ISSN 0031-0301, Paleontological Journal, 2018, Vol. 52, No. 5, pp. 550–562. © Pleiades Publishing, Ltd., 2018.
Original Russian Text © D.I. Pashchenko, I.T. Kuzmin, A.G. Sennikov, P.P. Skutschas, M.B. Efimov, 2018, published in Paleontologicheskii Zhurnal, 2018, No. 5, pp. 77–90.

On the Finding of Neosuchians (Neosuchia, Crocodyliformes) in the Middle Jurassic (Bathonian) Deposits of the Moscow Region

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Received April 27, 2018

Abstract—Remains of neosuchian crocodyliforms (isolated teeth, fragment mandibular bone) from the Middle Jurassic (Bathonian) Peski locality in the Moscow Region are described for the first time. The neosuchian from Peski is characterized by well-pronounced ornamentation on the dermal skull bones, and also bicarinate teeth oval in cross section without serration and with triangular conical crowns and fine striation of the enamel. The similarity of Bathonian vertebrate faunas of the Moscow Region, Great Britain, Western Siberia, and Kyrgyzstan is evidence of homogeneity of the vertebrate fauna throughout Laurasia.

Keywords: Crocodyliformes, Neosuchia, faunal homogeneity, Middle Jurassic, Bathonian, Moscow Region

DOI: 10.1134/S0031030118050118

INTRODUCTION

In the Central Region of European Russia, Middle Jurassic (Bathonian) continental deposits are usually represented by linear structures filling paleovalleys (paleochannels) and also karstic depressions or cavities. Bathonian continental deposits were formed at the beginning of a new sedimentation cycle, which was connected with the Middle Jurassic transgression of the epicontinental sea, when the climate became more humid and runoff from the continent intensified, and accompanied by more intense efflux of terrigenous matter. Although Middle Jurassic continental deposits are widespread in European Russia, fossil remains were rather rarely recorded in them, except for macroflora. Only as the unique Peski locality was discovered in the Moscow Region, a Bathonian vertebrate fauna became known in this region (Alekseev et al., 2001; Alifanov and Sennikov, 2001; Sennikov et al., 2005a; Starodubtsev et al., 2008). The uniqueness of this fauna is also caused by its geographical position: Peski is situated between Asian (e.g., localities of the Balabansai Formation in Kyrgyzstan and the Berezovsky quarry locality in the Krasnoyarsk Region, Russia) and West European (village of Kirtlington in England and Isle Skye in Scotland) localities with rich vertebrate faunas of the Bathonian Age (Evans and Milner, 1994; Evans and Waldman, 1996; Averianov et al., 2005, 2010, 2016). The discovery of a Bathonian continental vertebrate fauna in Eastern Europe expands essentially our knowledge of the distribution and composition of vertebrate faunas over the entire Laurasia. Some vertebrate specimens from the Peski locality were described in special publications (Krupin, 1995; Alifanov, 2000; Alifanov and Sennikov, 2001; Gambaryan and Averianov, 2001; Sukhanov, 2003, 2006; Bragin, 2005). Other faunal groups were identified only preliminary in survey works (Alekseev et al., 2001; Sennikov et al., 2005a; Starodubtsev et al., 2008). Such a faunal group is crocodyliforms known from rare records of isolated teeth and a fragmentary mandibular bone.

The purpose of the present study is a more detailed description of the section with tetrapod remains, the determination and description of taxonomic belonging of crocodyliform remains from the Peski locality, and discussion of the composition and paleozoogeographic relationships of the vertebrate fauna from this locality.

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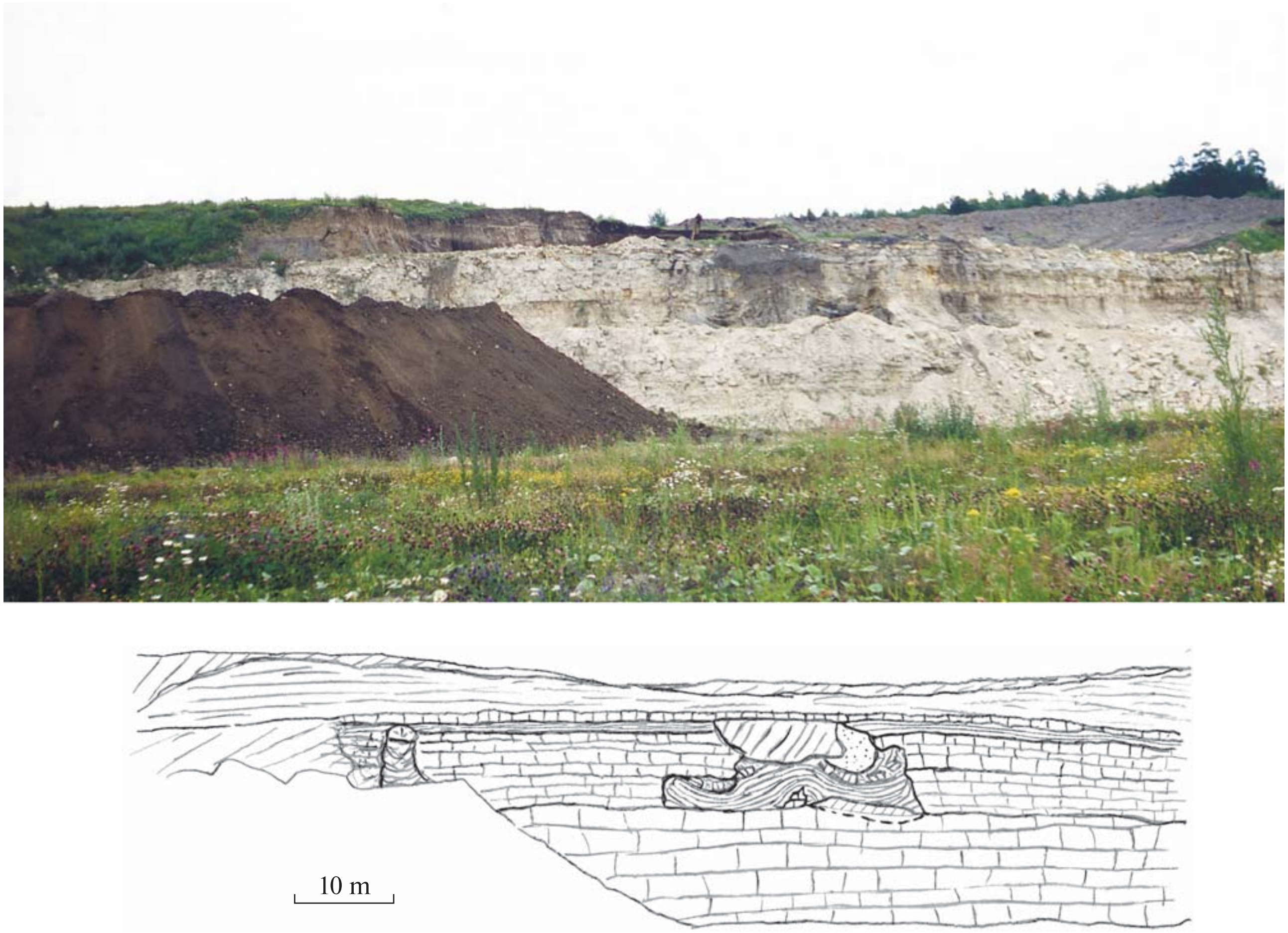

Fig. 1. Peski locality (Moscow Region, Kolomenskii District); general appearance of the northern slope of the Novopeskovskii quarry, with two karstic cavities filled with Bathonian deposits in Middle Carboniferous limestones (photograph, July, 1997, and drawing).

GEOLOGICAL STRUCTURE AND GENESIS OF THE PESKI LOCALITY

The Peski locality is situated in the Kolomenskii District of the Moscow Region in the area of the Peski Industrial Complex of Construction Materials (Novopeskovskii quarry). Deposits with vertebrate and plant remains belong to the Moskvoretskaya Formation (Meshchera Horizon, Late Bathonian). Bathonian dark gray, black, and green clays, clay siltstones with lenses of clay gravel, and light gray and yellowish wavy or obliquely layered sands with siltstone interbeds are deposited in a series of karstic cavities, scissures, and depressions in Middle Carboniferous limestones (Myachkov Horizon, Moscovian Stage) (Alekseev et al., 2001) (Fig. 1). These cavities were probably formed as a result of dissolution and washout of Carboniferous carbonate rocks in the pre-Bathonian time and, then, before the Callovian sea transgression, in the central part of the Russian Platform, they were rapidly filled with continental deposits. Both Carboniferous and Bathonian deposits are covered with washout by Upper Callovian and Oxford clays with abundant remains of marine invertebrates, including ammonites, belemnites, gastropods, bivalve mollusks, brachiopods, etc. (Alekseev et al., 2001).

Large karstic cavities, scissures, and depressions filled with Bathonian continental deposits, have a linear structure, that is, they are likely a system of relatively long channels of underground rivers rather than local karstic holes and funnels. This is supported by the character of deposits, which display signs of directed water flows and, in places, well-pronounced rhythmic structure. Bathonian continental sands, siltstones, and clay probably belong to the group fluvial facies, distinctive features of which are connected with specific underground sedimentation conditions in karstic caves and scissures. On the surface of the upper ledge of quarry, the extended linear shape and orientation of karstic cavities are clearly traced based on the shape and direction of subsidence of the overlying beds of either Carboniferous limestones or Callovian marine clays.

In the northern slope of the quarry, the first, largest karstic cavity with the most productive Bathonian deposits outcrops; it has yielded the majority of tetrapod specimens (Fig. 2). The surfaces of its walls and bottom are wavy rough, with rounded holes and ledges, which are typical of washout and dissolution of carbonate rocks in karstic cavities. The cavity is complex in structure; in the lower part, it is wider than in the upper part, in places, with some sites of the walls inclined inside and even overhanging the cavity. Close to the middle of its bottom, there is a limestone outlier complex in shape, with a narrow sharpened apex about 2 m high. The most complete and diverse vertebrate remains were found in Bathonian clays near this outlier; therefore, in the summer season of 1997 during expedition works of the Borissiak Paleontological Institute of the Russian Academy of Science (PIN), excavation was started here (Fig. 3). Originally, observations in 1997 showed that the cavity was about 20 m wide and up to 9 m high and was covered by the strata of Middle Carboniferous limestone (Fig. 2). This cavity was positioned submeridionally and gradually narrowed from the south to north, which is reflected in the direction of depression in overlying limestones and in the wall in the ledge of the quarry. At present, this site is demolished for about 100 m as a result of works in the quarry and, in this place, Bathonian deposits are not observed.

Bathonian continental deposits filling this karstic cavity were subdivided into two members; the lower member is darker clayey and clayey–silty, with abundant remains of vertebrates and plants; and the upper member is lighter sandy, with rare plant remains (Figs. 2, 3). The clay and siltstone beds enveloped the walls and roughnesses of the bottom; near the walls, they were strongly inclined to the center, which was probably connected with the sequence of filling and gradual condensation and subsidence of deposits. The clay and sand members were separated by a layer of horizontal and oblique, almost not rounded lumpy and platy limestones in broken enclosing matter (clays and siltstones); apparently, the cavity vault collapsed. Similar large isolated limestone fragments were also observed downward and upward in the section in clays and sands. The lower clayey part of the lens corresponds to slower filling by its silty deposits with periodic admixture of vertebrate and plant remains. Fossil remains were probably accumulated before rocky limestone ledges, such as the above-mentioned outlier, and in depressions at the bottom of an underground channel; and this was caused by the change in the hydrodynamic mode of the stream, so that water flow became slower. The upper part of the cavity was more rapidly filled with cross-bedded sand because of a more intense flow of the underground stream.

Later, in the northern and southeastern margins of the quarry, several similar karstic cavities and depressions filled with Bathonian continental clay and sandy deposits were revealed at the same level in the course of excavations; they enclosed remains of fish and macroflora. Undoubtedly, these were parts of a complex branching system of extended karstic cavities and underground channels (Sennikov et al., 2005a, 2005b).

The oryctocoenosis from the Peski locality contains spores and pollen, macroflora, and vertebrates belonging to continental (terrestrial or freshwater) organisms. The data on the presence in Bathonian deposits of marine invertebrates (ammonites, belemnites, bivalves: Krupin, 1995; Gambaryan and Averianov, 2001) is incorrect as representatives of these groups are known only from overlying marine deposits dated Callovian and Oxfordian. Plant macroremains are well-preserved, but fragmentary (leaves, branches, seeds, vegetative detritus, and lignified wood). Fishes are represented by isolated bones, fin spines, teeth, and complete skeletons. Sharks are usually represented by fin spines, although one complete specimen was also found. Dental plates of dipnoans are relatively frequent. The most abundant and well preserved remains belong to palaeoniscids, which are sometimes represented by complete skeletons with the scale cover and extremely rich in some clay and siltstone beds. Among tetrapods, aquatic turtles are best preserved, most abundant, and most complete, represented by a complete skull, large parts of armor, and articulated parts of a skeleton. Others terrestrial vertebrates (amphibians, choristoderans, crocodiles, dinosaurs, and mammals) are represented by individual isolated and sometimes rounded bones (Alekseev et al., 2001; Alifanov and Sennikov, 2001; Sennikov et al., 2005a; Starodubtsev et al., 2008; A.G. Sennikov, original data).

The unusual features of the geological structure and burial conditions complicate reconstruction of the genesis of the Peski locality. In the Bathonian, fossils were buried in the deposits of underground channels in a series of karstic cavities and scissures. Small rivers, creeks, or temporary streams could partially flow on the day surface and partially under the ground in karstic cavities. The richness and diversity of floral and faunal assemblages are evidence of the diverse biotopes and subtropical warm humid climate in this territory. The seasonal climate, with alternation of relatively dry and humid, rainy seasons is corroborated by the rhythmicity of the Bathonian deposits and annual growth rings in woods and presence of seasonally deciduous caytonials (Starodubtsev et al., 2008). Animals and plants dwelt on floodplains, in moist lowlands adjoining relatively more elevated sites, combined of karstic Carboniferous limestones. The wide range of biotopes is evidenced by the recognition of three plant communities adapted for dwelling under different conditions (Starodubtsev et al., 2008). Aquatic vertebrates inhabited relatively large water bodies (lakes and rivers), judging from the size of fishes and high abundance and diversity of bone remains. On the shores of these water bodies, the flora and fauna were rich and diverse. Plant and vertebrate remains were exposed to a more or less long transpor-

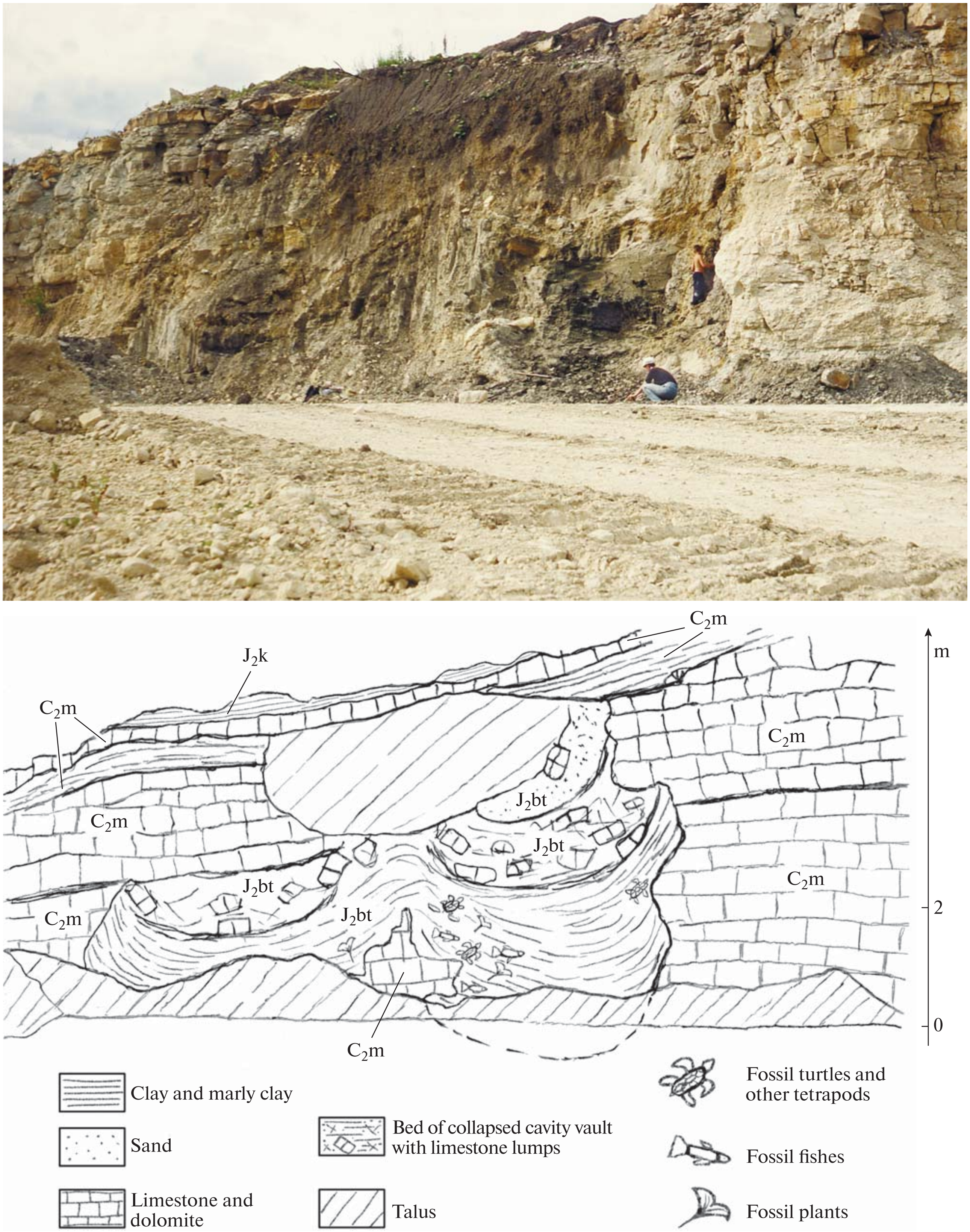

Fig. 2. Peski locality (Moscow Region, Kolomenskii District); northern slope of the Novopeskovskii quarry, largest karstic cavity filled with Bathonian deposits enclosing remains of tetrapods, fishes, and macroflora (photograph, July, 1997, and drawing). Designations: (C_2m) Middle Carboniferous, Moscovian Stage; (J_2bt) Middle Jurassic, Bathonian Stage; (J_2k) Middle Jurassic, Callovian Stage.

Fig. 3. Peski locality (Moscow Region, Kolomenskii District); northern slope of the Novopeskovskii quarry, the same karstic cavity as in Fig. 2, a site excavated in 1997; at the top right, karstic cavity surface; on the left, outlier of Middle Carboniferous limestones at its bottom.

tation from various habitats and maceration before they were buried. In deposits of karstic cavities, fossil specimens are usually isolated and fragmentary. This concerns plants and terrestrial vertebrates, while aquatic vertebrates, primarily fishes, could have been brought periodically (both alive or as dead remains) in these cavities by streams from neighboring water bodies during rainy seasons (Sennikov et al., 2005a; Starodubtsev et al., 2008). Thus, the oryctocoenosis from the Peski locality contains a mixed assemblage, including remains of aquatic, shore, and terrestrial vertebrate communities.

VERTEBRATE FAUNA FROM THE PESKI LOCALITY

The vertebrate assemblage from the Peski locality contains remains of cartilaginous and bony fishes, amphibians, reptiles, and mammals (Table 1). Cartilaginous fishes include the freshwater hybodont shark *Hybodus* sp. and chimera *Ischyodus* cf. *egertoni* (Buckland, 1835); these are the first records of fossil representatives of this group in continental deposits (Popov and Shapovalov, 2007). Bony fishes are represented in the Peski fauna by the dipnoan *Ceratodus segnis* Krupina, 1995 and actinopterygians *Lepidotes* sp., *Ptycholepis* sp., Coccolepididae, and Dapediidae (Krupin, 1995; Bragin, 2005; Sennikov et al., 2005a; Starodubtsev et al., 2008). Among amphibians, individual vertebrae of the relic brachiopoid temnospondyls cf. *Gobiops* and Caudata indet. have been recorded (Alekseev et al., 2001; Sennikov et al., 2005a, 2005b; Starodubtsev et al., 2008). Reptiles are represented by abundant bones of the basal turtle *Heckerochelys romani* Sukhanov, 2006 (Sukhanov, 2001, 2003, 2006), a jaw fragment of the primitive choristoderans *Cteniogenys ?* sp., teeth and claws of predatory dinosaurs (Alifanov, 2000; Alifanov and Sennikov, 2001). M.B. Efimov tentatively identified teeth and a cranial bone of the crocodyliform *Goniopholis* sp. (Sennikov et al., 2005a, 2005b; Starodubtsev et al., 2008), which are described below. Primitive mammals (probably representatives of Morganucodontidae) are represented by an isolated femur (Gambaryan and Averianov, 2001).

REMAINS OF CROCODYLIFORMS FROM THE PESKI LOCALITY

The material of crocodyliforms from Peski includes a lower jaw fragment (specimen PIN, no. 4767/8) and

Table 1. Vertebrate fauna from the Middle Jurassic (Bathonian) Peski locality, Moscow Region, Russia

Hybodontiformes	
	Hybodus sp. [=*Hybodus obtusus* in: Alekseev et al., 2000; *Hybodus* cf. *obtusus* in: Alifanov and Sennikov, 2001; *Hybodus hauffianus* in: Bragin, 2005]
Chimaeriformes	
	Ischyodus cf. *egertoni* (Buckland, 1835; Popov, 2005)
Ptycholepididae	
	Ptycholepis sp. [ptycholepids in: Alekseev et al., 2000] (Alifanov and Sennikov, 2001)
Coccolepididae	
	Coccolepididae indet. (Alekseev et al., 2000; Alifanov and Sennikov, 2001)
Lepisosteiformes	
	Lepidotes sp. (Alekseev et al., 2000; Alifanov and Sennikov, 2001)
Dapediiformes	
	Dapediidae indet. (Alekseev et al., 2000; Alifanov and Sennikov, 2001)
Dipnoi	
	Ceratodus segnis Krupina, 1995 (Krupin, 1995)
Temnospondyli	
	cf. *Gobiops* (Alekseev et al., 2000; Alifanov and Sennikov, 2001)
Caudata	
	Caudata indet. (Alifanov and Sennikov, 2001)
Testudines	
	Heckerochelys romani Sukhanov, 2006 (Sukhanov, 2006)
Choristodera	
	Cteniogenys? sp. [=*Cteniogenys* sp. in: Alifanov and Sennikov, 2001]
Crocodyliformes	
	Neosuchia indet. [=Mesosuchia: *Goniopholis* sp. in: Sennikov et al., 2005]
Theropoda	
	Tetanurae indet. [=Coelurosauria, Coelurosauria indet., *Richardoestesia* sp. in: Alifanov and Sennikov, 2001; Sennikov et al., 2005]
Mammalia	
	Morganucodontidae indet. [=Prototheria: triconodont? in: Alifanov and Sennikov, 2001; =Morganucodontidae indet. in: Gambaryan and Averianov, 2001]

isolated tooth crowns (specimens PIN, nos. 4767/9 and 4767/10).

Specimen PIN, no. 4767/8 (Fig. 4) is the middle part of a right angular bone directly adjoining the angle of the lower jaw, looking like a thin curved plate. One side of this plate has distinct dermal ornamentation consisting of grooves and irregular ridges over most of its area; therefore, it is interpreted as the external side. In the anterior part, it lacks such ornamentation, showing a facet for contact with the dentary. The medial side is mostly rounded; however, the posterior part of the fragment retains native structures, i.e., an oblique transverse crest and a paired nerve–vascular foramen anterior to it.

Specimens PIN, nos. 4767/9 and 10 are isolated teeth without roots (crowns) (Fig. 5), which are similar to each other and rather massive in structure. The crown is labiolingually flattened, the tooth base is oval in cross section. In longitudinal section, the tooth is an isosceles triangle; its lateral edges are approximately twice as long as the base. Medially and distally, there are distinct carinae without serration. The labial surface lacks enamel relief in both specimens (a natural characteristic of the teeth or consequence of the taphonomic processes); on the lingual surface, there is fine striation of enamel. The striae are discontinuous; some are straight, others fork at one end. The striae are rather regularly arranged throughout the internal crown surface from its base to the tooth apex.

The presence of a well-pronounced relief of pits and ridges on the external surface of cranial bones and features of the tooth crown (triangular conical shape, oval cross section, presence of two carinae without serration, striation of enamel) suggest that these spec-

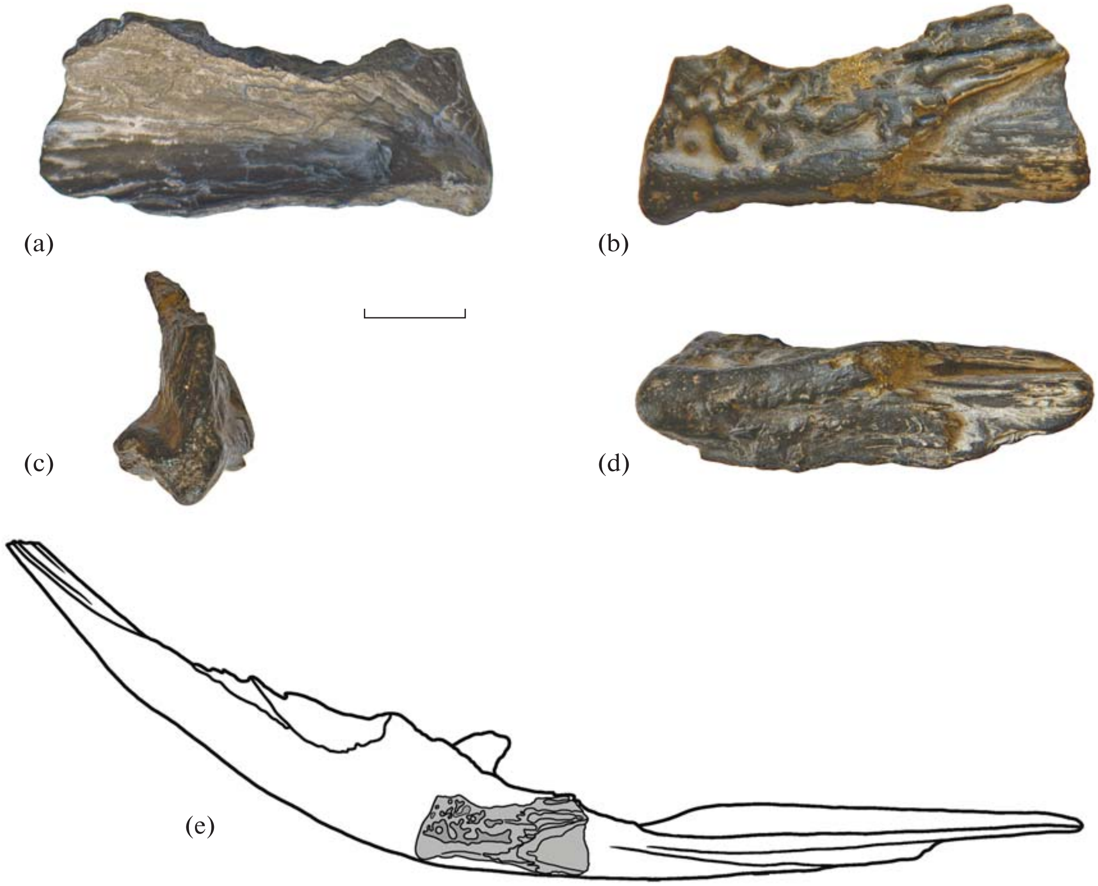

Fig. 4. Neosuchia indet.: (a–d) specimen PIN, no. 4767/8, fragment of the right angular of the lower jaw: (a) medial, (b) lateral, (c) transverse, and (d) ventral (flat external surface) views; (e) position of the fragment relative to the complete bone; white contour shows the angular of living *Crocodilus niloticus;* gray color shows specimen PIN, no. 4767/8. Moscow Region, Kolomenskii District, Peski locality; Middle Jurassic, Bathonian Stage. Scale bar, 1 cm in (a–d); (e) not to scale.

imens belong to Crocodyliformes (sensu Benton and Clark, 1988). Judging from the sizes of the mandibular bone fragment and teeth, all presently known remains can be assigned with caution to the same medium-sized taxon (about 2–3 m of body length). A more precise identification of these specimens within crocodyliforms is complicated because they are fragmentary. The presence of a distinct relief on the dermal skull bones distinguishes the crocodyliform from Peski from basal (Sphenosuchia) and aquatic (Thalattosuchia) crocodyliforms, because representatives of these groups are characterized by the absence or weak development of ornamentation on lower jaw bones (Walker, 1990; Wu and Chatterjee, 1993; Pierce and Benton, 2006; Martin and Vincent, 2013).

The teeth under study have a relatively simple conical structure, which is characteristic of representatives of many groups of Neosuchia, but distinguishes the crocodyliform from Peski from a number of taxa with specialized dental anatomy. In particular, the Hsisosuchidae from the Jurassic of China, the pelagic thalattosuchians Metriorhynchidae, which were globally distributed in the Jurassic and Early Cretaceous, and the majority of groups terrestrial Gondwanan Notosuchia frequently have teeth with serrated carinae and laterally compressed or even more complex crowns (Riff and Kelner, 2001; Peng and Shu, 2005; Larsson and Sues, 2007; Andrade et al., 2010; Pol et al., 2014). Some heterodont neosuchians (e.g., *Theriosuchus,* Bernissartiidae) have usual conical teeth in the anterior part of the tooth row and posterior teeth with distinctive crown morphology (lanceolate, flattened, tribodont) distinguished from that of the teeth from Peski (Buffetaut and Ford, 1979; Tennant et al., 2016).

The teeth in representatives of the families Goniopholididae (Late Jurassic and Early Cretaceous of Europe, Asia, and North America) and Paralligatoridae (Cretaceous of Asia) are similar to the teeth of the crocodyliform from Peski in size and shape, but differ in the presence of more massive, straight, regularly distributed ridges on the crown surface (Averianov, 2000; Maish et al., 2003; Schwarz-Wings et al., 2009; Wings et al., 2010; Kuzmin et al., 2013; Martin et al., 2016). A similar relief composed of narrow striae on the enamel surface is present on some teeth referred to

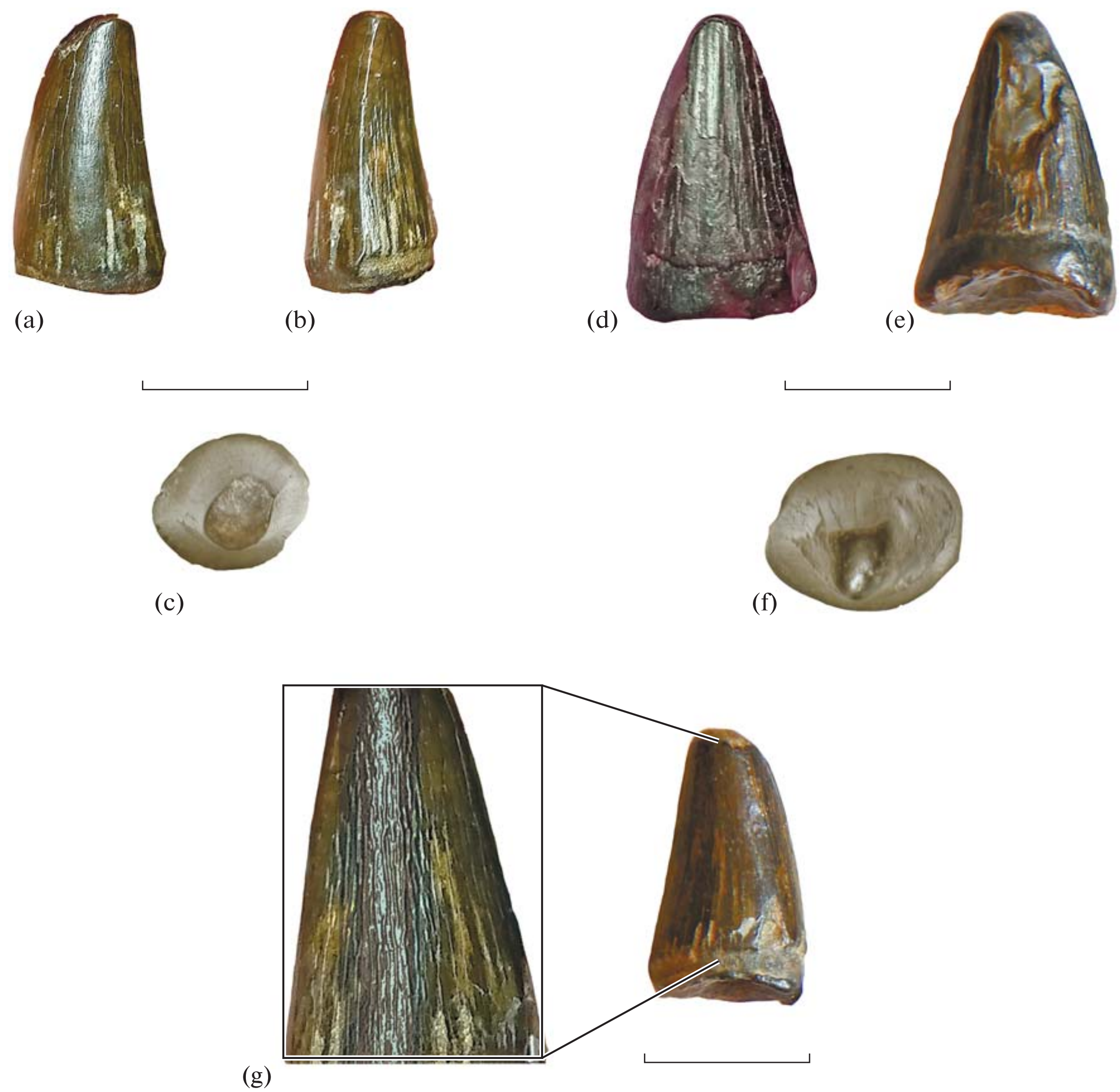

Fig. 5. Neosuchia indet.: (a–c) specimen PIN, no. 4767/9, isolated tooth crown: (a) labial, (b) mesial/distal, and (c) apical views; (d–f) specimen PIN, no. 4767/10, isolated tooth crown: (d) labial, (e) lingual, and (f) apical views; (g) specimen PIN, no. 4767/9, enamel relief on the lingual crown surface; Moscow Region, Kolomenskii District, Peski locality; Middle Jurassic, Bathonian Stage. Scale bar, 1 cm.

the family Atoposauridae, in particular, to the genus *Theriosuchus* (Schwarz-Wings et al., 2009, text-fig. 3A; Knoll et al., 2013, text-fig. 4g) and also on the teeth of some representatives of the thalattosuchian family Teleosauridae (Young et al., 2014, text-fig. 33A). The teeth of the crocodyliform from Peski differ from Atoposauridae in the large size and rougher morphology and from the majority of Teleosauridae in the less extended crown. In addition, the crocodyliform from Peski should not be assigned to Teleosauridae, because it is confined to continental deposits.

Taking into account the morphological characters listed above and also the continental genesis of enclosing deposits, it is highly likely that the crocodyliform from the Peski locality belongs to neosuchians of uncertain taxonomic position (Neosuchia indet.). This group comprises various semiaquatic taxa, including all extant crocodiles, and is a usual element of terrestrial vertebrate assemblages beginning from the Jurassic (Buffetaut, 1979; Benton and Clark, 1988; Efimov, 1988b; a review of Middle Jurassic crocodyliforms is provided below).

REVIEW OF CROCODYLIFORMS FROM MIDDLE JURASSIC DEPOSITS

In contrast to marine Thalattosuchia, which remains from the Middle Jurassic have been examined relatively thoroughly (Andrews, 1913; Benton and Spencer, 1995; Gasparini et al., 2005; Cau and Fanti, 2011; Young et al., 2013; Foffa and Young, 2014; Johnson et al., 2015; Wilberg, 2015), crocodyliform remains from continental deposits of this time are extremely fragmentary. They are mostly known from localities containing microremains of vertebrates and represented by isolated teeth and small bone fragments (Metcalf et al., 1992; Benton and Spencer, 1995; Kriwet et al., 1997; Evans et al., 2006; Flynn et al., 2006; Knoll et al., 2013; Knoll and López-Antoñanzas, 2014; Haddoumi et al., 2016). More informative remains come from Middle Jurassic continental deposits of Scotland (Evans and Waldman, 1996; Young et al., 2016; Yi et al., 2017), Asia (Averianov, 2000; Gao, 2001; Maish et al., 2003; Clark et al., 2004; Fu et al., 2005; Kuzmin et al., 2013), and Madagascar (Dal Sasso et al., 2017).

According to number of works, a rich neosuchian fauna existed during the Bathonian in the territory of modern Scotland (Evans and Waldman, 1996; Evans et al., 2006; Young et al., 2016; Yi et al., 2017). This fauna includes representatives Goniopholididae (isolated teeth and bone fragments and also an associated partially preserved postcranial skeleton with amphicoelous vertebrae and osteoderms having anterolateral processes), *Theriosuchus* sp. (dentary fragment), and probable representative of Hylaeochampsidae (represented by the only dentary fragment with a short mandibular symphysis, relatively shallow alveoli, and some heterodonty). Based on isolated teeth and bone fragments from Middle Jurassic continental deposits of Great Britain and France, the presence of Atoposauridae/*Theriosuchus* and Goniopholididae and also presumable presence in some assemblages of the thalattosuchian Teleosauridae indet. Were reported (Metcalf et al., 1992; Evans and Milner, 1994; Benton and Spencer, 1995; Kriwet et al., 1997; Knoll et al., 2013; Knoll and López-Antoñanzas, 2014). The crocodyliform assemblages revealed on the basis of fragmentary material from the Middle Jurassic of Europe (Goniopholididae, Atoposauridae/*Theriosuchus*, Hylaeochampsidae) are similar in composition to later and much more thoroughly investigated Late Jurassic–Early Cretaceous assemblages from this region (Salisbury and Naish, 2011). Apparently, relatively stable crocodyliform assemblages from the Late Jurassic–Early Cretaceous of Europe were formed during the Middle Jurassic (Yi et al., 2017).

From Middle Jurassic continental deposits of China, remains of relatively primitive representatives of Crocodylomorpha are known, including *Junggarsuchus sloani* (Clark et al., 2004) of the "sphenosuchian" morphofunctional level and also a basal crocodyliform of the family Hsisosuchidae (*Hsisosuchus dashanpuensis*; Gao, 2001). More evolutionarily advanced neosuchian crocodyliforms from the Middle Jurassic continental deposits of Asia are represented by numerous Goniopholididae from Kyrgyzstan (Averianov, 2000), China (Maish et al., 2003; Fu et al., 2005). and Western Siberia (Kuzmin et al., 2013). Some of these specimens are referred to the genus *Sunosuchus* known from the Late Jurassic of China and Mongolia (Young, 1948; Efimov, 1988a; Wu et al., 1996). According to the results of recent studies, the genus *Sunosuchus* is not monophyletic and all remains previously referred to it require a revision (Andrade et al., 2011; Halliday et al., 2015).

Crocodyliform remains from the Middle Jurassic continental deposits of Africa are known from Morocco (Haddoumi et al., 2016) and Madagascar (Flynn et al., 2006; Dal Sasso et al., 2017). Based on isolated teeth from the Bathonian of Morocco, three crocodyliform taxa have been recorded, i.e., the presumable atoposaurid cf. *Theriosuchus* sp., a thalattosuchian uncertain taxonomic position (Teleosauridae indet. and Thalattosuchia ?Metriorhynchidae indet.) (Haddoumi et al., 2016). In addition, the presence of Atoposauridae in coeval deposits of Madagascar has been established based on numerous, but undescribed in detail teeth and fragments of a cranial and postcranial skeleton (Flynn et al., 2006). According to a recent revision of the family Atoposauridae, a detailed examination of these remains is required for confirmation of the presence of Atoposauridae or the genus *Theriosuchus* in the Middle Jurassic of Madagascar; at the same time, the authors adhere to the assignment of isolated teeth from Morocco to the genus *Theriosuchus* (Tennant et al., 2016). *Razanandrongobe sakalavae* is one more crocodyliform taxon from the Bathonian of Madagascar known from fragmentary remains of a rostrum, lower jaw, and teeth with bilaterally serrated carinae (Dal Sasso et al., 2017). *Razanandrongobe,* which is the only and earliest known Jurassic representative of Notosuchia, reached a huge size and was apparently a terrestrial predator of the highest order (Dal Sasso et al., 2017).

It is noteworthy that identification of crocodyliform remains to genus/family based on isolated teeth and skeleton fragments is frequently incorrect, because these remains lack distinctive apomorphic characters of the taxonomic groups of low ranks. In particular, isolated teeth of Atoposauridae indet./*Theriosuchus* sp. from the Middle Jurassic of Europe (Kriwet et al., 1997; Knoll et al., 2013; Knoll and López-Antoñanzas, 2014) and Madagascar (Flynn et al., 2006) were referred to higher-rank taxa in a recent revision of the family (Neosuchia indet./Mesoeucrocodylia indet.), because this material is impossible to identify more closely (Tennant et al., 2016). The same concerns the identification of representatives of the family Goniopholididae based on isolated teeth (Metcalf et al., 1992; Evans and Milner, 1994; Benton and Spencer, 1995) or fragments of the postcranial skeleton (Evans and Waldman, 1996) lacking distinctive apomorphic characters. The analysis of published data has shown that diagnosable remains of Goniopholididae from Europe are only known from the Late Jurassic (Schwarz, 2002) and Early Cretaceous (Salisbury et al., 1999; Salisbury, 2002; Andrade et al., 2011; Puértolas-Pascual et al.,

Table 2. Comparison of the vertebrate fauna from the Peski locality with other Bathonian faunas of Laurasia (faunal elements occurring in Peski are given for comparison)

Peski locality	Bathonian faunas of Great Britain	Fauna from the Berezovsky section (Itat Formation, Western Siberia, Krasnoyarsk Region)	Bathonian faunas of Kyrgyzstan (Balabansai Formation)
Hybodontiformes			
Hybodus sp.	*Hybodus* sp.	*Hybodus* sp.	*Polyacrodus* sp.
Chimaeriformes			
Ischyodus cf. *egertoni*	–	–	–
Ptycholepididae			
Ptycholepis sp.	–	–	?Ptycholepididae indet.
Coccolepididae			
Coccolepididae indet.	–	–	–
Lepisosteiformes			
Lepidotes sp.	*Lepidotes* sp.	–	cf. Lepidotidae indet.
Dapediiformes			
Dapediidae indet.	–	–	–
Dipnoi			
Ceratodus segnis	–	Dipnoi indet.	*Ferganoceratodus jurassicus*
Temnospondyli			
cf. *Gobiops*	–	–	*Ferganobatrachus riabinini*
Caudata			
Caudata indet.	*Marmorerpeton freemani, M. kermacki, Salamander* A, *Salamander* B	*Urupia monstrosa, Kiyatriton krasnolutskii, Salamander* A	*Kokartus honorarius*
Testudines			
Heckerochelys romani	Pleurosternidae indet., Cryptodira indet.; *Eileanchelys waldmani*	*Annemys* sp.	*Xinjiangchelys tianshanensis*
Choristodera			
Cteniogenys? sp.	*Cteniogenys* sp.	cf. *Cteniogenys* sp.	Choristodera indet.
Crocodyliformes			
Neosuchia indet.	Goniopholididae indet., Atoposauridae indet.	Goniopholididae indet.	*Sunosuchus* sp.
Theropoda			
Tetanurae indet.	*Proceratosaurus* sp., *Megalosaurus* sp.	*Kileskus aristotocus*	Tetanurae indet.

2015; Martin et al., 2016; Ristevski et al., 2017); at that time, the Goniopholididae were a usual element of vertebrate assemblages (Salisbury and Naish, 2011; Buscalioni et al., 2013).

Thus, the Middle Jurassic was the time of diversification of the main neosuchian groups and formation of characteristic later crocodyliform assemblages; at the same time, remains of representatives of this group are extremely rare and fragmentary in continental deposits of that time (Yi et al., 2017).

ZOOGEOGRAPHICAL RELATIONSHIPS OF THE PESKI FAUNA WITH OTHER BATHONIAN VERTEBRATE FAUNAS OF LAURASIA

In addition to the Moscow Region, the Bathonian history of the continental biota is known in some other regions of Laurasia (Table 2). For example, vertebrate faunas of this age are rather thoroughly investigated in Great Britain, Kyrgyzstan, and Western Siberia (Evans and Milner 1994; Evans and Waldman 1996;

Averianov et al., 2005, 2010, 2016). A prominent feature of these faunas is significant similarity in taxonomic composition (especially the faunas from Great Britain and Western Siberia), which is evidence of faunal homogeneity throughout the territory of Laurasia during the Bathonian time (Averianov et al., 2010, 2016; Skutschas, 2013; Skutschas et al., 2016). The most typical components of Bathonian vertebrate faunas of Great Britain, Kyrgyzstan, and Western Siberia are caudate amphibians (one of the first in the fossil record), basal turtles, basal choristoderans, primitive mammals, and neosuchian crocodyliforms (Evans and Milner 1994; Evans and Waldman 1996; Averianov et al., 2005, 2010, 2016; Skutschas, 2013; Skutschas et al., 2016).

Despite the incompleteness of available data, the vertebrate fauna from Peski shows the presence of the elements characteristic of other Bathonian faunas (caudate amphibians, basal turtles, basal choristoderans, primitive mammals, and neosuchian crocodyliforms), which supports the concept of the homogeneity of Bathonian faunas of Laurasia, including Eastern Europe.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project nos. 17-04-00410, 16-05-00711, and 17-54-10013) and by the State Russian Government Program for Competitive Growth of Kazan Federal University among World's Leading Scientific and Education Centers.

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Translated by G. Rautian