

# FOURTH INTERNATIONAL CONODONT SYMPOSIUM. ICOS IV "PROGRESS ON CONODONT INVESTIGATION"



Editores: Jau-Chyn Liao  
José Ignacio Valenzuela-Ríos



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**FOURTH INTERNATIONAL CONODONT SYMPOSIUM**  
**ICOS IV**  
**“PROGRESS ON CONODONT INVESTIGATION”**

JOINTLY WITH:

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THE INTERNATIONAL SUBCOMMISSION ON SILURIAN STRATIGRAPHY ***ISSS***

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Upper right: Palaeozoic succession in the Volayer Area (Carnic Alps, Italy-Austria border). Photo by Carlo Corradini.

Middle left: Ancyrodelloides lineage proposal, lower to middle Lochkovian (Lower Devonian) in the Central Pyrenees (Spain). Photo by José I. Valenzuela-Ríos.

Middle centre: Pragjan-Emsian succession in the Baliera section, Benasque area, Aragonian Pyrenees. Photo by José I. Valenzuela-Ríos.

Middle right: Regional correlation in the southern part of the Central Pyrenees for the Middle to Upper Devonian. Photo by Jau-Chyn Liao.

Lower left: Orthoceras limestones (Lower Devonian) from Gerri La Sal section, Noguera Pallaresa valley. Photo by Jau-Chyn Liao.

Lower centre one: Reconstruction in 3D of the Epigondolella quadrata (Upper Triassic) of the Pizzo Mondelo (Italy). Photo by Michele Mazza and Carlos Martínez-Pérez.

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Lower right: Schiphocrinites from the Silurian/Devonian in Gerri La Sal section. Photo by Jau-Chyn Liao.

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## THE 4<sup>TH</sup> INTERNATIONAL CONODONT SYMPOSIUM "PROGRESS ON CONODONT INVESTIGATION"

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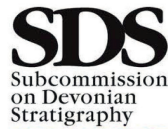
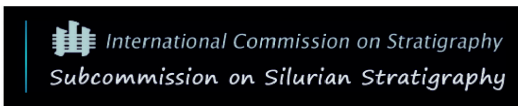
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## PREFACE

Primarily conodonts are one of the key fossil groups in establishing detailed biostratigraphical scales in many marine environments and are instrumental for practising sound correlations from Cambrian to Triassic strata. Consequently, they are one of the more important groups in establishing the boundaries of the International Chronostratigraphical Chart for the concerned Systems. In the last decades the importance of conodonts have greatly expanded to other aspects such as prospecting natural resources (hydrocarbons), detecting hydrothermal activity, geochemistry, apparatus reconstruction, zoological affinities, ... The controversy on the systematic position of conodont and on the interpretation of the apparatus function, has also been a hot on-going debate for the last 30 years. The recent application of non-invasive X-ray synchrotron microtomography has fuelled a new dimension in the study of conodonts, especially in the interpretation of the biological affinities. This Symposium will contribute to a better understanding of the group in a variety of topics and therefore, will contribute to the main objective of the Pander Society: to encourage the exchange of information about conodont research

Coinciding with the 50th Anniversary of the Pander Society, this is the first time that four European countries jointly organise the fourth International Conodont Symposium (ICOS IV). In the 3rd International Conodont Symposium held in Mendoza, Argentina, in 2013, Spain was elected for the next international meeting of conodont workers. Subsequently, two international subcommissions of stratigraphy (ISSS and SDS) asked to join ICOS IV for their annual meetings. This time about 100 participants from over 25 countries will attend the joint meeting.

The joint organisation of the three conferences is a unique opportunity for stimulating international and multidisciplinary discussions and fostering joint collaborations combining and exchanging data from various fields (palaeontology, stratigraphy, geochemistry, geophysics, sedimentology, tectonics, ...) Therefore, the conference will bring together three important scientific meetings for the Earth Sciences at the highest international level for the first time. This meeting will specially explore the value of conodonts for solving global bio- and chronostratigraphic problems and in integrating these data for supporting the calibration of the Timescale.

By encouraging attendance of experts from different disciplines, the ICOS IV will provide special emphasis in discussing both the current state-of-art in multidisciplinary conodont research and applications and their special role in calibrating the Silurian and Devonian time scale.

The conference will be held in the Burjasot Sciences Campus of the University of Valencia, Spain. A pre-conference fieldtrip is scheduled in the Spanish Pyrenees; a intra-conference field trip will visit the Upper Devonian strata of the Iberian Chains in Tabuena; a post-conference fieldtrip is scheduled in the Prague Synform and in the Carnic Alps.

This book reflects the passion, commitment and organizers vigorous effort in attracting colleagues from all the continents and diverse fields to come together to Spain and share their knowledge and state-of-the-art in all the topics targeted in this meeting.

As a result of participants effort, 85 works have been accepted after due revision. This constitutes a huge contribution to the progress of knowledge in Conodonts, Devonian and Silurian matters. These contributions range from Cambrian to Triassic, with special emphasis on Silurian and Devonian. The presentation of these works will be bracketed by an opening Conference given by Prof. Dr. Carls (Braunschweig, Germany) and a closing Conference by Dr. Manuel Rigo (Padua, Italy). The communications will be arranged in following eight sessions: 1) IGCP 653, The rise of conodonts prior to and during the Great Ordovician Biodiversification Event, 2) Silurian Integrated stratigraphy: conodont, graptolites, brachiopods fauna and isotope analysis, 3) Progress on Middle Devonian conodont investigation from 60's to present: High-Resolution Bio-Chronostratigraphy, regional Correlation and Global Event Stratigraphy, 4) Devonian Global Events, environments and time, 5) Carboniferous Conodont Stratigraphy, Sedimentology and Tectonothermal analysis, 6) Permian to Triassic conodonts: Biostratigraphy, Isotopes and Geochemistry, 7) GECKO: Global Events impacting Conodont Evolution and 8) Recent advances in conodont Palaeobiology.

In brief, this conference will play an important role in understanding the evolution of life in a long period of time and specially to improve our understanding of the Earth History for the Silurian and Devonian. Consequently, we are deeply grateful to the Spanish Geological Survey (IGME) for continuously supporting international research in all fields of Earth Sciences and make possible the publication of this enormous contribution to the improvement and dissemination of cutting-edge science.

*The editors Jau-Chyn Liao and José Ignacio Valenzuela-Ríos*

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## PROFESSOR PETER CARLS: TRIBUTE TO HIS CAREER



(Courtesy by Falk Lehnhoff)





## THE SCIENTIFIC AND HUMANISTIC CONTRIBUTION OF PROF. DR. PETER W. CARLS HOMAGE TO HIS LEGACY

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On the occasion of the 4th International Conodont Symposium that is held in Spain and coinciding with his 80<sup>th</sup> birthday, I want to pay heartfelt tribute to my scientific advisor, elder colleague and beloved friend, Prof. Dr. Peter Carls.

Peter Carls is a key figure for the progress of palaeontological and stratigraphical studies in the Palaeozoic of Spain, specially of Aragón, in demonstrating the worldwide relevance of Devonian strata from the Iberian Chains, in contributing to the progress of scientific research in several topics and in creating a multidisciplinary team and facilitating the establishment of a network of researchers that continues very active. His enormous contribution represents a "quantum leap forward" in the knowledge of the Devonian, and specially in many palaeontological aspects of several fossil groups, among them the conodonts stand out.



Fig. 1. Peter Carls in September 2017 in Nevada SDS fieldtrip. Upper Devonian Alamo Breccia.

Peter Carls was born in Hannover (Germany) on the 3<sup>rd</sup> January 1937. He started his BSc in Geology in Hamburg in 1957; the following year he leaved northern Germany and moved to the University of Würzburg in Bayern. There, he continued his learning in Geology and specially Palaeontology under the supervision of Prof. Dr. Klaus Sdzuy. Two years later, in August 1959, he came for the first time to Aragón (Spain), a tough territory with a complex Geology that captured Peter's attention. Aragón trapped Peter and he started one of the most prolific and outstanding scientific carriers on the Palaeozoic strata of the Iberian Chains. During these almost sixty years of love with Aragón's Geology and People, he spent large field campaigns, in occasions almost a year, walking up and down in the hills, rivers, paths... enjoying the torrid summers, the freezing winters and the chilly wind, and overall making friends everywhere he was. His skin turned brown and his ears were many times peeled off. Also his relation with thorny and spiny bushes, such as gorses, brambles, rosebushes... is remarkable. The combination of sun-dried skin with these spiny shrubs produced red-dyed patches; however, these by-products of field Geology in Aragón never suggested him to give up his job. Oak trees helped him in repairing the handle of many research field tools (hammers, pick-axes, mattocks, shovels, axes...). His tenacity and hardwork rendered soon the first results. In December 1962 finished his Master Thesis (*"Diplom-Hauptprüfung für Geologie"*) with the title *"Erläuterungen zur geologischen Kartierung bei Luesma and Fombuena in den Östlichen Iberischen Ketten"*. Subsequently, in July 1965 he successfully completed and defended his Ph. D. Thesis *"Jung-silurische und unterdevonische Schichten der Östlichen Iberischen Ketten (NE-Spanien)"* before Prof. Dr. Sdzuy and Prof. Dr. Knetsch. In this work, Peter already described with extremely precision the Silurian and Lower Devonian succession and introduced the subdivisions into formations and alpha-numeric units, which due to the enormous practical value are widely used for researchers everywhere. He continued his teaching and research activities as Assistant Professor under the direction of Prof. Dr. Sdzuy in the University of Würzburg until 1977. Then, he gained the position of Professor of Palaeontology at the Institut für Geologie und Paläontologie, TU Braunschweig. Shortly after, in January 1978 he is in charge of the Palaeontology Section until his retirement in 2002. During all these years and even after the retirement, his department, and in particular the charm, beloved and highly productive "Baracke" has been a mandatory visiting place for many researchers from all over the world. The Braunschweig Baracke, leaded by Peter, resulted in one of the more effectives places for generating massive amounts of important scientific data, sharing knowledge, fomenting interpersonal relations and at the same time favouring the development of individual learning in a family atmosphere. The cooperative character developed in the Baracke crossed political and economical boundaries and facilitated cooperation and understanding between geologists of different ages, from different cultures, many countries and with diverse educational backgrounds. Peter was able to manage this "multicultural pot" for making possible a huge transference of scientific, technical and vital knowledge in a healthy environment. Anyone who paid a visit to Peter returned home with the work well done and with the desire to come back as soon as possible to share again science and friendship with Peter.

Unfortunately, new university policies resulted in the recent demolition of the Baracke, one Scientific symbol in Braunschweig for all of us who worked there and one of the most Cost-efficient places in the world I know.

In Spain we are most grateful to Peter for his teachings and practical lessons in the field, as well. He has shown us with extreme passion and knowledge the Geology and Palaeontology of the Iberian Chains. He has also managed the lending of unpublished works (mostly Master and Ph. D. Thesis) of German students dealing with the Geology and Palaeontology of the Palaeozoic when the young Department of Palaeontology in the University of Zaragoza started to investigate the Palaeozoic outcrops. His vast knowledge on Geology was also instrumental for structural geologists, mineralogists, petrologists, stratigraphers and geomorpholo-

gists; all them have learnt and have been inspired from the great experience, knowledge and wisdom of this wise Professor. His contacts in Spain included also other research groups, as the Devonian group of Oviedo. The Members of this group will never forget the long and hot fieldwork days in the Aragonian hills, neither the long and well wine-watered nights in the Aragonian small country inns and taverns. Now they are not only colleagues but also deep friends. Besides his lectures in the Spanish field, he opened his department and laboratory for anyone who wanted to travel to Germany and keep learning with him. Even in the 1980's he organised a practical fieldwork on Actuogeology and Actuopalaeontology in Amrum, an island in the North Sea, for Spanish geologists. Also the several weeks-long teaching fieldtrips he organised for his Braunschweig students, both in Spain and in Germany, were always open for anyone who wanted to learn and enjoy an unforgettable experience.

Peter is a world-renowned specialist in conodonts, brachiopods and Devonian stratigraphy and Correspondent Member of the International Subcommittee on Devonian Stratigraphy (SDS). Other areas of expertise include other fossil groups, Geological Systems and laboratory techniques, especially those applied to Micropalaeontology. An example of this tenacity and meticulous application of a wide array of laboratory techniques to a single fossil, is the preparation (which lasted several years) of one of the more important and spectacular fossils housed in the Natural Sciences Museum, University of Zaragoza, the long-snouted arthrodire *Carolowilhelmina geognostica*.



Fig. 2. Peter Carls and the long-snouter arthrodire *Carolowilhelmina geognostica*. Sala Lucas Mallada, Palaeontology; University of Zaragoza. Currently at Natural Sciences Museum, University of Zaragoza.

He is so closely linked to Aragón that he named numerous genera and species after this region, its mountains and inhabitants. Here, I would like to highlight two of them. The genus *Baturria*, dedicated to the "Baturros", who are the inhabitants, especially the peasants, from Aragón; and the species *Baturria simonae* dedicated to his beloved "Tía Simona". The tremendous love that Peter has for the inhabitants of Aragón and especially for the Badulesian is reciprocal and in 2008, the city of Badules paid him an extremely moving homage that ended with the nomination of Peter as "Adoptive son of Badules".



Fig. 3. Commemorative plaque dedicated to Peter Carls as Adoptive Son of Badules. Badules, November 2008.

His extensive and excellent research is demonstrated by more than one hundred papers that are highly appreciated by colleagues, numerous reports to the SDS, the coordination and effective leadership of scientific fieldtrips, and the supervision of more than 30 Master Thesis and 5 Ph. D. Thesis. Regarding SDS, he was the first in opposing the current official criterion and position for the base of the Emsian in the SDS meeting held in Rennes in 1988. Subsequently, he has been very active in providing sound arguments against the "kitab-icus boundary" being the base of the Emsian. Currently, the SDS is considering the revision of this boundary according to his initial proposal.



Fig. 4. Peter Carls revising Emsian (Lower Devonian) conodonts at Kitab Geological reserve in Zinzilban. SDS Fieldtrip in Uzbekistan, August 2008.

His language ability allowed him to be a panel member of many Ph. D. Thesis defended in several European countries and a Member of the Editorial Board of diverse journals, reviewing papers written in different languages. His great cooperative spirit is demonstrated by the co-authorship with more than 40 colleagues from different nationalities from Europe, America and Asia.

Last but not least, I want to mention that his legacy goes further beyond the briefly aforementioned curriculum, and crosses generations and cultures. I'm very proud of being his disciple, to start a scientific carrier and promote a scientific network that tries to continue the labour of the Master, and more important, with him. His teachings, care, love, passion for the improvement of scientific knowledge, friendship and the liberal atmosphere that one can feel when approaching Peter are values that can be passed along through generations.

Thanks Peter for being the lighthouse that illuminates the way through the cloudiness and helps people to find the path of things that are important in life and science.



## WHAT DID REALLY KILL CONODONTS?

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**Keywords:** Conodont, Upper Triassic, extinction

Conodonts are elements of a feeding apparatus belonging to eel-shaped marine early vertebrates, which lived from the Early Cambrian (520 Mya) to the Late Triassic (200 Mya) when they did become extinct. Late-most Triassic was a period characterized by intense biological, climate and environmental changes, ending with the break-up of the supercontinent Pangaea and the occurrence of the End-Triassic mass Extinction (ETE), one of the big five extinctions documented during the Phanerozoic. Timing and causes of the ETE are still the subject of controversial discussion and several triggers have been proposed, including the emplacement of the massive Central Atlantic Magmatic Province (CAMP) in the uppermost Rhaetian; climate change associated to the basal flow degassing; bolide impact event; sea-level change; methane release; ocean anoxia etc. It is noteworthy that the ETE seems to be associated with significant  $d^{13}C$  perturbations (CIEs), named "precursor", "initial" and "main", commonly related to the CAMP eruptive phases. Recently, the occurrence of another carbon isotope perturbation at the Norian/Rhaetian boundary has been documented and associated with biotic crisis, and likely related to the Angayucham activity that is an Alaskan Large Igneous Province (LIP), late Norian in age. Thus, the base and the top of the Rhaetian appears to be characterized by a series of faunal turnovers, including conodont ones. In fact, starting below the Norian/Rhaetian boundary, platform conodonts documented a morphological evolution towards platform-less elements and then elements with a well-developed basal cavity, ending with the documentation of a single ramiform species before their final extinction. This evolution seems not be influenced by climate changes (temperature or environmental conditions), at least at the base of the Rhaetian, or major Rhaetian  $d^{13}C$  perturbations. Instead, they apparently died out during the short recovery phase after the "initial" CIE that is related to the ETE event and the intermediate CAMP unit.

At present, conodont extinction is still one of the biggest mystery of the conodont world, and comparisons with other periods characterised by conodont crisis can help to unravel the main cause that could have led to the decline and fall of conodont empire.





# CONTRIBUTIONS



# **IGCP 653: THE RISE OF CONODONTS PRIOR TO AND DURING THE GREAT ORDOVICIAN BIODIVERSIFICATION EVENT**





## UPPER CAMBRIAN TO LOWER ORDOVICIAN CONODONT RESEARCH IN SOUTHERN LAURENTIA, 1933–2017: BRANSON & MEHL, FURNISH, MÜLLER, MILLER, ETHINGTON & CLARK, AND REPETSKI

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**Key words:** Conodonts, Cambrian, Ordovician, taxonomy, biostratigraphy

### INTRODUCTION AND HISTORICAL REVIEW

Cambrian to Lower Ordovician conodont studies in Laurentia began when Branson and Mehl (1933) described conodonts from the middle Lower Ordovician Jefferson City Dolomite in Missouri. Furnish (1938) published his dissertation on Lower Ordovician conodonts from the partly coeval Prairie du Chien Group dolomites in Iowa and Minnesota. These authors' faunas came from green shale bands interbedded with dolomites, and the shales were disaggregated by boiling them in water. Acetic acid was not used until years later. The dolomites were deposited in waters with restricted circulation and probably high salinity. Both papers were mostly taxonomic.

In 1955 Klaus Müller spent some months at the University of Iowa with Bill Furnish, who gave him some unusual Cambrian conodonts(?) from the Gallatin Limestone in Wyoming. Müller visited the U.S. Geological Survey in Washington, DC, where Pete Palmer gave him additional Cambrian conodonts(?) from the lower Upper Cambrian Dunderberg Formation in Nevada. Palmer (pers. comm.) had shown these fossils to Wilbur Hass, the Geological Survey's conodont specialist. Palmer asked if they were conodonts, Hass asked about their age, and when Palmer said they were Cambrian, Hass said they could not be conodonts because there were no Cambrian conodonts. (!!!!) Palmer also gave Müller some primitive *Cordylodus* from the Signal Mountain Limestone in Oklahoma. Palmer's material all came from acetic acid dissolution of scraps of limestone that he had split to recover trilobites. Several German and Swedish paleontologists gave Müller Cambrian conodonts(?) that they found in northern Europe, some from stinkstone concretions in the Alum Shales. Müller (1959) published the first paper on Cambrian conodonts, in which he described these materials and named genera and species after colleagues who gave him specimens for study. Species were also named for the Gallatin and Dunderberg Formations. That paper was also primarily taxonomic. Müller's Cambrian conodonts(?) are now known to be protoconodonts (Phylum Chaetognatha) and paraconodonts, so, in a certain sense, Hass was correct about Palmer's material. *Cordylodus proavus* Müller, 1959 is a much younger ramiform euconodont.

In 1962 Raymond Ethington and David Clark began studying conodonts from the Ordovician Pogonip Group in the Ibex Area of western Utah. They worked with Lehi Hintze, who had measured many sections in the Pogonip Group and was studying its silicified trilobite faunas. In 1965 I began a masters program

with Clark at the University of Wisconsin. My thesis research was to look for conodonts in the Notch Peak Formation and to find the Cambrian–Ordovician boundary. Lehi Hintze directed my fieldwork in June–July of 1965. My samples yielded abundant conodonts that had not been described by Müller (1959), and they were mostly new species and genera of primitive coniform euconodonts. I published my thesis (Miller, 1969) and established many new taxa, in what was the first Cambrian study based on samples from carefully measured sections. Miller (1980) placed many of those 1969 species in new multi-element genera.

Ethington and Clark (1971) published a preliminary paper on Lower Ordovician conodonts from the Ibex Area and discussed various conodont “faunas” from the Pogonip Group. Ethington and Clark (1981) published a monograph on those conodont faunas and established a zonation that was tentative because they were not certain that the faunas were widespread geographically. Ethington directed student research on strata in Texas and New Mexico (Repetski, 1982) and in Oklahoma, and the faunas his students found were similar to faunas in the Pogonip Group in Utah.

Ross et al. (1997) published a monograph that documented ranges of conodonts in Utah and formalized the conodont zonation. They also summarized ranges of trilobites and other fossil groups from the upper Notch Peak Formation and the Pogonip Group. They also named several chronostratigraphic units that are used over much of Laurentia.

## LITHOSTRATIGRAPHY, BIOSTRATIGRAPHY, AND CHRONOSTRATIGRAPHY

The papers of Branson and Mehl, Furnish, and Müller were based on only a few samples. The papers of Miller, Ethington and Clark, and Repetski were based on large samples collected at regular stratigraphic intervals, and the data formed the basis for naming biostratigraphic units. Cambrian and Ordovician strata in western Utah are ~5.33 km thick, have low dip angles, and exposures extend for tens of km along strike. The Notch Peak Formation is 420–520 m thick and is divided into three members. The upper ~60% of the Notch Peak Formation and coeval strata in Nevada, Texas, and Oklahoma yielded hundreds of thousands of conodont elements and has been divided into eight conodont zones/subzones that can be correlated to many parts of the world.

The Pogonip Group is more than a km thick and is divided into six formal formations and 14 members. Ethington and Clark (1981) divided the Pogonip Group into 17 zones/subzones based on ranges of tens of thousands of conodont elements. The lower six zones/subzones can be correlated globally, but the upper eleven are less widely recognized globally because faunal provincialism developed during the Early Ordovician.

These faunas have been used together with trilobites to divide the upper Cambrian Furongian Series and the Lower Ordovician into four stages used in Laurentia (Ross et al. (1997). Miller et al. (2016) proposed the Lawson Cove section in the Ibex Area as an Auxiliary boundary Stratigraphic Section and Point (ASSP) for the base of the Ordovician System. The proposed boundary horizon was at the First Appearance Datum (FAD) of *Iapetognathus fluctivagus*, which was the boundary horizon chosen at the global stratotype at Green Point, Newfoundland, Canada. In addition to ~45,000 conodont elements at Lawson Cove, Miller et al. (2016) documented ranges of trilobites and brachiopods, a nearby graptolite occurrence, carbon isotope profiles, and sequence stratigraphy as correlation tools. The Subcommittee on Ordovician Stratigraphy accepted the proposal of Miller et al. (2016), so Lawson Cove is a “backup section” in a different facies and paleogeographic region compared with the stratotype section in Newfoundland.

## DIVERSITY AND TWO MASS EXTINCTIONS

The oldest faunas that I studied include a few protoconodonts but are mostly paraconodonts. Somewhat higher, the oldest named euconodonts are species of *Proconodontus* Miller, 1969. The fauna diversified slowly with the addition of two more coniform genera, but at the top of the *Cambroistodus minutus* Subzone of the *Eoconodontus* Zone, there is an abrupt mass extinction where five of the common euconodont species disappear between two beds, leaving only one common euconodont species that continued up section. Paraconodonts were much less affected. Also disappearing were virtually all species and several genera of trilobites and the two common genera of phosphatic brachiopods. Very different conodont genera, including *Clavohamulus*, *Cordylodus*, *Fryxellodontus*, and *Hirsutodontus*, plus different brachiopods and trilobites, appeared in overlying strata. The cause of this extinction is unknown but is associated with a rapid lowering of sea level. This extinction event is very useful for global correlation in the upper part of Cambrian Stage 10. As the conodont fauna recovered, diversity increased through the next several conodont zones as new coniform and ramiform taxa appeared. The conodont fauna of the Notch Peak Formation includes ~50 taxa of paraconodonts and euconodonts.

The Pogonip Group includes 151 conodont taxa. A second mass extinction occurred near the top of the *Rossodus manitouensis* Zone, which is near the top of the House Limestone. That extinction was less abrupt than the earlier one and occurred through an interval of ~10 m. Nearly all of ~24 taxa that occurred in underlying strata disappeared, including *Cordylodus*. The next ~100 m of the Fillmore Formation has few conodonts that have very generalized morphologies. These strata are identified as the Low Diversity Interval, which is recognized over much of Laurentia. The cause of this second mass extinction is unknown but was also accompanied by a drop of sea level.

## CONCLUSIONS

The thick stratigraphic succession and the favourable depositional environments in Utah made this an excellent place to document conodont faunal ranges. Decades of field and laboratory work provided the basis for detailed biostratigraphic frameworks. Another advantage of the Utah strata is that they also contain many other groups of fossils that are useful for correlation. For example, very detailed correlations are possible using conodont and trilobite ranges from the same section. Utah conodont faunas have been duplicated in many depositional environments, ranging from nearshore sandstones to slope deposits on both the western and eastern margins of Laurentia and in thin sections of deep-ocean cherts in Kazakhstan.

## Acknowledgements

With the exception of E.B. Branson and M.G. Mehl, I have known and worked in the field with all of the authors of the papers in the references. I am grateful for the help and companionship of many student and professional colleagues during 52 years of field work in remote areas of Utah, Nevada, Texas, and Oklahoma. The United States National Science Foundation and Missouri State University provided research and travel funding.



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## TOWARDS A MORE PRECISELY DEFINED CAMBRIAN/ORDOVICIAN BOUNDARY IN AUSTRALIA

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**Keywords:** Conodonts, Cambrian/Ordovician boundary, Australia

### INTRODUCTION

Carbonate-dominated Ordovician rocks are widely distributed in extensive intracratonic basins in the central, western and northern parts of the Australian continent, and are also present in eastern Australia and Tasmania as remnants of shelves or platform margins of the Craton, and flanking oceanic volcanic islands (Fig. 1). Conodont faunas crossing the Cambrian/Ordovician boundary are only known from western Queensland (Georgina Basin: Druce and Jones 1971), northern Australia (Bonaparte Gulf Basin: Jones, 1971), and western New South Wales (Koonenberry Belt: Zhen and Percival, 2006). Studies of the faunas from Black Mountain of western Queensland (Druce and Jones 1971; Shergold et al., 1991, Shergold and Nicoll 1992) provided the main sources of information for conodont biozonation and correlation of the Cambrian/Ordovician boundary interval in Australia until recently, when new data from western New South Wales became available, significantly increasing precision in defining and correlating the base of the Ordovician in Australia (Zhen and Percival, 2006).

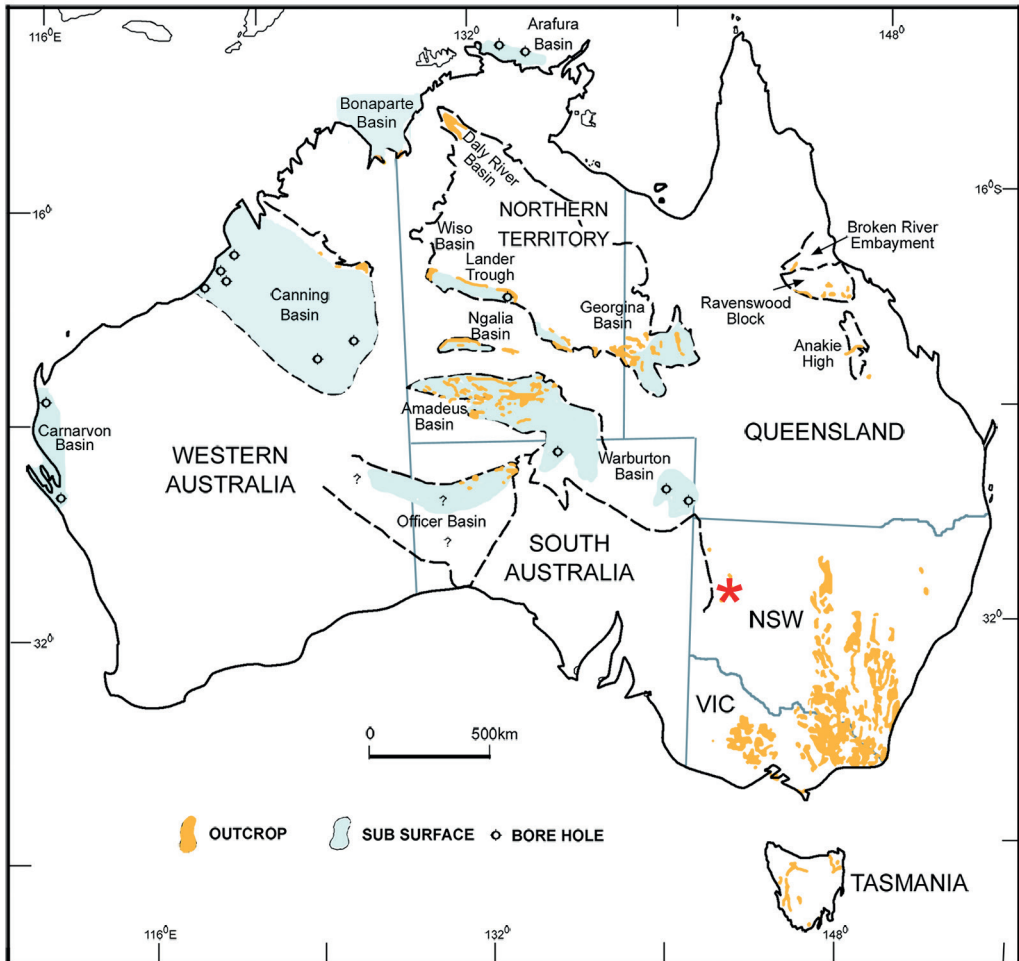


Fig. 1. Map of Australia showing distribution of the Ordovician rocks (modified from Webby et al., 1981), and the location (indicated by \*) of the *Lapetognathus* fauna in far western New South Wales.

## PREVIOUS STUDIES

Druce and Jones (1971) recognized six conodont biozones from uppermost Cambrian-Tremadocian successions in western Queensland, including (in ascending order) the *Cordylodus proavus*, *Oneotodus bicuspatatus*–*Drepanodus simplex*, *Cordylodus oklahomensis*–*C. lindstromi*, *Cordylodus prion*–*Scolopodus*, *Cordylodus rotundatus*–*C. angulatus*, and *Chosonodina herfurthi*–*Acodus* biozones. Although originally erected as form species, several index species recovered from western Queensland, such as *C. lindstromi* Druce and Jones, 1971, *Hirsutodontus simplex* (Druce and Jones, 1971), *Variabiloconus datsonensis* (Druce and Jones,

1971), and *Oneotodus bicuspatius* Druce and Jones, 1971, are now recognized as cosmopolitan and of global significance in defining the Cambrian/Ordovician boundary. Jones et al. (1971) subsequently established three regional stages for Australia, namely the Payntonian, Datsonian (spanning the *Cordylodus proavus* to *C. oklahomensis*–*C. lindstromi* biozones) and Warendian (from the *Cordylodus prion*–*Scolopodus* to *Chosonodina herfurthi*–*Acodus* biozones), and correlated the Datsonian and Warendian with the lower and upper Tremadocian of European successions. For the ensuing two decades the First Appearance Datum (FAD) of *C. proavus* (base of Datsonian) was utilised as the primary marker for the base of the Ordovician in Australia (Jones et al., 1971; Druce, 1978; Webby et al., 1981). Subsequently, Nicoll and Shergold (1991) regarded the Datsonian as the terminal Cambrian stage, and correlated the Datsonian/Warendian boundary in the Black Mountain section with the base of the Tremadocian. Based on a comprehensive revision of *Cordylodus* species and other forms from the Black Mountain upper Cambrian and Lower Ordovician succession (Nicoll, 1990, 1991, 1992a), Shergold and Nicoll (1992) recognized nine conodont biozones in this interval, and revised the boundaries of the Datsonian and Warendian. The base of the Warendian Stage, redefined by the FAD of *C. lindstromi*, was correlated with the base of the Tremadocian, but is now considered slightly older due to the establishment of the intervening *Iapetognathus fluctivagus* Biozone (Fig. 2).

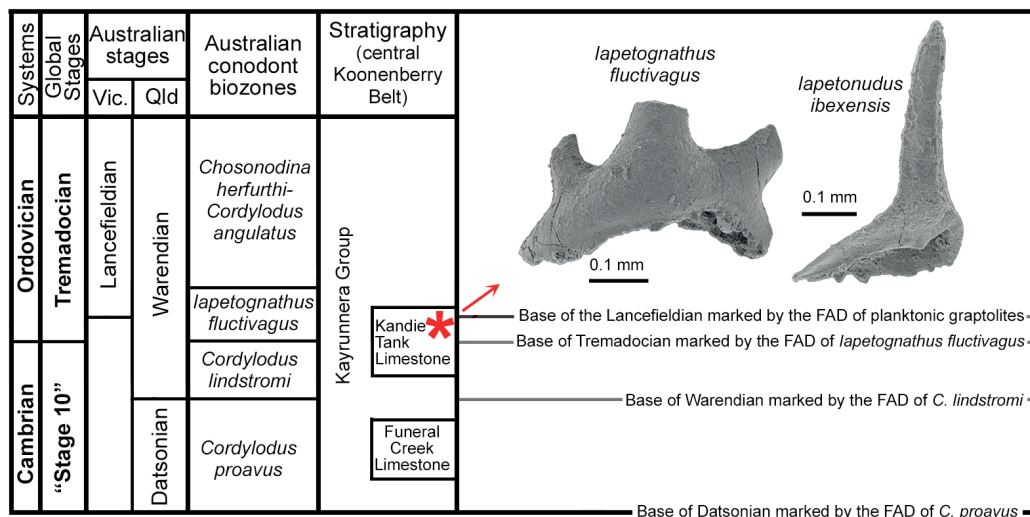


Fig. 2. Biostratigraphy of the Cambrian/Ordovician boundary beds and occurrence of *Iapetognathus fluctivagus* and *Iapetonodus ibexensis* from the Kandie Tank Limestone of the Kayrunnera Group in far western New South Wales.

## RECENT WORK IN FAR WESTERN NEW SOUTH WALES

Since 2000, the base of the Ordovician has been defined by the FAD of conodont *Iapetognathus fluctivagus* (see Cooper et al., 2001). With an age range restricted to the earliest Tremadocian, *I. fluctivagus* has been widely utilized in North America, South America, and Asia to establish the Cambrian/Ordovician boundary. However, only recently this distinctive species has only been recognized in Australia in the Kandie Tank Limestone of the Kayrunnera Group in far western New South Wales (Fig. 2), where it was found in

association with *Coelocerodontus* spp., *Cordylodus lindstromi*, *Cordylodus proavus*, *Hirsutodontus simplex*, *Iapetonodus ibexensis*, *Teridontus nakamurai* and *Variabiloconus* sp. This fauna can be closely compared with those recognized from the GSSP section at Green Point in western Newfoundland (Cooper et al., 2001) and from the Lawson Cove section (ASSP) in the Ibex area of Utah (Miller et al., 2016). Intensive sampling of limestone lenses and interlayers in the Nootumbulla Formation and correlative units in the Koonenberry Belt has defined the *Cordylodus proavus*, *Cordylodus lindstromi* and *Iapetognathus fluctivagus* conodont biozones in western New South Wales. These can be accurately correlated with corresponding biozones established in North America, South America, Asia and other parts of the world.

## CONCLUSIONS

Recognition of the *Cordylodus proavus*, *Cordylodus lindstromi* and *Iapetognathus fluctivagus* biozones crossing the Cambrian/Ordovician boundary interval in the Koonenberry Belt has significantly increased precision in defining the base of the Ordovician in Australia. The *I. fluctivagus* Biozone recognized in far western New South Wales correlates with the upper part of the *Cordylodus lindstromi* Biozone established in the Black Mountain succession in western Queensland.

Recent new discoveries of the *Iapetognathus* faunas in Australia, China (Dong et al. 2004) and Argentina (Albanesi et al. 2016) strongly supports the FAD of *I. fluctivagus* as the primary marker to define the base of the Ordovician System as ratified by the IUGS in 2000. However, in Australia, as well as in many parts of the world, *Iapetognathus fluctivagus* is relatively uncommon. In the absence of *I. fluctivagus*, *I. jilinensis*, or *Iapetonodus ibexensis*, the FAD of *C. lindstromi* remains a useful proxy to indicate the approximate level of the Cambrian/Ordovician boundary.

## Acknowledgements

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## UPPER CAMBRIAN FAUNAS AND BIOSTRATIGRAPHY FROM EASTERNMOST ALASKA

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**Keywords:** Conodonts, Cambrian, biostratigraphy, trilobites, Alaska

Recent collections made from the Jones Ridge Formation in easternmost Alaska contain rich but previously poorly known faunas of Cambrian and Early Ordovician age that are allowing significant refinement of the upper Cambrian (Furongian) biostratigraphy and correlations from this remote region. The formation has been known to contain Cambrian strata since the early 1900's, from samples collected, but unpublished, during reconnaissance mapping in that region. Brabb (1967) subsequently mapped the area, named the formation, and described several measured sections. At that time, it was thought that this area contained the westernmost exposures of Cambrian sedimentary rocks in North America. Material collected during that and earlier studies formed the basis of the most comprehensive treatment of Cambrian trilobites in Alaska to date (Palmer, 1968).

New collections from the Jones Ridge are now being studied for trilobites, conodonts, and other fossils, and here we discuss new data from the Upper Cambrian part of the type section area, an approximately 150 m thick interval of carbonate strata, mostly limestone, which was deposited at the platform margin near the [present-day] western margin of Laurentia. Recently, Taylor and others (2015) presented a preliminary report on trilobite and conodont faunas from the Jones Ridge, but that report concentrated on the Lower Ordovician segment; at that time only a few Cambrian samples had been examined for conodonts. Those yielded fairly long-ranging species diagnostic of the *Proconodontus muelleri* and *Eoconodontus* Zones. Our subsequent work now allows us to recognize the occurrence of all of the primary index conodont species for the *Proconodontus tenuiserratus*, *P. posterocostatus*, *P. muelleri*, *Eoconodontus*, *Cordylodus proavus*, and *C. lindstromi* Zones, as well as the *Eoconodontus notchpeakensis* and *Cambrooistodus minutus* Subzones of the *Eoconodontus* Zone. Other significant conodont taxa reported for the first time from the Jones Ridge Formation include *Eoconodontus alisonae*, *Cambropustula?* sp., a problematic genus known previously only from Sweden and Sardinia, *Proconodontus tenuiserratus bicostatus* Szaniawski and Bengtson, and an unnamed taxon with morphologic shape and features similar to *Fryxellodontus*. The recovery of *Eoconodontus alisonae* likewise is significant for extra-regional correlation, as this species has been reported previously only from eastern North America and Kazakhstan. As in those other sites, the Jones Ridge *E. alisonae* elements were recovered from the *C. minutus* Subzone within deeper water carbonate facies deposited at or seaward of the platform margin. The occurrence of probable *Cambropustula* also extends its known range upward into strata above the Paibian Stage, on the basis of associated trilobites and carbon isotopic data at Jones Ridge.



The shelfbreak to upper slope facies of the Jones Ridge Formation also yielded numerous new trilobite collections that significantly expand the documented diversity of faunas in the uppermost Cambrian (global Stage 10), from which only five genera and three species of trilobites had been reported previously (Kobayashi, 1936, Palmer, 1968). Our expanded data set from Stage 10 at Jones Ridge now comprises more than 20 faunal collections that contain at least 15 trilobite genera. Several of these genera, including *Eurekaia*, *Idiomesus*, *Tatonaspis*, and perhaps *Glaberaspis*, are represented by multiple species. Many of these taxa are shared with the uppermost Cambrian faunas in toe-of-slope limestone conglomerates in the northern Appalachians (Rasetti, 1944; Ludvigsen and others, 1989), but are more tightly constrained in age by their *in situ* occurrence and associated conodont faunas in the Jones Ridge Formation. For example, *Idiomesus ultimus*, previously reported only from uppermost Sunwaptan boulders in the Cow Head Group of western Newfoundland, was recovered in the Jones Ridge from less than a meter below the horizon that yielded *E. alisonae*.

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## LARAPINTINE SEAWAY ACROSS AUSTRALIA DISPROVED BY EARLY ORDOVICIAN CONODONT DISTRIBUTION

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**Keywords:** Early Ordovician, conodonts, palaeogeography, Australia

### INTRODUCTION

The Larapintine Seaway (or Larapinta Sea) was formally defined by Webby (1978) as an open "Ordovician seaway crossing Australia from east to west" connecting the Canning and Amadeus basins (Fig. 1A). The name "Larapintine Sea" was introduced into the literature much earlier (Keble and Benson, 1939, p. 50), and the existence of such a seaway was speculated by many earlier workers (see Webby, 1978, p. 55). Subsequently this seaway has been adopted in most Ordovician palaeogeographical reconstruction maps of Australia (Nicoll et al., 1988; Cook and Totterdell, 1991; Webby et al., 2000; Zhen and Nicoll, 2009; Metcalfe, 2011). However, mounting evidence from palaeontological, sedimentological and detrital zircon age studies of the Amadeus and Canning basins, particularly in recent years, strongly disputed the existence of such a marine connection (Haines and Wingate, 2007). Our current study of the Early Ordovician conodonts from both the Canning and Amadeus basins supports the latter view (Fig. 1B).

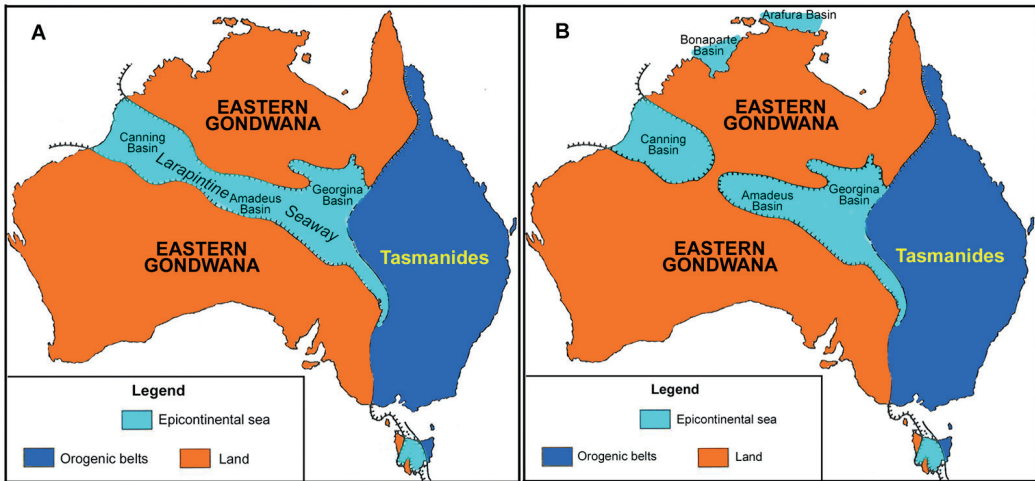


Fig. 1. A, Schematic palaeogeographic reconstructions of Australia during the Early Ordovician; A, showing the hypothetical Larapintine Seaway (modified from Webby, 1978); B, showing no marine connection between the Canning and Amadeus basins, as discussed in the text.

## PREVIOUS WORK

The concept of a narrow east–west seaway crossing the Australian Craton during the Ordovician was largely based on broad distributional patterns of sediments and faunal relationships derived from the data available at the time (Webby, 1978), before fossils of the abundant marine faunas inhabiting the intracratonic basins had been fully documented. However, based on the lithofacies patterns and trends of the Ordovician terrigenous sediments and carbonates in the Canning and Amadeus basins, Veevers (1976) had earlier presented an alternate view, suggesting that these two basins were not connected during the Ordovician, but represented embayment extending onto the craton from the west and east sides respectively. This interpretation was further advanced by Haines and Wingate (2007), who analysed the depositional settings, lithofacies, possible sources of terrigenous material and detrital zircon age data of the Ordovician rocks in both basins. They concluded that the Larapintine Seaway concept lacked compelling supporting evidence, and demonstrated that both basins opened to the ocean in different directions with lithofacies transferring from off-shore mud-dominated deposits, via carbonates to sand-dominated near-shore deposits (Haines and Wingate, 2007, fig. 4). Recently, Jakobsen et al. (2013a, 2013b, 2016) reported a very high degree of endemism among the brachiopods, trilobites and molluscs from the Stairway Sandstone (Middle Ordovician) of the Amadeus Basin, which exhibited significant differences from those recorded from the Canning Basin. Trilobites from the Horn Valley Siltstone of the Amadeus Basin also showed strong endemism (Laurie, 2006).

## NEW CONODONT STUDIES IN THE CANNING AND AMADEUS BASINS

Well-preserved and diverse conodont faunas from the Horn Valley Siltstone (47 species) of the Amadeus Basin and from the Nambheet (51 species) and Emanuel (over 24 species) formations of the Canning Basin were studied to provide precise biostratigraphic correlation (Fig. 2) and to form the basis of the current analysis. These more or less coeval units were deposited under similar depositional settings in both basins. The Emanuel Formation with more abundant carbonate beds was deposited in shallow and open marine conditions. Both the Nambheet Formation and Horn Valley Siltstone are dominated by fine grained clastic rocks with minor limestone, sandstone and sandy siltstone, and were deposited predominantly in slightly deeper water, more off-shore conditions. Detailed comparison between Early Ordovician conodont faunas from the Canning and Amadeus basins demonstrate significant differences at species and genus levels. The faunas from the Horn Valley Siltstone exhibit strong endemism characterized by the occurrence of a large number of taxa so far only reported from the Amadeus Basin, Georgina Basin or eastern Australia. Conodonts from the Canning Basin, particularly those from the middle to upper parts of the Nambheet Formation, show much less endemism and display a stronger palaeobiogeographic connection with faunas documented from the three major Chinese terranes. Several species of likely Chinese origin, including *Nasusgnathus dolonus*, *Rhipidognathus yichangensis* and *Triangulodus bifidus* dispersed eastwards from the Chinese terranes to the Canning Basin and other intracratonic basins along the western and northern margins of the Australian Craton, but failed to reach central and northeastern Australia (Zhen et al., 2003; Zhen and Nicoll, 2009). Several genera including *Bergstroemognathus*, *Protoprioniodus*, and *Triangulodus* are present in both the Canning and Amadeus basins, but pandemic species (e.g. *B. extensus*, *P. simplicissimus* and *T. brevibasis*) occur only in the Canning Basin. However, in central, northeastern and eastern Australia those species were replaced respectively by *B. kirki*, *P. yapu* and *T. larapintinensis*, which were likely endemic species restricted to the eastern side of the Australian Craton. This distribution pattern and the strong endemism of the Early Ordovician conodont fauna from the Amadeus Basin favours the interpretation (Haines and Wingate, 2007) that there was no effective continuous marine connection – the so called Larapintine Seaway – existing during the late Early Ordovician (Floian) to allow migration of fauna from the Canning Basin through the Amadeus Basin and eastwards to the Georgina Basin and the Delamerian margin, or *vice versa*. However, distribution of some taxa of latest Tremadocian age, such as the appearance of a new species of *Variabiloconus* in both the Canning and Amadeus basins, implies that a shallow-water connection may have existed intermittently during that time between the Canning and Amadeus basins.

System	Series	Stages	Canning Basin		Amadeus Basin		Conodont biozones
			Subsurface (Olympic No. 1)	Outcrops (Lennard Shelf)	Near-shore facies	Off-shore facies	
Ordovician	Middle	Dapingian	Willara Formation	Hiatus	Stairway Sandstone (lower)	Horn Valley Siltstone	<i>Histiodelia altifrons</i>
		Floian					Gap Creek Formation
	Lower	Tremadocian	Nambeet Formation	Emanuel Formation	Pacoota Sandstone	Goyder Formation	<i>Oepikodus communis</i>
		?	Kudata Dolomite Kunian Sandstone	Hiatus			<i>P. oepiki-S. bilobatus</i>
Cambrian	Furongian	Hiatus	Hiatus	Hiatus		<i>Paroistodus proteus</i>	
							?

Fig. 2. Correlation of the coeval stratigraphic units (Early Ordovician) in the Canning and Amadeus basins based on conodonts.

## CONCLUSIONS

New conodont data from both Canning and Amadeus basins indicate that there was no effective marine connection during much of the Early Ordovician, except for a possible intermittent faunal exchange during the latest Tremadocian.

During the Early Ordovician, conodont faunal exchange and dispersal in eastern Gondwana occurred primarily via the northern margin of the Australian Craton. The major faunal influxes from neighbouring Chinese terranes successfully reached the Canning Basin and Arafura Basin from the western and northern side of the Australian Craton, but failed to migrate further to the Amadeus and Georgina basins and eastern Australia (Gnalta Shelf and Tasmanian Shelf) on the other side of the continent.

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## BALTOSCANDIAN CONODONT DIVERSITY (UPPER TREMADOC AND MIDDLE ORDOVICIAN) COMPARED TO GOBE

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**Keywords:** GOBE, conodont diversity, Baltoscandia, Lower and Middle Ordovician

### INTRODUCTION

GOBE (Great Ordovician Biodiversification Event) is today considered fundamental for development of biodiversity for marine life, especially for shallow-marine shelly benthos. A study of conodont diversification from Baltoscandia is carried out from the upper Tremadoc (*Paltodus deltifer* Zone) to the Middle Ordovician (*Pygodus serra* Zone), i.e. the time interval, when Earth's brachiopod biosphere changed fast from relatively low diverse to high diverse in the early Darriwilian. On Baltica the Tremadocian–Darriwilian sedimentary rocks are composed mainly of cool to temperate limestone and marl with little input of siliciclastic sediments.

### MATERIAL AND METHODS

The study is based on hundreds of samples collected from many disparate sections covering the main part of the platform and margin and thousands of specimens have been inspected. The total material has been investigated during several decades of research and the study initiated with construction of a summary of the temporal distribution and proposed relationships amongst all known Lower and Middle Ordovician conodonts from the region. This provides an improved foundation for biostratigraphic and biochronologic studies in Baltoscandia additional to the investigation already prepared for the eastern Baltic.

### RESULTS

In this study several conodont highs and lows in diversity pattern are recognized during the investigated time interval. The conodont diversity highs include an acme in mid Floian (33 species in the *O. evae* Zone) and a second high but with a lower peak is recorded in the mid Darriwilian (23 species in the *Yangtzeplacognatus crassus*–*Lenodus pseudoplanus* zones). The upper Tremadocian diversity maxima is up to 23 species and



the following highs are separated by prominent diversity lows with a gradual decline characterizing the late Floian that persisted into earliest Dapingian. However, the most prominent conodont diversity minimum is from the upper *Lenodus antivariabilis* Zone (basal Darriwilian) - i.e. just prior to the fast early Darriwilian rise for the shallow-marine benthos - and the conodont diversity was reduced to 11 species.

## CONCLUSIONS

The recorded conodont diversity pattern for Baltoscandia matches the patterns already known from South China and the Tamir Basin and thus the recorded trend for the conodonts may represent a general development rather than only reflecting regional patterns.

The development of the conodont diversity, when compared with the regional case study on brachiopods from Baltoscandia and South China, is not identical with that displayed by the shallow-marine brachiopods. The fast steady increase in diversification of the brachiopods is not equally prominent for the conodontophorids, which show a rhythmic, moderate decrease and increase in diversity. The difference in the pattern of diversification may be caused by response to the challenges in the exchange of the seawater between the conodontophorids - being mainly nektobenthic and/or free swimming organisms - and the shallow-marine brachiopods (mainly sessile).

## NEW TAXONOMICAL INSIGHTS ON THE CONODONT GENUS *LENODUS* (LOWER DARRIWILIAN) FROM THE PRECORDILLERA, SAN JUAN, ARGENTINA

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**Keywords:** *Lenodus*, conodont, Precordillera Darriwilian

### INTRODUCTION

The type species of *Lenodus* Sergeeva was defined on the basis of *Lenodus clarus* Sergeeva, represented by an oistodiform element. Lindström (in Ziegler, 1973) considered the holodontiform (oistodiform) element as the M element belonging to the multielemental apparatus of "*Amorphognathus*" *variabilis* Sergeeva. Stouge and Bagnoli, (1990) proposed a multielement apparatus for the genus *Lenodus*, composed of seven morphotypes and included it in the Family Balognathidae. Dzik (1994) named for first time the species *Lenodus variabilis* (Sergeeva), with conformed a multielement apparatus. Since then, this species has been used as an important key conodont in the Darriwilian

Zhang (1997) described the species *Eoplacognathus crassus* Chen and Zhang, mentioning detailed taxonomical characters, even an ontogenetical variation between juvenile to mature elements. On the other hand, Zhang (1998a) erected the genus *Yangtzeplacognathus* composed of a bimembrate apparatus with stelliplanate and pastiniplanate elements. After that, Zhang (1998b) assigned the *E. crassus* to the genus *Yangtzeplacognathus*.

Löfgren and Zhang (2003) recognized for first time a septimembrate apparatus for the *Y. crassus*, identical to that of the genus *Lenodus*. These authors also proposed a close phyletic relationship between *Lenodus antivariabilis* An and *Y. crassus*. Thus, the supposed differences between these two genera seem to disappear.

Recent studies on lower Darriwilian conodonts have been developed from several sections in the Precordillera (Heredia and Mestre 2013; Mestre and Heredia 2013; Mestre 2014).

An extensive bibliographical revision and the great detailed observations of our own material, allow us reconsider the genus assignment of the species *crassus* to the genus *Lenodus* following different considerations such as number and disposition of elements into the apparatus, P elements morphology and surface texture.

### GEOLOGICAL CONTEXT

The Cambrian-Ordovician carbonate succession of the Precordillera is developed along a length of 400 km N-S with a width of 150 km E-W.

The Ordovician carbonate succession begins with the Lower–Middle Ordovician San Juan Formation, composed mainly of fossiliferous limestone and marly limestone. The San Juan Formation is conformably

overlain by grey and black shale and thin- to medium-bedded marly limestone and black shale of the Los Azules-Las Aguaditas formations of Middle to Late Ordovician age (Heredia and Mestre 2011; 2013; Mestre, 2014). The contact between the San Juan and Los Azules-Las Aguaditas formations is transitional; the first level of black shale has been used as the arbitrary boundary between these units.

From the contributions on Darriwilian conodont biostratigraphy developed by Heredia and Mestre (2011; 2013a; this volume) it is obvious that the Precordilleran conodont faunas showed a strong connection with Baltoscandia and South - Central China for this time interval. The *Lenodus antivariabilis*, *Lenodus variabilis*, *Lenodus crassus*, *Eoplacognathus pseudoplanus* and *E. suecicus* zones permit dividing the lower and middle Darriwilian.

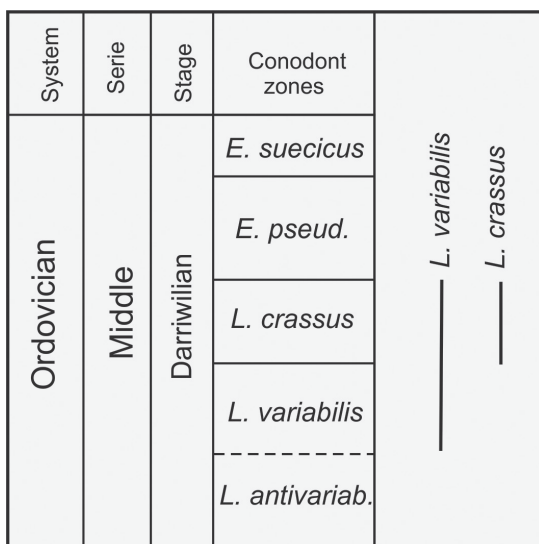


Fig. 1. Darriwilian conodont biostratigraphical chart with the vertical distribution of key conodonts in the Precordillera.

## MATERIAL AND METHODS

This study is based on the conodont faunas from seven middle Darriwilian sections of the Eastern and Central Precordillera (listed in Fig. 2) from which 40 kg of samples were processed, following the laboratory procedures described by Stone (1987), and recovered 180 complete and almost complete elements of the genus *Lenodus* were recovered.

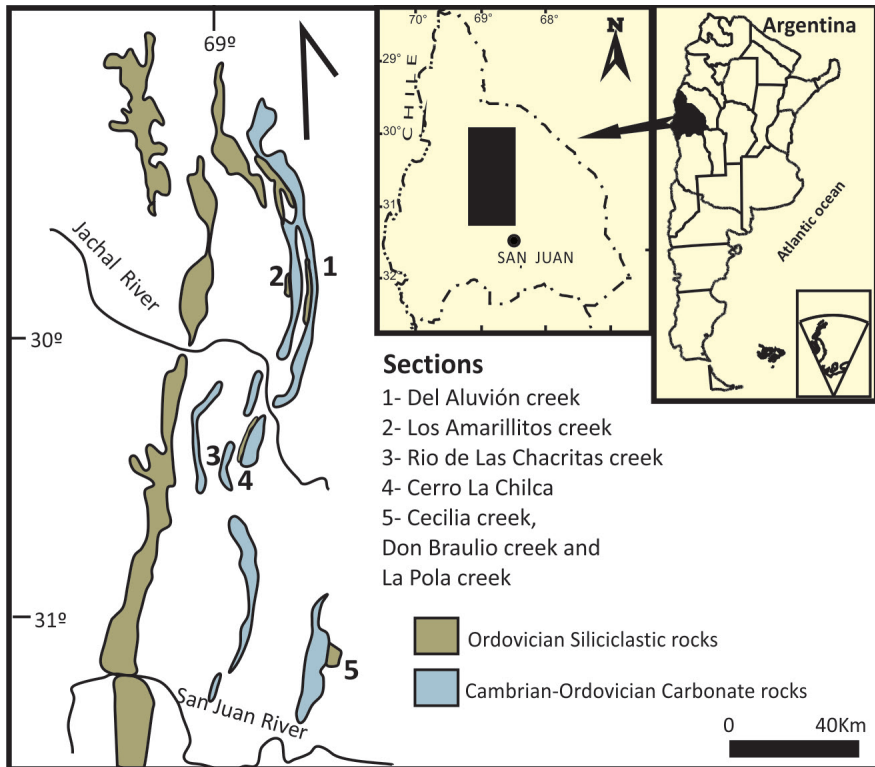


Fig. 2. Location map showing the distribution of the study sections.

## DISCUSSION

The apparatus of the genus *Lenodus* is composed of seven elements: Pa, Pb, Sa, Sb, Sc, Sd and M. The pectiniforms Pa and Pb are not mirror image elements (Stouge and Bagnolli, 1990). The Pa element presents pastiniscaphate morphology with denticulate lobes in posterior and anterior processes. The dextral Pa element presents a wide platform while the platform is slender in the sinistral Pa element. The Pb element presents a pastiniscaphate morphology. Both Pa and Pb element show micropattern structure (honeycomb) on the platforms and denticles, but is not always present. The S elements are alate Sa, tertio pedate Sb, bipennate Sc and quadriramate Sd with wartlike extensions on the tip of the cusp. The M element is a modified "geniculate" type.

*Eoplacognathus crassus* was named by Chen and Zhang (in Ding et al., 1993), after that Zhang (1997) offered a detailed taxonomical study of Pa and Pb elements of this species.

Zhang (1998b) assigned the *E. crassus* to the genus *Yangtzeplacognathus* since it would be composed by only unpaired marked dissimilar sinistral and dextral Pa and Pb elements. Also, she proposed a probable evolutionary relationship with *Y. foliaceus* based on the Pb element *Y. crassus* morphology where the posterior process is rounded. Later, Löfgren and Zhang (2003) described a multielemental apparatus for *Y. crassus*, with equal composition and spatial disposition from those elements of the *L. antivariabilis*, *L. variabilis* and

*E. pseudoplanus* (Viira). These authors support the generic assignation due to the bifurcations of the anterior and posterior outer lobes in *Y. crassus*, these are more distal to the cusp than those observed in the *L. variabilis* and *E. pseudoplanus*. Another generic diagnostic character for *Yangtzeplacognathus* introduced by these authors is the presence of micropattern (honeycomb) on the entire platforms of P elements. However, the polygonal pattern is observed on P elements of several genera such as *Dzikodus*, *Pygodus* and *Eoplacognathus*.

Heredia and Mestre (2013b) described and figured the mutlielement apparatus of the *L. variabilis* from the Precordillera, recognizing the micropattern (honeycomb) on the platform and denticles in the pectiniform elements.

Following the taxonomical criteria proposed by Mestre and Heredia (2013), we interpret that the morphological differences between the species *variabilis* and *crassus*, do not represent genus differences, since the main features of *crassus* species are all included in the genus *Lenodus*.

Our proposal recognizes the genus *Lenodus* with the following species: *L. antivariabilis*, *L. variabilis* and *L. crassus* within the Family Balognathidae.

The species of the genus *Lenodus* appear to follow an evolutionary trend that began in *Trapezognathus diprion* (Carlorosi and Heredia, 2014), mostly observed in the architecture of apparatus, the morphology of M elements, as well as the variation in the morphology of the Pa and Pb elements.

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## CONODONT $\delta^{18}\text{O}$ PALAEOETHERMOMETRY FROM CONJUGATED MARGINS OF THE SOUTHERN IAPETUS OCEAN DURING THE ORDOVICIAN PERIOD: A STORY OF DRIFTING?

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**Keywords:**  $\delta^{18}\text{O}$  palaeothermometry, Ordovician conodonts, Argentine Precordillera, terrane drift pattern, Iapetus Ocean

### INTRODUCTION

The shelly faunas of several fossil groups of the upper Cambrian-Lower Ordovician from the Argentine Precordillera, which evolved to have a paleogeographically mixed character during the Dapingian-Darriwilian, are of Laurentian affinity in general with an increasing number of colder-water taxa typical of Avalonia and Baltica. These paleontological records have allowed palaeobiogeographic interpretations of different contrasting models proposing either that a) the Precordillera rifted from the southwestern margin of Laurentia in low latitudes during the Cambrian, then drifted across the Iapetus Ocean, to collide with the Gondwanan margin during the late Middle Ordovician, and received glaciogenic sediments in the later Ordovician (e.g., Astini *et al.*, 1995), or b) the Precordillera originated as a low-latitude segment of Gondwana then drifted southward through episodes of major transform faulting toward high latitudes during the late Middle Ordovician to reach its present position during the Devonian (e.g., Finney, 2007).

Oxygen isotope compositions ( $\delta^{18}\text{O}_{\text{phos}}$ ) were determined from conodonts from Precordilleran and Laurentian carbonate successions to track changes in sea surface temperatures and investigate the hypothesized drift of the Precordillera, thereby testing the Laurentian-Gondwana palaeogeographic model.

### $\delta^{18}\text{O}$ PALAEOETHERMOMETRY AND METHODOLOGY

The  $\delta^{18}\text{O}$  compositions of conodonts were measured *in situ* at high spatial resolution (30 $\mu\text{m}$  spots) using the sensitive high resolution ion microprobe (SHRIMP II) at the Australian National University. The analytical approach follows that described previously in Ordovician, Silurian, and Triassic oxygen isotope studies (Trotter *et al.*, 2008, 2015, 2016).

Samples were taken from well studied stratigraphic sections, where firm biostratigraphic controls had been previously established, in the Precordillera of Argentina and from three geographically separated regions



in North America. These successions were: Precordillera, Argentina (Albanesi and Ortega, 2016); Alsate Creek and Woods Hollow, Ouchita embayment, Texas (Bergström, 1978); Wilcox Pass, Jasper National Park, Alberta (Pyle *et al.*, 2003); and Port au Port Peninsula and St Pauls Inlet, western Newfoundland (Ji and Barnes, 1994; Johnston and Barnes, 1999).

## RESULTS

The  $\delta^{18}\text{O}$  values of conodonts from Alberta, Texas, Newfoundland, and the Precordillera, show a consistent pattern of a cyclic but overall increasing trend (approx. 16 to 18‰) through the Lower and Middle Ordovician. An apparent change occurs at the basal Upper Ordovician, where values obtained from conodonts in the uppermost sample from the Precordillera are significantly higher (+1.5‰) than those from Laurentia. The higher values imply significantly cooler conditions, as would be anticipated if the Precordillera had drifted close to the Gondwana margin. Unfortunately, the virtual absence of conodont-bearing carbonates in the Upper Ordovician of the Precordillera has precluded analysis of additional samples and into younger levels.

## CONCLUSIONS

Our new isotope data support the model of a drift of the Precordillera from tropical to higher latitudes from the Late Ordovician, as suggested by cooler oceanic temperatures. This apparent cooling of the Precordillera is, however, based on only one sample. Thus, further detailed studies in the Precordilleran and North American successions are needed to clarify unequivocally whether the Precordillera originated from southern Laurentia (Ouachita Embayment), as advocated by many authors. Our record is also consistent with earlier studies (Trotter *et al.*, 2008) that reported an overall cooling trend throughout the Lower to Middle Ordovician with the same range in  $\delta^{18}\text{O}$  values.

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## REVISION OF THE DIAGNOSIS OF THE CONODONT GENUS *TRAPEZOGNATHUS* LINDSTRÖM BASED ON THE FINDING OF NEW ELEMENTS

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**Keywords:** Conodont, *Trapezognathus*, Baltoscandia, Ordovician

*Trapezognathus* Lindström is a typical conodont genus from Baltoscandia but in the last years has expanded its distribution to the southern China and Gondwana, these last mainly in the North-western Argentina and Peru outcrops. The discovery of complete new Pa elements allows making a modification to the diagnosis provided by Stouge and Bagnoli (1990). The early mention and illustration of new Pa elements was carried out by Viira *et al.* (2001); posteriorly Löfgren and Zhang (2003) recognized and described this element in the *Trapezognathus quadrangulum* Lindström (1955) apparatus: large Pa elements that develop a strengthening, weakly denticulated inner lateral extension from the posterior process supporting a wide bulge of the basal sheath.

Carlorosi and Heredia (2013) and Carlorosi *et al.* (2013) illustrated and described Pa elements from the North-western Argentina outcrops. All these Pa elements are mostly composed of basal fillings and fragments of crown. Carlorosi *et al.* (2016) recovered complete Pa elements besides others with part of crown with evidences of denticles and an elevated cusp. It is necessary to modify the diagnosis previously amended by Stouge & Bagnoli (1990) after these new findings introducing a new Pa element.

Stouge and Bagnoli (1990) diagnosis: "*The Trapezognathus Lindström apparatus is septimembrate, with pectiniform P elements, geniculate M elements and a complete series of S elements (alate, tertiopepate, bipennate, quadriramate). P elements are adenticulate to weakly denticulate. M element is adenticulate to denticulate and the cusp forms an angle about 90° with the upper margin of the base. S elements are stubby, with a base higher than the cusp, weakly denticulate to denticulate. All elements are albid and have a deep basal cavity and large basal sheath*". Stouge and Bagnoli (1990) and Bagnoli and Stouge (1997) reconstructed the apparatus of this genus and recognized Pa and Pb elements virtually indistinguishable from each other. These authors did not report pastiniscaphate Pa forms in their Baltic collections and they based their classification of P elements on subtle morphological differences. This proposal did not recognize that the apparatus of *Trapezognathus* includes a pastiniscaphate element (Pa).

Amended diagnosis, Carlorosi and Heredia: "*The Trapezognathus Lindström apparatus is septimembrate with a pastiniscaphate Pa and a pastinate Pb, geniculate M elements and a complete series of S elements (alate, tertiopepate, bipennate, quadriramate). P elements are denticulated to weakly denticulated. M element is adenticulate to denticulate and the cusp forms an angle about 90° with the upper margin of the base. S elements are stubby, with a base higher than the cusp, weakly denticulate to adenticulate. All elements have a deep basal cavity and large basal sheath*".

The finding of these new Pa elements in the North-western Argentina showing different levels of evolutionary development as was proposed by Carlorosi *et al.* (2016), suggests that these morphological differences can be used in biostratigraphical sense identifying early, middle and late representatives of the *Trapezognathus diprion* and *T. quadrangulum* Pa elements during Lower-Middle Ordovician (Figure 1).

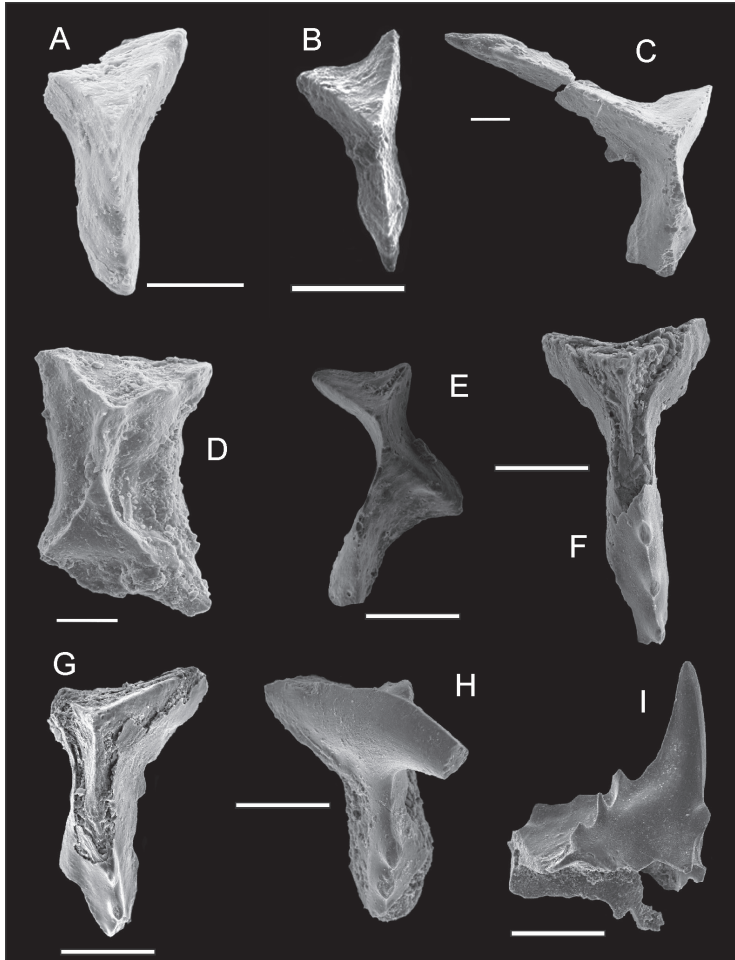


Fig. 1. Pa elements of *Trapezognathus* Lindström. A-C- *Trapezognathus diprion* (Lindström) D-I- *T. quadrangulum* Lindström. A: upper view, sample ED1, Acoite Formation, Espinazo del Diablo 5030(1). B: upper and antero-lateral view, sample LV12, Acoite Formation, Zenta, CML-C 3001(3). C: upper view, sample MS4, Alto del Cóndor Formation, Los Colorados, CML-C 5088(1). D: Primitive Pa element, upper view, sample MS4, Alto del Cóndor Formation, Los Colorados, CML-C 5090(1). E: upper view, sample L14, Altos de Lipán section, CML-C 1035(1). F - I: Pa elements with different evolutionary stages, upper and lateral views, samples SG2 and SG5, Santa Gertrudis Formation, CML-C 7015(1-4). The bar indicates 0.1 mm.

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## MIDDLE-UPPER ORDOVICIAN CONODONTS FROM THE FFAIRFACH AND GOLDEN GROVE GROUPS IN SOUTH WALES, UNITED KINGDOM

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**Keywords:** Conodont taxonomy, biostratigraphy, biogeography, Darriwilian-Sandbian

The conodont fauna of the reference succession of the British regional Llandeilian Stage of the Llanvirn Series was first described in a now classical study by Rhodes (1953) using single element (form) taxonomy. Although some subsequent authors have recorded a few additional conodont taxa from this late Darriwilian-Sandbian interval at Llandeilo and coeval strata in nearby areas (e.g. Bergström, 1964, 1971; Bergström and Orchard, 1985), the present study is the first to present a complete taxonomic review of these faunas, which include approximately 20 multielement species. Most prominent among the compound conodont taxa in these fauna from South Wales are representatives of *Amorphognathus*, *Baltoniodus*, *Eoplacognathus*, *Icriodella*, and *Plectodina*. Biostratigraphically diagnostic species indicate that the Llandeilo study succession ranges from the *Eoplacognathus lindstroemi* Subzone of the *Pygodus serra* Zone to the *Baltoniodus variabilis* Subzone of the *Amorphognathus tvaerensis* Zone.

The Llandeilo faunas have their own biogeographic character. The common occurrence of species of *Plectodina* and less common representatives of *Erismodus* and *Icriodella* are reminiscent of coeval North American Midcontinent faunas but the latter lack *Baltoniodus* and *Eoplacognathus*. The Llandeilo conodont species association is also somewhat similar to that of the Caradoc Series of Welsh Borderland (Bergström, 1971; Savage and Bassett, 1985) but the latter differs in lacking, among others, *Baltoniodus*, and *Eoplacognathus*. These two genera are common in coeval Baltoscandic faunas, but the latter also contain such characteristic genera as *Complexodus*, *Protopanderodus*, and *Pygodus*, which are not represented in our Llandeilo collections. Because specimens of *Plectodina* are quite rare, and *Erismodus* is missing, in the coeval Baltoscandic faunas, the faunal similarity between the Baltoscandic and the South Wales faunas is quite limited.

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## THE DARRIWILIAN CONODONT BIOSTRATIGRAPHY OF THE ARGENTINE PRECORDILLERA

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**Keywords:** Conodonts, Darriwilian, biostratigraphy, Precordillera, Argentina

Several localities at the Central and Eastern Precordillera have been studied: Del Aluvión (Cerro Viejo), Cerro La Chilca and río Francia (Cerro La Chilca region), Las Chacritas river section and de La Brecha creek (Las Chacritas river), Las Aguaditas, Los Amarillitos and Don Braulio/La Pola/Cecilia (Villicum) (Fig. 1). In these sections the carbonate, mixed and siliciclastic succession of the Lower-Middle Ordovician allows the study of the Darriwilian conodont biostratigraphy.

Previous studies on Darriwilian conodonts confirm that there exists a close affinity of the Precordillera biostratigraphical zonation with those of Baltoscandia and South-Central China (Heredia and Mestre, 2011, 2013; Heredia, 2012; Mestre, 2012; Mestre and Heredia, 2012; Mestre and Heredia, 2013; Heredia *et al.*, 2013, 2016). The main goal of this contribution is to incorporate recent conodont information to enlarge our biostratigraphic database, allowing an accurate Darriwilian conodont biostratigraphical chart for the Argentine Precordillera (Fig. 2).

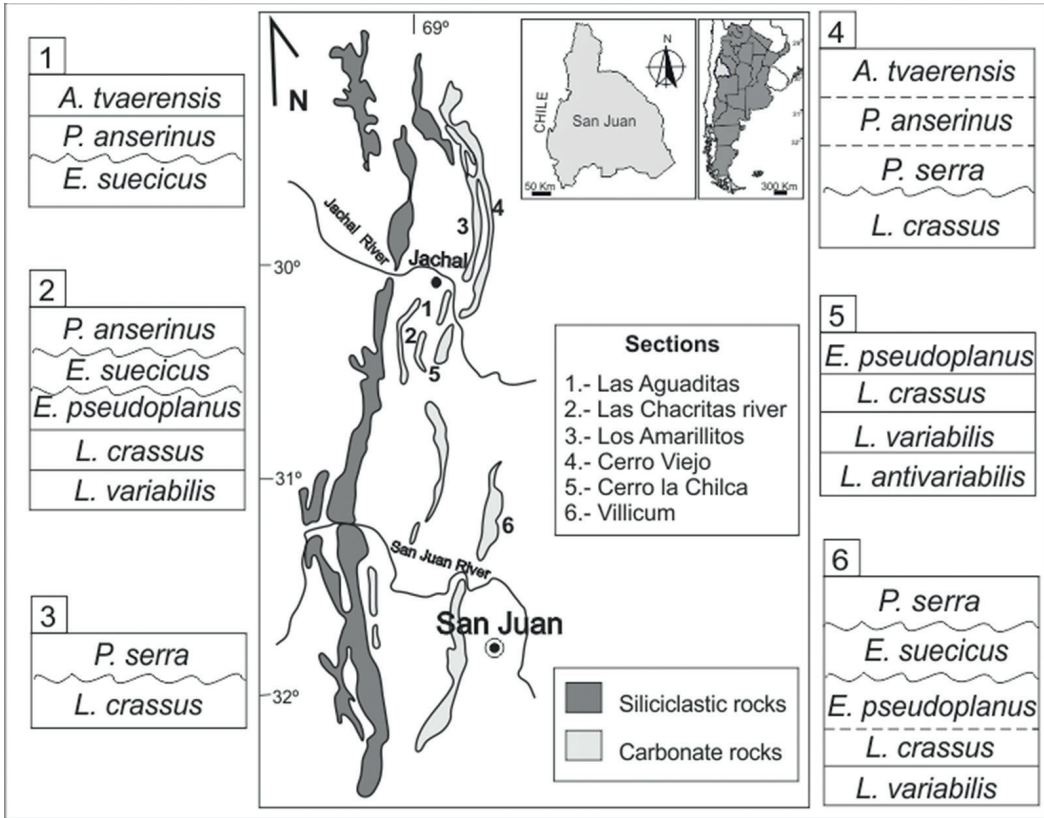


Fig. 1. Location map of study sections at the Central and Eastern Precordillera, showing the vertical distribution of the key species.

## GEOLOGIC SETTING

Each section begins with the Lower–Middle Ordovician San Juan Formation, composed mainly of fossiliferous limestone and marly limestone. The San Juan Formation is overlain by thin- to medium-bedded marly limestone and black shale of the Las Aguaditas/Los Azules Formation of the Middle to Late Ordovician age. Middle and Upper Ordovician strata of largely siliciclastic facies show great vertical and lateral heterogeneity, the siliciclastic units studied are the Los Azules, Las Aguaditas and La Cantera formations.

System	Series			Stages			Baltic Conodonts Zones & subzones			Conod. south China Zones & Subzones	Conodonts Precordillera	Conodonts Precordillera																		
	Global	Britain	N.Amer.	Global	Austr.	China	Löfgren (1978)	Bagnoli & Stouge (1997); Löfgren & Zhang(2003)	Zhang(1998)	Albanesi & Ortega (2002)	This study																			
Ordovician	U.	Car.			Gis.	Nei.					<i>A. tvaerensis</i>																			
								<i>Pygodus anserinus</i>	<i>Y. jianyeensis-P. anserinus</i>	<i>Pygodus anserinus</i>	<i>Pygodus anserinus</i>																			
							<i>P. serra</i>	<i>li.</i>	<i>P. serra</i>	<i>li.</i>	<i>Y. proramosus</i>	<i>P. serra</i>	<i>li.</i>	<i>ro.</i>	<i>re.</i>	<i>fo.</i>	<i>P. serra</i>	<i>li.</i>	<i>ro.</i>	<i>re.</i>	<i>fo.</i>	<i>P. serra</i>	<i>li.</i>	<i>ro.</i>	<i>re.</i>	<i>fo.</i>	<i>lindstroemi</i>	<i>robustus</i>		
	<i>ro.</i>	<i>re.</i>	<i>fo.</i>	<i>Y. foliaceus</i>																										
	<i>re.</i>	<i>fo.</i>																												
	Middle	Llanvirnian	Whiterockian	Darrivilian	Darrivilian	Zhejiangian	<i>E. suecicus</i>	<i>E. suecicus</i>	<i>P. anitae</i>	<i>E. suecicus</i>	<i>E. suecicus</i>	<i>P. anitae</i>	<i>E. suecicus</i>	<i>P. anitae</i>	<i>E. suecicus</i>	<i>P. anitae</i>	<i>E. suecicus</i>	<i>P. anitae</i>	<i>E. suecicus</i>	<i>P. lunnensis</i>	<i>M. ozarkodella</i>	<i>Dzikodus tablepointensis</i>	<i>M. ozarkodella</i>	<i>E. suecicus</i>	<i>H. kristinae</i>	<i>E. pseudoplanus</i>				
																											<i>P. lunnensis</i>	<i>M. ozarkodella</i>	<i>M. ozarkodella</i>	<i>M. ozarkodella</i>
																											<i>E. suecicus</i>	<i>S. gracilis</i>	<i>M. ozarkodella</i>	<i>M. ozarkodella</i>
	Arenig			Dapingi			<i>E. ? variabilis</i>	<i>E. ? variabilis</i>	<i>E. ? va.-M. ozarkodella</i>	<i>E. pseudoplanus</i>	<i>M. haegtiana</i>	<i>Dzikodus tablepointensis</i>	<i>M. haegtiana</i>	<i>L. variabilis</i>	<i>P. horridus</i>	<i>P. horridus</i>	<i>L. variabilis</i>	<i>P. horridus</i>	<i>P. horridus</i>	<i>Y. crassus</i>	<i>Y. crassus</i>	<i>Y. crassus</i>	<i>L. variabilis</i>	<i>P. horridus</i>	<i>P. horridus</i>	<i>L. crassus</i>				
																											<i>E. ? variabilis</i>	<i>M. flabellum</i>	<i>Y. crassus</i>	<i>Y. crassus</i>
																											<i>E. ? variabilis</i>	<i>M. flabellum</i>	<i>Y. crassus</i>	<i>Y. crassus</i>
							<i>B. norfandicus</i>	<i>Lenodus antivariabilis</i>	<i>Lenodus antivariabilis</i>	<i>Lenodus antivariabilis</i>	<i>Microzarkodina parva</i>	<i>Lenodus antivariabilis</i>																		
							<i>Trapezognathus quadrangulum</i>					?																		

Fig. 2. Biostratigraphical chart comparing Darrivilian conodonts zones of Baltoscandia, South-Central China and those recorded in Argentine Precordillera.

## CONODONTS AND BIOSTRATIGRAPHY

Heredia and Mestre (2011, 2013) proposed modifications to the Darrivilian conodont biostratigraphical chart including the *Lenodus variabilis* and *Yangtzeplacognathus crassus* zones, *Eoplacognathus pseudoplanus* Zone with *Microzarkodina* cf. *M. ozarkodella* Subzone and *E. suecicus* Zones with *Pygodus lunnensis* and *P. anitae* Subzones.

In this contribution, we report the vertical distribution of the following key taxa *L. antivariabilis* An and *P. serra* (Hadding) with *E. robustus* Bergström and *E. lindstroemi* (Hamar).

The Darrivilian conodont biostratigraphical chart (Fig. 2) proposed here includes this new information. The middle Darrivilian conodont fauna associated to these index conodonts in the all sections were mentioned previously in Heredia (2012), Mestre (2012, 2014), Mestre and Heredia (2012, 2013), Heredia and Mestre (2013) and Heredia *et al.* (2013, 2015, 2016).

**L. antivariabilis Zone:** This zone was recorded about 20 meters below the top of San Juan Formation from the río Francia section (Cerro La Chilca region), and represents the first mention for the Argentine Precordillera and South America indicating the lowest Darrivilian; it also supports the close relationship between Baltoscandia and South-Central China.

**L. variabilis Zone:** The *L. variabilis* Zone was documented about 15 meters below the top of the San Juan Formation in the Cerro La Chilca (Heredia and Mestre, 2013), río Francia and Las Chacritas river sections, and 2 meters below the top of this unit in Cecilia section (Villicum).

**L. crassus Zone:** We record this zone at the very top of the San Juan Formation from the Del Aluvion section (Cerro Viejo range) (Mestre and Heredia, 2013a), Los Amarillitos section and La Pola/Don Braulio/Cecilia sections (Villicum range) (Mestre, 2014). Also it is present from 4,5 m to 7 m below the top of the San Juan Formation in the Las Chacritas river section (Mestre and Heredia, 2013a). The *L. crassus* Zone is recorded from 9 to 3,5 m below the top of the San Juan Formation in the Cerro La Chilca (Mestre and Heredia, 2013a) and río Francia sections.

**E. pseudoplanus Zone:** This zone was recorded from the very top of the San Juan Formation in the Cerro La Chilca, de la Brecha creek and Las Chacritas river sections (Mestre and Heredia, 2013b). Also it was identified 2 meters above the base of the Los Azules Formation in the La Pola section (Villicum) and the base of the Las Aguaditas Formation in the de La Brecha creek section (Las Chacritas river region) (Heredia, 2012).

**E. suecicus Zone, P. lunnensis subzone:** The record of this subzone is present in Las Aguaditas Formation at the Las Aguaditas section (Heredia *et al.*, 2016). It is *ca.* 4 meters thick and unconformably overlain by beds with *P. anserinus* and *Baltoniodus variabilis*.

**E. suecicus Zone, P. anitae subzone:** This subzone was recorded several times in the Precordillera. We have registered it in La Pola creek (Villicum) with 8 m thick from the base of the La Cantera Formation (Heredia *et al.*, 2015, 2016) and Las Chacritas river section in Las Aguaditas Formation where it is 45 m thick (Heredia, 2012).

**P. serra Zone:** The record of the *P. serra* Zone is partial, only the *E. robustus* and *E. lindstroemi* subzones are present in the eastern outcrops such as Don Braulio/La Pola and Los Amarillitos sections (Heredia *et al.*, 2015, 2016). Until now the lower part of *P. serra* Zone, the *E. foliaceous* and *E. reclinatus* subzones are not reliably registered in the Precordillera.

**E. robustus Subzone:** It has been recorded from small outcrops of sandstone beds below the channel conglomerates of La Cantera Formation in the Don Braulio section (Heredia *et al.*, 2015).

**E. lindstroemi Subzone:** The presence of this species with *B. prevariabilis* and *E. robustus* suggests the upper *P. serra* Zone. This conodont association was recovered from sandstone beds of the La Cantera Formation in Don Braulio section, and the upper part of the middle member of the Los Azules Formation in the Los Amarillitos section (Heredia *et al.*, 2016).

**P. anserinus Zone Lower Subzone:** This time interval was not recorded until now in the Precordillera. The conodont association *P. anserinus*/*B. prevariabilis* is missing and the top of the Darrivilian Stage remains without record.

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## INTEGRATING ORDOVICIAN CONODONT STRATIGRAPHIC RANGE DATA AND OTHER FOSSILS MORE COMMON IN CARBONATE FACIES: A PLAN FOR THE ORDOVICIAN GEOLOGIC TIME SCALE 2020

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**Keywords:** Ordovician, GTS 2020, conodont, graptolite, CONOP9

The current Ordovician time scale is derived from a global CONOP9 composite of graptolite first and last appearance events with interpolated radiometric dates (Cooper & Sadler, in Gradstein et al., 2012). Local carbonate successions are correlated with graptolite zones derived from the composite using correlation charts in a rather subjective manner. The tie points are set by expert opinion on how the different sets of zones are related. We suggest that the direct integration of the stratigraphic range data from fossils that are more common in carbonate facies (e.g., conodonts and chitinozoans) into a global multi-clade CONOP9 composite Ordovician range chart would significantly increase the precision and usefulness of the Ordovician time scale. The construction of a global multi-clade composite poses a number of difficulties including the overall size of the data set, integrating the North American Midcontinent and North Atlantic conodont successions, and finding enough sections that contain species from both black shale and carbonate biofacies.

In this study we present several initial steps in constructing an integrated CONOP9 composite that may be used as the basis for the Ordovician GTS 2020. First, we constructed separate CONOP9 conodont composites from *Laurentia* and *Baltoscandia*, evaluated range similarities and inconsistencies, and attempted to establish common zonal boundaries. Second we present an example of a fully integrated graptolite, conodont, chitinozoan, and ostracod range chart from *Baltoscandia* that spans the Lasnamagi to Porkuni regional stages (middle Darriwilian to Hirnantian), and show how this range chart can be used to project graptolite zonal boundaries into carbonate sections and correlate the regional chitinozoan zonation more precisely with the standard global stages. Finally, because a great deal of chemostratigraphic data comes from carbonate-dominated sections, we investigate ways in which carbon isotope excursions can be successfully integrated into automated graphic correlation networks.

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# THE CONTROVERSIAL CONODONT FAUNA OF THE SANTA GERTRUDIS FORMATION (ORDOVICIAN), CORDILLERA ORIENTAL, NW ARGENTINA: A BIOSTRATIGRAPHIC APPRECIATION

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**Keywords:** Conodont taxonomy, biostratigraphy, Ordovician, Cordillera Oriental, Argentina

## INTRODUCTION

A number of articles have dealt with the age of the Santa Gertrudis Formation from the Ordovician System of the Cordillera Oriental in northwestern Argentina, as determined by means of conodont biostratigraphy following the first contribution by Sarmiento and Rao (1987). The particular conodont fauna of this unit represents a challenge for precise relative dating because of the lack of index taxa from standard biozonations. As frequently occurs, the conodont assemblages that includes mostly endemic new species, are difficult to be understood, and frequent mistakes are detected in the taxonomic determinations. For the study case, the misinterpreted reworking of certain species from the conodont assemblage of the referred formation (Carlorosi *et al.*, 2011), as well as mistakes in taxonomic determinations (Carlorosi *et al.*, 2016). The present contribution attempts to clarify a series of taxonomic confusions in order to shed light on the actual age of the conodont fauna that bears the Santa Gertrudis Formation.

## DISCUSSION

A recent publication by Carolrosi *et al.* (2016) concludes that the age of the Santa Gertrudis Formation is early Dapingian because of the presence of a new species of *Baltoniodus* following Heredia *et al.* (2015), and associated taxa. According to the referred authors, this new species named to as *Baltoniodus cooperi* was originally described by Cooper (1981) from strata of the Horn Valley Siltstone of Australia as *Baltoniodus navis*. This form, which occurs in the Sistema de Famatina of NW Argentina, was determined by Albanesi and Vaccari (1994) as *B. navis sensu* Cooper, and referred to the lower Dapingian because of the presence of other widely distributed associated taxa, such as *Baltoniodus navis s.s.*, *Jumudontus gananda* and *Erraticodon patu*. The two latter forms were also recorded by Cooper (1981) in association with *B. navis sensu* Cooper. Taxonomic mistakes are detected from the conodont plates of the papers by Heredia *et al.* (2015) and Carolrosi *et al.* (2016); namely, the elements illustrated as *Baltoniodus cooperi* Carolrosi *et al.*, and the Pa elements of *Baltoniodus triangularis*, which actually correspond to a new genus and species of the Balognathidae. The configuration of the cusp and denticles in the P elements are remarkably different, as

well as the presence of striae in *B. navis sensu* Cooper, which are not present in *B. cooperi*. The M element illustrated by the latter authors bears denticles on the upper margin of the base, which are not present in the original form illustrated by Cooper (1981), nor that one illustrated by Albanesi and Vaccari (1994) as *B. navis sensu* Cooper. On the other hand, the elements illustrated as *Trapezognathus quadrangulum* belong to a new species of *Zentagnathus* together with the S elements referred to as *B. triangularis*. The misinterpreted elements attributed to *Erraticodon patu* (Carlorosi *et al.*, 2014) actually belong to a different species of *Erraticodon*, as demonstrated by characteristic morphologies; for instance, that of the number, size, and distribution of denticles in the M element. Our conodont collection that was recovered from calcareous mudstones of the basal part of the Santa Gertrudis Formation (ca. 80 m thick) includes, apart from discussed taxa, specimens of "*Bryantodina*" aff. *typicalis* (i.e., n. gen. and sp. in the present contribution), which is a species consistently recorded from middle Darriwilian biozones in the Precordillera, and a new species of the genus *Erismodus*. Other taxa correspond to new species of the genera *Semiacontiodus* and *Polycaulodus*. All of these forms were originally illustrated by Albanesi in Moya *et al.* (2003). After numerous biostratigraphic records elsewhere, it is possible to confirm that the well-known genus *Erismodus* appears in the middle Darriwilian.

## CONCLUSIONS

The comparison of our conodont collection with assemblages of other correlative units from the same and neighbouring basins, as well as regional correlation with equivalent strata of the Precordillera, verify a Darriwilian age for the bearer strata, although the lack of key conodont species for intercontinental correlation precludes the assignment of discussed conodont species to a particular biozone (Albanesi and Aldridge, 2013; Albanesi and Ortega, 2016). The Capillas and Sepulturas formations, which crop out in the Cordillera Oriental and the Sierras Subandina, respectively, share several species with the Santa Gertrudis Formation but have also yielded remains of other forms and the oldest pteraspidomorph of South America, *Sacabambaspis janvieri* Gagnier *et al.* (Albanesi *et al.*, 2007). In the La Cantera Formation of the Eastern Precordillera, San Juan Province, Argentina, *Sacabambaspis* has been dated as Middle Darriwilian by its association with conodonts of the *Pygodus serra* Zone (Albanesi *et al.*, 1995). A similar age was assigned by other authors for fossil remains of the fish reported in different localities of the Gondwanan margin (Heward *et al.*, 2016). Consequently, the analysed conodont taxonomy, biostratigraphic records and geological correlations confirm a middle Darriwilian age for the bearer levels of the Santa Gertrudis Formation.

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# **SILURIAN INTEGRATED STRATIGRAPHY: CONODONT, GRAPTOLITES, BRACHIOPODS FAUNA AND ISOTOPE ANALYSIS**



# LATE ORDOVICIAN-LATE SILURIAN CONODONT BIOSTRATIGRAPHY AND BIOEVENTS, FROM BOTH SHELF AND SLOPE FACIES, CANADIAN ARCTIC ISLANDS, WITH IMPLICATIONS FOR REGIONAL STRATIGRAPHY, TECTONICS AND EUSTASY

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**Keywords:** Ordovician-Silurian, biostratigraphy and bioevents, Canadian Arctic Islands, shelf and slope facies, tectonics and eustasy

## INTRODUCTION

The Canadian Arctic Archipelago provides one of the world's best areas for establishing an integrated graptolite-conodont biozonation for the Late Ordovician-Silurian and for interpreting ocean-climate changes given the well-exposed interfingering relationship of the shale slope/basinal and carbonate shelf facies. Both the conodonts and graptolites are exceptionally well preserved. Two detailed conodont biostratigraphic studies have recently been completed for the two facies (Zhang et al. 2016, submitted) together with oxygen isotope work to interpret Silurian ocean paleotemperatures and events (Trotter et al. 2016).

## CONODONTS FROM THE CARBONATE SHELF FACIES, DEVON AND ELLESMERE ISLANDS

The conodont biostratigraphy for the Upper Ordovician – Upper Silurian carbonate shelf (Irene Bay and Allen Bay formations) and interfingering slope facies (Cape Phillips Formation) was recently established for parts of Devon and Ellesmere islands, central Canadian Arctic Islands (Zhang et al. 2016). Revisions to the interpreted regional stratigraphic relationships and correlations are based on the stratigraphic distribution of 51 conodont species representing 32 genera, identified from over 5000 conodont elements recovered from 101 productive samples in nine stratigraphic sections. The six zones recognized are, in ascending order: *Amorphognathus ordovicicus* Local-range Zone, *Aspelundia fluegeli* Interval Zone, *Pterospathodus celloni*, *Pt. pennatus procerus*, and *Kockellella patula* Local-range zones, and *K. variabilis variabilis*–*Ozarkodina confluens* Concurrent-range Zone. These provided a more precise dating of the members and formations and, in particular, the range of hiatuses within this stratigraphic succession.



The conodont biostratigraphic data establish the ages of the main stratigraphic units as follows: a) Irene Bay Formation and Lower Member, Allen Bay Formation — early Richmondian, Late Ordovician; b) Middle Member, Allen Bay Formation — Aeronian (Ae2) to late Telychian (Te5), Llandovery, Early Silurian; c) interfingering unit of Cape Phillips Formation — early Sheinwoodian (Sh1) to late Homerian (Ho3), Wenlock, Early Silurian; and d) Upper Member, Allen Bay Formation — Gorstian, possibly extending into the early Ludfordian, Late Silurian. Major hiatuses occur above the Lower Member, Allen Bay Formation, and possibly above the interfingering Cape Phillips unit.

Five main eustatic events and trends are recognized: a) a relatively high sea level represented by the Irene Bay and Lower Member, Allen Bay Formation (early Richmondian); b) a major Late Ordovician – Early Silurian regression marked by a hiatus between the Lower and Middle members, Allen Bay Formation (Hirnatian to early Aeronian); c) a modest transgression (Aeronian (Ae2) to late Telychian (Te4–Te5) marked by the Middle Member, Allen Bay Formation; d) a more significant transgression (early Sheinwoodian (Sh1)), marked by the interfingering 35 m unit of Cape Phillips Formation shale (Sheinwoodian (Sh1)) to the end of the Homerian (Ho3); and e) a regressive phase marked by the Upper Member, Allen Bay Formation (Gorstian and possibly to early Ludfordian).

These patterns show some differences to the interpreted global Silurian eustatic patterns, possibly because of regional geodynamic effects resulting in apparent sea-level changes from the collisions with Laurentia by Baltica to the east and Pearya to the north. Key paleoceanographic patterns and events in the area include the restricted circulation on the carbonate platform, a partly rimmed reefal bank margin at times with eastward backstepping to produce the interfingering Cape Phillips shale unit, and the relatively deep and anoxic offshore shale basin to the west.

The patterns of regional stratigraphy, facies changes, and hiatuses are interpreted as primarily related to the effects of glacioeustasy associated with the terminal Ordovician glaciation and smaller Early Silurian glacial phases, the backstepping of the Silurian shelf margin, and the geodynamic effects of the collision with Laurentia by Baltica to the east and Pearya to the north. Conodont colour alteration index values (CAI 1–6.5) do vary among the nine sections and complement earlier graptolite reflectance data in providing regional thermal maturation data of value in hydrocarbon exploration assessments.

## CONODONTS FROM THE SLOPE FACIES, CORNWALLIS ISLAND

In contrast, stratigraphic sections on Cornwallis Island, south-west of Devon and Ellesmere islands, reveal the well-exposed interfingering relationship of the slope/basinal shale and carbonate shelf facies. Building on earlier graptolite studies, 180 conodont samples were collected from nine sections of the Cape Phillips Formation, of which 118 yielded approximately 7600 conodont elements representing 54 species in 25 genera; the conodonts all have minimal thermal alteration (CAI 1) (Zhang et al. submitted).

Nine conodont zones are recognized and defined for this region, namely the *Amorphognathus ordovicicus*, *Distomodus kentuckyensis*, *Aspelundia expansa*, *As. fluegeli* and *Pterospathodus celloni* Interval zones, *Pt. a. amorphognathoides* Taxon-range Zone, *Pt. pennatus procerus* and *Kockeella ranuliformis* Highest-occurrence zones, and *K. ortus absidata* Taxon-range Zone. These are integrated with graptolite biozones established by others (e.g., Thorsteinsson 1958, Melchin 1987, 1989, Lenz and Melchin 1990), involving many of the same sections. Conodont community patterns have been previously established and compared to those from correlative faunas on Anticosti Island, Quebec (Zhang et al. 2006).

Paleontological and isotope geochemical studies have demonstrated the dynamic nature of the Silurian ocean-climate system and have identified major faunal turnovers or events, including those from the Baltica,

Avalonia, and Laurentia paleoplates where many Primo (P) and Secundo (S) Episodes and specific brief Events marking faunal turnovers occurred during the Hirnantian and early Silurian. Five of these are recognized in the Cornwallis conodont faunas and related to oceanographic and climate changes, particularly from oxygen isotope data ( $\delta\text{O}^{18}$  using ANU SHRIMP ion microprobe; Trotter et al. 2016) from Cornwallis conodonts: a) the Hirnantian mass extinction event (Ashgill), b) Sandvika Event (late Aeronian, Llandovery), c) Snipklint Primo Episode (early Telychian, Llandovery), d) Ireviken Event (late Telychian, Llandovery-Sheinwoodian, Wenlock) and e) the Mulde Event (early Homerian, Wenlock).

## CONCLUSIONS

The Canadian Arctic Archipelago exposes exceptional Lower Paleozoic stratigraphic sections for both the carbonate shelf and offshore shale/carbonate slope facies. Two detailed conodont studies of the Late Ordovician-earliest Late Silurian conodont faunas have been completed, with six zones recognized for the platform facies (on Devon and Ellesmere islands) and nine zones for the slope facies (on Cornwallis Island). These are combined with earlier graptolite studies to generate an integrated graptolite-conodont biozonation for this interval.

The patterns of regional stratigraphy, facies changes, and hiatuses are interpreted as primarily the effects of glacioeustasy associated with the terminal Ordovician glaciation and three smaller Early Silurian glacial phases, the backstepping of the Silurian shelf margin, and the geodynamic effects of the eastern and northern collisions with Laurentia by Baltica and Peary, respectively.

Conodont colour alteration index values are low on most of the carbonate shelf (CAI 1-3) and Cornwallis basin (CAI 1; buttressed by the Boothia Uplift), but increase to values CAI 4 and even over CAI 6 in the Parry Island and Central Ellesmere fold belts within the Innuitian Orogen to the north-west. These thermal maturation data complement earlier graptolite reflectance data in providing regional thermal maturation patterns of value in hydrocarbon exploration assessments.

$\delta\text{O}^{18}$  isotope data from Cornwallis conodonts reveal sea water paleotemperature changes correlating to five major faunal turnovers or events within this interval: the Hirnantian mass extinction event (Ashgill), Sandvika Event (late Aeronian, Llandovery), Snipklint Primo Episode (early Telychian, Llandovery), Ireviken Event (late Telychian, Llandovery-Sheinwoodian, Wenlock) and the Mulde Event (early Homerian, Wenlock).

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## UPDATED LLANDOVERY (SILURIAN) CONODONT PROVINCIALISM BASED ON QUANTITATIVE ANALYSIS

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**Keywords:** Llandovery, conodont, provincialism, quantitative analysis, longitudinal

### INTRODUCTION/BACKGROUND

Although the Early Palaeozoic conodont provincialism was already recognized in late 1950s (Sweet et al., 1959), provincialism of Llandovery conodonts has never been a major topic, particularly if compared with that of Ordovician faunas (e.g., Bergström, 1970; Barnes et al., 1973; Barnes and Fåhræus, 1975; Charpentier, 1984; Bergström, 1990; Zhen and Percival, 2003). Earlier studies of Llandovery conodont distribution were mostly based on the form taxa (e.g., Barnes et al., 1973; Charpentier, 1984), which is out-dated now. The first quantitative analysis on the basis of multi-element taxa by Bergström (1990) only focused on the data from Laurentia and Baltica, where the conodont faunas were well studied by then. Later, a restudy based on a larger database was carried out by Wang (1998), in which, the palaeogeographic pattern came from the intuitive recognition of endemism of typical species, rather than quantitative analysis. A quantitative restudy based on a large, taxonomy-updated dataset will be necessary in order to understand the conodont provincialism during the Llandovery.

### MATERIAL AND METHODS

The present dataset contains the data from 250 sections of 21 countries, which were collected from 124 publications. In order to unify identifications of taxa presented in all these publications for quantitative analysis, all published identifications were checked and, if needed, revised based on the multi-element concept of taxa. After this procedure, a total of 94 species of 18 genera can be used in the quantitative analysis.

Correlation of Llandovery conodont successions, particularly those from Rhuddanian and Aeronian, from different regions, and their correlation with the standard graptolite biozonation, is still complicated. So the two ages, the Rhuddanian and Aeronian are combined as one interval called 'Pre-Telychian'. The other analysed interval is Telychian.

The hierarchical scheme of provincial classification suggested by Zhen and Percival (2003) – Realm-Domain-Province – is accepted in this study. Recognition of a 'Realm' is generally based on water-depth. Con-

sidering the sedimentary features and/or the benthic assemblages, the sections in our database evidently represent two realms, Shallow-Sea and Open-Sea. 'Domains' are mainly defined by temperature and, in general, have latitudinal distribution. However, the quality of data, particularly from the high latitude zone, is not good enough to allow recognition of any 'Domain'. Delimitation of 'Provinces' in this study is based on faunal endemism recognized in 'Areas'. An 'Area' is composed of sections representing similar depositional environment, are located in short geographical distance from each other, and are characterized by similar conodont assemblages.

Three quantitative methods are adopted by using the program PAST (version 3.11; Hammer et al., 2001): cluster analysis (CA), non-metric multidimensional scaling (NMDS), and minimum spanning tree (MST). The advice of Huang (2011) is followed when choosing the coefficient for CA analysis. He noticed that a data frequency analysis is necessary before conducting the CA analysis, and suggested to choose coefficients according to the composition of faunas. Furthermore, he also indicated that CA analysis should be supplemented by other methods, such as NMDS analysis, to make the results more reliable and accurate.

## RESULTS

In both intervals, analysis of conodont provincialism is based only on data from the Shallow-Sea Realm. The information about faunas available from the Open-Sea Realm is too limited to allow reliable statistical calculations. After the frequency analysis, the Ochiai and Raup-Crick coefficients are selected for the CA analysis, and the Ochiai coefficient is chosen for the NMDS analysis. Both analyses indicate four provinces during the 'Pre-Telychian' interval, i.e., North American-Baltic-Siberian Province (NBS Province), Timan-Severnaya Zemlya Province, Australian Province and Yangtze Province, and only three during the Telychian interval, i.e., Baltic-Austrian-Siberian-Australian-North American Province (BASAN Province), Timan-Severnaya Zemlya Province and Chinese Province (Fig. 1).

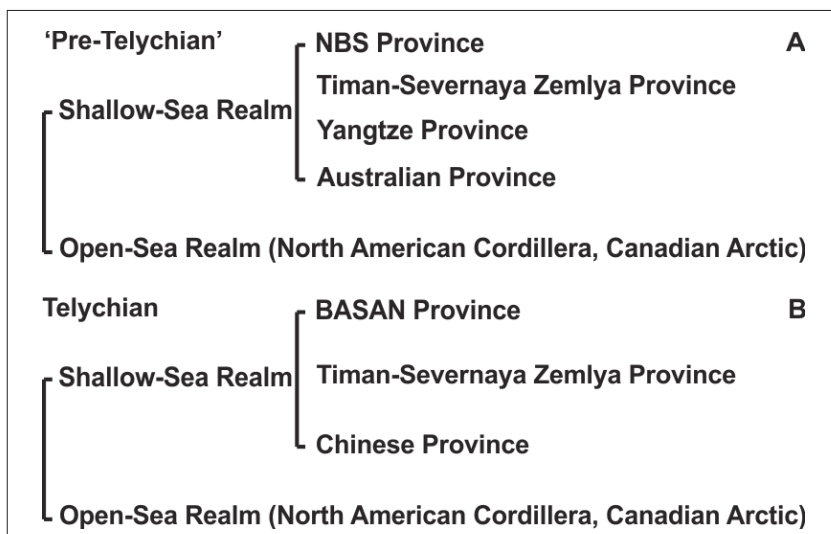


Fig. 1. Hierarchical scheme of biogeographic subdivisions used in this study.

## DISCUSSION

Temperature was considered as one of the essential factors controlling the provincialism of conodont (e.g., Sweet et al., 1959; Barnes and Fåhræus, 1975; Zhen and Percival, 2003). However, results of our study did not support this theory. The conodont faunas from Austria and Turkey located in the high latitude zone in Llandovery were quite similar to those from North America and Baltic region, both located in the mid-low latitude zone in that time. This is confirmed by the quantitative analysis: all these four regions are assigned to the same BASAN Province during Telychian. Moreover, the latitudinal distribution pattern of conodont provinces does not fit with the latitudinal pattern of the climatic zones (which explains why 'domains' are not recognized in this study). This indicates that temperature alone, i.e. distribution of climatic zones, was not the major factor controlling the Llandovery conodont provincialism.

## CONCLUSIONS

A large database of uniform taxonomy has been built up to analyze the Llandovery conodont provincialism. Three quantitative methods, including CA analysis, NMDS analysis and MST, have been adopted. The results indicate four and three provinces existed during 'Pre-Telychian' and Telychian intervals respectively. The latitudinal distribution pattern of conodont provinces suggests that temperature was not the major factor on conodont provincialism during Llandovery.

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# EARLIEST RASTRITIDS AND PETALOLITHIDS (GRAPTOLITES) IN CHINA AND THE CZECH REPUBLIC: COMPARISON AND PALAEOBIOGEOGRAPHIC IMPLICATIONS

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**Keywords:** Aeronian, *Petalolithus*, *Rastrites*, palaeobiogeography, correlation

## INTRODUCTION/BACKGROUND

Global correlation of Silurian rocks relies primarily on planktic graptolites, supplemented by chitinozoans and conodonts. Graptolites are the most common and stratigraphically important fossils to be found in anoxic black shales, which predominate in both Aeronian and Rhuddanian sedimentary successions worldwide. As part of the search for new Global Stratotype Section and Point (GSSP) for the Aeronian Stage by the Sub-commission on Silurian Stratigraphy, the most promising sections rich in graptolites are studied in South China and the Czech Republic.

Llandovery black shales rich in graptolites are widely distributed in the Yangtze Platform of South China. In the upper and middle part of the Yangtze region Rhuddanian and Aeronian stages are preserved within up to 80 m thick Lungmachi Formation. Shennongjia section of Hubei province and Yuxiancun section of Sichuan province exposes an uninterrupted succession ranging from the Ordovician-Silurian boundary interval to the upper Aeronian. Silurian of the Barrandian area of the Czech Republic belongs to sedimentary cover of the Teplá–Barrandian Unit, considered as a part of the Armorican Terrain assemblage, HUN super terrain, or an independent microplate named Perunica with close faunal affinities to other peri-Gondwanan terranes of the variscan Europe. Rhuddanian and Aeronian are represented by the Želkovice Formation, comprising somewhat condensed, 8–12 m thick black-shale succession with rich graptolite fauna.

Preliminary comparison of the upper Rhuddanian – lower Aeronian graptolite assemblages of South Chinese sections with those of European black shale succession (exemplified by Czech sections) revealed substantial difference in taxa involved. Despite the fact that Llandovery graptolite fauna has been considered as one of the most cosmopolitan of any throughout the graptolite fossil record (Berry & Wilde 1990), considerable differences between graptolite faunas of China, Siberia and northern North America on one side and those of Europe on the other side have been already discussed by Melchin (1989). Many taxa are specific either to Europe or China (plus Siberia and northern Canada), many species are more or less closely similar but differ in some characters and morphological details. Since many graptolite species are specific to either Atlantic cool-water realm (Europe) or Pacific warm-water realm (China, Siberia, northern Canada) *sensu* Berry & Wilde (1990) and truly cosmopolitan graptolite species are few, taxonomic re-assessment of morphologically similar, but apparently not identical, taxa recorded in comparable stratigraphic levels in the



two realms is a key prerequisite for high resolution and quantitative correlation of the sections considered in current search for new Aeronian GSSP. Lowermost part of the Aeronian Stage exhibits a rapid graptolite diversification event with closely spaced appearances of several morphological innovations and new evolutionary lineages: monograptids with isolated and hooked thecae (genera *Demirastrites*, *Rastrites* and *Campograptus*) as well as ancorate biserial *Petalolithus*. Early representatives of *Demirastrites*, *Rastrites*, *Campograptus* and *Petalolithus*, reported from many regions throughout the world, have been employed as important tools in high-resolution global correlation. Our study focused on early representatives of *Rastrites* and *Petalolithus* – graptolite taxa of major importance for identification and high-resolution correlation of the Rhuddanian-Aeronian boundary strata.

## MATERIAL AND METHODS

A detailed morphological and morphometric analysis based upon 20-30 characters was performed on Czech and Chinese collections comprising ca 400 specimens. The authors collected Czech material in Hlásná Třebaň, Karlík, Všeradice and Radotín tunnel sections. Type specimens of the species described by J. Barrande and J. Perner were studied in the National Museum, Prague. Newly collected Chinese material came from Shennongjia section in Hubei province and Yuxiancun section in Sichuan province. Type specimens illustrated by Chen & Lin (1978), Chen (1984) and Ni (1978) were studied at Nanjing Institute of Geology and Palaeontology CAS. All specimens were photographed in high magnification. Line drawings were prepared using Photoshop software. Morphometric data were obtained from line drawings by means of AutoCAD.

## RESULTS AND INTERPRETATION

Lower Aeronian strata studied in the Czech sections yield *Rastrites longispinus* (Perner) – single *Rastrites* species with FAD in the lower third of the *Demirastrites triangulatus* Biozone. The same species is recorded from the lower Aeronian sections throughout Europe. Several species assigned to *Rastrites* have been reported from the *triangulatus* Zone in Yangtze Platform. Chen & Lin (1978) recorded *Rastrites guizhouensis* (Mu *et al.*), *R. confertus* n.sp., *R. peregrinus* Barrande, *R. approximatus* Perner, *R. hybridus* Lapworth, *R. hemigyrtus* n.sp., *R. distans bellulus* Yin & Mu and *R. rastrum* Richter from the lower Aeronian of Tongzi area of Guizhou province. Ni (1978) recorded *R. guizhouensis* and *R. peregrinus* from the lower Aeronian of Yichang area of Hubei province. *R. guizhouensis*, *R. hybridus*, *R. cf. richteri* and *R. norilskensis* Obut & Sobolevskaya were identified by Chen (1984) in southern Shaanxi province. Bed by bed sampling of the *triangulatus* Zone carried out in Shennongjia and Yuxiancun sections recorded only two rastritid species: abundant *R. guizhouensis* and less common *Rastrites* aff. *longispinus*. *R. aff. longispinus* differs from *R. longispinus* in having shorter metathecae. DVW attains 2.1 mm in distal thecae in comparison with 2.9-3.2 mm attained in *R. longispinus*. Other taxa, recorded by Chen & Lin (1978), Ni (1978) and Chen (1984) are either conspecific with these two (*R. confertus*, *R. peregrinus sensu* Chen & Lin and Ni, *R. approximatus*, *R. hybridus sensu* Chen & Lin and *R. cf. richteri sensu* Chen) or belong to different genera and higher stratigraphic levels (*R. norilskensis*, *R. hemigyrtus*, *R. distans bellulus*).

Two species of *Petalolithus* were recorded in the lower Aeronian of central, southern and western Europe as well as in Great Britain and Scandinavia. *Petalolithus ovatoelongatus* (Kurck) made its lowest occurrence in the lowermost *triangulatus* Zone, just above the FAD of the zonal index species. Smaller *Petalolithus minor* (Elles) is known from slightly higher levels beginning with the middle *triangulatus* Zone. Surprisingly, there

are limited records of *Petalolithus* from the lower Aeronian of China. Chen & Lin (1978) recorded *Petalolithus folium* (Hisinger) from Tongzi area along with *Petalolithus palmeus* (Barrande), *Petalolithus dubovikovi* Obut & Sobolevskaya and *Petalolithus minor granulus* n. ssp. The former one has not been found in the *triangulatus* Zone of Shennongjia and Yuxiancun sections. Preserved specimens of *P. palmeus*, a species limited to the lowermost Telychian in Europe, as well as *P. dubovikovi* are not determinable. *P. minor granulus* is a single juvenile rhabdosome in need of further examination. Chen (1984) described *Petalolithus ovatus* (Barrande) and *Petalolithus minor brevicollis* n. ssp. from higher part of the lower Aeronian of Shaanxi. The former one is a species limited to the lowermost Telychian in Europe and the specimen assigned to *P. ovatoelongatus*, is poorly preserved. Also *P. minor brevicollis* is based upon single indeterminate specimen. Fairly common petalolithid was recorded in the *triangulatus* Zone in Shennongjia and Yuxiancun. It can be differentiated from *P. ovatoelongatus* by having lower angle of thecal inclination (30-35° compared to ca 40° at th1!), shorter, less everted and less overlapping proximal thecae, more gradual widening of the rhabdosome and lesser maximum width with mean value of 4.1 mm compared to 4.9 mm.

## CONCLUSIONS

Stratigraphically important monograptid genus *Rastrites* is represented by a single species (*R. longispinus*) in the lower Aeronian *triangulatus* Zone in Europe. The species does not occur in South China. In turn, *R. guizhouensis* and *R. aff. longispinus* – two species widespread in China – are missing in Europe. Similar difference attributed to palaeobiogeographic disparity can be observed in *Petalolithus*. *P. ovatoelongatus* and *P. minor* are common lower Aeronian taxa in Europe whereas closely similar *Petalolithus* sp. and some small rhabdosomes of questionable affinity occur China. Our results are consistent with the palaeobiogeographic model outlined by Melchin (1989) and point to palaeobiogeographic constraints in high-resolution biostratigraphic correlation on a global scale.

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## ECOLOGICAL GRADIENT OF A BRACHIOPOD FAUNA AFTER THE END ORDOVICIAN MASS EXTINCTION FROM SOUTH CHINA AND ITS SIGNIFICANCE

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Classification of extinction events and their severity is generally based on taxonomic counts. The ecological impacts of such events have been categorized and prioritized but rarely tested with empirical data. In a recent study, the ecological severity of the end Ordovician event was considered even less significant than that of the Serpukhovian, and is ranked only sixth within the eleven largest Phanerozoic crises since the beginning of the Ordovician Period (McGhee et al., 2013). South China offers a key opportunity to examine the ecological changes through the end Ordovician event in detail. The *Cathaysiorthis* Fauna is a shelly fauna dominated by brachiopods from the uppermost Ordovician to lowermost Silurian of SE China, succeeding the cool-water *Hirnantia* Fauna. The fauna is abundant and has a relatively high diversity; these data were reported with the detailed systematic descriptions of the fauna (Rong et al., 2013). The spatial and temporal ranges of more than 6,500 identified specimens, from 10 collections derived from 6 localities were investigated by network and cluster analyses, nonmetric multidimensional scaling and a species abundance model. The ecological circumstances of the survival brachiopod fauna after the end Ordovician mass extinction were evaluated.

Other, older brachiopod faunas, *Altaethyrella* Fauna and *Foliomena* Fauna, characterizing the late Katian within the same area (Zhan and Cocks, 1998) are compared in terms of diversity, population structure, benthic assemblage zones and relative abundance together with their major components to help further elucidate the ecological 'turnover' through the end Ordovician extinction event in South China. Depth zonations and structure of brachiopod assemblages along an onshore-offshore gradient in the late Katian were similar to those in the latest Ordovician–earliest Silurian (post–extinction fauna). The widths of ecological range are similar between before and immediately after the crisis that may suggest the limited ecological effect of the event (Fig. 1).

Within this ecological framework, deeper-water faunas are partly replaced by new taxa; siliciclastic substrates continued to be dominated by the more 'Ordovician' orthoides and strophomenoides, shallow-water carbonate environments hosted atrypoides, athyridoides and pentameroides, with the more typical Ordovician brachiopod fauna continuing to dominate until the late Rhuddanian. The end Ordovician extinctions tested the resilience of the brachiopod fauna without damage to its overall ecological structure; that commenced later at the end of the Rhuddanian.

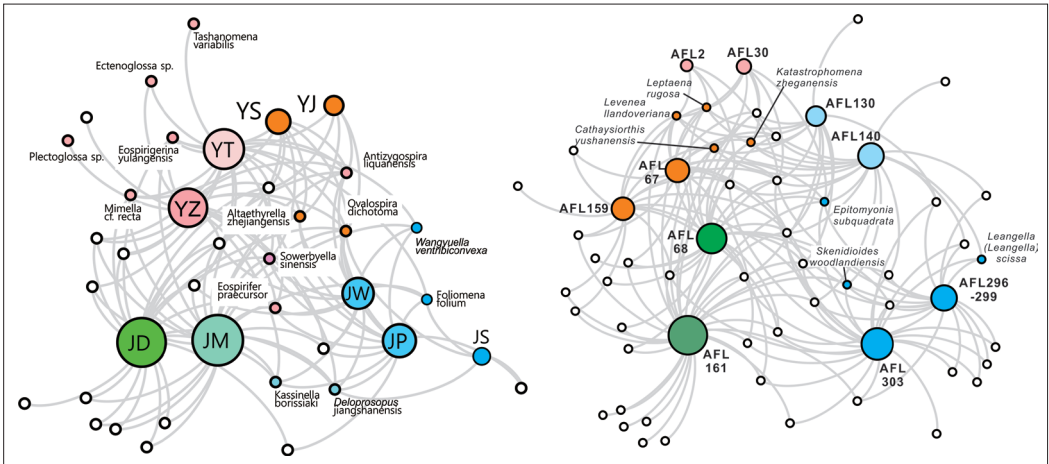


Fig. 1. The network diagram generated by NA shows an overview of the *Altaethyrella* Fauna, *Foliomena* fauna from upper Katian (left part), and the *Cathaysiorthis* Fauna from the uppermost Ordovician to lowermost Silurian (right part). The diagram indicates a similar bathymetric gradient for the brachiopod faunas before and after the end Ordovician mass extinction; the typical deeper-water taxa are distributed in the top right of the diagrams, whereas the shallow-water taxa are in the top left.

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## THE PRELIMINARY REPORT ON THE INTEGRATED STRATIGRAPHY OF THE LUDLOW IN THE BAUBLIAI – 2 WELL (WEST LITHUANIA)

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**Keywords:** Graptolites,  $\delta^{13}\text{C}$  isotope excursion, upper Silurian, West Lithuania

### INTRODUCTION

The Ludlow is a very dynamic epoch of the Silurian Period that witnessed several global bioevents and perturbations of carbon cycle. The *leintwardinensis*, *kozlowskii* and *spineus* graptolite global extinction events have been identified in the Ludlow (Koren' 1987). Three conodont events are distinguished in a same interval (Jeppsson, 1997): the Linde, Lau and Klev events, and the Linde and Lau positive  $\delta^{13}\text{C}$  isotope excursions are documented (Melchin, 2012). The *leintwardinensis* graptolite extinction seems to overlap with the Linde conodont bioevent and the positive  $\delta^{13}\text{C}$  excursion at the Gorstian/Ludfordian boundary. The lower part of the Lau positive  $\delta^{13}\text{C}$  excursion meets the lower part of Lau conodont event and the upper part coincides with *kozlowskii* graptolite extinction. The *spineus* graptolite extinction and Klev conodont bioevents distinguished at the Ludlow/Pridoly boundary are most probably synchronous. As the synchronicity of these events is not yet convincingly demonstrated, the aim of this study is to clarify the temporal relationships of these events.

### MATERIAL AND METHODS

The new material comes from the Baubliai-2 well in West Lithuania, located in the open shelf facies zone of the East Baltic Sedimentary Basin. The investigated interval ranges from 1644.7 to 1560 m depth (about 85 m). The core was not taken below and above this interval. The section of the investigated interval comprises mudstones with limestone interbeds.

The graptolite fauna was collected every 15–30 cm. Samples were prepared using a standard HF method. The samples for stable carbon and oxygen isotope analysis were collected at 1 m intervals. Ca 2 g of rock sample was Picked and the powdered material was analysed on the mass spectrometer Delta V Advantage and (for preparation of gases) GasBench II by Thermo Scientific.

## RESULTS

The *ludensis* (?), *nilssoni*, *progenitor*, *scanicus* and *leintwardinensis* graptolite biozones were distinguished in the investigated interval of the Baubliai-2 well. The presence of the *ludensis* Biozone that corresponds to the topmost Wenlock, is problematic in Baubliai-2 well. The lower part of the studied interval contains only *Colonograptus gerhardi* (Kühne) that appear in the *ludensis* biozone and disappears in the lower part of *nilssoni* Biozone in Lithuania (Radzevičius & Paškevičius, 2005) and in the Czech Republic (Štorch et al., 2016). The *nilssoni*, *progenitor* and *scanicus* biozones correspond to the Gorstian and the *leintwardinensis* Biozone represent the lower part of the Lutfordian Stage. The upper part of the investigated interval of Baubliai-2 well is barren of graptolites.

The initially low  $\delta^{13}\text{C}$  values (-3.29 ‰ - 1644.7 m) rise rapidly up to 0.49 ‰ over one meter and fall to -0.51 ‰ at 1641.7m depth. Then values are moderately stable between 1642.7 to 1605.7 m (from -0.9 to -0.19 ‰). Higher up, the values rise rapidly up to 0.44 ‰ (depth 1604.7 m) and fall rapidly to -1.91 ‰ (depth 1602.7 m). Slightly to moderately negative  $\delta^{13}\text{C}$  values (-1.91 ‰ to -0.13‰) are characteristic of the depth interval 1595.7- 1601.7 m. This is followed by an increase of  $\delta^{13}\text{C}$  values up to 0.63‰ at the depth 1591.7 m and a slow decline to -1.25 ‰ (depth 1583.7 m). Another rise of the curve, with some fluctuations, reaches 5.52 ‰ at the depth 1560.7 m). The core was not taken in the Baubliai-2 well higher up of this depth.

## CONCLUSIONS

There are two positive  $\delta^{13}\text{C}$  excursions in the investigated interval. The first one in 1592.7 – 1588.7 m interval is not very distinct and is confined to the *leintwardinensis* Biozone. This excursion could likely point at the Linde event but integration of the conodont material is required for accurate calibration of the isotopic and graptolite records. The second positive  $\delta^{13}\text{C}$  excursion started at 1581.7 m and reaches the end of studied interval). The increase of  $\delta^{13}\text{C}$  values starts higher than the last occurrence of *Pristiograptus tumescens* (Wood, 1900) and could point at the Lau event. This is also confirmed by the high  $\delta^{13}\text{C}$  values (5.52 ‰) that are specifically characteristic of the Lau Event.

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## BIOTIC RESPONSE TO LATE HOMERIAN ENVIRONMENTAL CRISIS: LUNDGRENI EXTINCTION EVENT AND SUBSEQUENT RECOVERY IN THE PRAGUE SYNFORM, CZECH REPUBLIC

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**Keywords:** Homerian, Lundgreni Event, graptolites, extinction and recovery, biodiversity indices

### INTRODUCTION

Silurian Period is widely recognized as a time interval of considerable changes in marine environment and biodiversity. Several global biotic crises associated with environmental perturbations have been identified, for the first time in graptolite and/or conodont faunal record, and subsequently correlated with facies changes and carbon isotope data. One of the most widely recognized biotic crises developed in the upper Homerian, beginning with the uppermost part of *Cyrtograptus lundgreni* graptolite Biozone. Dramatic reduction of graptolite diversity in the middle of the Homerian Stage, called Lundgreni Event or "Big crisis", was recognized by Koren' (1987) and Jaeger (1990) respectively. The late-Homerian crisis was also recognized as a prominent overturn and extinction of conodont faunas in Gotland sections and named the Mulde Event. Graptolite extinction slightly predated a double-peaked late Homerian <sup>13</sup>C isotope excursion (CIE) used as a chemostratigraphical correlation tool. Black-shale dominated offshore sedimentary successions spanning the stratigraphic interval from middle Sheinwoodian *Monograptus belophorus* Zone to the uppermost Homerian *Colonograptus ludensis-C. gerhardi* Zone is well accessible in the Kosov Quarry, in the Prague Synform of central Bohemia. Graptolite-rich shales with subordinate shelly fossils enabled detailed insight into offshore faunal dynamics across the late Homerian crisis from the incipient extinction in the uppermost *lundgreni* Zone, through a survival interval to a subsequent recovery in the *ludensis-gerhardi* Zone.

### MATERIAL AND METHODS

A series of 56 bulk samples, each about one cubic foot in volume, was collected from a 13 m thick shaly succession punctuated by numerous tuffitic intercalations. From all samples, all other macrofossils were collected along with 2582 determined graptolite rhabdosomes employed in statistical calculations. Basic biodiversity indices, such as Menhinick's and Margalef's richness indices and Dominance, Berger-Parker's, Shannon's and Simpson's indices of diversity, were calculated from quantitative graptolite data to evaluate changes in graptolite community associated with the *lundgreni* Event. The effect of sample size on graptolite species counts was investigated by rarefaction analyses. Rarefaction curves have shown the need to merge two (and in two cases three) neighbouring two (in two cases three) samples and reduce the original dataset



of 56 samples to 27 samples. Statistical significance of diversity changes between stratigraphically neighbouring two samples has been evaluated using a diversity t test. Statistical calculations were undertaken using the software package PAST, ver. 3.14 (Hammer *et al.* 2001).

## RESULTS AND INTERPRETATION

In the Kosov section the first signs of on-going collapse of the lower Homeric graptolite fauna coincided with about the last tenth of the *lundgreni* Zone when once common *Monoclimacis flumendosae* (Gortani) vanished in conjunction with substantial numerical decline of plectograptids. Cyrtograptids still flourished, being represented by *Cyrtograptus lundgreni* Törnquist, *Cyrt. hamatus* (Baily), *Cyrt. mancki* Bouček and *Cyrt. hemmanni* Bouček. The species richness remains almost constant in the upper part of the *lundgreni* Zone, alternating between seven and nine species per sample. However, low dominance typical of graptolite assemblages of the *lundgreni* Zone was rising towards the top of this interval. Rapid decline of species richness began when plectograptids and *Cyrt. lundgreni* vanished. Short-ranging successive proliferation of *Monograptus subflexilis* Bouček & Přibyl, and *M. ambiguus* Jaeger in the uppermost part of the *lundgreni* Zone could be interpreted as further diversification of an ecologically balanced fauna. However, coincidence with extinction of *Cyrt. lundgreni* and proliferation of opportunistic generalists *Monograptus flemingii* (Salter) and *P. pseudodubius* (Bouček) instead probably indicate changing conditions, given that this level is overlain by an interval with very low diversity assemblage of the two generalist survivors. We suppose that living conditions of the graptolite fauna deteriorated slightly before the end of the *lundgreni* Zone as defined herein.

A major drop in species richness and rise in dominance marked a thin interval assigned herein to *Monograptus flemingii* Zone, which preserved *M. flemingii* and *P. pseudodubius*, the only survivors from once prospering early Homeric fauna. Further stress resulted in extinction of *M. flemingii* and dwarfism of *Pristiograptus parvus* Ulst – the only and name giving species of the subsequent *parvus* Zone. In this interval, stressful conditions brought graptolites to near extinction. Carbonaceous level, developed in the *parvus* Zone, preserved a rich, although minute, relatively deep water shelly and trilobite fauna referred to as the *Decoroproetus-Ravozetina* benthic Community. Abundant occurrence of *Gothograptus nassa* (Holm) in the upper part of the *parvus* Zone may be interpreted as immigration and proliferation of either generalists or pre-adapted opportunists, rather than indigenous speciation.

Dominance and Berger-Parker index reached maximum values in *Pristiograptus frequens* Zone when a normal-sized morphotype of *Pristiograptus dubius* stem line – *P. frequens* (Jaekel) became the most common taxon by far in the low-diversity/high-dominance graptolite assemblage. Very low species richness (2–3 species per sample) continued until the base of *Colonograptus praedeubeli*-*C. deubeli* Zone when *Colonograptus praedeubeli* (Jaeger) and *Colonograptus deubeli* (Jaeger) took a dominant role among 2–4 co-existent species. Slow recovery of the post-extinction graptolite fauna commenced with lowest occurrences of the two cosmopolitan taxa as indicated by the fact that the *praedeubeli*-*deubeli* Zone is marked by true morphological differentiation derived from the *pristiograptid* stem. Early *colonograptids* exhibit remarkably high variability in curvature of the sicula, and its apertural width, shape and rutellum, as well as in the apertural shape and degree of isolation of the initial thecae. High intraspecific variability, which is observed also in *pristiograptid* rhabdosomes of this interval (*P. frequens* and *Pristiograptus jaegeri* Holland *et al.*), can be ascribed to incipient speciation under subsiding or relaxed environmental stress. In the lower part of the latest Homeric *ludensis-gerhardi* Zone, the zonal index *Colonograptus ludensis* (Murchison) is the only incoming monograptid taxon, later supplemented by *Pristiograptus auctus* Rickards and plectograptids *Spinograptus*

*munchi* (Eisenack), *Spinograptus clathrospinus* (Eisenack), and *Neogothograptus eximinassa* Maletz. Four species per sample were found in the lower part of the *ludensis-gerhardi* Zone, the uppermost combined sample yielded seven species. Relative increase of the species richness in the middle *ludensis-gerhardi* Zone was largely driven by plectograptine revival. Generally rare and inconsistent occurrence of plectograptid taxa in the post-extinction Homerian of the Kosov section does not allow for ecologically relevant interpretation when compared with more consistent records from Všeradice and Nesvačily sections. However, gradual increase of species richness and diversity measures, including Dominance, Berger-Parker's, Shannon's and Simpson's indices returning to pre-crisis values, account for the restoration of pre-crisis equilibrium by about the middle of the *ludensis-gerhardi* Biozone. Post-extinction recovery of the graptolite fauna grew into adaptive radiation which partly regained the former morphospace of planktic graptoloids by introduction of complex and diverse morphological novelties on thecae and rhabdosomes near the base of the Ludlow Series (hooded, hooked, lobate and spinose thecal apertures, ventrally curved and s-shaped rhabdosomes, sicular cladia).

## CONCLUSIONS

Obtained data reveals the anatomy of the mid-Homerian mass faunal extinction, survival, and subsequent recovery. Significant changes in graptolite community structure and species dominance predated major species extinctions and changes in benthic communities. The first victims of changing environment were large and specialized cyrtograptids, plectograptines and some monograptids whereas latest survivors *M. flemingii* and *P. dubius* represent long-ranging, ecologically-tolerant epipelagic taxa. Post extinction interval is represented by bioturbated shale, and argillaceous limestone with specific shelly fauna and slumped limestone lenses. This level witnessed a period of bare survival, in which the planktic graptoloids were close to extinction. Minute rhabdosomes of the only monograptid survivor *P. parvus*, were subsequently accompanied by the plectograptid *G. nassa*. Abundant benthic fauna of the post-extinction *Decoroproetus-Ravozetina* Community accounts for enhanced ventilation in the *parvus* Zone and, in conjunction with slumped limestone lenses in the overlying strata, indicate a shallowing pulse documented globally. The *frequens* Zone recorded incipient recovery of the graptolite fauna heralded by immigration of the standard-sized *P. frequens*. The subsequent *praedeubeli-deubeli* Zone brought novelties in morphology which gave rise to early colonograptids. Recurrent occurrences of the low-diversity small shelly fauna and trilobites of *Decoroproetus-Ravozetina* Community continued until the lower part of the *ludensis-gerhardi* Zone. Graptolite diversity increased and species dominance decreased in the uppermost part of the section which is referred to the lower-middle part of the *ludensis-gerhardi* Zone. Correlation with Nesvačily and Všeradice sections suggests that well-balanced environment returned and new adaptive radiation among graptolites developed as late as in the latest Homerian in the Prague Synform.

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## SILURIAN CONODONTS FROM THE "ORTHOCERAS LIMESTONES" (TAFILALT AND TINDOUF BASINS, NW AFRICA)

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**Keywords:** conodonts, biostratigraphy, "Orthoceras limestones", Silurian, NW Africa.

### INTRODUCTION

In contrast to the low to mid latitude Silurian conodont faunas from peri-Gondwanan Europe and Laurentia, little is known about the Silurian conodont faunas from the widespread cold-water limestones that developed in northern Gondwana. Few researchers have addressed the Silurian conodont faunas from NW Africa, where predominantly shale deposits expand with very uniform facies throughout scattered outcrops for several hundreds of kilometers, many of them affected by territorial disputes.

Based on published and unpublished reports of 40 stratigraphic sections, García López *et al.* (1996) analysed the main lithological features and conodont associations from a vast area of northern Gondwana, extending from northern France to the west–central Sahara. They recognized four pulses of limestone deposition during the early Llandovery, late Llandovery – early Wenlock, latest Wenlock – Ludlow, and Pridoli. The second two limestone packages are characterized by condensed outer shelf nautiloid and scyphocrinoid limestones and are distinct markers for regional correlation studies (Destombes *et al.*, 1985; Lubeseder, 2008).

The broad siliciclastic character of the Silurian sedimentary succession and the difficult working conditions in some regions of NW Africa resulted in that most of the conodont information from this area is obtained from spot samples. In the present contribution, we analyze two new conodont samples obtained from the "Orthoceras limestones" in the Tafilalt Basin (Eastern Anti-Atlas, Morocco) and the southern flank of the Tindouf Basin (W Sahara) (Fig. 1). Taking into account the recent conodont studies from NW Africa (e.g., Sarmiento *et al.*, 1997; Benfrika, 1999; Benfrika *et al.*, 2007; Männik *et al.*, 2011; Lubeseder, 2008; Corrigan *et al.*, 2014), they allow us to improve the knowledge on the Silurian conodont faunas and shed light into the episodic development of condensed limestone levels in northern Gondwana.

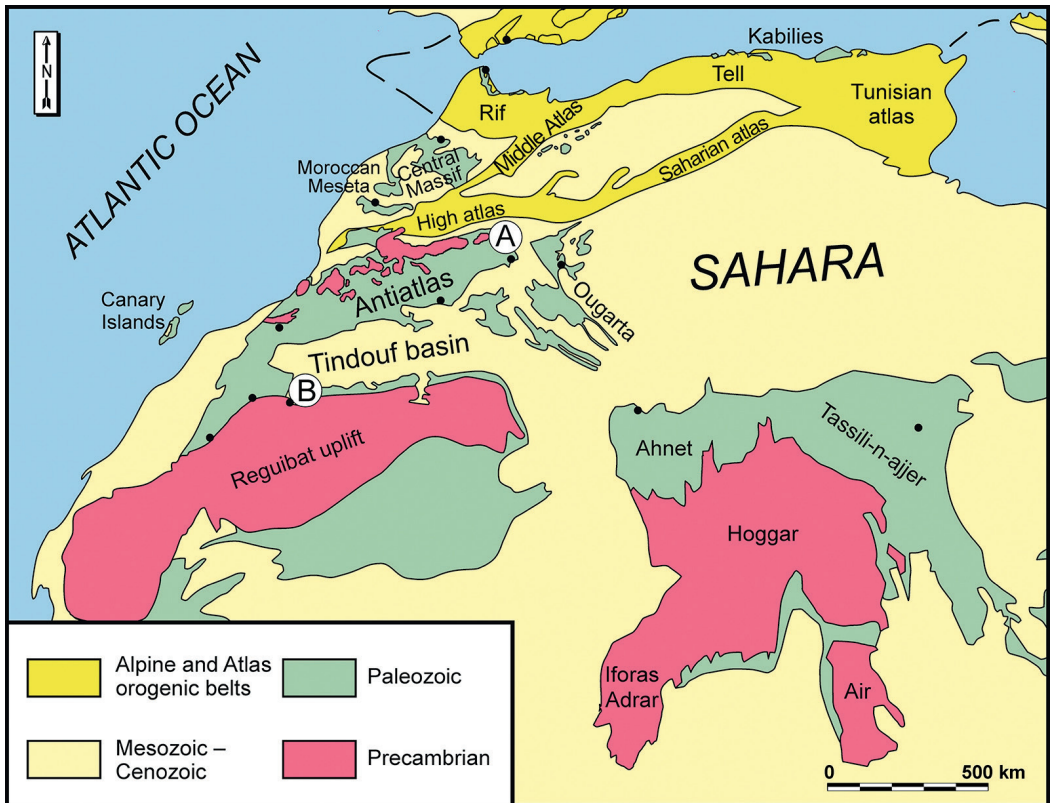


Fig. 1. Simplified geological map of Northwestern Africa with location of studied samples (modified from Julivert, 2003). (A): Khabt-Lahjar Section, Tafilalt Sub-basin, Eastern Anti-Atlas, Morocco. (B): Uad Tadaieght Section, Tindouf Basin, W Sahara. Black dots represent localities with previous Silurian – lower Devonian conodont reports (see text for references).

## CONODONT RECORDS FROM THE "ORTHO CERAS LIMESTONES"

In the Khabt-Lahjar section of the Tafilalt, located 21 km to the east of Erfoud, the Silurian succession is about 150 m thick. It is dominated by graptolitic black shale facies interbedded with nautiloids and scyphocrinoid limestone beds towards the top. Sarmiento *et al.* (1997) observed that the "Orthoceras limestones" cropping out in the Khabt-Lahjar section include conodonts referable to the *Polygnathoides siluricus* Zone, in agreement with previous conodont reports from the Tafilalt (Hollard, 1977). Lubeseder (2008) also recognized the *P. siluricus* Zone in the lower and upper beds of the "Orthoceras limestones" in the Dra Plain, south-western Anti-Atlas, but he did not discuss, according to the graptolite findings just above the upper bed that it may extend up to the Ludfordian–Pridoli transition. After a detailed biostratigraphic study in the Erfoud area, NW Tafilalt, Corrigan *et al.* (2014) established that the "Orthoceras limestones" are middle Ludfordian in age (*Ancoradella ploeckensis* – *P. siluricus* zones), whilst the "Scyphocrinites limestones" correspond to the late Pridoli – Lochkovian.

The conodont association from the "Orthoceras limestones" at the Khabt-Lahjar section was obtained after standard acetic acid digestion of a wackestone-packstone sample (500 g) taken ca. 60 m above the base of the Silurian deposits. It provided 61 conodont elements including *Coryssognathus dubius* (Rhodes), *Oulodus siluricus* (Branson and Mehl), *Ozarkodina* sp., *Pseudooneotodus beckmanni* (Bischoff and Sannemann), *Wurmiella excavata* (Branson and Mehl), *Kockelella variabilis variabilis* Walliser and the zonally diagnostic species *P. siluricus* (Branson and Mehl) (Fig. 2). The latter conodont species verifies a Ludfordian depositional age for the "Orthoceras limestones" at the Khabt-Lahjar Section, as its temporal range is restricted to the homonymous biozone.

The Tindouf Basin is a vast syncline (500 x 300 km) mainly unexplored, which crosses the borders between Morocco, NW Algeria, Mauritania, and the disputed territories of Western Sahara. The only study of the Silurian conodont faunas from the Tindouf Basin is that by Ethington and Furnish (1962), who analyzed four Silurian spot samples. Their faunal association suggests a broad Ludlow age, though two of the samples are apparently contaminated with Frasnian elements.

The conodont sample from the Tindouf Basin was collected during water prospect studies (Ron Martin, 2009) at the Uad Tadaieght section, 15 km SW of Hassi Meheiris Village (11°18'38.7"N, 26°11'41.4"W). There the Silurian succession is made up of ~40 m of graptolitic black shales in the lower part and ~60 m of fetid wackestone to packstone beds intercalated with thin argillaceous horizons in the upper part. The sample proceeds from a nautiloid rich level located at the top of the succession, and despite its low weight (100 g), it provided 38 conodont elements (Fig. 2). The conodont association includes *Pseudooneotodus beckmanni* (Bischoff and Sannemann), *Oulodus elegans elegans* (Walliser), *Oulodus elegans detortus* (Walliser) and "*Ozarkodina*" *eosteinhornensis* s.l. It is characteristic of the late Pridoli, probably corresponding to the Lower *Oulodus elegans detortus* Zone, following the biostratigraphic scheme of Corrigan *et al.* (2014) for the Eastern Anti-Atlas.



Fig. 2. Silurian conodont elements recovered from orthocone-rich limestones at the Khabt-Lahjar section, Eastern AntiAtlas (1–8, 19–20: *Polygnathoides siluricus* Zone) and the Uad Tadaieght Section, Tindouf Basin (9–18: *Oulodus elegans detortus* Zone). 1. *Oulodus siluricus* (Branson and Mehl), Sc element, DGO7969; 2. *Polygnathoides siluricus* Branson and Mehl, Pa element, DGO7970; 3. *Kockelella variabilis variabilis* Walliser, Sc element, DGO7971; 4. *Kockelella variabilis variabilis* Walliser, Pa element, DGO7972; 5. *Oulodus siluricus* (Branson and Mehl), P element, DGO7973; 6. *Pseudooneotodus beckmanni* (Bischoff and Sannemann), P element, DGO7974; 7. *Coryssognathus dubius* (Rhodes), M element, DGO7975; 8. *Polygnathoides siluricus* Branson and Mehl, Pb element, DGO7976; 9. *Oulodus elegans elegans* (Walliser), Sb element, DGO7977; 10. *Oulodus elegans detortus* (Walliser), Sc element, DGO7978; 11. *Ozarkodina eosteinhornensis* s.l., Pb element, DGO7979; 12. *Oulodus* sp., P element, DGO7980; 13. *Oulodus elegans detortus* (Walliser), P element, DGO7981; 14–15. *Ozarkodina eosteinhornensis* s.l., Pa element, DGO7982; 16–17. *Ozarkodina eosteinhornensis* s.l., Pa element, DGO7983; 18. *Ozarkodina eosteinhornensis* s.l., Sc element, DGO7984; 19. *Wurmiella excavata* (Branson & Mehl), Sb element, DGO7985; 20. *Wurmiella excavata* (Branson & Mehl), Sc element, DGO7986. Scale bar: 0.1 mm.

## DISCUSSION AND CONCLUSIONS

The "Orthoceras limestones" and the "Scyphocrinites limestones" are distinct stratigraphic markers for correlation of Silurian – lower Devonian deposits in northern Gondwana. Detailed biostratigraphic studies have shown that they may vary strongly in thickness and depositional age. Our new conodont sampling confirms that the outcrops of the "Orthoceras limestones" in the Khabt-Lahjar section, Eastern AntiAtlas, are Ludfordian in age (*P. siluricus* Zone). In the Tindouf Basin, an orthocone-rich level provided conodonts referable to the late Pridoli (*O. elegans detortus* Zone). These cool-water limestone levels have been related to upwelling episodes along the south-western margin of the Rheic Ocean (Lubeseder, 2008). Despite the fact that the taxonomy of the ozarkodinids is not yet stabilized and many samplings are exploratory, the high-latitude Silurian conodont faunas recovered from NW Africa show apparently no characteristic endemism nor major differences with the conodont faunas from peri-Gondwanan Europe and Laurentia.

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## ADVANCES ON SILURIAN-DEVONIAN CONODONT BIOSTRATIGRAPHY IN THE CENTRAL PRECORDILLERA, ARGENTINA

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**Keywords:** Silurian, Devonian, conodonts, biostratigraphy, Precordillera

### INTRODUCTION

Hünicken (1975) provided the first mention of Silurian conodonts in the Precordillera. Then, Hünicken & Sarmiento (1988) recognised the *Polygnathoides siluricus* Zone and the basal part of the *Pedavis latialata* Zone from the Los Espejos Formation at Sierra de Talacasto, defining the middle and upper Ludlow. Lehnert *et al.* (1999) described a Llandovery conodont association from the La Chilca Formation at Cerro del Fuerte, this association represents the *Distomodus kentuckyensis* Zone. Later, Albanesi *et al.* (2006) recorded conodonts indicative of the *Kockelella v. variabilis* Zone at Sierra de Talacasto. Heredia *et al.* (2007) defined the conodont biostratigraphy of the Los Espejos Formation at Cerro del Fuerte locality. In addition, Mestre (2009) documented Pridoli conodont assemblages from the Tambolar (Facies Pachaco) Formation. Subsequently, Heredia *et al.* (2010) proposed the first biostratigraphical chart of Silurian Precordilleran conodonts.

Gómez (2015) and Garcías (2016) carried out detailed biostratigraphical studies on Silurian conodonts from the Los Espejos Formation at Ancha and Poblete creeks, Talacasto region. These studies are used as a baseline for proposing a new conodont biostratigraphical chart for the Silurian-Lower Devonian of the Precordillera, adding former information from several sections already published.

### GEOLOGICAL CONTEXT

Los Espejos Formation crops out in the Central Precordillera; it is composed of marine siliciclastic strata, primarily green to brown sandstone and green siltstone, which vary in thickness to northwards from 25 to 510 m (Astini & Piovano 1992). Los Espejos Formation was deposited on middle to shallow platform setting including intercalations of storm deposits. Sinsedimentary deformation (convolute bedding) is frequent, mainly in the uppermost part of the unit (Astini & Maretto 1996). Brachiopods, trilobites, graptolites, tentaculitids, crinoids, acritarchs, edrioasteroids, conodonts, corals, eurypterids, nautiloids, gastropods and trace fossils are common fossils. Los Espejos Formation paraconformably overlies the La Chilca Formation and, in turn, is paraconformably overlain by the Lower Devonian shale of the Talacasto Formation.

## MATERIAL AND METHODS

Conodont samples were collected from coquinoids beds of the Los Espejos Formation at several sections in the Central Precordillera. About 3 kg of each sample was processed following the laboratory procedures described by Stone (1987). The insoluble fraction of each sample was picked for conodonts resulting in recovery of nearly 5,000 identifiable conodont elements. The conodonts are housed in the collection of the INGEO at the Universidad Nacional de San Juan, under the code INGEO-MP.

System	Serie	Stage	Walliser (1964)	Jeppsson <i>et al.</i> (2006)	Corradini <i>et al.</i> (2015) Corradini and Corriga (2012)	This study	
Devonian	Lower	Lochkovian			<i>pandora</i> β		
					<i>trigonicus</i>		
					<i>eleanorae</i>		
					<i>transitans</i>		
					<i>carlsi</i>		
					<i>postwoschmidti</i> <i>hesperius</i>	<i>hesperius</i>	
Silurian	Pridoli		<i>Oz. steinhorn.</i> <i>eosteinhorn.</i>		Upper <i>O. e. det.</i>	Upper <i>O. e. det.</i>	
					Lower <i>O. e. detortus</i>	Lower <i>O. e. detortus</i>	
					<i>Oz. eosteinhorn.</i> IZ	<i>Oz. eosteinhorn.</i>	
	Ludlow	Ludfordian	<i>S. crispus</i>	<i>Oz. crispata</i>	<i>Oz. crispata</i>		
			<i>I. latialatus</i>	<i>Oz. snajdri</i> "Icriodontid"	<i>Pe. latialata</i> - <i>Oz. snajdri</i> IZ		
			<i>P. siluricus</i>	<i>P. siluricus</i>	<i>P. siluricus</i>		<i>P. siluricus</i>
			<i>A. ploeckensis</i>	<i>A. ploeckensis</i> <i>K. v. variabilis</i> <i>Oz. exc. hamata</i> <i>Oz. excavata</i> n.sp.S	<i>A. ploeckensis</i> <i>K. variabilis</i> IZ		<i>K. v. variabilis</i>
		<i>Oz. crassa</i>	<i>K. crassa</i>	<i>K. crassa</i>			

Fig. 1. Silurian-Lower Devonian conodont biostratigraphical chart for the Precordillera and comparison with selected previous schemes.

## CONODONT BIOSTRATIGRAPHY

The conodont record allows the recognition of six biozones from the lower Ludlow (Gorstian) to the lower Lochkovian. The comparison of previous and newly obtained data enabled recognition of the following conodont zones (Fig. 1):

***K. v. variabilis* Interval Zone:** Apart from the *Kockelella variabilis variabilis* (Walliser), the following associated conodonts were identified: *Panderodus unicosatus* (Branson and Mehl), *Pseudoneotodus beckmanni* (Bischoff and Sannemann) and *Wurmiella excavata* (Branson and Mehl).

The zone is used herein in the sense of Cramer et al. (2011) as an interval zone above the last occurrence of *K. crassa* and below the entry of *Ancoradella ploeckensis*. Besides, this zone can only be indirectly documented by the presence of *K. v. variabilis* and absence of the index of the Zones above and below. The *K. v. variabilis* Interval Zone was documented in Poblete and Ancha creek sections.

***P. siluricus* Zone:** The conodont assemblage consists of *Coryssognathus dubius* (Rhodes), *Dapsilodus obliquicostatus* (Branson and Mehl), *K. o. absidata* (Barrick and Klapper), *K. maenniki* (Serpagli and Corradini), *K. v. ichnusae* (Serpagli and Corradini), *K. v. variabilis*, *Oulodus siluricus* (Branson and Mehl), *P. unicosatus*, *Ps. beckmanni*, *Ps. bicornis bicornis* (Drygant), *Ps. bicornis contiguus* (Corradini) and *W. excavata*. The index conodont is absent but the co-occurrence of *K. maenniki*, *K. v. ichnusae* and *K. v. variabilis*, indicates the basal part of *P. siluricus* Zone (Corradini et al., 2015) in the middle part of the Los Espejos Formation at Poblete section.

***Oz. eosteinhornensis* s.l. Interval Zone:** This zone is registered in the middle to upper part of the Los Espejos and Tambolar (Facies Pachaco) formations at Ancha creek and Pachaco sections. The conodont assemblages is composed by: *Belodella* sp., *C. dubius*, *D. obliquicostatus*, *O. e. elegans* (Walliser), *O. siluricus*, *Oz. eosteinhornensis* s.l. (Walliser), *P. unicosatus*, *Ps. beckmanni*, *Ps. b. bicornis*, *Ps. b. contiguus* and *W. excavata*.

**Lower *O. e. detortus* Zone:** The conodont fauna from this zone is: *C. dubius*, *D. obliquicostatus*, *O. e. elegans*, *O. elegans detortus* (Walliser), *Oulodus* sp., *Oz. eosteinhornensis* s.l., *Oz. eosteinhornensis* s.s. (Walliser), *Ozarkodina* sp., *P. unicosatus*, *Ps. beckmanni*, *Ps. bicornis bicornis*, *Ps. bicornis contiguus*, *W. excavata* and *Zieglerodina* sp. The occurrence of *Oz. eosteinhornensis* s.s. pointing out a well-defined horizon (Corradini and Corrigan, 2012). The Lower *O. e. detortus* Zone is recognized in the upper part of the Los Espejos Formation at Ancha and Poblete creek sections.

**Upper *O. e. detortus* Zone:** The conodont assemblage is composed by: *Ps. beckmanni*, *Ps. b. contiguus*, *Oulodus* sp., *Ozarkodina* sp., *Wurmiella* sp. and *Zieglerodina* sp. This zone is registered in the last meters of the Los Espejos Formation at Ancha creek section from coquinoid levels above the *Oz. eosteinhornensis* s.s. horizon. The absence of the latter key conodont and of *D. obliquicostatus* in the conodont assemblage allow us to recognize the Upper *O. e. detortus* Zone according to Corradini and Corrigan (2012).

***I. hesperius* Zone:** This zone is recorded in the upper part of the Los Espejos Formation at Poblete creek and the conodont assemblage is composed by: *Icriodus* cf. *hesperius* (Klapper and Murphy), *Oulodus* sp., *Ozarkodina* sp., *P. unicosatus*, *Ps. beckmanni*, *W. excavata* and *Zieglerodina* sp. The presence of *I. cf. hesperius* allow us recognize the basal Devonian for the first time in the Precordillera.

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## LATE SILURIAN AND EARLY DEVONIAN BIOEVENTS AND CONODONT BIOSTRATIGRAPHY IN THE PRAGUE SYNFORM

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**Keywords:** Conodont biostratigraphy, Silurian, Devonian, bioevents, Prague Synform

### INTRODUCTION

During the last years, chemostratigraphic and detailed biostratigraphic studies have demonstrated prominent global changes in the chemistry of Silurian and Devonian oceans and in marine faunas. However, reconstructions of the paleoclimatic and ecosystem settings of these events are not always easy due to the insufficient state of correlation at some stratigraphic levels.

Together with graptolites, conodonts are fundamental tools in Palaeozoic biostratigraphy. There, however, still exist significant problems concerning the stratigraphic distribution of the two fossil groups, and especially conodonts, and their global correlation. The problems were mostly caused by natural constraints (e.g., dearth of biostratigraphic information, environmental aspects), but also, in part by diverse scientific approaches to taxonomy and nomenclature. The use of ill-defined biostratigraphic units has seriously distorted the global correlation of various intervals of the Lower Paleozoic and particularly in the late Silurian – Early Devonian time. The global correlation of the Silurian is, at the same time, based principally on conodonts (carbonate-dominated sequences) and graptolites (shale-dominated facies). In the Devonian, where carbonate facies are dominating, the conodonts are the leading fossil group in biostratigraphy.

The main aim of the paper is to summarize the present state of conodont biostratigraphy in the late Silurian – early Devonian of the Prague Synform and to discuss the global context of the data. Another aim is bracketing of the major bioevents recognized in their respective time intervals.

### THE SILURIAN AND DEVONIAN OF THE PRAGUE SYNFORM – A BRIEF OVERVIEW

The Prague Synform is a part of the Teplá-Barrandian tectonic unit (Bohemium terrane) in the central part of the Bohemian Massif. The Prague Synform is an asymmetrical, elliptical structural depression and now represents an erosional relic of unmetamorphosed Lower Palaeozoic volcanic-sedimentary successions in the sense of Melichar (2004) and Knížek et al. (2010). Accordingly, the term „Synform“, is used herein rather than the frequently used term „Basin“, in order to stress the tectonic evolution of the unit.

The complete, non-metamorphosed Silurian and Devonian succession with richly diversified benthic and pelagic faunas is confined to the central part of the present Prague Synform. During the Silurian, gradual synsedimentary deformation of the basin was accompanied by strong submarine volcanism that culminated in the late Wenlock and early Ludlow. Thick accumulations of volcanoclastics gave rise to submarine highs (or

even an emerged island) that are surrounded by shallow water bioclastic limestones. Towards the top of the Silurian, black graptolitic shales prevailing in the Lower Silurian, are gradually replaced by carbonates. The carbonate sedimentation then continues from the Late Silurian to the Early Devonian with no interruption, except for a local gap at the top of the former volcanic island near Svätý Jan. Absolute prevalence of biode-trital types is a typical feature of the Silurian limestones in the Prague Basin. The Silurian deposits as a whole, originated in a shallow, warm-water environment, in about the subtropical climatic zone. The maximum thickness of the Silurian strata in the Prague Synform is 450 m.

The Devonian succession of the Prague Synform is characterized by two major lithofacies: shallow-water biode-trital, mostly crinoidal limestones that also include the reefal skeletal accumulation of Pragian age near Koněprusy, and a more pelagic facies that are represented mostly by calcisiltites. In Devonian, there are several prominent fluctuations in sea level, some of them can be traced globally, e.g., the Basal Pragian and Kačák Events of Chlupáč & Kukul (1986).

Devonian sedimentation culminated in siliciclastic flysch-type rocks (Srbsko Formation) of Givetian age that reflect the incoming Variscan Orogeny, which uplifted, folded and faulted the marine basin. The average thickness of the Devonian strata is 500 m in the Prague Synform. The highly diverse fauna with warm-water elements points to a well-oxygenated sea-water in the tropical climatic zone.

## ADVANCES IN CONODONT BIOSTRATIGRAPHY AND CORRELATION OF BIOEVENTS

More than 20 sections around the Prague Synform have been studied for conodonts in past years. Both the newly obtained and revised conodont data were integrated into the correlations scales for specific time intervals. Many of the established conodont zones can be recognized globally and enable more precise correlation of the major events. Among the most important results the following can be listed:

1. The regional zonation of the Wenlock/Ludlow boundary was established for the Prague Synform using refined data from updated conodont records (Slavík 2014). The following conodont zones have been recognized in the Prague Synform: the *Ozarkodina sagitta sagitta* Zone, the *Ozarkodina bohémica* Interval Zone, the *Kockelella crassa* Zone, the *Kockelella variabilis variabilis* Interval Zone and the *Ancoradella ploeckensis* Zone. The Bohemian conodont zonation was correlated with the recently proposed standardized zonation. The established conodont zones are tentatively correlated with global graptolite zonation and matched with generalized eustatic and carbon isotope curves.

2. Stratigraphic correlation of the Ludfordian Stage (Ludlow) in the Prague Synform was summarized using refined biostratigraphic data from updated conodont and graptolite faunal records (Slavík et al. 2014). The seven graptolite and seven conodont biozones and faunal intervals were correlated. The biozonations were integrated with generalized eustatic and carbon isotope curves. The proposed correlation chart is a basis for further high-resolution correlation of that region.

3. The stratigraphic level of a major biotic crisis (mass extinction - i.e. Lau/Kozłowski Event) in marine environment was precisely defined within the Ludfordian Stage (Manda et al. 2012, Slavík & Carls 2012). The major biotic crisis in the late Silurian was also linked to geochemical composition of the Ludfordian Ocean.

4. The regional conodont biozonation of the Přídolí in its stratotype area includes five conodont biozones. The Přídolí time is dominated by spathognathodontid conodonts which exhibit mostly rather conservative morphologies. These are the major constrain for taxonomical progress and resulting biozonal refinement. The provisional conodont biozonation for Přídolí in the Prague Synform is based on several morphologically distinct forms, which are short-lived and thus can precisely characterize very short time spans: *Zieglerodina*

*zellmeri*, *Zieglerodina ivochlupaci*, *Delotaxis detorta*, "*Ozarkodina*" *eosteinhornensis* s.s. and *Zieglerodina klonkensis*. The wide regional use of the proposed scale has still to be tested both within and outside of peri-Gondwana.

5. In the Lower Devonian, the most important progress has been attained in the Lochkovian where eleven regional zones have been recognized (Slavík et al. 2012). Most of them are global in the sense of Valenzuela-Ríos et al. (2015). The onset of icriodontids, shallowing and condensation around the Lochkovian/Pragian boundary reflect the Basal Pragian Event. The conodont crisis in the Pragian Stage negatively affected the development of global conodont biozonation of the Pragian Stage (Slavík 2004). In the Prague Synform, however, both the alternative correlation based on icriodontids (Slavík et al. 2007) and, with reservations, also the correlation based on eognathodontid and polygnathid lineages can be applied. Early Emsian conodont biostratigraphy has remained stable for more than four decades.

## CONCLUSIONS

In recent years, conodont biostratigraphy of the late Silurian (Ludlow and Přídolí) and early Devonian (Lochkovian, Pragian and Emsian) of the Prague Synform has been enhanced. Global correlation of the strata is supported by the integration of new biostratigraphic, sedimentological and petrophysical data; this has allowed a refined regional subdivision of the Upper Silurian Series and Lower Devonian Stages in the Prague Synform. The late Silurian conodont biozonal scale has been refined and a juxtaposition of conodont and graptolite biozones was suggested. The integration of conodont and graptolite biostratigraphy has also substantially improved correlation of the global extinction bioevents of the Ludlow Series. The development of the conodont biozonation of the Early Devonian in the Prague Synform is summarized and discussed.

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## CONODONTS ACROSS THE SILURIAN/DEVONIAN BOUNDARY IN THE CARNIC ALPS (ITALY-AUSTRIA)

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In the Carnic Alps one of the best exposed and most complete Palaeozoic successions in the world, ranging from the Middle Ordovician to the Upper Permian, is exposed. Uppermost Silurian and lowermost Devonian rocks are relatively widely exposed and mainly represented by limestones or black shales, belonging to five different formations: Seekopf Fm., Alticola Fm., Rauchkofel Fm., Nöbling Fm. and Bischofalm Fm.

Several sections have been measured in these units, and conodonts across the Silurian/Devonian boundary are documented, among others, in the Cellon section (Walliser, 1964; Corradini et al., 2015; Corrigan et al., 2016), Rauchkofel Boden (Schönlaub, 1980; Schönlaub et al., 2017), Oberbuchach II (Schönlaub, 1985), Seewarte (Suttner, 2007), Monte Cocco II (Corrigan & Corradini, 2009), Rifugio Lambertenghi Fontana III (Corradini & Corrigan, 2010) and Rio Malinfier West (Corrigan, 2011). The restudy of the original collections from these sections, often integrated with new samples, and data from new localities (Freikofel South, ...), allows to define a series of first or last occurrences of taxa in the latest Silurian and basal Devonian beds, which can be used to locate the Silurian/Devonian boundary:

- Last Occurrence of *Ozarkodina confluens* (Branson and Mehl), just followed by
- First Occurrence of *Zieglerodina remscheidensis* (Ziegler) and *Z. eladioi* (Valenzuela-Ríos), and by
- Last Occurrence of *Zieglerodina zellmeri* Carls et al.
- First Occurrence of *Icriodus hesperius* Klapper & Murphy and *Icriodus woschmidti* Walliser. In some sections the two taxa enters together (e.g., Monte Cocco II, Corrigan & Corradini, 2009; Oberbuchach II, Schönlaub, 1985), whereas elsewhere *Icr. hesperius* enters a few centimetres below *Icr. woschmidti* (e.g., 10 cm in the Cellon Section, Corradini et al. 2015, Corrigan et al. 2016).
- First Occurrence of *Zieglerodina* sp. A Corrigan et al., 2016.

The base of the Devonian is defined by the FAD of the graptolite *Monograptus uniformis* Přibyl, and the conodont taxon "with wide distribution that appears closest to the Lower Devonian boundary" is *Icr. hesperius* (Carls et al. 2007, p. 157-158). In case *Icr. hesperius* is not present in a section, all the events listed above may help to approximate the boundary.

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## CONODONTS OF FAMILY SPATHOGNATHODONTIDAE FROM THE SILURIAN/ DEVONIAN BOUNDARY, PRAGUE SYNFORM

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**Keywords:** conodont, Spathognathodontidae, Silurian/Devonian boundary, Prague Synform

### INTRODUCTION/BACKGROUND

The base of Devonian was defined by the entry of the graptolite *Monograptus uniformis* (see Chlupáč et Kukul 1977). As the occurrence of graptolites is largely linked to the shale-dominated facies, correlation of the Silurian/Devonian boundary in carbonate-dominated facies is based on other faunal groups. Among conodonts, the best marker of the base of Devonian is *Icriodus hesperius*, i.e. probably the oldest representative of the genus *Icriodus* (cf. Carls et al. 2007). This taxon is, however, relatively scarce worldwide, even in shallower facies. In contrast to icriodontids, the platform elements of the family Spathognathodontidae are relatively abundant component of conodont fauna around the Silurian/Devonian boundary. According to our preliminary results, spathognathodontids seem to be more tolerant to bathymetry and thus their correlation potential is considerably increased.

We have focused on two sections (Na Požárech and Praha-Radotín) in the Prague Synform – the classic area of the Silurian and Devonian strata (several GSSPs have been defined in the area). Both sections are developed in carbonate facies, but the Na Požárech section is much shallower than the Praha-Radotín section. The main objective of the study of conodont faunas is a search for regional time markers that occur in contrasting palaeoenvironments among spathognathodontids and to study microfacies in both sections.

### GEOLOGICAL CONTEXT

Prague Synform is located in the central part of the Czech Republic, south-west from Prague extending to Pilsen. It is an asymmetric elliptical structural depression, an erosional relic of unmetamorphosed Lower Palaeozoic volcanic-sedimentary successions in the sense of Melichar (2004). Fig. 1.

The upper Silurian (upper part of Ludlow and Přídolí) Požáry Formation is represented by the sequence of platy biomicritic and bioclastic limestones with intercalations of calcareous shales. Graptolites, brachiopods, trilobites and chitinozoans are abundant in the formation (see Kříž 1992).

Devonian carbonates lie concordantly on the underlying Silurian rocks. The so called "scyphocrinites horizon" is developed around the Silurian/Devonian boundary (i.e. up to few meters thick interval of mostly coarse bioclastic carbonates with lobolites and crinoid columnals). This horizon is, however, missing in deeper

water environments, e.g. in famous Klouk section (the GSSP of the Silurian/Devonian boundary), where is no prominent lithological change in lower Devonian.

The Lochkov Formation represents the lower Devonian and includes two different facies – the Radotín Limestones and the Kotýs Limestones. The Radotín Limestones are dark, micritic with calcareous shale intercalations. This facies is generally considered to be deeper water than the Kotýs Limestones, which are lighter grey, bioclastic, usually with high abundance of crinoids and other bioclasts (cf. summary by Chlupáč et al. 1998).

Each of the chosen localities represents one of the principal Lochkovian facies mentioned above. The contrasting depositional environment in both localities may serve as a test of difference in composition of conodont assemblages. The Lochkovian in the Na Požárech section is developed in the Kotýs Limestones, while the Praha-Radotín section is characterised by the Radotín Limestones.

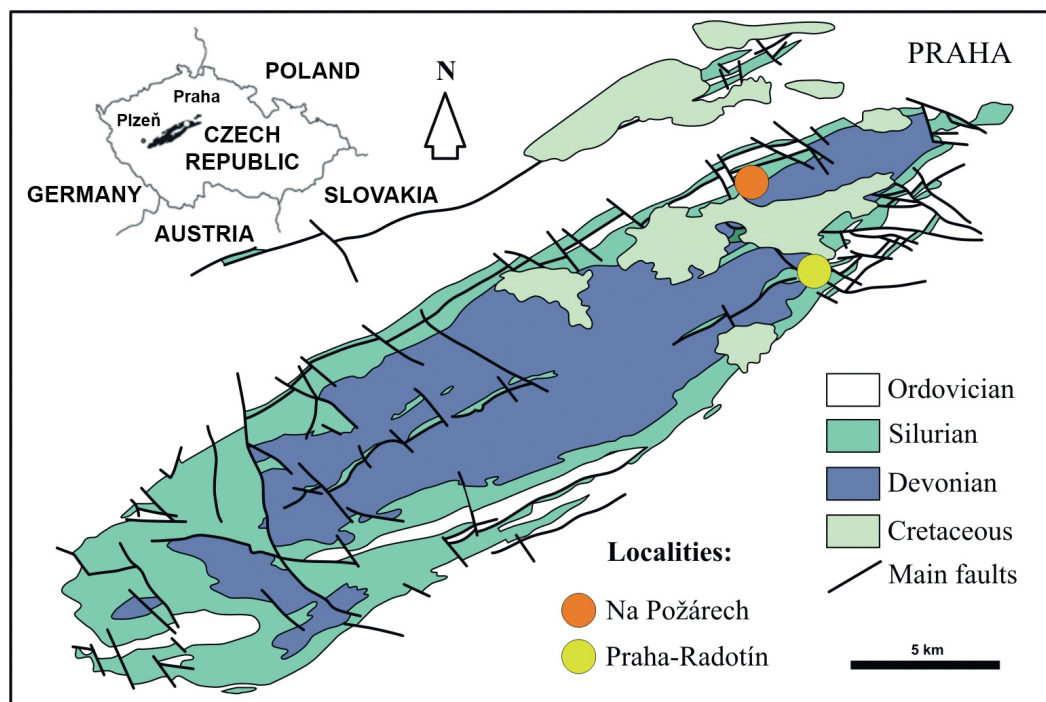


Fig. 1. Position of the Prague synform and the two localities – Na Požárech and Praha-Radotín (according to Ernst et al., 2013).

## MATERIAL AND METHODS

Samples for conodonts and thin sections were taken from both sections. Total of 9 conodont samples were taken from the locality Na Požárech and 13 from the locality Praha-Radotín. All samples have been processed in the acetic acid and then concentrated by heavy liquid separation. The conodont material obtained is relatively rich (cca 2000 elements). In total 23 thin sections have been taken for microfacies study and photographed.

## RESULTS

Samples from both sections contain diverse conodont faunas. Both in the Na Požárech and in the Radotín sections, the beginning of the Devonian can be precisely identified by the first occurrence of taxa of the genus *Icriodus*. In the critical samples with the first icriodontids, that mark the base of the Devonian, two new taxa of the Spathognathodontid family were identified. These taxa may have a great potential for the alternative identification of the Silurian/Devonian boundary, where other markers (graptolites and icriodontids) are missing. To prove that, further detailed study is, however, necessary.

The first study of conodonts at the Praha-Radotín section revealed that surprisingly, this locality seems to be the best for conodont studies of the critical Silurian/Devonian boundary interval. It is both because of conodont abundance and relatively high conodont diversity. The taxa: *W eosteinhornensis s.l.*, *Zieglerodina zellmeri*, *Ozarkodina typica*, *Ozarkodina optima*, *Wurmiella excavata* have been identified around the Silurian/Devonian boundary. The taxa belonging to *Icriodus* are also highly variable and several morphotypes can be distinguished. Above the Silurian/Devonian boundary, higher up in the Lochkovian, *Ancyrodelloides omus*, *Pedavis breviamus*, and representatives of *Lanea* are common.

Conodonts from the Na Požárech section are less diverse and the elements are mostly broken. The taxa *Zieglerodina sp.*, *Wurmiella sp.*, *Ozarkodina typica* and *Ozarkodina optima* occur around the boundary. In comparison to previous locality, in the section Na Požárech are icriodontids relatively rare (only about 25 element).

## DISCUSSION AND CONCLUSIONS

Both sections, Praha-Radotín and Na Požárech, provided relatively rich and diverse conodont faunas. Despite the fact that the locality Praha-Radotín was considered as the more deeper-water, 117 elements of *Icriodus* have been found, most probably belonging to different taxa. Surprisingly, the Praha-Radotín section is much more rich in conodonts than the Na Požárech section. Moreover, striking is, that the first graptolite *Monograptus uniformis* – a criterion for the Silurian/Devonian boundary GSSP definition and the first *Icriodus* sp. have been recorded from the same bed. This confirms that the first appearance of *Icriodus* sp. is probably the best marker of the Devonian base in the carbonate successions.

Usually, the size of the oldest icriodontids reported from elsewhere from the Silurian/Devonian boundary is small. The elements of *Icriodus* from samples from the Praha-Radotín section vary in size, containing both the small (juvenile) and large (adult) specimens.

In both sections, morphologically distinct taxa among spathognathodontids have been found. These might be promising for the identification of the Silurian/Devonian boundary regionally. Following studies at other localities/sections will test their regional applicability that could be a promising base for inter-regional correlation.

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## THE TAXONOMIC POSITION AND RANK OF BELODELLIDS

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**Keywords:** Belodellids, conodonts?, taxonomy, bilaterally symmetrical, Late Silurian

*Belodella* traditionally have been considered as conodonts, but at the same time it has been recognized that they are different in some fundamental ways from conodonts and that is why Sweet (1988) accorded them ordinal rank.

The presently known attributes of Belodellids that set them apart from conodonts are that they are very thin walled, the walls do not show peripheral layering, no basal filling has been observed, and organic matter is not retained in their elements because they don't change colour like conodonts when heated. Some very well preserved forms show closely spaced, transverse darker bands around the element and parallel to its base. We have observed this latter phenomenon in Late Silurian material from U topolů and Klouk, and from latest Ludlow and at the base of the Přidolí in the Požáry GSSP. These bands are present in several of the specimens figured from Klouk, especially the figures by Jeppsson (1989, pl. 1, figs. 5a, 13a, 13b, 14a, and, less obviously, in 18a), and also in Uyeno (1980, pl. 10, figs. 13, 15) from the Canadian Arctic. If these represent growth bands, a conclusion that is hard to escape, *Belodella*, is certainly not a member of the Conodonti and the presence of the bands supports placing belodellids in a separate taxonomic category as Sweet has done (1988, p. 45, Cavidonti).

Sweet (1988, p. 49) also pointed out in setting up the Order Belodellida that the various belodellid elements, "commonly have distinct anterior, posterior, and lateral keels or costae" and that the posterior edge may be bordered by fine, needle-like serration or denticulation. This statement fixes what is used here as the standard orientation for elements in the individual belodellid. The belodellids obviously are not conodonts and so orientation of their elements cannot be assumed to be the same as that in the simple conical elements of conodonts (e. g. *Panderodus*). We add that there is no evidence for what part of the organism these remains represent.

In summary then, the case for classifying the Belodellids as conodonts rests mainly on their phosphatic composition, the individual element has a mirror image pair, and that each animal had many elements in the same size range as conodonts.



## CONCLUSIONS

Belodellids are bilaterally symmetrical animals, that produced hard parts made of calcium phosphate but their function is unknown. Belodellids are not conodonts. If belodellids represent the central theme of the Cavidonti, Cavidonti also are not conodonts. If Conodonts are a phylum of animals, then so are belodellids.

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**PROGRESS ON MIDDLE DEVONIAN  
CONODONT INVESTIGATION FROM 60'S  
TO PRESENT: HIGH-RESOLUTION  
BIO-CHRONOSTRATIGRAPHY,  
REGIONAL CORRELATION, AND  
GLOBAL EVENT STRATIGRAPHY**





## LOCHKOVIAN (LOWER DEVONIAN) CONODONTS FROM THE CONCA DE TREMP-MONTSEC GEOPARK PROJECT; A UNIQUE CHARACTER OF GLOBAL RELEVANCE

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**Key words:** Conodonts, Lower Devonian, sustainability, Geopark Conca Tremp-Montsec

### BACKGROUND AND OBJECTIVES

Geoparks should play an important role in contributing to the sustainable development of territories by a multidisciplinary approach based on the exceptional geological content. Scientists, policy-makers and local entrepreneurs work together fomenting the economic growth and supporting the cultural and natural heritage through the continuous mutual cooperation and implementing programs that promote long-term scientific research in the territory. The subsequent dissemination of the geological values through the development of educational programs will diversify the cultural and touristic offering, encouraging local business to come together in benefit of local communities. It is obvious the impact of Geological heritage in developing local initiatives, that in turn will benefit local economy and will increase awareness of inhabitants regarding this heritage.

The Lower Devonian outcrops south of Gerri de la Sal represent an outstanding geological feature of the Conca de Tremp-Montsec Geopark Project. De Villalta & Rosell Sanuy (1969) described the stratigraphical section in the north flank of the Buscarró anticline spanning from the upper Silurian through the Middle Devonian and showed the international value of these rocks. Carls (1977) provided the first Lower Devonian conodont documentation of these beds and revealed the importance of this area in a palaeogeographic context. Valenzuela-Ríos (1990) presented the first detailed conodont succession from Gerri de la Sal sections, positioning the Silurian/Devonian boundary and recognizing seven biostratigraphic units. This work already showed the relevance of the Gerri de la Sal sections for global correlations and analysis of conodont evolution. Valenzuela-Ríos (1994a, b) further developed and documented this proposal. Valenzuela-Ríos & Murphy (1997) described a new genus present in the Gerri de la Sal sections, demonstrated a detailed middle Lochkovian correlation between the Spanish Pyrenees and Central Nevada and proposed a new global subdivision of the Lochkovian Stage. Valenzuela-Ríos & García-López (1998) compared sequences from Gerri and the Catalan Coastal Ranges. More recently Valenzuela-Ríos & Liao (2012) and Valenzuela-Ríos *et al.* (2015) considered the Gerri de la Sal sequences for demonstrating the indispensability of palaeontological data in correlating global events and in establishing a new Lochkovian global zonation.

The main objectives of this paper are: 1) to describe the stratigraphy and palaeontology of one selected Devonian outcrop (Gerri de la Sal) within the aspiring Geopark; 2) to present the singularity of this outcrop in the context of national Geoparks and 3) evaluate the relevance of the conodont succession in an international context.

## **GEOLOGICAL CONTEXT**

The Gerri de la Sal outcrops are developed in the Subfacies Compte of the Southern Facies area (Mey, 1967; Zwart, 1979) and represent the southernmost Palaeozoic strata of the Nogueras Zone. The stratigraphic interval studied herein consists of about 23 m of limestone alternating with marl and shale and corresponds almost completely to the Lochkovian (Fig. 1)



Fig. 1. Geological map of Conca Trep-Montsec Geopark Project with position of sections Ge 1.1 and Ge 1.2.

## MATERIAL AND METHODS

The stratigraphic sequence can be subdivided into two parts, a lower one of dominant shale and black colour and an upper one with clear colour limestone being the prevailing strata. Two sections, Ge 1.1 and Ge 1.2 were sampled bed by bed. All the samples were etched with formic acid (5-7%) and washed by decantation. Heavy liquids and magnetic separator concentrated large residues. Microfossils were handpicked with the help of a wet brush under the microscope.

## RESULTS

A large and outstanding conodont collection was obtained from these two sections. It contains both endemic (*Icriodus*, *Pelekysgnathus*) and more cosmopolitan conodonts (*Ancyrodelloides*, *Lanea*, *Flajsella*, *Masaraella*, *Pedavis*, *Wurmiella*, *Zieglerodina*, "*Ozarkodina*"). The conodont succession has been thoroughly described in the papers by Valenzuela-Ríos and co-authors referred above and are briefly summarized below.

The Silurian/Devonian boundary is close to Bed 1 in section Ge 1.1. There, *Icriodus woschmidti* has been recorded together with lobolites of *Scyphocrinites*. Up to Bed 11 the endemic conodonts prevail and records document two of the three evolutive early icriodids branches, the *transiens* and the *angustoides* branches. Bed 6 yielded the holotype and paratypes of a new taxon "*Ozarkodina eladioi*". The first *Ancyrodelloides*, *A. carlsi*, enters in bed 11 and it is followed by a continuous and rich conodont sequence spanning through the middle and upper Lochkovian. This sequence contains the evolutionary steeps of the genera *Ancyrodelloides*, *Lanea* and *Flajsella* that are used for defining, subdividing and correlating the middle Lochkovian and of *Masaraella* and *Pedavis* that are the key taxa for the definition, subdivision and correlation of upper Lochkovian. Besides, some scattered records of the more endemic *Pelekysgnathus* and *Icriodus* strength correlations between neritic and pelagic facies. Occasional records of *Kimognathus* and the new taxon "*Ozarkodina malladai*" increase the biodiversity of Gerri sections and augment tie points for fine correlation.

Section Ge 1.2 mostly mirrors the middle and upper Lochkovian sequence, but with slightly lower biodiversity. Lower Lochkovian is missing due to local tectonics.

## DISCUSSION AND CONCLUSIONS

The Lochkovian conodont sequence at Gerri de la Sal sections is one of the richest and more important worldwide and makes the Conca de Tremp-Montsec Geopark Project as one of the key regions for demonstrating the evolutionary steeps of several genera that are instrumental in establishing the finest Lochkovian subdivision and subsequent high-resolution correlation.

The holotypes of several taxa have been described from Ge 1.1 section ("*Ozarkodina eladioi*", "*Ozarkodina malladai*" and *Pelekysgnathus serratus* 20).

These two facts provide this aspiring Geopark with a singularity of global relevance that is neither present in the nearby UNESCO Global Geopark of Sobrarbe nor in any of the other UNESCO Global Geoparks.

Further, the combination of these sections with the section Compte-I (CP-I) just in the northern margin of the Conca de Tremp-Montsec Geopark Project and the Segre sections (Se 1-5), a few kilometre northeast of this aspiring Geopark, constitute one of the best Lochkovian data base for establishing the finest Lochkovian biostratigraphical subdivision that can be worldwide applied and, consequently, represents a relevant region for increasing our understanding on the geo-biological history of Earth. This added value of a natural resource

could be integrated in sustainable development programs to increase people awareness on their natural heritage and in seeking new ways of attracting scientist and tourist to the region, which in turn would foster local economy and help dissemination of this unique and precious geological signature.

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## PRELIMINARY MORPHOLOGICAL ANALYSIS OF *Polygnathus pireneae* (LOWER DEVONIAN) FROM SOUTH CHINA

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**Keywords:** Devonian, Shizhou Member, Liujing section, Dacun section, Guangxi

### INTRODUCTION

*Polygnathus pireneae* is a species of great stratigraphical and palaeontological significance. As one of the earliest polygnathids, it rapidly gives rise to many species around the Pragian-Emsian Boundary and also is the nominal species of the uppermost Pragian zonation (Yolkin et al., 1994). Since first described and named in the Spanish Central Pyrenees by Boersma (1973), *Pol. pireneae* has been widely reported around the world. According to Boersma (1973, pl. 2, figs 1–12), the extraordinarily small type specimens are characterized by a large and deep basal cavity, which covers the whole aboral side and whose flanks just reach the platform margins. In contrast, both the kitabiformis and sokoloviformis morphotypes of *Pol. pireneae* recognized by Izokh et al. (2011) possess an extraordinarily wide and large basal cavity with flanks obviously protruding beyond the platform margins. However, due to the scarcity of *Pol. pireneae* specimens previously reported around the world, whether the differentiation of the outline of basal cavity represents ontogenetic or in-traspecific variation is still unknown.

In the present study, we report the result of recent investigation based on relatively extensive sampling of two sections from Guangxi in South China, which yielded abundant immature and mature *Pol. pireneae* specimens from the lower part of the Shizhou Member of the Yukiang Formation. The new material enables to make a discrete morphological analysis of this species and contributes to expand our understanding of the early evolution of polygnathids.

### GEOLOGICAL CONTEXT AND MATERIAL

The Dacun section (Fig. 1) is situated approximately 300 m northwest of the Dacun Village and 1.8 km east of the Liujing section (for more details about the stratigraphical information of the Liujing section, see Lu et al., 2016). The lower part of the Shizhou Member, which mainly consists of thin to medium-bedded limestone intercalated with thin mudstone beds, is well-exposed at this section. The total thickness of the strata is 4.32 m, and seventeen conodont samples were collected. Conodonts were obtained from twenty-four samples (seven additional samples come from the Liujing section) weighting between 2.175–8.070 kg each. Samples were fragmented and then dissolved in diluted acetic acid (5–10%). All residues were then washed,

air-dried and finally hand-picked using a stereo microscope. Abundant conodonts including *Pol. pireneae*, *Pol. sokolovi* and *Pandorinellina exigua philipi* were obtained and temporarily assigned to the uppermost part of the *pireneae* Zone.



Fig. 1. The location of the Dacun section in Guangxi, South China.

## RESULTS

Mainly based on the different outlines of the basal cavity, *Pol. pireneae* is herein informally subdivided into the wider-cavity type, whose cavity has flanks clearly extending beyond the platform margins, and the narrower-cavity type, whose cavity has flanks just reaching the platform margins. Sixty-one relatively intact Pa elements of *Pol. pireneae* that include the Liujing and Dacun materials as well as specimens previously reported by other researchers (Wang, 1989, pl. 29, fig. 15; Izokh et al., 2011, pl. 1, figs 1–5; Martínez-Pérez and Valenzuela-Ríos, 2014, figs 9b–d) around the world are measured for their length and width (Figure 2A).

It is suggested that the length of platform (PL) systematically augments with the increasing of total length of the unit (TL) for both narrower-cavity and wider-cavity types, and the best-fit line of PL for the narrower-cavity type almost overlaps that for the wider-cavity type (Figure 2B), which strongly indicates that the platform in both types of *Pol. pireneae* grows simultaneously during all ontogenetic stages. Thus, for specimens without free blade the length of the platform (PL) can be considered as a good and reliable index to reflect the ontogenetic development of the specimens. The ratio of width of basal cavity to width of platform (CW/PW) ranges from 0.7598 to 1.1709 (averaging out to about 1) for the narrower-cavity type and from 1.1506 to 1.8409 (averaging out to about 1.3) for the wider-cavity type (Figure 2C). This ratio distinctly distinguishes the narrower-cavity type from the wider-cavity type at all ontogenetic stages, meaning that the former possess a basal cavity whose width usually equals to, or sometimes even smaller than, the width of the platform, whereas the latter has an extraordinarily capacious basal cavity whose width apparently surpasses the width of the platform. For specimens with the same width of the platform, wider-cavity type always has a basal cavity that is more laterally extended than that in the narrower-cavity one (Figure 2D).

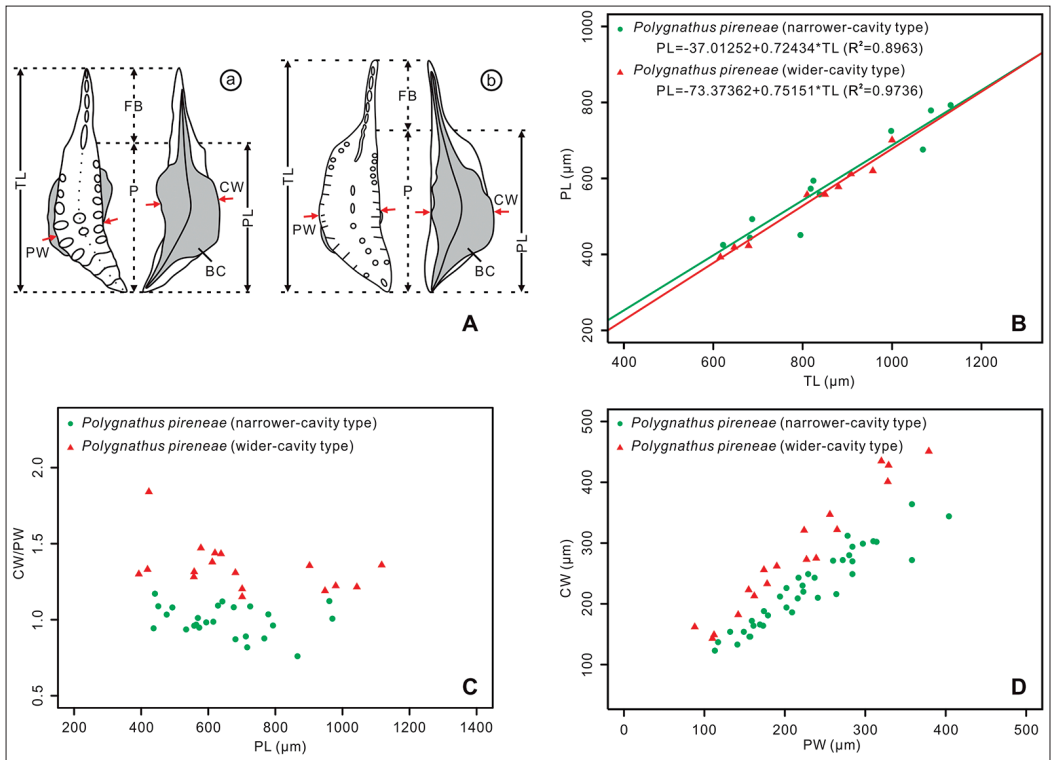


Fig. 2. **A**, Pa element of *Polygnathus pireneae* Boersma, 1973 showing the characters measured and their nomenclatures: a, the wider-cavity type of *Pol. pireneae*; b, the narrower-cavity type of *Pol. pireneae*. BC, basal cavity; CW, width of basal cavity; FB, free blade; P, platform; PL, length of platform; PW, width of platform; TL, total length of the unit. **B**, Scatter diagram showing the relationship TL and PL in wider-cavity and narrower-cavity types of *Pol. pireneae*. **C**, Scatter diagram showing the relationship between PL and CW/PW in wider-cavity and narrower-cavity types of *Pol. pireneae*. **D**, Scatter diagram showing the relationship between of PW and CW in wider-cavity and narrower-cavity types of *Pol. pireneae*.

## DISCUSSION AND CONCLUSIONS

Statistical analysis of *Pol. pireneae* reveals that differentiation of the basal cavity outline occurs at all ontogenetic stages of this species and consequently belongs to stable intraspecific variation. The basal cavity in the wider-cavity type of *Pol. pireneae* has its flanks protruding outside of the platform margins, whereas the flanks of the basal cavity in the narrower-cavity type only reach or even not reach the platform margins.

On the basis of the outlines of the basal cavity and outer platform margin, *Pol. pireneae* is further divided into  $\alpha$ ,  $\beta$  and  $\gamma$  morphotypes herein. The  $\alpha$  morphotype (Lu et al., 2016, figs 7C–F), corresponding to the kitabiformis morphotype of Izokh et al. (2011), has a rounded outer platform margin at the junction point of anterior and posterior platforms, and a capacious basal cavity with its flanks protruding beyond the platform margins. The  $\beta$  morphotype (Lu et al., 2016, figs 60–R, 7A–B) refers to the sokoloviformis morphotype of

Izokh et al. (2011). The  $\alpha$  and  $\beta$  morphotypes are assignable to the wider-cavity type but  $\beta$  is distinctly differentiable by its angular outer platform in the posterior part. *Pol. pirenae*  $\gamma$  morphotype (Lu et al., 2016, figs 5E–N, 7G–J), which belongs to the narrower-cavity type, also bears a rounded and smooth outer platform margin but has a basal cavity whose width equals to or is smaller than the width of the platform.

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## THE ROLE OF CONODONTS IN BUILDING STANDARDS OF REFERENCE FOR EXPRESSING THE HISTORY OF EARTH: THE GIVETIAN (MIDDLE DEVONIAN) EXAMPLE

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**Keywords:** Conodonts, Givetian subdivision, chronostratigraphic scale

### INTRODUCTION

The primordial objective of the International Commission on Stratigraphy (ICS) is to define global units with such a high precision that they can precisely be arranged to establish the International Chronostratigraphic Chart, which serves as a basis for the International Geological Time Scale.

Murphy & Salvador (1998) revise the principles and procedures of naming and classifying stratigraphic units with the benefit of improving accuracy in international communication. This, in turn will help scientist to communicate their results in a more effective way and, subsequently, to better integrate worldwide data into a global standard scale.

Conodonts represent one of the fossil groups that, has extensively contributed to achieve ICS objectives in the Palaeozoic Erathem, especially in the Devonian System, where all, but one, Stages are defined by the entry of a marker conodont. Further subdivision of Devonian Stages is also based on conodonts, and the accuracy reached by some conodont zones represents the highest possible resolution (less than 200,000 years) for global correlation and, consequently, are one of the best tools for setting a detailed standard scale for correlating and arranging the successive local and global Geo-bioevents of Earth. This, in turn, will facilitate a better understanding of the Earth's history.

Herein we analyse the historical development of the Givetian bio and chronostratigraphical scale based on conodonts, which is used globally and provides the best reference for arranging, correlating and testing synchronicity of the many events, sea-level and climatic changes that were common in the Givetian. Subsequently, we test the applicability of this scale in the Givetian sequences of marine carbonate sequences in the Spanish Central Pyrenees.

### GEOLOGICAL CONTEXT

This study is restricted to the Givetian marine strata that are exposed either in pelagic or in shallow-water environments in many localities around the world. Special attention is paid to the Pyrenean carbonate sequences in two different facies settings (Liao et al., 2008; Liao and Valenzuela-Ríos, 2008, 2013; Liao 2014; Gouwy et al., 2013, 2016).

## RESULTS

The base of the Givetian is defined in the GSSP at the base of Bed 123, section Jebel Merch Irdane, Tafilalt, Morocco coinciding with the entry of *Polygnathus hemiansatus* (Walliser et al., 1995; Walliser and Bultynck, 2011). The Givetian upper boundary coincides with the base of the Frasnian Stage, which has a controversial history.

Most of the Titular Members of the International Subcommittee on Devonian Stratigraphy voted in favour of subdividing the Givetian into three substages, Lower, Middle and Upper, supporting the report presented by Bultynck (2006).

The achievement of this proposal and subsequent affirmative vote would have been impossible without the previous work of many colleagues around the world (see a historical summary in Liao & Valenzuela-Ríos, 2016). These works lay out a fine stratigraphical scheme of ten conodont zones of global application for pelagic sequences. Klapper & Ziegler (1979) set the basis for the current Givetian conodont subdivision, especially for the lower and middle parts. Subsequently, Klapper & Johnson (1980, 1990) arranged the scheme for the upper part. These ten zones are from younger to older: *hemiansatus*, *timorensis*, *rhenanus/varcus*, *ansatus*, *latifossatus/semialternans*, lower *hermanni*, upper *hermanni*, lower *disparilis*, upper *disparilis* and *norrisi*.

The base of the *hemiansatus* Zone coincides with the bases of the Lower Givetian substage and, accordingly, with the base of the Givetian. It is defined by the first occurrence of the index *Polygnathus hemiansatus*. The lower boundary of the *timorensis* Zone coincides with the first occurrence of *P. timorensis*. These two zones, *hemiansatus* and *timorensis* further subdivide the Lower Givetian.

The lower boundary of the Middle Givetian coincides with the basis of the *rhenanus/varcus* Zone, which is defined with entry of either *P. rhenanus* or *P. varcus*. The first occurrence of *P. ansatus* marks the basis of the next Zone, the *ansatus* Zone. The last Zone of the Middle Givetian is the *latifossatus/semialternans*, which lower limit is defined by the entry of either *P. latifossatus* or "*Ozarkodina*" *semialternans*.

The lower boundary of the Upper Givetian coincides with the lower boundary of the lower *hermanni* Zone, which is defined with the lowest entry of *Schmidtognathus hermanni*. Above follows the upper *hermanni* Zone, which is defined by the first entry of *P. cristatus*. The lower limit of the lower *disparilis* Zone coincides with the entry of *Klapperina disparilis*. The entry of *P. dengleri* defines the lower boundary of the upper *dengleri* Zone. The base of the last Givetian *norrisi* Zone is defined by the appearance of *Skeletognathus norrisi*.

Bultynck (1987) presented an alternative zonation for neritic environments based on the sequential entries of icriodids. The base of the Givetian can be approximate in neritic facies with the entry of *Icriodus obliquimarginatus*. The entry of *I. brevis* falls within the *timorensis* Zone. The entry of *I. difficilis* correlates with upper parts of the *rhenanus/varcus* and the *difficilis* Zone last up to the top of the Middle Givetian. Subsequently Narkiewicz & Bultynck (2010) analysed the *Icriodus subterminus* Zone, which was subdivided into three parts (Lower, Middle and Upper) and correlate it with an interval between the topmost part of the *hermanni* Zone and the end of the Givetian.

## DISCUSSION AND CONCLUSIONS

Conodonts permit a detailed ten-fold global subdivision for the Givetian Stage, which are the basis for further subdividing this stage into three substages, Lower, Middle and Upper Givetian.

This zonation is based on pelagic sequences. An alternative zonation for neritic sequences can also be applied.

This example shows the relevance of conodonts as a tool for subdividing time in fine portions, which can accurately be globally correlated. Furthermore, the clear definition of the lower limits of successive stratigraphic units and the terminology used to communicate these concepts is internationally accepted. All this, result in an effective scientific communication and therefore contribute to main objectives of the International Commission on Stratigraphy.

This time-subdivision achieved in the Givetian represents the basis for further multidisciplinary studies aiming at a better understanding of the History of Earth for this Period.

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## THE PAST, PRESENT AND FUTURE OF THE UPPER EIFELIAN CONODONT ZONATION

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**Keywords:** Conodonts, Eifelian, biostratigraphy, biozone, Kačák Event

### INTRODUCTION

The precise conodont biostratigraphic subdivision of the uppermost Eifelian is important for tracing the Eifelian-Givetian stages boundary worldwide but also because it is crucial for determining and correlation of the levels attributable to the global events (Kačák or *otomari* Event, Late Eifelian Events, eustatic If transgression). During **the past** four decades the concept of the uppermost Eifelian-lowermost Givetian zonation has changed considerably (Fig. 1).

	Becker et al.(2012)	Weddige (1977)	Bultynck (1987)	Clausen et al. (1993) previous	Clausen et al. (1993) actual	Belka et al. (1997)	Walliser (2000)	Becker et al.(2012)
GIVETIAN	386	<i>varcus</i>	<i>rhenanus/</i> <i>varcus</i>	<i>varcus</i> Lower	<i>varcus</i> Lower			<i>varcus</i>
	387		<i>timorensis</i>					
EIFELIAN	387.7 ±0.6	<i>ensensis</i>	<i>hemiansatus</i>	Upper <i>ensensis</i>	<i>hemiansatus</i>	<i>hemiansatus</i>	<i>hemiansatus</i>	<i>hemiansatus</i>
			<i>eiflius</i>	Lower		<i>ensensis</i>	former Lower <i>ensensis</i>	<i>ensensis</i>
	389 Ma	<i>kockelianus</i>		<i>kockelianus</i>	<i>kockelianus</i>	<i>eiflius</i>	<i>kockelianus</i>	<i>kockelianus</i>

Fig. 1. Variants of the conodont zonation across the Eifelian-Givetian boundary.

The *ensensis* Zone has been introduced by Weddige (1977) as the uppermost Eifelian zone, with the lower boundary defined by the first appearance of *Polygnathus xylus ensensis* and upper - by the first appearance datum (FAD) of the Givetian species *P. timorensis*. Bultynck (1987) replaced the upper part of such defined unit with the *hemiansatus* Zone, attributed already to the Givetian, while the uppermost Eifelian has been

defined as the *eiflius* Zone. The uncertainties related to a correct identification of the taxa of the *P. ensensis* - *P. xylus* - *P. pseudofoliatus* group (Weddige, 1988) probably led to the abandonment of the *ensensis* Zone in the standard conodont zonation during the 1990s (e.g., Clausen et al., 1993). Nevertheless, its lower part, defined as the *ensensis* Zone in a narrower sense, has been applied by Belka et al. (1997) and this approach was also taken in establishment of the Eifelian-Givetian boundary (Walliser, 2000). In the respective GSSP in the Jebel Mech Irdane (Morocco) the zone comprises the interval between the Bed 116, where typical Eifelian taxa disappear, such as *P. robusticostatus*, *P. trigonicus* and *Tortodus kockelianus*, and the Bed 123 with FAD of *P. hemiansatus*. *Polygnathus x. ensensis* itself has not been indicated in this interval, however.

## MATERIAL AND METHODS

Common **present** approach to the uppermost Eifelian - lowermost Givetian stratigraphy is the application of the *kockelianus*, *ensensis* and *hemiansatus* zones (e.g. Becker et al., 2012). Whereas the last zone is well-defined in several sections worldwide, the usage of the uppermost Eifelian zonation appears less straightforward. In order to verify the definition of the *ensensis* Zone the re-investigation of several conodont collections was undertaken in addition to the evaluation of the literature. The key localities studied included Jirásek Quarry (Bohemia), Jbel Ou Driss Eastern and Bou Tchrafine (Morocco), Benner Bicken I, II and Blauer Bruch (Germany), Mont d'Haus and Couvin area (Belgium).

## RESULTS

The occurrence of the zonal taxon *P. x. ensensis* is rather uncommonly reported in the literature. In most of the sections investigated it is absent and the zone in question was previously defined based either on accompanying conodonts of questionable biostratigraphic significance or on other stratigraphic tools, e.g. on macrofauna or event correlation. Whenever present, the subspecies is frequently misidentified if its original diagnosis (Ziegler and Klapper, 1976) is respected. One of the main issues is the incorrect identification of juvenile specimens in which the diagnostic serrated anterior platform margins are found in individuals transitional to *P. pseudofoliatus* and in representatives of *P. pseudoeiflius* or *P. hemiansatus* (Bultynck, 1987; Walliser and Bultynck, 2011). More importantly, *P. x. ensensis*, if present, tends to occur in the lower Givetian strata (with *P. hemiansatus* or other typical Givetian forms). Its presence in the upper Eifelian appears questionable in most, if not all, of the investigated cases, and it has never been found with *T. kockelianus*, which defines the underlying zone. These observations refer also to the stratotype area in the Eifel Mts. (Weddige, 1977, 1988), Benner Bicken sections and the Moroccan localities, including the GSSP, in which the occurrence *P. x. ensensis* in the Eifelian strata has not been confirmed so far.

## DISCUSSION

In the opinion of the present authors the successful application of the *P. x. ensensis* Zone in **future** studies appears problematic. Consequently, alternatives for the uppermost Eifelian conodont biozonation were discussed in order to fulfil the needs of a global correlation. The review of pertinent literature data and the authors' own observations suggest that the uppermost Eifelian zone can be favourably based on the Eifelian range of *Polygnathus eiflius*. This species, erected by Bischoff and Ziegler (1957) has been recently revised by Walliser and Bultynck (2011). They narrowed its concept by excluding some forms described separately as *P. pseudoeiflius*, which appears earlier than *P. eiflius*.

The re-evaluation of *P. pseudoeiflius* and *P. eiflius* shows that the latter species is easy to determine, especially in comparison to *P. x. ensensis*, and is characterized by a widespread geographic distribution in deeper-water facies. It first occurs in the upper part of the *kockelianus* Zone, just below the last occurrences of *P. robusticostatus*, *P. trigonicus*, *P. angustipennatus* and *T. kockelianus* (Walliser and Bultynck, 2011). The uppermost occurrence of *P. eiflius* is in a lower part of the *timorensis* Zone of the lower Givetian (Walliser and Bultynck, 2011). The Eifelian range of the species in the studied sections was easily determined by its common co-occurrence with *P. hemiansatus*, whose appearance defines the upper boundary of the proposed *eiflius* Zone (=Eifelian-Givetian boundary). In its upper part the last appearance of *T. intermedius* and *Ozarkodina bidentata* have been noted, while several taxa first appear in this interval, including *T. sardinia*, *P. kluepfeli*, *P. linguiformis* n.ssp. A *sensu* Uyeno and Bultynck, 1993, *P. l. klapperi*, *T. variabilis* and *Icriodus arkonensis*.

## CONCLUSIONS

The concept of the *eiflius* Zone has its roots in the *eiflia* zone – the informal biostratigraphic unit introduced by Wittekindt (1966) for the (than) lowermost Givetian of the Rhenish area, and later extended to the Carnic Alps. The present concept refers directly to the *eiflius* Zone introduced by Bultynck (1987) for the uppermost Eifelian in Bou Tchrafine section (Morocco; Fig. 1) and later informally applied also by other authors in Morocco and in Pyrenees. It should be stressed, however, that due to the revision of the zonal species its biostratigraphic significance, particularly its lower range, also requires re-evaluation. In the present study forms ascribed to *P. eiflius* by Wittekindt (1966), Weddige (1977) and Bultynck (1987) were attributed partly to *P. pseudoeiflius* and other taxa. Such revision has further consequences for tracing the base of the proposed zone in respective sections.

The advantages of the proposed *eiflius* over the *ensensis* zone facilitate a worldwide detection of the uppermost Eifelian. The base of the zone (= FAD of *P. eiflius*) is clearly below the dark shales marking the Kačák Event and eustatic If transgression in Bohemia and in Morocco, thus having potential to enhance the event correlation with other sections worldwide.

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## CAPTURING AN EIFELIAN-GIVETIAN DROWNING EVENT IN THE NORTHWESTERN CANADIAN SUB-ARCTIC MAINLAND

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**Keywords:** Devonian, geochemistry, shale, Canada

### INTRODUCTION/BACKGROUND

The study area lies within Canada's Northern Interior Platform, around the Norman Wells area in the Northwest Territories (Fig. 1). Due to heavy hydrocarbon exploration, several wells were drilled and cored, a small subset of which were chosen for study by the first author. We used geochemical analysis, sedimentology, and conodont biostratigraphy from wells and outcrop sections to infer the paleo-environment of deposition of black shale called the Bluefish Member, and consider its possible correlation to global episodes of sea-level change.

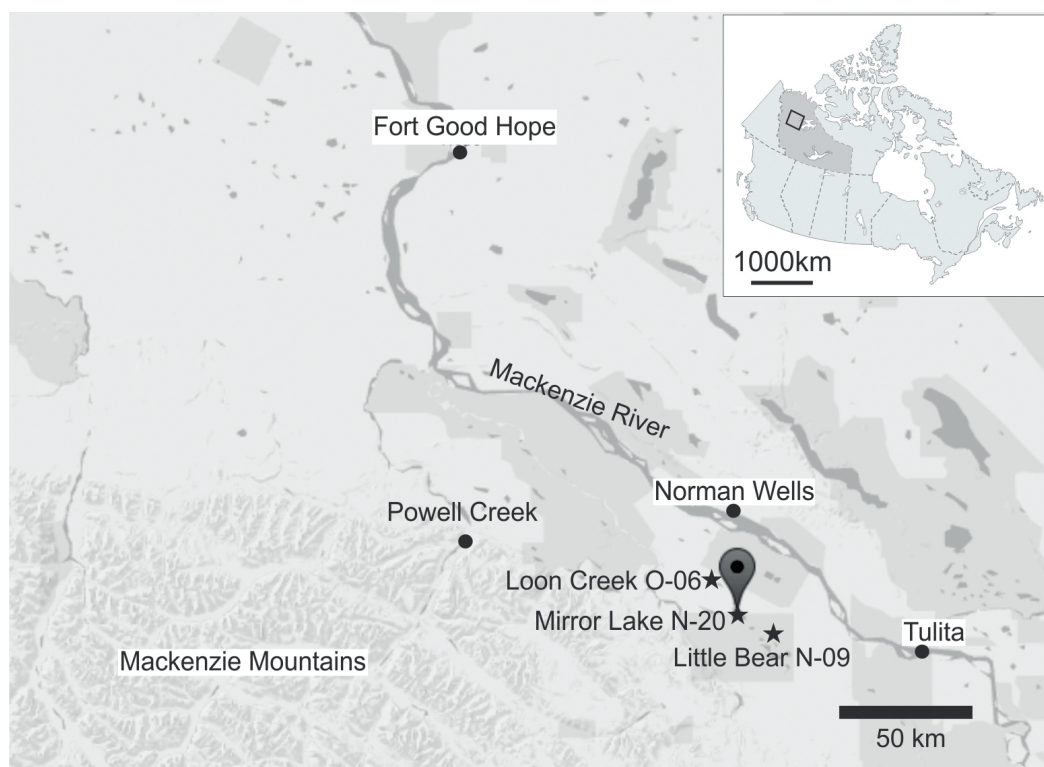


Fig. 1. Map of study area in the northern Canadian mainland (modified from Google maps).

## GEOLOGICAL CONTEXT

The area preserves Palaeozoic strata, from Cambrian siliciclastics to Devonian carbonates overlain by Devonian siliciclastics (Fritz et al., 1991). Within the Devonian siliciclastics, the Bluefish Member of the Hare Indian Formation, a succession of black, bituminous, Middle Devonian-age shale, was the first to be deposited (Pugh, 1983). This shale, part of the Horn River Group, sharply overlies the Hume Formation, an Eifelian limestone that was deposited in oxic waters. The Hume Formation contains a variety of well-preserved macrofossil assemblages including corals, brachiopods, and bivalves. The sharp limestone-to-shale contact is visually obvious. It is also present in spectral gamma ray logs and geochemical character. Above the Bluefish Member lies grey shale of the Francis Creek Member, which grades into the black shale of the Canol Formation overlain by Imperial Formation siltstone and shale.

Biostratigraphically, the Bluefish Member probably encompasses the base of the Givetian, where samples from the lower part of the Hare Indian Formation contain conodonts *Polygnathus linguiformis weddigei* and *Icriodus difficilis*, indicating an Early Givetian age (Gouwy, 2016; Uyeno, 2008). Given this age constraint, the onset of the Bluefish Member potentially coincides with the global Kačák Episode, a global phase of black shale deposition (Walliser & Bultynck, 2011).

## MATERIAL AND METHODS

The ConocoPhillips Canada Resources Corporation Mirror Lake N-20 well, drilled approximately 30 km south of Norman Wells and completed in 2013, contains a cored interval preserving the contact between the Middle Devonian Hume Formation and the overlying Hare Indian Formation (including the basal Bluefish Member). Approximately 50 metres of this core was described, including the Hume and Hare Indian formations, and the lower part of the overlying Canol Formation.

A geochemical database containing 28 well and outcrop sections was compiled from publications of the Geological Survey of Canada (GSC) and Northwest Territories Geological Survey (NTGS). Data consists of ICP-MS inorganic elemental geochemistry, Rock-eval, and X-ray Diffraction. Geochemical logs were created from calculations of redox and basin restriction proxies of two available nearby wells. Statistical Primary Components Analysis, a method of evaluating elemental covariance, was performed using this data compilation. Spectral gamma ray logs, collected using handheld scintillometer from GSC field programs in the summer of 2015 and 2016 were correlated to well gamma-ray logs.

## RESULTS

Core descriptions of Mirror Lake N-20 show the preservation of the sharp Hume - Bluefish contact; a slickensided surface marks the end of the Hume carbonates with the Bluefish black shales above. The Hume Formation preserved many rugose and other coral species, stromatoporoids, and shell fragments. The Bluefish Member preserves many calcareous, tentaculite-rich laminae in the lower third, pyritized bivalve shells and organic walled orthoconic cephalopods in the middle, and an arcritarch rich upper third which grades into the Francis Creek Member grey shales.

Geochemical analysis normalizing Molybdenum, Copper, and Nickel to TOC was used as a proxy for basin restriction (Tribovillard et al., 2006). The Hume contains relatively low ratios, while the Bluefish sharply contrasts with higher ratios (Fig. 2). The higher ratios indicate greater nutrient flux, where elements listed above are introduced. The boundary between the Hume and Bluefish also marks a strong shift from highly oxic conditions to euxinic (conditions with enrichment of hydrogen sulphide) waters when looking at the excess Mo and V (Fig. 2). The geochemical logs on Figure 2 show three distinct packages within the Bluefish Member: highly anoxic/euxinic conditions (high excess Mo and V), overlain by more oxygenated conditions (low excess Mo and V), in turn overlain by another anoxic event.



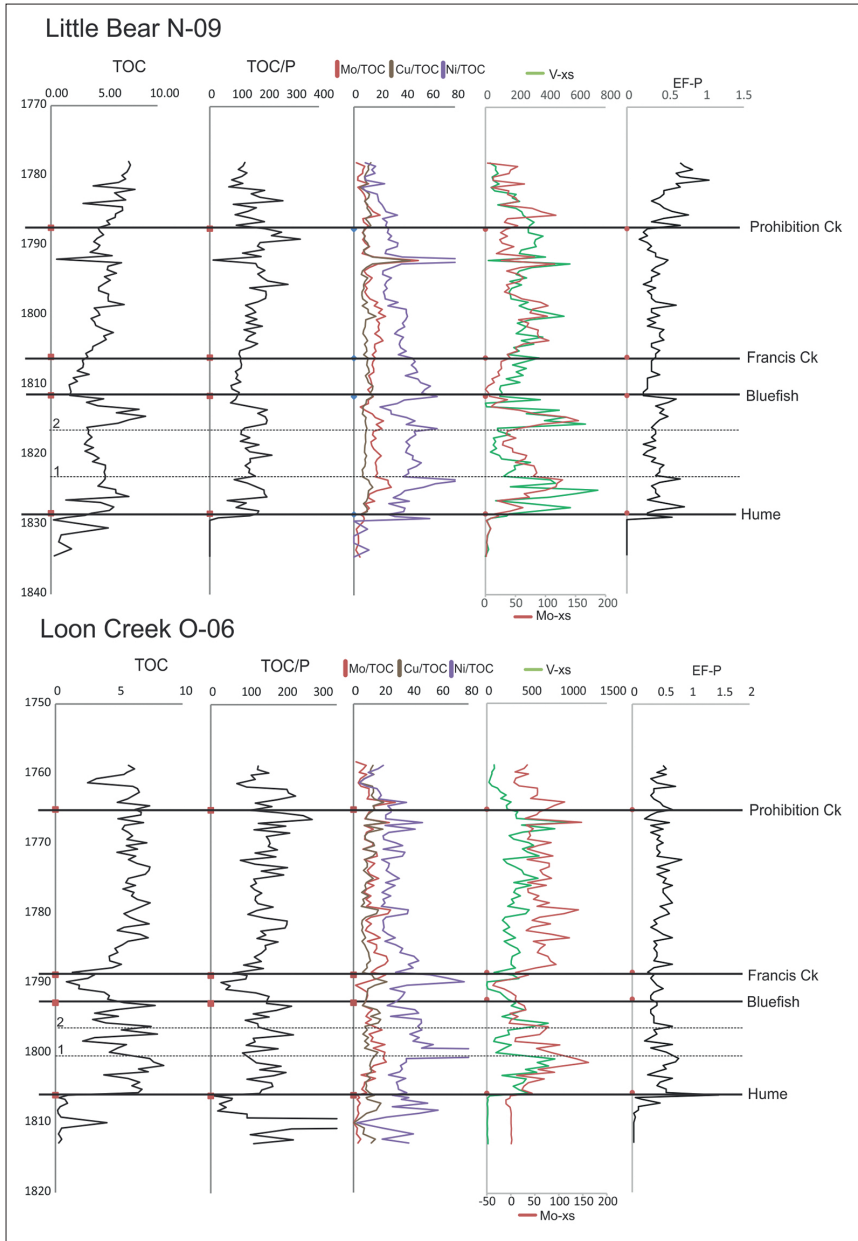


Fig. 2. Geochemical logs of basin restriction and redox proxies. "Xs" indicates excess while "EF-P" indicates enrichment factor of Phosphorus. TOC stands for total organic content, TOC/P for the TOC to Phosphorus ratio. Mo, Cu, Ni to TOC ratios are used as a basin replenishment proxy, while excess Mo and V are used for redox proxies. Solid black lines indicate unit tops, while dashed lines separate redox packages.

## DISCUSSION

The boundary from Hume to Bluefish shows a phase of deepening water depth. This is evident in the change from oxic-zone macro-fossils of the Hume, to the appearance of more pelagic species and pyritization of the Bluefish Member. This may also explain the geochemical signatures, where the redox boundary moves up when entering the Bluefish Member, as evidenced by the redox proxies of excess Mo and V. This could be attributed to the transgressive event, where the change in local water depth results in a shift in the redox boundary upward. These anoxic/euxinic conditions also coincide with basin nutrient flux, where Mo, Cu, and Ni are replenished more in the Bluefish Member than in the Hume Formation. Given the preliminary biostratigraphic constraint of Bluefish Member, the anoxic event may also coincide with the global Kačák Episode. This widespread event is attributed to a rise in global sea-level, which is also characteristic of the deposition of the Bluefish Member.

## CONCLUSIONS

The Hume-Bluefish contact represents a sharp boundary from shallow water oxic marine conditions to a transgressive anoxic deposition. Lithology from core descriptions shows a change from carbonate-shelf macrofossils in the Hume to pelagic rich shale in the Bluefish. This transgressive surface probably coincides with the onset of a global sea-level rise, called the Kačák Episode.

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## MIDDLE DEVONIAN BIOEVENTS FROM THE MARHOUMA SECTION (SAOURA, ALGERIA)

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**Keywords:** Chefar El Ahmar Formation, Middle Devonian bioevents, Saoura Algeria

### INTRODUCTION

The Marhouma section (also known as "km 30" section) is located around Béni Abbès, in the north-western part of the Algerian Sahara. This section has been studied by several authors since the XXth century. Devonian deposits are well exposed from Pragian to Famennian stages.

Sedimentological and biostratigraphical studies allow, for the first time, the recognition of all Middle Devonian bioevents in the Chefar El Ahmar Formation (marls-limestone alternation) of this Marhouma Key section and the location of stratigraphical boundaries recently refined in our previous papers. Several conodonts from the *Polygnathus* genus were recovered. Synthesis on zonations and bioevents is established from previous works (Göddertz, 1987 ; Ouali-Mehadji 2004, 2011 ; Maillet *et al.*, 2012) and our new recent results on conodonts, ostracods, goniatites and brachiopods.

### MAIN RESULTS

The Emsian-Eifelian boundary is located within the bed 8 of the the Chefar El Ahmar Formation, 2m higher than in the previous studies, with the first occurrence of *Polygnathus costatus partitus*,

The Choteč event (or *jugleri* event) is easily recognisable by its typical lithology. It appears after pentameridae micromorphs brachiopods and ends below the bed 11, in the *costatus* Zone

The *otomari* event is recognised by its lithology and is located within the bed 27. From this bed the Kačák horizon extends up to bed 28.

The *pumilio* event corresponds to an abundant and exclusive brachiopod fauna. It is located within the bed 56b in the *ansatus* Zone.

The Taghanic biocrisis occurs in the interval between beds 60 and 82. The Givetian-Frasnian transition has been identified in the tentaculite bed 82.

## CONCLUSIONS

This study allows to precise stratigraphy in the Marhouma section. Moreover, Middle Devonian bioevents, defined in several places in Gondwana, are for the first time highlighted in the Algeria Sahara.

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## BIOSTRATIGRAPHY AND SEQUENCE STRATIGRAPHY OF THE MIDDLE DEVONIAN (GIVETIAN) IN CENTRAL KENTUCKY, USA

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**Keywords:** Devonian, conodonts, sequence stratigraphy, Kentucky

### INTRODUCTION

The Middle Devonian (middle Givetian) of central Kentucky, USA, is represented by a thin but complex and somewhat enigmatic succession that until recently has been poorly dated and correlated with other classic Devonian successions. Recent studies have yielded unusual fossil echinoderms, as well as new conodont assemblages and sequence stratigraphic units that aid in the correlation of these units.

### GEOLOGIC CONTEXT

The Middle Devonian Boyle Formation of Kentucky comprises thin sandy dolomitic wackestones, echinoderm grainstones, and chert-rich wackestones. These are overlain by silty dolostones and thin dark gray to black shales of the Portwood Member of the New Albany Shale. The lower contact of the Boyle Formation is a distinct regionally angular unconformity that oversteps strata of mid Silurian to Late Ordovician age. The unit is sharply and disconformably overlain by the Portwood Member. Locally, this unconformity removes the Boyle Formation completely.

### MATERIALS AND METHODS

New road cut sections of Middle Devonian in Estill County, central Kentucky, have been measured and correlated in high resolution. The sections were also sampled for carbon isotopic and other geochemical analyses. Carbonates were processed using buffered acetic acid and residues were picked for conodonts.

### RESULTS AND DISCUSSION

New exposures reveal a series of distinctive depositional sequences in the Boyle Formation, each with a sharply erosive base, overlain by quartz sand rich in phosphatic pebbles, fish teeth, and bone fragments.

The lower sequences, forming the Kiddville Member, are siliciclastic-rich, *Zoophycos*-bioturbated, silty, dolomitic carbonates that contain typical Hamilton Group brachiopod associations (e.g. *Tropidoleptus*, *Athyris*, *Mediospirifer*). The thin basal Kiddville sequence may correlate with lower Hamilton Group sequences of the Appalachian Basin succession. The Kiddville is missing in some successions, apparently owing to erosional truncation and overstep by higher Boyle units; these yield the oldest datable conodont assemblages. Preservation of conodonts is poor; most specimens were fragmented or encrusted by matrix particles, suggesting deposition under a rather high hydrodynamic regime. The identifiable fragments consist of dominant *Lingui-polygnathus linguiformis* (almost 65 % of the fauna), some *Tortodus* (ca. 10 %), *Latericriodus latericrescens latericrescens* and broken icriodids indet. (ca. 12 %), and rare *Polygnathus timorensis*, *Po. ansatus*, and *Po. ovatinodosus*. The assemblage clearly falls in the higher part of the middle Givetian *Po. ansatus* Zone, based on *Po. ovatinodosus*.

Lenticular sandy echinoderm grainstones at the base of the upper or Casey Member have yielded an extraordinary echinoderm fauna, including the youngest known diploporitan cystoids and unusual schizotrematid blastoids; unfortunately these beds have not yielded diagnostic conodonts. The rest of the Casey Member is a massive and highly cherty carbonate, which is strongly variable in thickness, owing to major erosional truncation/karstification that locally removes the Boyle Fm. completely. The basal Casey Member in cuts near Waco, KY, is a linguipolygnathid facies, with a large dominance (> 90 %) of *L. linguiformis*. *Prioniodina* sp. and the long-ranging *Po. xylus* are accessory. In addition, Work et al. (2007) reported *Po. rhenanus* from the Casey Member of the J.K. Smith Power Plant section near Trapp, KY, a typical taxon of *ansatus* Zone faunas (e.g. Ziegler et al. 1976; Aboussalam, 2003). Conodont studies thus indicate that much of the Boyle is of *Po. ansatus* Zone and thus late middle Givetian in age. It is probably equivalent to the Moscow Formation of New York State.

The overlying Portwood Member of the New Albany Shale belongs to the *Po. ansatus* and "*Ozarkodina*" *semialternans* zones and consists of dark brownish gray shales and muddy dolosiltites. In many localities the basal unit is a lenticular dolomitic breccia, the Duffin Bed, which may represent a lowstand karst breccia that mantles the irregular upper contact of the Boyle at a regional unconformity. A lower dark shale locally contains the brachiopods *Emmanuella* and *Leiorhynchus*, in common with the lower Tully Fauna of the Appalachian Basin. A low-diversity conodont fauna from the Boyle/Portwood is interesting because of its distinctive composition, with relatively abundant *Po. varcus* besides the dominant *L. linguiformis*. The basal Portwood shale is overlain by a dolosiltite bed ("Megaburrow bed") with a highly distinctive trace fossil assemblage on its base yielding rare *Tullypothyridina*. The joint local entry of *Po. ansatus* and "*Po.*" *alveoliposticus* characterizes the top part of the *ansatus* Zone. As noted by Work et al. (2007), the latter species suggests correlation with the Carpenter Falls to Taughannock Falls beds of the western New York succession (top Lower to Middle Tully Limestone; see also Ziegler et al., 1976). This is particularly significant as the middle Portwood has been tentatively aligned with the middle Tully Formation (Carpenter Falls-Smyrna beds of New York) on the basis of the *Tullypothyridina*-*Emanuella* brachiopod assemblage (Heckel, 1973; see Baird and Brett, 2003). This bed somewhat resembles the distinctive Carpenter Falls bed of the lower Tully Limestone in the Appalachian Basin. It is overlain by dark gray to black calcareous mudstones of the middle submember of the Portwood. In many localities the middle Portwood Member shows highly contorted ball and pillow-like masses and internally discordant beds suggesting regional seismites.

An upper pale gray, lenticular, massive dolomitic bed rests sharply on the middle Portwood at a disconformable contact with relief of about 0.5 m. This bed yields poorly preserved corals, atrypid brachiopods and phacopid trilobites but apparently none of the distinctive lower Tully faunal elements, as is typical of the upper

Tully member. It passes upward into uppermost Portwood thinner bedded rhythmically bedded calcareous mudstones and dark shales. Conodonts of the *semialternans* Zone including "*Schmidognathus*" *latifossatus*; and "*Oz.*" *semialternans* in the upper shale-calcisiltite interval, confirm a correlation of this upper Portwood interval with the upper Moravia and Fillmore Glen beds of the uppermost Tully Formation in the Appalachian Basin. *L. linguiformis* is still present in this youngest middle Givetian conodont fauna of Kentucky, which falls in the Upper Taghanic Crisis Interval of Aboussalam (2003). The sharply overlying black Trousdale Member yields the first appearance of *Po. dubius* and *Po. limitaris*, indicating the (Lower) *hermanni* Zone and correlation with the lower Geneseo Formation black shales.

The variable thicknesses, complex internal discordances and abundant seismites in the Boyle-Portwood interval suggest a highly dynamic interval in the late middle Givetian, with regional far-field tectonics associated with the second tectophase of the Acadian Orogeny. Despite these tectonic effects the presence of a consistent internal sequence stratigraphy that correlates with that of the Appalachian Basin and elsewhere reflects strong eustatic effects.

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## A NEW ASSESSMENT OF THE MIDDLE AND UPPER DEVONIAN CONODONT BIOSTRATIGRAPHY OF THE HORN RIVER GROUP IN THE POWELL CREEK REFERENCE SECTION (NORTHERN MACKENZIE MOUNTAINS, NWT, CANADA)

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**Keywords:** Conodonts, Devonian, Northwest Territories, biostratigraphy, Canada

### INTRODUCTION

The Powell Creek section ( $65^{\circ}16'23.61''\text{N}$ ,  $128^{\circ}46'39.95''\text{W}$ ) and Tributary section (about 700m NW of the main section) (Fig. 1) were first described and studied by Basset and Stout (1967) and Lenz and Pedder (1972). They were first sampled for conodonts in 1969 by Mackenzie and Pedder and in 1971 by Uyeno (Uyeno, 1971, 1972). The Powell Creek outcrops are an almost continuous exposure of Devonian rocks, without structural complication from the sub-Devonian unconformity to the lowermost part of the Famennian. The remote setting of the outcrop, 100km from the nearest town (Norman Wells, Fig.1) makes it accessible only by helicopter. This section was selected as reference for the biostratigraphy of Western and Arctic Canada by Uyeno (1978) and is still considered the reference for the area.

In the summer of 2016 the Powell Creek outcrop and tributary section were revisited as part of the second phase of the Geo-mapping for Energy and Minerals (GEM) Program of the Geological Survey of Canada.

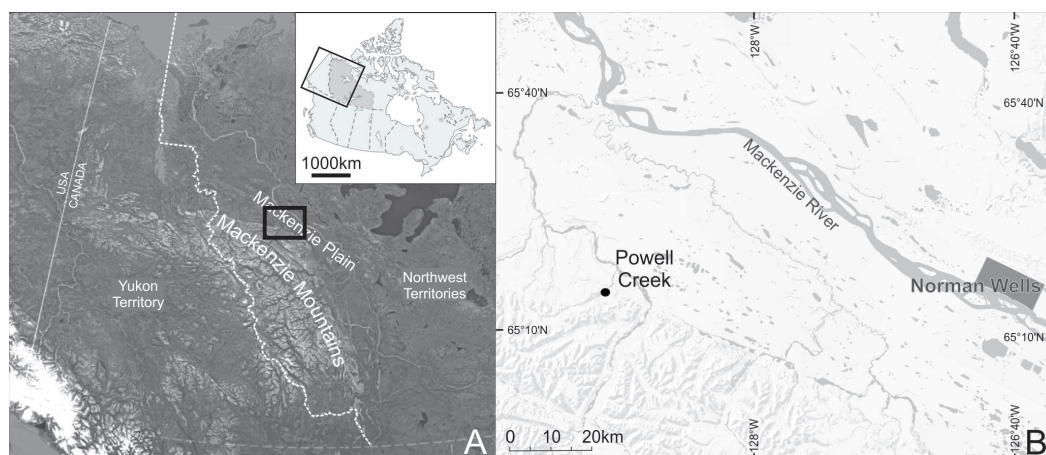


Fig. 1. Location map A: Location of the study area in the Mackenzie Mountains, NW Canada. Black rectangle shows part B. Inset shows the extent of NW Canada in A. B: Location of the Powell Creek section (black dot) at the front of the Mackenzie Mountains (modified from Google maps).

## GEOLOGICAL CONTEXT

The Horn River Group consists of the Hare Indian, Ramparts and Canol formations (Fig. 2). It conformably overlies the Eifelian Hume Formation, a more than 100m thick unit of fossiliferous and argillaceous limestone and calcareous shale that extends throughout the northern Mackenzie Mountains and Mackenzie Plain. The Horn River Group is overlain by interbedded sandstone and shale of the Frasnian-Famennian Imperial Formation.

The lower part of the Hare Indian Formation consists of the Bluefish Member, a black to dark grey shale with some thin interbeds of greyish limestone. This Member transitions upward into the Bell Creek Member, consisting of grey shale, calcareous siltstone and argillaceous limestone with a few calcareous interbeds near the top. In the Norman Wells and in the Powell Creek region, the Bell Creek Member is overlain by the Ramparts Formation, consisting of the Platform Member and the reefal Kee Scarp Member, separated by thin brownish grey calcareous shales of the Carcajou Member. In the Powell Creek section, the 1 m thick Carcajou Member overlying the Platform Member is followed by the Allochthonous Limestone Member, a cherty limestone showing slump structures and contorted bedsets (Kabanov et al., 2016). It is the lateral equivalent of the Kee Scarp Member exposed in the Powell Creek Tributary section and consists of debris flows originating from the reefal Kee Scarp Member. The Kee Scarp Member of the Ramparts Formation is the reservoir for the giant oil field at Norman Wells. The Canol Formation is composed of black siliceous bituminous shales with several calcareous beds and nodules (up to 1m diameter).

The deposition of the Hare Indian Formation on the Hume Formation marked the onset of siliciclastic sedimentation throughout the area, indicating a transgression in the Late Eifelian-Early Givetian. This deepening phase falls within the Kačák Episode (Uyeno et al., 2017).

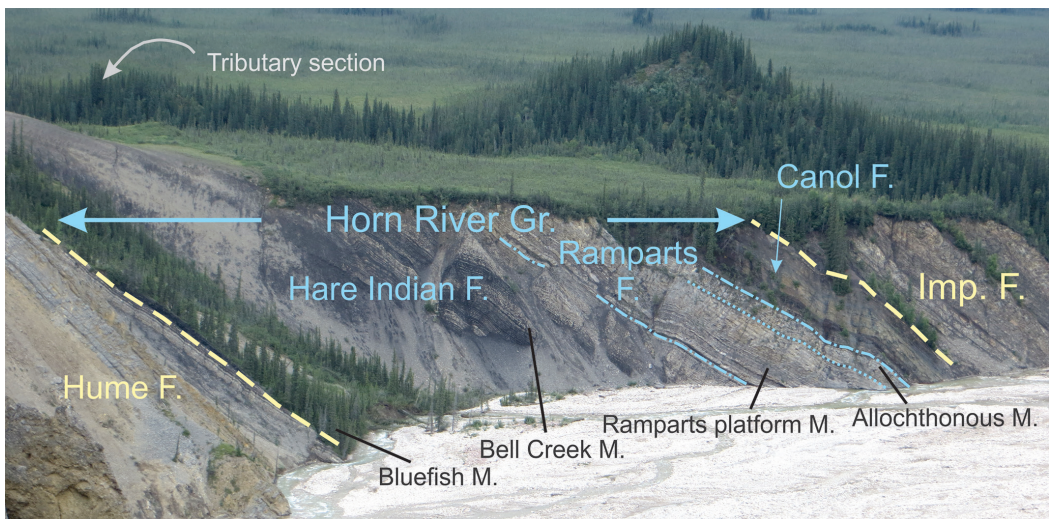


Fig. 2 The Powell Creek outcrop showing formations and members. Dotted line is the thin Carcajou Member.

## MATERIAL AND METHODS

A total of 92 conodont samples were collected in the 228m thick Horn River Group at Powell Creek and the Tributary section over the last 48 years by GSC researchers. Because the lower part of the Hare Indian Formation is covered in the Powell Creek section a combination of the two sections is used to study the local conodont biostratigraphy taking into account the differing lithologies within the Ramparts Formation between the Powell Creek and Tributary sections.

## RESULTS

The conodont data distinguish most of the Givetian and several Frasnian conodont zones. The base of the Hare Indian Formation is situated within the *ensensis* Zone. The base of this Zone was placed within the uppermost part of the Hume Formation at its type section located about 55Kms west (Uyeno et al., 2017). In the lowermost part of the Hare Indian Formation conodonts are rare, and do not allow assignment of the deposits specifically to the Eifelian or the Givetian. *Polygnathus hemiansatus* (which defines the base of the Givetian) has not been found in the sections.

The base of the *rhenanus-varcus* Zone, indicated by the local appearance of *P. rhenanus*, is positioned within the Bell Creek Member. The first *P. ansatus* (base of *ansatus* Zone) was identified 5m below the base of the Ramparts Formation. The base of the *semialternans/latifossatus* Zone could not be positioned: *Ozarkodina semialternans* appears higher up in the section; *P. latifossatus* was not found.

The base of the *hermanni* Zone is placed 12m above the base of the Ramparts Formation (local appearance of *Schmidognathus peracutus*). *Klapperina disparilis* indicates the base of the *disparilis* zone at 16m above the base of the Ramparts Formation. The base of the *norrisi* Zone (first occurrence of *Skeletognathus norrisi*) is placed in the top layer of the Ramparts Platform Member.

The first *Klapperina ovalis/Mesotaxis falsovalis* (indicating the base of the *falsovalis* Zone) appears 8m above the repositioned base (Kabanov et al., 2016) of the Canol Formation. Several limestone levels in the lowermost part of the Canol Formation and nodular levels in its upper part have been resampled and are currently being processed for conodonts. In the transition between the Canol and Imperial formations, *Palma-tolepis nasuta* indicates a late Frasnian age for the top of the Canol shales.

## DISCUSSION

The absence of several zone-defining taxa in the section does not necessarily mean there are diastems in the biostratigraphy in Powell Creek. The scarcity of conodonts (mostly coniform elements) at the top of Hume/base of Hare Indian Formation can explain the absence of *P. hemiansatus*. *Polygnathus latifossatus* was not found in a larger study area either; *Oz. semialternans* has a late appearance in the area. The Givetian/Frasnian boundary and the lower-middle Frasnian in the outcrop are still under investigation (samples are being processed). Additional sampling in this remote section in the near future is very unlikely. GSC bedrock mapping is now concentrated on an area south of the Powell Creek study area. Sampling these formations in the southern part of the Northern Mackenzie Mountains and combining the results with data from several shorter sections may give enough biostratigraphic information to complete the Givetian and Frasnian framework for the Northern Mackenzie Mountains.

## CONCLUSIONS

Powell Creek is by far the best studied section in the region and a good reference section for the Givetian/Frasnian even though part of the section (Canol Shale) is still being studied. So far most of the Givetian and several Frasnian conodont zones have been identified. Because of the remote setting of the Mackenzie Mountains this will probably remain the reference.

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## CONODONT BIODIVERSITY ANALYSIS FROM THE MIDDLE AND UPPER DEVONIAN OF THE SPANISH CENTRAL PYRENEES

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**Keywords:** Conodont biostratigraphy, biofacies, microfacies, Middle-Upper Devonian, Spanish Pyrenees

### BACKGROUND AND GOALS

Ziegler (1962b) recognised 27 Upper Devonian conodont zones (based on *Palmatolepis*) in the pelagic facies of the Renish Slate Mountains. Seddon (1970a) and Seddon & Sweet (1971) proposed two main Frasnian conodont biofacies, *Palmatolepis* (deep facies) and *Icriodus* (shallow facies) in the Canning Basin (W. Australia). Sandberg (1976), Sandberg and Dresden (1984) recognised five to nine conodont biofacies in widely distributed Upper Devonian strata from western USA and Europe. Sandberg et al (1989) studied conodonts around the Middle to Upper Devonian interval in the Renish Slate Mountains and several North American regions and recognised five conodont biofacies in different facies setting. Ovnatonova and Kononova (2008) analysed the Frasnian conodont taxonomic diversity from the Central and Eastern Russian Platform and distinguished two main conodont biofacies (*Mesotaxis-Palmatolepis* and *Polygnathus*) and also two secondary biofacies (*Mesotaxis-Polygnathus* and *Mesotaxis-Ancyrodella*).

In the Spanish Central Pyrenees (SCP), the ample conodont database from seven successions allows the recognition of the geographical and biostratigraphical distribution of these taxa.

The precise age control in each section allows the description bed by bed of the faunal content. Therefore, the changes in conodont composition can be recognised and evaluated with high-precision (smaller than zonal units). Similar studies in all considered sections permit great accuracy in demonstrating the time-equivalent of rocks and, hence, the conodont faunal sequences can be precisely correlated.

Combination of conodont biostratigraphy and microfacies studies in several sections from the same sedimentary basin possibilities the accurate correlation of rock units, the precise arrangement of the depositional events recorded in these rocks and the evaluation of whether they were related to local conditions or due to global sea-level fluctuations.

The goals of this study are: 1) to recognise the potential conodont biofacies; 2) to identify the sedimentary facies, and 3) to integrate these facies with high-resolution chronostratigraphical data from the SCP Southern Facies-area.

## GEOLOGICAL CONTEXT

We studied eight Middle to Upper Devonian selected successions from different paleogeographical sub-units (Sierra Negra, Renanué and Compte Subfacies) belonging to a larger unit, the Southern Facies-area (Mey 1967, Hartevelt 1970, Zwart, 1979; Valenzuela-Ríos & Liao 2006).

## MATERIAL AND METHODS

450 conodont samples, which recorded 86 taxa grouped into ten genera have been analysed through time and space. All samples come from Ampriú (Amp, AMP II), Basibé (Bas), Renanué (Re), Compte (CP), La Guàrdia d'Ares (LGA, LGA-I), and Villech (Vi-I).

## RESULTS

Fifteen conodont zones have been recognized by means of their index taxa.

The space-time analysis on the evolution of conodont faunas have led to the identification and characterisation of 14 conodont biofacies, their evolution and their distribution in the different sections. Five biofacies, in which only "one taxon (genera)" counts for over 75% of the total amount of conodont elements: *Polygnathus*, *Icriodus*, "*Ozarkodina*", *Schmidognathus* and *Ancyrodella*. Another eight biofacies are characterised by the presence of "two dominant elements", being the first name-bearer almost double in proportion than the second: *Polygnathus-Icriodus*, *Icriodus-Polygnathus*, *Polygnathus-Tortodus*, *Polygnathus-Coniformes*, *Polygnathus-Schmidognathus*, *Schmidognathus-Polygnathus*, *Polygnathus-Klapperina* and *Polygnathus-Ancyrodella*. Finally, a mixed *Polygnathus-Ancyrodella-Klapperina* Biofacies is also recognised.

The sedimentary facies analysis of the same sections have allowed the identification of four main facies (A, B, D and E) and seven subfacies (C1, C2, C3, F1, F2, G1 and G2), which correlate with the Standard Microfacies of Wilson SMF1-3, 5 and 12 with some variants.

## DISCUSSION AND CONCLUSIONS

The conodont radiation that took place in the Upper Givetian accounts for eight of the biofacies. The main one is the *Polygnathus* biofacies, which shows a remarkable change from narrow to wide platform of Pa element. Both types of platforms coexist in the lower part of Upper Givetian, but from the upper part of the Upper disparilis Zone upwards, the narrow-plaform Pa elements are not longer recorded in any Givetian rocks of all Pyrenean sections.

The only mixed corresponds to the *Polygnathus-Ancyrodella-Klapperina* Biofacies. *Polygnathus* is de dominant taxon from the Eifelian to Middle Givetian rocks and, consequently the *Polygnathus* Biofacies governs during this time span except form some spotty high abundances of *Icriodus*, *Tortodus* and coniforms that for particular time intervals and sections develop two components biofacies: *Polygnathus-Icriodus*, *Icriodus-Polygnathus*, *Polygnathus-Tortodus* and *Polygnathus-Coniforms*. The radiation of *Schmidognathus* and *Klapperina* in the Upper Givetian counts for the *Schmidognathus*, *Polygnathus-Schmidognathus*, *Schmidognathus-Polygnathus* and *Polygnathus-Klapperina* Biofacies. The innovation and subsequent radiation of *Ancyrodella* called for a Biofacies change in the Lower Frasnian, which is characterised by *Ancyrodella*, *Polygnathus-Ancyrodella* and *Polygnathus-Ancyrodella-Klapperina* Biofacies.

For the palaeoenvironmental interpretation: wackestone and/or packstone are dominant but grainstone are also common; mudstone is restricted to the Upper Givetian rocks of the Renanué section. Dacryconarids are the dominant bioclastic components. Oncoidal rudstone are restricted to the Middle Givetian in the Renanué section. Carbonate sedimentation dominates, but some siliciclastic input is recorded in the Middle and Upper Givetian. All identified facies correspond to an outer carbonate platform that comprises from the proximal platform to the deep basin.

In the Lower Givetian, facies with turbiditic deposits from deep environments dominate. Two settings are recognised: intrabasinal swell and toe-of-slope. During the Middle Givetian there is an ample spectrum of environments as reflection of sea-level fluctuations. In general, the environment changed from toe-of-slope at the *rhenanus/varcus* Zone to middle parts of talud during the *ansatus* Zone that locally, due to small storms, moved back to the toe-of-slope. At the end of the *ansatus* Zone and during the *semialternans/latifossatus* Zone a shallowing trend (proximal platform) developed in the westernmost sections while deeper environments ruled the eastern sections. During the Upper Givetian deep environments prevailed.

On the whole, a regressive trend is inferred for the Lower and Middle Givetian rocks that is followed by a transgressive tendency, which started earlier in the eastern part of the Pyrenean Basin.

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# **DEVONIAN GLOBAL EVENTS, ENVIRONMENTS AND TIME**



## CONODONT DATING OF REEF DROWNING AND EXTINCTION IN THE HÖNNE VALLEY (NORTHERN RHENISH MASSIF, GERMANY)

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**Keywords:** Devonian, reef complex, stratigraphy, conodonts, Frasnian Events, Kellwasser Crisis, Germany

### INTRODUCTION

During the Middle and Upper Devonian (Givetian to Frasnian), the growth of reefal build-ups was distributed all over the southern shelf of Laurussia. In the Rhenish Massif, ecologically diverse huge bioherms to small biostromes grew in a variety of palaeogeographical settings. In the northern Rhenish Massif, the Hagen-Balve Reef Complex represents one of the biggest reefs of central Europe. From west to east, basinal black shales, turbiditic flint limestones or pelagic nodular limestones overlie variably the reef limestones and indicate laterally different drowning processes and episodes. The thick reef succession of the Hönne Valley was and is in the focus of scientific research (e.g. Jux 1960; Schürger 1964; Schudack 1993; Becker et al. 2016) because of its economic importance as a major lime resource. Therefore, there are several large and partly active quarries operated by the LWL Rheinkalk, which generously supports our ongoing research and who provided complete drill cores. As a first step, our project focused on the reef drowning and extinction in the Hönne Valley area. It is based on bore holes and outcrops in the Beul area near Eisborn, which is famous for its Famennian ammonoid faunas (e.g. Wedekind 1914). Our aim was to document palaeoecological changes of the final reef phase by core logging and microfacies analysis, to date such facies changes by conodont sampling, and to correlate them with the established sequence of Devonian global events.

### GEOLOGICAL CONTEXT

The Hagen-Balve Reef Complex fringes in the northern Rhenish Massif the core of the Remscheid-Altena Anticline, which probably formed a syndimentary high in the Givetian (Paproth 1986). The initial reef growth started in the lower Givetian after a sudden and long-lasting depletion of the siliciclastic supply from the Northwest, probably as the result of climatic change (increasing aridity) on the Old Red Continent. The Hönne Valley Reef quickly evolved from a biostromal bank stadium to a real bioherm. Due to the occurrence of *Stringocephalus* near Binolen, its lowest part can be firmly assigned to the lower Givetian. The well-stratified lower carbonate succession grades into thick and cyclic, predominantly lagoonal limestones, followed by a final reef stage, which suddenly drowned (Stichling et al. 2015; Becker et al. 2016). The overlying sediments are open marine deposits, first still with some corals and stromatopores, then suddenly with Frasnian to upper Famennian pelagic faunas. This post-reefal interval also includes the famous top-Frasnian Kellwasser beds.

## MATERIAL AND METHODS

Most analyzed material originates from drill cores provided by the LWE Rheinkalk. Two cores (HON\_1101 and B102) sunk in the Beul area were logged and sampled at representative levels for large-sized thin sections/microfacies analysis. Results were compared with the adjacent only good outcrop of the reef top and early post reefal sediments (Becker et al. 2016). Rather small samples from halved drill cores (300-400 g) mostly yielded sufficient conodont faunas for precise dating. Outcrop biostrome samples were larger but often poor in conodonts.

## SUCCESSIONS AND STRATIGRAPHY

In the HON\_1101 drill core, the uppermost part of the reefal succession is formed by monotonous lagoonal limestone containing a characteristic fauna: dendroid *Amphipora* and *Stachyodes*, small sized bulbous stromatoporoids, and subordinate tabulate corals. This calm environment is overlain by storm-ridden reef core facies dominated by laminar and massive stromatoporoids. Within these debris deposits, at a depth of 83 meters (Bed -21), the first conodonts were encountered. Fragmentary *Ancyrodella rotundiloba ?pristina* and *Polygnathus alatus* indicate a basalmost Frasnian age, MN Zone 1. Therefore, the drowning of the reef rim and influx of open water organisms (ancyrodellids) can be correlated with an upper pulse of the global, transgressive Frasnian Event. In the next sample, one meter above and still within reefal debris, *Ad. rotundiloba rotundiloba* was found in addition to *Po. alatus*, which suggests MN Zone 2. The top of the reefal carbonate is reached at a depth of 78 meters (Bed -20), where *Icriodus subterminus* and *Pa. paradecorosus* were found, which are typical species in the lower Frasnian. This layers are open marine wackestones and floatstones with laminar and dendroid tabulates (alveolitids, thamnopores) and a few stromatoporoids. Bed -18 contains *Ad. ?gigas*, *Belodella* sp., *I. symmetricus*, *Zieglerina ovalis*, *Po. alatus*, *Po. webbi*, *Po. paradecorosus*, *Palmatolepis bohemica*, and *Pa. punctata*, which indicates a fully pelagic conodont biofacies in the middle Frasnian MN Zone 6. The final reef drowning occurred possibly in the course of the basal middle Frasnian Middlesex Event.

Above, black shales of Bed -15 were first assumed to represent Kellwasser beds, but that was disproven by conodonts from just above. Bed -14 still falls in the lower part of MN Zone 12, based on the association of *Ad. ioides*, *Ancyrognathus triangularis*, and *Pa. hassi*. Neither the Lower Kellwasser Bed, nor the Upper Kellwasser Bed were found in HON\_1101, possibly due to an unconformity. The youngest limestones are of early middle Famennian age, as an assemblage of *Pa. marginifera marginifera*, *Pa. glabra pectinata* M2, *Pa. glabra prima* M3 and, *Pa. quadrantinodosa inflexoidea* indicate the *marginifera* Zone.

Similar results are gained from the B102 drill core. Rudstones formed by storm transported laminar stromatoporoids form the youngest reefal carbonates (beds -30 to -28). They are also overlain by wacke-/ and floatstones with broken tabulate corals and stromatoporoids (beds -27 to -25). Nodular limestones form the overlying sequence and exhibit deep open marine conditions (*Palmatolepis* biofacies). *Palmatolepis plana* indicates MN Zone 10 or the top of the middle Frasnian (Bed -24). Facies conditions do not change much up to Bed -20. In contrast to drill core HON\_1101, both Kellwasser beds are represented by intercalated, finely laminated, black shales (beds -18 and -15). The lower level has the darkest (organic-rich) part at the base, followed by a non-laminated interval with ostracods, bivalves, and juvenile mantidoceratids, and then by poorly fossiliferous, dark laminites. The upper level shows a gradational contact to the underlying, very ostracod-rich, light-grey micrites, followed by a wackestone with bivalved ostracods and then by laminites with some thin layers of univalved ostracods. The subsequent nodular limestones fall in the basal Famennian

(Lower) *triangularis* Zone, based on *Pa. ultima*, *Pa. triangularis* (*praeterita* Morphotype), *Pa. subperlobata*, and *Pa. canadensis* in Bed -13.

In the Beul outcrop (Becker et al. 2016), a polygnathid conodont assemblage with *Po. alatus* and *Po. paradecorosus* indicates the *norrisi* Zone (uppermost Givetian) for the section base. In the course of the transgressive Frasnian Event, reef growth and carbonate production decreased rapidly. An open marine facies was established, dominated by wacke- and floatstones with subordinate reef organisms (Beul Facies). A brief recovery is marked by a thin alveolitid-thamnoporid biostrome with a poor, probably still lower Frasnian conodont fauna (*Mesotaxis guanwushanensis*). It represents the final stage of reef growth. *Ancyrognathus*, *amplicavus* and *Pa. plana*, date the overlying nodular limestones as MN Zone 10.

## CONCLUSIONS

The final reefal succession of the Beul area exhibits monotonous lagoonal limestone, dominated by dendroid stromatoporoids. At the top, these were replaced by reefal debris with dominant laminar and massive stromatoporoids. Conodonts clearly demonstrate that the first drowning occurred in the course of the global Frasnian Events. Reefal carbonate production did not reach the late middle Frasnian. The extinction proceeded in several steps and reef builders recovered only very briefly in open marine wacke- and floatstones with corals and stromatoporoids in the lower Frasnian. These last biostromes are overlain by pelagic nodular limestone dated as MN Zone 10. The two Kellwasser intervals post-date the regional reef extinction.

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## HIGH FRASNIAN CONODONTS FROM THE PIPE CREEK SHALE AND CANASERAGA SANDSTONE, JAVA GROUP, UPPER DEVONIAN, WESTERN NEW YORK

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**Keywords:** Lower Kellwasser, Frasnian, *Palmatolepis*, *Polygnathus*

### INTRODUCTION

This report represents updated information from the 1997 SDS meeting and field trip in New York as well as new material from the Canaseraga Sandstone.

### GEOLOGICAL CONTEXT

High Frasnian marine strata in the northern Appalachian Basin are characterized by nearshore sandstones that grade offshore to gray and black silty shales. The Pipe Creek Shale - Lower Kellwasser equivalent in western New York State - marks the base of the Java Group which regionally contains the Frasnian-Famennian Boundary, which has been narrowly constrained in western New York at numerous localities (Over, 1997, 2002; Haddad et al., 2016). The boundary strata are in the upper Hanover Shale which consists of light gray shale and thin black shale interbeds that grade shoreward (eastward) into siltstones and sandstones of the Canaseraga Formation. The Point Gratiot Bed - Upper Kellwasser equivalent - is recognized as far east as the Genesee River Valley.

### MATERIALS AND METHODS

Black shale strata were split and the bedding planes scanned for fossils. Calcareous cemented beds in the Canaseraga were cracked for macrofossils and dissolved in buffered formic acid to recover conodonts.

### RESULTS

The Pipe Creek Shale has yielded *Palmatolepis winchelli* in the eastern outcrop region. A fossiliferous calcite cemented conglomeratic sandstone at the base of a large channel feature in the Canaseraga Sandstone - formerly Wiscoy Sandstone at this locality in the Genesee River Valley - yielded a diverse *Polygnathus* fauna



in addition to the brachiopods *Cyrtospirifer whitneyi*, *Spinatrypa compacta*, *Nervostrophia* sp., *Protodouvillina* sp., *Protodouvillinaria* cf. *D. perversa*, and *Pseudodouvillina* cf. *P. euglepheia*, as well as bivalves, bryozoans, cephalopods, corals, crinoids, and fish. The conodonts include *Polygnathus aequalis*, *Po. alatus*, *Po. brevis*, *Po. webbi*, and at least one new *Polygnathus* taxon, *Icriodus alternatus*, as well as a palmatolepid suggestive of *Palmatolepis hassi*.

## DISCUSSION

*Palmatolepis winchelli* in the eastern outcrop region lead to revision of the stratigraphic assignments where the eastward equivalent to the Hanover Formation is the Canaseraga Formation (Bush et al., 2015). The Wiscoy Sandstone is equivalent to the Angola and Nunda formations. The brachiopod fauna is typical of an Upper Devonian offshore shelf environment; conodonts indicate Frasnian Zone 13 in the highest Frasnian based on the occurrence of *Palmatolepis* aff. *Pa. hassi*, high Frasnian *Polygnathus* species, and the absence of *Palmatolepis subperlobata* and *Pa. triangularis* which are known from the uppermost Hanover Formation (Day and Over, 2002). The diverse polygnathid fauna and palmatolepids indicates open circulation and a conodont biofacies similar to a carbonate deep shelf setting in the clastic dominated Appalachian Basin.

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## THE FRASNIAN-FAMENNIAN BOUNDARY IN VIETNAM AND THE EVOLUTIONARY MEANING OF FADS AND LADS

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**Keywords:** Conodont, Frasnian-Famennian boundary, N. Vietnam

The latest Frasnian and earliest Famennian conodont assemblages at the Si Phai section in northernmost Vietnam consist of species closely related to those from coeval strata in Europe, but their taxonomic diversity is significantly lower. Ramiform elements are relatively common enabling the apparatus approach to taxonomy and more reliable species identification than based just on highly variable P<sub>1</sub> elements. The succession seems rather complete. Immediately after the conodonts' abundance increased above a flat pebble horizon, presumably in result of the sea deepening, the assemblage became dominated by the polygnathid *Avignathus* in association with species of the palmatolepidids *Mantolepis*, among them '*Palmatolepis*' *linguiformis* being unusually well represented. In two subsequent sudden changes of ecological nature, a diverse set of polygnathids *Ctenopolygnathus* and *Polygnathus* followed species by *Klapperilepis ultima* enriched the assemblage. In the next faunal exchange event, all the palmatolepidids except for *K. ultima* disappeared. Although the general pattern of conodont succession is similar to that in other parts of the world, precise age correlation is difficult and relies on the assumption that changes in ecology controlling distribution of conodonts were globally synchronous. This may be true but requires an independent corroboration that could be potentially provided by data on the phyletic evolution of conodonts. Unfortunately, the evolutionary origin of none of the palmatolepidid species occurring in Si Phai (with possible exception of *M. winchelli*) has been determined. Probably the lineage of *Ancyrodella* is more reliable in this respect, but the sampling has yielded only few specimens of its species.



## A NEW APPROACH TO MIDDLE FAMENNIAN CONODONT BIOFACIES (UPPER BALLBERG QUARRY, NORTHERN RHENISH MASSIF)

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**Keywords:** Conodonts, stratigraphy, facies, Upper Devonian, Rhenish Massif, Germany

### INTRODUCTION

The northern Rhenish Massif is one of the classical regions in Europe for the study of Upper Devonian stratigraphy and facies. Famennian strata of a small belt along the northern flank and around the axial ramp of the Remscheid-Altena Anticline have been studied and described by numerous authors. Ziegler (1962) partly based his "standard" conodont zonation for the middle to uppermost Famennian on the pelagic limestone succession of the Ballberg section (near Balve). An initial survey of the near-by Upper Ballberg Quarry (N 51° 21'31.3", W 7° 54'47.8"), which has not been investigated previously, proved the presence of rich, diverse, and variable conodont faunas despite a rather uniform lithology. Therefore, we used the section to test the Rhenish middle Famennian conodont biostratigraphy and to explore its potential for a refined conodont biofacies analyses.

### METHODS

The lithological survey provided 28 limestone beds, twelve of which were sampled for conodonts. The carbonate microfacies analyses applied the modified facies types of Hartenfels (2011). Only the Pa elements of conodonts were counted and identified, as many middle Famennian multielement reconstructions are still doubtful and incomplete. The conventional conodont biofacies analysis is based on the models of Sandberg (1976), Sandberg & Dreesen (1984), and Ziegler & Weddige (1999), amongst others. It concentrated on the facies distributions of specific or morphologically similar (e.g. *Mehlina*, *Branmehla*, and single-row *Bispathodus*) genera. However, distribution differences between species groups within genera (e.g. of the *Po. nodocostatus* and *Po. semicostatus* groups, within *Icriodus*) were noted early (e.g. Savoy & Harris 1993; Corradini 1998). The classical genus-level approach is here expanded and refined by the separation of distinctive species groups within "mega-genera" (e.g. Hartenfels and Becker 2016). These seem to represent separate phylogenetic lineages with a potentially different palaeoecology, which is tested here. Some groups have been recognized by various authors as separate genera, either in multielement taxonomy, or based on morphological differences of the Pa element only (Lüddecke et al., sub. manuscript).

## RESULTS

The macroscopically homogeneous, light-grey, fine-grained flaserkalk-sequence is classified as micro-sparitic mud-wackestone (MF-A3b) sensu Hartenfels (2011), with bioclasts dominated by ostracods and fragmented thin-shelled bivalves. There are no significant microfacies changes throughout the carbonate succession. The micrites were deposited on the SE part of the drowned Hönne Valley Reef Complex, a persisting hemipelagic swell below the storm wave base. Most of the succession, at least from Bed 2 on, falls probably in the *Pa. marginifera utahensis* (Upper *marginifera*) Zone, which is often difficult to distinguish in the Rhenish Massif from the underlying *Pa. marginifera marginifera* (Lower *marginifera*) Zone.

Members of the genus *Palmatolepis* dominate the sampled section, which place the succession within the deeper-water Palmatolepid-Polygnathid Biofacies (Facies II, e.g. Ziegler and Weddige 1999). The *Pa. glabra* Group dominates the fauna, although it fluctuates in the middle part (45.3-68.5 %) and decreases at the top of the section (51.1 %). Second most abundant is the *Po. glaber* Group among representatives of the "mega-genus" *Polygnathus*. *Icriodus* enters as a very rare form in the higher part of the section (Bed 14d, 0.1 %) and increases upsection, in parallel with decreases in the *Pa. minuta/gracilis* and *Pa. glabra* groups. The fluctuations of different palmatolepid species groups and other genera at the Upper Ballberg Quarry enable the local recognition of five middle Famennian subfacies types. These do not correlate with fluctuations of general conodont frequency, neither in absolute numbers nor per kg sample weight.

### 1. *Pa. glabra - minuta/gracilis* Subfacies

Definition: The ***Pa. glabra* Group** is very dominant (ca. 60 % of the fauna); **together** with the ***Pa. minuta-gracilis* Group** it constitutes **more than 70 %** of the assemblage.

### 2. *Pa. glabra/marginifera - Po. glaber* Subfacies

Definition: The *Pa. glabra* Group is dominant (45-56 % of the fauna); together with the *Pa. minuta/gracilis* Group it constitutes ca. 53-67 % of the assemblage. Typically there are more than 9 % of the *Pa. marginifera* Group (up to 30 %) and **7-18 %** of the ***Po. glaber* Group**.

### 3. *Pa. glabra - Po. nodocostatus* Subfacies

Definition: The *Pa. glabra* Group is dominant (64 % of the fauna); together with the moderately common *Pa. minuta/gracilis* Group (8 %) it constitutes more than 70 % of the assemblage. Most typical (unlike as in Subfacies 1) is a small enrichment of the ***Po. nodocostatus/Polylophodonta* Group (6 %)**.

### 4. *Pa. glabra/marginifera - Branmehl/Mehlina* Subfacies

Definition: The *Pa. glabra* Group is dominant (53 %); together with the *Pa. minuta/gracilis* Group it constitutes less than 63 % of the assemblage. The *Pa. marginifera* Group is rather common (ca. 14 %) but most distinctive are the numerous - ***Branmehl/Mehlina* (16 %)**. A slightly increased content of *Icriodus* (ca. 3 %) is distinctive.

### 5. *Pa. glabra - Icriodus* Subfacies

Definition: The *Pa. glabra* Group is dominant (51 %); together with the rare (< 2 %) *Pa. minuta/gracilis* Group it constitutes less than 53 % of the assemblage. Most distinctive is the relative abundance of **deeper-water *Icriodus* species (12 %)**.

The vertical distribution patterns suggest a slightly deeper setting in the middle part of the section (*Pa. glabra - minuta/gracilis* Subfacies) and a minor shallowing towards the top. The new *Pa. glabra - Icriodus* Subfacies suggests an intergradation of palmatolepid and icriodid dominated assemblages without a parallel proliferation of polygnathids. This emphasizes that it is important to distinguish between neritic and pelagic icriodids and that bathymetry and turbulence were not the only significant palaeoecological factors that control assemblage structures. A conodont-barren interval (beds 22-24) is thought to reflect an episodic collapse of the trophic web during the minor sea-level fall. The latter correlates with the regressive eustatic trend in the lower part of the middle Famennian (e.g. Johnson et al. 1985; Becker 1993: UD II-H/I).

A comparison with previously described, contemporaneous assemblages of Sardinia, the Carnic Alps, and of some more distant regions (NW Canada, NW Thailand) suggests that our subfacies types, variants of them, and some different types can be recognized on a global (pantropical) scale.

## CONCLUSIONS

The Upper Ballberg Quarry succession is monotonous in terms of litho- and microfacies. In contrast, the conodont biofacies are more sensitive to environmental changes. Consequently, pelagic conodont assemblages are a much finer detector of palaeoecological variations than macroscopic lithology and carbonate microfacies. This opens prospects for a refined application of conodont biofacies once the palaeoecological control factors aside from palaeobathymetry become better understood.

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## UPPER DEVONIAN CONODONT BIOSTRATIGRAPHY IN THE CERRO LAS PINTAS AREA, NORTHEASTERN SONORA, MEXICO

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**Keywords:** Conodonts, biostratigraphy, Famennian, NW Mexico

### INTRODUCTION

The present work describes a biostratigraphic study based on conodonts from the Cerro Las Pintas area, northeastern Sonora, Mexico. The results of this work allow to identify the Upper Devonian (upper Famennian), previously recognized in the area by Gómez-Tagle (1967) and Peiffer-Rangin (1988), and to analyse their sedimentary palaeoenvironments during the middle Palaeozoic at the southwest margin of the North American Craton to northeast Sonora.

Based on previous work by Ransome (1904) in Bisbee, Arizona, where he described the Precambrian sequences and defined the Paleozoic and Cretaceous units, it was possible to establish the correlations between the sequences of the Bisbee Quadrangle and the Pintas Area.

Gómez-Tagle (1967) correlated the rocks of the Cerros Las Mesteñas with those identified by Ransome (1904), based on lithological and stratigraphic features and on the fossil content. In this way, he proved the presence of the Pinal Schist, the Bolsa Quartzite, the Abrigo Limestone, the Martin Limestone, the Escabrosa Limestone, the Naco Limestone and, of the Bisbee Group, the Glance Conglomerate and the Morita Formation.

Peiffer-Rangin (1988) carried out studies that included geological mapping in the region, where she recognized the spatial distribution of the sequences reported by Gómez-Tagle (1967). Moreover, Peiffer-Rangin (1988) discovered some conodonts in a Devonian sequence (Martin Limestone) but genera or species were not specified.

### GEOLOGICAL CONTEXT

The Cerros Las Mesteñas are composed of rocks that range from the Proterozoic, represented by the Granito Mesteñas (1,589 ± 3 Ma) and the Pinal Schist (1,640 Ma), to Quaternary alluvial deposits. The Palaeozoic rocks is represented by the Cambrian Bolsa Quartzite and the Cambrian Abrigo Limestone, the Devonian Martin Limestone, the Mississippian Escabrosa Limestone, and the Pennsylvanian Naco Limestone and is overlain by the Cretaceous sequences of the Bisbee Group. The Cenozoic is represented by plutonic rocks that



are affecting the Proterozoic and Palaeozoic sequences and by tuff deposits and rhyolitic flows. Finally, the Quaternary is represented by a poorly consolidated conglomerate and alluvial deposits (Gómez-Tagle, 1967).

## MATERIAL AND METHODS

A succession of 500 m was logged in the NE area of the Cerro Las Pintas. As a result, 43 samples were taken for thin sections and 18 of them also for conodont research. The latter were processed in the laboratory following the conventional method with formic acid, resulting in seven positive samples. Nine *Polygnathus* species, two *Palmatolepis* species and one *Icriodus* species were found. The conodonts were taken by SEM model TM3030 Plus brand Hitachi, hosted in the Estación Regional del Noroeste of the Universidad Nacional Autónoma de México (UNAM).

## RESULTS

The succession is mainly composed of limestone and sandy limestone and is exposed in medium to coarse strata at the base and in coarse to massive strata at the top. In the first 150 m trilobites and algae fragments, echinoderm plates were recognized. Above, 100 m of azoic limestone is cropped out. The next 110 m contains bryozoan and sponge remains at the base; and 50 m at the top, conodonts and echinoderms plates are abundant

The conodont analysis indicated the presence of *Palmatolepis perlobata postera*, *Pa. rugosa ampla* transitional to *Pa. rugosa rugosa*, *Polygnathus experplexus*, *Po. semicostatus*, *Po. perplexus*, *Po. obliquicostatus*, *Po. extralobatus*, *Po. symmetricus*, *Po. collinsoni*, *Po. carina*, *Polygnathus* sp. cf. *Po. Inornatus*, and "*Icriodus darbyensis*"; this indicates an age range from ca. the upper part of the Lower *postera* to Upper *expansa* (equals the lower part of the *Bi. ultimus* Zone, Corradini *et al.*, 2016) zones of the upper Famennian (Late Devonian).

## DISCUSSION

The carbonate sequence spans from the upper Cambrian Abrigo Limestone to the Upper Devonian Martin Limestone. Based on a lack of conodonts were not found at the base and in the middle part of the succession and based on the lithological characteristics and other fossil content, this part of the sequence may be related to the Cambrian deposits described by Peiffer-Rangin (1988) from the region.

The age of the last 50 m of the sequence was assigned by their conodont content and it corresponds to the upper part of the Lower *postera* to Upper *expansa* zones (upper Famennian, Late Devonian).

The depositional environment of this sequence may be determined through the biofacies of conodonts for the Upper Devonian (Sandberg, 1976). Based on conodont associations for each conodont level, we can determine a transition from the *Palmatolepis-Polygnathus* to the *Polygnathus-Icriodus* biofacies and possibly to the *Polygnathus-Pelekysgnathus* biofacies. This suggests a transition from shallow to moderately deep water on the continental shelf to moderately shallow water on the outer cratonic platform, with an important terrigenous contribution.

Besides, in a coral study by Huddle and Dobrovolny (1952) of this area, they divided the Martin Limestone in three members (from the base to the top): 1) conglomeratic sandstone and dolomitic limestone, 2) sandstone and limestone; and 3) calcareous sandstone, sandstone, limestone and shale. The first two members represent partially or completely the *Stromatopora* Zone (Middle Devonian) while the last one may be the

*Phillipsastrea (Pachyphyllum)* Zone (Upper Devonian) Martin limestone represents a southward carbonated development and it includes shale strata that increase their thickness northward of Bisbee (Huddle and Dobrovoly, 1952).

Considering the results of this work it is possible to establish comparisons between the upper member described by Huddle and Dobrovoly (1952) and the sequence here studied. Thus, the outcrops of the sequence of the Cerro Las Pintas, do not show the shale and sandstone strata characteristic of the upper member of the Martin Limestone, but shows an important siliciclastic input. This difference may be explained by a larger distance to the terrigenous source than those of the Bisbee sequences and other northernmost localities. The palaeoenvironments of the Cerro Las Pintas sequence correspond to the outer cratonic platform associated to the North American Craton.

A study of changing in the sedimentary environments suggests a sea level fall. According to Johnson *et al.* (1985) argues that for the *expansa* Zone in Euramerica, it is registered a slightly sea level rise (cycle II<sub>f</sub>) different from what is shown here and that is against the sea level fall tendency from the *triangularis* Zone to *postera* Zone (cycle II<sub>e</sub>); a sea level fall that begins during the Early Famennian (Johnson *et al.*, 1985).

Finally and due to the observations of Johnson *et al.* (1985) for the *expansa* Zone and our results in this sequence, it is proposed that the transgression cycle II<sub>f</sub> started in the middle-upper part of the *expansa* Zone in the west coast of the North American Craton and that is because the regression cycle II<sub>e</sub> effects are shown in that time.

## CONCLUSIONS

A total of nine species of *Polygnathus*, two species of *Palmatolepis*, and one of "*Icriodus*" have been identified in the studied section, which provide an age range from the upper part of the Lower *postera* to Upper *expansa* (equals to the lower part of the *Bi. ultimus* Zone, Corradini *et al.*, 2016) zones of the upper Famennian.

Based on conodont biofacies it was possible to infer a change in the depositional environment that ranged from shallow to moderately deep water on the continental shelf to moderately shallow water on the outer cratonic platform, with an important terrigenous input. The upper Famennian sequence described in this work contains characteristics that correspond to slightly deeper water than those of the upper member of the Martin Limestone, which represents an important continental influence in the northern localities, in Arizona (Huddle and Dobrovoly, 1952).

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## FIRST EVIDENCE FOR A LATE FAMENNIAN CARBON ISOTOPE EXCURSION IN FRANCONIA (GERMANY)

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**Keywords:** Carbon cycle, Epinette Event, *expansa* conodont Zone, biocrises, stable isotopes

### INTRODUCTION

The late Famennian episode comprises repeated successions of global eustatic and hypoxic events post-dating the late Frasnian (F/F "Kellwasser"; Buggisch 1991) and predating the D/C (Hangenberg Event; see Kaiser et al. 2015) mass extinction events. The events are characterized by global sea-level changes and transgressive/regressive pulses during deposition of black shales and organic-rich limestones within short time spans (Algeo & Scheckler 1998; House 2002). The late Famennian hypoxic events are accompanied by low-order biocrises, among them the *Annulata*, Dasberg, Epinette and Etreoungt Events, which are characterized by extinctions, originations and radiations of selected faunal groups (Hartenfels 2010; Hartenfels & Becker 2009, 2016; Kaiser et al. 2008; Streef et al. 2000). However, the ultimate causes of environmental changes during pre-Hangenberg Event times and their impact on fauna are still a matter of discussion (Racki 2005). Scenarios for this time span range for example from climate change, the onset of high-latitude glaciations, glacially induced sea-level changes, enhanced global wildfires, anoxia and increasing organic carbon burial (Joachimski & Buggisch 2002; Sandberg et al. 2002, Marynowski et al. 2010; Isaacson et al. 2008; Racka et al. 2010). Enhanced C<sub>org</sub> burial were suggested based on positive  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{org}}$  excursions which have been reported for the first time from the Middle and Upper *expansa* (*Bispathodus aculeatus aculeatus* and *Bi. ultimus ultimus*) Zone in the Carnic Alps (Austria; Kaiser et al. 2008). The increasing  $\delta^{13}\text{C}$  values of up to 3 ‰ (V-PDB) recorded in the Carnic Alps seem to coincide with an increase in sea water temperature of ca. 8° C, based on preliminary oxygen isotope data measured on coeval conodont phosphate (Kaiser et al. 2008).

Our study focuses on the stable isotope geochemistry in order to document environmental changes during pre-Hangenberg Event times. First results of carbon isotope analyses measured from middle to uppermost Famennian limestone successions in Franconia (Germany) are presented herein.

### RESULTS

A carbon isotope excursion with values up to 3 ‰ was measured for the first time in Franconia from limestones in the *Bispathodus aculeatus aculeatus* (Middle *expansa*) Zone. The studied Geuser (= Geyser, older literature) section exposes a 16.5 m thick, bedded, light to dark-grey, micritic, more or less homogenous

flaserkalk succession (Hartenfels 2003), which spans the *Palmatolepis rugosa trachytera* to *Siphonodella praesulcata* zones (Hartenfels 2011; old Lower *trachytera* to Lower *praesulcata* zones). The section is part of a large olistostrome, embedded overturned in argillaceous sediments with intercalated greywackes of Early Carboniferous age. The Geuser section became well-known since Münster (1840) collected Famennian ammonoids for his large collection at this location.

Carbon isotope analyses were conducted on samples from each limestone bed, with a higher sampling density in the *Bispathodus stabilis stabilis* to *B. ultimus ultimus* zones (*expansa* Zone). The carbon isotope values start to increase from around 2 to ca. 2.6‰ in the basal *Bispathodus aculeatus aculeatus* Zone (Middle *expansa* Zone), highest values of 2.9‰ are recorded in the middle part of this conodont zone. Values of up to 2.7 ‰ persist in the *B. ultimus ultimus* (Upper *expansa*) Zone.

## CONCLUSION

The  $\delta^{13}\text{C}$  excursion measured in Franconia can be correlated with the excursions reported from the Carnic Alps in the Middle *expansa* Zone by Kaiser et al. (2008). It is interpreted to record enhanced organic carbon burial and thus a perturbation of the global carbon cycle. It can be correlated with a low-order faunal turnover during the Epinette Event in the Middle *expansa* Zone (Streel et al. 2000), which is characterized by global sea-level changes and transgressive pulses. The geochemical changes recorded here and in the Carnic Alps do not correlate with changing sedimentation patterns but coincides with the Epinette Transgression in Belgium (Epinette Shale of Belgium, Streel 2007), which is characterized by the entry of the miospore *Retispora lepidophyta* in the higher part of the *Bi. a. aculeatus* (Middle *expansa*) Zone. This miospore taxa defines the *Retispora lepidophyta* – *Knoxisporites literatus* (= LL Zone), and the sudden global spread of this marker spore was interpreted to indicate more humid climate conditions (Streel & Marshall 2007). This study contributes to the understanding of complex successions of repeated bio- and lithoevents during rapid eustatic sea-level changes in the late Famennian. It can provide fundamental insights into the ultimate cause of environmental changes and associated biocrises during pre-Hangenberg Event times.

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## NEW CONODONT DATA FROM THE DEVONIAN-CARBONIFEROUS BOUNDARY INTERVAL IN THE KITAB RESERVE AREA (UZBEKISTAN)

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**Keywords:** Uzbekistan, conodonts, biostratigraphy, Devonian-Carboniferous boundary

### INTRODUCTION

The criterion for defining the base of the Carboniferous system is placed to coincide with the First Appearance Datum (FAD) of the conodont species *Siphonodella sulcata* within the *Si. praesulcata*-*Si. sulcata* lineage, and the GSSP (Global Stratotype Section and Point) is located in La Serre Trench E' section (Paproth et al., 1991). Difficulties in discrimination of *Si. sulcata* from the supposed ancestor *Si. praesulcata* have been known since a long time, and studies on the stratotype section have revealed other problems (for a summary refer to Aretz, 2013 and Corradini et al., 2016). A redefinition of the Devonian–Carboniferous boundary (DCB) was determined necessary, and in 2008 the International Commission on Stratigraphy established a working group with the goal of proposing a new criterion for defining the boundary and finding a new GSSP. For that purpose several sections are under investigation around the world, including already-known localities and new locations, and main fossil groups are subject to revision.

### GEOLOGICAL CONTEXT AND PREVIOUS RESULTS

Present study was aimed at tracing the DCB in the sections Kule 1 and Novchomok 22 in the eastern part of the Kitab Reserve Area (Uzbekistan) located in the Zeravshan-Gissar Mountains area (W-Tian Shan). The investigated part of the Kule 1 section comprised the boundary interval between the Upper Akbasay and Novchomok formations representing rather uniform, grey, fine-grained and pelitic limestones, massive in the lowermost part and becoming thin- to thick-bedded towards the top. In the Novchomok 22 section the present study comprised the top of the Yatavluk Fm. and the base of the Novchomok Fm. The first unit is composed of dark grey pelitic limestones with crinoids and corals, and cherry-coloured marly shales and marls. The Novchomok Fm. is developed as dark grey pelitic limestones and brown marly shales locally with crinoids.

Conodonts in both sections have been studied earlier by Erina (2008, and in: Kim et al., 2008), but the Novchomok 22 data have not been published so far. Our observations confirm that the taxonomic diversity is higher in the Kule 1 section than in the Novchomok 22 one. Previously, the DCB has been placed at the lithostratigraphic boundary between the respective formations in both sections. In Kule 1 the DCB has been detected by the first occurrence of *Si. sulcata* slightly above the entry *Siphonodella praesulcata*. However, the present re-examination of *Si. praesulcata* and *Si. sulcata* figured by Erina (2008, pl. 33, fig. 1, 2) revealed



that these are not typical forms and therefore they can hardly indicate the DCB position. Also the presence of *Si. quadruplicata* in the uppermost Famennian in the Novchomok 22 section (Erina, unpublished data) is questionable as the first appearance of the species is reported in the literature from the upper part of the lower Tournaisian (*sandbergi* Zone, Sandberg et al., 1978).

## MATERIAL AND METHODS

The investigated conodont material, comprising ca. 100 elements, was obtained from seven samples (all positive) from each of the studied sections. The frequencies per sample are low, mostly not exceeding 10 specimens, except for a few richer samples from the Kule 1 section. Overall, the preservation of conodonts is poor due to fracturing by a tectonic cleavage, particularly in the Novchomok 22 section. The dark brown (CAI 3, Kule 1) or black (CAI 5, Novchomok 22) colours indicate high temperature regime, from 110° up to 400°C.

The biostratigraphic analysis has been carried out based on a comparison of conodont stratigraphic ranges reported i.a. by Sandberg et al. (1978), Kaiser and Corradini (2011), Bahrami et al. (2011) and Corradini et al. (2016). For the Upper Devonian the standard zonation by Ziegler and Sandberg (1984) has been applied while for the lower Carboniferous the subdivision according to Sandberg et al. (1978), with modifications proposed by Kaiser et al. (2009) and Corradini et al. (2016), is followed.

## RESULTS

The studied forms have been attributed to the following genera: *Branmehla*, *Bispathodus*, *Palmatolepis*, *Polygnathus*, *Protognathodus*, *Pseudopolygnathus* and *Siphonodella*. In the case of a single well-preserved specimen the generic assignment appeared difficult - most probably the form represents a new genus. The genera *Branmehla*, *Bispathodus* and *Protognathodus* have not been described from Uzbekistan so far. More than 50 % of the whole collection is represented by genus *Polygnathus*, in which the dominant species is *Po. purus*. New, previously not documented *Polygnathus* taxa are: *Po. cf. tenuiserratus*, *Po. communis carinus* and two taxa of indetermined taxonomic affinity. Among siphonodellids the key species *Si. praesulcata* is not present in the uppermost Famennian and has been found only in the lower Tournaisian. The latter strata revealed the presence of the previously unknown *Si. jii* being the index species for the *jii* Zone (Becker et al., 2016) of a middle part of the lower Tournaisian. Other taxa found for the first time in Uzbekistan are: *Branmehla inornata*, *Bispathodus stabilis*, *Protognathodus kockeli* and an undetermined (probably new) form of *Pseudopolygnathus*.

The DCB in the Kule 1 section runs still within the uppermost part of the Akbasay Fm. based on the presence of *Polygnathus purus subplanus*, whose first appearance is at the base of the Carboniferous. The lowermost part of the section is attributed to the wide interval of the *trachytera*–*kockeli* zones based on the total stratigraphic range of *Palmatolepis gracilis sigmoidalis*. Presence of the *jii* Zone in the middle part of the section is indicated by the occurrence of *Si. jii* at the base and *Si. praesulcata* at the top of this interval. The uppermost part of the section is attributed to the *jii*-Lower *crenulata* zones interval (upper part of a lower Tournaisian) based on the last occurrence of *Po. p. purus* (Ji & Ziegler, 1993).

In the Novchomok 22 section the base of the Carboniferous is tentatively traced just below the top of the Yatavluk Fm., above the occurrence of *Protognathodus kockeli*. This species co-occurs with *Palmatolepis gracilis sigmoidalis* in the same sample, indicating that the latter taxon survived a little after the Hangenberg

extinction event. The other possibility is a presence of a reworked late Famennian fauna within the lowermost Tournaisian.

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## RECENT ADVANCES ON CONODONT BIOSTRATIGRAPHY IN SONORA, NW MEXICO

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**Keywords:** Laurentia, Ordovician, Upper Devonian, Mississippian, Pennsylvanian

### INTRODUCTION

Cambrian to Permian sedimentary rocks are widespread in Sonora. Their recent arrangement is determined by extensional tectonics as well as volcanism and deformation related to the Laramide orogeny, which resulted in scattered outcrops of different thickness. In some cases the actual total thickness of the sequence is up to 2000 metres, but in other cases only some tens of metres appear in a continue succession (see Stewart and Poole, 2002; Poole et al., 2005 for a complete list of Palaeozoic outcrops and studies in Sonora).

In spite of the abundance of Palaeozoic fossils in the northwestern Sonora, Palaeozoic studies published until now mainly deal with their stratigraphy, paleogeography and/or geodynamic context. Paleontological associations, especially conodont associations, have been used in some of these studies, but only as tools for identifying the depositional environment or dating. Some of these studies include biostratigraphic summaries listing conodont species, relative abundance and age range, but detailed descriptions of such associations have not been published (e.g. Stewart et al., 1999).

The aim of this work is to summarize the latest advances in conodont research on the Palaeozoic rocks from Sonora, which include detailed biostratigraphic studies on nine sections that contain Ordovician, Upper Devonian, Mississippian, and Pennsylvanian sequences.

### GEOLOGICAL CONTEXT

Three main depositional environments or facies have been traditionally differentiated in the Sonoran Palaeozoic (Peiffer-Rangin, 1988, Stewart and Poole, 2002, and references therein). The most abundant outcrops of Palaeozoic rocks appear in central Sonora, and correspond to shallow-water facies, which were deposited at the southern continental margin of the North American craton. These rocks also appear, in a lesser extent, to the NW of the state. Ocean-basin rocks related to the Rheic Ocean crop out in the central part of Sonora and are known as the Sonora Allochthon. Cratonic facies of the North American Craton crop out to the northeast of the state and have been traditionally correlated to those that appear in the southwestern United States. In addition, Palaeozoic metasedimentary rocks have been described by some authors in southern Sonora (King, 1939, and references therein).

The major structural feature of the Sonoran Palaeozoic is the Sonora Allochthon. During the Upper Permian, deep-water sequences (Sonora Allochthon) were emplaced over carbonate shelf strata following the deposition of the middle Permian Mina Mexico flysch (Poole et al., 2005). This event is related to the Ouachita-Marathon Orogeny, which is the western continuation of the Variscan Orogeny in Europe.

## MATERIAL AND METHODS

This contribution sums up conodont biostratigraphic results obtained in nine geological sections measured in central and northern Sonora. Most of these studies have been conducted in the shallow-water facies outcrops, both in cratonic and the platform sequences: Arivechi (Morales Zuñiga, in prep., Reyes Montoya, in prep.), Cerro El Yugo (Borjas, in prep.), Cerros Las Pintas (Lara Peña, 2017), Cerro La Cueva (Ramos Martínez, 2016), Sierra Agua Verde (Navas-Parejo et al., 2015), Puerto del Orégano (Casarrubias López, 2015). The sections studied in the Mina de Barita and Maviro canyons (Navas-Parejo et al., 2016a, b) and the Cerro El Guayacán (Borjas, 2014, in prep) are located in the ocean basin sequence. More than 60 samples from these sections yielded conodonts after dissolution by standard procedures with acetic or formic acid.

## RESULTS

The conodont associations found in the samples from the shallow-water sequences show a relatively high biodiversity. In the Carboniferous section of the Sierra Agua Verde, nine genera and 13 species have been identified. In the Cerro La Cueva three genera and seven species of the Famennian have been found. Three genera and 13 species with a Famennian age have been found in the Cerros Las Pintas. In the Puerto del Orégano, one genus and one species were identified, which allows to date them as Mississippian. In Arivechi, three genera and three species from the Ordovician, and six genera and 10 species from the Famennian-Mississippian have been found.

The conodont associations obtained from the Upper Devonian deep-water successions are more abundant and show also a relatively high biodiversity, including 10 genera and more than 20 species.

## DISCUSSION

The conodonts in the studied sections allowed to identify several biozones of the Ordovician, the Upper Devonian, the Mississippian, and the Pennsylvanian of Sonora, Mexico. These dates include the Ordovician and the uppermost Devonian-lowermost Carboniferous (in Arivechi), the *rhenana* Zone (in the Cerro El Yugo), the *crepida* Zone (in the Minas de Barita area), the *rhomboidea* Zone (in the Cerro El Guayacán), the *expansa* Zone (in the Cerro Las Pintas), the upper Famennian (in the Cerro La Cueva), the upper Tournaisian-middle Viséan (in the Puerto del Orégano), and the Mississippian/Pennsylvanian boundary (in the Sierra Agua Verde).

## CONCLUSIONS

Further studies on conodont biostratigraphy of the Sonoran Palaeozoic sedimentary rocks may generate a relevant information that will allow a better understanding of the phylogeny, taxonomy and biofacies of the group. This is due to the abundance and relative biodiversity of these conodont associations, together with the presence of relatively close palaeoenvironments. Furthermore, these studies will shed light on the paleogeographic setting of the southwestern margin of Laurentia and their relation to the Rheic Ocean.

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## CA STABLE ISOTOPES PLACE DEVONIAN CONODONTS AS FIRST LEVEL CARNIVORES

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**Keywords:** Calcium isotope, conodont, trophic position, early vertebrates

Conodont animals are an extinct group of jawless vertebrates whose tooth-like elements represent the earliest evidence of a mineralized skeleton in the vertebrate lineage. Those hard parts, also known as conodont elements, are made of bioapatite and are interpreted as a feeding apparatus, which, together with the presence of large eyes and microwear patterns, support the hypothesis that conodonts were macrophagous predators and/or scavengers rather than suspensivores. Nevertheless, conodont physiology, functional morphology of the conodont feeding apparatus, and the relationship between the conodont morphological disparity and dietary specializations, remain poorly understood. Here, we use the calcium (Ca) stable isotope compositions of five conodont genera (*Palmatolepis*, *Polygnathus*, *Ancyrodella*, *Ancyrognathus* and *Icriodus*) from two marine successions of the Montagne Noire (France) to reconstruct their trophic position within Late Devonian marine ecosystems. Once calibrated with the contemporaneous seawater Ca isotope composition, our data indicate a zooplanktivore - primary piscivore niche for conodonts, possibly according to a genus-specific pattern. The question of active predatory or scavenging cannot be resolved definitively, but considering the anatomy of conodonts animals, especially the presence of large eyes, our results suggest that these animals were active first level consumers. Although calcium isotope datasets of modern world food chains will have to be augmented, our results set the stage for using Ca isotope compositions of phosphatic fossils as a tool to investigate the trophic structure of early vertebrate assemblages.





# **CARBONIFEROUS CONODONT STRATIGRAPHY, SEDIMENTOLOGY AND TECTONOTHERMAL ANALYSIS**





## UPPERMOST FAMENNIAN TO LOWER TOURNAISIAN STRATIGRAPHY AT BORKEWEHR NEAR WOCLKUM (NORTHERN RHENISH MASSIF, GERMANY)

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**Keywords:** Upper Devonian, conodonts, biostratigraphy, elemental geochemistry, Rhenish Massif, Germany

### INTRODUCTION

The Devonian/Carboniferous boundary was the first chronostratigraphic level, which was formally defined in 1935 (Second Heerlen Congress, proposal by Paeckelmann and Schindewolf published in 1937), using the entry of the index goniatite *Gattendorfia subinvoluta* in the Oberrödinghausen railway-cut (Hönne Valley, Rhenish Massif). Unfortunately, subsequent studies on the Rhenish Stockum Limestone (e.g. Alberti et al. 1974) proved that the selected stratotype section contains a hiatus right at the boundary level, at the base of the regional Hangenberg Limestone and the base of the *G. subinvoluta* Zone. This resulted in more than 15 years of intensive search for a new Devonian/Carboniferous definition and stratotype. Finally, the entry of the conodont *Siphonodella (Eosiphonodella) sulcata* was chosen as the Carboniferous index fossil and the new GSSP was placed in an oolitic succession at La Serre trench E' (Montagne Noire, southern France, Paproth et al. 1991). In the course of geochemical studies, Kaiser (2005, 2009) discovered that the index conodont occurs at La Serre already below the GSSP level, just above a facies break and a conodont-free interval (compare Feist et al. 2000, Aretz et al. 2016). Since there are no other criteria to correlate the GSSP level with precision, another revision became necessary in the frame of an International Devonian/Carboniferous Boundary Task Group. During a workshop in Montpellier (20.-22. September 2016), the task group voted to use the entry of *Protognathodus kockeli* as the future GSSP level. Therefore, the search for suitable successions that record in the immediate post-glacial and transgressive Upper Hangenberg Crisis Interval (Becker et al. 2016; Kaiser et al. 2015) the phylogenetic change from ancestral *Pr. collinsoni* to *Pr. kockeli* has become crucial.

### INVESTIGATED SECTION, MATERIAL, AND METHODS

The Borkewehr is the so far insufficiently studied type section of the Wocklum Limestone and of important uppermost Famennian index clymeniids adjacent to the Borkewehr near Wocklum (= old quarry on the SW slope of the Burgberg; e.g. Denckmann 1902; Paeckelmann 1924; Luppold et al. 1994). The Famennian and Lower Tournaisian of Borkewehr belong to a small outcrop belt along the southeastern axial ramp of the Remscheid-Altena Anticline, ca. 1 km ESE of the Balve village center (map sheet 4613 Balve).

Exposed along the forest track is a cyclic succession of mostly greenish-grey shales/marls and grey nodular limestones, the type Wocklum Limestone, which top part (beds -3 to -1) is especially rich in ammonoids,

including the old type-specimen of *Epiwocklumeria applanata*, the index of UD VI-D2. In two lateral successions, this unit is sharply overlain by 20 cm of very fissile Hangenberg Black Shale (Bed 0), followed by ca. 80 cm of more solid, greenish-grey, silty Hangenberg Shale/Sandstone equivalents (beds 1a-b). Its top 3 cm are dark-grey and marly (Bed 1c). The 11 cm thick beds 2-3 (see section log in Becker et al. 2016) are a somewhat unusual interval of thin-bedded to laminated, dark-grey limestones yielding acutimitoceratid impressions on bedding plans. The overlying alternating marls and nodular limestones are rather poor in macrofauna and show no obvious distinction between Stockum and Hangenberg Limestone levels. In the old quarry there is a fine exposure from the top Hangenberg Limestone through the basal Middle Tournaisian Lower Alum Shale Event Interval to the lower Viséan.

## CONODONT STRATIGRAPHY

So far, 21 micritic limestones have been sampled for conodonts. These provide sparse to moderately rich faunas, which enable the location of zonal boundaries and, most importantly, the evolutionary succession of species within the genus *Protognathodus*. As is common practice in stratigraphic conodont studies, only the Pa element taxonomy has been utilized, because many Famennian and Lower Carboniferous multi-element reconstructions are still doubtful. All Pa elements have been identified and counted. Thin-sections of each conodont-bearing layer were investigated for microfacies analyses and these give no hints for reworking processes.

The immediate pre-Hangenberg Event Interval (bed -3a to -1b) falls in the *Si. (Eo.) praesulcata* Zone. Bed -1b, the last nodular limestone of the Wocklum Limestone, yielded a rich, typical pre-extinction fauna with, amongst others, *Branmehla suprema*, *Mehlina strigosa*, *Neopolygnathus communis communis*, *Palmatolepis gracilis gracilis*, *Pa. gracilis expansa* M1, *Pa. gracilis sigmoidalis*, both morphotypes of *Bispathodus costatus* and *B. ultimus ultimus*, *B. spinulicostatus*, *Ps. marburgensis trigonicus*, *S. (Eo.) praesulcata*, and siphonodelloids. A sample from Bed 2 was barren, but Bed 3, the second platy limestone above the Hangenberg Shale/Sandstone equivalents, yielded *Pr. collinsoni* in association with opportunistic *Neo. communis communis*. This assemblage marks the top of the *costatus-kockeli* Interregnum. The first solid post-event nodular limestone (Bed 4b, true Lower Stockum Limestone) contains a joint *Pr. collinsoni-Pr. kockeli* assemblage of the *Pr. kockeli* Zone. Unusual is an occurrence of *Polygnathus restrictus*. A second *Pr. kockeli* Zone fauna occurs in Bed 5 and consists of *B. stabilis vulgaris*, *M. strigosa*, *Neo. communis phasphaenis*, *Po. purus purus*, *Pr. collinsoni*, and *Pr. kockeli*. A poor fauna from Bed 8 is not yet diagnostic but Bed 10 yielded *Si. (Eo.) aff. duplicata* and *Si. (Eo.) sulcata* s.l.

## ELEMENTAL GEOCHEMISTRY

A Czech working group led by TK investigated in 2016 the section for geochemistry. Element concentrations were measured by ED-XRF on pulverised samples taken from the Wocklum Limestone to the Lower Alum Shale (189 samples from 9.2 m thickness). The Hangenberg Black Shale revealed a short transgressive trend (marked by decreasing Zr/Al values) incorporated in an episode of general regression (Zr/Al increase), with its maximum within the Hangenberg Shale/Sandstone equivalents and related to the well-known glacio-eustatic fall. A transgressive character is noted in the higher portion of the extended Hangenberg Crisis Interval, from the Hangenberg Sandstone equivalents into the Stockum Limestone levels. K/Al values reveal a systematically decreasing trend in the Hangenberg Crisis Interval, which may indicate an increase in products of intensive

weathering. High values of Pb/Al and Zn/Al and low Mn/Al in the Hangenberg Black Shale are results of deposition during higher productivity and low oxygenation, characteristic for the Lower Hangenberg Crisis Interval on a world-wide scale.

## CONCLUSIONS

A new survey and re-sampling of Rhenish sections showed that there is only one succession with a well-exposed, easily accessible, sufficiently thick, and fossiliferous *Pr. kockeli* Zone (Lower Stockum Limestone), the Borkwehr near Wocklum. Current data suggest that the phylogenetic change from ancestral *Pr. collinsoni* to *Pr. kockeli* is recognizable in the first few transgressive limestones immediately after the siliciclastics of the glacioeustatic Hangenberg Regression. Therefore, it conforms to the recently decided criteria for the future Devonian/Carboniferous GSSP level.

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## A NEW DEVONIAN/CARBONIFEROUS BOUNDARY SECTION IN THE STRATOTYPE AREA (LA SERRE, MONTAGNE NOIRE, FRANCE)

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A new section is studied near the Devonian – Carboniferous Boundary (DCB) stratotype at La Serre trench E' (LS-E'). This La Serre trench C (LS-C) section is situated 200 m east of the present Global Stratotype Section and Point (GSSP). Though slightly different in thickness, the section is similar to LS-E', exposing a more fine-grained oolitic sequence, indicating a more distal deposition. In contrast to the stratotype section, the Hangenberg Black Shale (HBS) equivalent is well-developed below the regressive oolitic sequence.

The conodonts are recorded through the uppermost Famennian - lower Tournaisian interval for detailed biostratigraphy and give evidence for a range from the *Bispathodus ultimus ultimus* (= Upper *expansa*) Zone to at least the *Siphonodella jii* (= upper part of Upper *duplicata*) Zone.

Sedimentological evidence and conodont record allow fine-scaled laterally correlations with the LS-E' GSSP.





## LATE DEVONIAN – EARLY CARBONIFEROUS CONODONTS FROM THE NORTHEASTERN SIBERIA, ARCTIC RUSSIA

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**Keywords:** Conodonts, biostratigraphy, devonian, Tournaisian, Arctic Russia

### INTRODUCTION/BACKGROUND

Upper Devonian, Lower Carboniferous and Permian sequences are cropped out in Northern Kharaulakh Ranges (the lower reaches of the Lena River). They contain brachiopods, ammonoids, foraminifers and ostracods (Bogush et al., 1965; Bushmina, 1970; Abramov and Grigor'eva, 1986; Kashirtsev et al., 1966; and others). First discovery of Famennian conodonts was reported by Menner and Sidyachenko (1975). Recently new finds on Famennian and Tournaisian conodonts were done (Grakhanov et al., 2013; Yazikov et al., 2013; Izokh, Yazikov, in press). Those data significantly specified the Paleozoic stratigraphy of the Northern Kharaulakh.

### GEOLOGICAL CONTEXT

Upper Devonian and Lower Carboniferous sediments are exposed in large bluff outcrops along the lower Lena River and delta islands. Devonian-Carboniferous sediments crop out, respectively, in the crests of anticlines and in synclinal folds within the Verkhojansk uplift (megaanticlinorium). The area is heavily faulted and folded, consisting of large monoclinical and complex isoclinal blocks and westward recumbent folds. Many faults are of thrust geometry and are often superposed by later thrusts or oblique- and reverse-slip faults. The left bank of the Lena River belongs to the Lena trough which, in turn, is a part of the Verkhojansk Foredeep. In the northeast, the trough borders the uplifted Verkhojansk block along a large uplift fault with vertical displacement reaching a few kilometers (Gogina, 1979).

### MATERIAL AND METHODS

During the fieldwork in 2012, research team of the Trofimuk Institute of Petroleum Geology and Geophysics (Novosibirsk) studied the Devonian, Carboniferous and Permian deposits in the lower reaches of the Lena River delta. A total 240 of carbonate and siliciclastic-carbonate samples for conodonts were collected in the Stolb Island and the right bank of the lower reaches of Lena River. Microfossils were isolated from 0.4 to 4.0 kg samples dissolved in 5-7% acetic acid. Examination of insoluble rock residue revealed conodonts in 60 samples from the Orto-Khaya and the Stolb beds (Upper Devonian), the Bastakh and the Atyrdakh formations

(Lower Carboniferous). The collection of conodonts comprises well and quite well preserved black color (CIA =5-5.5) platform elements of genera *Ancyrolepis*, *Bispathodus*, *Icriodus*, *Lenathodus* nov. gen., *Mehlina*, *Mestognathus*, *Neopolygnathus*, *Nothognatella*, *Palmatolepis*, *Pelekysgnathus*, *Polygnathus*, *Pseudopolygnathus*, *Spathognathodus*, *Neoprioniodus*.

## RESULTS

Obtained new conodont data essentially completed paleontological characteristic of the Upper Devonian – Lower Carboniferous sediments in the lower reaches of the Lena River. Four Late Devonian conodont assemblages were recovered at the Stolb Island. The Orto-Khaya Beds includes very rare *Polygnathus*. The Stolb Beds contain three more abundant conodont assemblages. The first assemblage includes *Palmatolepis triangularis* Sann., 1955, *Pa. praetriangularis* Z. & Sandb., 1988, *Palmatolepis delicatula* Br. & M., 1934, *Icriodus alternathus alternathus* Br. & M., 1934, *I. alternathus helmsi* Sandb. & Dreesen, 1984, *I. costatus* (Thomas, 1949), and other, of the triangularis Zone.

The second assemblage contains *Ancyrolepis cruciformis* Ziegler, 1959, *Icriodus alternathus alternathus* Br. & M., 1934, *Polygnathus nodocostatus* Br. & M., 1934, *Palmatolepis regularis* Cooper, 1931, *Pa. quadrantinosalobata* Sann., 1955, *Pa. perlobata schindewolfi* Muller, 1956, *Pelekysgnathus planus* Sann. 1955 *u* *Mehlina* sp. and other. This association could be correlated with the *crepida* Zone.

Stratigraphically the upper most assemblage comprises *Palmatolepis tenuipunctata* Sannemann, 1955, *Pa. glabra glabra* Ulrich & Bassler, 1926, *Pa. minuta loba* Helms, 1963, *Pa. minuta minuta* Br. & M., 1934, *Polygnathus semicostatus* Br. & M., 1934. The upper part of studied section in Stolb Island could be correlated with the base of the *rhomboidea* Zone.

The late Tournaisian assemblages of conodonts discovered in the type sections of the Upper Bastakh Member and the lower Atyrdakh Formation (Izokh, Yazikov, 2017, in press). The collection includes a new species of the *Lenathodus* nov. gen., a new subspecies of *Neopolygnathus communis*, as well as shallow-water cosmopolitan representatives of the genera *Neopolygnathus*, *Bispathodus*, *Pseudopolygnathus*, *Mestognathus*, *Spathognathodus* and *Neoprioniodus*.

The lowest assemblage comprises *Neopolygnathus communis communis* (Br. & M., 1934), *N. communis yazikovi* Izokh, nov. ssp., *Bispathodus aculeatus aculeatus* (Br. & M., 1934), and *Mestognathus* sp. This assemblage characterizes the *isosticha* – Upper *crenulata* Zone or event to a younger biozone.

The second assemblage includes *Mestognathus praebeckmanni* Sandberg et al., 1986, *Bispathodus aculeatus aculeatus* (Br. & M., 1934), *Spathognathodus* sp., *Neopolygnathus communis communis* (Br. & M., 1934), *N. communis yazikovi* Izokh, nov. ssp., *Pseudopolygnathus multistriatus* Mehl & Thomas, 1947 Morphotype 1, *Neoprioniodus* cf. *N. scitulus* (Br. & M., 1940).

The third conodont assemblage from the upper part of the Upper Bastakh Member includes a new genus and species. The *Lenathodus bakharevi* nov. gen. et sp. co-occurs with *Neopolygnathus communis communis* (Br. & M., 1934), *Pseudopolygnathus multistriatus* Mehl & Thomas, 1947 Morphotype 1, *Bispathodus aculeatus aculeatus* (Br. & M., 1934) and *Spathognathodus?* sp.

## DISCUSSION

The Late Devonian – Early Carboniferous conodont assemblages contain mainly cosmopolite taxa. At the Stolb Island the early Famennian assemblages characterize from the *triangularis* to Lower *rhomboidea*

zones. Similar the early Famennian conodonts were reported from the West Taimyr (Atlas..., 2003; Yolkin et al., 2006), the Selenyakh Ridge at the Chersky mountain system (Tarabukin et al., 1997). No conodonts were found in the middle and upper Famennian deposits in the Arctic region so far.

The Early Carboniferous conodonts are very rare in the eastern Arctic Russia and have been limited to Tournaisian of the Taimyr Peninsula (Aristov, 1988; Atlas..., 2003) and the northwestern Chersky Range (Indigirka River drainage basin) (Tarabukin et al., 1997).

The late Tournaisian assemblage was found in the Upper Bastakh Member of the Northern Kharaulakh and provided biostratigraphic constraints within zones: the *isosticha*-Upper *crenulata* Zone – the *anchoralis-latus* Zone. The new conodont data allow updating the Lower Carboniferous stratigraphy of the Northern Kharaulakh and cast doubt on the assignment of the Lower Bastakh Member to the entire lower Tournaisian.

## CONCLUSIONS

The new data of the Late Devonian conodonts in the Stolb Island in the Lena delta and the late Tournaisian conodonts in the Upper Bastakh Member provide more reliable base for inter-regional correlations of units of the Upper Devonian-Lower Carboniferous stratigraphic chart for the Northern Kharaulakh. Conodont biostratigraphic analysis suggests correlation of the Stolb Beds to the lower Famennian interval from the *triangularis* to *rhomboidea* zones and the Upper Bastakh Member within the upper Tournaisian *isosticha*-Upper *crenulata* – *anchoralis-latus* zones.

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## NEW EARLY TOURNAISIAN (MISSISSIPPIAN) SIPHONODELLID CONODONTS FROM THE RHENOHERCYNIAN ZONE

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**Keywords:** Rhenish Massif, Bohemian Massif, biostratigraphy, *Siphonodella*

### INTRODUCTION

Conodonts of genus *Siphonodella* are one of the most important index fossils for biostratigraphy of lower Tournaisian marine deposits. Siphonodellids are abundant in pelagic Tournaisian successions, where occur orally ornamented species, used for siphonodellid zonation sensu Sandberg et al. (1978), emended by Ji (1985) and Becker et al. (2016). Siphonodellids without oral ornamentation were subsequently described from neritic successions of Southern China and Urals, accompanied by rare "pelagic" species, which allows correlation between pelagic and neritic zonations (Ji - Ziegler 1992, Qie et al. 2014). Devonian/Carboniferous boundary beds in the Remscheid-Altena Anticline (Rhenish Massif, Germany) and in the Moravian Karst (Bohemian Massif, Czech Republic) have been studied using high-resolution conodont stratigraphy. New lower Tournaisian siphonodellids without ornamentation on oral platform side were recorded here from the pelagic and turbiditic successions.

### GEOLOGICAL CONTEXT

The studied Devonian-Carboniferous sections Oberrödinghausen, Oese and Haselbachtal are situated in the Remscheid-Altena Anticline of the northern Rhenish Massif and sections Lesní lom and Křtiny in the Moravian Karst Palaeozoic of the eastern Bohemian Massif. Both sequences belong to Variscan Rhenohercynian Zone, which represents remains of the Rhenohercynian Basin at southern Laurussian margin. Upper Famennian and Lower Tournaisian succession of the Remscheid-Altena Anticline is characterised by outer shelf nodular limestones with siliciclastic intercalation of the Hangenberg Events deposits. Upper Famennian and Lower Tournaisian of the Moravian Karst reveal two facies development: monotonous nodular limestone succession of upper slope and calciturbiditic succession of the lower slope with well-developed Hangenberg Events.

### RESULTS AND DISCUSSIONS

*Siphonodella* (*Si.*) *belkai* previously unknown from western Europe is the most abundant species among the unornamented siphonodellids. This conodont was previously recorded from the lower Tournaisian of east-

ern European and Uralian regions (e.g. Dzik 1997, Pazukhin 2009, Plotitsyn - Zhuravlev 2016), and is the index fossil of the eponymous *belkai* conodont Zone distinguished in these regions (Pazukhin 2009). Problems in the determination of *Si. (Si.) belkai* existed in literature. Before *Si. (Si.) belkai* has been defined by Dzik in 1997, specimens belonging to *Si. belkai* were often assigned for example to *Si. (Si.) obsoleta*, *Si. (Si.) sandbergi*, or *Si. (Si.) quadruplicata* due to a sudden ventral narrowing of *Si. (Si.) belkai* platform, and for the presence of more than three rostral ridges, which is characteristic also for *Si. (Si.) sandbergi* or *Si. (Si.) quadruplicata*. Such determinations partly led to stratigraphic misinterpretations. Furthermore, the incomplete specimen of the *Si. (Si.) belkai*-holotype established by Dzik (1997), and juvenile specimens considering by the author, hampered a precise recognition of the rostral-ridge arrangements, which were observed in studied material. Therefore, based on the arrangement of the rostral ridges, two morphotypes of *Si. (Si.) belkai* Dzik are defined. In addition, a new unornamented siphonodellid species *Si. (Si.) kalvodai* sp. nov. has been described from the Moravian Karst. Its occurrence was previously documented from the *crenulata* Zone in Tajikistan (*Siphonodella* sp. nov. B, Bardascheva et al. 2001).

*Si. (Si.) belkai* is accompanied by "standard" conodonts typical for the *jii* (= formerly *hassi* or Upper *duplicata* Zone), *sandbergi* and *quadruplicata* conodont zones from pelagic settings in the Rhenish Massif and Moravian Karst. The new fauna thus occurs in the *jii* (= formerly *hassi* or Upper *duplicata* Zone), *sandbergi* and *quadruplicata* conodont zones. FAD of *Si. (Si.) belkai* M1 and M2 is in the basal *jii* Zone in the studied regions. The *jii* Zone base can therefore be correlated with the base of the *belkai* Zone of the East European platform and Uralian Mountains. It results in a more precise correlation of lower Tournaisian biozones of N-America, European, east European and Uralian regions.

Unornamented siphonodellids are minor constituent of siphonodellid-polygnathid biofacies in studied sections. This biofacies is typical for an upper part of the lower Tournaisian of many regions, at least in Laurussia, peri-Gondwana or Southern China, where occurs both in distal and proximal facies of carbonate ramps and shelves. It implies low bathymetric dependency of siphonodellid-polygnathid biofacies. On the other hand, occurrences of diverse unornamented siphonodellid faunas are tied to siphonodellid-polygnathid biofacies only in Siberian and northern Paleotethys realms, showing their provincialism. Only *Si. (Si.) belkai* accompanied by other rare unornamented siphonodellids occur in western Paleotethys realm (Rhenohercynian Basin). Migration of unornamented siphonodellids into the Rhenohercynian basin may have passed from the southern Uralian sea-ways from eastern regions. On the other hand, unornamented siphonodellids were not able to migrate to peri-Gondwanian terranes, probably isolated by a cold ocean (Isaacson et al. 2008). Their absence in North American Realm is questionable, because specimens of *Si. (Si.) belkai* could be confused with another siphonodellid.

## CONCLUSIONS

The new lower Tournaisian unornamented siphonodellid conodonts were recorded from the Rhenohercynian Zone (Rhenish and Bohemian massifs). Two morphotypes of *Si. (Si.) belkai*, as well as new species *Siphonodella (Si.) kalvodai* nov. sp. are established based on new material and revision of published data. *Si. (Si.) belkai* has its FAD in the basal *jii* Zone in both Rhenohercynian regions. The *jii* Zone can therefore be correlated with the *belkai* Zone of the East European platform and Uralian Mountains. It results in a more precise correlation of lower Tournaisian biozones of N-America, European, east European and Uralian regions. Distribution of unornamented siphonodellids indicates their north Paleotethys Realm provincialism.

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## LOWER CARBONIFEROUS CONODONTS FROM TELLEGO SECTION (ASTURIAS, SPAIN): COMMENTS ON *LOCHRIEA* SPECIES

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**Keywords:** *Lochriea*, Viséan-Serpukhovian boundary, Spain

### INTRODUCTION

The Tellego section (Cantabrian Mountain, Spain) exposes cherts and limestones. It belongs to the Alba Formation (Viséan-Serpukhovian, Lower Carboniferous). Sedimentological and biostratigraphical studies were carried out, based on conodont content.

Ornamented *Lochriea* are a clue for the stratigraphy of Viséan - Serpukhovian stages, that's why the study focuses particularly on this genus.

### MAIN RESULTS

Most conodonts recovered belong to genera *Gnathodus*, *Vogelgnathus* and *Lochriea*, regarded as deep-water dwellers. Sedimentological study confirms inner ramp deposits.

*Lochriea* specimens are abundant in this section, especially ornamented *Lochriea* species. The species *L. ziegleri*, which is regarded as the most suitable index taxon for recognition of a revised Viséan-Serpukhovian boundary is also useful.

These *Lochriea* species are markedly informative in this section. Some species as *L. saharae* show their extended stratigraphical range and also, a new species is presented. Moreover, the study of the other elements of the *Lochriea* apparatus shows that the M elements, easily recognisable for *Lochriea* genus, present different morphologies that may correspond to different species. Thus, these M elements can be considered as a particular tool in discriminating *Lochriea* species.

### CONCLUSIONS

The recognition of Viséan-Serpukhovian boundary is a special interest, with recent proposals of GSSP for the base of the Serpukhovian Stage. Studies of ornamented *Lochriea* species are basically useful in this context. The discrimination of *Lochriea* species based on M elements may also be useful in few productive carboniferous samples.





## STUDY PROGRESS ON THE CANDIDATE GSSP OF THE VISEAN-SERPUKHOVIAN BOUNDARY IN SOUTH CHINA

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**Keywords:** Conodont, GSSP, Viséan, Serpukhovian, South China

### INTRODUCTION

The Task Group to establish a GSSP close to the existing Viséan–Serpukhovian (V/S) boundary was created in 2002 (Heckel, 2002; Richards, 2003). Significant progress toward selecting a basal Serpukhovian GSSP has been achieved since then. Before evaluation of potential GSSP sites, the Task Group had to decide on the biostratigraphical tool with which to identify the boundary. Candidate fossil groups were ammonoids, conodonts and foraminifera. By 2005, the most-favoured group was conodonts; in particular, an evolutionary lineage within the genus *Lochriea* was considered to offer the best possibility of providing a tool to identify the boundary.

The genus *Lochriea* contains about eleven species, including: *Lochriea commutata* (BRANSON AND MEHL, 1941), *Lochriea costata* (PAZUKHIN AND NEMIROVSKAYA, in Kulagina et al., 1992), *Lochriea cracoviensis* (BELKA, 1985), *Lochriea cruciformis* (CLARKE, 1960), *Lochriea monocostata* (PAZUKHIN AND NEMIROVSKAYA, in Kulagina et al., 1992), *Lochriea mononodosa* (RHODES, AUSTIN AND DRUCE, 1969), *Lochriea multinodosa* (WIRTH, 1967), *Lochriea nodosa* (BISCHOFF, 1957), *Lochriea saharæ* NEMYROVSKA, PERRET-MIROUSE AND WEYANT, 2006, *Lochriea senckenbergica* (NEMIROVSKAYA, PERET AND MEISCHNER, 1994) and *Lochriea zieglerei* (NEMIROVSKAYA, PERET AND MEISCHNER, 1994). The evolutionary relationships among most of these species are well studied in South China sections (Qi, 2008; Qi et al., 2014) and the evolution of the *Lochriea* species has great potential for stratigraphic application. Morphological trends within the genus *Lochriea* from simple unornamented to complex sculptured forms have been recognized in many sections in Europe and Asia (Nemirovska et al., 1994; Skompski et al., 1995; Pazukhin et al., 2009; Qi et al., 2014). The evolutionary appearance of strongly ornamented species of *Lochriea* has been regarded to be of great importance for the definition of the base of the Serpukhovian Stage and for the correlation of the V/S boundary.

Members of the Task Group agree that the evolutionary appearance of the conodont *Lochriea zieglerei* Nemirovska, Perret, and Meischner, 1994 in the lineage *Lochriea nodosa*–*Lochriea zieglerei* is the best biostratigraphic event for marking the boundary, although this marker still awaits formal ratification. *Lochriea zieglerei* appeared near the middle of the Brigantian Substage in Western Europe, at a level that is correlated to slightly below the base of the type Serpukhovian Stage in the Moscow Basin and at a substantially lower horizon than the lower boundary of the Namurian Stage in Western Europe (Sevastopulo & Barham, 2014).

When formally adopted, the new basis for defining the V/S boundary will mean that rocks previously regarded as upper Visean will become lower Serpukhovian. The *L. nodosa*–*L. ziegleri* lineage is best developed in relatively deep-water sections and has been identified at several sites in Western Europe, Russia, and China (Nemirovskaya et al., 1994; Skompski et al., 1995; Wang and Qi, 2003; Qi and Wang, 2005; Nemyrovska, 2005; Nikolaeva et al., 2005, 2009; Pazukhin et al. 2010; Groves et al., 2012; Qi et al., 2010, 2014). The lineage has not been documented in cratonic North America, but several relatively long-ranging species including *L. nodosa* (Bischoff, 1957) have been reported there under the genus *Paragnathodus*, a junior synonym of *Lochriea* (Lane and Brenckle, 2005; Groves et al., 2012). A single specimen of *L. ziegleri* was identified from the Barnett Formation at the J. R. Walker Ranch, central Texas, North America (Qi et al., 2010; Richards, 2010), thus, correlation of the V/S boundary between Eurasia and North America is possible.

## PROGRESS STUDY IN SOUTH CHINA

Carboniferous marine sediments are widely distributed and well developed in South China, where they form continuous sequences of marine carbonates that contain conodonts and foraminifera. The Naqing section is the most-studied section across the V/S boundary in South China. Abundant conodonts from Late Visean–Early Serpukhovian deposits of the Naqing section include numerous elements related to cosmopolitan species of *Gnathodus*, *Lochriea* and *Pseudognathodus*; *Vogelgnathus* and *Mestognathus* are also common. In this section, numerous P1 elements of *Lochriea* species are found, and their evolutionary lineages are quite clear with many transitional forms within each lineage. Two lineages are herewith proposed: 1) noded *Lochriea* species, such as *L. mononodosa*–*L. nodosa*–*L. ziegleri*, *L. senckenbergica* and *L. multinodosa*, and 2) ridged *Lochriea* species such as *L. monocostata*–*L. costata*–*L. cruciformis*.

In the Naqing section, the evolutionary lineage of *Lochriea nodosa* – *L. ziegleri* with many transitional specimens between the taxa seems to be quite reliable, therefore, it has the greatest potential to be used for defining the Visean–Serpukhovian boundary. In addition, the entry of strongly ornamented *L. ziegleri* is widespread in Eurasia as well as in North America. Furthermore, this species is easily recognizable and more numerous elsewhere than the other strongly ornamented *Lochriea* species. Thus, the FAD of *Lochriea ziegleri* is the best marker for the base of the global Serpukhovian Stage.

Foraminiferal successions across the V/S boundary in the type area of the Serpukhovian Stage (Moscow Basin, Russia), elsewhere in Russia, and in the central United States suggest that the appearances of *Asterochaediscus postrugosus*, *Janischewskina delicata*, *Eolasioidiscus donbassicus*, and specimens controversially referred to "*Millerella tortula*" are reliable, auxiliary indices to the base of the Serpukhovian (Groves et al., 2012; Kulagina et al., 2012). In southern Guizhou Province, China, Visean–Serpukhovian stratigraphic sequences from slope and platform settings have also yielded rich associations of foraminifera. The foraminiferal zone - *Janischewskina delicata* Zone (62.25–70.15 m) is identified in the Naqing section. The first occurrence of *Janischewskina delicata* marks the base of this zone. This nominal species is usually used as reliable marker for the Serpukhovian Stage. It is widely distributed in deep- and shallow-water carbonates in South China. This species occurs 2.15 m above the FAD of *L. ziegleri* (60.1m) at this section.

In addition, Chen et al. (2015) reported a high-resolution  $\delta^{13}\text{C}$  chemostratigraphy and detailed sedimentary facies of late Visean–early Serpukhovian carbonate platform-to-slope successions in southern Guizhou, South China. Multiple negative  $\delta^{13}\text{C}$  excursion ( $>1\text{‰}$ ) can be correlated across the V/S boundary interval in several slope sections including the Naqing, Luokun, and Narao sections. A long-term decrease in  $\delta^{13}\text{C}$  values through the Serpukhovian of the Yashui section likely records local influences on carbon cycling in a

restricted platform setting. This negative  $\delta^{13}\text{C}$  trend and associated depositional facies at the Yashui section can be correlated to the Arrow Canyon section, USA, which, together with other coeval global sedimentary and geochemical records, indicates a widespread eustatic drawdown in the late Viséan with initial buildup of Gondwanan ice sheets. They conclude that integrated sedimentary facies analysis and  $^{13}\text{C}$  chemostratigraphy can be used for stratigraphic correlation when interpreted within a well-constrained sedimentary and carbon-isotope regional framework.

## CONCLUSIONS

A synthetic study on biostratigraphy, sedimentology and geochemistry of the upper Viséan to Serpukhovian succession in South China was undertaken in order to comprehensively understand the evolutionary change of the biota and global correlation around the Viséan/Serpukhovian boundary. In addition, several volcanic ash beds have been collected from the Naqing section and await dating.

## Acknowledgements

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# MISSISSIPPIAN TO EARLY BASHKIRIAN CONODONTS FROM AN EXPOSED SHALLOW-WATER CARBONATE PLATFORM IN THE PICOS DE EUROPE UNIT, SPAIN

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**Keywords:** Conodont, Carboniferous, shallow-water, Cantabrian Mountains, Spain

## INTRODUCTION AND GEOLOGICAL CONTEXT

Nodular cephalopod limestone facies show a ubiquitous distribution in the Mississippian of the Variscan foreland basin in the northern Spain (from the Cantabrian Mountains to the Pyrenees). It yields abundant conodonts studied by a lot of authors (Lane et al., 1980; Higgins and Wagner-Gentis, 1985; among others). The occurrence of derived shallow-water carbonate platform components (conodonts, foraminifers, algae, corals, brachiopods, ...) in beds interbedded in the nodular limestone facies (Cózar et al., 2015, 2016) at the Vegas de Sotres locality of the Picos de Europa tectonic unit guided the search of an unknown shallow-water carbonate platform in the Cantabrian Mountains (Fig. 1). The conodont fauna here described, together with studies on other fossil groups (particularly foraminifers) are allowing recognized the extension and age of this carbonate platform.

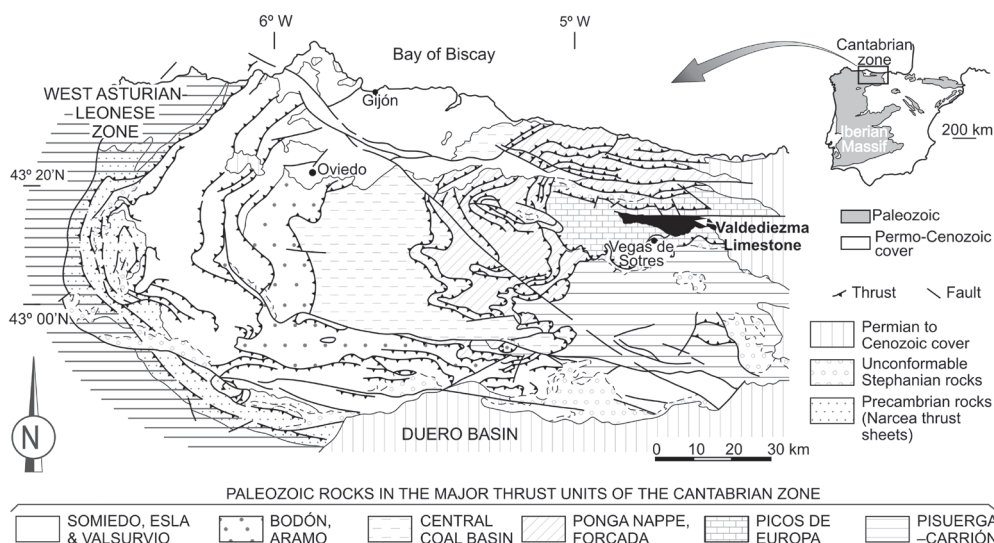


Fig. 1. Geological sketch of the Cantabrian zone showing the major tectonic units and the location of the outcrops of the Valdediezma Limestone in the Picos de Europa unit.



The Picos de Europa unit is located in the core of the Asturian arc and correspond to the younger Late Pennsylvanian emplaced thrust in the Cantabrian foreland basin. The stratigraphic succession consists of Late Famennian sandstones deposited through a regional unconformity above middle Cambrian to Lower Ordovician rocks. Sandstones are replaced by crinoidal limestones and a deep basinal sedimentation of reddish nodular limestones of the Alba Formation. This formation, 20–30 m thick, corresponds to a condensed interval deposited from the late Tournaisian to the late Serpukhovian (from the *Scaliognathus anchoralis* to the *Gnathodus truyolsi* Conodont zones according to Sanz-López and Blanco-Ferrera, 2012). Above, the Barcaliente Formation consists of late Serpukhovian to early Bashkirian dark, often laminated and with abundant organic matter limestone. Thickness is variable between 70 and 350 m, and its deposition coincided with the arrival of siliciclastic supplies from the Variscan hinterland at the western margin of the Cantabrian foreland. The Valdeteja Formation consists of Bashkirian to early Moscovian white colour limestone with bioclastic beds deposited in a carbonate ramp according to Bahamonde et al. (2007), where massive microbial carbonates were common in the internal zone. The Picos de Europa Formation consists of 500–700 m thick of light, usually bioclastic limestones forming a giant Moscovian platform.

## MATERIAL AND METHODS

A study led to get a map of distribution of the colour alteration index of conodonts showed an area of the Picos de Europa unit where conodont data are inconsistent with information included in the published geological maps (Blanco-Ferrera et al. 2016). Concretely, Bashkirian–Moscovian rocks yielded Viséan–Serpukhovian conodonts. Consequently, new samples for conodonts and foraminifers were collected through geological map revision and study of several partial stratigraphic sections. Seventy carbonate samples, five to ten kilos per sample, have been processed through standard techniques to obtain conodonts in laboratory.

## RESULTS

Conodonts and foraminifers from a new lithostratigraphic unit, the Valdediezma Limestone, correspond to late Tournaisian to early Bashkirian in age. This limestone crops out in several tectonic units of the eastern part of the Main imbricate of the Picos de Europa unit. The Valdediezma Limestone is defined for carbonate rocks, usually light in colour with varied shallow-water bioclasts. It is similar in facies to the younger Valdeteja and Picos de Europa formations, and, in the field, rock limestone is homogenized by surface weathering. The preserved thickness could be overpassing 800–900 m. The base of the unit is always faulted and above middle Cambrian rocks. The top corresponds to an erosive unconformity below beds of the Picos de Europa or younger formations. The units 2 and 3 of Blanco-Ferrera et al. (2008; see Cózar et al. 2015, 2016) at the Vegas de Sotres section are included as a wedge deposited to the basin from the platform of the Valdediezma Limestone. These units consist of a ten of meters of graded bioclastic limestone with intraclastic horizons in the Alba Formation and only are known in the southwards thrust sheets near the outcrops of the Valdediezma Limestone with kilometric thickness. Twenty-seven samples of the Valdediezma Limestone yielded conodonts. Diversity and abundance is low in comparison with samples studied in the Alba Formation. Basal beds yielded conodonts *Gnathodus pseudosemiglaber*, *Pseudopolygnathodus pinnatus*, '*Spathognathodus*' *macer* (Fig. 2e–f), together with *Hindeodus regularis* and *H. pulcher* (Fig. 2c). It is correlated with the late Tournaisian *Scaliognathus anchoralis* Conodont Zone or the early Viséan *Pseudognathodus homopunctatus* Zone (late Tournaisian to early Viséan). One to a few elements per sample of *Hindeodus regularis* (Fig. 2d–e) are recorded in beds considered middle Viséan. Late Viséan samples show locally a moderate diversity including

*Adetognathus* sp. (Fig. 2k), *Diplognathodus* sp. (Fig. 2f–g), *Gnathodus bilineatus*, *G. joseramoni*, *G. millarensis*, *G. pseudosemiglaber*, *G. truyolsi* (Fig. 2l), *Hindeodus cristula* (Fig. 2g–h), *Idioprinioides* sp., *Kladognathus* sp., *Lochriea commutata*, *Lochriea costata*, *L. monocostata*, *L. mononodosa*, *L. multinodosa*, *L. nodosa*, *L. saharae*, *L. ziegleri* (Fig. 2n), *Pseudognathodus homopunctatus*, *Ps. symmutatus*, *Vogelgnathus campbelli*, *V. cantabricus* (Fig. 2j) and *V. postcampbelli*. A lower Bashkirian bed yields *Declinognathodus lateralis* (Fig. 2m).

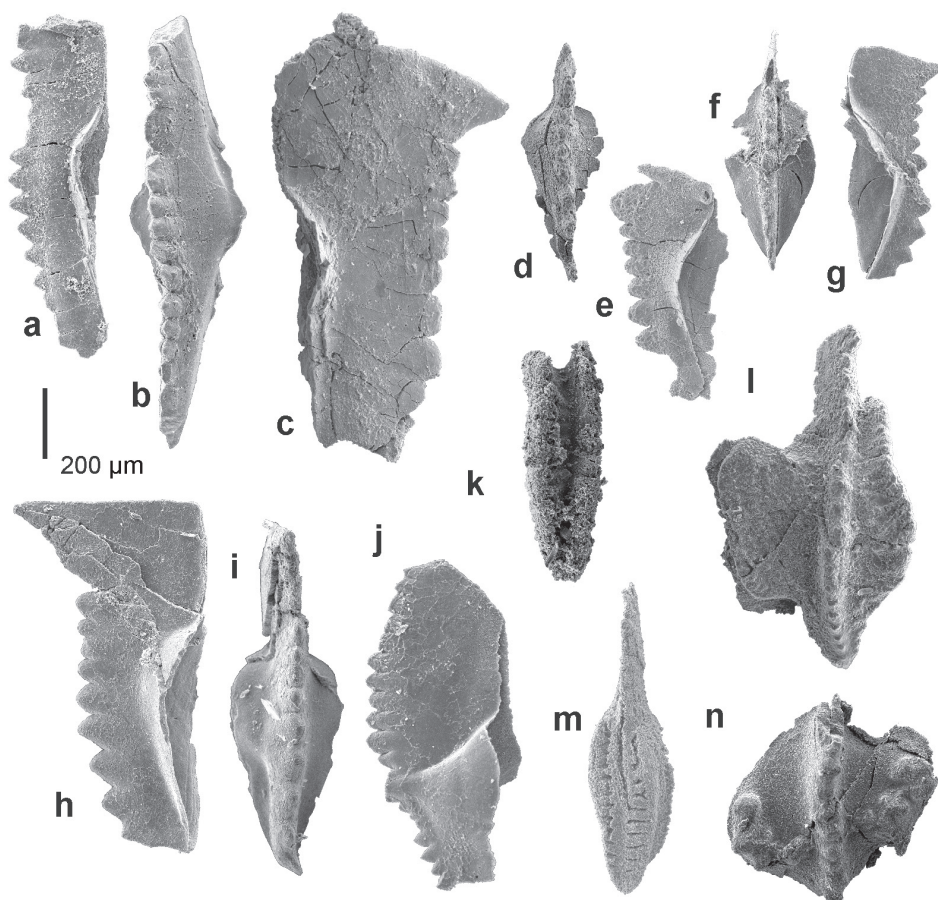


Fig. 2. SEM micrograph pictures of P1 elements of selected conodonts from the Valdediezma Limestone. Bar scale is 200  $\mu\text{m}$ . (a–b) "*Spathognathodus*" *macer* (Branson and Mehl), specimens DGO 15520–15521 from sample CPE-122. (c) *Hindeodus pulcher* (Branson and Mehl), specimen DGO 15516 from sample CPE-122. (d–e) *Hindeodus regularis* Branson and Mehl, oral and lateral views of specimen DGO 15538 from sample Sotres-4. (f–g) *Diplognathodus* sp., latero-aboral and oral views of DGO 15544 from sample VZM-3. (h–i) *Hindeodus cristula* (Youngquist and Miller), DGO 15543 from sample VZM-3. (j) *Vogelgnathus cantabricus* Nemyrovskaya, specimen DGO 15507 from sample CPE-111. (k) *Adetognathus* sp., specimen DGO 15553 from sample VZM-15. (l) *Gnathodus truyolsi* Sanz-López, Blanco-Ferrera, Sánchez de Posada and García-López, specimen DGO 15524 from sample CPE-245. (m) *Declinognathodus lateralis* (Higgins and Bouckaert), DGO 15549 from sample VZM-12. (n) *Lochriea ziegleri* Nemirovskaya, Perret and Meischner, specimens DGO 15513 from sample CPE-119.

## DISCUSSION

The Valdediezma Limestone yields conodonts from the late Tournaisian to the early Bashkirian and is correlated with the Alba and Barcaliente formations deposited in the basin and described in the rest of the Cantabrian Mountains. The conodont faunas from the Valdediezma Limestone include a component of shallow-water dwellers such as *Hindeodus cristula*, *H. pulcher*, *H. regularis*, *Diplognathodus* sp. and *Adetognathus* sp. in coincidence with lithological facies. The oldest European occurrence of *Diplognathodus* sp. is noticeable, since it only is known in Viséan beds of the Windsor Group in the Atlantic Canada (von Bitter and Plint-Geberl 1982). These shallow-water conodonts are together with taxa considered deeper water, such as species of *Gnathodus*, *Lochriea* and *Vogelgnathus*, particularly in late Viséan to Serpukhovian samples. *Hindeodus cristulus*, *Synclydognathus* sp. and species of *Mestognathus* were described as a minor component in prevailing deep-water faunas of the units 2 and 3 interbedded in the Alba Formation at the Vegas de Sotres section (Blanco-Ferrera et al., 2009).

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## MID-CARBONIFEROUS CONODONTS AND THEIR EVOLUTION: NEW EVIDENCES FROM LUODIAN, SOUTH CHINA

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**Keywords:** Mid-Carboniferous, Early Pennsylvanian, conodonts, evolution, South China

### INTRODUCTION

*Declinognathodus noduliferus* (Ellison & Graves, 1941) *sensu lato* was selected as the index for the mid-Carboniferous boundary (MCB) at the 10<sup>th</sup> International Congress of Carboniferous Stratigraphy and Geology (1983) in Madrid. The Global Stratotype of Section and Point (GSSP) for the MCB was placed in Arrow Canyon, Nevada, U.S.A. defined by the first occurrence of *D. noduliferus* within the lineage *Gnathodus girtyi simplex*-*D. noduliferus* (Lane *et al.*, 1999). *Declinognathodus noduliferus* comprises a group of related species/subspecies: *D. n. inaequalis* (Higgins, 1975), *D. n. noduliferus*, *D. n. japonicus* (Igo & Koike, 1964) and *D. lateralis* (Higgins & Bouckaert, 1968). Later, *D. praenoduliferus* Nigmadganov & Nemirovskaya (1992) and *D. n. berneseae* Sanz-López *et al.* (2006) were also included in this taxonomic plexus. The subspecies of *D. noduliferus* were subsequently regarded as discrete species by most conodont workers Nemirovskaya & Alekseev (1995), Mizuno, (1997), Kulagina *et al.* (2000), Wang & Qi (2003), and Sanz-López *et al.* (2013). By nodose or ridged parapets on P<sub>1</sub> elements, *Declinognathodus* species can be differentiated to nodose and ridged groups. The nodose group, i. e., *D. noduliferus*, *D. inaequalis* and *D. japonicus*, are characterized by nodose parapets/parapet and a groove extending to the dorsal end. The younger late Bashkirian and early Moscovian species *D. marginodosus* (Grayson, 1984) and *D. donetzianus* (Nemirovskaya, 1990) belong to this group as well. The ridged group, consisting of *D. praenoduliferus*, *D. berneseae*, *D. lateralis* and *D. pseudolateralis*, are typified by ridged parapets. In addition, a groove that does not extend to the dorsal end is also a characteristic feature of the former two species. The new species *Declinognathodus* sp. A and *D.* sp. B are placed in the ridged group.

Numerous evolutionary schemes have been proposed for the early Pennsylvanian conodont genera *Declinognathodus*, *Idiognathoides*, *Idiognathodus* and *Neognathodus* by Dunn (1970, 1971), Straka & Lane (1970), Lane & Straka (1974), Lane *et al.* (1985), Grayson *et al.* (1990), Nemirovskaya & Nigmadganov (1994), Nemirovskaya (1999) and Sanz-López & Blanco-Ferrera (2013). In these schemes (Fig. 1A), *Gnathodus girtyi simplex* Dunn (1965) and *G. bilineatus* (Roundy, 1926) were treated as the most likely ancestors of *Declinognathodus*. *Idiognathodus* was regarded as a direct descendent of *Declinognathodus*, probably *D. lateralis*. The origin of *Idiognathoides* was debatable. Many taxa, such as *G. defectus*, *Declinognathodus*, *G. bilineatus*, *G. postbilineatus* and *D. berneseae*, were regarded as possible ancestors of *Idiognathoides*. While *G. girtyi* was less controversial as the precursor of *Neognathodus*.

To better understand the evolution and international correlation of the mid-Carboniferous conodonts in South China, we investigated the MCB interval of two deep-water sections at Naqing and Luokun.

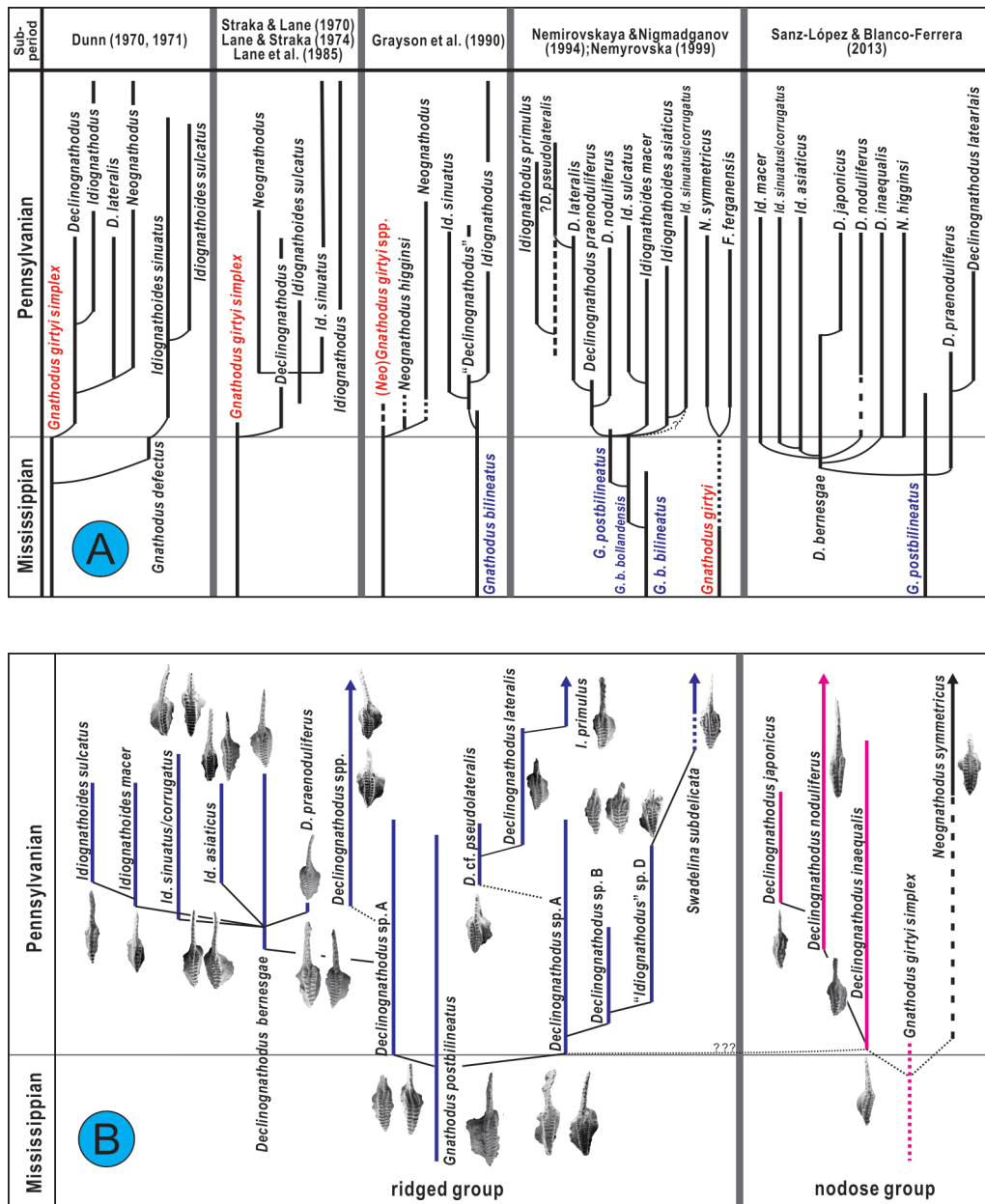


Fig. 1. A, Previously proposed evolutionary patterns of mid-Carboniferous conodonts. B, Evolutionary pattern of mid-Carboniferous conodonts from South China.

## GEOLOGICAL CONTEXT

Detailed geological setting of the study sections can be found in Qi et al. (2014) and Hu et al. (2017).

## MATERIAL AND METHODS

Limestone samples, one-hundred and four from the Naqing section and twenty-four from the Luokun section, were treated with acetic acid followed by separation with solution of lithium heteropolytungstates (LST heavy liquid). Thousands  $P_1$  elements were recovered from these samples. Forty-seven species/subspecies, including seven undetermined forms, assigned to fourteen genera were identified (Fig. 2). The conodont fauna throughout the study interval is dominated by the late Mississippian genera *Gnathodus* and *Lochriea*, associated with the early Pennsylvanian genera *Declinognathodus*, *Idiognathoides*, *Neolochriea*, *Idiognathodus* and *Neognathodus*. Rare specimens of shallow-water genera, *Rhachistognathus*, *Cavusgnathus* and *Ade-tognathus* also occur in several beds. The long-ranging genus *Hindeodus*, representing by *H. minutus* (Ellison, 1941), was found throughout the studied interval. Only platform elements are listed in the distribution chart.

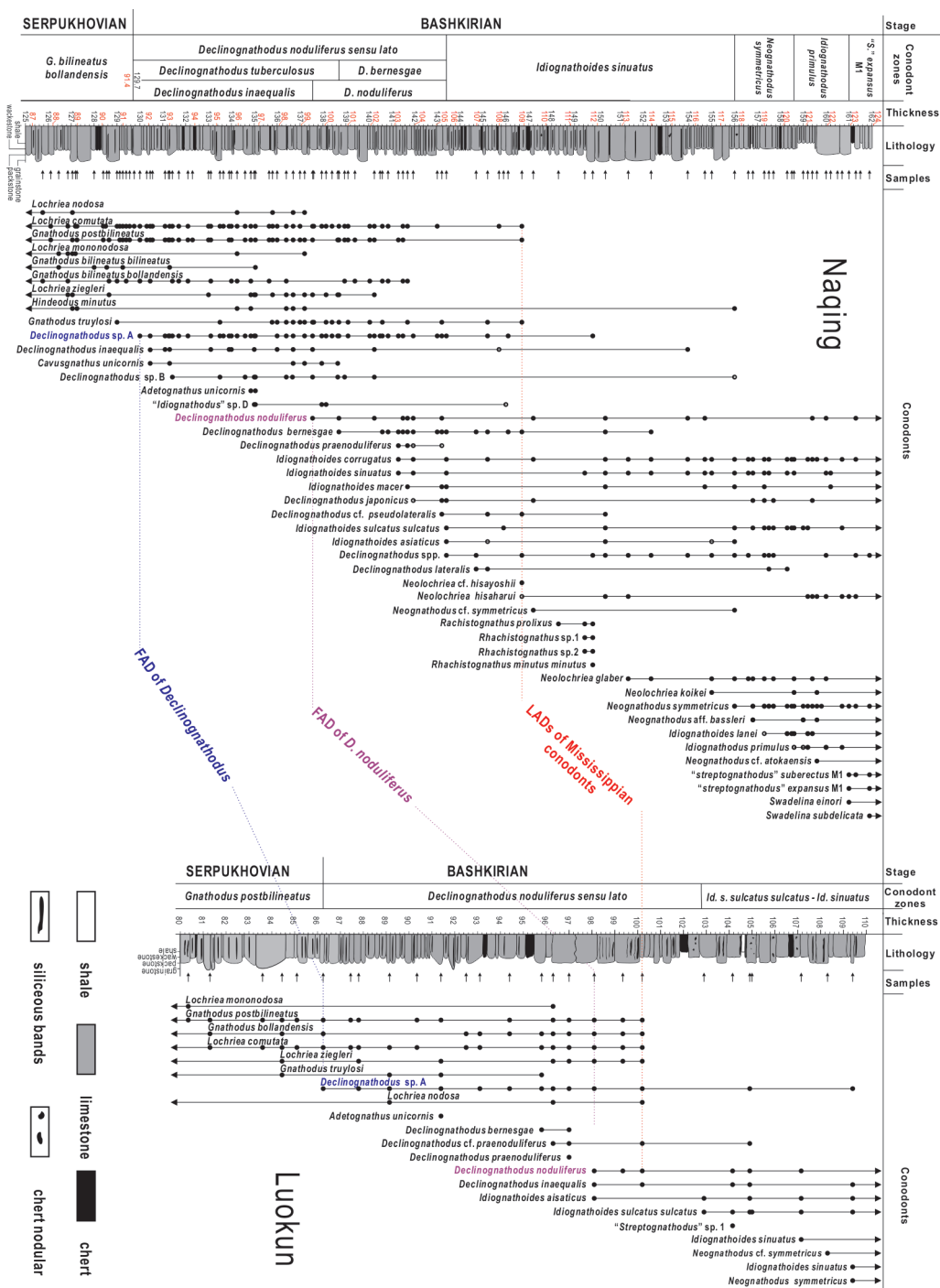


Fig. 2. Range chart of mid-Carboniferous conodonts from the Naqing and Luokun section.

## RESULTS

Based on the conodont succession from the study sections, several evolutionary patterns regarding the genera *Declinognathodus*, *Idiognathoides*, *Idiognathodus*, *Neognathodus* and *Swadelina* are proposed: 1) *D. sp. A*, *D. bernesgae* and *Idiognathoides*, 2) *D. sp. A*, *D. sp. B*, "*I.*" sp. D and *Swadelina*, and 3) *D. sp. A*, *D. cf. pseudolateralis*, *D. lateralis* and *I. primulus* (Fig. 1B).

## DISCUSSION

The mid-Carboniferous conodonts of South China are close to that of Central Asia and northern Spain but with different ranges. One of the main differences is that *D. sp. A* appears lower than *D. bernesgae* and subsequent *D. praenoduliferus* in the study sections. *Declinognathodus sp. A* is very similar to *D. bernesgae*, only differing by more than one node on ventral-rostral platform. In both the Naqing and Luokun sections, *D. sp. A* appears lower than *D. bernesgae*. In addition, some transitional forms with two nodes are found between the FADs of *D. sp. A* and *D. bernesgae*. Consequently, we interpret that the number of nodes on ventral-rostral platform in *D. sp. A* is gradually reduced to a single node. In other words, *D. bernesgae* was generated from *D. sp. A* by reducing nodes on the ventral-rostral platform. As *D. sp. A* evolved to *D. bernesgae* through reduction of nodes on the ventral-rostral platform, it is possible that *D. bernesgae* gave rise to *D. praenoduliferus* through the same process of node reduction.

*Declinognathodus sp. B* is found from the lower Bashkirian at the Naqing section. It was derived from *D. sp. A* by development of a caudal "lobe". Since many authors (e. g., Higgins, 1975; Grayson et al., 1990; Nemyrovskaya, 1999) considered that the first *Idiognathodus* species is probably the lobeless *I. primulus*, we interpret that *D. sp. B* was the ancestor of the troughed early Pennsylvanian species *Swadelina einori* (Nemirovskaya & Alekseev, 1993) and *Sw. subdelicata* (Wang & Qi, 2003).

We agree with Sanz-López and Blanco-Ferrera (2013) that *D. bernesgae* gave rise to *Idiognathoides asiaticus* and *Id. macer* by losing nodes and shifting the carina rostrally. *Idiognathoides sinuatus* and *Id. corrugatus*, however, were also likely generated from *D. bernesgae* directly.

The origin of the nodose *Declinognathodus* group has been controversial. The nodose *Declinognathodus* species may be descendants of *G. postbilineatus* (through *D. sp. A*) or *G. girtyi simplex*. In other words, it is possible that nodose and ridged *Declinognathodus* were respectively generated from different ancestors in America and Eurasia at the same time as Nemirovskaya & Nigmatdaganov (1994) suggested. In this case, the species of ridged *Declinognathodus* should be given a new genetic name.

## CONCLUSIONS

The conodont succession from the deep-water Naqing and Luokun sections provides a new understanding of the conodont evolution across the MCB. *Declinognathodus sp. A* and *D. sp. B* represent significant phylogenetic stages of early Pennsylvanian conodonts. *Declinognathodus sp. A*, which probably evolved from *G. postbilineatus*, gave rise to *D. bernesgae*, *D. cf. pseudolateralis* and *D. sp. B*. *Declinognathodus bernesgae* gave rise to *D. praenoduliferus*, *Idiognathoides macer*, *Id. sinuatus*, *Id. corrugatus*, and *Id. asiaticus*. *Declinognathodus cf. pseudolateralis* gave rise to *Idiognathodus primulus* through *D. lateralis*. *Declinognathodus sp. B* is the potential ancestor of *Swadelina subdelicata* and *Sw. einori* through intermediate "*I.*" sp. D. The origination of nodose *Declinognathodus* species *D. inaequalis*, *D. noduliferus* and *D. japonicus* is unclear. The no-



dose *Declinognathodus* was either a descendant of *G. girtyi simplex* or *D. sp. A*. *Gnathodus girtyi* group was the probable ancestor of genus *Neognathodus*. The origination of both ridged and nodose *Declinognathodus* probably took place at the same time. *Declinognathodus sp. A* may be slightly earlier than *D. inaequalis*, but close enough to be an equivalent marker for the MCB.

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## PALAEOENVIRONMENTAL CHANGES AND BIOSTRATIGRAPHY OF CONODONTS IN THE UPPER CARBONIFEROUS OF THE AMAZONAS BASIN, BRAZIL

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**Keywords:** Conodont, Carboniferous, Amazonas Basin

### INTRODUCTION AND GEOLOGICAL CONTEXT

The Amazonas basin was formed by extensional tectonics between the Guianas and Brazilian shields of north of Brazil. The most part of the filling took place during the Paleozoic, but younger rocks and/or a dense rainforest cover it. The Upper Paleozoic (Pennsylvania-Permian) is so called the Tapajós Group, which reaches up to 2,800 m in thickness and is limited by two regional unconformities (Cunha et al., 1994, 2007). The basal unconformity corresponds to a hiatus between the Viséan and the Bashkirian coinciding with an interval during which most of South America was located in high latitudes. From the Bashkirian, the Amazonas basin was located in low latitudes as a consequence of the northwards displacement of the western part of Gondwana. In this sense, the Tapajós Group records a change from hot and humid conditions to drier ones evidenced in a succession composed of basal fluvial and marine littoral sandstones (Formation Monte Alegre), shallow-water carbonates with occasional deposition of evaporites (Itaituba Formation) that are more frequent in lagoon facies (Nova Olinda Formation) and finally continental deposits (Andirá Formation).

### MATERIAL AND METHODS

The conodont study was focused on sixty-two positive samples from ninety-nine processed, weighing between 0.3 and 0.5 kilograms per sample. Their size is a consequence of their availability from core boreholes, which were drilled out by the company Petróleo Brasileiro SA. In addition, ten samples have been studied from limestone exposed in the Calminas quarry.

### RESULTS AND DISCUSSION

The conodont-based biostratigraphy allows establishing a correlation between the different localities. In particular, three interval zones (*Neognathodus symmetricus*, *Diplognathodus coloradoensis* and *D. ellesmerensis*), and a taxon-range zone (*Idiognathodus* aff. *incurvus*) are differentiated (Fig 1). The first record of *D. ellesmerensis* in the middle part of the Itaituba Formation is correlated with the base of the upper Moscovian and corresponds to an expansion of the marine sedimentation over the margins of the basin. In addition,

some isolated faunas are significant in the highest part of the succession. Among them, an upper Moscovian fauna with *Neognathodus inaequalis* is located below an unconformity detected by seismic profiles at the upper part of the Nova Olinda Formation (Cunha et al., 2007). Above, a shift towards more arid conditions is associated with the rare occurrence of marine beds yielding Upper Carboniferous *Streptognathodus firmus*. Conodont distribution is compared with the spores and pollen previously described in the Amazonas basin (Playford and Dino, 2000).

Fm	Playford and Dino (2000b)		this work		Global stage	Regional stage /substage		System		
	palynozone	substage	conodont zone	association		North America	Western Europe			
Nova Olinda	<i>Vitalina costalis</i>	Asselian–Sakmarian		<i>Streptognathodus</i> sp.				Permian		
				<i>Streptognathodus firmus</i>					Gzhelian–Kasimovian	Virgilian–Missourian
				<i>Neognathodus inaequalis</i>	Moscovian	Desmoinesian	Asturian	Carboniferous		
	<i>Raistrickia cephalata</i>	Westphalian D (Asturian)	<i>Idiognathodus</i> aff. <i>I. incurvus</i>	<i>Idiognathodus podolskiensis</i>					<i>Idiognathodus izvaricus</i>	
<i>Idiognathodus l. cf. l. obliquus</i>										
<i>Striatosporites heyleri</i>										
Itaituba	<i>Illinites unicus</i>	(probably) Bolsovian	<i>Diplognathodus ellesmerensis</i>			Atokan	Bolsovian			
	<i>Striomonosaccites incrassatus</i>									Langsettian Duckmantian
Monte Alegre	<i>Spelaeotriletes triangulus</i>	Langsettian–Duckmantian	<i>Neognathodus symmetricus</i>	<i>Idiognathodus incurvus</i>	Bashkirian	Morrowan				
				<i>Neognathodus</i> sp. A						
				<i>Idiognathodus sinuosus</i>						
				<i>Neognathodus bassleri</i>						

Fig. 1. Differentiated palynozones based on records from Monte Alegre, Itaituba and Nova Olinda formations, and correlation with the Western European regional sub-stages according to Playford and Dino (2000). Correlation of the conodont zones and faunas of the Amazonas basin with the regional stages/sub-stages in North America and Western Europe.

Conodonts, and particularly the *Idiognathodus* species, show a certain provincialism, as it has been described in several fossil groups of the Midcontinent-Andean Realm (fusulinaceans in Ross, 1967). Hitherto *Idiognathodus amplificus*, *I. crassadens*, *I. ignisitus*, *I. rectus* and *Diplognathodus iowensis* were exclusively known in North American “Midcontinent” region. Other Amazonian species of Moscovian age, such as *I. cf. obliquus*, *I. praeobliquus* and *I. podolskiensis* are also found in the sub-Arctic area of North America, but they

are typical of the Eurasian-Arctic Realm where they could have migrated through the northern primary corridor of the Arctic or Uralian- Franklinian Province (Fig. 2). However, the presence of *I. izvaricus*, a species previously known only in Eastern Europe but not in North America, suggests a secondary connection between the western Palaeo-Tethys and the eastern coast of Panthalassa oceans, either through the incomplete closure of the Rheic ocean, or through a corridor between North Africa and the Amazonas basin, as some authors have suggested (Baesemann et al., 1998, García-Bellido and Rodríguez, 2005).

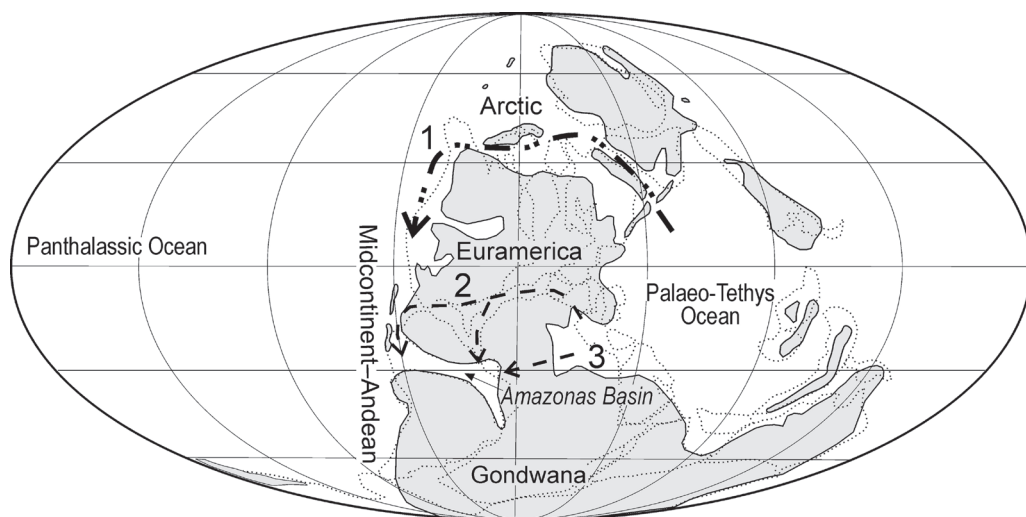


Fig. 2. Pennsylvanian paleogeography redrawn from Scotese (2002), which indicates the primary migratory route normally accepted from the Palaeo-Tethys (Eurasian-Arctic Realm) and eastern Panthalassa Ocean (the Midcontinent-Andean Realm) (1), the proposed connection through northern Africa according to Vai (2003) (2), and through the Amazonas basin in agreement with Baesemann et al. (1998).

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## TECTONOTHERMAL ANALYSIS OF A MAJOR UNIT OF THE CANTABRIAN ZONE (VARISCAN BELT, NW SPAIN) USING CONODONT COLOR ALTERATION INDEX

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**Keywords:** CAI, low-grade metamorphism, Variscan structure, tectonothermal history

The conodont color alteration index (CAI) is a useful parameter to analyze the transition between diagenesis and metamorphism in orogenic belts. It is cheap and easy to apply, and covers a large temperature range (from 50 to >600°C) (Rejebian *et al.*, 1987). As with other thermal maturity indicators that follow the Arrhenius reactions, it is time-temperature dependent, progressive and irreversible. The correlation of the conodont CAI with the Kübler Index (KI) has allowed to distinguish three prograding zones (diacaizone, ancaizone, epicaizone) in the transition diagenesis/metamorphism, with the ancaizone ranging between CAI 4–5.5 (García-López *et al.*, 2001). This zonation is very useful in areas where limestones are dominant and corresponds approximately to the KI zonation (diagenesis, anchizone, epizone).

Conodont CAI and KI methods have been applied to the Cantabrian Zone, the foreland fold and thrust belt of the Variscan orogen in NW Spain (Fig. 1). The Cantabrian Zone presents a near complete stratigraphic succession from the Cambrian to the upper Carboniferous, with important gaps in some areas, particularly in the Ponga study area. The Cantabrian Zone underwent thin-skinned tectonics with large thrust units and associated folds whose curved cartographic trend gives place to the "Asturian arc". The Variscan deformation developed mostly under low pressure and low temperature conditions, although very low- or low-grade metamorphism is reached in some areas. Analysis of distribution of CAI and KI values in relation to stratigraphy and structure allowed to construct a preliminary view of the tectonothermal evolution of the Cantabrian Zone (García-López *et al.*, 2007, and references therein). In this contribution, we analyze the distribution of conodont CAI values in the Ponga unit, one of the major of the Cantabrian Zone. This study completes the CAI framework of the Cantabrian Zone by connecting the eastern units (Picos de Europa and Pisuerga-Carrión units) with the western unit (Central Coal Basin) (Fig. 1).

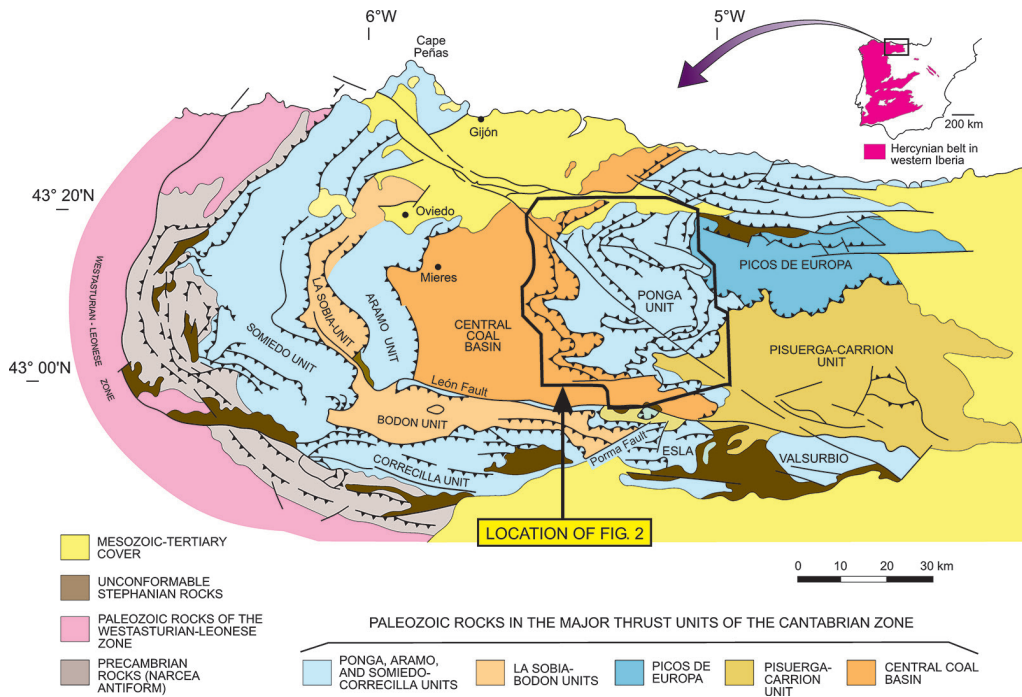


Fig. 1. Generalized geological map of the Cantabrian Zone (modified from Julivert, 1971) showing major thrust units and the location of the study area.

## GEOLOGICAL SETTING

The Ponga unit is located near the core of the Asturian Arc. Its most characteristic stratigraphic feature, when compared to the rest of the Cantabrian Zone, is the existence of a wide hiatus, comprising from the Middle Ordovician up to most of the Devonian. The unit is an imbricate system of E-directed thrusts, folded with E–W axial trace (Julivert, 1971; Álvarez-Marrón and Pérez-Estaún, 1988). These thrusts converge in depth towards a sole thrust located at the base of the Láncara Formation (lower Cambrian). The development of the thrusts gave rise to fault-bend folds associated with frontal or lateral ramps, and to some lateral tear faults. Subsequently, a notable N–S shortening gave rise to the development of new south-directed thrusts, to the reactivation of the tear faults and to the amplification of folds. Small outcrops of igneous rocks with U–Pb ages of c. 302 Ma (Valverde-Vaquero *et al.*, 1999) are present in the northern part of the Ponga. They produced contact metamorphism, skarns and economic mineralizations.

## RESULTS AND INTERPRETATION

The CAI data have a heterogeneous distribution due to the absence of limestone rocks in some areas, and the abundance of sterile samples. CAI values display a general increase southwards, and three E–W bands can be roughly distinguished (Fig. 2):

a) Northern band. It is a diacaizonal band with the exception of an ancaizonal sample located to the south of Infiesto. These low CAI values continue to the NE in the Ponga-Cuera unit (Blanco-Ferrera *et al.*, 2011).

b) Middle band (Rioseco–Campo de Caso–Beleño band). It is a dominantly diacaizonal band, but some samples are ancaizonal. In addition, two samples located at the eastern end of the band have high dispersion of CAI values.

c) Southern band. It exhibits mainly ancaizonal and epicaizonal CAI values. An exceptional diacaizonal value is located to the west of Burón.

The distribution of CAI values shown in Fig. 2 suggests that the CAI values are independent of the stratigraphic position of the samples. This implies that the maximum temperatures reached by the host rocks are not a result of sedimentary burial.

The ancaizonal value of the sample located to the S of Infiesto, in the northern sector of the Ponga (Fig. 2), is ascribed to a short term heating event produced by the late-Variscan igneous rocks that crop out in the area.



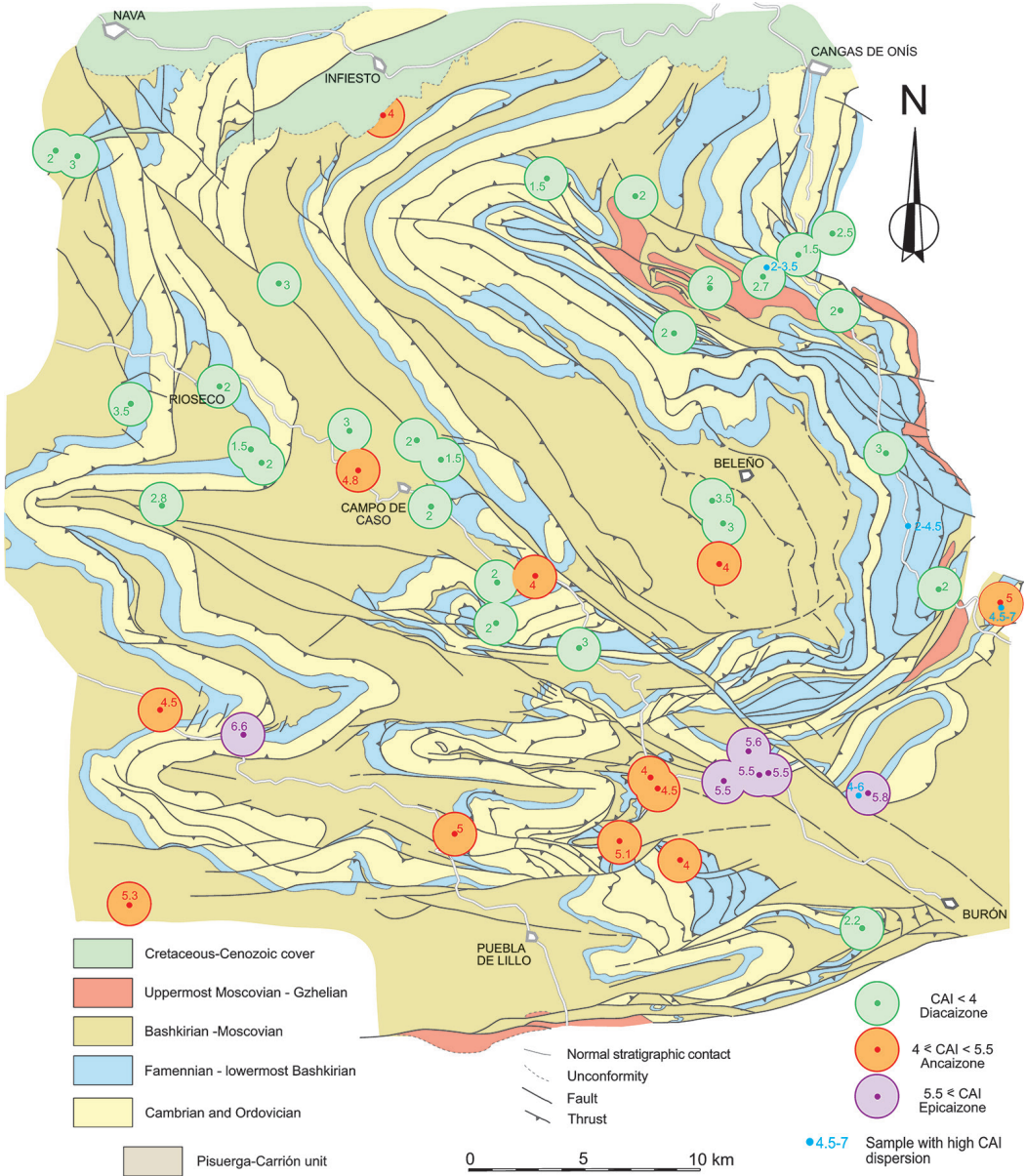


Fig. 2. Geological map of the Ponga unit with location of mean CAI values. The colored circles have been drawn in order to better visualize the metamorphic grade of the corresponding sample (geological map based on Julivert, 1967a and b, and Álvarez-Marrón *et al.*, 1989).

## DISCUSSION AND CONCLUSIONS: THE METAMORPHISM OF THE PONGA UNIT IN THE REGIONAL CONTEXT

The area with ancaizonal and epicaizonal values in the southern Ponga unit is part of a major E–W band that crosscuts the main Variscan structures. The width of this band is variable, being minimum in the Ponga unit. To the east, this metamorphic band occupies almost the whole Pisuega-Carrión and Valsurvio units (Fig. 1). To the west, in the Central Coal Basin, the band is also wider than in the Ponga unit. In both, the Ponga unit and the Coal Central Basin, the metamorphic band ends abruptly to the south on the León Fault. In the Pisuega-Carrión unit, it continues to the south of this fault.

The E–W metamorphic band has been interpreted as a result of an increase of the geothermal gradient related to a late-Variscan gravitational instability of the orogenic belt (Aller *et al.*, 2005; Valín *et al.* 2016). Among other evidences, the extensional deformation is recorded as a subhorizontal cleavage crosscutting the main Variscan folds in the units adjacent to the Ponga area (Central Coal Basin, Pisuega-Carrión and Valsurbio units), and it was subsequent to the Asturian Arc formation. Although the metamorphic grade in the Ponga is similar to that of the adjacent units, the absence of cleavage suggests less strain in this area, which does not affect the CAI response.

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# **PERMIAN TO TRIASSIC CONODONTS: BIOSTRATIGRAPHY, ISOTOPES AND GEOCHEMISTRY**



# THE NATURE OF PERMIAN TO LOWER TRIASSIC CONODONT BIOSTRATIGRAPHY

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**Keywords:** Evolution, Permian, Lower Triassic, gondolellids, biostratigraphy

## INTRODUCTION

The temporal ranges of conodont species have proven to be instrumental for the definition of many Global Stratotype Sections and Points and this is exemplified in the Permian where all nine stages are, or will be, defined by the First Appearance Datum of conodont species. I have recently summarized 40 Permian conodont zones and correlated 35 additional regional zones (Henderson, 2016). The next step is to review species definitions and attempt to determine evolutionary patterns that might point to a paleobiologic basis for this zonation.

## DISCUSSION

Permian ozarkodinid conodonts had 15 elements in their apparatus. The platform, or P1-elements, are discriminated at the species level because these elements have the greatest range of morphologic variability. They also exhibit significant trends in chemical elemental distribution. For example, in Permian gondolellid P1-elements the concentration of Na on the oral surfaces, comparable to that seen in modern shark teeth, indicates that these elements functioned as teeth exposed to seawater. In addition, the concentration of S in juvenile interlamellar tissue suggests a relationship of conodonts as stem cyclostomes and lamprey as paedomorphic descendants. The mineralized teeth of conodonts probably point to employment of a greater variety of food processing methods compared to lamprey. What can P1-element morphologic changes tell us?

The general shape of gondolellid P1-elements has not changed dramatically, suggesting, if this form relates to food type and food processing, that there were few significant changes in diet during their evolutionary history from Pennsylvanian to Triassic. Evolutionary changes to other elements in the gondolellid apparatus have discriminated numerous genera and families, but it is uncertain how these modifications affected food processing. There are three repetitive changes to P1-element morphology of significance. The reduction or loss of platform margins in naked species of *Gondolella*, *Neoclarkina* and *Neospathodus* represents the first pattern during the Late Pennsylvanian and Early Triassic. The second pattern involves the relative height and fusion of anterior denticles on the carina, which are low in *Gondolella*, variably high in *Mesogondolella*, low in most *Jinogondolella* and high in *Clarkina*. The third pattern represents the apparent association of the development of widely spaced discrete denticles on the carina, with third-order transgressive events during the Permian and Early Triassic. These patterns involve retention of juvenile characters or paedomorphic development that occurred during times of unstable environments, characterized by fluctuating temperature and shelf space. Is natural selection operating on some intrinsic aspect of the conodont animal or because of changes in food resource partitioning?

Upper Permian and Lower Triassic gondolellid taxa are largely discriminated by changes in the configuration of carinal denticles. The presence of discrete denticles in juvenile *Jinogondolella granti* specimens, and in adults of descendant *Clarkina postbitteri* subspecies, suggests a paedomorphic evolutionary process. This event is associated with a major sequence boundary and a Late Capitanian extinction and involves the evolution of a new gondolellid genus, *Clarkina*, defined by the lack of serration, high anterior blade-like denticles, and change in platform outline. The discrete denticulation of adult specimens coincides with a deepening event during the Early Wuchiapingian. However, younger Wuchiapingian taxa typically show increasingly closely spaced denticles that culminated in the wall-like carina of *C. wangi* at the Wuchiapingian-Changhsingian boundary. The smallest juveniles of *Clarkina* species are very similar, but comparing juveniles of *C. longicuspidata* and its descendant *C. wangi* hints at the evolutionary process. Juvenile *C. longicuspidata* have relatively discrete denticles compared to the increasingly fused denticles of intermediate and larger mature forms. In contrast, denticles of juvenile *C. wangi* are already partially fused, and in adults the anterior gap adjacent to the cusp, becomes fused, completing the high wall-like carina. This implies a heterochronic process involving acceleration or peramorphosis. These small-scale evolutionary events within an anagenetic series of *Clarkina* species is associated with relatively minor flooding surfaces. Younger Changhsingian taxa show a breakup of the wall-like carinal development, but they remain characterized by closely spaced denticles that decrease in height posteriorly. Discrete denticulate *Clarkina* species are again associated with the major flooding and extinction event during the Permian-Triassic boundary interval.

The high anterior (or ventral) blade in *Clarkina* may have served a similar function to the long anterior blade of other ozarkodinid conodonts like *Streptognathodus* and *Sweetognathus* by constraining element motion to the transverse plane, thereby maximizing food-processing efficiency. Combined with carinal denticulation, this may provide a paleobiologic basis for morphologic variation used in Upper Permian and Lower Triassic biostratigraphy, including the high anterior denticle of *Hindeodus parvus*, which defines the P-T boundary. The morphologic changes in these taxa may therefore relate to the parallel evolution or extinction of organisms representing potential food resources or to the availability of food resources along some environmental gradient. Profound provincialism during much of the Permian as well as timing and discrimination of migration events complicates these patterns.

## CONCLUSIONS

The cyclic nature of the carinal morphology and significant ontogenetic changes make species discrimination difficult, indicating the need for a sample population approach. This approach will allow the discrimination of the closely related taxa necessary to define a high-resolution biostratigraphic zonation, but there is still much "food for thought" regarding the paleobiologic basis of this zonation.

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## THE INDIAN CONODONT RECORD AT GURYUL RAVINE SECTION (KASHMIR, INDIA) AND ITS CONSEQUENCES FOR THE GRIESBACHIAN-DIENERIAN BOUNDARY

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**Keywords:** Conodonts, Permian-Triassic boundary, Griesbachian-Dienerian boundary, Guryul Ravine, Kashmir, climate change

### INTRODUCTION

The Permian-Triassic boundary (PTB) mass extinction (~252 Ma) was marked by the disappearance of more than 90% of all marine species (Raup, 1979) and by major changes in plant communities (Retallack, 1995; Hochuli et al., 2010). Contrary to most organisms, conodonts were not much affected by the main extinction event and thrived in the direct aftermath of the PTB (Orchard, 2007). Yet, at the Griesbachian-Dienerian Boundary (GDB), ca. 0.5 Myr after the PTB event, conodonts underwent a major faunal turnover.

Guryul Ravine is considered as one of the world's best locality for the study of the Early Triassic: it records a sub-continuous, relatively uniform, fossiliferous and expanded rock succession straddling the PTB and most of the Early Triassic (Kapoor, 1996). Yet, since the eighties and until a few years ago, the unstable political conditions in Kashmir have precluded access to the section, and it became urgent to reassess the conodont record of this important section in the light of the new taxonomical advances. Here we discuss the results concerning the conodonts from the basal Triassic interval (Member E of the Khunamuh Formation).

### RESULTS

Samples were collected at about 10-50 cm spacing. The first bed containing specimens of *Hindeodus parvus* (index species for the base of the Triassic), and therefore confidently assigned a Griesbachian age, is located ca. 6 metres above the base of the Khunamuh Fm. Towards the top of the Member E, we observe a radical faunal turnover from an exclusively neogondolellid assemblage to an exclusively neospathodid assemblage. The evolutionary origin of neospathodid conodonts is considered as a good marker of the GDB (for a review of the evolution of Early Triassic conodonts, see Orchard, 2007). At Guryul Ravine, we are able to constrain the GDB within a 40 cm interval in the upper half of sub-member E<sub>3</sub>.

We conducted Unitary Associations (UAs) analyses (for a description of the method, see Guex et al., 2015) in order to provide a robust biochronological model for the basal Triassic of the Tethys. Based on a dataset comprising five well-documented Chinese sections and the Guryul Ravine section, we define 10 Unitary



Associations Zones (UAZs) encompassing the PTB and the GDB. We propose to place the GDB in the interval of separation between UA<sub>7</sub> and UA<sub>8</sub>. UA<sub>7</sub> is characterized by the association of *Neogondolella discreta* with at least one of the following species: *Hindeodus parvus*, *Hindeodus typicalis*, *Hindeodus eurypyge*, *Hindeodus postparvus*, *Isarcicella staeschei*, *Neogondolella griesbachensis*, *Neogondolella nassichuki*, *Neogondolella meishanensis*, *Neogondolella kazi*, *Neogondolella lehmanni*, *Neogondolella krystyni*. UA<sub>8</sub> is characterized by the association of *Neogondolella discreta* and *Sweetospathodus kummeli*.

## DISCUSSION

Following this conodont-based definition of the GDB, we observe that the basal Dienerian co-occurs with a 3‰ positive excursion of the  $\delta^{13}\text{C}$  at Guryul Ravine, which suggests climatic changes around the GDB. This is corroborated by the fact that neogondolellid conodonts, which presumably favoured colder environments (Joachimski et al., 2012), were quickly restricted to the colder Boreal realm during the Dienerian and replaced by the newly evolved neospathodid conodonts at low and mid latitudes (Orchard, 2007; this study). Recent palynological studies (Schneebeli-Hermann et al., 2015; Hochuli et al., 2016) support this hypothesis as the GDB is also characterized by a major turnover in the floral composition at high and low latitudes (namely a swap from a gymnosperm-dominated floral assemblage to a lycopsid spore-dominated floral assemblage) that suggests a transition from a cool and dry climate to a hot and humid climate on a global scale (Hochuli et al., 2016).

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## INDUAN-OLENEKIAN BOUNDARY CONODONTS FROM OMAN

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The Induan-Olenekian Boundary (IOB), or Dienerian-Smithian boundary, is a stage boundary within the Early Triassic and the critical time period in the direct aftermath of the end-Permian mass extinction. The IOB still lacks a formal GSSP but a new STS working group has been constituted very recently and a final decision is expected soon. In terms of conodonts, the IOB corresponds to an explosive evolutionary radiation. Yet, most localities have only a very poor conodont record for the Late Induan (Dienerian), which led Orchard (2007) to propose for instance that some of the most important innovations in terms of multi-element apparatuses remained cryptic by lack of relevant fossils. Here we would like to summarize the conclusive bio-chronological results we obtained by analysing new, abundant, unpublished conodont material from several localities, in particular from Oman.

In Oman, the preservation of the conodont material is particularly exceptional since most P<sub>1</sub> elements and many S and M elements are preserved with at least some remains of basal body. To our knowledge this is the first report of S or M elements of Triassic age with preserved basal body. We will discuss how they may support previous hypotheses on the extent of basal body in Triassic elements and their consequences for the animated model proposed by Goudemand et al. (2011).

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## THE YOUNGEST OCCURRENCE OF *VJALOVGNATHUS* AT SELONG (TIBET)

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**Keywords:** Himalaya, Induan, biostratigraphic, extinction, *Vjalovognathus carinatus* sp. nov.

### INTRODUCTION/BACKGROUND

The end Permian mass extinction depleted over 90% of the marine species and about 70% of vertebrate families on land (Erwin, 1994; Retallack, 1995; Song et al., 2012; Sun et al., 2012; Yin et al., 2013). The conodont animal was considered less influenced by this lethal event since the input of abundant *Hindeodus* species and the new genus *Isarcicella* to both the tropical Tethyan area and high paleolatitude regions (Orchard, 1994; Mei, 1996; Algeo et al., 2012; Twitchett et al. 2004; Brayard et al., 2009; Payne et al., 2011). However, a cold-water conodont-*Vjalovognathus* is locally distributed in the Perigondwana region from Permian strata and is not present later. Reports from the Salt Range, Pakistan, Manang, central Nepal, and Guryul Ravine, Kashmir, all from Late Permian strata were believed to be the youngest occurrences of this genus (Wardlaw and Pogue, 1995; Nicora and Garzanti, 1997; Brookfield and Sun, 2015). Selong is one of the best-know Perigondwana Permian-Triassic (P-T) sections (Jin et al., 1996; Wignall and Newton, 2003; Shen et al., 2006). To address the considerable evolutionary complexity of *Vjalovognathus* in the Late Permian as well as the temporal changes of conodonts from high paleolatitudes, we sampled at Selong (in 2010) and herein present a new study of its conodonts.

### GEOLOGICAL CONTEXT

The Selong section is situated in the northwest of Selong in Nyalam County and is about 700 km southwest of Lhasa, Tibet, China. P-T strata in southern Tibet accumulated in inner shelf seas along the passive continental margin of Indian Perigondwana (Jin et al., 1996; Wignall and Newton, 2003). The P-T boundary beds at Selong are composed of the Coral Bed at the top of the Selong Group (Rao and Zhang, 1985; Wang et al., 1989; Jin et al., 1996) and then, at the base of the overlying Kangshare Formation, the Caliche Bed, the *Waagenites* Bed, the *Otoceras* Bed and the *Ophiceras* Bed (Jin et al., 1996; Wignall and Newton, 2003).

### MATERIAL AND METHODS

A total of 31 conodont samples from Selong, weighing 176 kg, were collected from 3.51 m of strata straddling the Permian-Triassic boundary. The samples were processed using the acetic acid dissolution

method (Jiang et al., 2007; Yuan et al., 2016) in the conodont laboratory of the China University of Geosciences (Wuhan).

## RESULTS

A total of 13 samples yielded 4746 conodonts, including 4124 P1 elements (2834 of them were broken) and 622 ramiform elements. Ten *Vjalovognathus* were recovered from the upper part of the Selong Formation. One new species *V. carinatus* sp. nov. and its proposed evolutionary lineage was described in this study (Fig. 1). The Sakmarian-Artinskian *V. australis* (A) is ovate-kidney-bean shaped and linearly compressed at its base with an anterior groove on the denticles. The Kungurian *V. shindyensis* (B) is distinguished by the absence of an anterior groove, but it develops a weak axial ridge on the posterior part of the denticles. Late Kungurian *V. nicolli* (C) develops a prominent axial ridge, which straddles the carina and is slightly appressed in the base of the denticles. *V. sp. nov. X* (D) has a round-ovate shaped cross-section of the denticles and is more thick-walled compare to *V. nicolli* (Zheng et al. 2007; Nicoll and Metcalfe 1998). The precise age of this species was not given by Zheng et al. (2007). The new specimens-*V. carinatus* sp. nov. reported from Changhsingian differ from previously reported species by their well-developed linear ridge between denticles, absence of groove and a basal cavity that is more excavated. The denticles are not compressed as compared with the older *V. australis* and *V. shindyensis*.

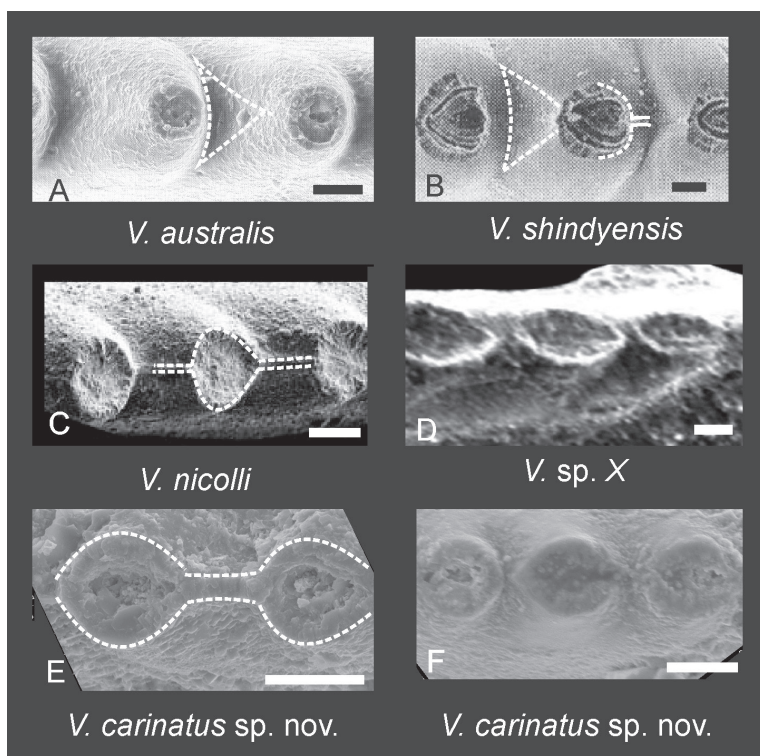


Fig. 1. Evolutionary trend of Permian *Vjalovognathus*. Scale bars represent 20µm.

## DISCUSSION: Changhsingian *Vjalovognathus* and its evolution during Permian

*Vjalovognathus* was first established by Kozur and Mostler (1976) and is characterized by an octomembrate apparatus (Yuan et al., 2015). It was used to establish the family Vjalovognathidae by Shen et al. (2015). It has been considered a cool water conodont typical of the Perigondwanan region especially during the Early Permian (Nicoll and Metcalfe, 1998; Mei et al., 1999a, b; Lai and Mei, 2000; Yuan et al., 2015). Five species have been assigned to *Vjalovognathus*. The earliest member of the *Vjalovognathus* group is *V. australis*, reported from Timor (Indonesia) and Western Australia where it ranges from late Sakmarian to early Artinskian (Van den Boogaard, 1987; Reimers, 1991; Nicoll and Metcalfe, 1998). The second species *V. shindyensis* is known from Kungurian or Roadian strata in the Pamirs (Kozur and Mostler, 1976), Western Australia (Nicoll and Metcalfe, 1998) and Shiquanhe, Tibet (Zheng et al., 2007). A third species *V. nicolli* was reported in late Kungurian strata from Western Australia (Nicoll and Metcalfe, 1998) and the central Lhasa block (Yuan et al., 2015). The youngest *Vjalovognathus* was reported in Changhsingian strata from the upper part of the Chhidru Formation in the Salt Range, Pakistan (Wardlaw and Pogue, 1995) and the basalmost part of the Khunamuh Formation at Guryul Ravine, Kashmir (Brookfield and Sun, 2015), but had not been described. At Selong, eight broken specimens with the distinctively truncated denticles are described here and considered the same species as those from Guryul Ravine and the Salt Range.

Kozur and Mostler (1976) suggested that *Vjalovognathus* was derived from *Neostreptognathodus pequopensis* through the fusion of the two opposite rows of denticles. However, *N. pequopensis* first appears during the late Artinskian (Magginetti et al., 1988; Jin et al., 1997), which postdates the first occurrence of *V. australis*, suggesting the relationship proposed by Kozur and Mostler (1976) is untenable. Yuan et al. (2015) proposed a possible relationship between *Vjalovognathus* and Gondolellidae (Nicoll and Metcalfe, 1998) by the similarity of the blade-like P1 element (cf. von Bitter & Merrill 1980). However, more data are clearly needed to establish any factual evolutionary relationship between *Vjalovognathus* and other conodont genera.

## CONCLUSIONS

We have investigated the conodonts from the Permian-Triassic Boundary interval at Selong, South Tibet and present a study on the youngest *Vjalovognathus* enabling us to establish an evolutionary lineage. The cold-water conodont *Vjalovognathus* went extinct at the end of the Permian, ending their more than 40 Myr history. Together with the Early Triassic size reduction of *Hindeodus* species in Perigondwana, this suggests that rapid global warming was the main driver of the conodont changes.

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# VARIABILITY OF LATE PALEOZOIC AND TRIASSIC CONODONT FAUNAS IN THE CACHE CREEK TERRANE OF WESTERN CANADA

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**Keywords:** Paleobiogeography, Canada, Cordillera, upper Palaeozoic, Triassic

## INTRODUCTION

The Canadian Cordillera consists of a number of fault bounded crustal blocks referred to as terranes. These contain rocks that share a common geological history and are distinct from those of neighbouring terranes. The various terranes have been interpreted to represent a number of different tectonic settings, including volcanic arcs and the remains of oceanic basins. The relationships between the terranes prior to their amalgamation and accretion to the North American margin are still enigmatic. Conodont paleobiogeography represents an important tool for helping to decipher the relative positions of the terranes. However, the degree of heterogeneity of conodont faunas within individual terranes is not well understood. In an attempt to understand the degree of internal variability, the conodont faunas from three separate geographic regions of the Cache Creek terrane are compared to each other.

## GEOLOGICAL CONTEXT

The Cache Creek terrane has been interpreted as representing ancient oceanic crust in a forearc accretionary complex (Mihalynuk, 1999). The terrane is exposed in a semi-continuous belt from southern to central British Columbia, and in a separate northern section in northern British Columbia and the southern Yukon, initially referred to as the Atlin terrane (Monger, 1975). The upper Palaeozoic to Mesozoic rocks of the terrane are assigned to the Cache Creek Complex (or Cache Creek Group), a unit defined in the southern part of the terrane near Ashcroft, and subsequently recognized in the central and northern regions. The composition of this complex is variable along the length of the terrane, but the rocks assigned to it are primarily limestone, chert, argillite, and volcanics (Beyers & Orchard, 1991; Orchard et al., 2001; Golding et al., 2016a). These range in age from Pennsylvanian to Early Jurassic in the central and southern parts of the terrane, and from Mississippian to Early Jurassic in the northern part.

## MATERIAL AND METHODS

A total of 306 productive conodont samples collected from limestone belonging to the Cache Creek Complex have been examined for this study. Of these, 53 are from the southern part of the Cache Creek terrane, 177 are from the central part, and 76 are from the northern part. These collections range in age



from the Mississippian to the Late Triassic. A number of these collections have previously been reported in publications (see Golding et al., 2016a for references). For many of the collections, the conodont taxonomy has been revised, and biostratigraphic ages updated. This allows accurate comparisons of conodont faunas between the three parts of the terrane.

## RESULTS

The three geographic areas of the Cache Creek terrane are variable in their conodont faunal content. Throughout the time interval studied, there are some species that are relatively widespread and occur in two or three of the areas (for example, *Neognathodus bothrops* in the Carboniferous; *Wardlawella movschovitschi* in the Permian; and *Epigondolella quadrata* in the Triassic). However, there are many species that appear in only one of the geographic areas; most notably, these species include *Sweetognathus* n. sp. A in the Permian and *Gladigondolella tethydis* in the Triassic. Both of these species only occur in the central region of the terrane.

## DISCUSSION

When discussing conodont faunas from the Cache Creek terrane, it is important to emphasize the fact that the faunal composition of the terrane is not homogenous. Therefore, comparisons between faunas from the Cache Creek terrane and others in the Canadian Cordillera must take into account this variability. For example, Orchard et al. (2001) conclude that the presence in the Cache Creek terrane of *Sweetognathus* n. sp. A during the Permian and of *Gladigondolella tethydis* during the Triassic indicates separation of the terrane from the North American continent at these times due to the absence of these species in contemporaneous faunas of the continental shelf. However, as noted above, both of these species occur only in the central part of the terrane. This may imply geographic separation between the three parts of the terrane during the Permian and Triassic, and that the Cache Creek terrane is not a homogenous tectonic unit. Alternatively, the presence of "exotic" species in the terrane may have implications other than that of paleogeography, such as facies dependence of species. Requiring the separation of the Cache Creek terrane from the North American margin during the Triassic based on conodont faunas is potentially in conflict with geological evidence in favour of proximity of the neighbouring Stikine and Quesnel terranes to the North American continent at this time (Beranek & Mortensen, 2011; Golding et al. 2016b).

## CONCLUSIONS

Analysis of conodont faunas is an important tool in deciphering the relative positions of terranes in the Canadian Cordillera prior to accretion. However, this methodology must take into account variability *within* terranes, as well as *between* terranes.

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## EARLY TRIASSIC CONODONT ZONATION OF SLOVENIA

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**Keywords:** conodont zonation, Early Triassic, Dinarides, Slovenia

### INTRODUCTION/ BACKGROUND

This contribution presents the results of a systematic conodont study in Slovenia with the aim to present a conodont biozonation of Early Triassic of the area. Conodont research in Slovenia started in the sixties of the last century, during the period of elaboration of Basic Geological Map of Yugoslavia 1: 100,000.

### GEOLOGICAL CONTEXT

Slovenia is situated in the area of four major geotectonic units: the Southern Alps, the Eastern Alps, the Dinarides, and the Pannonian Basin (Buser, 1989). All of the tectonic units of the Slovenian territory belong to the Adriatic lithospheric plate, which was originally connected to the African plate that existed as a separate plate from the Mesozoic Era to the present.

Conodonts were recovered from the Lower Triassic marine sedimentary rocks in the area of the Southern and Eastern Alps, the External Dinarides and the Transitional area between the External and Internal Dinarides. The Permian-Triassic boundary (PTB) interval containing conodonts is preserved only in the Idrija-Žiri area of the External Dinarides. Olenekian conodonts were identified also in all other mentioned units, except in the Slovenian part of the Eastern Alps.

### MATERIAL AND METHODS

The results presented herein are based on field work and systematic sampling carried out in the last two decades in Slovenia. Several sections were measured and carbonate samples, 2 kg each, were collected for the conodont study. Standard techniques with the use of diluted formic acid and acetic acid was applied. Then followed heavy liquid separation for conodont enrichment. The laboratory processing was done at the Geological Survey of Slovenia /Geološki zavod Slovenije.

### RESULTS

A succession of conodont zones can be identified in the Lower Triassic strata of Slovenia. Following conodont zones have been distinguished in the studied geotectonic units: *H. parvus* Z., *Isarcicella lobata* Z., *I. staeschei* – *I. isarcica* Z., *H. postparvus* Z., *Hadrodontina aequabilis* Z., *Ha. anceps* Z., *Eurygnathodus*

*costatus* Z., *Neospathodus planus* Z., *N. robustus* Z., *Platyvillosus corniger* Z., *Pl. regularis* Z., *Pachycladina obliqua* Z., *Foliella gardeane* Z., *Triassospathodus hungaricus* Z., *T. symmetricus* Z., *N. robustispinus - T. homeri* Z. and *T. triangularis* Z. (Kolar-Jurkovšek & Jurkovšek, 2015).

The lithostratigraphic development of Lower Triassic strata in all of the studied geotectonic units in Slovenia is more or less similar. The base of the Lower Triassic strata is composed of the Bellerophon Formation, which was the result of a general marine transgression onto a shallow shelf of western Paleotethys in the Late Permian. The External Dinarides were a part of an extensive carbonate platform during the Early Triassic interpreted as epeiric ramp located on the western margin of the Tethys. The epeiric ramp model is characterized by a large lateral extension, very low bathymetric slope, water depths of tens of meters, storms and nearshore currents (Aljinovič et al., 2011, 2014). A Spathian transgression occurred after a lowstand in the late Smithian (Aljinovič et al., 2011).

Despite lithological variations among the different Lower Triassic sedimentary areas in the External Dinarides, as well as in the Transitional area between the External and Internal Dinarides, their threefold division can be divided into: 1) an oldest part of Early Triassic consisting of carbonates, 2) dominantly red siliciclastics or mixed siliciclastic-carbonate part (shale, siltstone, sandstone), and 3) a youngest carbonate part represented by mudstones, marls and calcisiltites with ammonoids (representing Spathian-Anisian strata) (Buser, 1974; Aljinovič et al., 2013).

The Lukač section near Žiri in the External Dinarides represents a key section to define the PTB interval strata in Slovenia due to the presence of the conodont species *H. parvus* that is used as a marker according to an international criterion of the IUGS (Kolar-Jurkovšek & Jurkovšek, 2007). Therefore it is taken also as a standard for conodont zonation for the entire Dinarides area (Kolar-Jurkovšek et al., 2011, 2012, 2013).

## DISCUSSION

Certain Lower Triassic faunas in Slovenia show a very low diversity marked by shallow water and/or euryhaline genera (i.e. *Hadrodontina*, *Pachycladina*) that are an important regional biostratigraphic tool in western Tethys (Perri, 1991; Kolar-Jurkovšek, 1990; Kolar-Jurkovšek & Jurkovšek 1995, 1996). A limited geographic distribution of some taxa is confined to the European sections (*Foliella*, *Platyvillosus*) and it suggests they were ecologically restricted and probably adapted to shallow water environments (Chen et al., 2016). Most conodont faunas recovered from Dienerian and Smithian strata in Slovenia markedly differ from the contemporaneous conodont faunas of North America and Asia. *Triassospathodus hungaricus* is the species present quite frequently in Slovenia where it occurs as a single conodont species (Kolar-Jurkovšek & Jurkovšek, 2015).

## CONCLUSIONS

- Seventeen conodont zones have been distinguished in the Lower Triassic strata of Slovenia.
- The introduced Early Triassic conodont zonation of Slovenia can be applied also for the shallow shelf environments of western Tethys.
- Certain conodont taxa are of significant importance for biostratigraphic correlation between western and eastern Tethys.

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## NEW UPPER TRIASSIC CONODONT BIOZONATION OF THE TETHYAN REALM

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### INTRODUCTION/ BACKGROUND

The Upper Triassic was first divided by Mojsisovics (1869) into three stages, which are Carnian, Norian and Rhaetian. Originally, these stages were defined based on ammonoids (Carnian and Norian) and bivalves (Rhaetian) and described in different localities in the northern Alps. During the last decades, Triassic conodonts have been the subject of intensive investigations and a strong literature is now available. In fact, in recent years, the known species of Upper Triassic conodonts quickly increased, because of detailed research carried out in several sections worldwide, mostly in order to define the Upper Triassic GSSPs. The constantly increasing amount of available data of conodont distributions on long and continuous sections, sometimes tied to ammonoid, radiolarian and bivalve occurrences or chemo- and magnetostratigraphy, permit us to propose a conodont biozonation for the entire Upper Triassic. When possible, our biozonation is built on phylogenetic reconstructions, in order to provide a framework in which taxonomical attributions and biostratigraphic studies could be less aleatory. The reconstruction of Upper Triassic conodont phylogeny unveils the evolutionary trends of the class Conodonta during its last 40 Myrs.

This biozonation is based on 20 Interval Zones and 2 Taxon-range Zones, and it is thought to facilitate the discussion of the three Stages, even though only the base of the Carnian stage is formally defined and ratified by the International Commission on Stratigraphy (Mietto et al. 2012). When possible, the proposed conodont biozonation is compared with ammonoid, radiolarian or bivalve biozones and numerical ages. We consider this proposed biozonation as a starting point for future Upper Triassic investigations, wishing for a constructive integration in order to delineate a reference conodont biozonation, commonly applied for Tethyan and global correlations.

### UPPER TRIASSIC CONODONTS - OVERVIEW

The pectiniform conodont record of the Upper Triassic documents pulses of severe extinctions followed by recovery events, testifying that the evolutionary history of the class Conodonta in the last 38 Myrs of its existence is characterized by a continuous decline of conodont specific diversity (see e.g. Martínez-Pérez et al. 2014 and references therein). During the Late Triassic, conodonts suffer four main extinction events before



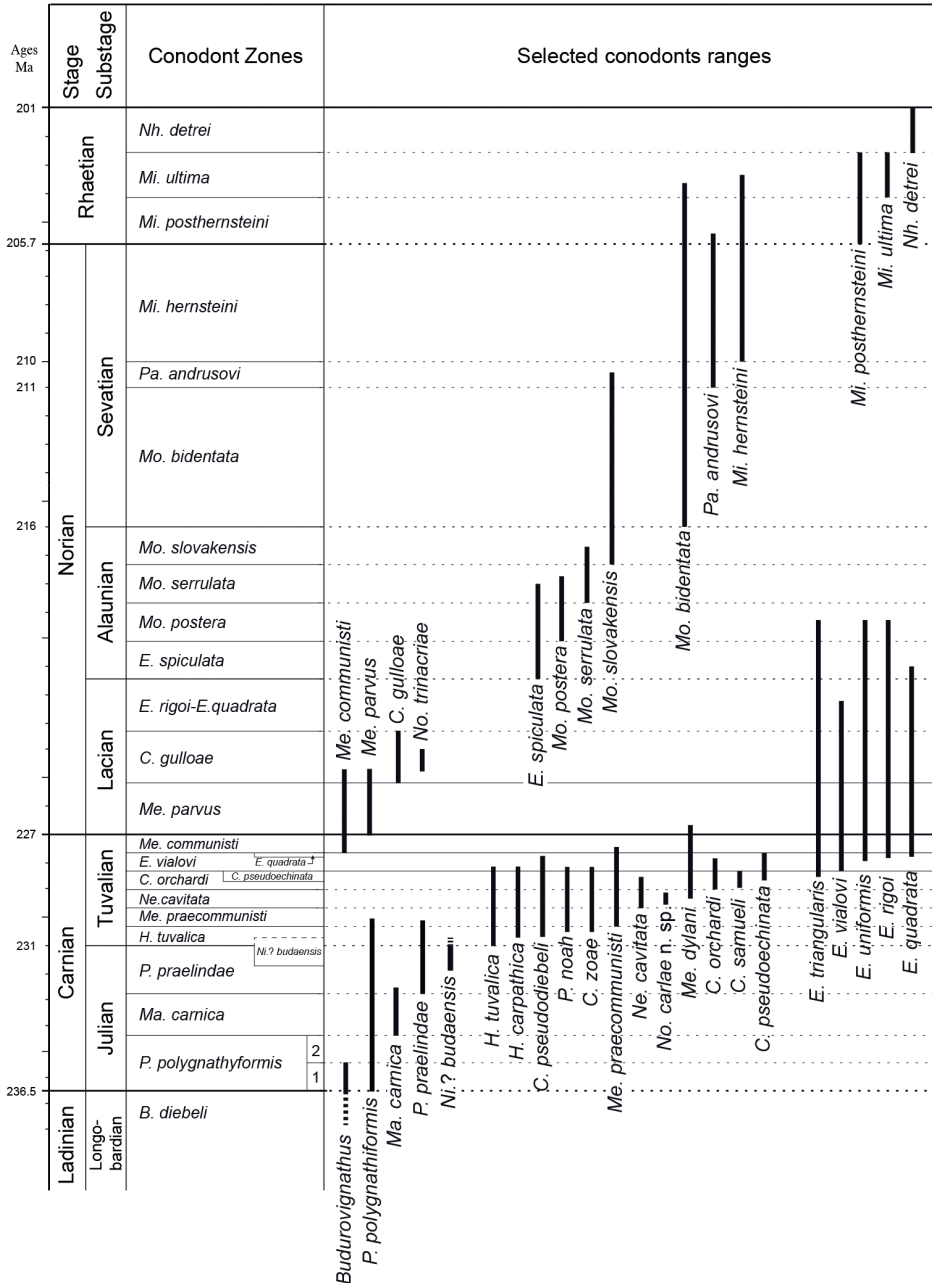


Fig. 1. New Upper Triassic conodont biozonation proposed and ranges of index species and most important conodonts for global correlations. B=Budurovignathus, C=Carnepigondolella, E=Epigondolella, H=Hayashiella, Ma=Mazzaella, Me=Metapolygnathus, Mi=Misikella, Mo=Mockina, No=Norigondolella, Ne=Neocavittella, Nh=Neohindeodella, Ni.?=Nicatoraella?, P=Paragondolella, Pa=Parvigondolella.

the final one at the end of the Rhaetian. The first is a weak one in the early Julian substage. The second is more significant at the Julian/Tuvalian substage boundary (middle Carnian). The third one, which is more similar to a faunal turnover rather than to a proper extinction, is at the Tuvalian/Lacian substage boundary. The fourth, occurs across the Norian/Rhaetian stage boundary testifying to a morphologic change towards simple cavitated species (i.e. genus *Misikella*). From the point of view of conodont morphology, each extinction is followed by a new speciation and by evident changes in the morphologic diversity of the platform elements. All these faunal turnovers seem to be related to climatic changes (Trotter et al., 2015).

## THE NEW CONODONT ZONATION

Conodonts are a leading fossil group for the definition of the biostratigraphic scale of the Palaeozoic. The incredible improvements reached in conodont research in the last years have shown the reliability of conodonts as a valid and sound biostratigraphic tool for also the Lower Mesozoic, making them a leading fossil group for the Upper Triassic (e.g. Orchard, 2016).

The conodont biozonation here presented is completely original and it is based on personal studies of Tethyan stratigraphic successions and comparisons with data from literature on conodonts from the Tethys and Boreal Provinces. The biozones proposed are based on phyletic lineages and conodont ranges from continuous pelagic successions with highly detailed and tightly spaced sampling. The main sources of data are the GSSP Tethyan candidate sections for the base of the Norian (Pizzo Mondello, western Sicily, Italy) and the base of the Rhaetian (Pignola-Abriola, southern Apennines, Italy), integrated with conodont distributions from other localities in all Tethyan provinces, and taken from the literature.

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## FAD OF *Metapolygnathus parvus*: PRIMARY MARKER FOR THE NORIAN GSSP

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**Keywords:** GSSP, Norian, conodont, Upper Triassic

### INTRODUCTION

Conodonts are the primary group for detailed biostratigraphy for most of the Palaeozoic Era and for the definition of Palaeozoic GSSPs. Recently researchers have reached an incredible level of detail also in the Triassic conodont biostratigraphy and phylogenesis, mainly due to the necessity of defining stage boundaries. We prove here how a conodont bioevent is the most preferable marker to define the base of the Norian stage, illustrating the great detail reached in the knowledge of conodont biostratigraphy across the Carnian/Norian boundary (CNB) in both the two GSSP candidate sections for the Norian stage: Pizzo Mondello (western Sicily, Italy) - PM (e.g. Nicora et al., 2007) and Black Bear Ridge (northern British Columbia, Canada)- BBR (e.g. Orchard, 2014). As a consequence of different paleolatitudinal depositional environments (western Tethys for PM and north-western Pangea margin for BBR), the conodont faunas of the two candidate sections for the Norian GSSP present differences related to endemism that have caused, during the years, divergences among specialists concerning conodont systematics. Nevertheless, after more than 10 years of detailed studies, it is now possible to recognize in both sections, common species and important phylogenetic lineages among the cosmopolitan forms, thus allowing to identify comparable conodont bioevents and turnovers (Rigo et al., 2017). In particular, the occurrence of a *Metapolygnathus* species, i.e. the FAD of *M. parvus* or *M. echinatus*, has been suggested as the possible marker for the base of the Norian stage (Nicora et al., 2007; Orchard, 2007). It is, in fact, possible to recognize in both provinces the entire lineage of *Metapolygnathus parvus*, descendent of *M. dylani* (Orchard, 2014). For this reason, we propose here the FAD of *M. parvus* as the primary marker to define the base of the Norian.

### METAPOLYGNATHUS PARVUS

The conodont *Metapolygnathus parvus* was established by Kozur in 1972, but the suggested holotype was a juvenile specimen. After more than 30 years, Noyan and Kozur (2007) presented a detailed analysis of the *Metapolygnathus communisti* group on new material from the Stefanion section (Argolis, Greece), emending a new description of *M. parvus* based on adult populations.

The occurrence of *M. parvus* is documented in other Tethyan successions, from Turkey, Slovakia, Southern Apennines (Italy), Hungary and at PM section (Sicily, Italy), as well as in North America at BBR, where three morphotypes named alpha, beta and gamma, characterized by three different stratigraphic distributions, were

described by Orchard (2014). Comparisons between the Tethyan and the North American populations easily prove that the Tethyan representative corresponds to *M. parvus* alpha of Orchard, which is the first morphotype to occur at BBR (Fig. 1).

Noyan & Kozur (2007) considered *M. parvus* as a probable descendant of *M. communisti*, as the terminal taxon of the phylogenetic lineage *Paragondolella noah* - *Metapolygnathus praecommunisti* - *Metapolygnathus communisti* - *Metapolygnathus parvus* (Mazza et al., 2011). Recently, Orchard (2014) suggested the newly established species *Metapolygnathus dylani* as ancestor of *M. parvus*, recognizing few specimens of *M. dylani* also at PM, within the morphologic variability of *M. praecommunisti*. The morphologic affinities between *M. praecommunisti* and *M. dylani* confirm the relationship between the two species, within their morphoclines, leaving no doubts about the presence of *M. dylani* in both the Tethys and North America.

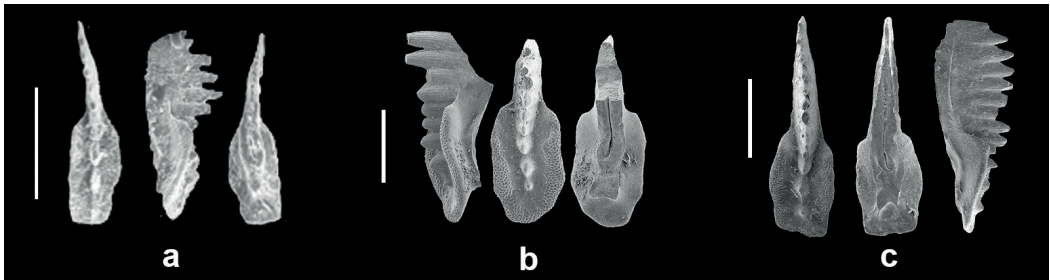


Fig. 1. (From Rigo et al., 2017) - Comparison between three different specimens of *Metapolygnathus parvus* Kozur from three separate regions: a) Northern Tethys (from Noyan & Kozur, 2007, fig. 7.1), North America (*Metapolygnathus* ex gr. *parvus* morphotype alpha; from Orchard, 2014, fig. 48, 23-25), and c) Neotethys (classified as "*M. communisti* morphotype without nodes" that, according to the description emended in Noyan & Kozur, 2007, corresponds to true *M. parvus*. From Mazza and Martínez-Pérez (2015, Pl. 6, fig. 23). Scale bars are 200  $\mu$ m.

## FAD OF METAPOLYGNATHUS PARVUS: PRIMARY EVENT FOR THE CNB

Since *Metapolygnathus parvus* is the descendant of *M. dylani* within the phylogenetic lineage *Paragondolella noah* - *M. praecommunisti* (or *M. ex gr. communisti* sensu Orchard, 2014) - *M. dylani* - *M. parvus*, it is possible to recognise easily the First Appearance Datum (FAD) of *M. parvus*, which first occurs above the FAD of *M. dylani* both at PM and BBR, documenting the transitional forms of its morphocline from *M. dylani*.

Also, occurrences of the representatives of the entire phylogenetic lineage that leads to *M. parvus* are recognisable in the same stratigraphic order (homotaxy) in both the North American and Tethyan provinces. The appearance of *M. parvus* is thus a synchronous bioevent in both Tethyan and North America realms and it can be thus considered as a real First Appearance Datum (FAD). Furthermore, the finding of *M. parvus* in all the provinces of the Tethys (southern, western and northern Tethys) in the same stratigraphic position, makes its FAD a cosmopolitan homotaxial bioevent.

## GLOBAL CORRELATIONS

In both Tethyan and North American realms the FAD of *Metapolygnathus parvus* also occurs within a few metres between the last occurrence (LO) of the last Carnian ammonoid genus *Anatropites* and the

first occurrence (FO) of the first Norian ammonoid genus *Geumbelites* (Rigo et al., 2017 and references herein).

Recently, the Subcommittee on Triassic Stratigraphy also recognised the occurrence of the bivalve *Halobia austriaca* as another possible primary marker event to define the base of the Norian Stage (Rigo et al., 2017). At both the GSSP sections proposed for the base of the Norian, PM and BBR, the bivalve *Halobia austriaca* occurs just above the occurrence of *M. parvus* (Rigo et al., 2017 and references herein). However, the occurrence of *H. austriaca* is also documented below the FAD of *M. parvus* and from undoubtedly Carnian strata and from the Carnian ammonoid *macrolobatus* Zone as reported by Orchard (2014 and references therein).

Furthermore, the first appearance of *M. parvus* occurs very close to the base of the positive  $\delta^{13}\text{C}_{\text{carb}}$  trend recognized in both PM and BBR sections and in other Tethyan sections, indicating a global trend recorded by the seawater chemistry. Noteworthy, this positive trend is coincident with a turnover (disappearance) of the typical Carnian conodonts to Norian metapolygnathids, named T2 at PM and also recognized at BBR, which are probably both related to a global spreading of oxygen depleted conditions (Rigo et al., 2017). The FAD of *M. parvus* also occurs within the upper part of magnetozone PM4n only at PM, because at BBR the original paleomagnetic signal has been cancelled by regional metamorphism (Nicora et al., 2007).

## CONCLUSIONS

We propose the FAD of *Metapolygnathus parvus* as the primary marker bioevent to define the base of the Norian, on the base of the following data:

1. it is easily recognizable,
2. it is in a lineage from its ancestor *M. dylani* and its FAD occurs close to a conodont faunal turnover (disappearance of the typical Carnian conodonts and mass occurrence of Norian metapolygnathids);
3. its FAD is homotaxial between indisputably Carnian *Anatropites* (below) and Norian *Guembelites* (above) ammonoids in both the North American and Tethyan provinces;
4. it occurs in correspondence with a positive  $\delta^{13}\text{C}_{\text{carb}}$  trend in both the 2 candidate sections;
5. it occurs in the uppermost part of the magnetozone PM4n at Pizzo Mondello section.

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## IMPACT EVENT AND CONODONT FAUNAL TURNOVER ACROSS THE MIDDLE-UPPER NORIAN TRANSITION IN THE UPPER TRIASSIC OF JAPAN

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**Keywords:** Upper Triassic, Norian, Panthalassa, impact, conodont

### INTRODUCTION

During the last 15 Myr of the Triassic, extinctions in major pelagic groups (such as conodonts and radiolarians) occurred in a stepwise fashion, unlike in a single mass extinction event such as occurred at the Triassic–Jurassic boundary. Available biostratigraphic data suggest that prominent faunal groups in the marine realm experienced a three-step extinction in the Late Triassic: at the end of the middle Norian, at the end of the Norian, and at the end of the Rhaetian. Catastrophic processes, such as episodes of anoxia and mantle plume volcanism, in the Central Atlantic Magmatic Province (CAMP) have been proposed to account for the second (end-Norian) and third (end-Rhaetian) extinction events. However, the cause of the initial (end-middle Norian) extinction event has been uncertain. Here, we show a possible temporal link between the end-middle Norian conodont extinction and a bolide impact, at a high level of precision.

### GEOLOGICAL CONTEXT

A Norian impact event has been inferred from anomalous concentrations of platinum group elements (PGEs) and negative Os isotope excursion in a claystone layer in an Upper Triassic bedded chert succession in the Sakahogi section, central Japan (Sato et al., 2013, 2016). Previous paleomagnetic studies of the Triassic bedded chert succession in the Sakahogi section suggest that these sediments accumulated in a pelagic, open ocean setting within a low- to mid-latitude zone of the Panthalassa Ocean, and accreted on to the eastern margin of the Asian continent during the Middle to Late Jurassic (Uno et al., 2015). In the Sakahogi section, the claystone layer ranges in thickness from 4 to 5 cm and extends laterally for at least 90 m. Studies of PGEs and Os isotopes have revealed that the anomalously high PGE abundances in the claystone layer resulted from a large chondritic impactor with a diameter of 3.3–7.8 km (Sato et al., 2016).

### MATERIAL AND METHODS

Samples for conodont biostratigraphy were collected from 53 chert beds across the claystone layer. To extract conodonts for biostratigraphic analyses, chert samples were soaked in a dilute HF solution (5%) for



24 h, and were then passed through a 63- $\mu\text{m}$  mesh sieve. This treatment was repeated 2–5 times to obtain sufficient residue for analysis. After drying the residue, conodonts were handpicked under a binocular microscope and were observed using a scanning electron microscope.

## RESULTS AND DISCUSSION

Based on the stratigraphic distributions of marker species, three conodont biozones are recognized in the Upper Triassic cherts of the study section: middle Norian *Mockina postera* zone; late Norian *Mockina bidentata* and *Misikella hernsteini* zones. A biostratigraphic analysis shows that four middle Norian taxa disappeared below the claystone layer, including *Mockina postera* and *M. spiculata*. Samples above the claystone bear *M. bidentata* along with more elongate *Mockina* elements resembling *Mockina mosheri*.

We propose that the impact event was probably the major factor responsible for the conodont extinction that occurred in the middle–upper Norian boundary. The base of the *Mockina bidentata* conodont zone provides the position in the middle–upper Norian boundary that is most closely aligned with the traditional base of the Sevastian, and which can be correlated with the impact event horizon in the study section (Onoue et al., 2016). The biostratigraphic record of conodonts suggests that a few *Parvigondolella* species survived across the claystone layer, but important middle Norian *Epigondolella* and *Mockina* species became extinct just below the impact horizon. The present data also shows the first appearance of late Norian *Epigondolella* and *Mockina* species within the first  $\sim 1$  Myr after impact. Conspicuous morphological changes occur in these genera across the impact claystone layer; the *Epigondolella* and *Mockina* species below the claystone layer are characterized by a wide platform, whereas species above the claystone have a longer and more narrow platform. The catastrophic collapse of the pelagic ecosystem after the impact event was probably the major factor responsible for the conodont turnover that occurred across the middle–upper Norian transition.

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## INTEGRATED BIO-MAGNETOSTRATIGRAPHY OF AN UPPER TRIASSIC PELAGIC SEQUENCE FROM PANTHALASSA OCEAN

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**Keywords:** Bedded chert, biostratigraphy, magnetostratigraphy, Panthalassa, Upper Triassic

### INTRODUCTION/BACKGROUND

The Late Triassic was characterized by several catastrophic events, such as widespread eruption of flood basalts, ocean acidification, and large extraterrestrial impact. The stratigraphic record of these events has been recently recognized in the Triassic bedded chert successions from the Jurassic accretionary complex in Japan. Because the Upper Triassic cherts in Japan have been deposited in a pelagic environment within a Paleo-Pacific (Panthalassa) deep basin, their stratigraphic record is particularly important for understanding the impact of global catastrophic events in the Late Triassic. Nevertheless, this process has been hampered by the poor age control for the cherts. The ages of the Triassic bedded cherts were predominantly determined from the radiolarian biostratigraphy, based on an indirect correlation with the ages determined from European and North American radiolarian biostratigraphies. However, the accurate calibration of chronostratigraphic stages and substages has been developed using ammonite and conodont biostratigraphies and magnetostratigraphy. In order to calibrate the Upper Triassic radiolarian zonation with the standard Triassic timescale, the conodont biostratigraphic and magnetostratigraphic studies are required in the pelagic chert successions in Japan.

This study undertook to establish the conodont biozones and magnetostratigraphy in exactly the same sections that Sugiyama in 1997 used as the type sections for his radiolarian biozones. The stratigraphic intervals from the Carnian to the Hettangian in his sections H, N, Q and R in the Inuyama area, central Japan were examined.

### GEOLOGICAL CONTEXT

Sections H, N, Q and R in which Sugiyama (1997) investigated the radiolarian biostratigraphy, are located in the Inuyama area of central Japan. The sections are part of the Kamiaso Unit, which is regarded as a Jurassic accretionary complex in the Mino Belt. The Kamiaso Unit consists mainly of Early Triassic 'Toishi-type' siliceous shale, Middle Triassic to Early Jurassic bedded chert, and Middle-Late Jurassic terrigenous clastic rocks. These rocks form the Sakahogi syncline and are exposed repeatedly as stacks of thrust sheets on the banks of the Kiso River. Yao et al. (1980) identified four chert thrust sheets and labelled them CH-1, CH-2, CH-3, and CH-4 in structurally ascending order. Section H, Q and R are included in CH-2, while section N is situated in CH-3, respectively.

## MATERIAL AND METHODS

In this study, 178 chert samples were collected from sections H, N and Q to achieve a biostratigraphic dataset of conodonts. In total, 140 samples were crushed into small pieces and immersed in a 5%–10% solution of hydrofluoric acid in a 100 ml plastic beaker for ca. 10 hour to remove the matrix.

477 oriented hand samples (red cherts) were collected from sections H, Q and R at average sampling interval of ~30 cm. Each hand sample was cored and cut into cylindrical specimens (25 mm in diameter, 22 mm in length). 357 specimens were subjected to progressive thermal demagnetization with a Natsuhara TDS-1 thermal demagnetizer. Natural remanent magnetizations were measured with a 2G Enterprises DC-SQUID cryogenic magnetometer and the component structure of the NRM was plotted on vector end-point demagnetization diagrams.

## RESULTS

This study described in detail the conodont zonation and some important conodonts including 29 species referred to 11 genera from the study sections. Based on recent conodont taxonomy and the stratigraphic distribution of marker species, eight conodont zones were defined: *Paragondolella tadpole* interval Zone, *Quadralella tuvalica* interval Zone, *Epigondolella quadrata* interval Zone, *E. triangularis* interval Zone, *Mockina postera* interval Zone, *Mockina bidentata* interval Zone, *Misikella hernsteini* interval Zone, and *Misikella posthernsteini* interval Zone. These were correlated with the coeval radiolarian zonation established by Sugiyama in 1997.

Thermal demagnetization showed four distinct remanent magnetization components from the cherts as mentioned in previous studies (e.g. Shibuya and Sasajima 1986). A reversal test is performed using the tilt corrected data set of the highest blocking temperature component, and an intermediate test result is obtained. We regarded the component as the primary remanent magnetization, which produced a magnetostratigraphy of the lower Carnian to Hettangian. The magnetostratigraphy consists of 20 substantive normal and reverse magnetozones, defined by measurement of 357 specimens. The mean inclination of the last demagnetized component suggests the bedded chert originated in an equatorial area.

## DISCUSSION

The Upper Triassic conodont fauna of sections H, N and Q yields several common species that can be biostratigraphically correlated with sections in British Columbia, Sicily, Salzkammergut, and the Chichibu and Tamba belts of Japan. The Carnian–Norian boundary interval in the studied sections is tentatively placed between the last occurrence of Carnian species (*Q. tuvalica*) and the first occurrence of Norian species (*E. quadrata* and *E. spatulata*) because of the absence of *Metapolygnathus parvus* and other diminutive elements reported from the GSSP candidate sections for the Carnian–Norian boundary.

Although the magnetostratigraphic data in the vicinity of the early-late Carnian boundary is the first record from the marine section, the magnetostratigraphy of samples in Carnian–Rhaetian interval was well correlatable with that of Tethyan marine sections (e.g. Pizzo Mondello and Silická Brezová sections). This correlation implies that the bedded chert of Inuyama area was deposited in the Northern Hemisphere, assuming that the rocks in the Tethyan marine sections were deposited in the Northern Hemisphere. The correlation of the magnetostratigraphic data also suggests that loss of the stratigraphic record at the Triassic–Jurassic boundary in the study sections, possibly due to structural erosion or hiatus.

By means of magnetostratigraphic correlation to the Newark astrochronological polarity time scale (APTS, Olsen et al., 2010), a new age model of sedimentation for the Upper Triassic bedded chert successions in the Inuyama area was obtained. This correlation places the Carnian-Norian boundary in the studied sections, at the top of Chron E7r in the Newark APTS (~227 Ma), and the Norian-Rhaetian boundary can be placed within Chron E20r (205-206 Ma). These ages contrast with the age constraints provided by the cyclostratigraphic data of the Triassic bedded chert successions in the Inuyama area (Ikeda and Tada, 2014).

## CONCLUSIONS

1) Based on recent conodont taxonomy, new conodont biostratigraphic data are presented from the Lower Carnian to the Rhaetian bedded chert succession in central Japan, where the standard radiolarian biostratigraphy has previously been investigated (Sugiyama, 1997). The defined conodont zonation of section H and N is comparable to that in North America, Tethys, and other sections in southwest Japan.

2) We established the lower Carnian to Rhaetian magnetostratigraphy of the bedded chert successions, which consists of 20 substantive normal- reverse polarity chrons. The magnetostratigraphy in the vicinity of the early-late Carnian boundary is the first record from the marine section.

3) Magnetostratigraphy from the bedded chert succession in the Inuyama area was correlated with that of Tethyan marine sections. Assuming that the rocks in the Tethyan marine sections were deposited in the Northern Hemisphere, the magnetostratigraphic correlation indicates that the bedded chert of Inuyama area was deposited in the Northern Hemisphere.

4) Based on magnetostratigraphic correlation with Newark APTS, the Carnian-Norian boundary in the studied sections can be placed at the top of Chron E7r in the Newark APTS, and the Norian-Rhaetian boundary falls within Chron E20r.

5) The intercalibrated conodont–radiolarian biostratigraphy and magnetostratigraphy from the studied sections accurately calibrates the radiolarian zones in Japan with standard chronostratigraphic stages and substages.

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# **GECKO: GLOBAL EVENTS IMPACTING CONODONT EVOLUTION**



## CONODONT SKELETAL ANATOMY AND APPARATUS COMPLEXITY THROUGH TIME

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**Keywords:** Dentition, skeletal architecture, evolutionary history, function, constraint

Knowledge of the conodont skeleton in terms of the morphologies of the elements and the positions they occupy provides the foundation of homology, taxonomy and evolutionary relationships in conodonts. Understanding that conodonts are vertebrates and that their elements functioned as a raptorial array and teeth provides the biological and evolutionary context within which to interpret their responses to external environmental drivers.

Our knowledge of conodont skeletal anatomy has seen great strides forward in recent decades, and it is now clear that in the context of vertebrate dentitions, conodonts are very unusual. In most major clades of vertebrates, teeth are more or less uniform in morphology (homodont); they can be assigned to relative positions based on whether they are on the bones forming the upper, lower or pharyngeal jaws, and numbered in terms of their location relative to landmarks such as the symphysis. But for such dentitions it is not possible to recognise homologous tooth positions in different taxa, and once teeth become disarticulated, any homology information is lost because teeth from separate locations are morphologically indistinguishable. The nature of the dentition of conodonts, like that of mammals, stands in marked contrast to this common pattern. In mammals and conodonts, homologous teeth from different taxa can be compared, and even where the morphology of teeth differs considerably, secure homologies can be established on the basis of the relative positions of tooth types. Also, the morphological complexity of teeth, and the degree to which they are differentiated into types that occur in particular locations in the mouth means that disarticulated, isolated teeth and elements retain evidence of homology and phylogenetic signal.

While these similarities allow parallels to be drawn between conodont and mammal dentitions, they also highlight some interesting and significant differences in the broad evolutionary patterns exhibited by the two groups. Across mammal phylogeny, and through time, dental formulas vary markedly, with significant changes between taxa in numbers of canines, premolars and molars. This in addition to the clear differences in morphology of the teeth. In contrast, articulated skeletal remains of conodont indicate that their dental plan was remarkably stable through much of their 300 million year existence, and direct evidence of the 'standard' 15 element arrangement has been recognized in natural assemblages representing diverse clades of conodonts ranging in age from Ordovician to Triassic.

Why, despite the major perturbations in the global marine biosphere they endured, did conodonts exhibit such anatomical stability? This is likely to be in large part a consequence of strong developmental and functional integration, and in this context, hypotheses that some taxa had fewer than 15 elements in their apparatus is worth closer scrutiny. Loss of elements from different domains of the apparatus has different



implications for function, taxonomy and our reading of the fossil record. The loss of occupants of positions in the S domain implies changes in food capture. The loss of elements from the P domain implies a change in food processing ability, perhaps linked to a shift towards foods that can be ingested with less slicing or crushing. Also, because the data for diversity and disparity in the conodont fossil record is primarily derived from P elements, evidence of loss of elements from the P domain has broad implications for understanding of evolutionary patterns.

## THE EVOLUTION OF CONODONT FORM THROUGH TIME

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**Keywords:** Conodont elements, conodont apparatuses, shape, size

Conodont elements are the only mineralized skeletal remains of an extinct group of soft-bodied, nektonic chordates that inhabited the oceans from the late Cambrian through the Triassic (some 300 million years). Interest in the effectiveness of conodont elements as chronostratigraphic markers, coupled with the search for the biological affinities of the conodont animal, has often obscured the fact that conodonts not only witnessed all major global changes during their 300 million year existence (e.g., major chemical perturbations to the ocean-atmosphere system, extinction and diversification events, the evolution of major new Bauplane as life emerged from the water and invaded the land), and were themselves affected by these changes. During this time the development of novel predation strategies initiated successive waves of "arms races". In addition, three major extinction events – two of which were among the largest in Earth's history – resulted in the complete taxonomic and ecological restructuring of marine communities. But curiously, irrespective of this tremendous explosion of environmental change, conodonts have generally been considered more-or-less static entities dwelling within the confines of their oceanic environment, a morphological "constant" in an ever-evolving world.

The classification of conodonts has traditionally been based on the analysis of their elemental morphology. Three main categories of conodont elements have been identified: coniform (including rastrate), ramiform, and pectiniform. If observed through their entire stratigraphic range, conodont elements and apparatuses have undergone substantial modification both in their architecture and in their elemental shapes. Apparatuses composed of only coniform elements characterize most of the earliest evolutionary history of the group, while multi-elemental shapes grew and diversified in later periods. Interestingly recent comparisons within the same morphological category have revealed both persistencies as well as morphologic innovations. For

example, Jones et al. (2012) explored morphological variation in *Wurmiella excavata* in order to better constrain the function of this element in food processing. We address this issue of characterizing the evolution of conodont element form (size + shape) quantitatively using both geometric and image-based approaches previously applied to the analysis of vertebrate, invertebrate and microplankton form within an explicitly phylogenetic context. Our intention is to document the evolution of conodont form independently from any interpretation of the function conodonts had in the living animal so that correlations between form and function can be investigated using standard statistical hypothesis tests.

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## EARLY AND MIDDLE ORDOVICIAN CONODONT EVENTS OF BALTOSCANDIA

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**Keywords:** Baltoscandia, conodonts, events, Lower and Middle Ordovician

### INTRODUCTION

The Baltoscandia region was a wide platform covered by an epicontinental sea on the Baltic Craton during Early to Middle Ordovician. In the same period the Baltica palaeoplate moved rapidly from high southern latitudes at about 50°S towards low southern latitudes reaching about 40°S in the mid Darriwilian. This northern directed movement crossed climate zones and the platform sedimentary succession changes from predominantly siliciclastic sedimentary rocks with minor carbonate in the late Cambrian to Early Ordovician to increasingly carbonate-rich rocks: first by cool, temperate shallow-water limestone (Orthoceras Limestone) and then by warmer temperate shallow-water carbonate and marl accumulation at the end of the Middle Ordovician (Darriwilian).

### RESULTS

True conodont faunal endemism within Baltica has not been observed. Instead Early and Middle Ordovician multielement conodonts from Baltoscandia record a series of faunal events comprising (1) conodont faunal phylogenetic developments, (2) migration events, (3) immigration events and (4) significant faunal turnovers.

The late Cambrian and earliest Ordovician (early Tremadocian) record of the conodont faunas is incomplete for the Baltic Platform, because of pronounced global sea-level lowstand. The conodont phylogenetic evolution starting from late Tremadocian (Early Ordovician) comprises the significant lineage of *Paltodus*, '*Acodus*' (= *Acodus deltatus* sensu stricto), *Trapezognathus* and to *Lenodus* and from the top Floian the lineages of *Baltoniodus* and *Microzoarkodina*. Several migration events include genera in the Tremadocian and the significant *Oepikodus evae* acme in the Floian. The dispersal of the bi-membrate genus *Eoplacognathus* (sensu stricto) in the Darriwilian was a significant migration event from deeper-water setting at the margin of the craton and onto the platform. Visitors (i.e. *Yangtzeplacognathus*) immigrating from other palaeocontinents or plates also reached the Baltica plate. These stayed only for a short period and disappeared equally fast as they appeared. However, the precise geographic source region for some invaders and the palaeoceanographic conditions that facilitated dispersal into the Baltoscandia platform is still poorly understood. Biogeographic analysis indicates that in the Early Ordovician communication exclusively with Laurentia prevailed. This line of communication was disturbed at the beginning of the Middle Ordovician (Dapingian), where communication with

Peri-Gondwana faunas also appeared on the Baltic platform. The Dariwillian invasions were multidirectional that involved taxa immigrating into the Baltoscandian region from both Laurentia and peri-Gondwana plates that approached continental margins of the Baltica palaeocontinent. The late Darriwilian – early Sandbian conodont faunas of Baltica show close similarities to faunas in the oceans, at margins of Laurentia, South China, and other adjacent tectonic plates and terranes, which indicate their semi-cosmopolitan distribution.

## **CONCLUSIONS**

The synchronicity of the geologic, climatic and oceanographic events supports the influence of geologic events on conodont evolution on Baltica. Causal links between the faunal turnovers includes predominantly (1) sea-level changes (2) tectonics and (3) global climate change. The trends also correlate with the perturbations in the carbon cycle, with the  $d^{13}C$  minima corresponding to the low diverse fauna and faunal turnover and the positive values generally occurring during radiations.

## DIVERSITY AND TURNOVER RATES OF CONODONT SPECIES FROM THE MIDDLE ORDOVICIAN OF THE ARGENTINE PRECORDILLERA

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**Keywords:** Conodonts, diversity, quantitative stratigraphy, Middle Ordovician, Argentine Precordillera

### INTRODUCTION

Studies on taxonomic diversity through time constitute useful tools for understanding evolutionary processes and patterns. In this sense, conodonts are particularly suitable due to their abundance, continuity in their stratigraphic record and excellent preservation (Sweet and Donoghue 2001[not in refs.]). The paleoecology of conodonts received much attention after the pioneering work of Seddon and Sweet (1971), Barnes and Fåhræus (1975), among others. Recently, the high diversity of Ordovician conodonts was considered to propose a combined ecological model, where conodonts occupied a variety of available ecological niches with different modes of life (Zhen and Percival, 2003). Lately, a recurring theme in conodont paleoecology has been the effect of eustatic sea level change in conodont community structures (Wu et al., 2014, and referred papers therein); for example, patterns of Middle Ordovician conodont diversity change were attributed mostly to oscillations in the sea level for the Argentine Precordillera (Albanesi and Bergström, 2004).

The Precordillera of western Argentina is characterized by a thick Cambro-Ordovician succession (ca. 2,200 m) of marine limestones that interdigitate with clastic slope deposits toward the west. Spanning a range of depositional environments, from shallow intertidal to marginal shelf and deep ramp settings, the Precordillera is the only lower Paleozoic basin of South America with a carbonate platform. A significant succession of black shales developed after the drowning of the carbonate platform associated with a rapid sea level rise during the early Middle Ordovician. The only remnants of carbonate deposits in the Precordillera concomitant with the referred black shales succession occur at the Las Chacritas and Las Aguaditas localities, and the Las Aguaditas Formation is the only unit that shows an environmental transition from platform to slope in the Middle Ordovician. The equivalent[do you mean correlative? Or, perhaps age-equivalent is better?] Gualcamayo Formation conformably overlies the San Juan Formation limestones and is characterized by black shales interbedded with calcareous strata, deposited on the outer platform (Astini, 1995).

Conodont species diversity is analyzed herein by means of conventional measures: estimated mean standing diversity (MSD) (Foote, 2000), total diversity and normalized diversity (Cooper, 2004), and a quantitative stratigraphic approach with the CONOP9 program (Sadler and Cooper, 2003). These measures are widely used in paleoecology and are discussed elsewhere (e.g., Foote, 2000, and referred works). The biostratigraphic intervals that span the *Lenodus variabilis*, *Yangtzeplacognathus crassus*, *Eoplacognathus pseudoplanus* and *Eoplacognathus suecicus* Zones are interpreted from 4 sections in the Argentine Precordillera from the

San Juan Province: Las Chacritas type section, Las Chacritas-south section, Las Aguaditas Creek and Cerro La Chilca sections.

## MATERIAL AND METHODS

This study is based on collections of Darriwilian (Middle Ordovician) conodonts from Las Aguaditas Creek, Las Chacritas River and Cerro La Chilca sections of the Central Precordillera. Fifty-one species were identified in the stratigraphic interval from the *Lenodus variabilis* to the *Eoplacognathus suecicus* zones, species listed with "?," "cf.," "aff." and subspecies were omitted, except for "*Bryantodina*" aff. *typicalis* which is a morphologically distinctive species. This database was used in CONOP9 program (Sadler and Cooper, 2003) to derive a composite succession and identify conodont zones to be used as time units. The MSD of conodonts was estimated using conventional measures: estimated MSD (Foote, 2000), total diversity, and normalized diversity ( $D_{norm}$ ) (Cooper, 2004). We also used a quantitative stratigraphic approach, CONOP9 software, in order to get a more reliable estimation of the MSD.

## RESULTS

A composite range chart for Darriwilian conodonts from the Central Precordillera is herein presented, where the *L. variabilis*, *Y. crassus*, *E. pseudoplanus* and *E. suecicus* Zones are identified (Fig. 1). Conodont diversity curves show the same trend based on the different approaches (Fig. 2a). The curves of  $D_{norm}$  and estimated MSD run parallel and are extremely close to each other, showing that the consideration of single interval taxa do not distort the results; on the other hand, total diversity tracked through increased values. Conventional measures show a gradual increase in species diversity from the *L. variabilis* Zone and reach a maximum peak in the *E. pseudoplanus* Zone, then decrease in the *E. suecicus* Zone. However, the later biozone is poorly represented in the study sections due to a stratigraphic hiatus. The diversity curve based on CONOP9 approach showed a rapid diversity increase throughout the *L. variabilis* Zone reaching a first diversity peak in the *Y. crassus* Zone and a second one in the *E. pseudoplanus* Zone, subsequently it decreases to a minimum through the *E. suecicus* Zone. Species appearance is considerably high during the *L. variabilis* Zone (19 species), and increases within the *Y. crassus* Zone with 23 species (Fig. 2b), decreasing upwards to its lowest point in the *E. suecicus* Zone (2 species). In the *E. pseudoplanus* Zone species disappearance is higher than in the previous zones (8 species); nonetheless, diversity reaches its highest value due to the high number of range-through species, and species that have their first appearance datum (30 and 7 species, respectively).

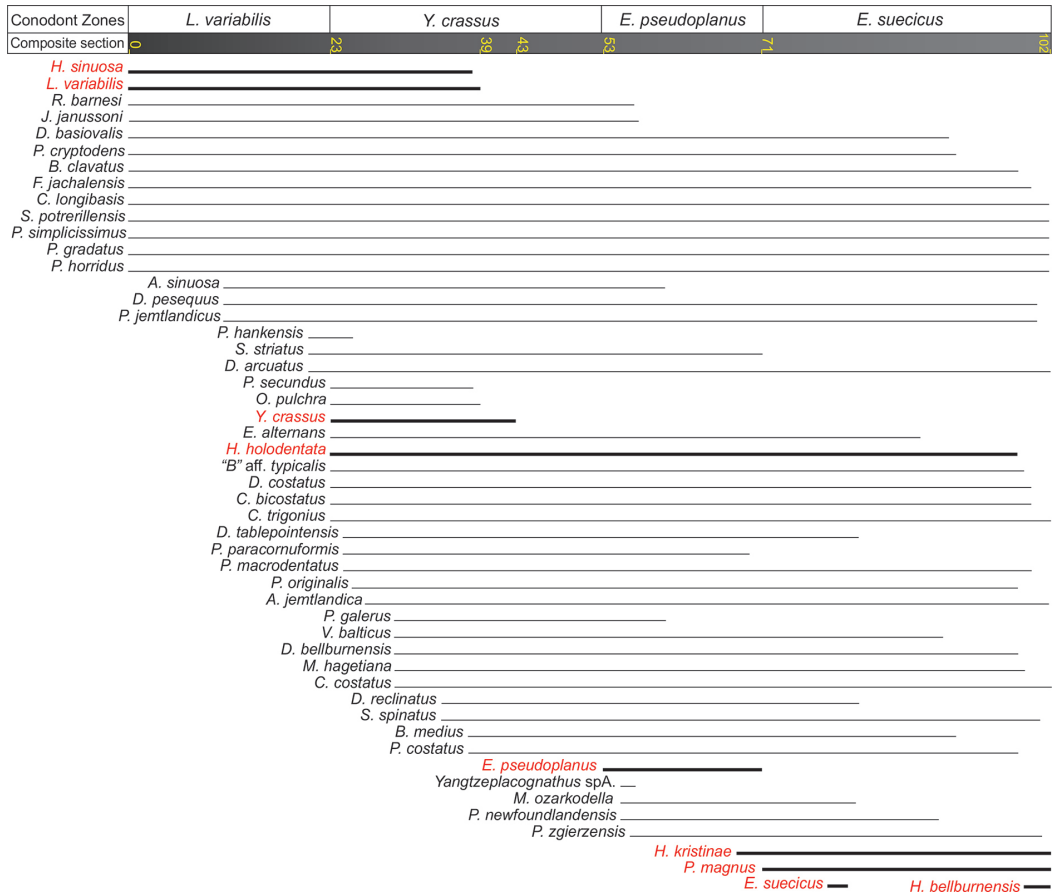


Fig. 1. CONOP9 composite range chart for Middle Ordovician conodonts from the Las Chacritas, Las Aguaditas Creek and Cerro La Chilca sections and identified conodont zones.



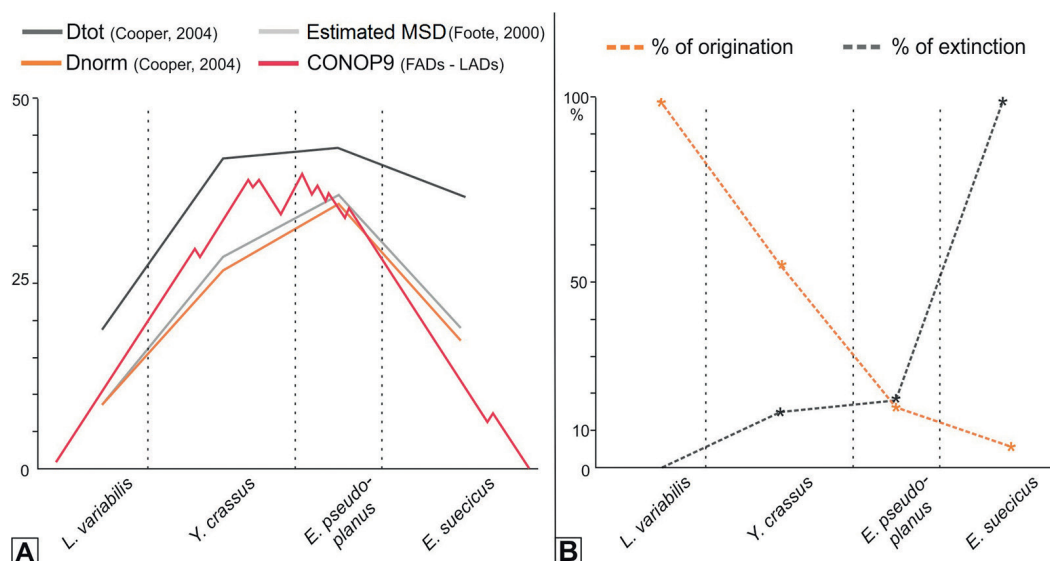


Fig. 2. A. Diversity curves of conodont species from the study sections after conventional approaches (Dtot, Dnorm and estimated MSD) and CONOP9 throughout the *L. variabilis*, *Y. crassus*, *E. pseudoplanus* and *E. suecicus* zones. B. Origination and extinction percentages of conodont species through the *L. variabilis*, *Y. crassus*, *E. pseudoplanus* and *E. suecicus* zones.

## CONCLUSIONS

Detailed conodont taxonomy and occurrence records were performed in 4 stratigraphic sections from the Central Precordillera. The data enabled the application of a quantitative stratigraphic approach (CONOP9), which led to the recognition and delimitation of the mentioned biozones. Different diversity measures showed similar trends for Darriwilian conodonts from the Argentine Precordillera. However, as shown by Hints et al. (2011), estimated MSD and normalized diversity tend to underestimate the CONOP9 diversity curve, while total diversity tends to overestimate it.

These results show a positive trend in conodont diversification throughout the Middle Darriwilian. Both methodologies reveal a rapid conodont diversification through the *L. variabilis* and the *Y. crassus* zones. According to the estimated MSD and normalized diversity approach, the highest conodont diversity is reached in the *E. pseudoplanus* Zone. On the other hand, total diversity and CONOP9 curves show increased diversity values, both in the *Y. crassus* and *E. pseudoplanus* zones. In the former, an important origination pulse occurs (45%) and reveals a 69% turnover rate, while in the *E. pseudoplanus* Zone a 16% of species origination and 34% of species turnover take place. A marked drop in conodont diversity is documented at the end of the *E. suecicus* Zone by the CONOP9 approach. This bias is the result of all conodont species having their last appearance datum due to a biostratigraphic unconformity; nevertheless, a total of 37 species ( $D_{\text{norm}} = 18.5$ ) are present in this interval. Here, the conventional measures seem to provide a more appropriate MSD estimation.

This pattern of diversity appears to be related to local sea level fluctuations. Most of the conodonts that appear in the *L. variabilis* and *Y. crassus* zones have their records in the upper San Juan Formation at the 4 study sections, where 42 out of 51 species were documented. The uppermost part of the San Juan Formation

represents the shallowest depositional environment from the units analysed, which is interpreted as distal ramp without storm influence. The facies transition between this formation and the overlying units at different localities is interpreted to have been caused by a flooding event over the carbonate platform. In these deeper environments the conodont species tend to disappear or to occur in low abundances, except for the middle and upper parts of the Las Chacritas Formation (*E. pseudoplanus* and *E. suecicus* Zones), and the uppermost strata of the lower member of the Las Aguaditas Formation (*E. pseudoplanus* Zone), where a shallowing event is responsible for a high number of species (45 records) and specimens (over 9000 specimens). These data [or, observations] reveal the profound effect of oceanographic cycles in faunal changes.

## Acknowledgements

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## DIRECTIONAL EVOLUTION IN THE *HISTIODELLA* LINEAGE

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**Keywords:** *Histiodellella*, elliptic Fourier analysis, Evolution, Darriwilian, Argentine Precordillera

### INTRODUCTION

Several species of the Ordovician genus *Histiodellella* have been used as index fossils (e.g., Sweet, 1984; Maletz, 2009; Stouge, 2012). This taxon is distributed through low to mid-high latitude latitudinal regions and characterizes deep platform or platform margin to slope depositional environments (Stouge, 2012). [But, many occurrences of *Histiodellella* species are from shallow platform sites, e.g., Oklahoma (Bauer; McHargue); U.S. Appalachians; Durness Gp., Scotland (R.Raine)] *Histiodellella* is particularly abundant in the Las Aguaditas creek stratigraphic section of the Central Precordillera, Argentina, where it presents a continuous record through the upper part of the San Juan Formation and the lower member of the Las Aguaditas Formation, Darriwilian in age (fig. 1). The upper part of the San Juan Formation presents a high diversity and abundance of conodont elements (Feltes *et al.*, 2016)[have not read this yet], including those of *Histiodellella*. In the lower and middle parts of the lower member of the Las Aguaditas Formation the conodont diversity decreases sharply because of the flooding event that submerged the carbonate platform. The sea level change caused unfavourable conditions for the development of the conodont fauna in this geological setting. In the upper part of the lower member, the diversity recovers and *Histiodellella* species reappears. In the study section, five species of *Histiodellella* were identified following Ethington and Clark (1981), McHargue (1982), Stouge (1984) and Bauer (2010); i.e., *H. sinuosa*, *H. serrata*, *H. holodentata*, *H. cf. holodentata*, and *H. kristinae*, which share a certain ancestor-descendant relation according to the phylogenetic hypotheses of McHargue (1982) (from *H. sinuosa* to *H. serrata*), and Stouge (1984) (from *H. holodentata* to *H. kristinae*). Elements that occupies the Pa position in the apparatus of *Histiodellella* are predominant in the collection; these are the most useful elements in the taxonomy to distinguish between different species of the genus. The aim of this work is to analyze the evolutionary transformation experienced by this taxon across the *Yangtzeplacognathus crassus* to the *Eoplacognathus pseudoplanus* zones.

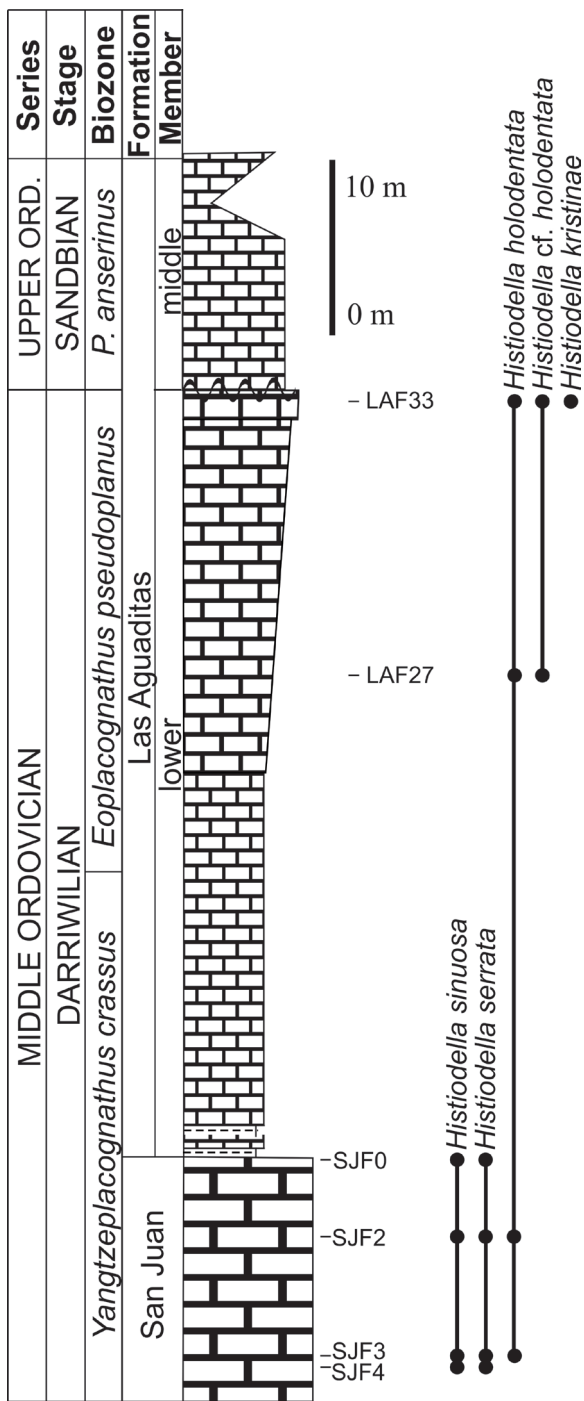


Fig. 1. Stratigraphic column of the Las Aguaditas Creek section, at the homonymous locality in Central Precordillera of San Juan Province, Argentina (sampled strata that provided the analysed elements of *Histiodella* are represented).

## MATERIAL AND METHODS

An elliptic Fourier analysis is carried out (Kuhl y Giardina 1982; Ferson *et al.*, 1985), using the free access software SHAPE v.1.3 (Iwata and Ukai, 2002) to evaluate the morphometry of *Histiodela* specimens. The data is treated in PAST v.2.17 (Hammer *et al.*, 2001) to perform a principal component analysis (Fig. 2) in order to represent the element distribution in the morphospace; also, a multivariate analysis of the variance is performed in order to consider if there exists significant difference between species. The outline of a specimen represents the inside shape of the element, linking the nadirs between denticles and the cusp (see Jones, 2006); thus, broken tips of denticles and cusp, do not modify the shape. Conodonts are characterized by continuous growth, for that reason, the outline includes only the five denticles closer to the cusp in the anterior process, in order to reduce the variation of the element shape due to differences in the ontogenetic state of development. In the case of the Pa element of *Histiodela* it corresponds to the length of the anterior process by successive addition of denticles. We decided to take into account five denticles because each specimen of the study collection presents at least five denticles. Moreover, with this number of denticles the shape of the element is representative of the maximum height reached by the denticles of the anterior process, which is taxonomically relevant. A total of 206 Pa elements of *Histiodela* are analysed, which were recorded (or recovered) through 55 m thick of the stratigraphic column, *i.e.* the uppermost 12 m of the San Juan Formation and the whole lower member of the Las Aguaditas Formation (43m).

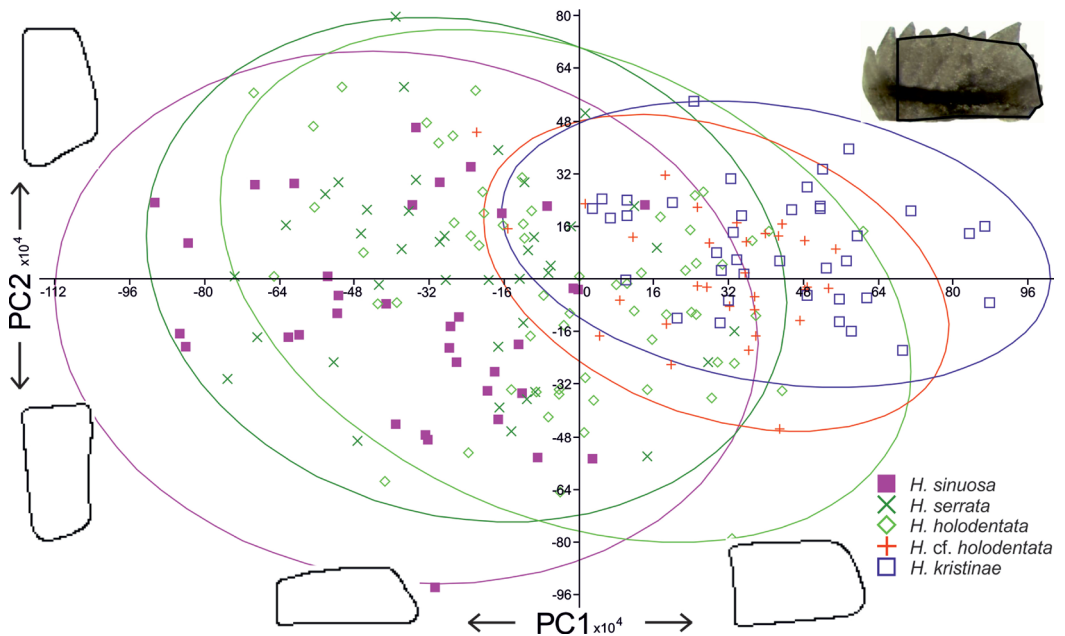


Fig. 2. Principal component analysis of specimens from *Histiodela* species recorded in the study section. PC1 and PC2 explain the 43.49% and 22.43% of the variation, respectively.

## RESULTS

The two first principal components are represented and explain 65.92% of the variance. The PC1 explains 43.49% of the change of the element form, and represents mostly a contrast in the element height. The specimens with positive values in this component have a high anterior process, where the oral margin becomes nearly parallel to the base due to a widening of the distal part of the anterior process (the length/height ratio of the element tends to 1). Conversely, the elements with negative values present a thinner anterior process, and the element acquires an elongated shape. The PC2 explains 22.43% of the variance, and the most evident change through this component is the height of the distal part of the anterior process relative to the height of the cusp. Elements with positive values in the PC2 have a distal part of the anterior process lower than the cusp region and elements with negative values have the opposite measures.

Multivariate analysis of the variance:

	<i>H. sinuosa</i>	<i>H. serrata</i>	<i>H. holodentata</i>	<i>H. cf. holodentata</i>	<i>H. kristinae</i>
<i>H. sinuosa</i>	0	0.984437	0.12873	0.298649	0.00993142
<i>H. serrata</i>	0.984437	0	0.513993	0.350823	0.010713
<i>H. holodentata</i>	0.12873	0.513993	0	0.0194556	0.00013136
<i>H. cf. holodentata</i>	0.298649	0.350823	0.0194556	0	0.966323
<i>H. kristinae</i>	0.0099314	0.010713	0.000131365	0.966323	0

The MANOVA performed with the Fourier coefficients shows significant difference between *H. kristinae* and all of the species, except for *H. cf. holodentata*, and between *H. holodentata* and *H. cf. holodentata*. No significant difference is verified between *H. serrata* and *H. sinuosa*, *H. holodentata* and *H. cf. holodentata*, neither between *H. sinuosa* and *H. cf. holodentata*.

## DISCUSSION

It is remarkable that the MANOVA does not reveal significant differences between *H. cf. holodentata* with *H. sinuosa* and *H. serrata*, due to the temporal and phylogenetic distance that separates them. On the other hand, it is not surprising that this method does not differentiate between *H. sinuosa* and *H. serrata*, since the distinctive characteristic of the latter is the beginning of the development of denticles in the posterior process, but preserving a similar inner outline. However, the 95% ellipse of *H. sinuosa* is located left in relation to that of *H. serrata* in the PC1 (Fig 2.). This topology means that elements of *H. sinuosa* are more elongated, or poses lower denticles in the anterior process, which is the principal variation in the shape as explained.

## CONCLUSIONS

The outline technique applied in our study results useful to detect continuous and subtle changes in the morphology of the elements. However, it implies the drawback of not considering the denticles shapes in the process, which is relevant in the evolution of this taxon. This may be the reason that explains the absence of differences between some species. It supports the hypothesis that the *Histiodela* lineage evolves anagenetically, through continuous changes in shape, and the appearance of novel characters, which can continue its

development in the descendant species. An evolutionary tendency of the denticles to surpass the height of the cusp is verified by this analysis. The scatter plot shows that the species limits are diffuse, while the elements are not grouped discreetly; which is supported statistically. However, the species are positioned in an order that coincides with the stratigraphic record and the phylogenetic hypothesis followed in this study; thus supporting the stratophenetic interpretations that were traditionally held for the *Histiodella* lineage. Finally, we suggest that *H. holodentata* descends from *H. serrata*, as supported by the PCA analysis.

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## NEW TYPES OF EXCEPTIONALLY LARGE CONODONT APPARATUSES WITH HYALINE ELEMENTS FROM THE MIDDLE ORDOVICIAN WINNESHIEK KONSERVAT-LAGERSTÄTTE IN IOWA, USA

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**Keywords:** Hyaline conodont apparatuses, Middle Ordovician, Iowa, impact crater, Konservat-Lagerstätte

### INTRODUCTION

Only about a dozen Ordovician Konservat-Lagerstätten are known globally and such deposits are more rarer in this system than in, for instance, the Cambrian. In view of this, the 2005 discovery of an in several aspects unique such deposit at Decorah, Iowa (Liu et al., 2006, 2009) was of special paleontological interest. The Winneshiek Lagerstätte is located in a circular meteorite crater, the Decorah Impact Structure, which has a diameter of 5.6 km and covers approximately 25 km<sup>2</sup>. It contains a crater filling a partly sandy, organic-rich, dark-grey shale, the Winneshiek Shale, which is exposed at only a single locality on the bank of the Upper Iowa River. However, two drill cores and chips from 29 wells show that this shale has a thickness of 17-27 m and overlies, with gradational contact, a thick impact breccia. The Winneshiek Shale is unconformably overlain by the widespread but largely unfossiliferous St. Peter Sandstone.

Tons of material excavated from the river bed have yielded more than 5300 cataloged specimens (Liu et al., 2017). Numerically, this collection is dominated by conodonts but it contains also representatives of a few other fossil groups (e.g. Lamsdell et al., 2015a, 2015b; Briggs et al., 2016) such as eurypterids with an estimated adult size of up to 1.7 m, phyllocarids (Briggs et al., 2016), and other non-mineralized arthropods. There are no benthic shelly fossils, such as articulate brachiopods, trilobites, bryozoans, bivalves, corals, and echinoderms, and also graptolites are missing. It appears that the Winneshiek Shale was deposited in a very quiet environment, possibly in brackish water, with a too low oxygen content in the bottom water to permit the establishment of a diverse benthic fauna.

Although not abundant, conodonts occur on many shale bedding surfaces and the conodont elements are excellently preserved in three dimensions. Very commonly, quite prominent basal bodies are preserved

attached to the crowns of the elements. A striking feature is that many elements have a gigantic size with a length of 10-15 mm and represent some of the largest conodont elements recorded anywhere.

The Winneshiek Shale fauna does not include fossils suitable for a very precise determination of the age of the unit. However, a recent chemostratigraphic  $\delta^{13}\text{C}_{\text{org}}$  investigation indicates that the unit represents Stage Slice Dw2 of Bergström et al. (2009) of the global Darriwilian Stage (Bergström et al., in preparation).

## CONODONT APPARATUSES

Of special interest is the fact that several of the approximately 12 conodont taxa present in the Winneshiek fauna are represented by more or less complete apparatuses. The two most common of the apparatuses were recently described and identified (Liu et al., 2017) as *Archeognathus primus* Cullison, 1938 and *lowagnathus grandis* Lui, Bergström, Witzke, Briggs, McKay and Ferretti, 2017. These are the first hyaline conodont apparatuses formally described in the global conodont literature.

*Archeognathus primus* has a 6-element apparatus of a previously unknown type. It includes one pair of blade-like multidenticulated coleodiform (S) elements and two pairs of archeognathiform (P) elements. All elements have very robust basal bodies that rival, or exceed, the crowns in size.

The apparatus of *I. grandis* includes 15 ramiform elements of alate (one element) and bipennate or angulate, and tertiopedate morphology (seven pairs). Bedding-plane apparatuses show that these elements were arranged in two opposing rows. In general architecture, this apparatus type shows a closer similarity to post-Ordovician apparatuses of ozarkodinid type than to those of *Promissum* and *Icriodella* (formerly *Notiodella*) from the Upper Ordovician Soom Shale of South Africa (Aldridge et al., 1995, 2013). However, the apparatus of *lowagnathus grandis* differs from these apparatus types in the arrangement and appearance of the elements. Detailed study and description of the several other apparatuses present in the Winneshiek Shale are expected to add substantial new information to our most incomplete knowledge about the apparatus organization of other hyaline Darriwilian taxa, which has remained essentially unknown.

Despite the fact that no soft parts have been identified in the Winneshiek specimens, the very large size of the apparatuses (up to 2-4 cm) suggests that the Winneshiek conodont animals reached a substantial size. Comparison with the apparatus size in the soft-part preserved conodont animals from the Carboniferous of Scotland suggests that the Winneshiek animals may have reached a length of 0.5 m or more.

The conodonts from the Winneshiek Shale provide a wealth of new information and this deposit has the potential to become one of the key Lower Paleozoic units for research on conodont apparatus architecture and element morphology.

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## INTEGRATING CONODONT TURNOVER, CARBON ISOTOPIC EXCURSIONS AND THE OCEANIC EVENTS IN THE LUDLOW OF THE SOUTHEASTERN BALTICA (MILAIČIAI-103 CORE, LITHUANIA)

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**Keywords:** Conodonts, brachiopods, graptolites, stable carbon isotopes, Lau event

Ludlow epoch of the Silurian period, according to the very detailed conodont record of Gotland area and to a lesser extent other areas of the world (Jeppsson and Aldridge, 2000; Jeppsson et al., 2012), experienced three major events, namely Linde, Lau and Klev. Apparently, Lau event was the most significant of all three biotic perturbations, since it is also coincident with the large scale genus level brachiopod depletion episode or so called "pentamerid event" (Talent et al., 1993). Chemostratigraphic studies revealed that these biotic disturbances were closely associated with significant stable carbon isotopic excursions, of which mid-Ludfordian excursion which is contemporaneous with the conodont Lau event was one of the strongest during the whole Phanerozoic (Melchin et al., 2012). The detailed association of Ludlow events to the biotic changes in different ecological settings is still poorly known.

Here we present an integrated record of conodont, brachiopod and graptolite succession in relation to the stable carbon isotopic excursions from the Milaičiai-103 (Western Lithuania) core section. The conodont data set is composed of 126 collections, which span almost the whole Ludlow starting from the *L. scanicus* and ending at the *Neoc. parultimus* graptolite zones. In total 26 conodont taxa are recognized in the section. Based on the distribution of time specific conodont species, *K. variabilis* interval zone is distinguished in the depth interval between 1301 and 1246 m. Lower portion of this interval zone, besides name bearing species, was characterized by other species characteristic of lower Ludlow, namely *Kockella stauros* Barrick and Klapper 1976 and *Wurmiella inflata* (Walliser, 1964), as well as several long ranging species. *Polygnathoides siluricus* zone is distinguished in the depth interval between 1246 and 1236 m. There is a single found of very rare massively built taxon *Silurognathus maximus* Jeppsson 2005 in the upper part of this zone, which confirms (at least regional) usefulness of this taxon for the upper Ludlow chronostratigraphy beyond the Gotland area. In the upper part of the section in the interval between 1182 and 1155 m *Oz. snajdri* zone is distinguished. This depth interval additionally is also characterized by the typical upper-most Ludfordian assemblage of conodont taxa, such as *Oulodus elegans* (Walliser, 1964), *Ozarkodina baccata* Miller and Aldridge 1997, and *Ozarkodina ambigua* (Viira, 1983).

The analysis of brachiopod fossil assemblages shows that during Ludlow time, there was steady long-term shallowing trend at the site. Lower portion of the section was characterized by deep water BA 5-4 *L.*

*obovata* – *J. grayi* brachiopod community, which transitioned in to the BA 4 *C. ? pubes*, later in to the BA 3-4 *I. amplificata*-*S. lewisii* and finally in to the BA 3 *I. ovalis* brachiopod community.

The biostratigraphic and paleoecological data were tied to the  $\delta^{13}\text{C}$  (whole rock) trend. The most prominent feature of the stable carbon isotopic curve is the pronounced mid Ludfordian Lau carbon isotopic excursion, which begins approximately at depth of 1253 m, peaks at depth of 1229 m, reaching maximum value of 5.02 ‰, and then gently declines through the section and ends approximately at depth of 1189 m.

Finally in order to test the influence of the oceanic events on the conodont paleocommunities compositional dynamics, so called recurrence plot and recurrence quantification analyses were employed. Recurrence plots are filtered distance matrices which reveal patterns of similarity between temporally or spatially ordered samples. In this case, samples were compared according to their conodont species compositions. The obtained patterns show that conodont communities were compositionally comparable (due to influence of long ranging dominant species) before and after the Lau event. On the other hand, the conodont communities which existed during the peak and the falling stage of the Lau carbon isotopic excursion represented transiently stable unique assemblages. This fact points to the possibility that environmental conditions that structured conodont communities were highly anomalous during this global perturbation.

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## LATE DEVONIAN CONODONTS FROM THE SHALLOW SHELF STRATA OF THE BROKEN RIB AND COFFEE POT MEMBERS, DYER FORMATION, CHAFFEE GROUP, COLORADO

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**Keywords:** Hangenberg, <sup>87</sup>Sr/<sup>86</sup>Sr, Devonian, Dyer

### INTRODUCTION

The Devonian-Carboniferous boundary is preserved in the Coffee Pot Member of the Dyer Formation, Chaffee Group, Colorado based on carbon isotope values of bulk carbonate and <sup>87</sup>Sr/<sup>86</sup>Sr of conodont apatite. Conodonts in the lower Dyer are *expansa* Zone; upper Dyer conodonts are tentatively identified as Carboniferous.

### GEOLOGICAL CONTEXT

The Dyer Formation in central Colorado is composed of carbonate strata deposited on a tropical carbonate platform during the Late Devonian. The Broken Rib Member is comprised primarily of biopackstones, biowackestones, and mudstones. The overlying Coffee Pot Member is comprised of dolomitized mudstones and intrarudstones characterized by rare stromatolites, karsted intervals, sandstones, and bioclastic beds.

### MATERIAL AND METHODS

Carbonate isotope samples and conodonts were collected from four measured sections in the White River area of central Colorado. Samples for magnetic susceptibility were collected at 5 cm intervals from the base of the Broken Rib Member through most of the Coffee Pot Member in a section along Deep Creek Canyon. Samples for conodonts were processed using buffered formic acid; <sup>87</sup>Sr/<sup>86</sup>Sr was determined from conodont fragments recovered from eight intervals below and above a significant carbon isotope excursion.

### RESULTS

The Broken Rib Member yields a relatively abundant and diverse conodont fauna characterized by *Bispathodus*, *Polygnathus*, *Pandorinellina*, *Icriodus*, and *Apatognathus*. The taxa are relatively long ranging,



indicative of the *granulosus* (Upper *trachytera*) Zone to *expansa* (Lower *expansa*) Zone based on the overlapping ranges of *Polygnathus obliquicostatus* and *Icriodus costatus costatus*. The MS and carbon isotope signatures are relatively stable,  $\delta$  MS is near -4, carbon isotopes are near -1 or 0 per mil. Conodonts from the Broken Rib have yielded  $^{87}\text{Sr}/^{86}\text{Sr}$  of 0.70874 to 0.70836. The Coffee Pot yielded conodonts from three horizons, in addition to a bed described by Sandberg and Poole (1977). Conodonts in the lower Coffee Pot include *Pandorenellina* cf. *P. insita*, *Icriodus costatus darbyensis*, and *Polygnathus perplexus*? In the upper Coffee Pot Member, above strata that exhibit unusually high (5-7 per mil)  $\delta^{13}\text{C}$  values, fused clusters of fragmented conodonts of ?*Siphonodella*, *Pseudopolygnathus*, have a  $^{87}\text{Sr}/^{86}\text{Sr}$  value of 0.70819. Magnetic susceptibility shifts further to the negative at the Broken Rib – Coffee Pot contact.

## DISCUSSION

Conodonts in the Broken Rib Member are relatively long ranging, indicative of the *granulosus* (Upper *trachytera*) Zone to *expansa* (Lower *expansa*) Zone based on the overlapping ranges of *Polygnathus obliquicostatus* and *Icriodus costatus costatus*. *Pandorinellina* cf. *P. insita*, *Icriodus costatus darbyensis*, and *Polygnathus perplexus*? are indicative of the *expansa* Zone to *ultimus* Zone. The conodonts in the lower Coffee Pot are similar; a more negative shift in  $\delta$  MS values indicates a drop in sea level. In the upper Coffee Pot Member, above strata that exhibit unusually higher (5-7 per mil)  $\delta^{13}\text{C}$  values characteristic of the highest Devonian Hangenberg Excursion, fused clusters of fragmented conodonts of ?*Siphonodella*, *Pseudopolygnathus*, and sand grains are suggestive of the Lower Carboniferous.

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## THE LAST PHASE OF CONODONT EVOLUTION: INTEGRATING BIOSTRATIGRAPHIC AND PHYLOGENETIC APPROACHES

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**Keywords:** Conodont, Upper Triassic, phylogenetics, morphoclines

### INTRODUCTION/BACKGROUND

Conodonts are elements of a complex feeding apparatus made of fluorapatite of an extinct marine vertebrate (e.g. Donoghue et al., 2000). Since the microstructure of conodonts is similar to that of the tooth enamel of present-day vertebrates, we have regarded conodonts as physiological analogues of teeth, and taken their morphology as a homologous characteristic, significant in phylogenetic reconstructions (e.g. Mazza et al., 2012). Integrated data both from available literature and from studied sections sampled in detail allow to draw a holistic stratigraphic distribution of Upper Triassic pectiniform conodonts. Basing on stratigraphic data, and on the apparatus reconstructions, most of the Triassic pectiniform conodonts belong to the Gondolelloidea family (Fåhræus and Ryley, 1989). One of the most important challenges for the reconstruction of the Upper Triassic conodont phylogenesis is to identify the praecursor of the genus *Misikella*. Different interpretations of the *Misikella* apparatus have been proposed (Fåhræus and Ryley, 1989; Budurov and Sudar, 1990) and Mastandrea et al. (1998) illustrated several clusters of ramiforms and pectiniform, all belonging to *M. ultima*. Basing on the similarity of the ramiform elements, Orchard assigned to the genus *Norigondolella* the likely precursor of the multielement *Misikella* apparatus (Pálfy et al., 2007). Our purpose is to arrange the uppermost Norian and Rhaetian phylogeny of the genera *Misikella* and *Parvigondolella*, in order to provide a theoretical framework for forthcoming taxonomical and biostratigraphic studies. We also recognized *Mockina bidentata* as the ancestor of *Misikella hernsteini*, the first species belonging to genus *Misikella*.

### MATERIAL AND METHODS

The phylogenetic analyses have been conducted on material from the Norian/Rhaetian successions of the Lagonegro Basin (Southern Apennines, Italy), consisting of ca. 400 m of hemipelagic cherty limestones with minimal facies variations. Thus, the depositional environment remained substantially the same, and the quality of conodont preservation should be consistent throughout the Formation. In particular, three stratigraphic sections have been investigated in detail, providing a great collection of conodonts around the Norian/Rhae-

tian boundary: the Monte S. Enoc, Pignola-Abriola and Monte Volturino sections. The excellent continuity and absence of condensed facies of the Calcarei con Selce Formation in these sections allowed to collect a complete and well-preserved conodont association across the Norian/Rhaetian boundary (Giordano et al., 2010).

This rich conodont collection from the Lagonegro Basin perfectly documents transitional forms between genera and species that are peculiar for the upper Norian (Sevatian) and Rhaetian. In particular, we documented the evolution of the genera *Misikella* and *Parvigondolella* from a common ancestor that is *Mockina bidentata*, which is characterized by two well-developed denticles on the lateral margins of the small tongue-shaped platform (an accessory tiny denticle can be present anteriorly), located in central portion and in correspondence to the pit. The blade consists of 5-6 high and well-fused denticles, ending in a carina that is composed of 3-4 denticles. Although the transitional forms between *M. bidentata* and genera *Misikella* and *Parvigondolella* are frequently collected during Norian/Rhaetian conodont investigations, the phylogenetic relationships among them are still debated and not clear, in particular during the Late Norian (Sevatian), which is a period of biotic turnovers and climate changes.

The phylogenic reconstruction based on the recognition of morphoclines, which are represented by a gradual transition from the ancestral to the descendant species, is the only method that can disentangle disagreements in the ranges of conodont species and taxonomic divergences. Only adult morphologies have been considered for phylogenetic analyses in this study. Moreover, the identification of the morphocline between ancestors and descendants allows to recognize the first appearance datum (FAD) of the descendant species.

## EVOLUTIONARY TRENDS OF THE NORIAN/RHAETIAN CONODONTS

### Morphocline between *Mockina bidentata*/*Parvigondolella andrusovi*

Genus *Parvigondolella*, the first representative of which is *P. andrusovi*, descends directly from conodont *M. bidentata* and their phylogenetic relationship is well proved (Kozur and Mostler, 1972; Kozur, 1989; Moix et al., 2007).

The morphocline between *Mockina bidentata* and *Parvigondolella andrusovi* is characterized by two phases that prove the quick evolutionary pace of this lineage: 1) the gradual loss of the platform of the *Mockina bidentata*, initially maintaining small denticles on both sides of the blade, which however decrease in size till the complete absorption by the blade; 2) the decrease (to 7-9) and the fusion of the blade denticles that are almost homogeneous in size and backwardly projected, with the cusp never located as the last denticles but followed by 1 to 2 denticles as in *Mockina bidentata*. The homogenization process of the blade denticles is reached by *Parvigondolella lata*, stratigraphically younger than *P. andrusovi* and its direct descendent. Notably is the total absence of significant variations on the basal side of both *Mockina bidentata* and *Parvigondolella andrusovi*, where the pit position is still central or slightly forwarded.

### Morphocline between *Mockina bidentata*/*Misikella hernsteini*

The evolutionary trend characterizing the morphocline between *Mockina bidentata* and *Misikella hernsteini* consists of the loss of the platform (vestigial bulges can be present in transitional forms) and the decrease in denticles composing the blade plus carina, reaching the number of 6 to 4 and similar in size. The denticles corresponding to the carina (posteriorly to the central cusp) in the species *Mockina bidentata* are progressively absorbed, leading the cusp to occupy the terminal position. Sometimes, it is possible to observe

a small vestigial denticle behind the cusp. The lower side develops a deep basal cavity that extends through the entire surface starting below the prominent denticle. The basal cavity has a typical teardrop shape with the largest part below, and thus terminal, the cusp.

## MISIKELLA TAXONOMIC ISSUE

Genus *Misikella* is affected by a taxonomic issue, related to its original definition. In fact, the genus *Misikella* is considered as the representative of uppermost Sevatian and Rhaetian stages. The genus *Misikella* was established by Kozur and Mock in 1974, who proposed *Misikella longidentata* as type species (1974a, p. 135). In the same year, the two authors assigned *Spathognathodus hernsteini* as new type species for the genus *Misikella* (Kozur and Mock, 1974b, p. 247). This issue was first noticed by Fähræus and Ryley (1989) who recognized two different conodont apparatuses within this group: a tetramembrate apparatus which corresponds to *Misikella longidentata* species, and a bitembrate conodont apparatus to all those species previously brought to *Misikella* genus (e.g. *Misikella hernsteini*, *M. posthernsteini*, "*M. rhaetica*", *M. koessensis*, "*M. lanceolata*"). Thus, they proposed a new generic name (*Axiothea*) for those upper Norian-Rhaetian species with a bitembrate conodont apparatus. Later, Budurov and Sudar (1990) gathered *Misikella longidentata* and all the *Axiothea* species into a single genus (*Misikella*) and retained *M. longidentata* as the type species (for priority reasoning). We agree with Fähræus and Ryley (1989) on assigning *M. longidentata* and the upper Norian-Rhaetian species to very different clades, and we should thus adopt the genus *Misikella* for the Carnian - lower Norian *M. longidentata* and genus *Axiothea* for the upper Norian-Rhaetian species proposed by Fähræus and Ryley (1989), basing of the principle of priority. Since the *Misikella* is largely used by the scientific community for the upper Norian and Rhaetian conodonts, we suggest to maintain the genus *Misikella* for the upper Norian-Rhaetian, accepting the species *M. (=Spathognathodus) hernsteini* as type species for genus *Misikella* as proposed Kozur and Mock (1974b). As a consequence, *Misikella* becomes a monophyletic genus, excluding only "*Misikella*" *longidentata*.

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## MINERALOGICAL CHARACTERIZATION OF APATITE BIOMINERALS: PRELIMINARY RESULTS

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**Keywords:** Conodonts, apatite, micro-diffraction, cell parameters

The term "bioapatite" has often been used improperly in the past and in different scientific fields to characterize apatite mediated by the intervention of organisms. Conodonts, for a long time considered enigmatic, represent an extinct group of jawless vertebrates that were the first among the group to experiment skeletal biomineralization with tooth-like elements in their feeding apparatus. Their use of apatite is shared with many other vertebrates that have applied calcium-phosphate biominerals to grow their skeletal structure and to shape their teeth. However, microbes are thought to play a role in apatite precipitation (e.g., Crosby and Bailey, 2012). Although development of mineralized parts seems controlled by specifically produced organic molecules that remain entrapped within the mineral units, the growth mechanisms and the diagenetic evolution of apatite fossils are still poorly understood.

Ferretti et al. (2016) recently described peculiar diagenetic apatite overgrowths on Late Ordovician (*A. ordovicicus* Zone) conodonts from Normandy. The conodont specimens exhibit a CAI of 4-5, indicating a heating up to 400°C. Diagenetic neo-crystals observed on the surface of conodont elements show distinctive large columnar, blocky or web-like microtextures. Apatite crystals were analyzed in terms of size, morphology, composition, geometry and spatial arrangement by integration of optical and scanning electron microscopy (SEM), environmental scanning electron microscopy coupled with chemical microanalyses (ESEM-EDX) and X-ray microdiffraction ( $\mu$ XRD). X-ray diffraction technique had been used in the past to characterize lattice parameters in apatite crystals (e.g., Ellisson, 1944; Pietzner et al., 1968; Nemliher and Kallaste, 2012). Microdiffraction, applied to conodont structural characterization, proved to be a reliable tool in describing overgrowths that otherwise cannot be resolved by the use of microscopic methods alone. In fact  $\mu$ XRD method allows for small volumes of material to be probed: X-rays are collimated to form a very small beam (up to 10  $\mu$ m in diameter) before irradiating a sample, giving the possibility to check for local "micro" environment such as defects or preferred orientations of the crystallites. Microdiffraction measurements were carried out on various points of the surface using a 50  $\mu$ m collimator and changing specimen orientation (fixed Omega revolution angle and varying Phi rotation angle). The integration of  $\mu$ XRD with chemical analyses allowed Ferretti et al. (2016) to reveal that diagenetic apatite neo-crystals exhibit the same chemical composition as the original fossil structure, and that no significant difference in unit cell parameters appears to exist between

the newly formed apatite crystals and those of the smooth (with no crystal overgrowth) conodont surfaces. In other words, diagenesis has strictly replicated the unit cell signature of the older crystals. The application of this approach, coupled with RAMAN analysis, has been extended to encompass conodont elements of different age and having diverse CAI in order to better constrain variability of apatite cell parameters. These results have been compared with those derived from apatite documented in other fossil and living organisms.

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# **RECENT ADVANCES IN CONODONT PALAEOBIOLOGY**







## CONTRIBUTION TO THE ORIGIN OF CONODONTS

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**Keywords:** Conodonts, origin, systematic, Chaetognatha, Early Palaeozoic

Origin and systematic position of conodonts is not clear and should be still studied. It is well known that in the late Cambrian and Ordovician deposits among typical conodonts commonly occur phosphatized grasping spines of chaetognaths and composed of them apparatuses. Until their recognition (Szaniawski, 1982) they have been treated as conodonts of the genus *Prooneotodus* (Muller and Nogami). Presently, despite of their morphological differentiation, they are assigned to one species of Chaetognatha - *Phakelodus tenuis* (Muller). Recently I had the opportunity to state that in the early Ordovician deposits, except of the elements of *Phakelodus*, occur other elements and apparatuses, which are similar in shape and construction to both - conodonts and grasping spines of chaetognaths (Szaniawski 2015). They are phosphatic, but probably in result of the secondary phosphatisation because some of them are deformed in a way suggesting original flexibility. Some of the elements are described and assigned to the conodont genera: *Coelocerodontus* Ethington, *Diaphonodus* Chen and Gong and *Viirodus* Dubinina. The elements have similar shape and construction to both - conodonts and grasping spines of chaetognaths. However their arrangement in apparatuses is clearly different than in conodonts of that age. The apparatuses are constructed of elements slightly differentiated in shape but fitting well to themselves. That means they were originally joined and could cooperate very well in action. Most probably they were originally composed of organic matter, constructed similarly to the grasping apparatuses of chaetognaths and similarly to them became diagenetically phosphatized. This suggests that the early Paleozoic chaetognath-like animals were strongly diversified and elements of their apparatuses can be confused with the co-occurring conodonts. Similarly as it has happened with the grasping spines of *Phakelodus*. It seems also possible that some of the fossils considered since a long time as conodonts have a common origin with Chaetognatha.

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## SIMILARITY AND DIFFERENCES OF MORPHOLOGICAL FEATURES OF PROTO- AND EUCONODONT ANIMALS

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**Keywords:** Protoconodont animals (Chaetognatha), euconodont animals, morphological features

### INTRODUCTION

The names of the proto- and euconodont animals come from the designation of histological types of their tooth elements (Bengtson, 1976). The extraordinary morphological similarity of the tooth elements of the proto- and euconodonts and the existence of a group of paraconodonts, which in pattern of the matter growth are sometimes considered to be transitional between the two former, made it possible to suggest the existence of a single evolution chain for all types of the conodont elements (Bengtson, 1983). H. Szaniawski compared the Lower Paleozoic protoconodont tooth elements of the *Prooneotodus? tenuis* (Müller) with the grasping spines of modern Chaetognatha and found their strong morphological and structural similarity. It was established that the protoconodont tooth elements are the hooks of Chaetognatha (Szaniawski, 2005). In essence, the proper conodonts are only the euconodonts.

### MATERIAL AND METHODS

Imprints of euconodont animals from the Lower Carboniferous deposits of the Polar Urals, Russia (Buryi et al., 2010) have been morphologically compared with the imprints of euconodont animals from the Upper Ordovician deposits in South Africa (Aldridge & Theron, 1993), the Silurian of Wisconsin (North America) (Mikulic et al., 1985), the Lower Carboniferous of Granton, Scotland (Briggs et al., 1983; Aldridge et al., 1993). The representatives of protoconodont animals – fossilized Chaetognatha *Protosagitta spinosa* from the lower Cambrian of China, *Paucijaaculum samamithion* from the upper Carboniferous of North America, as well as the modern ones of genera *Spadella*, *Aberrospadella*, *Bathyspadella*, *Heterokronia* and *Eukronia* (Kassatkina, 1982) have been studied.

### RESULTS

It was established that in the inner and outer structure of the proto- and euconodont animals there are many **common morphological features:**

**1. Presence of skeletal attaching elements.** The euconodont animals are similar to the protoconodonts in pattern of arrangement of the body supporting constructions. Our data show that the supporting

carcasses of the proto- and euconodonts are represented by the skeletal head attaching plates and the muscular system. The skeletal head plates of the Chaetognatha serve to attach and support a massive tooth apparatus -hooks (in protoconodonts) and teeth (in paraconodonts), as well as to attach the body muscular system (Kühl, 1938). The euconodont animals also had the pair head attaching elements (Buryi & Kassatkina, 2004) that served to attach the muscles connecting the tooth elements of the mouth apparatus, placed in the food sac, and to govern them in the feeding process.

**2. Similar muscular system.** In the protoconodont animals the transverse-banded muscular system is observed (benthic shallow-water *Spadella* and *Aberrospadella* and deep-sea *Bathyspadella*, as well as bathypelagic *Heterokronia* and *Eukronia*). In the euconodont animals there are also the inner transverse muscular structures of the body. The obliquely oriented and perpendicular muscular fibres are distinguished, whose orientation appears to depend on the direction of the animal movement. The convergence angle of the euconodont transverse muscular system can be directed towards the head or in the opposite direction – towards the tail (Kasatkina & Buryi, 2007).

**3. Absence of notochord.** In the picture of the sixth imprint of euconodont animal from Granton it is clearly seen that the longitudinal light structure is not a notochord. It is a gut with the excrements going out from its back end. In the imprint of the *Protosagitta spinosa* ancient Chaetognatha from the lower Cambrian of China a narrow light longitudinal structure (intestine) is also visible beginning from the head and ending with anus in the body back part. When the notochord is absent, the supporting structures of the body (both proto- and euconodont) are the longitudinal muscular bands and turgor.

**4. Similar reproductive organs.** The reproductive organs of the protoconodonts can be observed both in modern animals and in *Protosagitta spinosa* from the lower Cambrian of China. As judged from the first imprint from Granton, in the euconodont the tail division is supposedly filled with the male genitals. And on its fin rays one can see the structures that, probably, are the spermatophores similar to those in the protoconodonts. These spermatophores are, apparently, released from the cavity of the tail division.

### Taxonomic features that make the proto- and euconodont different:

**1. Different organs of food grasp.** On the example of the living now Chaetognatha, in the protoconodonts the hooks and teeth are situated on the head surface and serve to directly entrap (hooks) and retain (teeth) the mobile prey in the pharynx. In the euconodont animals all tooth elements are inside the body, in the food sac. This agrees well with S. Bengtson (1976) hypothesis that the tooth elements of the euconodont histological type were situated inside the animal body. The tooth elements of the euconodonts were able to filtrate the food particles from water.

**2. Different number of the attaching plates.** The essential difference of the proto- and euconodont animals is the different structure of their head skeletal apparatuses. In the protoconodonts they contain four skeletal plates (two pairs), and in the euconodont animals there are only two plates (one pair). The head plates play a very important role in the structure and evolution of these groups as in the protoconodont animals four massive muscular bands are attached to four skeletal plates, in the euconodonts – only two.

**3. Presence of the food sac in the euconodonts.** All skeletal and tooth elements and their connective tissues were in the rounded food sac localized on the outer ventral side of the animal. In the process of the food sac functioning, probably, the food particles in it were filtered from water, which was removed through special holes, and then a food clot was formed and migrated into the food channel (gut) (Guravskaya & Kassatkina, 2015).

## DISCUSSION

H. Szaniawski (2005) ascertained that the protoconodont elements are the hooks of the chaetogntha, and consequently, the animals, bearing them, must be assigned to the

Phylum Chaetognatha Leuckart, 1854. Our investigations show that, though the protoconodont and euconodont animals have some similar morphological features there are the fundamental differences between them in arrangement of the organs of the food grasp and their functioning. The protoconodonts, being predators, have a massive complex of hooks and teeth to catch, grasp, and retain the prey. The morphological structure of the mouth apparatus of the euconodont animals makes possible to suggest that they could not be the predators. The euconodont could, most likely, only gather the fine particles of detritus, bacteria, and unicellular algae with soft lobes, surrounding the mouth opening, and to pull them together with water into the food sac. The nutrient particles were filtrated with the help of the S elements from water and entered the pharynx, where the P elements formed a food clot of them, which went further to the gut. In our opinion, they apparently, being suspension feeders, belong to another type of animals - Euconodontophylea Kassatkina & Buryi, 1997 (Kassatkina & Buryi, 1997).

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## INTRASPECIFIC VARIATION AND EVOLUTIONARY TRENDS IN TWO CONODONT LINEAGES

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**Keywords:** Conodonts, evolution, developmental constraints, intraspecific variation, microtomography

### INTRODUCTION

How shape changes through evolutionary time? This question is central to paleontology as most of the record is morphological in nature. There is a long tradition of research on how forms are ruled, and therefore on how developmental processes determine the morphological variations of individuals in ontogeny and through evolution. Indeed, biological shapes are constrained by the basic rules of chemistry, physics and geometry, among others. The set of theoretically possible forms is thus bounded by the way these forms can be generated during ontogeny, possibly driving evolution into preferential directions. To date, patterns of shape variation in conodont elements have been documented mostly qualitatively and at the species level (e.g. within taxonomic diagnoses). Unlike other clades such as ammonoids, no generalized pattern of variation has been described for conodonts. Moreover little attention has been paid to the developmental origin of the taxonomical characters. Because conodont elements are used for feeding, their complex morphology, in particular recurrent homeoplasies, may reflect, to some degree, functional adaptations to specific diets. Yet, they must also reflect, to an unknown extent, developmental constraints. In order to constrain our interpretations of presumed adaptation to diets and environments, it is thus mandatory to better understand if and which traits might be adaptive or not. Conodont elements are likely highly integrated, that is their morphological characters are not independent but covary with each other. In this context, recognizing and measuring patterns of covariation and modularity in conodont elements will not only inform us about potential developmental rules, but will also allow us to make phylogenetic hypotheses that better reflect the true distances between taxa. In this study, we investigate patterns of intraspecific variation in two very distinct and distant evolutionary lineages, one from the Late Devonian, and one from the Late Triassic. In both cases, empirical observations have led some authors to hypothesize evolutionary trends in conodonts morphology. Here we are assessing those 'trends' in a quantitative way.

For this purpose, statistically meaningful populations of P1 elements of each species have been digitized using a CT-scanner. We performed geometric morphometrics both in 2D and 3D to compare the shape of the P1 elements quantitatively.

We are particularly keen to identify generic rules of conodont morphology, for instance patterns of covariation that would be shared by these two lineages and whose validity might then be extended to other taxa.



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## CONTRASTING SIZE TRENDS IN CONODONTS DURING THE SMITHIAN-SPATHIAN BOUNDARY EXTINCTION

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**Keywords:** Smithian-Spathian boundary, extinction, Lilliput effect, size change, conodonts, Northern Indian Margin

### INTRODUCTION/BACKGROUND

The pattern and timing of the biotic recovery of marine ecosystems after the end-Permian mass extinction is still a matter of debate. It has been suggested that the size of individuals was temporarily reduced in many marine clades during this recovery interval, a phenomenon coined 'Lilliput effect' (Schubert and Bottjer 1995, Twitchett 1999), with little knowledge about the underlying mechanism. On the other hand, Brayard et al. (2010, 2011) showed that previous conclusions drawn from the iconic gastropod case are not supported, and a recent study (Schaal et al. 2016) showed that several clades responded contrastingly in terms of size during the Early Triassic recovery.

Owing to their widespread and abundant distribution, conodonts are ideal for assessing temporal patterns at high resolution. Several global events occurred during the Early Triassic. The main one occurred at the Smithian-Spathian boundary (SSB) and it affected particularly nektonic organisms such as ammonoids and conodonts (Brayard et al. 2006, Galfetti et al. 2007, Orchard 2007, Goudemand et al. 2008). Chen et al. (2013) measured the temporal evolution of conodont sizes across the SSB by analysing a collection of 441 P<sub>1</sub> elements of segminate conodonts from the Nanpanjiang Basin (China) and concluded that their size decreased at the SSB, which they interpreted as a response to presumably extremely high seawater temperatures (Sun et al. 2012, Romano et al. 2013, see also Goudemand et al. 2013).

Our goal is to reassess this pattern for a larger geographical area and for a larger set of conodont genera.

### MATERIAL AND METHODS

We have measured more than 9000 conodont P<sub>1</sub> elements from three sections along the Northern Indian Margin (NIM): Tulong (South Tibet), Guryul Ravine (Kashmir) and Nammal Gorge (Salt Range, Pakistan).

Our study includes not only specimens of conodont taxa with a segminate P<sub>1</sub> element (*Neospathodus*, *Novispathodus*, *Triassospathodus*, *Icriospathodus*) but also neogondolellids, which have a segminiplanate P<sub>1</sub> element (*Neogondolella*, *Columbitella*, *Borinella*, *Scythogondolella*), as well as ellisonids.

## RESULTS

Our results support Chen et al.'s hypothesis that 'segminate conodonts' decreased in size at the SSB. Nonetheless, we also demonstrate that 'segminiplanate conodonts' underwent a remarkable size increase during the same interval. The largest measured elements belong to the ellisonids and are found during the early late Smithian.

## CONCLUSIONS

Our results contradict a direct causal link between seawater temperatures and conodont size. On the other hand they corroborate a previous suggestion (Joachimski et al., 2012) that 'segminiplanate conodonts' may have preferred colder environments than 'segminate conodonts'. In terms of size evolution, they responded contrastingly to the end-Smithian event.

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## QUANTITATIVE ASSESSMENT OF EVOLUTIONARY TRENDS IN A LATE TRIASSIC CONODONT LINEAGE

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**Keywords:** Conodonts, evolution, developmental constraints, intraspecific variation, microtomography

### INTRODUCTION

There is a long standing debate about whether evolution is driven 'internally' by developmental constraints or 'externally' by environmental factors and natural selection. Owing to their long and rich fossil record, conodonts have a great potential for shedding light on this debate. A few recent studies (Jones et al. 2012, Martínez-Pérez et al. 2016) have highlighted how some particular conodont morphologies/traits (e.g. the presence of white matter) might have been particularly useful for processing food and might have constituted the basis for functional adaptation to weaker or harder food. Nevertheless, too little is currently known about potential developmental constraints in conodont elements.

Here we scanned and analyzed about 180 P1 elements from a Carnian-Norian boundary collection from Sicily with the aim of quantitatively testing suggested evolutionary trends and identifying potential patterns of covariation that would reflect underlying developmental rules. This material has been the focus of an array of interesting studies by Mazza and coworkers for the last half decade or so (Mazza et al. 2012, 2015, 2016). In particular they reconstructed and described ontogenetic series on the basis of single P1 elements using synchrotron-based X-ray microtomography, and they performed cladistics analyses. Moreover, the material preservation is usually pristine. Hence this material lends itself for such quantitative analyses.

Specimens of the closely related genera *Carnepigondolella*, *Metapolygnathus* and *Epigondolella* were analyzed using both Elliptic Fourier contour analysis and landmark or semi-landmark-based geometric morphometrics. Because growth series are available throughout the sequence, ontogenetic and phylogenetic patterns of variation can be compared to the intraspecific patterns of variation among 'adult' forms. We will present our preliminary results.

### Acknowledgements

We would like to thank Michele Mazza (University of Milano, Italy) for granting us access to his Late Triassic conodont collections and Mathilde Bouchet (ENS Lyon, SFR Biosciences) for her invaluable help with the microtomograph. This research is supported by a French ANR @RAction grant to NG (ACHN project 'EvoDevOdonto').

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## SILURIAN CONODONT DIVERSITY: BEYOND THE ABIOTIC PARADIGM

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**Keywords:** Extinction, Sweden, turnover, stratigraphic bias

### INTRODUCTION

The relative importance of biotic and abiotic factors as controls of evolutionary dynamics and drivers of species diversity patterns has been hotly debated (e.g., Benton, 2009), but conodonts – despite their outstanding fossil record and major role in early Phanerozoic ecosystems – have been so far left untouched by this discussion. Concepts on the mechanisms shaping conodont diversity at the regional and global scale during the Silurian Period have been shaped by the models developed by Lennart Jeppsson. Based on over fifty years of work on the Silurian succession in the Swedish island of Gotland, he documented multiple new taxa, provided insight into the ecology of many species, and proposed one of the most detailed conodont zonation for the Baltic area (Jeppsson et al., 2006). His model linking conodont diversity and distribution with palaeoceanographic circulation and climate (Jeppsson, 1990; Jeppsson and Aldridge, 2000; Jeppsson et al., 1995) has been tested, rejected in its original form, and subsequently modified and developed, fuelling intensive research worldwide. The hypothesis which currently dominates in the literature posits that changes in conodont diversity during the Silurian were driven by external factors – such as environmental changes resulting from glaciations – which caused repeated carbon isotope excursions and associated intervals of elevated extinction rates of conodonts. However, the potential role of biotic interactions as an additional or even major driver of the observed diversity patterns have never been addressed. Testing the relative importance of the models attributing these patterns to external drivers is hindered by the following issues: (1) background extinction and turnover rates are not known; (2) quantitative data on conodont distribution and diversity at different spatial scales is not available; (3) reported diversity changes are partly based on new taxa which are not sufficiently documented to allow comparisons with other regions or which have uncertain ranks; (4) environmental niches of individual species are poorly contained; (5) the trophic position(s) of conodonts in Silurian ecosystems is (are) poorly constrained. We address primarily the first three issues and seek to develop alternative hypotheses to the present models.

### METHODS

We catalogued the content of all samples from Gotland in L. Jeppsson's collection and, wherever it was possible, reconstructed its stratigraphic position, exact or approximate position in the section, and the geographic coordinates. The information has been stored in the Palaeobiology Database (<https://paleobiodb.org>).



We preserved Jeppsson's original identifications in all cases and kept revisions at minimum by adding newer taxonomic opinions in clear separation from the original data. We photographed and documented problematic taxa, especially those reported only from Gotland, essential for stratigraphy or for diversity patterns proposed by Jeppsson. Exposures in Gotland provide onshore-offshore transects across the interval between the uppermost Telychian (Llandovery) through Ludfordian (Ludlow), classified into previously defined facies belts. Presence/absence data was used to calculate sample-level and total diversity in time and space (facies belts), as well as temporal and spatial turnover, at the stratigraphic resolution offered by the local zonation.

## CONCLUSIONS

Preliminary results indicate that previous estimates of the magnitude of extinctions were overestimated owing to the short time frames taken into consideration. Moreover, they are strongly affected by the taxonomic practice, e.g. how morphological evolution in a lineage is partitioned into genera, species, subspecies, and intraspecific variability. The recognition of environmental niches of conodonts are equally affected by how broad are their taxonomic diagnoses and indicate that part of the morphological variability can be attributed to morphological clines along the onshore-offshore gradient. Variation in the environmental preferences of species results also in elevated local extinction rates at sequence boundaries and other abrupt facies shifts. The continuous spatial record in Gotland, however, allows this stratigraphic bias to be accounted for in the total diversity changes. Finally, the turnover associated with external factors driving carbon isotope excursions does not exceed turnover between environments in the absence of external drivers, showing that the current model stressing the importance of external, abiotic drivers is insufficient to explain observed changes in diversity. Instead, high diversity at the assemblage level seems to be associated with higher morphological disparity, suggesting that biotic factors such as community structure and trophic diversity might contribute to conodont diversity dynamics.

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## CHARACTERIZING THE PHYSICAL STRUCTURE OF CONODONT ELEMENTS USING ELECTRON BACKSCATTER DIFFRACTION AND PTYCHOGRAPHIC X-RAY COMPUTED TOMOGRAPHY

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**Keywords:** Conodont, white matter tissue, Electron Back-Scatter Diffraction (EBSD), Ptychographic X-ray computed tomography (PXCT)

Conodonts are regarded as the earliest members of vertebrates evolutionary lineage to possess a mineralized skeleton, manifest as a feeding apparatus of tooth-like elements. As such, the conodont elements composed of calcium phosphate mineral are of great significance since they host general insights as an archive of seawater chemistry and temperature, providing fundamental understandings of the past climates. Conodont elements have two different clearly discernible units, a microcrystalline and organic rich basal body and crystalline crown composed of transparent crown tissue and the enigmatic white matter. There is little agreement on the physical nature of white matter, the principal tissue targeted for geochemical analyses, which has variably been interpreted as megacrystalline, microcrystalline, and non-crystalline. We attempted to test among these interpretations based on physical characterization of crystal dimension, orientation, porosity and permeability, of white matter using Electron Back-Scatter Diffraction (EBSD) and Ptychographic X-ray computed tomography (PXCT). PXCT reveals that while white matter is extremely porous, the pores are not, generally, connected. EBSD analyses demonstrate that white matter is comprised of a single crystal typically tens of microns in dimension. Combined with evidence that conodont elements grew episodically, these data suggest that white matter, which comprises the denticles of conodont elements, grew syntactically. Thus, while this tissue is a closed system and, therefore, a good potential geochemical archive, it is an archive representative of the different growth stages of the conodont element and organism. These insights should inform the interpretation of geochemical data derived from conodont elements, implying that bulk samples are time averaged, but also affording an opportunity to discriminate ontogenetic shifts in the ecology of habitat of these long extinct early vertebrates.



## FINITE ELEMENT ANALYSIS OF THE CONODONT APPARATUS

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**Keywords:** Conodont apparatus function, SXRTM, Finite Element Analysis

Conodonts are an enigmatic group of animals characterised by a complex array of oropharyngeal mineralised elements. Those elements conform a complex apparatus with a huge diversity of shapes, for which function, up to date, has been poorly studied. Within the Order Ozarkodinida, the conodont apparatus is extremely conservative, being normally composed by a series of 15 pieces classified as P, S and M elements. Interestingly, conodont functional analysis has been focused on just the P<sub>1</sub> elements, those that show the highest morphological disparity; meanwhile the function of the apparatus itself has been poorly studied, just based on analogies and qualitative analytical approaches (Purnell, 1994). The development of new computational techniques, assisted by computed tomography, are opening new opportunities to study quantitatively the function of these elements. Accordingly, in this work we attempted to shed some light on the function of the conodont apparatus using Synchrotron X-Ray Tomographic Microscopy (SXRTM), combined with Finite Element analysis (FEA).

To reach our goals, we have extracted a complete 3D conodont apparatus from a cluster of *Gnathodus bilineatus* (Carboniferous of UK), based on SXRTM, and analysed the different conodont types (S<sub>1-4</sub>, S<sub>0</sub> and M) by means of a Finite Element analysis, a conventional engineering technique used to analyse the stress and strain within complex shapes. *Gnathodus* P<sub>1</sub> elements are well known from a function viewpoint, with a complete analyses of their occlusion, microwear and microstructure showing that those elements performed an efficient tooth-like function (Donoghue & Purnell, 1999; Martínez-Pérez *et al.*, 2014). Therefore, the functional study of a complete apparatus of the same species, will allow us a better understanding of the role of the whole apparatus by unravelling the relationship between the morphology of the different teeth-like structures and the specific function that those elements could perform.

Based on the 3D models of the different elements of the apparatus, we constrained our FEA models simulating different loading scenarios, assuming that if the P<sub>1</sub> elements develop a tooth function, the ramiforms should be involved somehow in the processing, manipulation or merely grasping the food items. Given this scenario, we scaled the models to surface area, applying loads to the main denticles of each conodont type (S<sub>1-4</sub>, S<sub>0</sub> and M) in different directions (perpendicular to the main cusp, dorsal, ventral, and lateral) to simulate different element movements and/or functions, and constraining the elements by its basal cavity. Our preli-

minary results show that even though some element show clear morphological similarities, their mechanical performance apparently responds differently upon similar loading conditions, with some elements being more resistant than other, e.g. the  $S_{1-4}$  elements seem stronger than the M and  $S_0$  elements. On the other hand, the variation in the loading condition for each element allowed us to show their best mechanical scenario, opening a new line to investigate the relative movement of the different element on the apparatus based on their best mechanical performance. Therefore, although preliminarily, we can suggest that there is evidence of morphological and, consequently, functional specialization of individual elements, probably reflecting the different roles that the elements could perform within the apparatus. In addition, the combination of the study of complete well-preserved clusters, with the real topological position of the elements, and the application of these state-of-the art analytic techniques could shed light on the function and motion of the whole conodont apparatus.

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## AN ANIMATED, FUNCTIONAL MODEL OF *MOCKINA'S* APPARATUS

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**Keywords:** Conodont apparatus, modelling, synchrotron microtomography

The general architecture of conodonts' oral skeleton is a bilaterally symmetrical array of usually 15 phosphatic elements. Based on exceptional fused clusters of elements of *Novispathodus*, an Early Triassic conodont, Goudemand et al. (2011, 2012) revised the morphological interpretations of the S<sub>1</sub> and S<sub>2</sub> elements and proposed a realistic, animated reconstruction of the feeding apparatus at work. They suggested that the reconstructed movements were best explained by the putative presence of a lingual cartilage about which the elements were rotated by pairs of antagonistic muscles, i.e. a pulley-like mechanism similar to that found in extant cyclostomes.

As mentioned in an earlier abstract (Goudemand et al. 2013, 3<sup>rd</sup> ICOS), newly discovered and exceptionally preserved fused clusters of elements of the Norian *Mockina* (*Cypridodella*) that were imaged using propagation phase-contrast X-ray synchrotron microtomography, lend additional support to this model. In particular they seem to record the predicted pinching configuration whereby the S<sub>0</sub> and the pair of M elements would have been synchronized to grasp food.

Here we have segmented the individual elements within these clusters and re-analysed these clusters in details. The relative positions of the M elements recorded in one particular cluster led us to build a revised, animated model of these conodonts' apparatus.

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## MODELING THE GROWTH OF CONODONT ELEMENTS

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**Keywords:** Morphogenesis, development, computer simulations, conodonts

### INTRODUCTION/BACKGROUND

We are interested in the structure of intraspecific variation within conodont populations and how developmental constraints may have driven the evolution of conodonts in specific directions. In particular we want to understand the theoretical, developmental basis of phenotypic integration in conodont elements. For this purpose we are developing computational models, inspired by a cell-based model, initially developed by Salazar-Ciudad and Jernvall (2010), which is considered a realistic, simplified model of dental development.

### MATERIAL AND METHODS

Salazar-Ciudad and Jernvall's model is an agent-based model at the cellular level that simulates the interactions between the epithelium and the underlying mesenchyme. Initially, the model includes a set of identical epithelial cells lying above a set of identical mesenchymal cells. All cells can respond to mechanical cues as well as to three diffusing signaling molecules: an activator inducing enamel knots, an enamel knot-secreted inhibitor of enamel knot formation, and a growth factor regulating growth of the epithelium and mesenchyme. Because the enamel knot differentiation is irreversible, the model represents an irreversible reaction-diffusion-like model. Contrary to a standard reaction-diffusion model, the 3D domain within which the signals diffuse grows as the reaction-diffusion patterning mechanism operates. As a consequence, the way the signals diffuse is constrained by the domain but the growth of the domain depends also on the diffused signals. In other words, pattern formation and morphogenesis are mutually linked, a mode of development, they call morphodynamic (Salazar-Ciudad and Jernvall, 2002).

Denticles form when epithelial cells differentiate into non-dividing 'enamel knot' cells. This happens when the concentration of the activator reaches a set threshold. 'Enamel knot' cells then secrete the inhibitor, which inhibits the secretion of the activator and diffuses, thus also inhibiting the formation of additional denticles in the direct neighbourhood of the previous denticles.

### DISCUSSION

Although this model was developed for mammalian teeth (mice and seals), it is a generic model: the actual genetic and cellular interactions that regulate tooth-shape development are summarized in a few interactions and the model parameters code for the strength of these interactions, regardless of what actual



genes may be involved. Most of the cellular interactions are likely to be shared by other vertebrate epithelial appendages. Only the strength of these interactions is expected to vary. The genetic interactions are also reduced to a simple Turing model that is extended to enable cell differentiation and growth, and consequently we can expect the core of this model to be relevant for all odontodes, and thus for conodonts.

We are currently trying to extend the model to polyodontodes (or odontocomplexes) in order to match the specificity of conodonts' growth pattern (see Donoghue 1998).

## CONCLUSIONS

We show that it is possible to use this model to simulate the growth of conodont-like elements, in particular comb-like and molariform elements. The model can be used to suggest hypotheses about developmental modifications that may have underlie observed evolutionary innovations. Thus it could also provide estimates of the likelihood of evolutionary transitions between two given morphologies.

## Acknowledgements

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## SYNCHROTRON TOMOGRAPHY-BASED FUNCTIONAL ANALYSIS OF P<sub>1</sub> ELEMENTS OF THE *EPIGONDOLELLA-MOCKINA* LINEAGE

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**Keywords:** Conodont function, SXRTM, microwear analysis, gondolellids

### INTRODUCTION

Conodonts were eel-shaped soft-bodied organisms, their only hard-parts were a set of oral teeth-like elements. Their biological affinities and the function of those mineralised elements have attracted great attention. Until recently, conodont functional analysis has been limited to analogies and qualitative analytical approaches, but novel quantitative computational methods, as aided by computed tomography, are opening new opportunities to study the function of these elements. We have attempted to elucidate the evolution of feeding function within the Upper Triassic *Epigondolella-Mockina* lineage using Synchrotron X-Ray Tomographic Microscopy (SXRTM), combined with microwear analysis.

### MATERIAL AND METHODS

All the studied specimens belong to the *Epigondolella-Mockina* lineage (including taxa such as *Epigondolella* aff. *praeslovakensis*, *Epigondolella quadrata*, *Epigondolella rigo* and *Mockina slovakensis*), from the Seazza Creek (Roghi et al., 1995) and the Pizzo Mondello (Nicora et al., 2007) sections through the Upper Triassic of Italy. All exhibit a typical gondolellid morphology: a well-developed ventral free blade and a dorsal platform. Some species of this lineage are characterised by a high free blade and an abrupt interruption between the blade and the platform. This kind of morphology has never been studied from a functional viewpoint.

Our functional analysis was centred on the development of their occlusal cycle based on the 3D models (digital and physical) obtained from several *Epigondolella* aff. *praeslovakensis* P<sub>1</sub> clusters obtained using SXRTM at the Paul Scherrer Institut (Villigen, Switzerland). In addition, in an attempt to independently test inferred occlusal models, several disarticulated P<sub>1</sub> elements belonging to the same taxon, and from the same levels, were analysed for microwear (internal and external), using Scanning Electron Microscopy and SXRTM tomography.

## RESULTS

Analysis of the occlusal cycle of *Epigondolella* aff. *preaslovakensis* has allowed us to infer a model of a bilateral occlusion with an orthogonal component. Element occlusion was directed and controlled mainly by the denticles of the platform, not by the denticles of the carina.

Microwear analyses reveal evidence of element-element occlusion in the areas predicted by the occlusal model, that is, on the exterior denticles of the platform and on some parts of the free blade.

Our tomographic characterization of several exceptionally well-preserved specimens allowed us to identify internal wear and repair in the same functional areas predicted by the occlusal analysis. Interestingly, the same type of internal marks were identified in closely-related taxa with similar morphologies, such as *Epigondolella quadrata* and *Epigondolella rigoi*, as well as in unrelated taxa such as *Metapolygnathus linguiformis* and *Metapolygnathus communisti*.

## DISCUSSION AND CONCLUSIONS

Our digital occlusal analysis, combined with the internal and external microwear analyses of the *Epigondolella-Mockina* evolutionary lineage has allowed us to describe an occlusal cycle characterised by an orthogonal approach controlled by the lateral denticles of the platform and not by the denticles of the carina, showing that the great development of the carina and lateral denticles of the platform did not allow the typical rotational cycle described in other typical platform conodonts (Donoghue and Purnell, 1999a; Martínez-Pérez et al., 2014, 2016), highlighting again the occlusal diversity in conodonts. This cycle has been corroborated by the microwear analysis, finding clear evidences of wear on the surface of those denticles that controlled the occlusal cycle. In addition, the internal evidence of wear, recurrently located in areas where superficial wear was found, support the proposal that conodont elements were not shed and replaced by new ones as some authors suggested (Carls, 1977), but were retained throughout the whole life of the animal (Donoghue and Purnell, 1999b). The record of similar internal wear facets in other related taxa with similar morphologies, such as *Epigondolella quadrata* and *Epigondolella rigoi*, and unrelated taxa with dissimilar morphologies, such as *Metapolygnathus linguiformis* or *Metapolygnathus communisti*, demonstrate that this internal damage is not a taphonomic artifact.

Finally, our work confirms that typical platform gondolellids used their P<sub>1</sub> conodont elements as teeth to process their food. In addition, our results confirm that these elements were repaired, maintaining an optimal and functional efficiently morphology to process their food and, thus, were not shed and replaced during the life of the animal.

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## CONODONT CLUSTERS FROM THE MIDDLE TRIASSIC LUOPING BIOTA, SOUTHWEST CHINA

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**Keywords:** Conodont, clusters, Middle Triassic, Luoping biota, southwest China

### INTRODUCTION/BACKGROUND

Conodont clusters are relatively scarce in the fossil record from Permian to Triassic over the world, but extremely rare in China. Hitherto only four different conodont taxa have been recovered as clusters, including: *Neohindeoformella* from the Late Permian Changxing Formation, Kongtong Mountains, Datian, Fujian Province (Zhang and Zhang 1986), *Hindeodus* from the Early Triassic Feixianguan Formation, Shangshi, Guangyuan, Sichuan province (Jiang and Zhang 2015), *Novispathodus* from the Early Triassic Luolou Formation, Tiandong District, Guangxi Province (Goudemand et al. 2011), and clusters of *Nicoraella* from the Middle Triassic Guanling Formation, Luoping, Yunnan Province (Huang et al. 2010). All show several ramiform and/or platform elements preserving, in some cases, part of the three-dimensional structure of the multielement apparatus. Fused clusters are rare structures composed of several elements that are diagenetically fused and are extremely important for testing hypotheses on the architecture of apparatuses. However, they are fragile and very difficult to manipulate, and if more than two elements are involved, the external elements and/or matrix mask the morphology and arrangement of the different elements, making it very complicated to analyze. Here, using state of the art tomographic techniques, we study the first complete cluster of *Nicoraella* from Luoping biota, showing the complete characters of the conodont apparatus; allowing us to reconstruct its architectural model and revise the architecture of the superfamily Gondolelloidea apparatuses.

### GEOLOGICAL CONTEXT

Isolated conodont elements and fused conodont clusters of the genus *Nicoraella* were recovered from the lower fossil unit of the Luoping biota (Anisian, Middle Triassic; Zhang et al. 2009). The conodont-bearing strata belong to the member II of the Guanling Formation, which is widely exposed over the eastern Yunnan and western Guizhou provinces, at the southwestern part of the Yangtze Platform between the Nanpanjiang Basin and the Yangtze Platform (Enos et al. 2006). The Guanling Formation is well known because of the discovery of abundant articulated fossils at Luoping County. The Luoping biota is a rich and diverse fossil assemblage

of marine invertebrates and vertebrates, dominated by lightly sclerotized arthropods, associated with fishes, marine reptiles, bivalves, gastropods, belemnoids, ammonoids, echinoderms, brachiopods, foraminifers, ostracods and conodonts (Hu et al. 2011).

## MATERIAL AND METHODS

All conodont clusters and discrete elements here reported, come from the Luoping biota (Huang et al. 2010, 2011) and were extracted from limestone after acetic acid digestion of several samples in the Shangshikan and Dawazi sections. Specimens were photographed using a SEM located at the State Key Laboratory Geological Processes and Mineral Resources, China University of Geosciences, Wuhan, China. In addition, the cluster was scanned at the Synchrotron-radiation X-ray tomographic microscopy (SRXTM) in Swiss Light Source (Villigen, Switzerland). Accurate 3D models reconstructions were obtained after analysing the tomographic data using the specialized software Avizo (8 and 9) and Geomagic Studio.

## RESULTS

An important collection of discrete conodont elements and several fused conodont clusters was recovered from the Dawazi and Shangshikan sections. Previous work on the ratios of the discrete elements recovered revealed the presence of the whole conodont elements of a traditional Ozarkodinid apparatus in the collections, but neither the real composition nor the apparatus architecture was achieved (Huang et al. 2011). However, the study of a complete cluster of *Nicoraella* showed a 15 element conodont apparatus, including one pair of segminate  $P_1$  elements (nicoraellan), one pair of bipennate  $P_2$  elements (xaniognathiform), one alate  $S_0$  element (hibbardellan), a pair of dolobrate  $S_1$  elements (cypridodellan), a pair of breviform digyrate  $S_2$  elements (enantiognathiform), two pair of bipennate (hindeodellan)  $S_3$  and  $S_4$  elements, and one pair of digyrate M elements (cypridodellan). The relative position of the different elements in the clusters locates the  $S_0$  element at the middle and in an inner position of the apparatus, the dextral and sinistral  $S_1$  to  $S_4$  elements lay outside, one by one next to  $S_0$  element, and the M elements, fused together with S array, in the most external location.  $P_1$  and  $P_2$  elements were fused together, with their denticles opposing each other, and in a more caudal position.

## DISCUSSION

The cluster here described follows the classical 15 element Ozarkodinid apparatus ( $2P_1$ ,  $2P_2$ ,  $S_0$ ,  $2S_1$  to  $S_4$ , and 2M elements). Our architecture undoubtedly confirms the position of  $S_1$  and  $S_2$  elements in the multielement apparatus, confirming the last proposal of Goudemand et al. (2011), when they swapped the  $S_1$  and  $S_2$  positions in contrast with previous interpretations where the positions of the  $S_1$  and  $S_2$  were respectively occupied by the enantiognathiform and cypridodellan elements of the superfamily Gondolelloidea (Orchard, 2005). In addition, the multielement apparatus includes the  $S_0$ ,  $S_{3-4}$ , M and P elements, allowing us to reinterpret the architecture of the apparatus within the superfamily Gondolelloidea, for example, with the architecture of the natural assemblages of the genus *Neogondolella* from the Middle Triassic of Switzerland (Rieber, 1980; Orchard and Rieber, 1999); but also it permits us to compare the structure with the newly reconstructed apparatus of the genus *Novispathodus* (Orchard, 2005; Goudemand et al. 2011). Our results confirm that the  $S_3$  and  $S_4$  elements are much more conservative, showing similar outlines and at the same positions in of all the Gondolelloidea superfamily apparatus.

## CONCLUSIONS

The fused cluster and co-occurring isolated elements reveals the topological position and pattern of the *Nicoraella* conodont apparatus, allowing us to reconstruct its multi-element architecture (Fig. 1). The apparatus contains 15 elements, as proposed for other ozarkodinid conodont apparatus. The first reconstruction of a complete 3D conodont apparatus based on a complete cluster of *Nicoraella* represents the typical apparatus in the superfamily Gondolelloidea. Our specimens show a similar pattern of juxtaposition with the specimens of *Novispathodus*. These new data open a great opportunity to discuss the structure of the Gondolelloidea superfamily apparatus architecture.

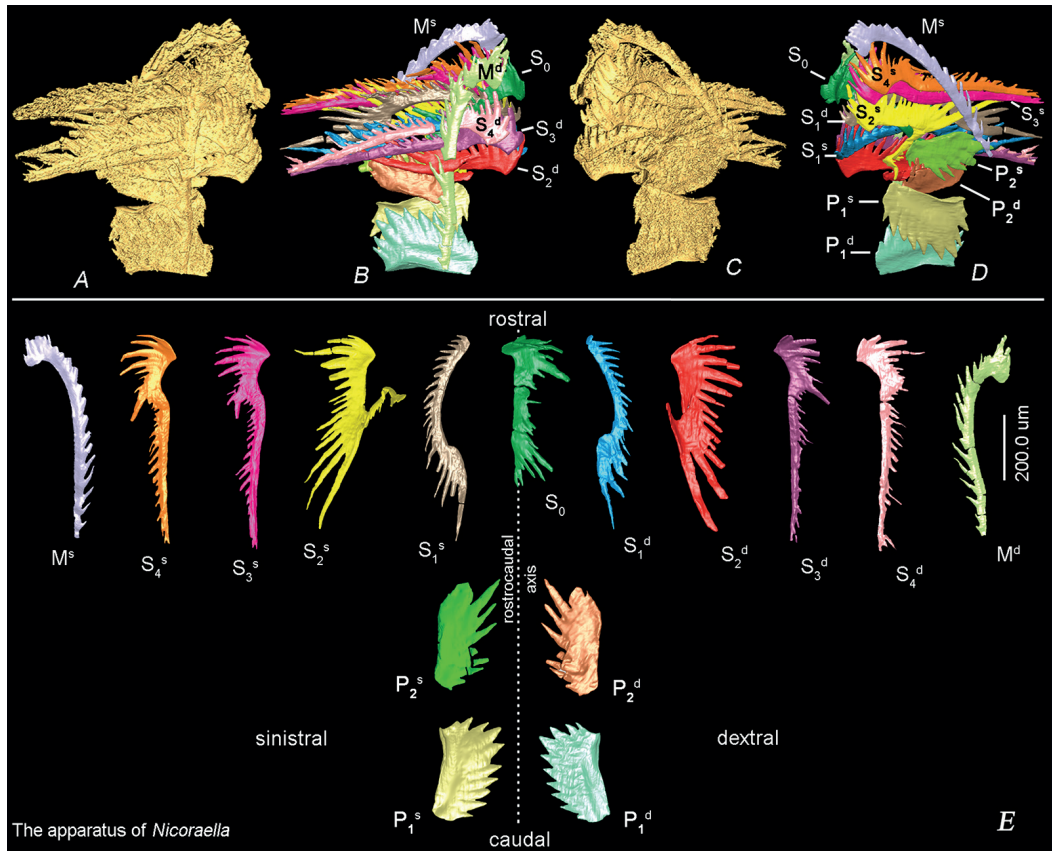


Fig. 1. A-D, complete fused cluster with fifteen elements ( $S_0$ ,  $S_1$  to  $S_4$ ,  $M$ ,  $P_1$  and  $P_2$  elements). E, Multielements of *Nicoraella* apparatus. Scale bar is 200 microns.



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## CONODONT AFFINITY – THE ULTIMATE PARLOR GAME

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Perhaps more than any other group of organisms, conodonts exemplify the difficulties inherent in interpreting incomplete fossil remains. For much of the century-and-a-half since their phosphatic skeletal elements were first described, there was little evidence and little consensus regarding many aspects of their anatomy, phylogenetic affinity, and function. After this prolonged period of almost unconstrained speculation, the discovery in the 1980s and 1990s of a series of fossils preserving non-biomineralised parts of the conodont body finally provided the key to establishing what kind of organism conodont elements came from. The remains from Scotland and South Africa are exceptionally well preserved and include authigenically phosphatized tissues, yet they also exhibit clear signs of decay and loss of anatomical information. These crucial specimens provide good evidence for the shape and orientation of the conodont body, and the presence of trunk musculature, interior rods and/or tubes, caudal fins and anterior sensory structures. Taken together with their skeletonized elements, the suite of soft-tissue characters evident from these remains indicates that conodonts were jawless vertebrates, broadly comparable to extant hagfish and lampreys. The presence of mineralized tissues comprising the conodont dentition, and their similarity to canonical vertebrate skeletal tissues, evidenced conodonts as the earliest skeletonizing vertebrates, and implicated them in scenarios that sought to explain the origin of the vertebrate skeleton. Until recently there was little scientific disagreement with this hypothesis in the literature, but a few recent papers have questioned it, and this has prompted us to reconsider all the available evidence in the light of current understanding of soft tissue taphonomy, relationships among vertebrates and their invertebrate relatives, and alternative approaches to phylogenetic analysis. Our results are clear: only by selectively excluding characters, failing to take anatomical decay into account, and by adopting narrow, character-based definitions of higher taxa (rather than basing assessments of affinity on hypotheses of relationships between clades) can conodonts be excluded from the vertebrates. However, rather than providing evidence of the origin of canonical vertebrate skeletal tissues, it appears that conodonts evolved their 'teeth', composed of enamel- and dentine-like tissues, entirely independently from, but in parallel with, gnathostomes.



## THE UPPER GIVETIAN TO LOWER FRASNIAN CONODONT SUCCESSION AND FRASNES EVENTS AT GIEBRINGHAUSEN (NE RHENISH MASSIF, GERMANY)

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**Keywords:** Givetian, Frasnian, conodont stratigraphy, Frasnian Events

### INTRODUCTION

The Giebringhausen section was one of the five key sections of the Rhenish Massif used by Ziegler (1966), Ziegler et al. (1976) and Ziegler & Klapper (1982) when the global middle/upper Givetian conodont zonation was first established and gradually refined. The original publication gave a rough section log for the NE face of the abandoned quarry with only 20 numbered beds. A range chart listed all identified taxa but zonal assignments of beds changed with ongoing faunal analysis. For example, the original (1966) record of *Palmatolepis transitans* (from Bed 17, marked with an "Ü" – probably for transitional), which would have indicated the late lower Frasnian *transitans* Zone (MN 4 Zone), disappeared later completely, leaving the original beds 17-19 in the *disparilis* to lowermost *asymmetricus* zones (all still Givetian). The identification of several figured polygnathids was left vague, which indicated that the faunal composition was never fully exploited. Unfortunately, the section was gradually forgotten and never re-visited during any later field trip.

### MATERIAL AND METHODS

New intensive field work in the eastern Sauerland led eventually to the re-discovery of the locality below the top of the Burghagen mountain, ca. 800 m NNE of Giebringhausen. The old quarry is now heavily overgrown and large parts were filled by rock debris. Some limestone cliffs still stick out and the best of it in the NE corner was measured and sampled bed-by-bed. It is not possible to recognize any of Ziegler's beds but some paint marks indicate that some previous sampling did take place. In the studied cliff, the middle Givetian is currently inaccessible and trenching would be very difficult. We took 39 samples from nearly all exposed limestone beds, which are either middle-grey, crinoidal turbidites (lower part, typical Padberg Limestone) or dark-grey to black, partly very argillaceous limestones and concretions embedded between dark-grey and black shale. We identified almost 10.000 platform elements that represent more than 80 taxa, including a high number of rare, unusual (possibly pathological), and new forms. The conodont yield fluctuates extremely, between 0 and 1540/sample. Coarse turbidites seem to be richer and dark limestones are often conodont-poor, but with exceptions from that rule (especially the argillaceous, black Bed 50d with 1130 specimens). We also counted fluctuations of alpha diversity, with a maximum of 42 taxa in one of the richest assemblages. The section is suitable for an analysis of hydraulic sorting by turbulence since there are very different amounts of ramiform elements in successive samples, with one bed being rich in ramiforms only.

## RESULTS

Throughout the section some taxa tend to be very common, especially *Polygnathus xylus* and *Po. varcus*. Zonal markers are mostly less common, with the exception of *Po. limitaris*, *Po. paradecorosus* and *Po. dengleri dengleri* in some upper Givetian beds. In the basal Frasnian, anyrodellids may reach up to 22 % of faunas.

In accord with the turbiditic nature of most limestones, there is some evidence of faunal reworking/mixing. The first two exposed beds (beds 3 and 4) are conodont-rich, with dominant *Linguipolygnathus linguiformis* (25-37 %) associated with common "*Ozarkodina*" *semialternans*, *Po. ansatus*, *Po. ovatinodosus*, some *Schmidtognathus latifossatus*, and rare *Schm. hermanni*, *S. pietzneri*, *S. wittekindti*, *Po. limitaris*, *Po. dubius*, and "*Oz.*" *sannemanni adventa*. This suggests the re-sedimentation of topmost middle Givetian (*semialternans* Zone) material in the basal upper Givetian (*hermanni* Zone). There are less than 5 % icriodids (mostly *I. brevis brevis*), which shows that the source was a pelagic slope, probably of an adjacent volcanic seamount. The overlying beds 6-9 are conodont-poor but *Schmidtognathus* is present.

*Polygnathus cristatus ectypus* enters as a subordinate species together with "*Oz.*" *sannemanni proxima* in Bed 10; *Po. limitaris* and *Po. xylus* are very common. The next two beds yielded a rare new *Schmidtognathus* species (with short side lobe) together with more abundant *S. pietzneri*, a single *Nicollidina brevis*, and the first local *Po. pennatus*. We assume that now rare specimens of *L. linguiformis*, a single *L. mucronatus*, and possibly also some *Po. timorensis* and *Po. ansatus* are reworked in the *cristatus ectypus* Zone. Based on *Klapperina vysotzkii*, we assign the subsequent beds 16-18 to the lower part of the *disparilis* Zone. Its zonal index species follows in the less rich fauna of Bed 19 together with *Kl. disparata* and *Kl. disparalvea*. This indicates a possible subdivision into successive subzones, which we like to prove by further sampling.

All *Klapperina* species continue into Bed 20A, which is marked by the sudden, moderately common entry of *Po. dengleri sagitta* and, less frequent, by *Po. paradecorosus* and (locally delayed) *S. peracutus*. This important fauna proves that the Moroccan *dengleri sagitta* Subzone of Aboussalam & Becker (2007) is well-developed in a Rhenish section and not only of regional (northern Gondwana) significance. The overlying Bed 20B is very conodont-poor and Bed 21b characterized by a *xylus-varcus* assemblage (82 %) with relatively frequent (12 %) "*Oz.*" *sannemanni adventa*. The *dengleri dengleri* Zone is restricted at our new Giebringhausen section to a single thin turbidite (Bed 22b). *Klapperina disparilis* and *Kl. disparalvea* are still present; there is no extinction at all at the base.

Beds 24-46 fall in a locally unusually thick and conodont-rich development of the *norrisi* Zone. *Skeletognathus norrisi* is a rather subordinate species, not only in Bed 24, and its characteristic Pb element is more often encountered than its Pa. The lower part of the zone (the very conodont-rich beds 24 and 26) is characterized by an acme of *Po. dengleri dengleri* (partly > 40 % of the faunas) and there are also blooms of *Po. dubius*, *Po. pennatus*, *Po. varcus*, *Po. ovatinodosus*, and *Po. ordinatus*. All three *Klapperina* species are still present, as in southern Morocco. The base of the zone is marked by additional index species, such as *Mesotaxis guanwuchanensis* (including its characteristic Pb element), *Po. aequidivisus*, *Po. alatus*, *Po. webbi*, *Po. "collieri M2"*, *Po. n. sp. aff. collieri*, *Ctenopolygnathus angustidiscus*, and *I. symmetricus*. There is also an interesting, small tortodid bloom in both beds (12 and 8.5 %, respectively), notably with *T. variabilis sardinia*, *T. variabilis variabilis*, *T. aff. weddigei*, and relatives of *T. subsymmetricus*, *T. schultzei*, *T. deformis*, and *T. ancyrognathoideus* (here re-assigned from *Ancyrognathus*). Other rare forms may be related to *Uyenognathus* (possible "*Po.*" *sculptilis*) and one specimen resembles the poorly known Chinese *S. furtivus*.

The higher part of the *norrisi* Zone, between beds 40 and 44, is poorer in conodonts and very dark. This first, topmost Givetian pulse of the global Frasnian Crises (Events) caused the extinction and local disappearance of some forms, such as "*Oz.*" *sannemanni adventa*, "*Oz.*" *plana*, *Po. cristatus ectypus*, and *Po.*

*ordinatus*; *Skeletognathus* is also not found any more although it continues elsewhere until MN Zone 2. It is currently not possible to place the Middle/Upper Devonian boundary with precision. *Ancyrodella rotundiloba soluta*, the index of the lower part of the MN 2 Zone, enters as a subordinate taxon (3.5 %) in Bed 48, which is dominated by *Po. pardecorosus* (58 %), followed by *Po. pennatus* (11 %). The early ancyrodellids disappear completely from the overlying, very dark and organic-rich interval of beds 49-50c. This resembles the conodont biofacies of the styliolinitic event beds of southern Morocco, which, therefore, were first wrongly placed in the *norrisi* Zone. Our second and more extensive pulse of the global Frasnian Crisis (beds 49-60) is interrupted by the conodont-rich, dark marl of Bed 50d, which yielded various index ancyrodellids, such as *Ad. rotundiloba soluta*, *A. rotundiloba rotundiloba*, and *A. recta*, together with the first (locally delayed) *I. subterminus* and *I. expansus*, as well as a species of *Zieglerina*. Therefore, the subsequent thickest black shale (Bed 53) and overlying concretionary black limestones (beds 54-58) fall in the upper part of MN Zone 2, which is also the age of the Lower Styliolinite of the Tafilalt and of the main pulse of the Frasnian Crisis (Events). Early ancyrodellids re-appear in Bed 64 but they are absent from a last limestone collected above the main section (Bed 67). This yielded another *xylus-varcus* assemblage, but with some other elements, such as *Elsonella rhenana*, *I. difficilis*, *I. brevis brevis*, "*Oz.*" *semialternans*, *Po. ovatinodosus*, and *L. linguiformis* (7.5 %). Without single records of *Po. webbi* and *Po. pardecorosus*, this fauna could be mistaken as from the Upper Taghanic Crisis Interval (*semialternans* Zone). It indicates a renewed input from a middle Givetian sediment source since beds 16-64 produced only single reworked linguipolygnathids in two much richer faunas.

## CONCLUSIONS

Our new section at Giebringhausen enables the recognition of all upper Givetian to basal Frasnian conodont zones and subzones, including the *denngleri sagitta* Subzone. On a global scale, Giebringhausen yielded the so far most diverse and richest top Givetian conodont faunas. There are several new and poorly known taxa of polygnathids, *Schmidtoognathus*, and *Tortodus*. Ranges of many forms are influenced by the two pulses of the global Frasnian Crisis (Events) in the higher *norrisi* and higher MN 2 zones. There is evidence for reworking and faunal admixture due to the turbiditic deposition in beds at the base and top but this mostly affected common middle Givetian species, notably of *Linguipolygnathus*.

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## THE IMPACT OF RE-SAMPLING ON CONODONT ABUNDANCE, PALAEO-DIVERSITY, BIOFACIES, AND STRATIGRAPHIC ANALYSIS – TWO FAMENNIAN CASE STUDIES

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**Keywords:** Conodonts, Famennian, diversity, biofacies, stratigraphy, statistics

### INTRODUCTION/ BACKGROUND

Conodonts were wide-spread in various Palaeozoic marine palaeoenvironments but it is common knowledge that samples variably have very small to large faunas, which are accordingly easy or difficult to interpret and compare with respect to stratigraphic age, palaeoecology (conodont biofacies, autecology, community structure), or palaeodiversity. Very inhomogenous local (alpha) diversity data build up regional (beta) or global (gamma) diversity, which fluctuations reflect important extinction and diversification trends. Therefore, it is rather surprising that there are so far no specific statistical studies that deal with the impact of sample size and re-sampling on conodont stratigraphy, biofacies, and palaeodiversity.

### GEOLOGICAL CONTEXT

In the frame of the B.Sc. Thesis of the first author, we used two ten kg samples from conodont-rich, oxic, and micritic pelagic limestone facies of the middle/upper Famennian of Franconia (Germany) as case studies. The microfacies suggests calm deposition without re-sedimentation and internal stratification by turbulence but with bioturbation, which homogenized the samples. The first was a loose block of the famous Köstenhof (= Schübelhammer) section (e.g. Tragelehn & Hartenfels 2002, 2011). It falls in the interval of the *Palmatolepis gracilis sigmoidalis* Subzone (higher *Pseudopolygnathus granulosus* = Upper *trachytera* Zone) below the global Lower *Annulata* Event. From local biofacies reasons, *Scaphignathus velifer velifer*, *Pa. rugosa trachytera*, and *Pa. minuta minuta*, which are normally common at this level, are absent. The second sample is from an unpublished section along a forest track NE of Losau, but in the vicinity of the former Rugendorf Quarry (Tragelehn 2016). It falls in the higher part of the (local) *Bispathodus stabilis stabilis* Zone (= Lower *expansa* Zone), from the interval below the global Dasberg Crisis, and includes both zonal markers, *Polygnathus styriacus* M1, the last *Po. nodocostatus nodocostatus*, and *Brammehla bohlenana bohlenana*, and the first *Br. fissilis*.



## MATERIAL AND METHODS

Both samples were split randomly into ten even subsamples before processing and picking. These can be statistically treated as if the beds were repeatedly sampled ten times. The weight differences between the (sub)samples was less than 0.5 %, which determines the maximum statistical error. Residues were picked completely but only all Pa elements were identified and counted. Our analysis addressed the following aspects:

1. The variability of absolute conodont abundance in all subsets;
2. The variability of alpha diversity and its correlation with absolute abundance (rarefaction aspects);
3. How much re-sampling is required to retrieve the complete local fauna, using ten random runs for each locality and cumulative counts;
4. An abundance ranking of all taxa (assignment to dominance classes) and its variability between subsets;
5. How reliably encountered are stratigraphical marker taxa (in how many subsets do they occur), leading to a stratigraphic reliability ranking;
6. Variability of conodont biofacies assignments;
7. Analysis of the assemblage structure based on the Shannon-Weaver Index and Evenness values *sensu* Washington (1982).

## RESULTS

The Köstenhof (sub)samples produced together ca. 1.950 Pa elements that fall in 25 taxa, Losau almost 2.250 Pa elements that fall in 31 taxa. At Köstenhof, the absolute yield varied between 157 and 282 specimens/kg, which gives a 37.4 % maximum negative to 45.1 % maximum positive difference to the average of 194.4 specimens (with 34 specimens = 17.4 % standard deviation). The equivalent values for Losau are even more variable, with between 172 to 410 specimens/kg and a 23.5 % maximum negative and 82.5 % maximum positive difference to the average of 224.7 specimens (66 specimens = 29.4 % standard deviation). This shows that there are large inhomogenities even in non-graded micrites, probably due to very variable bioturbation. The total abundance of conodonts has to be used very cautiously for environmental interpretations and differences up to 60 % between samples from the same bed may be meaningless (random).

The alpha diversity at Köstenhof differs between 14 and 17 taxa (average 14.9), which gives a rather low standard deviation. However, since different rare taxa are variably represented in (sub)samples, the encountered palaeodiversity fluctuates between only 56 and 68 % of the total amount of taxa; none of the samples represents the true alpha diversity to a satisfactory (90 %) extent. A similar picture emerges at Losau, with between 14 and 21 taxa/(sub)sample (average 17.8), but with a somewhat higher standard deviation. Individual (sub)samples record only between 45 and 68 % of the true alpha diversity. In other words, researchers have to realize that rare taxa could easily double the local palaeodiversity if sampling is continued. This high amount, however, applies probably only to species-rich (ca. > 20 taxa) assemblages. The random sequencing of (sub)samples, including extremes with the least and most diverse (sub)sample as the starting point for cumulative counts, showed that between five and ten (Köstenhof) and four and ten (Losau) (sub)samples were required to retrieve all encountered taxa (on average 7-8 runs). This is bad but realistic news: even if you take ten kg samples of conodont-rich strata you cannot be sure to get the complete faunal spectrum. We do not know how many more taxa would have to be added in 20 kg samples. However, with respect to the restricted standard deviation, significant changes of the observed number of taxa will probably reflect a true trend. In addition, there is only a weak positive correlation between conodont abundance and observed alpha diversity. At Köstenhof, (sub)samples with more or less identical numbers of specimens (ca. 200) included the minimum and maximum of observed species. At Losau, some (sub)samples

with ca. 200 specimens yielded more taxa (20-21) than samples that were double as rich (only 16 taxa). These rather variable courses of cumulative diversity rejects the idea of simple or linear factors that can be used in rarefaction calculations. A major change of the cumulative diversity curve slope occurs after the first sample, which, therefore, should not be smaller than a kg.

The encountered taxa can be ranked within assemblages as eudominant (> 32 % of specimens), dominant (10-31.9 %), subdominant (3.2-9.9 %), recedent (1-3.1 %), subrecedent (0.32-0.99 %), and sporadic (< 0.32 %). Between (sub)samples dominance can fluctuate, which may be relevant for biofacies terminology. For example, variably *Pa. gracilis gracilis* (five subsamples) or *Br. ampla* (four subsamples) are the most common (partly eudominant) taxa at Köstenhof and only one other form, *Bi. stabilis vulgaris*, becomes dominant in a single (sub)sample. Nine species are subdominant to recedent in total, with two more taxa that are recedent at least in one (sub)sample. This list includes all forms that are commonly used in stratigraphic analyses. Despite strong differences between the data subsets, it came out as a rule that only taxa that amount to at least ca. 1.5 % of the total fauna are found in all (sub)samples. Two further (sub)recedent taxa have to be judged as stratigraphically more unreliable; randomly they may not be encountered. Seven sporadic taxa occur in less than 50 % of the (sub)samples, five in even only one of them.

The situation is similar at Losau. Only *Pa. gracilis gracilis* is eudominant, reaching partly more than 50 % of the assemblages. *Bispathodus stabilis vulgaris* is consistently dominant, *Bi. stabilis stabilis* fluctuates strongly between recedent and weakly dominant. There are eleven recedent to subdominant taxa and four more are recedent in one or two (sub)samples. Here, only taxa with an abundance > 1.7 % of the total fauna are found in all 10 (sub)samples. *Palmatolepis gracilis expansa* is locally a sporadic taxon found in only three (sub)samples, which questions it as a zonal marker in the region. Six taxa occur only in one (sub) sample, which gives a rate of ca. 20 % extremely sporadic taxa at both localities. Among these, there are the upper ranges of stratigraphically significant forms, such as *Pa. gracilis manca*, *Pa. perlobata maxima*, and *Po. nodocostatus nodocostatus*.

The biofacies analysis leads to good news. All Köstenhof (subsamples) belong consistently to a *Pa. gracilis-Branmehla* Biofacies (with both groups together reaching 66-77 % of the total fauna), all Losau (sub) samples to a *Pa. gracilis-Bi. stabilis* Biofacies (reaching 64-80 %) with common (> 11 %) *Branmehla*. More disturbing is the partly widely fluctuating amount of subdominant genera, with up to 10 % difference (of total amount) between (sub)samples in *Bi. stabilis* (Köstenhof) and 6-8 % in *Alternognathus*, *Pseudopolygnathus*, *Neopolygnathus*, and the *Pa. perlobata* Group. This shows that conodont subfacies types should not be defined too strictly and only taxa that are at least subdominant should be considered for definition. There are no unusual spikes of rare groups in any of the (sub)samples.

The Shannon-Weaver Index fluctuates at Köstenhof between ca. 2 and 3.2, at Losau similarly, between 1.9 and 3.4. The resulting Evenness values of 0.62 and 0.56 reflect the similar assemblage structures characterized by strongly unequal frequencies of species. It underlines the significant amount of rare taxa, which are only episodically encountered and which point to a rather complex community structure, which synecology was certainly controlled by many factors, not only by palaeobathymetry.

## CONCLUSIONS

Our large data sets from two middle/upper Famennian localities of Franconia (Germany) show that there can be large fluctuations of conodont abundance, alpha diversity, and details of the assemblage structure between repeated samples of the same pelagic micrite. The high amount of rare (sporadic) taxa, manifested

in low evenness values, shows that in species- and specimen-rich facies even ten kg samples are not sufficient to obtain the complete fauna. This, however, does not affect the recognition of local palaeodiversity trends and conodont biofacies assignments.

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