# Fossil Roots from the Upper Tatarian Deposits of the Sukhona and Malaya Severnaya Dvina River Basin: Stratigraphy, Taxonomy, and Paleoecology

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# Fossil Roots from the Upper Tatarian Deposits in the Basin of the Sukhona and Malaya Severnaya Dvina Rivers: Stratigraphy, Taxonomy, and Paleoecology

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**Abstract**—Fossil roots *Radicites sukhonensis* sp. nov. and *R. erraticus* sp. nov are described from the Upper Tatarian Substage in the basin of the Sukhona and Malaya Severnaya Dvina rivers. Fossil roots are assigned to five distinct morphotypes. A model of catenic distribution of the root morphotypes is proposed. Paleoecological implications of the model are discussed.

## INTRODUCTION

Descriptions of fossil roots and root-like organs are scarce in the modern paleobotanical literature. These fossils deserve more attention since their studies can potentially reveal the diversity of root structures in extinct plants, with implications on facial and taphonomic analyses, as well as on the reconstruction of the habitats and ecological strategy of their plant producing species.

This paper gives morphological descriptions of the major fossil root types from the Upper Tatarian Substage in the basin of the Sukhona and Malaya Sever-

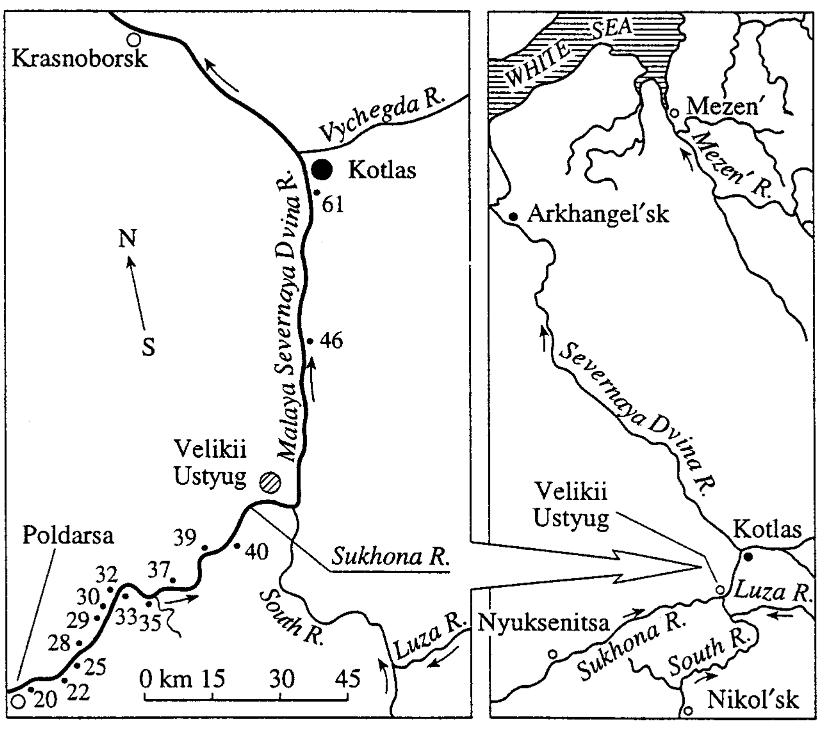



**Fig. 1.** Geographical position of root localities. Severodvinskii Horizon, Poldarskaya Formation 20—Nikulino, 22—Opoki, 25—Strel'na mouth, 28—Mutovino, 29—Konyavitsa, 30—Verkhnyaya Erga; Vyatskii Horizon, Poldarskaya and Salarevskaya formations: 32—Skoryatino, 33—Rovdino, 35—Bolshoye Kalikino; Salarevskaya Formation: 37—Klimovo, 39—Salarevo, 40—Odomchino, 46—Gorka, 61—Sokolki.

naya Dvina rivers (see localities in Fig. 1). We defined five distinct root morphotypes assigned to the formal genus *Radicites* Potonié, 1893. Open nomenclature is presently used for these morphotypes. In addition, two new species, *R. sukhonensis* sp. nov. and *R. erraticus* sp. nov. are erected.

The facial distribution of root morphotypes indicate a catenic structure of fossil soil and vegetation. Along the catena, different root morphotypes are here interpreted as representing ephemeroids and phreatophytes. Further, taxonomic assignments of putative Paleozoic ephemeroids and phreatophytes are discussed.

Fossil roots are, as a rule, difficult objects for taxonomic assignments. Sometimes they are confused with trace fossils or diagenetic structures. Characters that distinguish fossil roots from such enigmatic structures are the following:

(1) branches of second and higher orders that are morphologically different (in their dimensions, surface features or curvature) from the lower order axes;

(2) sedimentological features of aerial or subaerial origin;

(3) joint occurrence of roots and leafy shoots in one and the same or adjacent beds;

(4) lithological and geochemical characters of fossil soil (paleosoil).

The material was studied using a stereomicroscope MBS-9. The line-drawings were produced from photographs with tracings of morphological details using a stereomicroscope. The collection is deposited at the Paleontological Department of Moscow State University.

## STRATIGRAPHIC OVERVEIW

The root remains were collected from the Poldarskaya and Salarevskaya formations in their stratotypic area, the basin of the Sukhona and Malaya Severnaya Dvina rivers. Roots are lacking in the Sukhonskaya Formation of the same area. The Poldarskaya Formation consists of three members: the lower and upper greybed members (a) and (c) are separated by the redbed member (b) as described in *Opornyj Razrez of Tatarian Stage along the Sukhona River* (1981); see Fig. 2. The members (a) and (c) consist of calcareous clay, clayey limestones that are often dolomitized, clayey siltstones and marls. The member (b) consists of clayey siltstones, calcareous clay and sandstones. The latter comprises less marl and limestones than the two other members.

The outcrops of the Poldarskaya Formation in the Sukhona River Valley show five large sandstone lenses of different stratigraphic levels. The lenses are up to 16 m thick and 500 m long along the strike of the sequence. As a rule, they are irregular U-shaped cuts filled with quartz sandstones over thin basal gravelites or, more seldom, with siltstones or coarse breccia. All the lenses are topped with clayey siltstones that spread to the surrounding sediments. The overlying beds often show thin lenticulate structures formed of root remains. Such structures are evidence of paleosols (see "Genesis of deposits" below). The paleosols occur in all members and they are not restricted to the lenses.

The Poldarskaya Formation corresponds to the upper part of the Severodvinskii Horizon (*Resheniya...*, 1990). It contains ostracods *Suchonellina inornata* Spizh, *S. parallela* Spizh., *Prasuchonellina stelmakovi* (Spizh.), bivalves *Palaeomutela ovalis* Amal., *P. oleniana* Gus., *Prilukiella janischewskia* Plot. (*Resheniya...*, 1990), fishes *Boreolepis tataricus* Esin, *Amblipterina pectinata* Esin, *A. grandicostata* Esin, *Varialepis* sp., *Toyemia tverdokhlebovi* Min., *Acropholis* sp., *Issadia* sp. (determined by D.N. Esin), amphibia *Dvinosaurus primus* Amal., *Chroniosaurus dongusensis* Tverd., *C. boreus* (Ivach.), parareptiles *Raphanodon* sp., *Proelginia* sp., therapsids *Nuksenitia sukhonensis* Tat., *Suminia getmanovi* Ivach., *Saurochtonus* (?) sp. (determined by M.F. Ivachnenko and V.K. Golubev), mosses *Protosphagnum nervatum* Neub., lepidophytes *Fasciostomia delicata* Gom., ferns *Fefilopteris pilosa* Gom., *Pecopteris* sp. AVG-1, peltasperms *Peltaspermopsis* sp. AVG-1, *Tatarina* cf. *conspicua* S. Meyen, *Salpingocarpus bicornutus* S. Meyen, *S. variabilis* S. Meyen, *S.* cf. sp. SVM-2, *Phylladoderma (Aequistomia) annulata* S. Meyen, *P. (A.) rastorguevii* S. Meyen, *P. (A.) trichopora* S. Meyen, *Amphorispermum* (?) sp. SVM-1, *Raphidopteris* sp. indet., *Permotheca striatifera* S. Meyen et Gom., *P. vesicasporoides* S. Meyen, Esaul. et Gom., *Pursongia beloussovae* (Radcz.) Gom. et S. Meyen, conifers *Sashinia aristovensis* S. Meyen, *S. borealis* S. Meyen, *Quadrocladus dvinensis* S. Meyen, *Geinitzia* sp. SVM-1, plants incertae sedis *Arisada densa* S. Meyen (Gomankov and Meyen, 1986).

Variegated deposits of the Poldarskaya Formation are overlain by monochronous redbeds of the Salarevskaya Formation. The latter consists of red clayey siltstones and sandstones (Fig. 2). It also contains infrequent grey calcareous clays, limestones and bluish siltstones. There are also large asymmetrical sandy lenses as in the Poldarskaya Formation. The lenses are up to 12 m thick, 700 m along the strike. They consist of the basal gravelites or conglomerates overlain by polymictic sandstons. Four levels of sandy lenses, several at each level, are distinguished in the basin of the Sukhona and Malaya Severnaya Dvina rivers. Along the Sukhona River, six lenses of a single horizon are overlain by a thick paleosol. In the Malaya Severnaya Dvina River the lenses are normally not overlain by paleosols. In the Sokolki locality, a sandy lens is cut by ancient erosional channels, while in the Gorka locality it is levelled and covered by a layer of bluish siltstone.

The Salarevskaya Formation is assigned to the Vyatskii Horizon. It contains ostrocods *Suchonellina parallela* Spizh., *S. trapezoida* (Shar.), *S. fragiloides* (Zek.), *S. fragilinae* (Bel.), *S. inornata* (Spizh.), *Suchonella typica* (Spizh.), *S. cyrta* (Zek. et Jan.),

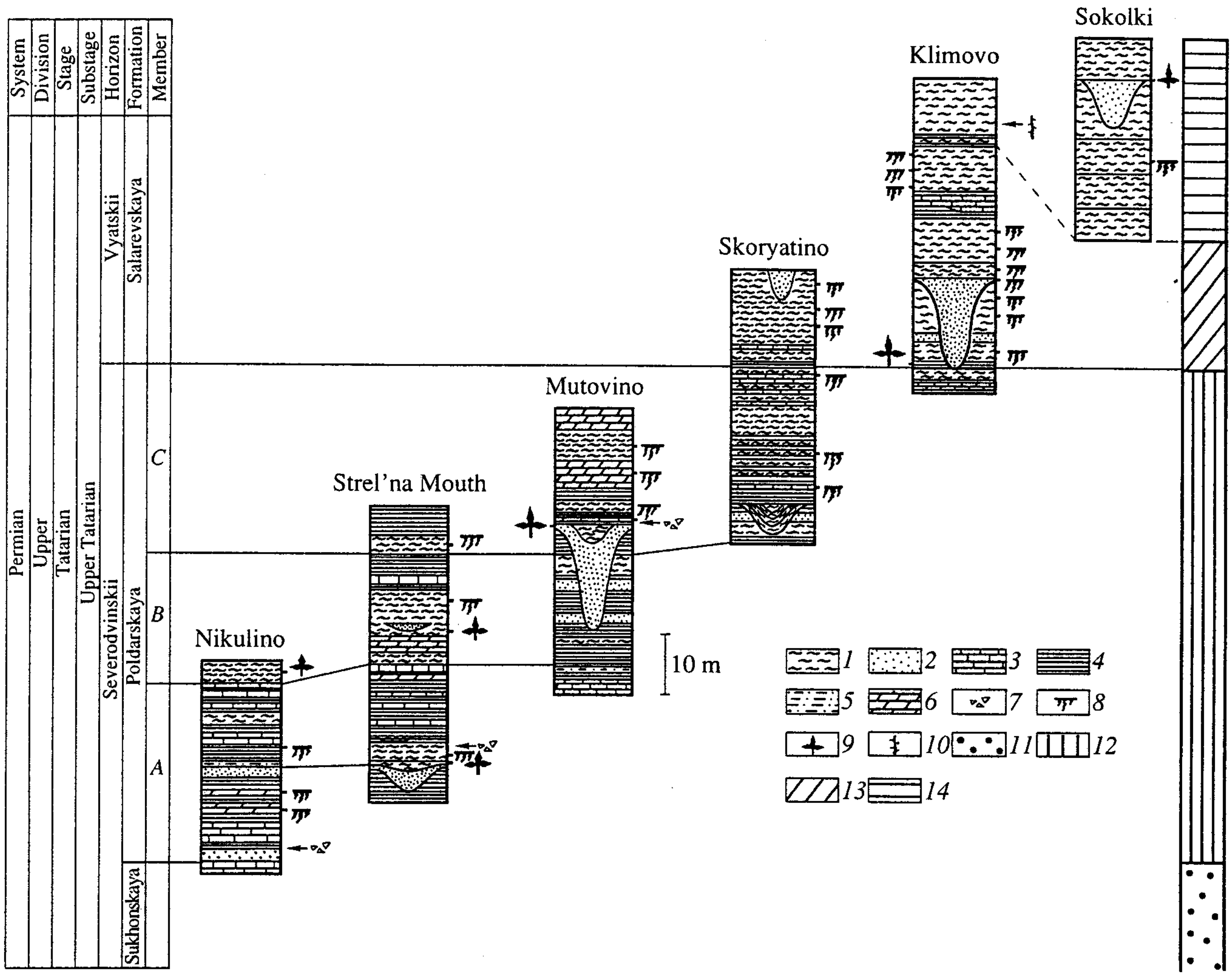



**Fig. 2.** Stratigraphic correlation of major localities and sedimentary environments: (*1*) clayey siltstones, (*2*) sands and sandstones, (*3*) limestones, (*4*) sandy clays, (*5*) sands with clayey siltstone interbeds, (*6*) marls, (*7*) clay-siltstone breccias, (*8*) fossil roots, (*9*) other plant fossils (leaves, shoots, reproductive organs), (*10*) horizons with typical *Radicites sukhonensis*, (*11*) basinal facies of the Sukhonskaya Formation, (*12*) marine and terrestrial deposits of shoals and coastal plains, the Poldarskaya Formation, (*13*) paleosol horizons in the lower part of the Salarevskaya Formation, (*14*) flood and playa lakes deposits with pedogenic carbonate cover, upper part of the Salarevskaya Formation.

*S. auriculata* (Shar.), *Darvinuloides svijazhicus* (Shar.), bivalves *Palaeomutela curiosa* Amal., *P. keyserlingi* Amal., *Opokiella tschernyschewi* Plot. (*Reshenia* ..., 1990), fishes *Amblipterina grandicostata* Esin, *Toyemia tverdokhlebovi* Min., *Mutovinia stella* Min., *Palaeoniscum* sp., *Watsonichthys* sp. (determined by D.N. Esin), amphibia *Dvinosaurus primus* Amal., *Jugosuchus licharevi* Riab., parareptiles *Scutosaurus* sp., *Kotlassia prima* Amal., *Karpinskiosaurus secundus* (Amal.), therapsids *Dicynodon trautscholdi* Amal., *Inostrancevia* sp., *Annaterapsidus* sp. (determined by M.F. Ivachnenko and V.K. Golubev), mosses *Pelliothallites tataricus* S. Meyen, *Protosphagnum nervatum* Neub., *Rhizinigerites neuburgae* S. Meyen, *Muscites* sp. SVM-1, *M.* sp. SVM-2, *M.* sp. SVM-3, lepidophytes *Fasciostomia delicata* Gom., *F.* sp. AVG-1, ferns *Fefilopteris pilosa* Gom., *Pecopteris* sp. AVG-1, peltasperms *Peltaspermopsis buevichiae* Gom. et S. Meyen, *P.* (?) sp. AVG-4, *Tatarina conspiqua* S. Meyen, *T. pinnata* S. Meyen et Gom., *Salpingocarpus bicornutus* S. Meyen, *S. variabilis* S. Meyen, *S.* cf. sp. SVM-2, *S.* sp. SVM-3, *S.* sp. SVM-5, *Phylladoderma (Aequistomia) aequalis* S. Meyen, *P. (A.) annulata* S. Meyen, *Permotheca striatifera* S. Meyen et Gom., *P. vesicasporoides* S. Meyen, Esaul. et Gom., *P. vittatinifera* S. Meyen et Gom., *Pursongia beloussovae* (Radcz.) Gom. et S. Meyen (Gomankov and Meyen, 1986), *P. amaltzkii* Zal (A.V. Gomankov, personal communication, and our data).

## MORPHOTYPES OF FOSSIL ROOTS DESCRIBED UNDER OPEN NOMENCLATURE

The genus *Radicites* was established by H. Potonié (1893) on material from the European Rotliegenden. Later, a new genus *Radiculites* was established by Lignier (1906). This latter genus is very similar, if not synonymous with *Radicites*. Two years later, Fritsch (1908) erected still another genus of root-like fossils *Rhadix* Frit. with the type species *R. corrugatus* from the Silurian (Barrandien) deposits of Czechia. However the structures described as *R. corrugatus* are problematic and may not even belong to the higher plants.

Numerous and diverse root remains were described and figured by Mader (1990a, 1990b) from the European Bundsandstein and Keuper deposits. Some of them are fairly close to those described in this paper. Thus the root tubes from the Otter Sandstones (New Red Sandstone in England) are morphologically quite similar to *Radicites erraticus* sp. nov. from the Tatarian deposits of the Russian Platform. Unfortunately, a comparison of these and other forms is hampered by the lack of detailed drawings showing morphological characters of fossil roots from European localities.

Some fossil roots described by Mader (1990a, 1990b) were related to other plant remains from the same deposits. It was possible to recognize roots of conifers and horse-tails.

Fossil roots preserved in paleosols were described from the Upper Triassic (?) locality Rozhdestvenskoye in Kazakhstan (Kapustin and Sivtsov, 1987). These roots can be assigned to two main root types. The first type includes thin axes forming root systems of several branching orders. The second type comprises vertical unbranched or seldom branched roots penetrating to depths of 0.5 m and more.

Root remains determined as *Radicites* sp. are often mentioned in paleofloristic papers, especially those containing paleoecological and taphonomic observations (Oshurkova, 1974, 1996; Naugolnykh, 1996). Unfortunately, the data on fossil roots assigned to *Radicites* are difficult to assess because they are defined as open nomenclature taxa or simply mentioned as associates of more distinct plant fossils. A synopsis of *Radicites* is yet to be compiled. Major root morphotypes from the Tatarian deposits are described below.

*Radicites* sp. 1 (Figs. 3i–3k; Pl. 6, fig. 14). Profusely branched systems of horizontal roots usually of three branching orders. The first order axes are curved, sometimes with small tubercles (Figs. 3i–3j). Width of the first order axes range from 2 to 8 mm, their lengths are more than 15 cm.

The second order axes are also curved but, as a rule, thinner than the first order axes. They arise from the first order axes irregularly at various angles and are often constricted at the point of divergence (Figs. 3i, 3j). The shortest second order axes are about 1–2 cm long, 3–4 mm broad respectively. Their maximum length exceeds 10 cm.

The second order axes often bear short hooked appendages, or third order axes. The latter are about 1.5 mm wide, 5–7 mm long. Similar appendages sometimes occur directly on the first order axes.

The figured specimens of *Radicites sentjakensis* Esaul. (Esaulova, 1986) is morphologically fairly close to our *Radicites* sp. 1. It differs however in showing central strands suggestedly corresponding to vascular bundles.

The root remains are preserved as strongly flattened clayey casts that are distinct from their rock matrix because of their different coloration. Sometimes they remain as three-dimensional casts. As a rule these roots do not show any evidence of distant transport. Therefore we consider most of *Radicites* sp. 1 localities as hypoautochtonous. The three-dimensional remains occurring in massive pelitomorphic limestones might have even been preserved *in situ*.

The material consists of ten specimens of satisfactory preservation collected from the Poldarskaya Formation (Fig. 4).

Microstructural characters have been studied in some roots of this type (Figs. 5a, 5b). The elements of primary xylem are tracheids with scalariform thickenings.

*Radicites* sp. 2 (Fig. 6b; Pl. 6, fig. 17). Root remains are aggregated, with a central subelliptical body 2 cm long and 1.5 cm broad. The first order axes arise radially from the central structure. They are curved or almost straight, sometimes with longitudinal striations or ribbed. Their width is about 3–4 mm, the length exceeding 50 mm. The second order axes arise at angles 70° to 90° to the first order axes. They are small straight or hooked appendages 5–8 mm long, 0.5–1 mm broad. Their densities seem to increase distally.

The distinctiveness of *Radicites* sp. 2 suggests a new species. However the material is not enough for erecting a new taxon.

The material consists of a single hand-specimen collected in the clayey limestone in the Mutovino locality, Poldarskaya Formation. The locality is here considered as hypoautochtonous.

*Radicites* sp. 3 (Fig. 6c). A system of horizontal roots with straight axes of the first and second orders. The first order axes are smooth, but with irregular coarse tubercles in presumably the proximal part. The proximal parts also bear thick side branches that are connected to adjacent first order branches. The axes are 2–3 mm wide and their width remains constant along the whole length of the preserved fragments which are up to 6 cm long.

The second order axes are straight, smooth, about 1 mm wide, 5–10 mm long, arising at a right angle or approximately so from the first order branches. They show occasional forking.

*Radicites* sp. 3 is similar to some specimens of *R. luganicus* Zal. (Zalessky, 1937) from the Lugan-

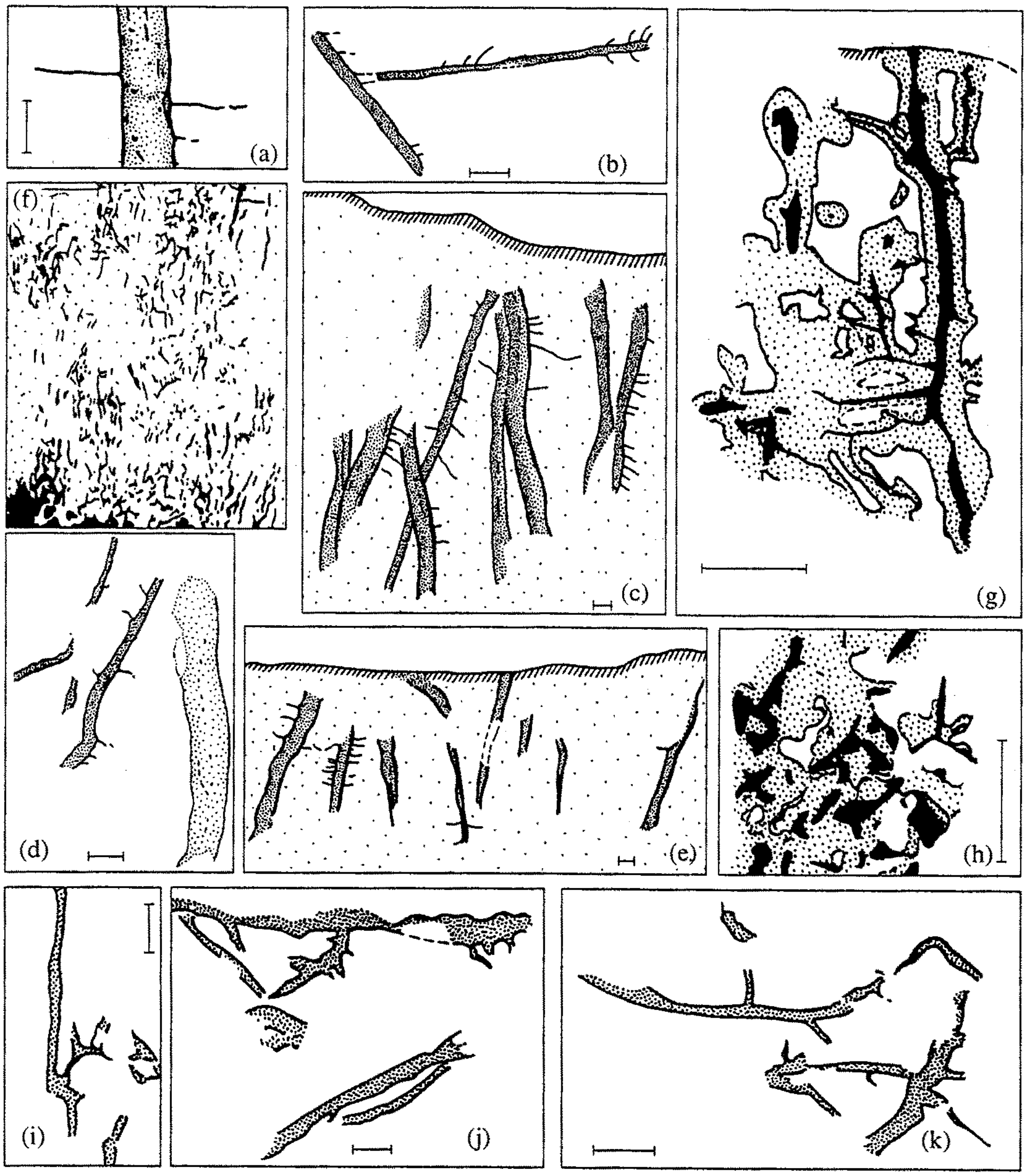



**Fig. 3.** Separate roots from the Upper Tatarian substage in the Sukhona Basin: (a), (c–e) *Radicites sukhonensis* sp. nov.; (a) holotype, Moscow State University, no. 276/4005, Odomchino, Salarevskaya Formation, vertical section; (c) specimen no. 276/4004, Odomchino, Salarevskaya Formation, vertical section; (d) specimen no. 276/2809-2, Mutovino, Poldarskaya Formation, horizontal sketch, (e) specimen no. 276/3010, Verkhnyaya Erga, Poldarskaya Formation, vertical section; (b) *Radicites* sp. 4, specimen no. 276/3701, Klimovo, Salarevskaya Formation, horizontal sketch; (f–h) *Radicites erraticus* sp. nov.; (f) Kostromskaya Region, Vetluga River, Makaryevo, Lower Triassic, Vokhminskiy horizon, Vokhminskaya Formation, vertical section; (g) holotype, Moscow State University, no. 276/3906, Salarevo, Salarevskaya Formation, vertical section; (h) specimen no. 276/2204, Opoki, Poldarskaya Formation, horizontal sketch; (i–k) *Radicites* sp. 1, horizontal sketch in all figures: (i) specimen no. 276/2811, Mutovino, Poldarskaya Formation; (j) specimen no. 276/2810, Mutovino, Poldarskaya Formation; (k) specimen no. 276/3313, Rovdino, Poldarskaya Formation. Scale bar 1 cm.

skaya Formation, Upper Carboniferous–Lower Permian of the Donets Basin. In the latter species the second order axes arise at approximately right angles to the first order axes. It is however distinct from our species in showing rhombic scars on the first order axes, as well as denser second order axes and in the occurrence of the third order axes that are lacking in *Radicites* sp. 3.

This form differs from *Radicites* sp. 1 in the straight first order axes and better developed second order branches that arise at right angles to their bearing axes.

Flattened clayey casts of *Radicites* sp. 3 were found in the hypoautochtonous locality within subaquatic Poldarskian deposits and as allochtonous remains in a

| System | Permian | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Division | Upper | | | | | | | | | | | | | |
| Stage | Tatarian | | | | | | | | | | | | | |
| Substage | Upper Tatarian | | | | | | | | | | | | | |
| Horizon | Severodvinskii | | | | | | | | Vyatskii | | | | | |
| Formation | Poldarskaya | | | | | | | | | Salarevskaya | | | | |
| Localities | 20 | 22 | 25 | 28 | 29 | 30 | 32 | 33 | 35 | 37 | 39 | 40 | 46 | 61 |
| | "Nikulino" | "Opoki" | "Strel'na Mouth" | "Mutovino" | "Konyavitsa" | "Verkhnyaya Erga" | "Skoryatino" | "Rovdino" | "Bol'shoye, Kalikino" | "Klimovo" | "Salarevo" | "Odomchino" | "Gorka" | "Sokolki" |
| *Radicites sukhonensis* | | | | + | | + | | | | | | + | | |
| *R. erraticus* | + | + | + | + | | | + | + | + | + | + | + | + | + |
| *R.* sp. 1 | + | | | + | + | + | + | + | + | | | | | |
| *R.* sp. 2 | | | | + | | | | | | | | | | |
| *R.* sp. 3 | + | | | | | | | | | | | | + | |
| *R.* sp. 4 | | | | | | | | | | + | | | | |
| *R.* (?) sp. 5 | | | | | + | | + | | | | | | | |

**Fig. 4.** Occurrences of roots and root-like fossils in the studied geological sections.

lens of the Gorka Village locality (Fig. 4). The material consists of five well preserved specimens.

*Radicites* sp. 4 (Fig. 3b). Horizontally disposed root systems of three order axes. The first order axes are straight, almost smooth, with indistinct tubercles, about 4 mm wide, more than 10 mm long. The second order axes are straight with small tubercles, often slightly constricted at the point of departure. They arise at 60° to the first order axes. The third order axes (appendages) are born at 60° to the second order axes. They are 2–6 mm long, 0.5–1 mm wide, hooked, pointed at the apex of their bearing branches. The appendages occasionally occur directly on the first order axes.

*Radicites* sp. 4 differs from *R.* sp. 1 and *R.* sp. 2 in straight first order axes that are almost smooth, while the third order axes–hooked appendages–set this form apart from *Radicites* sp. 3.

Two specimens of this form were found in allochtonous deposition in a lens of the Klimovo locality (Salarevskaya Formation).

*Radicites* (?) sp. 5 (Fig. 6e; Pl. 6, fig. 16). Vertical and subvertical repeatedly branching roots. The first order axes are strongly curved, their surface irregularly tuberculate, with thickenings that occasionally give rise to the second order axes. The first order axes taper from 8 mm thick at the base to 1 mm thick distally.

The second order axes and the occasionally developed third order ones are hooked appendages arising at 60° to 90°. They are 1–2 mm wide, more than 15 mm long.

The nature of *Radicites* ? sp. 5 remains problematic. This form differs from other root morphotypes in irregular branching and highly variable dimensions of the axes.

Two three-dimensional clayey casts of *Radicites* (?) sp. 5 from the Poldarskaya Formation (Fig. 4) were found in a vertical position. They are therefore considered as autochtonous.

## GENESIS OF THE ROOT-BEARING DEPOSITS

The Poldarskaya and Sukhonskaya formations are fairly similar, especially so within their transitional interval. They might have been formed in similar sedimentary environments. The consistent occurrence of the Sukhonskian redbeds on the western flank of the Sukhonskiy Ridge and the likewise consistent spread of the Poldarskian deposits on the eastern flank suggest their deposition in a single large epicontinental basin.

In distinction from the Sukhonskaya Formation, the Poldarskian deposits are more sandy, with more frequent sand lenses and predominantly terrestrial plants and vertebrates. These distinctions suggest deposition in near-shore environments close to the slopes of a sedimentary basin. Moreover, the Poldarskian deposits often show desiccation cracks and they contain numerous paleosol horizons with fossil roots of *Radicites erraticus* sp. nov. that can be taken as evidence of periodical emergence above sea level.

The root remains *Radicites erraticus* sp. nov. typically occur in variegated beds up to 1.5 m thick, with a patchy background of red spots and a light-bluish fringe around the lenticles. In the upper part of the bed, the roots (the proximal portion of the root system) form a dense mass. They gradually diverge distally to the bottom of the root-bearing bed where the first, second and third order axes are distinguishable. Further distally, the continuous root network is divided into separate clusters, supposedly belonging to different plant individuals. The root-bearing deposits are usually calcareous and contain small carbonate concretions up to 1.5 cm in diameter.

Major structural features of these beds suggest that they are paleosols. In the oppinion of pedologists V.O. Targulyan and Ye.Yu. Yakimenko the specific prismatic microstructures occurring in the deposits with *Radicites erraticus* sp. nov. are characteristic of illuvial horizons and suggest long exposure to weathering.

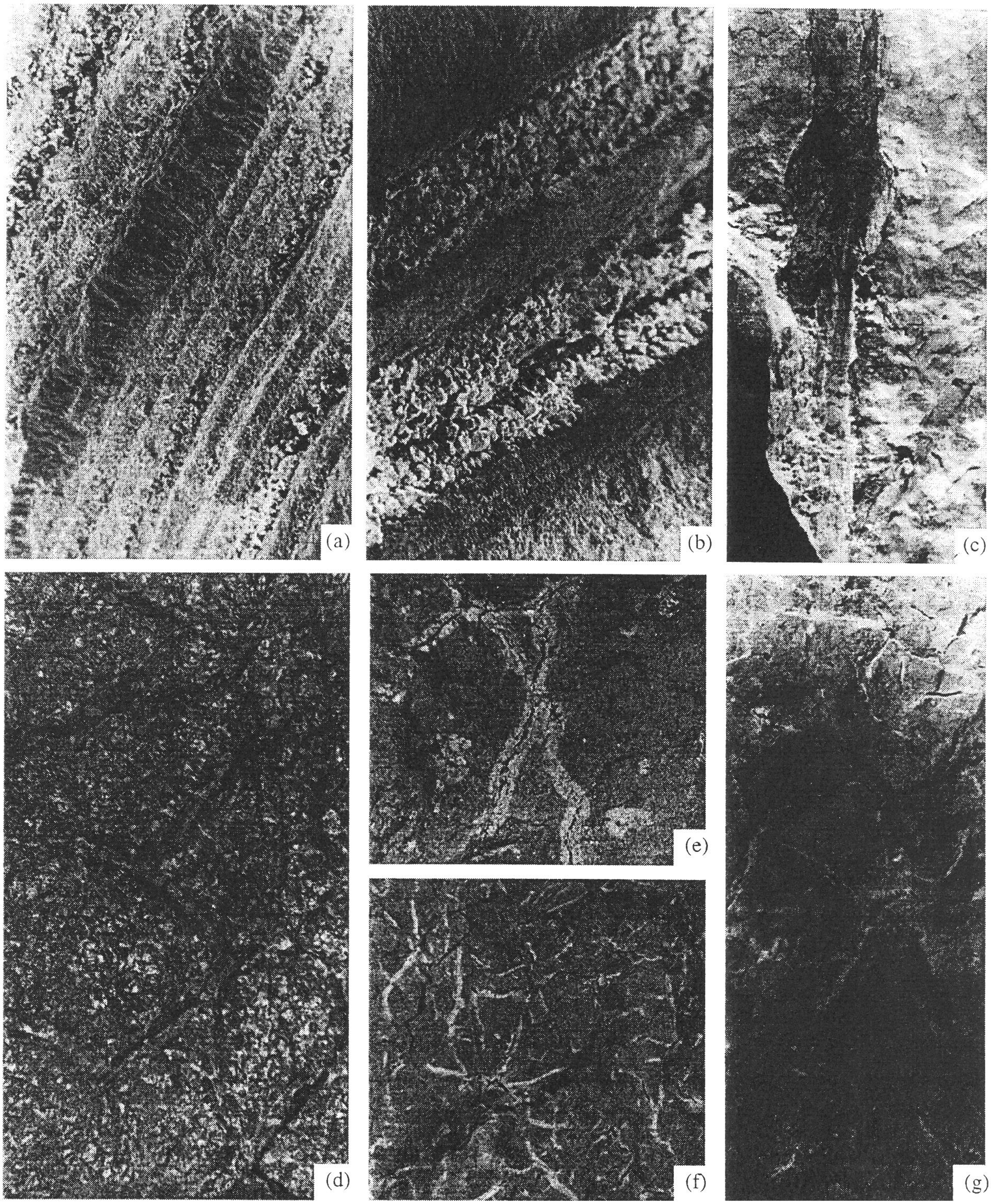



**Fig. 5.** *Radicites* root remains: (a, b) *R.* sp. 1, specimen no. 276/2231, ×150, Vologda Region, Sukhona River, Opoki, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, (c) *R. sukhonensis* sp. nov., holotype, Moscow State University, no. 276/4005, ×3, Vologda Region, Sukhona River, Odomchino, Upper Tatarian Substage, Vyatskii Horizon, Salarevskaya formation: (d–g) *R. erraticus* sp. nov.: (d) transverse section in the white spot zone on the bedding plane with desiccation cracks, field photograph, ×0.3, Nizhnii Novgorod Region, Vetluga River, Sarafanikha (Krasnye Baki), Lower Triassic, Vokhminskii Horizon, Vokhminskaya formation; (e) longitudinal section, specimen no. 276/7302, ×1.5, Nizhnii Novgorod Region, Vetluga River, Andreyevo, Lower Triassic, Vokhminskiy Horizon, Vokhminskaya formation; (f, g) transverse section showing two branching orders, specimen no. 276/7201, Nizhnii Novgorod Region, Vetluga River, Andreyevo, Lower Triassic, Vokhminskii Horizon, Vokhminskaya formation, (f) ×1, (g) ×1.5.

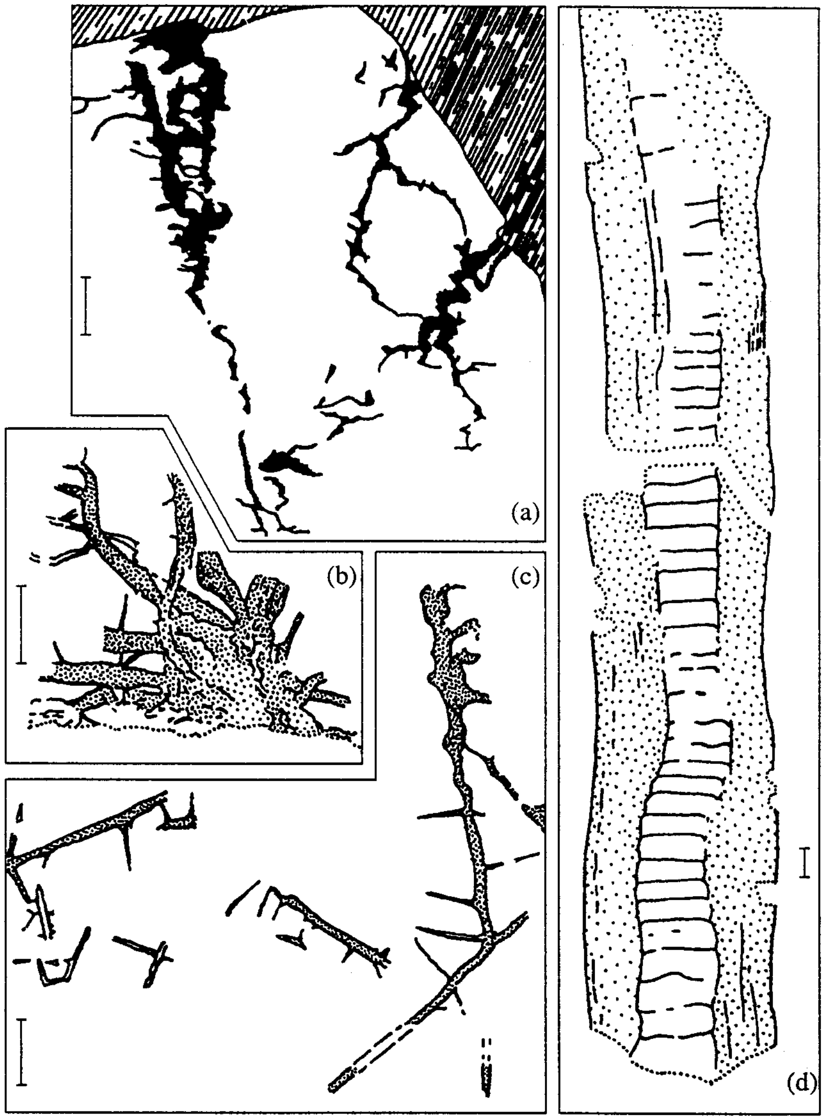



**Fig. 6.** Fossil roots (a–c) and a gymnosperm shoot? (d) from the Upper Tatarian Substage in the basin of Sukhona and Malaya Severnaya Dvina rivers: (a) *Radicites* ? sp. 5, specimen no. 276/3201, Skoryatino, Poldarskaya Formation, vertical section; (b) *Radicites* sp. 2, specimen no. 276/2812, Mutovino, Poldarskaya Formation, horizontal sketch; (c) *Radicites* sp. 3, specimen no. 276/4601, Gorka, Salarevskaya Formation, horizontal sketch; (d) *Artisia* ? sp., Strel'na mouth, Poldarskaya Formation. Scale bar 1 cm.

These features support interpretation of the root-beds as paleosols. Their high carbonate content is comparable with carbonate soils widespread in modern semiarid regions (*Obstanovki* ..., 1990). The occurrence of paleosols among the predominantly basinal Poldarskian deposits is evidence of extremely shallow-water environments with periodical emergence.

The Sukhonskaya Formation lacks organic remains. This and the occurrence of dolomites and silicites may suggest a relatively deep-water sedimentary off-shore environments, perhaps close to the sources of mineral solutions.

The Salarevskian deposits, despite their uniformly red coloration, lack the regular structure of the Poldarskaya Formation. They are fairly variable both in vertical section and laterally. Our data suggest that these deposits might have been polygenic. The lower part of the Salarevskaya Formation contains numerous paleosol horizons that form a thick sequence (up to 30 m thick in the Klimovo locality; see Fig. 2). The Salarevskian paleosols are variable in their root characters as well as in their carbonate inclusions (from small knots to carbonate carapaces and concretions up to 1 m in diameter). These structures await further study. In the upper part of the Salarevskaya Formation on the Malaya Severnaya Dvina River the paleosols became rare and are relatively thin.

Disappearance of paleosols from the upper part of the Salarevskaya Formation correlates with such sedimentary features as irregular thickness (varying from a

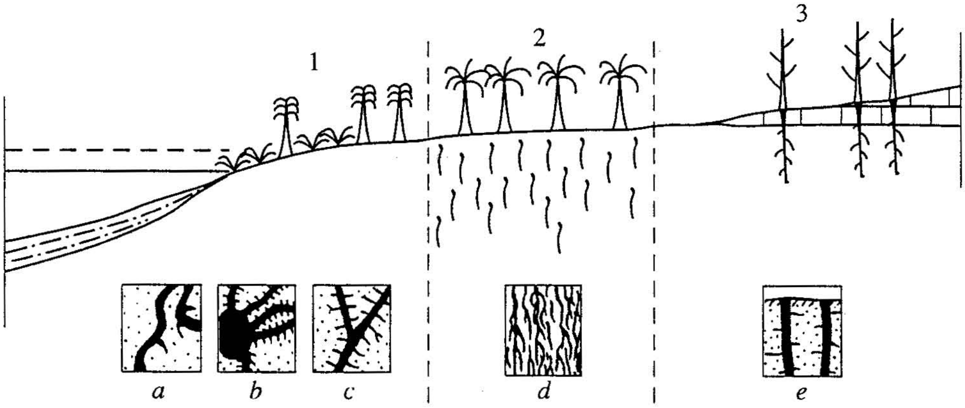



**Fig. 7.** Paleoecological interpretation of root type occurrences in sedimentary domains. (1–3) Preliminary defined catenic members: (1) periodically submerged coastal plain with ephemeroids; (2) terrestrial zone of active pedogenesis; (3) flood and playa lake deposition zone with pedogenic carbonates and with phreatophytes. Root types; (*a*) *Radicites* sp. 1, (*b*) *Radicites* sp. 2, (*c*) *Radicites* sp. 3, (*d*) *Radicites erraticus* sp. nov., (*e*) *Radicites sukhonensis* sp. nov.

few millimeters to several meters) and discontinuous distribution of individual beds, abundant small sand and siltstone lenses and widespread occurrence of bluish spots in the redbeds. The latter phenomenon is due to local concentration of reduced iron oxides. Also characteristic for the upper horizons are erosional cuts, pedogenic features, carbonate carapaces and granulometric sorting of clastic sediments (Verzilin *et al.*, 1993).

Such deposits can be met everywhere but they are most typically represented along the Malaya Severnaya Dvina River from the village of Aristovo to the city of Kotlas. They resemble modern talus fan deposits of distal piedmont zones. Tverdokhlebov (1996) noted proluvial characters of the upper Salarevskian horizons, assigning them to a special type of continental sediments–the plain proluvium. In his opinion, the plain proluvim accumulates over vast territories of arid and semiarid plains as a result of catastrophic floods. At the same time, these deposits are similar to those described by Mader (1992a, 1992b) from the Permian–Triassic fluvial basins of Central Europe. According to Mader, their textural characters indicate the plane erosion and flood accumulations with gradual transition to the playa lake deposits of small intermittent water bodies that arise during wet seasons in semiarid regions. Generally this interpretation agrees with that of Tverokhlebov and our observations that also support the flood and playa origin of the upper Saarevskian deposits.

The flood and playa sediments were covered with carbonate carapaces–limestone horizones up to 0.4 m thick that grade into carbonate concretions. Numerous horizons of underdeveloped carapaces appearing as concretion accumulations crop out along the Malaya Severnaya Dvina River. In a number of outcrops they contain vertical root remains, as in the Odomchino locality (see under description of *Radicites sukhonensis* sp. nov. below).

Opinions vary on the genesis of sand lenses. They were interpreted as (1) river channel deposits (Lutkevich, 1955), (2) shelf channels continuous with onland river systems (Efremov, 1950; Ignat'ev, 1963; Verzilin *et al.*, 1993), (3) break-through channels (V.T. Frolov's interpretation), (4) intermittent flow deposits (N.M. Chumakov's hypothesis).

We do not consider the lenses as shelf channel deposits for they are mostly cut into paleosols, flood or playa accumulations. At the same time the fluvial hypothesis does not seem convincing because it assumes a stable river system with permanent channels and their characteristic deposits. Sediments with typical flood-plain characteristics, as well as buried channels, have yet to be found in the region.

However we do not completely reject the fluvial model of the lens origin. In the absence of continuous plant cover in the areas of low relief a river with low non-cespitate banks could hardy maintain a permanent channel. Instead it seems logical to assume a shift of the flow at each high flood. Moreover, in the compensated depressions, such as the Moscow Syncline in the Tatarian–Early Triassic time, river valleys could barely have been formed at all. More probable is a system of shifting shallow channels that seem typical for the Tatarian deposits, with new channels appearing during high energy floods. This suggestion is supported by the widespread occurrence of flood deposits. This model assumes numerous intermittent flows, their sediments modified by eolian processes.

Thus, the Salarevskaya Formation can be considered as an assemblage of semiarid plain deposits with intermittent channels and playa lakes. Sedimentation in such an environment might totally depend on the periodicity of precipitation.

In addition to the above described deposits, the upper part of the Salarevskaya Formation in the Klimovo locality contains a 10 m thick uniform sequence of light-brown porous siltstones with cubical texture. This bed might have been of loess origin. Plant remains (leaves, shoots, rare fructifications) occur in lenses, as in the mouth of the Srel'na River, Mutovino (Isady) and Aristovo, or in occasional siltstone layers of near-shore marine origin, as in Nikulino, Opoki and Klimovo. The diverse roots of the Poldarskaya Formation are abundant in both the basinal facies and paleosols, rarely occurring in the clay-siltstone breccias that consist of non-abraded detrital, small pebble-size material included in the clay-siltstone matrix. In the Salarevskaya Formation the root remains are confined to paleosols, carbonate carapaces, rarely to the clay-siltstone breccias and sand lenses, as in the Klimovo and Gorka localities.

## RECONSTRUCTION OF THE CATENA

Reconstructions of catenae in the paleobotanical literature of the last decades are based on a synthesis of taphonomic, sedimentological and phytotaxonomic data (Krassilov, 1972; Retallack, 1977; Scott, 1979; Schweitzer, 1983; Shchegolev, 1991, etc.).

Certainly, such reconstructions are obligatory as a stage in the analysis of local florogenic processes and general trends of plant evolution (Krassilov, 1972; see also Teichmuller, 1958; Chandler, 1964; Knobloch, 1970).

In our material, most of the fossil roots and root-like remains occur in three different types of sedimentary environments suggesting a succession of respective deposition sites, as follows:

(1) shallow marine and, probably, adjacent coastal plain areas, with alternation of aquatic and terrestrial sedimentation characteristic of the Poldarskaya Formation (Fig. 7/1);

(2) terrestrial sites of active pedogenesis (Fig. 7/2) typically represented in the localities of Klimovo and Salarevo;

(3) terrestrial areas of flood and playa accumulations with carbonate carapaces (Fig. 7/3). This type is well represented in the outcrops along the Malaya Severnaya Dvina River from the village of Aristovo to the city of Kotlas.

The facial types (1–3) orderly replace each other upsection above the Sukhonian deposits (Fig. 2). Their succession represents a regressive series. Their regular stratigraphic occurrences reflect a landward directed sequence of sedimentary environments. Sites (1) are closest to the shore of the marine basin. Sites (2) are transitional between the periodically submerged and dry land zones. Sites (3) are most distant from the marine basin.

We observed a regular occurrence of root morphotypes in the above sedimentary facies. Thus the hypoautochtonous remains of horizontal root systems of *Radicites* sp. 1, *R.* sp. 2 and *R.* sp. 3 occur in sites (1), while the repeatedly branched autochtonous *Radicites erraticus* sp. nov. are confined to sites (2) and the long sparsely branched vertical *in situ* roots of *Radicites sukhonensis* sp. nov. are typical for sites (3). Therefore the coastal sites, the areas of active pedogenesis and the zones of pedogenic carbonates might correspond to segments of a single catena.

As we noticed before, the climate of the Late Tatarian time, as suggested by the characteristic sedimentological features, was semiarid with seasonal precipitation. Our paleoecological interpretation of fossil root occurrences against the succession of sedimentary facies together with paleoclimatic considerations have led to unexpected conclusions as to composition of the latest Permian vegetation. In semiarid climates coastal plains usually support ephemeroid communities. Ephemeroids are perennial herbaceous plants occurring in deserts and semideserts and adapted to strongly seasonal precipitation by developing dense shallow root system that absorb moisture form near-surface substrate layers. In contrast, the area of pedogenic carbonates might have been populated with phreatophytes that have strong sparsely branched vertical roots penetrating the deeper ground water sources.

The zone of active pedogenic process was ecologically transitional (ecotonal) between the ephemeroid and phreatophyte domains. Judging by the repeatedly branched *Radicites erraticus* sp. nov. root morphotype, it was populated by plants that were ecologically closer to ephemeroids than phreatophytes.

## TAXONOMIC ASSIGNMENTS OF LATE TATARIAN EPHEMEROIDS AND PHREATOPHYTES

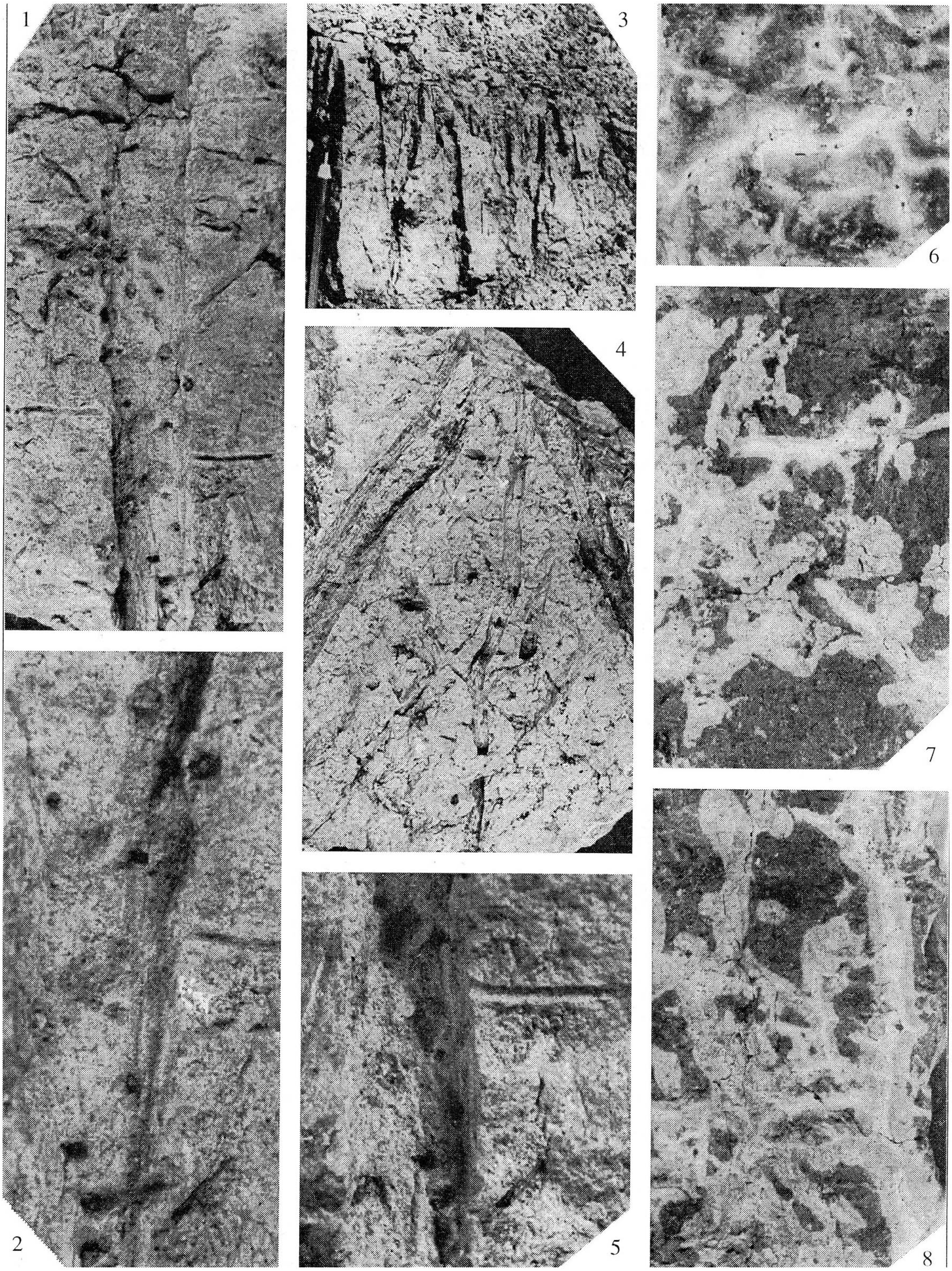
Unfortunately the root remains attached to other plant parts are totally lacking in our material. Therefore our taxonomic assignments of the root remains are based on oblique evidence alone awaiting further support of more complete finds of roots in organic association with aboveground organs.

At present the ecological information on habitats of Late Tatarian plants is very scanty. It was suggested, for instance, that representatives of the widespread genus *Tatarina* might have been hygro- or hydrophytes (Gomankov and Meyen, 1986). In our model of vegetational catena, the only habitat suitable for such life forms could be the sedimentary site (1). Tatarinas might grow along the coasts under conditions of seasonal precipitation.

In the Mutovino locality, the root remains *Radicites* sp. 1 and *R.* sp. 2 occur in deposits that contain a large plant-bearing lens with abundant leaves of *Pursongia* sp. (Pl. 6, figs. 5, 10, 12, and 15). A regular association of *R.* sp.1 and *R.* sp. 2 with *Pursongia*-type leaves may suggest their belonging to one and the same plant species.

Putative ephemeroids can perhaps be found among the Late Tatarian pteridophytes that were represented by predominantly herbaceous forms unable to produce

Plate 5



powerful root systems of the *Radicites sukhonensis* type. This ecological group might include some articulates (Pl. 6. figs. 2–4, 8, 18) widespread in the Upper Tatarian deposits but as yet little studied, e.g., *Paracalamites* sp., *Paracalamitina* sp., *Phylotheca* sp. (sp. nov.?), *Neocalamites* sp. (?), as well as lepidophytes (Pl. 6, fig. 9) and ferns (Pl. 6, fig. 11).

It seems easier to define the scope of potential phreatophytes. They might comprise a conifer genus *Geinitzia* (Pl. 6, fig. 7). Large fragments of pycnoxylic wood occasionally found in sand lenses might belong to these plants. The assemblage of conifers supposedly occupied most distant sites of the catenic sequence that agree with their suggested phreatophytic adaptation. Incidentally, *Geinitzia* remains are as rare as the typical *Radicites sukhonensis*, both probably belonging to phreatophytic vegetation that grew at a distance from the deposition sites.

## SYSTEMATIC PALEOBOTANY

### Genus *Radicites* H. Potonié, 1893

#### *Radicites sukhonensis* Aref'ev et Naugolnykh, sp. nov.

Plate 5, figs. 1–5

E t y m o l o g y. From the Sukhona River.

H o l o t y p e. Moscow State University, no. 276/4005, Odomchino locality, right bank of the Sukhona River opposite the village of Odomchino of the Velikoustyuzhskii District, Vologda Region, 9 km from the highway bridge in the direction of Velikiy Ustyug City, Upper Tatarian Substage, Vyatskii Horizon, Salarevskaya Formation.

D i a g n o s i s. Large vertical root axes, more than 15 cm long, 1.5 cm thick, unbranched, with dense small appendages. The appendages arise at 90° to the first order axes.

D e s c r i p t i o n (Figs. 3a, 3c–3e, 5b, 5c). Roots large, vertical, unbranched, with numerous small appendages. The first order axes long, straight, their surface scabrate with small tubercles and with longitudinal ridges (Pl. 5, figs. 2, 4). These axes are up to 15 cm long, 1.5 cm in diameter, with the diameters remaining constant along the whole lengths of the root fragments. Occasional specimens show forking of the main axes, with the diameters insignificantly decreasing in the fork arms that tend to be vertically oriented. The exceptional oblique or horizontal roots are exceedingly rare. Some specimens show elliptical bodies attached to the root axes and perhaps representing tubers (Fig. 5c).

Small appendages (second order axes) arise at about 90° from their bearing axes. They leave small (up to 2 mm in diameter) punctuate scars. Judging by the arrangement of the scars the appendages were sometimes disposed in regular vertical files (Figs. 3c, 3d). The appendages are more than 20 mm long, about 2 mm in diameter.

The preservation forms of these roots are predominantly three-dimensional, rounded in transverse section, tubes filled with soft greenish clay easily removed by water.

C o m p a r i s o n. From other species of the genus differs in large vertical main axes (the axes of the first order) as well as in numerous regularly disposed small appendages (the second order axes).

R e m a r k s. Almost all the specimens were collected in calcareous interbeds that are interpreted as pedogenic carbonates. Since these carbonate carapaces were formed as a result of long desiccation in a semiarid climate, the specimens might represent proximal parts of roots preserved in the zone of lime accumulation. The root diameters do not change in the available fragments suggesting that the roots penetrated to considerable depths. We consider localities of this type as autochtonous, with *in situ* root remains.

O c c u r r e n c e. Upper Tatarian Substage, Salarevskaya and, rarely, Poldarskaya formations in the basin of the Sukhona and Malaya Severnaya Dvina rivers, Vologda Region (Fig. 4).

M a t e r i a l. Eleven specimens of satisfactory and fine preservation.

#### *Radicites erraticus* Aref'ev et Naugolnykh, sp. nov.

Plate 1, figs. 6–8.

E t y m o l o g y. From Latin *erraticus* (wild, wandering).

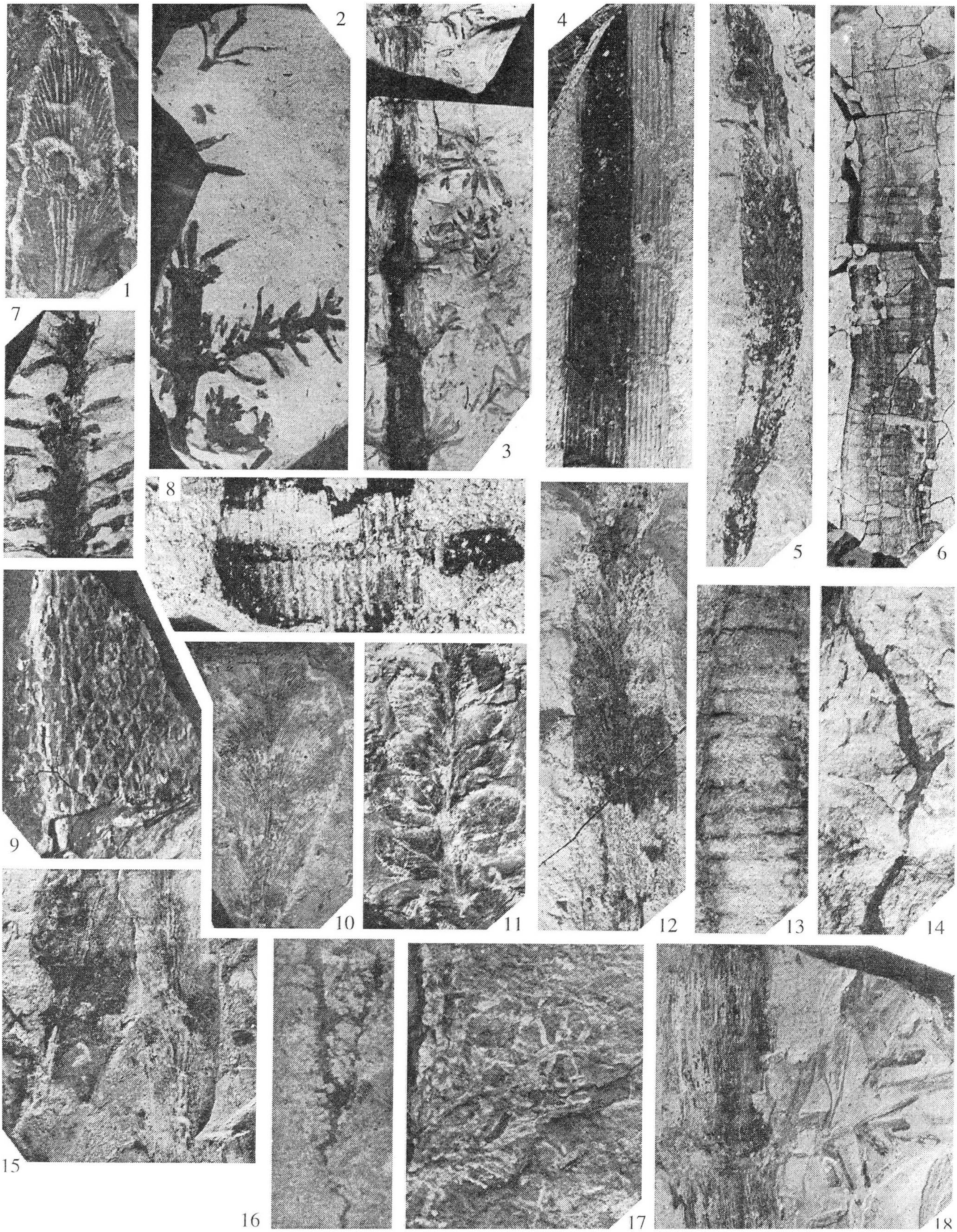
H o l o t y p e. Moscow State University, no. 276/3906; Salarevo locality, left bank of the Sukhona River opposite the village of Klimovo, Velikoustyuzhskii District, Vologda Region, 17 km from the highway bridge in the direction of the city of Velikiy Ustyug, Upper Tatarian Substage, Vyatskii Horizon, Salarevskaya Formation.

E x p l a n a t i o n o f P l a t e 5

Roots form the Tatarian Stage of Sukhona River.

**Figs. 1–5.** *Radicites sukhonensis* sp. nov.; (1,4,5) holotype, Moscow State University, no 276/4005, Vologda Region, Odomchino, Upper Tatarian Substage, Vyatskii Horizon, Salarevskaya Formation, vertical section; (1) ×1, (4) ×1.5, (5) ×1.7; (2) specimen no. 276/4004, same locality, vertical section, ×0.2; (3) specimen no. 276/2809-1, Vologda Region, Mutovino, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, horizontal sketch, ×0.5;

**Figs. 6–8.** *Radicites erraticus* sp. nov.; (6) specimen no. 276/2204, Vologda Region, Opoki, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, horizontal sketch, ×2.2; (7, 8) holotype, Moscow State University, no. 276/3906, Vologda Region, Salarevo, Upper Tatarian Substage, Vyatskii Horizon, Salarevskaya Formation, vertical section, ×1.8.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Explanation of Plate 6

Root-like fossils and leaves of their potential producing plants from the Tatarian Stage of the Sukhona Basin.

**Fig. 1.** *Marginopteris* sp. nov., leaf of a xeromorphic pteridosperm showing marginal spines, specimen no. 276/2209, Vologda Region, Opoki, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×1.5;

**Figs. 2, 3, 18.** *Phyllotheca* sp. (sp. nov.?): (2) specimen no. 276/2504, ×1; (3) specimen no. 276/2501, ×1; (18) specimen no. 276/2502, ×1.5, Vologda Region, Strel'na mouth, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation.

**Fig. 4.** *Paracalamites* sp. (ex gr. *P. frigidus* Neub.), specimen no. 276/2505, Vologda Region, Strel'na mouth, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×1.

**Figs. 5, 10, 12, 15.** *Pursongia beloussovae* (Radcz.) Gom. et S. Meyen: (5) specimen no. 276/2806, ×1.2; (10) specimen no. 276/2803, ×1.2; (12) specimen no. 276/2804, ×1.2; (15) specimen no. 276/2802, ×1.2, Vologda Region, Mutovino, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation.

**Figs. 6, 13.** *Artisia* (?) sp.: (6) Vologda Region, Strel'na mouth, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×0.2; (13) specimen no. 276/2510, same locality, ×1.5.

**Fig. 7.** *Geinitzia* sp., specimen no. 276/2805, Vologda Region, Mutovino, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×1.5.

**Fig. 8.** *Paracalamitina* sp., specimen no. 276/2506, Vologda Region, Strel'na mouth., Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×1.5.

**Fig. 9.** Lepidophyte cortex, specimen no. 276/2202, Vologda Region, Opoki, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×1.2.

**Fig. 11.** *Pecopteris* sp. AVG-1 (= *Dvinopteridium edemskii* Zal.), specimen no. 276/2201, Vologda Region, Opoki, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, ×1.5.

**Fig. 14.** *Radicites* sp. 1, specimen no. 276/1801, Vologda Region, Navoloki, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, horizontal sketch, ×0.5.

**Fig. 16.** *Radicites* (?) sp. 5, specimen no. 276/3201, Vologda Region, Skoryatino, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, vertical section, ×0.9.

**Fig. 17.** *Radicites* sp. 2, specimen no. 276/2812, Vologda Region, Mutovino, Upper Tatarian Substage, Severodvinskii Horizon, Poldarskaya Formation, horizontal sketch, ×1.

Diagnosis. Vertical repeatedly branched root system. Main axes slender, undulate, about 10 cm long, 1.5 cm in diameter.

Description (Figs. 3f–3h; 5d–5g). Well developed systems of vertical repeatedly branched roots. The first order axes are long, slender, undulate, up to 10 cm long with diameter constantly about 1.5 mm. Usually they are vertically oriented. The second order axes are thin, about 2 cm long, 1 mm in diameter arising irregularly at variable angles. They in turn give rise to the third order axes up to 5 mm long, 1 mm in diameter. Both the second and third order axes are hooked and often interlaced with the first order axes forming a dense uniform network.

The preservation forms of these roots are three-dimensional tubes or lenticles that are either hollow or filled with calcite. They are often encircled with a light-bluish fringe forming irregular spots against the predominantly red background.

Comparison. In their vertical orientation these roots are similar to *Radicites sukhonensis* sp. nov., but differ in the much smaller first order axes, almost equal diameters of the first, second and third order axes and copious branching.

From other species of the genus *Radicites* this form differs in the abundant axes and their copious branching.

Occurrence. Upper Tatarian Substage, the Poldarskaya and Salarevskaya formations in the basin of the Sukhona and Malaya Severnaya Dvina rivers, Vologda and Arkhangel'sk regions (Fig. 4); Lower Triassic of the Moscow Syncline.

Material. More than 15 satisfactory preserved specimens.

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## REFERENCES

Chandler M.E.J., *The Lower Tertiary Floras of Southern England. 4. A Summary and Survey of Findings in the Light of Recent Botanical Observations*, London: Brit. Museum (Natur. History), 1964.

Efremov, I.A., Taphonomy and Geological Record, *Tr. Paleontol. Inst., Akad. Nauk SSSR*, 1950, vol. 24, no. 1, pp. 1–177.

Esaulova, N.K., *Flora Kazanskogo Yarusa Prikam'ya* (Flora of the Kazanian Stage, Prikamie), Kasan: Kasan Univ., 1986.

Fritsch, A., *Problematica Silurica, Système Silurien du Centre de la Bohème*, Barrande, O., Ed., Prague, 1908.

Gomankov, A.V. and Meyen, S.V., *Tatarinovaya Flora* (The Tatarina's Flora), Moscow: Nauka, 1986.

Ignat'ev, V.I., *Tatarskii yarus tsentral'nykh i vostochnykh oblastei Russkoi platformy, Chast' 2. Fatcii, Paleogeografiya* (The Tatarian Stage of the Central and Eastern Regions of the Russian Platform, Part 2. Facies, Paleogeography), Kasan: Kasan Univ., 1963.

Kapustkin, G.R. and Sivtsov, A.V., Permineralized Roots of Plants in the Ancient Weathering Crust of Kempersay Massif, *Izv. Akad. Nauk SSSR, Ser. Geol.*, 1987, no. 5, pp. 127–132.

Knobloch, E., The Tertiary Floras of Moravia (Czechoslovakia), *Paleontol. Abh.*, 1970, vol. 3, nos. 3–4, pp. 381–390.

Krassilov, V.A., *Paleoekologiya nazemnykh rastenii. Osnovnye printsipy i metody* (Paleoecology of Terrestrial Plants, Main Principles and Methods), Vladivostok: Far East Research Center, Acad. Sci. USSR, 1972.

Lignier, O., *Radiculites reticulatus*, radicelle fossile de Sequoinée, *Soc. Bot. France Bull. Ser. 4*, 1906, vol. 6, pp. 193–201.

Lutkevich, E.M., Permian and Triassic Deposits in the North and Northwest of the Russian Platform. *Tr. VNIGRI, Nov. Ser.*, 1955, no. 86, pp. 1–236.

Mader, D., *Palaeoecology of the Flora in Buntsandstein and Keuper in the Triassic of Central Europe, vol. 1. Buntsandstein*, Stuttgart–New York: Gustav Fischer, 1990a.

Mader D., *Palaeoecology of the Flora in Buntsandstein and Keurep in the Triassic of Central Europe, vol. 2. Keuper and Index*, Stuttgart–New York: Gustav Fischer, 1990b.

Mader, D., *Evolution of the Palaeoecology and Palaeoenvironment of the Permian and Triassic Fluvial Basins of Europe, vol. 1. Western and Eastern Europe*, Stuttgart–New York: Gustav Fischer, 1992a.

Mader, D., *Evolution of the Palaeoecology and Palaeoenvironment of the Permian and Triassic Fluvial Basins of Europe, vol. 2. Southeastern Europe and Index*, Stuttgart–New York: Gustav Fischer, 1992b.

Naugolnykh, S.V., *Flora i fitostratigrafiya kungurskogo yarusa srednego Priural'ya* (Flora and Phytostratigraphy of the Kungurian Stage in the Middle Cis-Urals), *Cand. Sci. (Geol.) Dissertation*, Moscow: Geological Institute, Russian Academy of Sciences, 1996.

*Obstanovki osadkonakopleniya i fatcii* (Sedimentary Environments and Facies), Moscow: Mir, 1990.

*Opornyi razrez Tatarskogo yarusa reki Sukhony* (Reference Section of the Tatarian Stage on the Sukhona River), Saratov, 1981.

Oshurkova, M.V., Facial-Paleoecological Approach to the Study of Fossil Plant Remains, *Paleontol. Zh.* (Moscow), 1974, no. 3, pp. 87–96.

Oshurkova, M.V., Paleontological Parallelism between the Angaran and Euramerican Phytogeographical Provinces, *Rev. Palaeobot. Palynol.*, 1996, vol. 90, pp. 99–111.

Potonié, H.S., Die Flora des Rotliegenden von Thüringen, *Abh. Kgl. Preuss. Geol. Landesanst, N.F.*, 1893, vol. 9, no. 2, pp. 1–298.

*Resheniya mezhvedomstvennogo regional'nogo stratigraficheskogo soveshchaniya po srednemu i verkhnemu paleozoyu Russkoi platformy. Permskaya sistema* (Decisions of the Interdepartmental Regional Stratigraphic Meeting on the Middle and Upper Paleozoic of the Russian Platform. The Permian System), Leningrad, 1990.

Retallack, G.J., Reconstructing Triassic Vegetation of Eastern Australia: a New Approach for the Biostratigraphy of Gondwanaland, *Alcheringa*, 1977, vol. 1, pp. 247–278.

Schweitzer, H.-J., Die Unterdevon Flora des Rheinlandes, *Palaeontographica, Abt. B*, 1983, vol. 189, pp. 1–138.

Scott, A.C., The Ecology of Coal Measure Floras from Northern Britain, *Proc. Geol. Assoc.*, 1979, vol. 90, pp. 97–116.

Shchogolev, A.K., *Plaunovidnye i klinolisty pozdnego karbona* (Lycopsids and Sphenophylls of the Late Carboniferous), Kiev: Naukova Dumka, 1991.

Teichmuller, M., Reconstructionen Verschidener Moor Typen des Haupt-flores der Niederzheinischen Braunkohle, *Fortschr. Geol. Rheine Westf.*, 1958, pp. 599–612.

Tverdokhlebov, V.P., *Kontinental'nye aridnye formatsii vostoka evropeiskoi Rossii na rubezhe paleozoya i mesozoya* (Continental Arid Formations in the East of the Russian Platform at the Paleozoic–Mesozoic Boundary), *Doctoral (Geol.-Mineral.) Dissertation*, Saratov: Saratov Univ., 1996.

Verzilin, N.N., Kalmykova, N.A., and Suslov, G.A., Large Sand Lenses in the Upper Permian Deposits in the North of the Moscow Syneclise. *Tr. St. Petersb. Obshch. Yestestvoispyt.*, 1993, vol. 83, no. 2, pp. 1–111.

Zalessky, M.D., Sur une Division des Terrains Carbonifère et Permien du bassin du Donetz d'après leur Flore Fossile, *Problems of Paleontology*, 1937, vol. 2–3, pp. 143–153.