On the Permo-Triassic labyrinthodonts from the U.S.S.R.

I. The labyrinthodonts of the Campylian beds of Great Bogdo Mountain.

I. A. Efremov•

The Great Bogdo mountain, on the shore of Baskuntchak, a salt lake in the Astrakhan gov., has been known for a long time because of the splendid section of beds from the Upper Permian to the Lower Triassic. Aurbach even found here fragments of the bones of labyrinthodonts, which by mistake he referred to as *Mastodonsaurus* (1). Because of the extreme incompleteness, the labyrinthodont fauna of Great Bogdo remained unknown until 1912, when M. V. Bajarunas found two skulls and a few fragments there, defined by him as *Trematosaurus* and *Capitosaurus*. These skulls, belonging to the large species, were afterwards skillfully prepared and described by the late Academician, P. P. Sushkin, in his remarkable work (4). In 1926 I investigated Bogdo Mountain for the Geological Museum of the Academy of Sciences, and went there again in 1928 together with F. M. Kuzmin. During these two visits, it was possible to collect on the slopes of the mountain a small number of remains of labyrinthodonts, very fragmentary and incomplete. But it is possible, based on the above-mentioned discoveries of Bajarunas, to give the preliminary characteristics of the fauna of Great Bogdo and also to add one more geographic link of fauna of the oldest Tetrapoda in the U.S.S.R. The remains of labyrinthodonts are found in many thin beds of calcareous

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marls and clays of the upper part of the section, which is considered as belonging to the Campylian beds of the Lower Triassic (2). The last works of M. B. Bajarunas, who found an entirely different *Ceratites* fauna in the Triassic of Mangishlak, point out the remarkable similarity of the *Ceratites* of Great Bogdo Mtn. to the forms of Mangishlak and the Caucasus. This fact indicates the necessity of looking over the stratigraphy of Bogdo Mtn., and also makes us suppose that the calcareous layer of Bogdo Mtn. is stratigraphically lower than the Campylian beds. This hypothesis is accepted by M. B. Bajarunas. The skulls described by P. P. Sushkin, which were identical as to species, were studied by me for that purpose. The skull of *Trematosaurus*, which was preserved more fully than the rest, does not differ in any way from the typical *Tr. brauni*, to which I think it must belong. *Capitosaurus* is very incomplete, and its species cannot be determined, and what is more even its genus is not quite certain.

All these remains, except a number of undetermined fragments, belong to these two genera. The parts of the postcranial skeleton, which is generally very poorly known in *Capitosaurus* and *Trematosaurus.*

The skeletons of labyrinthodonts are very similar and differ only in adaptive characteristics, and there are many cases where the parts of the postcranial skeletons of two genera and even families cannot be distinguished. For this reason, in the following work the well-preserved ribs and parts of the vertebrae are left as incertae sedis because of the absence of absolute proof of their belonging to either genus.

GENUS *TREMATOSAURUS* BRAUN

Pl. 1, figs. 1–4.

1.

Imprint of the skull (N3 2247/14). On a plate of limestone with *Mytilus* shells is located a well-preserved imprint of the dorsal surface of a small skull (Pl. I, fig. 1). The nasal part is broken off. The sutures of the covering bones can be seen very clearly, probably because of the young age of the individual. The right orbit, as well as the whole right outside edge of the skull, were not preserved. The left orbit is small and located on the outside edge at the mid-length of the skull. A clearly distinguished lacrimal, connected by a suture to a large postfrontal, excludes the presence of the frontal among the bones of the edge of the orbit. Parietals are also elongated, their front ends narrowed. In the position of the parietal foramen, the stone is broken off. The supratemporal has the outline of a parallelogram in front surrounded by ? connected to the postfrontal, forming somewhat a narrowed outgrowth, which is turned toward the inside of the skull and connected with the postfrontal. Very well formed are the demosupraoccipitals, with square outlines. The squamosal, together with the tabular, surrounds a small auditory opening. The back outgrowth of the tabular is quite wide and not long. The parietal edge of the skull's surface forms a curve with a large radius, with its point toward the inside. Lacrimal ducts can be seen very clearly. The nasofrontal channel goes along the lacrimal, through the frontal to the postfrontal, where it ends. The operculo-maxillary canal forms a curve along the postorbital, of which only the upper part can be seen, going along the supratemporal and ending at the tabular, near the suture. The depth of the imprint indicates a comparatively high and narrow skull. The position and forms of the bones, the outlines of the lacrimal ducts, the general triangular form of the skull, and the position of the orbits fully correspond to *Trematosaurus*. The narrow, high skull also

supports this opinion. Because of the absence of the nasal part, the species cannot be determined exactly, but all of the present bones do not differ in any way from the typical *Trematosaurus brauni.*

2.

The cast of the skull (N1 2247/14) represents nothing but the inside cast of the left half of the middle part of the skull. No bones were preserved (Plate 1, fig. 2). The height of the skull, the lateral position of the orbit, and the wide interorbital part permits us to consider this fragment also as belonging to *Trematosaurus*, an individual of middle size.

3.

A fragment of the lower jaw (N6 2247/14) (Plate I, fig. 3), is a cast of the inside cavity of the middle part of the lower jaw, which was filled during life with Meckel's cartilage. On the inside part of the fragment can be seen a large nutrient foramen in the form of an elongated oval, which allows determining the position of the fragment. The small size of the Meckel's cartilage in this part of the jaw indicates a thin and narrow jaw, which cannot belong to *Capitosaurus* and which looks very much like a jaw of *Trematosaurus* represented in a drawing by Burmeister (3).

4.

Right clavicle (N16 2242/8) (plate I, fig. 4). The sternal edge and scapular process are broken off. The insignificant width of the fragment, the characteristic concavity of the inside edge of the proximal part, and a small sculpture permit us to consider the bone as belonging to *Trematosaurus*.

GENUS *CAPITOSAURUS* H. v. M.

(Plate II, figs. 1–6).

It must be noted that because of the absence of facts about the postcranial skeleton of *Capitosaurus*, while studying and determining the remains, I was guided chiefly by their tremendous size, basing upon the proven presence of *Capitosaurus* in the Bogdo Mtn. fauna.

1.

The lower jaw (N5 2247/14) (Plate II, fig. 1 and 1a) was preserved very incompletely and partly reconstructed by imprints preserved in the stone. Extremely hard work in the preparation of this jaw, which was surrounded by hard dolomite, was done by the preparator of the Institute, L. A. Gatnev. The left jaw is about 32 cm in length. The whole articular part is broken off so that the only remaining part is the narrow anterior end of the angular, which enters into the space between the dental and postsplenial. The rest of the sutures cannot be distinguished either on the external or internal sides because of poor preservation. The symphyseal part of the distal end is widened and holds two very large, prehensile teeth, external and internal, of which only the external is present. Its height is about 4 cm. A small tooth is located in front of the tusk-like tooth. All together, 19 teeth are preserved, including the fangs, 17 of which have their tips broken off. Alveoli for 12 teeth are also present. Undoubtedly the jaw belongs to a skull of large proportions, not less than 60 cm in length, and which by its size can be compared only with the skulls of *Mastodonsaurus*. But it definitely differs from the last by the massiveness of its distal end, forming a characteristic widening, which is absent in *Mastodonsaurus*, the distal part of whose jaw is comparatively very thin (5).

2.

A quadrate (N3 2242/8) (Plate III, fig. 2). A very large massive bone, belonging probably to *Capitosaurus*. Probably originally was part of the right upper jaw. Its internal edge has an outgrowth that comes close to the external side of the of quadrate ramus of the pterygoid. Must have belonged to a skull not less than 0.5 m in length, and to an old individual, judging by the full ossification of its articular surface.

3.

Left clavicle (N9 2247/14) (Plate II, fig. 3). The bone is well preserved, and has a massive, wide suprascapular process, broken off at the end. The distal part is very thick, very wide, and covered with rough and sharply furrowed sculpture. The edges of the distal plate are broken off and do not give any hint of the full size of the bone, but judging by the thickness of the plate, it must have been of considerable size—about 12 cm in length. The bone differs from the clavicles of *Trematosaurus*, the distal plate of which is elongated, and whose suprascapular outgrowth is narrow and triangular. I believe it belongs to *Capitosaurus*, to which the size of the described fragment corresponds.

4.

Interclavicle (N11 2247/14) (Plate II, fig. 4). The example represents the imprint of the right half of a very large interclavicle, covered with rough, radial sculpture. The upper part is widened. The sharp medial bending of its edge in the upper part of the fragment indicates a sharp narrowing of the bone in its continuation upward. The lower part does not narrow as sharply, thus differing from the interclavicle of *Trematosaurus*, in which the body of the bone itself has a correct rhombic form. The rays of the sculpture end at the internal edge of the fragment, indicating that the whole bone was at least twice

as wide as the fragment. Therefore it must have belonged to a labyrinthodont of gigantic size, which in the fauna of Bogdo Mtn. may be a *Capitosaurus*.

5.

Neural arch of a vertebra (N9 2242/8) (Plate II, fig. 5). Very well preserved. Has a high, slightly crescent-like spine, bent and ending with a massive thickening outgrowth. In the lower half, on the rear ridge of this outgrowth is a large oval deepening. Pre- and postzygapophyses are not developed. The transverse processes are long, nearly round in cross-section. The lower half of the neural arch carries two strong, straight-angled facets for connection with the vertebral centrum. All parts of the arch arc very massive and well ossified. The cerebrospinal canal is very narrow, and indicates that the animal was very slow moving. The type of structure of the arch is clearly stereospondylous. The great size of the arch indicates that it probably belongs to *Capitosaurus*. Mobile, aquatic forms such as *Trematosaurus* are characterized by comparatively low neural arch spines. High spines, on the contrary, are typical for large forms with enormous, heavy skulls, for support of which the powerful back muscles are necessary. The collection contains (Plate II, fig. 6) one more fragment of vertebral neural arch (N10 2242/8). A lower spine is preserved, bent even more backward with the same thickening at the end, and the right transverse process, nearly equal to the neural spine in length. This neural arch belongs to a vertebra from another part of the spinal column, probably lumbar.

Besides these bones, the collection contains many undetermined fragments, among which an enormous angular from a left lower jaw and a cast of the front part of Meckel's cartilage (N5 and N6 2242/8) belong to *Capitosaurus*, and fragments of the ribs and very badly preserved centra of the stereospondylous vertebra (N8 2242/8—to

Trematosaurus. I enclose the photographs of the four well-preserved ribs (Plate I, figs. 5–8) just to show their anatomical characteristics; because of the differences in the structure of the ribs of labyrinthodonts, in which even ribs from the same individual differ sharply according to the region of the skeleton. There is no definite knowledge about the structure of the ribs in *Capitosaurus* and *Trematosaurus*. The rib shown in Fig. 5 (N12 2248/8) probably belongs to the trunk region of the left side and has a strong uncinate process; by its size it may belong to the cervical region of *Capitosaurus*, just as the head of a large cervical rib (Fig. 7) (N8 2247/14), which is very much like the photograph of the cervical rib of *Mastodonsaurus* of Wepfer. A rib from the cervical region (fig. 6 (N11 2242/8) with a well-differentiated head and with characteristics of cervical ribs (widening of the distal end) probably belongs to *Trematosaurus*, to which I believe belongs the proximal part of a lumbar rib from a posterior vertebra, shown in Fig. 8 (N13 2248/8).

From the lower gray clay (2) were excavated two small bones (N17 and N18 2242/8) belonging to the metapodial region of the limb (Plate I, figs. 9 and 10). One of them, shown in Fig. 9, represents a proximal phalanx, and the other probably a metatarsal element or metacarpal. Definite proof of its belonging to either of the described genera is lacking.

Thus, although the remains are very incomplete, the presence of two genera, *Capitosaurus* and *Trematosaurus*, is absolutely determined in the fauna of Great Bogdo Mtn. Judging by the number of fragments of many different species, it will be of great interest in the future to get more detailed and exact knowledge of the fauna of Bogdo Mtn., because of the presence of genera nearly completely unknown in other

localities.....*Capitosaurus* and *Trematosaurus,* two cosmopolitan genera; and it is impossible to determine any zoogeographic region in Bogdo by them.

The discovery of typical *Trematosaurus brauni* indicates the European origin of the labyrinthodonts fauna of Bogdo. *Capitosaurus* is characteristic of the Lower Triassic; in the Upper and Middle, it is replaced by the closely related but more specialized *Cyclotosaurus*.

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3, 4, 5 follow in English or German, p. 62.

II. On the Morphology of the labyrinthodont *Dvinosaurus*.

The Permian labyrinthodont genus *Dvinosaurus*, which was discussed by V. P. Amalitsky, together with the pareiasaurian fauna in the sandy lenses of the Upper Permian of North Dvina, is very peculiar. The collection of the North Dvinsky Gallery of the Academy of Sciences (now the Division of Lower Vertebrates of the Paleontological Institute) contains one complete skeleton, 4 complete skulls, and a number of skull fragments and fragments of the postcranial skeleton of *Dvinosaurus*. These remains were described very incompletely by V. P. Amalitsky, and referred by him to two species, *D. primus* and *D. secundus*. After closer study of the remains, it may be said that these two species have no differences except in age.

All the material was worked on by P. P. Sushkin (7), who gave a full morphology of this genus. Nothing can be added to his excellent description, and because of that I will touch on only certain peculiarities in the structure of *Dvinosaurus*, which will be needed for the following conclusions.

1. An unusual sculpture of the dermal bones of the skull roof, clearly expressed by the radial arrangement.
2. Bones of the skull very thin in comparison with very massive endocranium.
3. Complete absence of traces of parietal foramen on the dorsal surface of the skull.
4. A peculiar connection of pterygoid with the parasphenoid without suture, but by direct contact of the bones. Basal part of pterygoid forms a hook-like outgrowth that presses upon the lateral part of the front edge of the parasphenoid body.
5. Descending paroccipital process tabular, sphenethmoid, basisphenoid, and supraoccipital did not ossify.

6. The quadrate ramus of the pterygoid is not united with the descending edge of the squamosal, palatal ramus continues much farther ahead.
7. Although the life was only in the water, the skull is comparatively high. The edges of the face, in particular the front part, are very flattened and undeveloped, as in the case of larval and very young individuals of Labyrinthodontia.
8. The ossified basioccipital, quite small and not participating in the formation of the condyles, and well-formed paired exoccipitals are present.
9. The postcranial skeleton is weak; short and quite straight ribs recall Amphibia.
10. The clavicles are narrow, as in a much-moving organism; in opposition to the weak skeleton.
11. The anterior palatal (?) foramen in all probability is absent. Eyes small; the nares and choanae poorly developed and may be considered as being in close relationship with gill breathing.

In looking over these characteristics on trends of the evolutionary development of labyrinthodonts, remarkably correctly determined by Prof. D. M. S. Watson, there appears a mixture of primitive and progressive characteristics in the form of *Dvinosaurus*. Such are nos. 4, 5, 6, 7, 8. Aquatic life with gill breathing did not involve a great flattening of the skull at the same time as in the Lower Permian *Trimerorachis*. The narrow clavicles are opposed to the whole structure of the skeleton of the animal, which was leading a slow-moving type of life. Very remarkable is the radial sculpture of the skull roof. Nearly all of the known labyrinthodonts have a perforate, furrowed sculpture of various kinds. The history of the development of the different types of sculpture are still absolutely unknown. In all labyrinthodonts the internal side of the bones of the skull roof contains definite traces of radial structure. Judging by the sculpture of the dermal bones of ganoid fishes, radial sculpture is characteristic of bony

structures that are located very close to the surface of the skin, in fact covered with a very thin layer of hard skin. With the further growth of the individual, increase in the thickening of dermal bones of the skull gradually continues. Depression in deep layers of the skin or under the skin brings out obliteration of the radial sculpture and changes it into an ordinary holed-harrowed (?) *Dvinosaurus primus* Am., and must represent nothing more than a younger individual of correspondingly smaller size with much more strongly expressed radial sculpture with sharp ridges. Larger and older individuals of *Dvinosaurus* (2 skulls, *D. secundus*) have more obliterated sculpture, which in the front part of the skull changes gradually into the holed-harrowed. Another even larger but incomplete skull of *Dvinosaurus* (N 43 Am.) has its radial sculpture obliterated to a great degree and broken into rows of separate elevations and ridges.

It is a remarkable fact that all known very young individuals of the aquatic Permian Labyrinthodontia have sculpture of the radial character on the dorsal surface of the skull. For example, such are the young individuals of *Archegosaurus* described by H. v. Meyer (5); *Brachyceps willinsoni* Steph. (6); young *Trematosaurus*, and others. The skull of a young *Eryops* described by Broom as *Eryops anatinus* (3) also contains traces of radial sculpture. Also young individuals of Labyrinthodontia are characterized by an extreme thinness of the bones of the skull roof, and comparatively massive bones in the endocranium, just as in *Dvinosaurus*. The undeveloped joints of the pterygoid and parasphenoid, although with massive bones, point again to the unfinished primitive stage.

Following the above-mentioned facts, it is possible to consider *Dvinosaurus* not as a correction to Dollo's Law about the anatomical impossibility of a backward trend of evolution, but just as sexually mature larva of the still unknown, more highly organized

form. Exactly similar examples we see in the conditions of life of axolotls. Just as in the case of the latter, which live in the dry climate of Central America, outside factors were unfavorable for *Dvinosaurus* and influenced the endocrine glands, thus stopping the development of the larva and permitting it to retain a gill-breathing life. The absence of the parietal foramen in *Dvinosaurus* is probably connected with changes in the hypophysis and epiphysis regulating the growth and development of the species and connected with the parietal organ. The larva might have reached a size nearly equal to that of the grown animal. The axolotl is marked by characteristics that are also present in *Dvinosaurus*—weak development of the sense organs and a very insignificant development of the skull roof. The key to understanding the conditions that made *Dvinosaurus* spend all its life in the water are in its relative relationships.

As Prof. D. Watson (8) remarkably guessed, *Dvinosaurus* is very close to the family Brachyopidae Broom. Particularly like it are three of the oldest genera of this family: *Brachyops* from Magli Province in India, *Bothriceps* from Australia, and *Batrachosuchus* from South Africa. All three genera—Stereospondyli—come from continental strata, the stratigraphical position of which has not been definitely determined, but supposedly belong to the very lowest Triassic.

The distribution of *Brachyops*, *Bothriceps*, and *Batrachosuchus* corresponds to the present geological understanding about Gondwanaland, which once included India, Australia, and Africa. The close relation of *Dvinosaurus* with the family Brachyopidae once more emphasizes the connection of the North Dvinsky fauna with Gondwanaland. The migration of the Gondwana forms of Tetrapoda to the Russian part of Laurasia began in the Lower Permian, as is shown by the mid-Permian Tetrapoda fauna of Kargalinsky

District of the western Near Urals, which also has Gondwanaland forms. The mature form of *Dvinosaurus* migrated together with representatives of Dinocephalia, Theriodontia, Dicynodontia and Pareiasauria. *Dvinosaurus* itself, with its gill breathing, was not able to migrate long distances on the continent, which once more proves our opinion. The period of dry climate that began in the Upper Permian made the life of land amphibians impossible. *Dvinosaurus* had to become extinct or remain in its larval form. The fact is very significant that, except for *Dvinosaurus*, the North Dvinsky fauna does not contain any other labyrinthodonts. Not having the adaptive changes of *Dvinosaurus*, all other forms became extinct in the district of the continental layers of North Dvina, in the same way as the mature form of *Dvinosaurus*. The North Dvinsky fauna belongs to the middle of the Tartaric strata, thus being not much older than its Gondwana relatives, Brachyopidae, but because of its larval condition preserved many of its primitive characteristics, which should have been extinct. Its mature form was probably more progressive.

Very interesting material [would result] from the careful exploration of the narrow strip of continental deposits of the Middle Permian along the Ural ridge. In them we probably should find many ancestral forms of the Tetrapoda fauna of the U.S.S.R., located in rare favorable facies. *Chalcosaurus rossicus* (4) from the mid-Permian facies, rich with the water of the copper-containing sands of Kargala, probably represents a relative of *Dvinosaurus*. New finds in this district will undoubtedly increase the number of proofs of the connection of the fauna of the ancient Tetrapoda of the U.S.S.R., and the mature form of *Dvinosaurus* may be discovered. This once more will be proof of the

truth of the methods of modern paleontology and the connection of Gondwanaland with Laurasia in the Permian epoch.

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2, 3, 4, 5, 6, 7, 8 are in German and English.

Summary in English follows.