Problems for Evaluation of the Scenario of the Permian - Triassic Boundary Biotic Crisis and of Its Causes

Heinz W. **KOZUR**

Abstract

Determination of the causes of the Permian-Triassic boundary (PTB) biotic crisis is hindered primarily by the diachronous nature of the used PTB, poor stratigraphic control of compared Upper Permian and Lower Triassic faunas, especially in continental biotopes, poor knowledge of the lower and middle Scythian faunas from many environments, and by interpolation of the unknown (lower and middle) Scythian diversity from the known Upper Permian and Middle Triassic diversity data in many major fossil groups. Most of these problems can be resolved by using the first appearance datum (FAD) of *Hindeodus parvus* as either an isochronous PTB, or as an isochronous marker level very close to the base of the Triassic; careful studies of fossil-rich, complete continental boundary sections (e.g., Dalongkou in Sinkiang), and utilisation of uninterpolated diversity data, which are based on known Scythian data, for the reconstruction of the extinction and recovery patterns in all fossil groups.

The most important features of the PTB biotic crisis are: (1) Among the marine biota, only the plankton and the warm-water benthos, nektobenthos and nekton are strongly affected by the PTB biotic crisis. (2) The recovery of the warm-water nekton and nektobenthos was very fast (after one conodont zone). The recovery of the warm-water benthos, some of the plankton (radiolarians) and the terrestrial plant productivity was strongly delayed for several million years, and occurred only in the upper Olenekian (upper Scythian) and in the Middle Triassic. (3) The number of the Lazarus taxa that re-appeared in the upper Olenekian and above all in the Middle Triassic, is very high (about 50%) and in some fossil groups 90-100% at generic level.

The reconstruction of the scenario for the PTB biotic crisis requires not only the consideration of the uninterpolated extinction and recovery patterns of all fossil groups across all environments, but must also account for the main features of geological evolution from the Middle Permian to the Lower Triassic. The most important causal factors in the PTB biotic crisis are the extinction event at the Guadalupian-Lopingian boundary that restricted the diverse Upper Permian warm-water benthos to the Tethyan shelves, the long-lasting, widespread Siberian Trap volcanism (Dzhulfian-lower Scythian) which was the greatest volcanic event during the Phanerozoic, and the very strong explosive felsic to intermediate volcanism around the PTB, close to the margin between eastern Tethys and Panthalassa. These volcanic activities resulted in those climatic changes that were directly and indirectly (as cause of the oceanic superanoxia) responsible for the PTB biotic crisis, such as periodic cooling of the climate by volcanic dust and sulphate aerosols (mainly caused by the Siberian Trap volcanism), acid rain, a 3-6 month "volcanic winter" at low latitudes and the strongly reduced input of sunlight during the uppermost Dorashamian (both caused by the very strong explosive volcanism at the Tethys/Panthalassa margin), followed by global warming in the lower Scythian, and uppermost Dorashamian to lower Scythian superanoxia.
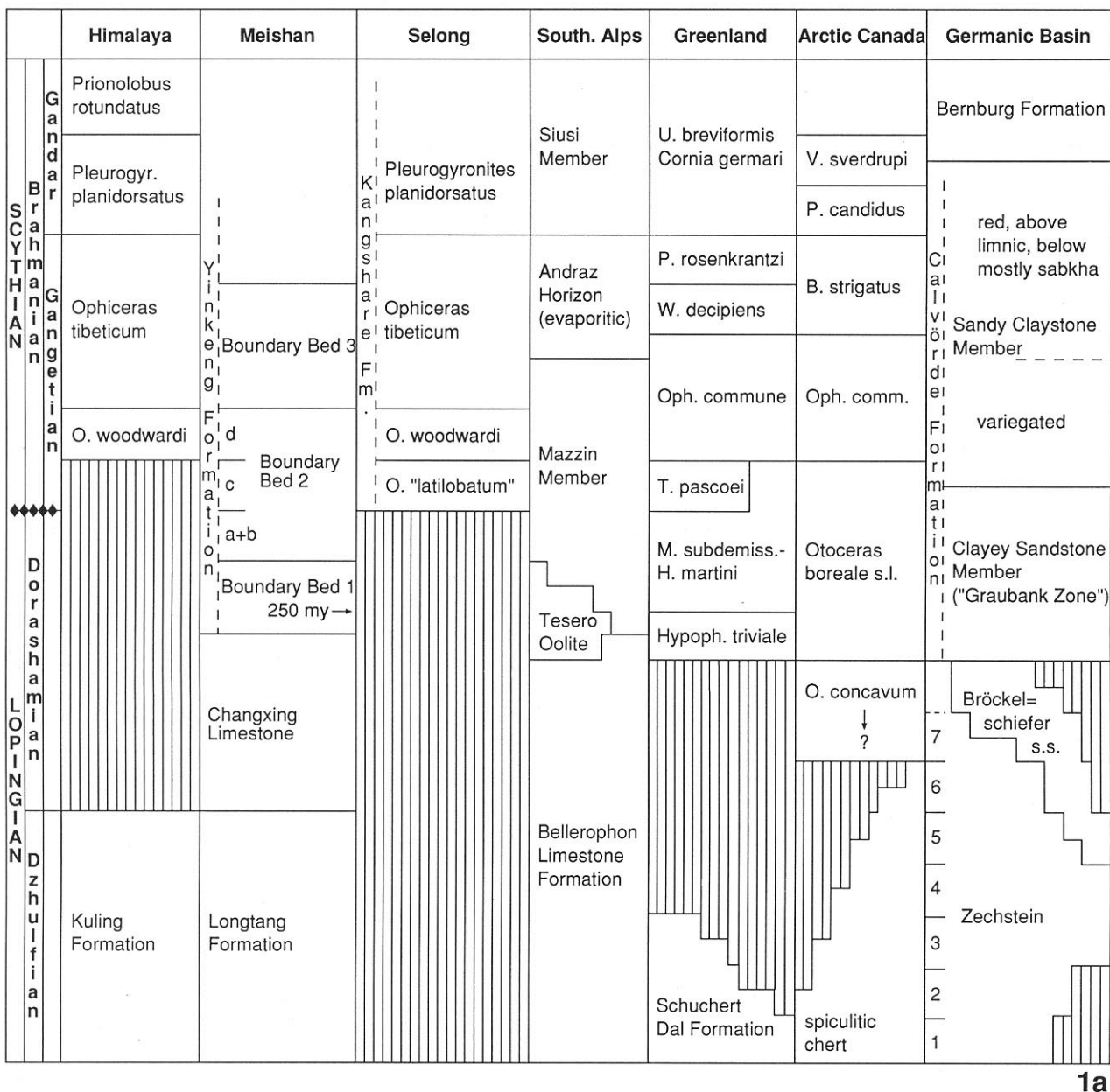
Rézsü u. 83, H-1029 Budapest, Hungary.

1. INTRODUCTION

The search for the causes of the biotic crisis around the Permian - Triassic boundary (PTB) requires the investigation of the exact scenario of the PTB biotic crises (extinction and recovery patterns among all major faunal and floral groups of all facies) and the exact global correlation of these patterns. It also requires consideration of accompanying geological phenomena (e.g., facies changes, climatic changes, age and character of volcanic activity around the PTB, changes in stable isotopes, the distribution and vertical range of the oceanic anoxia). These investigations have been hampered by (1) incorrect correlation of the PTB in different faunal realms and facies; (2) erroneous assignment of strong biotic changes at diachronous facies boundaries to the PTB biotic changes; (3) erroneous assignment of strong biotic changes, occuring between Permian and Triassic continental biota that are separated by a long time gap, to the PTB biotic crisis; (4) comparison of Permian and Triassic faunas with poor stratigraphic control; (5) inadequate knowledge of the lower and middle Scythian pelagic faunas; (6) interpolation of the unknown or poorly known (lower and middle) Scythian diversity of major fossil groups from known Upper Permian and Anisian diversities.

In the present paper some of the problems in the search for the real extinction and recovery patterns and the most important features of the PTB biotic crisis are indicated. On the basis of the real (not interpolated) extinction and recovery patterns of the major fossil groups, and with consideration of the geological phenomena in the Upper Permian and Lower Triassic, a possible scenario for the PTB biotic crisis is presented.

2. POSITION AND CORRELATION OF THE PERMIAN - TRIASSIC BOUNDARY

The following levels are, partly for historical reasons, the most important PTB levels used in marine and continental beds: (1) the base of the Buntsandstein in the southwestern Germanic Basin; (2) the boundary between the Bellerophon Limestone and the Werfen Group in the Southern Alps; (3) the base of the *Otoceras woodwardi* Zone in eastern Perigondwana; (4) the base of the *Otoceras concavum* Zone in the Arctic; (5) the first appearance datum (FAD) of *Lystrosaurus* in

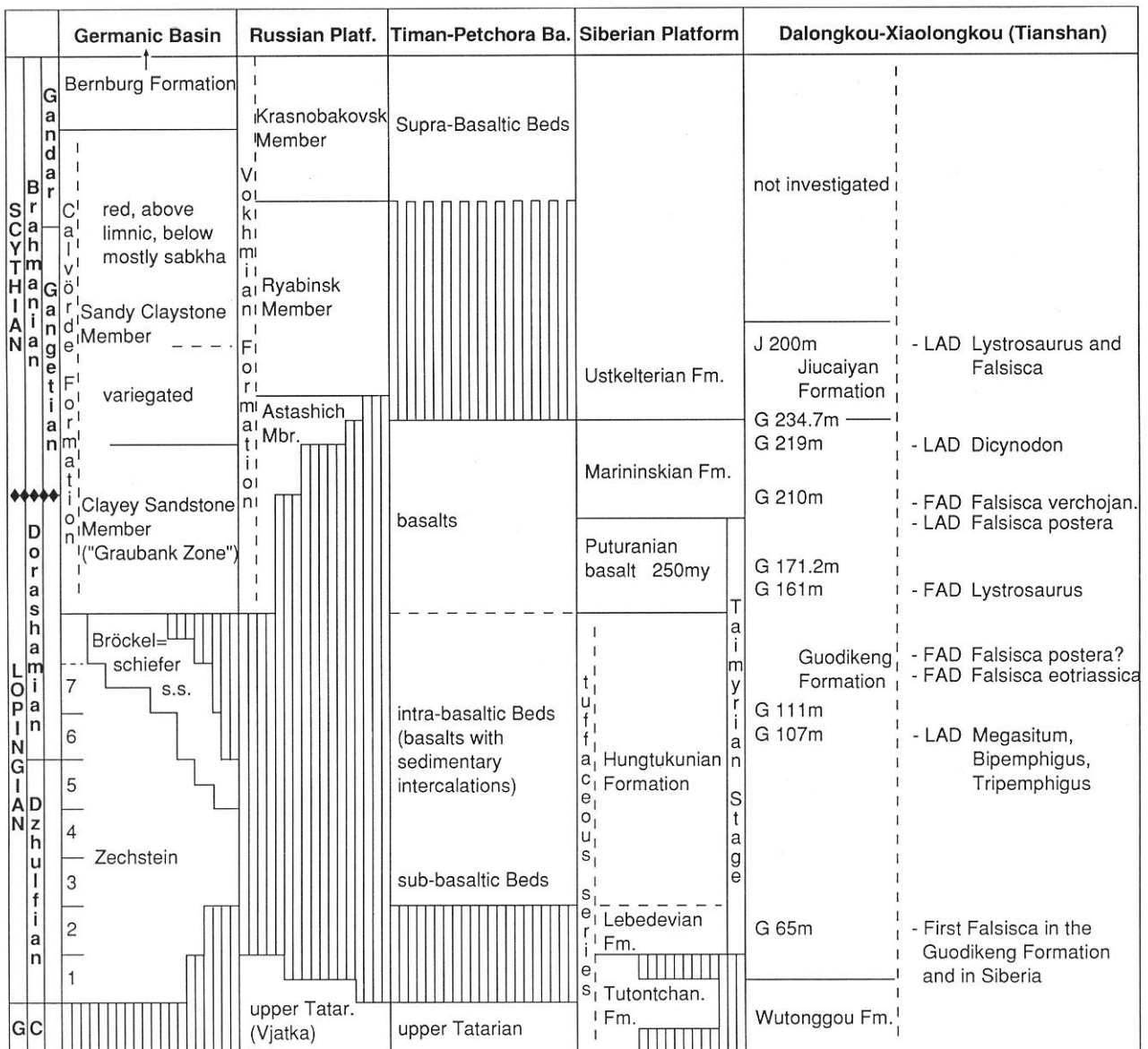|		Himalaya	Meishan	Selong	South. Alps	Greenland	Arctic Canada	Germanic Basin
SCYTHIAN	Brahmanian / Gandar	Prionolobus rotundatus			Siusi Member	U. breviformis Cornia germari	V. sverdrupi	Bernburg Formation
		Pleurogyr. planidorsatus		Pleurogyronites planidorsatus			P. candidus	red, above limnic, below mostly sabkha
	Gangetian	Ophiceras tibeticum	Yinkeng Formation — Boundary Bed 3	Kangshare Fm. — Ophiceras tibeticum	Andraz Horizon (evaporitic)	P. rosenkrantzi	B. strigatus	
						W. decipiens		Sandy Claystone Member
					Mazzin Member	Oph. commune	Oph. comm.	variegated (Calvörde Formation)
		O. woodwardi	Yinkeng Fm. d — Boundary Bed 2 c / a+b	O. woodwardi		Oph. commune		
				O. "latilobatum"		T. pascoei		
	Dorashamian		Boundary Bed 1 250 my →			M. subdemiss.- H. martini	Otoceras boreale s.l.	Clayey Sandstone Member ("Graubank Zone")
					Tesero Oolite	Hypoph. triviale		
LOPINGIAN			Changxing Limestone		Bellerophon Limestone Formation		O. concavum ↓ ?	Bröckel= schiefer s.s.
								7
								6
								5
	Dzhulfian	Kuling Formation	Longtang Formation					4
								3 / Zechstein
						Schuchert Dal Formation	spiculitic chert	2
								1

1a

Fig. 1 Correlation chart of some important marine and continental successions. Detailed only around the PTB. Vertical scale not thickness- or time-related! The upper Capitanian part is only shown for the Russian Platform and the Timan-Petchora Basin. After BAUD et al. (1996), CHENG et al. (1989), JIN et al. (1996), KOZUR (1989, 1994b, 1996b), KOZUR & SEIDEL (1983), KOZUR et al. (1996b), KRYSTYN & ORCHARD (1996), LOZOVSKY (1993), LUCAS (1993), PERCH-NIELSEN et al. (1974), RENNE et al. (1995), SADOVNIKOV & ORLOVA (1993), TEICHERT & KUMMEL (1976), TOZER (1967), TUZHIKOVA (1985), XIA & ZHANG (1992), YIN et al. (1996a, b). Figure 1a: Marine succession and Germanic Basin (marine and continental, PTB continental); Figure 1b (opposite page): Continental successions and Germanic Basin. Legend: ♦♦♦♦♦ = Used P/T boundary (FAD of *Hindeodus parvus* in marine beds). The following abbreviations are used only in Figure 1b: G = Uppermost Guadalupian Series; C = Upper Capitanian Stage; G 111 m = 111 m above the base of the Guodikeng Fm. in the Dalongkou section etc. Measurement after LUCAS (1996, during a joint project sponsored by the NGS, USA); J 200 m = 200 m above the base of the Jiucaiyan Fm. in the Xiaolongkou section.

continental beds; (6) the FAD of the conodont *Hindeodus parvus* (KOZUR & PJATAKOVA). These different PTB levels are mostly equated with each other, but are by definition situated at different stratigraphical levels.

The base of the Buntsandstein in SW Germany, the priority base of the Triassic (von ALBERTI, 1834), is a diachronous facies boundary within continental beds (KOZUR, 1994b, 1998a) which is only of historical interest. It has its lowest position at the margin of the Germanic Basin (including the Triassic type area in SW Germany), where Zechstein equivalents of the central Germanic Basin, such as the Bröckelschiefer, Leberschiefer and Tigersandstein were included in the Buntsandstein, but also lies in Upper Permian Dorashamian Stage within the centre of the Germanic Basin (Figs. 1a & b).

The base of the Werfen Group (base of the Tesero Oolite) was equated with the base of the Triassic in the Germanic Basin and placed at a level where the diversity of a rich Upper Permian fauna and marine flora of

	Germanic Basin	Russian Platf.	Timan-Petchora Ba.	Siberian Platform	Dalongkou-Xiaolongkou (Tianshan)
SCYTHIAN (Brahmanian / Gangetian; Gandarian; Dorashamian)	Bernburg Formation; red, above limnic, below mostly sabkha; Sandy Claystone Member; variegated; Clayey Sandstone Member ("Graubank Zone") — Calvörde Formation	Krasnobakovsk Member; Volkhmian Formation; Ryabinsk Member; Astashich Mbr.	Supra-Basaltic Beds; basalts	Ustkelterian Fm.; Marininskian Fm.; Puturanian basalt 250my	not investigated
					J 200m Jiucaiyan Formation — - LAD Lystrosaurus and Falsisca
					G 234.7m ———
					G 219m — - LAD Dicynodon
					G 210m — - FAD Falsisca verchojan. / - LAD Falsisca postera
					G 171.2m / G 161m — - FAD Lystrosaurus
LOPINGIAN / DZHULFIAN (Bröckel=schiefer s.s. 7, 6, 5, 4; Zechstein 3, 2, 1)			intra-basaltic Beds (basalts with sedimentary intercalations)	Hungtukunian Formation (Taimyrian Stage; tuffaceous series)	Guodikeng Formation — - FAD Falsisca postera? / - FAD Falsisca eotriassica
					G 111m / G 107m — - LAD Megasitum, Bipemphigus, Tripemphigus
			sub-basaltic Beds	Lebedevian Fm.	G 65m — - First Falsisca in the Guodikeng Formation and in Siberia
GC		upper Tatar. (Vjatka)	upper Tatarian	Tutontchan. Fm.	Wutonggou Fm.

1b

the Bellerophon Limestone Formation suddenly drops to a very low diversity fauna and flora of the Tesero Oolite. However, as shown by KOZUR (1994b), this boundary is also a diachronous facies boundary within the Upper Permian. The decrease in diversity is caused by the change from a highly diverse shallow-water shelf community into a low-diversity tidal flat community. Such facies change is always accompanied by a drastic decrease in diversity, independent of the stratigraphic level within the Permian or Triassic.

The base of the Triassic at the base of the Werfen Group is also only of historical interest, but this boundary has been, by many authors, erroneously correlated with the biostratigraphic PTB at the base of the *O. woodwardi* Zone (e.g. DIENER, 1912; TOZER, 1988; POSENATO, 1991). However, comparison of conodont distribution in the lowermost Werfen Group (KOZUR, 1989, 1994b, 1996b, 1998a) and in the *Otoceras* faunas (MATSUDA, 1981; KOZUR, 1989, 1994b, 1996b,

1998a; KRYSTYN & ORCHARD, 1996; KOZUR et al., 1996b; WANG et al., 1996; YIN et al., 1996a) indicates that the base of the *O. woodwardi* Zone is correlatable with the middle part of the Mazzin Member, considerably above the base of the Werfen Group (Fig. 1a).

The base of the *Otoceras woodwardi* Zone is the first biostratigraphically defined PTB (GRIESBACH, 1880), and the finally defined PTB should be at, or close to this boundary. The disadvantage of this boundary is that *O. woodwardi* GRIESBACH is only known from the Perigondwana margin of eastern Tethys. The FAD of *O. woodwardi* was, therefore, only tentatively correlatable with the Tethyan and the Boreal realms. Instead of biostratigraphic correlations, the FAD of *O. woodwardi* was equated with those different chronostratigraphic levels that were in different regions used as the PTB, e.g. with the base of the Werfen Formation (e.g. DIENER, 1912; TOZER, 1988), with the base of

the *Otoceras concavum* Zone (e.g. TOZER, 1967) or with the base of the *O. boreale* Zone (e.g. DAGYS, 1994). However, with the aid of conodonts, it can be shown that none of these boundaries corresponds to the FAD of *O. woodwardi* (KOZUR, 1989, 1994a, 1995a, 1996b, 1997c, 1998a).

The base of the *Otoceras concavum* Zone is preferred as the base of the Triassic by most ammonoid workers. This is largely based on the erroneous assumption that *Otoceras* begins in the Arctic and in Perigondwana at the same level (TOZER, 1967) and that *Otoceras* is the first Triassic genus. In reality it is the last representative of the Upper Permian Otoceratacea that straddles the PTB. The main disadvantage of definition of the PTB with the base of the *O. concavum* Zone are: (1) *O. concavum* is known only from very few localities in remote areas of Arctic Canada and NE Siberia; (2) *O. concavum* TOZER always follows after a gap or at least after a lengthy ammonoid-free interval; (3) the direct forerunner of *O. concavum* is unknown. The latter two reasons prevent the base of the *O. concavum* Zone from being palaeontologically defined within a phylomorphogenetic lineage between two species. This excludes the definition of the base of the Triassic with the FAD of *O. concavum*.

Moreover, conodont and sporomorph data have shown that the Boreal *Otoceras* faunas (with the exception of the uppermost O. boreale Zone s.l.) are Permian in age, if the FAD of *O. woodwardi* or the insignificantly older FAD of *H. parvus* Zone are used to define the base of the Triassic (KOZUR, 1989, 1994a, 1995a, 1996b, 1997c, 1998a; HENDERSON, 1993; HENDERSON & BAUD, 1996). This was subsequently confirmed by ammonoid data by KRYSTYN & ORCHARD (1996) who pointed out that *O. woodwardi* is more advanced than *O. boreale*, and that the *O. woodwardi* Zone occurs in the Selong section in Tibet in a stratigraphic succession above a fauna with *Otoceras* of the *O. boreale* group (*O. latilobatum* WANG & HE, according to KRYSTYN & ORCHARD a junior synonym of *O. fissisellatum* DIENER). This was the first usage of ammonoids to show the Perigondwana *O. woodwardi* Zone is younger than the Boreal *Otoceras* faunas, whereas all ammonoid workers prior to KRYSTYN & ORCHARD (1996) had correlated the *O. woodwardi* Zone either with the *O. boreale* Zone (e.g., DAGYS, 1994) or with the *O. concavum* Zone (e.g., TOZER, 1967). Therefore, the contradiction between the conodont and ammonoid correlations of the Boreal and Perigondwana *Otoceras* fauna has been resolved and the *O. concavum* Zone proven to be two ammonoid zones older than the *O. woodwardi* Zone (which is, according to priority the oldest Triassic ammonoid zone, see above).

The FAD of *Lystrosaurus* is used in continental beds to define the base of the Triassic. In most places, the first occurrence of *Lystrosaurus* is within the lowermost Triassic, but not necessarily at its base. The FAD of *Lystrosaurus*, however, can only be found in two

areas, in South Africa and in Dalongkou (Sinkiang). In both areas, there is an overlap with the Upper Permian index genus *Dicynodon*. In Dalongkou, the interval with the co-occurrence of *Lystrosaurus* and *Dicynodon* contains the conchostracans *Falsisca eotriassica* KOZUR & SEIDEL and *F. postera* KOZUR & SEIDEL. These conchostracans occur in the late Dorashamian (KOZUR, 1989, 1993; KOZUR & MOCK, 1993), whereas the lowermost Triassic (Gangetian Substage) contains *F. verchojanica* MOLIN. This latter species occurs in Sinkiang, in beds with *Lystrosaurus*, above the last occurrence of *Dicynodon*, and its FAD is in the uppermost beds with *Dicynodon*. Thus, the interval with the co-occurrence of *Lystrosaurus* and *Dicynodon* belongs to the Dorashamian, perhaps with the exception of its uppermost part, in which *F. verchojanica* is already present. The FAD of *Lystrosaurus* lies therefore within the uppermost Permian, but beds with *Lystrosaurus* that lack *Dicynodon* are of Triassic age.

The FAD of the conodont *Hindeodus parvus*, which is well recognizable within a phylomorphogenetic cline *H. typicalis - H. latidentatus praeparvus - H. parvus*, can be traced in all marine facies and faunal realms. It is common in ammonoid-free, shallow-water deposits of Tethys, Perigondwana, the Circum-Pacific area (western North America and Japan), and the Boreal realm. It is moderately common to rare in ammonoid-bearing pelagic rocks in Perigondwana and in the Arctic, where the cool-water *Clarkina carinata* group is better adapted to pelagic environments and mostly predominates. *H. parvus* is especially common in pelagic deposits of the basal Triassic *H. parvus* Zone in western and central Tethys. This facies is dominated by gondolellid conodonts (*Clarkina*) in the Upper Permian and in the Lower Triassic above the *H. parvus* Zone. However, after the disappearance of the Upper Permian warm-water gondolellid fauna (*C. subcarinata* group), at or a little below the PTB, the western and central Tethys has no gondolellid conodonts in the *H. parvus* Zone, not even in the slope facies favoured by Permian and Triassic gondolellid conodonts. In the *Isarcicella isarcica* Zone, gondolellids of the cool-water *C. carinata* group invaded the pelagic environments of the central and western Tethys, after they had adapted to warm-water conditions. In the Upper Permian, the *C. carinata* group is only present in the Arctic and in Perigondwana.

H. parvus begins in Perigondwana a few centimetres below the *O. woodwardi* Zone in the uppermost *O. boreale* Zone, and it occurs only in the uppermost part of the Boreal *O. boreale* Zone (KOZUR, 1995a, 1996b, 1997c; HENDERSON & BAUD, 1996). In Greenland, it occurs above the *Otoceras*-bearing beds of the *O. boreale* Zone s.s., and below the ammonoid-dated beds of the *Ophiceras commune* Zone, in beds with small *Hypophiceras*, *Tompophiceras gracile* (SPATH) and *T. pascoei* (SPATH) that indicate the *T. pascoei* Zone. According to DAGYS & ERMAKOV (1996) this zone corresponds to the uppermost *O. boreale* Zone s.l. It may be used, however, as an independent zone.

HENDERSON & BAUD (1996) reported two specimens of *Hindeodus* cf. *parvus* from the *O. boreale* Zone s.l. of Arctic Canada, without any indication of the exact level within this zone. In the lecture at the 30th IGCP in Beijing, they presented photos of these specimens that are fragmented forms that cannot be exactly determined because the cusp is broken away. It cannot be excluded that they belong to *H. parvus*. Their occurrence was shown in the uppermost part of the *O. boreale* Zone s.l. This occurrence fits well with the FAD of *H. parvus* in Greenland and in Perigondwana.

In Tethys, *H. parvus* was found in all conodont-bearing rocks of the lowermost Triassic, e.g., in Meishan and other localities of South China, in Malaysia, Iran, Azerbaidzhan, Armenia, Turkey, Hungary, in the Dinarides, Southern Alps, and in western Sicily (Italy). It is also present in the Circum-Pacific area (western North America and Japan - PAULL & PAULL, 1994; IGO, 1996; KOIKE, 1996). In contrast, gondolellid conodonts have a very restricted distribution in the lowermost Triassic *H. parvus* Zone. They are not only missing in the predominant shallow-water deposits of Tethys, Perigondwana and the Circum-Pacific area, but also in pelagic and slope deposits of the western and central Tethys. They are also absent in the most ammonoid-bearing deposits of NE-Siberia. Thus, the FAD of *H. parvus* is the only palaeontological datum that can be found in all the marine deposits of the world. Using this datum, the marine deposits around the PTB can be well correlated (Figs. 1a & b). As the FAD of *H. parvus* almost coincides with the base of the *O. woodwardi* Zone, the priority PTB, most authors regard the FAD of *H. parvus* as the most suitable marker for the base of the Triassic (YIN, 1985, 1993; KOTLYAR et al., 1993; KOZUR, 1994a, 1995a, b, 1996a, b, c, d, 1997a, b, c, d; PAULL & PAULL, 1994; WANG, 1994, 1995a, b, c, 1996; ZHU et al., 1994; DING et al., 1995, ZHANG et al., 1995, 1996; IGO, 1996; KOZUR et al., 1996b; LAI et al., 1996a; WANG et al., 1996; WIGNALL & HALLAM, 1996; WIGNALL et al., 1996; YIN et al., 1996a, b; YIN & ZHANG, 1996; HALLAM & WIGNALL, 1997; WANG & WANG, 1997; ZHU & LIN, 1997).

For evaluation of the PTB biotic crisis it is important that the FAD of *H. parvus* (base of the Triassic) is situated in the middle part of Boundary Bed 2 (middle part of Bed 27) in Meishan, within the middle Mazzin Member of the Southern Alps, within the E2 Member of the Khunamuh Formation of Kashmir, within the middle Kathwai Member of the Mianwali Formation of the Salt Range, in red shales immediately below large stromatolite bodies in Transcaucasia and NW Iran, and within the uppermost *O. boreale* Zone s.l. (= *T. pascoei* Zone) of the Arctic. In continental beds, this boundary is close to the disappearance of the typical Permian *Dicynodon* after an interval of co-occurrence of *Lystrosaurus* and *Dicynodon*. The direct correlation of the FAD of *H. parvus* in marine beds and the indirect correlations (mainly with conchostracans and sporomorphs) in important continental sections is shown in Figs. 1a & b.

3. PROBLEMS RELATED TO THE VARIOUS LEVELS OF THE PTB IN DIFFERENT FACIES AND FAUNAL REALMS

The exact correlation of a suitable marker level close to the PTB is more important than the actual position of the PTB for the evaluation of the PTB biotic crisis. The FAD of *H. parvus* is such a marker level, whether this bioevent is chosen as the base of the Triassic or not. As the base of the Perigondwana *O. woodwardi* Zone, the priority base of the Triassic, is only a few cm higher than the FAD of *H. parvus*, the finally approved PTB will be, in all cases either very close to, or at the FAD of *H. parvus*, which in the following discussions is used as the base of the Triassic.

The former diachronous correlations of the PTB between the Perigondwana margin and Tethys, within the Tethyan realm and above all, between Tethys and the Boreal realm, had strongly hindered the evaluation of the biotic crisis. For instance, the previous correlation of the Triassic base at the base of the *O. woodwardi* Zone with the base of the Werfen Group in the Southern Alps and with base of the *O. concavum* Zone in the Arctic, had the obvious following consequences for the age of the mass occurrences of fungi: in the pelagic to slope succession of South China, the mass occurrences of fungi were in the uppermost Permian, the percentage of fungal spores dropped below 1 % at the base of the Boundary Beds and fungal spores are practically absent in the Triassic. In the Southern Alps the mass occurrence of fungi would begin in the uppermost Permian and reaches its peak in the lowermost Triassic Tesero Oolite. In the Arctic, the mass occurrences of the fungi would be totally within the Triassic. Taking these distribution patterns, the mass occurrence of fungi around the PTB would not have any special significance.

Taking the FAD of *H. parvus* as an isochronous marker horizon and base of the Triassic, then the global mass occurrences of fungi, independent from the faunal and floral realm, would be before the FAD of *H. parvus* within the uppermost Permian. The mass occurrences decrease everywhere drastically a little before the FAD of *H. parvus* and above the FAD of *H. parvus*, fungal spores are very rare. Thus, the extinction pattern of fungi is totally different using previously accepted diachronous PTB correlations or the isochronous marker horizon (FAD of *H. parvus*). Similar modifications of the detailed extinction patterns can be observed for other fossil groups.

The former assignment of the Boreal *Otoceras* faunas to the Triassic has also caused assignment of all sporomorph associations with a high percentage of trilete cavate spores (e.g., *Lundbladispora obsoleta - Lunatisporites noviaulensis* association) to the Triassic

despite the fact that these associations begin in Tethys in the undoubtedly latest Permian deposits, e.g. in the lower Tesero Horizon of the Southern Alps, with upper Dorashamian conodonts (see below), fusulinids, Permian small foraminifers and Permian brachiopods. The revision of the conodont faunas in the *Otoceras* beds of Greenland (SWEET, 1976) by re-study of SWEET's collection allowed the re-evaluation of the age of the palynological events published by BALME (1979). The following succession of bioevents is present: Appearance of "Triassic" sporomorphs - end of the mass occurrences of fungal spores - FAD of *H. parvus*. The first two events are within the Dorashamian as in the Southern Alps, and the second event is also recognizable in the uppermost Dorashamian of South China. Erroneous correlation of the Perigondwana and Boreal *Otoceras* faunas caused erroneous determination of the PTB in continental beds, and erroneous circular conclusions, e.g., the "Triassic" age of the Boreal *Otoceras* faunas and of the lower Tesero Horizon of the Southern Alps due to the presence of "Triassic" sporomorphs.

Before the review of the conodont and ammonoid data by KRYSTYN & ORCHARD (1996), the erroneous placement of the PTB in the Arctic was difficult to recognize. There, neither at the base of the *O. concavum* Zone nor at the FAD of *H. parvus* nor in any horizon between these biostratigraphic levels, could a distinct drop in diversity be observed, because a very low-diversity fauna was already present before the *O. concavum* Zone. This was because a successive decrease in diversity occurred by the successive disappearance of warm-water faunas, beginning with the disappearance of fusulinids at the base of the Middle Permian (base of Guadalupian Series). This example clearly indicates that the Permian-Triassic biotic crisis was mainly a crisis in the warm-water biota that were restricted to Tethys at the end of the Permian.

Several other problems are related to the exact correlation of the PTB. Strong facies changes from tropical high-diversity shallow-water environments to low-diversity tidal flats are always accompanied by a drastic local drop in diversity. If such changes occur close to, but not at the PTB, such facies-controlled local diversity drops have generally been assigned to the PTB biotic crisis. A good example is the boundary between the Bellerophon Limestone Formation, with a high-diversity shallow-water fauna, and the lowermost Werfen Group (Tesero Oolite), with a low-diversity intertidal fauna. This boundary is related to a sea-level drop within the Dorashamian. In the eastern part of the Southern Alps (Carnic Alps), this sea-level drop caused a sudden shallowing within the Bellerophon Limestone Formation, but the high-diversity Permian shallow-water fauna continued. In the western part of the Southern Alps (Dolomites), the same sea-level drop caused in the originally shallower deposits a sudden change from high-diversity shallow-water fauna of the Bellerophon Limestone Formation to very low-diversity fauna of intertidal oolitic beds (Tesero Oolite of basal Werfen Gro-

up). Despite the fact that this drastic diversity drop has nothing to do with the PTB biotic crisis, but is an intra-Upper Permian facies-controlled diversity drop, it was used as a classical example for the severe PTB extinction event.

The situation in Meishan (South China) is different although a very distinct diversity drop can also be observed 18 cm below the FAD of *H. parvus*, at the base of Bed 25. This diversity drop is a real extinction event. It is distinctly younger than the Bellerophon Limestone Formation / Werfen Group boundary. According to the conodont fauna and the distribution of the fungal spores, this extinction level somewhat below the PTB corresponds to a level approximately 2 m above the base of the Tesero Oolite in the Tesero section and within the Tesero Oolite in other sections (e.g., Sass de Putia). At this level within the Tesero Oolite, the mass occurrence of fungal spores ends (as in pelagic beds at the top of the Changxing Limestone in Meishan at the top of Bed 24), but within a shallow-water upper Dorashamian conodont fauna with *Hindeodus latidentatus praeparvus* KOZUR, *Isarcicella ?prisca* KOZUR and *Stepanovites* cf. *dobruskinae* KOZUR & PJATAKO-VA, distinctly before the FAD of *H. parvus* within the Mazzin Member. No distinct change in the low-diversity fauna can be observed at this level in the Dolomites (Southern Alps) because the rich Permian fauna had already disappeared for facial reasons at the base of the Tesero Oolite, corresponding to a level within the upper Changxing Limestone (with a diverse Dorashamian warm-water fauna) of South China.

Particularly in continental environments, strong biotic changes at the PTB are assumed in sections with a long time-gap between the youngest Permian and the oldest Triassic faunas. For instance, between the Tatarian Stage and the lowermost Triassic on the Russian Platform, there is a long gap that comprises nearly the entire Upper Permian Lopingian Series (KOZUR, 1989, 1994b, 1998a). Despite the fact that the Tatarian is mostly regarded as uppermost Permian, on the Russian Platform (type Tatarian) it ends in different Capitanian to lowermost Dzhulfian levels. Therefore, the strong faunal changes between the continental Tatarian (Permian) and Vetlugian (Triassic) that were assigned to the extinction event at the end of the Permian, are in reality faunal differences between the Middle Permian Capitanian and different levels within the lowermost Triassic. Therefore, a summary effect of late Guadalupian and PTB biotic changes is assigned to the PTB biotic crisis.

In Dalongkou (Sinkiang), where a continuous, fossil-rich sequence is present in the Upper Permian and Lower Triassic, the change from the Permian to Triassic biota occurs in several steps of extinction and innovation that are mainly situated well below the oldest assumed PTB, the FAD of *Lystrosaurus*, at which level no extinction event in any faunal or floral group can be observed. Even the Upper Permian vertebrate guide form, *Dicynodon*, continued. A certain extinction event

Kozur: Problems for Evaluation of the Scenario of the Permian-Triassic Boundary...

141

is indicated by the disappearance of *Dicynodon*, in time-correlation close to the FAD of *H. parvus*, but this extinction is only the final replacement of the Permian *Dicynodon* by *Lystrosaurus* that appeared considerably earlier. Other Permian elements, such as Permian freshwater gastropods disappeared somewhat earlier, but also considerably above the FAD of *Lystrosaurus*.

Rather distinct changes can be observed considerably below the FAD of *Lystrosaurus*. The conchostracan genus *Falsisca* that straddles the PTB, begins about 96 m below the FAD of *Lystrosaurus*. The typical Permian conchostracan genera *Bipemphigus*, *Megasitum* and *Tripemphigus* disappear 65 m below the FAD of *Lystrosaurus*. Around this level, a distinct increase in trilete cavate spores can be observed.

It is very interesting that in the continental biota the "Triassic" elements (taxa that straddle the PTB and represent the lowermost Triassic faunas after the extinction of the Permian elements) all begin within the Upper Permian, long before the extinction of the Permian elements. Thus, the conchostracan *Falsisca* appear far below the FAD of *Lystrosaurus*, and after the later disappearance of typical Permian genera, also distinctly below the FAD of *Lystrosaurus*, the generic composition of the conchostracan faunas is already identical with that of the lowermost Triassic. Similar extinction and innovation patterns are known among the vertebrates, where the predominantly Triassic *Lystrosaurus* appeared within a Permian *Dicynodon* fauna, and the full Triassic character of the vertebrate fauna was established by the disappearance of *Dicynodon* close to the PTB (if defined with the FAD of *H. parvus*).

Only detailed investigations of such a continuous rich faunal record across the PTB as in Dalongkou can help to understand the extinction and recovery patterns of the continental faunas. Compilations of Upper Permian and Lower Triassic continental faunas with poor stratigraphic control hinder the evaluation of the biotic changes in the continental Upper Permian and Lower Triassic faunas rather than aid the progression of these studies.

4. PROBLEMS WITH THE RECOGNITION OF THE EXACT EXTINCTION AND RECOVERY PATTERNS OF MAJOR FOSSIL GROUPS CLOSE TO THE PTB

Interpolation of the unknown Scythian or lower-middle Scythian diversity of many major fossil groups from the known diversity in the Upper Permian and Anisian in literature compilations (e.g., ERWIN, 1993) is one of the major problems for the evaluation of the causes of the PTB biotic crisis.

The record of many pelagic, and also of shallow-water marine faunal groups in the lower and middle Scythian is very poor. A large percentage of taxa that disappeared at the PTB, re-appeared in the upper Scythian (upper Olenekian) or, more frequently, in the Middle Triassic. For several groups the percentage of re-appearing genera (Lazarus taxa) is 90-100 %. Nevertheless, these forms have not yet been found in the Scythian or lower-middle Scythian, not even in favourable facies. Good examples are the scolecodonts and the holothurian sclerites. Scolecodonts are common in shallow-water, gray or black limestones and shales during the Upper Permian and Middle Triassic. During the Lower Triassic, these sediments are widely distributed, but the examination of more than 1000 samples in facies favourable for the presence and preservation of scolecodonts has not yielded any specimens. All Upper Permian genera, bar one, re-appear during the Anisian and Ladinian. The only genus, *Delosites*, that does not re-appear in the Middle Triassic, is represented by its immediate successor, *Palurites*. In the broader definition of *Delosites* by ZAWIDZKA (1971) and KOZUR (1973), both genera are identical. Independent of this special taxonomic question, the number of Triassic scolecodont Lazarus genera is 100%, none of the Upper Permian genera that disappeared at or somewhat below the PTB, really became extinct.

Permian, Middle and Upper Triassic holothurian sclerites are common both in shallow-water and in pelagic deposits. They are especially common in Hallstatt Limestones, mainly reddish limestones with a very low sedimentation rate that are often stratigraphically condensed. Several hundred Scythian samples in the most favourable facies for the occurrence and preservation of holothurian sclerites, among them large samples from Hallstatt Limestones, have not yielded any holothurian sclerites. However, in the Middle Triassic, 9 out of 10 genera, which are present in the uppermost Permian, re-appeared in the Middle Triassic. The only Upper Permian genus, which does not re-appear in the Middle Triassic, is *Julfocaudina* MOSTLER & RAHIMI-YAZD. However, this genus does not occur in the upper *Paratirolites* beds and, therefore, disappeared distinctly before the PTB (MOSTLER & RAHIMI-YAZD, 1976). Holothurian sclerites underwent a rather rapid evolution of the form taxa that can be well related to natural species, and have considerable stratigraphic importance in the Middle and Upper Triassic (e.g., MOSTLER, 1969, 1973; KOZUR & MOCK, 1974). Despite this fact, 6 out of 8 species, which are present in the uppermost *Paratirolites* beds, also occur in the Middle and/or Upper Triassic (MOSTLER & RAHIMI-YAZD, 1976). Thus, the holothurian sclerites also belong to those groups, of which 100% of the genera survived the PTB biotic crisis. An interpolation of the unknown Lower Triassic generic diversity of the scolecodonts and holothurian sclerites to be constant from the Upper Permian to the base of the lower Middle Triassic would be formally, in a global aspect, correct. However, such an interpretation would mask the true picture that these fossils were not found in the Lower Triassic even in the most favourable facies (gray shallow-water limestones for scolecodonts and reddish Hallstatt Limestones for holothurian sclerites), despite investigation of a large number of samples in different

facies and areas. They have also not been reported by other specialists.

The fact that all Eunicida/Phyllodocida genera (their isolated jaws are the scolecodonts) and holothurian genera must have survived the PTB does not mean that they were not affected by the PTB biotic crisis. They were strongly affected and retreated to currently unknown relic areas from where they re-settled the Middle Triassic seas. Thus, even in this case, where the interpolations are formally correct, they do not show the real picture of the PTB faunal crisis.

Unfortunately, in and prior to ERWIN (1993), the Scythian, or at least the lower to middle Scythian diversity patterns of most of the fossil groups were interpolated from the known Upper Permian and Middle Triassic diversity. From this, a totally incorrect picture of the extinction and recovery patterns for many major fossil groups emerged. Only in HALLAM & WIGNALL (1997) a correct picture of the extinction and recovery patterns of some major fossil groups has been given, but no details (amount of the genera in the different Upper Permian to Middle Triassic stages) were presented and not all the major fossil groups were considered. Nevertheless, the exctinction - recovery patterns presented by HALLAM & WIGNALL (1997) can be used for evaluation of the character of the PTB biotic crisis. The exctinction - recovery patterns shown by ERWIN (1993) are mostly literature compilations and for most of the major fossil groups are so misleading that they mask rather than highlight the true extinction and recovery patterns. This is mainly the result of literature compilation and incorrect interpolation of the Lower Triassic (or lower to middle Scythian) diversity.

Lower Scythian diversity interpolation from known Upper Permian and Middle Triassic diversities produces an especially misleading picture in those fossil groups that have a high Upper Permian and Middle Triassic diversity, but were strongly affected at the PTB (real or largely real extinction, none, very few or a moderate amount of Lazarus taxa). In these groups the Middle Triassic high diversity is not caused by reappearance of Lazarus taxa as in the scolecodonts or holothurian sclerites, but by a strong radiation of a very low-diversity fauna which survived the PTB biotic crisis, or by the new development from skeleton-free representatives. A Scythian diversity interpolation of these groups shows no pronounced diversity drop at the PTB and a high diversity throughout the Scythian that was not present.

Two typical examples for a totally incorrect picture of the exctinction - recovery patterns of major fossil groups are discussed below.

The Radiolaria were shown by ERWIN (1993) to have a slight diversity drop from 4 to 3 families from the Capitanian to the Dzhulfian, and this level remains constant until the Anisian (Fig. 2). This diversity pattern is not only totally outdated, but it is interpolated for the Lower Triassic interval, because until recently no radiolarians were known from the Brahmanian and lower Olenekian. Only KOZUR et al. (1996a) described the first known radiolarians from this interval. Two species of two genera and two families were discovered. As these are Palaeozoic types, they probably have survived the PTB, but only in the upper Olenekian does the diversity of the radiolarians again become higher. Most of the upper Olenekian forms may have evolved from skeleton-free or simple spicular radiolarians. The real diversity pattern of the radiolarians is shown in Fig. 2. There is a strong drop in diversity immediately below the PTB, an extremely low-diversity fauna in the lower and middle Scythian (Brahmanian = "Induan", and in the lower Olenekian), a recovery to near Upper Permian diversity in the upper Olenekian and lower Anisian, and an explosive radiation in the middle and upper Anisian with a diversity far higher than that of the Upper Permian. The picture would be more impressive at genus and species level, but for a comparison to highlight the immense problems that were caused by interpolation of the Scythian diversity, the family level has to be used, as ERWIN (1993) used this taxonomic level. Whereas during the lower and middle Scythian the number of species, genera and families is the same (2), the number of the Dorashamian genera is about 2 times, the number of the upper Olenekian genera about 1.4 times, and the number of the upper Anisian genera about 2.5 times larger than the number of families. Dorashamian genera have on average 2 - 3 species, upper Olenekian genera 1 - 2 species and upper Anisian 2 species. As I have investigated these radiolarians by myself, the degree of splitting for the compared radiolarian faunas is the same.

The interpolated picture presented by ERWIN (1993) indicates that nothing happened with the siliceous plankton at the PTB. In reality, the skeleton-bearing radiolarians nearly died out, and the production of organic silica dropped close to zero. Even in the Panthalassa Ocean the lower and middle Scythian has no radiolarites, only shales that interrupt continuous Permian to Jurassic radiolarite sequences. In this example the interpolation of the diversity in the Scythian presents a totally incorrect picture.

A similar incorrect picture was presented by ERWIN (1993) for the non-fusulinid foraminifers (Fig. 2). Also for this group, a constantly high diversity was shown (19 families) from the Dorashamian to the Anisian. In reality, only the Upper Permian and Anisian foraminiferal faunas show this high diversity, whereas the Brahmanian and lower Olenekian foraminiferal faunas have a very low diversity. Even considering the fact that the Anisian foraminiferal families have a high percentage of Lazarus taxa, there is a very distinct diversity drop at the PTB.

A similarly incorrect, and for the Lower Triassic interpolated scenario, was shown by ERWIN (1993) for the siliceous sponges (Fig. 3). In this case, the reconstruction at family level is very difficult because the siliceous sponges are mostly not classified at family level, but in species, genus and order levels. Moreover,
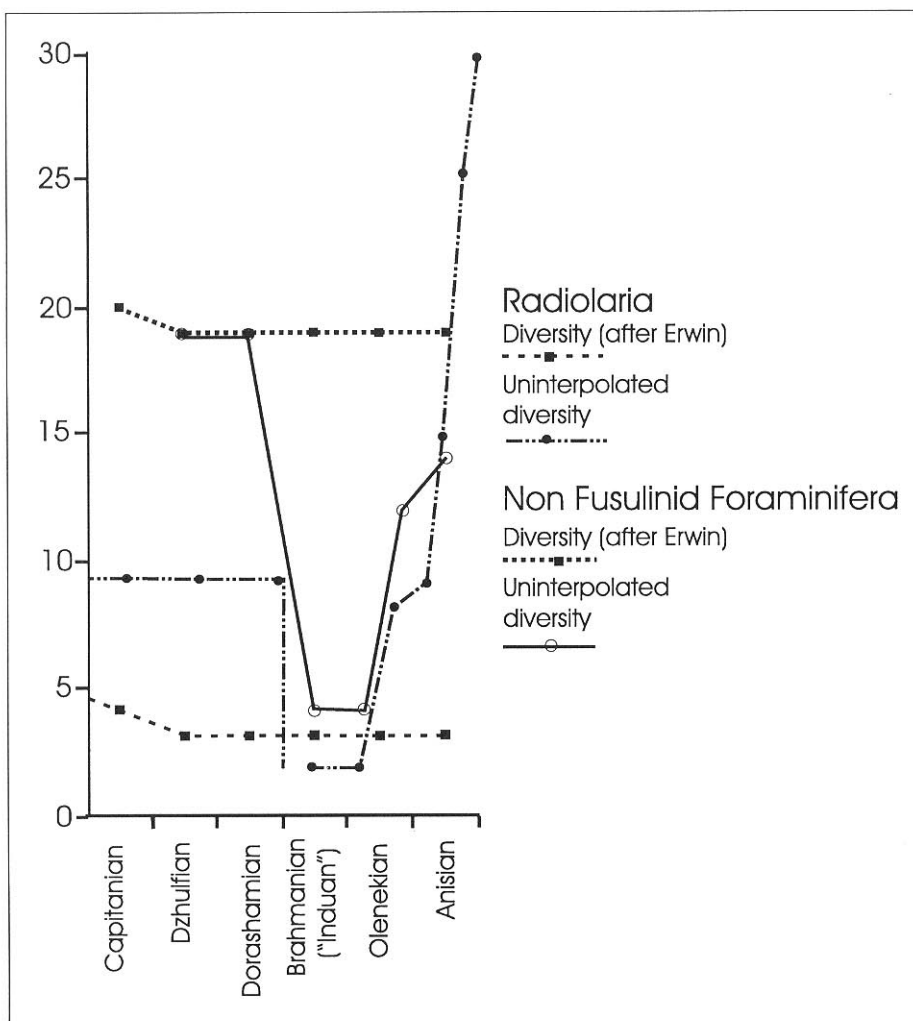
Fig. 2   Stage-level Capitanian-Anisian family diversity patterns of Radiolaria and non-fusulinid foraminifera after ERWIN (1993) in comparison with not interpolated diversity patterns. The Scythian radiolarian family diversity patterns by ERWIN (1993) is clearly interpolated, and shows no impact of the PTB biotic crisis on the diversity of Radiolaria in family level. The not interpolated family diversity pattern of Radiolaria shows a nearly complete extinction at the PTB, a beginning recovery in the upper Olenekian and a strong radiation in the Anisian. The diversity pattern of the non-fusulinid foraminifers by ERWIN (1993) for the Scythian part is also interpolated from the known Dorashamian and Anisian high diversity faunas because the distinct lower and middle Scythian minimum is missing. In the uninterpolated diversity curve for foraminifers, the Dzhulfian and Dorashamian family diversity was overtaken from ERWIN (1993), because it lies within the error range caused by different taxonomic scope of the families. The Anisian diversity at family level lies below the Upper Permian diversity. Lazarus taxa are dominant in family level. The diversity increase in family level from the upper Olenekian to Anisian is low, but in genus and species level it is high. The strong increase in family level diversity from the lower to upper Olenekian can be only observed in eastern Tethys and open-sea pelagic deposits in western Tethys (e.g., western Sicily). In upper Olenekian shallow-water deposits of western Tethys foraminifers are common but have a low diversity.

most of the taxa in the Dorashamian and Anisian have to be reconstructed from sponge spicules.

The Demospongiae (Fig. 3) were shown by ERWIN (1993) to have a very slight diversity drop from the Capitanian to the Dzhulfian (from 15 to 14 families), then a constant family diversity (14 families) until the uppermost Permian, and an increase to 15 families in the "Induan", a diversity that remained constant until the end of the Anisian. In reality, the Demospongiae have a strong diversity drop from the Capitanian to the Dzhulfian (from 12 to 6 families) and this diversity remains constant until the top of the Dorashamian. They disappeared at the PTB and are not known from the Scythian. They re-appeared in the Middle Triassic, where their diversity quickly became higher than in the Upper Permian. There are many Lazarus taxa, but several groups became extinct at the PTB.

The Hexactinellida (Fig. 3) are shown by ERWIN (1993) to have a drop in family diversity (6 down to 4 families) from the Capitanian to the Dzhulfian, and this diversity remained constant until the end of the Anisian.

Also this diversity pattern is interpolated for the Scythian because in 1993 only one Hexactinellida family (one genus, one species - RIGBY & GOSNEY, 1983) was known from the upper Scythian, and only KOZUR et al. (1996a) reported the first siliceous sponge spicules from the upper Brahmanian and lower Olenekian, which also belong to a single species, perhaps the same species as in the upper Olenekian.

The real distribution pattern of the Hexactinellida (based mainly on data of Prof. H. MOSTLER, Innsbruck, pers. comm.) looks totally different (Fig. 3). There was a drop in diversity from the Capitanian to the Dzhulfian from 6 to 3 families that continued until the end of the Dorashamian (2 families). There is a very distinct drop in species diversity from the Capitanian to the end of the Dorashamian (about 70% drop in diversity), nevertheless, Hexactinellida are still common in the uppermost Dorashamian (e.g., in western Sicily - KOZUR & MOSTLER, in prep.). In the upper "Induan" and Olenekian, one genus with one species is present. In the Anisian, the diversity of the Hexactinellida
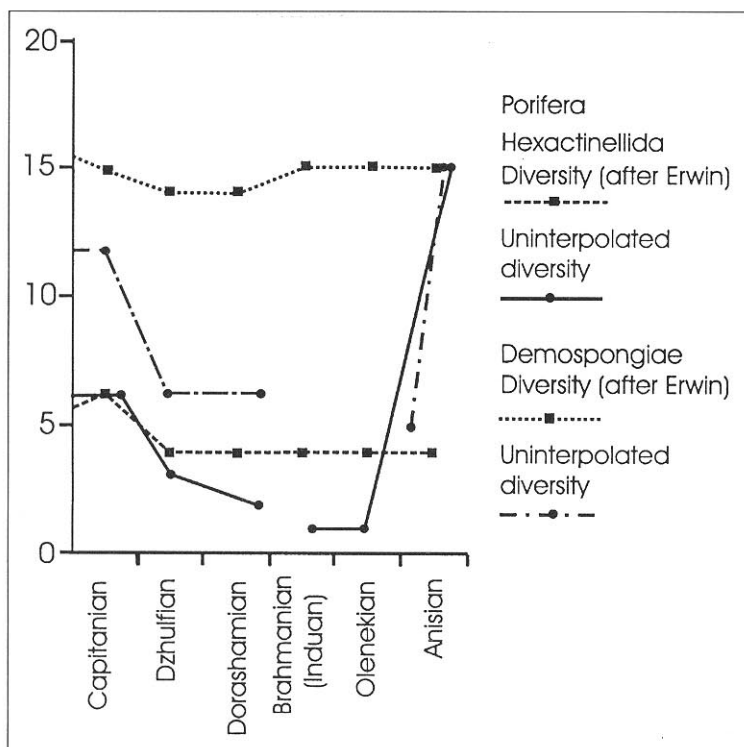
Fig. 3 Stage-level Capitanian to Anisian family diversi-
ty patterns of siliceous sponges (Demospongiae and
Hexactinellida). Comparison of the diversity pat-
terns with interpolated Scythian diversity by
ERWIN (1993) that show no PTB extinction event,
with the not interpolated diversity pattern that
shows the known Scythian diversity. Interruption
of the curve means that in the Scythian no Demo-
spongiae and in the lower Brahmanian (lower Indu-
an) no Hexactinellida are known. This curve shows
that the siliceous sponges have been strongly
affected by the PTB biotic crisis and recovered
only in the Middle Triassic, where many Lazarus
taxa appeared.

started with low diversity pioneer faunas, and the diver-
sity rapidly increased within the Anisian (15 families).
There are many Lazarus taxa of groups that disappeared
at the end of the Permian or earlier, but because the
diversity is mostly reconstructed from sponge spicules,
it cannot be excluded that some forms are not Lazarus
taxa, but homeomorphic forms that newly developed in
the Middle Triassic.

In all these cases the diversity drop is far higher
than indicated by ERWIN (1993). However, except for
the radiolarians, the number of the Lazarus taxa is
rather high, for instance, in the siliceous sponges more
than 50%. The important question is, why do they re-
appear only in the upper Olenekian, or mostly only in
the Middle Triassic.

The above examples have shown that interpolation
of the Scythian diversity from the Upper Permian and
Middle Triassic diversities leads to completely incor-
rect diversity patterns across the PTB and in the Scythi-
an. The true diversity patterns from the Upper Permian
to the Middle Triassic show a lot of details of the
extinction and recovery processes in different fossil
groups. But even true numeric diversity patterns are
mostly insufficient to show the real extinction and
recovery patterns. As most fossil groups comprise a
wide variety of taxa adapted to totally different facies,
it is important to study what were the extinction and
recovery patterns of different taxa within an investiga-
ted fossil group. Forms that lived in different environ-
ments must be separately investigated, warm-water ver-
sus cold-water taxa, shallow-water versus deep-water
taxa, fresh-water versus marine taxa, terrestrial versus
aquatic taxa, light-dependent taxa versus light-indepen-

dent taxa, taxa that need high oxygen content in the
water versus taxa that could live under reduced oxygen
content, taxa that lived in the northern hemisphere ver-
sus taxa that lived in the southern hemisphere etc.

For instance, only warm-water faunas were strongly
affected by the PTB biotic crisis. In the low-diversity
Boreal faunas no distinct extinction event can be
observed, neither at the base of the *O. concavum* Zone
nor at the much higher FAD of *H. parvus* or at any lev-
el in between. An exception is the disappearance of
sponge spicules a little below the FAD of *H. parvus*.
The Boreal land floras and the fungi were, however,
rather strongly affected, e.g., the end of the fungal mass
occurrences somewhat below the FAD of *H. parvus*.

Deep-water, cold bottom water, benthic faunas
(palaeopsychrospheric faunas), investigated mainly
among the ostracods (KOZUR, 1991), are not greatly
affected, but the upper Scythian and Middle Triassic
palaeopsychrospheric faunas consist mainly of Lazarus
taxa. However, these may not be true Lazarus taxa
because no lower and middle Scythian palaeopsychro-
spheric ostracod faunas are currently known.

Light-dependent taxa (corals, green algae) were
strongly affected, but as they are also warm-water taxa,
it is difficult to decide which factor (light or tempera-
ture changes or both) was decisive for the strong extinc-
tion event among these faunas and floras.

Fresh-water faunas with freeze- and/or drought-
resistant eggs were not affected by the PTB biotic crisis
(e.g., *Falsisca* and *Euestheria* among the conchostra-
cans, both present in temporary fresh-water lakes of the
tropical and Boreal realms). Also other fresh-water fau-
nal elements that occur in the Permian both in the Bore-

al and tropical realms, were not affected by the PTB (*Darwinula* among the ostracods).

Different aspects of the investigation of the extinction-recovery patterns can be well studied in the ostracods because this group has common representatives in fresh-water and marine, shallow-water and deep-water deposits, warm-water and cold-water biotopes, and among the ostracods there occur taxa that could live only under normal oxygen content and others that could live under reduced oxygen contents in the sea water.

If we compare Upper Permian with Lower to Middle Triassic ostracods as a whole, we cannot find many differences. The Upper Permian ostracod faunas are dominated by smooth Bairdiacea, such as *Bairdia*, *Cryptobairdia*, *Bardiacypris*, *Fabalicypris*, and in palaeopsychrospheric deep-water ostracod faunas also *Acathoscapha*. The same genera are predominant in the Upper Scythian and Middle Triassic ostracod faunas. Sculptured Bairdiacea are common in the Middle and Upper Triassic, but some are also present during the Upper Permian. This minor difference in the bairdiacean fauna is an evolutionary change.

Cavellinids (*Cavellina*, *Sulcella*) are very common both in Upper Permian and in Triassic ostracod faunas. During the Middle Triassic transitional forms to *Cytherella* occur, but this difference is also a normal evolutionary change.

Kymatophobe ostracod faunas (ostracods that avoid environments with turbulent water movements), are both in the Upper Permian and in the Middle and Upper Triassic rich in Healdiacea.

The Permian and Lower-Middle Triassic Cypridocopina and closely related forms are similar. *Acratia*, *Acratina* and *Microcheilinella* are common both in the Upper Permian and in the Middle-Upper Triassic. However, whereas they occur in both deep-water and shallow-water deposits during the Late Permian, they are restricted to deep-water deposits during the Triassic. *Triassocypris* is present both in the Upper Permian and in the Triassic. *Bashkirina* and *Haworthina* have closely related successors in the Lower and Middle Triassic. The only distinct difference is the disappearance of *Praepilatina* that is common up to the top of the Permian.

Cytherocopina are dominated during the Upper Permian by Bythocytheracea and in the palaeopsychrospheric deep-water faunas also by Tricorninacea. Most of the Upper Permian (and older) Bythocytheracea genera are also present in the Triassic, such as *Jonesia*, *Keijicythere*, *Nemoceratina*, *Paraberounella* and *Triassocythere*. Other Upper Permian Cytherocopina belong to the Youngiellidae, Cytherissinellinae and Judahellinae. The Youngiellidae end at the P/T boundary. In contrast, most of the Cytherissinellinae and Judahellinae genera also occur in the Triassic, such as *Callicythere*, *Judahella* and *Gruendelicythere* with the subgenus *Trodocythere*. Only *Visnyoella* is restricted to the Permian. Consequently, the Scythian Cytherocopina consists nearly of the same genera as the Upper Permi-

an ones. Beginning in the upper Scythian and above all in the Middle and Upper Triassic, numerous new Cytherocopina genera evolved, but this is a normal evolutionary process.

Except for the above mentioned ostracods, Hollinellacea of Paleocopida, Kloedenellacea of Platycopida and Kirkbyacea of Reticulocopida are common in Upper Permian shallow-water deposits. The commonly expressed view that the Palaeozoic and Triassic ostracods are very different because Paleocopida are present to the top of the Permian but absent in the Triassic, is not true. Firstly, the Paleocopida in the Upper Permian shallow-water deposits are only represented by the genus *Hollinella* and secondly, this genus is dominant in lower Scythian shallow-water deposits.

Kloedenellacea are very common in the Upper Permian, but mainly represented by 3 genera of Perprimitiidae: *Hungarogeisina*, *Italogeisina* and *Indivisia*. The last two genera are also present in the Lower Triassic. Other Kloedenellacea, like *Pseudobeyrichiopsis*, are very rare even in the extremely rich Upper Permian ostracod faunas of Hungary.

The Upper Permian Kirkbyacea are common and diverse in shallow-water environments. Several genera, especially *Carinaknightina*, continued in the Early Triassic of Perigondwana and of eastern Tethys. Within the Triassic, they have been replaced by typical Punciacea that evolved from small Kirkbyacea, but this transition had already begun within the Late Carboniferous-Late Permian time interval, where such characteristic punciid features evolved, such as the bracket teeth, and nearly all Kirkbyacea acquired a calcified inner lamella during the Late Permian.

No distinct changes can be observed within the Cladocopida and Myodocopida. *Polycope* is common in the Upper Permian and in the Triassic. Only some, rather rare specialized forms, such as *Nodopolycope*, are restricted to the Upper Permian.

Even such ostracods that are very rare or not yet known in the Permian survived the P/T boundary. The myodocopid Cypridinidae that are very rare in the Permian became a little more frequent in the Triassic, but no distinct differences between the Permian and Triassic forms can be observed. True and definitely not reworked "entomozoids" occur in the Triassic (KOZUR, in prep.).

Paraparchitacea and Binodicopina disappeared at the Permian-Triassic boundary, but the Upper Permian Binodicopina are only represented by the rare *Neoulrichia*.

The Dorashamian and Lower Triassic fresh water ostracod faunas consist of *Darwinula*.

As a whole, the faunal changes between the Upper Permian and Triassic ostracod faunas are insignificant. Most of the Permian ostracod families and genera survived into the Triassic. However, as shown below, this picture is oversimplified.

The Upper Permian Tethyan shallow, warm-water ostracod faunas are very diverse and consist both of

"modern forms", like Bairdiacea including sculptured Bairdiacea, Cytherocopina, Cypridocopina, and "Palaeozoic forms", like paleocopids, kirkbyaceans, kloedenellids, and cavellinids. In the Middle-Upper Triassic shallow-water ostracod faunas, the "Palaeozoic" forms are no longer present except for common transitional forms from cavellinids to cytherellids and very rare Punciacea that evolved from Kirkbyacea (KOZUR, 1998b). However, this does not mean that the extinction of the Palaeozoic forms occurred at the P/T boundary. On the contrary, in the Tethyan lower Scythian ostracod faunas the "modern forms" are missing. These faunas consist mainly of *Hollinella tingi* (PATTE), sometimes accompanied by a *Cavellina* or the cavellinid *Langdaia* species and/or an *Indivisia* species of Kloedenellacea. Thus, it appears that the mixed Palaeozoic-Mesozoic Tethyan Upper Permian shallow, warm-water fauna is followed by a 100 % Palaeozoic fauna. These forms, the cavellinids, the kloedenellids, but also the paleocopids are filter feeders (ADAMCZAK, 1969), able to live under dysaerobic conditions as has been shown for Meso-Cenozoic filter feeder faunas (BOOMER & WHATLEY, 1992; LETHIERS & WHATLEY, 1994, 1995; WHATLEY, 1995).

Thus, if we do not compare the Upper Permian and the Triassic faunas as a whole, but examine in detail what happened at the P/T boundary, then we can state that in the lowermost Triassic dysaerobic conditions also prevailed in shallow-water deposits, as in the Werfen facies. There was a kind of superanoxia (ISOZAKI, 1994, 1997), because at this time there were widespread anoxic conditions in oceanic deposits that reached to unusually shallow levels. These superanoxia were also determined by evaluation of sedimentological or microfacial and geochemical criteria (HALLAM, 1994; HALLAM & WIGNALL, 1997; LAI et al., 1996b; WIGNALL & HALLAM, 1992, 1993; WIGNALL et al., 1995, 1996, 1998). They lasted for an unusually long time, in many places throughout the entire Lower and Middle Scythian (Brahmanian = "Induan" and lower Olenekian), in other places only for one or two conodont zones (*H. parvus* or/and *I. isarcica* zones), as in the deep-water deposits in Sicily.

In the upper Scythian and Middle Triassic, the typical Palaeozoic, low-diversity fauna recovered first, with the re-appearance of numerous Lazarus taxa in the upper Scythian. Nearly all taxa that disappeared at the PTB, re-appeared in this level (see above). At the same time, the Hollinacea and Kloedenellacea became extinct in shallow marine faunas. Only a few Kloedenellacea survived in upper Scythian brackish environments, but became extinct in this facies at the end of the Scythian.

This extinction-recovery pattern can be found in all shallow marine, warm-water faunas of Tethys, from westernmost Tethys (KOZUR, 1985) to easternmost Tethys (e.g., WANG & WANG, 1997). However, the Boreal and Perigondwana ostracod faunas show a different extinction pattern at the PTB. In the Boreal realm both the Upper Permian and Lower Triassic ostracod faunas have a very low diversity, and no obvious changes occur at the PTB, wherever it is placed. In Perigondwana, there is also no distinct extinction event in the ostracod faunas at the PTB. Both in the uppermost Permian and in the Lower Triassic a moderately diverse temperate-water ostracod fauna is present. It contains common, but low-diversity Kirkbyacea (mainly *Carinaknightina* and other small forms, but mainly with other species as in Tethys), very low-diversity Bairdiacea without the tropical sculptured Bairdiacea, very low-diversity Cypridocopina (*Microcheilinella*), low diversity Cytherocopina, and a few Cavellinidae (SOHN, 1970). The *Hollinella*-cavellinid-kloedenellid boom of the lowermost Triassic of Tethys is missing. If we look the further differences to the tropical Tethys both in the uppermost Permian and in the Lower Triassic, then we can state that the uppermost Permian fauna is a cool-temperate fauna of moderate diversity, in which all the tropical forms, such as sculptured Bairdiacea, strongly sculptured representatives of Kirkbyacea and Kloedenellacea are missing. Moreover, the strong anoxic event in the *H. parvus* and *I. isarcica* zones is missing. Instead, the anoxia began immediately above the *I. isarcica* Zone (WIGNALL et al., 1996). The differences in the faunas between Perigondwana and the Tethys (cool-temperate versus tropical) and the distinctly later beginning of the strong anoxia in Perigondwana compared with the tropical Tethys allow testing of whether the anoxia were either directly responsible for the PTB extinction (HALLAM, 1994; HALLAM & WIGNALL, 1997; WIGNALL & HALLAM, 1992, 1993; WIGNALL et al., 1995, 1996, 1998) or only indirectly (by preventing the rapid recovery of the Tethyan warm-water fauna), and the assumed volcanic winter had the main killing effect on the Tethyan warm-water faunas (KOZUR, 1994a, 1996b, c, d, 1997b, c).

The moderate diverse Perigondwana cool-temperate ostracod fauna straddles the PTB without distinct changes. This could be due to the fact that the non-tropical ostracod fauna was unharmed by the short-lasting volcanic winter (the expected response of a cool-temperate fauna to a three-six month period of cooling). An other explanation may be the absence of anoxia in the Perigondwana *H. parvus* and *I. isarcica* zones. However, this ostracod fauna also straddles the onset of the anoxia above the *I. isarcica* Zone. For example, the same Kirkbyacea as in the uppermost Permian are common in the lower Mittiwali Member of the Mianwali Formation (SOHN, 1970), whereas the change to dysaerobic conditions had already occurred within the upper part of the underlying Kathwai Member (WIGNALL et al., 1996). There is some extinction connected with the beginning of the anoxia (main extinction horizon in WIGNALL et al., 1996), but the diversity drop in the macrofauna at the transition from highly oxygenated shallow-water to more basinal, poor oxygenated deposits is a normal reaction to such a facies change independent of the stratigraphic level in which this

facies change occurred, and unrelated to a mass extinction event. This is best proven by the fact that the same reaction to this facies change is found in Perigondwana at different levels (WIGNALL et al., 1996). It occurs sooner, where the anoxia began earlier (Kashmir) and later, where the anoxia began later (Salt Range). This may produce a local or regional, but not a global low-diversity fauna and flora, and no world-wide mass extinction. Therefore, even the superanoxia does not have a global killing effect on the tropical warm-water fauna, and it cannot affect the fauna and flora of the upper 10-20 m of the water column of the entire tropical Tethyan realm. However, this fauna and flora (green algae, reef community and other warm-water, shallow-water faunas) were the most strongly affected by the PTB biotic crisis.

The third type of change in the ostracod faunas was discovered by HAO (1992) in Guizhou, in the central part of eastern Tethys. As in the entire Tethyan realm, the Upper Permian ostracod fauna is a highly diverse fauna, consisting of "modern" and Palaeozoic types (see above). The southern part of the inner eastern Tethys should be the least influenced by a killing effect of the volcanic winter because it was further away from the huge volcanic eruption center close to the northeastern end of eastern Tethys (at the transition to Panthalassa), and it was close to the tropical Panthalassa, where obviously most of the Lazarus taxa of the Upper Permian shallow, warm-water fauna survived the PTB biotic crisis. As expected, this is the case despite the fact that the anoxic event in the *H. parvus* Zone is very pronounced. The latter is indicated by the booming of *Hollinella* and *Langdaia*. However, in the Guizhou fauna some of those ostracods are also present which disappear in most Tethyan warm-water faunas at the PTB, including *Acratia*, *Fabalicypris*, "*Paracypris*" and *Bashkirina* (the first three forms re-appear in the Upper Scythian or Middle Triassic, whereas instead of *Bashkirina* the closely related successor *Spinocypris* appears in the upper Scythian). Also the kirkbyid *Carinaknightina* is common in the *H. parvus* Zone. The inner eastern Tethyan area was therefore either close to or a part of the refuge for the Upper Permian shallow, warm-water benthic ostracods.

The extinction-recovery patterns of the ostracods yield many important data, including: the presence of pronounced anoxia in the Tethyan lower Scythian which reached to an unusually high level in the water column; the clear evidence that the killing effect at the PTB was caused by a temperature drop and not by the beginning of the anoxia; and suggestions, that the refuge of the numerous Lazarus taxa that re-appeared in the upper Scythian and Middle Triassic may have been situated in shallow-water areas in the tropical part of large oceans, such as Panthalassa and perhaps also in the southern part of eastern Tethys. To obtain these results however, it was necessary not to make any interpolations of the Scythian diversity, and in contrast, the diversity-recovery patterns in different areas, and

above all climatic zones, must be regarded separately.

Another, not so serious problem for most groups, is the elaboration of the diversity patterns at a too high taxonomic category. Often the diversity patterns of different groups are shown for the family level (e.g., ERWIN, 1993) because most authors work exclusively with data compiled from the literature and not with their own results from the study of a major fossil group. For many groups, the diversity patterns at family level show a fairly good picture of the extinction and recovery patterns around the PTB, but generally at genus level the results are more reliable. However, there are some groups, e.g., the conodonts, for which only the species level shows the impact of the PTB biotic crisis.

The conodonts show no diversity drop at genus level around the PTB. This lead to the repeatedly expressed assumption "that conodonts were almost unaffected by the P-T extinction" (HOFFMANN et al., 1998). This, however, is not correct. At species level, there is a distinct low diversity interval in the latest Permian and in the lower five Triassic conodont zones with two minima in the *H. parvus* Zone and in the *S. kummeli* and lower *N. dieneri* Zones. However, even the study of the conodont diversity at species level around the PTB gives an incorrect picture because among the conodonts the warm-water species (in the Dorashamian restricted to the tropical Tethyan area) and cool-water species (in the Boreal realm and at the Perigondwana shelf as well as in cold bottom-water in the Tethys) were affected in different manner by the PTB biotic crisis. Whereas the warm-water restricted *Clarkina subcarinata* group disappeared at the end of the Permian, the cold-water adapted *Hindeodus typicalis* and *Clarkina carinata* lineages flourished, with distinct diversification and occupation of the Tethyan biotopes after the disappearance of the warm-water forms. Therefore, a total turnover of the conodont faunas occurred at the end of the Permian, but because the diversification of the cool-water elements (started at the base of the *I. isarcica* Zone) occurred only a little after the extinction of the warm-water forms (mainly at the base and partly at the top of the last Permian conodont Zone, the *C. meishanensis-H. latidentatus praeparvus* Zone), the diversity drop in species level was not very significant.

At the top of the Gangetian Substage (top of the *H. postparvus-H. sosioensis* Zone = top of the *C. carinata* interval Zone), all hindeodid conodonts disappeared and the *C. carinata* group became very rare. At this second pronounced extinction event in the conodont fauna, only the cool-water conodonts that survived the mass extinction in the uppermost Permian and flourished in the lower three Triassic conodont zones were affected. Somewhat later a strong diversification of Tethyan warm-water conodonts began that also invaded the Boreal realm. The disappearance of the hindeodid conodonts especially indicates an important change in the conodont fauna, as this group had, in the lowermost Triassic, its strongest diversification and widest regional and facial distribution of its Late Palaeozoic to ear-

liest Triassic history. With the disappearance of this group, the mixed Palaeozoic-Triassic conodont fauna of the earliest Triassic was replaced by a low-diversity Triassic conodont fauna.

Thus, detailed conodont studies show that the conodonts were strongly affected by the PTB biotic crisis. At first the Late Permian warm-water conodonts totally disappeared in the latest Permian, and three conodont zones later the cool-water conodonts disappeared almost totally. This extinction pattern yields important data for the causes of the PTB biotic crisis: A drastic drop in the temperature in low latitudes during the uppermost Permian that coincided with a huge volcanic fallout in eastern Tethys (4-6 cm dust tuff over an area of 2 million km^2) and a strong global warming three conodont zones later.

5. SOME REMARKS ON THE ABIOTIC INDICATORS OF THE PTB BIOTIC CRISIS

There are no indications of an impact of a large extraterrestrial body (no iridium peak) close to the PTB (YIN & ZHANG, 1996). However, a little below the PTB an enrichment of microspherules can be found (Japan, China, Hungary). In Meishan, South China, they occur in Boundary Beds 1, at the level of a sharp drop in faunal diversity. According to YIN & ZHANG (1996), they are either of extraterrestrial or of volcanic origin, and the siliceous microspherules are similar to those found in the plume of the Mt. Etna volcano. As these microspherules occur both in an altered volcanic dust layer (Bed 25) and in an overlying anoxic layer (Bed 26), they may be of both volcanic and extraterrestrial origin. In the Bükk Mts. of Hungary, a few centimetre thick microspherule layer occurs about one metre above the top of the Nagyvisnyó Formation (equivalent of the Bellerophon Limestone Formation of the Southern Alps), in the basal Werfen Group with a low diversity latest Permian fauna, a few meters below the FAD of *H. parvus*. The big faunal drop occurs at the top of the Nagyvisnyó Formation, but may be facies-controlled. According to DETRE et al. (1998), the microspherules of this horizon are of extraterrestrial origin. This horizon may be contemporaneous with the Boundary Bed 1, because the sedimentation rate in the Bükk Mts. was high, whereas the Boundary Beds of Meishan are strongly condensed. Both horizons are above the LAD of fusulinids and a diverse Permian fauna and below the FAD of *H. parvus*. According to DETRE et al. (1998), these interstellar microspherules are related to a supernova explosion close to the Solar System (within a distance of 20 pc). Although this assumption is not proven, some aspects of the calculated effects of a supernova explosion close to the Solar System (depletion of the ozone layer, cooling of the troposphere) were probably present within the uppermost Permian, but this can also be explained by huge volcanic eruptions that caused a volcanic winter (KOZUR,

1998a). The explanation of the anoxia and increase in CO$_2$ by the high amount of dead biomass due to the mass extinction (DETRE et al., 1998) is surely incorrect. Nevertheless, the possible effects of a supernova explosion on the earth's biota should be taken into serious consideration, especially from the astronomy point of view: Can the gamma and roentgen radiation and later the corpuscular radiation and much later expanding gas and dust (as the assumed source of the microspherules) from a supernova explosion close to the Sun (within a distance of 20 or even of 10 pc) harm the earth's biota despite the protection by solar wind, Earth's atmosphere and magnetic field?

Regardless of the interstellar or volcanic source, a thin horizon of strong enrichment of microspherules a little below the PTB could be a good auxilliary marker for the base of the Triassic, if it will be discovered in the same level in other and distant well datable sections (e.g. in NW and Central Iran).

Terrestrial causes for the PTB biotic crisis are preferred. They may be also indicated by geochemical changes. Geochemical evidence, mainly changes in the ratios of stable isotopes are commonly used as indicators for the PTB biotic crisis (δ^{13}C) or for environmental or climatic changes (δ^{18}O, δ^{34}S, ^{87}Sr/^{86}Sr). WANG et al. (1994) attributed the drop in δ^{13}C to a catastrophic collapse of the marine primary productivity at the base of the Triassic. A productivity drop may contribute to the drop in δ^{13}C, but there are several other factors (diagenesis, dolomitization, sediment alteration by subaerial exposure connected with a gap, oceanic anoxia) that influence the δ^{13}C curve as discussed in KOZUR (1998a). For instance, in the Selong section (Tibet), there is a strong negative shift of the δ^{13}C curve at a caliche bed (YIN et al., 1996b) that is under- and overlain by beds with Gudadalupian cool-water conodonts, whereas no minimum in the δ^{13}C occurs in the basal Triassic. For this reason, the caliche bed was regarded as an equivalent of the Boundary Clay immediateely below the PTB in South China (WANG et al., 1989; MEI, 1996). The strong drop of δ^{13}C reported by WANG et al. (1994) from British Columbia may also be caused by sediment alteration during a long gap. Nevertheless, in many sections a primary minimum in the δ^{13}C curve is present at the very base of the Triassic. However, it is not certain that this drop depends on the drop in bioproductivity alone, or on other factors as well (or sometimes exclusively on the above mentioned other factors - FOSTER, 1997; KOZUR, 1998a). At the Guadalupian-Lopingian boundary, where there is a strong drop in bioproductivity, the δ^{13}C curve does not drop but it may even rise slightly (HOLSER et al., 1991). The possibility for stratigraphic misinterpretation is much higher for the onset of the drop in the δ^{13}C curve, or for its minimum, than for the biostratigraphically defined base of the Triassic (shortly discussed in section 2). Therefore, the proposal to use the carbon isotope shift for the exact definition of the base of the Triassic (NEWELL, 1994: minimum of the δ^{13}C curve

as base of the Triassic; HOFFMANN et al., 1998: onset of the drop in the $\delta^{13}C$ curve near the PTB as base of the Triassic) cannot be supported. Moreover, detailed investigations have shown that there are often two minima of similar magnitude of the $\delta^{13}C$ curve in somewhat different stratigraphic levels, which excludes the use of the minimum of the $\delta^{13}C$ curve for definition of the base of the Triassic. The lower minimum lies in different sections somewhat below, at or somewhat above the FAD of *H. parvus*. The onset of the drop in the $\delta^{13}C$ curve lies in the undoubtedly Permian *Clarkina changxingensis - C. deflecta* Zone. This was also stated by HOFFMANN et al. (1998), but explained that the conodonts are almost unaffected by the PTB extinction event, which is not the case because the warm-water conodont faunas disappeared. However, in the level, where the onset of the drop in the $\delta^{13}C$ curve occurs, there is not only a typical Permian conodont fauna, in Tethys dominated by warm-water species of *Clarkina*, but also a typical Permian *Pseudotirolites* ammonoid fauna, a typical Permian foraminiferal fauna with latest fusulinids, typical Permian brachiopod, radiolarian and sponge faunas. The carbon isotope shift yields only auxiliary data for the definition of the base of the Triassic which are neither as precise and invariably fixed to a precise time level nor situated at the level of the mass extinction or at the level of the appearance of the first Triassic fossils after the mass extinction.

A pronounced negative shift of $\delta^{13}C$ in the lowermost Triassic lies distinctly above the strong diversity drop close to the PTB, and was therefore not connected to the factors that caused this diversity drop (KOZUR, 1998a). Also the strong increase in $\delta^{34}S$ during the Scythian is obviously not related to any environmental change in connection with the PTB biotic crisis.

6. DATING AND COMPLEX EVALUATION OF THE EFFECTS OF THE EXTREMELY STRONG VOLCANIC ACTIVITY IN THE UPPER PERMIAN AND LOWERMOST TRIASSIC

There is a perfect time correlation between the PTB biotic crisis and the strongest volcanism in Phanerozoic history. As shown by KOZUR (1998a), this volcanism had both direct effects, such as acid rain and a short volcanic winter, and indirect effects, including strong UV radiation as a result of the destruction of the ozone layer by an extremely strong eruption, and the onset of superanoxia, as well as combined direct and indirect effects, such as climatic changes. The extremely strong volcanism was obviously the most important factor of the PTB biotic crisis.

6.1. DATING OF THE VOLCANISM AND ITS EFFECTS DURING THE VOLCANIC ACTIVITY

The effects of the volcanic activity on the biotic diversity around the PTB can only be estimated by very complex studies. First of all, the very exact dating of all occurrences is necessary to show whether volcanics, especially tuffs, are exactly contemporaneous over a large area and fit into the time interval of the biotic changes. This dating is easy and undisputed for the tuffs that belong to a volcanic centre situated at the northeastern margin of the eastern Tethys adjacent to Panthalassa. In South China, very fine-grained altered tuffs of felsic-intermediate composition, with a constant thickness of around 6 cm can be found in the uppermost Dorashamian in all sections, where the deposition was below the storm-wave base. They are best investigated in the Meishan section (Zhejiang Province) and in the Shangsi section (Sichuan Province), about 1500 km to the west of Meishan (for details and complete references see YIN et al., 1996 and LAI et al., 1996). Further tuff layers of the same chemical composition are present within the upper Dorashamian and in the lowermost Triassic. The tuff layer a few centimetres below the FAD of *H. parvus* is connected with the strongest extinction event, but some of the other tuff layers are also connected with extinctions. The northernmost known occurrence of tuffs of an upper Dorashamian explosive felsic-intermediate volcanism is in SE Siberia, about 2000 km NE of Meishan (ZAKHAROV et al., 1995). There, about 65 m of tuffitic layers is present, but with sedimentary intercalations; nevertheless the thickness of the upper Dorashamian volcanics is there much larger than in South China. The SE-Siberian occurrences were obviously closer to the eruption centres that were situated at the margin of Panthalassa, close to the northeastern margin of eastern Tethys. The South Chinese altered tuff layers are so fine-grained and their thickness is so constant over huge distances (about 2 million km²) that they may be partly related to a fall-out of aerosol dust. This huge explosive felsic-intermediate volcanism probably caused a volcanic winter in the uppermost Permian. The palaeolatitude of the eruption centre was in low northern latitudes. Therefore, the effects of the volcanic winter and of the reduction of sunlight should be strongest in the low northern latitudes that correspond to a large part of the Tethys, to which the latest Permian shallow warm-water benthos was restricted (except for insular occurrences in the tropical part of Panthalassa). Only the southern part of eastern Tethys (with the Perigondwana margin) was situated in low to middle southern latitudes. This part of southern Tethys, and above all the insular areas within tropical Panthalassa, had the greatest potential as a refuge for the shallow warm-water benthos.

The age of the Siberian Trap was disputed for a long time. Regarding its post-Tatarian age, DOBRUSKINA & MOGUTCHEVA (1987) assigned it to the Triassic. In this case, the Siberian Trap would be without any importance for the PTB biotic crisis. SADOVNIKOV & ORLOVA (1994) and SADOVNIKOV (1997) assigned the largest part of the Siberian Trap to the post-Tatarian, but Late Permian Taimyrian Stage. The conchostracans and the new radiometric data fully confirm

the post-Tatarian Late Permian age for most of the Siberian Trap. The predominantly tuffitic Hungtukunskian Formation of the Tungusska Basin contains *Falsisca* species (post-Tatarian conchostracan genus) that are present in the Dalongkou section considerable below the FAD of *Lystrosaurus*, and disappear 54 m below the FAD of *Lystrosaurus* in undoubtedly Upper, but not the uppermost Permian beds. The following Puturanian basalt and related intrusives have, according to RENNE et al. (1995), an age of 250 (±1.6) Ma. Bed 25 in the Meishan section, 14-18 cm below the base of the Triassic defined by the FAD of *H. parvus* was dated by the same authors as 249.98 (±0.20) Ma. The Puturanian basalt started, therefore, somewhat before the PTB and straddled this boundary. The Siberian Trap covers 2.5 million km². However, it is probably that in the subsurface of western Siberia, under a thick Meso-Cenozoic cover, large areas are also covered by the Siberian Trap, as the westernmost occurrence of the trap basalts is in the Urals. Thus, the area covered by the Siberian Trap may be far larger than 2.5 million km², but already this area covered by thick tuff layers followed by flood basalt indicates the greatest volcanic activity in the Phanerozoic.

The intra-basaltic layers of the Urals as the westernmost extension of the Siberian Trap volcanism were dated by TUZHIKOVA (1985) as lowermost Triassic and would therefore post-date the PTB biotic crisis. KOZUR (1989) agreed with TUZHIKOVA (1985) that the intra-basaltic layers of the Urals are post-Tatarian, but he pointed out that they are Upper Permian. A large part of the Zechstein palynodemes discriminated by VISSHER (1971) occur in the intra-basaltic layers that correspond therefore to part of the undoubtedly Permian Zechstein. Immediately below the lower volcanics, and in the lower part of the intra-basaltic sediments, *Lueckisporites virkkiae* POTONIÉ & KLAUS, mainly norm Ac, is common (up to 16% of the sporomorphs). This part of the sequence is not younger than the association with dominating *L. virkkiae* norm Ac sensu VISSHER that corresponds to the upper Zechstein 3. In the younger part of the intra-basaltic sediments *Lueckisporites* cf. *parvus* KLAUS (= *L. virkkiae*, norm Bc according to VISSHER, 1971) becomes dominant and then *Guttullapollenites* sp. (*L. virkkiae*, norm C sensu VISSHER, 1971) becomes increasingly frequent. According to the correlation of the Zechstein sporomorph associations with the international scale (KOZUR, 1994b), the post-Tatarian intra-basaltic beds are upper Dzhulfian to lower Dorashamian. The following main phase of the volcanism began in the upper Dorashamian and lasted until the lowermost Triassic (Gangetian Substage). It straddles, therefore, the PTB.

The two, close to the PTB contemporaneously active volcanic centres (Siberian Trap volcanism and huge explosive volcanism at the northern Tethys/Panthalassa transition), had surely a strong influence on the world climate. However, there are also other areas with tuffs and lavas close to the PTB. Dr. Spencer LUCAS, Albu-

querque, found altered tuff layers close to the PTB at the Dalongkou section in Sinkiang. Unfortunately, the material was confiscated and therefore neither radiometric nor geochemical investigations could be carried out. If these volcanics are related either to the Siberian Trap or to the volcanic centre at the transition between the northeastern Tethys and Panthalassa, this would very much enlarge the areas with volcanic ashes or dust fall-out of one of these two volcanic centres. But even if they would belong to an independent volcanic centre, this would further enlarge the areas affected in the uppermost Dorashamian by volcanic fall-out.

According to KOZUR (1998a), the long-lasting, initially mainly explosive Siberian Trap volcanism (very intense from the uppermost Dzhulfian to lowermost Triassic) caused some climatic changes that harmed especially the terrestrial biota (severe climate, cooling in high and medium latitudes, acid rain). During this time, the tropical warm-water faunas retreated to the tropical Tethys. Thus, in the medium-latitude Perigondwana Salt Range, the Dzhulfian is characterized by Tethyan warm-water conodonts. In the uppermost Dzhulfian and lowermost Dorashamian they were replaced by cool-water conodonts. The area with tropical warm-water faunas became in the Dorashamian very narrow and was restricted to the central and northern Tethys, where they remained highly diverse, and insular regions in the equatorial Panthalassa.

The huge explosive felsic-intermediate volcanism at the northeastern margin of Tethys a little below the PTB caused according to KOZUR (1998a), a 3-6 month volcanic winter in low latitudes. This period was long enough to kill the tropical warm-water faunas on the Tethyan shelves, but not long enough to bring the water temperature below the critical water-temperature for tropical warm-water faunas on the shelves of insular regions in the tropical part of Panthalassa. There, a large part of the warm-water faunas survived the PTB biotic crisis, and re-appeared on the Tethyan shelves in the upper Olenekian and in the Middle Triassic as Lazarus taxa.

A "side effect" of the huge volcanic eruption in the uppermost Permian that caused the volcanic winter, may be the destruction of the ozone layer by an especially violent eruption. Aerosols and gases of a huge explosive eruption could reach the ozone layer and deplete it. The consequence would be strong UV radiation. The sudden disappearance of the world-wide mass occurrences of fungi exactly at the level of the huge volcanic eruption at the northeastern margin of Tethys is best explained by strong UV radiation that is lethal for fungi. Strongly reduced sunlight would favour rather than harm the growth of fungi and also the cooling in a volcanic winter would not harm the *Tympanocysta* fungal association because it is common both in the tropical Tethyan and in the cold Boreal realm, and therefore adapted to both warm and cold climates.

The biotic expressions for a cooling event are obvious (KOZUR, 1998a). Mainly the tropical shallow,

warm-water fauna and flora as well as the plankton were affected by the PTB biotic crisis. The plankton mass extinction may also be related to a time of reduced sunlight that would accompany a volcanic winter, and the radiolarian extinction is probably partly related to oceanic anoxia. The mass extinction of tropical shallow-water biota could have been caused by a strong low latitude cooling or warming (the latter is favoured by HALLAM & WIGNALL, 1997, for the tropical areas), but according to KOZUR (1998a) a strong warming in low latitudes during the uppermost Permian can be excluded (strong extinction of warm-water faunas, but no pronounced extinction of marine cold/cool-water faunas and no continental extinction event in that stratigraphic level, contemporaneous equator-ward migration of high latitude cool/cold-water faunas). Moreover, the strong global warming at the base of the Gandarian (= base of Dienerian) post-dates the PTB extinction event except the delayed extinction event of cool-water conodonts. This global warming is directly related to the volcanic winter and the foregoing long-lasting Siberian Trap volcanism (see below).

The important question is why the warm-water faunas from the tropical Panthalassa could not return to Tethys earlier. A volcanic winter, accompanied by a strong reduction of sunlight, and the beginning of the long-lasting, strong and violent Siberian Trap volcanism within the Dzhulfian (with the culmination of the volcanic activity in the upper Dorashamian and lowermost Triassic) perfectly explain the observed extinction pattern affecting mainly the terrestrial communities (earlier than the marine faunas), the plankton, and the tropical shallow, warm-water faunas. However, this event alone can not explain that the recovery occurred only in the upper Scythian (upper Olenekian) and Middle Triassic, several million years after the PTB biotic crisis. After the end of the volcanic winter, the tropical shelf communities would recover very fast by migration of warm-water faunas that had survived on the shelves of intra-oceanic islands (see above). Both the extinction on the tropical shelves and the recovery of the tropical warm-water biota would happen in geologically a very short time. In the geological record only a moderate extinction event and innovations of new faunal elements would be observed. This can be, for instance, observed after the middle Carnian disappearance of the Tethyan reef communities.

6.2. DELAYED EFFECTS OF THE VERY INTENSE VOLCANISM AFTER THE END OF THE VOLCANIC WINTER AND AFTER THE END OF THE SIBERIAN TRAP VOLCANISM

The reason for the long delay in the recovery of the warm-water benthos on the Tethyan shelves was the oceanic superanoxia which reached an unusually high level in the water column (e.g., as shown by dysaerobic conditions in the Mazzin Member and similar shallow-water deposits above the storm-wave base, and black shales in all oceans). The recovery of the Tethyan warm-water faunas coincides with the end of the long-lasting lower-middle Scythian oceanic superanoxia in the sense of ISOZAKI (1994, 1997).

As these superanoxia reached a level above the storm-wave base, they were an effective barrier against the migration of the warm-water benthos that had survived on the shelves around oceanic islands in the tropical Panthalassa (and perhaps partly also within eastern Tethys) to the tropical Tethyan shelves. Moreover, such superanoxia also prevented the recovery of those radiolarians (plankton) that lived beneath the uppermost, oxygenated water column. Thus, only the phytoplankton (e.g., acritarchs), which occur in the uppermost oceanic layer, recovered quickly after the volcanic winter (and the accompanying strongly reduced sunlight).

The superanoxia were probably triggered by the unique volcanic activity in the Dzhulfian to lowermost Scythian interval. The huge amounts of dust and sulphate aerosols caused strong precipitation in areas that were normally dry, both in the low and high latitude dry belts. As a result large inputs of fresh-water occurred in the high latitude cold seas, and this caused a decrease in density of the heavy cold surface water. The sinking of heavy cold surface water strongly decreased or even ceased. This down-sinking of heavy, cold surface water in the high latitudes is, however, the "motor" for the cold bottom water currents that bring highly oxygenated cold surface water via deep-water currents in the tropical oceans, from where warm surface currents transport warm-water into high latitudes. If this oceanic current system disappeared or became very weak, oceanic anoxia were established.

The lengthy duration of the oceanic anoxia was caused by a strong global warming at the base of the Gandarian (= Dienerian) indicated by the appearance of Tethyan warm-water biota in unusual high latitudes, such as Spitsbergen (WIGNALL et al., 1998; KOZUR, 1998a). This caused a globally rather uniform climate during the upper Brahmanian (Gandarian Substage = Dienerian), indicated by world-wide rather uniform faunas (e.g., *Claraia* faunas), and a low temperature gradient in the Tethyan and Boreal oceans, that for a long period prevented the re-establishment of the cold bottom water currents. The temperature gradient between the Tethyan and Boreal realm became higher again during the lower Olenekian as indicated by increasing faunal differences between these realms. The upper boundary of the oceanic anoxia became lower during that time, but at least Panthalassa remained anoxic. In the upper Olenekian the cold bottom-water currents were re-established as indicated by the re-appearance of cold bottom-water palaeopsychrospheric ostracod faunas in Tethys. Contemporaneously, numerous Lazarus taxa among the shallow-water warm-water benthos migrated from their insular shelf relic areas within Panthalassa into Tethys.

The strong global warming at the base of the Gandarian (= Dienerian) was also caused by the volcanic

winter and the lengthy period of Siberian Trap volcanism. The very strong explosive volcanism that caused the volcanic winter, and the foregoing as well as contemporaneous Siberian Trap produced huge amounts of the greenhouse gas CO_2. As mentioned above, the huge amounts of dust and sulphate aerosols that caused a volcanic winter favoured strong precipitation also in the dry high latitude and in the arid low latitude girdles. The strong precipitations in the normally arid low latitude girdles caused a strong increase in the total amount of water vapour in the earth's atmosphere. As water vapour is an effective greenhouse gas, this caused an additional strong greenhouse effect. As long as the Siberian Trap volcanism continued, this greenhouse effect was counterbalanced by dust and sulphate aerosols. However, the Siberian Trap volcanism ended during the upper Gangetian, or at the latest by the top of the Gangetian because overlying sediments both in the Tungusska Basin and in the Urals yielded *Cornia germari* (BEYRICH) and other vertexiids that are guide forms of the Gandarian. After the end of the Siberian Trap volcanism the greenhouse effect resulted in a strong global warming that may have been as high as 6°C on average, as assumed by HALLAM & WIGNALL (1997).

The high precipitation, also in the formerly dry low and high latitude girdle, is an assumption (based on knowledge about the huge explosive volcanic activity in the Upper Permian and especially around the PTB) that needs to be verified by geological and geochemical data. The strong increase in precipitation in the upper Dorashamian and lower Scythian may have caused (at least partly) the significant increase in the $^{87}Sr/^{86}Sr$ ratio that indicates a large increase in chemical weathering triggered by increased humidity and atmospheric CO_2 levels. It is striking that in the uppermost Dorashamian and in the *H. parvus* and *I. isarcica* zones of the lowermost Scythian, no signs of hypersaline seas or continental arid climate can be found globally, not even in areas that were previously very arid, as in the Germanic Basin or the Alps. In the Germanic Basin, the hypersaline sedimentation and salt precipitation in the Zechstein ended in the central basin and large fresh water lakes with charophytes, *Darwinula* and conchostracans developed, whereas in the marginal part arid desert or sabkha conditions were replaced by fluviatile conditions. Thus, the predicted time interval of high precipitation in the normally arid low and high latitude girdles was really present during the uppermost Dorashamian *C. meishanensis - H. latidentatus praeparvus* Zone (starting with the very intense explosive eruption at the northeastern margin of the Tethys) and lowermost Triassic *H. parvus* and *I. isarcica* zones.

Above the *I. isarcica* zone the climate fluctuated rapidly. In the red upper Sandy Claystone Member of the Calvörde Formation and in the contemporaneous Andraz Horizon of the Southern Alps, the climate again became arid in the low latitude dry girdles. In the upper Calvörde Formation and Bernburg Formation (except for its uppermost part), and in the contemporaneous Seis Member of the Alps and Hungary, a rapid fluctuation of predominantly humid to semi-humid with semi-arid to arid climate can be observed. In the Bernburg Formation again a large fresh-water lake (or several large lakes) covered the central Germanic Basin, but periodically, the lake(s) dried out. The Seis Member was studied in detail for salt-content fluctuations in the northern Balaton Highland (Hungary), where deposition occurred in the marginal parts of the Seis shallow-water sea. The shallow-water deposits are in general normally marine, with a rich *Claraia* fauna and conodonts. However, in some parts the fresh-water influx was so strong that on some bedding planes the marine fauna was replaced by a rich fresh- to brackish-water fauna with mass occurrences of in situ conchostracans (KOZUR, 1993; KOZUR & MOCK, 1993). In other beds hypersaline rocks with anhydrite nodules occur.

Thus, the combination of climatic changes (principally the short cooling in the low latitudes due to a volcanic winter) and lower to middle Scythian superanoxia as the two main causes for the PTB biotic crisis were both caused by the unique large scale and violent explosive volcanism in the uppermost Permian and lowermost Triassic.

7. GENERAL EXTINCTION AND RECOVERY PATTERNS CONNECTED TO THE PTB BIOTIC CRISIS

Detailed knowledge of the exact extinction and recovery patterns in the Upper Permian and in the Lower Triassic (which can only be recognized by consideration of the data and problems presented in sections 2-4) is most important for the reconstruction of a scenario of the PTB biotic crisis and the recognition of its causes. KOZUR (1998a) reported the following extinction and recovery patterns related to the PTB biotic crisis:

- The (siliceous) plankton (radiolarians), and the warm-water benthos (highly diverse Upper Permian warm-water benthos was restricted to the Tethys), nektobenthos and nekton were the most strongly affected. The production of organic silica dropped so far that there is a lengthy, global radiolarite gap in oceans from a little below the PTB to the base of the upper Olenekian.

- The cold-water faunas were either not, or slightly affected by the PTB biotic crisis.

- Faunas of temperate zones with seasonal climate were slightly to moderately affected.

- There was a delayed extinction event in cold-water adapted faunas that survived the PTB without extinction, flourished and diversified in the lowermost Triassic after the extinction of the warm-water fauna in the Tethyan realm.

- The recovery time for the warm-water benthos and siliceous plankton was unusually delayed (about 5 Ma) as this recovery occurred only in the upper Olenekian to Middle Triassic interval.

- The recovery of the nekton and nektobenthos was mostly rapid, after one conodont zone (*H. parvus* Zone that had a short duration <0.1 my).

- The productivity of the terrestrial plants dropped strongly and the recovery occurred mainly in the upper Olenekian and in the Middle Triassic.

- Several extinction events occurred in the terrestrial faunas within the Upper Permian, considerably below the marine PTB, and for different fossil groups at different stratigraphic levels. At the marine PTB, only a very slight extinction event can be observed in vertebrates, when "remnant" Permian forms (*Dicynodon*) disappeared. At, or close to, the often used continental PTB (FAD of *Lystrosaurus*) no extinction event of any terrestrial faunal element can be observed.

Such terrestrial faunal elements mainly survived the PTB biotic crisis, which were able to survive some months of extreme climatic conditions, including severe drought, cold or even freezing conditions in low latitudes by hibernation-type live stages (vertebrates) or by drought- and freeze-resistant eggs (conchostracans). Good examples are the vertebrate *Lystrosaurus* which is known both from low latitudes and from high southern latitude areas with polar night, the conchostracan *Falsisca* which occurred both in low latitudes and in high northern latitudes within the Permo-Triassic polar circle, and the ostracod *Darwinula* which lived in tropical areas and high latitudes.

Distinct terrestrial floral changes (that were not of local character) occurred during the upper Dorashamian, when in most parts of the world the trilete cavate spores of lycopodiales became dominant, whereas several species of gymnosperme pollen disappeared. Until the end of the Permian a low diversity terrestrial flora was established and the terrestrial plant production became low.

During the lower and middle Scythian the terrestrial plant production remained low (global coal gap).

- About 50 % of the genera that disappeared at the PTB re-appeared in the Olenekian-Middle Triassic interval (Lazarus taxa). Some of them had changed in generic level but had undoubtedly evolved from genera that had disappeared at the PTB. In some groups the percentage of Lazarus genera is 90-100 % (e.g., holothurians, scolecodonts).

- Only very few major fossil groups totally disappeared at the PTB (without Lazarus taxa). Most of these groups had a very low diversity and/or a regional restriction at the end of the Permian to Tethys or

even to eastern Tethys (trilobites, rugose corals, fusulinids).

- The PTB is preceded by mass occurrences of marine (and continental?) fungi and the fungal spike ended abruptly a little before the PTB, in eastern Tethys at the base of the volcanic dust fall-out a little below the biochronologic PTB.

- The extinction was more severe in the northern than the southern hemisphere.

8. CONCLUSION - A POSSIBLE SCENARIO FOR THE BIOTIC CRISIS AT THE PTB

This scenario for the PTB biotic crisis originated by consideration of the data and problems presented in sections 2-7 and from earlier works (KOZUR, 1997c, 1998a). It incorporates facts such as the severe Dzhulfian-Dorashamian climate in many parts of the world caused by the continent-ocean configuration and by the Siberian Trap volcanism; the extinction event at the Guadalupian-Lopingian boundary that restricted most of the affected warm-water faunas to Tethys; and the Permian northward drift of Pangaea leading to a Middle and Upper Permian cooling of the Boreal area which caused a successive Middle Permian extinction of warm-water benthos and an interruption of the exchange of warm-water benthos between the Tethys and western North America during the Guadalupian.

The Permian northward drift brought large parts of Pangaea into the tropical-subtropical belt during the Middle-Late Permian resulting in rather severe climatic conditions over large parts of Pangaea during the Upper Permian, such as aridity and strong daily and seasonal temperature variations. Part of the fauna adapted to survive several months of very severe climate (long drought, low winter temperatures below freezing point in areas with hot or warm summers). At the same time, northern Pangaea reached the Boreal realm and the Middle-Upper Permian climate became colder and colder. This lead to extinction of major warm-water fossil groups in the Arctic long before the PTB, as shown by the disappearance of the fusulinids at the base of the Guadalupian. The faunal exchange of warm-water benthos between Tethys and the western shelf of America was interrupted. Therefore, a strong provincialism developed with different shallow, warm-water faunas on the western shelf of America and in Tethys. A very rapid and extensive regression at the Guadalupian-Lopingian boundary destroyed the habitats of large shelf areas (e.g., the Delaware Basin of southwestern North America changed into a hypersaline basin). In other basins, like the Phosphoria Basin, the warm-water fauna was additionally harmed by wide-spread upwelling of cold bottom water. Connected regional extinctions led to the disappearance of fusulinids on the western America warm-water shelf during the lowermost

Lopingian. As benthic warm-water faunas could no longer migrate between Tethys and western North America through the southern margin of the Boreal sea, major groups such as the fusulinids were restricted to the Tethys in the upper Dzhulfian and Dorashamian. This is also the case for the warm-water *Clarkina subcarinata* conodont lineage and for most groups of the reef communities.

Beginning in the middle Dzhulfian, the climate became periodically more severe by the influence of the (in that time) largely explosive Siberian Trap volcanism. The eruptions became stronger and stronger during the Dorashamian. The reduced strength of sunlight due to the presence of dust and sulphate aerosols favoured the development of marine (and continental?) fungi that became more and more common during the late Dorashamian (*Tympanicysta* association). Acid rain harmed the gymnosperm forests and most other plants, but did not influence swamp floras with Lycopodiales that were adapted to acid soil. Therefore in many parts of the world lycopodiales floras, as indicated by increasing amounts of trilete cavate spores became common and in many places dominant, whereas the amount of gymnosperms decreased in the uppermost Permian. Repetitive very short periods of cooling in low latitudes, connected with dust and sulphate aerosols from the Siberian Trap volcanism, led to a drop in the diversity of terrestrial vertebrates and fresh water faunas to the uppermost Permian. The larger terrestrial tetrapods were affected first while the conchostracans with drought- and freeze-resistant eggs were affected last. By these stepwise extinctions of different terrestrial faunal groups, in the upper Dorashamian a low diversity terrestrial and fresh-water fauna was present, in which forms prevailed that could survive severe climatic conditions, including short cooler periods in low latitude areas (*Lystrosaurus* among the terrestrial vertebrates, conchostracans, *Darwinula* among the freshwater ostracods). Forms adapted to a permanently warm climate become rare (*Dicynodon*). The cold climate in the Boreal realm and a regression followed by a transgression lead to the establishment of a very low-diversity fauna during the upper Dorashamian *Otoceras concavum* and *O. boreale* zones (the uppermost part of the latter zone s.l. belongs to the earliest Triassic *H. parvus* Zone). Highly diverse marine warm-water faunas were at that time restricted to Tethys, moderately diverse marine faunas occurred on the temperate Perigondwana shelves.

During the latest Dorashamian and earliest Triassic, around 252-250 Ma ago, the effusion of the Siberian Trap basalts covered an area of at least 2.5 million km², possibly even 4-5 million km². Furthermore in the northern hemisphere a huge highly explosive felsic to intermediate volcanism occurred at the northeastern Tethys-Panthalassa margin. Huge amounts of dust and sulphate aerosols were released into the atmosphere, and in the eastern Tethys a fall-out of volcanic dust over an area of at least 2 million km² occurred. Dust and sulphate aerosols lead to a drastic drop in temperature especially in low latitudes (Tethys!), which lasted about 3-6 months (volcanic winter with conditions similar to those calculated for a thermo-nuclear winter). Drastically reduced sunlight at the earth's surface and also a drop in water temperature on the Tethyan shelves strongly affected the phytoplankton, the basic element of the marine food-chain. Skeleton-bearing plankton (Radiolaria) that lived in different water depths was additionally affected by the onset of the oceanic anoxia. The Tethyan shelves, the refuge for most of the latest Permian warm-water benthos were cooled below the temperatures critical for reef communities, and the entire warm-water benthos, but in many places also most of the warm-water nekton or nektobenthonic faunas (e.g., warm-water conodonts) became extinct on the shelves. This climatic catastrophe was more severe in the northern hemisphere, where the two huge volcanic centres were situated, and especially severe in low northern latitudes, where the centre of the huge explosive felsic-intermediate volcanism was located.

The cold-water adapted fauna of the Boreal realm was not affected by this climatic catastrophe. The temperate to cool-water Perigondwana fauna was moderately affected because there was no tropical warm-water benthos, and the climatic catastrophe was not as severe as in the northern hemisphere. A bipolar fauna was established, as *Otoceras* from the Boreal realm invaded this area close to the PTB, probably in connection with the volcanic winter.

A global warming within the lower Scythian (indirectly related to the strong volcanism), which occurred at the base of the Gandarian (= Dienerian), caused the extinction of those cold-water adapted taxa that were not affected by the volcanic winter and flourished therefore during the uppermost Dorashamian and lowermost Triassic in Tethys, where they occupied all those biotopes, from which the Tethyan warm-water fauna had disappeared.

Continuing acid rain in the Gangetian (in connection with the continuing Siberian Trap volcanism) and the subsequent Gandarian global warming may be the reasons for the delayed recovery of the low latitude continental flora, especially in areas with a hot seasonal climate.

The low diversity uppermost Dorashamian terrestrial and fresh water fauna, to a large extent already adapted to shorter periods of severe climate (freezing temperatures or drought) survived to a large degree, after those faunal elements that were adapted to a permanently warm climate had died out earlier during the Dzhulfian and Dorashamian. Only rare last representatives of the latter fauna, like *Dicynodon*, became extinct close to the PTB.

The opportunistic swamp flora was not greatly affected by a short-lasting temperature drop in low latitudes and acid rain, but many Permian gymnosperms disappeared. In the eastern Tethyan humid-tropical Cathaysia province, rather distinct abrupt changes in

the flora can be observed. The tropical Filicales-Pteridospermophyta "rain forest" flora largely disappeared and the tropical highland flora with dominating gymnosperms survived. Therefore, the Cathaysia flora became rich in gymnosperms (sudden increase in bisaccate pollen) during the biotic crisis in connection with the volcanic dust fall-out, whereas in other floral realms the spores (especially of the Lycopodiales swamp flora) became dominant against the bisaccate pollen. As a whole, both in the terrestrial plant diversity and terrestrial plant bioproduction a minimum began with the volcanic winter within the latest Dorashamian (beginning of the world-wide coal gap) and the terrestrial plant diversity/bioproductivity remained very low during the lower and middle Scythian (coal gap). Only in the upper Scythian (upper Olenekian) the terrestrial land plant diversity recovered, but the first "post-crisis" coals are known only from Middle Triassic beds.

The explosive eruptions at the northeastern Tethyan volcanic centre were so strong that even the ozone layer was depleted. Due to the resulting strong UV radiation, the booming of marine (and continental?) fungi suddenly ends at the base of the volcanic dust fall-out in eastern Tethys and in contemporaneous levels in other parts of the world.

The drop in water temperature in the central tropical Panthalassa was not severe enough to kill the warm-water benthos on the narrow shelves of insular areas, where many warm-water taxa survived. However, these forms could not migrate to the faunistically depleted Tethyan shelves because of the wide-spread oceanic anoxia that reached in an unusually shallow level above the storm-wave base. Therefore, the recovery of the warm-water benthos on the Tethyan shelves was delayed for about 5 my until the end of the superanoxia in the upper Olenekian and Middle Triassic. As the shallow-water shelves around oceanic islands are unstable biotopes, many relic biotopes were destroyed during this period. Thus, finally, the strongly delayed recovery led to a delayed extinction, but many taxa survived this lengthy interval of relative isolation. After the end of the oceanic anoxia about 50 % of the genera that disappeared at the PTB re-appeared unchanged or slightly changed during the upper Olenekian and Middle Triassic. This reappearance of Lazarus taxa is followed by a radiation of the warm-water benthos during the Middle and Upper Triassic.

This scenario explains nearly all the details of the extinction patterns in continental and marine biotopes as well as the delayed recovery and the high percentage of Lazarus taxa that re-appeared during the upper Olenekian and Middle Triassic. Only two facts are difficult to explain. One is the strongly delayed recovery of the siliceous plankton (radiolarians) that began only in the upper Olenekian. This delayed recovery can partly be explained by the oceanic superanoxia because not all Palaeozoic-Mesozoic radiolarians lived in the uppermost, anoxia-free water column. However, those radiolarians that lived near the surface of the oceans should

have recovered very quickly as an anoxic ocean is especially nutrient-rich (HALLAM & WIGNALL, 1997). However, these radiolarians, to which the Oertlispongidae and a part of the Entactinaria belong, did also not recover before the late Olenekian or the Middle Triassic. A possible explanation for this is that nearly all skeleton-bearing Radiolaria became extinct near the PTB, and the Triassic radiolarian fauna developed anew from skeleton-less or spicular radiolarians (KOZUR et al., 1996a).

Superanoxia cannot explain the delayed recovery of the high productivity of terrestrial plants that also occurred in the upper Olenekian. In low latitudes with a hot seasonal climate this may be explained by a strong warming within the Gandarian (= Dienerian). However, such a global climate would favour the terrestrial plant productivity at high latitudes, but there the productivity also remained low. Thus, the high latitude Gondwana areas with Permian coals have no Lower Triassic coals, which do not exist anywhere else either. In the Gangetian, the terrestrial plant community may have been harmed by acid rain triggered by the continuing Siberian Trap volcanism, but in the Gandarian and lower Olenekian this volcanism was finished, and no distinct recovery of the terrestrial plant productivity can be observed in that time.

A possible explanation for the delayed recovery of the terrestrial plants is the strong extinction event of the fungi in the uppermost Permian, most probably caused by strong UV radiation due to destruction of the ozone layer. For dense vegetation comparable with tropical rain forest, the activity of microscopic fungi is decisive important. Without or with strongly reduced activities of these fungi such dense vegetation could not survive for longer time because the recycling of the organic matter would be very much disturbed, and the soil would become too poor for a dense vegetation.

As the recovery of the terrestrial plants, the planktonic radiolarians and of the warm-water benthos occurred contemporaneously in the upper Olenekian and Middle Triassic, there may still be some unknown factors that prevented the lower and middle Scythian recovery of the biota additional to the marine anoxia.

Some of the factors that lead to the PTB biotic crisis are today caused by man-made destructions of the environment, such as increase of atmospheric CO_2, air pollution, beginning destruction of the ozone layer, pollution of the sea, and destruction of the tropical rain forests. As the study of the Phanerozoic biodiversity has shown, the biosphere recovers very fast, if the harmful factors disappeared. This, however, is possible only until a certain level of environmental and biosphere destruction. Beyond this level, self-strengthening effects of the environmental and biosphere destruction come into existence that can lead to an environmental catastroph and biotic crisis (mass extinction etc.). The recent extinction rate, which is caused mainly by environmental and biotic destruction by negative effects of human activities, is very high. The estimations are

between a daily extinction rate of 74 species (SEPKOS-KI, 1997) and 150 species (EHRLICH & WILSON, 1991). According to BRIGGS (1994) the extinction rate is today highest in the Phanerozoic. Even at the lower estimation, the present extinction rate is close to the extinction rate around the PTB. Decisive important parts of the biosphere, such as marine plankton as the primary source of the food chain, are not yet affected in a global scale. However, this may happen in near future, if the destruction of environment and biosphere continue in the present level or even grow. Then the level will be reached, at which the self-strengthening and backfeeding processes of a biotic crisis will dominate. Thus, protection of the environment and of the biosphere diversity may become soon a question of survival for the mankind.

Acknowledgements

9. REFERENCES

ADAMCZAK, F. (1969): On the question of whether the palaeocope ostracods were filter-feeders.- In: NEALE, J.W. (ed.): The taxonomy, morphology and ecology of Recent Ostracoda. Oliver & Boyd, 93-98, Edinburgh.

ALBERTI, von, F. (1834): Beitrag zu einer Monographe des Bunten Sandsteins, Muschelkalks und Keupers und die Verbindung dieser Gebilde zu einer Formation.- Verlag der J.G. COTTA'schen Buchhandlung, Stuttgart and Tübingen, 366 p.

BALME, B.E. (1979): Palynology of Permian-Triassic boundary beds at Kap Stosch, East Greenland.- Medd. Grønl., 200/6, 1-37.

BAUD, A., ATUDOREI, V. & SHARP, Z. (1996): Late Permian and Early Triassic evolution of the northern Indian margin: carbon isotope and sequence stratigraphy.- Geodinamica Acta, 9/2, 57-77.

BOOMER, I. & WHATLEY, R. (1992): Ostracoda and dysaerobia in the Lower Jurassic of Wales: The reconstruction of past oxygen levels.- Palaeogeogr., Palaeoclimatol., Palaeoecol., 99, 373-379.

BRIGGS, J.C. (1994): Mass extinctions: factor fallacy?- In: GLEN, W. (ed.): The mass extinction debates: How science works in a crisis. Stanford University Press, 230-236, Stanford.

CHENG, Z., HAN, Y., HOU, J., LI, J., LI, P., LI, Y., LIU, S., LIU, Y., QU, L., SHEN, B., SUN, S., WU, S., XIAO, S., YANG, J. & ZHANG, Z. (1989): Research on the boundary between Permian and Triassic strata in Tianshan Mountain of China.- China Ocean Press, Beijing, 176 p.

DAGYS, A. (1994): Correlation of the lowermost Triassic.- Albertiana, 14, 38-44.

DAGYS, A. & ERMAKOV, S. (1996): Induan (Triassic) ammonoids from north-eastern Asia.- Rev. Paléobiol., 15/2, 401-447.

DETRE, Cs., TOTH, I., DON, Gy., SOLT, P., GUCSIK, A., KISS, A.Z., UZONYI, I. & BERCZI, Sz. (1998): A nearby supernova explosion at the Permo-Triassic boundary.- 23rd Symposium on Antarctic Meteorites, Juni 10-12, 1998, National Institute Polar Research, 23-24, Tokyo.

DIENER, C. (1912): The Triassic of the Himalayas.- Mem. Geol. Surv. India, 36/3, 176 p.

DING, M., ZHANG, K. & LAI, X. (1995): Discussion on *Isarcicella parva* of the Early Triassic.- Palaeoworld, 6, 56-63.

DOBRUSKINA, I.A. & MOGUTCHEVA N.K. (1987): About the age of the Tungusska Basin volcanics.- Geol. Geophys., 1987/1, 29-36 (in Russian).

EHRLICH, P.R. & WILSON, E.O. (1991): Biodiversity studies: science and policy.- Science, 253, 58-62.

ERWIN, D.H. (1993): The great Palaeozoic crisis. Life and death in the Permian.- Columbia University Press, New York, 327 p.

FOSTER, C.B. (1997): The Permian-Triassic boundary in Australia: where is it and how is it expressed?- In: SHI, G.R. (ed.): The Permian of eastern Tethys: biostratigraphy, palaeogeography and resources. Abstracts, Deakin University, Technical paper, 3, 51-52, Melbourne.

GRIESBACH, C.L. (1880): Paleontological notes on the Lower Trias on the Himalayas.- Rec. Geol. Surv. India, 13/2, 94-113.

HALLAM, A. (1994): The earliest Triassic as an anoxic event, and its relationship to the end-Palaeozoic mass extinction.- Canadian Soc. Petrol. Geol., Mem., 17, 797-804.

HALLAM, A. & WIGNALL, P.B. (1997): Mass extinctions and their aftermath.- Oxford University Press, Oxford-New York-Tokyo, 320 p.

HAO, W.C. (1992): Early Triassic marine ostracods from Guizhou.- Acta Micropaleont. Sinica, 9/1, 37-44.

HENDERSON, C.M. (1993): Are Permian-Triassic boundary events diachronous? Evidence from the Canadian Arctic.- Carboniferous to Jurassic Pangea, Program and Abstracts, 136, Calgary.

HENDERSON, C.M. & BAUD, A. (1996): Correlation of the Permian-Triassic boundary in Arctic Canada

on the basis of molluscan and conodont distribu-tion.- 30th International Geological Congress, Abstracts, 2, 63, Beijing.

HOFFMANN, A., GRUSZCZYŃSKI, M., MAŁKOWSKI, K. & SZANIAWSKI, H: (1998): Should the Permian/Triassic boundary be defined by the carbon isotope shift?- Acta Geol. Polonica, 48/2, 141-148.

HOLSER, W.T., SCHÖNLAUB, H.P., BOECKELMANN, K., MARGARITZ, M. & ORTH, C.J. (1991): The Permian-Triassic of the Gartnerkogel-1 core (Carnic Alps, Austria): synthesis and conclusions.- Abh. Geol. B.-A., 45, 213-232.

IGO, H. (1996): Silurian to Triassic conodont biostratigraphy in Japan.- In: First Asian Conodont Symposium. Acta Micropaleont. Sinica, 13/2, 143-160.

ISOZAKI, Y. (1994): Superanoxia across the Permo-Triassic boundary: Record in accreted deep-sea pelagic chert in Japan.- Canadian Soc. Petrol. Geol., Mem. 17, 805-812.

ISOZAKI, Y. (1997): Permo-Triassic boundary superanoxia and stratified superocean: Records from lost deep-sea.- Science, 276, 235-238.

JIN, Y., SHEN, S., ZHU, Z., MEI, S. & WANG, W. (1996): The Selong section, candidate of the global stratotype section and point of the Permian-Triassic boundary.- In YIN, H. (ed.): The Palaeozoic-Mesozoic boundary. Candidates of global stratotype section and point of the Permian-Triassic boundary. China University of Geosciences Press, 127-137, Wuhan.

KOIKE, T. (1996): The first occurrence of Griesbachian conodonts in Japan.- Trans. Proc. Palaeont. Soc. Japan, N.S. 181, 337-346.

KOTLYAR, G.V., KOZUR, H. & ZAKHAROV, Yu.D. (1993): The Transcaucasian sections Dorasham 2 (Azerbaidzhan) and Sovetashen (Armenia), two candidates for P/T boundary reference sections.- Albertiana, 12, 36-38.

KOZUR, H. (1973): Die Bedeutung der triassischen Scolecodonten insbesondere für die Taxonomie und Phylogenie der fossilen Eunicida. Hat sich die Synthese von "orthotaxonomischen" und "parataxonomischen" System in der Praxis bewährt?- Mitt. Ges. Geol. Bergbaustud., 21, 745-776.

KOZUR, H. (1985): Biostratigraphic evaluation of the Upper Palaeozoic conodonts, ostracods, and holothurian sclerites of the Bükk Mts., Part II: Upper Palaeozoic ostracods.- Acta Geol. Hungar., 28/3-4, 225-256.

KOZUR, H. (1989): The Permian-Triassic boundary in marine and continental sediments.- Zentralblatt für Geologie und Paläontologie, 1988/11-12, 1245-1277.

KOZUR, H. (1991): Permian deep-water ostracods from Sicily (Italy). Part 2: Biofacial evaluation and remarks to the Silurian to Triassic paleopsychrospheric ostracods.- Geol. Paläont. Mitt. Innsbruck, Sonderbd., 3, 25-38.

KOZUR, H. (1993): Range charts of conchostracans in the Germanic Buntsandstein.- In: LUCAS, S.G. & MORALES, M. (eds.): The nonmarine Triassic. New Mexico Mus. Nat. Hist. & Sci., Bull., 3, 249-253.

KOZUR, H. (1994a): The Permian/Triassic boundary and possible causes of the faunal change near the P/T boundary.- Permophiles, 24, 51-54.

KOZUR, H. (1994b): The correlation of the Zechstein with the marine Standard.- Jb. Geol. B.-A., 137, 85-103.

KOZUR, H. (1995a): Permian conodont zonation and its importance for the Permian stratigraphic standard scale.- Geol. Paläont. Mitt. Innsbruck, 20, Festschrift zum 60. Geburtstag von Helfried MOSTLER, 165-205.

KOZUR, H. (1995b): Some remarks to the conodonts Hindeodus and Isarcicella in the latest Permian and earliest Triassic.- Palaeoworld, 6, 64-77.

KOZUR, H. (1996a): Some remarks to the Permian standard scale.- Guadalupian II, Alpine, Texas, April 10-13, 1996, Abstracts, 7-11, 13, 14, Washington.

KOZUR, H. (1996b): The conodonts Hindeodus, Isarcicella and Sweetohindeodus in the uppermost Permian and lowermost Triassic.- Geol. Croatica, 49/1, 53-96.

KOZUR, H. (1996c): The Permian-Triassic boundary (PTB) in marine and continental beds - possible causes for the PTB biotic crisis.- 30th IGC, Abstracts, 2, 55, Beijing.

KOZUR, H. (1996d): Changes in marine ostracod faunas at the Permian-Triassic boundary.- 3ème Congrès Européen des Ostracodologistes - Paris - Bierville, 8-12 July 1996, 40, Paris.

KOZUR, H. (1997a): Pelagic Permian and Triassic of the Western Tethys and its paleogeographic and stratigraphic significance.- 48. Berg- und Hüttenmännischer Tag, Abstract, 21-25, Freiberg.

KOZUR, H. (1997b): The effects of the Permo-Triassic boundary biotic crisis on different faunal groups and its possible causes.- 13th International Symposium on Ostracoda ISO97, Abstract Vol., 31, London.

KOZUR, H. (1997c): Possible scenario for the biotic crisis of the Permian/Triassic boundary.- UNESCO-IGCP Project #335 "Biotic recoveries from mass extinctions", final conference "Recoveries '97", 18-22, Praha.

KOZUR, H. (1997d): The Permian conodont biochronoloy: Progress and problems.- In: SHI, G.R. (ed.): The Permian of eastern Tethys: Biostratigraphy, Palaeogeography and Resources. Abstracts, Deakin Univ., Technical paper, 3, 79-82, Melbourne.

KOZUR, H.W. (1998a): Some aspects of the Permian-Triassic boundary (PTB) and of the possible causes for the biotic crisis around this boundary.- Palaeogeogr., Palaeoclimatol., Palaeoecol., 143, 227-272.

KOZUR (1998b): Upper Triassic Punciacea, the connecting link between the Palaeozoic to Lower Triassic Kirkbyacea and the Cretaceous to Cenozoic Punciacea.- Bull. Centre Rech., Elf Explor. Prod. Mém., 20, 257-269.

KOZUR, H.W., KAYA, O. & MOSTLER, H. (1996a): First evidence of Lower to Middle Scythian (Dienerian-Lower Olenekian) radiolarians from the Karakaya Zone of northwestern Turkey.- Geol. Paläont. Mitt. Innsbruck, Sonderbd., 4, 271-285.

KOZUR, H. & MOCK, R. (1974): Holothurien-Sklerite aus der Trias der Slowakei und ihre stratigraphische Bedeutung.- Geol. Zborn., Geol. Carpathica, 25/1, 115-145.

KOZUR, H. & MOCK, R. (1993): The importance of conchostracans for the correlation of continental and marine beds.- In: LUCAS, S.G. & MORALES, M. (eds.): The nonmarine Triassic. New Mexico Mus. Nat. Hist. & Sci., Bull., 3, 261-266.

KOZUR, H., RAMOVŠ, A., WANG, C.Y. & ZAKHAROV, Y. (1996b): The importance of Hindeodus parvus (Conodonta) for the definition of the Permian-Triassic boundary and evaluation of the proposed sections for a global stratotype section and point (GSSP) for the base of the Triassic.- Geologija, 37/38, 173-213, Ljubljana.

KOZUR, H. & SEIDEL, G. (1983): Die Biostratigraphie des unteren und mittleren Buntsandsteins unter besonderer Berücksichtigung der Conchostracen.- Z. geol. Wiss., 11/4, 429-464.

KRYSTYN, L. & ORCHARD, M.J. (1996): Lowermost Triassic ammonoid and conodont biostratigraphy of Spiti, India.- Albertiana, 17, 10-21.

LAI, X., DING, M. & ZHANG, K. (1996a): The significance of the discovery of Isarcicella isarcica at the Meishan Permian-Triassic boundary stratotype section in Changxing, Zhejiang Province.- Exploration of Geosciences, 11, 7-11.

LAI, X., YANG, F., HALLAM, A. & WIGNALL, P.B. (1996b): The Shangsi section, candidate of the Global Stratotype Section and Point of Permian-Triassic Boundary.- In: YIN, H. (ed.): The Palaeozoic-Mesozoic boundary. Candidates of global stratotype section and point of the Permian-Triassic boundary. China University of Geosciencs Press, 113-124, Wuhan.

LETHIERS, F. & WHATLEY, R. (1994): The use of Ostracoda to reconstruct the oxygen levels of Late Palaeozoic oceans.- Marine Micropaleont., 24, 57-69.

LETHIERS, F. & WHATLEY, R. (1995): Oxygénation des eaux et ostracodes filtreurs: application au Devonien-Dinantien.- Geobios, 28/2, 199-207.

LOZOVSKY, V.R. (1993): The most complete and fossiliferous Lower Triassic section of the Moscow Syneclise: The best candidate for a nonmarine global time scale.- In: LUCAS, S.G. & MORALES, M. (eds.): The nonmarine Triassic. New Mexico Mus. Nat. Hist. & Sci., Bull., 3, 293-295.

LUCAS, S.G. (1993): Vertebrate biochronology of the Triassic of China.- In: LUCAS, S.G. & MORALES, M. (eds.): The nonmarine Triassic. New Mexico Mus. Nat. Hist. & Sci., Bull., 3, 301-306.

MATSUDA, T. (1981): Early Triassic conodonts from Kashmir, India. Part I: Hindeodus and Isarcicella.- Journal of Geosciences, Osaka City University, 24/3, 75-108.

MEI, S. (1996): Restudy of conodonts from the Permian-Triassic boundary beds at Selong and Meishan and the natural Permian-Triassic boundary.- In: WANG, H. & WANG, X. (eds.): Centennial Memorial Volume of Prof. Sun Yunshu: Palaeontology and Stratigraphy. China University of Geosciences Press, 141-148, Beijing.

MOSTLER, H. (1969): Entwicklungsreihen triassischer Holothurien-Sklerite.- Alpenkundliche Studien, 7, 53 p.

MOSTLER, H. (1973): Holothuriensklerite der alpinen Trias und ihre stratigraphische Bedeutung.- Mitt. Ges. Geol. Begbaustud., 21, 729-743.

MOSTLER, H. & RAHIMI-YAZD, A. (1976): Neue Holothuriensklerite aus dem Oberperm von Julfa in Nordiran.- Geol. Paläont. Mitt. Innsbruck, 5/7, 1-35.

NEWELL, N.D. (1994): Is there a precise Permian-Triassic boundary?- Permophiles, 24, 46-48.

PAULL, R.K. & PAULL, R.A. (1994): Hindeodus parvus - proposed index fossil for the Permian-Triassic boundary.- Lethaia, 27, 271-272.

PERCH-NIELSEN, K., BIRKENMAJER, K., BIRKELUND, T. & AELLEN, M. (1974): Revision of Triassic stratigraphy of the Scoresby Land and Jameson Land region, east Greenland.- Grønlands geol. Unders., Bull., 109, 1-51.

POSENATO, R. (1991): Endemic to cosmopolitan brachiopods across the P/Tr Boundary in the Southern Alps (Italy).- In: Proceedings of Shallow Tethys, Saito Ho-on Kai Special Publication, 3, 125-139, Sendai.

RENNE, P.R., ZHAN, Z., RICHARDS, M.A., BLACK, M.T. & BASU, A.R. (1995): Synchrony and

causal relations between Permian-Triassic boundary crises and Siberian flood volcanism.- Science, 269, 1413-1415.

RIGBY, J.K. & GOSNEY, T.C. (1983): First reported Triassic lyssakid sponges from North America.- J. Paleont., 57/4, 787-796.

SADOVNIKOV G.N. (1997): Taimyrian Stage of the terminal non-marine Permian.- In: PODEMSKI, M., DYBOVA-JACHOWICZ, S., JAWOROWSKI, K., JURECZKA, K. & WAGNER, R. (eds.): Proceedings of the XIII International Congress on the Carboniferous and Permian. Prace Pánstw. Inst. Geol., 157, 133-136.

SADOVNIKOV, G.N. & ORLOVA, E.F. (1993): The lower boundary and biostratigraphy of the nonmarine Triassic in Siberia.- In: LUCAS, S.G. & MORALES, M. (eds.): The nonmarine Triassic. New Mexico Mus. Nat. Hist. & Sci., Bull., 3, 421-422.

SADOVNIKOV, G.N. & ORLOVA, E.F. (1994): Taimyrian Stage - the terminal stage of the continental Permian.- Dokl. AN Russia, 338/5, 658-661 (in Russian).

SEPKOSKI, J.J. (1997): Biodiversity: Past, present, and future.- J. Paleont., 71/4, 533-539.

SOHN, I.G. (1970): Early Triassic marine ostracodes from the Salt Range and Surghar Range, West Pakistan.- In: KUMMEL, B. & TEICHERT, C. (eds.): Stratigraphic boundary problems: Permian and Triassic of Western Pakistan. University Press, 193-206, Kansas.

SWEET, W.C. (1976): Conodonts from the Permian-Triassic boundary beds at Kap Stosch, East Greenland.- Medd. Grønland, 197/5, 51-54.

TEICHERT, C. & KUMMEL, B. (1976): Permian-Triassic boundary in the Kap Stosch area, East Greenland.- Medd. Grønland, 197/5, 3-49.

TOZER, E.T. (1967): A standard for Triassic time.- Bull. Geol. Surv. Canada, 156, 1-103.

TOZER, E.T. (1988): Definition of the Permian-Triassic (P-T) boundary: The question of the age of the *Otoceras* beds.- Mem. Soc. Geol. It., 34, 291-301.

TUZHIKOVA, V.I. (1985): Miospory i stratigrafija opornych razrezov triasa Urala. Nizhnij trias, pogranichnaja verchnaja perm.- Akademia Nauk SSSR, Uralskij Nauchnij Centr, Sverdlovsk, 231 p.

VISSHER, H. (1971): The Permian and Triassic of the Kingscourt outlier, Ireland.- Geol. Surv. Ireland, Spec. paper, 1, 114 p.

WANG, C.Y. (1994): A conodont-based high-resolution eventostratigraphy and biostratigraphy for the Permian-Triassic boundaries in South China.- Palaeoworld, 4, 234-248.

WANG, C.Y. (1995a): Conodonts from the Permian-Triassic Boundary Beds and biostratigraphic boundary in the Zhongxin Dadui section at Meishan, Changxing County, Zejiang Province, China.- Albertiana., 15, 13-19.

WANG, C.Y. (1995b): Conodonts of the Permian-Triassic boundary beds and biostratigraphic boundary.- Acta Palaeontologica Sinica, 34/2, 130-151.

WANG, C.Y. (1995c): Upper Permian conodont standard zonation.- Permophiles, 26, 20-23.

WANG, C.Y. (1996): Conodont evolutionary lineage and zonation for the latest Permian and earliest Triassic.- Permophiles, 29, 30-37.

WANG, C.Y., KOZUR, H., ISHIGA, H., KOTLYAR, G.V., RAMOVŠ, A., WANG Z.H. & ZAKHAROV, Y. (1996): Permian-Triassic boundary at Meishan of Changxing County, Zhejiang Province, China - A proposal on the global stratotype section and point (GSSP) for the base of the Triassic.- In: First Asian Conodont Symposium. Acta Micropaleont. Sinica, 13/2, 109-124.

WANG, C.Y. & WANG, S.Q. (1997): Conodonts from Permian-Triassic boundary beds and evolutionary lineage of *Hindeodus - Isarcicella*.- Acta Palaeontologica Sinica., 36/2, 151-169.

WANG, K., GELDSETZER, H.H.J. & KROUSE, H.R. (1994): Permian-Triassic extinction: organic $\delta^{13}C$ evidence from British Columbia, Canada.- Geology, 22, 580-584.

WANG, Y., CHEN, C., RUI, L., WANG, Z., LIAO, Z. & HE, J. (1989): A potential global stratotype of Permian-Triassic boundary.- Development in Geoscience, Contribution to 28th International Geological Congress, 1989, Washington D.C. USA, Science Press, 221-229, Beijing.

WHATLEY, R. (1995): Ostracoda and oceanic palaeo-oxygen levels.- Mitt. hamb. zool. Mus. Inst., 92 (Ergbd.), 337-353.

WIGNALL, P.B. & HALLAM, A. (1992): Anoxia as a cause of the Permian/Triassic mass extinction: facies evidence from northern Italy and the western United States.- Palaeogeogr., Palaeoclimat., Palaeoecol., 93, 21-46.

WIGNALL, P.B. & HALLAM, A. (1993): Griesbachian (earliest Triassic) palaeoenvironmental changes in the Salt Range, Pakistan and southeast China and their bearing on the Permo-Triassic mass extinction.- Palaeogeogr., Palaeoclimatol., Palaeoecol., 102, 215-237.

WIGNALL, P.B. & HALLAM, A. (1996): Facies change and the end-Permian mass extinction in S.E. Sichuan, China.- Palaios, 11, 587-596.

WIGNALL, P.B., HALLAM, A., LAI, X. & YANG, F. (1995): Palaeoenvironmental changes across the

PLATE I

1   *Hindeodus latidentatus praeparvus* KOZUR, x275, sample 68 KC 33, East Greenland, Loc. 2.1 after TEICHERT & KUMMEL (1976), corresponds about beds 8 and 9 in River 1 section after TEICHERT & KUMMEL (1976). This level is situated in the river 1 section 1-15 m above the last occurrence of *Otoceras*, and *Claraia* occurs in the upper part of this level. Probably *T. pascoei* Zone. Lower part of *H. parvus* Zone.

2   *Hindeodus latidentatus praeparvus* KOZUR with very large, but broad cusp, but denticulation similar to *H. typicalis* (SWEET), x92, sample 68 KC 33 (see Fig. 1).

3   Very primitive *Hindeodus parvus* (KOZUR & PJATAKOVA), cusp still very broad as in *H. latidentatus praeparvus*, but this is seemingly partly caused by fusion with the following denticle in the lower half of the cusp, transitional form to *H. latidentatus praeparvus* KOZUR, x92, sample 68 KC 33 (see Fig. 1).

4   Primitive *Hindeodus parvus* (KOZUR & PJATAKOVA), x92, sample 68 KC 33 (see Fig. 1).

5   *Hindeodus latidentatus praeparvus* KOZUR, x92, sample 68 KB 8 b, River 1 section after TEICHERT & KUMMEL (1976), 1-7 m above the last *Otoceras*, somewhat below the first occurrence of *Claraia*. Probably *T. pascoei* Zone. Basal part of *H. parvus* Zone.

6   Transitional form between *Hindeodus parvus* (KOZUR & PJATAKOVA) and *H. latidentatus praeparvus* KOZUR, x92, sample 68 KB 8 b (see fig. 5).

7   Very primitive *Hindeodus parvus* (KOZUR & PJATAKOVA), x92, sample 68 KB 16 B, River 1 section after TEICHERT & KUMMEL (1976), beds with *Claraia*, >30 m above the last *Otoceras*. Probably *Ophiceras commune* Zone. *H. parvus* Zone.

8   *Hindeodus parvus anterodentatus* (DAI & ZHANG), x128, sample 68 KC 42 A, East Greenland, Loc. 2.1 after TEICHERT & KUMMEL (1976), 54 m above sample KC 33. *Isarcicella isarcica* Zone.

9   *Hindeodus latidentatus praeparvus* KOZUR, x92, sample 63 TA-122 (for sample position see SWEET, 1970), Pakistan, Chhidru West A, basal Kathwai Member, upper Dorashamian (uppermost Permian).

10 *Hindeodus latidentatus* (KOZUR, MOSTLER & RAHIMI-YAZD), x92, sample 63 TA-122 (see Fig. 9).

11 *Hindeodus latidentatus praeparvus* KOZUR, x92, sample 63 TA-122 (see Fig. 9).

12 *Hindeodus parvus* (KOZUR& PJATAKOVA), x64, sample 63 K 3-5 (for sample position see SWEET, 1970), Pakistan, Chhidru West A, lower Kathwai Member, clay bed ca. 1.3 m above sample 63 TA-122. *H. parvus* Zone of lowermost Triassic.
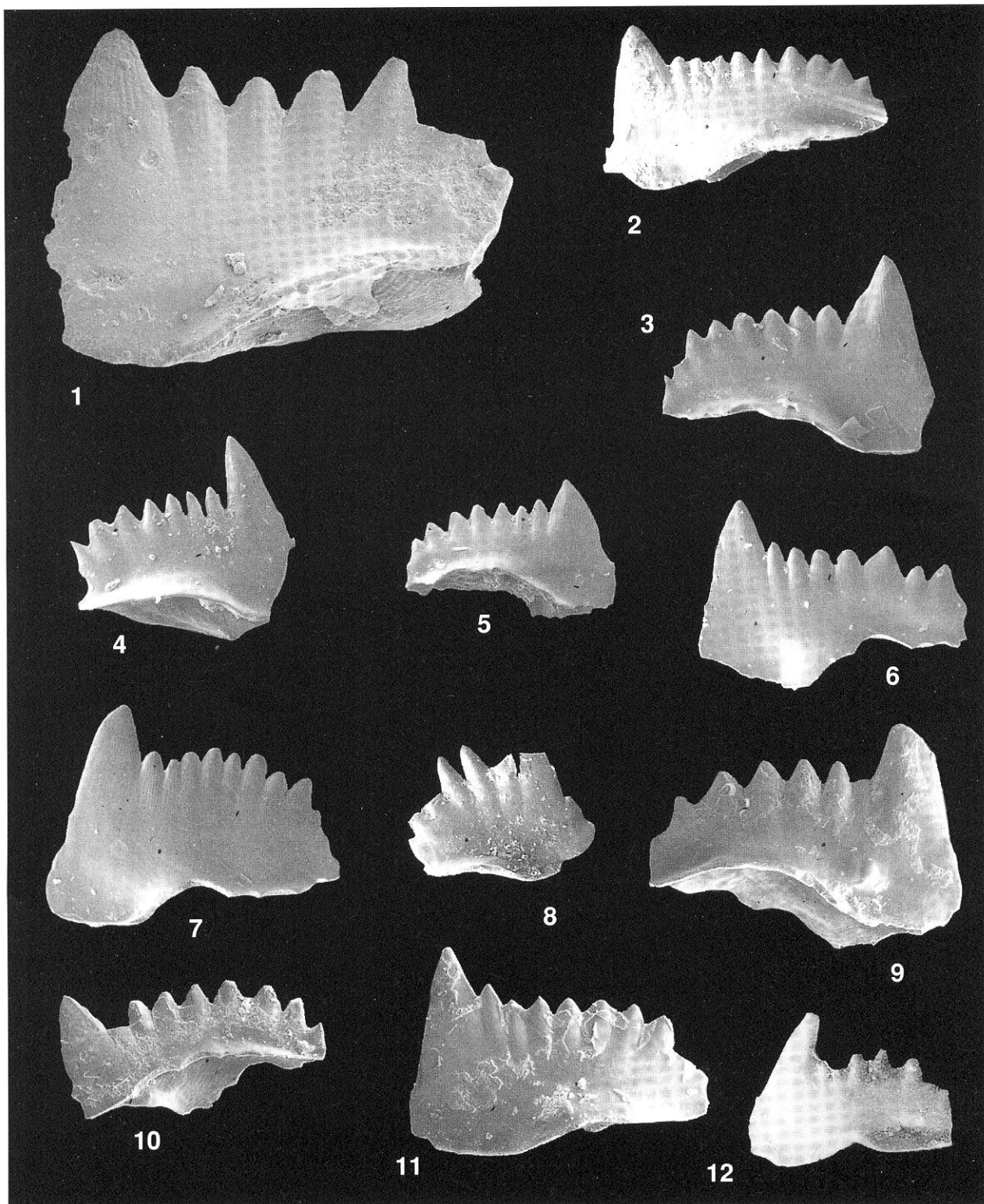
Permian/Triassic boundary at Shangsi (N. Sichuan, China).- Historical Biology, 10, 175-189.

WIGNALL, P.B., KOZUR, H. & HALLAM, A. (1996): On the timing of palaeoenvironmental changes at the Permo-Triassic (P/TR) boundary using conodont biostratigraphy.- Historical Biology, 12, 39-62.

WIGNALL, P.B., MORANTE, R. & NEWTON, R. (1998): The Permo-Triassic transition in Spitsbergen: $\delta^{13}C_{org}$ chemostratigraphy, Fe and S geochemistry, facies, fauna and trace fossils.- Geol. Mag., 135/1, 47-62.

XIA, F. & ZHANG, B. (1992): Age of the Selong Group, Selong of Xizang (Tibet) and the Permian-Triassic boundary.- Journ. Strat., 16/4, 256-263.

YIN, H. (1985): On the transitional beds and the Permian-Triassic boundary in South China.- Newsl. Strat., 15/1, 13-27.

YIN, H. (1993): A proposal for the global stratotype section and point (GSSP) of the Permian-Triassic boundary.- Albertiana, 11, 4-30.

YIN, H., SWEET, W.C., GLENISTER, B.F., KOTLYAR, G., KOZUR, H., NEWELL, N.D., SHENG, J., YANG, Z. & ZAKHAROV, Y.D. (1996a): Recommendation of the Meishan section as Global Stratotype Section and Point for basal boundary of Triassic System.- Newsl. Stratigr., 34/2, 81-108.

YIN, H., ZHANG, K., WU, S. & PENG, Y. (1996b): Global correlation and definition of the Permian-Triassic boundary.- In: YIN, H. (ed.): The Palaeozoic-Mesozoic boundary. Candidates of global stratotype section and point of the Permian-Triassic boundary. China University of Geosciences Press, 3-28, Wuhan.

YIN, H. & ZHANG, K. (1996): Eventostratigraphy of the Permian-Triassic boundary at Meishan section, South China. In: YIN, H. (ed.): The Palaeozoic-Mesozoic boundary. Candidates of global stratotype section and point of the Permian-Triassic boundary. China University of Geosciencs Press, 84-96, Wuhan.

ZAKHAROV, Yu.D., KOTLYAR, G.V. & OLENIKOV, A.V. (1995): Late Dorashamian (late Changxingian) invertebrates of the Far East and Permian to Triassic volcanism in the western Circumpacific.- Geol. Pac. Ocean, 12, 47-60.

ZAWIDZKA, K. (1971): A polychaete jaw apparatus and some scolecodonts from the Polish Middle Triassic.- Acta geol. Polonica, 21/3, 361-377.

ZHANG, K., DING, M., LAI, X. & LIU, J. (1996): Conodont sequences of the Permian-Triassic boundary strata at Meishan section, South China.- In: YIN, H. (ed.): The Palaeozoic-Mesozoic boundary. Candidates of global stratotype section and point of the Permian-Triassic boundary. China University of Geosciencs Press, 57-64, Wuhan.

ZHANG, K., LAI, X., DING, M. & LIU, J. (1995): Conodont sequence and its global correlation of Permian-Triassic boundary in Meishan section, Changxing, Zhejiang Province.- Earth Science, Journal of China University of Geosciences, 20/6, 669-676.

ZHU, X. & LIN, L. (1997): Typical Hindeodus parvus and its significance and discussion on P/T boundary.- Journ. Jiangxi Normal Univ., 21/1, 88-95.

ZHU, X.S., WANG, C.Y., LÜ, H., MU, X.N., ZHANG, L.X., QIN, Z.S., LUO, H., YANG, W.R. & DENG, Z.Q. (1994): Permian-Triassic boundaries in Jiangxi, China.- Acta Micropalaeont. Sinica, 11/4, 439-453.