



“Late Permian” vertebrate tracks from the Tumlin Sandstone of Poland—a commentary on some major implications

GRZEGORZ RACKI

The article by Ptasiński and Niedźwiedzki (2004) on vertebrate tracks from the well-known Tumlin Sandstone provides important documentation of the unique terrestrial ichnofauna of the Holy Cross Mountains in Poland. However, two of the major conclusions of this paper raise my objections. The authors propose a new position for the Permian–Triassic (P–Tr) boundary within the Buntsandstein succession of the regional lithostratigraphical scheme. In a conclusion of global significance, the authors find no signature of a mass extinction in the Late Permian land-dwelling tetrapod communities. Both of these issues are reviewed below.

Position of the Permian–Triassic boundary

Ptasiński and Niedźwiedzki (2004) claim that, although the footprint-bearing Tumlin Sandstone has been traditionally regarded as Early Triassic in age, its ichnogeneric characteristics indicate a Late Permian age. They infer, also evident in the article’s title, a Permian age for the Buntsandstein strata studied in surficial exposures. With reference to magnetostratigraphy, this conclusion is critically evaluated elsewhere by Nawrocki et al. (2005) when commenting on another article by these authors, and the controversial details of the placement of the P–Tr boundary in continental domains are dealt with comprehensively (see also reply by Ptasiński and Niedźwiedzki 2005). Therefore, only three methodological points are raised here:

(1) The vertebrate ichnofauna under study has been found at least several tens of meters above the horizon containing the *Lundbladispora obsoleta*–*Protohaploxylinus pantii* Assemblage Zone recognized in nearby boreholes by Fijałkowska (1994; see fig. 2 in Ptasiński and Niedźwiedzki 2004, noting that the index species are given in reverse order there). As was correctly noted by Ptasiński and Niedźwiedzki (2004: 290), the P–Tr boundary is defined at the base of the *Hindeodus parvus* Zone. They go on to claim that this key conodont zone “possibly corresponds to at least a considerable part of the *Lundbladispora obsoleta*–*Protohaploxylinus pantii* Assemblage Zone”. From this statement it seems inescapable that the Tumlin Sandstone, or at least its significant upper part, is Early Triassic (see Fijałkowska 1994), particularly as this palynozone has been recently consistently correlated with the lower Induan palynological assemblages of the Moscow Syncline (Yaroshenko and Lozovsky 2004). However, a few sentences below (p. 292), Ptasiński and Niedźwiedzki

make a final conclusion: “[...] the age of the Tumlin Sandstone is determined herein as the latest (uppermost) Permian (Dorashanian), very close to the Permian–Triassic boundary”. It is notable that these authors cite the papers and personal communication (sic!) of Kozur for this definition of the era boundary rather than the formal decision of the International Commission on Stratigraphy ratified by IUGS (Yin et al. 2001; see the currently operative time scale in <http://www.stratigraphy.org/>, where the latest Permian comprises Changhsingian). Of course, it is extremely difficult to find reliable stratigraphical tools to correlate the footprint-bearing Polish continental sections with the marine Global Stratotype Section, i.e., with the base of the Bed 27c of Meishan Section D, South China (Fig. 1; see also Nawrocki et al. 2005), especially given that Ptasiński and Niedźwiedzki (2005: 228) note the controversy regarding the magnetostratigraphical record in this reference succession.

(2) Ptasiński and Niedźwiedzki (2004) indicate an exclusive resemblance between the Tumlin Sandstone vertebrate tracks they studied and the “Val Gardena” ichnoassemblage, for which a Permian age is implied. However, the Italian ichnofauna was described in the 1970s and 1980s and the reliability of its chronostratigraphic position should be reassessed.

(3) The ichnotaxa from interdune deposits appear difficult to study, which is not helped by their poor preservation, and are placed by Ptasiński and Niedźwiedzki (2004) in open nomenclature (especially the amphibians) or are referred to five new reptilian ichnospecies. The possible endemicity of the assemblage causes severe problems for its use for correlation.

End-Permian mass extinction and terrestrial vertebrates

In a brief paragraph in their conclusions, Ptasiński and Niedźwiedzki (2004: 318) were unequivocal in stating that: “The transitional character of Late Permian vertebrate ichnofaunas provides no indication of the catastrophic mass extinction of terrestrial vertebrate faunas [...] While it is difficult to prove this evolutionary scenario, investigations of vertebrate body fossil assemblages seem to be compatible with it (Lozovsky 1997)”. Ptasiński and Niedźwiedzki (2004) selectively cite few, mostly not very recent, references for the support of this inference, with emphasis on “an incomplete stratigraphic and/or fos-

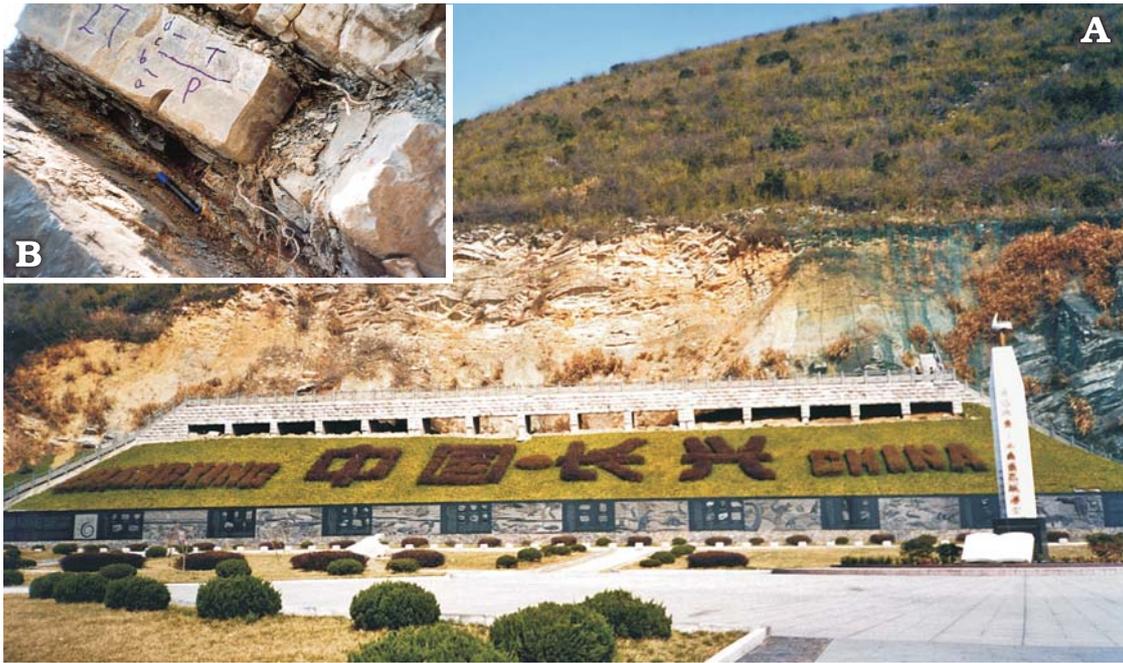


Fig. 1. Global Stratotype Section at Meishan Section D, South China. **A.** General view of the geological-educational protected site (note the monument of index Triassic conodont species *Hindeodus parvus*). **B.** Close-up of the “golden spike”-bearing Bed 27, with the biostratigraphically-defined boundary in the middle of Bed 27 at the first appearance of the conodont *Hindeodus parvus*. This level is underlain by bentonitic white clay, and black shaly horizons as a record of catastrophic processes in the crucial timespan. Photos by Dr. Maria Racka.

sil record” (Kozur 1998: 256), but this conclusion is indeed unexpected in 2004 in a light of review of broader literature data.

As Hallam and Wignall (1997: 110–111) noted: “Much of the literature of the past few decades has tended to downplay the existence of an end-Permian tetrapod extinction [...] As currently understood, the last few million years of the Permian witnesses a prolonged crisis in terrestrial tetrapod community [...] terminated by a rapid extinction event [...] which wiped out a broad spectrum of life styles”. Reorganization of vertebrate communities in a post-apocalyptic, greenhouse ecosystem is well seen in the Karoo Basin of South Africa (e.g., Retallack et al. 2003). Benton et al. (2004) explained aspects of the catastrophic turnover in a comprehensive survey of 289 localities spanning 13 successive geological intervals in the South Urals basin: “These changes in diversity and turnover cannot be explained simply by sampling effects. There was a profound loss of genera and families, and simplification of ecosystems, with the loss of small fish-eaters and insect-eaters, medium and large herbivores and large carnivores. [...] Even after 15 Myr of ecosystem rebuilding, some guilds were apparently still absent—small fish-eaters, small insect-eaters, large herbivores and top carnivores” (p. 97).

Benton (2003: 20–24) discussed the Triassic rise of both diapsid-derived dinosaurs and synapsid descendants, the mammals, as a final evolutionary effect of the post-extinction reptile renaissance (in some respects “the synapsid-diapsid-synapsid cycle” went full-circle after the end-Cretaceous mass extinction). Furthermore, the greater aerobic scope of the vertebrate survivors supports the hypothesis that potential respiratory adaptations to hypoxia probably evolved originally in burrowing animals (e.g., the non-mammalian cynodont *Trirachodon*; see Groenewald et al.

2001; Botha and Chinsamy 2004): physiological regulation was critical to their endurance under escalating stress during this time of lowered atmospheric oxygen and elevated carbon dioxide levels related to end-Permian atmospheric contamination from the massive dissociation of methane clathrate (for further discussion see Retallack et al. 2003 and Huey and Ward 2005).

Accordingly, the devastating demise of vertebrates at the P–Tr boundary, which had well-known major phylogenetic consequences, cannot and should not be dismissed lightly on the basis of ichnological data from a single region. The contribution of footprint analysis to understanding the response of vertebrates to this massive environmental perturbation may be substantial but is complicated, as shown elsewhere for the Triassic–Jurassic boundary extinction (Olsen et al. 2003).

Final remarks

Regarding the chronostratigraphical conclusions of Ptaszyński and Niedźwiedzki (2004, 2005), in the light of the above reservations I suspect that the thorough critique published by Nawrocki et al. (2005) is generally correct. Of course, re-assignment to the Permian of a Buntsandstein interval (or, more correctly, facies) cannot be totally excluded given our poor level of knowledge (see discussion in Nawrocki et al. 2005). This re-assignment requires, however, far more support from the comprehensive analysis of various geological data, including isotopic chemostratigraphy, and other high-resolution markers of global events at the P–Tr boundary (see summaries in Retallack et al. 2003, and Pang et al. 2005; also Lozovsky 1997), where material of extraterrestrial origin (microspherule-rich horizons; Bachmann et al. 2004) may

even be present. This multidisciplinary correlation approach is exemplified by a two-point research agenda for the Holy Cross succession:

(1) Recognition of a sedimentary response to the volcanism-induced climatic catastrophe (e.g., Visscher et al. 1996, 2004; Hallam and Wignall 1997; Benton 2003) which was coupled with higher sediment input and greater peak discharges in this arid drainage basin after vegetation loss; such a depositional switch is spectacularly seen in the fluvial systems of the Uralian foreland (Newell et al. 1999). Likewise, Ward et al. (2000) recognized in South African sequences a rapid decline in riverbank stability and thus a switch from meandering to braided-style channels. Is this catastrophic climatic/sedimentary event also reflected within the first Buntsandstein cycle of Fijałkowska (1994)? It is of note that this cycle was completed in mostly arid regimes during deposition of the desert Tumlin Sandstone (= complex C in Fijałkowska 1994).

(2) Identification of a prominent proxy for the crisis of life on land, the “fungal event” (*sensu* Visscher et al. 1996; see summary in Pang et al. 2005). Is this event recorded in the *Lundbladispora obsoleta*–*Protohaploxylinus pantii* microflora by the appearance of numerous *Tympanicysta* in the basal Buntsandstein units (see tables 1 and 3 in Fijałkowska 1994)? Although this correlation is granted by Ptaszyński and Niedźwiedzki (2004: 290), some doubts are raised by the results of Yaroshenko and Lozovsky (2004). This problematic (?algal) microfossil actually occurs also in the highest Buntsandstein palynozone (see tables 2 and 3 in Fijałkowska 1994).

In a broader context the Permian–Triassic boundary interval witnessed the most severe ecosystem collapse of the Phanerozoic, and any exception from this well-documented worldwide extinction pattern ought to be scientifically tested and proved in great detail. It seems that Ptaszyński and Niedźwiedzki (2004) did not fulfill this rigorous requirement, as is apparent even simply from their list of references. Thus, my final question is: do the ichnofaunas from the Polish Buntsandstein indicate a unique refuge for the Permian vertebrates that were exterminated elsewhere?

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