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ADVANCES IN TRILOBITE RESEARCH

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Editors: I. Rábano, R. Gozalo and
D. García-Bellido

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Cover:

Monotaxic cluster of complete specimens of *Asaphellus toledanus*, a species named after the Toledo province, Spain. Lower Oretanian (mid Darriwilian) slates of the Valongo Formation, Canelas quarry, Arouca, Portugal.

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PREFACE

The 4th International Trilobite Conference "TRILO 08" is a forum where researchers on trilobites and their allies review the latest advances on the Palaeontology of these arthropods. This year, the fourth edition of the conference will take place in Toledo (Spain), in the facilities of the *Real Fundación de Toledo* and at the *Diputación de Toledo*'s *Centro Cultural "San Clemente"* from the 16th to the 24th of June. These meetings have previously been held on July 1973 in Oslo (Norway), on August 1997 in St. Catharines (Ontario, Canada) and on April 2001 in Oxford (United Kingdom).

The main aspects of these conferences are (a) a extensive international contribution, in our case almost a hundred participants from more than 20 countries, (b) a multidisciplinary perspective, which includes presentations on systematics, biostratigraphy, palaeobiogeography, palaeoecology, taphonomy, evolution, etc., from both trilobites and kin groups, or related aspects, and (c) a continuous single session format, enabling participants to attend all the oral contributions as well as the poster presentations. These attributes have proven to be an effective way to promote cooperation and the exchange of ideas and experiences between specialists in different topics and/or ages, for the benefit of all the participants.

Another feature of these meetings is the partaking in field trips to the different localities with an important trilobite record, which allow attendees to enjoy, firsthand, some of the host-country's most significant fossil localities and discuss various issues *in situ*. In this case, two optional excursions have been organized, a pre-conference one to the Ordovician of Portugal and a post-conference one to the Cambrian of the Iberian Chains, plus a general mid-conference field excursion for all participants to visit the Ordovician of Montes de Toledo.

This event has been organized by the *Instituto Geológico y Minero de España* (Spanish Geological Survey), in collaboration with the universities of Zaragoza, Valencia and Trás-os-Montes e Alto Douro and the *CSIC* (Spanish National Research Council). All these institutions participate in this year dedicated to

"Planet Earth" by trying to provide society with the knowledge and information related to Palaeontology, a science bridging Earth Sciences and Life Sciences, aiming to unravel the history of life and its relationship with the planet where it develops.

The contents of this volume present a updated view of our knowledge on trilobites owing to more than 120 scientists. The various palaeobiological points of view of authors working on a range of regions and ages give us a better idea of the rich and complex world where these organisms lived, diversified and, ultimately, became extinct. Their dissemination, first to specialized scientists and later to the general public, is the only way these contributions will be useful to society.

The Spanish Geological Survey wants to contribute to the dissemination of these wonderful fossils, and to facilitate the understanding, not just of the history of life, but also the history of our Planet Earth, in this, its international year.

José Pedro Calvo Sorando
Director General
Spanish Geological Survey

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THE STATUS OF THE *CRUZIANA* (TRILOBITE TRACE FOSSIL) STRATIGRAPHY IN WESTERN GONDWANA: THE MIXING OF LOWER AND UPPER ORDOVICIAN ELEMENTS IN THE CENTRAL ANDEAN BASIN OF SOUTH AMERICA

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Keywords: Ordovician, *Cruziana*, trace fossil, chronology, South America, Argentina.

INTRODUCTION

A limited understanding of trace fossil distribution in the stratigraphic record and the partial interpretation of the meaning of this relation, precludes the correct interpretation of the potential values of ichnostratigraphy on "non fossiliferous" strata. Palaeozoic trilobite traces assigned to *Cruziana* and arthrophycids worm burrows (*Arthrophycus, Daedalus* and "*Phycodes*") are referred as important elements that provide clues evolution and behaviour of organisms during the Paleozoic (Seilacher, 2004). These have been used as important elements on the dating of the nearly barren fossiliferous Early Palaeozoic strata of Northern Africa (i. e. Seilacher, 1969; El-Khayal and Romano, 1988), and have been proposed as useful tools in biostratigraphy and palaeogeographic reconstructions (Seilacher, 2005; MacNaughton, 2007).

Crimes (1970) and particularly Seilacher (1970; 1992; 2007 with references) provided the conceptual framework for the Icnostratigraphical use of *Cruziana*, where several forms replace each other along the chronostratigraphy of Gondwana over 200 Million years (Cambrian – Lower Carboniferous). Even though *Cruziana rugosa* has been historically considered an index fossil for the Lower Ordovician of Gondwana (Crimes, 1970; Baldwin, 1977; Fillion and Pickerill, 1990; Seilacher, 2007 with references), the recent discovery of an Upper Ordovician association including *C. rugosa* in Bolivia and the current material from northern Argentina confirms that the group reaches on full health the Upper Ordovician in the Western Margin of Gondwana. *C. rugosa, C. furcifera, C. goldfussi C. rouaulti* and *C. yini* occur in successions where conodonts, graptolites, trilobites, brachiopods are common elements providing the needed solid biostratigraphic base to define the age of the bearer strata. In addition, the discovery of a new form, *Cruziana gutii* n. isp., adds a rare new ichnospecies of *Cruziana* in the Central Andean Basin of South America.

PROVENANCE OF MATERIAL AND CHRONOLOGICAL ASPECTS

The analyzed material was recovered from two different localities and units of Jujuy province in northwest Argentina: a) The Capillas Formation cropping out in Zenta Range and b) The sandstones and quartzites located above the Alto del Condor Formation in Los Colorados area. Both units are well dated chronologically, with an abundant fauna that includes the early fish *Sacabambaspis* in the second locality (Astini *et al.*, 2004 with references).

Particularly the Capillas Formation of Zenta comprises sandstones associated to randomly interbedded coquinoid lenses and carbonate-cemented sandstones bearing conodonts and broken inarticulate brachiopods. Conodonts are not abundant and preservation is variable, with frequent broken cusps and processes.

For the current analysis, four coquina samples were processed for conodonts with the conventional techniques (Stone, 1987); one of them yielded 132 conodont elements which have a light brown colour (CAI 2 of Epstein *et al.,* 1977). The recovered materials comprise *Erismodus* sp., *Trapezognathus diprion*, *Gothodus* aff. *costulatus*, *Gothodus* sp., *Drepanoistodus* aff. *pitjanti*, *Drepanoistodus* sp., *Oepikodus intermedius* and a non nominated Upper Cambrian paraconodont .

This association is interpreted as composed mainly by Floian allochthonous conodont fauna with Middle/Upper Ordovician autochthonous representatives such as *Erismodus* sp. The allochthonous fauna is present in carbonate sand grains mixed along with few autochthonous conodonts. The fauna composed by *Trapezognathus diprion*, *Gothodus* aff. *costulatus*, *Gothodus* sp., *Drepanoistodus* aff. *pitjanti*, *Drepanoistodus* sp., *Prioniodus intermedius* is common from the top of the Floian defining the *T. diprion* Zone. On the other hand, the presence of *Erismodus* sp. is an unequivocal genus for defining the true age of the Capillas Formation as Middle/Upper Ordovician. The allochthonous conodont genera are usually associated to a middle platform biofacies such the bedded fossiliferous lime mudstones of Horns Udde Formation (Bagnoli and Stouge, 1997), contrasting with the shallow sandstones facies of Zenta (Aceñolaza and Milana, 2005).

Figure 1. A-B., *Cruziana rugosa* association from Zenta range, Jujuy province, NW Argentina. Trace fossils are abundant on thick sandstone soles and upper surfaces of the upper sector of the Capillas Formation.

A review of the conodont faunas from the Capillas Formation in the Zapla Range recorded by Albanesi *et al.* (2007) display the same features with a Lower Ordovician conodont fauna and Upper Cambrian paraconodonts, such *Trapezognathus quadrangulum* (diagnosed by Albanesi *et al*. 2007 as *Icriodella?* nov. sp.), *Oepikodus intermedius* as *Plectodina* sp., an strange Pa element diagnosed as *Bryantodina* cf. *typicalis*, *Muellerodus* sp. and *Hertzina* sp. (the last ones being Upper Cambrian paraconodonts).

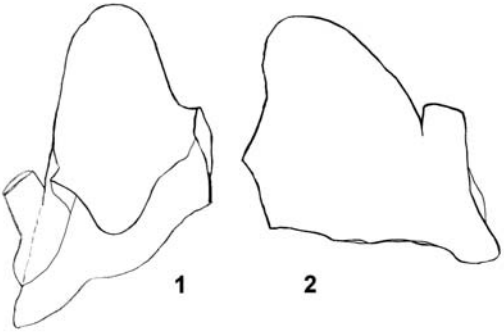

Figure 2. 1-2, *Erismodus* sp. from the Capillas Formation at Zenta Range, Jujuy province NW Argentina.

FINAL CONSIDERATIONS

Even though the stratigraphical distribution of *Cruziana* has been regarded as an important field method to date non fossiliferous sandstones, the presence of archetypical "Lower Ordovician" forms associated to diagnostic Upper Ordovician elements, and the clear extension of the *rugosa* group into the Upper Ordovician of the Central Andean Basin of South America represents an intriguing element to be evaluated in relation to facies, trilobite behaviour and evolution. Some elements of the *Cruziana rugosa* Group display a restricted value as a diagnostic Lower Ordovician form in northern and western Gondwana due to its wide chronological range in Baltica and the Central Andean Basin (Knaust, 2004; Egenhoff *et al*., 2007).

The appearance of most of the ichnospecies included in the *C. rugosa* group - including *C. gutii* n. isp. - on late Middle and Upper Ordovician strata in westren Gondwana may reflect an environmental aspect related of fauna (see discussion in Egenhoff *et al*., 2007) and/or a non synchronous convergent patterns of leg shape and burrowing behaviour, as early suggested by Seilacher (1993).

Even though *Cruziana* was firstly described in the Lower Paleozoic Central Andean Basin of South America (d´Orbigny, 1842), little detailed work towards the knowledge of its biostratigraphic framework has been done in the region. In addition, the *Cruziana* stratigraphical scheme has proved to work as a fast dating method for the "non fossiliferous" sandstone beds of northern Africa, the *C. rugosa* group in South America cannot be regarded as a reliable indicator of Lower Ordovician strata, supporting recent ideas of Egenhoff *et al.* (2007).

Figure 3. Holotype of *Cruziana gutii* n. isp. from the Middle/Upper Ordovician strata of the Capillas Formation, at Zenta Range. Jujuy province, NW Argentina. Scale bar = 1.65 cm.

The presence of conodonts, brachiopods, graptolites, molluscs and trilobites in the *Cruziana* beds of the Central Andean Basin provides a unique opportunity to test and detail on the biostratigraphic framework of *Cruziana* in the western margin of Gondwana.

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TAXONOMIC APPENDIX

Cruziana gutii n. isp.
(Figure 3)

Holotype: Figure 3; Invertebrate collection of the Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Argentina. PIL 14.548.

Stratum typicum: Capillas Formation, Middle/Upper Ordovician (Darriwillian/Sandbian), Zenta Range, Jujuy, Northwest Argentina.

Material and repository: 2 samples in the Paleontological Collection of the Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán (Argentina). Additional material *in locus*. PIL (14.548, 14.549).

Derivatium nominis: After Prof. Dr. Juan Carlos Gutiérrez-Marco, researcher of the Spanish Research Council (CSIC) and the Complutense University, Madrid (Spain).

Diagnosis: Trace fossil characterized by a mid-sized shallow elongated cruzianaeform furrow (mid width close to 4 cm) of the *rugosa* group, in which the multiple endopodal scratch marks meet the midline of trace at a close to perpendicular angle. A restricted longitudinal development also characterizes the form, representing a possible head-down ploughing procedure. Combed multi-clawed dig marks display up to 14 sharp-crested claw scratches. Characteristic fingerprint on *Cruziana gutii* n. isp. allows the inclusion of the new species into the *C. rugosa* group of Seilacher (1970).

Observations: Well preserved material and the unique shape of the multi-clawed scratch marks with its characteristic perpendicular disposition of scratches respect to the midline represent clear ichnotaxobases and support its separation as new ichnospecies. No other Ordovician *Cruziana* display such an uncommon pattern reflecting a peculiar behaviour of the producer organism. *C. gutii* n. isp. is a rare element in the association of Zenta, with 3 samples recorded out of 1200 analyzed traces. The new form has been found associated to *C. furcifera, C. goldfussi* and *C. rugosa*. *C. gutii* n. isp. could be compared to *C. balsa* from the Middle Ordovician of Bolivia, but the latter represents a deep rusophycid form with a differential scratch pattern with exopodal lateral brushing, all characters lacking in the new form.

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CRUZIANA YINI YANG, A PERI-GONDWANAN TRILOBITE TRACE WITH NEW RECORDS IN THE ORDOVICIAN OF SOUTH AMERICA AND IBERIA

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Keywords: Trilobite trace fossils, Ordovician, paleogeography, China, Iberia, Argentina.

INTRODUCTION

Armorican-type sandstones rich in trilobite traces of the *Cruziana rugosa* group are widely distributed around Gondwana, especially in the Lower Ordovician of south-western Europe (Durand, 1985; Romano, 1991; Neto de Carvalho, 2006 and references therein), north Africa – Middle East (Seilacher, 1970, 1990; El-Khayal and Romano, 1988; Ramos *et al*., 2006), Avalonia and Eastern Newfoundland (Crimes, 1970, 1975; Fillion and Pickerill, 1990), and in the Lower and Upper Ordovician of the Central Andean basin (a.o. Toro *et al*., 1990; Mángano *et al*., 2001; Aceñolaza and Aceñolaza, 2002; Mángano and Buatois, 2003; Aceñolaza and Milana, 2005; Egenhoff *et al*., 2007). Outside northern and western Gondwana, there are scattered occurrences of the *Cruziana rugosa* group in the Lower Ordovician of South China (Yang and Fu, 1985) and perhaps in Baltica (Knaust, 2004), but only the former show close resemblance with Gondwanan assemblages.

Here we report some South American and European records of an interesting member of the Chinese association of the *Cruziana rugosa* group, showing the wide peri-Gondwanan distribution attained by their corresponding, and somewhat-related, trilobite makers.

THE CHINESE RECORD OF *CRUZIANA YINI*

Yang (*in* Yang and Fu, 1985) originally described *Cruziana yini* from the Lower Ordovician quartzose sandstones of the Hongsiya (= Hungshiya, Hongshiyian) Formation in the section of Wuting, eastern Yunnan. The original description provided two figured specimens (Figs. 1 A and B), one of which was later designated as lectotype of the ichnospecies (Fillion and Pickerill, 1990, p. 27), while the other was considered as a compound specimen, transitional to *C. rugosa* d'Orbigny. In their brief review of *C. yini*, Fillion and Pickerill (1990) established the main ichnotaxobases to distinguish it as a valid and separate ichnospecies, as well as the criteria to differentiate it from its most closely related form, *C. breadstoni* Crimes, 1975, not considered by the Chinese author in the original description.

Although most members of the *Cruziana rugosa* group usually reached a wide geographical (and even stratigraphical) distribution through the Lower Paleozoic, *C. yini* was so far apparently restricted to the westernmost part of the Yangtze platform (South China Paleoplate). The stratotypical Hongsiya Formation is a 200-324 m succession of sandstones and shales with quartzose sandstones, where trace fossils are quite common, including *C. rugosa* d'Orbigny, *C. furcifera* d'Orbigny, *C. goldfussi* (Rouault), *Monomorphichnus, Dimorphichnus, Palaeophycus*, etc. (Yin, 1933; Xiong, 1944; Yang and Fu, 1985). Its type section lies in the western suburb of the Kunming city (Kuo, 1941), but the formation was later recognized along the eastern paleo-shore the old Kum-Yunnania Land from the type locality to Puge, in western Sichuan, either conformably overlying the Tangchi Formation (Tremadocian) or unconformably resting (with a 5 m-thick basal conglomerate) over Upper Cambrian rocks (Chen *et al*., 1995). Li (1991) defined the Hongsiya Formation as a near-shore, Armorican-type sandstone, which has been dated as late Floian by the occurrence in shale intercalations of some graptolites (*Baltograptus deflexus, B. turgidus*), trilobites (*Taihungshania, Symphysurus*) and acritarchs of this age.

CRUZIANA YINI FROM SOUTH-AMERICA

South American material assignable to *Cruziana yini* comes from three localities in the Eastern Cordillera of northwestern Argentina. The first is situated towards the upper part of the Ordovician sequence in the Chamarra Creek, north of the Los Colorados (Jujuy Province). A single specimen (Fig. 2 B) was collected in this section from a succession of sandstones and shales lying above the Alto del Cóndor Formation, which until very recently was regarded by different authors as an equivalent of the "Sepulturas" Formation (*sensu lato*). However, new records of different fossils in the *Cruziana*-bearing strata favored a different age dating to this unit, which ranges from late Middle Ordovician to early Upper Ordovician, as indicated by some conodonts and by the early fish *Sacabambapis janvieri* (Albanesi and Astini, 2003).

Additional Argentinian material of *C. yini* comes from two different outcrops placed in the Mojotoro Range, northeast and east of the city of Salta, respectively. A first specimen (Fig. 1C) from the Mojotoro Formation (middle to upper Arenigian) was presented by Mángano *et al.* (2001) from the Gallinato Creek section, being originally identified as *Cruziana furcifera* d'Orbigny (Mángano *et al*., 2001, fig. 3 C), and later as *Cruziana rugosa furcifera* (Mángano and Buatois, pl. 1, fig. 10) or again as *C. furcifera* (MacNaughton, 2007, fig. 8.4.B). The second specimen of *C. yini* (Fig. 2 A) comes from the San Bernardo Formation in the northern section of the Cerro San Bernardo, on the foothills of Salta City, being stratigraphically placed in late Tremadocian beds, because of their presence two meters below the FAD of the graptolite *Araneograptus murrayi*.

CRUZIANA YINI FROM IBERIA

The Iberian material assigned to this form was primarily recognized in the Portuguese part of the Central Iberian Zone of the Hesperian Massif by Sá (2005, p. 426), who described a specimen of *Cruziana* cf. *yini* from the fossil locality "Guadramil-6" in the Barreiras Blancas Hills, Bragança area. This sample is also presented here (Fig. 2 C) and comes from the Marão Formation, which is the equivalent to the Armorican Quartzite in the Trás-os-Montes region. Similar material derived from the same unit in the southern flank of the Moncorvo Syncline has been previously described as *C. furcifera* by Rebelo and Romano (1986, pl. 2, fig. 3), but in our opinion is better adscribed to *C. yini* (Fig. 1 E). A third occurrence of the ichnospecies in Portugal has been indicated by Sá *et al*. (2007, fig. 3 E) as coming from the Santa Justa Formation (also correlated with the Armorican Quartzite) in the Arouca region (Fig. 2 E).

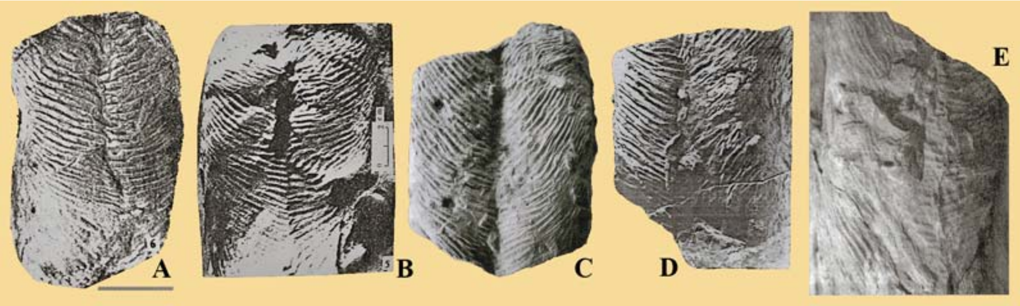


Figure 1. *Cruziana yini* Yang. Images of several specimens previously figured from China (A-B), Argentina (C), Spain (D) and Portugal (E) and discussed in the text. A-B, after Yang and Fu (1985, pl. 1, figs. 6 -lectotype- and 5 -paralectotype-, respectively). C, after Mángano *et al.* (2001, fig. 3C), specimen PIL 14629, also refigured by Mángano and Buatois (2003, pl. 1, fig. 10) and MacNaughton (2007, fig. 8.4.B), either identified as *C. furcifera* or as *C. rugosa furcifera*. D, after Crimes and Marcos (1976, pl. 1 a; specimen AMC 6270), described as *C. breadstoni*. E, after Rebelo and Romano (1986, pl. 2, fig. 3; specimen QS), identified as *C. furcifera*. Note that figures are not to scale.

Cruziana yini is so far represented in the Spanish part of the Central Iberian Zone by a single occurrence, recorded towards the base of the Armorican Quartzite Formation (= basal "I" unit of San José Lancha *et al*., 1974) in the Estena River section, within the Cabañeros National Park (Fig. 2 D).

Additional Spanish specimens of *C. yini* are also known from the Cantabrian Zone in the Cabo de Peñas section, Asturian coast. The material was originally described as *Cruziana breadstoni* by Crimes and Marcos (1976, pl. 1a, b; reproduced in part here, Fig. 1 D), and come from two quartzite-shale sequences located approximately 370-440 m below the top of the Barrios Formation, which includes the local equivalent of the Armorican Quartzite. This identification of *C. breadstoni* was taken as indicative of a Tremadocian age for the lower part of the section, in spite of its claimed co-occurrence with typical "Arenigian" traces like *C. rugosa, C. goldfussi* and *C. furcifera*, recorded from the same beds. The true *C. breadstoni* have a smaller V-angle than *C. yini* and their scratches are bunched in twos and threes, so that this ichnospecies still belongs to the stratigraphically older *C. semiplicata* group (Upper Cambrian to lower Tremadocian in north Gondwana). To this regard, and according to Mángano and Droser (2004), a significant trilobite turnover event, documented by ichnofossils in shallow-marine siliciclastic deposits of peri-Gondwana, is recorded by the post-Tremadocian replacement of the *C. semiplicata* group by elements of the *C. rugosa* group. Further evidence on the post-Tremadocian age of the beds yielding the Cantabrian specimens of *C. yini* (formerly assigned to *C. breadstoni*) comes also from the stratigraphic review of the same section by Aramburu and García-Ramos (1993). These authors restricted the exposure of the Barrios Formation in the Cabo de Peñas to the Tanes Member (Arenig), which here rests unconformably over the Cambrian to ?basal Tremadocian Oville Formation. The age of the Barrios Formation in the same Fold and Nappes Domain of the Cantabrian Zone was recently refined by Gutiérrez-Alonso *et al.* (2007), who place the Tremadocian-Floian boundary towards the lower-middle third of the Tanes Member.

MORPHOLOGICAL NOTES ON *CRUZIANA YINI*

According to the original description, and the later review provided by Fillion and Pickerill (1990), the more obvious and distinctive feature of *Cruziana yini* is the very large V-angle (>160 degrees) reached by the endopodal markings across the lobes. These could correspond to procline-induced scratches running transverse to a median furrow, which is very shallow, becoming remarkably faint in specimens preserved as wide U-shaped burrows. This procline ploughing could generate faint corrugations across the lobes, but without disrupting the course of individual scratches (Figs. 1 B, 2 C and D), unlike in the typical and coarse transverse corrugations of *C. rugosa*.

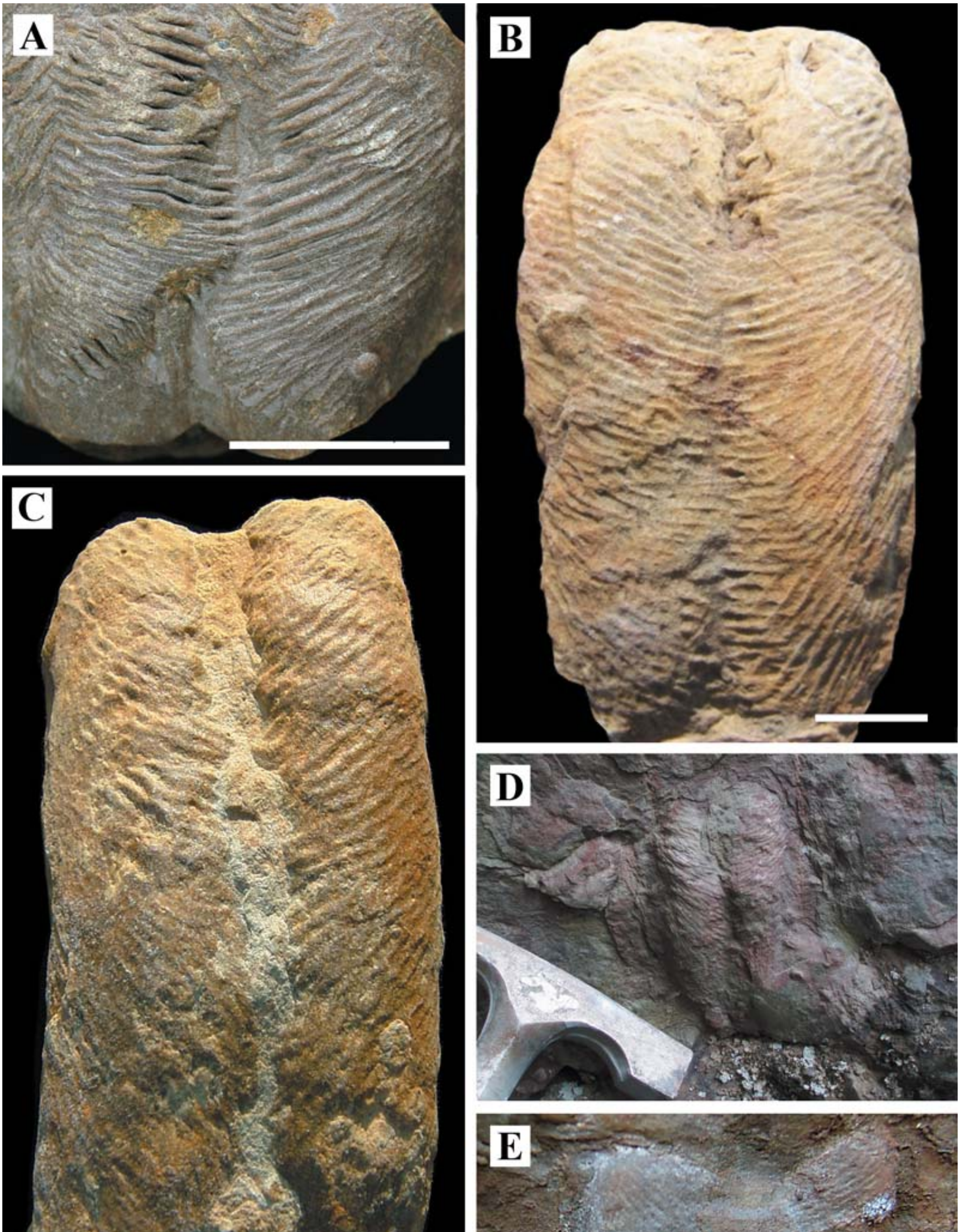
Some of the South American and Iberian specimens of *C. yini* have been previously misidentified as *C. furcifera* because a number of them showed endopodal markings crisscrossing at acute angles (Figs. 1 C to E). However, they lacked the characteristic reticulate scratch pattern on the lobes and the arrangement of successive sets of scratch marks may have occurred separately (Fig. 2 B). Even in the case of accepting the existence of compound specimens of *C. furcifera*–*C. yini*, the observed intergradation between other ichnospecies within the *C. rugosa* group (*e.g.*, Kolb and Wolf, 1979; Mángano *et al.*, 2001) show that the currently observed changes from procline to isocline (*C. rugosa* → *C. furcifera*) and isocline to opisthocline (*C. furcifera* → *C. goldfussi*) orientations of the tracemarker during excavation conflict with the isocline to procline pattern of critical material of *C. yini* (Figs. 1 C and D). This morphoethological and constructional variation also serves to justify the ichnotaxonomic separation of *Cruziana yini* from the remaining members of the *C. rugosa* group, which may be established either at the ichnospecific or ichnosubspecific level. The latter view was proposed by Seilacher (1996) without much support, other than Mángano and Buatois (2003). Likewise, the attempt by Kolb and Wolf (1979) to synonymize some of the most widespread forms of the *C. rugosa* group has also met the skepticism of most other authors (a.o., Pickerill *et al.*, 1984; Durand, 1985; Fillion and Pickerill, 1990; Egenhoff *et al.*, 2007).

While the type material of *C. yini* lacks lateral spine grooves (of pleural or genal origin), indications of such external furrows are observed in some of the Portuguese specimens (Figs. 1 E and 2 E). However, and as already described for other forms like *C. goldfussi, C. furcifera, C. rugosa* or *C. beirensis*, the presence/absence of marginal grooves is not truly diagnostic for particular ichnospecies within the *C. rugosa* group and may be partly due to preservational aspects.

Together with the very large V-angle of endopodal markings and the shallow median furrow, the main character of *C. yini* is the curved trend of individual scratches, passing from anterior obliquely oriented against the external border of each lobe to being perpendicular to the central furrow posteriorly. Within this arched scratch pattern, some of the endopodal ridges occasionally cross without interruption from one lobe to the other over the faint median furrow, giving the trace an unilobed aspect, very different to the ichnospecies presently included either under *Cruziana* or *Rusophycus*.

The repository information of the figured specimens is as follows: PIL, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán (Argentina); AMC, Alberto Marcos collection, Universidad de Oviedo (Spain); QS, José Rebelo collection, Instituto Nacional de Energia e Geologia, Lisbon (Portugal); GDM, Sá collection, Universidade de Trás-os-Montes e Alto Douro, Vila Real (Portugal).

Figure 2. New material of *Cruziana yini* from the Ordovician of Argentina (A-B), Portugal (C and E) and Spain (D). A, PIL 14551, Cerro San Bernardo, Salta; B, PIL 14550, Chamarra Creek, Jujuy; C, GDM-VI 42, Guadramil, Bragança; D, field photograph, Navas de Estena, Cabañeros National Park; E, field photograph, Paiva River Valley, Arouca. Scale bars, 2 cm.


A
B
C
D
E

CONCLUDING REMARKS

Cruziana yini is a peculiar trilobite trace whose stratigraphical and paleogeographical distribution is notably widened by its occurrences outside China in late Tremadocian to Sandbian strata from South America (Argentina) and Europe (Portugal and Spain).

Such peri-Gondwanan distribution of a trace fossil, originally described from the South China Plate, had also been recognized among the Lower Ordovician trilobites of the same area (Turvey, 2005). In this sense, the paleobiogeographical relationships of the Chinese trilobites point to a tropical or subtropical peri-Gondwanan association of South China with other Asian terranes, but also display faunal connections with north Gondwanan and South American regions.

The age and distribution of *Cruziana yini* agrees with that of the supossed tracemakers of the ichnospecies included in the *C. rugosa* group, which were possibly related with the feeding and locomotion of asaphid trilobites as already suggested by Bergström (1973) and later authors.

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A GLOBAL SPECIES DATABASE OF TRILOBITA: PROGRESS, RESULTS, AND REVISION OF THE *TREATISE*

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Keywords: Trilobites, diversity, classification, evolutionary faunas.

A comprehensive global species database of Trilobita includes 22,405 records of which 20,541 are valid species. The relational taxonomic database was compiled directly from the primary literature, and includes classification to traditional genus [compiled by Jell and Adrain (2003) with updates and corrections], subfamily, family, suborder, and order level. Stratigraphic information includes primary data such as formation, member, regional zone, stage, etc., and also assignment to a series of 37 global sampling bins from Lower Cambrian to Upper Permian. Geographic information is recorded as both modern geopolitical entities and tectonic elements. Data on type specimens are recorded. Historical published diagnoses are compiled for each taxon along with full synonymies, though this work is far from complete. Image fields will eventually include all published images of each species, but this task again has only just begun. An associated literature database includes over 5,400 systematic trilobite publications.

The compilation permits the first direct assessment of the performance of higher taxa as proxies of sampled species diversity. Trilobites have been proffered as an example of potential bias in this proxy relationship due to different amounts of taxonomic "splitting" in different time intervals, particularly in Cambrian versus post-Cambrian taxonomy. If the average number of species per genus changes non-randomly through time, higher taxic patterns might depart from species patterns. It is demonstrated that genera, somewhat surprisingly, are nearly exact proxies for sampled species diversity, but that families are very poor proxies and should probably not be used in paleobiological studies of summed diversity per unit time.

A temporally corrected species sampling curve reveals several features not previously apparent on curves derived from higher taxa (families and genera). Trilobites reached their peak species diversity much earlier during the Cambrian than previously appreciated. By the Late Cambrian, diversity had declined nearly to levels typical of the remainder of the Early Paleozoic. Further, the post-Cambrian peak in species diversity occurred during the Early Devonian, at which point trilobites were nearly as globally diverse as during the Late Cambrian.

Hierarchical cluster analysis (using Sorensen distance and flexible beta linkage) of all 165 trilobite families according to their species diversity in each of the 37 intervals reveals a striking pattern of six distinct evolutionary faunas. The Ordovician and post-Ordovician Ibex and Whiterock faunas of earlier analyses (Adrain *et al*., 1998, 2004), are confirmed by these much more detailed data. A further four Cambrian and Cambrian-Ordovician clusters are equally disjunct. All trilobite families belong to one of these evolutionary faunas, each with a unique pattern of temporal diversification.

It is anticipated that this database will form the foundation for the remaining revised trilobite volumes of the *Treatise on Invertebrate Paleontology*, for which I have agreed to serve as coordinating editor. While authors responsible for particular groups will (of course) be encouraged to adjust the classification and improve the database, the primary information has now been compiled for the entire group. It is hoped that the database can be made available to all as a web-based community resource. Funding avenues for further community-based development and for completion of the remaining *Treatise* volumes are being explored.

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SEGMENT VARIATION IN A CAMBRIAN TRILOBITE IN THE CONTEXT OF THE BURGESS SHALE FAUNA

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Keywords: Trilobite, Burgess Shale, dorsal flexure, segment variation.

INTRODUCTION

As in many other arthropod clades, trilobite displayed variation in the number of segments in the trunk region of mature specimens. A trend toward stabilization of mature thoracic segment numbers is evident both in the evolution of trilobite species, and also at higher taxonomic levels (McNamara, 1983; Hughes *et al.*, 1999). Hence the examination of individual species that vary in mature segment number offers potential microevolutionary insight into how trilobites generated the macroevolutionary diversity in segmentation found among the clade Trilobita. The middle Cambrian Burgess Shale located in Yoho National Park in the Rocky Mountains, near Field, British Columbia, Canada, offers the opportunity to examine this issue in unprecedented detail using the abundantly represented trilobite species *Elrathina cordillerae* along with the soft-bodied fauna that are found together at multiple bedding plane surfaces. By studying the covariation in mature segment number and the soft-bodied faunal assemblages, we can test whether variation in thoracic segment number is related to repeated paleoecological associations in soft-bodied fauna. We will use this to infer the adaptive basis for variation in trilobite segment numbers.

The greatest range of mature trunk segments is found in the basal trilobites, characteristically common in the Cambrian Period. The number of trunk segments ranged from less than 10 in some species to over 100 in others (Hughes, 2007). Within Cambrian species, mature trilobites commonly differed in total thoracic segment number by two or more (Hughes *et al.*, 1999). This stands in stark contrast to more derived trilobite groups in which the thoracic segment number remained constant among not only species, but at the family level and higher. The mature thoracic segments of more phylogenetically derived trilobite groups fall into a much smaller range from 6 to 22 (Hughes *et al.*, 1999). This suggests that mature thoracic segment numbers became progressively constrained as trilobites evolved (McNamara, 1983), although this constraint apparently could later be relaxed in certain environmental settings (Hughes *et al.*, 1999). Much work on the controls of mature segment number has been conducted on the Silurian trilobite *Aulacopleura konincki* (Fusco *et al.*, 2004), but there is now an important need to compare the mechanisms of variation in that trilobite with those operative in Cambrian species. Furthermore, the adaptive significance of variation in segment number in *A. konincki* remains elusive.

DISCUSSION

The Burgess Shale is special in that it preserves not only the 'hard parts' such as the biomineralized exoskeletons of trilobites, but also the rarely found soft tissues. This gives us the opportunity to explore the paleoenvironmental controls on segment variation in the context of taxonomic variations in the co-occurring soft-bodied fauna. About 90% of the *Elrathina* specimens examined in the preliminary study were fully articulated specimens showing no preferred attitude or orientation. These specimens are interpreted to have been living in a deep-basin depositional setting at the base of a carbonate bank and were buried very quickly in an obrution event (Caron and Jackson, 2006). By recording information on number of segments in the thorax and pygidium, as well as taking measurements between several landmark features on the dorsal exoskeletons, we will document the relationship between the paleoenvironment as recorded by the soft-bodied fauna preserved in this unit and variations in the trunk of mature specimens of *Elrathina cordillerae*. This is a unique opportunity because the soft-bodied fauna adapted to different ecological settings, and we hope to use this to infer the adaptive basis for variation in trilobite segment numbers. This fossil assemblage was selected not only because of the excellent preservation associated with this unit, but because of the high number (in some cases over 300 per bedding plane) of *Elrathina cordillerae* preserved in several of the bedding plane assemblages that make up the Greater Phyllopod Bed of the Burgess Shale (Caron and Jackson, 2006).

In this preliminary study, four separate slabs ranging in size from 26 x 22 cm to 55 x 48 cm containing a total of 104 *Elrathina* specimens were examined. True north was only known for two of the slabs, so it was necessary to assign an arbitrary north for those whose orientation was not recorded upon collection. These were treated separately when determining whether or not there was any preferred orientation among the specimens. The species diversity was very high but specifics have not yet been recorded. The segment count on these *Elrathina* was primarily seventeen or eighteen however at least one meraspid was found at this level and more are expected with the examination of more slabs.

UNUSUAL FLEXURE POSTURES

An interesting aspect of the Burgess Shale is the preservation of trilobites exhibiting dorsal flexure on one of the bedding planes. Dorsal flexure, like enrollment, is interpreted to be a response by the trilobite to rapid deep burial (Speyer and Brett, 1986; Hughes and Cooper, 1999). The difference is that dorsal flexure is interpreted to be an escape posture such that when the trilobites were inundated with sediment, they flexed their bodies up and down in an attempt to extricate themselves although those preserved were evidently unable to do so. Another possible reason for this flexure is as a behavioral response to adverse substrate toxicity or anoxia (Speyer and Brett 1986; Peters 2007). Marked flexure of this kind is seen only in the -420 layer of the Greater Phyllopod Bed, but also occurred in the late Ordovician Kope Formation (Hughes and Cooper, 1999). The taphonomic characteristics of this formation are strikingly similar to the -420cm level in the Burgess Shale with respect to specimen density and diversity of hard-part bearing taxa. Similar retroflexed postures are also known in homalonotid trilobites preserved in claystones (e.g. as in MCZ111053, a Devonian specimen assigned to *Digonus accraensis* and figured by Saul, 1967, pl. 144, fig. 7). Associations with this kind of density, articulation, attitude and posture may mark a distinctive assemblage style that occurred among trilobites of notably different age and phylogenetic position.

Flexing dorsally as an escape posture seems most likely, though why some trilobites show this behavior while others chose to roll up ventrally is not understood. Hunda *et al.* (2006) speculated that this choice might have related to paleoenvironment and depth of burial. The size measurements taken by Hughes and Cooper (1999) indicate that the majority of specimens in the "*granulosa*" cluster were 4-5cm in length suggesting some type of size segregation behavior. However, if this posture is indeed one of escape, it is possible that trilobites of other sizes than this were able to escape from the sediments and are therefore not represented. A study of the pattern of flexure compared to the size of the specimens in the *Elrathina* slabs might shed further light on this issue.

RESULTS

Preliminary analysis of 104 out of over 320 *Elrathina* specimens from the -420 cm layer of the Greater Phyllopod Bed shows that some 90% are fully articulated showing no preferred orientation or attitude, which suggests that these animals may have been buried alive by obrution events. This is supported not only by the in-place hypostome and apparently unopened sutures, but also by soft-tissue preservation, including dark carbonaceous stains which, in other Burgess Shale animals, are interpreted to represent a splay of ruptured gut contents released during compaction related decay. As such, these trilobites represent a population living on the sea floor at the time of burial. The average distance of the nearest neighbor ranged from 3.3 cm to 5.3 cm among the slab analyzed. The number of mature thoracic segments in these collections ranged from 17 to 19 and initial results suggest significant difference in mean thoracic segment number between bedding plane assemblages. No preferred orientation was observed and a set of nearest neighbor analyses showed that there was no significant sub clustering of trilobites within individual slabs.

Examination of other layers also bearing large numbers of *Elrathina* provides the opportunity to document mean segment variation by level in this unit, and initial results suggest significant difference in mean thoracic segment number between bedding plane assemblages. Examining the taphonomy of the trilobite and soft-bodied association in these beds will help up determine whether mature segment number correlates consistently with faunal variations in the soft-bodied assemblage, from this we hope to gain important insights into trilobite macroevolution.

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TREMADOCIAN TRILOBITE ASSEMBLAGES FROM THE ARGENTINE CORDILLERA ORIENTAL. A PRELIMINARY ANALYSIS

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Keywords: Trilobite assemblages, palaeoecology, Olenidae, Tremadocian, Santa Rosita Formation.

INTRODUCTION

A detailed study of biofacies coupled to a sequence stratigraphic framework is necessary if a comprehensive understanding of evolutionary palaeoecology patterns and processes is sought (Patzkowsky and Holland, 1999). Depositional sequences are the template for palaeoecologic and evolutionary studies, a concept that has been widely applied for the last ten years (Brett, 1998; Holland and Patzkowsky, 2007; Scarponi and Kowalewski, 2007). Trilobite "communities" and "biofacies" have been firstly described by Fortey (1975) and Fortey and Owens (1978), and this information has been of great importance in palaeoecologic and palaeobiogeographic reconstructions for the Early Paleozoic (Ludvigsen and Westrop, 1983). In view that trilobites are the most abundant preserved macrofauna for the Early Phanerozoic, the comprehension of their palaeosinecology and palaeoautoecology is fundamental in order to understand faunal dynamics during this interval (e.g. Adrain *et al*., 2000; Westrop and Adrain, 1998).

Due to the abundance and diversity of its fauna, continuity and excellent exposures of a relatively wide array of siliciclastic depositional environments, successions of the Central Andean Basin constitute a classical reference of the South American Cambro-Ordovician. Tremadocian trilobite faunas from Argentine Cordillera Oriental are known since the 18th century (Kayser, 1876), and much work has been done ever since (Kobayashi, 1935; Harrington and Leanza, 1957; Waisfeld and Vaccari, 2003, and reference therein). Indeed, these faunas were a cornerstone in Harrington and Leanza´s *opus magnum* Ordovician Trilobites of Argentina (1957). So far, most contributions dealt mainly with taxonomic and biostratigraphic aspects of this fauna, except for some approaches about autoecology of specific Tremadocian trilobite taxa (Tortello and Clarkson, 2003; Tortello and Esteban, 2003), as well as palaeoecological patterns of Floian trilobite assemblages by Waisfeld *et al.* (2003, and references therein). Despite their abundance and widespread nature, ecological and macroevolutionary dynamics of Argentine Tremadocian trilobites have received no attention, although they may give invaluable information about Early Ordovician trilobite history.

Here we present preliminary results of a large-scale study dealing with trilobite assemblages, palaeoecology, and biotic events throughout the Santa Rosita Formation (Late Cambrian-Tremadocian), in Northwestern Argentina. Due to the complex stratigraphic and tectonic history of this unit a diverse mosaic of trilobite biofacies is recorded. This contribution focuses on a detailed survey at a single locality (Arenal Creek, Huacalera, Jujuy) of a succession of trilobite assemblages. Main controls on their composition and distribution are briefly discussed

GEOLOGICAL SETTING

Although the knowledge of the Santa Rosita Formation (and its equivalents) dates from long ago (Harrington and Leanza, 1957; Aceñolaza, 2002; Benedetto, 2003, and references therein), only recently sequence stratigraphic analyses had been carried out (Astini, 2003; Buatois *et al*., 2006). These authors suggest that the Santa Rosita Formation records a wide array of depositional environments, ranging from storm dominated shallow marine deposits, usually associated with deltaic systems, punctuated by conversions towards complex tide dominated estuaries.

According to Buatois *et al*. (2006) lithostratigraphic nomenclature, the Santa Rosita Formation is subdivided in at least 5 members (Tilcara, Casa Colorada, Pico de Halcón, Alfarcito and Rupasca). These lithostratigraphic divisions are clearly observable at the Alfarcito area, 15 km further south from the studied area. The Alfarcito Member represents a single large-scale regressive succession, following a flooding event. This member, Early Tremadocian in age (partly included in the *Cordylodus angulatus* Zone), can be divided in three intervals (each one corresponding to a third order sequence) (Buatois *et al*., 2006) and it is represented mainly by open marine environments, ranging from shelf to lower shoreface facies. The Rupasca Member, constrained between the *Cordylodus angulatus* biozone and the *Paltodus deltifer pristunus* subzone, ranges up to the early late Tremadocian (Zeballo *et al*., 2005) and represents a stepwise flooding event consisting of at least three sequences in its type locality. This event has been recognized as one of the two most important flooding events at the basin scale (Buatois *et al*., 2006). The whole succession of this member is deeper than that of the Alfarcito Member, and no shallower than upper offshore environments are present.

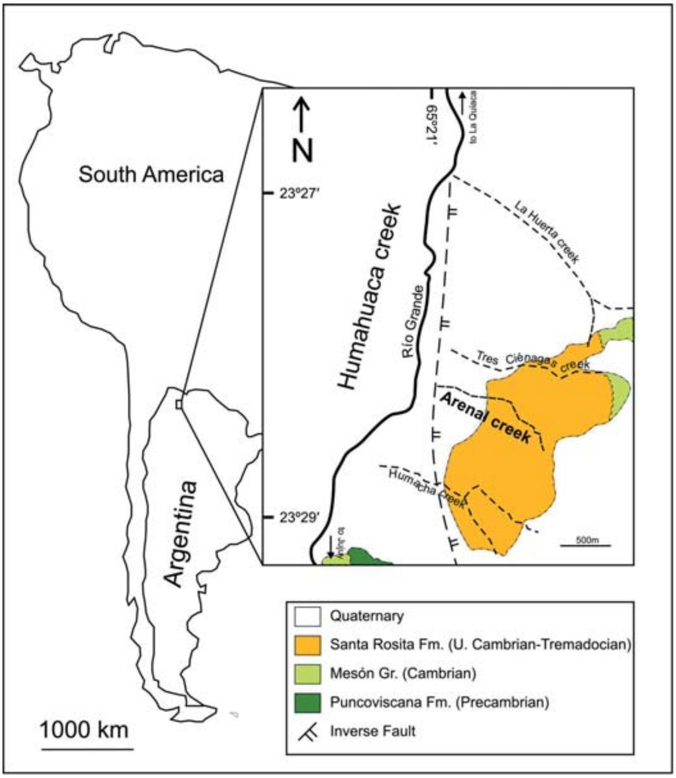

Figure 1. Location of the study area (modified from Moya *et al*., 1986)

The studied area, Arenal creek, is located in the east margin of the Humahuaca creek, north Jujuy Province, northwestern Argentina (Fig. 1). Along this creek the third interval of the Alfarcito Member and part of the Rupasca Member are recognized. A coarsening up, sandstone/ micaceous shale succession overlies the Rupasca Member. So far, there is not a formal lithostratigraphic designation for this interval. The high sandstone/shale ratio, abundance of shell beds and HCS structures suggest a more proximal setting than those present in the Rupasca and Alfarcito Member.

DATA AND METHODS

Twenty six field samples were taken from green/brown shales lithologies, corresponding to fair weather deposition in offshore and offshore transition (rarely corresponding to lower-middle shoreface) settings. Sampling was restricted to this type of lithologies in order to avoid bias due to different taphonomic signatures (e.g. Zuschin *et al*., 2005). Sampled stratigraphic thickness for each collection was in most cases around 10 cm, occasionally slightly thicker intervals (up to 20 cm) were considered. In every sample, all identifiable trilobite sclerites were counted, and the MNI protocol was followed for the number of individuals in each sample (Gilinsky and Bennington, 1994).

As sample size has an effect on sampled richness and abundance distributions (Buzas and Hayek, 2005), a minimum of 100 individuals was an *a priori* target sample size. Although this number was not always reached, it was usually achieved. A subsampling procedure could have been used to standardize sample size, but as in our database richness was not correlated with sample size (Spearman´s rank-order r_s=0,244 p>0,05), we preferred not to do so, to avoid unnecessary loss of information. The database consists on twenty six samples and 3208 individuals (mean sample size = 123 ind. per sample).

To analyze trilobite assemblages, both cluster and ordination analyses were performed. Cluster

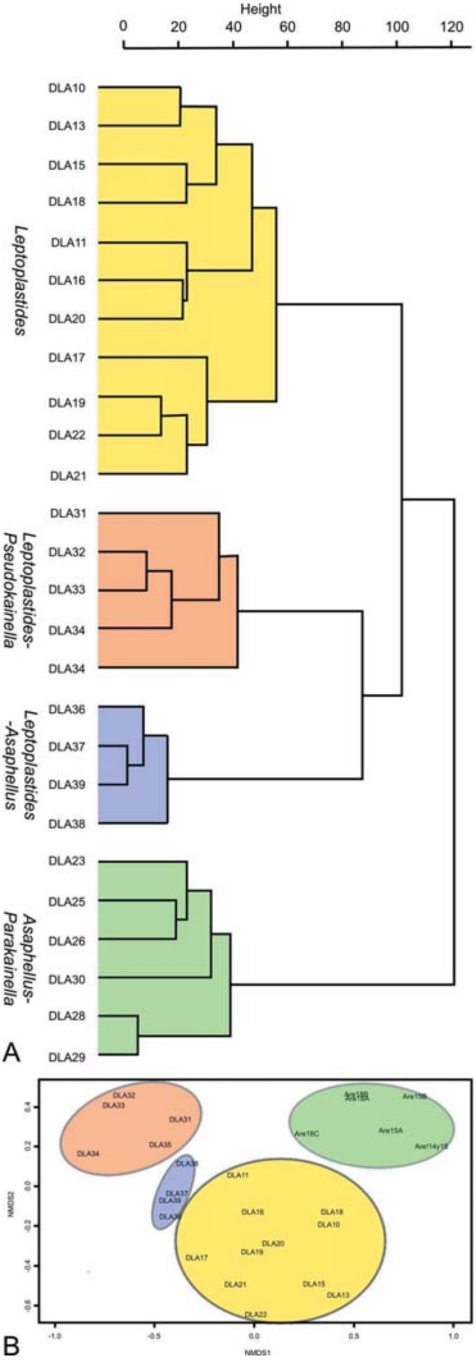

Figure 2. A. Cluster Analysis. B. NMDS, note that the colours correspond to the assemblages defined.

analysis is useful to define biofacies, while ordination methods are better for showing gradients. Preliminary analyses showed that the high dominance of one genus (*Leptoplastides*) in most samples blurred other biotic patterns. Hence, a log transformation was applied before relative abundances were calculated [to avoid 0 in case of abundance 1, the equation used was: $1+\ln(n_i)$]. A Q Cluster analysis was performed using Agnes in the Cluster package for R 2.5.1 (R Developmental Core Team). Euclidean distance and Ward´s clustering method were used. For Ordination analysis a Non Metric Multidimensional Scaling (NMDS) was performed using the metaMDS command from the Vegan package for R 2.5.1 with Bray-Curtis distance. The NMDS ordination was preferred against the widely used DCA because of its greater robustness and less gradient distortion, mainly when the actual distribution of the variables is unknown (Minchin, 1987).

RESULTS

Cluster Analysis defines four assemblages, three of them are dominated by *Leptoplastides* and the fourth is characterized by a different array of taxa, with *Leptoplastides* being subordinate or absent (Fig. 2).

Cluster 1: *Leptoplastides* assemblage. This assemblage clusters all samples collected from the Alfarcito Member (Fig. 3). It is highly dominated by *Leptoplastides,* while other genera (mainly *Parakainella*, *Kainella* and *Asaphellus*) are strongly subordinate in abundance. This assemblages exhibits a mean genus richness of 5,3, and its average evenness is very low J=0,402.

Cluster 2: *Asaphellus-Parakainella* assemblage. This assemblage cluster samples from the lower part of the Rupasca Member (Fig. 3). It is the most distinct, *Leptoplastides* is absent or in very low abundances, *Asaphellus* and *Parakainella* are invariable present in moderately abundances, and some forms otherwise occurring in minor abundances or absent, become more conspicuous elements (e.g. *Agerina*, *Onychopyge*, *Apatokephalus*). Besides, diversity among richardsonellids is remarkable. The mean genus richness and evenness in this assemblage are by far the highest (S=8 and J=0,766).

Cluster 3: *Leptoplastides-Pseudokainella* assemblage. Samples grouped in this assemblage are dominated by *Leptoplastides,* meanwhile *Pseudokainella* and *Asaphellus* display moderate abundances. It is important to note that occurrences of *Pseudokainella*, *Bienvillia* and *Peltocare* are restricted to these samples. Although the sample Are21 is clustered in this assemblage, its composition differs from other samples of the *Leptoplastides-Pseudokainella* assemblage (some of the core taxa are absent and the single occurrence of *Pharostomina* is recorded). The mean genus richness and evenness are 6 and 0,65 respectively. This assemblage represents all samples from the upper part of Rupasca Member (Fig. 3).

Cluster 4: *Leptoplastides-Asaphellus* assemblage. As assemblages in clusters 1 and 3, this one is dominated by *Leptoplastides*. Associated taxon is restricted to *Asaphellus* in moderate abundances, with a single record of *Apatokephalus* in one sample. The mean richness is the lowest and the mean evenness value is also low (S=2 and J=0,550). Here are clustered the samples that were obtained from the upper sandy interval overlying the Rupasca Member (Fig. 3).

The NMDS ordination should show underlying gradients, obscured by the cluster analysis. In this particular case, the ordination shows quite the same groups as the cluster does. Interestingly the *Leptoplastides-Asaphellus* assemblage appears between the *Leptoplastides* and *Leptoplastides-Pseudokainella* assemblages (Fig. 2).

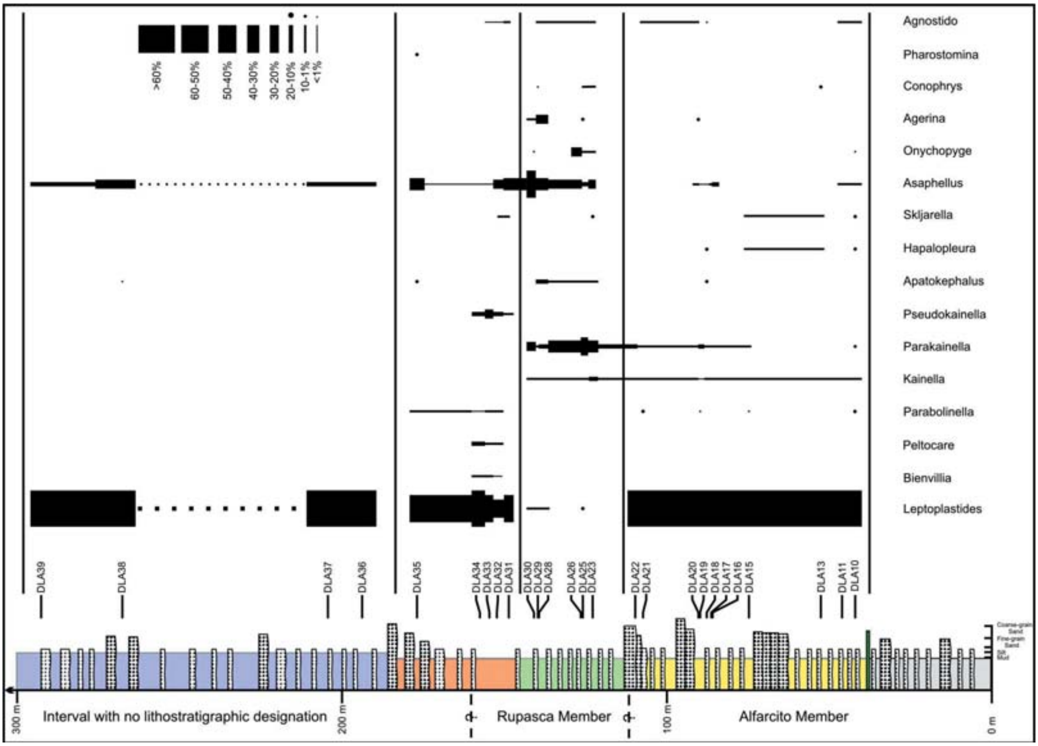

Figure 3. Stratigraphic ranges and relative abundances plotted against lithological column at the Arenal creek. The age of the studied interval is Early Tremadocian-Early Late Tremadocian. Colours correspond to the assemblages defined in Figure 2.

DISCUSSION AND CONCLUSION

Analysed trilobite assemblages are largely dominated by olenids and only secondarily by richardsonellids. Although both families are equally represented by four genera, relative abundance of richardsonellids become significant exclusively in the *Asaphellus-Parakainella* assemblage, while olenids (particularly *Leptoplastides*) predominate in all other assemblages. Remarkably, *Asaphellus* (probably represented by several species) is important in almost all assemblages. The difference between the *Leptoplastides* and the *Leptoplastides-Pseudokainella* assemblages might be related to the turnover of some genera (appearance of *Pseudokainella*, *Peltocare*, *Bienvillia* / disappearance of *Parakainella*, *Kainella*, *Hapalopleura*, *Skljarella*), both assemblages could represent a broadly similar habitat, although due to genera turnover the multivariate analysis represents them as different groups.

The *Asaphellus-Parakainella* assemblage is very distinct. The nearly absence of *Leptoplastides* is remarkable, as this taxon is persistently present and highly dominant in other assemblages. It is worth noting that this assemblage is not only the most rich but also the most even. Along a depth gradient, these features may characterize assemblages developed in a relatively deep setting (Gray, 2002). So, comparatively, the Asaphellus-Parakainella assemblage might have developed toward the deeper portion of the gradient The *Leptoplastides-Asaphellus* assemblage clearly corresponds to an impoverished assemblage.

This impoverishment and associated coarse grained facies, with frequent disturbances by storm events, allow placing this assemblage toward the shallowest portion of the gradient. In this context, it would be expected to occupy the extreme of the ordination, but its impoverished nature is probably the cause of its intermediate position in the gradient analysis.

These assemblages might shed light on the study of Olenidae autoecology. The group is highly abundant, though it does not match environmentally with the well-known "olenid biofacies" (Fortey and Owens, 1978; Fortey, 2000; Clarkson and Taylor, 1995, among others). Olenids were the dominant elements in slope to outer shelf biofacies all along their existence (Ludvigsen and Tuffnell, 1994). Almost all olenid species have been regarded as specialized to deep sea environments, usually completely or nearly depleted in oxygen. Interestingly in the assemblages studied herein, olenids are almost lacking in deeper facies, while thy are highly dominant in shallower facies. The group is particularly diversified in the *Leptoplastides-Pseudokainella* assemblage (four olenid genera), while in the *Leptoplastides-Asaphellus* assemblage they occur in great abundance (around 90% of individuals are *Leptoplastides*).

All the olenid genera present, with the exception of *Parabolinella*, correspond to the *Peltura*-type of Henningsmoen (1957). This type is the most active of all olenids, and is known to occur, beyond the "olenid biofacies" in associations with non-olenid trilobites (Edgecombe *et al.*, 2005; Fortey, 1985) However, even these active olenids have been usually treated as inhabitants of dysaerobic environments (e.g. Fortey and Owens, 1989; Fortey, 2000). On the basis of the record of *Leptoplastides*-dominated assemblages, even in the shallowest end of the gradient, it is possible to suggest that at least some members of the *Peltura*-type (*Leptoplastides* in our case) are not typically tied to deep, or restricted hypoxic/anoxic environments (Fortey, 1975, 1985, 2000). The later, might have been generalists that inhabited more oxygenated, frequently disturbed, and shallower environments than those inhabited by their much more specialized relatives.

Concerning the nature of the assemblages recognized herein there are two possible interpretations. On one hand, the assemblages may group samples due to their ecological similarity. On the other hand, it is possible that the assemblages represent temporal groups, segregated by genera turnover. At this early stage of our research and on the basis of the available data, it is difficult to differentiate between these two alternatives, because both factors are acting at the same time. Even considering this limitation, and taking in account significant changes in relative generic abundances, loss of taxa otherwise abundant in some assemblages and restriction of several forms to particular ones, suggest that ecological/environmental factors (probably related to shifts in depth) might have controlled their differentiation. Finally, further investigation, in coeval successions of other localities will provide a more accurate picture of assemblages changes in order to asses the real influence of spatio-temporal effects.

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ASPECTS OF SOME LATE MIDDLE CAMBRIAN TASMANIAN FAUNAL ASSEMBLAGES

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Keywords: Tasmania, late Middle Cambrian trilobite assemblages, faunal composition.

INTRODUCTION

Late Middle and early Late Cambrian faunas occur at numerous localities in western, northwestern and south-central Tasmania. Almost all of the faunas occur within siltstones deposited below wave base. All Tasmanian Cambrian faunas show the effects of tectonic distortion, although in many cases, including the Christmas Hills faunas discussed below, the effects are not significant. Brock *et al.* (2000, fig. 4) indicate that in the late Middle Cambrian Tasmania was about 10°N of the equator.

Faunal analyses of three contrasting late Middle Cambrian faunas (Que River Beds; lower and upper faunas from Christmas Hills) from northwestern Tasmania are presented herein. The present study quantifies the three agnostoid dominated assemblages discussed, largely qualitatively, by Jago (1973), who suggested that the Que River fauna, the Christmas Hills upper fauna and the Christmas Hills lower fauna occurred in progressively shallower water. However, all faunas are found in sediments deposited below wave base. The present study represents the start of a quantitative analysis of Tasmanian Cambrian faunas. All specimens in the three faunas occur as internal and external moulds; no original shell material remains.

COMPOSITION OF SOME LATE MIDDLE CAMBRIAN FAUNAS FROM TASMANIA

One fauna is from a black pyritic shale and siltstone of the Que River Beds from which Jago (1977) described poorly preserved agnostoid trilobites, lingulate brachiopods, sponges and a bradoriid. Quilty (1971, 1972) described the dendroids and a possible aglaspidid. The following agnostoid trilobites are present: *Hypagnostus* sp. aff. *H. parvifrons*, *Megagnostus* sp., *Valenagnostus* sp., *Ptychagnostus* sp., *Onymagnostus stenorrhachis*, *Ptychagnostus*? *murchisoni*, *Diplagnostus* sp., cf. *Kormagnostus* sp., and others. No polymerid trilobites are known from this fauna. Laurie *et al.* (1995) suggested an age of the *Euagnostus opimus – Ptychagnostus punctuosus* Zone. Representative examples of the Que River fauna are shown in Plate 1, figs L-P.

The other two faunas are from Christmas Hills where there is an abrupt faunal change over a few centimetres between two late Middle Cambrian faunas (Jago and Buckley, 1971; Bentley and Jago, 2007). The detailed regional geology is unclear due to a combination of thick vegetation cover, lack of outcrop and a deep weathering profile. However, 12 km to the north in the same stratigraphic succession, an early Late Cambrian fauna occurs within a proximal turbidite succession (Rickards *et al.,* 1990; Baillie and Jago, 1995). The lower fauna occurs within a buff coloured laminated siltstone; the upper fauna occurs in a darker more definitely laminated siltstone. However, regional borehole data suggest that unweathered siltstone from both faunas would be dark grey to black. In addition, the richly fossiliferous nature of both faunas suggests that in the unweathered state, the enclosing rocks would be quite calcareous.

The trilobites of the lower fauna (Plate 1, figs A-G) have been described by Jago and Daily (1974), Jago (1976a), Bentley and Jago (2004) and Jago and Bentley (2007). They include the polymerid trilobites *Nepea narinosa*, *Tasmacephalus platypus*, two species of *Dorypyge*, the anomocarellid *Mellacarella pulchella*, the anomocarid *Notacoosia plana*, an unassigned proasaphiscid and an unassigned damesellid. Agnostoid trilobites include *Tasagnostus debori*, *Valenagnostus imitans, Clavagnostus milli, Ammagnostus laiwuensis, Paraclavagnostus neglectus* and a single incomplete cephalon of what may be a very early *Glyptagnostus*. There are no representatives of common late Middle Cambrian agnostoid genera such as *Ptychagnostus, Goniagnostus, Lejopyge, Hypagnostus* and *Diplagnostus*. In addition a bradoriid, a lingulate brachiopod and several hyolithid specimens are known.

Of the upper fauna trilobites (Plate 1, figs H-K), only the agnostoids have been described to date (Jago, 1976a). These include *Lejopyge laevigata, Ptychagnostus aculeatus*, *Goniagnostus spiniger, Diplagnostus* sp., *Hypagnostus brevifrons, Tasagnostus debori*, and *Megagnostus* cf. *glandiformis*. The polymerids include the cosmopolitan genera *Centropleura*, *Fuchouia* and *Pianaspis* as well as rare nepeids and a few specimens of the conocoryphid *Elyx*. Dendroids, sponge spicules, lingulate brachiopods and bivalved arthropods have also been reported from the upper fauna (Jago, 1973; Quilty, 1971; Jago and Anderson, 2004), and are much more abundant in the upper fauna than the lower fauna. Jago and Bentley (2007) suggested a *Lejopyge laevigata* I or *Lejopyge laevigata* II Zone age on the northern Australia zonal scheme for both the lower and upper faunas.

All available specimens in the three faunas were counted; in order to avoid duplication only internal moulds were used. The results are shown in Figure 1. We have followed the same methodology as Pratt (1992) in which the number of individuals of a particular species is taken as the number of complete specimens plus whichever is the greater of the number of available cephala or pygidia. As noted above, the trilobite fauna from the Que River Beds comprises entirely agnostoids with 63 individuals counted (Fig. 1G). About 49.2% of the individuals occur as complete specimens. The fauna is dominated by *Ptychagnostus*? *murchisoni* which comprises 47.6% of the fauna. *Onymagnostus stenorrhachis* and *Diplagnostus* sp. comprise 19.0% and 12.7% of the fauna respectively.

Jago and Bentley (2007) counted 1044 individuals in the lower fauna at Christmas Hills; we now have a total count of 1049 (Fig. 1A-C). Of these 3.1% occur as complete specimens, with the same percentage for both agnostoids and polymerids. Agnostoids and polymerids respectively comprise 67.4% and 32.6% of the trilobite fauna. *Tasagnostus debori* is by far the most common taxon comprising about 79.8% of the agnostoids and 54% of the total trilobite fauna. The most abundant polymerid trilobite is the nepeid, *Nepea narinosa* that comprises 20.4% of the total fauna and 62.6% of the polymerids. The second most abundant agnostoid, *Valenagnostus imitans*, comprises 6.8% of the total fauna and 10% of the agnostoid fauna. The second most abundant polymerid, the wuaniid *Tasmacephalus platypus* comprises 6.9% of the total fauna and 21% of the polymerids. The anomocarid, *Notacoosia plana* comprises 3.1% of the total fauna and 9.4% of the polymerids.

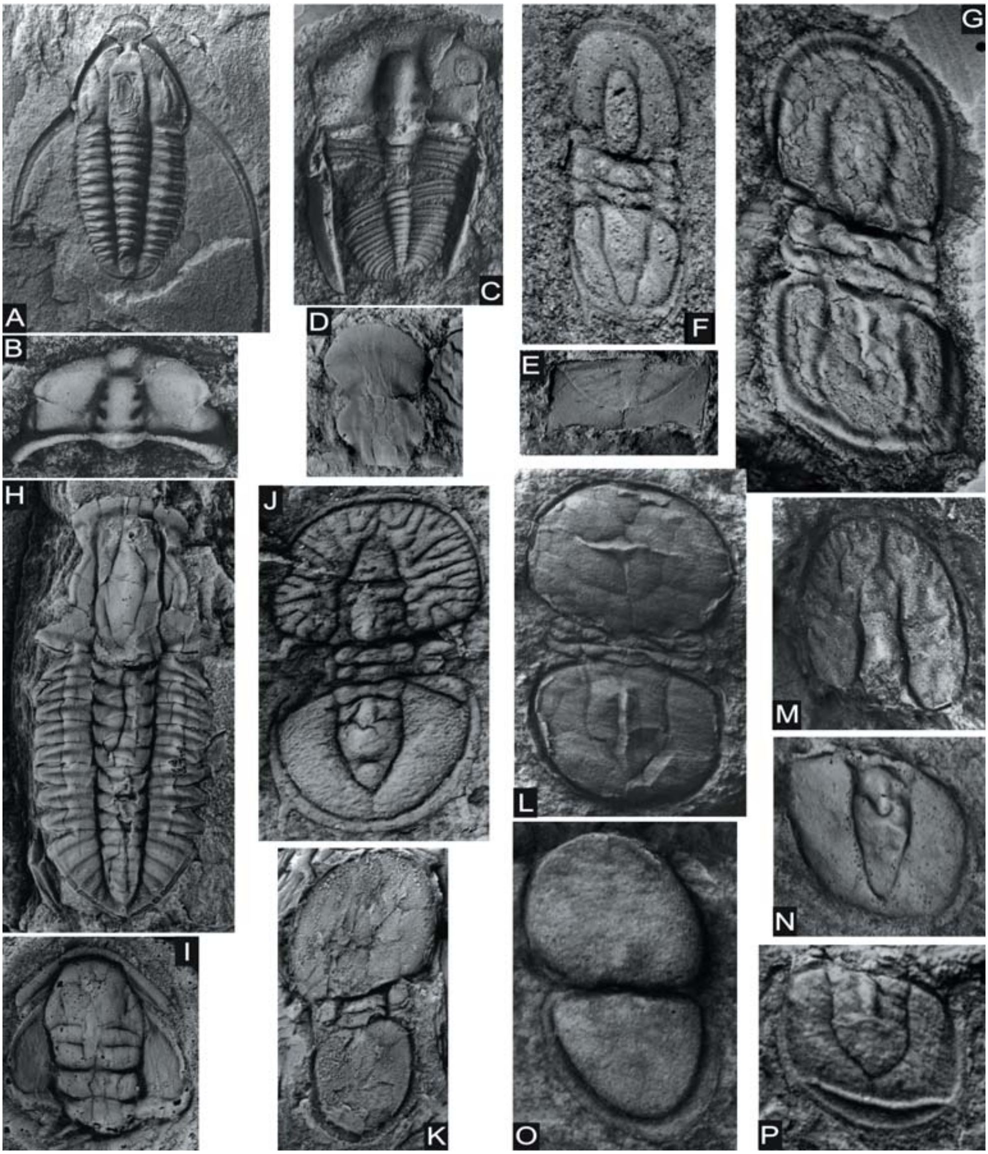

Plate 1. Some Tasmanian Cambrian trilobites. (IM = internal mould, EM = latex cast from external mould). A-G, Christmas Hills Lower Fauna. A, *Tasmacephalus platypus* Bentley and Jago, 2004, complete, IM, UTGD53647a, x1.1. B-C, *Nepea narinosa* Whitehouse, 1939, B, cranidium, EM, UTGD125432, x3.8; C, cephalon plus partial thorax, EM, UTGD125437, x5.7. D-E, *Notacoosia plana* Jago and Bentley, 2007, D, holotype cranidium, EM, UTGD125414, x3; E, pygidium, IM, UTGD125424, x3.8. F, *Clavagnostus milli* Jago and Daily, 1974, complete, IM, UTGD125459, x7.6. G, *Tasagnostus debori* Jago, 1976a, complete, EM, UTGD121112, x7.6. H-K, Christmas Hills Upper Fauna. H, *Fuchouia* sp., almost complete, lacking librigenae, IM, private collection, x1.5. I, *Centropleura* sp., cranidium, EM, private collection, x1.5. J, *Goniagnostus spiniger* (Westergård), complete, IM, UTGD92472, x6. K, *Megagnostus* cf. *glandiformis* (Angelin), complete, EM, prívate collection, x1.9. L-P, Que River Fauna. L, *Ptychagnostus? murchisoni* Jago, 1977, complete, IM, UTGD92509, x3.8. M-N, *Onymagnostus stenorrhachis* (Grönwall), M, cephalon, IM, UTGD92503, x5.3; N, pygidium, IM, UTGD95150 x4.5. O, *Valenagnostus* sp., enrolled specimen with cephalon visible, IM, UTGD92653, x6.4. P, *Diplagnostus* sp., pygidium, IM, UTGD92616, x8.7.

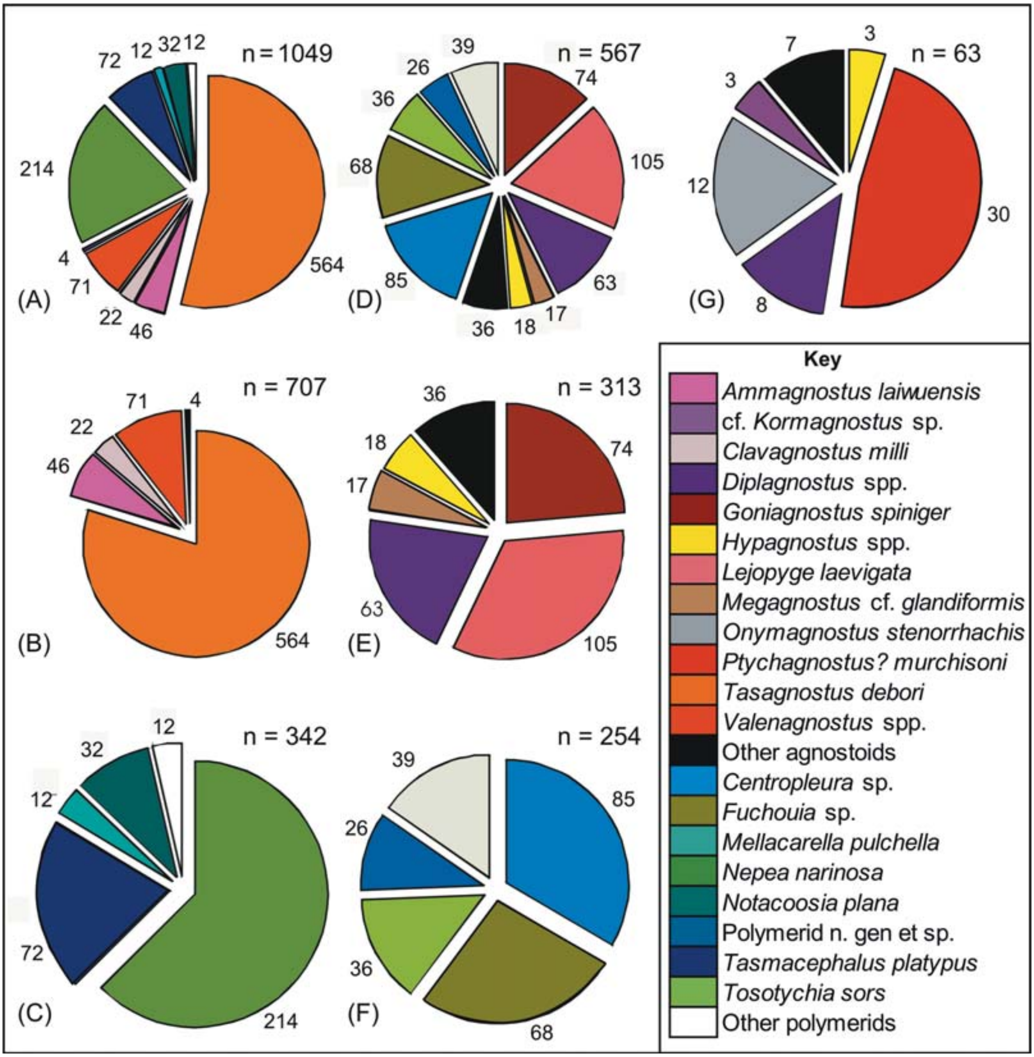

Figure 1. Relative abundances of trilobites from three Late Middle Cambrian faunas of Tasmania. A-C, Christmas Hills lower fauna. A, total counts of trilobites; B, counts of agnostoid trilobites only; C, counts of polymerid trilobites only. D-F. Christmas Hills upper fauna, D, total counts of trilobites; E, counts of agnostoid trilobites only; F, counts of polymerid trilobites only. G, Que River beds. G, total counts of trilobites (= counts of agnostoid trilobites).

The upper fauna at Christmas Hills has a much more even distribution of species when compared with the lower fauna. Agnostoids and polymerids respectively comprise 59.8% and 40.2% of the trilobite fauna. A total of 567 individuals have been counted from the upper fauna (Fig. 1D-F); of these about 9.7% of the individuals occur in complete specimens, with similar percentages for both the agnostoids and polymerids. The agnostoids *Lejopyge laevigata, Goniagnostus spiniger*, and *Diplagnostus* sp. respectively comprise 36.3%, 25.4% and 20.8% of the agnostoid fauna and 18.5%, 13.1% and 11.1% of the total trilobite fauna. The dominant species of the lower fauna, *Tasagnostus debori*, comprises only 3.5% of the agnostoids and 1.9% of the total trilobite fauna. *Centropleura* sp., *Fuchouia* sp. and *Pianaspis* sp. are the most abundant polymerid taxa comprising 33.5%, 26.8% and 14.2% of the polymerids and 15.0%, 12.0% and 6.3% of the total fauna. These figures are different from those given in Bentley and Jago (2007) because an extra 191 specimens have been added to the database.

DISCUSSION

Comparison with other Australian late Middle Cambrian faunas of *Euagnostus opimus* to *Lejopyge laevigata* Zone age is difficult, because although the Middle Cambrian agnostoids have been described in detail (e.g. Öpik, 1961, 1979; Laurie, 1988, 1989), studies on polymerid trilobite faunas are limited (e.g. Whitehouse, 1939; Öpik, 1961, 1967; Jell and Robison, 1978; Sloan and Laurie, 2004) or deal with particular trilobite groups (e.g. Öpik, 1970, 1982; Paterson, 2005). However, none of these papers gives details on the relative abundances of the different taxa. In addition, the faunas from the Georgina Basin (e.g. Öpik,, 1961, 1979) and northeastern New South Wales (Sloan and Laurie, 2004) occur in shallower water sediments than the Tasmanian faunas.

Three patterns can be discerned in the charts (Fig. 1). These are dominance by one taxon (the Christmas Hills lower fauna – Figs 1A-C; the Que River fauna – Fig. 1G); two or three taxa co-dominant (the Christmas Hills upper fauna agnostoids and polymerids, taken separately (Figs 1E-F); and several taxa subequal in numbers (the Christmas Hills upper fauna in total – Fig. 1D). Paterson and Laurie (2004), in their study of the slightly younger late Mindyallan-early Idamean Dolodrook Limestone faunas, found assemblages similar to Fig. 1B (their *Protemnites* assemblage) and to Figs 1E-F (their *Mindycrusta* assemblage). The Dolodrook faunas are preserved in limestone rather than the siltstones and shales of the present faunas and consist of relatively small numbers of individuals.

The three faunas discussed above all have a high agnostoid content, which generally indicates deep water, or at least outer shelf, deposition (e.g. Pratt, 1992). The complete absence of polymerid trilobites in the black pyritic siltstone of the Que River Beds indicates dysoxic/anoxic bottom conditions, although Jago (1974a) suggested that scavengers may be present. A similar situation is found in a *Lejopyge laevigata* II or *L. laevigata* III Zone age fauna from the Gunns Plains area, northwestern Tasmania (Jago, 1976b). Here, the fauna is dominated by agnostoids (*Lejopyge laevigata, L. armata, Hypagnostus brevifrons, Goniagnostus* sp.) with the only known polymerid, *Pianaspis leveni* Jago 1974b, being confined to a single stratigraphic horizon. The percentages of complete specimens from the Christmas Hills lower fauna, the Christmas Hills upper fauna and the Que River fauna are 3.1%, 9.7% and 49.2% respectively, thus indicating decreasing bottom energy levels and possibly increasing depth and/or anoxia.

The upper fauna at Christmas Hills includes several taxa (*Centropleura, Fuchouia, Pianaspis, Lejopyge, and Goniagnostus*) with a very wide distribution. In essence, it is a normal off-shore fauna for the late Middle Cambrian. The lower fauna at Christmas Hills is dominated by a single species of agnostoid, *Tasagnostus debori.* This may indicate that this fauna is under greater environmental stress than the upper fauna, but it is unclear as to why this should be the case. It could be argued that while agnostoids are generally considered to be pelagic (e.g. Robison, 1972, but see below), some, such as *Tasagnostus*, a genus of limited geographic extent, may be benthic. However, this is countered by the situation in the Trial Ridge Beds (*Lejopyge laevigata* Zone) of south-central Tasmania, where the cosmopolitan agnostoid *Goniagnostus nathorsti* comprises about 52% of the fauna (Jago and Brown, 2001). The question of the mode(s) of life of agnostoids is clearly relevant to this discussion, but is outside the scope of this paper and will be considered in the future. Fortey and Owens (1999, p. 455ff. and references therein) and Slavičková and Kraft (2001) have discussed the matter; further references are given by Peng and Robison (2000, p. 3).

Acknowledgements

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FLUCTUATIONS IN TRILOBITE PALAEOBIODIVERSITY DURING THE DEVONIAN IN THE ARDENNES MASSIF

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Keywords: Trilobite biodiversity, Devonian, Ardennes Massif, associations.

INTRODUCTION

Throughout Devonian, trilobite biodiversity was in gradual decline. During this period, trilobites were also affected by several and significant extinctions (Feist, 1991; Chlůpáč, 1994). Mostly benthic, trilobites were strongly sensitive to environmental changes. Sea-level fluctuations leading to paleoecological and paleoenvironmental changes had important effect on their biodiversity.

In the Devonian Ardennes Massif, faunas appear to be highly diverse but are poorly documented, not being as well known as those from the German Eifel or French Ardennes. In this context, our analysis examines trilobite-bearing sections of the Ardennes Massif, in order to evaluate the biodiversity and environmental control of trilobite assemblages (Crônier and van Viersen, 2007).

Thus, in the present study, a preliminary analysis based on some ecological indices and hierarchical clusters, has been performed 1) to define ecological and associative structure in biodiversity for Devonian trilobite faunas from Belgium and 2) to obtain evolution of trilobite associations and possible correlations with sea-level variations during the Devonian Period.

MATERIAL

The trilobite material used for this study comes from nine sections located along the southern and north-eastern margins of the Dinant Synclinorium (Fig. 1). These sections from Lower to Late Devonian are characterized by a trilobite record of varying quality. 33 genera and two subfamilies as well as a single and undetermined genus have been analysed through 19 samples.

ECOLOGICAL AND ASSOCIATIVE STRUCTURE

Associative biodiversity is generally characterized by taxa richness and relative abundance of the different taxa in samples. In order to characterize assemblages of trilobites, two ecological indices have been

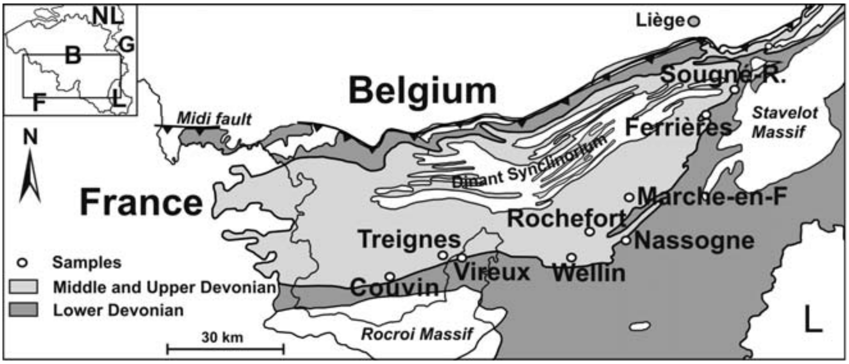

Figure 1. Location map of nine Devonian trilobite-bearing sections in the Ardennes Massif (modified after Dejonghe, 2001).

used: Diversity and Dominance indices (Brenchley and Harper, 1998). Diversity measures (Margalef Div = $S-1/\log N$; S = number of species, N = number of specimens) are standardized against the sample size. Dominance measures (Dom = $\Sigma (ni/N)^2$; ni = number of I^{th} species), based on relative abundance, have high values for assemblages with a few common elements, and low values where species are more or less evenly represented.

These ecological indices have permitted us to define four specific assemblage types (Fig. 2):

- Type A with only 1 species from Lower Devonian (SR-L, F-uP, N-uEs, T-uEs);
- Type B with important values of Dominance, characterized by a low diversity and the domination of 1 or 2 species (MF-lEs, MF-uEs, W-lEf, R-uEf, R-lG, C-mFr);
- Type C with moderate values of Diversity and Dominance (MF-uP/lEs, V-lEf, C-lEf, C-mEf, C-uEf/lG);
- Type D with important values of Diversity and low values of dominance (R-mEf).

Unfortunately, the distinction between ecological assemblages and those that arise from transport can be difficult. Thus, as noted by Brenchley and Harper (1998), 'pioneer' communities that are *in situ* or nearly *in situ* are dominated by one or two opportunistic species. Conversely, communities in 'equilibrium' are characterized by important Diversity and low values of Dominance, such as some samples of types C or D from the Belgium Eifelian (V-lEF; see Crônier and van Viersen, 2008).

Additionally, a hierarchical cluster analysis has been performed to identify typical associations of trilobites. Cluster analyses are commonly applied to paleoecological problems (Cugny, 1988; Brenchley and Harper, 1998; Botquelen *et al.*, 2006) and even on trilobites (Ludvigsen and Westrop, 1983). Here, the term association is used for similar taxonomic assemblages (Brenchley and Harper, 1998; Thomas and Lane, 1999).

The hierarchical cluster analysis, based on trilobite abundance classes, agglomerates assemblages by level of similarity (composition and relative abundance). Groups of samples (Q-mode clustering) and groups of taxa (R-mode clustering) were performed using paired-group method with the Pearson Similarity Coefficient. Groups of genera with a high probability of mutual occurrence are thus grouped together. This analysis has been performed using PAST 1.04 software (Hammer *et al.*, 2001).

Thus, six trilobite associations partly related to spatio-temporal gradients have been recognized in the Ardennes Massif (Fig. 3):

I) *Digonus* Association from Pragian-Emsian (F-uP, MF-lEs, N-uEs). Genus usually met in sandstone of the near-shore where turbulent environment has disarticulated specimens;

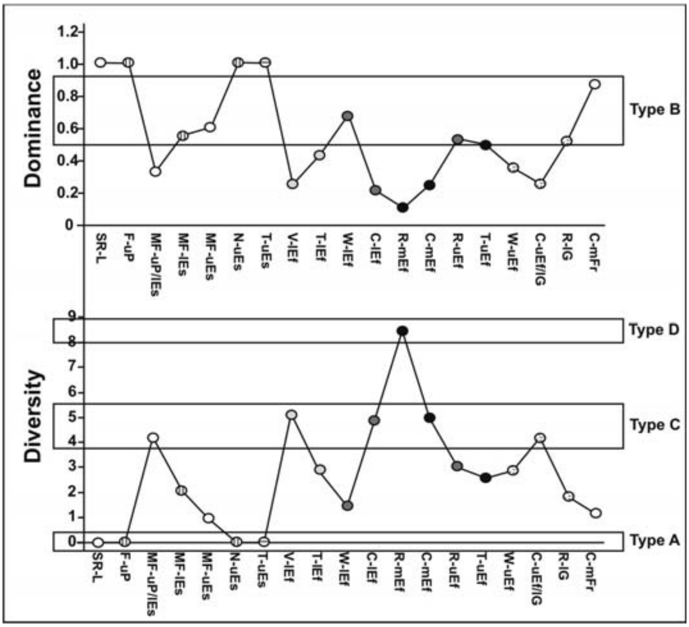

Figure 2. Trilobite faunal diversity and dominance variations through 19 samples of the Ardennes Massif from Lochkovian to the Middle Frasnian (C=Couvin, F=Ferrières, MF=Marche-en-Famenne, N=Nassogne, R=Rochefort, SR=Sougné-Remouchamps, T=Treignes, V=Vireux-Molhain, W=Wellin; L=Lochkovian, P=Pragian, Es=Emsian, Ef=Eifelian, G=Givetian, Fr=Frasnian; l=Lower, m=Middle, u=Upper).

II) Mixed Association from Eifelian which could be split in three sub-associations:
  IIa) *Calycoscutellum* Association (C-lEf, R-uEf). Couvin biota is found in argillaceous limestone beds and most of specimens are disarticulated. It is possible to find complete specimens of *Tropidocoryphe*, *Cyphaspis* and *Dohmiella* (van Viersen, 2006). Small individuals are locally accumulated. No complete specimens were found at Rochefort;
  IIb) *Geesops* Association (V-lEf). This biota is present in calcareous shales with fine lenticular clay laminae. Numerous specimens are articulated. This association is dominated by *Geesops* (50%); *Rhenocynproetus* (12%) and *Pedinopariops* (9%) are also well represented (Crônier and van Viersen, 2008);
  IIc) Association with abundant and diverse trilobites (C-mEf, R-mEf). Rochefort biota is characterized by dominant *Cyphaspis*, *Radiaspis*, *Kettneraspis*, *Cornuproetus* and *Gerastos*. Disarticulated and complete specimens are found. Couvin biota is characterized by dominant *Eifliarges*, *Cornuproetus* and *Gerastos*. Here, the biodiversity is less rich than Rochefort but with the same state of preservation;

III) Asteropyginae Association from Lochkovian-Emsian (MF-uEs, MF-uP/lEs, SR-L). Specimens are usually disarticulated and found in sandy layers;

IV) *Dechenella* and *Nyterops* Association from Upper Eifelian (Couvin and Wellin) and Lower Givetian (Couvin and Rochefort). Disarticulated and fragmented trilobites are found in crinoidal limestones;

V) *Kayserops* 'occurrence' from Upper Emsian (T-uEs). Since only one well-preserved cranidium of this taxon was found, the term of 'occurrence' is used pending the discovery of new data;

VI) *Bradocryphaeus* Association from Middle Frasnian (C-mFr). *B. supradevonicus* represents 69% of this association restricted to greenish shales. Trilobites are usually fragmented. Accumulations often occur.

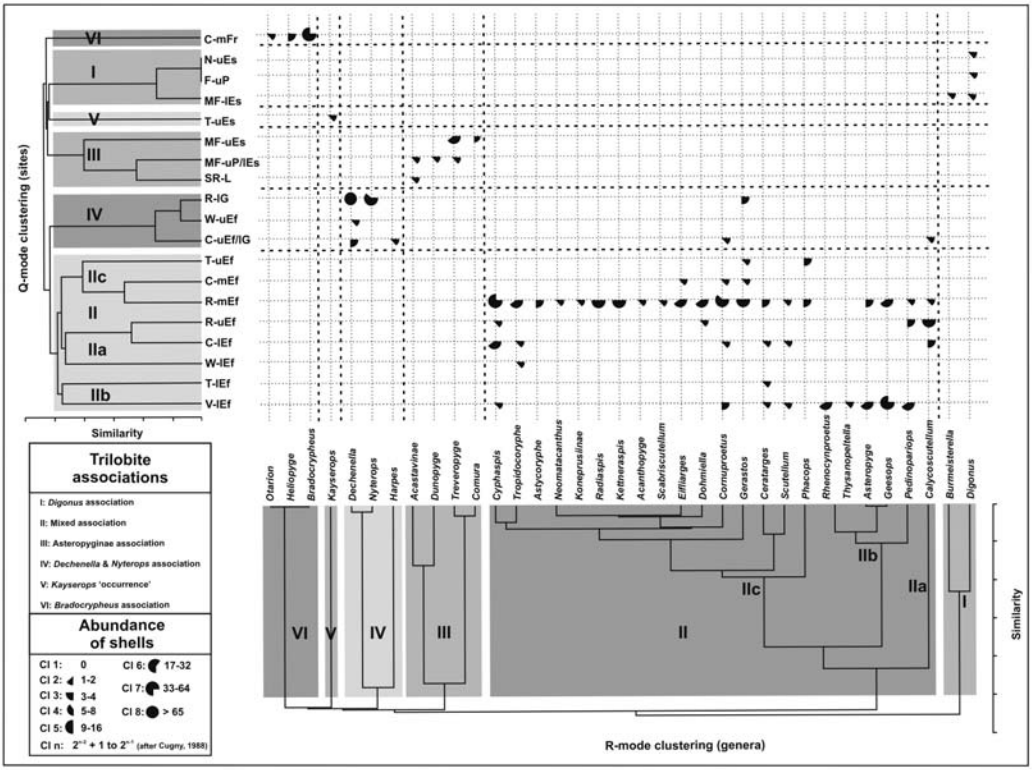

Figure 3. R and Q mode clustering analysis applied to Devonian trilobites of the Ardennes Massif (35 genera/subfamilies and 19 samples). Six clusters or associations are recognized after relative abundance classes of taxa (C=Couvin, F=Ferrières, MF=Marche-en-Famenne, N=Nassogne, R=Rochefort, SR=Sougné-Remouchamps, T=Treignes, V=Vireux-Molhain, W=Wellin; L=Lochkovian, P=Pragian, Es=Emsian, Ef=Eifelian, G=Givetian, Fr=Frasnian; l=Lower, m=Middle, u=Upper).

RELATIVE PALEOBATHYMETRIC POSITION

Palaeoecological indices, fossil preservation and nature of sediment are important tools to locate fossiliferous sites along a bathymetric profile (Fortey and Owens, 1997; Brenchley and Harper, 1998). Moreover, trilobite associations have been used for determining marine environments (Fortey, 1975).

Thus, the shoreline environment (0-15m), a shallow, proximal and agitated environment, is generally characterised by sandstone deposits. Ecological indices indicate usually a low diversity but this one may have been increased by transport of allochthonous specimens. *Digonus* Association (I) was possibly developed in such an environment.

The upper offshore or inner shelf environment is a quiet environment but occasionally disturbed by storm waves, so the deposits are mudstones interbedded with sandstones. Trilobites are commonly disarticulated or fragmented. *Bradocryphaeus* Associations (VI) could represent this environment.

The median offshore or middle shelf environment is characterised by mudstone deposits. Ecological indices point out usually an important abundance of specimens but decreasing with depth. Here associations were generally in 'equilibrium'. Well-developed eyes, commonly articulated trilobites are also characteristic of these quiet dynamic conditions. Mixed Associations (II) are found in such an environment.

CONCLUSIONS

Cluster analysis of 35 genera/subfamilies trilobite spatio-temporal distributions, has permitted the recognition of five associations and one occurrence in the Ardennes Massif during the Devonian.

These associations seem to be related to water depth and substrate type. Trilobites as vagrant epibenthos were sensitive to paleoenvironmental fluctuations and ecological parameters.

The distribution of the various trilobite associations in the Ardennes Massif, with their changing diversities and paleobathymetric preferences, seems to have been controlled by sea-level fluctuations (Godefroid *et al*., 1994; Steemans, 1989). Additionally, a species turn-over was also observed through time for trilobites occurring in the same environment. Thus, a period of low relative sea-level that occurred during the Early Devonian coincides with the expansion of *Digonus* and *Asteropyginae* associations, typical of shallow shoreline environments. Then, a rising sea-level period occurring during the Middle Devonian coincides with the blooming of Mixed associations known from the median offshore environment. In particular, a peak of diversity was reached during the Eifelian and coincides with deepening of the environment. Finally, a possible replacement of the *Dechenella* and *Nyterops* association from the Early Givetian by the *Bradocrypheus* association from the Frasnian seems to occur in the upper offshore or inner shelf environment.

This paper is a first step to improve our knowledge of Devonian Ardenne trilobites. To understand better the spatio-temporal distribution of trilobite associations, works on other trilobite-bearing sections such as Givet, Nismes, Glageon are in progress. Moreover, in order to enhance comparisons between fossil assemblages from different outcrops, new analyses with respect to current sedimentological and quantitative paleontological concepts and methods carried out level by level are necessary 1) to obtain a more precise and critical analysis of past biodiversity and relationships between faunas and their palaeoecological settings, and 2) to refine palaeoenvironmental reconstructions.

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MIDDLE CAMBRIAN TRILOBITES OF LA LAJA FORMATION, WESTERN ARGENTINA

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Keywords: Trilobites, Cambrian, biostratigraphy, paleobiogeography, Argentina.

The Cambrian–Lower Ordovician of the Precordillera of western Argentina is represented by a west- and southwest-facing continental shelf succession of mainly carbonate strata. It has been known for some time that the biotas preserved in these strata are similar or identical to those of Laurentia, implying close paleobiogeographic links which were gradually severed starting in the Middle Ordovician.

For our comprehensive study of the trilobite faunas of the Middle Cambrian La Laja Formation we measured sections in the San Juan area, in Quebrada de Zonda, Quebrada de La Laja and Cerro Tres Marias in Sierra Chica de Zonda, and Cerro Molle in Sierra de Villicum. These localities expose a heterolithic suite of facies characteristic of the platform interior, ranging from open-shelf ooidal grainstones to near-shore argillaceous mudstones. Storm activity was not intense but it was relatively frequent; there is evidence for occasional tsunami impact. Consequently the succession is poorly fossiliferous, trilobites are disarticulated, and sclerites are commonly broken.

Our work (Bordonaro and Pratt, in prep.) has revealed that the earliest Middle Cambrian is represented in the lowermost Soldano Member by *Eokochaspis nodosa* and other kochaspidids of the *Eokochaspis nodosa* Biozone and possibly other biozones of the generalized *Plagiura–Poliella* Zone, hitherto recognized in the Great Basin of western U.S.A. These overly a low-diversity fauna consisting of olenellids and a single antagmine ptychoparioid in the Estero Member, of latest Early Cambrian age. The succeeding *Albertella* Biozone may be present but this interval is badly folded and faulted and available material is as yet equivocal. The *Glossopleura* and *Ehmaniella* biozones occur in the middle and upper parts of the Soldano Member respectively. The former contains species belonging to *Glossopleura* and *Alokistocare*, while the latter contains species belonging to *Ehmaniella, Altiocculus, Elrathiella, Nyella* and *Polypleuraspis.* The *Bolaspidella* Biozone comprises the thickest portion of La Laja Formation, and includes the uppermost Soldano, the Rivadavia Member, the Juan Pobre Member (restricted) and the recently defined Las Torres Member. It contains species belonging to *Bolaspidella, Blainia, Altiocculus, Asaphiscus*, marjumiids and other genera. Several *Kootenia* and *Olenoides* species are present in the *Glossopleura* Zone and younger intervals, whereas agnostoids and oryctocephalids are lacking. Instead, La Laja faunas comprise a succession of inner-shelf biofacies distinct from those recognized in the Great Basin and the southern Rocky

Mountains of western Canada which are predominantly outer platform in their depositional setting (Bordonaro *et al.*, 2008).

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NEW POST-CAMBRIAN TRILOBITE ASSOCIATIONS FROM MONGOLIA

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Keywords: Mongolia, trilobites, Ordovician, Devonian.

INTRODUCTION

Although the trilobite faunas of Inner Mongolia has been recently thoroughly studied and discussed (e.g. Nan 1976; Zhang and Liu, 1986; Zhou and Campbell, 1990; Zhou *et al.*, 2000, and others), and despite of the common, stratigraphically and palaeontologically important Lower Palaeozoic faunas of Mongolia, mostly Cambrian trilobite faunas (e.g. Korobov 1980, 1989, and Dumicz *et al.*, 1970) have so far been published (with exception of Chernysheva, 1937). However, the findings of post-Cambrian trilobites are mentioned in the several mapping reports and excursion guides (Minjin *et al.*, 2001) or short papers (Minjin *et al.*, 2007) a.o. Our effort at least partially fills this perceptible gap; some new trilobite-bearing areas are described. These have been studied during the joint Czech-Mongolian geological mapping expeditions in 2000-2007, the IGCP 410/421 excursion in 2001 and during extensive field investigations guided by the Mongolian University of Science and Technology.

REVIEW OF SOME NEW POST-CAMBRIAN TRILOBITE LOCALITIES IN MONGOLIA

1. Mongolian Altai

Between Mongolian Altai and Gobi Altai Ranges, quite common, although anchi-metamorphosed trilobite remains were found by the first author during the joint geological mapping of the Chandmani somon area in the 1:50000 scale made by the Czech Geological Survey, Mineral Resources and Petroleum Authority of Mongolia (MRPAM) and the Geological Investigation Centre (GIC) in 2004-2007. These occur in two formations – the Middle Ordovician Bayantsagaan and the Lower Devonian Takhilt formations, respectively. In the Shine-Jinst area trilobites have been found in the Chuluun and in the Govialtai formations (Minjin *et al.*, 2001).

Figure 1. Sketch map of Mongolia. Stars mark position of the trilobite-bearing localities.
The numbers correspond to the numbering of the areas in the text.

1a. Bayantsagaan Formation – Middle Ordovician, Darriwilian? Stage

The Middle Ordovician age of this formation was supported by the occurrence of brachiopods (*Orthidiella* sp., *Productorthis* sp., *Orthambonites* sp. and Strophomenida div. sp.), crinoids (*Iocrinus* sp. and *Ramseyocrinus* sp.) in the chloritic shales and metasiltstones with intercalations of slightly re-crystallised, originally biodetritic limestones. The poorly preserved but quite common trilobite remains are represented by Asaphidarum indet. The marine, relatively deeper-water and rather quiet environment, yields periodic influxes of bioclastic material from elevations of the sea floor (biostromes?) that were probably caused by sea currents or storms.

1b. Takhilt Formation - Lower Devonian, Lochkovian to Emsian stages

The mostly clastic formation of Lochkovian to Emsian, most probably Pragian in age, contains banks of pink, white and grey coarse biosparitic to biomicritic, slightly re-crystallised limestones with common crinoids. Extremely rich faunal associations were found during mapping: *Asperocrinus* sp., *Trybliocrinus* sp., *Mediocrinus* sp., *Salairocrinus* sp., *Pentamerocystella* sp., *Mydodactylus* sp., *Pandocrinus* sp., *Sutherlandinia* sp., Rugosa indet., *Parastriatopora* sp., *Striatopora-Taouzia*? incert., *Bainbridgia*? sp., cf. *Cladochonus* sp., Syringoporida incert., and *Laccophyllum*, O*rthonychia* sp., *Cyrtocyclonema* sp., *Rugosatrypa*? sp., *Cymostrophia* sp., Phacopida? indet., Proetida indet., *Crotalocephalina* aff. *cordai* accompagnied by indeterminable bryozoans and nautiloids (*Kopaninoceras* sp.). The dacryoconarid tentaculites *Guerichina* sp. support a Lochkovian-Pragian age (determination P. Lukeš). This association indicate shallow-water marine environment in the photic zone, with biostromes or small reefs.

1c. Chuluun Formation – Lower Devonian, Emsian Stage

Brachiopod rich dark grey, thin-bedded limestones near the Tsakhir well contain numerous remains of a dechenelline proetid (*Basidechenella*? sp.).

2. Tsagaandel section, West from Bayanhongor city, Tsagaandel Fm., Sandbian to Katian stages

This very important section has been described by Rozman and Minjin (1981), Minjin *et al*. (2001), and Albanesi *et al*. (2003). Two authors (O.F. and R.F.) collected here in 2001, during the IGCP 410 and 421 field excursions, the rich but uniform trilobite faunas occurring in the brown-grey bioclastic carbonates which belong to the layer 6 sensu Minjin *et al*. (2001). The Upper Ordovician age is supposed for these strata (Upper Katian on the base of macrofauna, see Minjin *et al*. 2001) but Sandbian on the base of conodont dating, see Albanesi *et al*., 2003). The trilobites (*Ayushia baatar* gen. n. sp. n., Asaphidarum indet., Encrinurinae and Cybelinae indet. are accompanied by common but well-preserved brachiopods, corals, stromatoporates, bryozoans, tentaculites and crinoid debris (for the extensive list of non-trilobite fauna, see Minjin *et al*., 2001). The gathered association suggests rather shallow-water environment with locally developed organic build-ups.

3. Edrengijn Nuruu area, Lower Devonian, ?Pragian

Several trilobite remains including pygidium of *Scutellum* sp. have been collected and studied by the fourth author during the common Czech-Mongolian geological mapping expedition in 2000. The remains are of Lower Devonian age and have been found in dark grey biosparitic to biomicritic limestone of Ulgiyn Formation.

4. Chigertei section, Upper Ordovician, ?Sandbian to Katian

The locality has been recently described by Minjin *et al.* (2007). Possible trilobite remains (reminiscent effaced illaenids but too much deformed for any determination), brachiopods *Pionoderma* sp. (*Svobodaina* - like type) and/or *Comatopoma* sp. suggest the Upper Ordovician age and belong to the layer 2. sensu Minjin *et al.* (2007). Because of the very poor preservation, the trilobite remains are neither figured nor discussed in detail here but the region should be considered as potential for trilobite bearing. Recently, another trilobite remain (pygidium) has been collected by the Mongolian and Russian researchers but the material has not been at disposal.

SYSTEMATIC PART

Order Phacopida Salter, 1864
Family Phacopidae Hawle and Corda, 1847

Phacopidae? indet.
(Pl. 1 AE)

Material. One deformed negative of pygidium, two other questionable fragments, all anchi-metamorphosed.

Remarks. The preservation of all remains does not enable exact determination. Despite this, they are closer to phacopid than to proetid remains. However, the determination should be considered as provisional only and new findings are necessary to confirm an occurrence of this group in the area.

Occurrence: Takhilt Formation, Lower Devonian, Pragian?, Gichiginey nuruu, Chandmani somon area, Mongolia.

Family Pterygometopidae Reed, 1905
Subfamily Eomonorachinae? Pillet, 1954

Genus *Ayushia* gen.n.

Type species: *Ayushia baatar* sp.n.

Derivatio nominis. Ayusha, a masculine Mongolian name. In honour to our very open and friendly driver, who closely co-operated with us during the Mongolian Altai mapping expedition and collected nice fossils.

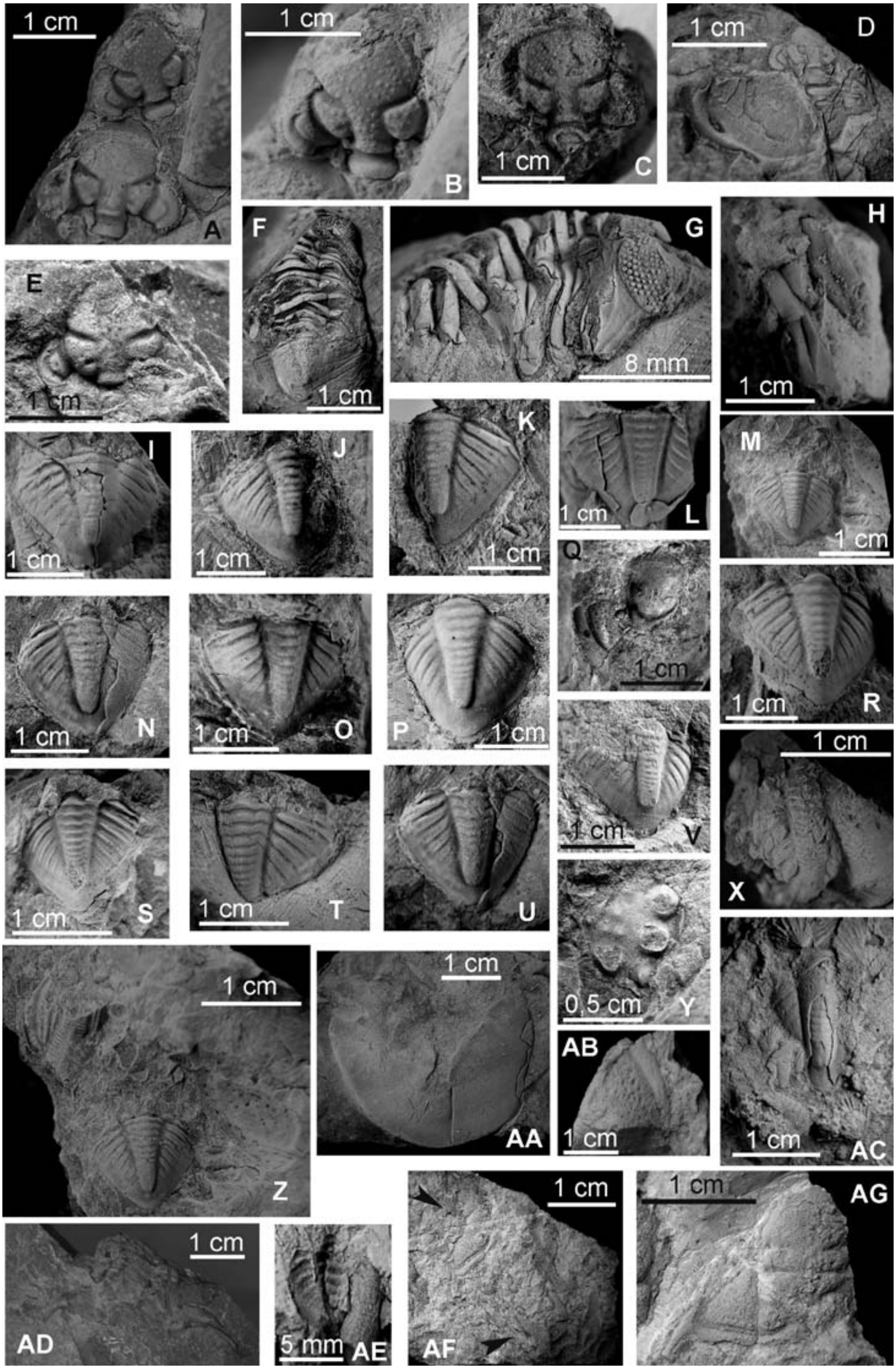
Diagnosis. Questionable eomonorachid with almost fused L2 and L3 forming inflated bicomposite lobe, separated from remaining glabella by prominent longitudinal furrow somewhat reminiscent of Monorakinae Kramarenko, 1952. S2 only slightly perceptible (especially adaxially on internal moulds), line-like, almost sub-paralell with posterior margin of L2. L1 and L2 very narrow (exsag.), L1 with minute but perceptible lateral lobes. L3 very wide, inflated. Eyes large, with more than 16-20 rows comprising up to 8-9 lenses (estimated). Glabella prominently granulated. Thoracic and pygidial axis vaulted, lateral axial lobes indistinct. Distal ends of thoracic pleurae well rounded, articulating facets expressive. Pygidium subtriangular with short blunt posterior process. Axis with 12-13 rings plus terminal piece. First 6-7 rings possessing apodemes rapidly narrowing backwards. Post-apodemal part of axis tapering more gradually, ending in ca 4/5 of the pygidial (sag.) length. Lateral lobes with 6-8 deep, narrow pleural furrows. Interpleural furrows line-like.

Remarks. The systematic position of *Ayushia* gen.n. is somewhat problematical. Although it surely belongs to the pterygometopids, its subfamily affiliation is not entirely certain. The general exoskeleton configuration strongly recalls *Eomonorachos*, *Calliops* and especially *Calyptaulax*. From all of these genera, it differs especially by strongly reduced L2 and inflated L3, forming a bicomposite lobe and by the presence of longitudinal glabellar furrows, suggesting the affiliation of the new taxon to the Monorakinae (see Holloway, 2004). However, the shape of L2 and the course of S2 resemble rather some specimens of *Calyptaulax* (see also Clarkson and Tripp, 1982).

Species assigned. Only type species.

Occurrence. Upper Ordovician (Sandbian) of Mongolia.

Plate 1. Tsagaandel Formation, Upper Ordovician. A-V, Z: *Ayushia baatar* gen. et sp. n. A-B, two cephala (holotype is the larger cephalon), CGS PB 350, A, general dorsal view. B, A detail of the smaller cephalon. C, E, incomplete cranidia, CGS PB 352-353, dorsal view. D, incomplete juvenile cephalothorax, CGS PB 354. F-G, damaged disarticulated specimen, CGS PB 355, dorsal and lateral view. H, fragments of thoracic segments, CGS PB 356, lateral view. I-P, R-V, incomplete pygidia, CGS PB 357-370, dorsal view. Q, hypostome and fragment of free cheek, CGS PB 371. X, Encrinurinae? indet.: damaged pygidium, CGS PB 372, dorsal view, x2. Y, Encrinurinae? indet. fragment of glabella(?), CGS PB 373, dorsal view. Z, Cybelinae indet., damaged pygidium (left top), and pygidium of *Ayushia baatar* gen. et. sp. n., dorsal view. AA, AC, Asaphidarum gen. et sp. I., incomplete pygidia, dorsal view. AA – CGS PB 374, AB CGS PB 375. Bayantsagaan Formation, Middle Ordovician. AD, Asaphidarum gen. et sp. II, deformed cephalon, CGS PB 376, dorsal view. Takhilt Formation, Lower Devonian. AE, Phacopidae? indet. – deformed, re-crystallized negative of the pygidium, dorsal view, CGS PB 381. AF-AG, *Crotalocephalina*? aff. *cordai* Barrande. Deformed, re-crystallized cranidium and pygidium, CGS PB 377. AF, general dorsal view. AG, detail of cranidium, dorsal view. AB, fragment of the free cheek, dorsal view, CGS PB 351.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Ayushia baatar sp.n.
(Pl. 1 A-V, Z)

Derivatio nominis. Baatar - Hero.

Holotype. Incomplete cephalon CGS PB 350.

Material. Two damaged incomplete specimens and almost fourty incomplete cephala, pygidia and other exoskeletal fragments.

Type locality. Bayankhongor area, W of Bayankhongor City, Tsagaan Del Section, Layer No. 6, Tsagaan Del Formation, Upper Ordovician (Sandbian).

Diagnosis. The same as for genus.

Remarks. It is unknown whether adults of *Ayushia baatar* gen. et sp.n. possess genal spines because in all specimens available the lateral cephalic border is damaged but seems to be rounded. It corresponds well to the general phacopid-like body morphology. Only the incomplete juvenile cephalothorax CGS PB 354 (Pl. 1 D) bears traces of spines on the right free cheek.

Occurrence. The type locality only.

Suborder Cheirurina Salter, 1864
Family Cheiruridae Salter, 1864
Crotalocephalus? aff. *cordai* (Barrande, 1846)
(Pl. 1 AB, AF-AG)

Material. Strongly deformed cranidium and pygidium on one rock piece, another fragment of free cheek.

Remarks. The preservation of remain allows only provisional affiliation.

Occurrence. Takhilt Formation, Lower Devonian, Pragian?, Gichiginey nuruu, Chandmani somon area, Mongolia.

Family Encrinuridae Angelin, 1854
Cybelinae and Encrinurinae indet.
(Pl. 1 X-Z)

Material. Two incomplete pygidia and several fragments of pygidia, cranidia and free cheeks.

Remarks. The pygidium figured on the Pl. 1. fig. X, reminiscent (especially by the prominently vaulted ribs) rather to encrinurids than to cybelids but its preservation does not enable an exact determination.

Occurrence. West of Bayankhongor City, Tsagaandel section, Tsagaandel Formation, Upper Ordovician (Sandbian).

Order Asaphida Salter, 1864
Asaphidarum gen. et sp. indet. I
(Pl. 1 AA, AC)

Material. Two deformed incomplete pygidia.

Remarks. The preservation of remains excludes exact determination.

Occurrence. West of Bayankhongor City, Tsagaandel section, Tsagaandel Formation, Upper Ordovician (Sandbian).

Asaphidarum gen. et sp. indet. II
(Pl. 1 AD)

Material. Cranidium and fragments of the pleurae conserved on the foliation planes, all anchi-metamorphosed.

Remarks. All remains available are very poorly preserved and indeterminable. Despite this, they indicate the presence of asaphids in the Mongolian Altai.

Occurrence. Bayan Tsagaan Formation, Middle Ordovician, Darriwilian. Northern slope of the Gichiginey nuruu mountain ridge, Chandmani somon area, Mongolia.

Order Proetida Salter, 1864
Proetidae indet.
(Fig. 2 A-D)

Material. Several incomplete poorly preserved, cranidia, free cheeks and pygidia, all anchi-metamorphosed.

Remarks. The preservation of remains does not enable any exact determination.

Occurrence. Takhilt Formation, Lower Devonian, Pragian?, Gichiginey nuruu, Chandmani somon area, Mongolia.

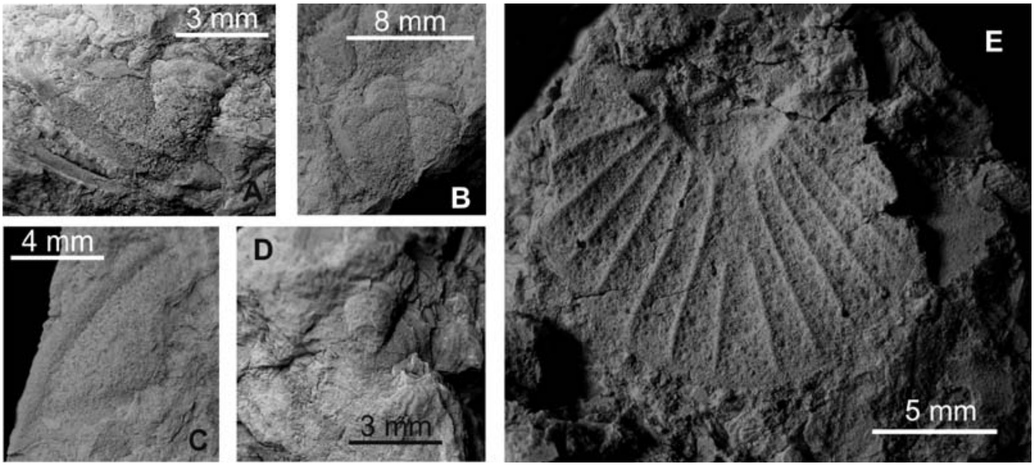

Figure 2. Takhilt Formation, Lower Devonian. A-D: Proetida indet. A, incomplete, deformed pygidium CGS PB 378, dorsal view; B, incomplete, deformed pygidium CGS PB 379, dorsal view; C, incomplete cranidium, CGS PB 380, dorsal view; D, incomplete, deformed pygidium CGS PB 378, dorsal view; Ulgiyn Formation, Lower Devonian. E, *Scutellum* sp., CGS PB 385, dorsal view.

Order Corynexochida Kobayashi, 1935
Suborder Scutelluina Hupé, 1953
Scutelluidae Richter and Richter, 1925
Scutellum sp.
(Fig. 2 E)

Material. Incomplete pygidium.

Remarks. The pygidium has wide (tr.), weakly trilobite axis and 7 pairs of narrow intercostal furrows that die out close to pygidial margin. There is a median unbifurcated rib which narrows extremely anteriorwards until being completely subsided adaxially, merging with neighboring ribs. Sculpture consists of irregularly spaced coarse granules. This configuration assigns the specimen to *Scutellum* Pusch. However, the specimen, a holaspid, is damaged. Specific determination needs supplementary material.

Occurrence. Ulgiyn Formation, Lower Devonian, Pragian?, Edrengijn Nuruu area, S. Mongolia.

CONCLUSIONS

Although only preliminarily described, the surprisingly rich trilobite assemblages indicate a great potential of this group for Mongolian stratigraphy and palaeogeography. From the palaeogeographic point of view, determinable Ordovician trilobites suggest possible connections with faunas from the Laurentia, Siberia or Baltica (occurrence of pterygometopids and encrinuroids), whereas some of the Devonian representatives show similarity to peri-Gondwana faunas (see also Feist, 2001).

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DALMANITOID AND ACASTOID TRILOBITES AND THEIR EVOLUTION IN THE PRAGUE BASIN (CZECH REPUBLIC)

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Keywords: Czech Republic, Dalmanitoidea, Acastoidea, Ordovician, Silurian, Devonian.

INTRODUCTION

The dalmanitoid and acastoid trilobites belong to the common and diversified trilobite groups in the Prague Basin as well as in other peri-Gondwanan regions, Australia, South America and Laurentia. They range there from the uppermost Lower Ordovician up to the Middle Devonian. Therefore, knowledge on these two superfamilies may be useful also for palaeogeography. The faunal migrations between the Prague Basin (Perunica) and other areas were discussed by Havlíček *et al*. (1994), Mergl *et al*. (2007, herein), Budil *et al*. (2007) and Fatka and Mergl (in press), meanwhile dalmanitids have been discussed by Budil (2001), Budil and Hörbinger (2006) and Budil *et al*. (submitted).

DALMANITOIDS AND ACASTOIDS EVOLUTION IN THE PRAGUE BASIN – MAIN PERIODS

In the Prague Basin several faunal exchange events could be recognized within dalmanititoids and acastoids *s.l.* (sensu Edgecombe, 1993),

Such events are characterized by appearance of newcomers known in other regions, alternating with periods of restricted communication, and/or even total absence of both groups, although their representatives were common in the neighbouring regions at the same time.

General facies dependence of dalmanitoid and acastoid trilobites (with benthic larvae, discussion see Budil *et al.*, submitted) represented probable constrain for their spreading.

The following main periods in the evolution of both groups have been observed in the Prague Basin (Figs. 2 and 3):

1) Onset of early dalmanitids (Floian to Dapingian): First representatives (*Ormathops*, *Toletanaspis*) in African Gondwana (present day Anti-Atlas), peri-Gondwanan Europe (Ibero-Armorica, Montagne Noire and Perunica and Avalonia; Fortey and Owens, 1987).

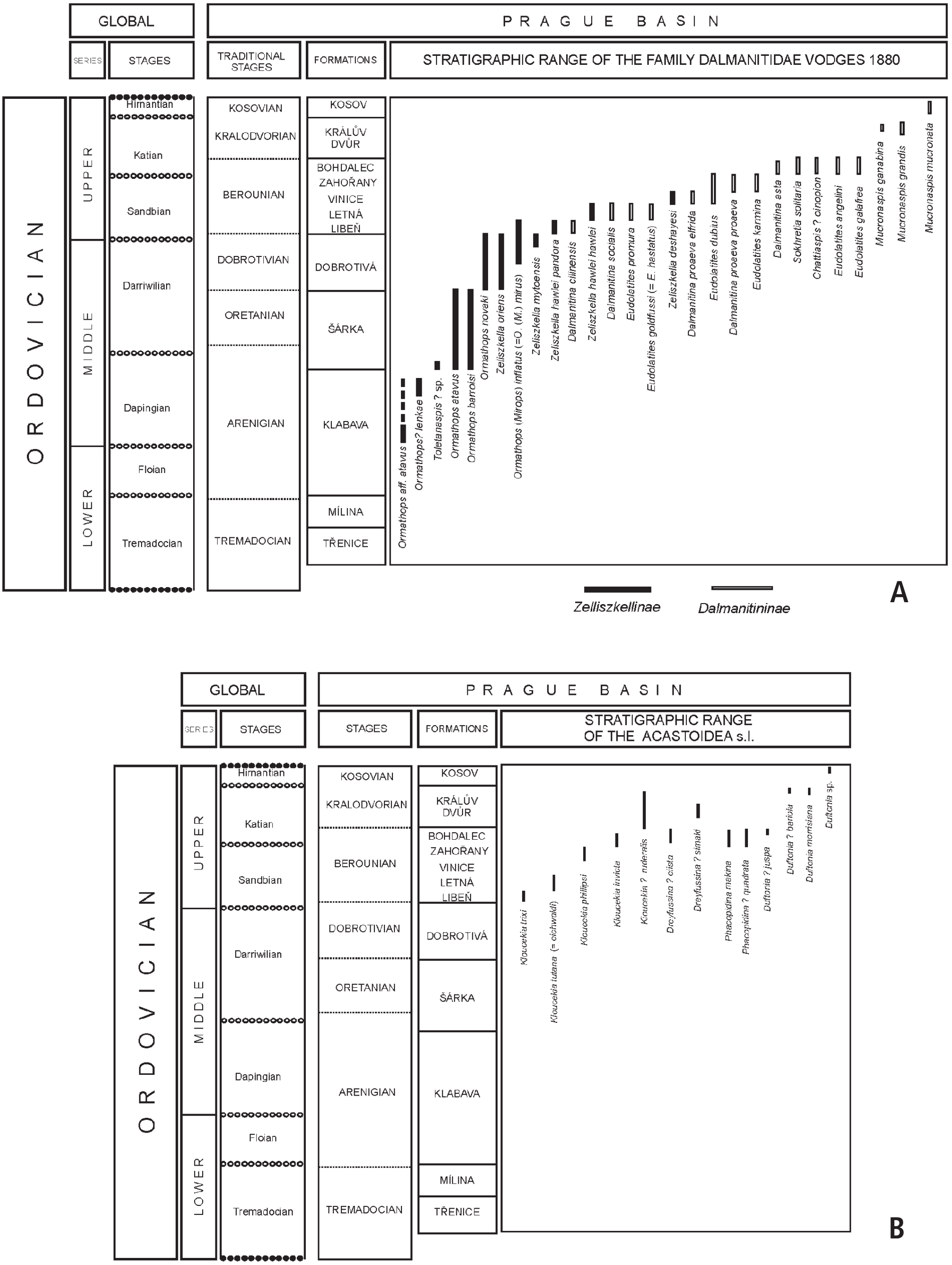

Figure 1. A review of the stratigraphical distribution of the dalmanitoids and acastoids in the Prague Basin.
A, Ordovician dalmanitids; B, Ordovician acastoids *s.l.*

2) Mid Darriwilian (Oretanian): First mass occurrence of dalmanitids in Perunica [shared species (*Ormathops*) in Massif Armoricain and possibly also in Avalonia] and Ibero-Armorica. Moderate species diversity but high intraspecific variability.
3) Endemic taxa in Dobrotivian (ca. upper Darriwilian): endemicity in African Gondwana (Morocco), Ibero-Armorica and Perunica.
4) Sandbian: *Dalmanitina-Eudolatites* spreading event. Probably Bohemian and/or Moroccan elements are known also in Armorica, Avalonia and present day Turkey. Advanced zelliszkelinids, immigration of the first acastoids probably from the Armorica or Avalonia.
5) Late Sandbian to early Katian: Immigration of *Phacopidina-Baniaspis* and *Dreyfussina* probably from African Gondwana (Morocco) and/or European peri-Gondwana (Montagne Noire or ?Avalonia). Shared *Dalmanitina*, *Kloucekia* and *Eudolatites*, rare *Duftonia*.
6) Late Katian: Onset of *Mucronaspis* and *Duftonia* (immigrating from Avalonia or southern Baltica). Analogy of Cystoid Limestones, short time warming (the global Boda Event sensu Fortey and Cocks, 2005).
7) Hirnantia Fauna (Hirnantian): *Mucronaspis* - cosmopolite character, the last rare acastoids in Perunica. Global event (cooling).
8) Lower Silurian without dalmanitoids and acastoids in Perunica.
9) A brief appearance of synphoriid *Delops* and *Struveria* (Avalonian elements) in Homerian (post-*lungreni* recovery?) in Perunica.
10) Upper Silurian to lowermost Devonian (Lochkovian): absence of dalmanitoids and acastoids in Perunica.

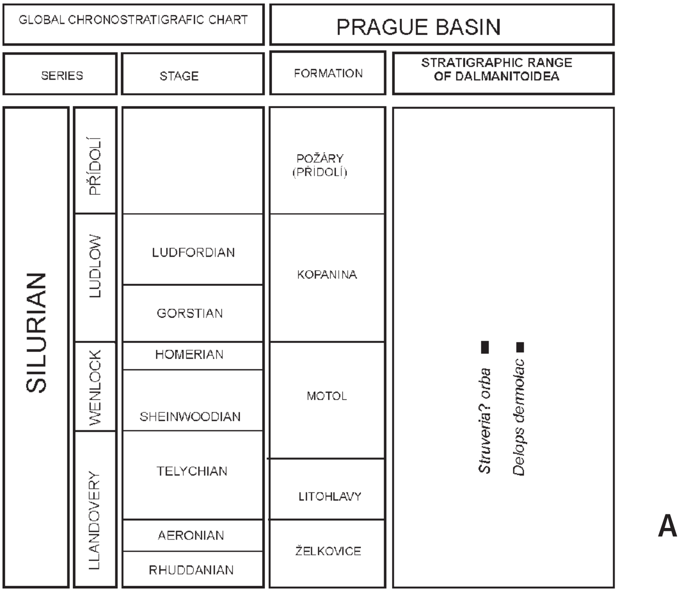

Figure 2. A review of the stratigraphical distribution of the dalmanitoids and acastoids in the Prague Basin.
A, Silurian dalmanitoids (synphoriids); B, Devonian dalmanitids (after Budil *et al.,* submitted)

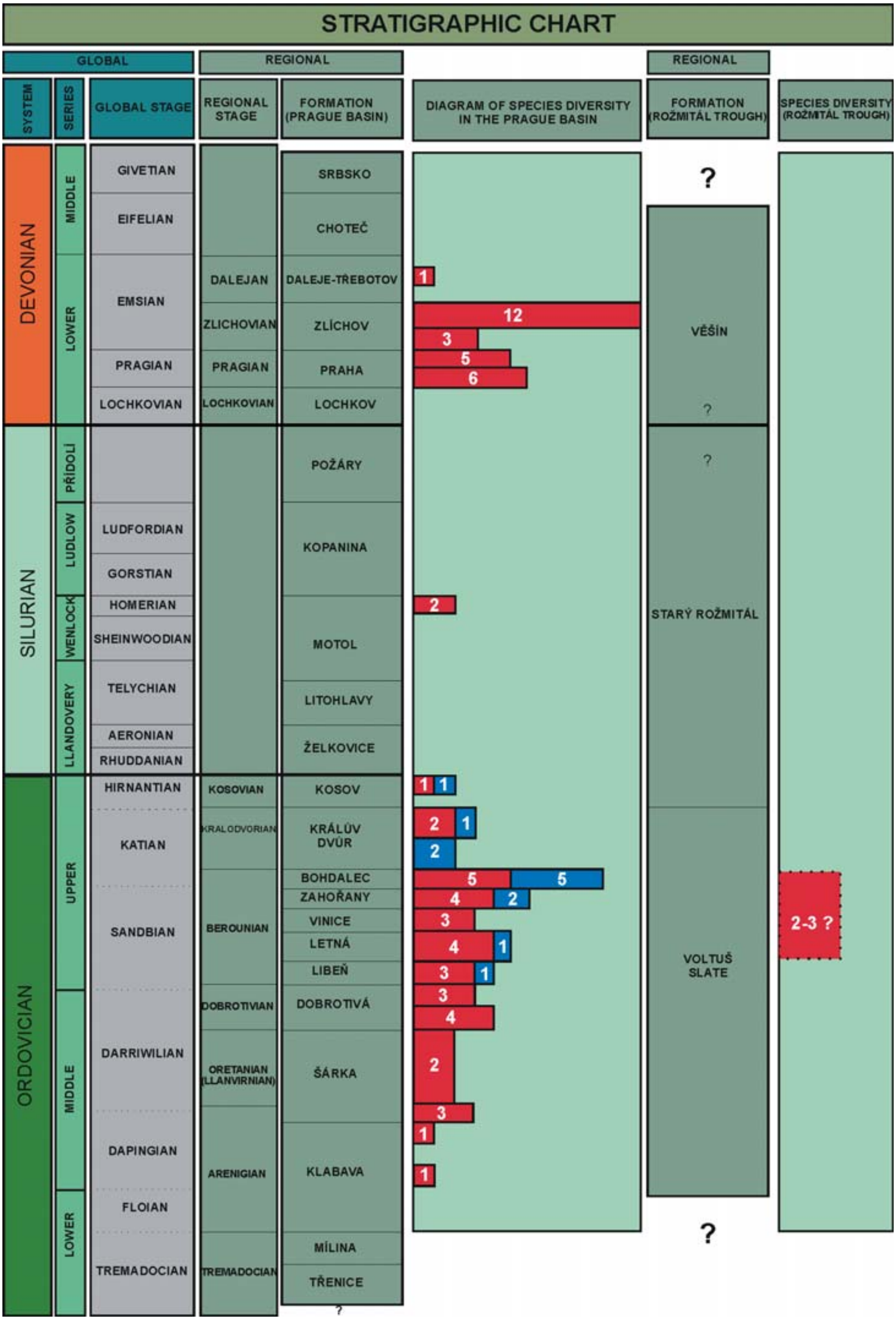

Figure 3. A review of the species diversity changes of the dalmanitoid and acastoid trilobites in the Prague Basin.

11) Lower Pragian Regression Event: onset of odontochilinids (*Reussiana*, *Odontochile*, *Zlichovaspis*) in Perunica. Immigration from present-day Kazakhstan, Morocco (along Gondwana margin) or from the "Ockerkalk" facies area? No synphoriids, no dalmanitids s.s. (Snajdr, 1987). Many taxa are shared with Gondwana (Morocco), rare in other peri-Gondwanan areas (Germany, France and Iberia).
12) Decrease and new extensive radiation in lower Emsian – *Zlichovaspis* (*Zlichovaspis*) and *Zlichovaspis* (*Devonodontochile*) in Perunica.
13) An abrupt extinction of large dalmanitids at the lower/upper Emsian boundary in Perunica.
14) Last two fragments of indeterminable dalmanitoids (discussed by Budil *et al*., submitted) - upper Emsian (Dalejan Regional Stage), Daleje-Třebotov Formation in Perunica.

CONCLUSIONS

High stratigraphical and palaeogeographical importance of dalmanitoids and acastoids is quite surprising. The sample from Perunica (Prague Basin) shows that these groups of trilobites may be well applied as indicators for the faunal exchanges within the peri-Gondwana realm (Dalmanitoidean Realm sensu Adrain *et al*., 2004).

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LINEAR CLUSTERS OF ARTICULATED TRILOBITES FROM LOWER ORDOVICIAN (ARENIG) STRATA AT BINI TINZOULIN, NORTH OF ZAGORA, SOUTHERN MOROCCO

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Keywords: Taphonomy, behaviour, palaeobiology, palaeoecology.

INTRODUCTION

In recent years Moroccan trilobite miners have found numerous examples of abundant, largely articulated, trilobite exoskeletons arranged in tightly packed linear patterns in otherwise barren or poorly fossiliferous shales and fine grained sandstones of the Arenig (Floian?) Zini Formation in southern Morocco. The strata have been dated using trilobites and graptolites. These specimens tell an interesting story of animal behaviour and taphonomy. The most abundant trilobites in these arrangements belong to the genus *Agerina*. However, examples dominated by *Ampyx*, cheirurids, asaphids and other trilobite taxa are known. Some of these associations include other invertebrate fossils, such as bivalves, echinoderms and hyolithids. Orthoconid nautiloids are found in these beds, but they do not occur in these linear arrangements. We think it likely that the burrows that contain these rows of trilobite exoskeletons were made by an unknown large organism, and that the trilobites took advantage of the shelter that they provided.

Numerous examples have now been published of trilobites occurring in tightly constrained rows in burrows (Chatterton *et al.*, 2003; Cherns *et al.*, 2006) or other hiding places (Brett, 1977; Chatterton *et al.*, 2003; Davis *et al.*, 2001; Hickerson, 1997; Suzuki and Bergström, 1999). Trilobites may have grouped together for feeding (Fortey and Owens, 1999), reproduction, moulting or protection (Speyer, 1985, 1990, 1991; Speyer and Brett, 1985); and some have been mechanically arranged in rows pre- or post-mortem by currents (Slavičková and Kocourek, 2000). The preponderance of entire exoskeletons in the Moroccan examples makes it very probable that there were assemblages of trilobites in vivo.

ARE THE TRILOBITE CLUSTERS BURROW FILLINGS?

A number of features about these linear clusters of exoskeletons suggest that they occupied burrows, similar to those of the Silurian trilobite *Acernaspis* (Chatterton *et al.*, 2003). Potentially, an echiuran worm could have formed such a burrow (Anker *et al.*, 2005), but where the rows of trilobites and or other invertebrate fossils occur they are not constrained by a distinct, visible burrow margin (as is sometimes the case in the *Acernapis* example referred to above). Elsewhere in the same beds, there are burrows of similar size (diameter) to those carrying the linear clusters, but without fossils inside them. These burrows occur in several distinct sizes, and each can be compared with one of the types of linear clusters described below. Where burrows can be seen, their margins are outlined by a thin sheet of iron oxide demarcating the burrow margin. This iron oxide often acts as a line of weakness when the rocks are broken, so that the shape of the burrow is apparent. These are often elliptical in cross section – but this may be an artifact of dewatering of the shale. Where calcareous fossils occur in these strata, the cuticles/shells have been dissolved during diagenesis, and the void left is partially filled by precipitates, including iron oxide. The fossils are preserved mainly as external and internal moulds. All of the locally available iron oxide has apparently been sequestered, during diagenesis, by the fossils, and so thus may not have been available locally for preserving burrow margins.

Other features that suggest these fossils are constrained in burrows include:

1) Intervals between the rows of fossils are usually barren or have very few fossils present.
2) The fossils in the intervening shales include planktonic or nektic forms – graptolites or nautiloids, respectively. The fact that these are NOT found in the burrows implies that their occupation is the result of purpose behaviour on the part of the trilobites. The very occasional large trilobite is found away from a burrow (e.g. a big *Asaphellus*) and these are outside the size range for the burrow occupiers.
3) Fossils that are longer than the width of the rows are arranged with their long axes roughly parallel to the trend of the row, but that is not the case for short fossils, which may be arranged so that their long axes are at high angles or even perpendicular to the long axis of the row. *Agerina* often seems to 'crowd' into the burrows in an irregular fashion, and the contrast with the cheirurids and *Ampyx* is striking.
4) The particular case of the spinose *Ampyx* specimens, described in detail below, where the trilobites appear to have been unable to turn around once confined in one of these linear arrangements.
5) No signs of cross beds or ripple marks have been seen, which might suggest that the exoskeletons were reoriented or concentrated mechanically before or after death into rows by currents or mass wastage on the sea floor. In any case, it is difficult to conceive of a purely physical process that would so effectively produce a linear arrangement of exoskeletons.
6) It should be added that one curious feature of the burrows is that they usually seem to recruit a cohort of similar sized trilobites. For example, there are few individuals that are conspicuously small in the rows illustrated in the plate herein (all are holaspides). It seems that not only do single species occupy the same burrow together in some cases (but far from invariably), but also individuals of that species are at a similar stage of growth. Perhaps this indicates a change in life habit for these forms, as they matured.

TYPES OF LINEAR CLUSTERS

There are several distinct types of linear clusters found in these Arenig strata. Some of these are monotaxic and some are polytaxic (see Paterson *et al.*, this volume). The rows also vary in size (primarily diameter/width), with some taxa only or usually occurring in narrow rows and others only occurring in wider rows. Some consist of only trilobites and others of trilobites with other fossils.


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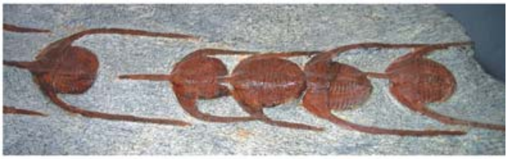
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Plate 1. All specimens from Bini Tinzoulin. All specimens in University of Alberta collections except 6, 7, which is a specimen in Tahiri Fossil Museum, Erfoud. 1. Row of *Agerina* X0.84. 2. Row of *Agerina* plus bivalves and *Asaphellus* X0.88. 3. Row of *Agerina* X0.68. 4. Two intersecting rows of *Agerina* X1.3. 5. Row of cheirurid trilobites X0.28. 6, 7. Views of row of *Ampyx* X0.35 and X0.68. 8. Row of *Ampyx* X0.66. 9. Row of *Ampyx* and *Asaphellus* X0.52. 10. Burrow, without fossils X1.

The most common linear association of trilobites in these beds consists of large numbers (up to hundreds) of specimens of a species of *Agerina* in comparatively narrow rows (usually less than 2 cm wide, and seen up to over 30 cm long). These rows are usually but not always monotaxic, with the trilobites arranged in a wide range of positions in relation to the trend of the row. Some specimens are enrolled, some are inverted, and a number of exoskeletons appear incomplete and appear to be moults. They are often several deep in the row. This type of row is comparable to the *Acernaspis* row in a burrow described by Chatterton *et al.* (2003).

A particularly interesting linear association of trilobites includes specimens with rows of *Ampyx* (*A.* cf. *cetsarum*). These may occur in monotaxic or polytaxic rows. The rows are wider than the *Agerina* rows, and usually contain fewer exoskeletons. However, a feature of almost every row of *Ampyx* that we have examined (at least 11 examples) is that all of the *Ampyx* exoskeletons are oriented antero-posteriorly along the row, are upright, are practically all carcasses rather than moults, and are **pointed in the same direction**. There is at least one exception known, with at least one *Ampyx* partial exoskeleton inverted and pointed in the opposite direction to other exoskeletons of the same taxon, and some *Ampyx* sclerites transversely arranged in the same row. These may have been re-arranged by other organisms later in the history of the row. Some of the *Ampyx* exoskeletons may be partly overriding specimens in front of them, but they are not enrolled or reversed in relation to other specimens of *Ampyx* in the same row as shown by all of the anterior cephalic spines pointing along the row in the same direction. Since *Ampyx* readily enrolled in the 'basket and lid' mode, the implication is that these were actively congregating animals at the point at which they died. Such strong unidirectionality does not apply to other trilobite taxa, such as the cheirurids, asaphids and calymenids, even in the same linear cluster. It seems likely that the long, anteriorly directed glabellar spines and posteriorly directed genal spines of this taxon prevented it from turning around once it was in a position that constrained the trilobite into a row. If practically all the *Ampyx* specimens pointed in the same direction we can ask whether this was an aggregation of trilobites to form a conga line on the sea floor to disperse or mate together before entering a burrow? The modern Caribbean spiny lobster *Palinurus argus* marches in a head to tail line across the sea floor, apparently in a behaviour associated with dispersal (Herrnkind, 1975). Speyer (1990) and Speyer and Brett (1985) suggested that trilobites assembled for mutual protection during reproduction and/or moulting. Another possibility is that if these were broad U-shaped echiuran worm burrows, with an entrance and an exit, then *Ampyx* species would orient themselves to face into any bottom current head first. They are clearly less likely to be overturned by a current if their medial spines faced into the current and their long genal spines were on or close to the sea floor (in the boundary layer). Head to tail rows could be the result of the aggregation of individuals who entered the burrow at various times, but always from the same direction in response to the promptings of ambient current directions. But they would still have to be subsequently trapped in the burrow. This hypothesis also requires that the entrances to these burrows sloped into the burrow at a moderate angle and were not close to vertical. It might also assume that the burrow openings were oriented in relation to bottom currents, perhaps to allow water to flow through the burrow.

A third type of linear association of trilobites in these beds consists of comparatively broad rows of trilobites, often with more than one species, which may include non-trilobite taxa. These larger burrows may have been easier for a variety of organisms to enter - or be washed or carried into. The trilobites' long axes are often, but not necessarily, parallel to the axis of the row (depending on the size of the trilobite and the width of the row). Nor are the trilobites pointed in the same direction. In fact, individuals of the Asaphida, Cheirurina and Calymenina often point in different directions in the same row. Unlike the *Ampyx* and *Agerina* cases there is more scope to regard the assemblages as concentrations produced by purely physical processes. However, it is still possible that they were the result of opportunistic strategies by the animals to avoid periods of inimical conditions (e.g. storm derived mud rains = obrution deposits, predator arrivals) on the sea floor.

FORMATION OF BURROWS

There are plenty of burrows present in the rock unit that contains the trilobite rows. There is very little information available on the nature of the burrow maker. There are no signs of distinct scratch marks on the margins of the burrows that we have examined (unlike the *Thalassinoides* burrows described by Cherns *et al.* (2006), that have been claimed to have been made by asaphid trilobites). While there are asaphid trilobites (*Asaphellus* '*Megalaspides*') present in this formation, they only occur in a few of the, almost always, larger burrows, and are unlikely to have been the trace makers. Apart from the trilobites present, there are no shelly organisms in these strata that are likely to have excavated the burrows. What we can say is that if our hypothesis is correct, then the burrows must have had sufficient rigidity to act as refugia for the trilobites. Soft-bodied organisms, such as echiuran worms, are the most likely candidates for the burrow makers. Modern studies of the echiuran "innkeeper worm" *Ochetostoma erythrogrammon"* suggests that "because of the size and semipermanent nature, burrows of larger echiuran worms (Phylum Echiura: Urechidae, Bonelliidae, and Thalassematidae) host a remarkable variety of symbionts. Most symbionts appear to be commensals" (Anker *et al.*, 2005, p. 157). Benton (1993) figured the range of the Echiura extending to the base of the Phanerozoic, and they are part of the basal radiation of phyla in the Cambrian, so there is circumstantial evidence that they would have been present in the Early Ordovician.

CONCLUSIONS

Dense rows of trilobites found in Ordovician strata in southern Morocco appear to be the result of trilobites entering a variety of sizes of burrows, possibly produced by echiuran innkeeper worms. The small size of some of these burrows may have controlled which trilobites could have entered them, but probably behaviour of the trilobites was as important as size, since narrow burrows with large numbers of the small trilobite *Agerina* often lack small, juvenile individuals of the other, larger trilobite taxa that occur in the same beds. *Agerina* is, however, sometimes common in the larger, wider rows of trilobite exoskeletons that are more often polytaxic.

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ORDOVICIAN TRILOBITES FROM VALONGO ANTICLINE: AN HISTORICAL AND SCIENTIFIC HERITAGE

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Keywords: Trilobites, Ordovician, Valongo Anticline, Natural History Museum of the University of Porto, Valongo Palaeozoic Park.

INTRODUCTION

The Ordovician trilobites from Valongo Anticline, neighbourhood of Porto (North-Western Portugal) are famous all over the world. These fossils are very important concerning the scientific significance and some of them are of a particular beauty. In the Ordovician of Valongo three formations were distinguished by Romano and Diggens (1974): Santa Justa, Valongo and Sobrido formations.

The Valongo Formation (Darriwilian) is one of the most fossiliferous lithostratigraphic units of the Ordovician of Portugal. This unit is equivalent to the ensemble of "*Didymograptus* slates", "*Orthis noctilio* slates" and "*Uralichas ribeiroi* slates" distinguished by Delgado in 1908. The fossil record shows a great palaeobiodiversity, evidenced by the presence of different forms of animal life, trace fossils and by the presence of seaweeds.

For about a hundred and half years ago the Valongo Formation has become an object of particular interest to several geologists. Sharpe (1849) in a paper on the geology of neighbourhood Porto presented the first palaeontological study of Valongo area, identifying six trilobite species, with the collaboration of the palaeontologist S.W. Salter, reviewed in 1853 by the last author. Since 1870 Nery Delgado developed several studies concerning the geology of this area, in particularly on palaeontology, having classified several species of arthropods, graptolites, cephalopods, gastropods, brachiopods, bivalves, echinoderms and other groups of uncertain affinity. In 1892 Delgado described thirty one trilobite species in the Ordovician of Valongo including the discovery of one of the biggest known trilobites, *Uralichas ribeiroi*. In 1908 Delgado presented a listing of the invertebrate fossils discovered in the Ordovician of Valongo, including about fifty trilobite species.

Throughout the 20th century, several papers concerning trilobites of Valongo were published. More than a hundred species of trilobites are known in Valongo Formation, some identified for the first time in the area and some of them being very unusual (Costa, 1931, 1942; Tôrres, 1936; Thadeu, 1949, 1956; Curtis, 1961; Romano, 1975, 1976, 1980, 1982, 1991; Henry and Romano, 1978; Romano and Henry, 1982; Rábano, 1990; Couto *et al.*, 1997; Tauber *et al.* 1997, among others).

Curtis in 1961 studied some trilobites from the "*Uralichas ribeiroi* slates", an horizon with a large abundance of trilobites, some of them attaining a large size. He described the species *Eccoptochile mariana*, a new species *Actinopeltis (Valongia) wattisoni* (reviewed by Tauber *et al.*, 1997), *Placoparia tournemini* and *Dionide formosa*. These specimens are housed in the Natural History Museum of London. Romano, in 1982, referred for the first time the presence of *Selenopeltis gallicus gallicus* in Valongo evidencing the palaeogeographic link of this region with Rennes (Bretagne, France) during the Darriwilian. In 1990 Romano described and figured an unusual and new species of *Protolloydolithus*. It was the first time that this genus was found outside Britain. Rábano (1990), in her PhD thesis about Ordovician Trilobites of Spanish Central Iberian Zone, established relationships with Ordovician Trilobites of the Portuguese Central Iberian Zone in what concerns palaeobiogeography and palaeoecology. Couto *et al.* (1997) presented a biostratigraphic synthesis of the fossil fauna occurring in Valongo area, including of course trilobites.

This palaeontological heritage has been object of attention in projects of the University of Porto, namely trough the Natural History Museum and Valongo Palaeozoic Park. Activities such as exhibitions, didactic and touristic field-visits are organized for schools and for the public in general.

ORDOVICIAN TRILOBITES IN NATURAL HISTORY MUSEUM OF THE UNIVERSITY OF PORTO

In the Natural History Museum there are collections of trilobites from Valongo area that have been collected by different naturalists and researchers, namely some of the authors cited above (Nery Delgado, Carrington da Costa, Tôrres, among others) since the end of XIXth Century. In the Catalogue of "Office of mineralogy and palaeontology" of Polytechnica Academy of Porto (1891) there are references to trilobites of Valongo area. Part of these old collections belongs now to the Natural History Museum of the University of Porto. Some exemplars that constitute the collection of the museum have been bought or offered lately. Among the species that make part of the collection there are several species of the genus *Nobiliasaphus, Isabelinia, Asaphellus, Neseuretus, Colpocoryphe, Salterocoryphe, Bathycheilus, Prionocheilus, Placoparia, Eccoptochile, Eoadalmanitina, Zeliskella, Ectillaenus, Uralichas, Dionide* and just one exemplar of *Eoharpes cristatus*.

Temporary exhibitions occur sporadically and actions within the "Geology activities in the summer" and "Science and Technology week", initiatives of the Ministry of Science and Technology, have been developed since 1999 focused on the geological and palaeontological heritage.

ORDOVICIAN TRILOBITES IN VALONGO PALAEOZOIC PARK

The Valongo Palaeozoic Park aims to preserve and promote the geological, palaeontological and geomining heritage of Valongo region, within the scope of a sustainable development. The Valongo Palaeozoic Park created in 1998 is a result of the joint efforts of the City Council of Valongo and the Faculty of Science of the University of Porto. The project, submitted in 1995, was financed by the European Community LIFE Programme, which aimed preserving the geological heritage and in particular the palaeontological heritage and the endangered species. Since 2000, a protocol of cooperation between the City Council of Valongo and the Geology Centre of the University of Porto provides technique and scientific support in preserving and promoting the Palaeozoic Park of Valongo. The Geoconservation Award 2005 was agreed to the City Council of Valongo by ProGEO Portugal for the work developed in the Valongo Palaeozoic Park.

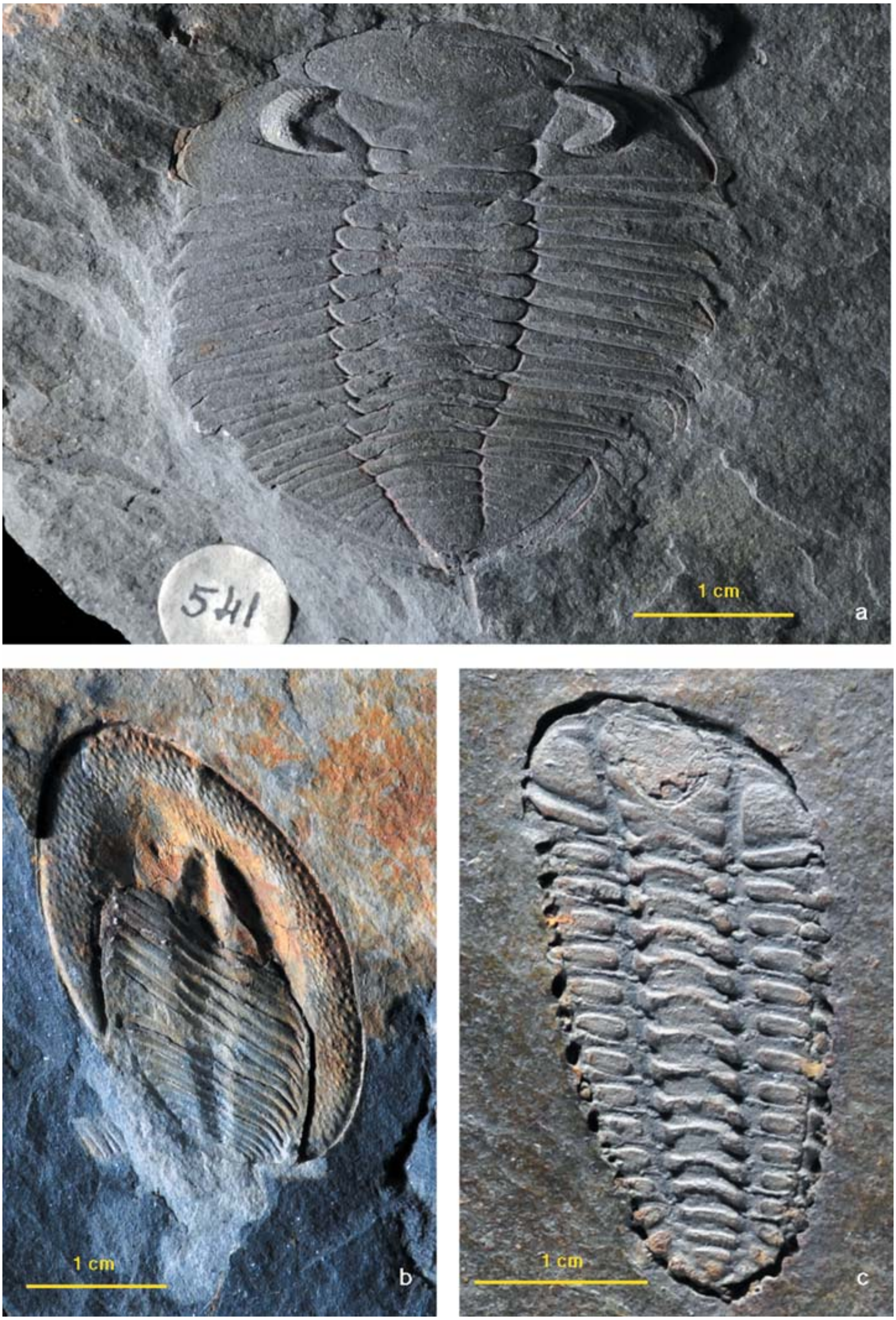

Figure 1. Ordovician trilobites from Valongo Anticline. a, *Eodalmanitina destombesi*, Covelo, Gondomar. b, *Eoharpes cristatus*, S. Pedro da Cova, Gondomar. c, *Placoparia tournemini*, Gondomar. Natural History Museum of the University of Porto.

From the vast and varied geological heritage present in the park, the internationally known Ordovician trilobites are of particularly interest due to their scientific and historic significance.

The palaeontological heritage of the Valongo region was integrated in a paper published in Episodes (Brilha *et al.*, 2005) in order to define the Portuguese Geological Frameworks of International Relevance. "Ordovician fossils from Valongo Anticline" was one of the fourteen proposed frameworks.

At the Valongo Palaeozoic Park, learning sessions for teachers and national and international scientific visits are organized. Several actions within the "Geology activities in the Summer" have been prepared since 1998 focused on the geological and palaeontological heritage. Throughout the years, several field excursions integrated in graduate and post-graduate courses have been organized in the Valongo Palaeozoic Park.

In the park an Interpretative Centre and an Interpretative Circuit are available to visitors. In the Interpretative Centre several materials concerning scientific papers, posters, books, didactic publications, leaflets, CD-ROMs, videos, topographic and geologic maps, and a 3D representation of the regional geomorphology and geology can be consulted. A binocular magnifying lens is available for the observation of fossil and mineral samples supported by identification cards (Couto, 2005; Couto and Lourenço, 2005). There is also a permanent exhibition of fossils of the region, namely trilobites, to exemplify the forms of life that populated the seas of Valongo about 500 million years ago. A web page (www.paleozoicovalongo.com) was also created.

CONCLUSIONS

The Ordovician trilobites of Valongo Anticline are recognized all over the world. They are important pieces not only for their beauty, but particularly for their scientific value. Consequently they are very required by fossil collectors and some important fossiliferous sites are sometimes in risk of being destroyed. The Palaeozoic Park of Valongo and the Natural History Museum of the University of Porto try to give a contribution for protecting this important palaeontological heritage and to provide material for scientific research. The University of Porto has developed the Index Rerum, a database for all the museums of the University. It consists of a program for divulgation with didactic components, still in implementation, that will be a good tool for the promotion of trilobites.

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A QUANTITATIVE COMPARISON OF THE ONTOGENY OF TWO CLOSELY RELATED TRINUCLEIDAE TRILOBITES FROM UPPER ORDOVICIAN

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Keywords: Upper Ordovician, trinucleid trilobites, ontogeny, quantification.

INTRODUCTION

The ontogeny of Ordovician trinucleids has been investigated since 1852 (Barrande). Nevertheless much progress has recently been made in the understanding of the ontogeny of Upper Ordovician trinucleid trilobites. The best insight into their development (Delabroye and Crônier, in press) has been obtained from a growth series of *Marrolithus bureaui* (Oehlert, 1895), from the Lower Caradoc of the Armorican Massif, Armorica, north-west France. In this study, a quantitative analysis has permitted the demonstration of a progressive shape change, in agreement with ontogenetic ordination and a comparison of the timing of size and shape changes. Changes that took place during the meraspid period included, in particular, the development of a more pronounced sub-quadrangular cephalic outline, a compression (sag.) of the glabella and a size decrease until disappearance of the alae in late stages.

In the present study, a morphometric approach based on landmarks has been used 1) to establish different size clusters from cephalic pieces, and 2) to establish the patterns of developmental variations in another marrolithine species *Onnia seunesi* (Kerforne, 1900), from the Lower Caradoc of the Armorican Massif too. Moreover, the ontogenetic trajectories of these two closely related species *Marrolithus bureaui* and *Onnia seunesi* have been compared to establish the patterns of developmental and evolutionary changes.

MATERIAL

The material used for this study was mainly collected by Luc Miclot (Cherbourg, France) and Philippe Courville (University of Rennes 1, France) from black shales in the upper part of the Andouillé Formation at 'La Touche', Andouillé in Mayenne, north-west of France (Fig. 1). *Marrolithus bureaui* was recovered primarily from the upper part of the Andouillé Formation where it is the dominant species (45%). *Marrolithus bureaui* has also been found in association with *Onnia seunesi*, another marrolithine, at the end of the upper part of the Andouillé Formation. Moreover, additional material assigned to *Onnia seunesi* came from ferruginous silty-deposit of Saint-Germain-sur-Ay and Saint-Sauveur-le-Vicomte, in the Cotentin area, north of France (Fig. 1).

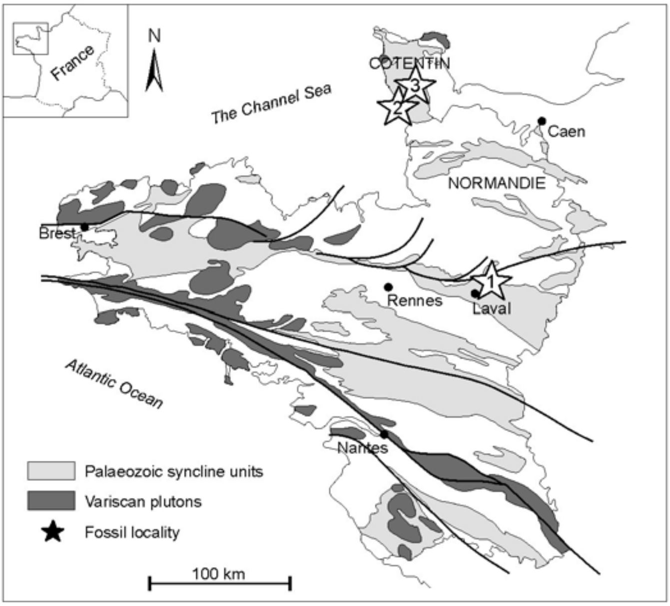

Figure 1. Location map of three fossiliferous sections from Armorica: (1) Andouillé-en-Mayenne locality, near Laval, at Pays de la Loire, (2) Saint-Germain-sur-Ay and (3) Saint-Sauveur-le-Viconte localities, at Normandie, France.

Numerous well-preserved disarticulated exoskeletons assigned to *Onnia seunesi* and *Marrolithus bureaui* and some articulated individuals assigned to *Marrolithus bureaui* have been sampled. The material includes different ontogenetic instars, primarily meraspides for *Marrolithus bureaui* and primarily holaspides for *Onnia seunesi*. Only sufficiently well-preserved cranidia/cephala, without apparent diagenetic distortion, were analyzed for morphometrical analyses.

Onnia seunesi material included 42 cranida/cephala for a traditional analysis and 36 cranidia/cephala for a geometric morphometric analysis. Additionally 111 cranidia/cephala for a traditional analysis and 69 cranidia/cephala for a geometric morphometric analysis of *Marrolithus bureaui* , described in Delabroye and Crônier (in press) have been added for comparative purposes.

ONTOGENETIC DEVELOPMENT

Various growth stages from the early holaspid period allow the morphogenesis of *Onnia seunesi* to be described.

Size series of distinct dimensional classes have been obtained in a previous work from bivariate plots of *Marrolithus bureaui*. More details are given in Delabroye and Crônier (in press). Each size class on cranida/cephala has been identified as follows: meraspid degrees 2, 3, 4 and 5 (called *mM2, mM3*, *mM4* and *mM5*, and holaspis (called *mH1, mH2* and *mH4?*), have been extrapolated based on the different pieces of the exoskeleton remaining in connection, and thus providing a reference for concordance between isolated pieces represented by cranidia/cephala.

In the same manner, in order to establish size series of isolated parts, the width (mm) as a function of length (mm) of 42 cranidia/cephala, in dorsal view, was measured and displayed on a bivariate plot for *Onnia seunesi* (Fig. 2). This size distribution allows growth to be described using relatively simple numerical models. The relative proportions of cranidia/cephala remain significantly constant ($y=ax+b$; r=0.97, $p<0.001$***) whatever the degree of development of individuals.

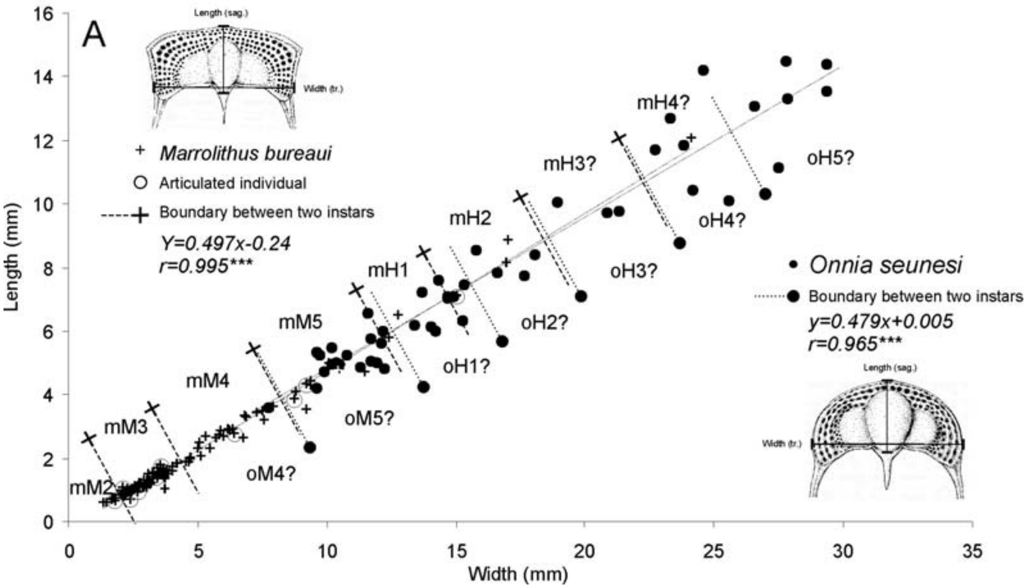

Figure 2. Size frequency diagram obtained from measurements of the width (tr.) as a function of the length (sag.); the numbers above the clusters correspond to the assumed instars defined after extrapolation from complete meraspid exoskeletons for *Marrolithus bureaui*, and an additional hierarchical classification for *Marrolithus bureaui* and *Onnia seunesi*.

Moreover, the size-frequency diagram exhibits more or less distinct dimensional classes for cranidia/cephala (Fig. 2). Unfortunately, the absence of complete individuals does not permit some of the instars to be recognized with certainty, on the basis of discrete features. Consequently, size remains an available parameter for assigning each individual to its own instar. Additionally, in order to assign an individual to a particular instar, we have performed an additional hierarchical classification, based on width and length linear size for *Onnia seunesi*. Thus, size series obtained for 42 cranidia/cephala show that this species has possibly seven instars in its ontogeny (Fig. 2): two meraspid degrees 4 and 5 (called *oM4?* and *oM5?*) and five holaspis (called *oH1?*, *oH2?*, *oH3?*, *oH4?* and *oH5?*).

The difference in size among instars was tested by an Univariate Analysis of Variance ANOVA. These ANOVA's performed on the linear size (width and length) of cranidia/cephala indicate the existence of a size differentiation among instars.

To complete the biometrical/traditional study, a Procrustes method that describes the morphology of the organisms by a set of landmarks (Bookstein, 1991) has been used. The *x*- and *y*-coordinates of 17 landmarks were automatically extracted on 36 cranidia/cephala for *Onnia seunesi* and 69 cranidia/cephala of *Marrolithus bureaui*.

To examine the major trend of shape variation, a Relative Warp Analysis (Rholf, 1993), which fits an interpolated function to the consensus configuration has been performed. It allows the emergence of principal independent axes according to a decreasing order of importance in the explanation of the shape variability. Significant relative warps (RWs) define a shape space into which it is possible to locate each individual according to its coordinates on these RWs.

Morphological relationships among individuals can be displayed by their representation in the morphological space (Fig. 3) defined by the first two principal axes, which provide a valuable approximation of the morphospace (83 % of the total variance). ANOVAs on the first three significant axes indicate a significant morphological differentiation among instars according to RW1-2. The set of individuals identified are ordinated in the morphospace according to their ontogenetic order along the first two axes for *Marrolithus bureaui* on the one hand, and *Onnia seunesi* on the other hand (Fig. 3).

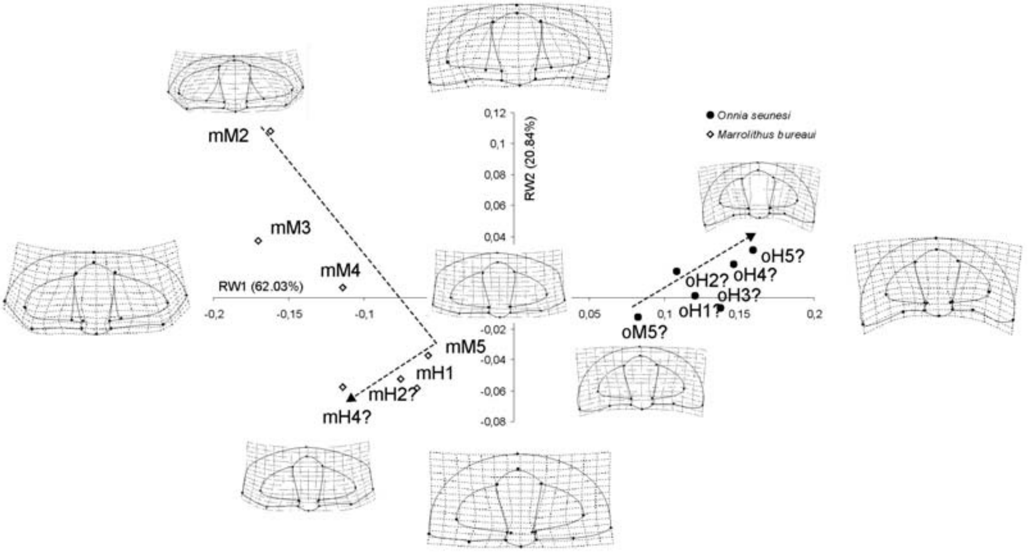

Figure 3. Location of 69 cranidia/cephala of *Marrolithus bureaui* (Oehlert, 1895) and 36 cranidia/cephala of *Onnia seunesi* (Kerforne, 1900) in the morphospace defined according to the first two relative warps RW1 and RW2. Axes RW1-2 represent 62% and 21% respectively of the total variance. Thin-plate spline deformation grids depicting patterns of shape change during cephalic development in *Marrolithus bureaui* and *Onnia seunesi*.

The morphological interpretation of the progressive shape changes during ontogeny is indicated by the thin-plate spline (TPS) warp grids showing the direction of maximum variance (Fig. 3). The first two relative warp axes shows that the main shape change in *Marrolithus bureaui* throughout its ontogeny results in more or less subrectangular cranidia/cephala (without the genal spines included) in outline: the youngest instars with a subovoid/elliptic cephalic outline and the latest instars with a subrectangular/inverse trapezoidal shape. This is linked to the insertion of internal short I arcs of a few pits. Additionally, RW1-2 describes variation in the relative lateral (tr.) compression of the glabella, and a 'lateral migration' of genal lobes backwards that involves a shortening of the posterior area between the glabella and genal lobes in later stages. This last point is linked to a disappearance of the alae (paired protuberances flanking the posterior sides of the glabella and situated between the axial and alar furrows) in late ontogenetic stages.

The first two relative warp axes show that the main shape change in *Onnia seunesi* through its ontogeny results in more or less sub-hemicircular cranidia/cephala (without the genal spines included) in outline: the youngest instars with a sub-hemicircular cephalic outline less protuberant forward and the latest instars with a sub-hemicircular shape more protuberant forward. This is linked to an important convexity of the cranidia/cephala in older specimens and the stretching of the genal angle backwards.

CONCLUSIONS

This quantitative study has provided a fuller description of two trinucleid growth series. Thus it has been possible to quantify shape change during ontogeny and to compare the ontogenetic trajectories between *Onnia seunesi* and *Marrolithus bureaui.*

Thus, on the basis of this material, the growth series of *Onnia seunesi* like that of *Marrolithus bureaui* exhibits a relatively simple pattern of instar development, with discrete instars during early ontogeny.

The outline analysis has shown a progressive shape change in *Onnia seunesi*, on the one hand and *Marrolithus bureaui*, on the other hand. Primary changes in shape appear to occur early in development.

Additionally, morphological changes related to ontogenetic process are opposed in these two species. Opposition of these ontogenetic trajectories may be a manifestation of developmental constraints: accentuation of the sub-quadrangular cephalic outline for *Marrolithus bureaui*; the trend is reversed at *Onnia seunesi* with an accentuation of the semi-circular cephalic outline with a stretching of genal angles backwards.

Such differences may be linked to ecological adaptation: *Onnia seunesi* seems to be a species which inhabited proximal environments; conversely, *Marrolithus bureaui* seems to be a species which occupied more distal environments.

The results suggest that ecological adaptation might well be studied by examining the developmental changes occurring within species through time and space.

Acknowledgements

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TRILOBITE BIOSTRATIGRAPHY AND BIODIVERSITY PATTERNS THROUGH THE MIDDLE-UPPER CAMBRIAN TRANSITION IN THE KYRSHABAKTY SECTION, MALYI KARATAU, SOUTHERN KAZAKHSTAN

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Keywords: Kazakhstan, trilobites, Middle Cambrian, Furongian, biostratigraphy, biodiversity

INTRODUCTION

The Cambrian sequence in the Malyi Karatau Range of southern Kazakhstan contains an abundant and diverse trilobite fauna that has been the subject of continued taxonomic and biostratigraphical studies over the last forty years. Data on the Lower Cambrian trilobite fauna were summarised by Ergaliev and Pokrovskaya (1977), and on the Middle to Upper Cambrian trilobite data were presented in numerous publications written mostly in Russian (for summary see Ergaliev and Ergaliev, 2004).

Middle to Upper Cambrian carbonate sequences exposed in the Kyrshabaty section were deposited on the seaward-prograding margin of a carbonate platform situated on an isolated sea-mount (Aisha-Bibi sea-mount; see Cook *et al*., 1991), which was on the passive continental margin of an early Palaeozoic microplate distant from terrestrial regions in low southern latitudes. Faunal affinities suggest that during the Cambrian - Early Ordovician it was situated in relative proximity to South China and the Australian segment of equatorial East Gondwana (Cook *et al*., 1991; Holmer *et al*., 2001).

Characters of carbonate sedimentation across the region in the mid Cambrian–Ordovician show no evidence of significant influence from local tectonics (Allen *et al*., 2001). Notwithstanding subsequent tectonic deformation, the ancient relief of the sea-mount is essentially preserved, and the lithofacies zonation can be reconstructed with a good degree of certainty (Cook *et al*., 1991). It exhibits a wide variety of carbonate deposits characteristic of environments across basin plain, carbonate slope, platform margin, platform interior and a transition to intertidal settings. Early Palaeozoic deep water sediments preserved mainly as dark carbonate shales and black cherts characteristic of the basin plain are well documented in surrounding areas, in particular in Bolshoi Karatau and north-east of Malyi Karatau towards the Shu-Sarysu basin.

The Kyrshabakty section comprises more than 600 m thickness of sediments, including: up to 100 m of basin plain lithofacies; about 465 m of carbonate slope deposits including lithofacies of an outer fan fringe (50 m); outer fan lobe (175 m); mid fan distributary channels (105 m); and inner fan feeder channels (135 m). There are some sedimentary slides and several units of debris flow breccias over 10 m thick, with clasts of shallow water carbonates including fragments of *Girvanella* build-ups. Deposits of the upper slope and platform margin with *in situ Girvanella* bacterial mats preserved are documented in the uppermost 60 m of the measured section (Cook *et al*., 1991).

The sequence of trilobite biozones established in Malyi Karatau was previously considered as a standard for the regional biostratigraphical subdivision of the Middle and Upper Cambrian within the former Soviet Union. Indeed the Kyrshabakty Section exhibits a continuous record of successive trilobite associations preserved in deep water carbonates deposited mostly well below storm wave base. Only a part of the fauna (e.g. agnostides, olenid trilobites, micromorphic linguliformean brachiopods) can be considered as autochthonous components of the original biota, whereas polymeroid trilobites and large obolide and rhynchonelliformian brachiopods were transported in significant part across the shelf into the basin by turbidity and mass flows. Influx of the allochthonous component probably increased towards the upper part of the sequence. Background trilobite assemblages mostly represent the agnostid biofacies, but associations of polymeroid taxa within the upper Cambrian units probably give a good representation of the total taxonomic diversity of the trilobite fauna that inhabited the narrow shelf of the sea-mount within a selected time interval. As a consequence, the sequence of trilobite biozones in the middle to upper Cambrian of the Kyrshabakty Section was not affected significantly by a bias of migrating biofacies belts resulting from sea-level changes. The lower boundary of each biozone is defined clearly by the first occurrence of the agnostide index species.

The time interval from the Middle Cambrian *Peronopsis ultimus* to the base of the *Pseudagnostus pseudagnostilobus-Acrocephalispina* Biozone representing the base of the Aksaian Regional Stage, as selected here for this analysis, includes the base of the newly established Drumian and Paibian stages defined by the FAD of *Ptychagnostus atavus* and *Glyptagnostus reticulatus* respectively, and the potential boundaries of the not yet formally recognised 7th and 9th Cambrian stages, which will be defined probably by the FAD of *Lejopyge laevigata* and *Agnostotes orentalis* (Fig. 1). A complete taxonomic revision of the agnostide trilobites comprising more than 140 species is now in an advanced stage of preparation, and the currently assembled data form a source for biodiversity analysis. Polymeroid trilobites described in existing publications comprise about 70% of the total species diversity of the Cambrian fauna, and current data can be considered as reliable for the biodiversity analysis at a generic level. With some additions they are based mainly on data published by Ergaliev (1980, 1981, 1990), Lisogor (1977), and Lisogor *et al*. (1988).

REVISED BIOSTRATIGRAPHY

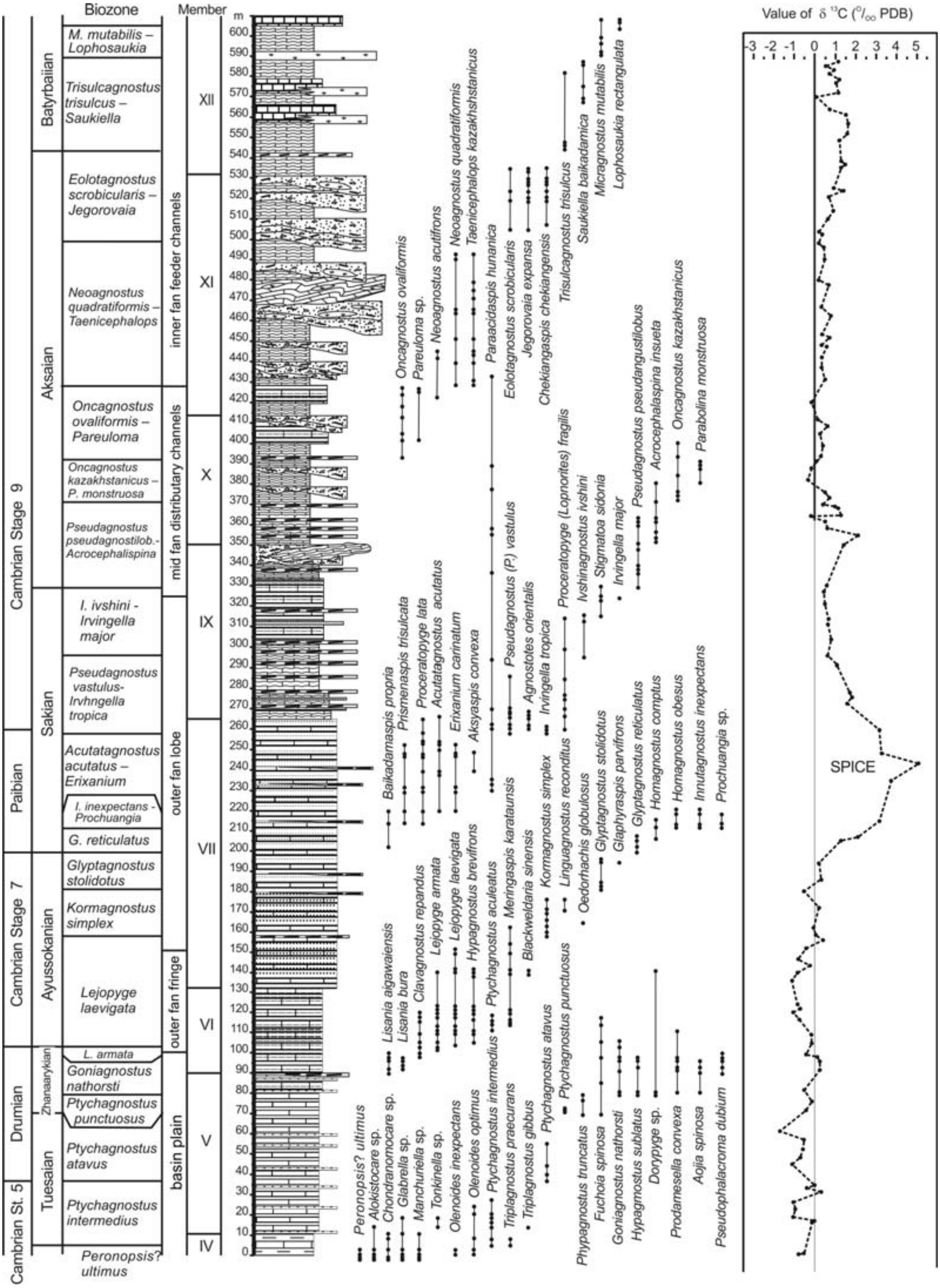
The oldest Middle Cambrian biostratigraphical unit in Malyi Karatau is the *Probowmania asiatica* Beds, which have a restricted distribution within the region and were considered previously as being within the Lower Cambrian (Ergaliev and Pokrovskaya, 1977). However, the low diversity fauna is synchronous with the *Shantungaspis* Biozone of North China and the *Orictocephalus indicus* Biozone of South China (Shergold and Geyer, 2003), and the index species of the latter biozone has received strong support as a potential indicator of the base of the Middle Cambrian Series (Peng, 2003).

The hitherto lowermost Middle Cambrian biostratratigraphical unit recognised at Kyrshabakty is the *Peronopsis ultimus* Biozone (Fig. 1), spanning the interval from -9 to 3.0 m of the measured section. The agnostide component within this interval is dominated by *Peronopsis,* accompanied by other characteristic genera including *Manchuriella, Olenoides, Prosymphysurina, Pseudamecephalus, Solenopleura* and *Tonkinella*, among others.

The succeeding *Ptychagnostus intermedius* Biozone spans the interval from 3.0 to 33.6 m in the measured section. It also defines the base of the Tuyesai Regional Stage. In addition to the index species, the assemblage within this biozone includes the biostratigraphically informative agnostide *Triplagnostus gibbus*. The uppermost biostratigraphical unit within the the Tuyesai Regional Stage is the *Ptychagnostus atavus* Biozone (33.6-70.6 m of measured section). Two other formal regional subdivisions recognised currently in the Middle Cambrian of Kazakhstan are the Zhanaaryk Regional Stage (including the *Ptychagnostus punctuosus* Biozone at 70.6-79.35 m in the measured section, the *Goniagnostus nathorsti* Biozone at 79.35-99.5m, and the *Lejopyge armata* Biozone at 99.5-102.5 m in the measured section), and the Ayussakan Regional Stage (including the *L. laevigata*, *Kormagnostus simplex* and *Glyptagnostus stolidotus* biozones). Recent studies reveal that the FAD of *L. laevigata* in the sequence is at 102.5 m, which is 39.7 m below the previously interpreted base of the Biozone (Ergaliev, 1980). Thus a significant part of the stratigraphical interval referred formerly to the *L. armata* Biozone is now assigned to the *L. laevigata* Biozone (Fig. 1). *L. laevigata* is currently considered as the probable index species for definition of the base of 7th Cambrian Stage; however, *Ptychagnotus aculeatus* deserves consideration as another short lived and easily distinguishable species of potential importance for definition of the Stage boundary. It appears at 104m in the Kyrshabakty section.

The *Glyptagnostus reticulatus* Biozone (182-199.2 m in the section) is the lowermost biostratigraphcal unit of the Sakian Regional Stage. The FAD of the index-species also defines the base of the globally recognised Furongian Series and the Paibian Stage. Other biostratigraphical units within the Sakian interval are the *Innutagnostus inexpectans–Prochuangia*, *Acutatagnostus acutatus-Erixanium*, *Pseudagnostus vastulus-Irvingella tropica* and *Ivshinagnostus ivshini-Irvingella major* biozones. The stratigraphical interval of the Paibian Stage at Kyrshabakty corresponds with the high magnitude positive carbon isotope SPICE excursion, with a peak value up to 4.82 δ13C ($^{O}/_{OO}$ PDB) at 243.50 m in the section within the middle of the *Acutatagnostus acutatus-Erixanium* Biozone (Fig. 1; Saltzman *et al*., 2000). The *Pseudagnostus vastulus- Irvingella tropica* Biozone (formerly known as the *Pseudagnostus "curtarae"* Biozone) spans the interval of 257.0-296.2 m. It is located close to the maximum value of the SPICE excursion, but occupies a somewhat higher position, where δC13 isotope values go down. The faunal assemblage of the Biozone includes *Agnostotes clavata*, which appears at 2.0 m above the FAD of *Irvingella* (257.0 m) and has a narrow range with its last occurrence at 270.8 m.

The succeeding Aksaian Regional Stage is subdivided into five biostratigraphical units, including the *Pseudagnostus pseudagnostilobus-Acrocephalispina*, *Oncagnostus kazakhstanicus-Parabolina monstruosa*, *Oncagnostus ovaliformis-Pareuloma*, *Neoagnostus quadratiformis-Taenicephalops* and *Eolotagnostus scrobicularis-Jegorovaia* biozones. Lithofacies within this stage comprise mid fan distributary channels and inner fan feeder channels characteristic of a sea-mount slope. A medium magnitude positive carbon isotope excursion is documented for the *Pseudagnostus pseudagnostilobus–Acrocephalispina* Biozone, with a peak value of 2.15 δC13 ($^{O}/_{OO}$ PDB) at 355.0 m in the middle of the Biozone (Fig. 1; Saltzman *et al*., 2000). Two uppermost biostratigraphical units, including the *Trisulcagnostus trisulcus-Saukiella* and *Micragnostus mutabilis-Lophosaukia* biozones are referred to the Batyrbaian Regional Stage, which constitutes the uppermost Cambrian subdivision used in Kazakhstan.


Biozone
Member
m
Cambrian St. 5
Cambrian Stage 7
Cambrian Stage 9
Tuesaian
Drumian
Zhanaarykian
Ayussokanian
Paibian
Sakian
Aksaian
Batyrbaiian
Peronopsis? ultimus
Ptychagnostus intermedius
Ptychagnostus atavus
Ptychagnostus punctuosus
Goniagnostus nathorsti
L. armata
Lejopyge laevigata
Kormagnostus simplex
Glyptagnostus stolidotus
G. reticulatus
I. inexpectans - Prochuangia
Acutatagnostus acutatus – Erixanium
Pseudagnostus vastulus- Irvhngella tropica
I. ivshini - Irvingella major
Pseudagnostus pseudagnostilob.- Acrocephalispina
Oncagnostus kazakhstanicus – P. monstruosa
Oncagnostus ovaliformis – Pareuloma
Neoagnostus quadratiformis – Taenicephalops
Eolotagnostus scrobicularis – Jegorovaia
Trisulcagnostus trisulcus – Saukiella
M. mutabilis – Lophosaukia
basin plain
outer fan fringe
outer fan lobe
mid fan distributary channels
inner fan feeder channels
IV
V
VI
VII
IX
X
XI
XII
0
10
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40
50
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70
80
90
100
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130
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430
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450
460
470
480
490
500
510
520
530
540
550
560
570
580
590
600
Peronopsis? ultimus
Alokistocare sp.
Chondranomocare sp.
Glabrella sp.
Manchuriella sp.
Tonkinella sp.
Olenoides inexpectans
Olenoides optimus
Ptychagnostus intermedius
Triplagnostus praecurans
Triplagnostus gibbus
Ptychagnostus atavus
Ptychagnostus punctuosus
Phypagnostus truncatus
Fuchoia spinosa
Goniagnostus nathorsti
Hypagmostus sublatus
Dorypyge sp.
Prodamesella convexa
Aojia spinosa
Pseudophalacroma dubium
Lisania aigawaiensis
Lisania bura
Clavagnostus repandus
Lejopyge armata
Lejopyge laevigata
Hypagnostus brevifrons
Ptychagnostus aculeatus
Meringaspis karataunsis
Blackweldaria sinensis
Kormagnostus simplex
Linguagnostus reconditus
Oedorhachis globulosus
Glyptagnostus stolidotus
Glaphyraspis parvifrons
Glyptagnostus reticulatus
Homagnostus comptus
Homagnostus obesus
Innitagnostus inexpectans
Prochuangia sp.
Baikadamaspis propria
Prismenaspis trisulcata
Proceratopyge lata
Acutatagnostus acutatus
Erixanium carinatum
Aksyaspis convexa
Pseudagnostus (P.) vastulus
Agnostotes orientalis
Irvingella tropica
Proceratopyge (Lopnorites) fragilis
Ivshinagnostus ivshini
Stigmatoa sidonia
Irvingella major
Pseudagnostus pseudangustilobus
Acrocephalaspina insueta
Oncagnostus kazakhstanicus
Parabolina monstruosa
Oncagnostus ovaliformis
Pareuloma sp.
Neoagnostus acutifrons
Neoagnostus quadratiformis
Taenicephalops kazakhshstanicus
Paraacidaspis hunanica
Eolotagnostus scrobicularis
Jegorovaia expansa
Chekiangaspis chekiangensis
Trisulcagnostus trisulcus
Saukiella baikadamica
Micragnostus mutabilis
Lophosaukia rectangulata
Value of δ 13C (0/00 PDB)
-3
-2
-1
0
1
2
3
4
5
SPICE

BIODIVERSITY PATTERNS

Trilobite diversity through the Kyrshabakty section has been analysed from the stratigraphical distributions of 61 agnostide and 101 polymeroid trilobite genera, plotted within a framework of 17 trilobite biostratigraphical units covering the interval from the Middle Cambrian *Peronopsis ultimus* Biozone to the Furongian *Neoagnostus quadratiformis-Taenicephalops* Biozone (Figs 1, 2). The geochronological time scale for the Cambrian period is based mainly on data from Gradstein *et al.* (2005). However, geochronology for the mid to late Cambrian still lacks precision, partly because of the problems related to inter-regional correlations and boundary definitions. Thus a provisional 510 Ma date was used for the base of the Middle Cambrian (which is not yet formally defined), and a 500.5 Ma date was applied for the base of the Furongian Series. The average duration of an individual trilobite biozone within the biostratigraphical succession at Kyrshabakty was probably close to 1Ma, and which was employed in the analysis as a close approximation. Generic origination/extinction rates, plotted as per lineage million years (Lma), were calculated as the number of genus originations/extinctions within the particular stratigraphical interval, divided by the total generic diversity within the interval, divided by the chronological duration of the corresponding time interval (for methodology and discussion see Patzkowsky and Holland, 1997). Biodiversity patterns were analysed separately for agnostide and polymeroid trilobites (Fig. 2).

For the mid Cambrian the agnostide component of the associations shows significant increase in generic diversity from the *P. ultimus* to *Kormagnostus simplex* Biozone, with origination rates considerably exceeding extinction rates (Fig. 2D). This was followed by a rapid decline during the *Kormagnostus simplex–Glyptagnostus reticulatus* biozones, with extinction rates exceeding 0.5 Lma and origination rates dropping to 0.1 Lma during the *Glyptagnostus stolidotus* Biozone. Decline of the agnostide diversity continued at a lower rate above the extinction horizon at the base of the *Glyptagnostus reticulatus* Biozone, and only from the *Acutatagnostus acutatus-Erixanium* Biozone does the agnostide fauna show a distinct sign of recovery. The interval from the *Ivshinagnostus ivshini-Irvingella major* to *Neoagnostus quadratiformis-Taenicephalops* biozones records a gradual decline in agnostide generic diversity, with extinction rates almost twice as high as origination rates (Fig. 2D).

Polymeroid trilobites exhibit a different biodiversity pattern, with five pulses of diversification, each of 2-3 Ma with origination rates exceeding 0.5 Lma. There are also two major extinction events recorded at the base of the *Ptychagnostus atavus* and *Glyptagnostus reticulatus* biozones. Extinction at the *P. atavus* base affected basin-dwelling taxa characteristic of the *P. ultimus* and *P. intermedius* biozones (e.g. *Alokistocare*, *Chondranomocare*, *Glabrella*, *Manchuriella*, *Tonkinella*). The unit of black, laminated limestone about 10m thick in the uppermost part of the *P. intermedius* Biozone contains a single olenid taxon, *Olenoides optimus*, and was probably formed in a disaerobic environment. After a period of low diversity stasis corresponding with the *Ptychagnostus atavus* Biozone, generic diversity increased significantly to a maximum at the *L. laevigata* and *Kormagmostus simplex* biozones, when trilobite assemblages included more than 20 polymeroid genera (Fig. 2A). This was followed by a significant decline in diversity, which is evident already for the *Glyptagnostus stolidotus* Biozone and terminated with the extinction of the families Damesellidae and Lisaniidae. The interval from the *Glyptagnostus reticulatus* to *Pseudagnostus vastulus-Irvingella tropica* biozones then records a period of biodiversity stasis

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Figure 1. Stratigraphical succession of the middle to upper Cambrian deposits in the Kyrshabakty section, Malyi Karatau Range, Kazakhstan, showing revised biostratigraphical units and ranges of selected trilobite taxa. Plots of $\delta 13C$ ($^{O}/_{OO}$ PDB) are after Saltzman *et al.* (2000, Table 1).

characterised by high faunal turnover and a relative abundance of genera with short stratigraphical ranges (e.g. *Baikadamaspis*, *Chuangiella*, *Erixanium* and *Eugonocare,* among others). This was followed by a major pulse of biodiversification through the *Ivshinagnostus ivshini-Irvingella major* to *Oncagnostus kazakhstanicus-Parabolina monstruosa* biozones, with high origination rates of about 0.5 Lma across the whole interval (Fig. 2B).

DISCUSSION AND CONCLUSIONS

The mid to late Cambrian trilobite fauna recovered from the Kyrshabakty section in Malyi Karatau inhabited slopes and a basin bounding the small, isolated Aisha-Bibi sea-mount on the margins of an intra-oceanic crustal terrane known as the Karatau-Naryn microplate (Holmer *et al*., 2001) or the Bailkonur-Talas Unit (Şengör and Natal'in, 1996). The early Palaeozoic trilobite and brachiopod faunas of that terrane show distinct equatorial peri-Gondwanan signatures, with closest similarity to contemporaneous faunas of South China (Ergaliev and Pokrovskaya, 1977; Ergaliev, 1980; Holmer *et al*., 2001).

The mid Cambrian polymeroid trilobite fauna from Kyrshabakty inhabited basin plain and outer fan fringe deposits, and it was thus dominated by basin-dwelling taxa. However, the biodiversity patterns of the polymeroid and agnostide components are markedly different, suggesting therefore that the physical factors controlling each group were different. The extinction event at the base of the *Ptychagnostus atavus* Biozone was probably a regional episode caused by anoxia, but it was selective and the agnostide component of the fauna was affected only slightly (Fig. 2).

The arrival of a new fauna in the *Ptychagnostus punctuosus* Biozone was probably an immigration event. However, unlike agnostides, the record of mid to late Cambrian polymeroid trilobites from equatorial peri-Gondwana is incomplete, and in some cases requires revision. This makes it difficult to discriminate the relative significance of immigration and radiation in local lineages within observed biodiversity patterns.

Extinction at the base of the *Glyptagnostus reticulatus* Biozone affected the whole trilobite biota, together with assemblages of micromorphic linguliformean brachiopods (Holmer *et al*., 2001). As demonstrated by Saltzman *et al*. (2000), this extinction occurred soon after the onset of the strong, positive δ13C SPICE excursion, probably related to major reorganization of global oceanic circulation, but the precise physical mechanism that caused the extinction remains unknown. Observed patterns suggest that a significant decline in trilobite biodiversity occurred already by the *Glyptagnostus stolidotus* Biozone, with larger scale effects on the polymeroid component. Therefore the pre-*Glyptagnostus reticulatus* Biozone extinction probably occurred in several steps. However, current data from the Kyrshabakty section are in part provisional, and further detail is required of biodiversity patterns at the species level across the mid to late Cambrian boundary.

By contrast, the onset of a moderate positive δ13C excursion at the base of the Aksaian Regional Stage and the *Pseudagnostus pseudagnostilobus-Acrocephalispina* Biozone (Fig. 1) coincides with a substantial increase of biodiversity turnover rates, but there was no sign of a decline in trilobite generic diversity that was to reach a maximum in the succeeding *Oncagnostus kazakhstanicus–Parabolina monstruosa* Biozone (Fig. 2). The gradual decline in agnostide biodiversity observed during the mid to late Furongian may be a preservational artifact. Additionally, sediments across this interval were deposited on the slope of the sea-mount and the influx of allochthonous components derived from the shallow shelf in the analysed assemblages increased significantly.

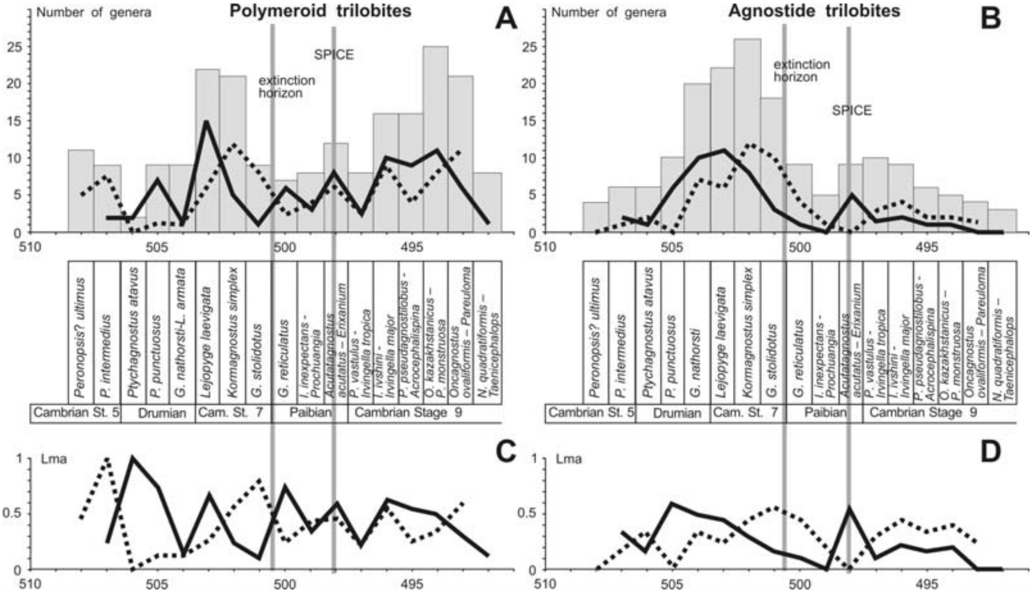

Figure 2. Plots of diversity, origination rates, and extinction rates in genera of the mid to late Cambrian polymeroid (A, C) and agnostide trilobites (B, D) from the Kyrshabakty section. The histograms (A, B) show changing total generic numbers; the solid line graph plots the number of new genera appearing within each biozone, and the broken line graph plots the number of genera becoming extinct within the biozone; numbers are plotted at the mid point in each unit. Diagrams C show D show origination and extinction rates (per lineage million years; Lma) for mid to late Cambrian trilobite genera. Lma for origination and extinction rates (y axis) is plotted as the number of genus originations (or extinctions) within the particular chronostratigraphical unit, divided by the total generic diversity within the unit, divided by the chronological duration of the interval (Patzkowsky and Holland, 1997); calculations for Lma are plotted at the mid point in each time interval.

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PARDAILHANIA THORAL, 1947 (SOLENOPLEUROPSINAE, TRILOBITA) FROM CAESARAUGUSTAN (MIDDLE CAMBRIAN) OF THE CADENAS IBÉRICAS (NE SPAIN)

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Keywords: Cadenas Ibéricas, middle Cambrian, Caesaraugustan, *Pardailhania*, evolutionary trend, Mediterranean Subprovince.

INTRODUCTION

The genus *Pardailhania* Thoral, 1947 is a biogeographically widespread trilobite from the middle Cambrian of the Mediterranean Subprovince. It was defined in the Montagne Noire (France; Thoral, 1947) and subsequently has been recognized in Spain (Sdzuy, 1958), Italy (Rasseti, 1972), Turkey (Shergold and Sdzuy, 1984) and Morocco (Geyer and Landing, 1995).

Pardailhania presents a short stratigraphical distribution that is confined to the middle Caesaraugustan substage and the lowermost part of the upper Caesaraugustan substage in the standard chronostratigraphical subdivision proposed for the middle Cambrian of the Mediterranean region (Liñán *et al*., 1993, 2002; Álvaro and Vizcaïno, 1998; Geyer and Landing, 2004; Dean, 2005).

DISCUSSION AND BRIEF REVIEW OF *PARDAILHANIA* THORAL, 1947

Pardailhania is a solenopleuropsinae genus characterized by the spines-like tubercle ornamentation, which shows regular arrangement in the glabella (see Sdzuy, 1968; Liñán and Gozalo, 1986). The number of rows in the preglabellar field, the number of rows in glabella and the size and density of tubercles have been used as diagnostic features to difference among *Pardailhania* species (Thoral, 1947; Sdzuy, 1968; Courtessole, 1973; Liñán and Gozalo 1986; Álvaro, 1996; Álvaro and Vizcaïno, 1997).

After Liñán and Gozalo (1986) revision, the genus comprises four species: *P. hispida*, *P. hispanica*, *P. multispinosa* and *P. sdzuyi*.

Pardailhania hispida Thoral, 1935, has one row of spine-like tubercles in the preglabellar field and four to five rows in the glabella.

P. hispanica Sdzuy, 1958 is characterised, according to the original diagnosis, by two rows of spine-like tubercles in the preglabellar field and five rows in the glabella.

P. multispinosa Thoral, 1948 shows two or tree rows of spine-like tubercles in the preglabellar field, and also five rows in the glabella; in spite of Thoral citation, who described the holotype with only two rows in the preglabelar field and five in the glabella (Álvaro and Vizcaïno, 1997). Previously, Sdzuy (1958, 1961, 1968) had differentiated between *P. multispinosa* and *P. hispanica* for the size and density of the spine-like tubercle.

Following its original description, *P. sdzuyi* Liñán and Gozalo, 1986 bears three tubercle rows of spine-like tubercles in the preglabellar field and seven to eight rows in the glabella. It can seem a species of *Solenopleuropsis* Thoral, 1947 due to the ornamentation with spine-like tubercles, but it differs in the lack of a symmetrical arrangement of the glabellar spine-like tubercles in *Solenopleuropsis*.

According to Álvaro (1996) and Álvaro and Vizcaïno (1997) the genus has also four species; they are *P. hispida*, *P. multispinosa*, *P. morisca* Álvaro, 1996 and *P. sdzuyi*.

P. hispida has the same diagnosis based on the preglabelar field but with four to six rows of spine-like tubercles on the glabella.

We follow *P. multispinosa* species diagnosis of Thoral (1948) with two rows of spine-like tubercles in the preglabelar field and four to six rows of spines-like tubercles in the glabella. Therefore *P. hispanica* is synonymized with *P. multispinosa.*

The new species *P. morisca* Álvaro, 1996 is defined with three rows of spine-like tubercles in the preglabelar field and four to six rows of spines-like tubercles in the glabella. This species includes the specimens considered as *P. multispinosa* by Liñán and Gozalo (1986). Finally, they followed the original diagnosis of *P. sdzuyi*.

We have collected numerous specimens sampling at decimetric scale in the RV_1 and RV_2 sections (Murero, Cadenas Ibéricas, see Liñán and Gozalo, 1986) during the last years. The new material shows an important variability in the number of the glabellar rows and size and density of the spine-like tubercles among specimens collected in the same level. Thus, although it is possible to recognise an evolutionary trend to increase the number of the rows from the oldest to the youngest specimens of *Pardailhania*, the number of rows in the glabella could be considered as intraspecific variability and not as diagnostic character.

The number of rows in the preglabellar field also shows an evolutionary trend to increase this number (see Álvaro and Vizcaïno, 2001); in this case this increment is produced in temporal order. The oldest specimens show only one row, and the youngest have three rows.

In summary, we propose to restring the number of *Pardailhania* species to three:

- *P. hispida* with one only row of spine-like tubercles in the preglabellar field as diagnostic character and four to six rows in the glabella.
- *P. multispinosa* with two rows of spine-like tubercles in the preglabellar field as diagnostic character and glabella bears among four to six rows. *P. hispanica* is considered as a junior subjective synonym of *P. multispinosa*.
- *P. sdzuyi* with three rows in the preglabellar field as diagnostic character and among six to nine rows in the glabella. *P. morisca* is considered as a junior subjective synonym of *P. sdzuyi.*

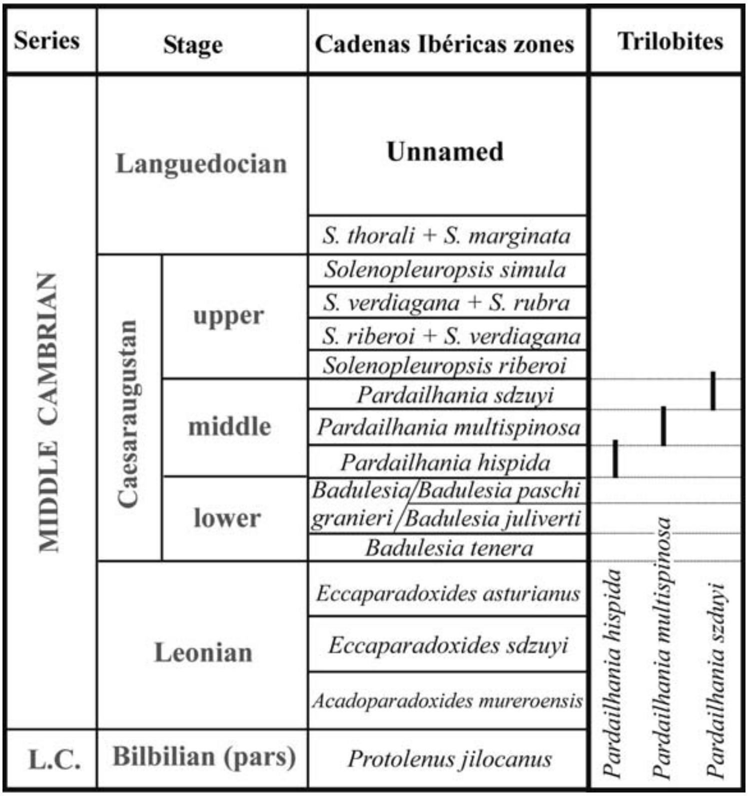

Figure 1. Proposal of a new zonation for the middle Caesaraugustan of the Cadenas Ibéricas.

MIDDLE CAESARAUGUSTAN ZONATION

The material studied in this paper was collected in several localities of the Cadenas Ibéricas (NE Spain) and come from the Murero Formation. The Murero Formation is represented by siltstone and marly siltstones with interbeded carbonate nodules containing trilobites (polimeroids and agnotids), bradoriids, other arthropods, echinoderms (cincta, eocrinoidea and edrioasteroidea), algae, linguliformea brachiopods, sponges, ecdisozoa, hyolits and trace fossils. This assemblage represents sublittoral-neritic biomas installed in tropical latitudes (Gozalo *et al.*, 2003; García Bellido *et al.,* 2007).

The Caesaraugustan stage was subdivided in three substages recognised by the presence of Solenopleuropsinae gena (Sdzuy, 1971; Liñán *et al*., 1993). The FAD of *Pardailhania hispida* characterises the beginning of the middle Caesaraugustan and the FAD of *Solenopleuropsis ribeiroi* characterises the beginning of the upper Caesaraugustan.

The middle Caesaraugustan substage was divided in three zones named *P. hispida*, *P. hispanica* and *P. multispinosa* (see Sdzuy, 1968) zones. According to Liñán and Gozalo (1986) and Gozalo *et al.* (2003) the two first zones are phylozones and the third one is a range zone. Álvaro and Vizcaïno (1998) proposed four range zones or the same substage: *P. hispida*, *P. multispinosa*, *P. morisca* and *P. sdzuyi*.

The new proposal of taxonomy for *Pardailhania* implies changes in this zonation which can be now subdivided in three interval zones, in which guide species are phylogenetically related (Fig. 1). These are the *Pardailhania hispida* zone, *Pardailhania multispinosa* zone [including the former *P. hispanica*] and *Pardailhania sdzuyi* zone [which include the former *P. multispinosa* zones of Sdzuy (1968) and Liñán & Gozalo (1986) and the *P. morisca* and *P. sdzuyi* zones of Álvaro and Vizcaïno (1998)].

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ENROLMENT IN MIDDLE CAMBRIAN SOLENOPLEUROPSINAE TRILOBITES

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Keywords: Solenopleuropsinae, *Pardailhania*, *Solenopleuropsis*, enrolment, coaptative structure.

INTRODUCTION

Trilobites are arthropods capable of enrolling. However trilobite enrolment mechanism has only been well studied in post-Cambrian specimens (Chatterton and Campbell, 1993; Clarkson and Whittington, 1997). The mechanism of enrolment is possible thanks to the presence of coaptatives structures. These structures have been recognized since Cambrian times.

According to Bergström (1973) there are two basic types of enrolment: incomplete and complete. Incomplete enrolment has been observed in some Lower Cambrian trilobites, whose enrolment comprises the coiled posterior part of a thorax (Bergström, 1973). Complete enrolment is the most common since Ordovician; although it is unusual in Cambrian trilobites, there are figurations since 19th Century (see Prado *et al.*, 1860: pl. VI fig. 8).

The complete enrolment has been subdivided into two subtypes: sphaeroidal and spiral (Bergström, 1973). In the first one, the pygidium leans on the ventral surface of the cephalon and in the second one the pygidium is undercovered by the cephalon. The sphaeroidal subtype, also could be subdivided in three types: cylindrical, *Asaphus*-type and inverted spiral (*Placoparia*-type). In the cylindrical enrolment, the most common in the Paradoxididae family (Middle Cambrian), pleurae do not close laterally the exoskeletal basket. *Asaphus*-type and inverted spiral enrolment (*Placoparia*-type) are the typical enrolment among post-Cambrian trilobites (Bergström, 1973; Speyer, 1988; Chatterton and Campbell, 1993; Bruton and Hass, 1997).

There are some complete Cambrian enrolled trilobites described in several species from North America (Palmer, 1958; Robinson, 1964; Stitt, 1983; Whittington, 2005) and Morocco (Geyer, 1990), most of them belonging to the spiral type. Sphaeroidal enrolment is very unusual in Cambrian specimens and we describe herein an example registered in two genera of Solenopleuropsinae.

Sixteen specimens of *Solenopleuropsis* and *Pardailhania* excellently preserved in 3D have been recently found in the Cadenas Ibéricas. This type of enrolment has not been described before in Cambrian species. The coaptatives structures observed and its role in the enrolment mechanism will also be analysed and discussed.

GEOLOGICAL FRAMEWORK AND PRESERVATION OF FOSSILS

The studied material has been found in the localities of Murero and Purujosa (Cadenas Ibéricas, NE Spain, fig. 1A). Fossils were collected in the levels of the Murero Formation (Caesaraugustan-Languedocian, Middle Cambrian; fig. 1B). This Formation consists of a siliciclastic succession with inter beded carbonate nodules deposited under sublitoral marine conditions in the western margin of Gondwana. Levels from both localities specially those from Purujosa are related with obruption deposits. Fossil assemblages are composed of echinoderms, brachiopods, trilobites and sponges.

The enrolled trilobites studied here are preserved as casts of the skeletons in authigenic verdine-type clay minerals. As a result of this preservation, specimens can be observed in three dimensions, a very atypical preservation style on middle Cambrian trilobites.

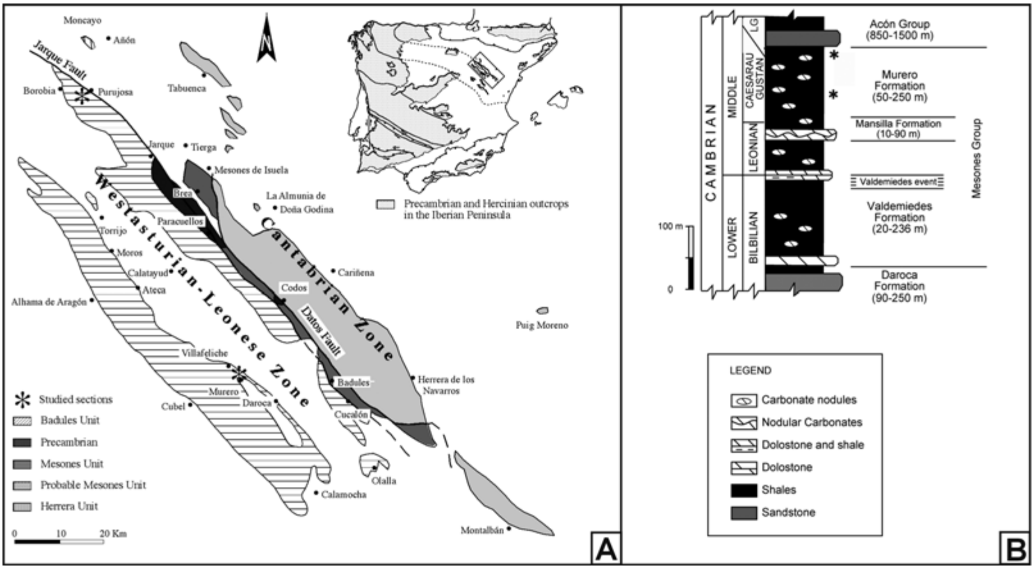

Figure 1. A, Geological framework of the Cadenas Ibéricas showing the studied localities (modified from Liñan *et al.*, 1996). B, Stratigraphy of the upper lower to middle Cambrian, Mesones Group (modified from Liñan *et al.*, 1996).

COAPTATIVE STRUCTURES

The different types of complete enrolment depend on morphological features called coaptative structures, which provide close interlocking of the opposing surfaces. The specimens of *Pardailhania* and *Solenopleuropsis* studied here have specific coaptative structures belonging to the *Asaphus* type of enrolment. These structures are localized in the cephalon, thorax and pygidium and they are briefly described below.

Cephalon: The cephalon has a concave anterior border with an upturned anterior margin. The ventral side bears a smooth vincular furrow and it is placed behind the cephalic doublure.

Thorax: The thoracic segments are arch on arches. The thorax bears articulation points placed between the axial rings (articulating half ring) and between adjacent pleurae, (fig. 2A). The axial rings show a preannulus that is divided into two parts: the articulating furrow and the intra annular furrow, which is very smooth and points the contact with the next thoracic segment (Harrington, 1959; Speyer, 1988; Bruton and Hass, 1997). The pleurae were articulated by fulcra joints with soft tissues connecting their inner margin of double as "ball and socket connection" (marginal connective device *sensu* Bergström, 1973) (fig. 2B). Thoracic pleurae doublures bears panderian protuberances consisting on elongated ridgelike protuberances.

Pygidium: It is very short and narrow with a little vincular hook fitting on the vincular furrow.

These coaptative structures make possible the mechanism of enrolment in Solenopleuropsinae trilobites. In this process pygidium rests with its dorsal side on the cephalic margin doublure. As a result cephalon and pygidium are in a opposite position.

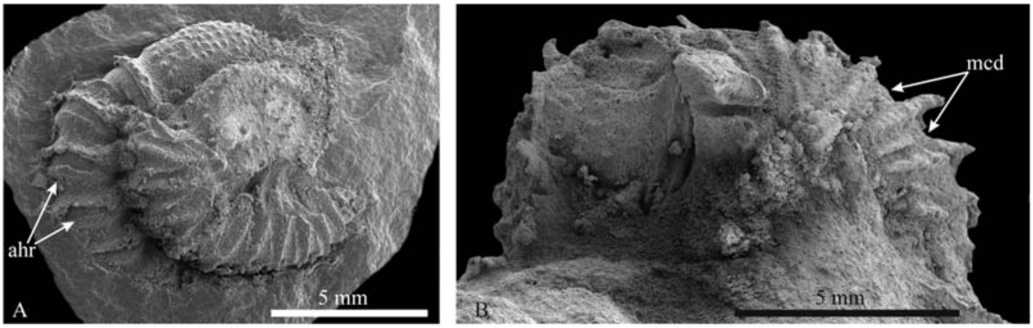

Figure 2. A, *Solenopleuropsis* sp., incomplete enrolled specimen in lateral view. ahr: articulating half ring. SEM picture of a latex cast. B, *Pardailhania* specimen enrolled in lateral view. mcd: marginal connective devises. SEM picture of a latex cast.

ENROLLING MECHANISM

The enrolment begins at the first articulation, between the occipital ring and the first axial ring, by the articulating half ring that allows the thorax bending. In the rest of the thorax, the ball and socket connections in pleurae execute the articulation between pleurae till they meet laterally the pygidium. Finally the most posterior thoracic segments have to fit the ventral the cephalon on its ventral part, through the vincular furrow, closing completely the trilobites.

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PYRITIZED TRILOBITE FAUNAS FROM THE ORDOVICIAN OF NEW YORK STATE: BEECHER'S TRILOBITE BED AND THE WHETSTONE GULF FORMATION NEAR LOWVILLE

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Beecher's Trilobite Bed (Ordovician, Caradoc, Frankfort Formation, NY) is a classic locality for the preservation of trilobite appendages. In particular, it is the source of our knowledge of the limbs of the olenid *Triarthrus* (Fig. 1) and the trinucleid *Cryptolithus*. The material studied by Beecher (1896) and Walcott (1894) came from the 4 cm-thick Trilobite Bed, which is dominated by trilobites, many of them complete, brachiopods and graptolites (Cisne 1973). This bed was rediscovered in 1984 and excavated in 1989; a detailed analysis of a ~30 cm sequence including the bed investigated possible controls on pyritization (Briggs *et al.*, 1991). A larger scale excavation by the Yale Peabody Museum of Natural History, Division of Invertebrate Paleontology, was initiated in 2004 to explore a much thicker sequence (2.8 m) incorporating the Trilobite Bed and to investigate lateral variation over a distance of at least 60 m (Fig. 2). This project aims to interpret the environment in which the trilobites lived, and the factors controlling the exceptional preservation.

The sequence containing Beecher's Trilobite Bed (Fig. 3) consists predominantly of dark-grey shales interbedded with medium grey mudstones/siltstones and fine sandstones. Most beds are unfossiliferous, or sparsely fossiliferous. Darker, finer mudstones yield bedding plane assemblages containing brachiopods, cephalopods, trilobite fragments, rare bivalves and graptolites. Thin layers dominated by graptolites occasionally show a preferred orientation (NE-SW). At least three new beds in addition to the original Trilobite Bed have been discovered that yield pyritized trilobites. These trilobite beds contain whole, often pyritized trilobites (>95% *Triarthrus*) within the bed, some shallow trace fossils at the top and rare graptolites and brachiopods. Overall, the sedimentary structures suggest a low-energy depositional regime, with frequent influx of distal turbidites.

A second locality yielding exceptionally-preserved olenids was discovered in 2005 in the Ordovician Whetstone Gulf Formation near Lowville, NY. The Lowville sequence also consists primarily of dark-grey to medium-grey siltstones and mudstones interbedded with fine sands, with an increase in sandy horizons towards the top of the sequence. The diversity and abundance of fossils is higher than at the Beecher's Trilobite Bed locality - in addition to *Triarthrus*, brachiopods and graptolites, there are crinoids, gastropods and bivalves. The trilobite *Cryptolithus* is common. Trilobites such as *Isotelus*, which are unknown at the Beecher's Trilobite Bed locality, also occur. However, soft-tissue preservation is confined primarily to the olenid trilobites which are generally found in low-diversity horizons. Overall the sedimentology suggests a slightly higher-energy, shallower depositional regime than that represented at the Beecher's Trilobite Bed locality.

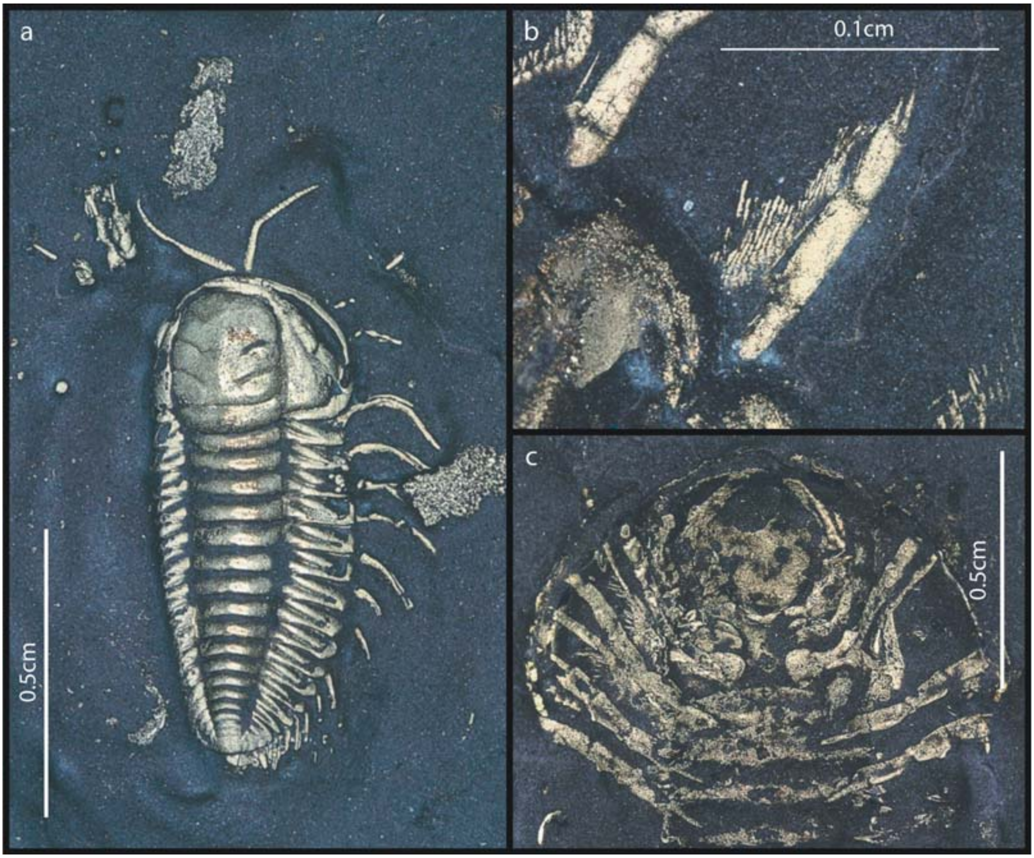


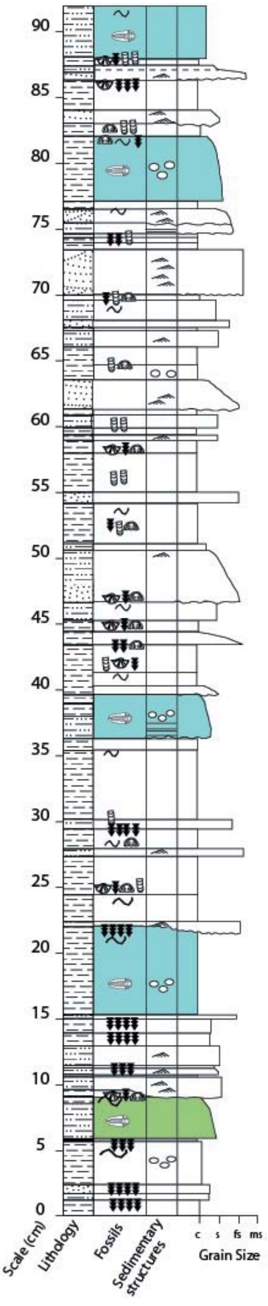
Figure 1. a, Dorsal view of *Triarthrus* from the original Trilobite Bed, showing antennae and limbs. b, Detail of biramous limb with filaments preserved. c, Ventral view of cephalon, showing appendages. Photos: Tom Whiteley.

Figure 2. Excavation at Beecher's Trilobite Bed, May 2005. This extended the original site laterally by about 60 m. Based on historical documents, this particular section is thought to be the location where C.E. Beecher worked in the late 1800's. Photo: Tom Whiteley.

Initial geochemical analyses of the Beecher's Trilobite Bed sequence showed that soft-tissue pyritization is associated with a high reactive iron content and high $\delta^{34}S$ values. The high iron content promoted iron reduction while the low organic content of the sediment ensured that sulphate reduction was concentrated at the decaying carcases, resulting in heavier isotope values as reduction continued after the system became closed (Briggs *et al.*, 1991). The sediment was enriched in highly reactive iron prior to sediment transport (Raiswell *et al.*, 2008). The new investigation involves analysis of the speciation of the highly reactive iron (FeHR) which comprises iron from those minerals that are reactive to sulphide on short diagenetic time-scales: iron associated with carbonate, magnetite iron, iron from oxides/oxyhydroxides and pyrite iron. The ratio of highly reactive iron (FeHR) to total iron (FeT) provides a method of distinguishing anoxic from oxic bottom waters (Raiswell and Canfield, 1996, 1998; Lyons and Severmann, 2006). The proportion of pyrite iron provides an indication of the possible presence of sulphide in the water column (Poulton and Canfield, 2005).

Preliminary geochemical, sedimentological and palaeontological results suggest that conditions in both the Beecher's Bed sequence and that at Lowville fluctuated, and were occasionally anoxic. The beds that contain pyritised trilobites correspond to peaks in the FeHR/FeT ratio, indicating low oxygen. They are also characterized by heavy $\delta^{34}S$ values indicating extended sulphate reduction associated with soft tissues (Raiswell, 1997).

The low diversity and high abundance of the trilobites in Beecher's Trilobite Bed, coupled with the geochemical signature, implies an unusual mode of life. It has been suggested that olenid trilobites such as *Triarthrus* had a symbiotic relationship with sulphur bacteria (Fortey, 2000) allowing them to live in



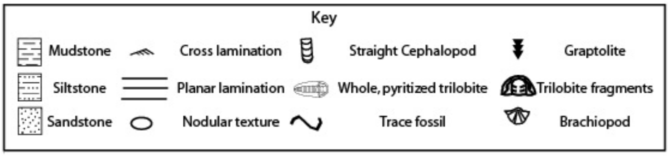


Figure 3. Sample section from the Beecher's Trilobite Bed locality. Newly discovered trilobite beds (i.e. beds with whole, pyritized trilobites) are highlighted in blue. The original Trilobite Bed is in green. Other fossiliferous beds contain varying percentages of straight cephalopods, brachiopods, trilobite fragments and graptolites. Trace fossils are rare and tend to be shallow with a simple straight, winding or branched morphology. The beds are flat-lying and can be traced over the length of the exposure.

environments that are toxic to most invertebrates. This is difficult to reconcile with the fluctuating conditions evident in both Beecher's Trilobite Bed and at Lowville: such instability would have been inimical to such a specialized mode of life. It remains a possibility, however, that the olenids migrated in and out of suitable settings, and that their remains were transported into the more oxygenated parts of the sequences.

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EXOSKELETAL CONFIGURATIONS OF CAMBRIAN AND ORDOVICIAN AGNOSTIDS: EXAMPLES FROM THE BARRANDIAN AREA OF CZECH REPUBLIC

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Keywords: Cambrian, Ordovician, agnostid trilobites, exuviation.

INTRODUCTION AND METHODS

For this study, all accessible specimens (several hundreds) of agnostids stored in collections of the Czech Geological Survey Prague, National Museum Prague, Museum of West Bohemia Plzeň, Charles University Prague, Museum of B. Horák Rokycany and in private collections have been utilized. From the thirty six species of miomerids (15 in Cambrian and 21 in Ordovician) known in the Barrandian area, complete specimen and at least one other exoskeletal configuration were observed in the following taxa:

Cambrian: *Condylopyge rex* (Barrande, 1846); *Pleuroctenium granulatum granulatum* (Barrande, 1846); *Phalagnostus prantli* Šnajdr, 1957; *Phalagnostus nudus* (Beyrich, 1845); *Phalacroma bibullatum* (Barrande, 1846); *Peronopsis integra* (Beyrich, 1846); *Onymagnostus hybridus* (Brögger, 1878); *Doryagnostus vinicensis* (Šnajdr, 1957); *Hypagnostus* cf. *parvifrons* (Linnarsson, 1869); *Tomagnostus* cf. *perrugatus* (Grönwall, 1902).

Ordovician: *Arthrorhachis tarda* (Barrande, 1846); *Corrugatagnostus refragor* Pek, 1969; *Corrugatagnostus perrugatus* (Barrande, 1872); *Corrugatagnostus morea* (Salter, 1864); *Geragnostus (Geragnostella) tullbergi* (Novák, 1883); *Leiagnostus bohemicus* (Novák *in* Perner, 1918).

The most common material was observed in Cambrian *Phalagnostus* and *Peronopsis* and Ordovician *Leiagnostus, Geragnostus* and *Corrugatagnostus* (several hundred specimens for each genus), more than twenty complete exoskeletons were observed in *Onymagnostus*, *Hypagnostus* and *Doryagnostus.* Number of specimens of other Cambrian and Ordovician taxa ranges from two to twenty exoskeletons. Major part of the materials used for this study was collected from different stratigraphical levels of the"Middle" Cambrian Jince Formation in the Príbřam-Jince and Skryje-Týřovice basins. Similarly, most of the Ordovician material comes from the three main stratigraphical levels of the Prague Basin: Šárka, Dobrotivá and Králův Dvůr formations (Darriwilian and late Katian, respectively).

The purpose of the contribution is (1) to present data on exoskeletal configurations of agnostids observed in "Middle" Cambrian and Ordovician of the Barrandian area, and (2) to propose an explanation of the observed modes of exoskeletal disarticulations.

Four major skeletal parts compose agnostid exoskeleton: (1) cephalic shield, (2) first and (3) second thoracic segments and (4) pygidial shield. The fifth mineralised part, the hypostome, is preserved only exceptionally and its presence or absence is not considered in this paper. The three joints existing between four parts of agnostid exoskeleton (joint I – III in figure 1) provide eight theoretical combinations of disarticulation of the exoskeleton. However, only the following three main exoskeletal configurations have been observed in the studied materials:

Exoskeletal configuration 0. Dead or moulted exoskeleton composed by fully articulated cephalic and pygidial shields and both thoracic segments (several hundreds observed specimens) – all joints are closed.

Exoskeletal configuration 1. Cephalic shield becomes detached from thorax; thorax still connected with pygidial shield – abundant (more than 80 observed specimens) – opening of the joint I.

In several specimens, the pygidial shield becomes detached from thorax, while thorax is still connected with cephalic shield.

Exoskeletal configuration 2. Pygidial shield becomes detached from thorax, e.g. cephalic shield already missing (more than sixty specimens observed) – opening of the joint III.

Rarely also the configuration was observed, when cephalic shield started to detach from thorax, when the pygidial shield was missing.

Stage 3. Thoracic segments become detached (both cephalic and pygidial shields missing); full disarticulation (observed in tens of samples) – opening of the joint III.

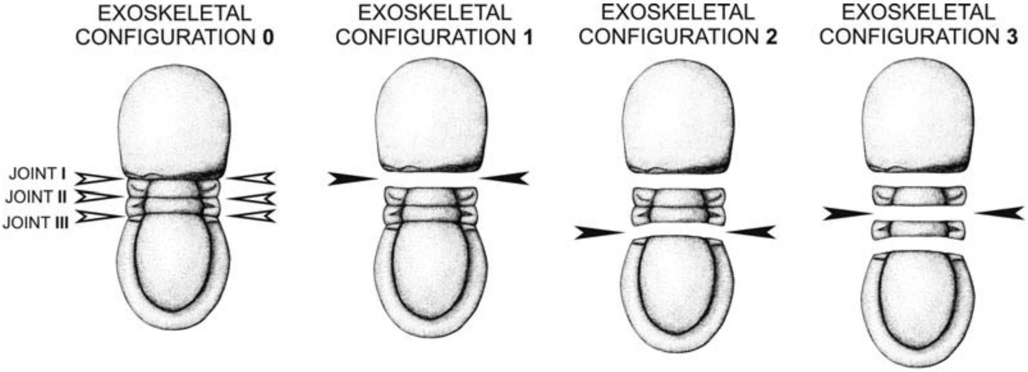

Figure 1. Generalized scheme of the main exoskeletal configurations in *Phalagnostus* Howell, 1955.

COMPARISON

Comparing to similar studies of the Pensylvanian-Permian xiphosurid genus *Paleolimulus* by Babcock *et al*. (2000) or the early Cambrian naraoiid arthropod genus *Naraoia* by Babcock and Chang (1997) and Zhang *et al*. (2007), preservation of the agnostid specimens did not provide the possibility to document decay of poorly sklerotised parts of body (e.g. appendages) and thus the detachment of gills, legs but also mineralised hypostome (which is generally rare) are not incorporated in the distinguished exoskeletal configurations.

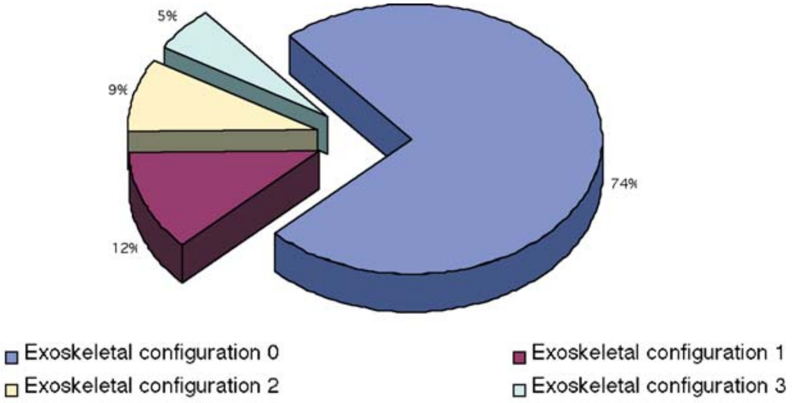

Figure 2. The doughnut chart of exoskeletal configurations for Cambrian and Ordovician agnostids of the Barrandian area.

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POSITION OF TRILOBITES IN CAMBRIAN ECOSYSTEM: PRELIMINARY REMARKS FROM THE BARRANDIAN REGION (CZECHIA)

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Keywords: Cambrian, trilobites, feeding, hiding, benthic and planctic life habits.

INTRODUCTION

Recently summarized feeding strategies of trilobites (e.g. Fortey, 1990, 2004; Fortey and Owens, 1999; Jell 2003), including evaluation of trilobite position in the Palaeozoic predator–prey system (Babcock, 2003) and some very special habits like the possible cryptic behaviour (Chatterton *et al*., 2003; Davis *et al*., 2001) show that trilobites occupied very diversified niches in Palaeozoic marine ecosystem. The goal of this contribution is to discuss selected findings documenting several major life habits of trilobites in Cambrian of the Barrandian region (Czechia).

BASE OF FOOD CHAIN IN CAMBRIAN OF THE BARRANDIAN REGION

Highly diversified and common planktonic primary producers (represented by up to several thousand of individuals and more than twenty species of acritarch and prasinophyte cysts in one gram of sediment, e.g. Fatka, 1989) as well as benthic microbial mat-bound substrates (containing different species of the filamentous genus *Siphonophycus* Schopf, 1968, emend. Knoll *et al*., 1991 and macroscopic algae *Marpolia spissa* Walcott, 1919, e.g. Steiner and Fatka, 1996) combined with the supposed bacterial decomposition (marine snow), document a rich and diverse source of food which was employed by different benthic and planktonic consumers, including the generally common trilobites.

BENTHIC LIFE HABIT

Assemblage of primary consumers feeding *in situ*

Several tens of slabs covered by entire specimens of the opportunistic polymerid trilobite *Ellipsocephalus hoffi* (Schlotheim, 1823) and tiny, evenly locally dominant hyolith *Jincelites vogeli* Valent *et* *al.* (in press) have been recently collected from higher levels of the Jince Formation, e.g. in sediments supposedly deposited in a shallow-water setting. On three of such slabs one to three articulated trilobite individuals together with several tens of articulated hyoliths are preserved on restricted surfaces directly inside the microbial mats, which contain well visible carbonaceous filaments (Pl. 1, fig. 8). Both the trilobites and hyoliths represent thus an *in situ* feeding assemblage of primary consumers.

Gardening of polymerid trilobites (= primary consumers)

Cephalon of the small, locally abundant agraulid trilobite *Litavkaspis rejkovicensis* Fatka *et al*., 1987 is characterized by a very specialized morphology of cephalon with lowered, only slihtly vaulted preglabellar area but conspicuously vaulted and abaxially narrowing frontal border combined with rounded librigena without postero-lateral spine. Entirely preserved articulated skeletons of the trilobite genus *Litavkaspis* are common inside of the ichnospecies *Rejkovicichnus necrofilus* Mikuláš *et al*., 1996 and represent the only articulated trilobite species preserved within this trace. Mikuláš (2001), logically designated *Litavkaspis* as the tracemaker and proposed the following scenario for origination of *Rejkovicichnus*.

The tracemaker produced a trench in the substrate, which subsequently filled with large bioclasts collected at the surrounding bottom. Bioclasts ascertained inside of *Rejkovicichnus* belong to isolated plates of ctenocystid and cinctan echinoderms (*Etoctenocystis bohemica* Fatka and Kordule, 1985, and *Asturicystis havliceki* Fatka and Kordule, 2001) and exoskeleton trilobite fragments (*Paradoxides* and *Conocoryphe*). The filled trench was left for the cultivation of bacteria for some time and than reopened by *Litavkaspis* to feed on the "cultivated" bacterial content.

Possible gardening and/or hiding of polymerid trilobites

Several tens empty conchs and rarely also complete individuals of the large hyolihid *Maxilites maximus* (Barrande, 1867) associated with a highly diversified fossil assemblage, have been recently discovered at the "Čihátko–milíř" locality. About 60 % of the more or less entirely preserved conchs contained a unique skeletal fauna entombed inside (Pl. 1, fig. 1). In different parts of conchs entire individuals and/or disarticulated exoskeletons of the polymerid trilobites *Skreiaspis spinosa* (Pompeckj, 1895), *Mikaparia mutica* (Hawle and Corda, 1847) and *Conocoryphe sulzeri atlanta* Šnajdr, 1982 are associated with skeletal parts of *Ctenocephalus (C.) coronatus* (Barrande, 1846), *Paradoxides (Eccaparadoxides) pusillus* (Barrande, 1846), isolated valves of the brachiopod *Luhotreta pompeckji* Mergl and Šlehoferová, 1990 and *Bohemiella romingeri* (Barrande, 1846) and dismembered echinoderm plates, including attachment disc of a tiny undescribed eocrinoid on the external surface of hyolithid conch of the genus *Oboedalites* Marek, 1981.

Cryptic behaviour or hiding combined with feeding directly on hyolith soft parts or on bacteria decomposing soft parts of the hyolith carcase or on bacteria growing inside of the hyolith conch (= gardening of *Skreiaspis*) is not possible to distinguish.

Similarly, several meraspid to early holaspid specimens of *Skreiaspis* have been collected under isolated cephalons of the much larger polymerid trilobites of the genera *Paradoxides (Eccaparadoxides)* and *Ptychoparia* (Pl. 1, fig. 6).

Feeding on organic matter accumulated under cranidia by currents or on bacteria growing under the exoskeleton or simple hiding of meraspid specimens associated with exuviation represent three plausible explanations of these findings.

Feeding or hiding of agnostids

Entire specimens of the tiny agnostid *Peronopsis* have been established entombed within and/or under carcases of the large *Paradoxides (Hydrocephalus) minor* (Boeck, 1827) (see Fatka and Szabad, in press). The agnostids could find here a hiding place in danger of predation existing within the water column or on the sea floor, or during bad weather periods associated with deterioration of physical conditions, and/or a rich and well protected source of food. Whether they were feeding directly on the soft parts of *Paradoxides* and/or on bacteria decomposing soft parts of the carcase is not possible to decide (Pl. 1, fig. 3).

Relation of trilobites to substrate

An obvious relation to the bottom substrate characterized by local dominance of trilobites associated with the stylophoran echinoderms has been established in the "Armoured" stylophoran biofacies of Lefebvre (2007). Hundreds of closely packed specimens of the primitive stylophoran *Ceratocystis perneri* Jaekel, 1901 associated with the small blind conocoryphid *Ctenocephalus (C.) coronatus* have been collected from a grainstone lens deposited under storm-dominated environments (above average stormbase) on proximal shelf at the Dlouhá Hora locality near Skryje.

Such accumulation evokes presence of restricted and rich but unfortunately unknown source of food for these opportunistic taxa at the water-sediment interface.

Similarly, the opportunistic, locally abundant occurrence of hundreds of articulated exoskeletons of the genus *Germaropyge*, associated with numerous specimens of *Mikaparia* and several other genera [*Lobocephalina*, *Conocoryphe*, *Ctenocephalus*, *Sao, Paradoxides (Eccaparadoxides)*] were possibly also associated with specific environment and a rich source of food.

Hunters/scavengers based on the hypostome morphology

After Fortey and Owens (1999) the general morphology of the hypostome and rostrum in the large genus *Paradoxides* supposedly corresponds with hunting/scavenging mode of life. We share this interpretation and preliminary analyses of rostra and hypostomes in paradoxiids of the Barrandian area most probably belong to this group. Our results show a surprising rarity of this habit within Cambrian trilobites of this area.

Soft parts of the digestive system

Internal molds of about twenty articulated specimens of polymerid genera *Germaropyge*, *Ptychoparia*, *Conocoryphe*, *Ctenocephalus* preserved in fine sandstones provide the occasion to study three-dimensionally preserved anterior, posterior and mid-gut morphology, including composition of their content (Steiner *et al.,* in prep.) (Pl. 1, fig. 2).

PELAGIC LIFE HABIT

The specialised exoskeleton morphology of *Luhops* Šnajdr, 1957 typified by a narrow streamlined exoskeleton with elongate genal spines and eyes, generally narrow but backward widening pleural areas continuing into large spiny pygidium at the fin-like posterior thorax-pygidial region combined with a wide rhachis.

Luhops as well as *Centropleura* and *Beishanella* show skeletal morphologies which have been interpreted as convergent with the pelagic Ordovician trilobites (e.g. *Bohemilla*) by Babcock (2003) and recently also by Fortey and Rushton (2007).

Exoskeletal disarticulation in agnostids

The recently established three different stages in disarticulation of agnostid exoskeletons (Fatka *et al.*, in press) support the earlier supposed coiled posture of this group proposed by different authors, e.g. by Müller and Walossek (1987).

Bite marks and healed injuries

Šnajdr (1978) described several specimens of paradoxidid trilobites with teratological exoskeletons, some of them could represent healed injuries after being attacked by unknown predator. Specimen of *Conocoryphe* and several other small trilobites show similar traces of lethal attacks (pl. 1, fig. 7).

TRILOBITE EXOSKELETONS AS SUBSTRATE FOR SETTLING AND BIOEROSION

Different exoskeleton parts, chiefly cephalic shields of the genera *Conocoryphe*, *Ptychoparia*, *Paradoxides (P.)* served as substrate for attachments of the eocrinoid echinoderm *Vyscystis ubaghsi* Fatka and Kordule, 1990; while attachment discs of the tiny undescribed eocrinoid have been established on cephalons of *Paradoxides (Hydrocephalus)* and *Skreiaspis* (Pl. 1, fig. 6).

The apparent preference to attach to trilobite exoskeletons, in comparison to the recent study by Lin *et al.* (in press), could be explained by the rarity of organophosphatic brachiopods in the deeper siliciclastic settings of the Barrandian region.

Straight, curved to irregularly ramified and/or net-like tunnels visible on internal moulds (less frequently slightly below the surface of internal moulds) of hyolithids and the trilobite genera *Ellipsocephalus* and

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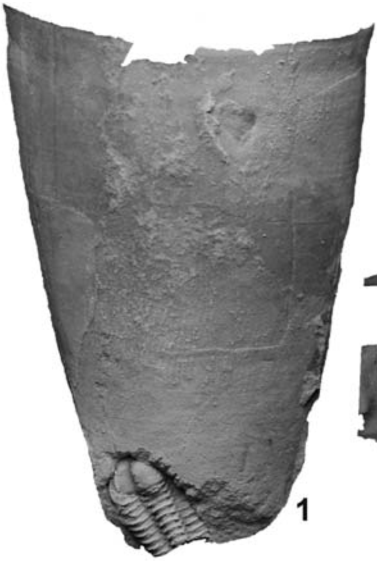
Plate 1. 1, Dorsal view on internal mould of the large hyolith *Maxilites maximus* (Barrande, 1867) with entombed exoskeleton of the wuanid trilobite *Skreiaspis spinosa* (Pompeckj, 1895). 2, Internal mould of *Conocoryphe* with three-dimensionally preserved alimentary structures of the digestive system in posterior sector of glabella and in the anterior thoracic segments. 3, Latex cast of two articulated specimens of the agnostid *Peronopsis integra* (Beyrich, 1846) entombed between the hypostome and dorsal exoskeleton of cephalic shield of the large *Paradoxides (H.) minor* (Boeck, 1827). 4, Internal mould of *Conocoryphe* with well developed *Arachnostega gastrochaenae* Bertling, 1992. 5, Latex cast of two specimens of the eocrinoid echinoderm *Vyscystis ubaghsi* Fatka and Kordule, 1990 attached to cranidium of the genus *Conocoryphe*. 6, Dorsal view of internal mould of cephalon of *Ptychoparia dubinka* Kordule, 2006 with two late meraspid specimens of *Skreiaspis spinosa*; on external surface of the isolated cephalon of *S. spinosa* (right upper) two attachment discs of an undescribed eocrinoid echinoderm are preserved. 7, Entire specimen of *Conocoryphe sulzeri atlanta* Šnajdr, 1982 with a bite mark on the left posterior margin of cranidium and missing first to sixth pleura on left thoracic side. 8, Entire specimen of *Elipsocephalus hoffi* (Schlotheim, 1823) and several tens of the tiny hyolithid *Jincelites vogeli* feeding *in situ* on the microbial mat.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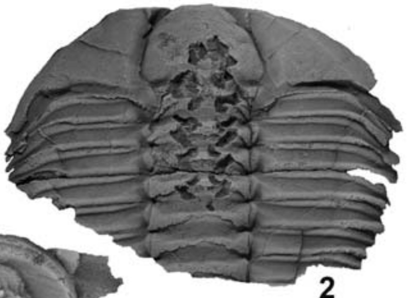
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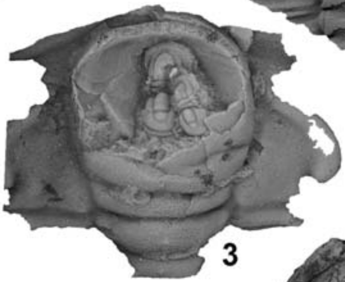
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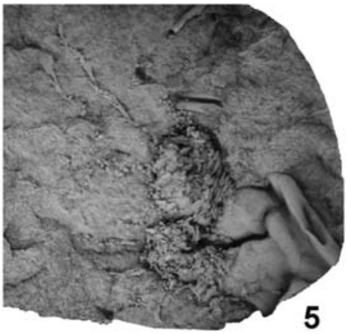
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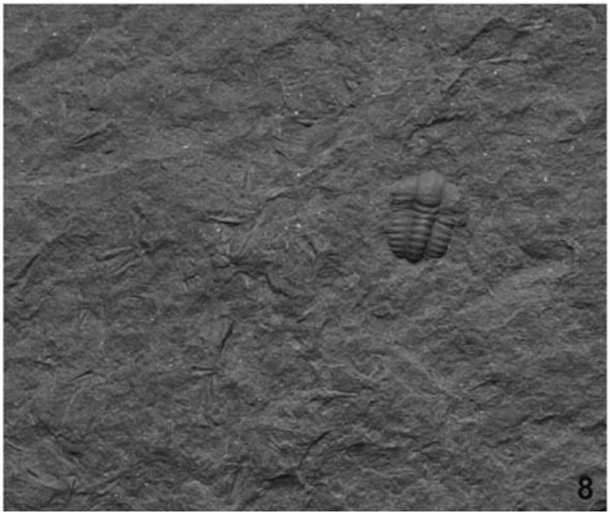
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Conocoryphe (Pl. 1, fig. 4) are classified as the ichnospecies *Arachnostega gastrochaenae* Bertling, 1992 by Fatka *et al.* (in press).

Study of locally common aggregates, including coprolites containing crushed skeletal debris represents still a poorly studied but very promissing source of data on trilobite ecology in different regions (Vannier and Chen, 2005), including Cambrian of the Barrandian area.

Acknowledgements

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ORDOVICIAN TRILOBITE GENUS *HUNGIOIDES* KOBAYASHI, 1936

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Keywords: Ordovician, trilobites, *Hungioides*, palaeobiogeography, taxonomic review.

ABSTRACT

Findings of the dikelokephalinid genus *Hungioides* Kobayashi, 1936 [type species *H. bohemicus* (Novák *in* Perner, 1918)] belong to rare elements of trilobite assemblages in the Lower to Middle Ordovician of Gondwana and peri-Gondwana.

The following six species and subspecies have been included in *Hungioides*:

1. *Hungioides acutinasus* Fortey and Shergold, 1984, from the "Arenig" Nora Formation of Georgina Basin (central Australia);
2. *Hungioides bohemicus bohemicus* (Novák *in* Perner, 1918), from the Middle Ordovician of Europe (Bohemia, Spain, Portugal and France), also documented (as *H.* cf. *bohemicus*) in West Yunnan, China (Zhou *et al*., 1988);
3. *Hungioides bohemicus graphicus* (Richter and Richter, 1954), from the Griffelschiefer Formation of Saxo-Thuringia (Germany);
4. *Hungioides constrictus* Lu, 1975, from the Lower Ordovician (upper Tremadocian) of China;
5. *Hungioides intermedius* (Harrington and Leanza, 1957), from the Suri Formation, late Lower Ordovician of the Famatina Basin (Argentina: Waisfeld and Vaccari, 2003);
6. *Hungioides mirus* Lu, 1975, from the "upper Arenig" of Hubei and Guizhou (south China).

The taxa *Hungioides novaki* Kobayashi, 1936 and *Hungioides bohemicus arouquensis* Thadeu, 1956 were synonimized by Rábano (1983) with *Hungioides bohemicus*. A recent revision of the original and additional specimens of *Hungioides graphicus* Richter and Richter, 1954 revealed that this taxon should be considered as a subspecies of *Hungioides bohemicus*.

The five known species of *Hungioides* have been documented from Gondwana (Argentina and Australia), peri-Gondwanan Europe (Ibero-Armorica, Thuringia and Bohemia) and China (North and South China palaeoplates and the Indo-China Terrane) and show thus a wide palaeogeographic distribution (Fig. 1).

Figure 1. Reconstruction of the world in the Lower Ordovician showing distribution of genus *Hungioides* (adapted from Cocks and Torsvik, 2002; ATA modified after Linnemann *et al.,* 2004).

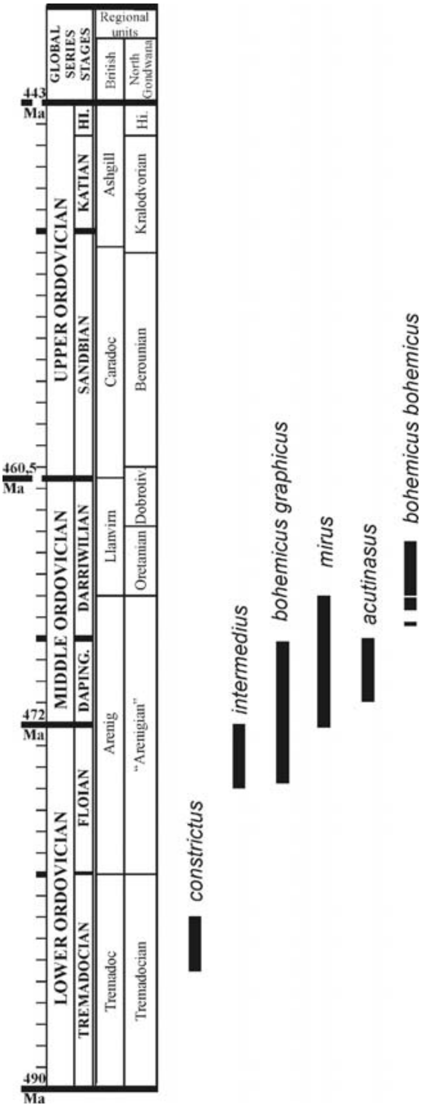

Figure 2. Chronostratigraphic ranges of the six different taxa of *Hungioides.*

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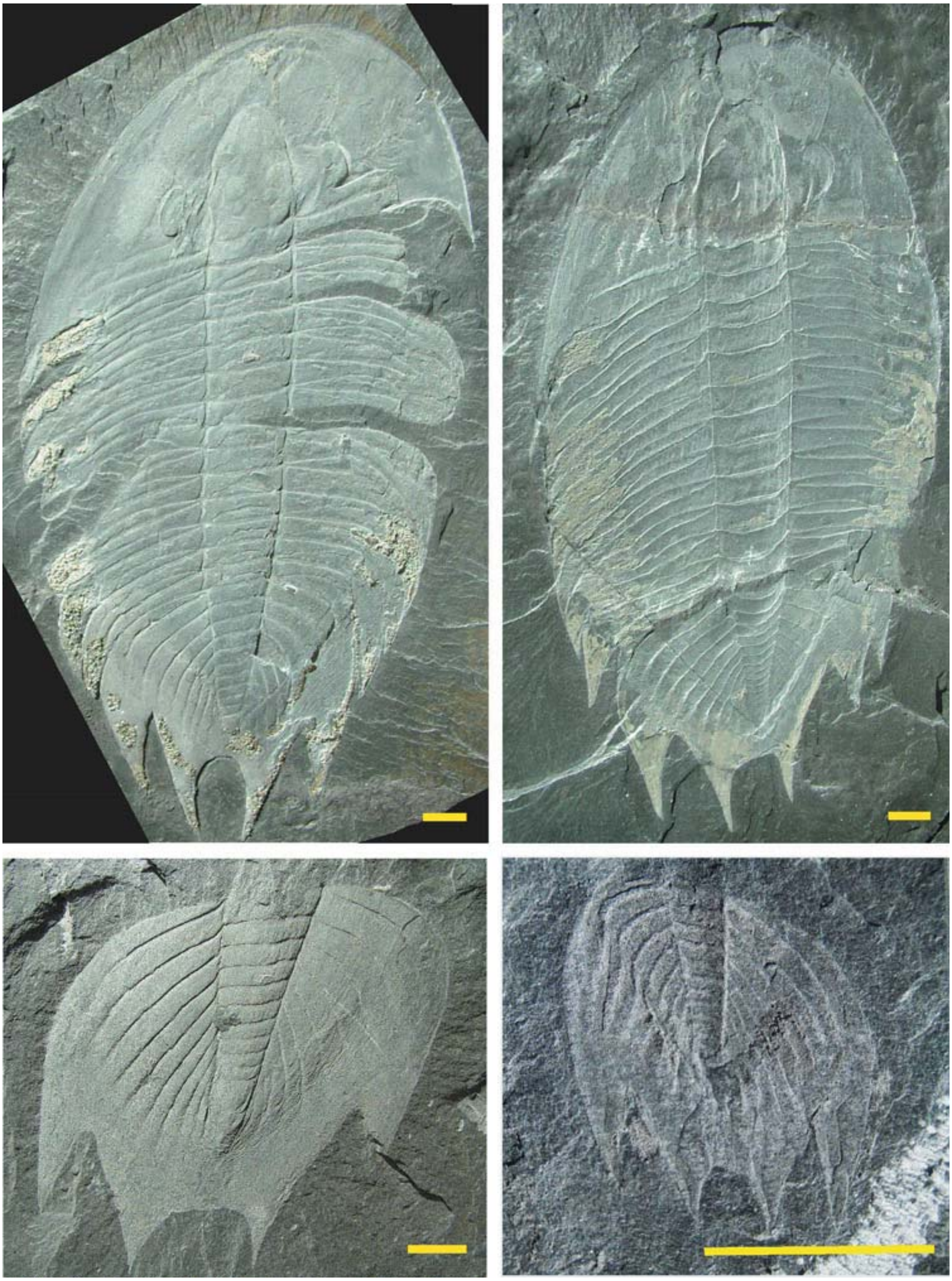

Figure 3. Some specimens of *Hungioides bohemicus bohemicus* from the Canelas quarry (Arouca, Portugal). Valongo Formation, lower Oretanian (middle Darriwilian) strata. Pictures reproduced from Sá *et al.* (2006). All are adult specimens except for the pygidium of the lower right corner, which corresponds to an early holaspis stage ("novaki-morphotype"). Scale bars = 2 cm.

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ASSESSING THE HYPOTHESIS OF A THIRD TAGMA IN SCUTELLUID TRILOBITES: ARGUMENTS FROM ONTOGENETIC, FUNCTIONAL, AND EVOLUTIONARY PERSPECTIVES

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Keywords: Trilobita, Scutelluidae, tagmosis, ontogeny, ecology, evolution.

INTRODUCTION

The morphology of the pygidium of scutelluids is unusual among trilobites. Its main characteristics can be summarized as follows: 1) a great size generally combined with a low dorsal convexity, 2) a short, transversally unsegmented but longitudinally trilobed axis, 3) a radial disposition of pleural ribs, and 4) a rather wide, far forwards extending doublure. These features easily discriminate pygidial segments from thoracic ones, leading to the suggestion that in scutelluids, unlike in most trilobites, the body was not composed of two but of three morphologically and functionally differentiated regions (i.e. tagmata): the cephalic, thoracic, and caudal tagmata (Hughes, 2003). The hypothesis that the pygidium of scutelluids may represent a distinct tagma is here assessed in light of their evolution and various aspects of the life history of these trilobites. Ontogenetic data are reviewed to document how and when the characteristic features of the adult pygidium differentiated during early growth. In addition, the functional and ecological consequences of the acquisition of this particular pygidial shape are evaluated. Lastly, major evolutionary trends recognized in the Scutelluidae are discussed with regards to the hypothesis of a third tagma.

DEVELOPMENT OF THE SCUTELLUID PYGIDIUM

The development of scutelluids is rather well known thanks to the description of rare but almost complete ontogenetic sequences. Ontogenetic data are thus available from representatives of four genera: the Silurian *Kosovopeltis* (Kácha and Šarič, 1991; Ludvigsen and Tripp, 1990) and the Early Devonian *Dentaloscutellum* (Chatterton, 1971), *Scutellum* (Chatterton, 1971), and *Meridioscutellum* (Feist, 1970; new data herein). The latter taxon is particularly interesting, as it documents a rare case of dissociation of the two main processes that regulate the development of the thorax: the creation of new segments and the formation of articulations. Unlike in most trilobite ontogenies, the periods of time during which these developmental processes are effective do not (or only slightly) overlap, as demonstrated by the discovery of protaspid larvae (i.e. growth stages devoid of articulations) with up to 9 (possibly 10) post-cephalic segments (Fig. 1a, b). These larvae are much larger than protaspides of other scutelluids, suggesting a delay in the onset of the formation of articulations.

The distinction between thoracic and pygidial segments is more or less clear from one taxon to another. In *Meridioscutellum* (e.g. Figs. 1c-g) and probably also *Scutellum*, future thoracic segments exhibit pleural spines as soon as they appear and can therefore immediately be distinguished from future pygidial segments. In *Dentaloscutellum*, the attribution of a segment to the future thorax or future pygidium is made possible by differences in pleural spine size. In *Kosovopeltis*, however, future thoracic segments display pleural spines no earlier than shortly before they are released into the thorax. Before that time, they are similar to future pygidial segments, making difficult the attribution to a given meraspid degree.

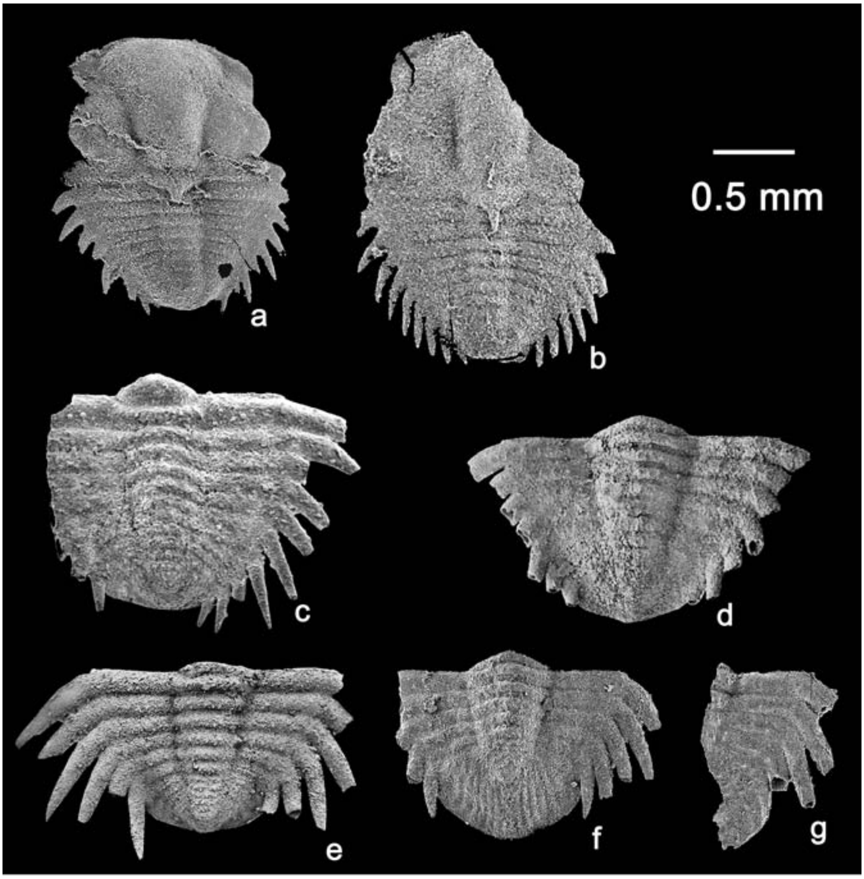

Figure 1. Selected growth stages of *Meridioscutellum*. a, Metaprotaspis with 8 protothoracic segments. b, Metaprotaspis with 9 protothoracic segments. c-g, Transitory pygidia. c, Meraspid degree 0, note the 10 pleural spines of future thoracic segments. d, Meraspid degree 3. e, Meraspid degree 4, note the segmented axis of the future pygidium. f, Meraspid degree 5, note the shortening of the axis of the future pygidium, the vanishing of its segmentation, and the flattening of the surrounding pleural field. g, fragment of Meraspid degree 6.

The four ontogenetic sequences demonstrate that a segmentation of the axis of the future pygidium still occurs in scutelluids, despite its absence in adults. The maximum number of axial rings present in the future pygidium reaches 4 in *Kosovopeltis* (M8, for meraspid degree 8), 5 in *Dentaloscutellum* (M5), 6 in *Meridioscutellum* (M0 to M4; Figs. 1c, e), and 7 in *Scutellum* (M7). However, all these axial rings rapidly disappear (compare Figs. 1e and 1f), except in *Kosovopeltis* where three of them remain discernible just in front of the trilobed part of the adult axis. The longitudinal trilobation of the axis becomes obvious a few stages after the disappearance of the axial segmentation in the four genera, around the boundary between meraspid and holaspid periods. The radial organization of pleural ribs apparently results from the limited growth of the axis of the future pygidium. The pygidial axis is relatively long (sagittally) in early growth stages (Figs. 1a-e), but after the disappearance of the axial segmentation it seems to grow relatively slower than the pleural field. In dorsal view, this relative shortening of the axis during the late meraspid period appears to proceed particularly rapidly, as it is accentuated by a concomitant flattening of the posterior part of the pleural field (Fig. 1f). Lastly, as soon as they are formed, the future thoracic and pygidial segments significantly differ in the width of their doublure. Thus, in transitory pygidia of *Meridioscutellum*, this latter doubles in width from the last future thoracic segment to the first future pygidial segment (Feist, 1970). A similar observation can be made in *Scutellum*, and in both taxa this difference increases during late ontogeny, when the doublure respectively narrows and widens in future thoracic and pygidial segments.

Thus, developmental data reveal that the main characteristics of the adult pygidium of scutelluids are secondarily acquired during ontogeny. The future pygidium initially follows the classic, ancestral mode of development of all trilobites, resulting in a segmented axis. However, this initial developmental process is rapidly replaced by others that are specific to the Scutelluidae. Some of these specific developmental processes affect almost synchronously all segments of the future pygidium (e.g. disappearance of the axial segmentation, appearance of axial trilobation). Others act so precociously in ontogeny that as soon as pygidial segments appear on the dorsal exoskeleton, they exhibit characteristic features enabling their distinction from thoracic segments (e.g. width of the doublure; absence of pleural spines in *Meridioscutellum* and probably also *Scutellum*). In conclusion, the particular morphology of scutelluid trilobites results from a highly modified development, which has retained only the necessary basics for the creation of segmental units from the ancestral developmental mode.

FUNCTIONAL ANATOMY AND LIFE HABITS OF SCUTELLUIDS

In extant arthropods, a tagma is a region of the body which is not only distinct morphologically, but also aimed at the practise of a particular function. Evaluating the hypothesis of a third tagma in the scutelluids therefore requires investigations on functional consequences of the acquisition of its particular pygidial morphology.

An apparently negative outcome of the acquisition of the typical scutelluid morphology (i.e. the ‘flat’ morphotype) is the loss of the ability to perfectly enroll the body. Indeed, Whittington (1999) demonstrated that cephalon and pygidium could not fit edge-to-edge, because the two body parts were too different in length (sagittally) and the thorax was not flexible enough ventrally to compensate their low convexity. Accordingly, he proposed that ‘flat’ scutelluids might have enrolled following a cylindrical mode of enrollment, which implicates the presence of unprotected lateral areas (Whittington, 1999: fig. 8). Alternatively, these trilobites might have no more been able to put in contact their pygidium and cranidium, as no example of a completely enrolled flat scutelluid is known. In the vaulted scutelluid *Paralejurus*, a complete enrollment has once been observed in a juvenile specimen (Barrande, 1852: pl. 42, fig. 29), but no more than a limited ventral flexion has ever been described in adults (e.g. Schraut and Feist, 2004: fig. 6.3). The supposedly partially enrolled specimen of the 'flat' *Bojoscutellum* figured by Whittington (1999: figs. 6.5-7 and p. 426) exhibits in fact a faint ventral flexion of the thorax and its cephalon is dislocated. Thus, both direct (anatomic) and indirect (absence of known examples) evidences suggest that the ability of complete enrollment might have been lost in most scutelluids, although it occurs in their sister group, the Styginidae. Apparently, and in contrast to most trilobites, where the pygidial shape has a particular significance in the enrollment process, the derived morphology of the pygidium in scutelluids was, to some extent, responsible for diminished capacities of enrollment. Given the importance of enrollment in trilobites, it can be reasonably speculated that this particular pygidial morphology has been selected for some considerable adaptive significance, most likely related to functional properties.

Several authors have suggested that the pygidium might have acted as a paddle in 'flat' scutelluids effecting up and down motions (Selwood, 1966; Chatterton, 1971). However, using this extremely large pygidial shield (Selwood, 1966: p. 203) to propel the animal on long distances would have had an enormous energetic cost, if not assisted by undulations of the body and movements of the thoracic appendages. Maybe only few flips of the pygidium were exerted, so that the animal could rapidly move away from a threat. This would explain the loss of the defensive strategy represented by enrollment in this group. The small axis, the short axial rings (when present), and the wide pygidial doublure are all evidences for strongly reduced (if present) pygidial appendages, that were probably too weak to support the pygidium. Instead, this support might have been provided by strong longitudinal muscles inserted on the two longitudinal furrows of the axis. Indeed, the relative position on the axis of these latter is analogous to the location of muscles scars on pygidial axis of many trilobites. For instance, in *Kosovopeltis*, these 'furrows' often form two series of depressed and small circular areas similar to those generally attributed to muscular attachments (e.g. Ludvigsen and Tripp, 1990: pl. 2, fig. 12). If we admit that strong muscles (including longitudinal muscles) were inserted on the longitudinal furrows of the axis, these might have not only supported the pygidial shield but also enabled its up and down motions.

Other morphological features support the view that scutelluids might have been, to some extent, free-swimmers. Chatterton (1971) pointed out particularities of thoracic articulations that explain the extreme dorsal flexibility of this body part in scutelluids (personal observations). This ability for flexing the body ventrally but also dorsally would have enabled to produce undulation, enhancing the action of the pygidium. Scutelluids also often display hypostomes with maculae partially covered with more or less arranged tiny tubercles (e.g. *Meridioscutellum*). These latter resemble in cross-section the biconvex lenses of the dorsal eyes (Harrington, 1959). The presence of visual organs on the ventral side of the body can only be understood if these animals were able to move away from the substrate. Thus, the acquisition of a novel pygidial morphology in scutelluids might have been associated with an ecological shift from an epibenthic to a more necto-benthic life style. However, this can be reasonably speculated in the case of the 'flat', typical forms of scutelluids, but certainly not in the vaulted *Paralejurus*. In this latter, several lines of evidences more likely suggest an endobenthic life style and burrowing habits (Schraut and Feist, 2004). It is more hazardous to explain the life-style of spiny forms such as *Ancyropyge* and *Andegavia*. However, their peculiar morphologies of the pygidium clearly suggests that, if it had some function in swimming (propulsion, control, etc.) in the ancestors, it was no longer the case in these highly derived forms, which might have returned to a more epibenthic life habit.

SECONDARY EVOLUTIONS OF THE PYGIDIUM IN SCUTELLUIDS

Most scutelluids are characterized by a flat, entire-edged, large pygidium. The highly vaulted body of *Paralejurus* is apparently a secondary evolution, as this genus is clearly phylogenetically related to the other members of the Scutelluidae and likely represents a distinct subfamily (Schraut and Feist, 2004). In addition to the particular case of *Paralejurus*, three main evolutionary trends can be described in Early to Middle Devonian scutelluids. All three consist in the great development of spines but following different modes.

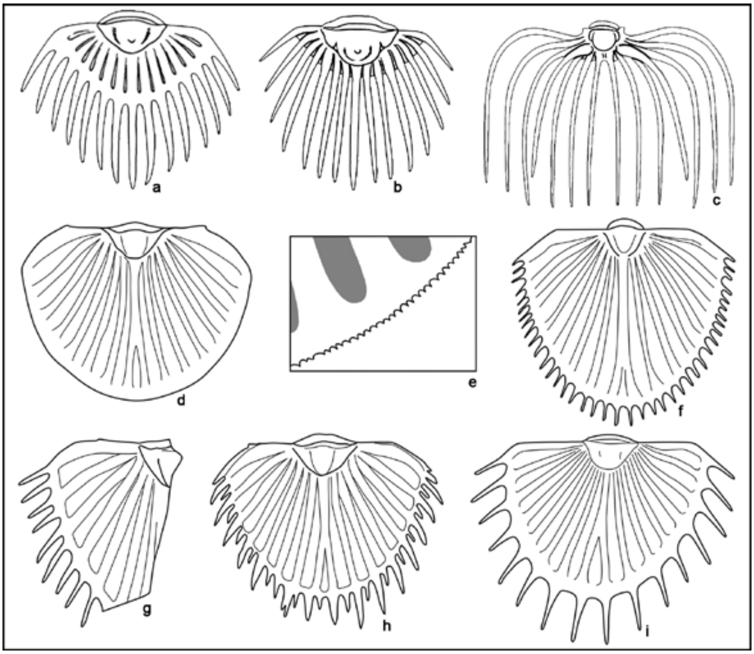

Figure 2. Morphological evolution of the pygidium in the *Weberopeltis* (a-c) and the *Thysanopeltis* (d-i) modes. a, *Exastipyx*. b, *Weberopeltis erbeni*. c, *Ancyropyge romingeri*. d-e, *Scabriscutellum hammadi*. d, General view. e, Detail of the margin. f, *Thysanopeltis speciosa*. g, *Thysanopeltella kerbelecensis*. h, *Septimopeltis trutati*. i, *Septimopeltis clementina.*

In the ***Weberopeltis* mode** overall size is maintained, but shape changes result from regression until complete disappearance of areas between pleural ribs (Erben, 1967; Fig. 2a-c). Theses latter extend into free spines far beyond the margin of the forwardly regressing platform. Whereas in *Exastipyx* this latter remains as long as the marginal spines (Fig. 2a), it becomes considerably reduced in other Early Devonian taxa (e.g. *Weberopeltis*, *Xyoeax*; Fig. 2b). In the Middle Devonian *Ancyropyge*, platform areas have completely regressed and free pleural spines directly project from the pygidial axis (Fig. 2c). However, the incompletely known cephalic morphology greatly varies from one taxon to another. Therefore, it is still not clear whether these spiny pygidial morphologies arose from iterative evolutions or if they really represent a straightforward evolutionary trend.

In the ***Thysanopeltis* mode** size and shape of the pygidial platform remain roughly unchanged (Erben, 1967 and data herein; Fig. 2d-i). Morphological changes affect the size, number, and disposition of spines along the pygidial margin. In initial stages, marginal spines are tiny, numerous (up to 120 in *Scabriscutellum hammadi*), and unrelated to pleural segmentation (Fig. 2d-e). Thereafter, they progressively increase in size while reducing in number (Fig. 2f). Further reduction in number proceeds by fusion of the spines, leading to configurations of spines related to the pleural segmentation in more derived taxa like *Thysanopeltella* and *Septimopeltis* (Fig. 2g-i). Interestingly, this modification of the pygidium, initiated in the *hammadi* group of *Scabriscutellum*, has not been associated to morphological changes on the cephalon and the thorax.

In the ***Kolihapeltis* mode** both size and shape are modified. The reduction of pleural field results from lateral compression, until a spine-like median rib remains (Fig. 3), proceeds as if a lateral compression occurs. With its slight inward flexion of the antero-lateral parts of the pleural field, the Emsian *Cavetia* may represent an earlier stage within this evolutionary trend (Fig. 3a). Within the Pragian genus *Kolihapeltis*, different pygidial morphologies can be observed from an elongated tongue shape (Fig. 3b-c) to a posteriorly pointed and laterally compressed lancet shape (Fig. 3d). In this latter, lateral ribs tend to become parallel to the median rib and to merge progressively with it posteriorly. In youngest representatives of the genus, this median rib already extends backwards in an extremely long spine (Fig. 3e). In the Emsian *Andegavia*, the postaxial pygidium is reduced to a single long medial spine, which is devoid of any traces rib differentiation. The cephala of all these taxa are nearly identical and also exhibit very long genal, occipital, and palpebral spines. However, morphological changes similar to those observed in the pygidium occur in the thoracic region. Thus, the shortening of adaxial parts of pleurae result in a thorax restricted to an axis with long, backwardly projecting pleural spines in *Andegavia*.

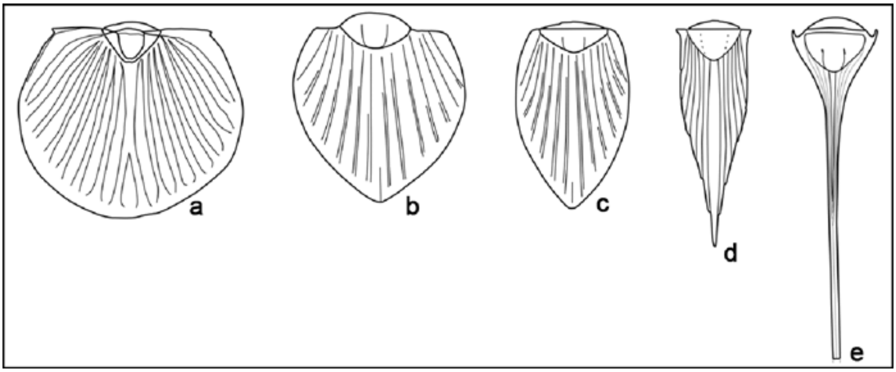

Figure 3. Morphological evolution of the pygidium in the *Kolihapeltis* mode. a, *Cavetia furciferum*. b, *Kolihapeltis briarea*. c, *Kolihapeltis magrebia*. d, *Kolihapeltis africana*. e, *Kolihapeltis titya.*

CONCLUSIONS

Ontogenetic data demonstrate that the development of the pygidium in scutelluids has been profoundly modified. Although speculative, our interpretations of the functional consequences of the acquisition of the scutelluid pygidial morphology suggest it has resulted in the gain and possibly also the loss of functional properties. Secondary evolution of the pygidium might have been concomitant with changes in the other body parts (*Paralejurus*; *Weberopeltis* mode), in the thorax only (*Kolihapeltis* mode), or completely independent of the rest of the body (*Thysanopeltis* mode). Considering all these elements, we conclude that the pygidium likely represented a morphologically and functionally differentiated body region or tagma in the Scutelluidae.

Acknowledgements

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DIGGING, SCRATCHING, AND WALKING IN THE STAIRWAY SANDSTONE OF CENTRAL AUSTRALIA: 'ARTHROPOD' ICHNOFOSSILS FROM THE ORDOVICIAN

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Keywords: Ichnofossils, Ordovician, Arthropoda, Australia.

INTRODUCTION

Recent fieldwork in the Amadeus Basin in central Australia yielded an abundance of trace fossils believed to have been made by various arthropods. The Stairway Sandstone is Darriwilian (Webby *et al.*, 2004) (Upper Llanvirnian to Llandeilian) and has been divided into three subunits: lower, middle and upper (Wells *et al.*, 1970). The traces collected are from the upper unit.

DISCUSSION

Numerous biogenic sedimentary structures occur in the uppermost unit of the Stairway Sandstone from the Ordovician of Australia. This poster is designed to illustrate the systematics of some of these traces and but steer away from proposing any particular organism as a producer of the traces. It should be noted that some trilobite fragments were found in association with the traces and they are of the appropriate size and shape to produce only some of the traces. As has been stated by numerous authors (Bromley and Fürsich, 1980; Ekdale *et al.*, 1984): "Identical structures may be produced by the activity of systematically different trace-making organisms, where behaviour is similar" (Kelly, 1990). With this said, Kelly (1990) pointed out that "ichnotaxa should be treated as non-biological form names *only* and their association with named organisms should be a matter of careful discussion, especially when there is no body fossil present. Even if there is a body fossil present, it may not be that of the original constructor". To follow that on "the nomenclature of trace fossils is based solely upon the morphological characteristics of the structure" (Kelly, 1990). Therefore, morphological characteristics required to produce the traces are considered. The behaviour of the organism responsible for the trace is indicative of digging, scratching and walking within or upon the substrate are subsequently preserved as casts. At this point, in my research, speculation as to what exactly the organism was doing: feeding, dwelling, resting, etc., will be left to subsequent research. These traces include a variety of ichnogenera, such as *Cruziana*, *Rusophycus* and *Monomorphichnus*.

CONCLUSIONS

The poster is meant to introduce the reader to 'arthropod' trace fossils from the Ordovician of central Australia and attempt to detach an organism from a particular trace. This is not to say that one cannot state the morphological characters that would be required to produce a trace and then propose possible candidates, this is a practice that should be encouraged.

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THE CAMBRIAN OF THE CADENAS IBÉRICAS (NE SPAIN) AND ITS TRILOBITES

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Keywords: Cambrian, stratigraphy, biostratigraphy, trilobites, Spain.

INTRODUCTION AND GEOLOGICAL SETTING

The Cadenas Ibéricas (Iberian Chains) are the two strings of Palaeozoic outcrops located in the central part of the Iberian System (NE Spain). The Cadena Ibérica Oriental is separated from the Cadena Ibérica Occidental by the Tertiary Calatayud continental basin. The Cadenas Ibéricas constitute a segment of the Hercynian fold-belt and their rocks are mainly deformed by the superposition of both Alpine and Hercynian orogenies. The Cadenas Ibéricas are separated from the Spanish segment of the Ibero-Armorican arch (i.e. the Iberian Massif) by Mesozoic and Cainozoic materials. Nevertheless, some of the tectono-stratigraphic zones of Lotze (1945) defined for the Iberian Massif may also be traced along the Cadenas Ibéricas. On the basis of tectonic, stratigraphic and palaeontological criteria, Gozalo and Liñán (1988) have suggested the prolongation of both the Cantabrian and West Asturian-Leonese zones trough the Sierra de la Demanda to the Cadenas Ibéricas (Fig. 1).

This structurally complex area has been divided into three geological units, from Southwest to Northeast are: Badules, Mesones and Herrera units (Lotze, 1929; Carls, 1983; Gozalo and Liñán, 1988). They are bounded by of two tectonic structures first order, the Jarque and Datos faults. The Badules unit shows a general sequence from late Neoproterozoic to early Ordovician rocks; these intensively faulted rocks dip primarily to the South. This unit shows a structure in nappes (Lotze, 1961; Liñán and Gozalo, 1986; Álvaro *et al*., 1992; Álvaro, 1994). The Mesones unit contains a folded stratigraphic sequence from late Neoproterozoic to Middle Cambrian rocks with a general dip to the North (Valenzuela *et al*., 1990). Finally, the Herrera unit shows a more complete and basically folded Upper Cambrian-Permian sequence.

STRATIGRAPHY

The Cambrian succession of the Cadenas Ibéricas (Fig. 2) is known through Lotze's work (1929) and was selected by Sdzuy (1971a, 1971b) as the reference section for the Spanish Lower and Middle Cambrian sequences because of their trilobite record. Since Lotze's study (1929), lithostratigraphic

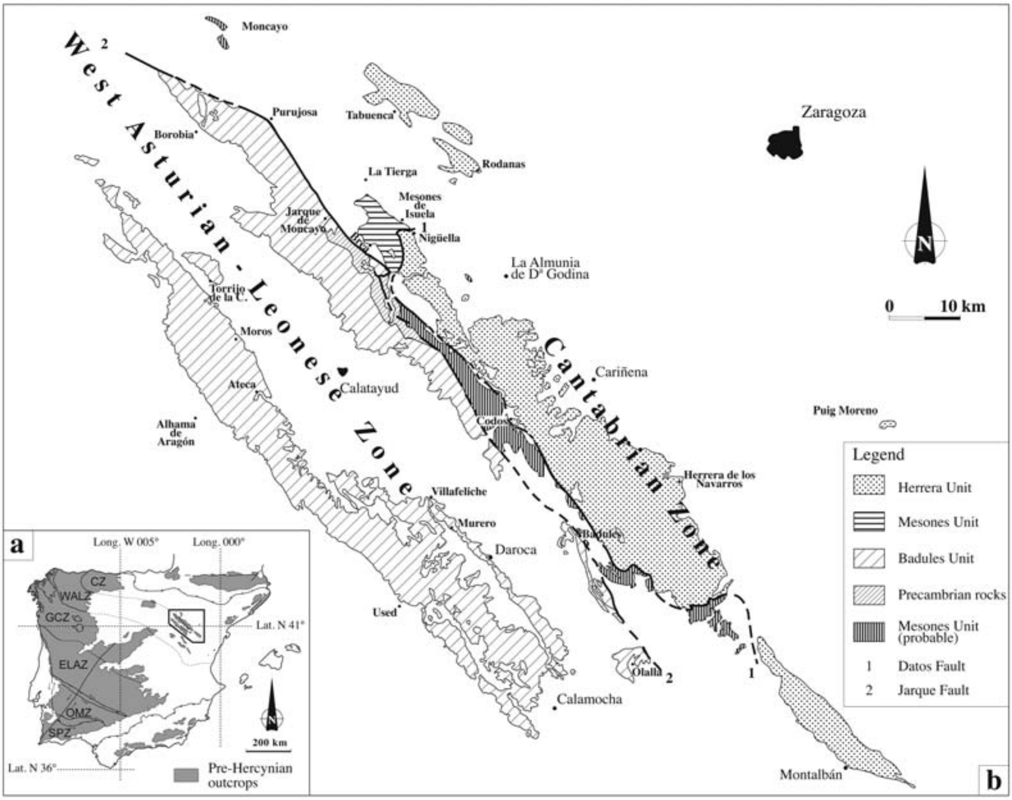

Figure 1. a, Pre-Hercynian outcrops and tectonostratigraphic zones of the Iberian Peninsula. The Iberian Chains are framed. Zones: CZ - Cantabrian, WALZ - West Asturian-Leonese, GCZ - Galician-Castilian, ELAZ - East Lusitanian-Alcudian, OMZ - Ossa-Morena, SPZ - South Portuguese. b, Pre-Hercynian outcrops and tectonostratigraphic zones and units of the Cadenas Ibéricas (from Gámez Vintaned, 2007).

nomenclature for the Precambrian and Cambrian rocks has been modified (Lotze 1958, 1961; Sdzuy, 1971a; Schmitz, 1971; Liñán and Tejero, 1988; Liñán *et al*., 1992; Álvaro, 1995), and was summarized by Gozalo (1995), Liñán *et al*. (1996a, 1996b, 2002, 2004) and Gozalo *et al*. (2004). The units along the Precambrian-Cambrian sequence are, in an ascending order: the Paracuellos Group, Bámbola Formation, Embid Formation, Jalón Formation, Ribota Formation, Huérmeda Formation, Daroca Formation, Mesones Group and Acón Group. This sequence shows plus 3,000 m thick with important fossiliferous levels consisting mainly of trilobites.

The Cambrian sedimentation of the Cadenas Ibéricas begun with the coarse sandstone and interbedded conglomerates of the Bámbola Fm; this unit lies unconformable on the Precambrian materials of the Paracuellos Gr. The Embid and Jalón Fms lie conformable on the Bámbola Fm; both formations are siliciclastic with sandstones and shales interbedded and the percentage of lutites increases towards the top; the first carbonate levels recorded appear in the Jalón Fm. The three first Cambrian formations were deposited after the Corduban regression, in a transgressive phase during the Corduban and Ovetian stages (see Liñán and Gámez-Vintaned, 1993; Liñán *et al.*, 2006). The fluvially influenced bottom of the Bámbola

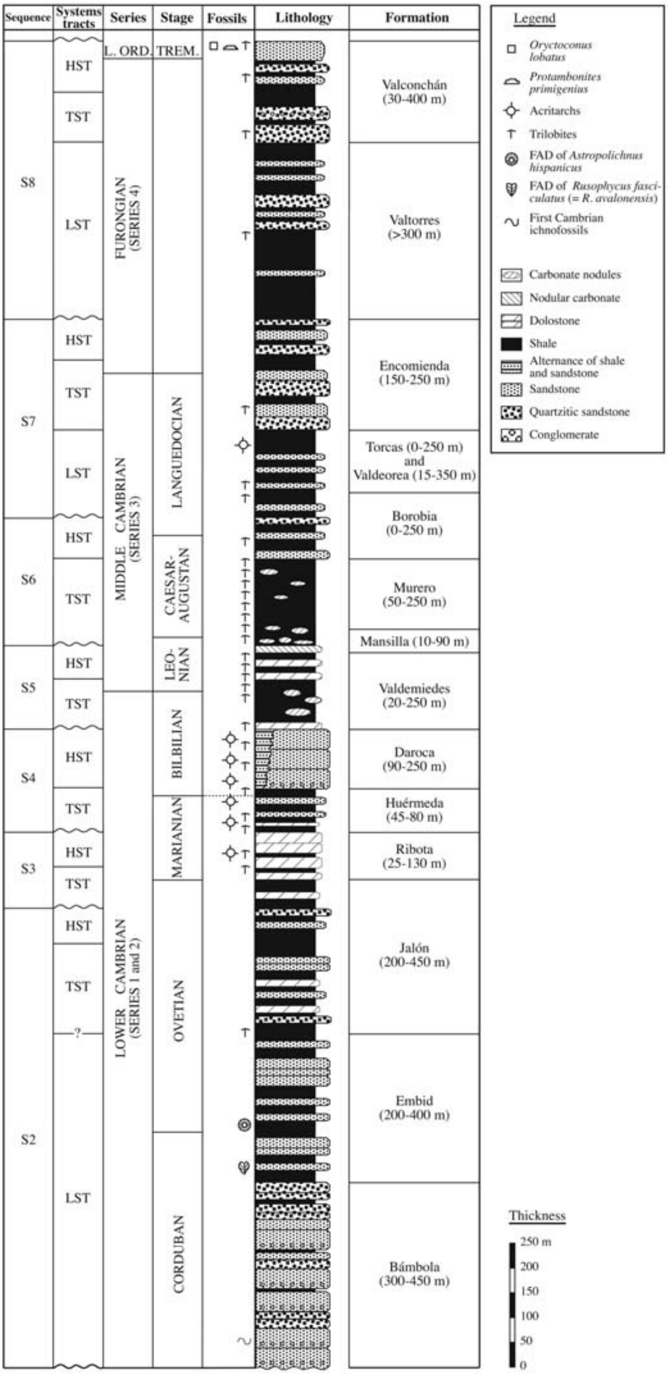

Figure 2. Cambrian stratigraphy of Cadenas Ibéricas and sequences recognised therein. Sequences after Schmitz (2006) and Gámez Vintaned *et al.* (in press).

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Fm evolved to shallow sublittoral conditions and, finally, to clearly sublittoral conditions in the base of Jalón Fm. The levels with stromatolites and mud cracks recorded in the upper part of the Jalón Fm indicate a littoral environment and it is considered as the beginning of another regressive pulse, that has been correlated with the Cerro del Hierro regression in the upper Ovetian (see Liñán and Gámez-Vintaned, 1993; Liñán *et al.*, 2006). The Jalón Fm shows red and violet colours and salt pseudomorphs that indicate arid conditions, which, in accordance with Sdzuy and Liñán (1993), were probably extended in the western Mediterranean area. The first trilobites (family Dolerolenidae) have been found in transitional beds between the Embid and Jalón formations indicating an upper Ovetian age (Sdzuy, 1987).

The Ribota Fm is a carbonate unit Marianian in age, which is composed of several metric levels of dolostones and limestones with lutites and marls intercalations. During the sedimentation of this formation, the environment changed from a littoral (sometimes supralittoral) environment in the bottom, with stromatolites and breccias, to a protected sublittoral environment, where invertebrate benthic communities could occasionally be developed (Álvaro *et al.*, 1995). Two successive trilobite assemblages are recorded in the shales; the first one is characterised by *Lusatiops ribotanus* and *Strenuaeva incondita*, and the second one contains *Kingaspis*, *Redlichia* and *Strenuaeva* species (Sdzuy, 1971a).

The overlying Huérmeda and Daroca Fms are siliciclastic. The first is mainly composed of lutites and siltstones, which were deposited in open sublittoral conditions during the upper Marianian times. Two trilobite assemblages have been described in the bottom of the formation. The assemblage of *Micmacca* aff. *coloi*, *Andalusiana*, *Strenuaeva incondita*, *Kingaspis (Kingaspidoides) velata*, *Redlichia* and *Triangulaspis* (Sdzuy, 1961, 1971a) suggests a Marianian age. The assemblage of *Strenuaeva* sp. and Protolenids (Sdzuy, 1971a) documents the disappearance of the Olenellids in Spain and indicates a Bilbilian age. The Daroca Fm (lower Bilbilian) supposed a new entry of coarse siliciclastic material to the basin; this formation shows important facies lateral changes, with coarse siliciclastic material southward and fine siliciclastic material northward (Álvaro and Vennin, 1998). The environmental conditions changed from a littoral with fluvial influences environment in the south to a shallow sublittoral environment in the north. Those shallow deposits marked the regressive phase of the lower Bilbilian named Daroca Regression, which has been correlated with the Hawke Bay Regression (Gámez *et al.*, 1991; Liñán and Gámez-Vintaned, 1993; Liñán *et al.*, 2006). The trilobites recorded in this formation are scarce: *Aragotus attacanus*, *Protolenus* sp., *Lusatiops* sp. and *Realaspis* sp.

The overlying Mesones Group (lower Bilbilian to upper Caesaraugustan/lower Languedocian) is composed of the Valdemiedes, Mansilla and Murero Fms. It is essentially composed of shales with carbonate nodules, dolostones and limestones interbedded, containing a rich assemblage of fossils, including Burgess Shale type fossils. These materials were mainly deposited in sublittoral environments (Sdzuy and Liñán, 1993). The middle part of the Valdemiedes Fm records the Valdemiedes Extinction Event (Liñán *et al.*, 1993a, 2002, 2006; Gozalo *et al.*, 1993b, 2007; Álvaro *et al.*, 1993). This global event is marked by a geochemical anomaly expressed in a pronounced $\delta^{13}C_{org}$ excursion, probably, coeval with the ROECE (Liñán *et al.*, in press). The first paradoxididis are recorded just above this event; they mark the base of Leonian stage (middle Cambrian) and the beginning of a new transgressive pulse. The top of Valdemiedes Fm and the bottom of Mansilla Fm coincide with the upper Leonian regression (Sdzuy *et al.*, 1999; Liñán *et al.*, 2002); the base of Mansilla Fm shows griotte facies, which were deposited in very shallow marine conditions and developped in perireefal environments. The Murero Fm shows a uniform sequence into a continue transgressive pulse, within a deep sublittoral environment, occasionally circalittoral. The trilobite biodiversity of the three formations is abundant in genera and species (see trilobite list).

The Acón Group (uppermost Caesaraugustan to Furongian) is characterized by a thick and conformable succession of siliciclastic rocks (Álvaro *et al*., 2007). The Acón Group conformably overlies the regionally diachronous top of the shaly green Murero Fm (Liñán *et al*., 2002, 2004), which marks the beginning of a new regressive pulse in the uppermost Caesaraugustan and lower Languedocian. Álvaro (1995) subdivided this group into five formations: Borobia, Valdeorea, Torcas, Encomienda and Valtorres formations. Shergold and Sdzuy (1991) summarized the biostratigraphic data and recognised six different assemblages, ranging from uppermost Languedocian to Furongian (former Upper Cambrian).

The Valconchán Fm consists mainly of quartzite with interbeds of mudstone deposited in littoral or shallow sublittoral environments. Trilobite and brachiopod faunas appear n the lower part of the formation and were considered Upper Cambrian in age by Shergold and Sdzuy (1991). At the top of this formation, there is another assemblage of trilobites, brachiopods and echinoderms which has been considered as either Upper Cambrian (Shergold and Sdzuy, 1991) or transitional Cambrian to Ordovician (Wolf, 1980; Villas *et al*., 1995; Álvaro *et al*., 2007).

BIOCHRONOLOGICAL FRAMEWORK

Using selected trilobite assemblages as chronomarkers, Sdzuy (1971a) defined three regional stages (in ascending order: Ovetian, Marianian and Bilbilian) for the Lower Cambrian of the Iberian Peninsula, and Sdzuy (1971b) proposed three informal Middle Cambrian stages (*Acadoparadoxides*, Solenopleuropsidae and Solenopleuropsidae-free stages). Liñán (1984) proposed the Corduban stage for the strata with Cambrian trace fossils that are overlain by rocks containing the first Ovetian fossil assemblages. These four regional stages were revised by Liñán *et al.* (1993b) using new data from trilobites, archaeocyatha and trace fossils. In the same paper, the Middle Cambrian stages were elaborated and the Leonian and Caesaraugustan were defined. Álvaro and Vizcaïno (1998) named the highest Middle Cambrian stage as Languedocian. Recent works on trilobite biochronology permit a more accurate zonation with trilobites (see figure 3).

TRILOBITES LIST

The list of trilobite taxa of the Cadenas Ibéricas has been extracted from several works: Richer and Richter (1948), Sdzuy (1958, 1961, 1971a, 1987), Liñán and Gozalo (1986, 1999, 2001), Valenzuela *et al*. (1990), Shergold and Sdzuy (1991), Gámez *et al*. (1991), Liñán *et al.* (1993a, 1993b, 1996b, 2003, 2004), Gozalo *et al*. (1993a, 1993b, 2003, 2007), Álvaro *et al*. (1993), Gozalo and Liñán (1996), Álvaro (1996), Sdzuy and Liñán (1996), Álvaro and Liñán (1997), Dies *et al*. (2001, 2004, 2007), Chirivella Martorell *et al*. (2003), Dies and Gozalo (2004, 2006). The specific names listed herein meet the last systematic proposals.

Transitional beds between the Embid and Jalón Fms (upper Ovetian)

Dolerolenus? sp. indet., *Anadoxides*? sp. indet., *Thoralaspis* n. sp. A.

Ribota Fm (Marianian)

Lusatiops ribotanus Richter and Richter, 1948, *Strenuaeva incondita* Sdzuy, 1961, *Kingaspis (Kingaspidoides) velata* Sdzuy, 1961 and *Redlichia* sp.

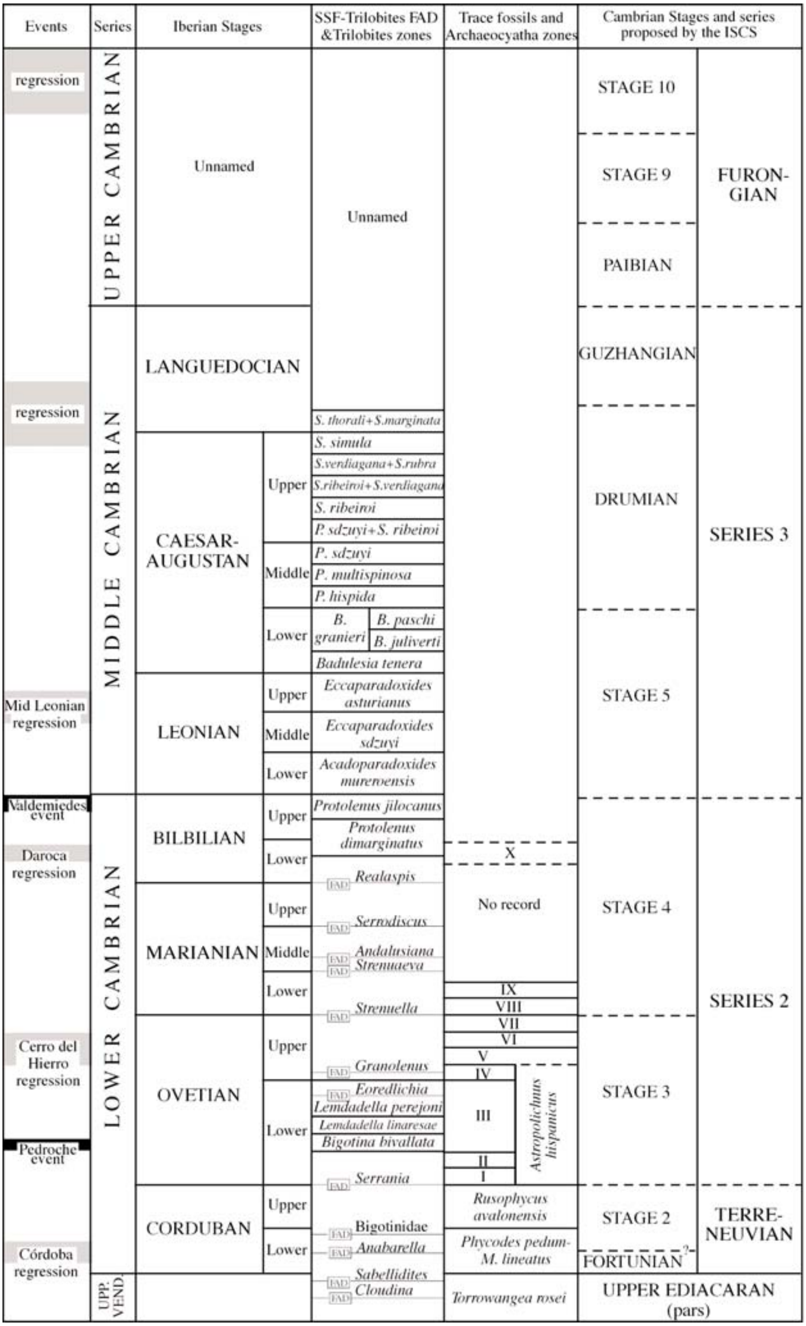

Figure 3. Cambrian chronostratigraphical and biochronological units in the Iberian Peninsula with the most relevant events and correlation with chronostratigraphical units proposed by the International Subcommission on Cambrian Stratigraphy (ISCS). FAD: first appearance datum; *B.*: *Badulesia*; *M.*: *Monomorphichnus*; *P.*: *Pardailhania*; *S.*: *Solenopleuropsis*; SSF: small shelly fossils.

Huérmeda Fm (Marianian)

Micmacca aff. *coloi* Hupé, 1953, *Andalusiana* sp., *Strenuaeva incondita*, *K. (Kingaspidoides) velata*, *Redlichia* sp. and *Triangulaspis* sp.

Huérmeda Fm (lower Bilbilian)

Srenuaeva sp., *Kingaspis (Kingaspidoides)* cf. *velata* and Protolenids.

Daroca Fm (lower Bilbilian)

Protolenus sp., *Realaspis* sp. and *Aragotus attacanus* Liñán and Gozalo, 2001.

Valdemiedes Fm (Bilbilian)

Protolenus termierelloides Geyer, 1990, *P. jilocanus* (Liñán and Gozalo, 1986), *P. dimarginatus* Geyer, 1990, *P. interscriptus* Geyer, 1990, *P. pisidianus* Dean *in* Dean and Özgül, 1994, *Hamatolenus (H.) ibericus* Sdzuy, 1958, *H. (Myopsolenus)* sp. A, *Kingaspis (K.) campbelli* King, 1923, *Alueva undulata* Sdzuy, 1961, *Sdzuyia sanmamesi* Liñán and Gozalo, 1999, *Tonkinella sequei* Liñán and Gozalo, 1999 and *Onaraspis altus* (Liñán and Gozalo, 1986).

Valdemiedes Fm (Leonian)

Acadoparadoxides mureroensis (Sdzuy, 1958), *Hydrocephalus* cf. *harlani*, *Eccaparadoxides sdzuyi* Liñán, 1978, *Hamatolenus (Lotzeia) lotzei* Sdzuy, 1958, *Alueva hastata* (Sdzuy, 1958), *A. moratrix* (Sdzuy, 1958), *Asturiaspis* sp., *Peronopsis* aff. *longinqua*, and *Condylopyge crucensis* Liñán and Gozalo, 1986.

Mansilla Fm (upper Leonian)

Eccaparadoxides asturianus Sdzuy, 1968, *E. sdzuyi*, *E. sulcatus* (Liñán and Gozalo, 1986), *Bailiaspis* aff. *tuberculata*, *Cainatops schirmi* (Sdzuy and Liñán, 1996), *Conocoryphe (Parabailiella) sebarensis* Sdzuy, 1968, *C. (P.) matutina* Sdzuy, 1968, *C. (P.) schmidti* Sdzuy, 1957, *Ctenocephalus* cf. *terranovicus*, *Holocephalina? leve* Liñán and Gozalo, 1996, *Asturiaspis inopinatus* Sdzuy, 1968, *Acadolenus* sp., *Parasolenopleura ouangondiana* (Hartt *in* Dawson, 1868) and *Peronopsella pokrovskajae* Sdzuy, 1968.

Murero Fm (Caesaraugustan)

Peronopsis acadica (Hartt in Dawson, 1868), *P. ferox* (Tullberg, 1880), *Peronopsella westergardi* (Sdzuy, 1968), *Condylopyge rex* (Barrande, 1846), *Corynexochus delagei* Miquel, 1905, *Eccaparadoxides sequeirosi* Liñán and Gozalo, 1986, *E. brachyrhachis* (Linnarsson, 1883), *E. pradoanus* Verneuil and Barrande, 1860, *Acadoparadoxides* sp., *Hydrocephalus donayrei* Liñán and Gozalo, 1986, *Badulesia tenera* (Hartt *in* Dawson, 1868), *B. granieri* (Thoral, 1935), *B. paschi* (Sdzuy, 1958), *Pardailhanica hispida* (Thoral, 1935), *P. multispinosa* Thoral, 1948, *P. sdzuyi* Liñán and Gozalo, 1986, *Solenopleuropsis ribeiroi* (Verneuil and Barrande, 1860), *S. truncata* (Sampelayo, 1935), *S. verdiagana* Sdzuy, 1958, *S. rubra* Sdzuy, 1958, *S. simula* Sdzuy, 1958, *S. marginata* Sdzuy, 1958, *S.* cf. *multigranifera*, *S. jarquensis* Álvaro, 1996, *S. vizcainoi* Álvaro, 1996, *Bailiaspis meridiana* Sdzuy, 1958, *Ctenocephalus antiquus* Thoral, 1946, *Conocoryphe (Parabailiella) languedocensis* Thoral, 1946, *C. (C.) heberti* Munier-Chalmas and Bergeron, 1889, *C. (C.) sdzuyi courtessolei* Liñán and Gozalo, 1986, *Agraulos longicephalus* (Hicks, 1872), *Skreiaspis* aff. *tosali* and *Jincella* sp.

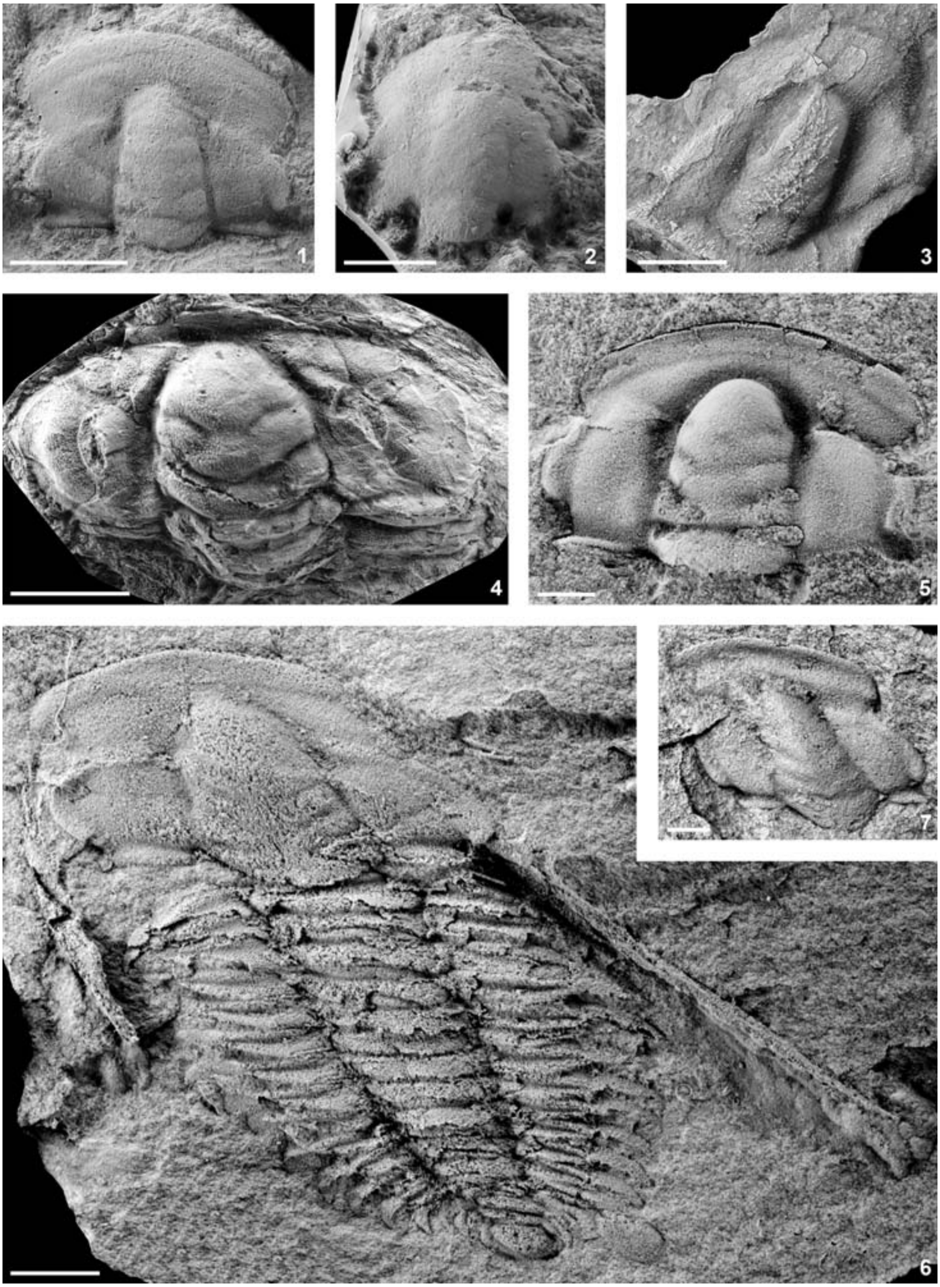

Plate 1. 1, *Lusatiops ribotanus*. Specimen MPZ 2005/91 (Museo Paleontológico de la Universidad de Zaragoza, Spain). Internal mould of cranidium. Scale bar = 5 mm. 2, *Kingaspis (Kingaspidoides) velata*. L 3230 (Lotze Collection, Universität Münster). Holotype. Latex replica of cranidium. Scale bar = 5 mm. 3, *Strenuaeva incondita*. SMF 11692 (Senckenberg Museum, Frankfurt). Holotype. Latex replica of cranidium. Scale bar = 5 mm. 4, *Aragotus attacanus*. MPZ 97/416. Cephalon and first thoracic segment of the holotype. Scale bar = 10 mm. 5, *Protolenus dimarginatus*. MPZ 01/100. Internal mould of cranidium. Scale bar = 2 mm. 6, *Hamatolenus (H.) ibericus.* MPZ 99/184. Complete specimen with the rigth librigena separated. Scale bar = 10 mm. 7, *Alueva undulata*. MPZ99/173. Internal mould of cranidium. Scale bar = 2 mm.

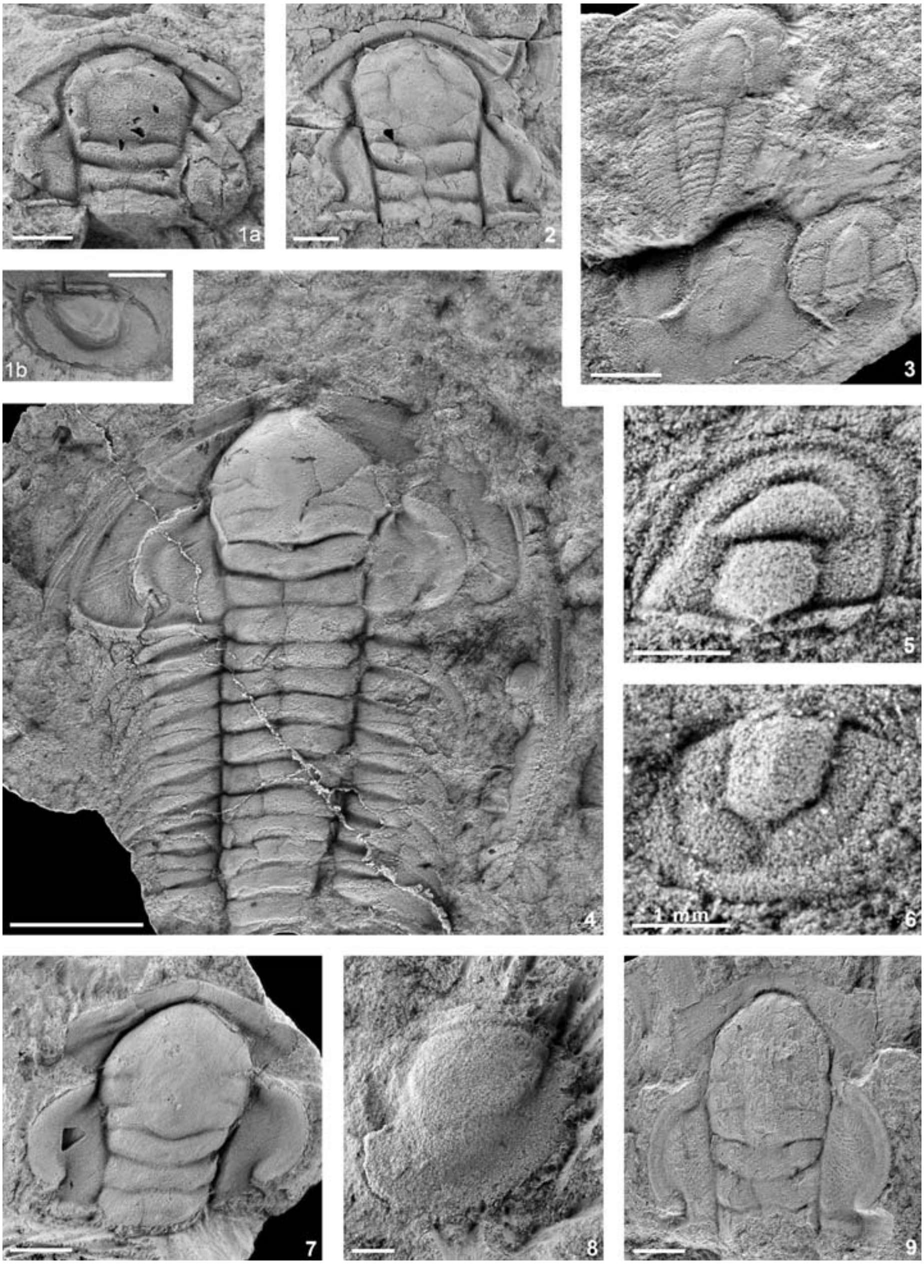

Plate 2. 1, *Acadoparadoxides mureroensis*. Specimen MPZ 2003/797 (Museo Paleontológico de la Universidad de Zaragoza, Spain). Internal moulds. 1a: cranidium; scale bar = 5 mm; 1b: pygidium; scale bar = 10 mm. 2, *Hydrocephalus* cf. *harlani*. MPZ 2004/96. Internal mould of cranidium; scale bar = 5 mm. 3, *Alueva hastata*. Specimens MPZ 2003/431 (upper one), MPZ 2003/432 (lower right) and MPZ 2003/433 (lower left). Internal mould. Scale bar = 5 mm. 4, *Eccaparadoxides asturianus*. MPZ 2007/559. Latex replica of cephalon and ten thoracic segments. Scale bar = 10 mm. 5, *Condylopyge crucensis*. MPZ 7826. Internal mould of cephalon. Scale bar = 1 mm. 6, *Condylopyge crucensis*. MPZ 804. Internal mould of pygidium. Scale bar = 1 mm. 7, *Eccaparadoxides sdzuyi*. MPZ 2007/604. Internal mould of cranidium. Scale bar = 5 mm. 8, *Eccaparadoxides sdzuyi*. MPZ 2007/615. Internal mould of pygidium. Scale bar = 2 mm. 9, *Eccaparadoxides sulcatus*. MPZ 2007/997. Internal mould of cranidium. Scale bar = 5 mm.

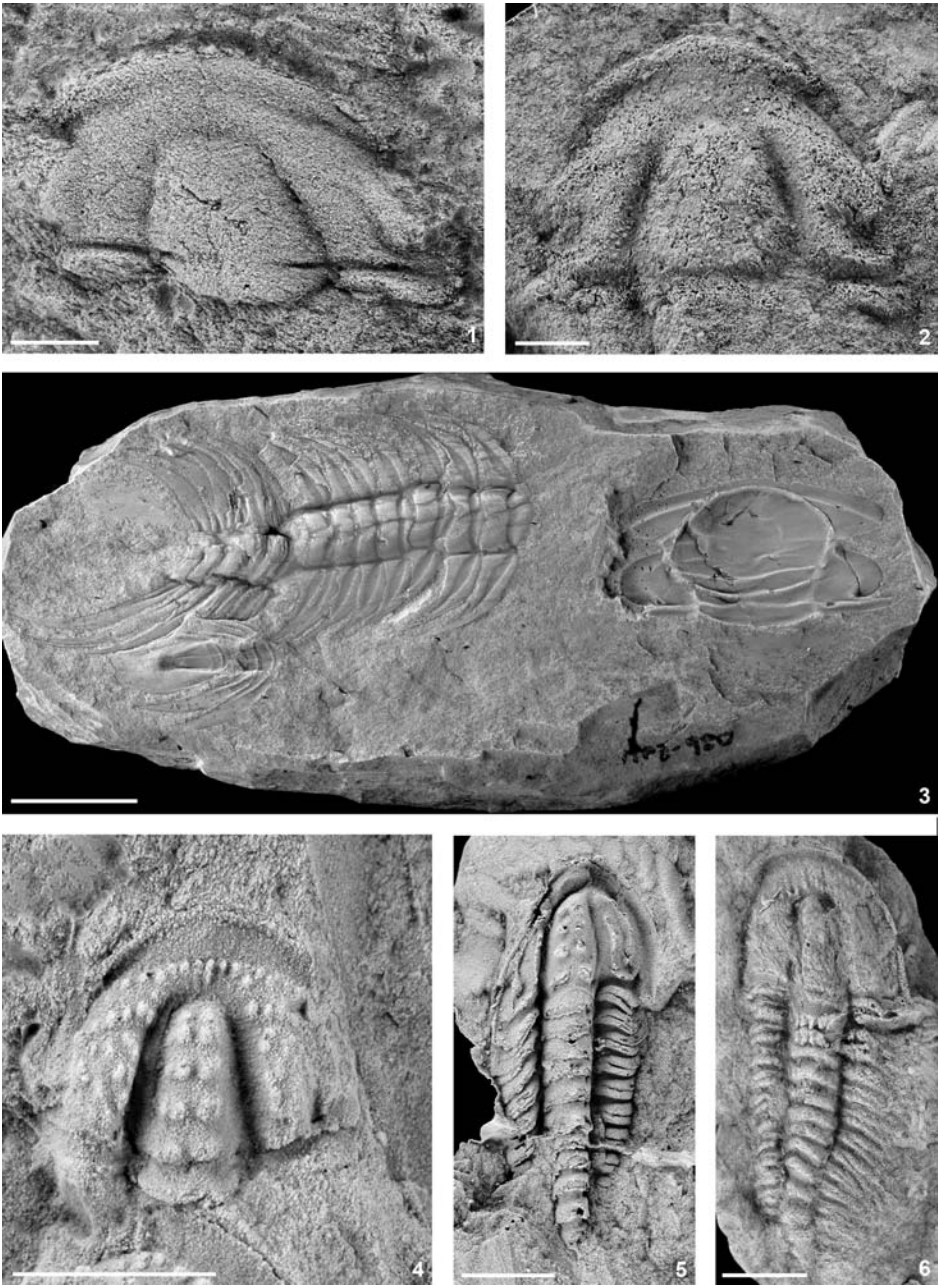

Plate 3. 1, *Asturiaspis inopinatus*. Specimen MPZ 2003/125 (Museo Paleontológico de la Universidad de Zaragoza, Spain). Internal mould of cranidium. Scale bar = 2 mm. 2, *Badulesia tenera*. MPZ 2007/1393. Internal mould of cranidium. Scale bar = 2 mm. 3, *Eccaparadoxides sequeirosi*. MPZ 980. Holotype. Internal mould of a molting specimen. Scale bar = 20 mm. 4, *Pardailhania hispida*. MPZ 3079. Internal mould of cranidium. Scale bar = 5 mm. 5. *Badulesia granieri*. MPZ 3072. Latex replica of a specimen without pygidium. Scale bar = 5 mm. 6, *Solenopleuropsis ribeiroi*. MPZ 2008/153. Internal mould of a specimen without pygidium. Scale bar = 5 mm.

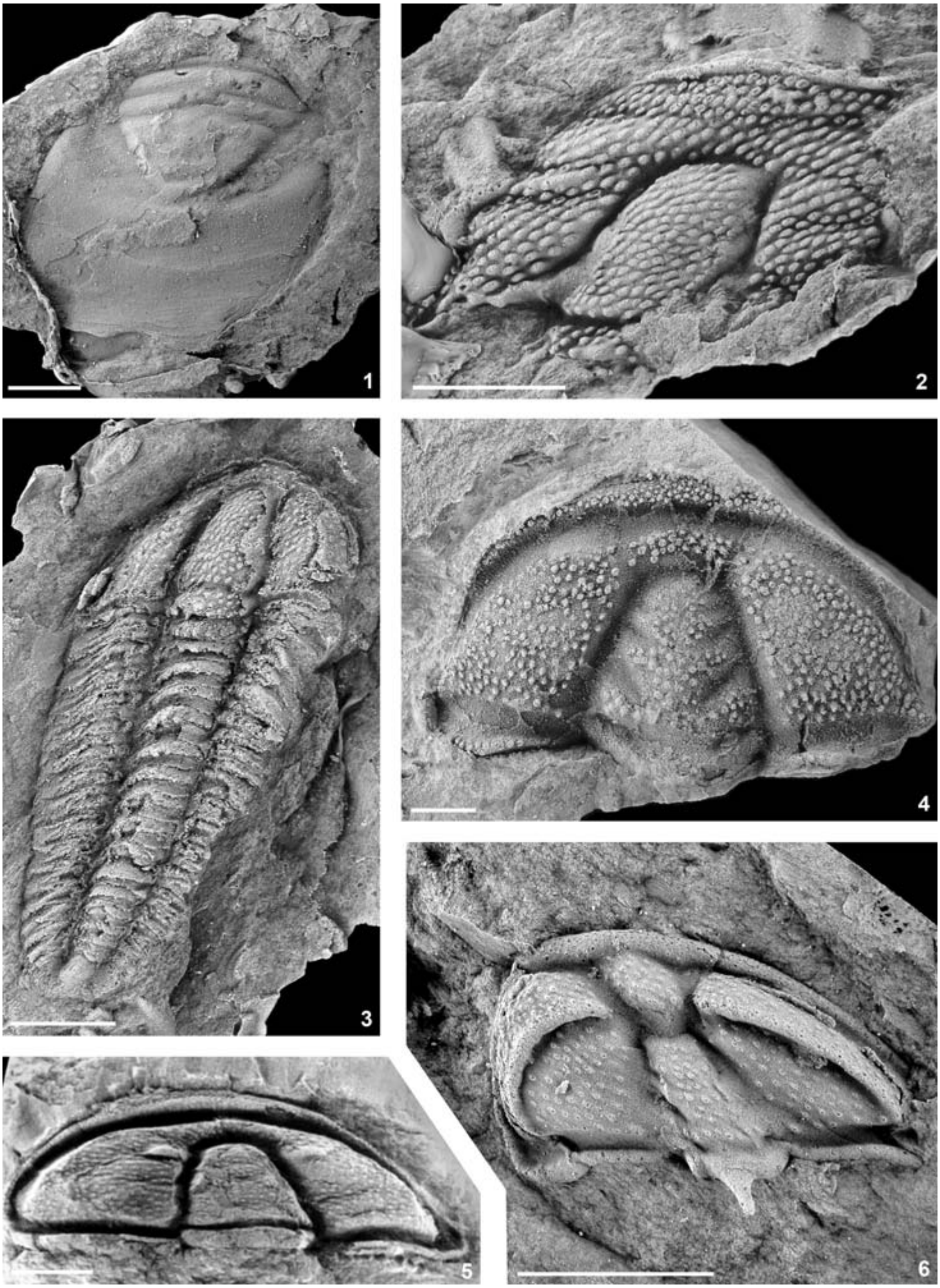

Plate 4. 1, *Eccaparadoxides melaguesensis*. Specimen MPZ 3044 (Museo Paleontológico de la Universidad de Zaragoza, Spain). Latex replica of pygidium. Scale bar = 5 mm. 2, *Solenopleuropsis simula*. MPZ 2008/155. Latex replica of cranidium. Scale bar = 5 mm. 3, *Solenopleuropsis thorali*. MPZ 2008/156. Latex replica of a complete specimen. Scale bar = 5 mm. 4, *Conocoryphe* (*Parabailiella) languedocensis*. MPZ 2008/154. Internal mould of cranidium. Scale bar = 5 mm. 5, *Conocoryphe (C.) sdzuyi courtessolei*. MPZ 3190. Holotype. Internal mould of cranidium. Scale bar = 10 mm. 6, *Ctenocephalus coronatus*. MPZ 2008/152. Latex replica of cranidium. Scale bar = 10 mm.

Acón Gr (Languedocian)

Peronopsis ferox, Eccaparadoxides brachyrhachis, E. melaguesensis Courtessole, 1973*, E. macrocercus* Courtessole, 1967*, Conocoryphe (C.) sdzuyi courtessolei, C. (C.) brevifrons* (Thoral, 1946) *C. (C.) ferralsensis* Courtessole, 1967*, Ctenocephalus* gr. *coronatus, Bailiella barriensis* Sdzuy, 1958*, B. levyi* Munier-Chalmas and Bergeron, 1889*, Solenopleuropsis marginata, S. thorali* Sdzuy, 1958, *Proampyx* sp. indet., *Parasolenopleura* n. sp.?, and *Solenopleura* s.l.

Acón Gr. and Valconchán Fm (Furongian)

Parachangshania? sp. indet., Aphelaspidinae aff. *Aphelaspis rara*, *Punctuaspis*? *schmitzi* Shergold and Sdzuy, 1991, *Valtorresia volkeri* Shergold and Sdzuy, 1991, *Elegantaspis* cf. *beta* and *Pseudagnostus (P.)* sp. indet.

Valconchán Fm (Tremadoc)

Pagodia (Wittekindtia) alarbaensis Shergold and Sdzuy, 1991 and olenid gen. et sp. nov (*Jujuyaspis*? sp. indet. *sensu* Shergold, 2000).

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EARLY ORDOVICIAN TRILOBITES FROM THE IBERIAN CHAINS, NE SPAIN: A TRIBUTE TO WOLFGANG HAMMANN

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INTRODUCTION

Wolfgang Hammann was a tireless palaeontologist who focused his research, among other topics, on the Ordovician trilobite biodiversity patterns and stratigraphy of southwestern Europe. When he passed away prematurely on 23rd September 2002 (see summarized biographies in Serpagli, 2003; Villas, 2005) he had recuperated the trilobite collections made by PhD students from the universities of Würzburg and Münster (Germany) in the Lower Ordovician of the Iberian Chains. The revision of this collection was still ongoing when our colleague died in the Carnic Alps. An unfinished manuscript found in his computer has been completed by the junior co-authors of this contribution and its preliminary implications are presented herewith.

STRATIGRAPHY

In the Iberian Chains the stratigraphic succession between the fossiliferous middle Cambrian strata (the Murero Formation) and the Armorican Quartzite comprise a thick (3600-4500 m) alternation of sandstones/quartzites and shales relatively poor in fossils. This succession has been given numerous lithostratigraphic names; we here subdivide it into the Acón and Ateca groups (after Álvaro, 1995), the latter containing the Valconchán, Borrachón, Dere and Santed formations (Wolf, 1980). The Acón and Ateca groups broadly correspond to the Iberian 'Series' of Schmitz (1971) and Josopait (1972). The trilobites on which this work is based were sampled in the Borrachón, Dere, Santed and Armorican Quartzite formations, among others, by Scheuplein (1970), Schmitz (1971), Josopait (1972), Wiemer (1975), and Wolf (1980).

The Borrachón Formation, 320-900 m thick, comprises mainly shales with minor sandy intercalations, which have yielded trilobites, linguliformean brachiopods, acritarchs and ichnofossils. The overlying sandstones and quartzites of the Dere Formation, 420-850 m thick, contain linguliformean brachiopods, trilobites and acritarchs, and are covered by the shale-dominated Santed Formation (200-950 m thick), which has yielded trilobites. Finally, the overlying Armorican-Quartzite Formation, 450-650 m thick, consists of two units rich in thick-bedded quartzites and sandstones with rare brachiopods, conularids, bivalves and trilobites (Babin and Hammann, 2001), separated by a shale-dominated middle part. Wolf (1980) subdivided the formation into three members.

Two volcanic episodes are recorded in the Lower Ordovician of the Iberian Chains: (i) a succession of Tremadocian-earliest Floian, eruptive felsic products, expelled explosively and characterized by the onset of rhyolitic and dacitic tuffs embedded in the Borrachón and Santed formations; and (ii) a Floian, effusive basaltic volcanic episode, represented by a single lava flow embedded in the Armorican Quartzite. The felsic explosive tuffs are associated with two ecosystem disturbance events: (i) a short-term colonization event of opportunistic linguliformean brachiopods that proliferated in the aftermath of a multi-event rhyolitic pyroclastic surge deposit; and (ii) several single-event mass-mortality horizons associated with dacitic pyroclastic flows responsible for the preservation of high-diverse allochthonous coquinas. The biodiversity patterns achieved by the benthic communities preserved in the poorly fossiliferous, siliciclastic strata of the Iberian Chains are, as a result, strongly biased by the presence of these interbedded skeletal tuffs (Álvaro *et al*., in press).

TRILOBITE ASSEMBLAGES

At least 15 families of trilobites are represented in the fossil record of the Borrachón, Dere, Santed and Armorican Quartzite formations, among which are: agnostoids (*Geragnostus*, *Micragnostus*, and *Leiagnostus*), leiostegiids (*Brackebuschia*), eulomids (*Euloma*), shumardiids [*Shumardia* (*Conophrys*)], olenids (*Angelina*, *Beltella*, *Hypermecaspis*, and *Leptoplastides*), bathycheilids (*Parabathycheilus* and *Prionocheilus*), asaphids (*Asaphellus*), dikelokephalinids (*Asaphopsoides*, *Dactylocephalus*, *Dikelokephalina*, *Megistaspis*, and *Niobe*), ceratopygids (*Ceratopyge* and *Macropyge*), remopleurids (*Apatokephalus*), nileids (*Symphysurus*), taihungshaniids (*Asaphelina*), orometopids (*Orometopus*), and phacopids (*Anacheirus*).

From a biostratigraphic point of view, the Lower Ordovician strata of the Iberian Chains can be correlated with the (regional) biostratigraphic chart proposed for the southern Montagne Noire, southern France, by Vizcaïno *et al*. (2001) and Vizcaïno and Álvaro (2003). The utility outside the Montagne Noire of this early Ordovician zonation is in some cases difficult due to trilobite endemism at species level, ranging from 33-36% in the Tremadocian to 71-91% in the Floian (Vizcaïno and Álvaro, 2003). Despite this palaeobiogeographic constraint, three Lower Ordovician biostratigraphic units of the southern Montagne Noire can be tentatively recognized in the Iberian Chains: the *Shumardia* (*C.*) *pusilla* Zone, the *Euloma filacovi* Zone, and the *Asaphelina barroisi berardi* + *Taihungshania miqueli* subzone.

The presence of several species of *Shumardia* (*Conophrys*) in the Borrachón Formation allows identification in the Iberian Chains of the *Shumardia* (*C.*) *pusilla* interval Zone, a unit recognized in the Montagne Noire both in limestones (Mounio Formation) and shales (lower part of the Saint-Chinian Formation). Recently, a diverse conodont fauna belonging to the *Paltodus deltifer* Zone has been discovered both in the interbedded limestones of the Val d'Homs and Mounio formations (Álvaro *et al*., 2007; Serpagli *et al*., 2007). This conodont zone includes, at least, the lower part of the *Shumardia* (*C.*) *pusilla* Zone.

The *Euloma filacovi* interval Zone of the French Saint-Chinian Formation contains two different trilobite assemblages that have never been found together in a same section (Vizcaïno and Álvaro, 2003). The assemblages were previously reported as distinct 'faunizones' (or informal units sharing litho- and biostratigraphic features), named *E* and *F* by Capéra *et al*. (1975) and Dolambi and Gonod (1992). Based on the presence of *Apatokephalus serratus* (also found in Scandinavia; Tjernvik 1956), Capéra *et al*. (1978) suggested that 'faunizone' *E* is of late Tremadocian age, although this inference needs confirmation. Trilobites of the *Euloma filacovi* Zone occurring both in the Montagne Noire and the Santed Formation of the Iberian Chains are *Asaphelina barroisi barroisi*, *Megistaspis* (*E.*) *filacovi* and *Prionocheilus languedocensis*. Another common trilobite is the agnostoid *Geragnostus crassus*, which occurs in the *Euloma filacovi* Zone and the *Asaphelina barroisi berardi* + *Taihungshania miqueli* subzone of Montagne Noire (Tortello *et al*., 2006), and in the Santed Formation of the Iberian Chains. Although the presence of *Taihungshania* was considered as indicative of an early 'Arenig' age (Capéra *et al*., 1978), this correlation also needs confirmation. As a result, the Tremadocian-Floian boundary cannot be identified with precision neither in the Iberian Chains nor the southern Montagne Noire.

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MID TO LATE ORDOVICIAN TRILOBITE PALAEOECOLOGY IN A MUD DOMINATED EPICONTINENTAL SEA, SOUTHERN NORWAY

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Keywords: Trilobite ecology, Darriwilian, Sandbian, Southern Norway.

INTRODUCTION

Trilobite ecology has been studied for decades (e.g. Fortey, 1975; Fortey and Barnes, 1977; Ludvigsen, 1978; Nielsen, 1995; Waisfeld *et al.*, 2003), providing a general knowledge on the palaeoenvironmental preferences of various trilobite taxa. Few authors, however, have been able to study the spatial distribution of trilobite assemblages and how these were affected by temporal changes in the environment due to physical factors such as sea-level and hydro dynamics.

The relatively thin (less than 100 metres thick) upper Middle to lower Upper Ordovician strata of southern Norway were deposited in a small sub-basin and offers with their easy accessibility and nearly complete fossil record through at least one major sequence cycle a unique possibility unravelling which physical factors that had the largest impact on the composition of the trilobite community.

GEOLOGICAL SETTING

The present study focuses on the upper Middle Ordovician to lowermost Upper Ordovician Elnes Formation of the Oslo area, southern Norway. This formation is a fully marine deposit dominated by concretionary siliciclastic clays and silts. It is the limestones of the Huk and Stein formations and is in turn overlain by concretionary marls and limestones representing the Vollen and Fossum formations.

During the Mid Ordovician Southern Norway was situated on the north-eastern margin of the small continent Baltica. The area was shielded from the Iapetus Ocean by a north-western island chain or land area, which was also the main sedimentary source (Fig. 1). The land area was separated from the main Baltoscandian carbonate platform by a WSW-ENE running foreland trough with dysoxic bottom conditions, effectively preventing most bottom dwelling animals from crossing during highstand periods (Bockelie and Nystuen, 1985; Nilssen, 1985; Hansen, *submitted*). The depositional environment was in contrast to the carbonate dominated, shallow water platform interior characterised by mainly siliciclastic clays and silts deposited in fairly quiet water well below fair weather wave base. Limestones and concretionary marls were deposited during lowstands, while fine-grained turbidites formed at certain intervals during the whole period, but especially in connection with the initial phase of the end Darriwilian sea-level fall. The water depth probably changed between something like 30 metres to perhaps more than 200 metres during the middle Darriwilian highstand (Hansen *et al.*, in prep.). At no time did the water temperature reach the threshold for chemical precipitation of carbonates, likely reflecting that a warm temperate climate prevailed (Jaanusson, 1973). The Cambro-Silurian deposits were later trusted and folded in connection with the Caledonian Orogeny.

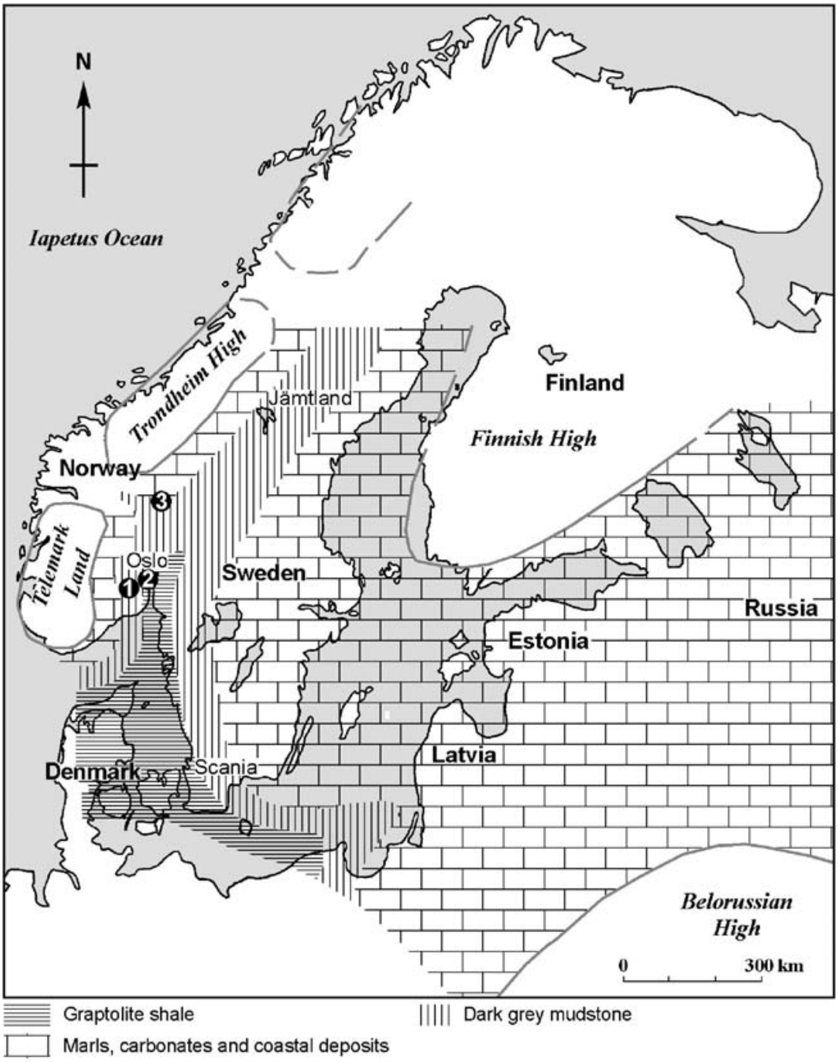

Figure 1. Lithofacies map of the mid Darriwilian epicontinental deposits in Baltoscandia showing the approximate distribution of the different sedimentary environments. The figure is based on data presented by Männil (1966), Jaanusson (1973), Nilssen (1985), Pålsson *et al.* (2002) and Hansen *et al.* (*in prep.*). The three main localities herein are indicated by numbers. 1, Råen at Fiskum, Eiker-Sandsvær district. 2, Slemmestad, Oslo-Asker district. 3, Nydal just north of Hamar, Mjøsa districts.

LOCALITIES AND METHODS

Three localities representing a south-north transect of the Oslo Region have been studied in detail. The southernmost succession is exposed at Råen west of the Fiskum Lake in the Eiker-Sandsvær district. The succession, which is pieced together from several exposures, is cut by a few faults but otherwise almost untectonized. The succession straddles the Huk and overlying Elnes Formation and even the base of the Fossum Formation at the top. The main profile investigated in this study is situated at Slemmestad in the central Oslo Region, and a nearly complete section through the Elnes Formation together with the uppermost Huk Formation and basal Vollen Formation. The rocks are relatively unmetamorphosed, although calcite shells typically have been dissolved during late diagenesis. A relatively fresh road-cut along highway E6 between Nydal and Furnes was sampled. The measured lower part of the profile represents the top of the Stein Formation equalling the basal part of the Elnes Formation further south. The rest of the profile exposes parts of the lower, middle and upper Elnes Formation. The exposure is disrupted by two large faults and the mudstone is completely tectonized, destroying all fossils, except those preserved within the concretions.

All three localities have been logged in detail and fossils were collected centimetre by centimetre. The relation between lithofacies and fossil content was investigated by compiling species data for each lithofacies and analysing the results using multivariable Principal Components Analysis available in the PAST computer program (Hammer *et al.*, 2001).

PALAEOENVIRONMENTAL DISTRIBUTION OF THE FAUNAL ASSOCIATIONS

The trilobite taxa form a number of associations or sub-associations, all being dominated by asaphid trilobites. The faunal associations exhibit a well-defined linkage with specific lithofacies, suggesting a strong palaeoenvironmental control on their distribution. Broadly speaking, they seem to reflect a depth transect as illustrated Fig. 2 for the Slemmestad locality.

In the most shallow water deposits limestones and concretionary marls the trilobites are dominated by representatives of *Asaphus* and *Megistaspis*, but also other forms like cheirurids, *Scotoharpes* and *Pliomera* occur. The limestones, which are also rich in partly current-orientated endoceratid cephalopods, probably represent a moderately energy-rich and well oxygenated environment where bottom waters were agitated above an early lithified carbonate substrate.

The marly sediments reflects a and slightly more soft-bottomed environment, still characterized by well oxygenated bottom waters. This was inhabited by an *Asaphus*-*Megistaspis*-*Illaenus* association completely dominated by the genus *Asaphus*. *Illaenus* was found only at the northern locality.

Sea-wards this fauna changed gradually into one dominatedby *Nileus*, raphiophorids and deeper water asaphids like *Ogygiocaris* and *Pseudomegalaspis*. They seem to have preferred an environment with a soft mud-marl substrate and fairly oxygenated but quiet bottom waters just above the storm wave base. The trilobite fauna is very diverse and the environment was probably also characterised by a moderately rich infaunal life as indicated by the strong bioturbation with trace fossils like *Planolites* and large *Chondrites*. The substrate shifted rapidly to dark grey siliciclastic mud deposits, reflecting less oxygenated bottom waters below storm wave base. The benthic faunas inhabiting this environment are low diverse and mainly dominated by brachiopods. Among trilobites the asaphids dominate. They occur in association with a few trinucleids and pelagic trilobites such as *Robergia* and *Sculptaspis*. The larger infauna disappeared due to

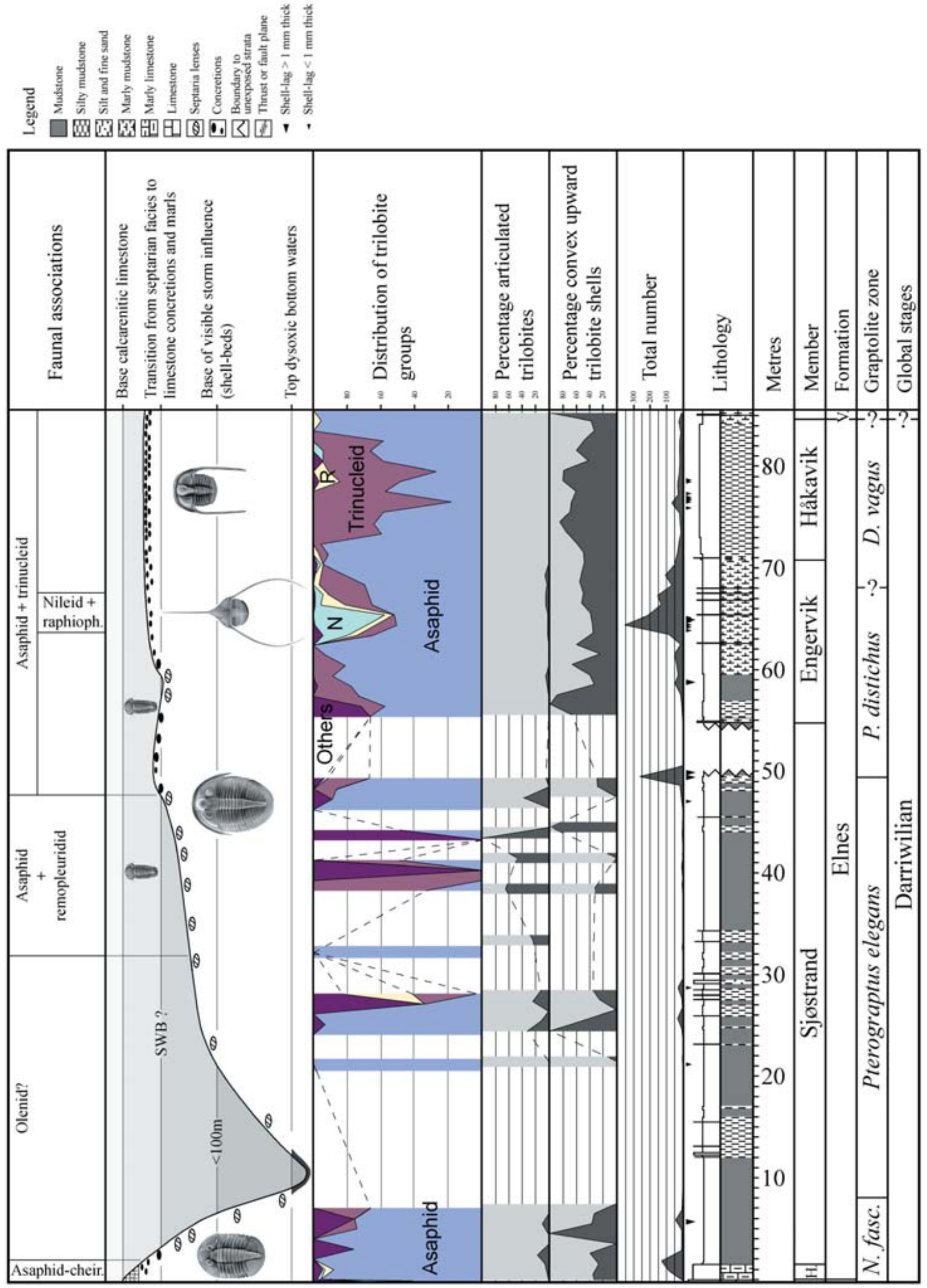

Figure 2. Distribution of trilobite groups in the Elnes Formation at Slemmestad, central Oslo Region. The percentages for articulated trilobites and orientation are given as an indicator of energy and current activity at the sea bottom. The small arrows along the lithological log indicate shell beds. N = *Nileus*; R = *raphiophorids*; SWB = *Storm Wave Base*; H = *Helskjer*; V = *Vollen*. N. fasc. = *Nicholsonograptus fasciculatus*; P. *distichus* = *Pseudamplexograptus distichus*; D. *vagus* = *Dicellograptus vagus*.

the dysoxic conditions within the sediment, but the sediments are still homogenised, likely reflecting the continued presence of smaller infauna. The near absence of trilobites is most likely due to the combined effects of a starved food-supply as well as low oxygen levels. The trilobites disappear completely in the most deep water setting characterised by dysoxic bottom water conditions and a related lack of infauna.

The silty turbidite settings are inhabited by a *Botrioides*-asaphid association, but in general the presence of turbidites is associated with a lowering in the trilobite diversity, probably due to stress.

REMARKS AND DISCUSSION ON FAUNAL ASSOCIATIONS

Numerous studies on Early Palaeozoic faunal associations and assemblages have been published (e.g. Fortey, 1975, 1980; Fortey and Barnes, 1977; Fortey and Owens, 1978, 1987; Ludvigsen, 1978; Nielsen, 1995; Pålsson *et al*., 2002). Higher taxa apparently exhibit a surprisingly large consistency with regard to preferred facies type and environmental settings, although species and genera obviously vary over space and time.

With regard to the trilobites, neither the shallow water pterygometopid-cheirurid-encrinurid association of Fortey (1975, 1980) and Ludvigsen (1978), nor the illaenid-lichid-telephinid-harpid biofacies of Ludvigsen (1978), said to characterize the middle to deeper carbonate platform of central Canada, are really present in the late Darriwilian depositional environment of the Oslo Region, although representatives of these associations may be found on the main carbonate platform further to the east (Schmidt, 1885, 1894; Holm, 1886; Jaanusson, 1957). Their scarcity in the Oslo Region, where even the most shallow water deposits are dominated by asaphids, is most likely related to the softer mud substrate and lower energy levels and perhaps also due to greater water depth and lower oxygen levels even at the time of local carbonate sedimentation.

The Elnes Fm of the Oslo Region is dominated by the Asaphid-trinucleid Association which quite closely corresponds to the nileid community of Fortey (1975) and resembling fossil associations elsewhere (Biofacies 4, the raphiophorid-trinucleid assemblage, the trinucleid biofacies or the raphiophorid community of Fortey (1975, 1980), Fortey and Barnes (1977), Fortey and Owens (1978, 1987), Ludvigsen (1978), Nielsen (1995), Zhou *et al*. (1998) and Pålsson *et al*. (2002). The listed fossil associations mainly comprise raphiophorids, nileids, asaphids and trinucleids and are thus corresponding very well with the Asaphid-trinucleid Association dominating most of the Elnes Formation, but they are typically associated with dark flaggy limestones to fine-grained clastic sediments representing proximal outer shelf to upper slope environments, whereas the Norwegian Asaphid-trinucleid Association lived in a mid shelf environment above storm wave base, probably in water depths of no more than 50 to 80 metres at the most (Hansen *et al*., *in prep*.). The local absence of this fossil assemblage further down-slope was probably because of a rapid decline in the oxygen level making it impossible for the infauna and larger benthic taxa to survive in deeper water.

In the present study raphiophorids and nileids are found within the Asaphid-trinucleid Association. They seem to form their own sub-association, but what precisely controlled their appearance is unclear as they are found in slightly different litho-facies and at quite deviating stratigraphical levels between the southern and northern Oslo Region. Raphiophorids are also common in parts of the slightly older Komstad Limestone Formation of Scania (Nielsen, 1995), but neither here does the material reveal a correlation with specific water depths.

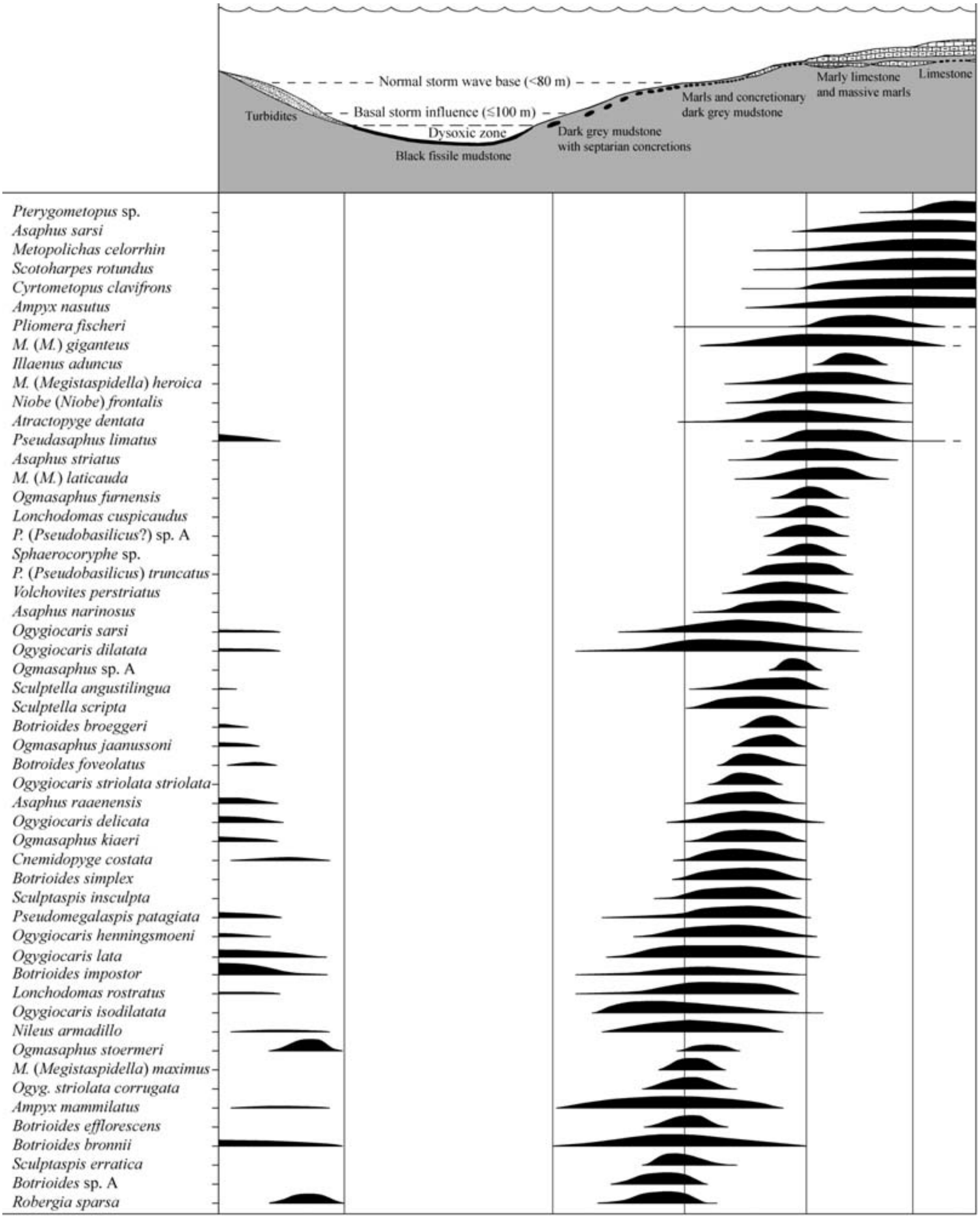

Figure 3. Summary figure showing inferred relation between faunas and palaeoenvironment.
Figure modified from Hansen (*submitted*).

Both Fortey (1975) and Månsson (in Pålsson *et al*., 2002) distinguish an olenid community, which down slope of the Asaphid-trinucleid Association defined here. For reasons unknown, olenids are very rare in the Oslo Region of southern Norway and have only been observed in the northernmost part, even though unmistakeable deep water facies are present in the central Oslo Region around Slemmestad. Olenids are also reported from Jämtland, central Sweden (Pålsson *et al*., 2002). Their presence in the northern district and Jämtland could somehow be related to the more open oceanic influence seen in these northern regions as interpreted by the local appearance of the Laurentian and cosmopolitan genera *Cybelurus*, *Primaspis*, *Robergiella*(?), *Raymondaspis* (*Turgicephalus*) and a carolinid trilobite found in the Mjøsa district, all of them absent further south (Hansen, *submitted*). The species of *Raymondaspis* (*Turgicephalus*) may actually originate from Baltica, as representatives of this subgenus are fairly common in older Baltoscandian deposits (Nielsen, 1995), and as it furthermore does not seem conspecific with the insular representative from the Otta Conglomerate north-west of the Oslo Region. Even so its strongly restricted geographical and stratigraphical appearance in the Baltoscandian deposits may suggest a peri-continental origin, thereby the suggested oceanic influence of the northern Oslo Region.

Alternatively it is possible that the thin-shelled olenid trilobite remains have been dissolved in the variably dysoxic environment in a similar manner of that described by Schovsbo (2001) from the Cambrian Alum Shale, but this is regarded less likely.

CONCLUSIONS

An extensive fossil material from the Elnes Formation and the very top of the Huk Formation, sampled at three stations in the Oslo Region representing a north-south transect of the area, reveals the general preferences of various trilobite taxa as summarized in figure 3 and facilitates recognition of a number of depth- or substrate dependent fossil associations. The overall compositions of the defined fossil associations agree well with those described by Fortey (1975, 1980), Fortey and Barnes (1977), Fortey and Owens (1978, 1987), Ludvigsen (1978), Nielsen (1995), Zhou *et al*. (1998) and Pålsson *et al*. (2002) from Lower Palaeozoic successions elsewhere.

In the most shallow water palaeo-environment, represented by the calcarenitic uppermost part of the Huk Formation and the marls of the Helskjer Member of the basal Elnes Formation, the trilobite fauna is completely dominated by asaphids such as *Asaphus* and *Megistaspis*, but includes more spiny taxa like the cheirurids and a single pliomerid. The trilobite association may be termed the Asaphid-cheirurid Association. The calcarenitic limestones and marls formed in an environment close to fair weather wave base characterized by well oxygenated and, in relative terms, moderately energy rich conditions.The Asaphid-trinucleid Association thrived further off-shore and inhabited an oxygenated but relatively low energy environment with a marly mud-dominated substrate deposited above the storm wave base. The fauna is generally diverse. This association, including the Nileid-raphiophorid Sub-association, is well-known from Lower Palaeozoic dark flaggy limestones to fine-grained clastic sediments predominantly deposited in outer shelf to upper slope settings (Fortey, 1975, 1980; Fortey and Barnes, 1977; Fortey and Owens, 1978, 1987; Ludvigsen, 1978; Nielsen, 1995; Zhou *et al*., 1998; Pålsson *et al*., 2002). However, in the Oslo Region this faunal association is found in a distal inner shelf setting, probably corresponding to a depth regime below 50 to 80 metres. Further offshore, the environment changes to one characterised by tranquil and slightly dysoxic bottom conditions with a muddy substrate formed below storm wave base but still within the zone influenced by storm induced bottom currents. Trilobites are few and low-diverse, mostly belonging to the asaphid genus *Ogygiocaris* and some rare pelagic forms, probably due to the dysoxic bottom conditions.

The deepest water setting recorded in the Elnes Formation represents off-shore tranquil waters well below the storm wave base. This environment was characterized by dysoxic bottom conditions with deposition of fine-grained, organic rich muddy sediments. Calcareous shelled taxa are nearly or completely absent, and no trilobites have been reported from this setting.

Turbidites, which occur in certain intervals of the Elnes Formation, likely represented a stress-factor as the benthic fauna generally exhibits a drop in abundance and diversity in the turbidite dominated units. The reason could be a regular wiping out of the infauna as indicated by the near absence of bioturbation in the sandy turbidite beds, but alternatively an increasing depositional rate 'diluted' the fossil content and gave little time for burrowing animals to inhabit the sea floor. Non-bioturbated turbidites may be as thin as half a centimetre. A few taxa belonging to the trinucleids may have benefited from the coarser and harder substrate as they show a slight increase in abundance.

Hemipelagic trilobites like remopleurids seem to be most abundant in inner shelf settings, probably reflecting a higher productivity in the surface waters close to land.

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CLADISTIC ANALYSIS OF PTYCHASPIDID TRILOBITES (UPPER CAMBRIAN), AND A NEW HYPOTHESIS OF INGROUP RELATIONSHIPS

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Keywords: Trilobita, Ptychaspidinae, Euptychaspidinae, Macronodinae, parsimony, Bayesian, Furongian, Sunwaptan.

INTRODUCTION

Ptychaspididae is a family of trilobites known from the Upper Cambrian (Furongian, Sunwaptan) of North America and Asia. Conventionally, ptychaspidid trilobites have been split into three subfamilies: the Euptychaspidinae, the Macronodinae, and the Ptychaspidinae (see Adrain and Westrop, 2005). Though a smaller analysis of euptychaspidine and macronodine trilobites has been conducted (Adrain and Westrop, 2001), a complete analysis of the Ptychaspididae has never been undertaken. Monophyly of the Ptychaspidinae was assumed but never fully tested.

THE ANALYSIS

To test the validity of the three subfamilies, I performed a parsimony and Bayesian analysis of over fifty species (an earlier version of this analysis was present in Hegna, 2006). Coding the taxa proved challenging as about half are known from heads alone, and some from a single illustrated head. Despite the missing data, the parsimony analysis resulted in 5,446 most parsimonious trees, which, in turn, generated consensus trees with a surprising amount of resolution. The consensus trees are most interesting for what they lack: a monophyletic Ptychaspidinae. Species belonging to *Ptychaspis* form a paraphyletic 'stem' to Euptychaspidinae, and species belonging to *Idiomesus* form a paraphyletic 'stem' to Macronodinae. *Asioptychaspis* proves monophyletic and falls out as the sistergroup to the Euptychaspidinae. All of these together (Euptychaspidinae, Macronodinae, and their 'stems') form a monophyletic clade. This clade excludes other genera previously assigned to the Ptychaspidinae (*Keithia* (Fig 1), *Keithiella*, and *Prioricephalus*), which form another possibly subfamily-level clade. The genera *Keithia* and *Proricephalus* form monophyletic clades, while *Keithiella* form a paraphyletic 'stem' to both.

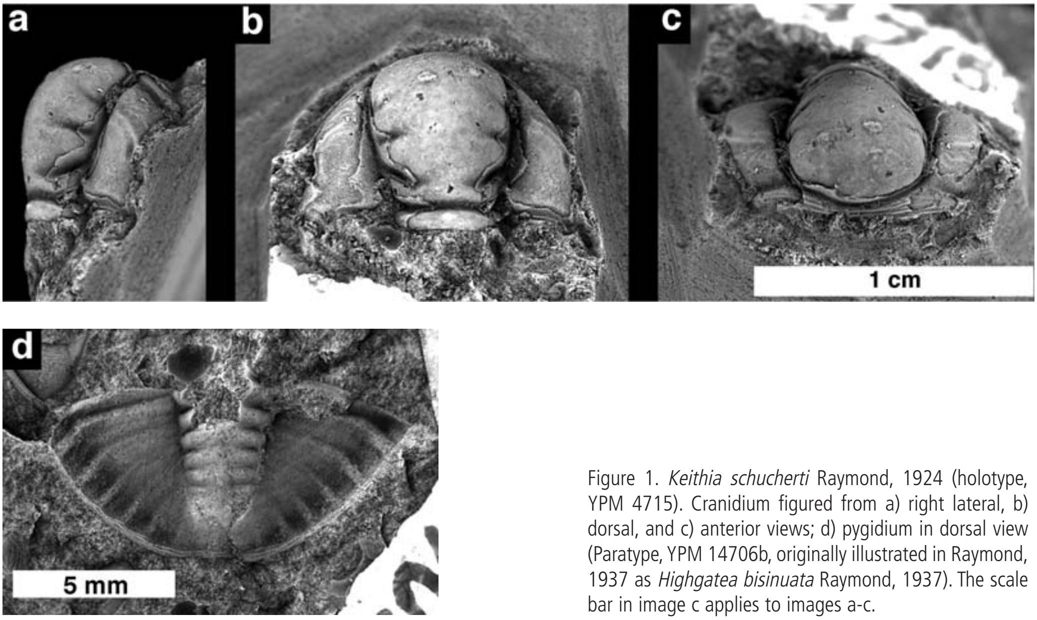

Figure 1. *Keithia schucherti* Raymond, 1924 (holotype, YPM 4715). Cranidium figured from a) right lateral, b) dorsal, and c) anterior views; d) pygidium in dorsal view (Paratype, YPM 14706b, originally illustrated in Raymond, 1937 as *Highgatea bisinuata* Raymond, 1937). The scale bar in image c applies to images a-c.

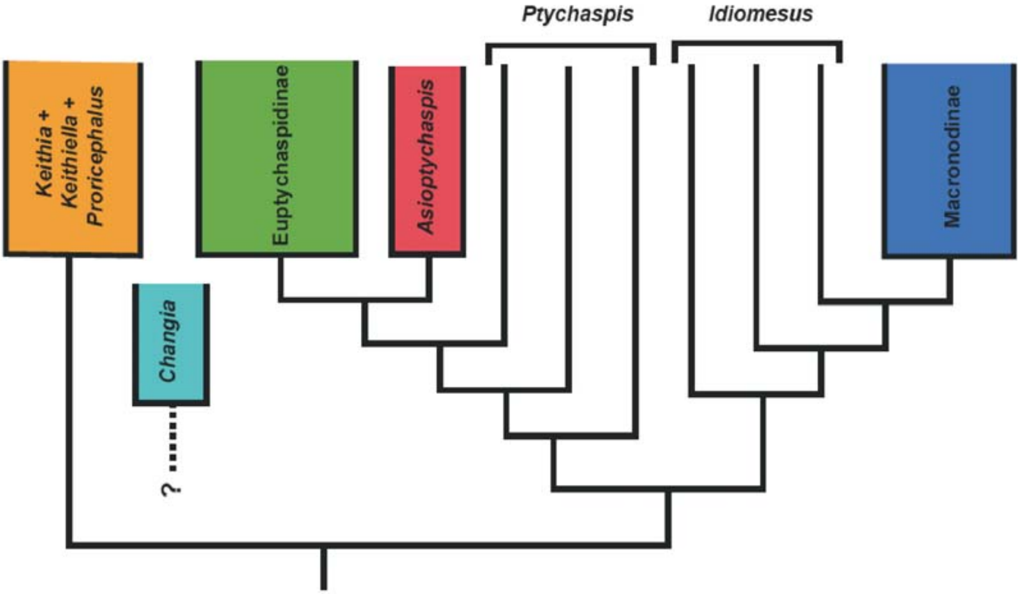

Figure 2. Schematic phylogeny illustrating the results of the parsimony analysis.

The result of the Bayesian analysis is similar to the parsimony analysis. It supports a Euptychaspidinae + *Asioptychaspis* clade, as well as a Macronodinae + *Idiomesus* clade. *Ptychaspis* falls out in a polytomy with these two clades. Both *Keithia* and *Proricephalus* retain monophyly, but *Keithiella* proves to be paraphyletic with regards not only to *Keithia* and *Proricephalus*, but also to the rest of the tree. Several trilobites belonging to the genus *Changia* were included in both analyses— they are quite labile, and therefore little can be said about their relationship to other ptychaspidid trilobites.

CONCLUSIONS

These analyses provide us with a new hypothesis (Fig. 2) of relationships within the Ptychaspididae. Macronodinae should be revised to include *Idiomesus* and Euptychaspidinae to include *Ptychaspis*. Better documentation of pygidial and librigenal characters will be necessary to evaluate the possibility of a new subfamily-level clade containing *Keithia*, *Keithiella* and *Proricephalus*.

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THE FIRST TRILOBITES IN LAURENTIA AND ELSEWHERE

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Keywords: *Fritzaspis* Zone, Laurentia, olenellines, bigotiniids.

INTRODUCTION

The identity of the first or oldest trilobite is an important milestone for understanding the early evolution of multicellular life on Earth. The earliest recorded trilobite occurrences in Siberia, and Morocco have been known for some time and seem to be approximately coeval (Geyer and Shergold, 2000). Recent discoveries of what appears to be the oldest trilobites in western North America (Laurentia) also seem to be about the same age (Hollingsworth, 2007). The morphology and biostratigraphy of these early trilobites should open new vistas of trilobite phylogeny and development.

Edgecombe and Ramsköld (1999) listed as the first apomorphic character of trilobites the calcification of the exoskeleton. Other criteria include dorsal faceted eyes with calcified visual surface and a circumocular suture. In their analysis, the Helmetiida forms a sister group to Trilobita, while the naraoiids are more remotely related. Fortey and Whittington (1997) also define trilobites as having calcareous cuticle. Thus the first trilobite is relatively easy to define in the field as the first to have the requisite calcareous exoskeleton.

Whenever discussing the "earliest" there is always the concern that an isolated specimen will be found significantly below the oldest reported trilobites. This problem is best addressed by extensive collecting efforts combined with detailed confirmation that the occurrence is in place and that the stratigraphy is not confused by local tectonics.

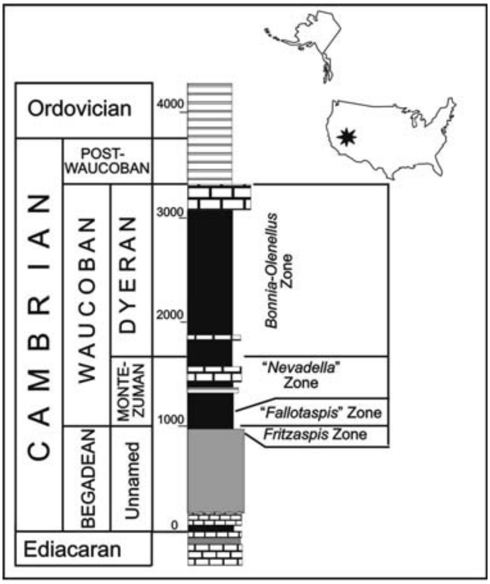

Figure 1. Cambrian rocks in the Esmeralda Basin, Nevada and California with Laurentian subdivisions and lower Cambrian trilobite biozones.

This type of problem occurred in western Laurentia. A single distorted but articulated trilobite was found about 400 m below known trilobites (Nelson and Hupé, 1964). The specimen occurred in a subrounded block suggesting transport. It was eventually identified as a distinct form that came from about 600 m higher in the section (Hollingsworth, 2005).

Trace fossils often attributed to trilobites such as scratch marks (*Monomorphichnus*), feeding traces (*Rusophycus*) and trackways (*Cruziana*) are locally present pre-trilobitic Cambrian rocks, but these were made by other, soft-bodied arthropods and thus cannot be used to indicate the presence of trilobites.

EARLY LAURENTIAN TRILOBITES

The earliest trilobites in Laurentia are in the Esmeralda Basin of western Nevada and eastern California (Fig. 1). They occur in the uppermost part of the Andrews Mountain Member of the Campito Formation as indistinct molds in quartzitic sandstone, and occasionally as internal molds with mineralized exoskeletal material in siltstone. *Fritzaspis*, a form lacking genal spines appears first, rapidly followed by *Profallotaspis*?, *Amplifallotaspis* and *Repinaella*? (Fig. 2). This group constitutes the *Fritzaspis* Zone (Hollingsworth, 2007), the lowest trilobite biozone in North America. These scarce trilobites occur in siliciclastic sediments deposited in oxic water conditions and they occur with an abundance of obolellid brachiopods (also calcareous), hyoliths, and a significant diversity of trace fossils.

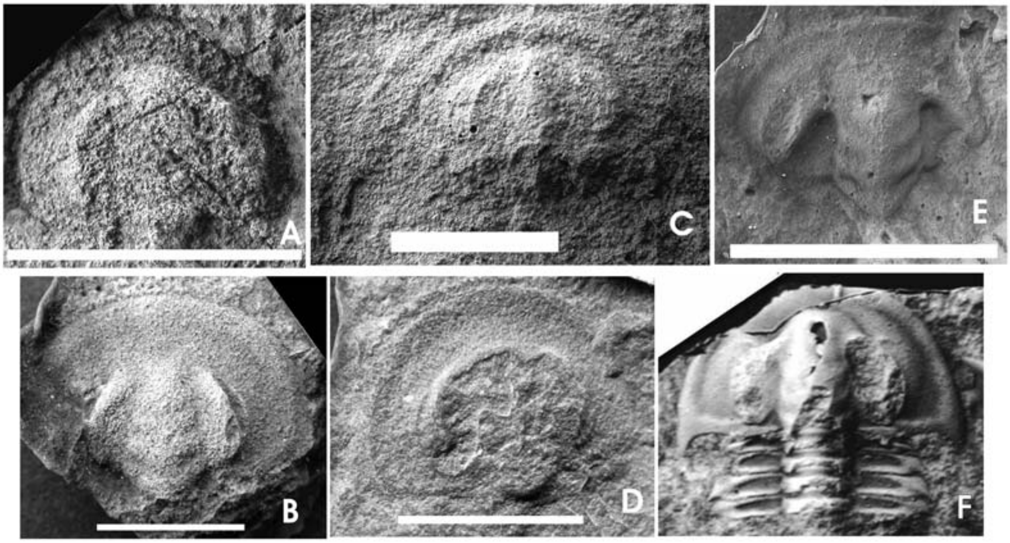

Figure 2. Early trilobites from Laurentia (A-D) and Siberia (E,F). A) *Profallotaspis*? sp.; B) *Fritzaspis generalis*; C) *Amplifallotaspis keni* (A-C from Hollingsworth, 2007); *Repinaella*? sp.; E) *Profallotaspis jakutensis*; F) *Repinaella sibirica* (E-F from ICS colletions). Scale bar 1 cm.

This *Fritzaspis* Assemblage Zone ranges from 58 to 126 m in thickness. Below this interval, the siliciclastic rocks are dark and unfossiliferous representing a dysoxic environment. Trilobites and brachiopods are absent in an earlier oxic interval about 110 m below, adding confidence to the interpretation that the earliest trilobites in the area have been located. Above the *Fritzaspis* interval, the sediments suggest a shift to a deeper-water, dysoxic environment. A 40 m interval is barren of body fossils, then *Archaeaspis* n. sp. is abundant in a 30 cm interval succeeded by several *Fallotaspis* species. This horizon is the base of the essentially continuous trilobite record in the area and, while trace fossils are common, associated brachiopods are quite scarce (Hollingsworth, 2005).

The *Fritzaspis* Zone trilobites have the requisite eye lobes and presumably multifaceted eyes. Calcified thoracic segments are present, but no articulated exoskeletons have been found. Hypostomes and pygidia are unknown. It is noteworthy that the *Archaeaspis* n. sp. that occurs at the base of the *Fallotaspis* assemblage clearly has a natant hypostome while no hypostome has been found for *Fallotaspis* either here or in Morocco (Geyer, 1996).

EARLY TRILOBITES ELSEWHERE

In Siberia, the base of the Atdabanian Stage is drawn at the first appearance of trilobites belonging to *Profallotaspis* which is succeeded by two species of *Repinaella* (Figure 2), plus *Bigotina*. This suite is most closely related to the western Laurentian assemblage. The next zone is characterized by *Pagetiellus* with *Archaeaspis hupei* at the base. These early trilobites occur in calcareous rocks and appear long after the archaeocyaths and brachiopods in the same area (Repina, 1981).

In Morocco, the first trilobites appear in carbonate rocks simultaneously with archaeocyaths. *Eofallotaspis*, an olenelline, appears just after *Hupetina*, a bigotinid (Geyer, 1996). In Spain and northwestern France, bigotinids appear at a similarly early position (Pillola, 1993; Liñan *et al.,* 2005).

The first trilobites in south China, *Parabadiella*, and in Australia, *Abadiella* (both redlichiids), appear to be somewhat younger than the early trilobites of Siberia, Morocco, and western Laurentia (Paterson and Brock, 2007). Additional radiometric dates-there being none from the Cambrian of western Laurentia-and geochemical studies should resolve these correlations. The Chengjiang Lagerstätte shows that arthropods were diverse and abundant in the soft bodied biota. Bradoriids which have a lightly calcified valves are common at Chengjiang (Zhu *et al*., 2001). In western Laurentia, they are scarce but present in and at the base of the *Fallotaspis* assemblage.

In other areas, Baltica, with *Schmidtiellus*, and western Avalonia, with *Callavia*, as the first trilobites locally are distinctly younger than the old trilobites of Siberia, Morocco and Laurentia.

DISCUSSION

The major innovation at the beginning of the Atdabanian was the development of the calcified exoskeleton. This may have been in response to 1) the evolution of predators (Bengtson, 1994; Babcock, 2003), or 2) in response to the availability of calcium or carbon dioxide in the oceanic waters. This latter explanation seems unlikely since the archaeocyaths and brachiopods developed calcareous hardparts several million years earlier.

The sudden appearance of *Amplifallotaspis* along with the other forms in the *Fritzaspis* Zone with the wide, stout genal spines and unusually long ocular lobes suggests that in this instance, the calcified trilobite exoskeleton may have originated independently in more than a single clade. Since several early trilobites (*Schmidtiellus*, *Fallotaspis*, *Montezumaspis*) have long, well-developed axial spines on the thorax, enlarged pleural spines on certain thoracic segments or large, stout genal spines (*Amplifallotaspis*), these calcified spines may have provided defense against predators, leverage to right an overturned trilobite or conveyed advantages during molting.

One consequence of the calcification of the trilobite cuticle was likely increased difficulty in molting as the calcareous sclerites would remain rigid during the process. The earliest trilobites in Laurentia and Siberia were olenellines and conventional wisdom would place these trilobites at the root of trilobite phylogeny. The circumocular suture was the only operable suture on the olenelline cephalon, while the cephalon readily cracked at the upper corners of the ocular lobes (Geyer, 1996). Bigotinids appear with the early olenelline trilobites in Siberia and Morocco. Jell (2003) among others has suggested that the sutured trilobites are a direct evolutionary improvement by developing cephalic sutures along pre-existing structural weaknesses thus presumably improving molt efficiency and perhaps reducing the temporary vulnerability to predators. A consequence of this would be that the bigotinids are polyphyletic. Among the early Laurentia trilobites, only a couple of poorly preserved specimens may have had sutures, but this feature is not convincing. In fact only a few of the thousands of fallotaspidoid cephala found in western Laurentia seem to have sutures. Meanwhile the olenelline trilobites with unsutured cephala persisted in Laurentia for about 10 million years. During this period, redlichiid trilobites were absent from Laurentia.

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FENESTRASPIS, AN UNUSUAL DALMANITID TRILOBITE FROM THE LOWER DEVONIAN OF BOLIVIA

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Keywords: Dalmanitidae, Synphoriinae, Devonian, Bolivia, fenestrae, eyes.

INTRODUCTION

The Lower and Middle Devonian of Bolivia is a rich source of trilobites, including representatives of the Proetidae, Aulacopleuridae, Brachymetopidae, Homalonotidae, Phacopidae, Dalmanitidae, Calmoniidae, Odontopleuridae and Lichidae. Dominating the faunas are the calmoniids, a family endemic to the Malvinokaffic Realm of the southern hemisphere (Eldredge and Ormiston, 1979; Boucot, 1988). The Bolivian calmoniids have been well documented in a number of publications (e.g. Kozłowski, 1923; Wolfart, 1968; Eldredge and Braniša, 1980; Lieberman *et al.*, 1991; Lieberman, 1993; Carvalho *et al.*, 2003); the other trilobite families present appear to be less abundant and diverse than the calmoniids, and have not received as much attention. Dalmanitids documented from the Devonian of Bolivia (Kozłowski, 1923; Braniša, 1965; Wolfart, 1968; Braniša and Vaněk, 1973; Edgecombe and Ramsköld, 1994) belong to five or six genera, of which two (*Chacomurus*, *Fenestraspis*) are not known to occur elsewhere, and another two (*Francovichia*, *Gamonedaspis*) have also been reported from Argentina, Brazil or South Africa (Eldredge and Ormiston, 1979; Cooper, 1982; Edgecombe, 1993). Some of these dalmanitid genera thus appear to be endemic to the Malvinokaffric Realm.

The most abundant Devonian trilobite faunas in Bolivia occur in three stratigraphical units located in separate geographical areas (Fig. 1): the Belén Formation on the northern Altiplano, La Paz Department, western Bolivia; the Icla Formation in the Sierras subandinas, northern Chuquisaca Department, central Bolivia; and the Gamoneda Formation of Tarija Department, southern Bolivia. The Belén, Icla and Gamoneda formations are regarded as broad stratigraphical equivalents, and their lowermost fossiliferous beds are assigned to the *Scaphiocoelia* Zone (Ahlfeld and Braniša, 1960; Eldredge and Braniša, 1980), of early Pragian age (Racheboeuf *et al.*, 1993). The upper boundaries of the Belén and Icla formations correspond approximately with the Eifelian–Givetian boundary (Blieck *et al.*, 1996).

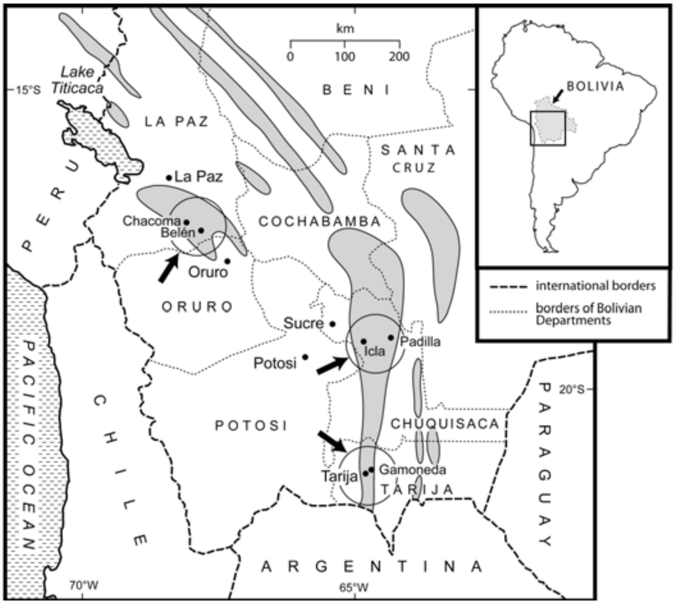

Figure 1. Map showing main regions of Bolivia from which Devonian trilobites have been documented (circled). Major areas of Devonian outcrop are shaded. Adapted from Isaacson (1977, text-fig. 1), and Isaacson and Sablock (1988, fig. 1).

FENESTRASPIS

Fenestraspis was proposed by Braniša and Vaněk (1973) as a genus of the Synphoriinae (Dalmanitidae), with type and only known species *F. amauta* from the Lower Belén Member (Pragian–Emsian) of the Belén Formation at Chacoma, southern La Paz Department, western Bolivia. The genus has been poorly known as the original diagnosis was brief and the only specimens of *F. amauta* illustrated show little more than the glabella. With the aim of revising *Fenestraspis* we have studied numerous specimens of *F. amauta* presented to the American Museum of Natural History by Leonardo Braniša and LeGrand Smith. These specimens, preserved as internal moulds in hard brown micaceous sandstone, consist mostly of cephalic remains including hypostomes, and a pygidium. The thorax is represented only by fragments of a few anterior segments attached to two of the cephala.

The most striking morphological feature of *Fenestraspis* is the presence of numerous openings or fenestrae in the pleural regions of the post-cephalic exoskeleton, where they are developed on the boundaries between segments. In the pygidium the fenestrae are situated on the pleural ribs and extend over virtually the entire width of the pleural field. Most ribs bear a single long fenestra but some have two or three shorter fenestrae; the pygidial fenestrae thus range in shape from slit-like to circular. A slit-like or elliptical fenestra on the line of articulation between cephalon and thorax is formed by a broad, shallow embayment in the posterior fixigenal margin, extending from near the axial furrow almost to the fulcrum, together with an opposing embayment in the front of the first thoracic segment. A shallow embayment in the anterior pleural margin of the pygidium suggests that a fenestra was also present on the thoracopygidial articulation. It is likely that fenestrae were present between all of the thoracic segments though this part of the exoskeleton remains poorly known. Fenestrae are rare structures in trilobites but have been documented in a few genera other than *Fenestraspis*, most of them belonging to the Asteropyginae. The function of the fenestrae remains uncertain but they may have allowed circulation of oxygenated water to the limb exites when the trilobite was enrolled, so that respiration could have been maintained.

Other notable features of *Fenestraspis* are the numerous upwardly directed spines on the cephalon, thoracic axial rings and pygidium, such spines being unusual in a member of the Synphoriinae, and the very large, highly elevated eyes with an outwardly projecting palpebral rim that markedly overhangs much of the visual surface. The eye of *Fenestraspis* is perhaps the largest of schizochroal type known in trilobites, having more than 900 lenses arranged in about 50 vertical files of up to 22 lenses each. The projecting palpebral rim is similar to that described in the asteropygine *Erbenochile erbeni* by Fortey and Chatterton (2003) and Chatterton *et al*. (2007), who suggested that it functioned in that species as an 'eyeshade' shielding the highly elevated and vertically oriented visual surface from sunlight coming directly from above. However, the palpebral projection in *Fenestraspis* would not have been very effective for this purpose, because the visual surface of *F. amauta* is inclined upwards and backwards from the vertical in its anterior part, where the projection is also narrowest.

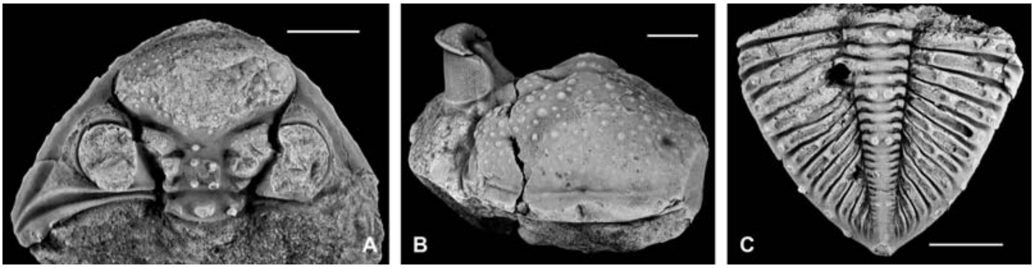

Figure 2. *Fenestraspis amauta* Braniša and Vaněk, 1973; Lower Belén Member (Pragian–Emsian), Belén Formation, southern La Paz Department, Bolivia. A, cephalon AMNH 51471, dorsal view, from Chacoma. B, cephalon AMNH 51470, anterodorsal view, from Patacamaya. C, pygidium AMNH 51474, dorsal view, from Chacoma. Scale bars are 10 mm.

Acknowledgements

We thank the collectors of the specimens, Leonardo Braniša and LeGrand Smith, for donating them to the American Museum of Natural History (AMNH); Bushra Hussaini for making them available for study; Petr Budil (Czech Geological Survey) and Vojtěch Turek (National Museum of Prague) for arranging for casts of the type specimens of *F. amauta* to be made for us; and Phil Lane for commenting on the manuscript.

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TRUNK SEGMENTATION OF THE EARLY CAMBRIAN EODISCID TRILOBITE *NEOCOBBOLDIA CHINLINICA*

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Keywords: Cambrian, trilobite, segmentation, *Neocobboldia*.

INTRODUCTION

Recent advances in molecular genetics permit fresh insights into the controls of development in living arthropods, and prompt comparative studies of trilobite body patterning. Trilobite development is unusual among arthropods in that segments from the meraspid pygidium, the posterior region of the exoskeleton comprising conjoined segments, are released into the thorax during the development of free-living juveniles. The number of thoracic segments in the meraspid pygidium reflects the dynamic balance between the rates of segment release and accretion (Hughes *et al.*, 2006). The early Cambrian eodiscid *Neocobboldia chinlinica* reportedly displays intraspecific variation in the development of segmentation in the pygidium in which some, but apparently not all, meraspid specimens possessed an additional segment when compared to the holaspid pygidium (Zhang, 1989). Zhang (1989) recognized two axial rings (including the terminal piece) in the pygidium of the smallest meraspid specimens recovered, followed by appearance of forms with three, four, and five axial rings progressively as pygidial size increased. A pygidial size interval then followed in which forms bore either five or six axial rings, succeeded by an interval in which all forms had five axial rings, which appears to be the final holaspid number.

This study aims to assess the pattern of segment accumulation and release in this taxon in order to test two models put forward recently to explain it (Fig. 1). One is offset between instars (molts) in which segments were added to the pygidium and those in which segments were released in the thorax, resulting in alternating pygidial segment numbers between three successive molts (Naimark, 2006). The other scheme is that addition and release of segments were coincident, but that members of the species followed two different ontogenetic pathways: one maintaining a constant number of pygidial segments by a coordinated transition in the termination of segment generation and release, while in the other both the start and the termination of the release of thoracic segments was offset by one molt cycle, with the result that the pygidium possessed an additional segment for a series of three consecutive molts (Hughes *et al.*, 2006).

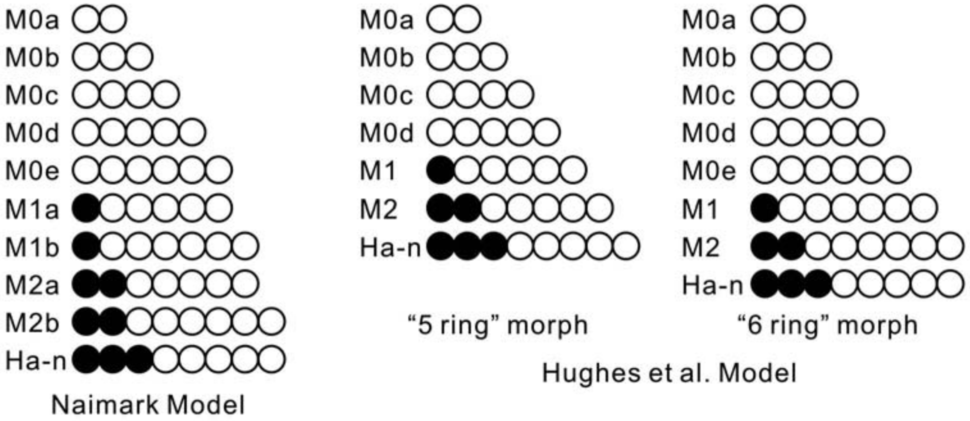

Figure 1. Segment accumulation schedules of the two models for *Neoccoboldia chinlinica* segmentation. M designates meraspid with degrees and instars within degrees given by numbers and letters, and H designates holaspid instars. Open shapes represent segments in the pygidium, and closed shapes represent thoracic segments (Hughes *et al.*, 2006; Naimark, 2006).

MATERIALS AND METHODS

Numerous phosphatized specimens of *N. chinlinica* occur in thin-bedded micritic limestone from the lower Cambrian Shuigoukou Formation from the Laozizhai section in Xichuan, Henan Province, China, together with species of the redlichiid *Ichangia*, bradorids, brachiopods, and sponge spicules. The assemblage sits immediately above a *Sinodiscus* horizon, and bed containing *Palaeolenus* overlies the *N. chinlinica* fauna (Zhang and Pratt, 1999). Due to lost of the original material, additional materials were collected from the same bed at a locality some 500 meters from the original.

To date about 300 specimens have been measured for statistical analysis, and hundreds more are scheduled to be processed. We are employing both a modeling approach based on predicted size frequency distributions and also shape based data to test between these and other possible hypotheses. The form of the posterior margin, the axis to width ratio, overall outline, and pleural rib structure have been identified as potential characters for additional subdivision of the ontogenetic series, and promise a finer resolution of the process of segmentation.

PRELIMINARY RESULTS

Preliminary results broadly parallel the original work, however, the intervals in which forms with either five or six axial rings occurred in specimens of similar size was much shorter than in Zhang's (1989) analysis. Despite the relatively small sample number, the consistency in size separation between meraspid forms with five and six axial rings suggests the minimal overlap is a correct representation of the true size distribution. However, slight temporal difference between the original material and the new collection cannot be discounted as a potential cause for this discrepancy.

The presence of a marked morphological jump between the small meraspid pygidia with five and six axial rings was also identified. Firstly, three pleural ribs are observed in small five-ring forms while five are present in six-ring forms. Secondly, a prominent posterior notch is present in all meraspid specimens except the six-ring forms. Given that morphological transitions between other instars are generally more gradual, it is possible that another instar occurred between the meraspid pygidia with five axial rings and the smallest of those with six axial rings. A few five-ring forms with four pleural ribs and a weak posterior notch are present in the new collection, but many more specimens must be analyzed in order to assess whether these likely reflect a discrete instar.

A consideration of the effect of segment release on the absolute length of the pygidium has implications for the developmental schedule. If a small six-ring form were to release a pygidial segment for a thoracic segment, as in Naimark's model, the remainder of the pygidium would have to grow by a factor of 1.23 to maintain its overall length, because the sagittal length of the anteriormost segment in the six-ring forms occupies, on average, 18% of the total pygidial length. If this is so, the meraspid five-ring forms would be expected plot close to the six-ring forms in the width-length graph, but initial results reveal no merapsid five-ring forms near the six-ring forms. In addition, meraspid forms with five segments immediately succeeded those with four rings a growth increment of about 1.4 is required, which is slightly higher than reported in other instances of pygidial meraspid growth, raising the possibility of multiple instars per stage.

CONCLUSIONS

Preliminary results suggest the presence of a single ontogenetic pathway in the new collection, with no substantive size overlap between meraspid pygidia with five and six rings. This suggests a different developmental pattern to that which both previous hypotheses sought to explain. As Zhang's original material is lost, it is unclear whether this is because of original differences between the samples, or in the way in which samples were described. These differences notwithstanding, the sequence found in the new sample resembles the developmental model proposed for one of the cohorts by Hughes *et al*. (2006), but one which may have contained a larger number of instars than proposed in that model [and in this respect more akin to the Naimark (2006) model]. More specimens from the meraspid stage are now necessary for further resolution of these and for testing additional hypotheses.

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MORPHOLOGICAL AND ONTOGENETIC CHANGE IN THE “EARLY” CAMBRIAN TRILOBITE *ZACANTHOPSIS* DURING AN INTERVAL OF ENVIRONMENTAL CHANGE

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Keywords: Geometric morphometrics, ontogeny, Great Basin, Cambrian, Trilobita, cladistics.

High-resolution stratigraphic sampling of silicified nodular limestone beds from Oak Springs Summit in the Delamar Mountains, east-central Nevada, United States, yielded undeformed ontogenetic material documenting a stratigraphic trend in samples of the trilobite *Zacanthopsis*. These limestone beds are interbedded with shales lying in the 10-meter interval immediately below the Dyeran-Delamaran (“Early-Middle” Cambrian) boundary in the Combined Metals Member of the Pioche Formation (Merriam, 1964; Palmer, 1971, 1998; Sundberg and McCollum, 2000). Regional stratigraphy is characterized by karsted calcareous sandstone and oncolitic limestones below the section of interbedded shales and nodular limestone beds and by ribbon limestones above the section (Sundberg and McCollum, 2000), indicating that water depth was increasing as these sediments were deposited (Webster, 2007).

Morphological shape change in the cranidium is documented using principal components analysis of geometric morphometric data (to be presented elsewhere) (Zelditch *et al*., 2004). Morphologically mature specimens were identified by plotting the Procrustes distance of each specimen from the mean of the smallest three specimens against centroid size: a sharp decrease in the rate of shape change away from the morphology of the smallest specimens indicates the onset of morphological maturity in *Zacanthopsis* cranidia. The primary change in morphologically mature specimens during this stratigraphic interval is a lateral expansion of the cranidium at the palpebral lobes relative to the width of the cranidium at the anterior facial sutures, accompanied by change in the orientation of the lobe (Fig. 1). Similar morphological change associated with increasing water depth has been documented in Ordovician trilobites from the Cincinnati area (Webber and Hunda, 2007) and from central New York State (Cisne *et al*., 1980).

Principal components analysis including morphologically immature specimens reveals that smaller specimens from all samples overlap in morphospace but that the stratigraphically youngest sample follows a unique trajectory of shape change as specimen size increases (data to be presented elsewhere). This ontogenetic divergence in morphospace is supported by statistical comparison of growth vectors extracted from Procrustes coordinates (methodology discussed in Webster *et al*., 2001). This sample is thus considered a distinct species and the appearance of the new species was accompanied by allometric repatterning (*sensu* Webster and Zelditch, 2005). The more subtle differences between stratigraphically older samples, however, are not associated with marked ontogenetic modification.

Phylogenetic analysis yielded over 700 most parsimonious trees, all inconsistent with a stratophenetic interpretation of the succession of samples (data to be presented elsewhere). Reconciling this inconsistency requires accepting complex facies tracking of multiple co-existing lineages, each sampled only once and in reverse order of the hypothesized order of phylogenetic branching, as well as long unsampled ghost lineages. However, trees that are consistent with the reading of the stratigraphic series as a phylogenetic trend of a single lineage are only one step longer. It is possible that the inconsistency between the most parsimonious trees and the stratigraphic series is due to uncertainty in choice of outgroup. Because *Zacanthopsis* is one of the oldest genera in the Family Zacanthoididae and the sister group to this family is unknown, outgroups included in the analysis include both derived groups as well as stratigraphically younger species ("Middle" Cambrian). Without appropriate outgroups, character polarity cannot be confidently determined.

We cannot yet determine whether the stratigraphic trend in older samples indicates non-evolutionary clinal variation or anagenesis concurrent with increasing water depth. Nonetheless, the results of the study indicate the usefulness of ontogenetic information in species delimitation. This study also highlights the difficulty in rooting trees where uncertainty in choice of outgroup reduces the confidence with which we can reconstruct ancestral morphologies.

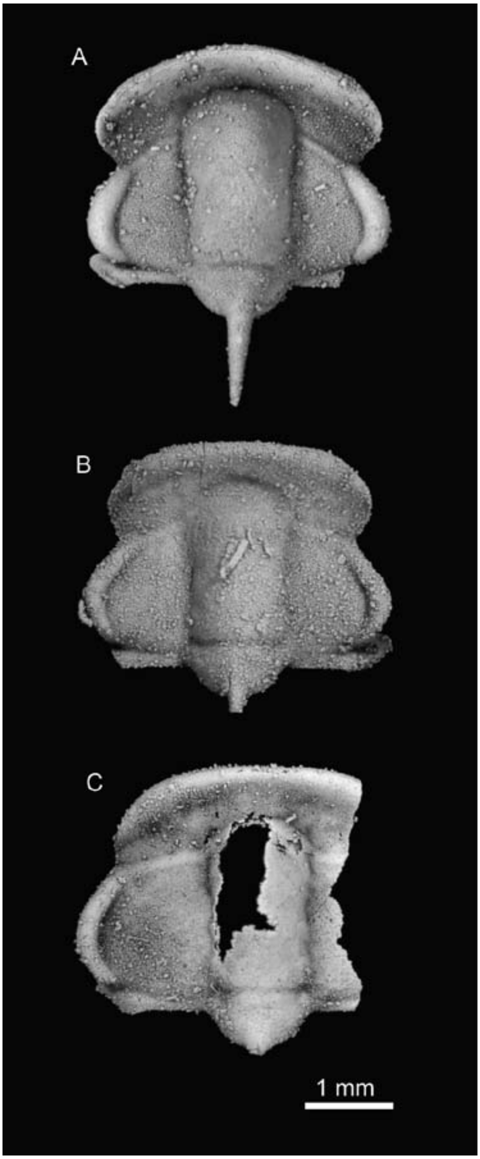

Figure 1. Morphological trend in *Zacanthopsis* cranidia from Oak Springs Summit, Nevada, during the latest Dyeran. Specimens are held at the Institute for Cambrian Studies (ICS). A, Cranidium from the oldest bed, 9.5 meters below the Dyeran-Delamaran boundary, ICS-1152. B, Cranidium from one of the middle beds, 5.5 meters below the Dyeran-Delamaran boundary, ICS-1159. C, Cranidium from the youngest bed, 1.6 meters below the Dyeran-Delamaran boundary, ICS-1287.

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TRILOBITE ASSOCIATIONS AND TAPHONOMY OF THE SILURIAN REEFS OF EASTERN NORTH GREENLAND

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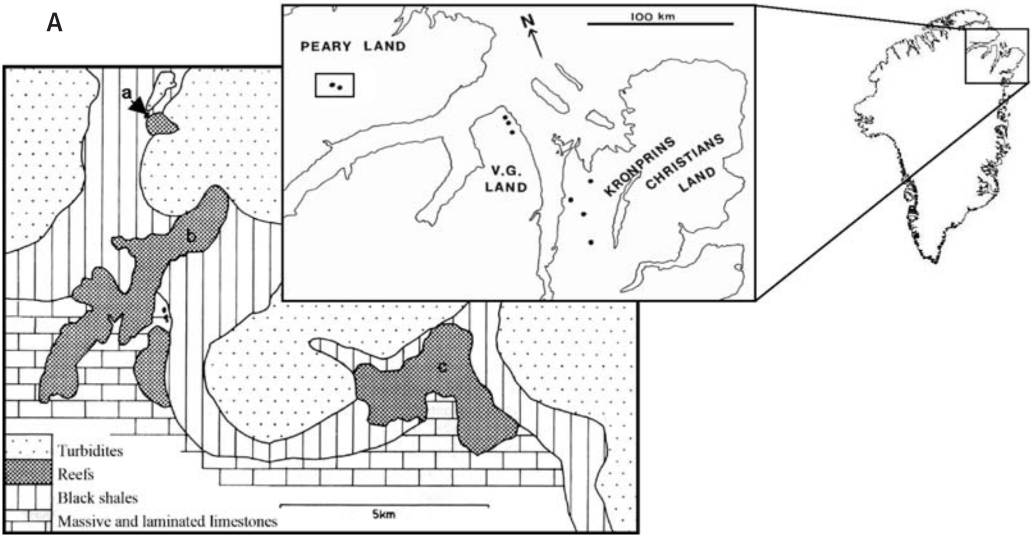
Keywords: Greenland, illaenid, reef, scutelluid, Silurian, taphonomy, trilobite associations.

INTRODUCTION

The Telychian (Upper Llandovery) reefs of Peary Land, North Greenland (Fig. 1) yield abundant and well preserved trilobite faunas belonging to the long-ranging Cheirurid-Illaenid Association. The trilobite fauna is dominated by scutelluids and illaenids. In approximate order of relative abundance, members of the Encrinuridae, Cheiruridae, Proetidae, Calymenidae, Lichidae and Harpetidae are also represented. The reefs belong to the Samuelsen Høj Formation and comprise pale crystalline limestones which lack extensive deformation and dolomitisation (Lane and Thomas, 1979). Published palaeontological and sedimentological studies of the reefs are few; Lane (1972) contributed the most substantial published work on Silurian trilobite faunas of eastern North Greenland so far. This study presents the combined results of lithofacies analysis, and the identification of trilobite associations and their taphonomic attributes. This has resulted, for the first time, in the application of a palaeoenvironmental and taphonomic context to the Silurian reef environments of North Greenland.

GEOLOGICAL SETTING

The reefs of North Greenland form part of the Franklinian reef belt, which extends ~2000 km from the Canadian Arctic Islands to eastern North Greenland (Sønderholm and Harland, 1989). They represent part of a passive margin succession comprising carbonate platform sedimentation. They are found associated with Telychian argillaceous limestones and shales, and at their stratigraphically highest points, are surrounded by turbidite deposits (Fig. 1B) representing drowning of the platform in the latest Telychian (Higgins *et al.,* 1991).



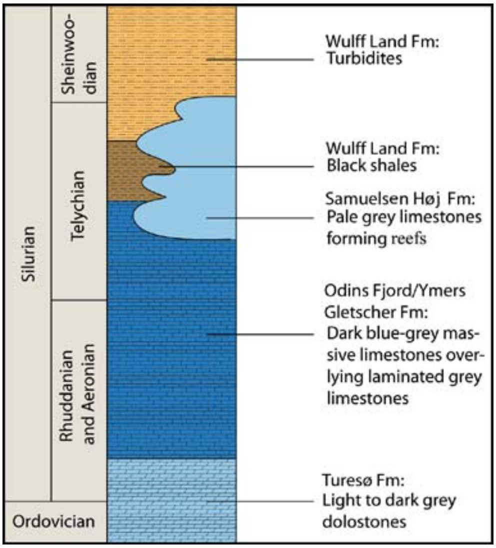


Figure 1. A. Detail of eastern North Greenland showing collection localities, represented by dots (V.G. Land = Valdemar Glückstadt Land). The boxed area within Peary Land is further expanded to show mapped relationships of Silurian strata; the three main reef outcrops are labelled a to c (adapted from Lane and Thomas, 1979). B. Simplified Silurian stratigraphy of eastern North Greenland.

THE REEFS AND THEIR TRILOBITE FAUNAS

Roughly 300 kg of reef limestones were collected from localities in Peary Land, Kronpins Chrisians Land and Valdemar Glückstadt Land during geological mapping expeditions in the 1970s and 80s. This account presents work completed so far on material collected from Peary Land (which constitutes roughly two thirds of the total material) from reef outcrops a-c (Fig. 1A). Trilobite sclerites were identified and counted, and these data form the basis for recognising trilobite associations. The associations can be regarded as varying combinations of three end-members.

End-member 1: Encrinurid Association

The Encrinurid Association occurs at the smallest, most northerly reef outcrop in Peary Land (locality a, Fig.1A). Within this association encrinurids (Fig. 2.A) comprise some 90% of the total trilobite fauna, and fragmented pygidia predominate. These are dispersed within the sediment and display no preferential orientation or stacking. Lichids (represented by *Dicranopeltis*; Fig. 2.D) are present within the rest of the fauna, as are rare examples of *Meroperix* and *Scharyia.* This association is found in a crinoidal grainstone lithofacies which comprises abundant crinoid fragments, with subordinate brachiopods, corals, bryozoans, and orthoconic cephalopods. A small proportion of microbially precipitated micrite is present.

The abundance of sclerites of similar size and shape, suggests that this association has been influenced by hydrodynamic sorting. This end-member represents the highest energy facies, indicated by the lack of micrite (other than that precipitated microbially) suggesting that mud was winnowed out above fair weather wave base. The fragmented nature of both crinoids and trilobite sclerites confirms this. The mapped relationships of reef outcrops a and b (Fig. 1A), suggest that the most northerly reef could be connected at depth to the main Y-shaped reef to the south. Its location (at the end of the main reef), and the presence of clean grainstones, suggest that the Encrinurid Association could be related to flank beds which represent the original surface of the reef.

End-member 2: Scutelluid Association

The lowest diversity association studied so far, is recognized from reef outcrops b and c (Fig. 1A) and is dominated by both fractured and complete *Ekwanoscutellum* pygidia (Figs 2.C, H). These occur as densely stacked layers, which typically comprise over 80% of the total trilobite fauna (where other fauna includes illaenids, *Meroperix*, cheirurids and proetids). In some layers, *Ekwanoscutellum* pygidia comprise up to 100% of the trilobite fauna. These pygidia are the largest trilobite fragments found in the reef material, reaching sagittal lengths of up to 100 mm. They occur in both convex- and concave-up orientations and commonly show preferred orientation. The Scutelluid Association occurs within a locally intraclastic, wackestone to peloidal packstone lithofacies which is rich in irregular stromatactis (spar-filled cavities). Crinoids, ostracods and brachiopods are present.

Dominance of pygidia of similar size and shape, vertical stacking and a preferred orientation of trilobite sclerites indicate sorting by hydrodynamic processes. This association represents a lower energy environment than that of end-member one, as indicated by the presence of micrite and the passive settling of sclerites. It commonly grades into end-member three.

End-member 3: Scutelluid-Illaenid Association

The most common association identified (and recognized from reef outcrops b and c; Fig. 1A) is dominated by scutelluids and illaenids, and is the highest diversity and most variable association. It is dominated by scutelluid (predominantly *Meroperix*; Figs 2.B, E, and less commonly *Ekwanoscutellum*) and illaenid (most commonly *Stenopareia*; Fig. 2.I, and *Failleana*; Fig. 2.F) pygidia and subordinate cephala, and these elements typically comprise well over 50% of the total trilobite fauna. Cheirurids are also conspicuous elements and are represented by *Cheirurus* (Fig. 2.G). Locally, smaller elements of this fauna are found associated with calymenids, encrinurids and proetids. This association is found in a similar lithofacies to that of the Scutelluid Association (stromatactis-rich wackestone to peloidal packstone).

Locally, shelter porosity is apparent, indicating a convex-up settling of sclerites producing cavities beneath. Like the trilobite fauna, non-trilobite elements display a high diversity; comprising common crinoid fragments, brachiopods, ostracods, bryozoans, corals, orthoconic cephalopods and gastropods.

Stacking patterns are common, indicating passive settling within an environment comparable to that of the Scutelluid Association. However, hydrodynamic sorting is less evident; there are variable orientations and greater diversity of sclerites, and therefore this association represents the lowest energy facies within the reef environment.

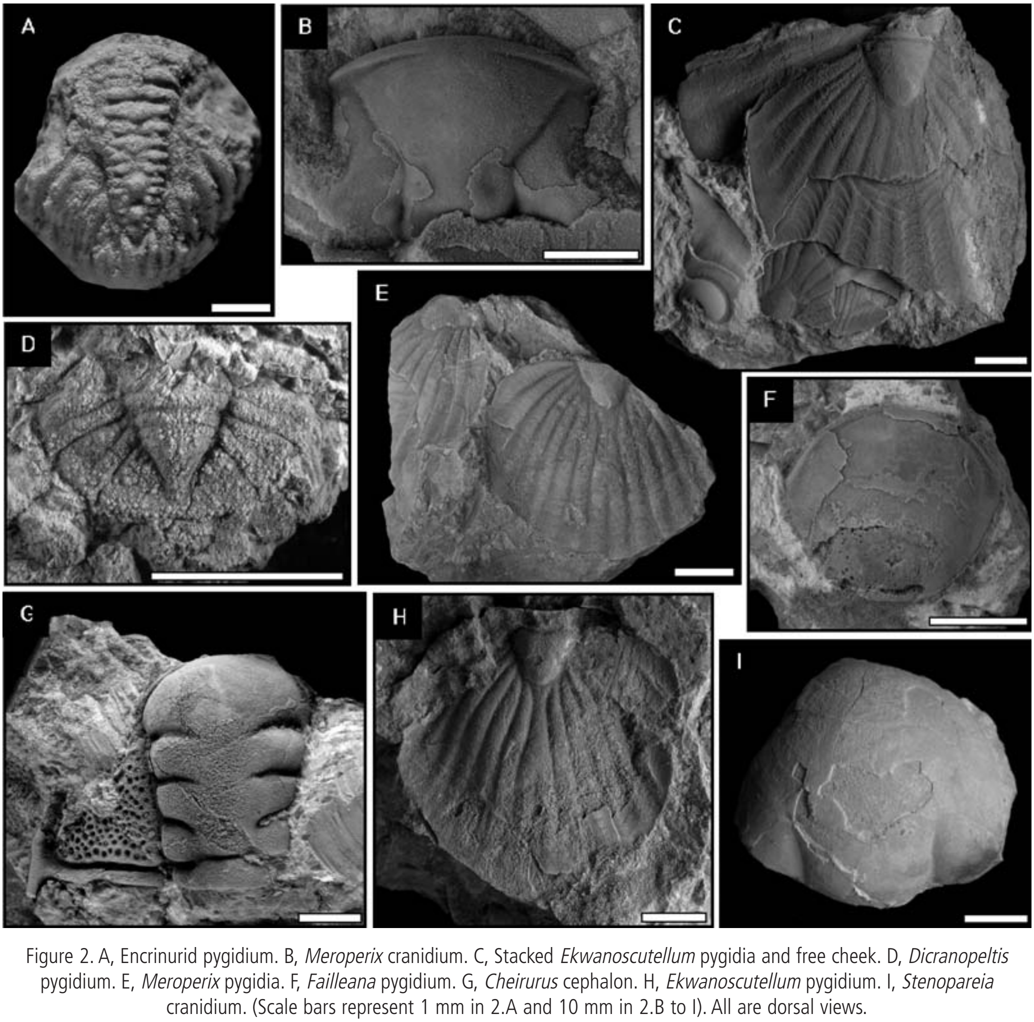


Figure 2. A, Encrinurid pygidium. B, *Meroperix* cranidium. C, Stacked *Ekwanoscutellum* pygidia and free cheek. D, *Dicranopeltis* pygidium. E, *Meroperix* pygidia. F, *Failleana* pygidium. G, *Cheirurus* cephalon. H, *Ekwanoscutellum* pygidium. I, *Stenopareia* cranidium. (Scale bars represent 1 mm in 2.A and 10 mm in 2.B to I). All are dorsal views.

Environments

The reefs comprise a variable suite of lithofacies; end-members include crinoidal grainstones, wackestones and peloidal packstones. Micrite, where present, is commonly recrystallized and displays evidence of microbial origin (indicated by clotted fabrics and the presence of filaments). Stromatactis cavities are found within all lithofacies and indicate early cementation of the reefs (they include syn-depositional turbid spars). The reefs therefore show evidence of early lithification and stabilization. Energy conditions were variable within the reef, with possible flank beds representing the greatest energy environments, and more micrite- and stromatactis-rich facies representing slightly lower energy reef core facies (as represented by end-members two and three).

CONCLUSIONS

Within the reef environment, three predominant trilobite associations occur, each found within varying lithofacies and displaying different taphonomic attributes. All associations have been influenced by some degree of hydrodynamic processes, resulting in size/shape sorting, the preferential occurrence of pygidia, and, locally, stacking patterns. Differences in trilobite associations, lithofacies and taphonomy, represent variations in energy conditions and processes within the reef. However, associations can not be explained by taphonomic processes alone; a strong segregation of species combined with limited transportation (as indicated by lack of abrasion of sclerites), suggests that the associations of trilobites occupied different niches within the reef environment. The phenomenon of stacking of flat scutelluid pygidia is also observed in classical localities such as the Pragian Koněprusy reef (Šnajdr, 1960, pl. 12) and in the Hamar Lagdad Lower Emsian pinnacle mudmounds from Southern Morocco (Alberti, 1981, fig. 8). The intense concentrations of sclerites provide further evidence for the presence of faunal pockets within some reef environments (Suzuki and Bergström, 1999; Chatterton *et al.,* 2003). End-members two and three are comparable with trilobite associations described from Early Silurian carbonate buildups from Wisconsin, Iowa, Ilinois and Canada (Mikulic, 1981; Mikulic and Kluessendorf, 1997). Particular similarities are found with associations from the coeval Attawapiskat Formation, Northern Ontario (Norford, 1981; Westrop and Rudkin, 1999), where end-member two is comparable with a monospecific to low diversity *Ekwanoscutellum* Association, and end-member three to a more diverse *Stenopareia-Meroperix* Association.

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GROWTH PROGRESSION IN TRILOBITES: A PRELIMINARY STUDY

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Keywords: Arthropods, ontogeny, growth rate, growth increment, Dyar's rule, size.

INTRODUCTION

Arthropod evolution has frequently been characterized by marked diversification, be it in the variety of segments or limbs along the body, or in aspects of the developmental schedule. Trilobite post-embryonic development comprised a long series of free-living instars, with transitions between successive instars generally characterized by modest morphological change. Such a condition apparently also characterized basal Crustacea (Waloszek and Maas, 2005), and may have been the primitive condition in basal euarthropods (Hughes *et al*., 2006). Is the increase in structural tagmosis witnessed in trilobite phylogeny (Hughes, 2007) matched by increased variety in growth modes, such as the among species variation in average growth rate, or departure from constant growth rate through ontogeny? We approached these questions through the analysis of trilobite ontogenetic growth progression. Over the last 50 years quantitative data on growth increments between putative successive instars have been published for over 65 trilobite species, from strata ranging from early Cambrian to Carboniferous in age. Such instar series have been posited for all of the articulation-based stages of trilobite life history, and for a broad range of environmental settings. A dataset of this information based on published records and our own analyses, accompanied by criteria with which to judge the reliability of the estimates, has been used to review trilobite growth.

Criteria for judging growth estimate reliability include both the degree of confidence in the morphological recognition of successive instars (see below) and in the preservational quality and degree of time-averaging in the sample. We have concluded that a significant number of putative cases of successive instars are weakly supported and that, even in cases which fulfil strict quality controls, estimates of growth increments can differ markedly even for the same ontogenetic stages of the same species. This requires caution to be exercised when assessing these results.

Exoskeletal growth in arthropods occurs in a stepwise manner, with post-embryonic development being paced by the moult cycle. Dyar's rule (Dyar, 1890) assumes a constant rate of size increase between moults, and is considered a "null model" for arthropod growth. The average per moult growth rate and (when possible) the degree of conformity to Dyar's rule across different ontogenetic stages have been calculated for all the species in the dataset.

MATERIALS AND METHODS

Values for linear dimensions were extracted either directly from published data tables, via the digitization of published graphs, of from our own analyses. This study is mainly based on *cross-sectional* data (Cock 1966), that consists of a series of static morphometric data, each relating to a different instar and a different set of specimens, where the grouping of specimens per instar is done on the base of a criterion independent of size, such as the number of trunk segments. However, for some species a size-independent criterion of stage assignment was not available (*mixed cross-sectional* data). Additional information on the phylogenetic affinities, stratigraphic age, developmental mode, and paleoenvironmental setting was recorded for each species. Due to ontogenetic allometry different morphometric characters may exhibit different growth rates within the same species and ontogenetic stage. We have summarized data as body length, body width and a compound measure of overall size (BoL, BoW and BoC, respectively), and analogously for the cephalon/cranidium (CeL, CeW and CeC) and pygidium (PyL, PyW and PyC).

All metric measures were transformed into their natural logarithms prior to statistical treatment, and are here referred to as logsize variables. A growth progression conforming to Dyar's rule is a geometric progression characterized by a constant growth rate (*GR*) called Dyar's coefficient. Log-transformation of the size variables transforms the geometric progression into a linear progression, i.e. a more statistically tractable version of Dyar's rule that is characterized by a specific constant growth increment ($GI = \ln GR$).

Because in the database only a fraction of the species exhibit growth at a constant rate, linear regression cannot be adopted as general model for logsize variables in trilobite ontogeny. The average growth increment (*AGI*) is thus calculated as the average logsize increment between pairs of contiguous instars in the ontogenetic series. This simplifies to:

$$AGI = \frac{X_f - X_i}{N - 1}$$

where X_f and X_i are the mean logsize of the last and the first instars of the series, respectively, and N is the number of instars. The average growth rate (*AGR*), a more traditional measure of ontogenetic growth progression, is than calculated as the anti-logarithm of the estimated average growth increment for the logsize variable.

Because ontogenetic series differ in the number of instars per series and, within a series, different instars are generally represented by a different number of specimens, it is not possible to distinguish between structural deviation from a constant growth model and sampling error with a comparable level of precision across the whole database. Hence we adopted a pragmatic approach to the evaluation of conformity to Dyar's rule. We devised a metric that evaluates the extent to which logsize calculated on the basis of a constant growth model is effective at predicting observed size. The two extreme instars are excluded, as these are used to calculate *AGI*. Our index of conformity to Dyar's rule (*IDC*) is thus calculated as:

$$IDC = \frac{\max\left|X_o - X_e\right|}{\rho(N-2)}$$

where X_o is the observed mean logsize of the instar that presents the maximum deviation from the corresponding expected mean logsize (X_e), r is the calculated average growth increment (*AGI*), and N is the number of instars. *IDC* varies between 0 (total growth realized in one moult) and 1 (perfect coincidence between expected and observed instar mean values). The metrics can give negative (i.e. nonsense) results in the case of ontogenetic size decrease.

PRELIMINARY RESULTS

While the ranges of variation for *AGR* and *IDC* values can give an estimate of the real variation in these parameters among trilobites, their mean values must be considered with more caution because they could be biased by unbalanced phylogenetic sampling and phylogenetic correlation, which are issues we have yet to explore. We have used the traditional, articulation-based trilobite life history scheme as a framework for presenting our preliminary findings.

Phaselus. The *AGR* of BoC for the two available examples are 1.80 and 1.63. These figures are notably high with respect to the comparable measure in protaspids of the same two species, 1.24 and 1.46 respectively. However the number of species sampled is too small to warrant further comment.

Protaspids. Most *AGR* values for BoC vary between 1.1 and 1.5, with a mean of 1.31. Within species, the *AGR* of BoL is generally greater than that of BoW (mean 1.33 vs. 1.29), and this may reflect the progressive addition of segments at the posterior of the trunk (anamorphosis). Conformity to Dyar's rule is quite variable, with about half the species with *IDC* values in the range 0.8-0.9 and the other half in the range 0.9-1.0 (for BoC, median 89.6).

Meraspids. With respect to length and width, the meraspid cephalon approximates to ontogenetic isometry in most cases, with similar *AGR* values for CeL and CeW. *AGR* for CeC is usually in the range 1.1-1.4 with a mean around 1.30, but there are conspicuous exceptions, and the highest *AGR* recorded approximate 2, i.e. doubling of linear size at each moult. Meraspid pygidia also show growth that is approximately isometric, with *AGR* for PyC usually in the range 1.05-1.25 with a mean around 1.16. Conformity to Dyar's rule is generally quite good for the cephalon, with most *IDC* values over 0.9 (for CeC, median 93.7). *IDC* values for the pygidium are usually smaller than the cephalon. Most values *IDC* are between 0.75 and 0.95 (for PyC, median 88.6), and within species the difference between *IDC* for PyW and PyL is often conspicuous.

Holaspids. Although holaspid instars have been claimed to be distinguished in a number of studies, there are few progressive morphological changes between putative instars upon which to base them. Most cases are based on gaps in size-frequency distributions that are interpreted to represent instar boundaries, but these are commonly of dubious significance. With respect to length and width, the holaspid cephalon approximates to ontogenetic isometry in most cases which fulfil a criteria of reliable instar assignment, with the *AGR* for CeC usually in the range 1.2-1.5, with a mean around 1.36. For the pygidium we have data for only two species (*AGR* of PyC, 1.24 and 1.22). *IDC* is larger than 0.90 for the two computable cases.

Transitions between stages: For a very few species we have growth data across two ontogenetic stages. In general, *AGR* tends to get smaller, both across the protaspid–meraspid transition and across the meraspid-holaspid transition. However there is no support for a generalized pattern of within-stage decrease in *GR*, neither for meraspids nor holaspids. In protaspid stage, early instar *GR* is frequently larger than later instar *GR*, but seldom this difference is conspicuous.

Stratigraphic trends. The upper limit of *AGR* tends to increase with stratigraphic age, while lower limit of *IDC* tends to decrease with stratigraphic age, although there are marked outlier to this generality, particularly in the Devonian. Thus neither an increase in among-species variation in growth rates, nor an increase in departure from Dyar's rule are supported by our preliminary analysis.

CONCLUSIONS

Although our results are preliminary, particularly because we have not yet assessed them in phylogenetic context, we see no suggestion of striking temporal trends in the degree of departure from Dyar's rule or in the variance in the average growth rate. Our results do not support Chatterton *et al*'s (1990) view that growth increments tended to increase, on average, during trilobite evolution, although particular clades of derived trilobites, such as certain "proetid" trilobites, do have notably high *AGR*. As with various and repeated experiments in skeletal tagmosis, it appears that changes in growth rates and degree of conformity to Dyar's rule occurred repeatedly and independently during trilobite evolution.

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CAMBRIAN TRILOBITES FROM THE PARAHIO AND ZANSKAR VALLEYS, INDIAN HIMALAYA: A SYNOPSIS

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Keywords: Himalaya, trilobites, Cambrian, biostratigraphy.

New collections of trilobites from the type section of the Parahio Formation in the Parahio Valley, Spiti, and from the Parahio, Karsha, and Kurgiakh formations in the Zanskar Valley provide for the establishment of a local biostratigraphic zonation for the top of the second and much of the third series of the Cambrian System. These collections form the basis for a monograph that we are currently completing. This zonation is based on collections precisely located within measured stratigraphic sections. Description of material preserved in limestone clarifies the concept of several Himalayan taxa known previously only from tectonically deformed specimens preserved in shale. New material can be assigned with confidence to 28 species described previously, and to 13 new species. Three new genera will be proposed. Ten Himalayan additional forms are assigned at the generic level only, and another 10 are questionably assigned to genera or species. The zonation includes 6 zones and 3 levels, including the the *Oryctocephalus indicus* level, the *Paramecephalus defossus* Zone, the *Oryctocephalus salteri* Zone, the *Iranonessia butes* level, the *Lejopyge laevigata* Zone, and the *Proagnostus bulbus* Zone. Other zones and levels will take the names of new taxa to be described in the monograph. Our sections span the upper part of the informal Stage 4 of the Cambrian System, about 511 Ma old, to the lower part of the *Proagnostus bulbus* zone, dated at about 501 Ma. This time interval is represented by about 2000m of section, which is remarkably thick compared similar intervals elsewhere globally and is consistent with high rates of sedimentation along the Himalayan margin at the time. The fauna is similar to others from equatorial peri-Gondwanaland, with closest similarity to those of South China. Juvenile trilobites are described for the first time from India. A Chinese new species of *Mufushania* will also be described.

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SHORT-TERM, PALEOENVIRONMENTALLY-RELATED MORPHOLOGICAL VARIATION IN THE ORDOVICIAN TRILOBITE *FLEXICALYMENE GRANULOSA*

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Keywords: Evolution, geographic, morphometrics.

INTRODUCTION

The ability to document changes in phenotype through time and space is one of the unique contributions that paleontology provides to evolutionary biology. However, interpretation of morphological trends in fossil species is complicated because observed morphological variability can arise through a variety of processes, such as: (1) genetic variability among populations, with the potential to lead to evolutionary changes; (2) environmental variability, perhaps with no genetic variability at all (ecophenotypy); (3) differences in growth and development (allometry); and (4) preservational (taphonomic) bias, often related to differences in rock type and preservation. The latter two factors can be easily accounted for. However, the degree to which variation among the phenotypes of individual organisms represents genetic variation among true biological populations cannot be addressed directly by the field of paleontology (Hageman, 2002). Nevertheless, examining the relationship between geographic and stratigraphic morphological changes can provide a null model of the correlation between morphology and environment that provides a means to control each of these factors through space and time in an effort to decipher process from pattern.

Paleobiological studies often rely on morphological changes as a means of characterizing species variability. In such cases, it must be determined whether differences in environmental variables (temperature, substrate conditions, salinity, etc.) are at least associated with, if not necessarily causing, different morphotypes within a species. This hinges on the ability to recognize accurately environmental signals within the available deposits. In the fossil record, the ability to link species to counterparts from modern environments provides a valuable gauge for understanding the relationship between species traits and environmental factors in preserved assemblages (e.g., Stanley and Yang, 1987; Cheetham and Jackson, 1995, 1996). This kind of information is necessarily lacking from older settings. Many Paleozoic studies rely on lithology, sedimentological characteristics, or larger-scale ecological associations to gain insight into environmental conditions. These approaches are certainly valuable, yet they potentially lack the resolution necessary to recognize subtle environmental shifts that may be coinciding with morphological trends, especially within depositional settings consisting of single lithofacies (Holland *et al*., 2001; Levy, 2003). What's more, being able to characterize the geographic component of temporal patterns 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.

The deposits of the Cincinnatian Series in its type locality are an ideal geologic setting in which to conduct spatial and temporal analyses of morphological change in *Flexicalymene granulosa*. The richly fossiliferous Kope Formation, a 70 meter thick stratigraphic interval of approximately 2 million years duration (Holland *et al.,* 2000), is currently the basis for ongoing, high-resolution correlation studies across a wide geographic area. Specimens of *F. granulosa* are sufficiently abundant throughout this interval and across all spatial environmental gradients. Environmental gradients within this setting have been modeled in detail and provide a quantitative model of shifting environments through space and time.

METHODOLOGY AND RESULTS

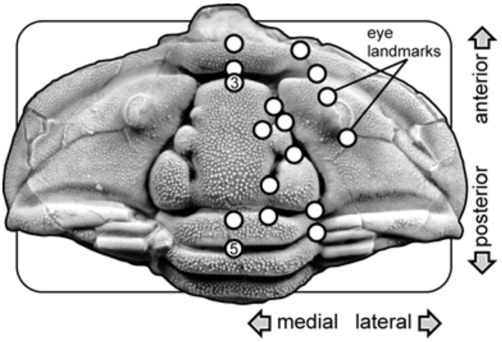

Figure 1. Landmarks on the cranidium of each specimen, after reflection, used in this analysis.

Initial research on the trilobite *Flexicalymene granulosa* has shown a significant correspondence between cranidial landmark positions and environment as quantified using Detrended Correspondence Analysis (Webber and Hunda, 2007). In this study, morphological change is measured using geometric morphometrics, or landmark-based analyses (Fig. 1), which quantifies shape and shape change at high resolution within an integrated morphological complex (e.g., Haney *et al*., 2001; Webster *et al*., 2001; Kim *et al*., 2002). This technique provides a more detailed characterization of morphology and morphological change than is possible with traditional morphometrics (e.g., measurements along single dimensions like length and width). A highly resolved characterization of environmental change is acquired through a bed-by-bed application of gradient analysis applied to strata of the type Cincinnatian by Holland *et al*. (2001) and Miller *et al*. (2001). Gradient analysis numerically evaluates the distribution and abundance of fossil remains and has been used to ordinate taxa according to underlying ecological gradients (e.g., Cisne and Rabe, 1978; Springer and Bambach, 1985; Patzkowsky, 1995). This has been shown to be a valuable tool for recognizing environmental signals, rather than relying on lithologic characteristics alone (Holland *et al*., 2001; Miller *et al*., 2001; Scarponi and Kowalewski, 2004). This suggests a relationship between cranidial shape and environment in the Kope Formation (Fig. 2).

Because the spatial and temporal components of this relationship have not been fully resolved at this point, it has not been determined whether morphological trends within *F. granulosa* represent evolution or habitat tracking of phenotypes in response to shifts in environmental gradients through time. This can be addressed by analyzing the morphology in nearly contemporaneous assemblages along spatial environmental gradients. To assess geographic variation, 239 specimens of *F. granulosa* were collected from a single bed correlated at seven localities of the Alexandria submember of the Kope Formation

(Cincinnatian Series). These sections are arranged along a southeast-to-northwest transect that spans approximately 98 kilometers. Geometric morphometric analyses have revealed phenotypic plasticity within *F. granulosa* that corresponds to an environmental gradient as proxied by water depth. This pattern mirrors that of previous analyses conducted by Webber and Hunda (2007).

CONCLUSIONS

This study of geographic variation in the trilobite *Flexicalymene granulosa* links paleoenvironmental variation expressed at a scale of no more than 10^3 years (Hunda *et al.*, 2006) to that which is persistent and evident across 2,000,000 years. Previous analyses show that a significant portion of the intraspecific morphological variation in *F. granulosa* from the lower type Cincinnatian is related to environment as quantified by gradient analysis. This suggests that a stable and persistent selective regime is operating within the Kope Formation. It suggests that while overall morphology is almost static, subtle and persistent variations do exist and demonstrate non-random patterns.

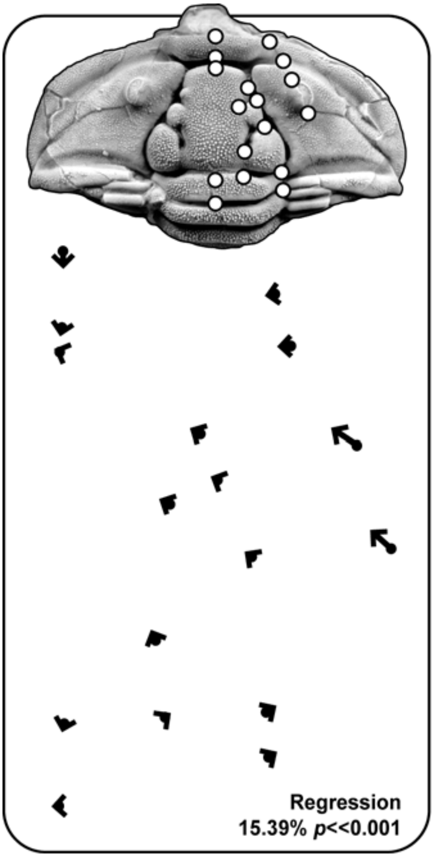

Figure 2. Vector diagram depicting the regression of DCA axis 1 sample scores against total morphological change (uniform and partial warps). Vectors indicate the portion of landmark movement that corresponds to DCA axis 1 scores.

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ORYCTOCEPHALID TRILOBITES FROM THE SIBERIAN PLATFORM

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Keywords: Oryctocephalids, early and middle Cambrian, stratigraphical distribution, Siberian Platform.

INTRODUCTION

Oryctocephalid trilobites existed at the late early Cambrian and middle Cambrian in the open-marine belt of the Siberian platform (Fig. 1). The rocks, in which they are found are widely distributed in the eastern part of the Siberian platform in the stratigraphical interval from the Botomian Stage to the Amgan Stage (Kuonamka and Inikan Formations). The maximum of genera and species diversity of the Oryctocephalids is on Ovatoryctocara and Kounamkites zones of the Amgan Stage. Oryctocephalids occur in many regions: Australia, North America, China (Shergold, 1969; Sunderg and McCollum, 2003; Sundberg, 1994; Yuan *et al.*, 2002; and others). Therefore those trilobites have high potential for interregional correlation. Lermontova (1940) studied the first Oryctocephalids from the Siberian Platform. She found and described several genera and species from Kuonamka Formation near the Anabar Uplift. In 1962 Chernisheva published an article on Siberian Oryctocephalids. Six genera and 12 species were described and the Oryctocephalidae family detailed characters were given in that article. The Siberian Oryctocephalids have not been studied since then.

SYSTEMATIC

Seven genera and 17 species of Oryctocephalids are now known from lower and middle Cambrian of the Siberian platform. New taxons of this family have been found in the Kuonamka Formation (Molodo River Section) (Fig. 1): *Sandoveria* sp. (Fig. 2, M, N), *Oryctocephalus granulatus* (sp. nov. 1) (Fig. 2, K, L), *Oryctocephalus* sp. nov. 2 (Fig. 2, Q, R), *Oryctocephalus* sp. nov. 3 (Fig. 2, T, U).

Besides these, some forms similar on morphology to the *Arthricocephalus* are found (Fig. 2, E, F). These finds considerably expand family of Oryctocephalidae on the Siberian Platform, and also allow more reliable correlations with middle Cambrian rocks from other regions. So, the finds of the representatives of the *Sandoveria* also are characteristic for the lower part of middle Cambrian of Australia. Numerous species of the *Arthricocephalus* genus are present in the Cambrian of China.

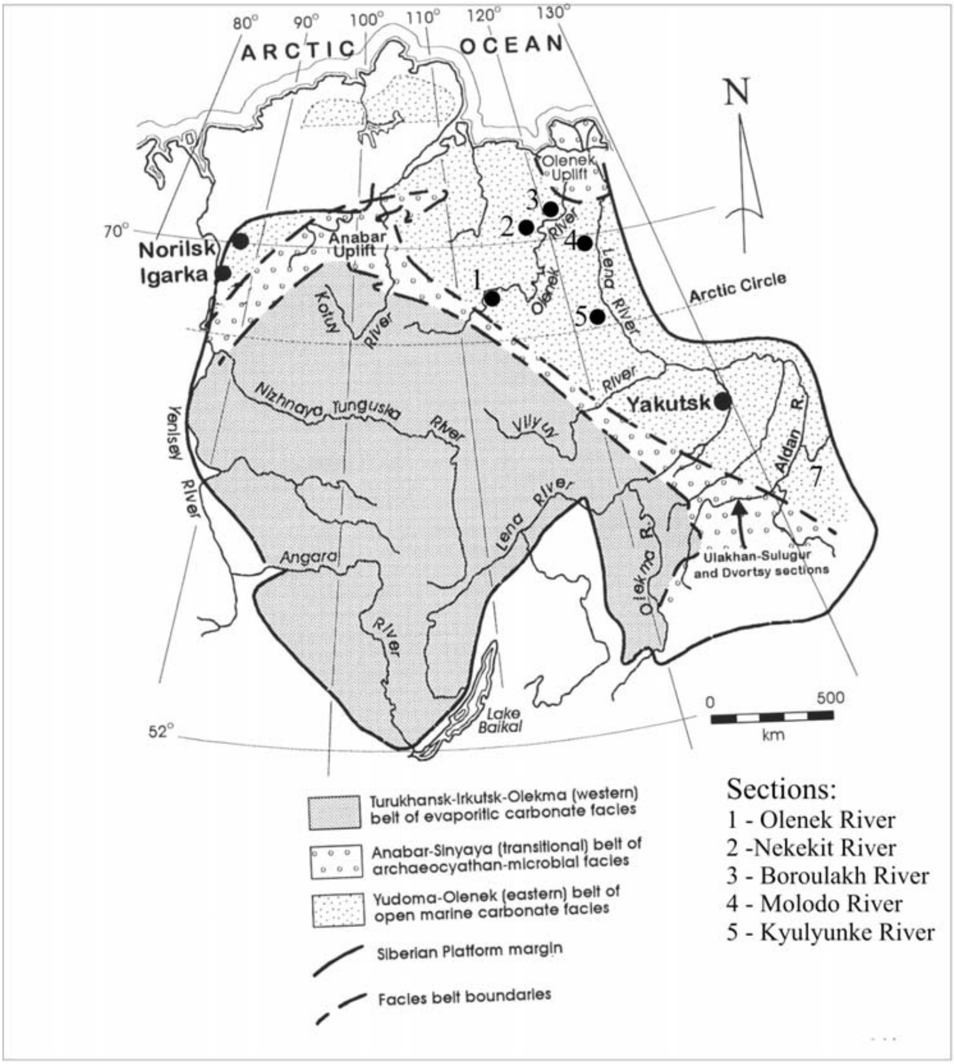
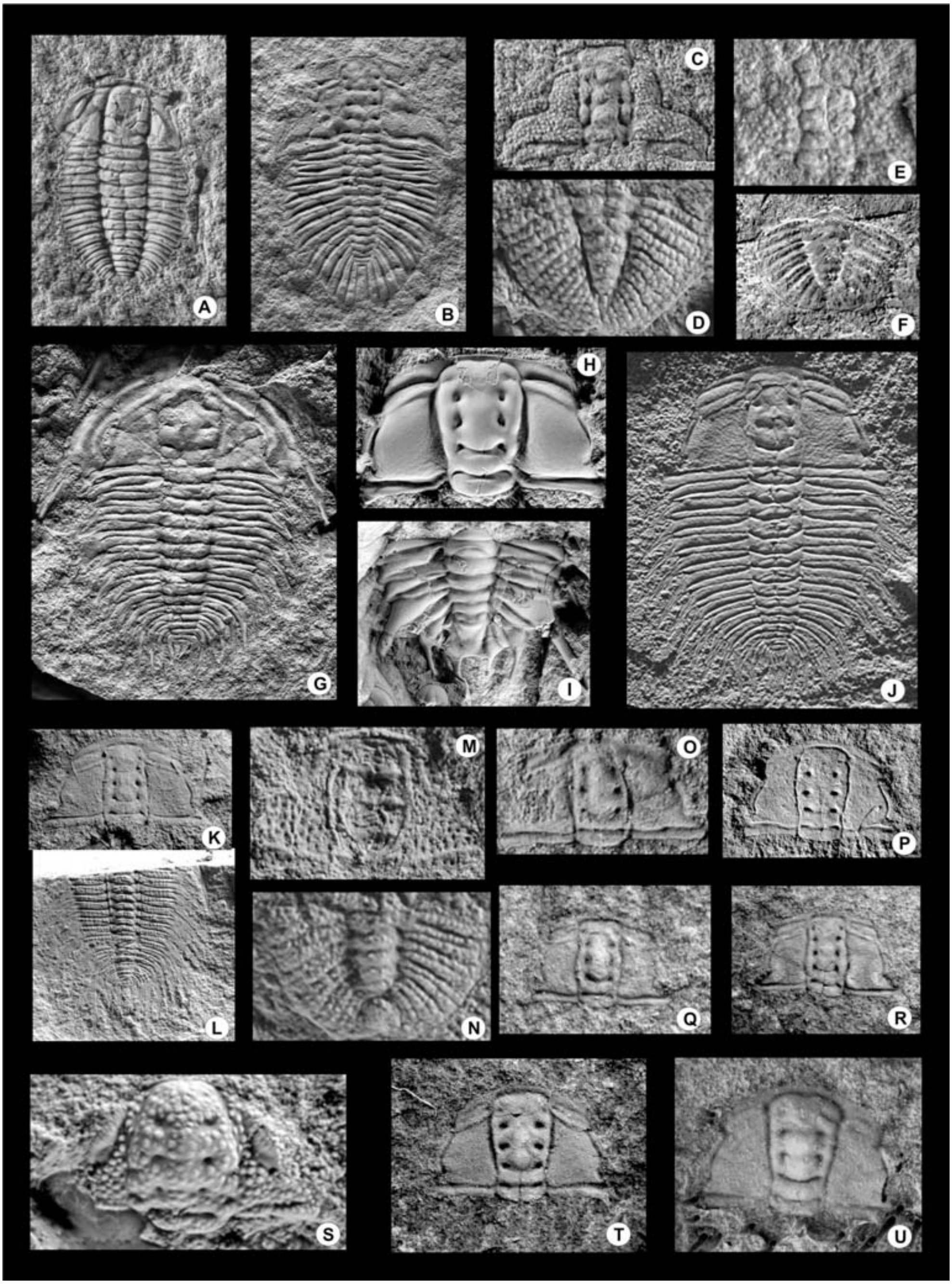


Figure 1. Map of the Siberian Platform, showing major modern rivers, distribution of major facies belts in late early middle Cambrian and major section of the Kuonamka Formation with Oryctocephalids.

Figure 2. Oryctocephalid trilobites from the Molodo River Section (Kuonamka Formation, early middle Cambrian). A, *Cheiruroides arcticus* N.Tcher., 1962, x 3, dorsal exoskeleton, N06/10a, Ovatoryctocara zone. B, *Ovatoryctocara ovata* (N.Tchern., 1960), x 4, dorsal exoskeleton, N06.3a, Ovatoryctocara zone. C-D, *Ovatoryctocara granulata* N.Tchern., 1962, Ovatoryctocara zone; C, cranidium, x 5, N06/4b(1); D, pygidium, x 8, N06/4b(2). E-F, *Arthricocephalus* sp., Ovatoryctocara zone; E, cranidium, x 4,5, N20a; F, pygidium, x 4, N20a(1). G, *Oryctocephalops frischenfeldi* Lerm., 1940, dorsal exoskeleton, x 6, N15a, Ovatoryctocara zone. H-I, *Oryctocephalus renoldsiformis* Lerm., 1940, Ovatoryctocara zone; H, cranidium, x 4, N06/15a(1); I, pygidium, x 4, N06/15(2). J, *Oryctocephalus reticulatus* (Lerm., 1940), dorsal exoskeleton, x 3, N24, Kounamkites zone. K-L, *Oryctocephalus granulosus* (sp. nov. 1), Kounamkites zone; K, cranidium, x 2,5, N28(1); L, pygidium, x 2,5, N28(2). M-N, *Sandoveria* sp., Ovatoryctocara zone; M, cranidium, x 4, N8(1); N, pygidium, x 4,5, N8(2). O, *Oryctocephalus reticulatus*? (Lerm., 1940), cranidium, x 3, N11b, Kounamkites zone. P, *Oryctocephalus*



vicinus N.Tchern., 1962, cranidium, x 2, N29, Kounamkites zone. Q-R, *Oryctocephalus* sp. nov. 2, Kounamkites zone; Q, cranidium, x 2,5, N31(1); R, cranidium, x 2,5, N31(2). S, Oryctocephalidae gen. et sp. indet, cranidium, x 4, N 06/27a, Kounamkites zone. T-U, *Oryctocephalus* sp. nov. 3, Kounamkites zone. T, cranidium, x 3, N31(3); U, cranidium, x 3, N32(1).

The family Oryctocephalidae is divided into three subfamilies: Oryctocephalinae, Tonkinellinae and Cheiruroidinae.

Subfamily Cheiruroidinae consists of one genus - *Cheiruroides*. On the Siberian platform 4 species are known: *Cheiruroides gracilis, Cheiruroides arcticus* (Fig. 2, A), *Cheiruroides maslovi* and *Cheiruroides fortis*. The most widespread are the first two species.

Subfamily Tonkinellinae on the Siberian platform is limited to three genera: *Ovatoryctocara, Tonkinella, Arthricocephalus*. The finds of the *Ovatoryctocara* are numerous in the lower part of the middle Cambrian, while the other two genera are seldom found.

Ovatoryctocara originally was included in the *Oryctocara* genus as subgenus (Chernisheva, 1962), which was included into Oryctocarinae. It was later allocated in an independent genus (Suvorova, 1964). It is known with the species: *Ovatoryctocara granulata* (Fig. 2, C, D), *Ovatoryctocara angusta* and *Ovatoryctocara ovata* (Fig. 2, B). *Ovatoryctocara angusta* is assigned to this genus with some reserves, as the species was established based only on the description of cranidia.

Arthricocephalus. Trilobites assigned to this genus in the Siberian platform were earlier described as *Oryctocara snegirevae* (Suvorova, 1964: 236).

Tonkinella. On the Siberian platform the following species have been found: *Tonkinella valida*, *Tonkinella khorbusuonkensis,* and *Tonkinella* ex gr. *flabelliformis* (Chernisheva, 1962: 33).

Subfamily Oryctocephalinae includes three genera: *Oryctocephalus, Oryctocephalops* and *Oryctocephalites*.

Oryctocephalites. One species on the Siberian platform - *Oryctocephalites incertus* is known.

Oryctocephalops. On the Siberian platform there is only one species - *Oryctocephalus frischenfeldi* (Fig. 2, G). The structure of glabella is very similar to that of *Oryctocephalites*, but glabellar furrows are very narrow.

Oryctocephalus. On the Siberian platform 4 species are known: *Oryctocephalus reticulates* (Fig. 2, J, O), *Oryctocephalus reynolsiformis* (Fig. 2, H, I), *Oryctocephalus vicinus* (Fig. 2, P), and *Oryctocephalus limbatus.* It is necessary to note that there are many forms which have attributes slightly different from the specified species. There is no absolute confidence whether these are local variants or it is new species. The study of this question requires additional and more detailed researches.

STRATIGRAPHICAL DISTRIBUTION

Oryctocephalids are distributed on the Siberian platform in the second part of the lower Cambrian and in the early middle Cambrian (Amgan Stage) (Fig. 3). These genera and species have very narrow stratigraphical intervals of distribution making them important for correlation of Siberian sections and for correlation with other regions.

Cheiruroides is distributed in the Lermontovia dzevanovskii-Paramicmacca petropavlovskii Zone (Toyonian Stage) and in the lower part of the Ovatoryctocara Zone (Amgan Stage). *C. gracilis* occurs in the middle part of this zone. *C. maslovi* and *C. fortis* occur in upper part of the Lermontovia dzevanovskii - Paramicmacca petropavlovskii Zone. *C. arcticus* is distributed in lower part of Ovatoryctocara Zone.

Ovatoryctocara is represented on the Siberian Platform by three species *O. ovata, O. granulata* and *O. angusta*. The finds of these species are dated basically for the first zone of the middle Cambrian: Ovatoryctocara Zone. But first two species also occur in the lower part of the Kounamkites Zone.

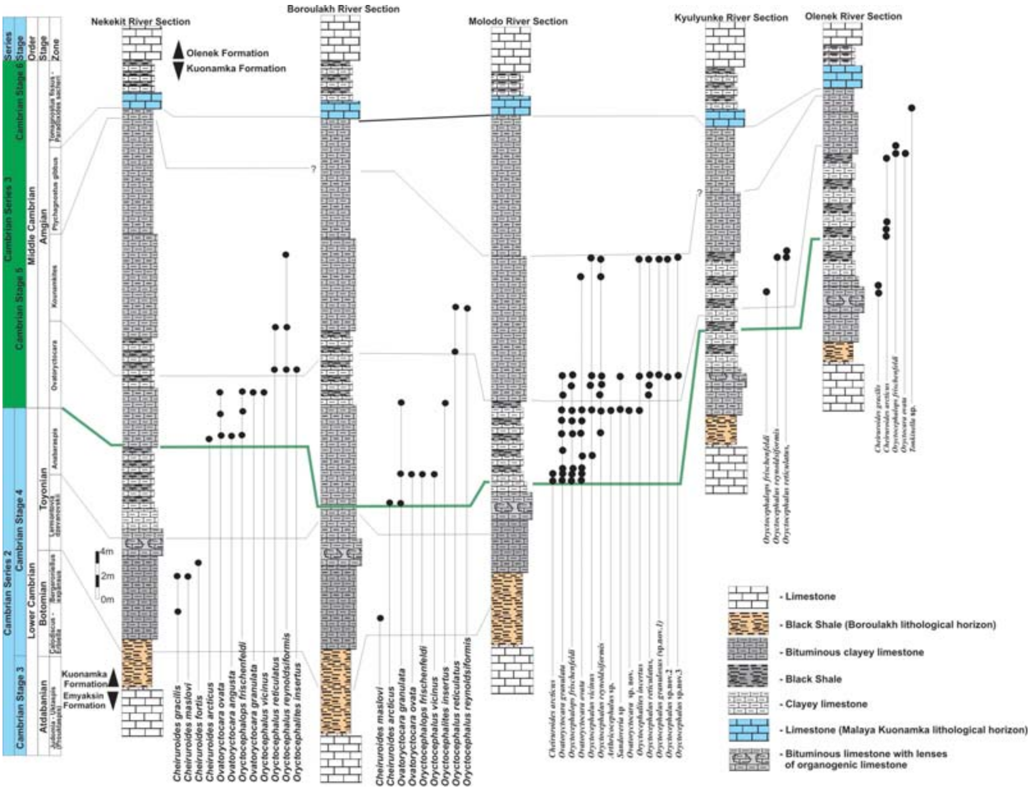


Figure 3. Stratigraphical distribution of Oryctocephalids in the Kuonamka Formation.

Artricocephalus is represented on the Siberian Platform by a single species (*A. snegirevae*). It is found in the lower part of the middle Cambrian.

Oryctocephalops occurs in two zones of the middle Cambrian: Ovatoryctocara and Kounamkites zones. It is represented by one species, *O. frischenfeldi*.

Oryctocephalus is also found in the Ovatoryctocara and Kounamkites zones. *Oryctocephalus vicinus* and *Oryctocephalus limbatus* occur in the middle part of the Ovatoryctocara Zone. *Oryctocephalus reticulatus* is characteristic for the Kounamkites Zone. *Oryctocephalus reynoldsiformis* occurs in Ovatoryctocara and Kounamkites zones.

Oryctocephalites, represented by the *O. incertus*, occurs in the second half of the Ovatoryctocara Zone, and it is also found in the upper part of the Kounamkites Zone.

Tonkinella. From the three species which occur on the Siberian platform, only the stratigraphical position of *Tonkinella khorbusuonkensis* has been determined with precision. The findings are dated within Triplagnostus gibbus and Tomagnostus fissus zones (Amgan Stage) (Solovjev, 1988).

It is impossible to determine the precise stratigraphical position of two other species (*Tonkinella* ex gr. *flabelliformis* and *Tonkinella valida*), which were described by Chernisheva (1962). She specified that these species occurred in the lower part of the middle Cambrian. Other co-occurring trilobites were not specified and thus we can’t specify a zone.

Besides these species, several other new species were found in the Molodo River Section (*Sandoveria* sp. and several new representatives of *Oryctocephalus*). The findings of *Sandoveria* sp. are located in the upper part the Ovatoryctocara Zone to the lower part of the Kounamkites Zone. All new forms of *Oryctocephalus* (*O. granulosus* sp. nov. 1, *Oryctocephalus* sp. nov. 2, *Oryctocephalus* sp. nov. 3) are found in the Kounamkites Zone.

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SPECIES RELATIONSHIPS IN THE PTYCHAGNOSTIDAE (CAMBRIAN, AGNOSTINA)

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Keywords: Ptychagnostidae, ?Trilobita, Cambrian, morphology, cladistic analysis.

INTRODUCTION

Disparate views of the taxonomy of the Ptychagnostidae have been presented by Öpik (1979), Laurie (1988, 1989), Robison (1982, 1984, 1994), Westrop *et al*. (1996) and Peng and Robison (2000). Öpik (1979) recognised 15 genus group names, and Laurie (1988, 1989) 12, while Robison (1984) recognised only five. Westrop *et al*. (1996) undertook a cladistic analysis of 42 species from the family, using *Agnostus pisiformis* and *Peronopsis brighamensis* as outgroups. The result was recognition of monophyletic groups such as *Aotagnostus* (Pl. 1, Figs 15-17) and *Goniagnostus* (Pl. 1, Figs 27-30, 34) however these were subsumed in a large, confused group of species which Westrop *et al*. (1996) referred to as *Ptychagnostus sensu lato*. Outside this, only *Lejopyge* and *Pseudophalacroma* were recognised as monophyletic groups. Consequently, Westrop *et al*. (1996) stated that their analysis did not support the "finely divided, gradistic classifications of Öpik (1979) or Laurie (1988, 1989) but are consistent with Robison's (1982) more conservative approach".In this paper, I attempt to demonstrate that the species belonging to the Ptychagnostidae can be readily divided into several groups, which reasonably should be assigned generic names. I also attempt to demonstrate that the 'conservative' approach of Robison (1982, 1984, 1994) and Peng and Robison (2000) is untenable.

WHAT IS A GENUS?

The genus should refer to the minimum number of species possible, as long as that group of species can be distinguished synapomorphically from all other species. This is not the approach adopted by Robison (1984, 1994). He has 'large' genera embracing many species and states that his taxonomic subdivisions parallel those of Öpik (1979), but that he prefers to recognise fewer genera (Robison, 1984, p. 10). Other than this stated preference, no reasons for recognising fewer genera are given. This is surprising given he believed *Ptychagnostus* to be paraphyletic. Although largely following the generic arrangements of Robison (1984, 1994), and similarly not elaborating on reasons for recognising fewer genera, Peng and

Robison (2000), used the results of the cladistic analysis of Westrop *et al*. (1996) to justify this small coterie of genera. However, one group which consistently appeared as monophyletic in all analyses of Westrop *et al*. (i.e., *Aotagnostus*) was ignored by Peng and Robison (2000). Thus, it appears their recognition of a genus is simply a matter of taste.

Unless we wish to be doomed to ever circling arguments over whose preference is to be preferred, we need a standard reproducible method of defining genera. Despite its many shortcomings, cladistic analysis is the only reasonable way of generic definition, if only because it is the most rigorous way of ordering morphological data. The genus could therefore be defined at a node close to the terminal taxa on a cladogram, and hence defined by at least one synapomorphy, provided all the relevant species are included in the analysis. 'Relevant species' would presumably mean all those species assigned to the particular higher taxon (family, subfamily) under study. This is itself a contentious point, in that not everyone agrees on what species belong in the Ptychagnostidae.

PREVIOUS ANALYSIS

Hasn't the cladistic analysis of Westrop *et al*. (1996) demonstrated that most of Öpik's genera are not able to be characterised by synapomorphies? I do not believe so. This is because in the analysis of Westrop *et al*. (1996), numerous morphological features were not included in the analysis. When I excavate a pygidium of any of the species *seminula*, *semiermis*, *hybridus* or *mundus* (which I would assign to *Onymagnostus*), I know as soon as I see the axis that it belongs to this group of species. I am also sure that this is true for other practitioners. Why can I immediately recognise an *Onymagnostus* pygidium as clearly distinct from an *Acidusus* pygidium, when according to the data matrix of Westrop *et al*. (1996), the only pygidial difference is that *Onymagnostus hybridus* lacks a postaxial median furrow? This is because they do not include the distinctly different convexity in their matrix. Furthermore, Westrop *et al*. (1996, p. 809) maintain that the only difference between the cephala of *O. hybridus* (Pl. 1, Figs 21-22) and *A. atavus* is that *O. hybridus* has short or slightly elongate basal lobes, while those of *A. atavus* are elongate. Nowhere do they mention the difference in the expansion or the posterior inflation of the

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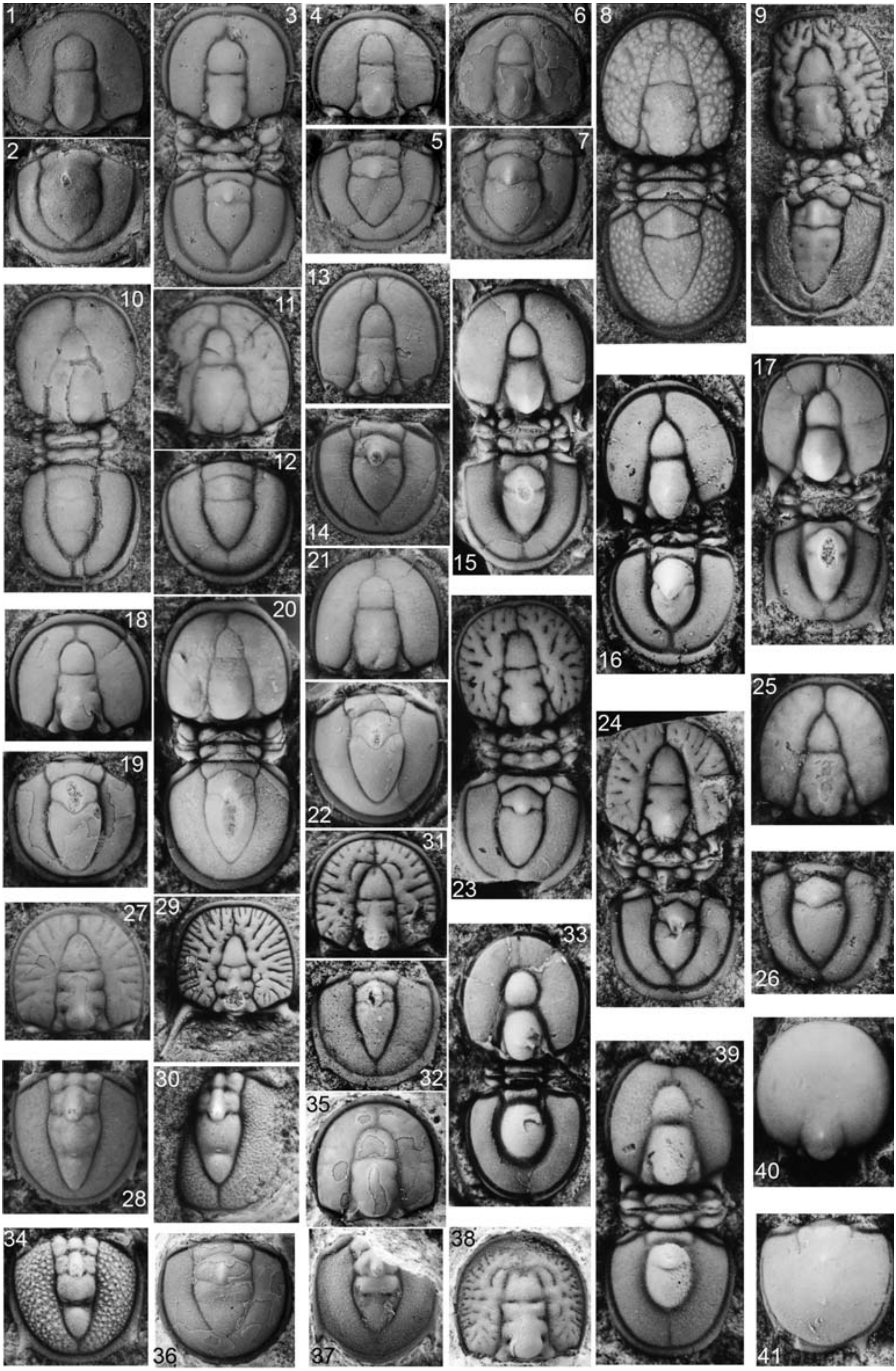
Plate 1 (opposite). Species of Ptychagnostidae. Repositories: NTM, Northern Territory Museum, Darwin; CPC, Commonwealth Palaeontological Collection, Geoscience Australia, Canberra; SGU, Swedish Geological Survey, Uppsala. 1-2, *Pentagnostus krusei*; 1, cephalon, NTM P3358, x5.5; 2, pygidium, NTM P3574, x6.5; 3, *Pentagnostus anabarensis*, complete carapace, CPC 37642, x6; 4-5, *Pentagnostus praecurrens*; 4, cephalon, CPC 37678, x4.5; 5, pygidium, CPC 37685, x4.5; 6-7, *Pentagnostus shergoldi*; 6, cephalon, NTM P3508, x4.5; 7, pygidium, NTM P3526, x5.5; 8, *Ptychagnostus punctuosus*, complete carapace, CPC 14190, x6.5; 9, *Ptychagnostus affinis*, complete carapace, latex mould, CPC 14198, x6; 10, *Zeteagnostus incautus*, complete carapace, latex mould, CPC 14239, x9; 11-12, *Zeteagnostus sinicus*; 11, cephalon, CPC 25679, x6; 12, pygidium, CPC 25680, x7.5; 13-14, *Triplagnostus gibbus*; 13, cephalon, SGU specimen with 4894, x3; 14, pygidium, SGU specimen with 4896, 4895, x3; 15, *Aotagnostus culminosus*, complete carapace, CPC 14166, x5; 16, *Aotagnostus aotus*, complete carapace, CPC 14151, x4.5; 17, *Aotagnostus magniceps*, complete carapace, CPC 14164, x6.5; 18-19, *Onymagnostus semiermis*; 18, cephalon, CPC 14294, x4; 19, pygidium, CPC 14279, x4.5; 20, *Onymagnostus mundus*, complete carapace, CPC 14281, x5.5; 21-22, *Onymagnostus hybridus*; 21, cephalon, CPC 14269, x4.5; 22, pygidium, CPC 14274, x5; 23, *Acidusus acidusus*, complete carapace, CPC 14248, x5.5; 24, *Acidusus occultatus*, complete carapace, CPC 14257, x6; 25, ?*Acidusus cassis*, cephalon, CPC 14261, x7; 26, ?*Acidusus leptus*, pygidium, CPC 25654, x7; 27-28, *Goniagnostus nathorsti*; 27, cephalon, SGU 4957, x4.5; 28, pygidium, SGU 4958, x5; 29-30, *Goniagnostus spiniger*, 29, cephalon, CPC 14342, x4; 30, partial pygidium, CPC 14344; x5; 31-32, *Criotypus lemniscatus*; 31, cephalon, CPC 14316, x4; 32, pygidium, CPC 14314, x5; 33, *Myrmecomimus saltus*, complete carapace, CPC 14188, x10.5; 34, *Goniagnostus fumicola*, pygidium, CPC 5840, x4; 35-36, *Tomagnostus fissus*; 35, cephalon, SGU 4841, x5.5; 36, pygidium, SGU 4839, x5; 37-38, *Tomagnostus perrugatus*; 37, partial pygidium, SGU 4855, x5.5; 38, cephalon, SGU 4854, x5.5; 39, *Myrmecomimus tribulis*, complete carapace, CPC 14179, x10; 40-41, *Lejopyge armata*; 40, cephalon, CPC 14349, x5.5; 41, pygidium, CPC 3615, x6.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posteroglabella, nor the position of the glabellar node. The conversion of "observed organismal variation into a data matrix has been considered as subjective, contentious, under-investigated, imprecise, unquantifiable, intuitive" (Hawkins, 2000, p. 22) and yet is the most important phase of any cladistic analysis. It needs to be taken much more seriously.

THIS ANALYSIS

While no cladistic analysis can ever deal with all the morphological characters of an organism, as the list of possible characters is effectively infinite, the process of character selection is 'unregulated' such that any characters can be selected and analysed. Character selection is essentially an hypothesis which subsequent workers can attempt to argue against. Such an argument can take two forms: either the selected characters and character states will be dismissed because they apparently lack rigour; or selected characters will be dismissed and other characters proffered. While the former can be countered by defining the characters and their states as rigorously as possible, the latter cannot be countered as it becomes a 'yes it is', 'no it isn't' argument.

The characters selected for this analysis are largely restricted to characters reflecting the morphological parameters of the glabella and pygidial axis, as I consider characters relating to spinosity, surface ornament, border width, etc., to, at best, simply confuse the analysis. This is of course making a priori assumptions, but this is done because numerous closely related species belonging in established genera often vary only in such characters as spinosity, surface ornament, border width and axial length. These characters are therefore not used. The characters selected here are as follows:

1. Taper of posteroglabella. This is a ratio given by distance between axial furrows level with F3 divided by distance between axial furrows at F1. This was expected to effectively be a continuous variable, but turned out not to be so. The states are: 0, Very weakly tapered; 1, Weakly tapered; 2, Moderately tapered; 3, Strongly tapered; 4, Very strongly tapered.
2. Expansion of posteroglabella. This describes whether the axial furrow between F1 and F3 is evenly convex abaxially. The states are: 0, Not expanded; 1, Expanded.
3. Basal lobes. This describes the shape and extent of the basal lobes. The states are: 0, Short; 1, Elongate with depressed anteriors; 2, Elongate with well developed anterior lobe; 3, Elongate with effaced anteriors.
4. Development of appendiferal pits. This describes the development of appendiferal pits adjacent to the anterior extremities of the basal lobes. The states are: 0, Absent; 1, Weak; 2, Strong.
5. Position of glabellar node. This is a ratio given by the distance of the glabellar mode from the rear of the posteroglabella divided by the sagittal length of the posteroglabella. This was expected to be a continuous variable, but, provided the measurements are obtained from late holaspides only, turned out not to be so. The states are: 0, Strongly posterior; 1, Moderately posterior; 2, Medial; 3, Moderately anterior; 4, Strongly anterior
6. Arcuate scrobicules. This refers to the presence or absence of large arcuate scrobicules. States are: 0, Present; 1, Absent
7. Posterior inflation of posteroglabella. This refers to the variation in height of the posterior portion of the posteroglabella. The states are: 0, Weakly inflated; 1, Moderately inflated; 2, Strongly inflated.
8. Development of preglabellar axial furrow. This refers not to whether this feature is well developed or weakly developed, but to whether it is developed evenly or variably from posterior to anterior. The

taxon\character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Pentagnostus krusei	1	0	0	0	1	1	2	0	0	0	1	0	0	2	0	0
Ptychagnostus punctuosus	2	1	2	0	3	1	0	2	1	2	1	1	0	2	1	0
Ptychagnostus affinis	2	0	2	0	3	1	0	2	1	2	1	1	0	2	1	0
Zeteagnostus incautus	4	1	3	0	1	1	0	2	0	1	0	0	0	0	0	0
Zeteagnostus sinicus	3	1	3	0	2	0	0	2	1	2	1	0	0	0	0	0
Pentagnostus praecurrens	1	0	0	1	2	0	2	2	1	2	1	0	0	2	0	0
Pentagnostus anabarensis	0	0	0	1	1	0	2	1	1	1	1	0	0	2	0	0
Pentagnostus shergoldi	1	0	0	1	2	0	2	2	1	2	1	1	0	2	0	0
Triplagnostus gibbus	1	0	2	1	1	0	2	2	1	2	2	1	0	2	0	0
Aotagnostus culminosus	2	0	1	0	1	1	2	2	1	2	2	2	0	0	0	0
Aotagnostus aotus	2	0	1	0	2	1	2	2	1	2	2	2	0	0	0	0
Aotagnostus magniceps	2	0	1	0	1	1	2	2	1	2	2	2	0	0	0	0
Onymagnostus semiermis	2	0	1	1	2	0	0	2	1	2	1	1	0	0	0	1
Onymagnostus mundus	2	1	1	0	2	1	0	2	1	2	1	1	0	2	0	1
Onymagnostus hybridus	2	1	1	0	3	1	0	2	1	2	1	1	0	2	0	1
Acidusus atavus	2	0	2	0	1	0	1	2	1	2	1	1	0	4	0	0
Acidusus cassis	3	0	2	0	1	1	1	2	1	2	1	1	0	?	0	0
Acidusus occultatus	2	0	2	0	1	1	1	2	1	2	1	1	0	4	0	0
Acidusus leptus	3	0	2	0	1	1	1	2	1	2	1	1	0	4	0	0
Acidusus aculeatus	2	0	2	0	1	1	1	2	1	2	1	2	1	0	0	0
Goniagnostus nathorsti	1	0	0	2	0	1	2	2	1	2	1	1	1	3	2	0
Goniagnostus spiniger	1	0	0	2	0	1	2	2	1	2	1	1	1	3	2	0
Goniagnostus fumicola	1	0	0	2	0	1	2	2	1	2	1	1	1	3	2	0
Criotypus oxytorus	1	0	0	2	0	0	2	2	1	2	1	1	0	3	0	0
Criotypus lemniscatus	1	0	0	2	0	0	2	2	1	2	1	1	0	3	1	0
Pseudophalacroma lundgreni	3	1	0	0	2	1	0	2	0	1	0	1	0	0	0	0
Pseudophalacroma scanense	3	1	0	0	2	1	0	2	0	1	0	1	0	0	0	0
Tomagnostus fissus	1	0	1	1	4	1	0	2	1	2	1	1	0	1	2	1
Tomagnostus perrugatus	0	0	0	2	3	0	0	2	1	2	1	1	0	1	2	0

Figure 1. Character matrix for Ptychagnostidae.

states are: 0, Developed as weak depression in front of glabella; 1, Developed as furrow shallowing anteriorly; 2, Evenly developed along entire length.

9. Development of pygidial F1. This describes the development of the pygidial F1 furrow. The states are: 0, Weak; 1, Well developed.
10. Development of F2. This describes the development of the pygidial F2 furrow. The states are: 0, Absent; 1, Weak; 2, Well developed.
11. Height of pygidial axial node. This describes the vertical development of the pygidial axial node. The states are: 0, Low; 1, Moderate; 2, High.
12. Posterior extent of pygidial axial node. This describes the horizontal extent of the pygidial axial node in the effect it has on the F2 furrow. The states are: 0, Minimal or no flexing of F2; 1, Moderate flexing of F2; 2, Extreme flexing of F2
13. Subdivision of M1 lobe. This describes whether the M1 lobe of the pygidial axis is subdivided by two exsagittal furrows into three portions. The states are: 0, Not subdivided; 1, Subdivided.
14. Presence of secondary axial node. This describes whether there is a secondary pygidial axial node on the posteroaxis and where it is located. The states are: 0, Absent; 1, Anterior; 2, Medial; 3, Posterior; 4, Terminal.
15. Presence of transverse depression on posteroaxis. This describes the presence or absence and degree of development of the transverse furrow associated with the secondary pygidial axial node. The states are: 0, Absent; 1, Weak; 2, Strong.
16. Pygidial convexity. This describes the orientation of the pygidial axis and indicates the convexity of the pygidial acrolobe. The states are: 0, Axis inclined rearwards; 1, Axis horizontal.

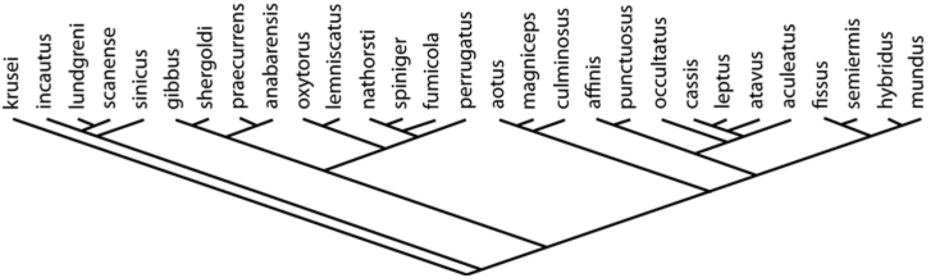

Figure 2. Majority consensus cladogram obtained by parsimony analysis of the character matrix (Fig. 1).

The species *Pentagnostus krusei* Laurie, 2006 was selected as the outgroup as it is the oldest possible ptychagnostid species in the Georgina Basin, preceding the appearance of both *Pentagnostus anabarensis* and *P. praecurrens* (Laurie, 2004, 2006). It shows some character states which would in the past have led it to be assigned to '*Peronopsis*', which belongs to a putative sister-group of the Ptychagnostidae. The parsimony analysis was performed using the palaeontological statistics package, PAST (Hammer *et al*., 2001). Because of the large number of species analysed, a Heuristic (Nearest Neighbour Interchange) algorithm with Fitch optimisation was used. While there are shortcomings to the heuristic algorithms in PAST, this is a preliminary analysis and precedes a more sophisticated analysis currently under way. Species assigned to the genera *Lejopyge* were excluded from the analysis because of the difficulty in coding effaced morphologies. Similarly, species assigned to *Myrmecomimus* were excluded from the analysis because of their small size and very unusual morphology.

CONCLUSIONS

Unlike the analysis of Westrop *et al*. (1996), the majority consensus tree (Fig. 2) generated from the data matrix (Fig. 1), shows clearly defined groupings of taxa. The first of these comprises *Zeteagnostus incautus* (Pl. 1, Fig. 10), *Z. sinicus* (Pl. 1, Fig. 11-12) *Pseudophalacroma lundgreni* and *P. scanense*. The association of *Zeteagnostus* and *Pseudophalacroma* was recognised by Westrop *et al*. (1996) and if confirmed by further analysis should perhaps lead to the suppression of *Zeteagnostus* in favour of *Pseudophalacroma*.

The second grouping comprises *Triplagnostus gibbus* (Pl. 1, Figs 13-14), *Pentagnostus shergoldi* (Pl. 1, Figs 6-7), *P. praecurrens* (Pl. 1, Figs 4-5) and *P. anabarensis* (Pl. 1, Fig. 3 and likewise, if confirmed by further analysis, should lead to the suppression of *Pentagnostus* in favour of *Triplagnostus*.

The third grouping comprises two subgroups. The first comprises *Criotypus oxytorus* and *C. lemniscatus* (Pl. 1, Figs 31-32), while the second comprises *Goniagnostus nathorsti* (Pl. 1, Figs 27-28), *G. spiniger* (Pl. 1, Figs 29-30), *G. fumicola* (Pl. 1, Fig. 34) and, strangely *Tomagnostus perrugatus* (Pl. 1, Figs 37-38). This arrangement could be used to argue for continued use of *Criotypus* and for *Goniagnostus*, but casts doubt on the assignment of *perrugatus* to *Tomagnostus*.

The fourth grouping comprises the species assigned to *Aotagnostus* by Laurie (1988). They are: *A. aotus* (Pl. 1, Fig. 16), *A. magniceps* (Pl. 1, Fig. 17) and *A. Culminosus* (Pl. 1, Fig. 15). This group was also recognised in the analysis of Westrop *et al*. (1996), but, as mentioned above, this was incorporated in a large confused group of species which they referred to *Ptychagnostus sensu lato*.

The fifth grouping again comprises two subgroups. The first comprises *Ptychagnostus punctuosus* (Pl. 1, Fig. 8) and *P. affinis* (Pl. 1, Fig. 9), while the second comprises *Acidusus occultatus* (Pl. 1, Fig. 24), *A. cassis* (Pl. 1, Fig. 25), *A. leptus* (Pl. 1, Fig. 26), *A. atavus* and *A. aculeatus*. As with *Criotypus* and *Goniagnostus* above, these groupings could be used to argue for the retention of *Acidusus* for the latter subgroup, and *Ptychagnostus* for the former.

The final grouping comprises *Tomagnostus fissus* (Pl. 1, Figs 35-36), *Onymagnostus semiermis* (Pl. 1, Figs 18-19), *O. hybridus* (Pl. 1, Figs 21-22) and *O. mundus*, (Pl. 1, Fig. 20) and argues for a common origin for these two generic taxa, and if this analysis is confirmed, could lead to suppression of *Onymagnostus*.

The recognition of such clear groupings of species argues for the concentration on features of the glabella and pygidial axis when attempting cladistic analyses of agnostids. Similarly, it demonstrates that the analysis of Westrop et al. (1996) suffered from the inclusion of too many extra-axial characters, giving rise to a confused cladogram among which only a few small groups could be discerned. Finally it demonstrates that the assignment by Peng and Robison (2000) of *Zeteagnostus incautus*, *Z. sinicus*, *Triplagnostus gibbus*, *Pentagnostus shergoldi*, *P. praecurrens*, *P. anabarensis*, *Aotagnostus aotus*, *A. magniceps*, *A. culminosus*, *Ptychagnostus affinis*, *P. punctuosus*, *Acidusus occultatus*, *A. cassis*, *A. leptus*, *A. acidusus* and *A aculeatus* to the genus *Ptychagnostus*, while excluding taxa assigned to *Tomagnostus*, *Onymagostus*, *Criotypus* and *Goniagnostus* is untenable.

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TAXONOMIC REAPPRAISAL AND EVOLUTION OF THE FURONGIAN SAUKIID TRILOBITES FROM KOREA

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Keywords: Saukiidae, *Mictosaukia*, *Eosaukia*, Furongian, Gondwana, Laurentia, taxonomy, evolution.

INTRODUCTION

The family Saukiidae Ulrich and Resser, 1933 is one of the diverse groups of Furongian trilobites in the paleo-equatorial region. The saukiids have been considered valuable for biostratigraphic correlation in Laurentia and their phylogenetic studies have attempted to explore their relationship in the Ptychaspid Biomere (Longacre, 1970; Edgecombe, 1992). However, fundamental taxonomic disagreement of the Saukiidae in Laurentia seems to make its biostratigraphic and/or phylogenetic significances questionable (Raasch, 1951; Taylor and Halley, 1974; Ludvigsen and Westrop, 1983).

Taxonomy of the saukiids appears to be more chaotic in eastern Gondwana. While numerous monotypic genera have been established based on poorly preserved materials, some genera, such as *Lophosaukia* Shergold, 1972 and *Mictosaukia* Shergold, 1975, embrace a number of species. These two genera have been used for inter-regional correlation. However, *Mictosaukia* was somewhat ambiguously defined for the forms having assorted cranidial morphologies of previously described *Saukia* Walcott, 1914 and *Tellerina* Ulrich and Resser, 1933. Subsequently, many Gondwanan species formerly assigned to *Ptychaspis* Hall, 1863, *Calvinella* Walcott, 1914, *Saukia* Walcott, 1914, *Tellerina* Ulrich and Resser, 1933, and *Eosaukia* Lu, 1954 have been reassigned to this genus (Shergold, 1975, 1991) and *Mictosaukia* became a large taxon in Gondwana comprising 23 species. This causes one of the major problems in saukiid taxonomy (Zhou and Zhang, 1985; Fortey, 1994; Zhang et al., 1995).

Recently, well-preserved silicified specimens of saukiids have been collected from the lower Paleozoic Taebaeksan Basin in Korea (Fig. 1a). This study aims to describe the Korean saukiids, to refine the generic concepts, and to contribute to understand the saukiid paleogeography and phylogeny.

OCCURRENCE OF SAUKIIDS IN KOREA

Five Furongian trilobite faunas have been recognized from the Hwajeol and the Dongjeom formations: i.e. *Asioptychaspis*, *Quadraticephalus*, saukiid-dominated, *Pseudokoldinioidia*, and kainellid-dominated faunas in ascending order (Choi *et al*., 2003; Lee and Choi, 2007; Sohn and Choi, 2007). They are well correlated with the uppermost Cambrian biozones of North China. Five saukiid species have been recognized in the boundary interval between Hwajeol and Dongjeom formations (Fig. 1b).

Based on the Korean materials and re-examination of the holotype of *Eosaukia latilimbata* Lu, 1954, previously poorly defined *Eosaukia* can be treated as a saukiid endemic to the eastern Gondwana, which is more diverse than previously thought: it is characterized by strong convexity in cephalon, oblique anterolateral preglabellar furrows, palpebral lobes away from the axial furrows, occipital node or spine, and pauci-segmented pygidium with distinct ridges on terminal piece. The emended diagnosis of *Eosaukia* enables to transfer many species formerly assigned to *Mictosaukia* and *Calvinella* to *Eosaukia*. Four Korean saukiids are assigned to the genus: namely, *Eosaukia* n. sp., *E. micropora* (=*Calvinella micropora* Qian, 1985), *E. bella* (=*Ptychaspis bella* Walcott, 1906), and *E. acuta* (=*Calvinella acuta* Kuo and Duan in Kuo *et al*., 1982).

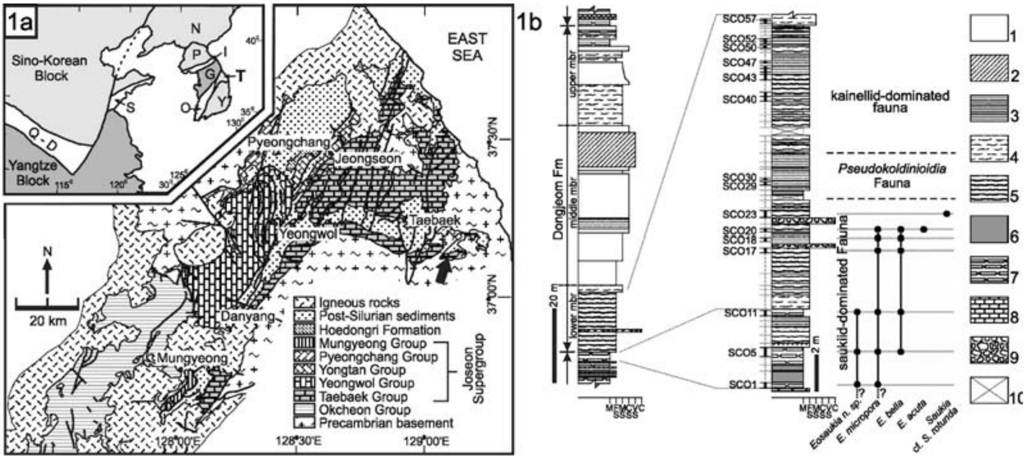
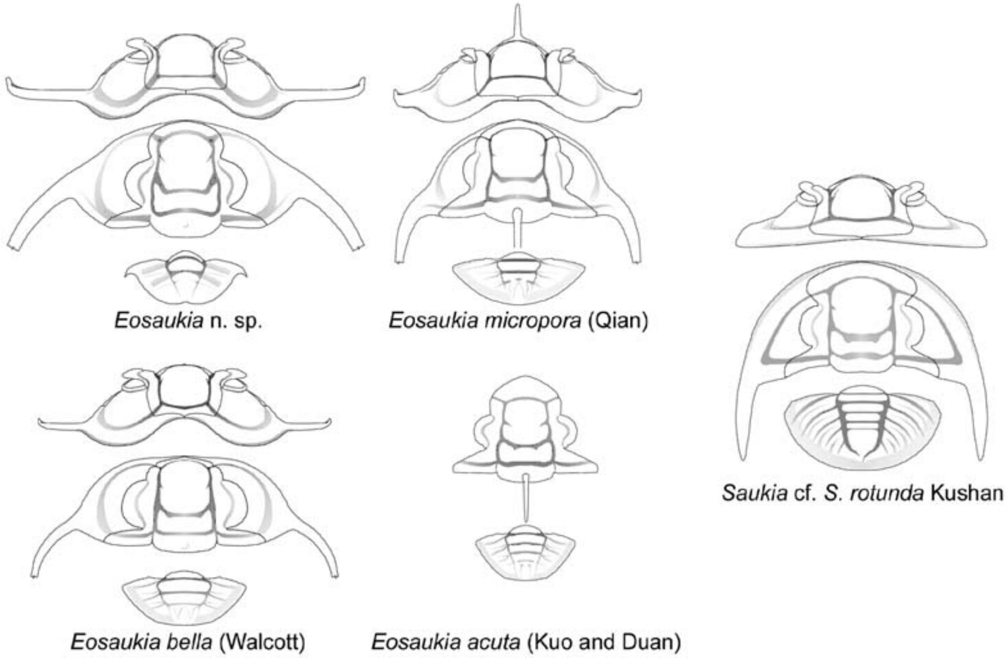


Figure 1. 1a. Simplified geologic map showing fossil locality (arrowed). 1b, Schematic stratigraphic columns indicating the occurrence of saukiids (modified from Lee and Choi, 2007). Legend: 1. massive or crudely stratified sandstone, 2. cross-stratified sandstone, 3. thinly-laminated sandstone, 4. sandstone intermingled with irregular mud layers, 5. thickly-laminated fine sandstone, 6. calcareous shale, 7. shale with limestone nodules, 8. limestone, 9. limestone conglomerate, 10. no outcrop.

The other Korean saukiid occurred in the highest stratigraphic level of the saukiid-dominated fauna can be referred to *Saukia* cf. *S. rotunda* Kushan, 1973 (Figs. 1b, 2). Previously, some species of *Saukia*, *Calvinella*, and *Tellerina* in Gondwana including *S. rotunda* have been transferred to *Mictosaukia* by Shergold (1975, 1991). However, these species are returned to *Saukia* herein based on low cephalic convexity, wide lateral border, and multi-segmented pygidium with broad border. Because the type species of *Mictosaukia* also has these features, *Mictosaukia* is regarded as a junior synonym of *Saukia*. All the species of *Mictosaukia* should be reassigned to *Eosaukia* or *Saukia*.


Eosaukia n. sp.

Eosaukia micropora (Qian)

Saukia cf. *S. rotunda* Kushan

Eosaukia bella (Walcott)

Eosaukia acuta (Kuo and Duan)

Figure 2. Dorsal and frontal reconstruction of the five saukiid species from the boundary interval of the Hwajeol and Dongjeom formations, Korea.

POSSIBLE PARAPHYLETIC EVOLUTION OF SAUKIIDS

The refined generic concepts enable to separate saukiids having Laurentian affinity from endemic forms in Gondwana. Saukiids occurred in both Gondwana and Laurentia (e.g. *Saukia*, *Prosaukia*) are characterized by multi-segmented pygidium with broad border, which are considered closely related to the Furongian dikelocephalid trilobites. Dikelocephalid affinity of Laurentian saukiids was advocated by Ludvigsen and Westrop (1983) and Ludvigsen *et al.* (1989). On the other hand, the Gondwanan forms (e.g. *Sinosaukia*, *Lophosaukia*, *Eosaukia*) possess small but wide pygidia with pauci-segmented axis and short border, which contrast to dikelocephalid-type pygidia of Laurentian saukiids. This difference in pygidia depending on the areas was already pointed out by Kobayashi (1957) who questioned the conventional application of Laurentian generic names (e.g. *Saukia*, *Calvinella*, and *Prosaukia*) to Gondwanan taxa with the pauci-segmented pygidia.

In addition, Gondwanan forms are distinguished by strong cranidial convexity and short preglabellar area, whereas the saukiids occurring in both continents generally have less convex cranidia with longer preglabellar areas differentiated into anterior border and preglabellar field. The cranidial characteristics of Gondwanan saukiids reminisce a ptychaspidid *Asioptychaspis*. *Asioptychaspis* and *Sinosaukia* or *Lophosaukia* share convex cranidium with undifferentiated preglabellar area as well as wide pygidium with narrow border. These features shared by Gondwanan saukiids and *Asioptychaspis* support the ptychaspidid affinity of Gondwanan saukiids, while the Laurentian saukiids may have evolved from a common ancestor with dikelocephalids.

It is interesting that widely distributed saukiids (e.g. *Saukia* and *Prosaukia*) have occurred intermittently in Gondwana: for instance, *Prosaukia* at the basal Fengshanian and *Saukia* at the terminal Fengshanian without any related forms in between. The discontinuous appearances of Laurentian forms in Gondwana can be possibly explained by mechanisms such as migration or dispersal.

CONCLUSIONS

The genus *Eosaukia* was redefined to accommodate a part of previous *Mictosaukia* species and *Mictosaukia* is synonymized with *Saukia*. In addition, this study suggests the independent evolution of Gondwanan saukiids and the occasional immigration of Laurentian saukiids into Gondwana. Further ontogenetic studies on *Asioptychaspis* and *Sinosaukia* will prove the ancestry and evolution of Gondwanan saukiids. However, the paleogeographic and phylogenetic history of saukiids may not be fully understood until taxonomy of Laurentian and the rest of Gondwanan saukiids is thoroughly revised.

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TRILOBITE BIOGEOGRAPHY AND PERMIAN BIOCHORES

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Keywords: Trilobita, biogeography, Permian.

INTRODUCTION

Trilobites have proved to be critical in constraining palaeogeographic models in the Lower Palaeozoic. In the Permian, they represent a minor component of benthic marine faunas, which explains why little attention has been paid to them with reference to the evolution of Permian palaeogeography. However, the evolution of trilobite biogeography during this period suggests that these organisms could contribute to the definition of major Permian biochores.

This contribution aims at 1) precisely depicting the evolution of trilobite biogeography during the Permian and 2) comparing this pattern to the evolution of Permian biochores, as they are recognized in other taxonomic groups. The recent review of the stratigraphical distribution of Permian trilobites (Owens, 2003) has been considered and new data from Australia, Oman, Russia, and Turkey have been added to the analysis. For practical reasons, the geographical distribution of trilobites is depicted for six time slices: Asselian-Sakmarian, Artinskian, Kungurian-Roadian, Wordian, Capitanian, and Wuchiapingian-Changhsingian (i.e. Lopingian). The Permian biochores are as defined by Grunt and Shi (1997).

ASSELIAN-SAKMARIAN

In the early Cisuralian (Asselian-Sakmarian), three of the biochores of Grunt and Shi (1997) are recognized by a certain degree of endemism of trilobites (Fig. 1): the North American Region (*Cheiropyge*, *Ditomopyge*), the Mediterranean Region (*Bedicella*, *Pseudophillipsia*), and the Cathaysian Region (*Weania*). There are more taxa in common between these two regions than between each of them taken separately and the North American Region. The Cisuralian Province, which belongs to the Mediterranean Region, is known to have particular affinities with the Cathaysian Region at that time, which is emphasized here with trilobites. The importance of the Euro-Canadian Region as a migration passage is evident from trilobites. Lastly, the Austrazean Province (*Doublatia*) may already be differentiated at the end of the Sakmarian.

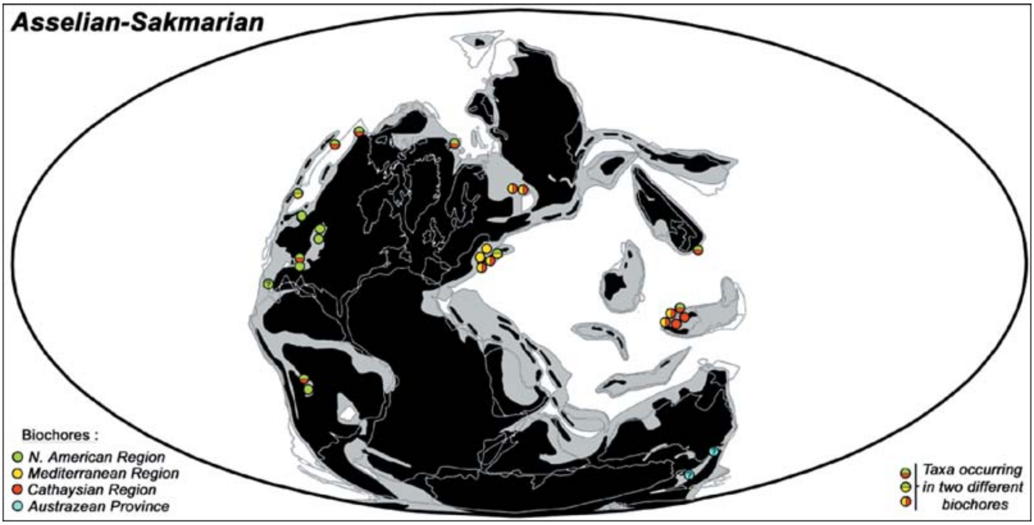

Figure 1. Trilobite biogeography in the early Cisuralian. Three, possibly four distinct biochores known from other groups of organisms can be recognized with trilobites despite their low diversity. Palaeogeographic reconstruction modified after Ziegler *et al.* (1997).

ARTINSKIAN

The distribution of Artinskian trilobites is particularly unbalanced, with most genera occurring on the North Gondwanan margin and neighbouring terranes. The North American and Euro-Canadian Regions cannot be distinguished using the trilobites alone. Most taxa occurring there are also present in the poorly differentiated Cimmerian Region (*Hentigia*, *Paraphillipsia*) and Westralian Province (*Hildaphillipsia*?, *Timoraspis*?), suggesting that migrations across the East European inland sea and the Arctic basin are still possible at that time. The only taxon found in the Cathaysian Region is not restricted to this region but is also known from the Westralian Province. In contrast, two atypical trilobite genera characterize the high latitudinal regions. The Kolyma-Omolon Province in the north is represented by the blind *Anujaspis* and the Austrazean Province in the south by *Doublatia*.

KUNGURIAN-ROADIAN

Only few taxa of that age are known. Nonetheless, the North American Region is particularly well individualized by a group of endemic forms (*Anisopyge*, *Delaria*, *Novoameura*, and *Vidria*). By contrast, the other biochores are virtually undifferentiated. The Austrazean Province may still be represented by *Doublatia* in the Kungurian. *Pseudophillipsia* is known from South China (Cathaysian Region) but possibly also from Turkey (Mediterranean Region). *Cheiropyge* may occur in both the North American Region (West Texas) and the Westralian Province (Timor), while *Triproetus* may be present in Svalbard (Euro-Canadian Region).

WORDIAN

The greater abundance of trilobites in the Wordian enables a better recognition of biochores. Like in the previous period of time, the North American Region is well individualized by the presence of the same four endemic genera. The Mediterranean Region is also characterized by a high degree of endemism, with six taxa out of nine exclusively known in the western coasts of the Paleo-tethys. *Neoproetus* and *Timoraspis* demonstrate that this biochore has some relationships with the Cimmerian Region. This latter is only differentiated by a single endemic genus, *Acropyge*, as is the Cathaysian Region by *Acanthophillipsia. Pseudophillipsia* has apparently a very wide geographic distribution, being known with confidence from the Mediterranean and Cimmerian Regions and possibly also occurring in the Cathaysian and Sino-Mongolian Provinces (Cathaysian Region).

CAPITANIAN

Trilobites are once again rare in the Capitanian, which limits the recognition of biogeographic units. However, the Sino-Mongolian Province is particularly well individualized by four endemic genera (*Acanthophillipsia*, *Ampulliglabella*, *Jimbocranion*, *Paraphillipsia*). Two other genera present in this province are common with the Cathaysian Province and the remaining ones can be found in various parts of the world (Kashmir?, Timor?, Tunisia).

WUCHIAPINGIAN-CHANGHSINGIAN

In the Lopingian, the Cimmerian and Mediterranean Regions cannot be distinguished from one to another, as noticed in other groups of organisms. Indeed, the four taxa found in the 'Mediterranean Region' are also known in the Cimmerian Region. Two of them (*Cheiropyge*, *Pseudophillipsia*) are cosmopolitan genera, which can also be found with *Acropyge* in the Cathaysian Region.

CONCLUSIONS

Trilobites have a particularly low diversity throughout the Permian, which logically affects the recognition of biogeographic units, especially at a low level (Provinces). However, most regions can be individualized using trilobites and in some cases, even changes in the affinity of one biochore with the others can be confirmed by trilobites. These observations suggest that some trilobite taxa should be included in the definition of Permian biochores. It is noteworthy that a slight difference of diversity from a period of time to another can significantly influence the potential of trilobites to discriminate biochores. Considering this, it seems crucial that more attention is paid to each newly discovered Permian trilobite.

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THE CEPHALIC MEDIAN ORGAN OF TRILOBITES

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Keywords: Trilobita, Arthropoda, cephalic median organ, morphofunctional anatomy, systematics.

INTRODUCTION

As in modern arthropods, a great variety of structures (tubercles, pits, ridges) are visible on the outer surface of the trilobite cuticle. The most obvious and/or common of them have naturally attracted particular attention (e.g. terrace ridges; see Whittington, 1997, p. 148, and references therein). Others, like the cephalic median organ (CMO), have never been subject to systematic investigations and remain almost unknown. The CMO is a small complex of structures located, as indicated by its name, on the sagittal line of the cephalon. This complex, generally composed of four pits arranged at the corners of an imaginary square, is rather common in odontopleurid and corynexochid trilobites where it has been called the 'occipital organ' (Whittington, 1956, 1965). However, its distribution within the Trilobita, as well as through time, and its morphological variability are virtually unknown. Here we report the preliminary results concerning these issues from a comprehensive study aimed at investigating every aspects of this enigmatic organ.

MORPHOLOGY AND VARIABILITY

The CMO is typically composed of four rather small pits, located on the occipital ring. An additional fifth pit, with a central position, is sometimes observed, especially in odontopleurids where it may represent a character that varies intraspecifically (e.g. *Meadowtownella ascita*; Whittington, 1956). Generally, the pits are equidistant, located at the corners of an imaginary square (Fig. 1a). However, other geometric shapes can be recognized, such as a rectangle (Fig. 1b, c), an isosceles trapezoid (Fig. 1d) or an inverted isosceles trapezoid (Fig. 1e).

The CMO is most often situated on a flat or slightly inflated surface (Fig. 2a), occupying a roughly central position on the occipital ring (sagittally). It is rather common, however, to observe it at the apex of a more or less developed tubercle (Fig. 2b, c), such as in several odontopleurids. Even when present on a flat surface, it is always on or near the highest point of the cranidium, suggesting a particular influence of this position on its function. This characteristic probably explains why in numerous species, the CMO is somewhat displaced relative to the centre of the occipital ring, usually backwards but in rare cases forwards. This positional constraint may also explain the likely migration of the CMO on to the preoccipital glabella in derived asaphids (*Tretaspis*, *Niobe*, and *Ogygiocaris*), which justifies abandoning the appellation 'occipital organ' in favour of a less restricted designation.

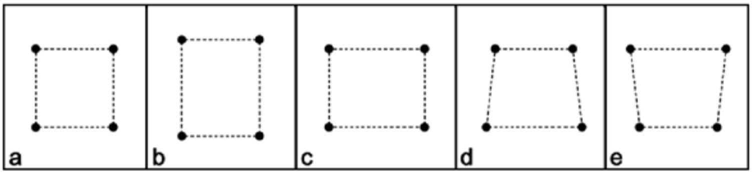

Figure 1. Geometric shapes suggested by the relative position of the four pits: square (a), rectangle elongated parallel (b) or perpendicular (c) to the sagittal line, isosceles trapezoid (d) or inverted isosceles trapezoid (e).

The CMO is more frequently observed on the largest specimens for a given species, but a great variability in relative size of the pits exists from one species to another. Large pits are particularly common in odontopleurids, although some Ordovician ptychopariids, phacopids, and corynexochids also display pits of significantly large relative size. Interestingly, phylogenetically close taxa can show important differences in pit size. In *Olenus wahlenbergi* (Clarkson and Taylor, 1995), a variant of the CMO is visible on early holaspid specimens and it is certainly present in earlier stages (meraspides) in some odontopleurid species (e.g. *Radiaspis norfordi*; Chatterton and Perry, 1983) and in *Aphelaspis* (Palmer, 1962). Moreover, it can be more visible in early growth stages than in adults in some species (e.g. *Eskoharpes palanasus*, McNamara *et al*., in press).

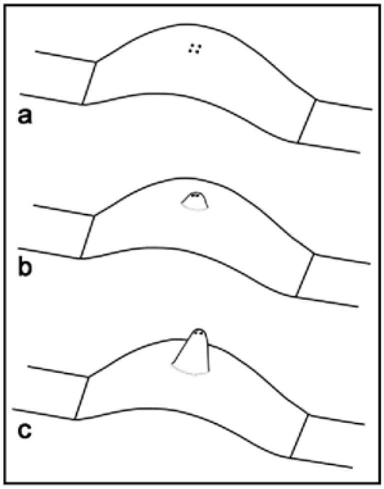

Figure 2. Relief of the area bearing the CMO. a, flat area. b, low tubercle. c, high tubercle/spine.

Four more or less developed tubercles arranged at the corners of a square can be observed on the occipital node of protaspid or early meraspid stages of the agnostid *Pagetia* and of some phacopides. The number, organization, and position of these structures suggest they might represent a modified/differently preserved CMO. A similar conclusion can be drawn for the four tiny tubercles displayed by adults of the Upper Cambrian olenid *Olenus wahlenbergi* (see Clarkson and Taylor, 1995). In *Aulacopleura konincki occitanica*, four small tubercles and a larger central one forming a quincuinx occur on internal moulds, while the dorsal surface of the carapace remains completely smooth. This suggests that the cuticle was thinner in these five areas, which is confirmed to some extent by rare specimens exhibiting four tiny dark spots on the dorsal surface of the occipital ring. In our opinion, these features are clear evidences of the occurrence of a CMO in this species, which raises the question of whether a similar barely discernible organ might not occur in many other species. Finally, the complex of pits located on the glabellar node (i.e. the highest part of the glabella) of *Agnostus pisiformis* represents another good example of a structure that probably evolved from the typical CMO of other trilobites. In this species, three relatively large pits are located on either side of the sagittal line, while a seventh, somewhat smaller, pit is located between the second pair of pits (Müller and Walossek, 1987). Despite this greater number of pits involved, the structure resembles the CMO both in terms of organization (paired pits surrounding a central, somewhat different pit) and relative position (highest part on the sagittal line of the glabella). We speculate that this structure evolved from the more 'typical' CMO.

DISTRIBUTION

The CMO, or a related structure, has been observed in representatives of all trilobite orders but one: the Lichida. It is especially frequent within the Odontopleurida, where we have recorded it in more than forty species (14 genera; Fig. 3). Likewise, it might have been an important structure in the Corynexochida, as demonstrated by the relatively large number (16 species/7 genera) and the taxonomic distribution of CMO bearing taxa within this group, being present in the three corynexochid suborders. In the seven remaining orders, only rare examples of trilobites equipped with this organ have been found. In terms of number of genera represented (Fig. 3), they rank as follows: Asaphida (4), Harpetida, Phacopida, Ptychopariida (3), Agnostida, Redlichiida (2), and Proetida (1).

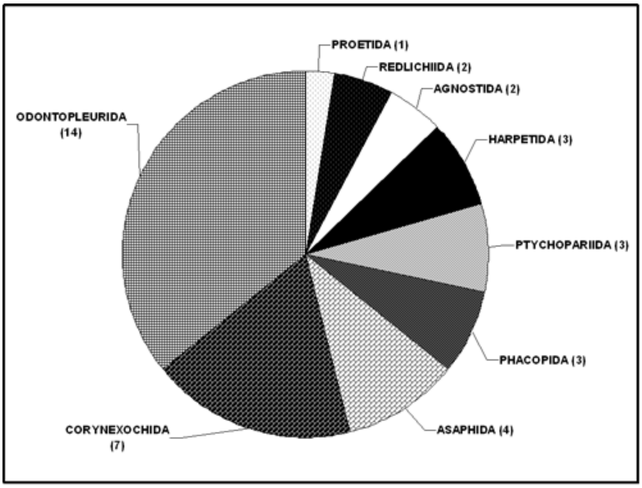

Figure 3. Generic abundance of the CMO in each trilobite order. The Lichida are not represented, as no example of CMO is known within this order.

The variability of abundance of known examples of trilobites with a CMO from one order to another logically influences their abundance through time. The oldest examples are of Middle Cambrian age and can be found within the Redlichiida, the Corynexochida, and possibly also the Agnostida (i.e. protaspides of *Pagetia*). In the Late Cambrian are found the first examples within the Asaphida and the Ptychopariida.

The organ is particularly frequent in Middle Ordovician to Silurian trilobites, especially in corynexochid and odontopleurid taxa. Its abundance, however, decreases in the Devonian and no occurrence younger than the Late Devonian has been recorded so far. The evolution of this abundance through time is manifestly correlated to the evolution of diversity of the different trilobite orders. Thus, a direct link exists between the greater number of CMO bearing taxa in the Silurian and the important diversity of odontopleurids during this period.

DISCUSSION

The CMO is a rare feature, but it can be observed in almost all the major groups of trilobites and it occurs as early as the Middle Cambrian. Despite the absence of known occurrences of the CMO within the earliest representatives of the class (i.e. the Olenellina), it can be speculated that this organ would have been inherited from the common ancestor of all trilobites (i.e. it is a plesiomorphic character). This assumption is reinforced by the great constancy of the CMO, both in terms of its morphology (nature, number, organization of structures) and of positioning. Most variants mentioned above are likely the results of differences of preservation or can be explained by probable functional constraint (i.e., the need to be located on the highest point of the cephalon). Therefore, multiple, independent origins of this organ appear to be a very unlikely evolutionary scenario to explain its wide distribution within the Trilobita. Moreover, its abundance is certainly underestimated, as suggested by the example of the Silurian proetid *Aulacopleura konincki occitanica*. In this species, only the 4+1 tubercles occuring on the internal moulds enable the presence of a CMO to be inferred, a presence which otherwise might have remained unoticed by the simple observation of the dorsal surface of the cuticle. These observations strongly suggest similar cases of CMOs having been overlooked during our survey, especially when we were examining photographs of whitened specimens. Indeed, in suppressing colour differences of the different parts of a specimen, this whitening technique eliminates any chances to observe the dark spots that could potentially reveal the presence of a 'hidden' CMO.

The hypothesis of the plesiomorphy of the CMO logically raises the question of the occurrence of a similar organ in other arthropods. Many crustaceans, from the Cambrian to Recent, display structures often referred to as the 'dorsal organ', that share with the CMO a sagittal location on the dorsal part of the head (Martin and Laverack, 1992). These structures have been shown to vary in internal and external morphologies and presumably also in function. Consequently, they probably do not represent homologous organs. A certain number of them, however, share a cluster of both external and internal characteristics that suggests they are variants of the same organ. As it supposedly had a sensory function, it has been called the 'sensory dorsal organ' as opposed to the broad term of 'dorsal organ' (Laverack *et al*., 1996). This sensory dorsal organ (SDO) and the CMO exhibit striking morphological similiarities, in addition to their common sagittal location on the dorsal side of the head. Indeed, both are generally represented externally by four obvious structures (pits/tubercles) arranged at the corners of an imaginary square. The SDO displays a fifth central structure, more variable in external aspect, which can be compared to the fifth pit or tubercle sometimes observed within the CMO of trilobites. Lastly, if a parallel is drawn between the two organs, the internal anatomy and the known variation in external aspect of the SDO may go some way to explaining almost all the variants of the CMO described above. For example, the thinnings of the cuticle associated with the five structures of the SDO (Laverack *et al*., 1996: fig. 5) may explain the presence of five tubercles on the internal moulds of *Aulacopleura konincki occitanica*. Similarly the fact the four outer papillae of the SDO can form slightly elevated bumps on the outer cuticle, as in *Anaspides tasmaniae* (Laverack *et al.*, 1996: fig. 1A), may explain the presence of four tubercles on the dorsal cuticle of *Olenus wahlenbergi*.

Like the SDO (Laverack and Macmillan, 1999), the CMO exhibits a rather high degree of consistency in external morphology and especially in organization. Given its wide distribution across the Trilobita, these two characteristics of the CMO not only justify that it be considered as an organ, but also suggest that it had an important function. Unfortunately, the similarities between the CMO of trilobites and the SDO of crustaceans does not help in determining its function in trilobites, because the function of the SDO has so far not been ascertained (Laverack and Macmillan, 1999).

The pattern of distribution of the CMO within the Trilobita demonstrated herein also raises questions concerning the relationships of some trilobite groups. In particular, the fact the CMO has never been observed in the order Lichida is particularly striking given the abundance of this organ in the Odontopleurida. This may be another argument against grouping the two taxa within a single order, as proposed by Fortey (1997; for other arguments against this grouping, see Whittington, 2002). The absence of a CMO in the family Illaenidae, despite it being present within the three suborders of the Corynexochida and especially in the Styginidae and the Scutelluidae within the Illaenina, is another interesting result of our survey. This observation may be of importance in the debate concerning the questionable common origin of the Styginidae, the Scutelluidae, and the Illaenidae and their grouping within the Illaenoidea (Whittington, 1999). On the other hand, this absence in some illaenids may be due to the presence of another organ, the glabellar 'tubercle'. Like the CMO this has a dorsal location along the sagittal line of the cephalon (Fortey and Clarkson, 1976). Likewise, no CMO has been observed in the superfamily Proetoidea during our survey, which explains the absence of a CMO in post-Devonian trilobites. Once again, a parallel can be drawn between the absence of this organ and the existence of a particular occipital node in this group (Fortey and Clarkson, 1976; Wilmot, 1991; Lerosey-Aubril and Feist, 2005). It is noteworthy that both the glabellar 'tubercle' of *Nileus* and other illaenids, and the proetoid occipital tubercle are associated with a thinning of the cuticle, as it supposedly occurs with the different elements of the CMO. Whether this observation is relevant with regard to possible morphological and/or functional evolution of these two 'organs' from the CMO, or if it simply reflects the fact the three organs were responding in a similar way with the external environment is unclear. However, the fact that the distribution of these three structures seems to be mutually exclusive appears to us worthy of consideration and further investigation.

CONCLUSIONS

The close resemblance between the dorsal organ of Crustacea and the CMO, or structures here considered as variants of the CMO, has already been stressed in the past (Barrientos and Laverack, 1986, and references therein). However, the variability and the wide distribution of the CMO within the Trilobita revealed by our survey combined with recent data concerning the crustacean SDO (Laverack *et al.*, 1996; Laverack and Macmillan, 1999), make the evolutionary scenario of a unique origin of these organs much more credible than ever. Considering the implications that this hypothesis, if proven, might have on the systematic position of Trilobita relative to extant arthropods, it seems crucial to continue investigations on both organs. As to the CMO alone, particular attention should be given to its ontogeny and especially to the modifications of the cuticle structure associated with its presence. This point is of the utmost importance for comparisons with the SDO and for determining the frequency of CMO bearing trilobites devoid of external structures (e.g. *Aulacopleura konincki occitanica*). Considering also the potential significance of this organ for the systematics of trilobites, we hope more attention will now be paid to its presence in descriptions of new taxa.

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CRYPTOPALAEONTOLOGY: MAGICAL DESCRIPTIONS OF TRILOBITES ABOUT TWO THOUSAND YEARS BEFORE SCIENTIFIC REFERENCES

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INTRODUCTION

Lapidaries are a particular type of literary text that describe and give names to a list of stones, which, like minerals or gems, have always stood out among the natural elements for their particular shape, shine or colour and to which magical and curative properties were attributed by ancient tradition. The first texts came from Mesopotamia and Persia; they then moved to classical Greece and later, highly impregnated by the Chaldean-Egyptian astrological tradition, were introduced into the west through the Arab culture. This emphasis on magical properties differentiates them from the more specifically pharmacological works of Hypocrates, Dioscorides and Galenus, in which references are also found to minerals and their by-products used as remedies, but without the mythological or astrological connotation of lapidaries.

Most of the original lapidary texts have been lost, but fragments of their content are known because they were the sources of subsequent works, among the most outstanding of which are Pliny The Elder's *Natural History* (1st century) and the Greek apocryphal "*Orpheus' Lapidary*" or "*Líthica Orphéôs*". It has been speculated that the latter is a copy based on a Greek original dating before the 2nd century B.C. (Halleux and Schamp, 1985). It is also worth pointing out that "*Lapidario Kerygmata*" or *Orpheus'* "*Lithica Kerygmata*" is an epitome or summary of "*Orpheus' Lapidary*".

Most of the stones referred to in these lapidaries are minerals and rocks, but there are also fossils, which are sometimes difficult to identify because their descriptions are ambiguous, whether because the emphasis is placed on their magical-medicinal properties alone, or because they intentionally use cryptic language that is only accessible to experts. The study of these ancient literary, medical and magical-religious texts with the aim of finding historical references to fossils and the meaning conferred upon them by primitive cultures can be referred to as Cryptopalaeontology. This discipline also includes findings of fossils in archaeological sites and the study of oral traditions that have survived until our times (Liñán, 2004).

Among the lapidaries mentioned, there are stones that are fossils beyond any doubt. Some have been known since ancient times, such as the Ammon's Horns Stone, but there are many others that still remain to be deciphered. One of the most enigmatic and interesting stones is the Scorpion Stone, which is present in Pliny's *Natural History,* Isidoro's *Ethimologies* (7th A.C.), Alfonso X's *lapidary* (1279) and also in the

Orpheus' two lapidaries. There is no doubt that this stone refers to a fossil, which we wish to analyse in this brief note, from a palaeontological viewpoint.

STONE DESCRIPTIONS

Stone of Scorpions ("*Líthica Orphéôs*", v. 494-497): "*Scorpion, the brilliant hero Orion was not aware of the existence of a stone with the same name as you, as I believe that, when his feet were crossed by sharp pain, he would have preferred to possess the stone than his constellation*".

Scorpion Stone ("*Orphéôs Líthica Kêrygmata*", 18): "*Stone called scorpion <skorpíos>, due to homonymy with the reptile* (sic), *which is said to have power against scorpions*".

As Liñán (2005a) pointed both texts very probably refer to the fossil group of the trilobites, which are extinct arthropods that populated the sea of the Palaeozoic Era. This supposition is based on three observations. In the first place, trilobites were already known and collected by Cromagnon Man in the Upper Palaeolithic Age as is suggested by the finding of trilobites drilled for use as a pendant in caves from Yonne, Central France (Oakley 1965, 1985; Chlupáč, 2000; Henry, 2001, St. John, 2007). In the second place, trilobites are by far the most common fossil arthropods on geological record worldwide and usually have the ability to roll up into a ball, thus taking on the appearance of scorpions, which roll up their abdomen when they feel attacked. The third circumstantial relation is constituted by the different common denominations that these fossils receive today in Spain. Thus, the locals refer to the Early Cambrian trilobites in San Nicolás del Puerto (Seville) as "stone scorpions" due to their segmented body and in Constantina (Seville) they are called "large ants of stone". Furthermore, as is well known, trilobites lived by forming communities of numerous individuals that left their skeleton when they shed their skin or died on the surface that fossilised them, giving rise to frequent accumulations on the rock surface, which could easily explain the plural used to designate this stone in "*Orpheus' Lapidary*".

Scorpitis Stone (Pliny XXXVII 187). From the Greek *Skorpíos*, scorpion: "*Some stones take the name of animals: ... **scorpitis**, from the colour or shape of the scorpion*". (Isidoro, *Etimologías* 16 19 "*scorpitis scorpionen et colore et effigie refert*").

The double reference to colour and shape may indicate the existence of two different sources. It would not seem likely that Pliny was referring here to real fossil scorpions, which even today are extraordinarily rare in the fossil record. He would not appear to be referring to fossil crabs because these are easy to recognise and because he previously mentions **Carcinias** (Crab stone, derived from the Greek *karkínos*) and says that they take their name "*from the colour of the sea crab*". He was most likely referring to trilobites, deposits of which are widely recorded in the classical world from Italy, Spain, Great Britain, France, Germany, Morocco, Algeria, Egypt, Turkey, Israel, Palestine, Jordan, Pakistan, Afghanistan and India.

As indicated above, trilobites are called stone scorpions and stone ants in some areas of Sierra Morena (South Spain). In this respect, the **Myrmecias Stone** (from the Greek *myrmex*, ant) "*The myrmecias is black and has excrescences similar to warts*" (Pliny XXXVII 174) and the **Myrmecitis Stone** ["*The myrmecitis is shaped like an upright ant*" (Pliny XXXVII 187), "*Myrmecitys formicae reptantis effigiem imitatur*" (Isidoro 16 19)] may also be a variety of trilobites. The shell of many trilobites is ornamented with spots and spines and its colour is often shiny black. Moreover, the partially rolled up shapes may look as though they are coiled up on themselves using the pygidium as a support point.

The interpretation of the **Cantharias** Stone (Pliny XXXVII 187) is more difficult (Liñán, 2005b). It comes from the Green *kántharos*, meaning beetle: "*The cantharias, the beetle stone*". Besides being rare, fossil beetles are delicate as they are conserved as fine carbon films in exceptional deposits of the *fossil-lagersttäte* type, which are formed in former lakes. However, agnostoids (pelagic trilobites exclusively from the Cambrian and Ordovician ages) are very common in the Mediterranean area and their appearance is very similar to that of beetles. If the Cantharias Stone is the interpretation of agnostoid trilobites, it could be one more explanation of why the beetle was considered a sacred animal in Egypt, as its "generation" inside rocks as well as the "Cornu Ammonis" stone, which would be a divine attribute.

The last reference is the **Albarquid** Stone contained in the Alfonso X the Learned of Castilla lapidary (I 13, 35) " ...*appears in this stone a scorpion figure; and we found the same figuration in the interior if they break*" which is considered the first palaeontological book in Spanish language (Liñán, 2006).

CONCLUSIONS

For his work, Pliny the Elder consulted writings that have not always been conserved but that date from before the 1st century B.C., one of which is "*De Lapidibus*" by Theophrastus (4th century B.C.) and other references are of Zoroastre (7th century B.C.) The disappearance of the Scorpion Stone and that of the Ostrite Stone in medieval lapidaries supports the relative antiquity proposed by *Orpheus' Lapidary,* the last codice in which these stones are found. That is, there are rational indications that trilobites were known in classical Greece and during the Roman Empire and were commercially valued as a sympathetic remedy against bites from poisonous animals. The different names Scorpion Stone, Myrmecias Stone, Myrmecitis Stone, Cantharias Stone and Albarquit Stone must have referred to different trilobite types and different geographical origins.

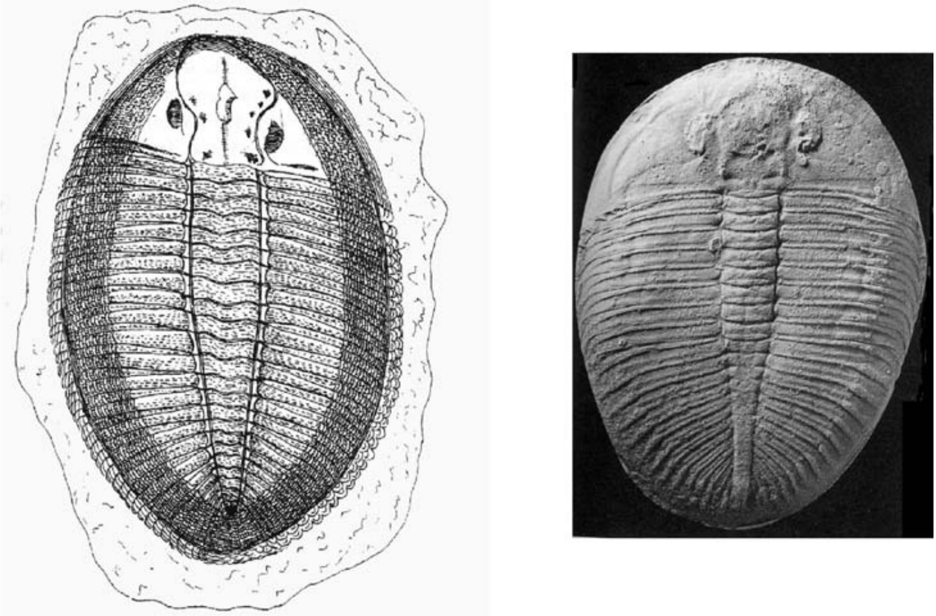

Figure 1. The 'flatfish' figured by Dr. Lhwyd (1698) and a photography of probably the same specimen of *Ogygiocarella debuchii* (after Fortey, 2000).

If this is the case, we must conclude that trilobites, like other fossils, were recorded in the primitive books of medicine and magic called lapidaries: almost two thousand years before Wan Shizhen (1689) mencioned trilobite pygidia in North China as "batstones" (John, 2007), before Lhwyd (1698), curator of the Oxford Museum, made the first known drawings of trilobites (Figure 1) representing the species *Ogygiocarella debuchii* of the Ordovician age (Fortey, 2000) and called them "Trinuclei"; before Zeno (1770) depicted the trilobite *Dalmania haussmanni* and called it "three-lobed shell" and before the German Walch (1771) coined the term "Trilobitae" (Whittington, 1992). In this way, lapidaries may be capable of filling part of the great information gap that exists in the History of Palaeontology for Palaeozoic invertebrates. The time that passed between the archaeological finding of trilobites *Ormathops* in Magdalenian from 15,000 years ago in France and Lhwyd's drawings. The latter might be considered as the point at which trilobites ceased to be interpreted as magical-medical stones.

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NEW TRILOBITE SPECIES FROM THE UPPER CAMBRIAN CHOPKO RIVER SECTION, RUSSIA

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Keywords: Termixes, description, comparison.

INTRODUCTION

The new trilobite genus and species *Tumoraspis tumori* gen. et sp. nov. is described from the Chopko Formation of the upper Cambrian Chopko River section (Norilsk region, northwestern Siberian Platform). The comparison of this taxon with specimens of *Langyashania felixi* Shergold (Río Urbión, Spain) is given; according to the results, we conclude that the Siberian and Spanish species belong to one genus. The Latin terminology established by Rosova and Makarova (2008) was used for nomenclature of trilobite morphological elements throughout the trilobite description.

DESCRIPTION

The Chopko River section is the key section for the upper Cambrian of the Norilsk region. New species specimens occur at some stratigraphic levels and characterize a significant interval of middle part of the upper Cambrian.

Data collected by A.I. Varlamov in 1988 and K.L. Pak in 2004 (section description by Varlamov) were used in the work. The stratigraphic column (Fig. 1) is taken from the work of Varlamov and co-authors (Varlamov *et al*., 2005) and partly given in the article.

The trilobite description was made with the use of Latin termixes (Fig. 2, also see Rosova and Makarova, 2008) applied earlier by other researchers (Rosova and Rosov, 1975; Rosova and Rosov, 1977; Rosova *et al*., 1985; Varlamov *et al*., 2005).

Class Trilobita Walch, 1771
Order Ptychopariida Swinnerton, 1915
Superfamily Ellipsocephaloidea Matthew, 1887
Family Agraulidae Raymond, 1913

Genus *Tumoraspis* gen. nov.

Etymology. From Latin *Tumor*: tumor, because of the shape of **Cr**, and Greek *aspis*: shield.

Type species. *Tumoraspis tumori* gen. et sp. nov. Northwestern Siberian Platform, Norilsk region, Chopko River, Chopko Formation. upper Cambrian, *Agnostotes (Pseudoglyptagnostus) clavatus – Irvingella perfecta, Norilagnostus quadratus – Irvingella cipita and Irvingella norilica* zones.

Diagnosis. **Cr** is of small size (2-6 mm), with almost square contours or slightly oblong in width ($\mathbf{a_1Cr} \le \mathbf{b_3Cr}$), from weakly to moderately convex, smooth on shell, with distinct furrows on core. **NCr** is arcuate. **CuCr** and **ArcCr** are uniformly arcuate. **G** is medium-sized ($\mathbf{a_1G}$~0.55$\mathbf{a_1Cr}$); truncate-fastigiate; smooth if shell is preserved and three pairs of vague **SG** are observed in core. **SD** has average width and depth. **Cor** is large ($\mathbf{a_1Cor}$ ~ 0.66 $\mathbf{a_1G}$), convex. **Bcl** are mid-sized (**bBcl**~0.5$\mathbf{b_3G}$), slightly convex, slightly suberected over **SD** and inclined outwards. **Pal** are median, large (**cPal** ~0.5$\mathbf{a_1G}$), curved, and are fused

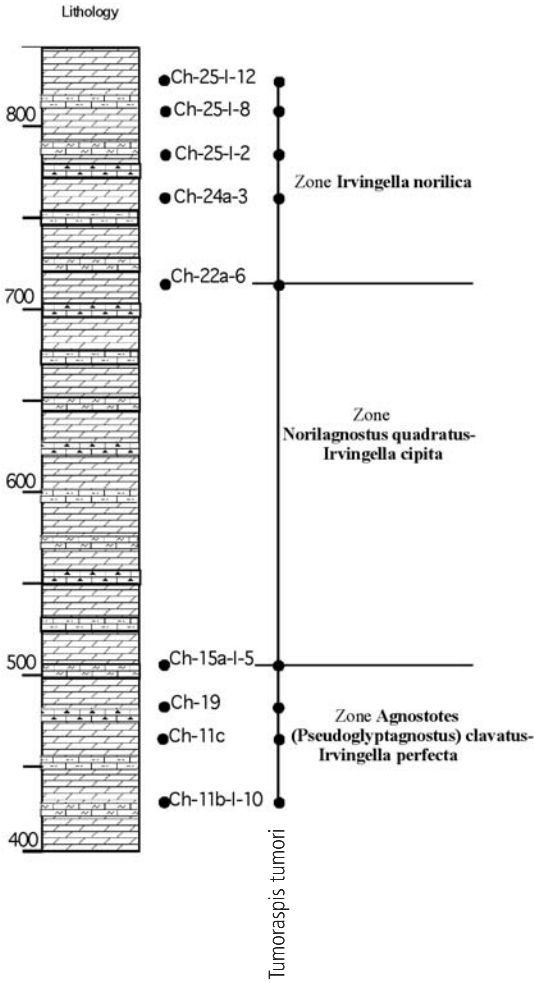

Figure 1. Distrubution of *Tumoraspis tumori* in the Chopko River section.

with **Bcl. O** is small ($\mathbf{a_1O}$~0.22$\mathbf{a_1G}$), enlarged in the middle, converged by flanks. **SO** is faintly saddled. **StCor** are almost parallel; **StPt** are divergent. **FcCr** is smooth on the shell and punctuate-pitted on the nucleus.

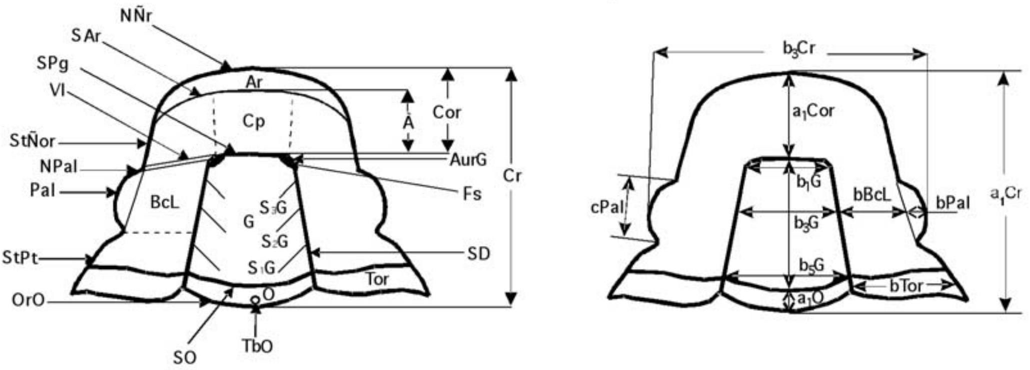

Figure 2. The main elements of **Cr** (cranidium) and its sizes.

Comparison. The new genus differs from Middle Cambrian genus *Agraulos* Corda, 1847 (type species *Arion ceticephalus Barrande*, 1846 (Walcott, 1913) by slightly more convex **Cr** less curved at the front, truncated conical and much less partitioned **G**: *Agraulos* has **G** rounded ahead and three pairs of distinct **SG**; and much longer **Pal**: **cPal** ~0.58$\mathbf{a_1G}$ (*Agraulos* has **cPal**~0.36$\mathbf{a_1G}$).

The new genus differs from the genus *Plethopeltis* Raymond, 1924 by almost square **Cr** (*Plethopeltis* has elongated **Cr**), quite large **Cor**~0.66$\mathbf{a_1G}$ (*Plethopeltis*~0.35$\mathbf{a_1G}$), wider **Bcl**~0.5$\mathbf{b_3G}$ (*Plethopeltis*~0.2$\mathbf{b_3G}$) and large size of **Pal**~0.58$\mathbf{a_1G}$ (*Plethopeltis*~0.23$\mathbf{a_1G}$).

Discussion. The genus *Tumoraspis* is similar to specimens of the Family Plethopeltidae Raymond, 1913 in flattening of **Cr**, but differs from them by almost square instead of oblong in length **Cr** and almost parallel and not divergent **StCor**. On the basis of these features the new genus is assigned to the Family Agraulidae.

Specimens of *Tumoraspis* are most similar to one of the species of *Agraulos* – *A. longicephalus* (Hicks, 1872) (see Sdzuy, 1961; Liñán and Gozalo, 1986). They differ from middle Cambrian specimens of this species only in the lack of depression on **Cor**, and as a result **Ar** is not separated and **Cor** has a single convexity. This feature also leads to a significant change in **Cr** profile that is almost a perfect arc in *Tumoraspis.* It is possible that the genus *Tumoraspis* is an upper Cambrian descendant of the Middle Cambrian genus *Agraulos*.

Langyashania felixi (Shergold *et al*., 1983) was described from a Spanish section at Rio Urbión, the specimens of which are morphologically similar to specimens of new *T. tumori* species. They also have almost square **Cr**, with very similar **CuCr**, large **Cor**, almost not partitioned, truncated conical **G**, wide **Bcl**, almost parallel or slightly divergent **StCor** and small and oblong transverse indentations diverging from **SPg** along back edges of **Cor.** At the same time, they differ significantly from the type species specimens of the genus *Langyashania* – *L. distincta* Lu and Zhu, 1980. The differences are in the shape of **Cr** (**Cr** of *L. distincta* is oblong, **Cr** of *L. felixi* has almost a square shape), in an anterior narrowing of **G** (*L. distincta*: $\mathbf{b_1G}$=0.58$\mathbf{b_5G}$, *L. felixi*: $\mathbf{b_1G}$=0.65$\mathbf{b_5G}$), in width and direction of **Bcl** (*L. distincta* has narrow **Bcl**: **bBcl**=0.26-0.30$\mathbf{b_3G}$, first slightly risen upwards, while the **Bcl** of *L. felixi* are much wider: **bBcl**~0.50-

0.56$\mathbf{b_3G}$, and they fall down immediately composing one arc with **G**), in the degree of **SD** definition (**SD** of *L. distincta* are more defined than *L. felixi*'s ones), regarding **SAr**: the **SAr** of *L. distincta* is observed quite distinctly, especially along the edges; *L. felixi*, judging by the description, sometimes has very poor **SAr**, but this is not seen from the photographs. In view of this data, the author considers that *L. felixi* refers to the new genus *Tumoraspis*.

Distribution. Northwestern Siberian Platform, Norilsk region. Middle layers of upper Cambrian. *Agnostotes (Pseudoglyptagnostus) clavatus – Irvingella perfecta, Norilagnostus quadratus – Irvingella cipita and Irvingella norilica* Zones. Spain, Rio Urbión section, horizons U 1/2, U 1/3. Middle part of the upper Cambrian.

Tumoraspis tumori gen. et sp. nov.
Pl. 1, Figs. 1-10

Etymology. From *tumor* (Latin): tumor.

Holotype. **Cr** CSGM 977/14, Pl. 1, Figs. 8, 8a and 8b. Ch-11c. Northwestern Siberian Platform, Norilsk region, Chopko River, upper Cambrian, *Norilagnostus quadratus – Irvingella cipita* Zone.

Locality and material. Ch-11b-I-10: 1 **Cr** (complete); Ch-11c: 2 **Cr** (complete); Ch-15a-I-5: 3 **Cr** (complete); Ch-19: 3 **Cr** (complete); Ch-22a-6: 2 **Cr** (complete); Ch-24a-3: 1 **Cr** (complete) and 1 **Cr** (incomplete); Ch-25-I-2: 2 **Cr** (complete); Ch-25-I-8: 1 **Cr** (complete); Ch-25-I-12: 7**Cr** (complete).

Diagnosis. **SPg** is shallow and narrower than **SD**, distinct furrows are seen on **Cor**, which are almost a continuation of **SD**, large **Pal** and medium-sized **O**.

Description. **Cr** sizes small [$\mathbf{a_1Cr}$=(3.55)[1] 2.1-5.4mm), with almost square contours or slightly oblong in width $\mathbf{a_1Cr \leq b_3Cr}$], slightly or moderately convex. **NCr** is arcuate. **CuCr** and **ArcCr** are uniformly arcuate, *i.e.*, **G** and **Cor** profiles, form almost a perfect arc, just as **G** and **Bcl**.

G is medium-sized ($\mathbf{a_1G}$=(0.52)-0.56 $\mathbf{a_1Cr}$), truncated conical ($\mathbf{a_1G}$=(0.97) 0.84-1.0; $\mathbf{b_3G}$; $\mathbf{b_1G}$=(0.60) 0.57-0.64$\mathbf{b_5G}$), uniformly converging ahead, **VG** in **CenG**, sometimes shifted to **NG**. The shell surface of **G** is smoothed, and three pairs of **SG** are clearly seen on the core.

$\mathbf{S_1G}$ are in the form of elongated, oblique, oval indentations with degraded boundaries, slightly narrower and much smaller than **SD**; $\mathbf{S_2G}$ are the same as $\mathbf{S_1G}$, but shorter, they are located almost in front of **NPal**; $\mathbf{S_3G}$ – are the same but very short and almost transverse, located near $\mathbf{S_2G}$ and very close to **AurG**. All **SG** are not joined to **SD**. The keel is lacking.

SD are straight, gradually converging ahead, sometimes they do not change all along, sometimes converge from **OrCr** to **NCr**. They are of average width and depth on the core, and shallow on the shell. Sometimes **SD** become deeper opposite **AurG** forming small **Fs**. **SPg** is straight or slightly arcuate, slightly narrower and more shallow than **SD**. Small, indistinct indentations that are visible only in oblique light diverge from **Fs** continuing **SPg**.

Cor is represented by merged **A** and **Ar**, and isolated **Cp**, separated on each side by furrows that continue **SD**. These furrows retain the depth and direction of **SD** and compose 0.41-0.42$\mathbf{a_1}$ **Cor**. They are best seen on the core. **Cor** is large [$\mathbf{a_1Cor}$=(0.70) 0.60-0.72$\mathbf{a_1G}$; a_1**Cor**=(0.36) 0.32-0.38 $\mathbf{a_1Cr}$] and convex; it rises as a small rung over **SPg**, and after **VCor** smoothly bends forward. **VCor** is located on **Cp**, and sometimes coincides with **VG**.

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[1] Numbers in parentheses indicate average values.

Bcl are mid-sized (**bBcl**= (0.50) 0.45-0.57**b$_3$G**), slightly convex, scarcely raised over **SD** and tilted outwards. **Pal** are medial, large (**cPal** =(0.59) 0.57-0.61**a$_1$G**; **bPal**=0.44-0.50**b$_3$G**), curved, and they have a common surface with **Bcl**.

O is small (**a$_1$O**=(0.22) 0.20-0.21**a$_1$G**), extended in the middle, converging to the sides, **TbO** is mid-sized, and shifted to **NO**. **SO** is slightly saddled; a little narrower and smaller than **SD** in the middle, becoming deeper to the sides and slightly dilated. **P** are small, almost flat and triangular. **Tor** are quite large (**bTor**~0.85**b$_5$G**), slightly convex, almost unchanged along the whole length.

StCor are almost parallel at first, then smoothly rounded and convergent. **StPt** are short, diagonally divergent. **FcCr** of the shell is smooth, and core are dotted/pitted.

Layers	№	**a$_1$Cr**	**a$_1$G:a$_1$Cr**	**a$_1$Cor:a$_1$Cr**	**a$_1$Cor:a$_1$G**	**b$_3$G:a$_1$G**	**b$_1$G:b$_5$G**	**bBcl:b$_3$G**	**cPal:a$_1$G**
Ch-11b-I-10	14e	5.4	~0.55	~0.35	~0.63	~0.93	0.61	0.55	~0.60
Ch-11c	14	3.55	0.52	0.36	0.70	0.97	0.60	0.50	0.59
	14b	2.1	0.54	0.35	0.65	0.86	0.59	0.57	0.60
	14c	~4.35	~0.52	~0.36	~0.69	0.95	0.57	0.54	
	14d	4.0	~0.55	0.37	~0.68	~0.90	0.62	0.55	
	18a	3.2	0.53	0.34	0.64	0.94	0.60	0.53	
Ch-19	16a	4.1	0.56	0.35	0.63	0.91	0.60	~0.47	
	17a	4.7	0.53	0.36	0.68	1.0	0.58	0.50	
	17b	3.35	0.53	0.32	0.61	0.94	~0.63		
	17d	4.6	0.54	0.32	0.60	0.90	~0.60		
Ch-15a-I-5	16	4.5	0.54	~0.35	~0.65	0.93	0.57		
Ch-22a-6	17e	~3.6	~0.58	~0.36	0.61	0.97	0.63	0.45	~0.61
	102b	2.6	0.57	0.34	0.60	0.86	0.64	0.46	0.60
Ch-25-I-12	17	4.2	0.52	0.38	0.72	0.95	0.62	~0.52	~0.59
	18	4.2	0.52	0.38	0.72	1.0	0.61	0.45	0.59
	18b	2.5	0.52	0.34	0.65	0.84	0.60	0.52	0.57
	18e	~2.55	~0.56	~0.35	~0.62	0.86	0.64	0.56	0.58

Table 1. Absolute and relative sizes of primary **Cr** elements.

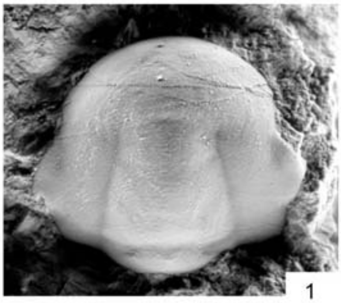
Variability. **Cor** (**a$_1$Cor**=(0.70) 0.60-0.72**a$_1$G**) and **Bcl** [**bBcl**= (0.50) 0.45 -0.57 **b$_3$G**] vary, as well as the degree of **SG** definition.

Comparison. *T. felixi* (Shergold) species differs from the type species *T. tumori* just in a little lower convexity of **Cr**, more distinct and deeper **SPg** relative to **SD** (**SPg** of *T. tumori* is on the contrary smaller and narrower than **SD**), in the absence of **SD** continuations on **Cor**, shorter **Pal**: **cPal** =0.4**a$_1$G**, slightly wider **O**: **a$_1$O**=0.21-0.25**a$_1$G** (*T. tumori* has **cPal** ~0.6**a$_1$G** and **a$_1$O**~0.21**a$_1$G**, respectively).

Discussion. Among *T. tumori* specimens there is a sharp distinction between specimen represented by core and specimen with a well-preserved shell. However, the shell from one specimen was partly removed during dissection (Pl. 1, fig. 3); after this, continuation of **SD** and **SPg**, as well as partition of **G**, became apparent.

In spite of some morphological distinctions, specimens of Siberian and Spanish species are similar, first, in the occurrence of transverse, oblong, shallow indentations going along back edge of **Cor**, which may be considered as extension of **SPg**. Both species, apparently occupy close stratigraphic position: *T. felixi* species is described from the lower third of upper Cambrian of Rio Urbión section (Shergold *et al.*, 1983), and the earliest specimens of *T. tumori* also appear in the lower third of upper Cambrian of the Chopko River section.

Distribution. Northwestern Siberian Platform, Norilsk region, Chopko River, upper Cambrian, from the upper *Agnostotes (Pseudoglyptagnostus) clavatus – Irvingella perfecta* Zone to the lower half of *Irvingella norilica* Zone, *i.e.,* distributed within *Irvingella* Biozone.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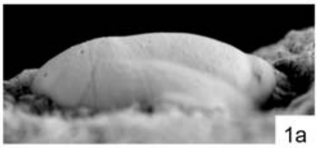
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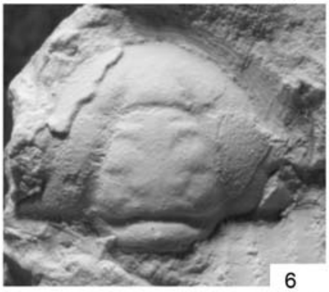
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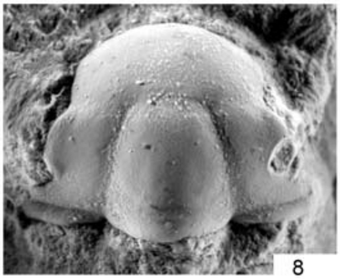
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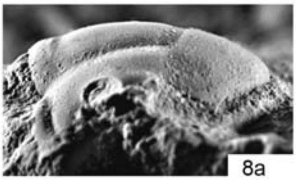
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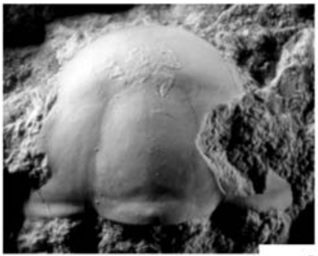
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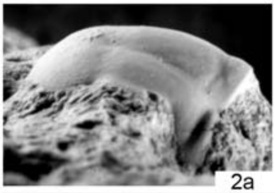
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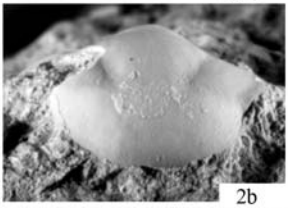
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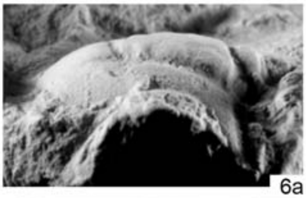
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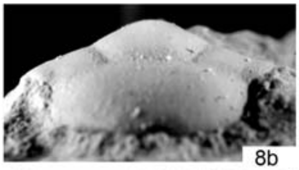
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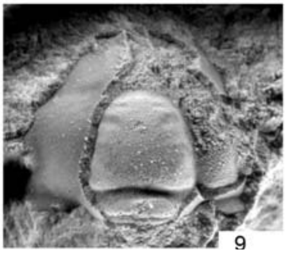
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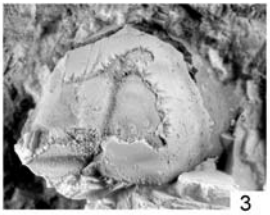
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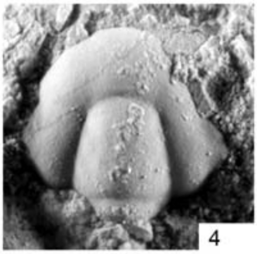
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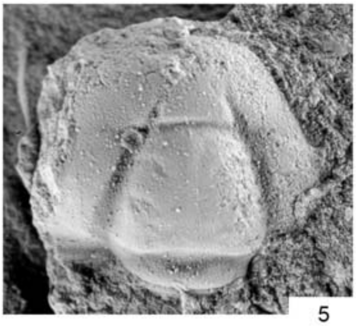
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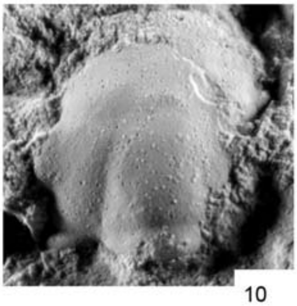
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CONCLUSION

Tumoraspis gen. nov. specimens occupy quite a broad stratigraphic position, characterizing the middle layers of the upper Cambrian and are encountered in at least in two sections of different world regions. Therefore they can be used for correlation of enclosing sediments. The description of new genus and species has been made with the use of Latin termixes. This significantly shortens the description, and serves to avoid ambiguity of morphological terms thus making presentation more clear for researchers speaking different languages.

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Plate 1. Figures 1-10: *Tumoraspis tumori* gen. et sp. nov. 1, CSGM 977/18 **Cr**, Ch-25-I-12, **a_1Cr**=4.2 mm, ı8.3; 1a: side view; 1b: front view; 2, CSGM 977/17 **Cr**, Ch-25-I-12, **a_1Cr**=4.0 mm, ı7; 2a: side view; 2b: front view; 3, CSGM 977/18e **Cr**, Ch-25-I-12, **a_1Cr**=4.7 mm, ı5.7; 4, CSGM 977/102b **Cr**, Ch-22a-6, **a_1Cr**=2.6 mm, ı11.4; 5, CSGM 977/16 **Cr**, Ch-15a-I-5, **a_1Cr**=4.5 mm, x9.3; 6, CSGM 977/17a **Cr**, Ch-19, **a_1Cr**=4.8 mm, x7.9; 6a: side view; 6b: front view; 7, CSGM 977/16a **Cr**, Ch-19, **a_1Cr**=4.1 mm, x10; 8, CSGM 977/14 **Cr** (holotype), Ch-11c, **a_1Cr**=3.6 mm, ı10; 8a: side view; 8b: front view; 9, CSGM 977/18a **Cr**, Ch-11c, **a_1Cr**=3.1 mm, ı10; 10, CSGM 977/14, **Cr**, Ch-11c, **a_1Cr**=4.5 mm, ı8.8.

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Cuadernos del Museo Geominero, nº 9. Instituto Geológico y Minero de España, Madrid, 2008. ISBN 978-84-7840-759-0

A NEW GENUS OF DIMEROPYGID TRILOBITES FROM THE LOWER ORDOVICIAN (IBEXIAN) OF WESTERN UTAH, USA

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Keywords: Dimeropygidae, systematics, cladistics, Ibexian, silicified.

Members of Dimeropygidae Hupé, 1953, are common components of silicified shallow water Ordovician trilobite faunas found in the type Ibexian area in the Tule Valley of Millard County, western Utah. Many undescribed species have been discovered in the course of a comprehensive, field-based revision of the Ibexian faunas described by Ross (1951) and Hintze (1953). Several new genera are represented, and description of this new diversity is underway (Adrain and Westrop, 2006, 2007; Adrain *et al*., 2001). Here we focus on a morphologically striking clade representing a new genus with species occurring in the Stairsian, Tulean, and Blackhillsian stages.

The new genus includes "*Psalikilopsis* (?)" *alticapitis* Young, 1973, along with six new species. Members of the new genus are small, highly vaulted, and most are robustly tuberculate. Synapomorphies include a linear or arcuate array of tubercles on the librigenal field, and pygidia with long fulcral spines and a pronounced "wall" structure of fused pleural bands similar to that seen in species of the younger *Dimeropyge* Öpik, 1937. Morphological diversity is high within the genus, particularly with respect to sculpture, pygidial features, and degree of effacement.

Relationships within Dimeropygidae and related groups are poorly understood (Adrain *et al*., 2001; Adrain and Westrop, 2007), mainly due to incomplete knowledge of many of the generally small and tuberculate species. Adrain and Westrop (2007) outlined the major unanswered questions in the phylogenetic structure of the family. In order to make progress, it is critical that new morphological data be developed to permit quantitative phylogenetic analyses. Adrain and Westrop (2007) carried out a parsimony analysis of their new *Bearriverops*, and we have conducted an analysis of the new genus reported herein.

Parsimony analysis of the seven species plus an outgroup species was based on 46 characters (16 cranidial, 15 librigenal, and 15 pygidial) and 109 character states. An undescribed dimeropygid from the Skullrockian Stage was selected as an outgroup. An exhaustive search with all characters unordered yielded a single most parsimonious tree of length 89, consistency index .708, and retention index .653.

Members of the new genus are usually relatively rare components of the diverse (typically 10-20 species) faunas in which they occur. Because of their highly characteristic morphologies, however, they may have considerable biostratigraphic potential.

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ORDOVICIAN (IBEX-WHITEROCK) TRILOBITES FROM CENTRAL EAST GREENLAND

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Keywords: Greenland, Ordovician, trilobites.

INTRODUCTION

The first detailed account of the Ordovician trilobite fauna of central East Greenland was by Christian Poulsen (1937), who described specimens collected by him and others during a series of expeditions in the 1920s to 1950s led by Lauge Koch. Detailed mapping of the Cambro-Ordovician rocks of the region was carried out in the 1950s by J.W. Cowie and P.J. Adams (1957). However, although they made extensive collections from the sections they studied, and provided preliminary identifications, they never published a detailed description of the fauna, although the Ordovician trilobites formed the basis of an unpublished MSc thesis (University of Bristol) by Gotto (1976). The present account is a preliminary report on the Ordovician (Ibex to Whiterock) trilobites collected by Cowie and Adams, which are now held at the National Museum of Wales, and for which full descriptions are in the process of being prepared. The collection includes over 30 genera, and several new species. The majority of the trilobites are bathyurids, although 13 other families are also represented.

STRATIGRAPHY

Cowie and Adams (1957) mapped the complete Cambro-Ordovician sequence in two main field areas of central East Greenland: Ella Island, and Albert Heim Bjerge in northern Hudson Land (Figure 1). The exposures are vast, with the Ordovician strata reaching thicknesses of over 2000 m on Albert Heim Bjerge, and over 1500 m on Ella Island. In both areas, the early Ibex (Gasconadian) Antiklinalbugt Formation (the Cass Fjord Formation of Poulsen, 1937, and Cowie and Adams, 1957; see Peel and Cowie, 1979) is overlain unconformably in by the Cape Weber Formation, of Jeffersonian to Cassinian age, followed conformably by the Narwhale Sound Formation, the lower part of which contains the Ibex-Whiterock series boundary (Figure 2). On Ella Island, the Narwhale Sound Formation is in unconformable contact with overlying Devonian rocks, but on Albert Heim Bjerge the Ordovician sequence continues conformably up into the Heimbjerge Formation (Whiterock), before giving way to Devonian strata.

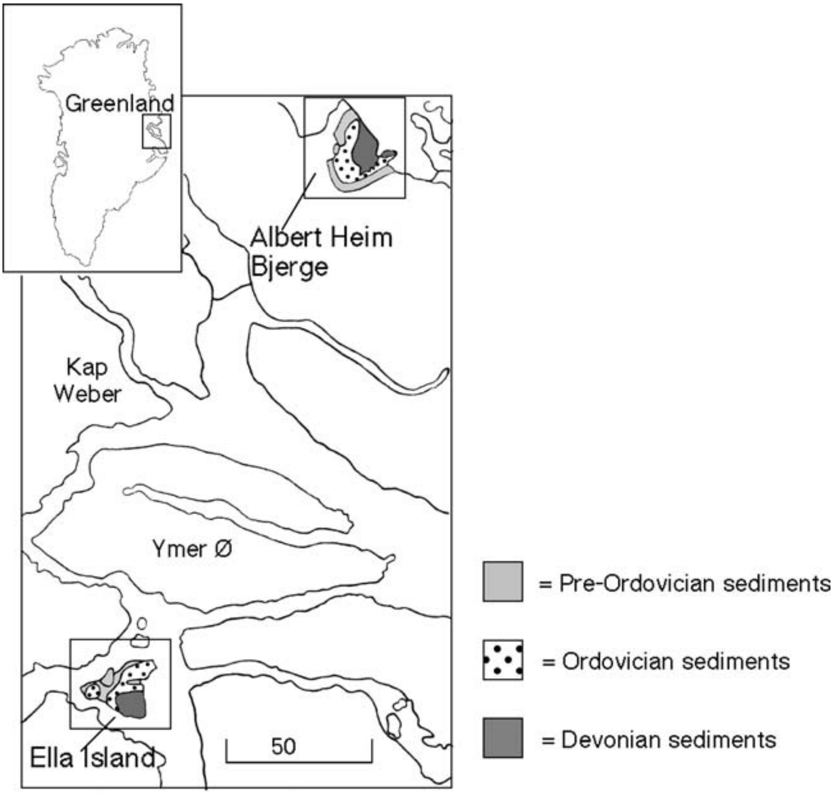


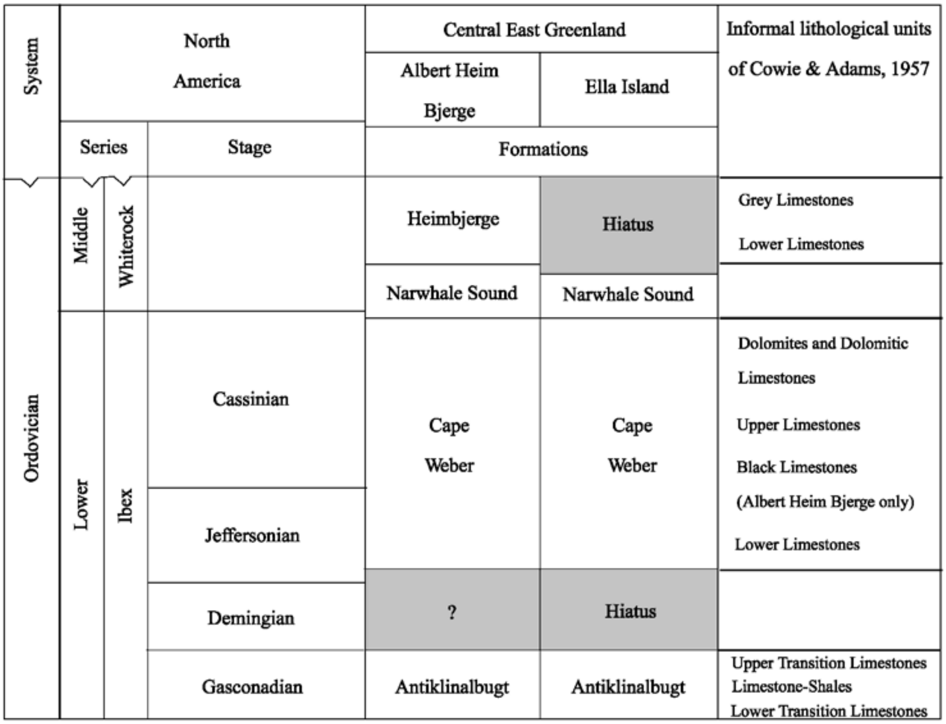
Figure 1. Map of central-east Greenland showing the outcrops of Ordovician rocks in the two main field areas, Albert Heim Bjerge and Ella Island.

The Antiklinalbugt Formation comprises over 200 m of carbonate sediments, including thinly-stratified peritidal to subtidal muddy and silty horizons interbedded with nodular limestones, and more massive subtidal limestone beds (Cowie and Adams, 1957; Stouge *et al.*, 2001). Stouge *et al.* (2001) described microbial (stromatolitic/thrombolitic) mounds from Ella Island, becoming larger in upper parts of the formation, in association with a late Cambrian/early Ordovician transgressive trend. The carbonate composition of the sediments varies from dolostone and dolomitised limestone to almost pure limestone. Cowie and Adams (1957) recognised three units, and fossils occur predominantly in the massive limestone beds of the middle one, the Limestone-Shales.

The Antiklinalbugt Formation has an unconformable boundary with the Cape Weber Formation, marking a depositional hiatus that is thought to include all of the Demingian and the lower part of the Jeffersonian Stage of the Ibex Series (Stouge *et al.*, 2001, 2002). Together with the overlying Narwhale Sound Formation, the Cape Weber Formation represents a conformable, shallowing-upward carbonate succession. The Cape Weber Formation generally comprises a great thickness (over 1000 m) of limestones, dolomitic limestones and dolomites. Although they viewed the formation as fairly homogeneous, Cowie and Adams (1957) recognised three main lithological units on Ella Island, while Stouge *et al.* (2002) made a different division into four mappable units. Fossils do not occur uniformly throughout the formation but are found in particular limestone beds within all lithological units. On Albert Heim Bjerge, Cowie and Adams (1957) recognised a fourth, distinctive, richly fossiliferous, lithological unit, which is not present on Ella Island. The 'Black Limestones' comprise 85m of thinly-bedded, dark grey to black limestones and shales, which Stouge *et al.* (2002) interpret as a deep-water marine incursion onto the carbonate shelf, due to a global sea level rise. This is marked in the faunal composition by the presence of some deeper water, cosmopolitan species, such as *Carolinites genacinaca*.

The Narwhale Sound Formation comprises a series of dolostones, dolomitic limestones and limestones, of various thicknesses. Some silicified beds in the formation have yielded fossils, but Cowie and Adams (1957) did not collect any identifiable trilobite remains.

On Albert Heim Bjerge, the Narwhale Sound Formation is succeeded conformably by the 320m thick Heimbjerge Formation, comprising shallow marine subtidal carbonate facies, in the form of mudstones, massive and platy limestones (Cowie and Adams, 1957; Stouge *et al.*, 2002). The Heimbjerge Formation represents the youngest lower Palaeozoic strata in central East Greenland and is overlain unconformably by Devonian strata.



System	North America			Central East Greenland		Informal lithological units of Cowie & Adams, 1957
				Albert Heim Bjerge	Ella Island	
	Series		Stage	Formations		
Ordovician	Middle	Whiterock		Heimbjerge	Hiatus	Grey Limestones Lower Limestones
				Narwhale Sound	Narwhale Sound	
	Lower	Ibex	Cassinian	Cape Weber	Cape Weber	Dolomites and Dolomitic Limestones Upper Limestones Black Limestones (Albert Heim Bjerge only) Lower Limestones
			Jeffersonian			
			Demingian	?	Hiatus	
			Gasconadian	Antiklinalbugt	Antiklinalbugt	Upper Transition Limestones Limestone-Shales Lower Transition Limestones

Figure 2. The Lower to Middle Ordovician stratigraphy of central East Greenland. After Stouge *et al.* (2002) and Cowie and Adams (1957).

FAUNAL COMPOSITION

Bathyuridae. The trilobite fauna is dominated by bathyurids, which are represented by 12 genera (?*Acidiphorus*, *Bathyurellus, Benthamaspis, Bolbocephalus,* ?*Jeffersonia,* ?*Lutesvillia,* ?*Peltabellia, Petigurus, Psephosthenaspis, Punka, Strigigenalis,* ?*Uromystrum*).

Dimeropygidae. Two new species of *Tulepyge* Adrain and Westrop, 2006.

Hystricuridae. Several taxa, including *Millardicurus armatus* (Poulsen) and *M.*? *nudus* have been recognised from the Antiklinalbugt Formation.

Telephinidae. The cosmopolitan species *Carolinites genacinaca* occurs in the 'Black Limestones' of the Cape Weber Formation, marking a period of deeper water incursion onto the shallow water carbonate shelf. Asaphidae. A single hypostoma of *Isoteloides* from the 'Black Limestones' awaits specific assignment. Asaphids are also represented in the same unit by two further unassigned hypostomata, and by fragmentary cranidia, free cheeks and pygidia of *Paraptychopyge* cf. *disputa*.

Styginidae. Two species are present, assigned tentatively to *Eobronteus* and *Raymondaspis*, which require further resolution.

Cheiruridae. A small number of cranidia of *Sphaerexochus*, too poorly preserved to allow specific assignment.

Illaenidae. Limited numbers of *Illaenus* and *Platillaenus* are present in collections from the Heimbjerge Formation.

Pliomeridae. Represented by a cranidium of *Cybelopsis* from the Cape Weber Formation, which probably belongs to *C. speciosa*, originally described by Poulsen (1927) from northwest Greenland. A cranidium of *Pliomerops* is recorded from the Heimbjerge Formation.

Pterygometopidae. A fragmentary cranidium of Calliops, from the Heimbjerge Formation.

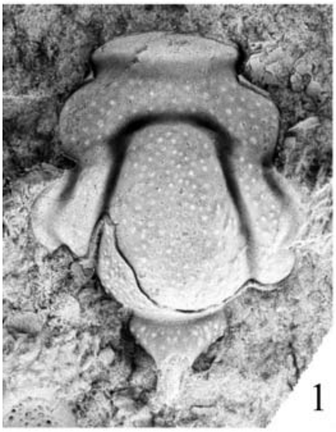
Remopleurididae. Several incomplete cranidia of *Remopleurides* from the Heimbjerge Formation, and a fragmentary cranidium from the Cape Weber Formation, which has been tentatively assigned to *Apatokephalus*.

Nileidae. At least two species of *Symphysurina* are present in the Antiklinalbugt Formation.

Catillicephalidae. A single fragmentary cranidium from the Cape Weber Formation is assigned to *Onchonotus*.

Agnostidae. One specimen of *Micragnostus* cf. *intermedius*, from the Antiklinalbugt Formation.

Plate 1. Trilobites from Central-East Greenland, from the J. W. Cowie Collection. 1. *Millardicurus armatus* (Poulsen), NMW97.56G.159b, cranidium, x3, Antiklinalbugt Formation. 2. *Tulepyge* sp. nov. A, NMW97.56G.149, cranidium, x8, Antiklinalbugt Formation. 3. *Tulepyge* sp. nov. B, NMW97.56G.169, cranidium, x8, Antiklinalbugt Formation. 4. *Isoteloides* sp., NMW97.56G.234, hypostome, x4, Kap Weber Formation. 5. *Bathyurellus* cf. *teicherti* Poulsen, NMW97.56G.116, pygidium, x4, Kap Weber Formation. 6. *Carolinites genacinaca* Ross, NMW97.56G.254, librigena, x8, Kap Weber Formation. 7. *Bolbocephalus groenlandicus* Poulsen, NMW97.56G. 20, cranidium, x9, Kap Weber Formation. 8. *Sphaerexochus* sp., cranidium, NMW97.56G.99a, x3, Heimbjerge Formation. 9. *Micragnostus* cf. *intermedius* (Palmer), NMW97.56G.156, x8, Antiklinalbugt Formation. 10. *Symphysurina porifera* Poulsen, NMW97.56G.265, pygidium, x4, Antiklinalbugt Formation. 11. *Remopleurides* sp., NMW97.56G.305, cranidium, x5, Heimbjerge Formation. 12. *Cybelopsis* cf. *speciosa* Poulsen, NMW97.56G.18, cranidium, x3, Kap Weber Formation. 13. *Illaenus* sp., NMW97.56G.299, librigena, x5, Heimbjerge Formation.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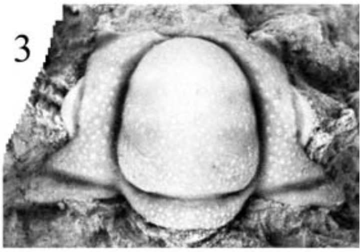
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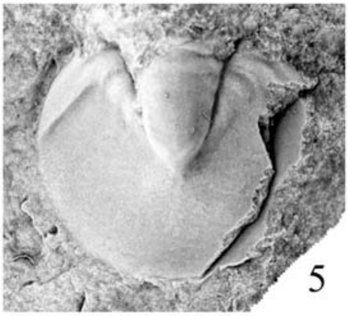
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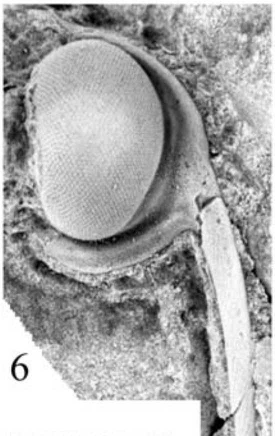
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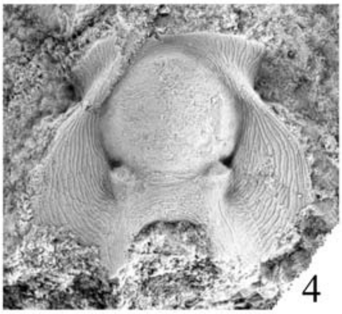
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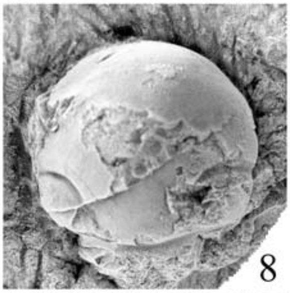
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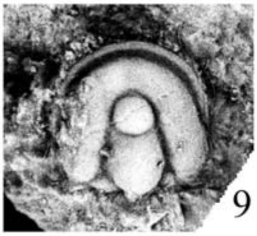
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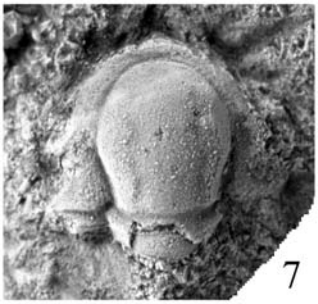
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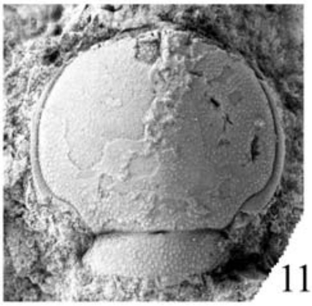
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CONCLUSIONS

Great thicknesses of Lower to Middle Ordovician (Ibex to lower Whiterock series) carbonates are exposed on Ella Island and Albert Heim Bjerge, in central East Greenland. Although only a few beds in the sequence are fossiliferous, Cowie and Adams (1957) amassed a significant collection of trilobites during their mapping of the Cambro-Ordovician stratigraphy of the area. The fauna is diverse and includes trilobites representing fourteen different families. However, almost half of the thirty or so genera present are bathyurids.

The fauna has elements in common with similar faunas from palaeogeographically adjacent regions, including north-west Greenland, Spitsbergen and western Newfoundland.

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BIOSTRATIGRAPHY AND SYSTEMATICS OF SELECT LOWER AND MIDDLE DEVONIAN PHACOPIDAE (TRILOBITA) FROM SOUTHERN MOROCCO

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Keywords: Phacopidae, *Austerops*, *Barrandeops*, *Boeckops*, *Reedops*, Devonian.

INTRODUCTION

Phacopid trilobites are almost ubiquitous fossils in the Lower and Middle Devonian strata of Morocco, and display a diversity of form seen at no other point in the history of the family. The southern and southeastern margins of Morocco make ideal field areas for studying the Phacopidae through this time interval, because rock units of this age are present in long, continuous exposures that are traceable for many kilometers along strike. Furthermore, the fossils themselves show articulation and preservation matched in few other regions (making complete, definitive descriptions possible), and are commercially mined by the local Berbers (making specimens available in large numbers). McKellar and Chatterton (in press) have recently described two new genera and eight new taxa of specific or subspecific rank within the Phacopidae, including: *Austerops kermiti*, *A. salamandar*, *A. smoothops*, *A. speculator punctatus*, *Boeckops stelcki*, *Barrandeops forteyi*, *Barrandeops granulops*, *Barrandeops lebesus*, *Barrandeops ovatus*, *Phacops araw*, and *Reedops pembertoni*. Additionally, new information was provided for *Reedops bronni* (Barrande, 1846), *R. cephalotes hamlagdadianus* Alberti, 1983, *Pedinopariops* (*Hypsipariops*) *vagabundus* Struve, 1990, *Drotops megalomanicus megalomanicus* Struve, 1990, and *D. armatus* Struve, 1995. The detailed examination of these new taxa, as well as other species still in open nomenclature, has presented an opportunity to use phacopid trilobites as biostratigraphic indicators. These taxa appear in correlatable strata from the three major Devonian basins in southern Morocco, the Tindouf, Tafilalt, and Ma'der basins (Fig. 1), and their presence is useful for correlation within and between these basins, as well as farther abroad. Here we concentrate upon the biostratigraphy of the phacopid trilobites of southern Morocco, and large-scale trends when their biostratigraphy and biogeography is considered alongside their phylogeny.

BACKGROUND TAXONOMY

The taxa outlined in the introduction will soon be appearing in a monographic work (McKellar and Chatterton, in press), so only a brief discussion of the new genera and a representative image of new species are presented here, to familiarize the reader.

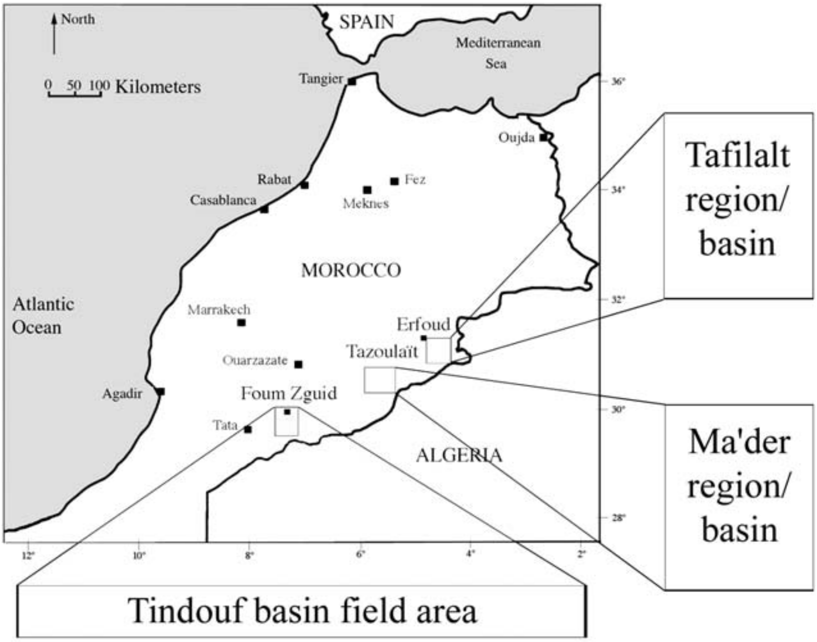

Figure 1 Generalized locality map for study sites within (Morocco indicating applicable Devonian basins. modified from Chatterton *et al*., 2006.)

Austerops McKellar and Chatterton

Discussion. This new genus is comprised of the Moroccan phacopids that are united by their shared possession of weak, sparse glabellar tubercles, an effaced lateral border furrow, a faint palpebral furrow, and prominent and continuous terrace lines upon their doublure. Grade-based taxonomy might place Austerops species within *Boeckops* or *Chotecops*, but members of *Austerops* clearly differ from these genera in terms of their sculpture (particularly doublure sculpture), glabellar proportions, and a number of eye-based characters. Currently there are only four species assigned to *Austerops* (Fig. 2), but additional work will likely increase this number greatly, and has the potential to expand the range of the genus outside Morocco.

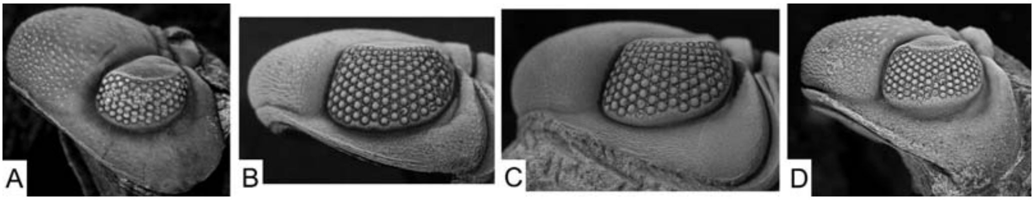

Figure 2. *Austerops* species. A, *Austerops smoothops* (Chatterton *et al*., 2006), UA13319, lateral view of isolated cephalon, X2.5. (Modified from pl. 6.6 of Chatterton *et al*., 2006.). B, *A. kermiti*, UA6884, lateral view of cephalon, complete individual, X2.3. (Modified from pl. 8.2 of McKellar and Chatterton, in press.). C, *A. salamandar*, UA6894, lateral view of cephalon, complete individual, X3.3. (Modified from pl. 10.8 of McKellar and Chatterton, in press.). D, *A. speculator punctatus*, UA6882, lateral view of isolated cephalon, X2.0. (Modified from pl. 6.2 of McKellar and Chatterton, in press.).

Barrandeops McKellar and Chatterton

Discussion. Barrandeops is comprised of a number of Moroccan phacopids that are united by their shared possession of a palpebral lobe that is lower than the palpebral area and bears no pits between its tubercles, and an eye that typically bears 19 vertical rows of lenses. *Barrandeops* species can be separated from the *Phacops* species found in Morocco on the basis of their conical glabellar tubercles, and can be separated from *Pedinopariops* and *Drotops* species, on the basis of their reduced scleral surface. Initial investigation has placed four species within *Barrandeops* (Fig. 3), but there are many undescribed phacopids within Morocco that likely belong within this genus.

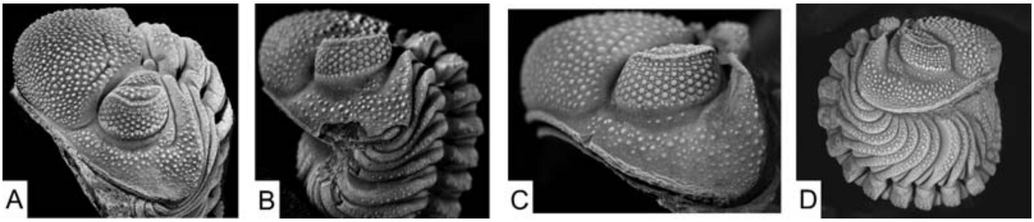

Figure 3. *Barrandeops* species. A, *Barrandeops granulops* (Chatterton *et al.*, 2006), UA13302, dorsolateral view of exoskeleton, complete individual, X1.1. (Modified from pl.2.11 of Chatterton *et al.*, 2006.). B, *B. lebesus* (Chatterton *et al.*, 2006), UA13304, lateral view of exoskeleton, complete individual, X3.0. (Modified from pl.3.7 of Chatterton *et al.*, 2006.). C, *B. ovatus*, UA6912, lateral view of isolated cephalon, X2.5. (Modified from pl. 14.1 of McKellar and Chatterton, in press.). D, *B. forteyi*, UA6920, lateral view of exoskeleton, complete individual, X1.0. (Modified from pl. 15.3 of McKellar and Chatterton, in press.).

BIOSTRATIGRAPHY

Perhaps the most useful product to arise from the study of Devonian phacopids within southern Morocco has been their newfound utility as local and regional biostratigraphic markers. Much of the initial work by researchers within and outside our research group has treated members of the Phacopidae as relatively ubiquitous and uninformative components of the Early and Middle Devonian fauna of southern Morocco, or used extreme morphologies for correlation (e.g. Schraut, 1998). This has led to a situation in which many section studies simply list all but the most extreme morphologies within Phacopidae as '*Phacops* sp. or spp.' in any given horizon, and horizons or 'couches' that produce large numbers of trilobites are often named on the basis of some of their most rare and exotic constituents. Phacopid species are usually the most abundant trilobites within these sections, and their detailed study has assisted in correlating horizons within different Devonian basins of Morocco, as well as between basins separated by up to 300 km, often suggesting connections to other faunal provinces.

In general, within the Devonian outcrop of southern Morocco, there is a succession of phacopid representatives, with basal (Pragian) horizons containing an assortment of *Reedops* species, intermediate horizons (Emsian to Eifelian) containing a mixture of *Austerops*, *Barrandeops* and *Phacops* species, and uppermost horizons (Givetian) hosting a relatively predictable succession of *Drotops*, and *Pedinopariops* species. Genera such as *Reedops*, *Barrandeops*, and *Drotops* occur in a range of facies, suggesting that they were not as environmentally restricted as other trilobite taxa, and have the potential to be superior macroscopic index fossils. Furthermore, many of the species within these genera possess very distinctive features that allow them to be identified easily in the field, with minimal or no specimen preparation.

Highlights of this approach to regional biostratigraphy include: the use of *Reedops bronni*, *R. pembertoni*, and *R. cephalotes hamlagdadianus* to identify quickly the '*Dicranurus* horizon' within the Ihandar Formation throughout the Ma'der Basin, and roughly correlate this horizon to crevasse-fills between the bioherms at Hamar Laghdad (Tafilalt Basin), and a basal horizon within an isolated section at El Mdaouer (Tindouf Basin); the use of *Barrandeops forteyi* to identify the '*Psychopyge* horizon' within the Tazoulait Fm. throughout the Ma'der basin, and correlate this horizon to the base of an isolated section at Talawarite (Tafilalt Basin); the use of *Austerops smoothops* and *B. lebesus* to identify the '*Thysanopeltis* horizon' at Zguilma (Tindouf Basin, Timrhanrhart Fm.) and correlate this to the '*Harpes/Thysanopeltis* horizon' at bou Dib (Ma'der Basin, El Otfal Fm.); and the use of the *Drotops megalomanicus* – *D. armatus* – *Pedinopariops* (*Hypsipariops*) *vagabundus* succession to correlate the lower portions of the Bou Dib Formation wherever it is present in the uppermost sections of the Ma'der basin. Additional taxa in open nomenclature bolster some of these correlations, such as *Reedops* n. sp. A (a recent addition to the '*Dicranurus* horizon'). Others suggest additional correlations, such as *Phacops* n. sp. A (found at the '*Ceratarges* horizon' of Zireg, a southern outlier of Ma'der Basin, as well as at Mrakib). Both of these trends are increasing with each new species that is described.

Attempting to identify phacopid trilobites to the level of species or subspecies in the field may be beyond the needs of many researchers pursuing trilobites within these sections, but very simplistic trends are also present among these taxa that provide a general sense of age within the studied rock units. These trends do not require any detailed knowledge of the Phacopidae, and can usually be observed in sections through phacopid cephala. One of the easiest character combinations to utilize is the nature of the sclera within the eyes, coupled with glabellar profile. Pragian strata are characterized by the presence of *Reedops* species, with very little sclera between their lenses (lenses are closely adpressed), and an elongate (exsag.), low (dors.) glabellar frontal lobe. Emsian to Eifelian stata contain a mixture of *Austerops* and *Barrandeops* species, with little sclera between the lenses of their eyes, but a progressive thickening of the sclera towards the dorsal portion of the visual surface, and this is accompanied by a relatively short (exsag.), inflated (dors.) glabellar frontal lobe. Within Eifelian strata, *Austerops* and *Barrandeops* species are often found alongside or are replaced by members of *Phacops* and *Morocops*, which possess massive, protruding sclera widely separating all lenses, and a bulbous glabella. Lower to middle Givetian strata, in addition to containing condonts from the lower *varcus* Subzone (Campbell *et al*., 2002), contain members of *Drotops* and *Pedinopariops*, which have thick sclera widely separating all lenses and small tubercles upon the sclera (at the six junctions between each lens and its closest neighbours), as well as relatively bulbous glabellar profiles.

SYSTEMATICS AND BIOGEOGRAPHY

The new Moroccan species generated in the McKellar and Chatterton study (in press) were subjected to cladistic analyses in an attempt to place them within monophyletic genera, and extend the phylogenetic hypothesis of Ramskold and Werdelin (1991) further into the Devonian. The basic nesting structure that emerged from these analyses is: (*Calyptaulax* sp. (*Acernaspis* sp. (*Ananaspis* sp. (*Reedops* spp. (*Chotecops* sp. (*Austerops* spp. (*Boeckops* spp. (*Barrandeops* spp. (*Paciphacops*/*Viaphacops*/*Kainops* spp. (*Phacops*/*Eldredgeops* spp. (*Geesops*/*Morocops* spp. (*Drotops* spp., *Pedinopariops* spp.))))))))))). It is beyond the scope of this work to discuss all of the systematic implications that arose from these analyses, but even with the limited number of taxa that were analyzed, some interesting biogeographic patterns emerged. In particular, it appears as though connectivity between the studied southern Moroccan basins and their surroundings varied through the Devonian.

The presence of *Reedops bronni* (Barrande, 1846) within the basal '*Dicranurus* horizon' suggests a strong connection between the Ma'der basin and the faunal contents of Bohemia, where *R. bronni* is used as a Pragian index fossil (Chlupáč, 1977). The *Austerops* and *Barrandeops* species that dominate the phacopid assemblages within the Emsian of Morocco represent a departure from this connection with many species, and perhaps whole genera endemic to Morocco. Communication with the neighbouring Rhenish realm must have improved within the Eifelian, since *Phacops* species very similar to the Rhenish type species *Phacops latifrons* (Bronn, 1825), are present within southern Morocco, and are followed in the Givetian by other Rhenish taxa such as *Pedinopariops*. During the latter portions of the Eifelian and within the Givetian, there may have been either mild isolation or unique environmental characteristics within the Ma'der basin in order to produce the gigantism seen in phacopids such as the *Drotops* species studied by Struve (1995).

CONCLUSIONS

Intensive sampling of the Early and Middle Devonian strata of southern Morocco has produced large sample sets of phacopid trilobites with a high degree of stratigraphic control. The new taxa recovered in these samples provide an opportunity for high-resolution biostratigraphy within the region, and provide alternatives to the cephalopod and brachiopod macrofossils that usually fill this role, but are often less abundant and more sporadic in occurrence than trilobites within the studied sections. Aside from improving the resolution of trilobite-based biostratigraphy, new taxa within the Phacopidae give us additional insight into the phylogeny of the group, and move us closer to having the resolution necessary for meaningful discussion of species distributions and the changes that these undergo. Initial work within southern Morocco has shown that there have been times where phacopids associated with the Rhenish and Bohemian faunal realms have been widespread in southern Morocco, and that there have also been time intervals where the Moroccan phacopid fauna has deviated substantially from that found elsewhere.

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LATE CAMBRIAN (FURONGIAN) TRILOBITES OF THE PELE LA GROUP, BLACK MOUNTAIN REGION, BHUTAN, AND THEIR SIGNIFICANCE FOR RECONSTRUCTION OF THE EARLY PALEOZOIC GONDWANAN MARGIN

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Keywords: Cambrian, trilobite, Bhutan, Himalaya, Gondwana, paleogeography.

INTRODUCTION

Despite nearly a century of work on the Himalaya region, its orogenic system is still poorly understood. A major contributor to this uncertainty is limited understanding of the stratigraphic architecture and the depositional systems of the strata throughout the Himalaya. The majority of literature focuses on the current geometric structure of the system, but without adequate understanding of the stratigraphic relationships of the units within it, the accuracy of orogenic models cannot be fully evaluated.

The Himalayan orogenic belt is the result of the continental collision of the Austral-Indian and Eurasian plates. The Himalaya proper is the southward verging thrust belt of the Indian subcontinent, separated from Eurasia by the Indus-Tsangpo Suture Zone (ITSZ), and is commonly divided into three major lithotectonic units with boundaries defined by major fault systems. The northern most of these units, the Tethyan Himalaya (TH), is comprised of Proterozoic through Eocene strata. The central Greater Himalaya (GH) consists of high grade metamorphic rocks, and the southern Lesser Himalaya (LH) is dominantly Precambrian-Cambrian strata. The TH is separated from the GH by the Southern Tibetan Detachment System (STD), the GH is separated from the LH by the Main Central Thrust (MCT), and the LH is separated from the southern Cenozoic foreland sediments, the Siwaliks, by the Main Boundary Thrust (MBT). The Frontal Thrust (FT) is southern most extension of the thrust system which cuts into the foreland deposits.

Debates exist on the original configuration of these units and the strata within them. Two primary models have been suggested for the origin of these units. The first postulates the LH and TH were not part of the same depositional system, with the two units either deposited in two basins separated by a topographic high (Aaron *et al.*, 1987), or the GH and TH representing exotic terranes juxtaposed against the LH during an early Paleozoic orogenic event (DeCelles *et al.,* 2000). The second model proposes these units were deposited in a single continuous margin, with the LH, GH, and TH representing proximal to distal portions of the margin, respectively (Brookfield, 1993). Recent work has provided evidence to support the continuous margin hypothesis, with chronostratigraphic data, sedimentological analysis, and biostratigraphy of Cambrian rocks in the TH demonstrating strong affinities with the LH in northern India (Hughes *et al*., 2005; Myrow *et al*., 2003, 2006), although Sr and Nd isotopic ratios suggest that some portions of the LH bear Cambrian rock may have been thrust southwards significantly (Richards *et al*., 2005).

Tethyan rocks in Bhutan yield some of the eastern-most fossiliferous rocks in the Himalaya. These strata allows for the opportunity to further test these hypotheses, as well as providing an unique perspective on the configuration of the early Paleozoic Gondwanan margin.

GEOLOGIC SETTING

The Pele La Group lies within the Black Mountain Klippe (BMK) in central Bhutan. The BMK has been described and mapped as the Chekha Formation, which considered to be distinct from the Tethyan sequence (Grujic *et al*., 2002). However,rocks in the hanging wall of the STD are generally considered of TH affinity, and these include the Chekha Formation. Hence we consider the BMK, in its entirety, part the TH sequence, in agreement with interpretations of Tangri and Pande (1995) and Yin (2006). Strata exposed in the Wachi La section of the BMK, from lowest to uppermost, include the Deshichiling Formation, the Maneting Formation, and the Quartzite Formation.

DISCUSSION

The Quartzite Formation yielded a low diversity faunal assemblage, consisting of three trilobite genera and a single brachiopod genus. Most abundant among the trilobite fauna was a species of the widespread and stratigraphically diagnostic equatorial Gondawanan genus *Kaolishania*, which occurs abundantly in various localities in North China, South Korea, and has also been identified in Australia (Shergold, 1971). The other two less widely distributed taxa include species belonging to the genera *Taipaikia* and *Lingyuanaspis*. Up until this discovery these taxa are thought to have had narrow geographic ranges with *Lingyuanaspis* having only been identified from a single locality in the Changshan Formation in the Liaoning Province of northern China, where it occurs along with *Kaolishania* and *Taipaikia* (Duan *et al*., 2005). *Taipaikia*'s only other known occurrence in the Taebaek Basin of South Korea (Kobayashi, 1960). A species of the early articulate brachiopod *Billingsella* was also abundant in the Quartzite Formation, and this genus is very widely distributed at this time.

The presence of *Kaolishania* in the assemblage allows us to estimate the approximate age of the deposits as about 493Ma, based on current but unpublished biostratigraphic age assignments of biozones formulated by the International Subcommission on Cambrian Stratigraphy. This assignment is based on the correlation of the North China *Kaolishania* zone with the *Eolotagnostus decoratus-Kaolishaniella* Zone of South China (Peng, 1992). These age assignments correspond with U-Pb detrital zircon data from the fossil bearing rocks of Bhutan that contain a youngest age peak at 500Ma.

Given that there is no structural evidence to suggest lateral discontinuity in the TH, the Quartzite Formation of the Pele La Group has yielded what are at present the only valid late Cambrian fossils currently known in the Himalaya, and this is of significance for reconstructions of the Cambrian peri-Gondwanan margin. While late early Cambrian trilobites in the western Himalaya show strong correlations with South China (Hughes *et al*., 2005), as does sedimentological evidence (Jiang *et al*., 2003), these eastern Bhutanese fauna show strong affinities to North China and South Korea. The spatially restricted occurrence of the genera *Taipaikia* and *Lingyuanaspis* is striking and since the three Bhutanese trilobite genera all co-occur stratigraphically in the Changshan Formation, this suggests that the North China Block may have been closer to the Himalayan margin, specifically the northeastern Indian subcontinent, than previously assumed (e.g. Metcalfe, 1996; Huang *et al*., 2000).

Further insight can be drawn from sedimentological comparisons between these two regions. In Bhutan there is a minimal age differences between the youngest zircons in the sample, which are about 500 Ma old, and the fossil constrained depositional age of ~494-493 Ma for the Quartzite Formation that implies a rapid exhumation, erosion, and re-deposition of these zircons, a signature of the Early Paleozoic orogenic event seen throughout the Himalayan margin (Garzanti *et al*., 1986; DeCelles *et al*., 2000; Gerehls *et al*., 2003; Myrow *et al*., 2003, 2006). Similarly, a tectonic event has been identified in the Taebaek Group, just above the *Kaolishania* zone, across the Cambro-Ordovician boundary (Kwon *et al*., 2006), which may be the result of the same event seen throughout the margin. The fact that this event is seen throughout the *Kaolishania* zone in Bhutan and above it in Korea could correspond to the eastern migration of the event along the Gondwanan margin suggested by Squire *et al*. (2006).

Recent paleogeographic models presented for the Cambrian eastern Gondwanan margin are in disagreement on the continental configurations of their constituents, with the location of the North China Block (equivalent to the Sino-Korean Block) showing inconsistency in placement in various reconstructions. Trilobite systematics may serve as a useful tool to further refine these paleogeographic reconstructions. As *Taipaikia* and *Lingyuanaspis* occur in limestones in the North China Block, and sandstones in Bhutan they do not appear to have a strong lithofacies preference. Rather, their distribution may reflect a close spatial and/or temporal relationship between these areas. These results are consistent with other recent suggestions that North and South Chinese Cambrian faunas show greater faunal similarity than once assumed. A detailed taxonomic revision of the Kaolishianidae and its many representatives, coupled with the formulation of sound biostratigraphic frameworks of these and other late Cambrian taxa should provide the necessary foundation to measure the degree of similarity between the early Paleozoic Gondwanan provinces, allowing for a further improved paleogeographic model.

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PATTERNS OF TRILOBITE EVOLUTION AND EXTINCTION DURING THE FRASNIAN/FAMENNIAN MASS EXTINCTION, CANNING BASIN, WESTERN AUSTRALIA

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Keywords: Late Devonian, Trilobita, evolution, extinction.

INTRODUCTION

The Frasnian/Famennian boundary marks one of the most significant events in the history of the Trilobita. Of the five orders present during the Frasnian – the Corynexochida, Odontopleurida, Harpetida, Phacopida and Proetida – only two, the Phacopida and Proetida, persisted into the Famennian. The two environmental crises that so adversely affected late Frasnian faunas of the Prototethys Ocean generally coincided with hypoxic deposits, the so-called "Lower and Upper Kellwasser horizons", which occurred at the end of conodont Zone 12 and during Zone 13c respectively. Sequences of the Late Devonian reef system in the northern part of the Canning Basin in Western Australia that straddle the Frasnian/Famennian boundary, are unusual as they are devoid of oxygen-depleted horizons. Despite this, the major trilobite extinction events occur contemporaneously with the Kellwasser horizons.

Late Devonian sedimentary rocks extend along the south-western margin of the Kimberley Block in northern Western Australia for about 350 km. They comprise a major reef complex that flourished during the latest Givetian to Famennian. Trilobites are only known from the marginal slope facies, the Virgin Hills Formation, that was deposited at depths between a few tens to at least 200 m (Becker *et al.*, 1991). The Virgin Hills Formation comprises a sequence of thinly bedded and gently dipping, very fine-grained wackestones, that are frequently haematite-rich. The oldest part of the Virgin Hills Formation that has yielded trilobites correlates with Frasnian conodont Zone 11 (Klapper, 2007). At McWhae Ridge, the classic site from where much of the material has been collected, the Frasnian section ranges from Zone 12 to Zone 13b. The overlying Famennian extends to the *rhomboidea* Zone, the earliest trilobites occurring in the Upper *triangularis* Zone.

Among the rich Virgin Hills Formation faunas, the Odontopleuridae (Feist and McNamara, 2007) and the Harpetidae (McNamara *et al.*, in press) reach the top of Zone 13b, as elsewhere. However, in contrast to all other occurrences, the Scutelluidae (McNamara and Feist, 2006) are shown for the first time to extend to the Upper Kellwasser Event. Of the two orders that survived the Kellwasser biocrises the Phacopida are represented by the Phacopidae (Feist *et al.*, in press), and the Proetida by the Proetidae; the

Tropidocoryphidae and Aulacopleuridae disappearing, respectively, at the Lower and the Upper Kellwasser crises (Feist *et al.,* submitted).

Here we document the changing trilobite biodiversity levels before and after the Frasnian/Famennian boundary. Moreover, we also describe the patterns of evolution prior to and following the mass extinction event. Where we have suitable ontogenetic information the role of developmental change in reflecting responses to changing environmental conditions is examined. In particular we investigate changes in eye morphology prior to and after the Frasnian/Famennian boundary. Some species are blind, while others show evolutionary trends of varying numbers of lenses. These trends are assessed with respect to fluctuating environmental conditions in the Canning Basin and other parts of the Prototethys Ocean.

SCUTELLUIDAE

Two species are known from the late Frasnian, *Telopeltis woodwardi* McNamara and Feist, 2006, which ranges from Zones 11 to 12, and *T. microphthalmus* McNamara and Feist 2006, from Zones 13a and 13b. This latter species is the last known representative of the order Corynexochida. Locally, *T. woodwardi* is a very common element of the zone 12 fauna, where it forms coquinas. The genus *Telopeltis* is an unusual scutelluid, as it has a very convex exoskeleton. The pygidium in particular is strongly convex, but reduces in convexity between the two species. Their ancestor/descendant relationship is shown by the occurrence of intermediate evolutionary forms. Reduced convexity is a feature that is paralleled in some other trilobite groups in the Virgin Hills Formation (see below). Furthermore, there is a reduction in the size of the eye lobe in the younger species of *Telopeltis*, also seen in other trilobite groups in the Frasnian part of the Virgin Hills Formation. A strongly vaulted transitory pygidium is characteristic of early ontogenetic growth series of scutelluids in general, suggesting that in *Telopeltis* this adult character is a paedomorphic feature. Six paedomorphic features have been identified in *T. microphthalmus* and nine in *T. woodwardi*, involving features such as glabellar furrow depth, development of occipital spine, and eye size, in addition to the exoskeletal vaulting (McNamara, 2006, p. 990). Given the species relatively small size it is possible that the paedomorphic features evolved in response to selection for earlier maturation in a stressed environment.

ODONTOPLEURIDAE

These are a rare element of the fauna, but forms present in zone 13b are the last representatives of the order Odontopleurida. Five species have been identified (Fig. 1), all within the genus *Gondwanaspis* (Feist and McNamara, 2007). Species attributable to this genus have been found in Morocco, Montagne Noire in southern France, the Harz Mountains in Germany and Rudny Altai, Siberia (Feist, 2002; Feist and McNamara, 2007). Of the Canning Basin species only two have been formally named: *G. spinosa* and *G. dracula*. This latter species also occurs in Germany. These species are confined to Zones 11 and 12, having become extinct at the Lower Kellwasser Event. Only two cephala have been found in Zone 13b, immediately prior to the Upper Kellwasser Event, and each appears to represent a distinct taxon. *Gondwanaspis* is characterised by a very low convexity, a wide cephalon, poorly defined glabellar lobes and the presence of spines or protuberances on the anterior margin of the cranidium. It has been suggested that the lack of an anterior cephalic arch, due to the downward flexure of the anterior margin, meant that unlike other odontopleurids, instead of having to assume both a 'resting' and an 'active'

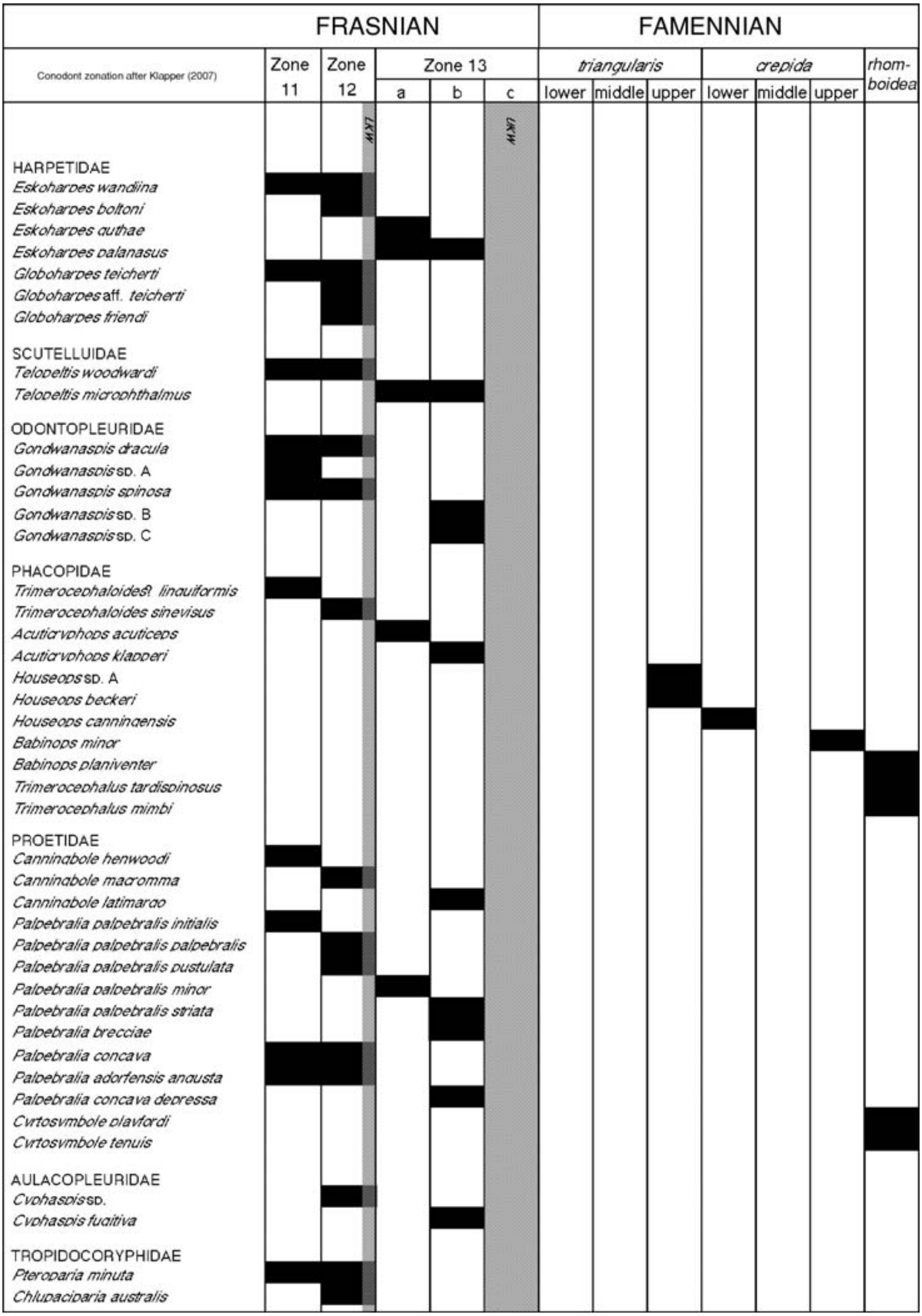

Figure 1. Range chart of Late Devonian trilobite species against conodont based biozonation, Canning Basin, Western Australia. Harpetid and phacopid taxa are currently in press; proetid taxa are submitted for publication; consequently, these taxa must be considered as *nomina nuda* until published.

posture, *Gondwanaspis* could assume a single, combined posture. Consequently, combined with the low convex cephalon and wide genal areas, the eye would have been positioned so as to minimise what would otherwise have been an appreciable anterior blind spot. Although the ontogenetic development of *Gondwanaspis* is not known, there are a number of consistent ontogenetic changes that occur in a wide variety of odontopleurids. These indicate that a number of cephalic features of *Gondwanaspis* evolved by paedomorphosis. These include the weakly developed glabellar lobes, the anterior position of the eye lobe in many species and the truncate frontal lobe.

HARPETIDA

The Frasnian part of the Virgin Hills Formation contains a diverse harpetid fauna (McNamara *et al.,* in press). Of the two genera described, *Eskoharpes* is the most diverse and long-ranging, including four species and extending from Zones 11 to 13b. The type species, *E. palanasus*, which is the sole representative of the genus in Zone 13b, represents the last known member of the order Harpetida. The four species of *Eskoharpes* (Fig. 1) show some significant evolutionary trends, particularly with regard to decreasing convexity of the cephalon and increase in brim width. The other harpetid genus, *Globoharpes*, is restricted to Zones 11 and 12, having been a casualty of the Lower Kellwasser Event. This genus shows dimorphism in the extent of development of a swollen anterior boss that is located immediately anterior to the frontal lobe. We argue that this represents a brooding pouch, analogous to similar structures reported in a large number of, predominantly, Cambrian forms (Fortey and Hughes, 1998). This is the first record of this structure in harpetid and post-Ordovician trilobites. Another structure recorded for the first time in this order, both in *Globoharpes* and *Eskoharpes*, is a median occipital pitted organ (see Lerosey-Aubril and McNamara, 2008).

PROETIDAE

This family with three genera and 15 species is the most abundant among the Late Devonian trilobites in the Canning Basin. The terminal Frasnian is marked by the presence of a number of lineages of early Drevermaniinae. Evolutionary changes mainly affected the eyes. In the new genus *Canningbole* large eyes and palpebral lobes are developed between Zone 11 and Zone 13b, i.e. up to the Upper Kellwasser extinction level. This "conservative" configuration, that we consider to reflect that of so far unknown proetoid ancestors, is observed for the first time in the Drevermanniinae. Field data indicate that these trilobites lived in shallow perireefal environments prior to gravitational transport in debris flows into deeper slope settings. *Canningbole*-like oculated predecessors gave rise to the *Palpebralia* lineage of worldwide distribution in off-shore or deeper ramp environments. This group is extremely diversified with regard to its trend towards eye-reduction and straightening of the palpebral suture. Whereas five different morphs of *P. palpebralis* with a variable degree of regression of the palpebral lobe are distinguished, four taxa of *Palpebralia* are blind. They are differentiated by the width of the genal field and the course of the facial suture. Both blind and reduced-eyed forms reach the Upper Kellwasser extinction level. As in Europe and North Africa proetoid recovery in the Famennian in the Canning Basin was delayed until the *rhomboidea* Zone, much later than that of the phacopids. The earliest *Cyrtosymbole* species are both oculated; their unknown ancestors must be searched for among sighted inhabitants of shallow water biotopes, such as may have developed on the Canning Basin reefal build-ups.

Late Frasnian aulacopleurids are fairly abundant in European sections but extremely rare in the Canning Basin. Only one free cheek and a single cranidium have been found. As elsewhere, *Cyphaspis* reaches the Upper Kellwasser extinction level. Tropidocoryphids, both oculated and blind, are abundant in mid-Frasnian strata prior to the equivalent of the Lower Kellwasser horizon. They are not present above this level in the Canning Basin, unlike the European and North African sections where they continue up to the Upper Kellwasser level. Interestingly, the blind *Pteroparia* from Western Australia takes an extreme position in the backward migration of the facial suture that characterises the *Pteroparia* evolutionary lineage.

PHACOPIDA

These trilobites are rare before the Lower Kellwasser Event, being only represented by the new genus *Trimerocephaloides*. The type species *T. sinevisus* is characterised by the absence of eyes and palpebral lobes like in the Famennian *Trimerocephalus*. Such blind phacopids were hitherto unknown in the Frasnian. Phacopids in the form of species of *Acuticryphops*, become common prior to the Upper Kellwasser Event (Feist *et al.,* in press). The reduction in eye lens number documented in *Acuticryphops* in Montagne Noire and in Morocco is also seen in the Canning Basin. However, rather than occurring within a single species the reduction occurred between two species. One new genus and six species of early Famennian phacopids are recognised. Phacopids have yet to be found immediately after the mass extinction event, the first occurring no earlier than in the middle *triangularis* zone. Unlike European sections where only blind phacopids are known in the earliest Famennian, initial recovery following the mass extinction event in the Canning Basin perireefal environments features oculated forms. These trilobites are likely to have evolved from conservative ancestors with normal eyes that had managed to survive the Kellwasser biocrises in reef-related shallow water niches. These discoveries have enabled the origin of post-event phacopids from shallow water environments to be demonstrated for the first time. Unlike the trends in eye reduction seen in the latest Frasnian, descendant lineages show increasing eye size, increased cephalic vaulting and effacement during the early Famennian, although some blind forms of *Timerocephalus* are also known.

CONCLUSIONS

To date 39 species of trilobites in 15 genera have been found in middle and late Frasnian and early Famennian strata in the Canning Basin, making it the richest fauna of this age known. The terminal Frasnian Kellwasser extinction events had a significant impact on the Canning Basin trilobite fauna, although the intensity of the two events differed, as reflected in the taxonomic levels at which extinction occurred. At the Lower Kellwasser Event 17 species, but only 4 genera, became extinct. Ten species, in seven genera became extinct at the Upper Kellwasser Event. These include three, *Telopeltis, Gondwanaspis* and *Eskoharpes*, that represent the extinction of three trilobite orders, demonstrating that the Upper Kellwasser Event was more deleterious to trilobite biodiversity than the earlier event. Post-event trilobite recovery was slow, with no forms found in the first two conodont zones. The proetids reappeared later than the phacopids. During the late Frasnian, evolutionary trends apparent include reduction in eye lens number in a number of unrelated lineages and trends in the latest Frasnian to selection for low convexity exoskeletons in some taxa. Reduction in lens number coincides with, and may be a reflection of, global rise of the sea level which culminated in an appreciable increase in water depth immediately before the Upper Kellwasser extinction. Reappearance of oculated forms in the early Famennian correlates with a period of regression and thus shallowing of water in the marginal slope environment. Canning Basin terminal Frasnian trilobites may thus have been victims of profound eustatic perturbations characterising the major pulse of the Kellwasser extinction event.

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LOWER AND MIDDLE ORDOVICIAN TRILOBITE ASSOCIATIONS OF PERUNICA: FROM SHOREFACE ENDEMICITY TO OFFSHORE UNIFORMITY (PRAGUE BASIN, CZECH REPUBLIC)

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INTRODUCTION

Trilobites of the Lower and Middle Ordovician of the Prague Basin have been continuously studied over 150 years, mostly for taxonomic purposes (summary see Bruthansová *et al*., 2007). Apart of brief autecological papers (e.g. Šnajdr, 1987), there are few papers devoted to trilobite synecology and biostratigratigraphy (e.g. Pek, 1977; Havlíček and Vaněk, 1990). Since the outstanding review on brachiopod and trilobite biostratigraphy by Havlíček and Vaněk (1966), only brief papers concerning trilobite associations have been published (Budil *et al.,* 2007; Mergl *et al*., 2007).

LOWER ORDOVICIAN TRILOBITE ASSOCIATIONS

The stratigraphically oldest trilobites of the Ordovician age appeared above base of the transgressive Třenice Formation of late Lower or early Upper Tremadocian age (Fig. 1). A remarkably diverse association of rhynchonelliform brachiopods (*Poramborthis*, *Kvania*, *Apheoorthina*, *Eoorthis*, *Protambonites*), cystoids (*Echinosphaerites*, *Glyptosphaerites, Paleosphaeronites*) and other rare benthic invertebrates preceded the first appearance of trilobites. The trilobite fauna occurs a little higher in the succession, being accompanied with different fauna of abundant and moderately diverse, mostly micromorphous lingulate brachiopods. The rhynchonelliform brachiopods are less diverse, with *Jivinella, Kvania* and *Poramborthis.* This change indicates that the first trilobites occupied the basinal floor subsequently after the initial spread of the more tolerant brachiopod associations. This trilobite immigration probably followed the progressive deepening of the sea basin associated with weakening of siliciclastic input.

The trilobite fauna has been observed only at two localities. It was recently designated as the *Hemibarrandia-Parapilekia* Association (Mergl, 2006; Mergl *et al*., 2007). This association is characterized by the large cheirurid *Parapilekia ferrigena*, large illaenimorph *Hemibarrandia holoubkovenis*, and

Holubaspis perneri, species of unclear affinity (probable eurekiid). These three taxa are accompanied by rare but characteristic calymenoids *Holoubkocheilus granulatus* and *Parabathycheilus krafti.* This moderately diverse benthic trilobite association contains generally small-sized species of the genera *Agerina*, *Anacheirurus*, *Apatokephalus*, *Ottenbyaspis*, and *Eulomina*, and larger but rare *Niobina* and *Platypeltoides* (Fig. 2). In total, twelve trilobite species have been ascertained, and the indeterminable fragments indicate presence of, at least, two other species. The stratigraphically earliest lichid *Holoubkovia klouceki* is rare element in this association (Whittington, 2003).

The stratigraphically younger and slightly different *Hemibarrandia-Parapilekia* Association is known from several sites of the Mílina Formation (Mergl *et al.,* 2007). The age of this unit, despite lack of the index microfossils, is likely isochronous with the *Ceratopyge* Regressive Event (*P. proteus* Zone). The key taxa are the same as in the preceding association. *Parapilekia olesnaensis* is associated with less abundant *Hemibarrandia klouceki* and generally dominant *Holubaspis perneri*. Some taxa derived from ancestors present in the Třenice Formation. It is evident from the couplets of closely related species in both formations (*Agerina ferrigena* - Třenice Formation and *A. clymene* - Mílina Formation, *Anacheirurus bohemicus* and *A. nanus*, *Apatokephalus* aff. *dagmarae* and *A. dagmarae*, *Holoubkocheilus granulatus* and *H. asopus*, *Holoubkovia klouceki* and *H.* sp. n., *Parabathycheilus krafti* and *P. vagans*). However, several other new taxa appear in the Mílina Formation for the first time. Apart of the agnostid *Geragnostus*, the incomers belong to genera *Ceratopyge*, *Dikelokephalina*, *Harpides*, *Niobina*, *Orometopus*, *Pricyclopyge* and *Proteuloma*. Scarce but reliable data indicate that shallower parts of the basin (exemplified by SW part of the Prague Basin) were characterized by cheirurids, illaenomorphs and calymenoids of the *Hemibarrandia-Parapilekia* Association (Mergl *et al.,* 2007). It is the early Ordovician equivalent of the Illaenid-cheiruid Biofacies in the peri-Gondwanan space, unique and from the younger and more equatorial trilobite associations distinguished by abundant calymenoids. Local deeper sites or substrate-based unique sites abound with *Orometopus* and *Harpides.* The NE part of the basin was somewhat deeper. Is it clear from the deficiency of cheirurids, illaenomorphs and calymenoids and prevalence of *Proteuloma*, *Ceratopyge* and rarely also *Pricyclopyge* and *Geragnostus.* This *Proteuloma-Ceratopyge* Association of Mergl *et al*. (2007) should be considered the equivalent of the offshore Nileid Biofacies. Total lack of the Olenid Biofacies in the Prague Basin in combination with the outstanding diversity and abundance of lingulate and orthid brachiopods, extensive sponge „gardens", presence of cystoids, is indicative of the well oxygenated bottom waters and generally shallow to moderate deep environments (maximum 100-150 m in NE, but probably shallower in SW). The true Cyclopygid Biofacies is still unknown here, similarly as in the Tremadocian and early Floian elsewhere.

The overlying Klabava Formation, with the thickness up to 300 m, represents comparatively long time interval. The lowermost parts represent the latest(?) Tremadocian, and middle and upper levels are probably Floian to lower Dapingian in age. However, apart of graptolite and chitinozoan data, the absence and/or poor knowledge of other index taxa weaken the accurate international correlation. It is lithofacially variable formation. This reflects the depth differentiation of the basin and also various sources of the sedimentary material. The red siltstones (product of lateritic weathering of the late Cambrian volcanites) along SE limb of the basin (= Olešná Member) are of shallow water origin. Other shallow to moderate deep lithofacies is represented as the rewashed tuffs (originated by contemporaneous volcanic activity) in the upper part of the formation (= Ejpovice Member). This member is bordering the ancient NW coast. The axial part of the basin was much deeper characterized by fine pelitic sedimentation (= Klabava Member), while the volcanogenic accumulations of the Komárov Volcanic Centre (active approximately from the Floian to Sandbian) obliquely crosses the longitudinal axis of the basin, forming the local shoals. This

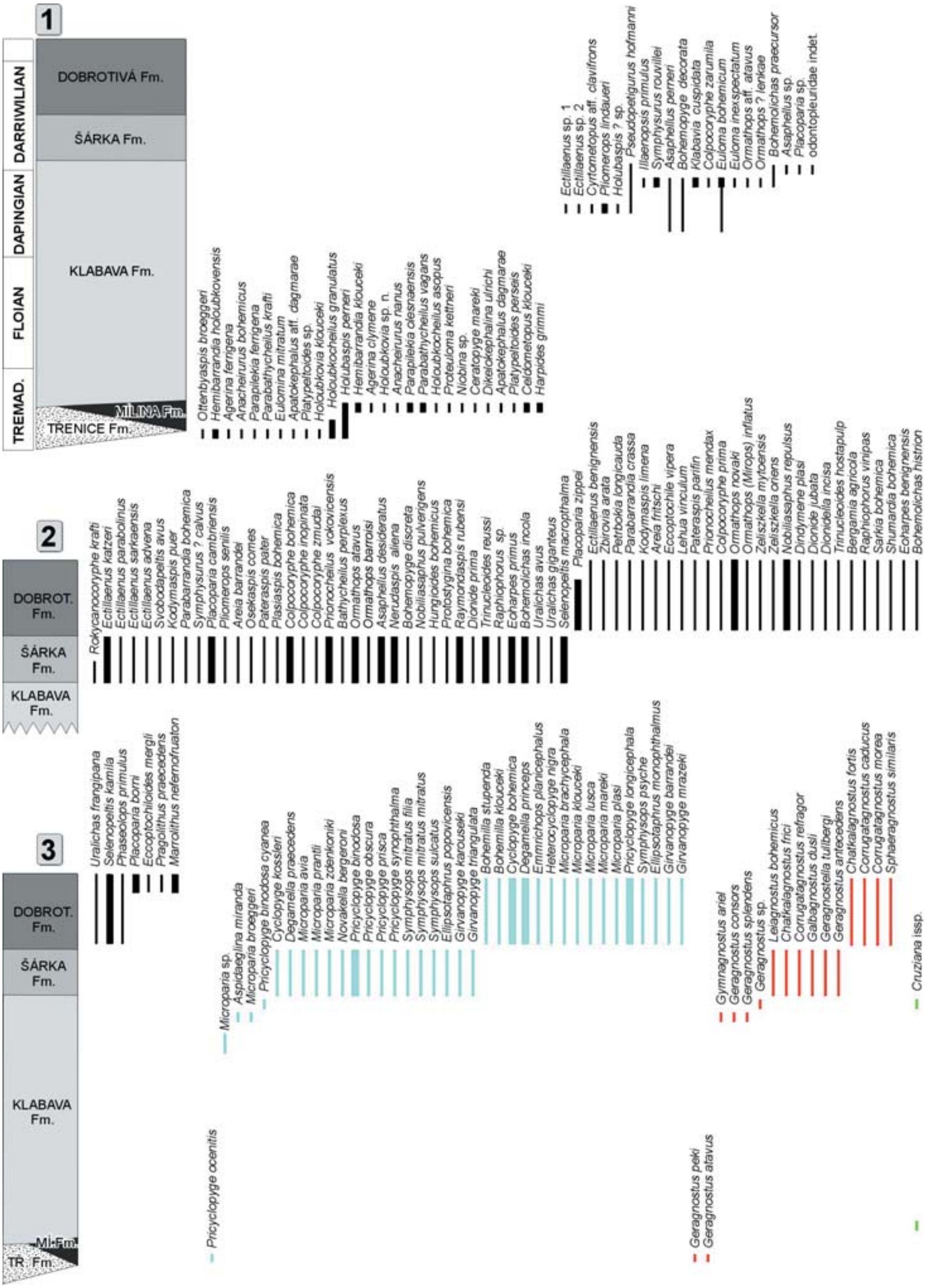

Figure 1. Stratigraphic range of trilobites and trilobite traces in the Lower and Middle Ordovician of the Prague Basin. 1, benthic and nektobenthic trilobites of Tremadocian to Dapingian (black); 2, benthic and nektobenthic trilobites of Darriwilian (black); 3, benthic and nektobenthic trilobites of Darriwilian (continued, black), pelagic trilobites (blue), agnostoid trilobites (red), and trilobite trace fossils (green) in Tremadocian to Darriwilian. Bold line: abundant occurrence; thin line: rare and very rare occurrence.

intricate lithofacies development is reflected by a mixing of the varied benthic facies-related or planktonic fossils. Trilobites are generally uncommon, being known from a few sites only.

Trilobite remains are still unknown in the Olešná Member, but the *Cruziana* trace fossils (10-15 mm broad) have been recently observed (Mergl and Mikuláš, *in prep.*). Presence of *Cruziana* indicates, that in some habitats the trilobites were quite common benthic biota and their absence in the Ole?ná Member could be taphonomically biased.

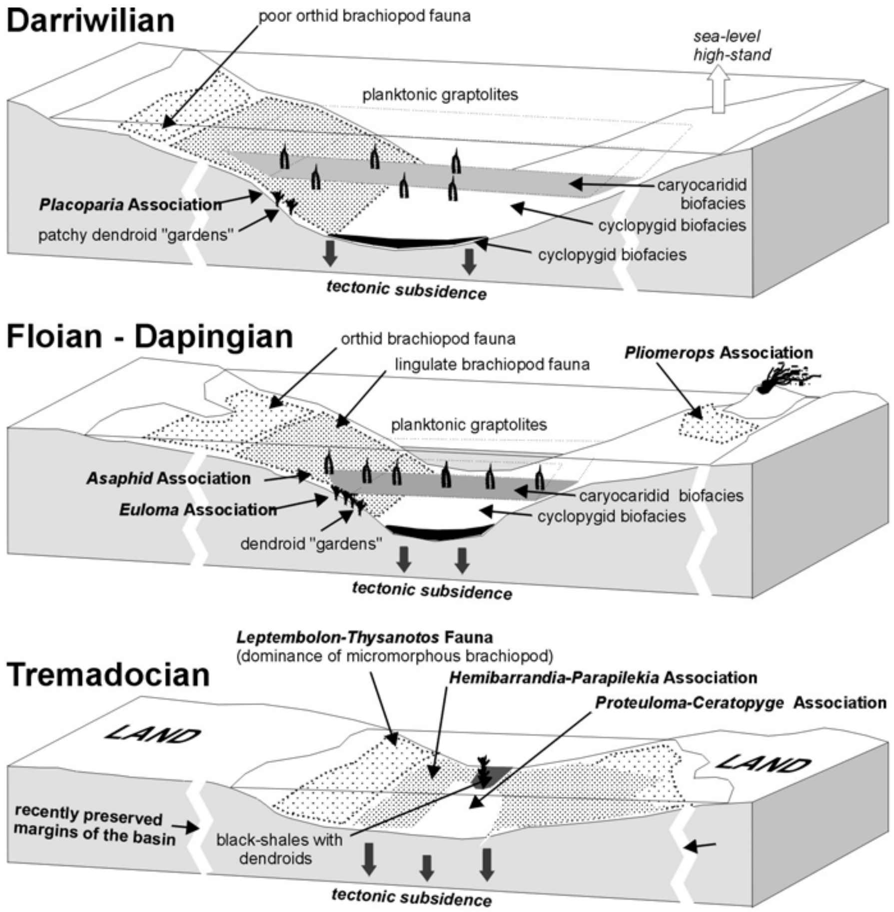

Figure 2. History of the Prague basin and its benthic and pelagic associations in the Lower and Middle Ordovician.

Trilobites of the moderately deeper environment, analogous to the Nileid Biofacies, are known from several localities in clayey shales in the middle to upper parts of the formation (*Holograptus tardibrachiatus* and *Azygograptus ellesi-Tetragraptus reclinatus abbreviatus* biozones). The trilobite remains are often complete or near complete in the Klabava Member, indicating deep and calm environment. The greater depth is also evidenced by the associated conulariids and nekto-planktonic groups such as cyclopygids, graptolites and caryocaridids. Rare and poorly preserved trilobite remains from some sites of the graptolite-bearing sequence indicate diagenetic dissolution of the calcareous material.

The *Euloma* Association is characterized by dominance of *Euloma bohemicum* and *Symphysurus rouvillei*. These two species are accompanied by several scarce species of *Asaphellus*, *Bohemopyge*, *Klabavia*, *Illaenopsis*, *Aspidaeglina*, *Cyclopyge*, *Microparia*, *Bohemolichas*, *Colpocoryphe*, *Ormathops*, *Geragnostus* and *Gymnagnostus,* The association includes some element characteristic of the offshore atheloptic association of Fortey and Owens (1987), e.g. *Illaenopsis*, *Ormathops* and *Colpocoryphe*. However the dominant *Euloma* and *Symphysurus* retain remarkably large eyes. Presence of cyclopygids should indicate depth zone 200 to 300 m (Fortey, 1985), but they are generally rare and their presence only indicates proximity of the Cyclopygid Biofacies in the deeper part of the basin. The deeper environment with the Cyclopygid Biofacies is indicated by very rare finds of cyclopygids in the Rokycany area, but the typical black-shale lithofacies is absent.

The stratigraphically younger *Asaphid* Association shares numerous common features with the above mentioned association. It is known in the Ejpovice Member in the upper part of the Klabava Formation. The association is characterized by *Asaphellus* and by the small species *Pricyclopyge binodosa cyanea.* The genera *Geragnostus*, *Bohemolichas*, *Placoparia* and small odontopleurids are rare. The ichnogenus *Cruziana* is fairly common element within the trilobite-bearing succession. The assemblage is associated with diverse fauna of orthids (*Ranorthis lipoldi, Nocturnellia nocturna*) small lingulate brachiopods, conulariids, ostracods, bryozoans, gastropod *Modestospira* and other invertebrates. Presumed depth inhabited by the *Asaphid* Association is up to 100-150 m which is consistent with a mixing of the benthic genera with the mesopelagic *Pricyclopyge* and the occurrence of typical offshore, depth related lingulate brachiopod *Paterula* just below the trilobite-bearing succession.

Entirely different, unique trilobite association is known in two sites of the Komárov Volcanic Centre. Although detailed stratigraphic and locality data are less clear, the late Floian age and a moderately deep environment (some tenths metres of the depth) of the fauna are supposed. The fauna is generally dominated by large orthids (*Ferrax*, *Nereidella, Prantlina*, *Styxorthis*) and rare gastropod *Mimospira*. Trilobites are generally scarce, with dominance of *Pliomerops lindaueri* accompanied by rare *Cyrtometopus*, *Ectillaenus* and ?*Holubaspis*. Another environmentally and stratigraphically similar site yielded *Pseudopetigurus hofmanni*. This fauna is highly endemic and can be considered the more offshore analogue of the Illaenid-cheirurid Biofacies. The brachiopods can be best compared with the Billingen brachiopod fauna of the East Baltic.

MIDDLE ORDOVICIAN TRILOBITE ASSOCIATIONS

The Šárka Formation (late Arenigian to Oretanian) is characteristic by dark-grey shales, penetrating laterally to more marginal, near-shore oolitic ferrolites. It is approximately equivalent of the early and middle Darriwilian but the exact correlation, despite some affords based on graptolites, is difficult. The trilobite fauna of the Šárka Formation is diverse, but this also reflects very intensive collecting in last 150 years. General character of trilobite associations shows a surprising similarity to the less diversified associations known from the upper Klabava Formation (*Asaphellus*, *Bohemolichas*, *Bohemopyge*, *Colpocoryphe*, *Cyclopyge*, *Ectillaenus*, *Microparia*, *Megistaspis*, *Ormathops*, *Placoparia*, *Pliomerops*, *Pricyclopyge* and agnostids). In addition, many new common nectobenthic taxa have appeared: *Dionide*, *Eoharpes*, *Plasiaspis*, *Prionocheilus*, *Trinucleoides* and *Uralichas*. Rare but significant elements represent *Areia*, *Bathycheilus*, *Hungioides*, *Kodymaspis*, *Osekaspis*, *Pateraspis*, *Raymondaspis* and *Svobodapeltis.*

Diverse association of cyclopygids with *Cyclopyge*, *Degamella*, *Microparia*, *Novakella*, *Pricyclopyge* and *Symphysops*, and the pelagic genera *Bohemilla* and *Girvanopyge* indicate proximity of the typical Cyclopygid Biofacies environment. However sedimentation of the Šárka Formation reflects rather medial shelf conditions. Despite this, the necto-benthic trilobite association can be well compared with the atheloptic association. Also other benthic fauna is taxonomically rich and diverse. Less common and weakly diverse sedentary brachiopods (*Eodalmanella*, *Euorthisima*) and small lingulides including dwarf *Paterula* are quantitatively surmounted by active benthic invertebrates: bellerophontids, bivalves, hyoliths, carpoids, asteroids, ophiuroids, ostracods, plumulitids and other groups. Abundance of conulariids, caryocaridids and graptolites confirms a communication with the deeper parts of the basin. Somewhat different composition of the trilobite fauna is known NE from Prague. Some different illaenids (*Ectillenus sarkaensis*, *E. parabolinus*), considerable variability of the eyes of *Ormathops atavus* and *Colpocoryphe bohemica*, and stratigraphically restricted occurrence of the dionidid *Trinucleoides* suggest probably deeper or variable depth conditions.

The information about the fauna of the Šárka Formation came mostly from the loose siliceous nodules. The attraction for private collectors, a common occurrence combined with generally good to excelent preservation, for almost 150 years is the main cause of our knowledge of the remarkably high diversity. However, detailed stratigraphical data about these fossils are scarce. The shales of the Šárka Formation are generally less fossiliferous although in some layers remarkable taxa have been observed (e.g. a proetid *Rokycanocoryphe krafti*). In general, the trilobite fauna of the Šárka Formation is more uniform, occupying a deep offshore more stabile environment with occasional episodes of local, possibly depth- and current-related oxygen deficiency. The latter is evidenced by local scarcity of benthic fauna and abundance of planktonic graptolites and caryocaridids (Chlupáč, 1970).

The Dobrotivá Formation is a several hundred metres thick unit, that can be roughly correlated with the late Darriwillian; zonation based on graptolites divides the unit to the lower *Hustedograptus teretiusculus* Biozone, and middle and upper parts of the formation belong to the *Cryptograptus tricornis* Biozone. The formation is predominantly formed by black shales, but margins of the basin are characterized by quartzitic sandstones (Skalka Quartzite Member) almost devoid of shelly fauna. In contrary to unique small orthids (*Tissintia, Tafilaltia*), the trilobites are rare in the Skalka Quartzite and do not differ significantly from trilobites of the clayey succession: *Mirops inflatus*, *Selenopeltis* sp. and fragments of asaphids have been determined. The trilobites of the clayey succession are known in shales but also in loose siliceous nodules. The quantitative taxonomic composition differs from locality to locality, and fluctuates within the succession. The cyclopygid trilobites and genera of the atheloptic trilobites are the key groups of the trilobite fauna. Unlike to the Šárka Formation, the trinucleoids are generally rare. Benthic fauna is less abundant and less diversified comparing to the underlying Šárka Formation, with prevalence of depth related taxa: conularids, *Paterula* and other minute lingulides, small plectambonitid and orthid brachiopods (*Benignites, Brandysia*) and unique carpoids (*Bohemiacystis, Prokopicystis, Mitrocystella* etc.).

Small blind *Placoparia zippei*, index form of the *Placoparia* Association, is characteristic for the lower and middle parts of the formation, being accompaned by diverse trilobite taxa. There are common genera but different species comparing to in the Šárka Formation. In the descending abundance there are *Ormathops novaki*, *Nobiliasaphus repulsus*, *Selenopeltis kamila*, *Zeliszkella oriens*, *Ectillaenus benignensis*, *Dionide jubata*, *Eoharpes benignensis*, *Zbirovia arata, Bergamia agricola* and other rare taxa (*Areia*, *Dindymene, Lehua*, *Pateraspis*, *Petrbokia*, *Raymondapis*, *Sarkia*, *Trinucleoides*). Agnostid trilobites are moderately diverse being represented by *Corrugatagnostus morea* and rare *Sphaeragnostus* and *Chatkalagnostus*. The benthic taxa occur together with the mesopelagic cyclopygid trilobites, of which

Cyclopyge bohemica, Degamella princeps, and *Pricyclopyge longicephala* belong to comparatively common forms. Apart of other cyclopygids (*Emmrichops*, *Heterocyclopyge, Microparia*), the other depth related mesopelagic trilobites are also known, with locally fairly common remopleuridids *Ellipsotaphrus monophthalmus*, rare *Girvanopyge occipitalis* and the nileid *Parabarrandia crassa*. Bohemiellid trilobites (*Bohemilla stupenda* and *B. klouceki*) and *Shumardia bohemica* are very rare but significant. For the deepest part of the basin the species *Zeliszkella mytoensis* is characteristic, being quite common locally.

The upper part of the formation has yielded somewhat different fauna. The characteristic *Placoparia (Coplacoparia) borni* is associated with *Mirops inflatus. Pragolithus praecedens* is common only locally, and *Prionocheilus mendax*, *Eccoptochiloides mergli, Areia fritschi* and other taxa are rare. Cyclopygid trilobites are less abundant and the necto-benthic trilobites prevail.

In general, the trilobite fauna of the Dobrotivá Formation occupied a deep offshore, low-oxygen environment; this is also evident from the black colour of the sediment rich by Corg, rich pyrite content and presence of lingulate brachiopod *Paterula* (*Paterula* Community *sensu* Havlíček 1982). In a few measured successions (Mergl, 1978,1996), the fine black shales with prevalence of cyclopygids, *Parabarrandia Ellipsotaphrus* and *Girvanopyge* are recurrently intercalated with the micaceous, silty bioturbated shales in which *Placoparia* and *Ormathops* (*Mirops)* are dominant. Deep shelf and upper slope environment, with depth below 100-150 m is supported be abundance of caryocaridids (Chlupáč, 1970)

CONCLUSIONS

The Tremadocian trilobite associations of the Prague Basin were moderately diverse, shore-related and highly endemic. Presence of early calymenoids support their peri-Gondwanan affinity, even in the episode of spread of the cosmopolitan *Ceratopyge* Fauna in the upper Tremadocian. Dominance of cheirurids, illaenomorphs and *Holubaspis* indicates a shallow to moderately deep environment and probably mild or temperate climate. Olenid trilobites, otherwise characteristic of the Tremadocian oxygen deficient basins never appearred in the Prague Basin.

Starting since the upper Tremadocian, and accelerating in the Floian Dapingian and ealy Darriwillian, the abundance of depth related taxa increases. Deep-water atheloptic trilobite associations appearred, with *Placoparia* and *Ormathops* dominated over other less common but characteristic genera (e. g. *Trinucleoides*, *Eoharpes*, *Dindymene, Selenopeltis*). Other cheirurid trilobites became rare, and illaenids, asaphids, trinucleids and lichids importance decreased in the late Darriwilian, with an exception of asaphid *Nobiliasaphus.* Diverse mesopelagic cyclopygids (with dominance of *Cyclopyge*, *Degamella*, and *Pricyclopyge*) became frequent to dominant trilobites in the fossil assemblages. Calymenoid trilobites characteristic of the Gondwanan shelves since the Dapingian are less common in the Prague Basin. Trinucleid and dionidid trilobites indicating deep offshore muddy bottom became numerically abundant in the Oretanian (= middle Darriwilian), but declined in the late Darriwilian, probably as the reponse to the spread of the oxygen deficient near-bottom waters. Peri-Gondwanan affinity of the Darriwillian fauna is especially manifested by presence of odontopleurid *Selenopeltis*, the genus which continued in the Prague Basin upward to late Sandbian, and also by abundance of the early dalmanitids. In Sandbian, *Selenopeltis* is associated with diverse advanced dalmanitids, trinucleids and calymenoids of the wide peri-Gonwanan affinity, which reflects the shallowing of the basin after the Darriwilian depth maximum but also the extensive faunal exchanges in this space and time (Budil *et al*., present volume).

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THE ENVIRONMENTAL SIGNIFICANCE AND FATE OF THE TRILOBITE FAUNA OF THE PYLE MOUNTAIN ARGILLITE (UPPER ORDOVICIAN), MAINE

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Keywords: Trilobites, Cyclopygid, Atheloptic, Laurentia, Ordovician.

INTRODUCTION

Perhaps the most profound effect of the end Ordovician extinction event on the trilobites was their disappearance from pelagic environments (e.g. Fortey in Adrain *et al*., 2004). Trilobite faunas dominated taxonomically and numerically by a mixture of large-eyed mesopelagic cyclopygids and eyeless ('atheloptic') benthic species characterise deep water peri-Gondwanan successions including those of Avalonia and South China throughout the Ordovician (Fortey and Owens, 1987; Owen and McCormick, 2003; Fortey in Adrain *et al*., 2004). Prior to the Late Ordovician, away from peri-Gondwa and terranes derived from Gondwana, cyclopygids, occasionally in some abundance, periodically extended onto the edge of mid-latitude Baltica associated with sea-level rises (Nielsen, 1995). Rare specimens are even known from the early Mid Ordovician of the Central Mobile Belt of Newfoundland (Williams *et al*., 1992; see also Fortey and Cocks, 2003, p. 284) which includes terranes of oceanic affinity from the Laurentian side of the Iapetus Ocean. By the early part of the Late Ordovician cyclopygids began to appear in low diversity deep water faunas in the Girvan district, Scotland (Rushton *et al*., 1996; Stewart and Owen, in press) which formed part of the Scottish Midland Valley terrane close to the margin of Laurentia (see Armstrong and Owen, 2001) and the late Caradoc and earliest Ashgill there contains a remarkably diverse cyclopygid-atheloptic faunas (e.g. Ingham in Thomas *et al*., 1984 and in prep). By the Ashgill, cyclopygids were present on Laurentia itself (Lespérance *et al*., 1987) as part of 'normal-eyed' faunas and here we document the only known cyclopygid-atheloptic fauna from North America.

THE PYLE MOUNTAIN ARGILLITE

The Pyle Mountain Argillite in Castle Hill Township, Aroostook County, northeastern Maine is a fine grained, olive coloured mudstone which, where calcareous, weathers to give a brown commonly richly fossiliferous 'gingerbread' crust. Black shales near the top of the underlying Winterville Formation contain graptolites of the *Climacograptus spiniferous* Biozone indicating that the Pyle Mountain Argillite is probably equivalent to a level in or close to the lower part of the *Pleurograptus linearis* Biozone and thus its faunas are broadly similar in age to the latest Caradoc–earliest Ashgill deep water faunas at Girvan noted above. Neuman (1994) summarised the previous work on the formation as part of his documentation of its brachiopods which he ascribed to the *Foliomena* fauna. In a recent multivariate statistical analysis of this widely documented brachiopod fauna, Zhan and Jin (2005) considered that the Pyle Mountain Argillite fauna lived towards the deeper water (Benthic Assemblage Zones 5-6) part of the environmental spectrum occupied by the *Foliomena* fauna.

TRILOBITE FAUNA

All of the trilobite specimens from the Pyle Mountain Argillite are isolated sclerites and, unlike the brachiopods which are all small, they represent a range of sizes ranging from a few mm in the case of some pygidia of *Cyclopyge* to a hypostome of *Nileus* 23 mm wide. A preliminary list of the trilobites was provided by Bruton (in Neuman, 1994) and we have now assessed all the available identifiable material (198 specimens), which belong to some 21 species which will be described in detail elsewhere. Table 1 lists the taxa present in the fauna.

Taxon	Pelagic	Benthic eyeless	Benthic with eyes
Cyclopyge sp.	18.5%		
Dindymene sp.		13%	
Panderia megalopthalma Linnarsson			11%
Dionide sp.		10%	
Trinodus cf. *tardus* (Barrande)		8%	
Nankinolithus granulatus (Wahlenberg)		5.5%	
Amphitryon radians (Barrande)	5.5%		
Symphysops sp.	4.5%		
cyclopygids indet	4.5%		
Lonchodomas sp.		3%	
lichid			2.5%
harpid fragments		2%	
Telephina cf. *fracta* (Barrande)	2%		
Pseudosphaerexochus sp.			1.5%
Raymondella sp.		1.5%	
Microparia ? sp.	1%		
Novaspis sp.		1%	
Staurocephalus sp.		1%	
asaphid ?			1%
calymenid			1%
Corrugatagnostus sp.		0.5%	
Nileus sp.			0.5%
Total pelagic trilobites	**36%**	**45.5%**	**17.5%**
of which cyclopygids	28.5%		

Table 1. List of trilobites in the Pyle Mountain Argillite in rank order of abundance of sclerites, their percentage abundance (n=198) and their broad palaeoautecology.

The fauna is dominated numerically by the mesopelagic cyclopygids *Symphysops*, *Microparia*? and, in particular, *Cyclopyge* itself. Together with *Amphitryon* which was also probably a swimmer and the epipelagic *Telephina,* these trilobites comprise well over a third of the fauna (36%). Benthic trilobites lacking eyes (*Dindymene, Dionide, Trinodus, Nankinolithus, Lonchodomas*, harpids, *Raymondella*, *Novaspis* and *Corrugatagnostus*) comprise 45% and apart from *Panderia*, no normal eyed trilobite species represents more than 2.5% of the fauna. Together they constitute only 17.5% of all the identifiable trilobite sclerites recovered from the formation. Although there are no taxa that lack eyes but have normal-eyed relatives, this is clearly a cyclopygid-atheloptic fauna in its broadest sense.

Cyclopygids comprise 28.5% of the fauna and yet are less diverse than in some other Late Ordovician faunas, possibly indicating that the Pyle Mountain Argillite trilobites do not represent the deepest part of the bathymetric spectrum seen elsewhere. The depth stratification of cyclopygid genera has been suggested by previous workers (e.g. Zhou *et al.*, 1994). Thus, whilst the presence of *Nankinolithus, Dindymene, Symphysops, Cyclopyge, Novaspis, Microparia* and *Telephina* in the Pyle Mountain Argillite indicate a strong similarity to some of the '*Novaspis*-cyclopygid' associations documented by Price and Magor (1984) in the mid-Ashgill (Rawtheyan) of North Wales (part of Avalonia), the deepest faunas there include a greater variety of cyclopygids including *Degamella* and *Psilacella*. Similarly the dominance of *Cyclopyge* and the co-occurrence of several benthic taxa (including relatively abundant *Panderia*) indicate some similarity to the 'Middle deep outer-shelf' *Ovalocephalus-Cyclopyge* biofacies described recently by Zhou *et al.* (2007) from the upper part of the Pagoda Limestone (upper Caradoc) on the north west margin of the Yangtze Block in China but again there is a deeper biofacies, in this instance dominated by the cyclopygids *Cyclopyge* and *Sagavia* together with *Ovalocephalus*. The Pyle Mountain Argillite also has several taxa in common with the latest Caradoc–early Ashgill deep water faunas of Girvan but the latter also include species of *Ellipsotaphrus, Psilacella, Girvanopyge, Degamella, Novakella* and *Sagavia* (Ingham in Thomas *et al.*, 1984, p. 40) suggesting deeper water environments there.

The pelagic trilobite fauna in the 'Cyclopygid Bed' in the Ashgill Punta S'Argiola Member of the Domusnovas Formation in Sardinia is very like that of the the Pyle Mountain Argillitte and comprises *Cyclopyge*, *Symphysops*, *Amphitryon* and *Telephina* (Hammann and Leone, 1997; Villas *et al.*, 2002). The cyclopygids as a whole comprise 30% and there are several elements of the benthic trilobite fauna in common. The *Foliomena* brachiopod fauna in the Sardinian unit plots very close to that of the Pyle Mountain Agillite in the Principal Components Analysis published by Zhan and Jin (2005) as did those of the Jerrestad Mudstone in Sweden and the Tangtou Formation in South China, both of which contain cyclopygid trilobite faunas dominated by *Cyclopyge*.

Lespérance *et al.* (1987) recorded species of *Cyclopyge*, *Heterocyclopyge* and *Symphysops* in the '*Stenopareia* Community' in the Ashgill of the Percé region of Quebec. Cyclopygids are locally dominant elements in this fauna but unlike the Pyle Mountain Argillite, 'normal eyed' taxa are a major constituent of the associated benthic trilobite fauna. In complete contrast, the *Foliomena* brachiopod fauna documented by Sheehan and Lespérance (1978) from Percé is accompanied by a trilobite fauna containing only a single specimen of cyclopygid out of 205 trilobite sclerites. The fauna is dominated by *Tretaspis* (173 specimens) and to a much lesser extent *Lonchodomas* (22 specimens). Such trinucleid-raphiophorid associations are common from the Arenig to Ashgill and are known from Avalonia, Baltica and South China (see Owen and Parkes, 2000, p. 227 for review). The contrast with the cyclopygid-atheloptic fauna that occurs with the *Foliomena* fauna in the Pyle Mountain Argillite and elsewhere is striking. Neuman (1994, p. 1218) excluded the Percé fauna from the *Foliomena* fauna because of an earlier reassignment of the *Foliomena* from there to *Proboscisambon* but it has been retained in its original genus by other workers since then (e.g. Zhan and Jin, 2005) and Prof. D.A.T. Harper of Copenhagen University suggests that the brachiopod fauna assemblage may be a low-diversity, shallower water member of the *Foliomena* fauna (pers. comm. 2008).

THE FATE OF THE TRILOBITE GENERA IN THE PYLE MOUNTAIN ARGILLITE

Despite their almost pandemic distribution, the pelagic and deep benthic trilobites were hardest hit of all the trilobite biofacies in the first wave of extinctions at the start of the Hinrnatian (Fortey, 1989; Owen *et al.*, 1991) suggesting a major oceanic event at the start of the Hirnantian glaciation. The Pyle Mountain Argillite fauna exemplifies this. Virtually all of the named genera persisted until the late Rawtheyan yet only *Staurocephalus* persisted into the Silurian as a very rare Ordovician hold-over. Even if all the indeterminate representatives of the Lichidae, Harpidae and Calymenidae belonged in genera that survived into the Silurian, less than 20 percent of the genera (and potentially less than 5%) of the Pyle Mountain Argillite genera survived the end Ordovician extinction event. In terms of the number of trilobite seclerites recovered from the Pyle Mountain Argillite, over 93% belong to taxa that did not persist into the Silurian.

Acknowledgements

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MIDDLE CAMBRIAN ACRITARCH ZONES IN THE OVILLE FORMATION AND THEIR CORRELATION WITH TRILOBITE ZONES IN THE CANTABRIAN MOUNTAINS, NORTHERN SPAIN

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Keywords: Acritarchs, trilobites, middle Cambrian, biozones, global correlation.

INTRODUCTION

This paper presents preliminary results of a restudy of acritarchs from the middle Cambrian Oville Formation based on sections in Porma and Oville in the Bodon Unit, Adrados in the Esla Unit and Barrios de Luna in the Correcillas Unit (Fig. 1). The continuous record of abundant and diverse acritarchs in these sections makes it possible to establish a detailed biozonation based on the most abundant and diagnostic cosmopolitan taxa. Five zones can be recognized in the Oville Formation of which the first four have been previously recognized in the Zafra area in southern of Spain. The co-occurrence of acritarchs and trilobites in the Porma and Barrios de Luna sections makes it possible to calibrate the two types of biozones.

IBERIAN MIDDLE CAMBRIAN ACRITARCH ZONES AND CORRELATION

Based on sections in the Cantabrian Mountains and the Zafra area five middle Cambrian acritarch zones are recognized, herein identified with the acronym IMC (Iberian Middle Cambrian). These are interval zones, with bases defined on the first appearance of a selected cosmopolitan taxon. Other characteristics of these biozones are also discussed.

The first four zones (IMC1-IMC4) have been previosly recognized in the Zafra area in south of Spain where they were referred to as the *Comasphaeridium silesiensis*, *Cristallinium cambriense, Adara alea* and *Timofeevia lancarae* Zones (Palacios *et al.*, 2006). A new zone, the IMC5, equivalent to the Languedocian regional stage, is identified in the study area. This zonation will be presented in greater detail in a future publication.

IMC1 Zone

The base of the zone is marked by the first appearance of *Comasphaeridium silesiensis*. The upper part of this zone is recognized near the base of the Oville Fm. (Genestosa Mb.) in the Porma section, with *Comasphaeridium silesiensis* (Fig. 3A), *Eliasum llaniscum* (Fig. 3F), *Solisphaeridium implicatum* and abundant specimens of Acritach gen. et sp. nov of Martin in Martin and Dean (1984) (Fig. 3B) first described from Newfoundland. This interval contains the trilobites *Eccaparadoxides asturianus* and *Tonkinella* aff. *brevicens* diagnostic of the *E. asturianus* Zone, equivalent to the upper Leonian regional stage (Sdzuy, 1995; Gozalo *et al.*, 2003a)

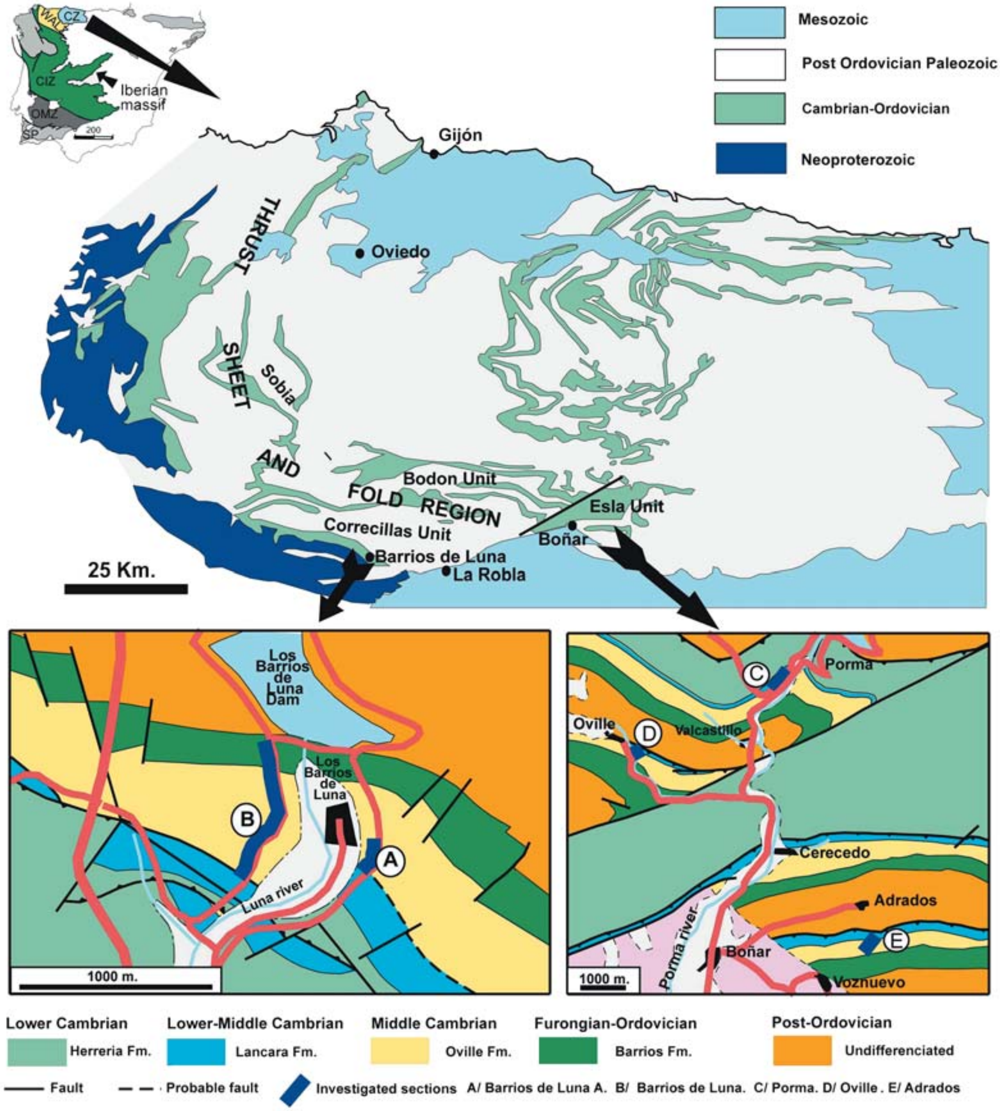


Figure 1. Geological sketch map of the Cantabrian Zone showing the main units and the location of the Porma and Barrios the Luna areas. Detailed geological maps of Porma and Barrios de Luna areas showing the location of studied sections. [Based on Aramburu *et al.* (2006) and other publications].

Correlations. Acritarch gen. et sp. nov Martin in Martin and Dean (1984), is a species whose first appearance is recorded near the top of Chamberlain Brook Fm. below a level that contains *Badulesia* aff. *B. tenera* (Martin and Dean, 1988, fig. 3). This species is also very abundant near the top of the Vallehondo formation in south Spain, which corresponds to the upper part of this zone (Palacios *et al.*, 2006).

IMC2 Zone

The first appearance of *Cristallinium cambriense* (Fig. 3D) defines the base of this zone. This zone has a high diversity of acritarchs and include *Celtiberium dedalinum, Eliasum pisiformis, Eliasum asturicum* (very abundant) (Fig. 3C), *Vulcanisphaera lanugo* (Fig. 3E) and *Baltisphaeridium pseudofaveolatum* (Fig. 3L). In the Porma section the base of this zone corresponds approximately to the first appearance of *Badulesia tenera* (Lower Caesaraugustan regional stage).

Correlations. In Avalonia the first appearance of *C. cambriense* and *Vulcanisphaera lanugo* is near the base of the Manuels River Fm. between the occurrence of *Badulesia* aff. *B. tenera* and *Paradoxides hicksii* (Martin and Dean, 1988, fig. 3). *Baltisphaeridium pseudofaveolatum* is a diagnostic acritarch species of the Kibartai Horizon in Baltica correlated with the *Eccaparadoxides insularis* Zone (Volkova and Kiryanov, 1995).

IMC3 Zone

The first appearance of *Adara alea* (Fig. 3G) defines the base of this zone. In the Oville section the first record of *A. alea* occurs ten metres above strata that contain *Badulesia juliverti* and a short distance below a level that contains *Solenopleuropsis* sp. (*Pardailhania zone*, Middle Cesaraugustian Gozalo *et al.*, 2003b). The upper part of this zone include the last appearance of *Eliasum pisiformis*, *Eliasum asturicum* and *Adara alea,* among others. Consequently IMC3 can be considered a range zone (*Adara alea* Zone)

Correlations. In Avalonia the first appearance of *A. alea* occurs in the Manuels River Fm. very close to last occurrence of *Paradoxides hicksii* and its last appearance is six meters below the occurrence of *Ptychagnostus punctuosus, Paradoxides davidis* and *Solenopleuropsis variolaris* (Martin and Dean, 1988, figs. 3, 7).

IMC4 Zone

The first appearance of *Timofeevia lancarae* (Fig. 3H) marks the base of this zone which also includes very abundant *Eliasum llaniscum* and *Cristallinium cambriense.* In the Barrios de Luna A section *Timofeevia lancarae* appears near the base (probably faulted, Fig.1) of the Oville Fm. (Genestosa Mb.) in levels that contain *Solenopleuropsis rubra* (Upper Caesaraugustan, Aramburu *et al.*, 2006, fig. 25)

Correlations. The lowest record of *T. lancarae* (indicative of Zone SK2 of Volkova and Kiryanov, 1995) in the East European platform is in the upper part of the *Paradoxides paradoxissimus* Zone. In Random Island (Eastern Newfoundland) the first appearance of *T. lancarae* occurs in the top of Manuels River Fm. in strata that contains *Paradoxides davidis* (Martin and Dean, 1981, fig. 3, table I), although the acritarch record at these levels is very scarce. This species is also very abundant in the Playón fm. (Palacios *et al.*, 2006) where it appears very close to levels that contain *Solenopleuropsis verdiagana*, attributed to the Upper Caesaraugustan (Gozalo *et al.*, 1994)

IMC5 zone

This zone is defined by the first appearance of *Symplassosphaeridium cambriense* (Fig. 3J), which in Barrios the Luna A section (Fig. 1) occurs three meters below the Simula Sandstone at levels bracketed

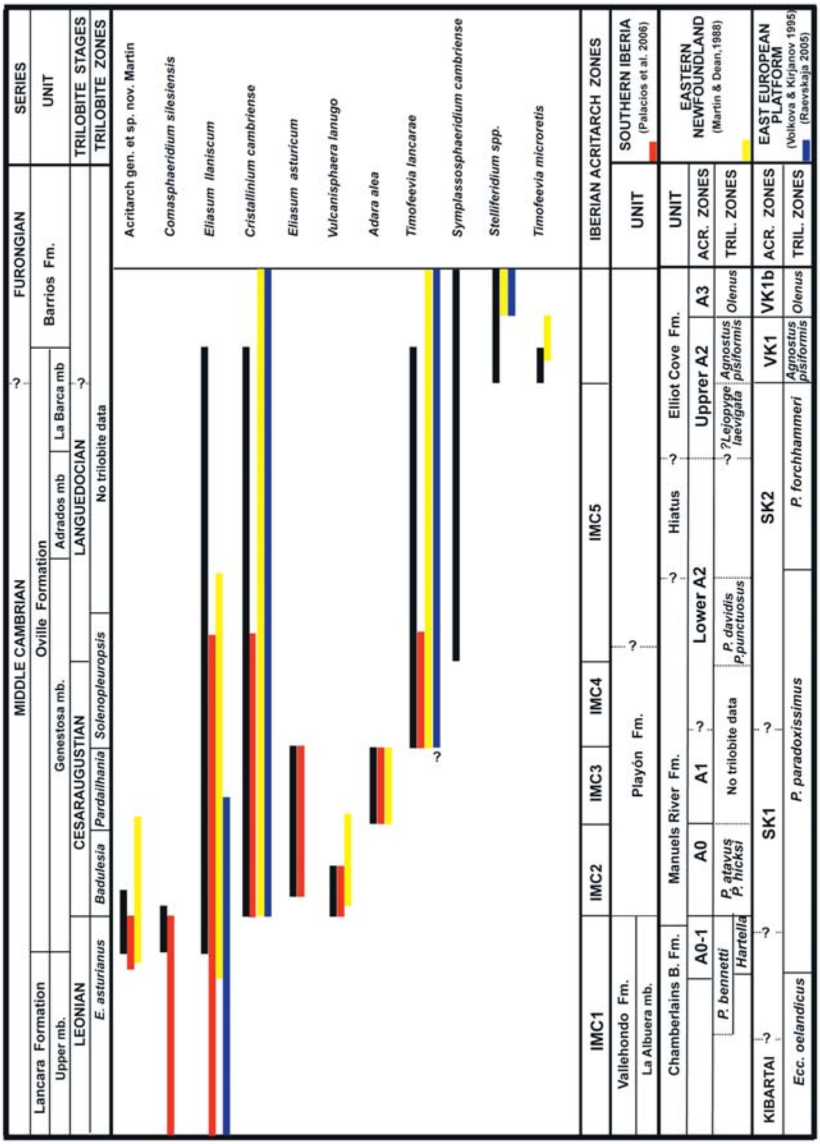
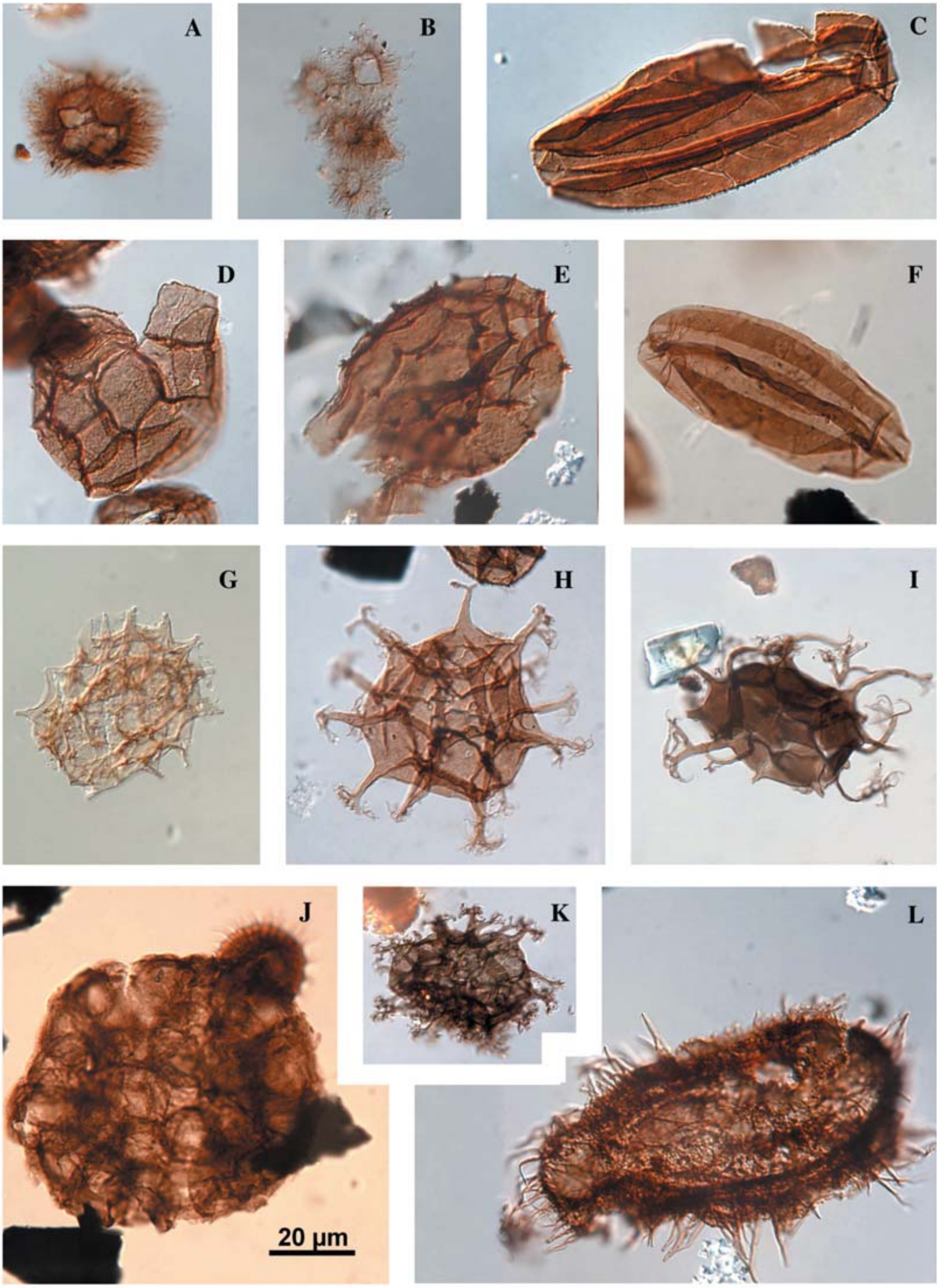


Figure 2. Stratigraphical ranges of selected acritarchs in Oville Formation and correlations with South Iberia, Eastern Newfoundland and East European Platform.

Figure 3. Acritarchs from the Oville Formation. In this figure is given: sample and slide number and England finder coordinates. (A) *Comasphaeridium silesiensis* Moczydlowska, 1998.PO106-13-N1;T-24-2. (B) Acritarch gen. et sp. nov Martin in Martin and Dean, 1984. PO106-13-N1;S-24-1. (C) *Eliasum asturicum* Fombella, 1977. OV06-2-2; B-28-2. (D) *Cristallinium cambriense* (Slaviková, 1968) Vanguestaine, 1978. AD06-2-2; P-22-2. (E) *Vulcanisphaera lanugo* Martin in Martin and Dean, 1988. OV06-2a-1; U-21-1. (F) *Eliasum llaniscum* Fombella, 1977. AD06-2-2; E-19-3. (G) *Adara alea* Martin in Martin and Dean, 1981.OV06-3N; O-37-2. (H) *Timofeevia lancarae* (Cramer and Díez, 1972) Vanguestaine, 1978. AD06-2-2; S-45-3. (I) *Stelliferidium* sp. BL06-17-1; F-46-4. (J) *Symplassosphaeridium cambriense* Slaviková,1968, validated in Fensome *et al.* (1990).AD06-2-2; J-35-3. (K) *Timofeevia microretis* Martin in Martin and Dean (1981). BL06-17-2; E-16-2. (L) *Baltisphaeridium pseudofaveolatum* Fridrichsone, 1971. OV06-2a-N; Z-22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between the *Solenopleuropsis thorali* + *S. marginata* Zone and levels with *Paradoxides* cf *davidis* (lower Languedocian, Aramburu *et al.*, 2006). In the Adrados section (Fig.1) the base of this zone is recognized in a similar position very close to the Simula Sandstone. The top of this zone is marked by the first appearance of *Timofeevia microretis* (Fig. 3K) and *Stelliferidium* spp. (Fig. 3I) in the upper part of La Barca Mb. in levels without trilobites. In the East European Platform Raevskaya (2005) recognized the VK1 Zone, equivalent to the Olenus Zone (Lower Furongian), by the presence of *Stelliferidium* spp. In Newfoundland *T. microretis* appears near the base of Elliot Cove Fm. in levels with *Agnostus pisiformis* (Martin and Dean, 1988). The first appearance of *Timofeevia microretis* and *Stelliferidium*, could indicate late Middle Cambrian or basal Furongian, but at the present it is not possible to tell with greater precisions.

Correlations. Slaviková (1968) erected the species S*ymplassosphaeridium cambriense* based on material from the middle Cambrian Jince Formation of the Czech Republic in levels assigned to the *Ellipsocephalus hoffi* sub-Zone or *Ellipsocephalus hoffi-Rejkocephalus* Abundance Zone *sensu* Fatka (2006), correlated to the upper Languedocian (Álvaro *et al.*, 2004). Palacios (1997) reported this species (as coenobial acritarchs) from the Acón Formation, assigned to the Languedocian (Palacios unpublished data). Erkmen and Bozdogan (1981) reported *Symplassosphaeridium cf. cambriense* from the Sonsink formation, Turkey and, from the same formation, Dean *et al.* (1997) reported (as coenobial acritarchs) in levels with *Solenopleuropsis* sp. In Nova Scotia (Palacios unpublished data) *S. cambriense* occurs near the base of the MacLean Brook Formation in a level bracketed between the occurrence of *P. davidis* and *P. forchhammeri*.

CONCLUSIONS

- Sections in the Cantabrian Mountains contain a record of acritarchs and trilobites that allows a precise correlation of their zones previously not possible for the Middle Cambrian of Gondwana.
- Five acritarch zones (IMC1-IMC5) are recognised in the Middle Cambrian of the Iberian Peninsula, which makes it one of the most finely divided acritarch successions of the Middle Cambrian.
- Detailed correlations betweenGondwana, Baltica and Avalonia is established on the basis of cosmopolitan acritarch species. Figure 2 shows the range of these zones and proposed global correlations.
- The excellent record of acritarchs and trilobites in the Oville Fm. (Genestosa and Adrados Mb.) from Adrados section shows that the Adrados mb. is middle Cambrian and not Upper Cambrian-Tremadoc as had been previously suggested (Fombella, 1986).
- The new acritarchs data contradicts the presence of a pronounced diachronism of the Oville Formation supported in recent publications.

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HIMALAYAN TRILOBITE FAUNA: PRESENT STATUS WITH RESPECT TO THE CAMBRIAN BIOSTRATIGRAPHY

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INTRODUCTION

The Himalayan trilobite fauna has been so far documented from the Kashmir, Spiti and Zanskar regions. The majority of taxa are known predominantly from Cambrian successions, with only a few records reported from the Palaeozoic. During the early twentieth century, Hayden (1904), Reed (1910, 1934), Wadia (1934), Kobayashi (1934) and King (1941) had attempted to document and interpret their stratigraphic significance in the Himalayan region. Subsequently, Shah (1973), Shah and Sudan (1982, 1983, 1987a,b) initiated the detailed investigation which yielded additional faunal data from the Cambrian successions of the Tethys Himalaya. Later on, Shah and his research team (Shah *et al.*, 1988, 1991, 1995a,b, 1996) and Parcha (1986, 1988, 1991, 1996, 1998, 1999, 2001, and 2005) extended their continued attempts to other parts of Tethys as well as Lesser Himalayan regions.

The present author, in collaboration with other trilobite researchers from India, China and USA (Nanjing Institute, California and Colorado universities) has been trying to develop comprehensive records of the Himalayan trilobite fauna with specific emphasis on their stratigraphic range and paleoenvironmental implications. Along with traditional faunal taxonomy, it is important to understand the intraspecific variation of various trilobite species with the added precision of computer graphic techniques and morphometric analyses for intraregional correlations. After detailed studies of all the fauna from these basins, a new scheme will be proposed for the Cambrian biostratigraphy in the Indian part of the Himalaya. Continuing studies on the agnostid-rich faunas of Ladakh will assist in producing a Cambrian scheme for the Tethyan Himalayan successions.

The Cambrian fauna of the Himalaya, first discovered by Hayden (1904) from the Spiti Valley and subsequently by Wadia (1934) from the Kashmir Basin, was later described by Reed (1910, 1934), Kobayashi (1934). Later, Kobayashi (1967) made the generic reassignment of Reed's identifications. The fauna from the Salt Range, collected earlier by Waagen (1899), was reviewed by King (1941). Subsequently, Shah and his research team substantially contributed by the additional records from Indian parts of the Himalaya. Further studies are being carried out at Wadia Institute of Himalayan Geology (WIHG), Dehra Dun (Parcha, 1986, 1988, 1991, 1996, 1998, 1999, 2001, 2005).

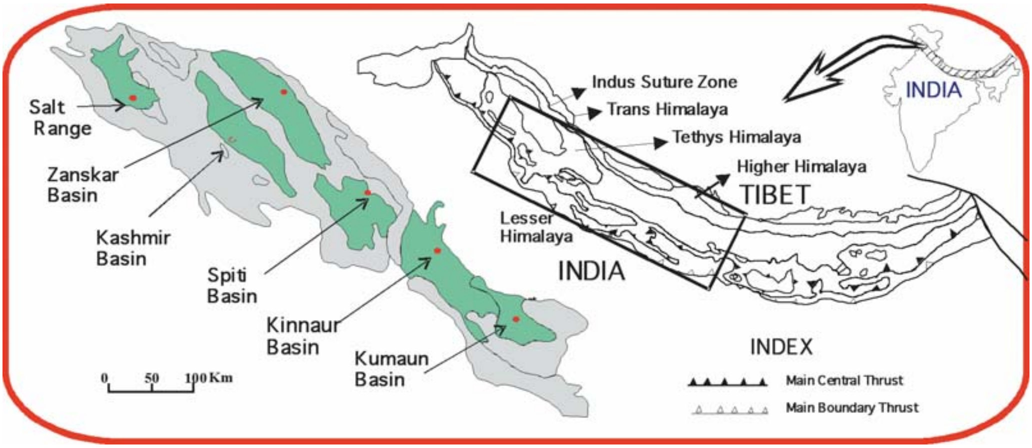

Figure 1. Map showing the different structural units of the Himalaya (modified after Gansser, 1964, 1974). The inset shows various sub-basins of the Tethys Himalaya.

EARLY CAMBRIAN

It has been observed that the earliest trilobites reported from the Himalayan belt represent the early Cambrian Botoman Stage. The early Cambrian fauna is well documented in the Lesser Himalayan regions; whereas, the middle Cambrian trilobites are so far only known from the Tethyan Himalayan successions (i.e. Kashmir, Spiti and Zanskar basins).

The trilobite records so far identified from the various Cambrian basins of the Himalaya (Fig. 1) are summarized in Table 1. Except for the fragmentary remains (free cheeks) reported from the Garbyang Formation in Garhwal area (Shah and Sinha, 1974), no early Cambrian trilobite fauna is yet known from this part of the Himalaya.

MIDDLE CAMBRIAN

The middle Cambrian taxa so far known from the Salt Range are represented by *Ptychoparia, Chittidilla* and *Yuehsienszella* reported from the Himalaya in Pakistan (King, 1941). In the Kashmir Basin the recorded fauna includes *Tonkinella*, (Kobayashi, 1934; Reed, 1934), *Bailiaspis*, *Bailiella*, *Holocephalina* and *Conocoryphe* (Shah, 1973). Later, Shah *et al*. (1986, 1987, 1988, 1991, 1995a,b) reported *Pagetia, Opsidiscus, Ptychoparia, Hundwarella, Iranoleesia, Peronopsis, Baltagnostus, Triplagnostus, Diplagnostus, Anomocaraspis*, *Kunmingaspis* and *Shahaspis* from Kashmir and *Oryctocephalus, Pagetia, Ptychoparia, Hundwarella, Iranoleesia, Baltagnostus* from the Spiti Basin. In the Zanskar Basin the middle Cambrian trilobite taxa reported by Whittington (1986) are *Diplagnostus, Hypagnostus, Lejopyge, Goniagnostus, Clavagnostus, Ptychoparia, Fuchouia, Torifera*, as well as *Damesops* and *Eoshengia* (Jell and Hughes, 1997). In addition to these forms Shah *et al.* (1996) described *Peronopsis, Baltagnostus*, and *Doryagnostus.* Ashok Kumar (1998) described *Hundwarella, Ptychoparia, Damesella, Lorenzella* and *Anomocare* from the Kurgiakh section. Afterwards Parcha (2001) recorded *Peronopsis, Hypagnostus, Diplagnostus, Clavagnostus, Iranoleesia, Kunmingaspis, Anomocarella, Blackwelderia*, *Damesella* from the

Tagzee and Kurgiakh sections. During fieldwork in the recent years, the author has recorded some other genera from the Cambrian successions of the Kurgiakh section, as well as from the Tangzee sections of the Zanskar region; the detailed studies are ongoing. This fauna ranges in age from the Solvan to Menevian stages of the middle Cambrian.

LATE CAMBRIAN

The late Cambrian trilobites are so far known only from the Kashmir and Spiti valleys. The fauna recorded from the Kashmir Basin is represented by *Damesella* (Shah and Sudan, 1983b, 1987b), *Hundwarella, Parablackwelderia*, *Amurticephalus, Walcotaspis, Pedinocephalus* (Sah *et al*., 1991), *Blackwelderia*, *Cyclolorenzella* and *Monkaspis* (Jell, 1986). In the Spiti Himalaya the fauna recorded are *Olenus, Hundwarella, Spitella* and *Tsinania* (Shah *et al*., 1991). Ongoing studies in the Cambrian successions of the Zanskar Basin are expected to yield additional faunal elements of the early late Cambrian, which would be significant for intrabasinal correlations in the Himalayas. In the Spiti and Zanskar basins, the topmost part of the Cambrian is marked by an angular unconformity, whereas in the Kashmir Basin, the Cambrian is conformably overlain by the Ordovician, where there is only facies change. Although there are reports of Ordovician trilobites from the Pin valley of Spiti (Shah, personal communication) there is a need to search for well preserved trilobites from the entire Lower Palaeozoic successions.

CONCLUSIONS

The trilobite fauna in the Cambrian successions of the Himalaya has historically had a relatively poor record, and has even been considered enigmatic. This may have been true up to the sixties but is no longer true, as a large variety of taxa from measured sections in Himalayan Cambrian of Kashmir, Spiti, Zanskar and Garhwal Himalaya have since been listed and described by various workers as mentioned above and in Table 1.

The Cambrian trilobite fauna of the Tethys Himalaya broadly correlates to the Chinese fauna, particularly in the presence of the *Pagetia, Anomocarella, Bailiella* and *Blackwelderia*. Other genera such as *Peronopsis, Diplagnostus, Lejopyge, Baltagnostus, Tonkinella, Damesella, Cylolorenzella* and *Ptychoparia* known from the Himalaya, however, are common to Australia and Kazakhstan. Therefore, it seems that the Cambrian fauna, particularly at generic level, is likely of cosmopolitan distribution, revealing that the Himalayan fauna may not be enigmatic or even provincial. Parcha (2005) gave a preliminary faunal correlation of the middle Cambrian successions of NW Kashmir Himalaya. Parcha (2005) indicated that the *Proasaphiscus* are common in contemporaneous faunas from China, as well as in Iran. The available faunal records reveal that, with the exception of a few species of geographically constrained distributions, a large part of Himalayan trilobite fauna shows affinity with that of China, Australia and Iran. It appears that during the late middle and early late Cambrian there was a reorganization of the early Cambrian trilobite families, with a peak occurrence during the middle Cambrian, but rapidly declined/terminated with simultaneous emergence of new forms around the beginning of the late Cambrian. This was essentially a global phenomenon and was sharply pronounced in the Kashmir and Spiti basins. In a broader angle, the Himalayan Cambrian trilobite fauna appears to be a part of East Asian province, showing affinities with China and Australia.

Late Cambrian				
Basin	**Area**	**Formation**	**Trilobite Taxa**	**Remarks**
Kashmir	**NW part (Kupwara)**	**Trahagam Formation**	*Parablackwelderia, Monkaspis* sp. cf. *M. serrata, Damesella shergoldi, Cyclolorenzella* sp., *Blackwelderoides monkei, Blackwelderia* sp., *Amurticephalus elongatus*	Shah & Sudan, 1983b; Jell, 1986; Shah & Sudan, 1987b; Parcha, 1988; Shah *et al.*, 1988; Shah *et al.*, 1991; Jell & Hughes, 1997.
Spiti	**Parahio Valley**	**Parahio Formation**	*Spitella barachuensis, Olenus haimentensis, Hundwarella interpres*	Reed, 1910; Shah *et al.*, 1991; Jell & Hughes, 1997; Parcha, 1999.
Middle Cambrian				
Kashmir	**NW part (Kupwara)**	**Nutunus Formation**	*Xingrenaspis daradapurensis, Tonkinella breviceps, Tonkinella kashmirica, Tonkinella quadrifida, Trilagnostus* kashmirensis, *Solenoplura* sp., *Solenoparia* sp., *Pagetia* sp., *Pagetia* sp. cf. *P. jinnanaensis*; *Peronopsis* cf. *tramitis, Ptychoparia* sp., *Opsidiscus* sp., *Kunmingaspis* sp., *Iranoleesia butes, Hundwarella memor, Holocephalina wadiai, Holocephalina wakhalooi, Conocoryphe reedi, Bailiaspis* sp., *Bailiella frangtengensis, Bailiella sejuncta, Baltagnostus* cf. *rakuroensis, Baltagnostus sp. Anomocarella* sp., *Anomocaraspis* sp.	Kobayashi, 1934; Reed,1934; Shah,1973,1982; Shah & Sudan,1987a; Shah *et al.*, 1988; Shah & Parcha, 1986; Parcha, 1988, Shah *et al.*, 1995a, 1995b; Jell & Hughes, 1997; Parcha, 2005.
		Trahagam Formation	*Shahaspis (=Bolaspidella) himalyensis, Shahaspis* sp., *Parachitidilla kashmirensis, Latilorenzella* sp., *Hundwarella* sp., *Diplagnostus* sp., *Amurticephalus elongatus*	Shah & Sudan, 1982; Parcha, 1988; Shah *et al.*, 1991, 1995a; Jell & Hughes, 1997; Parcha, 2005.
	SE part (Anantnag)	**Karihul Formation**	*Xingrenaspis dardapurensis, Ptychoparella* sp., *Anomocare* sp.	Kumar & Singh, 1983; Jell & Hughes, 1997.
Spiti	**Parahio Valley**	**Kunzum La Formation**	*Xingrenaspis maopensis, Kunmingaspis stracheyi, Kunmingaspis pervulgata, Ptychoparia* sp., *Pagetia significanc, Pagetia* sp., *Opsidiscus haimentensis, Peronopsis* sp., *Oryctocephalus salteri, Oryctocephalus indicus*	Reed, 1910; Shah & Paul, 1987; Shah *et al.*, 1988, 1991; Parcha, 1996; Jell & Hughes, 1997; Parcha, 1998, 1999.

Table 1. Tethys Himalaya.

	Pin Valley (Spiti region)	**Kunzum La Formation**	*Ptychoparia* sp., *Pagetia significance*, *Pagetia* sp., *Peronopsis* sp., *Oryctocephalus salteri*, *Oryctocephalus indicus*, *Opsidiscus haimentensis*, *Kunmingaspis stracheyi* , *Kunmingaspis pervulgata*, *Iranoleesia butes*, *Hundwarella* sp., *Anomocaraspis* sp.	Reed, 1910; Ranga Rao *et al.*, 1982; Shah *et al.*, 1991; Parcha, 1996, 1998, 1999, Jell & Hughes, 1997.
	Spiti Valley	**Kunzum La - Takche**	*Ptychoparia* sp., *Pagetia* sp., *Opsidiscus haimentensis*, *Kunmingaspis* sp., *Hundwarella* sp.	Reed, 1910; Ranga Rao *et al.*, 1982; Shah *et al.*, 1991; Parcha, 1996, 1998, 1999.
Zanskar	**Suru-Kurgiakh Valley**	**Kunzum La (= Parahio) Fm.**	*Goniagnostus*, *Lejopyge*, *Hypagnostus*, *Diplagnostus*, *Linguagnostus*, *Clavagnostus*, *Fuchouia*, *Damesops*, *Torifera*, *Eoshengai*, *Hundwarella*, *Iranoleesia*, *Ptychoparia*, *Damesella*, *Lorenzella*, *Kunmingaspis*, *Blackwelderia*	Dungrakoti *et al.*, 1974, 1975; Whittington, 1986; Jell & Hughes, 1997; Ashok Kumar, 1998; Parcha, 2001.

Early Cambrian

Kashmir	**NW part (Kupwara)**	**Lolab Fm.**	*Redlichia noetlingi*, *Redlichia* cf. *knjazevi*, *Tungusella obesa*	Shah *et al.*, 1980; Raina & Razdan, 1975.
	SE part (Anantnag)	**Lolab Fm.**	*Paokannia magna*, *Paokannia* sp.	Kumar & Verma, 1987; Jell & Hughes, 1997.
Spiti	**Pin Valley**	**Kunzum La Formation**	*Redlichia* sp.	Reed, 1910; Parcha, 1996, 1999.
Kumaon	**Pithoragarh**	**Milam Fm.**	*Redlichia*	Kacker & Srivastava, 1993.

Lesser Himalaya

Early Cambrian

Nigali Dhar Syncline	**Sirmur Himachal Pradesh**	**Tal Fm.**	*Redlichia noetlingi*, *Redlichia* sp., *Dolerolenus* (*Malungia*) cf. *M. laevigata*, *Drepanopyge gopeni*, *Protollenella* cf. *P. angustilimbata*	Kumar *et al.*, 1987; Jell & Hughes, 1997; Hughes *et al.*, 2005.
Mussoorie-Garhwal Synclines	**Kauriyal, Durmala**	**Tal Fm.**	*Xela mathurjoshi*, *Redlichia noetlingi*, *Redlichia* sp.	Joshi *et al.*, 1989; Mathur & Joshi, 1989; Rai & Singh, 1983; Jell & Hughes, 1997; Hughes *et al.*, 2005.

Table 1. Tethys Himalaya. (Continued).

In Tethyan Himalayan successions, polymerids and agnostids are the main trilobite taxa of paleoecological significance for interpreting the depositional history of Cambrian sequences. In the Lesser Himalaya, only lower Cambrian successions yield substantial data. Kashmir and Spiti basins yielded a good representation of polymerids, whereas the Zanskar Basin contains a good record of agnostids as well as polymerids. The trilobite fauna so far collected from the Tethyan and the Lesser Himalaya mostly belongs to the middle Cambrian. However, there seems to be a distinct separation in spatial distribution between the Kashmir, Spiti and Zanskar basins of the Tethyan Himalyan and the Lesser Himalayan regions. Although trilobite faunal ranges are variable along the Tethyan Cambrian successions of the Himalayan belt, there is a considerable percentage of similar taxa throughout the belt. The studies reveal that the faunal distribution is not uniform in all the Tethyan sub basins, and some faunal gaps at different intrasystem boundaries have been recorded.

Taxonomy of the various trilobite genera, as well as species, reported by earlier workers has been revised by Jell and Hughes (1997). This has revealed that the Cambrian trilobite fauna of the Himalayan regime shows considerable similarity with contemporaneous faunas from North and South China. In addition there are several species which are common with Australia and Iran. The difference between the middle Cambrian fauna of Spiti-Zanskar and Kashmir basins, are being interpreted based on the paleoenvironmental model proposed by Shah (1993).

The paleoecological interpretation of trilobite data generated from Tethys and Lesser Himalayas by the various researchers is difficult, mainly due to the lack of stratigraphic details, particularly from the Garhwal-Kumaun Lesser Himalaya. For this purpose it is essential to study the fauna of these basins, collected from the productive and closely measured stratigraphic sections. The identification and delineation of the various faunal levels in the different basins is practically difficult owing to lack of common taxa. For example, except the *Redlichia* in the early Cambrian, and some agnostids and polymerids in the middle–early late Cambrian, there are barely any common trilobite taxa (even at generic level) between Kashmir, Spiti and Zanskar basins. It has been observed that, barring cosmopolitan genera (i.e. *Peronopsis*, *Baltagnostus,* and *Hundwarella* etc.), the fauna of Spiti and Zanskar basins do not correspond with that of Kashmir Basin, though all these basins are situated in the same geographical realm.

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A SILICIFIED FURONGIAN TRILOBITE FAUNA FROM KOREA AND ITS IMPLICATION FOR MONOPHYLY OF THE ORDER ASAPHIDA

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Keywords: Late Cambrian, silicified fauna, trilobite, phylogeny, Asaphida.

INTRODUCTION

Trilobite phylogeny has still remained unsatisfactorily understood due mainly to our incomplete knowledge on the Cambrian relationships of the post-Cambrian trilobite clades (Fortey, 2001; Whittington, 2007). In order to solve such problems, Fortey and Chatterton (1988) and Fortey (1990) proposed the Order Asaphida which includes several Cambrian and Ordovician clades. They argued that the Order Asaphida can be generally characterized by having a globular protaspis and a ventral median suture. The concept of the Order Asaphida has stood the test of time for the past twenty years and has been generally accepted in trilobite classification. However, despite its widespread usage, the origin as well as the monophyly of this group has not been clearly proven yet.

We recently discovered a Furongian silicified fauna from the Hwajeol Formation, Taebaeksan Basin, Korea, which includes some trilobites that are significant for evaluating the phylogeny of the Order Asaphida; i.e. *Tsinania canens*, *Asioptychaspis subglobosa*, and *Haniwa sosanensis*. The family Tsinaniidae was considered as a phylogenetically intermediate between leiostegioidean and illaenoidean trilobites (Fortey 1990), and was placed in the Illaenoidea. However, Zhu *et al*. (2007) recently illustrated a tsinaniid trilobite, *Shergoldia laevigata*, and pointed out several features similar to the members of the Asaphidae. They went on further to assign the family Tsinaniidae to the Order Asaphida, disregarding previously suggested illaenoid/leiostegioid affinity of the Tsinaniidae. Therefore, the ontogeny of *Tsinania canens* is crucial in determining where the family Tsinaniidae fits into the Trilobita. The Dikelocephaloidea and Remopleuridioidea were considered to form a monophyletic clade within the Order Asaphida (Fortey and Chatterton 1988). However, the protaspid morphology of dikelocephaloid trilobites has not been reported so far, neither has that of the primitive Furongian remopleuridioids. The immature morphologies of the dikelocephaloid trilobite, *Asioptychaspis subglobosa*, and the remopleuridioid trilobite, *Haniwa sosanensis*, from the Hwajeol Formation will thus reveal whether these trilobites are truly related to other groups of the Asaphida.

RESULT AND DISCUSSION

The immature and mature morphology of *Tsinania canens* suggests a close phylogenetic relationship between the Tsinaniidae and the illaenoid/leiostegioid trilobites. Not only the adult morphology of *T. canens* is of 'illaenimorph', but also the protaspid morphology shows a strong affinity to the illaenid trilobites. The protaspid period of *T. canens* comprises two stages just as that of the Ordovician illaenid *Failleana calva* does; the first stage protaspis of rather globular shape and the second stage protaspis of benthic morphology. The late protaspid morphology is similar to those of leiostegioids and the Ordovician illaenids. Interestingly, the late protaspides of the Ordovician illaenids show a well-developed distinctive anterior cranidial border, whereas the late protaspis of *T. canens* and that of leiostegioid trilobites have no distinctive anterior cranidial border. Therefore, Fortey (1990)'s argument that the Tsinaniidae shows the leiostegioidean ancestry of Illaenoidea is supported. Given Zhu *et al*. (2007)'s demonstration that the Tsinaniidae is related to the derived families of the Order Asaphida (Asaphidae, Taihungshaniidae, Nileidae, and Cyclopygidae), the Illaenoidea and derived families of the Order Asaphida may have shared a common ancestry. Hence, the derived groups of the Order Asaphida likely originated from the leiostegioid/illaenoid trilobites: i.e., these families of conterminant hypostomal condition may have arisen from leiostegioid/illaenoid trilobites of conterminant hypostomal condition, not from the basal groups of the Asaphida (sensu Fortey, 1990) of natant hypostomal condition.

This is also significant in that it may shed light on the origin of the bulbous protaspid morphology of the Asaphidae. If the Asaphidae truly diverged from leiostegioid/illaenoid trilobites, the bulbous protaspid morphology of this family must have been related to the globular shape of the early protaspides of *T. canens* and the Ordovician illaenid *Failleana calva*. It can be inferred that the extension of the planktonic mode of life of this plesiomorphic condition led to the large bulbous protaspis of the Asaphidae which metamorphosed into benthic meraspis.

The protaspis of the dikelocephaloid trilobite, *Asioptychaspis subglobosa*, is not of globular shape, but rather of generalized ptychopariid protaspid morphology. Therefore the relationship of the Dikelocephaloidea with other groups of the Order Asaphida turns out to be doubtful. The late protaspid morphology of the primitive remopleuridioid trilobite, *Haniwa sosanensis*, is not as bulbous as that of the Ordovician remopleuridioids, implying that the highly bulbous protaspis of the Ordovician remopleuridioid trilobites may have been evolved independently within this clade, not being homologous with the globular protaspis of other asaphid trilobites. In addition, *Haniwa sosanensis* possesses a yoked free cheek, not a median ventral suture. This result indicates that the Dikelocephaloidea and Remopleuridioidea may have been neither closely related to other groups of the Order Asaphida, nor closely related to each other.

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XYLABION AND RELATED GENERA

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Keywords: Trilobita, Cheiruridae, Upper Ordovician, morphology, palaeogeography, Baltica, Laurentia.

INTRODUCTION

In his monographic study on British Cheiruridae, Lane (1971) assessed several new genera, including *Xylabion*. Two species originally described from Baltoscandia are recorded in its species list: *X. sexermis* (Öpik, 1937) and *X. helgoeyense* (Nikolaisen, 1961). Generic position of both species has been briefly discussed earlier by Pärnaste (2004) when revising the cyrtometopine genus *Reraspis* Öpik, 1937. However, a little preparation of the cranidium of *X. sexermis,* originally named as *Remipyga*? sp. (Männil 1958), revealed some new features of its morphology. Comparison of the apodemal pattern and muscle scars in the ventral side of the pygidia, including that of the type species *X. craigensis* (Tripp, 1954), reaffirms the assignment to *sexermis* to the genus *Xylabion*. The aim of this study is to clarify facts for future study on evolution and migration of cheirurid trilobites. It concentrates on the *Ceraurinus*-like cheirurids, those with parallel-sided or slightly anteriorly tapering glabella (e.g. *Ceraurinella* Cooper, 1953, *Osekaspis* Prantl and Přibyl, 1948, *Ceraurinus* Barton, 1913, *Xylabion*).

Institutional repositories as follows: GIT - Institute of Geology, Tallinn University of Technology; TUG 1085 - Öpik's collection, University of Tartu; HM - Hunterian Museum, Glasgow University; Ar - Swedish Museum of Natural History, Stockholm, and PMO - Natural History Museum, University of Oslo. Terminology follows that of Whittington (1997) with some additions (middle lobe: LM, and anterior lobe: LA of the glabella) used earlier by the present author (Pärnaste, 2003). Specimens on Pl. 1 are coated with ammonium chloride before being photographed, but those on Fig. 1 are not, to show the preserved muscle scars.

DISCUSSION ON SYNONYMY OF *XYLABION SEXERMIS*

Ralf Männil (1958, p. 175) described a cranidium under the name *Remipyga*? sp. (Pl. 1) collected from the Rakvere Stage at Munalaskme, western Estonia, suggesting that it possibly matched the pygidium of *Reraspis*? *sexermis* Öpik, 1937. The specimen was not completely prepared out at the time, especially its anterior part, which carries several features of diagnostic value. Similarly to *Ceraurinus*, it has an anteriorly tapering glabella with relatively long LA compared to *Cheirurus* cf. *glaber* Angelin, 1854 *sensu* Schmidt 1881 (= *Xylabion* sp. nova), and a slightly convex (sag) and trapezoidal anterior border. It resembles *X. craigensis* in its wide and deep, evenly medially concave anterior border furrow. The anterior border meets smoothly over the shallow anterior border furrow a relatively wide (tr) anterior fixigena. Thereby, the moderate eyeridge is developed. The eyes are at about L2/L3, opposite S2. The glabella is narrowest at LA, and rather flat. Measurements of three specimens (GIT 103-54, PMO 80805 and PMO 67937- the holotype of *P. helgoeyensis*) show ratios varying only within a few percentage points, proving that *helgoeyensis* is a junior synonym of *X. sexermis.*

Two pits on LA are visible on Schmidt's specimen, and often on *Ceraurus* or allied taxa (*Whittakerites, Borealaspis, Leviceraurus*), as well as on *Ceraurinella oepiki* Edgecombe *et al*. 1999, which are not traceable here. I have found the counterpart of the original fixigena in our collections (Pl. 1: C). These rock samples present also a cephalon with detached hypostome of *Achatella nieszkowskii* Schmidt, 1881, and a pygidium of *Erratencrinurus seebachi* (Schmidt, 1881). Two cheeks of *E. seebachi* could be seen together with the holotype pygidium (Pl. 1: J), proving they are of the same age: Rakvere Stage (top of *D. clingani* Zone).

X. craigensis closely resembles *X. sexermis*. The cranidium of the type species slopes down anteriorly more steeply, and the glabella seems shorter, flatter and slightly wider (tr.) in its centre, while genae are narrower (tr). Pygidium is also narrower, mainly on account of its pleural field.

DISCUSSION ON RELATED TAXA AND SOME DIAGNOSTIC CHARACTERS OF THE PYGIDIA

Remipyga Whittington, 1954 was first established mainly because of the vague understanding of *Ceraurinus marginatus* Barton, 1913, and was later synonymized with it by Ludvigsen (1977). In general, these species all have (1) their (pygidial) spines with blunt endings and a dorsal rim; (2) the innermost two pairs of pygidial spines follow in length the oval shape of the entire exoskeleton (it means also that the innermost pair is slightly longer or equal to the second pair); (3) and the anteriormost spine is larger, longer and curving downwards in relation with pleural field or axis. The peculiar oar-like shape of the first pair of spines in *Remipyga glaber* Whittington, 1954 could be interpreted as an extreme modification of that shape and still assessed within *Ceraurinus*. Accepting this means giving a relatively low priority to the shape of the anteriormost pair of pygidial spines in their taxonomy. Then, how about the validity of *Didrepanon* Lane, 1971, which has two long anterior pairs of spines of about equal length, but otherwise resembles *Hadromeros* Lane, 1971? Does *Xylabion* fall into the synonymy of *Ceraurinus*? In latter case, the only difference seems to be the spines in gradational of size (decreasing *versus* increasing adaxially), in addition to the different shape of the ending points of the spines. Even the characteristic rim on the dorsal side of the spines common on *Ceraurinus* appears on *Xylabion craigensis* (see Tripp, 1954, pl. 3, fig. 45). The adaxially decreasing pattern is common to *Hadromeros* and *Ceraurinella* as well. However, *Xylabion* could be defined based on the combination with the specific pattern of the apodemes.

Xylabion sexermis is rather similar to *Reraspis* and *Cyrtometopus* Angelin, 1854 (as mentioned in Lane, 2002; Pärnaste, 2004), and therefore one example is displayed here for comparison (see Fig. 1). Several characters of the thoracic pleurae are repeated on the first pleura of the pygidium. A light pleural furrow runs straight to the middle of the axial furrow (Fig. 1:D), as characteristic for Cyrtometopinae, but a much stronger and deeper one is curving towards the upper point of the axial furrow in others (Fig. 1:A, B, C).

Also a peculiar character of the articulating half-ring of the thoracic lobe but accordingly of the articulating furrow and the apodemes in it, are repeated on the first and often on the second axial ring of the pygidium. An axial furrow separating the first pair of pleurae from the axial ring is common for both, but one separating the second pair is missing on Cyrtometopinae, although it can be rather weak on Cheirurinae. The apodeme at the first interpleural furrow of Cyrtometopinae-type rises steeply from the junction of the axial furrow to run abaxially as a narrow rim, but is relatively low and blunt on the Cheirurinae-type. The junction point of the axial furrow with following interpleural furrows bearing apodemes is shifted aside abaxially, producing zigzag line through the entire axial furrow on the latter type. Cyrtometopinae have a large triangular apodeme at the interpleural furrow.

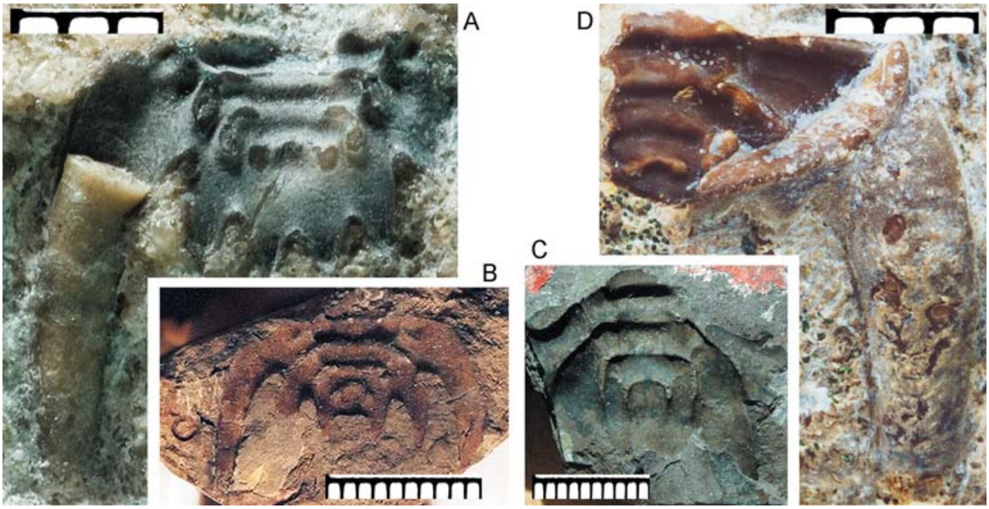

Figure 1. A, *Ceraurinella ornata* (Angelin) *sensu* Schmidt (GIT 319-6); B, *Xylabion craigensis* (HM A.3928b), original of Tripp 1954. C, *Hadromeros subulatus* (Linnarsson, 1869) (Ar 15281) presents a Cheirurinae-type pattern of pygidial apodemes and muscle scars, in comparison with the Cyrtometopinae-type pattern: D, (GIT 319-5) *Cyrtometopus* sp.

Several characters can be distinguished which differentiate between *Ceraurinella* specimens from various geographical areas: those inhabiting the eastern side (*i.e.*, northern side, based on Upper Ordovician paleogeography) of the Transcontinental Arch of Laurentia and those from the western side (*i.e.*, southern), those from the Girvan District, etc. The L1 glabellar lobe is slightly bigger and the second pair of pygidial spines longer on *Ceraurinella* inhabiting the western side than those on the *Ceraurinella* of the eastern side. *Ceraurinella* from the Girvan District differs a bit from the *Ceraurinella* from Laurentia by their bigger L1 (tr., sag.), which seems more triangular than rectangular, by shorter LA, wider axial part of the entire exoskeleton, and narrower lateral lobes (fixigena, thoracic pleurae and spines), as well as spines with sharp endings. I think we could assign it to geographical variation. Interestingly, this axial prevalence (in weight, capacity) brings up the emergence of the additional spines. In the case of the cheirurines of Girvan, we can see additional development of pygidial fulcral spines and small spines on the ventral side of the pygidial doublure. Probably these spines arose to balance weight/shape relation in certain environmental conditions. Strikingly, representatives of *Ceraurinella* from Girvan are very similar to the *Ceraurinus* of Laurentia, especially to those from limestones, like the type specimen. However, the

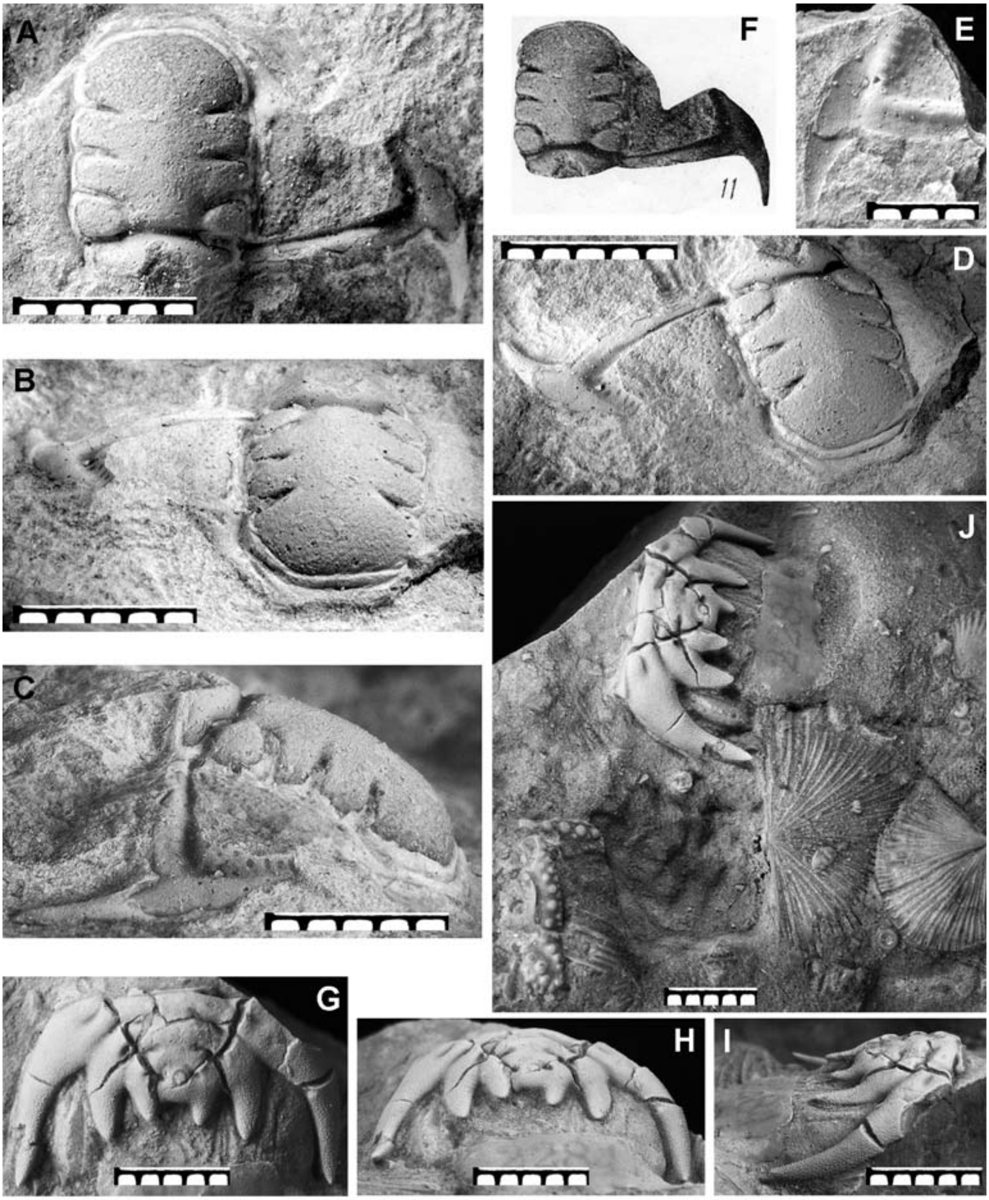

Plate 1. *Xylabion sexermis* (Öpik, 1937); A-D, (GIT 103-54, original of *Remipyga*? sp. Männil, 1958, pl. 3:11); E, (GIT 103-64) counterpart of previous specimen; F, figure of Männil; G-J, (TUG 1085, holotype, original of Öpik, 1937, pl. 12:4). Scale in mm.

shape of the anterior border in front of the LA is longer (exsag., sag.) and trapezoidal in dorsal view (partly due to not curving down) on *Ceraurinus*. In addition, the anterior spines of the pygidia of *Ceraurinella* curve up, and the innermost pair is usually shorter and conjoined. These two genera also differ in the shape of the apodemes. Based on these characters *Xylabion*, is closer to *Ceraurinus* than to *Ceraurinella.*

CONCLUSIONS

Paraceraurus helgoeyensis is a junior synonym of *Xylabion sexermis.* The first was collected from the Mjøsa Limestone at Bergevika, Helgøya, Norway, where patch reefs were developed (Harland, 1981) and the second comes from the micritic limestone of the Rägavere Formation at Munalaskme and Voore, northern Estonia. Interestingly, they are from contemporaneous beds of the *D. clingani* graptolite Zone (Rakvere Stage), but from different facies. Cheirurid trilobites are often strictly constrained to certain environments.

Xylabion, including *X. sexermis* shows the Cheirurinae-type pattern of pygidial apodemes in comparison with the Cyrtometopinae-type pattern.

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TRILOBITE CLUSTERS: WHAT DO THEY TELL US? A PRELIMINARY INVESTIGATION

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Keywords: Taphonomy, biostratinomy, behaviour, palaeobiology, palaeoecology.

INTRODUCTION

Clusters or aggregations of fully and/or partially articulated trilobite exoskeletons have fascinated palaeontologists and fossil collectors for well over a hundred years. Professional palaeontologists have been interested in their implications for trilobite palaeobiology (e.g., behaviour), whilst collectors have admired them for their aesthetic qualities (Johnson, 1985). Studies on trilobite clusters began over a century ago, with some of the earliest papers by Walcott (1875, 1881) and Beecher (1894). However, it was the pioneering work of S.E. Speyer (1985, 1987, 1990, 1991; Speyer and Brett, 1985) on Middle Devonian trilobite clusters from New York that brought trilobite behavioural palaeobiology to the fore. Since this time, there have been only a limited number of case studies on the interpretation of trilobite clusters (see Paterson *et al.*, 2007 and references therein).

DEFINING A TRILOBITE CLUSTER

The classic paper on Middle Devonian Hamilton Group trilobite assemblages by Speyer and Brett (1985) was the first to define what constitutes a trilobite cluster. They considered a 'cluster' to be "…a group of three or more trilobites along a single bedding plane in which adjacent individuals are no more than two centimeters from one another" (Speyer and Brett, 1985, p. 90); subsequent studies have found that the criterion of a maximum two-centimetre separation between individuals to be restrictive (e.g., Hughes and Cooper, 1999). Speyer and Brett further refined this definition by establishing two categories, 'body clusters' and 'moult clusters' to represent assemblages that contain fully articulated and partially articulated individuals, respectively. Other common characteristics of both cluster types observed in the Hamilton Group assemblages – but also noted in other studies (e.g., Paterson *et al.*, 2007) – include monospecific, size-segregated individuals assembled in an area rarely exceeding 200 cm^2 and forming discrete patches along the bedding surface.

But if one was to conduct a survey of trilobite clusters in the fossil record, would Speyer and Brett's

(1985) definition of a cluster be appropriate for any example and could the same type of behaviour be implied? The simple answer is 'no'. Trilobite clusters show a variety of biostratinomic (and sometimes taxonomic) variation, and, coupled with other data (sedimentologic, stratigraphic or otherwise), each example should be assessed against a variety of criteria to determine: (1) whether the cluster represents a true biological aggregation (or thanatocoenosis) or merely a "mechanical" association (or taphocoenosis), and (2) if a biological aggregation can be inferred, what evidence is available to determine the type of behaviour that is represented by the cluster.

Based on a recently compiled database of trilobite clusters, we herein revise a trilobite 'cluster' as: a discrete assemblage consisting predominantly of three or more partially and/or fully articulated exoskeletons occurring in a dense aggregation on a single bedding plane or within an event bed, cavity or burrow. This general definition does not take into account the size, taxonomic composition, orientation, posture or arrangement of the individuals, nor the three-dimensional space occupied by the cluster. It is also important to note that we consider 'partially articulated' exoskeletons to represent ensembles most reasonably interpreted as moults (e.g., McNamara and Rudkin, 1984, fig. 7; Chatterton and Ludvigsen, 1998, fig. 19.7; Paterson *et al*., 2007, fig. 8E), in addition to the following modes of preservation, which may or may not represent exuviae (*sensu* Henningsmoen 1975): cephala, axial shields, cephalothoraces and thoracopyga (or trunks). Since the aim of this study is to investigate the gregarious behaviour of trilobites, we have disregarded concentrations of disarticulated sclerites as such occurrences are evidently the result of extensive reworking and are, therefore, of no palaeobiologic significance.

TYPES OF TRILOBITE CLUSTERS

A review of trilobite cluster occurrences in the fossil record has enabled the recognition of several types. In some instances, cluster types clearly represent a behavioural aggregation, whilst examples of other types are more equivocal. Identification of a particular cluster type and, in turn, type of aggregation (behavioural or mechanical), can commonly be achieved by appraising a number of criteria:

1) Articulation.- Exoskeletons can be either fully articulated, which includes unbroken dorsal and ventral sutures, or partially articulated (as discussed above). Partially articulated individuals that do not represent obvious moult ensembles should also be examined in terms of the proportion of various elements, i.e., cephala, axial shields, cephalothoraces and trunks. Concentrations of disarticulated sclerites associated with clusters most likely represent background time-averaging due to sediment starvation prior to rapid burial.

2) Taxonomic composition.- Clusters will be composed of either a single species (monotaxic) or two or more species (polytaxic).

3) Size distribution.- Individuals may be size-segregated (unimodal; but not necessarily implying a single cohort) or show a range of sizes (polymodal).

4) Orientation.- This refers to the horizontal and vertical orientation of individuals in 3D space. Horizontal orientation is the facing direction of an individual within 360° on a horizontal bedding plane. Vertical orientation represents both the inclination of the individual relative to the horizontal bedding plane, in addition to the dorso-ventral attitude of the individual.

5) Posture.- Individuals may be prone (or outstretched) or display ventral flexure (including complete enrollment), dorsal flexure or torsion (*sensu* Hughes and Cooper, 1999).

6) Sedimentology/microstratigraphy.- Key features such as sedimentary structures, lithology and

microstratigraphic details (e.g., graded bedding within a microturbidite) may help elucidate the depositional setting and processes under which the cluster was preserved.

7) Palaeoecology.- Preservation of associated biota may also be useful biostratinomic tools, especially biostratinomically sensitive, sessile multielement (e.g., crinoids) and bivalved (e.g., brachiopods) taxa, in addition to groups that are excellent indicators of current direction (e.g., orthoconic cephalopods) (Speyer and Brett, 1988). These and other faunal elements, if articulated, unoriented and, in some cases, preserved in life position, would indicate autochthoneity.

In using these criteria, it is often possible to interpret whether the cluster is *in situ* (autochthonous), parautochthonous or allochthonous; the first indicating a behavioural aggregation and the latter two representing mechanical aggregations. Articulation of exoskeletons has long been considered an important factor in assessing the biostratinomic history of trilobites. Partially articulated exoskeletons, especially moult ensembles, are certainly the most informative indicators of autochthoneity and little to no pre-burial disturbance (Brett and Baird, 1986). In contrast, fully articulated exoskeletons must be interpreted with caution as biostratinomic indicators. Actualistic experiments have demonstrated that some modern arthropods do not suffer disarticulation soon after death due to transportation alone (Allison, 1986; Babcock and Chang, 1997; Babcock *et al*., 2000). So a trilobite that was transported whilst living (e.g., from a turbulent event) or recently dead may not have become disarticulated. Therefore, other criteria need to be considered when determining the autochthoneity or allochthoneity of a cluster primarily containing fully articulated individuals. Important biostratinomic information can be gleamed from the orientation and posture of individuals. For example, post-mortem, pre-burial disturbance of a cluster due to environmental factors (e.g., currents) may be implied from a preferred (uni- or bimodal) horizontal orientation and the presence of inverted (dorsum-down) individuals. As noted by Brett *et al*. (1999), although the dorsum- (or convex-) up orientation is the more hydrodynamically stable position in the presence of shallow, wave-induced currents, it is uncertain if this is the case in quieter deep marine settings. While this disturbance does not necessarily indicate allochthoneity, it would strongly suggest that the cluster was probably not a behavioural aggregation and could perhaps be considered parautochthonous. It should be noted that precaution must be taken with the interpretation of inverted individuals, as this attitude may result from behaviour, for example, an ecdysial posture (cf. Speyer, 1985; Karim and Westrop, 2002), or other biological (e.g., necrolysis, bioturbation or scavenging) and environmental (e.g., traction currents) causes; see Paterson *et al*. (2007) for an overview. A "chaotic" arrangement of individuals showing a combination of oblique orientations relative to a horizontal bedding plane, dorso-ventral flexure and torsion would perhaps imply that the individuals were caught up in a high energy event, transported and dumped (i.e., buried rapidly), thus resulting in an allochthonous cluster; however, flexure and torsion have also be interpreted as escape postures within an autochthonous cluster (cf. Hughes and Cooper, 1999). The underlying message is that trilobite clusters can be taphonomically complex and difficult to interpret. Given the number of variables, clusters should be assessed on a case-by-case basis, taking into consideration all of the above-mentioned criteria.

DECIPHERING GREGARIOUS BEHAVIOUR FROM TAPHONOMIC SIGNATURES

Unequivocal evidence of behaviour preserved in the fossil record, often depicting a moment frozen in time, is a rarity. Some interesting examples include the Middle Cambrian Burgess Shale arthropod *Marrella* caught in the act of moulting (García-Bellido and Collins, 2004), and a nesting oviraptorid dinosaur from the Cretaceous of Mongolia (Norell *et al*., 1995). However, in most instances, fossil behaviour must be inferred, usually from a unique biostratinomic signature of body or trace fossils and/or using modern analogues; the latter often associated with difficulties when trying to interpret fossils without extant exemplars.

Speyer and Brett's (1985) seminal study on the Hamilton Group clusters was a huge leap in our understanding the gregarious behaviour of trilobites. However, their 1985 paper and subsequent others by Speyer (1985, 1987, 1990, 1991), in discussing trilobite clusters and their palaeobiologic implications, only addressed body and moult clusters as representing an aggregation formed for purpose of synchronous moulting and copulation; although, Speyer (1985) recognised a separate cluster type, which he termed 'moult accumulations', but did not discuss the palaeobiology of these occurrences. While these and later studies (e.g., Karim and Westrop, 2002; Paterson *et al*., 2007) represent some of the most convincing examples of social reproductive behaviour in trilobites, a variety of cluster examples in the literature and our unpublished data indicate that trilobites were potentially capable of other forms of non-reproductive gregarious behaviour.

If a trilobite cluster is considered to be autochthonous, one can look for clues alluding to the type of behaviour represented. This can be challenging and, in many cases, behavioural inferences are speculative. From a neontological perspective, animal aggregation is complex, being widespread amongst most phyla and occurring for a variety of reasons (Parrish and Edelstein-Keshet, 1999). In general, animal aggregations can represent "self organisation" or form in response to extrinsic factors, and in many cases can be taxon-specific. Motives for aggregation amongst extant aquatic arthropods may include, amongst other reasons, protection, feeding and reproductive strategies.

A comprehensive survey of trilobite clusters and their behavioural implications are beyond the scope of this paper and will be investigated in a future study. However, the following examples aim to demonstrate the complexity of gregarious behaviour in trilobites by focusing on the various moulting strategies exhibited by disparate clades. Speyer and Brett (1985) noted the occurrence of moult clusters of *Eldredgeops* amongst *in situ* coral gardens, implying that these trilobites moulted in sheltered areas. More recent studies have also recognised moult clusters in more cryptic settings, notably burrows, nautiloid shells and cavities within carbonate buildups. Examples of dense, linear moult clusters preserved in burrows include: *Acernaspis orestes* from the Silurian of Canada (Chatterton *et al*., 2003); and *Placoparia cambriensis* from the Middle Ordovician of the Czech Republic (Mikuláš and Slavíčková, 2001). Davis *et al*. (2001, fig. 2) illustrated exuviae of *Flexicalymene meeki* entombed within a nautiloid shell from the Upper Ordovician of Ohio. Suzuki and Bergström (1999) reported pockets (representing cavities) within carbonate buildups containing moult clusters of several species from the Upper Ordovician of Sweden. In the majority of these examples, the species possess dorsal eyes, perhaps implying that they did not maintain a cryptic lifestyle, but sought temporary refuge from predators and other environmental disturbances during moulting. However, *Isocolus sjoegreni* and *Ityophorus undulatus* from the carbonate buildups of Sweden are blind, which may suggest that some trilobites were permanent residents of cryptic dwellings.

What these examples exemplify is that disparate trilobite clades throughout the Palaeozoic may have clustered for the same reasons and, in turn, show that the Trilobita exhibit the same complexities of social behaviour displayed by modern arthropods. While behavioural generalities may be a safer option when interpreting fossils, it is plausible that trilobite clusters forming for a particular purpose were taxon-specific, thus show a variety of strategies to achieve the same goal in the form of various taphonomic signatures. Whatever the mechanisms for aggregation, it is possible that this social behaviour contributed to the evolutionary success of the Trilobita.

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EARLY CAMBRIAN ARTHROPODS FROM THE EMU BAY SHALE LAGERSTÄTTE, SOUTH AUSTRALIA

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HISTORY OF RESEARCH ON ARTHROPODS FROM THE EMU BAY SHALE LAGERSTÄTTE

The Emu Bay Shale Lagerstätte, located on the north coast of Kangaroo Island, South Australia, is the most important Burgess Shale-type Cambrian fossil locality in Australia. In 1952, R.C. Sprigg first discovered fossils in the Emu Bay Shale near the Emu Bay jetty as part of the Geological Survey of South Australia regional mapping programme (Sprigg *et al*., 1954; Sprigg, 1955). However, due to an accident, Sprigg was unable to carry out detailed work to the east of Emu Bay. The Emu Bay Shale Lagerstätte site at Big Gully, located 3 km east of Emu Bay (Fig. 1), was discovered along the coastline immediately adjacent to Big Gully by B. Daily during his doctoral studies. The first fossils collected included superb articulated specimens of *Redlichia* up to 25 cm in length. Daily (1956, p. 126) was also the first to publish information on the Lagerstätte, recording the presence of the trilobites *Redlichia* n. sp. and cf. *Lusiatops*, plus *Isoxys* n. sp., an unidentified crustacean and annelids; this represented his Faunal Assemblage 12. The trilobite species referred to as "cf. *Lusiatops*" by Daily (1956) was later described as *Estaingia bilobata* by Pocock (1964), although the illustrated specimens were not sourced from the Lagerstätte. Jell (in Bengtson *et al*., 1990) formally described specimens of *Redlichia* from Big Gully as *R. takooensis* Lu, 1950. M.F. Glaessner, M. Wade and B. McGowran collected material (including nonmineralised taxa) in December 1956 (B. McGowran, pers. comm., December 2007), but no formal descriptions were published until Glaessner (1979) described the bivalved arthropods *Isoxys communis* and *Tuzoia australis,* the palaeoscolecid priapulid *Palaeoscolex antiquus*, plus *Myoscolex ateles* and *Vetustovermis planus* of uncertain affinities. Glaessner (1979) noted that there were no signs of trace fossils in his material; he suggested deposition as a thanatocoenosis within a reducing environment.

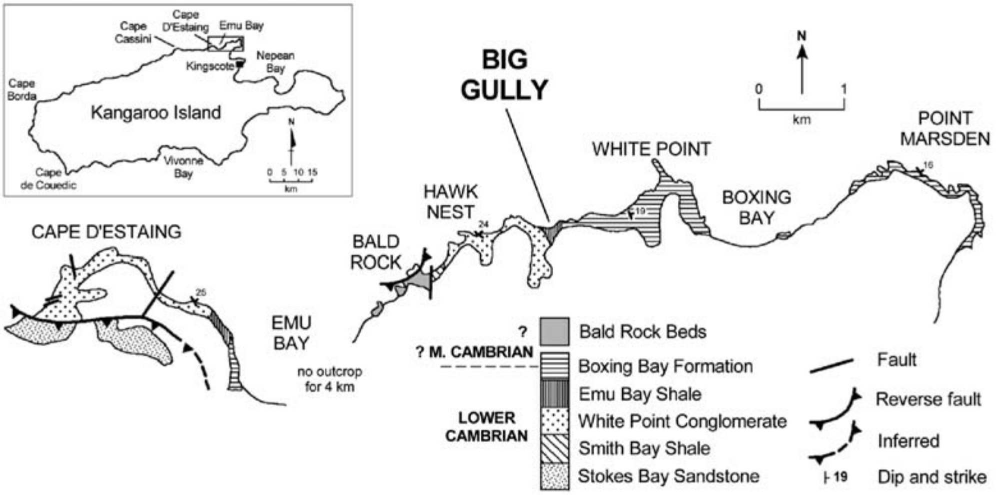


Figure 1. North east coast of Kangaroo Island showing Cambrian outcrop and the location of the Emu Bay Shale Lagerstätte at Big Gully; modified from Paterson and Jago (2006, fig. 1).

Studies during the 1980s and 1990s recognised the occurrence of putative stem-group arthropods in the Emu Bay Shale. Based on evidence of healed injuries in specimens of *Redlichia* from Big Gully, Conway Morris and Jenkins (1985) postulated the presence of predators in the fauna. This was confirmed when McHenry and Yates (1993) reported the occurrence of *Anomalocaris* at Big Gully; they also described and figured preserved antennae on a specimen of *Redlichia takooensis.* Nedin (1995a) subsequently recognised two species of *Anomalocaris*, but only formally naming *A. briggsi*. Briggs and Nedin (1997) reinterpreted *Myoscolex* as an *Opabinia*-like animal and stressed the importance of preserved mineralised (i.e., phosphatised) muscle tissue in *Myoscolex* as the oldest known at that time (and remains to hold true), with Nedin (1997) suggesting that early diagenesis was an important factor in preserving the muscle tissue. However, Dzik (2004) has recently swung back to Glaessner's original interpretation of *Myoscolex* in regarding it as the oldest known annelid.

Existence of trilobitomorphs or 'trilobite-allied' arthropods in the Emu Bay Shale Lagerstätte has been known for over 10 years. Nedin (1995b, 1999) reported the presence of two species of *Naraoia,* but recent studies (Lin *et al*., 2006; Zhang *et al*., 2007) have suggested that one of these species (illustrated by Nedin 1999, fig. 2A) has possible affinities to taxa such as *Primicaris* and *Skania*. However, new collections reveal that both of Nedin's species of "*Naraoia*" in fact represent new trilobitomorph taxa (discussed below). Nedin (1995b) also reported a single, poorly preserved specimen of *Xandarella*, but this has never been published.

The most recent research on the Emu Bay Shale Lagerstätte has focused on trilobites. Paterson and Jago (2006) described two new taxa, *Megapharanaspis nedini* and *Holyoakia simpsoni*; the former also representing a new monotypic emuelloid family, the Megapharanaspidae, and the latter representing the first occurrence of the genus outside of Antarctica. They also provided new morphological information on *Redlichia takooensis*, including a description of the hypostome and rostral plate. Paterson and colleagues (Paterson and Edgecombe, 2006; Paterson *et al*., 2007) have also conducted extensive research on emuellids, including material from the Emu Bay Shale type section at Emu Bay, although they have noted the rare occurrence of *Balcoracania dailyi* in the Lagerstätte.

STRATIGRAPHY AND AGE

At Big Gully, the Emu Bay Shale is about 78 m thick (Daily *et al*., 1979). The unit overlies the polymict conglomerates of the White Point Conglomerate that Daily *et al*. (1980) suggested were deposited as fanglomerates with a source area to the north. The Emu Bay Shale at Big Gully represents a minor facies comprising of dark laminated silty shales that were deposited below wave base in a fluctuating dysoxic-anoxic microenvironment (Conway Morris and Jenkins, 1985; Nedin, 1995b), which favoured the preservation of the Lagerstätte. Small scale slumping indicates a local southerly slope. There is at least one thin polymict conglomerate horizon within the unit. The Emu Bay Shale is conformably overlain by the 550 m thick Boxing Bay Formation, which comprises mainly subtidal feldspathic sandstones and arkoses with subordinate shales and thin conglomerate lenses (Daily *et al*., 1979). The lower part of the Boxing Bay Formation contains abundant trace fossils, including burrows and arthropod tracks, as well as exhibiting large scale soft sediment deformation.

The presence of the trilobites *Estaingia bilobata*, *Balcoracania dailyi* and *Redlichia takooensis* in the Emu Bay Shale suggests correlation with the lower Cambrian (Series 2) *Pararaia janeae* trilobite Zone within South Australia, the early-mid Canglangpuan Stage of China and the mid-late Botoman of Siberia (Jell in Bengtson *et al*., 1990; Paterson and Edgecombe, 2006; Paterson and Jago, 2006; Paterson and Brock, 2007). In a global context of lower Cambrian Lagerstätten, the Emu Bay Shale Lagerstätte is approximately coeval with the Balang Lagerstätte of China, but younger than the famous Chengjiang (aka Maotianshan Shale) and Sirius Passet Lagerstätten (Zhu *et al*., 2006).

CURRENT RESEARCH: NEW INSIGHTS INTO THE BIODIVERSITY OF THE EMU BAY SHALE ARTHROPODS

All previous research and collections from the Emu Bay Shale Lagerstätte have been sourced from outcrops along the shore platform and adjacent cliffs to the east of the mouth of Big Gully. A new study commenced in September 2007 with the excavation of a 15 m long trench covering about 8 m true thickness of the Emu Bay Shale, which is located about 500 m inland and along strike from the coastal outcrops. The trench section is highly fossiliferous, although soft-part preservation becomes rarer in the upper part of the section due to a higher frequency of interbedded siltstones and sandstones. The initial excavation has proved to be very successful with the discovery of several taxa previously unrecognised from the biota.

New collections from the trench are dominated by articulated trilobites (Fig. 2A, B). This faunal dominance was also noted in the assemblage from the coastal outcrops by Nedin (1995b) and Briggs and Nedin (1997). They proposed that trilobites constitute between 50 and 60% of the fossils, but our recent observations suggest that this percentage may be underestimated. Even considering the occurrence of a small percentage of moult remains, trilobites appear to dominate the biota. The trilobite fauna from the trench collections is dominated by *Estaingia bilobata* (Fig. 2A) and to a lesser extent by *Redlichia takooensis* (Fig. 2B), a few specimens of the latter possess antennae and poorly preserved biramous appendages. The other trilobite taxa known from the Emu Bay Shale are quite rare or absent in the new collections. For example, of the hundreds of trilobite specimens found, we uncovered only two specimens of *Balcoracania dailyi*. These specimens of *B. dailyi* are regarded as vagrants because this species is typically found in marginal marine environments (Paterson *et al*., 2007).

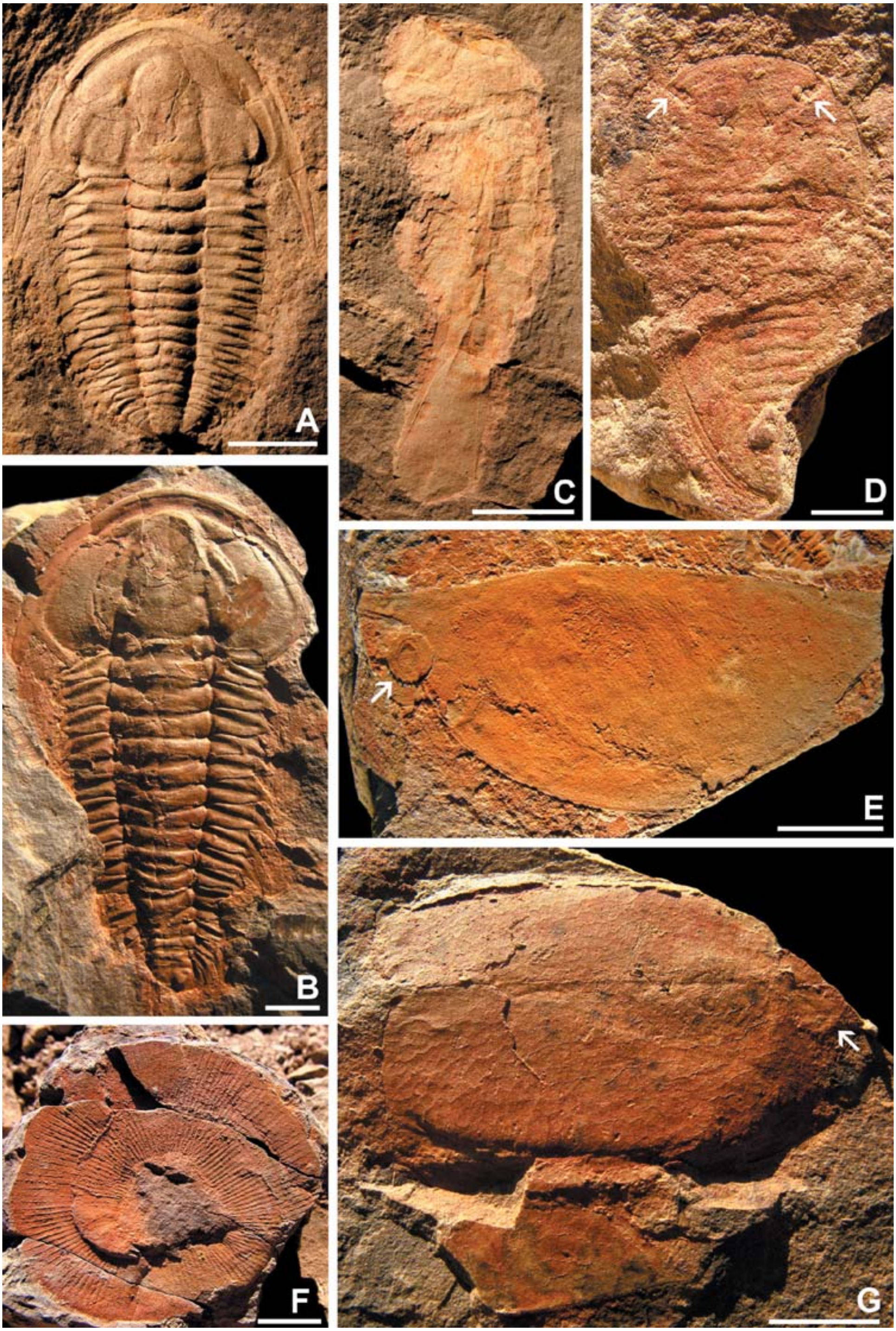
The excavation has also revealed an increased diversity of nonmineralised arthropods. The most common of these are the bivalved arthropods (Fig. 2E, G). Species include: numerous specimens of *Isoxys communis* (Fig. 2E), with considerably large cardinal spines, humped dorsal hinge line and hitherto undescribed very fine reticulated carapace, together with stalked eyes, alimentary canal and possible appendages; and a new species of *Isoxys* with straight dorsal hinge line and very short cardinal spines, also presenting soft-body preservation of eyes and gut; several specimens, including some in "butterfly" and dorsal orientation, of *Tuzoia australis* (Fig. 2G), three of which also possess eyes – a very uncommon occurrence (Vannier *et al*., 2007); and a few large fragments of a possible new species of *Tuzoia*.

Putative stem-group arthropods are relatively rare in the new collections. We have uncovered frontal appendages and lateral flaps of *Anomalocaris*. Specimens of *Myoscolex ateles* are also relatively uncommon. Previous studies (Nedin, 1995b; Briggs and Nedin, 1997) have indicated that *M. ateles* is the most abundant nonmineralised taxon from the coastal outcrops at Big Gully. The rarity of *M. ateles* at the new inland site could simply represent lateral and/or vertical stratigraphic variation of the assemblage; recent reconnaissance work indicates that the Lagerstätte extends across a greater stratigraphic range than previously thought (Briggs and Nedin, 1997).

The new excavation has revealed a number of previously undescribed arachnomorphs. Taxa include both 'trilobite-allied' arachnomorphs or Trilobitomorpha and 'chelicerate-allied' arachnomorphs or Cheliceramorpha (*sensu* Cotton and Braddy, 2004). The most common of these is a cheliceramorph taxon with probable megacheiran affinities (Fig. 2C). Body size and trunk morphology, especially the possession of 11 trunk segments and a spatulate telson, resemble forms such as *Alalcomenaeus* and *Leanchoilia*, but also *Utahcaris* and *Sanctacaris*. Many specimens also show gut traces and/or longitudinal carinae. Unfortunately, there are no preserved 'great appendages' in the specimens recovered to date. Other cheliceramorphs from the new site are rare and/or too fragmentary to make comment at this stage. Trilobitomorphs include two new taxa with preserved cephalic appendages that are likely allied to naraoiids because both have a natant hypostome, a short thorax, and a pygidium that is much longer than the head shield. One taxon has three thoracic segments and strong intersegmental furrows on the pygidium (Fig. 2D), whereas the other has a four-segmented thorax and effaced furrows on the pygidial pleurae. Discovery of articulated thoracic segments in the latter disproves its assignment to *Naraoia* or close affinities to *Primicaris* and *Skania* (discussed above). A few specimens represent a xandarellid, which is most likely to be conspecific with Nedin's (1995b) unpublished *Xandarella*.

Other (non-arthropod) fossils from the new collections include: several palaeoscolecid taxa (Fig. 2F), including *Palaeoscolex antiquus* and another with similarities to *Acosmia*; a variety of sponges, including leptomitid demosponges; an enigmatic form resembling *Eldonia*; hyoliths; chancelloriids; filamentous algae; a banffozoan; and several other problematic forms. Unfortuntately, we have not uncovered new material of the unusual *Vetustovermis planus* – now considered to share characteristics with molluscs, flatworms and nemertines (Chen *et al*., 2005) – but it is hoped future excavations will reveal important specimens to provide new information on the affinities of this taxon.

Figure 2. A, *Estaingia bilobata* Pocock, 1964, SAMP 14955; scale bar is 0.5 cm. B, *Redlichia takooensis* Lu, 1950, SAMP 14956. C, megacheiran arachnomorph, SAMP 14957. D, new trilobitomorph taxon with arrows indicating preserved antennae, SAMP 14958; scale bar is 0.5 cm. E, *Isoxys communis* Glaessner, 1979, with arrow indicating preserved eye, SAMP 14658. F, coiled palaeoscolecid, SAMP 14932. G, *Tuzoia australis* Glaessner, 1979 showing dorsal compression and arrow indicating preserved eyes, SAMP 14677. All scale bars are 1 cm, unless otherwise stated.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MORPHOMETRIC STUDY OF THE ORDOVICIAN PROETID TRILOBITE *CYAMELLA STENSIOEI* OWENS, 1978

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Keywords: Trilobita, statistical analysis, size range, carbonate mud mound, Boda Limestone, Siljan District, Sweden.

INTRODUCTION

The genus *Cyamella* was first described by Owens in 1978 as *Cyamops*, but was renamed (Owens in Owens and Hammann, 1990, p. 240) as the original genus name was preoccupied. *Cyamella stensioei* Owens is a small proetide trilobite from the Boda Limestone of the Siljan District in Dalarna (Sweden). The Boda Limestone (Upper Ordovician) is regarded as a carbonate mud mound showing core and flank facies (Jaanusson, 1982). Mass accumulations of trilobites within the Boda Limestone are regarded as a result of sedimentary infill and are termed pockets or cavities (Suzuki and Bergström, 1999). To our knowledge *C. stensioei* has not yet been described from outside these limited areas within the mounds. One rock specimen from the Boda Limestone in the quarry at Kallholn (NW part of the Siljan Ring between Orsa and Skattungsbyn) is investigated here. The aim of this study is to trace any morphometric variation of the proetid exoskeletons in one of such pockets, assuming this being a case of one particular accumulation and therefore representing variation in morphology within a species during as short a time period as possible.

MATERIAL AND METHOD

The limestone quarry at Kallholn is the type locality for *C. stensioei* (see Owens, 1978) and has yielded several slabs with mass accumulations of the species. One slab derived from Kallholn is investigated (Fig. 1) without any information given about the exact locality or orientation. Referring to Suzuki and Bergström (1999, p. 168; see also Owens 1978, p.202), it can be regarded as an *in situ* type of internal cavity filling.

Most trilobite specimens on the rock sample do not show all of the features regarded as important for the analysis. Twenty-four suitable cranidia were chosen for the final comparison. Specimens are named by using the following code: CTP stands for a complete specimen with cephalon/cranidium, thorax and pygidium, CTH stands for cephalothorax and CR stands for cranidium. The measurements were taken with a stereoscopic microscope using a measuring ocular. Longitudinal sections are termed lengths, all transverse sections are termed widths. All values are regarded as being absolute and measurements were taken in units, where forty units represent one millimetre. Later translation into millimetres does not affect the size ratios investigated. The trilobite specimens were oriented in a planar position (perpendicular to the optical path).

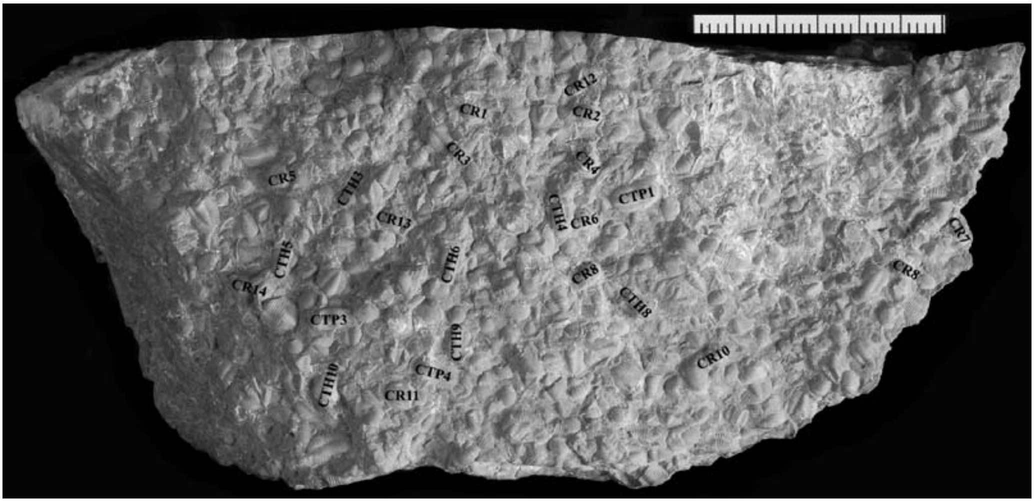

Figure 1. Rock specimen from Boda Limestone of Kallholn quarry, Sweden, showing a mass accumulation of the minute proetide *Cyamella stensioei*. Investigated remains are indicated using CTP for specimens with cranidium, thorax and pygidium, CTH for cephalothorax and CR for cranidium (Natural History Museum, Stockolm; Ar 45665). Scale graduated in mm.

A multiple orientation method was used for measuring the thirteen different sections of the cranidia (Fig. 2). By measuring from the centre of the graticule to the outer limit of the field of view, errors arising from the convexity of the exoskeleton were reduced. Measuring tracks were repeated three to five times to minimize measuring error. If a tolerance limit of six units between the highest and lowest values was exceeded, additional readings were made. An average value was calculated and chosen as the final measuring result. Where incomplete, some sections were measured in half length/width and doubled - assuming the measured specimens as being symmetrical in its feature.

The thirteen measurements used in the analysis are shown on Fig. 2. Their abbreviations stand for total cranidial length (Lmax), total cranidial width (Wmax), glabellar length (LGLABmax), glabellar width (WGLABmax), glabellar width at the middle of palpebral lobes (WGLAB_PALP), distance or position of palpebral lobes measured from posterior cranidial border (e.g. occipital ring) (LposPALP), length of preglabellar field (LPGFmax), width of preglabellar field (WPGFmax), length of palpebral lobes (LPALPmax), width of palpebral lobes (WPALPmax), length of occipital ring (LOCRmax), distance or position of median tubercle on occipital ring measured from posterior cranidial border (LposMTB), length of anterior cranidial border (LACBmax). In order to compare our values to those given by Owens (1978, p. 212), including those of the holotype, the palpebral width of the cranidium ($\sigma-\sigma$, sensu Owens) was calculated via WGLAB_PALP and WPALPmax. The dimensions of the cranidium of the holotype of *C. stensioei* (RM Ar47556) and an additional specimen (RM Ar47518) given by Owens (1978, p. 212) were compared with our measurements.

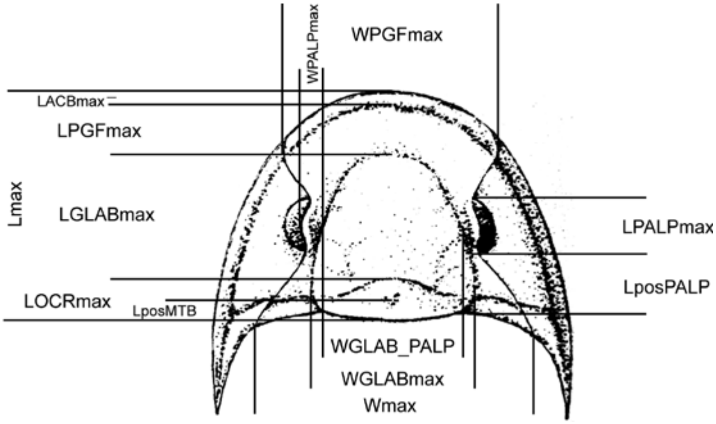

Figure 2. Measured sections on the cranidium of *C. stensioei*. L indicates length, W stands for width. (Figure modified after Owens, 1978).

RESULTS

As they are the most distinctive for identification and comparison, only cranidia were included in the investigation. The longest cranidium (CR13) shows a maximum length of 3.59 mm, whereas the shortest cranidium (CR12) measures 2.32 mm. The size difference is about 35 per cent and is a continuum, not showing grouping into separate instars (Fig. 3). The average is 3.007 mm, and calculated without the maximum and minimum values 3.011 mm. The median value is 2.955 mm. Cranidial widths could be measured on sixteen of the specimens. CR11 is the widest at 4.48 mm, the narrowest (CR12) measures 2.51 mm. The average is 3.43 mm, and calculated without the maximum and minimum values, 2.993 mm. The median value is 3.495 mm. The cranidial width-length ratio (Fig. 4A) changes from 78 to 97 per cent (average 87%, variability 19%), and that of the glabella (Fig. 4B) from 76–98 per cent (average 86%, variability 22%). Similar ratios (3/4–9/10) were described from the other slab (Owens, 1978, p. 211 here, and for following comparison). Sagittally the length of the preglabellar field occupies 34–52 per cent (average 42%, variability 18%) of the cranidial length, and is about 19–27 per cent (average 23%, variability 8%) of the length of the glabella. The ratio of the lengths of the palpebral lobe/glabella varies from 26 to 45 per cent (average 35%, variability 19%). For last two ratios 1/3 was described as diagnostic by Owens (1978). The width of the preglabellar field is equivalent to 63–89 percent of the maximum width of the cranidium, and 76–97 per cent of the length (variability 26% and 21% respectively). The occipital ring comprises from 21 to 36 per cent (average 29%, variability 15%) of the sagittal length of the glabella, which is more than was shown by Owens (1/4). The occipital tubercle is not positioned exactly to the middle length of the occipital ring, but slightly rearwards or forwards reaching to 5 per cent or 15 per cent respectively in comparison of LposMTB to LOCRmax (average 54%, variability 20%). The palpebral width of the cranidium (σ–σ) comprises 80% of the length of cranidium of holotype, but ranges from 57 to 74 per cent on this slab (Fig. 4C).

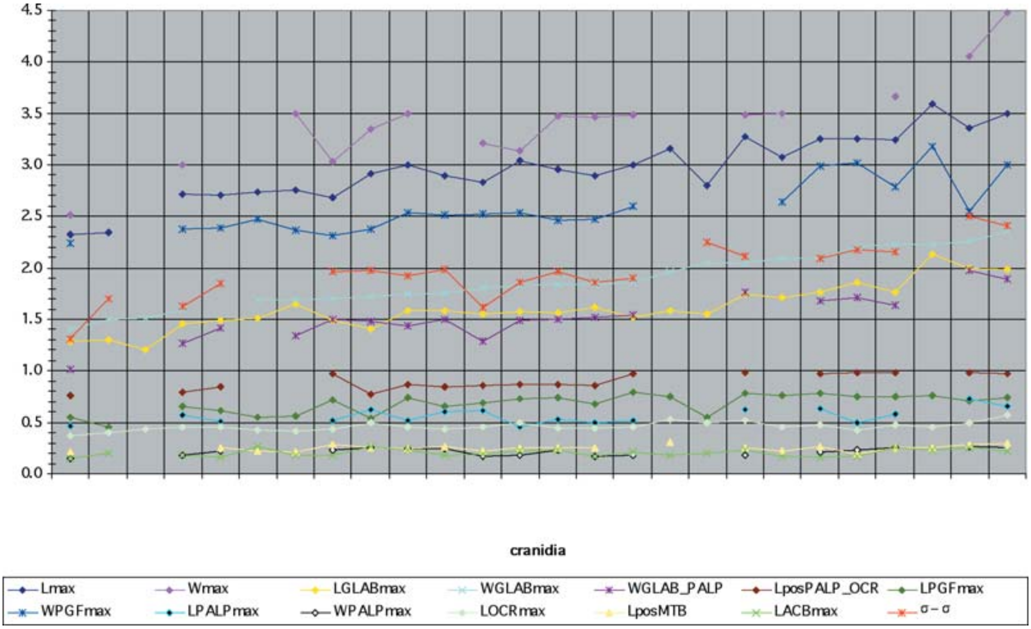

Figure 3. Measurements (in mm) for different trilobite sclerites. Sigma-to-sigma-values are calculated for our measurements. Additionally Owens' data (1978, p. 212) are used for comparison.

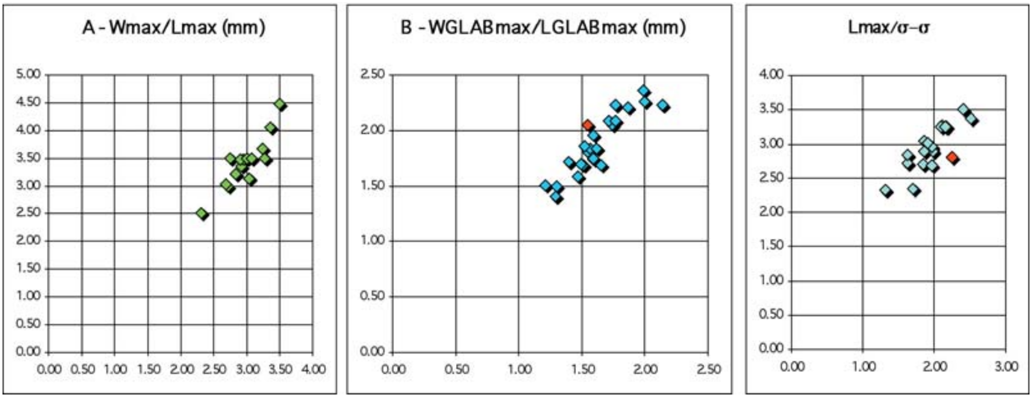

Figure 4. A–C, graphs plotting one character against another (see also Fig. 3). The holotype is shown by red.

While the maximum total length for the holotype (see Ar47556, Fig. 3) is situated in the lower part of the size distribution for all cranidia and differs by more than 1.2 mm from the longest cranidium measured, the maximum width is not given by Owens and therefore this ratio cannot be compared here. However, when sorted by the maximum width of the glabella the maximum cranidial length, glabellar length and the length of the preglabellar field show relatively lower values. The paratype cranidium (Ar47518) shows average cranidial length - glabellar width ratio, but again, somewhat lower value of the length of the preglabellar field. The differences described above in the data of the type specimens may be due to differences in measuring methods. The other possible reasons could be that these samples are from different pockets of the same or of possibly different age, or from different taphonomic situations.

The cranidial length and width only show a slight correlation, which could be a result of measuring errors (e.g. doubling the measured half-sections) superimposed on a small size variance signal. Another reason could be the small number of specimens used here. A better correlation is seen in the comparison of glabellar width and length, which show a proportional growth. More data are needed to clarify this in a more sophisticated way. The length of the occipital ring seems to change to a smaller degree compared to the increase of the cranidium. When plotted as graphs, most values of the thirteen measured sections show some peaks but these do not appear systematically. This can be seen, when sorting after one value first, than doing another plot with a different sorting of values. The sorting effect can be interpreted as a primary signal, showing variance on the species level. Also statistical explanations are possible.

CONCLUSIONS

Suzuki and Bergström (1999, p. 171) considered preservational reasons to be responsible for the relatively narrow size range for the minute trilobites *Ityophorus* and *Isocolus* also appearing within pockets and cavities of the Boda Limestone mounds. Maybe this is also the case for *Cyamella stensioei*.

Measurements of twenty-four cranidia of *C. stensioei* for one particular slab show 35 per cent of size difference, and no evidence for moulting instars or dimorphism. Maybe all individuals preserved belong to one generation, showing the natural size-variation. Further studies are needed to explain the differences between the type specimens and the specimens of this study. This also includes borrowing and re-measuring the type specimen and additional material stored in Stockholm. Besides statistical and morphometric analysis, further studies should also include sedimentological obeservations for supporting the theory of Suzuki and Bergström (1999) on life of *C. stensioei*.

Winnowing effects and trapping of hard-parts by algae were discussed by Suzuki and Bergström (1999) and further sedimentological analysis could help identifying the reason for the *Cyamella*-accumulations including whether or not they represent living communities within the cavities (or pockets). Smaller individuals including larvae can be expected if *C. stensioei* was fully adapted to this environment. Statistical analysis could also help to show morphometric differences within different *Cyamella*-accumulations, which could prove their separation from each other, being limited to one specific carbonate mud mound within the Boda Limestone facies.

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TAPHONOMY OF MIDDLE CAMBRIAN TRILOBITES: DISTINGUISHING TSUNAMIS FROM STORMS IN LA LAJA FORMATION OF WESTERN ARGENTINA

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Keywords: Trilobites, taphonomy, storms, tsunamis, carbonate platform, middle Cambrian, Precordillera, Argentina.

Coarse-grained strata deposited on continental shelves and epeiric seas in some tens of metres' water depth are conventionally ascribed simply to storms of varying intensity which interrupted the settling out of suspended mud. Storms eroded the sea bottom, concentrated and winnowed coarser particles, and delivered sediment from shallower water. Surprisingly, the possibility of tsunamis is virtually never evaluated even though they might, indeed should, have been common in many regions. Portions of the middle Cambrian La Laja Formation of the Argentine Precordillera formed in such a submerged epeiric platform or shelf. The taphonomy of trilobites in this unit provides the key that enables tsunami deposits (tsunamites) to be distinguished from storm deposits (tempestites) (Pratt, B.R. and Bordonaro, O.L. 2007: Tsunamis in a stormy sea: Middle Cambrian inner shelf limestones of western Argentina. *Journal of Sedimentary Research*, 77, 256–262).

The Soldano and Juan Pobre members of La Laja Formation comprise a suite of three limestone facies: variably argillaceous burrowed mudstone, bioclastic grainstone, and intraclastic conglomerate composed of pieces of mudstone including cemented haloes around burrows. Sporadically developed eocrinoid meadows and trilobite populations are recorded respectively by disarticulated ossicles and usually broken sclerites. The latter indicate that, generally, exoskeletons became fragmented by repeated bottom turbulence. Hence, the mudstones and grainstones show that, before stabilization by calcite cementation which began beneath the sediment–water interface and away from burrow margins, physical reworking of the surface sediment by storms was so frequent that it did not leave a specific signature of individual events. By contrast, scattered lenticular beds of intraclastic conglomerate were due to anomalous, brief episodes of deep scour and strong oscillatory flow due to powerful wave action. These conglomerates then escaped subsequent reworking. Because they are abruptly interbedded and encased within uniform mudstone, and there are no stratigraphic patterns, allochthonous material, or unconformities to indicate sea-level fluctuation, the events that created the conglomerates were more likely tsunamis, not storms. They could have been unleashed by faulting elsewhere on the shelf or rifting beyond the shelf margin to the (present-day) west to southwest. Those originating in the rift basin may have been diffracted by marginal shoals and attenuated by the shallowness of the platform, causing the waves to break some distance offshore. In any case, the study area near San Juan was not affected by backwash.

Recognition of tsunami-laid beds in this Cambrian unit urges a reexamination of the standard tempestite paradigm with its use of coarse-grained strata as a simple measure of storm frequency and intensity. Taphonomic observations prove critical in evaluating such events.

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THE NEW LOWER CARBONIFEROUS TRILOBITES FROM CZECH REPUBLIC

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Keywords: Carboniferous trilobites, Czech Republic, biostratigraphy, autecology.

INTRODUCTION

The active quarry-complex of Mokrá is situated in the southern part of Moravian Karst (Fig. 1). The studied sequence of the Mokrá quarry is part of the allochthonous Horakov development containing sediments from the Frasnian to the Viséan (Kalvoda and Ondrackova, 2003). It shows the transition from the platform carbonate sedimentation in Frasnian, *via* calci-turbidite sedimentation during deepening of the basin and its extension in the Famenian, to the basin inversion and gradual transit to a deeper-water siliciclastic sedimentation in Upper Tournaisian. Brezina Formation consists of reddish and olive greenish shales with calci-turbidites and siliciclastic turbidites. It ranges from Upper Tournaisian to Middle Viséan (Crha, 1987). There was no systematic study of the Lower Carboniferous trilobites from Moravia until the sixties of last century. Just a few papers on occurrence of sporadic fragments of trilobites were published.

Chlupáč (1966) found a trilobite assemblage in the vicinity of Mokrá near Brno, which came from several sporadic pits. All these trilobites were found in the Hady–Ricka limestones. No information has ever been published on the occurrence of Lower Carboniferous trilobites from the Brezina shales.

During the last years Lower Carboniferous shales of the Brezina Formation with very common fragments of trilobites were collected in the Mokrá quarry. After a comparison with material from other countries and published literature (Hahn, 1990; Hahn and Hahn, 1988;

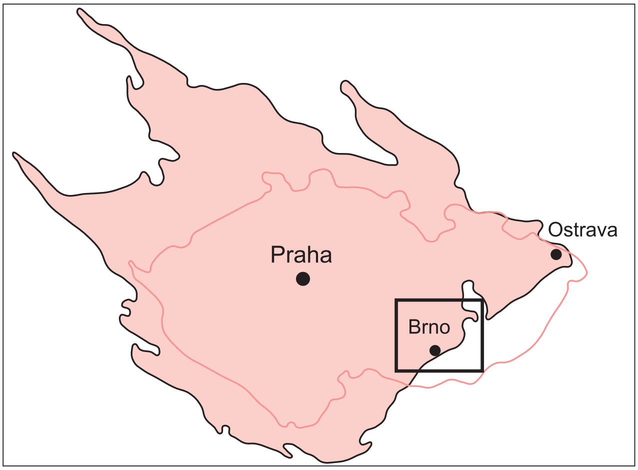

Figure 1. Sketch map of the Czech Republic with geographical position of Moravia and Brno city.

Hahn *et al*., 1996) a total of sixteen trilobite taxa were established. The occurrence of stratigraphically important conodont and foraminifera taxa dated trilobites as the youngest portion of the Brezina Formation. The main goal of this study is the systematic evaluation of the new trilobite assemblage from shales of this stratigraphical level.

CONCLUSIONS

In the Czech Republic, all studies on trilobite autecology have been focussed so far on the Prague Basin (Barrandian area). Chlupáč (1983) studied trilobite assemblages from the Ch?nice Limestone, including their ecology, while Chlupáč and Kukal (1985) studied trilobite assemblages from the Lochkovian–Pragian boundary. Havlicek and Vanek (1998) widely discussed brachiopod-trilobite assemblage and their main biofacies in the Pragian but they also pointed out some autecological aspects. Despite this, there has been no study focussing on autecology of Lower Carboniferous trilobites from the Moravian region. Based on specific functional morphology of studied taxa, four main groups were established in the studied assemblage from Mokrá quarry based on their supposed life style and feeding habits: (1) *Archegonus*, (2) *Liobole*, (3) *Bollandia*, and (4) *Tawstockia* morphotypes.

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ON THE APPLICATION OF LATIN TERMS AND THEIR INDICES ("TERMIXES") IN THE DESCRIPTION OF TRILOBITES

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Keywords: Trilobites, Latin term, "termix", measurements.

INTRODUCTION

When describing trilobites in a national language, we propose to use Latin terms and their indices, i.e., "termixes".

LATIN TERMS APPLICATION

The terminology used at present in descriptions of trilobites is ambiguous. One and the same morphological element has numerous synonyms in different languages, and even in the same language by different researchers, and sometimes a researcher uses different terms in different publications. This makes mutual understanding of specialists difficult and increases the probability of error when species of trilobites are determined. This problem becomes especially pressing when one has to do with foreign literary sources. A collective volume was published in 1975 under the name "Opisanie paleontologicheskih objektov s primeneniem latinskih terminov [*Description of paleontological objects by application of Latin terms*]" (Rosova *et al.*, 1975), in which a number of authors put forward Latin terms and their termixes to describe five groups of fossils: trilobites, monoplacophorans, brachiopods, conodonts and acritarchs. Rosova and Rosov (1975) proposed that a single Latin term and its "termix" should replace numerous polylingual synonym terms used for any particular morphological element. Latin is the international language of science. Biological and medical terminologies developed by the same procedure. We think this to be quite acceptable in paleontology as well, and Latin terms and their "termixes" assure unambiguity and conciseness of description in working out an international reference book on characteristics of genera and index species of trilobites. Rosova and Rosov (1975) collected Latin terms for morphological elements as follows: 1) they started by taking a previously known Latin term consisting of one Latin word and put forward its termix. For example: cranidium – **Cr**; glabella – **G**; pygidium – **Pyg**; rachis – **R** and so on; 2) in a previously used Latin term consisting of two words only one word was left. For example: annulus occipitalis was replaced by occiput - **O**; lobus palpebralis by palpebra - **Pal** and so on; 3) for an element that had no Latin term they chose a short harmonious Latin noun denoting an object which resembled a structure or position of that element by remote associations. For example: corona – **Cor**; arculum – **Ar**; buccula – **Bcl**; tempus – **Tm** and so on; 4) a Latin term for repeating elements (such as furrows, spines) was made up of two words: they took the main word (for example sulcus meaning *a furrow*) and added it to an attribute pointing out an element to which that sulcus belonged or the element it separated from another element. For example: sulcus glabellaris – **SG**; sulcus pygidialis – **SPyg**; sulcus rachialis – **SR**; sulcus occipitalis – **SO**; sulcus palpebralis – **SPal** and so on.

Several papers have been published in Russian using Latin terms (Zhuravleva and Rosova, 1977; Rosova *et al*., 1985; Lisogor *et al*., 1988; Varlamov *et al*., 2005), whereas in English there are only two (Varlamov *et al*., 2006; Makarova, this volume). Rosova and Rosov (1975) put forward a total of 290 Latin terms, which replace more than a thousand synonym terms describing trilobites in different languages: Russian, English, German, French, Spanish, Swedish and others.

Figures 1-3 show Latin terms of particular morphological elements.

Below we give just a small portion of the numerous synonyms used in the Russian literature, and one of the synonyms after almost each “termix” is taken from “Slovar morphologicheskih terminov i shema opisaniya trilobitov [*Dictionary of Morphological Terms and description scheme of trilobites*]” (Tchernyshova *et al*., 1982). Only one or two synonyms from English, German and French were employed. It is clear that if terms in other languages are applied, then this will expand the list of synonyms.

The list of Latin terms and their “termixes”[1]

“Termixes” and Latin terms are followed by synonym terms in Russian **(r)**, English **(e)**, German **(d)**, and French **(fr)**. In the cases where a Latin term is not followed by the synonym in any of the above languages, this means that the description consisting of a number of words is used instead of term.

A, area — **(r)** preglabellarnoe pole, preglabelnoe pole. **(e)** limb, frontal limb. **(d)** Vorglatzen feld (Richter and Richter 1940) (Fig. 1).

Ar, arculum — **(r)** kaima golovnogo tschita, frontalnaya kaima, perednyaya kraevaya kaima, perednyaya kaima, limb, kraevoi valik , kraevaya kaima cranidiya. **(e)** anterior border (Harrington *et al*., 1959). **(d)**

Stirnleiste (Barrande, 1868a); Kremple (Richter and Richter 1940). **(fr)** rebord frontal (Barrande, 1868b) (Fig. 1).

ArtPyg, artus pygidialis - **(r)** sotchlenovannoe polucoltso khvostovogo tschita, sotchlenovannoe polucoltso pygidiya. **(d)** Gelenkschuppe (Richter, 1912). **(fr)** denu – anneau articulaire (Hupe, 1953) (Fig. 1).

Bcl, buccula – **(r)** vnutreglaznoe pole, nepodvizhnaya tscheka, palpebralnaya tchast nepodvizhnoi tscheki. **(e)** palpebral area (of fixigena) (Harrington *et al*., 1959); fixed cheek (Howell *et al*., 1947) (Fig. 1).

C, cephala – **(r)** golovnoi tschit, cephalon, golova. **(e)** cephalon (Harrington *et al*., 1959). **(d)** Kopfschield (caput) (Zittel, 1881-1885); Kopf (Barrande, 1868a; Richter, 1912); caput (Dalman, 1828). **(fr)** tete (Barrande, 1868b) (Fig. 1).

Cor, corona – **(r)** frontalnii limb, frontalnaya tchast, perednyaya tchast cranidiya, limb, predglabelnaya tchast cranidiya. **(e)** frontal area (Harrington *et al*., 1959). **(d)** Rand, Stirnrandes (Barrande, 1868a). **(fr)** limbe, limbe frontal (Barrande, 1868b) (Fig. 1).

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[1] Total list of Latin terms and their “termixes” published in Rosova and Rosov (1975).

Cp, campus – **(r)** predglabelnoe pole, predglabelnoe prostranstvo, predglabelnaya plotschadka, predglabelnoe pole posredine. **(e)** praeglabellar field (20) (Fig. 1).

Cr, cranidium - **(r)** cranidii univ. **(e)** cranidium univ. **(d)** Mittelschild [scutum centrale (Zittel, 1881-1885)]; Festen Kopf, Mittelschild (Richter, 1912) (Fig. 1).

Schemes of polymer trilobite morphological elements.

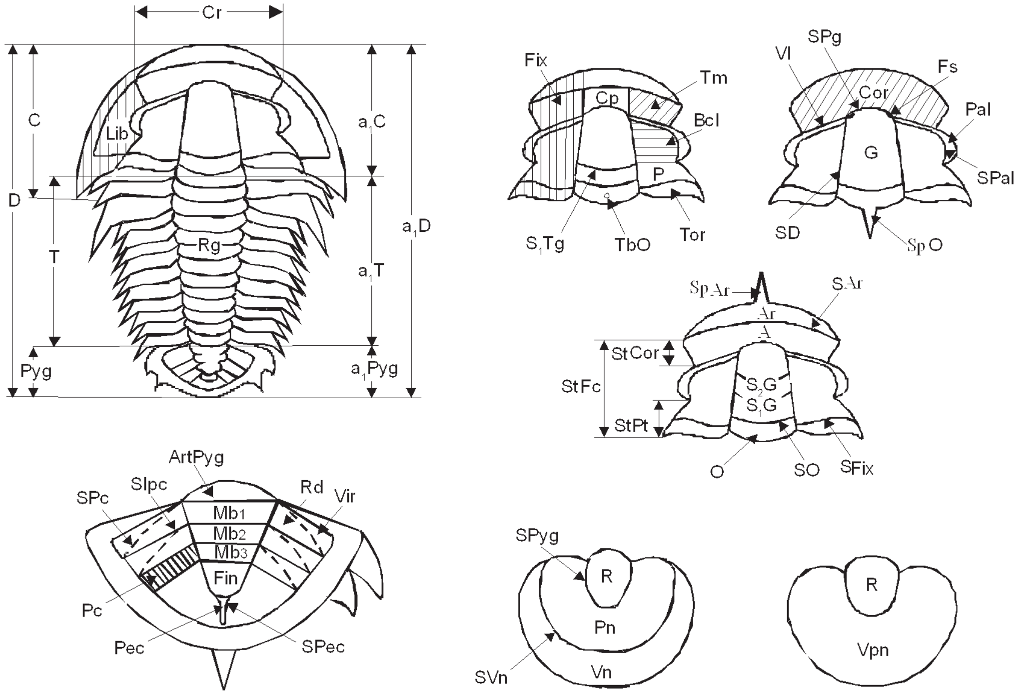

Figure 1. The main parts of **D** (dorsum), its sizes and the main elements of **Cr** (cranidium) and **Pyg** (pygidium).

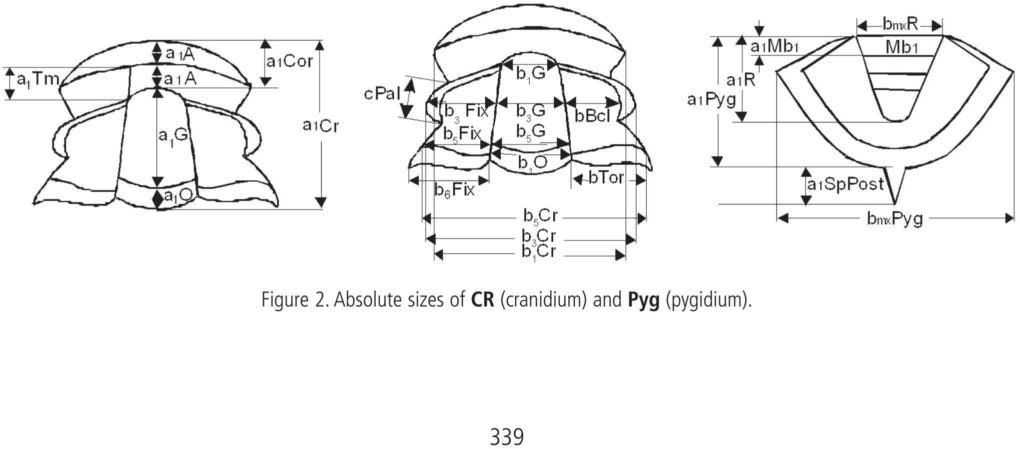

Figure 2. Absolute sizes of **CR** (cranidium) and **Pyg** (pygidium).

D, dorsum – **(r)** spinnoi tschit. **(e)** dorsal exoskeleton (Harrington *et al*., 1959). **(d)** Dorsalschale, Ruckenschale (Zittel, 1881-1885) (Fig. 1).

Fin, finis – **(r)** terminalnaya lopast, konechnaya tchast pigidiya, konechnaya lopast rahisa, zadnii uzkii konec rahisa. **(e)** terminal axial piece (or ring) (Harrington *et al*.,1959). **(fr)** piece terminale (Hupe, 1953) (Fig. 1).

Fix, fixigena – **(r)** nepodvizhnaya tscheka, tscheka. **(e)** fixigena (Harrington *et al*., 1959). **(d)** unbewegliche Wange (Barrande, 1868a); unbewegliche Theil der Wangen (jones fixed cheeks) (Zittel, 1881-1885); Fest Wange (Richter, 1912). **(fr)** joue fixe (Barrande, 1868b); fixigene (Hupe, 1953) (Fig. 1).

Fs, fossulae – **(r)** yamki spinnih borozd, perednie yamki, perednebokovie yamki, fossula. **(e)** anterior pit (Howell *et al*., 1947); fossula (Harrington *et al*., 1959) (Fig. 1).

G, glabella – **(r)** glabel univ. **(e)** hologlabella; glabella (Harrington *et al*., 1959; Howell *et al*., 1947). **(d)** Glabella (Barrande, 1868a); Glabella (Kopfbuckel) (Zittel,1881-1885); Glatze (Richter, 1912); Glabella (Prominentia frontalis) (Dalman, 1828). **(fr)** glabella (Barrande,1868b) (Fig. 1).

Lib, librigena – **(r)** podvizhnaya tscheka, svobodnaya tscheka. **(e)** free cheek (Harrington *et al*., 1959; Howell *et al*., 1947); librigena (Harrington *et al*., 1959). **(d)** beweglichen Wangen (Barrande, 1868a); Randschilder (scuta marginalia, joues mobiles, movable cheeks) (Zittel, 1881-1885); Frei Wange (Richter,1912). **(fr)** joue libre ou librigena, librigena (Hupe, 1953) (Fig. 1).

Mb, membrum – **(r)** coltso rahisa (u polimer), lopast (rahisa), osevoe kolco, segment rahisa. **(e)** axial ring (Harrington *et al*., 1959). **(fr)** anneaux axiaux (Hupe, 1953).

O, occiput – **(r)** zatylochnoe coltso univ. **(e)** occipital ring (Harrington *et al*., 1959; Howell *et al*., 1947). **(d)** der occipital Ring (Barrande, 1868a). **(fr)** l’ anneau occipital (Barrande,1868b) (Fig. 1).

P, planta - **(r)** zadnebokovaya lopast (cranidiya), zadnebokovaya lopast nepodvizhnoi tsheki (Fig. 1).

Pal, palpebra – **(r)** glaznie kryshki, palpebralnie lopasti. **(e)** palpebral lobe (Harrington *et al*., 1959; Howell *et al*., 1947). **(d)** Palpebral lobus (Barrande, 1868a); Augendeckel (Richter, 1912); Palpebralflugel (ala palpebralis) (Zittel, 1881-1885); lobus palpebralis (Dalman, 1828). **(fr)** lelobe palpebral (Barrande, 1868b; Hupe, 1953) (Fig. 1).

Pc, particular - **(r)** plevralnii segment, plevri pygidiya. **(d)** Pleura (Barrande, 1868a). **(fr)** plevre (Barrande, 1868b) (Fig. 1).

Pec, pecten - **(r)** osevaya poloska, terminalnii valik. **(e)** postaxial keel (Harrington *et al*., 1959). **(fr)** crete post-axiale (Hupe, 1953) (Fig. 1).

Pn, planum – (r) bokovye lopasti khvostovogo tschita. (Fig. 1).

Pyg, pigidium - **(r)** pygidii, khvostovoi tschit. **(e)** pygidium (Harrington *et al*., 1959). **(d)** Ischmanzchild (Pygidium) (Zittel, 1881-1885); Pygidium (Lobus scutum caudale) (Dalman, 1828) (Fig. 1).

R, rachis – **(r)** rahis, rahis pygidiya, os pygidiya. **(e)** axis of pygidium (Harrington *et al*., 1959). **(d)** axe (Barrande, 1868a); Spindel (Richter, 1912); Rhachis (Dalman, 1828); Rhachis caudalis (Lobus pygidii) (Dalman, 1828). **(fr)** axe (Barrande, 1868b); rachis ou axis (Hupe, 1953) (Fig. 1).

Rd, rudicula - **(e)** posterior pleural band (Harrington *et al*., 1959) (Fig. 1).

Rg, regula – **(r)** osevaya tchast tulovitscha, osevaya tchast (toraxa), rahis (tulovitscha). **(e)** axis (of thorax) (Harrington *et al*., 1959). **(d)** Spindel (Richter, 1912); Rhachis (Dalman, 1828) (Fig. 1).

S, sulcus – **(r)** borozda univ. **(e)** furrow univ. **(d)** Furche univ. **(fr)** sillon univ.

SAr, sulcus arcularis – **(r)** frontalnaya borozda, perednyaya kraevaya borozda, kraevaya borozda cranidiya. **(e)** anterior border furrow (of cephalon) (Harrington *et al*., 1959); marginal furrow (Howell *et al*., 1947). **(d)** Aussensaumfurche (Richter, 1912); Saumfurche (Richter and Richter, 1940). **(fr)** sillon frontal (Hupe, 1953) (Fig. 1).

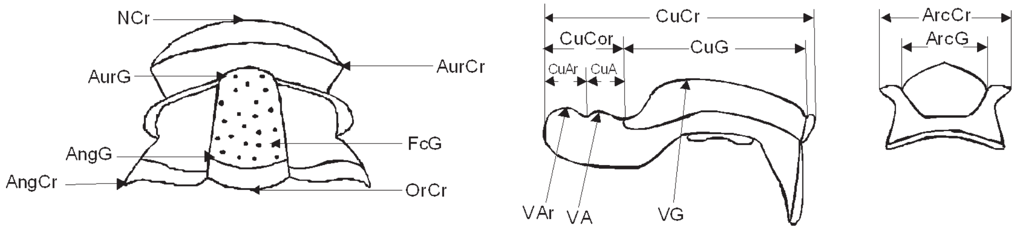

Figure 3. Additional terms for **Cr** (cranidium).

SD, sulcus dorsalis – **(r)** spinnaya borozda, spinnaya borozdka, dorzalnaya borozda, spinnaya borozda golovy. **(e)** axial furrow (Harrington *et al.*, 1959). **(d)** Ruckenfurchen (Barrande, 1868a); Dorsalfurchen (Zittel, 1881-1885). **(fr)** sillon dorsal (Barrande,1868b; Hupe,1953) (Fig. 1).

SFix, sulcus fixigenalis - **(r)** occipitalnaya borozda, zadnyaya kraevaya borozda, zadnebokovaya borozda. **(e)** posterior border furrow (of cephalon), posterior marginal furrow (Harrington *et al.*, 1959). **(d)** Occipitalfurche (sulcus occipitalis) (Zittel, 1881-1885); Hintersaumfurche (Richter, 1912). **(fr)** rainure (Barrande, 1868a); sillon posterieur (Hupe, 1953) (Fig. 1).

SG, sulcus glabellaris - **(r)** lunka, glabelarnie borozdki, borozdi glabeli, bokovie borozdi glabeli, poperechnie borozdi (glabeli), bazalnie borozdi glabeli. **(e)** lateral glabellar furrow, praeoccipital glabellar furrow (Harrington *et al.*, 1959). **(d)** Seitenfurchen (Barrande, 1868a; Richter, 1912); die hintere Furche (Barrande, 1868a). **(fr)** sillon posterieur (Barrande, 1868b); 1-4 sillons glabellaires (Hupe, 1953); sillon lateral (Barrande, 1868b) (Fig. 1).

SIpc, sulcus interparticularis - **(r)** mezhplevralnaya borozda, interplevralnie borozdi. **(e)** interpleural groove, interpleural furrow, rib furrow (Harrington *et al.*, 1959). **(d)** Nahtfurche (Richter, 1912). **(fr)** sillon interpleural (Hupe, 1953) (Fig. 1).

SO, sulcus occipitalis - **(r)** zatylochnaya borozda univ. **(e)** occipital furrow (Harrington *et al.*, 1959; Howell *et al.*, 1947). **(d)** Occipital Furche (Barrande, 1868a); Nackenfurche (Richter, 1912). **(fr)** sillon occipital (Barrande, 1868b; Hupe, 1953) (Fig. 1).

SPal, sulcus palpebralis - **(r)** glaznaya borozda, palpebralnaya borozda. **(e)** palpebral furrow (Barrande, 1868a; Howell *et al.*, 1947). **(d)** Deckelfurche (Richter, 1912). **(fr)** sillon palpebral (Hupe, 1953) (Fig. 1).

SPc, sulcus particularis - **(r)** mezhrebernaya borozda, plevralnaya borozda. **(d)** Schagfurche (Richter, 1912). **(fr)** sillon pleural (Hupe, 1953) (Fig.1).

SPec, sulcus pectinis - **(r)** zaosevaya borozdka, plevralnaya borozda khvostovogo tschita. **(e)** postaxial furrow (Harrington *et al.*, 1959) (Fig. 1).

SPg, sulcus preglabellaris - **(r)** predglabelyarnaya borozda, predglabelnaya borozda. **(e)** praeglabellar furrow (Harrington *et al.*, 1959). **(d)** Stirnliche Ruckenfurche (Richter and Richter, 1940). **(fr)** sillon praeglabellaire (Hupe, 1953) (Fig. 1).

SPyg, sulcus pygidialis - **(r)** spinnie borozdi (pygidiya). **(e)** axial furrow (Harrington *et al.*, 1959) (Fig. 1).

STg, sulcus transglabellaris - **(r)** transglabelyarnaya borozda, poperechnaya borozda (glabeli). **(e)** transglabellar furrow (Harrington *et al.*, 1959) (Fig. 1).

SVn, sulcus vincularis - **(r)** kraevaya borozda khvostovogo tschita, kraevaya borozda pygidiya. **(e)** inner margin of doublure (Harrington *et al.*, 1959). **(d)** Saumfurche (Richter, 1912) (Fig. 1).

Sp, spina – **(r)** ship univ. **(e)** spine (Harrington *et al*., 1959). **(d)** Dorn (Zittel, 1881-1885).

SpAr, spina arcularis (Fig. 1)

SpO, spina occipitalis – **(r)** zatylotchnii ship univ. **(e)** occipital spine (Harrington *et al*., 1959; Howell, *et al*., 1947). **(fr)** spine occipitale (Hupe, 1953) (Fig.1).

StCor, sutura coronalis - **(r)** perednie vetvi litcevogo schva univ. **(e)** anterior section (of facial suture) (Harrington *et al*., 1959). **(fr)** branche anterieure (Hupe, 1953) (Fig. 1).

StFc, suture facialis – **(r)** litcevoi schov. **(e)** facial suture (Harrington *et al*., 1959; Howell *et al*., 1947). **(d)** Gesichtnaht (Barrande, 1868a; Richter, 1912); Gesichtnaht (sutura facialis) (Zitte, 1881-1885); sutura (Dalman, 1828). **(fr)** suture faciale (Barrande, 1868b); trace dela suture faciale (Hupe, 1953) (Fig. 1).

StPt, sutura plantoralis – **(r)** zadnie vetvi litcevogo schva. **(e)** posterior section (of facial suture) (Harrington *et al*., 1959). **(fr)** branche posterieure (Hupe, 1953) (Fig. 1).

T, thorax – **(r)** tulovitschnii otdel, tulovitsche, torax. **(e)** thoracic region (Harrington *et al*., 1959). **(d)** Rumpf (thorax) (Zittel, 1881-1885) (Fig. 1).

Tb, tuberculum – **(e)** – tubercle.

TbO, tuberculum occipitale – **(r)** zatylochnii bugorok, bugorok, sredinnii bugorok. **(e)** occipital node (Harrington *et al*., 1959; Howell *et al*. 1947). **(d)** Nackenknotche (Richter, 1912). **(fr)** tubercule occipitale (Hupe, 1953) (Fig. 1).

Tm, tempus – **(r)** bokovie utchastki (frontalnogo limba), bokovie utchastki frontalnogo polya, bokovaya plotschadka frontalnogo limba, perednebokovie utchastki tschek. **(e)** anterior area (of fixigena) (Harrington *et al*., 1959) (Fig. 1).

Tor, torus – **(r)** zadnii valik tschek, zadnyaya kaima golovnogo tschita, zadnebokovaya kaima, zadnyaya kaima, zadnyaya kraevaya kaima, okcipitalnoe coltso, okcipitalnie valiki. **(e)** posterior border (Harrington *et al*., 1959). **(d)** hinter Wangenrand, hinter Rand der Wangen (Barrande, 1868a); Hintersaum (Richter, 1912); occipital ring (annulus occipitalis) (Zittel, 1881-1885); Truncus (Dalman, 1828). **(fr)** le bord posterior des joues (Barrande, 1868b) (Fig. 1).

Vir, virgula (Fig. 1)

Vl, vallum – **(r)** glaznie valiki, palpebralnii valik, valik glaza, glaznoi valik. **(e)** eye ridge (Harrington *et al*., 1959). **(d)** Augenleiste (Richter and Richter, 1940). **(fr)** crete ou ligne oculaire (Hupe,1953) (Fig. 1).

Vn, vinculum – **(r)** kaima khvostovogo tschita, kaima, kaima pygidiya, kraevaya kaima khvostovogo tschita, kaima (pygidiya). **(fr)** limbe ou bordure (Hupe, 1953) (Fig. 1).

Vpn, viplanum - **(r)** boka pygidiya, plevralnaya tchast khvostovogo tschita, plevralnaya tchast pygidiya. **(fr)** plevres (Hupe, 1953) (Fig. 1).

Additional Terms (Fig. 3)

Ang, angulus – the posterolateral angle of any element: **AngCr**, **AngG**, **AngCor**, and so on.

Arc, arcus – the transverse section of any element: **ArcCr**, **ArcG**, **ArcCor**, and so on.

Aur, auricular – the ventrolateral angle of any element: **AurCr**, **AurG**, **AurCor**, and so on.

Cu, curvature – the longitudinal profile of any element: **CuCr**, **CuG**, **CuCor**, and so on.

Fc, facies – the surface of any element: **FcCr**, **FcG**, **FcCor**, and so on.

N, nasus – the anterior end of any element: **NCr**, **NG**, **NCor**, **NPal**, **NR**, and so on.

Or, ora – the posterior end of any element: **OrCr, OrG**, **OrO**, **OrPal**, **OrR**, and so on.

V, vertex– the vertex of any element: **VCr**, **VG**, **VCor**, **VBcl**, and so on.

The main measurements of dorsum elements (Figs. 1 and 2)

a_1 – all sizes measured along axis **D** (dorsum).
b – all sizes measured transversely to axis **D** (dorsum).
cPal – all sizes measured at an angle to axis **D** (dorsum).

CONCLUSIONS

Latin is the international language of science. We hereby propose to use "termixes", abbreviations of Latin terms for the morphological elements of trilobites.

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LOWER DEVONIAN AULACOPLEURID TRILOBITES FROM ARGENTINA

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Keywords: Talacasto, Devonian, Aulacopleurids, Argentina.

INTRODUCTION

Aulacopleurids are widespread, frequent and diverse elements with long stratigraphic ranges (Ordovician-Devonian) out of the Malvinokaffric Realm. Nevertheless, their Malvinokaffric record almost exclusively restricted to the Devonian, is scattered and of low diversity. Due to this particularity and, probably, to the fragmentary nature of the type material, and the lack of proper illustrations and detailed studies, the only two genera recognized (*Malimanaspis* Baldis and Longobucco, 1977 and *Maurotarion* Alberti, 1969) (Adrain and Edgecombe, 1996), have received secondary attention, and no specific investigations have been carried out after the excellent review performed by Adrain and Edgecombe (1996).

The principal controversies about these faunas include their origin, their role in evolutionary events, and their paleobiogeographic significance (Elredge and Ormiston, 1979; Elredge and Braniša, 1980; Lieberman, 1993).

Lower and Middle Devonian information about *Maurotarion* from Bolivia is of great significance, accounting for a monophyletic small-scale radiation hypothesis that involves five formally nominated species, separated in two informal groups (Adrain and Edgecombe, 1996). The origin of this clade has been explained by means of two independent migration events of cosmopolitan groups from low latitudes, one for Lochkovian-Pragian and the other during the Emsian, that were be interpreted to represent cladogenetic pulses, according to Adrain and Edgecombe (1996).

Nevertheless, new evidences from eastern Bolivia confirm the presence of *Maurotarion* in South America already for the Silurian, questioning the nature and age of this evolutionary event (Edgecombe and Fortey, 2000).

A sixth Emsian species from the Bokkeveld group of South Africa, of discussed affinities to the proposed informal groups, completes the list of known Malvinokaffric *Maurotarion* species up to the present (Cooper, 1982; Adrain and Edgecombe, 1996)

In this scenario, the knowledge of Aulacopleurids from Argentina is very relevant. However, *Malimanaspis sarudianskii* (Baldis and Longobucco, 1977), Middle-Upper Devonian in age, from the

Chigua Formation in western Precordillera is the only one Aulacopleurid described from this country. Unfortunately, this species is known from a single specimen poorly illustrated, and thus several diagnostic features are obscured.

In this contribution the record of Lower Devonian Aulacopleurid trilobites from the Talacasto Formation in the Argentine Precordillera, is documented.

A detailed taxonomic study based upon abundant and well preserved materials as well as related evolutionary implications is now in progress. Hence, systematic aspects and evolutionary significance of these new faunas are preliminary analyzed herein.

MATERIALS

The Talacasto Formation is a classical, widespread lower Devonian unit from Argentine Precordillera, and has been dated as Early Lochkovian-Late Emsian, based on its rich brachiopod fauna (Herrera,1991,1993). It consists of a dominantly shaly succession at the base and a mainly psamitic succession toward the top, and was interpreted as deposited in a shallow muddy shelf under the fluvial influence (Astini,1991).

The Aulacopleurid material comes from several sections of the Talacasto Formation in San Juan Province: Río Talacasto, La Chilca, and Loma de Los Piojos (Fig. 1), and it mostly consist on molds, although occasionally shell remains are preserved.

So far, six species assigned to *Maurotarion* are recognized. They are closely related with congenerics from Bolivia and South Africa. Two species recovered from the Río Talacasto section, Early Lochkovian in age, probably are the most ancient Devonian Aulacopleurids for the Malvinokaffric Realm. The remainder taxa come principally from the Loma de Los Piojos section, and belong to the brachiopod assemblage zone B (Herrera, 1991) of Pragian age (Fig. 2). Together with the latter, other trilobites resembling assemblages recognized in the *Scaphiocoelia* zone from Bolivia

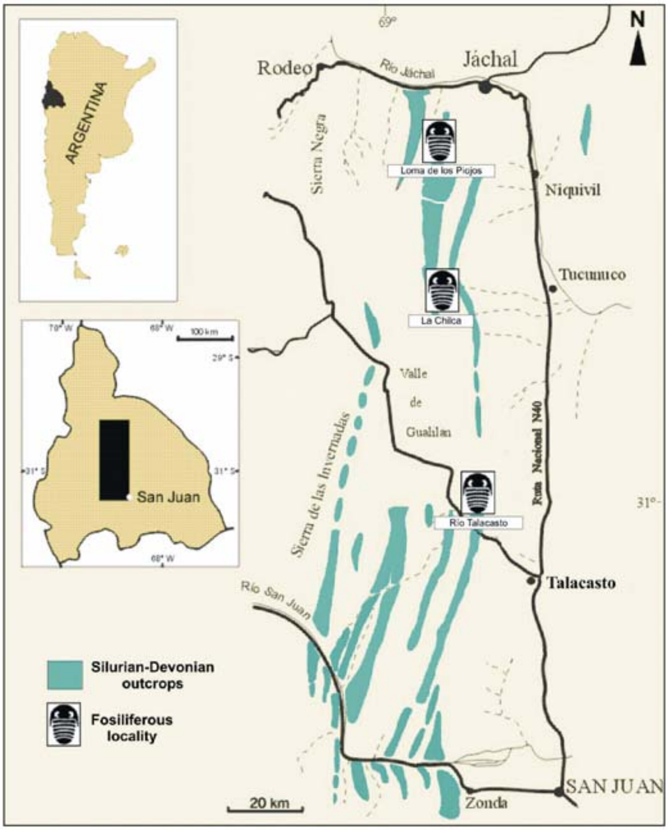

Figure 1. Location of Silurian-Devonian outcrops at eastern Argentine Precordillera, and fosiliferous localities with Devonian Aulacopleurids.

(Vaccari *et al.*,1994; Racheboeuf *et al.*, 1993, 1998) occur. In this stage of research, it is still not possible to confirm the presence of Aulacopleurids in Emsian levels.

All these species share the single prominent apomorphy indicated for Malvinokaffric *Maurotarion:* the extreme posterior expansion of the posterior and lateral librigenal borders, and the base of the genal spine (Adrain and Edgecombe, 1996).

They also exhibit a reduction of the ornamentation, the cephalic border usually flat and expanded forward, wide glabellae with often angular outline, effacement of the lateral border furrow, long wide and flat genal spines, absence of thoracic spines in the sixth segment, a constant number of 14 thoracic segments, and small pygidia.

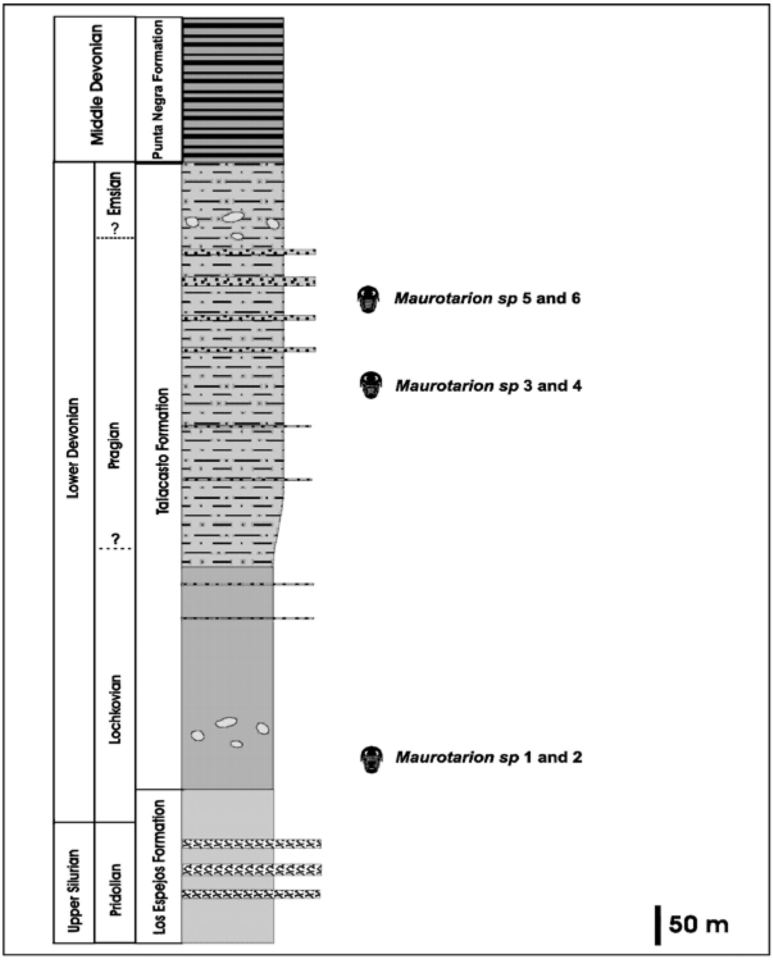

Figure 2. Schematic stratigraphic column of the Talacasto Formation, with references of Aulacopleurids position.

DISCUSSION

According to Adrain and Edgecombe (1996) expanded genal spines bases and wide posterior and lateral librigenal borders relate Bolivian *Maurotarion* with *M. periergum* (Haas, 1969) as a sister group of this subclade. At first glance, these apomorphies are also present in Argentine *Maurotarion* species, nevertheless, greater precisions based upon detailed morphologic studies now in progress would possible alter this proposed ancestry relation.

The Bolivian monophyletic radiation recorded in Altiplano and Tarija has been dated as post-Upper Lochkovian (Adrain and Edgecombe, 1996); nevertheless, the presence of *Maurotarion* in the late Silurian (Pridolian?) of eastern Bolivia (Edgecombe and Fortey, 2000), suggest an earlier age for this event. The early Lochkovian age of the oldest Argentine *Maurotarion* species, is in agreement with eastern Bolivia information.

The diversity of Argentine forms, their stratigraphic constrained data, and the morphological evidences, suggest that a diversification event within this subgroup of *Maurotarion* took place. Their relationship with Bolivian records, probably implies a more extended South American event.

These macroevolutionary events might be related with similar ones documented among other broadly coeval trilobite groups in these basins; for example, the paradigmatic event of the family Calmoniidae (Elredge and Ormiston, 1979; Elredge and Braniša, 1980; Lieberman, 1993; Vaccari *et al.*, 1994).

Several important aspects such as the cladogenetic structure of the event, phylogenetic relationships among proposed informal groups, the nature and age of possible migratory or exchange events and other significant aspects will be investigated and discussed in further contributions.

CONCLUSIONS

Our new records suggest that the diversity of Lower Devonian Argentine Aulacopleurids (with at least 6 taxa of specific level for *Maurotarion*) would to be comparable to that of the remainder of the Malvinokaffric Realm.

This one among other evidences would indicate a more ancient and complex South American Aulacopleurid diversification event (Pridolian? – Emsian) than previously thought, principally registered in Argentina and Bolivia.

The unravelling of evolutionary and phylogenetic aspects of these new faunas, would result of great importance in the discussion of similar events proposed for other trilobite groups in broadly similar times.

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DID THE TRABECULA IN PHACOPID LENSES ACT AS LIGHT-GUIDES?

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Keywords: Trilobite eye, visual system, internal reflection, light-guide bundles, schizochroal, trabecula.

Compound eyes are primary structures in arthropods, and are known in the most ancient trilobites of all. The earliest and plesiomorphic type is the *holochroal eye* (Fig. 1a), in which a few to several thousand lenses, contiguous and closely packed, are covered by a single pellucid corneal membrane. Such eyes ere found in most trilobites, from Lower Cambrian to Upper Permian. The tiny *abathochroal eye* (Fig. 1c) has separate lenses, each probably with its own cornea; it is restricted to the Lower to Middle Cambrian Eodiscina. As with the third type *schizochroal* eyes (Fig. 1b), these were derived by paedomorphosis from a holochroal precursor. Schizochroal eyes are found only in the Lower Ordovician to Upper Devonian Phacopina. They have usually fewer lenses than have holochroal eyes, but of significantly greater diameter (<1mm). Each lens is separate and has its own cornea; it is set at the summit of a cavity (alveolus) in the surrounding cuticle (sclera). In all trilobites the lenses are formed from primary calcite, which has the virtue of being transparent, but it is highly birefringent, and although the c-axis is normally aligned normal to the principal plane of the lens, any light rays travelling obliquely to this would produce ghost images.

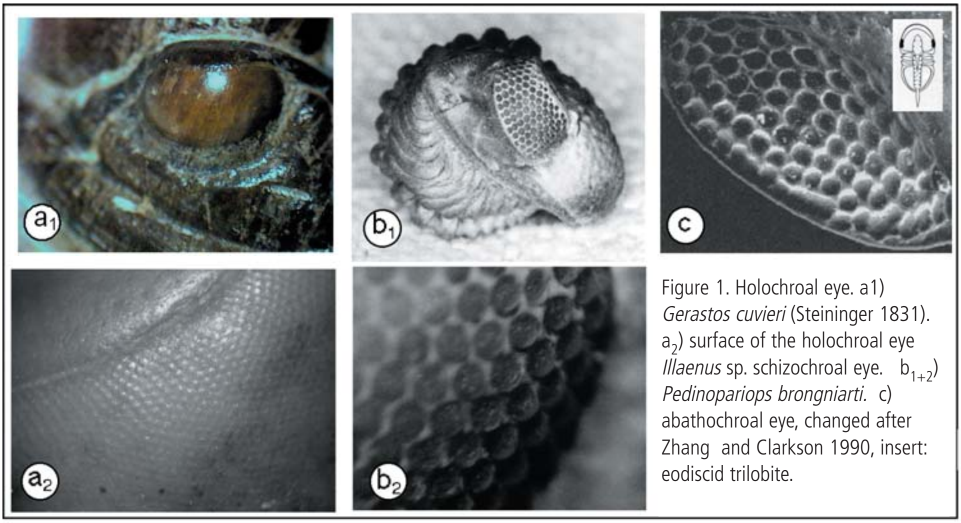

Figure 1. Holochroal eye. a1) *Gerastos cuvieri* (Steininger 1831). a_2) surface of the holochroal eye *Illaenus* sp. schizochroal eye. b_{1+2}) *Pedinopariops brongniarti.* c) abathochroal eye, changed after Zhang and Clarkson 1990, insert: eodiscid trilobite.

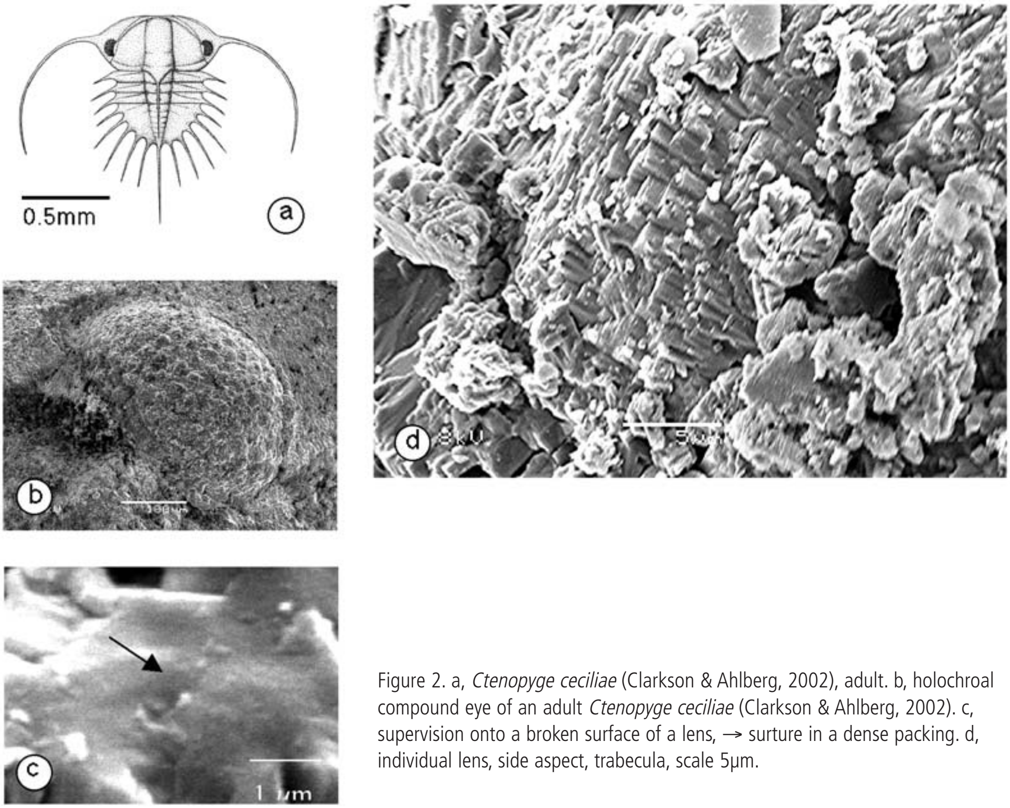

Figure 2. a, *Ctenopyge ceciliae* (Clarkson & Ahlberg, 2002), adult. b, holochroal compound eye of an adult *Ctenopyge ceciliae* (Clarkson & Ahlberg, 2002). c, supervision onto a broken surface of a lens, → surture in a dense packing. d, individual lens, side aspect, trabecula, scale 5μm.

In all trilobite eyes investigated, the lenses are constructed of microcrystallites of calcite, the trabeculae (~20μm), running vertically through the lens and fanning outwards towards the inner and sometimes the outer surfaces (Clarkson, 1979, 1997; Miller and Clarkson, 1980). Such trabeculae are illustrated here in the tiny holochroal eye of *Ctenopyge ceciliae* (Clarkson and Ahlberg, 2002) (Fig. 2 a-d) SEM analysis reveals that the trabecula remain very narrow in the holochroal lens, if not fused together so that they become optically one unit, as to be seen in Fig. 2 c. In this figure the upper surfaces of some trabecula of a broken lens shown here appear as a homogenous complex, whether this is original or a diagenetic effect is as yet unclear.

In phacopid eyes the structure of the trabeculae has been amply confirmed by Lee *et al.* (2007). In *Geesops* the trabecula fan outwards both to the outer and inner surfaces of the lens, widening slightly as they do so. In these thin sections very narrow spaces are visible between trabecula, which may have been enhanced by elutriation during diagenesis. During growth the trabecula were built by horizontal organic layers (Bruton and Haas, 2003), and it seems highly probable that the spaces between the trabecula were filled with organic material, readily destroyed after the death of the trilobite. If this was so, each of the trabecula, calcitic microcrystallites with a refractive index of 1.658 to 1.486, was surrounded by a thin film of organic material (e.g. body fluid with a refractive index of ~1.3). The optical characteristics of this

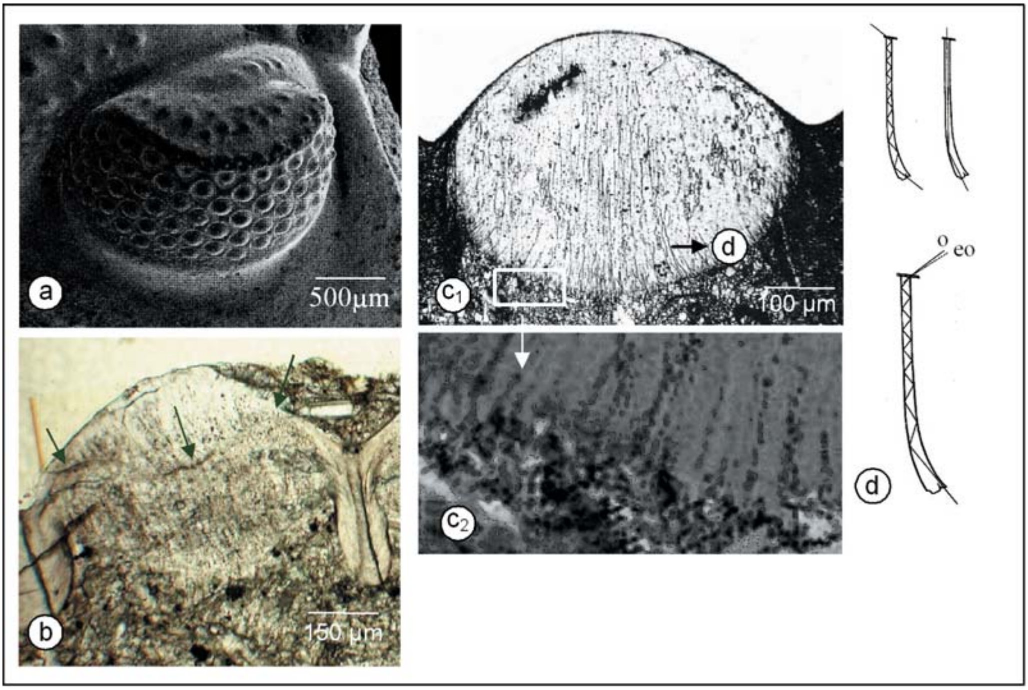

Figure 3. a) SEM eye of phacopid trilobite *Geesops schlotheimi* (Bronn, 1825) b) thinsection of lens of *Geesops schlotheimi*, → indicating the intralensar bowl as denser material. The lens is slightly distorted, the dark line-structures inside of the lens show the trabecula. c1) EBSD-scan of a lens of *Dalmanites* sp., showing the trabecula and the hollowspaces in between (dark structures). c2) lower rim of lens c1), trabecula showing at their proximal end. d) Total reflection inside of a trabeculum o: ordinary ray, eo: extraordinary ray. b) courtesy A. Owen and colleagues, c1) changed after Lee *et al*. (2007), the *Geesops* material courtesy H. Prescher.

system are total internal reflection of the incident light inside an angle to the optical axis of +/- 47.2° (ordinary ray), +/- 52.6° (extraordinary ray) (Fig. 3d), while more obliquely entering rays would pass right through the system on the other side of the protruding lens. The resulting image would thus be 'pixeled' and the resolution of the image would depend on the number of trabecula. Due to the narrow angle of capturing light, each "lens", or more exactly light-guide bundle, has a quite narrow opening angle due to its straight directional characteristics, while the opening angle of the entire "lens" determines the distance of the individual "lenses". These are arranged on a curved visual surface, ensuring in total a wide field of view. Because each "lens" probably has an individual retina some distance below, the images of the individual systems must finally be combined neuronally to a single coherent image. This is consistent with Schoenemann's (2007) hypothesis that the phacopid eye acted as a neural superposition system. Furthermore, this light-guide system gets rid of problems caused through birefringence. The phacopid lens, therefore, despite its shape, does not function as a refracting lens but as a bundle of light guides.

It has long been known that phacopid lenses are doublets, with an upper lens unit interlocking with an intralensar bowl. In some cases at least there is a central core as well. Clarkson and Levi-Setti (1975) showed how, if the bowl had a lower refractive index (1.3) than the upper unit (1.6), light would focus perfectly. Recent work by Lee *et al.* (2007) has confirmed the existence of these internal structures [previously doubted by Bruton and Haas (2003)]. It was shown that the bowl and core have a greater proportion of minerals, especially magnesium (Lee *et al*., 2007). This leads to a higher refractive index than of the upper lens unit. To what extent this reflects the original chemistry of the internal parts of the lens is not clear, and therefore our interpretations have to be tentative until more is known. Possibly due to their higher refractive index the bowl and core have the effect of slowing the light in various parts of the lens, so that despite the different lengths of the trabecula, the captured light rays arrive at the underlying photoreceptors all at the same time, which is in accordance with the idea of Bruton and Haas (2003) of index gradients inside of the lens.

This is a new and radical interpretation of the functioning of the phacopid eye, working not with usual light refracting lenses but with light-guide bundles, and needs to be sustained by further work on this extraordinary visual system, unique in the animal kingdom. But it explains the hitherto unsolved riddle how they managed the problems due to birefringence.

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SUBLENSAR CAPSULES IN PHACOPID EYES

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Keywords: Phacopid eyes, visual unit, eye system, schizochroal, ommatidium, ocellus, trilobite eye.

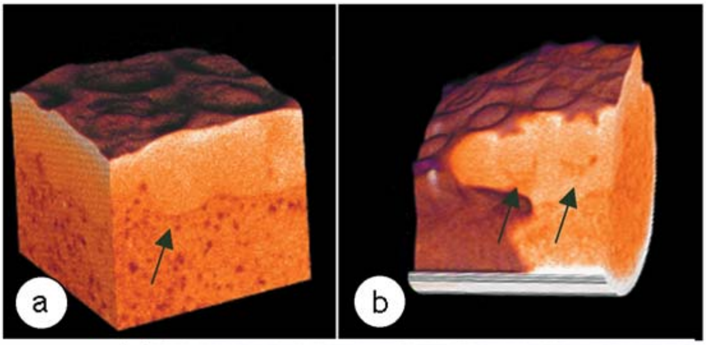
Although eyes are commonly preserved in trilobites, all that is normally retained is the calcareous lens array, and very little is known of the photoreceptive units which originally lay below the surface.

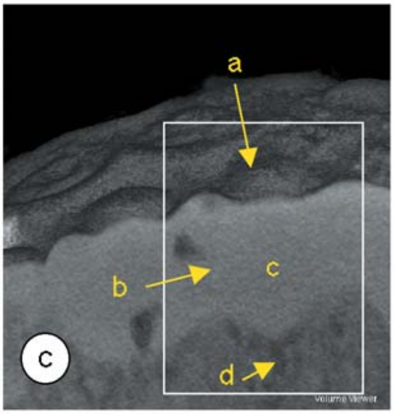
Holochroal eyes, which are the original type, found in the earliest trilobites, have many, small contiguous lenses, covered by a thin continuous pellucid membrane. They appear very similar externally to the eyes of living insects and crustaceans, and it is generally accepted that an apposition-type ommatidium lay below each lens.

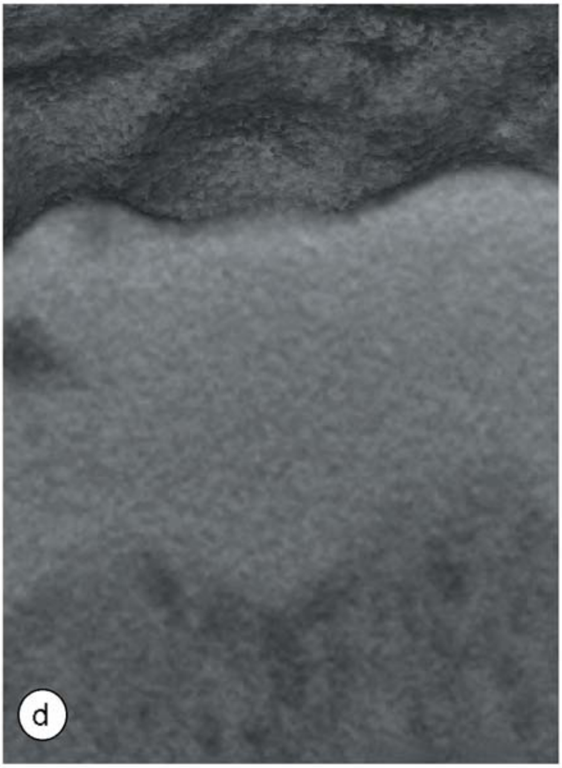
The schizochroal eyes of phacopid trilobites, however, have larger and fewer lenses, separated from each other by interlensar sclera, structurally similar to other parts of the exoskeleton. These eyes are very different from holochroal eyes, from which they were derived by paedomorphosis, and most authorities (Campbell, 1975; Clarkson, 1979, 1997; Fordyce and Cronin, 1993; Schoenemann, 2007) have postulated that rather than an ommatidium underlying each lens, there was some kind of sublensar capsule, floored by a retina of numerous photoreceptive cells. Whereas this was proposed on functional grounds, there is some structural evidence, albeit limited from sections made through the eyes of well-preserved Bohemian phacopids, the Silurian '*Phacops*' *fecundus* Barrande, the Devonian *Reedops cephalotes* Barrande (Clarkson, 1967, 1969) and *Pedinoparios broongniarti* Steininger from Gees, Germany (Bruton and Hass, 2003).

As has long been known, the thin corneal membrane overlying each phacopid lens as far as its margin, continues though the interlensar sclera as a cylindrical ring, which normally terminates at the inner surface of the sclera. In a single instance, in one specimen of *P. fecundus* this membrane is prolonged below the lens as a subcylindrical capsule with a flat floor. A similar structure is present in a solitary specimen of *R. cephalotes*, but the floor is missing; the interior is filled with sparry calcite, while a more or less hemispheric capsule is observed in *Pedinopariops brongniarti* Steininger. Only these examples are so far known.

Figure 1. a,b) 3D cubes showing sections of Geesops schlotheimi (Bronn, 1825) (upper parts of the lenses partly missing) arrows indicating the intralensar bowls (3D x-ray tomography, false-colour images).







c) The visual unit,
high resolution 3D x-ray tomographical images
of an eye of Geesops schlotheimi (Bronn 1825)

a lens
b interlensar sclera
c visual unit
d trace of an efferent structure?

d) section of a), white rectangle

Here we present further evidence for sublensar structures in *Geesops schlotheimi* (Bronn, 1825) from the Middle Devonian of the Eifel region, Germany, as revealed by high resolution 3D x-ray tomography (3D-µCT). The false-colour images (Fig. 2) and Fig. 1 show several cylindrical capsules, each with a rounded proximal termination and lying below an individual lens. These are picked out in bright yellow; they are all of the same overall form and extend a short distance below the inner margin of the sclera. Figs. 3a2 and 3b2 show the capsule even more clearly; the actual membrane or a 'ghost' thereof is picked out distinctly as a white band. This gives a good impression of the actual shape of the capsule, a slightly tapering cylinder

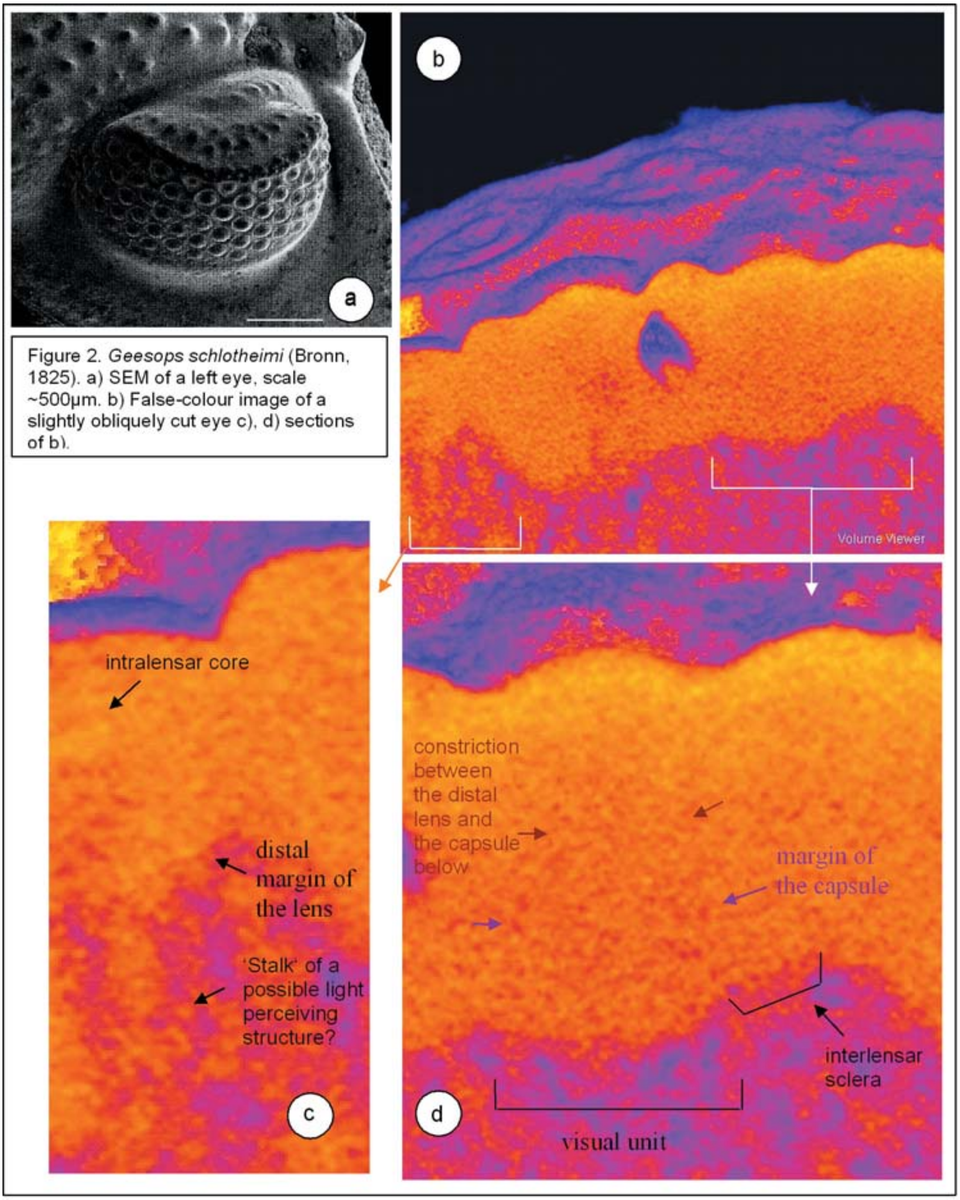


Figure 2. *Geesops schlotheimi* (Bronn, 1825). a) SEM of a left eye, scale ~500µm. b) False-colour image of a slightly obliquely cut eye c), d) sections of b).

Figure 2. *Geesops schlotheimi* (Bronn, 1825). a) SEM of a left eye, scale ~500µm. b) False-colour image of a slightly obliquely cut eye c), d) sections of b).

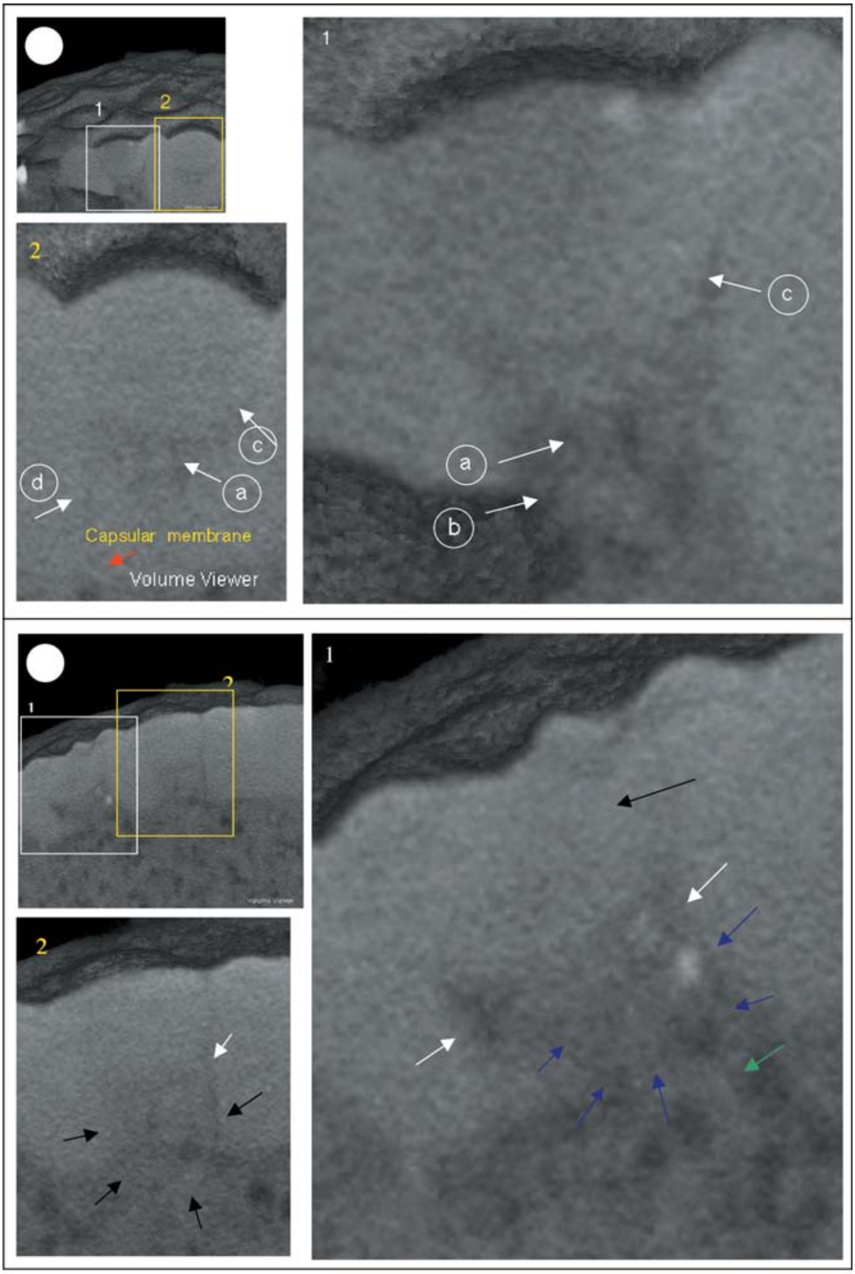


Figure 3. High resolution 3D x-ray tomography: a) and b) different sections of an eye of *Geesops schlotheimi* (Bronn, 1825), slightly obliquely cut, inserted rectangle indicate the magnifications. a) Centrally cut visual unit; a, 'stalk'-like structure below the lens; b, collar-like structure of spherical units; c, margin of the lens; d, capsule membrane. b) More peripheral cut visual unit; black arrows indicate the capsule, white arrows the sublensar structure, which encloses the 'stalk'. It is to be seen below a cuplike unit (blue arrows), green arrow: traces of efferent structure?

with a rounded base. Other internal structures are indicated and further tomography should reveal further details of sublensar structures, which should enable the functioning of the phacopid schizochroal eye, unique in the animal kingdom, to be more fully understood.

Acknowledgements and material

Geesops schlotheimi (Bronn, 1825), Middle Devonian, Ahrdorf Formation, Flesten Member, Salmerweg near to Gees, Germany. We greatly thank Fraunhofer Institut für Zerstörungsfreie Prüfverfahren (IZFP), Dresden for the support in 3D-μCT, H. Prescher for the trilobite material.

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A FURONGIAN POLYMERID PLANKTONIC TRILOBITE

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The invasion of the planktonic realm by adult polymerids was rare and sporadic during Cambrian times, although their juvenile stages may well have inhabited the plankton. Even pelagic Cambrian trilobites were uncommon, a recent convincing record before the Ordovician is *Beishanella* (Fortey and Rushton, 2007). Opinion is still divided as to whether the miomerids, with few thoracic segments (the agnostoids and eodiscoids) were planktonic (Robison, 1972), but accumulating evidence suggests that they were benthic too (Whittington, 1997; Chatterton and Speyer, 1997). A few Cambrian polymerids have beem thought to be planktonic, for example the tiny corynexochid *Thoracocare* (Robison and Campbell, 1974) and the burlingiids (e.g. Ebbestad and Budd, 2002), but such a habit was never claimed as certain. Other small arthropods inhabited the plankton from Lower Cambrian onwards (Butterfield, 2001). Here we report upon a miniaturised Furongian (upper Cambrian) olenid from Sweden, one of the smallest trilobites known, which we interpret as possibly the earliest unequivocally planktonic trilobite. The evidence for this mode of life comes from two sources, the optics of the visual system, and the extreme spinosity of the tiny body.

Ctenopyge ceciliae (Clarkson and Ahlberg, 2002) occurs in great numbers, at one locality only, in calcareous concretions found in a stream bed at Röstånga, in Skåne, Sweden. From the associated fauna it belongs to the *Peltura scarabaeoides* Zone. It is known only from disarticulated sclerites, and probably had no more than a few thoracic segments; here it is reconstructed with three, and although provisional, this restoration seems functionally realistic (Fig. 1). This miniature form was probably derived by progenesis from a normal-sized representative of the genus; even the earliest ontogenetic stages are exceptionally small, and the whole ontogeny is much compressed.

The mature *Ctenopyge ceciliae* has well-preserved reniform and holochroal compound eyes with about 150 calcitic lenses, the smallest juvenile eye has only about 10 and various intermediate stages of eye development are known (Fig. 2). Since the adult is tiny, the eyes are also exceptionally small, which raises the question of how they functioned. The application of the known laws of optics has considerable potential for addressing this vital question, even though only the lens array is preserved, and not the

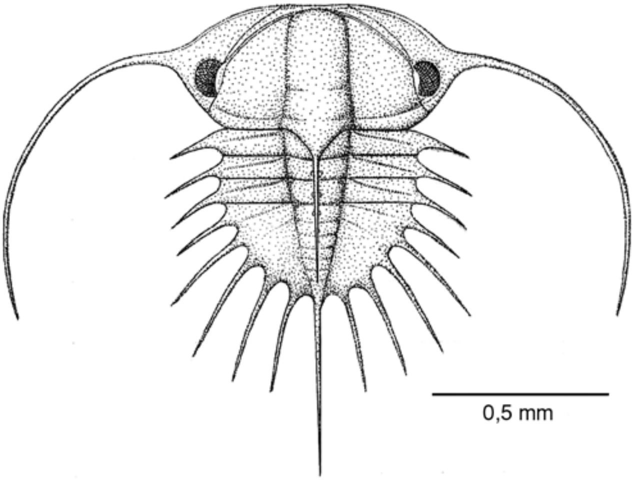

Figure 1. *Ctenopyge ceciliae* (Clarkson and Ahlberg, 2002), adult.

underlying structure. SEM photography has revealed that the lenses, some 21.33 +/- 2.39 µm in diameter (D), do not increase with growth and are much the same size in the smallest eyes as they are in the adult (Fig. 3a) Yet they are larger than they might be, for many arthropods have smaller lenses, as for example in the midge *Culex pipiens* (Linné, 1758) where the diameter is no more than 16µm. This indicates that the eyes of *Ctenopyge ceciliae*, even in the juveniles, are constructed to see; the visual system is not reduced in any way and remains a true compound eye. Since the material is largely undistorted it has proved possible to estimate the interommatidial angle $\Delta\varphi$ for various growth stages even though the packing of the lenses on the visual surface is not perfectly regular.

The thin, biconvex lenses, with the upper surface more convex than the lower, have a high refractive index (n=1.66 for calcite) and are functional in sea water, which a chitinous lens would not be. In Recent marine arthropods, the 'lenses' have planar surfaces and are never biconvex. With growth $\Delta\varphi$ decreases (Fig. 3b) and whereas the number of 'pixels', (represented by the lenses) increases, acuity improves only to a limited degree in the mature trilobite. This indicates that an optimal sensitivity was already established in the juvenile eye, which was not improved on with growth. As in all kinds of eyes, there is a trade-off between acuity and the brightness of the image, and the eyes of *Ctenopyge ceciliae* would only function in a well-lit environment, in other words in the uppermost waters of the sea. In the juvenile stages, they were not image formers, but worked as light detectors. The convex visual surface subtends a broad field of view, and even in the early stages the eye could detect the direction of light, of an object and its related movement, and would enable its bearer to stay within the photic zone. A somewhat improved acuity in the later stages of development would have enabled a better discrimination of the environment, and the recognition of social partners and other patterns.

Miniaturisation (*sensu* Fortey and Owens, 1990) would be in many instances a useful prerequisite for colonising the planktonic realm. Previously (Clarkson and Ahlberg, 2002), this minute trilobite was interpreted as planktonic on account of the very long spines, where the viscosity of the water relative to the dimensions of the animal is high. Study of the optical system greatly strengthens this interpretation: *Ctenopyge ceciliae* was a planktonic filter-feeder, and possibly the earliest known of all trilobites to

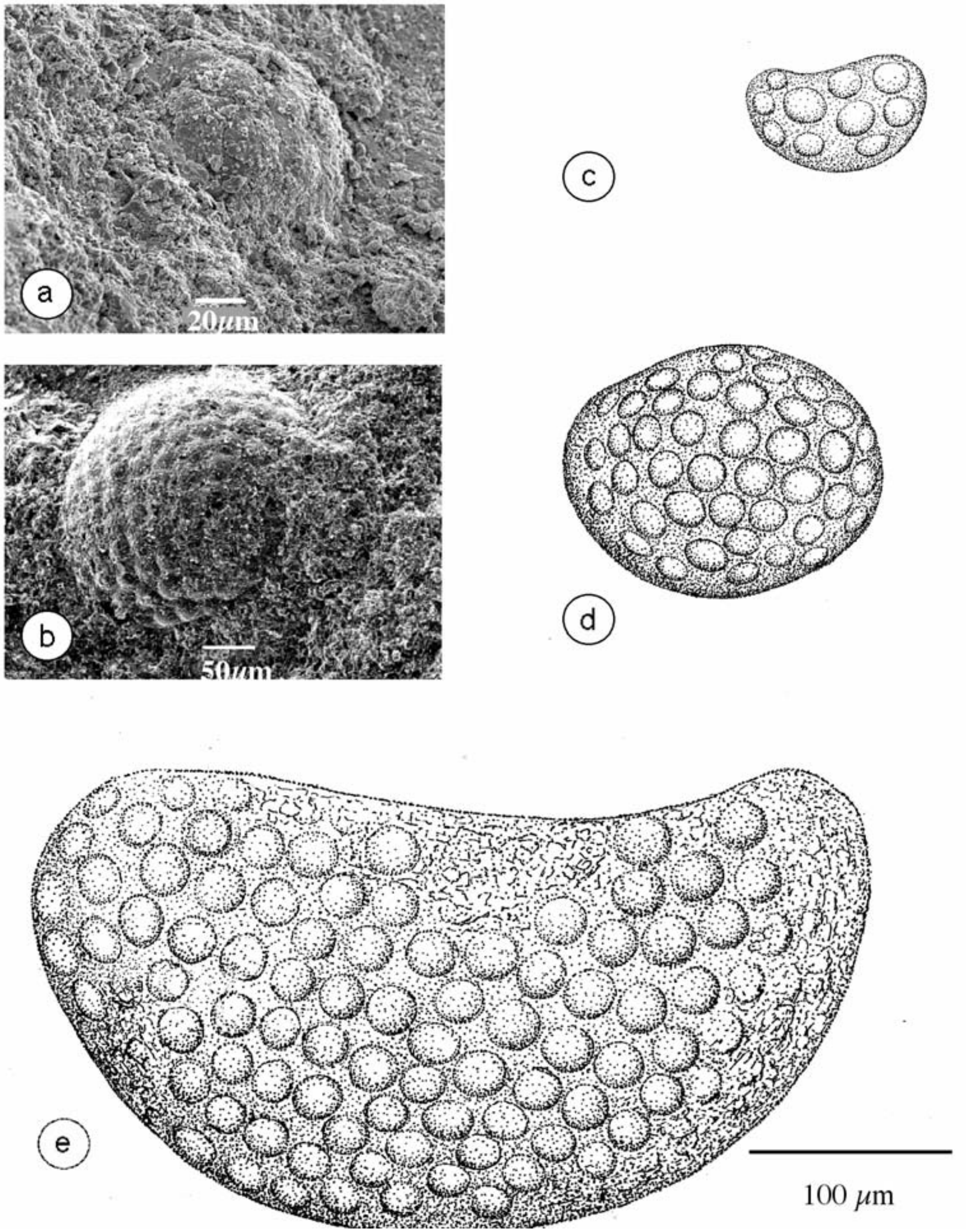

Figure 2. a, SEM juvenile eye. b, SEM almost adult eye. Drawings: c, juvenile eye; d, intermediate stage; e, adult eye (all drawings are at same scale).

colonise this niche. Planktonic life forms are normally widely distributed, but this species occurs at one locality only. It seems, however, to have been a short-lived species, and in any case individuals are very delicate and likely to be preserved only in rare and unusual conditions. Following its extinction, further colonisation did not take place until the great diversification of the Ordovician.

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ADDITIONAL CAMBRIAN TRILOBITES FROM KURGIAKH VALLEY ZANSKAR BASIN, NORTHWEST HIMALAYA

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INTRODUCTION

The Cambrian rocks that crop out in the Niri-Tsarap and Kurgiakh valleys of the southeastern Zanskar Basin are classified under four formational units i.e. the Phe, Parahio, Karsha and Kurgiakh formations (Nanda and Singh, 1977; Srikantia *et al*., 1980; Garzanti *et al*., 1986; Gaetani *et al*., 1986; Myrow *et al*., 2006). The Cambrian trilobites described in this contribution were recovered from the top part of the Teta Member (Karsha Formation) along the Tangze-Yogma-Kuru section (Kurgiakh Valley). The section yielded a diverse mixture of cosmopolitan agnostids and polymerids of Gondwanan affinities.

GEOLOGIC SETTING OF THE TANGZE-YOGMA-KURU (T-Y-K) SECTION

The Tangze-Yogma-Kuru (T-Y-K) section is situated at latitude 33° 09′ 21.1″ N and longitude 77° 12′ 03.5″ E on the right bank of the Kurgiakh Chu River at about 1.5 km North of the Tangze Yogma Village (in between the Tangze-Yogma and Kuru villages) of the Kurgiakh Valley. Along this, a 80.21-m-thick T-Y-K section has yielded a large number of polymerid and agnostid fauna embedded in an alternation of shale-grainstone limestone beds of the Teta Member (Karsha Formation). The measured section consists of orange dolostone (23 m) representing the top part of the Thidsi Member (Karsha Formation), followed by a 22-m-thick fossiliferous successions of alternating thin- to thick-bedded limestone grainstone, marl, shale and calcareous dolomite beds (individual beds ranging from 2 to 79 cm in thickness) which is characterized by the presence of well-preserved trilobites and a few ichnofossils, such as *Skolithos* and *Planolites*. This is followed by a 28.5-m-thick succession of shale-limestone grainstone and calcareous dolomite. The weathered marl beds (3-21 cm in thickness) are intercalated with the shale and calcareous dolomite beds. The top of the T-Y-K section, 4.8 m thick, consists of a succession of greenish-gray silt streaked shale beds, and represent the transition zone to overlying Surichun Member of Kurgiakh Formation.

FAUNAL COMPOSITION AND GLOBAL CORRELATION

The trilobite assemblage reported above consists of six agnostoid and five polymerid species: i.e., *Hypagnostus* sp., *Peronopsis* sp., *Lisogoragnostus hybus, Lejopyge armata*, *Diplagnostus planicauda, Clavagnostus* cf. *trispinus*, *Parablackwelderia* sp., *Fuchouia* cf. *oratolimba*, *Neoanomocarella asiatica*, *Fuchouia bulba* and *Damesops sheridanorum*. *Lejopyge armata* is the most abundant species of the processed fauna, representing more than 60 percent in relative abundance. The T-Y-K section contains several biogeographically widespread key agnostoid species, notably *Hypagnostus sp., Peronopsis sp., Lisogoragnostus hybus, Lejopyge armata*, *Diplagnostus planicauda* and *Clavagnostus* cf. *trispinus*.

Lejopyge armata is globally distributed in open-marine facies and has been previously documented from late Middle Cambrian strata of Greenland (Robison, 1984, 1988), Himalaya (Whittington, 1986; Jell and Hughes, 1997; Parcha, 2004), Korea (Hong *et al*., 2003), Sweden (Westergård, 1946; Axheimer and Ahlberg, 2003; Axheimer *et al*., 2006), Siberia (Lermontova, 1940), Kazakhstan (Ergaliev, 1980), western Zhejiang (Lu and Lin, 1989), Canada (Pratt, 1992), China (Peng and Robison, 2000), Australia (Öpik, 1967), Tasmania (Jago, 1976), and Antarctica (Cooper *et al*., 1996). In the late middle Cambrian of Scandinavia, Siberia, Australia, Kazakhstan, and China *Lejopyge armata* has also been reported co-occurring with *Lejopyge laevigata*. In China, *L. armata* first appears in the upper *Goniagnostus nathorsti* Zone, and ranges upwards into the *Lejopyge laevigata* and *Proagnostus bulbus* zones (Peng and Robison, 2000). In North America and Greenland, *L. armata* is known from the upper part of the *L. laevigata* Zone (Robison, 1984).

Diplagnostus planicauda is a long ranging species that ranges from the base of the *Ptychagnostus atavus* Zone to the upper *Lejopyge laevigata* Zone (Peng and Robison, 2000). It is known from Scandinavia, Siberia, North Greenland, the western United States, Australia, Argentina (Robison, 1988; Peng and Robison, 2000) and Himalaya (Jell and Hughes, 1997; Parcha, 2004).

Lisogoragnostus hybus is reported from the middle middleCambrian (*Acidusus atavus* Zone) to the middle Furongian of China (Yang *et al*., 1991, 1993; Peng and Robison, 2000), Australia (Jago, 1976; Shergold, 1982), Kazakhstan (Ergaliev, 1980; Lisogor *et al*., 1988), Laurentia (Rasetti, 1967; Pratt, 1992; Robison, 1994), and Korea (Lee and Choi, 1995).

Parablackwelderia has been mainly reported from the late middle Cambrian (*Blackwelderia*, *Drepanura*, and *Paradamesops jimaensis*-*Cyclolorenzella tuma* zones) of China (Walcott, 1905, Resser and Endo, 1937; Lu, 1957; Chu, 1959; Yang, 1978; Yin and Li, 1978; Qiu *et al*., 1983; Zhang and Jell, 1987; Zhu and Wittke, 1989; Zhang *et al*., 1995), England (Rushton, 1978), Korea (Kobayashi, 1935, 1960), and presumably in Kashimir (Jell and Hughes, 1997) and Zanskar (Singh, 2006, 2007).

Fuchouia cf. *oratolimba* is reported from the *Parablackwelderia* [=*Paradamesops*] *jimaensis* – *Torifera* [=*Cyclorenzella*] *tuma* Zone at Jiudiantang, Xinhuang (Zhou *et al*., 1977; Yin and Li, 1978; Yang, 1978; Lu and Lin, 1989) and at Huaqiao Formation in the Paibi and Wangcun sections of northwestern Hunan (Peng *et al*., 2004). *Fuchouia bulba* is reported from the Huaqiao Formation in the Paibi and Wangcun sections (Peng *et al*., 2001b, 2004) where it occurs with trilobites indicative of the *Pianaspis sinensis Zone (= Goniagnostus nathorsti* Zone and lower part of the *Lejopyge laevigata* Zone*)*. It has been also reported from south central China (Zhou *et al*., 1977), western Hunan and eastern Guizhou (Yang, 1978), Hunan (Liu, 1982).

Neoanomocarella asiatica has been mainly reported from Wangcun and Paibi sections of northwestern Hunan (Peng *et al*., 2004) where it occurs from *Wanshania wanshanensis* Zone to middle of the *Liostracina bella* zone which is equivalent to upper part of *Proagnostus bulbus* Zone to base of the *Glyptagnostus* *stolidotus* Zone. In Kazakhstan, it is reported from *Lejopyge laevigata* and *Kormagnostus simplex* zones (Ergaliev, 1980).

The species *Lisogoragnostus hybus, Clavagnostus* cf. *trispinus, Neoanomocarella asiatica and Fuchouia bulba* are recorded for the first time from the Zanskar region of Tethys Himalaya. The recorded agnostids and polymerids strongly support a correlation with the *Lejopyge laevigata* Zone - upper *Proagnostus bulbus* Zone or the *Pianaspis sinensis* Zone–*Wanshania wanshanensis* Zone of the Huaqiao Formation (late middle Cambrian age) of northwestern Hunan, China and similarly with Western Zhejiang, Australia, Sweden, United State, Canada, England, Kazakhstan, Antarctica, Greenland and Siberia (Lermontova, 1940; Robison, 1984, 1988; Hong *et al*., 2003; Westergård, 1946; Axheimer and Ahlberg, 2003; Axheimer *et al*., 2006; Ergaliev, 1980; Lu and Lin, 1989; Pratt, 1992; Peng and Robison, 2000; Öpik, 1967; Jago, 1976 and Cooper *et al*., 1996).

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HORNS, EGGS AND LEGS: EXCEPTIONALLY PRESERVED NEW ARTHROPODS FROM THE HEREFORDSHIRE (SILURIAN) LAGERSTÄTTE

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Keywords: Arthropoda, Crustacea, excepcional preservation, Herefordshire Lagerstätte, Marrellomorpha, Silurian.

INTRODUCTION

The Herefordshire Lagerstätte from the Welsh Borderland preserves a wide variety of invertebrates of mid-Silurian, Wenlock Series age. The fossils all show exceptional preservation of soft tissues in 3D, and are recovered through serial grinding, digital photographic and computer rendering techniques, which yield 'virtual fossils' in the round for study. The arthropod record from this deposit has recently been increased (Siveter *et al*., 2007a-c) by three new taxa: *Tanazios dokeron, Nymphatelina gravida*, and *Xylokorys chledophilia*.

TANAZIOS DOKERON (Fig. 1)

In *T. dokeron* the body tagmata comprise a head shield and a long trunk. The head shield bears six pairs of horn-like spines and the head five pairs of appendages. The presumed antennule and antenna, and the mandible, are all uniramous, and the mandible includes a gnathobasic coxa. Appendages four and five are biramous and similar to those of the trunk: each comprises a limb base with an endite, an enditic membrane, and two epipodites, plus an endopod and exopod. The hypostome bears a large cone-like projection centrally, and there may be a short labrum. The trunk has some 64 segments and at least 60 appendage pairs. A very small telson has the anus sited ventrally in its posterior part and it also bears a caudal furca. Comparative morphological and cladistic analyses of *T. dokeron* indicate a crustacean affinity, with a probable position in the eucrustacean stem group. The new species is interpreted as a benthic or nektobenthic scavenger.

Figure 1. *Tanazios dokeron*, (a) ventral stereo-pair, (b) dorsal stereo-pair, (c) left lateral view; x 3.6.

NYMPHATELINA GRAVIDA (Fig. 2)

N. gravida is an ostracod crustacean in which eggs and possible juveniles are preserved within its carapace, providing an unequivocal and unique view of parental brood care in the invertebrate fossil record. The female fossil belongs to Myodocopida, based on its soft-part anatomy. It demonstrates a remarkably conserved egg-brooding reproductive strategy within these ostracods over 425 million years. The soft-tissue anatomy urges extreme caution in classifying 'straight-hinged' Palaeozoic ostracods based on the carapace alone and fundamentally questions the nature of the shell-based Palaeozoic ostracod record. *N. gravida* was probably a nektobenthic species, and possibly a predator, scavenger, or detritivore.

XYLOKORYS CHLEDOPHILIA (Fig. 3)

In *X. chledophilia* the head and trunk are covered by a relatively featureless ovoid carapace, which comprises a domed central part and a flange-like border. The head bears five pairs of appendages. The first is uniramous, with dorsal and ventral projections distally. Appendages two to four are biramous and each

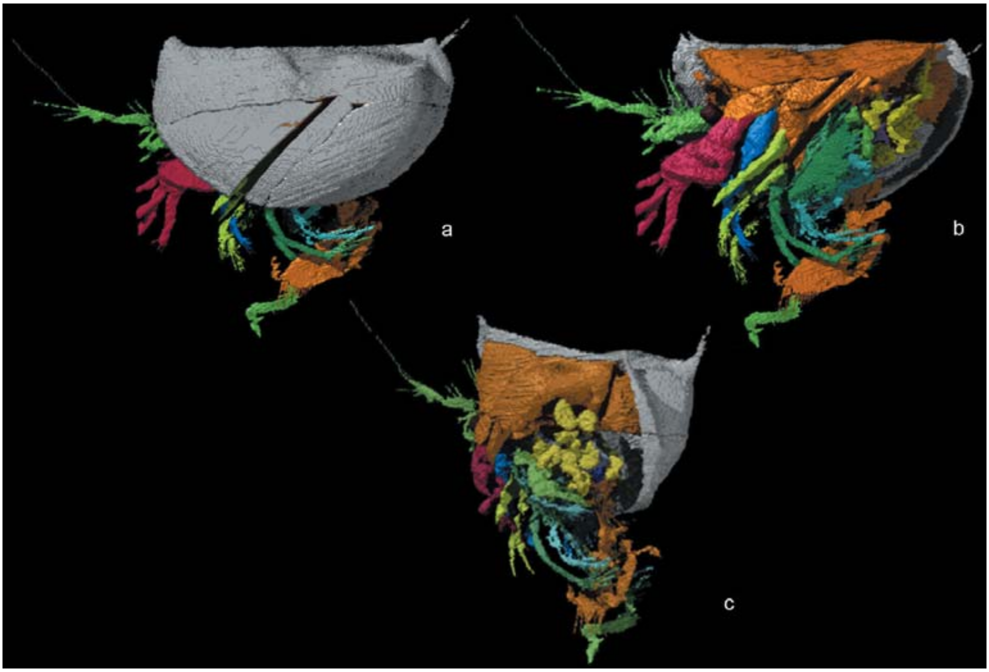

Figure 2. *Nymphatelina gravida*, (a) left lateral view, (b) left lateral view with left valve omitted, (c) posterior oblique view with left valve omitted; x 6.7.

endopod terminates in two projections. Appendage five is possibly biramous. The hypostome is very long and subrectangular in outline. There are approximately 35 pairs of biramous trunk appendages. Each exopod comprises a long slender shaft bearing numerous fine filaments; each endopod comprises a ribbon-like shaft bearing paddle-like endites. Morphological comparisons and cladistic analyses of *X. chledophilia* indicate affinity with *Vachonisia rogeri* from the Lower Devonian Hunsrück Slate, within the marrellomorphs, but assignment to Marrellomorpha is provisional pending revision of other members of this clade. *Xylokorys* is the first 'marrellomorph' to be reported from the Silurian. It is interpreted as a benthic particle filter feeder, which may also have consumed prey items.

CONCLUSIONS

Prior to the establishment of *Tanazios dokeron, Nymphatelina gravida* and *Xylokorys chledophilia*, arthropods were already one of the main components of the Herefordshire fauna (together with sponges), both in terms of number of specimens and also species. Those species described previously include a stem group chelicerate, a pycnogonid, a phyllocarid, and a cirripede (barnacle), together with a (second) myodocopid ostracod species. The new forms not only add to the arthropod species record from the fauna, but *Tanazios* (a probable stem crustacean) and X*ylokorys* (a 'marrellomorph') also increase somewhat the range of higher taxonomic arthropod groupings now known from the Lagerstätte. Most importantly, the detailed 3D morphology afforded by the remarkable preservation of all these Herefordshire Silurian arthropods is providing significant insights into the palaeobiology and phylogeny of the phylum, with the prospect of further revelations: there are several taxa that are still to be studied, including a trilobite.

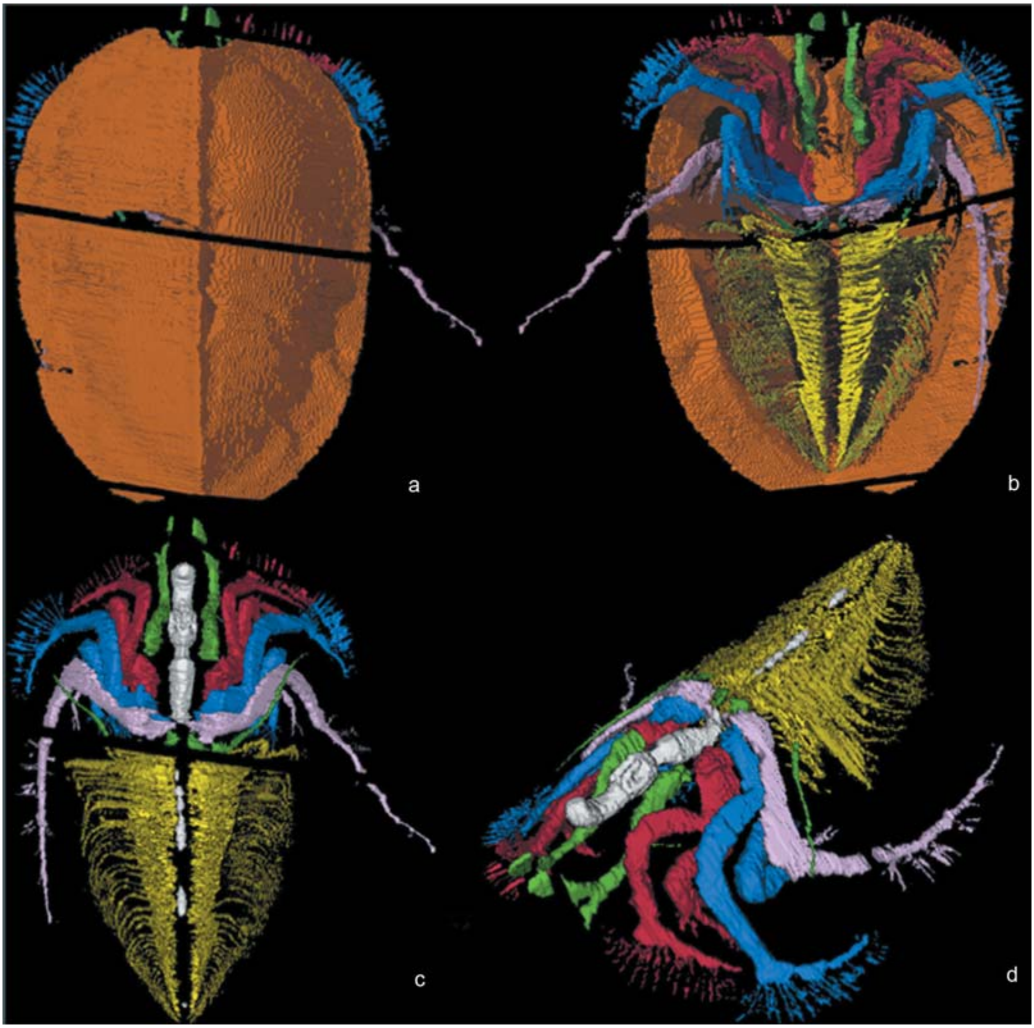

Figure 3. *Xylokorys chledophilia*, (a) dorsal view, (b) ventral view, (c) dorsal view with carapace omitted; x 1.9. (d) anterior oblique view with carapace omitted; x 2.3.

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A DEEP WATER TRILOBITE FAUNA FROM THE BRITISH LOWER LUDLOW

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Keywords: Trilobite, Bipartite Limestone, British, Lower Ludlow, Howgill Fells, Lake District Basin.

INTRODUCTION

Rich shelly faunas, including trilobites, are common in British Ludlow successions. The most abundant and diverse trilobite faunas occur in shelf and platform facies, with more basinal areas typified by graptolite- and cephalopod-bearing mudstones. Trilobites do occur locally in deeper water environments in the British Ludlow, however. The example described here occurs in the latest Wenlock/basal Ludlow Bipartite Limestone of the Howgill Fells, which then formed part of the Lake District Basin. This paper briefly summarizes work in progress on the Bipartite Limestone, its fauna and palaeoenvironmental significance.

GEOGRAPHICAL, GEOLOGICAL AND STRATIGRAPHICAL SETTING

The Howgill Fells of Cumbria, north-west England, are located north of the small town of Sedbergh and south of Ravenstonedale (Fig.1). The Howgill Fells are underlain by the Windermere Supergroup (Rickards and Woodcock, 2005), consisting of five groups and nine formations ranging from Ashgill to Přídolí in age. The Upper Ordovician Dent Group, at the base, consists largely of calcareous mudstones overlain by a conglomeratic sandstone. Shelly fossils such as trilobites, bryozoans and brachiopods occur throughout. Above the Dent Group, black graptolitic anoxic mudstone dominates, with nodular limestones below and green-grey mudstones above. These rocks make up the Stockdale Group, which spans the latest Ordovician to the topmost Llandovery. The overlying Wenlock to Gorstian Tranearth Group is composed largely of laminated siltstone and mudstone representing anaerobic bottom waters. The succeeding Coniston Group comprises sandstones and mudstones. A distinct lack of bioturbation and benthic faunas has been used to suggest continued anoxic conditions on the sea floor (Rickards and Woodcock, 2005). Finally the Kendal Group (Ludfordian–Přídolí) includes sandstones and mudstones representing a range of depositional environments. Bioturbation is observed at the top of the unit (Kirkby Moor Formation), indicating a return to aerobic conditions. The Windermere Supergroup was described in more detail by Kneller *et al.* (1994) and Rickards and Woodcock (2005). Overall, the sequence represents a foreland basin succession (King, 1994), developed as the microcontinent of Eastern Avalonia was loaded by Laurentia following the closure of the Iapetus Ocean.

The Coldwell Formation (Fig. 2) is a 10 m thick interval located in the middle of the Tranearth Group, and comprises fossiliferous silty limestones and calcareous mudstones. The formation includes what Rickards (1967) referred to as the topmost Wenlock – basal Ludlow Bipartite limestone ('Bipartite Limestone' herein). As its name implies, the Bipartite Limestone is split into two parts by graptolitic mudstone: a *Neodiversograptus nilssoni–Lobograptus scanicus* Biozone age has been identified for this mudstone interval (Rickards 1967, p. 230) providing a minimum age for the upper division of the Bipartite Limestone. The lower part of the Coldwell Formation contains graptolites of the late Wenlock *Monograptus ludensis* Biozone (Rickards and Woodcock, 2005, pp. 271-272).

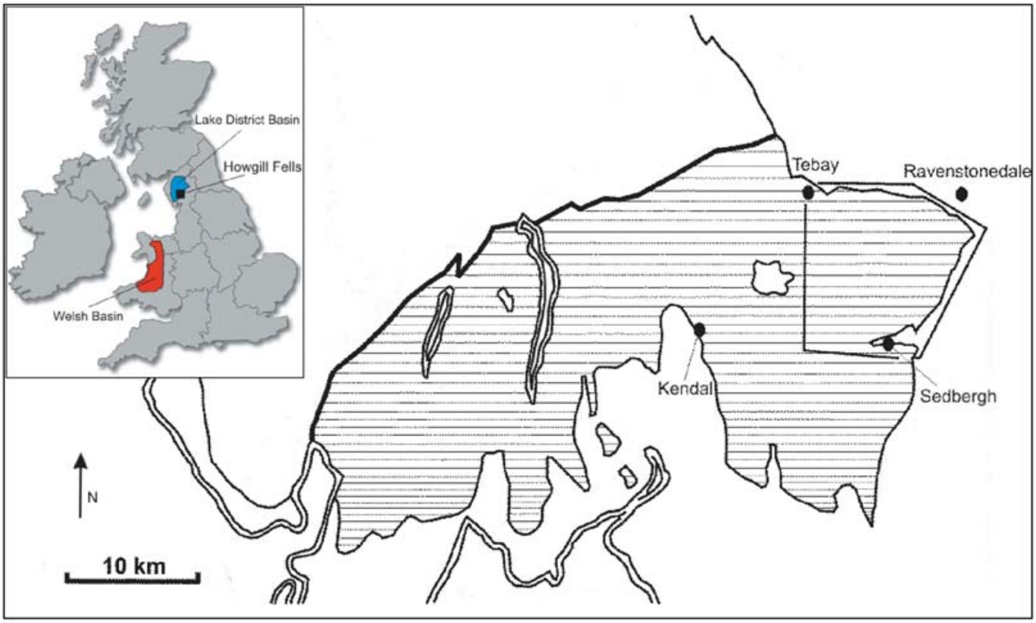

Figure 1. Map showing location of the Howgill Fells area within the UK. Silurian rocks indicated by horizontal ornament (adapted from Rickards, 1967, p. 216, and Woodcock, 2002, p.176).

THE BIPARTITE LIMESTONE AND ITS FAUNA

The Bipartite Limestone comprises impure bioturbated nodular carbonates with the occurrence of small-scale slumping (Rickards and Woodcock, 2005). The rocks contain a rich shelly fauna including disarticulated trilobites and brachiopods. Trilobites previously described or identified from the Bipartite Limestone include *Decoroproetus* (Owens, 1973; Rickards, 1965), *Miraspis, Delops,* and *Struveria* (Rickards, 1965; Thomas *et al.,* 1984, p. 55). The fauna was termed the *Delops-Miraspis* Association by Thomas and Lane (1999).

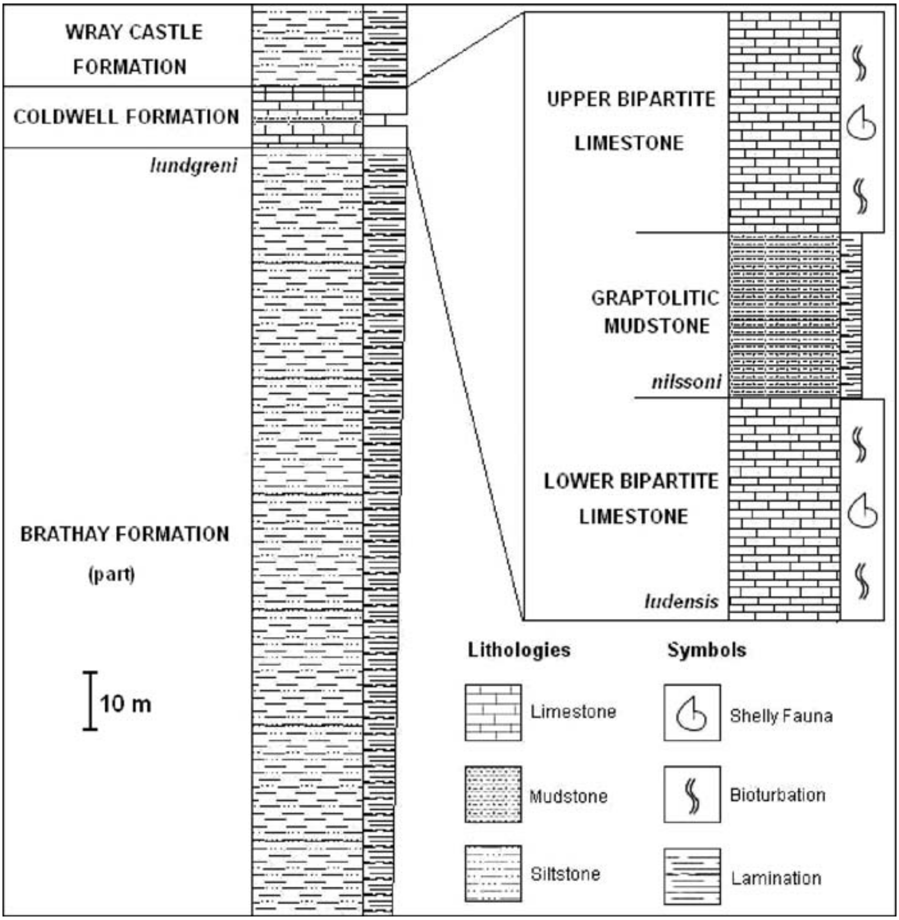

Figure 2. Summary stratigraphical log of part of the Tranearth Group, showing the position of the Bipartite Limestone. Based on data from (Rickards and Woodcock, 2005).

Substantial collections have been made from the Bipartite Limestone at intervals over the last 30 years, and work is in progress on these. Based on the material identified thus far, several observations can be made. Relative abundances were determined by counting left and right free cheeks, cephala and pygidia: the largest number indicates the minimum number of individuals per genus represented. Based on 250 specimens, representing a minimum of 106 trilobites, *Decoroproetus* makes up ~79% of the fauna with *Delops* ~17% and *Struveria* ~4%. *Miraspis, Scotoharpes,* and *Sphaerocoryphe* are rare, being represented by just one specimen each. Owens (1973, p. 52) recorded only one species of *Decoroproetus (D. scrobiculatus*) from the British Ludlow. This is the most abundant species in the Bipartite Limestone, but other *Decoroproetus* specimens occur that are distinguished by glabellar morphology, presence of a pygidial post-axial ridge, and raised first pygidial axial ring with deep furrows. These may represent one or more additional species.

The disparity between the number of cephala (55) and pygidia (84) of *Decoroproetus* in the Bipartite Limestone fauna, as well as the fragmentary nature of the assemblage, suggests that the material was transported, though some degree of disarticulation may have been caused by bioturbation. Specimens were probably transported fairly locally, and were certainly not derived from contemporaneous shelf environments, for none of the taxa recorded from the Bipartite Limestone are known from shallower water settings. The Bipartite Limestone assemblage therefore does appear to represent a fauna that inhabited deeper-water settings.

COMPARISON WITH OTHER TRILOBITE FAUNAS

Silurian Assemblages

Although the fauna of the Bipartite Limestone differs from the contemporaneous shelf faunas that occur in the UK, there are some localities with similar faunas. The Mottled Mudstone of North Wales for example, occurs in a basinal setting also, and yields a fauna containing brachiopods, trilobites and corals. Trilobites include dalmanitids and *Struveria* with rarer forms like *Miraspis*. However, there are marked differences, such as the dominance of *Ananaspis* and presence of *Calymene* and *Raphiophorus* (Warren *et al.*, 1984). Further afield, fauna described from the Swedish Colonus shale (Hede, 1915) also bears a resemblance to that of the Bipartite Limestone.

Assemblages of other ages

There are many descriptions of deep-water trilobite associations from the Ordovician (e.g. Fortey and Owens 1999, p. 452; Fortey 2006). These include "atheloptic" assemblages, characterized by blind benthic trilobites. No such associations are known from the Silurian, though deep-water faunas including blind trilobites evolved once again in the Devonian (they are known also in the Carboniferous, e.g. Owens and Tilsey, 1995). There are no blind trilobites in the Bipartite Limestone, and the only taxon with reduced eyes (*Scotoharpes* sp.) is represented by just one specimen. Both *Delops* and *Struveria* have large crescentic eyes of typical schizochroal type. It seems likely that the assemblage was adapted to life in deeper-water settings than those occupied by most trilobites found in the British Ludlow, but at shallower depths than those inhabited by atheloptic associations.

CONCLUSIONS

The sediments associated with the Bipartite Limestone are graptolitic shales and turbidites deposited below storm wave-base. The calcareous bioturbated sediments of the two divisions of the Bipartite Limestone, with their shelly benthic fauna, represent times when the sea-floor became ventilated (Kneller *et al.*, 1994), and this is most likely associated with temporary shallowing. The lower division of the Bipartite Limestone belongs to the latest Wenlock *ludensis* Biozone. That interval was a time of lowstand (Johnson, 2006) recognized from several palaeocontinents. In the UK, it corresponds with the younger part of the Much Wenlock Limestone Formation on the Midland Platform, and with the Upper Mottled mudstone in the basinal sequence of North Wales. It was thus a eustatic change, possibly associated with continuing glacial activity in the southern hemisphere (Johnson, 2006). The *ludensis* lowstand is followed by a widespread transgression at the start of the Ludlow. In the Lake District Basin however, the upper division of the Bipartite Limestone punctuates this transgressive sequence, representing a shallowing event that cannot be recognized elsewhere. This shallowing probably has a local tectonic cause therefore, reflecting the foreland basin setting of the Lake District Basin.

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POTENTIAL OUTGROUP FOR THE ORYCTOCEPHALIDS, A CLADISTIC ANALYSIS OF CAMBRIAN TRILOBITE HYPOSTOMES

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Keywords: Phylogeny, oryctocephalids, corynexochids, redlichids, olenellids

INTRODUCTION

One of the difficulties in a phylogenetic analysis of the oryctocephalid trilobites is determining the appropriate outgroup. If the oldest representatives are used, then the non-spiny oryctocephalids (Oryctocaridae) occur at the base of the clade. In turn, if the spiny oryctocephalids (Oryctocephalidae) are used because of their similarity to the redlichids, then the non-spiny oryctocephalids occur as the more derived taxa. Sundberg and McCollum (1997) avoided the problem by using the early representatives of the spiny oryctocephalids and limited their study to just the spiny forms. Unfortunately, none of these approaches can address the relationship between the two groups. An outgroup needs to be determined to resolve the phylogeny of the oryctocephalids.

The affinity of the oryctocephalids to the different groups, Redlichiida, Corynexochiida, and Ptychopariida, is unclear due to each group's distinctive morphology. However, the conservative morphological features of trilobites, such as the hypostome and rostral plates (Fig. 1), might provide a clue as to their interrelationship. For example, the corynexochids, including the oryctocephalids, are commonly linked together due to their fused hypostome and rostral plate (e.g. Moore in Harrington *et al*., 1959; Fortey, 1990). In this study, character states of the hypostomes of different "Lower" and "Middle" Cambrian trilobites are analyzed to see if an outgroup for the oryctocephalids can be identified.

CLADISTIC ANALYSIS

The analysis included 37 species of trilobites; 5 oryctocephalids are compared to 10 redlichiids, 6 olenellids, 12 other corynexochids, and 3 ptychopariids. The species selected are based on: 1) their well preserved and illustrated hypostomes; 2) a preliminary study of corynexochid hypostomes which identified groups with similar hypotomes, only representative of these corynexochids were used in this study; and 3) those for which I had in my reference library. The outgroup is the olenellid species *Nevadella faceta* and *Teresellus goldfieldensis* based on their age (*Nevadella* and *Olenellus* biozones), absence of facial sutures, multisegmented thorax, and small pygidium. The oryctocephalids consist of *Cheiruroides articus*, *Hunanocephalus ovalis*, *Oryctocephalus indicus*, *Oryctocephalites vicinus*, and *Tonkinella breviceps*. The hypostome typical of Oryctocaridae are not known or well preserved. *Shergoldiella vincenti* Geyer, 2006 (Oryctocaridae) has a poorly preserved hypostome that is similar to *Oryctocephalus* (Fig. 1C) and *Oryctocephalites*.

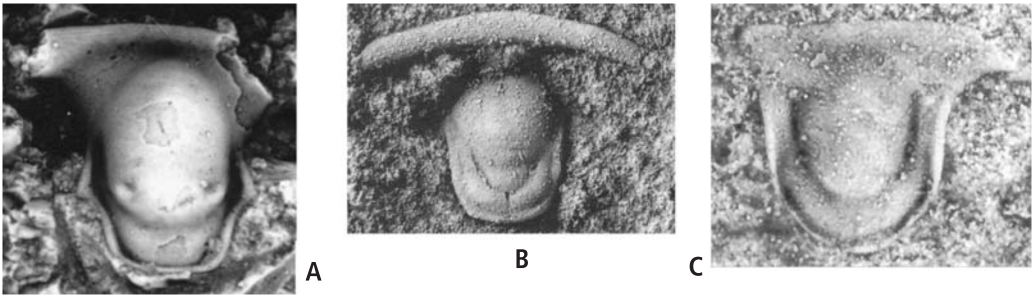

Figure 1. A, *Parkaspis* (corynexochid) hypostome and fused rostral plate (from Sundberg, 1994); B, *Redlichia* hypostome connected with extension to rostral plate (from Kruse, 1998); and C, *Oryctocephalus* hypostome and fused rostral plate (from Blaker and Peel, 1997).

Thirteen characters used in this cladistic analysis include: 1) hypostome fused to rostral plate (Fig. 1A, C); 2) hypostome touching rostral plate; 3) prominent macula; 4) location of macula above furrow (Fig. 1A); 5) secondary middle furrow; 6) anterior lobe oval; 7) posterior lobe extending to nearly to the middle of the anterior lobe (Fig. 1B, 1C); 8) posterior wing present (Fig. 1A); 9) posterior margin with spines; 10) strong anterior wing (Fig. 1A); 11) well defined lateral boarder reaching anterior end (Fig. 1C); 12) rostral plate with triangular ends; and 13) posterior lobe width. All are presences/absence characters with the exception of character 13 (see below). The analysis was done with PAUP using a heuristic search, with 1000 repetitions, and progressive reweighting based on the retention index (RI—setting the characters weights to 1000).

In some taxa, the position of the hypostome is not exactly known. In these situations the position of the hypostome is established by the location of the frontal lobe (see Whittington, 1987; Fortey, 1990). If the lobe is touching the anterior border or nearly so, then it is assumed that the hypostome is touching the rostral plate. If the frontal lobe is located some distance from the anterior border, then it is assumed that the hypostome is not touching the rostral plate. Some species of *Redlichia* (see Fig. 1B) have a thin anterior extension of the rostral plate that connects to the hypostome. This feature is only seen in a few trilobites and was coded as the hypostome not fused and not touching the rostral plate. The presence of a plectrum may indicate a thin anterior extension connecting the rostral plate and the hypostome (Fortey, personal communication). Of the taxa used, only *Olenellus* cf. *truemani* has a plectrum, but does not have an anterior extension (Blaker and Peel, 1997).

The relative size of the posterior lobe is based on the ratio the sagittal lengths of the posterior and middle lobes (character 13). The separation into different states is based on the gap coding which illustrates three groups of lengths. Codes are 0 = from 10 to 14 percent of the middle lobe, 1 = 16 to 30 percent, and 2 = 46 to 51%. The higher percentages are from *Ehmaniella fronsplanata*, *Hunanocephalus ovalis*, and *Cheiruroides articus*.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13
Albertella aspinosa	1	1	1	1	0	1	0	1	0	1	0	0	1
Bonnia columbensis	1	1	1	1	1	1	0	0	0	0	1	1	1
Bonnia brennus	1	1	1	1	1	1	0	1	0	0	1	1	1
Cheiruroides articus	1	1	0	0	0	1	?	0	0	0	1	1	2
Churkinia yukonensis	1	1	1	0	0	1	0	0	0	0	1	?	1
Dorypyge richthofeni	1	1	1	1	0	1	0	1	0	0	1	1	1
Dorypgye swasii	1	1	0	0	0	1	0	1	0	0	1	1	1
Drepanopyge mirabilus	0	1	1	0	0	1	1	1	0	1	1	0	1
Ehmaniella fronsplanata	0	0	1	0	0	1	0	0	0	1	1	0	2
Eokochaspis nodosa	0	0	0	0	0	1	0	1	0	1	1	0	?
Fieldaspis celer	1	1	1	1	0	1	0	1	0	1	0	0	1
Glossopleura walcotti	1	1	1	1	0	0	0	1	0	0	1	0	1
Guangyuanaspis shaanxiensis	0	0	1	0	0	1	1	0	0	1	1	0	1
Holmia inusitala	1	1	1	0	0	1	0	1	0	1	0	0	1
Hunanocephalus ovalis	0	0	0	0	0	1	0	0	0	1	1	?	2
Kootenia dawsoni	1	1	0	0	0	1	0	1	1	0	1	1	1
Malungia laevigata	0	0	1	0	0	1	1	0	0	1	1	0	1
Manchuriella macar	0	0	0	0	0	1	1	0	0	1	1	?	1
Nevadella faceta	0	0	1	0	0	1	0	0	1	1	0	?	1
Ogygopsis virgata	1	1	1	1	1	1	0	1	1	0	1	1	1
Olenellus cf. truemani	0	0	1	0	0	0	0	1	1	1	0	?	0
Olenellus sp.1	0	0	1	0	0	0	0	1	1	?	0	?	1
Oryctocephalus indicus	1	1	0	0	0	1	1	0	0	0	1	0	1
Oryctocephalus vicinus	1	1	0	0	0	1	1	0	0	0	1	0	1
Paradoxides davidis	1	1	1	0	0	1	0	1	0	1	0	0	0
Parkaspis drumensis	1	1	1	1	0	1	0	1	0	1	0	0	1
Polliaxis hanseni	0	1	1	0	0	0	0	1	1	1	1	?	0
Redlichia amadeana	0	0	0	0	0	1	1	0	0	?	1	0	1
Redlichia nobilis	0	0	1	0	0	1	1	1	1	0	0	0	1
Teresellus goldfieldensis	0	0	1	0	0	0	0	1	1	1	0	?	0
Tonkinella breviceps	1	1	0	0	0	1	1	0	0	0	1	0	1
Wannaria logani	0	1	1	0	0	0	0	0	1	0	0	?	0
Wenkchemia housensis	1	1	1	1	0	1	0	1	0	1	0	0	1
Xela drena	0	0	1	0	0	1	1	1	0	0	1	?	0
Xystridura verticosa	0	1	1	0	0	0	0	1	0	1	1	?	0
Xystriduria browni	0	1	1	0	0	0	0	1	0	1	1	0	0
Yiliangella forficula	0	1	0	0	0	1	0	1	1	1	1	?	1

Table 1. Character state distribution for the taxa used in the cladistic analysis. See text for characters. Source of illustrations used in the analysis are: Blaker and Peel (1997), Chang and Jell (1987), Chang *et al.* (1980), Ebbestad *et al.* (2003), Fritz (1972), Hollingsworth (2005), Jell and Hughes (1997), Jell in Bergston *et. al.* (1990), Kruse (1998), Öpik (1975), Palmer (1969), Palmer and Halley (1979), Sundberg (1994), Sundberg and McCollum (1997, 2000), and Whittington (1987).

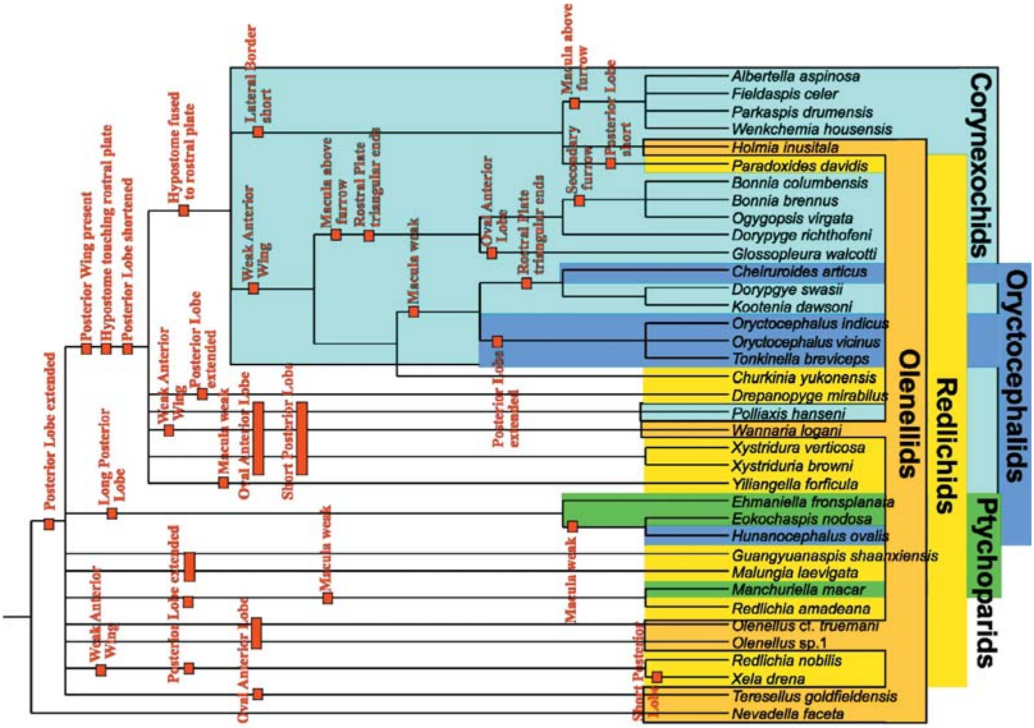

Figure 2. Majority rule cladogram of representatives of olenellid, redlichid, corynexochid, oryctocephalid, and ptychopariid hypostomes and rostral plates. Consensus tree is based on six trees that have TL = 10246, CI = 0.4733, HI = 0.5267, RI = 0.8944, RC = 0.42233.

RESULTS

The majority rule cladogram (Fig. 2) illustrates one well defined "Corynexochid clade," named because of the dominance of corynexochids. This clade is based on the presence of a posterior wing, the hypostome touching the rostral plate and a short posterior lobe. The taxa outside this clade have poorly resolved relationships and are generally a mixture of redlichids and olenellids.

Wanneria logani (olenellid) and five redlichids occur in the unresolved portion of the Corynexochid clade. Within the resolved portion of the clade two major subclades occur. The first major subclade contains *Holmia inusilata* (olenellid) and *Paradoxides davidis* (redlichid) with the corynexochids *Albertella*, *Wenkchemia*, *Parkaspis*, and *Fieldaspis* (Zacanthoididae and Dolichometopidae). The second major subclade contains the redlichid *Churkina yukonensis* with the corynexochids *Bonnia*, *Dorypyge*, *Glossopleura, Kootenia,* and *Ogygopis* (Dolichometopidae, Dorypygidae, Ogygopsidae) and the oryctocephalids *Cheiruroides*, *Oryctocephalus*, *Oryctocephalites*, and *Tonkinella*. This subclade can be divided into a clade containing *Bonnia*, *Dorypyge richthofeni*, and *Glossopleura* and a clade containing *Dorypyge swasii*, *Kootenia, Cheiruroides*, *Oryctocephalus*, *Oryctocephalites*, *Tonkinella* and *Churkina yukonensis*. This last clade is divided into three clades, one with the corynexochids *Cheiruroides*, *Dorypyge* *swasii*, and *Kootenia;* another with the oryctocephalids, *Oryctocephalus*, *Oryctocephalites*, and *Tonkinella*; and the redlichid *Churkina yukonensis* as a sister taxon to the other two clades.

The classical oryctocephalids *Oryctocephalus*, *Oryctocephalites*, and *Tonkinella* cluster together as a separate clade within the corynexochids. *Cheiruroides articus* however, falls within the sister clade to the oryctocephalids with *Dorypyge* and *Kootenia*. In contrast to the other four "oryctocephalids" which occur within the corynexochids, *Hunanocephalus ovalis* clusters with the ptychopariids *Eokochaspis* and *Ehmaniella*.

DISCUSSION

The purpose of this study is to identify a potential outgroup to the oryctocephalids. This outgroup is the redlichids, specifically in this study *Churkinia yukonensis. Churkinia yukonensis* occurs at the base of the clade containing the oryctocephalids. Yuan *et al.* (2001) suggested that *Cheiruroides* as the ancestral stock to the oryctocephalids. *Cheiruroides* occurs with corynexochids *Dorypyge* and *Kootenia* in a sister clade to the oryctocephalids. This suggests that *Cheiruroides* is related to the oryctocephalids, but is not an oryctocephalid itself.

Hunanocephalus ovalis is completely removed from the other oryctocephalids and corynexochids in this analysis. This taxon appears to be more closely related to the ptychopariids than to the corynexochids. *Taijiangocephalus* (Yuan *et al*., 2002) has a similar hypostome to *Hunanocephalus*, although too poorly preserved to use in this analysis. This similarity suggests that *Taijiangocephalus* is also not an oryctocephalid, but rather related to the ptychopariids.

Most workers consider the corynexochids as a monophyletic group and at first inspection of the cladogram here (Fig. 2) one would agree. However, with the occurrence of *Holmia*, *Paradoxides*, and *Churkinia* within the Corynexochid clade, a couple of possibilities present themselves for consideration. First, these olenellid and redlichid taxa have been incorrectly assigned and belong to the Corynexochida. Second, the corynexochids *Albertella*, *Wenkchemia*, *Parkaspis*, and *Fieldaspis* (essentially Zacanthoididae) were derived from the redlichids/olenellids independent of the rest of the corynexochids. If the latter is true, this suggests that the corynexochids have been artificially lumped together in a single order based on their elongated and expanding glabella, relatively large pygidia, and a fused rostral plate to the hypostome. Of course, keep in mind that this is a preliminary study based only on the hypostome and rostral plates of a few representative "Lower and Middle" Cambrian trilobites. As such, I would not advocate the construction of a new trilobite order for the Zacanthoididae, but rather the further exploration of separate origin of the group.

CONCLUSIONS

This preliminary study based only on the hypostomes and rostral plates of trilobites suggests that the oryctocephalids and corynexochids are potentially polyphyletic. The "oryctocephalid" *Hunanocephalus* is most similar to ptychopariids and the presumed ancestor *Cheiruroides* occurs in a separate clade from the other oryctocephalids. However, *Cheiruroides* and *Kootenia* appear to be a sister groups to the oryctocephalids. The closest outgroup to the oryctocephalids would be *Churkinia yukonensis* and other closely related redlichids (Metadoxididae?).

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AN ELECTRON BACKSCATTER DIFFRACTION STUDY OF *GEESOPS*: A BROADER VIEW OF TRILOBITE VISION?

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Keywords: EBSD, schizochroal eye, Phacopids, *Geesops*.

INTRODUCTION

The calcite eyes of trilobites have been studied for over 100 years using methods including light microscopy (e.g. Clarke, 1889; Campbell, 1975; Towe, 1973; Clarkson, 1979 and Bruton and Haas, 2003) and more recently cathodoluminescence (CL) imaging coupled with scanning electron microscopy (SEM) of samples etched in EDTA (Miller and Clarkson, 1980). This work has provided a great deal of information on the mechanisms by which lenses collected light, drawing attention to the importance of the crystallographic orientation of lens calcite for focusing, and leading to sophisticated models of trilobite vision (Clarkson and Levi-Setti, 1975; Gál *et al.*, 2000). The morphology and mode of life of phacopids, in particular *Geesops*, are well understood (Bruton and Haas, 2003a, 2003b) but observations on the internal structure of their lenses contradict the generally accepted models for image formation by schizochroal eyes. Recent technological advances have given new impetus to the analysis of crystalline materials and especially important has been electron backscatter diffraction (EBSD). This is a SEM-based technique that can be used to accurately 'map' variations in the crystallographic orientation of a sample down to the sub-micrometre scale by recording on a sensitive camera Kikuchi patterns that are formed by diffraction of an electron beam when focused on a polished sample tilted at 70°. Although this technique has been understood for over 50 years (Alam *et al.*, 1954) and has been extensively used in disciplines such as metallography (Humphreys, 2001), until recently its Earth Science applications were limited to studies of structural geology and petrology (Nuchter and Stockhert, 2007). Recent applications of EBSD to biomineralisation research (Dalbeck and Cusack, 2006; Griesshaber *et al.*, 2007) have mapped the crystal orientation and microstructure of calcite shells and in 2006 Lee *et al.* were able to apply this technique to investigating the microstructure of lenses in the schizochroal eye of *Dalmanites*. This paper describes results of an EBSD study of eyes of *Geesops schlotheimi* (Bronn, 1825) combined with more traditional microscopy techniques to reveal new aspects of trilobite lens structure.

METHODS

All work was undertaken on eyes in thin section and initial characterisation by optical microscopy (plane and cross-polarised transmitted light and reflected light) used a Zeiss Axioplan petrological microscope with a maximum magnification of 40 x. Optical CL imaging employed an equivalent microscope equipped with a CITL Technosyn 8200 MK4 luminoscope operated at 20 kV/200 nA. Images from the optical microscopes were collected digitally using a Nikon DN100 digital net camera. EBSD work used a FEI Quanta 200F SEM equipped with an EDAX/TSL system running OIM version 5.2 data collection software and using a Hikari high speed detector. Polished thin sections were produced by grinding specimens down and mounting, ground side down, on glass slides. Sectioning was carried out using a Buehler® Petrothin® and mechanical polishing used diamond lubricant, alpha alumina and colloidal silica.The thin sections were uncoated and studied with the SEM operated in low vacuum ($4.4e^{-1}$ Torr). Data were analysed and orientation maps and pole figures plotted using OIM version 5.2 analysis software. The lenses were chemically analysed qualitatively by simultaneous X-ray mapping during EBSD work and quantitatively by SEM spot analysis using EDAX Genesis hardware and software.

RESULTS

Eleven specimens of *Geesops schlotheimi* (Bronn, 1825) were analysed from the Eifelian of the Geeser Trilobitenfelder, Germany.

Lenses within the eye of *Geesops schlotheimi* vary significantly between specimens when viewed using plane polarised transmitted light and reflected light. Several thin sections contain lenses consisting of reasonably clear calcite crystals, others are more turbid and reflected light reveals microporosity as the source of this turbidity. A thin corneal covering, which can be traced into the alveolar ring, is present on the outer surface of some well preserved lenses; this too varies in appearance from optically clear calcite in some lenses to being darker and possibly iron stained in others. In transmitted light between crossed polarizers the central and basal areas of the lenses are in optically unity but extinction angles along an outer 'fringe' of the lens vary, producing a sweeping extinction pattern as the microscope stage is rotated.

Several specimens have lenses that contain intralensar structures similar to the core and bowl as described by Clarkson (1975; 1979) and others (Campbell, 1975; Miller and Clarkson, 1980; Lee *et al.*, 2007). These features are distinguishable from the rest of the lens by a distinct colour difference in plane polarised transmitted light. In some specimens the intralensar features are much darker than the enclosing lens calcite whereas in others they are optically clear and surrounded by a darker element of the lens. The clarity of the intralensar structures varies between thin sections.

Those lenses containing intralensar structures that are visible in transmitted light display equivalent features in CL images. The core luminesces more brightly than surrounding lens calcite whereas the intralensar bowl appears significantly duller. Cathodoluminesence imaging also reveals intralensar structures in lenses that apparently lack both intralensar bowls and cores when viewed in transmitted light (Fig. 1).

X-ray mapping has highlighted the presence of magnesium within the eyes. In addition to calcium, magnesium occurs throughout all of the lenses mapped although in several cases it is more highly concentrated in the central and basal areas of the lenses than the fringe. Quantitative spot analysis reveals that the concentration of magnesium in lens centres can be three times that of the rest of the lens. These magnesium-rich areas are not always coincident with intralensar structures visible using transmitted light. In marked contrast, magnesium concentrations are significantly lower in the intralensar sclera and in the host limestone.

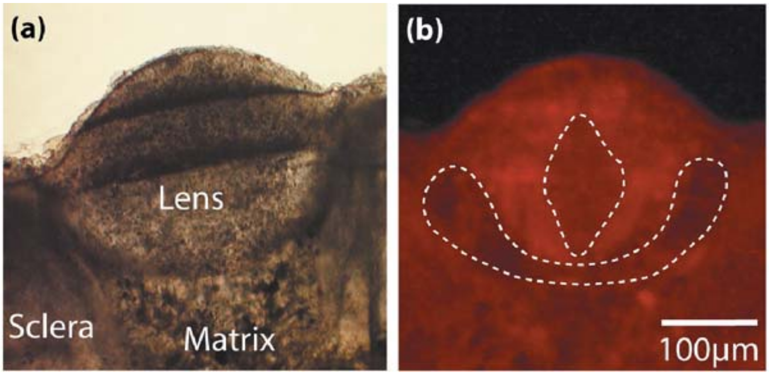

Figure 1. (a) Plane polarised transmitted light and (b) CL image of the same lens, seen in horizontal section. Note that an intralensar bowl and core (outlined) can be resolved only in the CL image. The eye has been cut perpendicular to the visual surface to produce horizontal cross-sections of the lenses, parallel to the plane in which the palpebral lobe lies.

EBSD maps reveal a consistent pattern in the crystallographic orientation of calcite in the lenses of all specimens. The central and basal areas of the lenses have uniform orientation with the calcite *c* axes oriented parallel to the lens axis. The upper area of the lens contains a 'fringe' within which calcite *c* axes are radially arranged (Fig. 2a) and pole figures highlight the orientation spread (Fig. 2b).

This radial fringe is visible in both horizontal and tangential sections of the lens. The thickness of the fringe varies between specimens although 40-55μm is typical. Fringe thickness can also vary by up to 50 μm between constituent lenses of the same eye. This microstructure does not extend into the cornea, the constituent calcite crystals of which have no preferred orientation. The interlensar sclera is very finely crystalline and has a distinct microstructure that is very different to that of lens calcite. The arrangement of crystals within the limestone matrix is random, although crystals immediately beneath the lens can share its orientation (Fig. 2a).

Calcite forming the fringe of a single lens can differ in *c* axis orientation from that of the lower part of the lens by up to 50°. EBSD misorientation profiles, which illustrate the change in crystal orientation from point to point along a line, show the change from uniform crystal orientation to the splaying of orientations to be gradual, as is the variation in *c* axis orientation within the fringe itself. Misorientation profiles can also highlight sub-grain boundaries within the lens; some lenses, possibly less well preserved, consist of several calcite crystals along the fringe, others display very fine scale crystallisation of a single crystal (Fig. 2a).

DISCUSSION

The lenses of all specimens studied here have a similar microstructure, which was initially observed by light microscopy and confirmed using EBSD. A similar arrangement of lens calcite crystals has been

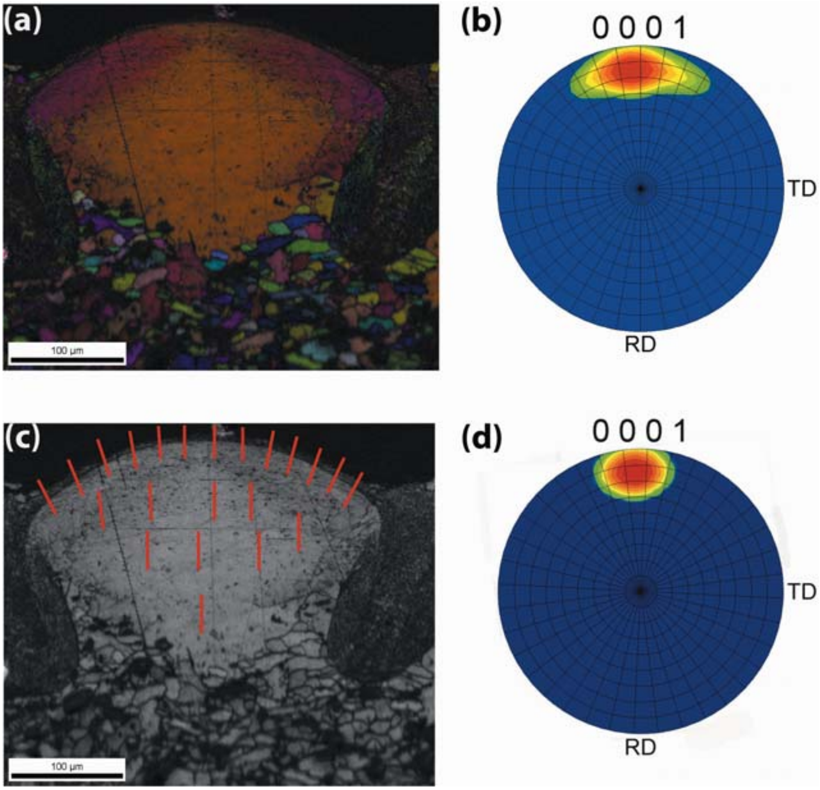

Figure 2. (a) EBSD orientation map of the lens in Figure 1. The gradual change in colour along the fringe denotes a change in *c* axis orientation. (b) Equal angle lower hemisphere pole figure showing the variation of crystal orientation throughout the lens in (a), the orientation of this lens is 75°. (c) EBSD map equivalent to (a) where orientation differences are not colour coded but indicated by the red lines, which are traces of the calcite *c* axis. (d) Pole figure of a *Dalmanites* sp. lens (from Lee *et al.*, 2006) showing a spread in crystal orientation of approximately 40°. Note the very significant difference in the spread of *c* axis orientations between lenses of the two species.

observed previously in several species of phacopids that have been variably diagenetically altered (Campbell, 1975) as well as in the lenses of other *Geesops* species from the same area which Bruton and Haas, (2003b) interpreted as being composed of aggregates of crystallites. EBSD has also highlighted how the thickness of the fringe and size of its constituent calcite crystals can vary significantly between lenses in a single eye. Some lenses appear to consist of a single calcite crystal in which the variation in *c* axis orientation around the fringe is extremely gradual (e.g. Fig. 2a). Although there are clear differences in crystallographic orientations within the lens, these results are consistent with Towe's conclusion (1975) that each lens was a single calcite crystal as EBSD misorientation profiles show no presence of sub-domains or crystallites. *Geesops* lenses analysed in the present study clearly differ in microstructure from those of *Dalmanites* sp. that were shown by Lee *et al*. (2007) to have uniform *c* axis orientation (Fig 2d). These results suggest that the phacopids developed at least two very different mechanisms for focusing light with the radiating fringe of *Geesops* possibly being used to guide peripheral light rays into a more central position within the lens.

The presence of the intralensar structures in CL images and the concentration of magnesium in the centres of lenses that are apparently featureless in transmitted light, support the suggestion by Campbell (1975), Clarkson (1975; 1979) and others (Clarkson and Levi-Setti, 1975; Miller and Clarkson, 1980) that these features are not the product of alteration, but original components of the lens (albeit partially modified during diagenesis). CL does not provide an exact indication of the lens chemistry but it does imply at least a subtle difference in composition between areas of varying luminescence. Features identified by CL imaging but absent in transmitted light may be remnants of the original intralensar structures.

CONCLUSIONS

EBSD and allied electron beam techniques have been used very successfully to confirm observations and interpretations made using traditional methods of analysis and to provide a wealth of new information. The spread of crystal orientation along the lens fringe may have new implications on the visual field of these trilobites. Previous studies into trilobite visual fields (Clarkson, 1966a; 1966b) have been based on the assumption that lens calcite is aligned parallel to the lens axis and that lens spacing allowed a latitudinal view of 15-20° (Stockton and Cowen, 1976). The 'intake range' of light travelling parallel to the lenses *c* axes orientation has here been shown to be much wider in the *Geesops* studied than previously calculated for phacopids, potentially providing the trilobite with a much broader field of vision and also a greater overlap of the visual fields of individual lenses, possibly enhancing the stereoscopic abilities of the eyes. Such wide visual field were also deduced by Schoenemann (2007) who argued these eyes functioned as a neural superposition system. EBSD and EDX results have not as yet provided conclusive answers as to how the schizochroal eye produced images but have raised important questions about the exact functions of each of the individual lens components.

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TRILOBITES FROM THE VARGAS PEÑA FORMATION (LLANDOVERY) OF ITAUGUÁ, EASTERN PARAGUAY

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Key words: Trilobites, Vargas Peña Formation, Llandovery, Itauguá, Paraguay.

INTRODUCTION

The Itacurubi Group (Harrington, 1972) represents the Lower Silurian of the intracratonic Paraná Basin in eastern Paraguay. The group comprises the Eusebio Ayala, Vargas Peña and Cariy formations, which document a Llandovery transgressive-regressive cycle. The clay-shales of the Vargas Peña Formation were deposited during the maximum flooding of the transgressive event, and contain trilobites and other marine invertebrates of malvinokaffric affinity (e.g. see Harrington, 1950; Wolfart, 1961; Benedetto *et al.*, 1992 and references therein; Uriz *et al.*, 2006 and references therein).

The trilobites from the type area of the Vargas Peña Formation (Vargas Peña clay pit =San Fernando Quarry) were originally studied by Harrington (1950, 1972), who described *Calymene boettneri* from the uppermost part of the unit. Subsequently Wolfart (1961) reported scarce material assigned to *Calymene* sp., *Calymene boettneri* Harrington, *Dalmanites*? sp. and *Eophacops* sp. In addition, Baldis and Hansen (1980) described the giant dalmanitid "*Guaranites*" *paraguayensis* from the San Fernando Quarry, but they did not provide information about its exact stratigraphic location.

New fossil samples from the Vargas Peña Formation at the San Fernando Quarry were recently collected. The aim of the present paper is to provide new data and records of trilobite species. This study includes the description of a columnar section representing the face of the quarry. The stratigraphic control is based on graptolites recorded from lower to upper parts of the formation (Uriz *et al.*, 2006, in prep.).

LOCATION AND AGE

The San Fernando Quarry is located close to Itauguá city, 60 km E of Asunción city, Paraguay (Fig. 1). Here, the Vargas Peña Formation is represented by light clays and micaceous shales about 25 m thick. The

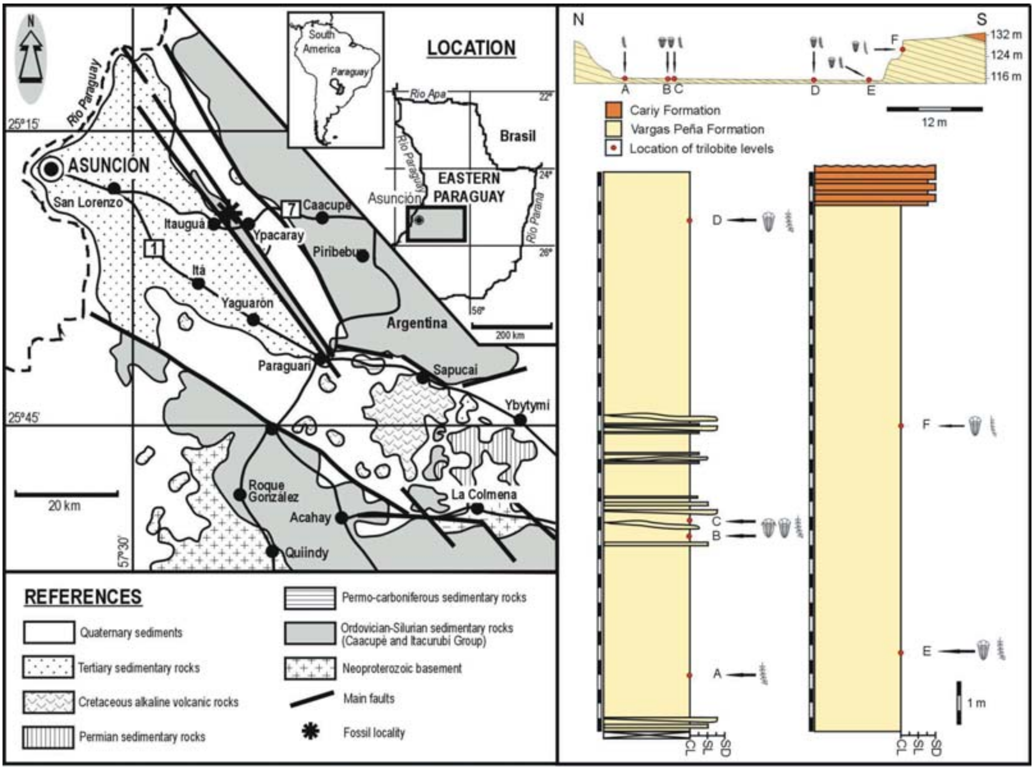

Figure 1. Geological map showing the location of the San Fernando Quarry, and stratigraphic section of the Vargas Peña Formation, showing all sampled horizons.

unit has yielded numerous macrofossils such as trilobites, graptolites, brachiopods, bivalves, gastropods, tentaculítids, nautiloids, hyoliths and crinoids. The trilobite levels are in the lower middle and upper parts of the formation (B-F, see Fig. 1). Levels A, B and C are characterized by the graptolite genera *Normalograptus* Legrand, 1987 and *Glyptograptus* Lapworth, 1873 (emend. Koren and Rickards, 1996), which suggest a Rhuddanian age (Uriz *et al*., in prep.). On the other hand, the graptolites recorded from the top of the section (level F) [*Monograptus* aff. *priodon* (Bronn), *Stimulograptus sedgwickii* (Portlock), ?*Demirastrites* sp.] are Aeronian – Telychian in age (Uriz *et al*., 2006).

NOTES ON THE FOSSILS

The specimens studied are very fragile external and internal moulds, so special care is needed during preparation. They are housed in the Museo de Ciencias Naturales de La Plata (MLP), Argentina.

Family Calymenidae Milne Edwards, 1840
Subfamily Calymeninae Milne Edwards, 1840
Genus *Calymene* Brongniart, 1822

Type species. *Calymene blumenbachii* Brongniart, from the Wenlock of England.

Calymene boettneri Harrington, 1950
(Pl. 1, figs. 1-7, 9)

1950. *Calymene boettneri* n. sp. Harrington, p. 73-76, pl. 1, figs. 1-3.

Material. Four complete specimens, 14 axial shields, 3 cephala, 4 cranidia, 11 thoraco-pygidia and 1 pygidium (MLP 31869-31901), levels ?C, D-F.

Remarks. Harrington (1950) provided a complete description of this species. *Calymene boettneri* differs from *C. ferrifera* Baldis and Blasco (in Baldis *et al*., 1976, pl. 1, figs. 1-3), from the Silurian Lipeón Formation (NW Argentina), by the presence of a more rounded preglabellar furrow, a more convex frontal lobe of the glabella, subtriangular lateral glabellar lobes (L1 and L2), and an occipital furrow of uniform width. It can be differentiated from *C. vallecitoensis* Waisfeld *et al*. (1988, pl. 1, figs. 1-8), from the Silurian Los Espejos Formation (Precordillera, western Argentina), by having a longer, not truncated glabella, a forward-curving occipital furrow, a slightly less raised pygidial axis which has 5-6 axial rings, less laterally expanded pleural fields, and fainter interpleural furrows.

Some materials from level C (3 axial shields and 2 thoraco-pygidia, MLP 31902, 31905, 31907, 31910; see Pl. 1, figs. 10, 11) could be conspecific with *C. boettneri*; however, they represent incomplete, slightly distorted individuals, so an unequivocal identification is not possible.

Calymene cf. *boettneri* Harrington, 1950
(Pl. 1, figs. 8, 12)

Material. One axial shield, 4 cranidia and 3 thoraco-pygidia (MLP 31903, 31908, 31911-31913, 31917, 31919, 31928), levels B, C.

Remarks. This taxon mostly resembles *Calymene boettneri* Harrington in having a rounded preglabellar furrow, a forward-curving occipital furrow, and eyes located moderately far the glabella, opposite glabellar lobe L2. However, the former differs in its less convex frontal lobe of the glabella and its less tumid L1 and L2.

Calymene sp. A
(Pl. 1, figs. 13-16)

1961. *Calymene boettneri* Harrington. Wolfart, p. 72, pl. 4, fig. 4,?5.

Material. Six cranidia (MLP 31904, 31906, 31911, 31914, 31916, 31935), levels B, C.

Remarks. *Calymene* sp. A is characterized by having a glabella constricted at L2, with a moderately convex, subquadrate frontal glabellar lobe, a larger, slightly more teardrop-shaped L1, and a wide, very slightly forwardly curving occipital furrow. These specimens are closely similar to the cephalon from the Vargas Peña Quarry assigned by Wolfart (1961, pl. 4, fig. 4) to *C. boettneri*. Similarly, an associated pygidium (see Wolfart, 1961, pl. 4, fig. 5) could be conspecific.

Subfamily Homalonotidae Chapman, 1890

Subfamily Homalonotidae Chapman, 1890

Genus *Trimerus* Green, 1832

Type species. *Trimerus delphinocephalus* Green, from the Wenlock of USA.

Trimerus sp.
(Figs. 2.5, 2.6)

Material. Two pygidia (MLP 31939, 31940), levels B, C.

Remarks. The pygidia found are ovate to subtriangular in outline, highly convex, with a gently tapering axis and indications of 10 axial rings, 7-8 pleural ribs and a short posterior mucro (see Fig. 2.5). These features enable the specimens to be assigned to *Trimerus*. Since the material is very scarce, it is left under open nomenclature.

Family Dalmanitidae Vodges, 1890
Genus *Dalmanites* Barrande, 1852

Type species. *Trilobus caudatus* Brünnich, from the Wenlock of England.

Dalmanites ypacarayensis (Baldis and Hansen, 1980)
(Figs. 2.1-2.4)

1980. *Makaspis ypacarayensis* sp. nov. Baldis and Hansen, p. 53-54, pl. 1, fig. A, pl. 2, fig. a.
1961. *Dalmanites*? sp. Wolfart, p. 74, pl. 4, fig. 8.

Material. Two cephala, 2 thoraco-pygidia and 3 pygidia (MLP 31922, 31930-31933, 31937, 31938), levels B, C.

Remarks. The cephala studied herein do not differ from that originally described as *Makaspis ypacarayensis* by Baldis and Hansen (1980, pl. 2, fig. a). Associated pygidia are slightly convex, subtriangular in outline, with a posterior process. The pygidial axis is conical in outline and composed of 8 rings and a terminal piece, whereas the pleural fields show 7 pairs of pleural furrows that are progressively curved backwards, and faint interpleural furrows.

According to Edgecombe (in Jell and Adrain, 2003), *Makaspis* Baldis and Hansen is a junior synonym of *Dalmanites*. As suggested by Baldis and Hansen (1980, p. 53), *D. ypacarayensis* seems to be conspecific with the poorly preserved cranidium from the Vargas Peña Quarry assigned by Wolfart (1961, pl. 4, fig. 8) to *Dalmanites*? sp. *Dalmanites ypacarayensis* differs from *D. sudamericanus* Benedetto and Martel in Baldis *et al.* (1976, pl. 3, figs. 1-3) from the Silurian Lipeón Formation (NW Argentina), mainly in having transverse, fainter glabellar furrows S1 and S2, and a narrower (sag.) occipital ring.

Dalmanites paraguayensis (Baldis and Hansen, 1980)
(Figs. 2.7-2.10)

1980. *Guaranites paraguayensis* sp. nov. Baldis and Hansen, p. 60-62, pl. 1, fig. C, pl. 3, figs. a-d.

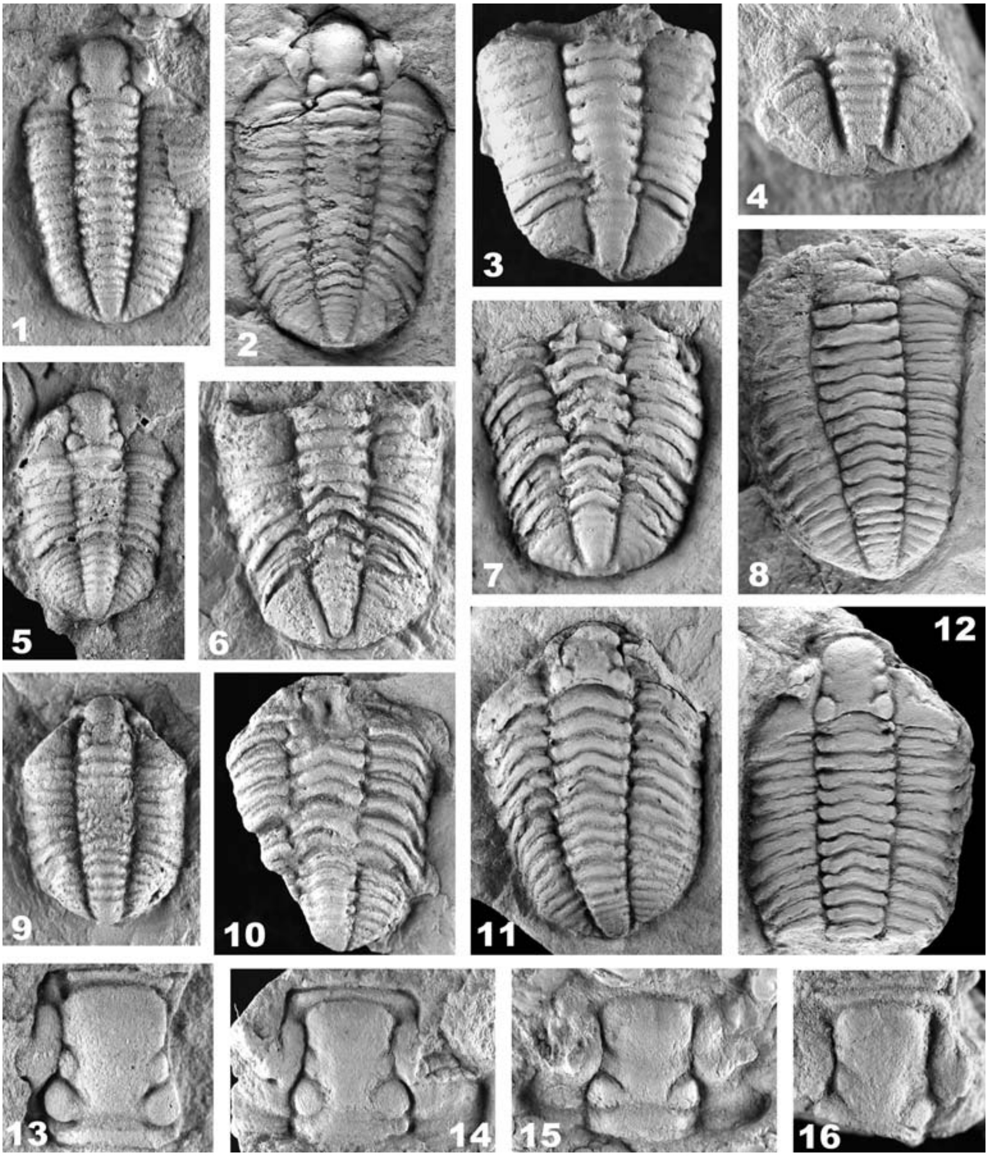

Plate 1. Calymenid trilobites from the Vargas Peña Formation at San Fernando Quarry, Itauguá. 1-7, *Calymene boettneri* Harrington; 1, axial shield, MLP 31888, level E, x1.5; 2, axial shield, MLP 31877, level E, x1.1; 3, thorax-pygidium, MLP 31869, level F, x1.1; 4, pygidium, MLP 31874, level F, x1.4; 5, axial shield, MLP 31879, level D, x1.9; 6, thorax-pygidium, MLP 31873, level F, x1.1; 7, thorax-pygidium, MLP 31896, level D, x1.4. 8, *Calymene* cf. *boettneri* Harrington, thorax-pygidium, MLP 31917, level C, x0.9. 9, *Calymene boettneri* Harrington, MLP 31885, level E, x1.6; 10-11, *Calymene boettneri*? Harrington; 10, hypostome, thorax and pygidium, MLP 31910, level C, x1.5; 11, axial shield, MLP 31902, level C, x1.2. 12, *Calymene* cf. *boettneri* Harrington, axial shield, MLP 31919, level C, x1.1. 13-16, *Calymene* sp. A, cranidium; 13, MLP 31906, level B, x1.9; 14, MLP 31904, level C, x1.5; 15, MLP 31916, level C, x1.9; 16, MLP 31909, level B, x2.1.

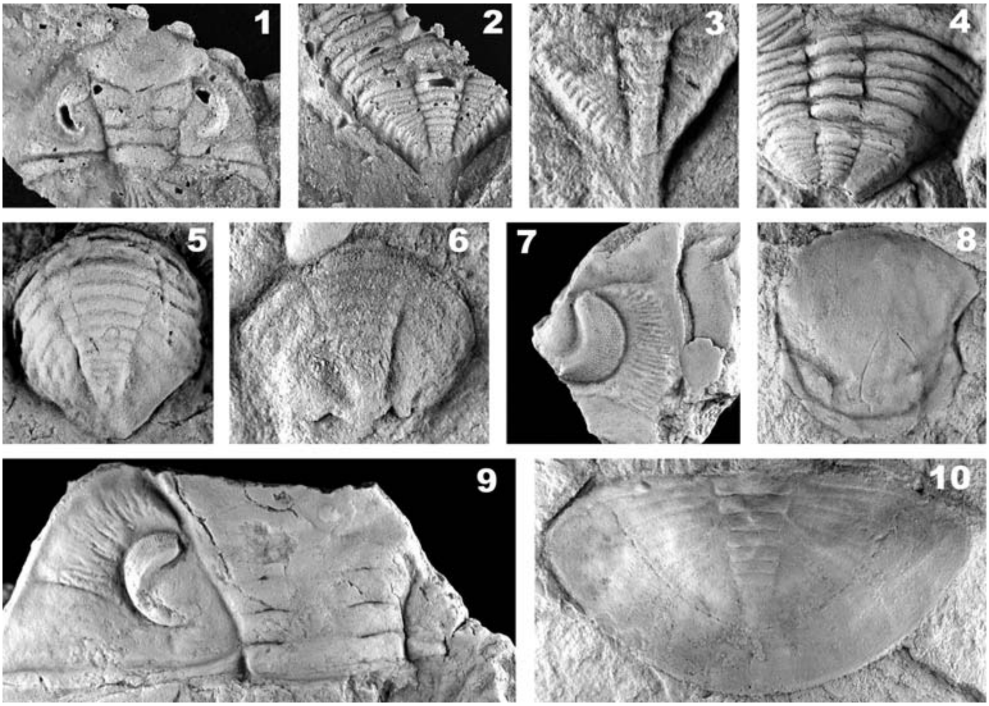

Figure 2. Dalmanitid trilobites from the Vargas Peña Formation at San Fernando Quarry, Itauguá. 1-4, *Dalmanites ypacarayensis* (Baldis and Hansen); 1, cephalon, MLP 31922, level C, x1.4; 2, fragmentary thorax-pygidium, MLP 31932, level B, x1.4; 3, pygidium, MLP 31930, level C, x2.2; 4, fragmentary thorax-pygidium, MLP 31938, level B, x1.1. 5-6, *Trimerus* sp., pygidium; 5, MLP 31939, level B, X1.2; 6, MLP 31940, level C, x1.9. 7-10, *Dalmanites paraguayensis* (Baldis and Hansen); 7, ocular area, MLP 31927, level B, x1; 8, hypostome, MLP 31926, level C, x0.8; 9, fragmentary cephalon, MLP 31923, level C, x0.8; 10, pygidium, MLP 31921, level B, x0.6.

Material. Six fragmentary cephala, 1 hypostome and 2 pygidia (MLP 31920, 31921, 31923-1927, 31929, 31936), levels B, C.

Remarks. *Dalmanites paraguayensis* is a giant dalmanitid that was fully described by Baldis and Hansen (1980) from the Itacurubi Group of the Vargas Peña locality. It was originally assigned to *Guaranites* Baldis and Hansen, a name that has been suppressed as a subjective junior synonym of *Dalmanites* (see Edgecombe in Jell and Adrain, 2003).

CONCLUSIONS

Both calymenid and dalmanitid trilobites are well represented in the Vargas Peña Formation at the type locality, Itauguá. Major diversity [*Calymene* cf. *boettneri* Harrington, *Calymene* sp. A, *Trimerus* sp., *Dalmanites ypacarayensis* (Baldis and Hansen), *Dalmanites paraguayensis* (Baldis and Hansen)] is recorded from the lower middle part of the section, where alternations of clays, shales and sandstones are indicative of changes in ventilation of bottom waters and nutrient supply. Lower graptolites suggest a Rhuddanian age. On the other hand, *Calymene boettneri* Harrington is restricted to the clays of the middle and upper part of the formation, where it forms a monospecific trilobite assemblage. The graptolites of the upper interval indicate an Aeronian – Telychian age.

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THE PROTO-ANDEAN MARGIN OF GONDWANA AND ACCRETED TERRANES: CONTRASTING BIOGEOGRAPHIC SIGNATURES BASED ON LATE CAMBRIAN-EARLY ORDOVICIAN TRILOBITES

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Keywords. Trilobite, Late Cambrian, Early Ordovician, South America, biogeography.

INTRODUCTION

Biogeographic affinities of Late Cambrian-Tremadocian trilobites from different South American Early Paleozoic geologic units are discussed. The latter involve the Cordillera Oriental and western Puna (in the Northwestern basin), as well as the Famatina and the Precordillera basins, which account for contrasting geodynamic settings and depositional histories (Fig. 1). New collections, progress in taxonomic revisions, and new age constraints of several biogeographically important taxa contribute to a more accurate picture of trilobite affinities in the Proto-Andean margin of Gondwana and accreted terranes for the Late Cambrian-Tremadocian.

The Northwestern basin involves major areas (Puna, Cordillera Oriental, Sierras Subandinas, Sierras de Santa Bárbara, and subsurface Chaco plains) that according to recent interpretations are regarded as adjacent depozones of a foreland basin system (Bahlbug and Furlong, 1996; Astini, 2003). Trilobites from Late Cambrian-Tremadocian units from the Cordillera Oriental (peripheral bulge depozone) and western Puna (volcanic arc complex) are considered. In the Argentine Cordillera Oriental, trilobites from the Lampazar Formation, Guayoc Chico Group and Santa Rosita Formation (mainly Casa Colorada, Alfarcito, and Rupasca members) are evaluated. The Guayoc Chico Group and the Santa Rosita Formation mostly record shallow wave-dominated subtidal, offshore to shoreface deposition, under the influence of deltaic systems, with conversions into tide-dominated estuarine complexes in the later unit (Buatois *et al*., 2006). The Lampazar Formation is largely represented by offshore deposits. In the Bolivian Yunchará segment, the northern continuation of the Argentine Cordillera Oriental, studied trilobites come from the Iscayachi Formation (Uppermost Cambrian-Tremadocian), interpreted as a storm-influenced prodelta to delta front setting (Egenhoff *et al*., 2004).

Trilobites from the Western Puna derive from the Las Vicuñas Formation, which has been interpreted as a shallow marine environment with strong volcanic influence. According to Coira and Koukharsky (2003) it records an early volcano-sedimentary episode indicating a calc-alkaline arc association. Its marginal position to Gondwana is largely interpreted from faunal data.

Figure 1. Location map of major geologic units mentioned in the text. Northwestern basin involves Sierras Subandinas, Cordillera Oriental, and Eastern and Western Puna.

In the Famatina Basin trilobites of the Volcancito Formation (Late Cambrian-Earliest Ordovician) are considered. This unit is mainly composed of carbonates and fine-grained siliciclastics, and has recently been interpreted as deposited in a passive continental margin (Astini and Dávila, 2004). According to these authors, later in the Ordovician this setting changed to a subduction zone related to a volcanic arc developed in the western Gondwana margin (Famatina Group).

The Precordillera represents an exotic terrane rifted from Laurentia and accreted to the proto-Andean margin of Gondwana (Benedetto, 2004 and references therein). Thick carbonate successions were deposited during the time interval included in this analysis. Trilobite-bearing units include the La Flecha Formation (Upper Marjuman–Furongian) that has been interpreted as a regional peritidal carbonate shelf by Cañas (1999). Other Upper Cambrian fossiliferous localities correspond to resedimented boulders of the Empozada and Los Sombreros formations in Mendoza and San Juan (Bordonaro *et al*., 1993).

FURONGIAN-EARLY TREMADOCIAN TRILOBITES

Late Cambrian trilobites are constrained to the *Neoparabolina frequens argentina* Zone, both in the Cordillera Oriental (Lampazar Formation, Casa Colorada Member of the Santa Rosita Formation) and in Famatina (Volcancito Formation). In the Cordillera Oriental the *Neopabolina frequens argentina* Zone is composed of *Neoparabolina*, *Parabolinella*, *Plicatolina*, *Beltella*, *Angelina*, *Hapalopleura, Onychopyge,* and *Akoldiniodinia* (Harrington and Leanza, 1957; Esteban and Tortello, 2007). Additionally, on the basis of new collections and the revision of the fauna described by Benedetto (1977), it is possible to anticipate the presence of *Golasaphus*, *Onchonotellus*, and *Rhadinopleura*. In Famatina, the trilobite fauna includes *Neoparabolina*, *Plicatolina*, *Parabolinella*, and *Angelina*, as well as *Asaphellus*, *Rhadinopleura*, *Onychopyge*, and *Conophrys* (Tortello and Esteban, 2007). In the Western Puna, the Las Vicuñas Formation (Uppermost Cambrian-basal Tremadocian) yielded a diverse trilobite association including *Prochuangia*, *Leiostegium*, *Amzaskiella*, *Onychopyge*, *Proceratopyge* (*Lopnorites*), *Australoharpes*, *Palquiella*, *Golasaphus*, *Hospes*, *Onchonotellus, Parabolinella*, *Plicatolina*, *Conophrys*, and agnostids. Some of these forms were previously recorded by Moya *et al*. (1993), Malanca *et al*. (1998), and Waisfeld and Vaccari (2003). Recent collections by the authors in classical localities from southern Bolivia (Tambo Guanacuno and Cuesta de Erquis) yielded rich trilobite associations from the Iscayachi Formation. In Tambo Guanacuno, *Onychopyge*, *Proceratopyge* (*Lopnorites*), *Palquiella*, *Golasaphus*, *Asaphellus*, *Parabolinella*, *Saltaspis*, and *Conoprhys*, are so far recorded. In Cuesta de Erquis *Asaphellus*, *Kainella*, *Parabolinella*, *Angelina*, and *Conophrys* are present. Some of these taxa were previously recognized by Kobayashi (1937), Suarez Soruco (1975), Přybyl and Vanek (1980), Vaccari *et al*. (2006), and Vaccari *et al*. (submitted).

In our collections from lower Tremadocian strata of the Cordillera Oriental, the olenids *Parabolinella*, *Leptoplastides*, *Angelina*, *Jujuyaspis*, *Saltaspis*, and *Bienvillia* occur. As well, *Leiostegium*, *Kainella*, *Parakainella*, *Apatokephalus*, *Asaphellus*, *Hapalopleura*, *Brackebuschia*, *Onychopyge*, *Conophrys*, and *Amzaskiella* are recorded. Some of these elements were previously recognized by Kobayashi (1935, 1936), Harrington and Leanza (1957), Tortello *et al*. (1999), Malanca and Brandán (2000), and Waisfeld and Vaccari (2003).

In the Precordillera terrane, Vaccari (1994, 1995) recognized the *Crepicephalus*, *Aphelaspis*, and *Saukia* zones in the La Flecha Formation. Trilobites from the Crepicephalus Zone are represented by *Crepicephalus*, *Cosella*, *Pemphigaspis*, *Madarocephalus*, *Welleraspis*, *Lonchocephalus*, *Kingstonia*, and *Komaspidella*. In the *Aphelaspis* Zone (Furongian) only the records of *Dytremacephalus* and *Cheilocephalus* are reported. An association dominated by plethopeltids, represented by species of *Plethopelthis* and *Stenopilus* (*Saukia* Zone) is recorded in the uppermost levels of the La Flecha Formation. The boulders of the Empozada and Los Sombreros formations yielded trilobites of the *Cedaria*, *Tricrepicephalus*, *Elvinia*, and *Saukia* zones (Borrello, 1971; Shergold *et al*., 1995; Bordonaro, 2003).

DISCUSSION

Some of the olenids recorded from both Famatina and Cordillera Oriental are traditionally included in the "olenid fauna" known from broadly similar environmental settings in biogeographically disparate regions such as Baltica, Avalonia, Laurentia, and Siberia. Olenids are associated with several widespread agnostids, as well as trilobites belonging to several families. However, Vaccari *et al*. (2006) noted that some early Tremadocian taxa documented in the Cordillera Oriental suggest east Gondwanan connections.

Onychopyge occurs in the Upper Cambrian of the Volcancito Formation and Upper Cambrian and Lower Tremadocian of the Cordillera Oriental, and the Yunchará segment. This taxon is known from several species in the Upper Cambrian of NE China (Lu *et al*., 1986). It is more widely distributed in the early/middle Tremadocian, with records in Australia and New Zealand, North and South China, and Mexico. *Australoharpes* occurs in the lower Tremadocian of the Cordillera Oriental, Famatina, and Western Puna, and it is known elsewhere form Victoria (Australia). Jell (1985) pointed out the affinities of the faunas from Argentina and Victoria, and Webby *et al*. (2000) also emphasized the records of *Australoharpes* and *Onychopyge* as good indicators of these connections. The record of *Amzasskiella* in the early Tremadocian of the Cordillera Oriental and Western Puna reported by Vaccari *et al*. (2006) is also significant. This form occurs in East Gondwanan settings (China, Australia, and New Zealand), as well as in Siberia and Kazakhstan. Hence, lower Tremadocian elements exhibiting restricted geographic distributions support faunal affinities with warm water settings.

New findings, recorded for the first time in Argentina, are now added. They include *Prochuangia*, *Proceratopyge* (*Lopnorites*), *Golasaphus*, and *Onchonotellus*. Although some of these taxa exhibit a relatively wide geographic distribution (e.g. *Onchonotelus*, *Proceratopyge* and *Prochuangia*), *Golasaphus* is restricted to warm areas of Gondwana (China, Australia, and the Oaxaca block). The record of *Brackebuschia* in the early Tremadocian of the Cordillera Oriental is also remarkable. Although the genus ranges into the early Sandbian (Ludvigsen, 1980; Ebbestad, 1999; Adrain in Jell and Adrain, 2003), the earliest records are so far restricted to the late Tremadocian of Scandinavia (Tjvernik, 1956; Ebbestad, 1999) and the Cordillera Oriental. Another taxon with a restricted geographic distribution is *Hospes*, otherwise recorded from Scandianvia and China. Hence, available data suggest that trilobite faunas exhibit close affinities with different areas developed in the eastern margin of Gondwana. Furthermore, links with other areas such as the Oaxaca block are highlighted.

Widely distributed forms (e.g. agnostids, *Irvingella*, *Parabolinella*), along with geographically restricted elements such as *Tricrepicephalus, Elvinia*, and *Hungaia*, are recorded in the Precordillera. Genera documented in the peritidal carbonates of the La Flecha Formation are so far only reported from Laurentia. The occurrence of several Upper Cambrian species shared between Laurentia and Precordillera is remarkable. These forms involve *Crepicephalus iowensis* (Owen), *Tricrepicephalus texanus* (Shumard), *Komaspidella laevis* Rasetti, *Madarocephalus laetus* Resser, *Cheilocephalus brachyops* Palmer, and *Elvinia roemeri* (Shumard), along with the pelagic trilobite *Irvingella major* Ulrich and Resser. Some of these species (e.g. *T. texanus*, *C. brachyops,* and *E. roemeri*) are widely represented in North America (Palmer, 1965; Westrop, 1986; Pratt, 1992; Chatterton and Ludvigsen, 1998, among others), while others are more narrowly distributed and suggest more closely related areas. Among them, *M. laetus* reported from Alabama, Tennessee, and Quebec (Rasetti, 1946, 1965), and *K. laevis* documented in Virginia, Missouri, and Newfoundland (Rasetti, 1961; Lochman, 1968; Westrop, 1992) are noteworthy. Accordingly, Late Cambrian trilobite faunas from the Precordillera belong to the biogeographic province of Laurentia; strong affinities with the eastern part of this palaeocontinent are evident. These records give strong support to the evidence that during the Late Cambrian there were no barriers to faunal exchange between the Precordillera and Laurentia.

CONCLUSIONS

According to the records discussed herein, Furongian-early Tremadocian trilobites from the proto-Andean margin of Gondwana are broadly composed of numerous taxa accounting for a wide geographic distribution. However, the presence of biogeographically sensitive taxa, such as *Onychpyge*, *Amzaskiella*, *Golasaphus*, and *Australoharpes* is significant. The fauna as a whole exhibits close links with coeval trilobite faunas reported from the Oaxaca block, in agreement with its position adjacent to the margin of Gondwana suggested by previous authors (cf. Fortey and Cocks, 2003).

Trilobite records throughout the Cambrian successions of the Precordillera point to a strong faunal identity with Laurentia, and also to the absence of faunal exchange with coetaneous areas of East Gondwana. This influence persisted until the Tremadocian. Accordingly, the Laurentian Precordillera terrane is as allochthonous to the margin of Gondwana as the Gondwanan Oaxaca terrane is to the margin of Laurentia.

Aceñolaza *et al.* (2002) proposed a parautochthonous model for the Precordillera, recently upheld also by Finney (2007). According to this model, Cuyania is located adjacent to the Gondwanan margin during the Cambrian, close to Antartica. In their reconstruction Australia, Antartica, and Cuyania are in a similar latitudinal position, with carbonate platforms developed in the three areas, without separation by oceanic barriers. Cambrian faunas from Antartica and Australia conform a closely related area within the well-known Redlichiid Realm. Surprisingly, no faunal elements are shared despite this geographic proximity. If the position of Cuyania relative to Antartica and Australia was that supposed in the parautochthonous model, a fluid faunal exchange among these blocks should be expected in both directions. Accordingly, Upper Cambrian-Lower Ordovician trilobite evidence does not support the parautochthonous model for the Precordillera proposed by Aceñolaza *et al*. (2002), and Finney (2007).

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HYOLITHS WITH ENTOMBED TRILOBITES – CRYPTIC BEHAVIOUR OF TRILOBITES?

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Keywords: Barrandian area, Cambrian, cryptic behaviour, Hyolitha, Skryje, trilobites.

INTRODUCTION

Occurrence of minute miomerid trilobites in "worm" conches from the Burgess Shale and findings of complete specimens of polymeroid trilobite exoskeletons in the Silurian sea-floor cavities have been documented recently (Chatterton *et al*., 2003). Whereas presence of complete trilobite exoskeletons inside cephalopod conchs from the Silurian of the Barrandian area have been known for a long time (e.g. Barrande, 1872, and Davis *et al*., 2001).

Findings of complete polymeroid trilobite exoskeletons and other remains of various skeletal fauna inside of large hyolithids are reported here.

MATERIAL

Five hyolithid genera were determined in the Cambrian sediment of the Skryje-Týřovice Basin since the 19th century. The biggest specimens belong to the genus *Maxilites* Marek, 1972 namely to the species *Maxilites maximus* (Barrande, 1867), which was ascertained at several localities (Buchava, Čihátko Hill, Dlouhá Hora Hill and Mlečice). Adult hyolithid conchs of this species reach up 150 mm.

Highly diversified skeletal fauna including relatively common conchs of *Maxilites maximus* (Barrande, 1867) has been recently discovered at the Milíř locality at Čihátko Hill (Buchava Formation, "Middle" Cambrian, Skryje-Týřovice Basin, Barrandian area, Czech Republic). Several tens of hyolithid conchs were found; about 60 % of specimens contain entombed remains of the following fauna.

1. Complete randomly orientated specimens as well as disarticulated parts of polymeroid trilobite exoskeletons of *Skreiaspis spinosa* (Pompeckj, 1895) and *Conocoryphe* sp.
2. Disarticulated remains of undeterminable echinoderm species.
3. Practically complete hyolithid conch (*Oboedalites* sp.) with attachment organ of eocrinoid gen. et sp. nov.

Figure 1. Dorsal view on the inside of adult hyolithid conch of *Maxilites maximus* (Barrande, 1867) with preserved remain of complete specimen *Skreiaspis spinosa* (Pompeckj, 1895).

At the studied locality the following accompanying fauna has been ascertained: abundant polymeroid trilobites [e.g. *Eccaparadoxides pusillus* (Barrande, 1846); *Ctenocephalus* (*C.*) *coronatus* (Barrande, 1846); *Mikaparia mutica* (Hawle *et* Corda, 1847); *Hydrocephalus carens* Barrande, 1846)], miomeroids [*Phalagnostus nudus* (Beyrich, 1845); *Diplorrhina cuneifera* (Barrande, 1846)], echinoderms (e.g. *Stromatocystites pentangularis* Pompeckj, 1895; *Trochocystites bohemicus* Barrande, 1846; *Ceratocystis perneri* Jaekel, 1901), rhynchonelliformean and acrotretid brachiopods [*Bohemiellla romingeri* (Barrande, 1848); *Acrothele quadrilineata* Pompeckj, 1895; *Luhotreta pompeckji* Mergl and ?lehoferová, 1990] and hyolithids [*Oboedalites oboediens* (Barrande, 1867); *Parentilites parens* (Barrande, 1867); *Slapylites signatulus* (Novák, 1891); *Maxilites maximus* (Barrande, 1867)].

DISCUSSION

We suppose the following succession of events leading to the origin of entombed association:

The large hyolith *Maxilites* died first, in several findings opercula are positioned not too distant from the conch aperture. The conchs are usually oriented by the flattened ventral side downwards. After release of the operculum, the decaying rests of soft tissue could attract trilobites as food. However the cavity inside the conch could stay free being filled by sediments and/or sediment with skeletal debris brought by currents. The free space could be also used as a protected environment during different periods of trilobite life.

The origin of entombed fauna in hyolithids can be caused by several processes.

1. According to the functional-morphological analysis of trilobite exoskeletons (Fortey and Owens, 1999, and Whittington, 1997) holaspid specimens of trilobite genera *Skreiaspis* and *Conocoryphe* had unattached (natant) hypostomes which have been interpreted as being associated with particle feeding life habits. It means that they could actively seek for place inside of hyolithid conch

to feed on more or less disintegrated soft tissues. This theory is supported by findings of complete trilobite exoskeletons (Fig. 1); in some cases with preserved axial spines (*Skreiaspis*) which strengthen probability of the *in situ* preservation.

2. The next plausible explanations of the above mentioned findings could be feeding on bacteria decomposing soft parts of the hyolith carcase or on bacteria growing inside of the hyolith conch (= possible gardening of *Skreiaspis*).
3. Another possible explication is seeking for sheltered space to perform the ecdysis or for mating.
4. Disarticulated exoskeletal remains of trilobites (*Skreiaspis* and *Conocoryphe*) as well as the isolated echinoderm plates are could represent result of postmortal accumulation.
5. The conch of hyolithid *Oboedalites* sp. with attachment organ of echinoderm on its dorsum is another example of postmortal placement.

The findings of large hyolithid conchs with entombed trilobite fauna show hyolithids as a potential refuge for ecdysis. This possible cryptic behaviour of trilobite provides another ecological aspect of the Cambrian fauna.

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TOWARD AN INTEGRATED STRATIGRAPHY OF THE MIDDLE CAMBRIAN-FURONGIAN-TREMADOCIAN FROM THE SOUTHERN MONTAGNE NOIRE, FRANCE

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Keywords: Lithostratigraphy, chronostratigraphy, chemostratigraphy, trilobites, biodiversity.

INTRODUCTION

Since the discovery in the Montagne Noire (Languedoc, France) of Barrande's "primordial fauna" (or *Paradoxides* Beds) and Ordovician faunas in the second half of the 19th Century, the southern prolongation of the Hercynian Central Massif has become one of the key outcrops to understand the evolution of early Palaeozoic trilobites in Gondwana. The strata of this Gondwanan margin mainly represent inner- to outer-platform environments, and so lack the cosmopolitan taxa more typical of distal basin settings. As a result, trilobites are dominated by Mediterranean and endemic taxa, and biostratigraphic correlations beyond this palaeogeographic domain are difficult (Álvaro *et al.*, 1999, 2003).

One useful approach to correlating Cambrian-early Ordovician GSSP's throughout the Mediterranean area is to couple regional bio- and eco-stratigraphic correlations with chemostratigraphy. Secular variations in $^{87}Sr/^{86}Sr$, ‰^{18}O and ‰^{13}C are not only of importance for chronostratigraphic correlation, but also for the reconstruction of trends in palaeoclimate, biogeochemical cycling, and tectonic evolution. The purpose of this paper is to summarize the chrono- and chemostratigraphic constraints on the replacement of trilobite assemblages throughout the middle Cambrian-Tremadocian of the southern Montagne Noire. This integrated stratigraphic framework (see sketch in Figure 1) is improving our knowledge of the biogeographic and biodiversity factors (such as immigration and subsequent multiplication of taxonomic lineages) that controlled the distribution of trilobites in NW Gondwana, and represents a further step in the achievement of an integrated stratigraphy for the Cambrian-Ordovician of the southern Montagne Noire (see previous synthesis in Vizcaïno and Álvaro, 2001).

MIDDLE CAMBRIAN

The middle Cambrian strata of the southern Montagne Noire mimic the carbonate-to-siliciclastic succession recorded in neighbouring platforms, such as the Cantabrian Mountains (northern Spain) and Sardinia (Italy). During the lower-middle Cambrian transition a large carbonate platform fringed West

Gondwana, which recorded a diachronous tectonic breakdown (responsible for the deposition of the condensed "griotte" limestone/shale couplets) and the final demise of carbonate productivity. The rich and diverse solenopleurid-paradoxidid-conocoryphid trilobite assemblage that colonized these substrates has allowed the subdivision of the middle Cambrian into three regional stages (named Leonian, Caesaraugustan, and Languedocian, respectively referred to the Cantabrian Mountains, the Iberian Chains, and the Montagne Noire). A correlation of these stages with the Moroccan ones was proposed by Álvaro *et al*. (2003) and Geyer and Landing, 2004). The time span involved in each stage is very different. The Leonian is mainly represented by condensed "griotte" units (reddish to purple alternations of centimetre-thick shales and limestones); on the assumption that their small-scale cycles were the result in the Iberian Chains of the influence of the obliquity and precession cycles, a rough estimate of the duration of these changes would reflect a time span of 1.33-1.45 Ma for the Leonian (Álvaro *et al*., 2000). The Caesaraugustan is represented by up to 150 m of offshore-dominated shales; its fossil record is characterized by a distinct phylogenetic plasticity of solenopleuropsine trilobites, which has allowed a fine biostratigraphic resolution into three substages and at least 10 zones (Álvaro and Vizcaïno, 1998). Finally, the Languedocian is represented by more than 500 m of sandstones, shales and interbedded limestones in the Montagne Noire, and seemingly represent a time span larger than that involved in the Leonian and Caesaraugustan stages.

Two chemostratigraphic shifts are recognized in the middle Cambrian of the Montagne Noire. (1) Although the ROECE (or Redlichiid-Olenellid Extinction Carbon Isotope Excursion; Zhu *et al*., 2006) negative shift in ‰ ^{13}C is not recognized in the Montagne Noire, Wotte *et al*. (2007) have identified a similar long-term trend to higher ‰^{13}C values that was punctuated by a succession of two Bilbilian shifts and two Leonian shifts both in the Cantabrian Zone and the Montagne Noire. By comparison with the Cantabrian Zone, the erosive contact that marks the Lastours/Pont de Poussarou lithostratigraphic boundary is consistent with the lower–middle Cambrian (Iberian) boundary. (2) The DICE (Drumian Carbon Isotope Excursion) event is a large negative excursion in ‰ $^{13}C_{carb}$ nearly coinciding with the beginning of the Drumian. The lower part of the La Gardie Formation in the Pardailhan nappe displays background ‰ $^{13}C_{org}$ values of -22 ‰ punctuated by a large negative shift in the middle Languedocian (Álvaro *et al*., in press). This negative excursion is similar in character to the DICE event reported close to the base of the Drumian, although the latter was exclusively based on ‰ $^{13}C_{carb}$ values.

FURONGIAN

The Furongian is devoid of significant gaps in the southern Montagne Noire. Sedimentation took place in a transgressive-dominated depositional system with common offshore deposits and clayey substrates. The Furongian is also associated with the onset of a tectonic instability that led to the episodic establishment of palaeotopographies and record of slope-related facies associations (Álvaro *et al*., 2007)

Although the base of the 'regional Upper Cambrian" was at first located at the FAD of the trilobite *Palaeadotes latefalcata* (Álvaro and Vizcaïno, 1998), a recent chemostratigraphic re-evaluation of the involved carbonate and shale strata has allowed the identification of the SPICE (Steptoean Positive Carbon Isotope Excursion) chemostratigraphic event in the Montagne Noire. As a result, the beginning of the 'regional Late Cambrian' pre-dated the Furongian. The top of the Furongian is interpolated below the FAD of Tremadocian conodonts, as a result of which the Furongian is reduced to less than 30 m in some condensed outcrops characterized by the presence of griotte units.

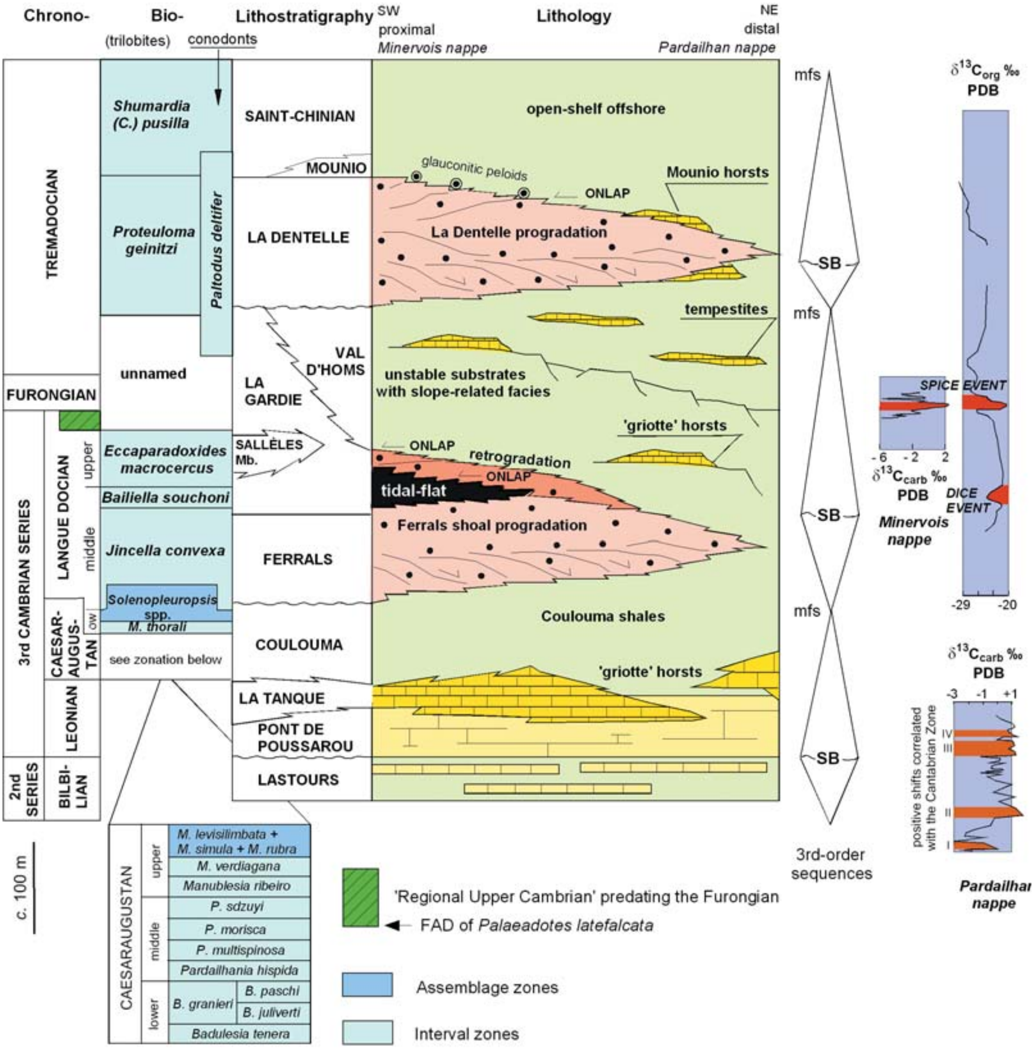

Figure 1. Updated sketch of the middle Cambrian-Furongian-Tremadocian stratigraphic framework from the southern Montagne Noire summarizing recent litho-, bio-, chrono-, sequence, and chemo-stratigraphic data (based on Álvaro and Vizcaïno, 1998; Vizcaïno and Álvaro, 2001, 2003; Álvaro *et al*., 2007, in press; Wotte *et al*., 2007); SB, sequence boundary; mfs, maximum flooding surface; PDB, Peedee belemnite reference.

TREMADOCIAN

The Tremadocian open-shelf shales of the southern Montagne Noire are punctuated by the progradation of a coarse-grained siliciclastic system (La Dentelle Formation). The subsequent transgression recorded the last episode of carbonate productivity (Mounio Formation) in the Montagne-Noire platform, finally flooded and replaced by offshore-to-basinal shales (Saint-Chinian Formation), in which the Tremadocian-Floian transition is tentatively included. The aforementioned carbonates display the last record of conodonts belonging to the *Paltodus deltifer* Zone, a biostratigraphic unit that contains the *Proteuloma geinitzi* trilobite Zone and a part of the *Shumardia (C.) pusilla* Zone. No chemostratigraphic shifts are identified in the Saint-Chinian Formation, which is characterized by a gradual (upward) increase in organic content.

TRILOBITE REPLACEMENTS AND PALAEOCLIMATIC IMPLICATIONS

Several immigration events are recognized throughout the latest middle Cambrian, Furongian and Tremadocian. The trilobites show a stepwise replacement of Acado–Baltic-type families (e.g., the typical Leonian-Caesaraugustan conocoryphid-paradoxidid-solenopleurid assemblage) characterized by: (i) a late Languedocian co-occurrence of middle Cambrian trilobite families with the first anomocarid, dorypygid and proasaphiscid invaders; (ii) a Furongian immigration, replacing previous faunas, composed of aphelaspidids, catillicephalids, ceratopygids, damesellids, eulomids, idahoiids, lichakephalids, lisaniids, onchonotinids, and pagodiids; and (iii) the subsequent input of asaphids, calymenids, catillicephalids, nileids and remopleurids that marks the base of the *Proteuloma geinitzi* Zone coeval with a distinct immigration of Tremadocian conodonts (representative of the *Paltodus deltifer* Zone; Álvaro *et al.*, 1999, 2003, 2007; Vizcaïno and Álvaro, 2001, 2003).

A shift from subtropical carbonate-dominated platforms to temperate-water siliciclastic platforms is attributed to changing oceanographic and palaeoclimatic conditions across the middle Cambrian-Furongian transition, when the southward-moving subtropical margin of NW Gondwana progressively invaded temperate and cold seas. The episodic development of Furongian-Tremadocian carbonate factories within temperate-water settings of the southern Montagne Noire (Val d'Homs and Mounio formations) signals short-lived warming episodes in meridional parts of NW Gondwana. These carbonate substrates represent sporadic development of Languedocian-Furongian *c*hancelloriid-*e*chinoderm-*s*ponge (*CES*) meadows, also rich in linguliformean brachiopods and trilobites. This association changed during the Tremadocian, as indicated by the disappearance of chancelloriids and the input of conodonts (Álvaro *et al.*, 2007).

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OXYGEN-CONTROLLED EARLY ORDOVICIAN TRILOBITE ASSEMBLAGES: THE THYSANOPYGE FAUNA FROM NORTHWESTERN ARGENTINA

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Keywords. Trilobite assemblages, paleoecology, Early Ordovician, Northwest Argentina.

INTRODUCTION

The well known *Thysanopyge* fauna, formerly defined as a group of endemic asaphids that flourished during the Floian in western Argentina (Harrington and Leanza, 1957), is re-evaluated upon new insights into its composition, spatio-temporal distribution, as well as ecological and environmental aspects.

Thysanopyge is a large aspahid, reaching 40 cm sagittal length, able to cope with a relatively wide range of environmental conditions, evidenced by its occurrence in a variety of lithologies, including green, grey, and black silts and shales. Although the *Thysanopyge* fauna was previously characterized by the presence of the alleged ubiquitous *Thysanopyge argentina* Kayser, six different species has been recently recognized by Waisfeld and Vaccari (submitted). Apart from *T. argentina*, *T. frenguellii* Harrington, *T. taurinus* (Harrington), *T. clavijoi* Harrington and Leanza, *Thysanopyge* n.sp. 1, and *Thysanopyge* n.sp. 2 are now established.

The *Thysanopyge* fauna is widespread in the Argentine Cordillera Oriental, the southern extreme of the Central Andean Basin, along present day 250 km, from nearby Salta city to Santa Victoria, in the border with Bolivia (Fig. 1). Its age is now bracketed between the late Tremadocian (*A. murrayi* Zone) to late Floian (upper part of *B. deflexus* Zone), involving about 11 m.y. The *Thysanopyge* fauna is recorded in different units (San Bernardo, Parcha, and Acoite formations), involving largely fine-grained successions, of overall 1500 m thickness. These successions display no significant lithofacies changes, except for shale/ silt variation in grain size and colour, and only locally, interbedded sandstones and shell beds account for high energy events mostly related to tempestite episodes.

According to recent interpretations the Cordillera Oriental represents the forebulge (or peripheral bulge) depozone of an extended Ordovician foreland basin systems in northwest Argentina. In the Cordillera Oriental platform deposits developed in a low gradient ramp-like setting, under the influence of large-scale prograding deltaic systems from the east, and of an active volcanic arc complex from the west (Bahlburg and Furlong, 1996; Astini, 2003).

The onset of the *Thysanopyge* Fauna is associated with a significant faunal turnover from the previous "*Notopeltis* Fauna", linked to a basin-wide flooding that took place since middle-late Tremadocian generating widespread subtidal environments throughout the basin (cf. Astini, 2003). Floian records occur in successions of dark, laminated silts and shales, that account for a relatively protracted interval of deficient oxygen content, related to environmental restriction in prodelta settings during aggradation stage of a highstand system tract (Astini, 2003; Waisfeld and Astini, 2003). In the uppermost Floian shallowing related to the progradation stage of the highstand system tract brought about a change in oceanographic conditions that led to the extinction of the *Thysanopoyge* Fauna and its replacement by the *Famatinolithus* Fauna (Waisfeld *et al.*, 2003, and references therein)

Thysanopyge conforms an array of assemblages that are here differentiated by their trilobite composition, richness, and co-occurrence of other benthic groups. The particular geodynamic and environmental setting featured particular ecological and biogeographical signatures which are briefly discussed.

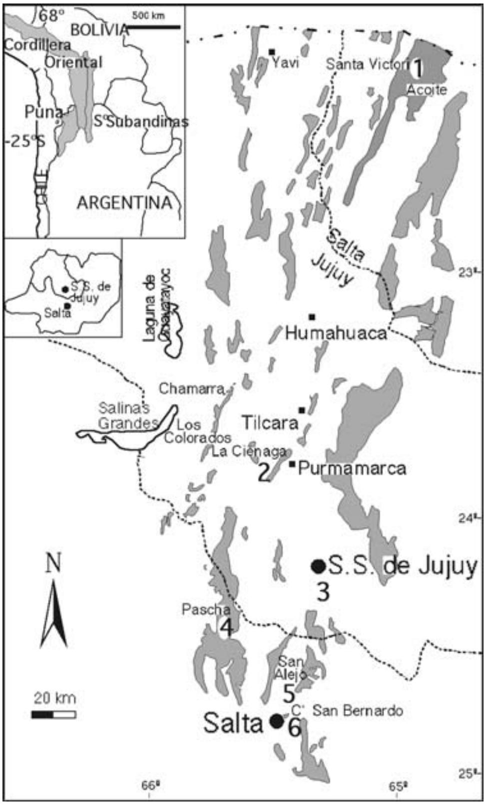

Figure 1. Location map showing areal distribution of undifferentiated outcrops of the Santa Victoria Group (Late Cambrian-Floian) in Northwestern Argentina (Cordillera Oriental). Numbers represent localities where *Thysanopyge* assemblages were recorded. 1, Santa Victoria; 2, La Ciénaga; 3, Dique Las Maderas; 4, Pascha-Incamayo; 5, Yacones; 6, Cerro San Bernardo.

THYSANOPYGE ASSEMBLAGES

Monospecific assemblages. *Thysanopyge* n.sp. 1 conforms monspecific aseemblages in the lower half of the Acoite Formation (lower Floian, Santa Victoria area). Low density, disarticulated sclerites of this species, restricted to few bedding planes, are recorded within a succession of approximately 100 m thickness of dark shales and silts. *Thysanopyge* n.sp. 1 is only occasionally found in association with crushed and flattened nautiloids. Infrequently, also *T. taurinus* conforms monospecific assemblages in the Parcha Formation.

Low diversity assemblages. Recorded in the the Parcha formation (upper Tremadocian, Pascha-Incamayo area). This sparsely fossiliferous assemblage is exclusively composed of trilobites (only asaphids and olenids). *T. taurinus* shows an overlapping distribution with other asaphids (*O. araiorhacis* and rare *Kayseraspis* sp.), extremely rare *Rhombampyx*, and olenids *Bienvillia parchaensis* and *B. jana*, as well as four species of *Hypermecaspis: H. armata*, *H. inermis*, *Hypermecaspis* n.sp. and *Hypermecaspis* sp. (cf. Waisfeld and Vaccari, 2006). Thoracic morphology of *Hypermecaspis*, relatively wide thoracic segments and their multiplication, is interpreted to represent adaptations to cope with oxygen restricted or depleted environments (Fortey, 1985; Fortey, 2000, and references therein).

Moderate diversity assemblages: Recorded throughout 150 m in the upper half of the Acoite Formation (upper Floian, Santa Victoria area), involving thick black shale and silt packages with dispersed trilobite sclerites, interbedded with high density winnowed pavements. Among trilobites, *T. calvijoi* is associated with asaphids (*Niobides armatus*, "*Thysanopyge*?" *latelimbata*, and a single olenid (*Porterfieldia* sp.). Pavements include, apart from the trilobites, high abundances of the bivalve *Goniophorina*? sp. and ostracods, as well as rare *Paralenorthis*. Diversity among trilobites is not significantly higher than in the low diversity assemblages, the main difference relies in the incorporation non-trilobite forms.

High diversity assemblage: Recorded in the San Bernardo Formation (upper Tremadocian) in green/grey shales occasionally interbedded with storm shell beds. Among trilobites, *T. argentina* is associated with *T. frenguelli*, *Kayseraspis asaphelloides*, *K. brackebuschi*, *Asaphellus kayseri*, *Australopyge* sp., *Sanbernardspis pygacantha*, "*Colpocoyphoides*" *trapezoidalis*, *Conophrys* sp.

Apart from trilobites, rhynchonelliformean (*Nanorthis grandis*), linguliformean, ostracods, bivalves (*Cienagomya bidentata*, *Ucumaropsis lermaensis*), gastropods, and equinoderms (*Lingulocystis*, crinoid ossicles, and pluricolumnals) are also very common.

BIOGEOGRAPHIC SIGNATURE

The endemic nature of this fauna, mainly among asaphids, has been largely recognized (Harrington and Leanza, 1957; Fortey and Cocks, 2003). *Thysanopyge* itself, *Australopyge*, *Niobides*, *Zuninaspis*, *Sanbernardaspis*, and "*Colpocoryphoides*", are associated with widespread forms (*Asaphellus, Ogygiocaris, Conophrys, Hypermecaspis, Bienvillia*). Biogeographic sensitive elements are scarse and restricted to *Kayserapsis* and the rare occurrences of *Rhombampyx*. The former is otherwise known from upper Tremadocian of north China and lower Floian of Korea, Australia, and Kazakhstan, and *Rhombampyx* has been recorded in Spitsbergen, Baltica, and South China. Both taxa account for weak connections with perigondwanan temperate areas.

DISCUSSION

Thysanopyge was among the dominant inhabitants of a broad shallow, nutrient rich, subtidal marine setting. Although association with other asaphids and olenids are common within dark fine-grained facies, this taxon appears to cope with the widest range of environmental conditions and bottom-water oxygen levels. *Thysanopyge* assemblages flourished in a relatively restricted, prodelta setting with high sedimentation rate and active subsidence, responsible of the scattered and diluted nature of some of these assemblages. They varied from monospecific or paucispecific to high diversity assemblages. Among them, variations in trilobite composition, presence of other benthic groups, and diversity are interpreted to account for variable paleo-oxygen levels, from dysoxic, to fully oxic conditions.

Several contributions discuss the driving mechanisms that may lead to different oxygen concentrations, and to a lesser extent, their effect upon the fauna (e.g. Sagerman and Bini, 1997; Levin, 2003; Gaines and Droser, 2003; Peters, 2006; Boyer and Droser, 2007, among others). Water column stratification is currently viewed as the main process in the development of ancient black shales; however, environmental stability and disturbance frequency, minor oscillations in sea level, seasonal and long term changes in the flux of metabolizable organic matter to the substrate, among others processes, control the frequency and intensity of the redox boundary fluctuations above the sediment water interface (Tyson and Pearson, 1991; Potter *et al*., 2005; Allison and Wright, 2005).

Among *Thysanopyge* assemblages, the high diversity assemblages are interpreted to occur in well oxygenated, and relatively shallow sites. Monospecific assemblages might represent brief colonization events in an otherwise barren oxygen restricted/depleted environment. Moderate diversity and low diversity assemblages appear to represent two distinct settings within the dysoxic environment.

Current views support a decrease in diversity associated with diminishing oxygen levels (e.g. Tyson and Pearson, 1991; Potter *et al*., 2005), thus, a trend of decreasing oxygen content between these assemblages might be suggested. However, an alternative explanation might relay, not just in the absolute oxygen content, but in its variability (transient or persistent) relative to ecological timescales (cf. Sageman and Bina, 1997). Persistent conditions might have prevented more oxygen–demanding forms, favoured diversification among particular olenids, and the development of morphological/physiological? adaptations to cope with oxygen restricted settings (as in *Hypermecaspis*). In contrast, more even redox conditions, possibly associated with occasional disturbances, favoured the development of associations characterized by the rare occurrence of olenids (except for triarthrinids), and inclusion of other groups such as benthic suspension feeders, and ostracods.

In summary, processes leading to the configuration of the assemblages are interpreted to result from the interplay of organism tolerance ranges and shifting redox conditions in the bottom and pore waters. These fluctuations are interpreted to be heterogeneous in space and time, not only in levels of oxygen concentrations, but also in the relative duration or persistence of dysoxic conditions. In this setting, particular biogeographic signature (endemic nature of many forms, and only weak connections with perigondwana temperate areas), might be the result of restricted circulation patterns in a peculiar basin configuration. The former promoted anoxia/dysoxia, variable in intensity and duration. The latter, a shallow seaway, with restricted connections to oceanic water masses, probably as a result of an active volcanic arc to the west, might have prevented a fluid exchange with other perigondwanan areas.

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INTEGRATION AND REGULATION OF DEVELOPMENTAL SYSTEMS IN TRILOBITES

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Keywords: Trilobita, developmental systems, integration, canalization, modularity, morphometrics.

INTRODUCTION

Developmental systems determine whether selectively useful variation arises (e.g., Maynard Smith *et al*., 1985; Wagner, 1988; Gerhart and Kirschner, 2007). They can reduce that variation via canalization or by structuring it into integrated complexes, thereby preventing organisms from varying one part without interfering with other parts (Wagner *et al*., 2007). Temporal or phylogenetic changes in intrinsic developmental factors may explain macroevolutionary trends in intraspecific variation (e.g., Webster, 2007) and clade diversification history, as proposed by the developmental or "genomic" hypotheses regarding the unique Cambrian radiation (Riedl, 1978; Valentine, 1995; Wagner and Laublicher, 2004; Budd, 2006; Davidson and Erwin, 2006; Erwin, 2007). Techniques for assessing and comparing patterns and levels of integration are becoming increasingly refined and powerful, but have yet to be applied to fossil taxa. As a result, the extent to which changes in developmental canalization and integration could have influenced macroevolutionary diversification is currently unclear. In this short paper, we discuss methods appropriate for quantifying the level and structure of variation in fossil taxa, permitting unparalleled insight into their developmental systems.

CANALIZATION, FLUCTUATING ASYMMETRY, AND MODULARITY

Canalization refers to the buffering of developmental systems, ensuring that the same phenotype is produced despite genetic and environmental perturbations (Waddington, 1942, 1952). Types of canalization are now typically distinguished according to the source of the perturbations being buffered. Thus genetic and environmental canalization are distinguished from each other, and environmental canalization is further subdivided into "macroenvironmental" canalization (the converse of phenotypic plasticity) and "microenvironmental" canalization (which is buffering against random perturbations within a constant environment; Debat and David, 2001). Theoretical studies have shown that genetic canalization evolves by natural selection only under highly restrictive conditions, in striking contrast to environmental canalization (Hermisson and Wagner, 2004). The distinction between macro- and microenvironmental canalization is equally important in that macroenvironmental canalization is expected only when the optimal phenotype is constant over the environmental range of a species, but microenvironmental canalization (resistance to developmental noise) is expected under all environmental conditions (Debat and David, 2001; Nijhout and Davidowitz, 2003).

Low levels of microenvironmental variation provide the primary evidence for well-buffered developmental systems, which can be measured in fossil taxa by fluctuating asymmetry (FA), i.e., random deviations from bilateral symmetry of a symmetric structure (e.g., Van Valen, 1962; Scheiner *et al*., 1991; Santos *et al*., 2005). One major advantage of using FA as a measure of microenvironmental variation is that its expected value is known—it is zero regardless of genotype and environment. A second major advantage is that it enables us to control for both genetic and macroenvironmental variation because both sides of an organism have the same genotype and develop within nearly identical environments.

FA has become of great interest in evolutionary developmental biology not only because it is regarded as a useful indicator of developmental noisiness, but also because it is now viewed as especially informative about modularity (Klingenberg and Zaklan, 2000; Klingenberg *et al*., 2003; Badyaev *et al*., 2005). The rationale is that FA can distinguish between two developmental causes of integration: (1) a process acting in parallel in different modules, and (2) direct interactions along or between intramodular pathways (e.g., Klingenberg and Zaklan, 2000; Klingenberg *et al*., 2003; Klingenberg, 2005). Only direct interactions are likely to explain correlated FA because the causes of parallel variation (i.e., common genetic or environmental factors) are controlled. Therefore, correlations found between (signed) asymmetries indicate direct intramodular interactions.

METHODS FOR STUDYING TRILOBITE DEVELOPMENTAL SYSTEMS

The methods of landmark-based geometric morphometrics (Bookstein, 1991; Zelditch *et al*., 2004) can be used to analyze phenotypic variation and FA. These methods extract information about shape variation by analyzing coordinates of landmarks (i.e., homologous, discrete, anatomical loci; Fig. 1). These methods retain information about the spatial relationships among landmarks, making it possible to relate abstract results of statistically powerful analyses to the physical structure of the organisms (Bookstein, 1991; Zelditch *et al*., 2004; Slice, 2007).

Analyzing FA and symmetrical variation of shape

The favored method for analyzing FA is the two-factor mixed-model analysis of variance, with the two main effects being "individuals" and "sides" (Leamy, 1984; Palmer and Strobeck, 1986). According to the recommended protocol, the right and left sides are measured two or more times, then the overall mean (over all replicates and sides) is estimated from the combined data, and deviations from the overall mean are partitioned into components due to the two main effects. The symmetric variation among individuals is quantified by the main effect of "individuals," after correction for asymmetry; directional asymmetry (handedness) is quantified by the main effect of "sides." The interaction term documents variation among individuals in right-left differences, which is FA. The statistical significance of FA is assessed by the F-ratio between the interaction mean square and measurement error mean square (Leamy, 1984; Palmer and Strobeck, 1986). After removing measurement error from the estimate of FA, populations can be compared using Levene's test, which is relatively insensitive to departures from normality (see Palmer and Strobeck,

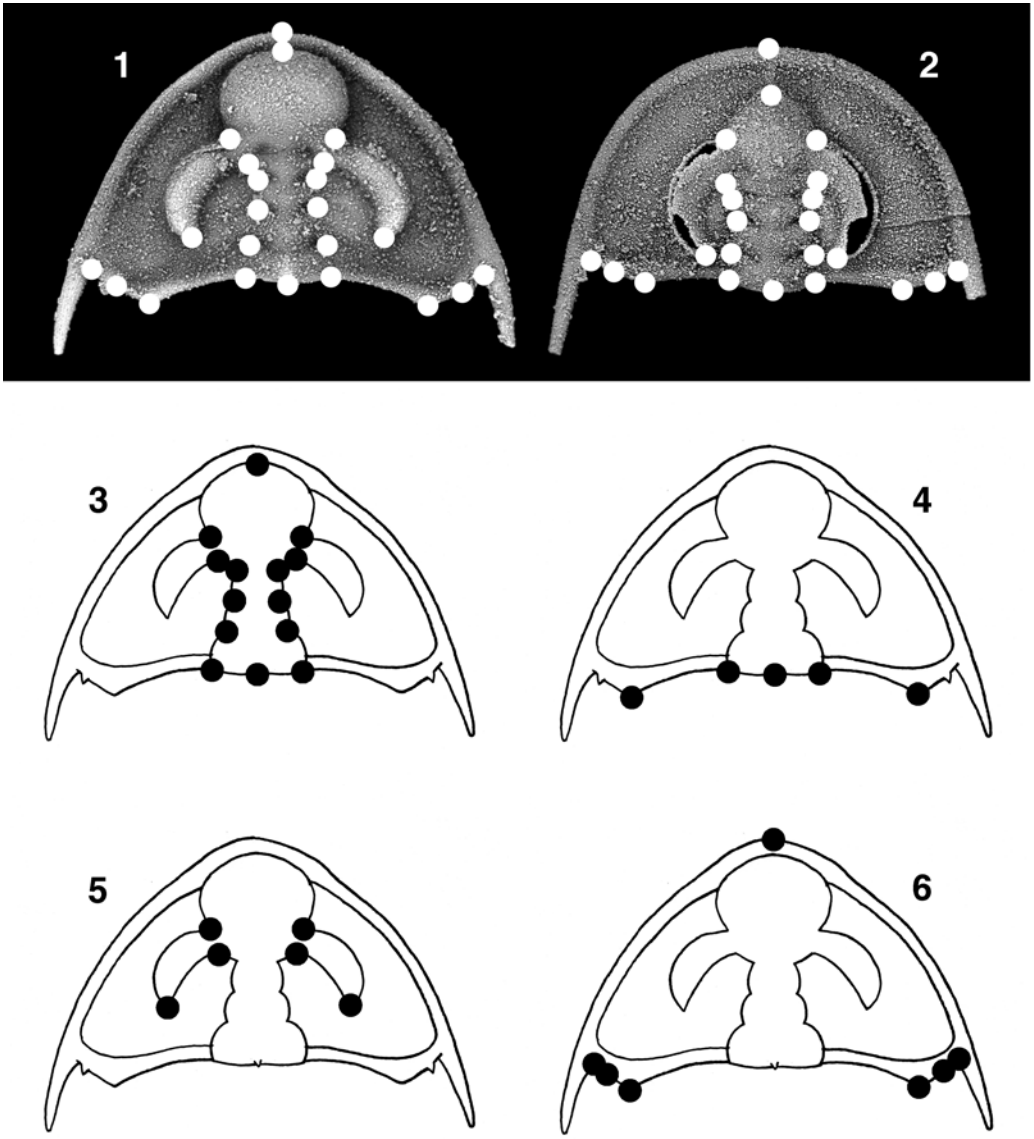

Figure 1. 1-2, Representative silicified cephala of olenelloid trilobites. White circles show location of landmarks appropriate for inclusion in the geometric morphometric study of developmental integration (see text). Both specimens from collection ICS-1173 (1.8 meters below top of Combined Metals Member, Pioche Formation, Dyeran, traditional "Lower" Cambrian) of Hidden Valley, Burnt Springs Range, Lincoln County, Nevada. *1*, *Nephrolenellus geniculatus* Palmer, 1998, UCR 9963.19, x12. *2*, *Olenellus gilberti* Meek in White, 1874, UCR 9963.120, x8. *3-6*, Landmarks associated with hypothesized developmental modules on the olenelloid cephalon, shown on the cephalic outline of *N. geniculatus*. 3, The "glabella module", covering and associated with the anterior portion of the digestive tract. 4, The "articulation module", associated with the functional articulation between the cephalon and first thoracic segment. *5*, The "ocular module", associated with the ocular lobes. 6, The "cephalic margin module", defining cephalic outline and associated with functional interaction with the substrate and feeding/respiratory currents.

1986 for additional details). The statistical approach outlined above has been adapted to the analysis of shape using Procrustes-based methods (Auffray *et al.*, 1996; Klingenberg and McIntyre, 1998; Klingenberg *et al.*, 2002). The same statistical model is used to partition variation. Using geometric data, the first step is to reflect the data for each specimen; the difference between the original and its mirror image quantifies the right-left difference of that specimen. The original and reflected copies are superimposed, with the mean shape being calculated over originals and reflected copies of all individuals. The main effect of "individuals" and sides can then be quantified as above, and the interaction between them estimates FA. The statistical significance of FA can be assessed by a permutation test and estimates for FA can be corrected for measurement error by the procedure outlined above. These estimates are also comparable across populations by Levene's test.

Analyzing modularity/morphological integration

The analysis of FA allows us to examine the extent to which morphological integration is structured by the intrinsic architecture of developmental pathways. Should morphological integration be largely due to that architecture, integration could be internally constrained in its evolutionary potential. That is because altering the structure of signaling interactions is thought to be less feasible than altering alleles acting in parallel within two or more modules (Klingenberg, 2005). Estimating the impact of direct interactions on integration therefore potentially provides important information on both causes and evolutionary potential of integration. This impact can be estimated from the matrix correlation between the FA and symmetric components of variance (e.g., Klingenberg and Zaklan, 2000; Klingenberg, 2005). It is then possible to assess (1) the level of integration, (2) the impact of direct interactions on integration, and (3) the stability of the structure of integration.

1. Measuring the level of integration: The most widely used measure of integration is the variance of the eigenvalues (Wagner, 1984) because high correlations/covariances produce one or few relatively large eigenvalues and many small eigenvalues, whereas low correlations/covariances produce nearly equal eigenvalues. Thus eigenvalues should be highly variable when morphologies are highly integrated but nearly equal when morphologies are weakly integrated. To eliminate the dependence of the variance on the mean eigenvalue, eigenvalues are typically standardized for overall variance before comparisons are made. The comparisons are done using a resampling procedure that repeatedly draws samples from each population; for each iteration, the standardized eigenvalue variance is calculated for each population then the difference is computed, yielding the distribution of differences against which the observed difference is compared.

2. Measuring the impact of direct interactions on morphological integration: The impact of direct interactions on morphological integration can be estimated by the matrix correlation between the symmetric and FA components of variation. If this value is high, then the direct interactions responsible for correlated FAs contribute highly to the structure of morphological integration. The complex morphology of the trilobite cephalon offers many readily identified anatomical loci and outlines ideal for landmark- and semilandmark-based morphometric analysis, especially of FA (Fig. 1). The cephalon can be subdivided into functionally defined structures (Fig. 1.3-6). The mosaic of functionally and anatomically diverse structures on the cephalon increases the likelihood that developmental systems controlling cephalic morphology were integrated into modules. The hypothesis that these cephalic regions associated with distinct functions constitute developmental modules can then be tested. Correlations between the FAs of these partitions can be estimated following the protocol of Monteiro *et al.* (2005), which estimates the pairwise Procrustes distances between all specimens for each partition, then computes the matrix correlation between those pairwise distance matrices between partitions. Thus, whereas the first test regarding the role of direct interactions involves simply estimating the correlation between the symmetric and FA components of variation, the second involves testing explicit hypotheses regarding the developmental architecture of integration.

3. Assessing the stability of the structure of integration: Interspecific comparison of integration structure can be achieved by comparing covariance matrices across species for both the symmetric and FA components of variance and by comparing correlation matrices for the partitions (as outlined above). Because morphological integration is usually measured in terms of correlations, comparisons should be based on the correlation matrices obtained from the procedure outlined above.

SAMPLING REQUIREMENTS

Given the focus on the measurement and biological interpretation of phenotypic variation and deviations from symmetry, taphonomic overprint on morphology is a particularly serious concern: tectonic or compaction-related deformation of fossils can introduce a strong non-biological signal into morphometric analyses (Webster and Hughes, 1999). To negate such issues, studies should utilize only high-quality, undeformed, three-dimensional fossils, preserved in carbonates either as testate material (recovered as "crackout" by physical breakage of the rock) or as silicified material (recovered as isolated sclerites by acid dissolution of the rock; Fig. 1). Any specimens showing evidence of tectonic or compaction-related deformation should be excluded from the study. Differences in phenotypic variation attributable to environmental heterogeneity, time-averaging, ontogeny, and phylogeny must also be taken into account and impose additional constraints on choice of study system when inter-sample comparisons are to be drawn.

DISCUSSION AND FUTURE WORK

The above methods for rigorously quantifying and comparing the level and structure of developmental integration have been successfully applied to evolutionary questions involving extant taxa (references above). However, the techniques have yet to be employed on fossil taxa, and many key questions involving long-term temporal dynamics of developmental systems therefore remain unanswered. A question of considerable theoretical importance is the direction in which integration evolves. A long favored model posits that integration increases over time (e.g., Cheverud, 1996). The primary alternative proposes that modularity evolves from an initially high level of integration. That second possibility is more difficult to achieve because integration must be decreased *between* modules but maintained or increased *within* modules (Wagner, 1996; Wagner *et al*., 2007). The best-supported theoretical model for the evolution of modularity by natural selection proposes that it evolves as a side effect of selection for canalization (Wagner and Mezey, 2004; Wagner *et al*., 2007). Despite the large number of comparative studies of integration, it is still not known whether integration or modularity tends to increase over time, or even if there is any temporal trend in either direction, much less whether modularity evolves in concert with canalization. Neither is it known whether regulation or integration of developmental systems changes on a timescale commensurate with macroevolutionary diversification trends, or whether they serve as a constraint explaining such trends.

Application of the above techniques to suitably well-preserved fossil taxa within a tightly constrained phylogenetic, stratigraphic, and environmental framework provides an avenue for addressing these questions. Such studies are already under way for several trilobite clades (e.g., Olenelloidea, Agnostina, corynexochines, Phacopida; unpublished data). These, and analogous studies of other fossil clades, will provide a fruitful research area in the evolutionary-developmental biology field over the coming years.

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A REVIEW OF CAMBRIAN BIOGEOGRAPHY OF CHINA

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INTRODUCTION

Eleven Chinese Cambrian geographic units, corresponding mainly to different allochthonous continental masses (plates and terranes), are divided largely on the basis of evidence from regional tectonics, palaeogeography and stratigraphy (Fig. 1). All the plates and most of the terranes in China may have been placed on the India-Australia margin of Gondwanaland and formed part of northeastern Peri-Gondwana during the Cambrian (e.g. Metcalfe, 1996).

With the exceptions of northern Xinjiang (Region 1 of Fig. 1) and southern Tibet (Region 10 of Fig. 1), Cambrian trilobites are widely recorded throughout China, however, most of them are described from South and North China, and Tarim (southern Xinjiang), in focus of which the Cambrian biogeography of China has previously been well delineated. The whole of China was considered to be assignable to a single biogeographic realm in the Cambrian by both Lu *et al*. (1974, named as the Oriental Realm) and Zhang (2003, as the Perigondwanan Realm; see also Kobayashi, 1976 and Palmer and Repina, 1993). This realm was recognised on the basis of several endemic clades, including, amongst others, the superfamilies Redlichioidea and Dameselloidea and families, such as, Crepicephalidae, Kaolishaniidae, Inouyiidae, Lisaniidae, Ptychaspididae, Sunaspididae and Tsinanidae. All of these flourished in China and are typical of most of the Chinese Cambrian faunas. As depicted by Lu *et al*. (1974 and references therein) and Zhang (2003 and references therein), outside of China, the distribution of most of the related genera was largely restricted to southeast, central and south Asia, Middle East, Australia and Antarctica, indicating that the primary biogeographic links of China are with the eastern Gondwana and other eastern Peri-Gondwana blocks.

A similar view was also held by Yang (1988b), who however suggested that the Hinggan Region (2 of Fig.1) may belong to an additional independent biogeographic unit. This point is supported by a few late Early Cambrian (Lungwangmiaoan) forms that were recently reported from the Yichun Terrane of this region by Duan and An (2001), including *Inouyina, Jangudaspis, Laminurus, Onchocephalina, Proerbia* and *Pseudozacanthopsis*, all of which exhibit a strong faunal affinity with Siberian assemblages.

In this paper, biogeographic links among the Chinese plates and terranes of eastern Peri-Gondwana are further reviewed on the basis of a complete dataset available for Cambrian trilobite record in China

(Zhou and Zhen, 2008). In the following discussion, the trilobites endemic to a particular plate or plates from in particular the platform/inner-shelf faunas are emphasized.

EASTERN PERI-GONDWANAN TERRANES

Only a few Cambrian trilobites were reported from several of the Peri-Gondwanan terranes in China. However, based on the incomplete data, the biogeographic attribute of each of these terranes is suggested as follows.

Middle Tianshan-Beishan Region/Terrane (Region 3 of Fig. 1): It was referred to the Tarim Province by Yang (1988b), though the occurrences of late Early Cambrian benthic trilobites such as *Edelsteinaspis, Serrodiscus, Calodiscus, Tannudiscus*, *Pagetides* and *Poliellina* (see Zhou *et al*., 1982; Xiang and Zhang, 1985; Zhang, 1987) in the region may suggest a close faunal link with Sayan-Altay and Tuva of Russia, and display evident affinities with Siberia and Laurentia rather than Tarim (Zhou *et al*., 1996). It is interesting to note that a similar contemporaneous fauna was also recorded from the Karaganda area, Kazakhstan (Ivshin, 1979). This indicates that, during the Early Cambrian, the Middle Tianshan-Beishan Region, or even possibly the entire Kazakhstan Mid-Plate, might have been located not far from the Siberia Plate. However, the early Mid Cambrian faunas of the region were characterized by the occurrences of *Galahetis* and *Xystridura* (Zhang, 1981; Zhou *et al*., 1982; Xiang and Zhang, 1985), indicating closest affinities with those of Australia and Antarctica (Lin and Jago, 1993; Brock *et al*., 2000). The late Mid-Late Cambrian trilobites recorded in this region are mostly slope-facies types, except for the Ejin Banner area, where a shallow-water fauna was reported (Lin *et al*., 1996a), including forms that are typical of the coeval fauna of North China Plate, such as *Amphoton* and *Crepicephalina*, and of Australia, such as *Amphoton*. Moreover, in the Late Cambrian, the occurrence of *Atopasaphus, Golasaphus* and *Lorretina* from a shallow-outer-shelf fauna in Ejin Banner (Lu *et al*., 1986) also supports a close biogeographic connection with Australia.

Hainan Region/Terrane (Region 11 of Fig. 1): Only a few inner-shelf-facies trilobites, such as *Galahetis* and *Xystridura*, have been reported from the early Mid Cambrian in the Sanya Area (11-2 of Fig. 1) (e.g. Lin and Jago, 1993), which are again taken to be indicative of a closest faunal link with eastern Gondwana as well as with the Middle Tianshan-Beishan Terrane.

Northern Qiangtang-Simao Region/Terrane (Region 7 of Fig. 1): Only a single genus *Kunmingaspis* was documented from the Early Cambrian of northwestern Yunnan (e.g. Hughes *et al*., 2002). Elsewhere, this form has been employed as a zonal fossil to define the uppermost horizon of the Lower Cambrian in South China and Tarim. There have also been three trilobite genera *Calvinella, Haniwa* and *Mictosaukia* described from Batang, western Sichuan (Zhu, 1982). All of them also frequently occur in the late Upper Cambrian (Fengshanian) of the North and South China plates, and *Mictosaukia* was also regarded as one of the key trilobite genera of the Australian Payntonian fauna (Brock *et al*., 2000).

Baoshan-northern Tibet Region/Terrane (Region 9 of Fig. 1): Only Late Cambrian shallow-outer-shelf-facies trilobites have been described from the Baoshan area, westernmost Yunnan (Luo, 1982, 1983; Sun and Xiang, 1979). Demonstrated by a number of common shallow-water elements that are associated in the faunas, such as *Blackwelderia, Changia, Chuangia, Dictyella, Easaukia, Haniwa, Kaolishania, Kaolishaniella, Mansuyia, Mansuyites, Mictosaukia, Monkaspis, Parachangshania (Parachangshania), Prosaukia* and *Tsinania*, the terrane shows a unique provincial link with South China, Australia and, in particular, North China.

EASTERN PERI-GONDWANAN PLATES

Cambrian trilobite faunas heterogeneously developed in the three Chinese cratonic plates, due to the differing geological evolution of each region. In the South China Plate (Region 8 of Fig. 1) and Tarim Plate (Region 4 of Fig. 1), the complete successions of the slope-facies Cambrian trilobites in the Jiangnan, Jiangbei and Southern Tianshan areas (respectively 8-2, 8-4 and 4-2 of Fig. 1), and the platform-facies Early Cambrian trilobites in the Yangtze Area (8-1 of Fig. 1) are well documented, but the platform-facies Mid-Late Cambrian trilobites only sporadically occur in the limestone intercalations of the dolomite strata. In contrast, in the North China Plate (Region 5 of Fig. 1), the platform-facies trilobites have been widely recorded in the late Early-Late Cambrian of the Yellow River Area (5-1 of Fig. 1), but none were recorded from the early Early Cambrian, as the strata of this interval (Chiungchussuan-lower Tsanglangpuan) are absent. The slope-facies trilobites are only distributed in the Qaidam and Middle Qilian terranes (Area 5-3 of Fig. 1), although Early Cambrian trilobites have not been found in this area.

All of the Chinese plates may have been situated in low latitude zones during the Cambrian (e.g. Burrett *et al*., 1990). Lu *et al*. (1974) was the first to note the ecological differentiation of the Cambrian faunas in the Chinese plates, and, accordingly, they classified the faunas into three types: North China, Transitional and Southeast China. Zhou *et al*. (1979) revealed that the Cambrian faunas were differentiated along a bathymetric gradient from the shallow platform in the west to the deep basin in the east of South China, and suggested that the North China, Transitional and Southeast China faunas may well represent the trilobite associations indicative of respectively platform, slope and basin environments. Since then, further research has been carried out in China (Yang, 1988b; Lin *et al*., 1992, 2001; Peng, 2000; Zhang, 2003) and the distribution patterns of the Cambrian trilobite faunas have well been established in time and space for all the Chinese plates, except the Qaidam and Middle Qilian terranes (Area 5-3 in Fig. 1), where the biofacies model is not well delineated yet. Despite this, judging from the faunal sequences and palaeogeographic framework (Lin *et al*. 1996b) of these two terranes, it is evident that most of the trilobites were associated with slope-facies environments, except for a few genera that might be classified as shallow-water dwellers.

Largely based on the similarity between the shallow-water trilobite faunas, Lu *et al*. (1974) referred both the North China and Yangtze platforms to a biogeographic unit, the North China Province. Yang (1988b), however, considered the South China, North China and Tarim plates to represent three independent provinces, but more recent research suggests that the Tarim Cambrian biota is most similar to that of the South China Plate (Zhou and Chen, 1992, p. ii; Zhou *et al*. 1996, pp. 11, 20).

Except for an endemic genus *Tianshanocephalus*, all the platform-facies trilobites that have been described from the Lower Cambrian in the Tarim, including *Bathynotus, Chittidilla, Jingyangia, Kepingaspis, Kunmingaspis, Meitanella, Paokannia, Redlichia* (*Redlichia*), *Tsuyidiscus* (*Tsunyidisus*), and *Ushbaspis* (see Zhang, 1981and Lin *et al*., 1992), are in common with the coeval faunas from the Yangtze platform, indicating that both blocks may have formed a single biogeographical unit at least during this period.

Following the Late Tsanglangpuan transgression, the Yangtze Sea became deeper (Zhou *et al*., 1979), whilst the North China Block was drowned, becoming a vast shallow epiric sea. This event caused many endemic taxa to evolve in both separate cratonic areas. According to Lin in Zhou and Zhen (2008), in the late Early Cambrian there are 26 genera and subgenera regarded as endemics to the North China Platform, belonging to the Ptychopariidae (15, e.g. *Probowmania* (*Probowmania*), *Paraziboaspis*), Redlichiidae (4, e.g. *Leptoredlichia, Neoredlichia*), Agraulidae (4, e.g. *Pseuoplesiagraulus*), Protolenidae (1), Zacanthoididae

(1) and Inouyidae (1), while there are 28 endemic taxa recorded from the Yangtze Platform, including eight from the Protolenidae (e.g. *Ichangia, Szechuanolus*), five from the Ptychopariidae (e.g. *Yuhsienszella, Xilinxia*), three each from the Redlichiidae (e.g. *Breviredlichia*) and Yinitidae (e.g. *Paokannia*), two each from the Zacanthoididae (e.g. *Chuchiaspis*) and Dolichometopidae (e.g. *Hoffetella*), and one each from the Agraulidae, Dorypygidae, Hicksiidae, Inouyidae and Palaeolenidae. Therefore, during the late Early Cambrian (late Tsanglangpuan-Lungwangmiaoan), significant differences between the platform-facies endemic trilobites from North and South China may signify them as separate biogeographic units, although

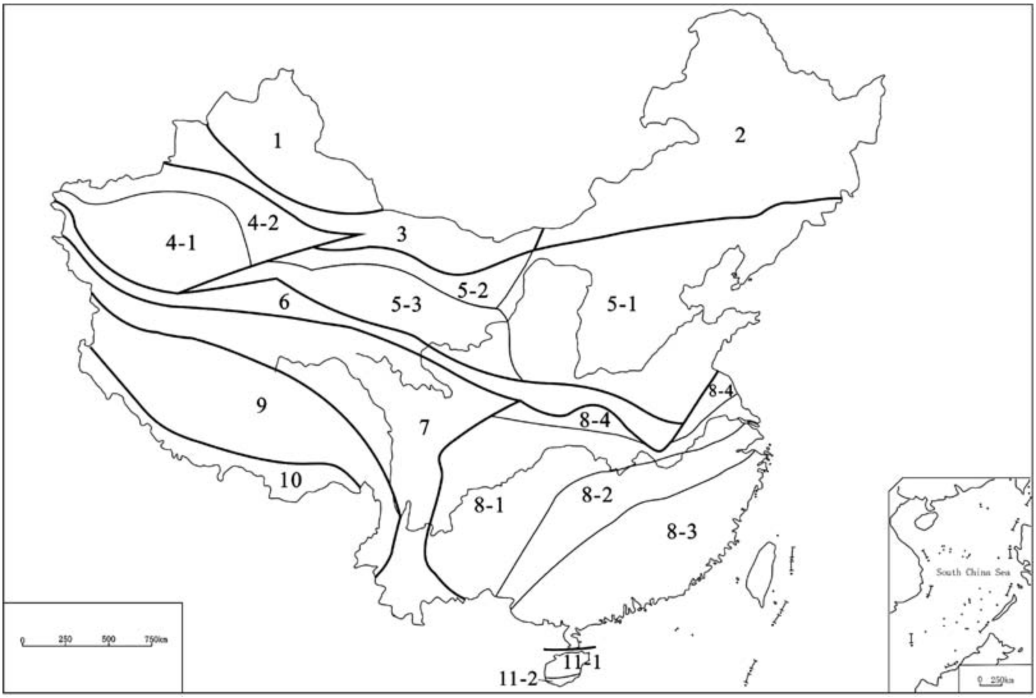

Figure 1. Map showing Cambrian geographic units of China. 1. Northern Xinjiang Region [part of the mobile zone between the Siberia and Tarim plates, see Zhou *et al.*, 1996; with no reliable Cambrian rocks reported (Lin *et al.*, 1996a)]; 2. Hinggan Region (mobile zone between the Siberia and North China plates, see Fan and Yang, 1994); 3. Middle Tianshan-Beishan Region (part of the Kazakhstan Mid Plate, see Zhou *et al.*, 1996); 4. Tarim Region: 4-1. Bachu-Kalpin Area (the Tarim Block proper, developed with platform or inner shelf facies), 4-2, Southern Tianshan Area (slope and marginal basin fringing the northern margin of the Tarim Block) (see Zhou *et al.*, 1996; Lin *et al.*, 1996a); 5. North China Region: 5-1. Yellow River Area (North China Platform, see Fan and Yang, 1994), 5-2. Dunhuang-Alexa Area (a dislocated old land lacking Early Palaeozoic deposits, possibly derived from the northern margin of the North China Platform, see Zhou *et al.*, 1996), 5-3. Qaidam-Qilian Area (consisting of the Qaidam and Middle Qilian terrances and the Altun faulted block, see Zhou *et al.*, 1996); 6. Kunlun-Qinling Region [polycyclic orogenic belt that crosses over the China mainland, see Fan and Yang, 1994; with intervening terranes or micro-blocks, including such as the Northern Qinling (Xiang *et al.*, 1981), a continent marginal terrane of the North China Plate (Yang, 1988b), and West Kunlun, a displaced landmass of the North China Plate proper (Zhou *et al.* 1996)]; 7. Northern Qiangtang-Simao Region (a northern extension of the Indochina or Annamia Terrane (e.g. Metcalf, 1996); 8. South China Region (modified from Lu *et al.*, 1974): 8-1. Yangtze Area (platform), 8-2. Jiangnan Area (southern shelf slope of the Yangtze Platform), 8-3. Cathaysia or Pearl River Area (deep basin), 8-4. Jiangbei Area [northern shelf slope of the Yangtze Platform, after Peng, 2000; = Middle and Southern Qinling terranes (Xiang *et al.*, 1981; Yang, 1988b)]; 9. Baoshan-northern Tibet Region (a northern extension of the Sibumasu Terrane, see Metcalf, 1996); 10. Southern Tibet Region (part of the India Plate, with no Cambrian trilobites yet found, see Fan and Yang, 1994); 11. Hainan Region (area subdivision see Wang, 1989): 11-1. Wuzhishan Area (deduced as a mobile zone edged the shelf), 11-2. Sanya Area (shelf).

a faunal link between both platforms is also indicated by the co-occurrence of dorypygids *Bonnia* and *Kootenia* (*Kootenia*), oryctocephalid *Cheiruroides*, Palaeolenid *Megapalaeolenus*, Ptychopariids *Eosoptychopaia* (*Eosoptychopaia*), *Kunmingaspis, Probowmania* (*Gunnia*) and *P*. (*Mufushania*), and redlichids *Redlichia* (*Redlichia*) and *R*. (*Pteroredlichia*).

In comparison with the highly diverse Mid-Late Cambrian trilobites recorded in the North China Platform, only a few taxa occur in the vast area of a restricted platform belt of the Yangtze Area (8-1 of Fig. 1), and almost all of them are identical with the contemporaneous forms of the North China Platform, such as, *Bailiella, Dapingia, Kailiella, Proasaphiscus, Kaotaia, Proasaphiscus, Probowmaniella, Solenoparia* (*Solenoparia*) and *Tonkinella* from the Maochuangian and Hsuchuangian (Yuan *et al*. in Zhou and Zhen, 2008); *Lisania, Manchuriella, Poshania, Protohedinia, Solenoparia* (*Solenoparia*) and *Szeaspis* from the Changhian (Yuan and Li in Zhou and Zhen, 2008); and *Blackwelderia, Calvinella, Enshia, Haniwa, Liaoningaspis, Mictosaukia, Prosaukia, Pseudosolenopleura* and *Saukia* from the Late Cambrian (Kushanian-Fengshanian) (Zhu in Zhou and Zhen, 2008). Lu *et al*. (1974) believed that the faunal difference between both platforms (North China and Yangtze) was lithofacies-controlled. This view was supported by a preliminary report on the Cambrian of southeastern Yunnan (Luo, 1984), where exposes a complete rock sequence of the open-platform-facies. It bears the Mid-Late Cambrian trilobite faunas that are identical with those of the North China Platform in terms of genus diversity and composition.

In order to express the preliminary observations more rigorously, cluster analysis of biogeographic links on the basis of trilobite genera and subgenera respectively from three time intervals [Lungwangmiaoan, Changhian, and Paibian (=latest Kushanian-middle Changshanian)] of the South and North China and Tarim plates was conducted using Simpson's coefficient (Fig. 2). This analysis reveals that the Chinese plates belonged to a single biogeographic unit during the Changhian and Paibian, and the platform/inner-shelf and outer-shelf/slope facies areas are separated into two distinct clusters (Fig. 1B, C). The Lungwangmiaoan clusters (Fig. 1A) suggest that the South China-Tarim and North China plates may well be referred to two independent biogeographic units, as evidenced by the occurrence of two different platform/inner-shelf faunas respectively in both units.

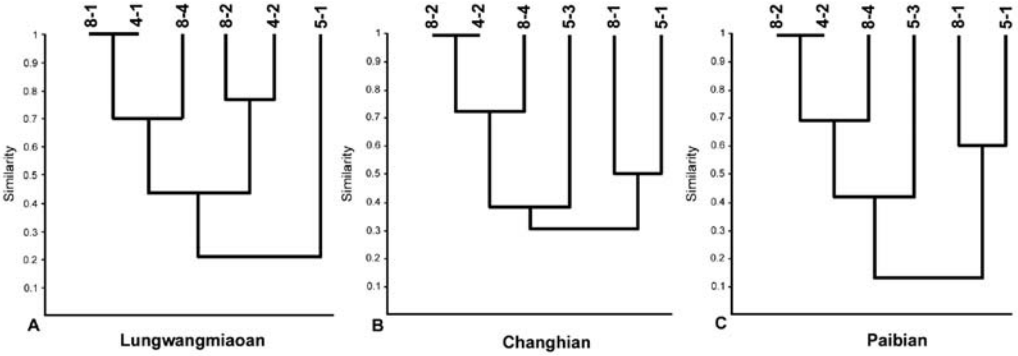

Figure 2. Clusters of Cambrian geographic units on the basis of trilobite faunas (dataset after Zhou and Zhen, 2008) using Simpson's coefficient, indicating the biogeographic affinities of Cambrian trilobites occurring in the shallow-water (4-1, 5-1, 8-1) and deep-water facies (4-2, 5-3, 8-2, 8-4) belts of Tarim (4), North China (5) and South China (8) plates (Fig. 1). A. Lungwangmiaoan; B. Changhian; C. Paibian. Note that the widespread agnostoids are excluded when coding; only a few pelagic trilobites were recorded in the Cathaysia Area (8-3) of South China, but most of them extended their distribution to the adjacent shelf slope (the Jiangnan Area, 8-2), all of which are not coded; and, as mentioned in the text, the coded trilobites from 5-3 are mainly deeper-water forms, but also mixed up with a few from shallow sites.

CONCLUSION

Although there are no Cambrian trilobites from the Northern Xinjiang and Southern Tibet terranes and no Early Cambrian trilobites from the Sibumasu and Hainan terranes have been reported, trilobite evidence indicates that all the plates and some of the other terranes in China exhibit a close biogeographic link and may have formed part of eastern Peri-Gondwana during the Cambrian, with the exception of the Hinggan Region and the Early Cambrian Middle Tianshan-Beishan Terrane where trilobite faunas instead show a strong affinity with those of Siberia and Laurentia.

Well-defined biogeographic patterns are depicted mainly by the shallow-water components of the Cambrian trilobites, especially in the South China, Tarim and North China plates. Synthetic analysis suggests that the Chinese eastern Peri-Gondwanan plates and terranes may be signified as belonging to a single biogeographic province during the Middle and Late Cambrian, but exhibit significant differences and may, therefore, be separated into two subprovinces during the Early Cambrian: one consists of South China, Tarim and Annamia, and the other is represented by the North China Plate only according to the information we yet have.

Acknowledgements

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REVISION AND VENTRAL STRUCTURE OF *GUANGXIASPIS GUANGXIENSIS* ZHOU, 1977 (TRILOBITA)

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Keywords: Trilobite, Ceratopygidae, *Guangxiaspis*, triangular rostral plate, conterminant hypostome, Cambrian, China.

INTRODUCTION

The type species of *Guangxiaspis* Zhou, 1977, *G. guangxiensis* Zhou, 1977 was erected only based on one almost complete exoskeleton and one cranidium, which were collected from the traditional upper Cambrian, Sandu Formation, Hewen Village, Jingxi County, southwestern Guangxi Province, China (Fig. 1). Abundant specimens of *G. guangxiensis* have recently been collected from Guole Town (Fig. 1), about 4.25km northeast of Hewen. Based on the new material, *G. guangxiensis* is revised and its triangular rostral plate and hypostome are herein described. One of the co-occurring trilobites, *Shergoldia laevigata*, as mentioned in the following text, has been described by Zhu *et al*. (2007).

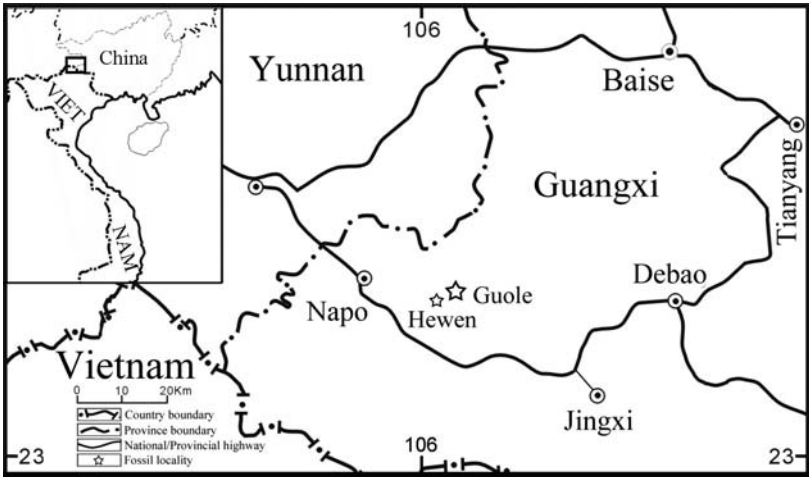

Figure 1. Location map of Hewen and Guole, Jingxi County, southwestern Guangxi Province, China.

REVISION OF *GUANGXIASPIS GUANGXIENSIS* ZHOU, 1977

The new material shows that the pygidium of *G. guangxiensis* Zhou, 1977 has a pair of pleural spines, which are unfortunately not preserved in the holotype (Zhou, 1977, pl. 47, fig. 11). The pygidial spines are stout and direct outward in the early holaspis (Fig. 2, A-B, F), but become slender and direct inward in the late holaspis (Fig. 2, D, E). Based on those observations, we consider that *Mansuyia laevigata* Zhou, 1977 and *Mansuyia pulchra* Zhou, 1977 may be both synonymous with *G. guangxiensis* Zhou, 1977, with the latter taking page priority. *Mansuyia laevigata* Zhou, 1977 and *Mansuyia pulchra* Zhou, 1977 both came from the same locality as *G. guangxiensis* Zhou, 1977, and the differences between them are accommodated by intraspecific variations. Qian (in Qiu *et al*., 1983) considered that the family assignment of *Guangxiaspis* was uncertain, but Jell and Adrain (2003) ascribed *Guangxiaspis* to Pterocephaliidae Kobayashi based on Zhou (1977)'s specimens. However, plenty evidence has proved that the hypostomal condition of pterocephaliids is natant and there is no rostral plate between librigenae, which are directly separated by a median suture (Fortey and Chatterton, 1988). Because the ventral structures of *Guangxiaspis* described below are significantly different from those of pterocephaliids, it seems unsuitable to refer *Guangxiaspis* to Pterocephaliidae Kobayashi. The new material of *Guangxiaspis* is reminiscent of *Mansuyites* Shergold, 1972, but *Guangxiaspis* is distinguished mainly by the medially rather than posteriorly situated palpebral lobes, the blade-like rather than band-like posterolateral limb, and the discernible rather than deep posterior pygidial border furrow. It is reasonably to infer that *Guangxiaspis* is closely allied to *Mansuyites*, and both of them may well be referred to the same family if further evidence could prove that the ventral structure of *Mansuyites* is similar to that of *Guangxiaspis*.

VENTRAL STRUCTURE OF *GUANGXIASPIS GUANGXIENSIS* ZHOU, 1977

The anterior facial sutures are sagittally merged on the border and then run forward to cross the cephalic margin, and finally extend ventrally to form a median suture (Fig. 2, A-B). The doublures of the libriganae are wide (Fig. 2, C) and separated from each other posteriorly by outward curved connective sutures. The rostral plate is triangular in outline, just like that of *Shergoldia laevigata* Zhu *et al*., 2007, and the hypostomal condition is conterminant (Fig. 2, G). The hypostome of *G. guangxiensis* is quadrate in shape with a straight anterior border and wide lateral and posterior borders, reflecting the presumed primitive hypostomal condition of Asaphidae Burmeister (Fortey and Chatterton, 1988). The cranidium and ventral structure of *G. guangxiensis* is similar to those of *S. laevigata*, which is closely related to Asaphidae and has been included in Tsinaniidae Kobayashi of Asaphoidea Raymond by Zhu *et al*. (2007). However, *G. guangxiensis* differs mainly in having a pair of lateral pleural spines on the pygidium, which resembles the pygidia of ceratopygides. This, combined with the overall resemblance of the exoskeletons, makes it reasonable to assign *Guangxiaspis* to Ceratopygidae Linnarsson.

CONCLUSION

Guangxiaspis Zhou is considered as belonging to the Family Ceratopygidae Linnarsson. Both *G. guangxiensis* Zhou and *Shergoldia laevigata* Zhu *et al*., have a triangular rostral plate, supporting the assumption that the median suture may finally be formed as a result of a progressive reduction in the width of the rostral plate (Fortey and Chatterton, 1988). *Guangxiaspis* is closely allied to *Mansuyites*, and, if

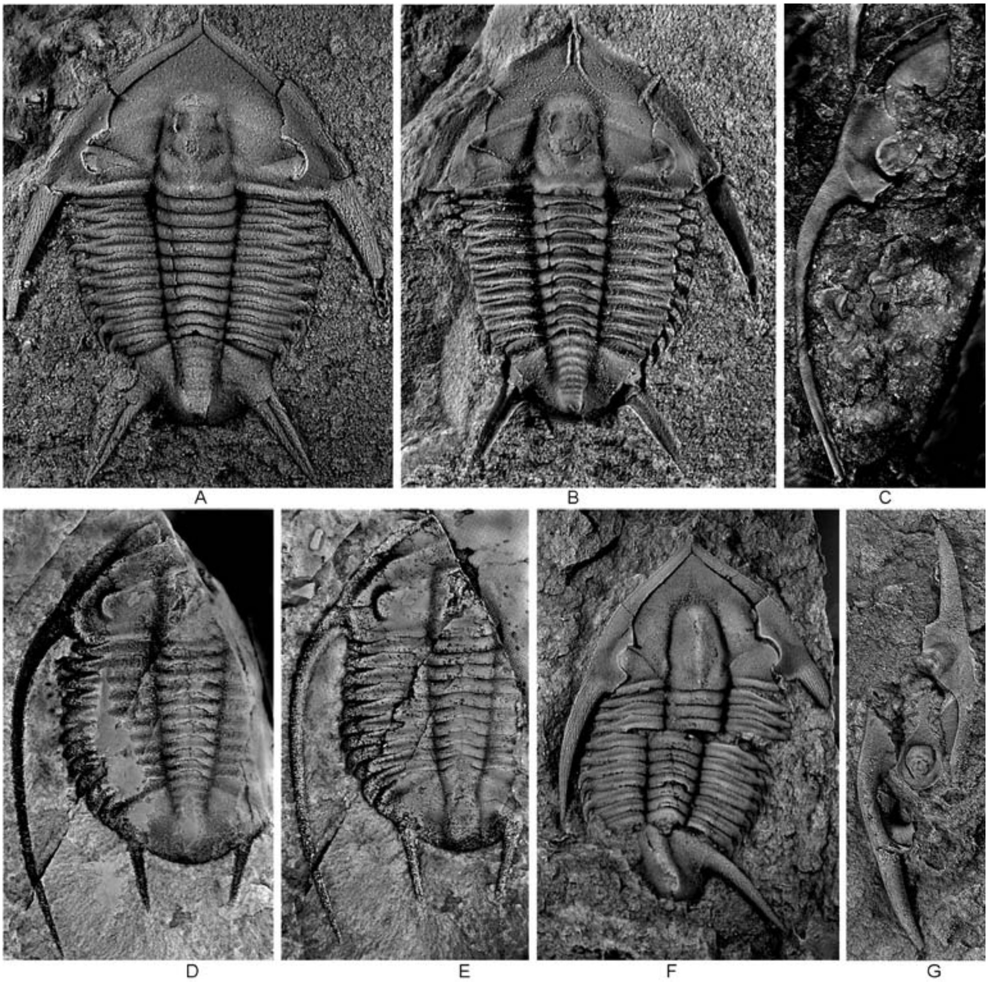

Figure 2. A-G, *Guangxiaspis guangxiensis* Zhou, 1977. A-B, NIGP 148327, x5.0. A, complete holaspid exoskeleton, latex cast from external mould; B, internal mould of complete holaspid exoskeleton. C, NIGP 148337, librigena, latex cast from external mould, x2.6. D-E, NIGP 148339, x2.3, incomplete holaspid exoskeleton, internal mould and latex cast from external mould. F, NIGP 148329, nearly complete holaspid exoskeleton, latex cast from external mould, x2.6. G, NIGP 148328, librigenae, rostral plate and hypostome, latex cast from external mould, x3.7.

further evidence could prove that the ventral structure of *Mansuyites* is similar to that of *Guangxiaspis*, both of them may well be referred to the same family that should be assigned to Asaphoidea Raymond; but, otherwise, both may be ascribed to different but closely related families.

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