Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeoecology

DIEGO BALSEIRO, BEATRIZ G. WAISFELD AND LUIS A. BUATOIS

LETHAIA

Balseiro, D., Waisfeld, B.G. & Buatois, L.A. 2011: Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeoecology. *Lethaia*, Vol. 44, pp. 58–75.

The study of biofacies has proven to be relevant in the understanding of trilobite palaeoecology, palaeobiogeography and macroevolution. The widespread Olenid biofacies is one of the best known, and is usually interpreted as occuring in dysoxic environments. Tremadocian successions of the Argentinian Cordillera Oriental bear a diverse and long-studied olenid-dominated fauna. Based on cluster analysis, five distinct biofacies are defined for the middle Tremadocian (Tr2 stage slice), distributed from shelf (below storm wave base) to lower-shoreface settings (above fair-weather wave base). Ordination shows biofacies along two gradients, a bathymetrical one and another related to oxygen content. All of them are dominated both taxonomically and ecologically by olenids. This detailed quantitative palaeoecological study challenges current views suggesting instead that the Olenidae dominated a broad range of environments, from oxygenated shallow-marine to dysoxic deep-marine. Comparisons with largely coeval trilobite records from geodynamically and palaeobiogeographically disparate sites suggest that siliciclastic sedimentation appears as the most influential controlling environmental factor upon olenid distribution and dominance. Further comparisons across different climatic belts show that siliciclastic input controlled trilobite diversity gradients, even more than latitude. From an autoecological viewpoint distribution of traditional olenid morphotypes shows no relation to depth or to oxygen content, and at least some members of the group appear to have had the possibility of coping with low oxygen content, rather than being restricted to oxygen-deficient environments. The analysis performed herein, together with recent research on the group, demonstrate that factors controlling olenid distribution are more complex than previously envisaged. ☐ *Biofacies*, *diversity*, *Olenidae*, *palaeoecology*, *Tremadocian*, *trilobite*.

Diego Balseiro [balsedie@gmail.com], Beatriz G. Waisfeld [bwaisfeld@efn.uncor.edu], CONICET CICTERRA-CIPAL, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Av. Vélez Sarsfield 299, X5000JJC Córdoba, Argentina; Luis A. Buatois [luis.buatois@usask.ca], Department of Geological Sciences. University of Saskatchewan, 114 Science Place, Saskatoon, SK S7N 5E2, Canada; *manuscript received on 08/07/2009; manuscript accepted on 24/03/2010.*

The study of biofacies provides important information about patterns and processes in evolutionary palaeoecology (Bennington & Bambach 1996; Patzkowsky & Holland 1999; Westrop & Cuggy 1999; Holland & Patzkowsky 2007). The analysis of trilobite biofacies has shed much light on trilobite palaeoecology, palaeobiogeography and macroevolution (e.g. Westrop & Ludvigsen 1987; Fortey 1989; Westrop & Cuggy 1999; Zhou *et al.* 2003; Adrain *et al.* 2004; Amati & Westrop 2006). In particular, the Olenidae has received much attention after the pioneer attempts of defining trilobite biofacies (Fortey 1975; Fortey & Owens 1978).

Henningsmoen (1957) was one of the first authors to point out that many olenids were probably related to dark-shale dysoxic facies. Ever since, these trilobites have been interpreted as a highly specialized clade that was restricted to dysoxic facies throughout their existence (Fortey 1989, 2000). Indeed, Fortey (1999, 2000) proposed that they were the first organisms to bear chemosymbiotic bacteria, an adaptation that allowed them to conquer oxygen-depleted environments.

These hypotheses are mostly supported by the olenid faunas from the Alum Shale (Middle Cambrian–Tremadocian) of Scandinavia and the Valhallfonna Formation (Floian–Dapingian) of Spitsbergen. Subsequent work corroborated this pattern around the globe (e.g. Fortey & Owens 1978; Ludvigsen & Westrop 1983; Clarkson & Taylor 1995; Pegel 2000; Esteban & Tortello 2007). Some olenids are present in diverse trilobite biofacies, always as lesser components (Fortey 1985). These cases were generally interpreted

DOI 10.1111/j.1502-3931.2010.00224.x

as the intergradations between oxygenated and dysoxic environments (e.g. Schovsbo 2001; Landing *et al.* 2007).

The Furongian–Lower Ordovician outcrops from the Argentinian Cordillera Oriental are with no doubt the best known from all coeval successions of the Central Andean Basin (Benedetto 2003 and references therein). The Central Andean Basin extends from Perú up to Norwestern Argentina (Fig. 1), the Argentinian Cordillera Oriental corresponding to the south edge of the basin. These strata bear an important and well-known olenid-dominated trilobite fauna (Harrington & Leanza 1957; Waisfeld & Vaccari 2003 and references therein). In particular, olenids were more abundant in this basin than anywhere else in the world during the Early Ordovician (Fortey & Cocks 2003). Previous studies have dealt mainly with systematic, biostratigraphical or autoecological issues of these faunas (e.g. Waisfeld 2001; Tortello & Clarkson 2003, 2008; Tortello & Esteban 2003; Zeballo & Tortello 2005; Waisfeld & Vaccari 2006, 2008b; Waisfeld *et al.* 2006; Esteban & Tortello 2007), while palaeosynecological questions have received little attention (Balseiro & Marengo 2008; Waisfeld & Vaccari 2008a). Therefore, the palaeobiological dynamics of these faunas is far from being understood.

In this context, Furongian–Lower Ordovician successions from the Argentine Cordillera Oriental are ideal to test different hypotheses concerning olenid palaeoecology. Here, we present a detailed analysis of trilobite biofacies for the earliest Middle Tremadocian (Tr2 stage slice, Bergström *et al.* 2009) from Northwestern Argentina (Fig. 1). This analysis shows that the distribution of olenids was not restricted to dysoxic facies as previously thought.

Geological setting

The Furongian–Early Ordovician tectonic and sedimentary history of the Cordillera Oriental is complex (Astini 2003). This succession developed in a back-arc foreland basin with variation in subduction angle

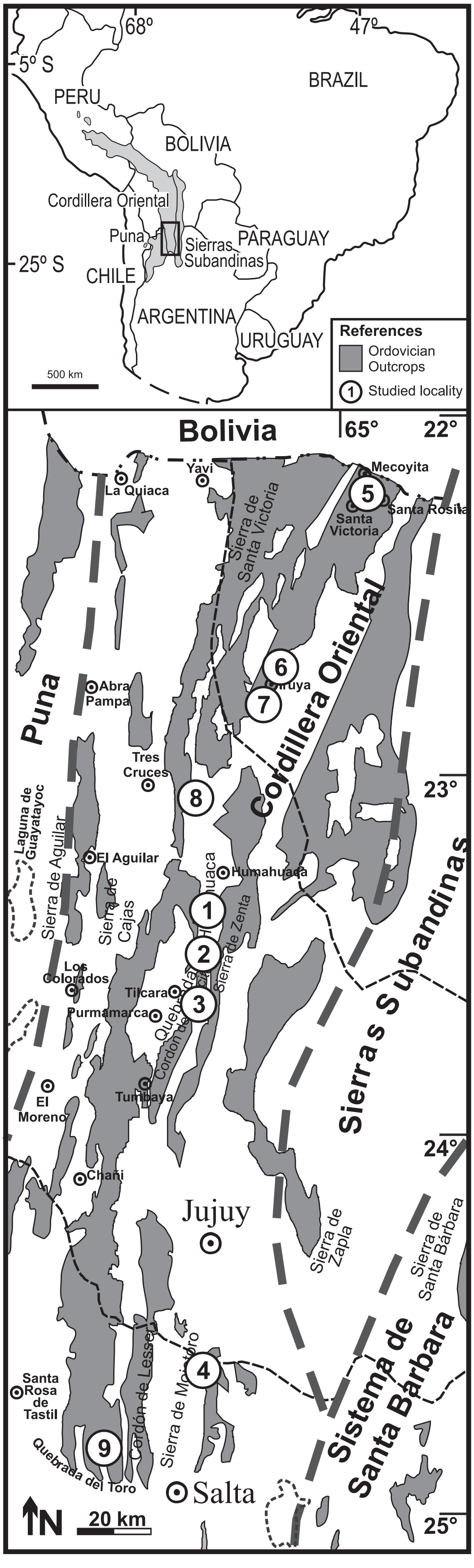

Fig. 1. Map showing location of Central Andean Basin and studied localities in the Argentinian Cordillera Oriental. Localities 1–4 were sampled for this study. Data from localities 5–9 come from the literature (Harrington & Leanza 1957), as well as additional samples from locality 3 (Zeballo & Tortello 2005). Localities: 1, Angosto del Ferrocarril, Angosto de Chucalezna; 2, Quebrada del Arenal, Huacalera area; 3, Alfarcito area (Quebrada de Casa Colorada and Quebrada de Rupasca were sampled for this study – Quebrada de San Gregorio and Quebrada de Casa Colorada based on literature); 4, Corte Ruta 9, Sierra de Mojotoro; 5, Santa Victoria; 6, Iruya, Nazareno; 7, Orán; 8, Azul Pampa; 9, Incamayo. Modified from Astini (2003).

(Bahlburg 1991; Astini 2003, 2008). There is growing evidence suggesting a doubly fed sedimentary system, with one source from the arc to the west, and the other from the craton to the east (Astini *et al.* 2003; Astini & Marengo 2006). Also, the development of areally restricted, incised fluvial conglomeratic and estuarine sandstone wedges indicates that some regions of the basin were partially exposed, while others were submerged during the Tremadocian (Buatois & Mángano 2003; Astini 2005, 2008; Buatois *et al.* 2006). As a result, an amazingly thick sedimentary succession with complex stratigraphical architecture and a diverse facies mosaic accumulated and is unlike that in any other coeval basin (Astini 2003; Buatois & Mángano 2003; Buatois *et al.* 2006).

The Furongian–Early Ordovician of the Cordillera Oriental is represented by the Santa Rosita Formation and partial equivalents (see Astini 2003, 2008 for a review). This formation records a wide array of depositional environments, ranging from shelf to storm-dominated shallow-marine deposits, usually associated with deltaic systems, punctuated by conversions towards complex tide-dominated estuaries (Astini 2003; Buatois & Mángano 2003; Buatois *et al.* 2006). The Santa Rosita Formation has recently been divided into different members combining the classic lithostratigraphical nomenclature proposed by Harrington (in Harrington & Leanza 1957) with a detailed sequence stratigraphical study (Buatois *et al.* 2006). According to these authors, in the Quebrada de Humahuaca area this formation is divided into at least six members. The Tilcara, Casa Colorada and Pico de Halcón members are Furongian (Late Cambrian) in age, the Alfarcito Member may include the Cambrian–Ordovician boundary, and the Rupasca and Humacha members range in age from the Middle Tremadocian up to the Late Tremadocian (Buatois *et al.* 2006).

The investigated time interval is represented in the Rupasca Member that is constrained to the lowest part of Tr2 stage time-slice (*Paltodus deltifer pristinus* subzone, Ortega & Albanesi 2005; Albanesi & Aceñolaza 2005; Zeballo *et al.* 2005). This member is represented in its type locality by three sequences that describe a stepwise flooding event (Buatois *et al.* 2006). Correlation of the Rupasca Member across the Cordillera Oriental is difficult due to the great diversity of lithofacies and common discontinuities. Nevertheless, integration of high-resolution graptolite, conodont and trilobite biostratigraphy with sequence stratigraphy helps the understanding of the sedimentary history and possible correlations (Ortega & Albanesi 2005; Buatois *et al.* 2006; Waisfeld & Vaccari 2008b). These analyses have allowed the correlation of the Tr2 along the Cordillera Oriental. Almost all known outcrops of this time-slice have been sampled for this study. The sampled localities include the Quebrada de Casa Colorada and Quebrada de Rupasca both in the Alfarcito area (Zeballo *et al.* 2005; Buatois *et al.* 2006), the Quebrada del Arenal in the Huacalera area (Moya 1988), and the Angosto del Ferrocarril in the Angosto de Chucalezna area (Albanesi & Aceñolaza 2005) (Fig. 1). Additional samples were taken from the broadly coeval Floresta Formation, from the Corte Ruta 9 in the Sierra de Mojotoro (Moya 1998). In addition, published data (Harrington & Leanza 1957; Zeballo & Tortello 2005) from the Santa Rosita Formation exposed at Santa Victoria, Iruya (Nazareno), Orán, Azul Pampa, Incamayo, and Alfarcito area (Quebrada de Casa Colorada and Quebrada de San Gregorio) were taken into account (Fig. 1).

The depositional environments (terminology after MacEachern *et al.* 1999) interpreted for this time-slice range from shelf (from storm wave base to shelf/slope break) to lower shoreface (immediately above fair-weather wave base) (Buatois *et al.* 2006). The deepest-water facies crop out at the Alfarcito area, while shallower-marine settings are recorded in the other localities exposed farther north (e.g. Quebrada del Arenal).

Sedimentary facies

Five sedimentary facies have been identified in the Rupasca Member, based on detailed sedimentological analysis in three areas, Alfarcito (Quebrada de Rupasca and Quebrada de Casa Colorada sections), Humacha (Quebrada del Arenal section) and Chucalezna (Angosto del Ferrocarril section) areas (Fig. 2). These facies are stacked, forming coarsening- and thickening-upward parasequences. Lower-shoreface deposits consist of light grey, hummocky cross-stratified, fine-grained sandstone forming amalgamated packages. Individual sandstone beds generally pinch out, but bedsets are laterally persistent. Thin mudstone partings are locally present. Gutter casts, load casts, ball-and-pillow structures and tool marks are common, while wrinkle marks are present locally. Physical sedimentary structures in these deposits indicate episodic storm wave activity, and wave-generated surges (Buatois & Mángano 2003; Buatois *et al.* 2006). High-energy oscillatory, and combined flows were the dominant processes during frequent storms. Flows were strongly erosive, and characterized by rapid influx of sand. Recurrent storms and continuous wave agitation during fair-weather removed most of the finer-grained particles, leaving only thin mudstone partings between sand units. These deposits are typified as strongly storm-dominated shorefaces (*sensu* MacEachern & Pemberton 1992). Lower-shoreface

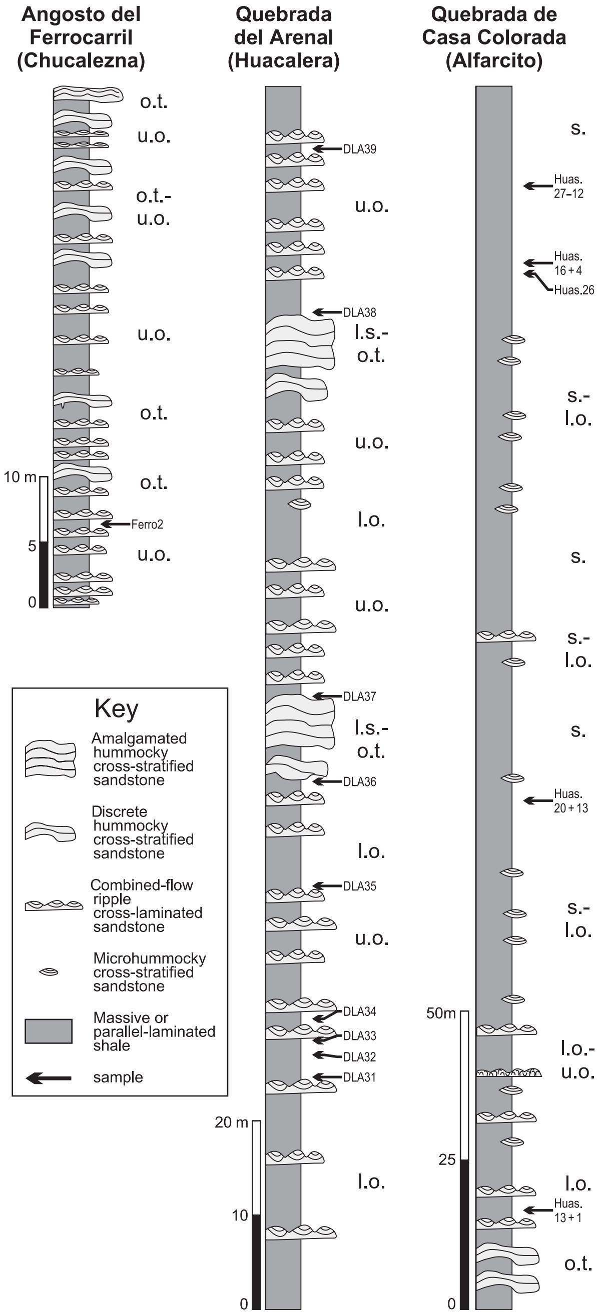

Fig. 2. Measured stratigraphical sections and inferred depositional environments of the Rupasca Member in the Cordillera Oriental. Neither base nor top observed in the Angosto del Ferrocarril section. Quebrada de Casa Colorada section after Buatois *et al.* (2006). Note different scales. l.s. lower shoreface, o.t. offshore transition, u.o. upper offshore, l.o. lower offshore, s. shelf.

deposits are uncommon in the Rupasca Member, being restricted to the tops of progradational packages in the Quebrada del Arenal.

Offshore-transition deposits consist of regularly interbedded, yellowish green and grey, parallel-laminated mudstone, and thin to thick, light grey, erosive-based, fine- to very fine-grained sandstone with hummocky cross-stratification, combined-flow ripple cross-lamination and/or symmetrical to near-symmetrical ripples at the top. Sandstone beds are usually laterally extensive, although displaying thickness variation. Hummocky cross-stratification is the dominant structure in the thickest sandstone beds, while combined-flow ripple cross-lamination tends to dominate in the thinnest beds. In contrast to lower-shoreface deposits, amalgamation of hummocky beds is uncommon. Common shell lags and intraclast layers are present at the base of hummocky beds. Gutter casts, load casts, tool marks and wrinkle marks are common. These deposits reflect alternation of quiet-water sediment fall-out, and combined and pure oscillatory flows due to frequent storms (Buatois & Mángano 2003; Buatois *et al.* 2006). The presence of thin mudstone intervals separating hummocky beds indicates periods of low energy between storm flows and deposition immediately below fair-weather wave base. Offshore-transition deposits are more abundant than lower-shoreface facies, but tend to be more common in the Huacalera area (e.g. Quebrada del Arenal) than in the Alfarcito area. In the latter, they invariably mark the tops of coarsening-upward parasequences, while in the former they may also occur immediately below lower-shoreface deposits.

Upper-offshore deposits consist of yellowish green, grey and brown parallel-laminated mudstone intercalated with thin light grey, tabular, erosive-based, very fine-grained silty sandstone. Sandstone usually displays parallel lamination, combined-flow ripple cross-lamination, symmetrical to near-symmetrical ripples, micro-hummocky cross-stratification, and hummocky cross-stratification. Load casts, tool marks and wrinkle marks are common. Upper-offshore deposits reflect alternating background suspension fall-out in a low-energy setting punctuated by distal storm deposition (Buatois & Mángano 2003; Buatois *et al.* 2006). The decrease in sand/mud ratio with respect to offshore-transition deposits indicates longer periods of fair-weather deposition of fines and sedimentation well below the fair-weather wave base. Upper-offshore deposits are abundant in the Huacalera and Alfarcito areas, as well as the section at the Angosto del Ferrocarril at the Angosto de Chucalezna.

Lower-offshore deposits consist of greenish grey, massive or thinly parallel-laminated mudstone. Mudstone units are laterally extensive, displaying sharp bases and are interbedded with grey, sharp-based, tabular, very thin, very fine-grained silty sandstone beds, exhibiting combined-flow ripple cross-lamination and symmetrical to near-symmetrical ripple tops. These deposits were formed in a low-energy setting, where suspension fall-out sedimentation was punctuated by rare, storm events (Buatois & Mángano 2003; Buatois *et al.* 2006). The presence of oscillatory structures in most of the interbedded sandstone layers indicates deposition immediately above storm-wave base. This environmental scenario is also supported by the scarcity of sandstone beds and the presence of thick mudstone intervals. Lower-offshore deposits are more abundant in the Alfarcito area, but are also present in the Huacalera area. In Huacalera, they commonly occur at the base of coarsening-upward parasequences immediately overlying flooding surfaces. In the Alfarcito area, they may also be present immediately above shelf deposits.

Shelf deposits consist of black, thinly parallel laminated shale. Shale units are laterally extensive, displaying sharp bases. Bioturbation is absent. This facies records deposition below storm-wave base in a low-energy environment due to suspension fall-out deposition in the absence of waves and currents (Buatois & Mángano 2003; Buatois *et al.* 2006). Absence of bioturbation indicates dominantly anoxic conditions at the sediment-water interface. However, oxygenation events leading to the establishment of periods of dysaerobic waters are indicated by the local presence of benthic fauna. This facies is restricted to the Alfarcito area where it forms thick packages.

Data and methods

Sampling method

Sixteen samples were collected from shales corresponding to fair-weather suspension-fallout deposition. This lithofacies was the only one sampled so taphonomical biases were minimized. The stratigraphical thickness of each sample was restricted to 10–20 cm, in order to avoid significant time-averaging signatures. A minimum number of 100 individuals was an *a priori* sample-size aim, which was usually but not always reached. Every identifiable trilobite sclerite was counted and the MNI protocol was used to obtain the number of individuals in each sample (Gilinsky & Bennington 1994).

One sample was obtained from the Floresta Formation from a homogeneous 1-m-thick shale interval. This interval was too thick compared with the strict sampling procedure applied for the other samples and had a greater sample size, therefore the original sample was divided in two sub-samples, whose sizes were randomly chosen from a normal distribution of mean 100 and standard deviation 10. For the sub-samples, the individuals were randomly chosen without replacement from the original sample until both sub-sample sizes were reached. A similar resampling technique was recently used by Bulinski (2007) and Layou (2009).

The final database ('abundance dataset', Table 1) consists of 18 samples, 3408 trilobite remains, 2018 individuals and 11 taxa (mean sample size: 112 individuals/sample).

In addition, 23 samples from similar lithologies were obtained from the literature (Harrington & Leanza 1957; Zeballo & Tortello 2005). Unfortunately, no counts are available for these literature samples, although the mean richness and variance is similar to our own dataset, implying a similar sample size. The complete database ('presence–absence dataset', Table 2) consists of 41 samples and 13 taxa. Agnostids were removed from all analyses because they are generally interpreted as planktonic (e.g. Robison 1972; see review by Fortey & Owens 1999), and some authors have even considered that they might not be trilobites (e.g. Walossek & Müller 1990).

Analytical methods

To analyse the data, a cluster analysis and an ordination were carried out. Cluster analysis has the tendency to define groups and due to this property is an ideal method for defining biofacies (Ludvigsen *et al.* 1986). This analysis was performed using the HCLUST and VEGDIST in the vegan package for R (R project 2008). The dendrogram was obtained using the square root of the Bray-Curtis similarity with the Ward grouping method. Because the used metric is ultrametric with binary data and possibly with abundance data (Legendre & Legendre 1998), it is suitable for Ward's method.

As cluster analysis has the tendency to break gradients into discrete assemblages, an ordination was conducted. This analysis was performed to see how biofacies intergraded along a biotic gradient and recognize the main underlying environmental factor (Webber 2004). The analysis was carried out by means of a correspondence analysis (CA) using the CCA function in the vegan package for R (R Project 2008). The CA was preferred against other commonly used ordination methods, because it has shown to be as effective as other methods (e.g. DCA) in finding gradients while it does not lose information due to detrending (Minchin 1987). Particularly, our ordination shows two gradients and a detrending procedure would obscure one of them.

A preliminary analysis showed that the high dominance of one genus (*Leptoplastides*) in most samples prevented a clear interpretation of the results, mainly of the ordination analysis. To avoid this problem, two alternatives were used. Firstly, the abundance dataset was log-transformed prior to a within sample

Table 1. Number of individuals per taxon in each sample of the abundance dataset.

Sample	Locality	*Leptoplastides*	*Bienvillia*	*Peltocare*	*Parabolinella*	*Asaphellus*	*Asaphellus?*	*Pseudokainella*	*Apatokephalus*	*Hapalopleura*	*Orometopido*	*Pharostomina*	Agnostid	Sedimentary environment
DLA31	Arenal	61	0	0	0	43	0	9	0	0	0	0	4	Upper offshore
DLA32	Arenal	110	2	7	13	66	0	49	0	0	0	0	1	Lower offshore
DLA33	Arenal	108	8	5	6	17	0	52	0	0	0	0	1	Lower offshore
DLA34	Arenal	134	2	20	1	6	0	34	0	0	0	0	0	Lower offshore
DLA35	Arenal	47	0	0	8	34	0	0	1	0	0	1	0	Offshore transition
DLA36	Arenal	54	0	0	0	6	0	0	0	0	0	0	0	Offshore trans.-Lower Shoreface
DLA37	Arenal	108	0	0	0	16	0	0	0	0	0	0	0	Offshore trans.-Lower Shoreface
DLA38	Arenal	128	0	0	0	35	0	0	1	0	0	0	0	Offshore trans.-Lower Shoreface
DLA39	Arenal	56	0	0	0	12	0	0	0	0	0	0	0	Offshore trans.-Lower Shoreface
Huas.13 + 1	Alfarcito	44	4	0	1	0	0	28	1	15	0	0	6	Shelf
Huas.20 + 13	Alfarcito	28	0	0	1	0	0	7	0	0	0	0	0	Shelf
Huas.26	Alfarcito	34	2	0	6	0	0	0	0	0	0	0	8	Shelf
Huas.26 + 4	Alfarcito	40	3	0	5	0	0	1	0	0	0	0	10	Shelf
Huas.27–12	Alfarcito	102	38	0	23	2	0	0	0	0	0	0	4	Shelf
Rupas.Sau	Alfarcito	37	7	2	1	0	0	6	0	0	0	0	0	Shelf
Ferro2	Chucalezna	64	0	0	0	12	0	0	0	0	0	0	1	Upper offshore
Flor.A	Mojotoro	0	36	0	26	10	30	0	0	0	1	0	0	Shelf
Flor.B	Mojotoro	0	41	0	17	15	33	0	0	0	2	0	1	Shelf

Table 2. Presence of each taxa in the samples of the presence–absence dataset.

Sample	Locality	*Leptoplastides*	*Pseudokainella*	*Parabolinella*	*Asaphellus*	*Asaphellus?*	*Hapalopleura*	*Apatokephalus*	*Bienvillia*	*Peltocare*	*Pharostomina*	*Conophrys*	*Plicatolina*	Orometopid	Agnostid
DLA31	Arenal	1	1	0	1	0	0	0	0	0	0	0	0	0	1
DLA32	Arenal	1	1	1	1	0	0	0	1	1	0	0	0	0	1
DLA33	Arenal	1	1	1	1	0	0	0	1	1	0	0	0	0	1
DLA34	Arenal	1	1	1	1	0	0	0	1	1	0	0	0	0	0
DLA35	Arenal	1	0	1	1	0	0	1	0	0	1	0	0	0	0
DLA36	Arenal	1	0	0	1	0	0	0	0	0	0	0	0	0	0
DLA37	Arenal	1	0	0	1	0	0	0	0	0	0	0	0	0	0
DLA38	Arenal	1	0	0	1	0	0	1	0	0	0	0	0	0	0
DLA39	Arenal	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Huas.13 + 1	Alfarcito	1	1	1	0	0	1	1	1	0	0	0	0	0	1
Huas.20 + 13	Alfarcito	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Huas.26	Alfarcito	1	0	1	0	0	0	0	1	0	0	0	0	0	1
Huas.26 + 4	Alfarcito	1	1	1	0	0	0	0	1	0	0	0	0	0	1
Huas.27−12	Alfarcito	1	0	1	1	0	0	0	1	0	0	0	0	0	1
Rupas.Sau	Alfarcito	1	1	1	0	0	0	0	1	0	0	0	0	0	1
Alf.CC-3	Alfarcito	1	1	0	0	0	1	0	1	0	0	0	0	0	1
Alf.CC-4	Alfarcito	1	1	1	1	0	1	0	1	1	1	0	0	0	1
Alf.CC-5	Alfarcito	1	0	1	1	0	0	0	1	1	0	0	0	0	1
Alf.CC-6	Alfarcito	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Alf.CC-7	Alfarcito	1	0	1	1	0	0	0	1	0	0	0	0	0	1
Alf.CC-8	Alfarcito	1	0	1	1	0	0	0	1	0	0	0	0	0	0
Alf.SG-4	Alfarcito	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Alf.SG-5	Alfarcito	1	1	1	0	0	0	0	1	1	0	0	0	0	0
Alf.SG-6	Alfarcito	1	1	1	0	0	1	0	1	1	0	0	0	0	0
Alf.SG-7	Alfarcito	1	0	1	0	0	0	0	1	0	0	0	0	0	0
Alf.SG-8	Alfarcito	1	0	0	0	0	0	0	0	0	0	0	0	0	1
J.Til-1	Alfarcito	1	1	0	0	0	0	0	1	0	0	0	1	0	0
J.Til-2a	Alfarcito	1	1	1	0	0	0	0	1	1	0	0	1	0	0
J.Til-2b	Alfarcito	1	1	1	0	0	0	0	1	1	0	0	0	0	1
J.Til-7	Alfarcito	1	0	1	0	0	0	0	1	1	0	0	0	0	0
J.Til-8	Alfarcito	0	0	1	1	0	0	0	1	0	0	0	0	0	1
Ferro2	Chucalezna	1	0	0	1	0	0	0	0	0	0	0	0	0	1
Flor.A	Mojotoro	0	0	1	1	1	0	0	1	0	0	0	0	1	0
Flor.B	Mojotoro	0	0	1	1	1	0	0	1	0	0	0	0	1	1
S.Ora-3	Orán	1	0	1	0	0	0	0	1	0	0	0	0	0	0
J.Hum-6	Azul Pampa	1	0	0	1	0	0	1	1	0	0	1	0	0	1
S.Iru-5e	Iruya	1	0	1	0	0	1	0	1	0	0	0	0	0	1
S.Ros12-P14	Incamayo	0	0	1	1	0	0	0	1	0	0	0	0	0	1
S.Ros12-P17	Incamayo	0	0	0	1	0	0	0	1	0	0	0	0	0	0
S.Vic-N47	Santa Victoria	1	0	0	1	0	0	0	0	0	0	0	0	0	0
S.Vic-N49	Santa Victoria	1	0	0	0	0	0	1	0	0	0	0	0	0	0

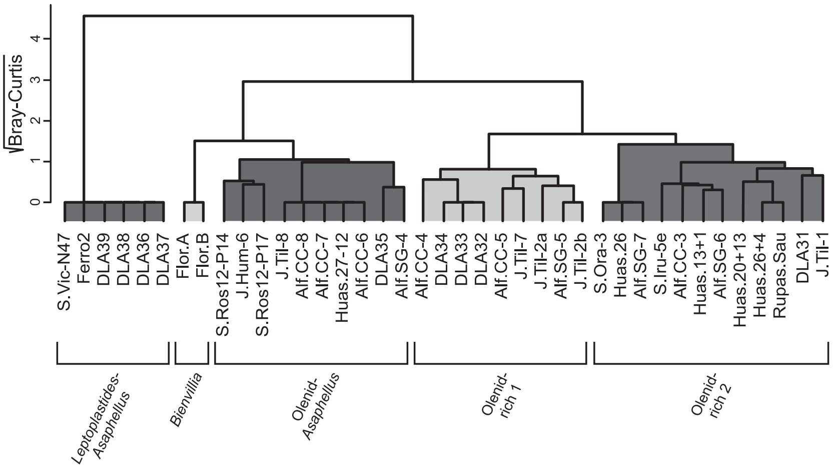

Fig. 3. Result of the cluster analysis carried out with the presence–absence dataset. Cophenetic correlation = 0.645.

percentage transformation. To avoid values of zero in cases of abundances of one individual, the equation used was (log*x*) + 1, while zero abundances remained as 0. Secondly, the dataset was transformed to a presence/absence matrix. This option has two advantages: it gives equal importance to all taxa, thus minimizing the effect of highly abundant ones; and, it also allows the possibility of analysing the literature data together with our own dataset. The preliminary analysis also showed that *Apatokephalus* was an outlier in the ordinations, so it was removed from both datasets for the cluster analysis and for the ordination.

The cluster and CA were carried out for both transformations after removing all taxa present in only one sample and all samples having only one taxon. The results were similar, although not identical, and all of them will be discussed in the next section.

In order to study the diversity gradient, two standardization methods were applied. Firstly, the samples from the abundance dataset were rarefied down to 90 individuals (E[Sn]) in order to obtain a standardized richness comparable with that of Westrop & Adrain (1998, 2001). Only samples with more than 90 individuals were taken into account for this analysis. Rarefaction was carried out with Analytical-Rarefaction 1.3 (Holland 2003), which is based on the analytical solution described by Hurlbert (1971). In addition, in order to compare the richness in each biofacies including the presence–absence dataset, a different re-sampling technique was applied (Alroy 2000a,b). This methodology is extensively explained by Alroy (2000a) and Bush *et al.* (2004), and has shown to be more accurate compared with the rarefaction based on occurrences and more useful in standardizing different datasets (Alroy 2000b). In this case, the quota used was 25, this is a very-low quota, but it is caused by the very-low richness in one of the biofacies. Nevertheless, using higher quotas, without taking into account the low richness biofacies, yields similar results. The re-sampling technique employed was the O2W (Alroy 2000a). Using other proposed coefficients such as 1.4 (O1.4W, Bush *et al.* 2004) gives comparable results. For the sake of clarity, only the O2W analysis with a quota of 25 is shown herein. The re-sampling was repeated 100 times in order to have confidence intervals.

Results

Cluster analysis

The cluster analysis of the abundance and presence absence data shows five groups that, following Ludvigsen *et al.* (1986), can be interpreted as biofacies. As some biofacies have rather different compositions in the abundance and presence–absence datasets, each cluster analysis will be discussed separately.

Presence–absence dataset. – The *Leptoplastides-Asaphellus* biofacies (Fig. 3) is clearly defined and groups samples consisting of *Leptoplastides*, with the asaphid as almost the only other genus present. All samples from this cluster lack other olenids but *Leptoplastides*. This biofacies occurs in offshore-transition deposits, and to a lesser extent in lower-shoreface and upper-offshore facies.

The Olenid-*Asaphellus* biofacies (Fig. 3) is composed of samples that have moderate olenid richness always associated with *Asaphellus*. The olenids include *Leptoplastides*, *Bienvillia* and *Parabolinella*. The samples of this cluster occur in upper-offshore to offshore-transition deposits.

The Olenid-rich 1 biofacies (Fig. 3) is dominated by olenids such as *Leptoplastides*, *Bienvillia*, *Parabolinella*, *Peltocare* and *Plicatolina*. While *Plicatolina* is present only in one sample, all other olenids are invariably present in this cluster. The richness of olenids is the highest, compared with any other biofacies in the analysis. Other trilobites present are *Asaphellus* and *Pseudokainella*, although they are randomly present in the samples defining this cluster. It occurs in lower-offshore deposits.

The Olenid-rich 2 biofacies is characterized by *Leptoplastides*, *Parabolinella* and *Bienvillia* (Fig. 3). As in the Olenid-rich 1 biofacies, *Pseudokainella* is present in many though not all samples. However, it is distinguished from the latter biofacies by the absence of *Asaphellus* and *Peltocare*. *Hapalopleura* is mostly restricted to this biofacies. The samples come mainly from dark shale interpreted as shelf facies (Buatois *et al.* 2006).

The *Bienvillia* biofacies corresponds to the subsamples from the Floresta Formation (Fig. 3). *Bienvillia*, *Parabolinella* and two asaphids define this biofacies. The absence of *Leptoplastides* is surprising as it is the only genus invariably present in every other biofacies. The samples from this cluster are also characterized by the occurrence of an orometopid not present in any other biofacies. These samples come from scarcely bioturbated brown shales interpreted as deposited in a shelf environment (Moya 1998).

Abundance dataset. – As in the case of the presence–absence dataset, the *Leptoplastides-Asaphellus* biofacies is clearly defined. It has almost the same membership (Fig. 4). *Leptoplastides* is highly abundant reaching 90% of individuals in some samples. *Asaphellus* is always present, though in low abundances (~10%).

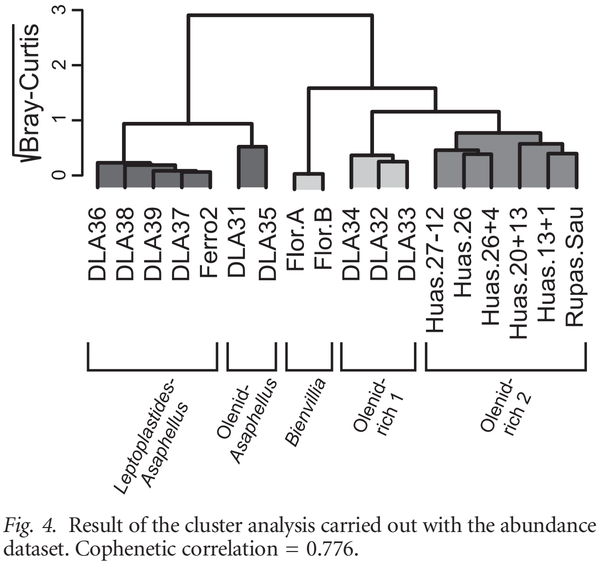

Fig. 4. Result of the cluster analysis carried out with the abundance dataset. Cophenetic correlation = 0.776.

The Olenid-*Asaphellus* biofacies exhibits some differences compared with its counterpart defined in the presence–absence dataset (Fig. 4). Here, it is only defined by two samples, one of which (DLA31) does not belong to this biofacies in the presence–absence analysis. The composition is also rather different, with *Leptoplastides* and *Asaphellus* present in moderate to high abundances, and other taxa, such as *Parabolinella*, in much lower abundances. Interestingly, *Asaphellus* has its highest relative abundances (~30%) in this biofacies.

The Olenid-rich 1 biofacies is very similar to its equivalent defined in the presence–absence dataset. Four olenids always occur: *Leptoplastides*, *Bienvillia*, *Parabolinella* and *Peltocare*, and a fifth (*Plicatolina*) is locally present. The only one with high relative abundance is again *Leptoplastides*. The main difference, compared with the presence–absence dataset, is that in every sample analysed here *Asaphellus* is present in moderate to low relative abundances. *Pseudokainella* also occurs in all samples in low to moderate abundance. This biofacies is again the one with more numerous olenid genera.

The Olenid-rich 2 biofacies is very similar to the one defined in the presence–absence dataset (Fig. 4). Its main feature is that *Asaphellus* is virtually absent in this biofacies, being present in only one sample in extremely low abundance (0.1%). Only three olenids are always present (*Leptoplastides*, *Bienvillia* and *Parabolinella*), and again *Leptoplastides* is the dominant taxon. Other taxa present are *Pseudokainella* and *Hapalopleura*, although not in every sample. This is the only biofacies where olenids may account for every individual in some samples.

The *Bienvillia* biofacies is clearly defined in this analysis (Fig. 4). The differences between this biofacies and the others resemble the results of the presence–absence analysis. The most important feature is the dominance of *Bienvillia* and the absence of the otherwise ubiquitous *Leptoplastides*.

Finally, the main differences between the biofacies defined in the abundance dataset and the presence–absence dataset are found in the Olenid-*Asaphellus* biofacies, and to some extent in the Olenid-rich 1 biofacies. Two possible causes might explain these differences. Firstly, the situation might result from the fact that the Olenid-*Asaphellus* biofacies includes numerous samples from the literature. This causes a difference in membership between biofacies when each dataset is analysed. Secondly, these two biofacies, as will be explained below, are in the centre of the gradient, and hence samples cluster in a different way when more importance is given to rare taxa, as

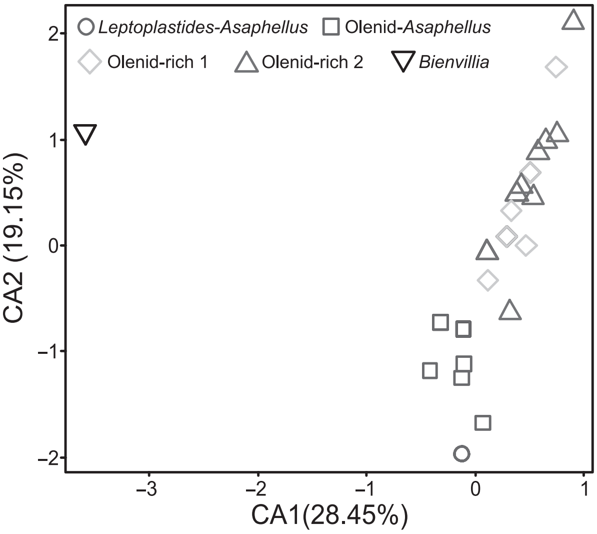

Fig. 5. Correspondence analysis performed with the presence–absence dataset. Each biofacies is depicted with a particular symbol. Numbers between brackets indicate percentage of total inertia associated with each axis.

is the case with the presence–absence transformation.

Ordination

When the presence–absence dataset is analysed, the major axis (CA1) segregates the *Bienvillia* biofacies from all other biofacies (Fig. 5). This may be caused by the presence of an environmental gradient developed towards the southeast of the basin (Sierrra de Mojotoro, Fig. 1) which is difficult to sample because broadly coeval successions are not properly exposed. If the *Bienvillia* biofacies was in or near the extreme of an unsampled gradient, in the CA analysis these samples would be separated from the others while the well-sampled gradient would be defined as a linear distribution of samples (Olszewski & Erwin 2009). Also, the possibility that the sampled interval from the Floresta Formation and the Rupasca Member of the Santa Rosita Formation are not strictly coeval should be considered. In this case, the compositional differences due to time alone would cause a similar pattern in the ordination space.

The second axis clearly distributes all other samples along a gradient (Fig. 5). The linear distribution of the samples along this gradient implies that one environmental factor is the responsible for most of the compositional differences along it. If depositional environments are taken into account, the gradient can be interpreted as a bathymetrical one. This interpretation is based on the occurrence of samples from near-shore depositional environments (lower shoreface) in low CA axis 2 scores, and samples from deeper-water (shelf) depositional environments in high CA axis 2 scores. The intermediate scores for the offshore-transition and upper-offshore samples are in agreement.

In this gradient, the *Leptoplastides*-*Asaphellus* biofacies lies at the shallowest extreme, followed by the Olenid-*Asaphellus* biofacies. However, there is a palaeoenvironmental overlap between these two shallow-water biofacies because both occupy the offshore-transition and upper-offshore zones. The Olenid-rich 1 and the Olenid-rich 2 biofacies are in similar positions, although most of the Olenid-rich 1 samples tend to be towards the shallow extreme (mainly lower offshore) and most of the Olenid-rich 2 towards the deep end of the gradient (shelf) (Fig. 5).

When individual genera are analysed along this gradient, it can be seen that *Leptoplastides* occurs all along the depositional profile, representing a facies-crossing taxon. While *Asaphellus* tends to be present towards the shallow end, *Bienvillia*, *Parabolinella,* and other olenids appear successively with increasing depth (Fig. 6, Table 2).

When the abundance dataset is analysed, the results are very similar to those of the presence–absence dataset (Fig. 7). As in the presence–absence dataset the CA axis 1 separates the *Bienvillia* biofacies from the rest of the biofacies (Fig. 7A), and the CA axis 2 defines the bathymetrical gradient (Fig. 7A). However, the bathymetrical gradient does not follow a linear distribution, indicating that more than one environmental factor controlled the distribution of taxa. When CA axis 3 is plotted against CA axis 2, this pattern can be clearly observed (Fig. 7B). The CA axis 2 possibly corresponds to depth. The interpretation is based on the arrangement of shelf environments towards one end and lower shoreface settings towards the other. The Olenid-rich 1 and Olenid-rich 2 biofacies are arranged along a distinct line when analysing the CA axis 3 and 2 together (Fig. 7B). This distribution is probably developed in response to a different gradient than depth. Based on sedimentological evidence, this second gradient can be interpreted as related to oxygen content. The samples with low CA axis 3 scores come from light coloured highly bioturbated shale, while samples with high scores come from dark, laminated, scarcely bioturbated shale. Buatois *et al.* (2006) interpreted this dark-shale facies as having accumulated in an oxygen-depleted environment.

The detailed analysis of the relative abundance of each genus in the ordination shows that once again *Leptoplastides* is the only taxon present in all samples, but the *Bienvillia* biofacies (Fig. 8). Other olenids are present in deeper-water settings, both oxygenated and dysoxic. *Asaphellus* is present in low to moderate abundances in the shallow end of the bathymetrical gradient and the oxygenated end of the oxygen gradient. Interestingly, the highest relative abundances of

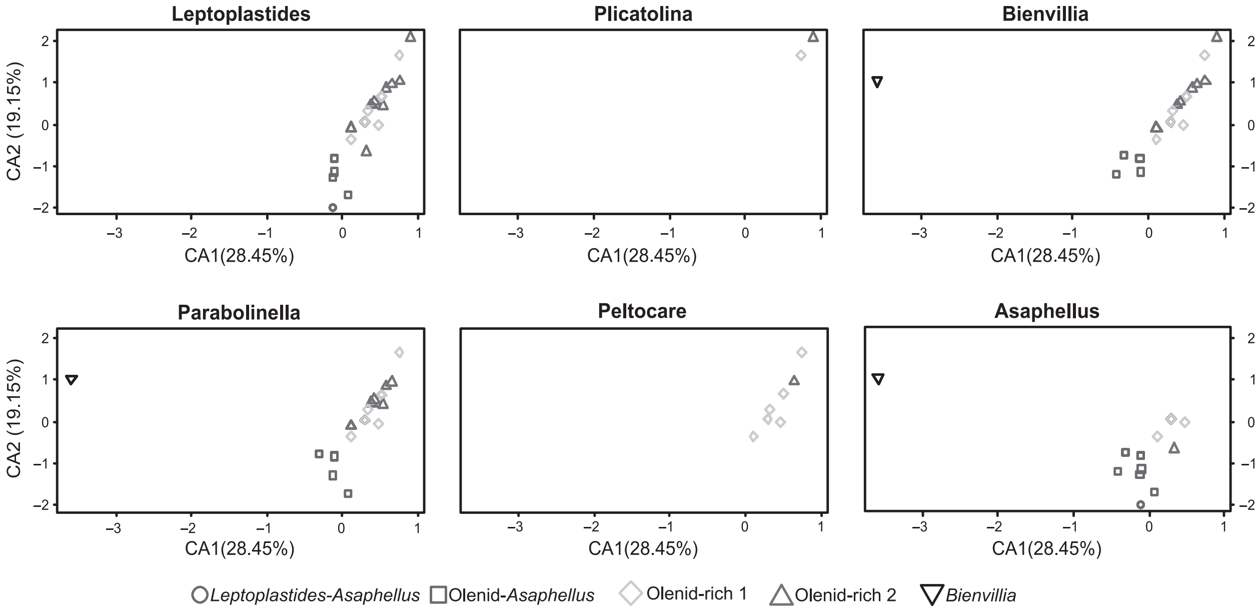

Fig. 6. Presence of main genera discussed in the text along the gradient in the presence–absence dataset. Each biofacies is depicted with a particular symbol. Numbers between brackets indicate percentage of total inertia associated with each axis.

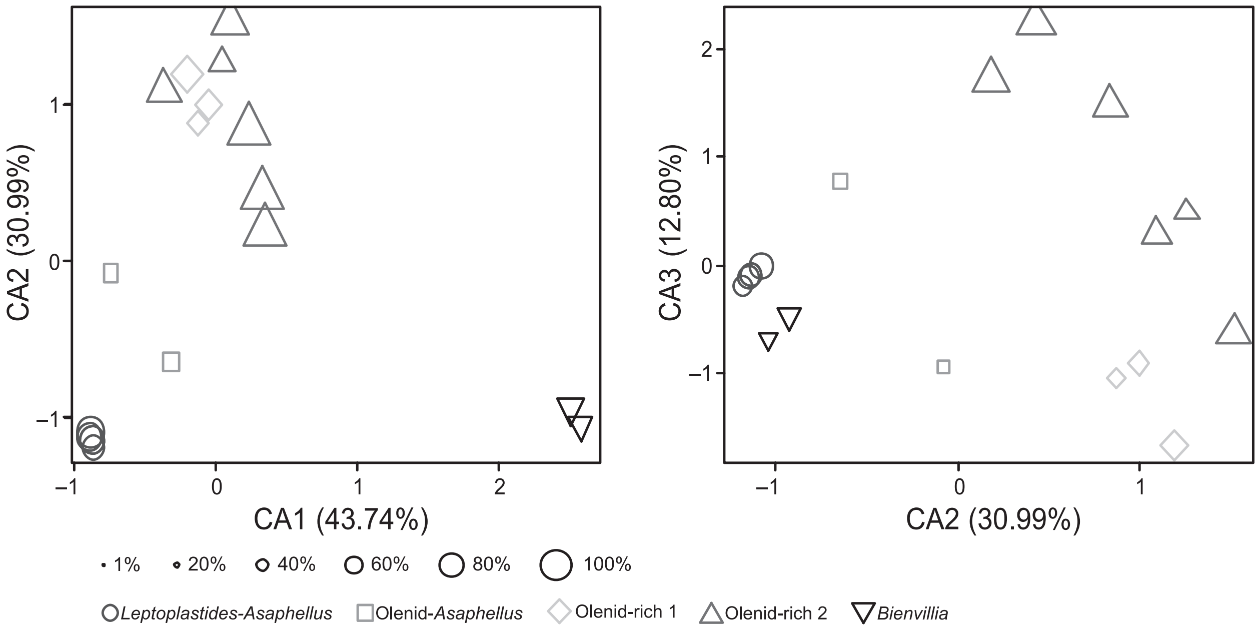

Fig. 7. Correspondence analysis performed with the abundance dataset. Symbol size represents the relative abundance of the family Olenidae in each sample. Each biofacies is depicted with a particular symbol. Numbers between brackets indicate percentage of total inertia associated with each axis.

Asaphellus are in the samples that lay in the middle of the bathymetrical gradient (Fig. 8).

Overall, both analyses, either based on the presence–absence or on the abundance datasets, show that a gradient is clearly present. This gradient is characterized in its shallower extreme by the *Leptoplastides-Asaphellus* biofacies, followed by the Olenid-*Asaphellus* biofacies. The interpretation of the position of the Olenid-rich 1 and Olenid-rich 2 biofacies is not straightforward. While the presence–absence analysis tends to place them along a bathymetrical gradient (Fig. 9), the abundance analysis reflects a broadly similar bathymetrical position, and a lateral variation that might reflect differences in oxygen content. As the oxygen content may covary with depth, neither the sedimentological analysis, nor this detailed palaeoecological study, provide enough support for differentiating which of these factors prevailed.

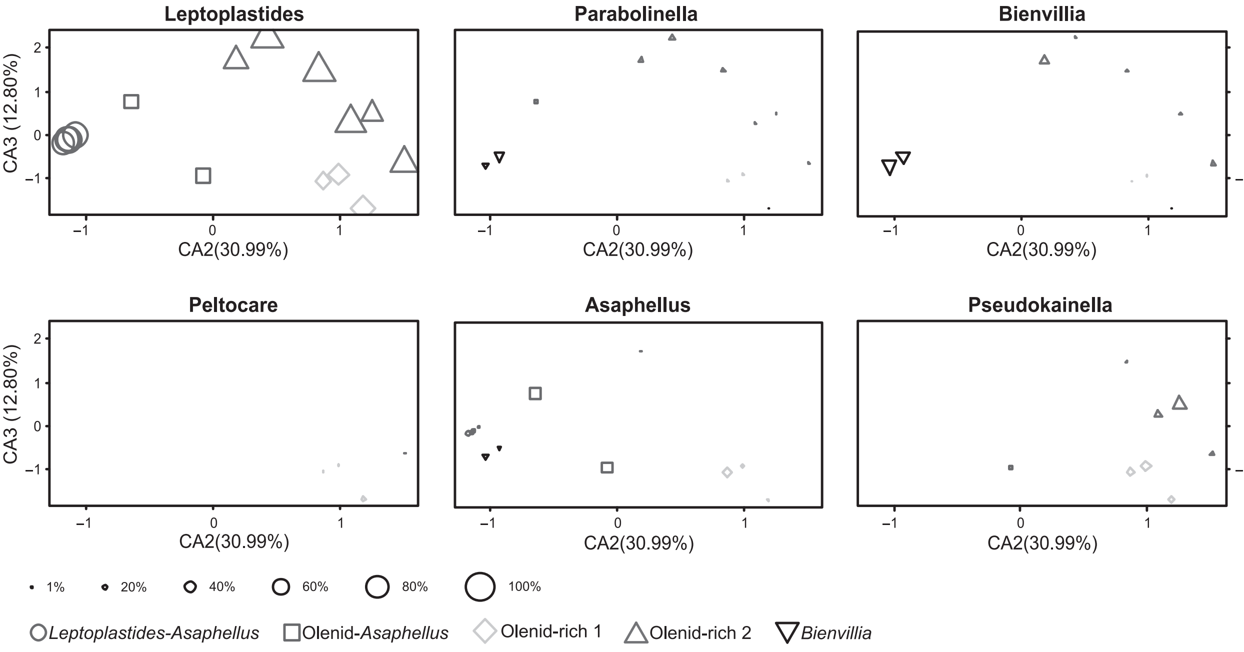

Fig. 8. Relative abundance of the main genera discussed in the text along the gradient in the abundance dataset. Symbol size represents relative abundance. Each biofacies is depicted with a particular symbol. Numbers between brackets indicate percentage of total inertia associated with each axis.

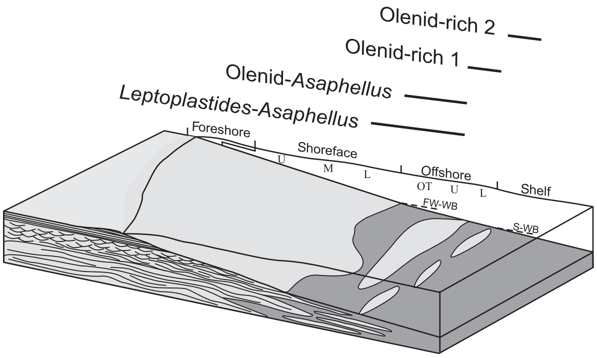

Fig. 9. Possible interpretations of the position of biofacies along the bathymetrical gradient. The gradient is depicted as shown by the presence–absence dataset, where the differences between Olenid–rich 1 and Olenid–rich 2 biofacies represent bathymetry.

Diversity

The diversity is lower in the shallow end of the gradient and rises towards the deep end, although the maximum is reached in the Olenid-rich 1 biofacies. This pattern is stable for both the alpha diversity of each rarefied sample and for the diversity of each biofacies (Fig. 10A).

For the rarefaction analysis, the shallowest (lower shoreface) samples have a diversity of two taxa, reaching almost six (average E[S] = 5.7) taxa in deep well-oxygenated settings (Fig. 10A). Other environments have rarefied diversities ranging between 4 and 5.5 taxa. The diversity of each biofacies follows the same pattern. The *Leptoplastides*-*Asaphellus* biofacies has the lowest richness with three genera, while the maximum richness is found in the Olenid-rich 1 biofacies with 5.93 genera. The Olenid-*Asaphellus* and Olenid-rich 2 biofacies have intermediate richness, being 4.89 and 5.23 genera respectively (Fig. 10A).

If the Olenidae is analysed as a whole, the pattern is surprising. They are present in every sample no matter what their position along the gradient. Indeed, at least half of the genera present in each sample belong to this family. When relative abundances are available, at least 50% of the individuals in every sample are olenids (Fig. 7). Interestingly, the highest relative abundances of olenids are found towards the extremes of the gradients: in the shallow samples it reaches 90% and in the deep less-oxygenated ones 100%. Nevertheless, the highest olenid richness (five genera) is found in the well-oxygenated deep samples (Fig. 7). Taking this into account, a clear dominance, both taxonomically and ecologically along the whole gradient, is evident.

Discussion

Development of an olenid-dominated gradient

As stated above, this is the first detailed account of an olenid-dominated bathymetrical gradient. Along this gradient, olenids dominated both oxygenated and

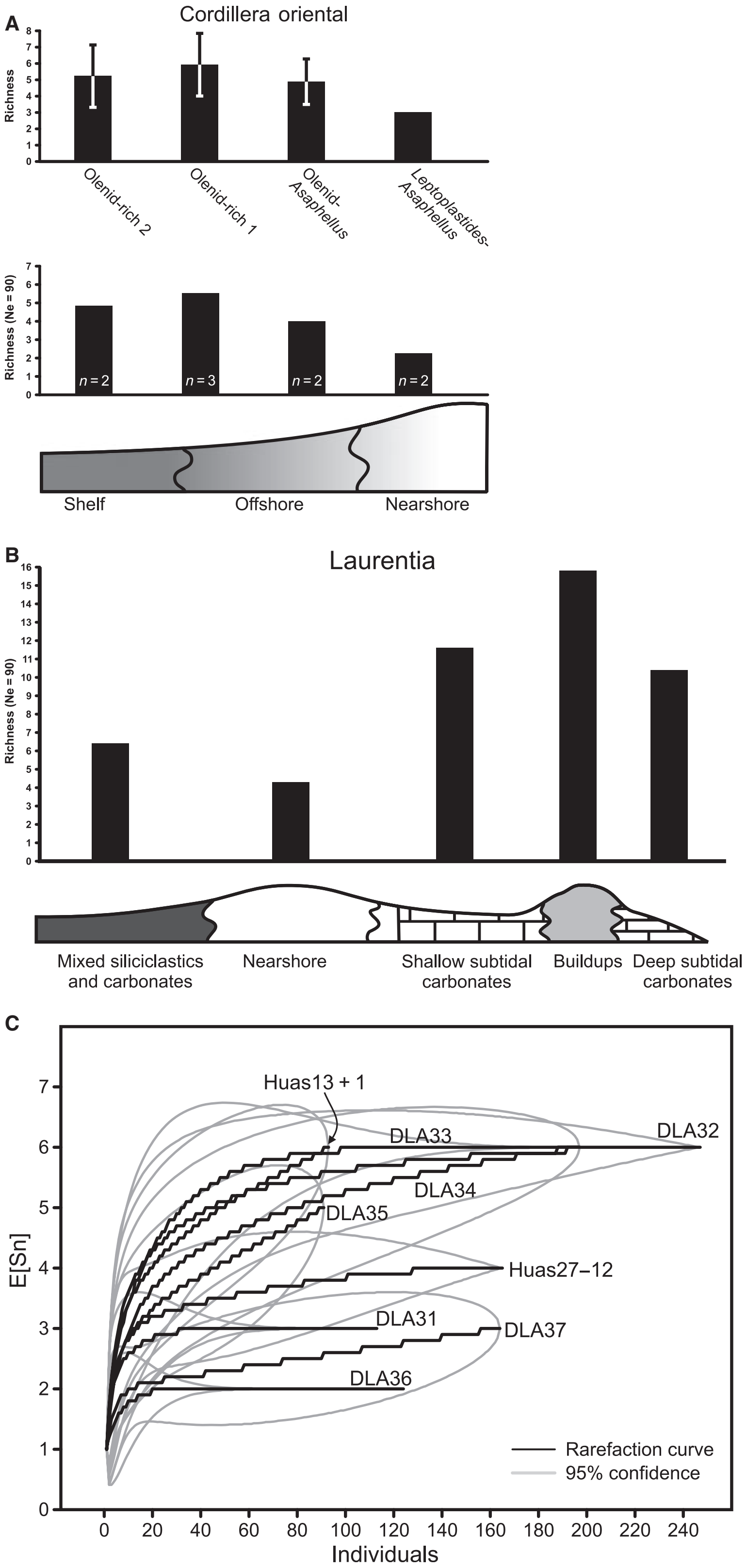

Fig. 10. Diversity gradients in Argentinian Cordillera Oriental and Laurentia. A, Diversity in Argentinean Cordillera Oriental. Diversity measured as richness for each biofacies (O2W, Alroy 2000a,b) and mean rarified richness for each biofacies (S[E = 90], Westrop & Adrain 2001). For O2W the error bars represent 95% confidence intervals. For the rarefaction *n* = number of samples. B, diversity gradient in Laurentia, for the carbonate platform and the mixed ramp. Diversity is measured as mean rarified richness (S[E = 90]). Modified from Westrop & Adrain (2001). C, Rarefaction Curves for the samples of Cordillera Oriental, note sedimentary environments of each sample in Table 1.

dysoxic environments, a remarkable pattern taking into account their broadly accepted palaeoecology (Fortey 1985, 2000; Clarkson & Taylor 1995). However, this seems not to be an isolated case. Although lacking a palaeoecological analysis as performed herein, the uppermost Cambrian–Tremadocian olenid dominated faunas from Poland, Finnmark (northern Norway), and Wales seem to share a similar pattern (Nikolaisen & Henningsmoen 1985; Fortey & Owens 1991, 1992; Żylińska 2002). The occurrence of similar olenid taxa also accounts for a similar biogeographical signature of these regions and the Cordillera Oriental (Nikolaisen & Henningsmoen 1985; Żylińska 2002). Interestingly, all these four regions have in common the thickness of their siliciclastic successions, which are composed of shale and interbedded sandstone beds, and absence of carbonates (Reading 1965; Bevins *et al.* 1992; Żylińska 2002; Astini 2003). In addition, successions from Finnmark and Cordillera Oriental developed in a broadly similar geodynamical/tectonical setting: a foreland basin (Astini 2003; A. Nielsen personal communication 2009).

Nikolaisen & Henningsmoen (1985) noted the similarities in composition of the faunas and, possibly, in sedimentation rates. They proposed that the olenids recorded in Finnmark were not adapted to the dysoxic environments usual of Alum Shale, but to an environment with much more input of siliciclastic material. Żylińska (2002) arrived at a similar conclusion in her study of the biogeography of the uppermost Cambrian from Poland. She proposed that these particular olenids flourished in the margin of Baltica, and migrated to Avalonia and South America.

The sedimentary history of these regions is completely different from those prevalent in other coeval epicontinental basins, such as Baltoscandia, Laurentia or Siberia. In the latter two areas, a carbonate platform with microbial reefs developed. Localized mixed carbonate-siliciclastic ramps are also recorded in the Upper Cambrian of Laurentia. Meanwhile, in Baltoscandia clastic sediment supply was extremely low, and carbonate production was restricted until the development of 'cool-water' carbonates during the Tremadocian (Jaanusson 1973; Nielsen 2004). In these cases, olenid-dominated faunas are known both for the Upper Cambrian and the Tremadocian (e.g. Henningsmoen 1957; Ludvigsen & Westrop 1983; Clarkson & Taylor 1995; Pegel 2000; Lauridsen & Nielsen 2005). These faunas are always restricted to black shale or dark limestone from outer-platform settings, in accordance to the 'usual' olenid biofacies defined by Fortey (1975). Recently, Karim (2008) described an olenid-dominated assemblage from a boulder in the Shallow Bay Formation (Newfoundland) interpreted as having been derived from a shelf-margin environment. Although an olenid-dominated assemblage was not previously reported from rather shallow carbonate environments, this record is difficult to interpret due to its restricted distribution and particular stratigraphical provenance.

These contrasting examples account for a distinct pattern. The 'usual' olenid-dominated biofacies occurs in outer-platform dysoxic settings, while a more 'unusual' olenid biofacies is present in environments with high sedimentation rates. The pattern implies that ecologically similar olenid faunas occur in basins with similar sedimentary regimes and geodynamical context, suggesting a common factor structuring these ecosystems.

The high input of siliciclastic material causes turbidity and soupy bottoms, apart from increasing nutrient supply (Pearson & Rosenberg 1987; Wignall 1993). The development of these environments, linked to high sediment input is interpreted to be a key factor, enabling olenids to inhabit shallower-water environments. Indeed, high sedimentation rates allow the development of deposit-feeder dominated communities (Pearson & Rosenberg 1987; Wignall 1993), as interpreted to be the case with the olenid biofacies (Fortey & Owens 1999). In contrast, environmentally different shallow-marine settings developed in epicontinental carbonate platforms, where bottoms are firmer and turbidity is almost absent (Shinn 1969; Tucker & Wright 1990).

Accordingly, oceanographical factors related to geodynamical context and sedimentation rates seem to control the structure of the biotic gradients. Olenids dominate all environments along the bathymetrical gradient where particularly high sedimentation rates are present, while they are almost restricted to deep-water dysoxic ones in environments involving carbonate accumulation and very low siliciclastic sedimentation.

Based on the palaeogeographical distribution of 'usual' and 'unusual' olenid biofacies, it could be argued that this pattern broadly mirrors a latitudinal gradient between equatorial/sub-equatorial settings and temperate to cold sites (e.g. Taylor 1977; Fortey & Owens 1978 among others). In fact, whether the pattern is climatically or sedimentologically driven is difficult to distinguish. Nevertheless, an independent line of evidence shows that clastic sedimentation rates may indeed be an important controlling factor. In Baltica, both 'unusual' and 'usual' olenid biofacies occur at broadly similar latitudes. While the usual one occurs in Baltoscandia (mainly Alum Shale Formation, Southern Sweden, Norway and Denmark), the unusual occurs in the other extreme of the palaeocontinent (Finnmark, northern Norway). Interestingly, this palaeocontinent rotated during the Cambrian and

Ordovician as much as 90° (Torsvik & Rehnström 2001 and references therein). Yet, this had little or no effect on its fauna, implying little climatic variation between its different regions (Fortey & Cocks 2003). Accordingly, different tectonosedimentary settings rather than climate between the Baltoscandian and Finnmarkian margins might have triggered the development of the usual and the unusual olenid biofacies, suggesting that sedimentation regime and geodynamic context are the major controlling factors of the biotic gradients.

Diversity patterns

Unfortunately, there are only very few studies describing detailed palaeosynecological patterns for the time interval analysed (latest Cambrian–Tremadocian). Most of these studies, if not all, come from Laurentia (e.g. Ludvigsen & Westrop 1983; Westrop 1996; Westrop & Adrain 1998, 2001; Westrop & Cuggy 1999). As mentioned above, in Laurentia both a carbonate platform and a mixed carbonate-siliciclastic ramp developed. This mixed ramp differs from the backarc-foreland system studied here, mainly because environments and oceanographical conditions prevailing in Palaeozoic epeiric seas were possibly very different from those in ocean-facing basin (Peters 2007; Miller 2008). Hence, comparisons have to be done carefully, as macroecological and macroevolutionary patterns might also have been different in these two settings (Peters 2007; Miller 2008). Nevertheless, when comparing synecological aspects of these two low-latitude Laurentian environments with the Cordillera Oriental, an interesting pattern arises. The biofacies differentiation in the carbonate platforms is surprisingly high, having at least five clearly defined biofacies (Ludvigsen & Westrop 1983; Westrop & Cuggy 1999). However, for the mixed carbonate-siliciclastic ramps, there are never more than three biofacies with low differentiation (Westrop 1986; Westrop & Cuggy 1999). The latter pattern is similar to the one described and discussed above (see Results). Indeed, almost the whole gradient along the mixed ramp is usually dominated by a unique family, as is the case in the Cordillera Oriental.

A similar case is present when comparing the diversity gradients in these environments. The carbonate platform has a mean rarified richness of more than ten species in almost all environments (Westrop & Adrain 2001; Fig. 10B), with the maximum reaching over 15 species in the reefs. The mixed ramp has a much simpler pattern with a gentle rise in richness towards the deepest-water settings, having just over six species in the richest environments (Westrop & Adrain 2001; Fig. 10B). This is particularly similar to the diversity gradient found herein for the Tr2 of the Cordillera Oriental. Here, the data confirm a gentle rise of diversity towards the offshore where the richest settings have almost six taxa (Fig. 10A).

Again the influence of sedimentary regime and climate is not easy to discriminate. However, these comparisons show that high biofacies differentiation occurs together with high alpha diversity in carbonate platforms, contrasting with siliciclastic shelves and mixed carbonate-clastic ramps. This difference accounts for the style of sedimentation as a major control on macroecological patterns, being even more important than latitude at least in trilobite-dominated assemblages. The style of sedimentation is a proxy for underlying environmental factors, in turn, highly influential on habitat complexity. In this scenario, independent evidence (e.g. sedimentological, microstratigraphical, geochemical) would be required to understand ecologically significant factors at different spatial scales for contrasting sedimentary regimes.

Implications for olenid palaeoecology

The development of a bathymetrical gradient dominated by olenids has important implication for understanding the ecology of these particular trilobites. Based on our findings, the olenids seem to have had the capability of coping with low-oxygen content if necessary, rather than being restricted to dysoxic environments.

The distribution of taxa throughout the gradient represents a broadly nested pattern (Boyer & Droser 2009). This pattern is more evident when comparing samples along the deepest settings (i.e. offshore through shelf). Particularly, *Leptoplastides* is the dominant taxon in every sample. This implies that it was not an opportunistic species (Dodd & Stanton 1981), but fully adapted to cope with dysoxic and normal conditions. The presence of taxa capable of being successful in this broad range of environments is not common in recent environments. This particular ecology has been recently described for the Middle Devonian brachiopod *Eumetabolotoechia multicostata* (Boyer & Droser 2007, 2009). The authors proposed that such distribution might be related to the more frequent dysoxic conditions in the Early Palaeozoic than in post-Palaeozoic times (Boyer & Droser 2007; Peters 2007). Our findings suggest that this capability might have been already present in the Early Ordovician in a completely unrelated taxon. More research is needed to see whether this pattern stands as a pervasive and unique characteristic of early Palaeozoic ecosystems.

Usually, the olenids have been divided in different morphotypes (Henningsmoen 1957). The *Peltura* type is interpreted as being more active, while the *Olenus* type as having a rather sluggish mode of life (Henningsmoen 1957; Fortey 1975, 1985). Representatives of the *Peltura* type are known to be present in oxygenated environments, though in low abundances (Fortey 1985). The olenids from the Rupasca Member belong to the *Peltura* type (*Leptoplastides*, *Bienvillia* and *Peltocare*) and to the *Olenus* type (*Parabolinella* and *Plicatolina*). As described above, members of both types occur in oxygenated environments and in dysoxic ones, achieving significant abundances and being the dominant elements of the assemblages. The distribution of these morphotypes is not related to bathymetry as both occur either in rather shallow or in deep environments, nor to oxygen content.

A similar pattern of distribution is recorded for the widespread *Hypermecaspis*, which is a classical *Olenus* type olenid, occurs in a wide range of environments in the Upper Tremadocian–Floian successions of the Cordillera Oriental. It is a common element in low-diversity dysoxic biofacies up to diverse well-oxygenated biofacies (Waisfeld 2001; Waisfeld & Vaccari 2008a). Some olenids may have had chemosymbionts (Fortey 1999, 2000), although our findings suggest that this might not have been the case for all of them, or for every morphotype. The interpretation of this life habit should be evaluated on a case-by-case basis taking into account independent evidence (e.g. Gaines & Droser 2003; Farrel & Briggs 2008).

Recently, Lee & Chatterton (2007) proposed that the environmental distribution of olenids might be related to adaptations in early ontogenetic stages, rather than to the adult morphology. These findings, along with the detailed analysis presented herein, suggest that the ecological factors controlling olenid distribution were much more complex than previously thought.

Acknowledgements. – This contribution benefited from discussion with the members of the Centro de Investigaciones Paleobiológicas (CIPAL). We are grateful to Arne Nielsen for his comments on the geology of Finnmark. Emilio Vaccari and Juan J. Rustán provided invaluable assistance in the field. Patricio Desjardins prepared figures 2 and 9. Associate Editor Alan Owen and two anonymous reviewers provided useful comments. Financial support was provided by CONICET (PIP 5599), ANPCyT-FONCyT (PICT 2004, Nº21857, PICT 2006, Nº1272), and Natural Sciences and Engineering Research Council (NSERC) Discovery Grant 311726-05/08.

References

Adrain, J.M., Edgecombe, G.D., Fortey, R.A., Hammer, Ø., Laurie, J.R., McCormick, T., Owen, A.W., Waisfeld, B.G., Webby, B.D., Westrop, S.R. & Zou, Z.-Y. 2004: Trilobites. *In* Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (eds): *The Great Ordovician Biodiversification Event*, 231–254. Columbia University Press, New York.

Albanesi, G.L. & Aceñolaza, G.F. 2005: Conodontes de la Formación Rupasca (Ordovícico Inferior) en el Angosto de Chucalezna, Cordillera Oriental de Jujuy: Nuevos elementos bioestratigráficos para una localidad clásica del noroeste argentino. *Ameghiniana 42*, 295–310.

Alroy, J. 2000a: New methods for quantifying macroevolutionary patterns and processes. *Paleobiology 26*, 707–733.

Alroy, J. 2000b: Successive approximations of diversity curves: ten more years in the library. *Geology 28*, 1023–1026.

Amati, L. & Westrop, S.R. 2006: Sedimentary facies and trilobite biofacies along an Ordovician shelf to basin gradient, Viola Group, South–Central Oklahoma. *Palaios 21*, 516–529.

Astini, R.A. 2003: The ordovician Proto–Andean basins. *In* Benedetto, J.L. (ed.): *Ordovician Fossils of Argentina*, 1–74. Secretaria de Ciencia y Tecnología Universidad Nacional de Córdoba, Córdoba, Argentina.

Astini, R.A. 2005: Las sedimentitas que apoyan en no concordancia sobre el 'granito rojo' en el angosto de la Quesera (Cordillera Oriental, Salta): una revisión crítica a más de 60 años de los trabajos pioneros de J. Keidel. *Revista de la Asociación Geológica Argentina 60*, 513–523.

Astini, R.A. 2008: Sedimentación, facies, discordancias y evolución paleoambiental durante el Cámbrico–Ordovícico. *In* Coira, B. & Zappettini, E.O. (eds): *Geología y Recursos Naturales de Jujuy Relatorio del XVII Congreso Geológico Argentino*, 50–73. Asociación Geológica Argentina, Buenos Aires, Argentina.

Astini, R.A. & Marengo, L.F. 2006: Paleoambientes y estratigrafía secuencial de depósitos marinos marginales del Ordovícico de la sierra de Zapla (sierras Subandinas, noroeste Argentino) y su relación con la Cuenca Andina Central. *Revista Geológica de Chile 33*, 247–276.

Astini, R.A., Marengo, L. & Rubinstein, C.V. 2003: The Ordovician stratigraphy of Sierras Subandinas (Subandean Ranges) in Northwestern Argentina and its bearing on an integrated foreland basin model for the Ordovician of Central Andean Region. *In* Albanesi, G.L., Beresi, M.S. & Peralta, S.H. (eds), *Ordovician From the Andes, Serie Correlación Geológica 17*, 381–386.

Bahlburg, H. 1991: The Ordovician back–arc to foreland successor basin in the Argentinian–Chilean Puna: tectono–sedimentary trends and sea–level changes. *In* Macdonald, D.I.M. (ed.), *Sedimentation, Tectonics and Eustasy. Sea–Level Changes at Active Margins, Special Publication of the International Association of Sedimentologists 12*, 465–484.

Balseiro, D. & Marengo, L. 2008: Tremadocian trilobite assemblages from the Argentine Cordillera Oriental. A preliminary analysis. In Rabano, I., Gozalo, R. & García–Bellido, D. (eds), *Advances in Trilobite Research, Cuadernos del Museo Geominero 9*, 33–40.

Benedetto, J.L. (ed.) 2003: *Ordovician Fossils of Argentina*, 561 pp. Secretaria de Ciencia y Tecnología Universidad Nacional de Córdoba, Córdoba, Argentina.

Bennington, J.B. & Bambach, R.K. 1996: Statistical testing for paleocommunity recurrence: are similar fossil assemblages ever the same? *Palaeogeography, Palaeoclimatology, Palaeoecology 127*, 107–133.

Bergström, S.M., Chen, X., Gutiérrez–Marco, J.C. & Dronov, A. 2009: The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ3C chemostratigraphy. *Lethaia 42*, 97–107.

Bevins, R.E., Bluck, B.J., Brenchley, P.J., Fortey, R.A., Hughes, C.P., Ingham, J.K. & Rushton, A.W.A. 1992: Ordovician. *In* Cope J.C.W., Ingham J.K. & Rawson P.F. (eds), *Atlas of Palaeogeography and Lithofacies, Geological Society (London) Memoir 13*, 19–36.

Boyer, D.L. & Droser, M.L. 2007: Devonian monospecific assemblages: new insights into the ecology of reduced-oxygen depositional settings. *Lethaia 40*, 321–333.

Boyer, D.L. & Droser, M.L. 2009: Palaeoecological patterns within the dysaerobic biofacies: examples from Devonian black shales of New York State. *Palaeogeography, Palaeoclimatology, Palaeoecology 276*, 206–216.

Buatois, L.A. & Mángano, M.G. 2003: Sedimentary facies, depositional evolution of the Upper Cambrian–Lower Ordovician Santa Rosita formation in northwest Argentina. *Journal of South American Earth Sciences 16*, 343–363.

Buatois, L.A., Zeballo, F.J., Albanesi, G.L., Ortega, G., Vaccari, N.E. & Mángano, M.G. 2006: Depositional environmets and stratigraphy of the Upper Cambrian–Lower Ordovician Santa Rosita Formation at the Alfarcito area, Cordillera Oriental, Argentina: integration of Biostratigraphic data within a Sequence Stratigrafic framework. *Latin American Journal of Sedimentology and Basin Analysis 13*, 1–29.

Bulinski, K.V. 2007: Analysis of sample–level properties along a paleoenvironmental gradient: the behavior of evenness as a function of sample size. *Palaeogeography, Palaeoclimatology, Palaeoecology 253*, 490–508.

Bush, A.M., Markey, M.J. & Marshall, C.R. 2004: Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling–standardization. *Paleobiology 30*, 666–686.

Clarkson, E.N.K. & Taylor, C.M. 1995: The lost world of the olenid trilobites. *Geology Today 11*, 147–154.

Dodd, J.R. & Stanton, R.J. Jr 1981: *Paleoecology, Concepts and Applications*, 559 pp. John Wiley & Sons, New York.

Esteban, S.B. & Tortello, M.F. 2007: Latest Cambrian sedimentary settings and trilobite faunas from the western Cordillera Oriental, Argentina. *Memoires of the Association of Australasian Palaeontologists 34*, 431–460.

Farrel, Ú.C. & Briggs, D.E.G. 2008: Pyritized Trilobites faunas from the Ordovician of New York State: Beecher's Trilobite Bed and the Whetstone Gluf Formation near Lowville. *In* Rabano, I., Gozalo, R. & García–Bellido, D. (eds), *Advances in Trilobite Research*, *Cuadernos del Museo Geominero 9*, 109–112.

Fortey, R.A. 1975: Early Ordovician trilobites communities. *Fossil and Strata 4*, 339–360.

Fortey, R.A. 1985: Pelagic trilobites as an example of deducting the life habits of extinct arthropods. *Transactions of the Royal Society of Edinburgh: Earth Sciences 76*, 219–230.

Fortey, R.A. 1989: There are extinctions and extinctions: examples from the Lower Palaeozoic. *Philosophical Transactions of the Royal Society of London B 325*, 327–355.

Fortey, R.A. 1999: Olenid trilobites as chemoautotrophic symbionts. *Acta Universitatis Carolinae, Geologica 43*, 355–356.

Fortey, R.A. 2000: Olenid Trilobites: the oldest known chemoautotrophic symbionts? *Proceedings of the National Academy of Science 97*, 6574–6578.

Fortey, R.A. & Cocks, L.R.M. 2003: Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. *Earth Science Reviews 61*, 245–307.

Fortey, R.A. & Owens, R.M. 1978: Early Ordovician (Arenig) stratigraphy an faunas of the Carmarthen district, south–west Wales. Bulletin of the British Museum (Natural History). *Geology 30*, 225–294.

Fortey, R.A. & Owens, R.M. 1991: A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine 128*, 437–464.

Fortey, R.A. & Owens, R.M. 1992: The Habberley formation: youngest Tremadoc in the Welsh borderlands. *Geological Magazine 129*, 553–566.

Fortey, R.A. & Owens, R.M. 1999: Feeding habits in trilobites. *Palaeontology 42*, 429–465.

Gaines, R.R. & Droser, M.L. 2003: Paleoecology of the familiar trilobite *Elrathia kingii*: an early exaerobic zone inhabitant. *Geology 31*, 941–944.

Gilinsky, N.L. & Bennington, J.B. 1994: Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. *Paleobiology 20*, 245–258.

Harrington, H.J. & Leanza, A.F. 1957: *Ordovician Trilobites of Argentina*, 276 pp. University of Kansas Press, Lawrence, USA.

Henningsmoen, G. 1957: The trilobite family Olenidae. *Skrifter Utgitt Av Det Norske Videnskaps–Akademi I Oslo, I. Matematisk–Naturvidenskapelig Klasse 1*, 1–303.

Holland, S.M. 2003: *Analytic Rarefaction 1.3*. http://www.uga.edu/~strata/software/index.html. Accessed 22 September 2008.

Holland, S.M. & Patzkowsky, M.E. 2007: Gradient ecology of a biotic invasion: Biofacies of the type Cincinnatian Series (Upper Ordovician), Cincinnati, Ohio Region, USA. *Palaios 22*, 392–407.

Hurlbert, S.H. 1971: The nonconcept of species diversity: a critique and alternative parameters. *Ecology 52*, 577–586.

Jaanusson, V. 1973: Aspects of carbonate sedimentation in the Ordovician of Baltoscandia. *Lethaia 6*, 11–34.

Karim, T.S. 2008: Olenid–dominated trilobite fauna from the Shallow Bay Formation (Cow Head Group), Cambrian–Ordovician boundary interval, western Newfoundland. *Canadian Journal of Earth Sciences 45*, 407–425.

Landing, E., Westrop, S.R. & Keppie, J.D. 2007: Terminal Cambrian and lowest Ordovician succession of Mexican West Gondwana: Biotas and sequence stratigraphy of the Tiñu Formation. *Geological Magazine 144*, 909–936.

Lauridsen, B.W. & Nielsen, A.T. 2005: The Upper Cambrian trilobite *Olenus* at Andrarum, Sweden: a case of iterative evolution? *Palaeontology 48*, 1041–1056.

Layou, K.M. 2009: Ecological restructuring after extinction: The Late Ordovician (Mohawkian) of the eastern United States. *Palaios 24*, 118–130.

Lee, D.-C. & Chatterton, B.D.E. 2007: Ontogeny of *Parabolinella panosa* (Olenidae, Trilobita) from the uppermost Furongian (Upper Cambrian) of northwestern Canada, with discussion of olenid protaspides. *Canadian Journal of Earth Sciences 44*, 1695–1711.

Legendre, P. & Legendre, M. 1998: *Numerical Ecology, Second English Edition*, 855 pp. Elsevier Science B.V., Amsterdam, The Netherlands.

Ludvigsen, R. & Westrop, S.R. 1983: Trilobite biofacies of the Cambrian–Ordovician boundary interval in North America. *Alcheringa 7*, 301–319.

Ludvigsen, R., Westrop, S.R., Pratt, B.R., Tuffnell, P.A. & Young, G.A. 1986: Dual biostratigraphy: zones and biofacies. *Geoscience Canada 13*, 139–154.

MacEachern, J.A. & Pemberton, S.G. 1992: Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America. *In* Pemberton, S.G. (ed.), *Applications of Ichnology to Petroleum Exploration*, *SEPM Core Workshop 17*, 57–84.

MacEachern, J.A., Zaitlin, B.A. & Pemberton, S.G. 1999: A sharp-based sandstone of the Viking Formation, Joffre Field, Alberta, Canada: criteria for recognition of transgressively incised shoreface complexes. *Journal of Sedimentary Research 69*, 876–892.

Miller, A.I. 2008: The secular decline of epicontinental seas through the Phanerozoic: Implications for marine diversification and extinction. *Abstracts, Palaeozoic Climates – International Congress, Lille*, 68.

Minchin, P.R. 1987: An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio 69*, 89–107.

Moya, M.C. 1988: Lower Ordovician in the southern part of the Argentine Eastern Cordillera. *In* Bahlburg, H., Breitkreuz, C. & Giese, P. (eds): *The Southern Central Andes, Lecture Notes in Earth Sciences*, 55–69. Springer Verlag, Berlin.

Moya, M.C. 1998: El Paleozoico inferior en la sierra de Mojotoro, Salta – Jujuy. *Revista de la Asociación Geológica Argentina 53*, 219–238.

Nielsen, A.T. 2004: Ordovician sea level changes: a Baltoscandian perspective. *In* Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (eds): *The Great Ordovician Biodiversification Event*, 84–93. Columbia University Press, New York, USA.

Nikolaisen, F. & Henningsmoen, G. 1985: Upper Cambrian and lower Tremadoc olenid trilobites from the Digermul peninsula, Finnmark, northern Norway. *Norges Geologiske Undersøkelse Bulletin 400*, 1–49.

Olszewski, T.D. & Erwin, D.H. 2009: Change and stability in Permian brachiopod communities from western Texas. *Palaios 24*, 27–40.

Ortega, G. & Albanesi, G.L. 2005: Tremadocian Graptolite–Conodont biostratigraphy of the South American Gondwana margin (Eastern Cordillera, NW Argentina). *Geologica Acta 3*, 355–371.

Patzkowsky, M.E. & Holland, S.M. 1999: Biofacies replacement in a sequence stratigraphic framework: Middle and Upper Ordovician of the Nashville Dome, Tennessee, USA. *Palaios 14*, 301–323.

Pearson, T.H. & Rosenberg, R. 1987: Feast and famine: structuring factors in marine benthic communities. *In* Gee, J.H.R. & Giller, P.S. (eds): *Organisation of Communities Past and Present. 27th Symposium of the British Ecological Society*, 373–395. Blackwell Scientific Publications, Oxford, UK.

Pegel, T.V. 2000: Evolution of trilobite biofacies in Cambrian basins of the Siberian platform. *Journal of Paleontology 74*, 1000–1019.

Peters, S.E. 2007: The problem with the Paleozoic. *Paleobiology 33*, 165–181.

R Project 2008: *R Version 2.8.1*, <http://www.r–project.org/>.

Reading, H.G. 1965: Eocambrian and lower Palaeozoic geology of the Digermul Peninsula, Tanafjord, Finnmark. *Norges Geologiske Undersøkelse Bulletin 234*, 167–191.

Robison, R.A. 1972: Mode of life of agnostid trilobites. *24th International Geological Congress 7*, 33–40.

Schovsbo, N.H. 2001: Why barren intervals? A taphonomic case study of the Scandinavian Alum Shale and its faunas. *Lethaia 34*, 271–285.

Shinn, E.A. 1969: Submarine lithification of Holocene carbonate sediments in the Persian Gulf. *Sedimentology 12*, 109–144.

Taylor, M.E. 1977: Late Cambrian of western North America: Trilobite biofacies, environmental significance, and biostratigraphic implications. *In* Kauffman, E.G. & Hazel, J.E. (eds): *Concepts and Methods of Biostratigraphy*, 397–425. Dowden, Hutchinson & Ross, Stroudsburg, USA.

Torsvik, T.H. & Rehnström, E.F. 2001: Cambrian palaeomagnetic data from Baltica: implications for true polar wander and Cambrian palaeogeography. *Journal of the Geological Society of London 158*, 321–330.

Tortello, M.F. & Clarkson, E.N.K. 2003: Ontogenia del trilobite olénido *Jujuyaspis keideli* Kobayashi (Ordovícico Temprano) del noroeste Argentino. *Ameghiniana 40*, 257–275.

Tortello, M.F. & Clarkson, E.N.K. 2008: Ontogeny, structure and moulting of *Parabolina frequens argentina* (Kayser) (Trilobita, Olenidae) from the Furongian of northwestern Argentina. *Ameghiniana 45*, 13–31.

Tortello, M.F. & Esteban, S.B. 2003: Trilobites del Cámbrico Tardío de la Formación Lampazar (sierra de Cajas, Jujuy, Argentina). Implicancias bioestratigráficas y paleoambientales. *Ameghiniana 40*, 323–344.

Tucker, M.E. & Wright, V.P. 1990: *Carbonate Sedimentology*, 483 pp. Blackwell Scientific Publications, Oxford, UK.

Waisfeld, B.G. 2001: Trilobites de la familia Olenidae en el Ordovícico Inferior (Arenigiano) de la Cordillera Oriental argentina. *Ameghiniana 38*, 195–211.

Waisfeld, B.G. & Vaccari, N.E. 2003: Trilobites. *In* Benedetto, J.L. (ed.): *Ordovician Fossils of Argentina*, 295–409. Secretaria de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba, Argentina.

Waisfeld, B.G. & Vaccari, N.E. 2006: Revisión de la Biozona de *Ogygiocaris araiorhachis* (Trilobita, Tremadociano tardío) en la región de Pascha–Incamayo, Cordillera Oriental, Argentina. Parte 2: Sistemática. *Ameghiniana 43*, 729–744.

Waisfeld, B.G. & Vaccari, N.E. 2008a: Oxygen-controlled Early Ordovician trilobite assemblages: The *Thysanopyge* fauna from Northwestern Argentina. *In* Rabano, I., Gozalo, R. & García–Bellido, D. (eds), *Advances in Trilobite Research*, *Cuadernos del Museo Geominero 9*, 421–425.

Waisfeld, B.G. & Vaccari, N.E. 2008b: Bioestratigrafía de trilobites del Paleozoico inferior de la Cordillera Oriental. In Coira, B. & Zappettini, E.O. (eds): *Geología y Recursos Naturales de Jujuy Relatorio del XVII Congreso Geológico Argentino*. 119–127. Asociación Geológica Argentina, Buenos Aires, Argentina.

Waisfeld, B.G., Vaccari, N.E., Toro, B.A., Rubinstein, C.V. & Astini, R.A. 2006: Revisión de la biozona de *Ogygiocaris araiorhachis* (Trilobita, Tremadociano tardio) en la región de Pascha–Incamayo, Cordillera Oriental, Argentina. Parte 1: Bioestratigrafía. *Ameghiniana 43*, 717–728.

Walossek, D. & Müller, K.J. 1990: Upper Cambrian stem–lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia 23*, 409–427.

Webber, A.J. 2004: Methodological advances in the use of faunal gradient analysis for regional high–resolution correlation in the type Cincinnatian Series (Upper Ordovician). *Palaeogeography, Palaeoclimatology, Palaeoecology 210*, 235–248.

Westrop, S.R. 1986: Trilobites of the upper Cambrian Sunwaptan stage, southern Canadian rocky mountains, Alberta. *Palaeontographica Canadiana 3*, 1–179.

Westrop, S.R. 1996: Temporal persistence and stability of Cambrian biofacies: Sunwaptan (Upper Cambrian) trilobite faunas of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology 127*, 33–46.

Westrop, S.R. & Adrain, J.M. 1998: Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. *Paleobiology 24*, 1–14.

Westrop, S.T. & Adrain, J.M. 2001: Sampling at the species level: impact of spatial biases on diversity gradients. *Geology 29*, 903–906.

Westrop, S.R. & Cuggy, M.B. 1999: Comparative paleoecology of Cambrian trilobite extinctions. *Journal of Paleontology 73*, 337–354.

Westrop, S.R. & Ludvigsen, R. 1987: Biogeographic control of trilobite mass extinction at an Upper Cambrian 'biomere' boundary. *Paleobiology 13*, 84–99.

Wignall, P.B. 1993: Distinguishing between oxygen and substrate control in fossil benthic assemblages. *Journal of the Geological Society of London 150*, 193–196.

Zeballo, F.J. & Tortello, M.F. 2005: Trilobites del Cámbrico Tardío–Ordovícico Temprano del área de Alfarcito, Tilcara, Cordillera Oriental de Jujuy, Argentina. *Ameghiniana 42*, 127–142.

Zeballo, F.J., Albanesi, G.L. & Ortega, G. 2005: Conodontes y graptolitos de las Formaciones Alfarcito y Rupasca (Tremadociano) en el área de Alfarcito, Tilcara, Cordillera Oriental de Jujuy, Argentina. Parte 1: Bioestratigrafía. *Ameghiniana 42*, 39–46.

Zhou, Z.-Y., Zhou, Z., Siveter, D.J. & Wenwei, Y. 2003: Latest Llanvirn to early Caradoc trilobite biofacies of the North–Western Marginal area of the Yangtze Block, China. *Special Papers in Palaeontology 70*, 281–291.

Żylińska, A. 2002: Stratigraphic and biogeographic significance of Late Cambrian trilobites from Lysogory (Holy Cross Mountains, central Poland). *Acta Geologica Polonica 52*, 217–238.