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1 **Permian-Triassic Osteichthyes (bony fishes): Diversity dynamics and body size evolution**

2

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23 **ABSTRACT**

24

25 The Permian and Triassic were key time intervals in the history of life on Earth. Both

26 periods are marked by a series of biotic crises including the most catastrophic of such events,

1 the end-Permian mass extinction, which eventually led to a major turnover from typical
2 Palaeozoic faunas and floras to those that are emblematic for the Mesozoic and Cenozoic. The
3 aim of this review is to examine trends in Permian and Triassic osteichthyans (Dipnoi,
4 Actinistia, Actinopterygii) in order to elucidate their response to important biotic events
5 during these periods. Our analyses are based on an updated data matrix adapted from primary
6 literature. We investigate different metrics, including taxonomic diversity and body size.
7 Diversity is measured separately for marine and freshwater bony fishes but also on global
8 scale (total diversity), across palaeolatitudinal belts and within different palaeogeographical
9 provinces. In addition, we examine body size to infer changes in trophic position. Our results
10 suggest a general trend from low osteichthyan diversity in the Permian to higher levels in the
11 Triassic. Diversity dynamics in the Permian are marked by a decline in freshwater taxa during
12 the Cisuralian, followed by a slight rise in global osteichthyan diversity towards the end of the
13 Permian. An extinction event during the end-Guadalupian crisis is not evident from our data.
14 However, basal actinopterygians ('palaeopterygians') experienced a significant body size
15 increase across the Guadalupian-Lopingian boundary and these fishes upheld their position as
16 large, top predators from the Late Permian to the Late Triassic. Smaller osteichthyans at lower
17 trophic levels mainly comprised neopterygians and 'subholosteans'. The effects of the end-
18 Permian mass extinction on bony fishes remain elusive due to taxonomic difficulties, however
19 two distinct diversification events are noted in the wake of this biotic crisis, a first one during
20 the Early Triassic (dipnoans, actinistians, 'palaeopterygians', 'subholosteans') and a second
21 one during the Middle Triassic ('subholosteans', neopterygians) – the latter event mediating a
22 significant global decrease in osteichthyan body size. Neopterygii, the clade that encompasses
23 the vast majority of extant fishes, experienced another radiation event in the Late Triassic.
24 The Triassic diversification of Osteichthyes, predominantly of Actinopterygii, which only
25 occurred after severe extinctions among Chondrichthyes during the Middle–Late Permian,
26 resulted in a profound change within global fish communities, from the chondrichthyan-rich

1 faunas of the Permo-Carboniferous to the typical Mesozoic and Cenozoic associations
2 dominated by actinopterygians. This ichthyofaunal turnover was not sudden but followed a
3 stepwise pattern over tens of millions of years, with leaps during extinction events.

4

5 *Key words:* Dipnoi, Actinistia, Actinopterygii, Osteichthyes, mass extinction, biotic recovery,
6 Permian-Triassic boundary, diversity, body size

7

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39 I. INTRODUCTION

40

1 Fishes (non-tetrapod vertebrates) comprise more than half of today's global vertebrate
2 diversity and they are important predators in aquatic ecosystems. Marine and freshwater
3 ichthyofaunas have been dominated by teleosteans since the later part of the Mesozoic, with
4 presently >28'000 species, followed by chondrichthyans (sharks, rays, ratfishes) as the second
5 largest clade with >1'100 extant species (Arratia, 2004; Nelson, 2006; Sallan, 2014). Other
6 groups, such as non-teleostean ray-finned fishes (bichirs, reedfishes, sturgeons, bowfin, gars),
7 lobe-finned fishes (lungfishes, 'coelacanth'), and 'Cyclostomata' (hagfishes, lampreys),
8 today constitute only a minor component, whereas other groups are only known as fossils
9 (Janvier, 1996, 2007; Nelson, 2006; Friedman & Sallan, 2012; Sallan, 2014). The diversity of
10 fishes has fluctuated in the past and groups that are rare or extinct today flourished at different
11 times (Thomson, 1977; McCune & Schaeffer, 1986; Patterson, 1994; Schultze, 2004; Klug *et*
12 *al.*, 2010; Sallan & Coates, 2010; Anderson *et al.*, 2011; Friedman & Sallan, 2012; Tintori *et*
13 *al.*, 2013). Questions concerning which factors led to the observed diversity patterns in fishes
14 and to what extent mass extinctions played a role have become increasingly important in
15 modern palaeoichthyology (e.g. McCune & Schaeffer, 1986; Patterson & Smith, 1987;
16 Benton, 1998; Cavin, 2002; Kriwet & Benton, 2004; Cavin, Forey & Lécuyer, 2007; Sallan &
17 Coates, 2010; Friedman & Sallan, 2012; Lloyd & Friedman, 2013; Sallan, 2014).

18 A critical time for both marine and continental life on Earth was the Permian-Triassic
19 interval (ca. 298.9–201.3 myr ago; Gradstein *et al.*, 2012), known for a series of extinction
20 events, amongst others the most devastating of all time: the end-Permian mass extinction
21 (~252.17 myr ago; e.g. Raup, 1978; Sepkoski, 1984; Benton, 2003; Erwin, 2006; Shen *et al.*,
22 2011). A few studies have already focused on diversity patterns of bony fishes (Osteichthyes)
23 or fishes in general in relation to the end-Permian mass extinction and most of them arrived at
24 the conclusion that these groups were only minorly impacted by this event (Schaeffer, 1973;
25 Thomson, 1976, 1977; Patterson & Smith, 1987; Benton, 1998; Reguant, 2007; Blicek, 2011).
26 Nevertheless, possible crises have been suggested for certain subsets of fishes, such as

1 durophagous forms (Friedman & Sallan, 2012) or marine taxa (Pitrat, 1973). Little is known
2 about the response of fishes to other extinction events of the Permian and Triassic, such as the
3 end-Guadalupian (Groves & Wang, 2013) and end-Smithian crises (Galfetti *et al.*, 2007a, b).
4 Moreover, previous studies were only based on anecdotal evidence or primarily on data from
5 old compendia, such as Benton (1993) or Sepkoski (2002). Note that the database of Sepkoski
6 (2002) was last updated in 1998 and his analyses were not specifically aimed at fishes. Hence,
7 earlier studies lack the data compiled over the last 15 to 20 years, including discoveries and
8 revisions of taxa and refinements in biochronostratigraphy. Finally, most previous studies
9 have only looked at taxonomic changes but not at other metrics.

10 Here we present a literature review and state-of-the-art study of the evolutionary
11 dynamics of the three dominant groups of Osteichthyes during the Permian and Triassic:
12 Actinopterygii (ray-finned fishes), Actinistia ('coelacanths') and Dipnoi (lungfishes). Trends
13 within Permian-Triassic Chondrichthyes (cartilaginous fishes) are examined elsewhere (Koot,
14 2013). Our analyses rely on an updated data matrix based on primary literature (see
15 Supplementary Tables A1–A3) and focus on changes in taxonomic diversity among various
16 osteichthyan groups, within different environments (marine, freshwater, global), and across
17 palaeolatitudes, but also on fluctuations in body size and accompanied implications for
18 aquatic trophic networks. The results are discussed primarily in the context of different biotic
19 crises and recoveries of the Permian-Triassic and the evolutionary dynamics of fishes are
20 compared to those of other taxa. The goal of this paper is to review the current state of
21 research and to highlight gaps in our knowledge as a guide for future research.

22

23 **II. MATERIAL AND METHODS**

24

25 (1) Dataset

26

1 This study is based on the more diverse osteichthyan groups of the Permian-Triassic,
2 namely Actinopterygii, Actinistia, and Dipnoi, which have been the dominant clades among
3 bony fishes since the Early Carboniferous and also include extant representatives (e.g.,
4 Nelson, 2006; Sallan & Coates, 2010; Friedman & Sallan, 2012). Chondrichthyes have been
5 studied separately (Koot, 2013). Conodonts, whose vertebrate affinities are still debated (see
6 Turner *et al.*, 2010), were studied by Orchard (2007). Other, rarer groups that lived during the
7 Permian-Triassic interval, such as ‘Cyclostomata’ (Janvier, 1996; Kuraku & Kuratani, 2006),
8 ‘Acanthodii’ (early gnathostomes; Mutter & Richter, 2007), and megalichthyid and
9 rhizodopsid sarcopterygians (Schultze & Heidtke, 1986; Witzmann & Schoch, 2012), are
10 excluded because of insufficient data for sound analyses. However, all groups of fishes, both
11 cartilaginous and bony clades, are taken into account in the discussion section.

12 Osteichthyes are divided into two major subclades: Sarcopterygii (lobe-finned fishes)
13 and Actinopterygii (ray-finned fishes). Sarcopterygians comprise the Dipnoi and Actinistia,
14 but also the Tetrapodomorpha (e.g. the Late Palaeozoic rhizodopsids and megalichthyids;
15 Janvier, 2007). Permian-Triassic actinopterygians are subdivided into the monophyletic
16 Neopterygii, which include Teleostomorpha (Arratia, 2004) and Holostei (to this group we
17 herein refer all non-teleostomorph neopterygians, see also Grande, 2010 and López-
18 Arbarello, 2012), as well as a paraphyletic group of non-neopterygian actinopterygians coined
19 ‘Palaeopterygii’ by Regan (1923). Many predominantly Triassic ‘palaeopterygians’ exhibit a
20 mosaic pattern of neopterygian characters (e.g. Brough, 1936; Schaeffer 1956). However,
21 these taxa have traditionally been excluded from Neopterygii and the term ‘Subholostei’ was
22 established for them by Brough (1936). Their similarities with neopterygians are mostly
23 considered the result of convergent evolution (Brough, 1936; Schaeffer, 1956).

24 Although some Permian-Triassic bony fishes have already been included in cladistic
25 analyses (e.g. Lund, Poplin & McCarthy, 1995; Forey, 1998; Coates, 1999; Schultze, 2004;
26 Gardiner, Schaeffer & Masserie, 2005; Poplin & Dutheil, 2005; López-Arbarello, 2012;

1 Benton *et al.*, 2013; Cavin, Furrer & Obrist, 2013), the phylogenetic position of many taxa is
2 still not well known. The taxonomic framework at family and order level is poorly resolved
3 for many osteichthyans, specifically for ‘palaeopterygians’ and ‘subholosteans’ (McCune &
4 Schaeffer, 1986; Patterson & Smith, 1987; Sallan, 2014). For these reasons, we refrain from
5 analysing osteichthyan diversity at family or order level and instead use the classical higher
6 groupings, i.e. Dipnoi, Actinistia, ‘Palaeopterygii’ (), ‘Subholostei’, Holostei, and
7 Teleostomorpha. We largely adopt Brough’s (1936) concept of ‘Subholostei’ but exclude
8 Saurichthyidae due to a lack of neopterygian-like traits (note that the sole character mentioned
9 by Brough, a vertical suspensorium, is absent in saurichthyids, cf. Stensiö, 1925).

10 For our analyses, we compiled a new database (last update: December 2013) and we
11 mostly follow the latest taxonomic interpretations (Supplementary Tables A1–A3). Our
12 database, resolved at species level (including species in open nomenclature), contains
13 information on geographical and stratigraphical occurrences as well as body size. Only taxa
14 whose stratigraphic occurrence can be dated at least at the epoch level are incorporated.
15 Occurrences of taxa represented by isolated skeletal elements (e.g. skull bones or scales) are
16 only included in the database if the remains can be identified with reasonable certainty at
17 genus level (e.g. jaw fragments of *Saurichthys*). Nominal taxa based on material we deem
18 non-diagnostic are omitted. Questionable occurrences are indicated by a ‘?’ or genera listed in
19 inverted commas in Supplementary Tables A1–A3.

20 Our database (see Supplementary Tables A1–A3; *nomina dubia/nuda* omitted) includes
21 a total of 697 named species (59 Dipnoi, 43 Actinistia, 595 Actinopterygii) belonging to 363
22 nominal genera (18 Dipnoi, 32 Actinistia, 313 Actinopterygii). Marine and freshwater
23 occurrences are treated as separate datasets. Assignment of occurrences as either marine or
24 freshwater mostly adheres to the interpretation of previous authors. Taxa from brackish water
25 environments are included in the marine dataset. All lungfishes are incorporated in the non-
26 marine dataset (note, however, that some dipnoans may have also dwelled in marine habitats;

1 e.g. Schultze, 2004). For the Permian-Triassic, we identified 212 marine genera (28
2 Actinistia, 184 Actinopterygii) and 172 freshwater genera (18 Dipnoi, 6 Actinistia, 148
3 Actinopterygii). Furthermore, 20 bony fish genera (2 Actinistia, 18 Actinopterygii) have been
4 reported from both marine and freshwater deposits and can thus be considered euryhaline. For
5 estimation of diversity on a global scale (i.e. marine plus freshwater combined), euryhaline
6 taxa were only counted once per interval. For comparison, the global average number of
7 genera per each Permian-Triassic epoch corresponds to ca. 0.5–1% of all extant osteichthyan
8 genera (~4'300; Nelson, 2006).

9 The Permian and Triassic are divided into three epochs each (Early, Middle, Late).
10 Permian epochs were originally named after geographically separated outcrop areas in Russia
11 (Cisuralian = Early Permian), the United States (Guadalupian = Middle Permian), and China
12 (Lopingian = Late Permian). The Cisuralian includes four stages (Asselian, Sakmarian,
13 Artinskian, Kungurian), the Guadalupian three (Roadian, Wordian, Capitanian), and the
14 Lopingian two (Wuchiapingian, Changhsingian). The Early Triassic is officially subdivided
15 into two stages (Induan, Olenekian; Kiparisova & Popov, 1956; Gradstein *et al.*, 2012) but
16 more commonly into four substages (Tozer, 1965) well defined by global faunal events
17 (Griesbachian, Dienerian, Smithian, Spathian). The Middle Triassic comprises two stages
18 (Anisian, Ladinian), and the Late Triassic three (Carnian, Norian, Rhaetian). Occurrences of
19 bony fishes are known from all stages of the Permian-Triassic interval (and substages of the
20 Early Triassic) and from all continents (Fig. 1a), with a focus on Europe due to the much
21 longer research history, starting with the dawn of palaeoichthyology in the early 19th century
22 (e.g. Agassiz, 1833–43).

23

24 (2). Diversity analyses

25

1 Diversity analyses herein are based on occurrences of genera (Supplementary Tables
2 A1–A3). Diversity of bony fishes is measured in terms of genus richness (counts of genera
3 per bin), boundary crossers (number of genera surviving an interval boundary), and mean
4 standing diversity. Mean standing diversity was calculated by counting first and last
5 occurrences of a given genus as 0.5 (assuming that taxa persisted, on average, for about half
6 of the duration of the origination or extinction interval, respectively) and range-through
7 occurrences as 1, whereas singletons (genera occurring in only one interval) are weighted as
8 0. Lazarus occurrences (virtual occurrences between known occurrences) were incorporated
9 for calculation of genus richness and boundary crossers. However, Lazarus occurrences
10 between intervals of questionable occurrence were omitted from the analyses. Numbers of
11 originations and extinctions were calculated, as well as per taxon origination and extinction
12 rates (counts of originations/extinctions divided by genus richness). Questionable occurrences
13 of taxa were ignored for these calculations.

14 For the assessment of palaeolatitudinal diversity, occurrences of bony fishes were
15 grouped into palaeolatitudinal belts (according to the palaeogeographic position of their find
16 locality, Fig. 1a) and equivalent belts of the northern and southern palaeohemisphere were
17 combined as follows: (1) low-palaeolatitudinal zone (30°N to 30°S), (2) mid-palaeolatitudinal
18 zone (31°N to 60°N and 31°S to 60°S), and (3) high-palaeolatitudinal zone (61°N to 90°N and
19 61°S to 90°S). Palaeolatitudinal diversity (marine, freshwater, global) is measured at epoch
20 level. Most Permian-Triassic bony fish localities in the northern palaeohemisphere were
21 deposited under marine conditions, whereas those from the southern palaeohemisphere
22 mainly represent continental deposits (Allison & Briggs, 1993; Fig. 1a).

23

24 (3) Body size analyses

25

1 In addition to diversity, we also examined variations in osteichthyan body size during
2 the Permian-Triassic. For this purpose, we compiled data on maximum standard lengths
3 (MSL) at species level (inclusive of some species in open nomenclature, Supplementary
4 Tables A1–A3). MSL of species only known from partial skeletons was estimated by
5 comparison with complete material of other species of the same genus. Based on the amount
6 of available data on body size for each time bin the data is pooled at the epoch level for the
7 Permian and Early Triassic, and at the stage-level for the Middle and Late Triassic (data for
8 the Norian and Rhaetian stages are combined). MSL of each species was counted only once
9 per interval regardless of number of occurrences. A Log₂ transformation was chosen to make
10 differences at smaller sizes better visible. Statistical analyses were performed using PAST
11 (Hammer, Harper & Ryan, 2001).

12 A recent study by Romanuk, Hayward & Hutchings (2011) demonstrates that body size
13 of extant fishes significantly correlates with trophic level (see also Trebilco *et al.*, 2013).
14 Accordingly, as a working hypothesis, body size of fossil fishes can be used as a proxy for
15 trophic position within ancient aquatic food webs. Note that a few extant taxa (e.g. large
16 planktivores) do show a negative correlation between body size and trophic level (Romanuk,
17 Hayward & Hutchings, 2011). Dietary data for Permian-Triassic bony fishes are limited (e.g.
18 Schaeffer & Mangus, 1976; Bürgin, 1996; Esin, 1997; Lombardo & Tintori, 2005; Boy &
19 Schindler, 2012; Bellwood *et al.*, 2014) and hence are only qualitatively discussed herein, but
20 many large-bodied species possess conical teeth typical for carnivores, suggesting that they
21 conform to the general trend. In fact, large suspension-feeding Osteichthyes did not evolve
22 before the Jurassic (Friedman, 2012). We herein use the following rough body length
23 categories as proxies for the spectrum (range) and dominance (median plus 25–75% quartiles)
24 of trophic position of Permian-Triassic Osteichthyes: small consumers (below ~200 mm
25 MSL), mid-sized consumers (ca. 200–500 mm MSL) and large consumers (above ca. 500 mm
26 MSL).

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(4). Quality of the osteichthyan fossil record

Inferring biological signals from the fossil record is often complicated because the patterns that emerge from it can be skewed by other factors, including biases in preservation, differences in sampling, and variations in research effort (see Benton *et al.*, 2011 for discussion). This is especially true for vertebrates because of their more sporadic stratigraphic distribution compared to other groups (e.g. many invertebrates). Nevertheless, fishes are an abundant group within the vertebrate fossil record and potentially useful for the study of evolutionary and macroecological patterns through time (e.g. Lloyd & Friedman, 2013).

For the evaluation of biases related to differences in palaeogeographical sampling, we compared the relative contribution of six macrogeographical provinces to the global fossil record of Permian-Triassic osteichthyans. These provinces are: (1) Boreal Sea, (2) east-equatorial Panthalassa, (3) south-western Pangaea, (4) Palaeotethys, (5) Neotethys, and (6) western and south-western Panthalassa (Fig. 1a).

To circumvent potential biases when comparing unevenly sampled assemblages, rarefaction methods are traditionally used (e.g. Gotelli & Colwell, 2011). However, this approach is not flawless. For instance, a rarefied richness of a Tropical assemblage may be strongly underestimated when compared to the richness of a Boreal assemblage. Chao & Jost (2012) provided an analytical solution for coverage-based rarefaction, “coverage” being a measure of sample completeness. Contrary to classical, sample size-based rarefaction, this rarefaction preserves the real degree of difference between the communities’ richnesses, even for small sample size, and provides a sampling ‘stopping rule’. Chao & Jost (2012) and Colwell *et al.* (2012) also provided an analytical solution for the extrapolation of sample richness to higher coverage instead of larger sample size, thus unifying coverage-based interpolation and extrapolation into a single curve [see Section III(1)].

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(5) Lagerstätten effect

One of the most important biases in the fossil record of bony fishes arises from the occurrence of Lagerstätten (Seilacher *et al.*, 1985). This is related to the fact that well-preserved material is essential for the identification of osteichthyan fossils at genus level, and this kind of preservation is usually linked to occurrences of dysoxic to anoxic facies (Tintori, 1992; Ware *et al.*, 2011). Because taxonomic richness at a particular site is dependent on the amount of specimens recovered, time slices containing fossiliferous localities with good quality of preservation frequently yield increased diversity compared to intervals without such sites. Moreover, localities yielding large quantities of well-preserved fossils are often also more extensively studied, leading to another bias through increased research effort.

In order to estimate the impact of the Lagerstätten effect we produced separate diversity curves for the marine and freshwater realms in which osteichthyan genera that are known *solely* from Lagerstätten are excluded and compared them with the trend lines derived from the complete datasets [see Section III(1)]. In addition, we calculated the degree of endemism of each Lagerstätte (i.e. percentage of genera that are exclusively known from that site during a given epoch, Fig. 3). In general, the higher the degree of endemism, the larger the Lagerstätten effect will be.

We herein identify osteichthyan Lagerstätten based on two criteria: (1) exceptional preservation quality, i.e. presence of well-preserved, (largely) complete specimens, and (2) high abundance of such fossils. Based on these criteria, the following Permian-Triassic Lagerstätten are determined for marine bony fishes: Marl Slate and Kupferschiefer formations (England and Germany, respectively; Late Permian; here treated together as a single Lagerstätte), Wordie Creek Formation (Greenland; Early Triassic), «couches à poissons et à ammonites» (NW Madagascar; Early Triassic), «fish horizon» (Spitsbergen; Early Triassic),

1 Sulphur Mountain Formation (British Columbia, Canada; Early Triassic), Luoping Biota
2 (Guizhou and Yunnan, China; Middle Triassic), Besano and Meride formations (Monte San
3 Giorgio area, Swiss-Italian boundary; Middle Triassic), Prosanto Formation (Switzerland;
4 Middle Triassic), and Zorzino Limestone (Bergamo Alps, Italy; Late Triassic). Note the
5 absence of marine Lagerstätten for the Early and Middle Permian (Fig. 3a).

6 For the freshwater record, we identify the following Lagerstätten: Autun, Bourbon
7 l'Archambault and Lodève basins (France; Early Permian; all three treated as a single
8 Lagerstätte), Krkonoše Piedmont Basin and Boskovice Graben (Czech Republic; Early
9 Permian), Upper Beaufort Series (Karoo Basin, South Africa; Early Triassic), Hawkesbury
10 Sandstone and Wianamatta Shale (New South Wales, Australia; Middle Triassic), and Chinle,
11 Dockum and Newark Groups (USA; Late Triassic; all three treated as one Lagerstätte). Note
12 that based on the criteria outlined above, no freshwater Lagerstätten could be identified for the
13 Middle and Late Permian (Fig. 3b).

14 Other methods to estimate sampling biases include division of taxonomic richness by (i)
15 number of localities or (ii) interval length (Supplementary Table B1). Note that division by
16 bin duration provides a time-standardised quantification of diversity, whereas division by
17 locality (or formation) number may suffer from redundancy (see e.g. Benton *et al.*, 2011). We
18 did not test for correlations between diversity and rock volume (see e.g. Thomson, 1977 for
19 discussion) but these two variables are likely governed by other factors (Hannisdal & Peters
20 2011).

21

22 (6) First and last appearance datums

23

24 The general incompleteness of the fossil record has important implications for the first
25 appearance datum (FAD) and last appearance datum (LAD) of taxa. Although, for practical
26 reasons, FADs are often equated with true originations and LADs with real extinctions, in

1 many cases this assumption is not correct (e.g. Signor-Lipps effect, Signor & Lipps, 1982).
2 Moreover, different biological meanings can be attributed to FADs and LADs. Apart from
3 true origination or extinction, the FAD and LAD of a given taxon could also suggest a
4 migration, for instance from a palaeoenvironment with a poor fossil record into one that has a
5 good record, or vice versa (cf. ‘*refugia taxa*’ during environmental crises, Kauffman &
6 Harries, 1986). Alternatively, a taxon may have stayed in its habitat prior to its FAD and/or
7 after its LAD but preservational conditions in that palaeoenvironment changed.

8 A famous example for migration as a likely explanation for a LAD is demonstrated for
9 actinistians. They are known from the Devonian up to the present, but lack a Cenozoic fossil
10 record (~70 Ma; Casane & Laurenti, 2013; Cavin, Furrer & Obrist, 2013). Until the discovery
11 of the extant coelacanth *Latimeria* in the 1930s (Smith, 1939), they were wrongly considered
12 extinct. *Latimeria* dwells in deep water environments, which have a poor fossil record. It was
13 hypothesized that such habitats could have been typical for post-Cretaceous actinistians,
14 providing a possible explanation for the gap in their fossil record (White, 1953; Forey, 1998).
15 However, it is noteworthy that actinistians are usually rare within fish assemblages and their
16 diversity in the fossil record is generally low, with a few exceptions (e.g. during the Early
17 Triassic; Schultze, 2004; Cavin, Furrer & Obrist, 2013). Although the migration scenario may
18 be a potential biological explanation for FADs and LADs of such less diverse or rare groups,
19 and generally at lower taxonomic ranks, it seems to be a more extraordinary assumption for
20 groups that are more diverse and abundant in the fossil record. At any rate, migration as well
21 as true origination and extinction of many taxa at the same time could still suggest an
22 underlying biotic event. As a working hypothesis, we herein follow previous authors and treat
23 FADs and LADs of taxa as genuine originations or extinctions, respectively, although
24 potential biases in the fossil record as well as the migration scenario may in some cases offer
25 alternative explanations.

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III. RESULTS

(1) Estimation of sampling bias and Lagerstätten effect

Most of the record for the Permian and the Middle–Late Triassic is dominated by data from the Palaeotethys, with important contributions from the western and south-western Panthalassa region, south-western Pangaea, and the east-equatorial Panthalassa province (Fig. 1b). In the Early Triassic, however, trends within osteichthyans are mainly based on either the Boreal Sea record (Griesbachian and Smithian) or the Neotethys record (Dienerian) because of occurrences of Lagerstätten [see Section II(5)]. The Spathian record of Osteichthyes is poor due to the absence of well-explored Lagerstätten and the data mostly come from China (western and south-western Panthalassa province, Fig. 1b). Other important sampling biases include large gaps in the Neotethys and western and south-western Panthalassa records during the Permian (Fig. 1b).

Sample-size rarefaction and extrapolation curves (following Chao & Jost, 2012 and Colwell *et al.*, 2012) indicate that the estimated osteichthyan richness at the species and genus levels is much higher for the Triassic than for the Permian (Fig. 2). Both time intervals show rather similar sample coverage values (~0.6 at the genus level and ~0.25 at the species level), indicating that data can be directly compared and are not likely to result from major differential sampling artefacts. However, Permian and Triassic sample coverage values are relatively low (especially at species level) suggesting that sampling effort for these two periods can be improved in the future and that endemic taxa largely dominate known bony fish records.

Our tentative evaluation of the Lagerstätten effect yielded different results for the marine and non-marine records. In the marine realm (Fig. 3a), we find the same main long-

1 term trend from lower diversity in the Permian to higher diversity in the Triassic, with a peak
2 in the Middle Triassic, whether taxa known only from Lagerstätten [see Section II(5)] are
3 omitted or not. The main difference between the two curves is, however, found in the Early
4 Triassic: here, osteichthyan diversity is similar to that found in the Late Permian if
5 Lagerstätten taxa are excluded from the dataset, whereas genus richness during the Early
6 Triassic is intermediate to Late Permian and Middle Triassic values if the complete marine
7 dataset is considered (Fig. 3a). The reason for this discrepancy lies in the similarity among
8 bony fish faunas in Early Triassic Lagerstätten as a result of increased cosmopolitanism
9 during this epoch [Piveteau, 1935; Schaeffer & Mangus, 1976; see Section IV(2a)]. Despite
10 the presence of high-diversity Lagerstätten in the Middle Triassic (Monte San Giorgio,
11 Luoping), removal of taxa restricted to these sites does not obliterate the peak in genus
12 richness during this epoch. In fact, this peak is due to high endemism at Middle Triassic
13 localities (Fig. 3).

14 For the freshwater record, we find high genus richness in the Early Permian and in the
15 Early to Late Triassic, and relatively lower diversity in the Middle to Late Permian if the
16 complete dataset (including Lagerstätten taxa) is considered. However, if genera restricted to
17 Lagerstätten are removed from the analysis, similar levels of genus richness are found
18 throughout the Permian-Triassic interval (Fig. 3b). Hence, it appears that the trends in the
19 freshwater record of Permian-Triassic bony fishes are influenced by the Lagerstätten effect.
20 The reasons for this may be twofold: (1) relatively high endemism at genus level in
21 freshwater Lagerstätten (>48%, Fig. 3b), and (2) mostly low freshwater diversity.

22 Division of genus richness (with or without inclusion of Lagerstätten taxa) by the
23 number of localities results in higher diversity in the Early and Middle Permian and again in
24 the Middle and Late Triassic (see Supplementary Tables A1–A3, B1). Lower genus richness
25 is found during the Late Permian and Early Triassic. These trends are evident in the marine
26 and the freshwater datasets, although in the marine record genus richness of bony fishes

1 reaches similar levels in the Early–Middle Permian and the Middle–Late Triassic intervals,
2 whereas in the freshwater record Middle–Late Triassic diversity is only about half of that
3 found in the Early–Middle Permian interval. Division of genus richness by interval length
4 yields peaks in the Early Triassic, usually followed by high values in the Middle Triassic and
5 the Late Permian, both with and without inclusion of Lagerstätten genera (Supplementary
6 Table B1). This pattern, which is found in the marine, freshwater and global datasets, mainly
7 results from relatively short interval lengths of the Late Permian and Early Triassic and high
8 diversity and short interval duration for the Middle Triassic.

9 Correlation indices (Spearman’s ρ , Kendall’s τ) calculated for genus richness versus
10 number of localities and for genus richness versus bin length suggest that global osteichthyan
11 diversity is independent of number of localities and interval length. A correlation ($p < 0.05$)
12 does exist, however, between freshwater genus richness and stage/substage duration, and
13 between marine genus richness and number of localities (Supplementary Table B2).

14

15 (2) General trends: Genus diversity, turnovers and turnover rates

16

17 Diversity dynamics of marine osteichthyans (Fig. 4a, Supplementary Table B3) show an
18 overall trend from low levels in the Permian to much higher values in the Triassic. Genus
19 richness of marine bony fishes gently rises from the Early to the Late Permian. However, this
20 trend is not seen in the mean standing diversity and boundary crossers curves. Two distinct
21 diversity peaks can be discerned in the marine record, one during the Early Triassic and one
22 in the Middle Triassic, followed by decreasing diversity towards the Triassic–Jurassic
23 boundary. The Early Triassic diversity peak spans the Griesbachian to Smithian interval
24 (maxima in the Dienerian) and is succeeded by low diversity during the Spathian [the latter
25 being due to incomplete sampling, see Sections II(4) and IV(2a)]. Marine diversity is highest
26 in the Ladinian.

1 Turnovers (sum of originations and extinctions) among marine bony fishes are higher in
2 the Triassic than in the Permian (Fig. 4b). Marine per taxon turnover rates (TR, relative to
3 genus richness) are also high throughout the Permian-Triassic interval when singletons are
4 included, with a peak in per taxon origination rates (OR) at the Spathian-Anisian boundary
5 (Fig. 3b, Supplementary Table B4). Per taxon extinction rates (ER) show a peak in the
6 Cisuralian (Sakmarian-Artinskian boundary), increase towards the end of the Permian and
7 remain elevated during the Triassic. If singleton genera are omitted (Fig. 4c, Supplementary
8 Table B4), marine TR mainly peak ($\geq 50\%$) in the late Cisuralian (Artinskian-Kungurian
9 boundary: 50% OR), at the Permian-Triassic boundary (65% OR, 57% ER), the Spathian-
10 Anisian boundary (94% OR, 64% ER) and the Ladinian-Carnian boundary (51% ER). ER
11 remain high ($>30\%$) from the Middle-Late Triassic boundary onwards (Fig. 4c,
12 Supplementary Table B4).

13 Diversity trends of the freshwater osteichthyan record (Fig. 5a, Supplementary Table
14 B3) differ from those described for the marine dataset. Permian freshwater diversity is largely
15 similar to that of the Triassic when comparing numbers of boundary crossers as well as mean
16 standing diversity. However, freshwater genus richness is distinctly higher in the Middle and
17 Late Triassic compared to the Middle Permian–Early Triassic interval. All three diversity
18 estimates studied herein (genus richness, boundary crossers, mean standing diversity) show
19 relatively high freshwater bony fish diversity during the early Cisuralian. Generally low
20 diversity levels are found in the late Early Permian to early Middle Permian and again in the
21 Early Triassic. Note, however, that low Early Triassic diversity is a sampling artefact and
22 related to the circumstance that many freshwater fishes from this interval (mostly from the
23 Karoo Basin in South Africa and the Tunguska Basin of Siberia, Russia) cannot be accurately
24 dated at substage level. At epoch level, a diversity minimum is not evident in the Early
25 Triassic (Fig. 3b).

1 TR of freshwater osteichthyans (including singletons; Fig. 5b, Supplementary Table B4)
2 peak at the Sakmarian-Artinskian boundary (62% ER), the Artinskian-Kungurian boundary
3 (56% OR), the Wordian-Capitanian boundary (62% OR), the Permian-Triassic boundary
4 (64% ER), and several times during the Triassic (Spathian-Anisian boundary: 73% OR;
5 Anisian-Ladinian boundary: 63% OR, 70% ER; Ladinian-Carnian boundary: 67% OR, 63%
6 ER; Norian-Rhaetian boundary: 56% ER). Increased TR in the Triassic are linked to
7 occurrences of relatively short-lived endemic taxa (mainly Sydney Basin, New South Wales,
8 Australia). In fact, when singleton genera are removed (Fig. 5c, Supplementary Table B4),
9 Triassic TR of freshwater bony fishes tend to be much lower. Omission of singletons restricts
10 peaks in OR to the Wordian-Capitanian boundary (55%) and the Ladinian-Carnian boundary
11 (56%), whereas maxima in ER are only found at the Sakmarian-Artinskian boundary (65%),
12 the Permian-Triassic boundary (60%) and the Norian-Rhaetian boundary (50%).

13 Diversity patterns of the global bony fish record (Fig. 6a, Supplementary Table B3)
14 largely resemble those of the marine dataset. This is due to the fact that marine osteichthyans
15 account for the highest taxonomic diversity throughout the Permian-Triassic interval. Global
16 diversity of Osteichthyes decreases during the Cisuralian (minimum in the Artinskian) and
17 rises again until the Wuchiapingian, followed by peak values in the Early Triassic (Dienerian
18 substage) and Middle Triassic. Global diversity of bony fishes then decreases towards the
19 Triassic-Jurassic boundary. The described patterns are evident from all three diversity
20 estimates studied here.

21 The number of turnovers of bony fishes globally is usually higher in the Triassic than in
22 the Permian, as in the marine record, but global TR are similar throughout most of the
23 Permian-Triassic record if singletons are included (Fig. 6b, Supplementary Table B4). Peak
24 OR are observed at the Wordian-Capitanian boundary (50%), the Permian-Triassic boundary
25 (50%) and the Spathian-Anisian boundary (84%), whereas peak ER are found at the
26 Sakmarian-Artinskian boundary (62%), the Permian-Triassic boundary (50%), the Dienerian-

1 Smithian boundary (57%), the Spathian-Anisian boundary (50%), the Anisian-Ladinian
2 boundary (52%), the Ladinian-Carnian boundary (60%) and at the Norian-Rhaetian boundary
3 (54%). However, if singletons are omitted (Fig. 6c, Supplementary Table B4), peaks in global
4 OR are merely found at the Permian-Triassic boundary (50%) and at the Spathian-Anisian
5 boundary (76%). Excluding singletons, peak ER are only obvious at the Sakmarian-
6 Artinskian boundary (55%), but are otherwise absent in the global record.

7

8 (3) Diversity dynamics within Osteichthyes

9

10 Actinistia generally show low diversity during the Permian-Triassic. Elevated levels of
11 marine actinistian genus richness (Fig. 7a) are reached during the Changhsingian-Smithian
12 interval and again in the Middle Triassic. Low actinistian diversity during the Spathian is
13 likely due to sampling biases [see Sections II(4) and IV(2a)]. Actinistian diversity in
14 freshwater environments (Fig. 7b) is mostly very low, but a diversity increase is observed in
15 the Late Triassic. Among bony fishes, relative genus diversity of actinistians is highest during
16 the Early Permian and in the Early Triassic but generally lower at other times (Fig. 8a;
17 Supplementary Table B5).

18 Actinopterygians are the most diverse group among marine Permian-Triassic
19 osteichthyans (Fig. 8). Permian ray-finned fishes predominantly belong to ‘Palaeopterygii’.
20 First representatives of ‘Subholostei’ (e.g. *Bobasatrania*, Stemmerik, Bendix-Almgreen &
21 Piasecki, 2001) and Holostei (*Acentrophorus*, e.g. Schaumberg, 1977) appear in the marine
22 record in the Lopingian. Whereas genus richness of marine non-subholostean
23 ‘palaeopterygians’ remains at similar levels from the Middle Permian to the Middle Triassic,
24 ‘subholosteans’ pass through a massive diversification event during the Early Triassic and
25 again in the Middle Triassic (Figs 7a, 8a). ‘Palaeopterygians’ and ‘subholosteans’ show a
26 decline in diversity from the Ladinian onwards (Figs 7a, 8a). In contrast, marine holosteans

1 (e.g. Semionotiformes) and Teleostomorpha diversified during the Middle and Late Triassic.
2 Although genus richness of marine neopterygians also decreases towards the Triassic-Jurassic
3 boundary after their diversity peaks in the Ladinian (Holostei) and Norian (Teleostomorpha,
4 Fig. 7a), their diversity relative to non-neopterygians continuously increases during the
5 Middle and Late Triassic and, by the Norian, exceeds that of any other group of marine bony
6 fishes (Fig. 8a).

7 Freshwater diversity of sarcopterygians is dominated by dipnoans (Fig. 7b,
8 Supplementary Table B5). Genus richness of lungfishes is generally higher during the
9 Triassic than in the Permian (Fig. 7b), and their relative diversity within freshwater bony fish
10 communities reaches peak values during the Early Triassic (Fig. 8b). Note, however, that the
11 significance of this peak is equivocal due to the generally low diversity during this interval.
12 Freshwater actinistians show relatively low genus richness during the Permian and the Early
13 to Middle Triassic interval, but slightly increased diversity in the Late Triassic (Chinle,
14 Dockum and Newark Groups; Figs 7b, 8b).

15 Diversity of actinopterygians within Permian freshwater environments is dominated by
16 ‘palaeopterygians’ (Figs 7b, 8b). So far, only one putative holostean has been described from
17 Permian freshwater deposits (*Brachydegma*; Hurley *et al.*, 2007; Near *et al.*, 2012). As in the
18 marine record, ‘subholosteans’ seemingly first appear in the Late Permian (*Ischnolepis*;
19 Murray, 2000) and they too become a larger component of freshwater bony fish faunas during
20 the Middle and Late Triassic. However, other than in the marine realm, holosteans and
21 teleosteomorphs account for only a small proportion of Triassic freshwater assemblages. In
22 fact, non-marine actinopterygian diversity in the Triassic is still dominated by
23 ‘palaeopterygians’ and ‘subholosteans’ (Fig. 8b).

24 Globally, changes in faunal composition within osteichthyans largely resemble those of
25 the marine record, with minor differences. Most notably, neopterygian dominance in genus
26 richness relative to other bony fishes in the Middle and Late Triassic is less pronounced in the

1 global record compared to the marine one (Figs 7c, 8c). Sarcopterygian diversity on a global
2 scale is relatively constant during the investigated time interval, with elevated genus richness
3 in the Artinskian and during the Changhsingian-Spathian (Figs 7c, 8c, Supplementary Table
4 B5).

5

6 (4) Palaeolatitudinal diversity

7

8 In the marine record, epoch-level-averaged palaeolatitudinal diversity of osteichthyans
9 is highest in the low-palaeolatitudinal belt throughout the Permian and again in the Middle
10 and Late Triassic. In the Early Triassic, however, low-palaeolatitudinal diversity is low and
11 maximum genus richness is found in the mid-palaeolatitudinal zone (Fig. 9a). Marine
12 diversity at genus level within the low-palaeolatitudinal zone during the Early Triassic is
13 similar to Permian values but distinctly lower compared to the Middle and Late Triassic. For
14 the whole Permian-Triassic record, genus richness of marine osteichthyans at mid-
15 palaeolatitudes is highest in the Early Triassic. The highest low-palaeolatitudinal osteichthyan
16 diversity is measured in the Middle Triassic.

17 Changes in palaeolatitudinal genus richness among freshwater bony fishes (Fig. 9b)
18 differ from those observed in the marine record. Non-marine genus richness at low-
19 palaeolatitude is similar to or higher than at mid-palaeolatitudes throughout the Permian and
20 again in the Late Triassic. However, in the Early and Middle Triassic, number of genera in the
21 low-palaeolatitudinal zone is distinctly lower than that in the mid-palaeolatitudinal zones.
22 Freshwater diversity at mid-palaeolatitudes is generally higher during the Triassic than during
23 the Permian, and highest in the Middle Triassic. High-palaeolatitudinal genus richness
24 normally constitutes the lowest values except in the Early Triassic, where it exceeds low-
25 palaeolatitudinal levels (Fig. 9b).

1 Globally, palaeolatitudinal distribution of osteichthyan genus richness during the
2 Permian and Triassic mostly resembles present-day conditions, with highest genus richness at
3 low-palaeolatitudes, lowest diversity at high-palaeolatitudes, and intermediate genus richness
4 at mid-palaeolatitudes (Fig. 9c). The only exception is found in the Early Triassic, where
5 palaeolatitudinal genus diversity is highest within the mid-palaeolatitudinal zones. High-
6 palaeolatitudinal genus richness also reaches maximum values during the Early Triassic. Peak
7 values in low-palaeolatitudinal global diversity are restricted to the Middle and Late Triassic
8 (Fig. 9c). Relative diversity of the three main groups of bony fishes investigated herein
9 (Dipnoi, Actinistia, Actinopterygii) is similar across palaeolatitudinal belts throughout the
10 Permian-Triassic interval (Supplementary Tables A1–A3).

11

12 (5) Body size

13

14 Permian-Triassic bony fishes show distinct fluctuations in the range and dominance of
15 species' maximum standard length (MSL). In the marine record, body size spectrum ranges
16 from ca. 20–900 mm in the Early Permian, to ca. 50–620 mm in the Middle Permian, to ca.
17 50–1500 mm in the Late Permian and Early Triassic, to ca. 20–1650 mm in the Anisian stage
18 to the Norian-Rhaetian interval (Fig. 10a, Supplementary Tables A1–A3). The Kolmogorov-
19 Smirnov test for overall equal distribution yields p -values < 0.05 only between the Early and
20 Middle Permian and between the Middle and Late Permian, and $p < 0.01$ exclusively between
21 the Early Triassic and Anisian (Supplementary Table B6). Differences in body size
22 distribution of marine osteichthyans between other consecutive intervals are not statistically
23 different ($p > 0.43$). Medians of marine osteichthyan MSL are also only significantly different
24 between the Late Permian and Early Triassic (Mann-Whitney U test, $p < 0.05$) and between
25 the Early Triassic and Anisian ($p < 0.01$; Supplementary Table B6). In general, body size
26 distribution of marine species shows a tendency (dominance) towards more mid-sized

1 consumers in the Early Permian, the Late Permian, and the Early Triassic. A tendency
2 towards small sized consumers is found in the Middle Permian and during the Middle–Late
3 Triassic (Fig. 10a).

4 MSL range in freshwater osteichthyans varies between ca. 40–1030 mm in the Early
5 Permian, to ca. 50–500 mm in the Middle Permian, to ca. 50–700 mm in the Late Permian, to
6 ca. 55–700 mm in the Early Triassic, to ca. 38–1000 mm in the Middle Triassic, to ca. 30–
7 1500 mm in the Late Triassic (Fig. 10b, see Supplementary Tables A1–A3). MSL
8 distributions are statistically different only between the Late Permian and Early Triassic
9 (Kolmogorov-Smirnov, $p < 0.01$), between the Early and Middle Triassic ($p < 0.01$) and
10 between the Middle and Late Triassic ($p < 0.05$; Supplementary Table B6). Differences in
11 median MSL are statistically different only between the Late Permian and Early Triassic as
12 well as between the Early and Middle Triassic (Mann-Whitney U, $p < 0.01$; Supplementary
13 Table B6). In the non-marine realm, body size distribution is skewed towards mid-sized
14 consumers predominantly in the Middle and Late Permian. In contrast, the bulk of freshwater
15 osteichthyans of the Early Triassic and the Late Triassic can be classified as small consumers
16 (Fig 10b).

17 Globally (Fig. 10c, see Supplementary Tables A1–A3), differences in the distribution of
18 osteichthyan MSL are only statistically significant between the Early Triassic and Anisian
19 (Kolmogorov-Smirnov, $p < 0.01$; Supplementary Table B6). Significantly different median
20 MSL is also only evident between the Early Triassic and Anisian (Mann-Whitney U, $p <$
21 0.01), although low p -values are also yielded between the Middle and Late Permian ($p < 0.05$;
22 Supplementary Table B6). On a global scale, body size distribution of Osteichthyes suggests
23 dominance of mid-sized consumers during the Permian and Early Triassic and dominance of
24 small consumers during the Middle–Late Triassic (Fig. 10c).

25 Body size distribution among the different groups of bony fishes during the Permian and
26 the Triassic suggests very similar patterns in marine and freshwater environments. Within

1 Actinopterygii, median MSL of 'palaeopterygians' tends to be larger than that of
2 'subholosteans', holosteans or teleosteomorphs throughout the studied interval (Fig 10a). In
3 the marine realm, median MSL of 'Palaeopterygii' varies between ca. 250 mm and 300 mm.
4 These fishes would therefore mostly fall into the mid-sized consumers' trophic category.
5 However, marine 'palaeopterygian' species tend to be much smaller during the Middle
6 Permian (median of 120 mm MSL) and larger during the Late Triassic (median of ca. 350–
7 1000 mm MSL, but note the smaller sample size). A significant size increase in marine
8 'Palaeopterygii' is noted across the Guadalupian-Lopingian boundary (Fig. 10a; Kolmogorov-
9 Smirnov and Mann-Whitney U tests, $p < 0.01$). Marine 'Subholostei' and Neopterygii have
10 median MSL ranging up to ~150 mm and, thus, these groups mainly comprise small
11 consumers throughout the Permian and Triassic (Fig 10a). Marine actinistians show similar
12 median body sizes as 'palaeopterygians' , but sample size is generally low. Small to mid-sized
13 'palaeopterygians' become rarer after the Middle Triassic, whereas holosteans continue to
14 extend the upper end of their size spectrum towards the close of the Triassic (although most
15 species remain in the small consumer's guild; Fig 10a). Body size range of teleosteomorphs,
16 on the other hand, remains small (23–155 mm MSL) throughout the studied interval (Fig.
17 10a).

18 Among Permian-Triassic freshwater fishes, there also is a tendency towards larger body
19 sizes in dipnoans and actinistians (median MSL >330mm, but note small sample size) and
20 'palaeopterygians' (median MSL 113–245 mm) compared to 'subholosteans', holosteans, and
21 teleosteomorphs (median MSL 55–120 mm; Fig 10b). Thus, like in the marine realm,
22 freshwater 'palaeopterygians' (and maybe alsosarcopterygians) predominantly occupied the
23 niche of mid- to large-sized consumers, whereas 'subholosteans' and neopterygians mostly
24 covered relatively lower trophic positions. However, other than in the marine realm, small
25 'palaeopterygians' do not become scarcer and holosteans do not seem to comprise larger
26 species towards the end of the Triassic in the non-marine domain (Fig. 10b).

1 Changes in osteichthyan body size across palaeolatitudes indicate that the slight increase
2 in global species' MSL between the Guadalupian and the Early Triassic (cf. Fig. 10) can be
3 observed both in the low- and the mid-palaeolatitudinal zones (Fig. 11), although these shifts
4 are not significant (Kolmogorov-Smirnov and Mann-Whitney U tests). The decrease in body
5 size between the Early and Middle Triassic that is evident in the marine realm and on a global
6 scale (Fig. 10), occur within both the low-palaeolatitudinal zone (statistically significant for
7 the marine and global datasets, Kolmogorov-Smirnov and Mann-Whitney U, $p < 0.01$, Fig.
8 11a, c) and within the mid-palaeolatitudinal belts (global, Mann-Whitney U, $p < 0.05$, Fig.
9 11c).

10

11

12 IV. DISCUSSION

13

14 (1) The Permian record

15

16 (a) "*Olson's gap*"

17

18 The Permian is marked by at least three biotic events, each of which affected marine and
19 continental life to varying extent. The first of these three events has been termed "Olson's
20 gap" (Lucas & Heckert, 2001) or "Olson's extinction" (Sahney & Benton, 2008) and it refers
21 to a global hiatus in the terrestrial tetrapod record during an interval spanning the latest
22 Kungurian and most of the Roadian (Lucas, 2004, 2013). It separates the Early Permian North
23 American tetrapod faunas, dominated by basal synapsids ('pelycosaurs') and temnospondyl
24 'amphibians', from the Middle Permian therapsid-dominated communities of Russia and
25 South Africa (Lucas, 2004; Sahney & Benton, 2008; Blicek, 2011). A diversity drop in
26 freshwater and euryhaline osteichthyan families coincident with "Olson's gap" was noted by

1 Pitrat (1973) and is also implied by the analysis of Blicek (2011), based on data from Benton
2 (1993).

3 No extinction event for bony fishes in the Kungurian or Roadian is evident from our
4 data (Figs 4–6). However, genus richness of freshwater osteichthyans notably decreased
5 earlier in the Cisuralian, which is mainly due to the disappearance of taxa native to the great
6 fluvio-lacustrine systems of Central Europe (Czech Republic, France, Germany) and the
7 southern United States (New Mexico, Oklahoma, Texas). Many of these taxa crossed the
8 Carboniferous-Permian boundary, such as the actinopterygians *Aeduell*a, *Bourbonella*,
9 *Paramblypterus*, *Platysella* and *Progyrolepis*, and the dipnoans *Conchopoma*, *Ctenodus*,
10 *Gnathorhiza*, *Megapleuron*, *Proceratodus* and *Sagenodus* (e.g. Štamberg, 1994, 2007; Heyler,
11 2000; Schultze, 2004; Poplin & Dutheil, 2005; see Supplementary Tables A1–A3). A few
12 chondrichthyan clades also vanished during the Early Permian, although the overall diversity
13 of these fishes remained relatively stable (Koot, 2013). Furthermore, megalichthyid and
14 rhizodopsid sarcopterygians (basal tetrapodomorphs, Janvier, 2007), which were confined to
15 Euramerican freshwater basins in the Early Permian, also seem to disappear from the fossil
16 record at that time (Schultze & Heidtke, 1986; Witzmann & Schoch, 2012). Another group
17 that potentially became extinct during the Cisuralian are the ‘acanthodians’, but there is
18 ambiguity regarding their LAD (either Early Permian or Middle-Late Permian, Mutter &
19 Richter, 2007). Both ‘acanthodians’ and basal tetrapodomorphs were more diverse during
20 their early evolutionary history but became minor faunal elements after the end-Devonian
21 Hangenberg extinction (Sallan & Coates, 2010; Witzmann & Schoch, 2012). ‘Acanthodians’
22 and basal tetrapodomorphs are frequently cited among the victims of the end-Permian mass
23 extinction (e.g. Schaeffer, 1973; Janvier, 1996; Mutter & Richter, 2007) but they might
24 already have become extinct during the general decline in freshwater fish diversity during the
25 Cisuralian. The diversity loss among Permo-Carboniferous bony fish taxa in Euramerican
26 fluvio-lacustrine systems during the Early Permian is probably linked to the reduction or

1 disappearance of their habitats (Pitrat, 1973; Schneider & Werneburg, 2012) as a result of
2 contemporaneous aridification trends and other climatic changes (Ziegler *et al.*, 2003;
3 Roscher & Schneider, 2006; Chen *et al.*, 2013).

4 Although there is no loss in genus richness among marine bony fishes during the
5 Cisuralian, we note elevated per taxon origination rates at the Kungurian-Roadian boundary
6 (Fig. 4c) and a possible reduction in body size across the Cisuralian-Guadalupian boundary
7 (Fig. 10a). Most Early Permian marine osteichthyans originate from the Eastern European
8 platform, based on which Esin (1997) observed a decrease in body size in the late Kazanian
9 (late Roadian; Menning *et al.*, 2006). However, whether this change in body length of marine
10 bony fishes is related to the continental “Olson’s gap” remains unknown.

11

12 *(b) The end-Guadalupian extinction event*

13

14 The second Permian event is the end-Guadalupian (or mid-Capitanian; Wignall *et al.*,
15 2012) extinction. This event is associated with shifts in the carbon and oxygen isotope record
16 (Chen *et al.*, 2013) and a first-order sea-level lowstand (see Groves & Wang, 2013 for a
17 summary). Although there is still disagreement about the timing and main triggers of the end-
18 Guadalupian extinction (Clapham, Shen & Bottjer, 2009; Groves & Wang, 2013), it seems
19 that the event is prolonged and possibly linked to a cool phase during the Capitanian
20 (‘Kamura event’, Isozaki, Kawahata & Ota, 2007) as well as to eruptive activity of the
21 Emeishan Traps (southern China) and the sea-level lowstand during the Capitanian-
22 Wuchiapingian transition (e.g. Wignall *et al.*, 2012; Clapham & Payne, 2011; Groves &
23 Wang, 2013). Victims of the Guadalupian crisis were predominantly marine invertebrates,
24 including fusulinoidean foraminifera, corals, bryozoans, brachiopods, and ammonoids
25 (Glenister & Furnish, 1981; Stanley & Yang, 1994; Clapham, Shen & Bottjer, 2009; Groves
26 & Wang, 2013; Wang & Sugiyama, 2000), although some terrestrial tetrapods also suffered

1 extinctions during the Middle Permian (Lucas, 2009; Fröbisch, 2013). Clapham, Shen &
2 Bottjer (2009) pointed out that the diversity decrease of various marine invertebrate groups
3 occurred over an extended interval (Wordian–Changhsingian) and mainly resulted from low
4 origination rates. Increased extinction rates at the Capitanian-Wuchiapingian boundary are,
5 nevertheless, found for some fusulinoidean families (Groves & Wang, 2013) and corals
6 (Wang & Sugiyama, 2000).

7 Chondrichthyan diversity trends imply that the Guadalupian crisis had an important
8 impact on these fishes, as it largely marks the tipping point of their dramatic diversity drop
9 towards the end of the Permian (Fig. 12; Pitrat, 1973; Koot, 2013). Strikingly, patterns in
10 bony fishes are very different. Global diversity of Osteichthyes is slowly rising between the
11 Kungurian and Wuchiapingian (Fig. 6a) and high per taxon turnover rates at the Guadalupian-
12 Lopingian boundary are not evident (Fig. 6c). Nevertheless, changes in trophic composition
13 of Middle–Late Permian ichthyofaunas from basins within the European part of Russia have
14 been documented by Esin (1997). Amongst others, he noted a decrease in diversity of
15 actinopterygians with a presumed durophagous diet in the late Urzhumian (late Wordian;
16 Menning *et al.*, 2006), in tandem with lowered benthic taxonomic diversity. This was
17 followed by reduced trophic diversity in the Sverodvinian (Capitanian–early Wuchiapingian;
18 Menning *et al.*, 2006), characterised by a high abundance of algal grazers. Diversity of
19 durophagous ‘palaeopterygians’ did not recover until the Vyatkian (late Wuchiapingian and
20 Changhsingian; Menning *et al.*, 2006). Esin (1997) interpreted these changes in trophic
21 communities as being related with alterations in local aquatic environments and sea-level
22 fluctuations, but they could be evidence for a potential crisis in relation to the end-
23 Guadalupian event.

24 During the Lopingian aftermath, global genus richness of Osteichthyes reached similar
25 levels to that of Chondrichthyes for the first time (Fig. 12; Koot, 2013). This diversity trend is
26 coupled with a significant body size increase among marine ‘palaeopterygians’ across the

1 Middle-Late Permian boundary. Following the scarcity of large osteichthyan consumers in the
2 Early and Middle Permian, Lopingian faunas bear several large-sized marine taxa (e.g.
3 species of *Acropholis*, *Mutovinia*, *Plegmolepis*) with similar body lengths as the osteichthyan
4 apex predators of the Triassic (e.g. species of *Birgeria*, *Saurichthys*, Lombardo & Tintori,
5 2005; Romano & Brinkmann, 2009; Romano *et al.*, 2012; see Supplementary Tables A1–A3).

6 The Late Permian is further characterized by the first appearance of ‘subholosteans’
7 (*Bobasatrania*, *Dorypterus*, *Ischnolepis*) in marine and freshwater environments, and small-
8 sized holosteans (*Acentrophorus*, *Archaeolepidotus*) in the marine realm (Figs 7, 8, 10; see
9 Supplementary Tables A1–A3). However, these groups, which greatly diversified later in the
10 Triassic [see Section IV(2)], make up only a small component of Lopingian ichthyofaunas
11 (e.g. Accordi, 1955; Jubb & Gardiner, 1975; Schaumberg, 1977; Stemmerik, Bendix-
12 Almgreen & Piasecki, 2001; Brinkmann *et al.*, 2010).

13

14 (c) *The end-Permian mass extinction event*

15

16 The end-Permian (late Changhsingian; Shen *et al.*, 2011) mass extinction is the most
17 devastating biotic crisis of the Phanerozoic (Erwin, 2006; Benton, 2003), wiping out an
18 estimated 96% of marine species (Raup, 1979) and about 49% of terrestrial tetrapod families
19 (Benton & King, 1989). This event, which was possibly linked to eruptions of the Siberian
20 Large Igneous Province (Ivanov *et al.*, 2013) and associated climatic and environmental
21 changes (e.g. Schneebeli-Hermann *et al.*, 2013; Benton & Newell, 2013), had a profound
22 impact on various marine invertebrate groups, including ammonoids (Brayard *et al.*, 2009),
23 gastropods (e.g. Batten, 1973; Payne, 2005), brachiopods (Shen & Shi, 2002), corals (e.g.
24 Wang & Sugiyama, 2000), and echinoderms (Twitchett & Oji, 2005), but also affected
25 terrestrial tetrapods (Lucas, 2009; Fröbisch, 2013). Land plants experienced a major change
26 from dominance of seed plants to spore plants at the Permian-Triassic boundary (Schneebeli-

1 Hermann *et al.*, 2013). However, fishes (and conodonts) are considered largely unimpaired by
2 the end-Permian event (e.g. Schaeffer, 1973; Thomson, 1976, 1977; Benton, 1998; Orchard,
3 2007; Reguant, 2007; Blicek, 2011).

4 Friedman & Sallan (2012) argued that the Late Permian record of fishes is very poor,
5 with many lineages ending before the boundary with the Triassic. However, our updated
6 database shows that the Lopingian record has improved with several lineages ending in the
7 Changhsingian, leading to elevated extinction rates at the Permian-Triassic boundary in both
8 the marine (57–70%, Fig. 4, Supplementary Table B4) and the freshwater record (60–64%,
9 Fig. 5, Supplementary Table B4). It should be noted that these high extinction rates are also a
10 consequence of the relatively low genus richness at the end of the Permian. Moreover,
11 extinction rates in the Changhsingian are lower at global scale (38–50%, Fig. 6,
12 Supplementary Table B4) due to the fact that some genera switch between marine and
13 freshwater environments during the Permian-Triassic transition (*Acrolepis*, *Atherstonia*,
14 *Palaeoniscum*, *Pteronisculus?*; see Supplementary Tables A1–A3). Others seemingly
15 survived the boundary without invading new habitats (e.g. *Bobasatrania*, *Elonichthys*,
16 *Pygopterus*; see Supplementary Tables A1–A3). Many genera crossing the Permian-Triassic
17 boundary are peculiarly long-lived and some probably represent ‘Elvis taxa’ (Erwin &
18 Droser, 1993). The impact of the end-Permian event on bony fish diversity remains elusive
19 until these taxa are subjected to critical re-examination and revision.

20 Body size changes across the Permian-Triassic boundary indicate no major shifts among
21 marine Osteichthyes suggesting relatively stable trophic communities in the oceans at epoch
22 level, whereas the significant body length decrease of freshwater bony fishes could indicate a
23 potential crisis for continental faunas (Figs 10, 11, Supplementary Table B6). Most Lopingian
24 marine apex predators among bony fishes (e.g. *Acropholis*, *Mutovinia*, *Plegmolepis*) did not
25 cross the Permian-Triassic boundary and by the Early Triassic, new osteichthyan taxa such as
26 *Birgeria* and *Saurichthys* (as well as marine tetrapods) became abundant and widespread

1 (Romano *et al.*, 2012; Scheyer *et al.*, 2014; Supplementary Tables A1–A3). Despite the rapid
2 recovery of oceanic trophic networks after the end-Permian event (Scheyer *et al.*, 2014), the
3 taxonomic turnover within marine apex predatory guilds across the Permian-Triassic
4 boundary suggests that higher trophic levels nonetheless suffered during the mass extinction.

5

6 (2) The Triassic record

7

8 (a) Early Triassic recovery

9

10 The Early Triassic has received increased research interest during recent decades due to
11 the study of biotic recovery following the end-Permian mass extinction (e.g. Benton, 2003;
12 Erwin, 2006, Foster & Twitchett, 2014). It is frequently assumed that the Triassic recovery
13 was unusually slow and protracted, with groups like corals (e.g. Deng & Kong, 1984; Qi &
14 Stanley, 1989; Roniewicz & Stanley, 1998; Payne *et al.*, 2006), some echinoderms (Twitchett
15 & Oji, 2005; Hagdorn, 2011), gastropods (Batten, 1973; Erwin, 1996; Fraiser & Bottjer,
16 2004; Nützel & Schulbert, 2005) or terrestrial vertebrates (e.g. Sahney & Benton, 2008)
17 possibly exhibiting delayed re-establishment of taxonomic diversity (i.e. not before the
18 Middle Triassic or later). However, in recent years it has been demonstrated that a number of
19 groups such as conodonts (Orchard, 2007), ammonoids (e.g. Brayard *et al.*, 2009) or the
20 benthos (Brayard *et al.*, 2011; Hautmann *et al.*, 2013; Hofmann *et al.*, 2013; Foster &
21 Twitchett, 2014) already display diversity peaks during the Early Triassic. These faster
22 recovering groups nevertheless experienced relapses in their diversity during the Early
23 Triassic (see below).

24 Carbon and oxygen isotope records, as well as spore-pollen ratios within sporomorph
25 assemblages show large fluctuations indicating iterative climatic changes in the wake of the
26 end-Permian mass extinction (Payne *et al.*, 2004; Galfetti *et al.*, 2007a, b; Hermann *et al.*,

1 2012; Sun *et al.*, 2012; Romano *et al.*, 2013), which may be linked to protracted eruptive
2 phases of the Siberian Traps (Ivanov *et al.*, 2013 and references therein). It has been
3 hypothesized that biotic recovery in the Early Triassic may have occurred whenever
4 favourable conditions prevailed, for instance during amelioration of temperatures, cessation of
5 anoxia or during transgressions (Orchard, 2007; Brayard *et al.*, 2011; Romano *et al.*, 2013).

6 Soon after the end-Permian mass extinction, bony fishes experienced a great increase in
7 global diversity (Fig. 6). This first osteichthyan diversification event at the onset of the Early
8 Triassic took place in both marine and freshwater environments (Figs 4–5) and involved both
9 sarcopterygians and actinopterygians (Figs 7–8; also see Cavin, Furrer & Obrist, 2013; Tintori
10 *et al.*, 2013). This origination peak at the onset of the Triassic cannot be dismissed as a mere
11 taxonomic artefact. Most Early Triassic bony fishes are morphologically very distinct from
12 their Permian relatives and their attribution to different genera is well justified. The Early
13 Triassic diversification pulse may partly be related to the prevalence of Lagerstätten (i.e.
14 Greenland, NW Madagascar, Spitsbergen, western Canada; Fig. 3) as well as to ideal
15 preservational conditions linked to widespread episodic anoxic events, i.e. in the Dienerian
16 and Late Smithian (Tintori, 1992; Hermann *et al.*, 2011; Ware *et al.*, 2011). Strikingly,
17 however, Early Triassic marine bony fish Lagerstätten comprise many shared genera
18 (indicated by low endemism rates, Fig. 3), a fact that has already puzzled previous researchers
19 (e.g. Piveteau, 1935; Schaeffer & Mangus, 1976; Brinkmann *et al.*, 2010). Cosmopolitanism
20 was also recognized for Early Triassic ammonoids, although only during certain intervals
21 (Tozer, 1982; Dagens, 1988; Brayard *et al.*, 2006; Brayard, Escarguel & Bucher, 2007). Some
22 sea-going tetrapods like trematosauroid ‘amphibians’ (*Aphaneramma*, *Wantzosaurus*) or early
23 ichthyopterygian reptiles like *Utatusaurus* were also wide-ranging during the Early Triassic
24 (Scheyer *et al.*, 2014 and references therein).

25 Cosmopolitan taxa are typical for post-extinction faunas and they are commonly
26 referred to as ‘disaster taxa’ (e.g. Sahney & Benton, 2008; Benton & Newell, 2013). Apart

1 from their wide palaeogeographic distribution, ‘disaster taxa’ (*sensu* Kauffman & Harries,
2 1996) are also typified as being r-strategists and as showing high fossil abundance within
3 post-extinction assemblages (short-term blooms). ‘Disaster taxa’ are usually rare among pre-
4 extinction communities and only become more frequent after competitor taxa declined. They
5 are also interpreted as having evolved to cope with stressful environmental conditions prior to
6 the extinction event, and hence were able to survive it and to thrive rapidly afterwards
7 (Kauffman & Harries, 1996).

8 , The cosmopolitan Early Triassic bony fish genera cannot be classified as ‘disaster
9 taxa’ for the following reasons. Firstly, none of them has a dominant occurrence in Early
10 Triassic Lagerstätten (e.g. Lehman, 1952; Nielsen, 1942, 1949, 1961; Schaeffer & Mangus,
11 1976; Stensiö, 1921, 1925, 1932). In fact, based on the inventory list published by Nielsen
12 (1961), Early Triassic osteichthyan Lagerstätten are characterized by relatively high evenness
13 (Simpson index 1-D): East Greenland (0.7907), north-west and south-west Madagascar
14 (0.7919), and Spitsbergen (0.8095). This is in sharp contrast to, for example, the Late Permian
15 German Kupferschiefer, where 90% of all fish fossils are identified as *Palaeoniscum*
16 *freieslebeni* (see Schaumberg, 1977). Secondly, although some cosmopolitan genera already
17 appear before the Permian-Triassic boundary, and some continue to exist after the Early
18 Triassic, none of them has yet been demonstrated to exhibit traits suggestive of adaptation to
19 stressful environments. Wen *et al.* (2013) speculated that Early Triassic actinistians may have
20 been ‘disaster taxa’ because they could have been adapted to low-oxygenation conditions, like
21 the extant coelacanth *Latimeria*. However, care must be taken not to assign biological traits of
22 one genus to a whole group, especially in the light of the great morphological variety
23 expressed by Early Triassic actinistians (Casane & Laurenti, 2013).

24 Schaeffer & Mangus (1976) assigned possible feeding habits to a number of Early
25 Triassic genera based on gape size, dentition type and body morphology. According to their
26 interpretations, Early Triassic osteichthyans exhibit a mixture of feeding strategies and

1 include small-bodied planktivores, grazers, and detritus feeders (e.g. *Australosomus*,
2 *Boreosomus*, parasemionotids), small to large predators (e.g. *Birgeria*, *Pteronisculus*,
3 *Saurichthys*), as well as durophagous forms (e.g. *Bobasatrania*). Stensiö (1921) also ascribed
4 a durophagous diet to some large Early Triassic actinistians (e.g. *Mylacanthus*,
5 *Scleracanthus*). These feeding habits are in agreement with the potential food sources of Early
6 Triassic seas, such as small vertebrates (including juvenile predators, conodonts; Orchard,
7 2007; Scheyer *et al.*, 2014), plankton (e.g. larvae of various stenohaline animals, acritarchs;
8 e.g. Schneebeili-Hermann *et al.*, 2013) and benthos (decapods, ostracods, bivalves, gastropods,
9 brachiopods, echinoderms, sponges, foraminifera; e.g. Garassino & Pasini, 2002; Twitchett &
10 Oji, 2005; Crasquin-Soleau *et al.*, 2007; Brayard *et al.*, 2010, 2011; Song *et al.*, 2011;
11 Hautmann *et al.*, 2013; Hofmann *et al.*, 2013). These potential prey organisms must have
12 been readily available during the Early Triassic to allow for the observed body size ranges of
13 marine osteichthyans (Fig. 10), including top piscine predators of 1 m length or more
14 (Romano *et al.*, 2012; Stensiö, 1921; Wendruff & Wilson, 2012), as well as the presence of
15 large marine tetrapods (Scheyer *et al.*, 2014). Marine predator diversity, distribution, and size
16 spectrum suggest that oceanic productivity during the Early Triassic was sufficient to sustain
17 such large predators (Romanuk, Hayward & Hutchings, 2011; Trebilco *et al.*, 2013; Scheyer
18 *et al.*, 2014).

19 The Early Triassic osteichthyan diversification event was seemingly restricted to mainly
20 mid-palaeolatitudes in the marine realm and largely to mid- to high-palaeolatitudes in the
21 non-marine domain, whereas in both realms the diversity at low-palaeolatitudes decreased
22 across the Permian-Triassic boundary (Fig. 9). Sun *et al.* (2012) mapped the palaeogeographic
23 distribution of fish and tetrapod localities between the Late Permian and Anisian and argued
24 for an ‘equatorial marine vertebrate eclipse’ in the Late Smithian – an interval that likely
25 lasted less than 150 kyr (Brühwiler *et al.*, 2010). Besides the fact that the quality of the fossil
26 records of Triassic fishes and tetrapods does not allow for recognition of palaeobiogeographic

1 patterns with this stratigraphical precision, the alleged gap in the distribution of vertebrate
2 sites is largely one between the equator and ca. 40°S. This area has an incomplete fossil
3 record throughout the Late Permian to Anisian interval (Sun *et al.*, 2012, fig. S1). Indeed, the
4 record of marine fishes from Gondwana is notoriously poor during the whole Triassic (Fig. 1;
5 e.g. López-Arbarello, 2004), partially related to the fact that sampling in the southern
6 hemisphere is generally poorer than in the northern one (Allison & Briggs, 1993). Hence, our
7 knowledge about low-palaeolatitudinal marine osteichthyan fish faunas of the Early Triassic
8 is entirely based on the northern equatorial realm (ca. 0°–30°N), i.e. on records from South
9 China and western North America (Fig. 1; see Supplementary Tables A1–A3). Note that low-
10 palaeolatitudinal vertebrate remains from the Early Triassic of Europe (Buntsandstein) are all
11 from continental deposits (e.g. Brinkmann *et al.*, 2010).

12 Early Triassic osteichthyans from South China are reported to be scarce (Tong *et al.*,
13 2006; Tintori *et al.*, 2013) and they have been much less extensively studied than those from
14 the Middle Triassic of this region. In western North America, Early Triassic fishes have been
15 described from British Columbia and Alberta, Canada, as well as from Idaho and Nevada,
16 USA (Brinkmann *et al.*, 2010). A relatively diverse fish fauna is known from British
17 Columbia, where new discoveries are still being made (e.g. Wendruff & Wilson, 2012). Early
18 Triassic fishes from other North American localities have either received very little research
19 interest during recent decades (Alberta and Idaho; e.g. Schaeffer & Mangus, 1976; Romano *et*
20 *al.*, 2012) or were only recently discovered (Nevada; Brinkmann *et al.*, 2010; Ware *et al.*,
21 2011). Peak diversity at mid-palaeolatitudes in the Early Triassic could be affected by the
22 presence of Lagerstätten (Greenland, NW Madagascar, Spitsbergen, Fig. 1), although their
23 impact on total diversity is minor due to many shared taxa (see above). In conclusion, bony
24 fish diversity may have been lower within equatorial latitudes than at mid-latitudes during the
25 Early Triassic (Fig. 9), but this discrepancy could at least partly be the result of differences in

1 sampling and research effort. An ‘equatorial eclipse’ during the Early Triassic is not evident
2 from our data.

3 A number of additional biotic crises occurred in the aftermath of the end-Permian event,
4 starting with the end-Griesbachian extinction. This event severely affected conodonts
5 (Orchard, 2007) but had no discernible effect on osteichthyan (Figs 4–6) and chondrichthyan
6 fishes (Fig. 12; Koot, 2013). Probably the most important crisis during the Early Triassic is
7 the end-Smithian event (Galfetti *et al.*, 2007a, b) less than two million years after the end-
8 Permian mass extinction. This event strongly decimated nekto-pelagic clades such as
9 conodonts (Orchard, 2007) and ammonoids (e.g. Brayard *et al.*, 2006, 2009), but seemingly
10 less so benthic communities (Song *et al.*, 2011; Hofmann *et al.*, 2013). The end-Smithian
11 extinction is associated with pronounced shifts in the carbon and oxygen isotope records as
12 well as changes in the net water balance between precipitation and evaporation, all of which
13 point to severe climatic changes possibly related to a late eruptive phase of the Siberian Traps
14 (e.g. Payne *et al.*, 2004; Galfetti *et al.*, 2007a, b; Ivanov *et al.*, 2013; Romano *et al.*, 2013).

15 After the diversification of osteichthyans at the onset of the Triassic and relatively stable
16 fish associations between the Griesbachian and Smithian, a first diversity minimum is noted
17 in the Spathian (Fig. 4). This low, however, is a consequence of the rarity of well-dated
18 Spathian occurrences (also see Tintori *et al.*, 2013) and does not necessarily reflect a crisis
19 across the Smithian-Spathian boundary. Strikingly, the taxonomic compositions of
20 Griesbachian to Smithian bony fish communities differs from that of Middle Triassic
21 associations suggesting that an important turnover occurred in between, analogous to other
22 groups (e.g. Crasquin-Soleau *et al.*, 2007; Hautmann *et al.*, 2013; Scheyer *et al.*, 2014).
23 Whether the Early-Middle Triassic taxonomic turnover within Osteichthyes was gradual or
24 whether extinction events such as the end-Smithian or end-Spathian crises (e.g. Orchard,
25 2007; Brayard *et al.*, 2009) were pivotal triggers remains unknown. If we want to improve our
26 understanding of the evolution of Triassic osteichthyans, filling the gap in their fossil record

1 during the Spathian, an interval that lasted ~3 million years and thus more than half of the
2 Early Triassic, becomes an important task.

3

4 *(b) The Triassic actinopterygian revolution*

5

6 The Middle Triassic is characterized by the appearance of several new osteichthyan taxa
7 (Figs 4–8). However, this major origination event may potentially have initiated already
8 during the Spathian for reasons outlined above. A diversity increase is coincidentally seen in
9 marine reptiles, for which a link to sea-level rise was postulated (Kelley *et al.*, 2012). This
10 explanation may also apply to fishes (Thomson, 1977). The second Triassic diversification of
11 bony fishes occurred in the marine environment mainly at low-palaeolatitudes, with many
12 taxa possibly originating in the South China region (Lombardo *et al.*, 2011), and in the
13 freshwater realm mostly at mid-palaeolatitudes (Fig. 9). Freshwater genus richness at mid-
14 palaeolatitudes remained high throughout the Triassic. This pattern may be explained by the
15 Pangaeon palaeogeographical configuration, because continental surface area was largest at
16 mid-palaeolatitudes in both hemispheres during the Triassic (cf. Fig. 1) and freshwater fish
17 diversity generally increases with area (e.g. Lévêque *et al.*, 2008). Scarcity of fishes in low-
18 palaeolatitudinal Pangaea in the Early and Middle Triassic could be related to prevalence of
19 generally more arid conditions in this zone (Ziegler *et al.*, 2003) and perhaps sampling bias
20 [see Section II(4)].

21 In the marine realm, the second Triassic bloom within Osteichthyes spawned a plethora
22 of small-sized consumers, most of which belong to ‘Subholostei’ and Neopterygii. In fact, the
23 statistically significant decrease of osteichthyan body size (marine, global) across the Early
24 Triassic-Anisian boundary is a direct consequence of the diversifications among these groups
25 (Figs 7, 10, Supplementary Table B6). Although there are differences in palaeogeographic
26 sampling [Early Triassic data mostly come from mid-palaeolatitudes and Anisian data largely

1 from low-palaeolatitudes, see Section III(4)] and body size tends to increase with latitude as a
2 function of temperature and productivity (e.g. Fisher, Frank & Leggett, 2010), the drop in
3 body size between the Early and Middle Triassic is unlikely to be a sampling artefact because
4 it is evident across palaeolatitudes (Fig. 11).

5 In the freshwater domain, body length increases across the Early Triassic-Anisian
6 boundary due to a rise in size and diversity of ‘palaeopterygians’ and ‘subholosteans’ (Figs 7,
7 10, Supplementary Table B6). Interestingly, Triassic freshwater assemblages contain
8 relatively fewer Neopterygii than marine communities (Figs 7–8). Moreover, Middle and Late
9 Triassic osteichthyan freshwater faunas comprise forms exhibiting more archaic bauplans that
10 are either rarer or absent in contemporaneous marine associations (e.g. saurichthyids with
11 more extensive scale coverage, Romano *et al.*, 2012), suggesting that Triassic fluvio-
12 lacustrine environments may have served as *refugia* for such groups. The Early Mesozoic
13 radiation of bony fishes led to a pronounced diversity peak in the Middle Triassic (Figs 4–6,
14 12), as the taxonomic richness of these fishes exceeded that of chondrichthyans for the first
15 time (Fig. 12; Sallan & Coates, 2010; Anderson *et al.*, 2011; Koot, 2013) The Triassic
16 osteichthyan revolution was accompanied by the emergence of several evolutionary novelties
17 (Tintori *et al.*, 2013), some of which convergently emerged in neopterygians and
18 ‘subholosteans’ (Brough, 1936; Schaeffer, 1956). These include optimizations of the fins (e.g.
19 reduction of fin ray number and modification of the caudal fin) as well as of the dentition and
20 jaw apparatus (e.g. Brough, 1936; Schaeffer, 1956). These anatomical novelties are associated
21 with new modes of life such as gliding (*Thoracopterus*; Tintori *et al.*, 2012), refined feeding
22 strategies (e.g. Perleididae; Bürgin, 1996) and new reproductive strategies including internal
23 fertilisation and (ovo-)viviparity. While changes in the feeding and locomotory apparatus
24 mainly pertain to ray-fins, new reproductive strategies are observed within both
25 actinopterygians (species of *Saurichthys* and *Peltopleurus*; e.g. Bürgin, 1990; Lombardo,
26 1999; Renesto & Stockar, 2009) and actinistians (*Luopingichthys eurylacrimalis*; Wen *et al.*,

1 2013). Note that although saurichthyids are known since the latest Permian, evidence for
2 viviparity has yet only been documented for some Middle and Late Triassic species (Romano
3 *et al.*, 2012). Viviparity evolved numerous times independently within vertebrates
4 (Blackburn, 2014), amongst others also in some Palaeozoic fishes (placoderms,
5 chondrichthyans). However, within osteichthyans evidence for viviparity older than the
6 Middle Triassic is still lacking. The case of viviparity in the Early Triassic *Birgeria nielsenii* is
7 erroneous (Bürgin, 1990; Lombardo & Tintori, 2005).

8

9 (c) “Carnian Pluvial Event”

10

11 The transition between the Middle and Late Triassic is characterized by a drop in genus
12 richness of marine bony fishes, followed by a decreasing diversity trend towards the Triassic-
13 Jurassic boundary (Fig. 4). The onset and maximum of the Late Triassic diversity decline of
14 marine Osteichthyes roughly coincides with another biotic crisis known as the “Carnian
15 Pluvial Event” (Simms & Ruffell, 1989). This early Carnian (late Julian) event is associated
16 with sedimentological evidence for increased continental runoff in the western Tethys, which
17 suggests an episode of intensified rainfall during the generally arid Late Triassic (e.g. Simms
18 & Ruffell, 1989; Ziegler *et al.*, 2003; Rigo *et al.*, 2007). Although the existence of a “pluvial
19 event” has been questioned (Visscher *et al.*, 1994), different lines of evidence indicate
20 climatic and biotic changes in the Carnian. These include a negative shift in the carbon
21 isotope record, possibly linked to eruptions of the Wrangellia Large Igneous Province in
22 western North America (Dal Corso *et al.*, 2012), as well as extinctions among, for example,
23 crinoids (Hagdorn, 2011), conodonts (Rigo *et al.*, 2007) and ammonoids (Brayard *et al.*,
24 2009), and a decline of carbonate platforms (Rigo *et al.*, 2007 and references therein).
25 Previously dominant groups, such as anomodont therapsids (Fröbisch, 2008), became rare
26 shortly before the onset of the Late Triassic and several important Mesozoic and Cenozoic

1 clades diversified in the wake of the Carnian event, such as dinosaurs, scleractinian corals,
2 and calcareous nannoplankton (Simms & Ruffell, 1989; Rigo *et al.*, 2007; Dal Corso *et al.*,
3 2012).

4 Among marine bony fishes, declining diversity across the Ladinian-Carnian boundary is
5 seen in all groups, yielding total extinction rates of 51–62% (Fig. 4, Supplementary Table
6 B4), followed by a rise in genus richness of Teleostomorpha during the Carnian and Norian
7 (Fig. 7). Osteichthyan communities of the Late Triassic are characterized by predominantly
8 ‘palaeopterygians’ within the large consumers’ guild and ‘subholosteans’ and neopterygians
9 among small-sized consumers (Fig. 10). Neopterygians underwent a radiation during the Late
10 Triassic and many taxa developed specialisations for durophagy (Tintori, 1998; Lombardo &
11 Tintori, 2005; Tintori *et al.*, 2013). Late Triassic teleostomorphs occupied both marine and
12 freshwater environments but their diversity remained relatively low until the Late Jurassic,
13 when also several of the extant clades emerged (Arratia, 2004, 2013).

14 The generally decreasing trend of marine osteichthyan diversity towards the end of the
15 Triassic may be linked to sea-level fall (cf. Kelley *et al.*, 2012). However, reduced Late
16 Triassic bony fish diversity could also partially be the result of sampling bias, because these
17 fishes have been less extensively studied than Middle Triassic ones. According to Lombardo
18 & Tintori (2005), many specimens from the Norian Calcare di Zorzino (northern Italy) are yet
19 undescribed, and the diversity may have been much higher than currently known. To what
20 extent a long-term sea-level fall or the Carnian extinction modulated the concurrent
21 ichthyofaunal changes, including the Late Triassic neopterygian radiation, requires further
22 research.

23

24 (3) Permian-Triassic turnover of fish communities

25

1 The series of extinction and diversifications during the Permian-Triassic interval had a
2 profound impact on marine and continental life. Typical Late Palaeozoic faunas and floras
3 were replaced by those that characterise the Mesozoic and Cenozoic (Sepkoski, 1984; Benton,
4 2003; Erwin, 2006). Marine invertebrate communities of the Permian consisting mainly of
5 goniatic ammonoids, brachiopods, rugose and tabulate corals as well as crinoid and blastoid
6 echinoderms were subsequently transformed into more modern assemblages dominated by
7 ceratitic ammonoids, bivalves, sea urchins, starfishes and scleractinian corals. Similarly,
8 turnover on land meant that tetrapod groups of the Late Palaeozoic gave way to
9 diversification of clades that ultimately evolved into dinosaurs and mammals. Fishes were no
10 exception to this trend.

11
12 The long-term change from low global genus richness of osteichthyans in the Permian to
13 higher levels in the Triassic is in direct contrast to the inverted diversity patterns documented
14 for chondrichthyans (e.g. Koot, 2013). The latter exhibit elevated diversity (at genus level and
15 higher taxonomic ranks) during the Lower and Middle Permian, but show severe extinctions
16 during the end-Guadalupian crisis followed by lower diversity in the Triassic (Fig. 12; Koot,
17 2013). The nature of the fossil record of these two fish clades is different, consisting mostly of
18 ichthyoliths (teeth, denticles or fin/cephalic spines) in Chondrichthyes and articulated material
19 in Osteichthyes (bony fish taxa based on isolated remains are normally considered invalid).
20 Regardless of these differences, however, comparison of the opposing diversity trends of
21 cartilaginous and bony fishes suggests a biological reason behind the patterns observed in
22 their fossil record. Since the radiation of Osteichthyes in the Devonian, global genus-level
23 diversity of actinopterygians remained below that of chondrichthyans and other fishes.
24 Sarcopterygians were diverse in the Devonian but did not recover taxonomically after the
25 end-Devonian Hangenberg extinction (Klug *et al.*, 2010; Sallan & Coates, 2010; Anderson *et*
26 *al.*, 2011). In contrast to the global trends at genus level, however, species richness of

1 actinopterygians was locally higher than that of chondrichthyans during the Carboniferous
2 (Sallan & Coates 2010). Despite their low global genus diversity, Carboniferous and Permian
3 bony fishes already display different body shapes and sizes as well as several trophic
4 adaptations (e.g. Schaumberg, 1977; Esin, 1997; Minikh & Minikh, 2009; Boy & Schindler,
5 2012). Permian bony fishes include general forms, as well as deep-bodied taxa (e.g.
6 *Platysomus*, *Dorypterus*, *Kargalichthys*, *Paranaichthys*) and the enigmatic
7 Discordichthyiformes (Schaumberg, 1977; Minikh & Minikh, 2009). However, advanced
8 anatomical features like those seen in Triassic and later taxa (e.g. viviparity, refined feeding
9 and locomotory apparatus; Brough, 1936; Schaeffer, 1956; Romano *et al.*, 2012; Wen *et al.*,
10 2013; Xu *et al.*, 2013; Blackburn, 2014) are either rare or absent among Palaeozoic
11 osteichthyans.

12 The Triassic saw the rise of the Neopterygii, a group that includes nearly all present-day
13 osteichthyans and more than half of all vertebrates (Nelson, 2006). Although neopterygians
14 experienced their first radiation in the Middle and Late Triassic (Figs 7–8; McCune &
15 Schaeffer, 1986; Tintori, 1998; Arratia, 2004, 2013; Tintori *et al.*, 2013), fossil data and
16 molecular clock analyses suggest that they evolved in the Late Palaeozoic (Hurley *et al.*,
17 2007; Near *et al.*, 2012; Betancur-R. *et al.*, 2013; Sallan, 2014). Palaeozoic neopterygians
18 were either rare and/or lived in environments with a poor fossil record. Neopterygian key
19 innovations in the feeding and locomotory apparatus (e.g. mobile maxilla, reduction of fin
20 rays), some of which convergently evolved in ‘Subholostei’ (Brough, 1936; Schaeffer, 1956),
21 probably led to the great success of ray-finned fishes during post-Palaeozoic times. The fact
22 that ‘subholosteans’ and neopterygians (and likely also actinistians and marine tetrapods;
23 Scheyer *et al.*, 2014) did not experience taxonomic blooms before the demise of several
24 chondrichthyan clades (e.g. Petalodontiformes, Eugeneodontiformes) between the late
25 Guadalupian and Early Triassic (Fig. 12, Koot, 2013) highlights the importance of Permian-
26 Triassic extinctions for this transformation of fish faunas, suggesting that macroevolutionary

1 trajectories in fishes mostly follow the Court Jester model (e.g. Benton, 2009). The associated
2 climatic and environmental changes and profound reorganisation of ecosystems allowed many
3 bony fish taxa to exploit new niches ultimately leading to the great Mesozoic radiation of
4 Osteichthyes. The processes and mechanisms involved in this ichthyofaunal turnover deserve
5 further research.

6

7 **V. CONCLUSIONS**

8

9 (1) Diversity of bony fishes changed from low during the Permian to relatively higher levels
10 in the Triassic as a result of origination events in the Early and Middle Triassic. In the marine
11 realm, these diversification pulses probably represent true biological signals and are not
12 merely the results of the Lagerstätten effect.

13

14 (2) During the Triassic revolution of Osteichthyes, many new taxa appeared exhibiting
15 evolutionary novelties in their locomotory and feeding apparatus, and for the first time in the
16 evolutionary history of the group, some species evolved viviparity. In the Early Triassic,
17 diversifications are noted for both sarcopterygians and actinopterygians, whereas in the
18 Middle Triassic the increase in taxonomic richness mainly pertains to Actinopterygii
19 ('Subholostei', Neopterygii).

20

21 (3) For most of the Permian-Triassic, the marine and global palaeolatitudinal diversity
22 gradients resemble present-day ones, with highest diversity found around the equator and
23 lowest towards the poles. However, during the Early Triassic, osteichthyan genus richness
24 was highest at mid-palaeolatitudes, whereas equatorial diversity was reduced compared to
25 Late Permian and Middle Triassic values. Although there could be an underlying biological

1 signal, this pattern is largely related to incomplete knowledge of low-palaeolatitudinal faunas
2 of Early Triassic age.

3
4 (4) Body size changes in Osteichthyes during the Permian-Triassic include a significant size
5 increase of marine ‘Palaeopterygii’ across the Middle-Late Permian boundary and these fishes
6 remain among the large apex predators during the Triassic. A significant body size reduction
7 of marine bony fishes is documented across the Early Triassic-Anisian boundary as a result of
8 diversifications of small taxa (mainly ‘Subholostei’ and Neopterygii). Dietary studies on
9 Permian-Triassic fishes are wanting and could further contribute to a better understanding of
10 macroecological changes during this critical interval.

11
12 (5) Composition of fish faunas changed profoundly during the Permian-Triassic interval:
13 typical chondrichthyan-rich communities of the Permo-Carboniferous diminished during the
14 end-Guadalupian crisis and, during the aftermath of the end-Permian mass extinction, piscine
15 diversity became osteichthyan-dominated – a condition that has prevailed up until today. This
16 ichthyofaunal turnover is a consequence of the series of extinction events during the Permian
17 and Triassic, each associated with severe climatic and environmental changes.

18

19

20

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13

14

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11 **VIII. SUPPORTING INFORMATION**

12

13 Supplementary Tables A1–A3. Excel spreadsheets listing occurrences and body size data of
14 Permian and Triassic Osteichthyes: Dipnoi (A1), Actinistia (A2), and Actinopterygii (A3).

15 For references cited in tables A1–A3 see Supplementary References.

16

17 Supplementary Tables B1–B6. Excel spreadsheets listing diversity data and results of
18 statistical tests.

19

20 Supplementary References. References for Supplementary Tables A1–A3.

21

22

23 **Figures captions:**

24

25 **Figure 1. Palaeogeography of Permian and Triassic Osteichthyes. A.** – Palaeogeographic
26 map of localities (partially summarized, cf. Supplementary Tables A1–A3) yielding bony fish

1 fossils of Permian (above) and Triassic (below) age and their allocation to palaeogeographic
2 provinces (1, Boreal sea; 2, east-equatorial Panthalassa; 3, south-western Pangaea and south-
3 eastern Panthalassa; 4, Palaeotethys; 5, Neotethys; 6, western and south-western Panthalassa).
4 Localities: ACU – Arctic USA (AK), AN – Angola; ANT – Antarctica (Transantarctic
5 Mountains); ARG – Argentina; ASA – Australia, South Australia, AU – Austria, BV –
6 Bolivia; CAA – Canadian Arctic Archipelago, CAN – China, Anhui, CG – China, Gansu,
7 CGX – China, Guangxi, CHB – China, Hubei, CHL – Chile; CHN – China, Hunan, CJI –
8 China, Jiangsu, CR – Czech Republic, CSC – China, Sichuan, CX – China, Xinjiang, CYG –
9 China, Yunnan and Guizhou, CZJ – China, Zhejiang; EE – Eastern Europe, EG – East
10 Greenland, EN – England/Ireland; EUS – eastern USA (MA, CT, NJ, PA, VA); FR – France;
11 GR – Germany; IT – Italy; IS – Israel; KG – Kyrgyzstan; KY – Kenya; KZ – Kazakhstan
12 (eastern, western, Mangyshlak peninsula); LS – Lesotho; LY – Libya; MOR – Morocco; MG
13 – Madagascar; NB – Namibia; NBZ – Northern Brazil (Maranhão, Paraná); NE – The
14 Netherlands; NER – Northern European Russia (Jaroslavl, Kostroma, Moscow Syncline,
15 Vologda, Vyatka-Kama depression, Wladimir); NP – Nepal; NSW – Australia, New South
16 Wales; PL – Poland; QL – Australia, Queensland; RFE – Russia Far East (Magadan,
17 Tunguska); RKJ – Russia, Krasnojarsk; RKP – Russia, Komi/Pechora; RNS – Russia, North
18 Siberia (Lena River Delta, Verkhoyansk); SA – Saudi Arabia; SAF – South Africa; SB –
19 Svalbard (Spitsbergen and Bjørnøya); SBZ – Southern Brazil (Rio Grande do Sul, Santa
20 Catarina, São Paulo); SCU – south-central USA (OK, TX); SER – Southern European Russia
21 (Astrachan, Cis-Urals, Kargala, Kazan, Kuznetsk, Orenburg, Perm, Samara, Saratov); SL –
22 Slovenia; SP – Spain; SW – Sweden; SZ – Switzerland; TAS – Australia, Tasmania; TH –
23 Thailand; TK – Turkey; TZ – Tanzania; UR – Uruguay; WA – Western Australia; WC –
24 western Canada (Alberta and British Columbia); WUS – western USA (AZ, CA, CO, ID,
25 NM, NV, UT); ZA – Zambia; ZB – Zimbabwe. **B.** – Relative contribution of the different

1 palaeogeographic provinces indicated in A to the total diversity of Permian and Triassic
2 Osteichthyes (only known occurrences).

3

4 **Figure 2. Rarefaction and extrapolation curves at species and genus level. A.** – Permian
5 dataset. **B.** – Triassic dataset. Solid lines: interpolation curves; dashed lines: extrapolation
6 curves; white circles: sample coverages (see text for details).

7

8 **Figure 3. Tentative evaluation of the Lagerstätten effect in the fossil record of Permian
9 and Triassic Osteichthyes. A.** – Marine and brackish realm. **B.** – Freshwater environment.

10 Upper graphs in A and B show a comparison of the diversity trends derived from the whole
11 dataset (black line) and with omission of occurrences at Lagerstätten (grey line, see text for
12 details). Lower graphs in A and B show genus richness at Lagerstätten (black bars).

13 Percentage values indicate proportions of endemic genera (partially summarized). Also see
14 Supplementary Table B1.

15

16 **Figure 4. Marine (and brackish) diversity dynamics of Permian and Triassic**

17 **Osteichthyes (including euryhaline taxa). A.** – Diversity (genus richness, mean standing
18 diversity, boundary crossers). **B.** – Originations/extinctions (bars) and per taxon origination
19 and extinction rates (shades), including singletons. **C.** – Originations/extinctions (bars) and
20 per taxon origination and extinction rates (shades) without singletons. First three unlabelled
21 intervals of the Early Triassic (in stratigraphic order): Griesbachian, Dienerian, Smithian.

22

23 **Figure 5. Freshwater diversity dynamics of Permian and Triassic Osteichthyes**

24 **(including euryhaline taxa). A.** – Diversity (genus richness, mean standing diversity,
25 boundary crossers). **B.** – Originations/extinctions (bars) and per taxon origination and
26 extinction rates (shades), including singletons. **C.** – Originations/extinctions (bars) and per

1 taxon origination and extinction rates (shades) without singletons. First three unlabelled
2 intervals of the Early Triassic (in stratigraphic order): Griesbachian, Dienerian, Smithian.

3

4 **Figure 6. Global diversity dynamics of Permian and Triassic Osteichthyes (euryhaline**

5 **taxa only counted once per interval). A.** – Diversity (genus richness, mean standing

6 diversity, boundary crossers). **B.** – Originations/extinctions (bars) and per taxon origination

7 and extinction rates (shades), including singletons. **C.** – Originations/extinctions (bars) and

8 per taxon origination and extinction rates (shades) without singletons. First three unlabelled

9 intervals of the Early Triassic (in stratigraphic order): Griesbachian, Dienerian, Smithian.

10

11 **Figure 7. Diversity dynamics of different groups of Osteichthyes during the Permian**

12 **and the Triassic. A.** – Marine and brackish environment, **B.** – Freshwater realm, **C.** – Global.

13 First three unlabelled intervals of the Early Triassic (in stratigraphic order): Griesbachian,

14 Dienerian, Smithian.

15

16 **Figure 8. Relative diversity of different groups of Osteichthyes during the Permian and**

17 **the Triassic. A.** – Marine and brackish realm, **B.** – Freshwater environment, **C.** – Global.

18 First three unlabelled intervals of the Early Triassic (in stratigraphic order): Griesbachian,

19 Dienerian, Smithian.

20

21 **Figure 9. Palaeolatitudinal diversity dynamics of Osteichthyes during the Permian and**

22 **the Triassic. A.** – Marine and brackish environment, **B.** – Freshwater realm, **C.** – Global. Left

23 column: Palaeolatitudinal gradient of epoch-level pooled genus richness (values of same

24 palaeolatitudinal belts of the northern and southern hemisphere combined). Right column:

25 Palaeolatitudinal diversity through time. Genera occurring within more than one

26 palaeolatitudinal belt are counted once per belt.

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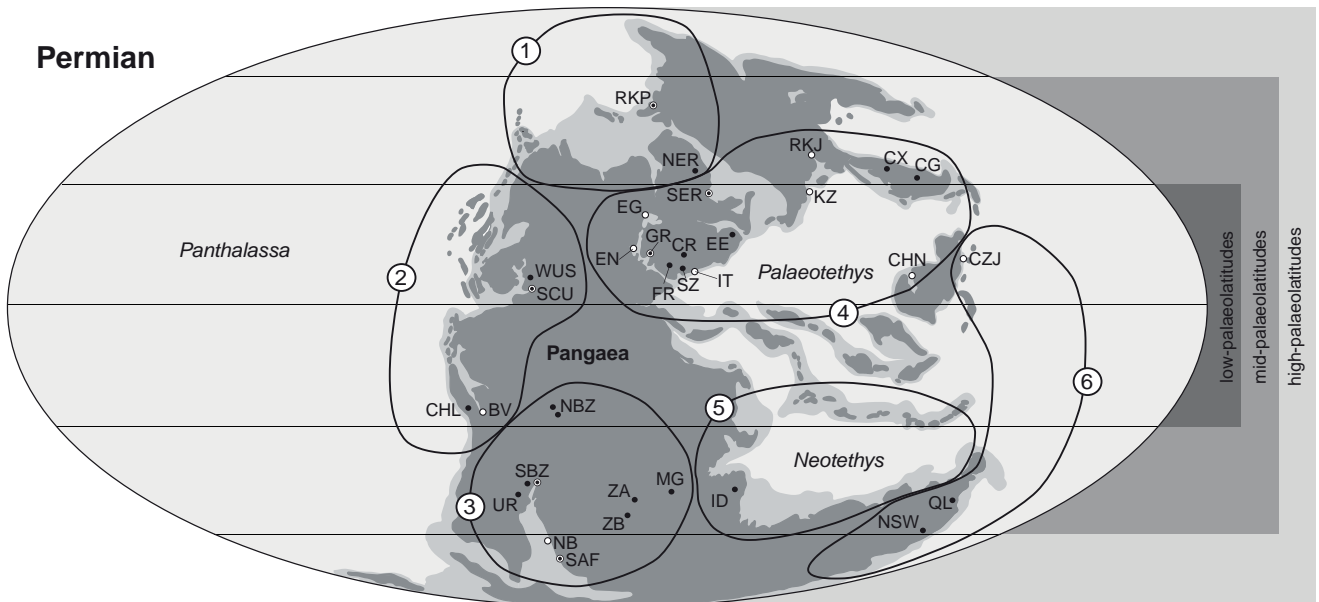
Figure 10. Body size evolution (Log₂ of species' maximum standard lengths) of Osteichthyes during the Permian and the Triassic. **A.** – Marine and brackish realm, **B.** – Freshwater environment, **C.** – Global. Left column: Box plots for all Osteichthyes. Solid lines mark the medians, boxes the 25–75% quartiles, whiskers the whole range of data. Right column: Distribution of body sizes of species belonging to different groups of bony fishes. Trend lines connect medians. SL = Standard length. Time intervals: Anis. = Anisian, Carn. = Carnian, EP = Early Permian, ET = Early Triassic, Lad. = Ladinian, LP = Late Permian, LT = Late Triassic, MP = Late Permian, MT = Middle Triassic, N.-R. = Norian-Rhaetian interval.

Figure 11. Body size evolution (Log₂ of species' maximum standard lengths) of Permian and Triassic Osteichthyes across palaeolatitudinal zones. **A.** – Marine and brackish realm, **B.** – Freshwater environment, **C.** – Global. Solid lines mark the medians, boxes the 25–75% quartiles, whiskers the whole range of data. Time intervals: EP = Early Permian, ET = Early Triassic, LP = Late Permian, LT = Late Triassic, MP = Late Permian, MT = Middle Triassic.

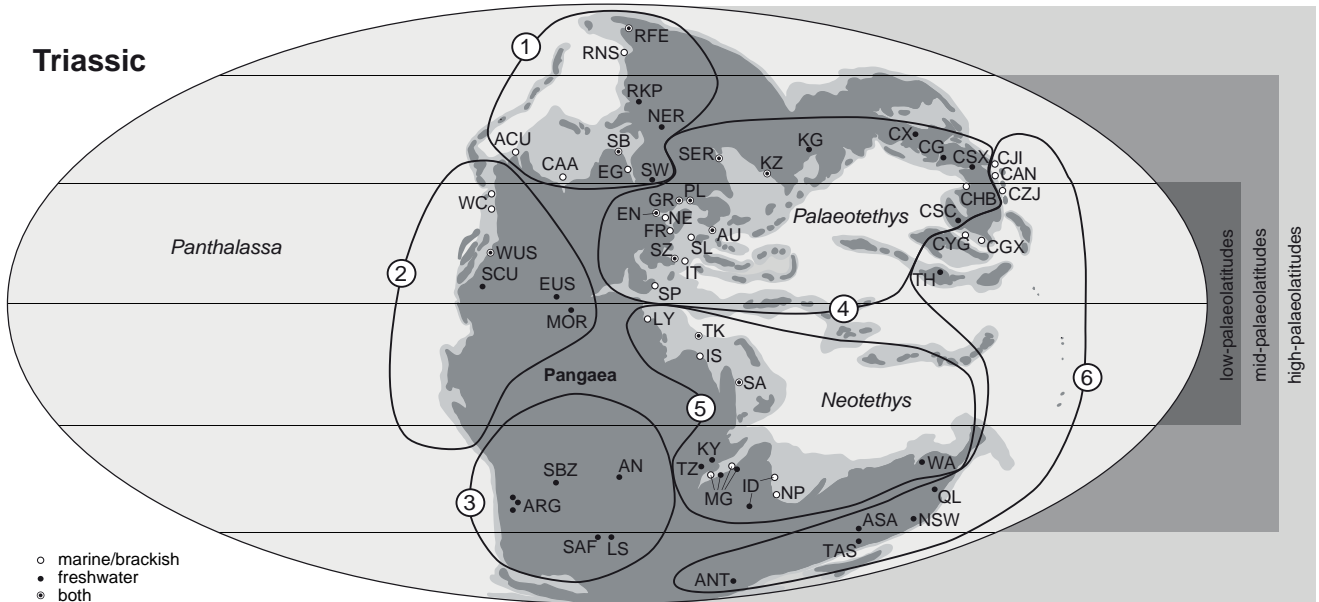
Figure 12. Diversity dynamics of Permian and Triassic fishes (Chondrichthyes, Osteichthyes). **A.** – Genus richness. **B.** – Relative diversity. Data for Chondrichthyes after Koot (2013), data for Osteichthyes from this study (Supplementary Tables A1–A3). First three unlabelled intervals of the Early Triassic (in stratigraphic order): Griesbachian, Dienerian, Smithian.

A

Permian



Triassic



- marine/brackish
- freshwater
- ◐ both

B

