

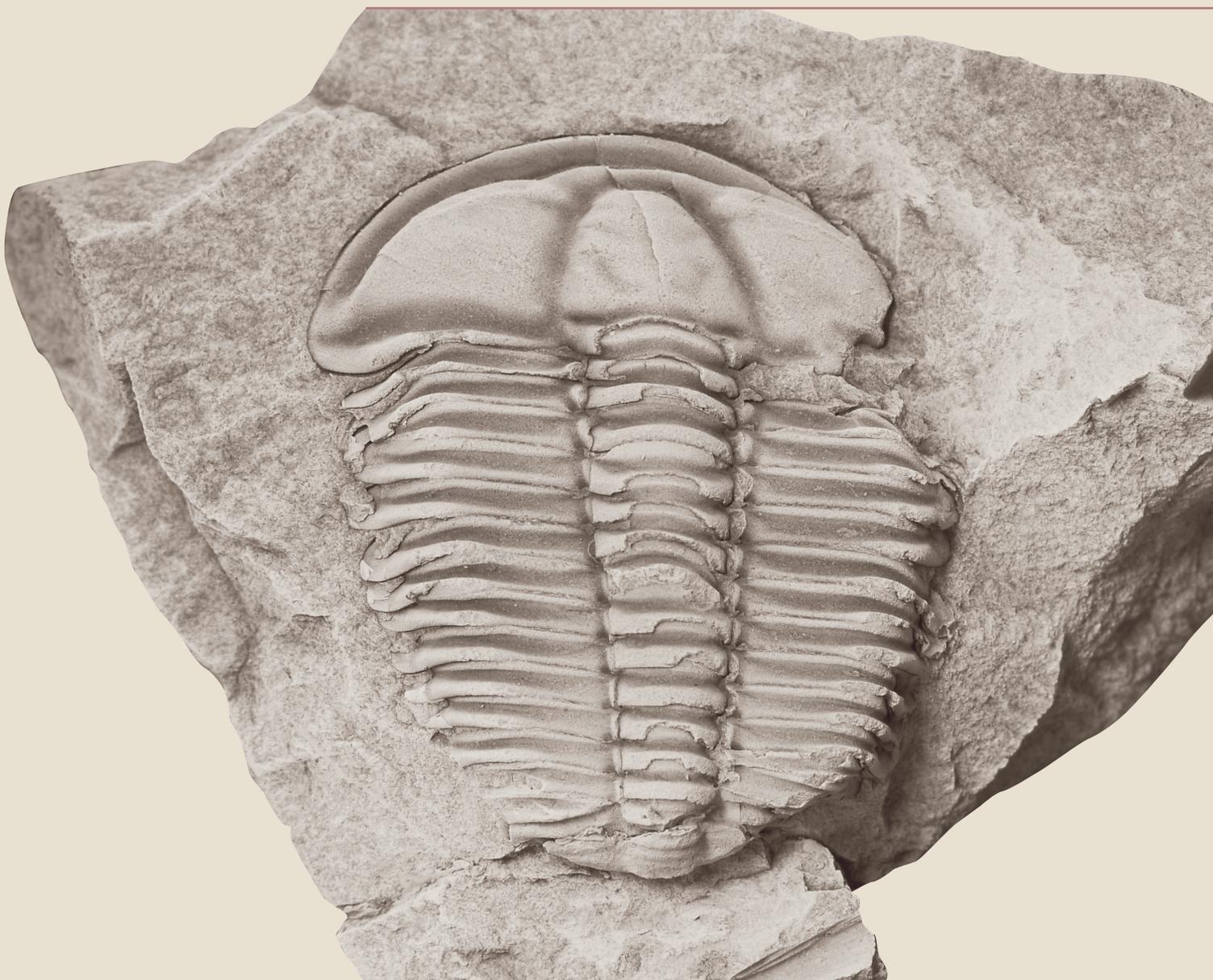


The 5th Conference on Trilobites and their relatives

1st July - 4th July 2012,
Prague, Czech Republic

A B S T R A C T S

Editors: Petr Budil & Oldřich Fatka



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on Trilobites
and their relatives**

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Cover illustration:

Conocoryphe sulzeri sulzeri

(Schlotheim, 1823). Entire specimen

(CGS VV 3) with healed injury

on the right gena. "Middle" Cambrian,

Drumian, Jince Formation,

Paradoxides gracilis Biozone. Locality

Rejkovice-Řešátko. Leg. L. Grigar, 1999.

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Petr Budil & Oldřich Fatka

CZECH GEOLOGICAL SURVEY
& CHARLES UNIVERSITY, PRAGUE



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FOREWORD

Dear colleagues and friends!

It is a great honour for entire Czech palaeontological community to welcome the participants of the 5th Conference on Trilobites and their relatives, held in Prague, Czech Republic on 1st July – 4th July 2012 and in Sardinia, Italy on 5th July – 8th July 2012.

The place for this great international event has been chosen also with respect to more than 240 years of intensive investigation of fossils, namely trilobites, in Bohemia (for review, see Bruthansová et al. 2007).

The oldest note on Bohemian trilobites was published by the Jesuit priest Franz Zeno (1770), who described and figured ‘*Cacadu* – order Käfer – Muschel’ or ‘*Concha triloba*’ and ‘*Echinites*.’ – apparently representatives of *Odontochile* (or *Zlichovaspis*) and *Phacops* (or *Boeckops*). Two, respectively five years later, Ignaz von Born (1772-1775) published a catalogue of his private collection of minerals, rocks, and fossils. In 1775, he described several new trilobite taxa, all of which are now considered invalid. Most probably, they represent the Cambrian species *Paradoxides gracilis* and *Conocoryphe sulzeri* and the Devonian genus *Odontochile*. The first valid trilobite taxon from the Bohemia was published by Brongniart (1822) as *Asaphus Hausmanni* (= *Odontochile hausmanni*). Schlotheim (1823) described two Cambrian species as *Trilobites hoffii* (now *Ellipsocephalus hoffii*) and *Trilobites Sulzeri* (now *Conocoryphe sulzeri*). Kaspar Maria Count Sternberg published important data on trilobite morphology (Sternberg, 1825, 1830, 1833). Cambrian and other trilobites were discussed by Boeck (1827), Emmrich (1839), Zenker (1833) and Beyrich (1845), and some of their species remain valid. Joachim Barrande was an exceptional personality who made a huge impact in understanding of Lower Palaeozoic stratigraphy and palaeontology, including trilobites. All of his studies are characterized by very precise observations, which have stood the test of time both technically and scientifically. Barrande (1846a, b) published his first trilobite studies when he was 47 years old. In 1852, Barrande began the publication of his monumental 22-volume work *Système Silurien du centre de la Bohême*, with two volumes dedicated to trilobites (1852, 1872). The large collections and the original types of Barrande’s *Système Silurien* are stored in the National Museum in Prague. Barrande (1852) was the first to describe trilobite larvae and ontogeny. He suggested a method for numbering growth stages during the meraspid period that is still in use (Chatterton and Speyer, 1997). Barrande (1852) also recognized three of the main types of trilobite enrollment (Harrington, 1959), and was the first to describe the presumed infilling of a trilobite alimentary canal (Whittington, 1997). Two Czech patriots, Ignatz Hawle, a local councilman and avid fossil collector, and August Carl Joseph Corda, a botanist at the National Museum, responded by publishing a monograph on Bohemian trilobites (Hawle and Corda, 1847). Unfortunately, this paper was compiled in great haste, with idealized drawings and numerous inconsistencies in the text. Barrande (1852, 1872) re-described and re-figured many of their species much more precisely. Unfortunately, the highly talented palaeontologist (chiefly a palaeobotanist) Corda died tragically in 1849. He did not have an opportunity to defend his and Hawle’s nomenclature priority over Barrande’s taxa. One of the most talented Czech palaeontologists, Ottomar Pravoslav Novák, was a student and disciple of Barrande. He was also appointed curator of Barrande’s gigantic collection and authorized to continue Barrande’s work on trilobites. After Barrande’s death, Novák (1880, 1884, 1885, 1886) continued the study of trilobites by publishing several papers on hypostoma and on Silurian and Devonian taxa (Novák, 1883, 1890). These papers included excellent, accurate drawings (although not quite comparable with those of Barrande). Unfortunately, his life and scientific activity were cut short when Novák died after a long illness at the age 41 in 1892. After Novák’s death, trilobite study underwent an interruption and crisis, which lasted until the end of the nineteenth century. This situation in palaeontological research continued up to the 1920s, when a slow regeneration started because of intensive research by enthusiasts (e.g., Celda Klouček, Karel Holub) and the young, next generation of professional scientists (e.g., Bedřich Bouček, Jan Koliha). One of Novák’s manuscripts (published in 1918) was arranged and finished for publication by Jaroslav Perner, who was not a trilobite specialist. Several new trilobite species were established in an extensive study by Pompeckj (1895). Other taxa were discussed by Jaekel (1909) and Raymond (1914). Trilobite reports were gradually produced by K. Holub (for example 1908, 1911), Koliha (1922a, b), Klouček (for example 1916), Želízko (for example 1921, 1922), Růžička (1926, 1927), Smetana (1921), and Šuf (1926), but trilobite research underwent another decline after this period. During the World War II and especially afterwards, Ferdinand Prantl and Alois Přibyl, later also Ivo Chlupáč, Ladislav Marek, Milan Šnajdr and Jiří Vaněk, began to publish on trilobites and several other groups of fossils. Trilobite study became more exacting during this period. An emphasis was placed on precise stratigraphic ranges as data



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needed by a new comprehensive geologic mapping of Czechoslovakia as a part of a search for raw materials. In the Barrandian area, the mapping conducted by the State Geological Survey focused on Palaeozoic stratigraphy, and the majority of palaeontologists, including trilobite specialists, participated in this extensive project. Intensive collecting at classic localities and the documentation of numerous new sections and outcrops provided voluminous new material. As a result, trilobite studies re-examined all of the Middle Cambrian–Middle Devonian groups (e.g., monographs by Prantl and Přibyl, 1949a; Šnajdr, 1958a, 1980a; Chlupáč, 1977b; Vaněk, 1959; Pek, 1977; Mergl, 1984). The years 1950–1980 could be designated as a “golden age of trilobite research” in the Barrandian area. The generation starting immediately after the war was active and their students made good use of the opportunity provided by the support to geology given by the official state policy. The decline in geology, including trilobite research, began during the 1980s, when the older generation slowly finished their activities. The attenuation accelerated at the beginning of 1990s, after the death of leading personalities, including Šnajdr (1989), L. Marek (1995), Pek (1999), later also Chlupáč (2002) and Vaněk (2004). After a ten years decline, the new generation of investigators, frequently in co-operation with foreign colleagues, started in teamwork with private, usually highly educated collectors. These new studies are not focussed on the systematics only but especially on diverse aspects of trilobite palaeoecology, taphonomy and ontogeny. Currently, several young, promising colleagues finish their studies in co-operation with foreign colleagues. Trilobites of the Barrandian area have been studied also by numerous foreign specialists (for example Delo, 1935; Kielan 1959; Bruton, 1966, 2008; Shaw, 1995, 2000; Hughes and Chapman, 1995; Hughes et al., 1999; Whittington, 1999, and many others). These researchers had contributed substantially to modern knowledge, and provided a better understanding of relation of Bohemian trilobites to those in other regions.

This Abstract Volume, and the entire conference, is dedicated to the memory of Professor Harry Blackmore Whittington FRS (March 24, 1916 – June 20, 2010).

This Abstract Volume includes contributions of almost one hundred scientists from more than twenty countries. The span of the contributions is also very wide – from the earliest Cambrian trilobites and anomalocaridids up to the Carboniferous trigonotarbids and the Cretaceous cirripeds. We thus believe that the Abstract Volume will be a useful source of information for all specialists focussed on the fossil arthropods and arthropod-related organisms.

Acknowledgment: We would like to express many thanks to all colleagues who helped us to organise the conference. We thank to all co-organisers and members of the scientific committee of the Conference. Namely, we would like to thank especially Dr. David Holloway for his generous help by very careful reviewing the abstracts. All responsibilities for any mistakes and omissions in the Abstract Volume have, however, the editors.

Oldřich Fatka and Petr Budil, editors (for organization committee)

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INVITED LECTURE

The early Ordovician trilobites of the Kirtonryggen Formation, Spitsbergen.

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More than thirty years after the description of the diverse trilobites of the Valhallfonna Formation the fauna of the underlying Kirtonryggen Formation has at last been investigated. This formation spans the Tremadocian to early Floian (Ibexian) stages, and has five successive and different trilobite faunas. All lived in inshore, carbonate habitats, and all were typically palaeotropical Laurentian trilobites, dominated by the bathyurid biofacies. 52 species have been identified, although we are obliged to keep many under open nomenclature because of shortage of material. The Spitsbergen section is important for 'stacking' several faunas that have otherwise been described from scattered Ordovician localities in Greenland, Newfoundland and elsewhere. For the most part, they include species close to other faunas from eastern Laurentia and are less similar to those from the Great Basin, an area that provides the Ibexian standard. The earliest fauna is Stairsian in age, with hystricurids and leiostegiids dominant. Two relatively sparse Tulean faunas follow, including equivalents of the classical "Jeffersonian" faunas. The following fauna with *Petigurus groenlandicus* was described as long ago as 1937 by Christian Poulsen in eastern Greenland, but we can now place it below a rich fauna with *Petigurus nero* that has been found widely to the south in Greenland, Newfoundland and eastern USA. This includes the faunas originally described by Elkanah Billings in 1865. Individual species like *P. nero* and *Punka flabelliformis* are widely distributed providing a reliable species-level biostratigraphy. An interesting aspect of the Kirtonryggen faunas is the occurrence of the earliest known proetid, illaenid, and styginid trilobites, all destined to radiate into many habitats. This provides support for Jablonski's hypothesis that major clades tend to start in inshore environments.



First Furongian (late Cambrian) trilobites from the Cantabrian Zone (northwestern Spain)

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The Spanish record of late Cambrian trilobites is very sparse, being so far restricted to few strata occurring in the Najerilla Formation of the Sierra de la Demanda (Colchen, 1967; Shergold *et al.*, 1983) and from the Valtorres, Valconchán and lowermost Borrachón formations of the western Iberian Chain (Shergold and Sdzuy, 1991, with earlier references). Outside Iberia, Furongian trilobites are also rare, in part due to the existence of major erosive unconformities and diachronic stratigraphic gaps related to the denudation of rift shoulders during a multi-stage rifting, probably connected to the opening of the Rheic Ocean (Alvaro *et al.*, 2007). Nevertheless, Furongian trilobite assemblages do occur in scattered peri-Gondwanan sections from the southern Montagne Noire (SE France: Feist and Courtessole, 1984; Shergold *et al.*, 2000; Alvaro *et al.*, 2001, 2003), SW Sardinia (Italy: Loi *et al.*, 1996), central Anti-Atlas (Morocco: Destombes *et al.*, 1987; Geyer *et al.*, 2002), and central Turkey (Shergold and Sdzuy, 1984).

During excavation of a tunnel for the Cantabrian Highway (A-8) in northern Spain, a thick intercalation of dark shales ('El Fabar Beds': ca. 40 m) was discovered within the La Matosa quartzite member of the Barrios Formation, located in the eastern Asturian domain (Aramburu and García-Ramos, 1993) of the Cantabrian Zone of the Iberian Massif. A palynological sample from these beds yielded a rich and well-preserved acritarch assemblage, composed of 19 taxa identified at the species level, and 7 more left in open nomenclature. Among them, the genera *Acanthodiacrodium*, *Lusatia* and *Cristallinium* are especially abundant, and the acritarch association was correlated by Albani *et al.* (2006) as equivalent to the *Protopeltura praecursor* trilobite biozone of eastern Newfoundland (basal Cambrian Stage 10 of the Furongian series: see Rushton *et al.*, 2011). In addition to the palynoflora, macrofossils from the El Fabar beds include some obolid brachiopods, phyllocarid crustaceans and rare olenid trilobites resembling *Parabolina* from the Furongian stages 9 and 10.

The record of late Cambrian trilobites from 'El Fabar Beds' was briefly mentioned by Gutiérrez-Marco and Bernárdez (2003) and Albani *et al.* (2006), but the material was never studied in detail. For the present work, we have examined all the specimens collected during the excavation of the "Túnel Ordovícico del Fabar" in the A-8 highway 7 km west of Ribadesella (Asturias). Our results confirm the preliminary identification of complete but poorly preserved olenid trilobites, adding the occurrence of several cranidia of the idahoiid *Maladioidella* cf. *colcheni* Shergold, Liñán and Palacios, 1983. This constitutes a probable further record of a species defined from the lower member of the Najerilla Formation of the Sierra de la Demanda, which was considered part of a trilobite assemblage of possible early Franconian age as suggested by Shergold *et al.* (1983) or, alternatively, correlated with the Iberian or Sunwaptan regional stages (Alvaro *et al.*, 2007). The widespread genus *Maladioidella* has numerous local synonyms and 'sister taxa' (*Kuruktageella*, *Iranella*, *Cedarellus*, *Saratogia* p.p., *Elrathiella* p.p., *Lakella* p.p., among others), and in Wales it ranges from the *Parabolina spinulosa* to the *Peltura scarabaeoides* trilobite zones (late Cambrian stages 9 and 10). Elsewhere it has been recorded from Furongian siliciclastic and carbonate rocks extending from northern Australia through South Korea and northern China into Siberia, Iran, Turkey and Europe (Wales, France, Spain and Sardinia): see Shergold *et al.* (1983), Shergold and Sdzuy (1984), Rushton and Hughes (1996), and Alvaro *et al.* (2003).

From a palaeobiogeographical point of view, the record in the Cantabrian Zone of the undetermined *Parabolina*-like olenid plus *Maladioidella* cf. *colcheni* is interesting because the second form belongs to a special group of trilobites that in the late Cambrian migrate into temperate, peri-Gondwanan platforms in intermediate paleolatitudinal settings. Also, according to Alvaro *et al.* (2007) this group includes Australasian invaders not only restricted to peri-Gondwanan margins, but co-occurring with cosmopolitan genera like *Maladioidella*, *Prochuangia*, *Onchonotellus*, *Olentella* and others. This is a contribution to Project CGL2009-07073 from the Spanish Ministry of Economy and Competitiveness (MINECO).



Evolutionary modifications of ontogeny: the example of three *Dechenella* species

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The historical section of the Givetian (Middle Devonian) in the Ardenne Massif has yielded three *Dechenella* species (Proetidae). *Dechenella givetensis* Bignon and Crônier, 2011 and *D. calxensis* Bignon and Crônier, 2011 occur in the basal Givetian, and *D. ziegleri* Struve, 1992 at the top of the lower Givetian (Bignon and Crônier, 2011). The numerous exuviae discovered provide the opportunity to compare their ontogenetic shape changes.

Since the seventies, most ontogenetic comparisons have been based on heterochrony theory. However, this concept needs a parallelism between ontogenetic trajectories to be applied. So, all modifications of ontogeny could not be classified as heterochrony. To resolve this problem, Webster and Zelditch (2005) suggested a comparison of species development under the concept of evolutionary modifications of ontogeny. They distinguished dynamic modifications, which compare the ontogeny of a descendant taxon with that of an ancestral one, from static modifications where the comparison only considers a particular stage. Three dynamic modes were described: rate modification, different speeds of ontogenetic modifications; timing modification, a change in the sequence of ontogenetic events; and allometric repatterning, different ontogenetic trajectories. The rate and timing modifications present a parallelism between ancestral and descendant ontogeny, and can thus be classified as heterochrony. Three static modes exist: heterotopy, a different morphological structure in the same place; heterotopy, the same structure in different places; and heterometry, a different number of the same structure.

The shape description of the three species of *Dechenella* was based on a morphometric approach, allowing us to remove size from the shape variation. Another focus of the analysis was to describe the shape under several dimensions, in order to test whether two ontogenetic trajectories are parallel. The cephalae and pygidia were described separately because no complete specimens were discovered. Moreover, in the absence of articulated specimens it is not possible to determine their ontogenetic stage. To resolve the problem, a multivariate analysis was performed in order to group the specimens of similar size. Three ontogenetic groups were determined for cephalae and four for pygidia.

The cephalic analysis of *D. givetensis* and *D. ziegleri* suggests an allometric repatterning. However, their pygidia present the same ontogenetic trajectory, enabling us to compare their rate of ontogenetic modifications. There appears to be a significant difference, suggesting that the rate is more important for *D. ziegleri* than for *D. givetensis*. In the case of *D. calxensis*, we are able to describe only its pygidial ontogeny because its cephalae are unknown. The analysis reveals an allometric repatterning with *D. givetensis* and, of course, *D. ziegleri*.

Concerning the static mode, a posterior medial notch is present in young specimens of *D. givetensis* but not in the two other species. Thus, two different structures are present in the same place, representing heterotopy.

This study reveals the effectiveness of the modes of evolutionary modifications of ontogeny associated with morphometric analyses in order to compare ontogenies. This work also demonstrates the important and complex role of ontogenetic modifications in evolutionary mechanisms leading to new morphologies. Thus, different structures in a species may be affected by different modifications of ontogeny: in the case of *D. givetensis* and *D. ziegleri*, an allometric repatterning of their cephalae and a rate modification for their pygidia. Also, the same structure in different species may be modified by different modes of ontogenetic change: pygidia of *D. givetensis* and *D. ziegleri* differ with a rate modification whereas an allometric repatterning has occurred in *D. calxensis*.

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Ölandian (Tremadocian to mid-Darriwilian) trilobite faunas along the Ural border of Baltica

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Baltoscandian trilobites have been studied for about two centuries by many authors in the region. Over five hundred species described from the Öland (Oeland) Series were counted in a recent list by Pärnaste, Bergström and Zhou. Less is known about the trilobites on the other side of Baltica - at the Uralian edge of it. Ancygin compiled a list of most of this fauna in 2001. The records of shared taxa even at the species level has proven the connection between these two margins of Baltica, especially during the late Tremadocian and mid Darriwilian.

In the Urals, the Ordovician facies run approximately meridionally as this mountain range is oriented today. The alluvial deposits in the westernmost area are replaced by shelf sediments eastwards and further on by deep oceanic and rifting sediments, which are allochthonous. The first, namely the Manitarynd Series, contains a cyclic succession of various sandstones alternating with conglomerates of mainly continental and costal shallow-water origin (without trilobite fossils). Eastwards, the Sakmara-Lemvinskaya facial zone consists of shelf sediments of the Pogurej Formation in the north and the Kidryas Formation in the south, where trilobites are known from the Lower Tremadocian onwards. This facial zone is a relatively narrow region with complicated relief often showing active hydrodynamic conditions (i.e. highly variable thickness of deposits). Due to transgression the shelf deposits reached further west during the Arenig. The easternmost series – the Grubeinskayan - is characterized by a thick complex of deep-water shales alternating with volcanic rocks representing the continental slope facies. During the Middle and Late Ordovician the deeper water conditions reach the Sakmara-Lemvinskaya zone. Most of the known trilobites come from this Sakmara-Lemvinskaya facial zone.

Altogether (including the non-trilobitic agnostid arthropods) some 220 species and 103 genera are recorded from the interval from the Lower Tremadocian to the Mid-Darriwilian in the Urals. The most common trilobites in the Tremadocian were olenids (*Peltocare*, *Saltaspis*, *Triarthrus*), hungaiids (*Leimitzia*, *Dikelokephalina*), cyclopygids (*Pricyclopyge*, *Tyrmancyclopyge*), remopleuridids (*Apatokephalus*), trinucleoids (*Orometopus*), asaphids (*Niobe*), shumardids (*Akoldinoidia*), and the possible hystricurid *Jadya*. *Nileus* and *Ottenbyaspis* together with *Harpides* became abundant by the Floian. Dapingian deposits bear mainly asaphids (*Niobe*, *Niobella*, *Megistaspis*, *Megalaspides*), plus remopleuridids (*Apatokephalus*, *Lakorsalina*, *Eorobergia*), *Euloma* and *Raymondaspis* in the Pai-Khoi district. From the southern part of the Urals trilobites of that age are known only from the Mayachnaya Gora, which is considered to represent island conditions slightly off the main shelf. All these genera except *Lakorsalina* have their distribution also in the Baltoscandian side of Baltica. The Darriwilian Karakol'-Mikhailov Stage has an even more diverse trilobite fauna shared with Baltoscandia (i.e. *Asaphus*, *Lonchodomas*, *Remopleurides*, *Pliomera*, *Cyrtometopus*, *Pateraspis*, *Illaeus*, *Platillaenus*, *Metopolichas*, and *Platylichas*), and other genera that are not shared with Baltoscandia. A few Tremadocian genera like *Kujandaspis*, *Nyaya*, *Amzasškiella* also known from Siberian paleoplate. The last of them is also known from Kazakhstan indicating the proximity of that area. *Cybelurus* from the Upper Tremadocian of the Pai-Khoi and Polar Urals is shared with Gornyj Altai and Spitzbergen, but arrived there later. Many genera are shared with South China (*Parabolinella*, *Macropyge*, *Apatokephalus*, *Niobella*, *Asaphellus*, *Parapilekia*, *Shumardia*, *Euloma*, *Platypeltoides*, *Harpides*), but these are mostly cosmopolitan. *Apatokephalus*, *Agerina*, *Harpides*, *Parapilekia* and *Pliomeroidea* have their oldest known occurrences in South America.



The evolution of limbs in Paleozoic horseshoe crabs revealed by an exceptionally preserved Silurian fossil

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A remarkable new horseshoe crab from the the mid-Silurian of Herefordshire, U.K. (~425 Myr) preserves biramous limbs in the prosoma that can be homologized with those of living *Limulus*. The fossil shows that a true biramous limb evolved in chelicerates as well as in crustaceans, in contrast to the endopod with exite present in trilobites. The evidence of the new fossil supports models for the origin of the limb morphology of living horseshoe crabs through loss of gene expression.



Preliminary report on articulated juvenile phacopid trilobites in the Prague Basin (Czech Republic)

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Complete early ontogenetic stages of phacopid trilobites left a very poor fossil record worldwide. Although phacopids are a common component of Devonian communities in the Prague Basin only two articulated juvenile individuals have been described until now.

A rich and diversified fauna, including common remains of meraspid and young holaspid specimens of *Pedinopariops superstes superstes*, has been found in the late Emsian Daleje shales (Daleje-Třebotov Formation) at the Čefinka Section near Bubovice. The distinctive association of skeletal fauna at this locality, in comparison with other known fossil sites within the Daleje shales, probably reflects the position of the locality close to the transition from the shale into carbonate facies.

The newly described association contains common moulted young holaspides, one entire meraspid and one poorly preserved but entire late meraspid-early holaspid specimen. The young individuals of *P. superstes superstes* closely resemble the ancestral *P. degener*; with the exception of the smaller eyes, they are somewhat similar to the coarsely tuberculate descendent *P. superstes superior*. The principal differences between the early stages of *P. superstes superstes* and the adult specimens include the relatively coarse tuberculation of the dorsal exoskeleton, its stronger vaulting and the smaller eyes in the young specimens. Co-occurring adult specimens, however, correspond with the diagnosis of typical *P. superstes*.

The newly collected material is supplemented by description of two, so far unpublished juvenile specimens of *Pedinopariops superstes* from other localities, a uniquely 3D preserved entire meraspid specimen of *Reedops* cf. *bronni*, and by a detailed discussion of two previously described specimens of *Pedinopariops insequens* and *Prokops hoeninghausi*.

The paucity of articulated meraspid and young holaspid specimens, compared with adult and sub-adult ontogenetic stages of phacopid trilobites and its possible causes are discussed.

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New discoveries of the oldest trilobites *Profallotaspis* and *Nevadella* in the Northeastern Siberian Platform, Russia

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Profallotaspis Repina, 1965 belongs to the Family Fallotaspidae Hupé, 1953, representatives of which are restricted to the Lower Cambrian in many regions of the world, including North America, Siberia, northwestern Eurasia, Morocco, Spain and eastern Germany. Repina described two *Profallotaspis* species, *P. jakutensis* (the type species) and *P. privica*, from the Lower Cambrian Pestrotsvet Formation in the middle reaches of the Lena River (southeastern Siberian Platform), where she identified the *Profallotaspis* Zone in the lower part of the Atdabanian stage of the Russian scale (Repina in Khomentovskii & Repina, 1965). *P. privica* was later found by Repina (1981) also in the Emyaksin Formation of the Fomich River (Anabar Region, northern Siberian Platform). She compared *P. jakutensis* and *P. privica* with older species of *Eofallotaspis* Sdzuy, 1978 from Morocco, the latter species being amongst the stratigraphically oldest trilobites (Palmer & Repina, 1993). In North America, Hollingsworth (2007) found *Profallotaspis?* sp. in the upper part of the Andrews Mountain Member, Campito Formation, Esmeralda County, Nevada, the poor preservation of the specimens preventing their identification with confidence.

In 2011, we examined the Lower and Middle Cambrian sections in the lower reaches of the Lena River (Ulakhan-Aldyarkhai Creek, Kharaulakh) in the northeast Siberian Platform. The first appearance of trilobites found was that of *Profallotaspis*, at 36 m above the base of the Lower Cambrian Tyusser Formation, in a layer of compact pelitomorphic lenticular algal limestone with thin interbeds of bioclastic limestone. Stratigraphically higher, 14.2 m above the horizon of *Profallotaspis*, in a layer of clayey, bioclastic, medium-grained limestone with thin, wavy bedding, we found trilobites of the *Nevadella* Zone: *Delgadella pervulgata* Laz., *D. anabara* Laz., *D. sakhaica* Nikif., *Nevadella effusa* Rep., *N. aff. subgroenlandica* Rep. This section was previously investigated by Lazarenko and Nikiforov (1962) Repina (1967) and Repina et al. (1974), and the latter authors published descriptions and photographs of all of the faunal groups found as well as a biostratigraphic chart of the Lower Cambrian of the Kharaulakh area. A fragmentary trilobite cephalon from 44.3 m above the base of the Tyusser Formation, or 11.9 m below the base of the *Nevadella* Zone, was identified by Repina (p. 20, pl. 25, fig. 5) as belonging to the Subfamily Fallotaspinae.

Several well preserved cephalons of *Profallotaspis* have recently been found in this section at two levels, 36 m and 38 m above the base of the Tyusser Formation, in layer 10 (or 18 of Repina) at the top of small bioherms composed of compact algal limestone that is pelitomorphic to fine-grained, grey and cloddy with interbeds of clastic limestone. The cephalons are well preserved and are assigned to the new species of *Profallotaspis tyusserica*. It differs from *P. jakutensis* and *P. privica* in several features, including: cephalon wider than long; concave preglabellar field; backwardly sloping anterior border; forwardly narrowing glabella with three pairs of glabellar furrows; curved posterior cephalic margin with distinct intergenal spine; medium-length occipital spine; distinct, narrow anterior ocular lines, beginning where ocular lobe merges with eye ridge and extending obliquely forward through anterior border; occipital furrow strongly curved backwards, deep, complete medially.

We have described and photographed five species of trilobites from the *Profallotaspis* and *Nevadella* zones in the Ulakhan-Aldyarkhai Creek section, and charted the biostratigraphic distribution of all trilobites from these zones in the Tyusser Formation in the lower reaches of the Lena River. The lithological column presented compares the latest description of the section and stratigraphic thicknesses of the Tyusser Formation with those given by Repina (1974) in order to identify the exact location of the new occurrences of trilobites and their distribution.



A bridge too far? Late Cambrian Laurentia – Gondwanan “saukiid” trilobite distribution, evolution, and dispersal

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The late Cambrian “Saukiidae” were a moderately diverse group with over thirty genera and more than 200 named species occurring in Afghanistan, Antarctica, Australia, north and south China, Oman, Iran, Kazakhstan, Korea, Myanmar, New Zealand, North America, Thailand, and Vietnam, consistently in shallow water, inshore facies. Although easily recognizable due to their distinctive glabellar morphology, like many groups of Cambrian trilobites their monophyly remains largely untested, yet their distinctive form, geographic distribution, and relatively restricted temporal range makes them of unusual potential value for global biostratigraphy and paleogeography. They thus make a challenging but potentially valuable target group for systematic analysis. Given their inshore environmental preference, their widespread distribution is both striking and perplexing due to the wide Iapetus ocean basin that lay between Laurentia and Gondwana during the late Cambrian. Thus, “saukiids” apparently managed to bridge the deep ocean basins between Laurentia and other continents and to disperse widely along coastal Gondwana. Moreover, unless Laurentian and Gondwanan “saukiids” are two independently derived clades and their morphological similarity the result of convergence, at least one “saukiid” species or species lineage (more likely if migration was achieved through a series of island hopping events) must have successfully migrated across an open ocean. Reports of various congeneric occurrences between Laurentia and Gondwana suggest that such migrations may have occurred more regularly, but it is also clear that some saukiid morphotypes were restricted to particular regions, even within equatorial Gondwana.

In order to better understand the distribution and utility of “Saukiidae” we are employing combined phylogenetic and morphometric approaches. Character-based phylogenetics will be the key to understanding the evolutionary history of the group and its biogeographic history. The morphometric approach aims to quantify changes in the observed overall morphological disparity of a group. The internal systematic relationships of “Saukiidae”, and their relationship to other groups of trilobites, have long been questioned. Various authors have considered the “saukiids” as a family not closely related to Dikelocephalidae; as a subfamily within the Ptychaspidae, allied with the Dikelocephalidae and the Ptychaspidae; as members of a superfamilial ranked Dikelocephalacea allied with the subfamily Remopleuridacea; or as members of a familial-level Dikelocephalidae with unresolved relationship to either the Ptychaspidae or the order Asaphida. Furthermore, a general lack of “saukiid” synapomorphies often confounds elucidation of within-group relationships. For example, “saukiid” taxa from separate paleocontinents are often so morphologically similar that they are assigned to the same genus, or even to the same species [(e.g. – *Mictosaukia globosa* (Robinson and Pantoj-Alor, 1968) reportedly occurs in both Laurentia and Gondwana, and thus may represent a taxon that crossed an ocean basin]. Alternatively, purely geographical constraints have been enforced for Gondwanan taxa that could clearly have been contained within Laurentian concepts (e.g. – *Thailandinium* Kobayashi is indistinguishable from *Prosaukia*).

As a test for both the ‘island-hopping’ hypothesis for “saukiid” migration, and the aforementioned problems with “saukiid” systematics in general, a comprehensive revision of the “Saukiidae” is underway. A cladistic analysis, including 25 well-preserved “saukiid” taxa from Laurentia and Gondwana, is presented based on 60 morphological characters, and phylogenetic hypotheses discussed.



Biodiversity fluctuations in phacopids through Upper Devonian time

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Trilobites were relatively abundant and diverse in marine Devonian habitats, and their abundance and taxonomic diversity fluctuated. After a peak of diversity during the Early Devonian, their diversity was restricted at high taxonomic levels by one of the most severe biological crises at the end of the early Late Devonian, during the Kellwasser event.

In this study, we focused our investigations on Upper Devonian sections in order (1) to evaluate the phacopid trilobite biodiversity through a global level and (2) to understand their fluctuations in time. This biodiversity is represented in our study by 71 relatively well-known phacopid species for 22 taxa.

Curves of diversity, origination, and extinction were achieved on the presence/absence database from the occurrence of phacopid taxa in the Upper Devonian stratigraphical column in order to estimate the biodiversity in Upper Devonian phacopids. Data are subjected to the range-through assumption for which the existence of a taxon is considered continuous between its first to last appearance. The occurrence of taxa was considered within 14 consecutive and discrete chronostratigraphic intervals from early Frasnian to late Famennian.

During the Upper Devonian, the eustatic variations had a major influence on the phacopid diversity and their evolution leading to major bioevents (Upper Kellwasser and Hangenberg events).

Pronounced sea-level deepening of the Frasnian and the Famennian led to major morphological adaptations such as the gradual regression of the visual complex leading to blindness of various taxa adapted to life in deep habitats. Rapid regressive fluctuations in sea level of the end Frasnian and of the end Famennian led to major extinctions within these deep benthic communities. The Kellwasser Extinction affected especially the phacopid biodiversity that precipitated the decline of phacopids. After a significant post-Kellwasser recovery during the late Early Famennian leading to a major faunal turnover, the Hangenberg Event, meanwhile, precipitated the extinction of all phacopids that as a group were already greatly impoverished.



Intraspecific variability in two Devonian trilobites from the Barrandian area: *Pedinopariops insequens* (Chlupáč, 1977) and *Prokops prokopi* (Chlupáč, 1971); surprising bimodalities

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Two parallel studies were conducted in order to estimate the intraspecific variability in two Devonian phacopid trilobites from the Barrandian area. *Prokops prokopi* (Chlupáč, 1971) and *Pedinopariops insequens* (Chlupáč, 1977) are abundant locally in the upper Pragian and lower Eifelian respectively in the vicinity of Prague. *Prokops prokopi* is easily distinguished from other Bohemian phacopids by the characteristic configuration of the visual surface that is reduced and asymmetrically kidney-shaped with 19-34 lenses, *Pedinopariops insequens* is regarded as closely related to the stratigraphically older species *P. superstes* (Barrande, 1852) on the basis of several similarities in the cephalic and pygidial morphology, including the characteristic configuration of the visual surface that is large and kidney-shaped with 18-20 dorsoventral files of lenses. Specimens of both species stored in the National Museum and the Czech Geological Survey, Prague, were investigated using quantitative methods. Landmarks were selected on cranidia/cephala, and 2-D projections of these landmarks were obtained by an optical image analyzer. All configurations of landmarks were scaled to unit centroid size and then superimposed using a Generalized Procrustes procedure. In order to find an eventual ontogenetic trend and to estimate the intraspecific variability, a Relative Warp Analysis was performed for each taxon.

For *Prokops prokopi*, our results show that: 1) there is a major shape change between two classes of individuals according to their visual surface; this bimodality is also observed according to the number of lens files and total number of lenses; 2) and there is no relationship between the size and shape of the visual surface throughout the studied part of growth. For *Pedinopariops insequens*, our results show that there are two classes of individuals according to their number of files and lenses. In *Prokops prokopi*, the bimodal distribution reflects individuals from two localities, whereas in *Pedinopariops insequens*, the bimodal distribution reflects individuals from only one locality but two different size classes. Could a disruptive selection cause adaptive divergence between conspecific groups that occupied different environments or utilized different resources?

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The morphology of *Anomalocaris* from the Burgess Shale and Emu Bay Shale

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The anomalocaridids are Cambro-Ordovician ecdysozoans commonly regarded as ancestors of the arthropods. They represent some of the most controversial taxa described from Cambrian fossil Lagerstätten, owing to the unusual morphology, complicated history of description and presumed role as apex predators. Recent research has revealed that the anomalocaridids are a highly diverse group in terms of their taxonomy and morphology, and that they had a wide global distribution ranging up into the early Ordovician. However, the name-bearing taxon of the group, *Anomalocaris*, is actually poorly known. Here we report new observations on the morphology of *Anomalocaris* from the Burgess Shale in Canada and the Emu Bay Shale in Australia.

The anomalocaridid oral cone is a unique structure that was thought to be highly conservative in its morphology, uniting at least the Burgess Shale taxa into the order Radiodonta. The “peytoia” oral cone was thought to consist of 32 subrectangular and spiny plates arranged around a square central opening, with four large plates situated 90° apart anteriorly, posteriorly and laterally. Re-examination of the Burgess Shale specimens has revealed that *Anomalocaris* does not possess this tetradial 32-plate oral cone. Instead, it has an oral cone with only three large plates and a highly variable number of smaller and medium-sized plates (Daley & Bergström 2012). The outer margins of all plates are increasingly subdivided into furrows or folds, and the large and medium-sized plates possess clusters of up to 16 small, scale-like nodes on their surfaces. This triradial oral cone has been found in 38 assemblages of *Anomalocaris* from the Burgess Shale, including three nearly-complete bodies. A single isolated triradial oral cone has also been found from the Emu Bay Shale, from which two different species of *Anomalocaris* have been described, confirming the shared presence of a triradial oral cone in different species of this genus. Tetradial oral cones likely belong to the animal previously referred to as *Laggania*, with the consequence that the correct name for this animal is *Peytoia nathorsti*. The morphology of the *Anomalocaris* oral cone throws into question the role of *Anomalocaris* as a highly specialized predator responsible for bite marks in Cambrian trilobites.

In addition to a triradial oral cone, the early Cambrian (Series 2, Stage 4) Emu Bay Shale (EBS) from South Australia yields anomalocaridid appendages, isolated swim flaps, extremely well preserved eyes (Paterson et al. 2011), and gill-like setae. Appendages include those of the highly spinose *Anomalocaris briggsi*, as well as a second species previously referred to as *Anomalocaris* sp. This second species is indistinguishable from *Anomalocaris canadensis* from the Burgess Shale, save for the presence of a proximal ventral spine with five terminal barbs instead of the usual three. Unique to any Cambrian fossil Lagerstätte, EBS also preserves several specimens of isolated swim flaps detached from the body. The triangular flaps have a straight margin of attachment, and evenly spaced transverse lines running along the length of the flap. In Burgess Shale material, the transverse lines of the swim flaps are highly-reflective and faint, but in the EBS the structure of these transverse lines is well preserved and consists of a string of high-relief, closely spaced, square or circular protrusions. Setal structures consisting of a series of lanceolate blades attached at one end and free-hanging at the other have also been found in the EBS, and are presumed to belong to *Anomalocaris* based on their similarity to the setae of *Hurdia* and *Peytoia* from the Burgess Shale. Though complete body specimens have yet to be found, the *Anomalocaris* material from the EBS has provided morphological data unavailable from the Burgess Shale and other Cambrian fossil Lagerstätten.

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The relationship between enrolment and caudalization in basal trilobites

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Caudalization is the trend in trilobites towards an increase in the number of segments allocated to the pygidium. Whereas many post-Cambrian trilobites have a trunk with a large, segment-rich pygidium, many basal trilobites such as redlichiids or ptychopariids have a trunk with a very small, segment-poor pygidium and generally a large number of segments allocated in the thorax. Enrolment in caudalized trilobites was more efficient at encapsulating soft tissues than in poorly caudalized trilobites so might selection for efficient enrolment have driven the trend towards caudalization in derived trilobites?

Although many phylogenetically basal, stratigraphically early, segment-rich trilobites were structurally incapable of encapsulated enrolment, the poorly caudalized redlichiid *Eccaparadoxides pradoanus* did enroll, so as to enclose most of the ventral surface, and possessed specialized articulating devices that facilitated this behavior. It provides a glimpse into the early evolution of characters necessary to achieve this stance.

Eccaparadoxides pradoanus occurs quite commonly in middle Cambrian (~506 m.y. old) rocks of the Mediterranean area and particularly common in the Purujosa trilobite assemblage (PTA) in the top of the Murero Formation (northeastern Spain). This unit (80 cm thick) is remarkable for the preservation of abundant enrolled trilobites belonging to a variety of taxa. Specimens of *E. pradoanus* preserved within this bed show different “degrees” of enrolment. We have been able to study the enrolment procedure over a sequential series. The width of the rear part of the trunk in *E. pradoanus* is as wide as or wider than the cephalon, and in this it is different most other members of the family Paradoxididae. This feature enabled the rear part of the trunk to cover the underside of the cephalon when enrolled, provided an early example of encapsulated enrolment. In addition to these unusual body proportions *E. pradoanus* also shows novel articulation devices such as fulcra, articulated pleura and half ring articulation that are poorly developed in the rear part of the trunk but well developed in the anterior part. This suggests that flexure was likely concentrated in the anterior part of the trunk.

The specimens preserved in the PTA confirm this inference by showing that enrolment began by first flexing the rear part of the trunk downward, and then by flexing more anterior trunk segments downward and forward from the rear in a progressive manner so as to lap the posterior of the trunk beneath the cephalon with the outer rim of the pygidium. Despite the flexion of the exoskeleton there is no indication, from the specimens preserved in the PTA, which the posterior portion of the trunk flexed significantly at any point during enrolment. In fact, most of the flexure was accommodated between the fourth to eight thoracic segments and segments to the anterior of this did not flex much during enrolment. Thoracic segments four to eight correspond with sort pleural spines in both homonomous and heteronomous morphotypes of this species, and these accommodated enrolment by swinging the anterior flanges of the pleurae abaxial to the fulcra beneath the doublure of the preceding segment, and by exposing articulating the half ring in the axial region.

Our results suggest that as flexure within the posterior part of thorax was apparently unnecessary in *E. pradoanus* any selective premium for caudalization would not have hindered encapsulation in trilobites of this morphotype. A trilobite of this morphotype may thus have been “pre-adapted” for caudalization.



Enrolment and life habit in agnostids from Cambrian series 3 of the Iberian Chains (northeastern Spain)

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Enrolled agnostids are relatively common fossils and in most cases specimens are exquisitely preserved as silica or phosphate replacements as well as articulated skeletons in limestones. These types of preservation allow very detailed descriptions of both articulations and coaptative devices, useful for enrolment, and there is no doubt about the ability of these arthropods for enrolment. Despite enrolled agnostids being well known there are many discussions and disagreements about the significance of enrolment in relation to their life habit. The reason for these disagreements is the preservation-type itself due to some palaeoecological and environmental data that are lost during the biostratigraphic and fossil diagenetic processes. Here we report on two new levels with enrolled agnostids from Cambrian series 3 from the locality of Purujosa (Iberian Chains, northeastern Spain). These levels shed new light on enrolment and life habit in agnostids.

The first level with enrolled agnostids is in the top of the Murero Formation and is known as the Purujosa trilobite assemblage (PTA). The Murero Formation (about 90 m thick) is a monotonous siliciclastic sequence with a high diversity of polymeroid trilobites that are commonly articulated, but agnostids are poorly preserved, mostly disarticulated (ca 98% of agnostids are disarticulated, JE unpublished data) and low in abundance in most of the beds. The PTA is a red mudstone bed (80 cm thick) and in contrast with the rest of the Murero Formation the percentage of articulated agnostids in it is very high (44% articulated), and of these specimens about 60% are enrolled. The PTA has also many other enrolled trilobites and the taphonomic features (e.g. low bioturbation, degree of articulation) suggest that this level is the result of a series of obrution events. In addition fully articulated fossils such as echinoderms, brachiopods and sponges have been found. Up to four monospecific clusters with articulated specimens (8 specimens on average) were found in the PTA and two of them consist of enrolled *Peronopsis ferox*. In addition isolated specimens of *P. ferox* and *Megagnostus* sp. have been found in enrolled position.

The second level with enrolled agnostids is in the bottom of the Valtorres Formation (about 300 m thick). This formation also is a siliciclastic sequence; however, trilobites as well as other fossils such as hyoliths, brachiopods and bradoriids are found in siliceous concretions up to 10 cm in diameter which occur embedded with their long axes lying parallel to the bedding plane. The concretions consist of a mixture of terrigenous material (quartz and phyllosilicates such as illite/muscovite and chlorite) and biogenic components (calcite and apatite-walled skeletons). Exoskeleton accumulations are within the concretions and specimens are mainly disarticulated although the presence of enrolled agnostids (*Peronopsis* cf. *insignis* and cf. *Megagnostus* sp.) as well as some prone and enrolled polymeroids is relatively high; however, unrolled agnostids are absent. The environmental deposit is currently under study.

The enrolled agnostids from PTA are especially interesting. Some authors suggest that agnostids spent much of their life partially enrolled and fed in a similar manner to ostracods, with the cephalon and pygidium gaping. However PTA shows cluster with both enrolled and unrolled specimens. On the other hand all the agnostids from the Valtorres Formation that appear articulated are also enrolled and they co-existed with typical marine benthic assemblages

All these factors suggest that at least some agnostid species probably had a benthonic lifestyle when they were adults and that adverse physical conditions were probably responsible for preservation in enrolled postures.



Evidence of lethal durophagous predation in Cambrian conocoryphid trilobites from the Barrandian area (Czech Republic)

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Reports of predation on trilobites are generally rare, although trilobites were abundant and diverse invertebrates in many Palaeozoic marine ecosystems. In the present contribution we discuss a relatively common type of bite mark in trilobite exoskeletons, the 'lateral bite mark'. This typically occurs in a restricted position on the left and/or right side of the thorax and in some cases also on the posterior cephalic margin. Trilobite specimens revealing 'lateral bite marks' used in this study were collected from the 'middle' Cambrian Jince and Buchava formations of the Barrandian area. 'Lateral bite marks' are interpreted as the result of predatory attacks on the postero-lateral side of trilobites in their living position. The predators aimed for the vital parts and muscle attachments to obtain the edible soft tissues. The agents responsible for most of the 'lateral bite marks' are unknown.

Exceptionally-preserved Early Cambrian arthropod eyes

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Recent discoveries from the early Cambrian (Stage 4) Emu Bay Shale (Kangaroo Island) of South Australia reveal arthropod compound eye details of unique quality and complexity for their age (~515Ma). The findings include seven specimens of isolated visual surfaces of an unknown, non-biomineralized arthropod¹, and two specimens identified as the eyes of *Anomalocaris*².

Most of what was known to date about the optical design of Cambrian arthropod eyes came from the study of the calcitic (and thus optically unusual) eyes of trilobites, such as the eodiscids *Shizhudiscus* and *Neocobboldia*, with fewer than 100 lenses, which were less than 50 µm in diameter and showed a square-grid arrangement. The isolated compound eyes¹ show flattening of the overall visual surface, with some degree of wrinkling and tearing, indicative of an originally non-biomineralized cuticle. However, fine features such as ommatidial lenses are preserved in superb detail and three-dimensional relief. These eyes have an ovoid visual surface with a long axis diameter of about 7–9 mm, covered by over 3,000 ommatidial lenses which are hexagonally close-packed in a highly regular six-neighbour arrangement. A specialized central area with the large lenses –each approximately 150 µm in diameter– can be interpreted as a ‘bright zone’ or ‘fovea’, with higher light sensitivity. Lens size gradually decreases towards the margins, with a minimum diameter of ~60 µm. Such lens numbers and their large size is unknown in biomineralized eyes of trilobites until 40 million years later, and in non-biomineralized arthropod eyes until about 85 million years later. Compaction of the fossils precludes exact quantification of the eye parameter ‘*p*’, but comparison with the younger trilobites *Carolinites* and *Priocyclopyge*, with similar sized lenses and eyes, allows extrapolation of *p* values, which correspond to those typical of taxa living in low-luminance environments. SEM-EDS analysis of the optical surface showed elevated levels of calcium and phosphorus, indicating a secondarily phosphatized structure.

The other set of eyes from the Emu Bay Shale are assigned to *Anomalocaris*², a common taxon in the same levels. They are stalked with a pyriform visual surface. This surface is much larger than the one described above: *c.* 22 mm long and with a maximum width of *c.* 12 mm in the most complete specimen, and >30 mm long and 16.9 mm wide in another specimen. The surface is covered by at least 16,000 hexagonally-packed lenses on the preserved side; the whole original eye could have had up to double this number. In typical arthropods and visual conditions, each lens produces a pixel of vision, and this high lens number rivals the most acute compound eyes in modern arthropods (e.g. dragonflies). The average lens diameter is ~95 µm, and allows estimates of a *p* (eye parameter) value of <2, characteristic of diurnal taxa living in well-lit environments. Until now, the eyes of anomalocaridids were known only from their outlines, but the newly recognized high visual acuity of this group, together with their large body size, robust spinose frontal appendages, mouth with a dentate inner margin and size and form of the midgut glands, confirms that these animals were highly mobile visual predators in the water column. Compound eyes also provide new evidence for the arthropod affinities of anomalocaridids, while suggesting that the compound eye evolved before such features as paired trunk appendages and a hardened exoskeleton. SEM-EDS analysis of these specimens shows two distinct modes of preservation: as iron oxide (after pyrite) and as calcium phosphate, demonstrating that disparate styles of early diagenetic mineralization can replicate the same type of extracellular tissue within a single BST deposit.

These findings show that the Emu Bay Shale has the potential for preserving aspects of early animal evolution that might not be observed in other Cambrian Lagerstätten, filling in some important gaps left by Sirius Passet, Chengjiang or Burgess Shale.

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***Rusophycus carleyi*: Evidence of cosmopolitan travellers**

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Rusophycus carleyi and similar morphologic traces *R. morgati*, *R. polonicus*, *R. radialus*, and *R. moyensis* have been found in a number of localities throughout the world: Argentina, Australia, Canada, France, Libya, Morocco, Poland, Spain, Wales, and the USA. These bilobed traces display two rows of coxal impressions between the striated lateral lobes, which would have been produced by the distal portions of the endites. They range in age from the late Cambrian (Furongian) to the Late Ordovician. Arthropod traces, including *Cruziana* species, have been suggested as useful chronostratigraphic tools for the Paleozoic, at least for Gondwana. *R. carleyi* has been definitively linked to, and was almost certainly made by, the trilobite *Asaphellus* aff. *fezouataensis*. The other *Rusophycus* species listed above, except *R. moyensis*, have also been correlated to asaphid trilobites. *R. moyensis* was possibly made by an olenid trilobite. The large size, non-adult-like form and multiple instars of known asaphid protaspides – asaphoids – suggest that they were long-lived and pelagic. This would have provided these organisms with expansive palaeogeographic circulation potential. The distribution of these distinctive traces is matched to the ranges of other Lower Paleozoic organisms, and the examination of late Cambrian to Late Ordovician geography, oceanic current flow patterns, and dispersal routes. Should these *Rusophycus* species prove to be valuable biostratigraphically, they have the potential to be advantageous for intercontinental correlation in non-fossiliferous strata.



Trilobites, brachiopods, and other microfossils resolve the paradox of conodonts reported in middle Cambrian rocks from the Parahio Formation of India

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The Parahio Valley of the Tethyan Himalaya provides the type section for the Cambrian of that lithotectonic zone. Early in the last century characteristically late Cambrian age trilobites such as *Olenus* and *Dikelocephalus* were described from the upper part of the Parahio Formation below an unconformity with Ordovician molasse deposits. This age assignment has endured in more recent literature and Bhatt and Kumar's 1980 report of conodonts and a paraconodont recovered shortly below the unconformity was also consistent with this interpretation.

Revision of Hayden's trilobite type material in the late 1990's re-evaluated systematic affinities and concluded that all trilobites collected *in situ* from the upper part of the Parahio Formation are of middle Cambrian age. Recent recollection recovered few new trilobite specimens in the uppermost part of this unit, but regional correlation with the Zanskar Valley suggests that this level is equivalent to the upper part of the *P. gibbus* Zone, at the top of Stage 5 of the Cambrian System, deeming it middle Cambrian. Although this age determination is consistent with the known range of paraconodonts, it precedes the range of euconodonts. To assess the disparity between the trilobite biostratigraphy and the occurrence of euconodonts we have employed two approaches. Firstly, the original material of Bhatt and Kumar was re-inspected. Of the illustrated specimens still available and identifiable, none are either paraconodonts or euconodonts. Rather, all are acrotretide brachiopods with laterally compressed and highly conical pedicle valves. Secondly, recently collected fossil-bearing carbonate samples from Parahio and Zanskar sections, including the horizon sampled by Bhatt and Kumar, were processed via acid dissolution. Such dissolution revealed a moderately rich fauna of lingulelliform brachiopods (including species belonging to *Prototreta*, *Dictyonina*, *Micromitra* and *Acrothele*), cancelloriids (species belonging to both *Chancelloria* and *Archiasterella*), hyolithids, molluscs, hexactinellid sponge spicules and a single meraspid trilobite. No euconodont or paraconodont specimens were recovered. The new brachiopod and microfossil age determinations for these sections are consistent with the Cambrian Stage 5 age estimate proposed using the revised trilobite biostratigraphy. Thus, the apparently paradoxical occurrence of diverse conodonts, including possible euconodonts, in middle Cambrian rocks has been resolved by showing that Bhatt and Kumar's fossil identifications were erroneous, as was the suggestion of a late Cambrian age for their host rocks.



New records of telephinid trilobites (*Carolinites* and *Oopsites*) from the Ordovician of the Central Andean Basin

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Epipelagic telephinids rarely occur in mid to high paleolatitudinal settings during the Ordovician. Extremely widespread taxa such as *Carolinites genacinaca* span the entire palaeotropical realm (McCormick and Fortey, 1999), while others, like the genus *Telephina*, seem restricted to the periphery of the continental paleoplates (Ahlberg, 1995).

The record of telephinids in the Ordovician of South America starts with the discovery of “*Keidelia*” (= *Carolinites macrophthalma* by Harrington and Leanza (1957) and *Telephina argentina* by Baldis and Blasco (1974) in the Argentinian Precordillera, plus “*Tafnaspis*” (= *Carolinites iglesiasi* by Leanza and Baldis (1975) in the eastern Puna belt of the same country. With the exception of a single occurrence of *Carolinites genacinaca* Ross from the Lower Ordovician of Bolivia (Aceñolaza *et al.*, 1999), the remaining South American telephinids were reported from Argentina, where they occur throughout the Floian-Sandbian of the Precordillera (*Carolinites macrophthalma*, *C. killaryensis* (Stubblefield), *C. constrictus* Benedetto and Cañas, *Telephina argentina* Baldis and Blasco, *T. calandria* Chatterton *et al.*, *T. chingolo* Chatterton *et al.* and *T. problematica* Chatterton *et al.*), as well as in the Lower Ordovician of the Famatina Basin (*C. cf. genacinaca* and *Oopsites* sp.): see Benedetto *et al.* (1986), Vaccari and Waisfeld (1994), Chatterton *et al.* (1989) and Waisfeld and Vaccari (2003). In the Argentinian part of the Central Andean Basin, *Carolinites* was known from three Lower Ordovician localities in the Jujuy province: one in the eastern Puna (*C. iglesiasi* of Leanza and Baldis, 1975) and two others in the Cordillera Oriental (*Carolinites* sp. of Waisfeld and Vaccari, 2003).

We here confirm the occurrence of *Carolinites genacinaca* in carbonate coquinas from the type section of the Sella Formation of the Cordillera Oriental of Bolivia, adding some new specimens (two cranidia and a pygidium) to the single cranidium illustrated by Aceñolaza *et al.* (1999) for the same locality. Also we report the first record of *Oopsites* in the Cordillera Oriental of southeastern Peru, occurring in Lower Ordovician siltstones of the San José Formation in a section located in the Apurímac river valley, northwest of the well-known site of Machu Picchu.

Both finds represent the northernmost occurrences of the genera *Carolinites* and *Oopsites* in present day South America, reported within the late Floian-early Dapingian *Famatinolithus* Fauna, which is assigned to intermediate paleolatitudes along the Famatinian and Central Andean basins (Benedetto *et al.*, 2009). The rare record of these telephinids has been related to warm water currents, probably due to equatorial surface gyres moving southwards and sporadically carrying epipelagic trilobites away from the tropics (McCormick and Fortey, 1999). This is argued by the latter authors to explain the individual records of *Carolinites* in the Lower Ordovician of southeastern France and Turkey.

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Ordovician trilobites and trilobite traces from the Cabañeros National Park (central Spain)

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The Cabañeros National Park is located within the Palaeozoic basement areas belonging to the southern part of the Central Iberian Zone of the Iberian Massif. It is mainly composed of Lower Cambrian to Middle Ordovician marine rocks, affected by Variscan folding and faulting and by differential erosion processes of the Palaeozoic formations leading to an Appalachian-like relief.

Starting from 2006, the present authors have been carrying out studies to increase the geodiversity knowledge within the extension of the National Park, especially aimed at identifying geosites of national and international interest, as well as implementing the geotouristic potential of some of the existing trails and 4WD routes through the park. This systematic research led to the discovery of important Ordovician fossil localities rich in trilobites or trilobite traces that are briefly examined in this note.

Occurrences of Ordovician trilobites are restricted to several outcrops of the lower part of the Navas de Estena Shales, close to the northern and southern boundaries of the Cabañeros National Park. The northernmost two sites lie at the periclinal end of two small synclines north of the Calanchera Fault (the points Calanchera 1 and 2), while the third is situated in the southwestern flank of the Navas de Estena syncline, northwest of the homonymous town (“Las Cuevas” locality). In the southern area, several fossiliferous sites occur in both flanks of the La Chorrera syncline: these are the Los Medianiles, Vallelobo, El Robledo and Solana del Cuervo 1 and 2 fossil localities. All of them come from the lower part of the Navas de Estena shales, ranging between 60 and about 200 m above the base of the formation, which represent a substantial part of the *Placoparia cambriensis* trilobite Biozone, here dated by graptolites as early Oretanian of the Mediterranean regional scale (approx. equivalent to the early-middle Darriwilian -lowermost Da2 substage- in the global scale). The whole assemblage comprises at least 13 different species belonging to three trilobite orders. The Asaphida include asaphines like *Nobiliasaphus delessei* (Dufet), isotelines such as *Asaphellus toledanus* (Gil), ogygiocaridines (*Ogyginus forteyi* Rábano) and some dikelokephalids as *Hungioides bohemicus* (Novák in Perner). The order Phacopida is the most diverse and is represented by the calymenids *Neseuretus avus* Hammann, *Colpocoryphe thoralis conjugens* Hammann and *Salterocoryphe ‘lusitanica’* (Thadeu), bathycheilids (*Bathycheilus castilianus* Hammann), dalmanitids (*Retamaspis melendezi* Hammann, *Klouceka drevermanni* Hammann), cheirurids (*Pateraspis mediterranea* Hammann) and pliomerids (*Placoparia cambriensis* Hicks). The single representative of the trilobite order Corynexochida is the illaenid *Ectillaenus giganteus* (Burmeister).

Trace fossils, currently attributed to a wide range of trilobite activities, are abundantly in the Armorican Quartzite, in the upper part of the ‘Intermediate Beds’ below it, and also in the upper Marjaliza Beds. The *Cruziana* ichnofacies represented in diverse localities along the Sierra Fría, Garbanzuelo and Cabañeros anticlines, yielded abundant specimens of *Cruziana rugosa* d’Orbigny, *C. furcifera* d’Orbigny, and *C. goldfussi* (Rouault), sometimes grouped in extensive beds indicative of the gregarious behavior of their tracemakers during collective moulting or mating. More sparse is the record of other ichnospecies such as *Cruziana problematica* (Schindewolf), *C. rouaulti* Lebesconte, *C. imbricata* Seilacher, *C. ‘vilanovae’* (Saporta and Marion) sensu Delgado (= *C. barriosi* Baldwin), *C. cf. cordieri* Rouault or *C. yini* Yang, as well as some scarce representatives of *Rusophycus* ispp. and *Monomorphichnus* ispp. Finally, a resting trace of giant size (70 cm long and 45 cm wide) has been identified as *Tumblagoodichnus?* isp., maybe related to an ichnogenus made by unknown amphibian non-trilobite arthropods.

Part of these ichnological localities are important and display a special interest for their geotouristic potential, having been already incorporated to the list of the Spanish geological heritage sites and being accessible to Park’ visitors throughout the Boquerón del Estena walking trail and through the Rocigalga route for 4WD-vehicles.

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Middle Cambrian (Series 3) trilobite and agnostid biofacies of East Gondwana: Beta diversity trends in space and time and implications for palaeogeography

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Cambrian Series 3 was a time of passive plate convergence on the eastern Gondwanan margin (comprising Australia, New Zealand and Antarctica), and a period of widespread carbonate and organic-rich sediment deposition. Extensive shallow shelf sediments of this age dominate northern Australian sedimentary basins, as well as those in South Australia, New South Wales, Victoria, Tasmania, New Zealand and Antarctica. Trilobite and agnostid assemblages are well documented for many Cambrian Series 3 successions in these regions, including material from outcrop and drillcore, and occur in a variety of marine lithologies, ranging from coarse-grained clastics to black shales, phosphorites and carbonates.

A preliminary binomial presence/absence matrix of all Cambrian Series 3 trilobite and agnostid genera from dozens of East Gondwanan localities has been constructed for each of the three stages (Stage 5, Drumian and Guzhangian) using the available literature. Genus level is considered the most appropriate taxonomic rank for an analysis of the various local assemblages of each stage, due to the endemism of many species even between regions of East Gondwana. Preliminary statistical analyses, using the software package PAST, have been performed, demonstrating similarities between regions based on shared genera. Initial results indicate that the clustering of faunal assemblages corresponds to the similar depositional environments they inhabited, ranging from very shallow inner shelf to deep outer shelf settings (below storm wave base), in addition to the continental slope. There is a considerable increase in East Gondwanan trilobite and agnostid diversity throughout Cambrian Series 3, with the Guzhangian showing a very marked increase in genera, perhaps reflecting a global marine transgression during this time that expanded the continental shelf along the East Gondwanan margin.



The new tropidocoryphid trilobite genus *Cirriticeps* (Proetida) from the Silurian of New South Wales

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The new tropidocoryphid genus *Cirriticeps* is represented in the Silurian of New South Wales by two species, one of them from the Wenlock to Ludlow of the Orange district, and the other from the upper Ludlow of the Yass Basin. The genus is most closely related to *Tropidocoryphe*, known from the Lower and Middle Devonian of Europe and North Africa, and was probably ancestral to it. The two genera are characterised, amongst other features, by very broad anterior and lateral cephalic borders that are poorly differentiated from the genal field and carry a strong epiborder furrow. The structure of the borders has been misinterpreted previously in *Tropidocoryphe*, the epiborder furrow having been regarded as the border furrow, and the inner part of the border as part of the genal field. *Cirriticeps* differs from *Tropidocoryphe* mainly in having deep longitudinal glabellar furrows extending from the occipital furrow to S3, numerous fine tropidial ridges on the genal field instead of a tropidium, eight instead of nine thoracic segments, and no median spines or spinose nodes on the posterior edges of the occipital and axial rings.



Agnostoid trilobites from the interval across the base of the Drumian Stage of the Machari Formation, Yeongwol Group, Korea

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The cosmopolitan agnostoid trilobite species *Ptychagnostus atavus*, ratified by the International Commission on Stratigraphy and the International Union of Geological Sciences as the species defining the base of the Drumian Stage, is reported for the first time from the Machari Formation of the Yeongwol Group in Korea. Well-preserved trilobites were collected from a newly discovered locality about 12 km northeast of Yeongwol where the lowermost 9-m-thick interval of the Machari Formation is well exposed. The lower part (ca. 5.8 m thick) is characterized by a massive bioclastic grainstone that yields Stage 5 trilobites previously known from the *Tonkinella* Zone. The middle part (ca. 1.7 m thick) is composed of gray to dark gray wacke- to packstone with a 60-cm-thick black shale bed at the base. *Ptychagnostus sinicus* and *Peronopsis* sp. occur in the wacke- to packstone beds at the lower 1.2 m interval, while *P. atavus* appears scarcely along with abundant *Yakutiana* (al. *Pseudophalacroma*) *ovale* in the upper 0.5 m interval. The upper part (ca. 1.5 m thick) is a succession of laminated lime mudstone, and *Lejopyge armata* is recovered from the horizon of the 1.2 m above the base of the interval, indicating that the boundary between the Drumian and the Guzhangian stages may lie somewhere within the interval. Landmark-based geometric morphometric methods are being utilized to evaluate quantitatively the morphological characters previously assigned for defining the ptychagnostoid species. Initial result displays a successful identification of significant shape differences between *P. sinicus* and *P. atavus*.



Dissecting controls on the development of the Czech Silurian trilobite *Aulacopleura koninckii*

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Ever since ontogenetic series for trilobites were first established (by Joachim Barrande 160 years ago) the remarkably rich preservation of the Czech middle Silurian trilobite *Aulacopleura koninckii* has provided a model system for understanding trilobite development. Over the last 20 years this species has been studied intensely, with a focus on growth, segmentation and the possible causes of its atypical pattern of morphological variation. These studies resulted in a seeming paradox. While on one hand, the growth of this animal was apparently tightly controlled, on the other this species' variation in holaspid thoracic segment number could suggest that developmental control of segmentation was not effective to the same degree.

To investigate further these and other apparently contrasting observations, a new dataset selected via a comprehensive survey of the highest quality specimens offers improved resolution of original morphology by all measures considered. Meraspid size increase was exponential and the meraspid growth rate per instar was strikingly constant. Meraspid growth proceeded along a tight developmental trajectory with variation both in size and shape at individual instars actively constrained by a process that channeled the development of both traits. Meraspid cranial allometry was subtle, with significant changes in instar form detectable only after several molts. Trunk segmentation in this synarthromeric trilobite also proceeded in a regular, progressive manner, with synchronous cessation of trunk segment appearance and release at the onset of the holaspid phase. Moreover, analysis of per-segment growth rates in the trunk also suggest tightly coordinated growth, which resulted in the position of the longest trunk segment moving posteriorly during ontogeny. Whether segments had individualized growth rates or were controlled by an overall growth gradient remains unresolved. Lastly, variation in mature segment number was more probably the manifestation of a polymorphism, rather than a polyphenic trait influenced by environmental conditions during meraspid development. Conversely, the posterior trunk of mature specimens shows varied malformations at the level of dorsal articulations, affecting some 10% of specimens. This sign of developmental instability concerns a single trait (articulation) and is expressed only late in the development of a particular region.

Both the "olenimorphic" form of *A. koninckii* and its pattern of occurrence on individual bedding planes suggest that the species may have thrived in conditions of reduced oxygen availability, but chemical alteration limits the recovery of geochemical proxies that might test specific adaptive hypotheses about variation in holaspid segment number.



Stability and Intensity of Clinal Regimes over Longer Time Intervals: Implications for Interpreting Stratophenetic Patterns in the Fossil Record

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Clines have long been documented in plants and animals and have been recognized as potentially important systems of speciation. Due to the heterogeneous nature of environmental conditions along a cline, interactions between environment and morphology can be described and modeled as the norm of reaction for a particular species. Nearly all traits will show some plasticity along a cline because phenotypes result from the interaction of genetics with environment, yet the response of phenotypic plasticity to variable environmental conditions still requires further understanding. Simply demonstrating that the environment affects phenotypic expression leaves unanswered the question of whether the phenotypic change over time is adaptive and arose through natural selection, or if this change is the reflection of phenotypic variation without a corresponding genetic change. While it is not possible to determine the role of genetics (ecotype) and/or environment (ecophenotype) in generating phenotypic plasticity along environmental gradients for deep time paleontological studies, the power of the fossil record is that it allows us to measure the spatial and temporal dynamics of morphological change within a species over longer time scales. This gives us the opportunity to understand how these clinal systems operate over longer-term intervals thereby elucidating their potential contributions to microevolutionary patterns routinely documented in the fossil record.

There are two primary steps in achieving this goal. Firstly, the geographic distribution of phenotypic variability within a species and how it corresponds to spatial environmental gradients (known as a *reaction norm*) must be documented accurately. This is a difficult task in the fossil record because it necessitates a detailed understanding of the relationship between morphology and environment and how both vary with geography. Assessing this relationship hinges on the ability to recognize accurately environmental signals within the available deposits. Most studies from the fossil record (particularly in settings older than the Neogene) rely on qualitative descriptions of environmental heterogeneity such as lithology, sedimentological characteristics, or larger-scale ecological associations. Although highly valuable, these approaches potentially lack the resolution necessary to recognize subtle environmental shifts that may be inducing phenotypic plasticity, especially within depositional settings consisting of single lithofacies. Being able to characterize geographic patterns in morphology and environment requires well established and highly resolved stratigraphic correlations. This is difficult in depositional settings where geographic coverage is limited or where fine-scale stratigraphic correlations are lacking. Secondly, once the reaction norm for a species is characterized, it must then be evaluated over time. This addresses whether the relationship between phenotypic expression and environment is stable or changes over time.

The richly fossiliferous Kope Formation makes an excellent setting in which to conduct this analysis because these strata currently form the basis for ongoing, high-resolution correlation studies across a wide geographic area. In addition, high-resolution faunal gradient analysis has revealed regionally traceable, fine-scale environmental variations in the Cincinnati that commonly occur irrespective of lithologic variations. Subtle non-random variations in morphology that may be attributed to these fine-scale environmental variations along the paleoramp can be characterized by utilizing high-resolution geometric morphometrics.

This study has quantified the norm of reaction in the trilobite *Flexicalymene granulosa* through geographic analyses at a temporal resolution of 10^3 years, and then tracked this relationship between morphology and environment stratigraphically over an interval of 10^5 years. Results indicate that clines are persistent, dynamic and responsive to environmental shifts. Within this clinal regime novel morphologies do not appear and stratophenetic patterns mirror patterns of environmental change due to the dominant process of clinal translocation. Therefore, clines will not be the site of speciation unless environmental perturbation is severe enough to require adaptation rather than migration, or the steepness of the gradient changes sufficiently enough to reduce gene flow and promote isolation.



The trigonotarbid arachnid *Maiocercus celticus* (Pocock, 1902) from the Late Carboniferous (Westphalian) of the Zlatník Formation (Western Carpathians, Slovakia)

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Trigonotarbids are an extinct order of diverse Palaeozoic spider-like arachnids (Chelicerata, Arachnida) which are currently known from the Late Silurian (Přídolí) to the Early Permian (Asselian). They are among the most familiar Carboniferous arachnid fossils. Arachnids in general are rare as fossils, therefore the discovery of any well preserved specimen is noteworthy. Trigonotarbids have been recovered most frequently from the Upper Carboniferous Coal Measures of Europe and North America where they are often one of the most abundant fossil arachnid groups (e.g. Dunlop & Rössler 2002; Garwood & Dunlop 2011). The trigonotarbid fossil presented here has been found during the routine revision of the macrofauna samples from the Upper Carboniferous (Westphalian) site near Dobšiná in Slovakia, which were collected in 1981 and deposited at the Department of Geology and Paleontology of the Comenius University in Bratislava. Fossil bearing strata of the Zlatník Formation near Dobšiná are one of the oldest documented sites with well preserved macrofossil content in Slovakia. The formation is composed of fine grained or slightly sandy siltstones and limestones which originated in a shallow marine-deltaic environment (Sitár & Čapo 1999). Organodetritic admixture mostly of fragmented bivalve, brachiopod or echinoid shells can sometimes be observed. The upper part of the formation is composed of fine- to coarse-grained organodetritic limestones with reefal communities such as corals, bivalves and crinoids (Bajaník et al. 1984). Differences in the faunal composition across the formation suggest a changing environment. According to trilobite and plant discoveries the age of the formation is Late Carboniferous (Westphalian). Bouček & Přibil (1960) identified several trilobite taxa: *Griffithides dobsinensis* Illés, 1902, *G. (Bolandia) rozlozsniki* Rakus, 1932, *Cunningella* aff. *balladoolensis* Reed, 1942, and *Paladin* aff. *eichwaldi* (Fischer, 1825). Some of these taxa are mentioned also by Osmólska (1970); no other research has been conducted with a focus on the trilobite fauna or other arthropods of the Zlatník Fm. Thus, the trigonotarbid specimen presented herein is a welcome find. It represents the first record of its kind from Slovakia and constitutes the first fossil member of the Chelicerata reported from the respective area. The trigonotarbid specimen is identified as *Maiocercus celticus* (Pocock, 1902). It shows a near-complete carapace and opisthosoma with fragments of appendages. Interestingly, the specimen does not come from the Coal Measures but from sediments of shallow marine environment with terrigenous influx. The specimen is flattened with the opisthosoma demonstrating features of both dorsal and ventral aspects, suggesting that only an exuvia with originally relatively thin cuticle is preserved. The opisthosoma of the living animal or a corpse would be filled with tissues which would prevent the observed preservation. Palaeogeographically the studied area was situated south of the East European Platform (close to the Equator) during the Westphalian (Dercourt et al. 2000). It was part of an intramontane post-tectonic Hercynian basin with prevailing river, swamp, lake and deltaic palaeoenvironments (Vozárová 1998). We thank J.A. Dunlop for helpful discussion on the identification of the specimen. The study was supported by research grants APVV-0644-10 and VEGA 2/0068/11.

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Systematic revision and taphonomy of the genus *Stramentum* Logan, 1897 (Cirripedia, Stramentidae) from the Bohemian Cretaceous Basin

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We present a preliminary report on the systematic revision, occurrence and taphonomy of the genus *Stramentum* Logan, 1897 from the Bohemian Cretaceous Basin (BCB). Most fossil cirripede taxa occur as disarticulated and isolated plates of peduncle and capitulum. The Cretaceous genus *Stramentum* Logan, 1897 is a notable exception, because its specimens are sometimes preserved as complete, articulated fossils. Unfortunately, finds of articulated stramentids are rare and their occurrence appears to be restricted to three exceptional circumstances: when cirripede larvae settled on planispirally coiled ammonite shells (examples of cirripedes on heteromorph ammonite shells are rather rare); when cirripedes were embedded in black shales; or when cirripedes were rapidly buried. The first is the case for articulated stramentid specimens from BCB, which were attached to *Collignonicerias woolgari* Mantell, 1822 or *Lewesicerias peramplum* Mantell, 1822. The geological record of the genus *Stramentum* is sparse and fragmentary within BCB. Preliminary study detected only seven specimens; one is housed in the Regional Museum in Teplice, Czech Republic, and other six others in the Palaeontological collections of the National Museum in Prague. All of these individuals belong to the subgenus *Stramentum* (*Stramentum*) Logan, 1897 and those from National Museum are assigned to the species *Stramentum* (*S.*) *pulchellum* (Sowerby, 1843). The specimen from the museum in Krupka is slightly different and its assignment to this species is uncertain. The stramentids from BCB occur in the Lower-Upper Turonian sediments at localities: Bílá Hora in Prague, Středokluky, Koštice, Lahošť and Džbán. Different numbers of peduncle scales indicate various ages of specimens, and small stramentids preserved as negative imprints on the sample from Džbán represent juvenile individuals.

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Ontogeny of *Sao hirsuta* (Barrande, 1846) in the Cambrian of Czech Republic

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The solenopleurid trilobite *Sao hirsuta* Barrande, 1846 is known from Drumian sedimentary rocks of the Czech Republic, Germany and Spain. It is one of the first trilobites in which the ontogenetic development was described in detail (Barrande, 1852). *S. hirsuta* was later revised by Růžička (1943), Whittington (1957) and Šnajdr (1958). The present research is the first modern revision of the ontogeny of this species for more than fifty years and is primarily based on quantitative methods and a detailed study of the morphology of the exoskeleton.

Changes in the dorsal exoskeleton during the ontogenetic development of *S. hirsuta*, including the discovery of post-protaspid intra-instar morphological and size variability and the transition from isometric to allometric growth, are described in detail by using quantitative methods (biometric measurements and geometric morphometrics). The study of segmentation in the species *S. hirsuta* shows hypoprotomeric development with the initial accumulation phase, middle equilibrium phase and terminal depletion phases.

Different instars of *S. hirsuta*, which can be recognized on length/width scatter plot, are described in the protaspid period. Detailed morphological studies reveal several different morphotypes of protaspid stages, some of which may represent different taxa. Metaprotaspid stages belonging to *S. hirsuta* shows typical adult-like morphology, and were probably benthic. It can be an explanation of low paleogeographic distribution of this species in western Gondwanan margin (see Álvaro et al., 2003).

The morphology and condition of the hypostome are described, including changes during ontogeny. Early developmental stages have a conterminant hypostome with a spiny margin. Holaspid stages of *S. hirsuta* have a natant hypostome with conservative morphology sensu Fortey (1990).

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Testing the Arachnomorpha and lamellipedian hypotheses: Whither the trilobites?

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Trilobites are the iconic invertebrate fossils of the Palaeozoic yet consensus on their relationships with other arthropods remains elusive. The Arachnomorpha hypothesis, formulated in the first half of the last century, placed trilobites with a range of predominantly early Palaeozoic arthropod taxa in the chelicerate stem lineage. The alternative placement of trilobites in the crustacean or mandibulate stem lineage has found its advocates but, during the last 60 years, most pundits have favoured Arachnomorpha. Among the non-trilobite taxa affiliated with the arachnomorphs, the megacheirans have garnered particular attention. Early proponents of the Arachnomorpha hypothesis identified these taxa with a large, preoral, ostensibly raptorial appendage as particularly close to the chelicerate crown group. This great appendage was considered to be homologous to the chelicera, a hypothesis that has recently been revived by some researchers. Subsequent workers have stressed the similarity of the postoral appendages in many arachnomorph taxa to the exclusion of megacheirans. The new Lamellipedia was interpreted as a paraphyletic grade of derivatives of the chelicerate stem lineage. Homology of the great appendage with the chelicera was discounted and the megacheirans considered derivatives of the euarthropod stem.

In the last decade, neuroanatomical and developmental data brought renewed momentum to the great appendage–chelicera hypothesis. This also led to a reevaluation of the relationships of lamellipedians, which are increasingly being discussed as possible stem-lineage mandibulates under a modified lamellipedian hypothesis. Most cladistic studies of fossil arthropods published since have focussed on the interrelationships of arachnomorph or lamellipedian taxa. Taxon sampling is usually limited to the supposed ingroups or only part thereof, with the outgroup frequently being a supposed basal lamellipedian or arachnomorph.

Here, we present a broader analysis, aimed at testing the Arachnomorpha hypotheses versus the modified lamellipedian hypothesis. Most of the over 80 included taxa are extinct, and the more than 170 characters coded focus on external morphology recognizable in the fossils. Euchelicerates are represented by three extant and 14 extinct species spanning synziphosurines, xiphosurids, chasmataspids, eurypterids, and scorpions. Three extant myriapods are included in acknowledgement of the Paradoxopoda versus Mandibulata controversy. Crustacea is represented by five extant and seven extinct taxa, including cephalocarids, branchiopods, mystacocarids, remipedes, and malacostracans, as well as four supposed derivatives of the crustacean stem lineage. Lamellipedians are represented by marrellomorphs, 16 artiopod species, three of which are trilobites, as well as *Cheloniellon calmani*, *Sidneyia inexpectans*, *Squamacula clypeata*, and *Aglaspis spinifer*. Among arthropods with a great appendage, five megacheirans and the bivalved *Isoxys acutangulus* were included. Also, several controversial or problematic taxa were included, such as *Canadaspis perfecta*, *Aagnostus pisiformis*, *Sanctacaris uncata*, *Kiisortoqia soperi*, and *Sarotrocercus oblita*. The stem-lineage euarthropod *Shankouia zhengei* was selected as outgroup. The matrix was run in TNT.

Results strongly support the position of all ingroup taxa except *Fuxianhuia protensa* within a well-supported Euarthropoda, contradicting earlier hypotheses that arthropods with a great appendage, *Canadaspis*, or *Sarotrocercus* represent stem-lineage euarthropods. Arthropods with a great appendage and *Kiisortoqia* are well supported as derivatives of the stem lineage of a monophyletic Chelicerata (Pycnogonida + Euchelicerata). *Canadaspis* is retrieved as an early derivative of the mandibulate stem lineage, and *Sarotrocercus* falls among the artiopod taxa which are rendered a paraphyletic grade giving rise to Crustacea. These results falsify the Arachnomorpha hypothesis, but are more in line with the modified lamellipedian hypothesis. Trilobites are likely representatives of the crustacean or pancrustacean/tetraconatan stem lineage.



Morphology and taphonomy of trilobite guts: recent developments and perspectives

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Digestive structures are the only internal organs of trilobites that are commonly preserved in Palaeozoic lagerstätten. As such, they offer unique insights into poorly known aspects of trilobite biology, especially their feeding strategies, through the study of their morphology and preservation. It has been repeatedly proposed that trilobite digestive systems could be grouped into one of two different types. One is characterized by a simple digestive tract narrowing progressively from front to rear and flanked laterally by metamericly paired digestive caeca. No differentiation of the foregut into a crop is observed in the type. In contrast, the second type of trilobite gut is characterized by the presence of a crop under the anterior glabella, followed posteriorly by a simple digestive tract devoid of digestive caeca. This type seems to be associated with trilobites having a large prefrontal glabellar lobe, as also confirmed by the distribution pattern of muscle scars supposedly related to the extrinsic musculature of the crop within the Trilobita. This characterization of two distinct digestive systems in trilobites and their association with different exoskeletal characteristics is supported by several new examples of fossilized guts. However, it is also challenged by the recent observations of 1) a crop co-occurring with digestive caeca in an early meraspid olenid, 2) a crop developed ventrally (and therefore invisible from the dorsal side) in a specimen from the Weeks Formation (Cambrian), and 3) a simple digestive tract devoid of digestive caeca in a typical ptychopariid from the Cambrian of China. Comparisons with extant arthropods fail to illuminate the functional significance of these gut morphologies due to the lack of data concerning key modern taxa such as remipedians. Current investigations on this topic might prove crucial for better understanding the palaeoecology of trilobites and of Cambrian arthropods.

The preservation of digestive structures of trilobites, and more generally of Cambrian arthropods, has received little attention, despite its potential importance for revealing aspects of their biology. For example, enhanced capacities for the storage of Ca and P ions and/or P-rich food (e.g. inarticulate brachiopods, microbial mats) have been recently proposed to explain the particularly extensive phosphatisation of the gut in some trilobites from the Cambrian Weeks Formation. New data will be presented supporting the second hypothesis. From an enrolled ptychopariid from the Cambrian of China with sediment-filled gut, it can also be demonstrated without ambiguities that other trilobites were truly deposit feeders. These two examples illustrate that taphonomic explorations can be as informative as morphological investigations in the study of fossilized guts of trilobites. Techniques such as scanning electron microscopy or energy dispersive x-ray analyses, which are now available to most scientists, provide critical data and should become indispensable tools for the study of trilobite guts in the future.

In summary, our current understanding of the digestive system of trilobites is still too limited to permit general inferences on the diversity of their feeding habits and their roles in Palaeozoic marine ecosystems. However, recent investigations demonstrate the importance of a taphonomic approach to understanding trilobite biology. Furthermore, renewed study of modern analogues hold promise for generating new insights into the architecture of trilobite digestive systems.



Trilobite associations and correlation of different facies deposits of lower part of the Upper Cambrian in the north-west of the Siberian Platform

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Different facies deposits contain various associations of fauna. In the north-west of the Siberian Platform in the early part of the Late Cambrian both open marine and lagoon environments with different trilobite associations existed. In the Chopko River section (Noril'sk area) many cosmopolitan forms have been found. Here the stratotype of the Omnian Stage (Varlamov & Rosova, 2009) was established in the lowermost part of the Upper Cambrian. It is subdivided into the *Glyptagnostus reticulatus*, *Stigmatia destructa* and *Erixanium sentum* zones. The *Glyptagnostus reticulatus* Zone, characterized by the index-species accompanied by numerous polymerid trilobites and agnostoids, is subdivided (bottom to top) into beds with *Nganasanella granulosa*–*Acrocephalites levatus*, beds with *Eugonocare tessellatum*, and beds with *Acrocephalaspis orientalis*–*Glyptagnostus nodulosus*. This part of the Chopko River section is assigned to the Chopko Formation, consisting of dark grey limestones, silty limestones with intercalations of marls, and breccias, interpreted as deposits of an open marine, relatively deep-water environment.

The Kulyumbe River section (Igarka area) contains very different trilobite associations from the Chopko River section despite its geographical affinity. Here *Glyptagnostus reticulatus* (Angelin) is absent and many of the species present are endemic. The Kulyumbe section, the stratotype of the lower Upper Cambrian Kulyumbian Stage (Rosova, 1964, 1968, 1984), is subdivided into the *Koldiniella convexa*–*Pedinocephalites minimus* Zone (Nganasanian horizon) and the *Koldinia minor*–*Pesaiella obnixa* Zone (Tavgian horizon). The section is assigned to the Oracta Formation, consisting of green-grey fine-grained limestones deposited in an inner shelf or lagoon environment.

Trilobite associations that evolved in different facies conditions have very few forms in common, and the correlation of such deposits is often difficult and ambiguous. Several variations in the correlation of the Chopko River and Kulyumbe River sections have been proposed. The base of the *Glyptagnostus reticulatus* Zone of the Chopko River section has been correlated with 1) the base of the *Koldiniella convexa* Zone (the stratotype for the base of the Nganasanian horizon) (Rosova, 1968, 1984; Rosova in Varlamov et al., 2005; Varlamov and Rosova, 2009); 2) the base of the *Koldinia minor* Zone (the stratotype for the base of the Tavgian horizon) (Varlamov, 2011); 3) the upper part of the *Koldinia minor* Zone (the upper part of the stratotype for the Tavgian horizon) (Anon... 1983); 4) the lower part of the *Maspakites-Idahoia-Raashellina* Zone (Lazarenko, 1968); or 5) the base of the *Acidaspidina plana* Zone (the stratotype for the base of the Maduan horizon) (Pak in Varlamov et al., 2005). Some other variations in correlation have also been proposed.

Recently obtained data confirm the correlation of the base of the *G. reticulatus* Zone with the lower part of the *Koldiniella convexa* Zone, as proposed by A.V. Rosova. Common forms present in both the Omnian and Kulyumbian stages are *Schoriecare latum* Rosova, and species of *Nganasanella* Rosova, *Acrocephalinella* Romanenko and *Pteraspis* Rosova et Makarova. Species of *Schoriecare* Rosova, *Acrocephalinella* Romanenko, *Acrocephalites* Wallerius and *Rina* Poletaeva are abundant in the upper part of the traditional Middle Cambrian in the stratotype of the Sakha horizon (lying just below the Nganasanian horizon) in the Kulyumbe River section. Representatives of these genera can also be found in the lower part of the *Glyptagnostus reticulatus* Zone (together with the index-species) of the Chopko River section. Hence the base of the Omnian Stage is correlated with the base or lower part of the Kulyumbian Stage (the lower part of the Nganasanian horizon).



The turbulent path of *Tariccoia arrusensis*: palaeoecology of an Ordovician nektaspid endemic to Sardinia.

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Tariccoia arrusensis Hamman, Laske & Pillola 1990 is a Late Ordovician trilobite-like arthropod endemic to Sardinia. This arthropod has a non-mineralized, smooth exoskeleton, presumably chitinous, without abaxial trilobation, devoid of eyes and with four thoracic segments. *Tariccoia* is found locally within the massive grey siltstones of the Riu Is Arrus Member (Monte Argentu Formation) that crops out extensively along the valley of the Riu Is Arrus Creek, south-east of Fluminimaggiore (SW Sardinia).

In order to shed light on the palaeoecology of this peculiar arthropod, taphonomic and sedimentologic studies of two stratigraphic sections of the Riu Is Arrus Member were made. The locality Roia Srappas is the most distinctive with regards the fossil content, which consists of *Tariccoia* and only a few other organic remains of plants and rare trace fossils. The facies analysis indicated that the clastic sequence of crudely stratified microconglomerate/sandstone levels, siltstones and massive and rippled sandstones was deposited by turbidity currents (hyperpycnal flows) generated by a flood-dominated fluvio-deltaic system entering lagoonal or protected shallow marine settings.

Detailed taphonomic analysis allowed the discrimination of two taphofacies. The first taphofacies consists of a high density of *Tariccoia arrusensis* exoskeletons of which 45% are articulated, and 92% of these are oriented ventral side-up. The second taphofacies is characterized by disarticulated sclerites only. The occurrence of the first taphofacies immediately above the microconglomerate/sandstone levels suggests that the arthropods were periodically engulfed and transported by the hyperpycnal plume and subsequently settle to the bottom upside down (falling leaf effect). In order to explain the preferred convex down position, supposedly related to the peculiar morphology and post-mortem rheotaxis, a Computational Fluid Dynamics (CFD) study was carried out. A commercial CFD code, based on the Finite Volume methodology that solves for the governing equations, simulates the interaction between the fluid and the exoskeleton during the post-mortem settling path. These integrated sedimentologic, taphonomic, ecologic and hydrodynamic approaches point to unfavorable ecological conditions in a quiet marginal/lagoonal shallow water environment.



Odontopleurid trilobites from the latest Katian of Bohemia, their ancestors and relatives

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Apart from *Selenopeltis*, odontopleurid trilobites are not common in the late Middle and Upper Ordovician succession of the Prague Basin, for at least two reasons. The first is the relatively mild to cool climate of the Perunica terrane in the late middle and early upper Ordovician, which was not favourable for many genera of the odontopleurid clade. The second reason is that the mainly deep-water succession of the Prague Basin was deposited in oxygen-deficient waters in a mid- to outer-shelf environment that was generally hostile for the clade. The changing climate in the Late Ordovician (the Boda Event in the Katian succeeded by a cooling and glacieustatic sea level drop in the Hirnantian) radically changed the physical environment in the basin, resulting in the appearance of new trilobite taxa, exemplified by the low-latitude *Staurocephalus* and the high-latitude *Mucronaspis*, as well as new odontopleurids. The characteristic high-latitude *Selenopeltis* disappeared in the early Katian.

Recent sampling in carbonate claystones informally referred to as the ‘Perník Bed’ at the top of the Králův Dvůr Formation (latest Katian) yielded taxonomically diverse odontopleurids. The specimens are very fragmentary but minute details of morphology are preserved in the claystone. The commonest odontopleurid is the minute *Diacanthaspis krizi* sp. nov., characterized by a pygidium having eight marginal spines, a number that is unique within the genus. The species arose allopatrically from the same clade as *Diacanthaspis* species present in the East Baltic, Spain and Sardinia. The medium-sized *Bojokoralaspis peregrina* (Barrande, 1846) (= ‘*Acanthaloma*’ *mirka* Marek, 1952; see Shaw 2000) first appears in the lower- to mid-Katian of the Králův Dvůr Formation, and other species are present in the Hirnantia fauna of the uppermost Hirnantian. Two other odontopleurids from the Perník Bed are very rare. *Chlustinia* sp. nov., known from a single pygidium, is the youngest member of the genus in the Prague Basin, and differs from older representatives in having shorter major border spines. *?Ceratourus* sp. is known only from an incomplete, rather deformed cranidium with robust occipital spines.

The presence of four odontopleurid species in the Perník Bed is unusual, and demonstrates the taxonomic diversity of the latest Katian benthic fauna and the influx of warm-water elements prior to the onset of climatic cooling in the Hirnantian.



Revision of Agnostina from Russian territory

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Members of the Suborder Agnostina described from the Siberian Platform and the Altay fold belt are revised, and their localities and ages given. There are representatives of 16 families, 70 genera and 210 species known from Russian localities, including 13 genera and 62 species originally identified from Russian territory, and 116 species previously known from elsewhere.

We suggest a taxonomic system for the Ptychagnostidae (9 gen., 22 sp.), summarizing current differing views. Ptychagnostidae comprises species with a fully developed preglabellar furrow, with a postaxial furrow developed at least in the meraspid stages, and with the pygidial F1 and F2 developed. Other features (the size of basal lobes, the shape of a posteroglabella and posteroaxis, the relative development of axial and glabellar F1 and F2) are considered to be useful in distinguishing genera; while features such as cephalic and pygidial spines, postaxial furrow and sculpture on the acrolobes are useful for distinguishing species. This taxonomy allows us to formally resolve the mosaic of features present in ptychagnostid genera and subgenera. *Zeteagnostus* is regarded as a subgenus of *Ptychagnostus*, and *Myrmecomimus* as a subgenus of *Aotagnostus*.

Revision of Peronopsidae (8 gen., 36 sp.) is based on the ontogenetic development of pygidial features. *Micagnostus* and *Eoagnostus*, both with effaced anteroglabella, are transferred to this family from the Spinagnostidae. *Itagnostus* and *Gratagnostus* have gained representatives from Siberian localities. *Peronopsis crassa* is assigned to *Ammagnostus*, while its lower “Middle” Cambrian forms are referred to as *Peronopsis montis*.

Doryagnostidae is represented only by *Euagnostus opimus* (= *Hypagnostus tesella* from Siberia) and *Doryagnostus incertus*.

Diplagnostidae (8 gen. 17 sp.) is divided into two subgroups. The first of these, comprising early diplagnostids originating from *Peronopsis*, is characterized by the absence or only incipient development of zonation on the pygidial border, and by poor development of F1 and F2. The other subgroup includes late diplagnostids, which probably descended from Baltagnostus. The Australian species *Diplagnostus atavorum* and *?Connagnostus zonatus* are synonymized with *Diplagnostus latus* and *Dolichagnostus levis* respectively. *Linguagnostus tricuspis* (= *L. paibiensis*) and *L. aristarius* (= *L. kierulfi* from Kazakhstan) appear to be the same as forms from China and Kazakhstan. Spinagnostidae (5 gen., 15 sp.) is unchanged, except that two genera are reassigned to the Peronopsidae, and *Phalacroma calva* Pokrovskaya, 1958 (= *Phalagnostus rasettii* Pratt, 1992) is assigned to *Lisogoragnostus*.

Ammagnostidae (5 gen., 14 sp.) is supplemented with representatives of *Hadragnostus*, previously unknown from Siberia.

Within the Agnostidae (9 gen., 19 sp.), six basic characters are useful for generic diagnoses: median preglabellar furrow, width of border furrow on cephalon and pygidium, length of pygidial axis, shape of pygidial axis, lanceolate field on the posteroaxis. An additional diagnostic feature may be the shape of the pygidial F1, though it varies between species. Other features seem to be insufficient to distinguish genera. *Eurudagnostus* Lermontova, 1951 (= *Salagnostus* Gabova, 2008) is revised and re-established for species having a wide border furrow on the cephalon and pygidium, and a short pygidial axis. Some species previously referred to *Micragnostus* should be transferred to *Eurudagnostus*, with *E?. brevispinus* being recorded in Siberia, Kazakhstan, northern China and Tasmania. *Distagnostus* conforms to the generic concept of *Trilobagnostus*.

From our revision of Pseudagnostidae (9 gen., 22 sp.) we infer the following. *Rhaptagnostus* differs from *Pseudagnostus* in having narrow border structures. The type species of *Pseudorhaptagnostus* (= *Neoagnostus* Kobayashi, 1955), *P. simplex* Lermontova, 1951, is represented in the type series by a mixture of two species, *P. simplex* and *Rhaptagnostus cyclopygeformis* Sun, 1924 (= *Pseudagnostus obsoletus* Lermontova, 1951), but the published description and illustrations are of *P. simplex* only. Therefore, *Pseudorhaptagnostus* appears to be valid. Well preserved specimens of *Triadaspis* demonstrates the features of Oidagnostidae instead of Clavagnostidae. *Tasagnostus compani* seems to be a junior synonym of *Oidagnostus eximius* Romanenko, 1967.



The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda

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Aglaspidids are an extinct group of Palaeozoic arthropods that are notorious for their unstable taxonomy and disputed affinities, acquiring a reputation as a "bucket taxon" for problematic taxa. The phylogenetic position of aglaspidids has been controversial for over 70 years, having been aligned with chelicerates or chelicerate-allied arachnomorphs. However, a position closer to trilobites and other closely related taxa (i.e. Trilobitomorpha) has been suggested based on the presence of an antenniform pair of anterior appendages and an hypostome. Here, we present a comprehensive cladistic analysis, including 10 genera of aglaspidids *sensu stricto*, 6 aglaspidid-like arthropods and 42 Palaeozoic arthropod taxa.

The results confirm an aglaspidid identity for several recently described arthropods, including *Quasimodaspis brentsae*, *Tremaglaspis unite*, *Chlupacaris dubia*, *Australaglaspis stonyensis* and an unnamed Ordovician Chinese arthropod. The problematic Bohemian arthropod *Kodymirus vagans* was recovered as sister taxon to *Beckwithia typa*, and both form a small clade that falls outside *Aglaspidida sensu stricto*, thus discarding eurypterid affinities for the former. The analysis does not support the phylogenetic position of *Kwanyinaspis maotianshanensis* at the base of *Conciliterga* as proposed in recent studies, but rather occupies a basal position within *Aglaspidida sensu lato*. The results indicate a close association of aglaspidid arthropods with xenopods (i.e. *Emeraldella* and *Sidneyia*) and cheloniellids (e.g. *Cheloniellon*, *Duslia*). The phylogenetic position of aglaspidid arthropods makes them good outgroup candidates for analysing the internal relationships within the groups that form Trilobitomorpha. This work provides a much clearer picture of the phylogenetic relationships among Lower Palaeozoic artiopodans.



Ancestral patterning of tergite border formation in a centipede suggests derived mode of trunk segmentation in trilobites

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Trilobites are some of the most common and abundant metazoans preserved in the fossil record, but little is known about the intrinsic mechanisms that orchestrate their body organization. The phylogenetic position of trilobites within total-group Euarthropoda, however, allows making inferences about the processes of segment formation in these extinct taxa, as some of the fundamental genetic processes for constructing the body segments are remarkably conserved among extant arthropods. This talk addresses the problem of trilobite trunk segmentation by drawing comparisons with conserved mechanisms for tergite (i.e. dorsal exoskeletal plates) formation, and its associated gene expression, in extant representatives. The results obtained from studying the development of the dorsal exoskeleton in the centipede *Strigamia maritima* clarifies the plesiomorphic correlation between the expression of the segment polarity gene *engrailed* and the formation of the tergites in euarthropods, and revives old trilobite segmentation models in which the tergite borders do not correspond directly to the underlying body segments. These observations suggest that trilobites, as well as other closely related taxa, had a considerable, and largely unsuspected, degree of developmental complexity.



Is the Guzhangian Stage (Cambrian) acceptable in Siberia?

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The Guzhangian Stage was ratified in 2008. The cosmopolitan agnostoid trilobite *Lejopyge laevigata* was chosen as the principal marker for defining its lower boundary, and its upper boundary coincides with the base of the Paibian Stage. *L. laevigata* occurs worldwide including Siberia, but its FAD in the Middle Cambrian strata of Siberia is noticeably higher stratigraphically than in the stratotype section of the Guzhangian Stage at Luojixi, Hunan, China. Comparison of the distribution of trilobites in the stratotype sections at Luojixi and Wangcun, China, compared with the stratotype section of the Maya stage in the southeast of the Siberian platform, shows a general correspondence in the succession of the main zonal species of agnostoids for this interval in the traditional Middle Cambrian: *Ptychagnostus gibbus*, *P. atavus*, *P. punctuosus*, *Goniagnostus nathorsti*, *Lejopyge laevigata*. Several other species have a wide stratigraphic range or appear at different levels in China and Siberia, and are not useful for accurate correlation: *Hypagnostus parvifrons*, *H. brevifrons*, *Diplagnostus planicauda*, *Linguagnostus kjerulfii*, *Glaberagnostus bituberculatus*, *Lejopyge armata*. Only three species can serve for rather precise correlation:

1. *Tomagnostella sulcifera* appears in the Luojixi section definitely higher stratigraphically than the FAD of *Lejopyge laevigata*, and much higher in the Wangcun section, whereas in the stratotype Maya section *T. sulcifera* appears distinctly lower than *L. laevigata*.
2. In the Luojixi section, the first appearance of *Goniagnostus spiniger* lies above the FAD of *L. laevigata*, and in the Maya section, *Goniagnostus longispinus*, a possible synonym of *G. spiniger*, appears much lower than the FAD of *L. laevigata*.
3. The FAD of the polymerid trilobite *Pianaspis attenuata* in the Luojixi section is higher than the FAD of *L. laevigata* and at the same level as that of *G. spiniger*, whereas in the Maya section *P. attenuata* appears far below the FAD of *L. laevigata* and a little above the FAD of *G. longispinus*.

Recovery of the cosmopolitan agnostoid trilobite *Ptychagnostus atavus* from the lowermost beds of the *Lejopyge laevigata* Zone in the Luojixi section provides indirect evidence for the much earlier appearance of *L. laevigata* in the Middle Cambrian of China than in Siberia. Apparently *Lejopyge laevigata* and *Ptychagnostus atavus* have never been observed to occur together. It seems that the FAD of *L. laevigata* in the Luojixi section corresponds to the uppermost part of the *Ptychagnostus punctuosus* Zone in Westergård's agnostoid biostratigraphy of Sweden. In this case the agnostoid zonation of Sweden does not quite correspond to that in China.

Comparison of the distribution of trilobites in the Middle Cambrian of Sweden and Siberia provides more information for evaluating the relative stratigraphic positions of FADs of *L. laevigata* in China and Siberia. The base of the Guzhangian Stage is confidently correlated with the base of the *Solenopleura? brachimetopa* Zone of Sweden, which thus corresponds with the lower part of the *laevigata* Zone in China. The assemblage of mainly polymerid trilobites of the *brachimetopa* Zone includes *Centroleura (loveni, angelini)*, *Proampyx (acuminatus, aculeatus, difformis, anceps)*, *Anomocarioides (limbatus)*, *Anomocarina (excavata, extornata)*, *Elix (laticeps)*, *Solenopleura* (many species), *Dasometopus (breviceps, ? incertus)*. Most of these genera and some of the species occur in Siberia in the *Anomocarioides limbataeformis* Zone, which lies above the *Anopolenus henrici* Zone (correlated with the *Ptychagnostus punctuosus* Zone) and below the *Lejopyge laevigata*-*Aldanaspis truncata* Zone. In addition, *Anomocarioides limbataeformis*, *Proampyx acuminatus* and *Centroleura angustata* disappear below or at the same level as the FAD of *Lejopyge laevigata*, and *Anomocarina splendens* appears lower than *L. laevigata*. Thus the FAD of *Lejopyge laevigata* in the Luojixi section can be correlated with the lower part of the *Anomocarioides limbataeformis* Zone in the Maya section. The FADs of *Lejopyge laevigata* in China and Siberia are therefore markedly diachronous. The only main principle for the establishing of the Global Standard Stages is a primary importance of the defining their lower boundaries which have to be isochronous. So one can conclude that the Guzhangian Stage is not acceptable in Siberia.



Evolution of the Furongian (late Cambrian) trilobite family Tsinaniidae

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Since the advent of cladistics, monophyly has been accepted as the only proper grouping for classification in biology. However, recent studies have increasingly addressed some problems involving the monophyly-obsessed classification. The cladistic classification system recognising only monophyletic taxa neither correctly reflects the underlying evolutionary process, nor is compatible with the Linnaean classification system. As the fossil data provide a temporal aspect of evolution, this issue is especially critical for palaeontology. Here we report successive occurrences of four species of the kaolishaniid genus *Mansuyia* and a tsinaniid trilobite *Tsinania canens* from the Furongian (late Cambrian) Chaomidian Formation in Shandong Province, China. A cladistic analysis including these taxa reveals that the four species of *Mansuyia* form stem-group taxa to the family Tsinaniidae, rendering *Mansuyia* and the Kaolishaniidae paraphyletic. The youngest species of *Mansuyia*, *M. taianfuensis*, turns out to be the immediate sister-taxon of the Tsinaniidae, displaying a closely similar morphology to the tsinaniid trilobite, *Shergoldia laevigata*. Nonetheless, it is proposed that the paraphyly of the genus *Mansuyia* and the family Kaolishaniidae should be maintained with the generic and familial boundary situated between *M. taianfuensis* and *S. laevigata*, because recognizing only monophyly is essentially impractical especially in palaeontology.



Morphology of the thoracic pleurae of *Evropeites*.

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Evropeites is a trilobite genus of the Suborder Cheirurina, first given subgenus status by Balashova in 1961. It was based on the East Baltic taxon first described as *Cheirurus* (*Cyrtometopus*) *primigenus* Angelin, 1854 var. *lamanskii* Schmidt, 1906, and as its name indicates it shows close resemblance to a taxon described from the western part of Baltoscandia. Other representatives of the genus have been reported from Spitzbergen. Further studies have showed that despite its similarities with *Pliomeroides primigenus* (Angelin) it represents a separate genus, and belongs together with another pliomereid taxon determined as *Pliomeroides toernquisti* by Holm in 1882. Holm's figure shows a thorax with ten pleurae bearing wide pleural furrows, and which are curved like those of asaphids and have a flat facet distally. A closer look at the specimen reveals a condition that is rather different from what is seen from the illustration. Preparation of the specimen led to the discovery of a pygidium that is tilted at about 90 degrees downwards from the end of thorax. The pygidium has only two pairs of pleurae and is similar in morphology to pygidia found together with the cranidia of *Evropeites lamanskii* and thought to be conspecific. These two taxa come from nearly(?) contemporaneous beds of Floian age.

Pliomeroides primigenus has (at least) eleven thoracic segments as does *Evropeites lamanskii*, but the number of pleurae on the pygidium is five in *P. primigenus* and two in *E. lamanski*. Two pairs of pygidial pleurae are more common in the Cheiruridae, such as in the earliest ones (not yet named) from Laurentia, or in much younger acanthoparyphines. The same number of pleurae, which are also similar in shape, are present in the Tremadocian *Anacheirurus frederici* (Salter, 1864) from Wales and Morocco, and in *A. bucenus* (Ancygin, 2001) from the Tremadocian of the Urals. However, species of *Anacheirurus* have fewer thoracic pleurae, of which the last ones end in long spines different from the situation in the Baltoscandian taxa.

Comparison of the details in the structure of the thoracic pleurae of *Evropeites* with those of several other pliomereids, cheirurids and encrinurids allows us to demonstrate rather large differences in these groups.



Artiopodan arthropod diversity from the early Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia

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The early Cambrian (Series 2, Stage 4) Emu Bay Shale Konservat-Lagerstätte is situated on the northeast coast of Kangaroo Island in South Australia. Recent excavations (2007–2012) at Buck Quarry have revealed a surprising diversity, with over 50 species now known. The Emu Bay Shale biota is dominated by arthropods (>50%), including anomalocaridids, a variety of artiopodans (including trilobites), bivalved taxa (e.g., *Isoxys*, *Tuzoia*, *Canadaspis*?) and cheliceramorphs (e.g., the megacheiran *Oestokerkus*), with the remaining species diversity comprising various other ecdysozoans (e.g., priapulids and a lobopodian), sponges, molluscs, brachiopods, a polychaete annelid, and a variety of problematic forms. Although the constituent taxa represent a typical Burgess-Shale-type (BST) fauna, Emu Bay Shale fossils commonly display a range of taphonomic modes that are otherwise rarely co-occur in most other BST deposits, particularly phosphatisation and pyritisation.

The Artiopoda was erected by Hou and Bergström to group trilobites and other allied ‘trilobitomorphs’, including nektaspids (i.e., naraoiids and kin), retificiids, concilitergans, petalopleurans, xenopodans and aglaspidids. Subsequent phylogenetic analyses have shown support for the Artiopoda as a clade, but the interrelationships of the major clades within it – including the sister group of Trilobita – have remained largely unresolved.

Trilobites are a dominant constituent of the Emu Bay Shale biota, especially the species *Estaingia bilobata* (>75% of individuals within the biota) and *Redlichia takooensis*. Mould ensembles and soft-shelled specimens of these species are known, and the preponderance of dorsum-down individuals (>75% within three densely sampled horizons at Buck Quarry) may be indicative of mass asphyxiation due to episodic benthic anoxia, with build-up of decay gases overturning carcasses. Three other species, *Balcoracania dailyi*, *Megapharanaspis nedini* and *Holyoakia simpsoni*, are very rare and possibly represent vagrants within the typical benthic assemblage.

Trilobites aside, other artiopodans are ubiquitous in Palaeozoic (especially Cambro-Ordovician) Lagerstätten, and the Emu Bay Shale is proving to be no exception. We have described two nektaspids, *Emucaris fava* and *Kangacaris zhangii*, that are resolved cladistically as a monophyletic group (the family Emucarididae) and is sister to Naraoiidae and Liwiidae (Paterson et al. 2010). The position of emucaridids as basal nektaspids, coupled with the stratigraphic and biogeographic data of other members of this clade, suggests that the Nektaspida may have emerged earlier than Cambrian Stage 3 (i.e., pre-dating the trilobite record). Other recently described artiopodans from the Emu Bay Shale include: *Squamacula buckorum*, the first occurrence of this genus outside of the Chengjiang Biota of South China; and *Australimicola spriggi*, a monotypic genus resolved in a cladistic analysis as a concilitergan – a clade otherwise consisting of Burgess Shale and Chengjiang taxa such as *Helmetia*, *Kuamaia*, *Saperion*, *Skioldia* and *Tegopelte* (Paterson et al. 2012). Specimens of *Squamacula* and *Australimicola* also exhibit three-dimensional, permineralised (phosphatised) midgut glands, similar to those seen in a diverse range of arthropods from other Cambrian Lagerstätten. A rare petalopleuran-like taxon with a short, semi-circular head shield, short antennae, and approximately 17 chevron-like thoracic tergites awaits formal description.

The discovery of these Emu Bay Shale taxa has extended the biogeographic range of at least two major clades within the Artiopoda – the nektaspids and concilitergans – to East Gondwana. Perhaps not surprisingly, the occurrence of *Squamacula* and *Kangacaris* in the Emu Bay Shale and Chengjiang biotas has strengthened the biogeographic ties between Australia and South China, as echoed by the more common biomineralised arthropod groups such as trilobites and bradoriids.

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Cambrian trilobite associations of the Diringde reef complex (northern Siberian Platform, Russia)

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The Diringde reef complex is located in the Kotuy River basin within the South-West Anabar Region (northern Siberian Platform, Russia). During the late mid-Cambrian-early Late Cambrian two detached carbonate buildup massifs were formed at the shelf margin of the epicontinental sea basin. The southern mid-Cambrian massif is replaced laterally by argillite-carbonate rocks of the open basin slope. The northern mid-Cambrian-Upper Cambrian massif is replaced laterally by inner shelf dolomites. The central parts (or cores) of each of the massifs are composed of algal limestone bioherms. There are narrow zones of facial transition (flanking layers) from the organic buildups to enclosing stratified floatstones/rudstones/grainstones to wackestone. Although being coeval, the trilobite associations of the cores and flanking layers are taxonomically different. The core trilobite assemblages consist of endemic polymerids, distributed mainly in interbeds and lenses of platy detrital limestone filling spaces between the algal buildups. Trilobite cranidia are usually convex, hemispherical in outline, with a massive glabella, narrow fixed cheeks and small palpebral lobes. Trilobite associations in the inner parts of bioherms are very scarce, monotypic or consisting of 2-3 species with rare individuals. Sometimes they form small gatherings. Trilobite associations in the marginal parts of the cores are more abundant and diverse, with a taxonomic composition similar to the trilobite associations of flanking layers. However, the latter ones differ in their greater abundance, higher taxonomic diversity, and the presence of rare agnostoids. Polymerids from the flanking layer associations often have flattened cranidia, different ratios of glabella and fixed cheeks dimensions, long and curved palpebral lobes and a long frontal area. The abundance and variety of agnostoids rises towards the open basin slope.

In the southern mid-Cambrian massif the core trilobite assemblage consists of *Maiaspis* Chernysheva, *Koldinia* Walcott et Resser, *Onchonotellus* Lermontova, *Plethopeltoides* Khramova, *Seletella* Ivshin, *Buttsia* Wilson, *Acidaspides* Lermontova, *Bonneterrina* Lochman and *Munija* Khramova. The trilobite assemblages from the coeval flanking layers include in addition *Olenekella* Khramova, *Acidaspidella* Rosova, *Sacha* Rosova, *Nganasanella* Rosova, *Trinia* Poletaeva, *Nericella* Rosova, *Schoriecare* Rosova, *Schmidaspis* Kobayashi and *Ammagnostus* Öpik. The youngest trilobite association from the filling strata in the rear side of the southern massif includes *Koldinia* Walcott et Resser, *Nganasanella* Rosova, *Catuniella* Egorova, *Pauciella* Rosova, *Raduginella* Egorova, *Grönwallina* Rosova, *Koldiniella* Lermontova, *Ammagnostus* Öpik and *Skryjagnostus* Šnajdr.

The trilobite association from the core base of the northern massif contains some genera common with the mid-Cambrian southern massif: *Seletella*, *Koldinia*, *Maiaspis* and *Munija*. In related flanking layers, species of *Schoriecare* Rosova and *Prismenaspis* Ergaliev occur. The remainder (overlying part) of the core and the flanking layers are characterized by younger trilobite associations, including various species of the Late Cambrian *Theodenisia* Clark together with species of *Albansia* Lochman, *Seletella* Ivshin, *Pagodia* Walcott, *Munija* Khramova, *Buttsia* Wilson and *Ritella* Khramova.

The trilobite assemblages of the core and flanking layers of the Diringde reef complex are similar to the mid to Late Cambrian assemblages of the reefal Chukuka Formation in the neighboring South Anabar Region. The flanking layer assemblages of the southern massif mainly consist of species distributed in the Cambrian upper slope deposits in the Kuljumba River reference section, northwestern Siberian Platform. The trilobite assemblage of the deeper water deposits joined to the seaward side of the Diringde reef complex combines typical elements of the mainly endemic shallow-water shelf associations described above and slope basin communities, with various cosmopolitan agnostoids (*Proagnostus bulbosus* (Butts), *Oidalagnostus trispinifer* Westergård, *Clavagnostus sulcatus* Westergård, *Hypagnostus (Tomagnostella) sulcifer* Wallerius, *Lejopyge laevigata* (Dalman), etc.). The Cambrian deposits of different facies of the Siberian Platform are correlatable in this region.



***Svobodapeltis* and other effaced illaenid trilobites from the Mediterranean Ordovician**

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Effacement in typical illaenimorph trilobites involves the trend towards increased exoskeletal convexity and a progressively 'smoother' appearance of the cephalon and pygidium, until only axial furrows are barely distinct. Widening of the thoracic axis and narrowing of the pleurae leads certain forms to resemble some other illaenids and styginids (i.e. *Bumastoides*, *Bumastus*, *Thomastus*, etc.), but these are rare forms among the twenty-odd different illaenids so far known in the Mediterranean Ordovician. Effacement of the dorsal exoskeleton tends to obscure many of the usual features of taxonomic value, making the generic affiliation of several species with bumastine appearance problematic. This is the case for some genera like *Svobodapeltis* that are not usually mentioned in the discussion on modern classifications of illaenid trilobites.

The genus *Svobodapeltis* Šnajdr 1957, so far restricted to its type species *S. avus* (Holub 1908) [= *Bumastus pragensis* Klouček 1916], is an apparently endemic form that is known from about 20 incomplete specimens, coming from very few localities of Oretanian (mid Darriwilian) age in the Prague Basin (Šárka Formation). Its diagnostic characters are the very wide glabella and thoracic axis, the length and curvature of the cephalic axial furrows, the size and position of the eyes, the narrow (tr.) fixigenae and narrow and rounded librigenae, 10 thoracic segments with short (tr.) pleurae, and a pygidium that is slightly smaller than the cephalon, with indistinct axis and narrow doublure. However, comparison of different photographs of the same material published in several papers (Šnajdr 1957; Horný and Bastl, 1970; Kraft, 1972; Bruthansová, 2003) allows the recognition of a wide pygidial axis in the type specimen, which also shows some remnants of segmentation, and the development of a marginal holcos (= concave border), which was confused by previous authors with a narrow doublure, still unknown in *Svobodapeltis*.

A possible second species of the genus is provisionally designated here as *Svobodapeltis?* *guillouorum* sp. nov. (nomen nudum), recorded from two localities near the top of the Traveusot Formation (*Marrolithus bureaui* Biozone) in the Armorican Massif, in beds of latest Dobrotivian (early Sandbian) age. The new species has been confused with either *Ectillaenus advena* (Barrande) or *Dysplanus* sp. by French amateur collectors, but its cephalic and thoracic features fit better with the type species of *Svobodapeltis*. Compared with *S. avus*, the anterior margin of the pygidium shows a more or less pronounced median arch and shallow indications of a short (sag.) and triangular axis on deformed internal moulds, as well as a relatively wide pygidial doublure.

A third form, somewhat similar to the previous ones, comes from younger beds in the central Anti-Atlas of Morocco (Lower Ktaoua Formation, undefined early to mid Berounian, Sandbian to Katian 2 age). It shows a slightly narrower cephalic and thoracic axis than in the former taxa, and the pygidium is longer than the cephalon but just as convex. With the exception of some Silurian and Devonian styginids, typical illaenimorph trilobites have a pygidium that is wider than long. In the new north-African form, the pygidium is subtriangular in outline, comparatively long, with almost completely effaced axial furrows and an axially-restricted holcos. These pygidial features, unique among known illaenid genera, may serve to diagnose the new form *Caudillaenus nicolasi* gen. et sp. nov. (nomina nuda), which also shows a striking sphaeroidal type of enrolment.

The presence of these bumastine-like illaenids, although scarce and limited to endemic forms, is interesting in order to complete the palaeobiodiversity range of the entire group in the high southern paleolatitude Gondwanan platforms before the Hirnantian extinction. Until additional material is found with details of the ventral exoskeleton preserved, such the rostral plate, hypostome and pygidial doublure, it is too early to say whether these three species constitute a single evolutionary lineage from mid Darriwilian (*S. avus*), early Sandbian (*S.?* *guillouorum*) to Sandbian or early Katian (*C. nicolasi*).

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A revision of the Late Ordovician marrellomorph arthropod *Furca bohemica* from Czech Republic

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The Upper Ordovician (Sandbian) Letná Formation, located in the Prague Basin, contains one of the most fossiliferous assemblages of Lower Palaeozoic invertebrates in the region. The quartzite beds of the Letná Formation have long been well-known as a sediments that contain abundant trilobites, brachiopods, conularids but also exoskeletons of rare arthropods: cheloniellids, bivalved ?phyllocarids and aglaspids (Chlupáč 1965, 1999b; Rak et al. 2009; Ortega-Hernández et al. 2010). Arguably one of the most unusual arthropods from this formation is *Furca bohemica* Fritsch, 1908a.

Despite being known for over a century (e.g., Hawle and Corda 1847), this taxon has only recently (Van Roy 2006) been unequivocally recognized as a member of the Marrellomorpha, a group of arthropods with exceptional preserved forms: *Marrella splendens* Walcott, 1912: Middle Cambrian Burgess Shale (Whittington 1971; García-Bellido and Collins 2006) and also from the Middle Cambrian of Kaili Formation (Zhao et al. 2003), *Mimetaster hexagonalis* (Gürich 1932) and *Vachonisia rogeri* (Lehmann 1955): Lower Devonian Hünsruck Slate (Gürich 1931; Stürmer and Bergström 1976; Kühl and Rust 2010) and *Xylorkorys chledophilina* Siveter et al. 2007: Silurian Herefordshire Lagerstätte (Siveter et al. 2007; Kühl et al. 2008).

New specimens of *F. bohemica* have been recently discovered in the Letná Formation on the southern slope Ostrý Hill in Beroun and in a debris of the Veselá Gorge (Beroun District, Central Bohemian Region) (see Chlupáč 1965 for locality details). The Letná Formation consists of thick, complex layers of sandstone, greywacke, siltstone and pelitic shales deposited within a shallow, near-shore basin (Kukal 1958, 1963).

Fossil preservation in the Letná Formation commonly consists of internal and external moulds of, generally disarticulated arthropods, brachiopods etc., frequently associated with sandstone or quartzite layers (Chlupáč 1999a). Heavily biomineralized organisms, such as trilobites are covered by a limonite layer, giving them a characteristic bright orange colouration.

The preservation of *F. bohemica* is typical for non-mineralizing organisms (Chlupáč 1999a). Most of the studied material is preserved in medium to coarse sandstone, predominantly in convex relief. In most cases, the outline of the fossils is clearly defined by the contrast of its colour and relief with the surrounding matrix.

Kühl et al. (2008) and Kühl and Rust (2010) recognised two clades of marrellomorphs: those with a dorsal cordate shield (i.e., *Xylorkorys* and *Vachonisia*), and those with prominent cephalic spines (i.e., *Furca*, *Marrella*, and *Mimetaster*). The results indicate that *Furca* should be removed from Marrellidae (sensu Chlupáč 1999a) and instead placed in Mimetasteridae. The presence of *F. bohemica* in a shallow marine environment indicates that marrellomorph arthropods probably had a much wider distribution and ecological versatility than that previously suggested.

The absence of appendage information in *F. bohemica* hampers the interpretation of its palaeoecology as well as its feeding strategies. Early interpretations of marrellomorph palaeoecology depicted them as active swimmers that spent most of their time in the water column (e.g., Rolfe 1969). Later studies have favoured a benthic (Whittington 1971; Kühl et al. 2008) or nektobenthic (Zhao et al. 2003; García-Bellido and Collins 2006) mode of life. Rolfe (1969) considered the long secondary spines of *Mimetaster* as an adaptation for a pelagic lifestyle. Bergström (1973) and Van Roy (2006) have regarded the presence of structures among marrellomorphs as a defensive adaptation based on the wide coverage of the spines over the body.



Infaunal molting in *Viaphacops orurensis* (Bonarelli 1921) and its evolutionary implications

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Infaunal molting behavior in trilobites has been only recently recognized. The hypothesis has been supported by direct taphonomic indicators based on a Late Silurian-Early Devonian phacopid lineage, involving three species of *Paciphacops* Maksimova 1972, from western Argentina. The infaunal molt pattern is characterized by the thoracopygidium being perfectly articulated, frequently exhibiting a gentle dorsal bending; the cephalon in front of the first thoracic segment being separated and nearly perpendicularly oriented; and the hypostome, when preserved, being barely displaced. Because no other taphonomic agents can be invoked for explaining this distinct three-dimensional arrangement, it has been interpreted as biologically produced during the molt, during which the trilobite was entirely buried in soft sediment. Since it is exclusively related to the most vulnerable period of the trilobite adult life (exuviation), this trait is understood as an evolutionary acquisition of a predator-deterrent behavior. In addition, an evolutionary trend toward the thickening of the carapace, development of spinosity, and increase in size have been documented in this *Paciphacops* lineage. These trends have been interpreted as escalated, in concert with the evolutionary-ecological context of the so-called Middle Paleozoic Marine Revolution. This bioevent is related to the sudden appearance of several groups of durophagous predators that greatly intensified predation pressure in Silurian-Devonian marine ecosystems, triggering coeval defensive trends in a number of prey groups.

Here we report new evidence based on several specimens of *Viaphacops orurensis* (Bonarelli 1921) coming from the Middle Devonian (Givetian?) of the Sica Sica Formation at Patacamaya, La Paz Department, Bolivian Altiplano. They are housed in the AMNH, New York, USA (Braniša collection), and consist of molt assemblages that conspicuously exhibit the very same described infaunal pattern. Although previous evidence suggested that the infaunal molt behavior was restricted to a monophyletic *Paciphacops* group of species, endemic to a single basin (Argentine Precordillera), the specimens of *V. orurensis* show that this behavior also existed in other genera and different basins, thus questioning the phylogenetic and paleobiogeographic context of the original proposal. In addition, since *V. orurensis* is much younger than the species of *Paciphacops* in which infaunal molting was reported, and also lacks pronounced spinosity, it would suggest a complex mosaic evolutionary pattern of these traits, implying that infaunalism, spinosity, and increase in size may have evolved more than once (i.e. is polyphyletic). A phylogenetic revision focused on genera closely allied to *Paciphacops* and *Viaphacops*, such as *Ananaspis*, *Kainops*, *Echidnops*, etc., is therefore necessary. Because this would be the first attempt to perform a phylogenetic study including behavioral characters in Trilobita, it would help to elucidate the phylogenetic patterns of responses previously supposed as escalated in nature. Moreover, taking into account that we now have data from a larger stratigraphic and geographic range and, eventually, a more significant stock of taxa to include in a phylogenetic test, such a revision would also help to solve the systematics and relationships of the complex group of phacopid trilobites usually grouped within the tribe Ananaspini of Haas, 1998.



Exquisite hydrodynamic morphology of the remopleuridid trilobite *Hypodicranotus striatulus*: Functional insights into the mode of life

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It has been suggested that the remopleuridid trilobite *Hypodicranotus striatulus* was an Ordovician swimming animal with a well-streamlined exoskeleton. In addition to the external smoothness, this species had a long, two-pronged hypostome extending below the pygidium, which is a unique characteristic among trilobites. As a preliminary step to understand the biological role of the long-forked hypostome for swimming, we theoretically demonstrated the swimming performance of the exoskeletal morphology using image-based modelling and computational fluid dynamics simulation techniques. The results using two models, one with and one without the hypostome, showed that the fork-bearing hypostome prevented the formation of prominent ventral vortices, and stabilised flow structures around the model regardless of the ambient flow velocities. Moreover, the hypostome reduced the drag coefficient as velocity increases, and maintained positive lift forces with stable lift coefficients under a wide range of velocities. Such a drag reduction with a modest lift force is an essential requirement for active swimming animals. Consequently, the morphology of the exoskeleton and hypostome of *Hypodicranotus* could be of advantage in an active and stable swimming system (see Shiino et al., 2012).

Simulated flow behaviours yielded a clue to consider the morphological implication of the two-pronged hypostome because a vortex was generated between the two branches of the hypostome. The vortex showed anteriorly-directed flows along the median internal surface of the exoskeleton, replicating the route of food transportation in the food groove of extant crustaceans. We conclude that the morphology of the exoskeleton including the long fork on the hypostome was an adaptation to enhance swimming performance and feeding efficiency.

Shiino, Y., Kuwazuru, O., Suzuki, Y. & Ono, S., 2012. Swimming capability of the remopleuridid trilobite *Hypodicranotus striatus*: Hydrodynamic functions of the exoskeleton and the long, forked hypostome. *Journal of Theoretical Biology*, 300, 29-38.



Sensory Structure of Phacopid Compound Eyes

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The nature of sublensar structures in trilobite eyes hitherto has remained unknown. Using x-ray ct-scanning (μ -ct) and synchrotron techniques the construction of original sensory structures in the eyes of phacopines is revealed for the first time. They are preserved as mineral coatings on the original components, and they form rosettes of cells lying within sublensar capsules. Their arrangement is very similar to that of modern apposition eyes, revealing this eye structure to have been effective since almost half a billion years. They resemble especially the apposition eyes of *Limulus*, which has obviously retained an ancient visual system, which successfully holds its own today among the modern visual principles.



Colour Patterns of Devonian Trilobites

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In several specimens of Middle Devonian scutelluid trilobites from the Rheinische Schiefergebirge colour patterns have been observed, especially on the pygidia. Two patterns have been distinguished. In the first type (*Scutellum flabelliferum* (Goldfuss, 1839)) a dark area around the end of the rachis on the plateau of the pygidium shows a black semicircular region, broadly corresponding to the area outlined by the inner margin of the doublure; while there is secondly a pale coloured broad band round the periphery of the pygidium. In the second form (*Scutellum geesense* Rud. & E. Richter, 1956) there is a single curving brown band along the median steepest part of the pygidial surface. These markings are shown in several specimens of each species, illustrated here.

Both patterns may enable some degree of camouflage in sunlit shallow water with a wave rippled surface.

There seem to be some dark dappled splotches on the glabella of *Eldredgeops rana milleri* (Stewart, 1927) from New York State, also suggestive of camouflage.



A Silurian three-dimensionally preserved ‘great appendage’ arthropod

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The mid-Silurian Wenlock Series Herefordshire Lagerstätte preserves invertebrates in three-dimensions as calcitic void infills in carbonate nodules within a volcanoclastic horizon. A new arthropod from this fauna belongs to the ‘short great appendage’ (megacheiran) group. Phylogenetic analysis, based on the most detailed panarthropod character matrix yet assembled, recovers the new Herefordshire genus with other short great appendage genera in a clade that is the most derived of the euarthropod stem. It thus provides new insights into the nature of this stem and the morphology of immediately pre-crown group forms; its phylogenetic position, as well as that of other short great appendage genera, contrasts with the position of this group as determined in many other studies, in which they have been considered to be part of the chelicerate stem lineage; and the new genus represents the first identification of a short great appendage form in strata younger than mid-Cambrian in age.



The function of terrace ridges associated with sensory setae in the carapace of the decapod *Pachygrapsus crassipes*: implications for trilobite biology

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The generally accepted biological role of terrace ridges is as burrowing sculptures or frictional devices. A generally known but sometimes overlooked feature is the close association of terrace ridges with cuticular pores, indicating the presence of sensory setae that are not fossilized. To understand the functional role of this combination of features, we documented their characteristics in the extant decapod *Pachygrapsus crassipes*, which exhibits agile retreating behaviour into intertidal rocky crevices.

Pachygrapsus crassipes bears densely spaced, short terrace ridges in regions a and b of the carapace; long and widely spaced ridges in c, d and e; and widely spaced, short to medium length ridges in f and g. In all of these regions the steep slopes of the terrace ridges face forward. The trend of the density of sensory setae appeared to correspond to these three divisions. A few thousand setae on the carapaces examined appear to fall into two morphological types, simple setae and hedgehog sensilla. Eighty-six to ninety percent of them are arranged in a row along or at the base of the steep slopes of terrace ridges. Around 75 to 90 % are simple setae that are 30~120µm in length, strongly inclined nearly parallel to the carapace surface, and never protrude above the top of the terrace ridges. The perpendicularly standing hedgehog sensilla are 40~70µm in length, and they exceed the height of the ridges. A few simple setae are commonly present between the terrace ridges. The sensory setae are of considerably higher density in f than in other regions of the carapace, and are also locally concentrated in regions where the carapace may hit the wall or ceiling of rocky crevices when the animal is retreating.

The role of the terrace ridges and associated setae is apparently to sense and distinguish stationary or motile contact with ambient objects. The animal stops retreating when region f comes into contact with the end of a crevice, and remains stationary when regions c, d and e are touching the ceiling. In trilobites, terrace ridges may have had a similar role in sensing and/or monitoring contact with ambient objects in order to determine swimming conditions or the extent of burying into the substrate.



The trilobite *Osmolskabole* from the Famennian of the Moravian Karst (Czech Republic): implications for the origin and descendance of the Cyrtosymbolinae

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The Famennian is a transitional period in the history of trilobites bounded by two major biocrises, the end Frasnian Kellwasser Event and the terminal Famennian Hangenberg Event. From the five orders of trilobites present in the Frasnian, only the Proetida survived until the Early Carboniferous. This latter period marked the renewal of trilobites through the appearance and spectacular diversification of the Phillipsiidae. The origin of these emblematic trilobites of the Late Palaeozoic is unknown, although several authors have proposed that they derived from the Famennian Cyrtosymbolinae. The Moravian Karst (Czech Republic) has long been known for its diversified Famennian trilobite fauna. However, since the major work of Chlupáč in the sixties, very few field investigations have occurred in the area. The recent discovery of several small outcrops has resulted in the collection of an abundant Famennian fauna mostly dominated by clymenids, orthocone nautiloids, trilobites, bivalves, and ostracods. A very significant outcrop in the Křtiny Limestone of the Líšeň Formation is a two-meters thick section. Conodonts in the most fossiliferous interval in this section are indicative of the Upper *Palmatolepis trachytera* to the *Palmatolepis postera* Biozones. More than a hundred trilobite remains, assigned to *Phacops granulatus*, *Osmolskabole neptis*, and “*O. prima*”, were collected. This is the first report of the presence of “*O. prima*” in the Moravian Karst.

“*O. prima*” has been variously regarded as a distinct species, a subspecies of *O. neptis*, or a synonym of *O. neptis*, depending on the significance accorded to differences observed on the pygidium. The discovery of numerous pygidia in the new localities reveals that a morphological continuum exists between the two extreme morphologies supposedly characterizing the two taxa. Considering that the two extreme morphs co-occur in the same beds and that no cephalic features permit discrimination, we regard “*O. prima*” as a subjective junior synonym of *O. neptis*.

The discovery of an almost complete articulated specimen of this species revealed that it possessed 10 thoracic segments. *Osmolskabole* has been considered the sister taxon of *Cyrtosymbola*, the type genus of the Cyrtosymbolinae and therefore, it can be reasonably assumed that 10 thoracic segments was the plesiomorphic condition for the subfamily and not the 7-8 segments observed in more derived forms (e.g. in *Calybole*). This observation supports the view that the Cyrtosymbolinae is a subfamily of the Proetidae, and that they might have evolved from Frasnian representatives of this family (e.g. *Palpebralia* and allies). On the other hand, some Mississippian phillipsiids (e.g. *Griffithidella*, *Ditomopyginae*?; *Dechenelloides*, *Schizophillipsia*, *Weaniinae*) also possesses 10 thoracic segments, instead of the 9 that supposedly characterizes the family. Accordingly, 10 segments in the thorax could also be a plesiomorphic condition for the Phillipsiidae, giving more credence to their evolution from cyrtosymbolines, as also suggested by similar protaspid morphologies. Thus, an origin of the Phillipsiidae from the Proetidae via the Cyrtosymbolinae seems more strongly supported than ever, but a reconsideration of the familial status of the Phillipsiidae should await a comprehensive cladistic analysis of Late Devonian/Early Carboniferous proetoids.



A Silurian *Bohemoharpes* twice used an empty shell of an orthocone nautiloid as refuge for moulting

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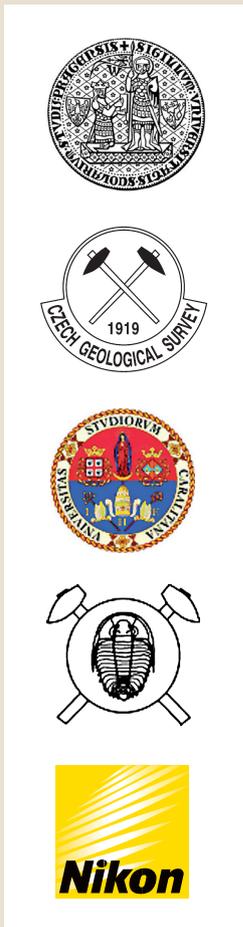
It is well known from the fossil record that empty shells of dead orthocone nautiloids have been used by benthic trilobites as shelter in critical situations or as refuge during moulting.

Orthocones from Silurian marl-limestone intercalations from Gotland (Sweden) often contain moult assemblages of calymenid trilobites but remains of harpetids in this situation are rare. A cephalon and an isolated lower lamella of *Bohemoharpes* cf. *acuminatus* (Lindström 1886) have been found inside the living chamber of an orthocone nautiloid from the Lower Gorstian Hemse Beds. The cephalon of the *Bohemoharpes* exceeds the dimensions of the lower lamella by more than 20 %. Both are parts of exuviae and they show the same pattern of injuries at the brim. The cephalon shows regeneration of the external rim, but the smaller lower lamella shows no signs of wound healing or regeneration. In addition, the pattern of pits in certain regions of the brim is the same on the cephalon and on the lamella. We therefore conclude that both parts belong to different moultings of the same trilobite. The implications of this extraordinary fossil material for our knowledge of paleobiology and paleobehaviour of harpetids in the Silurian will be discussed.



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Your remarks



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