

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/287723381>

Discovery of a Primitive Sauropterygian from the Lower Triassic of the Donskaya Luka (Don Basin) and the Range of Triassic Marine Reptiles in Russia

Article in *Paleontologicheskii Zhurnal* · January 2001

CITATIONS

4

READS

80

1 author:



[Andrey Gerasimovich Sennikov](#)

Russian Academy of Sciences

128 PUBLICATIONS 1,239 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Palynology and stratigraphy of the Middle (Ladinian) and Late Triassic deposits in the Timan-Northern Urals region and the Northern Middle Siberia. [View project](#)

Discovery of a Primitive Sauropterygian from the Lower Triassic of the Donskaya Luka (Don Basin) and the Range of Triassic Marine Reptiles in Russia

A. G. Sennikov

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117868 Russia

Received December 17, 1999

Abstract—A new primitive sauropterygian from the Donskaya Luka locality (Don River, European Russia) is described as a new genus and species of the family Cymatosauridae, *Tanaisosaurus kalandadzei* gen. et sp. nov. This is the first member of this group from the Early Triassic of Russia. The origin and early evolution of sauropterygians are considered. Triassic marine reptiles from Russia are reviewed.

INTRODUCTION

Donskaya Luka, an Early Triassic locality, occupies a special position among Triassic vertebrate localities of European Russia and the Fore-Urals (Pantelev, 1947; Rykov, 1951; Efremov and Vyushkov, 1955; Rykov and Otschev, 1966; Garyainov and Rykov, 1973; Sennikov, 1999). At the same time, it is incompletely characterized with reference to paleontological and geological features. It is located within a small field of the Lower Triassic beds on the southeastern slope of the Voronezh Anticline, on the right slope of the Don River valley. The beds enclosing vertebrates belong to the Lipovskaya Formation, the Gamskii Horizon of the Yarenskii Superhorizon of the Upper Olenekian Substage of the Lower Triassic; i.e., to the upper parts of the Lower Triassic.

The Triassic beds of the Lipovskaya Formation are eroded, overlie Carboniferous marine limestones, and are covered by Middle Jurassic continental sands and clays (Pantelev, 1947; Rykov, 1951; Rykov and Otschev, 1966; Garyainov and Rykov, 1973). The Lipovskaya Formation formed by terrigenous beds was considered to be of either continental (alluvial or lacustrine) (Rykov, 1951) or coastal marine (Pantelev, 1947) genesis. The genesis of these beds is associated with the coastal marine zone, where a large river discharged into a bay or other relatively detached and probably desalinated water body, and where an extensive water flow brought terrigenous material and terrestrial vertebrates. Thus, the latter were buried together with aquatic and coastal marine forms (Rykov and Otschev, 1966). Vertebrates from the Donskaya Luka locality were found in the first (basal), second (clay-silt with isolated sandstone lenses), and, mainly, in the third (sandstone-conglomerate) units of the Lipovskaya Formation (Rykov and Otschev, 1966). These are very fragmented specimens, including predominantly isolated bones of postcranial skeletons, skulls and,

occasionally, cranial fragments consisting of several bones. These bones are usually incomplete, broken into pieces, and rounded; since the main bone-bearing unit consisting of cross-bedded and undulate sand layers, friable sandstones, and conglomerates, the unit was formed under the conditions of intensive water flows that damaged and sorted the vertebrate bones. Therefore, identification and assignment of bones from this location to a certain taxon or even to a certain vertebrate group is extremely difficult.

The following forms were found in the Donskaya Luka locality: labyrinthodonts *Parotosuchus pantelevi* Otschev and *Batrachosuchoides lacer* Shishkin; a procolophonid, *Orenburgia enigmatica* (Tchud. et Vjusch.); *Coelodontognathus ricovi* Otschev and *C. donensis* Otschev, tentatively assigned to the Trilophosauria (Otschev, 1967); *Vitalia grata* Ivakhnenko (Ivakhnenko, 1973, 1979); *Doniceps lipovensis* Otschev et Rikov (Otschev and Rykov, 1968); a prolacertilian from the family Prolacertidae (not yet described), previously determined by Rykov and Otschev (1966) and Garyainov and Rykov (1973) as *Microcnemus* sp.; thecodonts of the family Rauisuchidae, *Tsylmosuchus donensis* Sennikov and *Scythosuchus basileus* Sennikov; and, probably, the erythrosuchid *Garjainia* sp. (Sennikov, 1999). Among the specimens from the Donskaya Luka locality, an articular of a medium-sized dicynodont and a premaxilla of a small dicynodont were recently found (Sennikov, 1999). M.V. Surkov (Saratov State University, SSU) assigned this premaxilla to a kannemeyeroide dicynodont (a new genus and species of the tribe Sinokannemeyeriini). In addition, a number of fragmentary fossils of vertebrates of uncertain taxonomic position were found in the Donskaya Luka locality. In particular, Otschev (1976) mentioned a peculiar tooth and assigned it to an ichthyosaur.

In the collection of the latest joint expedition (1998) of Saratov State University (M.G. Minikh) and the

Paleontological Institute of the Russian Academy of Sciences (PIN) (Novikov and Sennikov), a humerus and quadrates of eosauropterygians were found. Among the specimens collected earlier, a scapula and quadrates were also found. The humerus and the scapula are similar to those of early sauropterygians such as cymatosaurids. In the present study, this form is distinguished as a new genus and species belonging to the family Cymatosauridae. I refer the superfamily Pistosauroidea, including two families (primitive Cymatosauridae and the Pistosauridae, commonly considered to be intermediate between nothosaurs and plesiosaurs), to the suborder Eosauropterygia.

SYSTEMATIC PALEONTOLOGY

Order Sauropterygia

Suborder Eosauropterygia

Superfamily Pistosauroidea Zittel, 1887

Family Cymatosauridae Huene, 1948

Genus *Tanaisosaurus* Sennikov, gen. nov.

E t y m o l o g y. From *Tanais*, antique name of the Don River, and the Greek *saurus* (lizard).

T y p e s p e c i e s. *T. kalandadzei* sp. nov.

D i a g n o s i s. Quadrates extended, narrow in cross section, with square condyles strongly displaced inferiorly. Scapula massive and weakly curved; dorsal blade weakly detached from the bone body, relatively large, flat, wide, extended somewhat, thickened at upper edge, and weakly inclined posteriorly. Ventrocranial edge of scapular body almost straight; anterior part of bone body less massive and forming anteriorly small subtriangular projection. Ventrocranial edge of scapular body clearly isolated from ventrocaudal (glenoid) edge by curvature. Humerus gracil, strongly curved, and flattened dorsoventrally. Deltopectoral crest reduced. Distal part with small supinator process. External and internal epicondyles moderately or weakly developed. Ectepicondilar groove and entepicondilar foramen present. Distal articular surface flattened, located perpendicular to long axis of bone, complex in shape, and bearing well-pronounced facets for radius and ulna (capitellum and trochlea).

C o m p o s i t i o n. Type species.

C o m p a r i s o n. *Tanaisosaurus* is distinguished from other cymatosaurids by longer and narrower quadrates with square condyles strongly displaced inferiorly; by the scapula, the dorsal blade of which is weakly detached from the bone body, relatively large, flat, wide, extended, thickened at the upper edge, and weakly inclined posteriorly; by a more gracile and dorsoventrally flattened humerus possessing a flattened and complex distal articular surface located perpendicular to the long axis of the bone and clearly outlined facets for the radius and ulna. The new genus is distinguished from *Cymatosaurus*, *Chinchenia*, and *Kwangsisaurus* by a more strongly curved humerus; in addition,

it is distinguished from *Cymatosaurus* and *Chinchenia* by a weaker deltopectoral crest and external and internal epicondyles of the humerus. It is distinguished from *Chinchenia* and *Corosaurus* by an almost straight ventrocranial edge of the scapular body that is clearly isolated from the ventrocaudal (glenoid) edge by a curvature and by a less massive anterior part of the bone body forming a small subtriangular projection anteriorly; from *Chinchenia* and *Kwangsisaurus*, by the presence of the entepicondilar foramen; and from *Kwangsisaurus*, by a stronger ectepicondilar groove and a larger supinator process.

Tanaisosaurus kalandadzei Sennikov, sp. nov.

E t y m o l o g y. The species is named in honor of the Russian paleontologist N.N. Kalandadze.

H o l o t y p e. PIN, no. 1043/663, left humerus; Volgograd Region, Ilovnyanskii District, right slope of the valley of the Don River, village of Sirotinskaya, Lipovskaya Balka ravine, Donskaya Luka locality; Lower Triassic, upper part of the Olenekian Stage, Yarenskii Superhorizon, Gamskii Horizon, Lipovskaya Formation.

D e s c r i p t i o n (Fig. 1). The quadrates (Figs. 1a–1e) are extended and narrow in cross section (PIN, nos. 1043/520–522, 661, 662, and 707); the posterior edge bears an asymmetrical and weakly transversely expanded condyle; the anterolateral and anteromedial edges have extended depressions with rough surfaces for sutural articulation with other extended bones, i.e., for the squamosal (or the squamosal and the quadratojugal) and the pterygoid. The bone surface is covered by slender longitudinally undulate sculpturing characteristic of sauropterygians. Specimen PIN, no. 1043/522 has retained a fragmentary bone (probably, the squamosal) entering a depression in the quadrate and forming a sutural articulation with the latter. The lower ending of the presumed squamosal and depressions for this bone in large individuals only approach square condyles and terminate approximately 10 mm from the latter. Available quadrates are similar in shape, and certain differences between them are attributable to individual variation and the degree of bone preservation (deformation). Most bones are of approximately the same size, preserved parts in the most complete specimens are 55–60 mm long; only in PIN no. 1043/707 is the bone substantially smaller, 11 mm long. It is noteworthy that the shape and proportions of the bone are similar in the smallest and the largest specimens.

A quadrate characterized by a free lower part strongly displaced downwards could belong only to a reptile which possessed a deep incisure in the postorbital part of the skull and lacked the lower temporal arch, i.e., to a primitive sauropterygian. At the same time, in most eosauropterygians, the quadrates are substantially shorter and wider, the square condyles are displaced inferiorly to a lesser extent, and a larger part of the quadrate is covered by the squamosal and the quadratojugal. The new genus resembles *Cymatosau-*

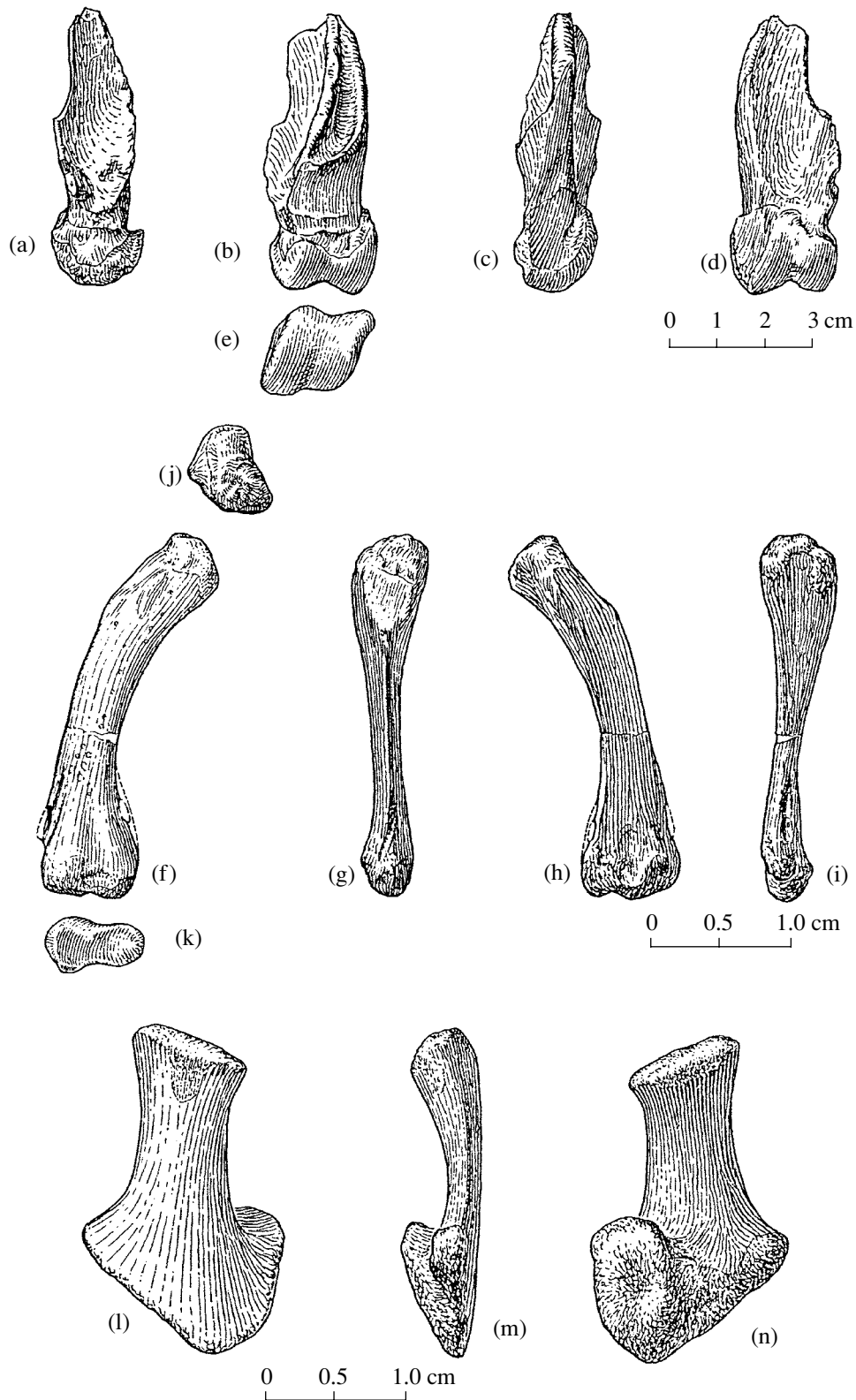


Fig. 1. *Tanaisosaurus kalandadzei* sp. nov.: (a–e) specimen PIN, no. 1043/520, right quadrate: (a) lateral, (b) cranial, (c) medial, (d) caudal, and (e) distal views; (f–k) holotype PIN, no. 1043/663, left humerus: (f) dorsal, (g) lateral, (h) ventral, (i) medial, (j) proximal, and (k) distal views; and (l–n) PIN, no. 1043/705, left scapula: (l) lateral, (m) cranial, and (n) medial views.

rus and *Pistosaurus* in the morphological features of the quadrates.

The left scapula (PIN no. 1043/705, Figs. 11–1n) is massive, weakly curved, and covered by surface sculpturing consisting of a longitudinal hatching or undulating pattern and the numerous small foramina that are characteristic of sauropterygians. The scapula together with the dorsal blade is 24 mm high, and the bone body is 14 mm long. The dorsal blade is relatively large, weakly detached from the bone body, flat, wide, somewhat extended and thickened at the upper edge, and weakly inclined posteriorly; posteriorly, it is isolated from the bone body (glenoid part) by an incisure or depression. The posterior part of the bone body is relatively massive, strongly thickened, projecting posteriorly, and bearing the glenoid articular surface at the ventrocaudal edge. Between the anterior and posterior parts of the bone, the inner side bears an incisure of the coracoid foramen (Rieppel, 1994). The ventrocranial edge of the bone body is only slightly convex and almost straight. The anterior part of the bone body is less massive and forms anteriorly a small subtriangular projection. The ventrocranial edge of the scapular body is isolated from the ventrocaudal (glenoid) edge by a well pronounced curvature. A relatively weak reduction and modification of the dorsal blade of the scapula probably indicate that the latter partially preserved the function of maintenance of the head and body (Carroll and Gaskill, 1985), i.e., *Tanaisosaurus* was adapted to the aquatic (marine) mode of life to a lesser extent than other known eosauroptrygians.

The humerus (holotype PIN, no. 1043/663, Figs. 1f–1k) is gracile, strongly curved, and flattened dorsoventrally; the proximal and distal endings are weakly extended. The bone is approximately 27 mm long. The bone surface is covered by thin longitudinal hatching or an undulating pattern and numerous small foramina, sculpture characteristic of sauropterygians. The deltopectoral crest is reduced. The bone surface has rugose areas for muscle attachment. On the dorsal side of the proximal part (above the curvature), there is a projecting ovoid tubercle, probably for the deltoideus muscle (Watson, 1924; Storrs, 1991). At the curvature of the bone, the lateral side bears a tubercle, probably for the attachment of the pectoral muscle (Watson, 1924; Storrs, 1991). On the ventral side of the proximal part (above the curvature), there is a rugose site, probably for the coracobranchialis brevis muscle (Storrs, 1991). The epiphyses are well ossified. The proximal articular surface is weakly convex and rounded. A semicircular fossa is located between the condyles on the dorsal side in the proximal part of the bone. The external and internal epicondyles are moderately or weakly developed (unfortunately, as the bone was dislodged from enclosing rock, both epicondyles were damaged). The distal part bears a small supinator process, the terminal piece of which (of approximately 1 mm long) is broken off. A sharp and strongly projecting crest extends proximally along the lateral side of

the bone from the supinator process to the point of the bone curvature (the attachment area of the pectoral muscle). A deep ectepicondilar groove extends almost vertically (only slightly obliquely) between the supinator process and the ectocondyle. The ending of the internal epicondyle is broken off (probably, for 2–3 mm); nevertheless, the edges of a large oval entepicondilar foramen are clearly visible; the latter passed somewhat obliquely and was probably closed. The distal articular surface is flattened rather than rounded convex, positioned perpendicular to the long axis of the bone, and complex in shape; it bears distinct facets for the radius and ulna (capitellum and trochlea). The surface and the facets considered are similar in shape to those of such reptiles as *Claudiosaurus* characterized by a relatively terrestrial mode of life. This indicates a considerable role of flexional movements of a wide range and rotation in the ulnar joint and, consequently, a more intensive use of the forelimbs as the main support on land, with a greater load falling on the articulations than in other known eosauroptrygians. The shape and position of the facets give evidence for a relatively weak modification of the forearm from the pattern of terrestrial supporting limbs to the fin pattern in comparison with those of other eosauroptrygians; the forearm is expanded and flattened to a lesser extent (the bone widths and the distances between the bones are relatively small); this indicates the relatively poor adaptation of *Tanaisosaurus* for an aquatic (marine) mode of life.

Specimens PIN, nos. 1043/706 and 750 are possibly two fragments of the left clavicle of a large *Tanaisosaurus*. They are covered by surface sculpture consisting of thin longitudinal hatching or the undulating pattern characteristic of sauropterygians. Specimen PIN no. 1043/750 is probably an extended anteromedial fragment; the ending is narrow and pointed and bears two extended depressions for sutural articulation with the other bones. The dorsal side has a short depression, probably for articulation with the medial process of the right clavicle and a high and sharp crest extending from the edge of the depression. On the ventral side, there is a long depression, probably for articulation with the lateral process of a narrow interclavicle. Specimen PIN no. 1043/706 is probably a laterocaudal fragment; the central part of the bone is massive, the posterolateral edge is narrow and expanded as a hood or semicone, and the dorsal side bears a sharp crest becoming lower towards the bone edge.

Variability. The great size variation of certain bones of *Tanaisosaurus* stands out. Thus, large measurements of most quadrates and clavicle fragments are evidence of large sizes of the individuals, the skulls were approximately 30–40 cm long and the body was 2–3 m long. The individuals possessing the quadrate PIN no. 1043/707, the humerus, and the scapula were approximately 0.5 m long. At the same time, ossified epiphyses and relatively well pronounced sites for the attachment of muscles indicate that the humerus most probably belonged to an adult or almost mature animal

rather than to a juvenile. This is evidence for considerable size variation in *Tanaisosaurus*, the largest adults being 4–6 times the size of the smallest. At the same time, the massiveness, shape, and proportions of bones are almost constant, i.e., mature or nearly mature *Tanaisosaurus* could continue growing and become several times larger without changes of body shape and proportions. This is characteristic of aquatic vertebrates, the bodies of which undergo less rigid constructive requirements in the course of growth and increase in size and weight than in terrestrial tetrapods, since they are supported by water. In general, eosauropterygians are characterized by a wide range of age variation in size (Sander, 1989; Storrs, 1991).

Material. In addition to the holotype, PIN nos. 1043/520–522, 661, 662, and 707, quadrates; PIN no. 1043/705, left scapula; and, probably, PIN no. 1043/706 and 750, fragmentary left clavicles from the same locality.

THE ORIGIN AND EARLY EVOLUTION OF SAUROPTERYGIANS

The discovery of a new eosauropterygian in the Donskaya Luka locality necessitates a consideration of its taxonomic position and the problem of sauropterygian origin. These marine reptiles characterized by the upper temporal fenestra, the temporal arch, and an incisure in the postorbital part of the skull were previously referred to as the subclass Synaptosauria. The ancestors of sauropterygians were proposed to belong to the Areoscelidia, small terrestrial lizardlike synaptosaurians (Saint-Seine, 1955; Tatarinov, 1964a; etc.); or to early diapsids, such as eosuchians (Kuhn-Schnyder, 1963, 1967, etc.); or they were considered to be of uncertain origin (Watson, 1957). The hypotheses of the origin of sauropterygians from theromorph reptiles (Huene, 1944, 1956) or directly from labyrinthodonts or even crossopterygians (Kuhn-Schnyder, 1961) are not generally accepted today.

Currently, sauropterygians are referred to as diapsids in the broad sense (Sues, 1987; Rieppel, 1989; Storrs, 1991; Carroll, 1988; Caldwell, 1997). *Claudiosaurus* from the Upper Permian of Madagascar is commonly considered to be a probable ancestor or a form closely related to the ancestors of sauropterygians (Carroll, 1981). When considering *Claudiosaurus* as the ancestor of sauropterygians, researchers regard it as a transitional form between typical early diapsids (eosuchians), such as the Younginidae, to typical sauropterygians (Carroll, 1981, 1988; Schmidt, 1987; Storrs, 1991; etc.). However, I believe that preference should be given to the hypothesis of sauropterygian origin from the most primitive early diapsids, such as areoscelidians or petrolacosaurus closely related to the latter (Rieppel, 1989).

Sauroptrygians are characterized by a broad, flattened, short body; long neck; relatively weak tail; and

powerful fins. Therefore, the propulsive function was performed mainly by the limbs, in particular, by the forelimbs (Robinson, 1975; Carroll and Gaskill, 1985; Storrs, 1991), whereas undulating flexure of the trunk in the course of swimming (and, hence, lateral flexion of the vertebral column) were absent or strongly restricted in these reptiles. The exception is probably provided by pachypleurosaurs possessing an extended body and, consequently, undulating movements may have played a certain role in the aquatic locomotion of these forms (Carroll and Gaskill, 1985; Sues, 1987). A number of paleontologists believe that sauropterygians were probably adapted for a swimming pattern resembling underwater flight and characterized by vertical waves of fins similar to the movements of marine turtles and penguins (Robinson, 1975). Other researchers propose that sauropterygians were probably adapted for rowing (oar-propelled) swimming characterized by fore-and-aft movements of finlike limbs (similar to those of many seals and sirenians) (Watson, 1924). Sauroptrygians most probably used both swimming patterns, as do sea lions (Godfrey, 1984; Storrs, 1991). This type of underwater locomotion of sauropterygians explains such morphological peculiarities as the shortened, expanded, flattened, consolidated, and essentially immobilized trunk and skeleton; the development of stout abdominal ribs; an increase in the number of the sacral vertebrae; modified limbs and limb girdles; flattened tail base; and elongated neck.

Two suborders of the order Sauroptrygia relatively primitive eosauroptrygians (or nothosaurs) and a more specialized group, plesiosaurs (Rieppel, 1998), are clearly distinguished by the extent to which they are adapted to aquatic environment. To date, eosauroptrygians are divided into the weakly specialized pistosauroids (probable ancestors of plesiosaurs), large specialized nothosauroids, and small specialized pachypleurosauroids distinguished by skeletal pachyostosis (Rieppel, 1998). The earliest sauropterygians from the Lower Triassic are presented by fragmentary fossils which are difficult to determine (Huene, 1951). In the case of more completely preserved forms referred to as the Early Triassic, such as *Corosaurus* from North America (Storrs, 1991) and *Kwangsisaurus* from China (Rieppel, 1999), dating is questionable or ambiguous. Therefore, the form from the Donskaya Luka locality is probably the earliest known Early Triassic eosauroptrygian.

Eosauroptrygians are characterized by strongly modified scapula and humerus developed as a result of adaptation to an aquatic (marine) mode of life. The dorsal blade of the scapula gradually became detached from the bone body, decreased in relative size, and acquired a posterior inclination. Such a reduction of the dorsal scapular blade is associated with the loss of the function as a supporter of the head and anterior part of the body because of the aquatic mode of life (Carroll and Gaskill, 1985). The humerus became flattened and strongly curved, the deltopectoral crest was strongly

reduced, the epiphyses were poorly ossified, and the articular surfaces of the latter became rounded convex and lacking the detached facets for the ulna and the radius on the distal surface. The latter was associated with the fact that the change of forelimbs into fins weakened and restricted the supporting function of limbs in the motion on land; as a result, the load falling between the bones was reduced, the flexional–extensional and rotary movements in the ulnar articulation were restricted, the forearm expanded, and the arrangement and movements of the antebrachial bones with reference to the humerus essentially changed (Storrs, 1991). In actual fact, the ulnar articulation changed in function and was substantially immobilized; as a result, only a flexible zone within the fin was inherited from a well developed and complex articulation of a supporting limb of terrestrial vertebrates. The humerus, forearm, and manus changed into an extended fin in which the limb parts were weakly distinguished and individual digits were virtually indiscernible. Regarding the extent of specialization, isolation of parts (functional units), and the role in terrestrial locomotion, the eosauroptrygian forelimbs are comparable to those of seals; in the extent to which the ulnar joint is modified, eosauroptrygians are comparable to whales. The eosauroptrygian hindlimbs lagged behind the forelimbs in the adaptation to an aquatic mode of life.

The limbs of plesiosaurs are shortened, modified in shape, and increased in massiveness by the changes of the humerus, femur, antebrachial, and lower leg bones; in addition, hyperphalangism is developed. The humerus became straight, and the forearm and manus also changed substantially. Regarding the degree of specialization and detachment of the units, the plesiosaur forelimb is a strongly specialized fin functioning as an integrated element comparable to those of whales and dolphins. Plesiosaurs are also characterized by a lowered disproportion between the forelimbs and the hindlimbs; the posterior fins became more similar to the anterior fins in measurements, shape, and, probably, in the role in aquatic locomotion.

It should be noted that the humeri of eosauroptrygians are initially gracile and usually preserve this state; only secondarily and in a small number of forms (certain pachypleurosaurs and lariosaurs) are they massive; in plesiosaurs, the humeri are secondarily extremely massive. This corroborates the hypothesis for the origin of sauropterygians from small gracile early diapsids in the broad sense (Carroll, 1981, 1988; Rieppel, 1989; Storrs, 1991). The humeri of certain primitive eosauroptrygians show individual structural characteristics undoubtedly inherited from their terrestrial ancestors and disappearing in advanced members of the group. Detached facets for the ulna and radius on the distal articular surface of the humerus were recorded in certain pachypleurosaurs (Rieppel, 1989) and cymatosaurids, such as *Cymatosaurus* (Rieppel, 1994). The nothosaurid *Sanchiaosaurus* (Rieppel, 1999), cymatosaurid *Chinchenia* from China (Rieppel, 1999),

and the eosauroptrygian humerus described by Huene (1944) possess a relatively well developed deltopectoral crest, although it is displaced distally.

In general, the scapula and the humerus of *Tanaisosaurus* are typical of eosauroptrygians. These bones have much in common with those of the most primitive members of the group. *Tanaisosaurus* possesses a well developed ectepicondilar groove, an entepicondilar foramen, and isolated facets for the ulna and radius on the distal articular surface of the humerus. At the same time, a number of characters observed in *Tanaisosaurus* have not been registered even in primitive eosauroptrygians and show the similarity of the new form to early terrestrial diapsids and presumable ancestor of sauropterygians, *Claudiosaurus*, or demonstrate an intermediate position of *Tanaisosaurus* in the morphological series between the above groups and typical eosauroptrygians. These characters include a relatively large size (weak reduction) of the dorsal scapular blade, a weak isolation of the blade from the bone body, a greater width, and a weak posterior inclination. It is noteworthy that the distal articular surface of the humerus is flattened rather than rounded convex, located perpendicular to the long axis of the bone, and complex in shape, i.e., includes clearly isolated facets for the radius and ulna (capitellum and trochlea). These characters provide evidence of a relatively more terrestrial mode of life in *Tanaisosaurus*, i.e., a lesser degree of specialization to an aquatic (marine) mode of life in comparison with other eosauroptrygians. Thus, *Tanaisosaurus* is not only one of the earliest eosauroptrygians but also one of the most primitive forms of this group known.

As mentioned above, eosauroptrygians were amphibious predators probably resembling seals in their mode of life. They probably inhabited sea shoals near sea coasts, occasionally visiting the coast, and fed mainly on fish. Eosauroptrygians flourished in western and central Europe in the Middle Triassic. They were widespread in the sea basin of so-called shell limestone (Germany, the Netherlands, and Poland), where warm and shallow epicontinental seas were rich in life and probably provided perfect conditions for these reptiles that showed intense adaptive radiation at this time. The overwhelming majority of specialized pachypleurosaurs, nothosaurs, and placodontids were found in these sites and in the deposits along the northern (Alpine) coast of the Tethys in Switzerland, Austria, France, Italy, and Spain (Storrs, 1991). In other continents, eosauroptrygian are relatively rare (the USA, Tunis, Israel, Saudi Arabia, China, and Japan), and their occurrence is also associated with the coastal zone of the Tethys (Storrs, 1991); however, in the Triassic coastal beds of southern Russia, *Tanaisosaurus* is the first find of this group. Even taking into account a relatively low adaptation of this form to an aquatic (marine) mode of life (in comparison with typical members of the group), the presence of *Tanaisosaurus* is an additional argument for the coastal marine genesis of the

Donskaya Luka locality associated with the northern coast of the Tethys, namely, with the western coast of the sea basin in the Caspian Depression. The finding of a new cymatosaurid in the south Eastern of Europe enables one to trace the distribution of these primitive eosauroptrygians along the sea coasts and shoals from western and central Europe through eastern Europe to China. Being the most primitive and among the least specialized eosauroptrygians, cymatosaurids had the widest range, including North America; western, central, and eastern Europe; and China.

TRIASSIC MARINE REPTILES OF RUSSIA

Marine reptiles were found in Russia in the Triassic coastal marine and shoal deposits. The finds of Triassic ichthyosaurs are usually fragmentary and occur mainly in Asiatic Russia.

(1) The above mentioned tooth from the Lower Triassic of Donskaya Luka is probably a tooth of an ichthyosaur (Otschev, 1976). However, this peculiar tooth could belong to a trematosauroid labyrinthodont. Unfortunately, to date, the specimen has been lost, and the assignment to ichthyosaurs cannot be tested.

(2) Two vertebrae of ichthyosaurs from the Triassic at the mouth of the Olenek River, Tumul Cape, were collected by S.G. Parkhomenko in 1921 (Nesov *et al.*, 1988).

(3) Ichthyosaurs were found in the Lower Triassic of the Primorie Region, Russian Island, Zhitkov's Cape (Shishkin and Lazovskii, 1979).

(4) Specimens tentatively identified as ichthyosaur vertebrae were found in the Mangyshlak Peninsula, Dollapa locality; Lower Triassic, Upper Olenekian Substage (collected by A.A. Shevyrev, 1960, housed at PIN). However, it is not ruled out that these vertebrae belong to dicynodonts. Accurate taxonomic identification of these specimens necessitates the preparation and thorough examination of the material.

(5) Ichthyosaurian bones were found in the interfluvium of the upper reaches of the Omolon and Bolshaya Germana rivers (southwestern part of the Omolon Mountains); Induan Stage, Lower Triassic (Polubotko and Otschev, 1972).

(6) Various ichthyosaurs, including *Pessopteryx niseri*, *P. arcticus*, *P. pinquis*, *Svalbardosaurus crassidens*, *Isfjordosaurus minor*, and *Grippia longirostris* from the family Omphalosauridae; *Pessosaurus polaris* and *Cymbospondylus* sp. from the family Shastasauridae; and *Phalarodon nordenskioeldii* from the family Mixosauridae were found in the upper part of the Lower Triassic and in the Middle Triassic of Spitsbergen (Maisch and Matzke, 1997; Motani, 1999; etc.). However, the taxonomic composition and assignment of these forms are currently under study. The fauna from Spitsbergen is the richest and most diverse fauna of primitive ichthyosaurs of the world. This was probably the center of origin and subsequent expansion of the group.

(7) Ichthyosaurian bones were found at the Russkaya River (tributary of the Omolon River) in the Omolon Mountains; Anisian Stage, Middle Triassic (Polubotko and Otschev, 1972).

(8) Indeterminable ichthyosaurian bones were found at the upper reaches of the Gizhiga River, the basin of the Sea of Okhotsk; Ladinian Stage, Middle Triassic (Polubotko and Otschev, 1972).

(9) An incomplete postcranial skeleton of a large ichthyosaur was found by Shishkin and Lozovskii (1979) in the Primorie Region, western coast of the Amur Gulf to the south of the Ugol'nyi Cape, *Daonella* slates; Ladinian Stage, Middle Triassic; not yet described, housed at PIN.

(10) Two vertebrae of *Shastasaurus nordensis* Otschev were found at the Dzhugadzhak River (tributary of the Omolon River); Ladinian Stage, Middle Triassic. A series of ribs and vertebrae of ichthyosaurs were found in the Carnian beds of the Upper Triassic of the same region (Polubotko and Otschev, 1972; Nesov *et al.*, 1988).

(11) An intervertebral cast of an ichthyosaur resembling *Shastasaurus careyi* was found in the upper reaches of the Khivach River (tributary of the Gizhiga River), the basin of the Sea of Okhotsk; Carnian Stage, Upper Triassic (Otschev and Polubotko, 1964; Nesov *et al.*, 1988).

(12) Ichthyosaurian bones were found at the Malaya Turomcha River (tributary of the Gizhiga River), the basin of the Sea of Okhotsk; Carnian Stage, Upper Triassic (Otschev and Polubotko, 1964; Polubotko and Otschev, 1972).

(13) A caudal vertebra of *Cymbospondylus*(?) sp. was found at the Kedon River (tributary of the Omolon River), near the mouth of the Omkuchan River; Carnian Stage, Upper Triassic (Polubotko and Otschev, 1972; Nesov *et al.*, 1988); ichthyosaurian ribs were found in the Rhaetian beds of the Upper Triassic of the same region (Polubotko and Otschev, 1972).

(14) A fragmentary ilium probably belonging to *Shastasaurus* was found in the upper reaches of the Burgagchan River (right tributary of the Korkodon River); lower part of the Norian Stage, Upper Triassic (Otschev and Polubotko, 1964; Nesov *et al.*, 1988).

(15) A vertebra referred to as *Shastasaurus sieversi* Riabinin, 1946 was found in the basin of the Igandzha River (right tributary of the Arman River), Magadan Region; Upper Triassic, Norian Stage (Riabinin, 1946; Polubotko and Otschev, 1972). Tatarinov (1964b) assigned this vertebra to *Mixosaurus* sp.

(16) Vertebrae and ribs of *Shastasaurus*(?) sp. were found 23 km from the mouth of the Russkaya River (tributary of the Omolon River), Omolon Mountains; upper part of the Norian or the Rhaetian, Upper Triassic (Otschev and Polubotko, 1964).

Triassic sauropterygians are represented in Russia by the superfamily Pistosauroidea.

(1) The discovery of the cymatosaurid *Tanaisosaurus kalandadzei* sp. nov. in the Donskaya Luka locality shows the presence of primitive sauropterygians in the upper part of the Lower Triassic of Russia (see above).

(2) The center of a large thoracic vertebra of *Pistosaurus*(?) sp., specimen SSU (Saratov State University), no. 104a/15, was found at the Taas-Krest River, the basin of the Lena River; Ladinian Stage, Middle Triassic (Lazurkin and Otschev, 1968). The vertebra is platycoelous and covered by peculiar thin longitudinal hatching (undulate surface sculpturing), the center is pierced by the foramina subcentralia. The neural arch is isolated from the vertebral center by a well pronounced suture. At the base of the neural arch, there is a partially preserved facet (synapophysis) located in the middle of the vertebral center.

(3) The center of a large sacral vertebra of *Pistosaurus* (?) sp., specimen PIN, no. 4466/14, was collected by Novikov in 1990 in the Synya-2 locality (point 4) along the Bolshaya Synya River, Pechora District, Komi Republic; coastal and lagoonal beds of the Bukobay Horizon, Ladinian Stage, Middle Triassic (Novikov, 1994; Ivakhnenko *et al.*, 1997). The vertebra is platycoelous, covered by peculiar slender longitudinal hatching (undulate surface sculpturing), and pierced by the foramina at the lateral sides of the center; the bases of thick sacral ribs located in the anterior part of the vertebral center are broken off.

(4) A large fragmentary posterior cervical vertebra resembling those of *Pistosaurus* (stored at PIN) was collected by G.N. Sadovnikov and E.F. Orlova (Sadovnikov, personal communication) below the mouth of the Ostantsovskaya River on the right bank of the Chernokhrebetnaya River, eastern Taimyr, Taimyr Autonomous Area, Krasnoyarsk Region; the bottom of the middle strata of the Ostantsovskaya Formation (or more specifically, not lower than this level, since the specimen was found in the talus), *Olenekites piniplicatus* Zone, Upper Substage of the Olenekian Stage, Lower Triassic (coastal marine strata). The vertebra is platycoelous and covered by peculiar thin longitudinal hatching (undulate surface sculpturing). The neural arch is isolated from the vertebral center by a weak suture. At the base of the neural arch in the posterior part of the vertebral center, there is an oval and almost vertically extending facet (parapophysis); a crest deviating from the upper edge of the latter probably connected the facet to the diapophysis located somewhat above on the neural arch. The vertebra is very similar in measurements and morphology to the vertebra from the Taas-Krest River (see above); however, poor preservation of the specimen and the great geological age (the end of the Early Triassic or even earlier) cast some doubt on the assignment of this vertebra to *Pistosaurus*.

ACKNOWLEDGMENTS

The study was supported by the Russian Foundation for Basic Research, project no. 00-15-97754, and by the Research Project of Young Scientists of the Russian Academy of Sciences on Basic and Applied Research (Biological Department), "Terrestrial Vertebrates from the Permian-Triassic Boundary Deposits of European Russia."

REFERENCES

- Caldwell, M.W., Modified Perichondral Ossification and the Evolution of Paddle-Like Limbs in Ichthyosaurs and Plesiosaurs, *J. Vertebr. Paleontol.*, 1997, vol. 17, no. 3, pp. 534–547.
- Carroll, R.L., Plesiosaur Ancestors from the Upper Permian of Madagascar, *Phil. Trans. R. Soc. London*, 1981, vol. 293B, no. 1066, pp. 315–383.
- Carroll, R.L., *Vertebrate Paleontology and Evolution*, New York: W.H. Freeman and Co., 1988, vol. 2.
- Carroll, R.L. and Gaskill, P., The Nothosaur *Pachypleurosaurus* and the Origin of Plesiosaurs, *Phil. Trans. R. Soc. London*, 1985, vol. 309B, no. 1139, pp. 315–383.
- Efremov, I.A. and Vyushkov, B.P., Catalogue of Localities of Permian and Triassic Terrestrial Vertebrates in the Territory of the USSR, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1955, vol. 46, pp. 1–186.
- Garyainov, V.A. and Rykov, S.P., The Southeastern Slope of the Voronezh Anticline, Obshchii Syrt and Fore-Urals near Orenburg, in *Stratigrafiya SSSR. Triasovaya sistema* (Stratigraphy of the USSR: Triassic System), Kiparisova, L.D. *et al.*, Eds., Moscow: Nedra, 1973, pp. 89–111.
- Godfrey, S.J., Plesiosaur Subaqueous Locomotion: A Reappraisal, *Neues Jahrb. Geol. Paläontol. Monatsh.*, 1984, vol. 11, pp. 661–672.
- Huene, F. von, Ein beachtenswerter Humerus aus unterstem Muschelkalk und seine Bedeutung, *Neues Jahrb. Miner. Geol. Paläontol., Abt. B*, 1944, vols. 7/9, pp. 223–227.
- Huene, F. von, Der älteste Sauropterygier-Rest, *Neues Jahrb. Geol. Paläontol. Monatsh.*, 1951, vol. 3, pp. 86–87.
- Huene, F. von, *Paläontologie und Phylogenie der niederen Tetrapoden*, Jena: VEB G. Fischer Verlag, 1956.
- Ivakhnenko, M.F., New Cotylosaurs from the Fore-Urals, *Paleontol. Zh.*, 1973, no. 2, pp. 131–134.
- Ivakhnenko, M.F., Permian and Triassic Procolophonidae from the Russian Platform, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1979, vol. 164, pp. 1–80.
- Ivakhnenko, M.F., Golubev, V.K., Gubin, Yu.M., *et al.*, Permian and Triassic Tetrapods from Eastern Europe, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1997, vol. 268, pp. 1–216.
- Kuhn-Schnyder, E., Der Schädel von *Simosaurus*, *Paläontol. Z.*, 1961, vol. 35, no. 3/4, pp. 95–113.
- Kuhn-Schnyder, E., Wege der Reptiliensystematik, *Paläontol. Z.*, 1963, vol. 37, no. 1/2, pp. 61–87.
- Kuhn-Schnyder, E., Das Problem der Euriapsida, *Colloq. Int. C.N.R.S.*, 1967, vol. 163, pp. 335–348.
- Lazurkin, D.V. and Otschev, V.G., The First Finding of Sauropterygians in the Triassic of the USSR, *Paleontol. Zh.*, 1968, no. 2, pp. 141–142.

- Maisch, M.W. and Matzke, A.T., *Mikadocephalus gracilirostris* n. gen., n. sp., a New Ichthyosaur from the Grenzbitumenzone (Anisian–Ladinian) of Monte San Giorgio (Switzerland), *Paläontol. Z.*, 1997, vol. 71, no. 3/4, pp. 267–289.
- Motani, M., Phylogeny of the Ichthyopterygia, *J. Vertebr. Paleontol.*, 1999, vol. 19, no. 3, pp. 473–496.
- Nesov, L.A., Ivanov, A.N., and Khozatskii, L.I., On the Finds of Ichthyosaurian Remains in the USSR and the Problem of Faunal Replacements in the Middle of the Cretaceous, *Vestn. Leningr. Gos. Univ., Ser. 7* (Leningrad), 1988, vol. 1, no. 7, pp. 15–25.
- Novikov, I.V., Biostratigraphy of the Continental Triassic of the Timan–North Ural Region Based on the Tetrapod Fauna, *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 1994, vol. 261, pp. 1–140.
- Otschev, V.G., A New Genus of Procolophonids from the Triassic of the Donskaya Luka Locality, *Izv. Vyssh. Ucheb. Zaved. Geol. Razved.*, 1967, no. 2, pp. 15–20.
- Otschev, V.G., An Unusual Tooth from the Lower Triassic of the Donskaya Luka Locality, *Izv. Vyssh. Ucheb. Zaved. Geol. Razved.*, 1976, no. 8, pp. 176–177.
- Otschev, V.G. and Polubotko, I.V., New Finds of Ichthyosaurs in the Northeast of the USSR, *Izv. Vyssh. Ucheb. Zaved. Geol. Razved.*, 1964, no. 7, pp. 50–55.
- Otschev, V.G. and Rykov, S.P., A New Genus of Small Reptiles from the Triassic of the Donskaya Luka Locality, *Paleontol. Zh.*, 1968, no. 1, pp. 140–141.
- Panteleev, F.P., On the Discovery of Lower Triassic Labyrinthodonts in the Donskaya Luka Locality, *Dokl. Akad. Nauk SSSR, Nov. Ser.* (Moscow), 1947, vol. 58, no. 9, pp. 2029–2032.
- Polubotko, I.V. and Otschev, V.G., New Finds of Ichthyosaurs in the Triassic of the Northeast of the USSR, *Izv. Vyssh. Ucheb. Zaved. Geol. Razved.*, 1972, no. 3, pp. 36–42.
- Rieppel, O., A New Pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland, *Phil. Trans. R. Soc. London*, 1989, vol. 323B, no. 1212, pp. 1–73.
- Rieppel, O., Osteology of *Simosaurus gaillardoti* and the Relationships of Steam-Group Sauropterygia, *Fieldiana (Geol.)*, N. S., 1994, no. 28, pp. 1–85.
- Rieppel, O., *Corosaurus alcovensis* Case and the Phylogenetic Interrelationships of Triassic Steam-Group Sauropterygia, *Zool. J. Linn. Soc.*, 1998, vol. 124, no. 1, pp. 1–41.
- Rieppel, O., The Sauropterygian Genera *Chinchenia*, *Kwangsisaurus* and *Sanchiaosaurus* from the Lower and Middle Triassic of China, *J. Vertebr. Paleontol.*, 1999, vol. 19, no. 2, pp. 321–337.
- Robinson, J.A., The Locomotion of Plesiosaurs, *Neues Jahrb. Geol. Paläontol. Abh.*, 1975, vol. 149, no. 3, pp. 286–332.
- Ryabinin, A.N., An Ichthyosaurian Vertebra from the Upper Triassic of the Kolyma Region, *Priroda* (Moscow), 1946, no. 9, pp. 57–58.
- Rykov, S.P., On the Question of the Stratigraphy of the Mesozoic Deposits of the Northern Part of Donskaya Luka, *Uch. Zap. Saratov Gos. Univ., Vyp. Geol.* (Saratov), 1951, vol. 28, pp. 158–164.
- Rykov, S.P. and Otschev, V.G., On the Localities of Triassic Vertebrates in Donskaya Luka, *Vopr. Geol. Yuzhn. Urala Povolzh.* (Saratov), 1966, vol. 3, part 1, pp. 58–62.
- Saint-Seine, P. de, Sauropterygia, in *Traite de paleontologie. Amphibians, reptiles, oiseaux*, Piveteau, J., Ed., Paris: Masson, 1955, vol. 5, pp. 420–458.
- Sander, P.M., The Pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the Description of New Species, *Phil. Trans. R. Soc. London*, 1989, vol. 325B, no. 1230, pp. 561–666.
- Schmidt, S., Phylogenie der Sauropterygier (Diapsida; Trias–Kreide), *Neues Jahrb. Geol. Paläontol. Abh.*, 1987, vol. 173, no. 3, pp. 339–375.
- Sennikov, A.G., New Data on the Rauisuchidae from Eastern Europe, *Paleontol. Zh.*, 1990, no. 3, pp. 3–16.
- Sennikov, A.G., Evolution of Postcranial Skeleton of Archosaurs in Connection with New Finds of the Early Triassic Rauisuchidae in Russia, *Paleontol. Zh.*, 1999, no. 6, pp. 44–56.
- Shishkin, M.A. and Lozovskii, V.R., A Labyrinthodont from the Triassic of the Southern Part of the Primorie Region, *Dokl. Akad. Nauk SSSR* (Moscow), 1979, vol. 246, no. 1, pp. 201–205.
- Storrs, G.W., Anatomy and Relationships of *Corosaurus alcovensis* (Diapsida, Sauropterygia) and the Triassic Alcova Limestones of Wyoming, *Bull. Peabody Mus. Natur. Hist.*, 1991, vol. 44, pp. 1–151.
- Sues, H.-D., Postcranial Skeleton of *Pistosaurus* and Interrelationships of the Sauropterygia, *Zool. J. Linn. Soc.*, 1987, vol. 90, no. 2, pp. 109–131.
- Tatarinov, L.P., The Subclass Synaptosauria, in *Osnovy paleontologii. Zemnovodnye, presmykayushchiesya i ptitsy* (Fundamentals of Paleontology: Amphibians, Reptiles, and Birds), Moscow: Nauka, 1964a, vol. 12, pp. 299–303.
- Tatarinov, L.P., The Subclass Ichthyopterygia, in *Osnovy paleontologii. Zemnovodnye, presmykayushchiesya i ptitsy* (Fundamentals of Paleontology: Amphibians, Reptiles, and Birds), Moscow: Nauka, 1964b, vol. 12, pp. 338–354.
- Watson, D.M., The Elasmosaur Shoulder-Girdle and Forelimb-Limb, *Proc. Zool. Soc. London*, 1924, no. 3, pp. 885–917.
- Watson, D.M.S., On *Millerosaurus* and the Early History of the Sauropsid Reptiles, *Phil. Trans. R. Soc. London*, 1957, vol. B240, no. 673, pp. 325–400.