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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)

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ABSTRACT

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.

Mots clés :
Faunes évolutives
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RÉSUMÉ

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

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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.

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