

A TEST OF BIOGEOGRAPHICAL, ENVIRONMENTAL, AND ECOLOGICAL EFFECT ON MIDDLE AND LATE TRIASSIC BRACHIOPOD AND BIVALVE ABUNDANCE PATTERNS

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ABSTRACT

Analysis of Middle Triassic data indicates that biogeography influences sample distributions, whereas depositional environment and stratigraphic position play secondary roles in governing sample patterns. During this time, taxa differed among biogeographic realms, while the general ecology remained the same: epifaunal benthos—pedunculate and epibyssate suspension feeders—dominate Middle Triassic samples much as they did in the Early Triassic. In contrast, Late Triassic data prove to be more complex in terms of ecology compared to Middle Triassic. Here, guild structure dictates the faunal patterns in addition to biogeographic realm and stratigraphic position, and an overall increase of infaunal life habits occurs—burrowing suspension and deposit feeders increase. Although diversity after mass extinction began to recover at the Early-Middle Triassic boundary, our results indicate that ecology remained stable through the Middle Triassic until the more modern life habits (e.g., infaunalization) increased in the Late Triassic. We conclude that the taxonomic and ecological differences among Late Triassic geographic regions recorded the initiation of a more mobile and infaunal life habit indicative of a modern lifestyle. Our results also indicate that this modernization did not necessarily unfold simultaneously and in coordinated fashion within regions and throughout time. Instead, details of guild expansion or stability may be region specific.

INTRODUCTION

Much work has gone into resolving large-scale Middle and Late Triassic brachiopod and bivalve abundance patterns, particularly diversity studies. Recent work has focused on abundance trends of marine benthos and reports an increase in ecological complexity within Jurassic faunas (Aberhan et al., 2006), between Jurassic and Cenozoic (Kowalewski et al., 2006) and between Paleozoic and post-Paleozoic faunas (Wagner et al., 2006). Aside from a recent study of the Upper Triassic Kössen Formation (Tomašových, 2006), abundance studies within the Middle and Late Triassic are still largely neglected. Many questions have been left unanswered, for example, What are the associated paleoecological details of this transition period? Are two major Phanerozoic events linked, and if so, how? Undoubtedly this interval of time holds a very complex macroevolutionary story, yet few rigorous paleoecological studies are completed. Geographic variance in ecological structure through time, including similarities and differences among geographic regions, provides additional evidence for the macroevolutionary complexity of large-scale biotic changes (Erwin et al., 1987; Sepkoski, 1993; Sepkoski and Kendrick, 1993; Raup, 1994; Benton, 1995; Jablonski, 1995, 1998).

To gain a fuller understanding of end-Permian mass extinction and the transitional period between it and the Mesozoic marine revolution, we examined abundance data from the Middle Triassic through the Late Triassic from several biogeographic locations. Using multivariate tech-

niques, we test (1) the environmental and biogeographic effects on sample-level faunal compositions, and (2) whether or not abundance patterns characterize taxonomic and ecologic membership.

Mass extinction is an important biological force not only for the taxa lost but also for the evolutionary diversification and ecological restructuring that occurs in postextinction events (Raup, 1986; Jablonski, 1998, 2002). The end-Permian mass extinction, one of the five major mass extinctions of the metazoan fossil record, was followed by a survival phase comprised of eurytopic, cosmopolitan, but depauperate faunas through the Early Triassic. Following this survival phase, a rapid recovery of global taxonomic diversity occurred in the Middle Triassic, which generated substantial long-term effects resulting in the most dramatic reorganization of marine communities (Vermeij, 1977; Gould and Calloway, 1980; Sepkoski, 1981; Erwin, 1994, 1998). Marine communities transitioned from mainly epibenthic sedentary suspension feeders (e.g., brachiopods, crinoids, anthozoans, and stenolaemate bryozoans—Paleozoic fauna) to a wide range of trophic levels ranging from deep infaunal suspension feeders to swimming carnivores (e.g., bivalve and gastropod mollusks, gymnolaemate bryozoans, echinoids, malacostracan arthropods, and bony fishes—modern fauna).

It has been argued that, beginning in the Jurassic, evolutionary changes in the effectiveness of shell-penetrating predators drove changes in the structure of marine communities and in the range of morphologies present in bivalves, gastropods and other marine prey (Vermeij, 1977, 1987, 1994). This Mesozoic marine revolution engendered such ecological changes as an increase in organisms possessing the abilities to utilize new infaunal habitats and resources.

STUDY AREAS AND GEOLOGICAL SETTING

This study focuses on four marine provinces throughout the Middle and Late Triassic: the Eastern Panthalassa Realm, the Northwestern Tethys Realm, the Northeastern Tethys Realm, and the Germanic Epicontinental Sea Realm (Fig. 1). Data sampling concentrated on the Anisian, Ladinian, Carnian, Norian, and Rhaetian stages of the Triassic (Fig. 2; Gradstein et al., 2004).

The overall geological setting consists of a series of transgressive-regressive cycles. Long-term sea-level changes indicate that a major transgression took place during the Anisian, which peaked in the Ladinian and regressed during the Norian through the Rhaetian (Haq et al., 1987; Michalik, 1987; Dagys, 1993; Hardenbol et al., 1998). General ocean-circulation reconstructions and taxonomic occurrence patterns indicate that free migration took place along the northern Tethys and into the Germanic Basin and from the eastern Tethys to the New World via the Boreal regions (Fig. 1). The low latitudes of the Eastern Panthalassa record occurrences of genera from Siberia and Alaska that confirm free migrations (Ager, 1988; Dagys, 1993). More specific geological information is discussed according to specific regions.

Germanic Epicontinental Sea Realm

The northern part of the Tethys was an epicontinental sea during a major global transgression of the Middle Triassic (Haq et al., 1987). This

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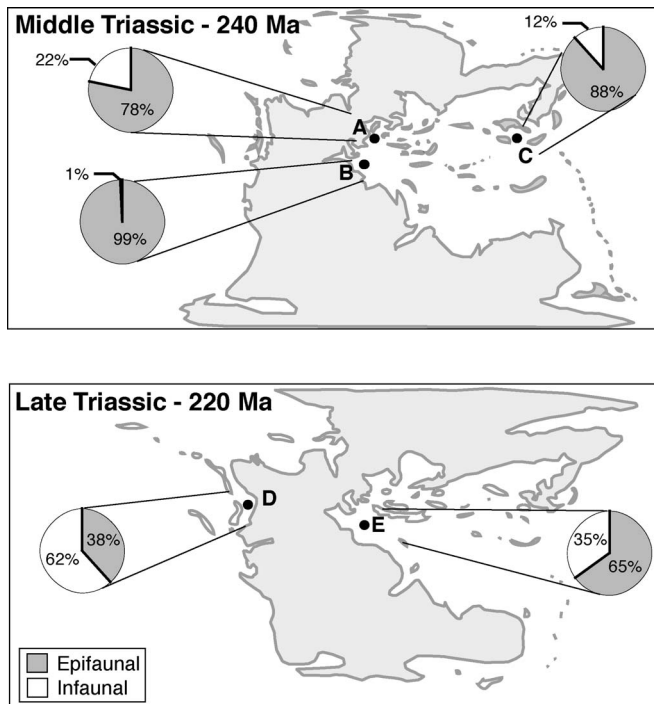


FIGURE 1—Middle and Late Triassic global paleogeography. Middle Triassic samples are differentiated into three realms: location A, the Germanic Epicontinental Sea Realm (GESR), location B, Northwestern Tethys Realm (NWTR), and location C, Northeastern Tethys Realm (NETR). Late Triassic samples are differentiated into two realms: location D, the Eastern Panthalassa Realm (EPR), and location E, representing the Northwestern Tethys Realm (NWTR). The pie diagrams represent percentage of general life habit preferences of benthos within each paleogeographic region

area is referred to as the Germanic Basin or Muschelkalk Sea (Kaim, 1997). At this time a connection between the Muschelkalk Sea and the Tethys Sea existed to the south; as a result, there are some similarities in the fauna between the two provinces (Pevny, 1988; Kaim, 1997). For this study, the area is termed the Germanic Epicontinental Sea Realm (GESR) for a more specific account of the area's depositional environment. Data from this region come from Upper Silesia of Poland (Kaim, 1997). These field sites sat paleogeographically on the southern margins of the Germanic Basin. By the Late Anisian (Middle Triassic), tectonic activity transformed the uniform carbonate platform into a combination of small, shallow, intraplatform basins (Galácz et al., 1985). Deposits from this area represent an open-carbonate platform and shallow intraplatform basins.

Northwestern Tethys Realm

The Northwestern Tethys Realm (NWTR) contains a diverse, excellently preserved invertebrate fauna of Middle and Late Triassic age (Fürsich and Wendt, 1977). Numerous reports have been published regarding faunal associations from the area (Ager, 1965, 1967, 1971; Pevny, 1988; Tamaro and Sartori, 1996) and are listed and described according to their well-known regional categories—West Carpathian, Northern Calcareous Alps, and Southern Alps.

The West Carpathian (Slovakia) carbonate platform was situated at the northwestern margin of the Tethys Sea (Kochanová and Pevny, 1982; Michalik, 1994; Tomašových, 2004a; Tomašových and Farkas, 2005). This extensive carbonate platform, due to tectonic activity, contained shallow, intraplatform basinal environments similar to that of the Upper Triassic (Rhaetian) Kössen Formation, which is also included in this study (Golebiowski, 1991; Tomašových, 2004b). Data reported from Kochan-

Geochronology		Stratigraphic position of samples according to paleogeographic realm (Figure 1)				Short-term sea-level change (after Embry, 1988)		
Ma	Epoch	Stage	EPR	NWTR	NETR	GESR	← Rise →	Fall →
200	Late Triassic	Rhaetian		Si1 G6 G2 G1				
204		Norian	L1 H4 H3					
217		Carnian	H2 H1	Si2 F2 F1				
228	Middle Triassic	Ladinian		To1 Ko1				
237		Anisian		P2 V3 P1 V2 Ga1 P3	S3 S2 S1	Ka3 Ka1		
245								

FIGURE 2—Geochronology from the Middle Triassic through the Late Triassic (after Gradstein et al., 2004). Samples categorized according to their appropriate stage and paleogeographic realm. Samples within stages are not arranged in stratigraphic order. GESR = Germanic Epicontinental Sea Realm; NWTR = Northwestern Tethys Realm; NETR = Northeastern Tethys Realm; EPR = Eastern Panthalassa Realm.

ova and Pevny (1982) contain macrofauna from the Slovak Zámosite Limestone Formation and Jasenie and Ráztoka Limestone Members.

The Northern Calcareous Alps represented an extensive carbonate platform situated on the western margin of the Tethys Sea during the Late Triassic (Ohlen, 1959; Piller, 1981; McRoberts et al., 1997). Data incorporated in this study are from the Kössen Formation, which records a regressive carbonate succession within a muddy intraplatform basinal environment separated from the open ocean to the east by an extensive carbonate platform (e.g., Dachstein Limestone; Golebiowski, 1989; McRoberts et al., 1997; Turnsek et al., 1999).

The Southern Alps, also situated in Western Tethys, record the disintegration of the Early Anisian carbonate platform (Gaetani, 1969; Fürsich and Wendt, 1977; Siblík, 1986; Vörös and Pálffy, 1989; Torti and Angiolini, 1997; Pálffy, 2003). By the Late Anisian, the tectonic activity related to a rifting phase in the western Tethys caused the deposition of laterally intercalated facies of patch reefs (Tagyon Limestone) and shallow basins with slopes (Felsöors Limestone) in fragments of the old platform (Galácz et al., 1985; Pálffy, 1990). Fürsich and Wendt (1977) studied the Upper Triassic Cassian Formation. The fossils from these areas are from shallow, intraplatform basins between carbonate buildups, similar to the Northern Calcareous Alps (Fürsich and Wendt, 1977; Gaetani and Jadoul, 1979; Gaetani et al., 1981; Jadoul et al., 1992).

Northeastern Tethys Realm

Data from the Northeastern Tethys Realm (NETR) come from the Middle Triassic Leidapo Member of the Qingyan Formation located in southwestern Guizhou, China (Stiller, 2001). During the Middle Triassic a normal marine epeiric sea, opened to the Tethys, existed in the southern part of the Guizhou Province. The Yangtze Platform, a shallow-water carbonate platform, was a stable paleogeographic feature from the Late Proterozoic through the Triassic (Enos et al., 1997).

TABLE 1—Locality, geology, age, and abundance information for Middle and Late Triassic samples.

Locality	Sample code*	Lithology	Realm	Depositional environment	Regional stage	Abundance
Trentino, Italy	Ga1	Limestone	NWTR	Middle shelf	Anisian	431
Poland	Ka1	Wavy limestone	GESR	Outer shelf	Anisian	1470
Poland	Ka3	Bivalve coquina	GESR	Outer shelf	Anisian	615
Male Karpaty Mtns., Slovakia	Ko1	Limestone	NWTR	Middle shelf	Ladinian	203
Balaton Highland, Hungary	P1	Biodetrital limestone	NWTR	Inner shelf	Anisian	786
Balaton Highland, Hungary	P2	Limestone	NWTR	Basin	Anisian	820
Balaton Highland, Hungary	P3	Limestone	NWTR	Middle shelf	Anisian	625
Guizhou, China	S1	Claystone-wackestone	NETR	Basin	Anisian	4323
Guizhou, China	S2	Bioclastic limestone	NETR	Outer shelf	Anisian	468
Guizhou, China	S3	Bioclastic limestone	NETR	Outer shelf	Anisian	263
Val Parina, Italy	To1	Limestone	NWTR	Shallow intraplatform basin	Ladinian	215
Veszprem, Hungary	V2	Dolomitic limestone	NWTR	Middle shelf	Anisian	304
Veszprem, Hungary	V3	Biodetrital limestone	NWTR	Inner shelf	Anisian	312
Trentino, Italy	F1	Marl-limestone	NWTR	Shallow intraplatform basin	Carnian	665
Trentino, Italy	F2	Packstone	NWTR	Middle shelf	Carnian	246
N. Calcareous Alps, Austria	G1	Clay marl	NWTR	Shallow intraplatform basin	Rhaetian	302
N. Calcareous Alps, Austria	G2	Bioclastic limestone	NWTR	Inner shelf	Rhaetian	3614
N. Calcareous Alps, Austria	G6	Limestone	NWTR	Middle shelf	Rhaetian	235
Nye County, Nevada, USA	H1	Bioclastic wackestone	EPR	Outer shelf	Carnian	3581
Nye County, Nevada, USA	H2	Lime mudstone	EPR	Basin	Carnian	692
Nye County, Nevada, USA	H3	Lime mudstone	EPR	Basin	Norian	218
Nye County, Nevada, USA	H4	Lime mudstone-wackestone	EPR	Basin	Norian	731
Gabbs Valley, Nevada, USA	L1	Packstone	EPR	Middle shelf	Norian	205
Silická Brezová, Slovakia	Si2	Limestone	NWTR	Middle shelf	Carnian	347

* Abbreviations: Ga1 = Gaetani (1969); Ka1, Ka3 = Kaim (1997); Ko1 = Kochanová and Pevny (1982); P1, P2, P3 = Pálffy (2003); S1, S2, S3 = Stiller (2001); To1 = Torti and Angiolini (1997); V2, V3 = Vörös and Pálffy (1989); F1, F2 = Fürsich and Wendt (1977); G1, G2, G6 = Golebiowski (1989); H1, H2, H3, H4 = Hogler (1992); L1 = Laws (1982); Si2 = Siblík (1986); GESR = Germanic Epicontinental Sea realm.

Eastern Panthalassa Realm

The Eastern Panthalassa Realm (EPR) extends along the margins of western North and South America (Fig. 1). Samples within this realm are from the Late Triassic of the Western United States. In this region, Upper Triassic rocks belong to various displaced terranes accreted onto North America via island-arc collision during the Cretaceous Sevier Orogeny (Hallam, 1986; Sandy and Stanley, 1993). Appropriate data are available from two units: the Gabbs Formation and the Luning Formation of Nevada (Laws, 1982; Hogler, 1992). These deposits represent an open-shelf carbonate platform environment with inner-shore to outer-shelf settings. Other data from this realm, however, are either unattainable, or sample sizes are not sufficient for meaningful statistical analysis (Sandy, 1994, 1997; Stanley et al., 1994; Gonzalez-Leon et al., 1996; McRoberts, 1997; Stanley, 1997; Goodwin, 1999; Sandy and Blodgett, 2002).

METHODS

Sample Collection and Processing

Our database consists of information on the age, sedimentary environment, and faunal composition of paleocommunities spanning the Middle and Late Triassic, gleaned mostly from the Paleobiology Database (PBDB)—a public, electronic resource of faunal data from published and unpublished (i.e., dissertation) sources. The PBDB collections represent the fossil content of a particular restricted stratigraphic and environmental interval. In assembling our database, we combined original PBDB collections into samples defined as closely spaced horizons from the same regional locality within similar primary lithologies to obtain as broad an environmental and temporal account of faunal changes as possible. The environmental framework used in this study is a very simple inner-shelf to outer-shelf gradient, much like the one used in Sepkoski and Miller (1985), with the exception of the intraplatform environment, which was present within the Triassic Tethys region. This framework is an extreme oversimplification of actual faunal environments, reducing the complex nature of marine benthic environments to the simple dimensions of depth

and distance from the shore. Our study, thus, provides only a first-order approximation of spatial and temporal differences among faunal associations.

Data were compiled into comprehensive, relative abundance data sets. Collections from one primary reference source, sampled from the same primary lithology within a 2° latitude and longitude variation, were combined as one sample within our data set (Table 1). Each sample consists of at least 200 specimens at the generic level. Original identifications were checked against museum collections and published photographs to confirm taxonomic identification. In total, 13 Middle Triassic and 11 Late Triassic samples with a total count of 21,671 specimens were analyzed (Table 1).

All samples represent marine level-bottom communities from a subtropical environment. The positioning of samples along the inner-shelf to outer-shelf gradient was based on the original primary lithology listed in the PBDB collections. That is, when new collections are entered into the PBDB, a primary lithology is selected, based on the literature reference, from a pull-down menu. The terms listed below are the specific terms used by the PBDB. An explanation of these terms can be found on the PBDB web site. Samples were placed into the inner-shelf environment if they were listed in the PBDB as limestone sandstone, biodetrital limestone, coquina limestone, crumpled limestone, shallow bioclastic limestone, and tuffaceous calcareous sandstone. Samples listed as carbonate, limestone, packstone, dolomitic limestone, shallow limestone, subtidal limestone, and marl were placed into the middle-shelf environment. Such lithologies as claystone-marl, lithified limestone, shallow limestone beds, subtidal limestone beds, wackestone-packstone, limy shale and mud, and wavy limestone were placed into the outer-shelf environment. Samples interpreted in the primary reference source as being from an intraplatform basin were placed within that environment. There is obvious uncertainty in placement of our samples caused by limited lithological data in paleontological literature. This problem reduces the resolution of the environmental data; however, it still provides a broad recognition of depth-related trends.

TABLE 2—Specimen information for Middle and Late Triassic genera.

Group	Order	Genus	Genus code	Ecological guild*	Geological periods
Brachiopod	Terebratulida	<i>Angustothyris</i>	ANG	Ped Susp	Middle Triassic
Brachiopod	Rhynchonellida	<i>Austrirhynchia</i>	AUS	Ped Susp	Late Triassic
Brachiopod	Rhynchonellida	<i>Caucasorhynchia</i>	CAU	Ped Susp	Mid–Late Triassic
Brachiopod	Terebratulida	<i>Coenothyris</i>	COE	Ped Susp	Middle Triassic
Brachiopod	Rhynchonellida	<i>Costirhynchopsis</i>	COS	Ped Susp	Late Triassic
Brachiopod	Terebratulida	<i>Cruratula</i>	CRU	Ped Susp	Middle Triassic
Brachiopod	Rhynchonellida	<i>Diholkorhynchia</i>	DIH	Ped Susp	Middle Triassic
Brachiopod	Rhynchonellida	<i>Fissirhynchia</i>	FIS	Ped Susp	Late Triassic
Brachiopod	Spiriferinida	<i>Leiolepismatina</i>	LEI	Ped Susp	Middle Triassic
Brachiopod	Spiriferinida	<i>Mentzelia</i>	MEN	Ped Susp	Middle Triassic
Brachiopod	Spiriferinida	<i>Nudspiriferina</i>	NUD	Ped Susp	Middle Triassic
Brachiopod	Athyridida	<i>Oxycolpella</i>	OXY	Ped Susp	Late Triassic
Brachiopod	Rhynchonellida	<i>Piarorhynchella</i>	PCHLA	Ped Susp	Middle Triassic
Brachiopod	Rhynchonellida	<i>Piarorhynchia</i>	PCHIA	Ped Susp	Middle Triassic
Brachiopod	Terebratulida	<i>Plectoconcha</i>	PLE	Ped Susp	Late Triassic
Brachiopod	Spiriferinida	<i>Qingyenia</i>	QIN	Ped Susp	Middle Triassic
Brachiopod	Terebratulida	<i>Rhaetina</i>	RHA	Ped Susp	Late Triassic
Brachiopod	Rhynchonellida	<i>“Rhynchonella”</i>	RHYC	Ped Susp	Late Triassic
Brachiopod	Athyridida	<i>Tetractinella</i>	TET	Ped Susp	Middle Triassic
Brachiopod	Rhynchonellida	<i>Trigonirhynchella</i>	TRI	Ped Susp	Middle Triassic
Brachiopod	Terebratulida	<i>Zeilleria</i>	ZEI	Ped Susp	Late Triassic
Brachiopod	Spiriferinida	<i>Zugmayerella</i>	ZUG	Ped Susp	Late Triassic
Mollusk	Neotaenioglossa	<i>Ampullina</i>	AMP	Epif Graz	Late Triassic
Mollusk	Pterioida	<i>Arcavicula</i>	ARC	Epib Susp	Middle Triassic
Mollusk	Pterioida	<i>Atreta</i>	ATE	Cem Susp	Late Triassic
Mollusk	Pterioida	<i>Bakevella</i>	BAK	Epib Susp	Late Triassic
Mollusk	Pterioida	<i>Cassianella</i>	CAS	Epib Susp	Mid–Late Triassic
Mollusk	Pterioida	<i>Daonella</i>	DAO	Epib Susp	Middle Triassic
Mollusk	Trigonioida	<i>Elegantinia</i>	ELE	Epib Susp	Middle Triassic
Mollusk	Pectinoidea	<i>Enantiostreon</i>	ENA	Cem Susp	Middle Triassic
Mollusk	Archaeogastropoda	<i>Eucycloscala</i>	EUC	Epif Graz	Middle Triassic
Mollusk	Pterioida	<i>Gervillaria</i>	GER	Epib Susp	Late Triassic
Mollusk	Pterioida	<i>Halobia</i>	HAL	Cem Susp	Late Triassic
Mollusk	Veneroidea	<i>Isocyprina</i>	ISO	Bur Susp	Late Triassic
Mollusk	Ostreoida	<i>Lopha</i>	LOP	Cem Susp	Late Triassic
Mollusk	Nuculoidea	<i>Nuculana</i>	NUC	Bur Dep	Late Triassic
Mollusk	Veneroidea	<i>Palaeocardita</i>	PAL	Bur Susp	Late Triassic
Mollusk	Veneroidea	<i>Pseudocorbula</i>	PSE	Bur Susp	Middle Triassic
Mollusk	Archaeogastropoda	<i>Rhaphistomella</i>	RHAP	Epif Susp	Late Triassic
Mollusk	Veneroidea	<i>Ruxingella</i>	RUX	Bur Susp	Middle Triassic
Mollusk	Veneroidea	<i>Septocardia</i>	SEP	Bur Susp	Late Triassic
Mollusk	Veneroidea	<i>Tutcheria</i>	TUT	Bur Susp	Late Triassic
Mollusk	Archaeogastropoda	<i>Wortheniella</i>	WOR	Epif Graz	Middle Triassic

* Abbreviations: Bur Dep = burrowing deposit feeders; Bur Susp = burrowing suspension feeder; Cem Susp = cementing suspension feeder; Epib Susp = epibyssate suspension feeder; Epif Graz = epifaunal grazer; Ped Susp = pedunculate suspension feeders.

Specimens were categorized as brachiopod or mollusk (bivalves and gastropods), life in relation to the sediment surface, and feeding habits. Table 2 lists all the specimen categorical information, including ecological guild assignments. Systematic and life-habit classifications were determined using primary references (Suess, 1854; Zugmayer, 1880; Knight et al., 1960; Stanley, 1968, 1970, 1972; Moore, 1969; Rudwick, 1970; Michalik, 1977; Linsley, 1978; Pojeta, 1980; Grant, 1981; Rowell, 1981; Thayer, 1981; Yin and Yochelson, 1983a, 1983b, 1983c; Pojeta et al., 1987; Rowell and Grant, 1987; Miller, 1990; Skelton et al., 1990; Bieler, 1992; Carter et al., 1994; Savage, 1996; Kaesler, 1997; Williams et al., 2000; Kondo, 1998; Carter et al., 2000; Steiner and Hammer, 2000; Carlson, 2001; Carlson and Leighton, 2001; Hautmann, 2001; Peck, 2001a, 2001b; Schneider, 2001; Chase, 2002). Unfortunately, information pertaining to original shell mineralogy (i.e., calcitic vs. aragonitic) was not available within the original PBDB records. Therefore, taphonomic biases were not controlled for in this study.

Sampled realms correspond roughly in similar amounts (Table 1). For the Middle Triassic, the GESR Realm contains 2085 specimens (17%), the NETR Realm consists of 5054 specimens (42%), and the NWTR Realm comprises 4906 specimens (41%). For the Late Triassic, the EPR

Realm consists of 5427 specimens (~50%), and the NWTR Realm contains 5409 specimens (~50%). In addition, analyzed facies and sampled stratigraphic intervals are approximately equal except in one stage, the Ladinian. Despite variation in the Ladinian, this stage comprises 418 specimens—an ample sample size for reliable statistical results. All other analyzed samples also have ample sample sizes to allow for reliable quantitative comparisons (Table 1).

Analytical Methods

Exploratory and confirmatory multivariate methods were used in this study. Data matrices are composed of compositional data with samples described by taxonomic percents. Specimens constituting <1% of a sample were deleted to reduce the amount of noise in the data sets and aid in interpreting results. In all, less than 26% of the total specimens were lost as a result of this operation. The data were log transformed before analysis because of the high degree of variation among attributes within samples.

Detrended correspondence analysis (DCA; see Hill, 1979) was used as our primary ordination technique; it is a popular method for indirect

gradient analysis (Shi, 1993; Scarponi and Kowalewski, 2004). It is worthwhile outlining a few key differences between the most popular statistical methods: nonparametric multidimensional scaling (NMDS), correspondence analysis (CA), and DCA. Some issues are relatively minor; for example, computation time is rarely an important consideration. Some issues are not entirely resolved; the degree to which noise affects NMDS and the degree to which NMDS finds local rather than global options need to be determined. Since NMDS is a distance-based method, all information about species identities is hidden once the distance matrix is created; this is the biggest disadvantage of NMDS. Perhaps the biggest difference between these methods is that CA and DCA are based on a unimodal model of species distributions, whereas NMDS locates species in the space where they are most abundant. As a result, the first axis usually turns out to be related to important environmental gradients. Correspondence analysis and DCA, thus, are closer to the theory of community ecology (Gauch, 1982; Pielou, 1984; Digby and Kempton, 1987).

Detrended correspondence analysis was chosen for this study because we aim to search for the underlying ecological gradient between specific localities within their appropriate geological stages. Detrended correspondence analysis, therefore, is an appropriate exploratory analysis for these data (Gauch, 1982), and we chose it over CA because DCA minimizes the arch effect, a defect of CA, and results in superior conclusions (Hill and Gauch, 1980; Gauch, 1982). The arch effect is considered a defect of CA because the unimodal model results in a compressed second axis, making the second CA axis an artifact. The arch effect is minimized in DCA by rescaling the first axis; therefore, distance in ordination space coordinates throughout the ordination diagram.

Since DCA is an indirect analysis and is considered exploratory, the researcher must interpret the ordination results (Gauch, 1982). To aid interpretation, we take a cross-validation approach to these analyses by combining the exploratory analysis of ordination with objective hypothesis testing of a nonparametric procedure: multiresponse permutation procedure (MRPP), which tests the hypothesis that there are no differences between two or more groups (McCune, 1997). For example, one could compare species composition between pelagic and benthic associations to test whether the two differ in faunal composition. Discriminant analysis and multivariate analysis of variance are parametric procedures used on the same general class of questions. The multiresponse permutation procedure, however, has the advantage of not requiring the assumption of normality, which is rarely met with ecological community data (Biondini et al., 1985). The method requires that groups of entities—samples or specimens in the matrix—be defined a priori. Here, MRPP is used as a comparative measure to assess relative performance of different grouping variables. It is, thus, merely a tool supplementary to ordination that measures the difference among precategorized samples based on Euclidean distances. Samples, in this case, are grouped with secondary information: biogeographic location, depositional environment, geological stage, taxonomic groups, sediment preference, and ecological guild. For those not familiar with MRPP, one important calculation is the T-statistic, which describes the distance or separation between analyzed groups of samples; the more negative the value, the more distance between the a priori groups (McCune et al., 2002). The calculated p-value determines whether the distance described by the T-statistic is statistically significant (McCune et al., 2002). For detailed description of MRPP see Mielke (1984). PC-ORD Version 4, software for multivariate statistical analysis of ecological data, performed both exploratory (DCA) and confirmatory (MMRP) analyses (McCune et al., 2002).

A large portion of this research examines whether biogeography, age, or depositional environment influences faunal patterns. As a means to test this, statistical ordination techniques were used as described above. In our study, ordination techniques search for redundancies within taxonomic relative abundance and plot samples according to the redundant similarity or differences between samples. Once the sample coordinates are plotted, if genera varied between two samples, those samples plot separate from one another in ordinal space. Likewise, if two samples shared taxa,

the samples will overlap in ordinal space. This inherent behavior of sample placement lends itself to discovering overall controlling mechanisms driving faunal patterns by coding samples according to their biogeography, age, and depositional environment. For example, if samples collected from a boreal region differ in taxonomic composition compared to samples from a tropical location, boreal samples would plot separate from the tropical samples. One could conclude from this example that biogeography is an important factor that influences faunal patterns. In contrast, if boreal samples plot in the same location as tropical samples (i.e., samples overlap), similar fauna occur in both locations, and as a result, biogeography is not a major factor influencing faunal patterns. Using this reasoning, once sample coordinates are calculated using ordination techniques, we can code samples according to their a priori biogeography, age, and depositional environment, thus revealing possible factors controlling sample placement by the amount of overlap exhibited between samples.

Since DCA calculates specimen and sample coordinates, the specimen coordinates were coded in the same manner as samples; thus, such criteria as sediment preference, feeding habit, and taxonomic groups (i.e., brachiopod versus bivalve) can be tested for control of faunal patterns. While ordination provides a visual interpretation of what influence faunal patterns, MRPP quantifies the amount of separation between a priori categories, thus testing whether the a priori categories differ significantly.

To aid in the interpretation of the ordination results, ecological guild structure was examined according to each paleogeographic region to capture the spatial and temporal details of guild expansion or stability. For this analysis, raw abundance data were converted to percentages within the appropriate guilds.

RESULTS

Multivariate Taxonomic Analysis

By using DCA, four data sets were originated from the raw data and analyzed independently: Middle Triassic genera, Middle Triassic orders, Late Triassic genera, and Late Triassic orders. Generic patterns produce more separation between samples and specimens than do ordinal patterns in both time periods. This indicates that decreasing the taxonomic resolution reduces drastically the amount of information preserved within faunal patterns. Similar results pertaining to loss of information at higher levels of taxonomic resolution have been found within the fossil record (Kowalewski et al., 2002) and within recent community assemblages (Lasiak, 2003). As a result, the rest of this paper focuses on results of the generic analyses.

The Middle Triassic ordinations indicate that the GESR, NETR, and NWTR Realms form separate groups with distinct taxonomic composition (Fig. 3). The separation, however, tends to be better for the genera than the orders (Figs. 3B, F). The samples indicate substantial overlap in each case when grouped by depositional environment and stratigraphic age (Figs. 3C–D, G–H). In addition, taxa overlap when genera are categorized into sediment relation, groups (i.e., brachiopod or mollusk), and ecological guild (Figs. 4A–C). Genera, however, vary along the first axis, indicating that taxa are responding to similar underlying factors in each case. Based on MRPP, biogeographic realm is the only a priori category that separates into statistically significant groups within the Middle Triassic (Table 3).

Late Triassic generic ordinations indicate that samples overlap when they are coded according to biogeographic realm, depositional environment, and geological stages (Figs. 5B–D). Late Triassic taxa show separation once coded according to their taxonomic group, ecology, and sediment preference. The greatest distinction is between brachiopods and mollusks (Fig. 6B). Pedunculate suspension feeders form a distinct cluster separate from other ecological guilds, although genera tend to overlap according to sediment preference and ecology (Fig. 6C).

Late Triassic MRPP results indicate that the a priori groups within

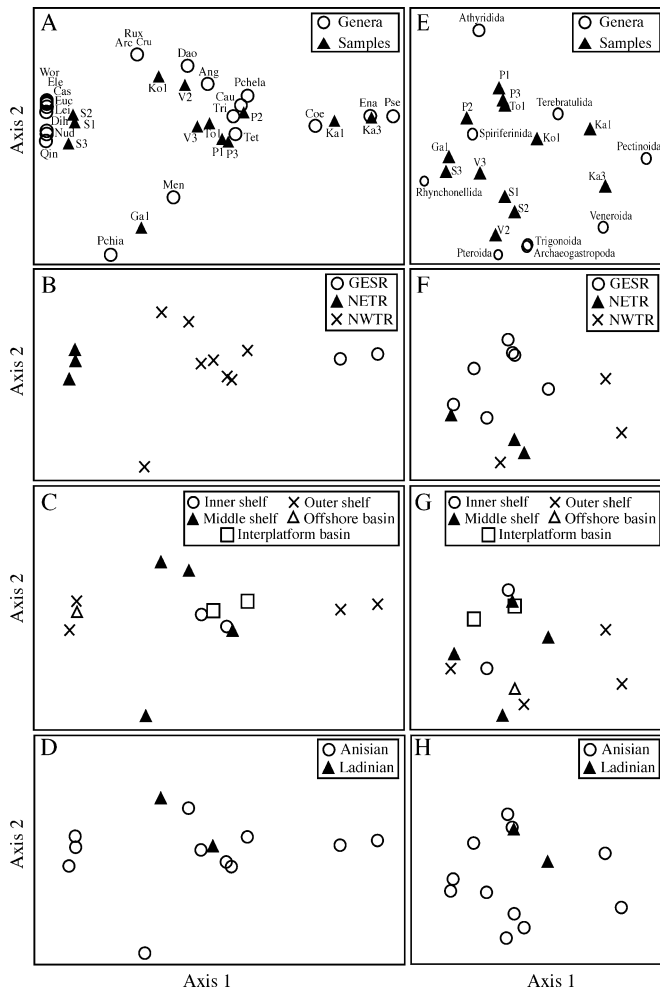


FIGURE 3—Middle Triassic detrended correspondence analysis of samples. Relative abundance data of genera (A–D) and orders (E–H) are plotted. Samples and taxa are plotted together in ordinal space (A and E). Sample codes listed in Table 1, and genera codes are listed in Table 2. B–D) Genus-level ordination plots for samples grouped by (B) biogeography, (C) depositional environment, and (D) stratigraphic stage. F–H) Order-level ordination plots of samples grouped by (F) biogeography, (G) depositional environment, and (H) stratigraphic stage. GESR = Germanic Epicontinental Sea Realm; NWTR = Northwestern Tethys Realm; NETR = Northeastern Tethys Realm.

sediment preference, taxonomic membership, guild structure, biogeography, and lithographic stages are all significantly different (Table 4).

Ecological Guild Structure

The most striking results are the differences in dominant ecological structure between the Middle and Late Triassic (Figs. 7–8). Pedunculate suspension feeders dominate the ecological structure in all Middle Triassic regions (Fig. 7). The second most dominant ecological guild, however, differs among Middle Triassic regions. Burrowing suspension feeders followed by cementing suspension feeders rank second and third for the GESR, whereas epibyssate suspension feeders and epifaunal grazers rank second and third in the NETR and NWTR. As a whole, epifaunal organisms dominate the Middle Triassic benthic ecosystem (Fig. 1).

In comparison, burrowing suspension feeders dominate the Late Triassic EPR followed by cementing suspension feeders and pedunculate suspension feeders (Fig. 8). Within the Late Triassic NWTR, pedunculate suspension feeders still are the dominant ecological category, and burrowing suspension feeders have increased compared to the Middle Triassic of this region. Epibyssate suspension feeders rank third in ecological

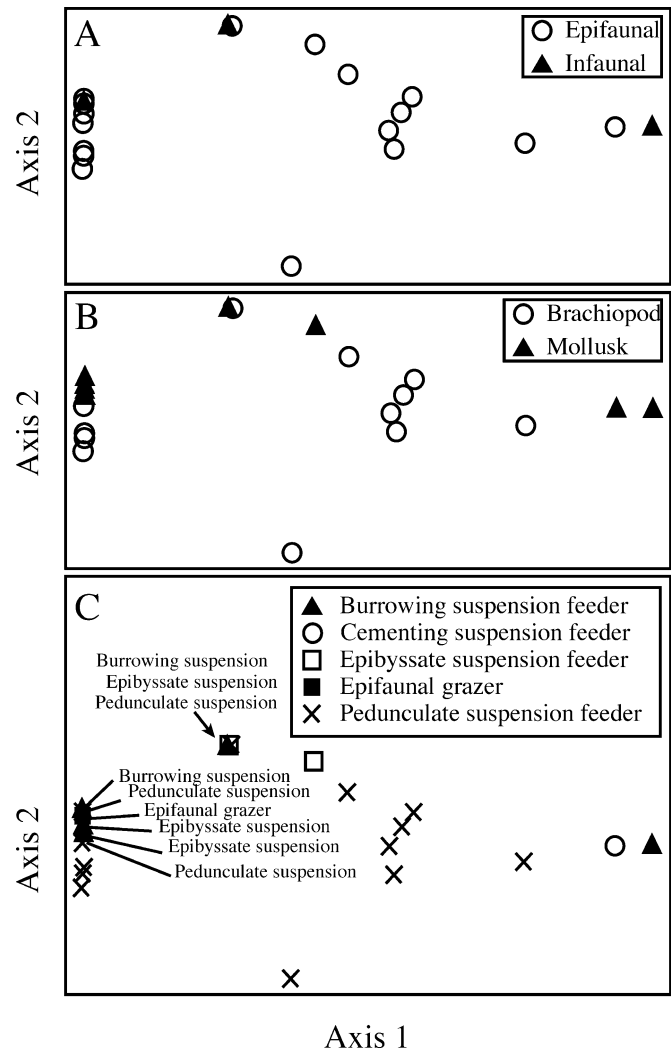


FIGURE 4—Middle Triassic detrended correspondence analysis of genera. Ordination of genera grouped by (A) sediment preference, (B) faunal group (i.e., brachiopod and mollusk), and (C) ecological guild.

dominance followed by epifaunal grazers. In addition to the dominant ecological guilds, a new ecological guild, burrowing deposit feeders, appears in both Late Triassic regions at low percentages (8%–10%). In part, this new ecological guild contributed to the overall increase of infaunal individuals during the Late Triassic (Figs. 1, 8).

TABLE 3—Multiresponse permutation procedure results for Middle Triassic taxonomic a priori groups (* $\alpha = 0.05$).

Group comparison	T-Statistic	<i>p</i> value*
Genera		
Substrate (infaunal vs. epifaunal)	−0.32	0.12
Brachiopod vs. mollusks	−0.98	0.82
Taxa ecology	−0.48	0.29
Paleogeographic realms	−3.09	0.01
Lithostratigraphic stages	−0.22	0.32
Depositional environment	−0.84	0.19
Orders		
Paleogeographic realms	−1.18	0.12
Lithostratigraphic stages	0.51	0.67
Depositional environment	0.99	0.85

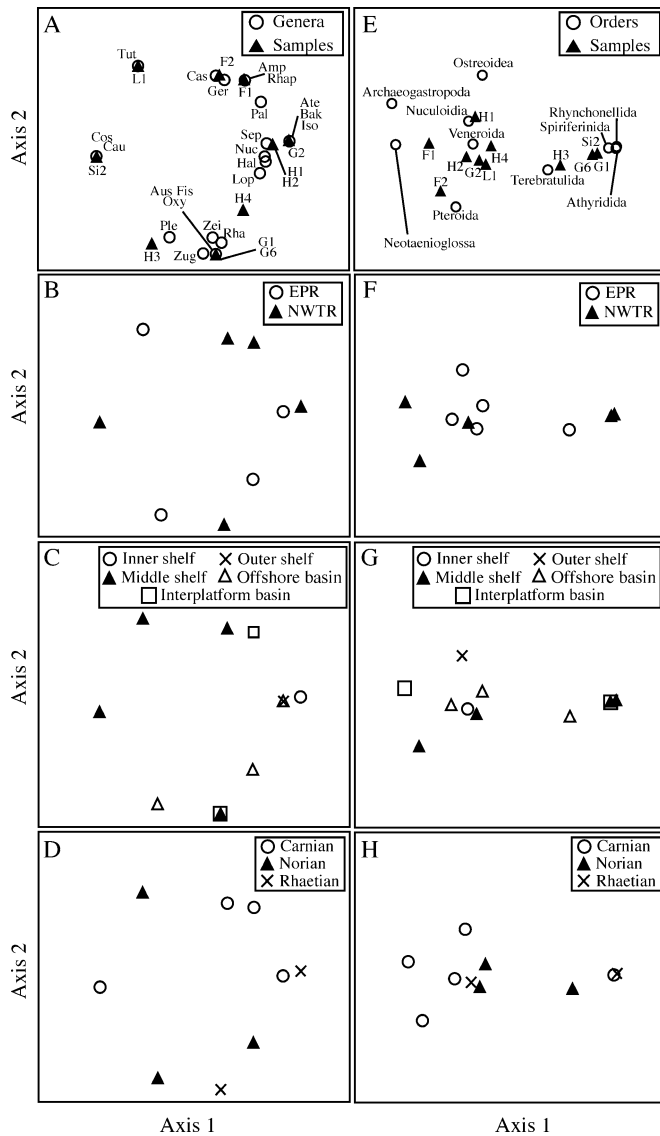


FIGURE 5—Late Triassic detrended correspondence analysis of samples. Relative abundance data of genera (A–D) and orders (E–H) are plotted. Samples and taxa are plotted together in ordinal space (A and E). Sample codes listed in Table 1, and genera codes are listed in Table 2. B–D) Genus-level ordination plots for samples grouped by (B) biogeography, (C) depositional environment, and (D) stratigraphic stage. F–H) Order-level ordination plots of samples grouped by (F) biogeography, (G) depositional environment, and (H) stratigraphic stage. NWTR = Northwestern Tethys Realm; EPR = Eastern Panthalassa Realm.

DISCUSSION

The Middle Triassic multivariate analyses indicate that paleogeographic variation between realms is the most important factor controlling differences among samples. At the scale of this study, depositional environment and stratigraphic position play a secondary role in the multivariate positioning of the samples. Differences between biogeographic realms are not attributed to geographic isolation because direct connections between the GESR, NWTR, and NETR existed during the Middle Triassic. As a result, two brachiopod genera are shared between biogeographic realms. For example, *Coenothyris* is in both GESR and NWTR samples, whereas *Mentzelia* is in both NWTR and NETR samples. All other taxa differ between samples within biogeographic realms. Perhaps this difference between samples is due to taxa selecting their biogeographic realm based on opportunity, much like Early Triassic brachiopod faunas. Recent work on brachiopod survival strategies suggest that certain surviving brachio-

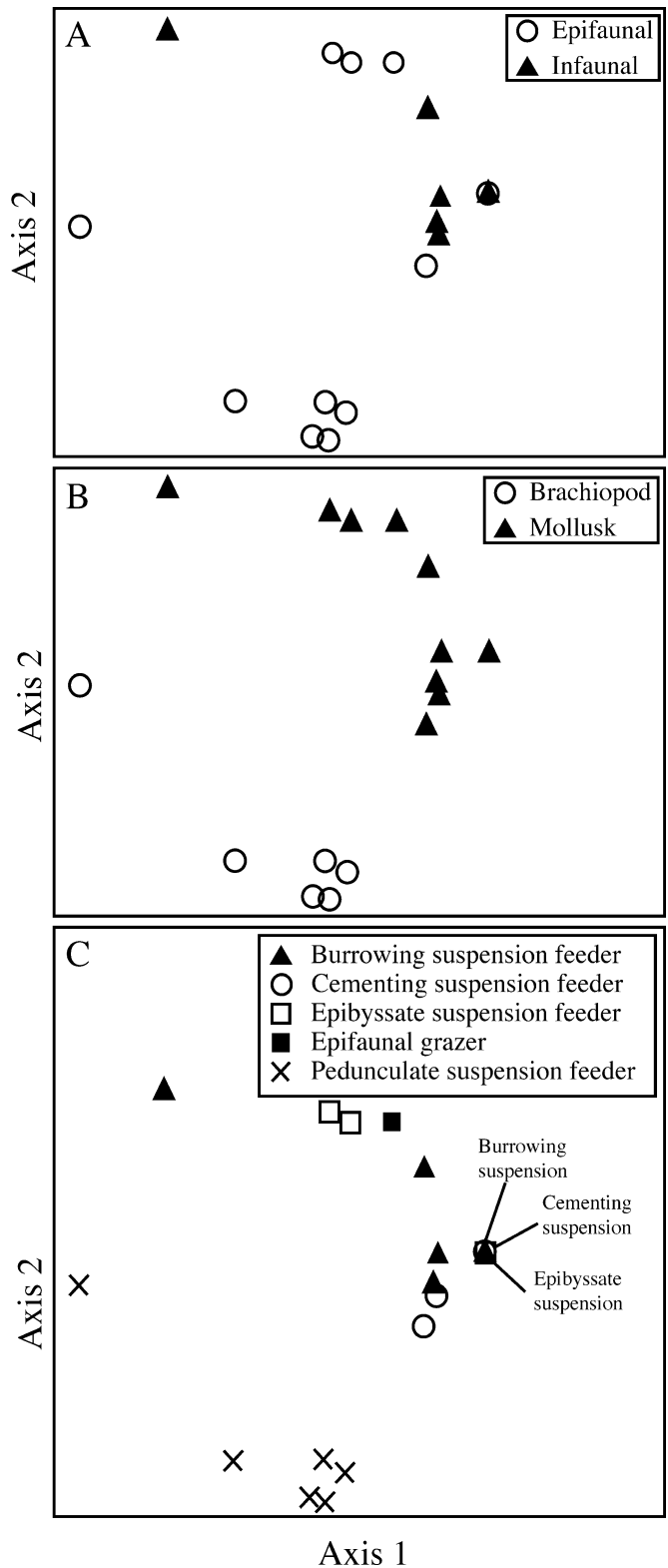


FIGURE 6—Late Triassic detrended correspondence analysis of genera. Ordination of genera grouped by (A) sediment preference, (B) faunal group (i.e., brachiopod and mollusk), and (C) ecological guild.

pod species prefer regions that were previously vacated by the end-Permian mass extinction or areas that were devoid of latest Permian taxa (Chen et al., 2005a, 2005b). The idea that biogeography selectivity occurs in the Middle Triassic, however, is speculative and beyond the scope of these data.

The poor quantitative discrimination of samples along the shelf most

TABLE 4—Multiresponse permutation procedure results for Late Triassic taxonomic a priori groups (* $\alpha = 0.05$).

Group comparison	T-Statistic	<i>p</i> value*
Genera		
Substrate (infaunal vs. epifaunal)	-6.04	0.001
Brachiopod vs. mollusks	-4.39	0.01
Taxa ecological guild	-3.17	0.01
Paleogeographic realms	-2.85	0.01
Lithostratigraphic stages	-2.35	0.02
Depositional environment	-0.44	0.30
Orders		
Paleogeographic realms	-1.27	0.11
Lithostratigraphic stages	-2.25	0.03
Depositional environment	0.60	0.67

likely reflects that sites were classified into very broadly defined environmental categories. As with sedimentary environment, stratigraphic position of the samples seems to be completely obscured by biogeographic variation. Perhaps the multivariate techniques fail to provide robust time indicators because only two samples are from the Ladinian stage, both of which come from the NWTR. While the results indicate that biogeography is important, the overlap and lack of significant difference between ecological guilds indicates that the general ecology between Middle Triassic samples remains similar through time.

Although the Middle Triassic analyses seem to agree, the Late Triassic multivariate analyses contrast one another. Ordinal results indicate that paleogeographic realms overlap, while the MRPP results indicate that the two realms differ significantly. These contrasting results might be a product of the different distance measures used by the two techniques; DCA uses chi square and MRPP uses Euclidean distance measure. Perhaps DCA is picking up on these similarities while MRPP is sensitive to the other taxa that are not shared between samples. We interpret these contrasting results as a signal that Late Triassic faunal patterns are more complex than Middle Triassic faunal patterns. Although recent work indicates that marine faunal abundance distributions increase in complexity within post-Paleozoic assemblages compared to Paleozoic assemblages (Wagner et al., 2006), our interpretations are tentative owing to the broad scale of this study. As an alternative, the conflicting results between DCA and MRPP could also be attributed to the limited number of samples within a priori groups. A greater number of samples within a priori groups would undoubtedly enhance the statistical validity of our data; however, until more samples are collected, we are limited to making broad-scale inquiries.

In sum, we conclude that biogeography is important in determining Late Triassic faunal patterns because only 4 taxa are shared out of 14 between biogeographic realms—*Cassianella*, *Nuculana*, *Zeilleria*, and *Zugmayerella*. Increased endemism is also supported by records of increased differentiation between brachiopod faunas due to extensive regression at the Norian-Rhaetian boundary, as well as the documentation of the first appearances of typical Mesozoic–Cenozoic brachiopod genera (Michalik, 1987; Golebiowski, 1989; Dagens, 1993).

Taxonomic ordination plots indicate a distinct separation between group membership. A clear line can be drawn between brachiopod and mollusk genera; MRPP results confirm this distinction. Although MRPP results indicate significant differences between sediment preferences, ordination results depict some overlap between epifaunal and infaunal taxa. Similar results appear within guild categories. Again, the two multivariate techniques could be picking up on complex aspects of faunal distributions equally as important to faunal patterns. Interestingly, both techniques indicate that brachiopods separate from mollusks and that pedunculate suspension feeders form a separate group from the rest of the ecological guilds, thus implying that the general ecology—the sum of abiotic and biotic factors—is extremely important in the distributions of Late Triassic

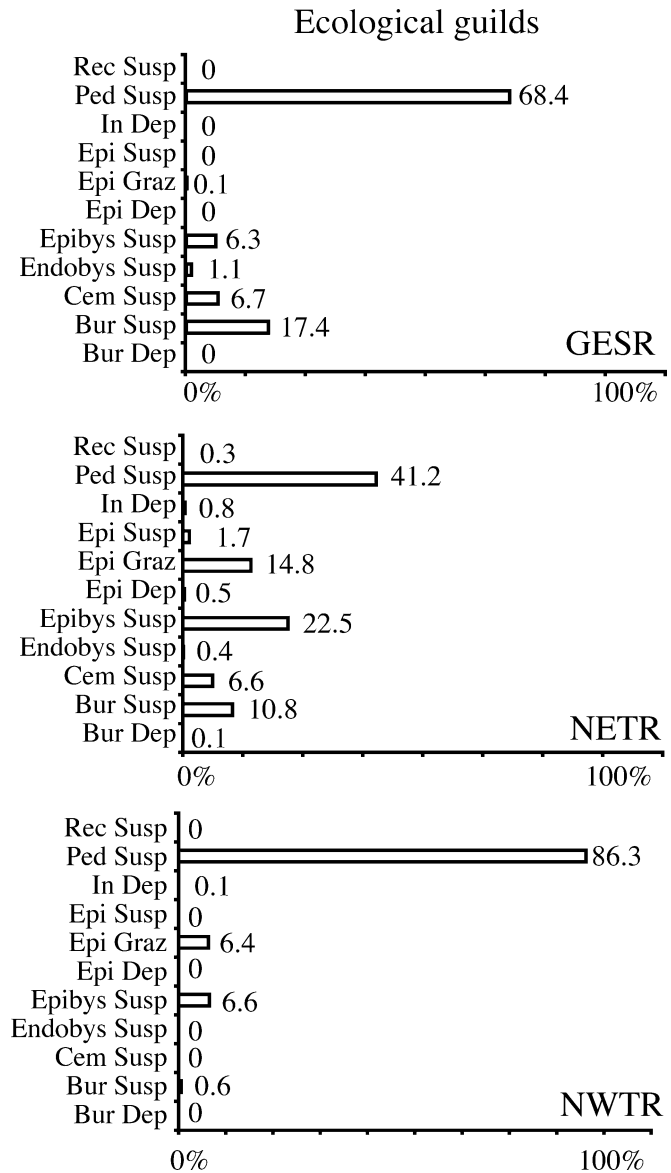


FIGURE 7—Middle Triassic guild structure and alpha diversity for the paleogeographic regions. GESR = Germanic Epicontinental Sea Realm; NETR = North-eastern Tethys Realm; NWTR = Northwestern Tethys Realm. Ecological guild abbreviations: Rec Susp = reclining suspension feeder; Ped Susp = pedunculate suspension feeder; In Dep = infaunal deposit feeder; Epi Susp = epifaunal suspension feeder; Epi Graz = epifaunal grazers; Epi Dep = epifaunal deposit feeders; Epibys Susp = epibyssate suspension feeders; Cem Susp = cementing suspension feeders; Bur Susp = burrowing suspension feeders; Bur Dep = burrowing deposit feeders.

samples. This is more evident when ecological guild structure is examined.

Early and Middle Triassic: Different Taxa but Similar Ecologies

One aspect of the reorganization between the Paleozoic and Modern faunas is the notable increase of infaunality. General discussion of this transition might leave some with the impression that this transition took place at the Paleozoic-Mesozoic boundary. In reality, this transition began later within the Late Triassic. Previous work recognizes the general lack of deep infaunal burrowers within the Early Triassic (Pruss, 2004; Pruss et al., 2005) and the trend of increasing infaunalization within the Late Triassic (Stanley, 1968, 1981; Thayer, 1979; Hallam, 1991; McRoberts, 2001).

Beginning with the survival interval of the end-Permian mass extinc-

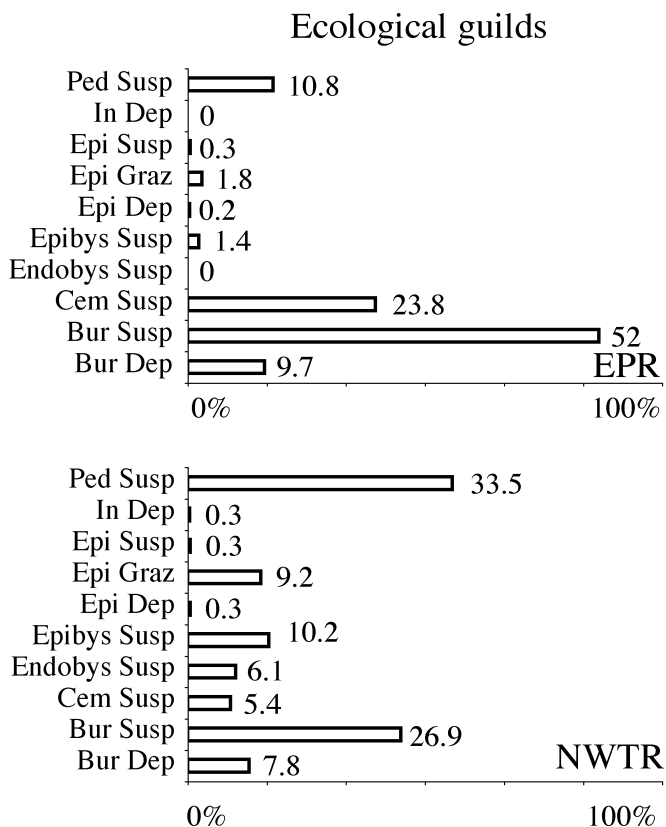


FIGURE 8—Late Triassic guild structure and alpha diversity for the paleogeographic regions. EPR = Eastern Panthalassa Realm; NWTR = Northwestern Tethys Realm. See Ecological guild abbreviations: Rec Susp = reclining suspension feeder; Ped Susp = pedunculate suspension feeder; In Dep = infaunal deposit feeder; Epi Susp = epifaunal suspension feeder; Epi Graz = epifaunal grazers; Epi Dep = epifaunal deposit feeders; Epibys Susp = epibyssate suspension feeders; Cem Susp = cementing suspension feeders; Bur Susp = burrowing suspension feeders; Bur Dep = burrowing deposit feeders.

tion, the fossil record indicates that epifaunal bivalves constitute one of the dominant Early Triassic groups of benthic taxa, many of which are considered low-oxygen and low-nutrient-tolerant organisms (Nakazawa and Runnegar, 1973; Waterhouse, 1983; Yin, 1985; Yang et al., 1986; Schubert and Bottjer, 1995; Twitchett, 1999; McRoberts, 2001; Twitchett et al., 2004; Fraiser and Bottjer, 2005, 2007). In fact, a variety of studies suggest that epifaunal bivalves tolerate stressed environments better than infaunal bivalves (Cranford and Grant, 1990; Jørgensen, 1990; McRoberts and Newton, 1995). Data from this study indicate that biogeography is important to brachiopod and bivalve abundance patterns and that general ecology remains the same throughout the Middle Triassic. Specifically, pedunculate suspension feeders, in this case epifaunal brachiopods, dominate all Middle Triassic regions, whereas epibyssate suspension feeders (i.e., epifaunal bivalves) constitute the second most dominant ecological guild.

Brachiopods, well known for their low-maintenance lifestyle, can survive poor environmental conditions, making them strong competitors in limited resource areas (Peck, 2001a, 2001b). The taxa, therefore, might differ between biogeographic realms, but the dominant ecological structure of the Middle Triassic remains similar: a stress-tolerant, epifaunal lifestyle, much like the dominant Early Triassic lifestyle, existed. This suggests that although diversity recovers at the Early-Middle Triassic boundary, the affects of the end-Permian mass extinction continued to shadow ecological patterns well into the Middle Triassic.

Late Triassic: Initiation of Ecological Change

From the Middle to the Late Triassic, our data reveal that Late Triassic faunal distributions become more complex as burrowing deposit and sus-

pension feeders (i.e., infaunal bivalves) as well as cementing suspension feeders (i.e., epifaunal bivalves) began to dominate ecological guilds. Both dominant life habits, infaunal and cementing, are considered defense strategies against shell crushing predators (Stanley, 1968, 1977; Harper, 1991). The appearance of different antipredatory adaptations within independent clades hints at increased predator pressures. While the initial cause of the Mesozoic marine revolution is debated (e.g., McRoberts, 2001), we show clear evidence that the abundance of infaunal and cementing life habits—modern Mesozoic marine revolution life habits—initiated within the Late Triassic much earlier than the original Jurassic prediction (Vermeij, 1977). Our Late Triassic ecological abundance patterns corroborate well with recent diversity studies (Stanley, 1968, 1972; McRoberts, 2001). Our study adds to these studies by substantiating that the abundance of infaunal habits increase beginning in the Late Triassic. In addition, reports of new ligament modifications within pteriomorph cementing bivalves, appearing in the Late Triassic, suggest that these modifications are an antipredator adaptation that effectively impedes valve shearing (Hautmann, 2004). Together, our study and previous studies provide compounding evidence that benthic fauna become more modernized within the Late Triassic. In addition, our results indicate that although infaunality increases on a global scale, spatial and temporal patterns differ between samples; therefore, local regions differ in the exact timing and initiation of modern life habits, in this case, infaunality. These initial results indicate that the transition from Paleozoic to modern faunas did not unfold simultaneously and in a coordinated fashion. Further studies are needed to understand the details surrounding this major ecological transition within the Late Triassic.

CONCLUSIONS

Recovery from the end-Permian mass extinction unravels in a very complex set of abiotic and biotic changes. Within this study, multivariate analyses and guild structure analysis reveal that brachiopod and bivalve abundance patterns vary in ecological structure and according to geographic location between the Middle Triassic and Late Triassic. Analysis reveals that biogeographic realms influenced the distribution of Middle Triassic samples and that depositional environment and stratigraphic position play a secondary role in sample distribution. In addition, both multivariate and ecological guild structure analyses indicate that Middle Triassic ecology remains generally the same across spatial and temporal fields, primarily consisting of epifaunal lifestyles or a more Paleozoic-type lifestyle. The Late Triassic proves to be more complex in terms of ecology compared to the Middle Triassic. Here, biogeography, stratigraphic position, and such ecological factors as sediment preference and guild structure all influence brachiopod and bivalve patterns significantly. We conclude from the Late Triassic results that this increase in ecological complexity records the initiation of the transition from Paleozoic lifestyles to the more modern lifestyle of today's oceans.

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