



Preservation of exceptional vertebrate assemblages in Middle Permian fluviolacustrine mudstones of Kotel'nich, Russia: stratigraphy, sedimentology, and taphonomy

Michael J. Benton ^{a,*}, Andrew J. Newell ^b, Al'bert Yu. Khlyupin ^c, Il'ya S. Shumov ^c, Gregory D. Price ^d, Andrey A. Kurkin ^e

^a School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

^b British Geological Survey, Maclean Building, Wallingford OX10 8BB, UK

^c Vyatka Palaeontological Museum, Ulitsa Drelevskii 22, Kirov, Kirov Region 610000, Russia

^d School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

^e Paleontological Institute, Russian Academy of Sciences, Ulitsa Profsoyuznaya 123, Moscow 117997, Russia

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ABSTRACT

The Kotel'nich locality in European Russia has long been a rich source of high-quality tetrapod fossils, including pareiasaurs, dicynodonts, gorgonopsians and theriodonts. The age of the Kotel'nich locality has been debated, but it corresponds to early Severodvinian in the Russian stratigraphic scheme, equivalent to the late Capitanian (late Middle Permian) on the international time scale. Remarkably, the majority of specimens are complete, quite unlike those from most Russian Permo-Triassic red bed localities; commonest of all are 1–2-metre long pareiasaur skeletons of the genus *Deltavjatia*, preserved in hollows on top of a consolidated palaeosol horizon. Previous taphonomic scenarios in the Russian literature have included suggestions that the animals were overwhelmed beneath sand dunes, mired in soft fluvial sediments, caught at the bottom of a deep lake, trapped in burrows, or dumped in fluvial scours. It is probable that the pareiasaurs were searching for water in a time of catastrophic aridification, and died, weakened, in shallow hollows. In this case, we also emphasise the importance of floodplain microtopography in creating the sedimentary conditions necessary for the preservation of exceptional vertebrate assemblages in a slowly aggrading fluviolacustrine setting.

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1. Introduction

Vertebrate skeletons in ancient river deposits are commonly preserved as lags within coarse-grained channel deposits where the remains have generally been transported, disarticulated and abraded. Less common, but often of greater paleontological importance, are skeletons preserved within fine-grained floodplain deposits that are often substantially complete and well preserved (Behrensmeyer, 1988; Smith, 1993; Rogers and Kidwell, 2000; Therrien and Fastovsky, 2000; Ryan et al., 2001; Smith and Swart, 2002; Straight and Eberth, 2002; Rogers, 2005; Eberth et al., 2007, 2010; González Riga and Astini, 2007). In comparison to coarse-grained channel deposits, floodplain mudstones often have a relatively uniform stratigraphy that can be masked by syndepositional soil-forming processes and this can lead to uncertainty regarding the original depositional environment of the muds as well as the life, death and preservation

of the enclosed vertebrate fossils. This uncertainty is exemplified by the renowned Permian vertebrate locality of Kotel'nich in Russia.

Kotel'nich has yielded hundreds of complete skeletons of fossil reptiles, predominantly pareiasaurs and dicynodonts. The mode of preservation of these skeletons has been debated (Hartmann-Weinberg, 1933, 1937; Kashtanov, 1934; Ivakhnenko, 1987; Gubin, 1989; Tverdokhlebov and Shminke, 1990; Ochev, 1995; Khlyupin, 2007; Sumin, 2009; Tverdokhlebov, 2009): were they preserved by miring in soft muds around water holes, deposited on the floor of a lake, buried in situ within burrows, or washed into floodplain hollows? Further, although the Kotel'nich locality has been known since the 1930s, and it has been referred to hundreds of times in the vertebrate palaeontological literature, the geology and taphonomy of the site have not been described. The aims of this paper are (1) to outline the stratigraphy and sedimentology of the Middle Permian continental red beds on the banks of the Vyatka River at Kotel'nich, which requires a presentation of the local stratigraphic scheme as well as new evidence for the dating of Kotel'nich in comparison to the Karoo tetrapod biozones and the international marine time scale, and (2) to describe the taphonomy of recently excavated tetrapod skeletons, and to present evidence that the exceptional

* Corresponding author. Tel.: +44 954 5400; fax: +44 925 3385.

E-mail address: mike.benton@bristol.ac.uk (M.J. Benton).

preservation of the fauna results largely from an arid episode and the rapid infill of floodplain hollows.

Museum abbreviations. KPM, Vyatka Palaeontological Museum, Kirov, Kirov Oblast, Russia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

2. Geological background

The Permo-Triassic red beds of Russia represent an enormous area of outcrop, covering 1.4×10^6 km² of European Russia (Fig. 1), and spanning over 40 million years, from the end of the Early Permian (Ufimian; Kungurian) to the end of the Middle Triassic (Bukobay; Ladinian). These units provide an important record of changing terrestrial environments and ecosystems before, during, and after the end-Permian mass extinction, including long-term aridification of climates and major changes in sedimentary regimes across the Permo-Triassic boundary (Newell et al., 1999, 2010; Golubev, 2000; Zharkov and Chumakov, 2001; Tverdokhlebov et al., 2003, 2005; Benton et al., 2004; Shishkin et al., 2006; Shcherbakov, 2008; Krassilov and Karasev, 2009; Benton, 2012).

One of the most remarkable localities in the Russian Middle and Late Permian is Kotel'nich, in Kirov Oblast, the source of hundreds of tetrapod specimens since their first discovery in 1893. In his seminal work on the stratigraphy of the Russian Permian tetrapods, Efremov (1937, 1941) established two lower, dinocephalian, complexes (I and II), and a third, pareiasaurian, complex (III) based initially on finds from Kotel'nich and Sokolki, a site on the North Dvina River. The pareiasaurian complex was subsequently divided into three, the Kotel'nich, Ilinsko'ye, and Sokolki subcomplexes, occupying the bulk of the Tatarian Russian Stage (details in Golubev, 2000). Kotel'nich was then one of the fundamental locations for understanding the evolution of Middle and Late Permian tetrapods from the earliest days of palaeontological work in Russia, and it was seen internationally as the equal and equivalent of the succession of tetrapod zones in the Karoo Basin in South Africa (e.g. Olson, 1962; Anderson and Cruickshank, 1978; Benton, 1983; Modesto and Rychczynski, 2000; Lucas, 2004, 2006).

Kotel'nich occupies a central position within the broad belt of Permian deposits on the Russian platform west of the Ural Mountains (Fig. 1), a north–south trending fold and thrust belt formed by the collision of the East European Platform and Siberian plate during the Carboniferous and Permian (Nikishin et al., 1996). On the Russian platform, Permian strata younger than the Roadian are predominantly siliciclastic terrestrial deposits that were largely derived from the Ural Mountains and deposited in a range of fluvial and lacustrine environments across the platform (Ignat'ev, 1962, 1963; Gorsky et al., 2003). Proximal to the Ural Mountains, in areas such as Perm', post-Roadian continental deposits are up to 1400 m thick and contain much cross-bedded pebbly sandstone and conglomeratic channel fills derived from the orogen, while in distal (western) locations Middle and Upper Permian deposits are generally much thinner and dominated by mudstones and evaporites deposited in fluvial lacustrine environments (Gorsky et al., 2003; Newell et al., 2010). Kotel'nich occupies a medial position within this westward thinning and fining clastic wedge.

3. Historical context of the Kotel'nich red beds and their fauna

Upper Permian red beds, comprising mudstones, siltstones, marls, sandstones, and conglomerates, are exposed on the right-hand (western) bank of the Vyatka River at, and for some 24 km south of, the town of Kotel'nich (Fig. 2), from Port Kotel'nich (58.29136N, 48.33060E) to Zemtsy (58.13931N, 48.36058E). Here the Vyatka River cuts westwards into an elevated escarpment of Permian rocks creating a discontinuous series of large outcrops in the generally flat-lying Permian succession (Fig. 3), ranging up to 40 m high at

Agafonovo (58.18637N, 48.32864E). The spectacular red, yellow, and brown colours of the near horizontally-bedded clastic sediments have been noted by previous authors (Fig. 4).

Geological work on the Kotel'nich red beds began rather late, with the first geological mapping only 100 years ago (Krotov, 1912). This was because the area was remote from major cities, and seemingly devoid of mineral potential. The Vyatka River had long been a major transport artery, but the town of Kotel'nich remained a very remote outpost of the Russian Empire until the railway from St Petersburg to Vyatka opened in 1905. Following continued repression during Soviet times, and substantial decline of industry after 1990, Kotel'nich remains a remote and undeveloped town. The geology of the Permian red beds was revised by Ignat'ev (1962, 1963) and Tikhvinskaya (1946), and reviewed by Nalivkin (1973) and Lozovskiy and Esaulova (1998). In these works, the sedimentary rocks were interpreted as fluvial and lacustrine. Tverdokhlebov and Shminke (1990) were the first to argue that the yellow sandstones of the Boroviki Member (Coffa, 1999) were aeolian in origin. Then, Goman'kov (1997), Coffa (1999), and Golubev (2000) presented summary accounts of the sedimentology and stratigraphy of the Kotel'nich succession, each based on original and independent fieldwork, and Tverdokhlebov (2009) added further first-hand observations.

The Kotel'nich red beds are renowned for their abundant and exquisite tetrapod fossils, and yet earlier geologists did not pay these much attention (see Ochev, 1995; Ochev and Surkov, 2000 for historical surveys). Krotov (1894, 1912) recorded isolated bones from the west bank of the Vyatka River just south of Kotel'nich, at a locality later termed 'Kotel'nich-1'. In 1933, S. G. Kashtanov, a young hydrogeologist from Kazan' University, discovered two complete pareiasaur skeletons near the village of Vanyushonki, on the river bank 18 km south of Kotel'nich (Figs. 2, 3), and he found a further two or three in 1935, 2 km upstream (Kashtanov, 1934). The skeletons were incomplete as they had been partially eroded by the action of the Vyatka River, but Kashtanov excavated some of this material and sent it to the Paleontological Institute (PIN) in Moscow. The Moscow palaeontologists came to Kotel'nich, beginning with expeditions led by A. P. Hartmann-Weinberg in 1935, and they found two incomplete skeletons and two skulls of pareiasaurs near the village of Volki (Fig. 3). In 1948, a team from PIN led by B. P. V'yushkov, found four pareiasaur skeletons, three of them damaged by erosion, near Boroviki village (Figs. 2, 3). The following year, the same team prospected 12 km of the banks of the Vyatka River, from Port Kotel'nich south to Boroviki, and they discovered a further seven complete and six incomplete skeletons. Two further skeletons were reported in 1950 from Boroviki village by D. M. Vologzhanin, but he could not extract them. In their overview of the Russian Permo-Triassic tetrapods, Efremov and V'yushkov (1955) reported 15 pareiasaur skeletons collected by PIN scientists at Kotel'nich.

Renewed investigations by PIN scientists Yu. M. Gubin, M. F. Ivakhnenko, and N. N. Kalandadze turned up isolated pareiasaur and therapsid specimens in several green sandstone lenses higher in the section, in what is now termed the Sokol'ya Gora Member near Agafonovo (Fig. 3), a locality they termed Kotel'nich-2. Further excavations began in the 1990s, thanks to the work of D. L. Sumin from Moscow, who collected many tetrapod skeletons, including dicynodonts, dromosaurs, therocephalians, and gorgonopsians, as well as pareiasaurs. He established a fossil-dealing company called Kamyennii Tsveyetok (= 'Stone Flower') that sold some of the fossils, but the company was dissolved in 1995. In the three years from 1990 to 1992, Sumin and colleagues collected 40 pareiasaur skeletons on the banks of the Vyatka, near the villages of Boroviki and Mukha (Figs. 2, 3). Since 1992, the work has been led by Al'bert Yu. Khlyupin, in conjunction with teams of locally based geologists, school children, and visitors from overseas (Fig. 5). These teams excavated both at Port Kotel'nich, where they found many dicynodont skeletons as well as rarer pareiasaurs, and along the southern portion of the section on the banks of the Vyatka

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