General Palaeontology, Systematics, and Evolution (Invertebrate Palaeontology)

Tempo and mode in the replacement of trilobite evolutionary faunas from the Cordillera Oriental basin (Northwestern Argentina)

Temps et mode dans le remplacement des faunes évolutives de trilobites du bassin oriental de la Cordillère (Nord-Ouest de l'Argentine)

Facundo R. Meroi Arcerito [a],[*], Karen Halpern [b], Diego Balseiro [c], Beatriz Waisfeld [c]

[a] Grupo de Entomología Edáfica Bonaerense Suboriental (GENEBSO), Universidad Nacional de Mar del Plata (UNMdP), Instituto de Investigaciones en Biodiversidad y Biotecnología (INBIOTEC), CONICET, 7600 Mar del Plata, Argentina
[b] Instituto de Geología de Costas y del Cuaternario (UNMDP-CIC), CONICET, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Dean Funes 3250, B7602AYJ Mar del Plata, Argentina
[c] Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), CONICET, Universidad Nacional de Córdoba, 5000 Córdoba, Argentina

A R T I C L E   I N F O

A B S T R A C T

Major ecological transitions among evolutionary faunas are matters of continual debate. Our study analyses the timing and mode of replacement of Ibex I and II Trilobite Evolutionary Faunas (TEF) in Lower Ordovician successions of northwestern Argentina, with special emphasis on olenids and asaphids as key groups of the Ibex I and Ibex II faunas, respectively. We explore richness by using the sample rarefaction method, and occupancy based on a presence–absence dataset. The late Tremadocian 2 (Tr2) represents an inflexion point in richness and occupancy trajectories of asaphids and olenids. While olenids diminish their generic richness through time, asaphids became the richest family since the Tr3 predating the global trend recognized for the expansion of the Ibex II Fauna. Asaphids gained diversity at the expense of other trilobites as well, their rise in diversity lags behind the increase in occupancy suggesting a displacement scenario as the probable mode of replacement between the Ibex I and II TEFs. Apparently, the processes of replacement variate among regions across the globe, configuring a complex global mosaic of regional patterns.

© 2017 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Les transitions écologiques majeures au sein des faunes évolutives font l'objet d'un débat continu. Le présent travail analyse le rythme et le mode de remplacement des faunes évolutives de trilobites (TEF) Ibex I et II au cours des successions de l'Ordovicien basal dans le Nord-Ouest de l'Argentine. Les olénidés et les asaphidés y sont particulièrement étudiés, car ils correspondent, respectivement, aux groupes principaux des faunes Ibex I et II. La richesse faunistique est caractérisée en utilisant la méthode de raréfaction des échantillons et leur répartition grâce à une base de données présence/absence. Le Trémadocien terminal (Tr2) représente une inflexion dans la diversité et la distribution des asaphidés et olénidés. Alors

* Corresponding author.
E-mail address: facundomeroi@hotmail.com (F.R. Meroi Arcerito).

que le nombre de genres des olénidés diminue au cours du temps, les asaphidés deviennent la famille la plus diversifiée à partir du Tr3, ce qui précède la tendance globale reconnue pour l'expansion de la faune Ibex II. Les asaphidés gagnent en diversité, contrairement aux autres trilobites ; de plus, ils voient leur diversification ralentie après la colonisation de nouvelles zones géographiques, ce qui suggère un déplacement comme mode probable de remplacement des faunes Ibex I et II. Apparemment, ces processus de remplacement varient suivant les régions, ce qui correspond à une mosaïque globale et complexe de patrons régionaux.

1. Introduction

The study of trilobites and their evolutionary history has a great impact on the understanding of the Paleozoic evolution of life (Sepkoski, 1981). In particular, during the Early Paleozoic, trilobites constitute the main marine fossil group and, therefore, they become the most important biological model to study paleocommunities for that time (Finnegan and Droser, 2008).

Following the concept of Great Evolutionary Faunas (Sepkoski, 1981), Adrain et al. (1998) introduced the concept of Trilobite Evolutionary Fauna (TEF) representing a group of different non-related families, which share a similar pattern of global diversity trajectory. Later, Adrain et al. (2004: fig. 24.1) characterized three different Early Ordovician evolutionary faunas, namely, Ibex I, Ibex II, and Whiterock, which had contrasting diversity trajectories. Considerable attention has been devoted to the study of the diversity, geographic and environmental distribution of the Whiterock Fauna, in part because of its implication for the understanding the post-Ordovician history of the group (Adrain and Westrop, 2005; Adrain et al., 2004; McCormick and Owen, 2001; Westrop and Adrain, 1998; Zhou et al., 2007; among others). However, little attention has been paid to the study of Ibexian faunas and to the possible pathways of replacement among either of these faunas.

According to the global analysis performed by Adrain et al. (2004), the two distinct Ibexian clusters show different diversity trajectories during the Early Ordovician. One group, the Ibex Fauna I, had high early Tremadocian diversity but steadily declined afterward, being Olenidae and Ceratopygidae typical of this fauna. A second group, the Ibex Fauna II, had very low early Tremadocian diversity, radiating rapidly during the late Tremadocian and reaching a peak during the early–late Floian, and then declined after the Darriwillian. The Asaphidae and Bathyuridae are typical families of this fauna (Adrain et al., 2004).

The processes underlying large-scale changes in marine ecosystems is a matter of continuous debate. After the pioneer work of Sepkoski (1981) and Sepkoski and Miller (1985) intense efforts have been made to understand the mode of replacement among evolutionary faunas. Two main pathways have been considered, named dilution or displacement (Westrop et al., 1995). Briefly, while displacement supposes that replacement was driven by interactions at geological time scales, dilution supposes a non-interaction scenario where the replacement is an illusion caused by the diversification of a group of taxa rather than an actual replacement. For instance, Westrop et al. (1995) assessed the replacement among trilobite-dominated communities (Cambrian Evolutionary Fauna) by brachiopod dominated communities (Paleozoic Evolutionary Fauna) during the Middle Ordovician in Laurentia. The authors found that trilobite diversity remained stable through the Ordovician, while other clades become more diverse and abundant and argued that the dilution process fits better the observed pattern (see also Adrain et al., 2000; Amati and Westrop, 2006; Westrop and Adrain, 1998).

For its rich and continuous fauna, Late Cambrian–Early Ordovician sedimentary deposits of the Cordillera Oriental basin became a natural laboratory for studying paleoecological patterns in South America (Balseiro, 2011; Balseiro and Waisfeld, 2014; Balseiro et al., 2011a, b; Waisfeld and Balseiro, 2016) and a key setting to provide new insights into West Gondwanan Ordovician ecosystems. Largely shallow-marine, siliciclastic successions are encompassed in the Santa Victoria Group, which includes the Santa Rosita (Furongian–Tremadocian) and Acoite (Floian) formations widely exposed in the Cordillera Oriental. The depositional history, paleogeography, biostratigraphic context and paleontological information of these units have been widely addressed by different authors (e.g., Albanesi et al., 2008; Astini, 2003; Astini et al., 2004; Benedetto, 2003; Benedetto et al., 2009; Buatois et al., 2006; Mángano and Buatois, 2011; Toro et al., 2015, among others). Besides, a wide array of paleoecological aspects of the trilobite assemblages from the Santa Victoria Group have been explored in successive contributions by Balseiro and Waisfeld (2013, 2014), Balseiro et al. (2011a, b), Waisfeld and Balseiro (2016). Among other aspects, they addressed new insights into the processes involved in the assembly of trilobite communities, biotic gradients structures, mechanisms linked to the stability and turnover rates, temporal trends in community structures at different scales, etc., and Meroi Arcerito et al. (2015) show changes in environmental distribution and relative abundance of asaphids for the earlier Tr2, pointing out the starting point of radiation of the Ibex II Fauna in local communities.

Our study analyzes the timing and mode of replacement of the Ibex I by the Ibex II TEF in Lower Ordovician successions of northwestern Argentina. We evaluate this faunal transition from an unexplored perspective, assessing regional trends in diversity and occupancy through time. We focused on the trajectories exhibited by olenids and asaphids as key groups of the Ibex I and Ibex II faunas, respectively.
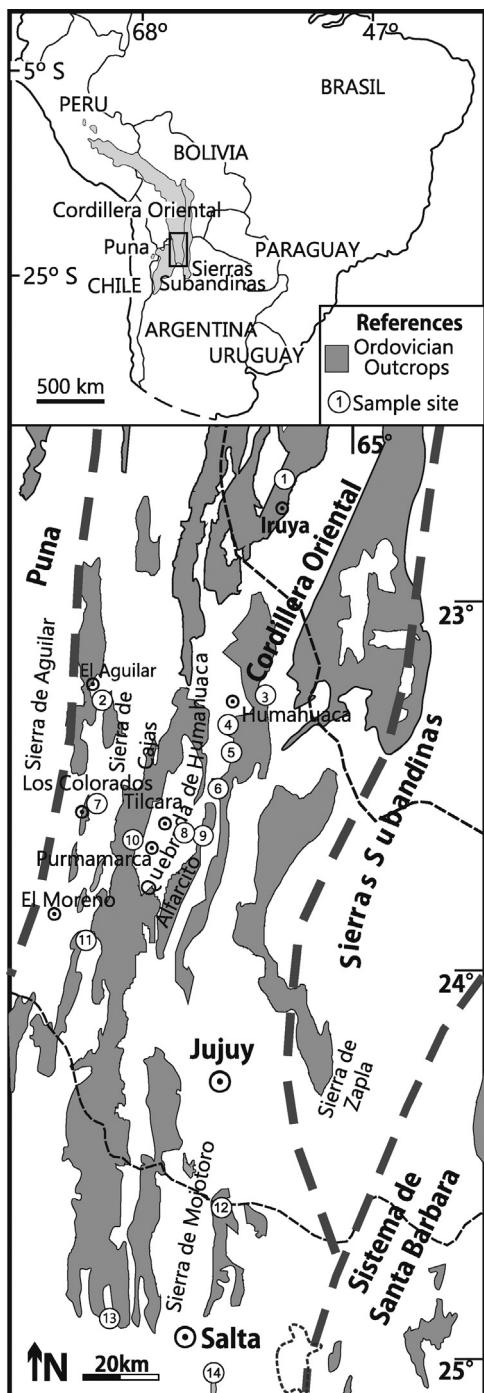
Fig. 1. Central Andean Basin, studied areas in the Argentinian Cordillera Oriental. 1: Santa Victoria Oeste (from late Tr2 to Fl2–3, see Toro et al., 2015). 2: Quebrada Amarilla (Tr1). 3: Quebrada de Humacha, Huacalera Area (early-late Tr2). 4. Quebrada de Moya (Tr1-early Tr2). 5: Quebrada del Arenal, Angosto del Ferrocarril, Angosto de Chucalezna. 6: Quebrada del Arenal (from Tr1 to early Tr2). 7: Quebrada Chamarra, Los Colorados Area (Fl2–3). 8: Quebrada del Salto (Tr1). 9: Quebrada Ruspasca, Alfarcito area (late Tr2), 10: Quebrada Coquena-Quebrada Chalala, Purmamarca Area (late Tr2). 11: Angosto del Moreno (Tr1). 12: Sierra de Mojotoro (late Tr2). 13: Pascha-Incamayo (Tr3). 14: Cerro San Bernardo (Tr3). Modified from Astini (2003).

Fig. 1. Bassin andin central, zones étudiées dans la Cordillère argentine orientale. 1 : Santa Victoria Oeste (du Tr2 terminal au Fl2–3, voir Toro et al., 2015). 2 : Quebrada Amarilla (Tr1). 3 : Quebrada de Humacha, zone de Huacalera (Tr2 basal-terminal). 4 : Quebrada de Moya (Tr1–Tr2 basal). 5 : Quebrada del Arenal, Angosto del Ferrocarril, Angosto de Chucalezna. 6 : Quebrada del Arenal (du Tr1 au Tr2 Basal). 7 : Quebrada Chamarra, Los Colorados Area (Fl2–3). 8 : Quebrada del Salto (Tr1). 9 : Quebrada Ruspasca, Alfarcito area (Tr2 terminal), 10 : Quebrada Coquena–Quebrada Chalala, zone de Purmamarca (Tr2 terminal). 11 : Angosto del Moreno (Tr1). 12 : Sierra de Mojotoro (Tr2 terminal). 13 : Pascha-Incamayo (Tr3). 14 : Cerro San Bernardo (Tr3). Modifié à partir d'Astini (2003).

2. Materials and methods

2.1. Data

Our dataset includes 193 fossil samples from the Lower Ordovician of the Cordillera Oriental, Argentina (Fig. 1). Part of the data set has been already analyzed by Balseiro and Waisfeld (2014), Balseiro et al. (2011a, b), Meroi Arcerito et al. (2015), Waisfeld and Balseiro (2016), while the rest are unpublished data (Meroi Arcerito, 2016). All samples are housed at the "Centro de Investigaciones en Ciencias de la Tierra" (CICTERRA, CONICET, UNC). All trilobite sclerites were identified in each sample at least to genus, according to the fossils' preservation, summing a total of 798 occurrences. It is important to remark that the taxonomy of asaphids has been recently revised (Meroi Arcerito, 2016; Meroi Arcerito et al., 2015), while the taxonomic resolution of other families is variable (e.g., Harrington and Leanza, 1957; Waisfeld and Vaccari, 2003), which would avoid a taxonomic bias in diversity estimation.

We considered six successive temporal bins for the Early Ordovician (Bergström et al., 2009): Tremadocian 1 (Tr1), early and late Tremadocian 2 (early Tr2 and late Tr2), Tremadocian 3 (Tr3), Floian 1 (Fl1) and Floian 2–3 (Fl2–Fl3) regionally recognized on the basis of graptolite, trilobite, and conodont biostratigraphy (Fig. 2). Time bins are here constrained upon the schemes proposed by Vaccari et al. (2010 and references therein) for the early Tremadocian and by Toro et al. (2015 and references therein) for the late Tremadocian–Floian.

The samples of the lower Tremadocian (Tr1) stratigraphic units correspond to the *Jujuyaspis keideli*, *Kainella andina* and *Kainella meridionalis* biozones, and the lowermost part of the *Kainella teiichii* biozone. We subdivided the Tremadocian 2 (Tr2) in two time intervals: early Tr2 consists of samples coming from the *Bienvillia tetragonalis* biozone and the *Asaphellus–Leptoplastides* association, and late Tr2 with samples coming from the *Notopeltis orthometopa* biozone (see Toro et al., 2015 for graptolite and conodont calibrations). The late
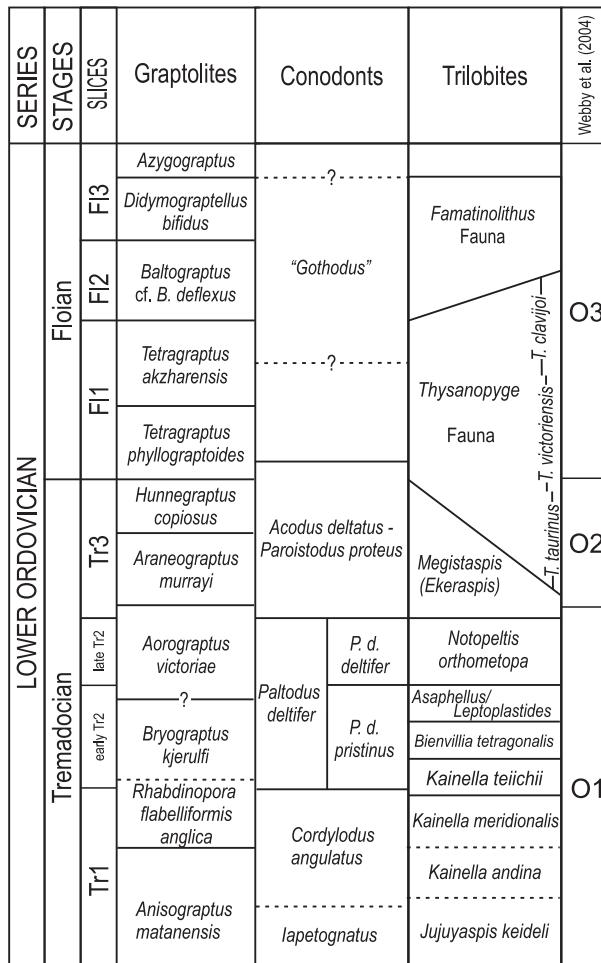
Fig. 2. Correlation chart between Ordovician stage slices and local biostratigraphy showing the studied time intervals. In accordance with Bergström et al. (2009). Modified from Vaccari et al. (2010) and Toro et al. (2015). Time slices after Webby et al., 2004.
Fig. 2. Table de corrélations entre les étages de l'Ordovicien et la biostratigraphie locale des intervalles de temps étudiés. Conforme aux travaux de Bergström et al. (2009). Modifié d'après Vaccari et al. (2010) et Toro et al. (2015). Tranches de temps selon Webby et al., 2004.

Tremadocian (Tr3) is represented by a few sparse samples coming either from the uppermost part of *Araneograptus victoriae* or the *Hunnegraptus copiosus* biozones. Unfortunately, Floian 1 was excluded because it has scarce samples to run the analysis. The Floian 2–3 interval corresponds to the uppermost Floian 2 (upper part of the *Baltograptus* cf. *deflexus* biozone) and the lowermost Floian 3 (lower part of the *Dydimograptus bifidus* biozone).

The data set comes from 15 different localities that are representative of the Lower Ordovician outcrops of the Argentine Cordillera Oriental (Fig. 1). However, the geographic coverage of individual bins varies. The samples from the Tr1 interval are the most geographically widespread (see Fig. 1). The samples from the Tr2 largely come from eastern outcrops of the Cordillera Oriental whereas no stratigraphic record of this interval is preserved to the west due to a regional unconformity (Tumbaya break, Astini, 2003 and references therein). As well, the samples from the Tr3 are scarce because the successions comprising this time bin are poorly fossiliferous or partially complete due to local faulting. In contrast, the records of Floian 1 deposits are relatively complete and widespread in the basin; however, they are weakly fossiliferous or even devoid of benthic fauna. Finally, samples from the Fl2–3 are concentrated in two areas, one in the west and the other in the North of the Cordillera Oriental.

3. Methods

In this contribution, we use one family as a proxy of each TEF, because this allows comparing the biological interaction between two monophyletic clades; on this scenario, the process of displacement can be evaluated on the fossil record more easily than if considering unrelated taxa. Olenids, asaphids and trinucleids were considered representative of Ibex I, Ibex II and Whiterock faunas for they are the best recorded families in the Cordillera Oriental basin.

To standardize the differential sampling effort of each temporal bin, we decided to use sample-based rarefaction to estimate diversity through generic richness (S) (Fig. 3). Sample-based rarefaction is a widely used method in the literature; it is used for estimating richness from a set of samples that are representative of an assemblage (Colwell et al., 2004; Hammer and Harper, 2006). We built sample rarefaction curves by temporal bin using Past 2.17 (Hammer and Harper, 2006), which estimates the diversity value and its standard deviation based on the analytical solution (for further explanation of the method, see Chiarucci et al., 2008).

To analyze the diversity of different samples sets under the same sampling effort is necessary to compare curves (Gotelli and Colwell, 2001; Sanders, 1968). The set of samples that contains the smallest number (25 samples) is the Tr3, and it determines the value at which we compare the estimated diversity value for all temporal bins. In decreasing order, the rest of the temporal bins Fl2–3, Tr1, late Tr2 and early Tr2 are represented by 47, 44, 32 and 29 samples, respectively (Table 1).

Since occupancy has shown to be a good proxy of abundance in both paleontological and neontological datasets (Holt et al., 2002; Ivany et al., 2009), we built
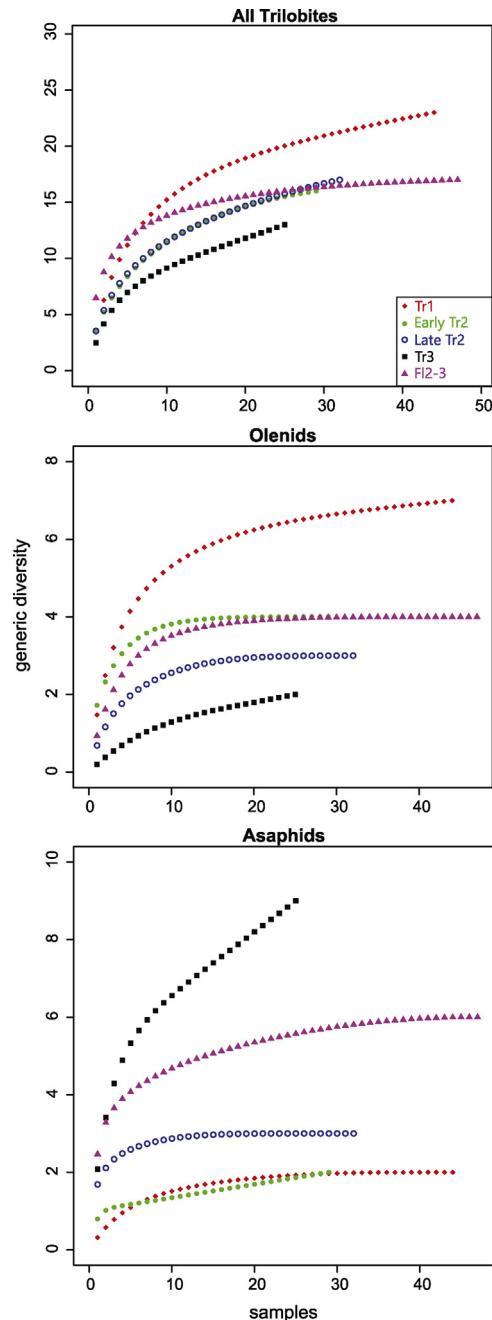
Fig. 3. Rarefaction curves show estimated generic diversity per time bin. A. All trilobites included in this analysis. B. Olenids. C. Asaphids.
Fig. 3. Courbes de raréfaction montrant la diversité générique estimée par intervalle de temps. A. Tous les trilobites inclus dans cette analyse. B. Olénidés. C. Asaphidés.

occupancy rank curves using R (R Core Team, 2017). Generic occupancy by temporal bin can be seen as analogous to rank-abundance or Whitaker plots (Magurran, 2004). In an occupancy rank curve, the number of taxa recorded at each time slice is sorted in descending order, and the proportion of the total number of samples is then plotted against the taxa rank. In this plot, we can identify

Table 1
Summary of the data used in this analysis.
Tableau 1
Résumé des données utilisées dans cette analyse.

Time slice	Samples	Taxa	Occurrences
Tr1	44	23	191
Early Tr2	29	16	102
Late Tr2	32	17	113
Tr3	27	15	67
Fl2–3	47	17	304
Total	193	59	798
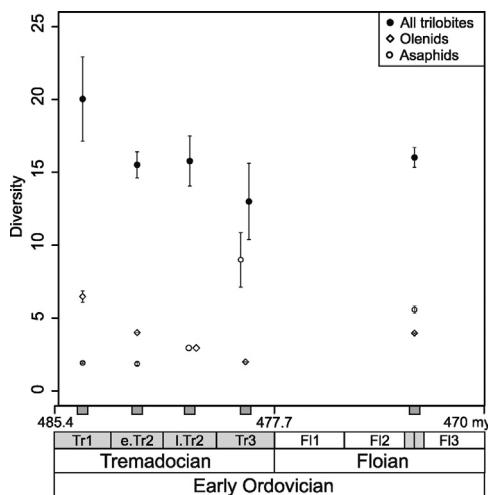
**Fig. 4.** Diversity trends of the TEF from Tr1 to Fl2–3. Note the steady decrease in diversity of olenids (white squares) from Tr1 to Tr3. Instead, the asaphids (white circles) show a peak of diversity during the Tr3. The whiskers represent one standard deviation.
Fig. 4. Tendances de diversité du TEF de Tr1 au Fl2–3. À noter la diminution stable de la diversité des olénidés (carrés blancs) du Tr1 au Tr3. Au contraire, les asaphidés (cercles blancs) présentent un pic de diversité durant le Tr3. Les boîtes représentent l'écart type.

the dominant genera of the families studied at each time bin.

Hence, we can independently analyze diversity and occupancy, and understand whether both parameters change synchronically or not during TEF replacement.

4. Results

4.1. Total diversity per temporal bin

The similarity between the raw data and the estimated sample trends is remarkable, reinforcing the fact that our sampling effort was enough to estimate total diversity (S_T) per temporal bin of 25 samples.

In Fig. 4, represented by black circles, we can see the diversity (S_T) pattern for the time sequence considered. The highest diversity recorded within the time bins was obtained for the Tr1; its S_T value is 20.031. A significant decrease in diversity can be detected by early Tr2, where $S_T = 15.511$. During late Tr2, generic diversity rises slightly and reaches $S_T = 15.772$. Later, in the Tr3, S_T falls to 13 genera. Finally, in the Fl2–3, diversity exhibits an increase ($S_T = 16.015$). In sum, we can observe that S_T remains

approximately stable, reaching its minimum values during the Tr3.

4.2. Olenids diversity per temporal bin

The temporal sequence for the estimated diversity for olenids (S_O) can be seen in Fig. 4 (white diamonds). In the Tr1, we registered the highest diversity value ($S_O = 6.48$). The number of genera in this family decreases drastically in the early Tr2 ($S_O = 4$), and their diversity continues declining by the late Tr2 ($S_O = 2.993$). By the Tr3, there are only two genera left ($S_O = 2$). Nevertheless, they exhibit a recovery during the Fl2–3, when their generic diversity doubles the previous record ($S_O = 3.959$).

Olenid diversity shows a very similar trend to the one observed in S_T described above (Fig. 4). Both S_T and S_O decline from Tr1 to early Tr2. The main difference is that S_O decreases steadily from Tr1 to Tr3 and, finally, an increase is recorded on the Fl2–3.

4.3. Asaphids diversity per temporal bin

Estimating the asaphids' diversity (S_A; see white circles in Fig. 4), we obtained a different pattern with respect to S_T or S_O. The temporal trend shows that S_A increases steadily from Tr1 ($S_A = 1.927$), passing through early Tr2 ($S_A = 1.862$) and late Tr2 ($S_A = 2.999$), reaching the highest diversity peak during Tr3 ($S_A = 9$) and then decreasing by Fl2–3 ($S_A = 5.572$).

The maximum difference observed between S_A and S_T is registered during the early Tr2 (Fig. 4). The lowest S_A value was recorded in the early Tr2 and it slightly increases from the early Tr2 to the late Tr2; then, during Tr3, asaphid diversity triples, reaching its highest proportion (69.3%) of S_T. Finally, in the Fl2–3, S_A is severely affected and reduced by almost one third. On the other hand, S_T shows it highest values on Tr1, and then its value remains relatively stable.

4.4. Occupancy of asaphids, olenids and other families

The occupancy rank plots show that the distribution of genera and families changed considerably throughout the Early Ordovician (see Fig. 5). In the Tr1, olenids (gray circles) dominate the communities with *Parabolinella*, *Leptoplastides* and *Angelina* occupying the 1st, 2nd and 4th places in the rank, respectively with occupancy values of 0.5, 0.4 and 0.32 during the time bin. Asaphids (white circles) are only represented by two genera, *Asaphellus* and *Golasaphus*, located at the 5th and 15th places.

In the early Tr2, although olenids remain as major components of the fauna (*e.g.*, *Leptoplastides*, *Parabolinella* and *Bienvillia*, ranked 1st, 3rd and 4th), they register a loss in diversity, and asaphids show an evident increase in occupancy. In this time bin, *Asaphellus* is the second most recorded genus with an occupancy of 0.76.

During the late Tr2 asaphids show a slight increase in diversity, now recording three genera: *Asaphellus*, *Notopeltis* and *Mekynophrys*. Unlike this, olenids decrease in diversity and also in occupancy: only *Parabolinella*, *Leptoplastides* and *Bienvillia* are left, occupying the 2nd, 8th, and
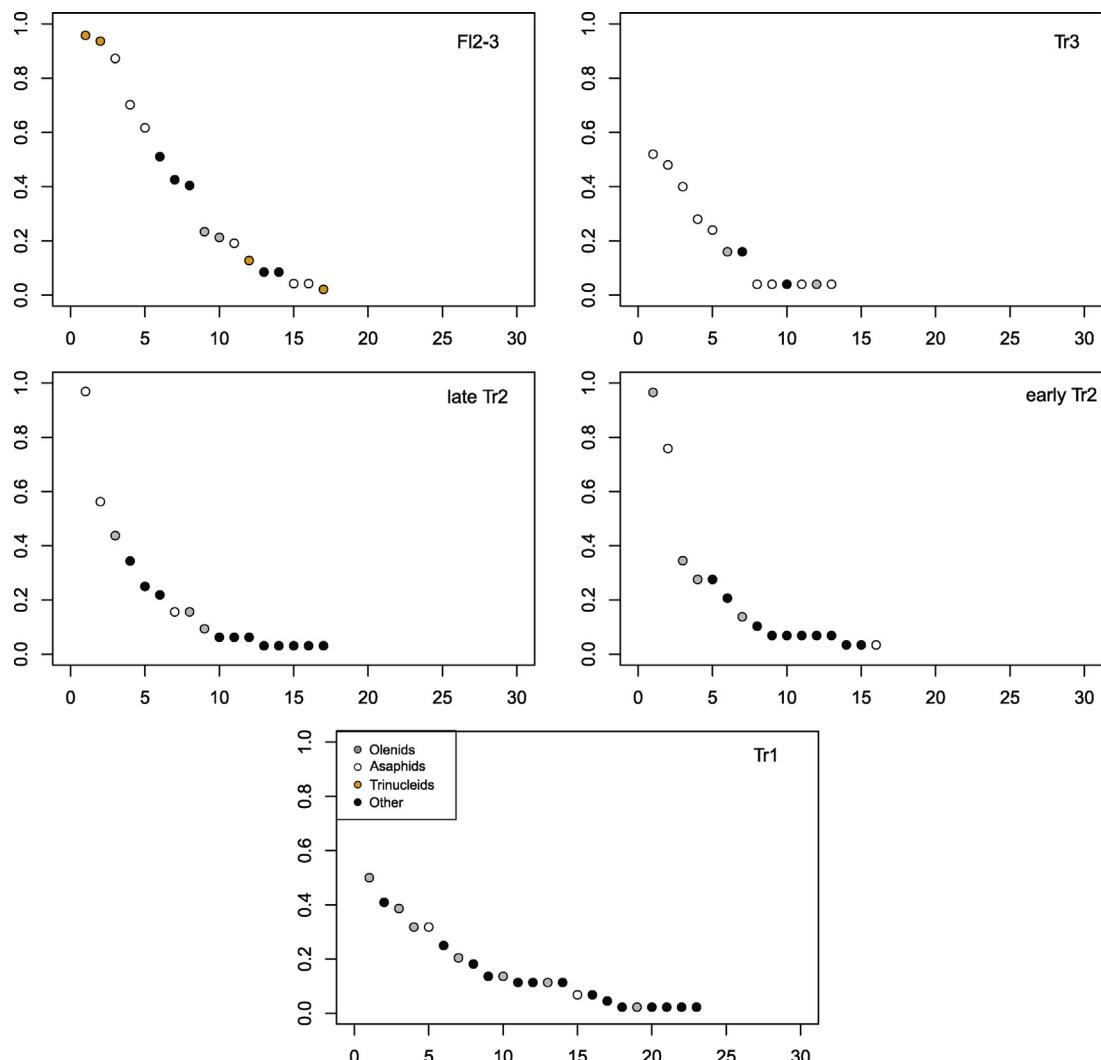
Fig. 5. Occupancy-rank plot showing the variation of the TEF distribution through time. Note the changing distribution of the trilobite families across the occupancy ranking plot: olenids (gray circles) exhibit their dominance during Tr1 and early Tr2; asaphids (white circles), reach their highest occupancy during the late Tr2 and Tr3, whereas trinucleids (orange circles) appear as dominant in the Fl2–3.

Fig. 5. Courbes du taux d'occupation montrant la variation de la distribution TEF au cours du temps. À noter la distribution changeante des familles de trilobites à travers les courbes du taux d'occupation : les olénidés (cercles gris) dominent durant le Tr1 et le Tr2 basal; les asaphidés (cercles blancs) atteignent leur occupation maximale au cours du Tr2 terminal et du Tr3, alors que les trinucléidés (cercles orange) apparaissent également dominants durant le Fl2–3.

9th places in the rank, with occupancy values of 0.56, 0.15 and 0.09, respectively.

By the Tr3, asaphids clearly exhibit the highest scores both in diversity and occupancy. The first five positions in the rank are occupied by *Thysanopyge*, *Kayseraspis*, *Asaphellus*, with values above 0.4, and *Notopeltis*, *Megistaspis (Ekeraspis)* with scores of 0.29 and 0.24 respectively. During this time bin, olenids record the lowest diversity (2) and occupancy values.

In the Fl2–3, trinucleids (orange circles) make appearance with *Famatinolithus* in the first place of the rank. Unfortunately, the lack of data from Fl1 does not allow one to identify when they were initially recorded. During this time bin, asaphids show a decrease in diversity and occupancy, but they are still one of the main constituents of

the Floian fauna. Moreover, olenids have a small increase in diversity and intermediate occupancy distribution, three genera ranked 9th, 10th, and 11th.

5. Discussion

5.1. Timing of faunal transitions

The regional scale analysis of diversity and occupancy of olenids and asaphids show an interesting pattern of turnover. While olenids diminish their generic richness through time, asaphids became the richest family since the Tr3. It is remarkable that both share the same diversity in the late Tr2, however, asaphids occupancy for the first time stepped up over olenids occupancy, rising then persistently

for the rest of the studied interval. Hence, the late Tr2 seems to be an inflexion point in diversity and occupancy trajectories of both groups, highlighting with high precision this turning point of the Ibex II Fauna in the Cordillera Oriental basin.

The early history of asaphids in Cordillera Oriental can be traced back in the Furongian by the occurrences of *Asaphellus*, the first member of the family recorded in the basin. During the Furongian, Balseiro et al. (2011a) found that *Asaphellus* was a quite rare component of the assemblages, occurring in low abundance and also very low occupancy. Interestingly, it was only present in high diversity and even olenid-dominated assemblages were restricted to intermediate environments of the onshore–offshore gradient. Based on the analysis of abundance distributions of trilobite taxa, Meroi Arcerito et al. (2015, fig. 4) observed that although *Asaphellus* was the only asaphid present in the early Tr2, it became abundant or even dominant in local communities. Our regional results, at the same interval, show that only one asaphid (*Asaphellus*) had high levels of occupancy (Fig. 5), whereas the rest of the high occupancies correspond to olenids. During the late Tr2, asaphids occupancy increased significantly, even they became dominant (Fig. 5); however, their diversity remained low (Fig. 4). Olenids are no longer dominant, remaining only one taxon with intermediate occupancy. Remarkably, during the Tr3, both asaphids diversity and occupancy increased drastically. Thus, a temporal decoupling between asaphids diversity and occupancy is recognized. The significant rise in diversity might be a consequence of the increase in occupancy in the Tr3. The diversity of asaphids in the Fl2–3 was markedly lower than in the Tr3 interval, but occupancy remains high. Nonetheless, a trinucleid, representing the Whiterock Fauna, shows the highest value of occupancy.

In sum, local and regional scale analyses portray the successive steps in the paleoecological dynamics of the asaphids and, hence, of the Ibex II Fauna in the basin. In general, a single (or more infrequently two) rarely present asaphid occurred in olenid-dominated communities since the Furongian to the early Tr2 (Fig. 5). However, in the latter interval, it became locally abundant and widespread, attaining high occupancy regionally. It was not until the late Tr2 that asaphids reached the highest occupancy scores, yet diversity remained low. At last, diversity peaked later in the Tr3 accounting for a diachronic diversity-occupancy relationship in the expansion of the Ibex II Fauna.

It is worth noting that previous paleoecological studies analyzed the timing of ecological shifts in the Cordillera Oriental (*e.g.*, Balseiro and Waisfeld, 2013; Mángano and Buatois, 2011; Waisfeld and Balseiro, 2016) and correlated them either with those derived from global analyses or issued mainly from Laurentian North America, where intensive studies resulted in comparable data (*e.g.*, Adrain et al., 2000; Finnegan and Droser, 2005; Peters, 2004, 2006; Westrop and Adrain, 1998, among others). For example, Balseiro and Waisfeld (2013) examined local richness and evenness in trilobite assemblages from the Cordillera Oriental and demonstrated that the rise in these parameters in the early-late Tremadocian (Tr2) lagged behind similar changes in the Late Cambrian of Laurentia (see Peters,

2004, 2006). As well, Waisfeld and Balseiro (2016) found that equitable assemblages developed since the Tr2 at the local scale and since the early Floian at the regional scale, whereas highly dominated and regionally equitable trilobite communities can be traced far back to the Middle Cambrian in Laurentia. In a similar vein, Mángano and Buatois (2011) argued that the occupation of the mid-tier infaunal ecospace took place in the Tr2 in the Cordillera Oriental and, hence, was delayed when compared with Laurentia or Baltica where the exploitation of the same tier began in the Early Cambrian. Despite same differences, these examples highlight the existence of diachronic ecological changes in the Cordillera Oriental occurring after those documented in Laurentia or globally.

Interestingly, unlike previous examples, the expansion of the Ibex II Fauna in the Cordillera Oriental predates the global signal. The reasons underlying this pattern are unclear. Paleogeographic constraints and the early phylogenetic history of the asaphids in the basin might have been influential in the observed pattern. The early phylogenetic history of asaphids should be traced far back in the Cambrian and it is far from being resolved. Besides, there are also limited studies in settings with paleolatitudes and sedimentary regimes, similar to those of the Cordillera Oriental, precluding to confirm how widespread is the pattern recognized herein.

Another interesting aspect of the analyzed transition is that the expansion of the Ibex II Fauna (late Tr2–Tr3) takes place after the remarkable change in the ecological structure (early Tr2) recognized by Balseiro and Waisfeld (2013) and Waisfeld and Balseiro (2016). These authors emphasized a shift toward more local and regional equitable communities that took place in the context of olenid-dominated communities. This change is coincident with the initial rise in abundance of *Asaphellus* in local communities as well as with its high regional dominance, accounting for the onset of the Ibex II Fauna in the basin. Therefore, it seems plausible that both patterns are somehow causally related. Further research will probably shed some light on the actual cause and consequence relationship of these coincident patterns.

Finally, the radiation of the Ibex II Fauna in the Cordillera Oriental does not match the global trend identified by Adrain et al. (2004). These authors indicated that the Ibex II Fauna radiated during their O2 interval (= late Tremadocian s.l.) and peaked in diversity during the O3 (=Floian 2–3). Even though the resolution of Adrain et al. (2004) global data is coarser than that derived from our regional analysis, a distinct diversity peak in the late Tremadocian (Tr3) is recognized, predating that reported by those authors. Thus, a decoupling in the development of the Ibex II Fauna results evident.

On the other hand, Adrian et al. (2004, fig. 24.12B) and Zhou et al. (2007, fig. 3) reported that in South China (Yangtze Block) the Ibex II Fauna (mainly represented by asaphids and nileids) began its radiation in the late Tremadocian (time slice 1d of these authors) reaching a distinct diversity peak during the middle Floian (time slice 2b). So, expansion of the Ibex II Fauna in South China is broadly coincident with the global signal, but took place later than in the Cordillera Oriental. This diachronism may suggest

that the radiation of the TEF Ibex II was heterogeneous in time and space, resembling the patterns recognized worldwide for the Whiterock TEF (*e.g.*, Adrain et al., 2004).

5.2. Faunal replacement

Little has yet been said about transitions between TEFs (Adrain et al., 2004; Zhou et al., 2007), although much has been discussed regarding great evolutionary faunas (Finnegan and Droser, 2005, 2008; Miller, 1998; Westrop et al., 1995). Our results could, however, shed some light on some aspects of the dynamics of TEF replacement at the regional scale.

Understanding the dynamics of faunal transitions is a challenge, mainly because underlying processes are very complex and multiple alternatives have been invoked (Alroy, 2004; Benton, 1987; Finnegan and Droser, 2005, 2008; Miller, 1998; Sepkoski, 1975, 1996; Westrop et al., 1995). In a simplified scenario, two models of replacement could be possible for transitions among evolutionary faunas or clades, namely dilution and displacement (Miller, 1998; Westrop et al., 1995). On the one hand, displacement involves biotic interactions over geologic time, with one clade actually displacing a previous one (Miller, 1998; Sepkoski, 1996; Westrop et al., 1995). Therefore, the rise in diversity of the diversifying clade goes hand in hand with the decrease in diversity of the displaced clade, resulting in the classic double-wedge pattern (Benton, 1987; Sepkoski, 1996). However, the double-wedge pattern is not the most probable result in a displacement scenario, where more complicated patterns should be more frequent in a realistically variable world (Sepkoski, 1996). On the other hand, the dilution process occurs when a clade holds a constant diversity, nevertheless its relative contribution diminishes, this happens as a consequence of the diversification of a new clade but not due to interaction between them (Westrop et al., 1995). While displacement can be easily ruled out for clades that occupy contrasting portions of the ecospace (Westrop et al., 1995), it becomes a plausible scenario when clades have similar life habits (Sepkoski, 1996). The latter is the case for the replacement between olenid-dominated (Ibex I) and asaphid-dominated (Ibex II) faunas of the Cordillera Oriental, as both occupied a similar portion of the ecospace, inhabited a similar variety of environments, and probably possessing similar feeding strategies. Olenids and asaphids occur along most of the bathymetric gradient, from lower shoreface to offshore, and shelf settings, and thrived either in well-oxygenated or oxygen-poor environments (Balseiro et al., 2011a, b; Waisfeld and Vaccari, 2008; Waisfeld et al., 2006). Feeding habits are difficult to assess among trilobites. However, based on different lines of evidence detritus feeding is currently considered as a primary strategy for olenids (Fortey and Owens, 1999). On the other hand, a similar feeding habit might be assumed for early asaphids with conservative hypostomes (e.g., early isotelinids, ogygiocaridiines) upon evidence provided by exceptional preservation of soft parts (Gutiérrez-Marco et al., 2017) and trilobite–trace fossil associations (Mángano and Waisfeld, 2004).

In the Cordillera Oriental, while asaphids underwent significant changes in diversity towards the latest Tremadocian (Tr3), regional diversity showed a stable trend through most of the Tremadocian to the Floian. Although this pattern is not a perfect double-wedge (Benton, 1997), it falls within the expected outcomes of competitive displacements (Sepkoski, 1996). These results suggest that asaphids gained diversity at the expense of other trilobites, what is expected in a displacement scenario. Moreover, the constant decline in diversity of olenids through the Tremadocian reaches a minimum during the Tr3, reinforcing the idea of displacement.

In a displacement scenario, occupancies of the displacing clade should increase before its diversity. This would happen because interactions should drive a rise in regional abundance of the displacing clade, until it becomes the dominant taxon, even before its diversity rises. However, if dilution was the main underlying dynamics, occupancies should increase only after, or together with, a rise in diversity. This is because regional abundance should increase hand in hand with the diversification of the clade as a diffusion process (Westrop et al., 1995). In the Cordillera Oriental, asaphids show a sharp increase in occupancy during the early Tr2, definitively reaching regional dominance during the late Tr2, but before their maximum diversity during the Tr3. Mirroring this rise in asaphids occupancy, olenids show a trend of decline in occupancy during the early Tr2–late Tr2. All in all, our results suggest, once again, a replacement driven mainly by displacement.

Moreover, integrating previously published local-scale relative abundance patterns during the Tremadocian of the Cordillera Oriental (Meroi Arcerito et al., 2015) reinforces the idea of the displacement scenario. At local scale, displacement should cause an increase in the relative abundance of the displacing taxon before the rise in regional occupancy. This is because regional occupancy could be delayed due to dispersal limitation or environmental preferences. Meroi Arcerito et al. (2015) showed that in the Cordillera Oriental, asaphids became the dominant taxon of local communities during the early Tr2, that is, before reaching regional dominance during the late Tr2 (Fig. 5).

Taking all three patterns into consideration, displacement stands as the most probable scenario for the regional replacement of the Ibex I Fauna by the Ibex II Fauna during the Tremadocian. Two things, however, need to be mentioned. First, the evidence for displacement blurs towards the Fl2–3 with the sudden appearance of Whiterockian taxa as dominant members coupled with a slight rise in olenid diversity and a clear drop in asaphid diversity (Fig. 4). Unfortunately, the lack of abundant data for the Fl 1 hinders the possibility of understanding the processes involved, but it could be possible that the dynamics driving the replacement between Ibex faunas changed with the rise of the Whiterock Fauna. Second, our analysis is restricted to the Cordillera Oriental, and therefore it is not easily to extrapolate them to other regions, even less globally. Indeed, it could be very possible that, in a fashion similar to the timing of the Ibex II fauna radiation, the processes involved in the replacement of the different faunas differ among regions across the globe, configuring a complex global mosaic of regional patterns similar to that observed

during the Ordovician Radiation (Miller, 2012; Miller and Mao, 1995; Waisfeld et al., 2003).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2017.09.001.

References

Adrain, J., Westrop, S.R., 2005. Evenness and diversity of lower Paleozoic trilobite faunas of Laurentian North America, 461. Geological Society of America.

Adrain, J.M., Fortey, R.A., Westrop, S.R., 1998. Post-Cambrian trilobite diversity and evolutionary faunas. Science 280, 1922–1925.

Adrain, J.M., Westrop, S.R., Chatterton, B.D.E., Ramsköld, L., 2000. Silurian trilobite alpha diversity and the end-Ordovician mass extinction. Paleobiology 26, 625–646.

Adrain, J.M., Edgecombe, G.D., Fortey, R.A., Hammer, O., 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. Columbia University Press, New York, pp. 231–254.

Albanesi, G.L., Ortega, G., Zeballo, F.J., 2008. Faunas de conodontes y grapttolitos del Paleozoico Inferior en la Cordillera Oriental Argentina , XVII Congreso Geológico Argentino. Geología y Recursos Naturales de la provincia de Jujuy. Relatorio, pp. 98–118.

Alroy, J., 2004. Are Sepkoski's evolutionary faunas dynamically coherent? Evol. Ecol. Res. 6 (1), 1–32.

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, Secretaria de Ciencia y Tecnología. Universidad Nacional de Córdoba, Córdoba, pp. 1–74.

Astini, R.A., Waisfeld, B.G., Toro, B.A., Benedetto, J.L., 2004. El Paleozoico inferior y medio de la región de Los Colorados, borde occidental de la Cordillera Oriental (Provincia de Jujuy). Rev. Asoc. Geol. Argent. 59, 243–260.

Balseiro, D., 2011. Biofacies de trilobites en sucesiones cambro-ordovícicas de la Cordillera Oriental argentina. Distribución, paleoecología y eventos bióticos. Tesis Doctoral, FCEFyN, Universidad Nacional de Córdoba, 209 p.

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

Balseiro, D., Waisfeld, B.G., Vaccari, N.E., 2011b. Paleoecological dynamics of Furongian (late Cambrian) Trilobite-dominated communities from northwestern Argentina. Palaios 26, 484–499.

Balseiro, D., Waisfeld, B.G., 2013. Ecological instability in Upper Cambrian–Lower Ordovician trilobite communities from Northwestern Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 370, 64–76.

Balseiro, D., Waisfeld, B.G., 2014. Evenness and diversity in Upper Cambrian–Lower Ordovician trilobite communities from the Central Andean Basin (Cordillera Oriental, Argentina). Palaeontology 57 (3), 531–546.

Benedetto, J.L., 2003. Ordovician fossils of Argentina. Secretaria de Ciencia y Tecnologia. Universidad Nacional de Cordoba, Cordoba, Argentina, 561 p.

Benedetto, J.L., Vaccari, N.E., Waisfeld, B.G., Sanchez, T.M., Foglia, R.D., 2009. Cambrian and Ordovician biogeography of the South American margin of Gondwana and accreted terranes. Geol. Soc. Lond. Spec. Publ. 325, 201–232.

Benton, M.J., 1987. Progress and competition in macroevolution. Biol. Rev. 62, 305–338.

Benton, M.J., 1997. Models for the diversification of life. Trends Ecol. Evol. 12 (12), 490–495.

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 δ^3C chemostratigraphy. Lethaia 42, 97–107.

Buatois, L.A., Zeballo, F.J., Albanesi, G.L., Ortega, G.C., Vaccari, N.E., Mángano, M.G., 2006. Depositional Environments 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 stratigraphic framework. Lat. Am. J. Sedimentol. Basin Anal. 13, 1–29.

Chiarucci, A., Bacaro, G., Rocchini, D., 2008. Quantifying plant species diversity in a Natura 2000 network: old ideas and new proposals. Biol. Conserv. 141 (10), 2608–2618.

Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85 (10), 2717–2727.

Finnegan, S., Droser, M.L., 2005. Relative and absolute abundance of trilobites and rhynchonelliform brachiopods across the Lower/Middle Ordovician boundary, eastern Basin and Range. Paleobiology 31, 480–502.

Finnegan, S., Droser, M.L., 2008. Body size, energetics, and the Ordovician restructuring of marine ecosystems. Paleobiology 34 (3), 342–359.

Fortey, R.A., Owens, R.M., 1999. Feeding habits in trilobites. Palaeontology 42 (3), 429–465.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4 (4), 379–391.

Gutiérrez-Marco, J.C., García-Bellido, D.C., Rábano, I., Sá, A.A., 2017. Digestive and appendicular soft-parts, with behavioural implications, in a large Ordovician trilobite from the Fezouata Lagerstätte, Morocco. Nature Sci. Rep. 7.

Hammer, Ø., Harper, D.A.T., 2006. Paleontological Data Analysis. Blackwell Publishing, Malden, MA, USA, http://dx.doi.org/10.1002/9780470750711.fmatter.

Harrington, H.J., Leanza, A.F., 1957. Ordovician trilobites of Argentina. Kansas University, pp. 1–259.

Holt, A.R., Gaston, K.J., He, F., 2002. Occupancy-abundance relationships and spatial distribution: a review. Basic Appl. Ecol. 3, 1–13.

Ivany, L.C., Brett, C.E., Wall, H.L.B., Wall, P.D., Handley, J.C., 2009. Relative taxonomic and ecologic stability in Devonian marine faunas of New York State: a test of coordinated stasis. Paleobiology 35, 499–524.

Magurran, A.E., 2004. An index of diversity. Measuring biological diversity. Blackwell publishing, pp. 100–133.

Mángano, M.G., Buatois, L.A., 2011. Timing of infaunalization in shallow-marine Early Paleozoic communities in Gondwanan settings: discriminating evolutionary and paleogeographic controls. Palaeontol. Electron. 14 (9A), 1–21.

Mángano, M.G., Waisfeld, B., 2004. Looking for the usual suspects: Trilobites as Cruziana-Rusophycus producers in Lower Paleozoic sandstones of northwest Argentina , Abstracts First International Congress on Ichnology (Ichnia 2004), Trelew (Argentina), pp. 50–51.

McCormick, T., Owen, A.W., 2001. Assessing trilobite biodiversity change in the Ordovician of the British Isles. Geol. J. 36 (3–4), 279–290.

Meroi Arcerito, F.R., 2016. Trilobites asáfidos del Ordovícico Temprano de la Cordillera Oriental Argentina. Sistemática, distribución y diversificación. Universidad Nacional de Cordoba, unpublished thesis, p. 324.

Meroi Arcerito, F.R., Waisfeld, B.G., Balseiro, D., 2015. Diversification of Asaphellus Callaway 1877 (Asaphidae: Trilobita) during the Tremadocian in south West Gondwana (Cordillera Oriental, Argentina). Geodiversitas 37, 131–150.

Miller, A.I., 1998. Biotic transitions in global marine diversity. Science 281, 1157–1160.

Miller, A.I., 2012. The Ordovician radiation: Macroevolutionary crossroads of the Phanerozoic. In: Earth and Life. Springer Netherlands, pp. 381–394.

Miller, A.I., Mao, S., 1995. Association of orogenic activity with the Ordovician radiation of marine life. Geology 23 (4), 305–308.

Peters, S.E., 2004. Relative abundance of Sepkoski's evolutionary faunas in Cambrian-Ordovician deep subtidal environments in North America. Paleobiology 30, 543–560.

Peters, S.E., 2006. Genus richness in Cambrian-Ordovician benthic marine communities in North America. Palaios 21 (6), 580–587.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.

Sanders, H.L., 1968. Marine benthic diversity: a comparative study. Am. Nat. 102, 243–282.

Sepkoski Jr., J.J., 1975. Stratigraphic biases in the analysis of taxonomic survivorship. Paleobiology 1, 343–355.

Sepkoski Jr., J.J., 1981. A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7, 36–53.

Sepkoski, J.J., Miller, A.I., 1985. Evolutionary faunas and the distribution of Paleozoic marine communities in space and time. In: Valentine, J.W. (Ed.), Phanerozoic Diversity Patterns. Princeton Univ. Press, Princeton, pp. 153–190.

Sepkoski Jr., J.J., 1996. Competition in macroevolution: the double wedge revisited. In: Jablonski, D., Erwin, D.H., Lipps, J.H. (Eds.), Evolutionary paleobiology. The University of Chicago Press, Chicago, pp. 211–255.

Toro, B.A., Meroi Arcerito, F.R., Muñoz, D.F., Waisfeld, B.G., de la Puente, S., 2015. Graptolite-trilobite biostratigraphy in the Santa Victoria area, northwestern Argentina. A key for regional and worldwide correlation of the Lower Ordovician (Tremadocian–Floian). Ameghiniana 52, 535–557.

Vaccari, N.E., Waisfeld, B.G., Marengo, L.F., Smith, L., 2010. *Kainella* Walcott, 1925 (Trilobita, Ordovícico Temprano) en el noroeste de Argentina y sur de Bolivia. Importancia bioestratigráfica. Ameghiniana 47, 293–305.

Waisfeld, B.G., Balseiro, D., 2016. Decoupling of local and regional dominance in trilobite assemblages from northwestern Argentina: new insights into Cambro-Ordovician ecological changes. Lethaia 49 (3), 379–392.

Waisfeld, B.G., Vaccari, N.E., 2003. Trilobites. In: Benedetto, J.L. (Ed.), Ordovician fossils of Argentina. Secretaría de Ciencia y Tecnología. Universidad Nacional de Córdoba, Córdoba, pp. 295–410.

Waisfeld, B.G., Vaccari, N.E., 2008. Bioestratigrafía de trilobites del Paleozoico Inferior de la Cordillera Oriental , XVII Congreso Geológico Argentino. Actas, pp. 119–127.

Waisfeld, B.G., Sánchez, T.M., Benedetto, J.L., Carrera, M.G., 2003. Early Ordovician (Arenig) faunal assemblages from western Argentina. Biodiversification trends in different geodynamic and palaeogeographic settings. Palaeogeogr. Palaeoclimatol. Palaeoecol. 196, 343–373.

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 tardío) en la región de Pascha-Incamayo, Cordillera Oriental, Argentina: Parte 1: Bioestratigrafía. Ameghiniana 43 (4), 717–728.

Webby, B., Cooper, R.A., Bergström, S.M., Paris, F., 2004. Stratigraphic framework and time slices. In: Webby, B.B., Paris, F., Droser, M.L., Percival, I.G. (Eds.), The Great Ordovician Biodiversification Event. Columbia University Press, New York, pp. 41–47.

Westrop, S.R., Tremblay, J.V., Landing, E., 1995. Declining importance of trilobites in Ordovician nearshore paleocommunities; dilution or displacement? Palaios 10, 75–79.

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

Zhou, Z., Yuan, W., Zhou, Z., 2007. Patterns, processes and likely causes of the Ordovician trilobite radiation in South China. Geol. J. 42, 297–313.