

Early Jurassic corals of the Pamir Mountains - a new Triassic-Jurassic transitional fauna

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ABSTRACT. Four microstructural groups of corals representing the orders Scleractinia and Hexanthiniaria are known in the Triassic and in the Early Jurassic of the Tethys realm. In the south-eastern Pamir Mountains, Lower Jurassic corals occur from the Hettangian to Toarcian sediments. Hettangian?-Sinemurian and Sinemurian coral faunas discussed in this paper come from the Gurumdy and Mynkhajir facies zones. Coral associations are composed of classical Early Jurassic West European and North African (Moroccan) taxa, accompanied by several genera previously unknown in the West Tethys. After the end-Triassic extinction, the Early Jurassic recovery faunas of the Pamir Mountains contain *Stylophylloopsis*, *Eocomoseris*, a genus related to *Elysastrea*, and a large number of Jurassic genera: *Oppelismilia*, *Archaeosmilia*, *Archaeosmiliopsis*, *Stylosmilia*, *Proaplophyllia*, *Cylismilia*, *Intersmilia*, *Prodonacosmilia*, *Pachysmilia*, *Placophyllia* and *Stephanastrea*. More or less fragmented corals and complete skeletons are found in detrital carbonate, oolitic, or micritic limestone facies. Phaceloid growth forms prevail over solitary and massive ones.

KEYWORDS: Scleractinia, Hexanthiniaria, Tethys, Central Asia, recovery fauna.

1. Introduction

Hettangian?-Sinemurian corals from the south-eastern Pamir Mountains occur soon after the end-Triassic mass extinction and while incompletely known represent the most taxonomically differentiated coral faunas of that time. This recovery fauna is composed of new taxa of relic Triassic groups as well as of newly evolved coral groups. The purpose of this paper is to present a summary of the fauna and its palaeogeographic relationships to the west Tethyan corals.

The earliest coral-bearing sediments in the south-eastern Pamir Mountains belong to strata of the late Hettangian? to Sinemurian age (Dronov & Melnikova, 1987, 2007; Melnikova, 2006, p. 173). These widely distributed sedimentary rocks composed of bedded, dark limestones of variable lithology, occur at the lower part of two structural zones (Fig. 1): south-west Gurumdy Zone and north-east Mynkhajir Zone, separated by the Istyk Uplift, directed NW-SE with marine transgressive facies of the Aalenian-early Bajocian (Andreeva & Dronov, 1972), all lying discordantly upon Triassic sedimentary strata. In each zone a number of sedimentary series were differentiated, each having a characteristic lithology, named with informal terms: suite (svita: Dronov & Melnikova, 1987), or formation (Melnikova, 2006).

Some of these finds were described in the past (Melnikova, 1975, 1989; Melnikova & Roniewicz, 1976;

Melnikova et al., 1993), providing a more complete insight in the coral recovery after the Triassic-Jurassic faunal crisis (Melnikova, 2006). This crisis was preceded by the intra-Norian decrease in coral diversity observed in the west Tethys, as documented by comparisons of faunas of the late Carnian-early Norian with those of the late Norian-Rhaetian time (Roniewicz, 2010, 2011). During the late Norian and Rhaetian bloom the coral fauna reached a different taxonomic composition in comparison with that of the preceding stage (Fig. 2).

A well known late Norian-Rhaetian fauna (e.g. Roniewicz 1989, Roniewicz & Michalik 1998, Melnikova, 2001) forms a basis for comparison of diversity between Late Triassic and Early Jurassic faunas. Dramatic diversity decrease of Rhaetian coral families after the T/J boundary is comparable to that of other marine organisms (Hallam, 1995). Knowledge of the composition of the Early Jurassic coral fauna is far from complete, but new finds from the south-eastern Pamir Mountains allow us to understand the proportion of Triassic corals to typical Jurassic genera in this Early Jurassic fauna. In defining the changes in coral fauna diversity at the level of high rank taxonomical units, a microstructural criterion has been used (Roniewicz & Morycowa, 1989, 1993).

2. Material

The characteristics provided herein are based on corals collected by G.K. Melnikova and on field observations that V.I. Dronov and G.K. Melnikova made between 1958 and 1980 (Institute of Geology, Dushanbe, Tadjik Republic). The material has been prepared in the form of thin sections. While the skeletons are recrystallized, they retain recognizable traces of the septal microstructure.

The collection of thin sections is housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland, under the repository number ZPAL H26.

3. World distribution of the Early Jurassic corals

From all Early Jurassic occurrences in the world, those from the West Europe, North Africa (Morocco) and the south-eastern Pamir Mountains in Central Asia are recognized the best. First taxonomic descriptions from the early Early Jurassic and middle Early Jurassic are these from the Belgium, Luxembourg, France (d'Orbigny, 1850; Chapuis & Dewalque, 1853; Fromentel, 1862; Dumortier, 1864; Terquem & Piette, 1865; Fromentel & Ferry, 1865-1869) and British Isles (Duncan, 1867-1868; Tomes, 1878, 1882, 1888). In the 20th century, this literature was increasing (Alloiteau, 1958; Weyer, 1965; Turnšek et al., 1975; Beauvais, 1976; Roniewicz & Michalik, 1998; Turnšek & Buser, 1999; Turnšek & Košir, 2000; Stolarski & Russo, 2002; Turnšek et al., 2003; Kiessling et al., 2009).

Stage	Structural Zones		
	Gurumdy Zone at the SW of the Istyk Uplift	Istyk Zone Istyk Uplift	Mynhadjir Zone at the NE of the Istyk Uplift
Late Sinemurian-Bajocian	Sedek Formation A	Karauldyn Formation	Zormynkhadjir Formation
Sinemurian	Ghurumdy Formation ** A	[land]	Mynkhadjir Formation **
Hettangian?-Sinemurian	** A <i>Cardinia</i> sp.sp.	Shahtesay Formation	** <i>Cardinia</i> sp.sp.
Hettangian	Darbazatash Formation		Kyzylbeles Formation
Upper Triassic deposits discordantly overlain by Lower-Jurassic conglomerates			

Figure 1. Structural-facies zonation of the lowest Early Jurassic strata in the South-East Pamir Mountains with distribution of Early Jurassic corals and ammonites. Legend: ** corals of Triassic and Jurassic relationships, A Early Jurassic ammonites.

Microstructural group	Family	LC - EN	LN - R	H - S
1 st	Stylophyllidae	—————	—————	—————
	Gigantostylidae		—————	
2 nd	Volzeiidae	—————		
	Protoheterastraecidae	—————		
	Archeosmiliidae			—————
	Coryphyllidae	—————	—————	
	Reimaniphyllidae	—————	—————	
	Distichoflabellidae		—————	
	Margarophyllidae	—————	—————	
	Procycolitidae		—————	
	Alpinophyllidae		—————	
3 rd	Actinastraecidae	—————	—————	—————
	Stylinidae			—————
	Placophyllidae			—————
	Conophyllidae	—————		
	Cycliphyllidae	—————	—————	
	Gablonzeridae	—————	—————	
	Curtoseriidae	—————	—————	
	Cuifastraeidae	—————	—————	
	Thamnasteriidae	—————	—————	●●●●▶
	Pamiroseriidae		—————	
	Tropiastraecidae	—————		
	Astreomorphidae	—————	—————	
	Microsolenidae	—————	—————	—————
	Latomeandridae			—————
Furcophyllidae	—————			
4 th	Zardinophyllidae	—————	—————	—————
	Amphiastraecidae	—————	●●●●▶	●●●●▶
	Donacosmiliidae			—————
	Intersmiliidae			—————
Corals of poorly preserved microstructure belonging to the 2 nd or 3 rd microstructural group	family A: <i>Hydrasmilia</i>	—————		
	family B: <i>Thamnasterites</i>	—————		
	family C: forking coral	—————		
	family D: solitary dwarfish coral	—————		
	No. of families/genera	24/ca.50	18/ca.40	10/>11

Figure 2. Coral families documenting the post-Early Norian and post-Rhaetian drops of faunal diversity. Legend: microstructural groups 1st fascicular; 2nd minitrabecular; 3rd thick-trabecular; 4th pachytheal after Roniewicz & Morycowa (1993); LC-EN families of the late Carnian-early Norian fauna; LN-R families of the late Norian-Rhaetian fauna, both observed in the Northern Calcareous Alps; H-S families in the Hettangian?-Sinemurian and Sinemurian fauna in the Pamir Mountains (after Roniewicz, 2010, 2011, modified).

The literature covers other Tethyan regions including Morocco with Early Jurassic fauna described by Beauvais (1986), and earlier results (Le Maitre, 1935; see also Melnikova et al., 1993), and the south-eastern Pamir Mountains with early Early Jurassic corals (Melnikova, 1975, 1989, 2006; Melnikova & Roniewicz, 1976; Melnikova et al., 1993; Dronov & Melnikova, 1987).

Early Jurassic corals also were described from the North America from the deposits of the Sinemurian from British Columbia (Beauvais 1982; Stanley & Beauvais, 1994), and from the Lower Jurassic of the South America: Peru (Wells, 1953; Senowbari-Daryan & Stanley, 1994), from the Hettangian to Pliensbachian of Chile (Prinz, 1991), and from the Pliensbachian of Argentina (Morsch, 2001). Although these other faunas will not be addressed in the comparisons, a common presence of stylophylline corals seems clear. Global changes in coral generic diversity during the Late Triassic and Early Jurassic as connected with reefal environment development were analyzed by Lathuilière & Marchal (2006) who presented range charts.

4. Early Jurassic coral environments

In the Recent reef ecosystem, scleractinians are important components of the fauna on continental shelves and volcanic

islands in subtropical and tropical zones, in the depth range of storm wave base, in oligotrophic, transparent, well aerated water, settled on hard bottom, in presence of green algae of similar preferences. The picture for Mesozoic coral environments is different when we consider the type of sedimentation, bottom conditions and associated organisms, among which are cyanobacteria.

The earliest Jurassic corals found in situ, formed associations of a few taxa, contained in fine detrital facies, so, they were developed on soft sediment bottom. In comparison to Triassic conditions, corals lost their significance in reef-building and as an influence on sedimentation, because high growing, bushy growth form, frequent in the Triassic, became replaced by solitary forms incapable of reef-building. Phaceloid corals developed only locally. Later in the Hettangian and Sinemurian, coral diversity was augmented by discoid, fungiform and incrusting colonial growth forms as well as rare cerioid or thamnasterioid branching colonies, but their influence on sedimentation as potential bafflers was restricted as well.

Early Jurassic coral-bearing deposits were described from many regions (Joly, 1936; Turnšek et al., 1975; Buser & Debeljak, 1996; Kiessling et al., 2009). In the Hettangian and Sinemurian of Europe, corals occur, as fragments or

complete skeletons, in marls, mudstones, sandstones etc; in the Pliensbachian, corals are known in the limestones (Slovenia). In the south eastern Pamir Mountains, early Early Jurassic corals occur in limestones: micritic through oolitic to pelletal-bioclastic or in marls and sandy marls; commonly, corals are associated with structures of cyanobacterial origin. In Europe and in the Pamir Mountains, early Jurassic corals settled on unstabilized sediment bottom; if branching (mostly phaceloid), corals formed meadow-like thickets at most, without making upward-growing bioconstructions.

The post-Triassic time was characterized with a global decrease of carbonate production in general and a rarity of reefs in particular. So, the corals, although present in Early Jurassic shallow seas, rarely developed reefs. The so called "Elmi Reef" in southern France, represents the only known example of an Early Jurassic reefal body, up to 20 meters thick, traceable laterally for 200 m and with smaller bodies in the immediate vicinity. It was described as coral-microbial reef, developing at a moderately deep water, but in range of storm-wave base (Kiessling et al., 2009).

5. Four evolutionary lines of Mesozoic corals

Micromorphology and microstructural aspects of the coral skeleton may be traced throughout the stratigraphical column, allowing us to recognize specific microstructural coral groups corresponding to high systematic units. This allows us to recognize the pressing problems of homeomorphy that is a troubling issue in taxonomic studies. Thanks to the microstructural studies, it was subsequently possible to differentiate four groups of corals by particular details of their skeletal structure (some detectable also in the micromorphology of septa). The recognition of these groups can be made from the Triassic throughout the Jurassic and three of the microstructural groups represent evolutionary stems. These are coral groups with the following skeleton microstructure types: 1st fascicular, 2nd minitrabecular, 3rd thick-trabecular (heterogeneous group) and 4th pachytheal (terminology: Roniewicz & Morycowa, 1989; 1993). Each group embraces one or more units of suprafamilial rank belonging to the orders Scleractinia (1st - 3rd groups) or Hexanthiniaria (4th group). In addition, an informal, heterogeneous scleractiniamorph-group, to which some Ladinian-Carnian corals were ascribed, defined by trabecular microstructure and broom-like arrangement of septa (Stolarski et al., 2004, Melnikova & Roniewicz, 2007). The microstructural groups exemplify evolutionary lines which are to be traced throughout the Mesozoic. The contents of the groups in the Early Jurassic will be characterized in the section 8.

Participation of these coral groups in the fauna of different geological periods allows us to differentiate a number of stages and developmental phases in scleractinian history (Roniewicz & Morycowa, 1989, 1993). The stages are determined by a share of given families in composition of fauna; phases differ from each other by a generic content of the families, changeable in time, thus, expressed in the faunistic spectrum, which is typical of a given time slice. The fauna considered in this paper developed during the Hettangian-Pliensbachian phase of the Early Mesozoic.

6. Characteristics of Early Jurassic corals from the West Tethys

Instability of environmental conditions and a collapse of coral development at the Rhaetian/Hettangian boundary was followed early in the Jurassic by the start of a coral recovery in the Tethys and neighbour epicontinental seas (West Europe, southern Europe, Carpathians, North Africa). Although corals are known from numerous localities, coral bearing sediments do not represent a significant volume within the early Jurassic column. The "Elmi Reef" is perhaps the exception to this (Kiessling et al. 2009).

In the western Tethys, the decline of the coral fauna at the T/J boundary is in both taxonomic and morphologic contrast between a rich end-Triassic fauna and that, impoverished one of the early Hettangian. A majority of Triassic families are missing during the Early Jurassic record (Fig. 2).

The descriptions of the earliest Jurassic corals from the British Isles, Luxemburg, and France (early Hettangian: *Psiloceras planorbis recte - Psiloceras spelae* ammonoid Zone) were not yet taxonomically revised. Judging from illustrations, this fauna is formed, first of all, from genera thriving from the Triassic, the most numerous corals from the fascicular microstructural group (the 1st group): *Stylophyllopsis* Duncan, (1867-1868; described as *Montlivaltia* in part), *Phacelostylophyllum* (in Duncan: *Thecosmilia* in part), *Heterastraea* (in Duncan: *Septastraea* and *Isastrea*), and from thick-trabecular group (the 3rd group): small-calicular, colonial corals, apparently were diversified taxonomically (described in the Duncan monograph as *Astrocoenia* and *Cyathocoenia*), among others containing *Chondrocoenia* of Triassic derivation under these names. In southern France, these groups are the best represented in the "Elmi Reef" (Kiessling et al., 2009), including subglobular *Rhaetiastraea*, another Triassic holdover. Stylophyllid genera from the *Oppelismilia*-group are frequent in the earliest Jurassic, as a novelty presenting septal apparatus made of isomorphic septal spines: *Oppelismilia* (Flügel, 1964), *Heterastraea* (Beauvais, 1976) and *Haimeicyclus* (Stolarski & Russo, 2002).

European corals of the minitrabecular and pachytheal (hexanthiniarian) groups (the 2nd and 4th groups) have not been mentioned in the literature as yet, although among *Thecosmilia*, *Montlivaltia*, or a coral erroneously attributed to *Elysastrea* in Duncan's monograph, are possible their representations. Their presence in the western Europe is expected as the minitrabecular archeosmiliids, in addition to those from the south-eastern Pamirs, are present in Morocco (Beauvais, 1986), and the pachytheal corals occur in the Pamirs.

A lack of Triassic, ecological conditions of coral habitats in the Early Jurassic may account for the observed changes in taxonomic character of coral fauna. This is evidenced by widespread solitary growth forms (terminology of Coates & Jackson, 1987), locally disc-like (British Isles, Luxemburg, Spain, Morocco, Sicily), in a smaller share of pseudocolonial phaceloid corals, than it was in the Late Triassic, and in appearance of small, disc-like and fungi-form cerioid colonies (Beauvais, 1976).

7. Early Jurassic corals in the South-East Pamir Mountains

The microstructural differentiation of Early Jurassic corals still relates to that of the preceding, late Norian-Rhaetian fauna (Roniewicz & Morycowa, 1993). However, the Pamirian corals differ from the latter fauna in taxonomic variability, i.e., in a different generic representation of Triassic families, and in appearance of typically Jurassic taxa that were ancestors of new families.

7.1. Geological characteristics of coral distribution

7.1.1. The Gurumdy Zone

In the Gurumdy Zone (Fig. 1), three superposed lithological units have been observed (Dronov & Melnikova, 1987, Melnikova, 1989, 2006): (a) the Darbazatash Formation estimated to be of the Hettangian age, transgressive, composed of terrigenous sediments overlying discordantly Permo-Triassic strata; (b) the Gurumdy Formation which will be discussed below as the only in this zone containing coral-bearing limestones; its stratigraphic position is determined by late Hettangian-Sinemurian ammonites, a schlotheimiid shell fragment, at its lower part, and an imprint of a Sinemurian ammonite *Angulaticeras* or *Gleviceras*, in its limits; (c) the Sedek Formation, overlying concordantly the preceding one, composed of bedded limestone and marls with abundant, taxonomically diversified ammonites from late Sinemurian at its lower part, through Pliensbachian up to Aalenian age at the top.

Lower Jurassic sediments of the Gurumdy Formation (from 40 m up to 400 m thick, depending the place) may be observed along the Alichur and Gurumdy rivers in the creeks ("says") opening to these river valleys and in the easternmost site, in the Gunyabay Say in the Teshiktash Massif.

In the creeks at the right side of the Alichur River, the sequence is composed of limestones of variable lithology. Its lower member (20-100 m thick) is composed of bioclastic limestones with frequent coral debris, limy shales, and marls with frequent corals, layers rich in bivalves *Cardinia* sp., and a peculiar, layered limestone bed of algal origin. In the upper part of the member, there are gray, micritic limestones with corals, especially phaceloid ones. The upper member (in a whole 20 m up to 300 m thick) is composed of oolitic and micritic limestones interbedded with oncolitic-bioclastic limestones of variable thickness, and of massive, thick-bedded limestone. The corals are represented by colonies of heavily recrystallized skeletons, rendering them difficult to determine taxonomically.

7.1.2. The Mynkhadjir Zone

Lower Jurassic sediments are observed in the valley of the Kizylbeles River, on the Kizylbeles Pass and in the West and East Mynkhadjir massif. Two Lower Jurassic lithological units were distinguished (Dronov & Melnikova, 1987, Melnikova, 2006): (a) the Kizylbeles Formation (30-50 m thick) discordantly overlying Norian-Rhaetian strata with transgressive facies, its tentative age is Hettangian; (b) the Mynkhadjir Formation (200 m) concordantly overlying the latter, composed of limestones, marls and limy shales, and divided into three parts; its tentative age is late Hettangian to Sinemurian. The formation is concordantly overlain by dark, well bedded limestone of (c) the Zormynkhadjir Formation (20-50 m), corresponding in lithology and fauna to the Sedek Formation of the Gurumdy Zone; its age being tentatively assigned as early Middle Jurassic.

The Mynkhadjir Formation, in the most complete development is observed in the Kizylbeles Valley: the lower part (50 m) is composed of dark micritic limestones of the late Hettangian?-Sinemurian age. A peculiar, layered limestone bed of algal origin and *Cardinia* beds correspond to those known from the Gurumdy lower member. On the Kizylbeles Pass, in the lower member, there are coral-bearing limestones; the middle member (50 m) mostly dolomitic in the upper part, contains limestone with corals in the lower part; the upper member (100 m) contains thick-bedded, grey, bioclastic limestone with oolites and oncolitic structures. In the Kizylbeles Valley, Sinemurian corals were observed.

7.2. General characteristics of the Pamirian coral fauna

In comparison with the fauna of the west Tethys, the ecological character of the Pamirian fauna is different, because

pseudocolonial, phaceloid genera (8-9) dominated over solitary genera (4). Nine genera with 12 species from the Hettangian?-Sinemurian of the south-eastern Pamir Mountains already were described (Melnikova, 1975, 1989, Melnikova & Roniewicz, 1976, Melnikova et al., 1993), and other seven taxa have been here identified on the generic level (Fig. 3). The list is not yet complete as the collection contains a number of genera awaiting description.

In the taxonomical spectrum of this fauna, Late Triassic genera of the stylophyllid, volzeioidean and hexanthiniarian (pachytheal) corals are present, as well as microsolenids. Corals of the suborder Stylophyllina, highly differentiated taxonomically in the Rhaetian, are represented by Triassic solitary/phaceloid genera *Stylophyllopsis*, and by Jurassic genus *Oppelismilia*, known also from the faunas of the west Tethys. The superfamily Volzeioidea contain two genera with a straight midseptal line, *Archaeosmilia* and *Archaeosmiliopsis*, from the family Archaeosmiliidae (originally attributed to the sub-order Amphistraeina) which is close to the Carnian Protoheterastraeidae. Hexanthiniarian corals are represented by the zardinophyllid genus *Pachysmilia* (originally attributed to the Amphistraeidae), by intersmiliid genus *Intersmilia* (originally treated as of unknown attribution in Eliášová, 1974, or considered to be linked with archaeosmiliids in Roniewicz & Morycowa, 1993), and by donacosmiliid genera *Cylismilia* and *Prodonacosmilia*.

From the thick-trabecular group of corals abundantly represented in the Triassic, two colonial genera with pennulae and meniana are present: regularly porous *Eocomoseris* and a coral related to *Elysastrea* Laube, 1865, having no common characters with corals described by Duncan, 1867 under this name. This links the Triassic fauna with two Jurassic groups: the first, the microsolenids and the second, the latomeandrids.

The remaining Early Jurassic corals of the south-eastern Pamirs belong to groups which, appeared for the first time in the Jurassic, then became typical of the Late Jurassic: phaceloid *Stylosmilia* and *Proaplophyllia* (Stylinidae) described in Melnikova (1989), and corals determined herein to the generic level as phaceloid *Placophyllia* sp. (Rhipidogyrina), colonial, lamellar *Stephanastraea* sp. (Actinastraeidae), and a coral determined provisionally herein as *Cyathocoenia?* sp. (Actinastraeidae?).

8. Discussion

The composition of the Pamirian coral fauna is especially interesting because the abundant fossils allow us to more accurately consider the familial composition of a transitional Triassic/Jurassic character with a slant towards those of the Jurassic.

With application of the microstructure as a taxonomical guide, differentiation of corals into four microstructural groups was possible (Roniewicz & Morycowa, 1989). Two groups of coral diversity have been recognized during the Late Triassic: the intra-Norian (post-early Norian) and the second at the Triassic/Jurassic boundary (Roniewicz, 2010, 2011). Interestingly, this shows different responses of each of corals groups (Fig. 2).

Late Norian-Rhaetian coral fauna, composed of 19 families, at least, and approximately of 40 genera (Roniewicz, 2011), most frequently occur in meadow-like associations (*constratal growth fabric* of Insalaco, 1998). These corals were well differentiated morphologically, abounding in solitary, phaceloid, high-growing, bushy forms and colonial forms of a variable corallite integration: cerioid, meandroid, thamnasterioid, astreoid, plocoid, kuhnastreoid (Roniewicz, 1989). Septal micromorphology (pennulae, meniana) of many Late Triassic corals was connected with their feeding specialization as was clarified using modern agariciid corals as the homology (compare Schlichter, 1992).

Such faunal composition changed by extinction of genera and families at the T/J boundary. During Early Jurassic, this fauna was replaced by a new one, exemplified by Pamirian corals, supplemented with new genera, but still composed of four microstructural groups (Fig. 3), each of them evolved at their own pace, as follows:

Microstructural groups	Taxa	growth forms			
		s	ph	c	t
1 st	<i>Stylophyllopsis</i> sp.	■	■		
	<i>Oppelismilia</i> sp.	■			
	<i>Pinacophyllum?</i> sp.		■		
2 nd	<i>Archaeosmilia beata</i>	■			
	<i>Archaeosmiliopsis densus</i>		■		
3 rd	<i>Stylosmilia alitschurica</i>		■		
	<i>Stylosmilia decemseptata</i>		■		
	<i>Proaplophyllia basardaraensis</i>		■		
	<i>Placophyllia</i> sp.		■		
	<i>Stephanastraea</i> sp.			■	
	<i>Cyathocoenia?</i> sp.			■	
	<i>Elysastrea?</i> sp.			■	
	<i>Eocomoseris gurumdyensis</i>				■
	<i>Eocomoseris lamellata</i>				■
4 th	<i>Pachysmilia prima</i>		■		
	<i>Prodonacosmilia dronovi</i>		■		
	<i>Cylismilia brevis</i>	■			
	<i>Cylismilia longa</i>	■			
	<i>Intersmilia djartyrabatica</i>		■		

Figure 3. Hettangian?-Sinemurian and Sinemurian corals recognized in the Pamir Mountains. Legend: microstructural groups 1st fascicular; 2nd minitrabecular; 3rd thick-trabecular; 4th pachytheal after Roniewicz & Morycowa (1993); growth forms: s solitary, ph phaceloid, c cerioid, t thamnasterioid after Coates & Jackson (1987); in bold style are marked taxa described in earlier papers (Melnikova, 1975, 1989; Melnikova & Roniewicz, 1976; Melnikova et al., 1993).

The first group: fascicular microstructure (sub-order Stylophyllina). The relic Triassic genera (*Stylophyllopsis*, *Phacelostylophyllum*, *Pinacophyllum*-like coral) are the most widely distributed palaeogeographically with occurrences in west Europe, north-western Africa, and the south-eastern Pamir Mountains. In addition, a new morphological trend appeared in this group with the formation, for example, of septa of thin, homogeneous septal spines that are observed in corals of diverse growth forms. In solitary corals this structure is known in taxa with ecologically conditioned ceratoid or discoid shapes of corallum connected with unloving on unstable sediment bottom: the first in *Oppelismilia* Duncan (re-described in Flügel, 1964), recognized also in the Pamirian fauna, and the second in *Haimeicyclus* Alloiteau (re-described in Stolarski & Russo, 2002).

The second group: minitrabecular microstructure (superfamily Volzeioidea). In the Hettangian-Sinemurian of the south-eastern Pamir Mountains, this group is represented by *Archaeosmilia* and *Archaeosmiliopsis*. Well illustrated, published photos allow us to recognize genus *Archaeosmilia* among the fauna of the upper Sinemurian of Spain, described as *Montlivaltia polymorpha* and *M. doriai* (Turnšek et al., 1975). Among Domerian corals of Morocco, five species of *Archaeosmilia* have been determined (Beauvais, 1986).

The third group: thick-trabecular diverse microstructures (heterogeneous group). The corals of this microstructural group were present during Hettangian and Sinemurian in the Tethys and also in the Pamirs. During Hettangian?-Sinemurian time in the south-eastern Pamir Mountains, the genera *Stylosmilia* (known also from the lower Domerian of Morocco) and *Proaplophyllia* occurred (described in Melnikova, 1989), as well as other Jurassic genera: *Eocomoseris* (described in Melnikova et al., 1993), *Placophyllia*, *Stephanastrea*, *Cyathocoenia* -like coral, and others, stated within the Pamirian collection. A rich representation of colonial genera makes this fauna similar to that of the Rhaetian time: however, abounding in different colonial taxa.

In this early Jurassic spectrum, genus *Eocomoseris* is especially interesting (described from Morocco as *Spongiomorpha crassa* by LeMaitre, 1935): the coral defined by a regular septal porosity, meniana-type micromorphology and a monotrabeular columella. It is a genus appearing during early Norian time (Roniewicz, 2011) and originally was described from the Rhaetian of the Alps as *Spongiomorpha ramosa* Frech, 1890. It was recognized among Early Jurassic corals of the south-eastern Pamir Mountains (Melnikova et al., 1993), and among Cenomanian, Late Cretaceous corals (Löser in Melnikova et al., 1993). Together with pennular coral resembling late Carnian *Elysastrea*, they may profitably be compared with the recent deep-water *Leptoseris fragilis* by a similar micromorphology of septa. In *Leptoseris fragilis*, septal sides bear meniana to support coelenteron ramifications provided with perforations related to the unusual anatomical adaptation by this coral to a filtering mode of feeding (Schlichter, 1992).

The fourth group: pachytheal microstructure (order Hexanthiniaria). During the Hettangian?-Sinemurian in the south-eastern Pamir Mountains, this coral group diversified into zardinophyllids, represented by phaceloid *Pachysmilia* (Melnikova, 1989), donacosmiliids, represented by solitary *Cylismilia* and phaceloid *Prodonacosmilia*, and intersmiliids represented by phaceloid *Intersmilia* (see Melnikova & Roniewicz, 1976), the latter attributed to the archaeosmiliid group in Roniewicz & Morycowa, 1993. Outside the Pamirs, this group has not been reported from the Lower Jurassic. It thus is thought to have migrated much later in the Upper Jurassic of the Tethys realm.

9. Conclusions

a) Early Jurassic coral faunas developed in ecological conditions different from those of the Late Triassic. They display a different taxonomic composition. West European, North-West African and south-east Pamirian corals of the Early Jurassic, show that the groups which characterized Late Triassic assemblages (solitary and phaceloid corals with minitrabecular septal microstructure), like *Retiophyllia*, *Distichophyllia*, *Margarosmilia* (see Roniewicz,

1989; Melnikova, 2001) or colonial corals of the Pamiroseriidae and Cuifastraeidae with thick-trabecular septa, were absent from the Jurassic.

b) In Europe, the earliest Jurassic corals (early Hettangian) have simple morphologies: that most frequently are solitary with ceratoid or patelloid shapes, as well as phaceloid. More complex colonial corals are rare, and these include small colonies of cerioid type, or very rare corals of thamnasterioid type. Solitary and phaceloid growth forms are typical of each of the four microstructural groups. This is a veritable "fauna of survival".

c) Meniana-bearing, regularly porous microsolenid *Eocomoseris* and the pennular, non-porous skeleton of the *Elysastrea* -like genus, both displaying Triassic micromorphological patterns typical of the Pamir fauna, showed the ability to adjust to varying environmental conditions and to pass through the end-Triassic mass extinction also characterized by a major drop of sea level at the T/J boundary. Following the extinction they then adapted to new conditions of the Early Jurassic.

d) Stylophyllid group, relatively rich morphologically during the Rhaetian, crossed the Rhaetian/Hettangian boundary with the most simple morphologies, and then diversified morphologically and taxonomically in the Early Jurassic.

e) Early Jurassic Pamirian and Moroccan faunas contain genera which later gave rise to coral lineages during the Late Jurassic and Early Cretaceous recovery of calcareous platforms. These corals evolved into the microsolenids, latomeandrids, stylinids, rhipidogyrinids (the 3rd group), and pachytheal amphistroids (the 4th group). In contrary, minitrabecular corals, (the 2nd group) disappeared from shallow waters. This microstructural line renewed itself in deep water environments (see also Roniewicz & Morycowa, 1993). The stylophylline coral lineage (the 1st group), presented throughout the Tethys during the Early Jurassic as well as Panthalassa, did not cross the boundary of the Middle/Late Jurassic. It occurred up to the Callovian. This is illustrated by a coral from Israël, determined as *Epistreptophyllum* (Gill, 1982) which shows all features of septal structure typical of the Stylophyllina.

f) A high ecological specialization of early Jurassic in particular and Mesozoic corals in general, is expressed in their evolution of skeleton structures adjusted to the following environmental characteristics: i) a soft-sediment bottom for corals settlement; ii) lowered water transparency resulting from intense precipitation of calcium carbonate, a part of which must remain temporarily in suspension; iii) a high nutrient content indicated by the relative abundance of the microbial development; iv) a strong paleoecological specialization of some coral genera in a filtering mode of feeding as indicated by their septal micromorphology (i.e., pennulae and meniana); v) a frequency of high-growing corals of phaceloid, uniserial form, which were different from many modern multiserial branching corals. This indicates that these Mesozoic corals preferred zones of less energetic water than those living in Recent reefs (Roniewicz & Stolarski, 1999).

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11. References

- Alloiteau, J., 1958. Monographie des Madréporaires fossiles de Madagascar. Annales Géologiques de Madagascar, 25, i-viii, 1-218.
- Andreeva, T.F. & Dronov, V.I., 1972. Pamirska geosynklinalnaja oblast, 224-237. Stratigrafia SSSR. Jurskaja sistema. Moskva, Nedra. [in Russian].
- Beauvais, L., 1976. Revision des Madréporaires liasiques décrit par Duncan (1867). Mémoires de la Société Géologique de France, n. s., 55, mémoire 126, 43-81.

- Beauvais, L., 1982. Étude de quelques coelentérés de la base du Mésozoïque du Canada occidental. *Canadian Journal of Earth Sciences*, 19, 10, 1963-1973.
- Beauvais, L., 1986. Monographie des madréporaires du Jurassique inférieur du Maroc. *Palaeontographica*, A194, 1-68.
- Buser, S. & Debeljak, I., 1996. Lower Jurassic beds with bivalves in south Slovenia. *Geologija*, 37/38 (1994/95), 23-62.
- Chapuis, M.F. & Dewalque, M.G., 1853. Description des fossils des terrains secondaires de la province de Luxembourg. *Mémoires de l'Académie de Sciences*, 25, 1-325.
- Coates, A.G. & Jackson, J.B.C., 1987. Clonal growth, algal symbiosis, and reef formation by corals. *Paleobiology*, 13, 363-378.
- Dronov, V.I. & Melnikova, G.K., 1987. Korrelacija jurskih otlozhenij Gurumdinskoj i Mynhajirskoj zon yugo-vostochnogo Pamira. *Izvestija A.N. Tadjikskoj SSR, otdelenije fiziko-matematicheskikh, himicheskikh i geologicheskikh nauk*, 4 (106), 58-64. [in Russian].
- Dronov, V.I. & Melnikova, G.K., 2007. Jura Pamira. *Trudy Instituta Geologii, Akademia Nauk, Respublika Tadjikistan, Institut Geologii*, n. s., 6, 32-53. [in Russian].
- Dumortier, E., 1864. Etudes paléontologiques sur les dépôts jurassiques du bassin du Rhône, pt. I. Infra-Lias. 1-187. Savy, Paris.
- Duncan, P.M., 1867-1868. A monograph of the British fossil corals. Second series. Part IV, No 1 (1867) Corals from the Zones of *Ammonites Planorbis* and *Ammonites Angulatus* in the Liassic Formation. No. 2.(1868) Corals from the Zone of *Ammonites angulatus*. *Palaeontographical Society of London*, i, ii, 1-73.
- Elišová, H., 1974. Genre nouveau *Intersmilia* (Hexacorallia) du Tithonien des calcaires de Štramberk (Tchécoslovaquie). *Časopis pro mineralogii a geologii*, 19, 415-417.
- Flügel, E., 1964. Ueber die Beziehungen zwischen *Stylophylloopsis* Frech, *Oppelismilia* Duncan und *Molukkia* Jaworski. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1964, 336-348.
- Frech, F., 1890. Die Korallenfauna der Trias. Die Korallen der juvavischen Triasprovinz. *Palaeontographica*, 37, 1-116.
- Fromentel, E., de., 1862. Coralliaires. In J. Martin (ed.), *Paléontologie stratigraphique de l'Infra Lias du Département de la Côte-d'Or*. *Bulletin de la Société géologique de France, série 2*, 16, 92-94.
- Fromentel, E. de, & Ferry, H.B.A.T., de., 1865-1869. *Paléontologie française. Terrains jurassiques. Zoophytes*, 240 p.
- Gill, G.A., 1982. *Epistreptophyllum* (Hexacoralliaires Jurassique): genre colonial ou solitaire? Examen d'un matériel nouveau d'Israël. *Geobios*, 15, 217-223.
- Hallam, A., 1995. Major bioevents in the Triassic and Jurassic. In Walliser O.H. (ed.), *Global events and event stratigraphy*.
- Insalaco, E. 1998. The descriptive nomenclature and classification of growth fabrics in fossil scleractinian reefs. *Sedimentary Geology*, 118, 159-186.
- Joly, H., 1936. Les fossiles du Jurassique de la Belgique avec description stratigraphique de chaque étage. II Lias inférieur. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 79, 244 p.
- Kiessling, W., Roniewicz, E., Villier, L., Leonide, P. Struck, U. 2009. An early Hettangian coral reef in southern France: Implications for the end-Triassic reef crisis. *Palaios*, 24, 657-671.
- Lathuilière, B. & Marchal, D., 2009. Extinctions, survival and renewal of corals from Triassic to Dogger. *Terra Nova*, 21, 1, 57-66.
- Laube, G.C., 1865. Die Fauna der Schichten von St. Cassian. I. Abteilung. *Denkschriften der Mathematisch - Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 24, 223-296.
- LeMaitre, D., 1935. Étude paléontologique sur le Lias du Maroc: Description des Spongiomorphides et des Algues. *Notes et Mémoires du Service des Mines du Maroc*, 34, 19-59.
- Melnikova, G.K., 1975. Novye rannejurskie predstaviteli Amphistraeina (skleraktinii) yugo-vostochnogo Pamira, 108-120. In Djalilov, M.R. (ed.), *Voprosy paleontologii Tadjikistana. Akademia Nauk Tadjikskoj SSR. Institut Geologii*. Dushanbe. [in Russian].
- Melnikova G.K., 1989. O novyh nahodkah rannejurskih skleraktinii na yugo-vostoche Pamira. 71-83. In Djalilov, M.R. (ed.), *Novye vidy fanerozojskoj fauny i flory Tadjikistana. Akademia Nauk Tadjikskoj SSR. Institut Geologii*. Dushanbe. [in Russian].
- Melnikova, G.K., 2001. Tip Coelenterata, 30-80. In Rozanov, A.Yu. & Sheveriev, R.V. (eds), *Atlas triasovyh bespozvonochnyh Pamira*. Moskva, Nauka [in Russian].
- Melnikova, G.K., 2006. The Early Jurassic fauna from the Gurumdy and Mynhajir Zones of the East Pamirs. *Dolkady Earth Sciences*, 407, 172-174.
- Melnikova, G.K. & Roniewicz, E., 1976. Contribution to the systematics and phylogeny of Amphistraeina (Scleractinia). *Acta Palaeontologica Polonica*, 21, 97-114.
- Melnikova, G.K. & Roniewicz, E. 2007. The Middle Triassic scleractinia-like coral *Furcophyllia* from the Pamir Mountains. *Acta Palaeontologica Polonica*, 52, 401-406.
- Melnikova, G.K., Roniewicz, E. & Loeser, H., 1993. New microsolenid genus *Eocomoseris* (Scleractinia, early Lias - Cenomanian). *Annales Societatis Geologorum Poloniae*, 63, 3-12.
- Morsch, M., 2001. Scleractinian corals of the Neuquen Basin (Lower Jurassic), Argentina. *Bulletin of the Tohoku University Museum*, 1, 320-332.
- Morycowa, E. & Roniewicz, E., 1995. Microstructural disparity between Recent fungine and Mesozoic microsolenine scleractinians. *Acta Palaeontologica Polonica*, 40, 346-385.
- d'Orbigny, A., 1850. *Prodrôme de Paléontologie stratigraphique universelle*, 3 vol., Victor Masson, Paris.
- Prinz, P., 1991. *Mezozoische Korallen aus Nordchile*. *Palaeontographica*, A216, 145-209.
- Roniewicz, E., 1989. Triassic Scleractinian corals of the Zlambach Beds, Northern Calcareous Alps, Austria. *Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Denkschriften* 126, 1-152.
- Roniewicz, E., 2010. Uniform habit spectrum vs. taxonomic discrepancy between two succeeding Triassic coral faunas: a proof of the intra-Norian faunal turnover. *Palaeoworld*, 19, 410-413
- Roniewicz, E., 2011. Early Norian corals from the Northern Calcareous Alps, Austria, and the intra-Norian faunal turnover. *Acta Palaeontologica Polonica*, 56, 389-416.
- Roniewicz, E. & Michalik, J., 1998. Scleractinian corals in the Rhaetian of the West Carpathians. *Geologica Carpathica*, 49, 391-399.
- Roniewicz, E. & Morycowa, E., 1989. Triassic Scleractinia and the Triassic/Liassic boundary. *Memoirs of the Association of Austral Asiatic Palaeontologists*, 8, 347-354.
- Roniewicz, E. & Morycowa, E., 1993. Evolution of the Scleractinia in the light of microstructural data. *Courier Forschungsinstitut Senckenberg*, 164, 233-240.
- Roniewicz, E. & Stolarski, J., 1999. Evolutionary trends in the epithecate scleractinian corals. *Acta Palaeontologica Polonica*, 44, 131-166.
- Schlichter, D., 1992. A perforated gastrovascular cavity in the symbiotic deep-water coral *Leptoseris fragilis*: a new strategy to optimize heterotrophic nutrition. *Helgoländer Meeresuntersuchungen*, 45, 423-443.
- Senowbari-Daryan, B. & Stanley, G.D., 1994. Lower Jurassic marine carbonate deposits in Central Peru: stratigraphy and paleontology. *Palaeontographica*, A233, 43-56.
- Stanley, G.D. & Beauvais, L., 1994. Corals from an Early Jurassic coral reef in British Columbia: refuge on an oceanic island reef. *Lethaia*, 27, 35-47.
- Stolarski, J. & Russo, A., 2002. Microstructural diversity of the stylophyllid (Scleractinia) skeleton. *Acta Palaeontologica Polonica*, 47, 651-666.
- Stolaski, J., Roniewicz, E. & Grycuk, T., 2004. A model for furcate septal increase in a Triassic scleractiniomorph. *Acta Palaeontologica Polonica*, 49, 529-542.
- Terquem, O. & Piette, E., 1865. Le Lias inférieur de l'Est de la France. *Mémoire de la Société Géologique de France*, 8, 175 p.
- Tomes, R.F., 1878. On the stratigraphical position of the corals of the Lias of the Midland and western countries of England and of south Wales. *Quarterly Journal of Geological Society of London*, 34, 179-195.
- Tomes, R.F., 1882. Description of a new species of coral from the Middle Lias of Oxfordshire. *Quarterly Journal of the Geological Society of London*, 38, 95-96.
- Tomes, R. F., 1888. On *Heterastraea*, a new genus of Madrepোরaria from the Lower Lias. *Geological Magazine*, 3/5, 207-218.
- Turnšek, D. & Buser, S., 1999. *Stylophylloopsis veneta* (Airaghi), a Liassic coral from the northern Dinaric Carbonate Platform (Slovenia). *Profil*, 16, 173-180.
- Turnšek, D. & Košir, A., 2000. Early Jurassic corals from Krim Mountain, Slovenia. *Razprave IV. Razreda SAZU*, 41, 81-113.
- Turnšek, D., Buser, S. & Debeljak, I., 2003. Liassic coral patch reef above the "Lithotid limestone" on Trnovski Gozd Plateau, West Slovenia. *Razprave IV. Razreda SAZU*, 44, 285-331.
- Turnšek, D., Seyfried, H. & Geyer, O.F., 1975. Geologische und Paläontologische Untersuchungen an einem Korallenvorkommen in Subbetschen Unterjura von Murcia (Süd-Spanien). *Razprave, Razred za prirodoslovne vede, SAZU*, 18, 120-151.
- Wells, J.W., 1953. Mesozoic invertebrate faunas of Peru, part 3, Lower Triassic corals from Arequipa region. *American Museum Novitates*, 1631, 14 pp.
- Weyer, D., 1965. *Heterastraea stricklandi* (Duncan, 1868) (Scleractinia) aus dem nordwestdeutschen Lias. *Geologie*, 14/8, 1004-1007.