Paleontological Journal, Vol. 39, No. 2, 2005, pp. 199–209. Translated from Paleontologicheskii Zhurnal, No. 2, 2005, pp. 88–97.

A New Specialized Prolacertilian (Reptilia: Archosauromorpha) from the Lower Triassic of the Orenburg Region

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Received December 29, 2003

Abstract—A new large specialized prolacertilian, *Vritramimosaurus dzerzhinskii* gen. et sp. nov., from the Lower Triassic of the Rassypnaya locality (Orenburg Region, European Russia) and new specimens of the Middle Triassic prolacertilian *Malutinisuchus gratus* are described. The diversity, phylogeny, systematics, and geographical and stratigraphic distribution of prolacertilians are discussed.

Key words: Archosauromorpha, Prolacertilia, diversity, systematics, phylogeny, Triassic, Eastern Europe.

INTRODUCTION

Diapsid reptiles are represented in the Permian and Triassic of eastern Europe by trilophosaurians, eosauropterygians, prolacertilians, archosaurs, eolacertilians, and, probably, by eosuchian and rhynchocephalian reptiles. Early thecodont archosaurs were examined particularly thoroughly; four families and more than twenty genera and species have been recorded, the historical development of this group in tetrapod communities has been reconstructed, and faunal assemblages characteristic of low-rank stratigraphic units were recognized (Sennikov, 1995; Ivakhnenko *et al.*, 1997).

The prolacertilians of eastern Europe have not been adequately studied. The Upper Permian beds yielded fragmentary remains of *Eorasaurus olsoni* Sennikov, 1997 assigned to the prolacertilian family Protorosauridae (Sennikov, 1997). This is a unique find of diapsid reptiles in the Permian of eastern Europe. The Triassic of eastern Europe yielded only members of the family Prolacertidae. *Microcnemus efremovi* Huene, 1940 (Huene, 1940) and *Boreopricea funerea* Tatarinov, 1978 (Tatarinov, 1978; Benton and Allen, 1997) were described from the Lower Triassic beds, while *Malutinisuchus gratus* Otschev, 1986 occurred in the Middle Triassic (Otschev, 1986). However, the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN) contains a number of Lower and Middle Triassic prolacertilians that have not been described yet.

In 1988, I.V. Novikov found a prolacertilian cervical vertebra in the Synya-2 locality in the northern Fore-Urals. This specimen is assigned with confidence to *Malutinisuchus gratus*, which was originally described from the Middle Triassic of the southern Fore-Urals (Otschev, 1986).

Among specimens from the Lower Triassic Rassypnaya locality (Orenburg Region, collected by B.P. Vjuschkov in 1953 and 1954), I found vertebrae of a large specialized prolacertilian which is described below as a new genus and species of the family Prolacertidae. This is the first prolacertid found in the Yarengian Regional Stage of eastern Europe.

The vertebrate fauna from the terminal Lower Triassic of the Rassypnaya locality (southeastern area of the Volga–Ural Anteclise) is rather similar to the vertebrate fauna of the same age from the Ural Foredeep. These bone beds are referred to the upper strata of the Petropavlovka Formation (Gamian Regional Stage, Yarengian Regional Superstage, Upper Olenekian Substage) (Novikov and Sennikov, 2001). The Rassypnaya locality yielded the capitosauroid labyrinthodont *Parotosuchus orenburgensis*; thecodonts, including the early erythrosuchid *Garjainia triplicostata* and the early rauisuchid *Jaikosuchus magnus*; and the therocephal *Silphedosuchus orenburgensis.* The discovery of a new prolacertilian substantially supplements the faunal assemblage from Rassypnaya and the tetrapod assemblage characteristic of the terminal Early Triassic of eastern Europe.

SYSTEMATIC PALEONTOLOGY

Order Prolacertilia

Suborder Protorosauria

Family Prolacertidae Parrington, 1935

Prolacertidae: Parrington, 1935, p. 205; Huene, 1956, p. 643 (pars); Romer, 1956, p. 522; Maleev, 1964, p. 458 (pars); Kuhn, 1969, p. 67; Gow, 1975, p. 118; Colbert, 1987, p. 2; Carroll, 1988, p. 199.

Askeptosauridae (pars): Huene, 1956, p. 645.

Protorosauridae (pars): Romer, 1956, p. 657; Tatarinov, 1964, p. 456; Chatterjee, 1980, p. 168; 1986, p. 297.

Type genus. *Prolacerta* Parrington, 1935.

Diagnosis. Squamosal with descending process. Interpterygoid depression long. Lower jaw symphysis lacking expansion. Marginal teeth isodont, prothecodont, sharp, and curved slightly posteriorly. Palatal teeth present on palatines, vomers, and pterygoids. Vertebrae with intercenters. Cervical region of vertebral column composed of seven vertebrae. Cervical vertebrae elongated. Neural spines of cervical vertebrae elongated, inverted trapezoid shaped, with expansion in upper part. Scapula relatively low and broad. Humerus with ectepicondilar notch. Manus with three proximal and four distal carpal elements. Pelvis with small thyroidean fenestra. Pes with three proximal and four distal tarsal elements. Fifth metatarsal element hooked and elongated.

Generic composition. *Prolacerta* Parrington, 1935; *Pricea* Broom et Robinson, 1948; *Trachelosaurus* Broili, 1918; *Macrocnemus* Nopcsa, 1931; *Microcnemus* Huene, 1940; *Megacnemus* Huene, 1955; *Prolacertoides* Young, 1973; *Cosesaurus* Ellenberger et Villalta, 1974; *Boreopricea* Tatarinov, 1978; *Kadimakara* Bartholomai, 1979; *Malerisaurus* Chatterjee, 1980; *Malutinisuchus* Otschev, 1986; *Vritramimosaurus* gen. nov.; *Rhombopholis* Owen, 1866; *Jesairosaurus* Jalil, 1997; and *?Langobardisaurus* Renesto, 1994.

Occurrence. Triassic; eastern, central, and western Europe, North America, northern Africa, India, China, Australia, and Antarctica.

Remarks. The taxonomic position of *Langobardisaurus* remains uncertain, because this prolacertilian combines diagnostic characters of both prolacertids and tanystropheids (Renesto, 1994).

Megacnemus from the Middle Triassic (lower shell limestone) of Silesia is only represented by an isolated very large, straight femur (Huene, 1956; Kuhn, 1969). *Megacnemus* is probably a very large prolacertid; however, it is not improbable that it is a member of the family Tanystropheidae, which is characterized by a more straightened femur than prolacertids.

Genus *Vritramimosaurus* Sennikov gen. nov.

Etymology. From *Vritra* (in Vedic mythology, a giant serpent or dragon killed by the God Indra), the Latin *mimicus* (seen, apparent, resembling), and the Greek *saurus* (lizard).

Type species. *Vritramimosaurus dzerzhinskii* sp. nov.

Diagnosis. Giant prolacertid (body probably at least 3 m long). Cervical vertebrae elongated, ratio of length to anterior height of cervical vertebral centra approximately 3.0. Axis of cervical vertebral centra positioned at 10° to horizontal line. Articular surfaces of cervical vertebral centra high. Neural spines of cervical vertebrae elongated, moderately high. Dorsal (upper) edge of neural spine thickened, expanded, and rugose. Spinal canal probably circular or its height somewhat greater than width. Prezygapophyses and postzygapophyses of cervical vertebrae positioned obliquely, their articular facets broad and short. Articular facets of postzygapophyses located in middle part of postzygapophyses and possessing specific ventromedial projections. Hyposphene probably present. Postzygapophyses terminated in flat, horizontal projections with rounded ends, extending posterior to articular surfaces. Diapophyses and parapophyses weakly projecting. Postdiapophyseal and postparapophyseal crests moderately projecting, seen in anterior half of centrum of cervical vertebrae. Anterior half of ventral surface of centra of cervical vertebrae possessing keel in shape of narrow, strongly projecting crest.

Species composition. Type species.

Comparison. *Vritramimosaurus* is distinguished from other prolacertids by its larger size; thicker, wider, and more rugose dorsal edge of the neural spine; and the presence of the hyposphene. It differs from other prolacertids, except for *Malutinisuchus*, in that the posterior ends of the postzygapophyses have a projection extending posterior to the articular facets. It differs from *Prolacerta, Microcnemus, Boreopricea, Malerisaurus, Malutinisuchus*, and *Rhombopholis* in the higher articular surfaces on the cervical vertebral centra, from *Prolacerta, Macrocnemus, Microcnemus, Malutinisuchus, Rhombopholis*, and *Langobardisaurus* in the greater inclination of the axis of the cervical vertebral centra. It differs from *Microcnemus, Boreopricea, Malerisaurus, Malutinisuchus*, and *Rhombopholis* in the higher spinal canal. It differs from *Prolacerta, Microcnemus, Boreopricea*, and *Malerisaurus* in having parapophyses and diapophyses which project to a lesser extent, and in the shorter and only slightly projecting postdiapophyseal crests. It differs from *Prolacerta, Boreopricea, Malerisaurus*, and *Malutinisuchus* in the longer neural spine of the cervical vertebrae. It differs from *Prolacerta, Boreopricea*, and *Rhombopholis* in the more elongated cervical vertebrae. It differs from *Langobardisaurus, Prolacerta*, and *Malutinisuchus* in the higher neural spine of the cervical vertebrae. It differs from *Microcnemus, Boreopricea*, and *Malutinisuchus* in the wider and shorter articular facets of the prezygapophyses and postzygapophyses and in the presence of specific ventromedial projections on the articular facets of the postzygapophyses. It differs from *Microcnemus* and *Boreopricea* in the position of articular facets in the middle part of the postzygapophyses. It differs from *Microcnemus* and *Malutinisuchus* in the shorter keel. It differs from *Langobardisaurus* in the shorter cervical vertebrae and the shorter neural spines of the cervical vertebrae. It differs from *Malutinisuchus* in the more oblique position of the prezygapophyses and postzygapophyses of the cervical vertebrae and in the flat, horizontal posterior protrusions of the postzygapophyses, with rounded ends. It differs from *Boreopricea* in the presence of the postparapophyseal crest and the keel. It differs from *Malerisaurus* in the weaker inclination of the axis of the cervical vertebral centra.

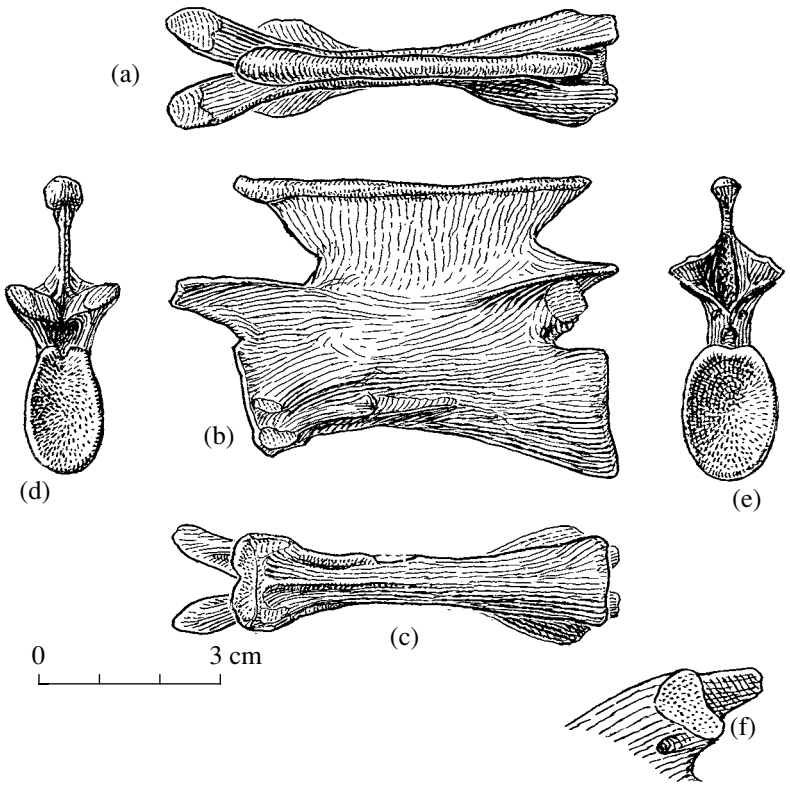

Fig. 1. *Vritramimosaurus dzerzhinskii* sp. nov.: (a–f) holotype PIN, no. 951/72, cervical vertebra: (a) dorsal, (b) left lateral, (c) ventral, (d) cranial, and (e) caudal views; (f) left postzygapophysis, ventrolateral view, complex structure of the facet is shown.

R e m a r k s. *"Tanystropheus" antiquus* has the posterior processes of the postzygapophyses of the cervical vertebrae similar to those of *Vritramimosaurus* and *Malutinisuchus* (Huene, 1931).

***Vritramimosaurus dzerzhinskii* Sennikov, sp. nov.**

E t y m o l o g y. The species is named in honor of the Russian zoologist F.Ya. Dzerzhinsky, a specialist in the field of comparative anatomy and functional morphology of vertebrates.

H o l o t y p e. PIN, no. 951/72, cervical vertebra; Orenburg Region, Ilekskii District, Rassypnaya locality; Lower Triassic, uppermost part of the Olenekian Stage, Yarengian Regional Superstage, Gamian Regional Stage, Petropavlovka Formation.

D e s c r i p t i o n (Fig. 1). The holotype is a cervical vertebra, which is probably from the middle part of the cervical region (from the third to the fifth). Judging from the compressed bone surface, the very small thickness of the middle part of the vertebra, and the asymmetrical displacement of the prezygapophyses, this vertebra was compressed laterally and somewhat deformed. The vertebral centrum of the holotype is 60 mm long; the entire vertebra from the anterior edge of the prezygapophyses to the posterior edge of the postzygapophyses is 75 mm long; anteriorly, the articular surface of the vertebral centrum is 20 mm high. Similar measurements have not been recorded in the cervical vertebrae of any member of the family Prolacertidae. Thus, this vertebra belongs to the largest known giant prolacertid, with the total body length not less than 3 m (as was reconstructed based on the skeleton proportions in *Prolacerta broomi*).

The vertebral centrum is elongated, the ratio of the length to the anterior height of the cervical vertebral centrum is approximately 3.0, which is typical for prolacertids. The middle part of the vertebral centrum is arched from below and strongly compressed laterally; however, the constriction of the centrum was obviously increased by postmortem compression and deformation of the bone. The axis of the vertebral centrum is positioned at an angle of 10° to the horizontal. As the dorsal (upper) edge of the neural spine is positioned horizontally and the anterior and posterior articular surfaces of the vertebral centrum are positioned vertically, the first is located higher than the second, while the vertebra is somewhat oblique in lateral view. The anterior and posterior articular surfaces of the vertebral centrum are relatively deeply amphicoelous and high (the height exceeds the width); however, the width probably slightly decreased because of postmortem lateral compression and deformation. The neural spine is moderately high, elongated, in the shape of an inverted trapezoid; this is also typical for prolacertids. The maximum length of the neural spine along the upper edge is

approximately 57 mm, i.e., a little shorter than the length of the vertebral centrum; the minimum length at the base is approximately 35 mm. The dorsal margin of the neural spine is thickened, straight, horizontal, and strongly rugose, with its edges somewhat projecting laterally, anteriorly, and posteriorly, forming a caplike structure above the spine, which is particularly clearly developed in the anterior part. This thickened dorsal end of the neural spine somewhat resembles an unpaired osteoderm fused with the neural spine; however, it is most likely an apophyseal bone rather than an osteoderm (Haines, 1969; Sennikov, 1999). This bone was probably formed because of the well-developed axial musculature–ligament apparatus in the neck of *Vritramimosaurus*.

The spinal canal is relatively small in diameter and probably almost circular in cross section; however, it is impossible to recognize its shape with certainty because of deformation. The prezygapophyses and postzygapophyses of the cervical vertebrae are large, elongated, and positioned at an angle of approximately 30° to the horizontal. Their articular facets are large. The articular facets of the prezygapophyses are relatively short, wide, and located close to their anterior ends. The articular facets of the postzygapophyses are short, wide, located in the middle part of the postzygapophyses, and have specific ventromedial protrusions or expansions. These ventromedial protrusions form thin projections, which come into contact in the middle, in the sagittal plane, and probably form the hyposphene. The presence of the hyposphene is evidence of the complication and strengthening of the articulations between the cervical vertebrae of *Vritramimosaurus*, which probably restricted twisting; this was necessary because of the long neck and large size of this animal. The development of ventromedial protrusions of the articular facets of postzygapophyses was also associated with the consolidation of articulation of the cervical vertebrae and complication of their relative movements. The postzygapophyses terminate in flat, horizontal projections with rounded ends extending posterior to the articular facets. These projections were probably formed in connection with the development of a strong musculature–ligament system in the neck of *Vritramimosaurus*, namely, with the attachment of the lateral flexors of the neck, the interarticulares muscles (Tschanz, 1985).

The diapophyses and parapophyses project only slightly. The postdiapophyseal and postparapophyseal crests project moderately and are distinctly developed in the anterior half of the vertebral centrum. The keel is in the shape of a strongly projecting narrow crest in the anterior half of the ventral surface of the centrum; in the posterior half, it is poorly developed.

In addition to the holotype, I tentatively assign the following specimens to *Vritramimosaurus dzerzhinskii*: PIN, no. 951/73, a cervical vertebra; PIN, no. 951/106, centrum of a caudal vertebra; and PIN, nos. 951/107 and 108, fragmentary vertebrae probably belonging to prolacertilians and distinguished from those of thecodonts from the Rassypnaya locality. Specimen PIN, no. 951/73 is probably a posterior cervical vertebra of a small juvenile. Its centrum is 25 mm long, the anterior articular surface of the vertebral centrum is 11 mm high. In the middle, the vertebral centrum is strongly laterally compressed and moderately elongated, the ratio of the length to the anterior height of the cervical vertebral centrum is approximately 2.3. The anterior and posterior articular surfaces of the vertebral centrum are high, amphicoelous. The axis of the vertebral centrum is at an angle of 10° to the horizontal. The spinal canal is high. The neural spine is broken off, but was probably short. The diapophyses and parapophyses project only slightly. The postdiapophyseal and postparapophyseal crests project moderately; the postdiapophyseal crest reaches the posterior edge of the vertebral centrum. This specimen differs from the holotype in its smaller dimensions and more elongated vertebral centrum and neural spine; these characters are probably attributable to a more caudal position of the vertebra in the vertebral column and the juvenile age of this animal (therefore, they are excluded from the diagnosis).

Material. In addition to the holotype, PIN, no. 951/73, cervical vertebra; PIN, no. 951/106, caudal vertebra; and PIN, nos. 951/107 and 108, fragmentary vertebrae from the type locality.

Genus *Malutinisuchus* Otschev, 1986

Malutinisuchus: Otschev, 1986, p. 172; Sennikov, in Ivakhnenko *et al.*, 1997, p. 25.

Type species. *Malutinisuchus gratus* Otschev, 1986.

Diagnosis. Large prolacertid (body approximately 2–2.5 m long). Cervical vertebrae elongated, ratio of length to anterior height of cervical vertebral centra 2.6–3.8. Axis of cervical vertebral centra positioned at 7–9° to horizontal line. Articular surfaces of cervical vertebral centra low. Neural spines of cervical vertebrae low, moderately elongated. Spinal canal low and wide. Prezygapophyses and postzygapophyses of cervical vertebrae positioned relatively close to horizontal, their articular facets large, slightly elongated, oval. Articular facets of postzygapophyses located in middle part of postzygapophyses. Postzygapophyses of cervical vertebrae terminated in narrow, pointed projections circular in cross section and extending posteriorly beyond articular facets. Diapophyses and parapophyses slightly projecting. Postdiapophyseal and postparapophyseal crests slightly projecting, distinctly visible in anterior half of cervical vertebral centrum. Keel slightly projecting, extending along entire length of ventral surface of cervical centrum. Humerus moderately elongated, with expanded epiphyses and short diaphysis. Epiphyses of humerus positioned at angle of 40–45°.

Species composition. Type species.

Comparison. *Malutinisuchus* is distinguished from the other prolacertids, except for *Vritramimosaurus*, by its larger measurements and the presence on the posterior ends of the postzygapophyses of projections extending posterior to their articular surfaces. It differs from *Prolacerta, Macrocnemus, Microcnemus, Rhombopholis*, and *Langobardisaurus* in the greater inclination of the axis of cervical vertebral centra. It differs from *Macrocnemus, Microcnemus, Boreopricea*, and *Rhombopholis* in the more elongated cervical vertebrae. It differs from *Prolacerta, Microcnemus, Boreopricea*, and *Malerisaurus* in the less projecting parapophyses and diapophyses and in the shorter and more poorly projecting postdiapophyseal crests. It differs from *Boreopricea, Prolacerta, Microcnemus*, and *Malerisaurus* in the less twisted humerus. It differs from *Boreopricea, Prolacerta*, and *Malerisaurus* in the lower spinal canal and in the positions of the prezygapophyses and postzygapophyses of the cervical vertebrae, which are closer to the horizontal line. It differs from *Langobardisaurus* and *Macrocnemus* in the shorter humerus with wider epiphyses. It differs from *Malerisaurus* and *Boreopricea* in the weaker inclination of the axis of the cervical vertebral centra. It differs from *Prolacerta* and *Malerisaurus* in the lower articular surfaces of the cervical vertebral centra. It differs from *Microcnemus* and *Boreopricea* in the longer oval articular facets of the prezygapophyses and postzygapophyses and in the position of the articular facets in the middle part of the postzygapophyses. It differs from *Boreopricea* in the presence of the postparapophyseal crest and keel. It differs from *Langobardisaurus* in the less elongated cervical vertebrae.

Malutinisuchus gratus Otschev, 1986

Malutinisuchus gratus: Otschev, 1986, p. 173, text-fig. 2; Sennikov, in Ivakhnenko *et al.*, 1997, p. 25, pl. 55, fig. 5.

Holotype. PIN, no. 4188/125 (SGU, no. 104/401), cervical vertebra; Orenburg Region, Sol'-Iletskii District, Bukobai 5 locality; Middle Triassic, Ladinian Stage, Bukobai Regional Stage, Bukobai Formation.

Description (Figs. 2, 3). The holotype (Figs. 2a–2f) is a cervical vertebra, probably a middle cervical vertebra (from the third to the fifth). The vertebral centrum of the holotype is 42 mm long, the vertebra from the anterior edge of the prezygapophyses to the posterior edge of the postzygapophyses is 60 mm long, and the anterior articular surface of the vertebral centrum is 11 mm high. No cervical vertebrae with similar measurements has been recorded in other members of the family Prolacertidae, except for *Vritramimosaurus* which was even larger. The total body length of *Malutinisuchus*, reconstructed based on measurements of its vertebrae and humerus and skeletal proportions of *Prolacerta broomi*, was approximately 2–2.5 m. The vertebral centrum is elongated, the ratio of the length to the anterior height of the cervical vertebral centrum is approximately 3.8. The centrum is arched from below in the central part and is strongly laterally compressed. The axis of the vertebral centrum is positioned at an angle of 9° to the horizontal line.

As the dorsal (upper) edge of the neural spine is positioned horizontally and the anterior and posterior articular surfaces of the vertebral centrum are positioned vertically, the first is higher than the second, while the vertebra is somewhat oblique in lateral view. The anterior and posterior articular surfaces of the vertebral centrum are amphicoelous and low (the width exceeds the height). The neural spine is low, only slightly elongated, in the shape of an inverted trapezoid, which is typical of prolacertids. The maximum length of the neural spine along the upper edge is substantially shorter than the centrum length, while the minimum length at the base is approximately 20 mm. The dorsal margin of the neural spine is thickened, straight, horizontal, and rugose, with its edges projecting somewhat laterally and anteriorly. The thickened dorsal end of the neural spine is most likely an apophyseal bone (Haines, 1969; Sennikov, 1999), which was probably formed in connection with the well-developed axial musculature–ligament apparatus in the neck of *Malutinisuchus*. The spinal canal is low and wide. The prezygapophyses and postzygapophyses of the cervical vertebrae are large, elongated, and positioned obliquely, at an angle of approximately 30° to the horizontal line. Their articular facets are large, slightly elongated oval. The postzygapophyses of the cervical vertebrae terminate in narrow, pointed projections circular in cross section and extending posterior to the articular facets. The presence of these projections is probably associated with the strong axial musculature–ligament apparatus of the neck of *Malutinisuchus*, namely, with the attachment of the lateral flexors of the neck, the interarticulares muscles (Tschanz, 1985). The diapophyses and parapophyses project slightly. The postdiapophyseal and postparapophyseal crests project only slightly and are distinct in the anterior half of the cervical vertebral centrum. The keel projects slightly and stretches along the entire length of the ventral surface of the cervical vertebral centrum.

Another cervical vertebra from the same locality (specimen PIN, no. 4188/126; Figs. 2g–2k) is somewhat larger and probably also belonged to the middle cervical vertebrae (from the third to the sixth). The vertebral centrum is 46 mm long, the total length of the vertebra from the anterior edge of the prezygapophyses to the posterior edge of the postzygapophyses is 65 mm, and the articular surface of the vertebral centrum is 15 mm high. The vertebral centrum is elongated, the ratio of the length to the anterior height of the centrum is approximately 3.0. The axis of the vertebral centrum is positioned at an angle of 7° to the horizontal line. The anterior and posterior articular surfaces of the vertebral centrum are amphicoelous, low, and almost circular (the width slightly exceeds the height). The neural spine is moderately elongated, the minimum

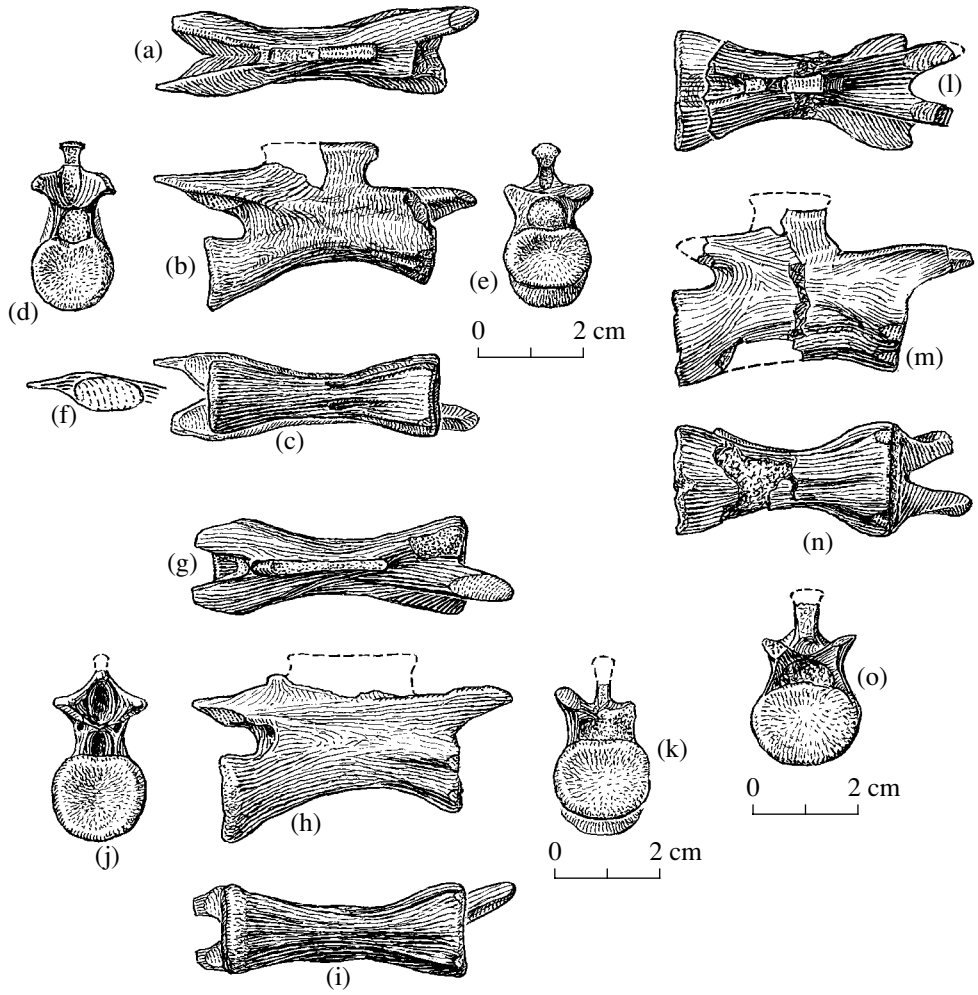

Fig. 2. *Malutinisuchus gratus* Otschev, 1986: (a–f) holotype PIN, no. 4188/125 (SGU, no. 104/401), cervical vertebra; Orenburg Region, Sol'-Iletskii District, Bukobai 5 locality; Middle Triassic, Ladinian Stage, Bukobai Regional Stage, Bukobai Formation: (a) dorsal, (b) right lateral, (c) ventral, (d) cranial, and (e) caudal views, (f) left postzygapophysis, ventrolateral view, complex structure of the facet is shown; (g–k) specimen PIN, no. 4188/126 (SGU, no. 104/405), cervical vertebra; the same age and locality: (g) dorsal, (h) right lateral, (i) ventral, (j) cranial, and (k) caudal views; (l–o) specimen PIN, no. 4466/7, posterior cervical vertebra; Komi Republic, Pechorskii District, Synya-2 locality; Middle Triassic, Ladinian Stage, Bukobai Regional Stage, Nadkrasnokamenskaya Formation: (l) dorsal, (m) right lateral, (n) ventral, and (o) cranial views.

length at the base is approximately 27 mm. Other characters of this vertebra are the same as in the holotype.

A cervical vertebra (specimen PIN, no. 4466/7; Figs. 2l–2o) from the Synya-2 locality probably also belongs to this species. It is a relatively massive (compared to the vertebrae described above) posterior cervical vertebra (probably, the fifth to the seventh). The vertebral centrum is 43 mm long, the anterior articular surface of the vertebral centrum is 17 mm high. The centrum is elongated, the ratio of the length to the anterior height of the cervical vertebral centrum is approximately 2.6. The axis of the centrum is positioned at an angle of 7° to the horizontal line. The anterior and posterior articular surfaces of the vertebral centrum are moderately amphicoelous, relatively low, and almost circular (the width slightly exceeds the height). The neural spine is slightly elongated, the minimum length at the base is approximately 18 mm. The hyposphene was probably present; however, it is impossible to make this statement with confidence because the posterior ends of the postzygapophyses are broken off. The fact that this vertebra and its neural spine are relatively shorter that those of the type series from the southern Fore-Urals is probably attributable to a more caudal position of this vertebra in the vertebral column. Other characters of this vertebra are the same as in the holotype and specimen PIN, no. 4188/126.

The humeri (specimens PIN, nos. 4188/127, 128; Fig. 3) are moderately elongated, with extended epiphyses and a short diaphysis. The humeri are approximately 95 (PIN, no. 4188/127) and 70 mm long (PIN, no. 4188/128). The proximal and distal articular facets

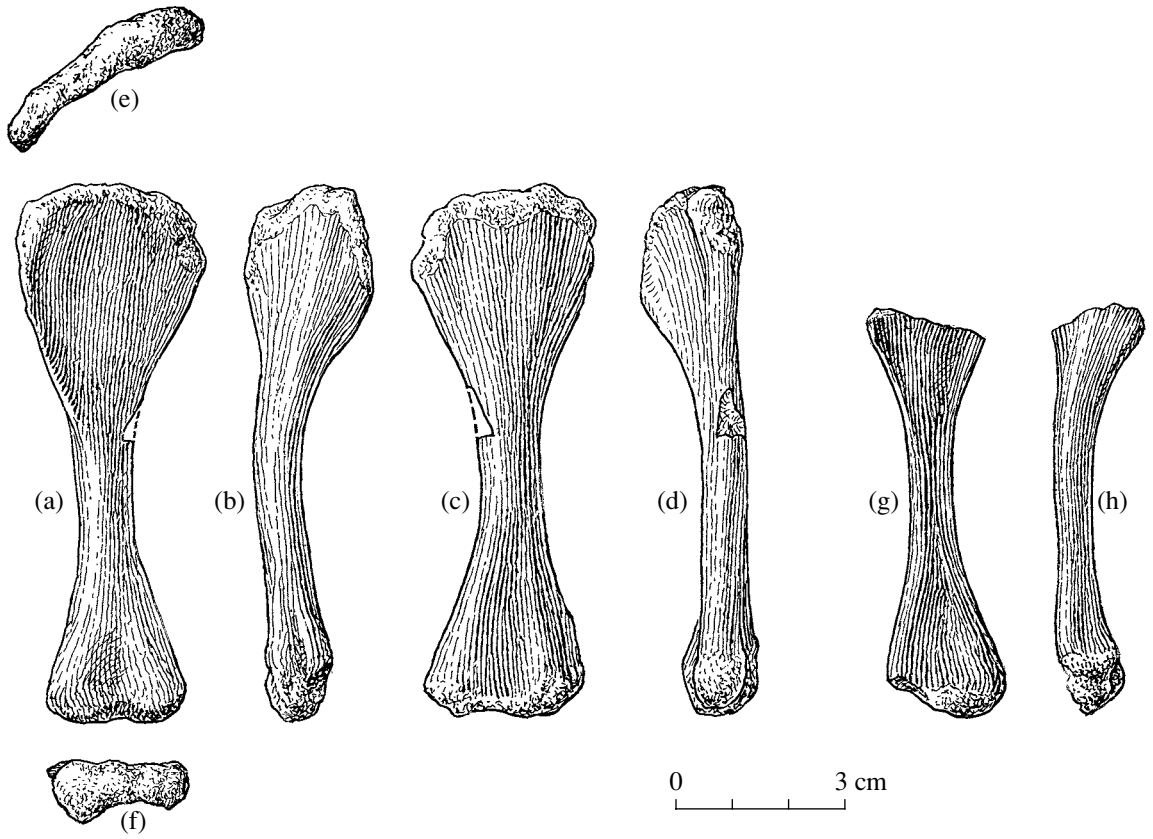

Fig. 3. *Malutinisuchus gratus* Otschev, 1986, right humeri; Orenburg Region, Sol'-Iletskii District, Bukobai 5 locality; Middle Triassic, Ladinian Stage, Bukobai Regional Stage, Bukobai Formation: (a–f) specimen PIN, no. 4188/127 (SGU, nos. 104/851, 852): (a) ventral, (b) lateral, (c) dorsal, (d) medial, (e) proximal, and (f) distal views; (g, h) specimen PIN, no. 4188/128: (g) ventral and (h) lateral views.

(epiphyses) of the humeri are positioned at an angle of approximately 40°–45°. The proximal articular facet is narrow and long (in specimen PIN, no. 4188/127, it is approximately 35 mm long); therefore, the proximal part of the bone seems strongly flattened. The deltopectoral crest projects moderately, is positioned close to the proximal end of the bone, at a distance of approximately 15–17 mm from it (i.e., one-sixth of the bone length). The distal part of the bone has a small supinator process. The lateral side of the bone has a moderately projecting crest that extends proximally from the supinator process for a quarter of the bone length. A short and relatively shallow ectepicondilar groove is located between the supinator process and the lateral condyle. The distal articular facet is relatively narrow, while the lateral condyle is somewhat larger than the medial condyle. Well-pronounced deep depressions are located between the condyles on the dorsal and ventral sides in the proximal part of the bone.

O c c u r r e n c e. Middle Triassic, Ladinian Stage, Bukobai Regional Stage; Orenburg Region, Komi Republic.

M a t e r i a l. In addition to the holotype, specimens from the type locality: PIN, no. 4188/126 (SGU, no. 104/405), cervical vertebra; PIN, no. 4188/129 (SGU, no. 104/497), caudal vertebra; PIN, nos. 4188/127 (SGU, nos. 104/851, 852) and 4188/128, right humeri. In addition, from the Synya-2 locality (Komi Republic, Pechorskii District; Middle Triassic, Ladinian Stage, Bukobai Regional Stage, Nadkrasnokamenskaya Formation), specimen PIN, no. 4466/7, posterior cervical vertebra.

R e m a r k s. In the original description of *Malutinisuchus gratus* (Otschev, 1986), an additional caudal vertebra (SGU, no. 104/3879 = PIN, no. 4188/129) was assigned to the type series. However, the collection includes only one caudal vertebra, SGU, no. 104/497. It is highly probable that both numbers were given to the same specimen.

VRITRAMIMOSAURUS AND ITS SIGNIFICANCE IN THE UNDERSTANDING OF THE PHYLOGENY AND SYSTEMATICS OF PROLACERTILIANS

The set of diagnostic characters of *Vritramimosaurus* shows that it is a typical prolacertid. The cervical vertebral centra of this form are considerably elon-

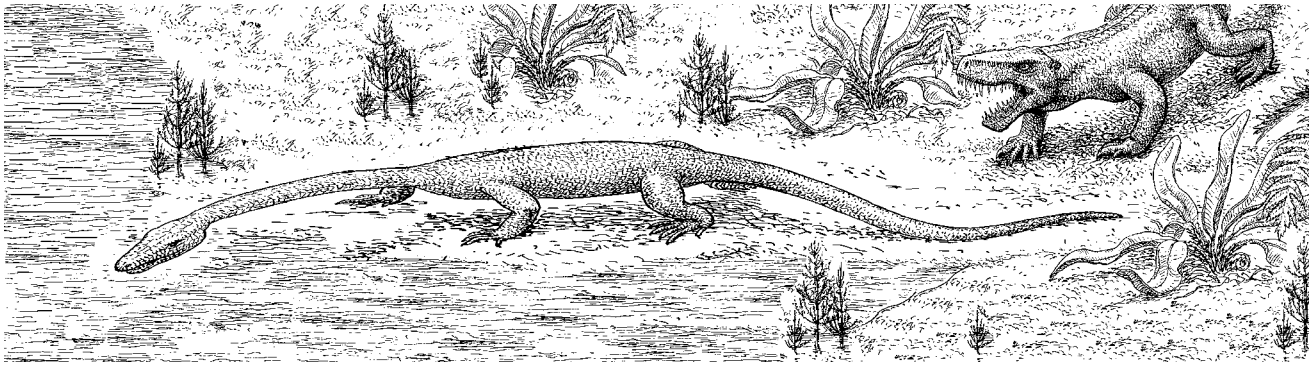

Fig. 4. Reconstruction of the appearance of the prolacertilian *Vritramimosaurus*; in the background, there is the predatory thecodont *Yaikosuchus*; the area near the Rassypnaya locality, Late Olenekian Time, end of the Early Triassic.

gated, as is characteristic of all prolacertilians; the neural spines are in the shape of an inverted trapezoid, which is a very typical character of prolacertids. This shape of the neural spine is probably associated with specific development, morphology, and functioning of the musculature–ligament apparatus of the neck of prolacertids, in particular, the epaxial muscles.

At the same time, *Vritramimosaurus* is distinguished by its relatively large size and high degree of specialization, which seems surprising in the case of an Early Triassic prolacertid. Apparently, only the Middle Triassic (Anisian) *Megacnemus* was similar in size to *Vritramimosaurus*; however, it is difficult to compare these genera, because *Megacnemus* is only represented by a femur. The Late Olenekian *Vritramimosaurus* is most similar to the Middle Triassic (Ladinian) *Malutinisuchus* and is even more specialized. However, it is impossible to regard *Vritramimosaurus* as a form ancestral to *Malutinisuchus*, because it is distinguished by a number of characters that are either more specialized or differ in manifestation (size, the shape of the neural spine of the cervical vertebrae, the presence of the hyposphene, complex structure of the articular facets of the postzygapophyses, and a different shape of the caudal processes of the postzygapophyses). The Early Triassic (Induan–Early Olenekian) prolacertid *Microcnemus* is also similar in morphology to *Vritramimosaurus*, although it is smaller in size and less specialized; they are probably closely related.

The large size and high specialization of *Vritramimosaurus* probably represent an attempt by prolacertids to realize the ecological type of a large terrestrial predator (Fig. 4). Actually, *Vritramimosaurus*, which reached 3 m in length, could probably have consumed not only insects and other invertebrates but also small vertebrates (for example, procolophonids). However, like other prolacertids, it had a long neck, small head, and was rather slender (Fig. 4), so that it was substantially weaker than more massive, bulky predatory thecodonts existing at the end of the Early Triassic, such as the Erythrosuchidae and Rauisuchidae feeding, among other forms, on the largest vertebrates. In the southern Fore-Urals and adjacent areas, the position of a dominant predator at the top of the food chain was occupied by the early erythrosuchid *Garjainia*.

The emergence of large terrestrial predators in different groups of Early Triassic reptiles, including those with inappropriate morphology, such as prolacertilians, is evidence of deficiency in predators in the terrestrial community, which arose as a result of mass extinction (ecological crisis) at the Permian–Triassic boundary. At the very beginning of the Triassic, terrestrial and aquatic continental communities were impoverished and included a small number of amphibians and reptiles, which were small in size and lowly specialized. Archosauromorphs were represented by small lizard-like prolacertilians (0.5–1 m long), while primitive thecodonts included proterosuchids (about 1–1.5 m long) and, from the middle of the Early Triassic, more advanced rauisuchids of the same size class. All of them were relatively small predators (in the broad sense), which probably fed on various prey, ranging from insects to vertebrates. It is worth noting that the terrestrial community was composed almost exclusively of the subdominant block, since phytophagous tetrapods (for example, lystrosaurs) were relatively rare (Sennikov, 1995).

During the Early Triassic, the terrestrial biota gradually restored its diversity; this process was completed only at the end of this epoch. Large specialized vertebrate taxa appeared, and the structure of their communities became almost as complex as before the crisis; the dominant block was restored (Sennikov, 1995). The presence of such a large predator as *Vritramimosaurus* among prolacertids is evidence of complexity and differentiation of vertebrate communities of that time.

At the end of the Early Triassic, the spatial differentiation and diversity of regional vertebrate faunas of eastern Europe also reached its maximum. The Late Olenekian fauna of the southeastern region (southern Fore-Urals and the southeastern peripheral areas of the

Table 1

Taxon	Length of the cervical vertebral centra, mm	Elongation of cervical vertebral centrum	Angle between the centrum and the horizontal line, degrees
Protorosauridae			
Eorasaurus olsoni	20	2.0	17–18
Protorosaurus speneri (after Seeley, 1887; von Meyer, 1856)	24–34	2.6–3.4	7–10
Prolacertidae			
Prolacerta broomi (after Gow, 1975)	19–20	2.7–2.8	5–6
Boreopricea funerea	5–6	2.0–2.2	10–12
Macrocnemus bassanii (after Peyer, 1937)	12–23	2.9–3.2	5–7
Microcnemus efremovi	10–15	2.6–3.4	6–8
Rhombopholis scutulata (after Benton and Walker, 1996)	12	2.6	5
Vritramimosaurus dzerzhinskii, sp. nov.	60	3.0	10
Malutinisuchus gratus	42–46	2.6–3.8	7–9
Malerisaurus robinsonae (after Chatterjee, 1980)	27–32	2.7–3.5	9–10
Malerisaurus langstoni (after Chatterjee, 1986)	29–31	3.1–3.5	12–13
New prolacertid from Donskaya Luka	14–43	3.0–6.5	4–5
Langobardisaurus pandolfii (after Renesto, 1994)	17–22	3.7–6.0	5
Tanystropheidae			
Tanystrachelos ahynis (after Olsen, 1979)	5–6	2.4–2.8	?2–4
"*Tanystropheus*" *antiquus* (after Huene, 1931; Wild, 1980, 1987; Wild and Oosterink, 1984)	24–85	4.8–6.5	2–5
Tanystropheus longobardicus (after Peyer, 1931; Tschanz, 1988)	27–260	6.0–10.0	0–3
Tanystropheus conspicuus (after Wild, 1973)	160–260	7.0–14.0	0–3

Russian Platform, where *Vritramimosaurus* was found) sharply differs from the fauna inhabiting the southern region (Voronezh Anteclise, where an essentially different prolacertid was found) and from the fauna of the same age from the northern regions of European Russia. At the same time, within the southeastern region, *Vritramimosaurus* is similar to *Malutinisuchus* from the Fore-Urals, although the latter genus is dated Middle Triassic.

The finding of *Malutinisuchus* in the northern Fore-Urals substantially enlarges the range of this prolacertilian and indicates (along with the presence of the rauisuchid *Energosuchus*) the presence of faunal contacts in the Ladinian Time. Based on the presence of the same archosauromorph species, the Nadkrasnokamenskaya Formation of the northern Fore-Urals is correlated with the Bukobai Formation of the southern Fore-Urals.

The discovery of *Vritramimosaurus* provides a better understanding of phylogeny and systematics of prolacertilians. The family Prolacertidae is divided into two groups, which should be ranked as subfamilies; the first includes relatively primitive small-sized taxa, while the second is composed of more advanced, large specialized forms. These groups are distinguished by a number of characters, including the length of the cervical vertebral centra, the elongation of the centrum (the ratio of the length to the anterior height of the cervical vertebral centrum), and the angle between the axis of the vertebral centrum and the horizontal line (see table).

Prolacerta, Pricea, Microcnemus, Boreopricea, and *Rhombopholis* belong to relatively primitive small prolacertids, while *Malutinisuchus, Vritramimosaurus, Malerisaurus* and, probably, *Macrocnemus* and *Megacnemus* compose the group of large specialized genera.

The large specialized taxa are characterized by elongated cervical vertebrae, a large angle between the axis of the vertebral centrum and the horizontal line, and relatively high neural spines. These characters indicate that the neck of these animals was long, with a considerable S-shaped curvature and relatively stout, well-developed musculature–ligament apparatus, in particular, strong epaxial muscles; the head was raised rather high, which was advantageous for searching for prey and hunting on land. This was probably a specialization mode of relatively more terrestrial prolacertids.

At the same time, tanystropheids had excessively elongated cervical vertebrae almost lacking neural spines, while the axis of the vertebral centra was close to the horizontal line. On this basis, it can be concluded that the neck of tanystropheids was very long, without S-shaped curvature, with the modified and partially reduced epaxial part of the musculature–ligament apparatus; the neck and head were positioned in the horizontal plane. These morphological features of tanystropheids are commonly considered to be associated with their adaptation to a semiaquatic or even aquatic mode of life (Wild, 1973; Tschanz, 1985).

It is interesting that *Langobardisaurus* (a new undescribed prolacertilian from the Donskaya Luka locality) and *"Tanystropheus" antiquus* are similar in a number of morphological characters and occupy an intermediate position between typical prolacertids and typical tanystropheids. These taxa probably represent a specialization mode of more aquatic prolacertids or transitional forms between prolacertids and tanystropheids.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project no. 01-04-48667), the Board of the President of the Russian Federation for Support of Leading Scientific Schools (project no. NSh-1840.2003.4), and the Program of the Presidium of the Russian Academy of Sciences "The Origin and Evolution of the Biosphere: Program 2."

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