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# **ICOS 2009 ABSTRACTS**

## **Edited by: Charles M. Henderson and Christine MacLean**



A pander of eggs (p.8).

International Conodont Symposium

A cluster of conodonts (p. 17).





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## Silurian to Early Devonian conodonts from Malaysia and Thailand

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Silurian and Early Devonian conodonts have been studied in Malaysia and Thailand. Although Igo and Koike (1967, 1968, 1973) described Middle Paleozoic conodonts through a series of studies, there has been no other biostratigraphic study of Silurian and Early Devonian conodonts in Southeast Asia. Here, we report on Silurian and Early Devonian conodont faunas from three areas in Malaysia and Thailand, including the first discovery of several species.

Malaysia-The Silurian carbonate succession distribution in northern peninsular Malaysia is called the Mempelam Limestone Formation (Cocks et al., 2005). Our investigation was made at the limestone exposure of this formation on the Langkawi Islands, northern peninsular Malaysia. The study section, about 300 m in thickness, yields abundant conodonts. The lower part of the section contains several representative species, Pterospathodus pennatus proceus, Dapsilodus hamari, Dapsilodus obliquicostatus and Panderodus langkawiensis. The upper part is characterized by occurrences of Ozarkodina excavata excavata, Ozarkodina remscheidensis remscheidensis, Ozarkodina remscheidensis eosteinhornensis, Pseudooneotodus beckmanni, Flajsella stygia, Flajsella Schulzei and Flajsella sigmostygia. These conodonts indicate that the lower and upper parts of the study section are compared with the Pterospathodus celloni to Ozarkodina segitta segitta Zones, upper Llandovery to middle Wenlock, and O. r. eosteinhornensis to Ancyrodelloides delta Zones, upper Pridoli to middle Lochkovian, respectively. Igo and Koike (1973) reported Icriodus woschmidti from the uppermost Mempelam Formation. The graptolite, Monograptus langgunensis, described by Jones (1968) from the basal Timah Tasoh Formation overlying the Mempelam Formation, is a typical species of the Pragian Monograptus yukonensis Zone. The lowermost part of the Timah Tasoh Formation also includes the dacryoconarids Nowakia and Styliolina, which indicate the Early Devonian (Jones, 1978). These stratigraphic data confirm the above-mentioned conodont age.

Thailand—Conodont faunas occur from the Silurian Kuan Tung Formation distributed in the Satun area, southern Thailand, to the so-called Thong Pha Phum Group, the Silurian and Devonian strata, in the Li area, northern Thailand. Conodont fauna from the limestone succession of the Kuan Tung Formation includes *O. e. excavata, Decoriconus fragilis, P. beckmanni* and *P. langkawiensis* and roughly suggests the Llandovery and Wenlock time. The study section in the Li area is made up of the limestone interbedded with black shale with abundant dacryconarids. The limestone beds contain *D. obliquicostatus, Dapsilodus* sp., *O. e. excavata* and *P. beckmanni* as representative species. On the basis of the conodonts and dacryconarids, the Li section spans from Ludlow or Pridoli to Pgarian in age.

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## Conodont biostratigraphy and paleoenvironments of the lower Sierra de La Invernada Formation, Middle Ordovician, San Juan Precordillera, Argentina

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The Sierra de La Invernada is a north-south trending range that extends for *ca*. 60 km in the in western Precordillera, in the San Juan Province, Argentina. The core of this range is composed by an early Darriwilian to early Katian dominantly siliciclastic succession known as the Sierra de La Invernada Formation.. This unit is largely composed by tabular sandstones and shales but conglomerates, calcarenites and fine-grained lime beds are also present. The formation is intruded by mafic dykes. A stratigraphic section along the provincial road 436 corresponds to the lower part of the Sierra de La Invernada Formation (337 m thick) and yields conodonts that indicate the Middle Darriwilian *Eoplacognathus* 

#### pseudoplanus Zone.

Five lithofacies were identified in the measured section: 1) Polymictic conglomerates and limestone rich-breccias with reverse to normal grading, indicating variably concentrated gravity flow deposits.

2) Coarse-grained graded sandy calcarenites with cross bedding indicating development of sand dunes under turbulent flow regimes reworking the coarser deposits of facies 1. Coarse sand grains within these beds are mostly lithic fragments with diverse limestone textures (ranging from skeletal packstones to mudstones) and minor proportions of quartz, feldspars, micas and few metamorphic and fine grained igneous lithics. Broken or slightly abraded bioclasts are also frequent components (*e.g.*, algae, bryozoans, bivalves, brachipods, pelmatozoans).

3) Sheet-like graded and laminated sandstones with pervasive development of climbing ripple lamination interpreted as eventbeds alternatively indicating turbidite deposits or storms beds under the reworking wave level. This is the volumetrically dominant facies in the profile.

4) Green silty-argillaceous shales interpreted as suspension deposits after the waning stages of facies 3 and under relatively quiet environmental intervals.

5) Laterally continuous fine-grained laminated calcarenites and lime-siltstones, with abundant cross-lamination and symmetrical rippled tops. This facies is the most conodont-rich facies and corresponds to event-beds that represent relatively diluted distal storm deposits. Parallel laminations and long wavelength wavy features (micro-hummocks) can be interpreted as high- flow regime features, whereas oscillation ripples are recorded at their tops indicating wave rework at relatively shallow depths. Components in these beds are mainly peloids, very fine-grained to silt size lime clasts and clacispheres together with very little quartz and small micas flaks. Whereas the limestone clasts and coarse sand size grains in the coarser facies 1 and 2 represent lithic fragments of older reworked limestones (non-coeval carbonates) the components in facies 5 seem to be represented largely by redeposited contemporaneous allochems, indicating that a coeval carbonate factory was active in the source area.

The conodonts were recovered from ten interbedded finegrained calcarenites in the Sierra de La Invernada Formation, throughout the measured profile, and also from two conglomerate samples in the lower section of the studied interval, summing up 22 kg of productive samples. The conodont collection includes about 3000 well-preserved specimens (CAI 3) that correspond to 40 species. The conodont biofacies of the lower Sierra de La Invernada Formation is dominated by Periodon macrodentata (over 50%), whereas other significant species such as Paroistodus horridus, Protopanderodus gradatus, Paroistodus originalis, Drepanodus arcuatus and Drepanoistodus basiovalis, are well represented. The conodont association yielded by this unit represents the Precordillera Province, in the Temperate Water Domain from the Deep-Water Realm. The conodont fauna is distinguished by the incorporation of typical species from the Laurentian and Baltoscandian regions, revealing a fluid exchange of taxa between these two paleobiogeographic units. The analyzed biofacies is characterized by a number of genera typical from the open deepwater environments such as Periodon, Protopanderodus, Pygodus,

Spinodus, Decoriconus, Dzikodus, Venoistodus, Eoplacognathus and Baltoniodus, although other forms, e.g., Fahraeusodus, Histiodella, Juanognathus, Parapaltodus, Protoprioniodus and Pteracontiodus, are representative of tropical shallow-water environments from the North-American Midcontinent region and elsewhere. Considering the presence of endemic species that complete the conodont association (Polonodus galerus, "Bryantodina" sp., Rossodus barnesi, Semiacontiodus potrerillensis) as well as other widely distributed forms of the genera Cornuodus, Costiconus, Erraticodon, Oistodus and Panderodus, a complex rich conodont fauna occurred. According to the stratigraphic distribution and relative abundance of genera throughout the profile, and considering the lithofacies arrangement and diverse models of conodont biofacies, the recorded conodont association represents a deep subtidal paleoenvironment in a distal siliciclastic platform or across the shelfal margin to the upper slope. This scenario is interpreted from the relative abundance of the genera Periodon, Paroistodus, Protopanderodus, Drepanoistodus, Costiconus and Drepanodus, which are common in the open deep-water biotopes.

A tectonic event is recorded at the exposed base of the studied section, where limestone clasts from the basal conglomerates, yielded allochthonous conodonts. These microfossils were reworked from strata correlative to the middle part of the San Juan Limestone, as inferred from the presence of the guide conodont *Oepikodus evae*, late Floian in age. The exhumed levels of the San Juan Formation that were eroded and redeposited on distal environments during the mid Darriwilian are interpreted as sourced from a westward advancing thrust belt related to docking of the Precordillera terrane against the South-American margin of Gondwana after crossing the Iapetus Ocean.

## The composition and architecture of primitive prioniodontid conodont apparatuses; a state-of-thescience review

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A consistent fifteen-element architectural template is now well established for ozarkodinin apparatuses, but it is becoming clear that early prioniodontid apparatuses had a greater variety of compositional patterns. Clusters of the basal prioniodontid *Paracordylodus gracilis* also indicate a fifteen-element apparatus (Tolmacheva and Purnell, 2002), but with the  $P_1$  and  $P_2$ elements more similar to each other than they are in ozarkodinins. A comparable apparatus structure has been reported for *Phragmodus*, on the basis of natural assemblages (Repetski *et al.*, 1998), and has been suggested for apparatuses of *Microzarkodina* reconstructed from large collections of well-preserved isolated elements (Löfgren and Tolmacheva, 2008). However, beddingplane assemblages of the unusual genus *Promissum* provide a nineteen-element model, with four pairs of P elements and with the  $P_1$  and  $P_2$  positions occupied by morphologically similar ele-

#### ments (Aldridge et al., 1995).

New natural assemblages of an *Icriodella*-like genus from the Late Ordovician Soom Shale of South Africa confirm an additional model, with seventeen elements; these include three pairs of P elements, all morphologically very distinct. A possible variant on this theme is presented by *Coryssognathus*, which was reconstructed by Miller and Aldridge (1993) to contain three distinct pairs of P elements, but to lack a symmetrical  $S_0$  element.

These models provide a range of templates on which to base possible reconstructions of other primitive prioniodontids and, of course, there may be other architectural patterns that have yet to be recognised. A revised cladistic analysis of early prioniodontids, incorporating the information from the new apparatuses, provides a predictive framework for such reconstructions.

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## Conodonts and the end-Devonian event stratigraphic chronology in the classic Pennsylvania "Oil Lands" region: Latest Famennian Riceville Formation – Berea Sandstone succession

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Traditionally, the end-Devonian Cleveland Shale, Bedford Shale, Berea Sandstone sequence in eastern Ohio has not been clearly traced into northwestern Pennsylvania due to apparent complex stratigraphy east of the Ohio/PA state line, compounded by poor outcrop coverage. New work, utilizing regional, conodontbearing, discontinuity-related lag deposits, event-stratigraphic markers, and sequence-stratigraphic principles, shows that Cleveland and Bedford-equivalent strata, understood by earlier workers to be absent near the PA/Ohio state line, reappear eastward across western and central Crawford County, Pennsylvania. These units reemerge below a regional disconformity flooring the Berea-equivalent Cussewago Sandstone. A condensed unit, characterized by dark, bioturbated siltstone and black shale partings and floored by a detrital pyrite/bone lag containing Bispathodus aculeatus aculeatus and Polygnathus symmetricus?, is tentatively identified as the Cleveland Shale and underlying Skinner Run Bed. This interval is overlain by a thin, unnamed, gray shale unit and a higher, erosion-related lag horizon ("Syringothyris Bed") containing Bi aculeatus aculeatus and Po. communis communis, which Caster (1934) interpreted as the base of the Bedford Shale-equivalent section in Pennsylvania. Strata 17 metres above this contact, within the "Drake Well Formation" (sensu Harper, 1998), yield Bi. aculeatus antiposicornis and "Icriodus" raymondi. Still higher units, the "Tidioute Shale" (sensu Harper, 1998), and the overlying Corry Formation, have not yet produced diagnostic conodonts. It is possible that the Tidioute Shale, where more complete than in sections examined to date, may include strata belonging to the Middle praesulcata zone and record the Hangenberg bioevent. The Devonian-Carboniferous boundary is presently placed at the base of the Bartholomew Siltstone Bed flooring the Orangeville Shale, but an unnamed shale unit below that bed might also be lower Carboniferous as well.

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## The fossil record from Pizzo Mondello (Sicani Mountains, Sicily) Norian GSSP candidate

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Pizzo Mondello (Sicani Mountains, western Sicily, Italy) is one of the best localities in the world for the definition of the Carnian/

Norian (C/N) boundary. This boundary is recorded within a succession of about 400 m thick Late Carnian-Late Norian "*Calcari* con selce", well known for the good primary magnetostratigraphic record and stable carbon isotope variations (Muttoni et al, 2001, 2004). This succession has become de facto the standard Tethyan marine reference for the Newark astrochronological polarity time scale (Kent et al., 1999; Muttoni et al., 2004) but it is also extremely interesting for the rich fossil record, consisting of ammonoids, conodonts, pelagic bivalves and radiolarians (Balini et al., 2008). Ammonoids are rather sparse but they provided accurate age constraints for the conodont and pelagic bivalve bioevents, that have been identified through very detailed bedby-bed samplings. Some radiolarian bearing levels also provide additional information for correlations.

The collected ammonoid faunas are very similar to the rich faunas described from western Sicily by Gemmellaro in his famous monograph (1904), but the new collection is bed-by-bed sampled. The most important ammonoid taxa so far identified document very well the Upper Carnian *Discotropites plinii* Zone and the Lower Norian *Guembelites jandianus* Zone, while in between the faunas are dominated by the group of *Anatomites sensu* Gemmellaro and by *Gonionotites*.

Conodont populations are very rich. The large number of specimens recovered in each sample allows statistical analyses of absolute abundances, the analysis of the different morphologies and the study of the relationships among genera and species, that are described in detail in separate contributions (Mazza et al., 2009; Rigo et al. 2009 in the present abstract volume). Currently 29 established conodont species, 5 new species and several transitional forms have been recognized. The classified species belong to 8 genera, among which the five most widespread Upper Carnian/ Lower Norian genera have been recognized: Paragondolella, Carnepigondolella, Metapolygnathus, Epigondolella and Norigondolella. Conodonts are the most abundant and promising fossil group, then possibly the selection of the Norian GSSP marker event will be chosen within this taxon. Two possible bioevents for the definition of the Carnian/Norian boundary have been identified: the FAD of Epigondolella quadrata Orchard and the FAD of Metapolygnathus communisti Hayashi.

The halobiids are undoubtedly the most common megafossil group recorded in the "*Calcari con selce*". Some 1100 specimens coming from about 230 beds were collected. Nine halobiid species and two sub-species have been recognized, grouped in seven assemblages spanning from the Upper Carnian to the Lower Norian. Of special interest is the occurrence in the C/N boundary interval of the sequence of species *Halobia areata*, *H. superba* and *H. styriaca*, which is typical of the Lower Norian in the North American (*Stikinoceras kerri* Zone; McRoberts, pers. comm., Krystyn *et al.*, 2002) and Thetyan successions (lower to upper *G. jandianus* Zone; Krystyn and Gallet, 2002). The abundance of halobiids and the great similarity of the faunas from Sicily with the faunas from North America suggest the possible selection of secondary C/N marker events within this group.

An additional tool for global correlations is represented by radiolarians, which were found in some samples with high diversity assemblages. In the 30 m-thick boundary interval there is an overlap between species previously considered Late Carnian with species usually regarded as Early Norian. The first Early Norian radiolarian assemblage occurs above the FAD of *E. quadrata*. This fauna consists of *Braginastrum curvatus* Tekin, *Capnuchosphaera deweveri* Kozur and Mostler, *Capnuchosphaera tricornis* De Wever, *Kahlerosphaera norica* Kozur and Mock, *Mostlericyrtium sitepesiforme* Tekin, *Podobursa akayi* Tekin and *Xiphothecaella longa* (Kozur and Mock).

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## Conodont biostratigraphy and biofacies of the Henryhouse Formation (Ludlow-Pridoli, Silurian), southern Oklahoma, U.S.A.

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The Henryhouse Formation in southern Oklahoma comprises up to 75 m of argillaceous to silty carbonate mudstone and wackestone that range in age from the earliest Ludlow to the latest Pridoli based on condont faunas. The Henryhouse Formation includes two distinct lithologic units, the boundary between which corresponds to the disconformity at the Lau Oceanic Event.

The lower unit is relatively thin, <12 m, and comprises extremely argillaceous and silty carbonate mudstones interbedded in the upper part with graptolite-bearing silty shale. The lower silty unit is restricted to the central and southern Arbuckle Mountain region. The conodont fauna of the lower silty unit shows that it ranges from the Kockelella crassa Zone through the Polygnathoides siluricus Zone. The conodont fauna is strongly dominated by elements of Dapsilodus and lesser numbers of Panderodus and Wurmiella excavata. Elements of Kockelella species are common in Gorstian faunas, but Ozarkodina confluens is more characteristic of early Ludfordian faunas. Biostratigraphic, isotopic, and physical evidence show that the lower silty unit is riddled with minor disconformities, which may account for the variation in thickness of the unit. Conodont elements tend to be badly broken in most samples, which suggests multiple intervals of exposure and perhaps minor reworking during deposition. Neither stable isotopes nor conodonts provide clear evidence of the Linde Oceanic Event.

The upper Henryhouse unit comprises moderately argillaceous carbonate mudstone and wackestone that rest unconformably on the lower silty unit. The upper unit constitutes the greater thickness of the formation in the Arbuckle Mountain region and all of the formation on the Lawrence Uplift to the northeast, where it attains its greatest thickness of 75 m. Nearly all of the characteristic "Ludlow" shelly fauna of the Henryhouse has been collected from the upper unit. The contact between the lower silty unit and upper unit lies at a disconformity surface where the pre–Lau Event *siluricus* conodont fauna ends and the post-Lau *Ozarkodina snajdri* fauna appears. The truncated isotopic record indicates that most of the time interval of the Lau Event is absent.

Conodonts of the upper Henryhouse unit occur as three successive faunas. The basal fauna, which characterizes several metres of relatively clean mudstone and wackestone, is strongly dominated by elements of *Dapsilodus*, *Belodella*, and *Wurmiella excavata*. The most characteristic species are *Ozarkodina auriformis* and *O. snajdri*; a few elements of *Pedavis latialata* occur. A few possible specimens of the late Ludlow species, O. crispa occur near the top of the basal fauna. The middle fauna is a low diversity fauna characterized by the abundance of Panderodus elements, with fewer Dapsilodus and Belodella elements in more argillaceous mudstones. Within this unit, small numbers of Dvorakia amdseni, Zieglerodina spp. and related forms, and Oulodus elegans elements occur sporadically. The upper fauna is characterized by a dominance of Belodella elements and variable numbers of Dvorakia, Dapsilodus and Panderodus. Elements of Ou. elegans and Zieglerodina spp. and related forms appear more regularly in the upper part of the fauna. Near the top of the third fauna, Ou. elegans detorta and a pronounced acme of Belodella coarctata occur. The base of the Pridoli and the early Pridoli Klev Oceanic Event cannot be identified. The Klonk Event, which crosses the Silurian-Devonian boundary, occurs in the uppermost beds of the Henryhouse and basal beds of the overlying Haragan Formation.

## Evolutionary patterns in conodont faunas of the Simpson Group, south-central Oklahoma

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The Simpson Group (Arbuckle Mountains) in southern Oklahoma records 700 metres of shallow-marine sedimentary rock that ranges from Dapingian to Sandbian in age or from early Whiterockian to early Mohawkian age. The Simpson is biostratigraphically important because it represents one of the thickest, virtually complete sections chronologically of fossiliferous rock in the eastern Midcontinent of North America.

The succession of Simpson conodont faunas represents a nearly continuous record of evolution in shallow-marine water. A striking turnover occurs at a level in the lowermost McLish Formation (middle Simpson Group) where species of the Oistodontidae and Multioistodontidae make their last appearance. That level marks the beginning of a transgression following a widespread regressive event (Sauk-Tippecanoe). Species that are affected by the extinction event are those with skeletal apparatuses that are morphologically simple compared to earlier forms in their respective families. The causal mechanism for extinction of the Oistodontidae and near extinction of the Multioistodontidae is likely a reduction in shallow water habitats which may have victimized species based on their level of specialization.

## The Ordovician conodont *Amorphognathus ordovicicus* Branson and Mehl and the evolution of *Amorphognathus* Branson and Mehl, a key genus in Ordovician conodont biostratigraphy

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In their classic monograph, Branson and Mehl (1933) described the genus *Amorphognathus* with the type species *A. ordovicicus* based on a collection from the Maquoketa -Thebes formations at a locality near Ozora, Missouri. Repeated attempts since the 1950s to find their imprecisely described site were unsuccessful until we re-discovered this 'lost' locality in 2005 (Leslie and Bergström, 2005). Our collections include several hundred conodont elements representing 14 multielement species, six of which were described from this locality by Branson and Mehl (1933). Of special interest was the recovery of several specimens of the diagnostic M element of *A. ordovicicus*, which was previously unknown from Ozora. As suggested by several authors, this element has a simple cusp without adjacent denticles (Figure 1).

Amorphognathus, which was a relatively rapidly evolving platform genus with a global distribution, is of major biostratigraphic significance and some of its species serve as zone indices. The evolutionary origin of the stratigraphically oldest known species, A. inaequalis Rhodes, is not firmly established, but its elements show similarity to those of Baltoniodus Lindström and related genera such as Rhodesognathus Sweet and Bergström. Based primarily on the M and Pa elements, several species are recognized in the Sandbian and Katian, such as A. tvaerensis Bergström, which evolved into A. superbus Rhodes in the early Katian. A distinctive species, A. complicatus Rhodes, probably evolved from A. superbus in early Katian and it ranges into the middle Katian. Among the several incompletely known Amorphognathus species recorded from the middle-upper Katian is A. primitivus (Winder), which has some morphological characteristics intermediate between A. superbus and A. ordovicicus. A. ventilatus Ferretti and Barnes from the A. ordovicicus Zone, which was based on only M elements, and A. duftonus Rhodes, of which now excellent specimens are available from its English type locality, are so close to A. ordovicicus that separation at the species level may be unwarranted. In areas with a suitable biofacies, representatives of Amorphognathus range into the Hirnantian, but there are currently no reliable records of the genus from the Silurian.

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Figure 1: SEM micrographs of some conodont species recently collected from the Ozora locality. Note the complete collection of P, M, and S elements of *A. ordovicicus*, and the simple cusp of the M element. (Leslie and Bergström, 2005).

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## The Middle Silurian (Wenlock) Eramosa Lagerstätte of the Bruce Peninsula, Ontario, Canada

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The Eramosa Lagerstätte of Ontario, Canada, contains wellpreserved, abundant vertebrates as articulated conodont skeletons and heterostracan fish. It is associated with taxonomically and taphonomically diverse, exceptionally preserved invertebrate and plant biotas, in the upper part of a 16 km outcrop belt of the ~15 m thick Eramosa Formation. The Eramosa Lagerstätte occurs in dolomitic rocks deposited along an environmental gradient that, based in part on the dominant conodonts present, we interpret to range from fully marine, through restricted marine, to lacustrinemarginally marine conditions.

At Wiarton, infrequent, but exquisitely preserved conodont skeletons of *Wurmiella excavata* (many/most preserving eyes), as well as rare ?fish remains, occur with a diverse, exceptionally preserved, soft-bodied marine fauna and flora, in organic-rich, flaggy carbonates. Based on the distribution of *Wurmiella excavata* in the Silurian of the Baltic, we interpret this environment to have been open marine, with good water circulation. Such an interpretation suggests the previous lagoonal interpretation be modified slightly to lagoonal, with open marine circulation.

At Hepworth, the Eramosa Lagerstätte is dominated by articulated conodont skeletons, many/most preserving eyes. Wurmiella excavata dominates, and is associated with much less frequent, Ozarkodina? sp. A, O.? confluens, Ctenognathodus cf. murchisoni, and Panderodus sp., with a shelly fauna in/on nodular carbonate and its encasing bituminous shale. About 3 km west, Ctenognathodus cf. murchisoni and Ozarkodina? sp. A dominate, and Pseudooneotodus bischoffi and Panderodus sp. are present, to the exclusion or near-exclusion of Wurmiella excavata, again associated with a shelly fauna in nodular carbonate and encapsulating bituminous shale. The several hundred conodont skeletons recovered from these two sites comprise at least seven taxa, and are the most abundant and diverse assemblage of articulated conodont skeletons known, quadrupling the number known from the Silurian. Conodonts preserving remains of soft tissues were previously limited to three genera from three localities; the Eramosa Lagerstätte adds two additional genera, with potential for more. Based on the distribution of closely related conodont taxa in the Silurian of the Baltic, the conodonts suggest an open marine environment at Hepworth, with more restricted, poorer marine water circulation, towards the west.

At Park Head, conodonts and shelly, open water, marine indi-

cators such as corals, brachiopods, and cephalopods are absent; flaggy carbonates contain corvaspid and rare tolypelepid dermal elements, together with rare complete skeletons of both of these groups of heterostracan fish. Previously, articulated Silurian heterostracans were known only from a single locality; those from Park Head preserve the first recorded traces of heterostracan soft-tissue remains as carbonaceous films associated with the calcium phosphate of the skeletal plates. The agnathans occur with eurypterids, polychaetes and ostracodes, tolerant of a broad range of salinities, and known to occur in non-marine to transitional marine-terrestrial settings.

Recent early vs. late Wenlock age determinations for the Wiarton and the Hepworth sections, respectively, raise questions regarding time and environmental equivalency of the two sections. Resolution likely depends on the identity and distribution of the *Ctenognathodus* species present.

## Possible Conodont Eggs from the Pennsylvanian (Middle Desmoinesian) of NW Illinois, U.S.A.

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A single part and counterpart specimen (ROM 59510 A and B) from the black shale associated with the Oak Grove Member of the Carbondale Formation on Court Creek, Knox Co., Illinois, U.S.A. preserves a group of 65 or more well-preserved, elongate, torpedo-shaped fossils, with one end blunt but rounded, the other pointed. They are 0.32 to 0.40 mm long, with measurement variation likely due to breakage of the pointed end. Some of the fossils are arranged sub-parallel to each other, with their pointed and blunt ends pointing in the same direction; others are arranged more randomly. The overall appearance of these fossils, and their relatively consistent size, partial sub-parallel arrangement, and grouping in a tight cluster, all suggest they are fossil eggs.



Figure 1: The grouping of eggs possibly represents a clutch (a ?pander) of conodont eggs. Bedding plane assemblages of the conodont *Gondolella pohli* von Bitter and Merrill 1996 are moderately common at Court Creek, suggesting a potential biological link. Other taphonomic associates, and thus possible biological candidates, are the conodonts *Idiognathodus*, *Neognathodus* and *Idioprioniodus*, as well as sharks.

The shape of the eggs is similar to those of hagfishes and lampreys, i.e. the agnathan groups to which conodonts are most commonly related. For example, eggs of the Atlantic hagfish *Myxine glutinosa* have been reported to be ovoid in shape, up to 25 mm long, with a horny shell; each female carries up to 30 eggs that she releases for external fertilization. Similarly, unfertilized eggs of the lamprey *Lampetra planeri* were described as ellipsoidal in shape and to be slightly pointed at the animal pole. The Illinois eggs are unlikely to be shark eggs; shark oviparity commonly involves eggs in complex protective egg cases.



Figure 2: Pacific hagfish eggs approx. 2cm long; white structures are the heads of dissecting pins holding the hagfish in place. Photograph courtesy of Dr. Joseph Thornton, University of Oregon

The comparison of egg to adult size, although having to be based on several variably reliable assumptions, is one of the few methods available to get closer to the identity and/or relationships of the Illinois fossil eggs. Three complete eggs are 0.39 mm long; a fourth is 0.40 mm long. Comparing these lengths with the adult length (55 mm) of the conodont *Clydagnathus windso*rensis (Globensky) from Scotland, suggests that adult conodonts may have been up to 137-141 times longer (larger) than their eggs. A similar comparison of the Atlantic hagfish (eggs to 25 mm long; adults 46-61 cm long; average adult length in one locale was 35.0 cm) suggests that adults of this species are 18.4 - 24. 5 times longer (larger) than their eggs, with the apparently smaller adult population being 14 times longer (larger) than their eggs. That the latter figure is almost exactly ten times less than the size relationship between the Illinois eggs and the adult conodont is probably not significant; however, the possibility that conodonts had very small eggs relative to their adult size may be significant, especially when compared with the egg-adult size relationship of other agnathans.

The chemical composition of the eggs, although assumed to be phosphatic, remains to be determined. Externally the eggs lack ornamentation, other than a series of seemingly irregular holes; internally, they are differentiated into an outer fibrous (? shell) layer of interlocking crystals, and a finer grained interior. Examination and documentation of the inner structure of the eggs using a synchrotron, is planned.

## Viséan to Serpukhovian (Carboniferous) occurrences of *Lochriea* species at the Vegas de Sotres section (Cantabrian Mountains, Spain)

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The Vegas de Sotres section (NE part of the Cantabrian Zone, Picos de Europa unit) exposes the condensed limestones of the upper part of the Alba Formation (Viséan-Serpukhovian), which can locally be subdivided into four units: red to pinkish-grey nodular mudstone (unit 1), light-grey nodular mud- to wackestone with bioclastic packstone beds (unit 2), black bioclastic limestone with shallow water fauna (unit 3), and laminated limestone and chert with siliceous sponge spicules (unit 4). This section bears particular interest since unit 2 and particularly unit 3 show bioclastic beds containing reworked foraminifera and algae (Blanco-Ferrera *et al.*, 2008), a type of fossil remains never described from the Alba Formation.

Most of the conodonts so far recovered from the section

belong to genera regarded as deep-water dwellers. However, a few elements of *Mestognathus*, *Kladognathus*, *Synclydognathus* and *Hindeodus*, which are considered to be abundant in shallow water settings, and have so far been rarely reported from this formation, occur throughout the section. On the other hand, the first appearances of several species of *Lochriea* (a genera frequently represented in the conodont assemblages reported from the Vegas de Sotres section) in unit 2, might bear stratigraphic significance and so they must be stressed.

The lowest bed containing reworked bioclasts registers a rising in the number of both elements and species of ornamented Lochriea. In fact, the species of the Lochriea nodosa Zone (L. mononodosa and L. nodosa) are associated to L. multinodosa, L. ziegleri and L. cruciformis (although only one fragment of the latter species has been found). Nemyrovska (2005) also reported coeval first occurrences of L. multinodosa and L. ziegleri from other Cantabrian Mountains section, even though in two other sections of the same area she observed that the first occurrence of L. ziegleri follows the first findings of L. multinodosa. Higgins and Wagner-Gentis (1982) proposed L. multinodosa as index fossil of the local L. multinodosa Zone established in the Cantabrian Mountains (uppermost Viséan to lower Namurian). However, this species has a restricted geographic distribution. Nemyrovska (2005) proposed the first appearance of L. ziegleri as the defining criterion of the base of the L. ziegleri Zone and the biostratigraphical index of the base of the Serpukhovian stage. Nowadays, the first evolutionary appearance of L. ziegleri is being discussed as a possible marker for the definition of the Viséan/Serpukhovian boundary, although that biostratigraphic event takes place in strata currently regarded as Viséan, middle of the Brigantian English Stage (Richards and Task Group, 2007). Actually, papers on the Carboniferous from Spain, published earlier than 1995, often confused L. ziegleri with L. nodosa and L. multinodosa. However, first findings of these strongly ornamented Lochriea elements from the Cantabrian Zone, quoted or described in many early papers, are close to the currently biostratigraphic event discussed for the definition of the Viséan/Serpukhovian stage boundary.

*L. cruciformis* occurs abundantly in the section at the top of unit 2. This horizon can probably be correlated with that registering the first occurrence of the same species at the Santa Olaja de la Varga section, a level that Belka and Lehmann (1998) used for recognizing the base of the Serpukhovian in the Cantabrian Mountains. In fact, the lower Serpukhovian ammonoids described by Kullmann (1961, 1963), and Wagner-Gentis (1963, 1980), probably come from strata occupying roughly the same position in the succession of the Alba Formation (either below or at the black limestones correlated with unit 3 of the Vegas de Sotres section).

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## Alteration and overgrowth on the conodont surface: a study case from NE Cantabrian Zone (Spain)

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The Cantabrian Zone is a foreland thrust and fold belt located in the southern branch of the European Variscan Belt and, concretely, in the core of the Ibero-Armorican arc. It has thin-skinned tectonics and it is mostly non-metamorphic. The north-eastern sector of the Cantabrian Zone corresponds to part of the Ponga Unit. The Variscan structure of this unit is formed by a south-directed imbricate system, whose thrusts converge towards a sole thrust. The thrusts gave rise to multiple repetitions of the Carboniferous succession, mainly consisting of Carboniferous limestones and shales. The structure was modified by the Alpine deformation that produced faults and reactivation of some thrusts.

The first studies about the Colour Alteration Index of conodonts (CAI) from this area were made by Blanco-Ferrera *et al.* (2006) and García-López *et al.* (2007). CAI values indicate diacaizonal conditions, prevailing values of 1-2, and exceptionally CAI 2-3. CAI values dispersion is low, except for a few localities. The conditions agree with the tectonothermal model proposed for the eastern Cantabrian Zone (García-López *et al.*, 2007) where a late Carboniferous to early Permian metamorphism reached anquizonal conditions southwards the Ponga Unit.

A few conodonts show smooth and light surfaces, but most of them have sugary texture with dull and corroded surfaces. The systematic study of one to fifteen conodonts from each positive sample under the scanning electronic microscope allows analysing in detail the sugary texture, which is seen as apatite overgrowths with a disperse distribution or forming an envelope around the conodont. A type of overgrowth gave rise to the external cast microtexture, which is formed by areas bounded by walls of small apatite crystals drawing a polygonal net different from the original polygonal microornamentation of conodonts. Polygonal areas of these nets can have different size and boundary walls with different height. In addition, the interior of these areas may be partially filled in with small apatite crystals, occasionally as casts of calcite twins. These microtextural features agree with the lithological characteristics of the host limestone.

Pierce and Langenheim (1970) reported diagenetic apatite overgrowths and crystal enlargement on the surfaces of conodonts and related it to deep burial, while other authors related these textural diagenetic alterations to dolomitization (see March Benlloch and de Santiesteban, 1993; Helsen, 1995, Nöth, 1998, among others). In the present case, the lack of dolomitization in the carbonate host rocks suggests a neocrystallization of apatite on surface of conodonts with low CAI values during diagenesis of the limestones. Most of the overgrowths are previous to processes making local corrosion which occur on the conodont surfaces and their overgrowths.

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## Possible function of the elements in the *Polygnathus linguiformis* linguiformis apparatus

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An evolved multi-element conodont apparatus should not be equated in a general way with an array of biting, chewing, grinding....vertebrate teeth. In the case of some specific genera or species (Purnell and von Bitter 1992; Purnell 1995) such comparisons have been made.

A different point of view is discussed herein on the basis of the seximembrate apparatus of *Polygnathus linguiformis linguiformis* Hinde 1879. Two groups of elements can be recognized in this species on the basis of their location and morphology. The anterior part of the apparatus consists of a set of ramiform elements (S and M) with mostly fine, delicate denticles. They were located in the anterior part of the buchal cavity (Nicoll 1985). They are generally considered, also in other conodont genera, as a food-grasping/-filtering system (*e.g.* Nicoll 1985; Purnell 1993; Walliser 1994).

The second part of the apparatus consists of two pairs of pectiniform elements. The first pair of comb-shaped P<sub>2</sub> elements, followed by a pair of platform elements  $(P_1)$ , were located in the posterior part of the buchal cavity, close to the opening of the gut. Grinding, crushing or cutting activities have been proposed for them (Nicoll 1985). The upper surface of the platform of the P<sub>1</sub> element in Polygnathus linguiformis linguiformis is characterized by a median, longitudinal crest (the carina) flanked on both sides by a longitudinal depression (the adcarinal troughs). The platform ends in a tongue-like structure, deflected inward and downward. During life the element was covered by tissue that can leave an imprint on the surface of the element. The course and the height of the carina, the depth of the adcarinal troughs and the form and orientation of the posterior end of the platform are variable and diagnostic for species, not only in the genus Polygnathus Hinde 1879. The morphology of this type of  $P_1$  element is not adapted for a good occlusion between the right and the left P, elements, and good occlusion is necessary for grinding, crushing. An alternative interpretation could be that contractions in the covering tissue bring the food particles via the P<sub>2</sub> elements to the P<sub>1</sub> elements and are then guided via the adcarinal troughs to the opening of the gut. The tongue-like posterior part could produce a swallowing movement at the opening of the gut.

Finally, it should be stressed that the architecture of at least some evolved multimembrate conodont apparatuses don't show convincing similarities with teeth arrangments in the buchal cavity of Agnatha or primitive Gnathostomata and functioned in a different way.

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## Imprint of euconodont animal from the Lower Carboniferous shale of the Northern Urals

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A complete imprint of a euconodont animal was first found in Russia in the Lower Carboniferous shale of the Kozhim River basin (the Northern Urals) (Zhuravlev, 1997; Zhuravlev et al., 2006). Binocular microscopic study of the carbonaceous argillite sample (Tz-59-1/95), the enclosing of this finding, showed that the rock dissected the upper surface of a long (about 4.8 mm), narrow (0.3-0.4 mm) worm-like body slightly curved in the horizontal and vertical planes (Fig.). On this imprint of a euconodont animal, the head, trunk, and tail parts are clearly seen. In the head part at a distance of 0.2 mm from its apical (anterior) end, a rounded H element or one of two skeletal attaching plates, characteristic of a euconodont animal, is seen in relief under a superposed soft tissue (Buryi, Kasatkina, 2004). Immediately adjacent to the H element contour, but beyond the head there is an incomplete set of tooth S-elements. In the trunk part, transversal, probably, muscular segments are present oriented most often perpendicularly and sometimes obliquely to the axis of the euconodont animal. These muscular segments are suggested to be an outer continuation of the transversal muscle fibres that we studied on the inside shears of imprints of the euconodont animals from the Lower Carboniferous Shrimp bed in Scotland and the Upper Ordovician shales of Soom in South Africa (Kasatkina, Buryi, 2007). Further backwards there is a tail tip on which two long rays are seen on the terminal end sides.



1 - head with a relief nose of a rounded structure (attaching H element), 2 - trunk with transversal segments, 3 - tail rays, 4 - a complex of tooth S-elements, 5 - head of another smaller imprint. Scale 0.2 mm.

A counterpart of the euconodont animal is also preserved. During the investigations the euconodont imprint was practically wholly extracted from the rock with the exception of the anterior apex where, probably, an insignificant destruction happened. Figure. Imprint of euconodont animal (specimen DVGI 2007, Tz-59-1/95):

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## Original data on ultramicroscopic structure of euconodont animal imprint from the Northern Urals

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The original results of the investigations of euconodont animal imprint on the ZEISS EVO 50XVP scanning electron microscope without spraying of its surface are done. Observations were carried out in the regime of the secondary electrons with the accelerating voltage of 20 kV. With small magnifications an integral picture of the subject was obtained and magnifications of 120 to 10 000 revealed numerous details of its structure. Most interesting are the fibrous structures – isolated fibre-like formations about 3  $\mu$ m thick and 10 to 107  $\mu$ m long, arranged, as a rule, either along the diagonal or across the euconodont body (Fig. 1).



Fig. 1. Fibrous structures on the upper surface of the euconodont animal imprint, x5000.

With close inspection one can see that these fibres are not scrappy – with their ends they go deep into the body. Essentially, the fibrous formations generally penetrate the euconodont body, going in some places beyond it. Thus, we can conclude that the fibrous formations we have recognized are an integral part of the study fossil. Also attention is drawn to the granulose surface of the trunk division of the study imprint (Fig. 2) that arises from large rounded cells.



Fig. 2. Granulose surface of the trunk division of the euconodont animal imprint, x350.

Besides, the surface of the euconodont animal body is covered with fine noses or papillae largely similar in the outer morphology to the papillae of *Aberrospadella verrucolosa* (Kasatkina, 1982). Other puzzling microstructures of funnel shape are also found on the surface of the euconodont animal imprint. They call for an interpretation. The funnel-shaped "pitted-foraminated" structures can be the duct bringing the secretions onto the animal surface. They, probably, have a secretory function, as in morphology they are similar to the gland structures or endocrine glands of chaetognaths of Spadellidae family. The ultramicroscopic study of them is reported in the paper by Casanova and co-authors (Casanova *et al.*, 1995). All of these structures – rounded cells, papillae, and funnel-shaped tumuli – create a granulose relief on the surface of the euconodont animal body.

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## Morphotypes in the early *Siphonodella* lineage: implications for the definition of the Devonian/ Carboniferous boundary

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The first occurrence of the conodont species *Siphonodella sulcata*, within the *Si. praesulcata – Si. sulcata* lineage define the base of the Carboniferous System (Paproth and Streel, 1984). The GSSP has been choose in the La Serre Section (Montagne Noire, France), at the base of Bed 89. However, previous (e.g., Flajs and Feist 1988) and recent studies (e.g., Kaiser 2005; Kaiser 2009) on the section have evidenced several problems on the stratotype section.

Recently several problems arose also in discriminating *Si. praesulcata* from *Si. sulcata*. Because the two taxa show a great variability and several specimens appear to be transitional between them, the attribution of a specimen to one or to the other species is subjective in many cases. It results that not only the determination of such specimens may depend on personal interpretations, but also the position of the Devonian/Carboniferous boundary may be strongly influenced.

The starting point of this research was a collection of *Siphonodella praesulcata* and *Si. sulcata* from La Serre section: we recognised several morphotypes and we refer specimens published by other authors to our groups. More than fifty published papers were considered. We added some groups recognized in the literature, to include in our scheme morphotypes missing in our collection from La Serre. A total of ten groups were discriminated, mainly based on the shape and curvature of the platform, the ornamentation pattern and the length/width ratio. Stratigraphic ranges and geographical distribution of different groups were also analyzed.

"Early" morphotypes which first occurred in the Lower *prae-sulcata* Zone, as well as "late" morphotypes which first occurred in the basal Carboniferous can be distinguished, but the paleogeographical distributions reveal that a certain origination of any of the groups is not evident. However, the great majority of collections has intermediate features between the two taxa. It results

that not only the determination of such specimens mainly depends on personal interpretations, but also the position of the Devonian/ Carboniferous boundary has been strongly influenced. Therefore, a taxonomic revision of the early siphonodellids is necessary, or another definition based on alternative faunas could be used to define the D/C boundary.

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## Conodonts from the Silurian and lowermost Devonian from the Rifugio Lambertenghi Fontana III Section (Wolayer area, Carnic Alps, Italy)

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In the Carnic Alps, located at the Italian-Austrian border, one of the most complete Paleozoic sedimentary successions is exposed. It is made up by rocks deposited almost continuously from Upper Ordovician to Permian. Silurian and Lower Devonian sediments are irregularly distributed within the Carnic Chain from the Monte Cocco area, at the East, to Lake Wolayer, at the West. In general the outcrops are quite small, mainly on the Italian side, with the only exception of Mt. Cocco e and La Valute areas.

The Rifugio Lambertenghi Fontana III (RLF III) Section is located just South of Lake Volayer. The area is well known for the abundant Upper Ordovician to Devonian sediments, mainly of shallow water, exposed in the area.

The RLF III Section, recently discovered, exposes about 15 m of grey-reddish "*Orthoceras* limestones". The abundant macrofauna, mainly crinoids, brachiopods, nautiloids and trilobites, indicates a shallow water environment.

In order to achieve a precise age placing for the section, seventeen conodont samples were collected and processed with the conventional formic acid technique. All the investigated levels were productive and about 1200 conodont elements were recovered. The state of preservation is generally quite good, even if a few elements are broken or slightly deformed. In general the Silurian part of the section is richer (up to 96 elements/ kg), whereas abundance strongly decreases in the upper part, in connection with a shallower depositional environment. The conodont colour is dark brown, corresponding to a Colour Alteration Index of 3.5-4. Twenty taxa, belonging to ten genera (*Belodella, Coryssognathus, Dapsilodus, Icriodus, Oulodus, Ozarkodina, Panderodus, Pseudooneotodus, Wurmiella* and *Zieglerodina*) were discriminated. *Wurmiella excavata* and *Panderodus unicostatus* are very abundant in the lower part of the section. *Belodella*, both *B. anomalis* and *B. resima* are constantly present.

It is difficult to precisely locate the Silurian/Devonian Boundary, due to the scarcity of the fauna in the upper part of the section. *Icriodus hesperius*, the taxon normally used to indicate a Devonian age, occurs only at very top of the section; however, it is possible to suppose that the boundary is about 3.5 m below, between the last occurrence of *Ozarkodina confluens* and the entry of *Zieglerodina remscheidensis*.

## Permian cool water environments within the tropics/ subtropics: Carboniferous and Permian of Western Pangea shelves.

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Large benthic foraminifera and planktic foraminifera with algal endosymbionts are particularly characteristic of warm, shallow waters and typically responded dramatically to environmental changes. Temperature is the most important physical factor that determines geographic distribution and affects the depth distribution of larger foraminifera by the development of a shallow thermocline that truncates the distribution of shallower species and excludes species adapted to the deepest euphotic zone. Temperature restricts larger foraminifera to those geographical regions or water depths characterized by temperatures never falling below 14 °C for several weeks. Three major biogeographic realms are usually recognized in the distribution of the Late Paleozoic foraminifers: Midcontinent-Andean (M-A), Boreal (B) and Tethyan (T). It has been seen long ago that taxonomic diversity in the M-A realm through the entire Late Paleozoic was relatively low compared to T and B realms. The number of common genera in Mississippian and Pennsylvanian (Rheic pathway open) among all realms is quite high. However, M-A realm exhibiting two-three times lower diversity than in the T and B realms. The origin of genera mostly takes place in the T and in B realms. These genera then dispersed in North America where they are developed at the species level, but diversity there was always half or less as that in B and T realms. Some cooler water taxa that mostly occur in northern and southern temperate zones are also

known to appear in the North American realm. Recent tropical larger foraminifera live within the depth of 0-150 m and optimal water temperature 30-20 °C. The suggested favourable depth for fusulinids in B realm subtropics is 5-70 m. The habitat of fusulinids in North American realm was much shallower (nearly one third) most probably due to cooler water conditions. The average temperature in the North American tropical shelves at the depth 0-10 m was 15-20 °C.

## Lower Famennian conodonts from the Burtebayian Formation in the western Kazakhstan

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The Burtebayian Formation is located in the south–east part of the Mugodzhar Mountains, in western Kazakhstan. The Burtebayian Formation belongs to the south-west flank of the Berchogur syncline, with its type locality 1 km south of the Berchogur village. The Berchogur syncline is characterized by a relatively simple tectonic structure; the west flank falls with an angle of approximately 35°, while on the east flank it is 5°. The central part of the syncline has a horizontal occurrence of deposits. The upper part of the structure clearly stands out in relief, which represents a small sloping range of Upper Devonian rocks. To the south of the structure it gradually expands and easily plunges. It is covered by the Mesozoic-Cenozoic deposits. The Berchogur syncline has a submeridional strike and it is approximately 80 km wide and 25 km long (Abdulin, 1973).

The Burtebayian Formation, 350 m thick, is characterized by the presence of limestones, with polymictic sandstones, conglomerates, clays and marls. The Burtebayian Formation is unconformably covering the Kurkudukian Formation and it is conformably overlying the Dzhanganinian Formation.

The Burtebayian Formation consists of deposits of the Makarian, Murzakaevian and Kushelginskian horizons of the Famennian (Kochetkova et al., 1986). The conodonts recovered from this Formation indicate that the deposits correlate with standard conodont zonation from the crepida Zone to the postera Zone. The fauna and biostratigraphy of the upper part of the Burtebayian Formation has been described in monograph (The fauna..., 1987). The author studied conodonts only from the lower part of the Burtebayian Formation. The conodonts mentioned here originate from the Makarian horizon, which consists of altered limestones. Major fossil groups such as coral, brachiopods, gastropods, crinoids, ostracods and algae are common. The conodonts were obtained from the Berchogur section, outcrops B1 and B2. Sample B/6695 (B1) contains Palmatolepis subperlobata helmsi, Pa. klapperi, Pa. glabra glabra, Pa. glabra prima, Pa. quadrantinodosalobata, Pa. subgracilis, Pa. regularis, Pa. perlobata perlobata, Pa. minuta minuta, Pa. minuta loba, Polygnathus semicostatus, Po. glaber glaber, Po. polesicus, Po. schinkaryovi and Po. berchogurensi.

Palmatolepis klapperi, Pa. minuta minuta, Pa. minuta loba, Polygnathus semicostatus, Po. polesicus, Po. schinkaryovi, Po. berchogurensi, Icriodus cornutus and Apatognathus varians were found in sample B/6698 (B2). The upper and uppermost crepida Zone was determined by the co-occurrence of Palmatolepis perlobata perlobata, Pa. quadrantinodosalobata, Pa. minuta loba and Pa. regularis (Sandberg, Ziegler, 1973). The presence of Palmatolepis subperlobata helmsi together with Pa. klapperi and Pa. subgracilis allow us to recognize the rhomboidea Zone. The species Polygnathus polesicus which is first described in the rhomboidea Zone in Belorusia has been found in the lower part of the Burtebayian Formation (Strelchenko, 2000). The upper crepida Zone - rhomboidea Zone are characterized by the presence of Icriodus cornutus, Polygnathus glaber glaber and Po. semicostatus (Ziegler, Sandberg, 1984). The author's studies of the Lower Famennian conodonts from the Burtebayian Formation in western Kazakhstan led to the discovery of the new regional species of Polygnathus (Po. schinkaryovi and Po. berchogurensi). New species belong to the group of Polygnathid: Polygnathus costatus-Po. inornatus (Barskov et al., 1991). Discovering new polygnathids is important for the subdivision and correlation of the Famennian shallow-water carbonates of western Kazakhstan.

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## Conodont evolution trend around Norian/Rhaetian boundary in the Lagonegro succession, Southern Apennines, Italy

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The Lagonegro Basin was part of the southernmost Mesozoic oceanic basins of the Tethyan realm, open during the Permian to the Miocene (Finetti, 1985; 2005; Stampfli and Borel, 2002; Ciarapica and Passeri, 2002).

Our studies focus on the Upper Triassic "transitional interval" (Amodeo, 1999) between the Calcari con Selce Formation (cherty limestones) and the overlying Scisti Silicei Formation (bedded cherts with radiolarians and radiolarites), where the Norian/Rhaetian boundary has been documented. This "transitional interval" is characterized by the progressive decrease in carbonate content and increase in shales and cherts; it documents the relative progressive lowering of the basin floor below the Carbonate Compensation Depth (CCD). This event occurred during the Carnian stage (Rigo *et al.*, 2007).

New data obtained by integrating conodonts and radiolarians improves the biostratigraphic resolution around the boundary, and permit us to calibrate the age of sedimentary events well. It also allows us to understand the evolution of the Tethys during the Late Triassic. A very rich and well preserved conodont fauna combined with a large collection of radiolarians characterize the Mt. S. Enoc and the Mt. Volturino successions. Furthermore, recognition of conodont transitional forms permits detailed phylogenetic and taxonomic studies between species *Misikella hernsteini* to *Misikella posthernsteini* that have both been proposed as possible biomarkers for the base of the Rhaetian Stage (Kozur and Mock, 1991; Krystyn *et al.*, 2007), thus improving the biostratigraphic resolution of the Norian/Rhaetian time interval.

According to Mostler et al., (1978) and Kozur and Mock (1991), M. posthernsteini descends from M. hernsteini by reduction of the blade denticle number and development of a heart-shaped basal cavity. Because of the finding of transitional forms between these two species, it has been possible to highlight the main features involved in M. hernsteini-M. posthernsteini evolution, in stratigraphic (and thus age) order. M. hernsteini is usually characterized by a long drop-shaped basal cavity, and a blade composed by 5-6 denticles pressed laterally; instead, M. posthernsteini bears 3 thick denticles on the blade and a wide heart-shaped basal cavity. Both of these two species have the cusp as the last posterior blade denticle. In the first step of evolution from M. hernsteini to M. posthernsteini, the shape of the basal cavity starts to enlarge in the posterior part and contemporaneously the number of blade denticles decreases, creating transitional forms with four-denticle blade and a large drop-shaped basal cavity (triangular in shape), without the inflexion peculiar of the heart. Second step, the first denticle of the blade, opposite to the cusp, becomes increasingly smaller until it melds with the second one and a little inflexion occurs on the posterior basal cavity margin. No incision or a very superficial one on the cusp backside is present. At the third step, only three denticles form the blade, even if a vestigial one could be present on the anterior side of the first denticle, the basal cavity

obtains the typical heart shape of the *M. posthernsteini* and a deep incision furrows the backside of the cusp. These detailed evolutionary steps permit us to better describe the origin of *M. posthernsteini*, attaching biostratigraphic importance to all of the transitional forms that might be used to well define the Norian/Rhaetian time interval.

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## Morphometry and specific differentiation from the example of Devonian *Palmatolepis* conodonts.

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Palmatolepis conodont elements have a fast evolution during the Late Devonian, which makes them good stratigraphical markers. It is therefore essential to have a good knowledge of the systematics of this genus. However, the taxonomic studies of conodonts present some difficulties to discriminate species. Indeed, it is not always easy to differentiate subtle shape variations between some P<sub>1</sub> elements. We propose here to use morphometric tools to test hypotheses relative to conodont taxonomy. We focus on one sample from the late Devonian (upper *crepida* conodont zone, Famennian) from the area of Mae Sam Lap (northern Thailand) that presents the interest of containing many conodonts of the genus Palmatolepis. We propose to test the validity of some of the taxonomic assignations of the genus Palmatolepis via an outline analysis, *i.e.* by an elliptic Fourier transform and a principal component analysis. The species Pa. adamantea, Pa. delicatula, Pa. mystica, Pa. regularis and Pa. tenuipunctata have been studied more particularly. These species are clearly distinguished with the geometric morphometry. Moreover, the existence of several morphotypes have been established for some species (Pa. regularis, Pa. delicatula), and the existence of Pa. angusta as a distinct species from Pa. regularis has been confirmed. But the strong intra- and inter-specific relationships between the species considered do not allow going further in the systematic interpretations. Nevertheless, this method is a useful complementary tool to discriminate conodont morphotypes and species and to solve the questions regarding some species.

## Early Triassic condont clusters from South China: Revision of the architecture of the 15-element apparatuses of the Gondolelloidea superfamily

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Several fused clusters of conodont elements of the genus *Novispathodus* were recovered from limestone beds at the Smithian-Spathian boundary (Luolou Formation., Early Triassic; Galfetti *et al.*, 2008) from several localities in Guangxi province, South China.

Conodont clusters are otherwise extremely rare in the Triassic and these are the first reported for the Early Triassic. The exceptional specimens partially preserve the relative three-dimensional position and orientation of ramiform elements and are therefore extremely important for testing hypotheses on the architecture of apparatuses.

These specimens partially confirm the reconstruction of the *Novispathodus* apparatus by Orchard (2005). Yet, they also demonstrate (see Fig. 1) that the elements previously identified as occupying the  $S_1$  and  $S_2$  positions occupy in fact the  $S_2$  and  $S_1$  positions respectively. This affects our interpretation of all apparatuses of the Gondolelloidea superfamily, which was based (Orchard, 2005) on bedding plane natural assemblages from the Middle Triassic of Switzerland (Rieber, 1980; Orchard and Rieber, 1999). The same applies to the elements in the  $S_3$  and  $S_4$  positions, whose positions are actually reversed, at least for the subfamily Novispathodinae (Orchard, 2005).

It was possible to reach these conclusions thanks to a X-ray synchrotron microtomography (Tafforeau *et al.*, 2006). In this particular case a pink beam setup at 17.6 keV - very recently developed at the ESRF on the ID19 beamline, and allowing submicron resolution ( $0.23\mu$ m) with a speed and an overall quality never reached before - has been successfully tested on these fossils. This technique appears as very successful for high quality and high resolution imaging of microfossils. It will certainly allow the non-destructive study or restudy of other known specimens, particularly of fused clusters, for which only exposed surfaces are otherwise accessible.

Co-occurring isolated elements from the same sample and pertaining to the same multi-element species were also scanned using this technique and it allowed us to reconstruct a virtual apparatus.

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Figure 1: fused cluster with four elements ( $S_1$  to  $S_4$ ). Scale bar is 400 microns.

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## An animated functional model of the Lower Triassic *Novispathodus* apparatus based on X-ray synchrotron microtomography and computer graphics.

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The starting point of this study was the discovery in South China (Goudemand *et al.*, 2009, this volume) of several fused clusters of conodont elements of the genus *Novispathodus* (Orchard, 2005). Some of these were scanned at the ESRF on the ID19 beamline using propagation phase contrast microtomography (Tafforeau *et al.*, 2006), as were isolated elements from the same sample. The high quality and high resolution (voxel size 0.23  $\mu$ m) imaging obtained using a newly developed pink beam setup at 17.6 keV, allowed us to reconstruct a virtual 3d apparatus.

The clusters impose constraints on the position and orientation of the  $S_{1.4}$  ramiform elements. Observing a striking resemblance between the posterior process of the  $S_0$  element and the  $S_1$  element (as revised by Goudemand *et al.*, 2009), we added further constraints on the position of the  $S_0$  element relative to the others. We have assumed that this position corresponds to the arrangement at rest, and thereafter considered their relative positions during feeding movement. New observations of geometric correspondence between elements allowed us to make new hypotheses and to derive a new functional model of the conodonts' feeding apparatus, presented in animated form.

In our view, the best solution implies the presence of a presumably cartilaginous 'copula' upon which the conodont elements are moving independently, more or less as do dental plates in extant lampreys, but not in the manner that was suggested in the pioneering work of Purnell and Donoghue (1997). This solution suggests that during retraction towards the caudally located platform elements, the  $S_0$  element first had a closing, rotating movement, most probably synchronized with the closure of the M elements, with which it would have performed a pinching, seizing function; this is followed by a sub-straight, dorso-caudally directed translation, by which it would have torn off the prey's 'flesh' and brought it towards the platform elements. The latter movement is accompanied by the closure of the other S elements, constraining the food in the desired direction.

Contrary to known Paleozoic apparatuses where all S elements seem to be oriented in the same direction, this apparatus shows (as previous reconstructions suggested, see Orchard and Rieber, 1999) that within at least some Triassic apparatuses, both  $S_1$  and  $S_2$  were oriented with the cusps pointing caudally, which in our interpretation suggests an evolutionary re-assignment of teeth from the 'palate/cheeks' to the 'tongue'.

Finally, considering that the presence of a cartilaginous copula associated with tongue protractor and retractor muscles has been asserted only for myxinoidea (hagfishes) and petromyzontida (lampreys) (see Donoghue, Forey and Aldridge, 2000, for further details), it led some authors (Yalden, 1985) to argue it would be a synapomorphous feature of cyclostomes and evidence of their monophyly. The debate is on-going but our new model may shed light and consequently hold important implications for the affinity of conodonts and for our general understanding of the origin of vertebrates.

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## Conodont deformation in the Devonian tentaculite limestone of the Villasalto area (SE Sardinia, Italy)

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On Sardinia (Italy), the most continuous outcrops deformed during the Variscan orogeny, are found in the central, southeastern and southwestern part of the island. Each of these regions had a different tectonic evolution during the Early Carboniferous collisional phases of the Variscan deformation (Conti *et al.*, 2001).

The outcrop in which deformed conodonts have been found is located in the southeastern region of the island. This region underwent three deformation phases during the Early Carboniferous: a N-S shortening phase with isoclinal folding and south directed nappe emplacement, an E-W shortening phase with W-directed emplacement of the Sarrabus nappe and another N-S shortening phase with refolding into upright synforms and antiforms with WNW-ESE strike (Conti *et al.*, 2001).

The conodonts were sampled in the "Calcari e scisti a tentaculiti" in the Gerrei tectonic unit, in a locality called Pranu Scandariu, close to the village of Villasalto. The "Calcari e scisti a tentaculiti" represent the Lower/Middle Devonian of SE Sardinia (Corradini et al., 1998). The deposits consist of an alternation of limestone and shale rich in tentaculites. The limestone is mainly composed of a micritic calcite matrix. Macrofossils are crinoids, brachiopods and rare trilobites. The conodont fauna in this limestone indicates an uppermost Lower Devonian to Upper Devonian age.

The outcrop is located close to the Villasalto overthrust, an E-W striking overthrust fault of regional importance, that was active during the second deformation phase.

The aim of this research is to see whether these deformed conodonts can be used locally as strain markers and if it is possible to deduce which tectonic phase(s) are the most important, and responsible for the deformation.

A study of microtectonics in thin section shows that at least two deformation phases can be distinguished and these can be linked to the first two deformation phases.

Several conodont deformation patterns are recognized: kinking, fracturing, stretching, torsion, buckling, boudinage and bending. They indicate shortening, angular shear strain and extension.

A problem is the orientation of those conodonts in the matrix of limestone. The normal extraction method used to retrieve the conodonts from the limestone does not preserve the original ori entation of the specimens. An attempt is in progress to extract them delicately from the limestone in order to determine their in situ orientation.

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## Gondolellid Cyclic Tooth Morphology: Conodont Paleobiologic Food for Thought

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Gondolellid species are largely discriminated by changes in the shape and spacing of carinal denticles on the  $P_1$  element and these morphologies tend to be very cyclic within the strati-

graphic record from widely spaced denticles to closely spaced and increasingly fused denticles. This pattern holds true throughout the Permian including in species of Mesogondolella during the Cisuralian (Lower Permian), Jinogondolella during the Guadalupian (Middle Permian) and Clarkina during the Lopingian (Upper Permian) and Lower Triassic. Genera are mostly discriminated on the basis of changes in the apparatus as well as ontogenetic shifts. For example, Jinogondolella is discriminated from Mesogondolella by changes in the S<sub>3</sub> element as well as the presence of serration on the P<sub>1</sub> element. In addition, the presence of discrete denticles typical of only juvenile Jinogondolella granti, in adults of the descendant Clarkina postbitteri suggests a heterochronic evolutionary process. This latter event is associated with a major sequence boundary and extinction event (Middle-Upper Permian boundary) and involved the evolution of a new gondolellid genus, Clarkina, defined by the lack of serration, high anterior blade-like denticles, and major change in platform outline of the P<sub>1</sub> element. The discrete denticulation appears to be typical of a deepening event during the Early Wuchiapingian and younger Wuchiapingian taxa typically show increasingly closely spaced denticles that culminated in the wall-like carina of C. wangi at the Wuchiapingian-Changhsingian boundary. Younger Changhsingian taxa show a breakup of the wall-like carinal development, but they remain typically characterized by closely spaced denticles that decrease in height posteriorly. Discrete denticulate Clarkina species are however again associated with the latest Permian major flooding event as well as with the Late Permian extinction. These changes in serration and denticle configuration clearly affect the complexity of the platform surface for food processing (see Purnell and Evans, this volume), but it is difficult to extract a paleobiologic basis for the cyclicity.

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 that constrain element motion to the transverse plane and apparently maximized food-processing efficiency, which will also be affected by denticle spacing. This may provide a paleobiologic basis for relating the morphologic variation used in Permian and Lower Triassic biostratigraphy. The importance of the carinal shape in these taxa may be related to the parallel evolution or extinction of organisms representing a potential food source or to the availability of food sources along some environmental gradient that provides selection pressure and competitive advantage to different configurations on a recurring basis. In fact, it is possible in gondolellid taxa to discriminate transgressive systems tract morphologies (widely spaced denticles) and regressive systems tract morphologies (closely spaced to fused) and the changes seem to operate on a similar temporal scale (about 3 my) as 3rd order stratigraphic sequences. Nutrient supply from upwelling and other oceanic chemistry will vary systematically in these sequences and this may point in the direction of potential food sources. Although it remains uncertain what conodont animals ate, the cyclic morphology of gondolellid P, elements at least provide some food for thought.

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Evolution and Geochronology of the *Sweetognathus* lineage from Bolivia and the Urals of Russia; Biostratigraphic problems and implications for Global Stratotype Section and Point (GSSP) definition

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Lower Permian conodonts have been known from Bolivia for a long time (Riglos *et al.*, 1987). Given the great distance from the potential Lower Permian GSSPs in the southern Urals of Russia, the Bolivian succession would represent a prime testing ground for correlation potential of the GSSP definitions. The Apillapampa section in Bolivia is ideal because of the cooccurrence of Streptognathodid and Sweetognathid conodonts, fusulinaceans and interbedded ash beds.

Conodonts from 28.2 and 54 metres include Streptognathodus spp. that correlate with the mid-Asselian Streptognathodus constrictus Zone and possibly some elements of the Late Asselian S. fusus Zone in the higher sample. The higher sample also contains Sweetognathus expansus and Sweetognathus cf. merrilli as well as transitional forms. The presence of S. merrilli would normally indicate correlation with the Lower Sakmarian S. merrilli Zone, but in the potential GSSP section at Kondurovsky Sweetognathus and Streptognathodus do not co-occur and Sweetognathus is generally thought to be an ecologic replacement for Streptognathodus. Higher samples yield the following taxa: Sweetognathus bucaramangus at 72.3 m; S. cf. binodosus and S. cf. anceps as well as transitional forms at 104.5 metres; S. aff. obliquidentatus at 132 and 145 metres; Diplognathodus cf. stevensi and S. cf. behnkeni at 153.5 and 157 metres; S. cf. behnkeni at 165.1 metres and S. cf. obliquidentatus at 224 metres. Sweetognathus behnkeni is not synonymized with S. whitei as suggested by Mei et al. (2002). In the Urals S. binodosus and S. anceps represent successive zones of the Sakmarian following the lowermost Sakmarian S. merrilli Zone (Chernikh, 2005, 2006) and S. obliquidentatus is typical of the Lower Artinskian S. whitei Zone at the potential GSSP at Dalny Tulkus. Furthermore, this succession is very similar to that from the mid-west USA (Ritter, 1986). Based exclusively on biostratigraphy, this succession seems to correlate with the mid-Asselian to lowermost Artinskian, despite some problems associated with endemic taxa and previously unknown overlapping ranges.

The geochronologic ages for these zones and Lower Permian stages have been determined in Russia (Schmitz *et al.*, 2007) based on abundant conodont faunas interbedded with ashes that indicate ages for the base-Asselian at 298.8 Ma, the base-Sakmarian at 293.99 Ma and the base-Artinskian at 290.9 Ma. Consistent high-resolution ages have also been determined at the Apillapampa section with a mid-Asselian age at 120 metres, early Sakmarian ages at 154 metres and 185 metres, and a mid-Late Sakmarian age at 242 metres. These ages do not match the apparent biostratigraphic correlations since forms comparable to *S. merrilli, S. binodosus* and *S. anceps* that represent successive Sakmarian zones in the Urals have geochronologic ages associated with the Asselian in Bolivia. A species from Bolivia comparable to Artinskian *S. obliquidentatus* from the Urals has a Sakmarian geochronologic age.

The question becomes how to resolve this significant correlation problem of at least 3 to 4 million years offset between biostratigraphy and geochronology. If we assume that the consistent high-resolution U-Pb geochronologic ages as determined by modern methods using high temperature annealing of individual zircons and ID-TIMS are correct, then we have to assume that evolution has somehow "repeated" itself, even if imprecisely. Modern evolutionary developmental biology suggests that this is definitely possible. This hypothesis would suggest that the Sweetognathus lineage evolved first in Bolivia (and possibly midwest USA) and was restricted to a region near the paleo-equator during the Asselian. Climate change near the Asselian-Sakmarian boundary may have provided the conditions to allow gene flow into the Sverdrup Basin of the Canadian Arctic and into the Urals of Russia and this subset of genetic material evolved similar morphologies by natural selection under similar ecologic conditions during the Sakmarian and Artinskian. If true, then subtle variations in morphology that previously were grouped as normal variability within a population must now be considered to be very significant for taxonomic discrimination. Furthermore, if true, it begs the question how many other apparent correlations are offset in time and suggests that the Lower Permian GSSP definitions will need to be reconsidered.

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#### About The Apparatus Of Triassic Gondolellacea

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Triassic Superfamily Gondolellacea consists of the families Gondolellidae and Gladigondolellidae, each having a distinct septi– or octomembrate apparatus.

The paired  $P_1$  pectiniform platform elements determine suprageneric, generic and specific taxonomy. At the suprageneric level, these paired ozarkodiniform  $P_2$ , cypridodelliform M and  $S_2$ , enanthiognathidoform  $S_1$ , diplododelliform  $S_3$ , hindeodelliform  $S_4$ and the single alate  $S_0$  may vary.

In the family Gondolellidae, subfamilies Neogondolellinae and Sephardiellinae have a bifid  $S_3$  element, which is not found in Epigondolellinae. Sephardiellinae may possibly have a sexually dimorph pollognathiform element  $P_2$  in the genus *Pseudofurnishius* and Neogondolellinae have a grodelliform  $S_2$  element (no anterior process).  $S_4$  elements occur in clusters and chirodelliform elements seem to accompany Gondolellidae.

In the family Gladigondolellidae, the ozarkodiniform  $P_{2a}$  element "saginata" probably alternates with the cratognathodiform  $P_{2b}$  element, the latter being rather a sexual dimorph  $P_2$  than a paedomorph  $P_1$ . Furthermore, paired cypridodelliform M "venusta" and  $S_2$  "spengleri", enanthiognatiform  $S_1$  "felsöörsi" n. form., bifid  $S_3$  "petrae-viridis" and hindeodelliform  $S_4$  "multihamata" elements and the single alate  $S_0$  "lautissima" element that may also develop as an anastrophognathiform elements, add to the very distinct appearance of the gladigondolellid apparatus. Dichodelliform may accompany the family.

Thermal Maturity within the Western Canada Sedimentary Basin, west-central Alberta to northeastern British Columbia and its Tectonic Implications for Pennsylvanian and Permian Strata

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The thermal history of Pennsylvanian and Permian strata is relatively poorly constrained within the Western Canada Sedimentary Basin. This study incorporates thermal maturation of conodont elements throughout the Western Canada Sedimentary Basin to better understand the tectonic processes and its implications that were occurring during the Pennsylvanian to Permian. A classification system developed by Epstein et al. (1977) assigns a conodont alteration index (CAI) value to conodont elements depending on their colour, which is a result of progressive and irreversible alteration of trace amounts of organic matter within lamellae of conodont elements. Alteration of organic matter is the result of heating and exposure time, and can be applied to burial of conodont elements in conjunction with the geothermal gradient. Colour variations are assigned CAI values of 1 through 8, with 1 being least altered and 8 being the most altered. Each numerical change in CAI value requires a sediment overburden of 1000 to 2000 metres under a normal geothermal gradient. Pennsylvanian and Permian strata exhibit generally the same thermal maturity patterns in the WCSB, but CAI values in the Pennsylvanian are locally more elevated than expected compared to that in Permian rocks. Pennsylvanian and Permian strata are generally very thin (no more than 500 metres thick and usually less than 150 metres) in the Western Canadian Sedimentary Basin, which cannot account for the elevated CAI values observed in some Pennsylvanian strata. The higher than normal CAI values observed in Pennsylvanian strata compared with overlying Permian rocks suggests that tectonic processes had a significant impact on the thermal maturity of the region. The anomaly may be attributed to a heating event prior to the deposition of Permian strata possibly associated with high heat flow from the Prophet Trough and/or may have been a result of hydrothermal fluids produced during the Laramide orogeny. Anomalies are localized, indicating hot fluid flow likely traveled through fault systems within the WCSB. Evidence of hydrothermal fluids comes in the form of Mississippi Valley-type lead-zinc deposits located along the western margin of North America, dolomitization of rock strata and corroded surface textures of conodont elements.

Hydrocarbon potential for the Western Canada Sedimentary Basin within Pennsylvanian and Permian strata is very promising as the majority of CAI values fall within the oil and gas potential zones; northeastern BC represents an important hydrocarbon exploration region at present. Western Alberta and easternmost British Columbia have CAI values that indicate oil potential in Pennsylvanian rocks. CAI values in northeastern British Columbia indicate potential for wet gas and dry gas in Pennsylvanian rocks. CAI values indicate oil potential in Permian units in Alberta, and wet gas in northeastern British Columbia.

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## Phylogeny of *Hindeodus-Isarcicella* across the Permian-Triassic Boundary

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The conodont genera Hindeodus Rexroad and Furnish, 1964 and Isarcicella Kozur, 1975, are taxa of prime importance in the biostratigraphy of the Permian-Triassic boundary (PTB) and in investigations of the end-Permian mass extinction event. The concept of Isarcicella was tentatively broadened by Kozur (1996), who included specimens referred to I? turgida and I? prisca; these lack denticles or a secondary blade on the cup, but have a thickened portion of the cup that is more than half of its width. The diagnosis of Isarcicella was subsequently emended by Perri and Farabegoli (2003, p. 296) to include forms without lateral denticles on the cup but with a 'weakly to highly asymmetrical and swollen cup.' This circumscription meant that Isarcicella would include not only species with denticles on the cup, such as I. isarcica and I. staeschei, but also I. turgida, I. prisca, I. peculiaris, I. lobata, I. inflata and I. changxingensis. In addition to these species, a wide range of Hindeodus species have been diagnosed from strata around the PTB: H. anterodentatus, H. eurypyge, H. inflatus, H. julfensis, H. latidentatus, H. parvus, H. pisai, H. postparvus, H. praeparvus and H. typicalis. However, the apparatuses of many Hindeodus species and all Isarcicella species are unknown or poorly known and most of these taxa have been diagnosed on the basis of the characters of P, elements alone.

In the literature, a considerable variety of phylogenetic hypotheses have been put forward to explain the relationships between these species. We have undertaken the first cladistic investigation of these taxa, based on  $P_1$  elements, testing the proposed phylogenies and establishing new hypotheses. We have coded a total of 24 characters for one syntype of *H. julfensis* and for the holotypes of 20 other species of *Hindeodus* and *Isarcicella*. The Carboniferous *Hindeodus cristulus*, type species of *Hindeodus*, was used as the sole outgroup taxon (Youngquist and Miller, 1949, pl. 101, fig. 1). Analyses were carried out using PAUP 4.0b10w (Swofford, 2002), and the cladogram converted to a phylogenetic tree using the stratigraphic distributions in the PTB stratotype section at Meishan, Changxing, Zhejiang Province, China. Initial results indicate that species referred to *Isarcicella* form a discrete clade, with *Hindeodus* species forming a paraphyletic ensemble. Nomenclatural revisions based on the cladogram are not recommended at this stage, as the apparatus structures of most taxa are unknown and the relationships to other genera, such as *Diplognathodus*, remain to be explored.

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Late Devonian to Early Mississippian conodont biostratigraphy of the uppermost Wabamun Group and Palliser Formation through to lower Banff Formation, Southern Alberta and Southeastern British Columbia, Canada

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The Late Devonian and Early Mississippian represent a critical time interval in the sedimentological, stratigraphic and tectonic history of the Western Canadian Sedimentary Basin, as well as in the rest of the world. Conodonts, along with other geochemical, sedimentological and stratigraphic data have been shown to have



Diagnostic conodont occurrences: • - this study, O - from literature

great utility in unravelling the timing and nature of sedimentological, stratigraphic and tectonic events in the Late Devonian to Early Mississippian in this part of the world.

In our study, ten conodont biostratigraphic assemblages were recognized in the subsurface Big Valley Formation of the Wabamun Group, the upper part of the surface Costigan Member of the Palliser Formation, the subsurface Bakken and surface and subsurface Exshaw formations and the lower part of the surface and subsurface Banff Formation.

Three conodont biostratigraphic assemblages are recognized in the Big Valley Formation and upper Costigan Member. One biostratigraphic assemblage is common and widespread. It contains morphotypes 1 and 2 of *Bispathodus stabilis* Branson and Mehl), *Branmehla inornata* (Branson and Mehl), species of "Icriodus", *Pelekysgnathus inclinatus* Thomas and narrow and wide-platformed species of *Polygnathus* (e.g. *P. communis* Branson and Mehl, *P. germanus* Ulrich and Bassler, *P. semicostatus* Branson and Mehl). The age commonly assigned to this assemblage is Lower *expansa* to *praesulcata* zones (Fig. 1). Figure 1. Chart showing correlation of Big Valley through to lower Banff formations in southeastern and southwestern Alberta to equivalent units elsewhere in Alberta and to the type Three Forks and overlying Lodgepole formations in southwestern Montana and to the "standard" conodont zonation. Diagnostic conodont occurrences also shown to illustrate conodont biostratigraphic control presently available from present and previous studies. Abbreviations: basal SAPP. = basal Sappington Member of Three Forks Formation, gy - gn sh = upper grey-green shale unit of Big Valley Formation in southern Alberta, upper SLST. MBR. = upper siltstone member of Exshaw Formation. PEK. FM. (pt.) = Pekisko Formation (part).

The second assemblage, characterized by the occurrence of species such as "Icriodus" costatus (Thomas), Palmatolepis distorta Branson and Mehl and P. marginifera Helms, occurs in basal strata of the upper Costigan Member as a discrete assemblage in several localities studied by us and other authors. Elements of this assemblage also occur as reworked elements in the first assemblage at one of our localities. The age assigned to this assemblage

is Uppermost *marginifera* to *trachytera* zones (Fig. 1). The third conodont biostratigraphic assemblage occurs only in the upper Costigan Member at Crowsnest Pass in southwestern Alberta. Characteristic species include *Palmatolepis marginifera*, *P. prima* Ziegler and Huddle, a form referable to *Polygnathus crowsnest-passensis* Johnston and Chatterton and *P. planirostratus* Dreesen and Dusar Morphotype 1. The age assigned to upper Costigan strata containing these species is Lower to Upper *marginifera* zones (Fig. 1).

The lower black shales of the Bakken and Exshaw formations contain a conodont assemblage consisting of species of *Palmatolepis* belonging to the *P. gracilis* (e.g. *P. expansa* Sandberg and Ziegler, *P. gracilis* Branson and Mehl land *P. sigmoidalis* Ziegler) and *P. perlobata* (e.g. having affinities with or referable to *P. perlobata* Ulrich and Bassler, *P. rugosa* Branson and Mehl and *P. schindewolfi* Müller) groups. It also contains species of *Bispathodus* (e.g. *B. aculeatus* [Branson and Mehl], *B. stabilis*) and *Branmehla* (e.g. *B. inornata*). This assemblage assigns a general age of *expansa* to *praesulcata* zones to the lower Bakken/ Exshaw black shales (Fig. 1). Another assemblage in these shales may be represented by faunas characterized by the sole occurrence of *Polygnathus communis*.

Only one conodont biostratigraphic assemblage occurs in the uppermost middle member of the Bakken Formation in a thin interval of lime wackestone. It includes many of the species of *Bispathodus* mentioned above and *Polygnathus communis*, and other polygnathid species such as *P. inornatus* E.R. Branson. This assemblage also includes species of *Pseudopolygnathus* including *P. primus* Branson and Mehl, and species of *Siphonodella* that include *S. quadruplicata* (Branson and Mehl) and forms referable to both morphotypes of *S. cooperi* Hass. This assemblage is tentatively assigned an age of *sandbergi* Zone (Fig. 1).

The upper black shale member of the Bakken Formation and lower black shale of the Banff Formation contain three condont biostratigraphic assemblages. One of these contains abundant specimens of *Bispathodus* and *Polygnathus communis*, as well as specimens of *Priniodina*, and rare *Pseudopolygnathus*. The other two assemblages contain species of *Bispathodus*, "*Branmehla*" ("*B.*" *abnormis* [Branson and Mehl]), *Dinodus*, *Elictognathus*, *Prioniodina* and *Siphonodella* (e.g. *S. obsoleta* Hass and forms suggestive of *S. sandbergi* Klapper). The age of the first assemblage is Lower *expansa* to *isosticha* – Upper *crenulata* whereas the ages determined for the other two assemblages are Upper *duplicata* to *isosticha* – Upper *crenulata* zones and *sandbergi* Zone (Fig. 1).

One definite and possibly one other conodont biostratigraphic assemblages occur in limestone and shale of the lower Banff Formation. They are characterized by the joint occurrence of species of *Gnathodus* (e.g. G. *cuneiformis* Mehl and Thomas, G. *delicatus* Branson and Mehl, G. *punctatus* Cooper, G. *semiglaber* Bischoff and G. *typicus* Cooper) and Siphonodella, as well as species of Bispathodus, "Branmehla", "Mehlina", Polygnathus and Pseudopolygnathus. The joint occurrence of Gnathodus and Siphonodella in this assemblage assigns an age of isosticha – Upper crenulata Zone (Fig. 1). A sample containing Gnathodus cuneiformis may suggest an age of lowermost typicus Zone for the strata that it came from.

Biostratigraphic and stratigraphic data show that major unconformities are interpreted exist within the upper part of the Costigan Member of the Palliser Formation and the Big Valley Formation, spanning the Lower and Upper postera zones and between the lower black shale member of the Exshaw Formation and the lower Banff Formation (Fig. 1). The latter unconformity spans up to several Late Devonian and Early Mississippian conodont zones (Fig. 1). Minor unconformities may have existed between the upper Costigan Member/Big Valley Formation and the lower black shale member of the Exshaw Formation and between the middle member of the Bakken Formation and the overlying Banff Formation and within the latter formation (Fig. 1). These unconformities are interpreted to have been the result of several periods and uplift and erosion during deposition of upper Palliser/Wabamun through to lower Banff strata, especially along the Fifth Meridian West in southern Alberta. These periods of uplift and erosion are considered to represent peripheral bulge development associated with Antler orogenesis and foreland basin development. Mapping of the stratigraphic units under consideration here shows the areal extent of these major and minor unconformities, as well as the distribution and thickness of the stratigraphic units.

## Test hypotheses of conodont ecology using element wear and damage

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Analysis of dental wear and damage is becoming an increasingly important tool in unravelling the trophic ecology of a wide range of vertebrates (Walker et al. 1978; Teaford 1988; Purnell et al. 2006), and when applied to fossils, it allows links between dietary change and morphological evolution to be investigated (Purnell et al. 2007). Conodonts have the best fossil record of any vertebrate group (Foote and Sepkoski 1999; Purnell and Donoghue 2005) and their skeletal elements are known to exhibit surface wear and damage (Purnell 1995; Donoghue and Purnell 1999); yet no systematic survey or analysis of the frequency and extent of this wear and damage in conodonts has hitherto been conducted. Here, we report on the first such study. Using focus variation optical microscopy, we acquired high resolution images of lateral and oral surfaces of P<sub>1</sub> elements from a range of taxa. Taxa were selected to span a range of nearshore and deeper water environments, and included Idiognathodus, Streptognathodus, Hindeodus, Gnathodus, Adetognathus, Mestognathus and

Patrognathus. Elements were selected on the basis of high quality of preservation, but were otherwise chosen randomly from within samples. Wear and/or damage were found in all elements sampled. Analysis revealed that morphologically similar elements have the most similar patterns of wear/damage. We also found consistent differences in the pattern of wear/damage in the blade region of the elements, potentially reflecting the differing environments occupied by the taxa (cf. Purnell et al. 2006). Oxygen isotope data obtained from the same taxa and samples suggest that wear/damage analysis may provide ecological information that could be used to constrain paleothermometry derived from isotopic analysis of conodont element apatite. The success of this technique has other, wide-ranging implications for unlocking the fossil record of conodonts; for example, offering a means of validating functional hypotheses, and furnishing direct evidence of the diet-mediated processes that may have driven observed patterns of evolutionary change.

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## Directional evolutionary character change in the conodont *Pterospathodus*

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The excellent fossil record of conodonts represents an ideal, yet under-utilized, resource for resolving fundamental issues of pattern and process in evolutionary theory. However, the quantitative understanding of conodont element morphology necessary to exploit this potential is currently limited. This work applies standardized morphometric protocols (Jones and Purnell 2007) to P<sub>1</sub> skeletal elements belonging to the conodont *Pterospathodus*, derived from a densely sampled core section from Estonia (Männik 2007). It has established a robust quantitative framework for morphological variation in Pterospathodus, permitting statistical analysis of the current qualitative hypotheses of evolutionary pattern within this genus for the first time. Apparent directional trends were statistically compared with patterns expected for directional evolution, an unbiased random walk and stasis, using maximum-likelihood model fitting (Hunt 2006), rescaled range analysis and the runs test. Results confirmed the presence of trends in size and shape change through time, and revealed additional patterns not previously reported. This has provided a rare example of convincing directional character change within a fossil lineage. The morphometric data have also allowed quantitative investigation of ontogenetic processes in Pterospathodus, rigorously testing the hypothesis of heterochrony in conodont elements for the first time. This has suggested that allometric repatterning (Mitteroecker et al. 2005, Webster and Zelditch 2005), and not heterochrony, was the proximal mechanism responsible for mediating the observed shifts in morphology through time. The results have demonstrated that data obtained using widely applicable morphometric protocols, subjected to straightforward time series analysis, can effectively unlock the potential of conodonts to elucidate evolutionary pattern and process in the fossil record.

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## Reworked conodonts of the Alexander Terrane: Utility and lithologic occurrence

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In southeastern Alaska, the former micro-continent and volcanic arc known as the Alexander Terrane has an extensive rock record spanning most of the Phanerozoic. Conodonts from every geologic period encompassing Silurian through Triassic time have been identified from carbonate units within the terrane's stratigraphic succession. As an oceanic micro-continent, the Alexander Terrane was a series of islands that had steep depositional slopes and a variable paleotopography over which a wide range of non-marine to deeper marine facies were deposited. Multiple episodes of tectonic uplift affected the terrane during its geologic history resulting in erosion and subsequent re-deposition of conodont-bearing units in younger rocks. This combination of features makes the stratigraphic record in the Alexander Terrane a natural laboratory for examining reworking and subsequent preservation of conodont elements in different rock types and depositional environments.

The Pennsylvanian through Late Triassic record of the Alexander Terrane contains numerous conodont-bearing carbonate units interbedded with, and sometimes lithologically mixed with, clastics and volcanics. Conodont samples were collected from every calcareous lithology in the field area, including: pure carbonate; conglomeratic, sandy, silty, and/or volcaniclastic carbonate; calcareous conglomerate, sandstone, and siltstone; and siliceous-matrix conglomerate/sandstone with carbonate lithoclasts. Conodont-bearing carbonates in the succession include: Early to Middle Pennsylvanian shallow- and deeper-water carbonate; Late Pennsylvanian to Early Permian mixed clastics, volcanics, and carbonate; Middle Permian carbonate; Middle Triassic clastics and carbonate; and Late Triassic mixed clastics, volcanics, and carbonate.

Reworked conodonts were only recovered from conglomeratic lithologies, with the exception of a single, calcareous, coarsegrained sandstone sample. Kasimovian to Asselian age lithoclastic conglomerates contained reworked Devonian and Pennsylvanian conodonts, Middle Triassic lithoclastic conglomerates contained reworked Permian and Early Triassic conodonts, Late Triassic lithoclastic conglomerates contained reworked Devonian and Permian conodonts, one Late Triassic lithoclastic sandstone contained abraded, reworked Devonian conodonts, and one Late Triassic intraclastic conglomeratic limestone contained reworked and sometimes abraded Late Triassic conodonts from the same biozone. Kasimovian to Asselian age reworking was mainly due to differential tectonic uplift and exposure of older units, Middle Triassic reworking was due to renewed tectonic uplift and previous exposure, and Late Triassic reworking was mainly due to erosion of previously uplifted and continuously exposed units.

The pervasive absence of reworked conodonts in non-conglomerate lithologies indicates the overall low preservation potential for reworked conodonts. This is despite 1) steep depositional paleo-slopes, which would have increased the likelihood of conodonts being transported into distal and/or finer-grained facies, 2) continuous exposure, erosion, and redeposition of Devonian and Permian units into younger units, and 3) abundant conodont elements in Devonian carbonate clasts in the field area. Reworked conodont elements are absent in most sandstones, despite an abundance of proximally deposited, angular, coarse to fine-grained sands, and display abrasion and rounding when found in these rock types. This supports that conodonts, being composed of apatite, erode as easily as their mineral hardness would suggest and are most easily reworked into younger units when inside a clast larger than the conodont element.

Conglomeratic units are the best place to find reworked conodonts, and are generally an easy rock type to see in the field, though careful lithologic examination is needed to identify the conglomeratic nature of some rock units, especially intraclastic conglomerates. Furthermore, reworked intervals yield tremendous insight into the depositional and erosional history of an area. They preserve records of deposition that have been otherwise completely removed by erosion, provide information on the timing and duration of erosion, and indicate which older units were exposed when erosion took place. Conodonts within clasts are one of the most useful tools for understanding the complex history of conglomerates and potential contamination of other lithologies with out-of-sequence conodonts is very unlikely.

## Revised Conodont-, Graptolite-, Chitinozoa-, and Event-Based Telychian-Lochkovian (Silurian-Early Devonian) Chronostratigraphy Developed Using Graphic Correlation

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Ranges of nearly 600 conodont, graptolite, and chitinozoan species, 36 bentonites, and three Global Boundary Stratotype Section and Points (GSSP) in over 80 stratigraphic sections in North America, Europe, and Australia comprise the framework for an upper Llandovery (Telychian)-lower Lochkovian (Silurian-Lower Devonian) chronostratigraphy developed using the graphic correlation method. The Telychian -Lower Devonian chronostratigraphy was recently revised with the addition of several stratigraphic sections containing much new range data, particularly of graptolites and bentonites. All of the series and stage boundaries officially recognized by the International Commission on Stratigraphy for the Silurian from the base of the Wenlock Series to the base of the Devonian System can be recognized with confidence in the revised Telychian-Lower Devonian chronostratigraphy. The GSSPs for the Llandovery/ Wenlock, Ludlow/Pridoli, and Pridoli/Lochkovian are part of the framework of the Telychian-Lower Devonian chronostratigraphy

and define the position of those boundaries in the Telychian-Lower Devonian composite. The Sheinwoodian/Homerian and Gorstian/Ludfordian boundaries are possible to recognize in the chronostratigraphic framework based on the ranges of graptolites or conodonts that are typically used to correlate the position of those boundaries in the official boundary stratotype sections in Homer and near Ludlow, United Kingdom, respectively. All of the original Silurian conodont zones proposed by Walliser (1964), and all of the Telychian-Pridoli conodont zones used by Aldridge and Schönlaub (1989), by the Subcommission on Silurian Stratigraphy (1995), by Corradini and Serpagli (1999), by Jeppsson et al. (2006), and by Männik (2007) are possible to recognize as chronozones or subchronozones in the revised Telychian-Lower Devonian chronostratigraphy, but not always at precisely the same stratigraphic positions at which they were recognized in those publications. The Telychian-lower Lochkovian chronostratigraphy currently includes 37 conodont chronozones, 25 graptolite chronozones, and 17 chitinozoa chronozones.

## Revised conodont zonation across the P/T boundary at Shangsi section, Sichuan, China

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The Shangsi section, formerly one of the candidate sections of the Global Stratotype Section and Point for the Permian-Triassic Boundary, is located near Guangyuan City, Sichuan Province, South China. Many achievements have been obtained from the research on the conodonts of the Shangsi section, which began with Dai et al. (1989) (in Li et al., 1989), followed by Lai et al. (1996) and Nicoll et al. (2002). In this study, large conodont samples (approximately 20 kg each) have been collected from the uppermost Permian and lowermost Triassic (beds 26-33) at this section. Almost all the samples have been entirely processed and over 3,000 specimens were obtained. For the first time, usable numbers of Neogondolella specimens have been found from the basal Triassic. The new data enable us to not only revise the ranges of some important conodont species, but also to establish parallel hindeodid and gondolellid conodont zones through a section that is similar to the Meishan section (Jiang et al., 2007). In ascending order, three newly established gondolellid zones are as follows: Neogondolella yini Zone (bed 26 and below), Neogondolella meishanensis Zone (beds 27a-27c) and Neogondolella taylorae Zone(beds 28a-29d). Also in ascending order, four revised and newly established hindeodid zones are as follows: Hindeodus changxingensis Zone (beds 28a-29b), Hindeodus parvus Zone (beds 29c-30a), Isarcicella lobata Zone (beds 30b-31a), Isarcicella isarcica Zone (bed 31b and above). According to the new data, the first appearance datum of *Hindeodus parvus* is about two metres lower than the previously reported horizon. Neogondolella taylo*rae* – a proposed earliest Triassic gondolellid marker species – is reported for the first time at this section with its first appearance at bed 28a. Unfortunately *I. staeschei* Zone is not identified at this section, which could be due to the lack of continuous sampling in beds 31a and 31b. However, the identification of the *I. lobata* Zone results in better conodont biostratigraphic correlation when comparing with the Bulla and Tesero sections (Western Tethys, Perri and Farabegoli, 2003).

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#### Graptolite Conodont and **Co-Occurrence** in **Ordovician Dark Shale Sequences**

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The co-occurrence of conodonts and graptolites on bedding planes in Ordovician shale sequences enhances the overall correlation precision between platform and deepwater successions. Shale successions in Tarim (western China), Alabama, Idaho, and Oklahoma in North America. central Scotland, and Bornholm, Denmark contain key conodont zonal indicator species. Oepikodus communis, Pygodus anitae, P. serra, P. anserinus, Amorphognathus tvaerensis, and A. superbus (as well as more long-ranging taxa) occur on bedding planes with *Didymograptus bifidus* to Diplacathograptus caudatus Zone graptolites. In the Phi Kappa Formation of central Idaho (Figure 1) we have also discovered bedding plane associations/partial assemblages of Oepikodus sp., P. serra, Periodon aculeatus, Pe. grandis, and A. tvaerensis. These bedding plane associations are difficult to interpret as the rocks containing the associations have been altered through a complex tectonic and thermal history. Nevertheless, they demonstrate that there is a high potential for apparatus reconstruction and paleobiological interpretation.

Collections across the Sandbian-Katian succession at the Hartfell Spa section near Moffat, Scotland (Figure 2) also contain biostratigraphically important conodonts. Amorphognathus tvaerensis is present 1.6 metres below the FAD of D. caudatus and A. superbus is present 9.4 metres above it. Thus, at Hartfell the A. tvaerensis Zone -A. superbus Zone boundary occurs within an interval of 11 metres in the D. caudatus graptolite Zone. This is similar

to what was discovered at Black Knob Ridge, and suggests in Trail Crack ratio in Trail Creek region that in dark shale successions A. superbus occurs relatively shortly after the FAD of D. caudatus. These bedding plane co-occurrences provide more precise ties between graptolite and conodont biozonations and support the potential for additional resolution with further collecting at these and other localities.

Not all Sandbian-Katian successions have yielded biostratigraphically important conodonts. For example, the succession on Bornholm is dominated by long-ranging, coniform conodont taxa (e.g., Scabbardella altipes). This suggests that graptolite-bearing dark shale successions contain at least two distinct conodont biofacies.

Figure 1. Conodont horizons within the Phi Kappa Formation., central Idaho. The occurrence of bedding plane conodonts with graptolites across the Sandbian-Katian boundary at Black Knob Ridge (Oklahoma) was a key factor in the selection of Black Knob Ridge as the GSSP for the base of the Katian. The A. tvaerensis Zone - A. superbus Zone boundary is tentatively identified at 5.7 metres above the base of the Bigfork Chert in the lower D. caudatus Zone.



Fault

section



Bedding plane co-occurrence of biostratigraphically useful conodonts and graptolites in Ordovician shale sequences are not uncommon. In every graptolite-bearing deep-water succession where we have taken the time to carefully collect and examine surfaces for conodonts, we have found them. Based on these collections, we think that there is great potential to enhance the overall correlation precision between carbonate-dominated successions, where conodont biostratigraphy has been well-established, and deep water siliciclastic successions where graptolite biostratigraphy is well established.

#### Early Ancyrodella from Basibé, a second extinction!

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The Middle and Upper Devonian stratigraphy from the Sierra Negra Subfacies in the Spanish Central Pyrenees is still unknown (Valenzuela-Ríos and Liao, 2006); therefore, any sound information is of great value for reconstructing the history of this subfacies and its relation to other areas. Such valuable information has been recorded from two short sections in the nearby of Benasque, the Ampriú and the Basibé sections. The former has been destroyed by road work aiming at a better access to a sky resort area; the latter will most likely suffer the same grace, but this time due to the megalomanous project seeking the building of a huge sky resort in the Pyrenees connecting several isolated sky stations.

The Basibé section has yielded an important fauna of early

Ancyrodella, including Ad. binodosa, Ad. soluta and a new form characterized by the presence of two nodes on each lobe, showing some variation on the arrangement of these nodes. Platform outline of some specimens shows an almost right angle disposition of the anterior and posterior carinas with respect to the secondary ones, and thus, giving them a "cross" aspect. Specimens with two large nodes on each side of platform have been recently described as Ad. postbinodosa (Uyeno and Wendte, 2005), but main outline and other ornamentation features are, somehow, different from the Pyrenean specimens.

The stratigraphic position of this Pyrenean taxon (MN1 and MN2 zones), and its morphological features hints at a position within evolution of early *Ancyrodella*.

Besides world-wide importance for a better understanding of the evolution of early *Ancyrodella*, this outcrop provides important information for the knowledge of the local Upper Devonian stratigraphy of the Subfacies Sierra Negra, and its comparison with other subfacies.

Therefore research in the area is of highest priority, however, human behaviour will most likely cause a new extinction of information, in this case, the second one for this taxon.

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## Permian Conodonts (Artinskian- Early Djulfian) from Ruteh and Nesen formations in Central Alborz, North Iran

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The suitable outcrops of Permian rocks are present in Northwest of Khur in Central Alborz, North Iran. This sequence consists of the Dorud (Asselian-Sakmarian), Ruteh (Artinskian-Murgabian) and Nesen (Early Djulfian) formations. The rich foraminifer fauna

indicates Artinskian to Early Djulfian (Early Wachiapingian) for the succession. The Ruteh (221m) and Nesen (13m) formations consist mainly of fossiliferous limestone. The Ruteh Formation disconformably overlies the Dorud Formation and in the studied section can be subdivided into three informal members, which are overlain disconformably by the Nesen Formation (Early Djulfian). According to International Conodont Biozonation, three conodont biozones have been distinguished in the Ruteh and Nesen formations. Conodont species Sweetognathus whitei has been obtained from member 1 of the Ruteh Formation that is the index for the whitei Zone (Artinskian). Sweetognathus hanzhongensis has been obtained from member 2 of the Ruteh Formation that is an index for the hanzhongensis Zone (Murgabian). Iranognathus tarazi also has been obtained from the Nesen Formation that indicates Iranoganthus tarazi Zone (Early Djulfian). These conodont biozones can be correlated with foraminiferal zones in the studied section including the Schubertella-Mesoschubertella Assemblage Zone (Artinskian), Dunbarula-Deckerella and Neoendothyra-Pachyphloia Assemblage Zones (Murgabian), and Paraglobivalvulina-Ictyolaria Assemblage Zone (Early Djulfian).

## Shallow-water conodonts of the Uppermost *margin-ifera* – Middle *expansa* zones in Poland

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Evolution of the Devonian epicontinental Pomeranian Basin (NW Poland) was controlled via proximity of the land areas representing uplifted parts of the East European Craton. The Pomeranian Basin was marine through the whole Famennian. A distinct and relatively rapid regressive event affected the study area probably at the end of the Late *marginifera* Chron or in the beginning of the Latest *marginifera* Chron. Marginal-marine siliciclastic and mixed siliciclastic-carbonate sediments, as well as shallow-water carbonates related to an inner carbonate ramp or platform were deposited during the middle-late Famennian times.

Conodont analysis permitted recognition of much of the Famennian "standard" conodont zones, up to the Uppermost *marginifera* Zone (Matyja, 1993). It should be noted that the base of a conodont zone has almost nowhere been adequately defined because of the paucity of diagnostic conodonts; the age of some fragments of the succession has presently been only broadly determined to intervals of 2-3 zones. Therefore, application of original zone definitions, based on index taxa, was not possible in most cases, and ranges of accompanying taxa, correlated with the standard conodont zonation, have been usually employed.

The Upper marginifera Zone is characterized by the range of *Palmatolepis marginifera marginifera* between the last occurrence of *Palmatolepis quadrantinodosa* and the first occurrence of *Scaphignathus velifer*. The range of *Palmatolepis marginifera marginifera* together with *Polygnathus glaber bilobatus* is here

taken to identify this zone. The most common association consists of Palmatolepis glabra pectinata, Palmatolepis glabra prima and endemic species Polygnathus pomeranicus. The Uppermost marginifera Zone is recognized by appearance of Alternognathus regularis and Polygnathus granulosus. The most common association consists of Polygnathus semicostatus, Polygnathus glaber glaber, Polygnathus glaber bilobatus and endemic species Polygnathus pomeranicus. Alternognathus pseudostrigosus, Polygnathus glaber glaber, Polygnathus glaber bilobatus, Polygnathus fallax, and Palmatolepis glabra distorta, as well as endemic assemblage represented by "Icriodus" chojnicensis and Polygnathus limbatus range to the top of the zone.

The shallowing-upward tendency has been observed in the conodont biofacies shift, from deeper polygnathid-palmatolepid biofacies during the Early-Late *marginifera* chrons to very shallow-water polygnathid one in the latest *marginifera* Chron. This bioevent was also related with final (definitive) retreat of the off-shore genus *Palmatolepis* from the Pomeranian Basin at the end of the *marginifera* Chron.

There is no evidence of the *trachytera* and *postera* conodont zones throughout the entire Pomeranian area. The inability to recognize these zones within the very shallow-water succession may be associated with the paucity or even absence of diagnostic conodonts. Taking into account the very shallow-water character of the succession and the low net sedimentation rate during the *trachytera* and *postera* chrons, it is not certain whether deposition was more or less continuous between the Latest *marginifera* and Early *expansa* chrons.

The Lower and Middle expansa zones were recognizable owing to the presence of numerous bizarre forms characteristic of extremely shallow environments. Fortunately, their vertical ranges have been correlated with the standard conodont zonation given by Sandberg and Ziegler (1979). The Lower expansa Zone is documented by the presence of *Polygnathus experplexus*, Polygnathus subirregularis and Scaphignathus ziegleri as well as by many other species, i.e., Clydagnathus ormistoni, "Icriodus" costatus darbyensis, "Icriodus" raymondi, Mehlina strigosa, Polygnathus bouckaerti, Pelekysgnathus inclinatus, Polygnathus communis communis, Polygnathus perplexus, Polygnathus semicostatus, "Pandorinellina cf. insita", Scaphignathus peterseni, and the endemic form Polygnathus szulczewskii. The Middle expansa Zone is characterized by the presence of Bispathodus aculeatus aculeatus, Bispathodus aculeatus anteposicornis, Branmehla inornata, Hemilistrona pulchra, Polygnathellus giganteus, Polygnathus delicatus and Polygnathus streeli.

As exemplified by the Pomeranian succession, the overall regressive tendency, observed during the Latest *marginifera* to Early *expansa* chrones is reflected by the gradual decrease in time, of the number of pelagic platform conodonts (palmatolepids and polygnathids of the *nodocostatus* group) and the simultaneous increase of the number of taxa that are characteristic of various restricted marine and peritidal settings (narrow polygnathids, "icriodids", pelekysgnathids, pandorinellinids, scaphignathids and clydagnathids). It is worth noting that *Polygnathus semicostatus* is the most abundant in the middle – late Famennian conodont population. A similar conodont fauna has been recognized both in the western United States and in Belgium.

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## Evolutionary patterns and phylogeny of the Carnian/ Norian conodonts from the Pizzo Mondello section, GSSP candidate for the base of the Norian

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The taxonomy and phylomorphogenesis of conodont pectiniform elements around the Carnian/Norian boundary is rather problematic for the apparent provincialism that affects many conodont species (Kozur, 2003; Mazza and Rigo, 2008a) and for the large number of morphotypes and transitional forms occurring during this stratigraphic interval. The mass presence of transitional forms among conodont species is explained by the rapid recovery and evolution of conodonts after the Carnian crisis (Julian/Tuvalian boundary), related to the Carnian Pluvial Event (Rigo *et al*, 2007).

In order to resolve the problems concerning evolutionary patterns and processes of the Upper Triassic conodonts, we conducted a detailed taxonomic study of the species belonging to the five most widespread genera (Paragondolella, Carnepigondolella, Metapolygnathus, Epigondolella, and Norigondolella) from the Pizzo Mondello section (Sicani Mountains, Western Sicily, Italy), candidate section as GSSP for the Carnian/Norian boundary (Nicora et al., 2007; Balini et al., 2008). The section is a 430 m thick continuous succession of marine limestones ranging from Late Carnian to Rhaetian in age (Nicora et al., 2007), characterized by almost uniform facies and a very rich conodont fauna. Taxonomic studies on conodont populations allowed us to recognize some discriminating morphological features for the separation of genera (the position of the pit, with respect both to the platform and to the keel end, the occurrence of nodes and/or denticles on the platform margins, the length of the platform and the shape of the keel end; see Mazza and Rigo, 2008b) and many others for the classification of species. Also morphometries have been applied to the measurable features (pit position with respect to the platform and to the keel end, platform length, keel width and free blade length) to obtain more precise and objective data for the analyses. The changes in the conodont platform morphology observed through the section, provided the following trends in the evolution of the pectiniform elements: a) the forward-shifting of the pit, b) the shortening of the platform and c) the appearance of nodes on the platform margins and the development of nodes into denticles (see Mazza and Rigo, 2008 and references therein). Species belonging to the five main Late Carnian-Early Norian genera have been thus assigned to two separate monophyletic lineages: i) the *Paragondolella-Metapolygnathus-Norigondolella* lineage and ii) the *Carnepigondolella-Epigondolella* lineage.

Nevertheless, the phylogenetic relationships of some species remained problematic. In order to solve these problems, a numerical cladistic analysis has been applied to the studied species. The morphological characters used to classify conodont species have been thus codified to generate numerical matrices to be analyzed by a program (PAUP, Swofford, 2002) for phylogenetic analysis under the parsimony criteria.

The produced cladograms demonstrate morphological relationships among genera and species, showing that the evolutionary trends listened above are supported by the most parsimoniuos character state distribution among taxa and confirming the importance of the considered characters for the conodont taxonomy. Furthermore, the consensus tree from the set of cladograms generated, allowed assigning some species to well identified sister groups, which coincides in this case with the conodont genera, and better defining the still uncertain systematic positions of some problematic species.

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## Middle Pennsylvanian conodonts (Carboniferous) from the Nevandi River Valley (Picos de Europa Unit, Cantabrian Zone, North Spain)

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The Picos de Europa Unit is in the eastern part of the Cantabrian Zone (Julivert, 1971; Pérez Estaún *et al.*, 1988). This structural unit exhibits a good Carboniferous succession comprising mainly marine limestones. Conodonts have been investigated for years in the Carboniferous of the area and provide important biostratigraphic data mainly in Lower Mississippian and Early Upper Pennsylvanian (Méndez y Menéndez, 1981; Truyols *et al.*, 1984; Blanco Ferrera *et al.*, 2005; Méndez, 2006).

The Nevandi River Valley Section is located in the South of the Picos de Europa Unit and consists of more than 800 m of an entirely marine succession predominantly calcareous with abundant dolomite at several levels.

Fusulinoideans, recorded for most of the succession except for its lower 171 metres, allowed us to distinguish Bashkirian, Lower Moscovian and Upper Moscovian in the series (Villa, 1985). The conodont faunas indicated some degree of precision in age mainly in the Lower-Middle Mississippian (Méndez and Menéndez, 1985). However, only a few conodont specimens were illustrated and no systematic descriptions were published. New biostratigraphic data concerning Moscovian conodont faunas can be reported from a re-study of the investigated ones and the research on additional material. The first 40 metres researched are within the upper part of the Valdeteja Formation and consist of grey massive limestones. The rest of the succession belongs to the Picos de Europa Formation. This lithostratigraphic unit consists of 300 metres with a lower member (about 50 m) made of thinbedded dark grey limestone with some intervals of chert and an upper member made of grey massive limestone topped with a few metres of dolostone.

Most conodont specimens recovered are  $P_1$  elements, and are generally well preserved. *Idiognathodus* and *Idiognathoides* are dominant. *Neognathodus* is present in several levels although it's not so abundant. Other genera recorded in the section are *Declinognathodus*, *Gondolella* and *Mesogondolella*. The investigated conodonts as a whole are integrated by cosmopolitan species and other forms that differ morphologically from those elsewhere.

The uppermost part of the Valdeteja Formation is dated as Lower Moscovian by fusulinoideans and provided scarce conodont elements mainly *Idiognathoides sinuatus*. Below this interval no conodonts were recovered in the formation.

Regarding the Bashkirian-Moscovian boundary one of the conodont events as potential boundary-defining datum is the evolutionary origin of *Idiognathoides postsulcatus* from *I. sulcatus* (Barry C. Richards and Task Group, 2004). We have registered *I. postsulcatus* only in a level close to the top of the bedded member of the Picos de Europa Formation, above the beds dated as Vereyan by conodonts.

Two cosmopolitan species: Declinognathodus marginodosus

and *Neognathodus atokaensis* are recorded together in a short interval in the lower part of the bedded member of the Picos de Europa Formation. This association occurs in the upper part of the Vereyan of the Moscow Syneclise so, a Vereyan age is suggested for that portion of the succession which agrees with the lower Moscovian age indicated by fusulinoideans.

*Idiognathoides sinuatus* is a cosmopolitan species extending through the succession that disappeared with the genus *Idiognathoides* in the lower part of the massive member of the Picos de Europa Formation. Several metres below, *Gondolella laevis* is present in the series. This fact suggests a Podolskian age for that portion of the section. *G. laevis* appears in the lower Desmoinesian of the U.S and was reported from the lower Podolskian of the Moscow Syneclise in Russia. The genus *Idiognathoides* is not recovered above the Podolskian in the Cantabrian Mountains. Data provided by fusulinoideans still indicate lower Moscovian for the same beds (Villa, 1985).

Significant for biostratigraphy too is the position of *Idiognathodus* cf. *I. expansus* close to the top of the investigated succession. *I. expansus* is reported from uppermost Desmoinesian in the Midcontinent (U.S.). Recently, we have recovered this species from Myachkovian in the Cantabrian Mountains (Picos de Europa Unit: Las llacerias Section), which can indicate the same age for the top of the series in this study.

The rest of the material are distinctive forms mainly idiognathodids. *Idiognathodus* is relatively abundant displaying a few morphologies in the lower part of the studied series.

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## Middle Pennsylvanian conodont biostratigraphy employing the genus *Neognathodus*

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Appalachian marine units are being restudied in great detail, the most active area of research employing biometric analysis of neognathodontid platform elements. There are about eight named marine units within the Pottsville and Allegheny Groups that have been assumed to be widespread, contiguous, and coeval. Work in southeastern Ohio demonstrates that they are none of these. Two classic exceptions to the continuity and contemporaneity rule include rocks called "Lower Mercer" that prove to be several, at least three and probably four, discrete heterochronous rock bodies. Another classic example is called "Vanport" and "Obryan" in southeastern Ohio and neognathodontid biometrics convinces me that these are five discrete slightly heterochronous rock bodies, from oldest to youngest, that near Pedro, that around the type Obryan, that near Wellston, that near Oak Hill, and finally that around McArthur.

In the Illinois Basin my original work there defined four conodont zones, in ascending order, the Neognathodus bothrops - N. bassleri Zone (Seville), N. medexultimus - N. medadultimus Zone (Seahorne), N. roundyi - N. medexultimus Zone (Oak Grove through Sparland), and N. dilatus – N. metanodosus Zone (Lonsdale). The fact that the entire Carbondale Formation contains just a single zone and with the very precise and detailed biostratigraphy that is proving possible with the genus elsewhere, led to some preliminary biometrics in an attempt to distinguish between the units. The results of this are that the Oak Grove can be distinguished from the other six units and the Hanover and St. David can be as well. So too can the Brereton and Pokeberry as can be the Sparland, although this last may be with a bit less confidence than with the others. Making distinctions between these pairs that differ little in age (Hanover - St. David, Brereton - Pokeberry) is a challenge for the future, but with the utility and sensitivity the genus has shown, it may be possible.

Samples from the Midcontinent are generally about the age they are supposed to be with a few exceptions. One potential reason for such exceptions and a note of caution: I have not done the detailed stratigraphic analysis and mapping in Missouri, Kansas, and Iowa that I did in Illinois and Ohio and I was generally forced to accept the "calls" made by those I followed in the field. The Tiawah I sampled appears to be a little older than the Seville in Illinois, the Scammon appears to be a little younger than the Seahorne and the Fleming appears to be a bit older than the Oak Grove, and the Excello and most of the Ft. Scott appears to be younger than the Sparland. More and better material (with well defined stratigraphic determinations) will be needed to establish these correlations precisely.

# Base of the *Cordylodus proavus* Zone (FAD of *Cordylodus andresi*) as a key horizon for Late Cambrian global chronocorrelation

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The base of the Cordylodus proavus Zone (FAD of Cordylodus andresi) is one of the most distinctive Upper Cambrian biostratigraphic horizons. In North America, this horizon is characterized by nearly complete faunal turn-overs among conodonts and trilobites. Underlying strata contain the coniform euconodonts Proconodontus muelleri, P. serratus, Cambrooistodus cambricus, and C. minutus. These taxa disappear abruptly at a level that coincides with the appearance of the oldest widespread ramiform conodont, Cordylodus andresi (base of C. proavus Zone). The lower part of this zone also contains the lowest occurrences of Hirsutodontus, Clavohamulus, Cordylodus proavus, and Fryxellodontus. The base of the C. proavus Zone coincides precisely with a major trilobite turnover (base of Eurekia apopsis Zone). These faunal changes are associated with the top of the Ptychaspid Biomere and are near the base of the Lange Ranch Lowstand, a global sea level event. These faunal changes characterize the base of the Ibexian Series in North America (Miller et al., 2003).

Several authors have disputed the age of the oldest *Cordylodus*. Landing (1983) inferred that the FAD of *Cordylodus* in Vermont is associated with somewhat older conodonts and trilobites than on the Laurentian platform. Taylor *et al.* (1991) collected three independent sets of conodont samples from Landing's sections but did not find *Cordylodus* associated with *Proconodontus*, except in one sample in which the youngest *Proconodontus* occurs with the oldest *Cordylodus*. They concluded that Landing's association of *Cordylodus* with uppermost Sunwaptan conodonts and trilobites resulted from miscorrelation between two sections and mixing of bioclasts in the edge of a debris flow precisely at the base of the Ibexian Series.

Szaniawski and Bengtson (1998) studied conodonts from Sweden and reported *Cordylodus andresi* from sediments immediately overlying strata containing their newly named subspecies, *Proconodontus tenuiserratus bicostatus*. They interpreted this occurrence as an unusually low FAD of *C. andresi* in the *Proconodontus tenuiserratus* Zone, which is four zones below the *C. proavus* Zone in the Laurentian zonation. However, elements of their new subspecies have anterior keels and thus cannot be assigned to *P. tenuiserratus*, which lacks such a feature. Thus, we consider their subspecies to be a junior synonym of *Proconodontus serratus*, a much younger species. Moreover, their reported co-occurrence of *C. andresi* with *P. muelleri* is from only one sample, collected in the matrix of a polymict conglomerate that has clasts that yield only conodonts of the *Eoconodontus* Zone.

Landing *et al.* (2007) reported that in Oaxaca, Mexico, *C. andresi* occurs with *P. serratus* and/or *P. muelleri* in two beds (within 1.3 metres of section) reported as fossil hash and intraclast wackestones and grainstones. Thus, the co-occurrence of these conodonts through section condensation and reworking is possible. They reported no independent dating of these beds, *e.g.*, by trilobites.

The turnover in conodont faunas at the base of the *Cordylodus proavus* Zone has been identified globally. *Cordylodus andresi* is a short-ranging species that occurs in facies ranging from nearshore sandstones to deep-marine radiolarian cherts. Associated trilobites are more endemic than conodonts, but changes in shallow-marine trilobites occur at this level on several paleocontinents. Other useful tools for correlating this horizon to other areas include brachiopods, sequence stratigraphy, and carbon-isotope geochemistry. This horizon is very useful for intra- and intercontinental correlation and is an excellent candidate for a global chronostratigraphic boundary that can be correlated by multiple criteria (Miller *et al.*, 2006).

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for conodont- and trilobite-based chrono-correlation. Journal of Paleontology, 65: 855–863.

## Upper Eifelian polygnathid-icriodid assemblages from Belarus and their biostratigraphic and paleogeographic significance

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The Middle Devonian of Belarus is dominated by restricted shallow-marine and continental facies represented by marlydolomitic and sandy, fossil-poor deposits. The exceptional open-marine intercalation of thin (3-10 m) carbonate-silty strata with abundant fishes, brachiopods and conodonts, is designated as the regional Kostyuokovichi Horizon. Its age was determined as Upper Eifelian based mainly on meiospores and fishes (Kruchek *et al.*, 2001; Obukhovskaya *et al.*, 2005; Valiukevičius *et al.*, 1995; Valiukevičius, 1998; Plaksa, 2007). A conodont fauna was initially described by Kruchek (1974), but it required verification based on new material obtained by the authors. The preliminary results indicate uniqueness of the fauna with respect to abundance, taxonomic diversity, biofacies and paleogeographic affinities (Narkiewicz and Kruchek, 2008).

We sampled nine borehole sections which yielded ca. 4600 specimens. Predominant are representatives of *Icriodus* and *Polygnathus* accompanied by *Belodella*, *Dvorakia*, *Ozarkodina* and *Tortodus*. Among icriodids we identified are *I. norfordi*, *I. stelcki*, *I. eriensis*, *I. formosus*, *I. xenium* and *I. orri*. *Polygnathus* is represented by *P. parawebbi*, *P. linguiformis linguiformis*, *P. ling. klapperi*, *P. ling. weddigei* and *P. ling.* n. subsp. *A sensu* Uyeno *et* Bultynck, 1993. Quantitatively most important are *I. orri* and *P. parawebbi*. Moreover, three new *Icriodus* species were recognized. We suggest amendment of *I. orri* Klapper and Barrick, 1983 whose holotype reveals features characteristic for the earlier described *Icriodus norfordi* Chatterton, 1978.

*Polygnathus* and *Icriodus* species are represented by a full spectrum of ontogenetic stages indicating lack of redeposition among studied assemblages which may thus be similar to the original biocoenoses. Predominance of *Icriodus* over *Polygnathus* (i.e. the icriodid-polygnathid biofacies) indicates a shallow-marine, moderately turbulent environment. The flourishing of the conodont fauna followed an immigration event due to a relative sealevel rise in the Belarus Basin.

The studied horizon is assigned to the middle to upper part of the *ensensis* Zone (uppermost Eifelian) based on the assessed total stratigraphic ranges of the key taxa: *I. formosus*, *I. stelcki*, *I. xenium*, *P. ling. klapperi*, *P. ling. weddigei*, *P. ling.* n. subsp. A and *Tortodus variabilis*. It may be possible to recognize a lower part of the *ensensis* Zone characterized by the first occurrence of *P. linguiformis klapperi* always followed by the appearance of *P. ling.* n. subsp. A, which appears characteristic for the upper part of the *ensensis* Zone.

The icriodid-*P. parawebbi* assemblage is characteristic for North America, whereas it has been found now for the first time in Europe. In contrast, representatives of *P. linguiformis* are widely known from North America, North Africa, Australia and Europe. The paleogeographic distribution of the two assemblages may be due to different environmental preferences responsible for the different migration pathways of icriodids and *P. linguiformis* subspecies.

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## **Mid-Carboniferous boundary conodonts of the Cantabrian Mountains** (Palencia, Spain)

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The deep water conodont succession across the Mid-Carboniferous boundary was discovered at the La Lastra section, Palentian Domain, eastern Cantabrian Mountains, Spain. The section embraces the uppermost part of the Genicera Formation (uppermost Visean) and the Barcaliente Limestone Formation, consisting of thinly bedded dark grey mudstones and wackestones, c. 60 metres thick. The greater part of the Barcaliente Formation is Serpukhovian in age and the upper part belongs to the lower part of the Lower Bashkirian.

The condont fauna and its distribution pattern is very similar to that of the other deep water sections throughout Eurasia especially to the Aksu section, South Tieanshan, Uzbekistan.

The conodonts are not abundant, but all important Serpukhovian and early Bashkirian species including those of the Mid-Carboniferous boundary conodonts occur here. The typical Serpukhovian and early Bashkirian species are of the Lochriea, Gnathodus, Declinognathodus and Idiognathoides genera. The sequence of Gnathodus postbilineatus, Declinognathodus praenoduliferus, D. bernesgae, D. noduliferus and early species of the genus Idiognathoides span the interval of the Mid-Carboniferous boundary deposits. The Mid-Carboniferous event, i.e. the changeover between the Mississippian and Pennsylvanian conodont faunas, is clearly apparent in the La Lastra section. Mississippian conodonts of the Gnathodus and Lochriea genera disappeared close to the level where the first Pennsylvanian Declinognathodus appear. Single specimens of the Mississippian conodonts were found a little above the Mid-Carboniferous boundary. The La Lastra as the other deep water sections contains the first representatives of the Declinognathodus noduliferus group of species with ridged margins but not yet nodular as occur in the shallower water areas. Later on they are supposed to have given rise to the nodular forms. Gnathodus girtyi simplex was not found. The sequence mentioned above supports the idea of the origin of Declinognathodus noduliferus group of species from the Gnathodus bilineatus group in Eurasia.

The Mississippian (Serpukhovian) part of the Barcaliente Formation is generally dominated by the *Gnathodus bilineatus* group of species. *Lochriea* species are common as well. The first early Pennsylvanian conodonts of the *Declinognathodus noduliferus* group were recorded in the deepest water part of the section. Above the Mid-Carboniferous boundary upwards the section in the uppermost part of the Barcaliente Formation the conodont yield increases with the appearance of the *Idiognathoides* species: *Id. asiaticus, I. sinuatus, Id. sulcatus* and *Id. macer.* Still higher in the section *Neolochriea glaber* occurs.

Six conodont zones were distinguished in the Barcaliente Formation: three of them in the Serpukhovain part and three in the lowermost Bashkirian. The Serpukhovian Stage is subdivided into the Lochriea ziegleri Zone, Gnathodus truyolsi Zone and Gnathodus postbilineatus Zone. The lowermost Bashkirian consists of the Declinognathodus praenoduliferus Zone, D. noduliferus Zone and the Idiognathoides sinuatus Zone. The correlation of the Serpukhovian at the La Lastra section to the other areas of Eurasia by conodonts is not difficult as the majority of conodont species are the same as well as their distribution pattern. The Bashkirian part of the Barcaliente Formation is best correlated to the deep water sections of the Tienshan Mountains, Uzbekistan, and the Cantabrian Mountains. In the shallower water areas the distribution pattern of conodonts differs. The conodonts of the Declinognathodus group of species span the interval of whole Homoceras Zone, and the species of Idiognathoides are known to appear there with the Reticuloceras transgression, so they join the Declinognathodus species later during the Reticuloceras time. Declinognathodus praenoduliferus Zone was not distinguished there. But if to compare the upper part of the Barcaliente Formation of the La Lastra section with the deep water ammonoidbearing Aksu section of South Tienshan, which yields an almost identical fauna, so all three the earliest Pennsylvanian conodont zones at La Lastra are supposed to correspond to the lower half of the *Homoceras* Ammonoid Zone. In shallow water sections the third zone – *Idiognathoides sinuatus* is known to belong to the *Reticuloceras* Ammonoid Zone. As the upper conodont-bearing beds of the Barcaliente Formation (above the Mid-Carboniferous boundary) are shallower and include *Neolochriea glaber* together with the *Idiognathoides* species the age of these beds could be extended but there is no data to prove that it could be younger than the *Homoceras* Ammonoid Zone

## Distribution of *Hindeodus wordensis* Wardlaw, 2000 in space and time

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The conodont species Hindeodus excavatus Behnken and Hindeodus wordensis Wardlaw have been used to correlate units in Oman with the Middle Permian stratotype sections in West Texas. The distinctive apparatus of Hindeodus excavatus was described by Behnken as Ellisonia excavata (1975) and is associated with a  $P_1$  element referred to *H. permicus* by Igo (1981). The lateral profile of the P<sub>1</sub> element is typically triangular in shape and all denticles point upward. According to the tables provided by Wardlaw (2000) this species appears earlier than H. wordensis and is apparently restricted to the Roadian of West Texas. Hindeodus wordensis was originally described as H. excavatus in Wardlaw and Collinson (1984, 1986), but Wardlaw (2000) named a new species because the name was preoccupied. Hindeodus wordensis has a distinctive apparatus with a P<sub>1</sub> element that is more rectangular in lateral profile and with posterior denticles are directed posteriorly. According to the tables provided by Wardlaw (2000) this species is long-ranging from mid-Roadian to earliest Capitanian in West Texas; as such, it is not exclusively diagnostic of only the Wordian as often suggested, but certainly typical of much of the Guadalupian.

In the Khuff Formation of Interior Oman, Hindeodus excavatus Behnken and Hindeodus wordensis Wardlaw along with Merrillina praedivergens Kozur and Mostler and Sweetina sp. were found associated with ammonoids, ostracods, foraminifers, bivalves, corals and brachiopods suggesting a Wordian age and a shallow water environment (Angiolini et al., 1998, 2003a, 2003b). A few specimens of Hindeodus excavatus and H. wordensis were also found in the lower part of the shallow water Saiq Formation (Saiq A2) of the Oman Mountains at Wadi Sathan section (Baud et al., 2001) and recently with the same range at the Saiq Plateau section. Both Hindeodus have also been founded on slope deposits of the lower Magam Formation (Magam A2) associated with Roadian ammonoids (L. Krystyn, oral communication) at Wadi Maqam (Sumeni nappe, NW Oman). Within the deep water of the Hawasina nappes at Wadi Wasit, Hindeodus wordensis is present in the lower part of the Al Jil Formations along with Iranognathus sp. and gondolellids suggesting Roadian to Wordian ages. Rare Hindeodus wordensis occurs in the red ammonoid limestones of the Rustag section. These conodont assemblages are similar to those described from North America (Wardlaw and Collinson 1984, 1986; Wardlaw 2000) and from the Salt Range, Pakistan (Wardlaw and Pogue, 1995). Recently the species Hindeodus wordensis has been found also in the lower Pamuçak Formation of the Curuk Dag section (Antalya nappes, SW Turkey). In South Tunisia, Jebel Tebaga de Medenine (Angiolini et al., 2008), in the Halq Jemel section the only conodont species found is Sweetognathus iranicus hanzhongensis (Wang). It occurs together with brachiopods and fusulinids (Chusenella rabatei Skinner and Wilde and Dunbarula ex gr. nana Kochansky-Devidé and Ramovs). Sweetognathus iranicus hanzhongensis, described from the Equatorial Warm Water Province (Mei et al., 2002), is a quite long-ranging conodont species spanning lower Roadian to middle Capitanian (Guadalupian), whereas the FAD of the fusulinid Dunbarula ex gr. nana is lower Midian that correlates with the upper Wordian and thus it matches the H. wordensis occurrence and allows the correlations of the Tethyan Scale with the Standard one. According to Angiolini et al. (1998, 2003a, 2003b) and Jan et al. (submitted), the distribution of marine bioprovinces and paleoflora during the mid- Permian along the northern Gondwana margin is consistent with the surface ocean-circulation pattern proposed by Archbold (1998) and the paleogeographic setting of Muttoni et al. (in press) and this may also explain the distribution of Hindeodus wordensis.

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## A brief history of Triassic conodonts and their role in time scale definition

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The role of conodonts in the formulation of a Triassic Time Scale is reviewed with emphasis on stage boundaries and GSSPs. The base Triassic (Induan), a time of rapid speciation rather than extinction for conodonts, is defined by the appearance of Hindeodus parvus, which developed from H. praeparvus; a parallel zonation is provided by Neogondolella species. For the Induan-Olenekian boundary (IOB), the appearance of Neospathodus (=?Novispathodus) waageni within a plexus of similar species is favoured as the defining index. The IOB was a time of extraordinary evolutionary radiation, unrivalled since the Late Devonian, with many new conodont taxa and apparatuses appearing without clear ancestry; the Smithian-Spathian boundary (mid Olenekian) is marked by an equally impressive extinction. The base of the Middle Triassic Anisian stage lies close to the appearance of Chiosella, with Triassospathodus and Spathicuspus characterizing the late Olenekian, and Gladigondolella tethydis and Nicoraella confined to the Anisian. The Anisian-Ladinian boundary is defined by an ammonoid, but the early development of Budurovignathus species provide a proxy. The basal Carnian, also defined by an ammonoid, lies close to first Metapolygnathus, including M. polygnathiformis and M. tadpole. The Carnian-Norian boundary is characterized by continuous faunal turnover featuring many new taxa, the succession of which is superbly displayed in British Columbia., where the favoured boundary is marked by an abundance of the M. primitius and M. echinatus groups. The Norian-Rhaetian boundary is likely to be based on evolution in Misikella in Europe, with concurrent changes recognized in North American 'Epigondolella'.

#### **Editor's note:**

The senior editor recognizes the PTB interval Gondolleids as *Clarkina*, not *Neogondolella*.

Conodonts, dacryoconarids, magnetic susceptibility, and placement of the Eifelian-Givetian Boundary in the Marcellus Shale of the lower Hamilton Group, Appalachian Basin, western New York State

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The Eifelian-Givetian (E-G) boundary, associated with the globally recognized Kačák-otamari events, is defined by the first occurrence of the conodont Polygnathus hemiansatus Bultynck; this horizon at the global section and stratigraphic point at Jebel Mech Irdane, Morocco, is above a black shale interval (otamarishale) and the Late Eifelian Magnetic Susceptibility Event. In western New York three widespread black shales occur in the Marcellus subgroup close to the E-G boundary. In the absence of Polygnathus hemiansatus the boundary is resolved to be between the Cherry Valley Member, which is assigned to the kockelianus Zone based on the occurrence of the nominative taxon, and below the Dave Elliot and Halihan Hill beds, 2 m higher in the Genesee River Valley, which have yielded the conodonts Icriodus angustus Stewart and Sweet, I. stephensoni Sparling, Polygnathus aff. P. robusticostatus Bischoff and Ziegler, and a species of Tortodus? - a fauna similar to that known from the Delaware Limestone and the upper Dundee Limestone in Ohio, Michigan, and Ontario which are associated with a Hamilton Group brachiopod fauna and goniatites that are considered Givetian. Polygnathus pseudofoliatus ranges through the boundary interval, recovered from the Cherry Valley Member, and the lower Chittenango Member above the Halihan Hill Bed. An abrupt and significant rise in magnetic susceptibility (MS) values from 1.5E-8 to 5E-8 m<sup>3</sup>/kg 40 cm above the base of the East Berne Member (top of the Cherry Valley) and before the brachiopod/conodont bearing beds, is similar to the MS shift measured in Morocco at the GSSP and other localities in Morocco and Europe. The E-G boundary is provi-

sionally placed where this shift stabilizes above the Cherry Valley Member within the black shale of the lower East Berne Member. The dacryoconarid *Nowakia* (*Dmitriella*) *sulcata postsulcata*? Alberti = *Nowakia halihanensis* n. sp.( Lindemann, submitted) recovered from the Halihan Hill Bed in the lower Chittenango Shale Member at Oatka Creek may serve as an additional indicator of lower Givetian strata.

## Conodonts and correlation of the Woodford Shale, Upper Devonian-Lower Carboniferous, in the subsurface of western New Mexico and western Texas

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The Woodford Shale in the type area of southern Oklahoma consists of approximately 75 m of predominately dark organicrich shale, as well as light shale, bedded chert, and interbedded phosphate-rich strata that lie unconformably on Middle Devonian or older units. The Woodford includes strata of Upper Frasnian, Famennian, and lower Carboniferous. In the subsurface of west Texas and eastern New Mexico the Devonian light and black shales assigned to the Woodford lie unconformably on Silurian or Lower Devonian carbonates, reaching a thickness of 120 m in Pecos County. Although Middle Devonian and lowest Frasnian deposition is indicated by conodonts recovered from cavity fills in the underlying carbonates and a thin basal green-grey shale, typical Woodford rocks in seven cores in the study area, from Chaves County NM to Howard County TX, consist of 4 to 20 m of Famennian strata that starts in the Upper crepida Zone, indicated by the conodonts Palmatolepis glabra unca, Pa. lobicornis, and Ancyrognathus bifurcatus, that is coincident with a global rise in sea level and deposition of other black shale units in the central and eastern United States, and ranges into the Upper marginifera Zone, indicated by the occurrence of Pa. perlobata maxima. The Lower marginifera Zone strata interval, indicated by the occurrence of Pa. distorta, Pa. inflexa, and Pa. inflexoidea correlates across 350 km of the Upper Devonian basin. A well in Glasscock County TX did not have lower Famennian Woodford, but preserves high Famennian strata of the Middle expansa Zone or higher, indicated by Bispathodus aculeatus aculeatus, as well as lower Carboniferous strata of the Upper duplicata Zone or higher based on the occurrence of Siphonodella cooperi. The Middle expansa Zone is characterized by deposition of another wide spread black shale interval in the eastern United States.

## Ontogenic Development of the Middle Triassic *Pseudofurnishius murcianus* (Van den Boogaard) and Reorientation of its P<sub>1</sub> element

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*Pseudofurnishius murcianus* is the most characteristic species in the Sephardic Province (Southern Tethys realm) during the Middle Triassic. It is also the dominant species in the Iberian Peninsula, sometimes entirely monospecific. Our material encompasses about 1500 specimens, in which the inner platform of the  $P_1$  element is very different from other contemporaneous species. In the reconstruction of the different stages of its ontogenic development, the earliest stage consists of a blade with 5 denticles and an insolated denticle in the inner side of the unit. Growth takes place by adding denticles to the blade and inner side that develops a discrete platform. In many elements (but no all) one or more denticles may be also present on the external side, which in the most advanced specimens develops into an outer platform.

Diebel (1956) was the first to illustrate the  $P_1$  element of *P. murcianus*, under the generic name *Spathognathodus* sp. But it was **Van den Boogaard (1966) who established the genus and spe**cies *Pseudofurnishius murcianus*. While, as in other conodont species, the denticles of the blade are inclined towards the anterior part, Van den Boogaard oriented the unit in the opposite direction. Comparing the ontogenic development of *P. murcianus* and *Sephardiella mungoensis*, along with the study of several clusters figured in the literature (Ramovs, 1977 and 1978 and Krivic and Stojanovic, 1978), we propose herein the reorientation of the  $P_1$  element.

The study of the ontogenic development of *Pseudofurnishius murcianus* (Plasencia, 2009) also leads to the recognition of the large variation within the species in space and time.

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## Conodont tooth complexity: quantification, convergence with mammals, and implications for dietary analysis

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That the shapes of conodont elements resemble the shapes of teeth in other vertebrates has long been known (*e.g.* Jeppsson 1971; Jeppsson 1979), and more recent work has explicitly stated that the morphology and interpenetrative occlusion of  $P_1$  elements from ozarkodinin conodonts was mammal-like in its complexity (Purnell 1995; Donoghue and Purnell 1999). Yet subjective assessments of general resemblance of this sort are scientifically unsatisfactory and are always open to dispute based on nothing more than differences of opinion. The degree to which conodont element morphology and complexity might resemble the teeth of mammals is hard to evaluate rigorously in the absence of homologous points of comparison. This is not surprising given the hundreds of millions of years of independent evolution that separates mammals from ozarkodinin conodonts.

New methods for routine acquisition of high-resolution threedimensional surface data from conodont elements, combined with new analytical protocols developed for investigating mammal tooth shape, are now allowing us to formulate robust answers to questions of complexity and convergence. Surface data for conodont elements from across the range of morphologically complex taxa assigned to the Priniodontida (taxonomy and taxon sampling based on Donoghue et al. 2008) were acquired using an Alicona Infinite Focus microscope. These data were then analysed using homology-free techniques developed for the measurement the phenotypic complexity of three-dimensional tooth shape in mammals (Evans et al. 2007), providing a metric that is directly comparable between taxa irrespective of homology and phylogenetic distance. The results of this analysis are, in some respects, unsurprising. Morphologically simple P<sub>1</sub> elements, such as those of *Plectodina* and Phragmodus, have lower complexity values than those with more intricate morphology and/or well-developed interpenetrative occlusion, such as Idiognathodus and Gondolella. More interestingly, the highest levels of morphological complexity in conodont P<sub>1</sub> elements are very close to the most complex mammal teeth, and allow levels of convergence to be quantified for the first time. Further interest arises from the close correlation between tooth complexity and diet. Complexity in mammals increases along a trophic gradient from carnivores, through omnivores, to herbivores (Evans et al. 2007); it would be premature to suggest that conodonts with the most complex elements were herbivorous, but differences in conodont complexity may prove useful as a proxy for differences in diet.

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## Conodont biostratigraphy of the Naqing (Nashui) section in South China: candidate GSSPs for both the Serpukhovian and Moscovian Stages

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In the Carboniferous, the endemism of biota, the strong glacialeustatic control over sedimentation and consequent widespread disconformities hamper the selection of acceptable GSSPs for the Carboniferous stages, including the Serpukhovian, Moscovian, Kasimovian and Gzhelian. Those relatively deeper-water, carbonate-slope and basinal sections can be served as potential candidate sections for GSSPs. The Naqing Section, which was formerly named as the Nashui section in Luosu, Luodian, Guizhou Province, South China, is such a slope facies section. More detailed biostratigraphy of both foraminifers and conodonts, mainly for the two GSSPs for the Serpukhovian Stage and Moscovian Stage, have been carried out in the last year. The sedimentary studies for the two stages have also been carried through with centimetre sampling.

Very abundant conodonts are found from both the Visean-Serpukhovian (V/S) boundary interval (28 species, including 1 new species, representing 6 genera) and the Bashkirian-Moscovian (B/M) boundary interval (31 species representing 9 genera). Three conodont zones occur at Naqing in the V/S boundary interval including, in ascending order, Gnathodus bilineatus, Lochriea nodosa and Lochriea ziegleri zones in an approximately 20 m interval. It is proposed herein that the FAD of L. ziegleri from the evolutionary lineage L. nodosa-L. ziegleri at 60.60 m above the base of the Naqing section could serve as the best marker for the base of the Serpukhovian. Four conodont zones are found in the Bashkirian-Moscovian boundary interval, in ascending order, the Streptognathodus expansus, Diplognathodus colouradoensis, Diplognathodus ellesmerensis and Gondolella donbassica-G. clarki zones in an approximately 15 m interval. We tentatively propose a new definition for the base of the Moscovian Stage, which is the FAD of Diplognathodus ellesmerensis from the conodont lineage Diplognathodus colouradoensis-D. ellesmerensis at 173.00 m above the base of the Naqing section in South China. This boundary approximately coincides with the entry of the fusulinid Profusulinella, making it easier for a global correlation.

More detailed foraminifer biostratigraphy and sedimentary research in the Naqing section are underway. A comparable section is the Yashui section. It is a shallow water facies and is about 50 km north of the Naqing Section that was selected to be studied in order to establish a correlation to the slope facies. The Yashui section contains abundant foraminifers and rugose corals among which the foraminifer *Neoarchaediscus postrugosus* is important because its first appearance marks the base of the Serpukhovian Stage in its type section in Zaborye Quarry, Moscow Basin, Russia. The successions of foraminifers and rugose corals will be taken out in the near future.

Keywords: conodont, Serpukhovian, Moscovian, candidate GSSPs, Naqing section in South China

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## Conodont faunas from the Durness Group, NW Scotland: determining the sequence stratigraphic history of a fragment of the Laurentian passive margin.

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The Durness Group of northwest Scotland represents a kilometre-thick succession of middle Cambrian to lower Middle Ordovician carbonates. Cambro-Ordovician rocks crop out in a narrow belt along the Caledonian foreland and within the Moine Thrust zone, stretching some 170 km from Loch Eriboll southwestwards to the Isle of Skye. The Cambro-Ordovician sediments in northwest Scotland represent deposition on a paleo-southeast facing, low latitude, passively subsiding continental margin. During this time Laurentia moved very little and Scotland was situated at around 25 degrees south.

Conodonts from the Durness Group have received little attention in comparison to sections in western Newfoundland and East Greenland. Conodonts were described from the uppermost formation (Durine) of the Durness Group by Higgins (1967) and the Cambrian-Ordovician boundary section (equating to the Eilean Dubh and Sailmhor formation boundary) was studied by Huselbee and Thomas (1998). However, conodonts from the intervening 580 m of carbonate strata have not been studied. Macrofossils are rare within the Durness Group and are principally restricted to the Croisaphuill Formation. Taxa suitable for biostratigraphic dating comprise three known trilobite specimens and poorly preserved cephalopods in museum collections. Conodonts are therefore crucial in developing a biostratigraphic framework for the Durness Group. Following detailed sedimentary logging and sampling for conodonts, the thicknesses of the subdivisions of the Durness Group are revised and the Sauk Megasequence and its subdivisions are recognized within the Scottish succession for the first time. Previously held views of stratigraphic breaks within the sequence (Palmer *et al.*, 1981) are now shown to be not of the duration or statigraphical positions suggested. The increased biostratigraphic resolution allows good correlation with Laurentian shallow water conodont zones.

The Sauk II and III supersequences are well represented by carbonates of the Durness Group and within these, a number of smaller sequences (interpreted as third-order) can be identified. The top of the Sauk sequence is not observed due to truncation of the section by Scandian thrusting. Conodonts show that the preserved top of the Durness Group lies within the *Histiodella altifrons* zone (Whiterockian) and corresponds to the Floian stage of the Middle Ordovician.

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## First finds of Changhsingian conodonts (late Permian) in radiolarites from northern Thailand: paleogeographic and paleoecologic implications

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The geology of northern Thailand is presently a fashionable subject, particularly to understand the paleogeography of Southeast Asia: timing of collisions, location of suture zones, etc. Therefore, during the last decades, geological and paleontological data have been accumulated in this region. Understanding stratigraphy is fundamental to elucidate the tectonics of the region. In this way, looking at the distribution and geological age of pelagic sediments is a clue for understanding the spatial extent and time of opening/ closure of the Paleo-Tethys Ocean. That is why this work is a part of a general study regarding the distribution and paleontological content of radiolarites in northern Thailand. Radiolarians content has been described by N. Wonganan (*e.g.* Wonganan *et al.* 2007). Conodonts were found simultaneously in some samples, which is of interest facilitating stratigraphical correlation of data between these two faunal groups. Conodonts have been already presented in the Chiang Dao area (Randon *et al.*, 2006). Here are presented the conodonts results from the Mae Sariang area, south of Mae Hong Son province.

From Mae Sariang sections, even if conodonts were found in several radiolarites samples, only a few samples have yielded significant conodonts. Less than 30  $P_1$  conodonts elements were discovered. All of these  $P_1$  elements belong to the species *Neogondolella changxingensis changxingensis* WANG and WANG 1981. They indicate a Changhsingian age for the studied sections. *Neogondolella changxingensis changxingensis* have been found previously mainly in the northern part (South China) and south-western part of the Paleo-Tethys (Iran, Tibet and Sicily).

These  $P_1$  elements are characteristic of the earlier ontogenetic stages of the species, confirming that the size reduction observed in the pelagic radiolarites of Devonian and Carboniferous age (Randon *et al.*, 2006) is also present in the Late Permian.

The presence of these Changhsingian conodonts in radiolarites confirms the still opening of the Paleo-Tethys in the Late Permian times in the Mae Sariang area and the relative close position of the SE Asian terranes at that time. It provides new information for the understanding of the SE Asia paleogeography. Moreover, conodont ages dating in radiolarites confirm and/or add precision to the data obtained from radiolarians. It is therefore essential to continue conodont studies in radiolarites.

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#### **Editor's note:**

The species *changxingensis* should be assigned to the genus *Clarkina*.

## The nektonic life of *Epigondolella praeslovakensis* and *Mockina slovakensis* conodont-animals: surface water dwellers of peritidal to basinal environments

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During Late Carnian to Norian time (Late Triassic), a wide peritidal carbonate platform called Dolomia Principale, occupied the western margin of Tethys, bordered to NE by the Slovenian (or Tolmino) Basin (De Zanche *et al.*, 2003). During the early rifting stage of the Tethys, the Dolomia Principale carbonate platform was dissected due to syndepositional transtensional tectonic activity. As a consequence, several intraplatform basins oriented NNE-SSW, site of dysoxic to anoxic environments, developed in the Dolomia Principale. Among them, the Aralalta Basins; the Dolomia di Forni Basins; the Seefeld Basins in Austria; and the Rezi Dolomite Formation in Hungary.

These intraplatform basins yielded abundant flora and fauna associations, such as pterodactyls, fishes, crustaceans and plants of Coniferales and ?Bennettitales. Also a very rich oligospecific conodont fauna has been collected from the anoxic basins (e.g. Roghi et al., 1995), consisting of the only two species Epigondolella praeslovakensis and Mockina slovakensis, the phylogenetic relationship of which has been recently described by Moix et al. (2007). Besides being distinctive of the Norian intraplatform basins, these conodont species are also common in pelagic sediments deposited in Late Triassic Neotethyan basins such as Lagonegro, Sicanian and Slovakian ones (Bazzucchi et al., 2005; Gullo, 1996; Channel et al., 2003). Because of the co-occurrences of Mockina slovakensis with other biostratigraphic tools (e.g. other conodonts, radiolarians) in open-marine sediments, it has been possible to constrain the occurrences of Epigondolella praeslovakensis and Mockina slovakensis to upper Alaunian and Sevatian (Upper Triassic) respectively (e.g. Gullo, 1996; Bazzucchi et al., 2005;

Moix *et al.*, 2007). Recently, conodont sampling was carried out on a subtidal level of Dolomia Principale, outcropping in Monte Pasubio (North Eastern Italy). In the supratidal stromatolitic portion of the same cycle, a trampled surface with 11 tridactyl and tetradactyl dinosaur footprints have been found. Unexpectedly, two conodont specimens of advanced *Epigondolella praeslovakensis* and *Mockina slovakensis* have been found (Belvedere *et al.*, 2008).

The discovery of Epigondolella praeslovakensis and Mockina slovakensis in the shallow water environment of the Dolomia Principale and their presence both in anoxic intraplatform basins (es. Dolomia di Forni) and pelagic environments enable to interpret these species as sea surface water dwellers, either benthic or nektobenthic or nektonic. In fact, Epigondolella praeslovakensis and Mockina slovakensis animal could have lived as bottom dwellers in the upper slope of the intraplatform basin characterized by the absence of anoxic conditions. However, the concomitant finding of these two species in very open-marine deposits permits to discharge the general idea that conodont-animals used to be nektobenthic since the bottom conditions of shallow-water, upper-slope and open-sea environments are totally different. For this reason, we suggest that Epigondolella praeslovakensis and Mockina slovakensis animals had to be nektonic, active swimmers that could easily live within the upper portion of water column, far from the sea-bottom, according to the subtidal lagoon environment of Dolomia Principale peritidal cycle.

The provenance of these two species might be located in the eastern sector of the Dolomia Principale, represented by the "Rio Resartico organic laminate Unit" that was directly connected to Slovenian Basin, an eastern branch of the Neothetys Ocean. The "Rio Resartico anoxic laminates Unit" yielded several specimens of species *Mockina slovakensis* and it has been thus interpreted as the passageway between the anoxic basins of the Dolomia di Forni and the open ocean, through which the conodont fauna migrated. The spreading of this oligospecific fauna has been probably supported by a concomitant strong marine transgression documented during the late Alunian- early Sevatian (middle-late Norian) (De Zanche *et al.*, 1993).

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## Generic turnovers of Carnian/Norian conodonts: climatic control or competition?

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Pizzo Mondello section (western Sicily, Italy) is a 430 m thick continuous succession of marine cherty limestones, named Calcari con Selce, ranging from Late Carnian to Rhaetian (Nicora *et al.*, 2007), characterized by almost uniform facies and rich in fossils (*e.g.* conodonts, radiolarians, ammonoids, bivalves) and, thus, suitable for detailed phylogenetic and taxonomic studies on conodont populations.

Conodont biostratigraphy around the Carnian/Norian boundary is still problematic due to an inferred provincialism that affects most of the conodont species and to the occurrence of a great number of transitional forms, linked to the fast recovery of conodonts after the Julian/Tuvalian crisis (Carnian, Late Triassic) (Rigo et al., 2007). The lower 144 metres of the succession, Tuvalian to Lacian in age (Carnian-Norian), were sampled in detail for a biostratigraphic and ecological study of five Upper Triassic conodont genera: Paragondolella, Carnepigondolella, Metapolygnathus, Epigondolella, and Norigondolella. After a taxonomic revision of the studied genera, meant to define the most significant morphological features for their classification, a statistical approach was applied to the study of conodont populations. Quantitative curves of the absolute abundances for each genus show potential ecological competition first between Paragondolella-Carnepigondolella and later between Metapolygnathus-Epigondolella (and partially between Epigondolella-Norigondolella). Recognition of morphoclines among species, integrated by a similar ecological behaviour, support the phylogenetic derivation of Norigondolella and Metapolygnathus from Paragondolella and that of Epigondolella from Carnepigondolella. Furthermore, cross checks of the quantitative curves demonstrate the presence of three major assemblage changes: at metre 64.76 (named event T1) Carnepigondolella is replaced by its descendant Epigondolella in a evolutionary step; at metre 80 (event T2) Epigondolella is substituted by the mass occurrence of Metapolygnathus and at

metre 95 (event T3) Metapolygnathus is succeeded by advanced Epigondolellae species and by Norigondolella. In looking for environmental explanations to these biological events, the quantitative curves of the conodont assemblages are compared to coeval  $\delta^{18}O$ and  $\delta^{13}$ C isotopic curves, based on new data from Pizzo Mondello section. The comparison shows a correspondence between higher <sup>13</sup>C/<sup>12</sup>C ratios and event T2 (and partially event T3), but not with T1. This is in accordance with the interpretation of event T1 as an evolutionary turnover, supported by the occurrence of the transitional forms between the genera involved in the turnover (i.e., Carnepigondolella and Epigondolella), and it demonstrates that conodont evolution is not affected by possible environmental changes Instead, a possible influence of environmental conditions on the absolute abundances of all the studied genera is observable: while *Epigondolella* proliferate when seawater  $\delta^{13}$ C ranges between 2.1‰ and 2.5‰, Carnepigondolella proliferate in the range between 1.6‰ and 2.1‰; Metapolygnathus instead appears to be limited to environmental conditions related to higher  $\delta^{13}$ C in seawater when  $\delta^{13}$ C is higher than 2.5‰. We explain this behaviour interpreting the genus Metapolygnathus as an opportunist taxon, exactly as its forerunner, the genus Paragondolella and thus, supporting their phyologenetic relationship

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# Morphological features, possible functions, and evolution of Late Carboniferous idiognathodid $P_1$ elements

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Late Carboniferous  $P_1$  elements that have been traditionally assigned to the genera *Idiognathodus* and *Streptognathodus* comprise a conservative group in terms of platform morphology. Like the closely related older genus *Gnathodus*, and the partially coeval genera *Neognathodus* and *Idiognathoides*, inversion of the basal cavity did not occur, nor did lateral processes develop during their evolutionary history. As a result, modification was limited to the oral surface of the basal cavity of the  $P_1$  element. Asymmetry of  $P_1$  elements was a common, but variable feature. No single trend in  $P_1$  element evolution through the Late Carboniferous is evident, only repetition of morphological features as small clades appeared and disappeared. This repetitive pattern of evolution has lead some workers to reject any hope of species-level taxonomy for these conodonts. We propose that one should attempt to discern which morphological features have functional significance, and that the use of these characters should lead to a stable taxonomy and also will elucidate the evolutionary history of these ubiquitous forms.

Detailed analysis of late Moscovian and early Kasimovian species of *Idiognathodus* has resulted in a system of taxonomy based on characters of functional significance. The use of characters that affect overall surface area and surface roughness of the element are considered of high functional and high taxonomic significance. Changes in the shape of the rostral and caudal lobes are most likely to affect the overall surface area of the platform. Changes in the length of the medial carina and the presence or absence of troughs or grooves are most likely to affect the surface roughness of the platform. Distribution of nodes, transverse ridges, and the characteristics of adcarinal ridges are considered last in this taxonomic hierarchy. Variation of these characters was investigated by scaled-image analysis of platform length, platform width, platform area, rostral lobe length, rostral lobe area, caudal lobe length, and caudal lobe area, as well as the distance from the caudal and rostral margins of the platform to the medial carina. Results from the late Moscovian Lost Branch Formation show distinctive differences in the rostral lobe characters used to distinguish the two species *I. expansus* and *I. swadei*.

The oldest species of *Idiognathodus* possess strong asymmetry in the  $P_1$  elements that was suppressed during most of the Late Carboniferous only to reappear briefly during the late Kasimovian, and then became fully expressed during the late Gzhelian and Early Permian radiation of *Streptognathodus*. Asymmetry is a result of the restriction of variation to features of the oral surface and the need for elements to compensate for sinistral blade behind dextral blade occlusion. In dextral elements of the Kasimovian species *I. magnificus*, the distance from the rostral margin to the medial carina is greater than the same measurement in equivalent-sized sinistral elements. The opposite is true for the distance from the caudal margin to the medial carina. This asymmetry of elements is expressed by shorter rostral lobe lengths and larger caudal lobe area in dextral elements than found in sinistral elements.

A long medial carina and a deep medial trough on the  $P_1$  element may reflect alternate approaches to platform modification. A deep medial trough ("*Streptognathodus*") occurs in the oldest species, disappears during the range of *Idiognathoides*, and then reappears at least three times, once during the Moscovian and twice during the Kasimovian.  $P_1$  elements with a long carina are rare during the Moscovian, during the range of *Neognathodus*, but then appear in *Idiognathodus* during the Kasimovian and again in the Gzhelian. Each time the carina retreated to form a deep medial trough in younger forms. The significant reoccurrence of a long carina and a deep medial groove has not been resolved, but its recurrence suggests either a strong functional aspect or perhaps a developmental constraint on platform morphology. One possible reason for the development of an elongated medial carina relates to a change in surface roughness along the medial axis of

the platform. Elongation of the carina is a positive relief feature to allow increasing contact between the oral surfaces of opposing elements. One possibility for the development of a trough is a negative relief modification that takes advantage of the asymmetry of elements resulting from sinistral behind dextral blade occlusion. The natural offset of elements will allow for increased vertical overlap of opposed oral surfaces, where the margin of one element overlaps into the trough of the opposing element.

Further investigation is needed to determine the validity of these and other potential reasons for these styles of modification.

## Probable presence of old species of *Declinognathodus* in the Mississippian and the correlation with the Mid-Carboniferous boundary in the Cantabrian Mountains (Spain)

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The GSSP of the Mid-Carboniferous boundary (base of the Bashkirian Stage and Pennsylvanian Subsystem) was situated at bed of sample 61B of the Arrow Canyon section, and the first occurrence of Declinognathodus noduliferus sensu lato was considered as the indicative biostratigraphic marker (Lane et al., 1999). However, an accurate correlation with the GSSP boundary depends on the taxonomy accepted for D. noduliferus s. l. Actually, this name includes several taxa with different specific or subspecific status after different authors (D. noduliferus, D. inaequalis, D. lateralis and D. japonicus) as well as two other taxa D. praenoduliferus and D. noduliferus bernesgae described recently. Sanz-López et al. (2006) discussed about the rarity of coeval origin events for six taxa, and on the contrary, stated that a succession of occurrences of different taxa is inferred from sequences of different basins. These authors concluded that a precise identification of the conodont species representing to the first entry of D. noduliferus s.l. at the Arrow Canyon, is necessary in order to achieve a high resolution correlation tool. On the basis of the pictures published by Brenckle et al. (1997), Sanz-López et al. (2006) concluded that the first entry of Declinognathodus at the Arrow Canyon section is the entry of D. inaequalis. In this case, the first occurrence of this taxon should be an accurate indicative for the recognition of the Mid-Carboniferous boundary, and the sequence of first occurrences of other taxa of Declinognathodus can be useful in the correlation of beds close to it.

Declinognathodus occurs in the black argillaceous limestones of Barcaliente Formation deposited on foreland platform in the Cantabrian Mountains (north of Spain). Méndez and Menéndez-Álvarez (1985), and Menéndez-Álvarez (1991) reported the first occurrence of Declinognathodus species and, above it, the first occurrence of Idiognathoides elements in the upper part of the Barcaliente Formation in several sections of the Cantabrian Mountains. These authors considered the entry of both genera as indicative of the earliest Bashkirian and Kinderscoutian beds respectively. Recently, Nemyrovska et al. (2008) have accurately located the entry of *D. inaequalis* together with *D. praenoduliferus* and *D. noduliferus* bernesgae at the La Lastra section. This occurs 68 m above the base of the Barcaliente Formation, and ten and twelve metres below the first occurrences of *Idiognathoides* and *I. sinuatus*, respectively, presumably in the upper part of the Barcaliente Formation.

However, the older findings of *D. noduliferus bernesgae* are in the first ten metres above the base of the Barcaliente Formation at the Barcaliente and Millaró sections (Sanz-López *et al.*, 2006; Blanco-Ferrera and Sanz-López, 2008). This is in agreement with the presence of *D. n. bernesgae* and *D. praenoduliferus* in the lower beds of the formation in other two localities of the Cantabrian Mountains (Figares and Bandujo in Sanz-López *et al.*, 2006). Furthermore, the specimen assigned by Higgins (1962) to *Cavusgnathus noduliferus* housed in the British National History Museum is, in fact, *D. n. bernesgae*. Since Higgins (1962) reported this fossil from the top of the formation underlying the Barcaliente Formation at the Getino, it comes from strata equivalent to those registering the earliest occurrences of *Declinognathodus* in the Cantabrian Mountains.

The Barcaliente Formation contains elements of Mississippian taxa such as *Gnathodus* and *Lochriea* that disappear in beds with *Declinognathodus*, in the upper part of the unit (Menéndez-Álvarez, 1991; Sanz-López *et al.*, 2006, Nemyrovska *et al.*, 2008). The youngest occurrences of those conodonts are close to the entry of *D. inaequalis* and hence probably close to the Mid-Carboniferous boundary (Nemyrovska *et al.*, 2008). Consequently, the findings of *D. n. bernesgae* and *D. praenoduliferus* in the first ten metres of the Barcaliente Formation should be considered as Mississippian. This age is supported by the finding of two small elements of *Adetognathus* cf. *unicornis* from a bed 6 m above the base that formation at the las Vegas de Sotres. The latter species is abundant in the Chesterian (upper Mississippian) of North America, and occurs below the Mid-Carboniferous boundary at the Arrow Canyon GSSP (Lane *et al.*, 1999).

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## Changes in the species of *Gnathodus* from the upper Tournaisian of the Cantabrian Mountains and Pyrenees (Spain and France)

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The condensed, pelmatozoan limestones of the Baleas Formation (Wagner *et al.*, 1971) in the Cantabrian Mountains and the lowest bioclastic beds of the Aspe-Brousset Formation (Perret, 1993) in the western Pyrenees are located on margins of basins filled by shale and chert in its deeper parts during the upper Tournaisian. Following it and along all studied area, nodular cephalopod bearing limestone ("supragriotte French facies") of the Alba Formation (Comte, 1959; Cantabrian Mountains) and the Aspe-Brousset Formation (Pyrenees) was widely deposited. Carbonates from these formations yielded a lot of conodonts, because stratigraphic successions are condensed. Conodonts are indicative of the standard Lower *typicus* Zone of Lane *et al.* (1980) or *cuneiformis* Zone of Belka (1985) to the standard *texanus* Zone of Lane *et al.* (1980) or *Pseudognathodus homopunctatus* Zone of Perret (1993).

Among the condont genera, the elements  $P_1$  of *Gnathodus* are abundant, because it is known as cosmopolitan genus dwelling preferably in marine deep-water settings. The abundance of  $P_1$  elements allows study of the variation in different species of

that genus in different sections of the Pyrenees and Cantabrian Mountains. Several hypothesis about change in different morphotypes can be discussed on the basis of variation in the morphologies along the sequences: 1) a group of elements corresponds to Protognathodus cordiformis; 2) another group are morphs close to Gnathodus delicatus; 3) there are elements close to G. cuneiformis and G. pseudosemiglaber; 4) G. punctatus includes several different morphologies, some of them probably corresponding to new taxa; 5) another group of morphs are related to G. typicus, 6) while serveral morphs seems to be close to G. semiglaber. The considered morphotypes and new taxa can also be compared with conodonts from beds of Belgium, England, Carnic Alps, Poland, South of China and North America (Sanz-López et al., 2008). The variation observed in different groups show a strong diversification in the upper Tournaisian where elements show trends towards the decreasing on the ornamentation and size of the platform, but increasing on the height and strength of the caudal, ventral parapet. Those trends on the morphology of the elements continued in spite of the sedimentary change to wide drowning platforms in the upper part of the upper Tournaisian. However, local abundance of some morphs occurs, while other ones went on to minor components of conodont faunas and disappeared in the lowermost Viséan.

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## Changes of the apatite overgrowth on the surface of diacaizonal conodonts from the Cantabrian Zone (Spain)

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The Cantabrian Zone is the external zone of the European Variscan belt in NW Spain. It is a mainly non-metamorphic foreland fold and thrust belt. Studies about the Colour Alteration Index of conodonts (CAI), clay minerals (IK) and coal ranks have allowed us to identify areas with very low- or low-grade metamorphism, and several thermal episodes have been distinguished (García-López et al., 2007). Diacaizonal (CAI < 4) or diagenetic conditions are prevailing in a great part of the Cantabrian Zone, and microtextural alterations on the surface of conodonts can be observed. Beautiful radial growths of apatite crystals are present in conodonts from several localities of the Baleas (upper Famennian-lowermost Carboniferous) and Alba (upper Tournaisian-Serpukhovian) formations. Both units are condensed limestones including porous rocks derived occasionally from bioclastic concentrations or from dissolution-seams in which enriched iron oxy-hydroxid grains and seams are common. CAI values range from 1.5 to 3.5.

The studied elements show sugary texture and grey patina. Microtextural alterations of conodont denticles and crystal fields are similar to those described by Helsen (1995), von Bitter and Austin (1984) and Nöth (1998). Fields of subhedral apatite crystals are observed at the oral surface of crowns and on the aboral crimp area of several carminiplanate *Polygnathus*, *Pseudopolygnathus* and primitive *Siphonodella* elements from the Baleas Formation. Blocky and, particularly, columnar crystals on the oral surface of conodonts can form fans diverging from the adcarinal grooves towards the ridges of the ornamented margins. Aboral fans developed on crimp areas show diverging trends from the pit and pseudokeel towards the platform margins. Corrosion is widely present on the crystalline faces, and big holes are mainly developed on the zones of recessive basal margin and basal pit.

Crystal growths on the surface of carminiscaphate platform and ramiform conodonts from the Alba Formation are different to those described above. Basal cavity and grooves can show corrosion of their margins and a filling of big spaced crystals. Oral surface overgrowths vary from small blocky crystals close to the aboral margins, columnar crystal developing towards flat surfaces, long columnar crystals with a fan arrangement in the middle part of the element and on the lateral surfaces and, finally, big hexagonal prisms developed on the denticles.

Grey patina and sugary texture are frequently associated with dolomitization in diagenetic conditions in other areas (Rejebian *et* 

*al.*, 1987, Helsen, 1995, Nöth, 1998; Königshof, 2003). However, Cantabrian conodonts were collected from pure or argillaceous limestones, where only a few rhomboedric dolomite crystals and silicified grains are present. Apatite grains are abundant in these limestones. The variation of the overgrowths observed in the Cantabrian samples show a trend from dissolution in the basal cavity to neoformation of crystals on the oral denticles. We suggest that this dissolution–neocrystallization trend was induced by diagenetic processes, and it seems to be related to the variation on the composition and structure of the hard mineralized tissues along the conodont.

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## Late Devonian conodonts and associated isotope geochemistry from northwestern Thailand.

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An eleven metre vertical section near the town of Mae Sariang, northwestern Thailand, has yielded conodont faunas of late Frasnian to late Famennian age. The section appears to include the Lower and Upper Kellwasser, Enkeberg, and the lower part of the Hangenberg events, as indicated by the conodonts and  $\delta^{13}$ C isotope excursions. The faunas are mostly cosmopolitan but include several new species. The  $\delta^{18}$ O isotope data are unreliable because of diagenetic overprint.

The 80 conodont faunas suggest the presence of the Late *rhenana*, *linguiformis*, *triangularis*, *crepida*, *rhomboidea*, *marginifera*, *trachytera*, *postera*, *expansa*, and *praesulcata* zones. The  $\delta^{13}$ C pattern closely resembles the global carbon isotope pattern of Buggisch and Joachimski (2006). In the *linguiformis* Zone the  $\delta^{13}$ C isotope data have values less than 0.9, but there are major positive spikes to between 3.0 and 4.0 during the Late *rhenana* and Early *triangularis* zones. In the succeeding samples the <sup>13</sup>C values fluctuate with a general trend down to about 2.1 but with a positive spike to 3.1 in the Middle *marginifera* Zone and an increase to approximately 2.8 during what is thought to be the lower and middle *praesulcata* zones near the top of the section.

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## Marine Ecotonal Transition and New Age Constraints of Ammonoids within the Dry Mountain Trough, Nevada

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Unique ammonoid faunas have been identified from the Dry Mountain trough (DMT), Nevada, a tectonic basin that developed along the western margin of North America approximately 291 - 285 million years ago (Snyder et al., 2008; 2002; Trexler et al., 2004). The DMT provides a snapshot of ammonoid paleoecology where an ecotone can be clearly defined based on the spatial segregation and presence of boreal (Uraloceras, Prothalassoceras, Metalegoceras), equatorial (Properrinites, Bamyaniceras), cosmopolitan (Crimites, Neocrimites, Agathiceras, Almites), North American (Akmilleria, Stenolobulites) and local endemic (Nevadoceras) forms (Schiappa, 1993; Schiappa et al., 2005). Their distribution and spatial segregation suggest an ecotone that is transitional between boreal and equatorial realms. Two key localities, Portuguese Springs (PS) and Beck Springs (BS), record the same depositional environment yet reflect distinct biological communities. The Portuguese Springs fauna consists of genera that are characteristic of equatorial, warm-water realms along with locally endemic, North American and cosmopolitan forms,

whereas the genera at Beck Springs are characteristic of boreal, cool-water environments along with North American and cosmopolitan forms. These distinct fauna in close proximity suggest the ecotonal boundaries for the basin lies between PS and BS.

An alternative explanation for the ammonoid spatial segregation between PS and BS is that a temporal difference exists. Preliminary results from conodont isotopic Sr analysis support an age difference between the two main ammonoid faunas and therefore a subsequent environmental change within the basin. A single analysis of conodont elements from both the PS and BS ammonoid matrix for their Sr isotopic concentration. The preliminary results from our analyses indicate that the conodonts from PS yield an <sup>87</sup>Sr/<sup>86</sup>Sr ratio value of 0.707769 +/- 21, corresponding to an age of 292.1 +/- 1.0 ma (Middle Sakmarian, Tastubian) according to the Urals calibration curve produced by Schmitz and others (2007). The single conodont analysis from BS indicates an  $^{87}$ Sr/ $^{86}$ Sr value of 0.707647 +/- 11, corresponding to an age of 289.6 +/- 0.3 ma (Early Artinskian, Burtsevian) according to the Urals calibration curve (Schmitz et al., 2007). Further analyses of conodont elements from these localities are necessary to verify these preliminary findings. Conodont elements will also be analyzed for the Neodymium content to estimate seawater temperature fluctuations within the basin to further refine the suspected environmental gradient within the DMT. These new data will provide further constraints on the timing of basin initiation, and a better understanding of environmental conditions and ammonoid migrations into the DMT.

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## Permo-Carboniferous Conodonts and Tuffs: High-Precision Marine Sr Isotope Geochronology

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Stratigraphic sections of the Southern Urals containing abundant and well-preserved fauna for precise biostratigraphic correlation and common instratified volcanic ash beds dated by U-Pb zircon geochronology offer a unique opportunity to constrain a temporally accurate Late Pennsylvanian-Early Permian seawater Sr curve. The 87Sr/86Sr compositions of conodonts from the Usolka and Dalny Tulkas stratigraphic sections were measured by high-precision thermal ionization mass spectrometry following rigorous pretreatment protocols, including ammonium acetate leaching and acetic acid partial dissolution. These data were plotted within an age model calibrated by >15 high-precision U-Pb zircon ash bed ages. The resulting seawater Sr curve shows a significant reduction in data scatter by comparison to earlier curves (Denison et al., 1994; Veizer et al., 1999; Bruckschen et al., 1999; Korte et al., 2006), suggesting that our conodont pre-dissolution treatment was highly effective for retrieving the original seawater Sr signal. The relatively flat Late Moscovian through Early Gzhelian seawater Sr curve of this study is generally consistent with that of Bruckschen et al. (1999). Beginning in the Early Gzhelian, our data define a decreasing trend in <sup>87</sup>Sr/<sup>86</sup>Sr through the base of the Artinskian, consistent with the results of Korte et al. (2006). Unlike earlier curves, our U-Pb zircon age calibrated data do not show any major inflections through the Early Permian. The monotonic nature of the decreasing seawater <sup>87</sup>Sr/86Sr composition across the Permo-Carboniferous transition lends itself to use as a geochronometer. By combining our high precision <sup>87</sup>Sr/<sup>86</sup>Sr measurements and U-Pb age calibration, the resolution of Sr isotope geochronology approaches 0.5 Ma in this interval. This highly resolved seawater <sup>87</sup>Sr/<sup>86</sup>Sr record obtained for the Late Moscovian through Sakmarian will aid in global carbonate chemostratigraphic correlation and contribute to our understanding of the timing of Late Paleozoic glacial and tectonic events.

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## Lopingian (Later Permian) high-resolution conodont biostratigraphic framework in South China and Iran

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South China and Iran are two of the very few places in the world with well-preserved marine Lopingian deposits. Correlation of the Lopingian Series in South China and Iran with its neighbouring Azerbaijan and Armenia has been a controversial issue with a long history. Rostovtsev and Azaryan (1973) proposed the Dorashamian Stage based on the strata containing the ammonoids from the Phisonites Bed to the Paratirolites Bed described by Ruzhentsev and Sarytcheva (1965); they also considered that the Changhsingian of South China proposed by Furnish and Glenister (1970) is equivalent to only the lower part of the Dorashamian. On the contrary, Zhao et al. (1981) and Sheng et al. (1984) studied the ammonoids and conodonts, and stated that the ammonoids in the Dorashamian are correlative with those of the Paratirolite-Shevyrevites Subzone in the lower part of the Changhsingian in South China. Sweet and Mei (1999a, 1999b) updated the Lopingian conodont sequence/zones in Iran and concluded that the Lopingian conodont succession between South China and Iran are correlative. Recently, Kozur (2004, 2005) questioned the completeness of the Changhsingian at Meishan in South China because some Clarkina species, such as C. iranica and C. nodosa, from Iran have not been found in South China. In this report we use a sample-population approach to develop a high resolution biostratigraphic framework for the Lopingian of South China and Iran. Seven Wuchiapingian conodont zones/subzones, including the Clarkina postbitteri postbitteri, C. dukouensis, C. asymmetrica, C. levini, C. guangyuanensis, C. transcaucasia and C. orientalis Zones, and five Changhsingian conodont zones including Clarkina wangi, C. subcarinata, C. changxingensis, C. yini, C. meishanensis Zones in South China are integrated based on our new collections and previously published materials. The high-resolution Lopingian conodont zonation in Iran is closely correlative with its counterpart in South China. However, slightly different evolutionary trends in Clarkina populations existed at the very end of the Changhsingian in Iran and South China. This reflects a geographical cline and/or facies dependence in Clarkina

rather than stratigraphic incompleteness of sections in either Iran or South China.

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## Apparatus reconstruction of *Lanea carlsi* (Spathognathodontidae, Conodonta) and mid-Lochkovian conodont stratigraphy

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The aim of the contribution is: (1.) to suggest reconstruction of apparatus of *Lanea carlsi* – a stratigraphically important member of middle Lochkovian Spathognathodontidae, (2.) to demonstrate stratigraphic significance of this taxon for the Lochkovian subdivision, and, (3.) to discuss its systematic position among known spathognathodontid genera in the Early Devonian.

## The nature and cause of the Great Ordovician Biodiversification Event (GOBE): new ideas and data from conodont paleothermometry

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What factors controlled the relative abundance and diversity of life on Earth and how have they changed through time? The Phanerozoic paleontologic record is marked by a few major shortterm events marking significant increases in biodiversification, but also offset by five mass extinctions. Periods of biodiversification follow the mass extinctions, but commonly represent slow recoveries lasting 5-10 million years. A few major biodiversification events occur that are not tied to a prior extinction event: for example, the Cambrian Explosion (near the base of the Cambrian) and the Great Ordovician Biodiversification Event (GOBE). The former has received much attention and speculation as to its cause. More recently, attempts have been made to better document and explain the GOBE, partly through projects of the International Geological Correlation Program (IGCP). Over the last year, two studies in particular present different analyses with alternative explanations for the initiation of GOBE (Trotter *et al.* 2008 and Servais *et al.* 2009); both will be reviewed in this presentation.

The GOBE is marked by about a five-fold increase in biodiversity. It marks the well-known change from the Cambrian Evolutionary Fauna to the Paleozoic Evolutionary Fauna documented by Sepkoski in several papers some decades ago. That transition appeared to occur over an extended interval, mainly because the Sepkoski data plots were calculated for each Ordovician Stage giving a coarse temporal resolution. The faunal transition occurred in the mid-Ordovician and has been explained by invoking effects of plate tectonics, paleogeography, a superplume event, and sea level change among others (*e.g.* Barnes 2004a, b; Servais *et al.* 2009).

A different approach was taken by Trotter et al. (2008), who established the paleotemperature record for the Ordovician by using oxygen isotopes from conodont microfossils using the ion microprobe SHRIMP II at the Australian National University. We presented a very different global climate record determined by ion microprobe oxygen isotope analyses of Early Ordovician-Silurian conodonts. The traditional view has been that the Ordovician was characterized by a supergreenhouse state with about 16X PAL (Present Atmospheric Level) of CO<sub>2</sub>, but that raised the question of how the terminal Ordovician glaciation could have developed. The new isotopic data show high temperatures for the earliest Ordovician equatorial seas, followed by a steady cooling trend through the Early Ordovician to reach modern equatorial temperatures by the mid-Ordovician, and then sustained throughout the Middle and Late Ordovician. This favourable climate regime not only implies that the isotopic composition of Ordovician seawater was similar to today, but that climate played an overarching role in promoting the unprecedented biodiversity increases that characterized this period. It suggests further that high ocean temperatures, which favoured particular faunal groups and suppressed biodiversity, may have controlled the lower biodiversity levels characteristic of the Cambrian Evolutionary Fauna. We are continuing this isotopic approach with more intensive sampling and through a wider stratigraphic range.

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## Devonian Conodonts from the Tor-Casamanya Synclinorium (Andorra); a preliminary report

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The Tor-Casamanya Synclinorium is an E-W oriented structure located between Andorra and Spain and it is composed of Silurian and Devonian rocks. Previous studies assigned the materials of this Synclinorium to the Sierra Negra Subfacies of the Sur Facies area according to the Dutch geologists. However, neither they, nor subsequent researchers were successful in terms of subdividing the Devonian rocks, either by age or by the lithological units that are recognized elsewhere in the Spanish Central Pyrenees. Main problems arise by the lack of accurate paleontological dating and by the dearth of characterizing stratigraphical units and their chronological arrangement. Due to these problems and because of the interest of this key area in regional geology a joint team from the University of Valencia and the Geological Survey of Spain has started a detailed work on the eastern edge of this synclinorium where a good, but heavily tectonised, section crops out.

Field-work allows recognition of eight stratigraphic units, and their preliminary sampling demonstrates the presence of the three Devonian Series (Lower, Middle and Upper). The lowest biostratigraphic relevant conodont record corresponds to the *Polygnathus linguiformis* group that would indicate an Upper Emsian-Eifelian age. Morphological features of an association composed of *Tortodus* sp. and *Polygnathus* sp. suggest a Givetian age; *Tortodus weddigei* and *T. bultyncki* document the Middle Givetian. *Ancyrodella africana*, *Acd. soluta* transitional to *Acd. rotundiloba*, *Icriodus alternatus* and *Mesotaxis falsiovalis* reveal the Lower Frasnian. *Acd. gigas* is recorded above this association.

Higher up, an association composed of *Ancyrognathus* sp., *Ancyrodella curvata* late form and *Tortodus* sp. indicates an upper Frasnian age.

Various species of *Palmatolepis*, *Icriodus*, *Polygnathus*, *Siphonodella sulcata* and *Protognathodus* sp. denotes the uppermost Famennian, close to the Devonian/Carboniferous Boundary.

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## Thermal Maturation and Burial History of the Lower Paleozoic in the Argentine Precordillera from Conodont Colour Alteration Data

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The Argentine Precordillera, as part of the Cuyania terrane, has been considered as an exotic terrane with a carbonate platform derived from low latitudes in the Early Cambrian, and attached to the proto-Andean margin of Gondwana in the Mid-Late Ordovician, according to most supported hypothesis. Subsequently, the Siluro-Devonian accretion of the Chilenia terrane to its proto-Pacific margin significantly overprinted the previous geologic history, producing a complex deformation and a low-grade metamorphism that affected mostly the Western Precordillera. The tectonic evolution of the Precordillera remained relatively stable until the Andean triggering of the thin-skinned fold and thrust belt. One decisive parameter, hitherto not explored, through which the tectonic history of the Cuyania terrane can be evaluated, is the thermal maturation history of its carbonate platform. Thermal analysis has been conducted in the Precordillera on the basis of previous and new reports of conodont CAI values in association with other published paleothermal data (e.g., illite crystallinity and mineral assemblages). 70 new conodont samples (rock weight = 250 kg), which correspond to about 70 localities and sections of the Precordillera yielded thousands of Cambrian to Silurian conodont elements.

The regional pattern of CAI values displays a rise of paleotemperatures to the west and south of the basin. This configuration shows a gradual and continuous transition from diagenesis to lowgrade metamorphism, which is apparently not controlled by any of the morpho-structural subdivisions of the Precordillera (*i.e.*, Western, Central, or Eastern). According to our results, the lower Paleozoic sedimentary burial played a secondary role in the heating of the Precordillera. Instead, the predominant component was the overloading by thrust sheets, resulting from the Devonian collision of Chilenia.

Conversely, our paleothermometric data from the easternmost exposures of the Precordillera do not show anomalies referable to any of the accretionary events that contributed to the early Paleozoic building of the southern proto-Andean margin of Gondwana. Instead, an Ordovician metamorphic event is recorded by means of conodont paleothermometry in the slope sedimentary sequences of the Western Precordillera. Allochthonous conodonts from reworked deposits of the eastern carbonate platform with CAI 4.5–5 and autochthonous conodonts from the slope facies with CAI 3 allow for constraining the metamorphic age within the *Paltodus deltifer* and *Lenodus variabilis* zones (*i.e.*, *ca.* 480– 465 Ma). The conodont data support an Ordovician instead of an alternative Devonian collision for the Cuyania terrane with the proto-Andean margin of Gondwana, which is consistent with the earlier proposed, but still contentious, microcontinent model. The occurrence of allochthonous and autochthonous conodonts in the slope facies of the Western Precordillera provides a time constraint for the early accretion of the Cuyania terrane and its transition to an evolving foreland mountain system in the Ordovician Period.

The Ordovician sedimentary sequences from the Western Precordillera were penetrated by a series of mafic sills, several metres in thickness, which intruded the sediments early after deposition. Conodont-rich mixed clastic-calcareous turbidites are common in the Ancaucha creek and allow for high resolution biostratigraphy through the sedimentary section. The conodont CAI has been used, together with X-ray diffraction analyses of clay minerals as well as petrography, in order to assess the effects of rapid thermal stress produced by basic intrusive rocks and subsequent regional low-grade metamorphism. The distribution of CAI values defines a thermal aureole of about 2.5 times intrusion thickness that prevailed over the subsequent very low-grade metamorphism. A metasomatic phenomenon at Ancaucha Creek is recorded by CAI values from 4 to 7, particularly restricted to a few layers close to the intrusive bodies, as indicated by conodont textures and rock fabrics. One-dimensional thermal computer simulation conforms to empirical data indicating temperatures higher than 600°C for the contact zone, although it points out slightly narrower thermal aureoles. The clay mineral assemblage of most of the analyzed samples (chlorite, illite, smectite and I/S mixed-layers) is complex and probably derives from several superimposed processes, thus representing non-equilibrium assemblages. In turn, KI values (0.27-0.32) indicate anchizone metamorphism, in agreement with the regional CAI 3 background; consequently, the occurrence of smectite and I/S probably resulted from retrograde diagenesis.

Additionally, the stable isotope studies, the conodont textural alterations and CAI values are not in agreement with heat transport by pervasive fluid migration or heat flow channelized along the thrust planes, which are usually invoked for the lower Permian San Rafael remagnetization. Hence, an alternative remagnetization mechanism should be investigated (*e.g.*, thermal metamorphism, maturation of organic matter, and diagenetic mineral transformations).

The CAI data also suggest that overburden depth varied from ca. 3.6 km in the shelf region of the Eastern Precordillera to *ca.* 12 km in the slope to rise deposits of the Western Precordillera, thus providing constraints for the palinspastic restoration across the orogen. On the other hand, the increase of peak paleotemperatures to the south of the Precordillera is associated with the exposure of deeper crustal levels at that sector, probably related to a significant shortening caused by a stronger collisional effect or, alternatively, a weaker mechanical response of its elastic lithosphere.

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## A mathematical approach to the assessment of the conodont colour alteration index (CAI)

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The conodonts have become a widely used tool in integrated basin analysis and in the exploration of oil and gas because of its coupled use as precise biostratigraphic markers and thermal maturity indicators. When subjected to heat, conodont elements experience progressive and irreversible chemical transformations of the organic matter interspersed with phosphatic lamellae in the crown ultrastructure. Unaltered conodonts present a pale yellow and a smooth surface with silky brightness (CAI 1). Gradually increasing temperature results in successive carbonization processes of conodont elements that outcome in the colour sequence light through dark brown (CAI 1.5-4) to black (CAI 5). Subsequent colour changes towards grey (CAI 6), white (CAI 7) and finally translucent (CAI 8) are consequences of oxidation of organic matter, release of constitutional water and recrystallization. The different CAI stages, which range in temperature from 50 to > 600°C, are directly related to temperature and duration of heating, conforming to the Arrhenius reactions (Epstein et al., 1977; Rejebian et al., 1987). From these pioneer works, much research has been conducted in order to quantify the conodont colour alteration index (CAI), employing electron spin resonance, organic geochemistry, spectral reflectance, and colour image analysis, among other techniques.

The Arrhenius equation is a rather simple, but precise formula for the temperature dependence of the rate constant, therefore, for the rate of chemical reaction. To evaluate this equation a pre-exponential factor, A (which is independent of temperature in the range of temperatures experienced by sedimentary basins), and the activation energy, E, are required. One of the major disadvantages in using the Arrhenius equation to model conodont thermal maturation directly is the selection of suitable values for these kinetic parameters (cf., Snowdon, 1979). Alternatively, the CAI values can be predicted directly from a time-temperature Arrhenius graph (Epstein et al., 1977; Rejebian et al., 1987). However, the application of this plot to complex geological histories is difficult because under natural conditions the heating occurs at variable temperatures, hampering the precise determination of paleotemperatures or geothermal paleogradients from CAI data (cf., García López et al., 2001).

We present a mathematical approach for determining the progress of conodont colour alteration by means of integration of time and temperature, based on the Arrhenius graphs of Epstein *et al.* (1977) and Rejebian *et al.* (1987). Although geochemical alteration of organic matter occurs through a series of complex, competing, parallel and/or successive reactions, the overall process of conodont alteration can be reduced to a series of simple pseudo-first-order reactions, from dominantly carbonization to oxidation of organic matter within the CAI 1.5–6 interval. Using the data from the published Arrhenius plots, we work out from the Arrhenius equation the dependance of the CAI values to temperature and time as:

where T is temperature in Kelvin and t is time expressed in years.

We compared the values of calculated CAI with the data of Epstein *et al.* (1977) and Rejebian *et al.* (1987) and found a standard deviation of only 0.1 up to CAI 6, much lower than the resolution of the visual CAI determination technique and without the need to access to the Arrhenius plot. Our approach is especially amenable to a spreadsheet program. Because maturation effects on the organic material are additive and irreversible, the total maturity for a given stratigraphic level results from the sum of the maturities acquired in each successive time-temperature interval.

The preliminary equation will derive in a definitive form, which will be presented in the final manuscript. The objective is to apply a CAI formula to optimize thermal history models by computing profiles of CAI values with depth and time; thus providing a new tool for quantitative CAI paleothermometric analysis.

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The Conodont Biostratigraphy of Middle Asselian to Early Sakmarian strata of the Fosheim–Hamilton sub-basin, Sverdrup Basin, Canadian Arctic: The retreat and extinction of genus *Streptognathodus* in response to interpreted thermocline shallowing and oceanic cooling.

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The Carboniferous and Permian conodont biostratigraphy and paleoecology of the Sverdrup Basin has been the focus of study for the last 2 decades (Henderson, 1989; Beauchamp and Henderson, 1994; Beatty et al., 2008). Conodonts, as well as ammonoids, fusulinaceans and small foraminifers have been used to both correlate Carboniferous and Permian strata of the Sverdrup Basin around the world and aid in paleoenvironmental analysis.

Recent studies of Asselian and Sakmarian conodonts and rocks of the Sverdrup Basin on west-central Ellesmere Island have suggested modifications to the biostratigraphy proposed by Henderson (1989), including recognition of new species and new correlations with Asselian and Sakmarian stratotype sections in the Urals (Chuvashov et al., 2002; Chernikh, 2006). Newly recognized species include Streptognathodus aff. S. sigmoidalis, S. longissimus, S. verus, Streptognathodus cf. S. fusus and Streptognathodus postfusus. Conodont zones P3, P4 and P5 of Henderson (1989) are proposed to be correlative with the constrictus, fusus and postfusus zones of Chernikh (2006), and are therefore Asselian in age. Sweetognathus aff. S. obliquidentatus, which was previously recognized as New genus A new species B Henderson 1989, was recovered in zone P3 (constrictus). The relative biostratigraphic position of this species is comparable to the Apillapampa Section, Bolivia, where it was recovered 12 metres above the last appearance of Streptognathodus constrictus (Henderson et al., 2009). Conodont zone P6a, although lacking genus Sweetognathus, is proposed to correlate with the Early Sakmarian. This correlation is justified by the recovery of advanced morphotypes of Sweetognathus merrilli in the overlying zone P6b, which is correlated as Early Sakmarian (Mei et al., 2002)

Exinction of genus *Streptognathodus* in the Sverdrup Basin is proposed as coeval with early onset of basinwide oceanographic cooling and transgression (Beauchamp, 1994; Beauchamp and Henderson, 1994), which is here proposed to have initiated during the latest Asselian (zone P5, *postfusus*). Genus *Streptognathodus*, whose biofacies previously corresponded with lithofacies of interpreted warm-water temperature (*chloroforam* allochem association), mid–shelf depositional environment, shifted proximally to inner– shelf and basin marginal lithofacies. This shift occurred during an interpreted shallowing of the warm-water temperatures (and thermocline) from mid– to inner–shelf depths, reinforcing the hypothesis that paleoecological distribution of genus *Streptognathodus* was in part controlled by warm–water temperature (Henderson, 1989). This extinction is likely correlative with the worldwide Permian conodont crisis (Mei and Henderson, 2001) and demise of continental glaciation on Gondwana (Isbell *et al.*, 2003), that resulted in a globally correlative transgression. The preservation of warm–water temperatures within the inner– shelf during this transgression likely allowed migration of genus *Sweetognathus*, of inner shelf, warm water biofacies, from equatorial regions to northwest Pangea (Sverdrup Basin, Ural Region).

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## On the age of *Gallowayinella* (fusulinids) based on conodonts

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The fusulinid genus Gallowayinella is widely distributed in South China. Fusulinid experts Prof. Sheng Jin-zhang and Rui Lin (1980) concluded that "the fusulinid Gallowayinella is a part of Changhsingian, the horizon bearing Gallowayinella is a very stable bed", "Gallowayinella is a zonal fossil for the lower part of the Changhsingian Stage, it is one of the markers for distinguishing the Wuchiapingian and Changhsingian Stages". Rui et al. (1984) subdivided the Changhsingian Stage into two parts: the upper Changhsingian Stage is represented by the Palaeofusulina siensis Subzone, the lower Changhsingian Stage is represented by the Palaeofusulina minima-Gallowayinella Subzone. These two genera, Palaeofusulina and Gallowayinella, are considered by these experts to be diagnostic zonal fossils for the Changhsingian Stage. This conclusion has been accepted by Chinese paleontologists and geologists, many strata bearing Gallowayinella or Palaeofusulina have been assigned to the Changhsingian. Yuan et al. (1993) listed 25 sections bearing Gallowayinella in South China and put all horizons containing Gallowayinella to the early Changhsingian.

Even in 2006, Zhao Bin *et al.* still assigned the Lapuchari Formation in Qinghai and Tibet, bearing *Codonofusiella-Gallowayinella*, to the Upper Changhsingian Stage based on the Sheng *et al.* (1980) conclusions.

Wang Chen-yuan *et al.* (1997) found, at the Qibaoshan section in Shanggao County, Jiangxi, that the strata bearing the *Gallowayinella* is not one "stable" bed; it is "unstable", comprising at least two beds or even more. The upper bed contains conodonts *Clarkina orientalis, Clarkina guangyuanensis, Clarkina deflecta* and *Clarkina demicornis*, belonging to the conodont *Clarkina orientalis* Zone, clearly indicating that this bed should be late Wuchiapingian in age. The lower bed is below the conodont *Clarkina leveni* Zone and ammonoid *Sanyangites* sp, roughly corresponding to the conodonts *Clarkina niuzhuangensis* (= *Clarkina*  *asymmetrica*) Zone. *Gallowayinella* has never been found in the Changhxing Formation at the type locality of the Changhsingian Stage at the Meishan in Zhejiang. The type locality and horizon of *Gallowayinella meitiensis* is in the Meitian district and in the Meitian limestone Member in Hunan. The conodont *Clarkina orientalis* and *C. mediconstricta* co-occur with *Gallowayinella* in the Meitian limestone Member. Therefore, the age of *Gallowayinella* definitely should be Wuchiapiangian rather than Changhsingian.

Because both *Gallowayinella* and *Palaeofusulina* appear as early as the early Wuchiapiangian (*Clarkina niuzhuangensis* Zone)(Wang *et al.*, 1997; Wang and Jin, 2006), these two genera are not diagnostic zonal fossils for the Changhsingian.

The Permian stages have long been defined by fusulinid genus zones, for instance the Palaeofusulina for the Changhsingian Stage and the Codonofusiella Zone for the Wuchiapingian Stage. Such fusulinid zones, from a historical point of view, have played important roles in China's stratigraphic research. However fusulinid genera that were selected as zonal indices of the Permian stages usually have long ranges and distributions that are endemic. Consequently, the zones cannot be clearly and accurately defined. In fact, such generic zones have caused some confusion in stratigraphic correlation. Palaeofusulina actually ranges from the early Wuchiapingian Stage to the late Changhsingian Stage rather than being limited to only the Changhsingian. The range of Gallowayinella is limited in the Wuchiapingian Stage. Chinese Early and Middle Permian stage names were declined by the International Commission on Stratigraphy. These stage names should not be used again. All of the Permian fusulinid genus zones have to be re-examined. Obviously, fusulinids are not suitable for defining the Permian stages. Conodonts are used as the leading fossil group in defining the 9 stages and 3 series of the Permian, as adopted by the International Commission of Stratigraphy. Two main tasks of Permian biostratigraphy research in the future are: (1) the establishment of phylogenetic relationships at the species level within every fusulinid genus; (2) exact correlation of the fusulinid sequence mainly in shallow water facies with the conodont zones mainly in deep water facies. Fusulinid genus zones established in China should not be used again.

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## Evolution of the Late Guadalupian Permian basin of West Texas and its *Jinogondolella* species

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The Permian basin of West Texas was connected to the open ocean by a seaway along the northwestern edge of the Ouachita Orogen. Vestiges of this seaway remain in the rocks of Las Delicias and El Antimonio, Mexico. Las Delicias displays basinal infilling of a tremendous amount of volcano-clastic debris and carbonate reef platform collapse megabreccias along the southern side of the seaway and El Antimonio displays shallow carbonate shelf deposition along the northern side of the seaway.

The Late Guadalupian stratigraphy of the Apache Mountains, central to the Permian basin reveals a gross cyclicity of sedimentary deposition. Each cycle is represented by one-to-several carbonate megabreccias at the base followed by mixed thin to medium bedded limestone, limey siltstone, and siltstone and rarely sandstone. The limestone beds are commonly graded going from fusulinid grainstone to packstone at the base, to radiolarian wackestone to mudstone at the top. Conodonts are common to the middle of each bed, but appear to occur throughout.

The megabreccias do not contain just Capitan reef limestone debris but also include limestone blocks and boulders of previous cycles of deposition. For instance, the megabreccia in one section (EF) contains a large stratigraphically coherent block of strata of the Lamar Limestone Member and a boulder of the Reef Trail Member, representative of the previous two cycles. Deposition of this unit was not simple highstand progradation of reef and mass shedding of reef debris into the basin, but appears to demand a more catastrophic margin collapse as a cause for its deposition.

Confirmation of the rocks involved is based on a new refined integrated biostratigraphy utilizing foraminifers, fusulinids, radiolarians and conodonts developed by bed-by-bed sampling of the entire section. From a single bed in another section (B), 8 cm thick, three different platform elements of *Jinogondolella* along with their entire apparatuses were recovered and provide

a template for the reconstruction of the apparatuses for most of the species of Jinogondolella. Lambert and Wardlaw (2006) and Lambert et al. (2007) also recently attempted the reconstruction of the apparatus of Jinogondolella. The Jinogondolella apparatus is distinguished from Neogondolellid apparatuses (Orchard, 2005) by having dimorphic  $P_2$  elements and polymorphic  $S_2$  elements. The apparatuses for Jinogondolella aserrata and J. postserrata which define the Wordian and Capitanian Stages, respectively, are illustrated. Several new species based on their apparatuses are also illustrated. The new species along with those described recently (Lambert et al., 2002, Nestell et al., 2006) prove useful in identifying each cycle of deposition in the Capitanian., especially a lineage of robust Jinogondolellids typified by Jinogondolella gladirobusta and J. artafrons. The ranges and probable evolution of the recognized species of Jinogondolella are illustrated in Figure 1.



Figure 1. General stratigraphy of the West Texas Permian basin and the ranges of *Jinogondolella* species. *Jinogondolella altudaensis* probably gave rise to *Clarkina* at the end of the Guadalupian (Lambert *et al.*, 2002).

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## Biostratigraphy of the Santa Rosita Formation (Furongian-Lower Ordovician), Cordillera Oriental of Jujuy, Argentina

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The Santa Rosita Formation crops out in the eastern margin of the Cordillera Oriental at the Quebrada de Humahuaca of Jujuy Province, northwestern Argentina, where it is composed of the Tilcara, Casa Colourada, Pico de Halcón, Alfarcito, Rupasca, and Humacha members. The formation overlies the middle-upper Cambrian Mesón Group and underlies upper Cretaceous-lower Paleocene strata of the Salta Group or Neogene-Quaternary sediments. The Santa Rosita Formation in this area is a heterolithic siliciclastic sequence with several transgressive-regressive cycles of open-marine environments and two fluvio-estuarine deposits incised into underlying rocks. This formation that belongs to the lower Santa Victoria Group is, on average, 900 m thick.

The conodonts were recovered from coquinas and calcarenites interbedded in the Alfarcito, Rupasca and Humacha members. 173 kg processed carbonate samples yielded *ca.* 9300 conodont elements. The *Cordylodus intermedius* (*Hirsutodontus simplex* Subzone), *C. lindstromi sensu lato, C. angulatus* and *Paltodus deltifer* conodont zones were identified. The Tilcara, Casa Colourada and Pico de Halcón members are barren of conodonts, despite other sections of the Cordillera Oriental with equivalent units (*e.g.*, Angosto del Moreno) records the *Cordylodus proavus* Zone. *Parabolina frequens argentina* (Kayser) is the most frequent trilobite in anoxic facies of the Casa Colourada Member. The *Cordylodus intermedius* Zone is represented by the hom-

onymous taxon together with the guide conodonts Hirsutodontus simplex (Druce and Jones), Albiconus postcostatus Miller, as well as species of Variabiloconus, Teridontus and Cordylodus. A high amount of proto and paraconodonts, such as Phakelodus, Problematoconites, Prosagittodontus and Westergaardodina was recovered from these facies as it occurs in other Cambrian basins with deeper environments. This assemblage is recorded in the lowermost part of the Alfarcito Member associated with the trilobite Jujuyaspis keideli keideli Kobayashi. This species was largely regarded as a marker of the Cambrian-Ordovician boundary, but the associated conodont fauna indicates a late Cambrian age (Furongian, Stage 10) for its lower record, although it is clear that this taxon continues into the Lower Ordovician (lower Tremadocian). C. aff. lindstromi is present in the C. lindstromi sensu lato Zone with Teridontus gallicus Serpagli et al., Variabiloconus datsonensis (Druce and Jones) and Utahconus n. sp. *Iapetognathus fluctivagus* Nicoll *et al.* was not recovered in the studied succession so far, being the Cambrian-Ordovician boundary tentatively traced at the lower-middle part of the Alfarcito Member, taking into account the most proximate conodont associations. The Cordylodus angulatus Zone is well represented in the upper part of Alfarcito Member including C. angulatus Pander, and species of Acanthodus, Drepanodus, Drepanoistodus, Kallidontus, Rossodus, Semiacontiodus, Teridontus, Utahconus and Variabiloconus. Graptolites, such as Rhabdinopora flabelliformis spp. and Adelograptus sp., were found in different sections of the middle-upper part of the Alfarcito Member, together with trilobites of the Kainella sensu lato Zone. The Paltodus deltifer Zone partly correlates with the Low Diversity Interval of North America; however, an interval with low diversity and high population as it occurs in Laurentia has still not been identified in this biozone. Paltodus deltifer pristinus (Viira) characterizes the eponymous subzone in the Rupasca Member, accompanied by species of Drepanodus, Drepanoistodus, Kallidontus, Teridontus, Utahconus, Variabiloconus, and Phakelodus. The corresponding trilobite zone for this member is the Bienvillia tetragonalis Zone although its upper part remains not well defined. In the Humacha Member and the Coquena Formation, the uppermost part of the Paltodus deltifer Zone is identified including the conodont Acodus n. sp. and species of Drepanodus, Drepanoistodus, Iapetognathus, Kallidontus, Paltodus, Parapanderodus, Protopanderodus, Tropodus, Utahconus, and Variabiloconus. The Acodus deltatus-Paroistodus proteus Zone is recorded in the Parcha-Incamayo area, southern Cordillera Oriental; however, the absence of the guide taxon Paroistodus proteus (Lindström) constrains the conodont fauna of the Humacha section to the latter lower biozone. The graptolites "Adelograptus" cf. altus Williams and Stevens, Aorograptus victoriae (Hall) and Ancoragraptus cf. bulmani (Spjeldnaes) are present in this lithological unit, representing the Aorograptus victoriae Zone. In the lower Humacha Member and the upper part of the Coquena Formation, Notopeltis orthometopa (Harrington) is a frequent trilobite that gives name to the zone.

The composition of the condont fauna reveals a particular mixture of Baltic and Laurentian taxa. The association of these taxa with endemic species characterizes the South Gondwana Province of the Cold Domain in the Shallow-Sea Realm. The Colour Alteration Index (CAI) of the condont elements is about 3, indicating overburden paleotemperatures of 110°-200°C. This value remains the same throughout the formation, except for the uppermost Humacha Member, where the conodonts exhibit a CAI 2, possibly due to its upper position in the column of the Santa Rosita Formation.

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## Refinement of Changhsingian conodonts and zonation from the Xiakou section, western Hubei Province, South China

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The Changhsingian conodont zonation in south China has been rationally discussed by many authors (Wang and Wang, 1981; Mei et al., 1998; Nafi et al., 2006). Because studying sections is restricted in the interior platform, many geographic clines have been ignored. Although the species assemblage reported by Kozur (2004) has some problems in stratigraphic subdivision (Henderson, 2008), recognition of them reminded us to explore available sections that can efficiently express the evolution of conodont faunas and their implication to end-Paleozoic extinction. For this purpose we selected a typical section that formed in the platform marginal environment in the town of Xiakou, western Hubei Province, China to gather all types of conodonts from different paleogeographic provinces. Twenty six species of genus Clarkina and five species of genus Hindeodus were described in detail and their stratigraphic ranges reveal following five standard zones in ascending order.

1) C. wangi Zone overlies the high diversity zone of the uppermost Wuchiapingian Stage, *i.e.* C. longicuspidata – C. prechangxingensis Zone. It is a low diversity zone and is distinguished by the first occurance (FO) of C. wangi (Zhang).

2) *C. subcarinata* Zone is also a low diversity zone and characterized by the FO of *C. subcarinata* (Sweet). Rare specimens of *C. orientalis* and *C. wangi* occur.

3) C. changxingensis – C. deflecta – C. xiangxiensis – C. abadehensis Zone is the high diversity zone and contains 9 new species and 7 evolved species of genus Clarkina. It is recognized

by the FO of *C. cha. changxingensis* (Wang and Wang) and existing new species.

4) *C. yini* Zone is a low diversity zone and is characterized by the FO of *C. cha. yini* (Mei, Zhang and Wardlaw). It also contains moderate number of *C. meishanensis zhangi*, *C. postwangi* and *C. cha. changxingensis*.

5) C. meishanensis – C. hauschkei Zone exhibits diversity reduction upward and expresses an interval between the FO of C. meishanensis meishanensis (Zhang, Lai and Ding) and C. hauschkei Kozur and the FO of Hindeodus parvus (Kozur and Pjatakova). The vertical change of diversity expresses three conodont faunas. The lower is the conodont acme fauna that contains 3 new species and 14 evolved species of the genus Clarkina. The second is a Clarkina-diversity reduced fauna (=C. meishanensis fauna) in which only half of the Clarkina species survive, but Hindeodus appears and begins to diversify; the upper fauna is represented by a diverse and abundant Hindeodus fauna (=H. typicalis fauna).

Conodont evolution through these five zones within the Changhsingian Stage reveals at least two cycles of end-Paleozoic extinction process.

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Keywords: Changhsingian, conodont, zonation, South China

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## Permian cyclic sedimentation of the Johnston Canyon Formation, southwestern Alberta and southeastern British Columbia, Canada

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The Permian Johnston Canyon Formation from southwest Alberta and southeast British Columbia has visible cyclic deposits alternating from phosphatic dolostone to silty shale. The description of facies and the quantification of cycles using a time series analysis helps to determine whether these deposits were influenced by the waxing and waning of late Paleozoic glaciation events, much like the cyclothems of the mid-continent of North America. The magnitude of sea level change exhibited by these cycles was determined by analyzing sediment components such as authigenic phosphate to determine the approximate water depth. The deepest facies interpreted is at a pycnocline, which, in normal marine conditions is 100 m or more. The shallowest facies occurs at or below storm weather wave base, which is at approximately 70 m water depth. This accounts for a sea level change on the order of 30 m.

A spectral analysis (time series analysis) was made possible using the conodont biostratigraphy from the Johnston Canyon Formation correlated with previously identified radiometric ages. The occurrence of *Sweetognathus merrilli* and *S. whitei* were located along both sections. The radiometric ages associated with these biostratigraphic markers permitted the calculation of sedimentation rates, which allowed for the identification of the time frame of cycles. The local first occurrence of the advanced form of *S. merrilli* found in this section (pre- *S. binodosus*) is estimated at 292.7 my (extrapolated from Schmitz *et al.*, 2007) and the base of the *S. whitei* zone (base of Artinskian) is at 290.1 my (Schmitz *et al.*, 2007). Given this information and the thickness of the unit, the sedimentation rate is about 226.1 kyr/m.

Considering the biostratigraphic problem outlined by Henderson *et al.* (this volume), there may be some question as to the validity of the biostratigraphic ages. However, the fact that these species occur within a transgressive sequence, above the major climatic event marked by the end of the Late Paleozoic ice age, indicates that these species properly represent the previously identified boundaries for the Sakmarian and Artinskian.

Based on the sedimentation rates, Milanovitch-scale cycles were identified ( $\sim 400$  kyr and  $\sim 100$  kyr). This indicates that these deposits were probably influenced by glacial eustacy, although the magnitude of these fluctuations was significantly less than the ones recorded in the Pennsylvanian cyclothems of the mid-continent of North America. This enables the term "cyclothem" to also be applied to the Johnston Canyon Formation cycles.

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