ISSN 0031-0301, Paleontological Journal, 2006, Vol. 40, Suppl. 4, pp. S475–S481. © Pleiades Publishing, Inc., 2006.

Vyazniki Biotic Assemblage of the Terminal Permian

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Received January 30, 2006

Abstract—A new unique and diverse biotic assemblage of the terminal Permian has recently been discovered in the town of Vyazniki (Central Russia). The Vyazniki terrestrial community is transitional between Permian and Triassic ones and represents the last, so far unknown stage of the global ecological crisis of the continental biota at the Permian–Triassic boundary. The successive development of land biotic crisis in the Late Permian, which was followed by mass extinction at the Permian–Triassic boundary, and long, successive postcrisis development and specialization of new Triassic groups as well as rearrangement and diversification of the biotic assemblage composition and community structure suggest predominance of intrinsic, biotic causes of this crisis, realized in destabilization, alteration, and new stabilization of continental communities and ecosystems.

DOI: 10.1134/S0031030106100078

Key words: Biotic assemblage, continental community, destabilization, stabilization, biotic crisis, Permian–Triassic boundary, Central Russia.

INTRODUCTION

A new unique and diverse terrestrial biotic assemblage of the terminal Permian was recently discovered in the town of Vyazniki (Vladimir Region of Central Russia) (Fig. 1).

Variegated Permian clays and sands were discovered for the first time in the town of Vyazniki in 1841 by R.J. Murchison during his expedition to European Russia (Murchison et al., 1845). Murchison also found Permian ostracodes and bivalves there. The Vyazniki vertebrate locality was discovered in 1951 and excavated in 1952, 1955, and 1956 by expeditions of the Paleontological Institute of the Academy of Sciences of the USSR headed by B.P. Vjuschkov (Efremov and Vjuschkov, 1955). This locality yielded a lot of vertebrates, including fishes, amphibians, and reptiles. Thus, a new Late Permian vertebrate fauna in Central Russia was discovered.

RESULTS AND DISCUSSION

Recent Discoveries in the Town of Vyazniki

After a long period, A.G. Sennikov, V.K. Golubev, and V.V. Bulanov (Paleontological Institute of the Russian Academy of Sciences, Moscow) rediscovered the Vyazniki locality and collected new vertebrate specimens in 1999 to 2003. Rich and diverse fossils were found in the town of Vyazniki and adjacent area in a

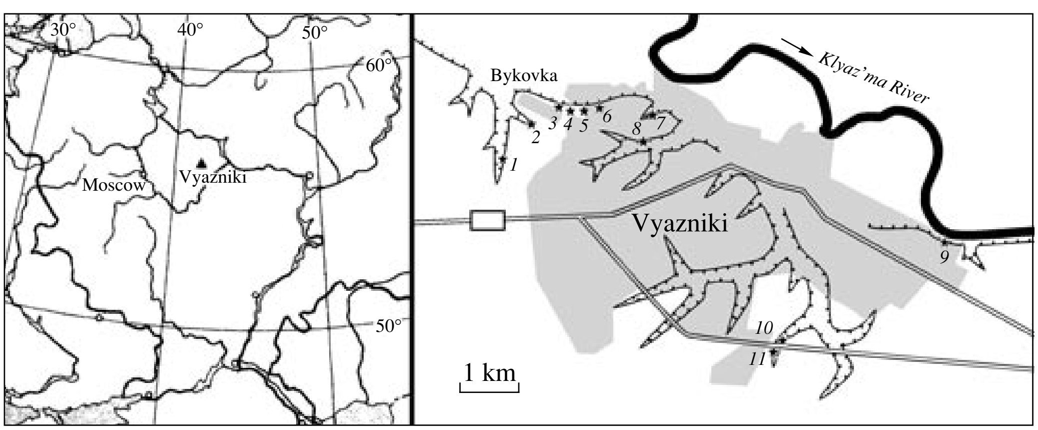

Fig. 1. Geographical position of the Late Permian Vyazniki locality. Sections studied: (*1*) Bykovka gully, (*2*) Zelenaya Gorka, (*3*) Bykovka lake, (*4*) Bykovka (Vyazniki-2), (*5*) Sokovka (Vyazniki-2), (*6*) Metallist, (*7*) Vyazniki-1, (*8*) Yartsevo, (*9*) Tolmachevo, (*10*) Balymotikha-1, and (*11*) Balymotikha-2.

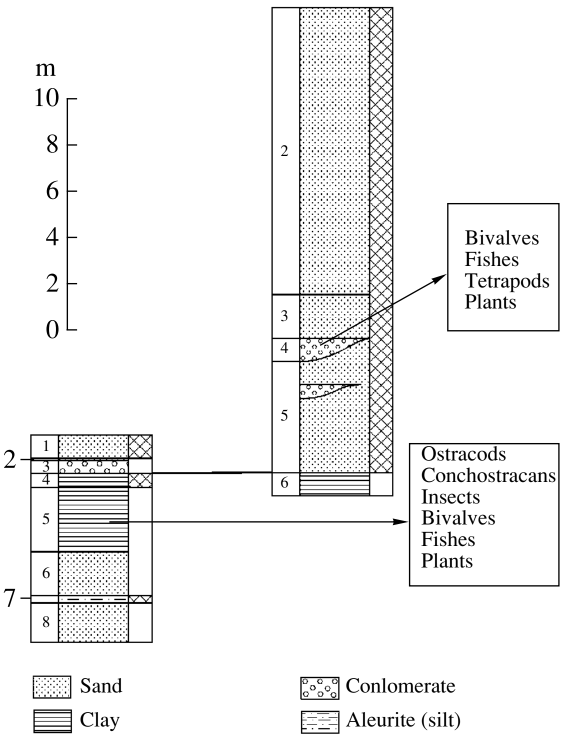

Fig. 2. The section of the Sokovka (Vyazniki-2) locality.

number of localities dated Late Permian during 2003–2005. Apart from vertebrates, this assemblage contained macrofloral remains, spores and pollen, bivalves, ostracodes, conchostracans, and insects. All fossils were found in sands and clays of alluvial genesis (Fig. 2). These deposits were accumulated in a number of channels and abandoned channels (or oxbow-lakes) of the vast flood-plain of a great river system directed from east to west, that is, from the Ural Mountains to the plain.

Vyazniki Continental Assemblage of the Terminal Permian from Central Russia

The Vyazniki Assemblage from the terminal Permian has no analogues in other continents and is the last, so far unknown stage in the history of the Late Permian continental biota. A tetrapod assemblage of the Vyazniki type is also known from the Purly locality (Nizhni Novgorod Region) and, perhaps, from a few other Upper Permian localities of European Russia (Ivakhnenko et al., 1997; Golubev, 2000; Ivakhnenko, 2003). In the Russian Platform, the Vyazniki Faunal Stage is intermediate between the Late Permian Sokolki and Early Triassic Vokhmian (Early Vetlugian) stages (Sennikov, 1995, 1996; Ivakhnenko et al., 1997; Golubev, 2000) (Fig. 3). The East European Sokolki Vertebrate Fauna, which includes pareiasaurs and gorgonorpians, is similar to the faunas from the terminal Permian of South Africa and other continents. The Vokhmian Fauna is correlated to the lystrosaurid–proterosuchid faunas of the beginning of Early Triassic in other continents.

The faunal assemblage from the type locality Vyazniki (Vladimir Region) is listed below.

The Vyazniki community is transitional between Permian and Triassic communities. The Vyazniki Tetrapod Fauna includes the temnospondyls *Dvinosaurus egregius* Shishkin and Microsauria (?) fam. indet., the kotlassiomorph *Karpinskiosaurus* sp., the elginiid pareiasaurs *Obirkovia* sp. and Elginiidae gen. indet., the anthracosaurs (chroniosuchians) *Bystrowiana permira* Vjuschkov and *Uralerpeton tverdochlebovae* Golubev, the thecodont *Archosaurus rossicus* Tatarinov (Fig. 4), the dicynodont Dicynodontidae gen. indet., and the therocephals *Moschowhaitsia vjuschkovi* Tatarinov and Moschorhinidae gen. indet. (Figs. 5, 6).

In addition to the Vyazniki locality, tetrapods, such as the therocephalians *Hexacynodon purlensis* Tatarinov, *Malasaurus germanus* Tatarinov, and Whaitsiidae gen. indet., were recorded in the Purly locality (terminal Permian, Nizhni Novgorod Region).

The most important feature was the disappearance of the pareiasaur–gorgonopian coadaptive pair, which were the dominant large herbivore and carnivore, and the appearance of new top predators (ultimate consumers), the proterosuchids (Fig. 7). The Vyazniki community documents the beginning of the major faunal replacement at the Permian–Triassic boundary and during the Triassic, that is, the replacement of therapsids by archosaurs. In its food chain structure, the Vyazniki terrestrial community (Fig. 5) was the first thecodont–dicynodont one. In this respect, the Vyazniki terrestrial community is more similar to Triassic communities. The anthracosaur *Bystrowiana* is the first record of bystrowianids, relict chroniosuchians typical of the Triassic. Dvinosaurs, kotlassiomorphs, chroniosuchids, elginiids, therocephalians, and dicynodontids are typical Upper Permian elements of the Vyazniki Assemblage (Golubev, 2000).

The fishes from Vyazniki include the hybodont shark *Wodnika* sp. and the actinopterygian *Saurichtys* sp. (Lozovsky and Yesaulova, 1998). The former is found in the Zechstein locality of Germany and the latter is typical of the Triassic faunas. The diverse paleonisciforms *Geryonichthys* (?) sp., *Mutovinia stella* Minich, *Mutovinia* sp. nov., *Toyemia blumentalis* A. Minich, *Toyemia* sp., and *Isadia* (?) sp. (A.V. Minikh, personal communication) belong to the Late Permian (Late Tatarian) ichthyoassemblage.

Fossil insects from Vyazniki are today under study. This insect assemblage, including the grylloblatids Tomiidae, beetles, cockroaches and many other groups, corresponds to the terminal Permian, probably close to the Permian–Triassic boundary (D.E. Shcherbakov, D.S. Aristov, and A.G. Ponomarenko, personal communication).

Ostracodes from Vyazniki (identified by I.I. Molostovskaya) include *Clinocypris* cf. *elongata* Schneider,

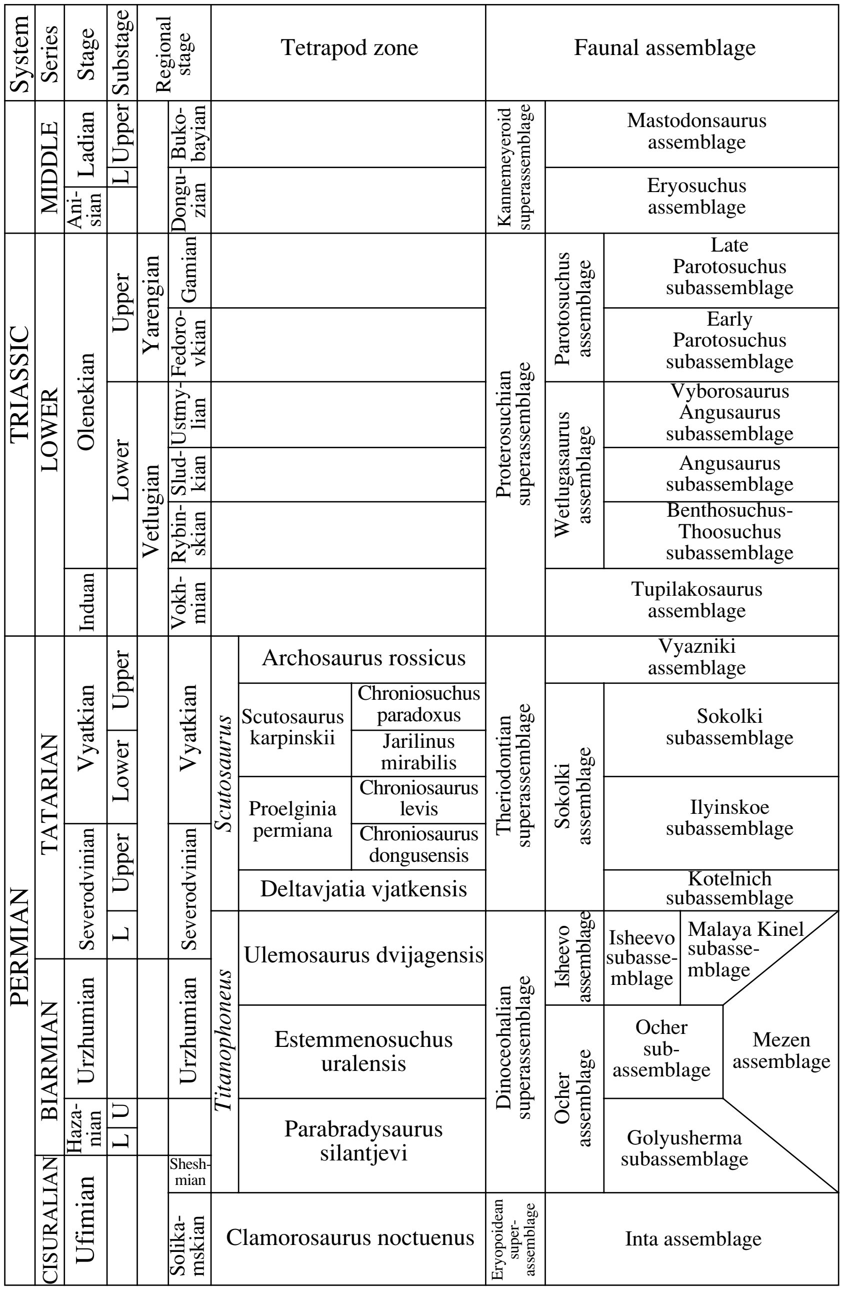

Fig. 3. Permian and Triassic tetrapod zonation and assemblages of Eastern Europe.

Clinocypris sp., *Darwinula* (?) *sima* Mishina, *D. (?) accuminata* Belousova, *D. (?) regia* Mishina, *D. (?) abscondita* Mishina, *Darwinuloides* ex gr. *svijazhicus* Sharapova, *Gerdalia* ex gr. *rixosa* Mishina, *G.* cf. *triassiana* Belousova, *G.* ex gr. *analoga* Starozhilova, *G. wetlugensis* Belousova, *Gerdalia* sp., *Marginella* (?) sp., *Nerechtina* cf. *plana* Mishina, *Suchonella* cf. *posttypica* Starozhilova, *S.* ex gr. *typica* Spizharskyi, *Suchonellina bulloida* (Mishina), *S.* cf. *anjugensis* (Mishina), *S.* ex gr. *anjugensis* (Mishina), *S. dispinosa* (Mishina), *S.* ex gr. *dispinosa* Mishina), *S.* ex gr. *trapezoida* (Sharapova), *S. perelubica* (Starozhilova) (= *S. alija* (Mishina), *S. pseudoinornata* (Belousova) (= *S. postparallela* (Mishina)), *Wjatkellina (?) pseudoobliqua* (Belousova), *W. fragilina* (Belousova), *W. vladimirinae* (Belousova), and *W.* cf. *vladimirinae* (Belousova). The composition of the Vyazniki Ostracode Assemblage is mostly characteristic of the Triassic, but includes a few Permian elements (Golubev et al., 2005).

The following conchostracans from Vyazniki were identified by N.I. Novozhilov: Limnadiopseidae gen. nov., Lioestheriidae Sphaerestheria sp. nov., *Pseudestheria suchonensis* Novojilov, *Pseudestheria* sp. nov. 1, *Pseudestheria* sp. nov. 2, *Loxomicroglypta* sp. nov., and

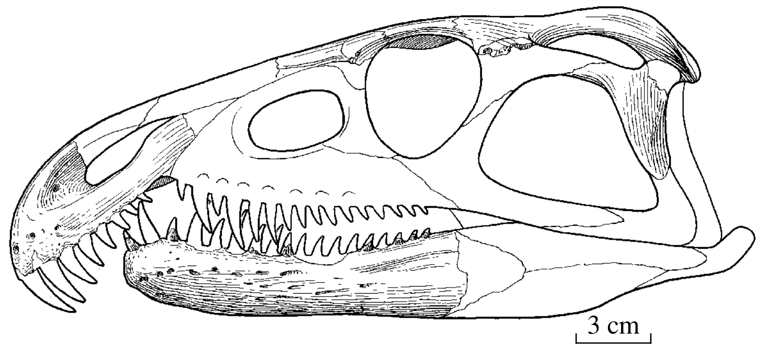

Fig. 4. Reconstruction of the skull of the proterosuchid *Archosaurus rossicus* from the Vyazniki locality.

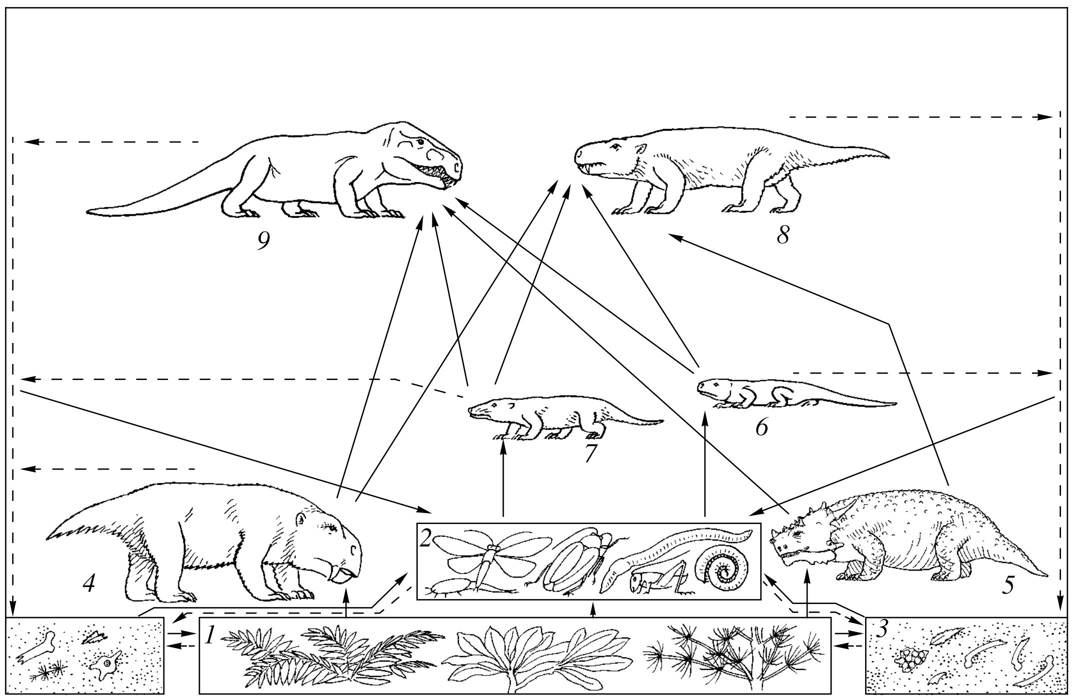

Fig. 5. Reconstructed food chain in the terrestrial Vyazniki community (Late Permian, Tatarian) of Eastern Europe. Lines with arrows indicate the circulation of energy through the community: solid lines show food relations, and dashed lines show decay relations: (*1*) plants, (*2*) invertebrates, (*3*) plant and animal detritus, (*4*) dicynodonts (Dicynodontidae gen. indet.), (*5*) elginiid pareiasaurs (*Obirkovia* sp. and others), (*6*) microsaurs (Microsauria fam. indet.), (*7*) small therocephals (*Malasaurus*), (*8*) large therocephals (*Moschowaitsia* and others), and (*9*) thecodonts (*Archosaurus*).

Concherisma sp. nov. This assemblage fits into the Late Permian (Tatarian) age of Vyazniki deposits.

Bivalves include *Palaeomutela oleniana* Amalitzky, *Palaeomutela plana* Amalitzky, *Palaeomutela* aff. *plana* Amalitzky, *Palaeomutela* cf. *solemyaeformis* (Netschajew), *Palaeomutela (?) concavocarinata* (Netschajew), and *Palaeomutela* sp. (V.V. Silantjev, personal communication). This bivalve assemblage is typical of the end-Permian (Tatarian) deposits of the Russian Platform.

The macroflora from Vyazniki is very special and diverse. The list of plants predominately consists of peltasperm seed ferns *Pursongia* sp. nov., cf. *Lepidopteris* (al. *Callipteris*) *martinsii* Townrow (? gen. et sp. nov.), *Peltaspermum* sp. nov., and also the fern *Prynadaeopteris* (?) sp., the arthrophyte *Neocalamites* cf. *mansfeldicus* Weigelt, the ginkgophytes *Sphenobaiera* sp. nov. and *Ginkgoites* sp., and the conifer cf. *Ullmannia* sp. (Naugolnykh, 2005). This macroflora assemblage is new, so far unknown in Eastern Europe, generally similar to the West European (Zechstein) assemblage of the terminal Permian.

The rich Vyazniki Palynological Assemblage is similar to the Molomian assemblage from Eastern Europe (Yaroshenko, 2005) and also to the assemblage from

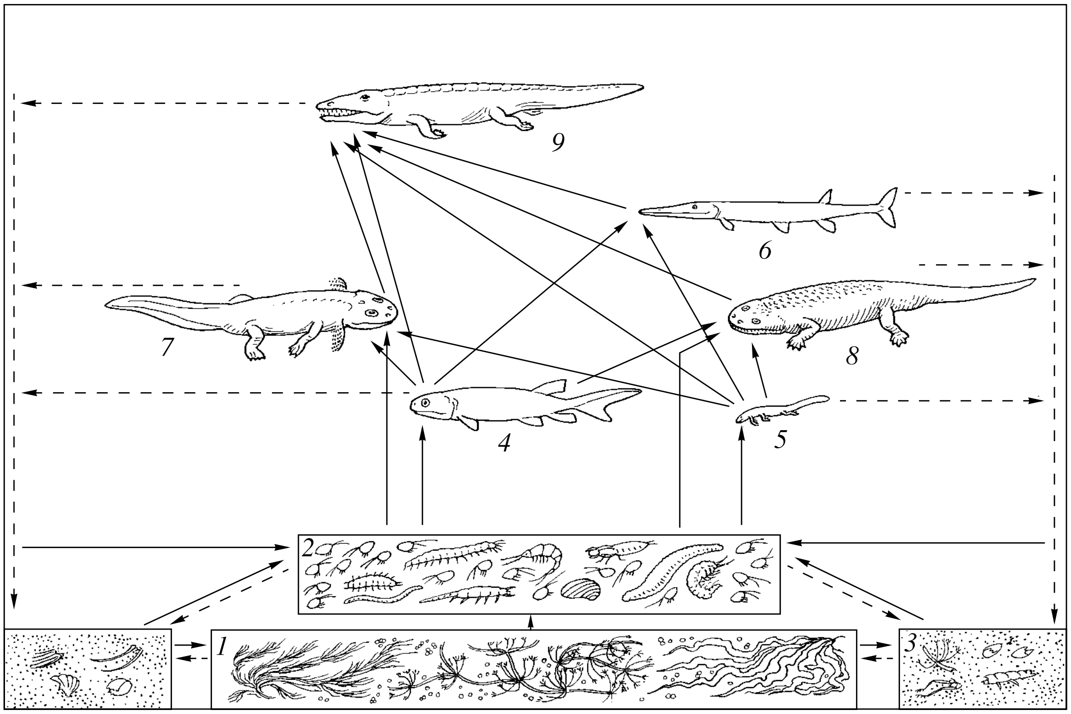

Fig. 6. Reconstructed food chain of the aquatic Vyazniki community (Late Permian, Tatarian) of Eastern Europe. Lines with arrows indicate the circulation of energy through the community: solid lines show food relations, and dashed lines show decay relations: (*1*) plants, (*2*) invertebrates, (*3*) plant and animal detritus, (*4*) palaeonisciforms and hybodont sharks, (*5*) larval aquatic tetrapods, (*6*) actinopterygians (*Saurichthys*), (*7*) temnospondyls (*Dvinosaurus*), (*8*) kotlassiomorphs (*Karpinskiosaurus*), and (*9*) chroniosuchians (*Bystrowiana* and others).

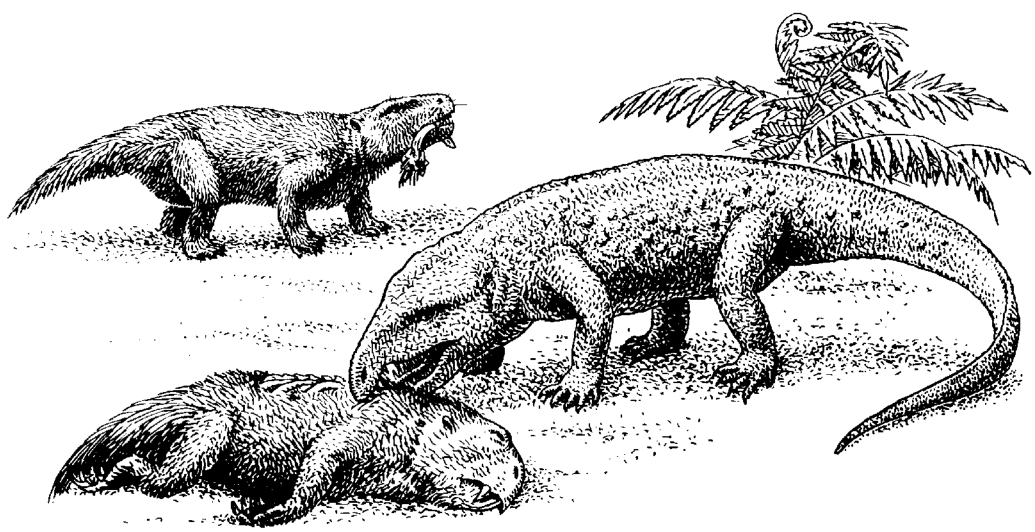

Fig. 7. A scene from the Vyazniki time; the proterosuchid *Archosaurus* and the therocephal *Moschowhaitsia* have captured a juvenile dicynodontid.

the upper part of the Lower Guodikeng Formation, Dalongkou, Xinjiang, China. The Vyazniki Palynoassemblage is transitional from the Permian to the Triassic ones, and includes elements characteristic of the Permian and of the Triassic, and a few taxa restricted to the Vyazniki Time (Afonin, 2005a, 2005b). Spores are represented by *Calamospora* sp., *Punctatisporites* sp., *Lophotriletes novicus* Singh, *Retusotriletes* sp., *Apiculatisporis* sp. cf. *A. cornutus* Hoeg et Bose, *Apiculatisporis* sp., *?Retitriletes* sp., *Laevigatosporites*, *Limatulasporites fossulatus* Helby et Foster, and *Kraeuselisporites* sp. Pollen grains include *Alisporites splendens* Foster, *Vitreisporites signatus* Leschik, *Klausipollenites schaubergeri* Jansonius, *Klausipollenites* sp. cf. *K. staplinii* Jansonius, *Platysaccus insignis* Ouyang et Utting, *Falcisporites* sp., *Potonieisporites*-like pollen grains, *Scutasporites* sp. cf. *S. unicus* Klaus, *Lueckisporites virkkiae* Clarke, *Protohaploxypinus* sp., *?Lunatisporites* sp., *Vittatina connectivalis* Waryukhina, *Ephedripites* sp., and *Cycadopites* sp. cf. *C. follicularis* Wilson et Webster. Algae are represented by *Actinastrum* (= *Syndesmorion*) *stellatum* Fijalkowska, *Reduviasporonites chalastus* (= *Tympanicysta stoschiana* Balme), *Quadrisporites* sp., *Botryococcus* sp. cf. *B. braunii* Kutzing, *Veryhachium* sp., and *Leiosphaeridia* sp. (Afonin, 2005a, 2005b).

Both macrofloral and palynological assemblages from Vyazniki demonstrate transitional features from the Paleophytic to Mesophytic, and gradual, non-catastrophic character of this transition (Golubev et al., 2005; Afonin, 2005a, 2005b; Naugolnykh, 2005; Yaroshenko, 2005).

Vyazniki Assemblage As the Last Stage of the Global Biosphere Crisis at the Permian–Triassic Boundary

New data on the uppermost Permian deposits of Vyazniki and a new transitional assemblage disagree with the hypothesis of a large gap in continental sedimentation and in the history of life in Eastern Europe close to the Permian–Triassic boundary (Golubev, 2004). New data contradict the commonly accepted opinion of a considerable increase in aridity around this boundary. During the Late Tatarian, the climate was generally subhumid in Eastern Europe.

On the whole, the Vyazniki Assemblage and the community structure demonstrate their transitional nature and present the last, so far unknown stage of the global ecological crisis at the Permian–Triassic boundary on continents (Sennikov, 1995, 1996, 2004; Sennikov and Golubev, 2005). Based on this new information, a scenario of global biotic crisis in the continental biota at this boundary exemplified by Eastern Europe may be suggested. The most complete Permian–Triassic stratigraphic succession on the Russian Platform presents a unique possibility for such a reconstruction, since at least eight stages in the Late Permian and eight stages in the Early and Middle Triassic are recognized in biotic history (Fig. 3). The major stages in the history of Eastern European continental communities are as follows (Sennikov, 1996; Golubev, 2000):

(1) Early Permian eryopoidean temnospondyl community of North American origin (Inta Assemblage).

(2) Typical Permian therapsid (theriodontian–dinocephalian) terrestrial and rhachitomous temnospondyl aquatic communities of the Late Permian (Ocher, Mezen, and Isheevo assemblages).

(3) Great tetrapod extinction at the Early-Late Tatarian boundary (at the end of the Guadalupian).

(4) Transitional terminal Permian theriodontian–pareiasaurian–dicynodontian (Sokolki) and the first thecodontian–dicynodontian (Vyazniki) (Fig. 5) terrestrial communities, as well as chroniosuchian (Sokolki and Vyazniki (Fig. 6) assemblages) aquatic communities.

(5) The major extinction at the Permian–Triassic boundary.

(6) Postcrisis thecodontian–dicynodontian terrestrial (including scarce Lystrosaurus) and temnospondyl aquatic communities of the Early Triassic (Vetluga and Yarenga assemblages).

(7) Typical Triassic thecodont–dicynodont terrestrial (including kannemeyeroids) and temnospondyl aquatic communities of the end of the Early Triassic and the Middle Triassic (terminal Yarenga, Donguz, and Bukobai assemblages).

CONCLUSIONS

The Permian–Triassic biotic transition was successive, gradual, and continuous, including a number of phases, and mosaic in various groups. The maximum level of mass extinction occurred at the Paleozoic–Mesozoic boundary both on the continents and in the seas (Sepkoski, 1978, 1979, 1984; Benton, 1985a, 1985b, 2003). The successive development of a land biotic crisis in the Late Permian was followed by mass extinction at the Permian–Triassic boundary, and long, successive postcrisis development and specialization of new Triassic groups as well as rearrangement and diversification of the assemblage composition and community structure suggest the predominance of intrinsic, biotic causes of this crisis, realized in destabilization, alteration, and new stabilization of continental communities and ecosystems.

ACKNOWLEDGMENTS

This research was supported by Russian Science Support Foundation, the Russian Foundation for Basic Research (project no. 05-05-65146), the Leading Scientific Schools NSh-1840.2003.4, 6228.2006.4, and by Program 25, 18 of the Presidium of the Russian Academy of Sciences "Biosphere Origin and Evolution," Subprogram 2.

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