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Was there more space in the late Early Devonian for marine biodiversity to peak than in the early Late Ordovician?: A brief note

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Abstract. After the so-called "Cambrian explosion", marine biodiversity peaked either in the early Late Ordovician (as shown by the "classical" curves based on the extensive palaeontological data compilation) or in the late Early Devonian (as shown by the "innovative" curve based on the sampling standardization). The brief review of the modern plate tectonic, palaeoclimatic, and eustatic reconstructions demonstrates that shelves, which likely provided the main space for biotic radiation, shrank, concentrated in the tropics, and were better connected in the late Early Devonian than in the early Late Ordovician. The results of the present analysis permit to hypothesize that there was more (or the same) space for marine organisms to reach their maximum in their number in the early Late Ordovician relatively to the late Early Devonian. This is the only particular hypothesis, and the other extrinsic and intrinsic factors should be considered in further discussions.

Key words: marine biodiversity, shelf, biotic radiation, Late Ordovician, Early Devonian.

Апстракт. После тзв. "камбријумске експлозије", морски биодиверзитет достиже свој максимум или у доњем делу горњег ордовицијума (као што је приказано "класичном" кривом заснованој на компилацији исцрпних палеонтолошких података) или у горњем делу доњег девона (што је приказано кривом заснованој на стандардном узорковању). Преглед података који се односе на савремену тектонику плоча, палеоклиму и реконструкцију нивоа мора, указује на смањење распрострањења шелфова, који су највероватније чинили главну средину за биотску радијацију. Шелфови су били ограничени на тропске пределе и били су боље повезани у горњем делу доњег девона него у доњем делу горњег ордовицијума. Резултати добијени у овом раду дозвољавају претпоставку да су морски организми имали више, или барем подједнако простора за достизање максимума своје бројности у доњем делу горњег ордовицијума него у горњем делу доњег девона. Ово је свакако само једна од претпоставки, а у будућим анализама биће разматрани и остали спољашњи и унутрашњи фактори.

Кључне речи: морски биодиверзитет, шелф, биотска радијација, горњи ордовицијум, доњи девон.

Introduction

The new reconstruction of the global Phanerozoic marine biodiversity dynamics (Alroy *et al.* 2008) has not only changed our understanding of the history of life, but it has posed new questions. One of the most important is about the Paleozoic diversity maxima. The "classical" curves (based on the latest version of the compendium by Sepkoski (2002)) depicting changes in the number of genera through the geologic time (e.g., Purdy 2008; Aberhan & Kiessling 2012) demonstrate clearly that the first outstanding maximum in the diversity of marine invertebrates after the famous "Cambrian explosion" (see review and synopsis of the key literature sources in Ruban 2010) was reached in the early Late Ordovician (Fig. 1A). Evidently, this peak was a quintessence of the Ordovician radiation (see reviews in Harper 2006; Servais *et al.* 2009; Ruban 2010; Miller 2012). In contrast, the "innovative" curve based on the sampling standardization (Alroy *et al.* 2008) postdates such a maximum by ~50–60 Ma and places it into the late Early Devo-

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nian (Fig. 1B), when another major biotic radiation culminated (RUBAN 2010). Although the both recognized events were true diversity peaks (see the curves based on the SEPKOSKI (2002)'s compendium (PURDY 2008; ABERHAN & KIESSLING 2012; ABERHAN *et al.* 2012) and the sampling standardization (ALROY *et al.* 2008)) resulted from major radiations in the marine realm (RUBAN 2010), it remains uncertain which of them was really bigger (Fig. 1).

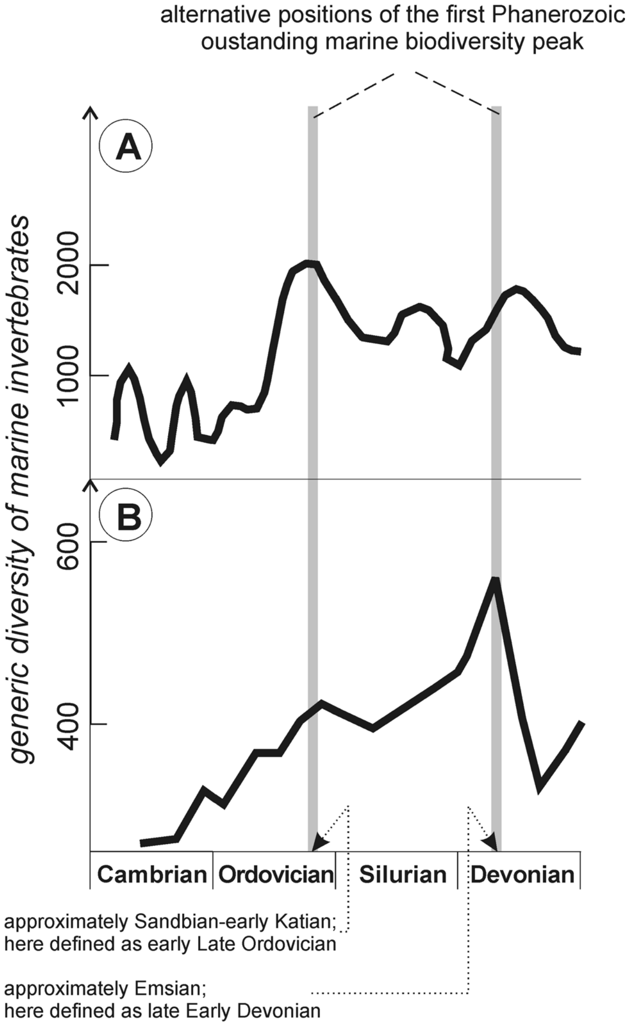

Fig. 1. Early–Middle Paleozoic marine biodiversity dynamics: **A,** "classical" diversity curve adapted from PURDY (2008) and based on the dataset by SEPKOSKI (2002); **B,** "innovative" curve adapted from ALROY *et al.* (2008) and based on sampling standardization. The scale of this figure and the correspondence of the curves follow RUBAN (2010).

The controversy between the two above-mentioned curves (or, better to say, data and approaches employed for their construction) is difficult to judge about, particularly because of different "philosophies" existing in the modern palaeobiology (e.g., BENTON 2011; RUBAN 2012). However, the discussion can be started from the "back" side, i.e., with evaluation of conditions that were or were not able to sustain higher marine biodiversity in the early Late Ordovician and the late Early Devonian. In the present note, the palaeoenvironments favourable for marine taxa to peak in their number in these two time slices are compared qualitatively. Of course, the outcome of such an analysis can be only hypothetical and particular. But even if this cannot resolve the above-mentioned controversy, the development of agenda for further investigations will be facilitated.

What space did the marine biodiversity need to peak?

Links between the space in oceans and seas that allowed marine biota to evolve and the diversity of this biota were probable, although this idea is addressed critically in the modern palaeobiological literature (ABERHAN & KIESSLING 2012; SMITH & BENSON, 2013). Generally, shelfal environments seem to be the most favourable for high biodiversity levels. On a global scale, their size depended on fragmentation of land masses, curvature of continental slopes, and sea level (ABERHAN & KIESSLING 2012; see also discussion by HOLLAND 2012). However, the existence of such a space did not necessarily lead to biodiversity acceleration. At least, two important constraints should be considered. The first constraint is climate. If warm seawater of the tropics was chiefly responsible for marine biodiversity, the only concentration of shelves near the Equator enlarged the latter. But there is an alternative point of view, which links higher number of taxa to palaeoclimatic differentiation (VALENTINE 1968; TROTTER *et al.* 2008; RUBAN 2010). In this case, the proportional pole-to-equator distribution of shelves was favourable for higher diversity. The second constraint is shelf connectivity. One may propose that either dispersal or isolation of marine organisms might have been a factor of their radiation (e.g., see RUBAN 2010). This means that the global connectivity of shelves or, in contrast, their separation by abyssal (*sensu lato*) domains might have enhanced peaks in the marine biodiversity.

The above said allows to compare the early Late Ordovician and the late Early Devonian global palaeoenvironments by the relative size, pole-to-equator distribution, and connectivity of shelves. Evidently, the uncertain importance of shelfal space for marine biodiversity to peak (ABERHAN & KIESSLING 2012), the complex relationships between the habitat size, sea-level changes, and biotic evolution (HOLLAND 2012), as well as the above-mentioned alternative interpretations of the constraints of space-biodiversity links should be further taken into account.

Comparison of two time slices

The available plate tectonic reconstructions (Scotese 2004; see also Cocks & Torsvik 2002; Lawver *et al.* 2002; Stampfli & Borel 2002; Torsvik & Cocks 2004; von Raumer & Stampfli 2008; Nance *et al.* 2012; Stampfli *et al.* 2013; see also scotese.com and ww2.nau.edu/rcb7/globaltext2.html) demonstrate that the fragmentation of land masses in the early Late Ordovician and the late Early Devonian was more or less comparable; and the degree of this fragmentation can be judged moderate (Ruban 2010). There were one large supercontinent of Gondwana and some other more or less "dispersed" middle-sized tectonic blocks in the both time slices (Fig. 2). Although Baltica and Laurentia already formed the continent of Laurussia in the Early Devonian (Stampfli & Borel 2002; Cocks & Torsvik 2005, 2011; Stampfli *et al.* 2013), and the Galatian terranes did not separate from Gondwana until the mid-Paleozoic (von Raumer & Stampfli 2008; Stampfli *et al.* 2013), there were the other relatively large and separate land masses, i.e., the Hunic terranes (von Raumer & Stampfli 2008; Stampfli *et al.* 2013) or the Kazakh continent with the related terranes (Wilhem *et al.* 2012).

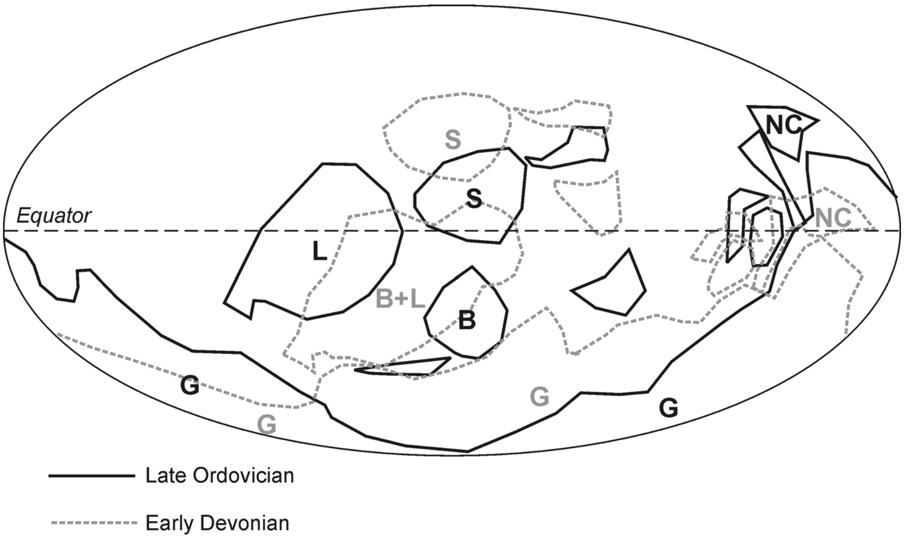

Fig. 2. Overlapped Late Ordovician and Early Devonian contours of the principal continental blocks (strongly generalized from Scotese 2004). Abbreviations: **B,** Baltica; **G,** Gondwana; **L,** Laurentia; **NC,** North China; **S,** Siberia (**B+L,** Baltica and Laurentia joined in the mid-Paleozoic to form Laurussia).

The same plate tectonic reconstructions (Cocks & Torsvik 2002, 2013; Lawver *et al.* 2002; Stampfli & Borel 2002; Scotese 2004; Torsvik & Cocks 2004; von Raumer & Stampfli 2008; Nance *et al.* 2012; Wilhem *et al.* 2012; Stampfli *et al.* 2013) permit to conclude about the comparable ratio between "active" and "passive" continental margins in the early Late Ordovician and the late Early Devonian. It can be assumed that the curvature of continental slopes, which is often controlled tectonically, was more or less similar on a global scale in these two time slices. Therefore, the established fragmentation of land masses and the curvature of continental slopes imply together the comparable size of shelfal environments in the analyzed time slices.

In contrast, significant difference is found with regard to the third factor affecting the size of shelves, i.e., the global sea level. The new eustatic reconstruction proposed by Haq & Schutter (2008) shows that this level was up to 200–220 m above the Present or even more in the early Late Ordovician, but it dropped by more than 1.5 times in the late Early Devonian, i.e., to only 120–140 m above the Present. This means that the shelfal environments in the former time slice were likely significantly larger. There were neither increase in the land mass fragmentation nor the smoothening of the continental slopes that would recompense the lower position of the global sea level in the late Early Devonian in comparison with the early Late Ordovician. Interestingly, the global palaeogeographical reconstructions by R.C. Blackey (available on-line at ww2.nau.edu/rcb7/globaltext2.html) demonstrate certain rise of the Gondwanan shelves in the Early Devonian; if so, the only moderate (if any) reduction of shelfal environments should be postulated for this time slice.

The knowledge on the early Late Ordovician climate remains controversial in somewhat (Miller 2012). It is more or less proven that the global temperature at the beginning of the Late Ordovician was high (e.g., see Fig. 8 in Zalasiewicz 2012). However, the cooling trend established by Trotter *et al.* (2008) and Boucot *et al.* (2009) and the evidence of glaciations that developed already since the Early Ordovician (Turner *et al.* 2011, 2012) imply that the Late Ordovician water masses were not exceptionally warm. It is not excluded, however, that the cooling trend was superimposed by a warming episode (Boucot *et al.* 2003; Fortey & Cocks 2005). In the late Early Devonian, the temperatures, including the low-latitude seawater surface temperatures, were high enough (Joachimski *et al.* 2009; Fig. 8 in Zalasiewicz 2012). However, the long-term cooling trend is interpreted (Joachimski *et al.* 2009). Finally, the equator-to-pole climatic gradient remained moderate in the both early Late Ordovician and the late Early Devonian (BOUCOT 2009). Speaking generally, the compared time slices were characterized by generally similarly global climatic conditions, and some pole-to-equator climatic differentiation was typical to the both of them. Evidently, it is important to realize whether there were differences in the pole-to-equator distribution of shelves between the two analyzed time slices. These can be deduced from the above-mentioned plate tectonic reconstructions (COCKS & TORSVIK 2002, 2013; LAWVER *et al.* 2002; STAMPFLI & BOREL 2002; SCOTESE 2004; TORSVIK & COCKS 2004; VON RAUMER & STAMPFLI 2008; NANCE *et al.* 2012; WILHEM *et al.* 2012; STAMPFLI *et al.* 2013). In the early Late Ordovician, the Gondwanan margin stretched from very high to very low latitudes in the Southern Hemisphere (and even entered the Northern Hemisphere), whereas separate middle-sized tectonic blocks were situated near the Equator. In the late Early Devonian, the Gondwanan margin remained large, but the interiors of the supercontinent occupied high latitudes of the Southern Hemisphere. In other words, the margin "shifted" towards Equator. The other tectonic blocks remained in the tropics with just a certain shift northwards. Therefore, it appears that the concentration of shelfal environments in the tropics increased together with the above-mentioned plate tectonic changes in the late Early Devonian relatively to the early Late Ordovician (Fig. 2). Of course, a portion of shelves remained in temperate and even high latitudes. Moreover, the global palaeogeographical reconstructions by R.C. BLACKEY (available on-line at ww2.nau.edu/rcb7/globaltext2.html) show that the Late Ordovician shelves of Gondwana also concentrated in the tropics, and they were narrower or lacking in the higher latitudes; the Early Devonian shelves of Gondwana, in contrast, were abundant in temperate latitudes. Consequently, it is sensible to suppose the only moderate (or even little) difference in the pole-to-equator distribution of shelves between the two analyzed time slices.

The connectivity of shelves changed through the early Paleozoic. At least, three features provide an evidence of its increase in the late Early Devonian in comparison to the early Late Ordovician. These include 1) the more "compact" grouping of land masses (e.g., SCOTESE 2004; STAMPFLI *et al.* 2013); 2) the shrinkage of the water space between Gondwana and Laurussia (DOJEN 2009), although the closure of the Rheic Ocean lasted through the Devonian and later (NANCE *et al.* 2012); 3) the lower global sea level (HAQ & SCHUTTER 2008).

Making hypotheses

The evidence presented above can be summarized as follows (Table 1). The global shelfal environments shrank, shifted towards Equator, and became better connected in the late Early Devonian relatively to the early Late Ordovician. If the very assumption that these environments provided the essential space for

Table 1. Comparison of global parameters considered in this paper (see text and RUBAN (2010) for more details and data sources).

Parameter	*early Late Ordovician (O3)*	*late Early Devonian (D1)*	*Comparison*
Fragmentation of land masses	moderate	moderate	O3 ≈ D1
Anticipate curvature of continental slopes			O3 ≈ D1
Global sea level	200–220 m above the Present	120–140 m above the Present	O3 > D1
Shelfal environments			O3 > D1
Climate (thermal regime)	moderately warm	moderately warm	O3 ≈ D1
Equator-to-pole climatic gradient	moderate	moderate	O3 ≈ D1
Pole-to-equator distribution of shelves	~ equal	certain concentration near the Equator	shelves in the tropics: O3 = D1
Connectivity of shelves	moderate	higher than moderate	O3 < D1

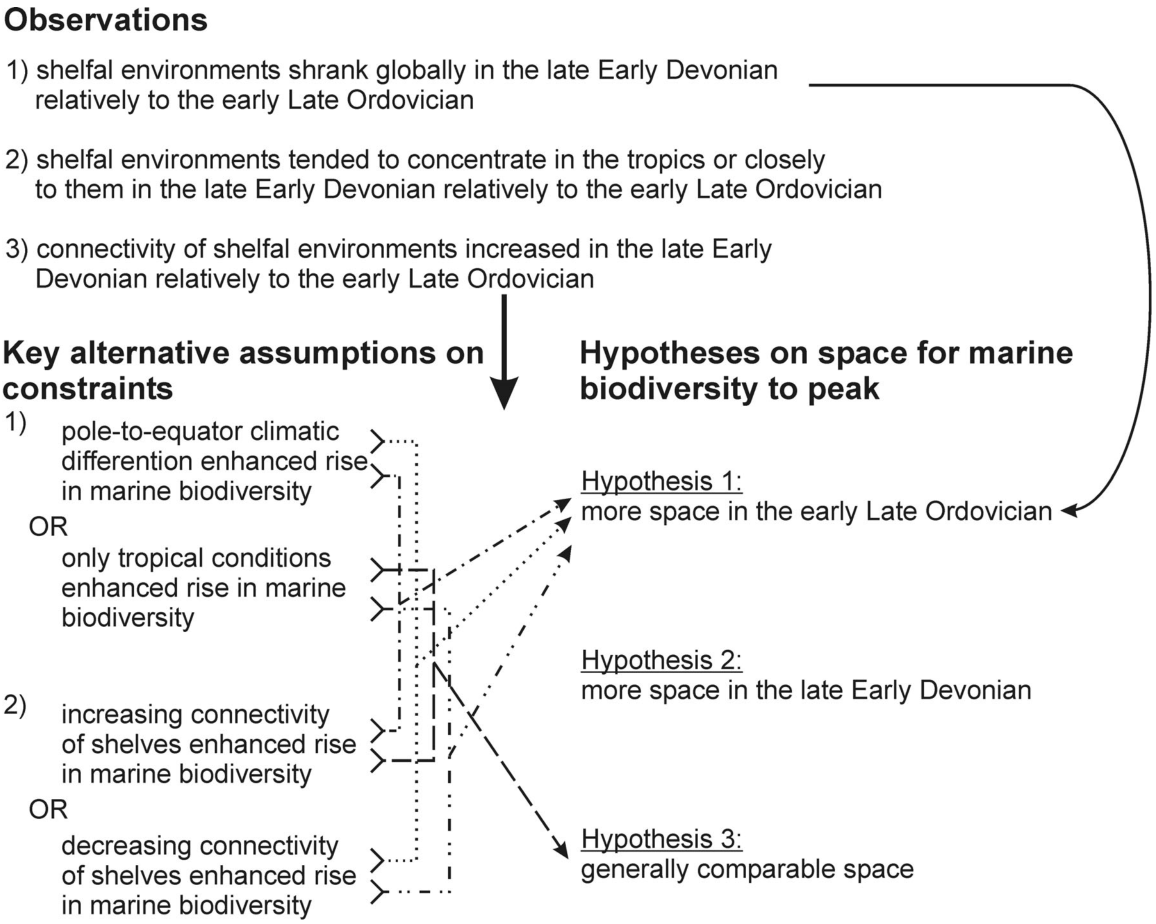

Fig. 3. Hypotheses that can be made based on the assumptions and the evidence employed in this paper (see text and Table 1). These considerations are sensible only if pole-to-equator distribution and connectivity of shelfal environments were true constraints and their importance was comparable.

the marine biodiversity to peak is valid, only two hypotheses can be proposed (Fig. 3). The first of them suggests that sea organisms had more space to peak in the early Late Ordovician, and the second hypothesis suggests that such a space was comparable in the analyzed time slices. Such a result is very interesting, because it matches better the "classical" biodiversity curves (Purdy 2008; Aberhan & Kiessling 2012; Aberhan *et al.* 2012; based on the data from Sepkoski 2002) than the "innovative" curve proposed by Alroy *et al.* (2008). One should note that the former curve indicates that the late Early Devonian peak was just a bit smaller than that early Late Ordovician (Fig. 1).

Of course, all considerations presented above are highly hypothetical, and it would be wrong to say that they are enough to support one of the alternative marine biodiversity curves. For instance, we do not know what was the relative importance of the discussed constraints of space-biodiversity links. It cannot be excluded that, say, the pole-to-equator differentiation was more important than the connectivity of shelfal environments, and so on. Moreover, the available plate tectonic, palaeoclimatic, and eustatic reconstructions still need serious improvement. However, the attempted qualitative analysis provides some important ideas for further discussions.

Conclusions

The qualitative analysis of the available information on the global Late Ordovician and Early Devonian plate tectonics, palaeoclimate, and sea level and the attempt to imply its results for judgements about the alternative biodiversity curves allow two main conclusions:

– apparently, global shelfal environments shrank, concentrated in the tropics, and were better connected in the late Early Devonian relatively to the early Late Ordovician;

– hypothetically, there was more (or the same) space for marine biodiversity to peak in the early Late Ordovician than in the late Early Devonian, which matches better the "classical" biodiversity curve.

Testing these too tentative ideas quantitatively appears to be an important task for further studies. However, quantification of the area of Late Ordovician and Early Devonian shelves is challenging because of two reasons. On one hand, the available global palaeogeographical reconstructions (e.g., that by R.C. Blackey - see on-line at ww2.nau.edu/rcb7/globaltext2.html) differ is some what from some other global plate tectonic reconstructions (e.g., Stampfli & Borel 2002; von Raumer & Stampfli 2008; Wilhem *et al.* 2012; Stampfli *et al.* 2013). On the other hand, the above-mentioned global plate tectonic reconstructions depict only tectonic blocks, not palaeoshorelines, and, thus, they cannot be employed directly for precise delineation of ancient shelves. The reconstruction proposed by Cocks & Torsvik (2013) is an exception (both tectonic blocks and palaeoshorelines are indicated there), but it embraces the only portion of the planetary space. Moreover, the summarized area of shelves around small oceanic islands (that are difficult to consider on the modern reconstructions) should not be ignored. And yet another caution is reasonable. As shown by Peters (2007), elongated shelves around land masses and widespread shelves of epeiric seas (better to say, such seas embraced only shelves) might have been different habitats. If so, further studies should differentiate palaeoenvironments, which are judged together as “shelfal” in this paper.

Of course, the size and the palaeogeographical distribution of shelves were not the only possible controls on the biodiversity. Many other forces, both extrinsic (i.e., environmental) and intrinsic (i.e., biological), as well as their interconnections should be considered – e.g., the content of the atmospheric oxygen (Berner 2006) and/or the perturbations in the sulphur isotopic record (Hannisdal 2011). Or, if there were teleconnections between marine and non-marine environments / ecosystems in the Late Devonian (Algeo *et al.* 1995), the rise and the dispersal of terrestrial floras in the Early Devonian (Niklas *et al.* 1983; Meyen 1987; Anderson *et al.* 1999) might have been also significant factor influencing the marine biodiversity. Finally, it would be wrong to forget that reaching the peak in the number of taxa depended on the geologic time itself, i.e., on the duration of the radiation, and the rate of global biotic evolution.

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Резиме

Да ли је за максимум морског биодиверзитета било више простора у горњем делу доњег девона него у доњем делу горњег ордовицијума? – кратак осврт

После тзв.”камбријумске експлозије“, морски биодиверзитет достиже свој максимум или у доњем делу горњег ордовицијума или у горњем делу доњег девона.Тешко је коментарисати неслагања која постоје око две криве биодиверзитета, мада би расправа могла бити започета са проценом услова који су погодовали развоју морског биодиверзитета у доњем делу горњег ордовицијума као и у горњем делу доњег девона. Највероватније су везе које су постојале између различитих делова мора и океана омогућиле развој и разноврсност морских организама одређених региона. У највећем броју случајева шелф се издваја као средина која је нарочито повољна за развој организмима и која је омогућила њихову велику бројност и разноврсност. Палеосредине које су имале широко распрострањене у доњем делу горњег ордовицијума као и у горњем делу доњег девона, поређене су на основу њихове релативне величине, распрострањења у односу на екватор и полове, као и њихове повезаности са шелфом. Постојећа реконструкција тектонских плоча указује да је фрагментарност континенталних маса током доњем делу горњег ордовицијума и горњем делу доњег девона, мање или више слична, као и да је степен ове фрагментараности био умерен. Такође би могло да се претпостави да је нагиб континенталних падина, који је често тектонски контролисан, био приближно сличан и то у глобалним размерама током ова два временска раздобља. Стога, успостављена фрагментација копнених маса као и нагиб континенталне падине указују на сличне величине шелфних средина у проучаваним раздобљима. Утврђена је значајна разлика у односу на ниво светских мора који је био трећи фактор који је утицао на величину шелфова, а који био 1,5 пута нижи у горњем делу доњег девона него у доњем делу горњег ордовицијума. Ово указује на то да су шелфне средине током овог последњег временског периода вероватно биле значајно веће. Уопштено говорећи, поменути временски периоди, чије је упоређење извршено, карактеришу се углавном сличним климатским условима, с тим што су за сваки од њих постојале и одређене специфичности везане за климу у областима полова и екватора. У горњем делу доњег девона долази до повећања концентрације шелфних средина у тропским областима, веће повезаности између шелфова, као и већег кретање тектонских плоча, него у доњем делу горњег ордовицијума. Претпоставка је да је било више (или исто) простора за достизање максимума у развоју морског биодиверзитета у доњем делу горњег ордовицијума него у горњем делу доњег девона, што се поклапа са ”класичном“ кривом биодиверзитета. Провера ове две идеје квантитативно представља важан задатак за будуће студије. Наравно, величина и палеогеографско распрострањење шелфова нису само могуће контроле биодиверзитета. Многи други фактори, како спољашњи (тј. животна средина) тако и унутрашњи (тј. биолошки), као и њихова међусобна повезаност мора бити разматрана. Најзад, било би погрешно запоставити да достигнути максимуми у броју таксона зависе од геолошког старости, тј. трајања радијације и степена глобалне биотске еволуције.

Б.Р.