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## THE SOUTHWESTERN MARGIN OF BALTICA IN THE PALEOZOIC- EARLY MESOZOIC: ITS GLOBAL CONTEXT AND NORTH AMERICAN ANALOGUE

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*Abstract* - Recent studies have provided evidence for long-termed activity of the shear zones at the southwestern margin of Baltica during the Paleozoic-early Mesozoic. In the late Paleozoic, the Northern Palaeotethyan Shear Zone formed the margin of Baltica and was one of the elements of the global system of megashears. The palaeotectonic analogue of the Paleozoic-early Mesozoic southwestern margin of Baltica may be found in North America, where long-distance displacements occurred at the western and southwestern margin during the Mesozoic-Cenozoic.

*Key words*: shear zone, palaeotectonic analogue, Baltica, North America, Paleozoic, Mesozoic.

### Introduction

The tectonic history of Baltica was reviewed by BOGDANOVA (1993), BOGDANOVA *et al.* (1996), NIKISHIN *et al.* (1996), TORSVIK *et al.* (1996), ARTEMIEVA (2003), and COCKS & TORSVIK (2005). A geologic abruptness of the western Baltica boundary was suggested much earlier (TORNQUIST, 1908). However, many relevant questions remain. The recent studies of the southwestern margin of Baltica (e.g., SAINTOT *et al.*, 2003; DADLEZ *et al.*, 2005; RUBAN & YOSHIOKA, 2005) suggest that the traditional concepts of the geodynamic evolution of this region need to be re-evaluated.

### Geodynamic outline

In the Paleozoic, Baltica, now a part of Eurasia, was a medium-sized continent, which included the present-day territory of European Russia, Ukraine, Belorussia, the Baltic countries, the northeastern part of Poland, and the Scandinavian Peninsula. COCKS & TORSVIK (2005) have described Baltica as a terrane. Two other terms “East European Craton” and “Russian Platform” are often referred to the same territory as “Baltica”. To avoid misunderstanding, I propose their definition herein. Baltica is considered only as a plate, which existed since the end-Proterozoic, when a solid continent appeared after the amalgamation of the Precambrian blocks, and already in the Paleozoic included into the larger continent of Laurussia and then Pangaea.

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In contrast, the East European Craton is the present-day tectonic unit, which comprises the second-order structures of former Baltica (Fig. 1). The Russian Platform may be referred to as the assembly of the stable structures between the Carpathians, the Scandinavian Caledonides, the Timan, the Urals, and the Caucasus, i.e., it includes the entire East European Craton, the Scythian Platform (often mentioned as the Scythian Plate), the Peri-Caspian Basin, the Donbass, and some other stable marginal areas. The southwestern margin of Baltica discussed in this paper comprises the present-day structures of the Ukrainian Massif (or the Ukrainian Shield), the Donbass, the Dniepr-Donets Basin, the Pripyat Trough, and the so-called Peri-Tornquist Basin (Fig. 1).

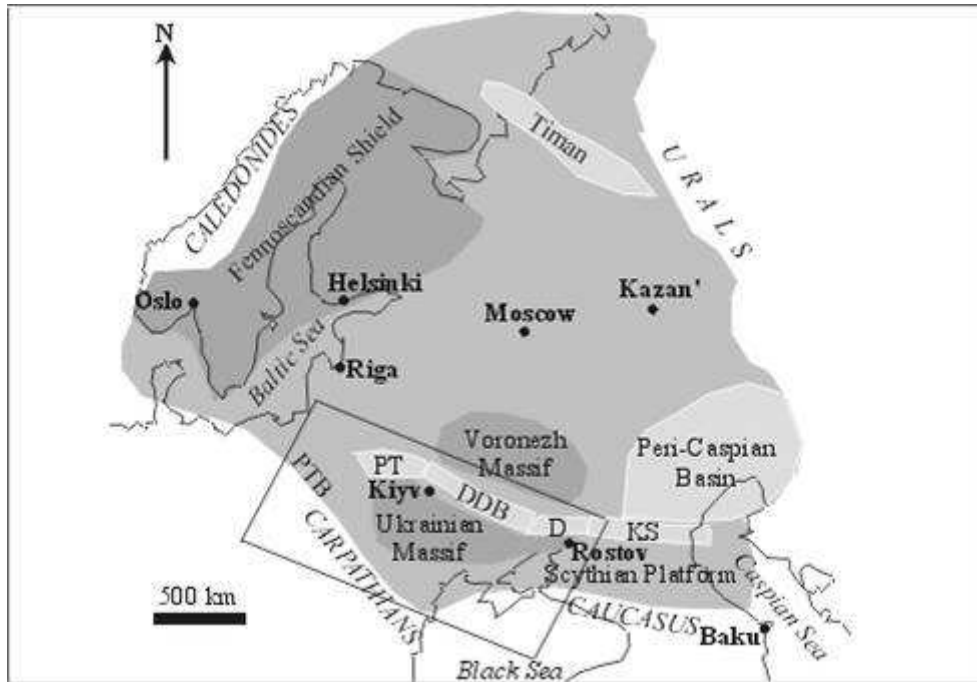


Fig. 1 - The present-day tectonic outline of the East European Craton (significantly modified after NIKISHIN *et al.*, 1996). Abbreviations: PT – Pripyat Trough, DDB – Dniepr-Donets Basin, D – Donbass, KS – Karpinsky Swell, PTB - Peri-Tornquist Basin. Rectangle delineates the southwestern margin of Baltica discussed in this paper.

There was not a unique continent named Baltica until the end of the Proterozoic. The assembly of large terranes in the Palaeoproterozoic did not result in a solid continent as traditionally accepted and described by NIKISHIN *et al.* (1996). Even if an orogeny ended, the boundaries between terranes might have stayed active in the Meso- and Neoproterozoic. BOGDANOVA (1993) and BOGDANOVA *et al.* (1996) argued for the existence of major shear zones with long-distance strike-slip displacements, and rifts between Fennoscandia, Sarmatia, and Volgo-Uralia. Possibly, they were related to previously existing Palaeoproterozoic active

structures. In the same way, the Neoproterozoic Pan-African Orogeny (alternatively named the Brasiliano-Pan-African Orogeny) resulted in the amalgamation of many plates and terranes to form the end-Proterozoic-Early Paleozoic Gondwana. This agglutination of continental masses was not an abrupt, but a continuous process, involving multiple and successive collisions (CORDANI *et al.*, 2000; HEILBRON & MACHADO, 2003). Major shear zones with strike-slip displacements became the boundaries between amalgamated cratons (CORDANI *et al.*, 2000; GUIRAUD *et al.*, 2000, 2005; AZZOUNI-SEKKAL *et al.*, 2003; CABY & MONIÉ, 2003; KLEIN *et al.*, 2005a,b). After the Neoproterozoic, Baltica became an individual ('solid') continent, which generally drifted to the Equator (SCOTese, 2004). However, ENEROTH & SVENNINGSEN (2004) have argued that Baltica was located close to the Equator by the end of the Proterozoic. Its mid-Paleozoic amalgamation with Laurentia led to the appearance of Laurussia, which in the late Paleozoic was included into the largest supercontinent, namely Pangaea (COCKS & TORSVIK, 2002, 2005; STAMPFLI & BOREL, 2002; SCOTese, 2004; TORSVIK & COCKS, 2004). After the breakup of Pangaea in the Mesozoic, Baltica, together with Siberia, India, and some large Gondwana-derived terranes, created Eurasia, which has existed until the present day.

Both DADLEZ *et al.* (2005), who analyzed the crustal structure of the Polish Basin, and RUBAN & YOSHIOKA (2005), who discussed the evolution of the Donbass, considered the evolution of the southwestern margin of Baltica in the context of the dynamics along the Paleozoic-Mesozoic major shear zones. The Early Paleozoic counterclockwise rotation of Baltica, documented particularly by TORSVIK *et al.* (1996) and COCKS & TORSVIK (2005), caused dextral strike-slip displacements along the Teisseyre-Tornquist Zone (Fig. 2A). As a result of this movement, a few small terranes were formed, including the Pomeranian Unit and the Kuiavian Unit (DADLEZ *et al.* 2005). It seems that those terranes were not moved far from the Baltic margin, though they were pushed along it. The re-accretion of the detached terranes and the Eastern Avalonian blocks with the southwestern margin of Baltica occurred in the Silurian (DADLEZ *et al.*, 2005). Some time later, in the Mississippian or (hypothetically) even earlier in the Middle-Late Devonian, a new and larger break-up of Baltica occurred (RUBAN & YOSHIOKA, 2005). It was caused by activity along the Northern Palaeotethyan Shear Zone. Counterclockwise rotation of Africa stimulated the dextral strike-slip movements along this zone (SWANSON, 1982; RAPALINI & VIZÁN, 1993) and caused the detachment of the Ukrainian Massif from Baltica (RUBAN & YOSHIOKA, 2005). The massif was transported off the margin of Baltica (KOSTJUTCHENKO *et al.*, 2004). Rapidly subsiding basins such as the Donbass, the Dniepr-Donets Basin, and the Pirpyat Trough, were opened during the late Paleozoic due to extension between Baltica and the Ukrainian Massif, which became an individual terrane (Fig. 2B). This was somewhat similar to the opening of the Red Sea, which began in the Oligocene and intensified in the Miocene (SHARLAND *et al.*, 2001; TAWADROS, 2001; BOSWORTH *et al.*, 2005; GUIRAUD *et al.*, 2005). Due to this breakup, the Arabian Plate became an individual tectonic block. The stress fields of Arabia and Africa are decoupled and during the next 10 My about 170 km of new crust will form in the Red Sea (BOSWORTH *et al.*, 2005).

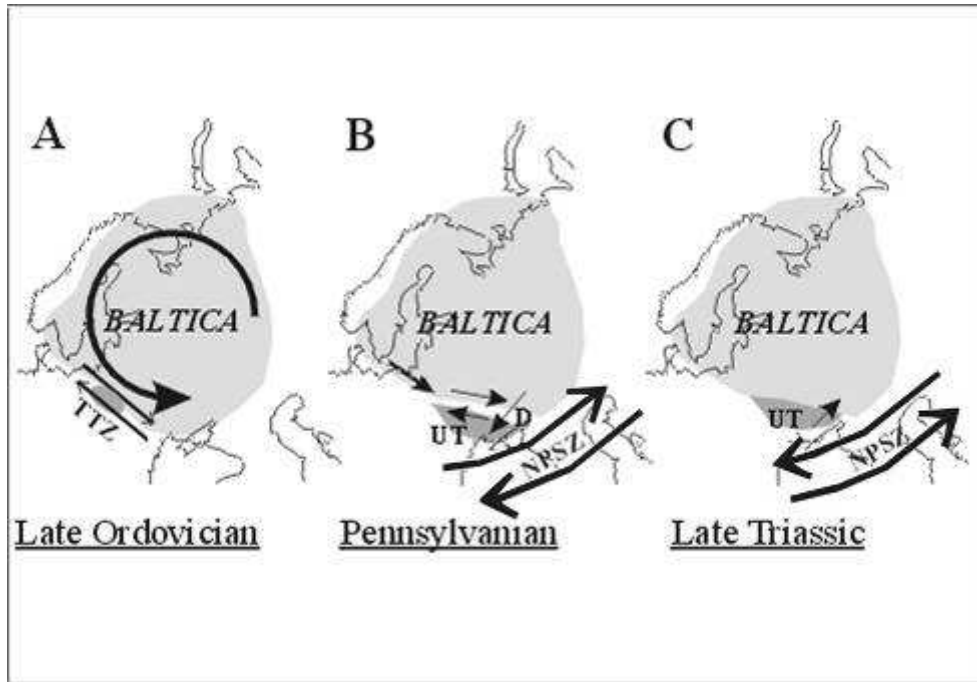


Fig. 2 - The southwestern margin of Baltica in the Late Ordovician (after DADLEZ *et al.*, 2005) (A), the Pennsylvanian (B), and Late Triassic (C). Abbreviations: TTZ –Teisseyre-Tornquist Zone, NPSZ –Northern Palaeotethyan Shear Zone, UT –Ukrainian Terrane, D – Donbass.

The extension hypothesized between the Ukrainian Terrane and Baltica probably took place with a significant oblique component. BELOUS & KOROLEV (1973), ARTHAUD & MATTE (1977), and later DE BOORDER *et al.* (1996) and SAINTOT *et al.* (2003) have shown some dextral displacements along the above-mentioned basins. The Variscan collision along the Teisseyre-Tornquist Zone also occurred with a dextral oblique component (DADLEZ *et al.*, 2005). In the Late Triassic, the displacements along the Northern Palaeotethyan Shear Zone changed from dextral to sinistral because of the clockwise rotation of Africa (SWANSON, 1982; RAPALINI & VIZÁN, 1993; RUBAN & YOSHIOKA, 2005). Consequently, the Ukrainian Terrane moved back to the margin of Baltica (Fig. 2C). Compression affected the basin located between them, i.e. the Donbass, as folding and thrusting demonstrate. This Late Triassic phase of contraction was documented by SAINTOT *et al.* (2003).

Thus, during the Paleozoic and at least the early Mesozoic, the palaeotectonic setting of the southwestern margin of Baltica was governed by the activity of the major shear zones. We only have indirect evidences for their continued activity in the Jurassic and the Cretaceous. For example, in the Donbass, Jurassic dykes occur on its southern flank near the Boldyrevka Village in the Rostov Region. Additionally, the Alpine phase of the Donbass deformation appeared in the Late Cretaceous-Tertiary (SAINTOT *et al.*, 2003). In the Atlasic domain of Africa, along

what was the western branch of the pre-existing Northern Palaeotethyan Shear Zone, shearing continued at least until the Late Jurassic (LÖWNER *et al.*, 2002). VAI (2003) noted that strike-slip displacements might have occurred between the Alps and the Himalayas in the Jurassic and the same was hypothesized by RUBAN (2007) for the Caucasus.

### Global context

The Northern Palaeotethyan Shear Zone—was not the only major shear zone in the late Paleozoic. The five shear zones considered most significant are described briefly below and located in Fig. 3.

(1) The Northern Palaeotethyan Shear Zone with right-lateral strike-slip displacements stretched from the Atlasic Domain of Morocco in the west to the Caspian region in the east (ARTHAUD & MATTE, 1977; STAMPFLI & BOREL, 2002; RUBAN & YOSHIOKA, 2005), although VAI (2003) places it closer to the African-Arabian margin of Gondwana than shown in Fig. 3.

(2) The Teisseyre-Tornquist Zone was characterized by dextral shear in Variscan times (DADLEZ *et al.*, 2005). The model of ARTHAUD & MATTE (1977) relates the activity along some other minor shear zones in Western and Central Europe to the Northern Palaeotethyan Shear Zone.

(3) The Appalachian Shear Zone stretched along the Appalachian Orogen, and it seems to be the westward extension of the Northern Palaeotethyan Shear Zone with

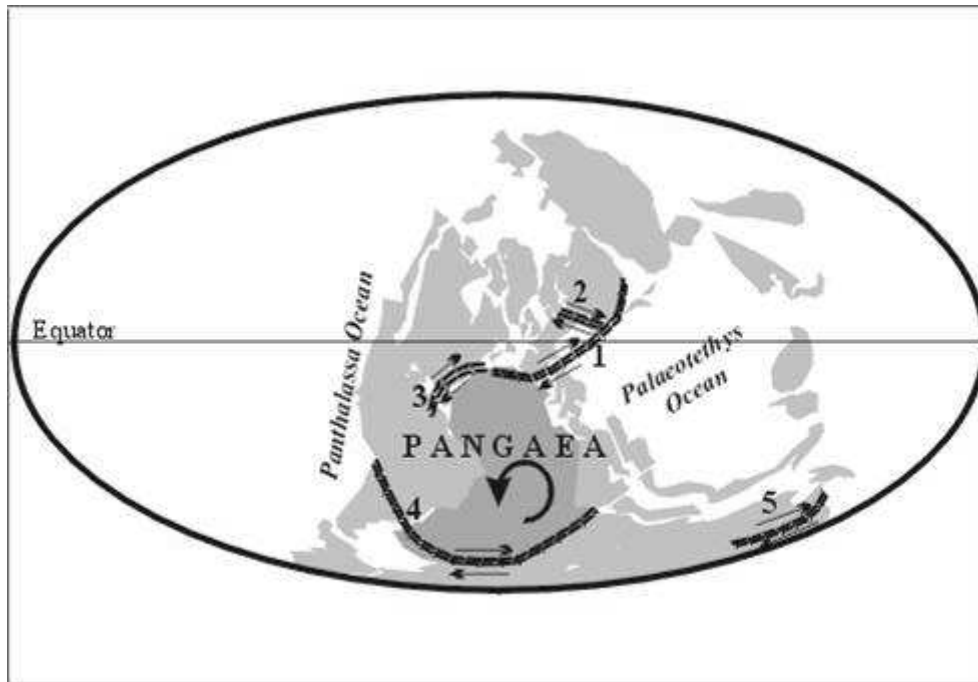


Fig. 3 - Global system of megashears in the late Paleozoic (palaeotectonic base map is simplified from SCOTESE, 2004). See text for explanation of the numbers of the major shear zones.

the same direction or sense of displacements (ARTHAUD & MATTE, 1977; SWANSON, 1982, 1999A,B, 2006; RAPALINI & VIZÁN, 1993; LAWVER *et al.*, 2002; VAI, 2003; HIBBARD, 2004; HIBBARD *et al.*, 2002).

(4) The Intrapangaeian Shear Zone was located within the Pangaea Supercontinent (RAPALINI & VIZÁN, 1993). Megashears are traceable in southern South America (particularly, in the Argentinian basins), and in South and East Africa.

(5) VEEVERS *et al.* (1994) indicated that significant dextral displacements occurred along the East Australian margin of Pangaea. It is unclear whether there was a separate shear zone, or a branch of the Intrapangaeian Shear Zone as an alternative to the branch along East Africa proposed by RAPALINI & VIZÁN (1993).

It seems that a global system of major shear zones existed in the late Paleozoic. Its development and activity may be explained in terms of global wrench tectonics (STORETVEDT, 2003), or at least by the rotation of the individual continents amalgamated into Pangaea. The beginning of the strike-slip activity in the Appalachians and in the Atlasic Domain of Morocco in the Devonian (ARTHAUD & MATTE, 1977; SWANSON, 1999a,b, 2006; HIBBARD *et al.*, 2002) corresponded well to the hypothesized Late Devonian onset of the Donbass structures (NIKISHIN *et al.*, 1996). If these regions were affected by a unique global system of major shear zones, such a correspondence validates an above-mentioned hypothesis that the Donbass structures were originated with the strike-slip displacements.

### **Palaeotectonic analogue**

A search for palaeotectonic analogues contributes to the understanding of the geological evolution of some poorly-known regions with the information from those better-known. Additionally, it produces a general knowledge on the fundamental mechanisms and regional peculiarities of the tectonic processes. Important examples of such studies were presented by MCCALL (2001), TAIRA (2001), CABY (2003), and RUBAN & YOSHIOKA (2005).

A well studied palaeotectonic analogue of the strike-slip continental margin is found in the west and southwest of North America (Fig. 4). Strike-slip movements, first sinistral and later dextral, occurred in the Sierra Nevada and Cordillera during the Late Jurassic-Early Cretaceous (WYLD & WRIGHT, 2001; DECELLES, 2004). At about 85 Ma, a ribbon of terranes, located along the margin of North, Central and South America, was translating northward (NOKLEBERG *et al.*, 2000; JOHNSTON, 2001; SCOTese *et al.*, 2001; LAWVER *et al.*, 2002) (Fig. 3A), resulting in the so-called oroclinal orogeny (JOHNSTON, 2001). It is important to note, that the oroclinal orogeny is also interpreted in Eastern Australia, where it was related to the activity of the late Paleozoic shear zones (VEEVERS *et al.*, 1994). Palaeobiogeographic interpretations of ABERHAN (1998, 1999) allowed him to conclude that Wrangellia and Stikinia, two Canadian terranes, moved northward by 1,000 km or more since the middle of the Early Jurassic. Thus, the major displacement occurred along the western margin of North America in the Mesozoic, and it lasted until the Present (NOKLEBERG *et al.*, 2000; SCOTese *et al.*, 2001; LAWVER *et al.*, 2002). ANDERSON & SILVER (1979) developed the concept of the Mojave-Sonora megashear with sinistral displacements, which occurred on

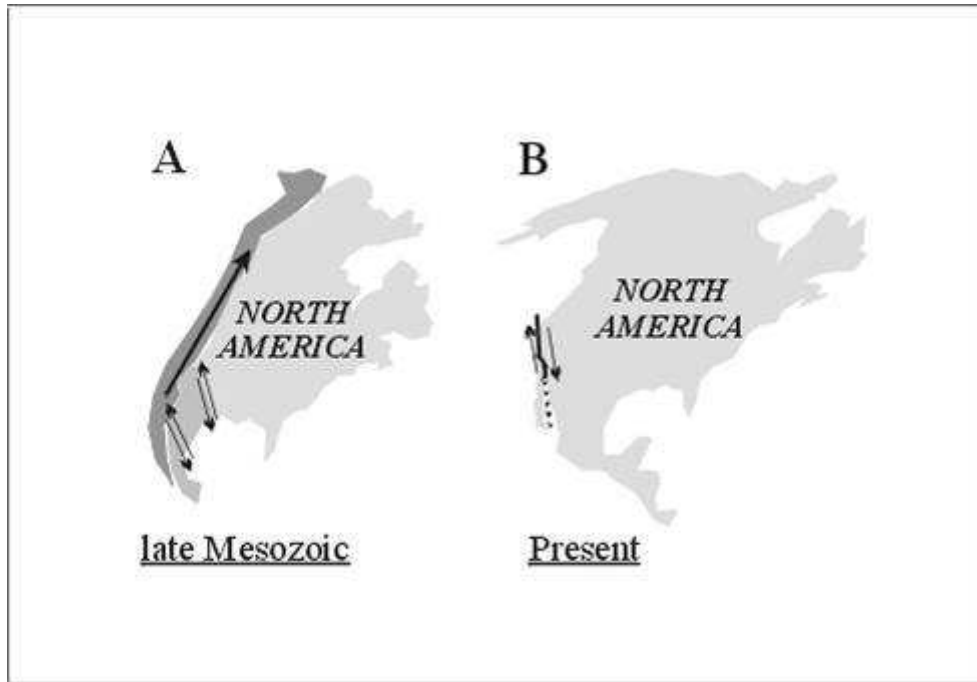


Fig. 4 - The western and southwestern margins of North America in the late Mesozoic (A) and the Present (B).

the southwestern margin of North America in the Late Jurassic. Recently, ANDERSON *et al.* (2005) proposed several subparallel megashears with sinistral strike-slip motions, which crossed the territory of present-day Mexico from southeast to northwest (Fig. 4A). At least some of the faults associated with those megashears might have been active even in the Cenozoic (MCKEE *et al.*, 1984). However, POOLE *et al.* (2005) found no evidence to support the concept of the Mojave-Sonora megashear. From the late Miocene to the Present, dextral displacements (up to 300-500 km) have occurred at the southwestern margin of North America along the San Andreas Fault and associated fault systems and aided in the evolution of the Gulf of California (ATWATER & STOCK, 1998; LEWIS & STOCK, 1998; NAGY, 2000; ARGUS & GORDON, 2001; OSKIN *et al.*, 2001; TSUTSUMI *et al.*, 2001; OSKIN & STOCK, 2003) (Fig. 4B).

The tectonic activity on the western and southwestern margins of North America was characterized by the presence and sometimes dominance of an oblique component during the Mesozoic and Cenozoic. Displacements of small and medium-sized terranes along shear zones were common in the geologic history of this region. Therefore, the western and southwestern margins of North America in the Mesozoic-Cenozoic are proposed as a palaeotectonic analogue of the Paleozoic-early Mesozoic strike-slip southwestern margin of Baltica. Although the forces-causing the activity along the major shear zones in these regions might have

been somewhat different, their further comparative study may contribute significantly to the understanding of the geodynamic evolution of these regions.

## Conclusions

This brief synthesis allows two conclusions that may aid in the geodynamic reconstruction of Baltica:

1) in the late Paleozoic, the shear zones on the southwestern margin of Baltica were included in the global system of megashears (Fig. 3);

2) a palaeotectonic analogue of the Paleozoic-early Mesozoic southwestern Baltic margin is found in North America - during the Mesozoic-Cenozoic, active megashears played a very important role in the evolution of the western and southwestern margins of that continent (Fig. 4).

In general, this paper should be considered as an invitation to a broad discussion, because many of palaeotectonic ideas presented herein are not finalized and, therefore, need to be verified, modified, or completed.

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## Review of Middle East Paleozoic plate tectonics

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### ABSTRACT

The Paleozoic Middle East terranes, neighboring the present-day Arabian and Levant plates, are shown by most authors to consist of ten major tectonic units: (1 and 2) the Helmand and Farah terranes of Afghanistan, southwest Pakistan and southeast Turkmenistan; (3 to 6) the Alborz, Central Iran (Lut, Yazd and Tabas) and Sanandaj-Sirjan terranes of Iran, and Northwest Iran (possibly extending into eastern Turkey); (7 and 8) the Pontides and Taurides terranes of Turkey; and (9 and 10) the Greater and Lesser Caucasus terranes between the Caspian and Black seas (Armenia, Azerbaijan, Georgia and southwest Russia). Published plate-tectonic reconstructions indicate that all ten terranes may have broken off from either: (1) the Gondwana Supercontinent in the mid-Silurian as part of the Hun Superterrane; or (2) the Pangea Supercontinent during the mid-Permian - Triassic as part of the Cimmeria Superterrane. To the north of Gondwana and Pangea, three successively younger Tethyan oceans evolved: (1) Proto-Tethys (Cambrian - Devonian); (2) Paleo-Tethys (mid-Silurian - Mesozoic); and (3) Neo-Tethys (mid-Permian - Cenozoic).

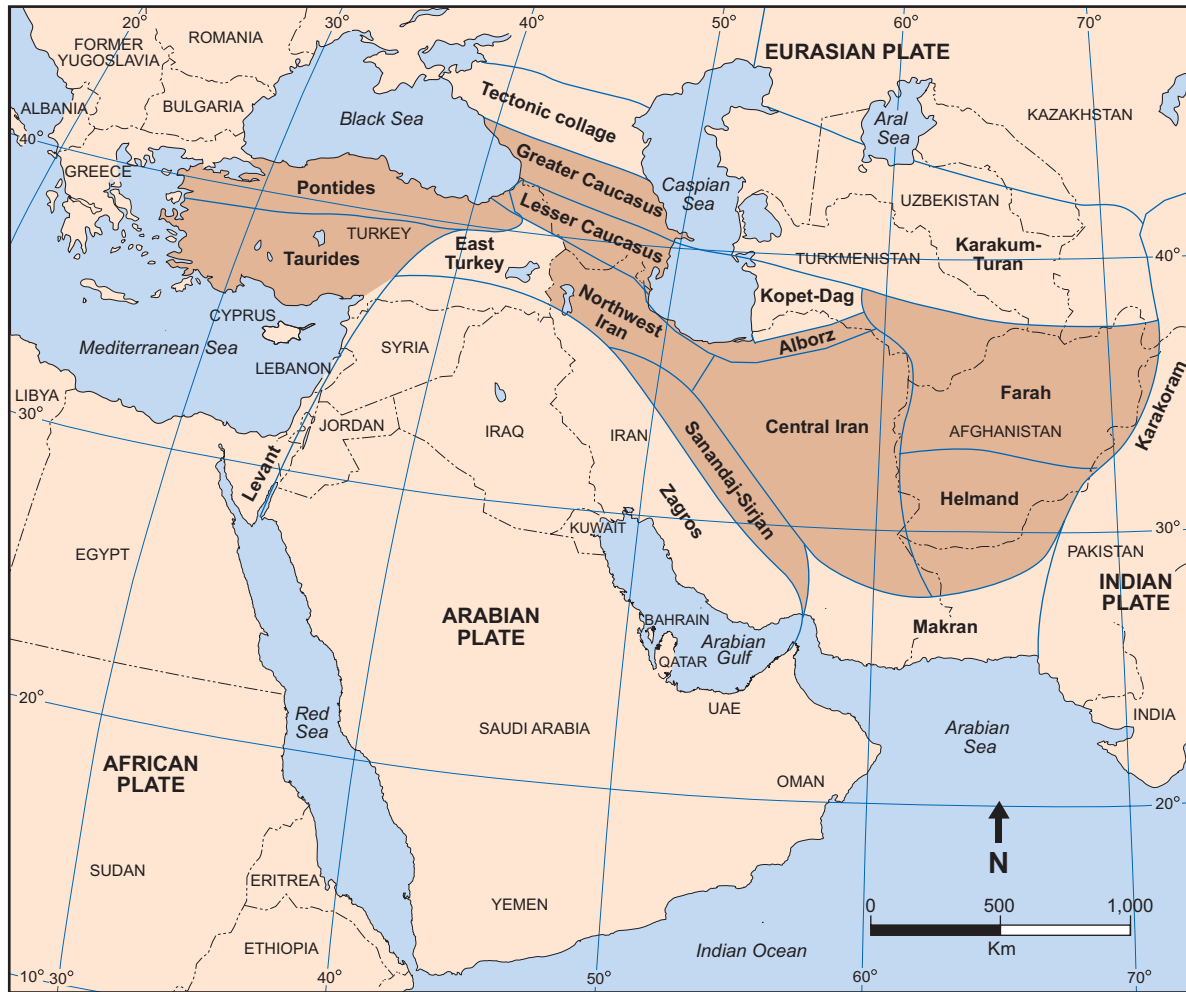
Two regional Paleozoic unconformities in the Arabian Plate are generally linked to major regional-scale structural events, and commonly correlated to the Caledonian and Hercynian orogenies. These orogenies took place many thousands of kilometers away from the Arabian Plate and are considered unlikely causes for these unconformities. Instead, the breakaway of the Hun and Cimmeria superterranes are considered as alternative near-field tectonic sources. The older unconformity (middle Paleozoic event), represented by a mid-Silurian to Middle Devonian hiatus in North Arabia (Iraq and Syria), reflects an episode of epeirogenic uplift, which might be related to the mid-Silurian rift of the Hun Superterrane. The younger mid-Carboniferous Arabia-wide angular unconformity involved compressional faulting and epeirogenic uplift, and might be related to the earliest phase of subduction by the Paleo-Tethyan crust beneath Cimmeria (Sanandaj-Sirjan and nearby regions) before it broke off. Based on our review and regional considerations, we assign the Helmand, Farah, Central Iran, Alborz, Sanandaj-Sirjan, Northwest Iran, Lesser Caucasus, Taurides and Pontides to Cimmeria, whereas the Greater Caucasus is considered Hunic.

### INTRODUCTION

During the past decade, our general knowledge on the geochronological evolution, paleopositions, paleotectonic compositions and paleogeographic outlines of the Phanerozoic supercontinents has significantly improved (e.g. Dalziel, 1997; Stampfli et al., 2001, 2002; Lindsay, 2002; Cocks and Torsvik, 2002; Lawver et al., 2002; Stampfli and Borel, 2002; Veevers, 2003; Pesonen et al., 2003; von Raumer et al., 2002, 2003; Golonka, 2004; Scotese, 2004; Torsvik and Cocks, 2004). Yet today, many uncertainties persist in reconstructing the geological evolution of the regions adjoining the supercontinents, especially for the Paleozoic Era (Cocks and Torsvik, 2002; Torsvik and Cocks, 2004; Scotese, 2004). These regions are in themselves vast, and consist of numerous plate-tectonic units that are sometimes referred to as microplates, terranes, blocks, structural domains, and sometimes grouped into superterranes. The Middle East is a typical example of a border-region that consists of a complex mosaic of tectonic units (Figures 1 and 2).

We identify the Middle East terranes, bordering the present-day Arabian and Levant plates, in Afghanistan, Iran, western Pakistan, Turkey, southeast Turkmenistan and the Caucasus (Armenia, Azerbaijan, Georgia and southwest Russia) (Figures 1 and 2). Several of these terranes are strongly deformed and stacked within a wide tectonic belt between the Eurasian, Arabian and Indian plates.

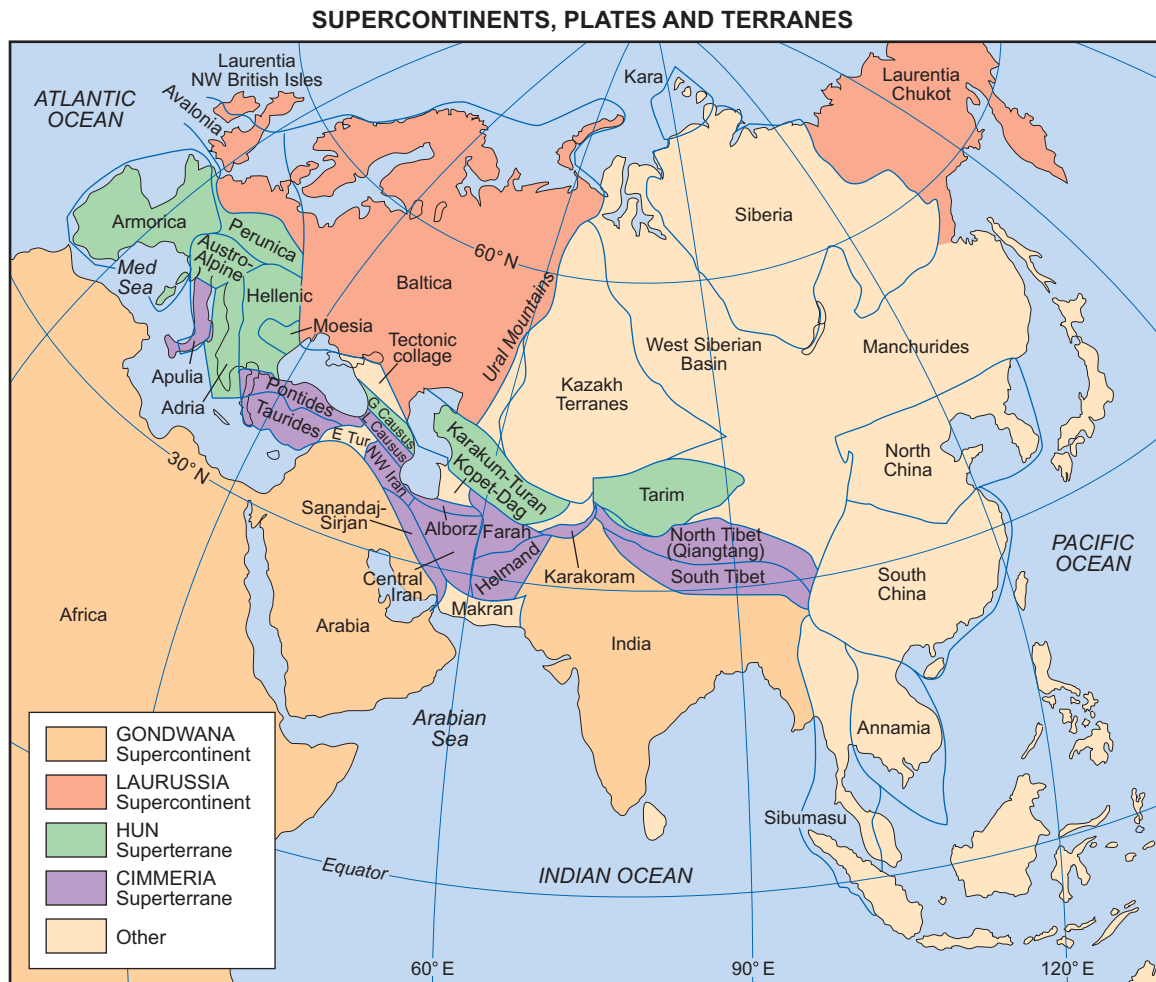
PLATES AND TERRANES OF THE MIDDLE EAST



**Figure 1:** The Middle East region consists of the present-day Arabian and Levant plates and numerous terranes (individual boundaries are shown in blue). During the Paleozoic ten large terranes are variably interpreted to have been adjacent to the Arabian and Levant plates (then attached to Gondwana and later Pangea). The Paleozoic Middle East terranes (colored brown) include Helmand and Farah (Afghanistan, southwest Pakistan and southeast Turkmenistan); Iran’s Alborz, Northwest Iran, Sanandaj-Sirjan and Central Iran; Turkey’s Pontides and Taurides; and the Greater and Lesser Caucasus between the Caspian and Black seas (Armenia, Azerbaijan, Georgia and southwest Russia). The Makran and East Turkey regions may have a Paleozoic core or could have formed as Mesozoic accretionary terranes.

Although their boundaries are generally traced along well-preserved or /and reactivated Paleozoic fault systems, in some cases the borders remain unclear. Correlation of the sedimentary core complexes, however, suggests that all of these terranes share a common ancestry during some time in the Paleozoic Era.

The Middle East terranes were affected by the evolution of the Paleozoic Tethyan oceans, the Hun (Hunic or Intermediate) and Cimmeria (Cimmerian) superterranes, and the Gondwana and Pangea supercontinents (Figures 3 to 11; e.g. Sengör, 1990; Stampfli, 1996; von Raumer, 1998; Cocks and Torsvik, 2002; von Raumer et al., 2002, 2003; Stampfli and Borel, 2002; Stampfli et al., 2001, 2002; Torsvik and Cocks, 2004; Natal’in and Sengör, 2005; Xypolias et al., 2006). At least three major Paleozoic rift episodes occurred along the margins of Gondwana and Pangea (Figures 4 to 11). The first was in the Early Ordovician when Avalonia broke off from Gondwana. This episode was unlikely to have influenced the Middle East region, which was located about 6,000 km away (Figure 4). The second involved the mid-Silurian breakaway of the Hun Superterrane (Figures 6 and 7), the detailed reconstruction of



**Figure 2: The majority of the plates and terranes discussed in this review are shown after Torsvik and Cocks (2004). Besides the NW British Isles and the Chukot Peninsula in Russia, the Laurentia Supercontinent included North America and Greenland (see Figures 4 and 5). Laurentia later collided with Baltica and Avalonia to form the Laurussia Supercontinent (Figure 7). Besides Arabia, Africa and India, the Gondwana Supercontinent included Antarctica, Australia and Madagascar (see Figure 4). Also shown are terranes that may have been part of the Hun and Cimmeria Superterrane. Note that Karakoram in north Pakistan is Cimmerian and different from the Hunic Karakum-Turan terrane.**

which is unresolved due to insufficient paleomagnetic and paleontological data. This episode is relevant to our review because parts of the superterrane may have involved the Middle East terranes. The third episode is the mid-Permian - Triassic breakaway of several Middle East Cimmerian terranes from Gondwana, by then a part of Pangea (Figures 10 and 11).

In most Paleozoic reconstructions, the Middle East region is interpreted as part of the passive margin of Gondwana and Pangea until the mid-Permian - Triassic, when Cimmeria started to rift away, causing the opening of the Neo-Tethys Ocean (e.g. Sharland et al., 2001; Stampfli et al., 2001). In addition, two regional unconformities are recognized. The first corresponds to a mid-Silurian to Middle Devonian hiatus – “middle Paleozoic hiatus” – that is sometimes correlated with the Caledonian Orogeny (e.g. Buday, 1980) (Figures 3, 5 to 7). The second unconformity represents a “mid-Carboniferous hiatus”, and is often correlated to the Hercynian Orogeny (e.g. Berberian and King, 1981) (Figures 3 and 9). These correlations do not provide a satisfactory plate-tectonic model for the Paleozoic evolution of the Middle East region because it was located far away from these two orogenies.

Our paper starts with a brief global review of the largest and relatively well-constrained Paleozoic

GLOBAL GEOCHRONOLOGY

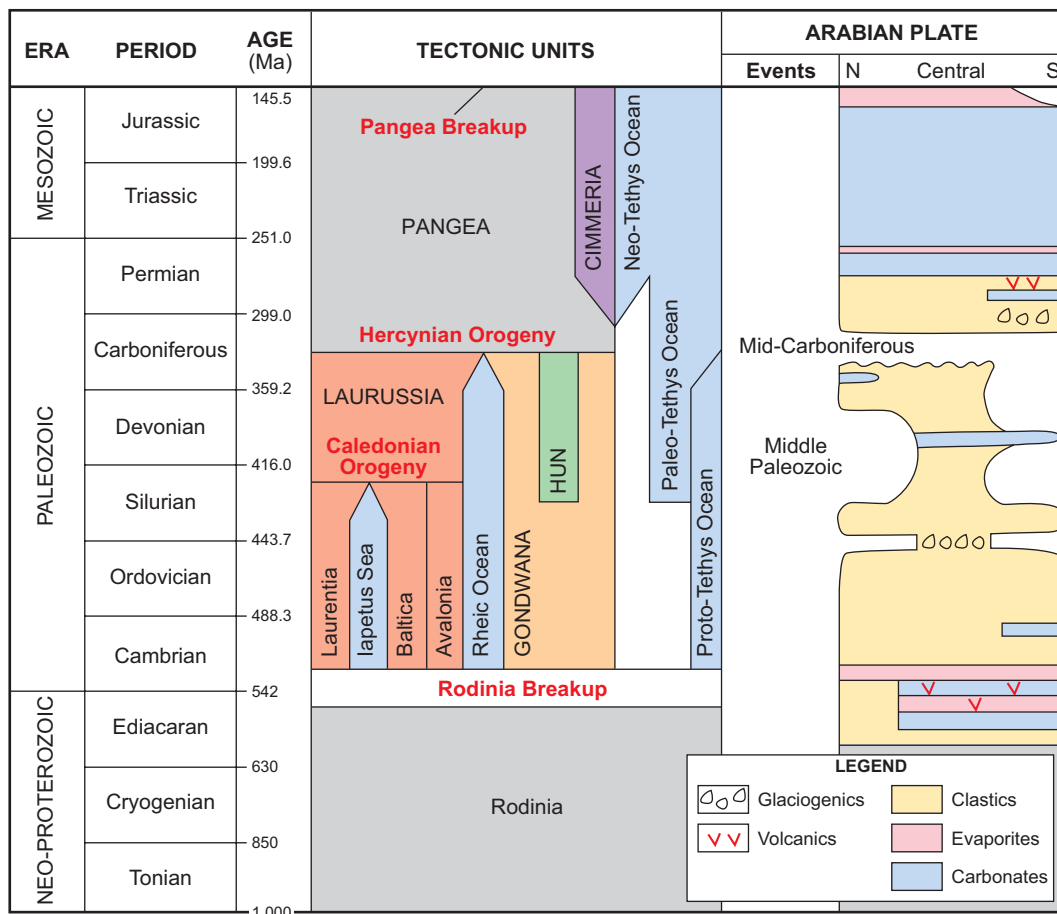


Figure 3: Simplified geochronology of the supercontinents, superterrane, oceans and seas, and generalized Arabian Plate stratigraphic column. The breakup of the Neo-Proterozoic Rodinia Supercontinent is not discussed in this paper. The geological time scale is after the ICS (International Commission on Stratigraphy; Gradstein et al., 2004). Two Arabian unconformities are associated with Gondwana glaciations: latest Ordovician-early Silurian (Figure 5) and late Carboniferous-early Permian (Figure 9). In Arabia the second glaciation followed a mid-Carboniferous structural event that coincided in time with the Hercynian Orogeny (Figure 9). Another North Arabian (and Oman) unconformity is associated with epeirogenic uplifting in the mid-Silurian (Wenlock) to Middle Devonian (middle Paleozoic event) and has been correlated to the Caledonian Orogeny (Figures 5 to 7). The Hercynian and Caledonian collisions were located many 1,000s of kilometers away from Arabia and could not therefore have transmitted significant lateral forces to its crust. Instead two near-field events may have played a more direct role: the breakaway of the Hun Superterrane in mid-Silurian (and possibly Devonian) (Figure 6), and the early compressional evolution of a subduction complex preceding the breakaway of the Cimmerian Superterrane (Figure 11). Color scheme for tectonic units follows Figure 2.

plate-tectonic units and seaways. We adopt the conventions of the ICS (International Commission on Stratigraphy; Gradstein et al., 2004) by not capitalizing informal qualifiers “late, middle, mid, early, etc.” except where defined (Ordovician and Devonian). After setting the global stage, we discuss the smaller and less constrained units of the Middle East, many of which have unfamiliar names and interpretations. Most of the illustrated global reconstructions follow Cocks and Torsvik (2002) and Torsvik and Cocks (2004), as the involved units are adequately represented. We have also considered the global reconstructions by von Raumer (1998), Stampfli and Borel (2002), von Raumer et al. (2002, 2003), Stampfli et al. (2001, 2002), Scotese (2004), Natal’in and Sengör (2005) and others. Our principal objective is to present the Paleozoic plate-tectonic framework and nomenclature for the Middle East, which can form a basis for further refinements.



## GLOBAL PALEOZOIC PLATE-TECTONIC SETTING

### Gondwana, Laurussia and Pangea Supercontinents

The global plate-tectonic configuration during the Paleozoic was dominated by three supercontinents: Gondwana, Laurussia and Pangea. Gondwana, the largest supercontinent on Earth from the Late Cambrian to mid-Carboniferous (Figures 2 to 8), consisted of several present-day plates including Arabia, Africa, most of Antarctica and Australia, India, Madagascar and most of South America, with numerous small terranes attached to their margins (Courjault-Radé et al., 1992; Cocks, 2001; Stampfli et al., 2001; Cocks and Torsvik, 2002; Stampfli and Borel, 2002; von Raumer et al., 2002, 2003; Fortey and Cocks, 2003; Scotese, 2004; Avigad et al., 2005).

During the Paleozoic Era, Laurussia was assembled out of three large plates (Avalonia, Baltica and Laurentia, Figures 3 and 5) and several island arcs in a series of orogenic phases (McKerrow et al., 2000; Stampfli and Borel, 2002; Scotese, 2004) (Figures 3 to 7). The collisional assembly of Laurussia caused the Caledonian Orogeny, an event that was redefined by McKerrow et al. (2000) to apply to the closure of the Iapetus Sea (Figures 3, 5 to 7).

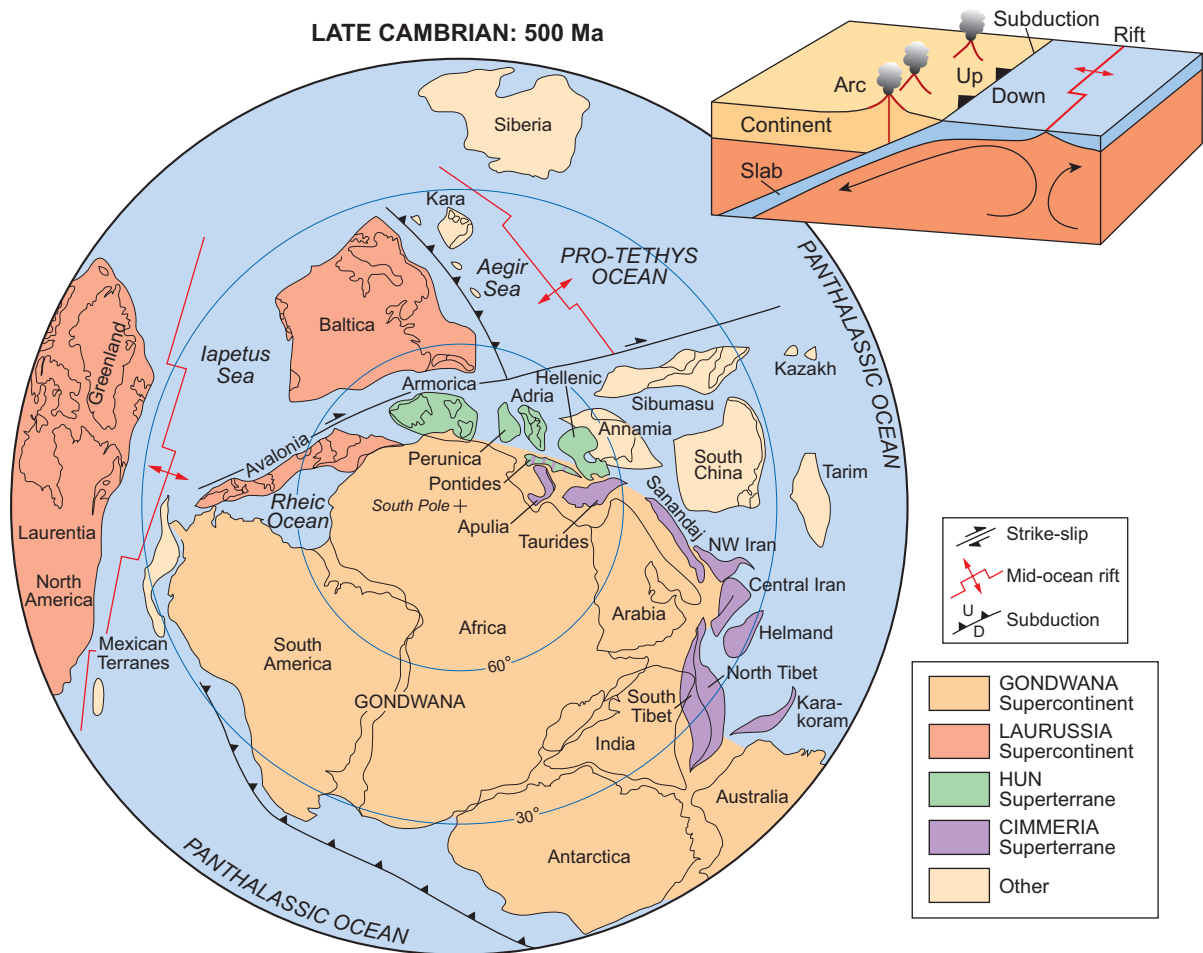
- Avalonia consisted of easternmost North America and parts of northwest Europe (Figures 2 and 3; also Avalonian-Cadomian Arc and Orogenic Belt of Linnemann et al., 2000, and Linnemann and Romer, 2002). Avalonia rifted from western Africa (in Gondwana) in the Early Ordovician (Cocks and Torsvik, 2002), and then drifted northwards until it collided with Baltica and Laurentia (Figures 4 to 7).
- Baltica consisted of the Russian Platform and extended to east of the Ural Mountains (Figures 2 and 3, Cocks and Torsvik, 2002).
- Laurentia consisted of most of North America, Chukot Peninsula of eastern Siberia, Greenland, Spitsbergen and the NW British isles (Figures 3 to 5; Cocks and Torsvik, 2002).

Gondwana and Laurussia remained separated by the Rheic Ocean until the mid-Carboniferous (c. 325–310 Ma) when they collided during the Hercynian Orogeny to form the Pangea Supercontinent (Stampfli and Borel, 2002; Scotese, 2004; Figures 3, 8 and 9, Torsvik and Cocks, 2004). In the late Carboniferous (Pennsylvanian) and Permian, Pangea was enlarged with the amalgamation of the Kazakh, Siberia, Kara and other terranes (Figure 10). The combination of Laurussia with these terranes would later in the Mesozoic form the Laurasia Supercontinent, a term that is easily confused with Laurussia.

### Three Tethyan Oceans

The names of the Paleozoic oceans that separated the supercontinents are not unique and vary to reflect somewhat different interpretations. The seaway that opened to the north of the Paleozoic Middle East terranes is called the Paleo-Tethys Ocean by some authors (e.g. Sharland et al., 2001; Bykadorov et al., 2003). Others refer to it as the Proto-Tethys (or Asiatic Ocean) and reserve the term “Paleo-Tethys” for the ocean that opened in the mid-Silurian along the trailing edge of the Hun Superterrane (Figures 3, 7 and 8; e.g. Ziegler et al., 2001; Stampfli et al., 2001; Stampfli and Borel, 2002; von Raumer et al., 2002, 2003). Most authors adopt the Neo-Tethys for the ocean that opened in mid-Permian - Triassic along the African-Arabian margin of Gondwana (e.g. Stampfli and Borel 2002; also Meso-Tethys of Metcalfe, 1999; Pindos Ocean of Golonka, 2004; Figure 10). Following Stampfli and Borel (2002), we adopt Proto-Tethys for the early Paleozoic ocean to distinguish it from the late Paleozoic Paleo-Tethys and Neo-Tethys oceans (Figures 3–10).

The interpretation of the lateral extent and evolution of the Tethyan oceans can vary. Hünecke (2006), for example, argued that the Middle-Late Devonian ocean between Gondwana and Laurussia was not as large as depicted by Stampfli and Borel (2002) and Torsvik and Cocks (2004). Stampfli and Borel (2002) and von Raumer et al. (2002, 2003) interpreted that in the Late Ordovician-early Silurian, the eastern branch of the Proto-Tethys Ocean might have closed when Serindia terranes (North China and

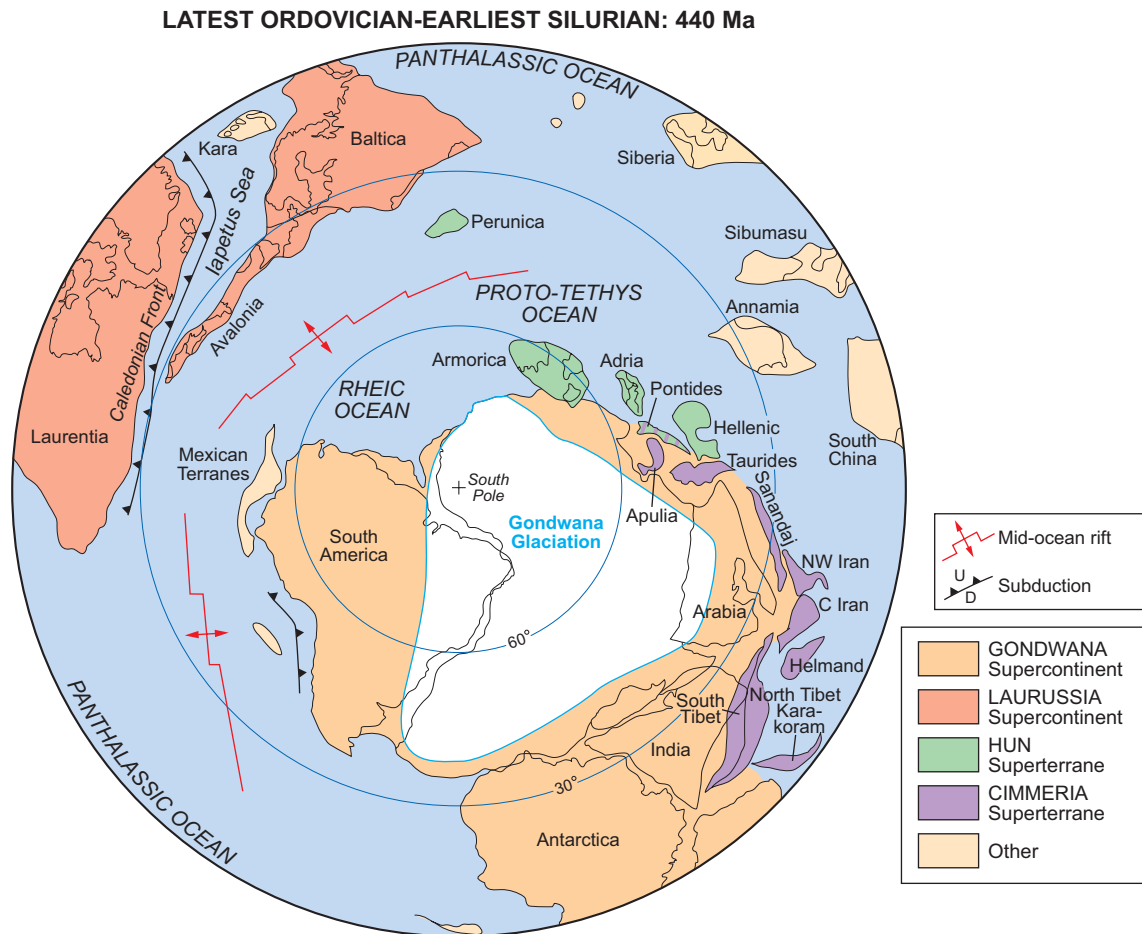


**Figure 4: Plate-tectonic reconstruction of the Late Cambrian times (modified after Cocks and Torsvik, 2002).** The terranes included in the Hun Superterrane (green) are mostly after Stampfli et al. (2001, see Figure 6). Torsvik and Cocks (2004) show several terranes breaking away from Gondwana in the middle Paleozoic but do not appear to recognize the Hun Superterrane (Figure 7). The Adria terrane (Figures 6 to 9, after Torsvik and Cocks, 2004) was not shown in Cocks and Torsvik (2002) and is located arbitrarily in Figures 4 and 5. Middle East terranes (Figures 1 and 2) not shown are Alborz, Farah and Caucasus. Pontides shown as Hunic by Cocks and Torsvik (2002), but considered Cimmerian in our paper (in stripes). Schematic diagram at top right illustrates oceanic slab subducting below (down or D) the continent (up or U).

Tarim) amalgamated with Gondwana. Several authors interpreted the initial opening of the Neo-Tethys Ocean in early rather than mid-Permian (Vannay, 1993; Garzanti and Sciunnach, 1997; Garzanti et al., 1994, 1996a, b, 1999; Stampfli and Borel, 2002; Angiolini et al., 2003), or to have started north of Australia in the Carboniferous and extended diachronously westwards into the Permian (Stampfli, 2000).

### Iapetus Sea and Rhecic Ocean

Two more Paleozoic seaways are significant for our review (Figures 3 to 7). The Iapetus Sea, which separated Laurentia, Avalonia and Baltica in the early Paleozoic, closed in the late Silurian when these terranes joined to form Laurussia (Figures 3 to 5). The Rhecic Ocean (also Rhecic-Mauritania, Rhenohercynian or Hercynian-Rhecic) opened in the Cambrian along Avalonia's northerly trailing edge (Figures 3 to 7). During the Devonian-early Carboniferous (c. 420–320 Ma), Gondwana drifted towards Laurussia, closing the Rhecic Ocean (Figures 7 and 8, Torsvik and Cocks, 2004). In the mid-Carboniferous, the Hercynian Orogeny occurred along a front between northwest Africa and southeast North America and closed the Rhecic Ocean (Figure 9; incorrectly referred to as the Iapetus Sea in Al-Husseini, 2004).



**Figure 5: Plate-tectonic reconstruction of the latest Ordovician-earliest Silurian times (modified after Cocks and Torsvik, 2002).** During the final Hirnantian Stage of the Late Ordovician, polar glaciers advanced over regions of Gondwana reaching western Saudi Arabia (Vaslet, 1990). Baltica and Avalonia were joined, closing the Iapetus Sea where the Caledonian Orogenic Front was located. Middle East terranes (Figures 1 and 2) not shown are Alborz, Farah and Caucasus. Adria terrane is located arbitrarily (see Figure 4 caption). Pontides shown as Hunic by Torsvik and Cocks (2004), but considered Cimmerian in our paper (in stripes).

### Hun Superterrane

Plate reconstruction of the mid-Silurian to mid-Permian northern margin of Gondwana fall into two general models (Figures 6 and 7). Whereas both show the breakaway of various terranes from Gondwana, they differ in detail and lateral extent – particularly near the Middle East region.

In the first model, following Stampfli et al. (2001) and Stampfli and Borel (2002), the ribbon-like Hun Superterrane extended from westernmost Iberia (in Spain) to Qiantang (Figure 6). This superterrane is also referred to as the Hun Composite Superterrane because it is divided into (Figure 6): (1) the northern Hun Cordillera terranes (also European Hunic terranes); and (2) the southern Hun Gondwana terranes (also Asiatic Hunic terranes) (von Raumer, 1998; Stampfli et al., 2001; von Raumer et al., 2002, 2003; Stampfli and Borel, 2002; Schulz et al., 2004). This division reflects the separate evolution of the two sets of terranes after they docked along Laurussia in the late Paleozoic. The Hun Superterrane rifted away from Gondwana in the mid-Silurian (possibly in different phases that lasted into the Devonian) and then drifted towards Laurussia, with which it collided in the Devonian-Carboniferous (Figures 3, 6 to 8). Interpretations of late Silurian paleocurrents indicate that the Panthalassic (north of the Proto-Tethys) waters did not mix with those of the Paleo-Tethys (Johnson et al., 2004), thus suggesting that the Hun Superterrane remained consolidated until at least the Early Devonian.

HUN SUPERTERRANE, LATE SILURIAN: 420 Ma

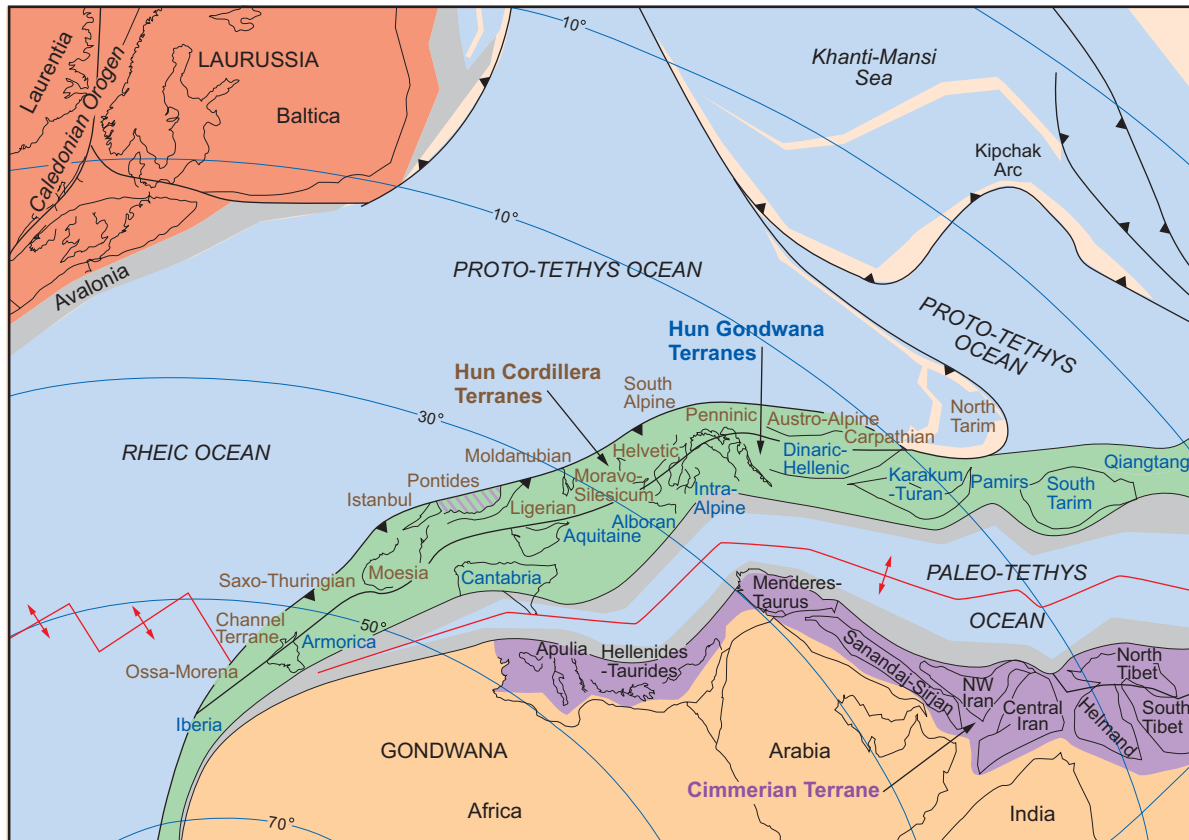
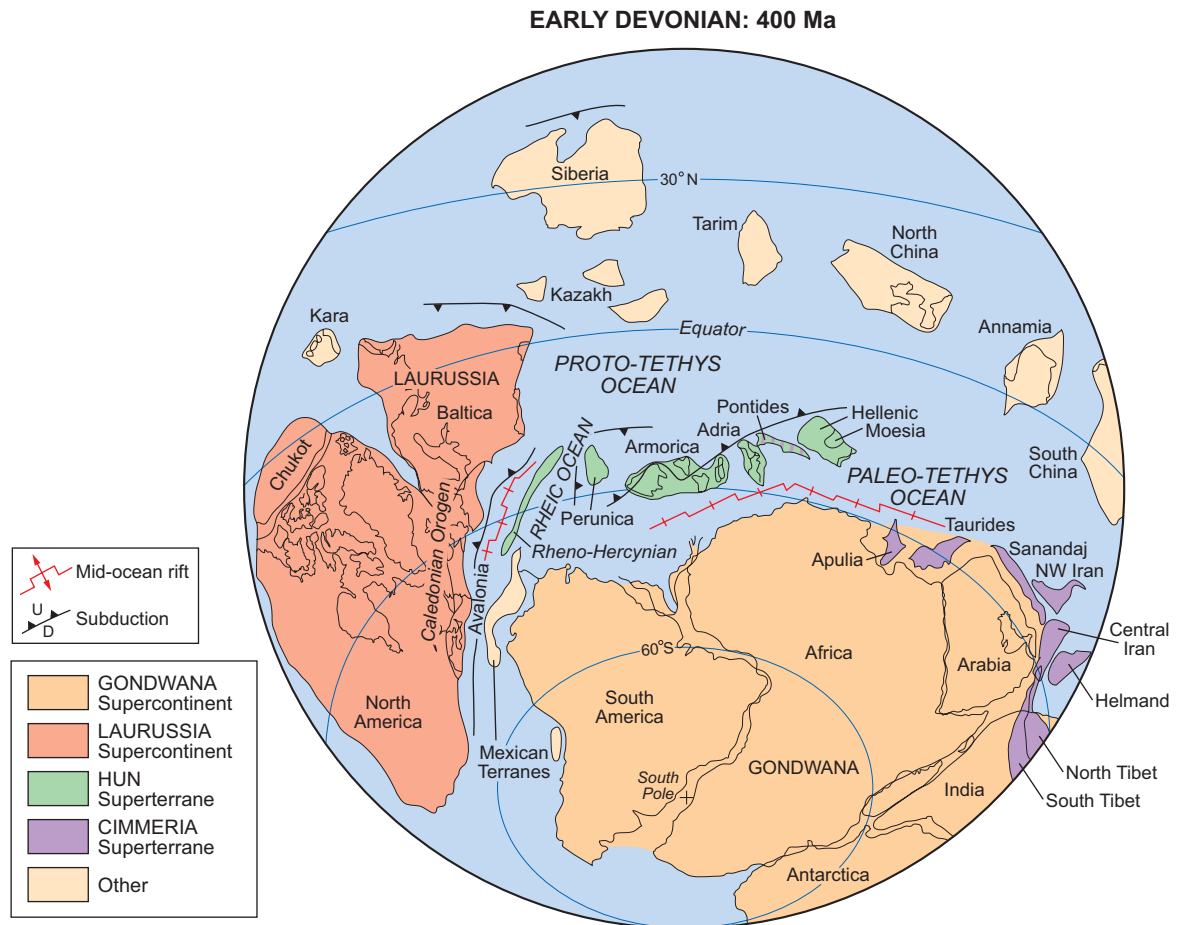


Figure 6: Plate-tectonic reconstruction of the late Silurian (Ludlow) by Stampfli et al. (2001) shows the Hun Superterrane rifted away from the Gondwana Supercontinent. The Paleo-Tethys Ocean formed between Gondwana and the superterrane. The superterrane is divided into the southern Gondwana and northern Cordillera terranes. Stampfli et al. positioned the Istanbul and Pontides terranes (North Turkey) near a subduction zone at the northern boundary of the Hun Cordillera terrane. In contrast, Sengör (1990; see Figure 11) placed the Pontides (in stripes) in the Cimmeria Superterrane and associated it with a middle Carboniferous-Mesozoic subduction-arc that continued into the Sanandaj-Sirjan terrane. Middle East terranes (Figures 1 and 2) not shown are Cimmerian Alborz, Farah and Lesser Caucasus. The Hunic Greater Caucasus may have been located further east beyond Qiangtang.

From west to east the Hun Cordillera terranes included: Ossa-Morena, Channel, Saxo-Thuringian, Moesia, Istanbul, Pontides, Ligerian, Moldanubian, Moravo-Silesicum, Helvetic, South Alpine, Penninic, Austro-Alpine, Carpathian and North Tarim (Figure 6; Stampfli et al., 2001). The Hun Gondwana terranes included: Iberia, Armorica, Cantabria, Aquitaine, Alboran, Intra-Alpine terranes (Adria, Carnic, Austro-Carpathian), Dinaric-Hellenic, Karakum-Turan, Pamirs, South Tarim, Qiangtang, North and South China, and Annamia terranes (Stampfli et al., 2001; Stampfli and Borel, 2002; the latter two easternmost terranes are shown in Figure 1, but not in Figure 6). In the Devonian, the Kazakh terranes may also have been close to the Hunic Cordillera Superterrane (Stampfli and Borel, 2002). The remaining adjoined with Pangea were Apulia, Hellenides-Taurides, Menderes-Taurus, Sanandaj-Sirjan, Northwest and Central Iran, Helmand, North and South Tibet.

In the second model, several terranes broke off and had drifted some distance away from the northwestern margin of Gondwana by the Early Devonian (Figure 7; Torsvik and Cocks, 2004). They also formed a ribbon-like superterrane that vaguely resembles the western part of the Hun Superterrane (compare Figures 6 and 7). The breakaway group included: Rheno-Hercynian, Armorica (includes Iberia), Adria, Pontides, Hellenic and Moesia (Figures 2 and 6). The Rheno-Hercynian and Perunica

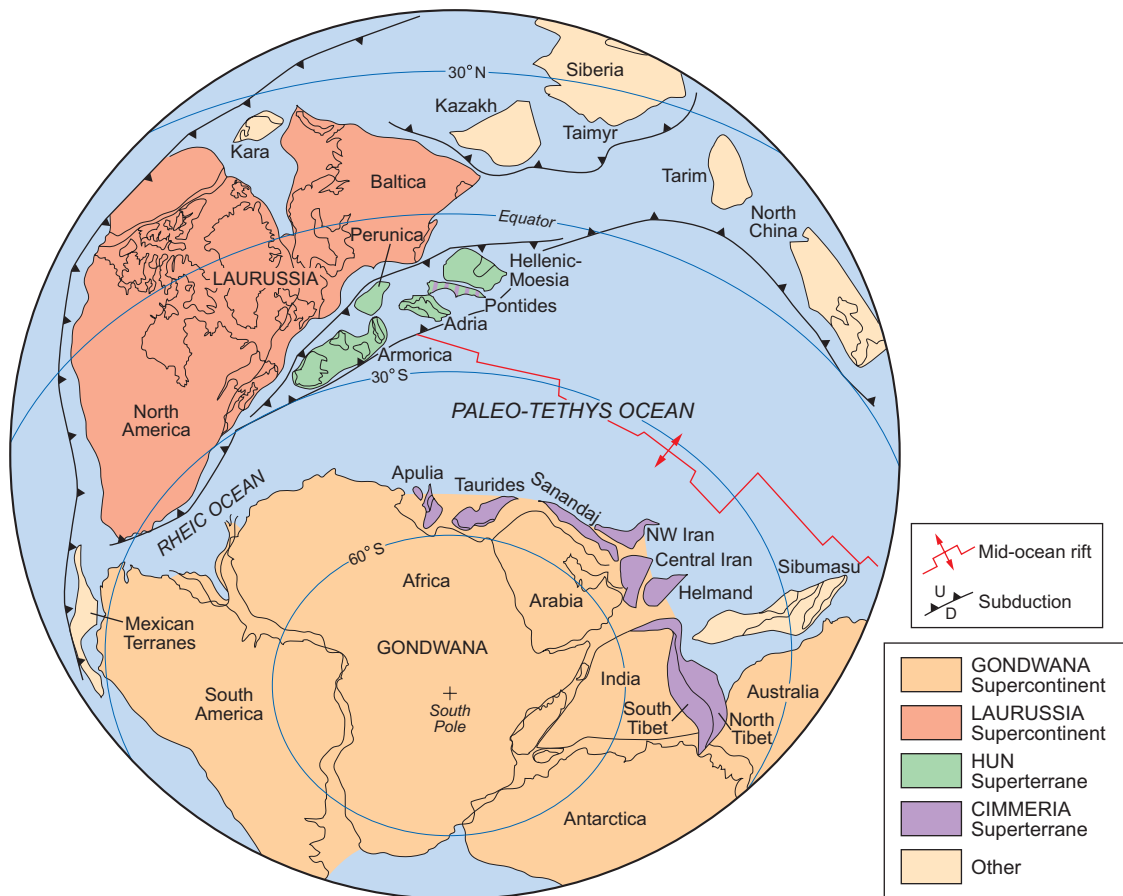


**Figure 7: Plate-tectonic reconstruction of the Early Devonian (modified after Torsvik and Cocks, 2004) shows the breakaway from Gondwana of several terranes that together resemble the western Hun Superterrane (Stampfli et al., 2001; Figure 6). Both reconstructions show the Pontides (in stripes) as Hunic whereas we favor a Cimmerian assignment. Middle East terranes (Figures 1 and 2) not shown are Hunic Greater Caucasus and Cimmerian Alborz, Farah and Lesser Caucasus. Note that North Tibet and Qiangtang are synonyms in Torsvik and Cocks, but two different terranes in Stampfli et al.**

are considered as separate terrane between the Hunic terranes and Baltica (in Laurussia) (Kříz et al., 2003; Torsvik and Cocks, 2004). Following the breakaway event, terranes adjacent to Gondwana were Apulia, Taurides, Sanandaj-Sirjan, Northwest and Central Iran, Helmand, South Tibet (Lhasa) and North Tibet (Qiangtang) terranes.

Some differences and confusion occur when comparing the two models in detail. The term Qiangtang (also Qangtang) is a synonym for North Tibet in Torsvik and Cocks (2004; Figure 2) and positioned next to South Tibet (Lhasa). In contrast, Stampfli et al. (2001) show Qiangtang as Hunic but North Tibet as Gondwanan (Figure 6). Other confusing terms are Karakum and Karakoram (also spelled as Karakorum). Karakum and neighboring Mangyshlak of Torsvik and Cocks (2004) are equivalent to the Karakum-Turan terrane (Figure 1). Karakum-Turan was not attached to Gondwana in the late Paleozoic (L. Angiolini, written communication, 2006) and probably Hunic (Figure 6). Karakoram is located in northern Pakistan (Gaetani, 1997; Figure 1), which belonged to Cimmeria (L. Angiolini, written communication, 2006). Further studies of the Cambrian-Ordovician rocks in Karakorum, based on the works of Gaetani et al. (1996), Gaetani (1997), Quintavalle et al. (2000) and Rolland et al. (2002), may provide new insights for its early Paleozoic paleoposition. Turan is often mentioned as a plate, but the Russian term 'plate' differs in meaning from 'tectonic plate', causing some further confusion (Laz'ko, 1975). It remains unclear whether Karakum and Turan formed one or several terranes.

**EARLY CARBONIFEROUS: 340 Ma**



**Figure 8: Plate-tectonic reconstruction of the early Carboniferous (Mississippian) (modified after Torsvik and Cocks, 2004). The Hun Superterrane had closed the Proto-Tethys Ocean and the Rheic Ocean was closing as Gondwana and Laurussia drifted towards each other. Middle East terranes (Figures 1 and 2) not shown are Hunic Greater Caucasus and Cimmerian Alborz, Farah and Lesser Caucasus. Pontides shown as Hunic by Torsvik and Cocks (2004), but considered Cimmerian in our paper (in stripes).**

**Cimmeria Superterrane**

In the mid-Permian - Triassic, Cimmeria started rifting away from Pangea and closing the Paleo-Tethys Ocean to the north, while opening the Neo-Tethys Ocean in its wake (Figure 10). Less clear is which terranes were Cimmerian, or Hunic or possibly neither. Torsvik and Cocks (2004, Figure 10) show Cimmeria to consist of Apulia, Taurides, Sanandaj-Sirjan, Northwest and Central Iran, Helmand and North Tibet (Qiantang). They place South Tibet (Lhasa) to the north of India, however noting that it is not constrained by paleomagnetic or faunal content. Stampfli et al. (2001) and Stampfli and Borel (2002) (Figures 1, 2 and 6) included in Cimmeria: Apulia, Hellenides-Taurides, Menderes-Taurus, Sanandaj-Sirjan, Northwest and Central Iran, Helmand, South and North Tibet. A comparison indicates that several Middle East terranes (Northwest and Central Iran, Taurides and Sanandaj-Sirjan) are considered Cimmerian by both groups of authors.

In contrast to the somewhat generalized Cimmeria of some authors (e.g. Sharland et al., 2001; Stampfli et al., 2001; Stampfli and Borel, 2002; Torsvik and Cocks, 2004), Sengör (1990, Figure 11) showed the Cimmeria breakaway event in substantial detail and to consist of three ribbons. He divided North Tibet into East and West Qiantang and considered the former as the leading Cimmerian ribbon. The “Intermediate” ribbon consisted of East Pontides, Dzirula Massif, Artvin/Karabagh, Sanadaj-Sirjan, Northwest Iran (including Alborz), Central Iran (Yazd, Tabas, and Lut), Farah, central Pamirs (China) and West Qiantang. The trailing third ribbon included Helmand and South Tibet. The latter two

ribbons connected to Australia, and the Neo-Tethys Ocean consisted of several seaways. Significantly for our paper, Sengör's model interpreted a subduction zone along the northeast front of Sanandaj-Sirjan and other northerly terranes, a subject that will be discussed later. The Intermediate ribbon of Natal'in and Sengör (2005) is generally comparable with the Cimmerian Superterrane.

## PALEOZOIC OROGENIES AND THE ARABIAN PLATE

In most of the pre-Permian Paleozoic reconstructions (Figures 4 to 9), the Arabian Plate is generally depicted inland from the Tethyan margins of Gondwana, or later Pangea. Until the mid-Permian (Figures 10 and 11), it is shown as bounded by the Middle East terranes and, for the most part, at latitudes of about 30° to 60° south. Two regional hiatuses that were associated with polar glaciations occurred in the Late Ordovician Hirnantian Stage (Figures 3 and 5; Vaslet, 1990; Abed et al., 1993) and in the late Carboniferous - early Permian (Figures 3 and 9; Osterloff et al., 2004).

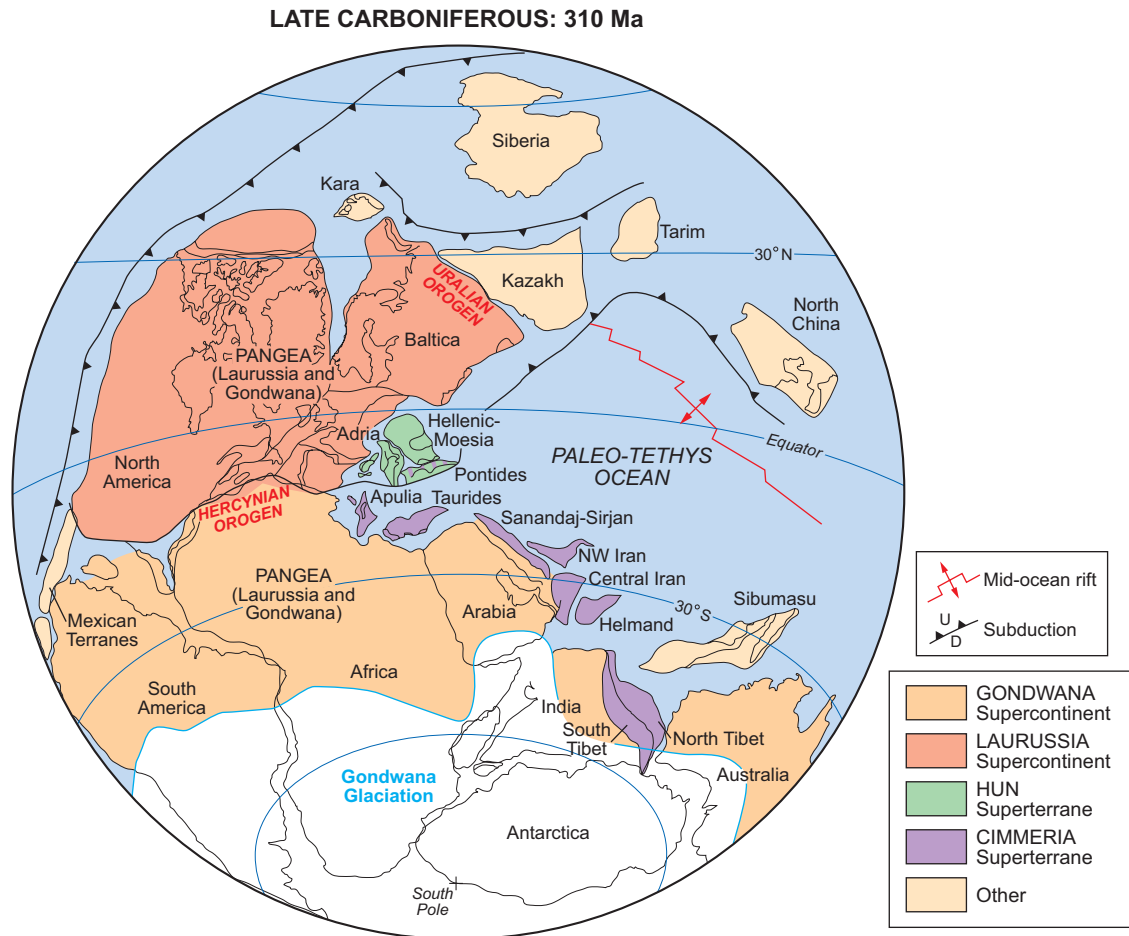
Two structurally significant unconformities have been recognized in the Arabian Plate (Figure 3). The mid-Silurian (Wenlock) to Middle Devonian hiatus is regionally manifested in Syria and Iraq, and possibly other parts of the Middle East (Brew and Barazangi, 2001; Al-Hadidy, 2007). Because of its age, it was correlated to the Caledonian Orogeny by some authors (e.g. Buday, 1980). In southeast Arabia (Oman), distinct hiatuses occur in the mid-Silurian (Wenlock) to earliest Devonian, and in the Middle Devonian to mid-Carboniferous (Millson et al., 1996; Droste, 1997; Osterloff et al., 2004). It would therefore appear that parts of Arabia could have been uplifted as highlands, most probably sometime between the mid-Silurian and Middle Devonian. These highlands may be related to pre-rift thermal swelling or post-rift isostatic rebound associated with the breakaway of the Hun Superterrane (Figure 6), rather than the Caledonian Orogeny (Figure 5).

The mid-Carboniferous unconformity is sometimes correlated to the Hercynian Orogeny, and the term "Hercynian unconformity" is adopted in regional and local studies by numerous authors (e.g. Stöcklin and Setudehnia 1972; Berberian and King, 1981). In Saudi Arabia, the angular pre-Unayzah unconformity correlates to the mid-Carboniferous hiatus (Figure 3, c. 325–310 Ma, Al-Husseini, 2004; at least Serpukhovian, Bashkirian and early Moscovian, Gradstein et al., 2004). The associated differential structural relief is manifested by broad epeirogenic swells (many 100s of kilometers in lateral extent) and laterally extensive (100s of kilometers) upthrown blocks (several 100s of meters), bounded by transpressional to reverse faults (Wender et al., 1998; Al-Husseini, 2004). The Hercynian Orogeny appears to have been too distant to account for the severity and style of this in deformation in Arabia (Figure 8 and 9).

An alternative to correlating the Hercynian Orogeny to the mid-Carboniferous Arabian unconformity is considered in the interpretation shown in Figure 11 of Sengör (1990). This Early Triassic reconstruction shows a SW-oriented subduction zone of the Paleo-Tethys oceanic crust beneath parts of Cimmeria. Next to the subduction complex, the Podataksasi Arc (a name Sengör derived from the initial letters of Pontides, Dzirula, Adzharia-Trialeti, Artvin-Karabagh and Sanandaj-Sirjan; Figure 11) was mainly a Carboniferous episode of orogenic deformation, metamorphism, and arc-type, calc-alkaline magmatism. This interpretation is based on a detailed study of successions in the involved terranes (see Sengör, 1990). Natal'in and Sengör (2005) included the Podataksasi Arc in the so-called Silk Road Arc, which stretched during the late Paleozoic-early Mesozoic from the Caucasus through north Iran and the Pamirs to China.

Further westwards, Xypolias et al. (2006) extended the subduction-arc model from the Pontides to the Hellenic terrane (External Hellenides) and northeast Greece. U-Pb dating of zircon from a granitic orthogneiss in the Kithira Island (southern Greece) yielded a late Carboniferous age of 324–323 Ma. Taken together with other geochronological data from the Aegean region it provides evidence for a restricted period of plutonism between 325–300 Ma (Xypolias et al., 2006). These authors concluded that northeast Greece (Cycladic and Palegonian basements) and northwest Turkey (Menderes Massif in the Taurides terrane and Sakarya Zone in the Pontides terrane) formed part of Cimmeria.

A reviewer (written communication, 2006) noted that a subduction complex does not transmit compressional horizontal stresses across broad regions and, moreover, a SW-directed compression

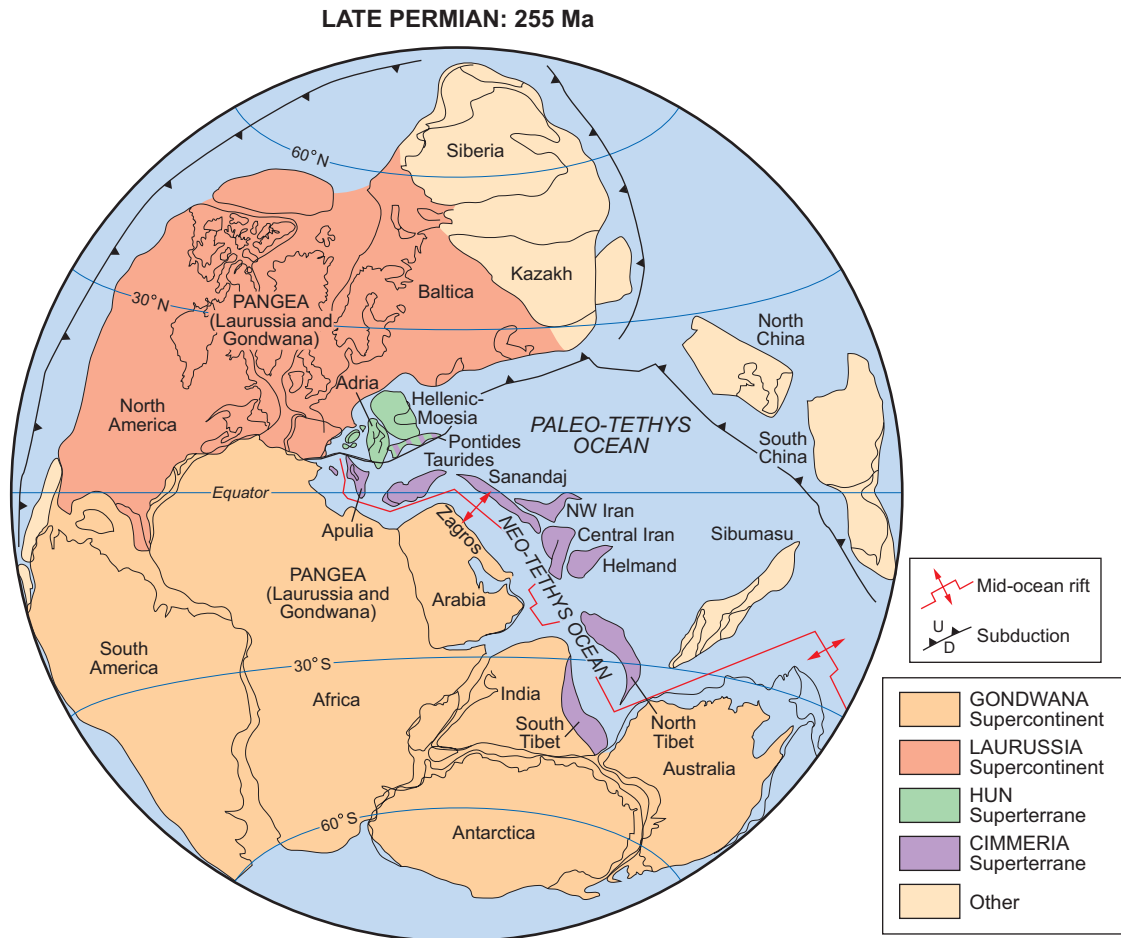


**Figure 9: Plate-tectonic reconstruction of the late Carboniferous (Pennsylvanian; modified after Torsvik and Cocks, 2004).** In the mid-Carboniferous times, the collision of Gondwana and Laurussia closed the Rheic Ocean causing the Hercynian Orogeny. Also in the late Carboniferous the collision of the Kazakh terranes with Pangea caused the Uralian Orogeny. In the Arabian Plate, an angular mid-Carboniferous unconformity is associated with epeirogenic swells and extensive compressional block faulting and a regional hiatus between about c. 325–310 Ma. The unconformity is widely referred to as “Hercynian” and associated with the Hercynian Orogeny. A more proximal tectonic event that may have caused the deformation of Arabia may have been the initiation of subduction along the Paleo-Tethyan margin of Cimmeria (Figure 11). The late Carboniferous - early Permian Gondwana glaciation extended into southern Arabia. Middle East terranes (Figures 1 and 2) not shown are Hunic Greater Caucasus and Cimmerian Alborz, Farah and Lesser Caucasus. Pontides shown as Hunic by Torsvik and Cocks (2004), but considered Cimmerian in our paper (in stripes).

appears inconsistent with the NS-trending grain of the fault-bounded Arabian structures. He pointed out that the initiation of subduction is commonly associated with a strong pulse of trench suction leading to roll-back, both processes exerting a strong extensional pull on the continental margin overlying the evolving subduction zone. As an analog to the Hercynian Orogeny’s influence in Arabia, he suggested the present-day Indian Plate. It is piercing into the anisotropic assembly of Central South Asia, with its effect reaching even the distant east coast of Asia. He concluded that a far-field relationship to Hercynian orogenic forces still cannot be completely excluded in Arabia.

Besides the data supporting a compressional mid-Carboniferous pulse due to a subduction-arc complex (Sengör, 1990, Figure 11; Xypolias et al., 2006), the concerns raised by the reviewer can be addressed. Whereas subduction complexes are indeed driven by slab-pull and associated with back-arc extension in the continental margin, this regime develops after an initial compressional stage. The pre-subduction stage involves first rupturing the entire oceanic crust (10 or more kilometers thick) and initiating





**Figure 10: Plate-tectonic reconstruction of the late Permian (Lopingian) time (modified after Torsvik and Cocks, 2004). In the mid-Permian - Triassic the Cimmeria Superterrane broke away from Gondwana, now part of the Pangea Supercontinent (Gondwana and Laurussia supercontinents, as well as Kazakh, Siberia and other terranes). Middle East terranes (Figures 1 and 2) not shown are Hunic Greater Caucasus and Cimmerian Alborz, Farah and Lesser Caucasus. Pontides shown as Hunic by Torsvik and Cocks (2004), but considered Cimmerian in our paper (in stripes).**

subduction along a new thrust zone. The horizontal forces required to fracture the brittle crust, then bend and push down the oceanic plate are not only compressional but of regional significance. In some cases, the thrust geometry is reversed and the compressional force is great enough to push the oceanic crust above the continental margin resulting in an obduction. It is considered here that the mid-Carboniferous event was an early pre-subduction compressional phase, while the mid-Permian - Triassic was the extensional one.

The relationship between a SW-directed compression and the NS-trending Arabian uplifted fault blocks was one of mid-Carboniferous transpression along pre-existing NS-oriented fault systems. The Arabian basement manifests a fault system with a NS-, NE- and NW-trending grain that was established in the late Proterozoic and Early Cambrian (Al-Husseini, 2000, 2004). We argue that a SW-directed compressional pulse would have caused the pre-existing Arabian basement-cored structures to be dislocated in a right-lateral transpressional style.

In summary, it seems likely that two regional angular unconformities in the Arabian Plate were related to plate-tectonic events that occurred in the vicinity of the Middle East terranes. The mid-Silurian to Middle Devonian unconformity (middle Paleozoic event instead of Caledonian Orogeny) may have involved the uplift of the northern Arabia margin (and Oman) in Gondwana. The uplift may have occurred along the newly formed Paleo-Tethys Ocean prior to, during or possibly after the breakaway

Research paper

# Evolutionary rates of the Triassic marine macrofauna and sea-level changes: Evidences from the Northwestern Caucasus, Northern Neotethys (Russia)

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## Abstract

A diverse Triassic marine macrofauna from the Northwestern Caucasus sheds new light on the biotic evolution after the end-Permian mass extinction. In the early Mesozoic, the study area was located on the northern margin of the Neotethys Ocean. Data on stratigraphic ranges of 130 genera of brachiopods, bivalves, ammonoids, corals, and sponges have been used to calculate the changes in two evolutionary rates, namely faunal transformation rate (FTR) and rate of transformation of the taxonomic diversity structure (TTDSR). The FTR demonstrates the changes in the generic composition of assemblages through geologic time, whereas the TTDSR indicates changes in the generic control of the species diversity. The Triassic marine macrofauna of the Northwestern Caucasus was characterized by very high FTR and TTDSR during the Early Triassic through early Late Triassic. The FTR slowed in the Middle Triassic, and accelerated again in the Carnian–Norian. In contrast, the FTR was abnormally slow in the Norian–Rhaetian. A remarkable turnover among macrofauna occurred at the Carnian–Norian transition. Regional sea-level changes were similar to the global eustatic fluctuations. It is difficult to establish their direct connections with changes in the evolutionary rates, although the turnover at the Carnian–Norian boundary coincided with a prominent regressive episode. In general, high evolutionary rates reported for the Triassic marine macrofauna of the Northwestern Caucasus may be explained as a consequence of the devastating end-Permian mass extinction. © 2008 Nanjing Institute of Geology and Palaeontology, CAS. Published by Elsevier Ltd. All rights reserved.

**Keywords:** Evolutionary rate; Marine macrofauna; Sea level; Triassic; Caucasus

## 1. Introduction

The greatest Permian/Triassic mass extinction devastated the Earth's marine biota about 251 Ma, and it was followed by a long-term and poorly-known recovery (Sepkoski, 1993; Hallam and Wignall, 1997; Peters and Foote, 2001; Benton and Twitchett, 2003; Bottjer, 2004; Pruss and Bottjer, 2004; Racki and Wignall, 2005; Erwin, 2006). The marine communities recovered only in the Anisian (Erwin, 2006), when the benthic fauna strongly diversified (Komatsu et al., 2004; Ruban, 2006a,b). However, the entire Triassic may be considered a recovery interval, during which biodiversity was less than in the Permian (Peters and Foote, 2001). Significant evolutionary changes, however, occurred during the Triassic; e.g., bivalves

began to dominate over brachiopods (Bonuso and Bottjer, 2005). The end of the Triassic was marked by a new mass extinction, which reduced the global marine diversity again (Sepkoski, 1993; Hallam and Wignall, 1997; Hallam, 2002; Pálffy et al., 2002). Thus, the Triassic recovery was unable to compensate for the biodiversity loss after the end-Permian mass extinction. Many factors, including sea-level changes, controlled the evolution of the Triassic marine biota. However, our knowledge of their influences remains limited.

This paper aims at a calculation of the evolutionary rates of the Triassic marine macrofauna of the Northwestern Caucasus (Fig. 1), where 130 genera of ammonoids, brachiopods, bivalves, sponges and corals are known from all Triassic stages (Ruban, 2006a). Previous studies analyzed the diversity dynamics of the Triassic marine biota of the Northwestern Caucasus (Ruban, 2006a,b,c), which was governed in particular by the changes in the basin depth. In this paper, the evolutionary rates are also compared to the sea-level changes, reconstructed for the study

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Fig. 1. Geographical and palaeogeographical location of the Northwestern Caucasus (slightly modified after Ruban, 2006a, 2007b). Palaeotectonics after Scotese (2004).

area. The main goals are to evaluate (1) how rapid was the Triassic evolution of the marine macrofauna, and (2) whether it was controlled by the sea-level changes.

## 2. Geological setting

The Northwestern Caucasus is a region in the south of Russia between the Kuban River and the Black Sea. During Triassic, the region was located on the northern margin of the Neotethys Ocean (Fig. 1), which was formed together with the northward drift of the Cimmerian terranes (Stampfli and Borel, 2002; Golonka, 2004; Scotese, 2004). The study area was situated much westwards from its present position, i.e., somewhere close to the Eastern Alps (Tawadros et al., 2006; Ruban, 2007a). According to Tawadros et al. (2006) and Ruban (2007a), this region was transported eastward to its present position along the major shear zone stretched along the Eurasian margin during the Late Triassic–earliest Jurassic. The sinistral displacements along this zone and rotation of Africa, which provoked them, have been discussed by Swanson (1982), Rapalini and Vizán (1993), and Ruban and Yoshioka (2005). Gaetani et al. (2005) pointed out the influences of the strike-slip movements in the Triassic evolution of the Northwestern Caucasus. In contrast, the traditional geodynamic model suggests that during Triassic, the study region was located on the southern periphery of the Russian Platform, where orogenic pulses occurred, coupled with extension (Ershov et al., 2003).

The Northwestern Caucasus was located close to the Tethyan region, although the global palaeobiogeographic differentiation was low in the Triassic (Westermann, 2000). This is supported particularly by the Caucasian signature of events documented in the “Boreal” bivalve evolution (Ruban, 2006c).

The Triassic stratigraphy and deposits of the Northwestern Caucasus were reviewed by Dagis and Robinson (1973), Jaroshenko (1978), Prozorovskaja (1979), Rostovtsev et al.

(1979), Gaetani et al. (2005), and Ruban (2006a,c). The regional lithostratigraphy is presented in Fig. 2. In general, the Triassic deposits, up to 1700 m thick, are: the Induan–Anisian carbonates, the Anisian–Carnian turbidites, and the Norian–Rhaetian carbonates, including reefal limestones. In some parts of the study area, shales interbedded with clastics and carbonates characterize the Norian. The major regional hiatuses are known in the Early Induan, Late Anisian, at the Carnian–Norian boundary, and in the Late Rhaetian. The age of the lithostratigraphic units was established based on an analysis of macro- and microfauna; ammonoids, brachiopods, and foraminifers were especially important for these purposes (Dagis and Robinson, 1973; Rostovtsev et al., 1979; Prozorovskaja, 1979; Efimova, 1991; Gaetani et al., 2005). Additionally, palynological studies by Jaroshenko (1978) and Gaetani et al. (2005) permitted a precise verification of these stratigraphic constraints.

## 3. Materials and methods

The data on the stratigraphic ranges of species, which belong to 130 genera of the Triassic marine macrofauna of the Northwestern Caucasus, were compiled from all available sources (Paffengol'tz, 1959; Djakonov et al., 1962; Dagis, 1963, 1974; Shevyryov, 1968; Dagis and Robinson, 1973; Jaroshenko, 1978; Prozorovskaja, 1979; Rostovtsev et al., 1979; Gaetani et al., 2005). These sources provided the reviews of the regional Triassic palaeontology that contain locality correlations and section-by-section compilations. The original data came from many sections (including those stretched along the valleys of the Belaja River and the Sakhraj River) within the study area. It appears that the compiled information is representative, because every interval of the regional Triassic succession was studied carefully (e.g., Dagis and Robinson, 1973; Rostovtsev et al., 1979).

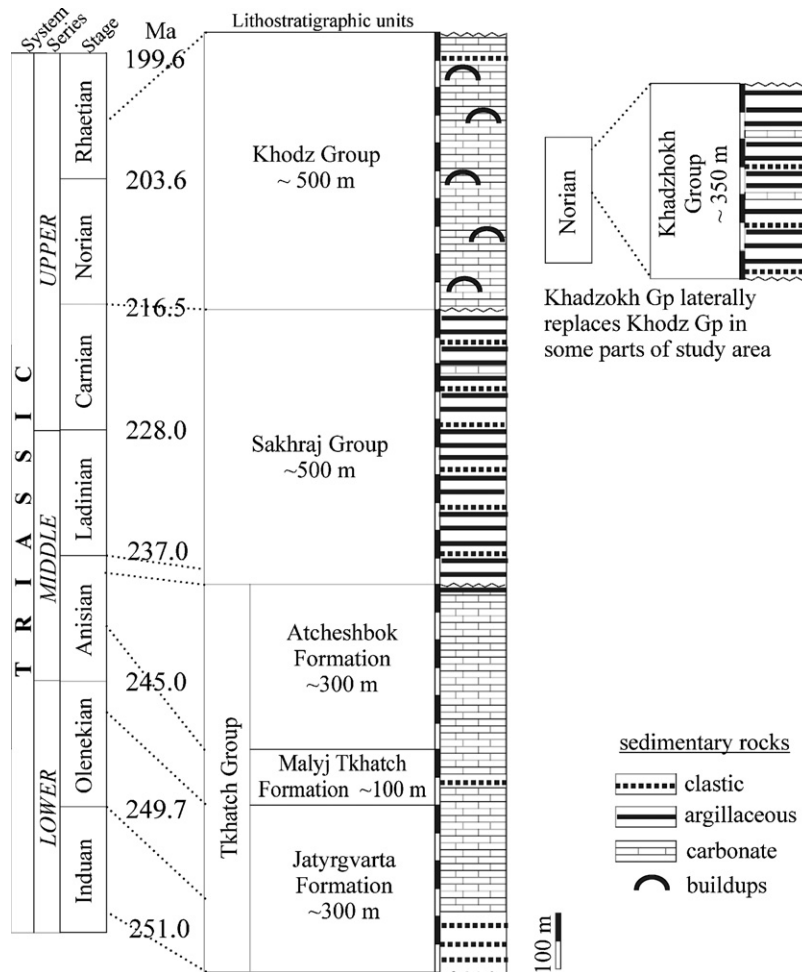


Fig. 2. Triassic lithostratigraphy of the Northwestern Caucasus (after Dagis and Robinson, 1973; Jaroshenko, 1978; Prozorovskaja, 1979; Rostovtsev et al., 1979; Gaetani et al., 2005; Ruban, 2006a,c). Absolute ages of stage boundaries are taken from Gradstein et al. (2004).

These data are essentially the same as those published by Ruban (2006a), although a few taxa identified with “sp.” were added. The distribution of fossils in each Triassic stage has been tabulated (Appendix A). It seems impossible to differentiate the data on the Induan and Olenekian, because they often were not differentiated in the available literature sources (e.g., Dagis and Robinson, 1973). The Triassic marine faunas of the Northwestern Caucasus were composed of 130 genera: 42 ammonoid, 61 brachiopod, 17 bivalve, 7 coral, and 3 sponge genera. These genera contain about 250 species, the ranges of which were well documented. When possible, a taxonomic correction was attempted to avoid under- or over-estimation of the evolutionary rates. The conclusions reached in this paper are limited regionally. And it appears to be complete on a regional scale. However, no regional database is complete enough to be used as a sole basis for further global constraints. An analysis of any regional database nevertheless provides the evidence for discussion of the planetary-scale patterns of biotic evolution with regards to their signatures in a given region.

The chronostratigraphy used herein follows that of the International Commission on Stratigraphy (Gradstein et al., 2004; Gradstein and Ogg, 2005, 2006).

Two evolutionary rates have been calculated herein. The methods of their quantitative evaluation were proposed by Ruban (2001a, 2002), and then described by Ruban and Tyszka (2005) and Ruban (2006d, 2007b). The first rate is the faunal transformation rate (FTR), which is estimated as  $1/R$ .  $R$  is a Jaccard’s (1901) similarity of two fossil assemblages, which characterize two successive stratigraphic intervals:

$$R = \frac{C}{[(N_1 + N_2) - C]}$$

where  $C$  is the number of common taxa for two assemblages,  $N_1$  and  $N_2$  are numbers of taxa in the earlier and later assemblages respectively. The FTR demonstrates how rapidly the changes occurred in the taxonomic composition of assemblages through geologic time. This paper is attempted to evaluate FTR for the generic assemblages of the entire marine macrofauna and particular fossil groups.

The second rate is the rate of transformation of the taxonomic diversity structure (TTDSR), which is estimated as  $1/Rst$ .  $Rst$  is a coefficient of Spearman’s rank correlation (Kendall, 1970) between two assemblages by presence/absence of genera, where the presence of a genus is indicated by the number of species that

belong to this genus in the particular assemblage. In other words, a correlation established takes into account the “weight” of each genus in a given age. This quantitative approach is described in detail by Ruban (2007b). The TTDSR shows how quick the changes in the generic control of the species diversity were, i.e., the change in significance of each genus for the determination of the species diversity. In general, this reflects the changes in the structure of taxonomic diversity and, therefore, in the structure of fossil assemblages. As in the previous case, TTDSR is evaluated for the entire marine macrofauna and particular fossil groups, whose genera and species are examined. It is always interesting to calculate Rst not only for the successive assemblages, but for those which existed in different times, e.g., for the Anisian and Carnian assemblages. This may have very interesting and important results (Ruban, 2001a,b, 2007b).

In this article, two patterns of regional sea-level changes are reconstructed with lithological data, namely transgressions–regressions and deepenings–shallowings. They are independent components of basin dynamics (Catuneanu, 2006; Ruban, 2007c). An appropriate general term to define both patterns is lacking. Tentatively, it is here called “sea-level changes”. Based on the analysis of the distribution of the Triassic deposits in the Northwestern Caucasus, with initial information compiled from Rostovtsev et al. (1979) and Gaetani et al. (2005), it is possible to recognize transgressive and regressive episodes. For these purposes, the presence or absence of marine strata in four particular areas of the study region was outlined. These areas were distinguished by Rostovtsev et al. (1979). Then, a cumulative curve for the entire Northwestern Caucasus was evaluated. Evidently, a wider distribution of marine deposits at each given time slice indicates a transgression, and vice versa, i.e., a restricted distribution indicates a regression. A critical analysis of the palaeoenvironmental interpretations of Gaetani et al. (2005) results in recognition of terrestrial, relatively shallow-marine, and slope environments using the same criteria as those by Ruban (2007c). This permits documenting the changes in the maximum basin depth. A somewhat similar approach was adopted by Landing and Johnson (2003). Used for a global reference were global eustatic curve of Haq et al. (1987) slightly modified by Haq and Al-Qahtani (2005) as well as reconstructed global base-level changes by Embry (1997).

#### 4. Evolutionary rates of marine macrofauna

The Triassic marine macrofauna of the Northwestern Caucasus was characterized by a very high FTR during the Early, Middle, and early Late Triassic (Fig. 3). The values of *R* were below 0.1. The FTR slowed in the Middle Triassic and accelerated again in the Ladinian–Carnian. This means very rapid changes in the generic composition of the assemblages until the Norian. In contrast, they were abnormally slow in the Norian–Rhaetian. The *R* value was as high as 0.415, which suggests a half similarity.

The TTDSR of the Triassic marine macrofauna of the Northwestern Caucasus was very high until the late Late Triassic (Fig. 4). Changes in the structure of taxonomic diversity slowed

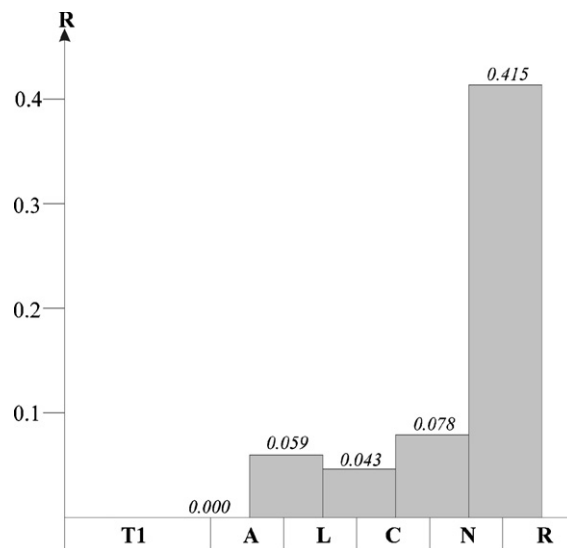


Fig. 3. *R* index of the entire Triassic marine macrofauna of the Northwestern Caucasus. Values of *R* are indicated above the columns. Stage abbreviations: A – Anisian, L – Ladinian, C – Carnian, N – Norian, R – Rhaetian; T1 – Early Triassic.

later. However, this evolutionary rate slightly accelerated in the Carnian–Norian. Therefore, this time interval was marked by a great turnover in the structure of fossil assemblages. Thus, the control of species diversity shifted strongly to other genera in the Norian in comparison to the Carnian. In contrast to the Rst index, the value of the *R* index decreased at the Ladinian–Carnian transition. The TTDSR became low in the Norian–Rhaetian. This suggests a high similarity of the taxonomic diversity structure between the Norian and Rhaetian assemblages.

Three fossil groups were responsible for the decrease in both evolutionary rates in the Norian–Rhaetian, namely, ammonoids,

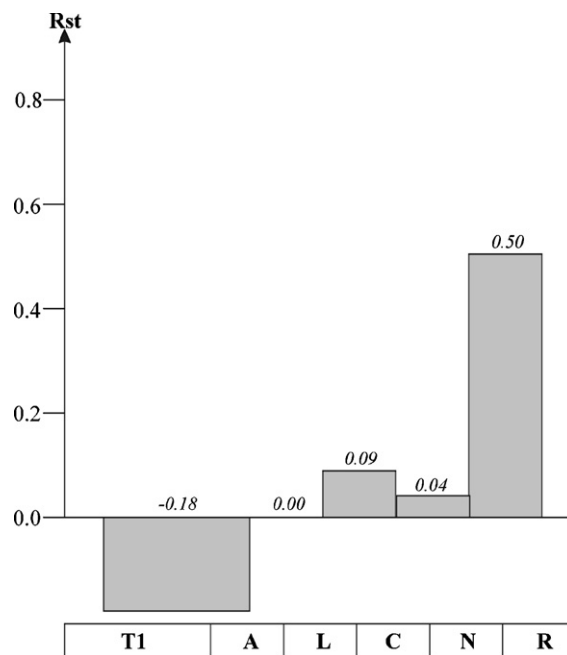


Fig. 4. Rst index of the entire Triassic marine macrofauna of the Northwestern Caucasus. Values of Rst are indicated above the columns. Stage abbreviations – see Fig. 3.

Table 1  
R index for the assemblages of particular fossil groups of the Triassic macrofauna from the Northwestern Caucasus

Fossil groups	E. Triassic–Anisian	Anisian–Ladinian	Ladinian–Carnian	Carnian–Norian	Norian–Rhaetian
Ammonoids	0	0.09	0	0	0.56
Bivalves	0	0.11	0.17	0	0
Brachiopods	0	0	0	0.14	0.48
Benthic macrofauna	0	0.04	0.06	0.09	0.39

corals, and brachiopods (Table 1). Many genera of these groups have representatives in both these stages. In contrast, no Rhaetian species of bivalves and sponges are found at all. However, as ammonoids, corals, and brachiopods belong to distinct ecological groups but all demonstrate similarly diminished evolutionary rates across the Norian–Rhaetian transition, it is possible that a real decline in the rate of fauna evolution took place at the Norian–Rhaetian transition. The whole benthic macrofauna, however, demonstrated the higher FTR at the Norian–Rhaetian transition than ammonoids did (Table 1).

A calculation of Rst among all assemblages (Table 2), both successive and non-successive, results in two important conclusions:

- (1) The Early Triassic assemblages are more different from the Anisian assemblages than from the Ladinian and Carnian assemblages;
- (2) The Norian and Rhaetian assemblages are more different from the Early Triassic, Anisian and Ladinian assemblages in comparison to the Carnian assemblage, although such a dissimilarity of the Rhaetian assemblage is slightly less.

The first conclusion coupled with the relatively high Rst value in the Ladinian–Carnian slightly reduces the importance of biotic changes during the Early Triassic through Carnian. The second conclusion suggests that the turnover at the Carnian–Norian transition was stronger than expected. It was something like a “revolution” in the regional history of the Triassic marine macrofauna. Both conclusions presented above are meaningful for the particular fossil groups (Table 3).

## 5. Sea-level changes

The documented evolutionary rates of the Triassic marine macrofauna of the Northwestern Caucasus might have been related to the regional sea-level changes. My reconstruction here documents the transgressions–regressions and deepening–shallowings in the Northwestern Caucasus, which

are compared with the global eustatic fluctuations (Haq et al., 1987; Embry, 1997; Haq and Al-Qahtani, 2005) (Fig. 5). Sea-level changes in the beginning of the Triassic are debated. Although Haq et al. (1987), Embry (1997), and Haq and Al-Qahtani (2005) pointed out the low sea level at the Permian–Triassic transition, Hallam and Wignall (1999) argued that a significant transgression occurred. In the Northwestern Caucasus, this transition is marked by the marine facies of the Abag Formation (Prozorovskaja, 1979), but these deposits are capped by an unconformity (Dagis and Robinson, 1973; Prozorovskaja, 1979; Rostovtsev et al., 1979; Gaetani et al., 2005; Ruban et al., in press). Perhaps this earliest Triassic hiatus was a result of local tectonic activity. After the short-term hiatus at the beginning of the Triassic, the sea rapidly transgressed over the study area (Fig. 5). This coincided with the global eustatic rise. However, in spite of global tendencies, a stepwise regression occurred in the middle-late Anisian. A global eustatic fall in the late Anisian corresponded to the regional hiatus. The next transgression, which also was very rapid, occurred in the latest Anisian and reached its maximum in the Ladinian. However, the sea occupied less territory, than during the previous cycle. This transgression corresponded well with the global eustatic rise. There is no evidence for the major late Ladinian regressive episode in the Northwestern Caucasus, although it occurred globally. In contrast, the gradual regional regression in the Carnian occurred at the same time, as the global sea level was rising. The global eustatic fall at the Carnian–Norian transition evidently coincided with the regional hiatus (Fig. 5). In the Norian, a new regional transgression occurred. It was the largest among the other Triassic regionally-documented transgressions, and it had analogues in the global record. Regression occurred abruptly in the Late Rhaetian, which is a well recognized global pattern. Therefore, three transgressive–regressive cycles are established in the Triassic history of the Northwestern Caucasus. Each began with a rapid transgression. Differences between the regional transgressions–regressions and global eustatic fluctuations may be explained in terms of local tectonics. Both eustasy and tectonics are responsible for the regional transgressions and

Table 2  
Rst index for the assemblages of the Triassic marine macrofauna from the Northwestern Caucasus

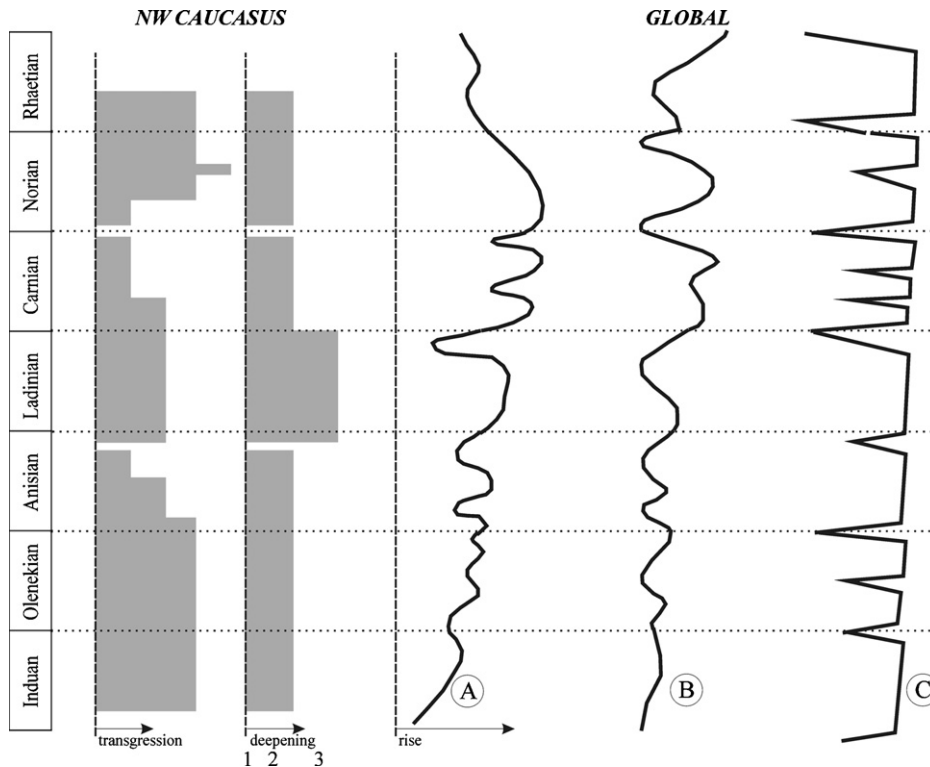
Assemblages	E. Triassic	Anisian	Ladinian	Carnian	Norian	Rhaetian
E. Triassic	–	<b>–0.18</b>	–0.07	–0.09	<b>–0.19</b>	–0.15
Anisian	–	–	0.00	–0.07	<b>–0.34</b>	<b>–0.28</b>
Ladinian	–	–	–	0.09	–0.15	–0.05
Carnian	–	–	–	–	0.04	0.06
Norian	–	–	–	–	–	<b>0.50</b>

Significant values are highlighted as bold.

**Table 3**  
Rst index for the assemblages of particular fossil groups of the Triassic macrofauna from the Northwestern Caucasus

Assemblages	E. Triassic	Anisian	Ladinian	Carnian	Norian	Rhaetian
<b>Ammonoids</b>						
E. Triassic	–	<b>–0.40</b>	–0.16	–0.12	–0.22	–0.21
Anisian	–	–	–0.03	–0.07	–0.23	–0.25
Ladinian	–	–	–	–0.07	–0.13	0.09
Carnian	–	–	–	–	–0.09	–0.09
Norian	–	–	–	–	–	<b>0.50</b>
<b>Bivalves</b>						
E. Triassic	–	–0.18	–0.13	–0.09	–0.16	0.00
Anisian	–	–	–0.17	–0.18	–0.46	0.00
Ladinian	–	–	–	0.22	–0.32	0.00
Carnian	–	–	–	–	–0.24	0.00
Norian	–	–	–	–	–	0.00
<b>Brachiopods</b>						
E. Triassic	–	–0.14	0.00	–0.09	–0.17	–0.15
Anisian	–	–	0.00	–0.01	<b>–0.38</b>	<b>–0.36</b>
Ladinian	–	–	–	0.00	0.00	0.00
Carnian	–	–	–	–	0.22	0.14
Norian	–	–	–	–	–	<b>0.56</b>
<b>Benthic macrofauna</b>						
E. Triassic	–	–0.10	–0.04	–0.06	–0.13	–0.10
Anisian	–	–	–0.05	–0.03	<b>–0.39</b>	<b>–0.29</b>
Ladinian	–	–	–	<b>0.22</b>	–0.15	–0.12
Carnian	–	–	–	–	0.00	0.05
Norian	–	–	–	–	–	<b>0.48</b>

Significant values are highlighted as bold.



**Fig. 5.** Regional and global sea-level changes. A – rescaled after Haq et al. (1987), B – rescaled after Haq and Al-Qahtani (2005), C – after Embry (1997). Numbers indicate environments: 1 – terrestrial, 2 – relatively shallow-marine, 3 – slope.

regressions (Catuneanu, 2006), and a balance between them enforces the shoreline shifts.

The Triassic seas in the Northwestern Caucasus were mostly shallow-water (Fig. 5). One long-term and pronounced deepening episode is documented. It occurred in the latest Anisian–Ladinian, when turbidites were accumulated (Gaetani et al., 2005; Ruban, 2006a). It seems that local tectonics enforced significant regional water-depth changes. However, the Ladinian deepening pulse documented in the study area coincided with the peak transgression in Western Europe (Jacquin and de Graciansky, 1998). This pulse may also be related to the eustatic rise documented by Haq et al. (1987), Embry (1997), and Haq and Al-Qahtani (2005). Undoubtedly, the marine basin, which embraced the Northwestern Caucasus in the Triassic, was not stable, but it fluctuated under both eustatic and tectonic controls. Those sharp changes in its extent and depth, which are established herein, indicate that the pulses are meaningful for further comparisons with the available palaeontological data.

## 6. A comparison of regional evolutionary rates and sea-level changes

The reconstruction of the regional sea-level changes (Fig. 5) allows comparison of them to the documented evolutionary rates (Figs. 3 and 4; Table 1). It seems that they did not directly coincide. However, some interesting relationships may be noted.

An increase of changes in the generic composition of assemblages and a major turnover in the diversity structure at the Carnian–Norian transition corresponds with the regional regressive episode. The latter provoked a significant interruption in the regional evolution of the marine macrofauna. When repopulation occurred in the early Norian, the marine macrofauna differed strongly from the Carnian assemblage because of the absence of transitional genera, which might have appeared in the end-Carnian and survived into the early Norian. It may be asked why there were no such significant changes in the late Anisian when another regression occurred. This can be easily explained by two reasons: (1) my data on the Anisian comprise the entire taxa, which existed both before and after the hiatus, and (2) the late Anisian regression was probably much shorter. Gaetani et al. (2005) suggested that the presence of late Carnian deposits is doubtful, and, consequently, the hiatus at the Carnian–Norian transition might have been even longer than traditionally assumed. Another hypothesis may be formulated. During Late Triassic, the Greater Caucasus Terrane began to move eastward (Tawadros et al., 2006; Ruban, 2007a), and, therefore, in the Norian, the region might be located in a palaeobiogeographically different area from where it was in the Carnian. But such an assumption requires strenuous testing. An easier explanation is a change in the character of sedimentation, which occurred within the Western Caucasus. The Sakhray Group is dominated by clastic deposits, whereas the overlying Khodz Group is composed of carbonates. However, carbonate beds already appeared in the Carnian (Fig. 2).

Another feature, which may be of interest, is relatively high similarity between the Norian and Rhaetian assemblages,

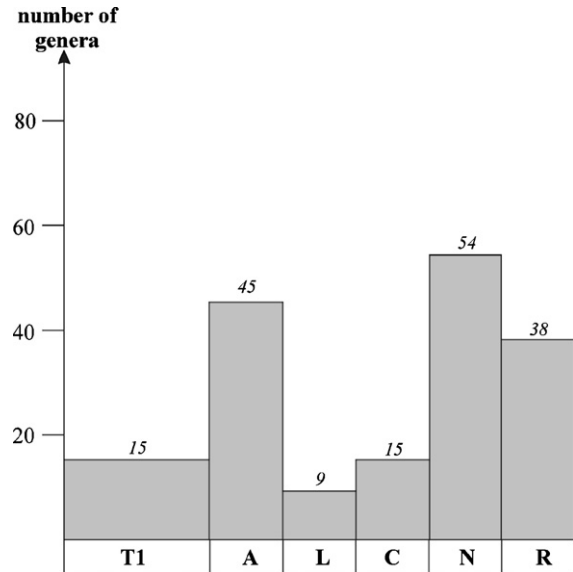


Fig. 6. Diversity dynamics of the Triassic marine macrofauna of the Northwestern Caucasus. Numbers of genera are indicated above the columns. Stage abbreviations – see Fig. 3.

which is suggested by both  $R$  and  $R_{st}$  values (Figs. 3 and 4; Table 1). The mentioned pair of assemblages corresponds to the transgressive–regressive cycle, i.e., the deposition was not interrupted during the Norian–Rhaetian intervals.

Therefore, sea-level changes were potentially able to control in part the evolutionary rates of the Triassic marine macrofauna in the Northwestern Caucasus.

## 7. Discussion

Fossil assemblages may be dissimilar not only in their taxonomic composition but also in their total diversity. In such cases, the values of  $R$  and  $R_{st}$  indices are usually low. To test this explanation for the Triassic marine macrofauna of the Northwestern Caucasus, the total number of genera in each stratigraphic interval has been calculated (Fig. 6). It is evident that the Anisian generic diversity increased about 3 times above that of the Early Triassic. The Ladinian diversity decreased five times. Differences in the number of genera between the Ladinian and Carnian are evident but not great. The Norian diversity was 3.6 times greater than the Carnian diversity, comparable to the Rhaetian diversity. Consequently, differences in diversity were strongly reflected in  $R$  and  $R_{st}$  values. However, no Early Triassic genera are known in the Anisian (see data in Ruban, 2006a). Therefore, high evolutionary rates in the Early Triassic–Anisian period occurred due to the real turnovers. Differences in the total diversity enforced the  $R$  and  $R_{st}$  for the Anisian–Ladinian. Three Anisian genera are known in the Ladinian, suggesting that the Ladinian assemblage was formed by the diminishing of the Anisian diversity, but origination of new taxa, and, consequently, turnover were stronger. This is reflected by the  $R$  and  $R_{st}$  values (Figs. 3 and 4), which are higher than during preceding intervals, although not significantly. It seems that the FTR and the TTDSR at the Ladinian–Carnian interval reflects mostly the



turnovers, because of small differences in their total diversity. As for the Carnian–Norian interval, documented acceleration of the FTR and the TTDSR occurred mostly due to the turnovers, but not the differences in the total diversity, because only five Carnian genera are known in the Norian. A similarity of both generic composition and diversity structure between the Norian and Rhaetian assemblages is a result of weak turnover, in which 27 genera are common to these stages. Thus, the real effect of the differences in the total generic diversity on the evaluation of the evolutionary rates was not so great in our case, and the decreases of the FTR and the TTDSR were mostly the result of turnovers.

The structure of global marine communities strongly changed after the Permian–Triassic mass extinction (Sepkoski, 1993; Hallam and Wignall, 1997; Benton and Twitchett, 2003; Bottjer, 2004; Pruss and Bottjer, 2004; Racki and Wignall, 2005; Erwin, 2006). Extremely high regional evolutionary rates, documented in the Northwestern Caucasus, might have been a result of a “restart” of the biotic evolution after the Permian–Triassic mass extinction. By extrapolating the regional knowledge on the evolutionary rates of the marine macrofauna to the global scale, it is possible to conclude that the Permian–Triassic catastrophe was so large as to be followed by a recovery, which lasted until the late Late Triassic. However, data from the other regions are needed to make a complete database in order to verify this conclusion.

## 8. Conclusions

The Triassic marine macrofauna of the Northwestern Caucasus evolved very rapidly. Rates of change in both the generic composition of assemblages and the structure of their taxonomic diversity were high. The real slowing of the evolution occurred only in the Norian–Rhaetian interval. The diversity structure of the assemblages sharply changed at the Carnian–Norian transition. The Triassic sea-level changes in the Northwestern Caucasus corresponded generally to the global eustatic fluctuations, although the local tectonic movements induced the particular features of the regional sea-level changes. The regional sea-level changes were among the important factors influencing the evolutionary rates of the marine macrofauna.

The calculation of the evolutionary rates of marine faunas may be significant for the chronostratigraphic developments. Using the Caucasian data, Tozer (1988, 1990) recognized the Rhaetian as a provincial substage of the Norian. The FTR and the TTDSR in the Norian–Rhaetian interval were lower than during earlier times (Figs. 3 and 4). But *R* and *Rst* values were about 0.5, which is not as large, and, consequently, transformations in macrofaunal assemblages at the Norian–Rhaetian transition were relatively slower. Thus, there is no clear evidence to support combining the Norian and Rhaetian into a unique stage.

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## Appendix A

Triassic macrofossil taxa from the Northwestern Caucasus. The number of species in each genus is indicated for stratigraphic intervals. The data are republished from Ruban (2006a) with few additions after a permission from the Editor of “*Revue de Paléobiologie*”.

Genera	Early Triassic	Anisian	Ladinian	Carnian	Norian	Rhaetian
<i>Abrekia</i>	1	0	0	0	0	0
<i>Acrochordiceras</i>	0	3	0	0	0	0
<i>Adygella</i>	0	0	0	1	1	1
<i>Adygelloides</i>	0	0	0	0	0	1
<i>Aegeiceras</i>	0	1	0	0	0	0
<i>Amphiclina</i>	0	0	0	0	1	2
<i>Ampliclinodonta</i>	0	0	0	0	1	0
<i>Angustothyris</i>	0	1	0	0	0	0
<i>Arcestes</i>	0	0	1	0	0	4
<i>Arpadites</i>	0	2	0	0	0	0
<i>Astraeomorpha</i>	0	0	0	0	2	1
<i>Aulacothyropsis</i>	0	0	0	1	0	4
<i>Austriella</i>	0	0	0	0	1	0
<i>Austrirhynchia</i>	0	0	0	0	0	2
<i>Badiotites</i>	0	0	1	0	0	0
<i>Balatonospira</i>	0	0	0	1	0	0
<i>Beyrichites</i>	0	1	0	0	0	0
<i>Bobukella</i>	0	0	0	1	1	0
<i>Cassianella</i>	0	0	0	0	1	0
<i>Caucasites</i>	0	2	0	0	0	0
<i>Caucasorhynchia</i>	0	0	0	0	1	1
<i>Caucasothyris</i>	0	0	0	0	1	0
<i>Cladiscites</i>	0	0	0	0	2	2
<i>Claraia</i>	4	0	0	0	0	0
<i>Coenothyris</i>	0	2	0	0	0	0
<i>Costirhynchia</i>	0	1	0	1	0	0
<i>Costispiriferina</i>	0	1	0	0	0	0
<i>Crurirhynchia</i>	0	0	0	0	1	0
<i>Crurithyris</i>	1	0	0	0	0	0
<i>Cubanothyris</i>	0	0	0	0	2	2
<i>Daonella</i>	0	0	2	0	0	0
<i>Decurtella</i>	0	2	0	0	0	0
<i>Dieneroceras</i>	1	0	0	0	0	0
<i>Dinarispira</i>	0	2	0	0	0	0
<i>Dioristella</i>	0	1	0	1	0	0
<i>Euxinella</i>	0	0	0	0	3	6
<i>Fissirhynchia</i>	0	0	0	0	1	1
<i>Flemingites</i>	1	0	0	0	0	0
<i>Flexoptychites</i>	0	1	0	1	0	0
<i>Guseriplia</i>	0	0	0	0	0	2
<i>Gymnites</i>	0	1	0	0	0	0



Genera	Early Triassic	Anisian	Ladinian	Carnian	Norian	Rhaetian
<i>Halobia</i>	0	0	1	5	0	0
<i>Hodsia</i>	0	0	0	0	1	0
<i>Hoernesia</i>	0	1	0	0	0	0
<i>Holcorhynchella</i>	0	1	0	0	0	0
<i>Hollandites</i>	0	3	0	0	0	0
<i>Indopecten</i>	0	0	0	0	1	0
<i>Japonites</i>	0	1	0	0	0	0
<i>Joannites</i>	0	0	0	1	0	0
<i>Juvavites</i>	0	0	0	0	1	0
<i>Koiveskallina</i>	0	1	0	0	0	0
<i>Koninckina</i>	0	0	0	1	1	0
<i>Laballa</i>	0	0	0	0	2	3
<i>Laboceras</i>	0	3	0	0	0	0
<i>Leda</i>	0	0	1	0	0	0
<i>Lepismatina</i>	0	0	0	0	0	1
<i>Leyophyllites</i>	0	4	0	0	0	0
<i>Limea</i>	0	1	0	0	0	0
<i>Lobites</i>	0	0	0	0	1	0
<i>Lobothyris</i>	0	0	0	0	2	0
<i>Longobardites</i>	0	1	0	0	0	0
<i>Lyssochlamys</i>	0	0	0	2	0	0
<i>Majkopella</i>	0	0	0	0	0	3
<i>Megaphyllites</i>	0	1	0	0	2	2
<i>Mentzelia</i>	0	1	0	3	1	2
<i>Mesocladiscites</i>	0	1	0	0	0	0
<i>Moisseievia</i>	0	0	0	0	2	1
<i>Molengraffia</i>	0	0	0	0	1	0
<i>Monophyllites</i>	0	1	3	0	0	0
<i>Monotis</i>	0	0	0	0	3	0
<i>Montlivaultia</i>	0	0	0	0	1	0
<i>Myophoria</i>	0	0	0	0	1	0
<i>Mytilus</i>	0	1	0	0	0	0
<i>Nannites</i>	1	0	0	0	0	0
<i>Neoretzia</i>	0	0	0	0	0	3
<i>Neowelerella</i>	1	0	0	0	0	0
<i>Norella</i>	0	1	0	0	0	0
<i>Owenites</i>	3	0	0	0	0	0
<i>Oxycolpella</i>	0	0	0	0	3	2
<i>Paleocardita</i>	0	0	0	0	1	0
<i>Paracladiscites</i>	0	0	0	0	0	2
<i>Paradanubites</i>	0	2	0	0	0	0
<i>Paragoceras</i>	1	0	0	0	0	0
<i>Parasageceras</i>	0	1	0	0	0	0
<i>Parussuria</i>	1	0	0	0	0	0
<i>Pexidella</i>	0	1	0	0	1	0
<i>Phyllocladiscites</i>	0	2	0	0	0	0
<i>Piarorhynchella</i>	0	1	0	0	0	0
<i>Pinacoceras</i>	0	0	0	0	1	1
<i>Placites</i>	0	0	0	0	1	1
<i>Posidonia</i>	0	1	1	0	0	0
<i>Proptychites</i>	1	0	0	0	0	0
<i>Pseudocyrina</i>	0	0	0	0	1	0
<i>Pseudomonotis</i>	0	0	0	0	2	0
<i>Pseudorugitella</i>	0	0	0	0	2	2
<i>Pseudosageceras</i>	1	0	0	0	0	0
<i>Punctospirella</i>	0	1	0	0	0	0
<i>Rhabdophyllia</i>	0	0	0	0	1	0
<i>Rhacophyllites</i>	0	0	0	0	1	2
<i>Rhaetina</i>	0	0	0	2	6	4
<i>Rhimirhynchopsis</i>	0	0	0	0	1	1
<i>Rhynchonella</i>	0	1	0	0	0	0
<i>Robinsonella</i>	0	0	0	0	0	1
<i>Sahraja</i>	0	0	0	0	1	0
<i>Schafhaeutlia</i>	0	1	0	0	0	0

Genera	Early Triassic	Anisian	Ladinian	Carnian	Norian	Rhaetian
<i>Sinucosta</i>	0	1	0	0	1	1
<i>Smithoceras</i>	0	1	0	0	0	0
<i>Spinolepismatina</i>	0	0	0	0	1	0
<i>Stephanocoenia</i>	0	0	0	0	1	0
<i>Sturia</i>	0	2	1	0	0	0
<i>Stylophylloopsis</i>	0	0	0	0	2	0
<i>Subowenites</i>	1	0	0	0	0	0
<i>Subvishnuites</i>	1	0	0	0	0	0
<i>Sulcatinella</i>	0	2	0	0	0	0
<i>Sulcatothyris</i>	0	0	0	1	0	0
<i>Tetractinella</i>	0	1	0	0	0	0
<i>Thamnastraea</i>	0	0	0	0	2	2
<i>Thecosmia</i>	0	0	0	0	6	2
<i>Thecospira</i>	0	0	0	0	1	0
<i>Thecospiropsis</i>	0	0	0	0	1	0
<i>Triadithyris</i>	0	0	0	0	2	1
<i>Trigonirhynchella</i>	0	0	0	0	1	2
<i>Velopecten</i>	0	1	0	1	0	0
<i>Volirhynchia</i>	0	2	0	0	0	0
<i>Wittenburgella</i>	0	0	0	0	1	1
<i>Worobievella</i>	0	0	0	0	1	1
<i>Wyomingites</i>	1	0	0	0	0	0
<i>Xenodiscus</i>	0	0	1	0	0	0
<i>Zeilleria</i>	0	0	0	0	3	6
<i>Zugmayerella</i>	0	0	0	0	0	1

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# Possible pitfalls in the procedure for paleobiodiversity-dynamics analysis

## Pułapki analizy paleo-bioróżnorodności

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### Abstract

The changes in the diversity of specific taxa during certain parts of the geological past (paleobiodiversity dynamics) can, in principle, be established by counting the number of the fossil taxa present (worldwide or in a specific study area) in rocks dated for the time interval under study. Numerous obstacles are present, however, for instance in the form of lacking field data, disappeared collections, ambiguous identifications, temporary 'disappearance' of taxa, and dating problems. One major problem is the fact that, particularly in regional studies in some countries, a local, regional or national chronostratigraphic terminology is used rather than the chronostratigraphy recommended by the International Stratigraphic Commission of the International Union of Geological Sciences. This hampers international correlation and makes precise global paleodiversity-dynamics analyses extremely difficult. A reliable insight into the true paleodiversity dynamics requires not only that the various problems are recognized, but also that their consequences are eliminated or, if this is impossible, minimized. This is particularly important if the effects of mass extinctions on fauna and flora are investigated. Each analysis of paleobiodiversity-dynamics analysis of phenomena related to mass extinctions should therefore try to quantify the impact that missing data or inaccuracies of any kind may have on the final results; such an analysis should, in addition, try to find a solution for the major problems, so as to avoid significant inaccuracies of the calculated values. Large electronic databases can help, since about a decade, to diminish possible errors in diversity estimates. Paleobiodiversity should preferably be expressed in the form of values with a certain band with, indicating the inaccuracy, rather than in the form of exact values.

**Keywords:** biodiversity, taxonomy, biostratigraphy, geochronology, Lazarus taxa

### Streszczenie

Zmiany w zróżnicowaniu gatunków w pewnych przedziałach czasu przeszłości geologicznej (dynamika paleo-bioróżnorodności) są z zasady ustalane poprzez zliczanie liczby taksonów skamieniałości (na świecie lub na wybranym obszarze) w skałach datowanych na badany interwał czasowy. Tym niemniej procedura ta napotyka wiele przeszkód, np. w postaci braku danych z jakiegoś obszaru, zagubionych kolekcji, niejednoznacznych identyfikacji, czasowego „zaniku” taksonów czy problemów datowania. Jednym z głównych problemów,

zwłaszcza w badaniach regionalnych w niektórych krajach, jest stosowanie lokalnej, regionalnej lub krajowej terminologii chronostratygraficznej, a nie chronostratygrafii rekomendowanej przez Międzynarodową Komisję Stratygraficzną przy Międzynarodowej Unii Nauk Geologicznych. Utrudnia to międzynarodowe korelacje i czyni niezwykle trudnym przeprowadzenie precyzyjnej globalnej analizy dynamiki paleo-bioróżnorodności. Wiarygodny wgląd w prawdziwą dynamikę paleo-bioróżnorodności wymaga nie tylko rozpoznania różnych problemów, ale również wyeliminowania ich konsekwencji, a gdy to niemożliwe, zminimalizowania ich. Jest to szczególnie ważne w przypadku, gdy badane są następstwa masowego wymierania fauny i flory. Dlatego każda analiza dynamiki paleo-bioróżnorodności zjawisk związanych z masowym wymieraniem powinna zawierać próbę ilościowego oszacowania wpływu, jakie brakujące dane lub niedokładności jakiegokolwiek rodzaju mogą wywierać na końcowe wnioski. Taka analiza powinna próbować znaleźć rozwiązanie dla głównych problemów, ażeby uniknąć znaczących niedokładności w obliczonych wartościach. Duże elektroniczne bazy danych, dostępne od około 10 lat, mogą pomóc w zmniejszeniu możliwych błędów przy szacowaniu różnorodności. Najlepiej, gdyby paleo-bioróżnorodność była wyrażana w formie wartości w pewnym zakresie, wskazującym na niedokładność, a nie w formie precyzyjnej wartości.

**Słowa kluczowe:** bioróżnorodność, taksonomia, biostratygrafia, geochronologia, taksony Łazarza

## Introduction

Since the end of the 1970s, hundreds of articles and books have been devoted to changes in global biodiversity, mass extinctions and – more in particular – the changes in biodiversity patterns of numerous fossil groups. Regional patterns were also established for numerous regions worldwide. The studies by Sepkoski (1993, 1997) and his co-workers (Sepkoski *et al.* 1981; Raup & Sepkoski 1982) are of great importance in this context, as they have initiated new developments in historical geology and paleontology. This type of work coincided in time, to mutual benefit, with multidisciplinary studies that have led to the insight that exceptional events in the Earth's history have greatly affected biodiversity in time (e.g., Alvarez *et al.* 1980), but there exists no general agreement yet about extraterrestrial (e.g. impact of a bolide) or Earth-related (e.g. global environmental change) causes that must be held responsible for the various events (e.g., Courtillot 2007).

Most research on paleobiodiversity has concentrated on faunas, commonly marine ones, probably because of their higher preservation potential and because of the commonly lower number and the commonly shorter interruptions (hiatuses) in their record. Diversity changes in terrestrial floras have, in contrast, been studied in much less detail, and paleobotanical evidence for biotic crises is still scarce, which may be ascribed – at least partially – to

the much less complete knowledge that is available nowadays about ancient terrestrial floras than marine biota. Attempts to estimate changes in the diversity of fossil plant assemblages have been undertaken by, particularly, Niklas *et al.* (1985), Boulter *et al.* (1988), Nishida (1991), Wing & DiMichele (1995), Tiwari (1996), Boulter (1997), and Philippe *et al.* (1999). The influences of mass extinctions on plants, including their diversity, were discussed by, among others, Tschudy & Tschudy (1986, Retallack (1995), Tiwari (2001), McAllister Rees (2002), and Wing (2004). Data about changes in paleobotanical diversity are still too scarce, however, to be reliable for statistically significant analyses. For instance, the highly interesting hypothesis of Guex *et al.* (2001) and Morard *et al.* (2003), later verified by Ruban (2004) and Ruban & Efendiyeva (2005) – which explains the end-Lias anoxia with the preceding plant growth – could not be supported by quantitatively sufficient data on changes in plant diversity, so that only qualitative and the simplest semi-quantitative data have been used. Most problems regarding the analyses of changes in paleobiodiversity (often referred to as 'paleobiodiversity dynamics') are similar for faunas and floras, although both groups have also their own specific problems because the evolution and preservation of both groups have their own specific aspects.

Some other aspects of paleodiversity-dynamics analysis have been reviewed and discussed by, among others, Benton (1995), Alroy

(2000, 2003), Foote (2000, 2007) and Hammer & Harper (2005). Several other works deal with the influence of differences in preservation potential and of the (in)completeness of the fossil record on diversity measurements and on the interpretation of the findings (e.g., Benton 1995; Peters & Foote 2001; Smith 2001, 2007; Twitchett 2001; Crampton *et al.* 2003; Vermeij & Leighton 2003; Bush & Bambach 2004; Boucot 2006; Peters 2006; Foote 2007). The present contribution is meant to present a brief overview of the more general problems related to the collection and compilation of data.

## Collection of data

The first problem, met immediately when starting an analysis of taxonomic diversity dynamics, is how and where initial data (in their most simple form data regarding the stratigraphic range of a particular taxon) have to be collected. This information should, obviously, be as complete as possible; in addition, it should be representative and scientifically correct.

Data from literature can be found in two forms: (1) as dispersed information, spread over numerous publications, each of which is highly incomplete; and (2) as already compiled, fairly complete information on the stratigraphic distribution of the taxa being studied.

It is evident that – if sources of the second type are available – they should be chosen as a starting point. Their disadvantage is, however, that they are commonly outdated. This implies that, even if such compilations exist, additional collection of data from ‘dispersed’ sources remains essential. Thus, the search for data can be realized in the following three ways:

(1) if there are no sources with compiled data at all, a search for all possible publications and unpublished reports with „dispersed” information should be carried out [as an example: when the diversity studies of the Phanerozoic megafloora from the Northern Caucasus (Ruban 2003) was started, thousands of potential sources were checked, which took about a year];

(2) if there are several sources with compiled, but evidently incomplete or outdated data, they should be chosen as the basic ones,

but the data found in them should be complemented with data from other sources with „dispersed” information (in exceptional cases, namely if the sources with compiled data seem neither incomplete nor outdated and if they seem sufficiently representative for the current knowledge, such basic sources may be used without additional search for complementary dispersed information);

(3) if there is only one source with previously compiled, but outdated information, it is necessary to search not only for complementary data in the literature that is devoted to the taxon/taxa under examination, but also for publications that might, as a ‘by-product’, contain information that might help to avoid shortcomings in the initial data (i.e., missing data, duplicate data).

Apart from carrying out the required literature search with great scrutiny, it is of utmost importance to decide carefully which of the three above approaches should be followed, as the choice of initial data is one of the most important factors that determine whether the inventory of data will result in a complete and reliable set of data that can form an adequate basis for the rest of the procedure.

## Compilation of data

The compilation of data, which have commonly to be collected from numerous sources, is one of the most difficult, time-consuming and bothersome activities when preparing a quantitative analysis of paleodiversity dynamics. This holds for both global and regional studies.

Among the problems that are met during data compilation, one of the most important is taxonomical synonymy. Incorrect identifications of taxa, which are sometimes obvious (Sohn 1994; Benton 1995) but which are more often difficult to find out, strongly influence the results of diversity analysis. If the problem of synonymy is ignored, one taxon (e.g. a species, genus or family) may be counted for two or even more, suggesting a too large diversity; on the other hand, fossils that may represent different taxa may have been identified erroneously as identical, thus giving rise to an appar-

ently too small number of taxa, and thus to an unduly low diversity. It is interesting in this context that DNA analysis becomes increasingly applicable to the establishment of taxonomic relationships [not only for fossils from the Pleistocene (see, among others, Rohland *et al.* 2007) but also for fossils that date back from tens of millions of years (see, among others, Wible *et al.* 2007)], thus suggesting that a DNA-based taxonomy may become feasible, as has been predicted already several years ago (Van Loon 1999). This might eventually help solving problems like those of synonyms and homonyms. In some cases (e.g., in the case of planktonic foraminifers), however, genetic explorations demonstrated that the available taxonomic classifications require fundamental re-consideration, which makes it difficult to measure diversity (Kucera 2007). The problems with synonymy should, indeed, be solved precisely, although sometimes (especially when „old“ data are used) this cannot be realized due to a low quality of the initial information (e.g. the absence of the original fossil collections, of descriptions used for the taxonomic identification and/or classification, or of figures); it might in many cases even be better not to include such fossils in a paleodynamics-diversity study at all.

### An example of synonymy

A characteristic example of a problem raised by synonymy is the confusion about two widespread Late Paleozoic plant genera, namely *Walchia* and *Lebachia*. According to Meyen (1987), *Lebachia* and *Lebachiaceae* are invalid taxa, which should be replaced by *Walchia* and *Walchiaceae*; but he also states, remarkably enough, that these names may continue to be used “due to tradition”. This ‘taxonomic flexibility’ is even more remarkable if one realizes that Carboniferous species are commonly identified as *Lebachia*, whereas Permian remains with the same characteristics are commonly classified as *Walchia*. This ‘tradition’ is also followed in the Northern Caucasus: *Lebachia* species are found in the Pennsylvanian (Novik 1978), whereas *Walchia* has been described from Early Permian strata (Miklukho-Maklaj & Miklukho-Maklaj

1966). The ‘Late Pennsylvanian’ (i.e., Kasiomovian and Gzhelian stages) assemblage consists of 34 genera, whereas the Permian flora contains only *Walchia* (Ruban 2003). An ‘outsider’ might conclude that – after the disappearance of the entire ‘Late Pennsylvanian’ flora – a new genus appeared in the Permian. The actual situation is, however, a sudden degradation of the flora at the end of the Carboniferous, with only one genus surviving into the Permian. This implies that a calculation of the rate of diversity dynamics on the basis of the disappearance of *Walchia* and the appearance of *Lebachia* would yield an incorrect value. Unfortunately, the name *Lebachia* still is found in recent publications, sometimes being even ascribed to the typical Permian *Walchia*, among others by Davydov & Leven (2003) who attempted, although they are not paleobotanists, to present a comprehensive overview for all kinds of stratigraphers/paleontologists.

### An example of a problem raised by lack of correct data regarding distribution in time and space

Another significant problem is the frequent absence of clear indications regarding the exact position of taxa in time and space. For example, the presence of a particular taxon may be indicated for a specific study area, without exact data about the precise site or the age of the rocks in which the fossils under study were found; or the occurrence of a particular taxon may be indicated without information about its distribution in zones or even stages. It is, as a rule, highly questionable whether such data could be used, as diversity dynamics should be based on “stage-by-stage” or “zone-by-zone” data.

A comparable problem is encountered if regional correlations become almost impossible by the use of different names for the same formation in sites far apart, or if different chronostratigraphic frameworks are used for different regions. A problem that is in many respects similar, but much more severe is posed by the frequent revisions of the geological time scale under the supervision of the International Commission on Stratigraphy (ICS) of the Inter-



national Union of Geological Sciences (IUGS) (see, as an example, Gradstein *et al.* 2004). In a case of stage boundary re-definition, it may become uncertain whether the stage name has a former or present meaning.

### Possible solutions

The above problems for data compilation may be (though sometimes only partly) solved in four ways:

(1) by revising the original data, for instance by re-examining the fossil collections;

(2) by recalculating data „as is”, taking into consideration the possible impact of the insufficiently unambiguous data when interpreting the results of the fossil dynamics analysis (but it should be emphasized that such a recalculation almost inevitably reduces the scientific value of the analysis!); this type of recalculation of data was followed by, among others, Ruban (2005) in his discussion of paleontological data gathered in the middle of the 19<sup>th</sup> century;

(3) by adapting the objectives of the project, i.e. lowering the resolution of the analysis in time and/or space; as an example, the above-mentioned diversity of the Phanerozoic macrofloras from the Northern Caucasus was, as a result of such an adaptation, studied by estimating the number of taxa not per stage (as had been originally envisaged), but per series only (Ruban 2003); other examples have been provided by McGhee (1996);

(4) by using purposely developed numerical equations to predict or to minimize the errors linked to the compilation problems; these equations are similar to those used for evaluation of the preservation bias.

Which of the above approaches should be followed in order to obtain an optimum result, depends on the specifics of the initial data and of the project targets. Sometimes, however, the problems may be so large that the best solution may be to postpone the analysis until more and/or more reliable and unambiguous data become available. It is worthwhile mentioning in this context that the increasing number of electronic paleontological databases provides ever more data for a successful compilation

process. The commonly not very clear original source of data from electronic data bases – and this holds even more for data found on internet – can, however, pose a problem; in addition, the reliability of data from not precisely known sources that cannot be trusted on the basis of peer review is dubious. Compilation of data on the basis of not generally recognized electronic sources is therefore not advisable.

### Application of the compiled data

Even if data compilation has been successful and a range chart for the various taxa under study has been prepared, the application of the compiled data – for analysis of the fossil diversity dynamics – can meet severe problems. Some of these problems may be exemplified on the basis of a simple hypothetical chart with the stratigraphic distribution of 5 species (belonging to 2 genera) in the Triassic of an imaginary study area (Fig. 1). The data are complete, and, therefore, represent the actual situation. If the diversity dynamics (as defined on the basis of species) within the Early-Middle Triassic is to be analyzed, first the number of species present during each stage must be calculated. This is simple, but the calculating the diversity dynamics is less simple as will be shown here, because some new species appear for the first time, whereas other species become extinct.

To calculate the rate of the origination of new species in the lowermost part of the inves-

chronostratigraphy		Triassic				
		Early		Middle		Late
species		Induan	Olenekian	Anisian	Ladinian	Carnian
genus 1	A	■	■	■	■	■
	B		■	■	■	■
	C	■	■	■	■	■
genus 2	D		■	■	■	■
	E					■

Fig. 1. Example of hypothesized ranges of taxa in the Triassic (see text for explanation)

Fig. 1. Przykład hipotetycznych zakresów taksonów w triasie (objaśnienia w tekście)

tigated stratigraphic interval, it is necessary to know how many taxa, absent in the previous stage, are present in this one. Commonly (as in this hypothetical case: Fig. 1) no data on fossils from the underlying strata are available. This implies that it is impossible to calculate the origination rate for the Induan stage, because the origination rate is the ratio between the number of new taxa in a chronostratigraphic unit and the number of new taxa in the immediately older chronostratigraphic unit of the same rank. Moreover, as the rate of change cannot be determined for the Induan, it is not possible to compare this ratio with that of the Olenekian.

In the example of Figure 1, the species A, B, and C belong to genus 1, whereas species D and E belong to genus 2. Genus 2 is represented by species during the Early, Middle and Late Triassic, but in the Carnian the earlier present species (D) was replaced by a new one (E), not present earlier. Data analysis of the Early and Middle Triassic should, obviously, take into account species A, B, C, and D. Species E should, however, also be taken into consideration: a calculation of the generic diversity on the basis of the above-mentioned Early-Middle Triassic chart requires also an evaluation of the extinction rate for the last stage, i.e., for the Ladinian. It is therefore necessary to determine whether species that were present in the Early-Middle Triassic survived into the Late Triassic. In addition, it must be checked whether the other species belonging to genera 1 and 2 that did not exist earlier, appeared for the first time in the Carnian. Without such a check, conclusions about the extinction of genus 2 (as in this example) will be incorrect.

This example shows that even well-prepared data may be insufficient for a correct analysis, because lack of data from older and/or younger stages can induce errors. Before starting a quantitative diversity analysis, it is therefore necessary to look for such potential errors and to try to eliminate them.

## The Lazarus taxa problem

A specific problem is formed by the so-called Lazarus taxa. The geological record shows frequent interruptions in the chronostratigraphic

range of taxa. The re-appearance of a taxon after an interruption is called the Lazarus effect, and taxa showing such interruptions are known as Lazarus taxa. These terms became widely used after the studies by Flessa & Jablonski (1983) and Jablonski (1986). Although the Lazarus effect is linked by some workers to re-appearances after mass extinctions only, it is more logical to consider any re-appearance after interruption in the fossil record as a Lazarus effect (as suggested by Rickards & Wright 2002; and by Ruban & Tyszka 2005), even though the Lazarus effect seems, indeed, most commonly related to mass extinctions (Jablonski 1986, Fara 2001). Several questions related to the Lazarus effect and its influence on the calculation of fossil diversity have been discussed extensively (Flessa & Jablonski 1983; Jablonski 1986; Urbanek 1993, 1998; Senowbari-Daryan & Stanley 1998; Wignall & Benton 1999, 2000; Arz *et al.* 2000; Basov & Kuznetsova 2000; Fara & Benton 2000; Twitchett 2000; Fara 2001; Rickards & Wright 2002; Watkins 2002).

The temporal interruption of the stratigraphic range of a taxon may be due to one of the following causes:

- recurrence, i.e. the appearance of a morphologically similar taxon during evolution (this implies that the interruption is only apparent, as the original taxon is replaced by what is, in fact, another taxon);
- preservation of the taxon in refugia, for instance at times of a global environmental crisis (a widely accepted concept; see, among others, Fara 2001);
- an extreme decrease of the taxon's abundance during a mass extinction, so that the quantity of specimen became too low to trace them in the paleontological record (Wignall & Benton 1999); if the taxon was preserved in refugia, the case is identical to the previous one, but it is also possible that the taxon survived in numerous areas worldwide, but with few individuals;
- temporal disappearance of the taxon from the study area, for instance by migration to the adjacent areas;
- incompleteness of the paleontological record due to hiatuses as a result of non-deposition or erosion, a reduced preserva-

tion of fossils, or errors in sampling (see the review by Fara, 2001);

- taxonomic errors, i.e., incorrect identification of a taxon that appears after the interruption as the same taxon that was present before the interruption (such taxa are also referred to as Elvis taxa: Erwin 2006).

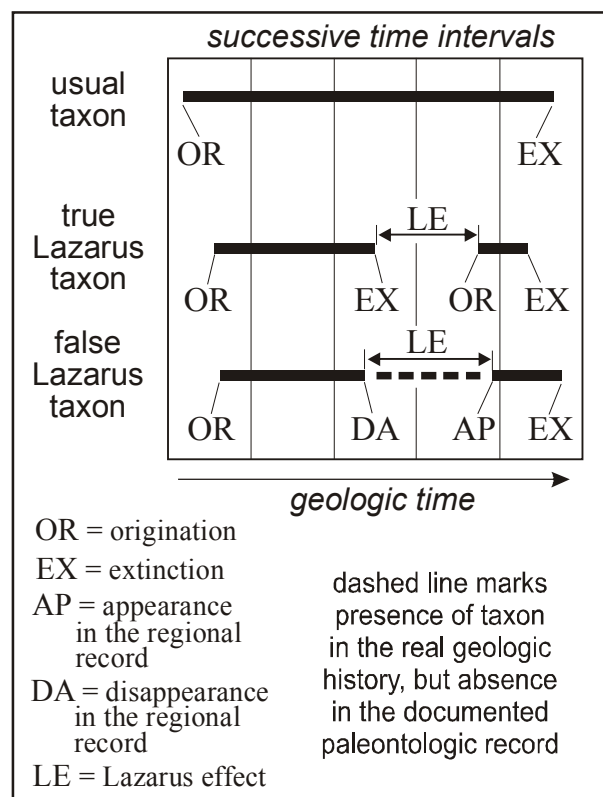
None of the above possibilities should be ignored, and pros and cons for each of these possibilities should be weighted in each particular case. Discussions on how to handle this are still going on (Wignall & Benton 1999, 2000; Rickards & Wright 2000; Twitchett 2000; Fara 2001). Ecological models explaining long survival of rare taxa (Yoshida 2002) support the concept of Wignall & Benton (1999). Meanwhile, refugia seem to play an important role, as suggested by paleoenvironmental studies of both of the geological past and the present (see, among others, Hladil 1994; Hladilova 2000; Riegl & Piller 2003). Possible other explanations for an apparent temporal interruption of the stratigraphic range of a taxon are a reduction in population size (resulting in less individuals that may be found in fossilized form) and a reduction in body size (resulting in less easily found fossil specimens) (Twitchett 2001).

### False Lazarus taxa

It is possible to divide the Lazarus taxa into two groups: true and false (Fig. 2). The true Lazarus taxa are those the evolution of which was really interrupted for a particular time interval. In contrast, a false Lazarus effect is obtained if the collected data are incomplete or if taxonomic errors are made while the taxon under study was actually present during all the time span during which its occurrence was only seemingly interrupted. Both survival in refugia and extreme decrease in number are essentially the same in this context: the studied taxa did not really disappear, only no fossil remnants have been found.

A fundamental problem with respect to Lazarus taxa is how to determine whether species or genera before and after the interruption are actually the same, which would imply a true Lazarus effect. If, however, a morphologically

similar taxon from before and after the interruption is erroneously considered as the same taxon, this is considered as a 'false Lazarus taxon', and the identification should simply be considered wrong. The fundamental paleontological problem in this context is on what basis species and genera should be distinguished from one another (see also Van Loon 1999; Kucera 2007). This question is closely related to another one: can convergence be so close that it becomes impossible to distinguish between different species (or genera) on the basis of morphology alone? This question is still under much debate, and an answer to this question is badly needed, if only to conclude how the Lazarus effect should be dealt with when determining the fossils' diversity. This is an important key to the systematic paleontology. Fortunately, it seems that application of genetic and other new approaches (such as microarchitectural analyses and investigations at even a molecular scale) may provide solutions for this key problem (see, e.g., Kucera 2007).



**Fig. 2.** True and false Lazarus taxa  
*Fig. 2. Prawdziwe i fałszywe taksony Łazarza*

Interruption of the stratigraphic range of a taxon increases the (apparent) extinction rate during the interruption interval and thus diminishes the (apparent) total fossil diversity. In contrast, the extinction rate during the next interval will be relatively low, because the 'extinct' taxon (re)appears (Fara 2001). A false Lazarus effect thus introduces a difference between the documented and the 'real' diversities, and therefore introduces erroneous values for the diversity dynamics. The fossil diversity and the diversity dynamics can therefore be estimated correctly only if the consequences of false Lazarus taxa are taken into account, and if the interruption of true Lazarus taxa is ignored. Dealing with a false Lazarus effect means that it is necessary to analyze the palaeobiodiversity during the stratigraphic range as if the occurrence of the pertinent taxon or taxa had not been interrupted.

All Lazarus taxa in the *global* geological record are, following the above-mentioned causes, false ones, except for the case of recurrence, but even in that case one has to consider the possibility that there is only strong morphological resemblance of two different taxa. It seems therefore that the influence of the Lazarus effect cannot be neglected when evaluating global paleobiodiversity. Fara & Benton (2000) and Fara (2001) have indicated how to handle this.

If paleodiversity dynamics are analysed for a relatively small *region*, more complications arise than if a continental or even global analysis is made. The reasons are that (1) the Lazarus effect occurs much more commonly at a small scale than at a large scale (but note that this is true almost exclusively when false Lazarus taxa are involved), and (2) it is more difficult to distinguish between Lazarus taxa that migrated for some time to come back later (for instance as a result of shifting environments due to climate fluctuations), and taxa that are not documented due to an incomplete sedimentary record.

It is, obviously, possible to recalculate the fossil diversity for the possible presence of taxa during the intervals corresponding to their temporal absence in the fossil record. Only the highest probable value (HPV) of the Lazarus effect, which suggests the maximum possible extent of the latter, is thus obtained (Ruban &

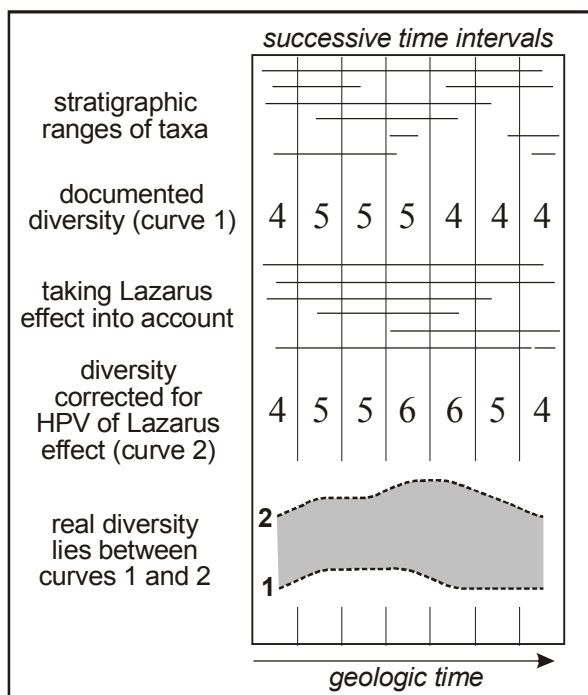


Fig. 3. Highest probable value (HPV) of the Lazarus effect and the estimation of regional fossil diversity.

Fig. 3. Najbardziej prawdopodobna wartość efektu Łazarza i oszacowanie regionalnego zróżnicowania skamieniałości

Tyszka 2005). In other words: the HPV represents the joint effect from both the true and the false Lazarus taxa. When an analysis of regional paleobiodiversity is made, the real diversity must be somewhere between the observed diversity curve and the curve corrected for the HPV (Fig. 3).

## Geochronological problems

A highly important aspect when preparing a quantitative analysis of fossil diversity dynamics is the choice of an appropriate geological time scale. The calculations must be carried out for specific chronostratigraphic units, but the 'translation' of lithostratigraphic units into chronostratigraphic units remains a great problem. Recently a great step forwards has been made because the International Commission on Stratigraphy (ICS) has provided an excellent framework for chronostratigraphy (Gradstein *et al.* 2004), so that - in principle - the same geological time table can be used worldwide. This

does not imply, however, that it has become easier to ascribe rock units to the correct chronostratigraphic unit. By far most datings of rock units are based on paleontological correlations, but if fossil diversity dynamics are investigated, it would be a vicious circle if the study would be based only on such paleontological data. Just like sedimentary facies shift in space with time, many fossils may show comparable diachronous occurrences. The first or last occurrence of a particular taxon at a certain place, where this occurrence coincides with a chronostratigraphically defined boundary, may therefore have a different age elsewhere in the world. Obviously, areas that are situated far from one another commonly are correlated through a number of intermediate correlations; the resulting inaccuracy of the correlation may be significant (Van Couvering 2000).

An entirely different problem is posed by the fact that the various chronostratigraphic units of one rank (e.g., stages) do not have an equally long duration. A stage that lasts twice as long as the previous one, has, obviously, a great chance to contain more species (and higher-order taxa) than its predecessor. It would be unjustified, however, to deduce that the longer stage is characterized by a higher biodiversity: at any given moment the biodiversity in both stages may be the same (within some band width), but the biodiversity in the longer-lasting stage may, at any given moment, also even be lower than the diversity at any given moment in the shorter stage! Biodiversity and the rate of fossil diversity dynamics should therefore preferably be determined for successive time-spans of approximately equal duration (Van Couvering 2000).

Such an approach may in practice turn out (almost) impossible with our present-day knowledge of correlations. Most areas are still described following a local or regional lithostratigraphic subdivision, and the duration of the time-span during which they were formed can often be estimated only roughly; in many cases attribution to an 'official' chronostratigraphic units is not even certain. This problem has to be solved, however, before reliable diversity dynamics can be determined. This implies (1) that the use of so-called "regional

stages", representing a regional time scale, should be avoided whenever possible, and (2) that, more than was done previously, attention should be paid to defining the boundaries between chronostratigraphic units, so that at least a reasonable correlation is established with the recent ICS „International Stratigraphic Chart“ (the most recent version is to be found at <http://www.stratigraphy.org>). Obviously, the decisions and recommendations of the ICS and its subcommissions should be followed. The presentation of data according to the International Stratigraphic Chart is, however, not yet always the case in a few countries (one of them being Russia), which should be regretted deeply as the use of any diverging stratigraphy prevents precise global paleodynamics analyses (or at least makes them more difficult and less reliable).

## Geochronology vs. dating

The term 'geochronology' is often considered as a synonym of 'dating' (particularly radiometric dating) or another kind of absolute time estimation, but this is based on misunderstanding (Walsh 2001). It seems, at first sight, that several of the problems sketched above would be solved if all stratigraphic observations were complemented with data about their absolute ages. It is true that some types of fossils evolved so rapidly that they can be considered to represent (geologically) very short time intervals. This is, for instance, the case with Late Carboniferous fusulinids. Only few of such 'time-specific' taxa have been dated precisely, however, by radiometric or other means, but this does not imply that well-dated taxa can always be used as chronostratigraphic markers. Imagine that a marine succession is interrupted by two levels of volcanic ashes that can be dated precisely, and which differ 1,000 years in age. If a species is present in the entire interval between the two ash layers, but neither underneath the lower ash layer, nor above the upper one, this does not imply that the species can be used as a precise time marker: it may well be that the conditions between the deposition of the two ash layers were so different from before

and after that the species found a good habitat in the region during the 1,000 'inter-ashes' years, but neither before nor afterwards. Elsewhere, however, the species may have occurred earlier or later. Using the well-dated time range once found for a particular taxon for all subsequent finds, is therefore in most cases without any doubt incorrect.

In addition, radiometric dating is not so absolute as sometimes believed. Much effort has been put by the ICS in establishing absolute ages for the boundaries between chronostratigraphic units (see the 'golden spikes' in the International Stratigraphic Chart), but new absolute ages for the various Devonian stages (Kaufmann 2006) were presented less than two years after the publication of the International Stratigraphic Chart of Gradstein *et al.* (2004). This is not amazing, as dating techniques become ever more refined, as expressed already much earlier by the successive editions of the Elsevier Geological Time Table [compare, for instance, the 4<sup>th</sup> edition (Haq & Van Eysinga 1987) with the recently published 6<sup>th</sup> edition (Haq, 2007)], where boundaries were changed sometimes for tens of millions of years. A comparison of the datings for the boundaries within the Mesozoic between the current International Stratigraphic Chart (ICS, 2006) and the 1999 GSA Geologic Time Scale (Palmer & Geissman, 1999) also shows that boundaries shifted in age sometimes more than the time-span of a stage. This means that the inaccuracies in absolute dating are sometimes larger than the duration of the chronological units themselves; it seems that such large changes do not – and will not – occur frequently anymore, but it should be a warning that adaptations of radiometric datings still take place. An example is the boundary (which is most important from a paleodynamics point of view because it is based on the largest mass extinction in the Earth history) between the Permian and the Triassic, which is indicated on the International Stratigraphic Chart (ICS, 2006) as 251.0 ( $\pm$  0.1) Ma, but which has, shortly after the publication of the 2004 ICS, been found to be 252.6 Ma ( $\pm$  0.2) (Mundi *et al.* 2004).

Similar conclusions have been drawn for other types of 'absolute datings'. There is, for instance, a gap of several hundreds of years between the

varve countings and the C-14 datings for Late Pleistocene and early Holocene glaciolimnic deposits in Scandinavia (e.g. Schove 1977) and for comparable datings elsewhere (e.g. Grayson & Plater 2007). And the necessity to use several types of C-14 dating, is proof in itself that this method has to deal with numerous 'internal' problems (cf. Buck & Bard 2007).

## Influence of changing astronomical parameters

Of academic interest only is the fact that paleodiversity dynamics is commonly calculated on the basis of diversity changes that occur in intervals of (usually) millions of years. These 'years' are, however, years with present-day length:  $\sim$  365 days of 24 hours each. One should realize, however, that these parameters have changed in the course of the geological history. It has been calculated that in the Ediacaran (the end of the Neoproterozoic) a year lasted 444 days and 20.4 hours (Nesterov 1999) with the result that, for instance, the 88 million years that are attributed to the Ediacaran (according to the recent International Stratigraphic Chart it lasted from  $\sim$  630 to 542 million years ago) lasted only 72 million years according to the astronomical years of the Ediacaran itself. As it is apparent that many organisms reproduce on the basis of yearly cycles, and that the rate of evolution depends (partly) on the velocity of reproduction (one of the reasons why *Drosophila melanogaster* is such a good 'guinea pig' for genetic research), it is obvious that the outcome of paleodiversity-dynamics analyses for Ediacaran (and other old) time intervals will give unduly low values. The change in the duration of a year had been deduced already much earlier, for instance for the Devonian (Wells 1963; Scrutton 1965). More recently, it has been concluded from the frequency modulation analysis of cyclic sedimentary successions that a Jurassic year had a duration intermediate between a Devonian and a recent one (Hinnov & Park 1998), and this confirms that a year on Earth has gradually become shorter. The gradual decrease in the number of days per year was

probably compensated – at least in part – by lengthening of the days. This lengthening may, indeed, have had an adverse influence on the reproduction velocity and thus on the value of paleodiversity dynamics, but the net result is still far from clear. It is certain, however, that evolution goes faster with geological time; it even seems likely that more new species are formed per unit of time now than ever before, and probably even at a higher rate than species becoming extinct (Van Loon 2003). In contrast, the paleodiversity dynamics must have been low in the Proterozoic (lack of sexual reproduction will certainly have played a role during this era, but this cannot explain the acceleration of evolution during the Phanerozoic). The reason for the apparently ongoing acceleration of evolution is not well understood, but it means in fact that equal values of paleodiversity dynamics calculated for two time units indicate that the rate of change in the younger unit is *relatively* lower than that in the older unit.

### Types of units for which the paleodiversity dynamics can be analysed

Paleodiversity dynamics can be determined for five types of units:

- non-diachronous lithostratigraphic units (results will be enforced by paleoenvironmental specifics);
- stages or epochs (results will be influenced by the uncertainties regarding the current chronostratigraphy);
- biozones (appropriate for particular fossil groups only);
- beds (appropriate only for the analysis of a given section; this is a common procedure particularly for microfossils);
- millions of years (not truly meaningful for fossils; moreover, fossils can rarely be dated within geologically restricted time boundaries).

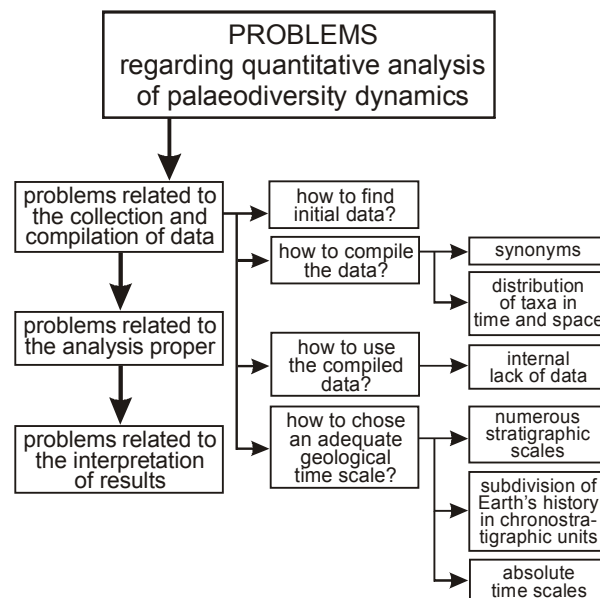
It seems to us that events that affected biodiversity significantly, such as mass extinctions and sudden faunal explosions, can be used to establish time units that comprise the same

number of biodiversity-affecting events (this extends the purpose of event stratigraphy as explained, particularly, by Walliser (1996) and Brett & Baird (1997). A possible alternative ecological approach in this context has been introduced by McGhee *et al.* (2004).

### Conclusions

The above-mentioned problems concerning the quantitative analysis of paleodiversity dynamics (for both animals and plants) are presented in Fig. 4. All problems can commonly be solved, though often only in a time-consuming way. It is not uncommon, however, that the problems can be overcome only partly, because of insufficient, ambiguous and/or insufficiently accurate data. In some cases the lack or inaccuracy of information may be even so significant that a detailed paleodiversity-dynamics analysis is not worthwhile; in other cases the problems can be minimized or taken care of in one way or another.

Fortunately, ongoing work in this field, supported by large electronic databases (e.g. NMITA, PaleoTax, The Paleobiology Database,



**Fig. 4.** Schematic overview of the problems related to the quantitative analysis of changes in paleobiodiversity

*Fig. 4. Schematyczne podsumowanie problemów związanych z ilościową analizą zmian w paleo-bioróżnorodności*

MIOMAP, FAUNMAP, Global Pollen Database, NOW, etc.) (Benton 1995; Budd *et al.* 2001; Alroy 2003; Löser 2004; Foote 2007), may help to diminish possible errors in the diversity estimates. Each analysis of paleodiversity dynamics or of phenomena related to the consequences of mass extinctions should, however, (1) try to quantify the impact that missing data or inaccuracies of any kind may have on the final results, and (2) try to find a solution for the major problems, so as to avoid significant inaccuracies of the calculated values.

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## Bryozoan diversity in Southern Siberia at the Devonian–Carboniferous transition: New data confirm a resistivity to two mass extinctions

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### ABSTRACT

Two spectacular mass extinctions, namely the Kellwasser and the Hangenberg events, affected the Earth's biota during the Late Devonian–Early Carboniferous. Diverse assemblages of bryozoans are known from the Fasnian–Tournaisian deposits of Southern Siberia, which includes such regions as the Kuznetsk Basin, the Kolyvan'–Tom' Zone, the Rudny Altay, and the Gorny Altay. Our new data establish the stratigraphic ranges of 154 species, which belong to 56 genera and 21 families. These data have been analyzed quantitatively to measure the patterns of diversity dynamics and the changes in the taxonomic diversity structure. The species diversity increased at the Frasnian–Famennian transition. After a short-term, but dramatic decrease in the middle Famennian, the total number of species accelerated in the late Famennian and the Tournaisian. A similar pattern occurred for both genera and families, although the radiation at the Frasnian–Famennian transition was not as large, and total family diversity decreased slightly in the Tournaisian. Changes in total species diversity differed between orders of bryozoans. Changes in taxonomic diversity structure were moderately rapid. The Tournaisian species diversity was governed by the other genera comparing to the early time intervals. Thus, our regional data suggest that bryozoans generally survived both the Frasnian/Famennian and the Devonian/Carboniferous mass extinctions, confirming similar conclusions made earlier with global data. However, a mid-Famennian regional crisis (diversity drop) in the evolution of bryozoans is documented within Southern Siberia. Bryozoan radiations coincided with pulses of basin deepening that occurred during both mass extinction intervals, perhaps explaining why bryozoans were resistant to extinction. The mid-Famennian crisis might have been caused by a rapid regression coupled with basin shallowing.

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### 1. Introduction

The marine biota was very diverse during the Devonian (Sepkoski, 1993; Benton, 2001; Newman, 2001; Peters and Foote, 2001). However, the end of this period was marked by two catastrophes that devastated the Earth's life, namely the Frasnian/Famennian (F/F) and the Devonian/Carboniferous (D/C) mass extinctions often referred as the Kellwasser and the Hangenberg events, respectively. Using the present absolute chronology for the Devonian (Gradstein et al., 2004; Kaufmann, 2006; Menning et al., 2006), the D/C mass extinction persisted for approximately 16 Ma after the conclusion of the F/F mass extinction. A number of possible triggers for these extinctions have been proposed. It is not possible, currently, to determine which, if any, is the likely cause of the extinctions (see review by Racki, 2005). These

events might have been linked with major eustatic changes, marine anoxia, global cooling, intense volcanism, and probable impacts (Copper, 1986; Buggisch, 1991; Copper, 1994; Algeo et al., 1995; McGhee, 1996; Hallam and Wignall, 1997; Algeo and Scheckler, 1998; Hallam and Wignall, 1999; Caplan and Bustin, 1999; Racki, 1999; McGhee, 2001; Copper, 2002; Gong et al., 2002; House, 2002; Godderis and Joachimski, 2004; Racki, 2005; McGhee, 2005; Girard and Renaud, 2007).

Were any groups of organisms resistant to inferred environmental perturbations at the end of the Devonian? It appears that the answer is yes. Hallam and Wignall (1997) and later Webster et al. (1998) discussed the effect of the F/F and D/C mass extinctions on the planetary biota and found that bryozoans were not stressed severely by these events. Horowitz and Pachut (1993) and then Horowitz et al. (1996) reported a significant crisis among bryozoans in the mid-Devonian, while the F/F event failed to produce dramatic reductions in diversity. This is confirmed by Horowitz and Pachut (2000), whose data also suggest against any major diversity decline after the D/C event. We are still far from a complete understanding of the causes and selectivity of mass extinctions (Jablonski, 2004). However, an

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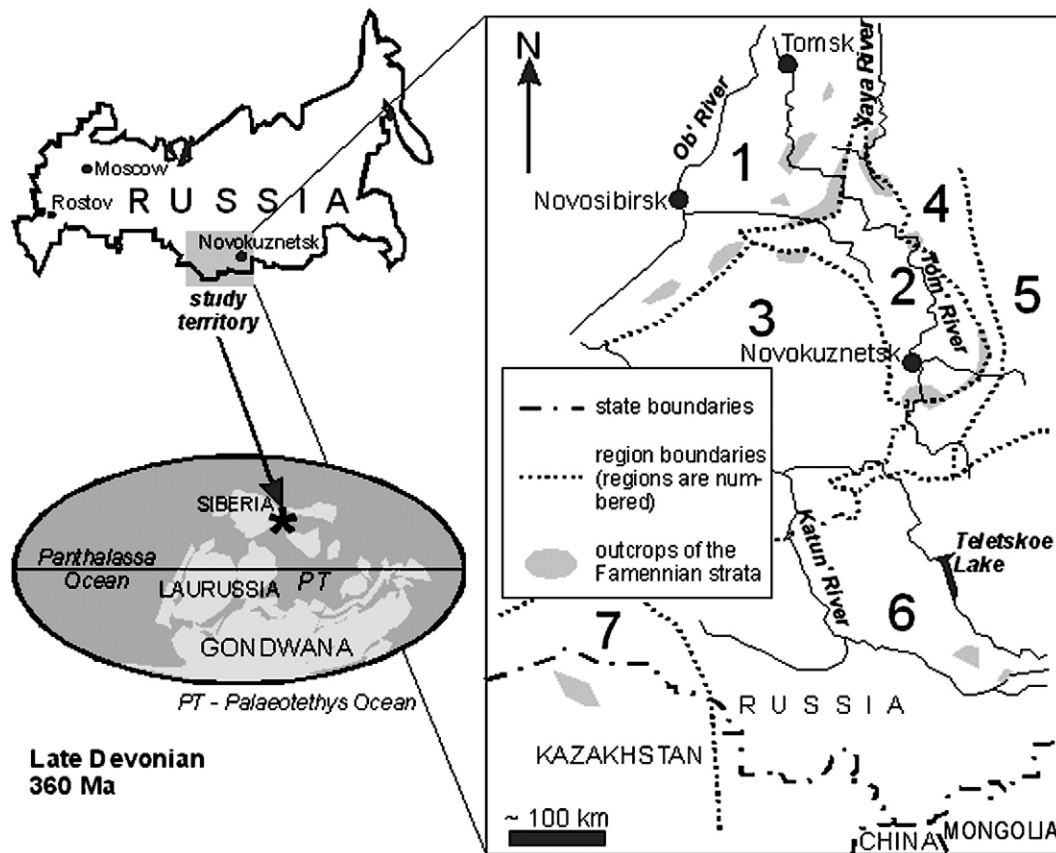


Fig. 1. Geographical and palaeotectonic location of the study territory. Global palaeotectonic map is simplified after Scotese (2004). Numbered regions: 1 – Tom'–Kolyvan' Zone, 2 – Kuznetsk Basin, 3 – Salair, 4 – Kuznetsk Alatau, 5 – Minusa Depression, 6 – Gorny Altay, 7 – Rudny Altay.

evaluation of the evolutionary dynamics of bryozoans from the Late Devonian–Early Carboniferous might be informative. Data are now available from Southern Siberia (Tolokonnikova, 2007) to attempt such a study. This region lies within the core of the present-day Eurasia (Fig. 1). Data include the stratigraphic ranges of 154 species, 56 genera, and 21 families of bryozoans from upper Frasnian, Famennian, and lower Tournaisian strata, making Southern Siberia a very important region to evaluate bryozoan diversity at the Devonian–Carboniferous transition and to discuss the effects of mass extinction on them.

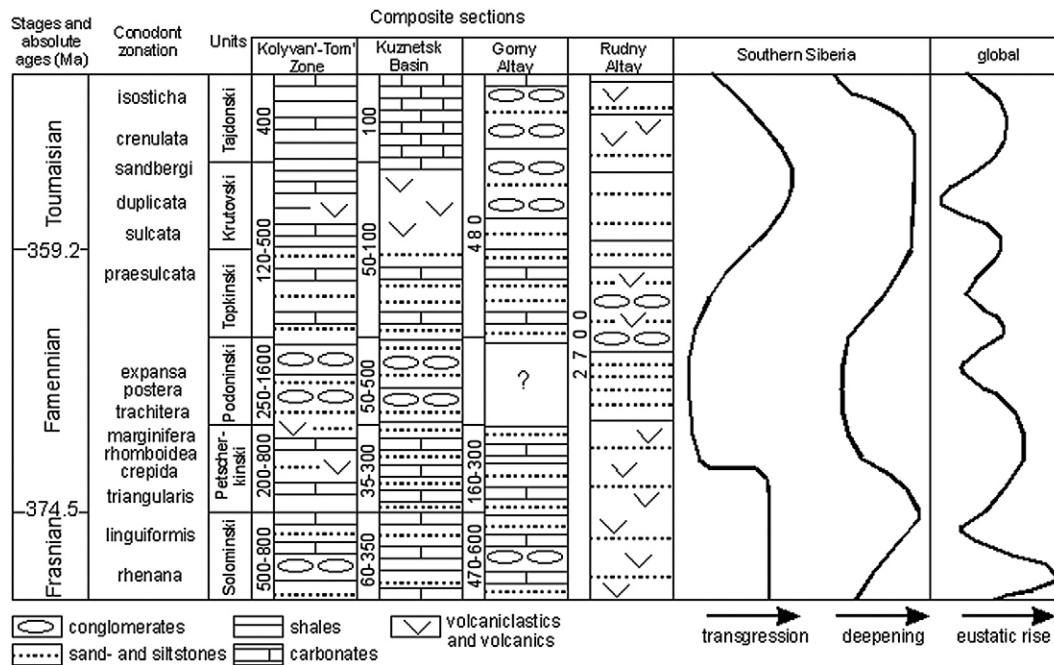
## 2. Geological setting

The study territory, generally referred as Southern Siberia, includes the Kuznetsk Basin (also called as the Kuzbass), the Kolyvan'–Tom' Zone, the Rudny Altay (the Ore Altay), and the Gorny Altay (the Mountaneous Altay) (Fig. 1). Using present global reconstructions for the Late Devonian and Early Carboniferous (Torsvik and Cocks, 2004; Scotese, 2004) and few regional palaeotectonical constraints (Yakubchuk, 2004; Cocks and Torsvik, 2007), it appears that these regions were attached to the margin of the Siberian Plate or were individual terranes (Fig. 1). The growth of present-day Southern Siberia appears to have been a stepwise process that occurred during the entire Paleozoic and even the Early Mesozoic.

Frasnian, Famennian, and Tournaisian deposits occur in many areas of Southern Siberia (Fig. 1). Their lithostratigraphic framework was established by Krasnov (1982) and was updated by Tolokonnikova (2007). These strata are subdivided into a number of horizons, based on chronostratigraphy and conodont zonation (Gutak and Rodygin, 2004; Tolokonnikova, 2007) (Fig. 2). Because the meaning of the term *horizon*, as it is used in international stratigraphic nomenclature (Salvador, 1994), differs from typical usage, we use the term *unit*. The

lowest of the units considered in our study is the Solominski Unit (upper Frasnian), that includes limestones and clastics with a total thickness of up to 800 m. They are overlain by the limestones, clastics, and in places, by volcanoclastics of the Petscherkinski Unit (lower Famennian) with a total thickness up to 800 m. The Podoninski Unit (middle Famennian) consists of red-colored clastic deposits, with occasional limestones and volcanoclastics, with a total thickness exceeding 1600 m (Fig. 2). The Topkinski Unit (upper Famennian) includes clastics and limestones that may reach a maximum total thickness of 500 m. The Krutovski Unit (lower Tournaisian) is dominated by volcanics and volcanoclastics with a total thickness of about 100–1500 m. The uppermost Tajdonski Unit (lower Tournaisian) is represented by limestones and clastics that have a total thickness of approximately 1100 m.

Palaeoenvironmental reconstructions (Bel'skaja, 1960; Gutak and Antonova, 2006a,b; Gutak and Ruban, 2007; Tolokonnikova, 2007) for the Late Devonian–earliest Carboniferous indicate that Southern Siberia was embraced by a large marine basin. The Kolyvan'–Tom' Zone represents the deepest facies deposited in that basin. The Kuznetsk Basin was occupied by extensive, relatively shallow-water, shelf environments. The Gorny Altay lay on a margin of this basin and, together with the Rudny Altay, was a center of regional volcanic activity. The regional Frasnian–Tournaisian transgression–regression (T–R) curve of Southern Siberia was reconstructed from lateral facies analysis, whereas the deepening–shallowing (D–S) curve was developed from analyzing facies stratigraphically. These were derived from Gutak and Ruban (2007). Our T–R curve differs from that proposed earlier by Karaulov and Gretschnikova (1997) and Yolkin et al. (1997) in the positioning of the D/C boundary and in proposing an alternative interpretation of facies (Gutak and Antonova, 2006a,b; Gutak and Ruban, 2007; Tolokonnikova, 2007). T–R and D–S patterns should always be distinguished (Catuneanu, 2006; Ruban, 2007a).



**Fig. 2.** The Frasnian–Tournaisian composite sections of the studied regions. Chronostratigraphy after Gradstein et al. (2004). Thickness (m) is indicated from the left side of each column. Regional transgressive–regressive and deepening–shallowing patterns are modified after Gutak and Ruban \*2007) and the global eustatic changes are given after Haq and Al-Qahtani (2005).

Transgressions and regressions reflect the shifting position of shorelines, whereas deepening and shallowing mark the changes in the depth of the basin. In Southern Siberia, the shoreline was stable during the Frasnian, and the F/F boundary is marked by a prominent, but short-term, deepening pulse (Fig. 2). A wide and abrupt regression and shallowing occurred in the early–middle Famennian. Marine deposits of this age have a very limited extent, whereas non-marine red-colored clastic deposits are known widely within the study region (Fig. 2). Both transgression and deepening occurred after the late Famennian reaching maximums in the Tournaisian when carbonates, often cherty, dominated regional deposition (Fig. 2). These regional patterns did not correspond well to the global eustatic fluctuations recorded recently by Haq and Al-Qahtani (2005). It appears to be nearly impossible to recognize the action of any planetary-scale events corresponding to their sea-level curve (Fig. 2).

### 3. Materials and methods

This study is based on data on the Frasnian–Tournaisian bryozoans collected in Southern Siberia by Tolokonnikova (2007). Data from a number of earlier studies (Nekhoroshev, 1926a,b; Krasnopeeva, 1935; Nekhoroshev, 1956; Trizna, 1958; Morozova, 1961; Volkova, 1974; Morozova, 2001) have also been reexamined including the distribution of each taxon (Solominski, Petscherkinski, Podoninski, Topkinski, and Tajdonski units; Supplementary Materials 1). No bryozoans have been found in the Krutovski Unit. The suprageneric taxonomy of the bryozoans examined in this study is presented in Supplementary Materials 2.

For species, genera, and families, we have examined changes in total diversity, number of appearances, and number of disappearances. The absence of bryozoans in the volcanics of the Krutovski Unit is expected (Tolokonnikova, 2007). Thus, to calculate the true number of appearances in the Tajdonski Unit and the number of disappearances for the Topkinski Unit, we have ignored the Krutovski Unit and compared the assemblages directly.

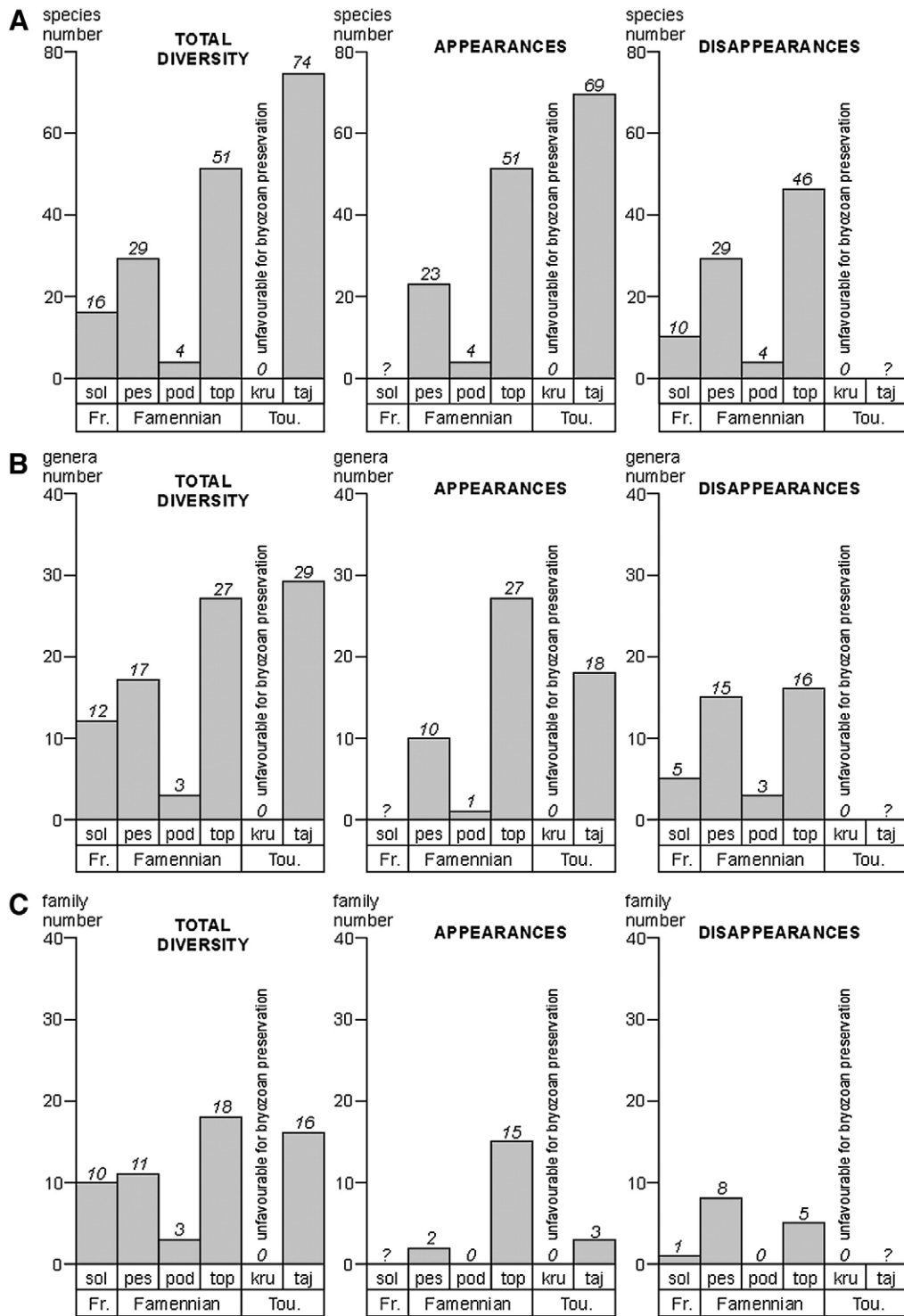
Regional evolutionary changes among bryozoans were measured using the Rst index. This index, and its interpretation, were presented by Ruban and Tyszka (2005), and Ruban (2007b). Rst is a coefficient of the Spearman's rank correlation (Kendall, 1970) between two

assemblages, where the presence of a taxon of higher taxonomic rank is indicated by the number of taxa of lower rank, which belong to that higher-ranked taxon in the particular time unit.  $1/Rst$  or  $1-Rst$  shows, how rapid were the changes in the control of the lower-ranked taxa diversity by the higher-ranked taxa. In other words, Rst indicates the changes in the structure of taxonomic diversity. It is intriguing to calculate Rst not only for the successive assemblages, but also for those, existing in different times. In this paper, we have calculated three Rst indices, namely the Genera-species Rst, the Families-genera Rst, and the Families-species Rst. This permits an evaluation of three patterns of regional change in the taxonomic diversity structure of bryozoans and provides a detailed picture of transformations across both the F/F and D/C mass extinctions.

### 4. Diversity dynamics

In total, 154 species of bryozoans are known from the upper Frasnian, the Famennian, and the lower Tournaisian strata of Southern Siberia. They belong to 56 genera, 21 families, and 6 orders. The most diverse were the orders Trepostomida (8 families, 22 genera, 53 species), Fenestellida (4 families, 16 genera, 54 species), and Rhabdomesida (4 families, 11 genera, 28 species). The Order Cystoporida was characterized by moderate diversity (3 families, 5 genera, 16 species), whereas the diversity of orders Cryptostomida (1 family, 1 genus, 2 species) and Tubuliporida (1 family, 1 genus, 1 species) was very low.

Species diversity nearly doubled at the Frasnian–Famennian (F–F) transition (increased 1.8 times; Fig. 3A) then decreased abruptly. In the late Famennian, bryozoans diversified again and the total number of species continued to rise into the early Tournaisian. Generic diversity rose slightly at the F–F transition (Fig. 3B) followed by an abrupt decline. The total number of genera was high in the late Famennian. A slight increase of 2 genera occurred in the early Tournaisian. It is intriguing that the number of generic appearances dropped dramatically in the early Tournaisian. Two new families appeared at the Frasnian–Famennian transition (Fig. 3C). After an abrupt drop in the mid-Famennian, the total number of families rose again in the late Famennian. A decrease of 2 families occurred at the Famennian–



**Fig. 3.** Species (A), genera (B) and family (C) diversity dynamics of the Frasnian–Tournaisian bryozoans of Southern Siberia. To calculate the numbers of appearances and disappearances the Topkinski Unit and the Tajdonski Unit are compared directly. Abbreviations: Fr. – Frasnian Stage, Tou. – Tournaisian Stage, sol – Solominski Unit, pes – Petscherkinski Unit, pod – Podoninski Unit, top – Topkinski Unit, kru – Krutovski Unit, taj – Tajdonski Unit.

Tournaisian transition (F–T). A comparison of total diversity changes documented at three taxonomic levels suggests differences especially at the F–F and F–T transitions. While species diversity rose significantly at the F–F transition (Fig. 3A), generic and familial diversity increased only slightly (Fig. 3B,C). At the F–T transition, the total numbers of species and genera increased (Fig. 3A,B), whereas the number of families declined slightly (Fig. 3C).

There is no direct evidence supporting either the F–F or the D–C mass extinctions among bryozoans in the regional record of Southern Siberia.

There was no major diversity decline at the F–T transition, confirming the conclusions of Horowitz et al. (1996), Hallam and Wignall (1997), and Webster et al. (1998). Updated data on global bryozoan diversity (Horowitz and Pachut, 2000) imply an existence 195 Frasnian species, 153 Famennian species, and 405 Tournaisian species. Thus, the total species diversity declined after the F–F event just in 1.3 times. This is too low in comparison with the Givetian–Frasnian transition, when the total diversity decreased in 3.2 times (Horowitz and Pachut, 2000). As for the D–

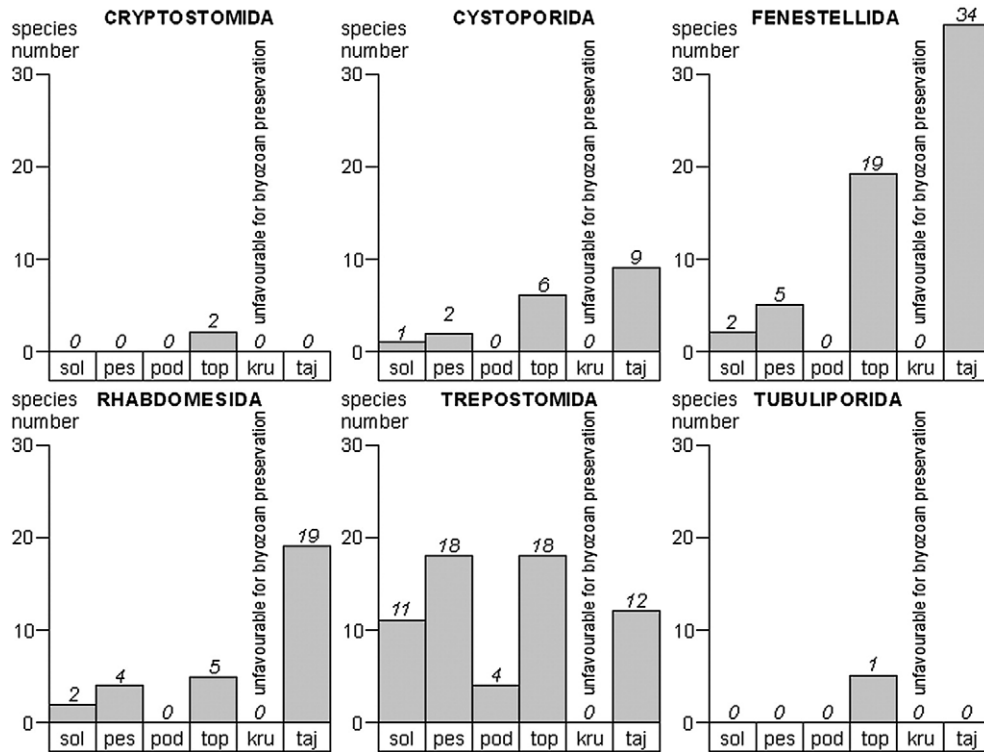


Fig. 4. Changes in the total species diversity among six orders of the Frasnian–Tournaisian bryozoans of Southern Siberia. Abbreviations – see Fig. 3.

C mass extinction, it did not affect either global or regional species diversity at all. On a global scale, the total diversity increased in 2.6 times (Horowitz and Pachut, 2000). The similar acceleration is documented in Southern Siberia.

As potential, but “minor” effect of the F–F and D–C mass extinctions the rate of disappearance of species, genera, and families at the beginning and end of the Famennian increased (Fig. 3A–C). Additionally, the number of appearances of genera and families decreased in the early Tournaisian (Fig. 3B,C). A unique crisis, documented regionally within the studied stratigraphic interval, occurred in the mid-Famennian (the Podoninski Unit) when a short-term but abrupt diversity decline occurred. However, in spite of their low diversity bryozoans are quite abundant in the Podoninski Unit.

The species diversity dynamics of the Cystoporida, Fenestellida, and Rhabdomesida were similar (Fig. 4), with diversity rising throughout the late Frasnian–early Tournaisian. In contrast, the species-level diversity dynamics of the Trepostomida was quite different (Fig. 4). Total species diversity was similar in the early and late Famennian, but declined rapidly in the early Tournaisian. Surprisingly, the Trepostomida was unique in surviving at the time of the mid-Famennian crisis. Both Cryptostomida and Tubuliporida radiated in the late Famennian, but they did not survive into the Carboniferous (Fig. 4). Thus, no orders were removed by the F/F mass extinction, whereas the D/C mass extinction might have been responsible for the disappearance of Cryptostomida and Tubuliporida and the decline

of the Trepostomida. A comparison of species diversity (Fig. 3A) with that of orders (Fig. 4) suggests that the decline of Trepostomida did not affect the stepwise increase in bryozoan diversity.

### 5. Changes in taxonomic diversity structure

Changes in the taxonomic diversity structure of the Frasnian–Tournaisian bryozoans of Southern Siberia are presented in Tables 1–3. The Genera-species Rst suggests relatively slow changes across the F–F transition, whereas the changes that followed were much more rapid (Table 1). This suggests that control of species diversity shifted to new genera in each successive time unit. Rst for the F–T transition also increased. A comparison of the non-successive assemblages suggests 3 important conclusions:

- (1) genera responsible for species diversity in the late Frasnian, continued to control species diversity in the late Famennian (Rst for the Solominski and the Topkinski units is as high as 0.24);
- (2) no remarkable changes in the taxonomic diversity structure occurred in the mid-Famennian based on an Rst for the Petscherkinski and Topkinski units of 0.48;
- (3) changes in species diversity occurred in the Tajdonski Unit at the Devonian–Carboniferous transition that was controlled by genera other than those that were responsible for species diversity at earlier times.

Table 1  
Genera-species Rst for the Frasnian–Tournaisian bryozoans of Southern Siberia

	sol	pes	pod	top	taj
sol	1.00	0.54	–0.01	0.24	–0.15
pes		1.00	0.04	0.48	–0.01
pod			1.00	–0.15	–0.12
top				1.00	0.27
taj					1.00

Abbreviations – see Fig. 4

Table 2  
Families-genera Rst for the Frasnian–Tournaisian bryozoans of Southern Siberia

	sol	pes	pod	top	taj
sol	1.00	0.81	0.47	0.39	0.22
pes		1.00	0.48	0.37	0.47
pod			1.00	0.15	–0.20
top				1.00	0.65
taj					1.00

Abbreviations – see Fig. 4

**Table 3**  
Families-species Rst for the Frasnian–Tournaisian bryozoans of Southern Siberia

	sol	pes	pod	top	taj
sol	1.00	0.82	0.43	0.13	−0.11
pes		1.00	0.11	0.51	0.29
pod			1.00	−0.13	−0.21
top				1.00	0.68
taj					1.00

Abbreviations – see Fig. 4

The Families–genera Rst indicates some additional peculiarities (Table 2). Changes in diversity structure were minor at the F–F and the F–T transitions but were higher during the middle- and late Famennian. Rst values between the non-successive assemblages were also high, suggesting gradual changes in family control of generic diversity. Similar patterns occur in the Families–species Rst (Table 3). An exception is relatively high Rst calculated for the Petscherkinski and Tajdonski units.

Changes in diversity structure of late-Frasnian–early Tournaisian bryozoans of Southern Siberia suggest moderately rapid evolution. A number of higher-ranked taxa, that controlled the diversity of lower-ranked taxa in the late Frasnian and/or early Famennian, were similarly important in late Famennian and/or early Tournaisian assemblages. No catastrophic patterns are documented, except those established at the Devonian–Carboniferous transition reflected by the magnitude of the Genera–species Rst. Thus, only the effect of the D/C mass extinction can be recognized in the regional record of bryozoans although this effect was weak.

## 6. Discussion

Transgressions/regressions and deepenings/shallowings might have been important factors, influencing regional diversity changes among bryozoans. A comparison of the reconstructed T–R and D–S curves (Fig. 2) with changes in the total species diversity of bryozoans (Fig. 3A) suggests a better correlation with the regional D–S pattern. Diversity rose as basin depth increased at the F/F boundary. Similarly, late Famennian–middle Tournaisian deepening coincided with rapid bryozoan diversification. In contrast, it appears that bryozoans were able to radiate at times of both a weak regression (early Famennian) and strong transgression (late Famennian–early Tournaisian). Regression and shallowing in the mid-Famennian coincided with a remarkable crisis (diversity drop) among bryozoans.

Racki (2005) suggested that a controversy existed in the interpretation of global sea-level changes across the F–F transition. Hallam and Wignall (1997, 1999) had suggested a eustatic rise, that was later confirmed by Haq and Al-Qahtani (2005). The end-Devonian experienced a global sea-level fall according to Hallam and Wignall (1997, 1999) and Racki (2005), while Haq and Al-Qahtani (2005) suggested the opposite (i.e., an eustatic peak, although preceded by a “minor” fall) (Fig. 2). If bryozoans really diversified as deepening occurred as suggested from Southern Siberia, the global eustatic rises documented by Haq and Al-Qahtani (2005) may explain why this group was little affected by the F/F and D/C mass extinctions on a global scale.

## 7. Conclusions

The Frasnian–Tournaisian bryozoans were diverse in Southern Siberia. Our calculations suggest that both the F/F and D/C mass extinctions did not affect diversity dynamics. Species-, genus-, and family-level diversity did not decline, and no large changes in the taxonomic diversity structure were observed, except for few minor exceptions. Thus, the resistivity of bryozoans to the Late Devonian environmental crises (or the selectivity of the event) is confirmed for a representative regional record from Southern Siberia. Currently, it

appears that regional changes in basin depth might have affected bryozoan diversity, causing it to increase as deepening occurred. An enigmatic mid-Famennian crisis might have been caused by rapid regression and basin shallowing. One question awaiting further investigation is whether the mid-Famennian crisis was regional or global in scale. The global data (Horowitz and Pachut, 2000) indicate just a slight general diversity decline in the Famennian. A diversity drop in the middle of this age might contribute to such a decline. To understand why bryozoans survived both the F/F and D/C extinctions on a global scale depends strongly on the causes of the catastrophes. If diversity increased, at least in part, thanks to the eustatic rises, a preference for deeper basins by bryozoans might adequately explain their survival. This is another subject for further investigations.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2008.04.009.

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# How global are the Jurassic–Cretaceous unconformities?

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## ABSTRACT

The reality of the global-scale sedimentation breaks remains controversial. A compilation of data on the Jurassic–Cretaceous unconformities in a number of regions with different tectonic settings and character of sedimentation, where new or updated stratigraphic frameworks are established, permits their correlation. Unconformities from three large reference regions, including North America, the Gulf of Mexico, and Western Europe, were also considered. The unconformities, which encompass the Jurassic–Cretaceous, the Lower–Upper Cretaceous and the Cretaceous–Palaeogene transitions are of global

extent. Other remarkable unconformities traced within many regions at the base of the Jurassic and at the Santonian–Campanian transition are not known from reference regions. A correlation of the Jurassic–Cretaceous global-scale sedimentation breaks and eustatic curves is quite uncertain. Therefore, definition of global sequences will not be possible until eustatic changes are clarified. Activity of mantle plumes is among the likely causes of the documented unconformities.

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## Introduction

Phanerozoic unconformity-bounded sequences defined in North America by Sloss (1963) have led to the development of global cycle charts and a possible eustatic curve (Vail *et al.*, 1977; Haq *et al.*, 1987). An updated curve for the entire Phanerozoic has been recently proposed by Haq and Al-Qahtani (2005). However, any eustatic constraints should always be tested to avoid errors and inconsistencies (Miall, 1992; Hallam, 2001; Catuneanu, 2006). Thus, it is sensible to return to the original concept of Sloss (1963) and to attempt broad correlation of the unconformities across the world. Interregional correlations like those previously performed by Soares *et al.* (1978), Petters (1979), Ross and Ross (1985), Embry (1997) and Hallam (2001) suggest the efficacy of such an approach.

During the past decade, new stratigraphic frameworks have been established for the Jurassic and Cretaceous successions of a number of important sedimentary basins of Eurasia, Africa, and America. These provide enough data to substantiate global-scale sedimentation breaks during this time interval.

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## Geological setting

To be global, an unconformity should be present not only in many regions in the world, but it should also be traceable in far-located regions with various tectonic settings and sedimentation types. A number of regions worldwide with the newly-established Jurassic–Cretaceous stratigraphic frameworks have been selected in order to correlate the Jurassic–Cretaceous unconformities (Fig. 1). Their tectonic settings differed strongly, which helps to avoid recognition of unconformities that result from specific tectonic events. Most of the above-mentioned basins were dominated by marine sedimentation, except the non-marine basins of Africa. In the Neuquén Basin, continental sedimentation since the Late Cretaceous has been established (Howell *et al.*, 2005). This permits us to outline the nearly-global unconformities traceable within a broad spectrum of depositional settings. Good correspondence in stratigraphic architecture between marine and non-marine strata is not so unusual (Catuneanu, 2006; Ruban *et al.*, in press). In all the studied regions, the lithological composition of the Jurassic–Cretaceous strata is quite diverse and the total thickness exceeds several hundreds of metres.

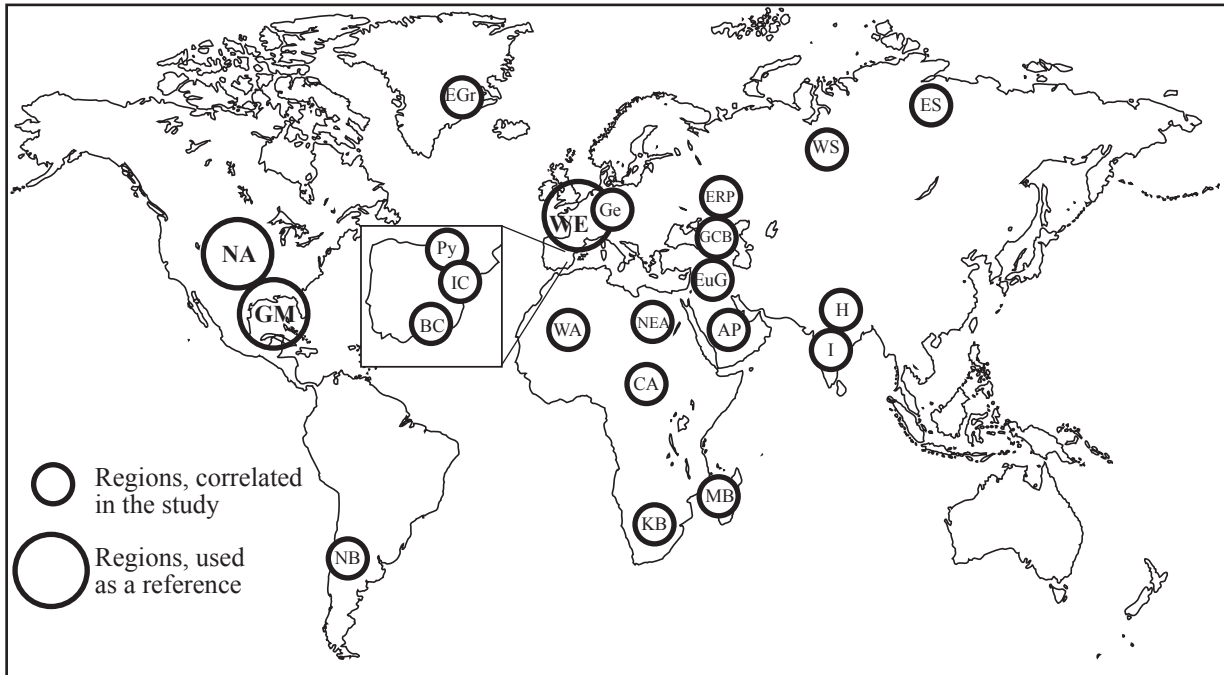
Available stratigraphic frameworks for the studied regions allow delineation of the hiatuses, which are estab-

lished within at least the main part of each region. These hiatuses mark regional unconformities. An interregional correlation then becomes possible. We do not omit regional unconformities with probable tectonic origin, because an interregional correlation is itself important for understanding the nature of hiatuses.

## Correlation of unconformities

Numerous unconformities are recognized, but not one unconformity is identified within all studied regions (Fig. 2). However, five nearly-global unconformities are common for at least 2/3 of the studied regions. They characterize the base of the Jurassic (T–J), the Tithonian–lower Valangian interval (J–K), the Albian–Cenomanian (K1–K2), the Santonian–Campanian (S–C), and the Maastrichtian–Danian (K–T) transitions.

A striking feature of all the above-mentioned unconformities is their strong diachroneity. This is especially significant for the T–J and the J–K transitional intervals. They cannot be recognized by any unique surface, but only by a concentration of regional hiatuses. Three Cretaceous unconformities seem to be less diachronous. This diachroneity may have at least two possible causes, namely (1) errors in the dating of the unconformity in given regions, (2) tectonic influence. In the first case, a diachrony can be proclaimed as an artefact of the



**Fig. 1** Location of regions, considered in this study. ERP – eastern Russian Platform, Ge – Germany, Py – Pyrenees-Basque-Cantabrian domain, IC – Iberian Cordillera, BC – Betic Cordillera, EGr – East Greenland, WS – West Siberia, ES – East Siberia, EuG – Euphrates Graben, AP – Arabian Plate, WA – Western Africa, NEA – Northeastern Africa, CA – Central Africa, KB – Karoo basins, MB – Morondava Basin, GCB – Greater Caucasus Basin, NB – Neuquén Basin, H – Himalayas and adjacent blocks, I – India, WE – Western Europe, GM – Gulf of Mexico, NA – North America.

stratigraphic analysis. In contrast, tectonic influences are able to create a true diachroneity. It is possible to hypothesize two kinds of tectonic influences. Any given unconformity may have resulted from the global-scale tectonic pulse. If so, diachroneity of such an activity resulted in diachroneity of the unconformities. Alternatively, an unconformity is resulted from a global eustatic fall. But the age of the unconformity corresponds to the time of such a fall only in those regions that were tectonically stable. Tectonic uplift causes the unconformity to occur earlier, whereas subsidence causes a later unconformity.

It is sensible to correlate the identified unconformities with those established earlier for other regions. We concentrated our attention to three such regions. They are Western Europe, where the principal unconformities have been used to outline the major cycles of sedimentation (Jacquin and de Graciansky, 1998), North America, where some key unconformities were used as major sequence boundaries (Sloss, 1963, 1988) and the

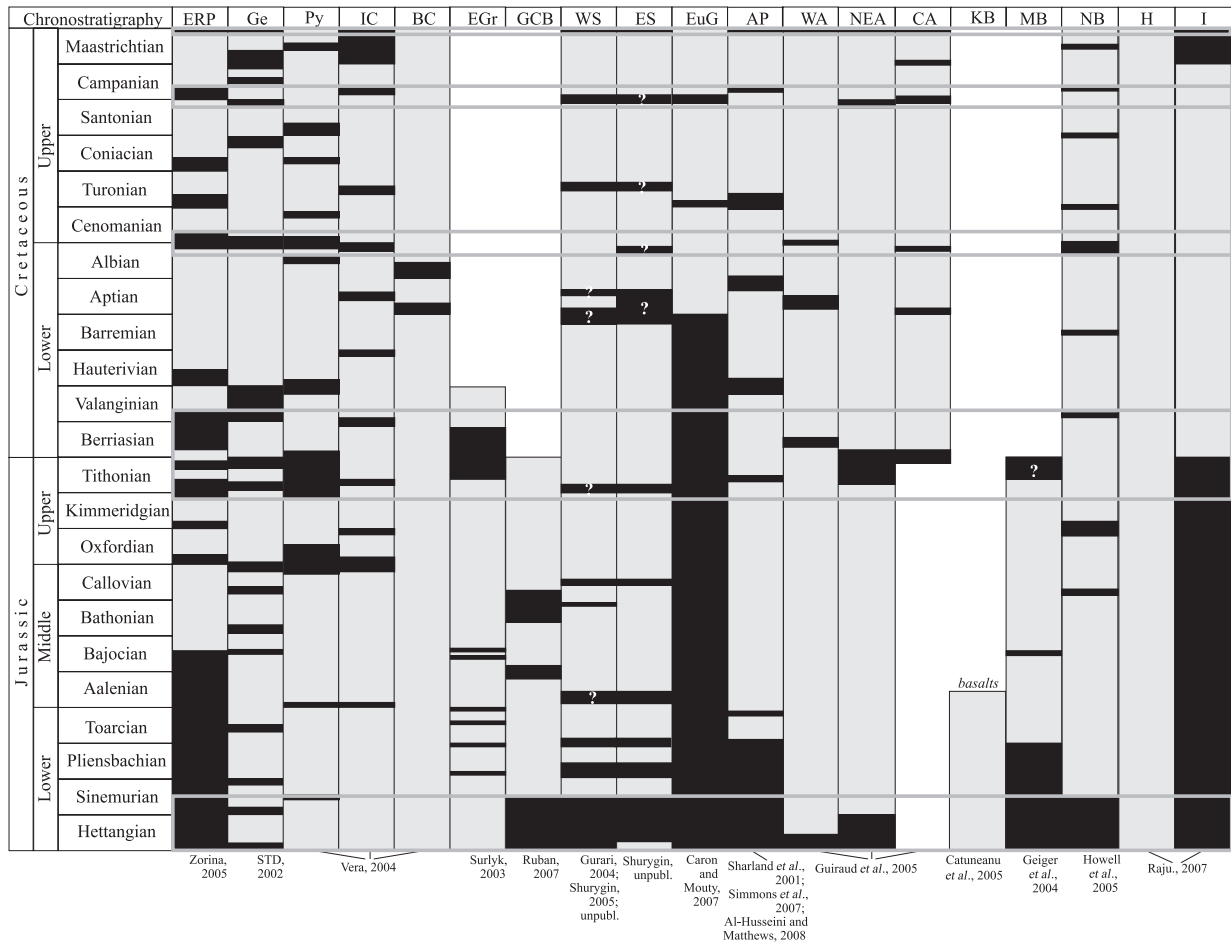
Gulf of Mexico, where Salvador (1991) identified a number of extensive unconformities. We observe that the J–K, the K1–K2, and the K–T unconformities are identified in these reference regions (Fig. 3). However, only the oldest is established in all three regions. Note that two unconformities relevant to the latter in the Gulf of Mexico, are not considered by Salvador (1991) among major. Intriguing are the T–J and the S–C unconformities. Their global extent is evident from our correlation (Fig. 2), but it is difficult to identify them in three reference regions (Fig. 3). However, one should take into consideration the absence of pre-Late Jurassic record in the review of data from the Gulf of Mexico by Salvador (1991) and the presence of the Early Cimmerian unconformity at the Norian/Rhaetian boundary.

#### Sedimentation breaks and eustatic curves

As the five above-mentioned sedimentation breaks are known from many

regions and can be labelled as *potentially*-global, they might have been caused by eustatic drops. We use the present Phanerozoic curve of Haq and Al-Qahtani (2005), the curve of Hallam (1988) and Hallam (2001) for the Jurassic, and the curve by Miller *et al.* (2005) for the Late Cretaceous to test this hypothesis (Fig. 3). The first two curves are based on the global compilation of data. However, Hallam (2001) pointed out that the earlier constraints by Haq *et al.* (1987) were based on information from the North Sea and some European sections. The curve reconstructed by Miller *et al.* (2005) is based on data from the New Jersey margin, although compared with those from other regions.

The T–J, the J–K and the K–T sedimentation breaks corresponded to the eustatic lowstands depicted by the curve of Haq and Al-Qahtani (2005). In contrast, the K1–K2 break coincided with a remarkable global sea-level rise. The situation at the S–C transition is unclear, although some eustatic drops are known from there. The other curve (Miller *et al.*, 2005)



**Fig. 2** The Jurassic–Cretaceous hiatuses in the studied regions. The considered intervals are highlighted as grey. No sufficient data are available for the rest intervals of some regions, which are shown by white. Bold dark-grey rectangles outline the common sedimentary breaks. See Fig. 1 for abbreviations.

establishes that both the K1–K2 and the S–C sedimentary breaks corresponded to the prominent global sea-level falls. However, why are there no global sedimentation breaks associated with some other remarkable eustatic drops, such as those in the Bathonian (Haq and Al-Qahtani, 2005) or Turonian (Haq and Al-Qahtani, 2005; Miller *et al.*, 2005)? In some regions, we may easily recognize the unconformities, which correspond to these eustatic falls (Fig. 2). But in some other regions, these unconformities do not exist. This may be explained by the above-mentioned tectonic influences. Rapid tectonic subsidence in some regions did not allow the unconformities to be formed during a time of eustatic fall. Moreover, in deep-marine environments,

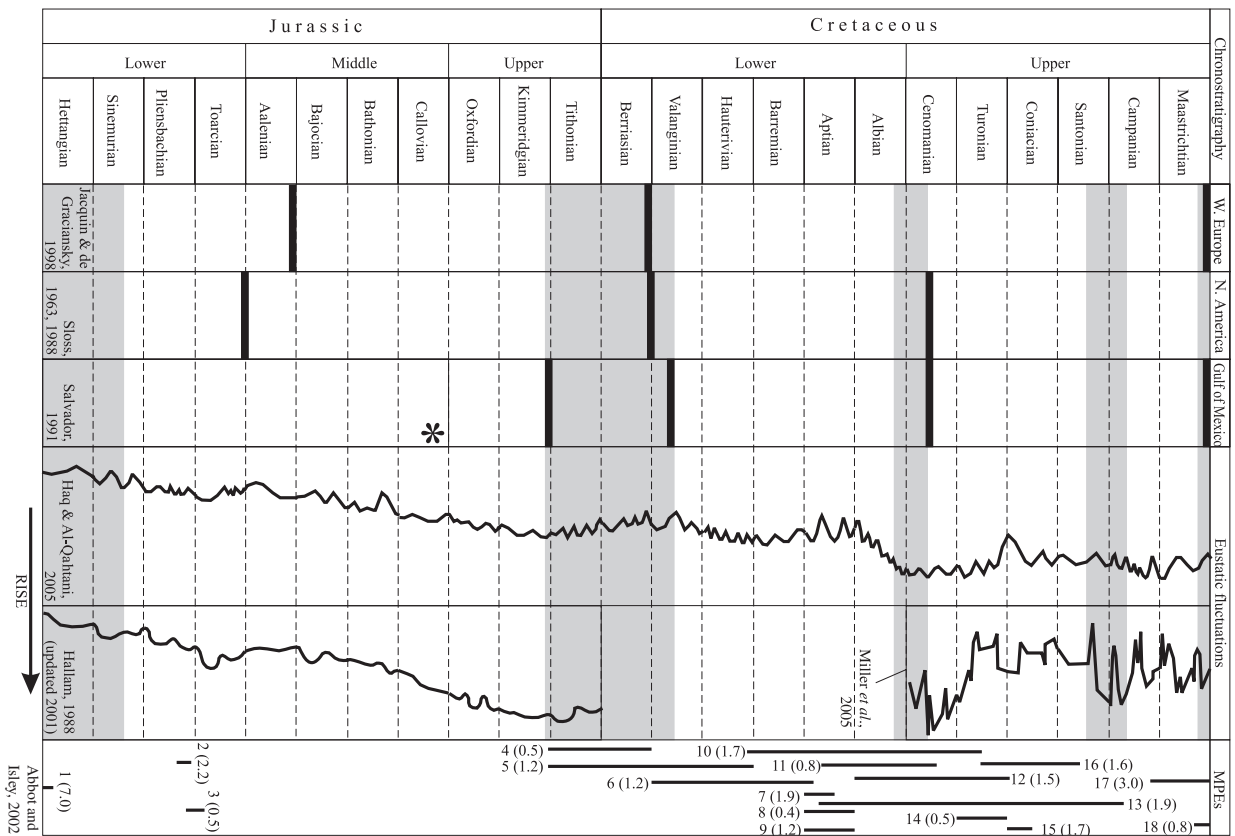
we do not necessarily see unconformities caused by the sea-level falls. Alternatively, those global falls, not reflected by the presence of wide-spread sedimentation breaks, are artefacts. According to Hallam (2001), regressions were mostly regional events, whereas transgressions are better traced across the world. If so, one should be careful interpreting the eustatic falls. The results of our unconformity correlations agree with Hallam (2001), suggesting the presence of many drops on the global sea-level curves not reflected by wide-spread unconformities, but also question the reliability of proposed eustatic curves.

If potentially global unconformities exist, they may be used to outline the global sequences similar to those

proposed by Haq *et al.* (1987). However, it is necessary to remember that a sequence is bounded by both unconformities and correlative conformities (Van Wagoner *et al.*, 1988; Cataneanu, 2006). If so, sequence boundaries may exist at those levels, where unconformities are not so common across the globe. Thus, a more precise reconstruction of global sea-level changes will permit us to outline the global sequence boundaries.

### Discussion

Although correspondence between documented sedimentation breaks and eustatic curves remains controversial, one may emphasize that only eustasy could cause them. If so, the next question is what factors would



**Fig. 3** Unconformities of reference regions, common sedimentary breaks for the studied regions (grey lines), eustatic fluctuations and MPEs. The horizontal scales of the eustatic curves are not identical. Each MPE is shown as a range accounting the dating errors. 1 – Central Atlantic, 2 – Karoo Province, 3 – Ferrar Dolerite, 4 – Magellan Rise, 5 – Shatsky Rise, 6 – Parana–Serra Gelal, 7 – Ontong Java Plateau, 8 – Wallaby Plateau, 9 – Manihiki Plateau, 10 – Alpha Ridge Plateau, 11 – Hess Rise, 12 – Kerguelen Plateau, 13 – Venezuelan–Colombian, 14 – Broken Ridge, 15 – Rio Grande, 16 – Madagascar, 17 – Peary Land, 18 – Deccan. Number in brackets means a size of volcanic province ( $\times 10^6$  km<sup>2</sup>). \*Salvador (1994) constrained sedimentary cyclicity since the Late Jurassic.

control the T–J, the J–K, the K1–K2, the S–C and the K–T eustatic drops? Two best candidates are changes in the ice-volume and tectonics. Data from Gondwana establish that the climate was generally warm during the most of the Cretaceous with a noted exception at the Jurassic/Cretaceous boundary, when temperatures dropped by about 10 °C (Scotese, 1998; Anderson *et al.*, 1999; Scotese *et al.*, 1999). A recognizable cooling took place near the end of the Cretaceous (Keller, 2001; Nordt *et al.*, 2003). Miller *et al.* (2005) suggested episodic occurrences of ephemeral glaciations during the Late Cretaceous. Undoubtedly, these cooling phases were able to cause some eustatic drops. However, glaciation episodes are also known from the Pliensbachian (Morard *et al.*, 2003),

the Callovian (Dromart *et al.*, 2003), the Early Cretaceous (Alley and Frakes, 2003) and the Turonian (Frakes and Francis, 1988; Frakes and Krassay, 1992; Frakes *et al.*, 1992), but none of them is associated with large unconformities. Several regional hiatuses can be brought into correspondence with these climatic episodes (Fig. 2). But why were other minor cooling phases more important in producing global-scale sedimentation breaks? Moreover, relative to the J–K transition, the present evidence relies on controversial climatic interpretations for this time (Husinec and Read, 2007; Zorina and Ruban, 2007).

Tectonic events such as supercontinent amalgamations and break-ups caused long-term influences on the global sea level (Miller *et al.*, 2005). But to explain relatively short-term

sedimentary breaks like those documented by our study within the Jurassic–Cretaceous interval, only abrupt and intense tectonic processes are likely. The clue is given by Hallam (2001) who underlined an importance of the large-scale plume tectonics for sea-level changes at the Triassic–Jurassic transition. The available record of episodes of mantle plume activity (MPE) (Abbott and Isley, 2002) permits us to relate the T–J unconformity with the Central Atlantic MPE, the J–K unconformity with the Magellan Rise MPE and the Shatsky Rise MPE, the K1–K2 unconformity with the Alpha Ridge Plateau MPE, the Hess Rise MPE, the Kerguelen Plateau MPE, and the Venezuelan–Columbian MPE, and the K–T unconformity with the Peary Land MPE and the Deccan MPE

(Fig. 3). No plume activity is known around the Santonian/Campanian boundary (Abbott and Isley, 2002). But taking into consideration the uncertainty in the age of the Venezuelan–Colombian MPE, one may suggest its coincidence with the S–C sedimentation break. Many other MPEs took place at times, when no sedimentation breaks occurred (Abbott and Isley, 2002).

Neither climatic nor tectonic origin of the Jurassic–Cretaceous sedimentation breaks should be excluded, but our knowledge of them remains incomplete. Moreover, local tectonic subsidence could have countered their influences on regional sedimentation. The above-mentioned considerations suggest that MPE is a more likely cause of the potentially global sedimentation breaks.

## Conclusions

An attempted correlation of the Jurassic–Cretaceous unconformities established in a number of regions with new or updated stratigraphic frameworks allows recognition of three potentially global sedimentation breaks, which occurred at the Jurassic–Cretaceous, the Lower–Upper Cretaceous and the Cretaceous–Palaeogene transitions. The unconformities established at the base of the Jurassic and at the Santonian–Campanian transition are not recognized in the reference regions of Western Europe, North America and the Gulf of Mexico, but they are common within those regions considered herein. Moreover, there are no unconformities existing within all considered regions. Five unconformities mentioned above are diachronous and their relationships with the eustatic falls are uncertain, because of the differences in the global sea-level constraints. The Jurassic–Cretaceous potentially global unconformities might have been caused by glaciations or MPE, among which the latter appears to be a more likely cause.

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of the Hun Superterrane. The mid-Carboniferous unconformity (instead of Hercynian unconformity) may have resulted from deformation caused by a compressional subduction-initiation phase along the outer margin of Cimmeria before it broke off in the Middle Permian-Triassic.

## DISCUSSION OF THE MIDDLE EAST TERRANES

In this section, we discuss the various plate-tectonic interpretations of the individual Middle East terranes (Figures 1 and 2). We highlight conflicting interpretations and suggest preferred interpretations where data and regional considerations allow. The terrane-by-terrane sections follow from present-day northwest to southeast (Figure 1).

### The Pontides and Taurides Terranes

Turkey (Figure 1) presently occupies the active collision zone between the Arabian and Eurasian plates (Bird, 2003), and interpretations of its Paleozoic history vary from a single terrane to several. Scotese (2004) positioned Turkey next to the Levant and Egypt (Figures 1 and 2) throughout the Paleozoic and early Mesozoic, and in the Cretaceous showed it drifting northwards until it collided with Eurasia in the middle Cenozoic (c. 30 Ma). Similar single-terrane models involving only Mesozoic rifting were adopted by others (e.g. Grabowski and Norton, 1995; Sharland *et al.*, 2001).

Göncüoğlu and Kozlu (2000) separated Turkey into the northern Pontides and southern Taurides by a Paleozoic ocean that closed in the Carboniferous. They correlated post-collisional granitoids and suggested that the Taurides was originally Gondwanan. As discussed earlier, Sengör (1990, Figure 11) considered the Pontides (and Kersehir) and Taurides (Menderes-Taurus) terranes to be parts of two Cimmerian ribbons with the intervening Neo-Tethys (Inner Taurides) Ocean.

Several authors, however, interpreted the Pontides as Hunic and the Taurides as Cimmerian (Figures 6 and 7; Stampfli *et al.*, 2001; Cocks and Torsvik, 2002). Moreover, based on a detailed analysis of foraminiferal paleobiogeography and plate tectonic review, Kalvoda (2002) concluded that Turkey was Laurussian, rather than Gondwanan. An investigation of the Carboniferous (Viséan) foraminiferal and algal paleobiogeography suggests that the Taurides was located along the northwestern border of the Paleo-Tethys (Okuyucu and Vachard, 2006).

Therefore it appears that the Paleozoic paleopositions of the main Pontides and Taurides terranes of Turkey remain unresolved in the literature. As discussed above, we favor the interpretation of these two terranes as Cimmerian and specifically within the regional context of the mid-Carboniferous subduction-arc complex (Figure 11, Sengör, 1990; Xypolias *et al.*, 2006).

### The Caucasian Terranes

The Greater Caucasus terrane is presently located south of the Russian Platform (Gamkrelidze, 1997; Tawadros *et al.*, 2006) (Figures 1 and 2, i.e. Baltica), and its Paleozoic sedimentary complexes crop out in the central Greater Caucasus Mountains (Ruban, 2006). Paleontological data from Silurian (Ludlow) carbonates (bivalve and ammonoid assemblages, Bogolepova, 1997), Pennsylvanian paleobotanical data (Anisimova, 1979), and middle and upper Paleozoic paleomagnetic data (Shevljagin, 1986) suggest that the Greater Caucasus was not a part of Baltica, as traditionally proposed (e.g. Laz'ko, 1975; Bykadorov *et al.*, 2003). The faunal and floral assemblages, as well as the lithostratigraphic architecture, are similar to those of Hunic Perunica and Carnic Alps (Central and Alpine Europe, Figures 2 and 7). Moreover, its lower Silurian mainly clastic and volcanoclastic succession resembles that of the Hunic margin of the Paleo-Tethys.

In the Middle-Late Devonian (until Famennian) about 4,500 m of mixed volcanoclastics and volcanic rocks were deposited in the Greater Caucasus (Kizeval'ter and Robinson, 1973). The volcanic activity may have been due to tectonism between the Greater Caucasus and other Hunic terranes. Alternatively, the magmatic activity may have been associated with the closure of the Rheic Ocean (Stampfli and Borel, 2002; Figure 6). We therefore follow Tawadros *et al.* (2006) in assigning the Greater Caucasus to the Hun (probably Cordillera) Superterrane.



The early Paleozoic location of the Greater Caucasus before the Hunic breakaway is uncertain. Tawadros et al. (2006) positioned it along the African-Arabian margin of Gondwana, but without constraining data. In the mid-Paleozoic, it was located near the easternmost extremity of the Hun Cordillera terranes with westward strike-slip dislocation along the northern Paleo-Tethys Shear Zone in the Carboniferous - Middle Triassic, and eastward dislocation in the Late Triassic - Early Jurassic (not depicted in figures in this paper). Such a late Paleozoic to Mesozoic shear zone may have stretched along the southern margin of Laurussia and connected with an intra-Pangean shear zone (Arthaud and Matte, 1977; Swanson, 1982; Rapalini and Vizán, 1993; Lawver et al., 2002; Stampfli and Borel, 2002; Bykadorov et al., 2003; Vai, 2003; Garfunkel, 2004; Natal'in and Sengör, 2005; Ruban and Yoshioka, 2005; Tawadros et al., 2006).

Stampfli and Borel (2002) positioned Kazakhstan (or parts of it) along the easternmost part of the Hun Superterrane suggesting proximity to the Greater Caucasus in the Devonian. Available paleontological data does not support this suggestion. The trilobite species *Paciphacops* occurs in the upper Silurian to Lower Devonian strata and its distribution encompasses the circum-Pacific (Merriam, 1973; Wright and Haas, 1990; Ramsköld and Werdelin, 1991; Edgecombe and Ramsköld, 1994). Its presence in Kazakhstan (Maksimova, 1968) and absence in Europe suggests the former was located on the margin of the Panthalassic Ocean, i.e. too far to be Hunic. This is also confirmed with other paleontological data (Blodgett et al., 1990; Campbell, 1977; Chlupác, 1975; Kobayashi and Hamada, 1977; Maksimova, 1972; Ormiston, 1972; Perry and Chatterton, 1976; Pedder and Oliver, 1990; Pedder and Murphy, 2004).

The Lesser Caucasus (Transcaucasus) terrane is presently located south of the Greater Caucasus, and north of Turkey and Iran (Figures 1 and 2). Interpretations based chiefly on paleomagnetic and paleontological data (Lordkipanidze et al., 1984; Gamkrelidze, 1986), indicate that it was apparently a separate terrane. It appears to have drifted northwards together with Cimmeria ("Iran-Afghan" microcontinent of Gamkrelidze). In the absence of conflicting evidence, we assign the Lesser Caucasus to Cimmeria. We also conclude that the paleopositions of the Caucasus along the margin of Gondwana or within the two superterranes remain unconstrained.

### **East Turkey, Northwest Iran and Alborz Terranes**

The Eastern Turkey, Northwest Iran and Alborz regions are inconsistently interpreted in published reconstructions. Sengör (1990) interpreted Eastern Turkey as a Neo-Tethyan accretionary prism. Northwest Iran is considered Cimmerian and similarly depicted by several authors (e.g. Sengör, 1990; Sharland et al., 2001), but is sometimes referred to as the Alborz terrane by others (Stampfli et al., 2001; Torsvik and Cocks, 2004). In this review we consider Northwest Iran and Alborz as separate terranes (Figures 1 and 2).

Based on paleobiogeographic studies, Kolvoda (2002) suggested that the Alborz terrane was a part of the late Paleozoic Laurussia Supercontinent. Angiolini and Stephenson (in press), based on a re-examination of early Permian (Asselian-lower Sakmarian) brachiopods of the lower Permian Dorud Formation in the Alborz Mountains and a new study of palynomorphs from the same formation, also concluded that there is little affinity with Gondwana and the peri-Gondwanan region. Brachiopod fauna shows affinities with those of Baltica (Urals and of the Russian Platform), and to a lesser extent to the Trogkofel Limestone (Carnic Alps) in the west. The palynomorph assemblage is completely different from those recorded from the Asselian-Sakmarian *Granulatisporites confluens* Biozone, which is ubiquitous in the Gondwana region. L. Angiolini (2007, written communication) and coworkers, based on their studies and published data, concluded that the Alborz, Northwest and Central Iran remained adjacent to one another throughout most of the Paleozoic. This is reflected by the continuity and common evolution of their Paleozoic sedimentary rocks, and uniform distribution of biota. They attribute the similarity of the fossil record to the Urals to surface currents and the low latitudinal position of the Iranian terranes.

In summary, Eastern Turkey may not have been a Paleozoic terrane. The Alborz, Northwest and Central Iran terranes were apparently adjacent to one another. Their paleobiogeographic signature suggests a Laurussian affinity, but in the absence of more definitive data we follow most authors and assign them to the Cimmerian Superterrane.

EARLY TRIASSIC: 245 Ma

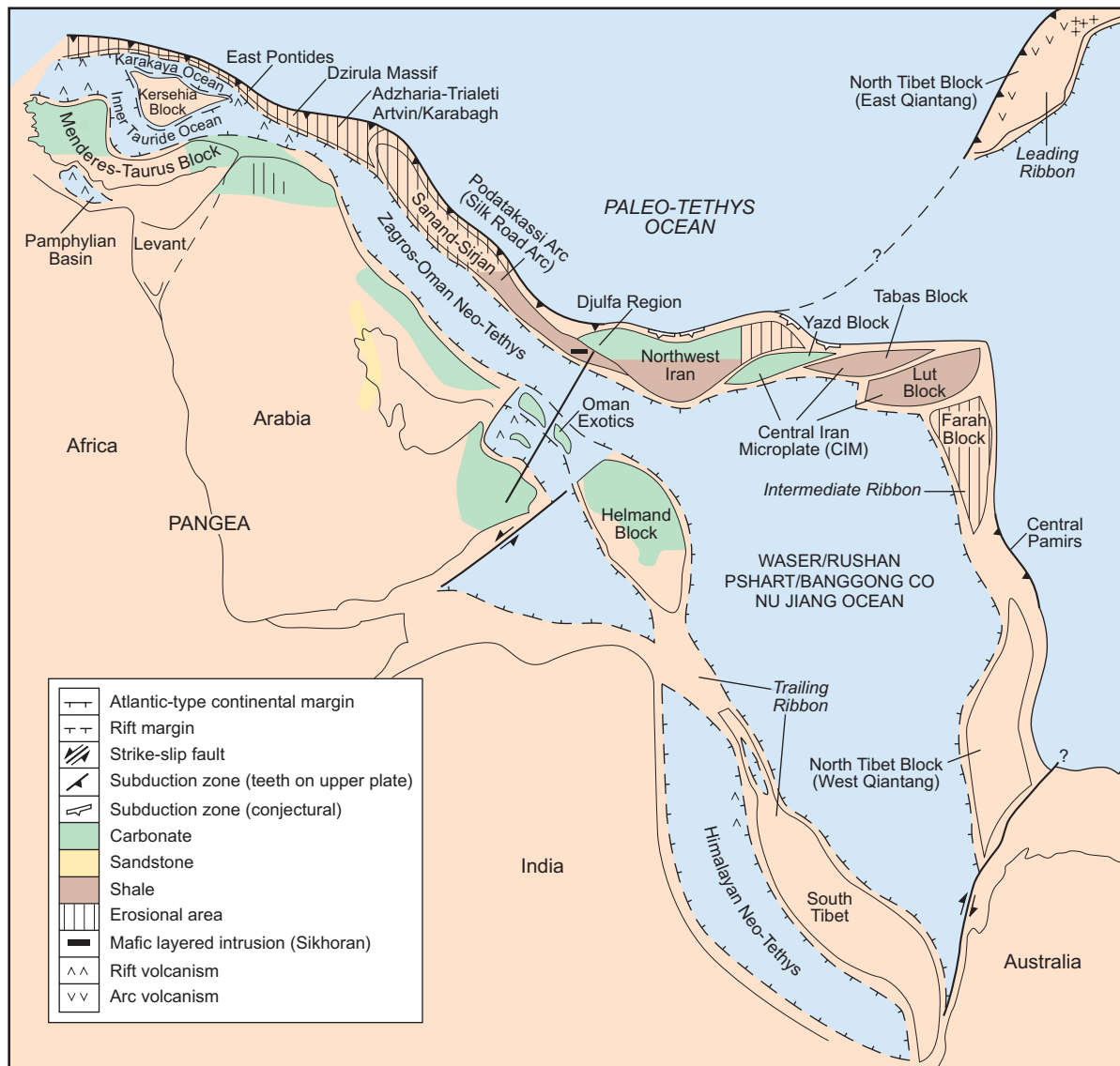


Figure 11: Plate-tectonic reconstruction of the Early Triassic (modified after Sengör, 1990). Sengör interpreted the breakaway of the Cimmeria Superterrane to consist of three ribbons that detached at different times from Pangea. L. Angiolini (2007, written communication) and coworkers believe that this model is probably valid although it is very difficult to prove in detail. For example, their data suggests that the Helmand terrane may have been attached to the middle ribbon. Sengör interpreted the embryonic Neo-Tethys Ocean to consist of several seaways: Inner Taurides, Zagros-Oman, an unnamed sea south of Oman, Himalayan and Waser/Rushan-Nu Jiang. A subduction-arc complex is interpreted along the Paleo-Tethyan margin adjacent to the Sanandaj-Sirjan terrane and possibly extending further to the southeast and west. The initiation of subduction in mid-Carboniferous times may have caused the epeirogenic swells and compressional faulting in the Arabian Plate.

### Sanandaj-Sirjan Terrane

The Sanandaj-Sirjan terrane (Figures 1, 2, 4 to 11) was attached to the Zagros Mountains (and the Arabian Plate) until it broke off as part of Cimmeria in the mid-Permian - Triassic (Berberian and King, 1981; Sengör, 1990; Grabowski and Norton, 1995; Stampfli et al., 2001; Sharland et al., 2001; Scotese, 2004). Most authors show the Paleozoic position of Sanandaj-Sirjan adjacent to the Zagros Suture, effectively implying that today it occupies the same approximate position as 250 million years ago.

This seems remarkable as it was involved in the opening and closing of the Neo-Tethys Ocean. During the opening it may have subducted the Paleo-Tethys (Sengör, 1990), and during its closing, the Neo-Tethys (Ghasemi and Talbot, 2005).

### **Central Iran**

Sengör (1990) divided the Central Iran microplate into the Lut, Tabas and Yazd blocks (Figure 11). Other authors consider Central Iran and Lut as synonyms (Stampfli and Borel, 2002; von Raumer et al., 2002, 2003; Torsvik and Cocks, 2004; Scotese, 2004; Golonka, 2004); or two neighboring terranes: Central Iran and Lut, or Yazd and Lut (e.g. Sharland et al., 2001; Stampfli et al., 2001). We adopt Sengör's Central Iran terrane and follow others by considering it as Cimmerian.

### **Zagros Mountains and Makran Region**

The Zagros Mountains region in southwest Iran forms a part of the Miocene-Pliocene collision zone between the Arabian and Eurasian plates (Figure 1). This region was a part of the Arabian Plate from the late Neoproterozoic to the present-day (Berberian and King, 1981; Sepehr and Cosgrove, 2004). During the Permian-Triassic (Figures 10 and 11), the opening of the Neo-Tethys Ocean along the Zagros Suture Zone was accompanied by normal faulting and horsts and graben systems (Sepehr and Cosgrove, 2004).

South of the Zagros Mountains, the Makran region in Iran and Pakistan (Figure 1) consists of the Inner Makran ophiolites and the Cenozoic Makran and Saravan accretionary prisms (McCall, 1997, 2002, 2003). This region is associated with the NE-directed subduction of the Gulf of Oman oceanic crust (a remnant of the Neo-Tethys Ocean) beneath Iran. The Makran core may have amalgamated with Central Iran and Sanandaj-Sirjan during the Triassic (McCall, 2003). Therefore, Makran may have formed a part of Mesozoic Cimmeria.

### **Helmand and Farah Terranes**

Afghanistan, western Pakistan and southeast Turkmenistan are cored by the southern Helmand and northern Farah terranes and considered Cimmerian (Figures 1 and 2; Sengör, 1990; Sharland et al., 2001; Stampfli et al., 2001; Golonka, 2004). Scotese (2004) adopted Sengör's (1990) model showing Helmand and Farah formed parts of two Permian-Triassic ribbons (Figure 11). Together with Karakoram in north Pakistan, the Farah and Helmand terranes are considered Cimmerian.

## **CONCLUSIONS**

Recent publications that interpreted the Paleozoic tectonic units of the Middle East and their paleopositions were reviewed in the global context of supercontinents and exhumed vast oceans, to individual terranes. Adjoining the Arabian and Levant plates, ten Paleozoic Middle East terranes were apparently involved in the evolution of the Gondwana and Pangea margins and the Hun and Cimmeria superterranes. The Cimmerian terranes that broke off from Gondwana in mid-Permian - Triassic appear to have been: (1 and 2) Turkey's northern Pontides and southern Taurides; (3 to 6) Alborz, Central Iran (Lut, Tabas and Yazd), Sanandaj-Sirjan and Northwest Iran; (7 and 8) Helmand and Farah of Afghanistan, western Pakistan and southeast Turkmenistan; and (9) the Lesser Caucasus. The Greater Caucasus may have been Hunic.

The Caledonian and Hercynian orogenies occurred far away from Arabia. Correlation between these two orogenies and deformations in Arabia can be misleading. They imply that far-field stresses were transmitted many thousands of kilometers from the orogenic fronts to Arabia's crust. The terms Caledonian and Hercynian should not be applied to the tectonic evolution of Arabia. Instead two significant and more proximal tectonic events were identified as possible near-field sources of regional deformation. The mid-Silurian breakaway of the Hun Superterrane is identified as a candidate that may be related to the mid-Silurian to Middle Devonian (middle Paleozoic) uplift in North Arabia and possibly Oman. The initiation of subduction, which could have preceded the mid-Permian - Triassic breakaway of Cimmeria, is considered a possible force for the regional mid-Carboniferous faulting and epeirogenic deformation in Arabia.

Middle East plate-tectonic models require much more data and investigations if they are to be firmly constrained. The first step is to adopt common boundaries and names for the terranes, not only for the Middle East, but also of those in Asia and Europe (Figures 1 and 2). The second step requires constructing a regional tectono-stratigraphic framework that crosses from the interior of the Arabian Plate and its outer margins (Oman, Zagros, North Iraq, Syria and Southeast Turkey) to the ten and possibly more Middle East terranes. The framework requires correlating stratigraphic rock units that are much better constrained by age (biostratigraphy), paleontology and tectonics. Additionally, paleomagnetic and age data, together with the descriptions and interpretations of volcanic rocks could better clarify many aspects of the tectonic events.

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