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

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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 fluviatile sediments, caught at the bottom of a deep lake, trapped in burrows, or dumped in fluviatile 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.

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

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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 km^2 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 Rybczynski, 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 fluviolacustrine 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 fluviatile 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, dromasaurs, therocephalians, and gorgonopsians, as well as pareiasaurs. He established a fossil-dealing company called Kamyennii Tsvyetok (='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

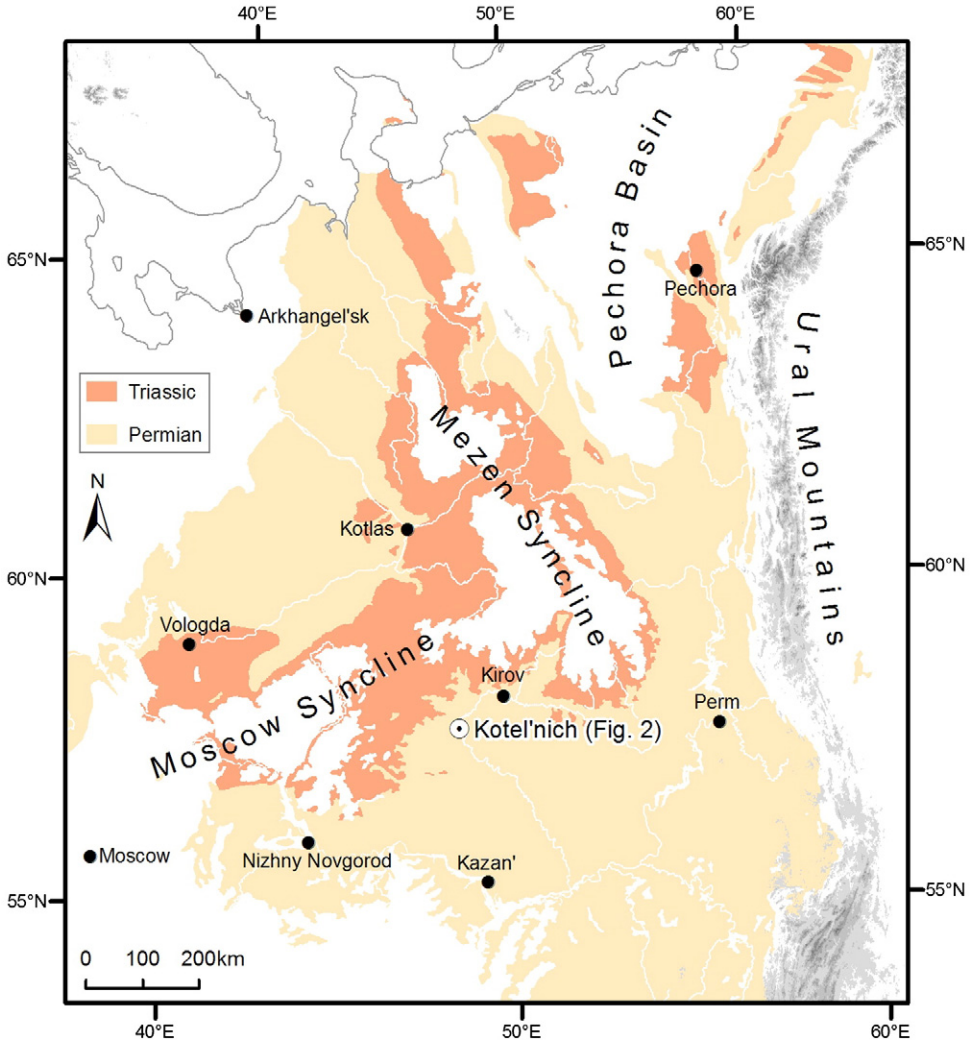

Fig. 1. Map showing the location of Kotel'nich 400 km NE of Moscow in the Russian Federation. Kotel'nich occupies a central position within the broad belt of Permian strata that was deposited on the Russian platform west of the Ural Mountains. It is located just to the south of the Moscow Syncline which contains a core of Triassic and younger strata.

where they excavated many pareiasaurs and the extraordinary small climbing reptile *Suminia*. Khlyupin established a museum in Kotel'nich in 1994, and it has since been designated as a regional museum, the Vyatka Palaeontological Museum. Since 1992, the Museum group has excavated and documented over 390 tetrapod skeletons.

4. Kotel'nich fauna and flora

4.1. Tetrapod fauna

The fossil amphibians and reptiles from the main Kotel'nich section are well known, including the plant-eating pareiasaur *Deltavjatia* (Hartmann-Weinberg, 1937; V'yushkov, 1953; Ivakhnenko, 1987; Lee, 2000; Kordikova and Khlyupin, 2001) the galeopid anomodont *Suminia* (Ivakhnenko, 1994; Rybczinski, 2000; Fröbisch and Reisz, 2009), and the gorgonopsian *Viatkogorgon* (Tatarinov, 2004a), as well as the small insect-eating parareptile *Emeroleter* (Ivakhnenko, 1997), and small carnivorous theriodonts (Tatarinov, 1968, 1995a, b, 1997, 1999a, b, 2000, 2004a, b). The dicynodont *Australobarbarus* (Kurkin, 2000) and two pareiasaurs found in 2009, possibly also *Deltavjatia*, come from the separate Port Kotel'nich locality. Further, the fish-eating chroniosuchian *Chroniosaurus* (Golubev, 1998, 2000), the basal biarmosuchian *Proburnetia* (Tatarinov, 1968), and the pareiasaur *Proelginia permiana* (=*Scutosaurus karpinskii*) are known from the younger Sokol'ya Gora locality.

The fauna has always been recognised as stratigraphically significant. Ivakhnenko (1987, 1992) established the 'Kotel'nich Subcomplex' (Kotel'nichskii Subkompleks) as the lowest of three faunal assemblages within the Sokolki Complex that spanned the Severodvinian and lower Vyatkian gorizonts, as part of the traditional tetrapod-based division of the Russian Permo-Triassic red beds (Fig. 5; Efremov, 1939, 1941; Lucas, 2004, 2006).

4.2. Flora and non-tetrapod fauna

The Kotel'nich red beds have produced plant fossils in addition to the famous tetrapods. V'yushkov (1953) and Ignat'ev (1963) mentioned the occurrence of plants, and Goman'kov (1997) provided a detailed study, reporting a detrital macroplant assemblage from the Chizhi Member channels referable to the *Tatarina* flora, with the conifers *Phylladoderma* and *Geinitzia*, the peltaspermalian pteridosperms (seed ferns) *Tatarina*, *Pursongia*, and *Permotheca*, and the horsetails *Paracalamites* and *Phyllotheca*, as well as miospores of the same plants that may be used in biostratigraphy.

These same organic-rich sandstone units of the Chizhi Member have produced further fossils, including ostracod tests, fish scales, and isolated tetrapod bones (Tverdokhlebov and Shminke, 1990; Goman'kov, 1997; see below).

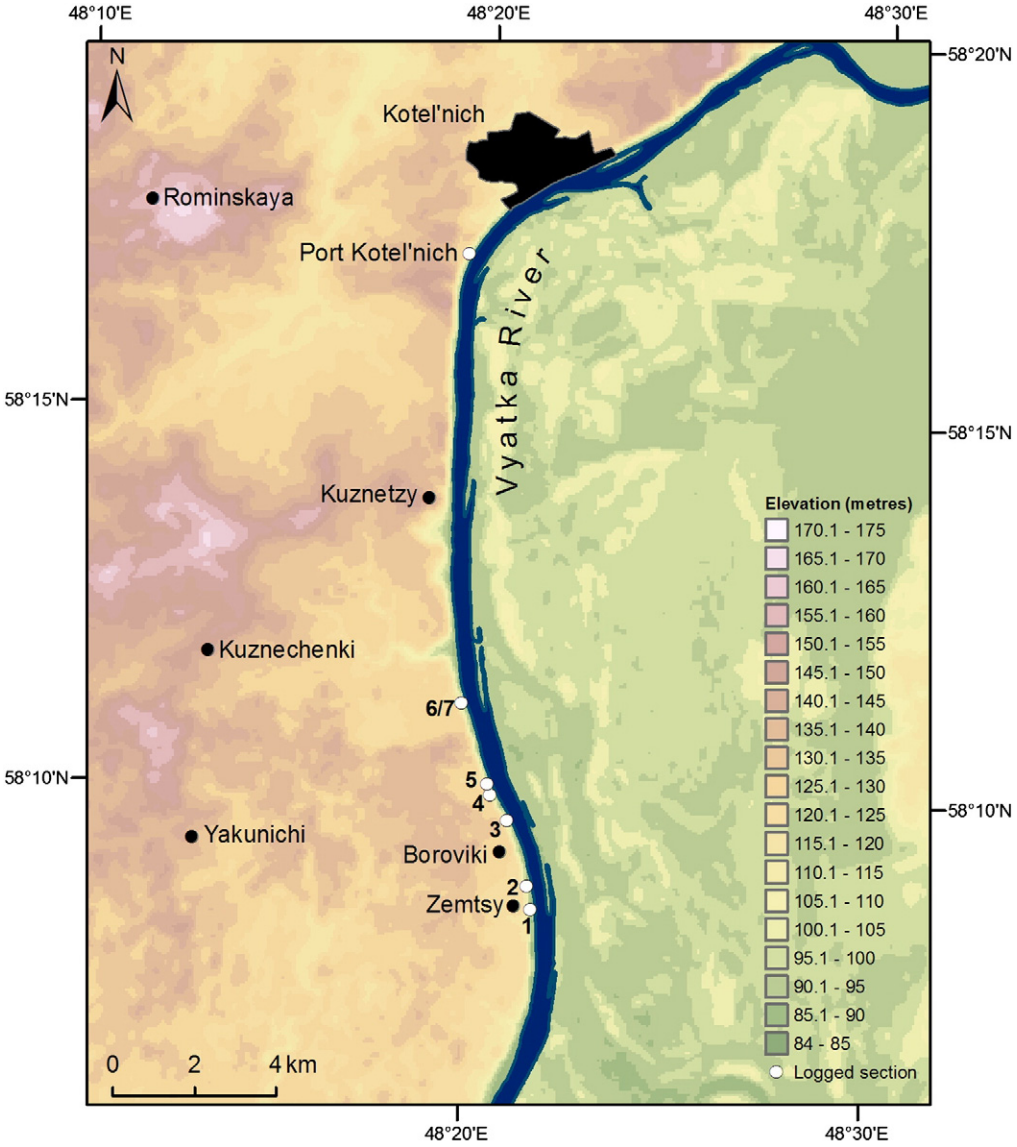

Fig. 2. Map of the Kotel'nich area showing the relatively straight, south-flowing reach of the Vyatka River to the south of the town. Permian strata are exposed on the elevated escarpment along the western bank of the Vyatka River, with most of the vertebrate localities close to the village Boroviki. Numbers with white markers show the locations of logged sections in Fig. 4.

5. Stratigraphy

5.1. Nomenclature and correlation

We distinguish three portions of the Kotel'nich succession, each with different tetrapod faunas and different modes of preservation, and each of which has to be related to the other appropriately in order to establish the succession. From north to south (Figs. 2, 3), these are (1) the Port Kotel'nich locality (58.29136N, 48.33060E), (2) the long southern succession from Shestakovy (58.2452N, 48.3179E) to Zemtsy (58.13931N, 48.36058E) with a conformable sequence of the Vanyushonki to Shestakovy members (Fig. 3), and (3) the Sokol'ya Gora Member at Agafonovo (58.18637N, 48.32864E). The relationships of the last two are straightforward: the Sokol'ya Gora Member follows directly above the Shestakovy Member. The Port Kotel'nich section is harder to correlate to the other two (see Section 6.7).

In addition to the geographic separation of portions of the Kotel'nich section, there has been some confusion over the nomenclature of these localities and the stratigraphic divisions. In general, the whole sequence was simply referred to as the 'Kotel'nich red beds', or an equivalent term, even though distinct horizons of red mudstone, conglomerates, and channels of green-brown sandstone had been noted. In traditional style, each fossiliferous locality was named, Port Kotel'nich being termed Kotel'nich-1, and this term was then extended to many other distinct sites in the southern section, but still in red mudstones and siltstones. The southernmost locality, called sometimes Agafonovo or Sokol'ya Gora, was termed Kotel'nich-2. This second location is well constrained both geographically and stratigraphically, but Kotel'nich-1 is not, extending over 20 km along the banks of the Vyatka River, and encompassing up to four distinct stratigraphic levels. Coffa (1999) noted a published example of how the terminology became confused when Tatarinov (1995a, b) stated that the holotype specimens of the theriodonts *Viatkosuchus* and *Karenites* both came from Kotel'nich-2, when in fact they came from the older Kotel'nich-1 horizon. The traditional habit among Russian geologists and palaeontologists of naming locations, but not horizons, often led to confusions of this kind.

Ochev (1995) distinguished three layers, clearly visible along the banks of the Vyatka River (Fig. 3): at the base a unit of reddish-

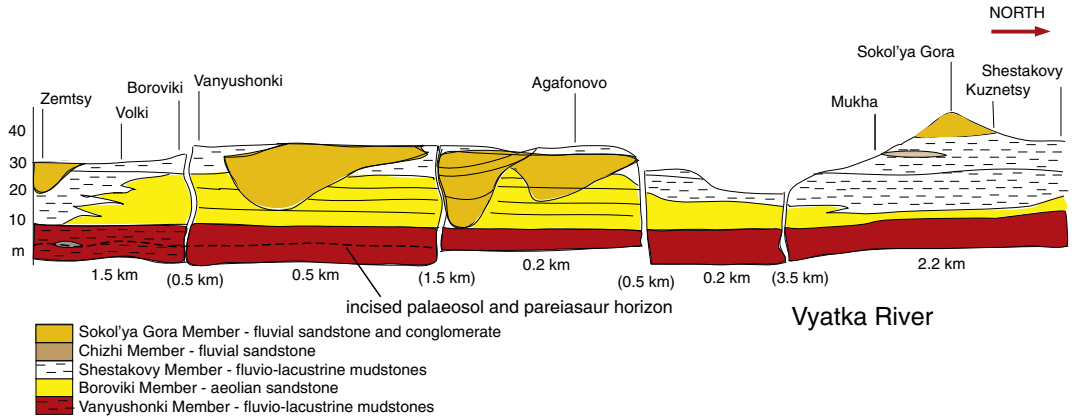

Fig. 3. Sketch section along the western bank of the Vyatka River between Zemtsy in the south and Kuznetsy in the north (see Fig. 2 for locations) showing the arrangement of the main stratigraphical units. The Vanyushonki Member is predominantly fluviolacustrine mudstone, which is overlain by the Boroviki Member, a flat-based, lensoid, predominantly aeolian sandbody, and the Shestakovy Member, a further series of fluviolacustrine mudstones. These are followed by the channel forms of the Chizhi and Sokol'ya Gora members, which comprise coarse-grained fluvial sandstones and intraclast conglomerates in lenticular bodies spectacularly incised into the older units. Vertebrates are primarily found in mudstones toward the base of the cliff in the Vanyusonki Member, in the marked palaeosol horizon. Distances (km) in brackets indicate breaks in exposure that are not shown in the diagram.
Figure is adapted from Tverdokhlebov (2009).

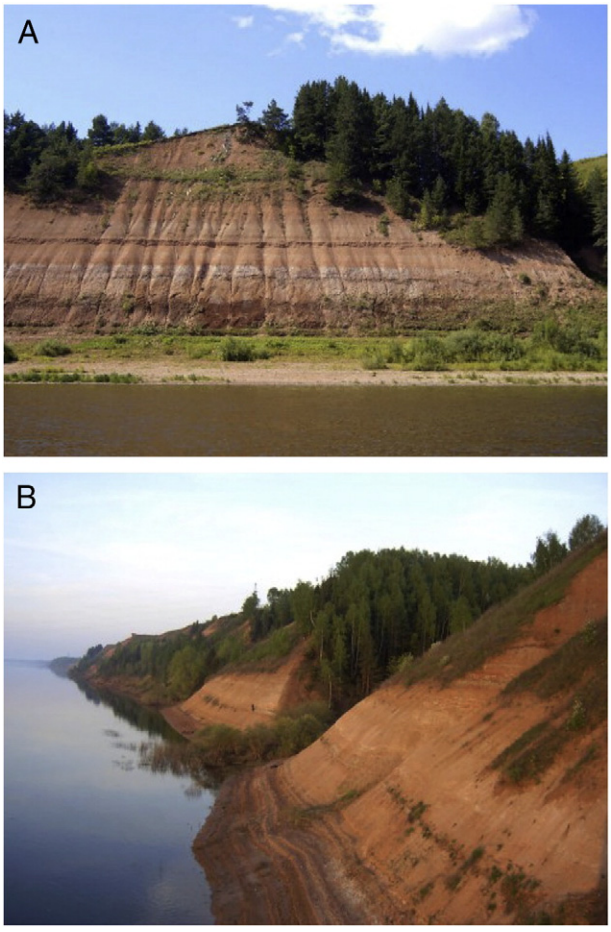

Fig. 4. Two views of the Kotel'nich tetrapod localities. (A) The right (west) bank of the Vyatka River, 15 km south of Kotel'nich town, near Boroviki village, at about 58.16092N, 48.34928E, showing a typical section through the red sediments of the Vanyushonki Member on the foreshore and in the lower one-third of the cliff, a thin strip of the overlying Boroviki Member sandstones, and the red sediments of the Shestakovy Member above. (B) The steep-sided cliff at Port Kotel'nich (58.29136, 48.32449), close to the 'dicynodont quarry', excavated in the early 1990s. Photographs by Al'bert Yu. Khlyupin.

brown siltstone with thin interbeds of shelly mudstone, bluish siltstone, calcareous mudstone, and detrital sand; above this a 15–18 m thick, kilometre-scale lens of reddish and yellowish fine-grained argillaceous, cross-bedded sandstones; and an upper unit, some 10 m thick, of brown and brownish-red sandy mudstone interbedded with greenish- and brownish-grey sandstone. Ochev (1995) also used the Kotel'nich-1 and Kotel'nich-2 terminology, but did not name the units within the succession he described.

Coffa (1999) was the first to divide the Kotel'nich red beds formally, and he named five stratigraphic members. These are, from the base of the succession, the Vanyushonki, Boroviki, Shestakovy, Chizhi, and Sokol'ya Gora members (Fig. 3). Andre Coffa worked with Russian geologists and palaeontologists in the mid-1990s for his Masters and PhD theses at Monash University, Australia, as part of a wider Russian–Australian collaboration, but his work was published only as two conference abstracts (Coffa, 1997, 1998) and as a summary paper in a conference fieldtrip volume (Coffa, 1999). The latter is the key reference and source of the nomenclature we use here. Coffa (1999) states that his stratigraphic scheme was agreed with key Russian stratigraphers at the time, and indeed was used by Kordikova and Khlyupin (2001). Further, his scheme was in use when we did our fieldwork in 2009: accordingly, we adopt Coffa's stratigraphic terminology here.

Further stratigraphic work was done on the Kotel'nich section by Goman'kov (1997), Golubev (2000), and Tverdokhlebov (2009), and they supplied three different informal numbering schemes for the succession. Coffa's (1999) five members correspond, in sequence from bottom to top, to Goman'kov's (1997) beds 1, 2, 3+4, 5, and 6, and Golubev's (2000, pp. 84–88, 117–120) beds 1+2, 3+4, 6, 5, and 7+8. Tverdokhlebov (2009) identified four sedimentary 'packets', numbered I, II, III, and IV from the bottom, and corresponding respectively to the Vanyushonki, Boroviki, Shestakovy, and Sokol'ya Gora members.

Goman'kov (1997), Coffa (1999), and Golubev (2000) differ in some details of their interpretation of the Kotel'nich succession, Coffa measuring a composite section of 65 m in all, and Golubev only 35 m. This discrepancy arises from differences in measurements of the five constituent units, but partly in the placement of the Port Kotel'nich section (see Section 6.7). We prefer to refer to the main section at Kotel'nich as 35 m thick, and make no assumptions about how much of the Port Kotel'nich succession might sit on top.

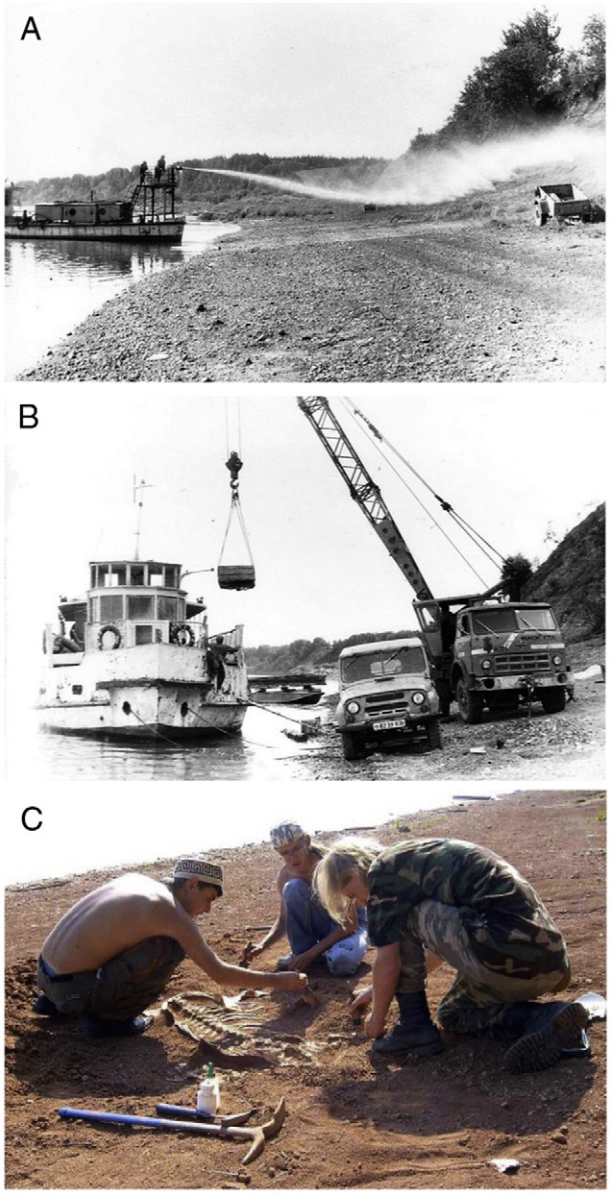

Fig. 5. Excavating pareiasaur skeletons from the Vanyushonki Member. (A, B) Scenes from the river-based 1992 joint paleontological expedition of "Stone Flower Company" (Moscow) and Moscow Paleontological Institute, using a fire-fighting barge equipped with a high-pressure hose (A) to blast sediment from the low-lying palaeosol horizons to expose pareiasaur skeletons, and then heavy lifting gear to remove the crated specimens to a small river vessel (B), for transportation up the Vyatka River to Port Kotel'nich, where they were loaded onto rail wagons for transport to the Paleontological Museum in Moscow. (C) Palaeontological expedition of the Kotel'nich Palaeontological Museum in 2006: from left to right, Maxim Kovalyov, Alexey Toropov, and Il'ya Shumov remove sediment from a complete pareiasaur specimen near Boroviki, with the Vyatka River at top left. Photographs by A. Yu. Khlyupin.

5.2. Dating

Traditionally, the Russian tetrapod faunas (e.g. Efremov, 1937, 1941) were dated by comparison with the succession of faunas in the Karoo Basin in South Africa (e.g. Anderson and Cruickshank, 1978; Benton, 1983; Modesto and Rybczynski, 2000) as Late Permian and late Tatarian. Comparison of the pareiasaurs (Lee, 2000) and dicynodonts (Kurkin, 2011) suggests that the Kotel'nich succession is broadly equivalent to the *Pristerognathus* Zone, although earlier overviews (e.g. Kurkin, 2000) correlated the Kotel'nich beds with the higher *Cistecephalus* Zone. This approach is unsatisfactory for two reasons: first, the Russian and South African tetrapod taxa are generally not identical, but merely close relatives, and so any matching can be based only on broad assumptions about phylogeny; and second, the South African succession is not yet securely dated to the international marine standard, so establishing a correlation with an approximate tetrapod biozone in the Karoo is a distraction, and it does not help in establishing the actual age of the Russian units. It will be better to seek auxiliary evidence to date the Russian and Karoo successions, such as marine intercalations, magnetostratigraphy, and radiometric dates (Newell et al., 2010; Benton, 2012), and then to use the vertebrate biozones (e.g. Lucas, 2004, 2006) to cross-match between the two successions.

There are two steps in the dating procedure: first, the Kotel'nich succession has to be placed in the context of the Russian system, and then this must be equated with the international marine standard by the use of biostratigraphy, magnetostratigraphy, and other evidence.

Evidence for dating the Kotel'nich succession within the Russian system comes from comparative biostratigraphic studies and matching with sections that have also yielded magnetostratigraphic evidence (see Appendix 1; Fig. 6). In summary, the whole Kotel'nich succession is Severodvinian (middle Tatarian), belonging to the *Suchonellina futschiki* ostracod zone (Molostovskaya in Tverdokhlebov and Shminke, 1990), equivalent to the *Suchonellina inornata* ostracod zones (Fig. 6). The sequence spans the *Deltavjatia vjatkensis* tetrapod zone and the *Chroniosaurus dongusensis* subzone of the *Proelginia permiana* tetrapod zone, the *Amblypterina costata* and *Amblypterina pectinata* ichthyozones (=*Toyemia tverdokhlebovi–Mutovinia stella* Ichthyozone; Fig. 6; Esin, 1995; Esin and Mashin, 1998), and the PK 5 palynocomplex (Golubev, 2000, p. 123). The Vanyushonki, Boroviki, and Chizhi members (Golubev's beds 1–5) in the Kotel'nich succession were said to be equivalent in age to the Nyuksenitskaya, Mikulinskaya, and lower Strelenskaya packets, the Shestakovy Member (Golubev's bed 6) to the upper Strelenskaya, Isadskaya, and Purtovinskaya packets, and the Sokol'ya Gora Member (Golubev's beds 7 and 8) to the upper Purtovinskaya and lower Kichugskaya packets (Golubev, 2000, pp. 118–120).

Having broadly established the placement of the Kotel'nich fossiliferous beds in the Russian system, this must now be linked to the international stratigraphic standard. Hitherto, this has been achieved through magnetostratigraphy (Khramov et al., 2006; Taylor et al., 2009), comparison with red bed palynomorphs, ostracods, fishes, and tetrapods, and importantly by comparisons of marine fossils (e.g. ammonoids, brachiopods) in intercalated beds of Early and Middle Permian age (full details in Newell et al., 2010).

The magnetostratigraphic scheme for the Upper Permian red beds of Russia is well established (Khramov, 1963; Molostovskiy et al., 1979; Molostovskiy, 1983, 2005), and it has recently been revised and matched to the international standard (Khramov et al., 2006; Taylor et al., 2009). Unfortunately, the Kotel'nich section is characterised by reverse magnetisation throughout (Burov et al., 1996), and there are no long measured sections with corrected magnetostratigraphic data from the wider Kotel'nich area that would allow direct age determination (Golubev, 2000). This means that links must be made through correlation across country and by using biostratigraphy (Golubev, 2000; Goman'kov, 2001). In the Russian magnetostratigraphic scheme (Fig. 6), major normal and reversed chrons in the Upper Permian are named R_1P, N_1P, R_2P, N_2P, and R_3P, and measurements on many sections show that these extend from the base to the top of the Russian Tatarian stage. The three divisions of the Tatarian are matched tentatively to the magnetostratigraphic scale, with the Urzhumian/Severodvinian boundary falling within N_1P and the Severodvinian/Vyatkian boundary within N_2P. The Permo-Triassic boundary is within, but near the base, of a normal interval at the top of R_3P (Lozovskiy and Esaulova, 1998; Golubev, 2000; Molostovskiy, 2005; Taylor et al., 2009). The succession of repeated reversals in magnetic sense corresponds to the international Illawarra Hyperchron, which succeeds the

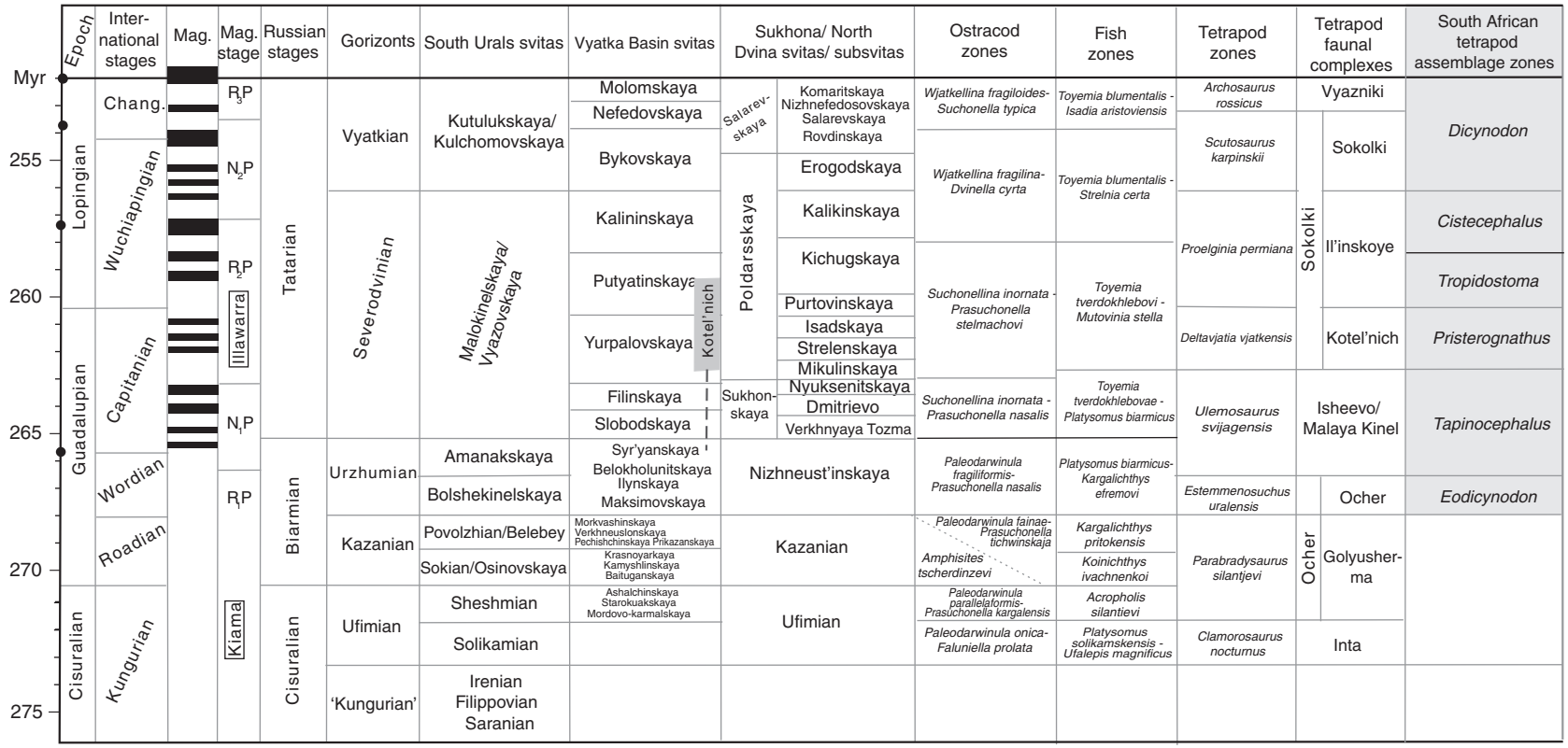

Fig. 6. Stratigraphic summary of the Middle and Late Permian of northern and eastern parts of European Russia, showing the international marine scale with radiometric tie points indicated by black dots (Gradstein et al., 2004; Ogg et al., 2008), the international magnetostratigraphic scale (Steiner, 2006), the Russian magnetostratigraphic stages (Molostovskiy 1979, 2005; Khramov et al., 2006; Taylor et al., 2009), the standard Russian gorizonts, biostratigraphic subdivisions of the Ufimian, Kazanian and Tatarian stages, key svitas in the Vyatka basin (Esaulova et al. 1998; Goman'kov, 2001), the Sukhona and North Dvina basin (Golubev, 2000) and biostratigraphic schemes for palynomorphs, ostracods, fishes and tetrapods (Golubev, 2000). Names of svitas are in basic Russian nominative form & all end in -aya, the feminine ending in agreement with the gender of the term Svita. The gorizont and tetrapod biozone terms are anglicised because many are already well established in western literature, such as Ufimian [Ufimskiy], Kazanian [Kazan'skiy], Tatarian [Tatarskiy], Yrzhumian [Urzhumskiy], Severodvinian [Severodvinskiy] & Vyatkian [Vyatskiy]. Tetrapod complexes/biozones are anglicised as follows, using simply the place name from which each is derived, rather than the genitive Russian form: Inta [Intinskiy], Golyusherma [Golyushermskiy], Ocher [Ocherskiy], Isheevo [Isheevskiy], Kotel'nich [Kotel'nichskiy], Il'inskoye [Il'inskiy], Sokolki, Vyazniki [Vyaznikovskiy].
Based on information in Newell et al. (2010).

Kiama Hyperchron when reversals were rare or non-existent. Comparison with the international magnetostratigraphic scale (Steiner, 2006) suggests that N_1P may be Capitan N (including P2), R_2P includes P3, N_2P is Chang N (including P4), and R_3P includes P5 (Taylor et al., 2009).

This review suggests that the Russian Vyatkian (= late Tatarian) is broadly equivalent to latest Wuchiapingian and Changhsingian, as suggested by Grunt (2006), Lozovskiy et al. (2009), and others. An alternative view, that the Vyatkian is equivalent to the whole of the Lopingian (i.e. Wuchiapingian + Changhsingian) has been suggested by Golubev (in Newell et al., 2010, Fig. 2), but we prefer the former, because it is a view of longer standing and it is supported by magnetostratigraphic data (Steiner, 2006; Taylor et al., 2009).

The Kotel'nich section apparently falls largely in the palaeomagnetic zone of reversed polarity R_2P, by comparison with the Sukhona River section (Khramov et al., 2006). The upper boundary of the R_2P magnetozone falls within the Kalikinskaya Packet, and the lower boundary is no higher than the middle of the Nyuksenitskaya Packet. Comparisons to the global standard stratigraphic scale indicate that the whole Kotel'nich succession is late Capitanian in age (Benton et al., 2004; Grunt, 2006; Newell et al., 2010). Further, if the Kotel'nich tetrapod assemblage is most comparable with the *Pristerognathus* Assemblage Zone in South Africa (e.g. Kurkin, 2011), new radiometric dates from the Karoo also confirm the age of the latter as late Capitanian (Rubidge et al., 2010). This then provides a strong indication of the age of all other Russian localities that have been confirmed from their fossil content as belonging to the Kotel'nich or Il'inskoye subcomplexes.

6. Sedimentology

6.1. Overview

The Kotel'nich red beds occur in near-continuous exposure along the west (right-hand) bank of the Vyatka River, a tributary of the Volga which flows south at this point (Figs. 1–4). The sedimentary rocks dip gently to the east, which is evident only to the north of Kotel'nich town, where the Vyatka flows southwest, before bending to the south through most of the section (Fig. 2). Sections were measured from the water's edge, across the broad, flat-lying beach beside the river, and up the cliffs, which range in height from a few metres to 40 m at Agafonovo. The beds lie nearly horizontally in relation to their north–south exposure, and so individual beds may be followed along the eroded riverside platform and the cliff line for long distances. Six detailed sedimentary logs were taken along a 10 km near-continuous section, from Shestakovy to Zemtsy (Figs. 3, 7), as well as at Port Kotel'nich, some 10 km north (Fig. 7).

The stratigraphy comprises five main lithological units dominated by brown, reddish brown, and grey mudstones of the Vanyushonki and Shestakovy members which extend vertically from river level to the top of the escarpment in areas to the south of Zemtsy and north of Kuznetsy (Figs. 2, 3, 7). Most of the vertebrate fossils are found in the mudstones of the Vanyushonki Member at relatively low elevations close to summer river levels (Fig. 7). Between Zemtsy and Kuznetsy the mudstones of the Vanyushonki Member are overlain by fine-

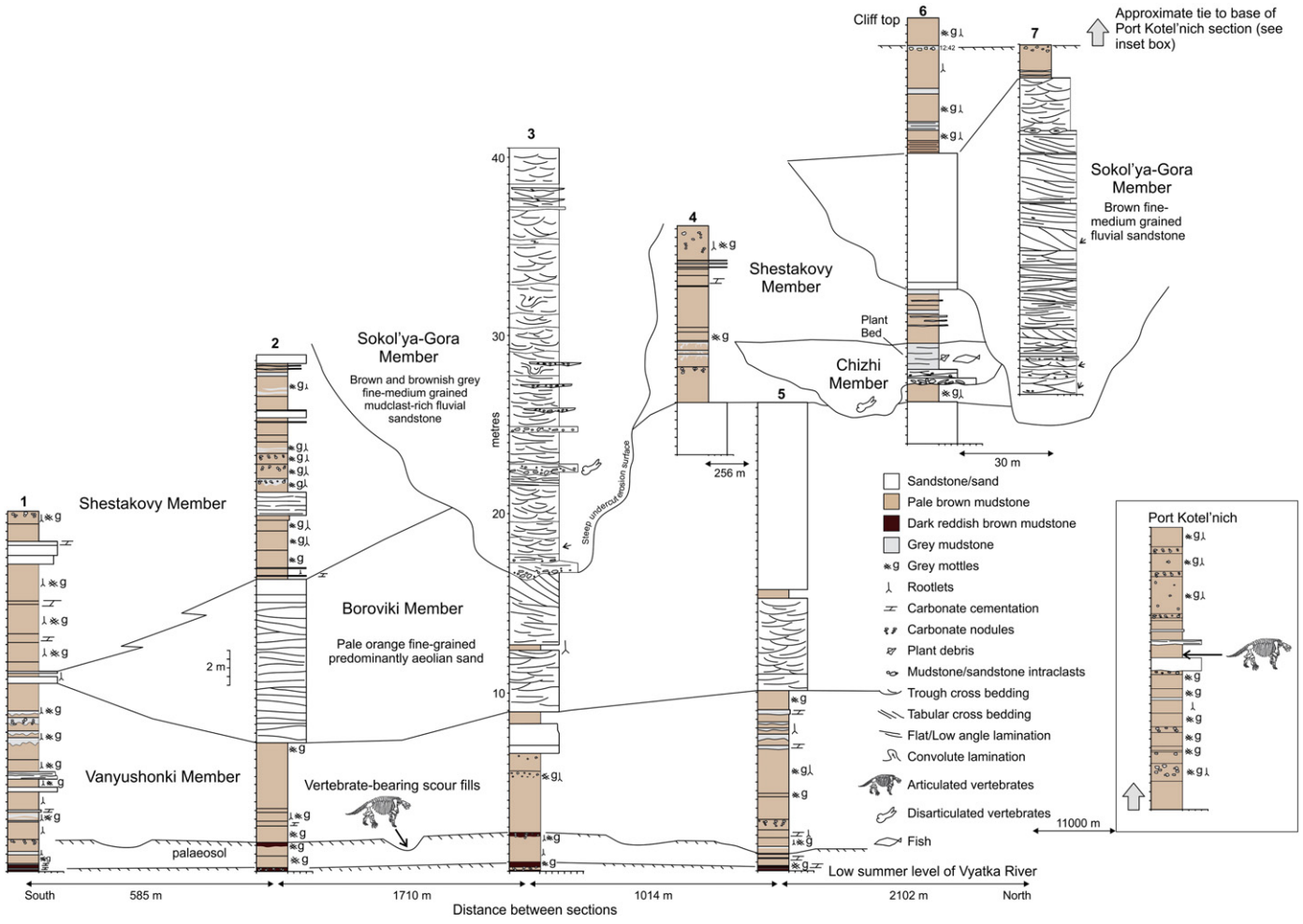

Fig. 7. Logged sections of the river escarpment exposures around Boroviki (see Figs. 2 and 3 for location of sections). The base of the logs corresponds to river level at low summer flows. Vertebrate fossils are primarily found close to river level in a series of mudstone-filled scours cut into a dark red, calcrete-bearing palaeosol within the Vanyushonki Member.

grained, pale orange, weakly cemented sandstones of the Boroviki Member, which form a broadly flat-based, lenticular body that reaches a maximum thickness of around 16 m close to Boroviki (Fig. 2). The Boroviki Member and overlying mudstones of the Shestakovy Member are incised by several bodies of brownish-grey, fine- to coarse-grained sandstone and intraclast conglomerate which infill remarkably steep scours into underlying mudstones and sandstones. These scour-filling sandstones reach a maximum thickness of 25 m and are named the Sokol'ya Gora Member after the large cliff of the same name near Boroviki. The Chizhi Member is a smaller channel-fill sandstone within the Shestakovy Member distinguished by the preservation of abundant plant material and some vertebrate remains in associated grey mudstones. The Kotel'nich red beds are described in upwards sequence of the five members named by Coffa (1999): the Vanyushonki, Boroviki, Shestakovy, Chizhi, and Sokol'ya Gora members.

6.2. Vanyushonki Member

6.2.1. Description

Coffa (1999) named this unit after the village of Vanyushonki, 18 km south of Kotel'nich on the west bank of the Vyatka River, the site of the first positively identified pareiasaur found by Kashtanov in 1933. The maximum thickness seen at outcrop is around 10 m, with an additional 83.5 m subsurface thickness measured from the Kotel'nich borehole, SKV 1. The basal mudstones of the Vanyushonki Member may be traced in surface outcrop to approximately 700 m south of the Kotel'nich River Port where they disappear beneath the surface.

The Vanyushonki Member is dominated by mudstones (silty clays and clayey silts with small quantities of fine-grained sand) that are predominantly pale or moderate brown in colour, but include common horizons and patches of grey and bluish-grey mudstone and two conspicuous horizons of dark red mudstone at the base of the exposure (Fig. 8A). Primary bedding and lamination are not generally seen in the mudstones, which mostly show an irregular, angular blocky structure. Root traces are common and typically consist of many millimetre-diameter tubules with short branches diverging at right angles. Rootlet structures are commonly highlighted by grey-coloured haloes around a black centre or by white calcite mineralisation. Carbonate forms a minor component of the mudstones either in the form of diffuse calcareous horizons up to 1 m thick or as small (<2 cm) isolated or coalesced nodules which generally occur in zones up to 0.5 m thick (Fig. 8B).

Horizons of grey and bluish-grey mudstone vary in thickness from 10 to 50 cm and generally have an irregular undulating top and an interfingering basal contact with underlying brown or reddish brown mudstones (Fig. 8A). Residual patches of brown or reddish brown mudstone are common in the grey horizons. Grey mudstones are generally clayey siltstones with a massive blocky structure and common rootlets. At Boroviki, grey mudstones occur in several clusters of up to 5 beds over an interval of several metres.

Dark red mudstones occur in two parallel beds spaced 1 m apart at the base of the exposure close to (summer) river level and can be traced laterally over several kilometres in the Boroviki area (Fig. 7). The thickness of the dark red units ranges from a few decimetres to 1 m and they contain rootlet structures, small centimetre-scale carbonate nodules and patches or mottles of grey or bluish grey mudstone. The dark red mudstones are relatively clay-rich, with clays often forming slickensided coatings on the exterior surfaces of angular blocks.

The stratigraphically higher dark red mudstone is notable for the development of a sharp erosional upper surface that forms a series of scours that partially or entirely cut out the bed (Fig. 8C, D). Scours vary from broad (several 10s of metres) and shallow to narrow and relatively steep sided and are infilled by pale brown mudstone which, in addition to being a markedly different colour from the underlying dark red mudstone, does not show the development of extensive rooting and carbonate nodules. Pareiasaur skeletal remains are commonly found within the scour-filling pale brown mudstone, and this single layer 3–4 m below the sandstones of the Boroviki Member (Figs. 3, 7) has produced most of the articulated reptile fossils formerly assigned to the Kotelnich-1 locality, although skeletons are found at all levels, both above and below the palaeosol horizon, and even below the Vyatka River water line. The majority of the

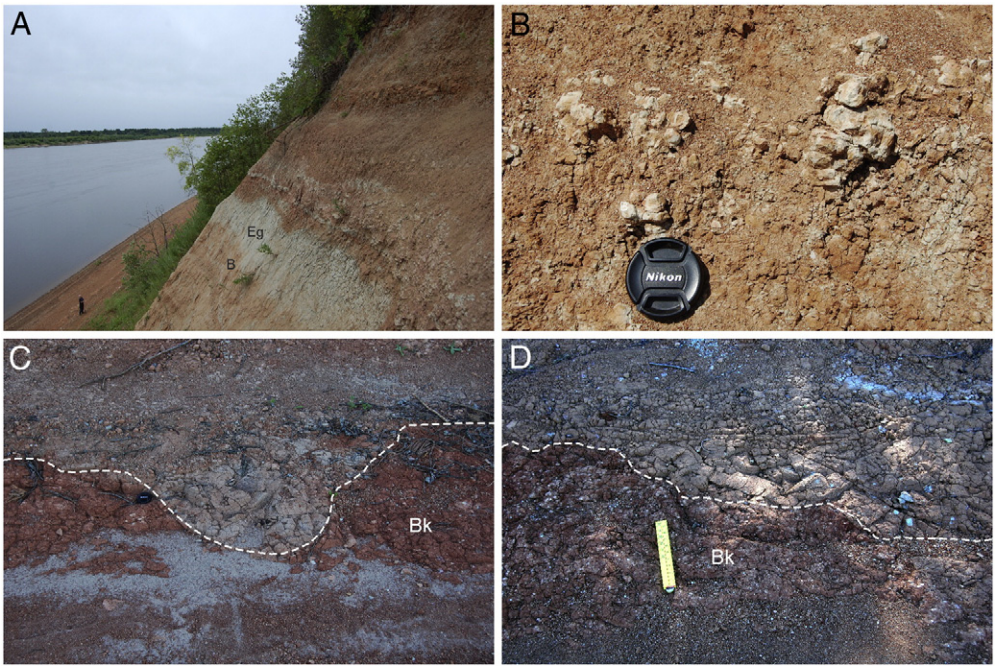

Fig. 8. Photographs showing typical features of the Vanyusonki Member mudstones, (A) alternation of pale brown, grey and moderate reddish brown mudstones, (B) small coalesced carbonate (calcrete) nodules, (C) undulating scour infilled with pale reddish brown mudstone cut into dark reddish brown mudstones with small carbonate nodules and grey mottles and (D) sharp erosional contact between pale brown mudstone above and dark reddish brown mudstone below.

finds by Sumin from 1990 to 1992 came from this level near the village Boroviki, but some from near the village Mukha (Ochev, 1995). The scours or hollows containing pareiasaurs are roughly circular in plain view, as determined from individual excavated skeletons, but it cannot be demonstrated that all skeleton-bearing hollows are circular; some might also be channel-shaped. Skeletons are usually intact, but sometimes the lenses contain clusters of well-preserved bones. The bones are either red-brown or chocolate-black in colour, excellently preserved, and with an internal calcite filling. The taphonomy of these remarkable tetrapod finds is discussed in detail below (Sections 7.3, 7,4).

The mudstones contain a number of thin sandstone beds that are usually only a few decimetres thick, but can reach 1.5 m. The sandstones are mostly fine-grained, massive and have sharp lower and upper boundaries. Coffa (1999) reported 16 fossil tree stumps measuring from 0.15×0.05 m to 0.4×0.3 m from some of the sandstone beds. The wood was carbonised and compressed and oriented in various directions, but with a strong west–east component.

6.2.2. Interpretation

The mudstones of the Vanyushonki Member were probably deposited from suspension in standing water bodies on floodplains or in shallow ephemeral lakes, but the precise environment cannot be determined because of the general absence of primary sedimentary structure. The presence of pareiasaurs, plant fossils, and ostracods indicates a terrestrial or freshwater environment, with the common occurrence of rootlets, carbonate nodules (calcretes) and colour horizonation suggesting that deposition was episodic with many extended periods of subaerial exposure and soil formation which obliterated most of the primary structure. The predominant brown and reddish brown colouration of the mudstones results from oxidation of iron-bearing minerals during weathering in soils that must have been relatively well drained between depositional events, although common grey and bluish grey mottles and horizons suggest phases of poor drainage and redoximorphic conditions.

The two laterally extensive dark red mudstones that occur toward the base of the outcrop at Boroviki are distinctive parts of the stratigraphy (Fig. 7). They are relatively clayey with nodular accumulations of calcium carbonate and red iron oxides and probably represent the illuvial (Bk) horizons of moderately developed palaeosols that formed during long breaks in sedimentation. Centimetre-scale, micritic carbonate nodules probably represent pedogenic calcretes, given their association with rooted and colour-variegated horizons and these typically form in well-drained soil profiles in sub-humid, semi-arid and arid climates (Alonso-Zarza, 2003). Given the presence of carbonate nodules and the common development of clay coatings around peds, the palaeosols could be classified as calcic Argillosols or Calcisols (Mack et al., 1993). The upper palaeosol horizon is spectacularly incised by a series of shallow scours which are infilled by pale brown mudstones which, although massive, lack the relatively mature pedogenic features of the underlying bed and were probably deposited rapidly from floodwaters with a high suspended load in the gullied landscape. Scour systems within successions of floodplain mudstones are not uncommon (Kraus and Middleton, 1987), but generally require a colour contrast in the eroded and infill materials to be recognised. At Boroviki these scour fills formed preferential sites for the burial and preservation of pareiasaur skeletons. Microtopography has an important control on the distribution and rate of sedimentation across floodplains because lows tend to form the sites of recession pondage with higher rates of deposition (Walling and He, 1998). High rates of sedimentation are an important factor in the preservation of terrestrial vertebrates because burial prevents skeletal remains being destroyed by scavenging or subaerial weathering.

Grey and bluish grey bleached mudstones occur as haloes around roots, small mottles and patches within reddish brown mudstones and as more continuous horizons (Fig. 8A). Grey colours generally denote the depletion of non-silicate-bound iron under redoximorphic conditions and they probably represent eluvial-gley (Eg) horizons developed in the upper part of the soil profile. Yakimenko et al. (2004) describe closely comparable grey Eg horizons in Upper Permian palaeosols from the Sukhona River in the northern part of the Russian platform. Gleying typically results from a raised water table or from impeded drainage within the soil profile and appears to contradict the evidence for well-drained conditions suggested by the predominant red or brown colouration of the mudstones, lack of organic preservation, common rooting and presence of calcretes. Yakimenko et al. (2004) explain the coexistence of oxic and redoximorphic features by postulating a strongly seasonal, semiarid climate, together with the possibility that precipitation fluctuated on a longer time scale.

Mudstones of the Vanyushonki Member contain several metre-thick beds of fine-grained sandstone that are generally sharp-based and massive. These were probably deposited from relatively unconfined flows, which distributed water and sediment across the flood basin. One sandstone toward the top of the exposure shows a well-developed upward-fining sequence from a basal intraclast conglomerate, through trough cross-bedded sandstone to a crudely laminated mudstone that contains much plant material. This probably represents a minor channel fill with the abandoned channel forming a long lasting water hole, which allowed the accumulation and preservation of plant material. The abundance of rootlets and large herbivores suggests a relatively humid and well-vegetated landscape.

6.3. Boroviki Member

6.3.1. Description

Coffa (1999) named this unit after the village of Boroviki, 15 km south of Kotel'nich on the west bank of the Vyatka River. It lies conformably above the Vanyushonki Member. The sandbody reaches a maximum thickness of around 16 m thick at Boroviki and can be traced over a distance of 10 km along the west bank of the Vyatka River from Zemtsy in the south to Kuznetsy in the north (Figs. 2, 3, 7).

The Boroviki Member is a body of pale orange, weakly cemented, fine- to medium-grained sand. The sandstones are compositionally mature with high quartz content (more than 65%) and a uniform grain size, with more than 90% of grains in the size range 0.05–0.5 mm, with only 8.5% in the clay fraction as measured by Tverdokhlebov and Shminke (1990). The sandbody has a relatively flat, or in places gently downcutting, base and a convex-up top, pinching out laterally into adjacent mudstones. Internally the sandbody is characterised by a range of bedding types. To the south, around log position 2 at Boroviki (Fig. 2) the sandbody is 10 m thick and dominated by large-scale, low-angle (15–20°) cross-bedded sandstone in thick wedge-shaped sets (Fig. 9A) with distinctive pinstripe laminae (Fig. 9B) and thin granule lags. Further north at log position 3 (Figs. 7, 10B) the basal part of the sandbody comprises small-scale trough cross-bedded sandstone with occasional thin rooted mudstones (Fig. 10), while the upper part includes low-angle laminated sandstone and large-scale cross-bedded sandstone with foresets dipping toward 050°. The unit may be capped by pale blue fine-grained sandstone, 0.4 m thick, corresponding to Bed 4 of Golubev (2000).

6.3.2. Interpretation

The Boroviki Member has many features that suggest a predominantly aeolian origin, including the well-sorted, friable texture of the pale orange sandstones, presence of large-scale cross bedding, well-developed pinstripe lamination, deflation granule lags and frosted, pitted quartz grains (Coffa, 1999). There is a corresponding absence of features suggesting a predominantly fluvial origin such as large-scale channel scours and mudstone intraclasts, although some of the small-scale trough cross-bedding associated with rooted mudstones at the base of log position 3 (Fig. 7) may have a fluvial origin. In

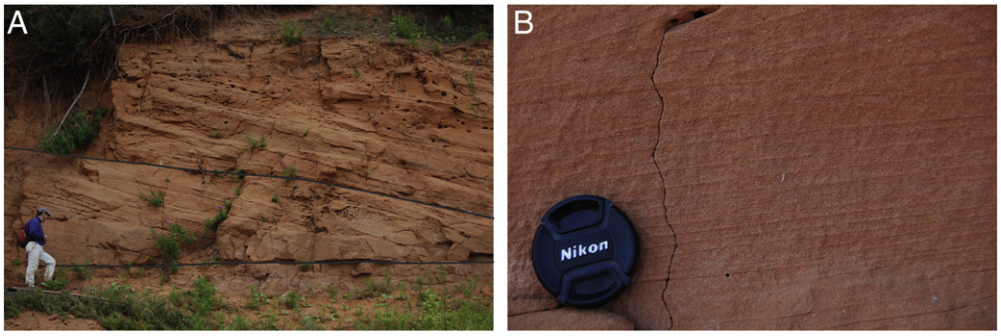

Fig. 9. Photographs showing typical features of the Boroviki Member in the southern part of the outcrop near logged Section 2 (see Figs. 2 and 7), (A) wedge-shaped sets of low-angle cross-bedded, friable, fine-grained pale orange sandstone, and (B) sandstone with well-developed, low angle pinstripe lamination probably deposited by migrating wind ripples.

the first sedimentological description, Ignat'ev (1963) interpreted the Boroviki sandstones as fluvio-deltaic, and the aeolian interpretation was given first by Tverdokhlebov and Shminke (1990), and accepted by Coffa (1999) and Tverdokhlebov (2009). Cross-stratification azimuths indicates a general wind direction from the west (Coffa, 1999), with most of the steeper foresets inclined toward the northeast.

The geometry and internal structure of the sandbody suggest that it developed as a localised aeolian erg in a floodbasin setting. Thick accumulations of aeolian sands in the upwind (SW) portion of the erg pass downwind into flanking areas where the sandbody contains a mixture of fluvial and lacustrine facies. The predominance of relatively low-angle wind-ripple lamination over steeply dipping aeolian avalanche strata may indicate a relatively wet aeolian system, with a high groundwater table and limited sand supply suppressing the construction of large dunes and favouring the development of low-relief sandsheets and poorly developed mounded dunes (Tverdokhlebov, 2009). Alternatively, the scarcity of steep aeolian cross-strata may reflect low rates of basin subsidence which favours the preservation of low angle dune aprons close to the water table rather than elevated parts of the dune (Fryberger, 1993). The Boroviki Member rests on a marked unconformity that cuts out 1–3 m of the underlying Vanyushonki Member, indicating a phase of cessation of floodplain deposition and some erosion. The low relief of the erosion surface and the absence of overlying mudclasts suggest it results from aeolian deflation rather than fluvial processes.

6.4. Shestakovy Member

6.4.1. Description

Coffa (1999) named the succession of reddish brown and grey mudstones lying above the Boroviki and Vanyushonki members the 'Shestakovo Member' after the village of Shestakovy, 5 km south of Kotel'nich on the west bank of the Vyatka River. We change the name from Shestakovo to Shestakovy to match the direct linkage of place name and stratigraphic unit, as with all the other member names. The mudstones of the Shestakovy Member are laterally continuous throughout the 20 km exposed southern section, and it may extend to Port Kotel'nich (see Section 6.7). Member thickness varies from 5 m to a maximum thickness of 20 m at the southernmost extent of the section, 18 km south of Port Kotel'nich. In the southern part of the section, the Shestakovy Member can locally be divided into two, the Shestakovy-1 and Shestakovy-2 divisions, lying respectively below and above the Chizhi Member, an intermittent plant-rich sandstone lens (Figs. 3, 7). Where the sandstones of the Boroviki Member are absent it is difficult to define the bottom of the Shestakovy Member because there seems to be no interruption in the sequence of fine-grained red sediments.

The primary lithology of the Shestakovy Member is similar to the Vanyushonki Member, with a predominance of pale brown or reddish brown mudstone, commonly grey mottled, alternating with irregular horizons of pale grey mudstone (Fig. 8A). The mudstones are generally massive and blocky, with common calcrete nodules and evidence of rootlets and bioturbation. Fragments of the pareiasaur *Deltavjatia* have been found. Fine-grained sandstone beds, generally less than 1 m thick, occur throughout, and these are largely massive but occasionally show a discontinuous horizontal lamination.

6.4.2. Interpretation

The Shestakovy Member indicates a return to shallow lacustrine or floodplain conditions, similar to the Vanyushonki Member. The combination of red, oxidised mudstones with calcrete and grey reduced mudstones indicates fluctuating drainage conditions. The thin beds of sandstone have been interpreted by Tverdokhlebov (2009) as distributary channels within an inland delta or terminal fan.

6.5. Chizhi Member

6.5.1. Description

Coffa (1999) named this the 'Chizhy Member' after Chizhi, a khutor, or one-settlement village, that is closest to the member, 12.8 km south of Kotel'nich on the west bank of the Vyatka River. The unit had been termed the Chizhebekaya Lens by Russian geologists. We correct the spelling from Chizhy to Chizhi to match the spelling of the village name, and as used by Russian geologists. The member is a laterally isolated lens with a thickness not greater than 8 m. In places, it cuts down into the Boroviki Member (Figs. 3, 7).

At the base the lithology is a grey, fine-grained sandstone that overlies an erosion surface covered in reworked mudstone clasts. This passes upward into crudely laminated grey mudstone with abundant comminuted plant and fish debris.

The unit has yielded a rich macroflora, consisting of carbonised tree stumps, fossilised leaf impressions, and a palynoflora consisting of pollen and spores (Golubev, 2000). The plant fossils reported (Goman'kov, 1996, 1997) are *Algites* sp. AVG-1, *Phyllotheca* aff. *Turnaensis*, *Paracalamites* sp., *Pecopteris* sp. AVG-1, *Peltaspermopsis* (?) sp., *Permotheca sardykense* Zalessky, *Alicospermum* sp., *Tatarina conspicua* Meyen, *Persongia beloussovae* (Radczenko) Gomankov et Meyen, *Phylladoderma* (*Aequistomia*) sp. indet., and *Geinitzia* sp. These are associated with fish remains, mostly scales, from the organic-rich mudstones near the top of the lens, identified as the actinopterygians *Platysomus biarmicus* Eichwald, *Toyemia tverdochlebovae* Minich, *Amblypterina* sp., and *Watsonichthys* sp., as well as 'Crossopterygii fam. indet.' (Esin, 1995; Esin and Mashin, 1998). Pareiasaur teeth with 13, instead of 11, cusps, as well as flat osteoderms were found in the Chizhi lens in 2009, and these resemble *Scutosaurus* ('*Proelginia*') rather than *Deltavjatia*. Further remains include *Suminia* teeth, a therocephalian tooth, teeth and a maxilla with teeth from a gorgonopsian, a canine tooth and vertebra of a dicynodont, and fragments of chroniosuchid osteoderms. These tetrapod fossils, especially the *Scutosaurus* remains,

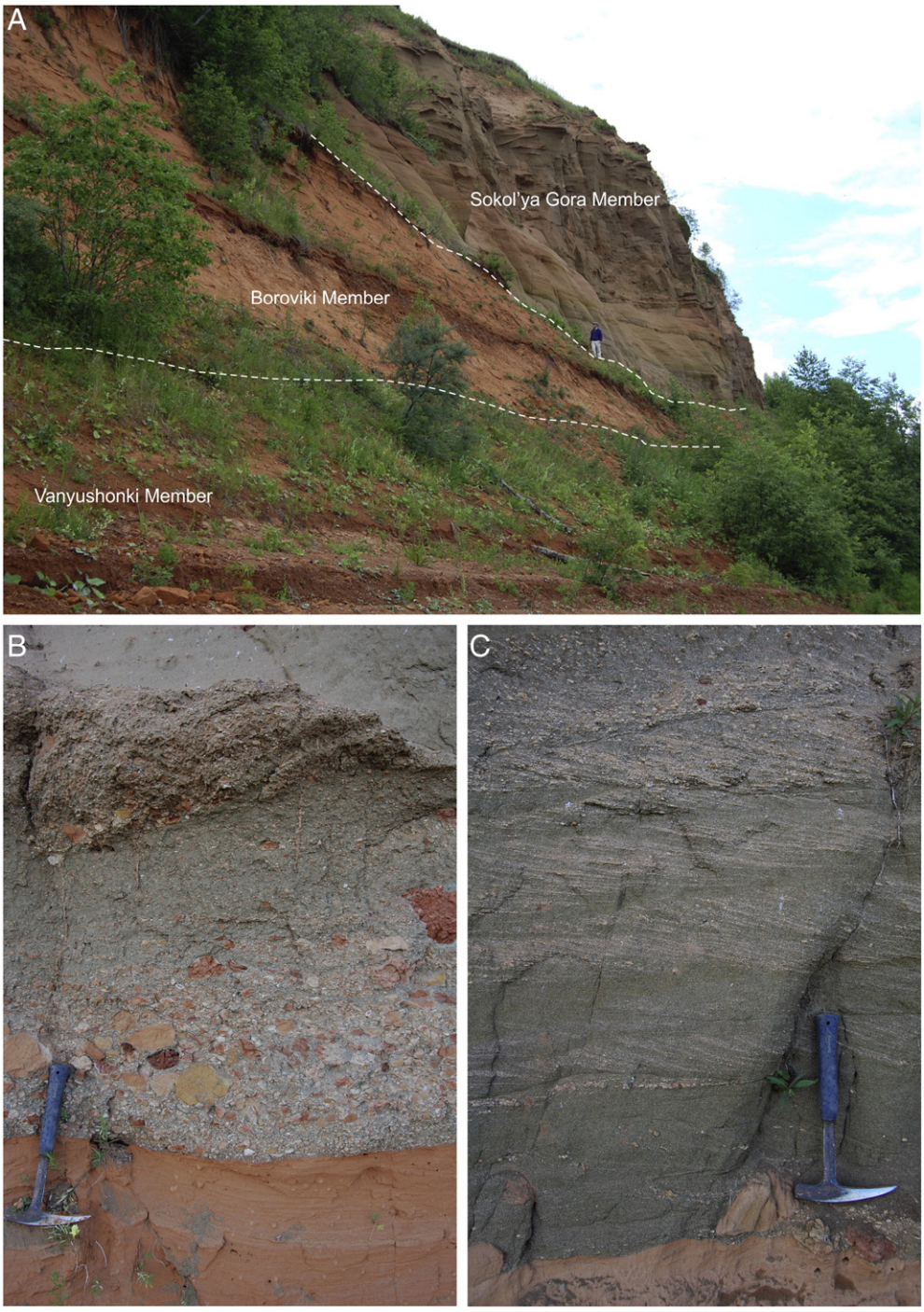

Fig. 10. Photographs showing typical features of the Sokol'ya Gora Member fluvial sandstones, (A) large-scale stratigraphic relationships near logged Section 3 (see Fig. 2 for location) showing fluvial sandstones of the Sokol'ya Gora Member overlying a high-relief erosion surface cut into pale orange aeolian sandstones of the Boroviki Member. Mudstones of the Vanyushonki Member form the base of the exposure, (B) sharp erosion surface between the brownish grey fluvial sandstones Sokol'ya Gora Member above and the pale orange sandstones of the Boroviki Member below. Basal parts of the Sokol'ya Gora Member contain many large, well-rounded mudstone and sandstone intraformational clasts (C) small to medium sets of trough cross bedding in grey sandstones of the Sokola Gora Member erosively overlying orange sandstones of the Boroviki Member.

suggest the Chizhi lens assemblage equates with that from the Sokol'ya Gora Member.

6.5.2. Interpretation

This discontinuous, erosively-based and upward-fining lens probably represents a channel fill which following abandonment, for example by meander cut-off, formed a relatively long-lived pond with poorly oxygenated bottom conditions which accumulated grey laminated mudstones and plant material. The abundant fish remains confirm a subaqueous environment and together with the plant taxa and point toward fluviolacustrine conditions (Goman'kov, 1996, 1997).

6.6. Sokol'ya Gora Member

6.6.1. Description

Coffa (1999) named this unit after the most prominent sandstone lens of the member, called Sokol'ya Gora (='falcon rock'), located

18 km south of Kotel'nich (Figs. 2, 3). A maximum thickness of 90 m is measured from the top, but this full thickness is preserved only north of Kotel'nich. It lies unconformably above the Shestakovy Member. The name has been given as 'Sokolya-gora' (e.g. Coffa, 1999), but we correct it to the place name as used by Russians.

The Sokol'ya Gora Member comprises several individual bodies of grey and brownish grey, fine-medium grained sandstone that occupy spectacular scours cut into the pale orange aeolian sandstones of the Boroviki Member and the fluviolacustrine mudstones of the Vanyushonki Member (Fig. 7). At Boroviki there are two major scour-filling grey sandstones that are up to 25 m thick and extend laterally for several hundred metres (Fig. 3). The sides of the scours are remarkably steep (Fig. 10A) and locally undercut. Flow direction, determined from cross-sets exposed in three dimensions, is generally toward the west so the north–south orientated exposures at Boroviki represent a cross section perpendicular to the elongation direction of the sandbodies. The sandstones are fine- to medium-grained, locally highly micaeous, and at the base contain large reworked clasts of mudstone and pale orange sandstone up to 30 cm in diameter (Fig. 10B). Internally the sandbodies are dominated by sets of trough, and occasionally tabular cross bedding, which are typically 0.1–0.3 m thick but can reach 1 m thick (Fig. 7). These are typically grouped into cosets 1–2 m in thickness (Fig. 10C), which may have a basal erosion surface overlain by an intraclast conglomerate. Some cosets are capped by thin units of highly micaeous, flat-laminated fine-grained sandstone. Convolute bedding is common in the centre of the sandbody exposed at log position 3, while the tops are characterised by layers and nodules of carbonate cementation and interbedded reddish brown mudstones.

Rare, disarticulated fossil bones and occasional bivalves are found in the fluvial sandstone of the channels. The tetrapod remains have been identified as *Chroniosuchus levis*, *Proelginia* cf. *permiana* (=*Scutosaurus karpinskii*), *Proburnetia viatkensis*, and *Dvinosaurus primus*, all typical of the Il'inskoye Subcomplex, the basal Vyatkian unit (Fig. 6; Golubev, 2000, p. 87). The upper red mudstones (Golubev's bed 8) are characterised by an extensive invertebrate fossil assemblage, comprising ostracods and bivalves.

6.6.2. Interpretation

The grey and brownish grey sandstones of the Sokol'ya Gora Member show many features that suggest a fluvial origin, including an abundance of large- and small-scale scouring, intraclast conglomerates, trough cross-bedding, and abundance of mica. The sandstones were deposited in deep scours that were incised up to 25 m into the underlying aeolian sandstones and fluviolacustrine muds. The presence of numerous erosion surfaces and intraclast conglomerates within the scours suggests that these were not cut and filled in a single event but acted as long-term conduits for multiple flow events. The gradual abandonment of these flow paths is marked by decreasing grain-size and extensive carbonate cementation toward the top of the sandbodies. The westerly flow direction is consistent with the mineralogy of the sandstones, which indicates a heterogeneous metamorphic source in the Ural Mountains to the east (Coffa, 1999). These sandbodies appear to have been deposited by major fluvial distributary channels carrying water and sediment hundreds of kilometres from their Uralian source far west onto the Russian Platform.

6.7. The Port Kotel'nich section

An excellent high exposure of red beds is seen at Port Kotel'nich, and it extends 400 m south to Gorodishe (Figs. 2, 4B, 7). The site was excavated from 1990 onwards, and over 70 skeletons and bone associations were discovered, nearly all of them dicynodonts (Kurkin, 2000, 2011). Most of the Port Kotel'nich section comprises relatively homogeneous pale brown and reddish brown mudstones with grey mottling and calcrete nodule horizons at regular intervals (Fig. 7). However, toward the middle of the section, immediately below the dicynodont site, the mudstone is interrupted by a sharp-based sandstone bed, 0.1–0.5 m thick, which is predominantly grey at the base and dark red toward the top. Carbonate concretions become common at the top of the sandstone bed. The top contact with the overlying mudstone is sharp and planar. The sandstones do not contain any fossils, and these are concentrated in the 2 m of mudstone immediately above the sandstone bed.

The Port Kotel'nich section might relate to the main Kotel'nich (southern) section in one of three ways: (1) it could be a lateral equivalent of the Shestakovy Member, as Goman'kov (1997), Coffa (1999), and Golubev (2000) argued, (2) it could be a lateral equivalent of the Vanyushonki Member, also a red mudstone unit and at the base of the main section (Figs. 3, 7), or (3) it could be something else altogether. Poor exposure between Port Kotel'nich and the main section makes it hard to walk out the section and confirm the correlation unequivocally. Coffa (1999) noted that the basal 'sandwich layer' of the Shestakovy-2 Member in the northern part of the Kotel'nich section disappears underground because the bedding dips up-river. Through the lack of recognisable marker horizons, investigators assumed that the site corresponded to the highest facies of the Vanyushonki Member, but detailed observation of the outcrop south of Gorodishe revealed that the base of the Shestakovy-2 Member could be traced along the lower part of the Vyatka River bank. In a bank exposure cleared by a creek just south of the dicynodont site at Port Kotel'nich, the most northern appearance of the 'sandwich layer' was observed, only 1.5 m higher than the water level of the Vyatka River during the summer of 1997 (Coffa, 1999).

We confirm the view presented by previous authors, that the base of the Port Kotel'nich section lies within the Shestakovy Member, but the correlation of the top is debated. Goman'kov (1997) presents the most thorough case, using the 200-m deep SKV-1 borehole at Kotel'nich (Ignat'ev, 1962, pp. 222–223) to provide the link from the southern Kotel'nich section (Fig. 3) to that at Port Kotel'nich (Fig. 7): he correlates the borehole depth 83.8 m with the top of the Chizhi Member, and the ground surface roughly with the Sokol'ya Gora Member, even though that conglomeratic unit is represented only by a thin band in Goman'kov's section. Then, he argues that the Port Kotel'nich section is higher, with the base equivalent to the Shestakovy-2 Member, and the 15-m borehole depth matching a transition from siltstone to sandstone near the base of the Port Kotel'nich section. Golubev (2000, p. 118) also makes the Port Kotel'nich section equivalent to his bed 6 (=Shestakovy Member), and places it below his bed 7 (=Sokol'ya Gora Member). As Goman'kov (1997) indicates, regional dips mean that it is perhaps not appropriate to assume that the Port Kotel'nich section (Fig. 7) simply sits in its entirety on top of the Sokol'ya Gora Member, but that much of it is laterally equivalent to those upper members.

6.8. Synthesis of depositional systems shown in the Kotel'nich exposures

The Permian exposures south of Kotel'nich show a remarkable range of sedimentary facies within a relatively thin stratigraphic interval and include mudstones deposited in shallow fluviolacustrine environments that were subject to numerous episodes of sub-aerial exposure and soil development, aeolian sandstones, and deeply-incised fluvial channel-fills. The environmental story recorded by the Kotel'nich outcrops starts with relative geomorphic stability and the formation of mature and laterally-extensive dark red, rooted palaeosols with calcretes on what must have been a well-vegetated and well-drained floodplain (basal Vanyushonki Member). This phase of stability was brought to an abrupt end by a high magnitude flood event that scoured the surface of the floodplain and deposited a layer of mud, which was locally of sufficient thickness to encase and preserve many complete pareiasaur skeletons. Further aggradation of fluviolacustrine mudstones was terminated by the development

of a local aeolian dune field (Boroviki Member), which migrated across the eroded surface of the former floodbasin. It is uncertain whether this was caused by a change toward greater climatic aridity, or simply a shift in the position of the active floodbasin away from Kotel'nich. The return of fluviolacustrine sedimentation to the Kotel'nich area is initially marked by mudstones (Shestakovy Member) and thin channel sandstones (e.g. Chizhi Member), but then by the incision of major fluvial conduits (Sokol'ya Gora Member), which eroded deeply into underlying deposits. These westward-flowing rivers probably record the abrupt shift (avulsion) of channels into the Kotel'nich area, which may have been cutting a pathway through the Kotel'nich depositional lobe to establish new floodbasins at more distal, topographically lower, locations on the Russian platform.

7. Kotel'nich tetrapod assemblages

7.1. Tetrapod-bearing horizons

As noted earlier, tetrapod fossils occur at three levels in the Kotel'nich section. The isolated detrital bones in the plant-bearing mudstone conglomerates of the Chizhi lens and the basal intraclast conglomerates and cross-bedded sandstones of the Sokol'ya Gora Member are not further considered here. Their preservation is uncontroversially explained as a result of high-energy channelized flows that entrained or reworked carcasses or isolated bones from older bank materials, as well as plants and invertebrates in certain cases, and transported them some distance before burial.

Here, we focus on the preservation of complete skeletons, and there are two occurrences:

(1) The great majority of fossil tetrapods from Kotel'nich come from the Vanyushonki Member, the basal red mudstones, and they are typically labelled 'Kotel'nich', even though most come from locations some distance south of the town. Further, the majority of recent finds, from the 1990s onwards, have come from this level, along the west bank of the Vyatka River from Zemtsy to Shestakovy villages (Figs. 2, 3).
(2) The lower parts of the red mudstones at Port Kotel'nich have also produced fossil tetrapods, namely the dicynodontid *Tropidostoma* and the pareiasaur *Deltavjatia* cf. *vjatkensis*.

Recent collecting, since 1990, has yielded more than 390 skeletons and partial skeletons of tetrapods, of which 290 come from the Vanyushonki Member (Table 1; Modesto and Rybczynski, 2000; Fröbisch and Reisz, 2009). The fauna is dominated numerically by herbivores, comprising 79% of the specimens, and small numbers of the insect-eating *Emeroleter* (5%), as well as small (12%) and large (3%) carnivores. Among herbivores, there are numerous articulated skeletons of the larger pareiasaurs (52%) and the small *Suminia* (27%).

Ochev (1995, p. 57) reported on the skeletons collected from the Vanyushonki Member:

> '… most of the skeletons are concentrated at levels that are located in bone-bearing deposits, from 3 to 4 m below the overlying sandstones [of the Boroviki Member]. In addition to numerous individual skeletons in varying degrees of preservation, at Kotel'nich were also found several clusters of isolated bones of several individuals, among which sometimes co-exist relatively large remains of pareiasaurs and smaller animals, therapsids. It is possible that some of these clusters, occurring in the laminated rock, were formed by the movement of bone flows.'

In the description below, we deal first with the preservation of the Port Kotel'nich dicynodonts, then the smaller skeletons in the Vanyushonki Member, before focussing on the extraordinary preservation of complete pareiasaur skeletons in the Vanyushonki Member.

Table 1
Faunal composition of the Kotel'nich locality, Russia (Vanyushonki Member), based on collections made since 1990. Abbreviations: Del, *Deltavjatia*; Eme, *Emeroleter*; Insect., Insectivores; Sum, *Suminia*; The, Therocephalia; Via, *Viatkogorgon*. * means unknown number of skeletons in accumulations. Table from Il'ya Shumov, updated from version in Fröbisch and Reisz (2009). Additional identified materials come from other localities and members, as follows: Port Kotel'nich: the dicynodont *Australobarbarus* (83 specimens, collected as follows: 1991 (2), 1992 (32), 1993 (12), 1994 (3), 1995 (1), 1996 (1), 1997 (26), 1998 (3), 2002 (1), 2009 (2)); Shestakovy Member (*Deltavjatia*, 3, collected 1995, 2002, 2008; Dicynodontia indet.,1, collected 2008); Chizhi Member (one *Scutosaurus* collected 2007; all others 2009: *Scutosaurus*, 2; *Suminia*, 1; Dicynodontia indet., 1; gorgonopsian, 2; *Chroniosaurus*, 1); Sokol'ya Gora and Agafonovo lens (*Scutosaurus*, 1 [1996]; Therocephalia indet., 4 [1995–6]; *Dvinosaurus*, 1 [1996]; *Chroniosaurus*, 1 [1996]), and Iskra, 7 km north of Kotel'nich (Dicynodontia indet., 1 [1995]).

Diet	Herbivores		Insect.	Carnivores	
Year	Del	Sum	Eme	The	Via
1990	14	4	–	–	–
1991	18	1	–	1	–
1992	16	10*	1	2	2
1993	7	5	2	3	–
1994	18	13*	2	7	1
1995	7	2	2	5	–
1996	6	1	–	3	1
1997	2	*	1	–	–
1998	6	5*	3	2	2
1999	10	22*	–	3	–
2000	11	3	–	5	–
2002	5	2	1	–	–
2004	6	1	–	–	1
2005	2	2	2	–	1
2006	3	–	–	–	–
2007	9	3	2	2	–
2008	3	3	–	2	1
2009	3	1	–	–	–
2010	3	1	–	1	–
Totals	149	79	16	36	9
Totals (%)	51.6	27.3	5.5	12.5	3.1
Diet grp. (%) [289]	78.9		5.5	15.6	

7.2. Dicynodont skeletons at Port Kotel'nich

At the Port Kotel'nich locality, probably within the Shestakovy Member (see Section 6.7), numerous dicynodont skeletons (*Australobarbarus*) were excavated in the early 1990s (Kurkin, 2000). All 86 skeletons came from a single layer about 0.5 m thick. Some of the remains were individual pieces, such as isolated skulls or jaws, and other elements. However, many of the finds were complete skeletons often forming clusters, consisting of the bones of one or two individuals. Some showed an unusual orientation of the skull and skeleton, as if the skull had been anchored in the sediment by the canine teeth, and the postcranial skeleton moved more freely in the flowing water. In one case, a dicynodont skeleton was found lying on its right side, with its legs underneath. Another skeleton was buried in an inverted position, with the backbone arched. Entirely unlike the pareiasaur skeletons in the Vanyushonki Member, there is only one case of a large specimen of a dicynodont found standing on its legs, as if preserved in life position. The abundance of thin layers of sandstone in the clay marl with the remains of dicynodonts, as well as the large number of calcareous concretions and pellets indicate that these carcasses had all been transported to a greater or lesser extent, presumably by rivers, and then dumped in waning currents.

7.3. Taphonomy of therapsid skeletons in the Vanyushonki Member

The smaller reptiles in the Vanyushonki Member are found either as isolated pieces or, in the case of *Suminia*, sometimes as assemblages of skeletons, a monotaxial, monodominant bonebed (Eberth et al., 2007). Ochev (1995, p. 57) noted further: 'The death of the *Suminias* took place in their life positions — with their backs looped by bending the body. The theriodont died, fell on his side and stiffened, with the backbone straightening, the legs and tail outstretched, and with the head

lightly bent down. These poses quite definitely indicate a place of death near the burial spot.' Fröbisch and Reisz (2009) illustrate a remarkable block containing at least 15 individual *Suminia* skeletons (PIN 2212/116; Fig. 11), and they note that the skeletons were well preserved and show little sign of weathering, predation, or scavenging, and so were presumably buried rapidly, 'possibly as a result of a catastrophic event'. Six of the 15 identified skeletons (specimens 1–5, 11) are approximately aligned, with two curled up (specimens 6, 12), two roughly at right angles (specimens 10, 13), and five incomplete and uncertain (specimens 7–9, 14, 15). Of the ten specimens whose orientations can be measured, all have the head oriented from 0 to 180°, and six have the head oriented from 0 to 60°; none of the specimens is oriented in the 180–360° quadrants. The rose diagram (Fig. 11C) has a mean orientation of 68.84° for all ten specimens, and the orientations are non-random, indicating a preferred orientation ($R = 0.636$, $p = 0.014$; chi-squared = 13.2, $p = 0.004$).

The alignment of skeletons may have been produced by current flow at the site of death or following short-distance transport. The incomplete specimens may have lost bones by current winnowing. Despite Ochev's (1995) suggestion that the various straight-backed

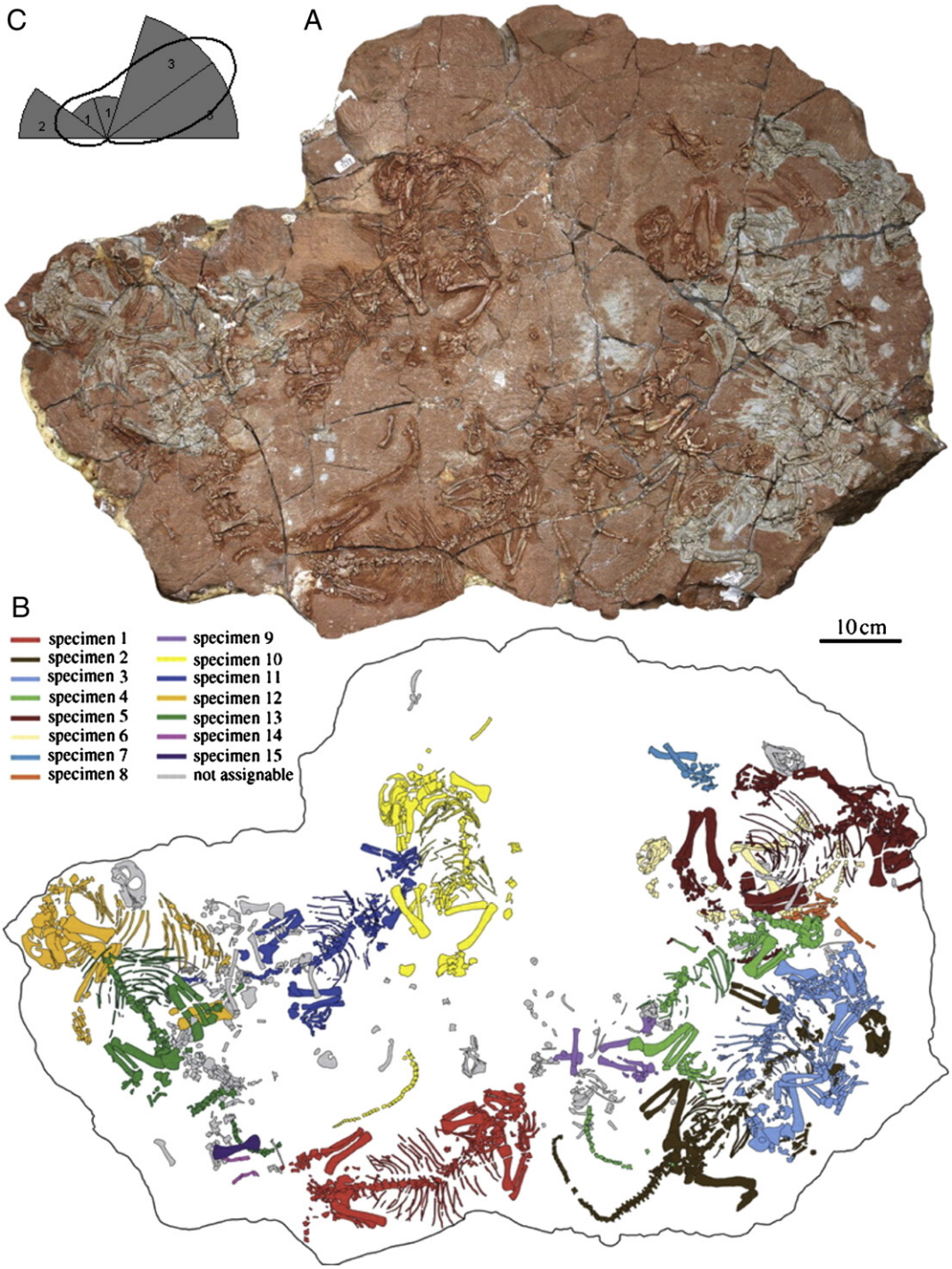

Fig. 11. *Suminia getmanovi*, large block with articulated skeletons. (A) Photograph and (B) colour-coded outline drawing of PIN 2212/116, showing the presence of at least 15 specimens. (C) Rose diagram, showing distribution of the ten specimens (numbers 1–6, 10–13) for which orientations could be assessed; orientations were measured as the angle of a straight line aligned with the dorsal vertebral column, from pelvis to neck, measured in degrees from zero (pointing right).

and curved skeletal postures indicate death positions, it is not clear that these features can be used to distinguish such an interpretation from the more likely suggestion that the carcasses were transported, or moved and winnowed, under the influence of water currents.

7.4. Taphonomy of pareiasaur skeletons in the Vanyushonki Member

7.4.1. Description

The numerous complete pareiasaur skeletons from Kotel'nich have attracted most attention in previous accounts. First, the key features of these skeletons from the Vanyushonki Member will be enumerated, and then the most likely model for their preservation will be developed, by comparing a range of possible models.

The Kotel'nich pareiasaur skeletons, most of which occur at one horizon in the Vanyushonki Member, show a number of characteristics: (1) the skeletons all sit in hollows scoured into a palaeosol surface; (2) there is usually just one – sometimes two – skeletons per hollow; (3) the skeletons are remarkably complete and articulated; (4) the skeletons are almost never belly-up; (5) the bones sometimes show evidence of exposure; (6) the animals are of uniform size, and small; and (7) pareiasaurs were terrestrial herbivores. These observations will be explained further.

(1) *Skeletons all sit in hollows on a palaeosol surface*: The preservation of complete pareiasaur skeletons is unusual and localised. They occur in mud-filled hollows, the majority of them on a single palaeosol horizon, some 3–4 m below the contact with the overlying sandstones of the Boroviki Member (Figs. 3, 7), a fact noted before (Ochev, 1995; Tverdokhlebov and Shminke, 1990; Tverdokhlebov, 2009). This skeleton-rich horizon is marked by a narrow bench standing out as a slightly positive feature, because the palaeosol horizon is indurated with carbonate, and it extends for several kilometres along the foreshore of the Vyatka River, close to water level (Fig. 12).
The hollows are 3–5 m wide and 1.5 m deep, and in places they are closely spaced, some 1–10 m apart, and many of the hollows at this level do not contain skeletons or bones. The hollows are infilled by pale brown, locally grey mottled, massive blocky mudstone which contrasts with the underlying dark red or reddish brown palaeosol with calcrete nodules (Fig. 8C, D). These overlying pale brown massive mudstones do not show any of the colour stratification or calcrete nodules of the underlying mature palaeosols. This suggests relatively rapid deposition. The actual process (e.g. massive sediment flows or from suspension) is impossible to determine because all the primary structure has been removed by weak pedogenesis. However, because the mudstones were only weakly modified by soil-forming processes it is likely they were deposited rapidly as a relatively thick bed.

(2) *Usually just one – sometimes two – bodies per hollow*: More than 90% of pareiasaur finds consist of a single skeleton per hollow. In 1999, two pareiasaur skeletons were found in a single mudstone-filled hollow, one lying on top of the other (KPM 234, Fig. 14E). The upper skeleton was buried with its back downwards, and the lower skeleton, preserved complete, lay beneath at the bottom of the pit, with its legs sprawled to the side and its backbone arched.

(3) *Skeletons are remarkably complete and articulated*: All older records, outlined above, and more recent excavations, have confirmed the remarkable completeness of the individual pareiasaur skeletons. Ochev (1995, p. 57) and Sumin (2009) report from their first-hand observations of the 1990–2 excavations that 23 of the skeletons were fully articulated, and nine were associated clusters of scattered bones, each from a single individual. The majority of specimens though were so complete that they retained the dermal ossicles in situ on the back and all hand and foot elements intact — commonly these small elements become detached and can be removed by low-energy currents (Eberth et al., 2007). Although most of the skeletons are in good condition (Figs. 13, 14), they all show some damage: some lack one or both hands, feet, legs, the front part of the skull or lower jaw. These small marks of damage are not a result of poor excavation, but were inflicted pre-burial either by scavenging or weathering of the carcass. Evidence for scavenging may include the discovery of a

Fig. 12. Excavation of vertebrate fossils in 2009 from pale brown mudstones of the Vanyushoni Member, erosively cut into the dark reddish brown palaeosol below. Dashed lines in (A) mark the extent of the palaeosol horizon, and the field workers are beginning to plaster a pareiasaur skeleton found in a scour on top of the palaeosol. (B) Plastered skeletons of [i]Sumnia[/i] on top of the palaeosol, ready to be lifted. The crew are excavating the next specimen, some 12 m away.

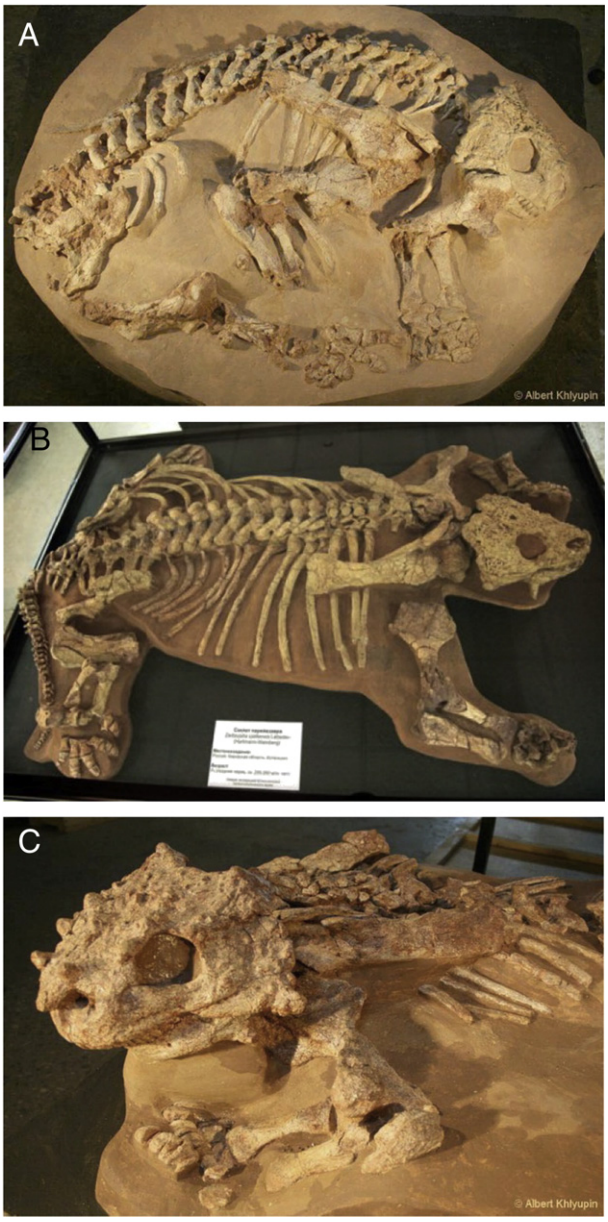

Fig. 13. Photographs of prepared specimens of *Deltavjatia vjatkensis*, as preserved: (A) skeleton lying on its side, KPM 290; (B) skeleton lying belly-down and with the limbs outstretched, KPM 232; (C) close-up of skeleton, with head and forelimbs raised, KPM 289. Photographs by Al'bert Yu. Khlyupin.

fragment of a small predator's tooth – possibly from a theriodont – found near one skeleton (Ochev, 1995), but predatory teeth are not at all as common at Kotel'nich as reported by Sander (1992), for example, around the postulated mired *Plateosaurus* of the Late Triassic.

Pareiasaur skeletons from coeval deposits elsewhere, such as those from the Sokolki locality on the banks of the North Dvina River, south of Kotlas collected by Amalitzkii in the early twentieth century are also remarkably complete (Ochev and Surkov, 2000), but these deposits were more typical fluviatile assemblages with piles of skeletons in close association within coarse channel sands.

(4) *Skeletons are almost never belly-up*: The posture of the skeletons is particularly interesting: they are nearly always preserved belly-down or on their sides. Of 14 complete skeletons recorded in situ, Ochev (1995) noted that four were lying on their sides (Figs. 13A, 14C) and eight were buried backupwards (Figs. 13B, C, 14A, B, D–H). The commonest position, with the dorsal side facing up, the head and tail down, and the limbs vertically below, with the feet down (Fig. 13B, C), led early discoverers (e.g. Hartmann-Weinberg, 1933, 1937; Kashtanov, 1934) to suggest the animals had died while standing up, and with their feet stuck in the mud. In many skeletons the vertebral column was arched — it was this feature that Hartmann-Weinberg (1937) interpreted as 'a swimming pose'. In some cases, the skeletons are at an angle to the bedding planes, with the limbs down on one side only and up on the other, or with the head and front quarters up (Fig. 13C), and the rear quarters at the base of the hollow.

These observations are confirmed by recent work in which more than 40 skeletons were observed in situ (Khlyupin et al., 2000; Khlyupin, 2007; Sumin, 2009). These authors note that most skeletons were found as if standing upright in the mud, and without any signs of transport (Figs. 13, 14). Only two specimens have been noted preserved belly-up. One (KPM 5/97; Fig. 14B) was badly damaged, suggesting that, unlike the others, this skeleton had been preserved on the flat surface, and not in a hollow, and had been predated and weathered, so causing an unusual level of damage. In 1998, near the village of Mukha, a small pareiasaur skeleton (KPM 286; Fig. 14A) was found, also lying on its back, with the limbs offset to one side and the ribs virtually absent. This partial skeleton lay in grey-coloured clay marl, containing numerous scattered bones of small reptiles and carbonised plant remains, evidence perhaps of water transport. This upright posture was noted also by Sander (1992) in his study of Late Triassic *Plateosaurus* bonebeds of central Europe.

(5) *Bones may show evidence of exposure*: In some cases, the bones appear to be bleached, perhaps suggesting that they were exposed at the surface for some time prior to burial (Ochev, 1995), but they might just as well have been altered by groundwater or diagenesis. One recently excavated specimen consisted of a well-preserved postcranial skeleton, but with a fragmentary skull lying in pieces at the front of the vertebral column. The context of the skeleton in the field suggested that the body was in the hollow and covered with sediment, while the head remained exposed for some time, when it may have been attacked by scavengers or weathered.

(6) *Animals are of uniform size, and small*: The Kotel'nich pareiasaurs all belong to one taxon, *Deltavjatia vjatkensis* (Hartmann-Weinberg, 1937), named originally as a new species of the South African genus *Pareiasuchus*. Over the years, additional species names were given to Kotel'nich material – *Anthodon rossicus* Hartmann-Weinberg, 1937, *A. chlynoviensis* Efremov, 1940 – but these all belong to the one taxon (Ivakhnenko, 1987; Lee, 2000). *D. vjatkensis* is a moderate-sized pareiasaur, about 2 m long, smaller than the other famous Russian pareiasaur *Scutosaurus karpinskii* (Amalitskiy, 1922), which is typically 3 m long. *Scutosaurus* was the first pareiasaur to be found in Russia, and *Deltavjatia* was always said to be small in comparison. This presumably gave rise to the repeated statement that the Kotel'nich pareiasaurs are juveniles (e.g. Hartmann-Weinberg, 1937; V'yushkov, 1953; Ochev, 1995), an assertion that is clearly unjustified. This casts doubt on earlier claims by these authors that the Kotel'nich site shows evidence of selective trapping of a juvenile size class and that the larger adults managed to escape because they were stronger. All that can be said is that the Kotel'nich pareiasaurs belonged to a single species, *D. vjatkensis*, and that this species was rather smaller than the geologically younger *S. karpinskii* that lived some 300 km to the north.

(7) *Pareiasaurs were terrestrial herbivores*: Pareiasaurs were stocky animals, with rather massive bodies, short legs and tails, and

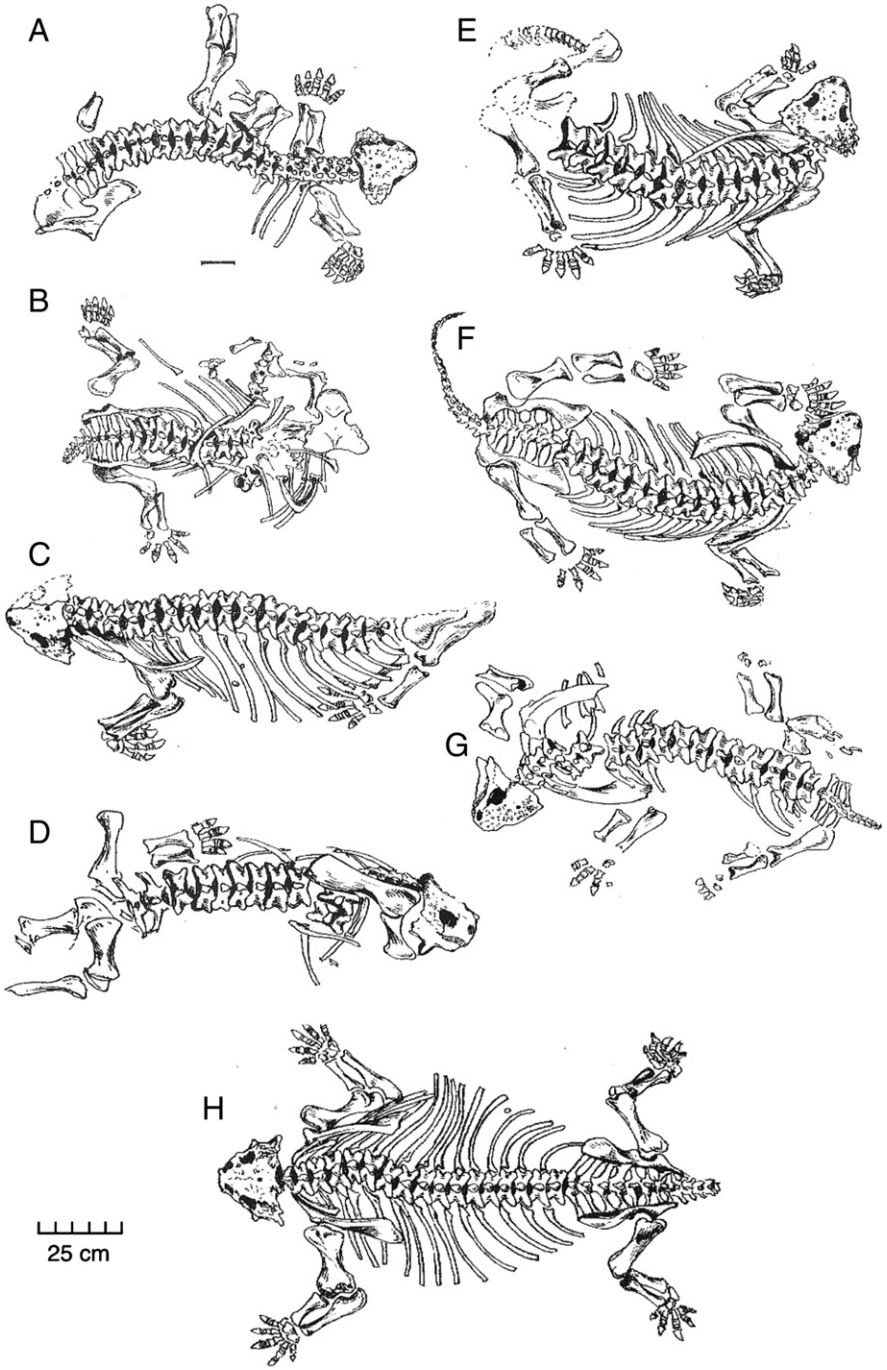

Fig. 14. Drawings of recently excavated pareiasaur skeletons from the Vanyushonki Member at Kotel'nich. Specimens are KPM 286 (A), field number KPM 5/97 (B), KPM 26 (C), KPM 23 (D), KPM 234 (E), private collection, traded by 'Stone Flower' in the 1990s (F, G), Museum "Exportsamotzvety", Moscow (H). Drawings made after collection and specimen preparation by Al'bert Yu. Khlyupin.

an armoured head (Fig. 15A). Their relatively small, somewhat leaf-shaped teeth indicate a herbivorous diet, supported also by their massive trunk capable of housing a vast gut. They ranged in length from 0.6 to 3.5 m, the larger ones weighing perhaps 600 kg. The majority of interpretation of pareiasaur palaeobiology is that these were terrestrial animals, capable of efficient semi-erect locomotion (Lee, 2000; Sumida, 2001; Fig. 15B). An alternative view was, however, promulgated by Ivakhnenko (1987), Gubin (1989), and Khlyupin (2007), that pareiasaurs were essentially aquatic, being similar to the modern dugong in spending most of their time in relatively deep water, swimming and feeding on water plants at the bottom and sides of watercourses and lakes (Fig. 15C). Evidence in favour of the terrestrial life mode and against the swimming mode comes from their limb morphology and from abundant tracks formed in the same way as the majority of other Middle and Late Permian tracks, in slightly damp, but not submerged, mud (Gubin et al., 2003; Voigt et al., 2010). *Deltavjatia* is a basal pareiasaur in phylogenetic terms (Lee, 2000), being smaller and less armoured than more derived forms.

7.4.2. Hypotheses of burial

The skeletons of the pareiasaurs at Kotel'nich largely occur in hollows on top of a palaeosol unit in the Vanyushonki Member.

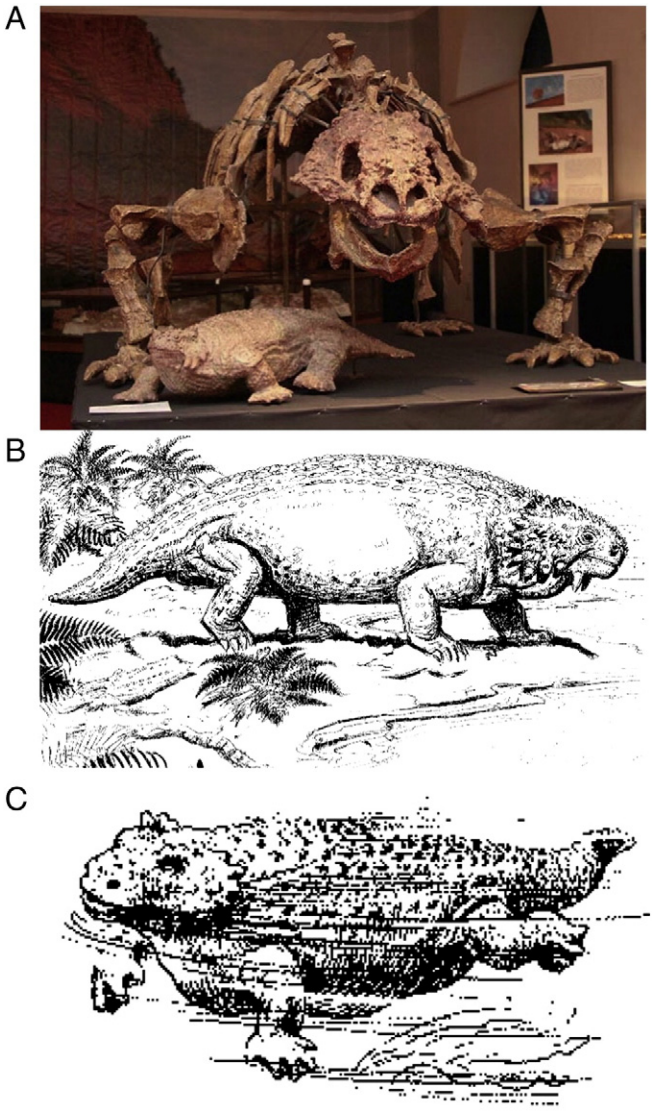

Fig. 15. The anatomy and reconstruction of pareiasaurs. (A) Mounted skeleton of the geologically younger pareiasaur *Scutosaurus* from Sokolki on the North Dvina, as mounted at PIN. (B, C) Life reconstructions, as a terrestrial (B), and aquatic, dugong-like animal (C). A, Photograph by AYK; C, drawing by Y. D. Kalganov.

The taphonomy of these strikingly complete skeletons has been interpreted in eight ways, as: (1) stuck in the mud of deep lakes; (2) killed by desertification events; (3) buried under sand dunes; (4) trapped in burrows, perhaps following hibernation; (5) carcasses dumped in fluviatile scours; (6) animals caught in hollows while digging for water; (7) animals trapped in shallow wallows; or (8) animals mired when weakened by an arid season. These eight models will be considered in turn.

(1) *Stuck in the mud of deep lakes:* Gubin (1989), who interpreted pareiasaurs as aquatic (see above), argued that their carcasses became trapped in the mud on the floor of a deep lake. He suggested that the back-upward posture of most of the skeletons, and especially those with the legs on one side down and one side up, indicated that the animals were already dead when they became stuck in the mud, and that they were not struggling to free themselves. Gubin (1989) argued that the pareiasaurs had died for any number of reasons, while swimming about in the lakes, and the carcasses sank to the bottom under the influence of their heavy weight. They then became stuck in the thick mud at the bottom of the lake, and so could not rise as decomposition gases filled the belly. This view is rejected here because there is no evidence for deep lacustrine environments in the Vanyushonki Member. With the exception of local grey mottling, the mudstones are well oxidised and show calcretes and rootlets, evidence for frequent episodes of extended subaerial exposure.

(2) *Killed by desertification events*: The alternative 'underwater' view, expressed by Ivakhnenko (1987) was that the more or less fully aquatic pareiasaurs died when their ponds dried up periodically. This model does not necessarily imply miring, but does suggest that the pareiasaurs either could not flee the drying conditions, or that the drying happened too fast for them to escape to another pond. This model is unlikely, however, because pareiasaurs were almost certainly terrestrial animals, and so could walk from lake to lake.

(3) *Buried under sand dunes*: The Boroviki Member sandstones are aeolian, indicating an advancing dune field over the alluvial sediments of the Vanyushonki Member. The close proximity of these aeolian sands, 3–4 m above the pareiasaur-bearing horizon could suggest death under an advancing dune field, as has been suggested for tetrapods in the Late Triassic Lossiemouth Sandstone in Scotland (Benton and Walker, 1985) and the Late Cretaceous of Nemegt, Mongolia (Loope et al., 2001), although this has not been proposed in print for the Kotel'nich tetrapods. This would in any case be unlikely because the sediments above the pareiasaur-rich horizon are fluviolacustrine (Figs. 7, 8), and so the tetrapods died some long time before the sedimentation regime switched temporarily from alluvial to aeolian.

(4) *Trapped in burrows*: Sumin (2009) suggested that the pareiasaurs were trapped in burrows. As evidence, he noted the excellent preservation of the skeletons, the fact they seemed to occur in distinct hollows in the sediment, and that they were reptiles living in a highly seasonal, tropical environment with distinct dry seasons. He did not refer to the fact that this is indeed a key mode of preservation of tetrapod skeletons in analogous sedimentary settings of similar age in South Africa (Smith, 1987, 1993; Groenewald et al., 2001; Damiani et al., 2003; Abdala et al., 2006; Modesto and Botha-Brink, 2010; Bordy et al., 2011). None of these reports from the Karoo identified burrowing pareiasaurs, however; the fossil evidence shows that the Karoo burrowers were dicynodonts, cynodonts, and procolophonids. Importantly, however, the field data from the excavation of 390 skeletons at Kotel'nich since 1990 has shown no evidence of burrow structures around the skeletons based on comparisons with the convincing burrows in the Permo-Triassic of the Karoo. Admittedly, abandoned burrows that collapse before infilling has begun may be hard to detect (Smith, 1993), but there is no evidence at Kotel'nich of impressions of nesting material on a scratch-marked surface, or articulated skeletons in typical hibernation pose, as found in the Karoo sediments. Our main reason for doubting that any of the skeletons from the Vanyushonki Member at Kotel'nich were preserved in burrows is that the hollows in which the pareiasaur skeletons sit are shallow and do not extend over the skeletons: the sediments above are laminated alluvial mudstones and siltstones that drape over the hollow and skeleton in continuity. This absence of burrows at Kotel'nich is somewhat unexpected, as all complete skeletons from the Permo-Triassic of the Karoo, whether curled up or with a straight backbone, have been interpreted (Smith, 1993) as preserved in burrows. Note, however, that only 10% of a sample of 329 Karoo skeletons fell into Smith's (1993) two 'complete skeleton' taphonomic categories, compared to the much higher percentage among the 390 Kotel'nich skeletons.

(5) *Carcasses dumped in floodplain scours*: A further suggestion is that the pareiasaur carcasses were entrained, transported and deposited by a major overbank flood event. As the carcasses were moved slowly by low-energy flows in shallow water, it could be that they lodged in erosive scours produced by earlier, stronger currents. As evidence, it might be noted that complete pareiasaur skeletons in hollows may be associated with isolated bones, accumulations of bones, or complete skeletons of smaller contemporaries. For example, under the skull of one of the recently excavated pareiasaurs (Fig. 14G), a complete skeleton of *Suminia getmanovi* was found, together with an isolated, crushed mandibular bone of a pareiasaur, and two broken ribs probably from a gorgonopsian. Other rare examples of this kind have been noted earlier, including the 1998 skeleton from Mukha (KPM 286; Fig. 14A), which was unusually on its back, and associated with water-transported bones of small reptiles and plant remains. A further pareiasaur skeleton found in 1994 below the village of Nizhnaya Vodskaya (KPM 23; Fig. 14D) was lying on its left side, and the backbone was broken into several fragments, abutting each other, as if the skeleton of the animal had been twisted several times along the longitudinal axis. Further, ribs and small bones of the skeleton, including the phalanges and the tail vertebrae, were missing. It is not certain whether these disturbances were caused by transport or by scavenging. However, such finds are rare, and most pareiasaur skeletons are complete, back-upwards, and apparently standing in their hollows.

The possibility of water-borne transport of the carcasses has been rejected, or not even mentioned, by most previous authors. Sumin (2009), for example, noted that there is little evidence for transport and dumping because the skeletons are isolated and not preserved in overlapping masses, there is little evidence for massive erosion that might be associated with currents strong enough to carry the bulky carcasses, the carcasses ought to be associated with massive boulders, tree trunks and other large objects indicative of high-energy flow, and the carcasses would surely be oriented randomly, some belly-down, some belly-up, and some on their sides. Here, Sumin (2009) makes the assumption that large objects such as tree trunks and coarse sediment grades were actually available for transport, which is unlikely given the distal, fine-grained floodplain/lacustrine setting and he also limits himself to considering only high-energy flows, and not more gentle water movement over a consolidated palaeosol surface that might resist erosion. It is therefore possible that some carcasses were moved by later water movement, and dumped in the hollows following short-distance transport, although this does not explain the consistent belly-down orientation.

(6) *Animals caught in hollows while digging for water*: Perhaps the pareiasaurs were digging down for water, or roots, and created the hollows in which they are now trapped, and many failed to escape. The pits might have been long-term structures, excavated to shallow depth initially to allow water to pool, and then visited time after time, and deepened progressively to reach water as the dry season continued. Eventually, the hole became too deep, and the last animal, or animals, to try to reach water was trapped, some indeed scrabbling at the sides of the pit to escape. Modern mammals dig narrow holes to reach water in dried-up river channels (e.g. Hamilton, 1985; Haynes, 1988; Emmons et al., 2004), but large mammals today tend to trample in great numbers around water holes, and enlarge the ponds (Butler, 1995, p. 95). Discrete pits are not seen. Such widely trampled areas around waterholes have been identified as an interpretation for certain mass dinosaur accumulations (Rogers, 1990), but there is no evidence for such trampling at Kotel'nich. Further, although there is ample evidence that medium-sized and large mammals today dig holes for water in drying conditions, there are no records of those animals being trapped in the holes, or dying in such a manner that individual carcasses would be distributed one per hole. The holes are not so deep, nor the animals so weak, that they cannot climb out and walk away.

(7) *Trapped while wallowing*: Large mammals today, such as buffalo, pigs, and elephants may create shallow hollows around their bodies as they wallow. Wallowing is partly to cool down in hot weather, and partly to dislodge parasites. Perhaps pareiasaurs also wallowed when there was enough water in the mud, and their wallow holes retained their depth because of the semi-consolidated palaeosol substrate. It is unlikely, however, that the animals would have become trapped in such shallow hollows unless they were weakened by hunger and drought.

(8) *Mired in soft sediment*: This leads us back to a version of the first proposal about the unusual preservation of the Kotel'nich carcasses (Hartmann-Weinberg, 1933, 1937; Kashtanov, 1934; Khlyupin, 2007), which was that the pareiasaurs had become trapped in boggy muds, and they were preserved more or less in situ. The evidence is the posture of most of the skeletons with the dorsal side facing up and the limbs down, as if they had died standing, as well as the excellent quality of preservation. These authors also suggested that the animals had been alive when they were in the hollows, and indeed were trying to escape: some skeletons were at an angle to the bedding planes, either with the limbs down on one side and up on the other, as if they had been flailing in a mud bath, or with the head and arms up on the edge of the hollow and the feet on the bottom, as if trying to climb out of a hole head-first. Finally, the size range of animals was said to suggest that the larger animals had been strong enough to escape, while tiny juveniles either never entered the area or were small enough not to get stuck. As noted earlier, there is no evidence that the Kotel'nich pareiasaurs are not all normal-sized adults.

We do not accept a pure miring model, where the mud itself was somehow so tenacious that the animals, in normal, healthy condition somehow became stuck. However, Ochev (1995), Khlyupin (2007), and Tverdokhlebov (2009) presented a plausible modification in which the animals all died at the same time during a particularly devastating aridification event. In the wet season, herds of pareiasaurs ranged over the flat plains, feeding on waterside plants. As conditions became worse at the onset of the dry season, the pareiasaurs congregated around remaining ponds, and smaller and weaker animals died. As the ponds dried out completely, soils were formed. Ochev (1995) also argues that the deaths probably did not happen en masse, as a single, sudden catastrophe, but that the pareiasaur carcasses accumulated over some time.

7.5. Miring as a cause of death

Miring is commonly cited as a means by which large terrestrial animals can become trapped (Rogers and Kidwell, 2007), and modern examples (e.g. Weigelt, 1989; Mellink and Martin, 2001) show how cattle, for example, become so weak during droughts that they simply cannot haul themselves to their feet, and they die of exhaustion and hunger in a hollow produced partly by their weight and partly by their feeble scrabbling. In some modern cases, the cattle had one or more feet trapped in the mud, but generally they did not. As preserved in fossil examples, one need not then expect to find a thick underlying layer of mud, and numerous animals might well be trapped on a single extensive horizon representing a single harsh summer. The absence of thick layers of mud or of evidence of trampling around the depressions need not then speak against the general miring model.

Miring has rarely been suggested for preservation of Permian vertebrates elsewhere. One example is a *Diadectes* skeleton, probably preserved upright in red mudstones of the Lower Permian Nocona Formation of West Texas, which Sander (1989) interpreted as mired and buried rapidly as an explanation for the posture and relative completeness of the specimen in comparison with the much more common channel lag bonebeds nearby. Other examples from the Permian are hard to identify, and the Kotel'nich deposit may be unique for that time.

Miring has been proposed as the cause of death of many later vertebrates, particularly dinosaurs and mammals (reviewed by Sander, 1992 and Rogers and Kidwell, 2007), and the normal assumption has been that these larger animals became stuck in the mud and could not extricate themselves. This is what is claimed for one of the closest taphonomic equivalents to Kotel'nich, the Late Triassic *Plateosaurus* and *Sellosaurus* bonebeds in the Stubensandstein (=Löwenstein Formation) and Knollenmergel (=Trossingen Formation) of SW Germany, where numerous near-complete skeletons are preserved in upright (belly-down) posture (Sander, 1992; Hungerbühler, 1996). These dinosaurs are preserved at the interface of fluvial sands overlain by finer grained floodplain deposits, and presumably became stuck in the wet sand. There is no hint that any of the skeletons of *Plateosaurus* stood in hollows in the underlying sediment, nor was there a palaeosol. Further, there is abundant evidence for scavenging in the form of associated teeth of predators, and disarticulation and removal of certain skeletal parts. A third difference is that the *Plateosaurus* skeletons occur at several different stratigraphic levels, so the mode of death, if it were miring possibly associated with aridification, must have happened repeatedly. The fourth difference is that the *Plateosaurus* were much larger, weighing more than 2 tonnes, and so Sander (1992, p. 291) could argue that the adults perhaps became stuck and could not escape, despite strenuous efforts, whereas the smaller juveniles could escape and so were not preserved. Finally, the *Plateosaurus* skeletons are disarticulated and scattered in parts, suggesting some long period of exposure after death.

In all these five points, the Kotel'nich pareiasaurs differ: (1) the carcasses stand in hollows on top of a palaeosol; (2) they have not been much scavenged; (3) they occur all at one stratigraphic level, suggesting a single killing event; (4) the pareiasaurs are perhaps not so massive, weighing perhaps 50–100 kg, that they could readily become trapped in the mud in normal health; and (5) the skeletons show almost no evidence of disarticulation, and so were buried quickly or at least without disturbance.

In another dinosaurian example, Varricchio et al. (2008) described a small herd of juvenile and subadult ornithomimids trapped in a mud unit in the Upper Cretaceous of Mongolia. The carcasses were all belly-down, but scattered, and somewhat overlapping, on a single bedding plane, somewhat aligned, and associated with isolated bones. These were interpreted as having died in a drying lake or pond. An even more unusual dinosaurian example from the Jurassic Shishugou Formation of Xinjiang, China consists of numerous small theropods apparently trapped in viscous mud within deep sauropod footprints (Eberth et al., 2010).

Eberth et al. (2010) note that most reported examples of miring make the assumption that the animals became trapped in viscous mud and could not free themselves. In particular, they report that attempts by the animals to free themselves can increase the stickiness of the mud, and so make their efforts to escape even harder. As noted, the Kotel'nich pareisaurs show no evidence for such viscous mud trapping the feet

7.6. Landscape microtopography and the preservation of skeletons

The Kotel'nich outcrops show the importance of microtopography of the landscape in providing taphonomic windows that locally increase vertical sedimentation rate and allow preservation of the vertebrate fauna. Here, we use the term 'microtopography' to refer to the landscape-scale shape of the land surface, rather than the plant-scale soil surface, as often used by ecologists (e.g. Beatty, 1984).

The microtopography in the fine-grained fluviolacustrine settings at Kotel'nich was generated in two ways (Fig. 16). First, the erosion of a stable, mature palaeosol surface formed a series of shallow scours. It seems most likely that the erosion was caused by a high-magnitude flood event. A common cause of high-magnitude flood events in floodplain settings is the abrupt shift (avulsion) of a drainage system into a low-lying area. Erosion of the Vanyushonki Member palaeosol created a series of shallow scours that became sites for enhanced rates of sedimentation and the mass burial of articulated pareiasaur skeletons. It is uncertain if the flood event was responsible for the mass death of the pareiasaurs, if a concentration of pareiasaur carcasses had simply accumulated on the stable palaeosol surface prior to flooding and erosion, or indeed, and this seems most likely, if the animals were actually entering and dying in the hollows with no physical transport.

The second type of microtopography generated in the Kotel'nich succession is above thin, erosionally based sandstones, and these probably represent lows formed above abandoned or cut-off river channels. In some cases, these abandoned channels formed floodplain lakes, which ponded water and allowed the accumulation of laminated grey lacustrine sediments, plant remains, and fishes. Fragmentary remains are seen in the channel lags of the Chizhi and Sokol'ya Gora members, and these probably represent weathered and disarticulated skeletal elements that entered the channel deposits by processes of scour and bank erosion and they may have been transported considerable distances from the site of death.

8. Discussion and conclusion

Complete skeletons of terrestrial tetrapods may be preserved in many settings, ranging from sand bars in the middle of rivers, overbank deposits, burrows, offshore marine sites, ash falls, and mummified beneath aeolian dunes. Behrensmeyer (1988) distinguished two modes of vertebrate preservation in fluvial channels, the channel-lag and channel-fill modes. *Channel-lag bones* are preserved in the lower part of erosional channels, generally associated with pebbles and intraclasts, often immediately above an erosive contact with finer-grained sediments below. Bones and teeth are generally heavily disarticulated, abraded, and concentrated in scours. This is the mode of preservation of bones and other fossils in the Chizhi, and especially the Sokol'ya Gora members. *Channel-fill bones* may be preserved in fine or coarse clastic sediments that fill a channel after it has been abandoned by active flow, and the bones tend to be less transported than in channel-lag examples, and sometimes carcasses may be more or less complete. U-shaped channels and lenses indicate abandoned channels, and a fill of fine-grained sediment suggests sudden abandonment and either a drastic reduction in the energy needed to transport coarser sediment or a barrier (e.g. vegetation) to the supply of sediment (Bridge, 1985; Behrensmeyer, 1988). This may be the mode of preservation of the dicynodont skeletons at Port Kotel'nich.

Skeletons preserved in fluviatile settings are generally assumed to have been transported some distance, as noted by Behrensmeyer, and the channel-lag preservation mode is most familiar. Less well understood are her channel-fill deposits, where skeletons appear to be nearly or completely undamaged, and so presumably minimally transported. Since 1988, several examples of such preservation have been noted among Permo-Triassic tetrapods (Smith, 1993; Smith and Swart, 2002) and dinosaurs (Rogers and Kidwell, 2000; Therrien and Fastovsky, 2000; Ryan et al., 2001; Straight and Eberth, 2002; Rogers, 2005; González Riga and Astini, 2007). The channel-fill deposition mode is often associated with major erosive surfaces below, and so has figured in debates about the significance of such levels in terms of omitted time and major sequence stratigraphic

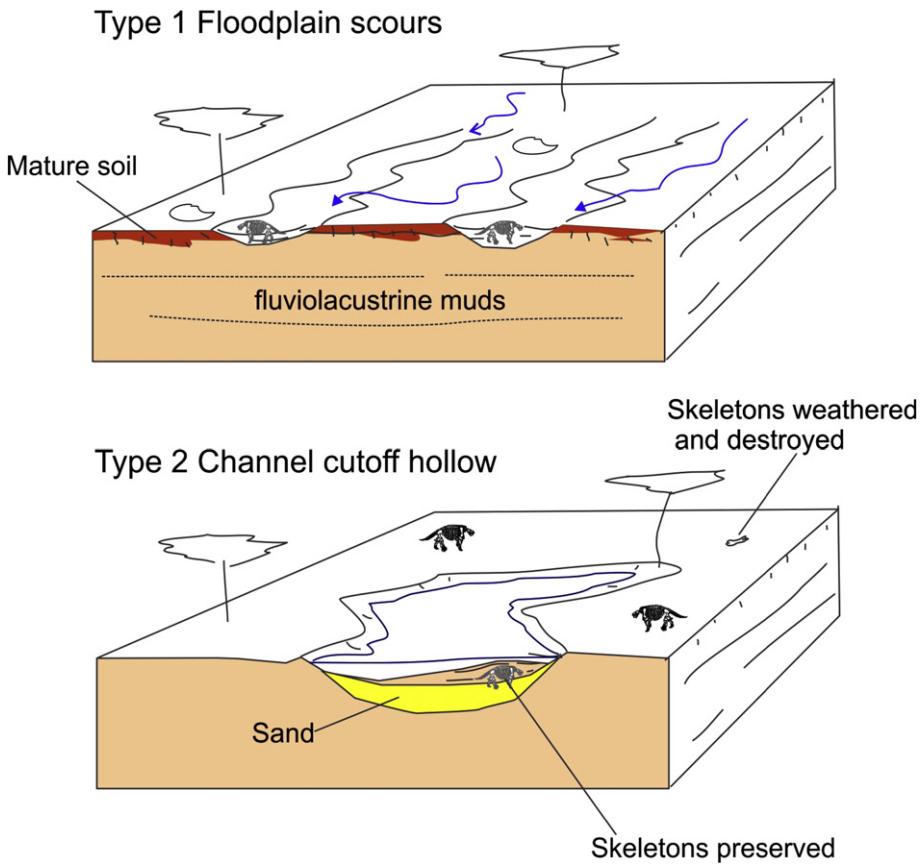

Fig. 16. Block models showing the two main modes of exceptional vertebrate preservation in fluviolacustrine deposits at Kotel'nich (Type 1), in floodplain scours in the Vanyushonki Member, and in channel cutoffs in the ?Shestakovy Member at Port Kotel'nich, and the channel lags of the Chizhi and Sokol'ya Gora members (Type 2).

marker horizons, whether they do (Straight and Eberth, 2002) or do not (Rogers and Kidwell, 2000) coincide with major stillstands and scour surfaces that delimit sedimentary packets. Behrensmeyer (1988) outlined four categories of channel fill, A–D, representing fine to coarse sediment fills and increasing energy and speed of channel fill; she observed categories B–D in the Pliocene of the Siwaliks, and A–D in the Lower Permian of Texas. Her category-A channel fills, indicating the finest grain sizes and the slowest rate of channel filling, are likely to preserve the finest and least damaged vertebrate skeletons. Independent channels, as opposed to sheet sands, suggest high rates of subsidence.

Behrensmeyer (1988) noted that bones in channel-fill deposits were preserved in mixed to fine-grained deposits that filled channels after they had been abandoned by sustained, active flow. Such deposits usually occur in middle to later parts of channel fills, but occasionally, as here in the Vanyushonki Member, occur immediately above the basal eroded surface. Bones may be preserved in a variety of modes, but complete and undamaged skeletons are commoner in channel fills than in channel lags. The channels are abandoned and have sporadic, waning flow with minor reworking of banks and bedload sediments. Bones and skeletons in channel fills are either at the site of death or transported short distances; most are autochthonous with respect to the local channel.

Behrensmeyer (1988) noted five correlates of the preservation of bones and skeletons in fluvial channels: (1) topographic lows likely to receive and protect organic remains, (2) concentrations of animals near abandoned channels due to localised availability of food and water, particularly during times of restricted resources on the alluvial plain, (3) localised transport, sorting, and hydraulic concentration of bones, such as might occur during sporadic floods, (4) sedimentation patterns characterised by periods of non-deposition when attritional remains could accumulate, alternating with periods of relatively rapid deposition that would bury bone-rich horizons, and (5) low rates of destruction by soil organisms and chemical dissolution because of the combined effects of rapid burial and (perhaps) anaerobic conditions.

Fine-grained fluviolacustrine depositional environments in subsiding sedimentary basins typically have exceptionally low surface relief and sediments are dispersed as thin sheets across large areas. Rates of vertical sediment aggradation are typically slow and punctuated by frequent episodes of non-deposition, weathering and soil formation. This style of sedimentation has considerable implications for the vertebrate fossil record of fluviolacustrine deposits because background sedimentation rates will generally be insufficient to conceal large skeletal remains before they are destroyed by physical weathering and scavenging. To achieve long-term preservation local conditions must be developed that rapidly remove vertebrate skeletons from the zone of subaerial destruction.

At Kotel'nich, the succession is mostly fine-grained and deposited in laterally extensive, shallow lacustrine and floodplain environments that aggraded slowly and were continuously modified by syndepositional soil-forming processes that were generally not conducive to the preservation of large vertebrate skeletons. Only at one level, on top of a palaeosol that corresponds to a time of non-deposition, were hollows formed by water erosion or by animal activity, and an episode of unusual aridity caused mass deaths of the dominant herbivores, the pareiasaurs, as they feebly searched for food and water. They entered pre-existing hollows, or created those hollows, in search of sustenance, and lacked the strength to escape, dying on the spot, and generally showing little evidence of scavenging, perhaps because flesh-eating tetrapods had also died or had left the basin. Following the mass death, the carcasses became entombed under

subsequent fine-grained sediments deposited under water, but without lateral currents that would have disturbed the carcasses.

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Appendix 1. Dating the Kotel'nich fossil assemblage

The Russian stratigraphic system for the Permo-Triassic red beds has been developed over the past hundred years as a result of extensive fieldwork and comparative study. The closest 'standard' section for comparison to Kotel'nich is the classic Sukhona River succession, some 275 km to the NNW, in the Dvina-Sukhona basin, Vologda Province (Goman'kov, 1997; Golubev, 2000), and this was identified as part of an extensive campaign since the 1960s to map throughout the basins west and south of the Ural Mountains, including the Vyatka, Sukhona, and Dvina river basins (Fig. 1). In each basin, svitas (≈formations, although used as chronostratigraphic, not lithostratigraphic, units) have been named, and these are sometimes further subdivided into 'packets' (≈members). Sections are correlated by means of mapping, magnetostratigraphy, and biostratigraphy (palynomorphs, ostracods, fishes, tetrapods). The stratigraphic scheme (Fig. 6) is organised according to gorizonts, biozones defined on the basis of key fossil groups.

The key relevant divisions are those of the Tatarian Stage, formerly the last stratigraphic unit of the standard international time scale, but now replaced by the Chinese marine standard. Russian stratigraphers subdivide the Tatarian into three, the Urzhumian, Severodvinian, and Vyatkian substages (Fig. 6), and magnetostratigraphic work (Molostovskiy et al., 1979; Molostovskiy, 2005; Khramov et al., 2006; Steiner, 2006; Taylor et al., 2009) has shown that the Tatarian is much longer than formerly assumed (3–4 Myr), spanning in fact 14–15 Myr of the upper Middle Permian and all of the Late Permian, equivalent to the Capitanian, Wuchiapingian, and Changhsingian international stages.

The Kotel'nich succession has always been dated as late Tatarian, but not terminal Tatarian, because it is overlain by the late Permian Sokolki and Vyazniki tetrapod complexes, and its span is within the Severodvinian (Fig. 6). There has been a difference in interpretation of the total time span represented at Kotel'nich, with the geological maps indicating that the Vanyushonki, Boroviki, and Chizhi members are parts of the P_2jur (=Yurpalovskaya) beds, the Shestakovy Member corresponds to the P_2pt (=Putyatinskaya) beds, and the Sokol'ya Gora Member to the P_2bk (=Bykovskaya) beds, as shown on USSR State Geological Map (1990): sheet number O-39-XIII (1:200,000) (Fridman, 1990; Goman'kov, 1997). The Yurpalovskaya and Putyatinskaya svitas were named by Ignat'ev (1962) and Forsch (1963) in the Vyatka Basin, including the Kotel'nich area (Fridman, 1990; Gusev, 1998; Goman'kov, 2001). Coffa (1999), on the other hand, stated that the first four members are components of the Yurpalovskaya Svita, and the Sokol'ya Gora Member is at the base of the overlying Putyatinskaya Svita. Finally, V. K. Golubev has suggested two correlations with the Sukhona section, first (Golubev, 2000, p. Fig. 35) equating the Kotel'nich succession with the Nyuksenitskaya to Purtovinskaya packets (Fig. 6), and then (Golubev, in Newell et al., 2010, Fig. 2) with the Strelenskaya to Kalikinskaya packets (Fig. 6). These assignments indicate variously a short (Yurpalovskaya-Putyatinskaya) or long (Yurpalovskaya-Bykovskaya) span for the Kotel'nich succession (Fig. 6), and the differences must be resolved. The unexposed older parts of the succession, perhaps dating back to the Urzhumian, as detected in the Kotel'nich borehole (Ignat'ev, 1962; Goman'kov, 1997) are not further considered here.

In his detailed biostratigraphic work, Golubev (2000, pp. 117–120) assigned primacy to the tetrapod-based biostratigraphic scheme. Russian palaeontologists have always recognised two stratigraphic units in the Kotel'nich succession, an upper unit represented by the Sokol'ya Gora Member, and a lower unit comprising the four members beneath. The finds of the chroniosuchid *Chroniosaurus levis*, the batrachomorph *Dvinosaurus primus*, the pareiasaur *Proelginia* cf. *permiana* (=*Scutosaurus karpinskii*), and the biarmosuchian theriodont *Proburnetia viatkensis* in the sandstone lens of the Sokol'ya Gora Member at Agafonovo and Sokol'ya Gora indicate assignment to the Il'inskoye Subcomplex, the middle division of the Sokolki Tetrapod Complex (Fig. 6). The other tetrapod finds, listed earlier, from Port Kotel'nich and from the localities south of Kotel'nich on the Vyatka River, from the Vanyushonki, Shestakovy, and Chizhi members respectively (Golubev's beds 1, 6, and 5), are integral to, and type exemplars of, the Kotel'nich Subcomplex, the lowest division of the Sokolki Complex (Fig. 6).

In comparison with the standard Sukhona River sections, the key biostratigraphic indicators, according to Golubev (2000, p. 119), are the chroniosuchids, basal tetrapods (='amphibians') that were widespread throughout Russia from the late Middle Permian to the Middle Triassic. In the Sukhona River sections, *Chroniosaurus levis* is known from the top of the Kichugskaya Packet (Mutovina and Mar'yushkina Sluda-C localities), while *C. donguesensis* is found some 20 m lower (lower part of the Purtovinskaya Packet, Mikulino locality). Golubev (2000, p. 119) argues that the *C. levis* from Sokol'ya Gora is intermediate in terms of evolution between the Mikulinskaya and Mutovina chroniosuchids. Remains of chroniosuchids like those from Sokol'ya Gora are found on the Sukhona at the top of the Purtovinskaya or at the bottom of the Kichugskaya packets, indicating possible equivalence with the Sokol'ya Gora Member of the Kotel'nich section (Fig. 6). Thus, based on data from tetrapod fossils, the Kotel'nich section is correlated with the middle part of the Poldarsskaya Svita (Strelenskaya to Purtovinskaya packets) in the standard Sukhona River section, as noted by Golubev (in Newell et al., 2010, Fig. 2).

Additional age data for correlation within the Russian system comes from the fishes and plants in the Chizhi Member plant-bearing lens. Goman'kov (1996, 1997) identified the macroplant assemblage from the Chizhi Member as of 'typical upper Tatarian appearance', whereas the pollen spectrum appears 'archaic', and dates this unit at least as older than Vyatkian, and places it just below the age of the plant-bearing deposits at Isady on the Sukhona River, assigned to the Purtovinskaya Svita (Fig. 6). This is confirmed by pollen associated with the plants in the Chizhi Member, which indicate assignment to the rather broad palynocomplex (PK) 5 *Vesicaspora–Vitreisporites* (Shelekhova, 1995), equivalent to the *Vitreisporites pallidus–Protohaploxypinus dvinensis* Palynocomplex (Yaroshenko and Goman'kov, 1998). In Goman'kov's (1997) view then the plant-bearing Chizhi Member of the Kotel'nich succession is dated to the Yurpalovskaya Svita, roughly equivalent to the Isadskaya Svita on the Sukhona River (Fig. 6).

The fishes indicate an early Tatarian placement of the bed, but the ichthyocomplex (Fig. 6) cannot be determined exactly. *Platysomus biarmicus* suggests the *Platysomus* Complex of the Ufimian, Kazanian, and lower Tatarian, while *Toyemia tverdochlebovae* points to the overlying *Toyemia* Complex, characteristic of the upper Severodvinian. The occurrence of *Amblypterina* sp. suggests a more detailed assignment, either to the *Amblypterina costata* Subcomplex, the uppermost of four subcomplexes in the *Platysomus* Complex, and characteristic of the lower Tatarian, or the overlying *Amblypterina pectinata* Subcomplex, lowest of three subcomplexes in the *Toyemia* Complex and matching the Il'inskian Tetrapod Complex (Esin, 1995; Esin and Mashin, 1998; Golubev, 2000).

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