

The First Gliding Reptiles from the Upper Permian of Russia

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Abstract—Two new gliding reptiles from the Late Permian Kul’chumovo-A locality (Orenburg Region), *Rautiania alexandri* gen. et sp. nov. and *R. minichi* sp. nov., are described and assigned to the family Weigeltisauridae. These finds substantially expand the knowledge of the morphology of this group and suggest the climax state of terrestrial tetrapod communities of eastern Europe in the pre-Triassic Time, which resulted in the development of ecological niches not typical of earlier terrestrial vertebrate faunas.

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INTRODUCTION

Paleontological data suggest that tetrapods developed aerial forms no later than the end of the Paleozoic. The first successful adaptation of this kind was probably achieved by Weigeltisauridae (Coelurosauravidae), a family that was widespread as early as the Late Permian (central and eastern Europe, Great Britain, and Madagascar) and persisted in the Early Triassic (Canada) (Piveteau, 1926; Pettigrew, 1979; Brinkman, 1988). This tetrapod lineage (which is apparently related to primitive diapsids) adapted to gliding flight by the development of wide skin folds on the lateral sides of the body, which were supported by a framework of hollow rodlike bones (Frey et al., 1997). The structure of this membrane allowed the animal to change its orientation during flight, and to fold it after landing (Evans, 1982).

All known Weigeltisauridae have been described based on isolated, more or less disarticulated specimens. This complicates the understanding of a number of their morphological features and their relationships with other Paleozoic reptiles.

In 2005, an expedition in the southern Fore-Urals (Orenburg Region) resulted in the discovery of the first Russian locality with Weigeltisauridae (Kul’chumovo-A), which was in Late Permian lacustrine facies of the Severodvinian–Vyatkian. Fossil remains of diapsids clearly predominate in this oryctocenosis, so that the locality has yielded the greatest number of individuals. Based on the material collected, a new weigeltisaurid genus, *Rautiania*, with two species, *R. alexandri* sp. nov. and *R. minichi* sp. nov., are established. The two species differ in the structure of the parietal and upper jaw. *R. minichi* comprises specimens that, like *Weigeltisaurus jaekeli* from Germany, have conical osteoderms and jaws with the same number of maxillary teeth as in *Weigeltisaurus*, i.e., 22 or 23. *Rautiania alex-*

andri has lower and wider osteodermal expansions on the parietal and a greater number of maxillary teeth (30 or more). More complete diagnoses of the new taxa are given below.

The material consists predominantly of isolated bones; however, some elements of the postcranial skeleton, including the sacral vertebrae and manus, were found articulated. Because of the absence of complete skeletons, it is impossible to associate these and many other specimens with particular species. However, they substantially increase the knowledge of the morphology of the Weigeltisauridae. In particular, certain structural details of the otic–occipital region, the quadrato-articular articulation, humerus, and sacrum are established in this family for the first time.

The type locality is the first Upper Permian Russian locality where diapsids prevail in the number of specimens. In general, this group is rather infrequent in the Permian because it evolved in xerophilous ecotopes of highlands far from burial sites. Vertebrate remains accumulated under conditions of short-lived and gradually dried streams in an open lake basin (an arm of an underwater part of the delta or a bed of a nearshore current). Due to the unusual origin of the locality, the oryctocenosis is apparently composed of new taxa; therefore, it is difficult to date the locality based on tetrapods. In addition to Weigeltisauridae, the material collected includes seymouriamorphs, chroniosuchians (?), unidentified small diapsids, and palaeonisciforms of the family Eurynotoidiidae.

SYSTEMATIC PALEONTOLOGY

Family Weigeltisauridae Kuhn, 1939

Genus *Rautiania* Bulanov et Sennikov, gen. nov.

E t y m o l o g y. The genus is named in honor of the Russian zoologist Aleksandr Sergeevich Rautian.

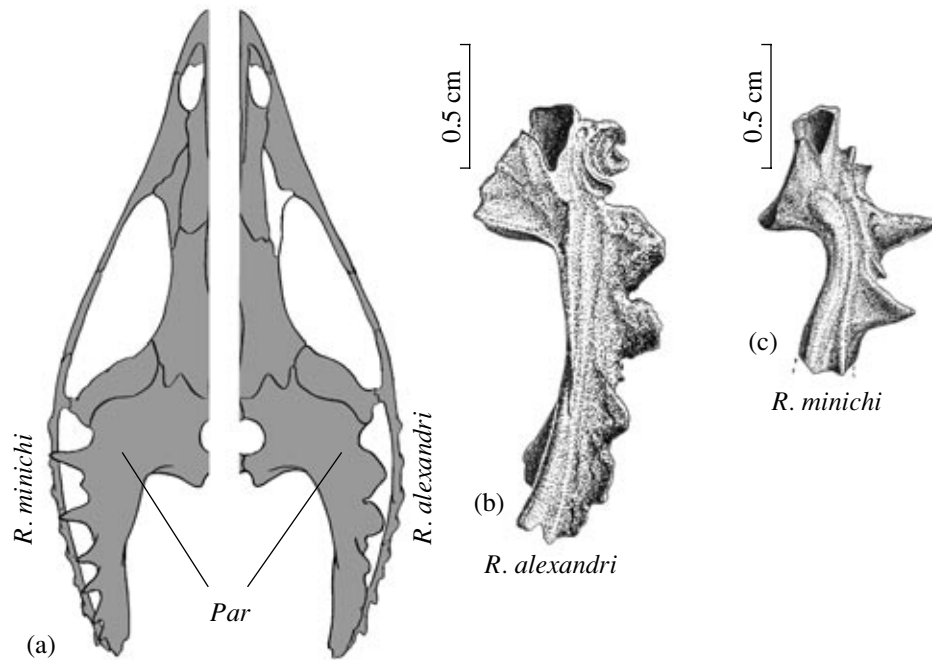


Fig. 1. *Rautiania alexandri* sp. nov. and *R. minichi* sp. nov.: (a) differences between the two species in parietals; (b) right parietal of adult *R. alexandri*, mediadorsal view (holotype PIN, no. 5130/1); (c) right parietal of adult *R. minichi*, mediadorsal view (holotype PIN, no. 5130/2). Designation: (*Par*) parietal.

Type species. *Rautiania alexandri* Bulanov et Sennikov sp. nov., Severodvinian (Vyatkian?) Stage; Orenburg Region, Russia.

Diagnosis. Caudal process of parietal sculptured with high osteodermal spines. Postfrontal with wide dorsal flank and narrow postorbital process. Premaxilla with 11 teeth. Crowns of jaw teeth longitudinally flattened, with wide anterior cutting border. Sacrum composed of three vertebrae; second and third sacral ribs expanding distally into wide plates fused with vertebral center for more than half of its extent.

Species composition. Two species, *Rautiania alexandri* sp. nov. and *Rautiania minichi* sp. nov.

Comparison. The new genus differs from other genera of the family Weigeltisauridae in the presence of high spines on their parietals, the wider dorsal region of the postfrontal, the narrow postorbital process, the greater number of premaxillary teeth, and in the flat crowns of the jaw teeth with a broad anterior cutting border.

***Rautiania alexandri* Bulanov et Sennikov, sp. nov.**

Etymology. The species is named in honor of the Russian zoologist Aleksandr Sergeevich Rautian.

Holotype. PIN, no. 5130/1, right parietal of adult; Russia, Orenburg Region, Saraktashskii District, Kul'chumovo-A locality; Upper Permian, Severodvinian (Vyatkian?) Stage.

Diagnosis (Figs. 1b, 2a). Osteoderms on caudal process of parietals flat and wide, adjoining each other

at bases. Maxilla with 30 densely spaced teeth. Tooth crowns widest in posterior part of tooth row. Externally, orbital flank of maxilla in shape of high ridge.

Occurrence. Type locality.

Material. In addition to the holotype, specimen PIN, no. 5130/4, maxillary bone.

***Rautiania minichi* Bulanov et Sennikov, sp. nov.**

Etymology. The species is named in honor of the paleontologist Maksim Georgievich Minikh.

Holotype. PIN, no. 5130/2, right parietal of adult; Russia, Orenburg Region, Saraktashskii District, Kul'chumovo-A locality; Upper Permian, Severodvinian (Vyatkian?) Stage.

Diagnosis (Figs. 1b, 2a). Osteoderms on caudal process of parietals high-conical and spaces between their bases as wide as bases. Maxilla with 23 widely spaced teeth. Tooth crowns widest in middle part of tooth row. Ridge along orbital flank of maxilla undeveloped.

Comparison. The new species differs from *Rautiania alexandri* in the high-conical osteoderms on the parietal, the presence of wide gaps between them, the smaller number of the widely spaced maxillary teeth, the wider tooth crowns in the middle part of the tooth row, and in the absence of a ridgelike expansion on the orbital flank of the maxilla.

Occurrence. Type locality.

Material. In addition to the holotype, specimen PIN, no. 5130/3, maxillary bone.

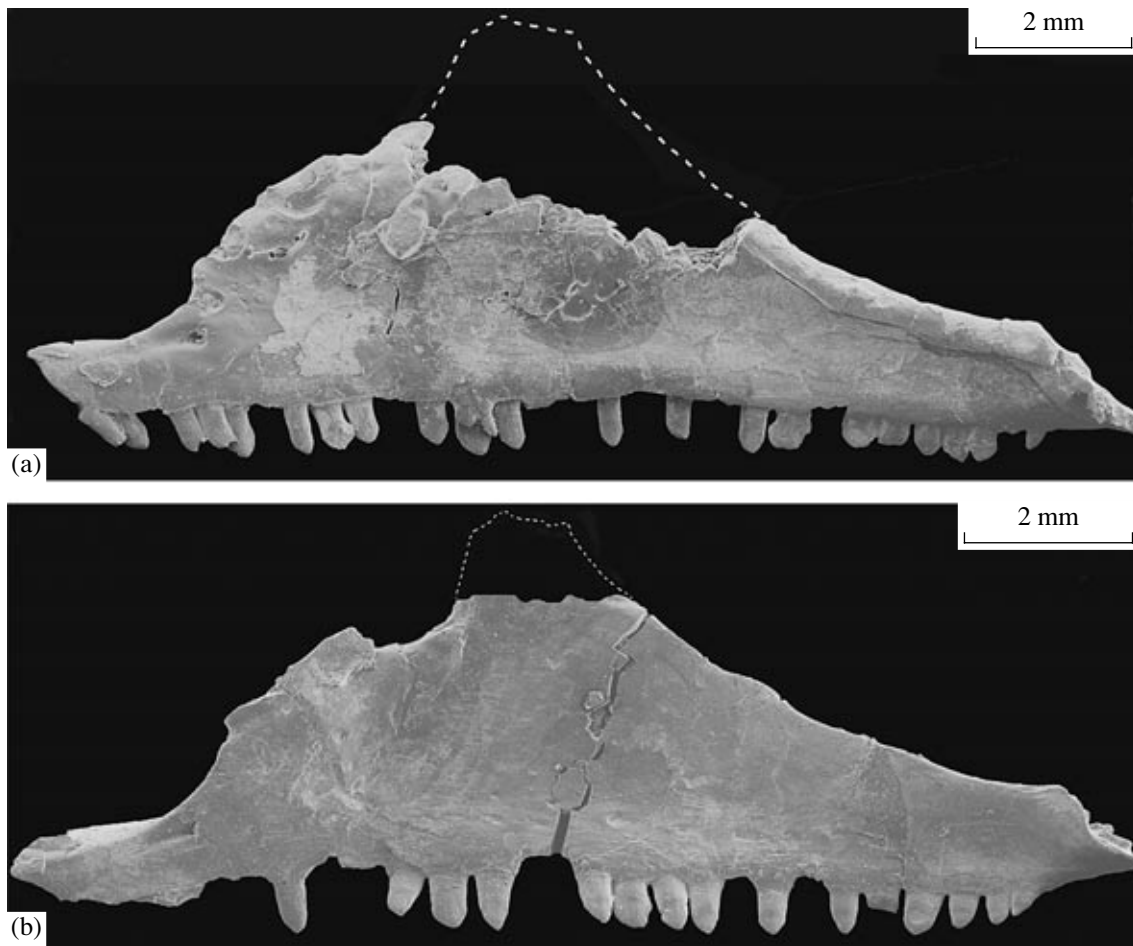


Fig. 2. The maxillae of *Rautiania*: (a) left maxilla of *R. alexandri* (specimen PIN, no. 5130/4), labial view; and (b) left maxilla of *R. minichi* (specimen PIN, no. 5130/3), labial view.

Notes on Functional Morphology of Rautiania

The morphological evolution of the Weigeltisauridae was influenced by their obligatory arboreal mode of life, which was atypical for Paleozoic tetrapods, and by the adaptation for gliding flight. The wing skeleton is composed of long, hollow needle-shaped bones, radiating from the area of the humeral articulation, which are apparently newly formed structures (Frey et al., 1997). To reduce weight, many membrane skull bones contain extensive cavities. The unguis phalanges are sharp, laterally compressed, and hooked, as in extant arboreal lizards (Spielmann, 2005). The landing load caused the consolidation of the sacrum, which is composed of three vertebrae due to the inclusion of the posterior presacral vertebra. The second and third sacral ribs form broad distal plates, which increase the area of attachment to the centers. The humerus is long, with well ossified spherical articular surfaces, which provided free movement of the forelimbs when the animal climbed trees or landed. The dentition suggests that the

Weigeltisauridae were insectivores, which is consistent with the feeding mode of extant ecological analogues.

The presence of gliding diapsids in the Late Permian of Russia suggests the climax state of terrestrial tetrapod communities of eastern Europe in the pre-Triassic Time, as it shows the development of ecological niches not typical of earlier terrestrial vertebrate faunas. The efficiency of specialization of the first gliding diapsids is proved by their cosmopolitan distribution in the Late Permian and the survival of this group into Triassic tetrapod communities (Brinkman, 1988).

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