The Age of Dinosaurs in Russia and Mongolia

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VITALII G. OCHEV AND MIKHAIL V. SURKOV

Introduction

Rich finds of tetrapods have been made in the mainly continental Upper Permian and Triassic deposits in the east of European Russia, west of the Ural Mountains. This territory, stretching from the Barents Sea to the Pre-Caspian, is covered with forests in the north and with steppe in the south. There are no vast badlands, yielding abundant fossil finds, as in South Africa or the Gobi Desert. The rocks are exposed only in river valleys and in ravines. Nevertheless, during almost two centuries of study, more than a thousand localities of Upper Permian and Triassic tetrapods have been discovered. They indicate a number of fossil faunas through time.

First discoveries in the Copper Sandstones (Late Permian)

The first of the local faunas to be discovered was one of the most ancient, the dinocephalian, from the early Kazanian to the early Tatarian (Late Permian). The localities of the dinocephalian fauna coincide mainly with the belt of Copper Sandstones, stretching for hundreds of kilometres along the western slope of the Ural Mountains. These finds were for a long time the oldest fossil reptiles from Europe. Their discovery was thanks to extensive mining works for copper, which were conducted in the eighteenth and nineteenth centuries. However, the finds which reached palaeontologists came only from a small number of mines in the present Orenburg Province, in Bashkortostan, and a very small number from Perm' Province. The distribution of the fossils probably reflects the presence of people in charge of the mines who understood the great scientific significance of fossils.

The first indications of bones in the copper mines of the Cis-Urals are found in the works of participants of the 'Academical Expeditions' which were conducted by the Russian Academy of Sciences from 1765 to 1805 with the aim of studying the natural environment of Russia. However, the naturalists at that time did not fully understand the nature of these remains: the corresponding member of the Russian Academy of Science, P.I. Rychkov, mentioned his discovery of cupriferous fossil reptile bones (judging by their size, a dinocephalian) in the diary of his Orenburg travels (1770), but he took them for the remains of ancient mining workers.

The first scientific description of the remains of terrestrial vertebrates from the Copper Sandstones (of Perm' Province) was made by a Professor of the University of Saint Petersburg, S.S. Kutorga (1838). He established new taxa of predatory dinocephalians, *Brithopus* and *Syodon,* which were described on the basis of fragments of the humerus and tusk respectively. Kutorga took them for mammals, ascribing the first to the edentates, and the second to the pachyderms. Thus he was the first to notice the similarity between mammal-like reptiles and mammals.

Among a number of active collectors of fossils from the Copper Sandstones, there was a captain of the mining engineers corps, Sobolevskii, who gathered materials from the mines of Perm' Province. Especially notable was F. Wangenheim von Qualen, director of a number of mines in Ufa (Bashkortostan) and Orenburg Provinces, who assembled a large number of remains of fossil vertebrates. In the 1840s

he began to publish a series of important essays in Russian scientific journals. Even before Murchison (1841) had distinguished the Permian System, he correlated the Copper Sandstones of the Cis-Urals with the Zechstein of Germany. We are indebted to him for the only data available now about the richest localities, as well as valuable information on the conditions of the burial of bones (Wangenheim von Qualen, 1845).

Materials from the collections of von Qualen were also studied by S.S. Kutorga and other Russian naturalists. Thus, a Professor of Moscow University, G.I. Fischer von Waldheim (1841) described a new genus of dinocephalian, *Rhopalodon*, and a corresponding member of the Academy of Science of Saint Petersburg, E.I. von Eichwald (1846), established the genus *Deuterosaurus*, and also described (Eichwald, 1848) the temnospondyl amphibian *Zygosaurus* on the basis of a complete skull.

A number of eminent foreign palaeontologists also studied the vertebrates from the Copper Sandstones. A significant part of von Qualen's collections was taken to Germany and later distributed to a number of museums, but most of these materials were destroyed during the Second World War. These specimens were studied by Hermann von Meyer. In 1866 he published a large monograph on terrestrial vertebrates from the Cis-Urals, in which he made many significant corrections to earlier researches. However, his understanding of the taxonomic content of the fauna was still not very clear: like the majority of naturalists at that time, he did not distinguish between amphibians and reptiles.

The material from the Copper Sandstones was first introduced to Richard Owen when it was brought from Russia to England after the 1841 expedition of Roderick I. Murchison (Figure 1.1). Owen took the Cis-Uralian dinocephalians for archosaurs. Later, he studied the materials in the British Museum, which had been collected in the Kargala mines in the Cis-Urals by the English company 'Russia Copper & Co.'. Owen (1876) gave the most complete analysis of this fauna: he compared the remains of the reptiles from the Copper Sandstones with the South African therio-donts, a new order which had been established by him. Another English researcher, W.H. Twelvetrees, published in 1880–2 a number of articles on remains of the vertebrates from the Kargala mines, which he had visited. From here, he established the new temnospondyl genus *Platyops* on the basis of a skull. The monograph by H.G. Seeley (1894) was highly significant: he worked out in detail the collections of the Saint Petersburg Mining Institute and those of Kazan' University, and gave excellent drawings. However, Seeley's opinion that the Cis-Uralian reptiles were related to the Placodontia and Nothosauria delayed for a long time a correct understanding of the Copper Sandstones fauna.

The interest of foreign scientists in the fauna did not diminish at the beginning of the twentieth century. New reconstructions and descriptions were made on the basis of data from the literature, mainly from the work by Seeley. The eminent German palaeontologist Friedrich von Huene (1905) for the first time emphasized the similarity between the Cis-Uralian reptiles and the pelycosaurs. The famous English palaeontologist D.M.S. Watson (1914) concluded that all the genera of reptiles described from the Copper Sandstones belonged to the Dinocephalia. The last restudy of the original material in the Saint Petersburg Mining Institute was completed by F. von Nopcsa (1928). His work, although containing many mistakes, concluded with the correct assessment that the reptiles of the Cis-Urals were synapsids, and that they include forms intermediate between the pelycosaurs from the Early Permian of Texas, and the therapsids of South Africa.

With the gradual cessation of copper mining from the 1880s, and its termination at the beginning of the twentieth century, new discoveries of vertebrates from the Copper Sandstones of the Cis-Urals almost completely stopped. The main collections from this time were made in slag heaps of the old mines. Thus, the Russian geologist P.N. Venyukov found fragments of the jaws of dicynodonts in the slag heaps of Kargala mines, which were described posthumously by V.P. Amalitskii (1922) as the new genus *Venyukovia* and ascribed by him at first to the mammals. The first

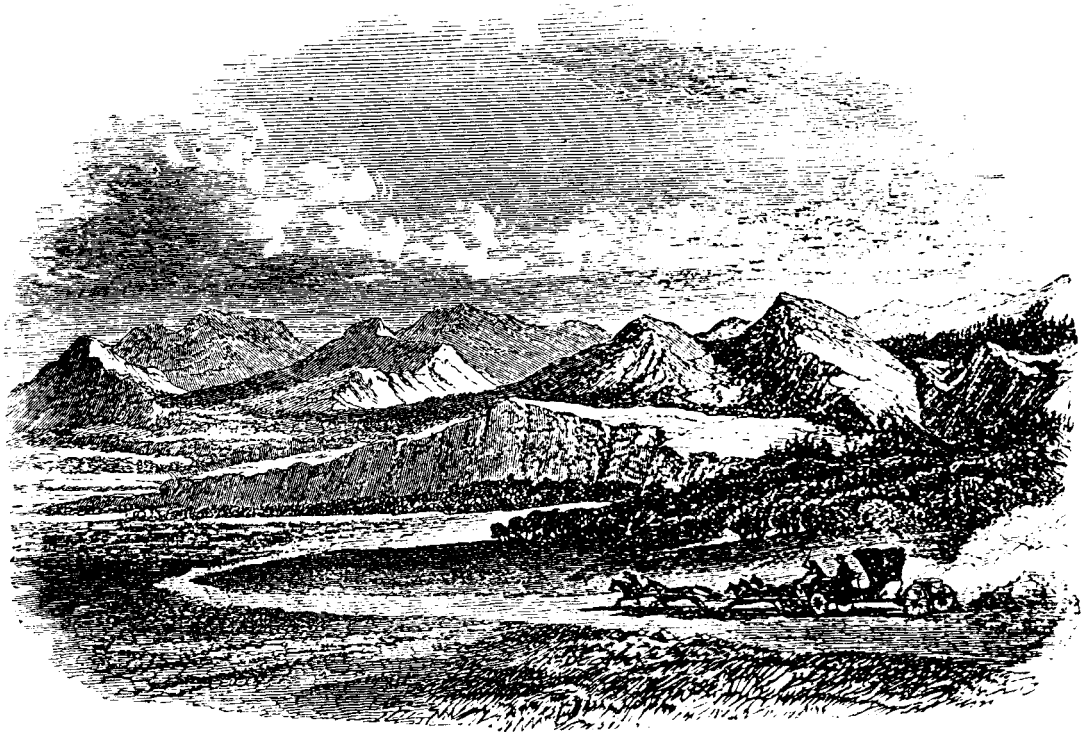

Figure 1.1. The Gurmaya Hills of the South Ural Mountains, as seen from the steppes of Orenburg. This engraving shows the scene as witnessed by Sir Roderick Impey Murchison when he visited Russia in the early 1840s, and first recognized the Permian System. (From Murchison and de Verneuil, 1845.)

localities in natural exposures, not in mines, were found only in the 1890s by a Kazanian geologist, A.A. Stuckenberg (1898).

Amalitskii and the Late Permian of the North Dvina River

The main attention of Russian researchers at this time was drawn to new, younger (Late Tatarian) Permian faunas with pareiasaurs, gorgonopsians, and dicynodonts (Figure 1.2). We are indebted to a professor of Warsaw University, V.P. Amalitskii, for the discovery of this fauna on the River North Dvina (eastern Poland at that time was part of Russia). His work was an heroic episode in the history of Russian palaeontology. Amalitskii began to study the Permian deposits of the Middle Volga region and found bivalves, which proved to be very similar to freshwater forms known from deposits of the same age from South Africa. It led Amalitskii to the suggestion that there should be other shared fossils, including the large reptiles (pareiasaurs and various mammal-like reptiles). This idea was supported by the fragmentary remains of dicynodonts, which were found by Amalitskii.

Amalitskii's idea was not greeted sympathetically at first, since it was in opposition to the generally accepted idea at the time that the animal and plant worlds were completely different in the northern and southern hemispheres in the Permian. But the enthusiasm of the scientist was strong and, with scanty resources, which he obtained from the Saint Petersburg Naturalists' Society, he began a field study along the banks of the Sukhona, North Dvina, and other smaller rivers.

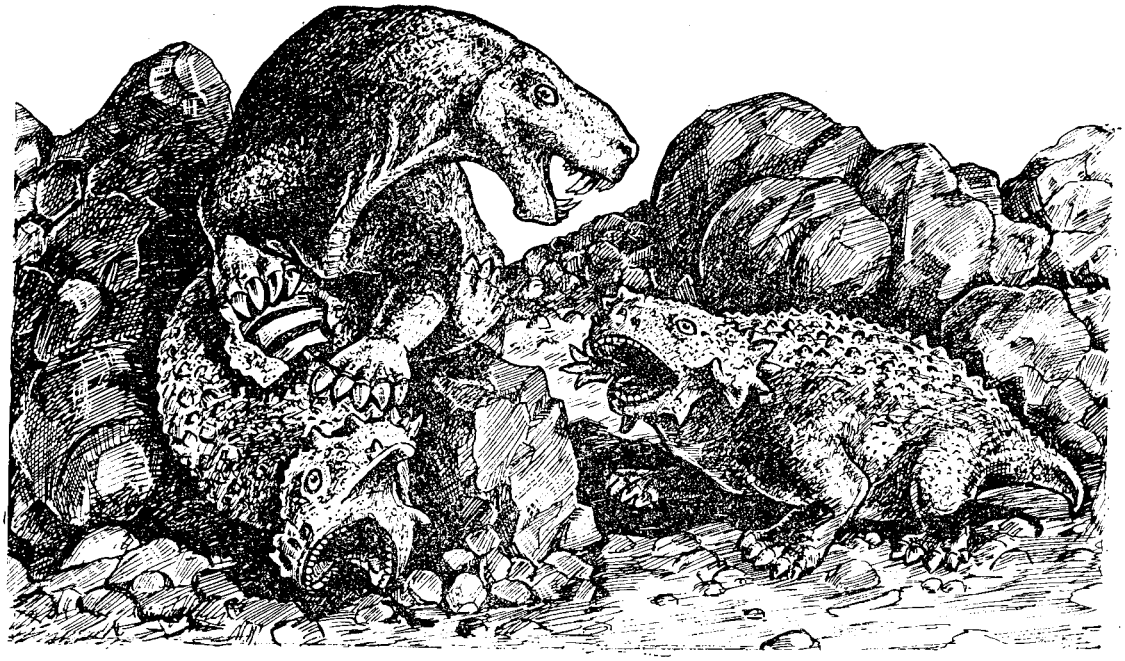

Figure 1.2. A Late Permian fauna from the North Dvina River, containing reptiles excavated by V.P. Amalitskii. A gorgonopsian, *Inostrancevia*, attacks two large herbivorous pareiasaurs, *Scutosaurus*. (Restoration by A.P. Bystrov.)

These researches were conducted in difficult conditions. Amalitskii, with his wife, travelled along the northern rivers by boat under the open sky, and took shelter under the boat at night and in rainy weather. This continued each summer from 1895 to 1898. They became accustomed to midges, a very poor diet, and to the constant dampness and mists. After four years of determined searches, Amalitskii's efforts were rewarded. The fauna of Late Permian reptiles found by him, known before only from South Africa and India, became one of the greatest discoveries in palaeontology of the nineteenth and early twentieth century.

When Amalitskii delivered his first findings to a meeting of the Saint Petersburg Naturalists' Society, opinions changed, and he received a small grant for excavations, which were started in 1899. In the beginning the main work was conducted on the right bank of the River North Dvina, above Kotlas rail station, in the area called Sokolki. Here, striped marls with several large lenses of sand and sandstone are exposed, and in the lenses, he observed large spherical concretions, sometimes containing bones and remains of plants. Amalitskii chose one of these lenses for excavation. However, the absolutely vertical cliff did not allow access to the lens either from below or above. Only after removing sediment from above was it possible to get deeper into the sandstone to quarry the concretions from it. There were plenty of them, but often without fossils, and Amalitskii searched for a long time before he came across concretions with skeletons. To extract them, he dug a gallery 7 m long, 4 m wide, and the same in height. Altogether, he found 39 large bone-bearing concretions. All the collections were packed in 64 boxes, which filled two rail carriages and weighed 20 tonnes.

These were the results of the first organized excavations in the history of Russian palaeontology, and no-one doubted Amalitskii's success after that. A large sum of money, 50 000 roubles was given to him, which allowed him to continue excavation on a much more

significant scale for many years. These resources also gave him the opportunity to organize the first palaeontological workshop in Russia, where the skeletons were prepared and mounted. This formed the nucleus of 'The North Dvina Gallery', created by Amalitskii. The present Palaeontological Museum of the Russian Academy of Science later developed from this gallery.

In the history of excavations by Amalitskii, there were many unexpected events and difficulties. The local people for a long time did not believe that he was searching for antediluvian animals, but thought that he was digging for gold. Only the finds of well-preserved jaws and skulls convinced them. The first season of excavation could have ended tragically, because of the appearance of the livestock plague, Siberian ulcer, in surrounding villages. A rumour spread that the professor was digging up an old cattle grave, and that the decayed corpses were spreading infection to the livestock. Fortunately, a veterinarian arrived and stopped the cattle plague, and the disturbances by the local people subsided.

The beginning of the First World War in 1914 marked a break in excavations on the North Dvina, and the unexpected death of Amalitskii stopped the research. The significant part of his results was published post-mortem, mainly in a special series by the Academy, *The North Dvina Excavations by Professor V.P. Amalitskii* (1921–7). These included preliminary descriptions and diagnoses of a number of new taxa of Permian tetrapods: the temnospondyl *Dvinosaurus*, the reptiliomorph amphibian *Kotlassia*, the gorgonopsian *Inostrancevia*, and others. The other materials of gorgonopsians were studied by a student of Amalitskii, Professor P.A. Pravoslavlev (1927). Academician P.P. Sushkin, known for his ornithological works, and since 1922 a curator of the North Dvina Gallery, used these collections for his classic works on the evolutionary morphology of vertebrates (Sushkin, 1926, 1927, 1936). These studies became widely known in the West.

The work of drawing geological maps, which was developing in Russia after the organization in 1922 of a Geological Committee, led to the discovery of numerous vertebrate localities in natural sections in the Permian and Triassic. Valuable finds were made in European Russia by famous early twentieth century Russian geologists, N.G. Kassin, P.M. Zamyatin, V.A. Tsaregradskii, M.A. Zhirmunskii, and by many of their followers. The excavations and search expeditions started by the North Dvina Commission and Geological Museum, were particularly activated after the organization in 1930 by Academician A.A. Borisyak of the Palaeozoological (later, Palaeontological) Institute in the Academy of Sciences of the USSR. Before the Second World War, Permian and Triassic tetrapods were studied by a few researchers. A.P. Hartmann-Weinberg, who was the curator of the North Dvina Gallery after the death of P.P. Sushkin, worked on the rich materials discovered in the North Dvina, and she established (Hartmann-Weinberg, 1933) that the local pareiasaurs belonged to the new genus *Scutosaurus*. However, the main role at the beginning of the new stage of study belonged to a student of P.P. Sushkin, Professsor I.A. Efremov (Figure 1.3).

Ivan Antonovich Efremov (1907–72)

Efremov gained world fame as a vertebrate palaeontologist, the founder of a new science, taphonomy, and as a writer of science fiction, widely popular in Russia. His scientific activity began very early. In 1925, when he was 18 years old, he became a preparator in the Mining Museum in Leningrad and straightaway started independent expeditions. In 1926 he studied the conditions of burial of temnospondyl amphibians on the mountain Bolshoe Bogdo, near Lake Baskunchak in the Cis-Caspian, where at the end of the nineteenth century, I.B. Auerbakh, and subsequently M.M. Bayarunas, found amphibian bones in the marine Lower Triassic (see Efremov, 1928).

From 1927 to 1930, Efremov excavated localities yielding temnospondyls and small reptiles (archosaurs and others) in the continental Triassic on the Volga–Dvina watershed. As a result, very rich material was obtained and led him to the discovery of the hitherto unknown most ancient fauna of Early Triassic amphibians. Here a group of new genera was established by him, and partially by Professor A.I. Ryabinin,

Figure 1.3. Professor Ivan Antonovich Efremov (1907–72), most celebrated Russian vertebrate palaeontologist of the twentieth century.

named by Efremov the Neorachitomi. The description of the most richly represented form, *Benthosuchus sushkini*, completed later jointly with a skilled morphologist and excellent artist, Professor A.P. Bystrov (Efremov and Bystrov, 1940), was awarded a Diploma of the Linnean Society in London. The remains of small reptiles collected by Efremov from the Early Triassic of European Russia were described by Huene (1940).

In 1930, Efremov became head of the Ural–Dvina Expedition of the Palaeontological Institute, which embraced the study of the Permian and Triassic of the north of European Russia and the Cis-Urals, and from 1934 to 1939 he led the Volga–Kama Expedition. Now he gave his main attention to Permian vertebrates, first of all from the Cis-Uralian Copper Sandstones. His aim was to make new finds in the old mines and to study the conditions of deposition of the bones, and this study was continued up to 1939. He went down into the the old pits, often at considerable risk. His work at the Kargala mines and at the Akbatyrovo mines in the Kirov Province (former Vyatka Gouvernement) in 1934 did not lead to significant new finds of bones, but they provided the first information on the conditions of burial of vertebrates in the Copper Sandstones.

Efremov summarized his research on tetrapods from the Copper Sandstones of the Cis-Urals in a fundamental monograph (Efremov, 1954). Having revised the systematic content of this fauna, he added to the list new genera of predatory dinocephalians and other therapsids.

Studies by geologists, and expeditions from the Palaeontological Institute of the Academy of Sciences, in the regions west of the zone of the Copper Sandstones led to the discovery of large new vertebrate localities of roughly the same geological age. A rich dinocephalian fauna was found near the village Isheevo in Tatarstan. From this locality, excavated from 1934 to 1939, complete skeletons of dinocephalians were obtained, similar to the latest forms from the Copper Sandstones. Efremov named this the Isheevo Dinocephalian Complex, to distinguish it from the Cis-Urals dinocephalian fauna. Yu.A. Orlov (1958) partially studied the findings from Isheevo, and described from this locality the carnivorous dinocephalians. Efremov (1946) established here a new genus of reptiliomorph amphibian, *Lanthanosuchus*, the analysis of which led him to distinguish the Subclass Batrachosauria.

Two further large localities of Permian vertebrates in the Cis-Urals were studied by Efremov, one low on the River Mezen' in northern Russia, and the other near the town Belebey in Bashkortostan. They were discovered by Ya.D. Zekkel in 1934–5, and by an assistant of Efremov, N.I. Novozhilov in 1937–8. In these localities, in contrast to the Dinocephalian complexes, the remains of small anapsid reptiles dominated. This gave Efremov the basis for the Mezen'–Belebey Cotylosaurian Complex, coeval with the Dinocephalian, but originally thought to be younger. In 1938–40, he established here the genera of anapsid reptiles *Nycteroleter*, *Nyctiphruretus*, *Rhiphaeosaurus*, an eotheriodont *Phthinosaurus*, and the pelycosaur *Mesenosaurus*.

Information on the younger North Dvina Pareiasaurian Complex was supplemented in the

1930s by the discovery of two new large localities: near the village of Il'inskoe on the Volga River near the town of Tetyushi in Tatarstan, and near the town of Kotel'nich on the Vyatka River in Kirov Province. However, the unique character of the tetrapod assemblages found here, which is slightly older than that from the North Dvina lenses, only became clear later.

Before the Second World War, Efremov summarized all the Permian and Triassic tetrapods from the former USSR (Efremov, 1940a, 1941). On the basis of his accumulated data, he created a zonal scheme for the stratigraphy of the continental Permian and Triassic on the basis of tetrapods (Efremov, 1937). It gained wide fame among geologists and was revised many times (Efremov, 1939, 1944, 1952) and is the basis of the current scheme.

Efremov had an early interest in the processes of burial of fossil vertebrates, and his wide experience of many cases led him to a number of important generalizations. In 1940 Efremov published an article on 'Taphonomy – the new branch of palaeontology' (Efremov, 1940b). In 1950, he published his monograph 'Taphonomy and the fossil record', in which he gave a broad outline of the study on burial of organic remains and formulated a number of generalizations. Although this book was published in Russian, it became widely known first in the USA, and in other Western countries.

Among researchers who worked with Efremov in the 1930s on Permian and Triassic tetrapods was Professor A.P. Bystrov. He combined the gifts of the morphologist and artist, and had created in 1935 reconstructions of the North Dvina fauna, and later of the dinocephalian fauna. He completed a number of studies on the histology of bones and teeth, the circulatory system of Palaeozoic amphibians (Bystrov, 1938, 1939, 1947) and, in the 1940s and early 1950s, he published detailed descriptions of some Permian amphibians and reptiles (e.g. Bystrov, 1944, 1957).

Researches in European Russia in the 1950s

Researches on Permian and Triassic tetrapods began in the late 1940s after a gap caused by the Second World War. Many new localities were discovered by surveyors working on a new programme to create the States geological map of the USSR at a scale of 1:200 000. A number of geologists gained fame as fossil hunters. Those working mainly in the northern regions of European Russia were Dr G.I. Blom from Nizhnii Novgorod, and Professor V.I. Ignat'ev from Kazan' University. Significant finds were made in southern regions by Dr V.V. Butsura and Dr V.A. Garyainov (Figure 1.4).

Figure 1.4. Dr Valentin Petrovich Tverdokhlebov surveys Lower Triassic sediments at Petropavlovka, north of the Sakmara River, north-east of Orenburg. These river deposits have yielded isolated bones of temnospondyl amphibians, procolophonids, and other tetrapods. (Photograph taken on the 1995 Saratov–Bristol Expedition to the South Urals.)

Figure 1.5. Peter Konstantinovich Chudinov, one of the leading Russian experts on mammal-like reptiles. He began his studies in the 1950s. He is pictured here, ready to go fishing, accompanied by the camp cook's dog, Jimmy Carter. (Photograph taken on the 1995 Saratov–Bristol Expedition to the South Urals.)

At this time, new researchers were beginning to work on fossil tetrapods. In the Palaeontological Institute in Moscow these were E.D. Konzhukova, the wife of I.A. Efremov, and two of his young students, B.P. V'yushkov (who died tragically at the age of 32) and P.K. Chudinov (Figure 1.5). Konzhukova gave the first description (1953) of eryopoid temnospondyls from the coal-bearing deposits of the basin of the Pechora River near the city of Inta, found in a mine by the geologist G.A. Dmitriev and others. Now they are ascribed to the lowest part of the Upper Permian. Later, Konzhukova (1955) established the presence in the southern Cis-Urals of the temnospondyl *Mastodonsaurus,* which suggested a Middle Triassic age. With this, she gave palaeontological evidence for the uppermost zone in the stratigraphic scheme of Efremov.

V'yushkov began his studies very early, at the age of 19–20, in 1945 with the discovery of the previously-mentioned Middle Triassic fauna with *Mastodonsaurus*, in southern Bashkortostan. He graduated from Saratov University, began to work at the Palaeontological Institute, and soon became the most energetic researcher in Efremov's laboratory. In 1947–9, V'yushkov and Konzhukova, as well as N.I. Novozhilov, conducted an expedition in the Orenburg region, where they excavated a locality of latest Permian (late Tatarian) batrachosaurs near the village of Pron'kino. In the same years, V'yushkov studied the still poorly known localities of the same age near the city of Gorky (now Nizhnii Novgorod), and also a number of other places in the European and Asian parts of the former USSR. V'yushkov's studies of these localities formed the basis for his establishment of the Gorky Batrachosaur Complex as part of Efremov's stratigraphic scheme, equivalent to the North Dvina Pareiasaur Complex. V'yushkov (1957b) described from here new genera of batrachosaurs, including the chroniosuchians. His study of theriodonts from Isheevo and from North Dvina (V'yushkov, 1955) supported Efremov's opinion that there was a significant gap in evolution between the Cis-Uralian Dinocephalian and Pareiasaur faunas.

We are indebted to V'yushkov and Chudinov (1956, 1957) for the first information on a number of groups of ancient tetrapods, previously unknown from Russia, whose remains had been collected by geologists and palaeontologists: unequivocal North American elements (captorhinids and caseids) from the Upper Permian of the northern regions, and procolophonids from the Lower Triassic of central and southern regions of the east of European Russia. In addition, V'yushkov (1957a), following finds in the basin of the Vetluga River made by the geologists G.I. Blom and V.I. Ignat'ev, recognized for the first time in

Figure 1.6. A scene from the early Triassic of the Urals Region, showing a large erythrosuchid, *Garjainia*, chasing some temnospondyls which are lingering at the water's edge. The theriodont *Silphedosuchus* is hunting some small prolacertiforms and procolophonids in the foreground. (Illustration by A.A. Prokhorov.)

Russia the amphibian *Tupilakosaurus*, which had previously been found in marine Induan deposits of Greenland. This was a critical stratigraphic marker, linking the continental basal Triassic of European Russia to the global standard stratigraphic scheme based on ammonoids.

However, V'yushkov's main interests were still in the Orenburg region of the Cis-Urals. In 1954, he conducted large excavations there using bulldozers, the first time this had been done in Russia, but commonplace later. Excavations near the village of Perovka, where the geologist P.N. Klimov had once found specimens of *Rhadiodromus* which were described by Efremov (1940c), yielded a diverse fauna of gigantic kannemeyeriid dicynodonts. A Lower Triassic locality near the village of Rassypnoe, found by V.A. Garyainov, produced the first whole skeletons of proterosuchian archosaurs (Figure 1.6). The untimely death of V'yushkov prevented him from completing these researches.

Efremov and V'yushkov (1955) published a catalogue of localities of Permian and Triassic terrestrial tetrapods from the territory of the USSR, which gave the results of the discoveries and researches of the first half of the twentieth century. This catalogue concluded the Efremov era in the study of the ancient tetrapods of Russia, and it was made available widely in English in an abbreviated version (Olson, 1957).

P.K. Chudinov, the last of Efremov's students, began research on the collections of small reptiles of the Mezen'–Belebey Cotylosaur Complex (Chudinov, 1955, 1957). However, his main achievement was the study of numerous early therapsids based on rich new material collected by him during excavations of the locality Ocher in Perm' Province. This was one of the greatest localities of Permian tetrapods, discovered in Upper Kazanian deposits, and it was the scene of perhaps the largest excavations in the history of Russian palaeontology. It was excavated by Chudinov during four field seasons (1952, 1957, 1958, 1960) with the use of bulldozers. The area of excavation reached 6000 square metres. This yielded an unknown number of individuals, but the known cranial remains indicate at least 50 animals. The results of the study of

those remains were given by Chudinov (1983), who considered the morphology, phylogeny, and origin of the eotheriodonts, dinocephalians, and early dicynodonts, the Venyukoviidae. The vast Ocher fauna revealed one of the most important pages in the fossil record of the Late Permian of Russia.

1960–95: new specimens, revised biostratigraphy, and phylogeny

At the beginning of the 1960s, a new generation of researchers started to study ancient tetrapods, and the number of specialists grew with each decade. In addition, field geologists, primarily Prof. V.R. Lozovskii (Moscow Geological Prospecting Institute) and Dr V.P. Tverdokhlebov (Figure 1.4) contributed their efforts in the hunt for specimens and in establishing stratigraphies. From this time, Saratov University took an active part in the excavation and field study of localities, this work having been conducted earlier only by the Palaeontological Institute in Moscow. The largest excavations, using bulldozers, were conducted by V.G. Ochev (Figure 1.7) in the southern Cis-Urals. First of all, a group of taphonomically diverse large localities were dug out along tributaries of the Ural, the Donguz and Berdyanka Rivers in the Sol'-Iletsk district, Orenburg Province. This small territory with numerous finds of tetrapods was named the 'Sol'-Iletsk phenomenon'.

All these localities were considered earlier as Lower Triassic. As a result of the excavations it was possible to obtain, besides kannemeyeriid dicynodonts, theriodonts and basal archosaurs, complete skeletons of capitosauroid temnospondyls (in one of the localities on the River Berdyanka, a concentration of 20 skeletons was dug up; Figure 1.8), and for the first time in Russia mass remains of plagiosaurs were collected. On the basis of the temnospondyls, it was possible to date this assemblage as Middle Triassic, but older than the fauna with *Mastodonsaurus*, which had been found here earlier. This assemblage was named the *Eryosuchus* Fauna, after its dominant genus of capitosauroids.

As a result of overviews of the new material, mainly from the Moscow Syncline and the southern Cis-Urals, M.A. Shishkin (Palaeontological Institute) and V.G. Ochev (Saratov University) suggested in 1967 a more complete and detailed scheme of stratigraphy of the continental Triassic, based on tetrapods, in which a number of sequential faunas where distinguished: Lower Triassic Neorachitome (Zone V in the scheme of Efremov), *Parotosuchus* (Zone VI of Efremov), Middle Triassic *Eryosuchus* (not distinguished in Efremov's scheme), and *Mastodonsaurus* (Zone VII of Efremov). Some of these were subdivided in more detail. A similarly improved scheme for the Permian

Figure 1.7. Vitalii Georgievich Ochev, Professor at Saratov University, leading expert on the fossil reptiles and amphibians, and the biostratigraphy, of the Triassic of the south Urals. He began his studies in the late 1950s. (A) V.G. Ochev wields a pick at the Koltaevo III locality, site of numerous finds of dicynodonts in the 1960s. (B) V.G. Ochev and Misha Surkov (foreground) working at the Koltaevo III locality. (Photographs taken on the 1995 Saratov–Bristol Expedition to the South Urals.)

Figure 1.8. Map of a mass accumulation of temnospondyl (*Eryosuchus*) skulls and other elements (jaws, rhomboid interclavicle plates, ribs, vertebrae, and limb bones) from a site discovered on the Berdyanka River in the early 1960s by V.G. Ochev.

was suggested by Chudinov (1969). It was based mainly on three successive faunas: the Ocher and Isheevo, both dinocephalian (Zones I and II of Efremov) and the North Dvina or Sokolki, according to M.F. Ivakhnenko, the pareiasaurian (Zone IV of Efremov; in his opinion, a gap corresponded to Zone III).

Since the 1960s, further work has been carried out on the morphology of vertebrates, using the older specimens, as well as newly collected materials. L.P. Tatarinov (1974, 1976) described new therapsids. Among other new taxa of tetrapods established by him, was the first Upper Permian archosaur, *Archosaurus*, from the locality Vyazniki in the Oka River basin (Tatarinov, 1960).

M.A. Shishkin concentrated his attention on amphibians. In publications on brachyopoids and plagiosaurs respectively, Shishkin (1973, 1987) considered the morphology and development of the head of temnospondyls, and the evolution of the middle ear and of the vertebral column in the lower tetrapods. He established for the first time the brachyopoid affinities of *Tupilakosaurus*, long regarded as a palaeontological puzzle. Shishkin described a number of new genera of temnospondyls. Of particular significance for the correlation of the continental and marine Triassic was his description of finds of temnospondyls from nearshore marine deposits: *Parotosuchus* from the Upper Olenekian from the Mangyshlak Peninsula, the benthosuchid *Benthosphenus* from the Lower Olenekian of the Far East, and the rhytidosteid *Boreopelta* from the Lower Olenekian of the River Olenek basin in Siberia. The interest of these findings were increased by Shishkin's (1994) identification of the Gondwanan genus *Rhytidosteus* in the *Parotosuchus* Fauna of the southern Cis-Urals.

V.G. Ochev studied the systematics and phylogeny of the largest group of Lower Triassic temnospondyls, the Capitosauroidea, and gave the results in two monographs (Ochev, 1966, 1972). Among a number of new taxa, the genus *Eryosuchus* was established, an index fossil of the new Middle Triassic fauna already noted. Later, Ochev focused his attention on the early archosaurs, described the first rauisuchid from the Triassic of Russia, *Vjushkovisaurus* (Ochev, 1982), and considered the phylogeny of proterosuchians in a special monograph (Ochev, 1991).

N.N. Kalandadze (1969, 1973) studied the extensive material of Middle Triassic dicynodonts of the southern Cis-Urals, which allowed him to recognize this fauna as one of richest in the world. A big event was the identification by Kalandadze (1975) of the first *Lystrosaurus* in Russia from materials which had been collected by G.I. Blom from the lowermost Triassic on the Vetluga River.

M.F. Ivakhnenko studied the fossil material of the most primitive reptiles and reptiliomorph amphibians. He published monographs on procolophonids (Ivakhnenko, 1979) and on the Permian reptiliomorph amphibians of the former USSR (Ivakhnenko, 1987).

In 1980, jointly with G.I. Tverdokhlebova from Saratov University, he published a monograph on Chroniosuchia. Subsequently, he identified some North America elements, such as the captorhinid *Rjabininus* in the Inta fauna on the River Pechora (Ivakhnenko, 1990). Ivakhnenko and Tverdokhlebova (1987) reported three skeletons of *Belebey*, described earlier from the Belebey locality, in the Upper Kazanian locality Krymskoe in Orenburg Province. Ivakhnenko (1990) suggested *Belebey* was related to *Bolosaurus* and he described a related genus, *Davletkulia*, from the southern Cis-Urals.

Since the second half of the 1970s, a number of new researchers at the Palaeontological Institute took an energetic part in field studies in the east of European Russia and in research on ancient tetrapods. S.N. Getmanov (1989) published his monograph on the Lower Triassic temnospondyl family Benthosuchidae on the basis of new materials, especially from the locality Tikhvinskoe, near Rybinsk, on the Upper Volga, which has yielded an astonishingly abundant collection of skulls. Yu.M. Gubin (1991) studied archegosauroid amphibians. M.A. Shishkin and I.V. Novikov, as a result of field work from 1984 to 1990, assembled new data on the little-known localities of Triassic tetrapods of the Timan–North Urals region. Novikov (1994) added to the systematic and stratigraphic distribution of Triassic amphibians and procolophonids. A.G. Sennikov (1995) studied the basal archosaurs of the eastern part of European Russia, and he revealed here for the first time Lower Triassic rauisuchids and Middle Triassic euparkeriids.

The vast amount of material accumulated by the 1990s indicated new conclusions on the evolution of the Cis-Uralian tetrapods and their stratigraphy. The largest excavations are being conducted now at an Upper Permian locality near Kotel'nich in Kirov Province, which is producing an abundance of pareiasaur skeletons. A rich assemblage of therapsids was also found there, the study of which has just started. This is a more ancient fauna of vertebrates than the North Dvina (Sokolki). The tetrapod complex with the oldest archosaur, *Archosaurus* (the locality of Vyazniki in Vladimir Province and others), was dated as uppermost Permian. This suggested the recognition of a specific stratigraphic horizon, with tetrapods transitional to the Triassic (Shishkin, 1990; Sennikov, 1991). Eventually, the work by Novikov (1994) on the assemblage from the Timan–North Urals region indicated the 'Tsyl'ma Tetrapod Complex' transitional between the 'Neorachitome' Fauna and the *Parotosuchus* Fauna.

Since the 1980s, general questions about the history of ancient tetrapods, a characteristic of Efremov's approach, were addressed. A series of articles on biogeography were published by N.N. Kalandadze, A.G. Rautian, M.A. Shishkin and V.G. Ochev, on the global stratigraphic correlation of Triassic faunas of terrestrial vertebrates (Ochev and Shishkin, 1989) and on the origins of faunas (M.F. Ivakhnenko and others).

In recent times, in the east of European Russia, about 1000 localities of Permian and Triassic tetrapods have been recorded. The growth of data on the Cis-Urals faunas can be observed in a number of review documents, in Efremov's and V'yushkov's (1955) catalogue and in the textbook by Orlov (1964). Recently, the number of Permian and Triassic genera described from Russia reached 150.

The lion's share of study of the Permian and Triassic tetrapods from the former Soviet Union still falls in the east of European Russia. The rest of this territory in general is poor in finds. The most significant were made in Central Asia. First were the large localities of discosauriscids discovered in the late 1950s and in the early 1960s in the Upper Carboniferous or Lower Permian of Kazakhstan and in the Lower Permian of Tadzhikistan. The largest excavation was conducted by an expedition of the Palaeontological Institute under the leadership of N.N. Kalandadze in 1975. Even more interesting is the Madygen locality in the Fergana Valley in Kirgizstan, first recognized for its rich plant remains. The palaeontologist, A.G. Sharov, when searching for fossil insects in the 1960s, found here, and described, the peculiar small reptiles *Longisquama* and *Podopteryx* (now *Sharovipteryx*; Figure 1.9). Continental deposits in Siberia have so far yielded only a few finds of temnospondyl larvae and a fragmentary dicynodont (probably *Lystrosaurus)*. The Asian part of Russia still awaits more intensive researches.

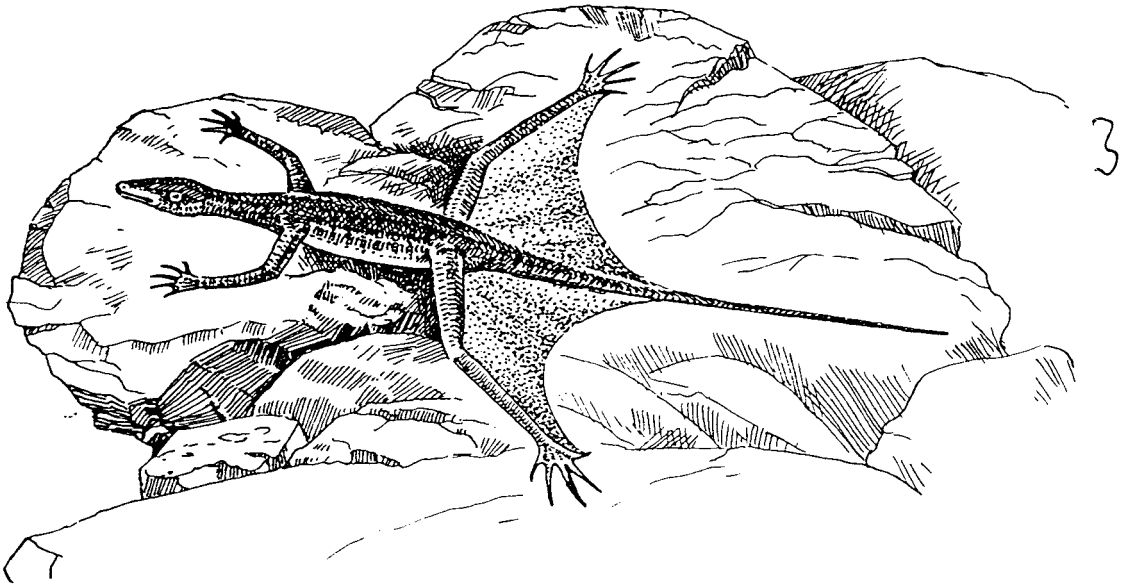

Figure 1.9. The enigmatic small gliding reptile *Sharovipteryx* from the Middle-Late Triassic of Kirgizstan. (Reconstruction by A.A. Prokhorov.)

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