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Bivalves and evolutionary resilience: old skills and new strategies to recover from the P/T and T/J extinction events

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Diversity dynamics among bivalves during the Triassic and Early Jurassic provides the opportunity to analyse the recovery patterns after two mass extinctions: Permian/Triassic and Triassic/Jurassic (T/J). The results presented here are based on a newly compiled worldwide genus-level database and are contrasted to the main morphological characters of the different taxonomical (orders and their constituent families and genera) and ecological groups. Many of such morphological characters are innovations appearing during the time span considered. Diversity and evolutionary rates were assessed and compared between these groups. During the Early Triassic there was a slow recovery, dominated by epifaunal taxa, the order Pectinida being the most diverse. The major post-Permian radiation took place during the Anisian, with several morphological and ecological innovations appearing and/or diversifying. The Late Triassic was a time of great diversification and ecological specialisation. Although the T/J was a true mass extinction for bivalves, it was not indiscriminate as its impact was stronger on specialised orders and not all ecological categories were equally affected. Recovery during earliest Jurassic was fast, confirming the high-evolutionary resilience of bivalve molluscs, except for groups with thick shells and tropical distribution, probably because of a biocalcification crisis.

Keywords: bivalvia; mass extinction; recovery; taxonomic diversity; Triassic; Early Jurassic

Introduction

Bivalves are one of the most useful groups of invertebrates for the study of diversity and evolutionary dynamics, as their shells have high preservation chances and thus are quite abundant in the fossil record. Bivalves appeared in the Early Cambrian (Runnegar and Pojeta 1974) and are highly diversified nowadays, but it was not until the beginning of the Mesozoic when they started to be ecologically dominant (Fraiser and Bottjer 2007). It was then that they diversified dramatically (Stanley 1968; Skelton et al. 1990) and replaced brachiopods, which occupied similar ecological roles during the Paleozoic (Bottjer et al. 2008).

The Triassic is an interesting period for analysing diversity dynamics in this group, as it is delimited by two mass extinctions; it started with the recovery from the biggest mass extinction ever, the end-Permian one (Raup 1979; Erwin 1993), and ended with the Rhaetian extinction. It was during this period that many novel adaptations became evident and their effects could be seen [e.g. diversity increasing in taxa with fused mantle lobes allowing for exploitation of infaunal habit (Stanley 1968) and expansion of foliated calcitic microstructure among Pteriomorphia allowing for the development of new life habits such as swimming and cementing (Esteban-Delgado et al. 2008)].

Bivalves were one of the less affected groups of the end-Permian extinction (Yin 1985). Nevertheless, they experienced an extraordinary adaptive radiation after it (Stanley 1968), suggesting that they are a particularly resilient group. The Triassic was a period of initial recovery and posterior diversification of the biota, which suffered not only a strong taxonomic depletion but also a drastic reorganisation of marine ecosystems (Erwin 2006; Wagner et al. 2006); complete recovery was not fulfilled until the Middle Triassic (Erwin 1993; Benton 2003). During the Late Triassic, bivalves reached their maximum diversity (McRoberts 2001; Hautmann 2007; Ros 2009), but at the Triassic/Jurassic (T/J) boundary a new mass extinction caused the loss of 42% of genera, although it did not affect ecospace occupation (Ros 2009). Once again, the Early Jurassic was a time of recovery, which was fully achieved by the Pliensbachian with the reappearance of coral reefs (Hallam and Wignall 1997).

In this paper, we focus on the study of both the taxonomic and the ecological diversity of bivalves and their variations during the Triassic and the earliest Jurassic. The results reported here are based on a new genus-level database (Ros 2009), and are interpreted in the

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context of the main morphological characters of the different taxonomical (orders and their constituent families and genera) and ecological groups, in which many of such characters are innovations evolved during the period considered. This approach allows for a more complete interpretative scheme about the establishment and radiation of post-Paleozoic bivalve faunas.

The diversity dynamics of bivalve orders was dealt with by Hallam and Miller (1988) and Skelton et al. (1990), who used the family as the taxonomic unit and dealt with the whole Phanerozoic and post-Paleozoic, respectively, while here we use genera as units and focus only on the interval Induan–Sinemurian, emphasising the main variations and events during this restricted time interval. Other authors analysed the diversity dynamics of bivalve orders during the Triassic at a sub-genus level, but either they restricted the study to a few particular orders (Hautmann 2007) or they focused mostly on the ecological factors more than on the taxonomic groups (McRoberts 2001).

Database and methods

Database

The results reported here are based on the data provided by Ros (2009), with a revision of the stratigraphic ranges of megalodontids based on Végh Neubrandt (1982). This database is a new worldwide stage-level compilation of genera of marine bivalves, following a coherent systematic scheme. It provides data on stratigraphic range, paleogeographic distribution, autoecology and shell mineralogy of all marine bivalve genera ranging from Induan (Early Triassic) to Sinemurian (Early Jurassic) based on a critical revision of the available literature on each genus and the advice from experts on different subgroups or specific geographic areas, to minimise taxonomic and stratigraphic inconsistencies (summarised data in Ros 2009, p. 366–374). Data of every genus and the species included in them were carefully revised, and only records accompanied by full descriptions and figures were included. The species were considered to minimise the diverse systematic interpretations that different authors made for some of them.

We follow the systematic arrangement by Amler (1999) and Amler et al. (2000) with some modifications discussed by Ros (2009). The assignment of genera to different orders is based on Cox et al. (1969) and subsequent specific systematic literature as detailed in Ros (2009). As systematic interpretation of the order Ostreoida and the position of family Mysidiellidae are highly controversial, in the appropriate sections we include a short note on those issues. Nevertheless, as the systematic revision of all the Triassic marine bivalves is beyond the scopes of this paper, we do not discuss all the different systematic schemes.

The stratigraphic resolution of our analyses is stages/ages, with the absolute ages for their boundaries taken from Gradstein and Ogg (2004). Different time scales in the analysed papers were updated using the conversion tables in Paleobiology Database (Available from: http://paleodb.org) and GeoWhen (Available from: http://www.stratigraphy.org/geowhen/index.html). Although the Triassic time scale is still unstable (Schultz 2005) as most boundary stages lack a definite global standard section and point, Ros' database (2009) was based on a well-defined stratigraphic scheme linked to absolute ages. When this scheme could not be directly applied (either because the papers were too old, the authors did not follow it, or the stratigraphic assignment of the records was too vague), the stratigraphic provenance was carefully checked and adjusted to this scheme. Possible changes in the interpretation of the stage boundaries, would not affect the reliability of the database, as long as absolute ages of this stratigraphic scheme remain robust. A special problem was the stratigraphic provenance of Norian and Rhaetian faunas in papers published between Tozer (1979), who initiated the tendency of relegate the Rhaetian as Norian substage, and the redefinition of Rhaetian by Dagys and Dagys (1994) (see discussion in Hallam 2002). At least the Kössen formation in Austria and the Gabbs formation in USA were considered to be truly Rhaetian in age (Dagys and Dagys 1994; Hallam 2002). For other units from the Norian–Rhaetian interval, the ages were carefully verified, so the resolution for these data is significantly improved over previous databases. Time ranges used here are observed ranges, defined by first appearances datum (FADs) and last appearances datum (LADs), and therefore they are only proxies for actual origination and extinction times. It must be taken into account that sample biases, stratigraphic gaps, regression and transgression effects and many other factors can affect first and last appearances (Holland 1995), and that bivalve temporal ranges are especially influenced by lithologic facies.

The orders Solemyida and Myida are not considered in the taxonomic analysis because of their low number of included genera. The first one only includes *Solemya* and *Acharax*. Myida has only one fully marine genus in the study interval. We did include them in the ecological analyses, except for *Acharax* which was recorded before and after the study interval but not during it, and which is morphologically very similar to *Solemya* anyway.

The taxonomic unit used in this database is the genus. Although the use of subgenera is frequent in the literature (Raup 1978; Jablonski et al. 2003), experience shows that in several cases subgenera were erected taking into account species level criteria, and sometimes even based on superficial shell structures easily influenced by taphonomic processes. The families Entoliidae or Halobiidae provide good examples (see discussion in Ros 2009). The use of subgenera to minimise the 'Pull of the Recent' (Raup 1972, 1978) is not pertinent in this case, as no stratigraphic range was extended in the analysed time interval due to the presence of an extant species.

Assessment of diversity and evolutionary rates

Two different metrics were used to analyse the changes in diversity: (1) the Boundary Crossers (BC) metric (Sepkoski 1979; Alroy 1996; Foote 2000); and (2) the mean standing diversity (MSD). The last one was calculated summing all the continuous ranges, one half for each FAD and LAD (Foote 2000) and one third for each singleton (Hammer 2003; Hammer and Harper 2006). In the absence of singletons, the MSD for a given stage is the mean between the BC at its base and the BC at its top; as a result, for graphical purposes they appear equivalent (the trend between base and top will be the same). The addition of singletons increases this value and consequently the trend changes. We consider this change an important fact to be analysed (there was higher origination in the stage than what is shown by the BCs alone) and so we decided to plot them together to get a better understanding of the diversity dynamics (the MSD was plotted as a point at the mid-value of each stage). Nevertheless, it must be noted that they are different metrics, while the BC is an actual metric of the diversity at one time-point, the MSD is a standardised estimation of the diversity for a whole stage; we specify on which metric each conclusion is based.

Origination rate was calculated as the number of FADs divided by MSD and standardised by the stage duration while extinction rate was obtained as LADs divided by MSD and also standardised by the stage duration; diversification rates were calculated by the subtraction of extinction rate from the origination rate (Sepkoski 1978). We did not calculate the evolutionary rates for the orders in two situations: (1) stages in which there were no records (either because the order was not yet present or because of a gap in its record); (2) stages of the first appearance (either the origination of the order or its reappearance after a gap), as standardisation is not possible in this case. The extinction pattern for the Paleozoic survivals (from now on the Paleozoic genera) was characterised by the proportional loss of genera for each stage divided by the stage duration; the same metric was applied to the other genera (from now on the post-Paleozoic genera).

Autoecological traits categorisation

The autoecological trait categorisation is a simplification of the animal marine ecospace considered by Bambach et al. (2007) for tiering and degree of motility/attachment. Assignment of taxa to these subdivisions is discussed by Ros (2009). Feeding type was excluded from this analysis as in the time interval under study there are only two categories: deposit feeders and filter feeders. The former is present only in the order Nuculida, being included as one of the traits for this taxon. Tiering includes the following categories: epifaunal, shallow infaunal and deep infaunal. Semi-infaunal bivalves were included either among the epifauna or among the shallow infauna depending on their biology; endobyssate bivalves, which have to burrow to certain degree and live with the anterior part buried, were grouped within this category; free lying bivalves living partly buried – because of their heavy massive shell, instead active burrowing activity – were grouped with the epifauna. For the degree of motility/attachment, other three categories were established: motile, sedentary and attached. These two traits produce an ecospace of nine categories, of which marine bivalves occupy six during the time interval: epifaunal–attached (either epibyssate or cemented; these two different modes of life will be dealt with in the discussion of the orders in which they are present), epifaunal–sedentary (reclined), epifaunal–motile [swimmers, facultative swimmers – as defined according to the morphology by Stanley (1970) – and pseudoplanktonic; again the differences will be dealt with in each order], shallow infaunal–attached (endobyssate), shallow infaunal–motile (shallow burrowers regardless of their feeding type) and deep infaunal–sedentary (deep burrowers).

At first glance, the inclusion of such varied habits in the epifaunal–motile category may look somewhat counterintuitive. While swimmers and facultative swimmers rely on muscular activity for their movements (implying high and moderate energy consumption, respectively), pseudoplanktonic forms can be regarded as physiologically sedentary; on the other hand, the distances they can drift away are far greater than those attained by swimmers and facultative swimmers (no bivalve has acquired a true nektonic habit; Stanley 1970). Nevertheless, what we are considering here is only the ability of the taxa to move to, and so to explore, different environments, regardless of their physiological needs or the distances involved. Actually, for the T/J extinction, both the main categories of motile forms (i.e. pseudoplanktonic vs. swimmers and facultative swimmers) share a similar extinction pattern regardless of the kind of motility (Ros and Echevarría in prep.).

As the life habits of bivalves may change through ontogeny and due to different environmental conditions, some practical considerations are required. Genera that are usually attached but can detach and move for a certain time were included in the motile category; all genera that in their adult life do not attach but practically do not move (although they can have high motility or be attached as juveniles) were considered as sedentary. Although adult *Solemya* is motile, it was grouped with the remaining deep burrowers, which are sedentary. The borer *Lithophaga* was coded as shallow infaunal–attached, while *Pichleria* was considered as infaunal but could not be codified in any motility/attachment category.

Results

Diversity measures and evolutionary rates

The proportional extinction of Paleozoic genera (Figure 1) shows that extinction was initially high among this group, and then diminished until the Middle Triassic; during the Late Triassic they suffered progressively higher extinction and during the Hettangian–Sinemurian they underwent no extinction at all. The proportional extinction among post-Paleozoic genera (measured in the same way) is likewise shown for comparison.

Evolutionary rates for the whole data set, together with the two diversity metrics, are shown in Figure 2. Apart from the Rhaetian high-extinction rates (and great-diversity depletion), the high-evolutionary rates during the Early Triassic and the high-origination rates (and sudden increase in diversity) during the Anisian are also significant. The Carnian diversity peak (MSD) is important too, not for the numerical value itself (exceeded by later Triassic values), but for its difference with the trend shown by the BC measures; the difference between both the curves shows the importance of singletons on this stage. There is also a Norian peak, similar to the Carnian one, although the difference is lower. Unlike the results shown by McRoberts (2001, fig. 1A), we obtained a growing diversity curve for most of the Late Triassic in coincidence with Hautmann (2007, fig. 8).

The diversity measures were discriminated according to the autoecological trait categories (Figure 3), and this clearly emphasises the importance of performing detailed analysis on ecological grounds when trying to assess diversity interpretations, as it shows that the apparent

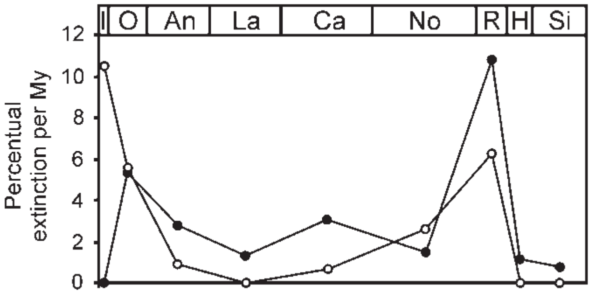

Figure 1. Extinction among bivalves during the Induan-Sinemurian interval (percentage of genera x My-1) - Empty symbols: genera originated during Paleozoic times; filled symbols: genera originated during the Induan-Sinemurian interval.

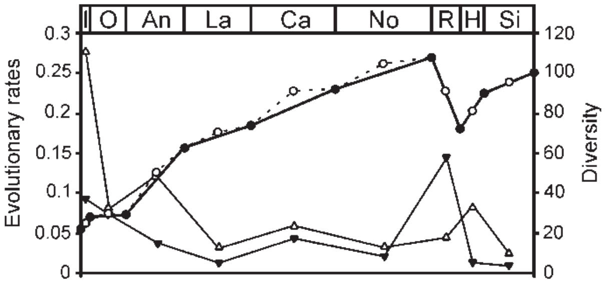

Figure 2. Diversity and evolutionary rates among bivalves during the Induan–Sinemurian interval – Filled circles: diversity in number of genera (BC metric); empty circles: diversity in number of genera (MSD metric); filled triangles: extinction rate in number of genera × genus^{-1} × my^{-1}; empty triangles: origination rate in number of genera × genus^{-1} × my^{-1}.

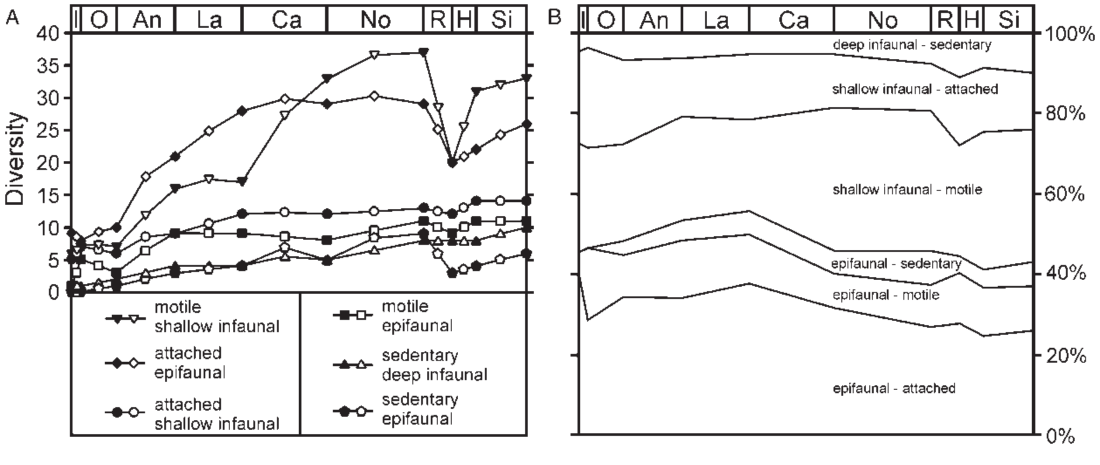

Figure 3. Diversity among the different ecological categories. (A) Absolute diversity among ecological categories during the Induan–Sinemurian interval; Filled symbols: diversity in number of genera (BC metric); empty symbols: diversity in number of genera (MSD metric). (B) Proportional diversity among ecological categories during the Induan–Sinemurian interval.

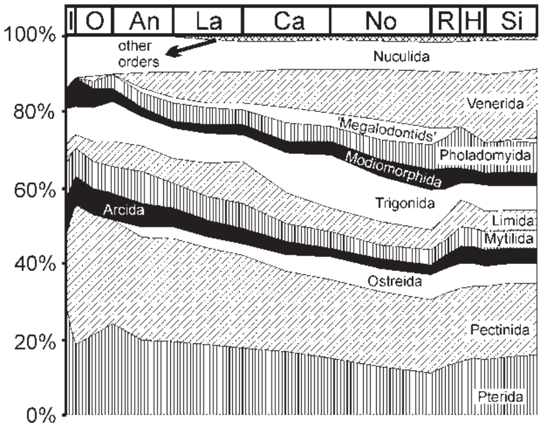

Figure 4. Proportional diversity among the analysed orders during the Induan–Sinemurian interval.

simple and constant growing trend in diversity between Ladinian and Norian ages is actually far more complex, showing important changes in the absolute and relative abundance of the different categories.

Orders evolutionary history and diversity dynamics

Figure 4 shows the variation in proportion of genera among orders during our study interval, while diversity estimates and evolutionary rates for all orders are summarised in Figures 5 and 6. To ease the discussion on these data, we also provide below a short characterisation of each order. This is not intended to be a detailed description of the anatomy and biology of each order, but just a short review of those characters that we consider relevant to explain the diversification and extinction patterns observed.

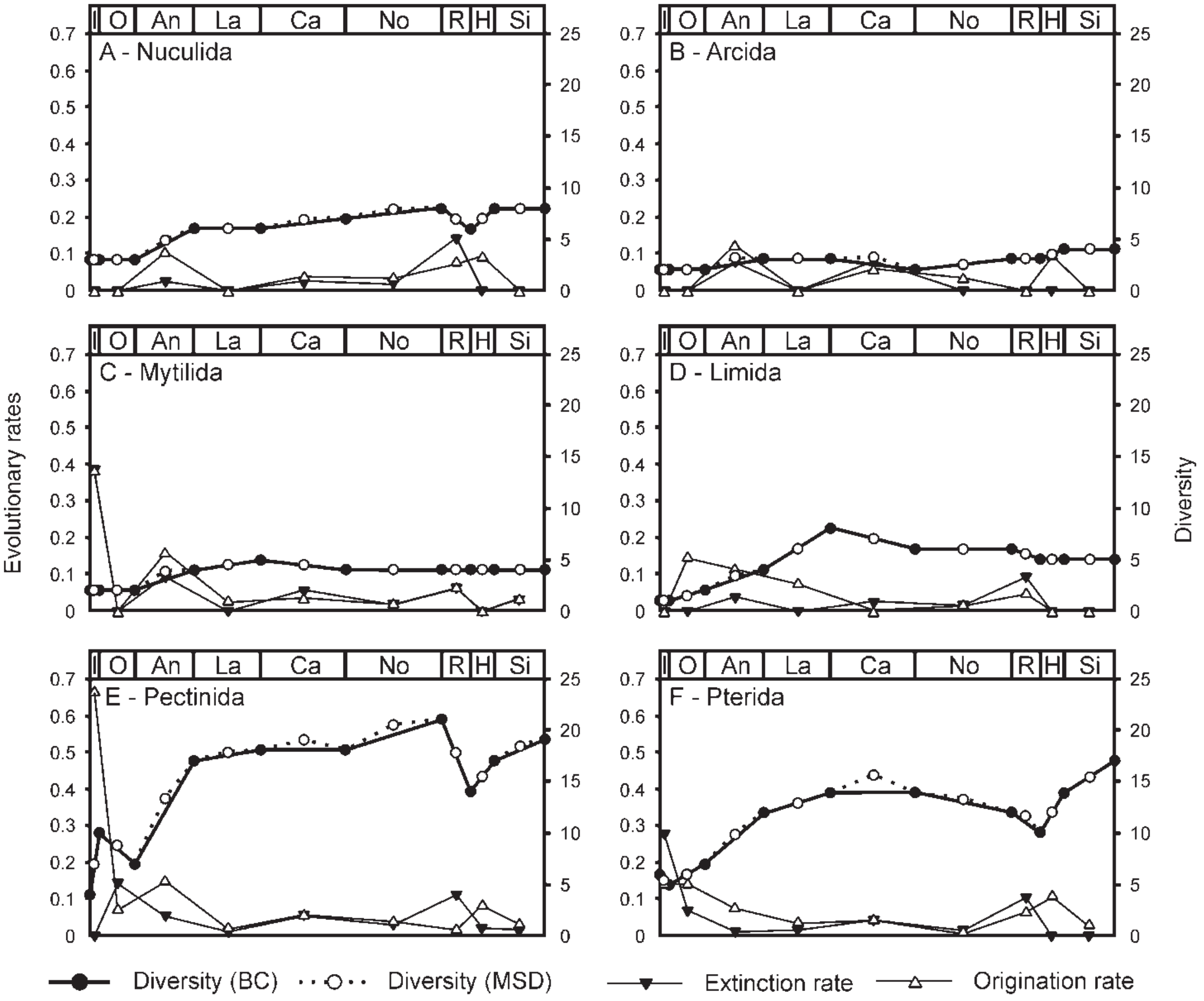

Figure 5. Diversity and evolutionary rates of the analysed orders during the Induan–Sinemurian interval – diversity in number of genera (BC, boundary crossers metric; MSD, mean standing diversity metric); evolutionary rates in number of genera × genus^{-1} × my^{-1}.

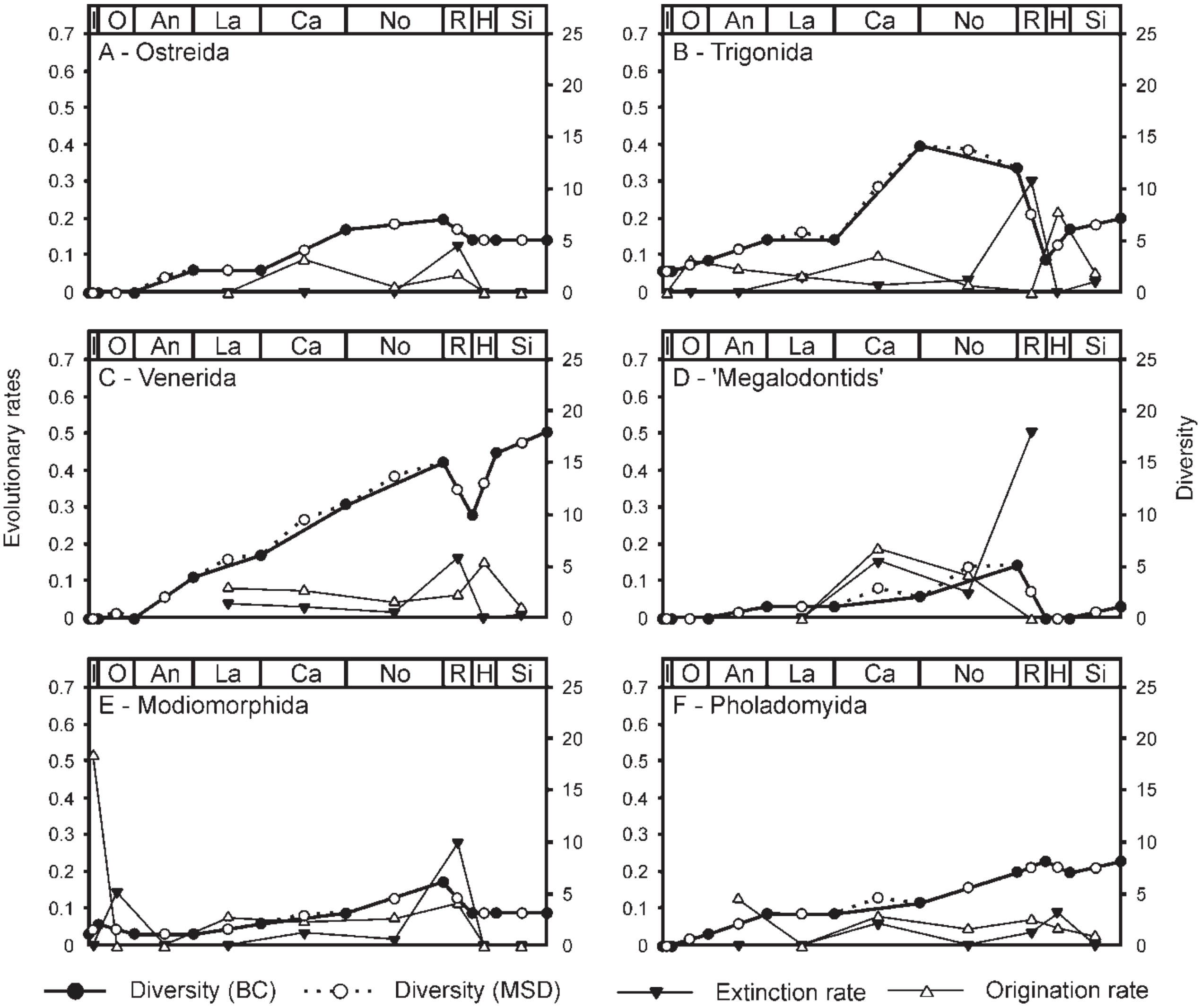

Figure 6. Diversity and evolutionary rates of the analysed orders during the Induan–Sinemurian interval – diversity in number of genera (BC, boundary crossers metric; MSD, mean standing diversity metric); evolutionary rates in number of genera × genus^{-1} × my^{-1}.

Order Nuculida

These are deposit feeding shallow burrowers, constantly moving due to the nature of their food source. This feeding type has also been interpreted as the reason for their conservatism, as they are generally longer lived and with lower turnover rates than suspension-feeding bivalves (Levinton and Bambach 1970; Levinton 1974). At present, their highest diversity is in deep-sea environments, probably as a result of competition with other suspension-/deposit-feeding bivalves (i.e. the Tellinoidea; see Cadée 1984).

Three genera survived the end-Permian mass extinction (Figure 5(A)), representing half of the shallow burrowers. Nevertheless, they did not begin to diversify until the Middle Triassic. Unlike suspension-feeding bivalves, they only diversified moderately during the Late Triassic, although they underwent some turnover along its stages. They were affected by the end-Triassic extinction, but thanks to originations the overall diversity decreased by only two genera (BC). Diversity was fully recovered by the end of the Hettangian.

Since the Ordovician, when Nuculida originated, they showed little diversity variation, at least at family level (Hallam and Miller 1988). This seems to be also the case for the genera in our study interval. It is remarkable that the end Triassic extinction affected only genera with a restricted distribution.

Order Arcida

The history of the order Arcida is dominated by certain evolutionary conservatism. The early adoption of simple means for increasing shell size and complexity by serial repetition of simple structures (simple teeth of taxodont dentition, sheets of fibrous and lamelar material in the duplivincular ligament) imposed on this group a number of morphogenetic and phylogenetic constrains (Thomas 1978a). The result of this conservatism is a generalised group of bivalves, well suited for unstable and rigorous environments (except for constantly mobile soft substrates), using a 'recovery strategy' mostly made possible by the well-developed foot (Thomas 1975, 1978a, 1978b). The generalised structure also allows for frequent changes in life habit from burrowing to byssate and back to free burrowing (Stanley 1972). The few examples of specialisation among the group usually result in convergence – albeit less efficiently – with other orders (Thomas 1978a).

During the study interval, the diversity dynamics of the group is dominated by the family Parallelodontidae – a family important during the Late Paleozoic and from which the other families may have evolved (Thomas 1978a). Long-ranging genera are common in this family. *Parallelodon* and *Grammatodon* date from the Permian, having a worldwide distribution and high diversity and abundance during the study interval (Ros 2009), and another genus (*Catella*) originated in the Norian; the three crossed the T/J boundary and were present in the analysed Early Jurassic stages. There was also a singleton in the Anisian. During the Triassic, the highest diversities were reached during the Anisian and Carnian (MSD), caused by some radiation occurring in the families Phylobryidae and Pichleriidae; nonetheless these were short events, as most of the genera of this stage were singletons. The family Cucullaeidae (the only living family of the interval) appeared at the beginning of the Jurassic.

The main radiation of this order occurred during the Mesozoic (Jurassic and Cretaceous), with the origination of the extant families (Thomas 1978a; Oliver and Holmes 2006). Thomas (1978a) considered the Parallelodontidae as byssate, and thus the burrowing life habit developed during this radiation, with the Cucullaeidae as their first representatives.

The consequences of this morphological conservatism can be clearly seen in the evolution of diversity within the order (Figure 5(B)): the reduced possibilities of specialisation resulted in a low diversity during the whole study interval, although with many abundant and long-lived genera. Their immunity from the end Triassic extinction event shows their ability to survive in unstable environments, and the establishment of the burrowing habit after it is evidence of the plasticity of a generalised structure. Some biological features, such as the quick production of a new byssus and gregarious behaviour (Morton and Peharda 2008), may have aided in the stability and resilience of the order.

Order Mytilida

The order Mytilida can be considered as morphologically more derived, including specialised endo- and epibyssate genera. According to Morton (1992), the development of a single posterior inhalant current from a primitive scheme of two inhalant currents (one anterior and one posterior as seen in Arcida) would have been a key innovation in the evolution of the group, allowing for the reduction of the anterior part and expansion of the posterior one. The result is the heteromyarianisation and the occurrence of the typical 'mytilid' and 'modiolid' shapes, highly specialised for the epi- and endobyssate life habits, respectively. This would have allowed also a gregarious behaviour with densities of hundreds or even thousands of individuals in a square metre (Seed 1969; McGrorty et al. 1990; Creese et al. 1997; Sukhotin et al. 2008); this behaviour is considered a strong adaptation against predation (Peterson and Black 1993; Casey and Chattopadhyay 2008). The thick, persistent periostracum of the group is also noteworthy (Harper 1997); although this feature allowed the exploitation of new habits, like the boring one (genus *Lithophaga*) (Thomas 1978a), it probably limited the acquisition of other ones, such as cementing habit (Harper and Skelton 1993).

Besides their structure, much more specialised than that of the Arcida, the Mytilida developed some other biological strategies that allowed them to resist environmental crises, such as the ability to live intertidally (Skelton et al. 1990; Harper and Skelton 1993), short life cycles (Seed 1969; Creese et al. 1997) and high fecundity and fast growing rates (Creese et al. 1997). They are usually mentioned in the literature as invaders of different environments (Darrigran and Pastorino 1995; Creese et al. 1997; Lachowicz 2005). The gregarious behaviour also excludes other suspension feeding bivalves (Creese et al. 1997; Lachowicz 2005), and some of them are considered strong competitors for space and food (Öztürk et al. 2002).

The study interval comprises two families: Mytilidae and the exclusively Triassic Mysidiellidae. This last family, as characterised by Waller and Stanley (2005), has curved beaks, inflated umbones, a non-myophoric anterior septum on which neomorphic hinge teeth may be developed and a variably developed byssal invagination of the anterodorsal shell margins; the nearly flat anterior margin may have facilitated strong byssal attachment conferring stability in turbulent shallow-water environments (Newton et al. 1987). Mysidiellidae probably appeared in the Induan (*Joannina timorensis* (Krumbeck) from Dienerian of Timor) and it includes short-ranging genera, thus experimenting high turnovers along its history; it is almost exclusive of the Tethys domain, except for *Mysidiella* and *Promysidiella*, which are also present in the Circumpacific domain. During the Middle Triassic radiation they dominated the diversity of the group, but they were slowly replaced by the Mytilidae during the Upper Triassic, and went extinct in the Rhaetian. Mytilidae, on the other hand, includes longer-lived genera, presenting a more stable history. As a result of this slow replacement, the diversity of the order did not change during the Upper Triassic and the Hettangian, and the loss of the last Mysidiellidae genus in the Rhaetian is compensated by the origination, at the same age, of *Inoperna* among Mytilidae. This evolutionary history resembles that of Arcida (Figure 5(C)), although the relative immunity from the extinction of the group may be related more to its biological strategies than to its morphology. The development of the boring habit in the Norian with the appearance of *Lithophaga* (Kleemann 1994) is also significant.

The systematic position of Mysidiellidae was discussed by many authors [see discussion in Waller and Stanley (2005), Hautmann (2008), and see Ros (2009) for a summary on the topic] and its exclusion from the order Mytilida would entail some changes, with a diversity growing trend for the order Mytilida during the Late Triassic. Yet, there is still a replacement of probably ecological equivalents regardless of the taxonomic scheme preferred.

Order Limida

They are monomyarian, mostly orthothetic bivalves (Beesley et al. 1998) with a biauriculate shell, although the anterior auricle can be reduced or absent in some forms (Cox and Hertlein in Cox et al. 1969). Living species are mostly epibyssate or nestlers (Jefferies 1960), and some can swim short distances in response to disturbance (Gilmour 1967; Stanley 1970). One peculiarity of their anatomy is the foot reversal: during settlement, the shell and visceral mass show a counter-clockwise horizontal rotation through 180° relative to the foot. This phenomenon is considered as an adaptation to balance the visceral mass and shell during settlement, but it could be also related to some unique adult adaptive features, such as (a) the great development of tentacles arising from the mantle middle fold (initially to help in balancing but later being use for defence thanks to mucus secretion and autotomy), (b) the muscular mechanism for rejection of pseudofaeces (which can be related to swimming and nest-building behaviour) and – related to this last feature – (c) the elaboration of the lips (which, together with peculiar labial palps and gills, aid in an unusual method of food collection and waste rejection) (Gilmour 1990).

Only one genus – *Palaeolima*, which was cosmopolitan during the Paleozoic – survived from the Permian (Figure 5(D)). Limida experienced great diversification during the Middle Triassic, with two of the genera originated then currently living (*Limatula* and *Limea*). During the Late Triassic their diversity declined, especially during the Carnian, although *Limea* remained as a common genus (especially outside the Tethys domain) (Ros 2009). Despite the diversity reduction at the T/J boundary, this depletion was not as dramatic as in other groups (overall diversity decreased only in one genus from the base to the top of the Rhaetian), so it can be considered as one of the orders which was almost unaffected by this major event. There was no change in diversity during the first two stages of the Jurassic.

The low-diversity values along the study interval, together with the presence of long-ranging genera, seem to indicate a relatively generalistic stock, its survival possibly aided by some of their unique adaptive anatomical features mentioned above (e.g. tentacles as defensive structures, enlarged and fused lips aiding in food collection; Gilmour 1990).

Order Pectinida

It is the most diverse order within the study interval, with 63 genera, all epifaunal with representatives in the three motility categories. They can be considered as a specialised group, showing important morphological changes throughout the study interval. The evolution of the order is strongly connected to the retention of the byssus, as it is for Pteriomorphia in general (Pojeta 1978) and as can be inferred from the presence of a byssal notch in the right valve at least in early growth stages (Waller 1978). But unlike the Mytilida, they developed a pleurothetic mode of life (Waller 1978). This fact, together with some other structural features of the ligament and the hinge line that will be detailed in the following paragraphs, explains in great extent the success of the group, especially during the study interval.

Four genera survived the Permian/Triassic (P/T) extinction (Figure 5(E)), but during the Induan the group experienced an initial radiation, ending the stage with 10 genera. Some of these genera were important in terms of abundance (*Eumorphotis*) or species-richness (*Claraia*) (Fraiser and Bottjer 2007; He et al. 2007). During Olenekian diversity decreased, but this was one of the most successful orders of bivalves in the Middle Triassic. The major radiation occurred during the Anisian: from 7 genera crossing its base to 17 crossing its top. During the Upper Triassic, they maintained a slowly growing diversity. The Rhaetian extinction had a strong effect on the order, reducing the number of genera from 21 at the base of the stage to 14 at the base of the Hettangian, but they showed their recovery capacity reaching a diversity of 19 genera at the top of the Sinemurian.

At the family level they show a high turnover along the Triassic. Four Paleozoic families (Pterinopectinidae, Deltopectinidae, Leptochondriidae and Prospondylidae) had a continuous stratigraphic range at the P/T boundary and were represented at the lowest Triassic, with three of them going extinct during the Triassic, while the fourth, Prospondylidae, is remarkable for being one of the first groups of bivalves developing the cementing habit, and may be related to the origin of other cementing groups, although this has not been well established yet (Hautmann 2001a, 2006a; Márquez-Aliaga et al. 2005). During the Early Triassic, two families reappeared (Oxytomidae within the Monotoidea and Aviculopectinidae among Aviculopectinoidea) and three new families originated (Syncyclonemidae [= Entoliidae] in the Induan, and Monotidae and Pectinidae in the Olenekian). With the evolution of Syncyclonemidae and Pectinidae, key morphological innovations appeared. These families have a straight hinge line with the resilium below it, hence the ligament is completely internal (Newell 1938); this innovation, together with the expansion of the foliated shell microstructure, subsequently allowed the group to master the swimming habit (Hautmann 2004a; Waller 2006; Esteban-Delgado et al. 2008). Although the swimming and facultative swimming mode of life was already present at the end of the Permian [with genus *Pernopecten* (Stanley 1972) and also some Permian species of *Claraia* were interpreted as facultative swimmers by Yang et al. (2001)], this kind of ligament can be considered as an improvement related to this habit. One of the families originated in the Paleozoic (Pterinopectinidae) went extinct during the Olenekian. During Anisian, four new families appeared (Halobiidae in the superfamily Halobioidea, Buchiidae and Asoellidae within the Monotoidea, and Propeamussidae within the Pectinoidea), while Deltopectinidae coming from the Paleozoic disappeared. The motile habit increased among the group, either the pseudoplanktonic (in the superfamilies Monotoidea and Halobioidea, although some interpretations are controversial, see discussion and references in Ros 2009) or the swimming and facultative swimming (in the Pectinoidea). During the Ladinian, Aviculopectinidae and the exclusively Triassic Halobiidae had their highest diversity, beginning to decline by the Carnian. Only one family appeared during the Late Triassic (Pergamiididae among the Monotoidea in the Carnian), while the Halobiidae and the Leptochondriidae went extinct by the Norian and the Aviculopectinidae by the Rhaetian. Since then, only two superfamilies were represented: the Monotoidea – mainly inequilateral prosocline forms – and the Pectinoidea. The former superfamily had a greater number of families (six during the two first stages of the Jurassic, against three among the Pectinoidea), and was important during the remaining of the Mesozoic, with some genera biostratigraphically significant; it went extinct at the K/T event. The Pectinoidea had more genera and is highly diversified nowadays.

The high resilience of the group, evidenced at both recovery events, seems to be strongly related to the variety of habits they can adopt (epibyssate, reclined, swimmers, facultative swimmers, pseudoplanktonic, cementing). The frequent development of genera that are usually known as ‘flat clams’ is also noteworthy; these are considered to be epifaunal reclined or byssate (although with a weak byssus) opportunistic forms and include members of the families Halobiidae, Monotidae and Pterinopectinidae (McRoberts 2010).

The specialisation of its constituent members made the order vulnerable to the Rhaetian extinction event, although the ecological categories they occupied at that moment were not among the most strongly affected (the reclined habit appeared in the group during the Hettangian with *Weyla*), but they were able to recover quickly.

Order Pteriida

They are mostly epi- and endobyssate forms, with a byssal notch at least in juvenile stages. They are considered as primitively epibyssate on hard substrata, secondarily acquiring the endobyssate habit (Beesley et al. 1998), although the endobyssate habit is inferred as primitive for some families such as Bakevellidae (Aberhan and Muster 1997). Some of them have lost the byssus acquiring a nestling (Beesley et al. 1998) or a reclining habit, notably the Cassianellidae in the study interval [see Ros (2009, p. 110) and references therein], and a few even took advantage of the byssus to acquire a semiplanktonic mode of life (like the Inoceramidae *Pseudomytiloides*).

The diversity of the end-Permian survivals is dominated by the typically Paleozoic family Myalinidae, representing half of the genera (3/6); this family was already declining in Permian times and almost disappeared during the Early Triassic; its last record is the Anisian genus *Aviculomyalina*, of dubious systematic position (McRoberts 2005; Waller and Stanley 2005; but see discussion in Ros 2009). The other families extending from the Permian are Bakevellidae (two genera) and Isognomonidae (one genus). The declining of the Myalinidae during the Early Triassic was compensated by the diversification of other families, reappearance of the family Pinnidae and evolution of the families Pteriidae and Posidoniidae, so the diversity of the order remained relatively constant.

During the Middle Triassic, the group took part in the proliferation of epifaunal habits, experiencing a high diversification (Figure 5(F)), but only one family appeared at this time – the Cassianellidae of pleurothetic reclined habit and characterised by a radial depression with a corresponding internal ridge or septum. Otherwise, the diversification was due to the radiation of the families already present, especially Bakevellidae.

During the Carnian, the order reached its highest diversity (MSD measure) for the Triassic; this value expresses a great number of singletons, especially among the Cassianellidae. From this time on, the diversity of the group slowly fell along the Late Triassic, especially due to the decline of that family, which went extinct by the

Rhaetian; the Pteriidae also lost some diversity at this stage. But strikingly, after the T/J crisis, the order experienced a sudden recovery, reaching its highest diversity (17 genera) by the end of the Sinemurian. This diversification is due mostly to the radiation of the Bakevellidae and the origination and radiation of the Inoceramidae.

The general stability within the families of this order is remarkable; there was not a great family turnover as happened among the Pectinida. Most families maintained a relatively constant diversity and long-ranging genera are common; the Cassianellidae seems to be an exception to this trend, as well as to the general life habit for the order. The evolution of the Posidoniidae is also interesting; they are included among the ecological group of the 'flat clams' (McRoberts 2010). The family Bakevellidae clearly dominated the diversity of the group, representing between 20 and 50% of the genera; together with the Inoceramidae they were the important components of the Jurassic and Cretaceous bivalve faunas as well, but they went extinct by the end-Cretaceous (Aberhan and Muster 1997; Harries and Crampton 1998). The stability of the group, together with the frequent switching of habits (from epibyssate to endobyssate and back to epibyssate), suggests a relatively generalised group with some specialised offshoots.

Order Ostreida

The evolution of the order is strongly related to the cementing habit, and is the only order here analysed that originated in our study interval. Like most pleurothetic bivalves they are monomyarian, with the exception of the Dimyidae (which have two adductor muscles), and they lack a foot and byssal notch in the dissoconch, becoming cemented at the beginning of the post-larval stage (Waller 1978). All of them have a shell with a calcitic outer layer, and the Ostreidae and Gryphaeidae acquired also calcitic inner layers (Carter 1990), while Dimyidae and Plicatulidae have aragonitic inner shell layers (Carter 1990; Malchus 2000). Here, we follow the systematic arrangement by Amler (1999), grouping these four families together like many authors do (Waller 1978; Carter 1990), but there is some controversy about the monophyly of the order, and other phylogenetic and systematic proposals are available (Yonge 1978; Hautmann 2001a; Bouchet and Rocroi 2010). If this was the case, then the diversity dynamics shown here by the order would actually correspond to most cementing bivalves instead.

Ostreida was absent in the Early Triassic, and its earliest record is Anisian [genera *Umbrostrea* within Ostreidae (according to Márquez-Aliaga et al. 2005), *Protostrea* within Dimyidae (Chen et al. 2006) and *Pseudoplacunopsis* within Plicatulidae (Posenato 2008a)], radiating strongly during the Carnian (Figure 6(A)). They reached their maximum diversity in the Rhaetian, when almost all the genera of the study interval are present (the only exception being *Protostrea*, which is a singleton), but they were moderately affected by the extinction and they did not recover during the first two stages of the Jurassic. Almost all the extinct genera belong to the family Plicatulidae; the family Ostreidae lost one genus (*Umbrostrea*) but also had one origination during the Rhaetian (*Actinostreon*), so the overall diversity remained constant. Although there are frequent Sinemurian and Hettangian references in the literature (Ros 2009), they did not form reefs during those ages, probably because of the Early Jurassic calcification crisis (Hautmann 2004b, 2006b; Van de Schootbrugge et al. 2007; Hautmann et al. 2008; Črne et al. 2011); the first reefs after the T/J boundary appeared during the Pliensbachian, and were produced by bivalves of the family Lithiotidae (Fraser et al. 2004). The order Ostreida was ubiquitous in bivalve faunas for the remaining of the Mesozoic.

Order Trigoniida

The only living genus is a shallow burrower, and all extinct forms are interpreted in the same way (Stanley 1977a). They are characterised by a strong schizodont hinge, its development was probably correlated with the occurrence of strongly muscular foot; this, together with a varied ornamentation pattern, made them moderately rapid burrowers and allowed them to become one of the most abundant and diverse stocks of shallow burrowers during the Jurassic and early Cretaceous in shallow marine environments (Stanley 1977a). According to Newell and Boyd (1975), the hinge of the group evolved in parallel more than once.

There were two genera extending from the Permian (*Costatoria* and *Neoschizodus*), and their diversity remained relatively low during the Early Triassic (Figure 6(B)). During the Middle Triassic they experienced a moderate diversification, but as shallow burrowers, they had their diversity peak in the Late Triassic, particularly during the Carnian. They were highly affected by the end Triassic mass extinction, but they had the highest diversification rates among bivalves during the Hettangian, although they did not recover their previous diversity in the study interval. They were abundant and diverse for the remaining of the Mesozoic. The order went almost extinct at the K/T, showing the vulnerability of the group to major environmental disruptions.

The schizodont hinge (and presumably the strong muscular foot) evolved during the Triassic, perhaps by parallel evolution (Newell and Boyd 1975; Stanley 1977a). Hence, the key innovations for the success of the group were produced during this time interval, and resulted in their rapid diversification (Stanley 1977a).

Order Venerida

They are mostly infaunal, either shallow or deep burrowers. Although the evolution of siphons was a key feature in the evolution of the group, during the analysed time interval they were mainly shallow burrowers, either asiphonate or with poorly developed siphons; their general shape during the Triassic and Early Jurassic points to slow to moderately rapid burrowers (Ros 2009).

Although originating during the Ordovician, they seem to have been severely affected by the end-Permian extinction event, as their first record in the study interval is a genus from the Olenekian stage (Hautmann and Nützel 2005). During the Middle Triassic they underwent a moderate radiation (Figure 6(C)), but it was in the Late Triassic when they became important components of bivalve faunas (11 genera at the base of the Norian and 15 genera at the base of the Rhaetian). During the end Triassic extinction event they were highly affected (10 genera crossing the top of the Rhaetian), but they recovered soon, reaching even higher diversities in the first two stages of the Jurassic. This order is one of the most diverse nowadays, although only after the K/T event it became dominant, with many families appearing at the base of the Cenozoic (Kondo and Sano 2009) and several forms exploiting progressively deeper habitats (Lockwood 2004). Within the order, Lucinoidea is a peculiar superfamily characterised by the presence of chemosymbiotic organisms, which allowed them to inhabit suboxic environments; this symbiotic relationship probably began in the Paleozoic (Taylor and Glover 2000, 2006). The first genus of our study interval appeared in the Olenekian (*Sinbadiella*) (Hautmann and Nützel 2005), but the group remained with a very low and almost constant diversity during the whole range (approximately one genus with a peak of two genera at the end of the Sinemurian).

The superfamily Crassatelloidea dominated the diversity of the group, including half of the genera for the whole order (18 out of 36); they are asiphonate, being mostly shallow burrowers. Among them, the Astartidae were the most diverse, although they reached their maximum diversity at the top of the Sinemurian (eight genera), being the major contributors to the Jurassic diversity recovery of the order. Strikingly, two of its genera, *Opis* and *Coelopis*, had an epifaunal habit (Hautmann 2001b). Myophoricardiidae is a Triassic family, being important during the Middle and Late Triassic, but they all went extinct during the Rhaetian; the family Cardiniidae had many short-ranging genera, although their diversity remained without much change.

The superfamilies Cardioidea (family Cardiidae) and Carditoidea (family Carditidae) are superficially similar, with strong radial sculpture producing an internally crenulated shell margin. They appeared in our study interval in the Late Triassic (Carnian for the Carditidae and Norian for the Cardiidae), and diversified through this period, but they decreased during the Rhaetian, being the major responsibles (together with the Myophoricardiidae) for the diversity drop within the order. The superfamilies Tellinoidea and Arcticoidea remained with low diversities in the study interval since their appearances. Although the Tellinoidea now comprises deposit-feeding genera, this nutrition type did not appear in the group until Early Cretaceous (Jablonski and Bottjer 1990).

'Megalodontids' (Order Hippuritida?)

Megalodontids are an extinct group of bivalves of uncertain affinities (Bouchet and Rocroi 2010). They date back from the Devonian (Skelton 1978), but although abundant, they were not diverse during the Paleozoic. It was proposed that megalodontids (superfamily Megalodontoidea) could have established photosymbiotic relationships (Freitas et al. 1993; Yancey and Stanley 1999), like the rudists in the Cretaceous (Kauffman and Johnson 1988) or the family Alatoconchidae in the Permian (Isozaki 2006). Although megalodontids have certain characteristics common with modern forms which bear photosymbionts (Vogel 1975; Seilacher 1990; Jones and Jacobs 1992), many living species with this nutrition type do not have any specialised shell modification, and, conversely, some species with those modifications do not have any symbiont (Jones and Jacobs 1992; Savazzi 2001). Whether they had photosymbionts or not, they were epifaunal sedentary forms, most frequently found in carbonate and tropical facies (Végh Neubrandt 1982). They were almost exclusively distributed along the Tethys (Ros 2009), although *Wallowaconcha* (family Wallowaconchidae) was recorded in the Pacific domain (Yancey and Stanley 1987, 1999). They had thick heavy shells, reaching great sizes during the Norian and Rhaetian (up to 42 cm, Végh Neubrandt 1982, p. 45; or even 50–60 cm, Allasinaz 1992, p. 447). All these characters point to highly specialised forms.

There are no Early Triassic records; *Physocardia arthaberi* (Kutassy) from the Anisian of Turkey (Fantini Sestini 1984) is the first mention for our study interval. They had a first diversification during the Carnian (radiation of the Dicerocardiidae), reaching their diversity peak in the Norian (Figure 6(D)); they are a group with high turnover rates, with short-ranging genera and many singletons. They were strongly affected by the end Triassic extinction event, being unrepresented in the fossil record until Sinemurian (genus *Pachyrisma*). The high vulnerability of this group is not surprising, as they were mostly tropical forms. These are usually much more prone to suffer from environmental disturbance, and the end Triassic extinction event was not an exception in this regard (Kiessling and Aberhan 2007). As in Ostreida, the recovery of the group may have been delayed by the Early Jurassic calcification crisis.

Order Modiomorphida

Modiomorphida is an extinct order which was highly diverse and abundant during Paleozoic times. It was strongly affected by the end-Permian event, and only a few geographically restricted genera survived the P/T boundary (Damborenea 2004). They are a complex group, from both a systematic and an ecologic viewpoint. During our study interval, only the superfamily Kalenteroidea was represented (see Fang and Morris 1997; Damborenea 2004). The life habit considered for the Triassic and Early Jurassic genera is that of shallow burrowers or endobyssate, although none of them has conclusive evidence of the presence of neither byssus nor siphons (Ros 2009). Nevertheless, some species of the genus *Permophorus* (Kalenteridae) had some modifications suggesting that they had a byssus, e.g. a reduced anterior part (Stanley 1972; Quiroz-Barroso and Perrilliat 1998); the same feature is shared by most species of *Myoconcha* (Myoconchidae) [Stanley 1972; see Ros (2009) for a discussion on each genus].

Diversity remained low in the group during the Early and Middle Triassic, then rising during the Late Triassic (Figure 6(E)); it showed a diversity peak at the base of the Rhaetian. Despite having the highest origination rate for this last age, it was strongly affected by the extinction, losing 62% of its genera. The three families in our study interval (Kalenteridae, Myoconchidae and Hippopodiidae) crossed into the Jurassic with one genus each, but they did not diversify during its first two stages. They did not fully recover during the rest of the Mesozoic, and probably went extinct by the end of the Cretaceous, although there might be a record for the group for Tertiary times (Griffin and Pastorino 2006).

Order Pholadomyida

They originated during the Ordovician, becoming widespread in the Late Paleozoic and Mesozoic, but less common in the Tertiary (Runnegar 1974). Most genera included herein were deep burrowers, although there are also shallow burrowers and – less commonly – modern genera include reclining, endobyssate and cementing forms (Runnegar 1974; Harper et al. 2000). Mantle lobes are ventrally fused, leaving only three (sometimes four) pallial apertures and the dorsal fusion of the periostracum is common, forming a secondary ligament (Runnegar 1972; Morton 1974, 1976, 1977; Sartori and Domaneschi 2005). There is a common trend among several lineages towards a progressive anterior elongation of the shell, resulting in a more anteriorly directed foot (Runnegar 1974). Although juveniles can be active burrowers, adults are generally considered sedentary forms unable to reburrow once disturbed from their life position (Runnegar 1972; Morton 1973).

Two families seem to cross the P/T boundary, Pholadomyidae and Chaenomyidae, according to Runnegar (1974). However, there is a gap in the record of the order as no Induan genera have been described (Figure 6(F)). *Pleuromya* first appeared in the Olenekian (Posenato 2008b), and since then the order showed an almost constant trend of increasing diversity. All genera recorded in the Early and Middle Triassic belong to the superfamily Pholadomyoidea, having an external ligament (Runnegar 1974). During the Carnian they experienced some diversification, with a large proportion of singletons; they reached a diversity peak at the end of the Rhaetian with eight genera and six families present. After a small decrease in the Hettangian, they recovered during the Sinemurian.

Several morphological changes occurred in the group during the study interval. The most notorious one is the internalisation of the ligament with the evolution of the superfamilies Ceratomyoidea (semi-internal ligament) and Pandoroidea (internal ligament). Ceratomyoidea went extinct in the Cretaceous, while Pandoroidea experienced certain diversification during the Cenozoic, with more families than Pholadomyoidea (Runnegar 1974). The slow but almost constant diversification of this group during the study interval, and its immunity from the Rhaetian extinction, might be related to the protection of the deep infaunal habit against environmental perturbations.

Discussion

Post-Permian faunal recovery among bivalves

The end-Permian extinction eliminated about 95% of animal species on the planet (Erwin 1993). This huge diversity reduction must have produced a strong relaxation of many selective biotic pressures such as predation and competition. In a hypothetical scenario, such relaxation would allow the survivor species to vary and develop new morphologies. Structural innovations that would have been deleterious (or at least would have reduced fitness) under high-competition conditions could develop and proliferate during the beginning of the Triassic leading to new adaptations for many of the lost niches, and even creating new ones.

Bivalves were one of the least affected groups of marine invertebrates during the end-Permian mass extinction (Yin 1985; Hallam and Miller 1990). So, from the beginning of the recovery, they had the advantage of having more phenotypic (and genetic) variability available to face the challenge of new environmental requirements. The high turnover of families (which of course are defined by morphology and hence represent trials of innovative morphologies) during the Early and Middle Triassic shows this morphological renewal in many bivalve taxa.

If we look at the diversity curve (Figure 2), there is a high increase in diversity by the Anisian, with a lower and somewhat more stable increasing trend during the Ladinian, Carnian and Norian. Nevertheless, if we also consider the diversity dynamics of the different ecological categories (Figure 3(A,B)), there are still important changes occurring among these stages, especially during the Carnian. From this stage on, shallow burrowing bivalves become dominant but, more important, relative proportions of the ecological categories remained stable (with the exception of the end-Triassic extinction). Something similar occurred among the orders (Figure 4), although the response to the T/J extinction varied among them (see below). From these observations, we can infer that only at the end of the Carnian the faunal recovery was completed.

Returning to a hypothetical scenario, at this point we would expect biological pressures to regain importance, and so competition and predation may have started to define specialisation trends among the newly settled morphologies, with an increasing diversity yielding progressively more specialised taxa. If this was the case, one would expect a high number of short-ranging genera, as implied by the many singletons in the MSD values for the Carnian and Norian (Figure 2). Competition is difficult to prove, so this statement may probably remain somewhat speculative, but there are many evidences for increasing predation pressures during the Late Triassic (Nützel 2002; Hautmann 2004a; Nützel and Erwin 2004; Harper 2005; Bonuso and Bottjer 2008; Vermeij 2008; Baumiller et al. 2010; Ros 2009).

Concerning ecological strategies, epifaunal life habits dominated the initial recovery. There were 22 genera extending from Paleozoic times in our study interval (excluding *Acharax*). Of those genera, 10 (45.4%) were epifaunal, most of them attached but one motile; five (22.7%) were endobyssate and seven (31.8%) were infaunal, mostly shallow burrowers with only one deep burrower. By the end of the epoch, the proportions changed a little (48.3% for epifaunal, 20.7% for endobyssate and 31.0% for infaunal), and the generic radiation was modest (from 22 to 29 genera). It was not until the Anisian that the major generic radiation occurred. The epifaunal forms experienced certain turnover, and there is a relatively high number of families with this mode of life appearing (or reappearing) by then. Two main explanations of this pattern can be offered; on one hand some of the physical disturbances linked to the end-Permian extinction continued during the Early Triassic. Oceans were likely anoxic and euxinic, with anoxic waters reaching shallow environments probably twice (Woods 2005; Wignall and Racki 2009 and references herein). Infaunal animals are expected to be more sensitive than epifaunal ones under anoxic conditions (Erwin 2001; Aberhan and Baumiller 2003), and in this case endobyssate genera may be considered as ecologically closer to epifaunal ones. This could explain why the typically infaunal orders showed almost no variation during the Early Triassic while epifaunal forms showed certain diversification and turnover. When favourable environmental conditions were re-established during the Anisian (Isozaki 1997), recovery was faster for both groups. On the other hand, infaunal bivalves were less common than epifaunal ones during the Paleozoic (Stanley 1968), so what was represented at the base of the Mesozoic is an impoverished version of Paleozoic faunas (Ros et al. in prep.), maintaining to a certain degree the relative relationships among categories. As a consequence, the recovery pattern resulted from a reduced set of survivors extending from the Permian exploiting the empty niches, showing more variability among epifaunal forms (hence faster diversification). However, this recovery pattern was somewhat delayed by the Early Triassic environmental perturbations (Woods 2005).

Diversity dynamics among bivalves during the Triassic and earliest Jurassic

Early Triassic

At this time bivalves started to be ecologically dominant (Fraiser and Bottjer 2007). As stated before, it was a time of great turnover, with high-extinction rates (Figure 2) probably due to the stressful environments (Woods et al. 1999; Woods 2005). While epifaunal attached (mostly epibyssate), shallow burrowers and endobyssate were the most diverse ecological categories, some of the categories less represented or absent during Late Paleozoic either expanded (epifaunal motile) or reappeared (epifaunal sedentary) by this time (Figure 3).

The Order Pectinida clearly dominated diversity during this time at both genus and family levels (it had 37% of genera and 35% of families at the Induan/Olenekian boundary); the turnover at these times is clear at both taxonomic levels, resulting in structural modifications (i.e. an internal ligament associated to straight hinge line and expansion of foliated shell microstructure) that allowed pectinids to subsequently improve the swimming habit. Also, some of the most frequent and abundant Early Triassic genera belong to this order. The second most diverse order, Pteriida, also showed some turnover, although not as strong as Pectinida, it is among this group that our epifaunal–sedentary ecological category reappeared – in *Bositra* (Posidoniidae). Probably the great number of empty niches, together with the relaxation of predation pressures, allowed for a diversification of epifaunal habits [normally more vulnerable to predation (Stanley 1977b; Skelton et al. 1990)] and favouring the development of new morphologies. Shallow burrowers were far less represented with only six genera extending from Permian times, three were Nuculida, two were Trigonida and one was Modiomorphida.

Middle Triassic

During this time a fast diversification of most habits took place, with the epifaunal ones being dominant during both stages and representing more than 50% of genera; among them, epifaunal attached were quantitatively the most important. The most significant radiation occurred during the Anisian (from 29 genera at the base to 63 at its top), with the second highest origination rate of all stages (only surpassed by the Induan rate). Largest categories (epifaunal–attached and shallow infaunal–motile) had strong rises at this stage, but differed during the Ladinian, with epifaunal ones still rising in diversity (10 genera at the base of the Anisian, 21 at the Anisian/Ladinian boundary and 28 at the top of the Ladinian), while shallow burrowers remained almost unchanged (from 7 genera at the base of the Anisian to 16 at the boundary and 17 at the top of the Ladinian). Endobyssate genera, although rising in number, decreased in proportion compared to other categories (Figure 3). Epifaunal–motile genera, mostly belonging to the order Pectinida, reached a diversity of nine genera at the base of the Ladinian, and after that they remained almost unchanged in diversity for most of the Triassic. Deep burrowers and epifaunal sedentary forms showed some diversification, but they still maintained low diversities (four genera at the top of the Ladinian for each one).

All orders diversified during this epoch, although sometimes the diversification was low. Diversity is still dominated by Pectinida and Pteriida, but proportionally reduced (Figure 4) because of the radiation of other groups, either epifaunal (Limida and to a less extent, Mytilida and Arcida) or infaunal (Trigoniida, Venerida and Nuculida). The cementing habit spread during this time interval, with the appearance of the order Ostreida (or perhaps, of three unrelated lineages of cementing bivalves). Family turnover of epifaunal bivalves continued during the Middle Triassic, and began in infaunal ones too, especially in the orders Trigoniida and Venerida, indicating major morphological modifications in these groups.

Late Triassic (Carnian and Norian)

The Carnian underwent what seems to be the saturation of epifaunal niches (mainly attached and motile), suggested by the strong turnover and high-evolutionary rates without substantial increases in diversity. At this stage, infaunal habits (including the endobyssate one) surpassed the epifaunal ones (Figure 3); this is mostly due to diversification of shallow burrowers (from 17 genera at the base of the stage to 33 at its top), which for the first time outnumbered epifaunal–attached genera (from 28 to 29 genera, respectively), and from then on they were always more diverse (except at the T/J boundary, when both groups had the same number of genera). The remaining categories show low-diversification rates, but in some instances, like the epifaunal–sedentary habit, with peaks of MSD at the stage (i.e. high number of singletons). At this point, food webs might have been completely re-established and predation pressure would have started to determine progressive specialisation trends in the protection against predators (perfection of swimming in Pectinida, diversification of cementation in Ostreida and some Pectinida, radiation of shallow burrowers in Venerida, Trigonida and Modiomorphida, continuation of the slow diversification of deep burrowers in Pholadomyida). These trends seem to be maintained throughout the Late Triassic. There was a diversification of the less represented categories during the Norian (from five genera at the base to eight at the top for deep burrowers, from five to nine for epifaunal–sedentary, and from 8 to 11 for epifaunal–motile); once again there was a high number of singletons among epifaunal sedentary bivalves, although the MSD did not exceed the BC value for the top of the Norian.

Rhaetian and Early Jurassic (Hettangian and Sinemurian)

During the Rhaetian, bivalve faunas suffered an important reduction in diversity (42% of genera present at the Rhaetian went extinct then, with the BC diversity falling from 108 genera at its base to 72 at its top, about 33%). Shallow burrowers and epifaunal–attached forms were the most numerous by this time, and were strongly affected (shallow burrowers experienced a 46% reduction while epifaunal–attached lost 31% of genera), and thus determining that pattern. Of the less represented categories, epifaunal–sedentary forms were the most affected, losing 67% of the diversity between the base and the top of the Rhaetian, while the remaining categories were unaffected (deep burrowers) or had few losses (8% among endobyssate, 18% among epifaunal–motile).

Regarding systematic groups, there is a negative correlation between the Carnian and the Rhaetian for the diversification rates of the different orders (Figure 7), meaning that the taxa with highest diversification during the Carnian suffered highest diversity depletions during the Rhaetian ($r = -0.56$; $p = 0.059$). This suggests that extinction was stronger among specialised taxa.

The previous analysis shows that, during the first two stages of the Jurassic, one can recognise in the diversity dynamics of orders the following three main responses to the end-Triassic extinction:

(1) *Orders that were almost unaffected by the extinction event*. These include the orders Mytilida, Arcida, Limida and Pholadomyida. The former three showed similar dynamics along the study interval, with low diversities reaching their relative maximum peaks during Middle Triassic (at most during the Carnian). They are mostly morphologically (Arcida) or ecologically (Mytilida and possibly Limida) gener-

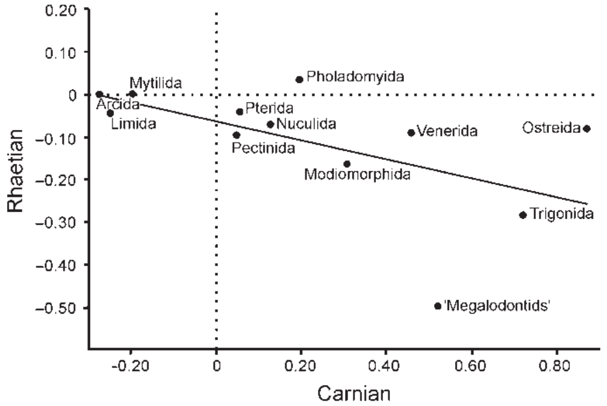

Figure 7. Relationship between Carnian diversification rates (x-axis) and Rhaetian diversification rates (y-axis) with the regression line – diversification rates in number of genera × genus^{-1} × my^{-1}.

alised forms. Pholadomyida is different; although always showing low diversities, they exhibit an almost continuous increase rate along the study interval. As they are mostly – and almost the only – deep burrowers, they reflect the history of this life habit; they represent about 5–7% of genera between the Olenekian and the Norian, and since the Rhaetian they were about 9–11% of genera. The immunity of the group may be due to the stability of this life habit against environmental perturbations.

(2) *Orders affected by the extinction event but with quick recoveries (highly resilient orders)*. These include the orders Pectinida, Pteriida, Venerida, Nuculida and probably Trigoniida. Pectinida, Venerida and Nuculida show a very similar pattern, with higher diversities at the top of the Norian (Nuculida with lower diversities than the other two), strong reductions at the boundary and an almost total recovery of diversity during the first two stages of the Jurassic. In Pteriida, the pattern is somewhat different; they reached a diversity peak in the Carnian (MSD) and then their number of genera was reduced along the Late Triassic, reaching a minimum at the top of the Rhaetian. After the boundary they rose again in diversity, even surpassing the Carnian peak; this response seems to be intermediate between the more generalised epifaunal orders of the first group and the more specialised ones like the Pectinida. Trigoniida can be included also in this group; although their maximum diversity attained during the first two Jurassic stages (seven genera) is far from the Triassic peak (14 genera at the end of the Carnian), diversification rates were the highest in this order. Their inability to reach previous diversity values may be due to the strong Rhaetian depletion (their diversity rate is one of the lowest, being surpassed only by that of the megalodontids) and the low diversities at the beginning of the Jurassic (only three genera). Despite this low diversity, the order would be one of the most conspicuous in Jurassic and Cretaceous shelf-environments.

(3) *Orders affected by the extinction event and with almost no recovery during the first two Jurassic stages (less resilient orders)*. These include the orders Ostreida, Modiomorphida and the megalodontids. Diversities are usually low in these groups, with the highest diversities at the base of the Rhaetian (just seven genera for the Ostreida and even less for the others), high losses during this stage and almost no recovery during the Hettangian and Sinemurian. The constituent lineages of the order Ostreida were the less affected, and most of the losses were among the Plicatulidae; although their diversity remained constant during the Jurassic stages of our study interval, they would become important components of the Jurassic and Cretaceous faunas. Modiomorphida was strongly affected, and its diversity was low for the rest of its geological history. Megalodontids suffered pseudoextinction (sensu Allasinaz 1992) at the T/J boundary, reappearing in the Sinemurian; hence, the existence of Hettangian ghost lineages can be inferred.

Properties of the end-Triassic extinction event

Although the end-Triassic has been questioned as a true mass extinction (Bambach et al. 2004; Tanner et al. 2004; Bambach 2006; Lucas and Tanner 2008), the sudden diversity drop during the Rhaetian (Figure 2) clearly shows a mass extinction, at least for bivalves, although not necessarily catastrophic, at the end of the Rhaetian (Hallam 2002). Nevertheless, some peculiarities indicate that this mass extinction was not indiscriminate. On ecological grounds, there was a clear selectivity against certain habits, such as epifaunal–sedentary and shallow burrowers, while others seem to be favoured, as was the case of deep burrowers, endobyssate and epifaunal–motile (Ros and Echevarría in prep.).

There is also a differential response among the different orders, i.e. some orders were clearly unaffected, while others were affected to various degrees. As stated before, the event did not affect morphologically or ecologically generalised forms, but was strong among the specialised ones. It is highly suggestive that the orders with the highest diversification rates during the Carnian also had the highest diversity depletions during the Rhaetian. So extinction was not indiscriminate in the different orders, but instead was stronger in more specialised ones. An important exception is the order Pholadomyida, a highly specialised order of deep burrowers. In this case, the protected life habit may have aided in the survival of the group.

Summary

(1) Epifaunal bivalves dominated – in diversity terms – the initial recovery after the P/T extinction, probably due to their greater diversity among Paleozoic survivors and to their higher tolerance to environmental stress (e.g. anoxia).

(2) During Early and Middle Triassic bivalves clearly qualify as an evolutionary resilient lineage, undergoing a morphological renovation with the appearance of many innovations within different orders; the most important radiation occurred during the Middle Triassic, with a sharp increase in the numbers of genera.

(3) Faunal recovery (at least for bivalves) was completed during Carnian times, marked by the dominance of infaunal habits over the epifaunal ones, and from then on, the Late Triassic represented a time of high-ecological pressures, defining many specialisation trends among bivalves.

(4) The end-Triassic extinction among bivalves was a mass extinction, but it was not indiscriminate, as some ecological categories were unaffected or little affected and generalised orders were positively selected, whereas specialised ones were greatly reduced in diversity.

(5) During the Hettangian–Sinemurian, diversity recovered quickly, approaching pre-extinction values; nevertheless, the performance varied among the orders with some of them, mainly those thick-shelled related to reef or tropical environments (Ostreida and 'Megalodontids'), showing a delayed response; this was probably due to the biocalcification crisis occurring during that interval.

(6) The different diversity dynamics shown by the various categories during both recovery phases clearly demonstrate that evolutionary resilience also varied in different taxonomic and ecological groups of bivalves.

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Note

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