

CALIBRATED DIVERSITY, TREE TOPOLOGY AND THE MOTHER OF MASS EXTINCTIONS: THE LESSON OF TEMNOSPONDYLS

by MARCELLO RUTA and MICHAEL J. BENTON

Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK; e-mails M.Ruta@bristol.ac.uk; Mike.Benton@bristol.ac.uk

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Abstract: Three family-level cladistic analyses of temnospondyl amphibians are used to evaluate the impact of taxonomic rank, tree topology, and sample size on diversity profiles, origination and extinction rates, and faunal turnover. Temnospondyls are used as a case study for investigating replacement of families across the Permo-Triassic boundary and modality of recovery in the aftermath of the end-Permian mass extinction. Both observed and inferred (i.e. tree topology-dependent) values of family diversity have a negligible effect on the shape of the diversity curve. However, inferred values produce both a flattening of the curve throughout the Cisuralian and a less pronounced increase in family diversity from Tatarian through to Induan than do observed values. Diversity curves based upon counts of genera and species display a clearer distinction between peaks and troughs. We use rarefaction techniques (specifically, rarefaction of the number of genera and species within families) to evaluate the effect of sampling size on the curve of estimated family-level diversity during five time bins (Carboniferous; Cisuralian; Guadalupian–Lopingian; Early Triassic; Middle Triassic–Cretaceous). After applying rarefaction, we note that Cisuralian and Early Triassic diversity values are

closer to one another than they are when the observed number of families is used; both values are also slightly higher than the Carboniferous estimated diversity. The Guadalupian–Lopingian value is lower than raw data indicate, reflecting in part the depauperate land vertebrate diversity from the late Cisuralian to the middle Guadalupian (Olson's gap). The time-calibrated origination and extinction rate trajectories plot out close to one another and show a peak in the Induan, regardless of the tree used to construct them. Origination and extinction trajectories are disjunct in at least some Palaeozoic intervals, and background extinctions exert a significant role in shaping temnospondyl diversity in the lowermost Triassic. Finally, species-, genus-, and family trajectories consistently reveal a rapid increase in temnospondyl diversity from latest Permian to earliest Triassic as well as a decline near the end of the Cisuralian. However, during the rest of the Cisuralian family diversity increases slightly and there is no evidence for a steady decline, contrary to previous reports.

Key words: cladogram, extinction, diversity, ghost lineages, origination, phylogeny, rarefaction.

A LARGE proportion of the literature on Phanerozoic diversity draws from Sepkoski's (1992, 2002) two monumental compendia on families and genera of marine fossil animals. Modifications, additions, and refinements to both compendia provide the foundations for analyses of origination and extinction rates, reconstruction of trajectories of taxonomic diversity through time, and quantification of biotic turnover. The development and enrichment of databases for macroevolutionary investigations have a prestigious and long tradition in palaeobiology. As a result, data on diversity are now available for several groups (e.g. Benton 1993; see also online resources such as The Paleobiology Database: <http://paleodb.org/cgi-bin/bridge.pl> and FossilPlot: <http://geology.isu.edu/FossilPlot/Index.htm>). However, there is a

dearth of quantitative macroevolutionary studies for the vast majority of fossil vertebrate groups (but see Benton 1985a, b, 1987, 1994, 1995, 1996a, b, 2003, Maxwell and Benton 1990, Benton and Simms 1995, and Benton and Hitchin 1996). In addition, only a very small number of papers have addressed specifically large-scale evolutionary patterns in early tetrapods (e.g. Pitrat 1973; Benton 1985b, 1987; Olson 1989; Maxwell 1992; Benton *et al.* 2004; Laurin 2004; Ruta *et al.* 2006; Wagner *et al.* 2006).

As the most species-rich and widespread of all groups of early tetrapods, temnospondyl amphibians are suitable for macroevolutionary studies. In an early account of this group's diversity, Carroll (1977) provided a stratigraphic plot of family ranges, but offered no qualitative or quantitative frameworks for investigating faunal turnover or

extinction/origination rates. More recently, Milner (1990) built a large-scale (albeit not a computer-assisted) cladistic analysis of family-level relationships for temnospondyls as a whole. This analysis was employed to assess timing and magnitude of the main diversification and extinction events in temnospondyl history as well as patterns of biogeographic dispersal and ecological partitioning.

In this paper, we undertake a new analysis of temnospondyl diversity. This study is certainly timely, given the large number of temnospondyl species described since Milner's (1990) paper (representing an increase of almost 20 per cent) and the availability of analytical techniques for macroevolutionary inference. Specifically, we address the following issues:

1. the impact of different taxonomic ranks on trajectories of raw (i.e. observed) diversity;
2. the influence of cladogram shape, ghost lineages, and range extensions on these trajectories;
3. the correlation (if any) between rates of family extinctions and originations (i.e. faunal turnover);
4. the effect of sample size on diversity profiles, in particular during periods of depauperate taxonomic richness (especially Olson's gap; see below);
5. the impact of the end-Permian mass extinction on temnospondyl diversification near the Palaeozoic-Mesozoic boundary and the pattern of taxonomic recovery in the aftermath of that extinction.

Taxonomic rank is an important, yet often neglected component of any macroevolutionary analysis. Empirical work demonstrates that diversity trajectories produced using a variety of ranks may differ to a considerable extent. These differences ultimately result in different models of diversity expansion and contraction during a group's history, including the fitting of appropriate curves for assessing patterns of increasing taxonomic growth (e.g. see Bambach 1989 and Lane and Benton 2003). The use of different ranks can alter profoundly models of recovery in the aftermath of large-scale extinctions, e.g. by either diluting or exaggerating the magnitude of the latter. Similarly, ranks can impact our perception of rates of originations (e.g. a gradual increase in taxonomic richness as opposed to a burst of diversification).

Jablonski (2007) provided a detailed treatment of the scale effect in macroevolutionary studies while Benton and Emerson (2007) discussed some problems associated with the use of species for large-scale macroevolutionary inference. Such problems range from errors introduced by

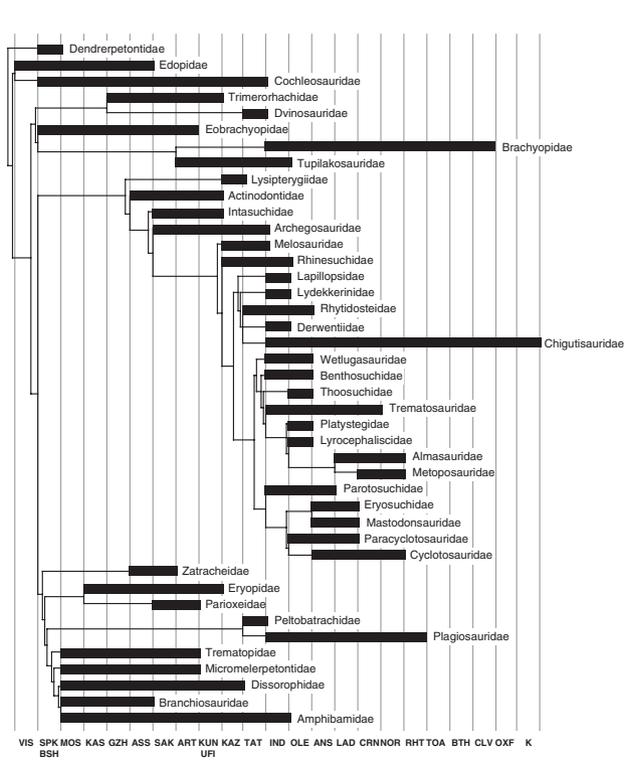
synonymy to the amount of effort and time required for data collection at a low taxonomic level, and from precision in dating to sampling bias. However, in the case of temnospondyls the number of species is 'manageable', not least because recent compendia cover the majority of described species and include detailed reviews of their synonymy. Dating and sampling problems are certainly more difficult to tackle. However, for the main purposes of the present paper, the assignment of species to stages will suffice. Although certain species pose difficulties in this respect (i.e. their precise assignment to a stage is dubious), they represent only a small fraction of the total number. As far as sampling is concerned, we assume that the group's record forms an unbiased collection from its entire stratigraphic range. This may seem unwarranted, given the fact that several temnospondyl assemblages (e.g. in the Carboniferous) show characteristic ecological fingerprints (see Milner 1990). For this reason, their probability of preservation would be higher than that of species living in environments that are not conducive to preservation. The impact of ecological and/or biogeographic factors on the trajectories of observed diversity will be considered in a separate publication (but see also Benton 1985*a, b*, 1987).

As far as the topology of phylogenetic trees is concerned, we seek to assess differences in profiles of family-level temnospondyl diversity when ghost lineages and range extensions (e.g. Norell 1992; Smith 1994) are taken into account. To this end, we use three recently published temnospondyl phylogenies. The use of families is dictated by the fact that species- or genus-level phylogenies for temnospondyls are not available, despite the number of cladistic data sets published so far. Only some of these data sets have considered a significant proportion of all major temnospondyl clades (see Yates and Warren 2000 and Ruta and Bolt 2006); many others (e.g. see Schoch and Rubidge 2005; Damiani *et al.* 2006; Laurin and Soler-Gijón 2006; Witzmann and Schoch 2006 and Schoch *et al.* 2007) have tackled small sections of the temnospondyl tree, e.g. to assess the phylogenetic placement of a few key species.

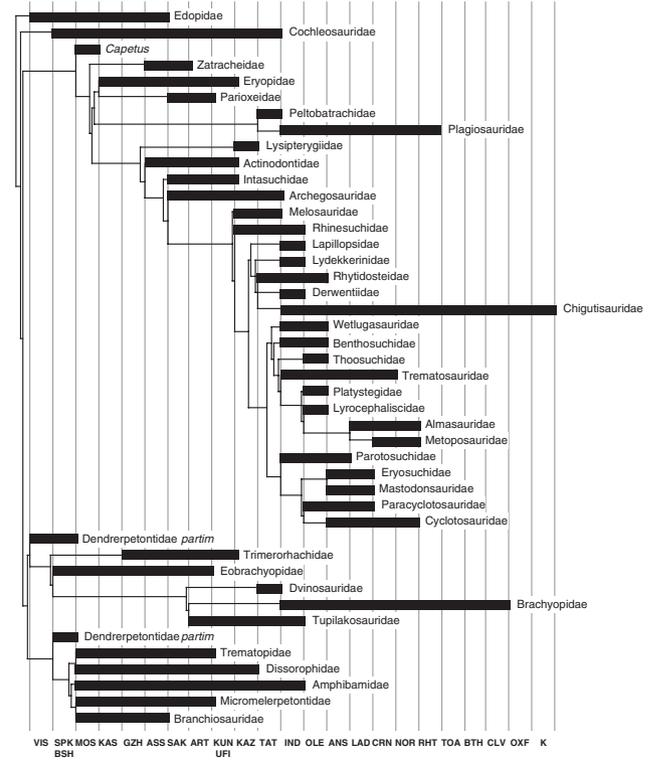
Our use of the expressions 'range extension' and 'ghost lineage' conform strictly to Smith (1994). A range extension of a taxon is the minimum stratigraphic range added to (or extended below) the earliest occurrence of that taxon in order to join an older taxon. In Text-fig. 1A–C, the range extensions are represented by the thin horizontal lines drawn immediately to the left of observed family ranges

TEXT-FIG. 1. Family-level relationships of temnospondyls superimposed on a time scale. A, Milner's (1990) tree; B, Ruta and Bolt's (2006) tree; C, Yates and Warren's (2000) tree. In Milner's (1990) and Ruta and Bolt's (2006) trees, the interrelationships of stereospondyls follow Schoch and Milner (2000); in Yates and Warren's (2000) tree, the interrelationships of several Palaeozoic families follow Milner (1990). D, hypothetical pattern of relationships among three families with schematic illustration of a ghost lineage and a range extension (see text for details).

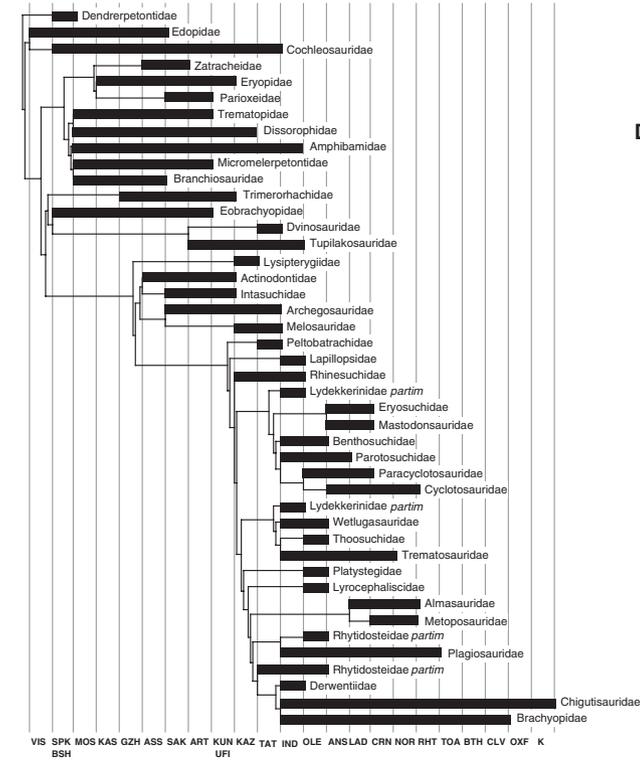
A



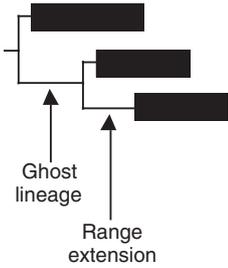
B



C



D



(black rectangular bars). A ghost lineage is an internal branch of a tree superimposed on a time scale, and for which no fossils are documented (Smith 1994). The thin horizontal lines that connect internal nodes in Text-fig. 1A–C are ghost lineages. Text-figure 1D illustrates the distinction between ghost lineages and range extensions.

The rates of family origination and extinction per unit time are constructed using a variety of metrics (see below), and inform the dynamics of faunal turnover. We are particularly interested in assessing the impact of the end-Permian mass extinction event on temnospondyl evolution. This issue was dealt with at length by Milner (1990) who employed ghost lineages and range extensions to quantify background family extinctions.

Finally, rarefaction techniques similar to those employed by ecologists and population biologists are applied to raw diversity values in order to re-calibrate diversity curves via taxon subsampling. Rarefied diversity for different time bins (e.g. see Raup 1975; Miller and Foote 1996; Hammer and Harper 2006 and references therein) permits more accurate comparisons among values of diversity when a reference sample of constant size is used (e.g. Benton *et al.* 2004).

Results from this work are brought together to quantify changes in diversity profiles near the Permo-Triassic boundary and recovery patterns in the aftermath of the end-Permian mass extinction. We want to see whether a so-called post-extinction ‘rebound’ (*sensu* Erwin 1993) best accounts for the elevated taxonomic richness in the lowermost Triassic (especially when compared to diversity values during the mid to late Permian). Furthermore, we are interested in the dynamic interplay between originations and extinctions immediately before and after the end-Permian extinction and in the correlation between raw diversity and faunal turnover.

Hereafter, ‘diversity’ is employed exclusively in the sense of, and interchangeably with, ‘taxonomic richness’, that is count of taxonomic units (e.g. Raup 1975). ‘Curve’, ‘profile’, and ‘trajectory’ are also used interchangeably. Finally, ‘raw’ data are ‘observed’ data (e.g. Miller and Foote 1996).

MATERIAL AND METHODS

All material used in this study is available upon request and can be used for further analytical protocols and statistical calculations.

A note on the use of old stage names

We have used the traditional scheme of stage subdivisions for the Guadalupian-Lopingian time interval instead of

the international stage names, for two pragmatic reasons. First, assignment of temnospondyls to the international stages is less straightforward than assignment based upon old stage names, because the latter have been used more often in the most recent compendia (e.g. Schoch and Milner 2000; Ward *et al.* 2006). Second, five species are known from the combined Kungurian and Ufimian time interval; therefore, these two stages have been lumped together as a single time unit to represent total observed diversity at the end of the Cisuralian (but see also stratigraphic notes in the supplementary data to Ward *et al.*'s 2006 paper). The Roadian and Wordian diversity, during the first half of the Guadalupian, can be mostly summarised using the old Kazanian stage, which includes 22 species. This leaves us with the distribution of diversity in the late Permian (21 species) being spread over the period from Capitanian (upper half of the Guadalupian) through to Wuchiapingian and Changhsingian (both stages spanning the entire Lopingian). This period corresponds approximately to the old Tatarian (Benton *et al.* 2004).

Large-scale interrelationships of temnospondyls

This work considers three family-level cladograms of temnospondyls projected on a stratigraphic time scale (Text-fig. 1A–C). Family ranges are shown by black rectangular bars. All stages are illustrated as having an identical length for simplicity. Stage names are mostly based upon Gradstein *et al.* (2004; see also the note above on the use of older stage names). Ghost lineages and range extensions (Norell 1992; Smith 1994) extend through all stages comprised between the first appearances of adjacent (i.e. sister) families (or groups thereof). The total count of recognised families follows Milner (1990) and Schoch and Milner (2000).

The selection of comprehensive cladistic analyses for temnospondyls is problematic (see above); the only study providing a coverage of all families is Milner (1990). Ruta and Bolt (2006) have published a character-based analysis of (mostly) Permo-Carboniferous temnospondyls, whereas Yates and Warren (2000) have proposed a radically different pattern of relationships for stereospondyls (the largest group of temnospondyls) from Milner (1990) and Schoch and Milner (2000). While acknowledging that there is no satisfactory solution to the issue of encompassing as much family diversity as possible, given the published phylogenies, we have to start somewhere. The plot of Milner's (1990) cladogram is shown in Text-fig. 1A. The species-level tree of Ruta and Bolt (2006) was first converted to a family-level tree (mostly by replacing species with the families to which they belong). However, a number of additional modifications were introduced. First, a basal archegosauriform-stereospondyl clade, represented by the

species *Sclerocephalus haeuseri* (Actinodontidae) and *Cheliderpeton latirostre* (Intasuchidae) in Ruta and Bolt's (2006) analysis, was replaced by the basal archegosauriform-stereospondyl clade in Milner's (1990) tree (i.e. the latter clade was 'grafted' onto Ruta and Bolt's 2006 tree without changes; Text-fig. 1B). Although the topology of the stereospondyl part of Milner's (1990) tree matches well Schoch and Milner's (2000), we opted for the latter in Text-fig. 1A–B, as Schoch and Milner's (2000) analyses provide greater resolution for stereospondyl interrelationships than Milner's (1990). In the case of both Milner's (1990) and Schoch and Milner's (2000) studies, no formal computer analysis was undertaken. We do not regard this as a major issue, as several subsequent analyses of temnospondyls based upon a small sample of species have retrieved patterns of relationships (although these cover smaller sets of all families) that resemble closely those proposed by Milner (1990) and Schoch and Milner (2000). In this context, we note that Ruta and Bolt's (2006) tree represents a novel topology as far as the relationships among major groups of Permo-Carboniferous temnospondyls are concerned.

Second, the family Dendrerpetontidae is monophyletic in Milner's (1990) analysis, but polyphyletic in Ruta and Bolt's (2006) analysis; specifically, Ruta and Bolt (2006) retrieved one of the species in the genus *Dendrerpeton*, *D. acadianum*, at the base of the clade Dvinosauria, whereas a second species, *D. confusum*, was placed at the base of the clade Dissorophoidea. Here, we divide Dendrerpetontidae into two separate families to take into account the distribution of the two *Dendrerpeton* species in Ruta and Bolt's (2006) tree. The two groups deriving from the subdivision of Dendrerpetontidae are regarded as having separate family status (identified by the *partim* notation; Text-fig. 1B). Furthermore, we assume that the range of the family that comprises *D. acadianum* extends back to the Viséan, through inclusion of *Balanerpeton woodi*. The latter occurs in phylogenetic proximity to *Dendrerpeton* in several recent analyses, although not necessarily as its sister taxon (e.g. Laurin and Soler-Gijón 2006; Ruta and Bolt 2006; see also Milner and Sequeira 1994 and Milner 1996 for discussions). However, a number of small-scale phylogenies (e.g. Sequeira 2004) have retrieved *Balanerpeton* and *Dendrerpeton* as each other's closest relatives, and small perturbations of several recently published data sets (e.g. through character and or taxon inclusion or exclusion) also cause these taxa to cluster together. Such finds may be accounted for in terms of the weakly supported phylogenetic placement of both *Balanerpeton* and *Dendrerpeton* (e.g. due to the array of generalised, plesiomorphic traits of both taxa); however, we cannot at present rule out the possibility that they form a distinct radiation. We point out that our results and conclusions are not affected if the stratigraphic range of the

family Dendrerpetontidae is not extended back in time via inclusion of *Balanerpeton* (see above).

Third, the range of *Capetus palustris* is taken to coincide with that of a monotypic family, but counts of inferred family diversity per stage and origination/extinction rates are not affected when this taxon is excluded (see comments on 'isolated species' in the next section) from counts of total family diversity.

Fourth, we have conservatively placed several non-stereospondyl families that do not appear in Ruta and Bolt's (2006) study in the same position that they have in Milner's (1990) tree (e.g. Parioxeidae).

Fifth, the first appearance datum of Edopidae is based upon Milner and Sequeira's (1994) discussion of an *Edops*-like taxon in the Viséan of East Kirkton, Scotland. The occurrence of some isolated, large and nearly straight ribs bearing uncinat processes was used by Milner and Sequeira (1994) to argue in favour of the presence of a presumed *Edops*-like taxon at East Kirkton. The evidence is not conclusive, however, because ribs with similar features occur in other tetrapods (e.g. see Clack and Finney 2005). For the purpose of the calculations presented in this paper, however, the extended range of Edopidae is not problematic, as it implies addition of the Viséan only to the inferred record of this family for at least one of the three analyses used in this paper, and does not alter calculations to a significant degree in any of the case studies presented herewith.

Finally, the plot of Yates and Warren's (2000) tree on a stratigraphic scale (Text-fig. 1C) required a few additional assumptions. The total number of temnospondyl families is not agreed upon, as different authors tend to group or separate species differently. An easy, although perhaps not entirely satisfactory way to deal with the problem of non-overlapping families in different analyses is to graft families onto a node, based upon their phylogenetic position in other analyses. As an example, Schoch and Milner's (2000) Derwentiidae is placed between Rhytidosteidae and Chigutisauridae in their tree. Rhytidosteidae and Chigutisauridae also appear in Yates and Warren's (2000) tree, conveniently placed in proximity to one another. In this simple example, Derwentiidae can therefore be grafted between Rhytidosteidae and Chigutisauridae. Other situations pose slightly more complicated problems. Thus, Yates and Warren's (2000) family Capitosauridae is almost co-extensive with Schoch and Milner's (2000) Capitosauroidae, including Parotosuchidae, Eryosuchidae, Mastodontosauridae, Paracyclotosauridae, and Cyclotosauridae. Yates and Warren's (2000) Clade 22 [Mastodontosauridae (Benthosuchidae Capitosauridae)], referred to as 'capitosauroids', comprises 'Capitosauridae (including *Parotosuchus*)' (see Yates and Warren 2000, p. 96). Thus, it includes a genus (*Parotosuchus*) that belongs in Schoch and Milner's (2000) basalmost family of capitosauroids

(Parotosuchidae). To preserve as much of the topological structure in Schoch and Milner's (2000) Capitosauroidae as possible, and to adapt Yates and Warren's (2000) own concept of Capitosauridae, we have thus replaced the latter with the clade [Parotosuchidae (Paracyclotosauridae Cyclotosauridae)], outside which Benthosuchidae and a (Eryosuchidae Mastodontosauridae) group form more distal outgroups (via a small modification to Schoch and Milner's 2000 preferred topology).

Additional modifications of the Yates and Warren (2000) cladogram are more straightforward. As in the case of the family Dendrerpetontidae in Ruta and Bolt's (2006) study (see discussion above), two of Schoch and Milner's (2000) families, the Lydekkerinidae and the Rhytidosteidae, were each subdivided into two small family-level groups. This subdivision was made to take into account Yates and Warren's (2000) placement of two genera of Lydekkerinidae, *Lydekkerina* and *Luzocephalus*, as sister taxa to the 'capitosauroids' (Clades 21 and 22) and Trematosauroidae (Clades 25 and 26), respectively, as well as their placement of one genus of Rhytidosteidae, *Laidleria*, as sister taxon to Plagiosauridae (Clade 30), with remaining Rhytidosteidae as sister taxon to (Chigutisauridae Brachyopidae) (Clade 31). With such proposed subdivisions, the stratigraphic ranges of Lydekkerinidae and Rhytidosteidae were altered (e.g. the stratigraphic range of the group containing *Laidleria* coincides with the range of this genus).

Genus-, species- and family-level diversity trajectories

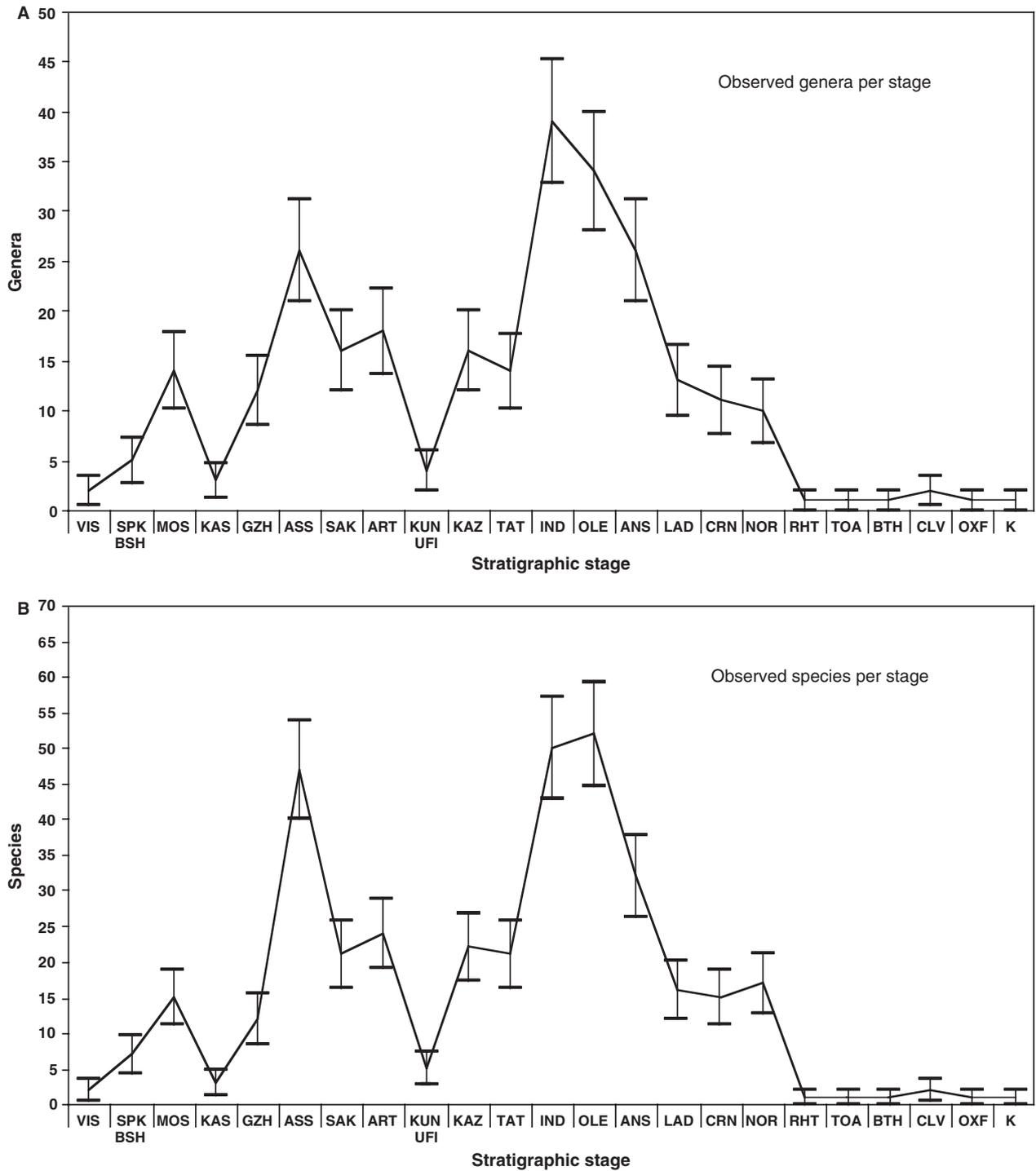
Both genus- and species-level diversity trajectories (Text-fig. 2) were reconstructed from counts of taxa in each stage. Error bars were calculated as $\pm\sqrt{D}$ (see Sepkoski and Raup 1986 and Foote 1994a, 1995), where D is the observed diversity (i.e. the number of genera or species) per stage; each value of D for a stage includes also counts of genera or species known from other stages. This procedure for calculating error bars '... provides an estimate of counting error associated with discrete events ... [and] does not allow absolute statistical confidence but only relative statements, if it is assumed that ... sampling error is constant throughout the time series' (Eble 2000, p. 61). Earliest and latest occurrences of each family are based upon the age of the first and last documented occurrences of species in the family. However, a few species do not fit easily into any of the well-established families and have been excluded from observed and inferred diversity values. However, this does not represent a problem for various reasons. First, some of these 'isolated' species occupy a basal position relative to certain families (or clusters of families), i.e. they form the plesiomorphic sister taxa to them. Thus, when cladistic relationships among families are superimposed on a time scale, reconstructed ghost

lineages and range extensions will often include such 'isolated' taxa within their range (i.e. they are included in calculations of inferred family-level diversity). Second, instances of 'isolated' species are very rare. Based upon Milner (1990) and Schoch and Milner (2000), we recognize 43 temnospondyl families (observed number of families).

We have attempted, so far as possible, to encompass all described genera and species using available compendia (e.g. Milner 1990; Schoch and Milner 2000; see also the supporting appendix to Ward *et al.* 2006) supplemented by more recent literature, where applicable.

Known families are, for the most part, monophyletic. Although some have uncertain status and may represent grades rather than clades (e.g. Milner 1990), they constitute only a small proportion of family diversity. In addition, many grade-group families have been subsequently redefined to represent clades. Some families, however, are truly problematic and we are forced to assume their monophyly, pending further phylogenetic analyses that will help clarify their status and intrinsic relationships. An example is offered by Archegosauridae. Thus, Gubin (1991) and Schoch and Milner (2000) discussed characters in support of archegosaurid monophyly, although they did not present a formal cladistic analysis. In Yates and Warren's (2000) phylogeny, the family is monophyletic, although represented only by three taxa, i.e. *Archegosaurus*, *Konzhukovia*, and *Platyoposaurus*. Conversely, Gubin (1997) and Witzmann and Schoch (2006) found archegosaurids to be paraphyletic relative to Stereospondyli. Different sets of characters used in these studies certainly exerted an impact on the issue of monophyly or paraphyly of archegosaurids. The issue will be explored in detail in a separate publication. Overall, we found that, if species are removed from paraphyletic families in order to create monophyletic groups, then the major conclusions from our analyses are not affected.

For the reconstruction of inferred family diversity, we adopt several conventions and simplifications as follows. First, if two families form sister taxa and their earliest records occur in different stages, then the range extension occupying all stages that intervene between the first documented occurrences of such families is taken to represent a single family extension. This extension can be interpreted in many ways, e.g. either as a new family that occurs in continuity with the more recent of the first documented records of the two sister families or as an extended range of the younger family. In either case, it counts as one, and the same, inferred family for each of the stages that it ranges through. Also, if two clusters of families form sister taxa, then the ghost lineage joining them occupies all stages intervening between the first documented family records of both clusters



TEXT-FIG. 2. Observed diversity of temnospondyl genera (A) and species (B) in different stages. Error bars represent $\pm\sqrt{D}$ (Sepkoski and Raup 1986; Foote 1994a, b, 1995), where D represents the observed diversity per stage (see text for details).

(Text-fig. 1A–C). For simplicity, a range extension added to a family is not counted as a separate family. However, a ghost lineage subtending a cluster of families (i.e. two or more) is regarded as a separate family and thus added to the total count of observed plus inferred families.

Second, if the earliest known records of two or more families within a clade occur in the same stage, then we assume that the hypothetical latest common ancestor of those families also occurs in that stage. This might appear as an unrealistic speciation scenario, since it assumes that

a series of simultaneous or nearly simultaneous branching events separate families which first appear in the same stage. However, it provides a conservative estimate for the number of inferred family originations, and thus circumvents the problem of assigning a specific duration to a ghost lineage or a range extension (i.e. the problem of assigning an arbitrary length to each of the horizontal lines that connect internal nodes to earliest family occurrences within the same stage; Text-fig. 1).

Originations and extinctions

For each stage, family originations and extinctions are expressed as a percentage of the total number of families (both observed and inferred) that existed throughout the group's recorded history (i.e. from the Viséan to the Aptian; Milner 1990; Holmes 2000). In a separate series of calculations, each percentage is then divided by the duration of the stage where originations and extinctions occur. Un-calibrated and time-calibrated methods represent 'total diversity' methods (Foote 2000a; Hammer and Harper 2006).

Note that such calculations differ from other methods, such as those presented by Van Valen (1984) and Foote (2000a) (see Hammer and Harper 2006 for reviews). Various proposed measures of the rates of originations/extinctions, e.g. Foote's (2000a), aim to minimize the influence of singleton taxa (that is taxa that originate and become extinct within an interval) as well as interval duration (see discussion in Hammer and Harper 2006). Temnospondyl genera and species are mostly singletons. As such, they are not amenable to the calculations presented by Foote (2000a). For his analyses, Foote (2000a) selected only genera that cross interval boundaries, as they give estimates '...of instantaneous standing diversity that does not increase systematically with interval length and that, by ignoring single-interval genera, is not expected to be as sensitive to variation in preservation rate as is the total number of genera ... from an interval' (Foote 2000a, p. 579). For each time interval, let N_b represent the number of taxa that cross the bottom boundary of the interval, N_t the number of taxa that cross the top boundary, N_{bt} the number of taxa that cross both boundaries, and Δt the interval duration. The origination and extinction rates for that interval, p and q , are expressed by the formulae:

$$p = -\ln[(N_{bt})/N_t]/\Delta t \text{ and}$$

$$q = -\ln[(N_{bt})/N_b]/\Delta t.$$

Foote's (2000a) method could be applied to families, although this requires a few caveats. First, the precise placement of numerous temnospondyl species in a stage

is unknown. Indeed, there are cases in which even the broad assignment of a species to a certain stage is dubious. Second, each stage (except for the first and the last) has at least one family that ranges through its entire duration (that is, it crosses both its lower and its upper boundaries). However, identifications of N_b and N_t families pose problems, as the origin and/or the extinction of a family cannot be located accurately within a stage as they would correspond to the earliest and latest recorded occurrences of a species in that family, respectively). For this reason, all plots of family ranges assume that extinctions and originations took place, respectively, at the end and at the beginning of a given stage. It follows that the ranges of singletons extend from the lower to the upper boundary of an interval (Text-fig. 1A–C).

Unfortunately, Foote's (2000a) formulae can be applied only to temporal ranges in our data between the Asselian and Artinskian stages and between the Kazanian and Carnian stages. For remaining stages, either N_b or N_t (or both) values are zero, and thus invalidate the use of the formulae. For this reason, we include a third method proposed by Van Valen (1984) to calculate rates of originations and extinctions. In this method, we consider a quantity termed the mean standard family-level diversity of a stage. This is calculated by adding up the following quantities:

1. number of families that cross the lower and upper boundaries of a stage; each of these families has a value of 1 (these families correspond to Foote's 2000a N_{bt});
2. number of families that originate in a stage and cross its upper boundary to extend into one (or more) of the subsequent stages; each of these families has a value of 0.5 (these families correspond to Foote's 2000a N_t);
3. number of families that originate before a given stage, cross its lower boundary, and terminate in the same stage; each of these families has a value of 0.5 (these families correspond to Foote's 2000a N_b);
4. singleton families; each singleton has a value of 0.3 (Hammer and Harper 2006).

Next, we calculate the origination rate for a stage by dividing number of originations in that stage by mean standard diversity of that stage; the resulting value is then divided by Δt . Similarly, the extinction rate is calculated as the ratio between number of extinctions and mean standard diversity, again divided by Δt . For simplicity, we discuss only calculations based upon observed family-level diversity. It is important to note that the assignment of 'weights' to families is arbitrary. Thus, singletons receive approximately one-third of the weight given to families that cross lower and upper stage boundaries. Because many families in this study are represented by singletons, we decided to explore the effects of altering weights. As numerous options are possible, each one depending upon the weights assigned to families, we opted for the equal

weighting of all families, in which both singletons and families that cross one or both stage boundaries are given a value of 1.

We consider only the mean standard diversity for each stage, as standard diversities at the upper and lower boundaries of a stage often show identical or similar values (but see Foote 2000a for comments), so that there is no ground for a detailed investigation of partial correlations between changes in rates of originations (Δp) or extinctions (Δq) and change in diversity (ΔD) throughout each interval. The use of these partial correlations for short-term variations of p and q was introduced by Foote (2000a) to avoid the influence of factors (e.g. pseudo-extinctions; pseudo-originations; preservation potential; inaccurate absolute taxon dating; biological causes) that often introduce positive or negative correlations between Δp and Δq . Although we cannot rule out the influence of one or several of the above-mentioned factors on the diversity trajectory of temnospondyls, we note that the use of families (as opposed to species or genera) may partly dilute small-scale fluctuations of p and q . A compromise solution to the problem of a spurious correlation between p and q , such as was noted by Alroy (1996) and Foote (2000b) (see also Foote 2000a) and linked to the presence of singletons, is the assignment of small values to singletons in the computation of mean standard diversities (see above and comments in Hammer and Harper 2006).

Our preferences for the total diversity and Van Valen (1984) methods are ultimately justified by our attempt to employ all families in the rate calculations, including singletons (with the recommendations provided by Hammer and Harper 2006). After all, singleton families make up approximately 25 per cent of the total observed diversity of temnospondyls. However, we are aware of the potential problems that singletons may pose, including inflating the correlation between p and q through artificially increasing the lower of either p or q rate values (e.g. when such values differ remarkably). For detailed discussions of temporal patterns of origination and extinction, see Foote (2003).

Origination and extinction values are chosen to represent the dependent and independent variables, respectively, for the purpose of assessing their degree of correlation (measure of faunal turnover). Both least-squares regressions and their associated statistics were performed with StatView v. 5.0 (SAS, Berkeley, CA, USA). We also calculated reduced major axis regressions (discussed briefly below; see Appendix). In each scattergram we include:

1. regression equation;
2. R , correlation coefficient (a measure of the strength of the linear association, or covariation, between the dependent and independent variables);
3. R^2 , coefficient of determination (percentage of variation of the independent variable that is explained by variation of the dependent variable);

4. P value (probability that a random sample of values for the two variables gives the observed amount of covariation R).

Finally, the degree of correlation between origination rate and extinction rate was evaluated through two non-parametric coefficients, namely Spearman's r and Kendall's τ (all calculations were performed with StatView v. 5.0 and PAST v. 1.67; e.g. Hammer *et al.* 2001 and <http://folk.uio.no/ohammer/past/>). We employ Spearman's r to measure the amount and direction of a linear relationship between the two variables, when these are ranked into two ordered series (i.e. the variables are on an interval scale). For Kendall's τ , we contrast the probability that the variables are in the same order that we observe with the probability that they are in different orders. Specifically, Kendall's τ is used to measure the tendency of two variables to change in the same (or opposite) direction. Given a pair of bivariate observations (i.e. two points in a scattergram, each identified by a value on the horizontal axis and a value on the vertical axis), if the difference between the values on the horizontal axis and the difference between the values on the vertical axis (taken in the same order) show an identical sign (positive or negative), then the two points form a concordant pair. If the signs differ, then the two points form a discordant pair. If we now consider the value of the difference between all concordant and all discordant pairs, this value can vary from large and positive (strong positive correlation) to large and negative (strong negative correlation) following standardization by number of bivariate observations (i.e. sample size).

Rarefaction curves

Rarefaction (Sanders 1968), originally devised in ecological studies of marine benthos, has since found a wide range of applications in palaeobiology including, among others: analyses of taxonomic richness profiles during the Phanerozoic (e.g. Alroy *et al.* 2001; Peters 2006); studies of biofacies compositions in relation to depositional environments (e.g. Amati and Westrop 2006); assessments of fluctuations in alpha diversity during time intervals of major biotic crisis, or in response to environment modifications (e.g. Adrain *et al.* 2000; Hammer 2003); investigations of the effects of sample size on overall diversity data (e.g. Benton *et al.* 2004). For mathematical treatments of rarefaction methods, see Hurlbert (1971), Simberloff (1972), Raup (1975), and Hammer and Harper (2006). Useful discussions about refinements to rarefaction methods can be found in Gotelli and Colwell (2001).

Raup (1975) offered an elegant, succinct treatment of rarefaction using post-Palaeozoic echinoids as a case study. Briefly, rarefaction gives an estimate of the diver-

sity of higher taxonomic categories when lower taxonomic units are subjected to a series of subsample collections (rarefaction), i.e. collections of smaller magnitude than the raw data. Thus, rarefaction allows the investigator ‘... to compare estimated diversities at a constant sample size’ (see Raup 1975, p. 333). The fundamental issue with rarefaction is to assess if the observed fluctuations in taxonomic richness through time are the result of differences in sample size. Rarefaction is time-dependent (that is, we expect to sample a larger number of taxonomic units during longer time intervals). Thus, a way to correct for time-related biases in diversity estimates is to consider approximately equal time intervals (e.g. Raup 1975). This is particularly relevant to those cases in which identical (or similar) diversity values for a given taxon result from ‘balancing’ effects of originations and extinctions. In these cases, as Raup (1975) noted, diversity estimates for fractions of a time interval will be necessarily lower than the diversity estimate applied to the entire interval. We note that at least some of our selected bins for the analysis of calibrated temnospondyl diversity profiles are of approximately equal duration. In other cases, time bin durations differ to some degree.

However, there is no need for a strict application of the equal time bin correction if, for instance, we have reasons to assume that interval lengths are not the only factor responsible for different magnitudes of observed taxonomic richness. Temnospondyls illustrate this: the explosive radiation of this group in the aftermath of the end-Permian extinction took place during a very short period (<1 million year), in the earliest part of the Early Triassic (Milner 1990). This rapid burst of diversification might be correlated to ecological factors, e.g. exploration of various ecological options across Laurasia (it is widely acknowledged that a clade of Gondwana-based species initiated the colonisation of the Northern Hemisphere). Also, intense collecting efforts from such a crucial time interval in Earth’s history (post-extinction period) and availability of well-sampled Early Triassic sites may also partly account for this unusual diversity (discussions in Erwin 1993 and Benton 2003). However, Benton *et al.* (2004) showed that, although sampling in the five Early Triassic time units of the Russian basin was more intense than before or after, the overall diversity of tetrapods (i.e. amphibians plus amniotes) was much reduced.

There appears to be much scope for comparisons between observed and rarefied diversity values. In a seminal paper on the effects of sample size and time interval durations on patterns of taxonomic and morphological diversification, Miller and Foote (1996) showed that, based upon observed data, marine diversity in the Ordovician was characterized by an initial increase from Tremadoc to Arenig, followed by a small decrease in the

Llanvirn, and by a steady and rapid increase during Llandeilo and especially Caradoc, when diversity peaked before dropping again during the Ashgill. After rarefying the observed diversity values for each Ordovician stage at a taxon sampling size comparable with the smallest raw diversity value (in the Llanvirn), Miller and Foote (1996) showed that Ordovician diversity increased quite rapidly from Tremadoc through Arenig to Llanvirn, and stabilized after the Llanvirn. Miller and Foote (1996, p. 308) pondered the possible impact of sampling on other portions of Phanerozoic life, particularly during time intervals of biotic crisis (e.g. large-scale extinctions). In their words, ‘... the apparent diversity decline during the Late Permian mass extinction may be exaggerated because of a sparse Upper Permian record, relative to that of the Lower Permian’. This observation prompted us to address the possible effects of the Upper Permian terrestrial record using temnospondyls as a test case.

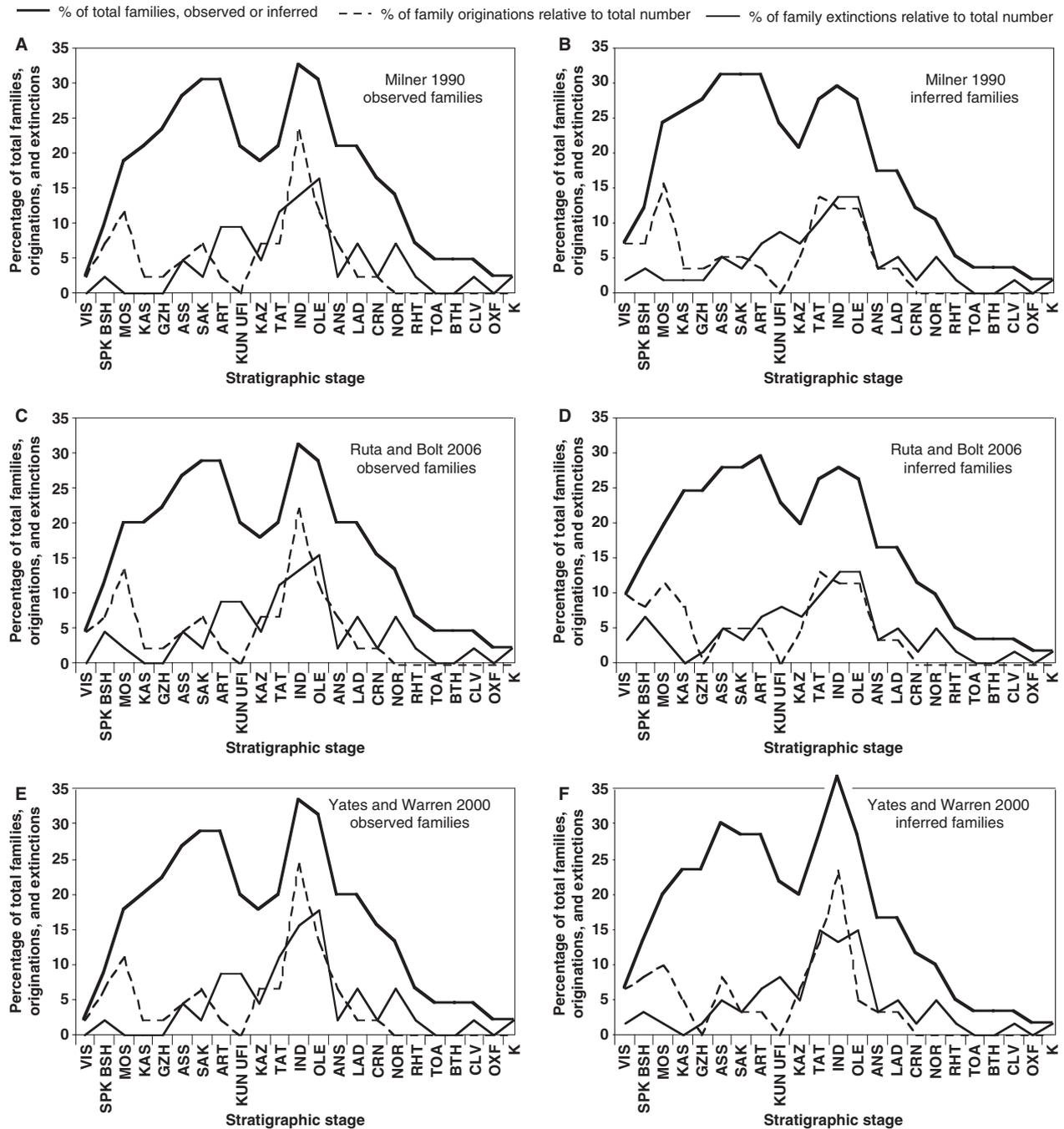
All rarefaction analyses were performed with the program Analytic Rarefaction v. 1.3 for Macintosh OS X platforms (see <http://www.uga.edu/strata/software/>).

RESULTS

Diversity profiles

Both genus- and species- based diversity curves show an Early Permian and an Early Triassic peak; the difference between the values of these peaks appears more pronounced in the genus-level curve (Text-fig. 2A). Alternating with these peaks are two troughs, in the earliest part of the late Pennsylvanian and in the early to mid Guadalupian, with similar values for both curves. The second trough reflects a well-known drop in mid Permian tetrapod diversity, generally referred to as Olson’s gap (e.g. see Lucas and Heckert 2001 for a review), and extending from the latest Kungurian to the earliest Kazanian (i.e. from the late Cisuralian to the middle Guadalupian; see also Lucas 2002, fig. 1 and Lucas 2004, fig. 9).

Following the Early Triassic peak, diversity decreases steadily and rapidly until the Middle Triassic, when its value is slightly lower than in the latest Permian. Throughout most of the Late Triassic, genus-level diversity diminishes slowly, in contrast to species-level diversity, which reaches a plateau. In both curves, however, diversity is marked by a sudden drop in the latest Late Triassic, and remains low from then onward. The apparent post-Triassic plateau is an artefact due to the way in which both curves have been reconstructed (i.e. only Jurassic and Cretaceous stages with recorded temnospondyl diversity have been included, whereas ‘empty’ stages have been omitted).



TEXT-FIG. 3. Profiles of observed (A, C, E) and inferred (B, D, F) family-level diversities based upon Milner’s (1990) (A, B), Ruta and Bolt’s (2006) (C, D), and Yates and Warren’s (2000) (E, F) trees. For each stage, we include: the percentage of families (thick solid lines); the percentage of family origins (thin dashed lines); and the percentage of family extinctions (thin solid lines). All percentages refer to the total number of observed or inferred families (i.e. the total diversity from all time periods); origins and extinctions are un-calibrated.

The family-level diversity curves (thick solid lines; Text-fig. 3) differ considerably from both genus- and species-level curves (Text-fig. 2). Both observed (Text-fig. 3A, C, E) and inferred (Text-fig. 3B, D, F) trajectories of family diversity show a Cisuralian peak (either span-

ning the Asselian or ranging from Asselian to Artinskian, or from Sakmarian to Artinskian) and an Induan peak. A trough in the Kazanian is offset by one stage relative to the troughs that characterise genus- and species-level curves and marks the only substantial drop in diversity

between Cisuralian and Induan peaks. A steady and rapid increase in diversity from Viséan through to most of the Cisuralian is mirrored by a similarly rapid decline from Induan to Aptian. In particular, the drop in diversity from the Early to the Middle Triassic appears even more conspicuous than in the species-level curve.

The overall profiles of observed and inferred family-level diversities do not differ substantially from one another, or when different trees are considered. However, among significant differences introduced by ghost lineages and range extensions is a modification of the increase in diversity from Moscovian to Artinskian. Relative to the observed diversity curve, this modification is indicated by a 'flattening' and widening of the curve during these time bins. No differences in overall pattern affect the diversity drop in post-Olenekian intervals.

Patterns of family originations and extinctions

Text-figures 3 and 4 display curves of family originations and extinctions through time. When originations and extinctions are expressed as a simple percentage of the total number of families (either observed or inferred), without considering the duration of the time bins, we obtain the two curves (thin dashed lines and thin solid lines represent originations and extinctions, respectively) underneath the overall diversity trajectory (thick solid line) in Text-fig. 3. If the origination and extinction percentages are divided by time interval lengths, then we obtain the graphs in Text-fig. 4A–F (once again, thin dashed lines and thin solid lines represent originations and extinctions, respectively). The diagrams in Text-figs 3A, C, E and 4A, C, E are constructed from the observed numbers of families whereas those in Text-figs 3B, D, F and 4B, D, F are obtained from inferred numbers (based upon the stratigraphic plot of trees in Text-fig. 1A–C). Text-figure 4G, H depicts origination (thin dashed lines) and extinction (thin solid lines) trajectories built using Van Valen's (1984) method, and applied to observed families only. Text-figure 4G considers different weights for families, whereas Text-fig. 4H assumes equal weights for all families (see also above).

Time-calibrated origination and extinction trajectories are similar to one another, in agreement with Foote's (2000a) and others' observations. This similarity appears

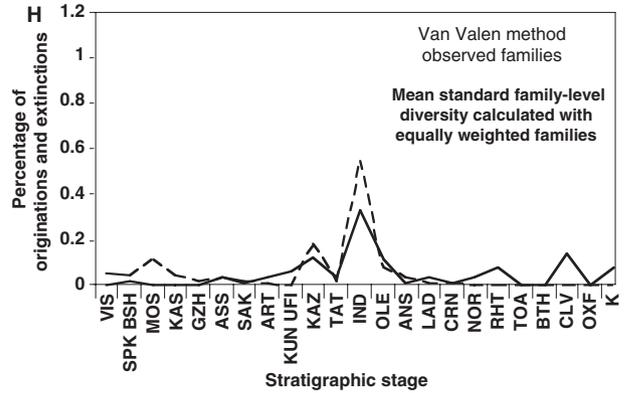
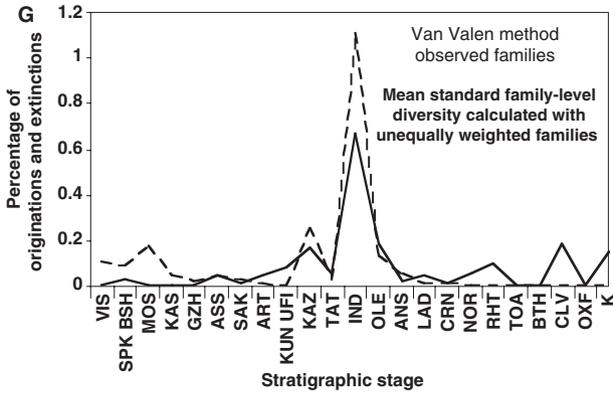
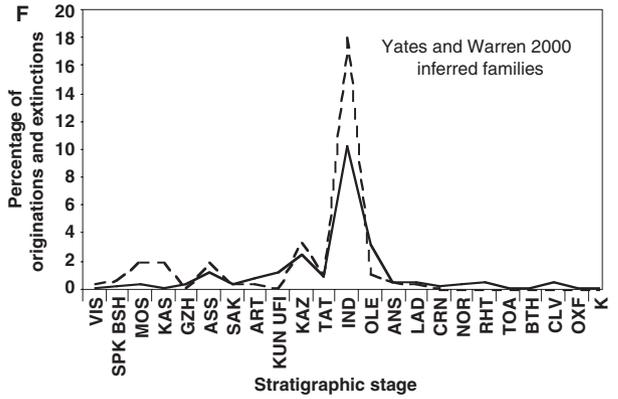
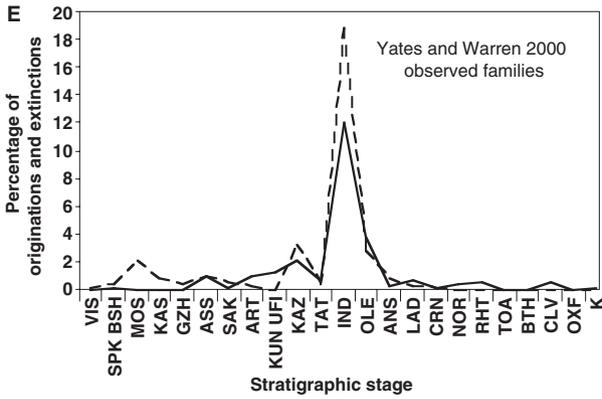
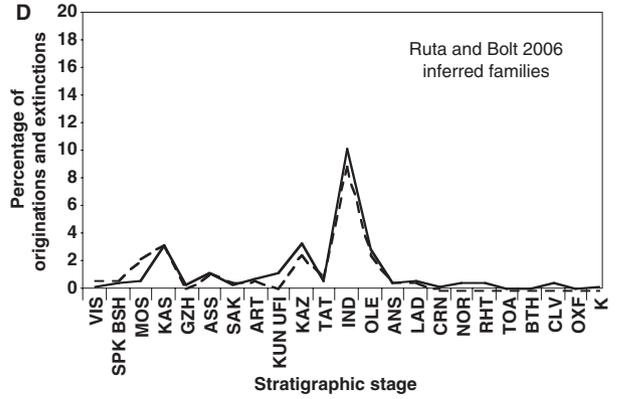
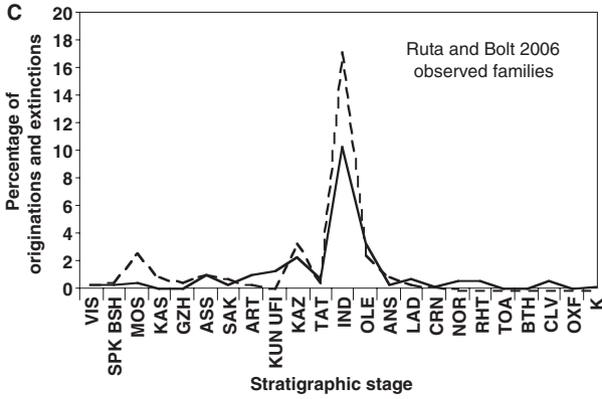
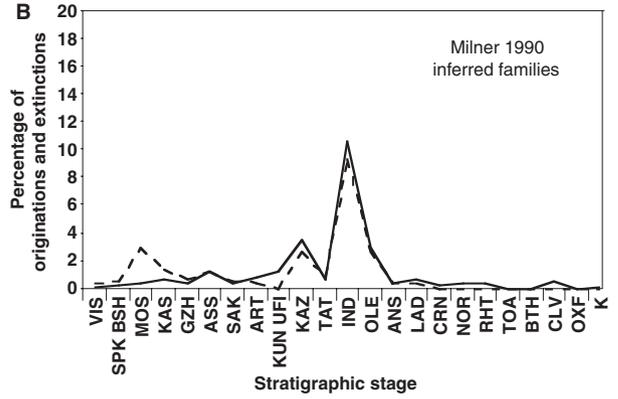
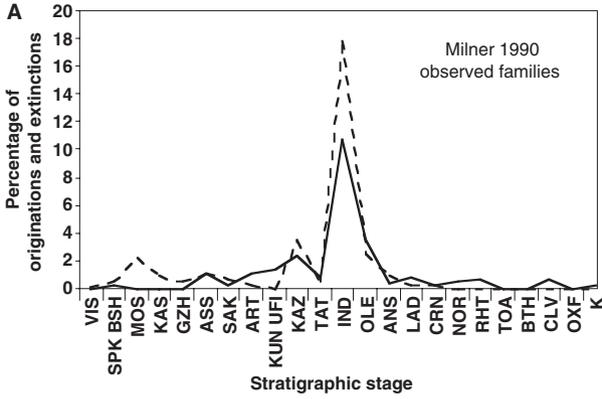
less obvious when time calibration is not introduced (Text-fig. 3), regardless of whether raw or inferred data are employed.

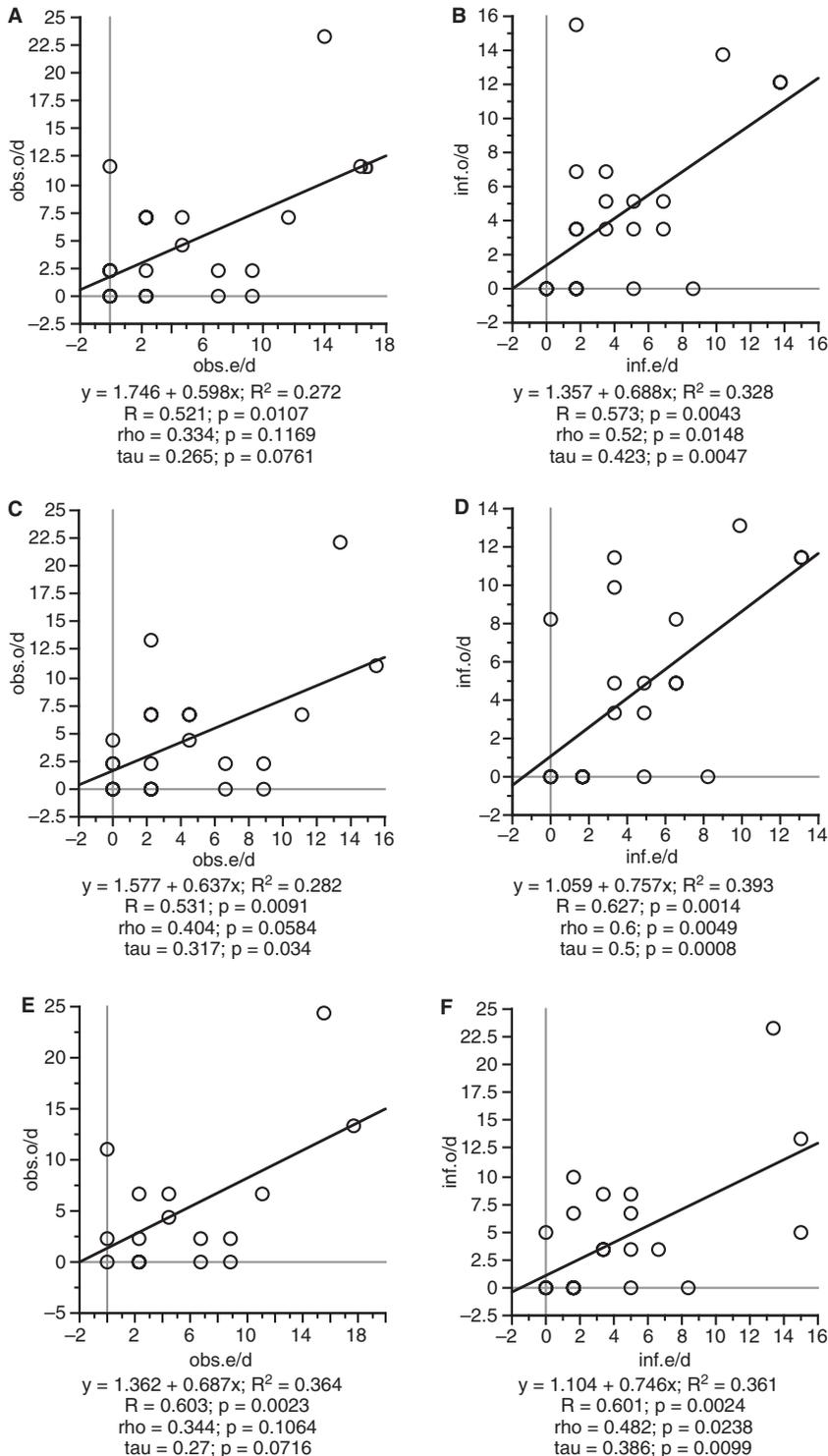
Another way to look at the correspondence between the two curves is via correlation between values of origination and extinction rates both for un-calibrated (Text-fig. 3) and for time-calibrated (Text-fig. 4A–F) curves (all calculations consider both observed and inferred numbers of families). Specifically, we want to establish whether a linear model is a good fit for the origination and extinction rate values. (Text-figs 5, 6). In Text-fig. 7, all regressions for the time-calibrated curves have been re-calculated after removal of data related to the Induan outlier, clearly visible in all scattergrams in Text-fig. 6, as this outlier may exert a strong influence on the fitting of the regression line. Our major conclusions are not affected if all data are log-transformed.

Inspection of all scattergrams reveals that the correlation between rates of origination and extinction is always positive, significant, and considerably stronger in the case of time-calibrated curves, even in the absence of the Induan outlier. Overall, the levels of originations and extinctions in the lowermost Triassic are comparable only when inferred family-level diversity is considered. This is true for most of the un-calibrated and time-calibrated curves. The only exceptions are the curves based upon Yates and Warren's (2000) analysis, in which the origination rate considerably exceeds the extinction rate during the Induan (Text-fig. 4F). Significant and positive correlations between origination and extinction rates are also found with the curves generated using the Van Valen's (1984) method. In this case, however, the Induan outlier exerts a strong influence on the correlation. This is evident in the scattergrams and associated statistics in Text-fig. 8A, B, which are based upon the curves in Text-fig. 4G, H. After the outlier is removed, the correlation is much less strong and non-significant (Text-fig. 8C, D).

Spearman's r and Kendall's τ coefficients and their associated P values are calculated for both un-calibrated and time-calibrated curves (inferred and observed) and appended to the graphs in Text-figs 5–8. Generally, a correlation between rates of originations and extinctions is much stronger in the case of inferred family curves than in the case of observed family curves, regardless of whether time-calibration is considered. A non-significant correlation is invariably found when Van Valen's (1984) method is used, even in the presence of the Induan outlier.

TEXT-FIG. 4. Profiles of time-calibrated rates of origination (thin dashed lines) and extinction (thin solid lines) for observed (A, C, E) and inferred (B, D, F) family-level diversities; rates are expressed as percentages of the total number of families (either observed or inferred; i.e. family diversity from all time periods), and based upon Milner's (1990) (A, B), Ruta and Bolt's (1996) (C, D), and Yates and Warren's (2000) (E, F) trees. G, H, time-calibrated rates of origination (thin dashed lines) and extinction (thin solid lines) based upon Van Valen's (1984) method (for observed families only in both cases) and constructed with different and identical family 'weights', respectively, as input for calculations of mean standard family-level diversity in each stage (see text for details).





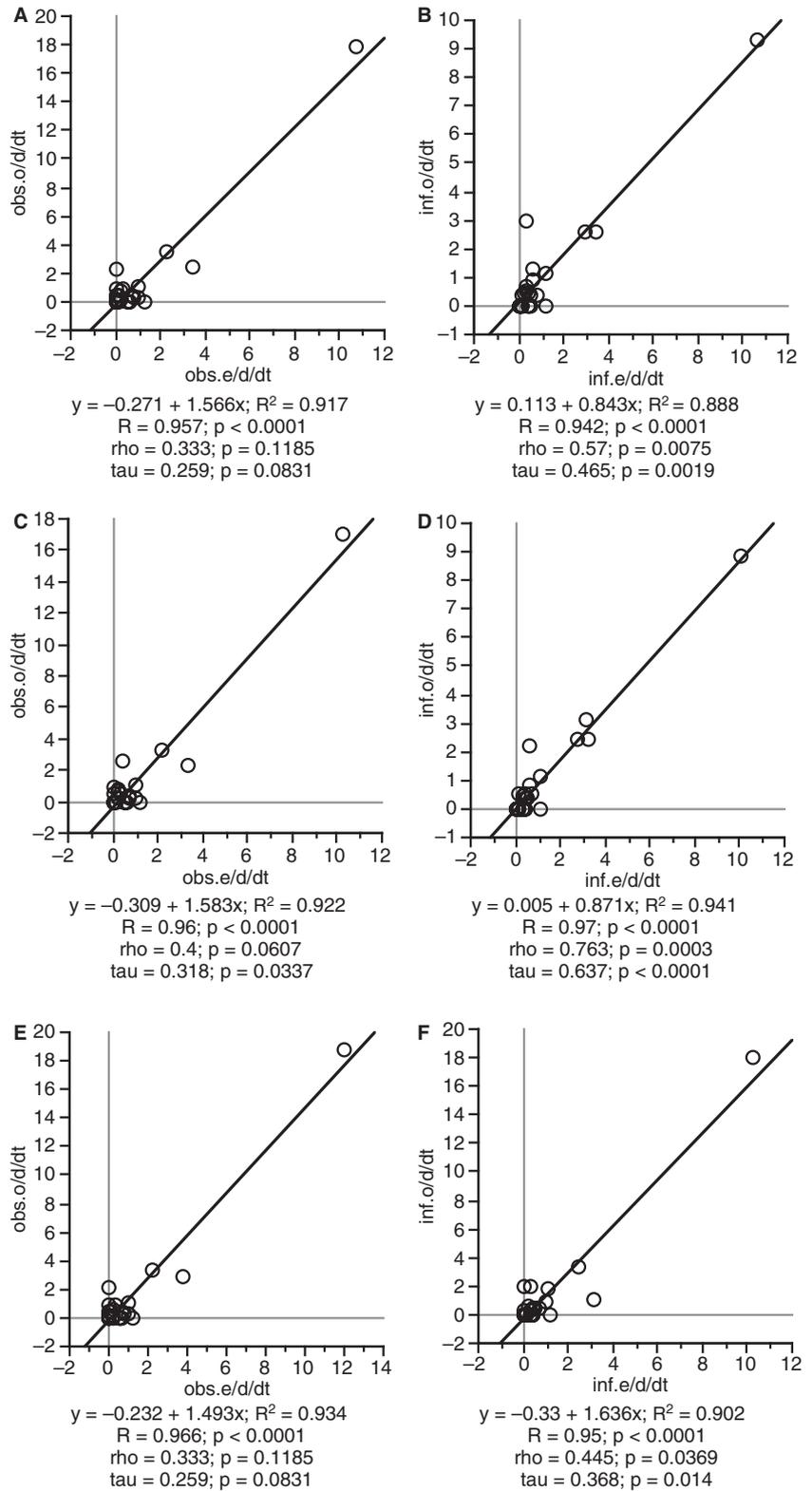
TEXT-FIG. 5. Least-squares scattergrams, regression lines, and regression statistics for the correlation between un-calibrated values of originations (o) and extinctions (e) for observed (obs; A, C, E) and inferred (inf; B, D, F) family-level diversities in relation to total number (d) of families (either observed or inferred; i.e. total diversity from all time periods), and based upon Milner's (1990) (A, B), Ruta and Bolt's (1996) (C, D), and Yates and Warren's (2000) (E, F) trees. We also report statistics related to Spearman's r (ρ) and Kendall's τ (τ), with significance values corrected for ties (where present).

Reduced major axis regression

In addition to performing least-squared regressions, we conducted reduced major axis regression on all time-calibrated data following removal of the Induan outlier.

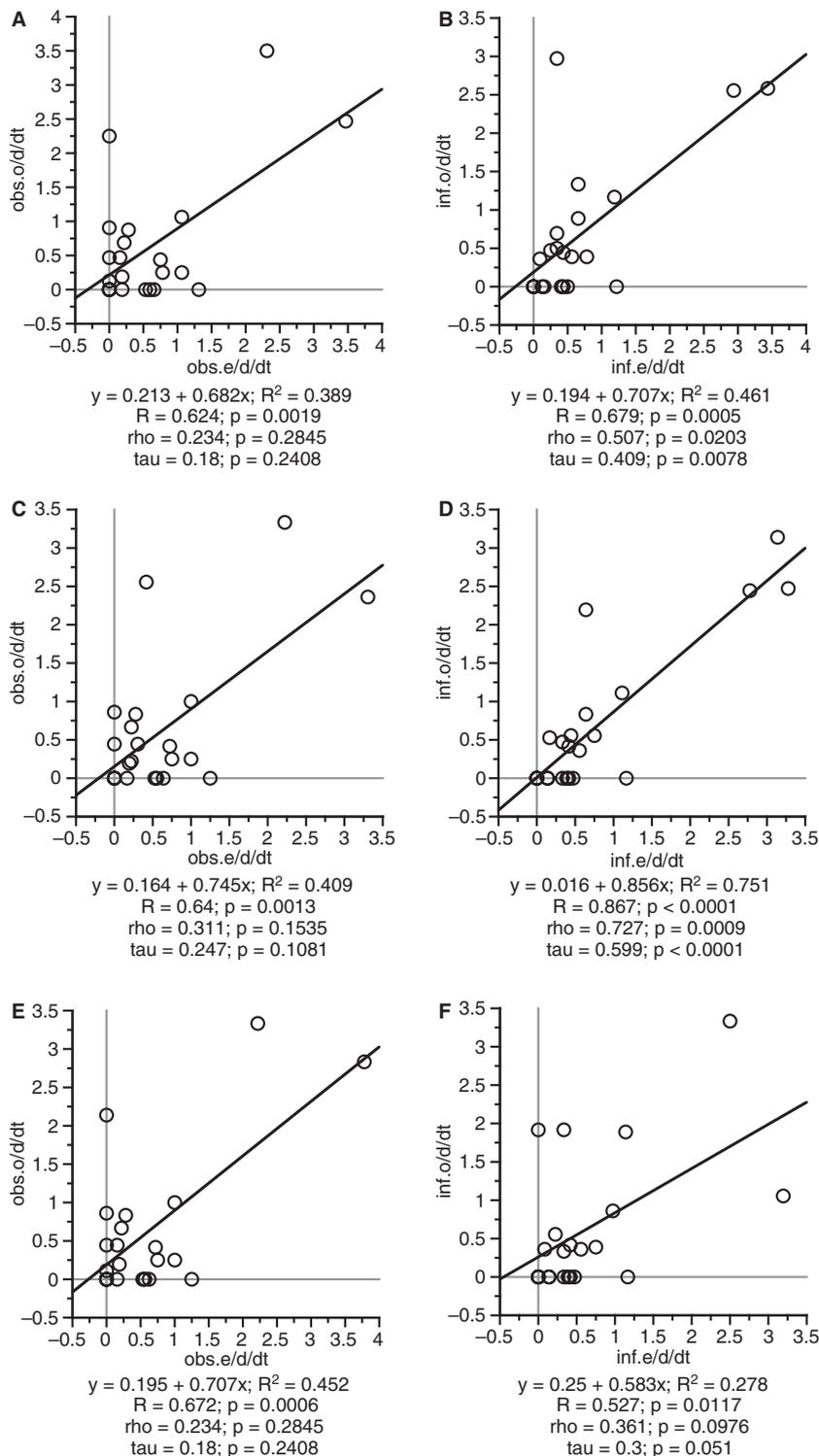
Reduced major axis regression is suitable when the independent variable is subject to error rather than being known accurately. All calculations were performed with the program RMA (Bohonak and Linde 2004). The output (see Appendix) shows estimates of intercept and slope

TEXT-FIG. 6. Least-squares scattergrams, regression lines, and regression statistics for the correlation between time-calibrated values of originations (o) and extinctions (e) for observed (obs; A, C, E) and inferred (inf; B, D, F) family-level diversities in relation to total number (d) of families (either observed or inferred; i.e. diversity from all time periods) and stage duration (dt), and based upon Milner's (1990) (A, B), Ruta and Bolt's (1996) (C, D), and Yates and Warren's (2000) (E, F) trees. We also report statistics related to Spearman's r (ρ) and Kendall's τ (τ), with significance values corrected for ties (where present). Note the Induan outlier.



for the RMA regression line, calculated using both a linear regression approximations method and a one-delete jackknifing method. The 95 per cent confidence intervals

on linear estimated values are output via standard statistical procedures as well as via bootstrapping (1000 replicates for all calculations) (for additional information, see

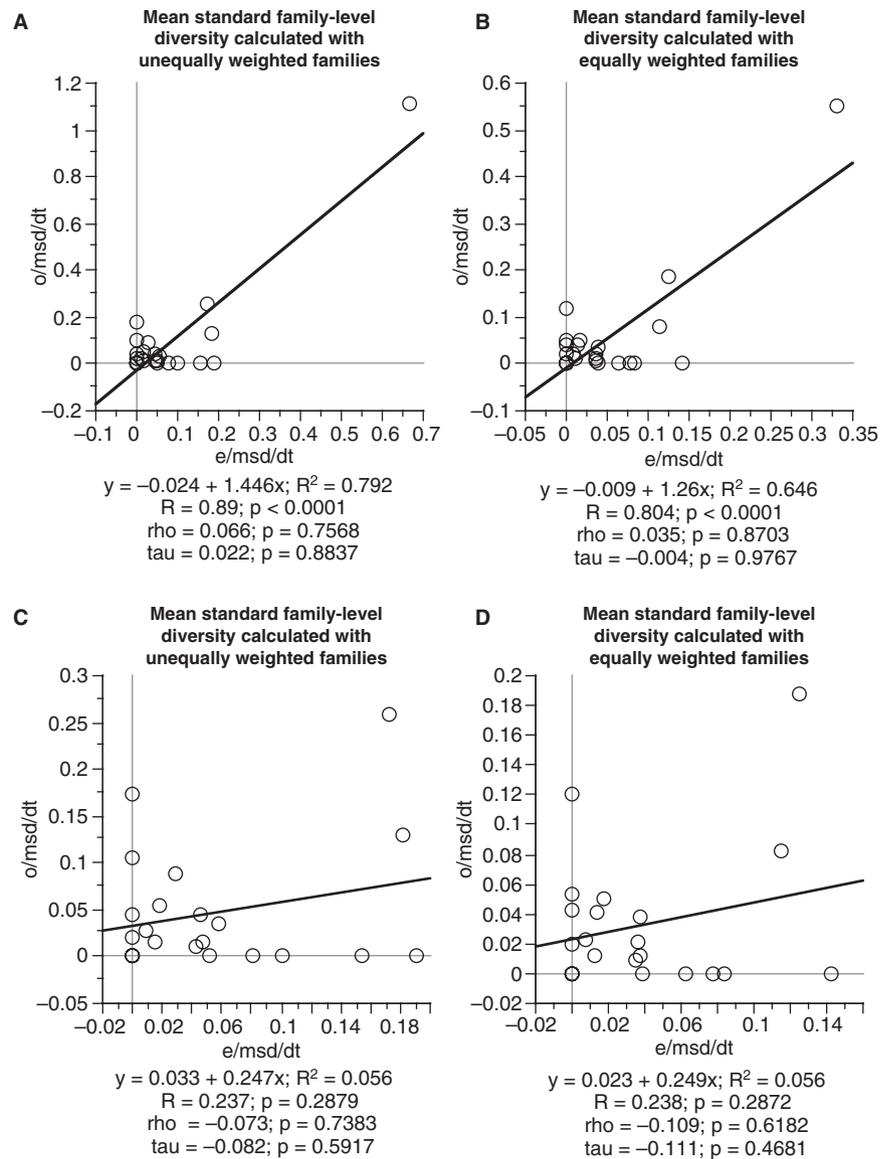


TEXT-FIG. 7. Least-squares scattergrams, regression lines, and regression statistics for the correlation between time-calibrated values of originations (o) and extinctions (e) for observed (obs; A, C, E) and inferred (inf; B, D, F) family-level diversities in relation to total number (d) of families (either observed or inferred; i.e. diversity from all time periods) and stage duration (dt), and based upon Milner's (1990) (A, B), Ruta and Bolt's (1996) (C, D), and Yates and Warren's (2000) (E, F) trees. We also report statistics related to Spearman's r (ρ) and Kendall's τ (τ), with significance values corrected for ties (where present). Calculations have been performed after removal of the Induan outlier (see text for details and Text-fig. 6).

Bohonak and Linde 2004 and discussion available online at: http://www.palass.org/modules.php?name=palaeo_math&page=7). A comparison among the regression equations in Text-figs 7, 8C, D, based upon least-squares regressions, and those based upon RMA (Appendix) offers a

crude evaluation of differences in slopes and intercepts. Generally, slope and intercept values obtained with least-squares regression are either close to or fall within the range of confidence intervals around those same values calculated with RMA regression. A series of comparisons between the

TEXT-FIG. 8. Least-squares scattergrams, regression lines, and regression statistics for the correlation between time-calibrated values of originations (o) and extinctions (e) for observed family-level diversities in relation to mean standard family-level diversity (msd) per stage and stage duration (dt), and based upon Van Valen's (1984) method (see text for details and Text-fig. 4G, H). We also report statistics related to Spearman's ρ (rho) and Kendall's τ (tau), with significance values corrected for ties (where present). The scattergrams are constructed both with different (A, C) and with identical family 'weights' (B, D) and in the presence (A, B) or absence (C, D) of the Induan outlier.



correlation coefficients (R) associated with least-squares and RMA regressions was devised to assess the significance of differences for these two independent correlations. Specifically, the R value for each of the regressions in Text-figs 7, 8C, D was compared with the R value for the RMA one-delete jackknifing method applied to the same set of data points. This test can be justified on the ground that we try to determine the difference between two independent correlations, one of which (RMA) is based upon a sampling routine (jackknifing) of the same data points (that is, the time-calibrated origination and extinction rates). As an example, the R value for the least-squares graph in Text-fig. 7A is 0.624. The R value for the same set of data, calculated under jackknifing in RMA, is 0.639 (i.e. square root of $R^2 = 0.4079$ in the Appendix). The significance of the difference between the two R values is $P = 0.54$). All significance tests were performed with online

statistical programs at: <http://www.quantitativeskills.com/sisa/statistics/correl.htm>. Results are reported in the Appendix at the bottom of each major block of numbers describing the output of RMA for time-calibrated origination and extinction rates.

Comparisons among rarefaction curves

Rarefaction was carried out using occurrences of both genera and species within observed families in each time bin. Rarefaction is based upon numbers of taxa (genera and species; see below) rather than collections (Alroy *et al.* 2001). To evaluate the effects that time bin durations and taxonomic richness in each bin have on diversity resampling, we constructed rarefaction curves at different temporal levels. Specifically, at the most general

level we contrasted rarefied diversity estimates for the Palaeozoic and Mesozoic. At the next level, we considered Carboniferous, Permian, and Mesozoic. We further divided the Permian into Cisuralian and Guadalupian–Lopingian, in order to contrast the diversity in those bins with the estimates for the Carboniferous and Mesozoic. Finally, the Mesozoic was divided into Early Triassic and Middle Triassic–Early Cretaceous, giving a total of five bins (Carboniferous; Cisuralian; Guadalupian–Lopingian; Early Triassic; Middle Triassic–Early Cretaceous). In the rest of this section, the term ‘curve’ refers to the rarefied curve of observed family-level diversity.

When either genera or species are rarefied within families in the Palaeozoic and Mesozoic bins, the rarefaction curves associated with these bins display almost identical shapes and run very close to each other (the curves based upon genera basically overlap each other, and those based upon species diverge only slightly in the right half of their course). The null hypothesis of no difference between the mean values of estimated family diversity cannot be rejected under non-directional t-tests, when genera ($F = 1.42$; $P = 0.24$) or species ($F = 1.81$; $P = 0.18$) are rarefied.

When Carboniferous, Permian, and Mesozoic diversities are compared, it emerges that the Mesozoic and Permian curves almost overlap if genera are used and run nearly parallel to each other if species are used. Both curves plot out well above the Carboniferous curve. In order to test for differences among the mean estimated diversity values for these three curves, we carried out an analysis of variance (ANOVA). Overall, there are significant differences among the three mean values of estimated family diversity when genera are rarefied ($F = 33.8$; $P < 0.0001$). A post-hoc, Tukey’s HSD test found that, of the three pairwise comparisons among the three bins, the only non-significant difference is between Permian and Mesozoic diversities (Carboniferous vs. Permian and Carboniferous vs. Mesozoic comparisons differ significantly at $P < 0.01$). We obtain comparable results when species are rarefied (ANOVA; $F = 61.71$; $P < 0.0001$), but with a noteworthy difference, namely the Tukey’s HSD test reveals a significant difference between Permian and Mesozoic diversities ($P < 0.05$), beside showing Carboniferous vs. Permian and Carboniferous vs. Mesozoic diversities to differ at $P < 0.01$.

A comparison among Carboniferous, Cisuralian, Guadalupian–Lopingian, and Mesozoic diversities shows the curves associated with such bins to be well-separated (in the case of both rarefied genera and species; however, a partial overlap occurs between the Carboniferous and Cisuralian curves). ANOVA shows that the mean estimated diversity values differ significantly ($P < 0.0001$). Specifically, of the six pairwise comparisons, one (Carboniferous vs. Guadalupian–Lopingian) is non-significant, while the others are significant at $P < 0.01$. Apart from the F statis-

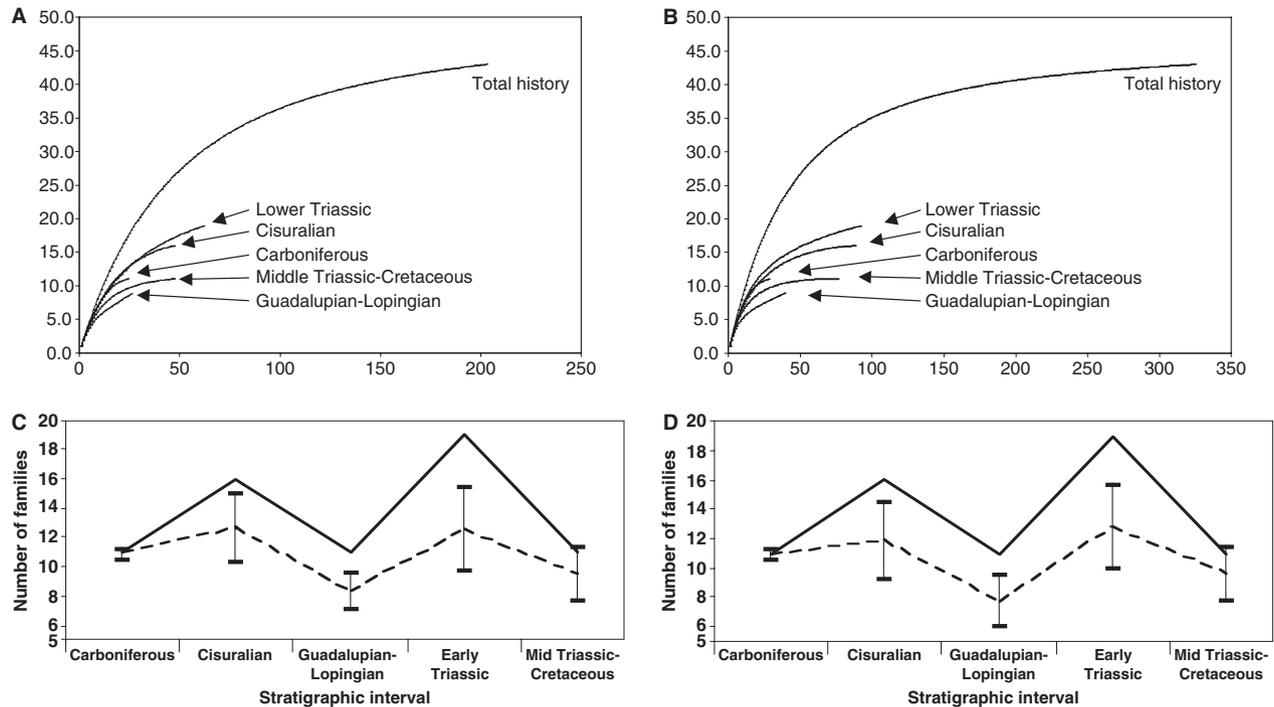
tic ($F = 133.73$), ANOVA results from rarefied species do not differ from those based upon genera.

Finally, when diversities in Carboniferous, Cisuralian, Guadalupian–Lopingian, Early Triassic, and Middle Triassic–Early Cretaceous bins are compared, we observe that for genus-based rarefactions, the Cisuralian and Lower Triassic curves overlap throughout most of their course, as do Carboniferous and Cisuralian, and Carboniferous and Lower Triassic curves (Text-fig. 9A). For species-based rarefactions (Text-fig. 9B), the only substantial overlap occurs between the Carboniferous curve and the Cisuralian and Lower Triassic curves. Mean estimated values of family diversity differ significantly (ANOVA; $F = 23.07$; $P < 0.0001$) when we use genera. Seven pairwise comparisons are significant ($P < 0.05$: two cases; $P < 0.01$: five cases). Remaining comparisons are non-significant (Cisuralian vs. Lower Triassic; Carboniferous vs. Middle Triassic–Early Cretaceous; Carboniferous vs. Guadalupian–Lopingian). If we rarefy species, then ANOVA results ($F = 49.4$) are nearly identical to those based upon rarefied genera, except that all seven significant pairwise comparisons are at $P < 0.01$.

Rarefied diversity trajectories and Olson’s gap

The trajectory of observed family-level diversity consists of an identical number of families (11) for the Carboniferous, Guadalupian–Lopingian, and Middle Triassic–Early Cretaceous time bins. The diversity peaks in the Cisuralian (16) and in the Early Triassic (19) complete the trajectory. We use a rarefaction approach (see above) to cast a re-calibrated profile of diversity following the method outlined by Miller and Foote (1996). Specifically, we are interested to assess whether the burst of diversification in the Early Triassic represents a real phenomenon or results from concentration of collecting efforts and abundance of densely prospected sites related to an interval of great palaeobiological significance on a global scale (i.e. the immediate aftermath of the end-Permian extinction).

We further employ rarefaction as a means of assessing the effect of notoriously depauperate tetrapod faunas from Olson’s gap on the overall shape of diversity curves. Here, the fundamental issue concerns the degree to which the re-calibrated profile of taxonomic richness matches (if only in terms of relative proportions) the profile based upon raw data when different subsamples of observed values of diversity are considered. This translates into the following question: what is the estimated family-level diversity associated with a time bin, when smaller, standard reference samples for the total number of genera or species in that bin are considered? It is important to note that rarefaction cannot overcome taphonomic or rock availability biases, but only differences in taxonomic richness.



TEXT-FIG. 9. A, B, rarefaction curves built from number of genera (A) or species (B) (horizontal axis) within families (vertical axis). Rarefaction is based upon numbers of taxa (genera and species) rather than collections (see Alroy *et al.* 2001). We report curves that relate to five time bins. For a given genus or species number, each curve gives an estimated value of family-level diversity in the related time bin. To avoid crowding of lines, we have excluded confidence intervals around each curve. C, D, comparisons between profiles of observed (thin solid lines) and estimated (thin dashed lines) family-level diversity values in five time bins; the observed values derive from counts of family occurrences in each bin, whereas the estimated values derive from rarefaction of genera (C) and species (D) within families; all error bars represent 95 per cent confidence intervals.

The horizontal coordinate value of the right extremity of each rarefaction curve (Text-fig. 7A, B) is a direct reading of the total number of genera or species in the bin to which the curve in question refers. For both sets of curves, the smallest horizontal coordinate value belongs to the Carboniferous curve. A vertical line through the right extremity of this curve intersects the remaining curves at different levels. The vertical coordinate values of the intersections represent rarefied estimates of family-level diversity. In practice, rarefied estimates are obtained from the outputs of Analytic Rarefaction.

A few noteworthy features emerge from the recast diversity trajectories. First, temnospondyls show greater family-level richness in the Carboniferous than they do in either the Guadalupian–Lopingian or the Middle Triassic–Early Cretaceous intervals. Second, diversity reaches its lowest value throughout the Guadalupian–Lopingian. Third, only a slight increase in trajectory slope occurs from Carboniferous to Cisuralian. Fourth, Cisuralian diversity emerges as being slightly lower than Early Triassic diversity when species are rarefied (Text-fig. 9C), but slightly higher when genera are rarefied (Text-fig. 9D). Fifth, the Middle Triassic–Early Cretaceous diversity decline is less conspicuous than raw data suggest.

The second of these observations is potentially the most interesting but also the most problematic. A diversity decline during the Guadalupian–Lopingian is usually attributed to the impact of Olson's gap, regardless of whether this gap marks a genuine decrease in diversity or results from a rock record bias. However, estimates of diversity through rarefaction point in the direction of an overall decrease during mid to late Permian. We selected time bins in such a way that all latest Permian temnospondyl genera and species are considered. This choice should ensure that re-calibrated values are not biased towards a decrease of estimated diversity for the mid to late Permian (a likely outcome, had the time interval that spans Olson's gap been chosen as a bin). In short, inclusion of latest Permian diversity in calculations of re-calibrated diversity is expected to compensate in part for the effects of Olson's gap for the time interval encompassing Guadalupian and Lopingian. Rarefaction independently supports an overall drop in mid to late Permian diversity (Text-fig. 9C, D). Crucially, however, it shows that the upper limit of the confidence interval for the re-calibrated Guadalupian–Lopingian diversity value barely reaches the lower limits of the confidence intervals associated with the Cisuralian and/or the Early Triassic, and is also con-

sistently lower than the lower limit of the confidence interval for the Carboniferous.

DISCUSSION

Taxonomic ranks

The use of different taxonomic ranks has little effect on the overall shape of the diversity trajectories in the time period from the Induan onward, during which the pattern is one of steady and rapid decline. In the Palaeozoic, however, different ranks imply different perceptions of the expansion/contraction trend, and this is nowhere better illustrated than in the Pennsylvanian. The alternation of troughs and peaks in the genus- and species-level curves (Text-fig. 2) is replaced by a smooth, rapid increase in family-level diversity (Text-fig. 3). However, the species-, genus-, and family-level trajectories consistently display a rapid increase in diversity from the latest Permian to the earliest Triassic and a decline near the end of the Cisuralian. In the rest of the Cisuralian, however, family-level diversity is either relatively constant or shows a small increase. Thus, we could find no evidence for a steady diversity drop, *contra* Maxwell (1992). However, a drop is evident when either genus- or species-level curves are considered. Also, the impact of Olson's gap is equally emphasized by all curves, regardless of taxonomic rank.

A treatment of Olson's gap is beyond the scope of the present paper. However, some comments are necessary. Lucas (2004) offered a detailed account of this gap, giving evidence in support of its global extent, and arguing in favour of a remodelling of Permian tetrapod faunas throughout its duration. His emphasis was on comparisons between synapsid faunas, but other tetrapod groups were discussed as well. According to Lucas (2004), the dynamics and magnitude of this remodelling cannot be dealt with satisfactorily until new discoveries from this crucial hiatus help us quantify major evolutionary steps that bridge the faunal transitions (see Milner 1990 for discussions of temnospondyl family turnover). In the time bin (Artinskian) immediately preceding Olson's gap (Kungurian/Ufimian), 13 temnospondyl families are recorded. Nine of them are represented during the gap itself. Also, five of the 13 families extend into the following time bin (Kazanian). A simple application of the range-through assumption to observed family diversity (i.e. families extend in continuity from their earliest to their latest appearance datum; Hammer and Harper 2006) shows that there is no radical restructuring of family composition, at least as far as temnospondyls are concerned. More than 69 per cent of all families observed immediately before the hiatus survive during the latter, and more than 38 per cent of pre-hiatus diversity is

recorded just after the gap (however, three new families first appear during the Kazanian). Differences between values of diversity are attenuated (especially between hiatus and post-hiatus family counts and survival levels) when ghost lineages and range extensions are introduced.

From this brief exercise, we conclude that further investigations on other tetrapod groups are needed before the dynamics of community remodelling before, during, and after Olson's gap can be quantified.

The influence of choice of tree

Plotted family-level phylogenies, and the introduction of inferred family ranges, modify slightly overall patterns of family diversity. Some of these changes have been highlighted above. Again, we emphasize a remarkable decrease in absolute difference between Tatarian and Induan family records (except in the case of Yates and Warren's 2000 study). Our results indicate a steady increase in family diversity from Kazanian to Induan (again in contrast to Maxwell's 1992 finding that relative stability characterises the late Permian–earliest Triassic interval). Observed and inferred data support post-extinction 'rebound' as an explanation for the elevated diversity in the Early Triassic (Milner 1990; Erwin 1993, 2006; Benton 2003). Also, reshuffling of families associated with different trees exerts only a small impact on overall diversity, but note localised changes in the Permian profiles (especially for the Cisuralian).

Faunal turnover

Originations and extinctions display a more complex pattern during the Palaeozoic than they do in the Mesozoic. In agreement with previous works (summary in Erwin 1993), extinction increases irregularly throughout the Palaeozoic until the Early Triassic, after which period it decreases irregularly (Text-fig. 3). This pattern is not greatly affected by the introduction of ghost lineages and range extensions. More importantly, levels of extinction comparable to those in the latest part of the Permian are also found in the Early Triassic. It is thus clear that temnospondyls did not simply undergo an explosive radiation after the mass extinction at the end of the Permian. Rather, elevated family-level cladogenesis took place in parallel with intense extinction. The origination curves reconstructed from observed family-level diversity values display a large peak in the Induan but the corresponding extinction value for this stage is lower. This difference, however, disappears in the case of the inferred diversity curves based upon Milner's (1990) and Ruta and Bolt's (2006) phylogenies. Yates and Warren's (2000) phylogeny

differs from the two previous phylogenies, in that originations exceed extinctions in the Induan, when inferred diversity is considered (Text-fig. 3F). The influence that Lower Triassic extinctions have on the pattern of biotic turnover and timing of recovery for terrestrial vertebrates requires further scrutiny.

A peculiar aspect of the time-calibrated curves of origination and extinction rate is the occurrence of two peaks, one in the Asselian and one in the Kazanian (a third peak, in the Kasimovian, is observed in the curve in Text-fig. 4D). These are the only Palaeozoic time bins during which the curves run close to each other. Elsewhere, their trajectories do not match (a decrease in origination rate may correspond to an increase in extinction rate, or vice versa). All curves show a considerable peak in both origination and extinction rates in the lowermost Triassic. In the rest of the Mesozoic, no obvious patterns emerge. Extinction rates are invariably higher than origination rates from middle Late Triassic onward, when no more originations take place. However, note the irregularity of the extinction rate curve when the Van Valen (1984) method is employed (Text-fig. 4G, H). This irregularity results from exaggerations of the Ladinian, Rhaetian, and Callovian peaks. These peaks are also seen in other curves, either un-calibrated (Text-fig. 3) or (to a lesser degree) time-calibrated (Text-fig. 4A–F). In comparing the two graphs built with the Van Valen (1984) method, we observe that the only substantial difference associated with the use of unequally weighted vs. equally weighted families is a drop in the percentage of originations and extinctions during the Induan in the case of equally weighted families.

Time-calibrated origination curves are considerably more irregular than the extinction curves. Thus, a peak during the Moscovian is followed by a rapid drop in the late part of the Pennsylvanian, whereas a new rise occurs in the Cisuralian (either as a peak or as a plateau). Origination then drops to nil in the Kungurian/Ufimian, while extinction in this interval reaches its second largest value (after the Tatarian) for the Palaeozoic.

Our study confirms previous empirical observations that rates of origination and extinction appear to be correlated. This correlation is stronger when originations and extinctions are calibrated with time bin durations. Calibration permits more direct comparisons between rates than the un-calibrated curves do. A peak in the Induan, observed for both rates, stands out, as it is associated with a time bin of relatively short duration. This implies high levels of turnover in the aftermath of the Permian extinction event. In addition, time-corrected curves deriving from inferred family-level diversity values show that much of the Palaeozoic history of temnospondyls points in the direction of three major cladogenetic events, one in the mid Pennsylvanian and one each at the beginning and at the end of the Permian. These events are counteracted

by nearly synchronous extinction episodes. Perhaps more intriguingly, origination rates in the Moscovian are not accompanied by comparable levels of family extinction, but the significance of this unique lack of correlation for the two rates is obscure.

End-Permian extinction and post-extinction recovery

Genera (Text-fig. 2A) and species (Text-fig. 2B) occurrences highlight a remarkable diversity increase across the Permo-Triassic boundary (Milner 1990) but perhaps the most intriguing patterns derive from counts of inferred family ranges. Thus, two of the three curves of inferred family-level diversity display only a small difference between Tatarian and Induan values. This contrasts with the larger difference between the values associated with these stages when raw diversity is considered. Milner's (1990) tree implies an increase of over 55 per cent in raw family-level diversity values across the Permo-Triassic boundary, but only a 6.25 per cent increase if inferred diversity is taken into account (Text-fig. 3A, B). A similar set of figures is obtained when Ruta and Bolt's (2006) tree is employed (Text-fig. 3C, D). However, Yates and Warren's (2000) tree is *sui generis*, as it implies a remarkable diversity increase from Tatarian to Induan (Text-fig. 3E, F). Relative to the Tatarian, the Induan peak marks an increase of over 66 per cent in observed diversity and of about 30 per cent in inferred diversity.

In terms of recovery, temnospondyls reach diversity levels comparable to that in the Tatarian during the Anisian, in the case of raw values, or the Olenekian, in the case of inferred values, regardless of tree shape (Text-fig. 3). A post-extinction recovery (using the diversity in the Tatarian as the pre-extinction reference value) thus occurs earlier for families than for genera or species (mid to late Middle Triassic).

From Kazanian to Induan, origination and extinction levels rise steeply (the former more so than the latter) in the case of the observed family trajectories. When inferred ranges are introduced, originations and extinctions tend to balance each other off across the Palaeozoic-Mesozoic boundary, at least in the case of two of the three cladograms shown here (Text-fig. 3A–D). In these, origination is actually lower than extinction (albeit only marginally) in the Induan. It is interesting to observe that rise in origination and extinction levels from the latest Permian to the Early Triassic is accompanied by overall increase in observed as well as inferred family diversity. Such a correspondence occurs rarely in other Palaeozoic time intervals, and usually involves no more than two adjacent stages. An interpretation of this pattern appears, of course, less straightforward and may be correlated with a variety of causes, e.g. a model of ecological displacement

among different temnospondyl clades or geographically constrained, selective diversification and extinction events throughout the latest Palaeozoic. When time is introduced in rate calculations, however, the above-described pattern disappears. We are in the process of investigating a series of causal factors underlying the shape of time-calibrated rate profiles (Text-fig. 4), including the dramatic drop in rates per million years immediately before the end-Permian crisis. What seems to be clear, however, is that temnospondyls as a whole undergo an explosive radiation after the end-Permian, although the effects of background extinctions in the latest Permian exerts an equally strong impact on both the shape of diversity curves and the pattern of post-extinction recovery.

Origination and, to a lesser extent, extinction rate values across the Permo-Triassic boundary appear to be lower when family range extensions are considered. A similar result was found by McGowan and Smith (2007) in their analysis of generic diversity of Permo-Triassic ceratitid ammonoids.

Only four families survive the Permian mass extinction, namely the Amphibamidae, Rhinesuchidae, Rhytidosteidae, and Tupilakosauridae (but see also Milner 1990). To these, we may add Brachyopidae, which perhaps extend back to the late Permian. In Text-fig. 1, we have attributed the earliest known occurrence of this family to the earliest Triassic, but much uncertainty surrounds the age of some basal species (see Damiani and Kitching 2003 for a recent review).

The Amphibamidae dominate in Permian and Carboniferous deposits of North America and Europe. Its last documented representatives come from the Early Triassic of South Africa. Amphibamids are of great zoologically interest, as they are thought to be ancestral to at least some of the three extant crown amphibian orders (e.g. Ruta and Coates 2007). In Schoch and Rubidge's (2005) phylogenetic analysis, the latest known amphibamid, *Micropholis stowi*, forms the sister taxon to all other amphibamids. This hypothesis implies the occurrence of as yet undiscovered taxa bridging the gap between Carboniferous and Triassic amphibamids. In turn, this suggests a broad geographic distribution for this family as well as the possibility of an early dispersal event into Laurasia.

The Tupilakosauridae are also characterised by a broad distribution. The earliest records come from the Cisuralian of North America and the Lopingian of Western Europe. The latest records are from the Induan of South Africa, Greenland, and Russia (for a review, see Werneburg *et al.* 2007). In agreement with Benton *et al.* (2004), we consider Tupilakosauridae to represent a 'disaster taxon', i.e. an example of '... long-ranging opportunistic [and] generalist [groups] that briefly proliferate in the aftermath of mass extinctions, invading vacant ecospace until [they are] forced to return to more marginal settings through competition with specialist taxa returning from refugia'

(Rodland and Bottjer 2001, p. 95). In the case of tupilakosaurids, evidence in support of proliferation rests on the occurrence of three Induan taxa, altogether encompassing a wide geographic range (see above). However, ecological displacement is far more arduous to prove. Candidates responsible for this displacement (if any) may be sought from a vast array of Early Triassic families that were also present in South Africa, Greenland, and Russia.

Finally, the Rhinesuchidae and Rhytidosteidae appear phylogenetically basal to other stereospondyls (the largest radiation of post-Palaeozoic temnospondyls). The former family is noteworthy because it is thought to represent the very inception of the stereospondyl radiation (in phylogenetic terms) as well as its geographic 'cradle' (all known rhinesuchids come from South Africa).

As an overview of changes in overall diversity across the Permo-Triassic boundary, we observe that three families recorded before the Tatarian survive into the Induan (i.e. Amphibamidae; Rhinesuchidae; Tupilakosauridae). A fourth family (Rhytidosteidae) appears in the Tatarian, and is last recorded in the Olenekian. Three families are last recorded during the Tatarian (i.e. Archeosauridae; Cochleosauridae; Melosauridae), while a further two (Dvinosauridae; Peltobatrachidae) are singletons in that stage. In the Induan, ten families make their first appearance. The Benthosuchidae, Brachyopidae, Chigutisauridae, Parotosuchidae, Plagiosauridae, Trematosauridae, and Wetlugosauridae extend beyond this stage, while the Derwentiidae, Lapillopsidae, and Lydekkerinidae constitute singletons.

A final, brief note concerns the status of temnospondyls. Throughout this paper, we have considered them as a coherent and well-characterised group (Milner 1988; Schoch and Milner 2004). However, the status of temnospondyls, regarded either as a monophyletic group (that is, a plesion *sensu* Patterson and Rosen 1977) branching from the tetrapod stem (e.g. Vallin and Laurin 2004), or as a set of plesions on the lissamphibian stem, i.e. a grade group (e.g. Milner 1988; Schoch and Milner 2004; Ruta and Coates 2007), has not generated consensus thus far (for recent reviews of the amphibian origin debate, see also Schoch and Milner 2004 and Lee and Anderson 2006). The implications of such contrasting hypotheses of temnospondyl affinities are far-reaching, and bear on the issues of diversity profiles and dynamics of major extinctions. As an example, the origins of some or all of the three extant orders of lissamphibians (frogs, salamanders, and caecilians) may be traced back to one or possibly two families of dissorophoid temnospondyls, according to some authors (review in Ruta and Coates 2007). Two of these families, in particular, have played an almost unrivalled role in the temnospondyl hypothesis: Branchiosauridae and Amphibamidae (see Milner 1993; Schoch and Milner 2004, and references therein). Amphibamidae are in strati-

graphic continuity with the earliest recorded crown-group amphibians (i.e. *Triadobatrachus* and *Czatkobatrachus*, two Lower Triassic stem-group frogs from Madagascar and Poland, respectively; see Evans and Borsuk-Bialynicka 1998 and Rocek and Rage 2000). The same is true for *Tungusso-gyrinus*, a dissorophoid of uncertain phylogenetic affinities from the Permo-Triassic of Siberia (Shishkin 1998; but see also Werneburg 2004 for an interpretation of *Tungusso-gyrinus* as a branchiosaurid). Regardless of the status of these dissorophoid families, their postulated phylogenetic proximity to lissamphibians increases both observed and inferred family-level diversity immediately after or, possibly, before the Permo-Triassic boundary, and thus impacts estimates of rates of origination and extinction. However, exclusion of lissamphibians does not invalidate major conclusions from this paper, as our study centres on a specific group of early tetrapods and does not consider the global trajectory of terrestrial vertebrate diversity (see Benton 1985a, b, 1987, 1994, 1995, 1996a, b).

CONCLUSIONS

This paper tackles temnospondyl diversity through time. It assesses the impact of taxonomic rank, tree topology, and sampling size on profiles of taxonomic richness, as well as the effect of the end-Permian mass extinction on the group's pattern of radiation and recovery. Major conclusions are as follows.

1. In comparison with the raw family diversity curves, curves built from inferred family counts (such as are obtained from a stratigraphic plot of three cladograms of family-level relationships) show (in all but one analysis) a small increase in diversity across the Permo-Triassic boundary. Furthermore, they point to a rather steady diversity from late Pennsylvanian through to early Permian. The post-Triassic decline is invariably rapid and steep.

2. Un-calibrated origination and extinction curves do not appear to be closely associated. However, the curves are close to each other when time calibration is introduced. Two of the highest origination rates in the Palaeozoic (Asselian; Kazanian) are matched by very similar extinction values, but in other time bins, the origination and extinction rate curves follow almost opposite trends (an increase in one curve corresponds to a decrease in the other). An extinction rate peak occurs in the Moscovian/Kasimovian. When the two rate curves are built using inferred family ranges, then extinction and origination values in the Induan are similar (extinction is only slightly higher than origination); however, the Yates and Warren (2000) analysis represents an exception to this pattern. Origination exceeds extinction when observed family-level diversity is considered (and this holds true for all three cladograms).

3. The recast trajectories of temnospondyl diversity, based upon rarefaction estimates of family counts, indicate that the group was approximately as diverse during the Carboniferous and Cisuralian as it was in the Early Triassic. The only significant drop in diversity is throughout the Guadalupian-Lopingian. A relatively small confidence interval is placed around the rarefied diversity value for this time period, in contrast to the values associated with the preceding and following bins, both with large error bars. Thus, if diversity values are rarefied using smaller samples of genera and/or species, then estimated diversity declines dramatically. We interpret such a decline as a real phenomenon rather than as an artefact of the taxonomically impoverished Olson's gap. Similarly, after rarefaction the Lower Triassic still stands out as a time interval of remarkable taxonomic richness (considering its short duration).

Differences between estimated mean diversities are not appreciable when time bins of considerable duration are employed. Thus, Palaeozoic and Mesozoic diversities are comparable. Using subsampling of species occurrences (i.e. rarefying species within families), we demonstrate that there are significant differences between estimated mean diversity values in all pairwise comparisons for the Carboniferous, Permian, and Mesozoic; the comparison between Permian and Mesozoic values is non-significant when genera are rarefied. Also, mean estimated diversities for the Carboniferous and Guadalupian-Lopingian are not significantly different in a four-bin analysis. At the finer time bin subdivision considered in this study (five-bin analysis), Carboniferous/Guadalupian-Lopingian, Carboniferous/Middle Triassic-Early Cretaceous, and Cisuralian/Lower Triassic comparisons are not significant.

When either genera or species are rarefied within families using five time bins, a recast trajectory of family-level diversity appears consistent with the raw data in displaying an Early Permian and an Early Triassic diversity peak. Unlike in the raw data trajectory, however, no conspicuous discrepancy occurs between the estimated diversity values associated with these peaks, and both values are only marginally higher than the Carboniferous value. Rarefaction shows that diversity in the Guadalupian-Lopingian is even lower (compared with Carboniferous and Middle Triassic-Early Cretaceous values) than raw data suggest. Also, data are silent about the causal factors underlying this depressed Guadalupian-Lopingian diversity. Preservation bias (e.g. Maxwell 1992) may be responsible for it. However, we point out that a higher extinction level is not necessarily correlated with greater observed or inferred diversity values, as even a cursory glance at Text-fig. 3 reveals. The hypothesis that '[a larger number of] amphibian families in the Early Permian led to a greater number of extinctions ... [whereas] fewer families [in] the Late Permian led to fewer extinctions' (Erwin 1993, p. 124) can thus be ruled out.

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APPENDIX

Results of the reduced major axis regression applied to time-calibrated (dt; stage duration) values of originations (o) and extinctions (e) for observed (obs) and inferred (inf) family-level diversities using either mean standard diversity (msd) of families per stage (Van Valen's 1984 method for observed families only; Text-fig. 8C, D) or total diversity (d) of families from all stages (based upon Milner's 1990, Ruta and Bolt's 2006, and Yates and Warren's 2000 trees; Text-fig. 7).

obs-o/d/dt vs. obs-e/d/dt based upon Milner's (1990) tree (see also Text-fig. 7A)

	Intercept	Slope	R ²
Linear model			
Estimate	−0.04037	1.093	0.3894
Standard error	0.1987	0.1909	
Jackknife			
Estimate	−4.059e ^{−3}	0.9795	0.4079
Standard error	0.1909	0.4168	0.2754
95% confidence intervals			
Linear	−0.4548, 0.3741	0.6944, 1.491	
Bootstrap	−0.413, 1.035	−1.493, 1.628	9.496e ^{−3} , 0.7483

Least-squares R = 0.624; RMA jackknife R = 0.639; difference between the two R values = 0.015; 95 per cent confidence interval for the difference = −0.400884 < 0.015 < 0.441915; z = 0.10877; P = 0.54331.

info/d/dt vs. infe/d/dt based upon Milner's (1990) tree (see also Text-fig. 7B)

	Intercept	Slope	R ²
Linear model			
Estimate	-0.03096	1.041	0.4615
Standard error	0.1872	0.1709	
Jackknife			
Estimate	1.361e ⁻³	0.9295	0.4163
Standard error	0.1295	0.3118	0.372
95% confidence intervals			
Linear	-0.4216, 0.3596	0.6849, 1.398	
Bootstrap	-0.4364, 0.2186	0.7825, 2.302	0.01021, 0.9076

Least-squares R = 0.679; RMA jackknife R = 0.645; difference between the two R values = -0.034; 95 per cent confidence interval for the difference = -0.470118 < -0.034 < 0.370573; z = -0.26401; P = 0.39589.

obs'o/d/dt vs. obs'e/d/dt based upon Ruta and Bolt's (2006) tree (see also Text-fig. 7C)

	Intercept	Slope	R ²
Linear model			
Estimate	-0.09961	1.165	0.4092
Standard error	0.2005	0.2002	
Jackknife			
Estimate	-0.04556	1.014	0.4118
Standard error	0.2029	0.4765	0.2467
95% confidence intervals			
Linear	-0.5179, 0.3187	0.7473, 1.583	
Bootstrap	-0.5059, 0.9541	-1.452, 1.98	2.196e ⁻³ , 0.7548

Least-squares R = 0.64; RMA jackknife R = 0.642; difference between the two R values = 0.002; 95 per cent confidence interval for the difference = -0.41882 < 0.002 < 0.424403; z = -0.26401; P = 0.5.

info/d/dt vs. infe/d/dt based upon Ruta and Bolt's (2006) tree (see also Text-fig. 7D)

	Intercept	Slope	R ²
Linear model			
Estimate	-0.08745	0.9871	0.7513
Standard error	0.1366	0.1101	
Jackknife			
Estimate	-0.07976	0.9616	0.7707
Standard error	0.09421	0.1269	0.1761
95% confidence intervals			
Linear	-0.3724, 0.1975	0.7575, 1.217	
Bootstrap	-0.2819, 0.08694	0.8191, 1.49	0.3073, 0.953

Least-squares R = 0.867; RMA jackknife R = 0.878; difference between the two R values = 0.011; 95 per cent confidence interval for the difference = -0.382985 < 0.011 < 0.458773; z = -0.20095; P = 0.58.

obs'o/d/dt vs. obs'e/d/dt based upon Yates and Warren's (2000) tree (see also Text-fig. 7E)

	Intercept	Slope	R ²
Linear model			
Estimate	-0.0161	1.053	0.4516
Standard error	0.1862	0.1743	
Jackknife			
Estimate	0.04422	0.8762	0.4915
Standard error	0.1933	0.437	0.2868

95% confidence intervals

Linear	-0.4045, 0.3723	0.689, 1.416	
Bootstrap	-0.3934, 0.989	-1.493, 1.628	9.496e ⁻³ , 0.7905

Least-squares R = 0.672; RMA jackknife R = 0.701; difference between the two R values = 0.029; 95 per cent confidence interval for the difference = -0.375467 < 0.029 < 0.465678; z = -0.23923; P = 0.59.

inf_o/d/dt vs. inf_e/d/dt based upon Yates and Warren's (2000) tree (see also Text-fig. 7F)

	Intercept	Slope	R ²
Linear model			
Estimate	-0.07231	1.107	0.2777
Standard error	0.2106	0.2103	
Jackknife			
Estimate	-0.03772	0.9837	0.2137
Standard error	0.1658	0.481	0.2726
95% confidence intervals			
Linear	-0.5117, 0.3671	0.6679, 1.545	
Bootstrap	-0.3948, 0.3059	0.4303, 2.01	5.761e ⁻³ , 0.7932

Least-squares R = 0.527; RMA jackknife R = 0.462; difference between the two R values = -0.065; 95 per cent confidence interval for the difference = -0.489792 < -0.065 < 0.348314; z = -0.37544; P = 0.35.

o/msdd/dt vs. e/msd/dt using Van Valen's (1984) method with unequally weighted families (see also Text-fig. 8C)

	Intercept	Slope	R ²
Linear model			
Estimate	-9.987e ⁻³	1.042	0.05625
Standard error	0.01887	0.2264	
Jackknife			
Estimate	-0.08707	2.617	-0.04804
Standard error	0.08338	1.788	0.1254
95% confidence intervals			
Linear	-0.04935, 0.02937	0.5699, 1.514	
Bootstrap	-0.04266, 0.1108	-1.183, 1.477	4.468e ⁻⁴ , 0.4515

Least-squares R = 0.237; RMA jackknife R = -0.219; difference between the two R values = -0.456; 95 per cent confidence interval for the difference = -0.722977 < -0.456 < -0.014543; z = -2.0234; P = 0.02.

o/msdd/dt vs. e/msd/dt using Van Valen's (1984) method with equally weighted families (see also Text-fig. 8D)

	Intercept	Slope	R ²
Linear model			
Estimate	-7.566e ⁻³	1.047	0.05642
Standard error	0.01314	0.2274	
Jackknife			
Estimate	-0.0594	2.565	-0.07895
Standard error	0.05729	1.761	0.1234
95% confidence intervals			
Linear	-0.03498, 0.01985	0.5727, 1.522	
Bootstrap	-0.03174, 0.07654	-1.188, 1.474	2.916e ⁻⁴ , 0.4661

Least-squares R = 0.238; RMA jackknife R = -0.519; difference between the two R values = -0.519; 95 per cent confidence interval for the difference = -0.753531 < -0.519 < -0.081584; z = -2.31641; P = 0.01.