

The Late Permian (Lopingian) and Early Triassic flora of the Moscow Syncline

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Abstract

The Late Permian (Lopingian) and Early Triassic successions of the Moscow Syncline have been studied in twenty localities. We recognized of two phases of development of the Late Permian flora. First, the phase of rise and maximum diversity and second phase of suppressed and unstable stage of the flora development. The taxonomic diversity curves were prepared at genus and species level. The curves indicate that floral richness continuously declines from the Late Permian to Early Triassic. The main factor in reducing of the number of taxa is a decrease the number of transit taxa and an increase of the rate of extinction.

Keywords: Late Permian, Early Triassic, paleobotany, phytostratigraphy, taxonomic diversity

Introduction

There were many new data of flora composition of the Moscow basin was received from Late Permian and Early Triassic deposits during last 20 years. The new information on the composition of plant assemblages has been obtained both from well-known and recently discovered localities [e.g. 1–3]. Significant progress in the study of the Late Permian vegetation is also observed in Europe [e.g. 4–6] and China [7, 8]. The reference framework for the present study is the classical book of A.V. Gomankov and S.V. Meyen [9], and certain a few review and descriptive papers published later [3, 10–13]. Gomankov and Meyen [9] monographically studied the flora of the East European Platform and the Fore-Urals, and named it the Tatarina flora after the dominant leaf genus *Tatarina*. The uniqueness of the plant assemblages of the Tatarina flora made it possible to recognize the Subangara paleofloristic area [14].

Gomankov [15] traced and identified changes in the floristic assemblages clearly marked at the boundaries of the Urzhumian, Severodvinian and Vyatkian Stages. He notes the maximum taxonomic diversity of the Late Permian vegetation in the sediments of the upper part of the Severodvinian Stage (Wuchiapingian) on the East European Platform. This stratigraphic level we take as the lower boundary of interval that were analyzed.

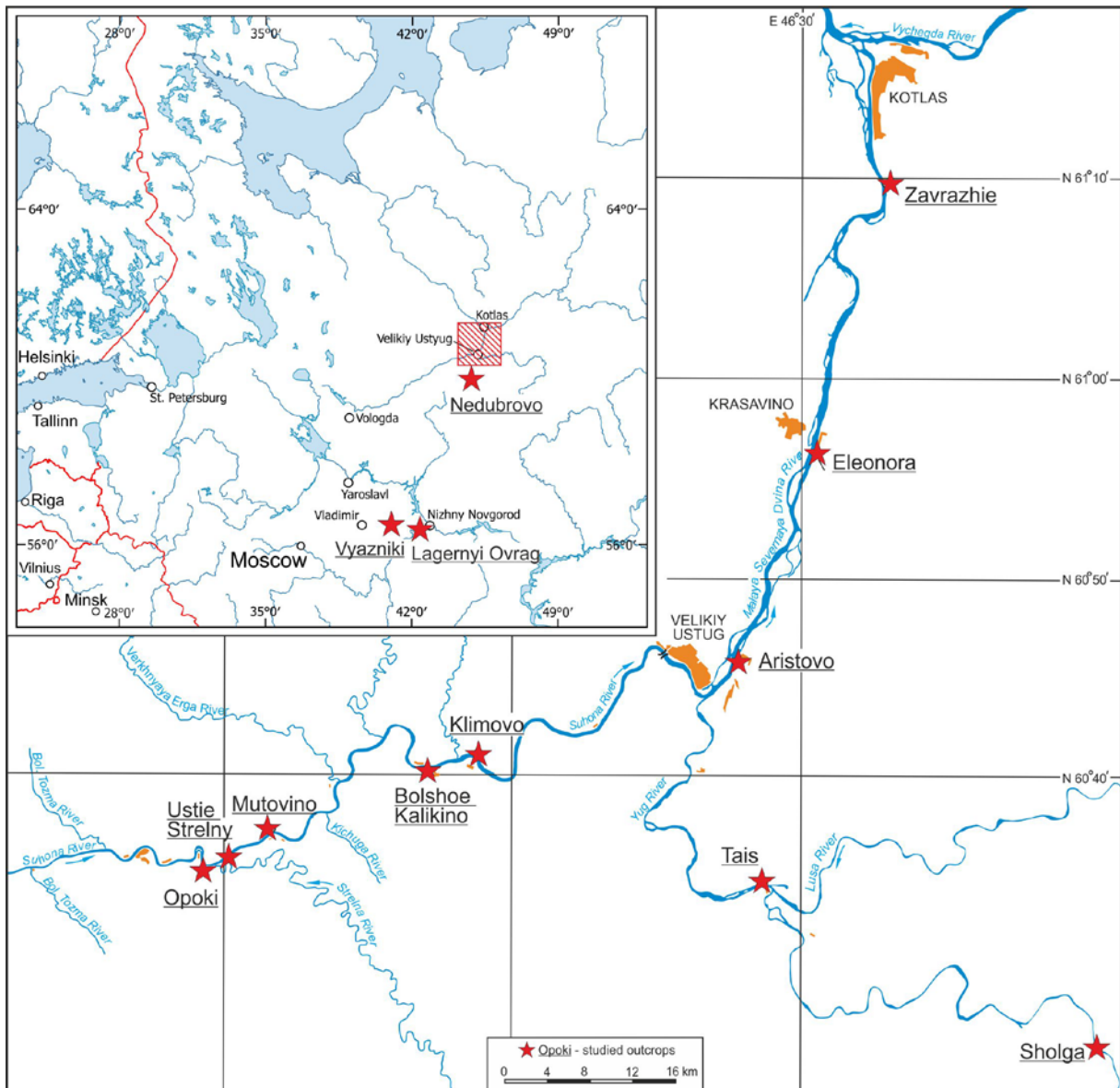


Fig.1: Map of the studied localities

In the last century, the prevailing view was that stratigraphic hiatus exists between the Late Permian and the Early Triassic in European Russia. The terminal Permian and earliest Triassic deposits were discovered later [16–18]. Until this time the paleobotanical characteristic of the last stage of Tatarina flora was absent. The plant assemblages were described from the latest Vyatikian (Changhsingian)–basal Vetlugian (terminal Changhsingian–Induan) of the Volga–Dvina Rivers Basins, European Russia [1].

In this paper, we clarify the stratigraphic spread and systematic composition of fossil plants of these assemblages. Also we estimate a local scale diversity of the higher plants in the Late Permian and Early Triassic of the Moscow Syneclise. The present investigation utilizes quantitative methods to assess the taxonomic diversity of flora at the genus and species levels.

Methods

The diversity assessment at the present study is based on a dataset that has recently been assembled as part of a review of the stratigraphic correlation of the Permian and Triassic of the Severnaya Dvina and Sukhona Rivers Basin [19]. Localities from the southern part of the Moscow Synclise (Vyazniki, Lagernyi Ovrage) applied to the composite stratigraphic column based on the correlation of the fauna of ostracods and tetrapods [20–23].

We divide taxa into classes following terminology of M. Foote [24]. All taxa divided into four classes with respect to occurrence in the stratigraphic interval. This is taxa that cross the top boundary only (first appeared taxa - F), taxa that cross the bottom boundary only (last appeared - L), taxa confined to the interval (Singletons - S) and taxa that range through the entire interval, crossing both the top and bottom boundaries (Transited – T). The total diversity is given as $N_{TOT}=F+L+S+T$.

The present dataset incorporates a total of 84 species in 45 genera from five floristic assemblages (Fig. 2). Quantitative analyses of diversity taxa were performed and plots generated using R software with IDE Rstudio [25, 26].

Materials

Actual data for the analysis of taxonomic diversity in this work are drawn from the central and southern part of the Moscow Syncline. We analyzed the stratigraphic distribution and variation of the diversity of higher plants from ten localities on the Sukhona and Malaya Severnaya Dvina Rivers Basin (Vologda region) and two localities from the Vladimir and Nizhny Novgorod regions (**Fig.1**). A brief paleobotanical characteristic of each analyzed localities is given below.

Ustie Strelny Locality

Horsetails are dominated in the Strelna Member of the Ustie Strelny Locality. Gomankov [11] noted impressions of stems of *Paracalamites* sp. and *Neocalamites* sp. and leafy shoots close to the *Asterophyllites* sp. S.V. Naugolnykh described a new species *Neocalamites tubulatus* Naugolnykh, noting that this plant dominated in this flora [27].

Opoki Locality

Plant remains in the locality are represented by well-preserved impressions. Numerous remains of leaves and bark of the lycopsid *Lepidophylloides* cf. *delicata* (Gomankov) Gomankov were collected from the bottom of the Purtovino Member. The sphenophylls *Paracalamites* sp. and fragments of pinnae of the fern *Dvinopteridium edemskii* (Zalessky) Naugolnykh are less frequent.

Mutovino (=Isady) Locality

Fossil plants from the Mutovino are dominated by shoots of the conifer *Quadrocladus schweitzeri* Meyen in association with strobili of *Dvinostrobus sagittalis* Gomankov et Meyen. Subdominant fossils include leaves of the peltasperms *Tatarina conspicua* Gomankov et Meyen associated with peltate ovuliphores of *Peltaspermopsis* cf. *buevichae* Gomankov et

Meyen, seeds of *Salpingocarpus bicornutus* Meyen, *Salpingocarpus variabilis* Meyen and sporangia of *Permotheca striatifera* Meyen et Gomankov and *Permotheca vesicasporoides* Meyen, Esaulova et Gomankov [9]. There are also abundant leaves of the cardiolepid *Phylladoderma (Aequistomia) annulata* Meyen, *Phylladoderma (A.) rastorguevii* Meyen and *Phylladoderma (A.) trichophora* Meyen. In addition, Gomankov and Meyen [9] reported on leaves of the *Rhaphidopteris* type and fragmentary leaves of uncertain systematic position *Arisada densa* Meyen. Spore-bearing plants are represented by leaves of the lycopsid *Lepidophylloides delicata* (Gomankov) Gomankov and associated dispersed megaspores. Other fossil plants include leaves with venation of the *Taeniopteris* type produced probably by ferns (*Fefilopteris pilosa* Gomankov) or seed ferns, and the moss *Protosphagnum nervatum* Neuburg.

Klimovo and Bolshoe Kalikino Localities

In 1993, M.P. Arefiev collected horsetail stems of *Paracalamites* sp. and *Phyllopytis* sp. from red beds of the Klimovo Locality underlying paleosols. In 2014, we found fragments of pinnae of *Pecopteris* sp. At approximately this stratigraphic level from the Bolshoe Kalikino section, Gomankov [11] listed horsetail stems of *Neocalamites*, leaves of the peltasperms *Pursongia angustifolia* Zalesky and leaves of the gymnosperm *Rhipidopsis* cf. *ginkgoides* Schmalhausen.

Aristovo Locality

The Aristovo is the richest and best studied locality for plant remains in the basin of the Severnaya Dvina and Sukhona rivers. Gomankov and Meyen were the first who studied of the floristic assemblage of the Aristovo section [9]. Seed ferns of the families Peltaspermeaceae and Angaropeltaceae are dominant. Peltasperms are represented by leaves of *Tatarina conspicua* Meyen, *Ustyugia pinnata* (Meyen et Gomankov) Gomankov, *Pursongia belousovae* (Radcz.) Gomankov et Meyen, ovuliferous discs of *Peltaspermopsis buevichiae* (Gomankov et Meyen) Gomankov and associated ovules of *Salpingocarpus bicornutus* Meyen, *S. variabilis* Meyen and *Salpingocarpus* sp. The family Angaropeltaceae is represented by leaves of *Phylladoderma (Aequistomia) aequalis* Meyen and *P. (A) annulata* Meyen. Synangia of seed ferns affiliated to three species: *Permotheca striatifera* Meyen et Gomankov, *P. vesicasporoides* S. Meryen, Esaul. et Gomankov and rare sporangia of *P. vittatinifera* Meyen et Gomankov [9]. Conifers are represented by shoots of *Quadrocladus dvinensis* Meyen and *Geinitzia* sp., ovuliferous dwarf-shoots of *Sashinia aristovenssis* Meyen and strobili of *Dvinostrobus sagittalis* Gomankov et Meyen. Leaves of the lycopsid *Lepidophylloides delicata* Gomankov are less abundant. There are occasional pinnae of *Pecopteris* sp. and plants defined as incertae sedis *Arisadia densa* Meyen. Perfectly preserved bryophyte leaves have been restudied by Ignatov [28] and assigned to *Pelliothallites tataricus* Meyen, *Thallites* sp., *Arvidia elenea* Ignatov, *Gomankovia latifolia* Ignatov, *Aristovia subcordata* Ignatov, *A. microcellulata* Ignatov, *Protochryaea polymorpha* Ignatov, *Ignatievia papillosa* Ignatov, *Rhizinigerites neuburgae* Meyen, *Protosphagnum nervatum* Neuburg,

Palaeosphagnum meyenii Ignatov, *Vorcutannularia minima* Ignatov, *Servicktia acuta* Ignatov, and *S. vorcutannularoides* Ignatov.

Zavrazhie Locality

The Zavrazhie is at the same stratigraphic level as the Aristovo locality. Plant remains are represented by well-preserved impressions and occasionally small fragments of poorly preserved cuticles. Here you can find peltasperms, represented by leaves of *Pursongia amalitzkii* Zallesky and ovuliferous discs of *Peltaspermopsis polyspermis* Naugolnykh[29].

Eleonora Locality

The plant mesofossils include dispersed megaspores and numerous fragmentary cuticles of gymnosperm and rare bryophyte leaves. The megaspore assemblage contains many megaspores of *Erlansonisporites?* sp.; and only one specimen of *Maiturisorites* sp. was found. The fragments of bryophyte leaves belong to the order *Protosphagnales* (Ignatov, 2015, pers. comm.). Most fragments of dispersed leaf cuticles of gymnosperms belong to pteridosperms of the family *Angaropeltaceae* of genus *Phylladoderma* (*Aequistomia*) Meyen.

Tais Locality

The plant remains of the Tais Locality are represented by well-preserved impressions and occasionally by small fragments of poorly preserved cuticles. The plant macrofossils include the shoots of mosses *Muscites* sp., numerous shoots of the horsetail *Neocalamites* sp. and fragmentary sterile pinnae of ferns *Sphenopteris* sp. and *Pecopteris* sp. Conifers are represented by shoots of *Quadrocladus dvinensis* Meyen. The linear-lanceolate leaves of peltasperms *Tatarina conspicua* Gomankov et Meyen are sub-dominant. Rare fragments of large leaves were preliminarily identified as *Rhaphidopteris* (?) sp.

Vyazniki (Sokovka) Locality

Dominants of the Vyaznikovsky assemblage are leaves of *Permophyllocladus polymorphus* Karasev et Krassilov and species *Vjaznikopteris rigida* Naugolnykh. Leaves of *Tatarina conspicua* Gomankov et Meyen and *Phylladoderma*(*Aequistomia*) *aequalis* Meyen, typical of the Vokhomsky assemblage, are in a subordinate amount in the Vyaznikovsky assemblage. In association with leaves of peltaspermalean pteridosperms, ovuliferous disks of *Peltaspermum capitatum* Naugolnykh and numerous dispersed seeds were found. Ovuliferous organs of *Stiphorus ovatum* Naugolnykh occur in single specimens; conifers are represented by fragments of leaves of *Ullmannia* cf. *frumentaria* (Schlotheim) Göppert and *Quadrocladus* sp. In the middle part of the plant bearing lens is an interlayer with rather numerous shoots of sphenopsids *Neocalamites* cf. *mansfeldicus* (Weigelt) Weigelt. In addition, the Vyaznikovsky assemblage is characterized by much evidence of intense interaction of parasitic arthropods with plants [1, 30].

Lagernyi Ovrage-3 Locality

The Lagernyi Ovrage-3 was temporarily available for study in 2011 due to large-scale road works to expand the street Okskiy S'yezd of Nizhny Novgorod. The locality is a gray mudstone lens where some remains of plants, ostracod shells, conchostraca and bivalves, scales and bones of fishes and rare tetrapod bones [31]. Coniferous shoots of the genus *Quadrocladus* sp. and dispersed seeds of the genus *Salpingocarpus* sp. The most numerous among the fossil remains of plants. Lobate leaves of *Vjaznikopteris* cf. *rigida* Naugolnykh and ovuliferous discs of *Peltaspermum* cf. *capitatum* Naugolnykh are found here, as well as several lanceolate leaves of *Tatarina* sp. Two samples are presented by imprints of shoots of *Paracalamites* sp. and one impression of the leaf of *Rhipidopsis ginkgoides* Schmalhausen.

Nedubrovo Locality

The Nedubrovo section is exposed in a series of large outcrops on the left bank of the Kichmenga River. The plant remains are fragmentary but with well-preserved cuticles. In 1999, Krassilov, Afonin and Lozovsky published the first data on the assemblage of plant remains from the Nedubrovo section [16]. They showed that the floristic assemblage from the Nedubrovo Locality includes elements typical of both the Tatarian flora of the East European platform (*Tatarina conspicua* Meyen and *Phylladoderma (Aequistomia) annulata* Meyen) and Zechstein flora (*Ullmannia* cf. *bronnii* Goeppert and *Quadrocladus* cf. *solmsii* (Gothan et Nagathard) Schweitzer). Mesofossils are represented by megaspores of *Otynisporites tuberculatus* Fuglewicz characteristic of the Induan of Central Europe and megaspores of *Otynisporites maculosus* Karasev et Turnau, *Maexisporites grosstriletus* (Liu, Zhu et Ouyang) Karasev et Turnau, *Maexisporites* cf. *pyramidalis* Fuglewicz and *Maexisporites rugulaeferus* Karasev et Turnau characteristic of the megaspore assemblage of the Sholga locality (see below). Well preserved ovuliferous organs (peltoids) of *Navipelta resinifera* Karasev [32] and fragmentary leaves of *Permophyllocladus* cf. *polymorphus* Karasev et Krassilov are also found in the Nedubrovo Locality.

Sholga Locality

The megaspore assemblage comprises at least nine species of megaspores, among them two new species, one of the genus *Maexisporites* and the other *Otynisporites*. Additionally, megaspores referable to *O. tuberculatus* Fuglewicz, *Hughesisporites* sp. cf. *H. simplex* Fuglewicz, *Maexisporites pyramidalis* Fuglewicz, *Trileites* sp. cf. *T. vulgaris* Fuglewicz, and *Verrutriteles* sp. were identified. The taxa identified are known from the Lower Triassic deposits of Eastern Europe, Central India, East China and Southern Australia. The assemblage from Sholga contains species typical of the *Otynisporites eotriassicus* Zone including *O. tuberculatus*, *H. simplex* and *Trileites vulgaris*. Thus, the megaspore assemblage from the upper part of the Astashikha Member and from the Ryabi Member of the Vokhma Formation can be confidently compared with that of the lower Buntsandstein of Eastern Europe. We also found rare dispersed cuticles that show epidermal structures the same as in the genus *Tatarina*.

Discussion

Two phases of the Tatarina flora

Two phases of florogenesis were in the Late Permian of the Moscow Syncline. The first or early phase is a rise and the maximum taxonomic diversity of Tatarina flora. The Tatarina flora on this phase divided into three paleofloristic assemblages: Kotelnichsky, Alexandrovsky and Vokhomsky [15] (Fig. 2). According to Gomankov [15] the Alexandrovsky paleofloristic assemblage differed from the preceding the Kotelnichsky assemblage by the almost total disappearance of Cordaitales and the absence of sphenophytes of the genus *Sphenophyllum* Brongniart. The Vokhomsky assemblage is characterized by the peltasperms of *Usyugia pinnata* (Meyen et Gomankov) Gomankov and conifers *Sashinia aristovens* Meyen.

The late or second phase of Tatarina flora corresponds to the last and most unstable stage of development of the Late Permian flora. The typical elements of Tatarina flora were found at this phase regularly, but less frequently. The common and most characteristic element of the second phase is leaves of the genus *Permophyllocladus*. Plants close to *Permophyllocladus* appear in small numbers in the Vokhomsky assemblage on the Russian platform and noted as *Lepidopteris archaica* Gomankov. Leaves of similar to *Permophyllocladus* common in the latest Permian deposits of Western Europe and known as *Germaopteris* [5, 6] and from the Upper Permian of Sunjiagou Formation of China as *Lepidopteris baodensis* Zhang, Zheng et Naugolnykh [8]. A significant quantity of cells of *Reduviasporonites chalastus* (Foster) Elsik were found in the microfossil assemblage from deposits with *Permophyllocladus* [33-34]. The proliferation of *Reduviasporonites chalastus* recorded from the Permian–Triassic deposits in various localities (e.g. China, Israel, Southern Alps, Australia, South Africa) has been closely associated with the Permian–Triassic mass extinction event [35–37].

The second phase of the Tatarina flora are subdivided into two paleofloristic assemblages: the earlier is the Vyaznikovsky assemblage and later is the Nedubrovsky assemblage (Fig. 2).

The Vyaznikovsky assemblage is characterized with short-lived genera *Vjaznikopteris* Naugolnykh. Krassilov and Karasev described a two the Sokovka and the Balymothikha floral assemblages near Vyazniki city [1]. We revised the taxonomic composition of the Balymothikha locality (Vladimir region) and combined it together with the Sokovka locality into the Vyaznikovsky assemblage. This assemblage also includes the plant assemblage of the Lagernyi Ovrage-3 locality.

The Nedubrovsky assemblage is characterized by the presence of the genus *Navipelta* and dispersed megaspores of the lycopsids of the genera *Otynisporites* and *Maaxisporites*. The composition of plants from Nedubrovo and Sholga localities refers to this assemblage. Probably, some elements of the Nedubrovsky assemblage found in the Spasskoe locality (Nizhny Novgorod region) with ovuliferous organs of genus *Vetlugospermum* which is very similar to the genus *Navipelta* [38].

Thus, the upper boundary of the stratigraphic distribution of the Tatarina flora is located in the terminal Permian deposits (Nedubrovo locality, Nedubrovo Member of Vokhma Formation). It is worth noting the dispersed cuticles indistinguishable by epidermal

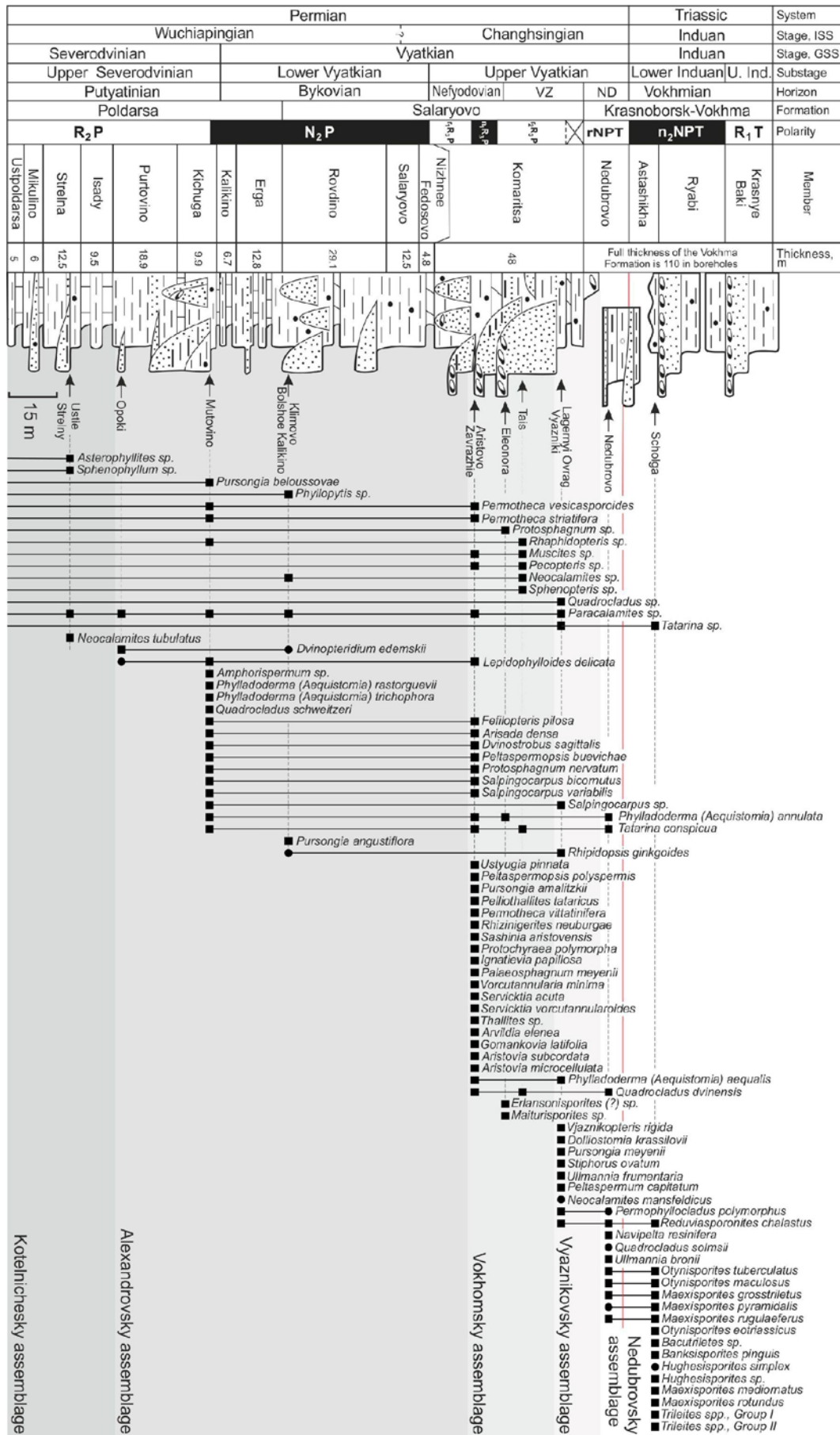


Fig 2: Stratigraphic range chart of the Late Permian-Early Triassic plants at the Moscow Syncline

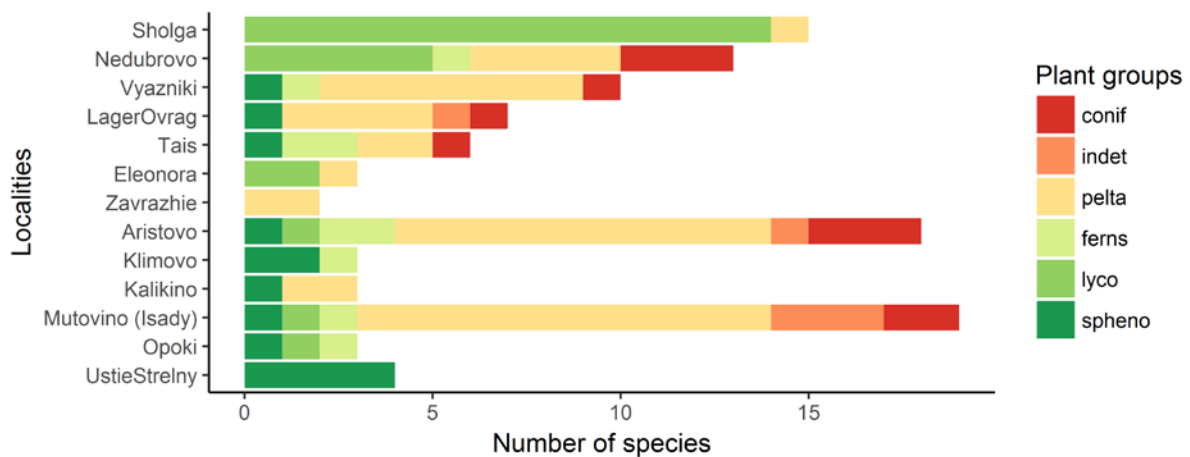


Fig. 3: The recognized and published number of taxa in each locality. Colors show the main groups of higher plants in proportion.

characters from the genus *Tatarina* occur in Induan of the Vetluga Horizon (Sholga locality, Ryabi Member of Vokhma Formation).

Taxonomic diversity

The actual number of described taxa and the ratio of the main plant groups from one oryctocoenosis to another are distributed extremely unevenly (Fig 3). This is due primarily to the various burial conditions (how long material was transported, diagenesis, etc) and nature of the paleolandscape in which formed this taphocoenosis. In addition, in some cases, the ratio of the main plant groups is affected by the volume of collected fossil material. We supplement the taxonomic composition of each of the orcotocenoses with taxa known from both earlier and later beds of the studied area (Fig. 4). This reduced the influence of "window of preservation" on the ratio of the main groups of plants in the oryctocoenosis [39].

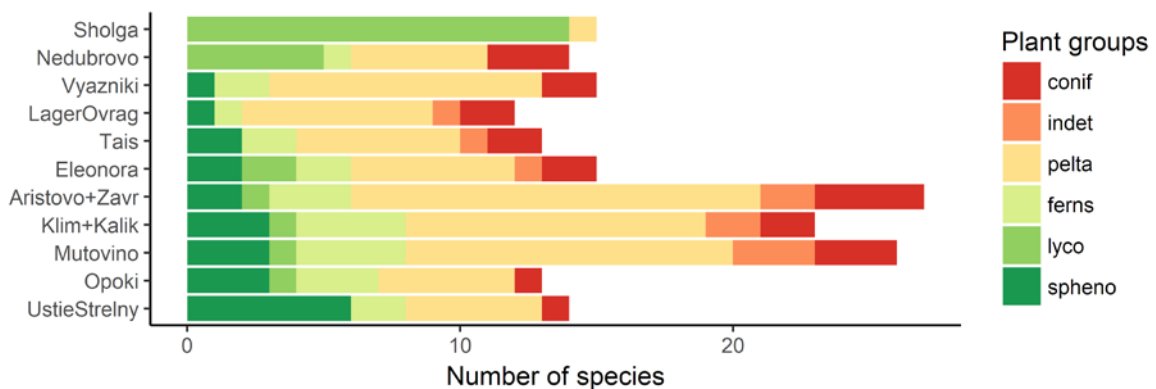


Fig. 4: The total number of taxa in each time interval including transited taxa. Intervals included one or more localities of the same age. Colors show the main groups of higher plants in proportions.

The non-vascular plants (algae and mosses) were excluded from the analysis because they require specific of conditions burial. In addition, the most of the species of bryophytes of the Late Permian of the Moscow Syncline are described from one locality [28], which introduces a strong misrepresentation in the taxonomic diversity of this group.

The total diversity curves of genus and species level (Fig. 5) indicate that the maximum of diversification of peltasperms and conifers reach on intervals from "Mutovino"

to "Aristovo+Zavr"(the Alexandrovsky and the Vokhomsy assemblages) and gradually decline to "Nedubrovo" interval.

On the interval "Vyazniki" there is a small increase in the diversity of peltasperms (Fig. 6.). This is due to the fact that in the terminal Permian (Vyaznikovsky and Nedubrovsky assemblages) there is a replacement of dominant forms among peltasperms [1]. In the Vyaznikovsky assemblage a new genera and species (*Vjaznikopteris*, *Permophyllocladus* etc.) were added

to the conspecific peltasperms of Tatarina flora. On the "Nedubrovo" interval the number of conifer taxa increased because the typical Zechsteinian conifers (*Ullmannia* cf. *bronnii* Goepfert and *Quadrocladus* cf. *solmsii* (Gothan et Nagalhardt) Schweitzer) were recognized[1].

The Fig. 6 shows the change in the number of taxa of spore plants and gymnosperms. The interval from "Nedubrovo" to "Sholga" (Nedubrovsky assemblage) shows a significant increase in the diversity of lycopsids, in contrast to a gradual reduction in the number of taxa of spore plants throughout of the Alexandrovsky and Vokhomsy assemblages.

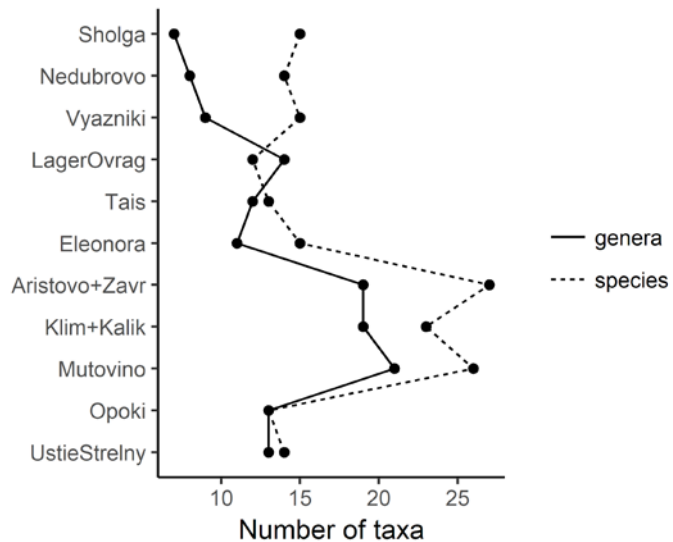


Fig. 5: Genus and species diversity curves of total richness

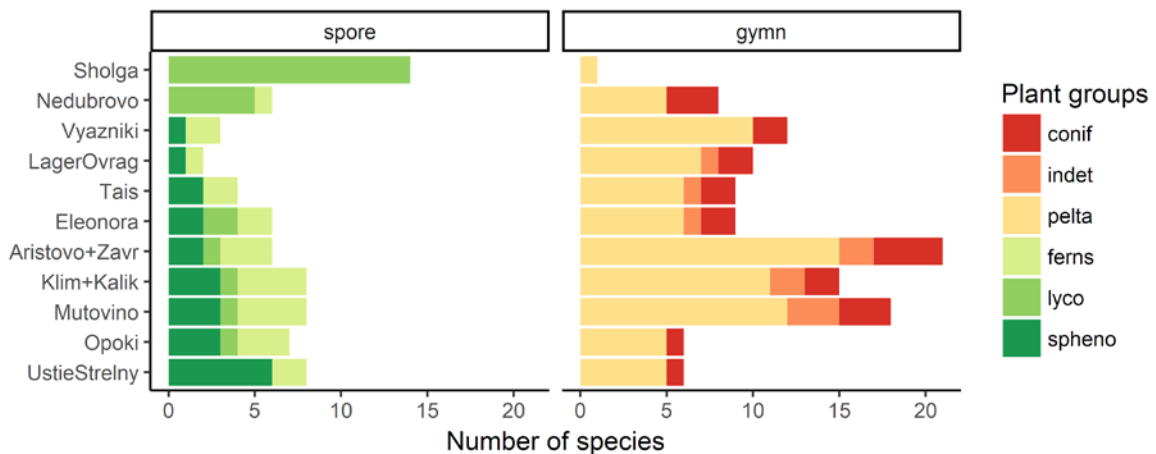


Fig. 6: The total number of taxa in each time interval including transited taxa and separated to spore-bearing and gymnosperm plants.

The observed different trends in the number of genera and species in the Nedubrovo and Sholga interval (Fig. 5) can be explained by the large number of species of disperse megaspores in relation to a smaller number of genera. In turn, this is due to the fact that disperse megaspores were classified according to the formal system of H. Potonié [40].

A significant increase in the proportion of lycopsids in relation to other groups of plants in the oryctocoenosis is considered quite common for crisis communities [41]. This is the first peak of diversity lycopsids near the boundary of the Permian and Triassic.

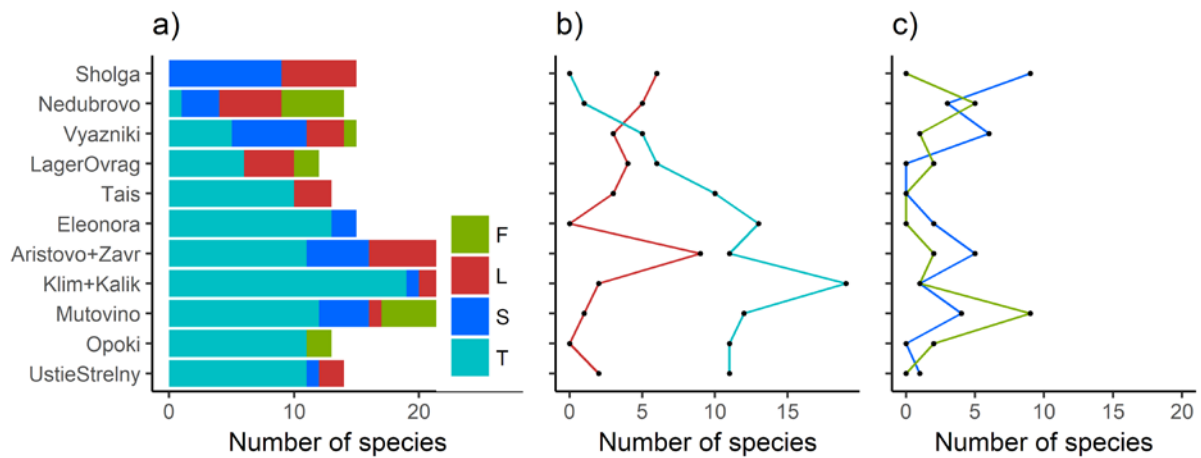


Fig. 7: The four classes of taxa in each interval. a) Total number of taxa; b) Transited and last appeared taxa; c) Singletons and first appeared taxa. Colors are according to class of taxa (see text for explanation).

On the territory of the Moscow Syneclise, the second distribution of lycopsids is better known as the mass distribution of the *Pleuromeia* forming monodominant assemblages in the Olenekian [1, 10, 42].

The next graph (Fig. 7a) shows the dynamics of the number of taxa change for each of the four classes. The turquoise fill corresponds to transit taxa (T), blue - singletons (S), red - meets last time (L), green - taxa occurs for the first time on a certain interval (F). The curves of changes of transit and disappearing taxa (Fig. 7b) show that gradually reducing diversity of Tatarina flora occurred within Lopingian. The main factor in reducing of the number of taxa is a decrease the number of transit taxa and an increase of the rate of extinction. At the same time, the rate of appearance of new taxa and the proportion of short-lived taxa remain approximately almost at the same level (Fig. 7c).

Conclusions

- We recognized of two phases of development of the Tarina flora. First, the phase of rise and maximum diversity and second the terminate and unstable. The characteristic genus of the second phase is *Permophyllocladus*.
- The second phase are included two paleofloristic assemblages: Vyaznikovsky with the characteristic genus *Vjaznikopteris* and Nedubrovsky with the characteristic genus *Navipelta* and dispersed megaspores of *Otynisporites* and *Maexisporites*.
- The taxonomic diversity of the Tatarina flora declined throughout Late Permian gradually. The main factor in reducing of the number of taxa is a decrease the number of transit taxa and an increase of the rate of extinction.

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