

Diversity dynamics of Early–Middle Jurassic brachiopods of Caucasus, and the Pliensbachian–Toarcian mass extinction

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Taxonomic diversity of NW Caucasus brachiopods changed cyclically in the Early–Middle Jurassic. Diversifications took place in the Late Sinemurian–Early Pliensbachian, Middle–Late Toarcian and Late Aalenian–Early Bajocian, while diversity decreases occurred in Late Pliensbachian–Early Toarcian, Early Aalenian and Late Bajocian. Outstanding diversity decline in the Late Pliensbachian–Early Toarcian corresponds to a global mass extinction interval, whose peak has been documented in the Early Toarcian. Similar diversity changes of brachiopods are observed in other Tethyan regions, including the well-studied Bakony Mountains, although in NW Caucasus the recovery after demise have begun earlier. The causes of Pl-To mass extinction in the studied region are enigmatic. Probably, it could be linked to anoxia, but its correspondence to the beginning of transgression is not coincident with the global record, so eustatic causes seem to be doubtful for this region.

Key words: Brachiopoda, taxonomic diversity, mass extinction, Jurassic, Caucasus, Russia.

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Introduction

The Late Pliensbachian–Early Toarcian (Early Jurassic) mass extinction is one of the most significant events in geological history. Although it is often called a “small” mass extinction in relation to such great biotic crises as Permian–Triassic or Cretaceous–Tertiary ones, it has been recognized for many principal groups of fossil organisms: foraminifers, bivalves, brachiopods and ammonoids (Hallam and Wignall 1997). Moreover, it provides an excellent example to study possible causal relations of mass extinctions to anoxia, major sea-level changes and intensive volcanism. The knowledge on the Early Jurassic mass extinction has grown thanks to the studies of Hallam (1961), who analyzed the fossil record, and Jenkyns (1988), who identified oceanic anoxia. In the past decade numerous publications on Liassic biotic changes by Hori (1993), Bassoulet and Baudin (1994), Little and Benton (1995), Aberhan and Fürsich (1997, 2000), Hallam and Wignall (1997, 1999), Harries and Little (1999), Guex et al. (2001), Wignall (2001), Jenkyns et al. (2002), and others have substantially added to previous results. A special study was dedicated to establishing the precise absolute radiometric age of the mass extinction, which is now accepted as 183 ± 2 Ma (Pálffy et al. 2002).

Although one of the main fossil groups used to discuss the Late Pliensbachian–Early Toarcian (Pl-To) mass extinction are Bivalvia (Aberhan and Fürsich 1997, 2000; Harries and Little 1999), Brachiopoda seem to be no less important. Their significance in discussion of this decimation has been shown in articles of Hallam (1987), Bassoulet and Baudin (1994), and Vörös (1993, 1995, 2002).

Every mass extinction should be studied both using comparative global and regional data analyses to understand better its appearance in geological time and space. Results of quantitative analysis of taxonomic diversity dynamics of Early–Middle Jurassic brachiopods of Northwestern Caucasus are presented in this paper. The appearance of a biotic crisis in this Tethyan region allows one to extend the area where this mass extinction can be documented.

Geological setting

In the Mesozoic the Caucasus region was located on the northern active periphery of Tethys (Lordkipanidze et al. 1984; Meister and Stampfli 2000). Although brachiopods have been found in Jurassic deposits in this entire region, the most complete data are from NW Caucasus (Fig. 1). In tectonical aspect this territory covers 3 major tectonic zones: Labino-Malkinskaja zone, Pshkish-Tyrnyauzskaja zone and Arkhyz-Guzeripl'skaja zone (Rostovcev et al. 1992).

The Lias to Dogger stratigraphy and lithology of NW Caucasus have been described by Krymgolc (1972), Rostovcev et al. (1992), Granovskij et al. (2001), Ruban (2002), and also in *Stratigrafičeskij slovar'* (1979). The Rhaetian–Hettangian interval corresponds to a major regional hiatus. Smaller hiatuses divide Pliensbachian from Toarcian strata and Aalenian from Bajocian ones. Sinemurian–Pliensbachian deposits about 500 m thick include conglomerates, sandstones, dark shales and rare limestones. Lower–Middle (lower interval) Toarcian deposits (up to 70 m thick) are

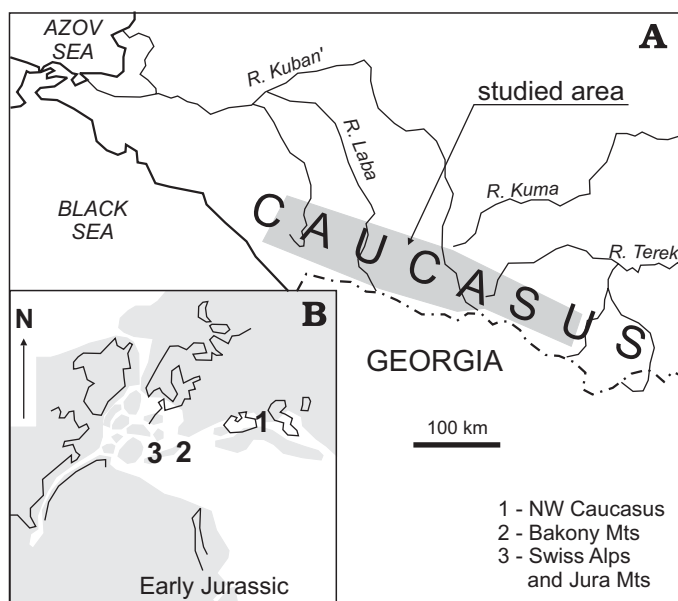


Fig. 1. Geographic location of studied area (A) and paleogeographic situation of areas discussed in the text (B; studied area indicated by 1). Paleogeographic base map is modified from Owen 1983 and Dommergues et al. 2001.

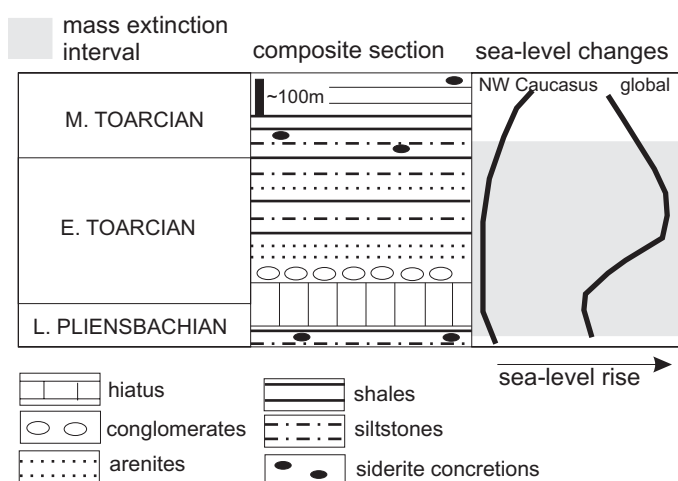


Fig. 2. Liassic composite lithological section of NW Caucasus and comparison of regional and global (simplified from Hallam and Wignall 1999) sea-level changes.

terrigenous (Fig. 2), but in the Middle (upper interval)–Upper Toarcian and Aalenian 1500 m of laminated dark to black shales have been accumulated. Bajocian deposits are represented by dark shales (up to 1200 m), often with interbeds of terrigenous or volcanogenous deposits. Dark shales contain siderite concretions. The highest concentration of them has been observed in the Middle–Upper (lower interval) Toarcian (Ruban 2002). But both rare dark shales horizons and concretions have been found also in the Middle (lower interval) Toarcian deposits.

The Jurassic paleoenvironments of the studied territory have been described in thanks of geochemical studies and

numerous paleogeographical reconstructions by Âsamanov (1978). The Sinemurian sea was relatively shallow with normal salinity, the climate was subtropical and humid, and in the Pliensbachian the basin became deeper. Regression took place in Late Pliensbachian–Early Toarcian times followed by a fast transgression that started in the end of Middle Toarcian and in the Late Toarcian–Early Aalenian marine basin was deep. Dark shales of this interval are interpreted as slope deposits (Granovskij et al. 2001). The paleotemperatures of sea-water were about 20–22°C. Regression occurred in the Aalenian, and the climate became more moderate. Paleotemperatures decreased to 10°C, while in the Late Aalenian they were once again about 20–23°C. In Bajocian the sea became deep and the climate returned to be subtropical and humid. Paleotemperatures identified were 25–27°C. In general terms, during all the Early–Middle Jurassic the Caucasus basin was not separated from the Tethyan ocean too much.

Materials

Early to Middle Jurassic brachiopods of NW Caucasus are rather well-studied. The first complete revisions have been made by Neumayr and Uhlig (1892), and then by Moiseev (1934) followed by the works by Makridin and Kamyšan (1964), Prosorovskaya (1986, 1989, 1993), and Rostovcev et al. (1992).

The most complete and taxonomically revised data on stratigraphic distribution of brachiopods have been presented by Makridin and Kamyšan (1964), Prosorovskaya (1989, 1993) and Rostovcev et al. (1992). These sources have been used to compile the diversity data, following by some revisions and stratigraphical corrections. In the whole 83 species from the Lower Jurassic and 51 ones from Middle Jurassic were recognized (see Appendix). The stratigraphical ranges of taxa are as detailed as the substages recognized in the ammonite succession (Rostovcev et al. 1992).

Total species quantity, and number of originations and extinctions have been calculated for each substage from Sinemurian to Bajocian to analyze the taxonomic diversity dynamics.

Species diversity dynamics

Species diversity of brachiopods changed dramatically in NW Caucasus (Fig. 3). After the great diversification in the Sinemurian–Early Pliensbachian (up to 54 taxa), a severe diversity decline occurred in Late Pliensbachian. This trend continued into the Early Toarcian, when brachiopods disappeared entirely. In the Middle–Late Toarcian a new gradual diversification took place (total diversity reached 14 taxa), although it did not compensate for the previous decline. Once again brachiopods disappeared in the Early Aalenian (probably two taxa are

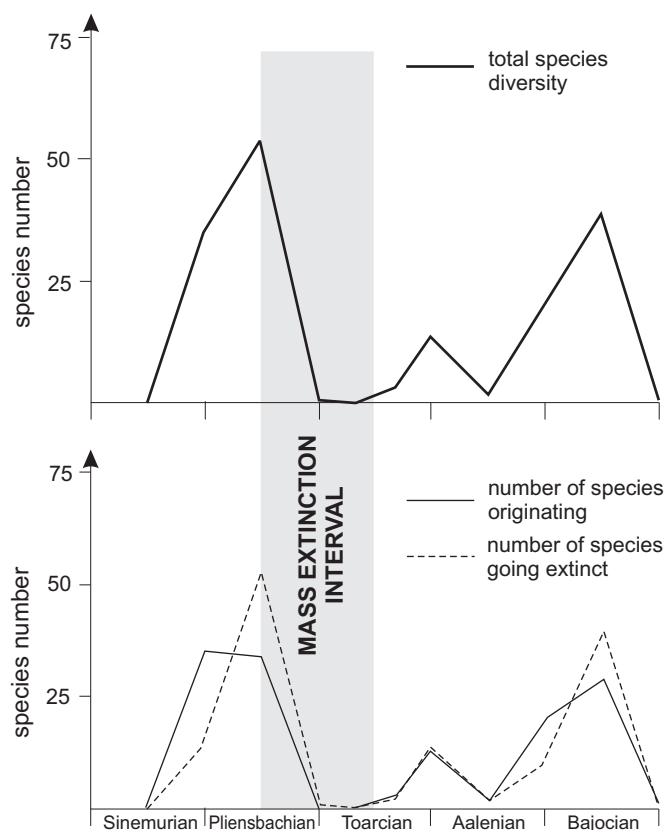


Fig. 3. Total species diversity changes, origination and extinction rates of NW Caucasus brachiopods in Early–Middle Jurassic.

known). Then a new acceleration of diversity is observed during Late Aalenian–Early Bajocian. Later Middle Jurassic brachiopod communities became extinct again. But the most outstanding features of the regional brachiopod history are the Late Sinemurian–Early Pliensbachian acme followed by Late Pliensbachian–Early Toarcian demise.

The origination and extinction rates help us to understand the causes of such turnovers (Fig. 3). Late Sinemurian–Early Pliensbachian diversification has been followed by increase both of origination and extinction. When the disappearance rate became higher, a regional diversity drop occurred. Also the Late Pliensbachian–Early Toarcian demise of brachiopods corresponded to collapse of origination rate. The Early Aalenian and Late Bajocian crises also can be explained in the same way.

An analysis of events connected with disappearance of fossils should always take into account so-called Lazarus-taxa (Flessa and Jablonski 1983; Jablonski 1986; Wignall and Benton 1999; Fara 2001). The Lazarus effect causes a significant gap in any taxon's range. Among Early–Middle Jurassic brachiopods of the studied region only three Lazarus-taxa have been found (see Appendix). The interval of their absence covers the Late Pliensbachian–Early Toarcian in the NW Caucasus, and for two of them—also the Middle Toarcian. It is evident, that such a negligible Lazarus effect could not significantly influence the above mentioned results.

Discussion

Regional record of Pl-To crisis.—As shown above, the most intensive drop in brachiopods diversity occurred in Late Pliensbachian–Early Toarcian. This time interval approximately corresponded to the mass extinction, whose most intensive phase embraced the Early Toarcian (Hallam and Wignall 1997). As the Caucasus sea was connected with Tethys, there was no barrier to isolate the local biota from the disastrous global factors.

The ecosystem collapse was indeed the most profound in the Early Toarcian, when brachiopods regionally disappeared. However, whilst the decrease of diversity began only in the Late Pliensbachian; the decline of origination rate was documented already in the Early Pliensbachian. In this timespan, the benthos disappearance also intensified, and the initial phase of the crisis took possibly place in the Early Pliensbachian. The recovery of brachiopods has been documented in the Middle Toarcian. But only the intensification of benthic colonization and total species diversity increased (i.e., the repopulation stage) in the Late Toarcian can be considered as a record of the final crisis termination. So, severe extinction have certainly influenced development of the Caucasus brachiopod biota during the Late Pliensbachian–Middle Toarcian.

It is important to compare the brachiopods diversity data with those of other shelly benthos like bivalves. The most recent compilative paper devoted to Jurassic pectinoids from the southern regions of the former Soviet Union, including Caucasus, has been published by Romanov and Kasum-Zade (1991). Stratigraphic ranges chart presented by these authors allows the recalculating of the total species quantity changes through the Late Liassic (Fig. 4). After a rather strong diversification of pectinoids in the Pliensbachian a relatively small diversity drop (~30%) is recognizable in the Early Toarcian. The species number was relatively low till the Bajocian when a new rise occurred. This diversity changes means: (1) decline of bivalves was not as significant as that of the brachiopods, and (2) it occurred after a great diversification event which is similar to those observed for brachiopods.

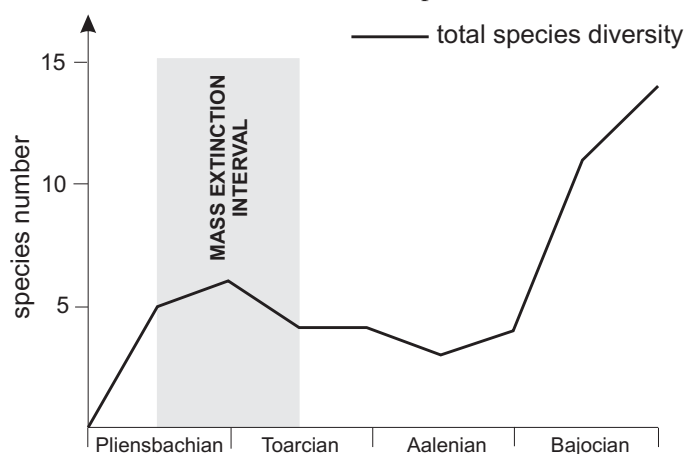


Fig. 4. Diversity changes of Spondylydae, Limidae, Plicatulidae, Anomioidea (Pectinoida) from the South of former Soviet Union (after Romanov and Kasum-Zade 1991).

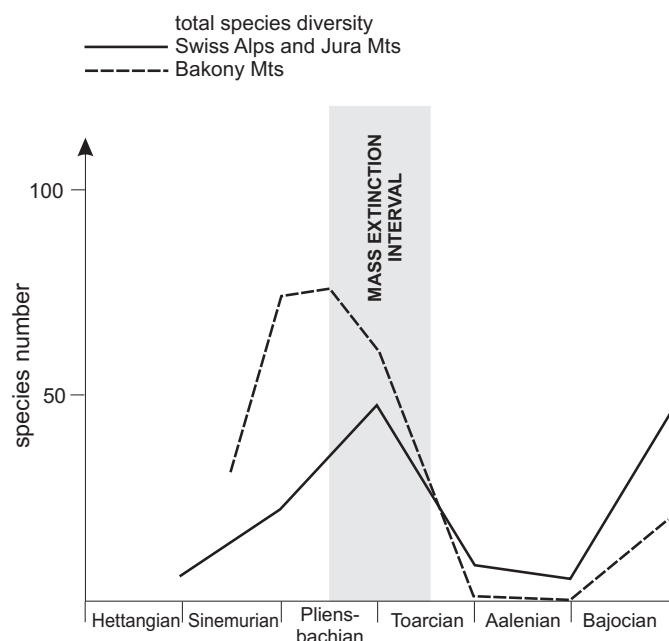


Fig. 5. Brachiopods diversity changes in Lias of Bakony Mts (after Vörös 1993, 1995) and Swiss Alps and Jura Mts. (after Sulser 1999).

Comparison with other regions.—Early Jurassic brachiopod diversity patterns was studied in other Tethyan regions, the best exemplified being in the Bakony Mountains in Hungary (Vörös 1993, 1995). The results show that total species number increased from the Hettangian to the Early Pliensbachian (Fig. 5). Then in the Late Pliensbachian a decrease began, while through the Toarcian–Aalenian interval brachiopods disappeared almost entirely. Origination rate began to decrease in the Carixian, and extinction rate increased the same time but more intensively in the Domerian. A new radiation has been documented in the Bajocian.

Diversity dynamics of Swiss Alps and Jura Mountains brachiopods could be calculated from data of Sulser (1999). Although in this monograph only partial stratigraphical ranges are shown (i.e., where taxa are abundant), the Sinemurian–Pliensbachian diversification phase, and Toarcian–Aalenian diversity fall are evident as well (Fig. 5).

Therefore, temporal diversity patterns of Tethyan brachiopods are very similar to those of NW Caucasus brachiopods although a recovery of diversity in the Late Toarcian shows a shorter crisis duration. But another feature is common for these regions: the mass extinction occurred after significant diversification, which seems to be connected with a radiation phase.

Causes of the shelly benthos collapse in NW Caucasus

The Early Jurassic mass extinction is thought to be causally connected mainly with anoxia and major sea-level changes (see reviews by Hallam and Wignall 1997, 1999; Wignall 2001). As the Pliensbachian–Toarcian boundary transition is

marked in Caucasus by a hiatus, it is considered that at this time a local uplift took place; after the accumulation of Early Toarcian inner shelf sediments, the progressive deepening has begun in the Middle Toarcian (Granovskij et al. 2001).

The global sea-level curve (Haq et al. 1987; Hallam 1988, 2001; Hallam and Wignall 1999) shows eustatic rise that occurred distinctly earlier (in the Early Toarcian), and a regressive phase has already begun in the Middle Toarcian. A difference between the NW Caucasus and global sea-level record is evident (Fig. 2), while the results of diversity studies are similar. So, the Pl-To extinction among brachiopods in the studied region possibly should be explained by additional causes. It is necessary to note that previous attempts of explanations of Pl-To biotic crisis by sea-level fluctuations led to conclusion about the absence of direct links between these phenomena (McRoberts and Aberhan 1997).

Anoxic conditions are well established world-wide in Toarcian seas (Jenkyns et al. 2002). Although the broad shallowing trend has been observed, oxygen-depleted conditions can be tentatively inferred due to black colour of shales, common occurrence of siderite concretions and pyrite grains presence (Fig. 2). The dark colour may be interpreted as a result of the organic lamination. In the sections exposed along the Belaja River, the author has found interlayers fully consisted of siderite concretions in terrigenous deposits of the Lower–Middle (lower interval) Toarcian succession (Ruban 2002). Meantime, siderite is not considered as a direct indicator of anoxia.

It is necessary to point out that taking into consideration different regional factors may lead us to the correction of assumptions presented above; e.g., regional subsidence if it was intense could have disguised any local evidence of anoxia. The accounting of the same factor also may enforce us to reestimate the importance of transgressions–regressions. So, this a matter for further studies and discussions.

Nevertheless, the Caucasus record gives another opportunity to analyze the causes of possible anoxia themselves in the light of a recent scenario by Guex et al. (2001). The marine oxygen depletion is connected with the terrestrial plants diversification in the Early–Middle Liassic and linked with extensive land inundation during a transgressive pulse, when this accumulated organic material was able to initiate the anoxia. Macrofloral remains in the Domerian–Early Toarcian deposits are abundantly found in all studied sections (Ruban 2000), which might indicate a major plant diversification just before the beginning of Pl-To mass extinction. The same temporal link is observed in the global record (Philippe et al. 1999).

Conclusions

Three diversification episodes of brachiopod faunas, followed by diversity decline, have been documented in NW Caucasus marine basin, and the benthos diversity changed cyclically in the Early–Middle Jurassic. But the most dra-

matic change occurred in Late Sinemurian–Early Toarcian when diverse brachiopod communities experienced a severe extinction. Similar diversity patterns have been reported from coeval biota in other Tethyan regions (e.g., Vörös 1993, 1995). Such benthos collapse was obviously related to killing environmental factors operating globally through the Late Pliensbachian to the Early Toarcian (?anoxia), even if the direct causal mechanisms remain still enigmatic in the region studied. Expanding oxygen deficiency is a main candidate, and frequently discussed as a main environmental trigger of Palaeozoic brachiopod demises (e.g., Racki 1998; see also Hallam and Wignall 1997; Harper and Rong 2001; Rong and Shen 2002).

In comparison to the Bakony Mts, Jura Mts., and Swiss Alps, brachiopod recovery began earlier in this northern Tethyan domain. Therefore, the regional diversity pattern of the Early Jurassic biotic crisis could be traced even more clearly, and this is a promising perspective for elaboration of other fossil groups. The Caucasus sequences can serve a “reference” for further high resolution stratigraphical and ecological-geochemical studies of this biotic turning point in the Mesozoic.

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Appendix

List and stratigraphic ranges of Liassic Brachiopoda of Northwestern Caucasus (compiled from Makridin and Kamyshan 1964; Prosorovskaya 1989, 1993; Rostovtsev et al. 1992). S2, Sinemurian; P1, Early Pliensbachian; P2, Late Pliensbachian; T1, Early Toarcian; T2, Middle Toarcian; T3, Late Toarcian.

Species	S2	P1	P2	T1	T2	T3
<i>"Rhynchonella" babala</i> Dumortier						+
<i>"Rhynchonella" latifrons</i> Geyer		+				
<i>"Rhynchonella" reinesi</i> Gemmelaro	+					
<i>"Rhynchonella" ex gr. obtusiloba</i> Rollier					+	
<i>"Spiriferina" moeschi</i> Haas	+	+				
<i>Aulacothyris griffini</i> Rollier						+
<i>Aulacothyris resupinata</i> (Douville)		+				
<i>Aulacothyris salgirensis</i> Moissejev		+				
<i>Aulacothyris waterhousi</i> (Davidson)		+				
<i>Bodrakella</i> aff. <i>bodrakensis</i> Moissejev		+				
<i>Calcirhynchia plicatissima</i> (Quenstedt)	+	+				
<i>Caucasorhynchia visnovskii</i> Moissejev		+				
<i>Cincta leptonumismalis</i> (Rollier)		+				
<i>Cincta</i> cf. <i>numismalis</i> (Valenciennes)		+				
<i>Cirpa borissiaki</i> Moissejev		+				
<i>Cuersithyris radstockensis</i> (Davidson)		+				
<i>Cuneirhynchia dalmasi</i> (Dumortier)		+				
<i>Cuneirhynchia gussmani</i> (Rollier)		+				
<i>Cuneirhynchia persinuata</i> (Rau)		+				
<i>Cuneirhynchia rauae</i> Rollier		+				
<i>Curtirhynchia</i> sp.						+
<i>Digonella subdigona</i> (Oppel)		+				
? <i>Disculina liasina</i> Deslongchamps		+				
<i>Flabellirhynchia lycetti</i> (Davidson)		+				+
<i>Furcirhynchia laevigata</i> (Quenstedt)	+					
<i>Gibbirhynchia curviceps</i> (Quenstedt)		+				
<i>Gibbirhynchia gibbosa</i> Buckman	+	+				
<i>Gibbirhynchia heiningensis</i> Rollier						+
<i>Grandirhynchia capitulata</i> (Tate)						+
<i>Homoeorhynchia deffneri</i> Oppel	+	+				
<i>Homoeorhynchia</i> sp. 1		+				
<i>Homoeorhynchia</i> sp. 2						+
? <i>Linguithyris bimammata</i> Rothpletz	+					
<i>Liospiriferina alpina</i> (Oppel)		+				+
<i>Liospiriferina obtusa</i> (Oppel)	+	+				
<i>Liospiriferina rostrata</i> (Schlotheim)	+	+				
<i>Liospiriferina</i> cf. <i>obtusa</i> (Oppel)		+				
<i>Lobothyris havesfieldensis</i> Rollier						+
<i>Lobothyris punctata</i> (Sowerby)		+	+			
<i>Lobothyris subpunctata</i> (Davidson)		+				
? <i>Lobothyris ovatissima</i> Quenstedt		+				
<i>Piarorhynchia juvenis</i> (Quenstedt)	+					
<i>Piarorhynchia rostellata</i> (Quenstedt)		+			+	
<i>Piarorhynchia triplicata</i> (Phillips)		+				

Species	S2	P1	P2	T1	T2	T3
<i>Piarorhynchia variabilis</i> Davidson		+				
<i>Piarorhynchia</i> aff. <i>albertii</i> (Oppel)		+				
<i>Praemonticlarella schuleri</i> (Oppel)						+
<i>Prionorhynchia greppini</i> (Oppel)	+					
<i>Prionorhynchia serrata</i> (Sowerby)					+	+
? <i>Prionorhynchia regia</i> Rothpletz		+				
<i>Pseudogibbirhynchia jurensis</i> (Quenstedt)						+
<i>Pseudogibbirhynchia moorei</i> (Davidson)						+
<i>Ptyctorhynchia</i> sp.						+
<i>Rimirhynchia rimosa</i> (Buch)		+				
<i>Rudirhynchia belemnitica</i> (Quenstedt)	+					
<i>Rudirhynchia calcicosta</i> (Quenstedt)	+					
<i>Scalpellirhynchia scalpellum</i> (Quenstedt)	+					
<i>Securina partschi</i> (Oppel)	+	+				
<i>Spiriferina haasi</i> Makridin and Kamyschan	+					
<i>Spiriferina haueri</i> (Suess)	+	+				
<i>Spiriferina ilminsteriensis</i> Davidson	+					
<i>Spiriferina walcottii</i> (Sowerby)	+	+				
<i>Spiriferina angulata</i> Oppel		+				
<i>Squamirhynchia squamiplex</i> (Quenstedt)		+				
<i>Tettrahynchia pontica</i> Moissejev	+					
<i>Zeilleria cornuta</i> Quenstedt	+	+				
<i>Zeilleria davidsoni</i> Makridin et Kamyschan	+	+				
<i>Zeilleria engelhardii</i> (Oppel)		+				
<i>Zeilleria indentata</i> (Sowerby)	+	+				
<i>Zeilleria lunaris</i> (Zieten)		+				
<i>Zeilleria mutabilis</i> (Oppel)	+	+				
<i>Zeilleria ovalis</i> Rollier	+					
<i>Zeilleria ovimontana</i> (Boese)	+	+				
<i>Zeilleria perforata</i> (Piette)	+					
<i>Zeilleria rehmanni</i> (Roemer)	+	+				
<i>Zeilleria retusa</i> Martin	+	+				
<i>Zeilleria roemeri</i> (Schloenbach)	+					
<i>Zeilleria scalprata</i> (Quenstedt)	+	+				
<i>Zeilleria stapia</i> (Oppel)	+	+				
<i>Zeilleria subsphaeroidalis</i> Rollier	+					
<i>Zeilleria thurvieseri</i> Boese	+	+				
<i>Zeilleria vicinalis</i> (Schlotheim)	+	+				