

OLENEKIAN (EARLY TRIASSIC) FOSSIL ASSEMBLAGE FROM EASTERN JULIAN ALPS (SLOVENIA)

Tea KOLAR-JURKOVŠEK¹, Valery J. VUKS², Dunja ALJINOVIĆ³, Michael HAUTMANN⁴,
Andrzej KAIM⁵ & Bogdan JURKOVŠEK¹

¹ Geological Survey of Slovenia, Dimičeva ulica 14, 1 000 Ljubljana, Slovenia; e-mail: tea.kolar@geo-zs.si,
bogdan.jurkovsek@geo-zs.si

² Federal State Unitary Enterprise “A.P. Karpinsky Russian Geological Research Institute” Sredny pr. 74,
199106 St.-Petersburg, Russia; e-mail Valery Vuks@vsegei.ru

³ University of Zagreb, Faculty of Mining, Geology and Petroleum Engineering, Pierottijeva 6, 10 000 Zagreb, Croatia;
e-mail: dunja.aljinovic@rgn.hr

⁴ Paläontologisches Institut und Museum, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland;
e-mail michael.hautmann@pim.uzh.ch

⁵ Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, PL-00-818 Warszawa, Poland;
e-mail: kaim@twarda.pan.pl

Kolar-Jurkovšek, T., Vuks, V. J., Aljinović, D., Hautmann, M., Kaim, A. & Jurkovšek, B. 2013. Olenekian (Early Triassic) fossil assemblage from eastern Julian Alps (Slovenia). *Annales Societatis Geologorum Poloniae*, 83: 213–227.

Abstract: New palaeontological and sedimentological data from the Lower Triassic strata of the eastern Julian Alps in Slovenia are presented. They are unusual for the Early Triassic of the Alps in representing a relatively deeper, unrestricted marine (mid-ramp) setting. There are two basic microfacies types in the section investigated (types A and B), which are organized as couplets with coarse-grained tempestitic deposits (microfacies A), overlain by laminated or bioturbated lime mudstones and/or marls (microfacies B), frequently containing ammonoids. This pattern is interpreted as storm deposition with occasional winnowing of bottom sediments and the formation of coarse-grained skeletal deposits (lags), followed by the slow settling of suspended particles, when the storm waned, in addition to background deposition. Dominantly lime mud deposition and the presence of ammonoids indicate deposition on a more distal, deeper ramp with an unrestricted connection to the open sea. Intense reworking of bottom skeletal-rich sediment and accumulation of storm lags suggest deposition above the storm wave base, possibly in a wide low-energy mid-ramp environment. Faunas from such settings have been reported relatively rarely from the Early Triassic of the Alps. The macrofauna contains ammonoids, bivalves and gastropods, whereas the microfauna is represented by foraminifer tests and conodont elements; rare fish remains also occur. In the foraminifer assemblages, species of *Ammodiscus*, *Hoyenella*, *Glomospirella* dominated, corresponding to the widespread “*Glomospira-Glomospirella*” foraminifer community, with some miliolids and nodosariids. The conodont fauna is characterized by *Triassospathodus hungaricus* (Kozur et Mostler), indicating an early Spathian (Olenekian) age. The fossil assemblage highlights the wide distribution of Early Triassic taxa in the Tethys and facilitates its worldwide correlation. Its relatively low diversity by comparison with shallow marine settings is interpreted as an evolutionary proximal-distal trend in the wake of the end-Permian mass extinction. Re-diversification first occurred in nearshore settings and expanded into deeper/distal marine environments through geological time.

Key words: Olenekian, Early Triassic, foraminifers, bivalves, gastropods, conodonts, sedimentology, Julian Alps, Slovenia.

Manuscript received 4 August 2013, accepted 23 December 2013

INTRODUCTION

The end-Permian mass extinction event was pivotal in the Phanerozoic history of marine life, terminating the incumbency of the “Palaeozoic Evolutionary Fauna” that had dominated life in the sea for nearly 250 million years (Sepkoski, 1984). In the wake of the extinction event, the eco-

logical structure of the present-day biosphere evolved from the stock of the surviving taxa, shaping the “Modern Evolutionary Fauna” that characterizes marine ecosystems until today (Sepkoski, 1997). The recovery from the end-Permian mass extinction is therefore crucial for understanding

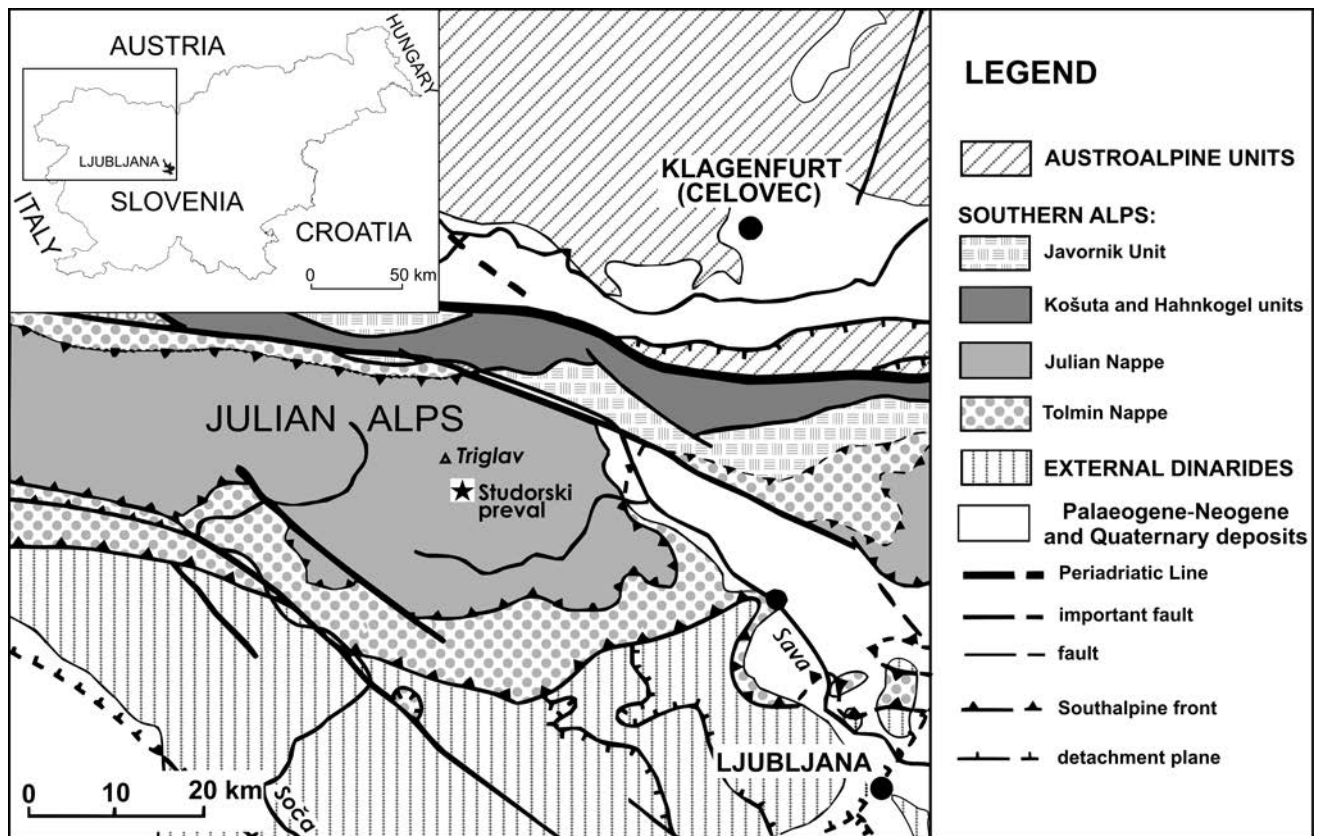


Fig. 1. Location of Lower Triassic strata at Studorski preval in Julian Alps (Slovenia)

how the present-day biosphere evolved. An indispensable prerequisite in this context is a census of the faunas that lived and evolved during the Early Triassic, i.e., the epoch that followed the crises. Thus, collecting and interpreting new field data from the Early Triassic has been a major research agenda during the past decade (e.g., Brayard and Bucher, 2008; Posenato, 2008; Kumagai and Nakazawa, 2009; Kaim *et al.*, 2010, 2013; Hautmann *et al.*, 2011, 2013; Brühwiler *et al.*, 2012; Wasmer *et al.*, 2012; Hofmann *et al.*, 2013a, b). However, Early Triassic benthic faunas have been described mostly from relatively shallow marine sections, particularly in Europe, where deeper shelf settings are rare. The section investigated is also known as the location, where an isolated temnospondyl bone (Lucas *et al.*, 2008), was found and therefore represents an important site of Slovenian natural heritage. In this study, new sedimentological and palaeontological data are presented from the Spathian (late Early Triassic) section in the Julian Alps (Slovenia). They contribute to a better understanding of how diversity and faunal composition changed along depth gradients during re-diversification from the greatest crisis in the history of life.

GEOLOGICAL SETTING

The study area is in the Julian Alps, NW Slovenia (Fig. 1). Structurally they form the easternmost continuation of the Southern Alps, where the South Alpine and the Dinaric structures now overlap (Placer, 1999). The largest

overthrust unit in the Slovenian part of the Julian Alps is represented by the Julian Alps Overthrust (Jurkovšek, 1987a, b) or the Julian Nappe, which is composed of successions, ranging from Early Triassic to Cretaceous strata, though a major part of it is made up of Late Triassic carbonates. Early Triassic strata are scattered in narrow disconnected belts or patches in the wider Julian Alps area. They usually occur within smaller tectonic slices (Figs 2, 3).

The area investigated is located in the uppermost tectonic slice of the Julian Alps Overthrust, SE of Triglav Mt. (2863 m), the highest peak in Slovenia. The lower part of these strata is in tectonic contact with the Norian–Rhaetian Dachstein Limestone, whereas upwards they pass continuously into Anisian limestones and dolomites (Jurkovšek, 1987a; Celarc and Kolar-Jurkovšek, 2008).

The Studorski preval section is strongly tectonized (coordinates: N46°21'14.46", E13°52'55.80"; WGS 84). Thick lime mudstones and marls and thin beds enriched in coarse-grained bioclastic material, predominate. The fauna is characterized by Early Triassic mollusks, dominated by bivalves and gastropods. The microfauna is diversified, but consists mainly of foraminifer assemblages in association with rare conodont elements and fish remains.

Lithology

The Studorski preval section mainly consists of thick mudstones (Fig. 4A) and marls (Fig. 4B), and thin beds, enriched in coarse-grained bioclastic material. These lithologies form units, in which coarse-grained bioclastic material

is concentrated at the base and gradually passes upward into mudstones/marls. Thus, the microfacies in the Studorski preval section correspond to two microfacies types: microfacies type A, fossiliferous floatstone/packstones, and microfacies type B, dense or laminated lime mudstones that may pass gradually into marls.

Centimetre- to decimetre-thick fossiliferous floatstone/packstone beds (A) have distinctive sharp lower erosional boundaries. The floatstone/packstone interbeds gradually change upward to much thicker mudstone/marl intervals, which locally were intensively reworked by organisms (Fig. 4C).

Floatstones/packstones of microfacies type A consist of coarse (usually > 2 mm) well preserved skeletal detritus (Fig. 4F). Among the skeletal fragments bivalves, gastropod, and ammonoid detritus predominate. Echinoderm ossicles and foraminifer tests are rare. In the floatstone/packstone a bimodal sorted biofabric is found, which consists of large bioclasts and micritic matrix. Very frequently, the matrix is non-homogenous and contains a high proportion of peloidal particles and some micrite (Fig. 4E). Whole valves are dominantly oriented parallel to the bedding surface, very often in a convex-up position. Completely preserved bivalve or gastropod shells are geopetally infilled with sparry calcite. Some shelter pores, at the concave side of bivalve shells, are also infilled by sparite.

Microfacies type B consists of dense, laminated or bioturbated mudstones and/or marls. Sparse, well preserved fossils can be dispersed in the mudstones (Fig. 4D). The mudstones consist of homogenous micritic mud or micrite-rich laminae. Disturbance of the lamination is due to reworking by infaunal organisms. Lime mud is slightly recrystallized. In both microfacies types euhedral pyrite crystals and large celestite crystals (determined by EDS analysis) are present.

MATERIAL AND METHODS

The present study is based on field work, carried out in 2011 at Studorski preval in the Julian Alps. Approximately 10 m of the Lower Triassic strata was sampled just below the contact with the Anisian dolomite. Nine samples (SP 1–9) were collected for examination from the Lower Triassic strata; sample SP 1 is the lowest and the sample SP 9 is the highest. Rock samples with an average weight of 4 kg were processed for conodont study, using standard laboratory techniques. Several thin sections were made for the study of foraminifers as well as for petrographic purposes. Laboratory preparation was carried out at the Geological Survey of Slovenia (Geološki zavod Slovenije) where all of the micropalaeontological material is stored and inventoried under repository numbers 4429, 4548–4555, 4901–4904 and abbreviated GeoZS. The collection of macrofossil specimens: Jurkovšek Paleontological Collection, Kamnica 27, Dol pri Ljubljani, Slovenia, has been registered with the Natural History Museum of Slovenia, Ljubljana and abbreviated as BJ. The determinations of conodont elements presented here and the SEM/EDS analyses were carried out, using the JEOL JSM 6490LV Scanning Electron Microscope at the Geological Survey of Slovenia.

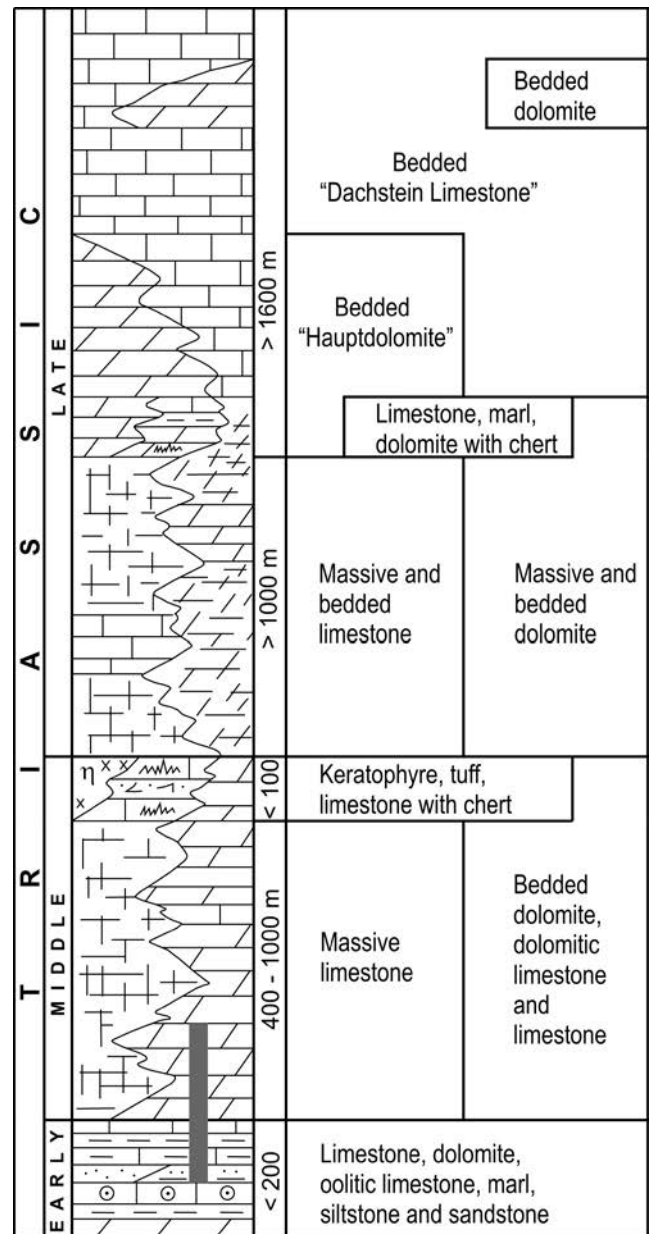


Fig. 2. Generalized stratigraphic section of Triassic strata in Julian Alps. Thick dark bar indicates section studied in tectonic slice at Studorski preval

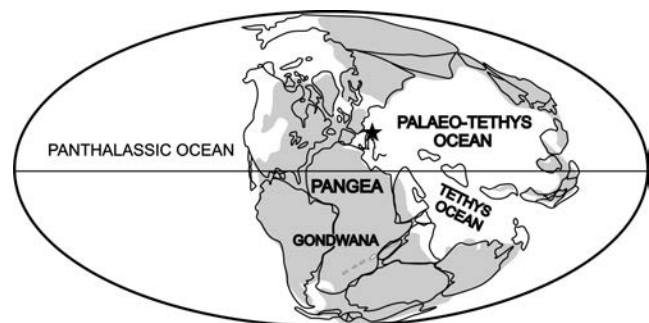


Fig. 3. Palaeogeographic map for Early Triassic with position of the Julian Alps marked (star), modified from Scotese (2001)

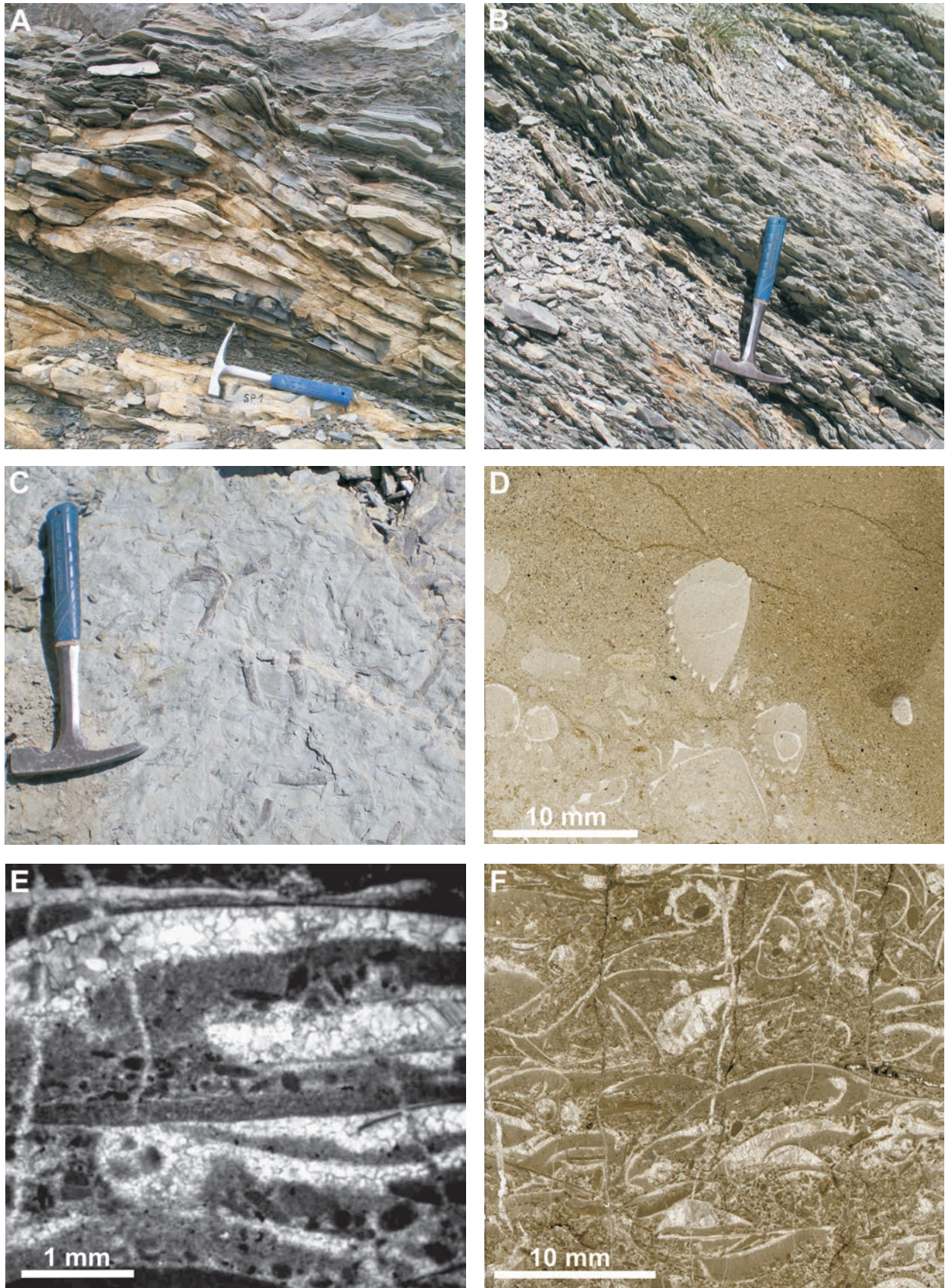


Fig. 4. Microfacies types from Early Triassic of Studorski preval, Slovenia. Hammer length 26.5 cm (A) and 29 cm (B, C). **A.** Laminated, thin-bedded mudstones. **B.** Homogenous marl interval. **C.** Bioturbated lime mudstone. **D.** Rare skeletal fragments in dominantly muddy sediment – microfacies type B. **E.** Floatstone (microfacies type A) with coarse skeletal detritus and inhomogeneous matrix containing high proportion of pelloidal particles and some micrite. **F.** Floatstone of microfacies type A consists predominantly of bivalves and gastropod detritus. Note convex-up position of most valves

PALAEOENVIRONMENT

The Studorski preval section can be compared to the Werfen Formation of the Southern Alps that represents deposition on a storm-influenced ramp (Brandner *et al.*, 2012). Sedimentation of the dominantly fine-grained microfacies type B can be interpreted as slow deposition in a deeper marine environment below the fair-weather wave base, which corresponds to the distal part of a ramp. The presence of ammonoid shells indicates a good connection with the open unrestricted sea and also implies deposition in a deeper-ramp environment. Nevertheless, the interlayering with limestone of microfacies type A suggests that slow deposition of fine-grained sediments (microfacies type B) was periodically interrupted by the deposition of coarse skeletal detritus during high-energy events (microfacies type A). The sharp and erosive lower boundaries of microfacies type A beds imply the abrupt commencement of sedimentation. The well-preserved skeletal detritus in the floatstones/packstones and the upward-increasing proportion of matrix indicate deposition during storms, in a zone above the storm-weather wave base. As the beds of microfacies type A are overlain by laminated or bioturbated calcareous mudstones and/or marls (microfacies type B), their deposition reflects short storm events in a deeper low-energy ramp environment, where the deposition of lime mud prevails. The intense bottom-shear conditions during the storm peak concentrated shells of living and dead organisms from the sea bottom, either by burying them under a sudden influx of storm-suspended particles or by exhuming previously buried shells by ripping up the underlying weakly consolidated sediments and forming skeletal concentrations (lag deposits). Therefore, well-preserved fossils within a fine micritic/peloidal matrix of microfacies type A are interpreted as the result of storm events, which preserve whole fossils by burying and protecting them from normal destructive processes. The presence of foraminifera indicates detritus derived by storms from the shallow proximal ramp. Valves oriented parallel to the bedding plane in a convex-up position also indicate deposition under short-term high-energy conditions. Furthermore, winnowing and suspension of fine sediment resulted in the deposition of the upward-fining units above coarse lag deposits. As the storm waned, more mud was deposited from suspended material, resulting in fining-upward grading. Intense colonization by organisms and bioturbation could reflect the cessation of the storm and a return to normal low-energy ramp sedimentation below the fair-weather wave base. The presence of pyrite also indicates low-energy, and possibly partly anaerobic conditions, whereas the genesis of celestite is considered as diagenetic in deep-sea sediments, as explained by Baker and Bloomer (1988) although it also has been described from shallow marine settings (Hautmann, 1997). Storms are frequently recorded both in the inner and outer shelf/ramp in the Induan/Olenekian sediments of the wider Dinaric region (Aljinović, 1995; Aljinović *et al.*, 2006, 2011), while this investigation points to deposition in wide mid-ramp zone (the zone between the fair- and storm- weather wave bases), as defined by Burchette and Wright (1992).

There are only a few outcrops of Lower Triassic strata in the Julian Alps and they occur in small tectonically con-

finned areas (e.g., Mavrinc, Lipanca). There is some similarity in their development and macrofossil content (*Natiria costata* and badly-preserved ammonoids). Conodont and other micropalaeontologic analyses were negative and therefore a detailed geological comparison of these strata had not been possible.

PALAEONTOLOGY

Microfauna

The microfossil material recovered from nine conodont samples (SP 1–9) was examined in the present study. The associations consisted of conodont elements, rare fish remains, as well as some recrystallized free specimens of foraminifera from two samples (SP 1 and SP 5). In addition, several thin sections were prepared from each sample for foraminifera study. The conodonts recovered are white with CAI = 1 (Epstein *et al.*, 1977).

The list of microfossils determined is presented in Table 1.

Foraminifera

The foraminifer classifications of Loeblich and Tappan (1988) and Mikhalevich (2000) are combined and used here. The foraminifer descriptions are short, because these foraminifera are mainly well-known and the preservation of these forms is not particularly good.

Genus *Ammodiscus* Reuss, 1862

Type species: *Ammodiscus infimus* Bornemann, 1874

Ammodiscus? parapriscus Ho, 1959
Fig. 5A–D

*1959 *Ammodiscus parapriscus* n. sp. – Ho: p. 408, pl. 2, figs 3–6.

Table 1

Distribution of microfossils in samples
from Studorski preval

Taxa	Sample	SP1	SP2	SP3	SP4	SP5	SP6	SP7	SP8	SP9
<i>Ammodiscus? parapriscus</i> Ho		va	a	va	a	va	va	r	r	a
<i>Glomospirella facilis</i> Ho		va		r	r	va	a			
<i>Glomospirella shengi</i> Ho		va		vr		a	a			
<i>Glomospirella</i> sp.		a		r		r	a			
<i>Pilamina? cf. praedensa</i> Urošević							vr			
<i>Arenovidalina? sp.</i>				vr						
<i>Meandrospira? sp.</i>										vr
<i>Agathammina? sp.</i>			vr						vr	
<i>Hoyenella sinensis</i> (Ho)		va	a	va	a	a	a			r
<i>Dentalina splendida</i> Schleifer		vr	vr	vr					vr	
<i>Nodosaria? spp.</i>		a	vr		r		r	vr	r	
<i>Triasospathodus hungaricus</i> (Kozur & Mostler)		a		va		r				
fish teeth		r		r						

Vr – very rare (1 specimen), r – rare (2–4 specimens), a – abundant (5–10 specimens), va – very abundant (more than 11 specimens)

- 1976 *Ammodiscus parapriscus* Ho – Zaninetti, p. 89, pl. 2, figs 1–2.
- partim 1983 *Ammodiscus parapriscus* Ho – Salaj *et al.*, p. 61, pl. 1, ?non fig. 2, pl. 6, figs 3–5, ?non fig. 6, non 7–8.
- 1992 *Ammodiscus parapriscus* Ho – Trifonova, p. 9, pl. 1, figs 3–5, pl. 6, fig. 10.
- ?non1995 *Cornuspira? parapriscus* (Ho) – Rettori, p. 102, pl. 19, fig. 6.

Material: 75 sections in samples SP 1, 2, 3, 4, 5, 6, 7, 8, 9 and 61 free specimens from the sample SP 1.

Description: The test is circular, discoid; periphery rounded and concave on both sides. The spherical proloculus is followed by a closely planispiral enrolled undivided tubular second chamber, gradually increasing in diameter. The number of whorls is 3–5. The wall is agglutinated and compact. The aperture is at the end of the tube.

Remarks: This species was assigned to *Cornuspira* with a question mark by Rettori (1994), but the material of the present study is not well-preserved. Therefore, it is not possible to support his conclusion, but the question mark is retained here for definition of the genus. The preservation of the wall of the specimens studied is not good, because they are recrystallized and in some cases pyritized.

Stratigraphic and geographic occurrence: The species *Ammodiscus? parapriscus* was first found in the Lower and Middle Triassic of China (Ho, 1959). This species occurs also in the Lower and Middle Triassic (Anisian) of the Dinarides, Albania, Hungary, Bulgaria, Greece, Turkey, Iran, China (Zaninetti, 1976; Pantić-Prodanović and Radošević, 1977a; Dager, 1978; Oravec-Scheffer, 1987; Pirdeni, 1988; Salaj *et al.*, 1988; Trifonova, 1992; Rettori, 1995) and in the Anisian and Rhaetian of the West Carpathians (Salaj *et al.*, 1983).

Genus *Glomospirella* Plummer, 1945

Type species: *Glomospira umbilicata* Cushman & Waters, 1927

Glomospirella facilis Ho, 1959

Fig. 5E, F

- *1959 *Glomospirella facilis* n. sp. – Ho, p. 414, pl. 6, figs 8–12.
- 1976 *Glomospirella facilis* Ho – Zaninetti, p. 95, pl. 2, fig. 18.
- partim 1983 *Glomospirella facilis* Ho – Salaj *et al.*, p. 63, pl. 2, figs 9–12, figs 14–15, ?non figs 13, 16.
- 1992 *Glomospirella facilis* Ho – Trifonova, p. 18, pl. 2, figs 13, 15–16, pl. 6, figs 13–14, 26.

Material: 21 sections in the samples SP 1, 3, 4, 5, 6, and 43 free specimens from the samples SP 1 and 5.

Description: The test is small, the equatorial section rounded, the axial section plain or concave on the both sides. The spherical proloculus is followed by a streptospirally enrolled undivided tubular second chamber and the last 2–3 whorls become planispirally coiled and abruptly increasing in diameter. The last whorl is wider than others and a little angular in cross-section. The wall is agglutinated, thin, and smooth. The aperture is at the end of the tube.

Remarks: The characteristic features of this species are a round form in the equatorial section and a concave form in the axial section, with a very small streptospiral stage of coiling. The above mentioned features of *Glomospirella facilis* differ from those of *Glomospirella shengi*. The preservation of the wall of the specimens studied is not good, because they are recrystallized and in some cases pyritized.

Stratigraphic and geographic occurrence: The species *Glomo-*

spirella facilis was first described from the Lower and Middle Triassic of China (Ho, 1959). Later this species was reported from the Lower and Middle Triassic (Anisian) of the Alps, Dinarides, Albania, Hungary, Bulgaria, Caucasus, Iran (Zaninetti, 1976; Pantić-Prodanović and Radošević, 1977b; Pisa *et al.*, 1979; Oravec-Scheffer, 1987; Pirdeni, 1988; Efimova, 1991; Trifonova, 1992; Rettori, 1995) and in the Upper Triassic of the West Carpathians (Salaj *et al.*, 1983).

Glomospirella shengi Ho, 1959

Fig. 5G, H

- *1959 *Glomospirella shengi* n. sp. – Ho: p. 413, pl. 5, figs 20–25.
- 1976 *Glomospirella shengi* Ho – Zaninetti, p. 104, pl. 2, figs 14–16.
- partim 1983 *Glomospirella shengi* Ho – Salaj *et al.*, p. 65, pl. 3, figs 1–10, 13–16, non 11–12, pl. 5, figs 10–11, 15–16, ?non figs 12–14
- partim 1992 *Glomospirella shengi* Ho – Trifonova, p. 18, pl. 2, fig. 4, pl. 6, figs 20, 27, ? non fig. 28.

Material: 17 sections in the samples SP 1, 3, 5, 6, and 30 free specimens from the samples SP 1 and 5.

Description: The test is small, equatorial section oval, axial section mainly plain or convex on the both sides. The spherical proloculus is followed by a streptospirally enrolled undivided tubular second chamber and the last 2–3 whorls become planispirally coiled and gradually increasing in diameter. The streptospiral stage of coiling is wider in the axial section than the last whorl. The wall is agglutinated, thin, and smooth. The aperture is at the end of the tube.

Remarks: The characteristic features of this species are the oval form in the equatorial section and the convex or plain form in the axial section, the streptospiral stage of coiling is wider in the axial section than the last whorl. The above mentioned features of *Glomospirella shengi* are different from those of *Glomospirella facilis*. The preservation of the wall of the specimens is not good, owing to recrystallization or pyritization.

Stratigraphic and geographic occurrence: This species was first found in the Lower and Middle Triassic of China (Ho 1959). Later the species was described from Lower and Middle Triassic (Anisian) of the Dinarides, Hungary, Bulgaria, Turkey, Caucasus (Pantić, 1970; Urošević and Jeličić, 1973–1974; Zaninetti, 1976; Dager, 1978; Oravec-Scheffer, 1987; Efimova, 1991; Trifonova, 1992; Rettori, 1995) and from the Rhaetian of the West Carpathians (Salaj *et al.*, 1983).

Genus *Pilammina* Pantić, 1965

Type species: *Pilammina densa* Pantić, 1965

Pilammina? cf. praedensa Urošević, 1988

Fig. 5I

- *1988 *Pilammina praedensa* n. sp. – Urošević: p. 372, pl. 1, figs 1–6.
- partim 1995 *Pilammina praedensa* Urošević – Rettori, p. 56, pl. 3, figs 1–3, 5, ?non fig. 4.

Material: One section in the sample SP 6.

Description: The test is free. It is close-coiled, consisting of a round proloculus and another insepate, tubular chamberlet. The initial winding covers two and a half to three close coils. The last whorl is much wider than first whorls.

Remarks: The section studied is similar to the holotype. The preservation is not good, because the test is not complete. Therefore there is no possibility to describe the inner structure in detail. Usu-

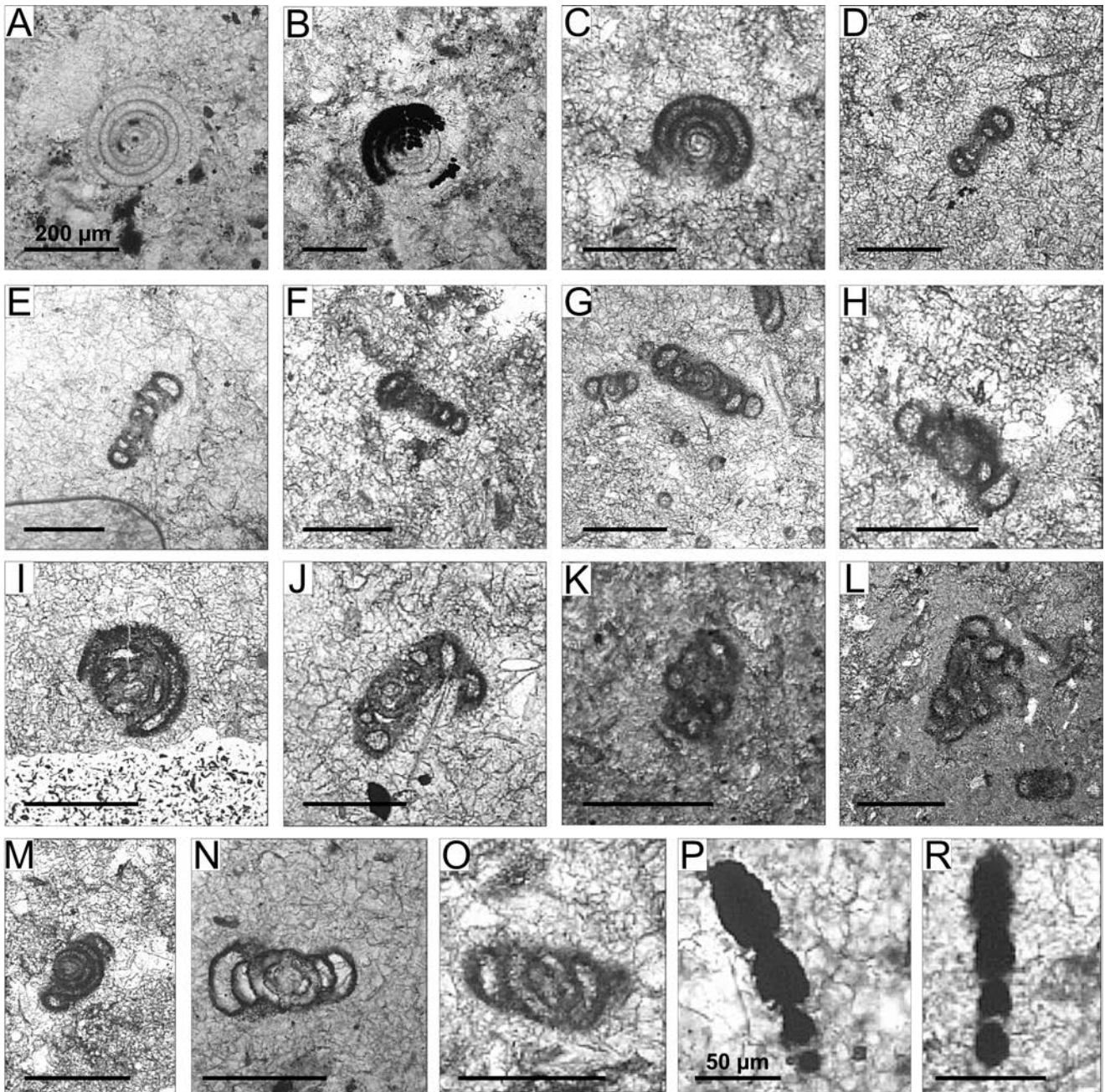


Fig. 5. Foraminifera from Early Triassic of Studorski preval, Slovenia. Scale bar 200 µm (A–O), 50 µm (P, R). **A–D.** *Ammodiscus? parapriscus* Ho, 1959, A. SP 7, equatorial section. B. SP 1, equatorial section. C. SP 6, equatorial section. D. SP 3, axial section. **E, F.** *Glomospirella facilis* Ho, 1959, E. SP 6, F. SP 1, subequatorial sections. **G, H.** *Glomospirella shengi* Ho, 1959, G. SP 6, H. SP 6, subequatorial sections. **I.** *Pilamina?* cf. *P. praedensa* Urošević, 1988, SP 6, oblique section. **J.** *Arenovidalina?* sp., SP 3, oblique section. **K.** *Meandrospira?* sp., SP 9, subequatorial section. **L.** *Agathammina?* sp., SP 2, subtransverse section. **M–O.** *Hoyenella sinensis* (Ho, 1959), M. SP 1, subaxial section. N. SP 2, axial section. O. SP 3, subaxial section. **P, R.** *Dentalina splendida* Schleifer, 1961, P. SP 2. R. SP 3, sublongitudinal sections

ally the preservation of the wall of this species is not good and there is no confidence that this species belongs to *Pilamina* and this is true for the studied specimen too.

Stratigraphic and geographic occurrence: Species *Pilamina praedensa* was first described from the Lower Triassic of the Dinarides (Urošević, 1988) and after it was found in the upper part of Olenekian of Greece and the Lower Triassic of China (Rettori, 1995).

Genus *Hoyenella* Rettori, 1994

Type species: *Glomospira sinensis* Ho, 1959

Hoyenella sinensis (Ho, 1959)

Fig. 5M–O

*1959 *Glomospira sinensis* n. sp. – Ho, p. 410, pl. 3, figs 16–34.

1959 *Glomospira sinensis* var. *rara*, n. sp. n. var. – Ho, p.

- 410, pl. 4, figs 1–2.
- 1972 *Glomospirella elbursorum* n. sp. – Brönnimann, Zaninetti, Bozorgnia and Huber, p. 9, pl. 3, figs 1–10.
- partim 1974 *Glomospirella elbursorum* Brönnimann, Zaninetti, Bozorgnia and Huber – Baud *et al.*, pl. 30, figs 4–6, 8–11, non figs 7, 12, pl. 31, figs 1–6, 8–10, non fig. 7.
- partim 1975 *Glomospirella* sp. – Zaninetti and Brönnimann, pl. 36, figs 1, 3–6, 10–12, non fig. 9.
- 1994 *Hoyenella sinensis* Ho – Rettori, p. 342.
- partim 1995 *Hoyenella* gr. *sinensis* Ho – Rettori, p. 126, pl. 24, figs 1–15, pl. 25, figs 1–3, 5, 8, non figs 4, 6–7, 9, pl. 26, figs 1–3, 6–8, 10–12, 14, non 4–5, 9, 13, 15–17, pl. 27, figs 5–7, 10, non 1–4, 8–9, 11.

Material: 29 sections in the samples SP 1–6, 9 and 10 free specimens from the samples SP 1 and SP 5.

Description: The test is free and small, mainly ellipsoidal in shape, the spherical proloculus is followed by an undivided tubular second chamber, gradually increasing in diameter. In coiling, early whorls are miliolid-like, later ones are short with 1–2 planispiral whorls. The wall is dark and compact in transmitted light. The aperture is simple, terminal.

Remarks: *Glomospirella elbursorum* Brönnimann, Zaninetti, Bozorgnia and Huber (1972) could be placed into synonymy with the species studied, because of the very similar structure of the test and in this point, the decision of Rettori (1994) is followed. *Glomospirella* sp. (Zaninetti and Brönnimann, 1975) is placed into synonymy with the species studied, according to the morphological features of this species. The preservation of the wall of the specimens studied is not good owing to recrystallization or pyritization.

Stratigraphic and geographic occurrence: The species *Hoyenella sinensis* was first found in the Lower and Middle Triassic of China (Ho, 1959). Moreover, it is known from the Lower and Middle Triassic (Anisian) of the Alps, Dinarides, Albania, Hungary, Bulgaria, Greece, Turkey, Caucasus, Iran, Pakistan, Himalaya (Dimitrijević *et al.*, 1968; Baud *et al.*, 1974; Zaninetti and Brönnimann, 1975; Zaninetti, 1976; Pantić-Prodanović and Radošević, 1977a, b; Dager, 1978; Pisa *et al.*, 1979; Kristan-Tollmann, 1984; Oravec-Scheffer, 1987; Pirdeni, 1988; Salaj *et al.*, 1988; Efimova, 1991; Trifonova, 1992; Rettori, 1995) and in the Upper Triassic of the West Carpathians and Bulgaria (Salaj *et al.*, 1983; Trifonova, 1992).

Genus *Dentalina* Risso, 1826

Type species: *Nodosaria (Dentaline) cuvieri* (d'Orbigny, 1826)

Dentalina splendida Schleifer, 1961 in Gerke (1961)
Fig. 5P, R

- *1961 *Dentalina splendida* n. sp. – Schleifer in Gerke: p. 233, pl. 29, figs 5–6.
- 1991 *Dentalina splendida* Schleifer – Efimova, pl. 1, fig. 7.
- 1994 *Dentalina splendida* Schleifer – Trifonova, p. 37, pl. 4, figs 7, 11–12, 18.

Material: Four sections in the samples SP 1, SP 2, SP 3 and SP 8.

Description: The small test is almost rectilinear or slightly curved. The proloculus is usually oval. The number of elongated oval chambers is from 4 to 8. They usually increase very gradually in size and are, comparatively loosely jointed in all chambers. The sutures are depressed. The wall is very thin. The aperture is simple, terminal.

Remarks: The typical feature of this species is usually the oval proloculus and other chambers are oval and elongated. The holo-

type is broken, without a proloculus. The preservation of the specimens is not good, because they are mainly recrystallized, but there is proloculus present in all specimens.

Stratigraphic and geographic occurrence: Species *Dentalina splendida* was first described from the lower part of the Olenekian of the North Siberia (Gerke, 1961). Later this species was found in the Olenekian of the North Caucasus and Precaucasus (Efimova, 1991), and in the upper part of the Lower Triassic and in the lower part of the Anisian of Bulgaria (Trifonova, 1994).

Remarks on foraminifer fauna. The foraminifer assemblage consists of *Ammodiscus? parapriscus* Ho, *Glomospirella facilis* Ho, *Gl. shengi* Ho, *Gl. sp.*, *Pilamina? cf. P. praedensa* Urošević, *Arenovidalina? sp.*, *Meandrospira? sp.*, *Agathammina? sp.*, *Hoyenella sinensis* (Ho), *Dentalina splendida* Schleifer, *Nodosaria? spp.* (Fig. 5A–R). Species of the genera *Ammodiscus*, *Glomospirella* and *Hoyenella* are dominant. An overview on the foraminifer taxa determined is given in Table 1.

The main feature of the taxonomic composition of this foraminifer assemblage from the Studorski preval locality in the Julian Alps of western Slovenia is the dominance of primitive agglutinated foraminifers (*Ammodiscus* and *Glomospirella*) and some miliolids and nodosariids. The foraminifers are very small and not well-preserved. The generic composition of this foraminifer assemblage is mainly similar to the composition of the Early Triassic and Anisian assemblages from different parts of the Tethys, from the Alps to China. Several authors have indicated that there are “*Glomospira-Glomospirella*” foraminifer communities at different levels of the Lower Triassic and the lower Anisian in the Tethyan Realm (Zaninetti, 1976; Salaj *et al.*, 1983; Trifonova, 1992; Vuks, 2007). The foraminifer assemblage from the Studorski preval locality has some species common with the foraminifer assemblages from the Lower Triassic of China (He, 1993), the Olenekian of the Caucasus area (Efimova, 1991), the Lower Triassic and Anisian of Bulgaria (Trifonova, 1992) and Hungary (Oravec-Scheffer, 1987), and it can be correlated with foraminifer assemblages from these areas. In the Alps and the Dinarides the “*Glomospira-Glomospirella*” foraminifer communities with some miliolids and nodosariids are known mainly from the Lower Triassic (Dimitrijević *et al.*, 1968; Pantić, 1970; Pantić-Prodanović and Radošević, 1977b; Pisa *et al.*, 1979; Resch, 1979; Broglio Loriga *et al.*, 1990).

Earlier in western Slovenia, the “*Glomospira-Glomospirella*” foraminifer assemblages with some nodosariids were reported from the Lower Triassic and Anisian (Ramovš, 1972). The foraminifer assemblage from western Slovenia is mainly similar to the foraminifer assemblages mentioned above, because they have a common generic composition. In eastern Slovenia “*Glomospira-Glomospirella*” foraminifer assemblages are known from the Anisian (Aničić and Dozet, 2000).

In only one thin-section a *Meandrospira*-like specimen has been detected, but the preservation of the internal structure is poor. In Triassic time, the representatives of *Meandrospira* are typical for the Early Triassic and the Anisian.

It is reasonable to conclude that the foraminifer assemblage from the Studorski preval locality of the Julian Alps in western Slovenia occurred in Early Triassic–Anisian time, or that it was probably restricted to the upper part of the Early Triassic.

Conodonts

The conodont taxonomy follows the classification of Orchard (2005).

Genus *Triassospathodus* Kozur, 1998 in Kozur, Mostler and Krainer (1998)

Type species: *Spathognathodus homeri* Bender, 1970

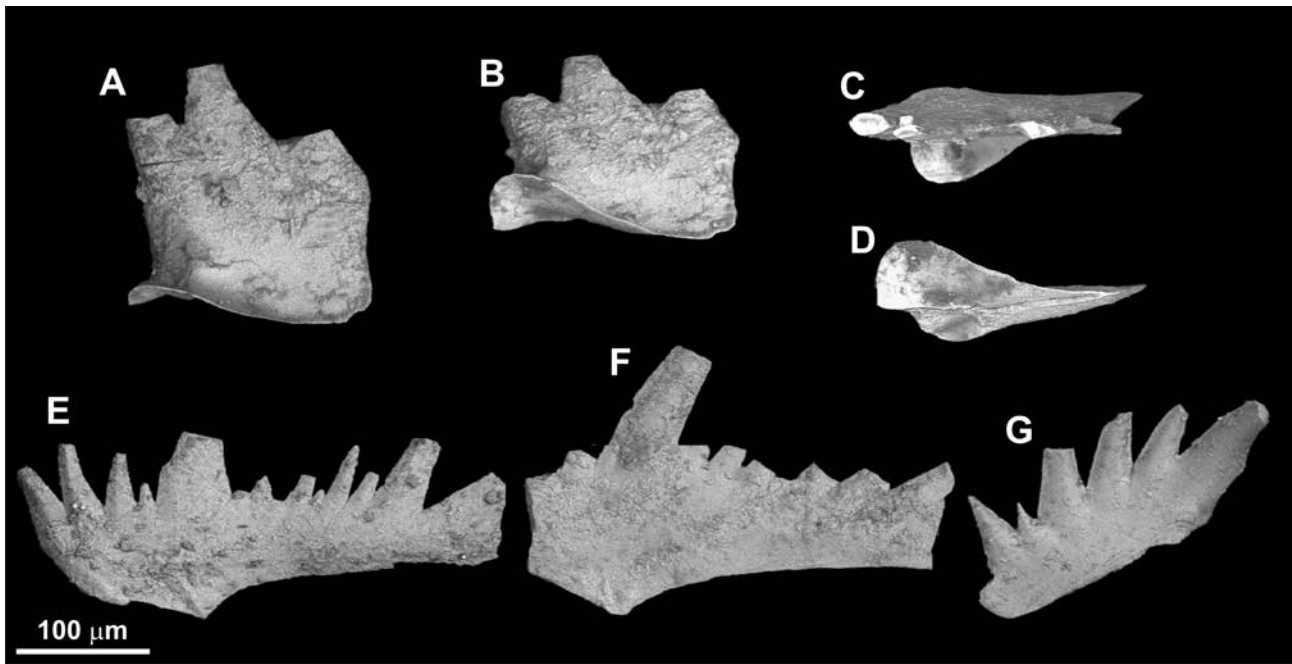


Fig. 6. Conodonts from Early Triassic of Studorski preval, Slovenia. **A–G.** *Triassospathodus hungaricus* (Kozur and Mostler, 1970). **A–D.** P1 element (upper, lower, lateral views), SP 1. **E–G.** ramiform elements (?M, ?S1, S3 elements), SP 3

Triassospathodus hungaricus (Kozur and Mostler, 1970)
Fig. 6A–G

*1970 *Spathognathodus hungaricus* n. sp. – Kozur and Mostler: p. 453, pl 4, figs 8–11.

Material: Five P-elements and eleven ramiform elements (samples SP 1, 3, 5) of moderate preservation.

Description: The spathodid P-elements examined are similar in length and bear three denticles. The basal cavity is wide and open. However, part of the posterior margin in the illustrated specimen is broken in the aboral view (Fig. 6D). It is obvious that the elements have an expanded basal cavity.

The ramiform elements are mostly fragmented and they do not permit reconstruction. Some of them are determined as ?M, ?S1 and S3 elements.

Remarks: *Triassospathodus* can be easily distinguished from *Neospathodus* Mosher, 1968, which has a terminally upward-directed lower margin of the basal cavity (Mosher, 1968). On the other hand, there exists a morphologic similarity in the P elements of *Triassospathodus* Kozur, 1998 (in Kozur *et al.*, 1998) and *Novispathodus* Orchard, 2005 (Orchard, 2005); the latter has a shorter and more widened basal cavity and it has also a different apparatus composition (Heinz Kozur, pers. comm., 2012).

From the Spathian strata of the Thaynes Group in Nevada, Lucas and Orchard (2007) reported elements that are morphologically close or identical with “*Neospathodus*” cf. *hungaricus*.

Stratigraphic and geographic occurrence: Species *T. hungaricus* was first described from the *Tirolites* beds of Felsőrs in Hungary (Kozur and Mostler, 1970). *Triassospathodus* is an important Lower Triassic genus that comprises the majority of Upper Olenekian (Spathian) index species (Kozur *et al.*, 1998).

In an integrated ammonoid and conodont zonation of the Triassic, Kozur (2003) presented *T. hungaricus* as the marker taxon for the basal Spathian equivalent to the *Tirolites cassianus* ammonoid Zone. According to H. Kozur (pers. comm., 2012), in the shallow western Tethys the *T. hungaricus* fauna lies within the lower Spathian, where the fauna with *Icriospathodus collinsoni* is missing.

There are several records of Early Triassic conodonts from Slovenia, but most of them are older than Spathian (see Kolar-Jurkovšek *et al.*, 2011). Recovery of the spathodid Spathian fauna has been documented only from the borderland of the Ljubljana depression in central Slovenia (Dozet and Kolar-Jurkovšek, 2007). In Slovenia, a conodont fauna, high in spathodid elements and with few denticles, is abundant in the Spathian of Slovenia (Idrija-Žiri and Krško areas; unpublished data). From the External Dinarides, the Muć section in Croatia was proposed as a standard section for the European Upper Scythian. This section is well-known for its rich macrofauna and also contains *Triassospathodus triangularis* (Herak *et al.*, 1983).

Macrofauna

The macrofauna collected contains bivalves and gastropods, as well as a few badly preserved specimens of ammonoids of the genus *Tirolites* that indicate an Early Spathian age.

Bivalves

Genus *Bakevellia* King, 1848

Type species: *Avicula antiqua* Graf zu Münster in Goldfuss, 1836 [non *A. antiqua* DeFrance] = *Avicula binneyi* Brown, 1841, by original designation

Bakevellia cf. *incurvata* (Lepsius, 1878)
Fig. 7A–C

*1878 *Gervillia incurvata* sp. n. – Lepsius: p. 353, pl. 1, figs 3a–b.

1908 *Gervillia incurvata* Lepsius – Wittenburg, p. 31, pl. 4, fig. 7.

1923 *Gervillia incurvata* Lepsius – Diener, p. 91 (cum syn.).

Material: One well-preserved specimen with conjoined valves

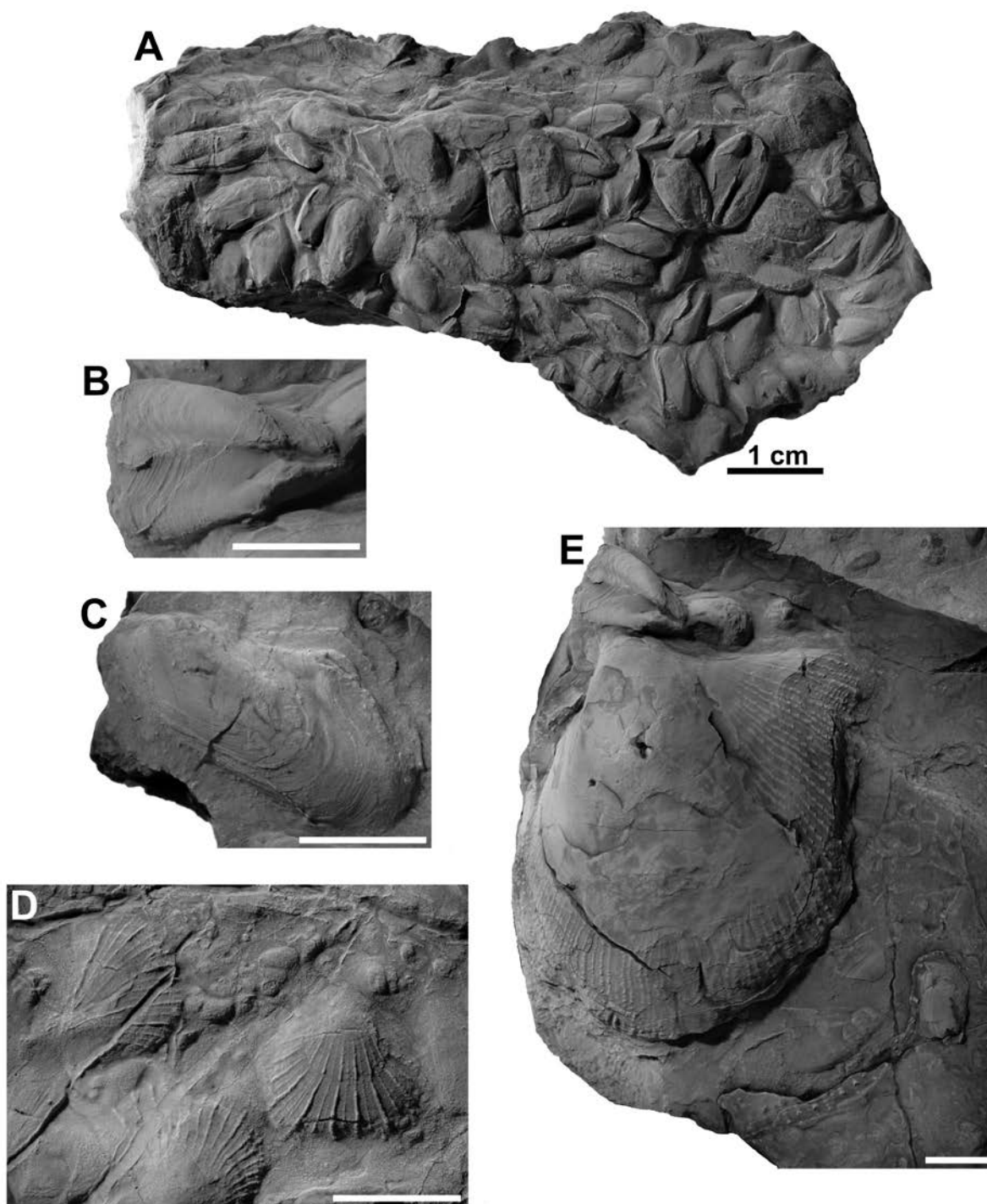


Fig. 7. Bivalves from Early Triassic of Studorski preval, Slovenia. Scale bar 1 cm. All specimens blackened with graphite emulsion and coated with ammonium chloride. **A–C.** *Bakevella* cf. *incurvata* (Lepsius, 1878). **A.** shell accumulation of mostly conjoined valves, BJ 2764. **B.** Specimen with conjoined valves, anterior shell end to right, BJ 2766. Note orientation with valves slightly opened and dorsal margin upside. See text for explanation. **C.** Left valve, BJ 2763. **D.** *Avichlamys* sp., one left valve (individual on right) and two valves with unknown side orientation, BJ 2765. **E.** *Eumorphotis* cf. *gronensis* (Wittenburg, 1908), left valve, BJ 2766

(BJ 2766), one left valve and one specimen with conjoined valves (BJ 2763), ca. 40 moderately preserved specimens mostly with conjoined valves (BJ 2764).

Description: Relatively slender, posteriorly elongated *Bakevella*, with left and right valve more or less equally convex. Beaks pointed, projecting above hinge margin in both valves.

Remarks: This species is unusual for its genus in having more or

less equally convex left and right valves. On this basis, the material is tentatively assigned to *Bakevella incurvata*, although there are slight differences in the outline by comparison with the single right valve, figured by Lepsius (1878, pl 1, figs 3a, b). Lepsius (1878, p. 353) indicated that the beak of the right valve did not project above the hinge line, whereas in the material described, it does. Another difference to the description by Lepsius (1878) is

the apparent lack of a shell sulcus at the ventral margin, but the intraspecific variability of this feature is unclear.

A peculiarity of the present material is an unusual orientation of specimens that have both valves conjoined. Frequently, these specimens have their valves opened up to 30° and rest on the ventral valve margins, i.e. the hinge margin lies in a dorsal position, more or less parallel to the substrate. It is unlikely that this was the life position of the animal, because constructional morphology (elongated shape, long hinge axis, similar convexity of valves) indicates life as an endobryssate mud sticker with the hinge axis oriented more or less vertically to the sediment surface (Seilacher, 1984, text-fig. 7; Muster, 1995, p. 98). Because the fauna occurs at the top of a tempestitic bed, as indicated by hummocky cross-stratification, a possible explanation is that the animals were excavated and displaced by storm waves and then smothered by the resettling silt-clay suspension. The observed orientation in the Studorski preval material might thus be an unnatural dying position of this species.

Genus *Eumorphotis* Bittner, 1901

Type species: *Pseudomonotis telleri* Bittner, 1898 by subsequent designation (Cossman, 1902)

Eumorphotis cf. *gronensis* (Wittenburg, 1908)

Fig. 7E

*1908 *Mysidiopetra gronensis* sp. n. – Wittenburg: p. 31, pl. 4, fig. 4.

Material: One left valve with a partly preserved external shell layer (BJ 2766), questionable three abraded left valves (BJ 2701).

Description: Very large *Eumorphotis* with about 70 radial ribs near the shell margin. Ribs nodose, increasing in number by intercalation during ontogeny. Outline of shell typical of the genus, but posterior wing relatively elongated.

Remarks: The largest specimen is about 8 cm long and more than 8 cm high. This is to the knowledge of the authors the largest *Eumorphotis* specimen, reported so far from the Early Triassic.

Although the type material of *E. gronensis* (Wittenburg, 1908) is incomplete, the specimen in the present study is tentatively assigned to that species on the basis of the similar ornamentation. The shell exterior of the specimen is dorsally eroded, but an increase in the number of ribs by intercalation of additional ribs is observed on the posterior wing. Therefore, it is assumed that the higher number of ribs in this specimen (ca. 70) by comparison with the holotype of *E. gronensis* (28) could be related to its larger size.

Species *E. kittlii* Bittner, 1901 differs from *E. gronensis* chiefly in its stronger development of the ten to twelve most posterior radial ribs, which cover the posterior wing and the adjacent part of the disc. Although the present authors currently treat both species separately, they wish to note that the difference in ornamentation might turn out to be a preservation effect or as lying within the range of intraspecific variation. In this case, *E. kittlii* would have priority over *E. gronensis* and species assignment of the specimen would change accordingly (see also Broglio Loriga and Mirabella, 1986).

Genus *Aviclamys* Allasinaz, 1972

Type species: *Pecten csopakensis* Frech, 1905 by original designation

Aviclamys? sp.

Fig. 7D

Material: One complete left valve and two incomplete valves (BJ 2765).

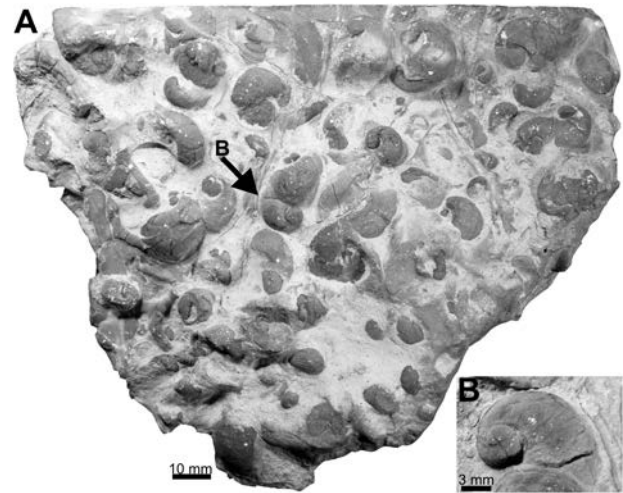


Fig. 8. Neritimorph gastropod ?*Naticella costata* (Münster, 1841) from Early Triassic of Studorski preval, Slovenia, BJ 2480. **A.** General view of rock fragment with numerous poorly preserved individuals. **B.** Close-up of the specimen arrowed on A, showing mode of preservation

Description: Disc nearly circular, covered with about ten strong first-order radial ribs plus the same number of intercalated weaker second-order ribs. The posterior auricle is without a sinus.

Remarks: The state of preservation does not allow specific determination of this taxon. However, the circular disk, truncated posterior auricle and style of ornament are typical of *Aviclamys*. *Pecten vajolettensis* Wittenburg, 1908, subsequently referred to *Aviclamys* by Allasinaz (1972, p. 225), has a similar ornament. However, the presence of an elongated anterior auricle, as figured by Wittenburg (1908, pl. 1, fig. 9), cannot be verified in the material described.

Gastropods

Genus *Naticella* de Koninck, 1881

Type species: *Naticella lyrata* Phillips, 1836 by monotypy (de Koninck, 1881, p. 5)

?*Naticella costata* (Münster, 1841)

Fig. 8A, B

- *1841 *Naticella costata* sp. n. – Münster: p. 101, pl. 10, fig. 14.
- 1892 *Naticella costata* Münster – Kittl, p. 67.
- 1967 *Naticella costata* Münst. – Leonardi, pl. 20, figs 15–16.
- 1985 *Naticella costata* (Münster) – Neri and Posenato, p. 91.
- 2002 *Naticella costata* (Münster) – Hips and Pelikán, p. 356, fig. 8A.
- 2005 *Naticella costata* (Münster) – Nützel, p. 440, fig. 6.

Type locality: Most likely Groneshof, South Tirol, Italy; Werfen Formation, Olenekian, Early Triassic (compare Kittl, 1892: 67).

Material: Single rock piece, composed of gastropod coquina from Studorski preval. The association is monospecific, the shells are recrystallized and mostly weathered out from the visible surfaces. Sample BJ 2480.

Remarks: In spite of the mass occurrences of this gastropod in the Werfen Formation, its taxonomic – both generic and specific – status remains unclear. The type species of *Naticella* was described from the Visean (Lower Carboniferous) of Yorkshire (Phillips, 1836), while the species *Naticella costata* was defined by Münster (1841) in a monograph on gastropods from the Carnian (Upper

Triassic) St. Cassian Formation. It seems, however, that the type series of *N. costata* came from a locality of the Werfen Formation, rather than of the Cassian Fm. Kittl (1892, p. 67) suggested that the material of Münster (1841) could have come from an outcrop of the Werfen Fm at Groneshof, where it occurs abundantly. Taking into account approximately 100 million years and the P-T extinction event between the occurrences of *N. lyrata* and *N. costata*, it is doubtful that both forms are congeneric (see also discussion in Yin and Yochelson, 1983, p. 523). Unfortunately, despite the ubiquity of the material from the Lower Triassic, no protoconch of *N. costata* has been discovered yet.

The material recovered at Studorski preval is poorly preserved and does not contribute any new morphological information to the existing descriptions. In fact the identification itself is poorly constituted and only conditional, on the basis of gross shell morphology. Nevertheless, no other gastropod of this morphology and size is known from the Werfen Formation and therefore the identification seems to be plausible and it is yet another piece of data, confirming the wide distribution of this gastropod in the Early Triassic Tethys.

Stratigraphic and geographic occurrence: *Natiria costata* along with *Werfenella rectecostata* are the most typical gastropods of the Early Triassic Werfen Formation (e.g. Nützel, 2005). These two species occur in Europe, coinciding roughly with outcrops of the upper Werfen Formation or its equivalents. Occurrences include in Italy (e.g., Leonardi, 1967; Neri and Posenato, 1985, Nützel, 2005), Hungary (Broglia Loriga, 1990; Hips and Pelikán, 2002), Austria (Diener, 1926; Kutassy, 1940), Croatia (Prlj-Šimić, 2006), and Slovenia (Pavšič, 2003; this paper). Recently, poorly preserved *Natiria* cf. *costata* has also been reported from the Spathian of Utah, USA (Hofmann *et al.*, 2013a, b).

DISCUSSION AND CONCLUSIONS

This paper presents detailed documentation and interpretation of sedimentological data on a remarkable Early Triassic fossil site in the Julian Alps of Slovenia. The report on the palaeontological material, collected at Studorski preval, confirms the wide distribution of mollusk and foraminifer taxa in the Early Triassic Tethys. The recovery of the earliest Spathian conodont fauna with *Triassospathodus hungaricus* indicates an Olenekian age of the fauna and is an important correlative element for comparison with coeval faunas in the Dinarid area and worldwide.

The sedimentological data presented here indicate that the strata of Studorski preval in the Julian Alps of western Slovenia were deposited in a more distal, storm-influenced ramp. A ramp setting was also mentioned for the deposition of the Werfen Formation in the Southern Alps (Brandner *et al.*, 2012). Two types of beds were recognized, designated here as microfacies types A and B. These alternate vertically and form a sedimentary architecture that consists of coarse-grained skeletal lag deposits of microfacies A, overlain by the laminated or bioturbated mudstones and/or marls of microfacies B. Units with such organization imply the occasional winnowing of bottom sediments during storm peaks and the deposition of coarse-grained skeletal material as the storms waned, followed by the slow settling out of fine-grained material during intervals without storms. Ammonoids encountered in microfacies B imply a barrier-free connection of the depositional environment with the open sea, i.e. deposition in a more distal, deeper-ramp setting.

Numerous trace fossils in the mudstones and marls of microfacies B type beds suggest deposition in a low-energy deeper part of the ramp. A low-energy, poorly aerated environment is also indicated by the presence of pyrite and celestite. Periodic reworking of the bottom skeletal-rich sediment and the sedimentation of storm beds suggest deposition in a zone above the storm wave base, possibly in a wide low-energy mid-ramp environment.

Foraminifer assemblages mainly consist of the primitive agglutinated foraminifers, typical for the Lower Triassic and the Anisian. The foraminifer assemblage is represented by *Ammodiscus? parapriscus* Ho, *Glomospirella facilis* Ho, *Gl. shengi* Ho, *Gl. sp.*, *Pilamina? cf. praedensa* Urošević, *Arenovidalina? sp.*, *Meandrospira? sp.*, *Agathammmina? sp.*, *Hoyenella sinensis* (Ho), *Dentalina splendida* Schleifer and *Nodosaria? spp.* The main feature of the taxonomic composition of this foraminifer assemblage is the dominance of primitive agglutinated foraminifers (*Ammodiscus*, *Glomospirella*, *Hoyenella*), associated with some miliolids and nodosariids. It can be assigned to the time range from Early Triassic to Anisian “*Glomospira-Glomospirella*” foraminifer community. An Early Triassic age is more plausible.

The mollusk fauna includes taxa comparable to those of the *Tirolites* beds of the (Upper) Werfen Fm. Gastropods form monospecific coquinas that are most likely of the shells of *Natiria costata*, a typical faunistic element of the Tethyan Early Triassic. The bivalve fauna includes three genera that differ in stratigraphical range and geographical distribution. *Bakevellia* is a long-lived genus, known worldwide from the Permian up to the Cretaceous. *Eumorphotis* was cosmopolitan in the Early Triassic and reached its acme in the Olenekian, although the genus might have persisted locally into the Middle Triassic. In contrast, *Aviclamys* was restricted to the Olenekian and is currently known only from the western Tethys. The bivalve species include *Bakevellia* cf. *incurvata*, *Eumorphotis* cf. *gronensis* and *Aviclamys* sp. One of the specimens of *Eumorphotis* displays unusually large dimensions, seemingly constituting a record for the largest size of this genus, so far reported from the Early Triassic. The unusual position of articulated *Bakevellia* specimens is in accordance with storm-event deposition, inferred from sedimentological observations. By comparison with other recently described bivalve faunas from the Spathian (Neri and Posenato, 1985; Wasmer *et al.*, 2012; Hautmann *et al.*, 2013) and even from the Griesbachian (Kumage and Nakazawa, 2009; Hautmann *et al.*, 2011), the bivalve diversity is low in the Studorski preval section, and no infaunal taxa are present. However, the normal to large growth sizes of the specimens indicate that this low diversity is not related to environmental stress. Rather, it may be related to the relatively greater water depth, provided that the specimens have not been transported over very large distances, which is unlikely given the low level of fragmentation. Miller (1988) demonstrated an evolutionary onshore-offshore trend in the Palaeozoic history of bivalves, in which taxa mainly evolved in shallow marine settings and expanded later into deeper/distal settings. This onshore-offshore or proximal-distal trend can be easily applied to the weakly inclined ramp situation, as depicted for

the site investigated. The low bivalve diversity in the relatively deeper distal setting described here may thus reflect an evolutionary delay of re-diversification in distal settings, compared to the more diverse faunas in shallower settings of the same age (e.g., Neri and Posenato, 1985; Hautmann *et al.*, 2013). The data indicate a general evolutionary trend that is onshore-offshore (see also Jablonski *et al.*, 1983), seldom considered in analyses of the timing of biotic recovery after mass extinctions.

Acknowledgements

The authors thank the Triglav National Park (Triglavski narodni park) for permission to collect samples at Studorski preval (no. 35607-1/2011-2 dated 9th June 2011). Communication with [Heinz Kozur](#) on the conodont fauna is appreciated. Alex Nützel (Münich, Germany) is acknowledged for the discussion on *N. costata*. The study was partly supported by the Slovenian Research Agency (Programme Number P1-0011 and Project Number J1-9465) and Croatian Ministry of Science (Project Number 195-0000000-3202). The research of AK was supported by the Alexander von Humboldt Foundation Return Fellowship and the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw. The authors thank two anonymous reviewers and editor for careful reading and thoughtful comments. This is a contribution to IGCP-Project 572 (“Recovery of ecosystems after the Permian–Triassic mass extinction”).

REFERENCES

- Aljinović, D., 1995. Storm influenced shelf sedimentation – an example from the Lower Triassic (Scythian) siliciclastic and carbonate succession near Knin (southern Croatia and western Bosnia and Herzegovina). *Geologia Croatica*, 48: 17–32.
- Aljinović, D., Kolar-Jurkovšek, T. & Jurkovšek, B., 2006. The Lower Triassic shallow marine succession in Gorski Kotar Region (External Dinarides, Croatia): lithofacies and conodont dating. *Rivista Italiana di Paleontologia e Stratigrafia*, 112: 35–53.
- Aljinović, D., Kolar-Jurkovšek, T., Jurkovšek, B., Hrvatović, H., 2011. Conodont dating of the Lower Triassic sedimentary rocks in the External Dinarides (Croatia and Bosnia and Herzegovina). *Rivista Italiana di Paleontologia e Stratigrafia*, 117: 135–148.
- Allasinaz, A., 1972. Revisione dei pettinidi Triassici. *Rivista Italiana di Paleontologia e Stratigrafia*, 78: 189–428.
- Aničić, B. & Dozet, S., 2000. Younger Paleozoic and Mesozoic rocks in the northern Krško depression borderland, Slovenia. *Geologija*, 43: 13–36 Ljubljana. [In Slovenian, English summary].
- Baker, A. P. & Bloomer, H. S., 1988. The origin of celestite in deep-sea carbonate sediments. *Geochemica et Cosmochimica Acta*, 52: 335–339.
- Baud, A., Brönnimann, P. & Zaninetti, L., 1974. Sur la présence de *Meandrospira pusilla* (Ho) (Foraminifère), dans le Trias inférieur de Kuh-e-Ali Bashi, Julfa, NW Iran. *Paläontologische Zeitschrift*, 48: 205–213.
- Bender, H., 1970. Zur gliederung der Mediterranen Trias II., Die conodontenchronologie der Mediterranen Trias. *Annales Géologiques des Pays Helléniques*, 19: 465–540.
- Bittner, A., von, 1898. Beiträge zur Paläontologie, insbesondere der triadischen Ablagerungen centralasiatischer Hochgebirge. *Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt*, 48: 689–718.
- Bittner, A., von, 1901. Über *Pseudomonotis telleri* und verwandte Arten der unteren Trias. *Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt*, 50 (for 1900): 559–592.
- Bornemann, L. G., 1874. Über die Foraminiferengattung *Involuntina*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 26: 702–749.
- Brandner, R., Horacek, M. & Keim, L., 2012. Permian-Triassic-Boundary and Lower Triassic in the Dolomites, Southern Alps (Italy). Field Trip Guide 29th IAS Meeting of Sedimentology, Schladming/Austria. *Journal of Alpine Geology*, 54: 379–404.
- Brayard, A. & Bucher, H., 2008. Smithian (Early Triassic) ammonoid faunas from northwestern Guangxi (South China): taxonomy and biochronology. *Fossils and Strata*, 55: 1–179.
- Brönnimann, P., Zaninetti, L., Bozorgnia, F. & Huber, H., 1972. Ammodiscids and ptychocladids (Foraminifera) from the Triassic Elika Formation, Nessa-Hassanakdar section, Central Alborz, Iran. *Rivista Italiana di Paleontologia e Stratigrafia*, 78: 1–28.
- Broglio Loriga, C., Goczan, F., Haas, J., Lenner, K., Neri, C., Oravec-Scheffer, A., Posenato, R., Szabo, I. & Makk, A. T., 1990. The Lower Triassic sequences of the Dolomites (Italy) and Transdanubian Mid-Mountains (Hungary) and their correlation. *Memorie di Scienze Geologiche, Università di Padova*, 42: 41–103.
- Broglio Loriga, C. & Mirabella, S., 1986. Il genere *Eumorphotis* Bittner 1901 nella biostratigrafia dello Scitico formazione di Werfen (Dolomiti). *Memorie di Scienze Geologiche, Università di Padova*, 38: 245–281.
- Brown, T., 1841. Description of some new species of fossil shells, found chiefly in the Vale of Todmorden, Yorkshire. *Transactions of the Manchester Geological Society*, 1: 212–229.
- Brühwiler, T., Bucher, H., Ware, D., Hermann, E., Hochuli, P. A., Roohi, G., Rehman, K. & Yassen, A., 2012. Smithian (Early Triassic) ammonoids from the Salt Range. *Special Papers in Palaeontology*, 88: 1–114.
- Burchette, T. P. & Wright, V. P., 1992. Carbonate ramp depositional systems. *Sedimentary Geology*, 78: 3–57.
- Celarc, B. & Kolar-Jurkovšek, T., 2008. The Carnian–Norian basin-platform system of the Martuljek Mountain Group (Julian Alps, Slovenia): progradation of the Dachstein carbonate platform. *Geologica Carpathica*, 59: 211–224.
- Cossmann, M., 1902. Rectification de nomenclature. *Revue de la Nomenclature*, 6: 1–233.
- Cushman, J. A. & Waters, J. A., 1927. Arenaceous Paleozoic Foraminifera from Texas. *Contributions from the Cushman Laboratory for Foraminiferal Research*, 3: 146–153.
- Dager, Z., 1978. Les Foraminifères du Trias de la Péninsule de Kocaeli – Turquie. *Notes du Laboratoire de Paleontologie de l'Université de Geneve*, 3 : 23–69.
- Diener, C., 1923. *Lamellibranchiata triadica. Fossilium catalogus I: Animalia. Pars 19*. W. Junk, Berlin, 257 pp.
- Diener, C., 1926. *Fossilium Catalogus I: Animalia, Pars 34 – Glossophora triadica*. W. Junk, Berlin, 242 pp.
- Dimitrijević, M., Pantić, S., Radoičić, R. & Stefanovska, D., 1968. Lithostratigraphic and biostratigraphic Mesozoic columns in the Gacko-Sutjaska-Drina region. *Bulletin Institut de Recherches Géologiques et Géophysiques, Series A*, 26: 35–114.
- Dozet, S. & Kolar-Jurkovšek, T., 2007. Spodnjetriasne plasti na južnovzhodnem obrobju Ljubljanske kotline, osrednja Slovenija. *RMZ – Materials and Geoenvironment*, 54: 361–386. [In Slovenian].
- Efimova, N.A., 1991. Triassic system. In: Azbel, A. Y. & Grigelis, A. A. (eds), *Practical Manual on Microfauna of the USSR 5. Mesozoic Foraminifers*. Nedra, Leningrad, pp. 16–25. [In Russian].

- Epstein, A. G., Epstein, J. B. & Harris, L. D., 1977. Conodont color alteration – An index to organic metamorphism. *U.S. Geological Survey Professional Paper*, 995: 1–27.
- Frech, F., 1905. Nachträge zu den Brachiopoden und Zweischalern der Bakonyer Trias (Werfener und Cassianer Estherien-schichten). *Resultate der wissenschaftlichen erforschung des Balatonsees, Anhang: Palaeontologie der Umgebung des Balatonsees*, 1(1): 1–29.
- Gerke, A. A., 1961. *Foraminifers of the Permian, Triassic and Liassic Deposits of the Petroliferous Regions of the North Central Siberia*. *Trudy Naučno-Issledovatel'skogo Instituta Geologii Arktiki*, 120, Leningrad, 519 pp. [In Russian].
- Goldfuss, G. A., 1826–1844. *Petrefacta Germaniae tam ea, quae in museo universitatis regiae Borussicae Fridericae Wilhelmae Rhenanae servantur quam alia quaecunque in museis Hoeninghusino, Muensteriano aliisque extant, iconibus et descriptionibus illustrata*. Verlag lithographische Anstalt Arnz & Co, Düsseldorf, 312 pp.
- Hautmann, M., 1997. Geochemische Untersuchungen im Unteren Muschelkalk bei Jena (Thüringen). *Zeitschrift für geologische Wissenschaften*, 25: 599–616.
- Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A. & Nützel, A., 2011. An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. *Geobios*, 44: 71–85.
- Hautmann, M., Smith, A. B., McGowan, A. J. & Bucher, H., 2013. Bivalves from the Olenekian (Early Triassic) of south-western Utah: systematics and evolutionary significance. *Journal of Systematic Palaeontology*, 11: 263–293.
- He, Y., 1993. Triassic foraminifera from northeast Sichuan and south Shaanxi, China. *Acta Palaeontologica Sinica*, 32: 170–187. [In Chinese, English summary].
- Herak, M., Ščavničar, B., Šušnjara, A., Đurđanović, Ž., Krystyn, L. & Gruber, B., 1983. The Lower Triassic of Muć – Proposal for a standard section of the European Upper Scythian. *Schriftenreihe der Erdwissenschaftlichen Kommissionen, Österreichische Akademie der Wissenschaften*, 5: 93–106.
- Hips, K. & Pelikán, P., 2002. Lower Triassic shallow marine succession in the Bükk Mountains, NE Hungary. *Geologica Carpathica*, 53: 351–367.
- Ho, Y., 1959. Triassic foraminifera from the Chialingkiang Limestone of South Szechuan. *Acta Paleontologica Sinica*, 7: 387–418. [In Chinese, English summary].
- Hofmann, R., Hautmann, M., & Bucher, H., 2013a. A new paleoecological look at the Dinwoody Formation (Lower Triassic, Western USA): intrinsic versus extrinsic controls on ecosystem recovery after the end-Permian mass extinction. *Journal of Paleontology*, 87: 854–880.
- Hofmann, R., Hautmann, M., Wasmer, M., & Bucher, H., 2013b. Palaeoecology of the Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica*, 58: 149–173.
- Jablonski, D., Sepkoski, J. J., Bottjer, D. J. & Sheehan, P. M., 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science*, 222: 1123–1125.
- Jurkovšek, B., 1987a. *Basic Geological Map of SFRY, Sheet Beljak and Ponteba, 1:100.000*. Zvezni geološki Zavod, Beograd.
- Jurkovšek, B., 1987b. *Explanatory Book, Sheet Beljak and Ponteba L 33–51 L 33.52. Basic Geological Map of SFRY 1:100.000*. Zvezni geološki zavod, Beograd, 1–58. [In Slovenian English summary].
- Kaim, A., Nützel, A., Bucher, H., Brühwiler, T. & Goudemand, N., 2010. Early Triassic (Late Griesbachian) gastropods from South China (Shanggan, Guangxi). *Swiss Journal of Geosciences*, 103: 121–128.
- Kaim, A., Nützel, A., Hautmann, M. & Bucher, H., 2013. Early Triassic gastropods from Salt Range, Pakistan. *Bulletin of Geosciences*, 88: 505–516.
- King, W., 1848. *A Catalogue of the Organic Remains of the Permian Rocks of Northumberland and Durham*. Published by the author, Newcastle-upon-Tyne, 16 pp.
- Kittl, E., 1892. Die Gastropoden der Schichten von St. Cassian der süd-alpinen Trias. 2. Theil. *Annalen des K. K. Naturhistorischen Hofmuseums*, 7: 35–97.
- Kolar-Jurkovšek, T., Jurkovšek, B. & Aljinović, D., 2011. Conodont biostratigraphy across the Permian–Triassic boundary at the Lukač section in western Slovenia. *Rivista Italiana di Paleontologia e Stratigrafia*, 117: 115–133.
- Koninck, L. G., de, 1881. Faune du calcaire carbonifère de la Belgique, troisième partie, Gastéropodes. *Annales du Musée Royal d'Histoire Naturelle de Belgique, Série Paléontologique*, 6, 1–170.
- Kozur, H., 2003. Integrated ammonoid-, conodont and radiolarian zonation of the Triassic. *Hallesches Jahrbuch für Geowissenschaften*, 25: 49–79.
- Kozur, H. & Mostler, H., 1970. Neue Conodonten aus der Trias. *Berichte Natur-Medizin Vereins Innsbruck*, 58: 429–464.
- Kozur, H., Mostler, H., & Krainer, K., 1998. *Sweetospathodus* n. gen. and *Triassospathodus* n. gen., two important Lower Triassic conodont genera. *Geologia Croatica*, 51: 1–5.
- Kristan-Tollmann, E., 1984. Trias-Foraminiferen von Kumaun im Himalaya. *Mitteilungen der Österreichischen Geologischen Gesellschaft*, 77: 263–329.
- Kumagai, T. & Nakazawa, K., 2009. Bivalves. In: Shigeta, Y., Zakharov, Y. D., Maeda, H. & Popov, A. M., (eds), *The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia*. National Museum of Nature and Science Monographs, 38: 156–173.
- Kutassy, A., 1940. *Fossilium Catalogus I: Animalia, Pars 81 – Glossophora triadica II*. G. Feller, Neubrandenburg, pp. 243–477.
- Leonardi, P., 1967. *Le Dolomiti, Geologia dei Monti tra Isarco e Piave*. Manfrini, Rovereto, 552 pp.
- Lepsius, R., 1878. *Das westliche Südtirol*. Verlag Wilhelm Hertz, Berlin, 375 pp.
- Loeblich, A. R. & Tappan, H., 1988. *Foraminiferal Genera and Their Classification. 2 V*. Van Nostrand Reinhold Company, New York, 970 pp.
- Lucas, S. G. & Orchard, M. J., 2007. Triassic lithostratigraphy and biostratigraphy north of Currie, Elko County, Nevada. *Bulletin, New Mexico Museum of Natural History and Science*, 40: 119–126.
- Lucas, S. G., Kolar-Jurkovšek, T. & Jurkovšek, B., 2008. First record of a fossil amphibian in Slovenia (Lower Triassic, Olenekian). *Rivista Italiana di Paleontologia e Stratigrafia*, 114: 323–326.
- Mikhalevich, V. I., 2000. The phylum Foraminifera d'Orbigny, 1826 – Foraminifers. In: Alimov, A. F., (ed.), *Protista: Manual on Zoology. P. 1*. Nauka, St.-Petersburg, 533–623. [In Russian, English summary].
- Miller, A., 1988. Spatio-temporal transitions in Paleozoic bivalvia: an analysis of North American fossil assemblages. *Historical Biology*, 1: 251–273.
- Mosher, L. C., 1968. Triassic conodonts from western North America and Europe and their correlation. *Journal of Paleontology*, 42: 895–946.
- Münster, G.G. zu, 1841. *Beiträge zur Geognosie und Petrefactenkunde des Südöstlichen Tirol's vorzüglich der Schichten von St. Cassian*. Buchner'schen Buchhandlung, Bayreuth, 152 pp.

- Muster, H., 1995. Taxonomie und Paläobiogeographie der Bakevelliidae (Bivalvia). *Beringeria*, 14: 1–161.
- Neri, C. & Posenato, F., 1985. New biostratigraphical data on uppermost Werfen Formation of western Dolomites (Trento, Italy). *Geologisch-Paläontologische Mitteilungen Innsbruck*, 14: 83–107.
- Nützel, A., 2005. Recovery of gastropods in the Early Triassic. *Comptes Rendus Palevol*, 4: 433–447.
- Oravecz-Scheffer, A., 1987. Triassic foraminifers of the Transdanubian Central Range. *Geologica Hungarica, Series Palaeontologica*, 50: 1–134.
- d'Orbigny, A., 1826. Tableau méthodique de la classe des Cephalopodes. *Annales de Sciences Naturelles*, 1: 245–314.
- Orchard, M. J., 2005. Multielement conodont apparatuses of Triassic Gondolelloidea. *Special Papers in Palaeontology*, 73: 73–101.
- Pantić, S., 1965. *Pilamina densa* n. gen., n. sp. and other Ammodiscidae from the Middle Triassic in Crmnica (Montenegro). *Geološki vjesnik*, 18 (for 1964): 189–193.
- Pantić, S., 1970. Caractéristiques micropaléontologiques de la colonne triasique de l'anticlinal de Zdrelo (Serbie orientale). *Bulletin Institut de Recherches Géologiques et Géophysiques, Series A*, 28: 377–385.
- Pantić-Prodanović, S., & Radošević, B., 1977a. The lithostratigraphic characteristics of Triassic sediments on Tara mountain Inner Dinarides, Yugoslavia. In: Kallergis, G. (ed.), *Proceedings of the VI Colloquium on the Geology of the Aegean Region*. Institute of Geological and Mining Research, Athen, pp. 1159–1167.
- Pantić-Prodanović, S. & Radošević, B., 1977b. Geological section of Scythian and Anisian stages in the Jelovica River valley (southeastern Serbia). *Bulletin du Museum d'histoire naturelle de Belgrade, Series A*, 32: 75–93.
- Pavšič, J., 2003. *Paleontologija. I. del Paleobotanika in nevretenčarji*. Univerza v Ljubljani, Naravoslovnotehniška fakulteta, Oddelek za geologijo, Ljubljana, 451 pp.
- Phillips, J., 1836. *Illustrations of the Geology of Yorkshire*. John Murray, London, 253 pp.
- Pirteni, A., 1988. The Triassic benthic foraminifera of Albania. *Revue de Paléobiologie*, Vol. Spec. 2: 145–152.
- Pisa, G., Farabegoli, E. & Ott, E., 1979. Stratigrafia e paleogeografia dei terreni Anisici della conca di Agordo e dell'alta val di Zoldo (Dolomiti sudorientali). *Memorie della Società Geologica Italiana*, 18 (for 1978): 63–92.
- Placer, L., 1999. Contribution to the macrotectonic subdivision of the border region between Southern Alps and External Dinarides. *Geologija*, 41 (for 1998): 223–255.
- Plummer, H. J., 1945. Smaller Foraminifera in the Marble Falls, Smithwick and lower Strawn strata around the Llano uplift in Texas. *University of Texas Publications*, 4401: 209–271.
- Posenato, R., 2008. Patterns of bivalve biodiversity from Early to Middle Triassic in the Southern Alps (Italy): Regional vs. global events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 261: 145–159.
- Prlj-Šimić, N., 2006. *Stratotip*. Hrvatski prirodoslovni muzej, Zagreb, 47 pp.
- Ramovš, A., 1972. Mikrofauna der alpinen und voralpinen Trias Sloweniens. *Mitteilungen der Österreichischen Geologischen Gesellschaft*, 21: 413–426.
- Resch, W., 1979. Zur Fazies-Abhängigkeit alpiner Trias-Foraminiferen. *Jahrbuch der Geologischen Bundesanstalt*, 122: 181–249.
- Rettori, R., 1994. Replacement name *Hoyenella* gen. n. (Triassic Foraminiferida, Miliolina) for *Glomospira sinensis* Ho, 1959. *Bolletino Società Paleontologica Italiana*, 33: 341–343.
- Rettori, R., 1995. Foraminiferi del Trias Inferiore e Medio della Tetide: revisione tassonomica, stratigrafia ed interpretazione filogenetica. *Université de Genève, Département de Géologie Paléontologie*, 18: 1–150.
- Reuss, A.E., 1862. Entwurf einer systematischen Zusammenstellung der Foraminiferen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe*, 44 (for 1861): 355–396.
- Risso, A., 1826. *Histoire naturelle des principales productions de l'Europe meridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, tome 4*. F.-G. Levrault, Paris, 439 pp.
- Salaj, J., Borza, K. & Samuel, O., 1983. *Triassic Foraminifers of the West Carpathians*. Geologický Ústav Dionýza Štúra, Bratislava, 213 pp.
- Salaj, J., Trifonova, E., Gheorghian, D. & Coroneou, V., 1988. The Triassic foraminifera microbiostratigraphy of the Carpathian-Balkan and Hellenic realm. *Mineralia Slovaca*, 20: 387–415.
- Scotese, C. R., 2001. *Atlas of Earth History. Volume 1, Paleogeography, PALEOMAP Project*. University of Texas, Arlington, Texas, 52 pp.
- Seilacher, A., 1984. Constructional morphology of bivalve: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology*, 27: 207–237.
- Sepkoski, J. J., 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology*, 10: 246–267.
- Sepkoski, J. J., 1997. Biodiversity: Past, present, and future. *Journal of Paleontology*, 71: 533–539.
- Trifonova, E., 1992. Taxonomy of Bulgarian Triassic foraminifera. I. Families Psammosphaeridae to Nodosinellidae. *Geologica Balcanica*, 22: 3–50.
- Trifonova, E., 1994. Taxonomy of Bulgarian Triassic foraminifera. III. Families Spirolocuniidae to Oberhausereliidae. *Geologica Balcanica*, 24: 21–70.
- Urošević, D., 1988. Microfossils from the Triassic of the Inner belt of the Yugoslavian Carpatho-Balkanides. *Annales Géologiques de la Peninsule Balkanique*, 52: 371–379.
- Urošević, D. & Jeličić, L. 1973–1974. Conodonts and foraminifers from Hanbulog limestone of Serbia, Bosnia, Herzegovina and Montenegro. *Bulletin Institut de Recherches Géologiques et Géophysiques, Series A*, 31–32: 251–263.
- Vuks, V. J., 2007. Olenekian (Early Triassic) foraminifers of the Gorny Mangyshlak, Eastern Precaucasus and Western Caucasus. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 252: 82–92.
- Yin, Hong-fu & Yochelson, E. L., 1983. Middle Triassic gastropoda from Qingyan, Guizhou Province, China: 2 – Trochacea and Neritacea. *Journal of Paleontology*, 57: 515–38.
- Wasmer, M., Hautmann, M., Hermann, E., Ware, D., Roohi, G., Ur-Rehman, K., Yaseen A. & Bucher, H., 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. *Palaeontology*, 55: 1043–1073.
- Wittenburg, P., von, 1908. Beiträge zur Kenntnis der Werfener Schichten Südtirols. *Geologische und Paläontologische Abhandlungen, Neue Folge*, 8: 251–289.
- Zaninetti, L., 1976. Les Foraminifères du Trias. Essai de synthèse et corrélation entre les domaines mésogéens européen et asiatique. *Rivista Italiana di Paleontologia e Stratigrafia*, 82: 1–258.
- Zaninetti, L. & Brönnimann, P., 1975. Triassic foraminifera from Pakistan. *Rivista Italiana di Paleontologia e Stratigrafia*, 81: 257–280.