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Differentiation of Tetrapod Communities and Some Aspects of Biotic Events in the Early Triassic of Eastern Europe

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Abstract—The patterns of spatial differentiation of the Early Mesozoic terrestrial biota in Eastern Europe and Australia–Tasmania demonstrate that the tetrapod faunal recovery following the Permian extinction was characterized by both global and regional heterogeneity. Local distinctions observed in the development of Early Triassic tetrapod assemblages of European Russia allow the recognition of the following realms: (1) the central and northern regions of the East European Platform (Moscow–Mezen Syncline) and the Timan–North Ural Region; (2) the southern Fore-Urals, including the Obshchii Syrt Plateau; and (3) the southern regions of the East European Platform (the slope of the Voronezh Anticline). Climatic conditions at the initial stage of the development of local communities were characterized by an increase in aridity and seasonal contrasts of climate. Therefore, terrestrial assemblages mostly concentrated in the aquatic and coastal biotopes. Accordingly, vertebrate assemblages of the region were dominated everywhere by aquatic amphibians and semiaquatic reptiles, while the accompanying palynomorph assemblages show the predominance of hygrophilous vegetation indicative of swampy mangrove setting. With respect to amphibians, a peak of local biogeographic differentiation falls on the onset of the Early Triassic and, in the case of reptiles, on the end of this time span. This change conforms to the increasing role of reptiles in the overall taxonomic diversity with time. Among the three main biogeographic units of the region, the Southern Fore-Ural Realm is distinguished by the maintenance of distinct faunal links with Gondwanan regions. The Southern Realm shows a connection with the Germanic Basin and more western Euramerican areas, which is documented for the Late Olenekian and occurred under influence of coastal marine conditions.

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INTRODUCTION

The initial (Early Triassic) stage of the recovery of the terrestrial biota after the Late Permian mass extinction developed against a background of a general uplift and integration of land masses under special climatic conditions. The major climatic features combined global warming, evening out of temperature distinctions, and increasing aridity of climate inherited from the Permian Time (Ochev, 1992a; Ochev and Shishkin, 1998; Zharkov and Chumakov, 2001). This resulted in the ultimate formation of the circumequatorial arid belt, which extended to the tropical latitudes (Tucker and Benton, 1982; Lozovsky, 1993). At the same time, an increase in seasonal and spatial climatic contrasts is detected. The latter were manifested in the general zonal differentiation of abiotic conditions (with a substantial decrease in aridity in temperate and high latitudes) and, apparently, in the local distinctions associated with the dissection of the relief and increased contrasts in humidity between elevated and lowland sites. All these factors resulted in the fragmentation of the former biotopes suitable for terrestrial vertebrates.

Accordingly, tetrapod communities of that time, contrary to widespread opinion (e.g., Shubin and Sues, 1991), show a clearly pronounced spatial nonuniformity. The first steps in their restoration after the Late Permian extinction passed on the basis of local evolutionary experiments, with a high degree of endemism of newly emerging faunas and an essential role in their structure of ephemeral genera and groups with very short geological history (Shishkin and Ochev, 1993a, 1993b, 1999, 2001). These groups include the few cosmopolitan taxa of that time. They were represented by exclusively aquatic or amphibiotic forms (some genera of amphibians and the dicynodont *Lystrosaurus*), which mostly managed to disperse at the Permian–Triassic transition, before the establishment of the circumequatorial climatic barrier.

Due to such run of events, the Early Triassic is the first stage in the geological history for which the global biogeographic zonation based on terrestrial vertebrates is possible (Shishkin *et al.*, 1996). This contrasts with concominant changes in the flora with the provincial borders existing since the Paleozoic becoming less distinct (Dobruskina, 1982). The general appearance of the vertebrate fauna at this time enables a recognition of the Southern Gondwanan (in the strict sense), Australian–Tasmanian, and Euramerican regions and, tentatively, the North Asian Region, on which very few data are so far available.

On this heterogeneous background, a more detailed differentiation of local tetrapod communities (Shishkin and Ochev, 2001) is also recognized. The study of this differentiation is limited by the incompleteness of the available Triassic fossil record for certain continents. At the present state of knowledge, it is possible to point out only two regions with a sufficiently detailed record for the analysis. These are the Australian–Tasmanian Region in Gondwana and Eastern Euramerica, including, first of all, European Russia (the East European Platform and the Ural Foredeep) in Laurasia. The eastern and western areas of the Australian–Tasmanian Region were inhabited by essentially different Early Triassic (mostly amphibian) faunas. The eastern fauna, dominated by the widespread capitosaurid *Rewanobatrachus* ("*Parotosuchus*")[1] and diverse primitive rhytidosteids; it was recorded in the Arcadia Formation in eastern Australia (Queensland). The western fauna (= "*Blinasaurus–Deltasaurus*" fauna) is most completely represented in the Knocklofty Formation in Tasmania and the Blina Shales in western Australia (Cosgriff, 1984). Although it is not improbable that the two communities differ in age, they most likely belong to the Early Olenekian Time. The borehole data in the Perth Basin, where the rhytidosteid *Deltasaurus* was found in coastal marine deposits of the Kockatea Formation in an interval characterized by Early Smithian ammonites and conodonts, support this age for the western community (compare with Cosgriff, 1965; McTavish and Dickins, 1974). The strictly continental fauna from the Arcadia Formation bears no unequivocal age markers (Balme, 1990) and, consequently, its correlation remains disputable (compare Anderson and Cruickshank, 1978; Thulborn, 1984; Warren 1985; Battail, 1988). However, judging from the presence of nonlonchorhynchine trematosaurids (A. Warren, personal communication) and from the evolutionary level of a number of reptiles (M.A. Shishkin and I.V. Novikov, personal observations), it should also be dated Early Olenekian.

In comparison with the Australian–Tasmania, the Lower Triassic of European Russia provides much better opportunities for the analysis of spatial differentiation of tetrapod communities, essentially being a model object for the study of post-crisis events in the history of the Early Mesozoic land biota. In the evolution of Early Triassic vertebrates, five or six successive faunal episodes are recognized in this region, as opposed to at most two known in Gondwana. Moreover, at least half of these episodes are represented by local modifications. Unlike records from other regions, most of the East European faunal sequence is reliably correlated with the standard biostratigraphic scale (Shishkin *et al.*, 2000). This minimizes the risk of taking purely chronological distinctions of particular assemblages for biogeographic varieties.

The results of preliminary analysis of the spatial differentiation of tetrapod faunas of Eastern Europe during the Early Triassic, and, partly, the factors that caused it are briefly reviewed below for three time intervals, i.e., the Induan, the Lower Olenekian, and the Upper Olenekian. They represent the major episodes in the development of Early Triassic tetrapods in the region (Shishkin and Ochev, 1999; Shishkin *et al.*, 2000). The Induan (Early Vetlugian) and Lower Olenekian (Late Vetlugian) intervals correspond to the *Benthosuchus–Wetlugasaurus* Fauna and include up to four consecutive episodes in its development; the Late Olenekian (Yarenskian) interval, comprising two (Fedorovskian and Gamskian) episodes, corresponds to the *Parotosuchus* Fauna. Local distinctions in the structure of synchronous communities, allow the recognition of several biogeographic units within this territory (Fig. 1). These are (1) central and northern areas of the East European Platform (Moscow and Mezen syneclises) along with the Timan–North Ural Region; (2) the Southern Fore-Ural Region, including the Obshchii Syrt (the slope of the Volga–Ural Anticline and the Ural Foredeep); and (3) southern areas of the platform (the slope of the Voronezh Anticline and, probably, the Caspian Depression). The first unit also demonstrates some hitherto poorly studied local distinctions. As all the Early Triassic faunas of the region are numerically dominated by temnospondyl labyrinthodont amphibians, the observable geographic distinctions in their composition are usually most reliable (at least for the early faunas).

Among the factors that underlay the spatial heterogeneity of the tetrapod communities considered is most clearly connected with the external biogeographic influences of regional biotas outside Eastern Europe and, partly, with the major habitats, for example, coastal marine or lacustrine environments.

The role of the climatic factors by themselves in this differentiation seems to be of little significance at the present state of knowledge. It is worth noting that, in the Early Triassic, the entire territory considered was situated at the periphery of the northern arid belt (Tucker and Benton, 1982, fig. 1; Lozovsky 1993, fig. 1) and might be relatively homogeneous in relation to the degree of climatic aridity. It is also necessary to take into account weak temperature gradients for the whole

[1] The proposed synonymy of the Australian *Rewanobatrachus* (Schoch and Milner, 2000) with the later *"Watsonisuchus"* from the base of the *Cynognathus* Zone of South Africa (Damiani, 2001; Steyer, 2003) is incorrect. The latter is a junior synonym of the South African *Kestrosaurus*, which is closely related to the European *Parotosuchus* of the same age (Shishkin *et al.*, 2004; Shishkin, 2005).

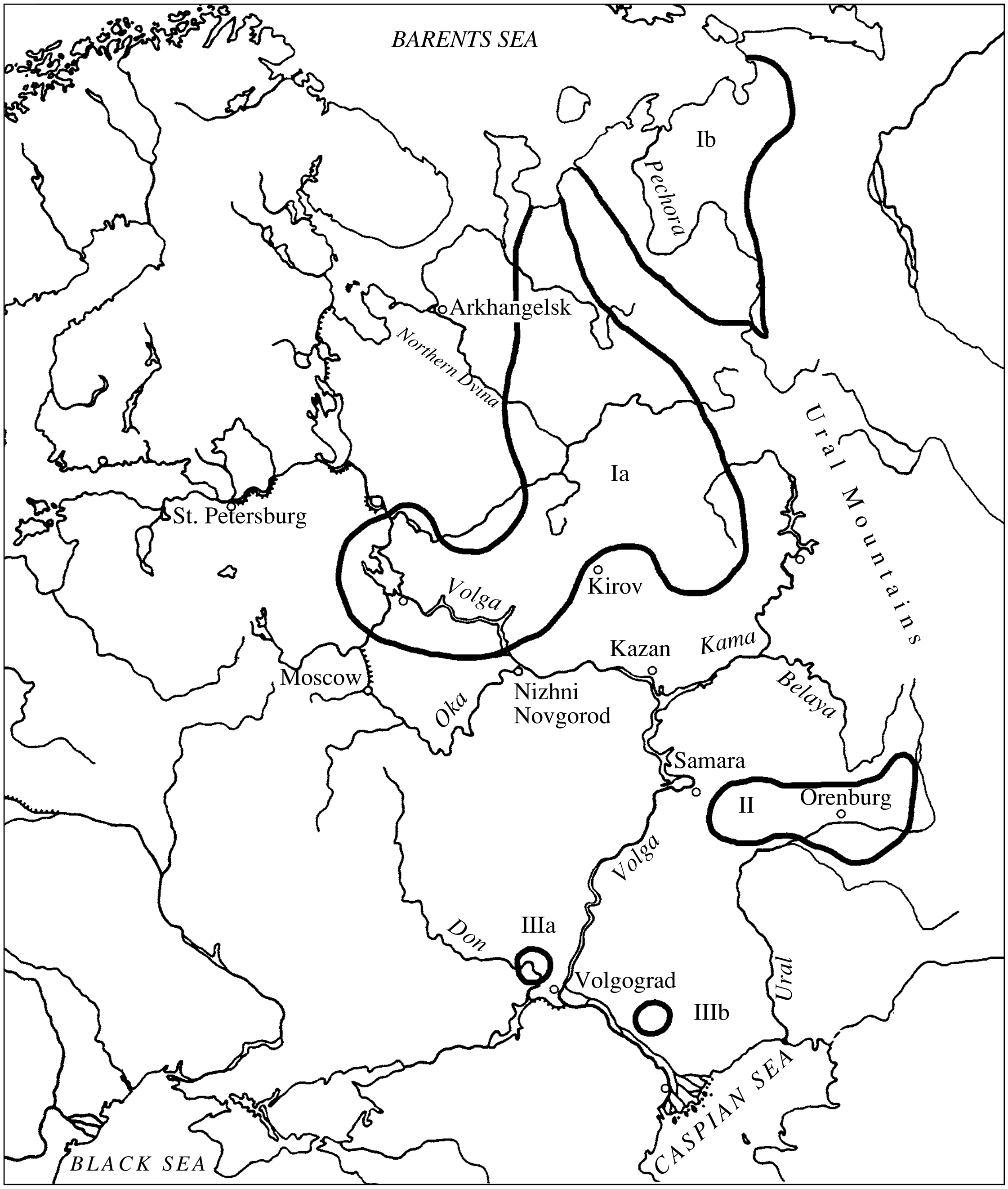

Fig. 1. Areas of occurrence of bone-bearing continental deposits of the Lower Triassic in European Russia (generalized). Designations: (I) northern and central, (II) Southern Fore-Ural, and (III) southern regions; (Ia) Moscow and Mezen syneclises; (Ib) Timan–North Ural Region (Pechora Depression; Korotaikha and Bol'shaya Synya depressions of the Ural Foredeep); (II) Southern Fore-Ural Region (slope of the Volga–Ural Anticline and the southern part of the Ural Foredeep); (IIIa) the slope of the Voronezh Anticline; and (IIIb) Caspian Depression.

of the Early Triassic land (Ochev, 1998, 2000; Ochev and Shishkin, 1998), which allowed the existence of herpetofauna even in the subpolar paleolatitudes.

On the other hand, under conditions of a rather dry seasonal climate, the entire East European Region should be characterized by sharply expressed gradients of humidity at transition from the final drainage areas (lowland lakes and rivers with their banks) to more elevated sites. Accordingly, terrestrial animals and vegetation of that time were overwhelmingly accumulated in the coastal zones of water basins and immediately around them, that is, in the most humid biotopes. In particular, over 90% of all remains of Early Triassic tetrapods of the region belong to aquatic labyrinthodont amphibians or to semiaquatic coastal reptiles (basically to proterosuchian archosaurs), which were markedly larger than the other members of local communities (Ochev, 1992a, 1994; Shishkin and Ochev, 1993a, 1993b, 1998, 1999; 2001). Likewise, the palynological assemblages of the region during almost the entire Early Triassic are dominated by spores of hygrophilous plants (lycopsids or ferns), indicating the prevalence of swampy-mangrove vegetation. Taeniate pollen of the xerophytic conifers plays only a subordinate role; its presence may result from distant transportation from elevations mainly occupied by this component of flora (Yaroshenko *et al.*, 1991; Ilyina and Novikov, 1994; Ilyina, 2001a, 2003).

Such conditions of plant microfossils are especially important because they are much more resistant to a distant transportation than bone remains. Therefore, their total composition for a given biota reflected in the final burials seems less biased by taphonomic factors than in the case of vertebrates. In general, the influence of the above considered climatic features on the composition of tetrapod communities, were likely comparable in all areas of the region.

INDUAN EPOCH: VOKHMIAN HORIZON, *BENTHOSUCHUS–WETLUGASAURUS* FAUNA: *TUPILAKOSAURUS* GROUPING

This epoch corresponds to the maximum of the Early Triassic aridization, which is reflected in both the composition and general pattern of East European tetrapod communities, in which the strictly terrestrial animals are only represented by small-sized forms (Ochev, 1992a).

The peak of aridity obviously corresponds to the beginning of the Induan. This is evident from features of the poor Early Vokhmian Palynomorph Assemblage of the Moscow Syneclise, described as the associations of *Cycadopites* sp.–*Klausipollenites schaubergeri* and *Striatoabieites richteri–Klausipollenites schaubergeri* (Yaroshenko and Lozovsky, 2004). Even taking into account the probability of an important role in this assemblage of redeposited Permian taxa, it is possible to infer the total domination of pollen of xerophytic gymnosperms, which indicates a very restricted role of swampy–lacustrine biotopes at this time. The high-latitude analogues of this association from the Arctic basin, known in East Greenland and on the shelf of the Barents Sea (the Harvet Formation), are dated to Lower Griesbachian (Yaroshenko and Lozovsky, 2004; Mangerud, 1994). However, in the last case, the palynomorph assemblage is much richer and shows a prevalence of spores of moisture-loving plants. It is remarkable that, in general, the composition of plant microfossils from this interval points to a marked uniformity of the flora of the entire Northern Hemisphere (Mangerud, 1994).

The successive interval of the Induan (the Upper Griesbachian–Dienerian) is characterized in Eastern Europe by quite noticeable expansion of wet lowland biotopes. Accordingly, the dominant role among plant remains is played here by spores of lycopsids, as illustrated by the composition of *Densoisporites complicates–Ephedripites* sp. and *Ephedripites permasensis–Pechorosporites disertus* assemblages in the Moscow Syneclise and their analogues in the Timan–North Ural Region (assemblage of *P. disertus*) (Yaroshenko *et al.*, 1991; Ilyina, 2001a; Yaroshenko and Lozovsky, 2004). Almost all vertebrate records of the Vokhmian Horizon belong to this interval.

Regional differences in the composition of the East European tetrapod communities of that time are quite clearly expressed. The specific feature of the amphibian fauna of the Obshchii Syrt Plateau is the presence of some taxa of southern Gondwanan origin that remain unknown in other areas discussed. This is primarily the earliest capitosaurid of the genus *Wetlugasaurus* (represented by the archaic *W. samarensis*), which is closely related to the Australian *Rewanobatrachus* from the Arcadia Formation and the most widespread labyrinthodont in the Southern Fore-Ural Region at that time interval. Another Gondwanan element is the primitive trematosauroid cosgriffiid, which is probably a relict of Permian archegosauroids. In contrast to the early *Wetlugasaurus*, it is extremely scarce. It is not improbable that this genus is synonymous to the poorly known synchronous *Gonioglyptus* from the Panchet Group of India (Shishkin, 2002). Apparently, another distinctive feature of the Fore-Ural community is the presence of primitive benthosuchids, such as (*"Parabenthosuchus" uralensis* Ochev, 1958), which appeared in the northern areas as late as in the Early Olenekian (Rybinskian).

In the Moscow Syneclise, on the contrary, synchronous temnospondyl amphibians are nearly totally dominated by a member of the brachyopoid family Tupilakosauridae (*Tupilakosaurus wetlugensis*), the cosmopolitans of the Induan. Among the strictly aquatic amphibians known for the beginning of the Early Triassic, they are the smallest forms, and obviously predominantly inhabited shallow basins. Tupilakosaurids were also found in Greenland, India (Shishkin, 1973), South Africa (Warren, 1999), and Antarctica (unpublished data of M.A. Shishkin); however, their remains are abundant only in the northern regions, which suggests that they emerged in the Laurasian Region. In the southern Fore-Urals, they are usually represented by isolated finds (the only exception is the locality near the city of Perevolotsk in the Orenburg Region in the interfluve of the Samara and Ural rivers. Another cosmopolitan group of amphibians that occur in the Moscow Syneclise and is characteristic of the beginning of the Early Triassic is the family Lydekkerinidae. It is represented there by very rare finds of the only Laurasian member, i.e., the genus *Luzocephalus*. This family, unlike tupilakosaurids, undoubtedly emerged in Gondwana where it is widely represented (Shishkin *et al.*, 1996). Its penetration into the northern regions most likely proceeded along the continental coasts, which is probably indicated by frequent finds of *Luzocephalus* in coastal marine Induan deposits of Greenland. The dispersal of lydekkerinids from the north or the west into European Russia was apparently limited.

Another characteristic difference in the composition of tetrapods between the Northern Region and Southern Fore-Urals, detectable as early as the Induan (Early Vetlugian), concerns the relict chroniosuchian anthracosaurs of the family Bystrowianidae. During the entire Early Triassic of the Moscow Syneclise, they were mostly represented by narrow-scute members of the genus *Axitectum*. On the contrary, in the Southern Fore-Ural Region and on the Obshchii Syrt Plateau, where bystrowianids appeared later (in the Rybinskian Time), they are represented exclusively by taxa with wide dorsal scutes, such as *Synesuchus* and *Dromotectum* (Shishkin and Novikov, 1992; Novikov and Shishkin, 1995, 2000; Novikov *et al.*, 2000). In the northern areas, taxa of this type appeared only at the end of the Early Triassic (unpublished data of M.A. Shishkin).

Differences in the composition of reptiles between local Induan tetrapod communities are not so conspicuous. Parareptiles of that time are characterized by wide spread of primitive procolophonids (*Phaanthosaurus* and *Contritosaurus*) in the central areas of the East European Platform, versus their rare presence in the Southern Fore-Ural Region. As for proterosuchid archosaurs, the primitive small genera *Vonhuenia* and *Blomosuchus* were found only in the central areas; however, it is difficult to draw unequivocal conclusions from this fact because of the restricted material available. The same is even truer for the scattered finds of the lystrosaurid dicynodont *Lystrosaurus* (*L. georgi*) in the basal Lower Vetlugian (Astashikha and Ryabinsk) beds of the Vyatka–Vetluga basin (Kalandadze, 1975; Ochev, 1992b; Lozovsky, 1983). Lystrosaurids, which emerged in Gondwana, also expanded in Asia, as is evident from their presence in the southeast of the continent, in China and central Siberia; therefore, it is highly improbable that their migration routes to the central areas of European Russia did not involve the Fore-Ural Region. The extremely short-term (up to the Middle Induan) presence of this unique and rather rare phytophagous component of the local Early Triassic tetrapod fauna indicates relatively severe climatic conditions and limited resources in coastal biotopes that hosted these amphibiotic animals (Ochev and Shishkin, 1998).

EARLY OLENEKIAN EPOCH: RYBINSKIAN–USTMYLIAN HORIZONS, *BENTHOSUCHUS–WETLUGASAURUS* FAUNA: LATE GROUPINGS

The Early Olenekian Time is characterized by a eustatic maximum (Lozovsky, 1992), which resulted in the expansion of lakes in Eastern Europe. Accordingly, the sporomorph assemblages of that time were dominated by spores of hygrophylous plants (with typically Triassic elements prevailing), with lycopsids being gradually replaced by ferns. These changes are documented in the Moscow Syneclise by the assemblage from the Rybinskian Horizon (Strok *et al.*, 1984). Its analogues in the Timan–North Ural Region is the *Densoisporites nejburgii–Lundbladispora variabilis* Assemblage, which is dated based on the correlation with the Early Smithian coastal marine palynomorph assemblages of northern Siberia (Ilyina and Novikov, 1994; Ilyina, 2001b).

At that time, the tetrapod fauna of this region demonstrated an intensive diversification of taxa inhabiting mainly lake basins. These are the autochthonous benthosuchid amphibians and their derivatives from the subfamily Thoosuchinae, which gave rise to typical trematosaurids. The genus *Benthosuchus* shows clear racial distinctions in the northern areas and the Southern Fore-Ural Region. Its descendants, toosuchines, are especially diverse on the Obshchii Syrt Plateau, where they include several endemic genera (*Prothoosuchus, Trematotegmen*, and a number as yet undescribed forms). These taxa coexisted with more widespread *Thoosuchus* and *Angusaurus*. Substantial changes are recorded for the distribution pattern of capitosaurids, which are represented by *Wetlugasaurus*. Its main range, contrary to the Induan epoch, is shifted from the Southern Fore-Ural Region to the central and northern areas, where the Rybinskian and Sludkian intervals are characterized by the presence of a single species of *Wetlugasaurus* (*W. angustifrons*). The Late Vetlugian time (the Ustmylian interval) is characterized by the presence of *Wetlugasaurus malachovi* and, apparently, another closely related species described as *Vladlenosaurus alexeyevi*[2] (Ivakhnenko *et al.*, 1997; Morkovin and Novikov, 2000). This species was confined to lacustrine habitats and, hence, acquired the external appearance of benthosuchids, the most typical inhabitants of these biotopes. At the same time, the archaic *W. samarensis* probably persisted in the Fore-Ural Region at the beginning of the epoch considered, being later replaced there by *W. angustifrons.*

In the late phase of the Early Olenekian Time (Ust'-Myla Horizon), the areas of Mezen and Pechora syneclises also demonstrated certain faunal specificity, with the presence of benthosuchid ancestors of yarengiids (*Vyborosaurus*). In general, characteristic features of tetrapod differentiation in the Ustmylian time remain poorly understood, mostly because of difficulties in the recognition of vertebrate assemblages of this age outside the northeastern areas of the platform.

The appearance of advanced procolophons with differentiated teeth in the Early Olenekian was accompanied by the first regional differences in their composition. Along with the genera common for the northern areas and Southern Fore-Ural Region (*Tichvinskia* and *Orenburgia*), endemic taxa are found in the Timan–

[2] M.A. Shishkin believes that this species should be assigned to the genus *Wetlugasaurus*.

North Ural Region (*Timanophon, Insulophon, Lestanshoria*) and on the Obshchii Syrt Plateau (*Samaria*).

Some local differences are also obvious in diapsid reptiles. The group of archosaurs, with proterosuchids (*Chasmatosuchus*) and the first rauisuchids (*Tsylmosuchus*), is represented by different species in the northern areas and Southern Fore-Urals. The Fore-Ural species of *Chasmatosuchus* and *Tsylmosuchus* were larger and apparently appeared earlier than in the north (the former in the Vokhmian, and the latter, in the Rybinskian time). It is also noteworthy that *Tsylmosuchus* is much more frequent in the Moscow Syneclise. Other distinctions are so far less significant as they are based on isolated finds. This concerns the presence of the prolacertid *Boreopricea* in the northern areas and the proterosuchid *Exilisuchus* in the Fore-Urals.

LATE OLENEKIAN EPOCH: YARENSKIAN HORIZON, *PAROTOSUCHUS* FAUNA

The Late Olenekian retains a seasonal semiarid climate, but with the growing tendency towards milder conditions (see below). Indirectly, this is in accordance with the concept that the northern margin of the European continent along with the Arctic shelf shifted into the humid belt by the end of the Early Triassic (Mangerud and Romund, 1991). The general decrease in aridity in Eastern Europe is documented both in lithological features and the composition of the tetrapod fauna. The fauna shows a sharp increase in the proportion of terrestrial taxa (reptiles) in the total taxonomic diversity in comparison with aquatic amphibians, and an essential body size growth in members of both groups (Ochev, 1992a). At the same time, the absolute prevalence in abundance of amphibian remains, combined with the extreme rarity of theromorph reptiles and the absence of typically phytophagous taxa in these communities, indicate that a set of biotopes favorable for tetrapods remained approximately the same as in the previous epoches of the Early Triassic. The bulk of taxa continued to occupy the areas connected with lowland water basins.

Accordingly, plant microfossils are still dominated by spores of coastal hygrophilous taxa with the leading role of ferns. The best studied association of this time from the Timan–North Ural Region is known as the *Aratrisporites robustus–Verrucosisporites pseudomorulae* Assemblage (Yaroshenko *et al.*, 1991; Ilyina, 2001a); a similar assemblage was described from the Mezen Syneclise (Strok *et al.*, 1984, p. 117). At the same time, there are signs of differentiation of plant communities, which were probably caused by various factors. In particular, in the Mezen Syneclise, along with the Upper Yarenskian association of hygrophylous type from the basin of the Vychegda River, there is a synchronous assemblage described from the Mezen River area with the prevalence of pollen of conifers (Minikh and Makarova, 1990). In the Southern Fore-Ural Region, deposits of the same age (Petropavlovskaya Formation) are characterized by a poor palynological assemblage, which pollen component, according to Makarova and Vergai (1995), is dominated by Ginkgoaceae. The extremely low taxonomic diversity of this association could have been caused by the predominant elevated relief forms in this realm, with thin vegetation and with the restricted area of local water bodies and adjacent biotopes.

According to the data on the Timan–North Ural Region, the Late Olenekian palynomorph assemblage includes two successive evolutionary stages with the later stage characterized by the presence of some Middle Triassic taxa (Ilyina, 2001a, 2003). These stages most likely correspond to two phases in the development of Late Olenekian tetrapods (see below).

In comparison with the preceding intervals, the analysis of regional distinctions of tetrapod communities for the Yarenskian are extended by new data on the faunal composition at the southern peripheral areas of the East European Platform (slope of the Voronezh Anticline; Lipovskaya Formation of the Don River basin) (Rykov and Ochev, 1966; Garyainov and Rykov, 1973; Novikov *et al.*, 2001, 2002; Sennikov and Novikov, 2002).

In general, the faunal stage considered includes two phases or groupings corresponding to the Fedorovskian and Gamskian horizons of the Moscow Syneclise and their analogues. Although vertical ranges of taxa typical for these groupings, as well as exact dating of some relevant localities are not always well defined, some major features of the spatial differentiation of the Late Olenekian communities are, nevertheless, quite clear.

The dominant groups of Late Olenekian amphibians everywhere show a decrease in the taxonomic diversity. Capitosaurids and brachyopids (the genera *Parotosuchus* and *Batrachosuchoides*, respectively) in different areas differ only at the species level. At least for the genus *Parotosuchus*, which shows two successive Early Triassic evolutionary grades, i.e., the *helgolandiae* and *nasutus* types from the Fedorovskian and Gamskian horizons, respectively, (Ochev *et al.*, 2004), some species-level diversity is recorded within the same (Gamskian) interval. In paticular, forms of the *nasutus* type comprise *P. panteleevi* from the Don River basin, corresponding to *P. orenburgensis* from the Southern Fore-Urals and *P. komiensis* from the Vychegda River basin.

The spatial differentiation of trematosaurids has not been recognized so far. The stratigraphic analogues of the Fedorovskian Horizon in the Caspian Region (the Bogdo Formation) yielded *Inflectosaurus*, which is apparently also present in synchronous deposits of the northern areas in the Vyatka River basin. The Lipovskaya Formation of the Don River basin has yielded a more specialized Central European genus, *Trematosaurus* (undescribed new species), which is probably accounted for by the younger (Gamskian) age of the host deposits. The possibility of this species' presence in Gamskian deposits of the Moscow Syneclise in the Vychegda River area is not excluded. On the other hand, the relatively well studied community of the Don River basin, unlike the northern fauna of the Gamskian age, bears no evidence of the presence of descendants of benthosuchids, closely related to trematosaurids of the family Yarengiidae (Novikov *et al.*, 2002).

With regard to other groups of amphibians, the most biogeographically significant record is the presence in the southern Fore-Urals of the Gondwanan family Rhytidosteidae represented by the South African genus *Rhytidosteus* (Shishkin, 1994). Although it is extremely rare, the presence of this genus is in accordance with other data on the Early Triassic faunal links between the southern Fore-Urals and Gondwana (see above). In the central parts of the platform (Fedorovskian Horizon of the Luza River basin), another rare allochthonous element is represented by a trematosauroid that is close to the almost synchronous *Cosgriffius* from North America (Shishkin, 2000).

Unlike amphibians, reptiles of the Late Olenekian Time, which essentially increased in taxonomic diversity (Ochev, 1992a), reached the maximum of regional differentiation for their entire Early Triassic history. Partly, these differences are observable in the composition of procolophons; thus, the Lipovskaya Formation of the Don River basin retains the relict *Orenburgia*, whereas the synchronous Gamskian deposits of the Moscow Syneclise contain a new genus, *Macrophon*.

The most prominent differentiation is shown by diapsids, which nearly lack common genera in the three regions compared, i.e., the North and South Fore-Ural, and the Southern (Don River basin) realms. A specific feature of prolacertids of the Southern Fore-Ural Region (Obshchii Syrt Plateau) is the presence of the giant genus *Vritramimosaurus* closely resembling the Middle Triassic (Bukobai) *Malutinisuchus* from the same region (Sennikov, 2005). At the same time, the Southern Region (Donskaya Luka locality) gives evidence of a new prolacertilian, probably belonging to a primitive tanystropheid, similar to *"Tanystropheus" antiquus* from Central and Western Europe (Novikov *et al.*, 2002).

Within the archosaurian group, proterosuchids (*Gamosaurus*) are known only in the north. Rauisuchids of the same area are represented by the genus *Tsylmosuchus* (Fedorovskian Horizon) and *Vytschegdosuchus* replacing it (Gamskian Horizon), whereas on the Obshchii Syrt Plateau, they are replaced by *Jaikosuchus*, and in the south (Don River basin), predominantly by *Scythosuchus* accompanied by a small endemic species of the genus *Tsylmosuchus*. In the southern Fore-Urals, the fauna of archosaurs shows additional indications of connections with Gondwana, manifested by the presence of early eyrthosuchids (*Garjainia*), which have close analogues in the synchronous lower subzone of the *Cynognathus* Zone of South Africa (Shishkin *et al.*, 1995). In the Moscow Syneclise, these taxa have not been recorded, whereas in the south, their presence is questionable.

In general, the highest specificity of the reptile component of the East European Late Olenekian faunas is found in its southern part (Don River basin). This area presents a unique record of such reptilian groups, as trilophosaurs (genera *Coelodontognathus, Doniceps*, and *Vitalia*), and among synapsids, of the most ancient representative of kannemeyerid dicynodonts, known by very rare remains (Novikov *et al.*, 2001, 2002; Surkov, 2005). Paleogeographic features of this area, which was situated at the western coast of the northern gulf of the Tethys, explain the presence here of some marine taxa. In particular, these are crossopterygians, coelacanths among fishes, ichthyopterygians (?) among reptiles (Ochev, 1976), and the cymatosaurid *Tanaisosaurus* representing the most ancient eosauropterygians (Sennikov, 2001). The composition of this local fauna clearly points to its connections with central European and more western Euroamerican communities, which is supported by the presence of the labyrinthodont *Trematosaurus*, trilophosaurs, a representative of cymatosaurids, a primitive tanystropheid, and by the predominance of the early rauisuchid archosaurs.

CONCLUSIONS

(1) During the entire Early Triassic, the East European Platform and adjacent areas show biogeographic differentiation in the fauna of terrestrial vertebrates. This heterogeneity developed against a background of relatively similar conditions of a seasonal semiarid climate, with the accumulation of animal population and vegetation in the biotopes connected with lowland water bodies.

(2) The greatest spatial differentiation in the taxonomic composition of vertebrates is recorded for amphibians at the beginning of the Early Triassic (Induan), and for reptiles, at the end of the Early Triassic (Late Olenekian).

(3) These two episodes correspond to the peaks of taxonomic diversification of the respective groups (Ochev and Shishkin, 1998). The increase in the diversity of reptiles during the Early Triassic is, in its turn, explained by a gradual trend to a milder climate in comparison with the initial, most arid conditions, which gave an advantage to obligatory inhabitants of strictly aquatic biotopes.

(4) Of the three basic biogeographic units recognized in Eastern Europe (the East European Platform and the Ural Foredeep), the southern Fore-Ural Realm throughout the Early Triassic is specific in the preservation of distinct faunal connections with Gondwana. The southern area in the Late Olenekian shows a connection with the Germanic Basin and more western areas of Euramerica. The northern area demonstrates a high degree of faunal unity with the northern shelf of Europe (Greenland) in the Induan, and individual connections with North America in the Late Olenekian.

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REFERENCES

1. J. M. Anderson and A. R. I. Cruickshank, "The Biostratigraphy of the Permian and the Triassic: Part 5. A Review of the Classification and Distribution of Permo-Triassic Tetrapods," Palaeontol. Afr. **21**, 15–44 (1978).
2. B. E. Balme, "Australian Phanerozoic Timescales: 7. Triassic Biostratigraphic Charts and Explanatory Notes," Austral. Bureau Miner. Res. **37**, 1–28 (1990).
3. B. Battail, "Biostratigraphie des formations permo-triasiques continentales à vertébrés tétrapodes et biogéographie du Gondwana," Ann. Soc. Géol. Nord **107**, 37–44 (1988).
4. J. W. Cosgriff, "A New Genus of Temnospondyli from the Triassic of Western Australia," J. Roy. Soc. West. Austral. **48** (3), 65–90 (1965).
5. J. W. Cosgriff, "The Temnospondyl Labyrinthodonts of the Earliest Triassic," J. Vertebr. Paleontol. **4** (1), 32–46 (1984).
6. R. J. Damiani, "A Systematic Revision and Phylogenetic Analysis of Triassic Mastodonsauroids (Temnospondyli: Stereospondyli)," Zool. J. Linnean Soc. **133**, 379–482 (2001).
7. I. A. Dobruskina, "Triassic Floras of Eurasia," Tr. Geol. Inst. Akad. Nauk SSSR, no. 365, 1–196 (1982).
8. V. A. Garyainov and S. P. Rykov, "The Southeastern Slope of the Voronezh Anteclise, Obshchii Syrt and Orenburg Fore-Urals," in *Stratigraphy of the USSR: Triassic System* (Nedra, Moscow, 1973), pp. 89–111 [in Russian].
9. N. V. Ilyina, *Palynostratigraphy of the Middle Triassic of the Timan–North Ural Region* (Inst. Geol. Komi Nauchn. Tsentr Ural. Otd. Ross. Akad. Nauk, Yekaterinburg, 2001a) [in Russian].
10. N. V. Ilyina, "Palynology of the Triassic of the Lena–Olenek Facies Zone," in *Triassic of Western Siberia: Materials of Stratigraphical Meeting on the Mesozoic of the West Siberian Plate* (SNIIGGiMS, Novosibirsk, 2001b) [in Russian].
11. N. V. Ilyina, "Analogues of the Upper Olenekian Substage in the Timan–North Ural Region," Syktyvkar. Paleontol. Sborn., No. 5, 118–139 (2003).
12. N. V. Ilyina and I. V. Novikov, "Early Olenekian Miospore Assemblage of the Pechora Syneclise," in *Palynology in Stratigraphy: Papers to the 8th Palynological Conference, France, 1992* (Nauka, Moscow, 1994), pp. 59–61 [in Russian].
13. M. F. Ivakhnenko, V. K. Golubev, Yu. M. Gubin, *et al.*, "Permian and Triassic Tetrapods of Eastern Europe," Tr. Paleontol. Inst. Ross. Akad. Nauk **268**, 1–216 (1997).
14. N. N. Kalandadze, "The First Find of *Lystrosaurus* in the European Part of the USSR," Paleontol. Zh., No. 4, 140–142 (1975).
15. V. R. Lozovsky, "On the Age of Beds with *Lystrosaurus* in the Moscow Syneclise," Dokl. Akad. Nauk SSSR **272** (6), 1433–1437 (1983).
16. V. R. Lozovsky, "The Early Triassic Stage in the Development of Western Laurasia," *Extended Abstract of Doctoral Dissertation in Geology and Mineralogy* (Mosk. Geol.-Razv. Inst., Moscow, 1992).
17. V. R. Lozovsky, "Early Triassic Pangea," Bull. New Mexico Mus. Natur. Hist. Sci. **3**, 289–291 (1993).
18. I. S. Makarova and I. F. Vergai, "Miospores," in *Biostratigraphy of the Continental Triassic of the Southern Fore-Urals*, Ed. by M. A. Shishkin (Nauka, Moscow, 1995), pp. 120–129 [in Russian].
19. G. Mangerud, "Palynostratigraphy of the Permian and Lowermost Triassic Succession, Finnmark Platform, Barents Sea," Rev. Palaeobot. Palynol. **82**, 317–349 (1994).
20. G. Mangerud and A. Romund, "Spathian–Anisian (Triassic) Palynology at the Svalis Dome, South-Western Barents Sea," Rev. Palaeobot. Palynol. **70**, 199–216 (1991).
21. B. A. McTavish and J. M. Dickins, "The Age of the Kockatea Shale (Lower Triassic), Perth Basin—A Reassessment," J. Geol. Soc. Austral. **21** (2), 195–201 (1974).
22. M. G. Minikh and I. S. Makarova, "On the Stratigraphic Position of the Gamian Formation in the Triassic of the Mezen Syneclise," in *Mineral Resources of the Northeastern European USSR* (Syktyvkar, 1990), pp. 233–239 [in Russian].
23. I. V. Morkovin and I. V. Novikov, "A New Labyrinthodont from the Lower Triassic of the Luza River Basin (Komi Republic)," Izv. Vyssh. Uchebn. Zaved., Geol. Razved., No. 3, 29–35 (2000).
24. I. V. Novikov, A. G. Sennikov, M. G. Minikh, *et al.*, "New Data on the Early Triassic Vertebrates from the Donskaya Luka Locality in the Volgograd Region: Part 1," Izv. Vyssh. Uchebn. Zaved., Geol. Razved., No. 6, 33–38 (2001).
25. I. V. Novikov, A. G. Sennikov, M. G. Minikh, *et al.*, "New Data on the Early Triassic Vertebrates from the Donskaya Luka Locality in the Volgograd Region: Part 2," Izv. Vyssh. Uchebn. Zaved., Geol. Razved., No. 2, 43–53 (2002).
26. I. V. Novikov and M. A. Shishkin, "Palaeozoic Relic in Triassic Tetrapod Communities: The Last Anthracosaurian Amphibians," in *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota* (China Ocean Press, Beijing, 1995), pp. 29–32.
27. I. V. Novikov and M. A. Shishkin, "Triassic Chroniosuchia (Amphibia, Anthracosauromorpha) and Evolution of Dermal Thoracic Scutes in the Bystrowianidae," Paleontol. J. **34** (Suppl. 2), 165–178 (2000).
28. I. V. Novikov, M. A. Shishkin, and V. K. Golubev, "Permian and Triassic Anthracosaurs from Eastern Europe," *The Age of Dinosaurs in Russia and Mongolia*, Ed. by M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (Cambridge Univ. Press, Cambridge, 2000), pp. 60–70.
29. V. G. Ochev, "New Data on the Triassic Vertebrate Fauna of the Orenburg Fore-Urals," Dokl. Akad. Nauk SSSR **122** (3), 485–488 (1958).

30. V. G. Ochev, "An Unusual Tooth from the Lower Triassic of Donskaya Luka," Izv. Vyssh. Uchebn. Zaved., Geol. Razved., No. 8, 176–177 (1976).
31. V. G. Ochev, "On the History of the Triassic Vertebrates of the Fore-Urals," Byull. Mosk. O–va Ispyt. Prir., Otd. Geol. **67** (4), 30–43 (1992a).
32. V. G. Ochev, "On the Second Reliable Find of Anomodonts in the Lower Triassic of the East Europe Platform," Izv. Vyssh. Uchebn. Zaved., Geol. Razved., No. 2, 132–133 (1992b).
33. V. G. Ochev, "On the Biogeography of Triassic Tetrapods," Byull. Mosk. O–va Ispyt. Prir., Otd. Geol. **69** (2), 84–90 (1994).
34. V. G. Ochev, "On the Distinctive Features of Early Triassic Ecosystems of Southern Africa and Fore-Urals," Byull. Mosk. O–va Ispyt. Prir., Otd. Geol. **73** (2), 63–66 (1998).
35. V. G. Ochev, "Climatobiogeography and Tetrapods of the Permian–Triassic Pangea," Byull. Mosk. O–va Ispyt. Prir., Otd. Geol. **75** (3), 42–46 (2000).
36. V. G. Ochev and M. A. Shishkin, "A Shift in the Continental Biota at the Paleozoic–Mesozoic Boundary of Eastern Europe: 4.1. Communities of Terrestrial Vertebrates," in *The Permian–Triassic Boundary in the Continental Series of Eastern Europe*, Ed. by V. R. Lozovsky and N. K. Esaulova (Geos, Moscow, 1998), pp. 59–74 [in Russian].
37. V. G. Ochev, M. A. Shishkin, D. A. Kukhtinov, *et al.*, "On Some Unsolved Problems of the Triassic Stratigraphy of Eastern Europe," Stratigr. Geol. Korrelyatsiya **12** (3), 51–64 (2004).
38. S. P. Rykov and V. G. Ochev, *On the Localities of Triassic Vertebrates at Donskaya Luka* (Sarat. Gos. Univ., Saratov, 1966) [in Russian].
39. R. R. Schoch and A. R. Milner, "Stereospondyli," in *Handbuch der Paläoherpetologie*, Ed. by P. Wellnhofer (Friedrich Pfeil, München, 2000), Part 3B, pp. 1–203.
40. A. G. Sennikov, "Discovery of a Primitive Sauropterygian in the Lower Triassic of the Donskaya Luka and Distribution of Triassic Marine Reptiles in Russia," Paleontol. Zh., No. 3, 76–85 (2001) [Paleontol. J. **35** (3), 305–314 (2001)].
41. A. G. Sennikov, "A New Specialized Prolacertilian (Reptilia: Archosauromorpha) from the Lower Triassic of the Orenburg Region," Paleontol. Zh., No. 2, 88–97 (2005) [Paleontol. J. **39** (2), 201–210 (2005)].
42. A. G. Sennikov and I. V. Novikov, "The Lower Triassic Donskaya Luka Locality, As an Example of Regional Specificity of the Vertebrate Fauna," in *Paleontology and Stratigraphy of the Permian and Triassic Continental Beds of Northern Eurasia: IV All-Russia Conference, Moscow, April 4 and 5, 2002* (Paleontol. Inst. Ross. Akad. Nauk, Moscow, 2002), p. 88 [in Russian].
43. M. A. Shishkin, *Morfologiya drevnikh zemnovodnykh i problemy evolyutsii nizshikh tetrapod* (Nauka, Moscow, 1973) [in Russian].
44. M. A. Shishkin, "A Gondwanan Rhytidosteid (Amphibia, Temnospondyli) in the Lower Triassic of Southern Fore-Urals," Paleontol. Zh., No. 4, 97–110 (1994).
45. M. A. Shishkin, "Olenekian–Anisian Boundary in the History of Land Tetrapods," in *Workshop on the Lower–Middle Triassic (Olenekian–Anisian) Boundary, June 7–10, Tulcea, Romania, Conference of the Section of the International Union of Geological Sciences: Triassic Subcommission*, Ed. by E. Gradinaru (Bucharest, 2000), pp. 60–69.
46. M. A. Shishkin, "On Possible Relicts of the Paleozoic Archegosauroids (Amphibia, Temnospondyli) in the Triassic of Euramerica," J. Vertebr. Paleontol. **22** (3), 106–107 (2002).
47. M. A. Shishkin, "The Patterns of Evolution of Early Triassic Tetrapod Communities in Europe and Southern Gondwana: Comparison and Implications," in *Herpetologia Petropolitana*, Ed. by N. Ananjeva and O. Tsinenko (Nauka, St. Petersburg, 2005), pp. 301–303.
48. M. A. Shishkin and I. V. Novikov, "Relict Anthracosaurs in the Early Mesozoic of Eastern Europe," Dokl. Akad. Nauk **325** (4), 829–832 (1992).
49. M. A. Shishkin and V. G. Ochev, "On the Spatial Differentiation of the Land Vertebrate Fauna in the Early Triassic," in *Fauna and and Ecosystems of the Geological Past* (Nauka, Moscow, 1993a), pp. 98–108 [in Russian].
50. M. A. Shishkin and V. G. Ochev, "The Permo–Triassic Transition and the Early Triassic History of the Euramerican Tetrapod Fauna," Bull. New Mexico Mus. Natur. Hist. Sci. **3**, 435–437 (1993b).
51. M. A. Shishkin and V. G. Ochev, "On the Patterns of Change in Tetrapod Communities during Paleozoic–Mesozoic Transition," in *International Symposium: Stratotypes of the Upper Permian of the Volga Region*, Ed. by B. V. Burov *et al.* (Kazan, 1998), pp. 136–137.
52. M. A. Shishkin and V. G. Ochev, "Tetrapods As a Basis for Stratification and Correlation of the Continental Triassic of European Russia," in *Questions of General Stratigraphical*, Ed. by V. G. Ochev (Sarat. Gos. Univ., Saratov, 1999), pp. 52–73 [in Russian].
53. Terrestrial Vertebrate Communities during Paleozoic–Mesozoic Transition," in *Proceedings of International Symposium on Global Stratotype Permian–Triassic Boundary and Paleozoic–Mesozoic Events*, Ed. by Jiaxin Yan and Yuanqiao Peng (China, Changxing, 2001), pp. 90–93.
54. M. A. Shishkin, V. G. Ochev, V. R. Lozovsky, and I. V. Novikov, "Tetrapod Biostratigraphy of the Triassic of Eastern Europe," in *The Age of Dinosaurs in Russia and Mongolia*, Ed. by M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (Cambridge Univ. Press, Cambridge, 2000), pp. 120–139.
55. M. A. Shishkin, B. S. Rubidge, and P. J. Hancox, "Vertebrate Biozonation of the Upper Beaufort Series of South Africa: A New Look on Correlation of the Triassic Biotic Events in Euramerica and Southern Gondwana," in *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Ed. by A. Sun and Y. Wang (China Ocean Press, Beijing, 1995), pp. 39–41.
56. M. A. Shishkin, B. Rubidge, and J. Hancox, "Comparison of Tetrapod Faunal Evolution during Early Triassic in Eastern Europe and South Africa," in *Abstracts of the 9th Biennial Conference of the South African Paleontological Society* (Stellenbosch, 1996), unpaged.
57. M. A. Shishkin, B. Rubidge, J. Hancox, and J. Welman, "Re-evaluation of *Kestrosaurus* Haughton, a Capitosaurid Temnospondyl Amphibian from the Upper Beaufort

Group of South Africa," Russ. J. Herpetol. **11** (2), 121–138 (2004).

58. M. A. Shishkin, B. S. Rubidge, and J. W. Kitching, "A New Lydekkerinid (Amphibia, Temnospondyli) from the Lower Triassic of South Africa: Implications for Evolution of Early Capitosauroid Cranial Pattern," Phil. Trans. Roy. Soc., Ser. B **351**, 1635–1659 (1996).
59. N. H. Shubin and H.-D. Sues, "Biogeography of Early Mesozoic Continental Tetrapods: Patterns and Implications," Paleobiology **17** (3), 214–230 (1991).
60. J. S. Steyer, "A Revision of the Early Triassic "Capitosaurs" (Stegocephali, Stereospondyli) from Madagascar, with Remarks on Their Comparative Ontogeny," J. Vertebr. Paleontol. **23** (3), 544–555 (2003).
61. N. I. Strok, T. E. Gorbatkina, and V. R. Lozovsky, *Upper Permian and Triassic Deposits of the Moscow Syneclise* (Nedra, Moscow, 1984) [in Russian].
62. M. V. Surkov, "The First Dicynodont from the Terminal Lower Triassic of European Russia, with Special Reference to the Evolution of the Masticatory Apparatus of These Therapsids," Paleontol. Zh., No. 1, 76–82 (2005) [Paleontol. J. **39** (1), 73–79 (2005)].
63. R. A. Thulborn, "Early Triassic Reptiles of Australia," in *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, Ed. by S.-E. Reif and F. Westphal (Attempto Verl., Tübingen, 1984), pp. 243–248.
64. M. E. Tucker and M. J. Benton, "Triassic Environments, Climates and Reptile Evolution," Palaeogeogr., Palaeoclimatol., Palaeoecol. **40**, 361–379 (1982).
65. A. Warren, "Two Long-Snouted Temnospondyls (Amphibia, Labyrinthodontia) from the Triassic of Queensland," Alcheringa **9**, 293–295 (1985).
66. A. Warren, "Karoo Tupilakosaurid: A Relict from Gondwana," Trans. Roy. Soc. Edinburgh, Earth Sci. **89**, 145–160 (1999).
67. O. P. Yaroshenko and V. R. Lozovsky, "Palynological Assemblages from the Continental Lower Triassic of Eastern Europe and Their Interregional Correlation: 1. Palynological Assemblages of the Induan Stage," Stratigr. Geol. Korrelyatsiya **12** (3), 65–75 (2004).
68. O. P. Yaroshenko, L. P. Golubeva, and I. Z. Kalantar, "Miospores and Stratigraphy of the Lower Triassic of the Pechora Syneclise," Tr. Geol. Inst. Akad. Nauk SSSR, No. 470, pp. 1–135 (1991).
69. M. A. Zharkov and N. M. Chumakov, "Paleogeography and Conditions of Sedimentation during the Permian–Triassic Biosphere Reorganizations," Stratigr. Geol. Korrelyatsiya **9** (4), 29–54 (2001).