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Taxonomic diversity dynamics of Early Cretaceous brachiopods and gastropods in the Azerbaijanian domains of the Lesser Caucasus (Neo-Tethys Ocean)

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Abstract. Palaeontological data available from the Azerbaijanian domains (Somkhit-Agdam, Sevan-Karabakh, and Miskhan-Kafan tectonic zones) of the Lesser Caucasus permit reconstruction of the regional taxonomic diversity dynamics of two groups of Early Cretaceous marine benthic invertebrates. Stratigraphical ranges of 31 species and 14 genera of brachiopods and 40 species and 31 genera of gastropods are considered. The total number of species and genera of brachiopods was low in the Berriasian–Valanginian and then rose to peak in the Barremian. Then, the diversity declined in the Aptian, and brachiopods are not known regionally from the Albian. Gastropods appeared in the Hauterivian and experienced a strong radiation in the Barremian. The diversity of species and genera declined in the Aptian (with a minor radiation in the Middle Aptian), and no gastropods are reported from the Albian. Globally, the number of brachiopod genera remained stable through the Early Cretaceous, and the number of gastropod genera increased stepwise with the maximum in the Albian. The regional and global patterns of the diversity dynamics differed for the both groups of marine benthic invertebrates. The Barremian maximum of the taxonomic diversity coincided with the regional flourishing of reefal ecosystems. The taxonomic diversity dynamics of brachiopods in the Azerbaijanian domains of the Lesser Caucasus is very similar to those of the Northern Caucasus, which is an evidence of proximity of these regions during the Early Cretaceous.

Key words: brachiopods, gastropods, taxonomic diversity, transgression, Early Cretaceous, Lesser Caucasus, Azerbaijan, Neo-Tethys Ocean.

Апстракт. Палеонтолошки доступни подаци из Азербејџански домена (Сомкхит-Агдам, Севан-Карабаху, и Мискхан-Кафан тектонске зоне) Малог Кавказа дозвољавају реконструкцију динамике регионалних таксономских разноликости две групе доњокредних морских бентоских бескичмењака. Разматран је стратиграфски опсег 31 врсте и 14 родова брахиопода и 40 врста и 31 род гастропода. Укупан број брахиоподских врста и родова је био низак у беријас-валендину, а врх разноликости достигао у барему. Затим, разноликост опада у апту, а од алба брахиоподи нису регионално познати. Гастроподе су се појавиле у отриву и доживела јаку експанзију у барему. Разноликост врста и родова опада у апту (са мањом експанзијом у средњем апту), а ниједан гастропод се не појављује од алба. Глобално, број брахиоподских родова остао је стабилан током доње креде, а број гастроподских родова је постепено повећаван, са максимумом у албу. Регионални и глобални обрасци динамике различитости разликовала су се за обе групе морских бентоских бескичмењака. Баремски максимум таксономске разноликости поклопио са регионалним процватом гребенског екосистема. Динамика таксономске разноликости брахиопода у азербејџанским деловима Малог Кавказа је веома слична онима на северном Кавказу, што је доказ близине ових региона током ране креде.

Кључне речи: брахиоподи, гастроподи, таксономска разноврсност, трансгресија, рана креда, Мали Кавказ, Азербејџан, Неотетис.

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Introduction

Reconstructions of regional changes in taxonomic diversity of marine organisms are highly important for understanding spatial differences of biodiversity changes registered with the available global palaeontological data (SEPKOSKI 1993, 2002; ALROY *et al.* 2008; PURDY 2008; ALROY 2010). Particularly, the fossil record of the Caucasus, a large region stretching between the Black Sea and the Caspian Sea, is useful for analysis of the Cretaceous biotic evolution (RUBAN *et al.* 2011). Representative palaeontological data from this region were already compiled and published, but still unemployed for the analysis of diversity dynamics.

The present paper focuses on the Azerbaijanian domains of the Lesser Caucasus (Fig. 1). Two groups of marine benthic macroinvertebrates, namely brachiopods and gastropods, are common in the Lower Cretaceous deposits of the study area (AKOPIAN & KHALILOV 1986; ALI-ZADEH 1988). These groups seem to be suitable for the analysis of the regional taxonomic diversity dynamics and its further comparison with the global patterns. This study is a part of the palaeobiological re-evaluation of the information about Cretaceous marine invertebrates from the Caucasus (see also RUBAN 2006, 2011a; RUBAN *et al.* 2011).

Geological setting

The Lesser Caucasus comprises a large southern portion of the Caucasus (Fig. 1). It occupies Armenia and parts of Azerbaijan and Georgia, as well as the neighbouring parts of Turkey and Iran. According to SHIKHALIBEYLI (1972), the Azerbaijanian domains of the Lesser Caucasus include the Somkhit-Agdam, Sevan-Karabakh, and Miskhan-Kafan tectonic zones (the names are given in Russian transliteration). The exact Mesozoic plate tectonic setting of the Lesser Caucasus, which is a Gondwana-derived terrane (RUBAN *et al.* 2007), has been debated (LORDKIPANIDZE *et al.* 1984; GAMKRELIDZE 1986; GOLONKA 2004; ISMAIL-ZADEH 2007; ADAMIA *et al.* 2011). This terrane was located either in the midst of the Neo-Tethys Ocean or near its northern periphery (e.g., STAMPFLI & BOREL 2002; GOLONKA 2004) (Fig. 1). The Lesser Caucasus was affected by active tectonic processes in the Early Cretaceous, including hot-spot activity (AZIZBEKOV *et al.* 1972; ISMAIL-ZADEH 2007; ADAMIA *et al.* 2011; ROLLAND *et al.* 2009, 2011).

The regional Lower Cretaceous stratigraphy has been developed, particularly, by KHALILOV & ALIYEV (1972, 2007), AKOPIAN & KHALILOV (1986), ALI-ZADEH (1988), and ALIYEV & KHALILOV (2007). Generally, Lower Cretaceous deposits constitute the carbonate- and volcanoclastic-dominated successions with a total thickness of ~1500 m and more (KHALI-



Fig. 1. Geographical location of the study area. Spatial distribution of the Lower Cretaceous deposits in the Lesser Caucasus is shown schematically after KHALILOV & ALIYEV (1972), AKOPIAN & KHALILOV (1986), and ALI-ZADEH (1988). Plate tectonic reconstruction for 120 Ma is simplified from SCOTSE (2004). Approximate position of the Lesser Caucasus is shown according to GOLONKA (2004).

LOV & ALIYEV 1972, 2007; AKOPIAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007) (Figs. 2, 3). The Urgonian limestones and reefs are abundant in the Barremian (JASAMANOV 1978; AKOPIAN & KHALILOV 1986; ALI-ZADEH 1988; AKHMEDOV *et al.* 2003; ALIYEV & KHALILOV 2007; KHALILOV & ALIYEV 2007) (Fig. 3). Clastic lithofacies are common in the upper part of the regional Lower Cretaceous succession (Fig. 2). The Lower Cretaceous deposits of the study area were accumulated in a shallow-marine open basin; the seawater was warm with normal salinity (JASAMANOV 1978; ALI-ZADEH *et al.* 1982). The sea was populated by different marine organisms, including ammonites, belemnites, bivalves, brachiopods, and gastropods (KHALILOV & ALIYEV 1972, 2007; AKOPIAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007). Palaeobiogeographically, the fossil assemblages belonged to the Mediterranean–Caucasian Subrealm (WESTERMANN, 2000).

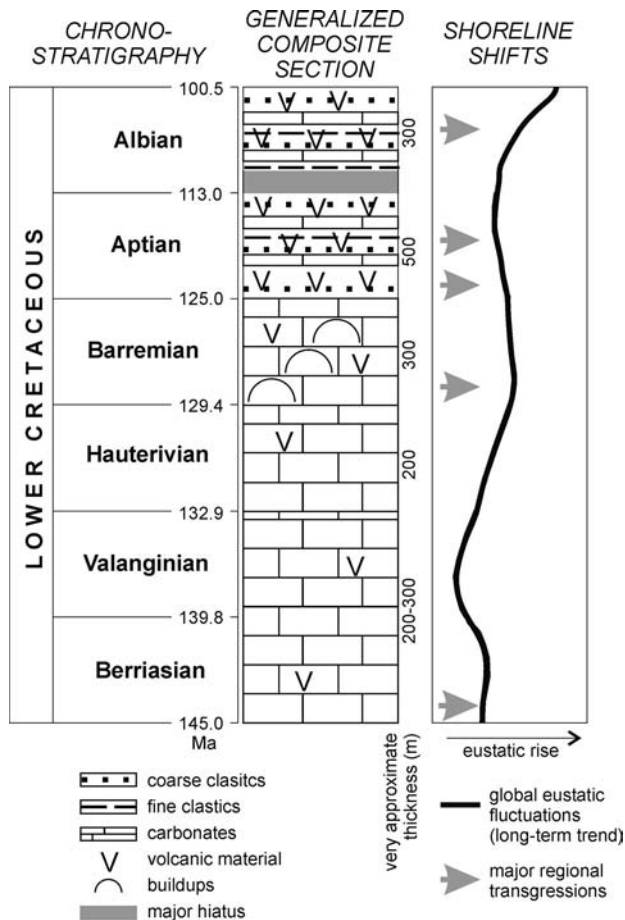


Fig. 2. The stratigraphical outline of the Lower Cretaceous deposits of Azerbaijan. Lithology and regional transgressions are based on information summarized by KHALILOV & ALIYEV (1972, 2007), AKOPJAN & KHALILOV (1986), ALI-ZADEH (1988), and ALIYEV & KHALILOV (2007); chronostratigraphy after GRADSTEIN *et al.* (2012) (see the updated time scale on-line: stratigraphy.org); global eustatic fluctuations after HAQ (2014). Regional transgressions should be distinguished from global eustatic changes, because the latter did not necessarily appear regionally.

The available stratigraphical information (KHALILOV & ALIYEV 1972, 2007; AKOPJAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007) permits to indicate five regional transgressions (Fig. 2). These are interpreted on the basis of consideration of relative spatial distribution of marine deposits, erosional surfaces, and transgression surfaces. For instance, the limited occurrence of the pre-Barremian deposits in the Azerbaijanian domains of the Lesser Caucasus relatively to the distribution of the Barremian desposits implies landward shoreline shift, i.e., transgression (*sensu* CATUNEANU 2006), peaked in the Barremian. The largest was the Albian transgression (JASAMANOV 1978; KHALILOV & ALIYEV 2007), which coincided with the global long-term sea-level rise (HAQ 2014) and was, probably, triggered by the

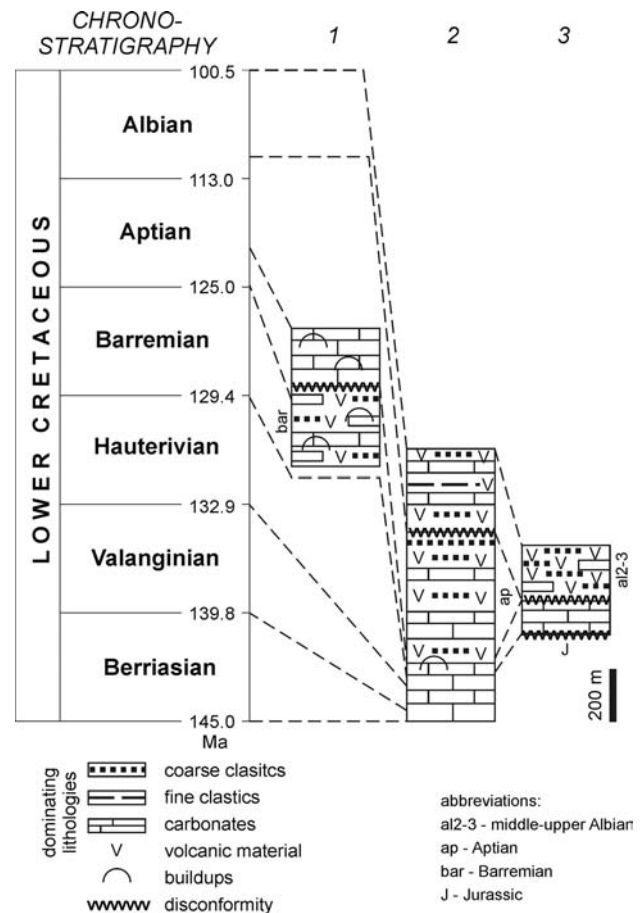


Fig. 3. Correlation of three Lower Cretaceous reference sections (1 – Dashalty, 2 – Dolanlar, 3 – Dashushen) in the Azerbaijanian domains of the Lesser Caucasus (based on the information from ALIYEV & KHALILOV 2007). These sections are given as examples; many other sections and outcrops are also known in the study area, and they were investigated by KHALILOV & ALIYEV (1972, 2007), AKOPJAN & KHALILOV (1986), ALI-ZADEH (1988), and ALIYEV & KHALILOV (2007). Formal lithostratigraphical units are yet to be established for the study area. Chronostratigraphy follows GRADSTEIN *et al.* (2012) (see the updated time scale on-line: stratigraphy.org).

latter. Deposits of this age are the most widely distributed among the Lower Cretaceous sedimentary packages (ALI-ZADEH 1988; ALIYEV & KHALILOV 2007; KHALILOV & ALIYEV 2007). This transgression took place in the Middle Albian, and it is documented locally by transgressive surface between the Middle Albian and underlying deposits (ALIYEV & KHALILOV 2007; KHALILOV & ALIYEV 2007).

Materials and methods

This study employs regional and global stratigraphical ranges of Early Cretaceous brachiopods and gas-

tropods. The regional data on brachiopods (Appendix 1) were taken from AKOPJAN & KHALILOV (1986) and ALI-ZADEH (1988) with certain updates (e.g., *Cyrtothyris pseudosella* (LOBATSCHIEVA) and *Praelogithyrus pseudosella* LOBATSCHIEVA given as two distinct species in the original data source seem to be synonyms; *Cyrtothyris gillieronii* PICTET, *C. picteti* BURRI, and *C. renauxiana* D'ORBIDNY can be attributed to the genus *Lamellaerhynchia*). The work by AKOPJAN & KHALILOV (1986) synthesizes the information on the regional stratigraphy, and, among others, it lists common brachiopod taxa. The chapter by ZEYNIYEV & LOBATSCHIEVA in ALI-ZADEH (1988) is the first comprehensive taxonomic review of Cretaceous brachiopods from Azerbaijan, which remains essential source of the relevant information up to nowadays. These data are the result of regional sampling of many Early Cretaceous fossil localities in the Azerbaijanian domains of the Lesser Caucasus. The global generic diversity of brachiopods was established by CURRY & BRUNTON (2007). The regional data on gastropods (Appendix 1) were extracted from ALI-ZADEH (1988). ALIYEV in ALI-ZADEH (1988) reviewed all available information about Early Cretaceous taxa reported from Azerbaijan, including those described earlier by ALIYEV (1963). As in the case of brachiopods, the above-mentioned data were collected during sampling of many localities, and it is regionally representative. The global data on gastropods were taken from the compilation of SEPKOSKI (2002; see database on-line: <http://strata.geology.wisc.edu/jack/start.php>).

For the purposes of this quantitative analysis, two regional datasets were composed (Appendix 1). The first of them comprises stratigraphical ranges of 31 species of brachiopods belonging to 14 genera. The second dataset shows the stratigraphical distribution of 40 species of gastropods belonging to 31 genera. The presence of taxa is recorded at the scale of stages, but the distribution of Early Hauterivian–Middle Aptian gastropods (Late Aptian taxa were not reported at all) is also recorded at the level of substages (Appendix 1). All regional data were collected from numerous localities within the study area. As the data are given in the original sources, they characterise the entire region (not individual sections or outcrops), which is typical for palaeontological syntheses from the former USSR. Such information is very suitable for palaeobiological studies (see RUBAN (2011b) for discussions).

The present quantitative analysis of the regional taxonomic diversity dynamics of brachiopods and gastropods includes evaluation of the total diversity (=total number of taxa), the number of appearances, and the number of disappearances by stages of the Early Cretaceous. Appearances and disappearances are preferred to originations and extinctions respectively, because the formers could be only temporal in regional records (see RUBAN & VAN LOON 2008). This

analysis is done for both species and genera. For further comparisons of diversity patterns, the global changes in the total number of brachiopod and gastropod genera are also considered (no data on the global number of species are available). The taxonomic diversity dynamics are described herein at the level of stages. This resolution enables direct comparisons with the global diversity trends. Uncertainties related to different understandings of substages are avoided (cf. RUBAN & VAN LOON 2008). Also, a major part of the original data is attached to stages only. However, the available information on gastropods allows a tentative reconstruction of their diversity dynamics on the level of substages.

This study is based on the Early Cretaceous chronostratigraphical framework established by the International Commission on Stratigraphy (GRADSTEIN *et al.* 2012; see the updated time scale on-line: stratigraphy.org). Some cautions are necessary when using data from the older palaeontological literature (RUBAN 2011b). Particularly, there may be some differences between the regionally established Lower Cretaceous stages (KHALILOV & ALIYEV 1972, 2007; AKOPJAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007) and the actual global stages (GRADSTEIN *et al.* 2012; see the updated time scale on-line: stratigraphy.org). A brief examination of the regional biostratigraphy (KHALILOV & ALIYEV 1972, 2007; AKOPJAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007) suggests that some stage boundaries may be replaced downwards or upwards by about a triple of the stage length, but their exact position can be fixed only after detailed special investigations, and this is not the purpose of the present paper. However, the possible influence of the noted problem is considered in the interpretations of the results of this study (e.g., minor diversity changes are supposed to be within the error, and, thus, they are ignored). It should be also noted that the stratigraphical ranges employed for the purposes of the present study are based on generally consistent chrono- and biostratigraphical frameworks used in the original sources (AKOPJAN & KHALILOV 1986, ALI-ZADEH 1988), and no major errors linked to differences in stage understanding in different works are expected.

Results

The number of brachiopod taxa changed significantly in the Azerbaijanian domains of the Lesser Caucasus during the Early Cretaceous (Fig. 4). Few brachiopods are reported from the Berriasian and Valanginian deposits. However, the total brachiopod diversity increased in the Hauterivian and duplicated in the Barremian. The Aptian brachiopod assemblages were poor again, and the Albian brachiopods are unknown. The number of appearances tended to remain below

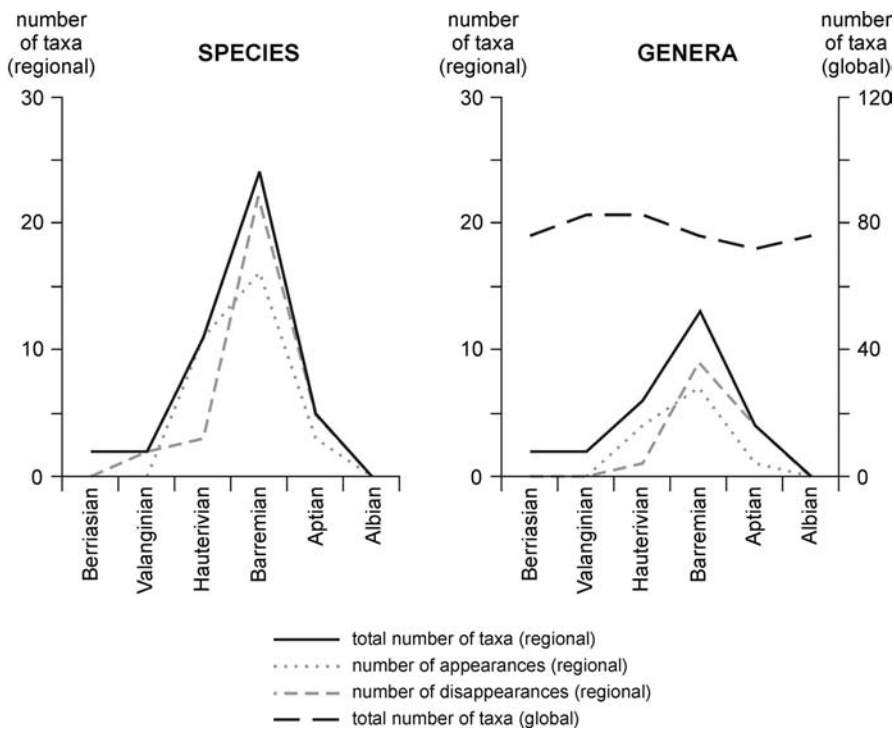


Fig. 4. Regional taxonomic diversity dynamics of Early Cretaceous brachiopods in the Azerbaijanian domains of the Lesser Caucasus. Changes in the global number of brachiopod genera (after CURRY & BRUNTON 2007) are given for reference.

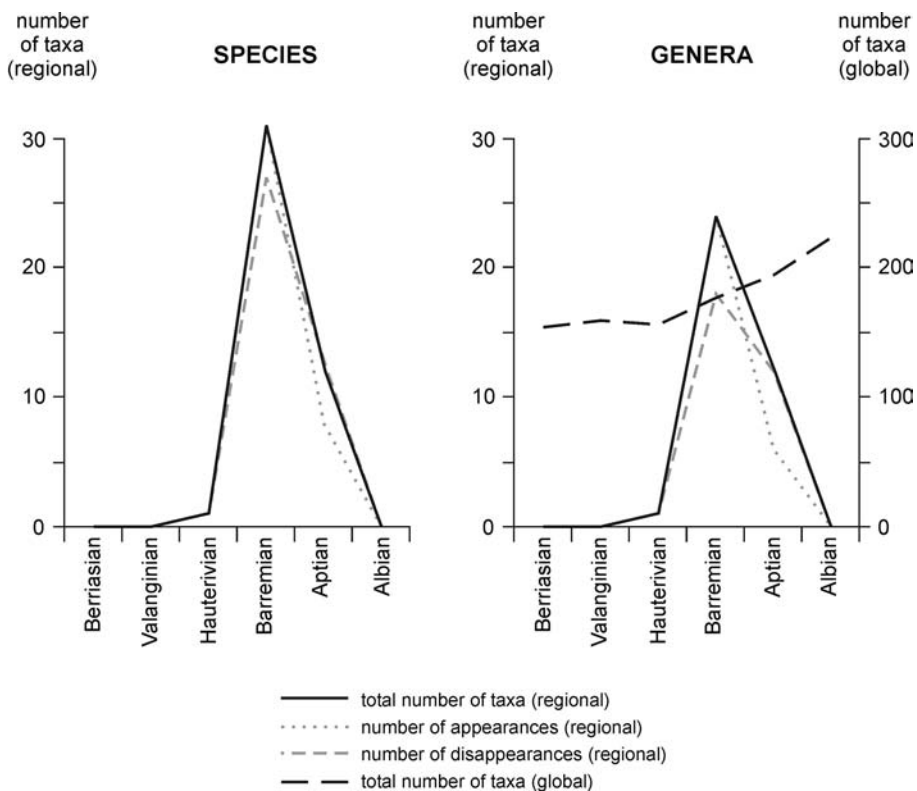


Fig. 5. Regional taxonomic diversity dynamics of Early Cretaceous gastropods in the Azerbaijanian domains of the Lesser Caucasus. Changes in the global number of gastropod genera (on the basis of data from SEPKOSKI 2002) are given for reference.

the number of disappearances (except for the Hauterivian). The Barremian total diversity maximum is a result of 16 species appearances in this stage and only 3 species disappearances in the Hauterivian. Very similar patterns of the generic diversity dynamics are registered (Fig. 4).

The number of gastropod taxa also varied during the Early Cretaceous (Fig. 5). The first gastropod taxon appeared regionally in the Hauterivian. The Barremian stage is characterised by a strong radiation of gastropods. The total diversity declined by about a half in the Aptian, but they remained relatively diverse in this stage. No gastropods are reported from the Albian deposits of the study area. The Barremian diversity maximum was a result of striking increase in the number of appearances in this stage. 27 species disappearances in the Barremian and only 8 species appearances in the Aptian reduced the gastropod diversity in the latter stage. As in the case of brachiopods, very similar patterns of the generic diversity dynamics are registered (Fig. 5). Consideration of the total diversity dynamics at a higher resolution demonstrates that gastropods radiated gradually through the Barremian, and their diversity increased slightly in the Middle Aptian to be followed by the total disappearance of gastropods already in the late Aptian (Fig. 6).

The comparison of the regional taxonomic diversity dynamics of the two groups of marine benthic invertebrates (Figs. 4, 5) implies that the both reached the maximum in their total species and generic diversity in the Barremian. However, the brachiopod assemblages were more diverse in the Hauterivian than in the Aptian, whereas gastropods

were relatively diverse in the Aptian and much less diverse in the Hauterivian. In other words, brachiopods experienced a gradual radiation and less gradual decline (Fig. 4), whereas gastropods experienced a strong radiation and gradual decline (Figs. 5, 6).

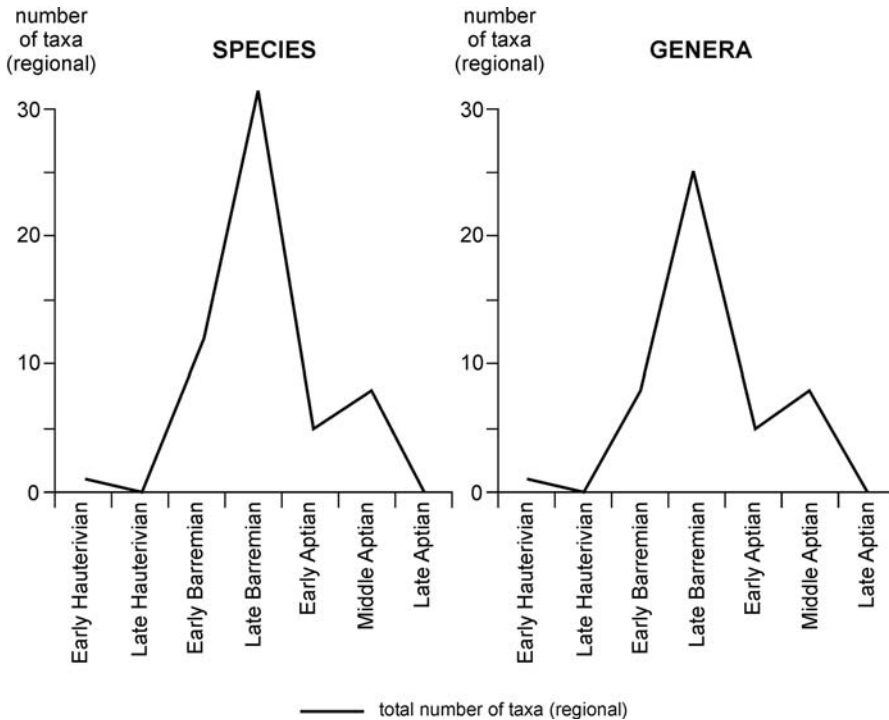


Fig. 6. Regional taxonomic diversity dynamics of Hauterivian–Aptian gastropods in the Azerbaijanian domains of the Lesser Caucasus calculated per substages. The names of the regional sub-stages are not capitalized, because these units are provisional.

Discussion

Globally, the total generic diversity of brachiopods remained stable in the Early Cretaceous, which is different from the regional pattern (Fig. 4). The maximum in the total diversity that occurred in the Azerbaijanian domains of the Lesser Caucasus is not established globally. And, vice versa, brachiopod communities were poor or absent regionally, when this group diversified globally. Gastropods experienced a stepwise diversification on a global scale, which contrasts with the regional changes in the number of genera (Fig. 5). The only Barremian regional diversity maximum coincided with the onset of the late Early Cretaceous diversification, but the latter was not as striking global feature as the above-mentioned regional strong radiation of gastropods. Moreover, the global diversity of these fossils peaked in the Albian, whereas no gastropods of this age are reported from the Azerbaijanian domains of the Lesser Caucasus.

This comparison suggests that there was a fundamental difference between the regional and global diversity dynamics of both brachiopods and gastropods.

Moreover, these fossils were more similar by changes in the total number of genera on a regional scale than on a global scale. Therefore, it is unlikely that the regional taxonomic diversity dynamics was controlled by the global changes in the number of taxa. Of course,

this conclusion is valid if no bias is significant. For instance, the restricted distribution of pre-Barremian strata (ALIYEV & KHALILOV 2007; KHALILOV & ALIYEV 2007) may explain the low number of brachiopods and gastropods reported from them. The investigations that provided data for the compilations of AKOPJAN & KHALILOV (1986) and ALI-ZADEH (1988) were regional in scale essentially. As shown in their works, each interval was studied with an equal attention. Thus, it is unlikely that sampling bias affect the taxonomic diversity reconstructions presented in this paper. As for the preservation bias, carbonate rocks, which are favourable for fossil preservation, are frequent in the entire Lower Cretaceous successions of the study territory (KHALILOV & ALIYEV 1972, 2007; AKOPJAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007) (Fig. 2).

Some regional palaeoenvironmental controls on diversity should be considered. The geological information summarized by KHALILOV & ALIYEV (1972, 2007), AKOPJAN & KHALILOV (1986), ALI-ZADEH (1988), and ALIYEV & KHALILOV (2007) allows to outline several landward shoreline shifts that occurred in the Azerbaijanian domains of the Lesser Caucasus and either coincided with or differed from the global eustatic changes (HAQ 2014) (Fig. 2). It is unlikely that these transgressions (Fig. 2) were an ultimate control on the regional taxonomic diversity dynamics of either brachiopods or gastropods because of their different correspondence to the diversity changes (Figs. 4, 5). However, it cannot be excluded that the transgression peaked in the Barremian facilitated (or, at least, did not preclude) the rapid diversification of marine benthic macroinvertebrates, and the Aptian transgressions were, probably, responsible for the minor radiation of gastropods (Fig. 6). Interestingly, the global diversity of brachiopods (Fig. 4) and gastropods (Fig. 5) also did not correspond to the long-term eustatic changes reconstructed by HAQ (2014) (Fig. 2).

Another possible palaeoenvironmental control on the reconstructed diversity dynamics was seawater temperature. It was evaluated regionally on the basis of isotope studies of benthic molluscs and belemnites. Results from such studies should be used with caution because of certain difficulties with isotopic data interpretation (e.g., LONGINELLI 1996, pers. comm.). The investigation by JASAMANOV (1978) showed some cooling during the late Early Cretaceous. The seawater temperature dropped by 4–5 °C down to ~18 °C. Still, the water remained warm, and the basin was situated in or near the tropical climatic belt (JASAMANOV 1978). The palaeotemperature analysis by ALI-ZADEH *et al.* (1982) showed cooling in the marine basin of Eastern Azerbaijan from ~22 °C to ~16 °C during the Valanginian–Barremian and then warming to ~22 °C in the Albian. The above-mentioned data from JASAMANOV (1978) do not permit to judge about direct influences of seawater temperature on the fossil diversity. The results of ALI-ZADEH *et al.* (1982) imply that the diversity maximum was reached when the seawater was the coldest. If the latter is true, this is an unusual coincidence (one would expect fauna flourishing in warm-water conditions), and further investigations are necessary to confirm and to explain this.

The Barremian deposits of the Azerbaijanian domains of the Lesser Caucasus bear reefs with diverse corals (AKOPJAN & KHALILOV 1986; ALI-ZADEH 1988; AKHMEDOV *et al.* 2003) (Appendix 2). It is broadly accepted that coral ecosystems sustained high taxonomic diversity in the geological past (KIESSLING *et al.* 2010). The Urgonian facies with reefs are established in the study area (JASAMANOV 1978; AKOPJAN & KHALILOV 1986; ALI-ZADEH 1988; ALIYEV & KHALILOV 2007; KHALILOV & ALIYEV 2007). These are also typical for many European regions (CSÁSZÁR 2002; IDAKIEVA & IVANOV 2002; MASSE *et al.* 2003, 2009; BODIN *et al.* 2006; GODET *et al.* 2010; MILLAN *et al.* 2011; STEIN *et al.* 2012; CAREVIC *et al.* 2013; GODET 2013; HUCK *et al.* 2013; MASSE & FENERCI-MASSE 2013), where they were formed in environments favourable for diversification of benthic invertebrates. The development of reefal ecosystems in the Barremian provides a plausible explanation of the strong diversification of brachiopods and gastropods relatively to Hauterivian and Aptian intervals. Anyway, the low diversity of these benthic macroinvertebrates in the Berriasian and the Valanginian, as well as their absence in the Albian remain enigmatic, because the regional palaeoenvironments (relatively shallow-water and warm seas with carbonate sedimentation) do not appear restrictive for diverse fossil communities (Fig. 2).

Globally, the Barremian is not known as a stage with the highest global distribution of reefs. Their quantity rose gradually through the Early Cretaceous, but the peak (not as pronounced as that of the Late Jurassic) was reached near the end of this epoch (KIESSLING *et al.*

1999; see also BOGGS 2006). The global generic diversity of Barremian corals (LÖSER 1996, 2005) was high, but not as exceptionally high (relatively to older and younger stages) as it was regionally (ALI-ZADEH 1988). Probably, the regional growth of reefal ecosystems in the only Barremian explains why the diversity maximum of marine benthic invertebrates is registered in the Azerbaijanian domains of the Lesser Caucasus, but not globally in this stage.

The quantitative analysis by RUBAN (2011a) permitted to register the taxonomic diversity dynamics of brachiopods in the Northern Caucasus, i.e., the northern part of the Greater Caucasus Basin. This dynamics can be compared with the diversity patterns established by the present study. The two regions are now located in the proximity of each others, but their relative position during the Early Cretaceous remains quite uncertain because of debates on the exact plate tectonic location of the Lesser Caucasus (LORDKIPANIDZE *et al.* 1984; GAMKRELIDZE 1986; GOLONKA 2004; ISMAIL-ZADEH 2007; ADAMIA *et al.* 2011). However, it is clear that the Lesser Caucasus was located to the south of the Greater Caucasus and within the same tectonic sector of the Neo-Tethys Ocean.

The total brachiopod species diversity in the Azerbaijanian domains of the Lesser Caucasus was lower than that in the Northern Caucasus in the Berriasian, the Valanginian, and the Albian (Fig. 7). However, the total species number changed very similarly in these regions, and the Barremian diversity maximum was reached synchronously (Fig. 7). The total brachiopod generic diversity in the Azerbaijanian domains of the Lesser Caucasus was lower than that in the Northern Caucasus during the Early Cretaceous, except for the Barremian and the Aptian. The only difference in the generic diversity dynamics between the two compared regions is the peak that was reached in the Barremian in the Azerbaijanian domains of the Lesser Caucasus and in the Hauterivian in the Northern Caucasus. Such a similarity of the brachiopod taxonomic diversity dynamics between the two regions can be treated as an indirect evidence of their proximity in the Early Cretaceous. This matches the scenario, where both regions were situated at the northern margin of the Neo-Tethys Ocean. The comparison of assemblage composition between the Azerbaijanian domains of the Lesser Caucasus and the Northern Caucasus (RUBAN 2011a) indicates certain number of common species and genera, which supports the conclusion about their proximity.

Conclusions

The quantitative analysis of the Early Cretaceous taxonomic diversity dynamics of two groups of marine benthic invertebrates, namely brachiopods and gastropods, allows some conclusions:

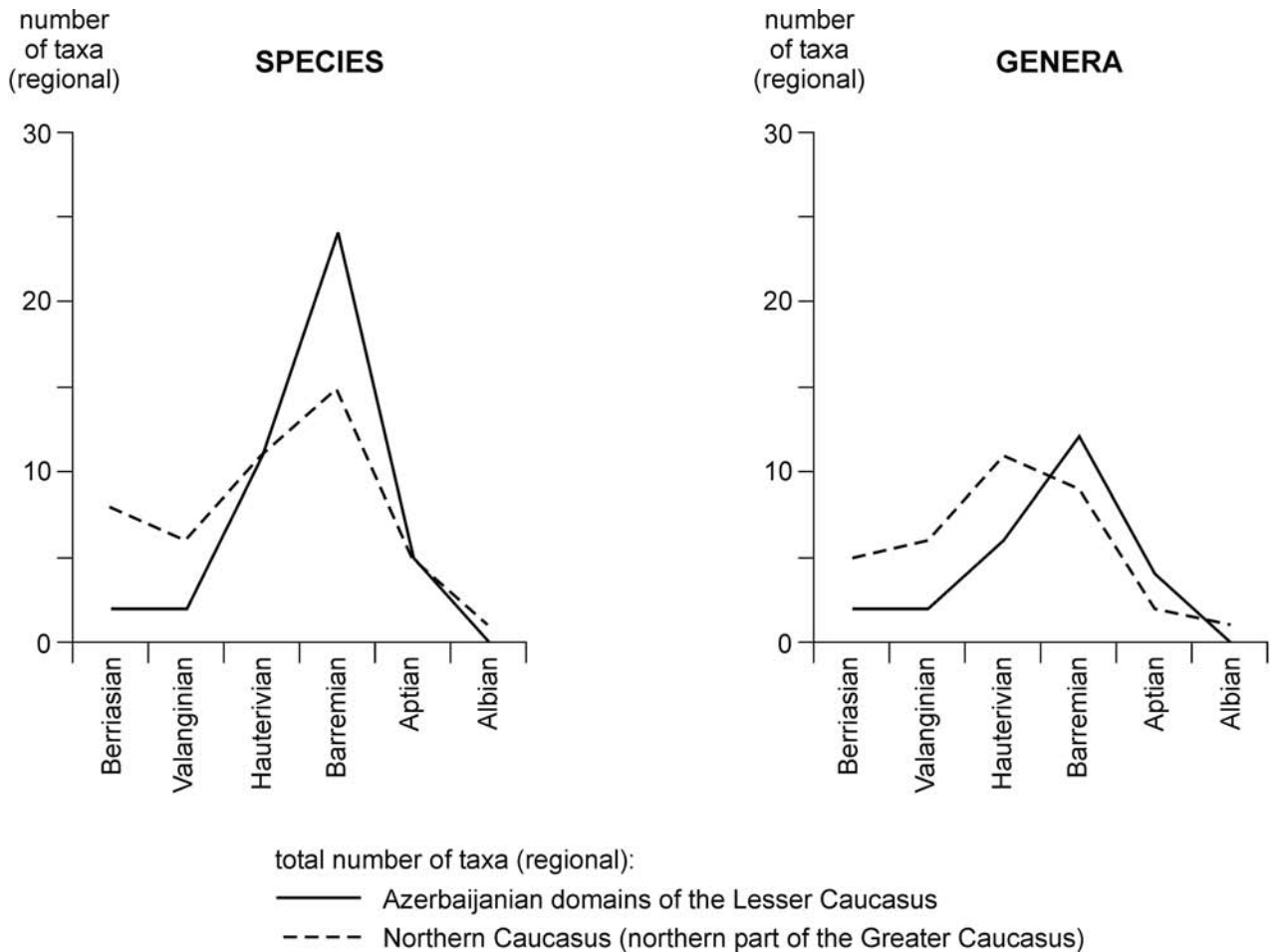


Fig. 7. Regional changes in the total number of species and genera of brachiopods in the Azerbaijanian domains of the Lesser Caucasus and the Northern Caucasus (after RUBAN 2011a).

- the number of species and genera of brachiopods increased in the Hauterivian, peaked in the Barremian, and dropped rapidly in the Aptian;
- the number of species and genera of gastropods increased in an strongly in the Barremian and then declined in the Aptian;
- the regional and global changes in the total generic diversity differed for each fossil group;
- the regional development of reefal ecosystems in the Barremian was likely responsible for the regional diversity maximum of marine benthic macroinvertebrates;
- the patterns of the taxonomic diversity dynamics of brachiopods were similar between the study area and the Northern Caucasus.

Further investigations should be aimed at evaluation of the Early Cretaceous diversity dynamics of such fossil groups as ammonites and belemnites. Sequence stratigraphical architecture and palaeoenvironmental changes also need accurate reconstruction to judge about the possible extrinsic controls on the fossil diversity.

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Резиме

Динамика таксономске разноврсности доњокредних брахиопода и пужева у Азербејданским областима Малог Кавказа (Нео-Тетис)

Фосилни налази Кавказа, велике области која се протеже између Црног мора и Каспијског мора, је користан за анализу биотичке еволуције креде. Брахиоподи и пужеви су чести у доњокредним наслагама у Азербејданским областима Малог Кавказа. Ове фосилне групе су погодне за анализу регионалне динамике таксономске разноврсности као и за њено даље поређење на глобалним нивоу. Азербејданске области Малог Кавказа обухватају Сомхит-Агдам, Севан-Карабах и Мисхан-Кафан тектонске зоне. Седименте доње креде чине карбонати и вулканокластити, који доминирају у сукцесијама укупне дебљине од ~ 1500 m и више. У овој студији коришћени су подаци који се односе на регионално и стратиграфско распрострањење доњокредних брахиопода и пужева. Сачињене су две регионалне базе података. Прва обухвата стратиграфско распрострањење 31 брахиоподске врсте, који припадају 14 родова. Друга база података приказује стратиграфско распрострањење 40 врста пужева који припадају 31 роду. Квантитативна анализа обухватила је процену укупне разноврсности таксона, као број њиховог појављивања и ишчезавања током доње креде. Број брахиоподских таксона значајно се променио у Азербејданској областима Малог Кавказ за време доње креде. Из берјаских и валандинских седимената познато је само неколико брахиоподских таксона. Међутим, укупна разноврсност брахиопода повећава се у отриву, а дуплира у барему. Током апта брахиоподске заједнице поново постају сиромашне, а у албу су потпуно непознате. Број гастроподских таксона такође варира током

доње креде. Први гастроподски таксон у проучаваном простору појавио се у отриву. Баремски век се карактерише значајном радијацијом пужева. Током апта њихова укупна разноврсност опада и упола је мања, мада су ипак и даље релативно разноврсни. Наласци гастропода нису потврђени из албских наслага проучаваног подручја. У албским седиментима проучаваног подручја пужви потпуно изостају. Поређење динамике регионалне таксономске разноврсности ове две групе морских бентоских бескичмењака указује на то да су обе групе достигле максимум у укупном броју врста и генеричке разноврсности у брему. Међутим, код брахиопода је дошло до постепене радијације и бржег опадања разноврсности, док је код пужева радијација била израженија и било је присутно постепено опадање разноврсности таксона. Постојала је фундаментална разлика између регионалне и глобалне динамике диверзитета како код брахиопода тако и код пужева. Штавише, ови фосили показују већу сличност у променама укупног броја родова на регионалном нивоу него што је то био случај на глобалном нивоу. Мало је вероватно да су регионалне трансгресије биле главни фактор који је контролисао динамику регионалне разноврсности брахиопода и пужева. Занимљиво је да глобални диверзитет брахиопода и пужева такође не одговарај дугорочним променама нива мора. Развој спрудних екосистема у барему би могао да буде објашњење за велику разноврсност брахиопода и пужева у односу на отривске и аптске интервале. На глобалном нивоу барем није познат као век са највећим распрострањењем спрудова. Њихова бројност је постепено расла током доње креде, али су врхунац достигли тек крајем ове епохе. Вероватно да регионални раст спрудних екосистема у барему објашњава због чега је максимум разноврсности морских бентоских бескичмењака забележен у Азербејданским областима Малог Кавказа али не и глобално у овом беку. Вјероватно, регионални раст спрудних екосистема само у Барему објашњава зашто максимална разноврсност морских бескичмењака бентосним је регистрована у Азербејданским доменима Мали Кавказ, али не глобално у овом кату. Сличност у динамици разноврсности брахиоподских таксона између Азербејданских области Малог Кавказа и Северног Кавказа је индиректан доказ њихове близине током доње креде. Даља истраживања би требало да имају за циљ процену доњокредне динамике диверзитета фосилних група као што су амонити и белемнители. Структура секвентне стратиграфије као и промене палеосредине такође захтевају прецизну реконструкцију како би могло да се суди о могућој спољашњој контроли фосилног диверзитета.

Appendix 1. Stratigraphical distribution of Early Cretaceous brachiopods and gastropods in the Azerbaijanian domains of the Lesser Caucasus. Based on data from AKOPJAN & KHALILOV (1986) and ALI-ZADEH (1988) with improvements. See text for more explanations.

BRACHIOPODS

T a x a	S t a g e s					
	Berriasian	Valanginian	Hauterivian	Barremian	Aptian	Albian
<i>Cruralina cruralinica</i> SMIRNOVA				×		
<i>Cyclothyris ardescica</i> (JACOB et FALLOT)			×	×		
<i>Cyclothyris castellanensis</i> (JACOB et FALLOT)			×	×		
<i>Cyclothyris contractoides</i> JACOB et FALLOT			×			
<i>Cyclothyris irregularis</i> (PICTET)			×	×		
<i>Cyclothyris kiparisovae</i> (MOISSEEV in LOBATSHEVA)			×			
<i>Cyclothyris larwoodi</i> (OWEN)				×		
<i>Cyclothyris lata</i> (D'ORBIGNY)			×	×	×	
<i>Cyclothyris tenuicostata</i> LOBATSHEVA				×		
<i>Cyrtothyris kentugajensis</i> (MOISSEEV)				×		
<i>Cyrtothyris middlemissi</i> Calzada					×	
<i>Cyrtothyris minor</i> (LOBATSHEVA)				×		
<i>Cyrtothyris pseudosella</i> (LOBATSHEVA)				×		
<i>Dzirulina marianovkaensis</i> (MOISSEEV in SMIRNOVA)				×		
<i>Fortunella decipiens</i> (D'ORBIGNY)				×		
<i>Lacunosella cherenmensis</i> (JACOB et FALLOT)			×	×		
<i>Lacunosella malbosi</i> (PICTET)	×	×		×		
<i>Lamellaerhynchia gillieronii</i> (PICTET)				×		
<i>Lamellaerhynchia picteti</i> BURRI				×		
<i>Lamellaerhynchia renauxiana</i> (D'ORBIGNY)				×		
<i>Loriolithyris russillensis</i> (DE LORIOI)			×	×		
<i>Moutonithyris karakaschi</i> MOISSEEV				×		
<i>Moutonithyris moutoniana</i> (D'ORBIGNY)				×		
<i>Nucleata</i> cf. <i>strombecki</i> (SCHLOENBACH)				×		
<i>Sellithyris campichei</i> (PICTET)	×	×				
<i>Sellithyris sella</i> (SOWERBY)			×	×	×	
<i>Terebrirostra?</i> aff. <i>neocomiensis</i> D'ORBIGNY			×	×		
<i>Terebrirostra taurica</i> (MOISSEEV)				×		
<i>Torquirhynchia astierana</i> (D'ORBIGNY)					×	
<i>Torquirhynchia aurea</i> (ELLIOTT)					×	
<i>Tropeothyris salevensis</i> (DE LORIOI)			×			

GASTROPODS (listed per stages)

T a x a	S t a g e s					
	Berriasian	Valanginian	Hauterivian	Barremian	Aptian	Albian
<i>Ampullospira kurdistanica</i> (ALIEV)					×	
<i>Ampullospira subupensis</i> ALIEV				×		
<i>Archimedeia archimedi</i> (ORBIGNY)				×		
<i>Balkanella garthisensis</i> (ALIEV)					×	
<i>Campichia azerbaijanensis</i> ALIEV et LYSENKO				×		
<i>Campichia margaritae</i> ALIEV et LYSENKO				×		
<i>Columbellina maxima</i> LOR.				×		
<i>Confusiscula</i> sp.					×	
<i>Contortella cylindrica</i> ALIEV				×		
<i>Contortella tuberculata</i> ALIEV				×		
<i>Culindrobulina geuialensis</i> ALIEV					×	
<i>Cylindroptyxis pellati</i> (COSSMANN)				×		
<i>Dalmatea bicarinata</i> ALIEV				×		
<i>Diozoptyxis coquandi</i> (ORBIGNY)				×	×	
<i>Diozoptyxis renauxi</i> (ORBIGNY)				×		
<i>Diozoptyxis traversensis</i> PICT. et CAMP.				×		
<i>Diptyxiella transcaucasica</i> ALIEV et LYSENKO				×	×	
<i>Diptyxis subdistincta</i> ALIEV				×		
<i>Funiptyxis pcelincevi</i> ALIEV				×		
<i>Harpogodes pelagi</i> (BRONG.)				×	×	
<i>Helicaulax caucasicum</i> ALIEV				×		
<i>Lissochilus subantonii</i> (ALIEV)					×	
<i>Lyosoma capduri</i> COSSMANN				×		
<i>Microchiza nickchici</i> PCELINCEV				×		
<i>Neoptyxis formosa</i> PCELINCEV				×		
<i>Nerinella algarbiensis</i> CHOFF.				×	×	
<i>Oonia pseudoovalis</i> ALIEV				×		
<i>Phaneroptyxis arnaudi</i> (MATH.)				×		
<i>Phaneroptyxis balkanensis</i> (PCELINCEV)				×		
<i>Pleurotomaria subjaccardi</i> PCELINCEV			×			
<i>Proacirsa provencali</i> COSSMANN					×	
<i>Purpuroidea pcelincevi</i> ALIEV					×	
<i>Salinea alizadei</i> (ALIEV)					×	
<i>Salinea pseudobella</i> (DVALI)				×		
<i>Sculpturea fogdtiana</i> (MORT.)				×		
<i>Trochonatica bruguierii</i> (MATH.)				×		
<i>Tylostoma depressum</i> PIC. et CAMP.				×		
<i>Tylostoma paranaticoide</i> ALIEV				×		
<i>Tylostoma rochatianum</i> PIC. et CAMP.				×		
<i>Umbanea favrei</i> ALIEV				×		

GASTROPODS (listed per substages)

T a x a	Substages					
	Early Hauterivian	Late Hauterivian	Early Barremian	Late Barremian	Early Aptian	Middle Aptian
<i>Ampullospira kurdistanica</i> (ALIEV)						×
<i>Ampullospira subupensis</i> ALIEV				×		
<i>Archimedeia archimedi</i> (ORBIGNY)				×		
<i>Balkanella garthisensis</i> (ALIEV)						×
<i>Campichia azerbaijanensis</i> ALIEV et LYSENKO			×	×		
<i>Campichia margaritae</i> ALIEV et LYSENKO			×	×		
<i>Columbellina maxima</i> LOR.				×		
<i>Confusiscala</i> sp.						×
<i>Contortella cylindrica</i> ALIEV				×		
<i>Contortella tuberculata</i> ALIEV				×		
<i>Culindrobulina geuialensis</i> ALIEV						×
<i>Cylindroptyxis pellati</i> (COSSMANN)			×	×		
<i>Dalmatea bicarinata</i> ALIEV				×		
<i>Diozoptyxis coquandi</i> (ORBIGNY)			×	×	×	
<i>Diozoptyxis renauxi</i> (ORBIGNY)			×	×		
<i>Diozoptyxis traversensis</i> PICT. et CAMP.			×	×		
<i>Diptyxiella transcaucasica</i> ALIEV et LYSENKO				×	×	
<i>Diptyxis subdistincta</i> ALIEV				×		
<i>Funiptyxis pcelincevi</i> ALIEV				×		
<i>Harpogodes pelagi</i> (BRONG.)				×	×	
<i>Helicaulax caucasicum</i> ALIEV				×		
<i>Lissochilus subantonii</i> (ALIEV)						×
<i>Lyosoma capduri</i> COSSMANN			×	×		
<i>Microchiza nickchici</i> PCELINCEV				×		
<i>Neoptyxis formosa</i> PCELINCEV				×		
<i>Nerinella algarbiensis</i> CHOFF.				×	×	
<i>Oonia pseudoovalis</i> ALIEV				×		
<i>Phaneroptyxis arnaudi</i> (MATH.)				×		
<i>Phaneroptyxis balkanensis</i> (PCELINCEV)				×		
<i>Pleurotomaria subjaccardi</i> PCELINCEV	×		×			
<i>Proacirsa provencali</i> COSSMANN					×	×
<i>Purpuroidea pcelincevi</i> ALIEV						×
<i>Salinea alizadei</i> (ALIEV)						×
<i>Salinea pseudobella</i> (DVALI)			×	×		
<i>Sculpturea fogdtiana</i> (MORT.)			×	×		
<i>Trochonatica bruguierii</i> (MATH.)			×	×		
<i>Tylostoma depressum</i> PIC. et CAMP.			×	×		
<i>Tylostoma paranaticoide</i> ALIEV				×		
<i>Tylostoma rochatianum</i> PIC. et CAMP.			×	×		
<i>Umbanea favrei</i> ALIEV				×		

Appendix 2. Stratigraphical distribution of Early Cretaceous coral genera in the Azerbaijanian domains of the Lesser Caucasus. Only Barremian and Aptian taxa were reported from this region. Based on data from ALI-ZADEH (1988) with improvements.

T a x a	Stages	
	Barremian	Aptian
<i>Actinastrea</i>	×	
<i>Clausastrea</i>	×	
<i>Cryptocoenia</i>	×	
<i>Dimorphocoenia</i>	×	
<i>Eohydnohora</i>	×	
<i>Eugyra</i>	×	
<i>Holocystis</i>	×	×
<i>Hydnophoromeandraraea</i>	×	
<i>Mesomorpha</i>	×	
<i>Metaulastraea</i>	×	
<i>Microsolena</i>	×	
<i>Placocolumastrea</i>	×	
<i>Polyphylloseris</i>	×	
<i>Pseudopolytremacis</i>	×	
<i>Rhipidomeandra</i>	×	
<i>Stelidioseris</i>	×	
<i>Thecosmilia</i>	×	