

Ostracod recovery in the aftermath of the Permian–Triassic crisis: Palaeozoic–Mesozoic turnover

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Abstract During the earliest Triassic, the neritic environments were completely devastated and the recolonization of biotopes was very slow. Besides some small foraminifera and bivalves, ostracods are among the few neritic organisms that were able to survive and/or to thrive in the inhospitable environments after the disaster events. But the Permian–Triassic boundary marks also a great change in the ostracod assemblages. The Palaeozoic ostracods left room for the “modern” fauna. New data on the Early Triassic

neritic fauna in South China (Sichuan and Guangxi Provinces) and bibliographic synthesis on other areas yield a first description of the timing of this turnover. First “typically modern” forms appear already in the Late Permian. The Early Triassic (Griesbachian to Spathian) ostracod faunas display a mixture of Palaeozoic and Mesozoic taxa. Completion of the Palaeozoic–Mesozoic turnover could be located in the Middle Triassic (Anisian).

Keywords Ostracods · Palaeozoic – Mesozoic turnover · mass extinction · recovery · Late Permian · Early Triassic

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Ostracodology – Linking Bio- and Geosciences

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Introduction

The end-Permian mass extinction led to drastic change in marine diversity (Fig. 1). The protracted upper Permian biodiversity decline lasted some 10 Ma. The Triassic recovery can be divided into three phases (Erwin, 1993). The mass extinction is followed by a phase of biotic poverty during the Scythian. Most of the Early Triassic deposits are characterized by abundant microbial limestone, generally interpreted as disaster form (Schubert & Bottjer, 1992). Early Triassic communities exhibit low diversity. Based on the ages proposed by Gradstein et al. (2005), the lag phase lasts around 6 million years

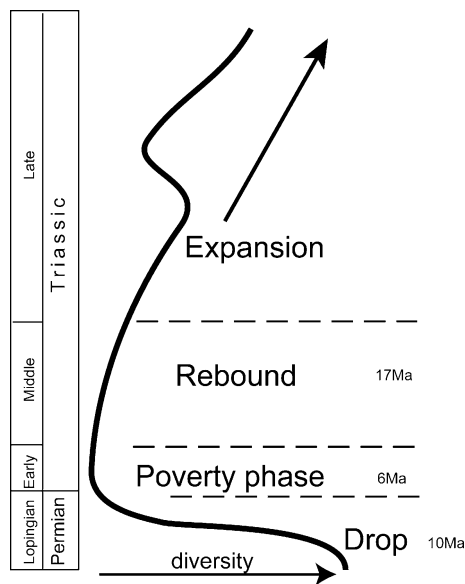


Fig. 1 Divisions of the post-extinction recovery (modified after Erwin, 1993)

(between 251 Ma-PT boundary- and 245 Ma-end of Scythian). We shall see later that recent data of Ovtcharova et al. (2006) revise this estimate slightly. The rebound phase characterizes the Middle Triassic with a return to normal marine fauna. The true expansion of Mesozoic marine faunas took place during the Late Triassic.

Ostracods are known to inhabit all aquatic environments. Despite its remarkable adaptive potential, the sub-class was deeply affected, as are all other neritic fauna, by the end-Permian mass extinction. This period marks the great change in the ostracod group evolution. The Palaeozoic fauna were replaced by the “modern” assemblages, which grew during the Late Triassic. The transition between Palaeozoic and Meso-Cenozoic fauna is poorly documented. In order to understand the changes in ostracod taxa throughout the extinction and recovery, this paper synthesizes the current state of knowledge of all ostracod faunas described from different areas, and aims to identify major features and trends in ostracods throughout the interval. In this paper, we take into account only the neritic forms. Palaeopsychrospheric ostracods, deep benthic inhabitants below the thermocline, are not considered in this work because the basinal environment is very conservative and the evolution and

disappearance of this biotope, somewhere in the Anisian, is a problem per se.

The Palaeocopids, ostracods with straight dorsal border, were considered for a long time to have gone extinct during the Late Permian and their occurrence was thought to be restricted to the Palaeozoic. Gramm (1995) figured an undetermined *Kirkbyocopina* of early Anisian age from Primor’ye (Russian Far East). If recorded specimens indubitably belong to *Kirkbyocopina*, then the dating of the sample seems more questionable. No other fossils were associated with these ostracods. Crasquin-Soleau et al. (2004a, b) and Crasquin-Soleau & Kershaw (2005) showed that Palaeocopids survived into the earliest Triassic.

The recent studies on ostracods around the Permo-Triassic boundary in Western Taurus, Turkey (Crasquin-Soleau et al., 2004a, b), Saudi Arabia (Crasquin-Soleau et al., 2005) and South China in Sichuan Province (Crasquin-Soleau & Kershaw, 2005) and Guangxi Province (Crasquin-Soleau et al., 2006 and this paper) allow further precision to the mapping. Some unpublished data on Early and Middle Triassic of Rumania are taken into account.

Late Permian ostracod fauna (examples illustrated on Fig. 2, 1–6)

We do not discuss here the progressive disappearance of Palaeozoic forms within the Permian. This topic will be dealt with in a separate paper. The first Mesozoic forms appear in the Late Permian (Fig. 2). Some typical strongly shelled and ornamented Bairdiidae, which comprise an important part of the Late Triassic Tethyan fauna, are recognized in the Wuchiapingian and Changhsingian (Fig. 3). For example, *Sinabairdia nodosa* Becker & Wang, 1992 is described in the Wuchiapingian of Sichuan as well as *Ceratobairdia sinensis* Becker & Wang, 1992 in the Changhsingian of Zhejiang Province (Becker & Wang, 1992).

In the latest Permian of Hubei Province, Chen & Shi (1982) present four species of *Ceratobairdia* Sohn, 1954, three of *Petasobairdia* Chen, 1982 and three of *Mirabairdia* Kollmann, 1963.

In the Changhsingian of Meishan section, Shi & Chen (1987) recognized three species of *Mirabairdia* Kollmann, 1963 and two of *Lobobairdia* Kollmann, 1963. These Triassic genera have their maximum development during Ladinian–Carnian time interval. The genera *Petasobairdia* Chen, 1982 (very close to *Ceratobairdia* Sohn, 1954, described also by Kristan-Tollmann (1970) in the Late Triassic of Alps) and *Abrobairdia* Chen, 1982 (very close to the Triassic genus *Mirabairdia* Kollmann, 1963) are represented by four and two species, respectively. The systematics of the ostracods of Meishan section still need an important systematic revision which is currently in progress. As noted by Chen & Shi (1982, p. 146), the Triassic genera *Parurobairdia* and *Mirabairdia* seem to be a transitional type between Late Palaeozoic to Early Mesozoic genera. This group of strongly shelled and ornamented Bairdiidae is called “*Petasobairdia–Ceratobairdia–Mirabairdia–Parurobairdia* fauna” by Chen & Shi (1982). This confirms the phyletic proximity of all these forms through the PT boundary and the necessity of the systematic revision.

Some other genera which are first representatives of Mesozoic inhabitants are recognized by different authors:

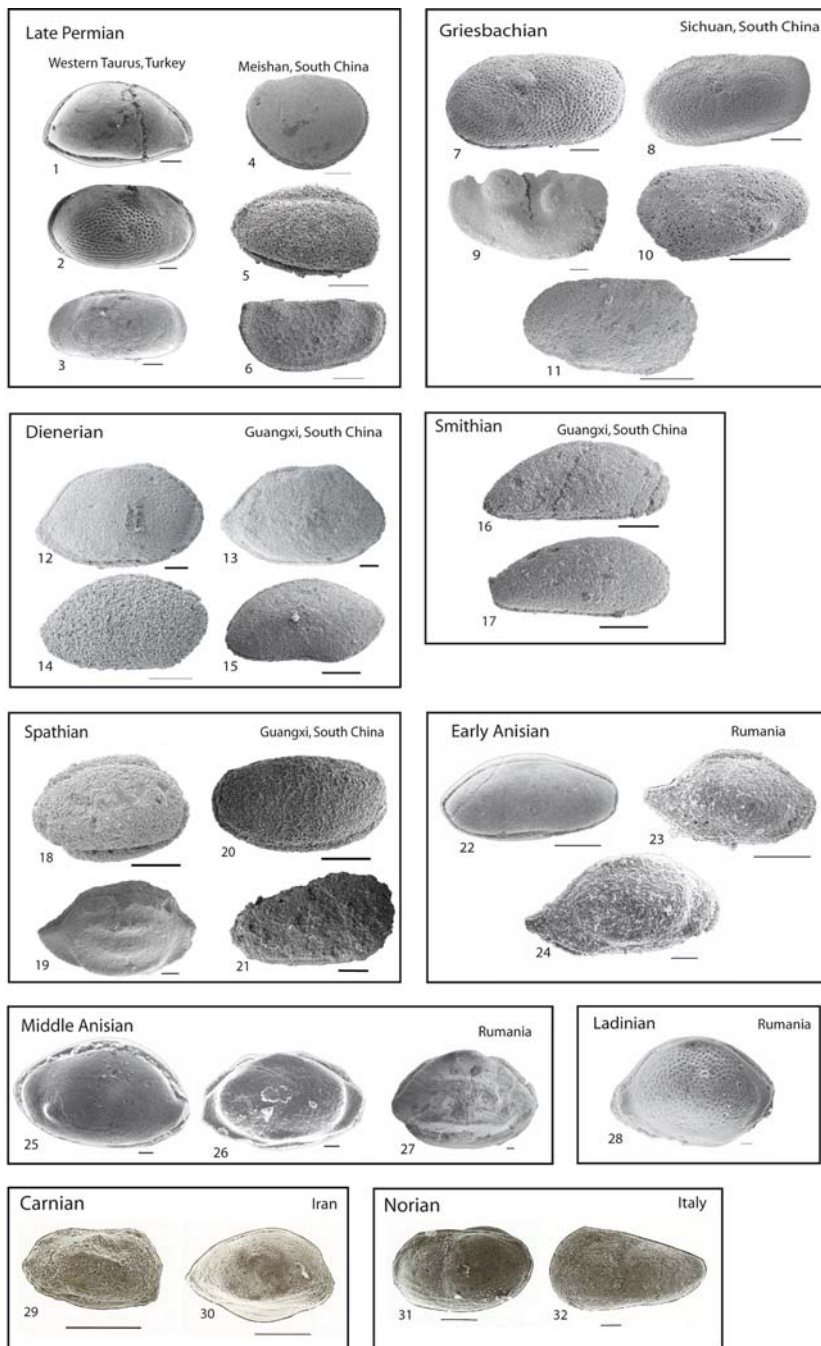
- By Kozur (1985) in the Bükk Mountains: *Judahella bogschi bogschi* Kozur, 1985 in the Changhsingian, *Callicythere mazurensis* (Styk, 1972) in the early Wuchiapingian, *Gruendeliclythere (Trodocythere) permica* Kozur, 1985 and *Fueloepicythere pulchra* Kozur, 1981 in the middle Wuchiapingian;
- By Gerry et al. (1987) and Honigstein et al. (2006) in the Late Permian of Israel: five species of *Arqoviella* Gerry & Honigstein, 1987. As it was underlined by these authors this genus shows typical Mesozoic features;
- By Crasquin-Soleau et al. (2004a, b) in the Lopingian (Wuchiapingian–Changhsingian) of Antalya Nappes (Western Taurus): *Petasobairdia nantongensis* Chen 1987, *Petasobairdia* cf *subnantongensis* Chen, 1987 sensu Crasquin-Soleau et al. 2004a, b *Arqoviella tahtaliensis* Crasquin-Soleau, 2004a, b *Callicythere lysi* Crasquin-Soleau, 2004, gen. et sp. indet.
- By Crasquin-Soleau et al. (2005) in the Lopingian Khuff Formation of Saudi Arabia with four species of *Arqoviella* genus.

Scythian (Early Triassic) and early Anisian (Middle Triassic) ostracod fauna (examples illustrated on Fig. 2, 7–32)

The Early Triassic neritic ostracods are poorly known. Psychrospheric faunas are known from early Anisian of Rumania (Crasquin-Soleau & Gradinaru, 1996).

Some neritic species were recognized (or just quoted) in the Early Triassic (Induan–Olenekian) and early Anisian of Australia (Jones, 1970), Pakistan (Sohn, 1970), Nepal (Bunza & Kozur, 1971), Greece (Kozur, 1971b; Ardens et al., 1979), Germanic Basin (Kozur, 1973b), Israel (Hirsch & Gerry, 1974), Kashmir (Agarwal, 1979, 1980, 1981; Agarwal et al., 1980) and South China (Wang, 1978; Wei Ming, 1981; Hao, 1992, 1994).

Recent works on Permian–Triassic sections in Western Taurus (Crasquin-Soleau et al., 2004a, b), in Saudi Arabia (Crasquin-Soleau et al., 2005) and South China (Crasquin-Soleau & Kershaw, 2005; Crasquin-Soleau et al., 2006 and this paper) give new data on the latest Palaeozoic and earliest Mesozoic ostracods. It was evidenced that a transitional interval existed for this group. Some forms of Mesozoic affinities were discovered in the latest Permian mixed with typical Palaeozoic forms (Crasquin-Soleau et al., 2004a, b). In the earliest Triassic, some survivors are associated with the newcomers. The presence of survivors was first evidenced by Jones (1970) in Perth Basin (Australia) and Sohn (1970) in Salt Range (Pakistan). It was confirmed in South China by Wang (1978) in Guizhou and North Yunnan Provinces, Wei (1981) in Sichuan Province, Hao (1992, 1994) in Guizhou Province. More recently, Palaeozoic survivors were recognized in Western Taurus (Crasquin-Soleau et al., 2004a, b) and South China in Sichuan Province (Crasquin-Soleau & Kershaw, 2005). The problem is to date the final disappearance of Palaeozoic forms and complete conquest of environments by typical Triassic inhabitants.



The ostracods analyzed in this paper are dated by ammonoids from Griesbachian up to Spathian. The Table 1 compiles the available data on Early Triassic ostracods, from bibliography and from personal works. Unpublished data on Early–Middle Triassic ostracods from

Dobrogea (East Rumania) are added. In this table, only the species which have typical Palaeozoic or Mesozoic affinities are reported. Species which are representative of panchronic genera (as smooth *Bairdia* or *Paracypris*, ...) are not quoted.

◀ **Fig. 2** Examples of ostracod associations during the different phases of extinction—recovery patterns at Permian–Triassic boundary. PF, Palaeozoic form; MCF, Mesozoic form (1–6: latest Permian): (1) PF, *Acratia changxingensis* (Shi, 1987) from Western Taurus (Turkey; Crasquin-Soleau et al., 2004); (2) MCF, *Arqoviella tahtalensis* Crasquin-Soleau, 2004 from Western Taurus (Turkey; Crasquin-Soleau et al., 2004); (3) MCF, *Callicythere lysi* Crasquin-Soleau, 2004 from Western Taurus (Turkey; Crasquin-Soleau et al., 2004); (4) PF, *Samarella* sp.1 from Meishan section (level 15) (Crasquin-Soleau et al., unpubl.); (5) PF, *Microcheilinella* sp.1 from Meishan section (level 15) (Crasquin-Soleau et al., unpubl.); (6) PF, *Kirkbyidae* sp.1 from Meishan section (level 22) (Crasquin-Soleau et al., unpubl.); (7–11) Griesbachian of Sichuan (South China; Crasquin-Soleau & Kershaw, 2005); (7) PF, *Langdaia laolongdongensis* Crasquin-Soleau & Kershaw, 2005; (8) PF, *Langdaia suboblonga* Wang, 1978; (9) PF, *Hollinella* sp. 1; (10–11) MCF, *Callicythere postangulata* Wei, 1981; (12–15) Dienerian of Guangxi (South China; Crasquin-Soleau et al., 2006); (12–13) MCF, *Ptychobairdia luciae* Crasquin-Soleau, 2006; (14) *Bairdia fengshaensis* Crasquin-Soleau, 2006; (15) *Bairdia wailiensis* Crasquin-Soleau, 2006; (16–17) Smithian of Guangxi (South China; Crasquin-Soleau et al., 2006); (16) PF, *Acratia nostrica* Monostori, 1994; (17) *Paracypris jinyensis* Crasquin-Soleau, 2006; (18–21) Spathian of Guangxi (South China; Crasquin-Soleau et al., 2006); (18) PF, *Microcheilinella* cf. *venusta* Chen, 1958; (19) MCF, *Ptychobairdia aldae* Crasquin-Soleau, 2006; (20) PF, *Carinaknightina?* sp. *sensu* Crasquin-Soleau et al., 2006; (21) MCF, *Kerocythere?* sp. *A sensu* Crasquin-Soleau et al., 2006; (22–24) Early Anisian of Dobrogea (Rumania; Crasquin-Soleau & Gradinaru, 1996); (22) *Bairdiacypris galbruni* Crasquin-Soleau & Gradinaru, 1996; (23) MCF, *Urobairdia fauconnierae* Crasquin-Soleau & Gradinaru, 1996; (24) MCF, *Urobairdia uzumensis* Crasquin-Soleau & Gradinaru, 1996; (25–27) Middle Anisian of Dobrogea (Rumania; Crasquin-Soleau, unpublished data); (25) MCF, *Ogmoconchella* sp.2; (26) MCF, *Ptychobairdia* sp.6; (27) MCF, *Ptychobairdia* sp.5; (28) Ladinian of Dobrogea (Rumania; Crasquin-Soleau, unpublished data). MCF, *Lobobairdia* cf. *salinaria* Kollmann, 1963; (29–30) Carnian of Zagros (Iran; Crasquin-Soleau & Teherani, 1995); (29) MCF, *Moscovitschia* cf. *interrupta* Kristan-Tollmann, 1983 *sensu* Crasquin-Soleau & Teherani 1995; (30) MCF, *Metacyteropteron?* *zagrosensis* Crasquin-Soleau & Teherani 1995; (31–32) Norian of Northern Italy (Crasquin-Soleau et al., 2000); (31) MCF, *Rhombocythere dimorphica* Crasquin-Soleau et al., 2000; (32) MCF, *Kerocythere quateralsi* Crasquin-Soleau et al., 2000

Griesbachian

Griesbachian ostracod fauna is recognized in South China (Guizhou, Sichuan, Yunnan and Guangxi Provinces), Western Taurus, and Tibet (Table 1). Many Palaeozoic forms are still pres-

TRIASSIC	Late	Rhaetian	
		Norian	
		Carnian	
	Middle	Ladinian	
		Anisian	
	Early = Scythian	Olenekian	Spathian
			Smithian
		Induan	Dienerian
			Griesbachian
	PERMIAN	Late = Lopingian	Changhsingian
Wuchiapingian			

Fig. 3 Late Permian—Triassic stratigraphic subdivisions (from Gradstein et al., 2005). No vertical scale

ent, with genera like *Hollinella*, *Carinaknightina* and *Langdaia*. Even if the *Hollinella* specific attributions are wrong in Hao (1992, 1994) and Wang (1978), this genus is recognized without ambiguity (Crasquin-Soleau et al., 2004a). Few genera present Late Triassic features: *Callicythere* in Sichuan, *Kerocythere* in Guangxi, both in South China, *Lutkevichinella*, *Judahella*, *Hungarella*, *Monoceratina* in Tibet (see Table 1).

Dienerian

Before this work, we had no data on Dienerian ostracods. In the Jinya/Waili section (Guangxi Province, South China—Crasquin-Soleau et al., 2006), we recognized three species in the Dienerian: *Bairdia fengshanensis* Crasquin-Soleau, 2006, *Bairdia wailiensis*, Crasquin-Soleau, 2006 and *Ptychobairdia luciae* Crasquin-Soleau, 2006. This last species presents typical Mesozoic characters.

Smithian

As for the Dienerian, the only Smithian available data come from the *Flemingites* beds of Jinya/Waili section (Crasquin-Soleau et al., 2006). We found four species (*Bairdia fengshanensis* Crasquin-Soleau, 2006, *Acratia nistorica* Monostori, 1994, *Bythocypris?* sp.3 and *Paracypris jinyensis*

Table 1 (1) Hao (1992, 1994)—South China; (2) Crasquin-Soleau & Kershaw (2005)—South China; (3) Crasquin-Soleau et al. (2004a, b)—Turkey; (4) Crasquin-Soleau et al. (2006)—South China; (5) Wang (1978)—South China; (6) Wei Ming (1981)—South China; (7) Jones (1970)—Australia; (8) Sohn (1970)—Pakistan; (9) Kozur (1973a, b)—Germanic Basin; (10) Crasquin-Soleau (unpublished data)—Rumania; (11) Crasquin-Soleau & Gradinaru (1996)—Rumania; (12) Gramm (1995)—Far East Russia

Species	Guizhou Griesbachian parvus zone	Sichuan Griesbachian parvus zone	Taurus Griesbachian parvus – staeschei zone	Guangxi Griesbachian	W Guizhou NE Yunnan Griesbachian	Sichuan Griesbachian	Australia Griesbachian Late Griesbachian	Pakistan Late Griesbachian	Guangxi Dienerian	Guangxi Smithian
	1	2	3	4	5	6	7	8	4	4
<i>Hollinella</i> cf. <i>plana</i> Jiang <i>sensu</i> Hao, 1992	♦									
<i>Hollinella</i> <i>unispinata</i> Hao, 1992	♦									
<i>Hollinella tingi</i> (Patte) <i>sensu</i> Wang and Hao	♦				♦	♦				
<i>Hollinella</i> cf. <i>tingi</i> (Patte) <i>sensu</i> Hao, 1992	♦									
<i>Carinaknightina</i> <i>carinata</i> Sohn, 1970	♦									
<i>Carinaknightina</i> <i>zhenfengensis</i> Hao, 1992	♦									
<i>Langdaia</i> <i>suboblonga</i> Wang, 1978	♦				♦					
<i>Acratia</i> <i>symmetrica</i> Hao, 1992	♦									
<i>Hollinella</i> sp.1 <i>sensu</i> CS & Kershaw, 2005		♦								

Table 1 continued

Species	1	2	3	4	5	6	7	8	Guangxi Dienerian	Guangxi Smithian
	Guizhou Griesbachian parvus zone	Sichuan Griesbachian parvus zone	Taurus Griesbachian parvus – staeschei zone	Guangxi Griesbachian	W Guizhou Yunnan Griesbachian	Sichuan Griesbachian	Australia Griesbachian	Pakistan Late Griesbachian		
<i>Langdaia laolong</i>		◆								
<i>Langdaia dongensis</i>										
CS & Kershaw, 2005										
<i>Langdaia suboblonga</i>		◆				◆				
Wang, 1978										
<i>Acratia</i> sp.1		◆								
<i>Callicythere postiangusta</i>		●								
Wei Ming, 1981										
<i>Reyvia curukensis</i>			◆							
Crasquin-Soleau 2004										
Paraparchitacea indet			◆							
“ <i>Healdia</i> ” sp.A				◆						
<i>sensu</i> CS et al., 2006										
<i>Kerocythere?</i> sp.A <i>sensu</i> CS et al., 2006				●						
<i>Triassinella cuneiformis</i>					●					
Wang, 1978										
<i>Carinaknightina neutrum</i>							◆			
Jones, 1970										
<i>Hollinella</i> sp.										◆

Table 1 continued

Species	Guizhou Griesbachian parvus zone	1	Guizhou Griesbachian parvus zone	2	Sichuan Griesbachian parvus zone	3	Taurus Griesbachian parvus – staeschei zone	4	Guangxi Griesbachian	5	W Guizhou Yunnan Griesbachian	6	Sichuan Griesbachian	7	Australia Griesbachian	8	Pakistan Late Griesbachian	Guangxi Dienerian	Guangxi Smithian
<i>Truncobairdia beaglensis</i> Jones, 1970																			
<i>Carinaknighthina discarinata</i> Sohn, 1970																	◆		
<i>Carinaknighthina</i> aff. <i>carinata</i> Sohn, 1970																	◆		
<i>Carinaknighthina carinata</i> Sohn, 1970																	◆		
<i>Lutkevichinella? ornata</i> Sohn, 1970																	•		
<i>Judathella? sp.</i>																	•		
<i>Hungarella? sp.</i>																	•		
<i>Monoceranita? sp.</i>																	•		
<i>Ptychobairdia luciae</i> Crasquin-Soleau, 2006																		•	
? <i>Acratia nostrica</i>																			◆

Table 1 continued

Species	Pakistan Spathian	Guangxi Spathian	Germanic Basin Spathian	Dobrogea Rumania Spathian	Germanic Basin Early Anisian	Dobrogea Rumania Early Anisian	Far East Russia Early Anisian
Kirkbyidae gen. indet. sp.	8						
<i>Microcheilinella</i> sp. sensu Sohn, 1970	◆						
<i>Reubenella?</i> sp. sensu CS et al., 2006; Sohn, 1970	•						
<i>Carinaknightina?</i> sp. sensu CS et al., submitted	◆	4	9	10	9	10 and 11	12
<i>Microcheilinella?</i> cf. <i>venusta</i> sensu CS et al., 2006	◆						
<i>Microcheilinella?</i> sp.1 sensu CS et al., submitted	◆						
<i>Ogmoconcha?</i> sp.A sensu CS et al., 2006	•						
<i>Psychobairdia aldae</i> CS, 2006	•						
<i>Psychobairdia</i> sp.A sensu CS et al., 2006	•						
<i>Psychobairdia luciae</i> CS, 2006	•						
<i>Luikevichinella</i> (<i>Cytherissinella</i>) <i>bisulcata</i> (Kozur)			•				
<i>Luikevichinella</i> (<i>Cytherissinella</i>) <i>nodosa</i> (Kozur)			•				
<i>Judahella pulchra</i> & Kozur			•		•		
<i>Judahella</i> <i>tsorfaria</i> Sohn, 1968			•		•		
<i>Luikevichinella simplex</i> <i>simplex</i> Kozur			•		•		
<i>Acratia</i> sp.2				◆			
<i>Ogmoconchella</i> sp.5				•			

Table 1 continued

Species	Pakistan Spathian	Guangxi Spathian	Germanic Basin Spathian	Dobrogea Rumania Spathian	Germanic Basin Early Anisian	Dobrogea Rumania Early Anisian	Far East Russia Early Anisian
<i>cf. Langdaia suboblota</i> Wang, 1978	8	4	9	10	9	10 and 11	12
<i>Cultella? levis</i> Kozur					♦		
<i>Cytherella jenesis</i> Kozur					•		
<i>Lutkevichinella</i> (<i>Cytherissinella</i>)					•		
<i>lata lata</i> Kozur					•		
<i>Triassocypris</i> <i>pusilla</i> (Kozur)					•		
<i>tenuis</i> (Kozur)					•		
<i>Urobairdia</i> sp.1						•	
<i>Urobairdia</i> sp.2						•	
<i>Pychobairdia</i> sp.1						•	
<i>Pychobairdia</i> sp.2						•	
<i>Metacytheropteron</i> sp.2						•	
<i>Urobairdia fauconniereae</i> CS & Gradinaru, 1996						•	
<i>Hungarella</i> sp.2						•	
<i>Lobabairdia cf. salinaria</i> Kollmann, 1963						•	
<i>Metacytheropteron</i> sp.						•	
<i>Kirkyocoppina</i> sp.	♦						♦
	•						
		Palaeozoic affinities					
		Mesozoic affinities					

Crasquin-Soleau, 2006) which are smooth Bairdiacea. These species belong to panchronic genera (smooth Bairdiacea) and are not informative for our purpose.

Spathian

In the Spathian, the ostracod assemblage becomes diversified again. Faunas were published by Sohn (1970—dating reviewed by Pakistani-Japanese Research Group (1985) and Wignall & Hallam (1993). Ostracods known from the Salt Range occur in the lower part of Mittiwali member of Mianwali Formation (late Griesbachian) and in the Narmia Member of Mianwali Formation (Spathian). We add here data on Luolou Formation, Guangxi Province, South China (Crasquin-Soleau et al., 2006).

Kirkbyidae indet, *Microcheilinella* and *Carinaknightina* (see Table 1) are late Palaeozoic forms documented in the Spathian of Tibet and Guangxi Province. In the Germanic Basin (Kozur, 1973a), all the representatives have Mesozoic affinities.

Early Anisian

Available data come from the Germanic Basin (Kozur, 1973a), from Dobrogea in Rumania (Crasquin-Soleau & Gradinaru, 1996 and Crasquin-Soleau, unpublished data) and from Far East Russia (Gramm, 1995). Two imprecisely determined species exhibit Palaeozoic affinities: cf. *Langdaia subobloga* Wang, 1978 (Kozur, 1973a) and *Kirkbyocopina* sp. (Gramm, 1995). These two species are the latest Palaeozoic representatives.

Middle (late Anisian) and Late Triassic ostracod fauna (Fig. 3):

The Tethyan Upper Triassic ostracods were studied particularly by Méhes (1911—Hungary), Anderson (1964—Great Britain), Kollmann (1963, 1960—Austria), Kristan-Tollmann (1970, 1973, 1983, 1986, 1991—Alps, South China, Papua-New Guinea, Iran), Sohn (1968—Israel), Bolz (1969, 1970a, b—Alps), Will (1969—Germany),

Kozur & Nicklas (1970—Alps), Monostori (1994—Hungary).

The Upper Triassic neritic fauna is very characteristic and well known in the Tethyan domain. Most of the forms are massive and thick-shelled, as exemplified by representatives of Cytherellidae (as *Reubenella* Sohn, 1968, *Leviella* Sohn, 1968, ...), Bairdiidae (as *Carinobairdia* Kollmann, 1963, *Cornutobairdia* Kristan-Kollmann, 1970, *Lobobairdia* Kollmann, 1963, *Dicerobairdia* Kollmann, 1963, *Nodobairdia* Kollmann, 1963...), Kerocytheridae (as *Kerocythere* Kozur & Nicklas, 1970, ...), Mesozoic Healdiidae (as *Hungarella* Méhes, 1911; *Ogmoconchella* Gründel, 1964; *Hermiella* Kristan-Tollmann, 1977; *Triadohealdia* Kristan-Tollmann; 1971, *Soëlla* Kristan-Tollmann et al., 1987, ...), Cytheruridae (as *Metacytheropteron* Oertli, 1957, ...), Judahellidae (*Judahella* Sohn, 1968), Glorianellidae (*Lutkevichinella* Schneider, 1956, ...).

For the Middle Triassic, all the published neritic ostracods of upper Anisian and Ladinian age are typical Mesozoic forms. Palaeopsychrospheric assemblages (not taken in account in this paper) were published by Kozur (1970) from late Anisian of Hungary.

Data on upper Anisian neritic ostracods are found in Sohn (1968—Israel), Gramm (1975—South Primorye, Far East Russia), Kristan-Tollmann (1983—South China) and Monostori (1995—Hungary).

For the end of Middle Triassic, we can mention the work in Israel by Sohn (1968), in the Alps by Kozur (1971a–c), in Southern Spain by Kozur et al. (1974), in Himalaya by Agarwal & Kumar (1981), in NE Iran by Kristan-Tollmann (1991), in India by Goel et al. (1984), in Alaska by Sohn (1987), in Slovenia by Kolar-Jurkovsek (1991).

Discussion and conclusion

This analysis emphasizes that the first occurrences of ostracods exhibiting modern features are recorded from the Late Permian of South China, Western Taurus, Israel and Saudi Arabia. They include *Callicythere*, *Arqoviella*, and representatives of the “*Petasobairdia*–*Ceratob-*

airdia–Mirabairdia–Parurobairdia fauna” of Chen & Shi (1982).

Palaeozoic forms survive in the Early Triassic, as indicated by the occurrences of *Hollinella*, *Carinaknightina*, *Langdaia*, *Microcheilinella*, *Acratia*. The latest representatives are from the early Anisian.

It is also important to note that the Early Triassic ostracod assemblages from the Luolou Formation, Guangxi Province, South China (Crasquin-Soleau et al., 2006) do not differ significantly from Late Permian ones. Data obtained in Early Triassic strata in Pakistan (Sohn, 1970), in Western Taurus (Crasquin-Soleau et al., 2004a, b) and in Eastern Sichuan (Crasquin-Soleau & Kershaw, 2005) show exactly the same features: composition similar to Late Palaeozoic assemblages and open marine environments. Twitthett et al. (2004) stated that “the hypothesis that the apparent delay in the recovery after end-Permian mass extinction event was due to widespread and

prolonged benthic oxygen restriction and in the absence of anoxia, marine recovery is much faster”, a statement which may well apply to our data. But, contrary to those authors, the “pre-extinction fauna” of Late Palaeozoic aspect occurs on the borders of Neo-Tethys, at least in South China, Tibet, and Western Taurus. The “mixed fauna interval” extending from latest Permian to Spathian separates Palaeozoic ostracod communities from the modern ones. For the moment, we have only few data on ostracod fauna from the Late Permian–Triassic interval and in a next future we expect to provide further data and quantitative distributions. Nevertheless, we can try to compare our results with the recovery of other well-documented groups as ammonoids, conodonts and brachiopods.

The conodonts have an explosive radiation during the Smithian when the fauna contains four-times as many conodont genera as those known in the

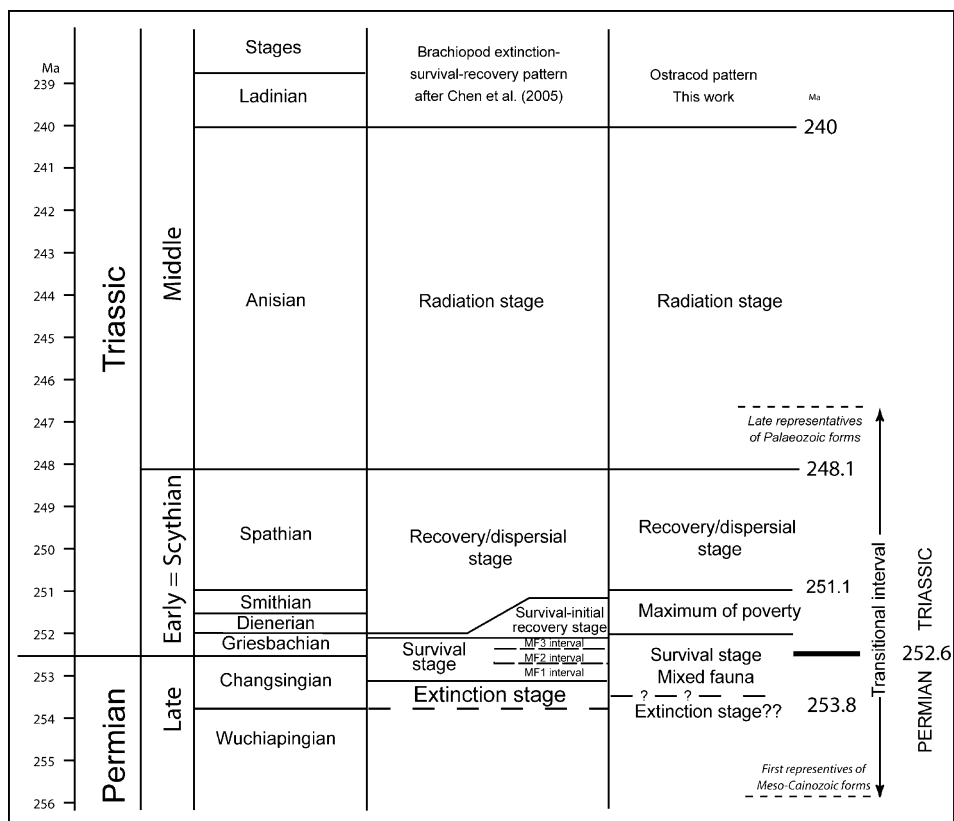


Fig. 4 Comparison between extinction and recovery patterns of brachiopods and ostracods through Permian–Triassic boundary events. Brachiopod data after Chen et al. (2005). MF: mixed fauna (datations from Ovtcharova et al., 2006)

Late Dienerian (Orchard, 2005). The ammonoids return to full diversity in the Spathian (Brayard et al., 2006) i.e., 1–3 Ma after the PTB. For the Brachiopods, Chen et al. (2005) described different phases of extinction-survival-recovery pattern across the end-Permian extinction (Fig. 4): an extinction stage during the early Changhsingian, three survival stages (mixed fauna 1, 2 and 3 intervals) from late Changhsingian to middle Griesbachian, a survival-initial recovery stage in late Griesbachian, three phases of recovery/dispersal stage from Dienerian to the end of the Spathian and finally the radiation stage from the Anisian.)

At the present date, we do not have enough data to precisely date the end of the “extinction stage”. The survival stage exists also for the ostracods. It seems to be longer than for brachiopods (Palaeozoic survivors still exist in the Spathian). The survival-initial recovery stage may begin earlier for the ostracods than for the Brachiopods (Mesozoic representatives are present from the Late Permian). The radiation stages seem to coincide for the two groups during the Anisian.

The final turnover of ostracods from Palaeozoic to Mesozoic faunas took place later during the Anisian.

If we consider a 252.6 ± 0.2 Ma age for the PTB (Mundil et al., 2004) and a late Spathian *N. haugi* Zone age of 248.1 ± 0.4 Ma (Ovtcharova et al. 2006) a minimal duration of ca. 4.5 ± 0.6 Ma can be inferred for the Early Triassic. The recovery phase is significantly shorter than previous estimates.

This study is a first step in the knowledge of ostracod fauna recovery after the events of the Permian–Triassic boundary. Detailed analysis of reference sections are in progress and may lead to a quantitative approach.

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References

- Agarwal, P. N., 1979. Scythian Ostracodes from the ‘Khunamuh Foramation’, Khreuh, Kashmir Himalayas. *Current Sciences* 48: 442–443.
- Agarwal, P. N., 1980. A record of Lower Triassic Ostracodes from Guryul Ravine, Kashmir. *Geoscience Journal* 1: 93–94.
- Agarwal, P. N., 1981. An account of marine Triassic Ostracodes and their possible utility in biostratigraphy, with special reference to *Judahella* SOHN, in certain Lower Triassic sections in Kashmir Himalaya. *Proceeding of IX Indian Colloquium on Micropalaeontology and Stratigraphy* 146–155.
- Agarwal, P. N. & S. Kumar, 1981. An ostracod assemblage from the Kalapani limestone, Malla Johar Area, Kumaun Himalaya In Sinha, A. K. (ed.), *Contemporary geoscientific research in Himalaya*. Dehra Dun 1: 217–224.
- Agarwal, P. N., S. N. Singh & S. Ashok, 1980. Scythian Ostracodes from Kashmir Himalayas. *Journal of the Palaeontological Society of India* 23/24: 110–114.
- Anderson, F. W., 1964. Rhaetic Ostracoda. *Bulletin of the Geological Survey of Great Britain* 21: 133–174.
- Ardens, R., J. P. Colin & H. Kozur, 1979. Sur la présence de Scythien supérieur fossilifère dans la chaîne du Vardoussia (Grèce continentale). *Conséquences paléogéographiques*. *Comptes rendus sommaires de la Société Géologique de France* 3: 132–135.
- Becker, G. & S. Q. Wang, 1992. Kirkbyacea and Bairdiacea (Ostracoda) from the Palaeozoic of China. *Palaeontographica A* 224: 1–54.
- Bolz, H., 1969. Der “bairdoppilate” Verschluss und Skulptur–Unterschiede bei Bairdien (Ostrac.) der alpinen Obertrias. *Senckenbergiana lethaea* 50: 411–431.
- Bolz, H., 1970a. Einige Cytherelloidea - Arten (Ostracoden) aus der alpinen Obertrias. *Senckenbergiana lethaea* 51: 239–263.
- Bolz, H., 1970b. Late Triassic Bairdiidae and Healdiidae. *Bulletin du Centre de Recherche Pau - SNPA* 5 supplément, 717–745.
- Brayard, A., H. Bucher, G. Escarguel, F. Fluteau, S. Bourquin & T. Galfetti, 2006. The Early Triassic ammonoid recovery: Paleoclimatic significance of diversity gradients. *Palaeogeography, Palaeoclimatology, Palaeoecology* 239: 374–395.
- Bunza, G. & H. Kozur, 1971. Beiträge zur Ostracodenfauna der tethyalen Trias. *Geologisch-paläontologische Mitteilungen Innsbruck* 1: 1–76.
- Chen, Z. Q., K. Kaiho & A. D. George, 2005. Early Triassic recovery of the brachiopod faunas from the end-Permian mass extinction: A global review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 224: 270–290.
- Chen, D. Q. & C. G. Shi, 1982. Latest Permian ostracoda from Nantong, Jiangsu and from Miannyang, Hubei. *Bulletin of Nanjing Institut of Geology and Palaeontology, Academia Sinica* 4: 105–152 (in Chinese with English abstract).

- Crasquin-Soleau, S., F. Berra & R. Rettori, 2000. A Late Triassic Ostracod assemblage from the Quattervals Nappe (Austroalpine, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 106: 181–190.
- Crasquin-Soleau, S. & E. Gradinaru, 1996. Early Anisian ostracode fauna from the Tulcea unit (Cimmerian North Dobrogean Orogen, Romania). *Annales de Paléontologie* 82: 59–116.
- Crasquin-Soleau, S. & S. Kershaw, 2005. Ostracod fauna from the Permian - Triassic boundary interval of South China (Huaying Mountains, eastern Sichuan Province): palaeoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 217: 131–141.
- Crasquin-Soleau, S., J. Marcoux, L. Angiolini & A. Nicora, 2004a. Palaeocopida (Ostracoda) across the Permian - Triassic events: new data from South-Western Taurus (Turkey). *Journal of Micropalaeontology* 23: 67–76.
- Crasquin-Soleau, S., J. Marcoux, L. Angiolini, A. Nicora & Y. Bertho, 2004b. New ostracode fauna from Permian - Triassic boundary in Turkey (Taurus, Antalya Nappes). *Micropalaeontology* 23: 67–76.
- Crasquin-Soleau, S. & K. Teherani, 1995. Première découverte d'ostracodes triasiques dans la Formation de Khanet Kat, Montagne de Michparvar (Ouest Iran). *Revue de Micropaléontologie*, 38: 27–36.
- Crasquin-Soleau, S., D. Vaslet & Y. M. Le Nindre, 2005. Ostracods from Permian -Triassic boundary in Saudi Arabia (Khuff Formation). *Palaeontology* 48: 853–868.
- Crasquin-Soleau, S., T. Galfetti, H. Bucher & A. Brayard, 2006. Early Triassic ostracods from Guangxi Province, South China. *Rivista Italiana di Paleontologia e Stratigrafia* 112: 55–75.
- Erwin, D. H., 1993. *The Great Palaeozoic Crisis: Life and Death in the Permian*. Columbia University Press, New York.
- Gerry, E., A. Honigstein, B. Derin & A. Flexer, 1987. Late Permian Ostracodes of Israel. Taxonomy, distribution and paleogeographical implications. *Senckenbergiana lethaea* 68: 197–223.
- Goel, R., H. Kozur & S. S. Srivastava, 1984. Middle Anisian (Pelsonian) Ostracoda from Spiti (Himachal Pradesh), India. *Geoscience Journal* 5: 53–62.
- Gradstein, F. M., J. G. Ogg & A. G. Smith, 2005. *A Geological Time Scale 2004*. Cambridge University Press, Cambridge.
- Gramm, M. N., 1975. Marine Triassic Cytheracea (Ostracoda) from South Primorje (Soviet Far East). *Palaeontographica A* 151: 102–110.
- Gramm, M. N., 1995. Ostracodes of the suborder Kirkbyocopina from the Middle Triassic of Southern Primor'ye (Far East). *Paleontological Journal* 29: 154–156.
- Hao, W. C., 1992. Early Triassic Ostracods from Guizhou. *Acta Micropalaeontologica Sinica* 9: 37–44 (in Chinese with English abstract).
- Hao, W. C., 1994. The development of the Late Permian - Early Triassic ostracod fauna in Guizhou Province. *Geological Review* 40: 87–93.
- Hirsch, F. & E. Gerry, 1974. Conodont and ostracode biostratigraphy of the Triassic in Israel. *Schriftenreihe der Erdwissenschaftlichen Kommissionen, Österreichische Akademie der Wissenschaften* 2: 107–114.
- Honigstein, A., A. Rosenfeld & B. Derin, 2006. Late Permian ostracodes from Israel: New subsurface data. *Micropaleontology* 51: 405–422.
- Jones, P. J., 1970. Marine Ostracoda (Palaeocopida, Podocopida) from the Lower Triassic of the Perth Basin, Western Australia. *Bulletin of Bureau of Mineral Resources, Geology and Geophysics* 108: 115–142.
- Kolar-Jurkovsek, T., 1991. Microfauna from the Upper Triassic (Norian) of Karavanke Mts. (Slovenia), Symposium on Triassic Stratigraphy, Lausanne, Switzerland, 15 pp.
- Kollmann, K., 1960. Ostracoden aus der alpinen Trias Österreichs. I.- *Parabairdia* n.g. und *Ptychobairdia* n.g. (Bairdiidae). *Jahrbuch der Geologischen Bundesanstalt Wien* 5: 79–105.
- Kollmann, K., 1963. Ostracoden aus der Trias. II.- Weitere Bairdiidae. *Jahrbuch der Geologischen Bundesanstalt Wien* 106: 121–203.
- Kozur, H., 1970. Neue Ostracoden-Arten aus dem Obersten Anis des Bakonyhochlandes (Ungarn). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck* 58: 384–428.
- Kozur, H., 1971a. Die Bairdiacea der Trias. Teil I: Skulpturierte Bairdiidae aus mitteltriassischen Flachwasserablagerungen. *Geologisch-paläontologische Mitteilungen Innsbruck* 1: 1–27.
- Kozur, H., 1971b. Die Bairdiacea der Trias. Teil 2: Skulpturierte Bairdiidae aus mitteltriassischen Tiefseefablagerungen. *Geologisch-paläontologische Mitteilungen Innsbruck* 1: 1–21.
- Kozur, H., 1971c. Die Bairdiacea der Trias. Teil 3: Einige neue Arten triassischer Bairdiacea und Bemerkungen zur Herkunft der Macrocyprididae (Cypridacea). *Geologisch-paläontologische Mitteilungen Innsbruck* 1: 1–18.
- Kozur, H., 1973a. Die Bedeutung triassischer Ostracoden für stratigraphische und paläoökologische Untersuchungen. *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten in Österreich* 21: 632–660.
- Kozur, H., 1973b. Einige Bemerkungen zur Systematik der Ostracoden und Beschreibung neuer Platycopida aus der Trias Ungarns und der Slowakei. *Geologisch-paläontologische Mitteilungen Innsbruck* 2: 1–27.
- Kozur, H., 1985. Neue Ostracoden-Arten aus dem Oberen Mittelkarbon (Höheres Moskovian), Mittel- und Oberperm des Bükk-Gebirges (N-Ungarn). *Geologisch-paläontologische Mitteilungen Innsbruck* 2: 1–145.
- Kozur, H., W. Kampschuur, C. W. H. Mulder-Banken & O. J. Simon, 1974. Contribution to the Triassic ostracode faunas of the Betic zone (Southern Spain). *Scripta Geologica* 23: 1–56.
- Kozur, H. & L. Nicklas, 1970. Ostrakoden aus dem Plattenkalk-Niveau des Hauptdolomites (Rhätikon). In Mostler, H. (ed.), *Beiträge zur Mikrofazies und Stratigraphie von Tirol und Vorarlberg 1971* (Festband des Geologischen Institutes, 300-Jahr-Feier Universität Innsbruck 1970), 309–320.

- Kristan-Tollmann, E., 1970. Einige neue Bairdien (Ostracoda) aus der alpinen Trias. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 135: 268–310.
- Kristan-Tollmann, E., 1973. Zur Ausbildung des Schliessmuskelfeldes bei triadischen Cytherellidae (Ostracoda). Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 6: 351–373.
- Kristan-Tollmann, E., 1983. Ostracoden aus dem Oberanis von Leidapo bei Guiyang in Südchina. Schriftenreihe der Erdwissenschaftlichen Kommissionen, Österreichische Akademie der Wissenschaften 5: 121–176.
- Kristan-Tollmann, E., 1986. Beobachtungen zur Trias am Südostende der Tethys – Papua/Neuguinea, Australien, Neuseeland. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 4: 201–222.
- Kristan-Tollmann, E., 1991. Ostracods from the Middle Triassic Sina Formation (Aghdarband Group) in NE Iran. Abhandlungen der Geologischen Bundesanstalt 38: 195–200.
- Méhes, G., 1911. Über Trias-Ostrakoden aus dem Bakony. Resultate der wissenschaftlichen Erforschung des Balatonsees 1: 1–38.
- Monostori, M., 1994. Ostracod evidence of the Carnian salinity crisis in the Balaton Highland, Hungary. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 193: 311–331.
- Monostori, M., 1995. Environmental significance of the Anisian Ostracoda fauna from the Forras Hill near Felsoors (Balaton Highland, Transdanubia, Hungary). Acta Geologica Hungarica 39: 37–56.
- Mundil R., K. R. Ludwig, I. Metcalfe & P. R. Renne, 2004. Age and Timing of the Permian Mass Extinctions: U/Pb Dating of Closed-System Zircons. Science 305: 1760–1763.
- Orchard, M. J., 2005. On the explosive radiation of Lower Triassic Conodonts: A new multielement perspective. Albertiana 33: 65.
- Ovtcharova, M., H. Bucher, U. Schaltegger, T. Galfetti, A. Brayard & J. Guex, 2006. New Early to Middle Triassic U–Pb ages from South China: Calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. Earth and Planetary Science Letters 243: 463–475.
- Pakistani-Japanese Research Group, 1985. Permian and Triassic Systems in the Salt Range and Sughar Range, Pakistan. In Nakazawa, K. & J. M. Dickins (eds), The Tethys. Her paleogeography and paleobiogeography from Palaeozoic to Mesozoic. Tokai University Press, Tokyo, 221–312.
- Shi, C.-G. & D.-Q. Chen, 1987. The Changhsingian ostracodes from Meishan Changxing, Zhejiang. Stratigraphy and Palaeontology of Systemic Boundaries in China; Permian and Triassic Boundary 5: 23–80 (in Chinese with English abstract).
- Schubert, J. K. & D. J. Bottjer, 1992. Early Triassic stromatolites as post-extinction disaster forms. Geology 20: 883–886.
- Sohn, I. G., 1968. Triassic Ostracodes from Makhtesh Ramon, Israel. Geological Survey of Israel Bulletin 44: 1–71.
- Sohn, I. G., 1970. Early Triassic Marine Ostracodes from the Salt Range and Surghar Range, West Pakistan. In Kummel, B. & C. Teichert (eds), Stratigraphic boundary problems: Permian and Triassic of West Pakistan. Department of Geology, University of Kansas, Special publication, Lawrence, 149–206.
- Sohn, I. G., 1987. Middle and Upper Triassic Marine Ostracoda from the Shublik Formation, Northeastern Alaska. U.S. Geological Survey Bull., Shorter contribution to Paleontology and Stratigraphy (1664), C1–C47.
- Twitchett, R. J., L. Krystyn, A. Baud, J. R. Wheeley & S. Richoz, 2004. Rapid marine recovery after the end-Permian mass-extinction event in absence of marine anoxia. Geology 32: 805–808.
- Wang, S. -Q., 1978. Late Permian and Early Triassic ostracods of Western Guizhou and Northeastern Yunnan. Acta Palaeontologica Sinica 17: 307–308 (in Chinese with English abstract).
- Wei, M., 1981. Early and Middle Triassic Ostracods from Sichuan. Acta Palaeontologica Sinica 20: 501–510 (in Chinese with English abstract).
- Wignall, P. B. & A. Hallam, 1993. Griesbachian (Earliest Triassic) palaeoenvironmental changes in the Salt Range, Pakistan and southeast China and their bearing on the Permo-Triassic mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 102: 215–237.
- Will, H. J., 1969. Untersuchungen zur Stratigraphie und Genese des Oberkeupers in Nordwestdeutschland. Beihefte zum Geologischen Jahrbuch 54: 1–240.