

Biochronology of Triassic bivalves

CHRISTOPHER A. McROBERTS

Department of Geology, State University of New York at Cortland, P.O. Box 2000, Cortland, NY 13045, USA (e-mail: christopher.mcroberts@cortland.edu)

Abstract: Substantial advances by numerous researchers over the past 20 years have made it possible to develop a composite biochronological scheme for the Triassic based on the bivalves *Claraia*, *Peribositria*, *Enteropleura*, *Daonella*, *Halobia*, *Eomonotis* and *Monotis*. These bivalves exhibit temporal durations nearly equal to ammonoids and conodonts. Widely distributed across the Tethys, Panthalassa and Boreal regions, these bivalves occur in a wide variety of marine facies and water depths, but are most notable for their thick shell accumulation in deeper-water oxygen deficient environments. They were most likely resting or reclining benthos, may have housed chemosymbionts, and were part of episodic opportunistic palaeocommunities in or near oxygen deficient settings.

A new biochronological zonation for bivalves is presented that encompasses the entire Triassic and is integrated with standard ammonoid schemes. The Lower Triassic is characterized by 2–3 zones of *Claraia*, most notably from the eastern Tethys representing the entire Induan and lower portion of the Olenekian. Later in the Olenekian, and most notably from the Boreal realm, species of *Peribositria* (included by some workers within *Bositra*) provide useful zonal indexes. The Middle Triassic is well represented by *Enteropleura* (Middle Anisian) and *Daonella* (Upper Anisian through Ladinian) in the Tethys and North America with significant occurrences throughout the circum-Pacific and Boreal realms. The Upper Triassic can be subdivided into 8–13 bivalve zones based on the succession of *Halobia*, *Eomonotis* and *Monotis sensu lato* species with best representation in the Tethys, Boreal and eastern Panthalassa regions.

Following the end-Permian mass extinction, benthic marine ecosystems underwent a remarkable reorganization associated with the post-extinction recovery and subsequent adaptive radiation during the Mesozoic. Among shelly benthos, this reorganization resulted in the diminishment of typical Late Palaeozoic brachiopod, pelmatozoan, and stenolaematid bryozoan dominated level-bottom marine communities in favor of communities characterized by bivalve and gastropod molluscs, bony fishes, gymnolaemate bryozoans, echinoids and certain crustaceans, representing an increase in trophic variety ranging from deep infaunal suspension feeders to active nektonic carnivores (Vermeij 1977; Sepkoski 1981). A significant component of this essentially modern fauna are bivalve molluscs, which in the Triassic dominate many level-bottom, reefal, and pelagic settings (McRoberts 2001; Fraiser & Bottjer 2007).

Among the bivalves of the Triassic radiation, those belonging to the genera *Claraia*, *Peribositria*, *Enteropleura*, *Daonella*, *Aparimella*, *Halobia* and *Monotis*, are arguably the most abundant macrofauna in deep-water marine facies of the Triassic (Fig. 1). Often referred to as ‘flat clams’ because of their very thin shell width and narrow valve convexity, these bivalves generally have widespread distributions and very high species turnover rates making them excellent biochronological macrofossils of the Triassic. Their biochronological value

was recognized soon after their discovery, and within the past 30 years they have become standard components of biochronological schemes (e.g. De Capoa Bonardi 1984; Polubotko 1986; McRoberts 1997; Zakharov *et al.* 1997; Yin 2003). Even though bivalve zonations have been provided for specific regions and or limited portions of the Triassic, this paper provides the first global summary of bivalve zonation for the entire Triassic (Figs 1, 3, 5, 6).

Taxonomic and nomenclature issues

Perhaps the largest problem with the use of Triassic bivalves in biochronological studies is a combination of the multitude of available species names, many of which are in open nomenclature, and a high degree of uncertainty in species and higher taxonomy of this heterogeneous grouping of bivalves. These issues are due to several factors including: poor understanding of significant morphological traits and their variation in natural populations, their frequently poor preservation resulting in a misinterpretation of such traits, and palaeogeographical/palaeoceanographical provincialism that is in many cases unrecognized.

As construed herein, Triassic ‘flat clams’ represent a morphologically and taxonomically diverse group belonging to at least three separate bivalve

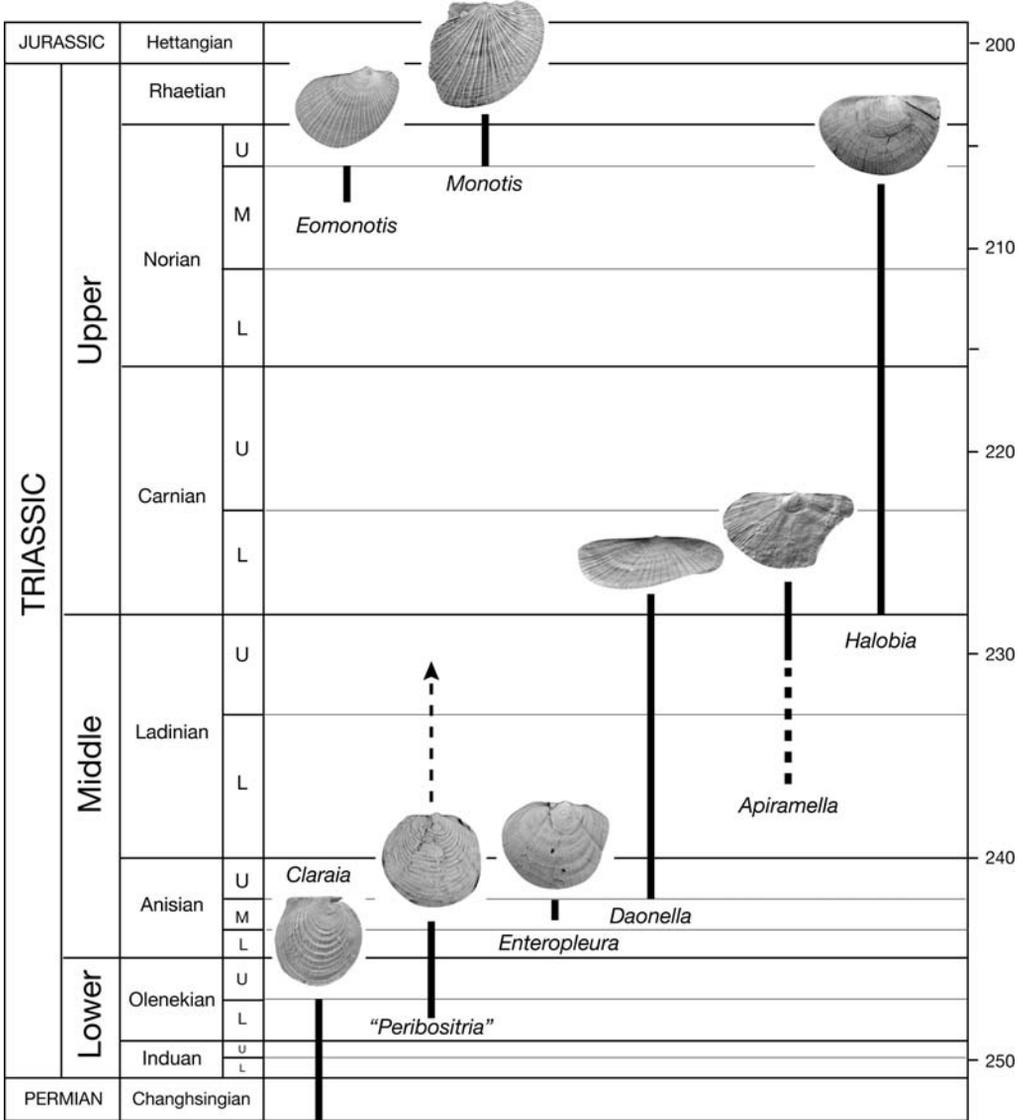


Fig. 1. Temporal distribution of Triassic flat clam bivalve genera with biochronological utility.

clades distributed across four family-group taxa: the Posidonidae, Halobiidae, Monotidae and Pterinoplectinidae. Further compounding the taxonomic clutter has been the introduction of lower-level groups (genera and subgenera) which have proliferated in recent years but which have often been constructed on limited morphological evidence without regard to natural morphological variation within species or populations or phylogenetic considerations. The primary genus-group taxa used here are broadly construed (*sensu lato*) and include *Claraia*,

Ellesmerella, *Enteropleura*, *Daonella*, *Halobia*, *Eomonotis*, and *Monotis*. Brief summaries of these accepted taxa and comments on group membership and affinities are provided in Appendix 1 and representative species are illustrated in Figures 4 and 7.

The sheer number of species in some of these genera is another subject of concern. For example, following Mojsisovics' (1874) impressive monograph, Kittl (1912) alone recognized 66 species of *Daonella* and 116 species of *Halobia*. More recent workers have not fared much better and the pace of

naming species has accelerated. In the past 50 years, workers have introduced more than 50 new species of *Monotis*, more than 75 new species of *Daonella*, and more than 200 new species of *Halobia*. Not surprisingly, a vast majority of these new species are based on wholly inadequate material – either very small sample sizes of only one or two specimens and without regard to natural morphological variation within populations, or they are based on taphonomically compromised specimens. While a thorough assessment of individual species validity is beyond the scope of this paper, an attempt has been made to include only species that have biochronological value, are morphologically distinctive, are based on sufficient material, and are generally accepted by modern workers.

Palaeoecological and palaeogeographical controls on biochronology

Although the mean duration of bivalve species is estimated to be *c.* 15 Ma (Stanley 1979), Triassic flat clam species are closer to the average durations for ammonoid species (1–2 Ma or less). What makes these bivalves different from other level-bottom bivalves likely lies in their evolutionary palaeoecology which can, in the absence of modern analogs or genetic information, be inferred from morphological adaptations, their unique facies occurrence, and analogous yet anecdotal similarities from other non-pelagic bivalves.

Palaeoecology

A significant attribute of Triassic flat clams is their episodic occurrence in monospecific or paucispecific shell accumulations. Although many of these shell beds occur in deep-water oxygen deficient settings, they also occur in significant abundance in deep so called ‘pelagic’ or ‘filamentous’ limestone (e.g. Hallstatt facies) that represent fully oxygenated marine settings (McRoberts *et al.* 2008). In addition, many examples are known from presumably shallower-water environments from Russia, New Zealand and Japan among other regions (see Miroshnikov & Burii 1969; Ando 1987; Campbell 1994). Within these settings, Triassic flat clams occur within a continuum of accumulation modes that are interpreted to be nearly *in situ* to occasional or episodic shell accumulations with varying amounts of re-working and time-averaging. Although some taxa (e.g. *Claraia* and *Enteropleura*) typically form thin shell beds less than 10 cm thick, the shell beds comprised of other taxa (e.g. *Halobia* and some *Monotis*) can achieve thicknesses of greater than 2 m (McRoberts *et al.* 2008; Grant-Mackie, pers. comm.). A ubiquitous

feature of the bivalve accumulations is that they are almost exclusively monospecific, or, more rarely, composed of two or three species. Similar shell beds are often labeled as ‘stagnation deposits’ (e.g. Seilacher *et al.* 1985) and may contain an admixture of palaeoecological and/or time-averaged associations. Following Kidwell & Bosence (1991), many are best described as either census assemblages or within-habitat time-averaged assemblages. These accumulations can be interpreted as *in situ* biogenic deposits representing episodic population expansion or immigration.

An extensive literature exists on the hypothesized living habit of Triassic flat clams (see Gruber 1976; Ando 1987; Wignall & Simms 1990; Campbell 1994; Schatz 2005; Waller in Waller & Stanley 2005 for useful summaries). While there certainly exists morphological disparity between genera, and no one-size-fits-all approach with respect to their autecology, Triassic flat clams are most likely either freely resting or reclining without byssal attachment (e.g. *Peribositria*, *Enteropleura*, *Daonella* and *Halobia*) or attached with a feeble or weakly functioning byssus (e.g. *Claraia*, *Eomonotis*, and *Monotis*). Although it has also been proposed that several of these genera were pseudoplanktonic and attached to drifting seaweed, wood, or other epiplanktic host (e.g. Jefferies & Minton 1965; Tozer 1982; Wignall & Simms 1990; McRoberts 1997), shell-bed attributes, facies occurrences, and lack of demonstrably attached specimens point to a benthic life mode for all of the genera considered here. A benthic living habit, however, does not in itself explain their unusual occurrence nor their biochronological utility.

It is also possible that some Triassic flat clams harbored symbiotic bacteria that enabled them to live in the presence of hydrogen sulfide in dysaerobic palaeoenvironments. Seilacher (1990) proposed that the anterior tube of *Halobia* served as a sulphur pump and perhaps served as the locus for chemosynthetic bacteria. This view was recently advocated by Waller (in Waller & Stanley 2005) who reinterpreted structures on *Halobia*'s anterior tube interior as radial mantle muscle scars and thus suggesting open passage from the tube to the mantle cavity. It should be noted, however, that neither *Daonella* (ancestral taxon to *Halobia*) nor other halobiids, monotids, or claraids exhibit this shell tube, yet occur in similar settings and shell accumulation modes. It should be further noted that extant bivalves with sulphur-oxidizing or methanotrophic endosymbionts (e.g. lucinid, thyasirid and solemyid bivalves) typically have relatively large gills which host the endosymbionts which would not be accommodated in the slender valve cavity of the Triassic forms (most notably halobiids and claraids). Furthermore, known chemoautotrophic endosymbionts

and methanotrophs occur where both sulfide and limited oxygen co-exist (Scott & Cavanaugh 2007), and that free oxygen is necessary for metabolic function employing glycolysis (Oschmann 1993).

Hydrothermal vent and, to a lesser extent, methane seep faunas are notably dominated by endemic species (Tunnickliffe 1991) which is atypical for these Triassic bivalves. Lastly, although the Triassic flat clams are notable for their densely-packed accumulations, which resemble some of the dense faunal communities surrounding methane seeps, the shell beds are laterally continuous in exposures up to one kilometer in lateral extent, which is atypical for modern chemo-symbiotic communities whose distribution is patchy.

Based on facies occurrences and shell-bed attributes, many of the Triassic flat clams can be best described as belonging to opportunistic populations which Levinton (1970) described as unstable populations that are not resource limited but primarily controlled by the physical and not the biotic environment. Opportunistic fossil populations appear to be a major component of the exaerobic biofacies (*sensu* Savrda & Bottjer 1987, 1991) that are characterized by organic-rich laminated sediments and epibenthic macrofossil assemblages in oxygen deficient (dysaerobic) benthic conditions. Claroids, halobiids and monotids in particular fit the opportunistic model in several ways as demonstrated by several empirical studies on similar biofacies. Wignall (1993) established a positive correlation between decreasing oxygen gradients and decreasing benthic diversity, reaching zero at essentially the anaerobic/dysaerobic boundary. Gradient analyses of Jurassic oxygen-deficient faunas by Etter (1995) demonstrate the macrofaunal succession of equilibrium species being displaced by low diversity, high abundance opportunistic species and again by low abundance higher diversity chemosynthetic specialists at the lower end of the dysaerobic/anaerobic interface.

Many of these Triassic flat clam palaeocommunities are interpreted to have inhabited and dominated environments near a threshold oxygen minimum boundary which other shelly benthos found unsuitable. The spatial distribution and mode of occurrence of these bivalve palaeocommunities conform to an incumbent dominance model (e.g. Rosenzweig & McCord 1991; Sepkoski 1996) where the first individuals of a species to occupy a niche, dominate and hold the spot until replaced or removed from that niche. It has also been proposed that rapid fluctuations in environmental conditions tend to favor eurytopic species with high genetic diversity (Sanders 1968; Bretsky & Lorenz 1970). The episodic nature of many of the shell beds suggests that Triassic flat clams also appear to have exhibited low resistance to environmental perturbations but are resilient in being able to recover

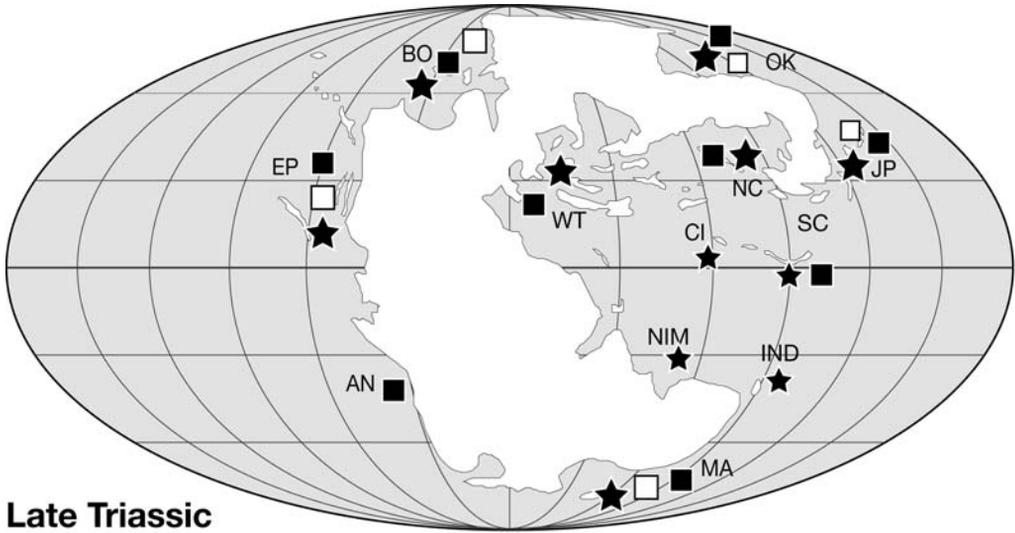
quickly (see Tang 2001 for a review of resistant v. resilient species). With respect to flat clams in general, and *Monotis* in particular, Shaner & McRoberts (2000) proposed that once colonization occurs, the bivalve assemblages dominate substrate to the exclusion of other benthic organisms. This dominance may continue even if oxygen conditions become favorable. This model of episodic replacement of bivalve assemblages provides ample room for the repeated colonization of different flat-clam species and even genera along oxygen or other resource threshold boundaries.

Palaeobiogeography

The assembly of the supercontinent Pangaea by Triassic time had resulted in more than half of the Earth's surface being covered by the Panthalassa Ocean, which spread from pole to pole, and an east-west tropical seaway – the Tethys (Fig. 2). Within these broad palaeogeographical constraints, geographical distribution of Triassic bivalves with biochronologic significance is controlled by the location of suitable environments. Major constraints in the distribution of bivalves are bathymetry, substrate, temperature, chemistry (e.g. dissolved oxygen), and oceanographical currents needed for dispersal.

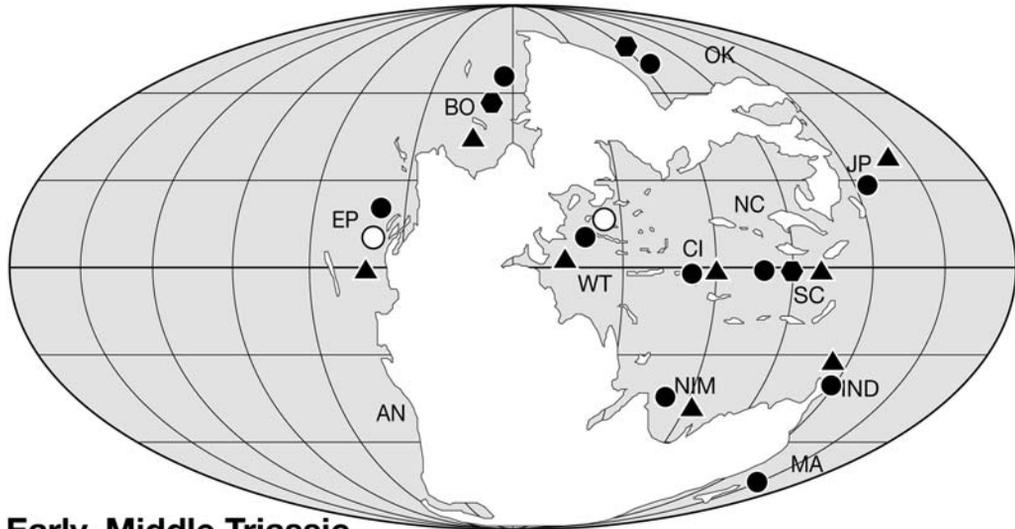
Palaeocurrents within Panthalassa and the Tethys can be determined through actualistic principles applied to palaeogeographical reconstructions and have been summarized by several workers (e.g. Tollmann & Kristan-Tollmann 1985; Yan & Zhao 2001). In general, the major palaeocurrents of the Triassic can be summarized as: (a) a low latitude north and south equatorial current from the margin of Pangaea moving westwards across Panthalassa and into the Tethys with an equatorial counter current moving eastward; (b) a clockwise gyre in northern Panthalassa feeding warm currents along the northeast margin of Pangaea and a cold-water current moving down the northwest margin of Pangaea; and (c) a counterclockwise gyre in southern Panthalassa bringing warm water across southeastern Tethys, Australia and perhaps as far south as New Zealand and cooler water northwards adjacent to the Andean margin of Pangaea. It should be noted, however, that distributional patterns of many Triassic macrofauna are quite complex and may require additional dispersal models, such as the Pantropical model of Newton (1988) or tectonic displacement or some combination thereof (e.g. Silberling 1985; Stanley & González-León 1995).

Dispersion of bivalve species across Panthalassa and the Tethys would most likely have been through passive transport of larvae via surface currents. Although some Triassic flat clams may have had planktotrophic larvae (McRoberts 2000), almost nothing is known about the larval development of most species. Regardless, even short-lived planktic



Late Triassic

- *Monotis* □ *Eomonotis* ★ *Halobia*
- “*Peribositria*” ○ *Enteropleura* ● *Daonella*
- ▲ *Claraia*



Early-Middle Triassic

Fig. 2. Biogeographical distribution of significant occurrences of Triassic bivalves. Abbreviations for informal regions include: WT, Western Tethys; NIM, Northern Indian Margin (e.g. Salt Range, Kashmir); CI, Cimmeria (e.g. Tibet); NC, North China; SC, South China; IND, Indonesia; JP, Japan; MA, Maori; AN, Andean; EP, Eastern Panthalassa including pericraton regions (e.g. Nevada and northeastern British Columbia) and allochthonous terranes (e.g. Wrangallia, Stikinia); BO, Boreal (Arctic Alaska, Arctic Canada, Greenland, Svalbard, northern Siberia); OK, Okhotsk (e.g. northeastern Siberia). Palaeogeographic reconstructions modified from Blakey (2005).

larva could be transported great distances – for example, larvae having a pelagic stage of 2–6 weeks could be transported up to 500 km by only moderate coastal currents; longer pelagic larval

stages (e.g. 3 months or more) could effectively cross entire deep ocean basins (e.g. Sheltema 1977). Except for the broadly construed Tethyan, Panthalassan, and Boreal realms, Triassic seas are

not easily differentiated into biogeographical provinces. With few notable exceptions discussed later, Triassic flat clams are distributed across most regions in which marine strata are preserved. Although too numerous to list here in detail, Triassic pelagic bivalves commonly occur in the Western Tethys (including the northern and southern Alps, Sicily, Carpathians, and into the Balkans). Major occurrences in the central and eastern Tethys are also significant, with many species known from both the southern branch of the Tethys northern Indian margin (e.g. Salt Range) as well as from the central and northern branches (e.g. Caucasus, Crimea, Kashmir, Spiti, Nepal and Tibet). In the far eastern Tethys, significant occurrences of flat clams are also known from both the North and South China Blocks, Timor, and in many localities in what is now southeast Asia (e.g. Thailand, Vietnam, etc.). The Boreal region appears to be a center of diversity among bivalve species having significant occurrences in northern and northeastern Siberia, northern Alaska, the Canadian Arctic Archipelago, northeast Greenland and Svalbard. The northwest margin of Panthalassa includes Primorye and the terranes of Kamchaka and Korayak. Many of these regions contain mixtures of faunas from more than one province. For example, bivalves of low to mid palaeolatitudes of western offshore Pangaea (e.g. Nevada and northeastern British Columbia) contain a mixture of Boreal

and Tethyan elements (see discussion in Silberling 1985; Newton 1988).

Biochronology and bivalve zones of the Triassic

This section presents a summary of the temporal distribution and global/interregional correlation of bivalve (chiefly flat clam) occurrences having demonstrably biochronological significance during the Triassic. These data are based on an extensive literature compilation and first-hand study of field and museum collections, and integrated, to the extent possible, with other biochronologically important fossils, most notably ammonoids and conodonts. The temporal ranges of species are depicted here as zones and, except where noted, these are total range zones and are based on the ranges of individual species. These zones, however, remain tentative and informal as they lack appropriate stratal and geographical definitions. Where possible, the bivalve ranges are resolved to standard ammonoid zones as depicted in the zonal charts (Figs 3, 5 & 6). In species whose range is demonstrably shorter than an ammonoid zone (e.g. uppermost Olenekian *Ellesmerella*, uppermost Anisian *Daonella* or uppermost Norian *Monotis*) the zonal limits may be artificially extended upwards and downwards for the entire interval.

	STAGE	AMMONOID ZONES		BIVALVE ZONES			
		North American	Tethys	Eastern Tethys	North America	Boreal	
LOWER TRIASSIC	OLENEKIAN	Spathian	<i>Keyserlingites subrobustus</i>	<i>Neopanoceras haugi</i>		<i>Ellesmerella aranea</i>	
			<i>Olenikites pilaticus</i>	<i>Prohungarites-Subcolumbites</i>		<i>Peribositria sibirica</i>	
				<i>Procolumbites</i>			
				<i>Columbites parisianus</i>			
				<i>Tirolites cassianus</i>			
	Smithian	<i>Anawasatchites tardus</i>	<i>Anawasatchites / Anasibirites</i>		<i>*Pseudomonotis* occidentalis</i>	<i>*Pseudomonotis* occidentalis</i>	
		<i>Euflemingites romunderi</i>	<i>Meekoceras gracilitatis</i>			<i>Peribositria mimer</i>	
		<i>Hedenstroemia hedenstroemi</i>	<i>Euflemingites</i>			<i>Peribositria borealis</i>	
			<i>Flemingites griesbachi</i>				
	INDUAN	Dienerian	<i>Vavilovites sverdrupi</i>	<i>Rohillites rohilla</i>			
			<i>Propyrites candidus</i>	<i>Prionobolus</i>	<i>Claraia aurita</i>		
		Griesbachian	<i>Bukkenites canstrigatus</i>	<i>Gryonites frequens</i>			
			<i>Ophiceras commune</i>	<i>*Pleurogryonites* planidorsatus</i>	<i>Claraia stachei</i>	<i>Claraia stachei</i>	<i>Claraia stachei</i>
				<i>Discophiceras rotelliformis</i>			
<i>Ophiceras boreale</i>	<i>Ophiceras tibeticum</i>	<i>Claraia wangi</i>					
		<i>Otoceras woodwardi</i>	<i>Claraia dieneri</i>				

Fig. 3. Bivalve zones of Early Triassic *Claraia*, *Peribositria* and *Ellesmerella* for the western and eastern Tethys (including both northern Indian margin and South China), and Boreal realm. Sources for bivalve zonation discussed in text. Ammonoid zones modified from Orchard & Tozer (1997), Zakharov *et al.* (1997) and Kozur (2003).

Temporal assignments rely on integration of several zonal schemes from various taxa taken across widely distributed regions as discussed in each appropriate section below. Stage and substage nomenclature and definitions are largely taken from Ogg (2004) and in several cases have been modified as recent advances in selection of GSSPs in defining the standard chronostratigraphic scale of the Triassic.

Early Triassic

As with other parts of the Triassic, biochronological schemes of the Early Triassic are largely based upon conodonts and ammonoids. Following the formal definition of the base of the Triassic with the first occurrence of the conodont *Hindeodus parvus* from the base of bed 27c at Meishan South China (Yin *et al.* 2001), the Triassic Subcommittee on Stratigraphy has recently adopted the use of subdividing the Early Triassic into two stages, the Induan and Olenekian. Progress has been made at defining the base of the Olenekian at the Mud section of Spiti by the first occurrence of the conodont *Neospathodus waageni sensu lato* which is less than one metre above the base of the *Rohillites rohilla* ammonoid Zone (Krystyn *et al.* 2007a). The Lower Triassic is subdivided into between 10 and 15 ammonoid zones (Kozur 2003) and recent estimates suggest that the entire Early Triassic was of only 5 Ma or so (Mundil *et al.* 2004; Ogg 2004) in duration.

As mentioned earlier, the Early Triassic is dominated by low diversity but locally abundant bivalve faunas, which largely include representatives of Permian hold-over clades (e.g. Permophoridae, Myalinidae and Pterinopectinidae). Included in this group are species *Eumorphotis* and *Promyalina*, and most importantly the flat clam *Claraia* that has long been recognized as a zonal taxon for the Early Triassic. Although *Claraia* has often been regarded as a cosmopolitan taxon, a majority of its species are of local or regional importance. It should also be noted that *Claraia* species are quite rare in the lowermost Triassic *Otoceras* beds and are often found above the disaster fauna (e.g. microbialites and *Lingula* zone) associated with the end-Permian mass extinction. Furthermore, individual species ranges (and subsequent zones) for *Claraia* are somewhat long when compared to ammonoid ranges of the same interval, yet they are comparable to bivalve zones of the Middle and Late Triassic. In spite of this, zonal schemes for *Claraia* have been developed for a number of Tethyan, Boreal, and circum-Pacific regions (Fig. 3).

Of the numerous successions, those of the eastern Tethys, including the Northern Indian Margin and South China are the best known and integrated into other biochronological scales using

conodonts and ammonoids. Nakazawa (1977, 1981) developed a zonation based on *Claraia* from the uppermost Permian through Lower Olenekian (*Meekoceras* beds of the Smithian) from Kashmir and Iran. Nakazawa listed 33 *Claraia* species belonging to 4 species groups. A complimentary zonation from south China was provided by Yin (1985, 1990) who identified six *Claraia* acme zones distributed across much of the Lower Triassic. Presented here is a composite zonation beginning with a zone of *Claraia dieneri* Nakazawa correlative to the *Otoceras woodwardi* Zone that is well established in Kashmir, South China, and the Perth Basin of Australia (Nakazawa 1977; He *et al.* 2007). A zone of *C. wangi* Patte associated with the conodont *Isarcicella isarcica* and the ammonoid *Ophiceras sinense* and largely restricted to South China and Vietnam is in part correlative with *C. dieneri* Nakazawa, yet ranges into somewhat younger strata (Yin 1990; Tong & Yin 2002). *Claraia griesbachi* (Bittner) and *C. concentrica* (Yabe) also occur in the Lower Induan (*Ophiceras-Lytophiceras* ammonoid Zone) of Anhui Province China (Tong *et al.* 2004). *Claraia wangi* Patte has been reported from several localities in south China and is frequently associated with the ammonoid *Ophiceras* and the conodont *Isarcicella isarcica* but never with lowermost Induan ammonoids *Otoceras woodwardi* nor the conodont *Hindeodus parvus*. This east Tethyan zone can be correlated to the western-Tethys, where at the Tesero section in the Italian Dolomites, *Claraia griesbachi* (Bittner) first appears about 15–20 m from the base of the Mazzin Member of the Werfen Formation (e.g. Broglio Loriga *et al.* 1986; Broglio Loriga & Cassinis 1992; Wignall & Hallam 1992). Tethyan *Claraia* can be correlated to North America, where several species including *C. clarae* (Emmrich) (Fig. 4h) and *C. stachei* Bittner occur in the central Rocky Mountains in the western United States (Newell & Kummell 1942; Ciriacks 1963; Newell & Boyd 1995) and also northern Rocky Mountains in British Columbia and Alberta Canada (Tozer 1970). It should be noted, however, that reports of Permian *C. stachei* (e.g. Muromtseva 1984) have not been adequately illustrated, and their validity remains in question. Generally above the sequence of *C. stachei* Bittner is a zone of *C. aurita* (Hauer) that has proven to be of regional significance extending from the western Tethys eastward into the Praecaucasus, the northern Indian Margin, South China and northeastern Russia and with a little more precision to the *Tirolites harti* ammonoid Zone (Gavrilova 2004).

Above the *Claraia* zones of the Induan and lowermost Olenekian are several demonstrable zones of *Peribositria* that are largely relegated to the Boreal realm. Several *Peribositria* species are

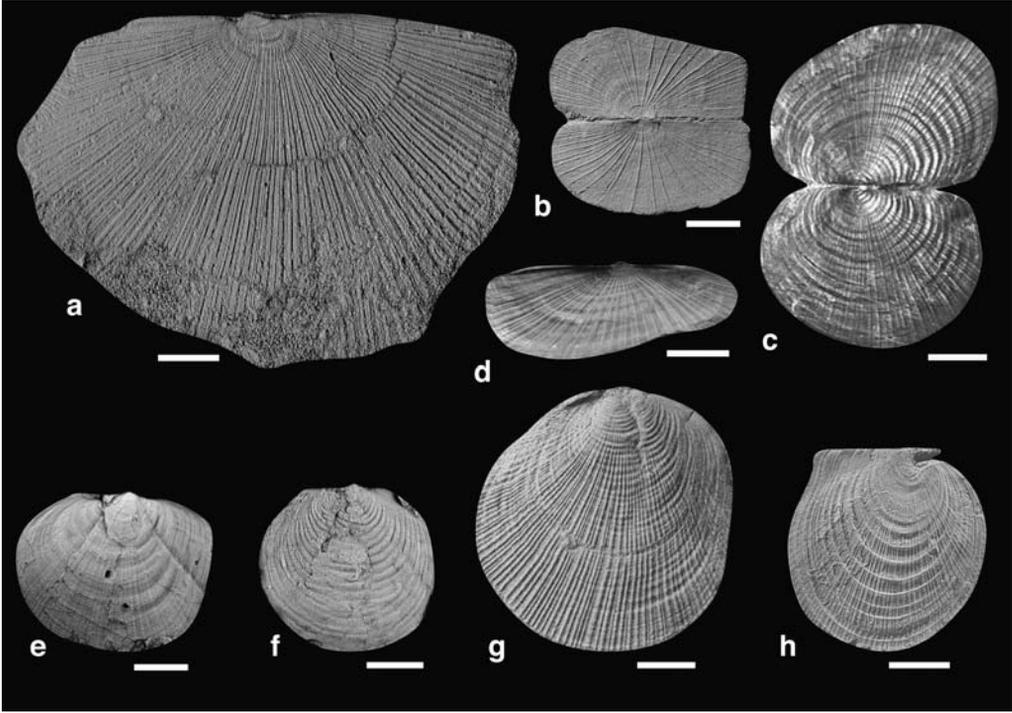


Fig. 4. Representative Lower and Middle Triassic pelagic bivalves. All scale bars = 1 cm. (a) *Daonella elegans* McLearn, Upper Ladinian, *Frankites sutherlandi* Zone from Toad Formation, Halfway River area, British Columbia, Canada (SUCP collection). (b) *Daonella subarctica* Popov, Upper Ladinian, Botneheia Formation, Svalbard (SM M1285, from Campbell 1994, pl. 5, fig. 2). (c) *Daonella moussoni* (Merian), Upper Ladinian, *Prototrachyceras gredleri* Zone (PIMZ collection, from Rieber 1969, pl. 2, fig. 3). (d) *Daonella* cf. *D. sturi* (Benecke), Upper Anisian, *Parafrechites meeki* Zone, Favret Formation, Lone Peak, Nevada (SUCP collections). (e) *Enteropleura jenksi* Hopkin & McRoberts, Middle Anisian, *Balatonites shoshonensis* Zone, from Favret Formation, New Pass Range, Nevada (USNM 526057, from Hopkin & McRoberts 2005, fig. 3.1). (f) *Peribositria mimer* (Oberg), Upper Olenekian, Otuk Formation, Brooks Range, Alaska (SUCP collection). (g) *Ellesmerella aranea* (Tozer), Upper Olenekian (Smithian) Svalbard (SM G1281, from Tozer & Parker 1968, pl. 25, fig. d). (h) *Claraia clarae* (von Hauer), Lower Induan, Brazeau River, Alberta (GSC 14196, from Newell & Boyd 1995, fig. 17.7; see also Tozer 1961, pl. 28, fig. 3).

relegated to the lower Olenekian including the most common forms *P. borealis* Kurushin & Trushchelev and *P. mimer* Oeberg (Fig. 4f), which comprises two distinctive zones of the upper Smithian. Tozer (1963) reports *P. mimer* Oeberg from the *Euflemingites romunderi* Zone of the Toad Formation of northeastern British Columbia, from the same interval in the Blind Fiord Formation of Ellesmere Island in Arctic Canada and likely from the Yukon area. Other species of *Peribositria*, including *P. backland* (Wittenburg) from the lower Olenekian from Siberia and Svalbard (Kurushin & Trushchelev 1989), are rather poorly constrained but are known to co-occur with the ammonoids *Arctoceras blomstrandii* and *Euflemingites* and *Hedenstroemi* equivalents of the Early Olenekian (Kurushin & Trushchelev 1989). Somewhat longer in duration

is *P. siberica* Kurushin (1980) which seems to have some biochronological value (Zakharov *et al.* 1997), yet it is long-ranging, encompassing nearly the entire Spathian (*Bajarunia euomphala* through *Parasibirites grambergi* ammonoid Zones) from central Siberia, Arctic Canada, and British Columbia (Kurushin & Trushchelev 1989).

In high to mid northerly latitudes, *Ellesmerella aranea* (Tozer) (Fig. 4g) comprises the youngest bivalve zone of the Olenekian and is fairly well constrained by ammonoids of the *Keyserlingites subrobustus* ammonoid Zone. Tozer (1973) summarized the distribution of this species which is now known from several localities in Svalbard (Tozer & Parker 1968), and Ellesmere Island in the Canadian Arctic (Tozer 1961, 1967), northeastern British Columbia (Tozer 1963, 1970) and northeastern Siberia

MIDDLE TRIASSIC	STAGE	AMMONOID ZONES		BIVALVE ZONES			
		North American	Tethys	West Tethys	North America	Boreal	
		LADINIAN	U	<i>Frankites sutherlandi</i>	<i>Frankites rogoledanus</i>	<i>Daonella lormmeli</i>	<i>Daonella elegans</i>
<i>Maclearnoceras maclerni</i>	<i>Prototrachyceras archelarus</i>			<i>Daonella nitinae</i>			
<i>Megincoceras meginae</i>	<i>Prototrachyceras longobardium</i>				<i>Daonella piccheri</i>		
L	<i>Tuchodoceras poseidon</i>			<i>Prototrachyceras gredleri</i>	<i>Daonella moussoni</i>	<i>Daonella rieberi</i>	<i>Daonella frami</i>
				<i>Prototrachyceras margaritosum</i>			<i>Daonella lindstroemi</i>
	<i>Eoprototrachyceras matutinum</i>		<i>Eoprototrachyceras curionii</i>				
ANISIAN	U		<i>Frechites occidentalis</i>	<i>Nevadites sacedensis</i>	<i>Daonella elongata</i>	<i>Daonella dubia</i>	<i>Daonella dubia</i>
			<i>Parafrechites meeki</i>	<i>Reitziites reitzi</i>		<i>Daonella cf. D. sturi</i>	
			<i>Gymnotoceras rotelliformis</i>		<i>Daonella sturi</i>	<i>Daonella americana</i>	<i>Daonella americana</i>
			<i>Gymnotoceras mimetus</i>				
		<i>Gymnotoceras weitschati</i>					
	M	<i>Balatonites shoshonensis</i>	<i>Balatonites balatonicus</i>	<i>Enteropleura bittneri</i>	<i>Enteropleura jenski</i>		
		<i>Nevadisculites taylori</i>	<i>Nevadisculites taylori</i>				
		<i>Acrochordiceras hyatti</i>	<i>Acrochordiceras ismidicus</i>				
	L	<i>Paracrochoceras americanum</i>					
		<i>Lenotropites caurus</i>	<i>Lenotropites caurus</i>				
		<i>Silberlingites mulleri</i>	<i>Silberlingites mulleri</i>				
		<i>Pseudokeyserlingites guexi</i>	<i>Pseudokeyserlingites guexi</i>				
	<i>Japonites welteri</i>	<i>Japonites welteri</i>					

Fig. 5. Bivalve zones of Middle Triassic *Peribositra*, *Enteropleura* and *Daonella* for the western Tethys, North America and Boreal realms. Sources for bivalve zonation discussed in text. Ammonoid zones modified from Mietto & Manfrin (1995), Orchard & Tozer (1997), Zakharov *et al.* (1997), Kozur (2003) and Monnet & Bucher (2005).

UPPER TRIASSIC	STAGE	AMMONOID ZONES		BIVALVE ZONES				
		North America	Tethys	West Tethys	North America	Boreal		
		RHAETIAN	U	<i>Choristoceras crickmayi</i>	<i>Choristoceras marshi</i>	<i>Rhaetavicula contorta</i>		<i>Tosapecten efimovae</i>
<i>Cocholoceras ameonum</i>	<i>Vandafites stuerzenbaumi</i>			<i>Monotis rhaetica</i>				
	<i>Sagenites reticulatus</i>			<i>Monotis salinaria</i>	<i>Monotis subcircularis</i>	<i>Monotis ochotica</i>		
NORIAN	M		<i>Gnomaharites cordilleranus</i>	<i>Sagenites quinquepunctatus</i>				
			<i>Mesohimavites columbianus</i>	IV	<i>Halarites macer</i>	<i>Halobia distincta</i>	<i>Eomonotis pinensis</i>	<i>Eomonotis scutiformis</i>
				III				
				II	<i>Himavatites hogarti</i>	<i>Halobia norica</i>	<i>Halobia fallax</i>	<i>Halobia obruchevi</i>
			I	<i>Himavatites watsoni</i>	<i>Halobia halorica</i>	<i>Halobia halorica</i>		
	<i>Drepanites rutherfordi</i>		<i>Cryptoleurites bicrenatus</i>	<i>Halobia darwini</i>				
	L		<i>Juvavites magnus</i>	<i>Juvavites magnus</i>	<i>Halobia mediterranea</i>			
		<i>Malayites dawsoni</i>	<i>Malayites paucicki</i>					
		<i>Stikinoceras kerri</i>	<i>Guembelites jandianus</i>	<i>Halobia beyrichi</i>	<i>Halobia beyrichi</i>	<i>Halobia verchojanensis</i>		
			<i>Gonionotites italicus</i>	<i>Halobia radiata</i>	<i>Halobia radiata</i>	<i>Halobia kawadai</i>		
		<i>Anatropites</i>	<i>Discotropites plinii</i>					
CARNIAN	U	<i>Klamathites macrolobatus</i>	<i>Tropites subbullatus</i>	<i>Halobia lenticularis</i>	<i>Halobia superba</i>	<i>Halobia kiparisovae</i>		
		<i>Tropites welleri</i>			<i>Halobia ornatissima</i>	<i>Halobia omskutcharica</i>		
		<i>Tropites dilleri</i>	<i>Tropites dilleri</i>	<i>Halobia superba</i>		<i>Halobia ornatissima</i>		
	L	<i>Sirenites nanseni</i>						
		<i>Austrotrachyceras obesum</i>	<i>Austrotrachyceras austriacum</i>	<i>Halobia rugosa</i>	<i>Halobia rugosa</i>	<i>Halobia popowi</i>		
		<i>Trachyceras desatoyense</i>	<i>T. aonoides</i>	<i>T. aonoides</i>		<i>Halobia zhilnensis</i> <i>Halobia zitteli</i>		

Fig. 6. Stratigraphical ranges of Late Triassic, *Halobia*, *Eomonotis*, and *Monotis* for western Tethys, North America and Boreal realms. Ammonoid Zones modified from Orchard & Tozer (1997) Zakharov *et al.* (1997), Kozur (2003) and Gallet *et al.* (2007).

(Vozin & Tikhomirova 1964; see also Zahkarov *et al.* 1997).

Middle Triassic

The Middle Triassic comprising the Anisian and Ladinian stages lasted approximately 10–12 Ma (Brack *et al.* 2005; Lehrmann *et al.* 2006; Ovtcharova *et al.* 2006). The Anisian, whose base is as yet undefined, contains 7–13 ammonoid zones (Silberling & Tozer 1968; Tozer 1994; Mietto & Manfrin 1995; Orchard & Tozer 1997; Monnet & Bucher 2005). As shown in Figure 5, the Ladinian, whose base is now accepted to be the first occurrence of *Eoprototrachyceras curionii* (Brack *et al.* 2005), can be subdivided into approximately seven standard ammonoid zones (Tozer 1994; Mietto & Manfrin 1995).

No global or regionally applicable bivalve zones have been identified for the Lower through Middle Anisian. The first globally useful bivalve zone of the Middle Triassic occurs in the upper part of the Middle Anisian (*Balatonites shoshonensis* ammonoid Zone) where several species of *Enteropleura* (Fig. 4e) appear in different and widely-spaced regions including the west Tethys, North America and China (Waller in Waller & Stanley 2005; Hopkin & McRoberts 2005; Chen & Stiller 2007).

Beginning at the base of the *Gymnotoceras weitschati* ammonoid Zone, a succession of *Daonella* species permits subdivision of the Upper Anisian through uppermost Ladinian into approximately 5–7 *Daonella* zones of regional and global significance. Perhaps the best-represented succession of daonellas is known from the Monte San Giorgio section, Switzerland (Rieber 1968, 1969; Schatz 2004), and from the Italian Dolomites (Brack & Rieber 1993). A composite succession begins with *Daonella sturi* (Benecke) in the Upper Anisian (*Paraceratites trinodosus* Zone) overlain by the *Daonella elongata* Mojsisovics group (co-occurring with *D. pseudomoussoni* Rieber) that dates as uppermost Anisian and lower Ladinian (*Reitziites reitzi* through *Eoprototrachyceras curionii* Zones). Above this is a distinct zone containing *D. moussoni* (Merian) (Fig. 4c) which ranges close to the base of the upper Ladinian (*Prototrachyceras gredleri* Zone), although it may extend a short time above its uppermost boundary. This is in turn followed by two successive *Daonella* zones: *D. picheri* Mojsisovics overlain by *D. lommeli* (Wissmann) that are well represented in the Southern Alps and provide useful correlations to elsewhere in the Tethys and North America.

A North American sequence of daonellas can be constructed using the well documented succession from western Nevada (e.g. Silberling & Tozer 1968; Silberling & Nichols 1982) and northeastern British Columbia, Canada (e.g. Tozer 1967, 1970).

The sequence provides several links to the Tethyan succession (e.g. *D. moussoni* (Merian) near the middle/upper Ladinian boundary) and with the Boreal Realm (e.g. *D. americana* Smith and *D. dubia* (Gabb) in the upper Anisian). In North America, the youngest *Daonella* of the Ladinian, *D. elegans* McLearn, is well constrained to the *Frankites sutherlandi* ammonoid zone from north-eastern British Columbia (Tozer 1967) and possibly from western Nevada (Balini *et al.* 2007). Although they remain poorly documented, several occurrences of *Daonella* are known from lower Carnian strata overlapping with true *Halobia*.

Upper Triassic

The Upper Triassic is subdivided into three stages: in ascending order Carnian, Norian and Rhaetian. The basal Carnian has recently been defined as the base of the *Daxatina canadensis* ammonoid Zone (Mietto *et al.* 2007). Several potential candidates are being considered for a base-Norian GSSP including ammonoids (e.g. *Stikinoceras kerri*) slightly above the first occurrence of *Epigondolella primitius* datum and below several other potential conodont-based levels including first occurrence of *Epigondolella quadrata* (see Orchard 2007). Of the three potential levels for the base Rhaetian, the conodont *Misikella posthernsteini* is the leading candidate (Krystyn *et al.* 2007b).

The Carnian through middle Norian can be subdivided into several zones based on *Halobia* species (Fig. 6). Zonal schemes are provided for the western Tethys Alpine-Mediterranean belt (taken from Gruber 1976; Cafiero & De Capoa Bonardi 1982; De Capoa Bonardi 1984), western North America including the allochthonous and autochthonous elements of British Columbia, southeastern Alaska, Oregon and Nevada (McRoberts 1997, personal observations), and the Boreal regions encompassing northeastern Siberia (Kiparisova *et al.* 1966; Polubotko 1980, 1984, 1986), Arctic Alaska (Blome *et al.* 1988; Dutro & Silberling 1988), Arctic Canada (Tozer 1961, 1967), and Svalbard (Campbell 1994). It should be noted that other regions including China (Chen 1964), SE Asia and Melanesia (e.g. Krumbek 1924; Vu-Khuc 1991; Chonglakmani & Grant-Mackie 1993) and New Zealand (e.g. Marwick 1957; Campbell 1994) have significantly contributed towards our understanding of *Halobia* biochronology and provide valuable interregional and global correlations.

The Early Carnian *Trachyceras desatoyense* through *Sirenites nanseni* ammonoid zones and equivalents are rather poorly represented by pelagic bivalves in most regions. It is perhaps best represented by *Halobia zitteli* Lindstöm (Fig. 7k) in the Boreal regions of Russia, Canada, and

Svalbard (e.g. Tozer 1961; Polubotko 1980; Campbell 1994). In NE Siberia, *H. zitteli* Lindstöm may be restricted to the earliest Carnian (*Trachyceras desatoyense* Zone) and is subsequently overlain by four halobiid zones including *H. zhilnensis* Polubotko with *H. talajaensis* Polubotko, *H. popowi* Polubotko, *H. ornatissima* Smith with *H. subfallax* Efimovae, and *H. asperella* Polubotko (Polubotko 1980, 1986; Zakharov *et al.* 1997). In western North America, however, *H. zitteli* Lindstöm is poorly represented, and *H. rugosa* Mojsisovics is more characteristic of the lower Carnian, yet it too may extend into the upper Carnian extending into the *Klamathites macrolobatus* Zone or even *Stikinoceras kerri* Zone where it co-occurs with *H. superba* Mojsisovics and *H. radiata* Gemmellaro (McRoberts 1997, 2007, personal observations).

The base of the Norian stage (as yet undefined, but here taken as the first occurrence of the ammonoid *Stikinoceras kerri*) closely corresponds to the first occurrence of *Halobia styriaca* (Mojsisovics) (Fig. 7i) and *H. beyrichi* (Mojsisovics) and similar species best represented in low palaeolatitudes with notable occurrences in the western and eastern Tethys and eastern Panthalassa (Gruber 1976; De Capoa Bonardi 1984; McRoberts 1997). A temporally-limited zone spanning the Carnian-Norian boundary is based on *H. radiata* Gemmellaro that is well represented across the Tethys, Boreal, and low to mid latitude strata in western North America (De Capoa Bonardi 1984; Nicora *et al.* 2007; McRoberts 2007). Above the zone of *H. beyrichi* (Mojsisovics) and *H. styriaca* (Mojsisovics) are a suite of similar forms referable to *H. cordillerana* Smith (Fig. 7g), *H. obruchevi* Kiparisova in NE Russia (e.g. Kiparisova *et al.* 1966; Polubotko 1984) and *H. hochstetteri* Mojsisovics in New Zealand (Campbell 1994). In the western Tethys, this interval is characterized by a sequence of zones in ascending order: *H. mediterranea* Gemmellaro, *H. darwini* Cafiero & De Capoa Bonardi, *H. halorica* Mojsisovics, *H. norica* Mojsisovics, and *H. distincta* Mojsisovics (Gruber 1976; De Capoa Bonardi 1984). Of particular importance is *H. halorica* Mojsisovics, a short-lived species found in the western Tethys, Russia and in North America which is well constrained to the middle Norian *Drepanites rutherfordi* into lowermost *Mesohimavittes columbianus* Zones and equivalents (De Capoa Bonardi 1984; McRoberts 1997).

Eomonotis contains at least 10 species, primarily in the circum-Pacific, and notably absent in the western Tethys, that are all largely restricted to the upper part of the Middle Norian (e.g. below the conodont *Epigondolella bidentata*). The oldest *Eomonotis*, *E. daonellaeformis* Kiparisova and slightly younger *E. pinensis* (Westermann) (Fig. 7e) are found in association with *Halobia* near the first

appearance of the conodont *Epigondolella postera* and ammonoid equivalents (e.g. *Mesohimavittes columbianus* II Zone) in western North America and with *E. scutiformis* (Teller) at approximately the same level in far-east Russia and New Zealand (Westermann & Verma 1967; Bychkov *et al.* 1976; Grant-Mackie 1980; Grant-Mackie & Silberling 1990).

Above *Eomonotis*, the Upper Norian (*Gnomohalorites cordilleranus* Zone and equivalents) is characterized by numerous species of *Monotis* (*sensu lato*) that have proven to be of global biochronological significance (e.g. Ichikawa 1958; Westermann 1973; Bychkov *et al.* 1976; Grant-Mackie 1978; Tozer 1980; Silberling 1985; Silberling *et al.* 1997). Although there are about 30 well-defined species of *Monotis* that demonstrably occur in the upper Norian, only a few are noteworthy because of their regional and global correlation potential. These include the distinctive *M. subcircularis* Gabb in the circum-Pacific, *Monotis ochotica* (Keyserling) across the circum-Pacific and into the Boreal Realm, and *Monotis salinaria* (Schlotheim) common in the Tethyan Province and perhaps elsewhere in the circum-Pacific. Some authors have differentiated an uppermost Norian into two zones, a lower consisting of *M. subcircularis* Gabb (Fig. 4f) and an upper zone of *M. ochotica* (Keyserling) and *M. alaskana* Smith in certain mid to high-latitude settings (e.g. Grant-Mackie & Silberling 1990; Silberling *et al.* 1997). It should be noted that both *M. subcircularis* and *M. ochotica* provide valuable correlations to the upper Norian of South America (e.g. Jaworski 1922; Westermann 1970; Geyer 1973) which are mostly lacking in marine strata during earlier Triassic times. It has been long assumed that *Monotis* experienced mass extinction close to the Norian/Rhaetian boundary as defined by first appearance of the conodont *Misikella posthernsteini* and its ammonoid equivalents (various *Paracochloceras* and perhaps *Sagentites reticulatus*). Recent finds in the Hallstatt limestone in Austria record two surviving and dwarfed species of *Monotis* above this event, one of which, *Monotis rhaetica* McRoberts *et al.* (Fig. 7d) is new (McRoberts *et al.* 2008).

Although species of *Otapiria* are known from strata as old as Carnian and continue through the Early Jurassic, they take particular temporal significance in the Norian and Rhaetian. For example, *Otapiria ussuriensis* (Voronetz) is the name bearer of a well established zone in the Middle Norian of Siberia (Kiparisova *et al.* 1966; Zakharov *et al.* 1997) and *Otapiria dissimilis* (Cox) is distinctive of the Rhaetian of New Zealand (Marwick 1957; Campbell 1997) and the closely related *Otapiria alpina* Zapfe (Fig. 7b) is restricted to the Rhaetian of the Austrian west-Tethys (Zapfe 1973).

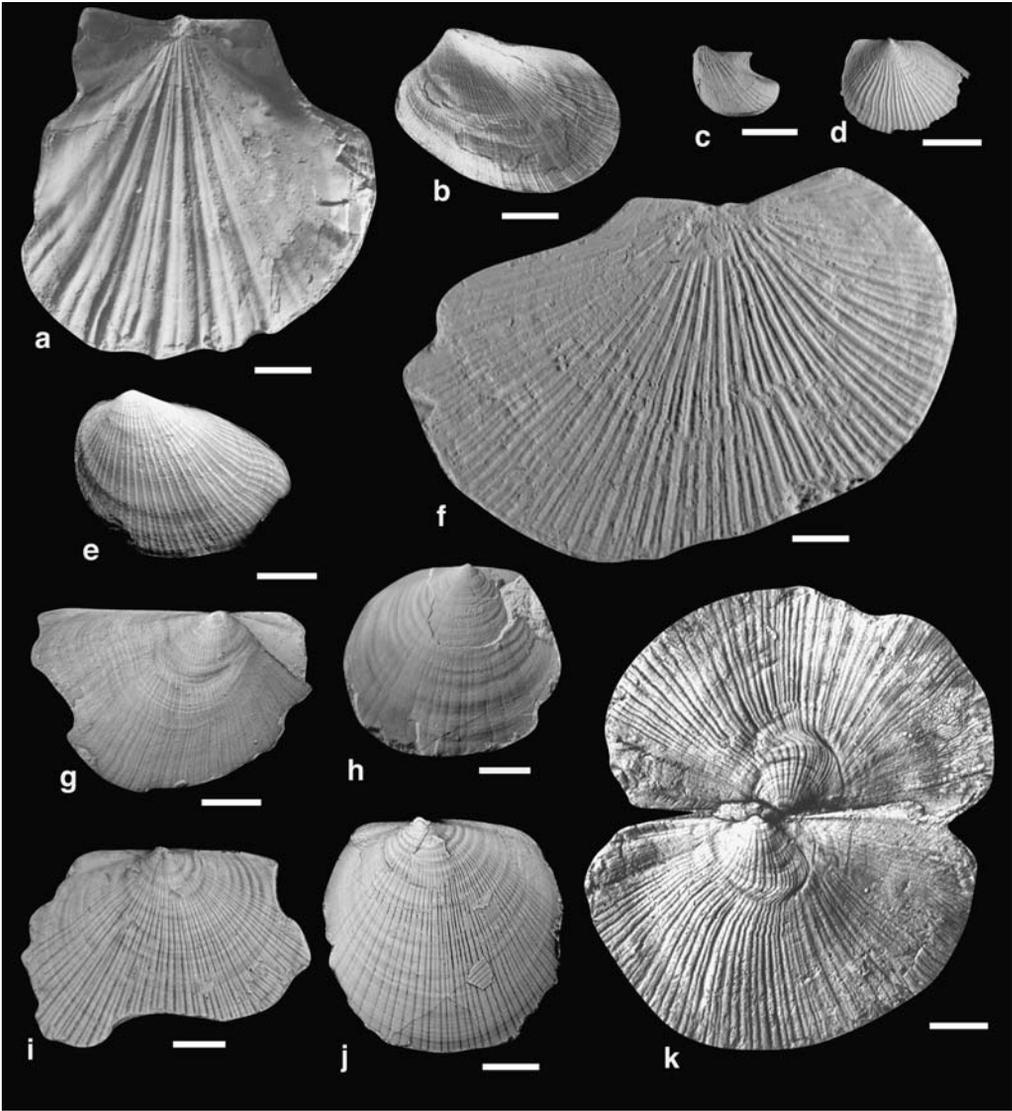


Fig. 7. Representative Upper Triassic pelagic Bivalvia. All scale bars = 1 cm. (a) *Tosapecten efimovae* Polubotko, Rhaetian, Olomon River area, NE Siberia, Russia. (TsNIGR collection, same specimen as in Bychkov *et al.* (1976, pl. 71, fig. 4). (b) *Otapiria alpina* Zapfe, Rhaetian, Zlambach Formation, Rossmoosgraben, Austria (NHMW 1973/1623, from Zapfe 1973, pl. 1, fig. 1). (c) *Rhaetavicula contorta* (Portlock), Rhaetian, Kössen Formation, Hochalm, Austria (SUCP collection). (d) *Monotis rhaetica* McRoberts *et al.*, Lower Rhaetian, *Paracochloceras suessi* Zone, Hernstein, Austria (NHMW 2007z0111/0012, from McRoberts *et al.* 2008, pl. 1, fig.15). (e) *Eomonotis pinensis* (Westermann), Middle Norian, *Mesohimavites columbianus* III Zone, Peace River area, British Columbia, Canada (SUCP collection). (f) *Monotis subcircularis* (Gabb), Upper Norian, *Gnomahalorites cordilleranus* Zone, California (USNM 32492, see Martin, 1916, pl. 30, fig. 2). (g) *Halobia cordillerana* Smith, Middle Norian, *Drepanites rutherfordi* Zone, Peace River area, British Columbia, Canada (SUCP collection). (h) *Halobia lenticularis* Gemmellaro, Probably uppermost Carnian, Pizzo Mondello, Sicily (UNIMI FNP67/68, from Nicora *et al.* 2007, pl. 2, fig. 1). (i) *Halobia beyrichi* Mojsisovics, Lower Norian, *Stikinoceras kerri* Zone, Vancouver Island, British Columbia, Canada (GSC 13712). (j) *Halobia styriaca* (Mojsisovics), Lower Norian, *Guembelites jandianus* Zone, Sommerkogel, Austria (SUCP collection). (k) *Halobia zitteli* Lindström, Lower Carnian, Axel Heiberg Island, Arctic Canada (GSC 85851).

Other Late Triassic bivalves of notable biochronological significance

With few exceptions, the uppermost stage of the Triassic is characterized not so much by the emblematic pelagic bivalves, but by level bottom bivalve assemblages with long-ranging species. A few notable species, however, have proven biochronologic value but are mostly relegated to the western Tethys or the Boreal realm of northeastern Russia.

The distinctive pterioid bivalve *Rhaetavicula contorta* (Portlock) (Fig. 7c) is perhaps the most commonly recognized bivalve and key index of the Rhaetian in shallow-water facies of the western Tethys, southern Germany and across northwestern Europe. Golebioski (1990) provided a most useful summary of the facies, geographical, and temporal distribution of *R. contorta* (Portlock). Based on recently published high-precision chemostratigraphic correlations between the NW European and Tethys sections (see Hesselbo *et al.* 2002; Kuerschner *et al.* 2007), and accepting the base of the Rhaetian to be the first occurrence of the conodont *Misikella posternsteni* (Krystyn *et al.* 2007b) which is present in the basal Hochalm Member of the Kössen Formation (Kozur 1996), all true *R. contorta* (Portlock) are now interpreted to be confined to the Rhaetian. Other claims of *R. contorta* in the eastern Tethys and circum-Pacific (e.g. Healey 1908; Muller & Ferguson 1939) may indeed be Rhaetian, but have yet to receive satisfactory study to warrant assignment to *R. contorta* (Portlock).

In the Boreal realm and in far-east Russia in particular, the Rhaetian is characterized by the pectinid *Tosapecten*. Although *Tosapecten sensu stricto* appears as early as the Carnian of Japan and other east-Asian, western Panthalassa, and Boreal regions, other representatives of the family group such as *Janopecten* and *Nevadapecten* occur in the Middle Triassic (see Arkhipov & Truschelev 1980; Waller in Waller & Stanley 2005). *Tosapecten efimovae* Polubotko (Fig. 7a) has been a key index for the Rhaetian strata of Boreal far-east Russia (e.g. Polubotko & Repin 1990). This zone encompassing the entire Rhaetian can be subdivided into a lower *Camptonectes nanus* subzone and an upper *Tosapecten efimovae* subzone (Polubotko & Repin 1990; Dagens & Dagens 1994). Zakharov *et al.* (1997) seem to have inverted the *Tosapecten efimovae* and *Camptonectes nanus* subzones.

Conclusions

The reorganization of marine benthic communities following the end-Permian extinction marked the onset of an essentially modern fauna dominated

by bivalve molluscs during Triassic time. The radiation of bivalves during the Triassic coincided with the origination and proliferation of many pelagic 'flat clam' species, which, because of their high evolutionary turnover and widespread distribution, makes them one of the best macrofossils for biochronological studies. Based on more than a century of work on pelagic bivalves of the Triassic in conjunction with detailed taxonomic study, high-resolution stratigraphic sampling and integration with more traditional biostratigraphic schemes using ammonoids and conodonts, the Triassic Period can be temporally subdivided into more than 30 discrete bivalve zones with a mean duration of typically less than 2 Ma. These bivalve zones can be identified across most of the marine Triassic with significant occurrences in the Tethyan Panthalassa and Boreal realms. Still, there remain many uncertainties in taxonomy of the zonal bivalves and the temporal limits of the established zones.

I would like to thank the numerous colleagues who have made their collections available to me. Funding for aspects of this research were made available through the National Science Foundation (EAR-9706040 and EAR-0518605) and the donors to the Petroleum Research Fund of the American Chemical Society. I. Polubotko, J. Grant-Mackie and Yin Hong-Fu made available photographs and additional information on Triassic bivalves which greatly aided in the preparation of this manuscript. S. Damborenea, N. Silberling, D. Taylor and B. Waterhouse provided helpful reviews that substantially improved the manuscript. This is a publication of IGCP Project 467, Triassic Time and Correlations.

Appendix 1. Taxonomic Notes

Family Pterinopectinidae: Claraia sensu lato

Claraia Bittner is a cosmopolitan pectinoid genus originating in the Permian but achieving peak diversity in the Early Triassic. Stemming back to Bittner (1901), it was recognized as a key index of the Early Triassic, and since that time, there have been various opinions as to the familial affinity of *Claraia*. Most recent workers now consider them to be pectinoids aligned with the Pterinopectinidae (e.g. Zhang 1980; Gavrilova 1995, 1996; Newell & Boyd 1995; Waterhouse 2000, 2008). Following recent workers (e.g. Newell & Boyd 1995; Yang *et al.* 2001; He *et al.* 2007) *Pseudoclaraia* Zhang, and *Claraioides* Fang are considered to be junior synonyms for *Claraia*. Other newly proposed clariid genera are based on either surficial morphology (e.g. *Rugiclaraia* Waterhouse) or represented by poorly known endemic genus-group taxa (e.g. *Periclaraia* Li & Ding and *Epiclaraia* Gavrilova) and can be included within current concepts of *Claraia*. Of the approximately 75 species names for *Claraia*, 30 or so are considered valid.

Family Monotidae: Monotis sensu lato and Eomonotis

A diverse group of which several genus-level taxa have biochronological significance in mostly Upper Triassic strata *Eomonotis* Grant-Mackie and *Monotis* Bronn *sensu lato* (here including the subgenera *Monotis* Bronn, *Entomonotis* Marwick, *Pacimonotis* Grant-Mackie & Silberling and *Maorimonotis* Grant-Mackie) represent a coherent clade arising from a likely *Meleagrinnella* ancestor during the Early or Middle Norian. Waller (in Waller & Stanley 2005) considered the Monotioidea to be a superfamily within the Pectinoidea and included the families Asoelidae, Monotidae and Oxytomidae. Waterhouse (2001, 2008) relegated the Monotidae to suborder rank and suggested they were derived from a eurydesmatoid ancestor. Although it is acceptable practice to subdivide this species group into several subgenera and/or species groups that may have some phylogenetic significance (Ichikawa 1958; Grant-Mackie 1978; Grant-Mackie & Silberling 1990) none of the proposed genus-groups have been adequately tested with a rigorous cladistic analysis. Of these proposed names, this paper follows the lead of Tozer (1980) in recognizing two broadly construed genus-group taxa: *Monotis* and *Eomonotis*.

Family Posidoniidae: Peribositria and Ellesmerella

Waller (in Waller & Stanley 2005) elevated Posidoniodea to superfamily and included the families Posidoniidae and Halobiidae. Included in this clade are five genus-group taxa including the posidoniid *Peribositria* Kurushin & Trushchelev and the halobiid genera *Enteropleura* Kittl, *Daonella* Mojsisovics, *Aparimella* Campbell, and *Halobia* Bronn. As noted by several workers (e.g. Campbell 1994), the traditional classifications of the Posidoniidae (*sensu* Cox & Newell 1969) contain an artificial grouping of several thin-shelled taxa that are now considered to belong to several different clades. Waterhouse (2008) placed some of these taxa within the Pterinopectinidae along with *Claraia* (e.g. *Halobia*, *Aparimella*, *Daonella* and some *Enteropleura*) and some (including true Jurassic *Bositra*) with several *Enteropleura* into his new genus *Wallerobia* (order Ostreoida). A more conservative approach used herein considers all to be pterioids.

The Early and Middle Triassic contains several flat clams which have global biochronologic utility and have been variously placed in *Posidonia* Bronn, *Peribositria* Kurushin & Trushchelev, *Bositra* de Gregorio, and even *Daonella* Mojsisovics (e.g. Kurushin 1980; Waller in Waller & Stanley 2005). Waller (in Waller & Stanley 2005) placed most of the species attributed to *Posidonia* and *Peribositria* into an expanded view of *Bositra*. Because of some outstanding issues regarding morphological detail of the ligament systems of the Triassic forms, and, less so, because the large stratigraphic gap between

the Early and Middle Triassic forms and the Jurassic (Oxfordian) representatives, *Peribositria* is provisionally retained until further evidence can be brought to light. At present, about 15 species of *Peribositria* are known ranging from base of the Olenekian through the Middle Anisian.

Although most other species historically attributed to *Posidonia* are rather poorly known, the radial-ribbed *Posidonia aranea* Tozer from the Olenekian of the Boreal province is sufficiently distinct from other so called *Posidonia* and *Peribositria* to warrant recognition. Waterhouse (2008) used this species as the basis for his new aulacomyellid genus *Ellesmerella* that he interpreted to be closely aligned to *Bositra* (etheripectinoid order Ostreoida). Although *Ellesmerella* appears to be valid (its sole species does not appear to belong in an existing genus-group taxon), it is perhaps better placed with the pterioid families Posidoniidae or Halobiidae (*sensu* Waller in Waller & Stanley 2005).

Family Halobiidae: Enteropleura, Daonella, Aparimella and Halobia

Enteropleura Kittl, here considered to belong to the Halobiidae, is an interesting genus narrowly restricted to the late Middle Anisian. Like other Triassic flat clams, there is some controversy regarding its affinity, but most who have addressed this matter consider them to be the stem group for the Halobiidae derived from the Posidoniidae (Encheva 1978; Campbell 1994; Waller in Waller & Stanley 2005; Chen & Stiller 2007). Departing from the generally accepted view, however, is Waterhouse (2008) who placed some *Enteropleura* (including the type species *Enteropleura gumbelli* Mojsisovics) with etheripectiniids in the Ostreoida and others, including his new *Wallerobia* (including *Enteropleura jenkisi* Hopkin & McRoberts) within his new family Bositridae. Approximately five species of *Enteropleura* are known from Europe, Asia, and North America (Chen & Stiller 2007).

A complex evolutionary transition from *Daonella* Mojsisovics to *Halobia* Bronn (either directly or via *Aparimella* Campbell) occurred near the base of the Carnian. For example, *Daonella elegans* McLearn passes into *Halobia* gr. *H. zitteli* Lindström within beds that containing both of the ammonoids *Trachyceras* and *Frankites*. At about the same time *Daonella nitainae* McLearn is found below *Halobia daonellaformis* McRoberts from similar aged strata in British Columbia. The taxonomy of species groups, subgenera and genera here included within *Halobia sensu lato* are provided by Kittl (1912), Encheva (1978), Gruber (1976), Polubotko (1984, 1988), Campbell (1994) and McRoberts (1997). Although there exist more than 300 available species names for *Halobia*, slightly more than 30 species of *Halobia* are likely valid with significant occurrences in Alpine-Mediterranean (Austria, Italy, Balkans) and circum-Pacific (Canada).

Repository abbreviations

Repositories for illustrated specimens as follows: GSC, Geological Survey of Canada, Ottawa; NHMW, Naturhistorisches Museum, Vienna; PIMZ, Paläontologischen Instituts und Museum, University of Zurich; SM Sedgwick Museum, Department of Earth Sciences, Cambridge University; SUCP, SUNY Cortland Paleontology Collections, Cortland, New York; TsNIGR, Central Geological Research Museum, St. Petersburg; UNIMI, Dipartimento di Scienze della Terra 'Ardito Desio', University of Milano; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

References

- ANDO, H. 1987. Paleobiological study of the Late Triassic bivalve *Monotis* from Japan. *The University Museum, The University of Tokyo, Bulletin*, **30**, 1–110.
- ARKHIPOV, Y. V. & TRUSHCHELEV, A. M. 1980. A new genus of pectinid from the Triassic of northeast USSR and central Siberia. In: DAGYS, A. S. (ed.) *Paleontology and Stratigraphy of Middle Siberia*. Academy of Sciences of the USSR, Siberian Department, Transactions of the Institute of Geology and Geophysics, Novosibirsk, **448**, 10–17, 109–110. [In Russian.]
- BALINI, M., JENKS, J. F., MCROBERTS, C. A. & ORCHARD, M. J. 2007. The Ladinian–Carnian boundary succession at South Canyon (New Pass Range, central Nevada). *New Mexico Museum of Natural History & Science Bulletin*, **40**, 127–138.
- BITTNER, A. 1901. Trias Brachiopoda and Lamellibranchiata. *Palaeontology of India, Series 15 Himalayan Fossils*, **3**(2), 1–76.
- BLAKEY, R. 2005. *North American paleogeographic maps, Paleogeography and geologic evolution of North America*. [Updated December 4, 2006] <http://jan.ucc.nau.edu/~rbc/namD385.jpg> [Accessed August, 2007].
- BLOME, C. D., REED, K. M. & TAILLEUR, I. L. 1988. Radiolarian biostratigraphy of the Otuk Formation in and near the National Petroleum Reserve in Alaska. *U.S. Geological Survey Professional Paper*, **1399**, 725–776.
- BRACK, P. & RIEBER, H. 1993. Towards a better definition of the Anisian/Ladinian boundary: new biostratigraphic data and correlations of boundary sections from the Southern Alps. *Eclogae Geologicae Helvetiae*, **86**(2), 415–572.
- BRACK, P., RIEBER, H., NICORA, A. & MUNDIL, R. 2005. The Global Boundary Stratotype Section and Point (GSSP) of the Ladinian Stage (Middle Triassic) at Bagolino (Southern Alps, Northern Italy) and its implications for the Triassic time-scale. *Episodes*, **28**, 23–244.
- BRETSKY, P. W. & LORENZ, D. M. 1970. Essay on genetic-adaptive strategies and mass extinctions. *Geological Society of America Bulletin*, **81**, 2449–2456.
- BROGLIO LORIGA, C. & CASSINIS, G. 1992. The Permian–Triassic boundary in the Southern Alps (Italy) and in adjacent Periadriatic regions. In: DICKINS, J. M., YANG, Z., YIN, H., LUCAS, S. G. & ACHARYYA, S. K. (eds) *Permo-Triassic Events in the Eastern Tethys*. Cambridge University Press, World and Regional Geology, **2**, 78–97.
- BROGLIO LORIGA, C., NERI, C. & POSENATO, R. 1986. The early macrofauna of the Werfen Formation and the Permian–Triassic boundary in the Dolomites (Southern Alps, Italy). *Studi Trentini Scienze Naturali, Acta Geologica*, **62**, 3–18.
- BYCHKOV, Y. M., DAGYS, A. S., EFIMOVA, A. F. & POLUBOTKO, I. V. 1976. *Atlas of the Triassic Fauna and Flora of Northeastern USSR*. Ministry of Geology of USSR, Moscow. [In Russian.]
- CAFIERO, B. & DE CAPOA BONARDI, P. 1982. Biostratigrafia del Trias pelagico della Sicilia. *Bollettino della Società Paleontologica Italiana*, **21**, 35–71.
- CAMPBELL, H. J. 1994. The Triassic bivalves *Halobia* and *Daonella* in New Zealand, New Caledonia, and Svalbard. *Institute of Geological & Nuclear Sciences Monograph*, **4**, 1–166.
- CAMPBELL, J. D. 1997. Otapirian Stage: its fauna and microflora. In: DICKINS, J. M., YANG, Z., YIN, H., LUCAS, S. G. & ACHARYYA, S. K. (eds) *Late Paleozoic and Early Mesozoic Circum-Pacific Events and Their Global Correlation*. Cambridge University Press, World and Regional Geology, **10**, 229–234.
- CHEN, C.-C. 1964. On the occurrence of *Halobia* fauna from the Ganzi region, western Sichuan (Szechuan) and its significance. *Acta Palaeontologica Sinica*, **2**, 75–78.
- CHEN, J.-H. & STILLER, F. 2007. The halobiid bivalve genus *Enteropleura* and a new species from the Middle Anisian of Guangxi, southern China. *Acta Palaeontologica Polonica*, **52**, 53–61.
- CHONGLAKMANI, C. & GRANT-MACKIE, J. A. 1993. Biostratigraphy and facies variation of the marine Triassic sequences in Thailand. *International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies and Paleontology*, **1**, 97–123.
- CIRIACKS, K. W. 1963. Permian and Eotriassic bivalves of the middle Rockies. *American Museum of Natural History Bulletin*, **125**, 1–100.
- COX, L. R. & NEWELL, N. D. 1969. Family Posidoniidae. In: MOORE, R. C. & TEICHERT, C. (eds) *Treatise on Invertebrate Paleontology, Part N, Mollusca 6*. Geological Society of America and Kansas University Press, Lawrence, N342–N344.
- DAGYS, A. S. & DAGYS, A. A. 1994. Global correlation of the terminal Triassic. *Mémoires de Géologie (Lausanne)*, **22**, 25–34.
- DE CAPOA BONARDI, P. 1984. *Halobia* zones in the pelagic Late Triassic sequences of the central Mediterranean area. *Bollettino della Società Paleontologica Italiana*, **23**, 91–102.
- DUTRO, J. T. & SILBERLING, N. J. 1988. Megafossil biostratigraphy of some deep test wells, National Petroleum Reserve in Alaska. *U.S. Geological Survey Professional Paper*, **1399**, 667–675.
- ENCHEVA, M. G. 1978. Phylogenetic development of the Family Posidoniidae and the genera *Daonella* and *Halobia* (Bivalvia, Triassic). *Geologica Balkanica*, **8**(2), 55–67.

- ETTER, W. 1995. Benthic diversity patterns in oxygenated gradients: an example from the Middle Jurassic of Switzerland. *Lethaia*, **28**, 259–270.
- FRAISER, M. L. & BOTTJER, D. J. 2007. When bivalves took over the world. *Paleobiology*, **33**, 397–413.
- GALLET, Y., KRYSZYN, L., MARCOUX, J. & BESSE, J. 2007. New constraints on the end-Triassic (upper Norian–Rhaetian) magnetostratigraphy. *Earth and Planetary Science Letters*, **255**, 458–470.
- GAVRILOVA, V. A. 1995. A new pterinopectinid genus (Bivalvia) from Lower Triassic of the Mangyshlak. *Paleontological Journal*, **29**(1), 154–160.
- GAVRILOVA, V. A. 1996. On the systematics of Triassic Pterinopectinidae (Bivalvia). *Paleontological Journal*, **30**(5), 7–15.
- GAVRILOVA, V. A. 2004. Triassic Bivalvia and Ammonoidea of the Central and Eastern part of the Praeucasus. In: BOGDONOVA, T. N. & GAVRILOVA, V. A. (eds) *Atlas of the Most Important Groups of Fauna of Mesozoic-Cenozoic Deposits of the Northern Caucasus and Praeucasus*. VSEGEI Press, St. Petersburg, 22–39. [In Russian.]
- GEYER, O. F. 1973. Das präkretazische Mesozoikum von Kolumbien. *Geologisches Jahrbuch*, **5**, 1–155.
- GOLEBIEWSKI, R. 1990. The Alpine Kössen Formation: a key for European topmost Triassic correlations. *Albertiana*, **8**, 25–35.
- GRANT-MACKIE, J. A. 1978. Subgenera of the Upper Triassic bivalve *Monotis*. *New Zealand Journal of Geology and Geophysics*, **21**, 97–111.
- GRANT-MACKIE, J. A. 1980. Systematics of New Zealand *Monotis* (Upper Triassic Bivalvia); subgenus *Eomonotis*. *New Zealand Journal of Geology and Geophysics*, **23**(5–6), 639–663.
- GRANT-MACKIE, J. A. & SILBERLING, N. J. 1990. New data on the Upper Triassic bivalve *Monotis* in North America, and the new subgenus *Pacimonotis*. *Journal of Paleontology*, **64**, 240–254.
- GRUBER, B. 1976. Neue Ergebnisse auf dem gebiete der Ökologie, Stratigraphie und Phylogenie der Halobien (Bivalvia). *Mitteilungen der Gesellschaft der Geologie und Bergbaustudenten in Österreich*, **23**, 181–198.
- HE, W., FENG, Q., WELDEN, E. A., GU, S., MENG, Y., ZHANG, F. & WU, S. 2007. A Late Permian to Early Triassic bivalve fauna from the Dongpan section, southern Quangxi, South China. *Journal of Paleontology*, **81**, 1009–1019.
- HEALEY, M. 1908. The fauna of the Napeng beds or the Rhaetic beds of Upper Burma. *Palaeontologia Indica*, **2**(4), 1–88.
- HELSELBO, S. P., ROBINSON, S. A., SURLYK, F. & PIASECKI, S. 2002. Terrestrial and marine extinction at the Triassic–Jurassic boundary synchronized with major carbon-cycle perturbation: a link to initiation of massive volcanism. *Geology*, **30**, 251–254.
- HOPKIN, E. K. & MCROBERTS, C. A. 2005. A New Middle Triassic flat clam (Pterioidea: Halobiidae) from the Middle Anisian of north-central Nevada, USA. *Journal of Paleontology*, **79**(4), 796–800.
- ICHIKAWA, K. 1958. Zur Taxonomie und Phylogenie der triadischen ‘Pteriidae’ (Lamellibranch), mit besonderer Berücksichtigung der Gattungen *Claraia*, *Eumorphotis*, *Oxytoma* und *Monotis*. *Palaeontographica A*, **3**, 131–212.
- JAWORSKI, E. 1922. Die marine Trias in Südamerika. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **47**, 93–200.
- JEFFERIES, R. P. S. & MINTON, P. 1965. The mode of life of two Jurassic species of ‘*Posidonia*’ (Bivalvia). *Palaeontology*, **8**, 156–185.
- KIDWELL, S. M. & BOSENCE, D. W. J. 1991. Taphonomy and time-averaging of marine shelly faunas. In: ALLISON, P. A. & BRIGGS, D. E. G. (eds) *Taphonomy: Releasing Data Locked in the Fossil Record, Topics in Geobiology*. Plenum Press, New York, 115–209.
- KIPARISOVA, L. D., BYCHKOV, Y. M. & POLUBOTKO, I. V. 1966. *Upper Triassic bivalve molluscs from the northeast USSR*. Ministry of Geology of the USSR, All Union Geological Research Institute (VSEGED), Magadan. [In Russian.]
- KITTL, E. 1912. *Materialen zu einer Monographie der Halobiidae und Monotidae der Trias*. Resultate der Wissenschaftlichen Erforschung des Balatensees, I Band, I Teil. Paleontologie Anhang., Wien.
- KOZUR, H. 1996. The position of the Norian–Rhaetian boundary. *Berichte aus dem Sonderforschungsbereich*, **313**(76), 27–35.
- KOZUR, H. 2003. Integrated ammonoid, conodont and radiolarian zonation of the Triassic. *Hallesches Jahrbuch der Geowissenschaften*, **B25**, 49–79.
- KRUMBECK, L. 1924. *Die Brachiopoden, Lamellibranchiaten und Gastropoden der Trias von Timor II*. E. Schweizerbart’sche Verlagsbuchhandlung, Stuttgart.
- KRYSZYN, L., RICHOSZ, S. & BHARGAVA, O. N. 2007a. The Induan–Olenekian Boundary (IOB) in Mud – an update of the candidate GSSP section M04. *Albertiana*, **36**, 32–45.
- KRYSZYN, L., BOUQUEREL, H., KUERSCHNER, W., RICHOSZ, S. & GALLET, Y. 2007b. Proposal for a candidate GSSP for the base of the Rhaetian stage. In: LUCAS, S. G. & SPIELMANN, J. A. (eds) *The Global Triassic. New Mexico Museum of Natural History and Science Bulletin*, **41**, 189–199.
- KUERSCHNER, W. M., BONIS, N. R. & KRYSZYN, L. 2007. Carbon-isotope stratigraphy and palynostratigraphy of the Triassic–Jurassic transition in the Tiefengraben section – Northern Calcareous Alps (Austria). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **244**(1–4), 257–280.
- KURUSHIN, N. I. 1980. New Triassic Molluscs of Central Siberia. In: DAGYS, A. S. (ed.) *The Paleontology and Stratigraphy of the Triassic of Central Siberia*. Academy of Sciences of the USSR, Siberian Department, Transactions of the Institute of Geology and Geophysics, Novosibirsk, **448**, 81–85. [In Russian.]
- KURUSHIN, N. I. & TRUSHCHELEV, A. M. 1989. Posidonids from Triassic deposits of Siberia and the Soviet Far East. In: DAGYS, A. S. & DUBATOLOV, V. (eds) *The Upper Paleozoic and Triassic of Siberia*. Academy of Sciences of the USSR, Siberian Department, Transactions of the Institute of Geology and Geophysics, Novosibirsk, **732**, 57–71, 154–155, 168–171. [In Russian.]
- LEHRMANN, D. J., RAMEZANI, J. ET AL. 2006. Timing of recovery from the end-Permian extinction: geochronologic and biostratigraphic constraints from south China. *Geology*, **34**, 1053–1056.

- LEVINTON, J. S. 1970. The paleoecologic significance of opportunistic species. *Lethaia*, **3**, 69–78.
- MARTIN, G. C. 1916. Triassic rocks of Alaska. *Geological Society of America, Bulletin*, **27**, 685–718.
- MCRROBERTS, C. A. 1997. Late Triassic North American halobiid bivalves: stratigraphic distribution, diversity trends, and their circum-Pacific correlation. In: DICKINS, J. M., YANG, Z., YIN, H., LUCAS, S. G. & ACHARYYA, S. K. (eds) *Late Paleozoic and Early Mesozoic Circum-Pacific Events and Their Global Correlation*. Cambridge University Press, World and Regional Geology, **10**, 198–208.
- MCRROBERTS, C. A. 2000. A primitive *Halobia* (Bivalvia: Halobioidea) from the Triassic of northeast British Columbia, Canada. *Journal of Paleontology*, **74**, 599–603.
- MCRROBERTS, C. A. 2001. Triassic bivalves and the initial marine Mesozoic revolution: a role for predators? *Geology*, **29**, 359–362.
- MCRROBERTS, C. A. 2007. The halobiid bivalve succession across a potential Carnian/Norian GSSP at Black Bear Ridge, Williston Lake, northeast British Columbia, Canada. *Albertiana*, **36**, 142–145.
- MCRROBERTS, C. A., KRYSZYN, L. & SHEA, A. 2008. Rhaetian (Late Triassic) *Monotis* (Bivalvia: Pectinoida) from the eastern Northern Calcareous Alps (Austria) and the end-Norian crisis in pelagic faunas. *Palaentology*, **51**, 571–535.
- MIETTO, P. & MANFRIN, S. 1995. A high resolution Middle Triassic ammonoid standard scale in the Tethys Realm. A preliminary report. *Bulletin de la Société Géologique de France*, **166**(5), 539–563.
- MIETTO, P., ANDRETTA, R. ET AL. 2007. A candidate of the Global Boundary Stratotype Section and Point for the base of the Carnian Stage (Upper Triassic): GSSP at the base of the *canadensis* Subzone (FAD of *Daxatina*) in the Prati di Stuoeres/Stuoeres Wiesen section (Southern Alps, NE Italy). *Albertiana*, **36**, 78–97.
- MIROSHNIKOV, L. D. & BURIJ, L. V. 1969. Conditions of accumulation of the Triassic *Daonella* shales in the southern Maritime Province. *Lithology and Mineral Resources*, **5**, 80–85. [In Russian.]
- MOJSISOVICS, E. von. 1874. Über Die Triadischen Pelecypoden—Gattungen *Daonella* und *Halobia*. *Abhandlungen der k. k. Geologischen Reichsanstalt*, **7**, 1–35.
- MONNET, C. & BUCHER, H. 2005. Anisian (Middle Triassic) ammonoids from North America: quantitative biochronology and biodiversity. *Stratigraphy*, **2**, 281–296.
- MULLER, S. W. & FERGUSON, H. G. 1939. Mesozoic stratigraphy of the Hawthorne and Tonopah quadrangles, Nevada. *Geological Society of America Bulletin*, **50**, 1573–1624.
- MUNDIL, R., LUDWIG, K. R., METCALFE, I. & RENNE, P. R. 2004. Age and timing of the Permian mass extinctions: U/Pb dating of closed system zircons. *Science*, **305**, 1760–1763.
- MUROMTSEVA, V. A. 1984. Genus *Vnigripecten* Muromtseva n. gen., and Genus *Morrisopecten* Muromtseva and Guskov. In: MUROMTSEVA, V. A. (ed.) *Permian marine deposits and bivalve molluscs of the Soviet Arctic*. USSR Ministry of Geology, Nedra, Leningrad, 65–66, 75. [In Russian.]
- NAKAZAWA, K. 1977. On *Claraia* of Kashmir and Iran. *Journal of the Palaeontological Society of India*, **20**, 191–204.
- NAKAZAWA, K. 1981. Permian and Triassic bivalves of Kashmir. In: NAKAZAWA, K. & KAPOOR, H. M. (eds) *The Upper Permian and Lower Triassic Faunas of Kashmir Palaeontologia Indica*, **46**, 89–122.
- NEWELL, N. D. & BOYD, D. W. 1995. Pectinoid bivalves of the Permian–Triassic crisis. *American Museum of Natural History Bulletin*, **227**, 1–95.
- NEWELL, N. D. & KUMMEL, B. 1942. Lower Eotriassic stratigraphy, western Wyoming and southeast Idaho. *Geological Society of America, Bulletin*, **53**, 937–995.
- NEWTON, C. R. 1988. Significance of ‘Tethyan’ fossils in the Cordillera. *Science*, **242**, 385–391.
- NICORA, A., BALINI, M. ET AL. 2007. The Carnian/Norian boundary interval at Pizzo Mondello (Sicani Mountains, Sicily) and its bearing for the definition of the GSSP of the Norian Stage. *Albertiana*, **36**, 102–115.
- OGG, J. G. 2004. The Triassic Period. In: GRADSTEIN, F. M., OGG, J. G. & SMITH, A. G. (eds) *A Geologic Time Scale 2004*. Cambridge, University Press, 271–306.
- ORCHARD, M. J. 2007. A proposed Carnian–Norian boundary GSSP at Black Bear Ridge, northeast British Columbia, and a new conodont framework for the boundary interval. *Albertiana*, **36**, 130–141.
- ORCHARD, M. J. & TOZER, E. T. 1997. Triassic conodont biochronology, its calibration with the ammonoid standard, and a biostratigraphic summary for the Western Canada Sedimentary Basin. *Bulletin of Canadian Petroleum Geology*, **45**(4), 675–692.
- OSCHMANN, W. 1993. Environmental oxygen fluctuations and the adaptive response of marine benthic organisms. *Journal of the Geological Society, London*, **150**, 178–199.
- OVTCHAROVA, M., BUCHER, H., SCHALTEGGER, U., GOLFETTI, T., BRAYARD, A. & JEAN GUEX, J. 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.
- POLUBOTKO, I. V. 1980. Early Carnian Halobiidae of northeast Asia. *Paleontological Journal*, **1**, 34–41.
- POLUBOTKO, I. V. 1984. Zonal and correlation significance of Late Triassic halobiids. *Sovetskaya Geologiya*, **6**, 40–51. [In Russian.]
- POLUBOTKO, I. V. 1986. Zonal complexes of Late Triassic halobiids in the northeastern USSR. In: YANSHIN, A. L. & DAGYS, A. S. (eds) *Mesozoic Biostratigraphy of Siberia and the Far East*. Transactions of the Institute of Geology and Geophysics, Novosibirsk, **648**, 118–126. [In Russian.]
- POLUBOTKO, I. V. 1988. On the morphology and systematics of the Late Triassic Halobiidae (bivalve mollusks). *Annual of the All-Union Paleontological Society*, **31**, 90–103. [In Russian.]
- POLUBOTKO, I. V. & REPIN, Y. S. 1990. The Triassic/Jurassic boundary in northeastern Asia (sedimentological and biotic features). *Les Cahiers de l'Université Catholique de Lyon, Série Sciences*, **3**, 191–205.

- RIEBER, H. 1968. Die Artengruppe der *Daonella elongata* Mojs. aus der Grenzbitumenzone der mittleren Trias des Monte San Giorgio (Kt. Tessin, Schweiz). *Paläontologische Zeitschrift*, **42**, 33–61.
- RIEBER, H. 1969. Daonellen aus der Grenzbitumenzone der mittleren Trias des Monte San Giorgio (Kt. Tessin, Schweiz). *Eclogae Geologicae Helvetiae*, **62**, 657–683.
- ROSENZWEIG, M. L. & MCCORD, R. D. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology*, **17**, 202–213.
- SANDERS, H. W. 1968. Marine benthic diversity: a comparative study. *The American Naturalist*, **102**(925), 243–282.
- SAVRDA, C. E. & BOTTJER, D. J. 1987. The exaerobic zone, a new oxygen-deficient marine biofacies. *Nature*, **327**(6117), 54–56.
- SAVRDA, C. E. & BOTTJER, D. J. 1991. Oxygen-related biofacies in marine strata: an overview and update. In: TYSON, R. V. & PEARSON, T. H. (eds) *Modern and Ancient Continental Shelf Anoxia*. Geological Society, London, Special Publications, **58**, 201–219.
- SCHATZ, W. 2004. Revision of the subgenus *Daonella* (*Arzelella*) (Halobiidae; Middle Triassic). *Journal of Paleontology*, **78**(2), 300–316.
- SCHATZ, W. 2005. Palaeoecology of the Triassic black shale bivalve *Daonella* – new insights into an old controversy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **216**, 189–201.
- SCOTT, K. M. & CAVANAUGH, C. M. 2007. CO₂ uptake and fixation by endosymbiotic chemoautotrophs from the bivalve *Solemya velum*. *Applied and Environmental Microbiology*, **73**, 1174–1179.
- SEILACHER, A. 1990. Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology*, **3**, 289–311.
- SEILACHER, A., REIF, W. E., WESTPHAL, F., WHITTINGTON, H. B. & CONWAY MORRIS, S. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten [and Discussion]. *Philosophical Transactions of the Royal Society of London, Series B, Biological Science*, **311**, 5–24.
- SEPKOSKI, J. J. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, **7**(1), 36–53.
- SEPKOSKI, J. J. 1996. Competition in macroevolution: the double wedge revisited. In: JABLONSKI, D., ERWIN, D. H. & LIPPS, J. H. (eds) *Evolutionary Paleobiology*. University of Chicago Press, 211–255.
- SHANER, J. S. & MCROBERTS, C. A. 2000. The life history of the Late Triassic ‘flat clam’ *Monotis subcircularis*: taphonomic evidence from British Columbia. *Geological Society of America, Abstracts with Programs*, **32**(2), A 73.
- SHELTEMA, R. S. 1977. Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. In: KAUFFMAN, E. G. & HAZEL, J. E. (eds) *Concepts and Methods of Biostratigraphy*. Hutchinson and Ross, Stroudsburg, 73–108.
- SILBERLING, N. J. 1985. Biogeographic significance of the Upper Triassic bivalve *Monotis* in circum-Pacific accreted terranes. In: HOWELL, D. G. (ed.) *Tectonostratigraphic Terranes of the Circum-Pacific Region*. Earth Science Series, Circum-Pacific Council for Energy and Mineral Resources, 63–70.
- SILBERLING, N. J. & NICHOLS, K. M. 1982. Middle Triassic molluscan fossils of biostratigraphic significance from the Humboldt Range, northwestern Nevada. *U.S. Geological Survey Professional Paper*, **1207**, 1–38.
- SILBERLING, N. J. & TOZER, E. T. 1968. Biostratigraphic classification of the marine Triassic in North America. *Geological Society of America Special Paper*, **110**, 1–63.
- SILBERLING, N. J., GRANT-MACKIE, J. & NICHOLS, K. M. 1997. The Late Triassic bivalve *Monotis* in accreted terranes of Alaska. *U.S. Geological Survey Bulletin*, **2151**, 1–21.
- STANLEY, G. D. JR. & GONZÁLEZ-LEÓN, C. 1995. Paleogeographic and tectonic implications of Triassic fossils and strata from the Antimonio Formation, northwestern Sonora. In: JACQUES-AYALA, C., GONZÁLEZ-LEÓN, C. & ROLDÁN-QUINTANA, J. (eds) *Studies on the Mesozoic of Sonora and Adjacent Areas*. Geological Society of America, Special Paper, **301**, 1–16.
- STANLEY, S. M. 1979. *Macroevolution: Pattern and Process*. W. H. Freeman and Company, San Francisco.
- TANG, C. M. 2001. Stability in ecological and paleoecological systems: variability at both short and long time-scales. In: ALLMON, W. D. & BOTTJER, D. J. (eds) *Evolutionary Paleoecology*. Columbia University Press, New York, 1–8.
- TOLLMANN, A. & KRISTAN-TOLLMANN, E. 1985. Paleogeography of the European Tethys from Paleozoic to Mesozoic and the Triassic relations of the eastern part of the Tethys and Panthalassa. In: NAKAZAWA, K. & DICKINS, J. M. (eds) *The Tethys. Her Paleogeography and Paleobiogeography from Paleozoic to Mesozoic*. Tokai University Press, Tokyo, 3–22.
- TONG, J. & YIN, H. 2002. The Lower Triassic of South China. *Journal of Asian Earth Sciences*, **20**, 803–815.
- TONG, J., ZAKHAROV, Y. D., ORCHARD, M. J., YIN, H. & HANSEN, H. J. 2004. Proposal of Chaohu section as the GSSP candidate of the Induan–Olenekian boundary. *Albertiana*, **29**, 13–28.
- TOZER, E. T. 1961. Triassic stratigraphy and faunas, Queen Elizabeth Islands, Arctic Archipelago. *Geological Survey of Canada Memoir*, **316**, 1–116.
- TOZER, E. T. 1963. Illustrations of Canadian fossils: Triassic of western and Arctic Canada. *Geological Survey of Canada Paper*, **62-19**, 1–26.
- TOZER, E. T. 1967. A standard for Triassic time. *Geological Survey of Canada Bulletin*, **156**, 1–103.
- TOZER, E. T. 1970. Marine Triassic faunas. In: DOUGLAS, R. J. (ed.) *Geology and Economic Minerals of Canada*. Geological Survey of Canada, Economic Geology, Report 1, 5th edition, 633–640.
- TOZER, E. T. 1973. Lower and Middle Triassic ammonoids and bivalves from Nordaustlandet (Spitsbergen) collected by Dr Oskar Kulling in 1931. *Geologiska Föreningens i Stockholm Föreläsningar*, **95**(1), 99–104.
- TOZER, E. T. 1980. Latest Triassic (Upper Norian) ammonoid and *Monotis* faunas and correlations. *Rivista Italiana Paleontologia e Stratigrafia*, **85**, 843–876.

- TOZER, E. T. 1982. Marine Triassic faunas of North America; their significance for assessing plate and terrane movements. *Geologische Rundschau*, **7**, 1077–1104.
- TOZER, E. T. 1994. Canadian Triassic ammonoid faunas. *Geological Survey of Canada Bulletin*, **467**, 1–663.
- TOZER, E. T. & PARKER, J. R. 1968. Notes on the Triassic biostratigraphy of Svalbard. *Geological Magazine*, **105**(6), 526–541.
- TUNNICLIFFE, V. 1991. The biology of hydrothermal vents: ecology and evolution. *Annual Reviews of Oceanography and Marine Biology*, **29**, 319–407.
- VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245–258.
- WALLER, T. R. & STANLEY, G. D. JR. 2005. Middle Triassic pteriomorphian Bivalvia (Mollusca) from the New Pass Range, west-central Nevada: systematics, biostratigraphy, paleoecology, and paleobiogeography. *Paleontological Society Memoir*, **61**, 1–64.
- WATERHOUSE, J. B. 2000. Early Triassic Pectinidina (Mollusca: Bivalvia) from Dolpo and Manang, Nepal Himalaya. *Records of the Canterbury Museum*, **14**, 155–186.
- WATERHOUSE, J. B. 2001. Late Paleozoic Brachiopoda and Mollusca, chiefly from Wairaki Downs, New Zealand, with notes on Scyphozoa and Triassic ammonoids and new classifications of Linoproductoidea (Brachiopoda) and Pectinida (Bivalvia). *Earthwise*, **3**, 1–195.
- WATERHOUSE, J. B. 2008. Aspects of the evolutionary record for fossils of the bivalve subclass Pteriomorpha Beurlen. *Earthwise*, **8**, 1–220.
- WESTERMANN, G. E. G. 1970. Occurrence of *Monotis subcircularis* Gabb in central Chile and the dispersal of *Monotis* (Triassic Bivalvia). *Pacific Geology*, **2**, 35–40.
- WESTERMANN, G. E. G. 1973. The Late Triassic bivalve *Monotis*. In: HALLAM, A. (ed.) *Atlas of Palaeobiogeography*. Elsevier, Amsterdam. 251–258.
- WESTERMANN, G. E. G. & VERMA, H. 1967. The Norian Pine River Bridge section, British Columbia, and the succession of *Monotis*. *Journal of Paleontology*, **41**(3), 798–803.
- WIGNALL, P. B. 1993. Distinguishing between oxygen and substrate control in fossil benthic assemblages. *Journal of the Geological Society, London*, **150**, 193–196.
- 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. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**, 21–46.
- WIGNALL, P. B. & SIMMS, M. J. 1990. Pseudoplankton. *Palaeontology*, **33**, 359–378.
- YAN, J. & ZHAO, K. 2001. Permo-Triassic paleogeographic, paleoclimatic and paleoceanographic evolutions in eastern Tethys and their coupling. *Science in China (Series D)*, **44**(11), 968–978.
- YANG, F., PENG, Y. & GAO, Y. 2001. Study of the Late Permian *Claraia* in South China. *Science in China (Series D)*, **44**(9), 797–807.
- YIN, H. F. 1985. Bivalves near the Permian–Triassic boundary in South China. *Journal of Paleontology*, **59**, 572–600.
- YIN, H. F. 1990. Paleogeographical distribution and stratigraphical range of the Lower Triassic *Claraia*, *Pseudoclaraiia* and *Eumorphotis* (Bivalvia). *Journal of China University of Geosciences*, **1**(1), 98–110.
- YIN, H. F. 2003. Triassic biostratigraphy of China. In: ZHANG, W., CHEN, P. & PALMER, A. R. (eds) *Biostratigraphy of China*. Science Press, Beijing, 379–422.
- YIN, H. F., ZHANG, K., TONG, J., YANG, Z. & WU, S. 2001. The Global Stratotype Section and Point (GSSP) of the Permian–Triassic boundary. *Episodes*, **24**, 102–114.
- VOZIN, V. F. & TIKHOMIROVA, V. V. 1964. *Field atlas of Bivalvia and Cephalopoda in the Triassic deposits of northeastern USSR*. Institute of Geology, Siberian Branch, USSR Academy of Sciences, Moscow. [In Russian.]
- VU-KHUC, D. 1991. *Paleontological Atlas of Vietnam, volume 3, Mollusca 3*. Geological Survey of Vietnam, Institute of Geology and Mineral Resources, Science and Technics Publishing House, Hanoi.
- ZAKHAROV, V. A., BOGOMOLOV, Y. I. ET AL. 1997. Boreal zonal standard and biostratigraphy of the Siberian Mesozoic. *Russian Geology and Geophysics*, **38**(5), 927–956.
- ZAPFE, H. 1973. *Otapiria* (Monotidae, Bivalvia) aus der alpinen Trias. *Annals der Naturhistorisches Museum Wien*, **71**, 149–158.
- ZHANG, Z.-M. 1980. On the ligament area, systematic position and evolutionary relationship of *Claraia*. *Acta Palaeontologica Sinica*, **19**(6), 433–443.