

Article

Species Diversity of *Radulopecten* (Pectinoidea, Bivalvia) in the Jurassic Seas of the Northern Central Neotethys: Reconsidering the Paleontological Information

Dmitry A. Ruban 

Department of Management Technology in Tourism Industry, Institute of Tourism, Service and Creative Industries, Southern Federal University, 23-ja Linija Street 43, Rostov-on-Don 344019, Russia; ruban-d@mail.ru

Abstract

Radulopecten Rollier, 1911 was a common bivalve genus in the Middle–Late Jurassic seas of the northern Central Neotethys. The present work offers measurements of the species diversity dynamics of this genus after reconsideration of the species names and the related corrections of their stratigraphic ranges. Information from four large domains of the northern Central Neotethys is employed. It is established that *Radulopecten* included seven species and evolved during the Bathonian–Tithonian interval in this region. The total number of species peaked in the Callovian, after which it declined. Globally, this genus had a slightly wider stratigraphic range (Bajocian–Tithonian), and its species diversity peaked in the Oxfordian. The regional diversity dynamics of *Radulopecten* may reflect some global regularities of changes in the species number modified by specific regional paleoenvironmental changes.

Keywords: diversity dynamics; marine bivalves; Mesozoic; paleobiology; stratigraphic ranges

1. Introduction

Diversity dynamics of fossil organisms has been the focus of paleobiological research for many decades. The seminal works by Alroy [1], Benton [2], Hallam [3], Peters and Foote [4], and Sepkoski et al. [5] stimulated related studies, which have addressed multiple aspects of diversity changes. The most recent examples of such studies are those, in particular, of Close et al. [6], Huang et al. [7], and Mannion [8]. Bivalves have evolved throughout the Phanerozoic, and their outstanding diversity and ecological differences make them interesting to paleobiologists [9–17]. The works by Aberhan and Fürsich [18], Ayoub-Hannaa et al. [19], Caswell and Dawn [20], Hallam [21], and Ros et al. [17] demonstrated that the diversity of Jurassic bivalves deserves special attention.

In order to examine the diversity of Jurassic bivalves, appropriate paleontological information is required. Despite the potential importance of tools such as the Paleobiology Database [22], traditional compilations of published paleontological data still matter. These compilations should be coupled with taxonomical and stratigraphical updates. Johnson [23] introduced many changes in the systematics of pectinoid bivalves, and Carter et al. [24] revised the suprageneric taxonomy of the entire class. These and many other changes are reflected, for instance, in the online reference system MolluscaBase [25].

Several generations of paleontologists have examined Mesozoic fossils in the vast territory of the former USSR. Most of the related information was published before the



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1990s and remained poorly known to the international research community. As a result, many important regions are true “white spots” in paleobiological research. Indeed, such gaps in the knowledge should be filled. Ruban [26] reviewed the information on Jurassic pectinoids from the Caucasus and used this information to reconstruct the diversity dynamics of these fossils. In the course of this analysis, it was realized that significant taxonomic updates were necessary: some specialists followed the “splitting” tradition, which resulted in an apparently unjustified increase in the number of taxa. Ruban [26] tried to solve this problem at the generic level, but also noted challenges for taxonomic revisions of species. The urgency and the complexity of these challenges make it reasonable to focus on particular genera that possessed many species and were widespread in the Jurassic seas. A typical example is *Radulopecten* Rollier, 1911, which was a Middle–Late Jurassic pectinoid genus; it was a rather common representative of the marine benthic macroinvertebrates in the Neotethyan tropical and subtropical seas, where it was an epifaunal suspension feeder [22,23,25]. This fossil was common in several domains of the northern Central Neotethys, where it evolved during the Bathonian–Tithonian interval [26,27]. Nonetheless, the regional diversity of this genus is yet to be fully understood, and the related international knowledge is limited [22,26]. This is a significant gap in the knowledge due to the large size of the considered territory (Figure 1a) and the duration of the above-mentioned time span (Figure 1b).

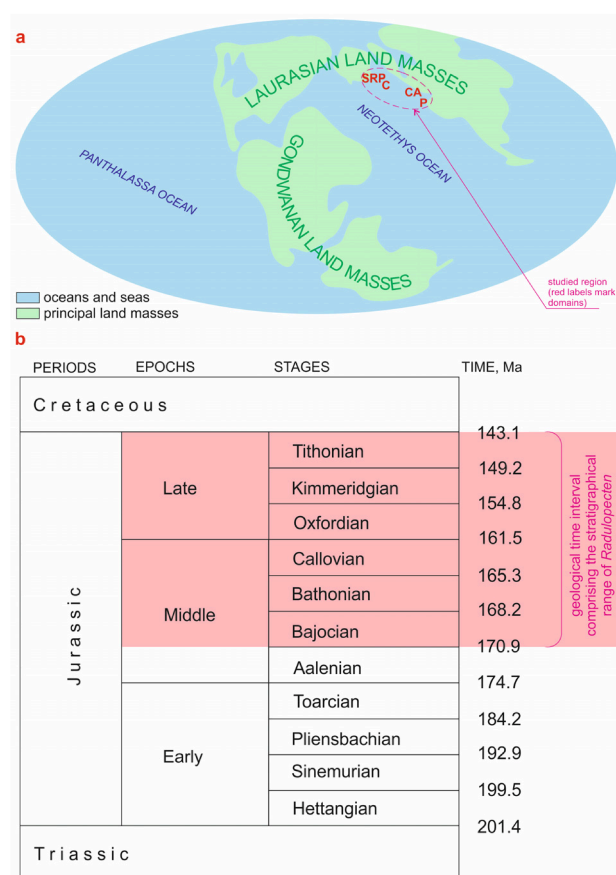


Figure 1. General geological context of the present study: (a) paleogeographical position of the studied region and its considered domains (C—Caucasus, CA—Central Asia, P—Pamir, SRP—southern Russian Platform and vicinities) at the Middle–Late Jurassic transition (indicated by the highly simplified information from [28]), (b) the considered time span (highlighted in rose color) on the geological time scale (according to [29]).

The present paper aims at a reconsideration of the available paleontological information on *Radulopecten* from several domains of the northern Central Neotethys and

subsequent reconstruction of its regional dynamics of species diversity. The achievement of these tasks contributes to filling the above-mentioned gap in the knowledge. The data from the studied region are important on the global scale, and it is very difficult to realize the changes in *Radulopecten* in the Jurassic without lines of evidence from the territory of the former USSR. It should be stressed that this study does not employ a full-scale taxonomic revision of the paleontological data, which would be an (almost) impossible task, but tries to take into account the most principal changes in the nomenclature of the above-mentioned genus. Also, the present work intends neither to support nor to question the utility of the major paleontological databases.

2. Materials and Methods

2.1. Studied Region

The studied region corresponds geographically to the wide belt stretching across southwestern Eurasia between the Black Sea and the Central Asian high mountains such as the Pamir (approximately 38–55° N and 30–75° E). It comprises four large domains, namely, the Caucasus (a late Cenozoic orogen between the Black and Caspian seas that includes the Greater Caucasus and the Lesser Caucasus), Central Asia (tectonic blocks between the Caspian Sea and the Pamir), the Pamir (a northeastern segment of the huge Cenozoic Hindu Kush–Pamir collision system), and the southern Russian Platform and vicinity (peripheral parts of a Precambrian craton and adjacent parts of a post-Hercynian plate and depressions). Presently, these are distinct territories, but they represent an important and still poorly known paleogeographical area. In the Jurassic, the very large Neotethys Ocean separated the Gondwanan land masses in the south from the Laurasian land masses in the north [28]. The studied region and its four considered domains were in a wide northern periphery of the central segment of this ocean (Figure 1a).

During the Middle and Late Jurassic epochs, which together lasted ~30 million years (Figure 1b), the studied region was embraced by large, semi-enclosed, relatively shallow, generally warm, marginal seas with common carbonate deposition (nonetheless, siliciclastics also accumulated) and very rich ecosystems [30–32]. Pectinoid bivalves and, particularly, *Radulopecten* were common in benthic macroinvertebrate communities [26,27].

2.2. Paleontological Data

In the present study, the data were gathered and treated through several procedures (Figure 2). The main source of the paleontological and stratigraphical information on *Radulopecten* is the detailed monograph by Romanov [27]. It characterizes representatives of this genus from the southern part of the territory of the former USSR. All established species were formally described in that monograph, and their stratigraphic ranges were indicated. This source established the presence of many species of *Radulopecten* in the Caucasus, Central Asia, the Pamir, and the southern Russian Platform and vicinity. Ruban [26] extended and slightly corrected the information related to the Caucasus. These updates permitted improvement of the knowledge of the stratigraphic distribution of this genus in the noted domain. The broadly-accepted definition of the Jurassic stages [29,33] was followed.

The monograph by Romanov [27] appeared almost simultaneously with the seminal work by Johnson [23]. Although the species nomenclature of *Radulopecten* followed in the data sources [26,27] can be treated within the terms of the “splitting” tradition, one should note that Romanov [27] did not propose many new species, but simply followed the works published before Johnson [23] and, apparently, supported a “narrow” understanding of species. In other words, when this specialist described numerous species, this was not an intentional “splitting”.

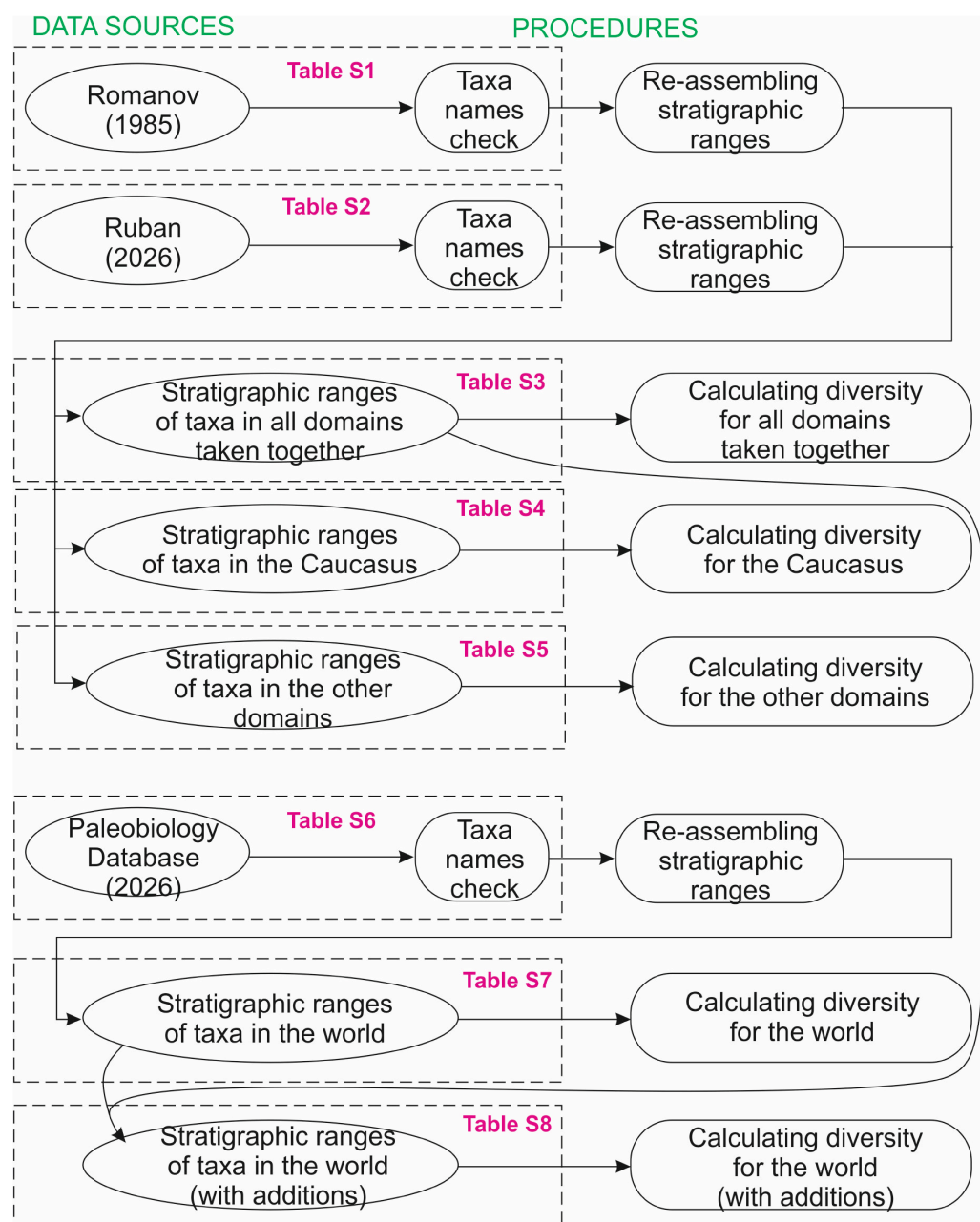


Figure 2. Information treatment and analytical procedures of the present study (some text labels are highlighted in green and violet for better visibility). Tables S1–S8 are presented in Supplementary Information. The sources indicated in the figure: Paleobiology Database (2026)—[22], Romanov (1985)—[27], Ruban (2026)—[26].

A principal task of the present study was the reconsideration of the available data. For this purpose, the names of all species considered by Romanov [27] and Ruban [26] were checked on MolluscaBase [25], with its extensive coverage of bivalve taxa and implementation of the up-to-date species nomenclature (the latter is reflected in Tables S1–S8). This solution, when the names are checked, seems optimal because re-examinations of original collections are a challenging task due to the questionable accessibility of the collections (this is why a full-scale taxonomic revision seems to be unrealistic). A kind of limitation is that the names of bivalves become dependent on the information from MolluscaBase [25]. Published sources with original taxonomic descriptions can be engaged if one decides to revise not only taxa names but also the previous identifications of specimens. This ambitious task is left for further investigations. In the present study, some species were reconsidered

as junior synonyms, as invalid taxa, or as belonging to other genera. Various taxonomic improvements required the creation of updated lists of species of *Radulopecten* for the entire region and its domains, with related changes in the stratigraphic ranges (Tables S1–S8). Moreover, it was reasonable to merge data from Romanov [27] and Ruban [26]. These procedures resulted in the generation of a new set of paleontological information, which was employed in this work (Figure 2).

2.3. Analytical Procedures

The stratigraphic ranges of species permitted an examination of the diversity dynamics of *Radulopecten* according to the stages of the Jurassic Period (Figure 2). The stages are understood according to the recommendations of the International Commission on Stratigraphy and the current version of the geological time scale [29,32]). The basic procedures for the analysis of the species diversity dynamics (e.g., [34]) were employed as follows.

First of all, the total number of species in the entire studied region was calculated for each stage. Then, the numbers (rates) of appearances and disappearances were counted. One should note that “appearance” and “disappearance” are more detailed terms than “origination” and “extinction”. The former takes into account that a given species might have appeared in a particular region later than in other loci due to relatively long-term migration or regionally unfavorable environments, and that it might have disappeared earlier in a specific region than is recorded globally. The unavoidable incompleteness of the regional fossil records related to sampling procedures or preservation potential also matters. Some stratigraphic ranges were interrupted by temporary disappearances and subsequent re-appearances of taxa. Therefore, the numbers of appearances and disappearances are reasonable parameters. Additionally, attention was paid to singletons, which are taxa with existence limited to one stage [35].

The patterns of the species diversity dynamics were also analyzed in particular domains, with special attention to the Caucasus. Its record of Jurassic bivalves seems to be relatively better because of more extensive studies synthesized by Ruban [26]. For the Caucasus, the total species diversity and the numbers of appearances and disappearances were considered. Then, the changes in the total number of species in this domain were compared with those in the three other domains.

3. Results

3.1. Reconsidered Paleontological Data

Reconsideration of the original paleontological information was extensive. Romanov [27] mentioned 14 species of *Radulopecten* from Jurassic deposits of the studied region. However, one species is attributed to a different genus (*Pseudopecten* Bayle, 1878), and the remaining 13 species are reconsidered as only seven valid species (Table S1). Notably, *Radulopecten ilolikensis* Romanov, 1985 remains valid. Regardless, the total regional diversity of *Radulopecten* was halved. Ruban [26] indicated stratigraphic ranges of 14 species of *Radulopecten*. They were reevaluated (Table S2). Many earlier established species were attributed to *Radulopecten scarburgensis* (G. Young & Bird, 1822).

After combining the revised lists (Tables S1 and S2), seven valid species of *Radulopecten* were registered in the Jurassic record of the studied region (Table S3). Their presence was established in the Bathonian–Tithonian deposits, and a single taxon, namely, *Radulopecten scarburgensis* (G. Young & Bird, 1822), was found in all five stages of the noted stratigraphic interval. Singletons are represented by *Radulopecten fibrosodichotomus* (Kasansky, 1909), *Radulopecten ilolikensis* Romanov, 1985, and *Radulopecten subinaequicostatus* (Kasansky, 1909).

3.2. Regional Diversity Dynamics

The stratigraphic ranges of the species of *Radulopecten* (Table S3) imply that this genus reached its maximum diversity in the Callovian, after which the number of species decreased gradually (Figure 3). Several representatives of this genus appeared in the Bathonian, and the genus diversified quickly due to the high rate of appearances (Figure 3). Subsequently, this rate declined, but the number of disappearances remained rather stable (Figure 3). New species did not appear in the Kimmeridgian–Tithonian, and several species that appeared in the earlier stages continued to exist (Figure 3). Notably, singletons existed only in the Callovian–Oxfordian, and they can be related to short-term invasions or evolutionary “experiments”.

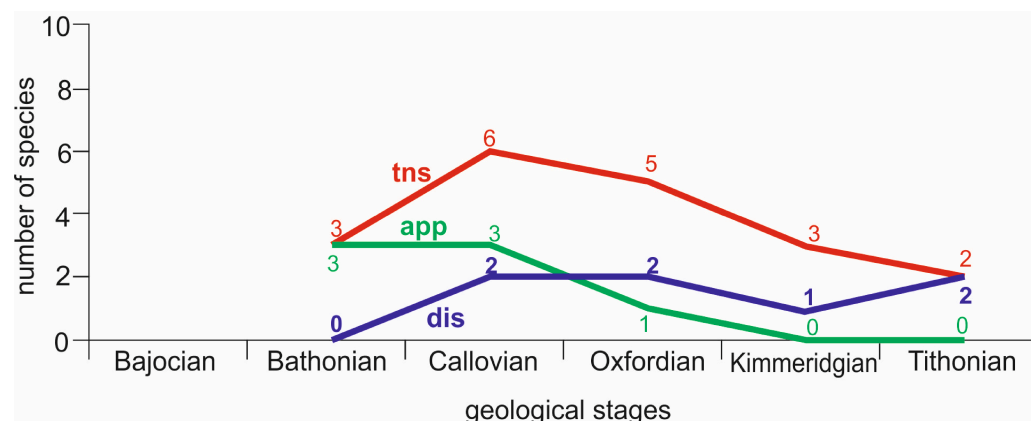


Figure 3. Diversity dynamics of *Radulopecten* in the studied region (four domains taken together): tns—total number of species (red line), app—number of appearances (green line), dis—number of disappearances (blue line) (based on the data from Table S3). Numbers above lines indicate values; the colors of the numbers correspond to the colors of the lines.

The stratigraphic distribution of *Radulopecten* in the Jurassic of the Caucasus (Table S4) reveals chiefly the same patterns of diversity dynamics (Figure 4a). Three differences are as follows: (a) the Callovian total diversity peak was more pronounced (Figure 4a), (b) the total diversity declined in the Kimmeridgian and rose slightly in the Tithonian (Figure 4a), (c) new species did not appear in the Late Jurassic, whereas the rate of disappearances accelerated in this stage (Figure 4a). Two singletons existed in the Callovian (Table S4). An interesting feature is the disappearance of *Radulopecten scarburgensis* (G. Young & Bird, 1822) in the Oxfordian and its re-appearance in the Tithonian (Table S4).

The stratigraphic ranges of species in the considered domains of the studied region (Tables S4 and S5) permit outlining similarities and differences between these domains. The Callovian diversity peak and the lower diversity in the Late Jurassic were common to all domains (Figure 4b). The second peak in the number of species in the Kimmeridgian is recorded only in the southern Russian Platform and vicinity (Figure 4b). Moreover, the Caucasus was the only domain where *Radulopecten* existed in all stages of the Bathonian–Tithonian interval (Figure 4b). The dissimilarities between the domains can be explained by differences in their paleoenvironments or preservation potential. Because the main portion of the data is taken from the monograph by Romanov [27], it is expected that the information from the four domains is rather homogenous regarding stratigraphic resolution and paleontological sampling.

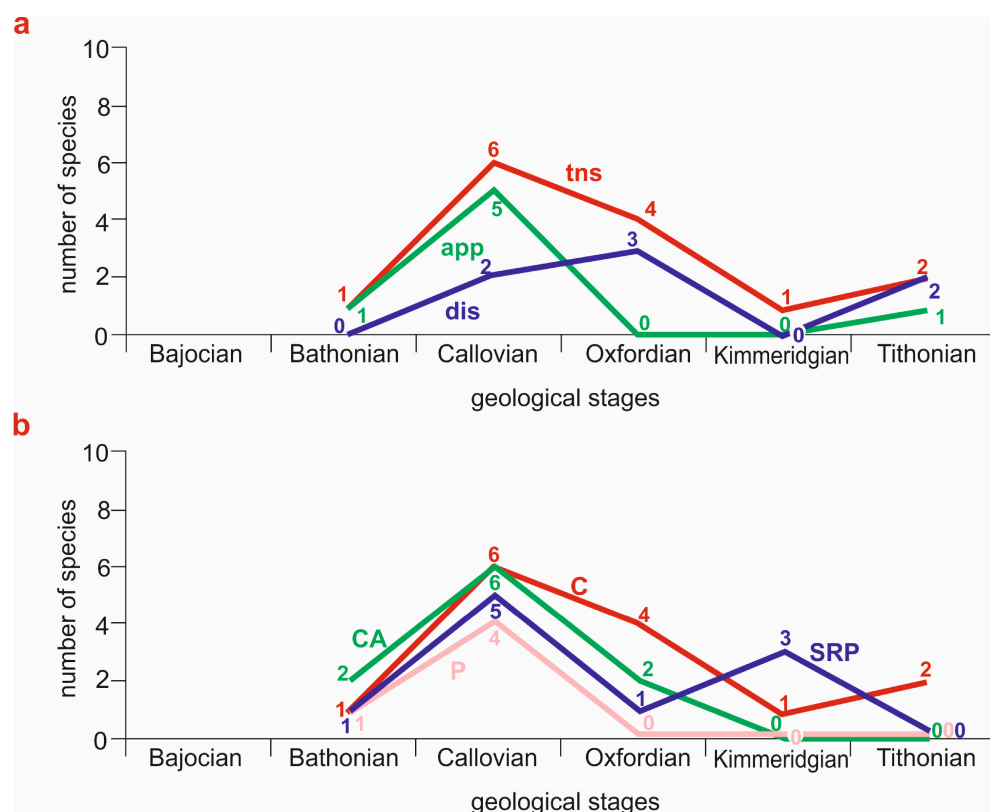


Figure 4. Diversity dynamics of *Radulopecten* in the different domains of the studied region: (a) changes in the total number of species (tns, red line), number of appearances (app, green line), and number of disappearances (dis, violet line) in the Caucasus (based on the data from Table S4); (b) changes in the total number of species in the Caucasus (C, red line), Central Asia (CA, green line), the Pamir (P, pink line), and the southern Russian Platform and vicinities (SRP, blue line) (based on the data from Table S5). Numbers above lines indicate values; the colors of the numbers correspond to the colors of the lines.

4. Discussion

4.1. Global Versus Regional Diversity Changes

The species diversity dynamics established in the present study reflects the history of *Radulopecten* in the northern Central Neotethys. However, the geographical distribution of this genus was much wider [22,23,36–38], and, thus, it is reasonable to compare the regional and global diversity. Despite the criticism regarding its completeness and biases [39,40], the Paleobiology Database [22] appears to be the most evident and up-to-date source of paleontological information for discussions of global diversity changes in particular groups of fossils. The genus *Radulopecten* was found there, and the information about the stratigraphic ranges of its species was extracted “manually” from the compilation presented in the window “Age range and collections” of the record of this genus in the considered database (this procedure was carried out in March 2026). When the same species were mentioned two or more times, the joint stratigraphic ranges were composed. The stratigraphic distribution of more than a dozen species was recorded (Table S6). Surprisingly, the knowledge of *Radulopecten* contained in the Paleobiology Database [22] does not seem to be perfect regarding the names of species and the completeness of the information. To address these challenges, some taxonomic improvements were carried out (Table S6), and the stratigraphic ranges of species were updated accordingly (Table S7). Moreover, it was found reasonable to couple this information with the lines of evidence from the studied region (Table S8) (Figure 2).

After the above-mentioned revisions, it was established that *Radulopecten* developed during the Bajocian–Tithonian interval, i.e., it appeared one stage earlier than in the northern Central Neotethys (Table S8). No species was reported from all stages of the noted interval, and singletons were typical of the Callovian–Oxfordian (Table S8). The global species diversity of *Radulopecten* remained relatively low during the Bajocian–Callovian, which was followed by the Oxfordian peak, and then the number of species decreased (glb-imp curve in Figure 5). The addition of the information from the studied region changes the total diversity curve. A gradual diversification through the Bajocian–Oxfordian becomes evident, and the diversity decline in the Tithonian seems to be less strong (glb-add curve in Figure 5).

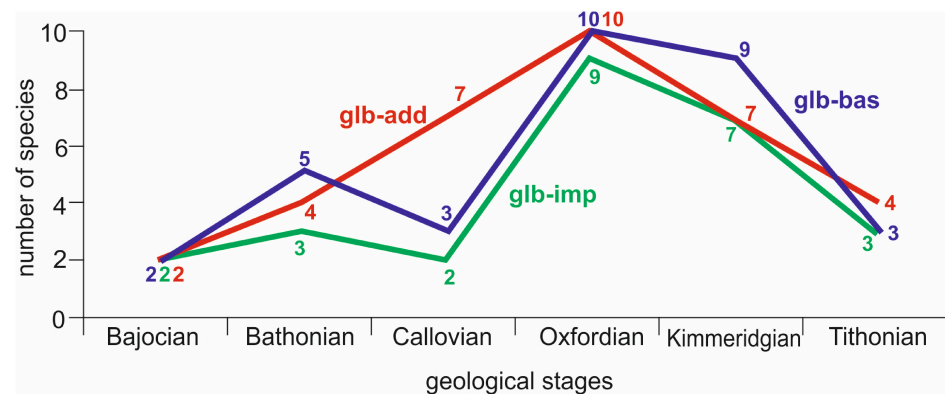


Figure 5. Global changes in the total number of species of *Radulopecten*: glb-bas—on the basis of the baseline data from the Paleobiology Database [22] (blue line) (see Table S6), glb-imp—on the basis of the improved data from the Paleobiology Database [22] (green line) (see Table S7), glb-add—on the basis of the improved data from the Paleobiology Database [22] coupled with the reconsidered data from the studied region (red line) (see Table S8). Numbers above lines indicate values; the colors of the numbers correspond to the colors of the lines.

The single wave-like changes in the total number of species are observable both regionally (Figure 3) and globally (Figure 5). However, there is a striking difference in the Callovian–Oxfordian interval. *Radulopecten* reached the regional peak in the Callovian and the global peak in the Oxfordian (Figure 5). The position of the global peak is not changed even after the addition of the regional information (compare glb-imp and glb-add curves in Figure 5).

The interpretations presented above should be treated with certain caution, and, thus, they remain tentative. On the one hand, the Paleobiology Database [22] could be incomplete. For instance, the novel information from Tibet [41,42] needs attention. On the other hand, the present diversity estimates in the northern Central Neotethys are based on the avoidance of the “splitting” tradition. However, it was explained above that this tradition appeared more as a narrow understanding of species than an unjustified multiplication of taxa. If so, the avoidance of this tradition may not be necessarily correct (it is correct only with respect to the contemporary and “mainstream” research), and the related discussions can be revitalized in the future. This also means that the outcomes of the present study do not challenge the previous interpretations (e.g., [26]), but simply follow a different point of view. Moreover, the fundamental developments by Johnson [23] and those reflected by MolluscaBase [25] may also be incomplete or geographically biased, and, therefore, a new reconsideration of the regional and global knowledge of *Radulopecten* will be required in the future.

4.2. Possible Factors of Diversity Changes

The results imply that the regional species diversity of *Radulopecten* did not remain stable during the Middle–Late Jurassic, and the related changes need to be explained. First

of all, one should note the similar shape of the regional (Figure 3) and global (Figure 5) diversity curves. This similarity itself indicates the presence of some global control on the regional dynamics.

The planetary climate experienced strong changes during the considered geologic time interval: a cooling trend started in the beginning of the Middle Jurassic and culminated in the Callovian coldhouse conditions, and greenhouse conditions were restored only in the Tithonian [43]. Somewhat similar changes took place in the northern Central Neotethys, although they are better expressed in the domains with a relatively northward position [32]. Regardless, the global climate shifts affected the northern Central Neotethys, as well as the entire Neotethyan sector of the Earth because they remained at generally the same latitudes during the Middle–Late Jurassic, as evidenced by the plate tectonic reconstructions of Scotese [28]. According to Haq [44], a tendency to a global sea-level rise was established in the Bathonian and culminated in the Late Jurassic. Indeed, this tendency could be responsible for wide transgressions and the development of large shallow-water seas with siliciclastic or mixed siliciclastic–carbonate sedimentation near the Middle–Late Jurassic transition [31,32,34]. Further warming resulted in the growth of carbonate platforms [31,34]. These paleoenvironmental changes can explain the observed similarity of the regional (Figure 3) and global (Figure 5) diversity curves.

Apparently, some regional factors modified the signatures of the global patterns in the northern Central Neotethys. For instance, the establishment of vast, shallow-water marine environments in the Caucasus in the Callovian [32,34] could explain the relatively early diversity peak of *Radulopecten*. The local salinity crisis in the Late Jurassic [34] could explain the reduction in the regional species diversity in the Kimmeridgian. It is worth considering the preservation potential related to the lithological changes. In the Caucasus, the preservation of bivalves in Callovian siliciclastics is much better than that in Oxfordian–Kimmeridgian carbonates. However, the overall bivalve diversity in the Callovian and the Oxfordian was comparable [34]. This is why it would be difficult to suppose a difference in the preservation potential between these stages.

One can also take into account the different durations of the stages (Figure 1b). The present version of the geological time scale [29] implies that the Oxfordian was significantly longer than the two preceding stages and slightly longer than the two next stages (Figure 1b). Although this may be used as a tentative explanation of the global peak in the species diversity of *Radulopecten* in the Oxfordian (Figure 5), this explanation is not applicable to the studied region where the number of species peaked in the relatively short Callovian (Figure 3). Moreover, the different durations of the stages may only have played a role if the rates of speciation remained more or less constant during the entire history of *Radulopecten*. Evidence in support of this assumption is not available.

5. Conclusions

The reconsideration of the species diversity of *Radulopecten* from four domains of the northern Central Neotethys permits us to draw three general conclusions.

- (1) The total number of species of *Radulopecten* peaked in the Callovian, and this peak was registered in all four considered domains of the studied region.
- (2) The species diversity of *Radulopecten* peaked globally in the Oxfordian, and the addition of the information from the northern Central Neotethys does not change this pattern.
- (3) The established diversity dynamics of the considered genus can be explained by the interplay between global and regional factors.

Radulopecten is one of many bivalve genera reported from Jurassic deposits of the territory of the former USSR. A huge amount of work is required to reconsider the information on other genera, and their full-scale taxonomic revision will be an even more challenging

task. Nonetheless, the outcomes of the present study demonstrate that this ambitious work can be continued step by step to contribute to the global knowledge of Jurassic bivalves.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/geosciences16070280/s1>. Table S1: Reconsideration of the information on *Radulopecten* from Romanov (1985). Table S2: Reconsideration of the information on *Radulopecten* compiled by Ruban (2026). Table S3: Stratigraphic distribution of the valid species of *Radulopecten* in all considered domains (based on the information from Tables S1 and S2). Table S4: Stratigraphic distribution of the valid species of *Radulopecten* in the Caucasus (based on the information from Tables S1 and S2). Table S5: Stratigraphic distribution of the valid species of *Radulopecten* in three considered domains (based on the information from Table S1). Table S6: Reconsideration of the information on *Radulopecten* from the Paleobiology Database (PBDB, 2026). Table S7: Stratigraphic distribution of the valid species of *Radulopecten* in the world as can be deduced from the Paleobiology Database (PBDB, 2026) (based on the information from Table S6). Table S8: Stratigraphic distribution of the valid species of *Radulopecten* in the world as can be deduced from the Paleobiology Database (PBDB, 2026) with additions from all considered domains (based on the information from Tables S3 and S7). The sources mentioned in the tables: MB (2026)—[25], PBDB (2026)—[22], Romanov (1985)—[27], Ruban (2026)—[26].

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