

PALEOECOLOGICAL DYNAMICS OF FURONGIAN (LATE CAMBRIAN) TRILOBITE-DOMINATED COMMUNITIES FROM NORTHWESTERN ARGENTINA

DIEGO BALSEIRO,* BEATRIZ G. WAISFELD, and N. EMILIO VACCARI

Consejo Nacional de Investigaciones Científicas y Técnicas, Centro de Investigaciones en Ciencias de la Tierra (CONICET CICTERRA), Centro de Investigaciones Paleobiológicas (CIPAL), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sársfield 299, X5000JJC Córdoba, Argentina

e-mail: balsedie@gmail.com

ABSTRACT

The Cambrian–Ordovician boundary interval is a critical moment in the ecology of trilobite communities. To understand this transition, we studied—at three different spatial scales—changes in the structure of olenid-dominated communities included in the *Parabolina* fauna, which flourished in the latest Cambrian, largely storm-dominated, successions of northwestern Argentina. At the local (~meter) scale, species-poor communities occur in shoreface deposits. Relatively flat species-abundance distributions (SADs) and high evenness characterize upper offshore to offshore transition settings of the early highstand systems tract (HST), whereas uneven SADs in species-poor communities are typical of the lower offshore and shelf environments of the transgressive systems tract (TST). This pattern is unlikely to be caused by a change in time averaging and is consistent with the intermediate disturbance hypothesis predicting unimodal diversity gradients. The pattern is thus interpreted to be related to a trend in intensity and frequency of storm disturbance along local shallowing-upward gradients. At the regional scale (~100 km), the diversity trend across the sampled west-east transect is rather variable and does not match the depth or oxygen-related gradients. At the biogeographic scale, the patterns of abundance of two key taxa (*Parabolina* and *Asaphellus*) show contrasting abundance and occupancy patterns between the Cordillera Oriental siliciclastic settings and the more carbonate-rich settings of Famatina (Argentina) and Oaxaca (Mexico). The presence of these genera in settings spatially adjacent, but environmentally different from their preferred habitats can represent a signature of source-sink dynamics. Low sample evenness values for the Cordillera Oriental contrast with those of coeval Laurentian communities, implying that a secular increase in evenness took place earlier in Laurentia than in Gondwana.

INTRODUCTION

The Cambrian–Ordovician (C–O) boundary interval is a pivotal moment in the ecology of marine benthic communities, particularly those dominated by trilobites (e.g., Ludvigsen and Westrop, 1983; Westrop and Cuggy, 1999; Peters, 2004a, 2004b). Cambrian communities had low alpha diversity (Sepkoski, 1981b), low evenness (Peters, 2004a), simple species-abundance distribution (Wagner et al., 2006), and low beta diversity between communities (Sepkoski, 1988). During the Cambrian–Ordovician boundary interval, however, trilobite-dominated communities achieved high evenness (Peters, 2004a) and biofacies differentiation (Ludvigsen and Westrop, 1983), changing the typical ecological signature of Cambrian communities (Sepkoski, 1981b; Wagner et al., 2006). Most of the available detailed ecological information comes from Laurentia, while little is known from other paleocontinents (Adrain et al., 2000). Although previous studies dealing with C–O faunas have accounted for contrasting regional paleoecolog-

ical dynamics and diversification patterns among settings at different latitudes (e.g., Westrop, 1991; Waisfeld and Sánchez, 1996; Miller, 1997; Waisfeld et al., 2003), quantitative paleoecological data capturing a wider biogeographic view are needed in order to understand regional to global biotic dynamics during critical intervals.

The study of species-abundance distributions (SADs) has allowed increasing levels of comprehension of processes controlling species diversity, although it is clear that different processes can generate similar shapes of SADs (Magurran, 2004; McGill et al., 2007). The long-term debate concerning the ecological interpretation of SADs, evenness, and richness (e.g., Whittaker, 1972; Huston, 1979; Frontier, 1985; Gray, 1987; Rosenzweig, 1995; Hubbell, 2001; Magurran, 2004; McGill et al., 2007) resulted in several models explaining multiple ecological patterns (McGill et al., 2007). Therefore the study of temporal and spatial changes in SADs along with other ecological indices such as beta diversity provides a useful approach to explore processes leading to community assembly during critical transitions in the evolution of benthic fauna. Only recently, fidelity of community-level relative abundances and diversity in the subfossil record have been addressed quantitatively (Kidwell, 2001; Tomašových and Kidwell, 2009a), and the analysis of SADs has become a valuable tool for paleoecology (e.g., Olszewski and Erwin, 2004; Wagner et al., 2006; McElwain et al., 2009; Tomašových and Kidwell, 2009b, 2010a; Fall and Olszewski, 2010).

In this contribution we study the ecological patterns of a typical trilobite-dominated assemblage known as the *Parabolina* (*Neoparabolina*) *frequens* fauna (Harrington and Leanza, 1957). This widespread fauna developed in the Central Andean Basin, Famatina, Oaxaquia, Avalonia, Baltica, and Łysogóry during the latest Cambrian (Shergold, 1988). It is dominated by olenid trilobites, and its main characteristic is the presence of the olenid *Parabolina* (*N.*) *frequens* (Barrande), which is an intercontinental biostratigraphic marker for the latest Cambrian (Shergold, 1988; Zylinska, 2002; Esteban and Tortello, 2007). Distribution, stratigraphic range, and different fossil groups associated with this taxon have been extensively investigated from a biostratigraphic perspective, whereas few quantitative ecological studies have been conducted. Our analysis is constrained to the Central Andean Basin (Argentine Cordillera Oriental, southwestern Gondwana), a reference site for the study of the *Parabolina* fauna (Fig. 1). We analyze changes in species-abundance distributions, alpha and beta diversity, and evenness related to environmental gradients at three spatial scales. First, at the local (~meter) scale we study these attributes in three sections exposing shallowing-upward successions. Second, we analyzed diversity patterns at a regional scale, across a fairly well-sampled, west-east transect (of ~80 present-day km) within one basin. This analysis is further complemented with literature data from every site where the *Parabolina* fauna is recorded encompassing about ~3500 km² throughout northwestern Argentina. Third, we analyze abundance and occupancy of two taxa at a biogeographic (~1000 km) scale, including the Cordillera Oriental, and two close peri-Gondwanic shelves, namely Famatina and Oaxaca.

* Corresponding author.

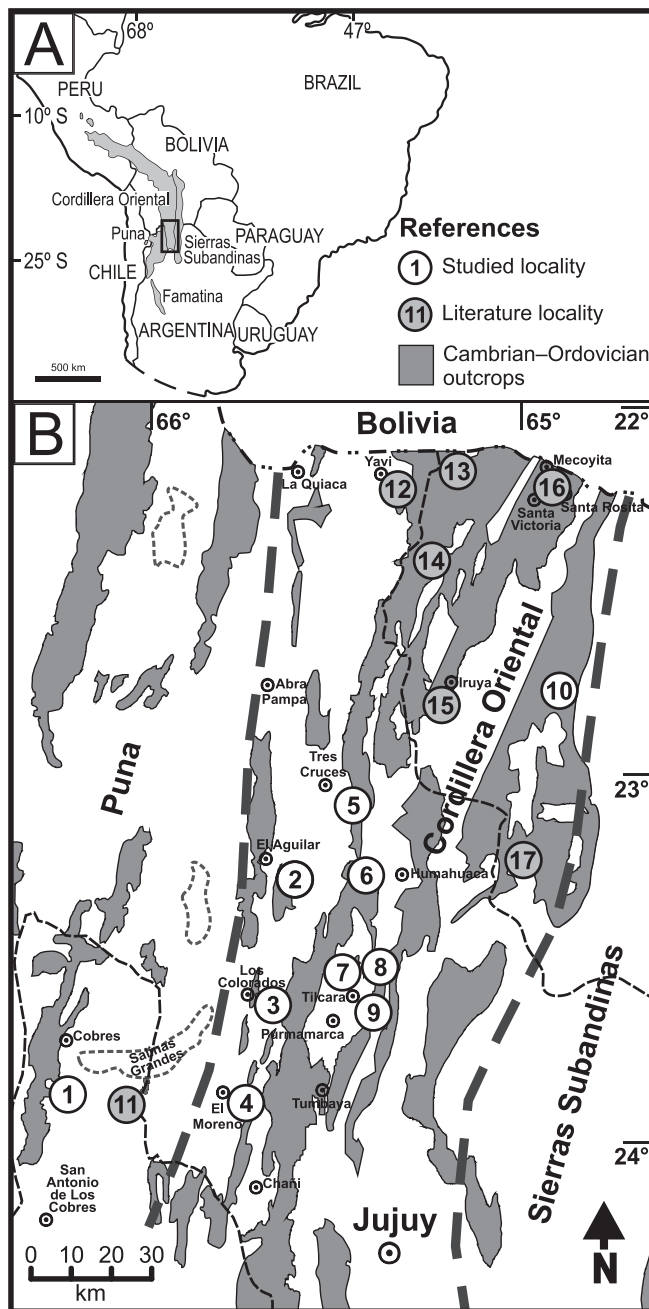


FIGURE 1—Location of the study area in South America. A) Regional map showing major areas of the Central Andean Basin and present-day position of the Famatina terrane. B) Detailed map of study localities in the Northwestern basin. 1 = Taique; 2 = Quebrada Vizcacha, Quebrada Azul, and Quebrada Llama; 3 = Quebrada Totora; 4 = El Moreno; 5 = Azul Pampa; 6 = Yacoraité; 7 = Jueya; 8 = Abra Blanca; 9 = Quebrada Huasamayo and Quebrada San Gregorio; 10 = Matancillas; 11 = Cangrejillos; 12 = Yavi; 13 = Río Tres Lagunas; 14 = Quebrada Colorada de Fundición; 15 = Iruya; 16 = Río Mesón; 17 = Orán. Segment 1 = localities 1 and 11; Segment 2 = localities 2–4; Segment 3 = 5–7; Segment 4 = 8–9; Segment 5 = 10 and 15.

Metacommunity Concept in Paleocology

The metacommunity concept provides a framework for the discrimination of ecological processes affecting species composition at multiple spatial scales (Chase and Bengtsson, 2010). A metacommunity is a collection of semi-isolated communities of potentially interacting species that are interconnected by dispersal with a very large species pool (mainland-island model; Leibold et al., 2004; Volkov et al.,

2007; Chase and Bengtsson, 2010). Currently, different models of metacommunities have been proposed that can vary in several ways, such as in the importance of local and regional processes, in the role of population regulation and stochasticity at local scales, and in the dynamics of speciation (see Leibold et al., 2004; Leibold and Miller, 2004; Chase and Bengtsson, 2010, for reviews).

On one hand, this concept requires that multiple local assemblages are treated in a spatially explicit framework, because distinguishing spatial autocorrelation from environmental effects on composition is one of the primary means of discriminating among metacommunity types. This can be difficult to apply to successions with fossil assemblages where spatial variation in environment is coupled or replaced by temporal variation instead. On the other hand, paleoecological samples of fossil assemblages rarely capture signals of short-term population-scale processes that are studied in community ecology at local spatial scales owing to time-averaging effects (Fürsich and Aberhan, 1990; Kowalewski, 1996). The structure of many local fossil assemblages can rather resemble that of metacommunities by integrating species composition at a given site over longer temporal duration (Tomašových and Kidwell, 2010a).

It is important that some metacommunity models have been implicitly used in paleoecology for a long time. For example, the studies of biofacies or biotic gradients in the fossil record (Westrop and Cuggy, 1999; Holland and Patzkowsky, 2007; Olszewski and Erwin, 2009) assume that species tracking of local environmental conditions primarily determines the composition of fossil assemblages. This concept corresponds to a species-sorting or habitat-filtering metacommunity model which predicts that dispersal limitation is negligible in structuring gradients in species composition (Leibold et al., 2004). Discriminating the role of local and regional effects via diversity partitioning (Patzkowsky and Holland, 2007), and accounting for spatial (Tomašových and Kidwell, 2010b) or temporal variation (Tomašových and Kidwell, 2010a) in composition among fossil assemblages, however, clearly provide quantitative tools that allow testing the importance of other mechanisms such as dispersal limitation or the strength of local dynamics in structuring paleocommunities. Paleocommunity analyses performed at multiple spatial scales can thus help to unravel patterns underlying the structure of paleocommunities and, among other aspects, patterns of alpha and beta diversities among communities. More recently, the metacommunity concept has begun to be applied more broadly to understanding paleoecological patterns (e.g., Jackson et al., 1996; Pandolfi, 1996; Zuschin et al., 2007; Tomašových and Kidwell, 2009a, 2010a; Fall and Olszewski, 2010).

GEOLOGICAL SETTING

The Central Andean Basin includes five major areas (Puna, Cordillera Oriental, Sierras Subandinas, Sierras de Santa Bárbara, and subsurface Chaco plains) that were traditionally considered as separate basins due to recent Andean tectonic influence. Newer interpretations, however, regard these areas as adjacent early Paleozoic depozones of a large-scale foreland basin system (Bahlburg and Furlong, 1996; Astini, 2003, 2008) developed at the active, proto-Andean margin of southwestern Gondwana.

Our study is mostly constrained to the Cordillera Oriental, interpreted to represent the peripheral bulge depozone (Astini, 2008) of the foreland system, where platform siliciclastic deposits developed in a low gradient, ramp-like setting. The latter was largely influenced by large-scale prograding deltaic systems developing as a consequence of drainage systems drowning from the craton to the east, and of an active volcanic arc complex in the west (Bahlburg and Furlong, 1996; Astini, 2003). Wave-dominated siliciclastic shelf environments with rare conversions into tide-dominated estuarine complexes during lowstands (Buatois and Mángano, 2003; Buatois et al., 2006; Astini, 2008) characterize the depositional history of Furongian–Tremadocian

Period	Stage	Age	Biostratigraphy		Lithostratigraphy					Sequence stratigraphy
			Trilobites	Conodonts	Segment 1	Segment 2 and 3	Segment 4	Segment 5		
Cambrian	Stage 10	488	<i>Jujuyaspis keideli</i>	<i>lapethognathus</i>	Potrefilos Fm.	Guayoc Chico Gr.	Alfarcito Mb.	Santa Rosita Fm. (undifferentiated)	TST	
	Stage 10	489	<i>Parabolina (N.) frequens</i>	<i>Cordylodus proavus</i>	Taique Fm.	Lampazar Fm.	Pico de Halcón Mb. Casa Colorada Mb.		FSST	
					Padrioc Fm.	Tilcara Mb.		HST		
								TST		
								LST		

FIGURE 2—Correlation chart showing biostratigraphy, lithostratigraphy, and third-order sequence stratigraphy for the uppermost Cambrian of northwestern Argentina. Trilobite zones based on Waisfeld and Vaccari (2008), conodont zones on Albanesi et al. (2008), lithostratigraphy on Astini (2003) and Buatois et al. (2006), sequence stratigraphy on Buatois et al. (2003, 2006), and absolute ages on Ogg et al. (2008).

successions of the Cordillera Oriental. Based on biogeographic signatures of the diverse shallow-water, benthic invertebrate faunas, the position of the Cordillera Oriental during the late Cambrian–Early Ordovician is broadly agreed upon to be at generally intermediate latitudes (Vaccari et al., 2006; Benedetto et al., 2009).

The studied interval is constrained to the *Parabolina (N.) frequens argentina* zone (Waisfeld and Vaccari, 2008), which at least partially correlates with the *Cordylodus proavus* zone (Albanesi et al., 2008). According to Buatois et al. (2003, 2006) this time span records one of the most important basin-wide transgressions in the Cordillera Oriental which thus allows intra-basinal correlation (Buatois et al., 2006). It also represents the transgressive and early highstand systems tracts of the lowermost sequence of the Cajas Supersequence (Astini, 2003).

Furongian–upper Tremadocian successions of the Cordillera Oriental have been assigned to different lithostratigraphic units depending on their position in the basin (see stratigraphic nomenclature in Astini, 2003; Buatois et al., 2006). We mostly constrained our study to the fully marine units, the Lampazar Formation and its lateral equivalent, the Casa Colorada Member of the Santa Rosita Formation (Fig. 2).

Our paleoecological analysis was performed at local, regional, and biogeographic scales. For the local scale analysis, extensive sampling is concentrated on the Lampazar Formation which crops out at the western area of the Cordillera Oriental. The unit is represented by a shallowing-upward succession, overlying the sandstones of the Padrioc Formation, which is interpreted to represent the initial lowstand (Buatois and Mángano, 2003). Environments represented by the Lampazar Formation mostly range from shelf (below maximum storm wave base) to lower offshore and upper offshore to offshore transition (between storm wave base and fair-weather wave base), and to a lesser extent to lower shoreface (above fair-weather wave base) (Buatois et al., 2003). The Lampazar Formation starts with a distinct drowning surface followed by a shale interval (Fig. 3) that may record variable oxygen levels (Esteban and Tortello, 2007). Toward the middle to upper levels, thin tabular sandstones (1–2 cm) or occasional shell beds are present, while in the uppermost part, sandstone beds progressively become more frequent (Fig. 3). The latter interval is interpreted to represent an upper offshore to offshore transition setting (Buatois et al., 2003; Esteban and Tortello, 2007). The top of the formation is marked by a regressive surface of marine erosion that records the start of the falling stage systems tract, which characterizes the base of the Guayoc Chico Group (Astini, 2003; Buatois et al., 2003). The sequence-stratigraphic framework proposed by Buatois et al. (2003) establishes that deep environments at the lower part of the Lampazar Formation represent the late transgressive systems tract (TST), while shallower facies (from lower offshore to offshore transition) developed in the middle and upper part of the unit represent the highstand systems tract (HST).

For the analysis at the regional scale, Furongian successions exposed at ten additional localities were evaluated. These localities follow a basin-wide west-east transect and in turn can be divided in five segments. The segments are arranged following a regional bathymetric gradient, based both on regional analysis and local sedimentary facies (Astini, 2003, 2008; Buatois et al., 2003, 2006; Spagnuolo et al., 2005; Egenhoff, 2007).

Segment 1 is unique, as the depositional history of the Cambrian–Ordovician successions there is related to a volcanic arc setting, while all other segments are ordered following a general onshore-offshore trend. Segment 2 represents the deepest parts of the basin, while at the other extreme, Segment 5 represents the most proximal settings. This bathymetric change along the sampling transect is possibly of similar magnitude to local shallowing-upward trends recorded at local scales; however, as the regional gradient records important deltaic systems in shallower environments that are not registered at local scales, both gradients have contrasting depositional environments.

Localities from Segment 1 correspond to the eastern Puna Belt, a Furongian–Lower Ordovician volcano-sedimentary complex located to the west of the Cordillera Oriental (Coira et al., 2009). Sedimentary facies are similar to those found in the Lampazar Formation that record offshore environments (Esteban and Tortello, 2007).

Segment 2 includes all three localities studied at local scales. In addition to what has been described above, this segment is the only one that records clear shelf (below storm wave base) environments during the TST (Buatois et al., 2003).

Localities from Segment 3 of the Cordillera Oriental exhibit strong structural deformation. Though the stacking pattern of Furongian successions resembles the shallowing-upward trend of other regions, integration of this area into the general stratigraphic framework is difficult. Samples from this area (Quebrada Jueya and Quebrada Yaoraité) were considered in the analysis because they complete the regional trend in ecological patterns.

In Segment 4, depositional environments vary from estuaries to fully marine. The marine environments recorded here range from lower offshore to upper offshore environments and the stacking pattern of these sections indicates a general shallowing-upward trend (Buatois et al., 2006).

Facies associations in the easternmost fifth segment represent a range of deltaic subenvironments with frequent influence of marine episodes (Spagnuolo et al., 2005). Several authors have pointed out the more proximal signature of this succession when compared with coeval ones to the west (Spagnuolo et al., 2005; Astini and Marengo, 2006; Astini, 2008), suggesting that the depositional history of this region is linked to the wide deltaic systems developed to the east.

At the biogeographic scale, further comparisons were conducted with two other peri-Gondwanan regions where the *Parabolina* fauna is well known. During the early Paleozoic, the Famatina Range was located south (Astini, 2003) and the Oaxaca block (southern Mexico) was situated northwest of the Cordillera Oriental (Fortey and Cocks, 2003; Landing et al., 2007). In the Famatina Ranges the *Parabolina* fauna occurs in the lower part of the Volcancito Formation, a carbonate-siliciclastic succession composed of calcarenites, marls, and laminated siltstones deposited on a storm-dominated mixed platform. The latter is interpreted to have been developed during a short-lived passive margin stage that predated the Lower Ordovician fore-arc to back-arc history (Astini, 2003). In the lower Paleozoic passive margin succession of the Oaxacan Complex, the *Parabolina* fauna occurs in the upper Cambrian lower Yudachica Member of the Tiñu Formation. The Yudachica Member is composed of a largely condensed succession of wackestones and grainstones interbedded with silty shales, deposited in cool to temperate waters on a storm-influenced ramp (Landing et al., 2007). This member has been recently subdivided into three depositional sequences (Landing et al., 2007). Based on conodont biostratigraphy (Landing et al., 2007), only the second sequence correlates with the *Parabolina* fauna (i.e., the *Cordylodus proavus* zone).

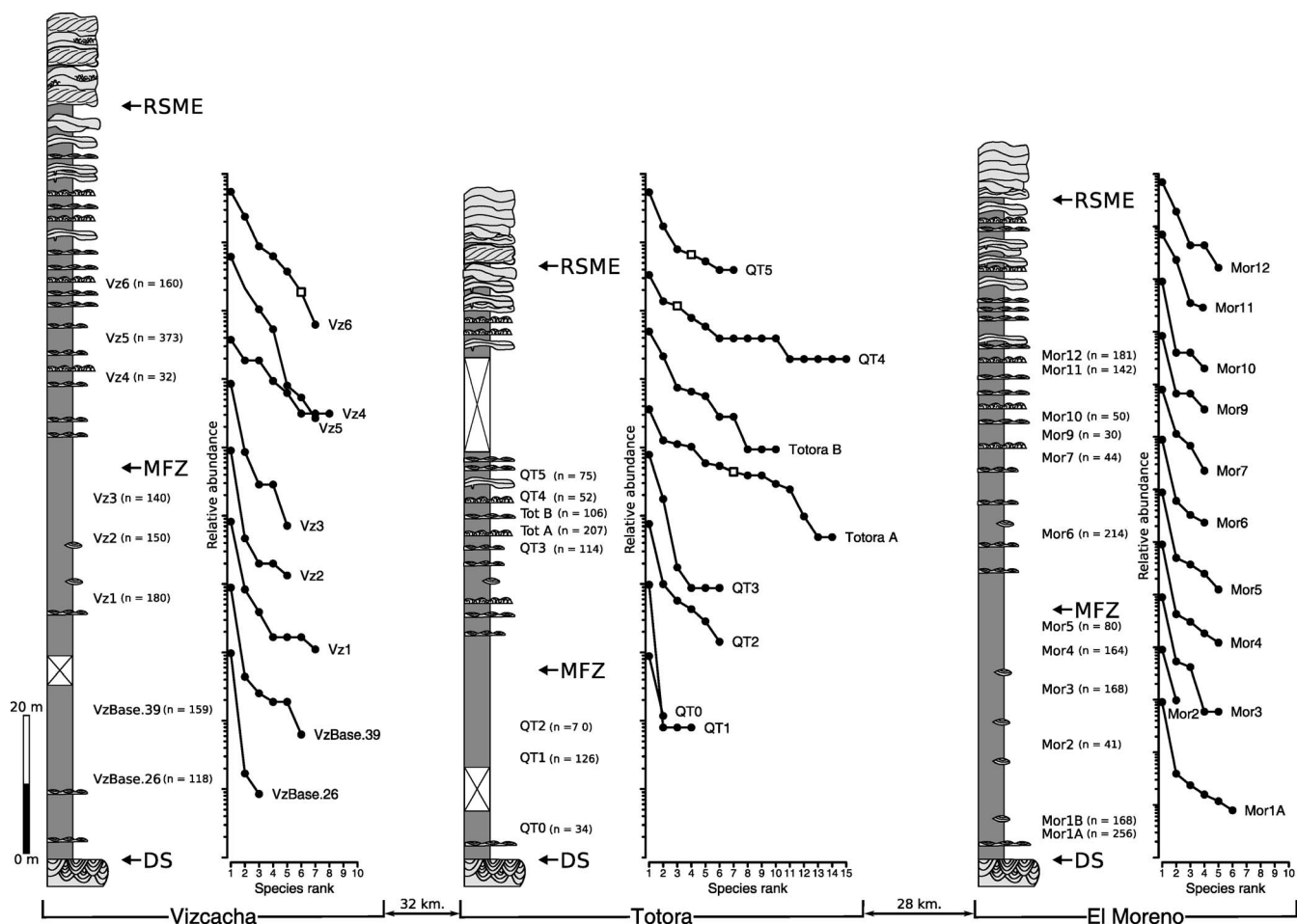


FIGURE 3—Stratigraphic logs for the Lampazar Formation and Whittaker plots for the localities analyzed at local scale. The curves are ordered in relative stratigraphic position. Note that the relative abundance axis is relative to each curve and hence absolute values are not displayed. Open boxes = *Asaphellus*; solid circles = other trilobites; RSME = regressive surface of marine erosion; MFZ = maximum flooding zone; DS = drowning surface. Sequence stratigraphy based on Buatois et al. (2003).

MATERIALS AND METHODS

Sampling Protocol

Forty-four samples were collected from shales interpreted to represent fair-weather suspension-fallout deposition (Esteban and Tortello, 2007). Samples were collected from restricted 10–20 cm intervals, in order to avoid significant time-averaging signatures. Sandstone-dominated shoreface environments recorded in the study interval (Buatois et al., 2003) were not sampled for scoring species-abundance distributions due to the increased effect of taphonomic distortion of live-dead assemblages and also to the low preservation potential of shale intervals in these high energy settings. Nevertheless, we did record species richness in these environments. Every identifiable trilobite sclerite was identified to the lowest taxonomic level possible and the MNI (minimum number of individuals) protocol was used to obtain the number of individuals in each sample (Gilinsky and Bennington, 1994). The database consists of 29 taxa (mean sample size = 104 individuals per sample; see Supplementary Data¹ for further information).

Sampling intensity varies among segments. SADs analysis derives exclusively from samples collected by the authors, whereas richness was evaluated also from literature sources, in order to achieve a more complete regional framework (Table 1).

Sampled localities are shown in Figure 1 and include from west to east:

1. Segment 1 (eastern Puna Belt): Taique section (2 samples).
2. Segment 2 (western flank of the Cordillera Oriental): El Moreno (12 samples), Quebrada Totorá (8 samples), and Quebrada de la Vizcacha (8 samples).
3. Segment 3 (central Cordillera Oriental): Azul Pampa (1 sample), Quebrada Yacoraite (1 sample), and Quebrada Jueya (3 samples).
4. Segment 4 (central-east Cordillera Oriental): Quebrada de Abra Blanca (6 samples) and Quebrada de Casa Colorada (1 sample). Additional localities, such as Punta Corral, Purmamarca, Ruta 16 yielded one monospecific sample each.
5. Segment 5 (easternmost Cordillera Oriental): A single sample from the upper course of the Río Iruya (Matancilla area) is available.

Fossil Preservation

The degree of articulation of the multielement trilobite exoskeleton, levels of fragmentation, and proportions of disarticulated sclerites of different size and shape provide important taphonomic clues to evaluate post-mortem reworking and relative time of residence on the sea floor prior to burial (Speyer and Brett, 1986; Pratt, 1998; Karim and Westrop, 2002; Hunda et al., 2006; Webster et al., 2008). Unraveling these processes is crucial for getting reliable abundance and diversity data and for interpreting paleoecological aspects of fossil assemblages.

¹ palaios.ku.edu

TABLE 1—Literature localities analyzed in this work. Richness values are medians; minimum and maximum values are given in parentheses. N = number of samples. Qda. = Quebrada. References: a = Harrington and Leanza (1957); b = Esteban and Tortello (2007); c = Zeballo and Tortello (2005); d = Esteban and Tortello (2008).

Locality	Segment	Richness	N	References
Cangrejillos	1	3.5 (2, 5)	6	a, b
Qda. Azul	2	5 (2, 11)	11	b
Qda. Llama	2	3 (1, 7)	11	b
El Moreno	2	3 (1, 7)	7	b
Jueya	3	2.5 (2, 7)	4	b
Qda. San Gregorio and Huasamayo	4	1 (1, 3)	9	a, c
Iruya	5	4 (2, 8)	5	a, d
Other localities not assigned to segments				
Yavi (Rincón de Cajas)		2 (1, 5)	3	a
Orán (Río Santa Cruz)		4 (2, 5)	4	a
Río Tres Cruces		3 (1, 9)	5	a
Río Mesón		1 (1, 2)	3	a
Qda. Colorada de Fundición		2 (4, 1)	9	a

The trilobites in the study area lie parallel to the bedding planes and are largely dispersed in the shale intervals, with few contacts in most samples. In other samples bioclasts are slightly more densely packed with frequent contacts among sclerites (Figs. 4A–F). In *Parabolina* (*N.*) *frequens*, thoracic segments are prolonged in spines, the seventh segment is macropleural, and a long axial spine protrudes backward from the twelfth thoracic axial ring (Fig. 4D). Yoked free cheeks, united by a narrow band of cephalic doublure, which yields the long genal spines, are frequently preserved (Fig. 4A). These fragile features are consistently preserved in most samples with a very low frequency of breakage (except for the axial spine, which is seldom preserved in its entirety) implying low degradation rates and/or low residence time in the taphonomic active zone.

Most trilobites occur frequently articulated, either as complete or nearly complete carcasses or as molt ensembles with different degrees of articulation (Figs. 4B–C). The occurrence of sclerites indicates that these fossil assemblages consist of a mixture of rapidly buried remains and remains that were exposed on the sea floor for a longer period of time. Such a range of well- and poorly preserved sclerites can be expected when skeletal remains accumulate under low energy conditions and slow background sedimentation rates, but are subjected to episodic storm-related burial. The percentage of sclerites preserving some degree of articulation is variable, ranging from 5% to 66% among samples of the TST and from 4% to 35% in collections from the HST.

Studied samples record the co-occurrence of hardparts of a wide range of sizes (Fig. 4A). Articulated meraspides of *Parabolina* (*N.*) *frequens* (~0.6 cm length) are common and are associated with articulated holaspides (3–3.5 cm length) in the same bedding planes. In addition, fairly complete growth series can be observed among cranidia of *Parabolina* (*N.*) *frequens* from early meraspides (0.1–0.3 cm length) to adults (1.1–1.2 cm length). Other forms (e.g., *Plicatolina*, *Angelina*, and *Onychopyge*), although much less abundant than *Parabolina* (*N.*) *frequens*, also preserve sclerites with a wide range of sizes. Disarticulated trilobite sclerites with different shapes and dissimilar hydrodynamic properties (see Westrop, 1986; Lask, 1993) in the same bedding plane, along with hardparts of a wide range of sizes, suggest minimal sorting and negligible pre-burial winnowing and/or transport, supporting the largely *in situ* source of the material. Accordingly, taphonomic attributes of the analyzed samples, such as low levels of sorting coupled with variable but generally high articulation levels, suggest a relatively rapid burial preventing intense degradation. Given this scenario it is likely that time averaging of the whole assemblage was not extensive and took place within one habitat type.

It should be noted that minimal size sorting has been documented in most samples from both the TST and HST, even in those collections in which articulation levels were low. The similarity in preservation between these two assemblages can also imply that they do not differ much in time averaging, although the expected differences in net sedimentation rates between the TST and HST might indicate that assemblages from the latter could be even less temporally averaged than TST assemblages. As we argue below, however, the comparison of diversity patterns between TST and HST environments indicates that changes in time averaging do not account for the major trends in diversity observed in this study.

Trilobite remains exhibit an uneven distribution across the thin sampled intervals rather than being restricted to particular bedding planes, suggesting that their preservation might have been favored by suspension fallout under moderate to high sedimentation rates in combination with sporadic rapid burial.

Analytical Methods

Analysis at Local Scale.—We analyzed the change in species-abundance distributions, diversity, richness, evenness, and beta diversity along temporal shallowing-upward gradients and along three single stratigraphic sections, namely Quebrada Totorá, Quebrada de la Vizcacha, and El Moreno (all from Segment 2). The analysis of single sections provides an understanding of local environmental gradients, although some temporal effects cannot be ruled out. In the localities under study, most of the TST records deep marine environments below storm wave base (shelf), while HST records the progradation of shallower environments, usually ranging from lower offshore to offshore transition (Buatois et al., 2003). Therefore, we used the sequence-stratigraphic framework as a proxy for sedimentary environments.

In order to analyze species-abundance distribution (SAD) we employed an empirical approach (McGill et al., 2007) assessing the change in SADs by Whittaker rank plots (Magurran, 2004), in addition to model fitting. We fitted common SAD models to our data, namely geometric, log-normal, broken-stick, Zipf, and Zipf-Mandelbrot. To do this, we used only the 22 samples that had >90 individuals, as low sample size may bias model fitting (Wagner et al., 2006). In order to select the best model we used Akaike weights (Anderson et al., 2000), based on the Akaike information criteria (AIC). At a second stage, we combined their Akaike weights to test Zipf–Zipf-Mandelbrot models versus all other models, because the shape of the Zipf and Zipf-Mandelbrot species-abundance models is similar (Frontier, 1985). For the model fitting we used the *radfit* function in the *vegan* package for R (Oksanen et al., 2010; R Development Core Team, 2010).

To analyze diversity, richness, and evenness, we used the decomposition formula put forward by Hayek and Buzas (1997). This approach states that diversity measured as Shannon's Entropy (H') is decomposed in richness and evenness based on the formula:

$$H' = \ln(S) + \ln(E)$$

where S is richness and E is evenness calculated as $E = e^{H'/S}$ (Buzas and Gibson, 1969).

As H' , S , and E are dependent on sample size, we rarefied our samples to a quota of 50 individuals. This procedure was carried out by resampling individuals, without replacement, within samples. H' , S , and E were calculated as mean values of 1000 replicate subsamples. This analysis was performed using a code written in R (R Development Core Team, 2010) by one of the authors (D.B.). For all comparisons between HST and TST we used a Wilcoxon rank test (Quinn and Keough, 2002) using the *wilcox.test* function in R (R Development Core Team, 2010).

We also analyzed beta diversity between samples of the TST and HST. As a measure of beta diversity, we used multivariate dispersion in

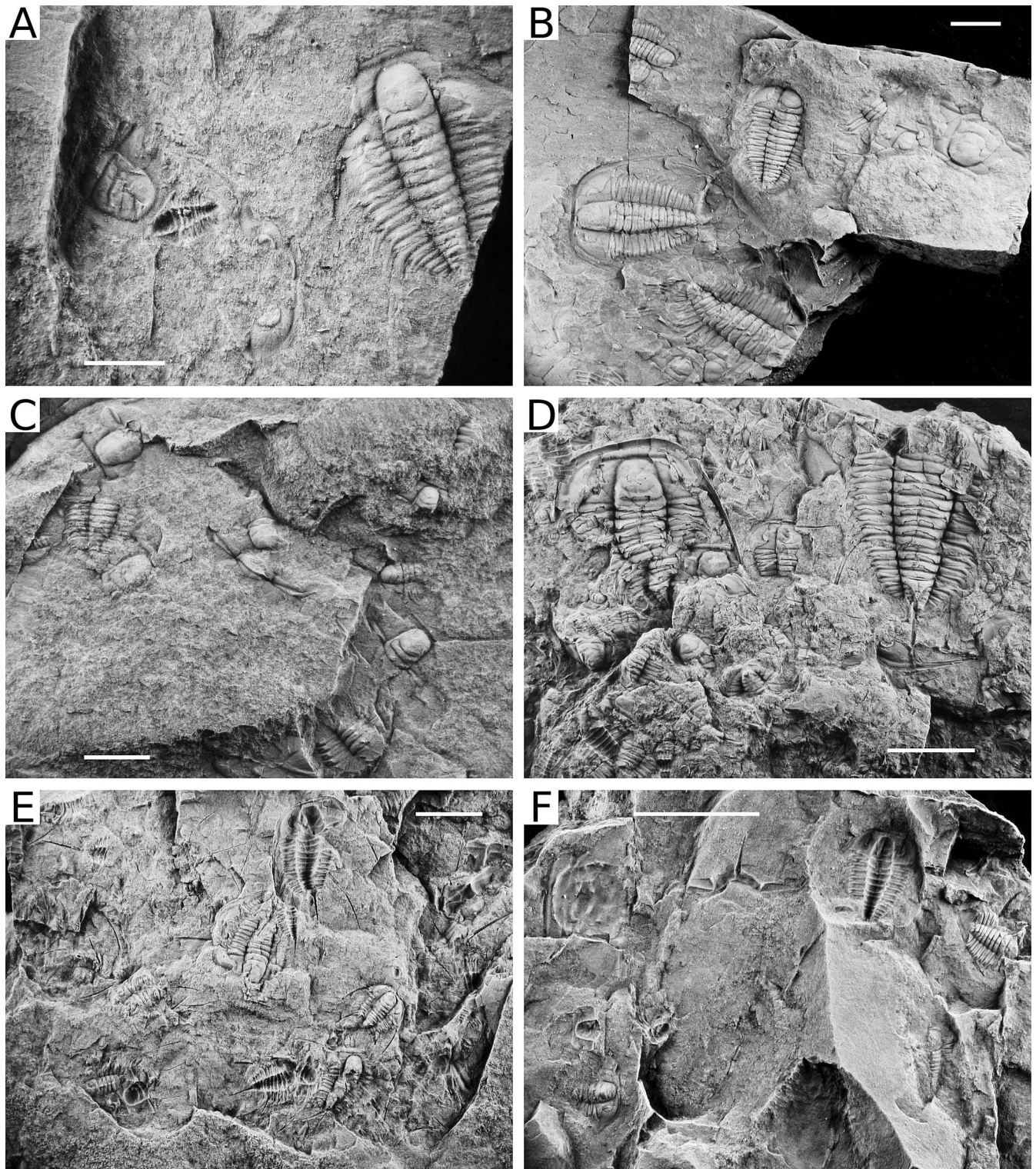


FIGURE 4—Slabs showing high degree of articulation and low levels of sorting in the trilobite assemblages analyzed in the text. A) Sample from Vizcacha (Vz6); scale bar = 2 mm. B) Sample from Totorá (QT0); scale bar = 2 mm. C) Sample from Vizcacha (Vz6); scale bar = 5 mm. D) Sample from Totorá A; scale bar = 10 mm. E) Sample from Totorá B; scale bar = 5 mm. F) Sample from El Moreno (Mor4), scale bar = 10 mm. See Figure 3 for stratigraphic location of samples.

a space defined by principal coordinates (Anderson et al., 2006). This measure was calculated using Morisita-Horn dissimilarity using relative abundances, as this dissimilarity index is less influenced by sample size than other dissimilarity distances (Wolda, 1981), and has been used in similar analyses (Heim, 2009; Tomašových and Kidwell, 2010b). Since Bray-Curtis dissimilarity has also been used for the analysis of beta

diversity (Ellingsen, 2002), we also tested beta diversity using this distance. For this analysis we used 14 samples of the HST and 13 samples of the TST. The sample Mor1B was excluded due to its particularities in composition and relative abundances (see Results). We tested the differences in beta diversity between TST and HST using a permutation test (Oksanen et al., 2010). The analysis was carried out

using *vegdist* and *betadisper* functions in the *vegan* package for R (Oksanen et al., 2010; R Development Core Team, 2010).

We also evaluated the trends in composition and relative abundances along environmental gradients using an indirect gradient analysis, i.e., a correspondence analysis (CA) (Legendre and Legendre, 1998). The CA was preferred against the detrended CA because the latter might distort the underlying nature of the ordinations due to the detrending (Wartenberg et al., 1987). On the other hand, nonmetric multidimensional scaling (NMDS) gave similar results to CA, but the stress value was too high (>0.5) to be interpretable (Clarke, 1993). Prior to this analysis, samples with only one species and species present just in one sample were both removed. In addition, a square root transformation was applied after calculating relative abundances per sample. The CA was performed using the *cca* function of the *vegan* package for R (Oksanen et al., 2010; R Development Core Team, 2010).

Analysis at Regional Scale.—At this scale diversity patterns were studied following the west-east sampling transect which follows a bathymetric regional gradient. Using our field collections, we analyzed diversity, richness, and evenness using the decomposition approach (Hayek and Buzas, 1997), and the sample standardization method described for the analysis at local scale with the same quota of 50 individuals. To check if the regional richness patterns found were robust in our dataset, we added two samples from one locality that lacks abundance data (Taique, see Supplementary Data¹) and surveyed the literature for more information (Harrington and Leanza, 1957; Tortello and Esteban, 2003; Zeballo and Tortello, 2005; Esteban and Tortello, 2007, 2008). Using both our field collections and the literature data, we analyzed richness trends along the sampling transect and also looked for possible trends in northern localities that were not assigned to segments. Kruskal-Wallis rank test (Quinn and Keough, 2002) was used for statistical comparisons between more than two segments using the *kruskal.test* function in R (R Development Core Team, 2010).

Analysis at Biogeographic Scale.—For this level we compared the abundance and occupancy of the two most common taxa between Cordillera Oriental, Oaxaca, and Famatina. We focused on *Parabolina (N.) frequens* and *Asaphellus*, as these are the most abundant taxa in those regions. We studied their relative abundance per sample and their occupancy. Occupancy is the proportion of total sites (i.e., samples) where a taxon is present, and is also known as proportion of occurrence (Fall and Olszewski, 2010); several literature sources were used to analyze patterns in Famatina and Oaxaca (Robison and Pantoja-Alor, 1968; Tortello, 2003; Tortello and Esteban, 2007).

We also calculated the probability of interspecific encounter (PIE; Hurlbert, 1971) in order to compare our evenness values to those calculated by Peters (2004a) for the Cambrian–Ordovician of Laurentia. PIE has been shown to be the most robust evenness index in small sample sizes (Bulinski, 2007), but has the disadvantage of not being independent of richness. Peters's (2004a) sampling design is very similar to ours, as he sampled only fair-weather shales and sample sizes close to 100 individuals. As Peters (2004a) did not rarefy to a common sample size, and calculated PIE using the actual abundances in each sample, we followed the same procedure.

RESULTS

Species-Abundance Distributions along Local Stratigraphic Gradients

The species-abundance distributions analyzed in El Moreno, Vizcacha, and Totorá sections (Fig. 3) show clear variations along local temporal shallowing-upward gradients. When analyzed along each stratigraphic section, the SADs gradually change from very uneven distributions to more equitable ones. The SADs from the deepest settings of the TST have high dominance and many rare species. They are depicted as a hollow curve in a Whittaker plot (Fig. 3). SADs in shallower environments of the HST are variable (Fig. 3) and many of

them, particularly the ones from Quebrada Totorá (Fig. 3), are flatter, showing less dominance, more intermediate-abundant species, and fewer rare species.

The change between these two extremes in species-abundance distributions is mostly gradual along the shallowing-upward trend documented in each section; however, not every section shows this pattern clearly. For example, El Moreno shows little change in SADs along the shallowing-upward succession (Fig. 3). In spite of this change in dominance and general structure of the SADs, *Parabolina (N.) frequens argentina* occurs persistently as the most abundant taxon in every sample from each stratigraphic section. A particularly interesting sample is Mor1B from El Moreno, which is the only one that is not dominated by *Parabolina*. Here the most dominant species is an agnostid (*Micragnostus*), whose relative abundance attains 31%. *Plicatolina* is also abundant (20%), while *Parabolina* only reaches 1%. This sample also has many species with intermediate abundances. This peculiar sample resembles an outage (Brett and Baird, 1997), which is a thin stratigraphic horizon where a usually abundant taxon is very rare or absent. Hence, this sample was removed from all other analyses at the local scale.

A temporal change in SAD shape is observed when fitting species-abundance models to the data. In most samples, Akaike weights do not allow the selection of one model over others (Table 2); however, most samples are better supported by the Zipf (14 samples) or the geometric model (6 samples). When we combine the weights of the Zipf and Zipf-Mandelbrot versus other models, many samples have very high Akaike weights (Table 2). In this case, 75% of samples coming from the TST are better fitted by the Zipf–Zipf-Mandelbrot model. HST samples usually have lower Akaike weights and hence the selection of one model is not clear (Table 2). Thus, the change in SAD shape is better described by Zipf–Zipf-Mandelbrot SADs in deep environments of the TST and by higher variation in the shape of SADs in shallower environments of the HST.

Diversity measured as Shannon entropy (H') also changes between deep environments of the TST and shallower settings from the HST, increasing in the latter (Fig. 5). The Wilcoxon test shows that the change in median H' value is statistically significant ($W = 103.5$, $p = 0.0026$). The decomposition of diversity indicates that both richness and evenness increase between TST and HST (Fig. 5). Only samples coming from the HST have more than five species, while samples from the TST have richness values around 2–4 species. The Wilcoxon test gives significant results for the change in median richness ($W = 87.5$, $p = 0.041$) and median evenness ($W = 96.5$, $p = 0.0098$) between systems tracks. Fossil concentrations from shoreface environments are always mono- to paucispecific having no more than three species (namely *P. (N.) frequens*, *Angelina hyeronimi*, and *Leiostiegium douglasi*) (Esteban and Tortello, 2007; our personal observation, 2008).

The results of the analysis of beta diversity show that the TST yields significantly lower beta diversity than the HST (Fig. 6). This is true both for Bray-Curtis ($p = 0.002$) and Morisita-Horn ($p = 0.001$) distances.

The general pattern in the ordination analysis is a concentration of samples from deep environments and a higher dispersion of samples from shallower settings. The samples from a single stratigraphic section tend to be clustered and separated from other sections. For example, samples with low CA1 axis scores come almost exclusively from Quebrada de la Vizcacha, while most samples from Quebrada Totorá have high CA1 axis scores (Fig. 7A). This pattern, however, is most characteristic in samples from shallower settings of the HST (Fig. 7B). Samples from the deep environments typical of the TST lie more or less close to each other regardless of the section they come from (Fig. 7B). Such concentration of TST samples at intermediate CA1 values and low CA2 values is related to high dominance of *Parabolina*, while species relative abundances are more variable in those with flatter SADs from the HST. This pattern is consistent with the results of the analysis of

TABLE 2—Model selection criteria for each sample with >90 individuals. AIC = Akaike information criteria; w_i = Akaike weights. See text for further details.

Sample	AIC					w_i					w_i	
	Broken stick	Geometric	Lognormal	Zipf	Maldelbrot	Broken stick	Geometric	Lognormal	Zipf	Maldelbrot	Zipf-Maldelbrot	Other models
VzBase+26	102.21	NA	18.62	16.35	18.35	1.35E-019	NA	0.19	0.592	0.218	0.81	0.19
VzBase+39	181.79	61.87	48.9	36.15	37.53	1.58E-032	1.73E-006	0.001	0.665	0.334	0.999	0.001
Vz1	181.26	71.27	54.22	37.5	39.5	4.45E-032	3.41E-008	0	0.731	0.269	1	0
Vz2	152.69	47.74	41.1	29.45	31.06	1.20E-027	7.38E-005	0.002	0.69	0.308	0.998	0.002
Vz3	86.33	31.76	31.55	24.02	26.02	2.10E-014	0.0148	0.016	0.708	0.261	0.969	0.031
Vz5	166.3422	38.74	43.49	62.87	42.73	1.59E-028	0.814	0.076	4.68E-006	0.111	0.111	0.889
Vz6	59.2	33.89	34.44	39.17	36.54	1.53E-006	0.4765	0.363	0.034	0.127	0.161	0.839
MOR1A	297.68	82.49	62.47	42.28	44.28	2.53E-056	1.35E-009	3.02E-005	0.731	0.269	1	0
MOR1B	51.93	58.34	59.7	73.26	62.06	0.936	0.038	0.019	2.19E-005	0.006	0.006	0.994
MOR3	14.88	10.72	12.71	12.71	NA	0.067	0.536	0.198	0.198	NA	0.198	0.802
MOR4	162.19	50.41	43.5	31.78	33.78	3.50E-029	6.57E-005	0.002	0.729	0.268	0.998	0.002
MOR6	148.77	43.76	41.42	28.75	30.75	6.32E-027	0.0004	0.001	0.73	0.268	0.998	0.002
MOR11	49.17	23.47	26.96	29.35	27.45	1.92E-006	0.733	0.128	0.039	0.1	0.139	0.861
MOR12	75.3	31.97	31.99	30.33	31.61	7.13E-011	0.183	0.182	0.416	0.219	0.635	0.365
QT1	150.18	NA	28.38	22.47	24.47	1.30E-028	NA	0.037	0.704	0.259	0.963	0.037
QT3	102.42	28.79	30.4	28.95	29.61	3.38E-017	0.3301	0.147	0.304	0.218	0.523	0.477
TotoraA	74.69	77.47	65.54	71.95	73.15	0.0096	0.002	0.93	0.038	0.021	0.058	0.942
TotoraB	61.78	44.41	41.46	41.57	42.49	1.39E-005	0.082	0.36	0.342	0.216	0.557	0.443
Yacor1	56.51	52.59	59.47	71.48	56.87	0.109	0.775	0.025	6.13E-005	0.091	0.091	0.909
Jueya2B	78.15	20.93	21.58	20.23	22.23	1.02E-013	0.273	0.197	0.388	0.143	0.53	0.47
Jueya3B	61.82	35.56	33.99	26.34	28.34	1.41E-008	0.007	0.016	0.714	0.263	0.977	0.023
MAT10-Iruya	79.22	54.99	46.83	37.93	39.93	7.81E-010	0	0.008	0.725	0.267	0.991	0.009

beta diversity. All samples from El Moreno, which usually have high dominance of *Parabolina*, occur in this sector of the ordination space. Therefore, the flattening in the shape of SADs (and thus the increase in richness and evenness) and the increase in beta diversity correlate with local shallowing-upward patterns.

Regional Diversity Patterns

The change in abundance distributions across the sampled east-west transect is not monotonic. In any case, the flat SADs tend to be

restricted to Segment 2 and Segment 5 (Figs. 2, 8). Segment 3 has either SADs with similar abundances of the first two ranked species or hollow curve-shaped distributions (Fig. 8). Finally, Segment 4 samples are pauci- to monospecific which precludes any discussion of the abundance distributions. Overall, the shape of SAD does not follow any clear trend across a regional gradient. *Parabolina (N.) frequens* is always the most abundant taxon in diverse samples and it is the only species present in all monospecific samples.

Richness at the regional scale is very variable, ranging from monospecific samples up to diverse ones with >11 taxa in rarified

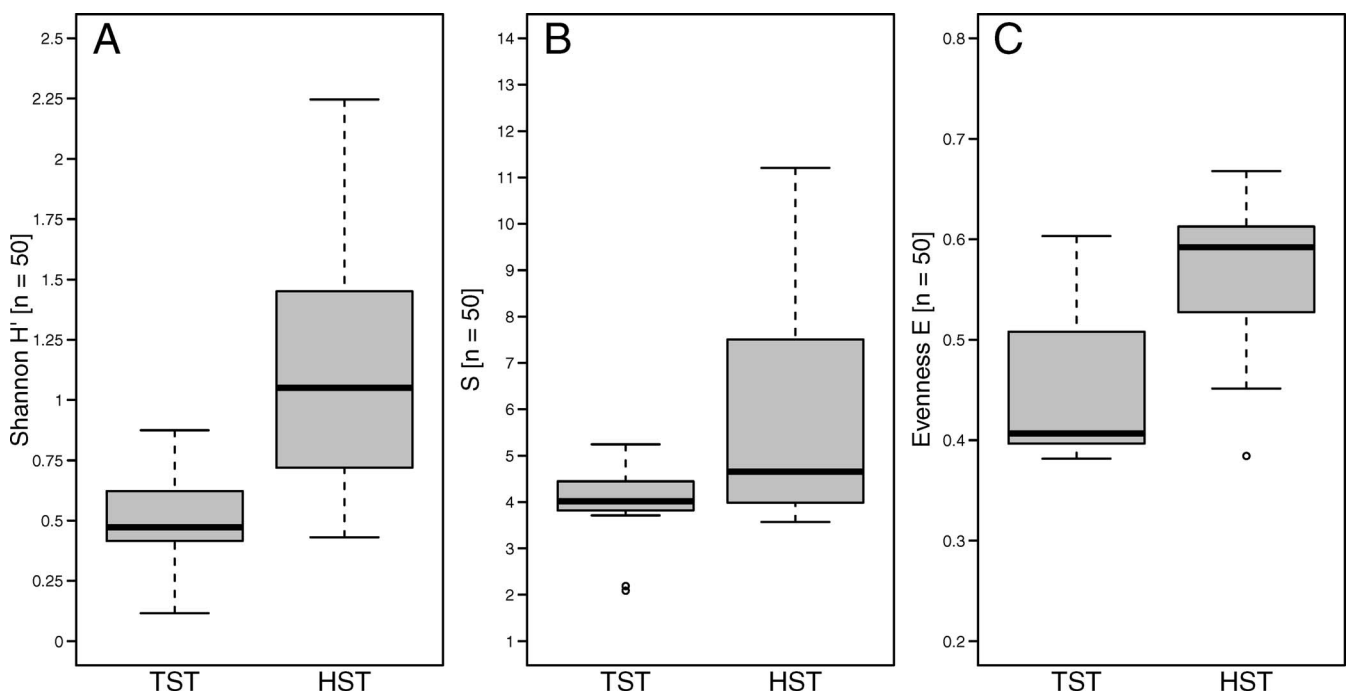


FIGURE 5—Box plots for rarefied diversity, richness, and evenness binned by systems tract. A) Rarefied diversity measured as Shannon's H' . B) Rarefied richness. C) Rarefied evenness measured as Buzas-Gibson's E . Box plots show medians, first, and third quartiles; whiskers extend to 1.5 times the interquartile range from the box, and open circles are extreme values.

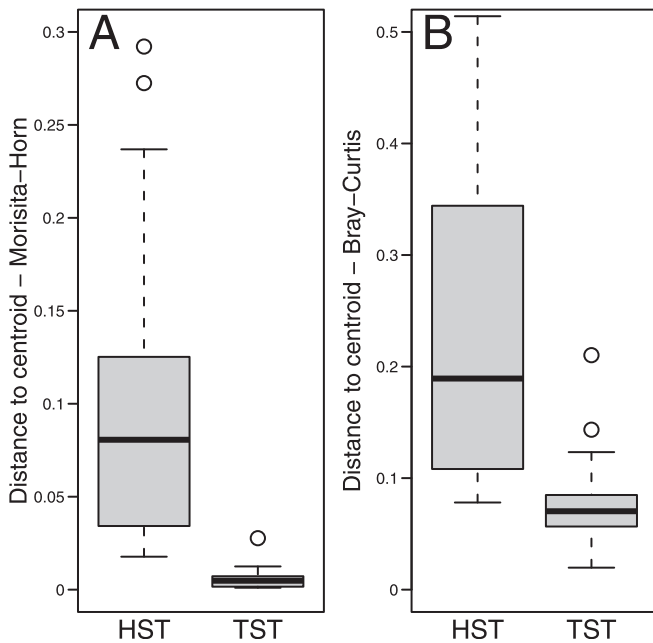


FIGURE 6—Box plots for beta diversity binned by system tract. A) Beta diversity measured as distance to the centroid based on Morisita-Horn distance. B) Beta diversity measured as distance to the centroid based on Bray-Curtis distance. Box plots show medians, first, and third quartiles; whiskers extend to 1.5 times the interquartile range from the box, and open circles are extreme values.

samples (Fig. 9B). As can be seen in Figure 10, there is no trend in standardized diversity at a regional scale. Shannon's H' is high at Segment 2 with mean values of 0.844, decreasing toward Segment 3 (mean $H' = 0.591$), and reaching its minimum at Segment 4 where H' is 0. Shannon entropy rises again at segment 1 where the only sample has $H' = 1.01$. The Kruskal-Wallis rank test shows that the differences between median H' of Segments 2, 3, and 4 are significant ($K-W X^2 = 8.08$, $df = 2$, $p = 0.017$).

The decomposition of diversity shows that the richness trend along the sampled transect is very similar to the trend in H' (Fig. 10). High richness is found toward Segment 2 (Fig. 10), exhibiting sample rarefied richness between 3–6 species (mean $S[50] = 5.28$). In this segment, samples from Quebrada Tatora are particularly interesting as they display the highest levels of sample richness (≤ 14 species). At Segment 3 richness is lower (Fig. 10) and after rarefaction samples yield between 3 and 4 species (mean $S[50] = 3.6$). Richness decreases even more at Segment 2, where samples become pauci- to monospecific. Although all samples with >50 individuals at Segment 2 are monospecific, there is one small sample (AB6) with two species. Finally, at Segment 1 sample richness rises again and reaches rarefied richness of 5.542 species. A Kruskal-Wallis rank test gave significant results for differences in median rarefied richness between Segments 2, 3, and 4 ($K-W X^2 = 10.21$, $p = 0.006$).

There is no obvious trend in evenness across the sampled transect. Evenness measured as Buzas-Gibson E has similar values at different segments (Fig. 10). We compared Buzas-Gibson E only between Segments 2 and 3 because samples in Segment 4 are mostly monospecific and hence evenness values are $E = 1$. The differences between these two segments are not significant (Wilcoxon test, $W = 42$, $p = 0.81$). The fact that there appears to be no change in evenness indicates that the regional change in diversity along the sampling transect is mainly caused by changes in richness.

Raw sample richness values from the literature are summarized in Table 1 and Figure 11. They are consistent with the ranges found in sampled segments, supporting the trend in rarefied richness described above. A Kruskal-Wallis rank test yielded significant results for the change of median raw richness between all segments ($K-W X^2 = 33.13$,

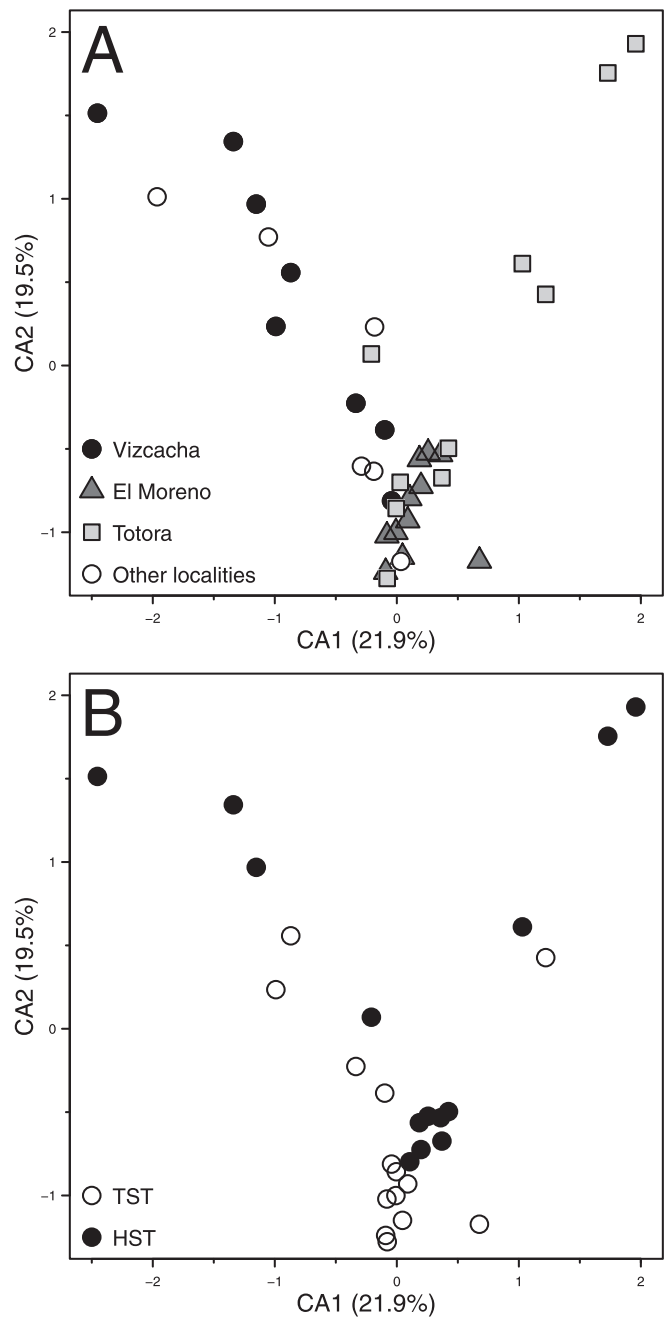


FIGURE 7—Results of the correspondence analysis. A) Ordination of samples by localities. B) Ordination of samples by systems tract. Parentheses show percentage of inertia explained by the axis.

$df = 4$, $p = 1.12 \times 10^{-06}$). Other northern localities not assigned to segments also show that there is no clear regional trend in richness in this part of the basin (Fig. 1, Table 1).

Biogeographic Diversity Patterns

When comparing trilobite assemblages found in Cordillera Oriental with those from Famatina and Oaxaquia, striking differences appear. All three regions have a close biogeographic relationship as they share many species. Polymeroid trilobite species such as *Parabolina (N.) frequens argentina*, *Angelina hyeronimi*, *Plicatolina scalpa*, *Asaphellus aspinus*, *Asaphellus* sp., and *Rhabdinopleura* sp. are in at least two of these three regions (Robison and Pantoja-Alor, 1968; Esteban and

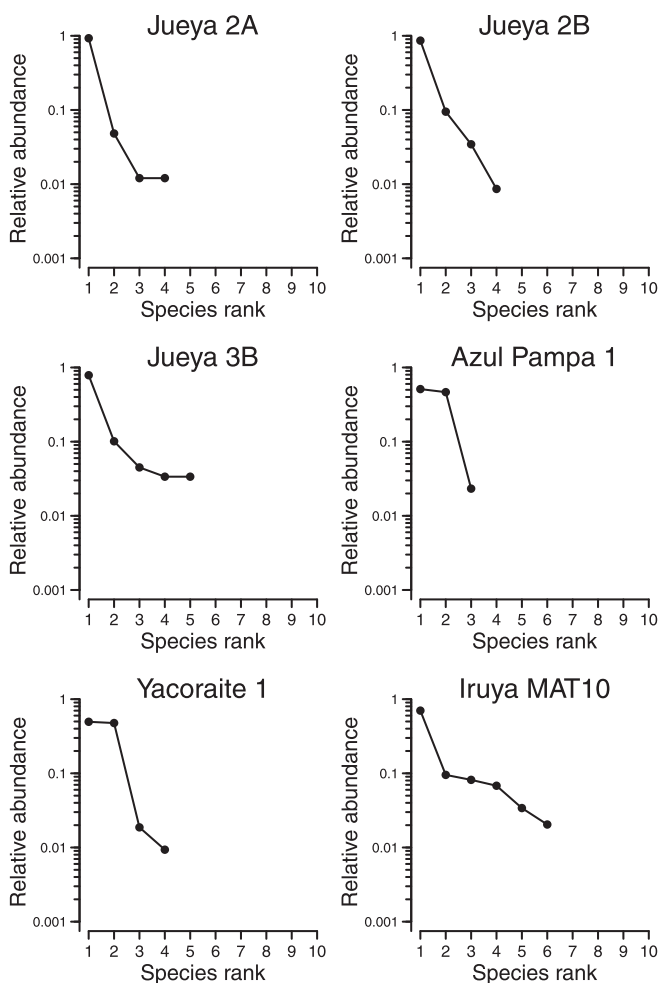


FIGURE 8—Whittaker plots for other samples in the Cordillera Oriental.

Tortello, 2007; Tortello and Esteban, 2007; this study). When relative abundances and proportion of occurrences are taken into account, however, significant differences between these regions become evident.

At the Cordillera Oriental, *Asaphellus* is found only as a rare element. In our dataset, *A. aspinus* is present in low abundances; mean relative abundance, calculated only from samples where it is present, is 8.4%. Rarity is not only expressed in relative abundance, but also in occurrence, as the species is present only in 4 of 44 samples of our database. Literature also shows this taxon to be rare (Esteban and Tortello, 2007) and reveals one additional rare species from the genus (*Asaphellus* sp.; Harrington and Leanza, 1957; Esteban and Tortello, 2007). These published sources together with our dataset indicate a very low occupancy of *Asaphellus* (including both species), because this genus occurs in 7% of the samples (8 of 111 samples). This occupancy pattern contrasts with the one of *Parabolina (N.) frequens*. The latter is almost invariably the most abundant species in our dataset; its occupancy in our dataset and literature data is 99% (110 of 111 samples).

In contrast, in both Famatina and Oaxaquia, *P. (N.) frequens* is a rare member of the communities, while *Asaphellus* is very abundant (Robison and Pantoja-Alor, 1968; Tortello and Esteban, 2007). Only a few samples attributable to the second sequence of the Yudachica Member of the Tiñu Formation (Robison and Pantoja-Alor, 1968; Landing et al., 2007) are known. Although numerical abundance data are not available for the Tiñu Formation, both Robison and Pantoja-Alor (1968) and Landing et al. (2007) indicate that *Asaphellus* is abundant, being present in 3 of 6 samples. *Parabolina (N.) frequens*

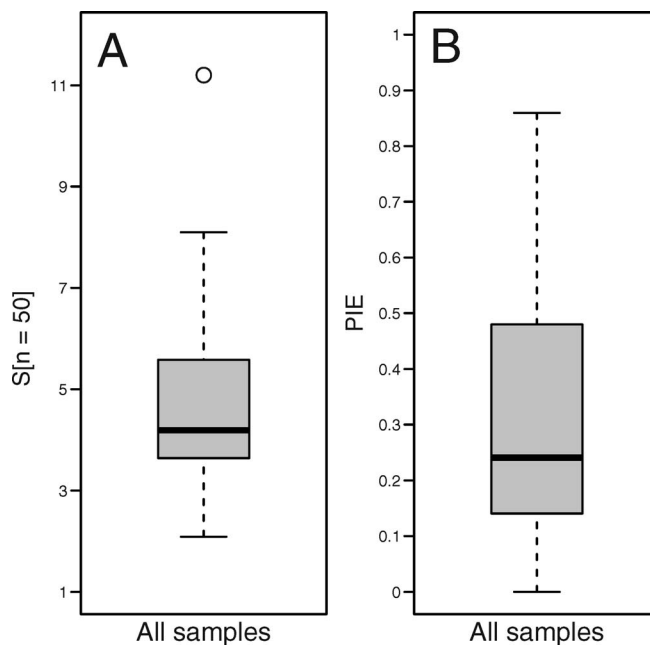


FIGURE 9—Box plots for regional richness and evenness for all samples along the regional sampling transect. A) Rarefied richness. B) Evenness measured as PIE (probability of interspecific encounter) based on actual sample sizes. Box plots show medians, first, and third quartiles; whiskers extend to 1.5 times the interquartile range from the box, and open circle is an extreme value.

occurs in a single sample as just three cranidia (Robison and Pantoja-Alor, 1968).

Most of the samples that come from Famatina contain *Asaphellus* (4 of 6), while only two contain *P. (N.) frequens* (Tortello, 2003; Tortello and Esteban, 2007). Relative abundances reported by these authors show a broadly similar pattern to that of the Yudachica Member, indicating high abundance of *Asaphellus* and paucity of *P. (N.) frequens* (Tortello and Esteban, 2007). Figure 12 shows relative abundances of these two taxa at Famatina compared to the only four samples that contain *Asaphellus* in our dataset.

Evenness measured as Hurlbert's PIE is low in samples from the Cordillera Oriental. Its median value is 0.34, while values >0.75 are present in only two samples (Fig. 9B).

DISCUSSION

Local Paleocological Patterns

The best supported pattern found in the *Parabolina* fauna is the trend toward higher sample richness, evenness, and beta diversity in HST environments. This pattern occurs together with the change in SADs in those environments. In addition, samples in the ordination analysis show a similar response to local shallowing-upward trends. It can be argued that documented patterns in sampled diversity and ordination analysis might be the result of time averaging and reflect largely biased ecological relationships (or distorted biological signals) (Finnegan and Droser, 2008; Tomašových and Kidwell, 2010b). If this were the case, time averaging should augment alpha diversity, while beta diversity should decrease (Tomašových and Kidwell, 2010b). When an increase in alpha diversity is not accompanied by a decrease in beta diversity, however, the pattern is most probably biological in origin (Tomašových and Kidwell, 2010b). Our samples from the HST not only have higher alpha diversity and evenness but also yield higher beta diversity. This combination is difficult to interpret based on time averaging alone, and implies a true increase in diversity at regional scales.

Local-Scales Explanations.—Different ecological processes might be invoked to explain the observed patterns. One possible alternative to

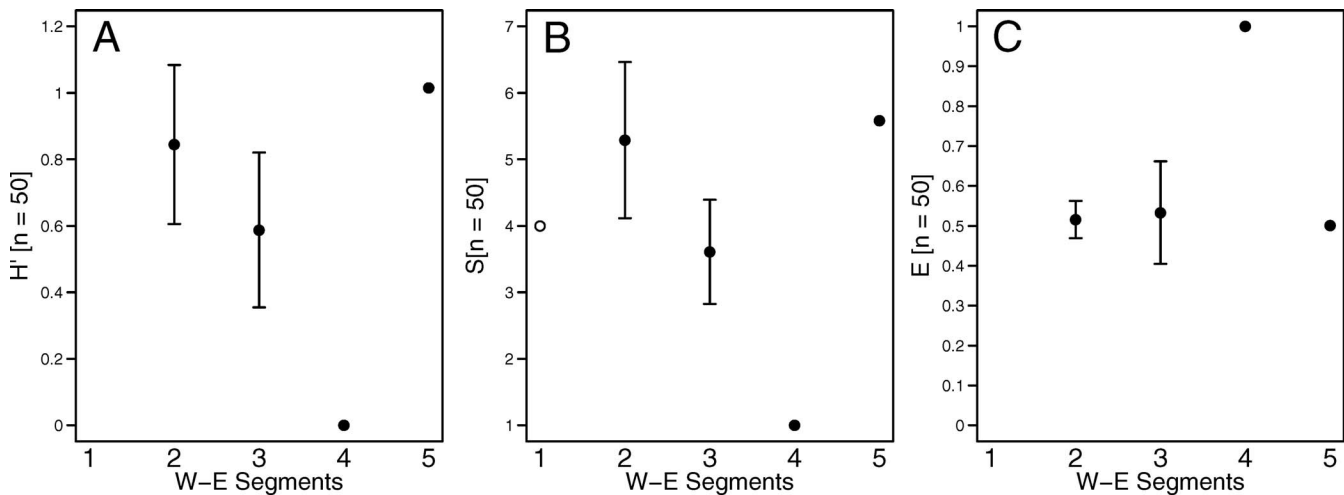


FIGURE 10—Plot for rarefied diversity, richness and evenness binned by regional sampling segment. A) Rarefied diversity measured as Shannon's H' . B) Rarefied richness. C) Rarefied evenness measured as Buzas-Gibson's E . Points are means and lines represent two standard errors for the mean.

account for the trend in higher sample richness and evenness in HST environments might be largely related to the intermediate disturbance hypothesis (Levin and Paine, 1974; Connell, 1978). Along a disturbance gradient, maximum diversity and evenness are predicted to be found at intermediate values of both intensity and frequency of disturbance (Connell, 1978). This pattern can be caused by multiple processes that may act at different spatial and temporal scales (Roxburgh et al., 2004). The disturbances cause spatio-temporal heterogeneity mainly by renewing limiting resources, reducing dominance, and/or creating opportunities for new species to colonize because disturbance can disrupt equilibrium and allow inferior competitors to colonize habitats (Levin and Paine, 1974). If disturbance is too frequent, however, it prevents species with lower colonization rates and less dispersal capability from entering the community. This creates a rather

homogeneously disturbed environment where only the species that have a high colonization capacity can survive, causing diversity to decrease (Connell, 1978). Thus, intermediate disturbance is related to maximal heterogeneity, a factor which is known to enhance species diversity (Ellingsen, 2002; Begon et al., 2006).

The depositional profile of wave- and storm-dominated shallow marine siliciclastic platforms is represented by the progressive offshore decrease in water depth, wave energy, and associated reworking processes (Dalrymple and Choi, 2007). The energy gradient is easily interpreted from primary sedimentary structures and facies analysis (e.g., Walker and Plint, 1992) and could be largely correlated with a concomitant variation in the intensity and frequency of disturbance. Hence, the seaward decrease in wave energy can be linked to a similar trend in disturbance. Storms are the most frequent source of disturbance preserved in ancient shallow marine shelves; however, storms occurring at short (monthly to yearly) time scales were much more frequent than those actually preserved in the geological record.

In accord with the prediction of unimodal diversity gradients, in our case study, the richest and most even communities occur above storm wave base, a largely unstable setting due to frequent storm-induced disturbances, whereas the stable deep environments of the late TST yield low richness and low evenness communities. At the other extreme, the shoreface communities, which are continually disturbed by fair-weather waves and frequent storms, are impoverished and exhibit no more than three taxa (this study; Esteban and Tortello, 2007). Thus the diversity-disturbance relationship broadly matches the expectations of the intermediate disturbance hypothesis (Connell, 1978; Roxburgh et al., 2004). Although it is possible that we did not sample the shallowest environments, we conclude that as disturbance increases so does the diversity, whereas when disturbance is very high, diversity is low.

It should be noted that possible underlying mechanisms shaping diversity are currently very complex and a subject of enduring controversy. Although the intermediate disturbance hypothesis has not been thoroughly tested in the fossil record (Wilson, 1987; Allmon et al., 1998, among others), it provides a reasonable approach to interpret the observed diversity patterns. Notably, the intermediate disturbance hypothesis was considered by Turvey (2005) to explain regional diversity trends in trilobite associations across an onshore-offshore gradient. The author recognized maximum trilobite diversity at intermediate water depths on the basis of a detailed quantitative analysis of Floian associations of the South China Plate.

As explained above, environments with intermediate disturbance can be expected to record habitats with the highest spatial heterogeneity. Species rank position and relative abundances in such environments

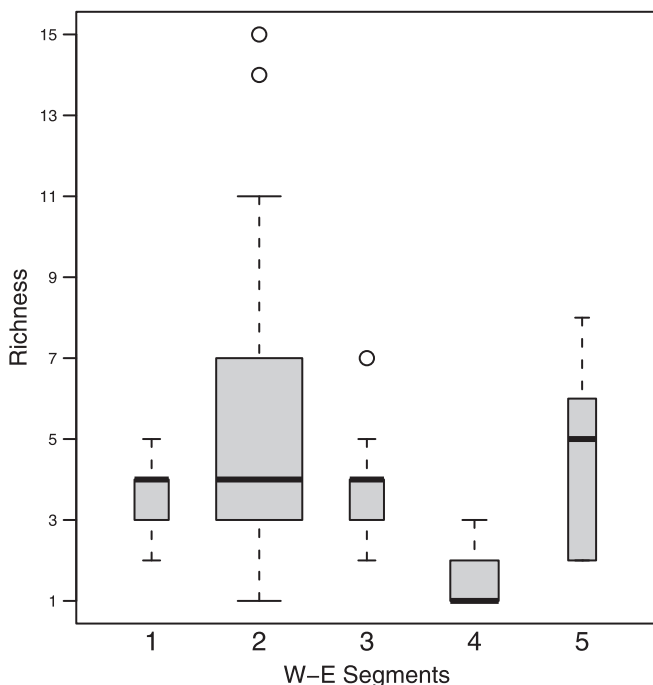


FIGURE 11—Box plots for non-rarefied richness binned by regional sampling segment. Data from our dataset and literature sources. See Table 2 for further information. Box plots show medians, first, and third quartiles; whiskers extend to 1.5 times the interquartile range from the box, and open circles are extreme values.

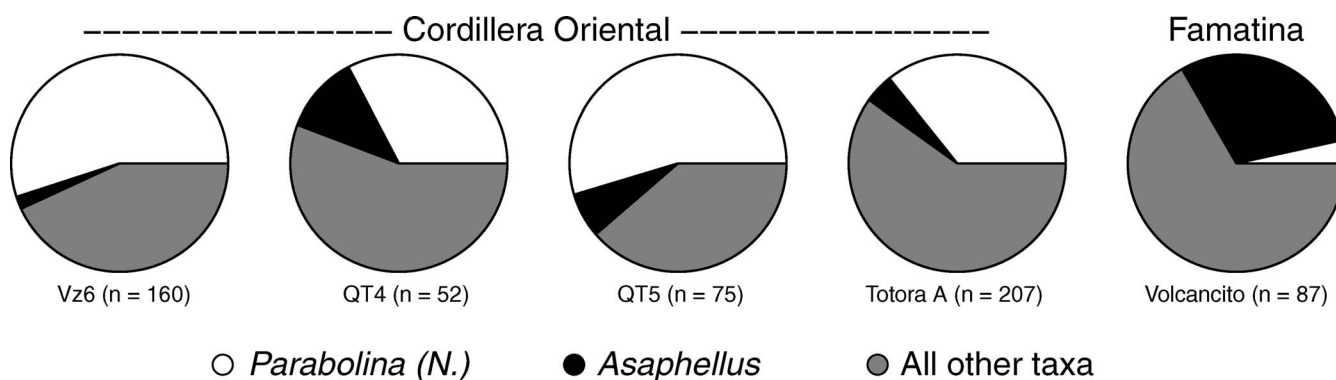


FIGURE 12—Pie plots showing relative abundances of *Parabolina* (*N.*), *Asaphellus*, and all other taxa for the four samples where *Asaphellus* is present at Cordillera Oriental and data available from Famatina (Famatina data from Tortello and Esteban, 2007).

should be much less spatially constant than in other, less heterogeneous settings. In agreement with this idea, samples from deep environments of the TST tend to be concentrated in the ordination space, while the shallower HST samples are much more dispersed, showing that beta diversity was higher in HST than in TST. Such distribution of samples in the ordination has already been noted by Scarponi and Kowalewski (2004) who found the very same pattern in their Quaternary samples from Italy. In a subsequent analysis, however, Scarponi and Kowalewski (2007) found that beta diversity decreased and alpha diversity increased toward the TST and hence it is likely to be a taphonomic pattern. We note that although the pattern found in our case study might be expected from higher time averaging in TST samples, the simultaneous decline in alpha and beta diversity toward the TST more likely reflects a biological explanation (Tomašových and Kidwell, 2010b).

Regional-Scales Explanations.—Another possible alternative that might explain higher sample richness in HST environments could be related to different abundances of species with preferences for habitats with varying disturbance in the regional species pool. It is possible that the regional species pool was dominated by taxa with preferences for environments with intermediate disturbance. Such a scenario could be expected if these environments were more frequent and hence had more area and/or temporal duration, which in turn would yield higher richness via higher opportunity for immigration or speciation (Rosenzweig, 1995). Our regional data might suggest that diverse samples from these environments are not very frequent and that similar depositional environments do not always bear diverse assemblages. Although the intermediate disturbance hypothesis seems to better explain the reported trends in richness and evenness, the environmental preferences of the regional species pool cannot be ruled out as a factor influencing higher richness in these environments.

Regional Paleocological Patterns

A regional paleogeographic scenario of a west-dipping, low gradient ramp is envisaged by several authors for early Paleozoic successions of the Cordillera Oriental (Astini, 2003, 2008; Egenhoff, 2007). Interestingly, the trend in diversity of the associations encompassed in the *Parabolina* fauna across the sampled west-east transect does not follow an obvious regional depth-related gradient. First, there is no clear richness trend across the transect, but only a clear decrease in richness at Segment 4 (Fig. 11). Second, the pattern of diversity in relation to environments observed at local scales seems to be masked by higher regional variability. At Segment 2, offshore environments of the HST yielded the most diverse samples (Fig. 5), while at Segment 4 samples coming from similar environments were pauci- to monospecific.

This pattern raises a question about the environmental factor causing very low richness at Segment 4. Factors that might account for such

depletion in diversity are usually related to minimum oxygen zones (Boyer and Droser, 2007); however, there are at least two reasons to think that very low richness in Segment 4 was caused by more complex factors than oxygen alone. Firstly, in Cordillera Oriental oxygen levels during the latest Cambrian were probably very variable and intervals that have evidence of dysoxic settings usually yield diverse samples (Esteban and Tortello, 2007). Secondly, an actualistic interpretation of low diversity caused by dysoxic conditions might be flawed in pre-Devonian times, because it has recently been proposed that physiological requirements for oxygen in the macrofauna were much lower than today (Dahl et al., 2010). Furthermore, it is possible that this lack of relationship between bathymetric gradients and compositional-diversity gradients at regional scales indicates that different aspects of metacommunity dynamics, other than species sorting to environmental gradients, affected ultimate changes in diversity and composition of the *Parabolina* fauna. Neutral or mass-effect models can lead to spatial autocorrelation that is unrelated to environmental gradients, causing a poor fit to environmental structure (Hubbell, 2001; Cottenie, 2005).

Biogeographic Patterns

At the biogeographic scale, the pattern of difference in relative abundances and occupancy of core taxa (*Asaphellus* and *Parabolina* (*N.*)) between Cordillera Oriental, and Famatina and Oxaquia, can be further related to processes underlying metacommunity dynamics at such a scale. Variations in these parameters associated with significant differences in environmental properties approach the mass effect model. Mass effect assumes that patches differ in their environmental conditions and species can partly sort themselves along environmental gradients, but high dispersal between patches results in source-sink dynamics that lead to patterns unexpected by environmental gradients (Leibold et al., 2004). This means that rare species are present in areas where they tend to go extinct (sinks) because of immigration from areas where they are abundant (sources) (Amarasekare and Nisbet, 2001).

Such requirements are, at least partially, fulfilled by Famatina, Oxaquia, and Cordillera Oriental (Fig. 13), because all three areas are characterized by distinct environmental conditions. The first two were neighboring peri-Gondwanic shelves (Astini, 2003; Landing et al., 2007) that shared a broadly similar depositional environment, interpreted as storm-wave influenced, mixed (carbonate-siliciclastic) ramps (Astini, 2001; Landing et al., 2007). Meanwhile, the Cordillera Oriental was a tectonically active setting, with high siliciclastic sedimentation rates (Astini, 2003). Balseiro et al. (2011) suggested this sedimentation rate enhanced olenid abundances, while the group became very rare or absent in shallow carbonate settings or areas with low sedimentation rates. The mixed ramps with low sedimentation rates should have been sources for some taxa (e.g., *Asaphellus*), while clastic platforms with high sedimentation rates were for others (e.g., *P. (N.) frequens*).

Furongian 490 Ma

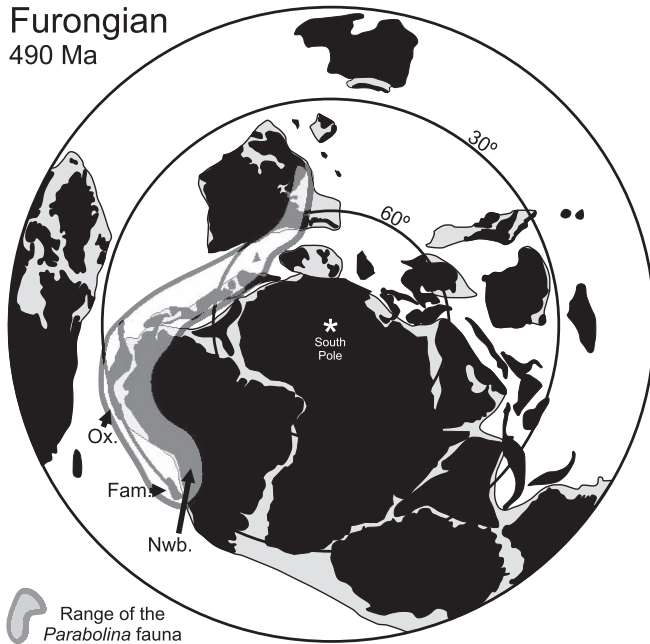


FIGURE 13—South polar view of global paleogeographic reconstruction showing the position of Northwestern Basin (=Nwb.), Famatina (=Fam.), and Oaxaca (=Ox.) and the biogeographic distribution of the *Parabolina* fauna. Reconstruction based on Cocks and Torsvik (2002); range of the *Parabolina* fauna based on Harrington and Leanza (1957), Robison and Pantoja-Alor (1968), Nikolaisen and Henningsmoen (1985), Shergold (1988), and Zylinska (2002).

Therefore, in environmentally disparate, biogeographically related areas, dispersal should allow the coexistence of these two taxa in the same local community, even when they likely had different environmental requirements. Although it is possible that their rarity in less favorable environments corresponds to extreme tails of their environmental tolerances and thus can still be explained by a sorting model, it is likely that without continuing immigration from source regions, the small populations would quickly go extinct in the face of environmental perturbations.

This finding is particularly interesting taking into account that olenids (e.g., *P. (N.) frequens*) and asaphids (e.g., *Asaphellus*) are the core taxa of Trilobite Evolutionary Faunas (TEF) Ibex I and Ibex II, respectively (Adrain et al., 2004). The TEF concept defines groups of trilobite families that followed broadly similar diversity trajectories (Adrain et al., 2004). Patterns of diversification of the Whiterockian TEF in different environmental and paleogeographic settings have been studied by several authors (e.g., Adrain et al., 2004; Zhou et al., 2007), whereas Ibex-I and Ibex-II TEFs have received comparatively little attention. Usually the dynamics of evolutionary faunas were tackled by the analysis of their replacement based on diversity trajectories through time (Sepkoski, 1981a; Westrop and Adrain, 1998; Adrain et al., 2000). Another perspective to explore is related to the study of the potential patterns of coexistence between different TEFs.

In the communities under study, Ibex-I and Ibex-II faunas are represented only by a few families, namely Olenidae and Agnostidae (Ibex I) and Asaphidae (Ibex II). These communities shed some light on the issue of trilobite evolutionary faunas' initial development, as they record the onset of the Ibex-II fauna. We suggest that the coexistence of taxa belonging to different TEFs was related to environmental variability at many scales, even when members of each evolutionary fauna had differential environmental preferences. Further studies on the post-Cambrian ecological dynamics of trilobite communities in different environmental and paleogeographic settings are needed in order to test if the hypothesis proposed here might also explain the later success of members of the Ibex-II TEF.

Evenness in Cambrian–Ordovician Communities

As explained above, evenness in our samples is rather variable, mainly between TST and HST. Though some samples have a PIE > 0.7, most values are near 0.4 (Fig. 9B), which is much lower than the evenness documented for the latest Cambrian of Laurentia but similar to middle Cambrian values (Peters, 2004a). Peters (2004a) found that the Furongian witnessed a major breakthrough in evenness. Laurentian upper Furongian communities had evenness values much closer to Ordovician (PIE ~0.7–0.8) than to middle Cambrian (PIE ~0.3–0.5) communities. The difference in evenness between Laurentia and Cordillera Oriental shows that the change in the ecological structure of benthic communities across the Cambrian–Ordovician boundary interval took place earlier in Laurentia than in Gondwana. Such a diachronic change between these two paleocontinents has been also documented using a different set of ecological features, such as the composition of local communities, guild structure, and diversity gradients (Waisfeld et al., 2003; Balseiro et al., 2011). Therefore, we suggest that in Cordillera Oriental evenness values typical of Laurentian shelf environments were reached only later during the late Tremadocian or even the Floian. Such a result is expected if global patterns represent just the addition of processes acting at regional scales (Miller, 1998).

In addition, as biodiversity has an important biogeographic component (Miller, 1997; Waisfeld et al., 2003), differences in evenness can also be explained by differences in the size of species pools at biogeographic scales. Laurentia exhibits a much larger species pool than the Central Andean Basin, due to factors such as area (shelf area of Laurentia was larger than on southwestern Gondwana; Cocks and Torsvik, 2002), style of sedimentation (Balseiro et al., 2011), and paleogeographic position (Fortey and Cocks, 2003). Local richness depends at least in part on regional richness (Ricklefs, 1987), and for similar sample sizes, PIE is related to richness (Olszewski, 2004; Bulinski, 2007). We can hypothesize that higher evenness in Laurentia is also a consequence of higher richness in the paleocontinent that might be coupled to the diachronic ecological change discussed above.

CONCLUSIONS

1. At the local scale, species-abundance distributions (SADs), diversity, richness, and evenness follow a predictable pattern along stratigraphic shallowing-upward gradients. SADs can be described by Zipf–Zipf–Mandelbrot models in samples from the TST, whereas samples from HST depart from these models. Sample diversity, richness, and evenness show an increase from the TST to the HST. These patterns could be interpreted in the light of the intermediate disturbance hypothesis (Connell, 1978).

2. At the regional scale, SADs, diversity, richness, and evenness do not follow a clear trend along a regional bathymetric gradient. In particular, samples from Segment 4 are pauci- to monospecific. Although low oxygen levels are usually interpreted to be the cause for such patterns, different lines of evidence in our study suggest that this might be a more complex case.

3. At a biogeographic scale, patterns in abundance and occupancy of two key taxa (*Parabolina (N.) frequens* and *Asaphellus*) among Cordillera Oriental, Famatina, and Oaxaca, suggest mass effect metacommunity dynamics. For example, *P. (N.) frequens*, which is locally abundant and persistent in siliciclastic environments, can persist even at low abundances in adjacent carbonate environments via constant immigration from its source environment. Such mechanisms can explain the coexistence of these taxa which belong to different Trilobite Evolutionary Faunas, in spite of their distinct environmental preferences.

4. Sample evenness during the latest Cambrian of Cordillera Oriental is much lower than during the late Cambrian of Laurentia, which may

account for the diachronic change in the ecological structure of the communities in these two regions.

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