

PART N, REVISED, VOLUME 1, CHAPTER 25: EARLY TRIASSIC–EARLY JURASSIC BIVALVE DIVERSITY DYNAMICS

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INTRODUCTION

Bivalves are a highly diversified molluscan class, with a long history dating from early Cambrian times (COPE, 2000). Although the group already showed a steady diversification trend during the Paleozoic, it only became highly successful and expanded rapidly from the Mesozoic onward. The Triassic was, for bivalves, first a recovery period and later a biotic diversification event. It was also the time bivalves first fully exploited their evolutionary novelties.

Whereas brachiopods are typical elements of the Paleozoic Fauna (*sensu* SEPKOSKI), bivalves belong to the Modern Fauna, characterized by a dramatic increase in diversification rates just after the Permian (SEPKOSKI, 1981, 1984). The Permian/Triassic (P/T) extinction did not affect bivalves to the same degree that it affected many other marine invertebrate groups (YIN HONG-FU, 1985; ERWIN, 1993). Furthermore, during the Triassic, bivalves underwent an extraordinary evolutionary radiation, due, in part, to mantle fusion and siphon development (STANLEY, 1968), which allowed them to fully exploit infaunal niches unfilled by both bivalves and brachiopods during the Paleozoic. This evolutionary radiation coincided with a relatively warm Triassic–Jurassic episode in Earth history, when latitudinal climatic gradients were moderate and polar ice was virtually nonexistent (HALLAM, 1982; SEPTON & others, 2002).

The Triassic is bounded by two severe biotic crises: the Permian/Triassic (P/T) and Triassic/Jurassic (T/J), both of which are included in the so-called big five extinction events, which had devastating

effects on a global scale (NEWELL, 1967; RAUP & SEPKOSKI, 1982). The P/T extinction event was the most severe biotic crisis in the history of life on Earth (RAUP, 1979; RAUP & SEPKOSKI, 1982; ERWIN, 1993, 2006), not only in terms of taxonomic losses, but also in terms of the drastic reorganization of marine ecosystems (ERWIN, 2006; WAGNER, KOSNIK, & LIDGARD, 2006). The subsequent recovery of ecosystems was slow, compared with other extinction events (ERWIN, 1998), and did not end until Middle Triassic times (ERWIN, 1993; BENTON, 2003).

From a paleoecologic viewpoint, bivalves (together with brachiopods, although the latter were disproportionately decimated) were the main shelled invertebrates to use both epifaunal and infaunal strategies during the recovery of the P/T (BOTTJER & others, 2001). Bivalves became the dominant shelled marine invertebrates in benthic communities during the earliest Triassic, replacing the role previously played by brachiopods (FRAISER & BOTTJER, 2007), although their abundance had already considerably increased during the late Permian (CLAPHAM & BOTTJER, 2007). A bivalve diversification phase began during the Anisian, early Middle Triassic, and continued into the Late Triassic (with a diversity peak during the Norian), when extinction played an important role once more (MCROBERTS, 2001; ROS, 2009). The T/J extinction event was less important than the previous one, and, according to BAMBACH, KNOLL, and WANG (2004) and LUCAS and TANNER (2008), it unfolded during the entire Late Triassic. These authors concluded that it reflects high

extinction and low origination rates. Its intensity may be overestimated due to the compiled correlation effect of imprecise stratigraphic data, the Signor-Lipps effect (SIGNOR & LIPPS, 1982) and extrapolation of local data to a global scale (LUCAS & TANNER, 2008). On the other hand, HALLAM (1981, 2002) recognized a single extinction event at the end of the Triassic. The real magnitude of this T/J extinction event is difficult to evaluate due to the widespread facies changes that characterize the T/J boundary (JABLONSKI, 2005), with the disruption of calcareous sedimentation by dominant siliciclastic deposits, which do not favor the preservation of calcareous skeletons (HAUTMANN, 2004).

The earliest Jurassic saw a new biotic recovery period that, although not as well studied as the one in the Triassic, was apparently faster. Already during the Hettangian, the initial stage of the Jurassic, significant diversification is observed among marine invertebrates, culminating during the Pliensbachian, middle Early Jurassic, with the reappearance of reef organisms (HALLAM & WIGNALL, 1997).

There are three main issues related to the history of marine life after the Paleozoic: the environmental conditions near the P/T boundary, the end-Permian extinction, and the Mesozoic Marine Revolution (MMR) (VERMEIJ, 1977; FRAISER & BOTTJER, 2007). This chapter will deal with these and other topics related to the evolution of bivalve diversity from the beginning of the Mesozoic. We cover the interval of time from just after the P/T extinction (Induan, earliest Triassic) to the T/J recovery in the Sinemurian, Early Jurassic. We will deal not only with taxonomic diversity dynamics, but also with the evolution of bivalve ecospace during this period, with special emphasis on the T/J extinction. An important aspect of this chapter is the infaunalization observed during the Late Triassic (MCROBERTS, 2001) and later times (ABERHAN, KIESSLING, & FURSICH, 2006), and its relation to the MMR.

DATA AND METHODS

The data for this chapter were compiled by ROS (2009), and include stratigraphic ranges, paleogeographic distributions, autoecology, and shell mineralogy for all marine bivalve genera during the Induan–Sinemurian study interval. Data were compiled from all available literature containing descriptions and/or illustrations of bivalves for this interval, with generic assignments revised where needed. In addition, some stratigraphic ranges reflect data from DIENER (1923), KUTASSY (1931), COX and others (1969), VOKES (1980), SEP Koski (2002), the *Zoological Record*, and the Paleobiology Database (PBDB; <http://www.paleodb.org/>), among other sources, when it was not possible to find other sources of literature.

Genera were assigned to families following COX and others (1969) and more recent literature, when available. We follow the systematic arrangement by AMLER (1999) and AMLER, FISCHER, and ROGALLA (2000), with some modifications discussed in ROS (2009). For the purposes of this paper, this classification does not differ significantly from the scheme proposed more recently for the *Treatise on Invertebrate Paleontology*, Part N (revised), by CARTER and others (2011).

We used GRADSTEIN and OGG (2004) for numerical ages. Different time scales in the analyzed papers were updated using the conversion tables in PBDB and GeoWhen (<http://www.stratigraphy.org/geowhen/index.html>). A special problem was the time value of Rhaetian faunas in papers published prior to the redefinition of this stage by DAGYS and DAGYS (1994). The Kössen Formation in Austria, the Gabbs Formation in the United States, and the Otapirian deposits in New Zealand at least were considered to be truly Rhaetian in age (DAGYS & DAGYS, 1994; HALLAM, 2002). The time ranges used here are observed ranges defined by first appearances (FADs) and last appearances (LADs) and are therefore only proxies for actual origination and extinction times. Sample biases, stratigraphic

gaps, regression and transgression effects, and many other factors can affect first and last appearances (HOLLAND, 1995). It should be remembered that bivalve temporal ranges are especially influenced by lithologic facies.

Paleoecologic data were framed, with some adjustments discussed later, into BAMBACH, BUSH, and ERWIN (2007) ecospace, which considers three main factors: relationship with the water column/substrate, feeding type, and degree of motility/fixation. Each genus was assigned to a living strategy (ROS, 2009; annex fig. 5.6, p. 482–484; and see Table 1 and Fig. 13). Taxonomic data were also classified according to relation with the substrate (epifaunal or infaunal). Endobysate semi-infaunal bivalves were grouped with infauna, while free-lying bivalves with heavy shells and semi-infaunal habits (e.g., some megalodontids) were grouped with epifauna.

TAPHONOMY AND DIVERSITY

Evolutionary readings of the fossil record should be preceded by a consideration of the taphonomic factors that can distort or disguise interpretations of paleobiologic processes (DE RENZI, 1992). Shell mineralogy, shell size, and even the scale of geographic and stratigraphic sampling can potentially compromise interpretations of the fossil record.

Shell Mineralogy

The effect of rarefaction by geologic age must also be considered, and this probably affects the more ancient fossil record (RAUP, 1976a, 1976b; RAUP & STANLEY, 1978; DE RENZI, 1992). Rarefaction by age can produce bias against aragonitic shells, and this bias could potentially influence the Triassic fossil record (DE RENZI & ROS, 2002; ROS & DE RENZI, 2005). Bivalve shells can be entirely aragonitic, calcitic except for aragonitic myostracal (muscle scar) and ligament mineralization, or any proportion of aragonite and calcite in the major shell layers (CARTER, 1990). The differential solubility of aragonite and calcite (KERN & WEISBROD, 1964;

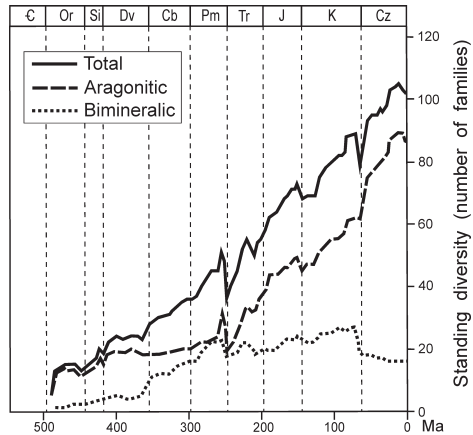


FIG. 1. Diversity of bivalve families according to shell mineralogy; C, Cambrian; Or, Ordovician; Sl, Silurian; Dv, Devonian; Cb, Carboniferous; Pm, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Cz, Cenozoic (adapted from Ros & De Renzi, 2005).

ROLFE & BRETT, 1969; MORSE, MUCCI, & MILLERO, 1980; KIDWELL, 2005) can result in underestimation of aragonitic bivalve diversity (HARPER, 1998; DE RENZI & ROS, 2002; BUSH & BAMBACH, 2004; ROS & DE RENZI, 2005; VALENTINE & others, 2006). Inorganic calcite is 35% less soluble than aragonite, but other factors, such as crystal size and shape (HARPER, 2000; VALENTINE & others, 2006) and the amount of organic matter (HARPER, 2000) can also influence solubility. However, KIDWELL (2005) did not find a significant mineralogical effect on estimates of family-level bivalve diversity in the fossil record. The plesiomorphic condition in the Bivalvia is entirely aragonitic shells. Bivalves are presently divided into two categories: aragonitic and bimineralic. Bivalves with even a thin calcitic outer shell layer, such as many Paleozoic pterioids and pectinoids, were classified as bimineralic because such a layer increases their preservational potential. As shown in Figure 1, richness of aragonitic bivalves grows remarkably slower than that of bimineralic ones. This difference between rates, however, can reflect the aragonite bias. This figure also shows that aragonitic families increased at a more rapid

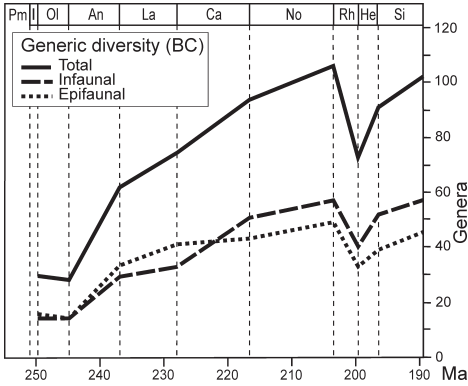


FIG. 2. Bivalve generic diversity (boundary crosser estimation) during the Induan–Sinemurian for infaunal, epifaunal, and all life strategies; *Pm*, Permian; *I*, Induan; *Ol*, Olenekian; *An*, Anisian; *La*, Ladinian; *Ca*, Carnian; *No*, Norian; *Rh*, Rhaetian; *He*, Hettangian; *Si*, Sinemurian (data from Ros, 2009).

pace than the bimineralic ones throughout the Mesozoic, although the aragonitic ones may be underrepresented.

Substrate Relationship and Shell Size

Relationship to the substrate apparently does not influence family-level diversity estimates in the fossil record (HARPER, 2000; ROS & DE RENZI, 2005), but there is a negative bias against smaller bivalves (COOPER & others, 2006). This is a serious problem for analyzing diversity just after an extinction, since organisms tend to be smaller during survival and recovery stages (the so-called Lilliput effect; see TWITCHETT, 2006). Bivalve diversity could therefore be underestimated for the Early Triassic because of this bias (HAUTMANN & NÜTZEL, 2005).

Geographic and Stratigraphic Range

Geographically restricted taxa are more likely to be overlooked in the fossil record, thereby leading to underestimations of diversity (VALENTINE & others, 2006; ROS, 2009). The same applies to taxa with more restricted stratigraphic ranges: the longer the stratigraphic range, the more likely a taxon is to be recorded. Furthermore, time and geographic range appear to be positively correlated (MILLER & FOOTE, 2003; FOOTE & others, 2008).

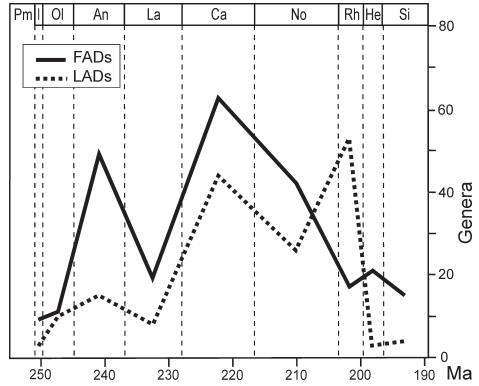


FIG. 3. First appearances (LADs), and last appearances (FADs), during the Induan–Sinemurian; see Figure 2 for key to abbreviations (adapted from Ros, 2009).

INDUAN–SINEMURIAN TAXONOMIC DIVERSITY DYNAMICS

Standing Generic Diversity

Total bivalve generic diversity (boundary crosser estimation) steadily increased from the Induan, earliest Triassic, to the Norian, middle Late Triassic (Fig. 2). The total number of genera then diminished through T/J and then rose again during the Early Jurassic. Generic first appearances (FADs) reached a maximum in the Carnian (63 genera), then diminished to a minimum during the Rhaetian (Fig. 3). The trend of last appearances (LADs) follows that of FADs from Induan to Norian, but differs from FADs by peaking in the Rhaetian (Fig. 3). Not all bivalve orders contributed equally to this diversity change (Fig. 4). Pectinida, Pteriida, Venerida, and Trigoniida are the most diverse orders during the study interval. The first two are mostly epifaunal bivalves whose orders were well represented in the Paleozoic and reached a diversity peak during the Carnian, with a slight decrease from then on. Other, mainly infaunal orders, such as Venerida, progressively increased in generic diversity through the entire interval, with only a slight decrease

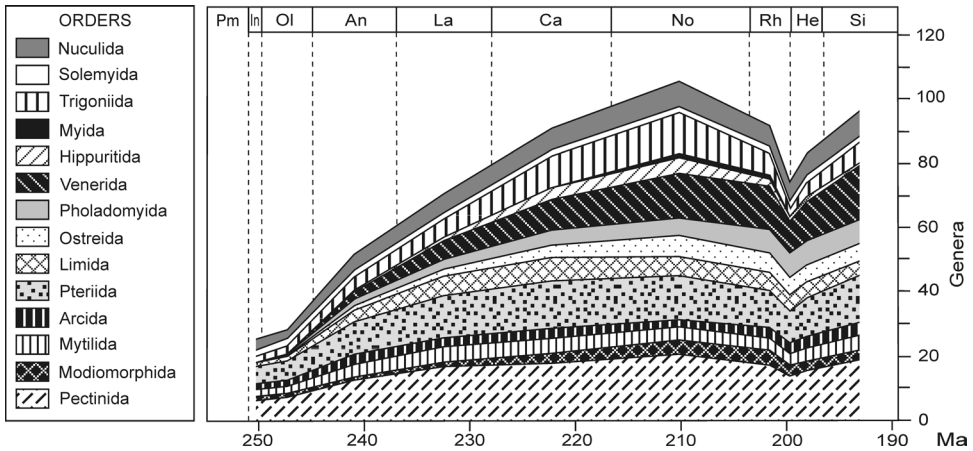


FIG. 4. Bivalve generic diversity (Mean Standing Diversity and Boundary Crosser in T/J limit) by order during the Induan–Sinemurian. In the order Hippuritida, all Triassic genera went extinct at the T/J boundary, but the order reappeared in the Sinemurian with *Pachyrisma*; see Figure 2 for key to abbreviations (data from Ros, 2009).

at the T/J boundary. The Trigoniida also increased during all of the Triassic then clearly declined in generic diversity at the T/J boundary.

When infaunal and epifaunal bivalves are analyzed separately (Fig. 2), epifaunal generic diversity is slightly greater than infaunal diversity until the Carnian, when both lines intersect, and from then onward to the present, infaunal bivalves are always more diverse than epifaunal ones. Note that the diversity of epifaunal and infaunal bivalves decreases in parallel, with infaunal diversity remaining greater than epifaunal diversity. During the study interval, generic diversity climaxed during the Norian. The diversity of each group declined after its maximum until the end of the Rhaetian.

Evolutionary Rates

Origination rates during the Triassic show an overall diminishing trend (Fig. 5), with three successively lower peaks (Induan, Anisian, Carnian), then decreasing from the Carnian to a minimum just at the Norian. Then, it began to grow until the T/J boundary and increased sharply during the Hettangian. Infaunal generic origination rates are greater than epifaunal ones from the Carnian onward (Fig. 6.2). During the

Hettangian, although both infauna and epifauna show a peak, origination rates are significantly greater for the infauna.

A peak in extinction rates during the Induan stage is entirely due to a decline in epifaunal genera, and its high value is probably influenced by the short duration of the stage and the small number of surviving taxa (Fig. 6.1). This value is only exceeded in Rhaetian times (also a short stage), when as many as 53 genera disappeared (42%). After the Induan stage, generic extinction rates show a decreasing trend until Ladinian, after which there are 2 peaks: the first during

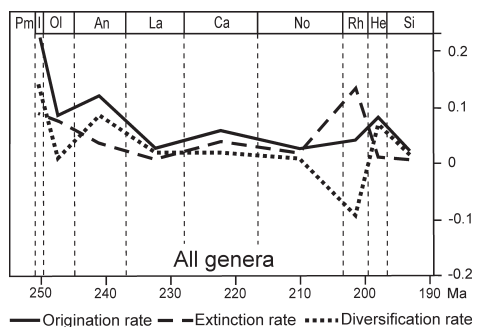


FIG. 5. Bivalve evolutionary rates for the Induan–Sinemurian interval for total bivalve genera; see Figure 2 for key to abbreviations (data from Ros, 2009).

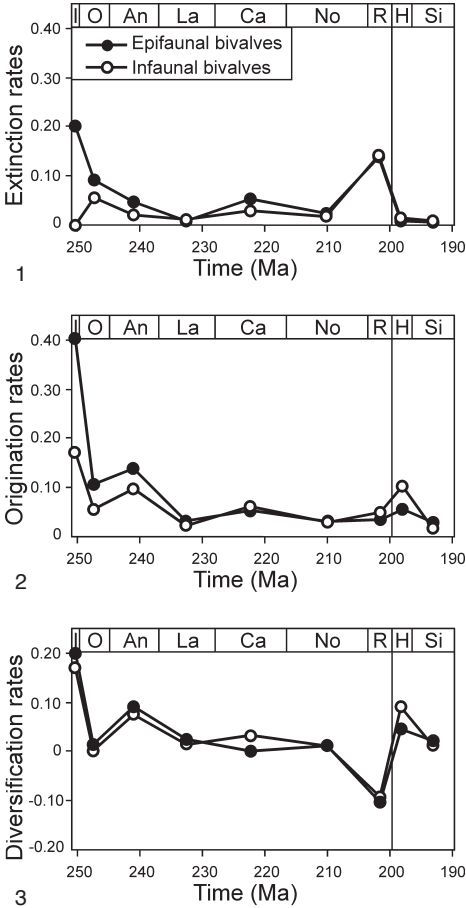


FIG. 6. Evolutionary rates of epifaunal and infaunal bivalves. 1, Extinction rates; 2, origination rates; 3, diversification rates; see Figure 2 for key to abbreviations (data from Ros, 2009).

the Carnian and the second (larger) during the Rhaetian (Fig. 5). In the Anisian and Carnian, the generic extinction rate was particularly severe for epifaunal taxa, among which most genera were represented by a single species, but it was similar for both collectives during the T/J event (Fig. 6.1).

Within the Triassic, the Carnian is characterized by a maximum diversification rate for infaunal genera relative to epifaunal genera (Fig. 6.3). The generic diversification rate is positive during the Triassic except around the T/J boundary, when a negative value is observed, with epifauna declining faster than

infauna due to a greater origination rate of this collective during the Rhaetian. During the Hettangian, infaunal generic diversification rates were far greater than for epifauna.

New Taxa

The preceding analyses indicate that one of the most significant events in the history of Triassic–Early Jurassic bivalve diversity was the change from an epifauna-dominated to an infauna-dominated fauna (Fig. 2). Considering only the genera with Induan to Sinemurian FADs, the number of originations for infaunal bivalves greatly exceeded that of epifaunal bivalves from the Carnian onward (Fig. 7–8).

When one examines the fate of stage-delimited cohorts of bivalve genera originating in the Triassic (Fig. 9–12), the Early and Middle Triassic cohorts are most stable, with the exception of the Olenekian cohort, which underwent three extinction events, at T/J boundary, in the Late Jurassic, and in the Early Cretaceous. After steadily diminishing throughout the Triassic, the Anisian and Ladinian Middle Triassic cohorts suffered no major losses until the K/T extinction (Fig. 10). In contrast, the Carnian, Norian, and Rhaetian Late Triassic cohorts show more pronounced decay during the Jurassic and the Cretaceous, culminating in profound losses during the K/T

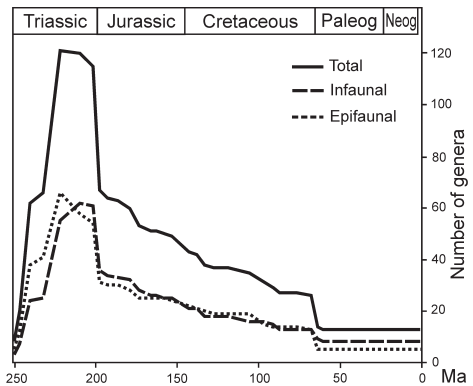


FIG. 7. Bivalve genera originating during the Triassic (Induan–Rhaetian) and their fate since the Hettangian times; *Paleog*, Paleogene; *Neog*, Neogene (data and figure from Ros, 2009).

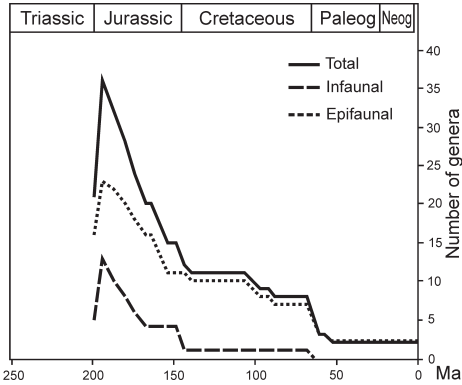


FIG. 8. Bivalve genera originating during the Hettangian and Sinemurian Early Jurassic, and their fate since the Pliensbachian; *Paleog*, Paleogene; *Neog*, Neogene (data and figure adapted from Ros, 2009).

extinction (Fig. 11). The differential success of the earlier and later Triassic generic cohorts may reflect the progressive biotic filling up of ecospace, with a parallel increase in competition (DE RENZI & ROS, 2004; HAUTMANN, 2007), and the resultant progressive increase in origination rates of stenocore genera, with smaller geographic distributions and shorter durations (ROS, 2009). Interestingly, the Hettangian and Sinemurian Early Jurassic generic cohorts show a stability intermediate between the Early and Late Triassic cohorts, comparable to the Middle Triassic cohorts (Fig. 12). This may reflect the different intensity of the P/T and T/J extinction events. This pattern confirms the observation by MILLER and FOOTE (2003) that marine post-Paleozoic taxa originating during recovery periods tend to persist longer than others.

INDUAN–SINEMURIAN BIVALVE ECOSPACE DYNAMICS

Much has been written about long-term changes in the use of ecospace by marine invertebrates, especially in relation to the decline of the Paleozoic fauna and the rise of the modern fauna (BAMBACH, 1983; BOTTJER, SCHUBERT, & DROSER, 1996; CLAPHAM & BOTTJER, 2007). Such analyses can help identify the traits that have been important in bivalve evolutionary dynamics, and

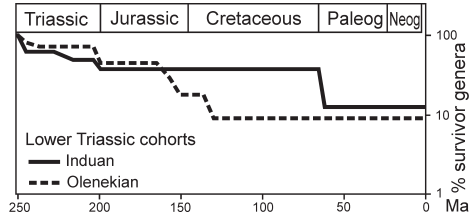


FIG. 9. Bivalve genera originating during the Early Triassic (Induan and Olenekian cohorts) and their subsequent fate; *Paleog*, Paleogene; *Neog*, Neogene (data and figure adapted from Ros, 2009).

perhaps point to ecological factors during the T/J extinction. We have analyzed bivalve ecospace utilization during the Induan–Sinemurian interval.

TRIASSIC–EARLY JURASSIC BIVALVE ECOSPACE CATEGORIES

The presently utilized ecospace categories for the Triassic and Early Jurassic are: tiering (epifaunal, semi-infaunal, shallow infaunal, deep infaunal), motility level (fast motile, slow motile, facultative attached, facultative unattached, sedentary attached, sedentary unattached), and feeding strategy (suspensivorous, detritivorous) (Table 1). These categories differ slightly from those proposed by BAMBACH, BUSH, and ERWIN (2007) for all marine animals, and from the so-called Bambachian megaguilds of DROSER, BOTTJER, and SHEEHAN (1997). BAMBACH, BUSH, and ERWIN (2007) divided ecospace by feeding type, degree of mobility or attachment, and tiering. Unlike BAMBACH, BUSH, and

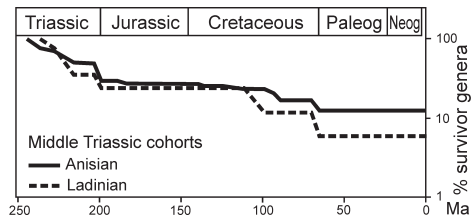


FIG. 10. Bivalve genera originating during the Middle Triassic (Anisian and Ladinian cohorts) and their subsequent fate; *Paleog*, Paleogene; *Neog*, Neogene (data and figure adapted from Ros, 2009).

TABLE 1. Ecologic categories for tiering, motility level, and feeding mechanism recognized here for bivalves. The main differences with the invertebrate ecospace of BAMBACH, BUSH, and ERWIN (2007) are: (1) only four tiering categories are considered, because no bivalves with pelagic or erect mode of life are known; (2) motility level: the two first categories only include burrowing bivalves, because they are the only ones that can move continuously, and the other four categories are always for epifaunal or semi-infaunal bivalves; (3) feeding mechanism: only two categories are considered, because no other mechanisms are inferred in bivalves from the study time interval (adapted from Bambach, Bush, & Erwin, 2007).

Category	Description
Tiering	
Epifaunal	Benthic, living above substrate or water interface
Semi-infaunal	Partly infaunal, partly exposed to the water column
Shallow infaunal	Infaunal, living in the top 5 cm of the substrate
Deep infaunal	Infaunal, living more than 5 cm deep in the substrate
Motility level	
Fast motile	Fast burrower
Slow motile	Slow burrower
Facultative, unattached	Reclined free-lying with ability to swim
Facultative, attached	Byssate with ability to swim or pseudoplanktonic
Nonmotile (sedentary), unattached	Not capable of self-propulsion, free-lying, reclined
Nonmotile (sedentary), attached	Not capable of self-propulsion, attached (cemented or byssate)
Feeding mechanism	
Suspension feeder	Capturing food particles from the water
Deposit feeder	Capturing loose particles from the substrate

ERWIN (2007), we use only four categories of tiering because no Triassic or Early Jurassic bivalves with pelagic or erect life habits are known. Also, our motility category is restricted to burrowers and swimmers (with swimmers being regarded as facultative motile) in relation to epifaunal and infaunal strategies, and our feeding category is restricted to suspensivores and detritivores. Carnivorous bivalves (e.g., Septibranchia) did not appear until the Middle Jurassic. Burrowing mobility is presently divided into fast and slow, as

suggested by shell morphology, but fast-burrowing bivalves did not appear until the Cenozoic (CHECA & JIMÉNEZ-JIMÉNEZ, 2003). Only adult life habits are presently considered, because some bivalves change their mode of life during ontogeny.

In order to examine trends in ecospace utilization among Induan–Sinemurian bivalves, we recorded the boundary crosser estimate of generic diversity by stage representing each life habit category (for details see ROS, 2009; fig. 5.6, p. 481–484; and see Fig. 13–14).

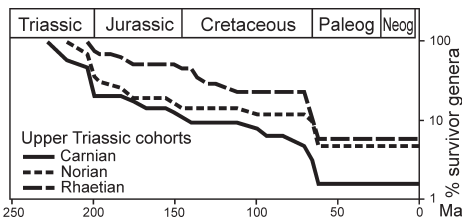


FIG. 11. Bivalve genera originating during the Late Triassic (Carnian, Norian, and Rhaetian cohorts) and their subsequent fate; *Paleog*, Paleogene; *Neog*, Neogene (data and figure adapted from Ros, 2009).

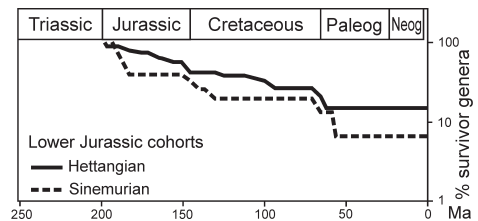


FIG. 12. Bivalve genera originating during the Early Jurassic (Hettangian and Sinemurian cohorts) and their subsequent fate; *Paleog*, Paleogene; *Neog*, Neogene (data and figure adapted from Ros, 2009).

Variations in the Ecospace Utilization

All life strategies followed by Induan bivalves were already occupied during the Permian. Therefore, Induan ecologic biodiversity reflects only the life strategies persisting after the P/T crisis. The best represented of these is suspensivorous, epifaunal, sedentary attached taxa, most of which were epibyssate (Fig. 14.1–14.2). The epibyssate and shallow burrowing life habits (comprising several ecospace categories) are the most diverse life strategies during the Induan stage. The cemented mode of life is represented during Induan time only by *Pegmavalvula*, which did not survive into the Middle Triassic (NEWELL & BOYD, 1995). However, cemented genera subsequently diversified in the Middle and Late Triassic when epibyssate genera decreased in diversity (Fig. 14.2).

During the Olenekian stage, two Permian life strategies reappeared: deep burrowers, represented by *Pleuromya*, and epifaunal, sedentary, unattached bivalves, represented by *Bositra*. Bivalves using the former strategy became increasingly diverse during the Triassic and Jurassic, and they were only barely affected by the end-Triassic extinction (one genus lost) (Fig. 14.5). However, epifaunal, sedentary, unattached bivalves peaked during the Norian, were reduced in generic diversity during the Rhaetian, and then remained roughly constant to the Sinemurian (Fig. 14.1). The reclining mode of life, including free epifaunal and semi-infaunal, nonmotile, unattached forms, increased in diversity up to the Late Triassic (Fig. 14.1 and 14.6). Semi-infaunal bivalves reach a maximum in the Norian, only to disappear altogether at the end of the Rhaetian (all Triassic forms). Nevertheless, the latter strategy was resumed in the Hettangian by *Weyla* and in the Sinemurian by *Weyla* and *Pachyrisma*.

During the study interval, endolithic bivalves first appeared in the Late Triassic, probably in the Norian (KLEEMANN, 1994). They are here gathered with deep burrowers,

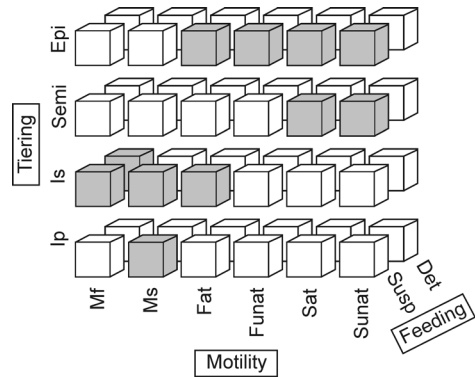


FIG. 13. Theoretic bivalve ecospace in the Induan–Sinemurian interval defined by the three variables (with their categories): tiering (Epi, Semi, Is, Ip), motility level (Mf, Ms, Fat, Funat, Sat, Sunat), and feeding strategy (Susp, Det). The strategies occupied by bivalves are colored; *Susp*, suspensivorous; *Det*, detritivorous; *Epi*, epifaunal; *Semi*, semi-infaunal; *Is*, shallow infaunal; *Ip*, deep infaunal; *Mf*, fast motile; *Ms*, slow motile; *Fat*, facultative attached; *Funat*, facultative unattached; *Sat*, sedentary attached; *Sunat*, sedentary unattached (new).

because deep infaunal habitat and boreholes produced by endolithic activity are both safe places. Facultative mobile, infaunal, attached (endobyssate) genera had Carnian first records, and they were represented by some Kalenteridae and Carditidae, which probably could burrow but spent almost all their lives being endobyssate. However, the latter strategy was apparently not very successful just after the Rhaetian, being occupied in the Hettangian and Sinemurian by only one genus, *Kalentera* (Fig. 14.4).

Among infaunal bivalves, the most successful strategy seems to have been suspensivorous, shallow burrowers, although this was severely reduced by the end-Triassic crisis (Fig. 14.4). Detritivores were always less abundant than suspensivores during the study interval (Fig. 14.3). Fast burrowers (either suspensivorous or detritivorous) were more seriously impacted by the T/J extinction than slow burrowers (Fig. 14.3–14.4).

Tiering

During the P/T extinction, epifaunal tiering considerably decreased in soft bottom

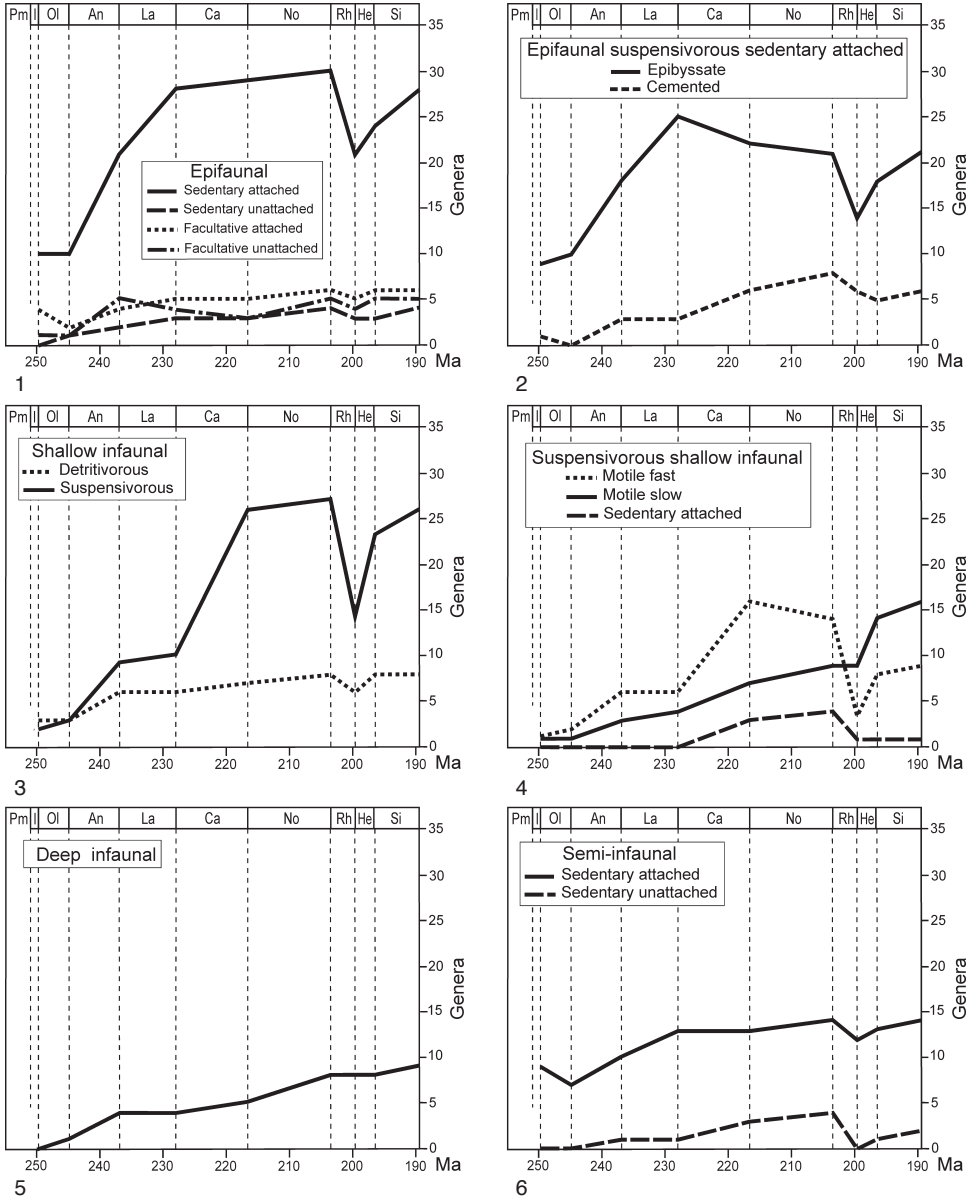


FIG. 14. Ecospace occupied by Induan–Sinemurian bivalves. The generic diversity (Boundary Crosser estimation) corresponding to each life strategy is shown by stage. 1, Epifaunal; 2, epifaunal, suspensivorous, sedentary (nonmotile), attached strategy decoupled in terms of cemented and epibyssate animals; 3, shallow infaunal; 4, suspensivorous shallow infaunal; 5, deep infaunal; 6, semi-infaunal; see Figure 2 for key to abbreviations (data from Ros, 2009).

suspensivorous communities (BOTTJER & AUSICH, 1986; BOTTJER, SCHUBERT, & DROSER, 1996; AUSICH & BOTTJER, 2001). Infaunal tiering also declined, at least in the equatorial realm (KNAUST, 2010), and this is

coincident with the absence of deep infaunal burrowers during Induan times. Nevertheless, tiering rapidly recovered to Permian levels and was not affected by the T/J extinction (AUSICH & BOTTJER, 2001) (Fig. 14.5).

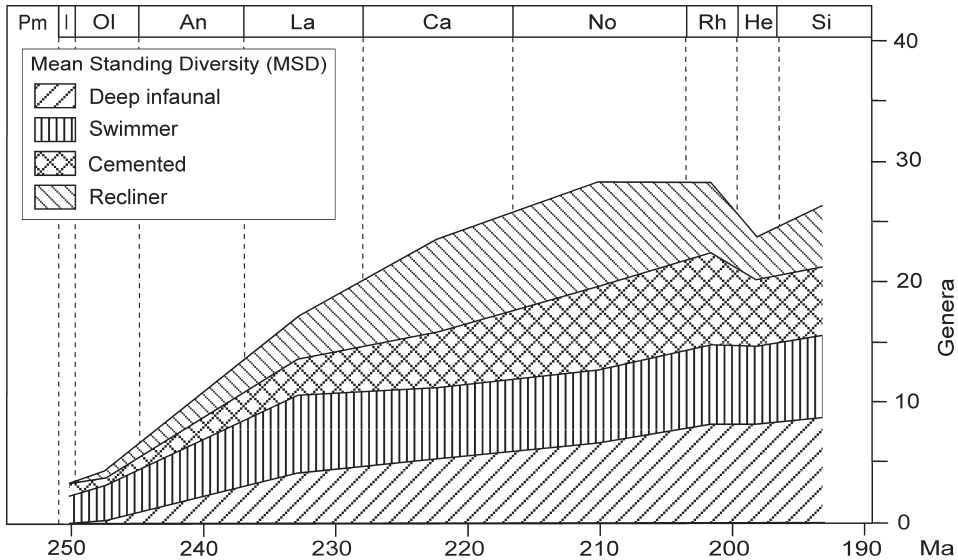


FIG. 15. Generic diversity (Mean standing diversity) trends for four composite life strategy categories during the Induan–Sinemurian. Reclined bivalves are all suspensivorous, sedentary (nonmotile), and unattached, and include epifaunal and semi-infaunal taxa. Swimming bivalves are all suspensivorous and epifaunal and include facultative attached and facultative unattached taxa. Cemented bivalves are all suspensivorous, epifaunal (nonmotile), and attached. Deep burrower bivalves are all suspensivorous, deep infaunal, slow motile taxa; see Figure 2 for key to abbreviations (new).

Deep infaunal tiering was, for bivalves, one of the most stable ecologic categories during the study interval. The reinstallation of tiering is a good measure of recovery after extinction (TWITCHETT, 1999), and during the Anisian Middle Triassic, deep burrowing bivalves reappeared and diversified.

Bivalves occupy only the lowest levels of epifaunal tiering, but they can be secondary tierers, using skeletons of primary tierers to lift themselves above the substrate, thereby reaching elevations up to 20 cm (BOTTJER & AUSICH, 1986). Cemented and occasionally swimming byssate bivalves increased throughout the study interval (Fig. 14.1–14.2, Fig. 15). In comparison with brachiopods, which developed only very slight tiering throughout the entire Phanerozoic (between -6 cm and $+5$ cm; BOTTJER & AUSICH, 1986), bivalves came to occupy the deepest infaunal levels, down to -100 cm (AUSICH & BOTTJER, 1982) due to siphon development (STANLEY, 1968, 1977). Thus, Triassic bivalves occupied tiering ecospace

vacated during the Early Triassic, whereas brachiopods remained in tiering ecospace that were never vacated and that were therefore characterized by intense competition from other marine invertebrates.

LATE TRIASSIC INFAUNALIZATION AND THE MMR

As noted by McROBERTS (2001), infaunal bivalves increased throughout the Triassic, more noticeably from Late Triassic onward. At the same time, cemented bivalves diversified during the Middle and Late Triassic (HARPER, 1991). Both infaunalization (STANLEY, 1977; VERMEIJ, 1977) and cementation (HARPER, 1991, 2003, 2005; HAUTMANN & GOLEJ, 2004) were part of the Mesozoic Marine Revolution (MMR), which reflects an increase in durophagous organisms. HARPER (1991) verified experimentally that some predators (asteroids and crabs) prefer byssate rather than cemented bivalves. HAUTMANN and GOLEJ (2004) observed that post-Paleozoic cemented

bivalves had more complex hinge plates than Late Paleozoic ones, and interpreted this as a defensive strategy against valve torsion and predator manipulation. The main predator groups had already appeared during the Triassic but were apparently not sufficiently abundant to seriously influence biotic communities (McROBERTS, 2001; but see ROS & others, 2011). Several examples of predation on bivalves are known from the Triassic (VÉGH-NEUBRANDT, 1982; FÜRSICH & JABLONSKI, 1984; NEWTON & others, 1987; KOWALEWSKI, DULAI, & FÜRSICH, 1998; McROBERTS & BLODGETT, 2000) and Early Jurassic (HARPER, FORSYTHE, & PALMER, 1998; HARPER, 2003), but it seems that predation pressure increased significantly only from the Early Cretaceous, when predators became both abundant and diverse (VERMEIJ, 1977; KOWALEWSKI, DULAI, & FÜRSICH, 1998). HARPER, FORSYTHE, and PALMER (1998) suggested that predation levels can be underestimated for poorly preserved faunas because of the difficulty of observing predation marks. Because of the generally poor preservation of early Mesozoic bivalves (often preserved as molds) (ROS & DE RENZI, 2005), it is possible that Triassic predation levels have been underestimated and that increased predation is responsible for some of the life habit changes documented for this period (HARPER, FORSYTHE, & PALMER, 1998; HARPER, 2003). Probably because of their entirely calcitic shells, articulated brachiopods usually preserve predation marks better than bivalves (HARPER, 2003). Perhaps not surprisingly, therefore, predatory drilling has been judged to be higher for brachiopods than for bivalves during the Mesozoic (HARPER, 2003). Some brachiopods, such as terebratulids and rhynchonellids, already show a trend of ornamentation reinforcement during the Triassic and Jurassic. This trend has been interpreted as a response to increased diversity of predators (VÖRÖS, 2010).

Free-lying, epifaunal, and semi-infaunal bivalves increased in diversity during the Triassic (Fig. 14.1, 14.6, Fig. 15; see also

HARPER, 2003, 2005), but from the Norian on they were less diverse, and they were strongly affected by the T/J crisis. Note that, whereas cementing, swimming, and deep burrower bivalves increase in diversity throughout the Triassic, the reverse trend is observed for sedentary, reclined bivalves during the Late Triassic and Early Jurassic (Fig. 15).

The patterns summarized above were interpreted by McROBERTS (2001) to result from greater competition in the epifauna than in the infauna, and from the biotic structure during the recovery phase after the P/T extinction. It is clear that siphonate bivalves (STANLEY, 1968, 1977), with access to many available niches without direct competition from other infaunal organisms during the Early Triassic (BOTTJER & others, 2001), had a splendid opportunity to radiate and that their radiation was probably favored by the presence of the post-Paleozoic predators.

THE TRIASSIC–JURASSIC EXTINCTION AND RECOVERY

Bivalve generic origination rate decreased continuously during the Triassic, probably due to saturation of niches. Bivalve extinction rates show a different pattern than that suggested for the global biota by LUCAS and TANNER (2008), wherein extinction rate decreased and origination rate increased continuously during the Late Triassic. Bivalves demonstrate a high extinction rate during the Early Triassic, the Carnian, and especially the Rhaetian (Fig. 5), but not during the Norian, despite the fact that some groups, such as halobiids and monotiids, suffered extinction at the Norian-Rhaetian boundary (McROBERTS, 2007), and pectinids did so as well at the Carnian-Norian boundary (JOHNSON & SIMMS, 1989). The Trigoniida and Hippuritida show a maximum extinction rate during the Carnian; their diversity then diminished during the entire Late Triassic (ROS & ECHEVARRÍA, 2011a). Nevertheless, the generic diversification rate is negative for

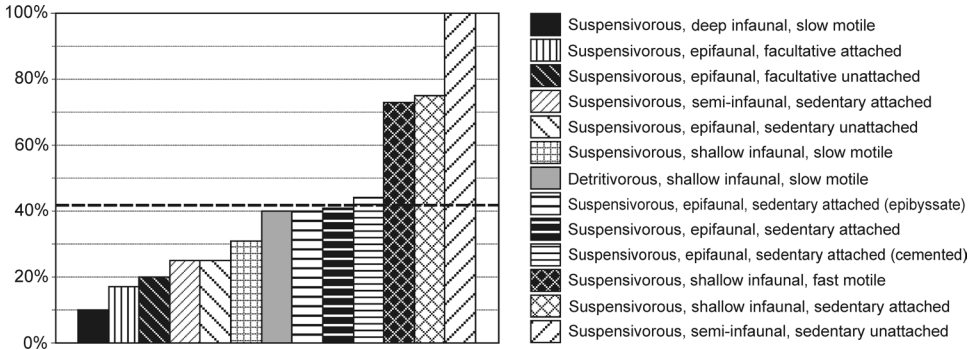


FIG. 16. Generic extinction percentages into each life strategy at the T/J crisis. The only significant differences from the global percentage extinction are observed for the suspensivorous semi-infaunal sedentary unattached and suspensivorous deep infaunal slow motile strategies; *broken line*, extinction for all categories combined (42%) (new).

bivalves only around the T/J boundary (Fig. 5). As explained by BAMBACH, KNOLL, and WANG (2004), the T/J global crisis was not characterized by extremely high extinction rates (as happened during the P/T crisis), but by moderate extinction rates combined with very low origination rates. This seems not to be the case for bivalves, since their extinction rate is high (compared with the rest of the Triassic) and their origination rate is only slightly low (ROS & ECHEVARRÍA, 2011b).

Triassic–Jurassic Extinction Selectivity

The present study does not support previous conclusions that infaunal bivalves suffered greater extinction than epifaunal ones during the T/J extinction (MCROBERTS & NEWTON, 1995; MCROBERTS, NEWTON, & ALLASINAZ, 1995, in Europe; HAUTMANN & others, 2008, in Tibet; KIESSLING & others, 2007, for the whole bivalve biota) (Fig. 4). The extinction rate is similar for both collectives, as noted by MCROBERTS (2001), although origination rate is higher for infaunal ones and therefore the diversification rate is higher for this collective. The data also indicate that during the Carnian, Norian, and the post-Triassic recovery phase, the extinction rate was lower, while the origination rate was higher for infaunal bivalves (Fig. 6; see also KIESSLING & others, 2007).

The statistical significance of selectivity in extinction was tested using a resampling algorithm for each ecologic strategy (performed by JAVIER ECHEVARRÍA, La Plata Museum, 2010). In the case of tiering and motility, extinction rate was found to be highest for epifaunal and semi-infaunal, sedentary, free bivalves ($p = 0.04$), and lowest for deep infaunal bivalves ($p = 0.02$). When examining all life strategies, extinction rate was greatest for reclined, semi-infaunal bivalves ($p = 0.01$; 100% of Triassic genera became extinct; Fig. 16), and mobile shallow infaunal bivalves ($p = 0.035$), and lowest for deep infaunal bivalves ($p = 0.03$; with only one genus disappearing at the T/J boundary, i.e., 11%; Fig. 16).

Regarding shell mineralogy, HAUTMANN (2004, 2006) and HAUTMANN, BENTON, and TOMAŠOVÝCH (2008) suggested that ocean acidification at the T/J boundary should cause wholly aragonitic bivalves to suffer greater extinction than bimineralic ones. But it is noteworthy, in this context, that shell mineralogy and mode of life are highly correlated (DE RENZI & ROS, 2002), with burrowing bivalves being nearly exclusively aragonitic. The present study confirms that during the T/J crisis (Fig. 17.1), wholly aragonitic bivalves suffered proportionally more extinction than bimineralic ones, although no statistically significant

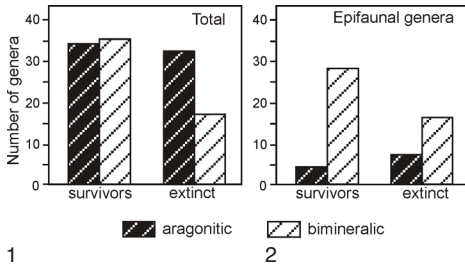


FIG. 17. Comparison of genera becoming extinct or surviving the T/J boundary crisis according to mineralogy; 1, total number of genera; 2, epifaunal genera (new).

differences are detected in the results. However, this could reflect their predominantly infaunal mode of life instead of shell mineralogy. According to KIESSLING and others (2007, p. 216), aragonitic epifaunal bivalves were more vulnerable to extinction during the Triassic and Jurassic than bimineralic epifaunal bivalves. However, our data (Fig. 17.2) demonstrate that most of the epifaunal bivalves that became extinct were bimineralic, and the extinct epifaunal aragonitic genera were almost all recliners (epifaunal and semi-infaunal, nonmotile, unattached).

KIESSLING and ABERHAN (2007) suggested a climatic factor in the T/J extinction, with tropical genera being more affected by the crisis. The climatic factor was not considered in the present study.

Taxonomic versus Ecologic Changes in the Triassic/Jurassic Extinction

HALLAM (1981) proposed a more severe generic-level T/J extinction for bivalves (50%) than the 42% extinction indicated by our data. Our percentage is most similar to that in McROBERTS (2001; 40%), and higher than that in HALLAM (2002; 31%), KIESSLING and others (2007; 26% ± 5%), and HAUTMANN (2007; 34%). Our generic data do not reflect the global Norian–Rhaetian extinction event described by LUCAS and TANNER (2008) for bivalves and other organisms. Instead, we see a mild extinction rate during the Carnian and Anisian and a much higher

rate during the Rhaetian, but no extinction peak during the Norian.

Despite the loss of 42% of genera, bivalves were unaffected in terms of life habit strategies at the T/J boundary (ROS & others, 2011). The taxonomic and ecologic impact of the extinction was therefore decoupled, as previously noted by DROSER and others (2000) and MCGHEE and others (2004) for other extinction events for the whole biota. DROSER, BOTTJER, and SHEEHAN (1997) developed a system to evaluate the severity of ecologic change produced during mass extinctions and recoveries. They considered four paleoecological levels, all nonadditive and nonhierarchical, but ordered by severity. They also indicated some characteristic signals for each level. We have modified these levels and their signals to evaluate the ecological severity of extinction in the Bivalvia (Table 2). We conclude that the T/J boundary saw no change in the ecology of bivalve communities, no loss of any bivalve life strategy, and only third- and fourth-level ecologic changes *sensu* DROSER, BOTTJER, and SHEEHAN (1997, p. 168), indicated by “thinning” within life strategies and taxonomic changes. In contrast, the P/T extinction was characterized by second-level ecologic changes for bivalves, with the transition from brachiopod-dominated to bivalve-dominated shelf communities during the Early Triassic (GOULD & CALLOWAY, 1980). The T/J extinction did not see a change in infaunal tiering, with deep burrowers losing only one genus.

Post-P/T and post-T/J Recovery

A comparison of bivalve diversity at the beginning of the Triassic and Jurassic indicates that the two post-extinction recoveries were quite different. The Early Triassic was characterized by several generalistic bivalves with wide paleogeographic distributions, whereas the Early Jurassic was characterized by much greater bivalve diversity. One shared feature was the small size of the recovery bivalves (TWITCHETT, 2001), as clearly shown by megalodontids at the T/J

TABLE 2. Paleocological levels and their typical signals to evaluate the effects of extinctions and recoveries among bivalves (see also Droser & others, 2000; new).

Level	Signals
First	1: initial radiation of the clade 2: total extinction of the clade
Second	1: changes in dominance with respect to other clade 2: appearance/disappearance of bivalve ecospace strategies
Third	1: increase and/or decrease of tiering complexity 2: filling or thinning within bivalve ecospace strategies
Fourth	1: taxonomic changes within the clade 2: appearance/disappearance of the clade in certain communities

boundary (VÉGH-NEUBRANDT, 1982; ALLASINAZ, 1992; HAUTMANN, 2006) and by other bivalves at the P/T boundary (HAUTMANN & NÜTZEL, 2005). Although ecologic tiering is usually affected during extinction events (e.g., the P/T extinction event), no such changes are evident for bivalves at the T/J boundary.

During the Hettangian and Sinemurian (Early Jurassic), the rapid recovery of infaunal bivalves correlates with the Jurassic infaunalization described by ABERHAN, KIESSLING, and FURSICH (2006).

The number of new genera appearing during the Hettangian (21) is nearly the same as during the Early Triassic (20), but the time involved is much shorter, i.e., 3.1 Ma for the Hettangian and 6 Ma for the Induan + Olenekian. The faster rate of recovery during the Early Jurassic reflects the smaller magnitude of the T/J crisis compared with the P/T crisis, and probably also the greater ecologic impact of the P/T event.

CONCLUSIONS

The present analysis indicates that, although the Triassic–Jurassic extinction strongly impacted bivalve taxonomic diversity, it had little impact on bivalve ecologic diversity. Not a single bivalve life strategy was eliminated at the end of the Triassic.

The process of infaunalization began for bivalves in the Late Triassic and proceeded unabated throughout the Mesozoic. This process and the selectivity against free-lying forms during the same period of time, together with an increase in diversity of cemented and facultative motile bivalves, seem to reflect the influence of the MMR. However, possibly due to the generally poor preservation of early Mesozoic bivalve faunas, the link between these changes and increased predation in the Triassic has yet to be demonstrated.

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