**Benthosaurus sushkini**, a new labyrinthodont from the Permo-Triassic deposits of the Sharshenga River, government of North Duna

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This work is a brief systematic description of the cranium of a labyrinthodont, about which I delivered a preliminary lecture in the IIIrd General Congress of Zoologists and Anatomists in 1927. The skull was found by me in the varicolored Permo-Triassic deposits upon the shore of the Sharshenga River in the year 1927. The loose conglomerate-like sandstone** that contained the bones of the labyrinthodonts lies between the varicolored marl, clay, and sand of the middle and upper portions of the variegated strata, and according to all indications belongs to the Permo-Triassic deposits. The paleontological material is found scattered in the fossiliferous stratum, and portions of the postcranial skeletons of several individuals of varying ages and sizes are intermixed.

In the present work only 1 skeleton is described. Because regular excavation must yet be made, and new material should be expected, the great number of the available portions of the postcranial skeletons will be subjected to a detailed study in the near future.

The appreciable softness of the stony formation, the absence of any deformation, and the perfect preservation of the bones afford an exceptionally detailed preparation. The skull (fig. 1, a and b) is almost completely preserved, with the exception of the slightly damaged left temporal region where a portion has chipped off, and a corner of the tabular bone, as well as the cultriform process of the parasphenoid, which are likewise broken off.

[Fig. 1. *B. sushkini*, gen. et sp. n.: (a) upper cranial aspect (1/2 nat. size); (b) ventral aspect (1/2 nat. size); (c) posterior cranial aspect (approx.1/2 nat. size).]


** J. Efremov, Gisements de stégocéphale dans le nord - est de la partie Européenne de l’URSS. *Cras.-A*, 1929, p. 15.
The skull probably belongs to a young, smallish individual (140 mm. in length), and the sutures separating the bones can be observed to the minutest detail.

The dorsal surface of the cranium. The form of the cranium is a regular triangle (fig. 2); the rostrum is small and rounded. The skull in the occipital region is somewhat dextroversally deformed, and has resulted in a longitudinal construction of the maxillae. The general cranial configuration is flat. The facets of the articulations in the lower jaw are retracted backward and lie in a line with the posttemporal process of the tabular. Upon the anterior end of the rostrum is the triangular interpremaxillary foramen. The large nasal apertures, oval in form, are found in the middle of the first quarter of the cranial length, very close to the exterior margin of the skull.

Fairly large, somewhat oval orbital foramina are placed entirely in the posterior half of the cranium, close to each other, and directed upward.

[Fig. 2. *Benthosaurus sushkini*, g. et sp. n.

The margins of the orbits are incrassate and elevated, thus forming a concave interorbital region; 8 mm behind the margins of the orbits is the round parietal foramen, 3 mm in diameter.

The deep otic incisures are well expressed. The occipital margin of the cranium has a lightly expressed parabolic excision behind the posttemporal process of the tabular bone.

The position and form of the cranial roof do not show any marked peculiarities. As in all forms with orbits retracted backward, the preorbital elements are strongly developed and elongate, whereas the postorbitals are compressed with abbreviated square outlines. In the forms where the orbits are situated in the front, we observe the opposite—here dominate the postorbital elements, and the preorbitals are compressed and abbreviated.

The premaxillae occupy the whole anterior portion of the well-developed snout. The broad and long nasals are bounded behind by the log and narrow frontals and by the well-
developed, triangular prefrontals. The lacrimal bones are large, of an elongate oval form. They are pushed far from the orbit by the prefrontals and the anterior portions of the elongated jugals.

The maxillae are narrow and very long; the parietals are relatively not large and are elongate in the anterior direction. The postfrontals are broad, sickle-like bones that together with the broad and short postorbitals form the whole posterior half of the orbits.

The supratemporals, almost square in form, became narrower in the posterior direction and articulate with well-developed tabulars and the broad square dermosupraorbitals. The squamosal, jugal, and quadratojugal bones are likewise well-developed. In terminating the description of the cranial roof bones, we must indicate an interesting feature—the left ring of the orbits is formed inwardly and posteriorly by the postfrontal and postorbital, from the outside by the jugal, from the front and inside by the prefrontal and the small process of the frontals, which are enclosed between the pre- and postfrontals.

The right orbit is formed by the same elements, without however any participation of the frontals which are displaced toward the midline. Thus there are joined in one individual, two structural types of orbits, which serve as important indices in systematics. Through the fragments of other crania, it may be positively established that the structure of the right orbital ring is typical for our form: namely the exclusion of the frontal from the orbit. It is likely that here is a case of an atavistic asymmetrical anomaly. The sculpture is strongly expressed and is of a fossa-and-furrow-like type, and the radial striation is weakly indicated in the squamosal, jugal, and quadratojugal bones.

The mucous canals are well developed and, in their outlines, resemble those of *Mastodonsaurus* and *Trematosaurus*. The nasofrontal canal (fig. 2 nfk.) begins at the posterior margin of the orbit in the postfrontal, whence winding in the form of an “S” it passes through the frontal, prefrontal, and around the nasal aperture into the premaxilla. The marginal canal begins at the posterolateral edge of the cranium, passes along the suture between the squamosal and the quadratojugal, here giving origin to an upward branch, directed to the posterior orbital margin (fig. 2 rpmk.). It then extends [p. 761] further over the suture of the jugal and maxilla, and approaching the nasofrontal canal, forms a loop from the maxilla into the lacrimal, and descends again into the maxilla, disappearing under the nasal aperture. A short supratemporal canal, beginning at the suture between the supratemporal and the tabular and ending at the postorbital, attains a close propinquity to the outward-directed
branch of the marginal canal. The short and deep anterior diagonal canal extends through both premaxillae, over the intermaxillary foramen, and does not join with the other canals. At the bottom of the mucous canals numerous minute openings for the branches of the sensory nerves are observable in few places.

The ventral surface of the cranium. The ventral surface of the cranium has all the peculiarities of the highest labyrinthodonts (fig. 3). The interpterygoid and infratemporal cavities are fairly large.

The parasphenoid—a leaf-like, flat bone—is connected on both sides with the pterygoids by almost imperceptible sutures. It becomes narrower in the backward direction and is joined by its deep sutures to both exoccipitals. The free posterior margin of the parasphenoid extends in the form of a thin lamina only to the base of the condyles. The cultriform process has broken off in our specimen entirely, but judging from the extended ends of the prevomer, it was very small. The whole interior end of the parasphenoid body articulating with the pterygoids is covered with granular shagreen teeth.

The pterygoids are joined by deep sutures with the transverse middle section of the palate. The small anterior process of the palatine ramus of the pterygoid articulates with the posterior palatine process, which is supported by the anterior part of the ectopterygoid [transversum] and does not reach the prevomer. The external margins of the pterygoids are delicate, bent downward, and covered by a sulcus-like sculpture. The anterior and middle portions of the pterygoids, like the parasphenoid, are covered with shagreen teeth. The quadrate rami of the pterygoids are massive and extend diagonally from the bottom of the auditory cavity, articulating with the quadrates. The upper margins of these rami of the [p. 762] pterygoids become delicate and surround the ear cavity from the front and external sides.

The quadrate—massive and cylinder-like—is very securely joined to the quadratojugal and is surrounded by a spongy mass—the remnant of a lime-incrusted cartilage.

[Fig. 3. B. sushkini, g. et sp. n.
Lower cranial aspect (approx. 1/2 half of n. size.): pmx. – premaxilla; mx. – maxilla; ecpt. – ectopteryoid (transversum); qj. – quadrojugal; q. – quadrate; pvo. - prevomer; pal. – palatine; pt. – pterygoid; rqpt. –quadrate ramus of the pterygoid; psp. – parasphenoid; exoc. – exoccipital; cdoc. – occipital condyle; apf. – anterior palatal foramen; fz. – canine; nzpv. – dentition of the prevomers; shbp. – shagreen dentition of the parasphenoid and pterygoid.]
The ectopterygoids—small, long bones joined tightly with the maxillae and palatines—bear a row of teeth that extends to the margins of the infratemporal cavities.

The palatines are rather long and well developed; they are contiguous from behind and outside the ectopterygoids; anteriorly they are bound by their broad sutures to the prevomers, building thus the posterior margins of the choanae. They also bear a row of stout teeth.

The maxillae—exceptionally long and narrow bones—commence at the anterior margins of the infratemporal fossae where they articulate with the quadratojugals. They closely adjoin the ectopterygoid, palatine, and prevomer bones, thus forming the outer walls of the choanae, and also bear a row of teeth that likewise reaches the anterior edges of the infratemporal fossae. In the middle of the exterior walls of the anterior palatal foramina, the maxillae are joined by their serrated sutures to the powerful premaxillae which form the entire front end of the snout and the anterior walls of the anterior palatal foramina.

[p. 763] The prevomers—are very large and broad bones bearing a great number of teeth. They form the rear walls of the anterior palatal foramina and the inner walls of the choanae; behind, the prevomers are elongated into long and narrow projections that extend to almost 1/3 of the interpterygoid fossae and join with the narrow cultriform process of the parasphenoid. There are no traces of a penetration of the cultriform process under the prevomers or its wedging between them.

Each of the prevomers bears 2 large prechoanal canine-like teeth on each side and a row of teeth extending from the first canine-like tooth suture between the prevomers, which form a wedge-like figure. In addition the prevomers are provided with a row of small teeth that surround the choanae.

The round anterior palatal cavities are separated by an imperfect septum; they are formed by cylinder-like processes of both prevomers from behind, and similar processes of the premaxillae from the front. Apparently this septum becomes ossified in later age. The described cavities open onto the anterior portion of the nasal cavity, which in turn opens into the nasal aperture via the interpremaxillary foramen.

The choanae, of a regular oval form, are of the same size as the outer nasal apertures. They are bounded from the front and inside by the prevomers, from the outside by the maxillae, and from behind by the palatines.

The teeth, of typical labyrinthodont plicated structure, are provided with longitudinal
sulci. The tooth crown is round, slightly bent backward. The base is compressed from the front toward the back and is elliptical in diameter. The principal tooth row covers the premaxillae and maxillae and varies little as to size. The second row extends over the palatines and ectopterygoids, paralleling the first row, and has similar teeth; on each side are three large canines. The first 2 teeth rest upon the bridge between the choanae and the anterior palatal cavity. In our specimen only 1 tooth on each side has been preserved; the third canine rests upon the posterior wall of the choana at the beginning of the palatine tooth row. The entire first third of the prevomer is occupied by a supplementary wedge-shaped row of small teeth beginning at the posterior margin of the anterior palatal cavities. Similar teeth surrounding the inner walls of the choanae (fig. 4, bzp.).

[p. 764] The occipital region of the skull (fig. 4.). The occiput of a flattened type is slightly compressed by a dorsoventral deformation. In its general construction it reminds one of the skulls of late Rhachitomi and Capitosauridae. The exoccipitals are large, well-developed bones that play an important part and bear the occipital condyles. The condyles have the form of cylinder out diagonally and in an inward direction. At the base of the condyles and under the parotic process of the exoccipitals are seen large apertures for the 10th pair of cranial nerves (vagus nerve foramen fig. 4. X).

[Fig. 4. B. sushkini g. et sp. n. Posterior cranial aspect (8/11 n. size); pshp. – parasphenoid; rqpt. – quadrat ramus of the pterygoid; q. – quadrat; sq. – squamosal; t. – tabular; dsoc. – dermosupraoccipital; exoc. – exoccipital; cvt. – tympanic cavity; pdt. – descending processus of the tabular; psex. – ascending superior processus of the exoccipital; pbex. – lower basioccipital process of the exoccipital; fq. – quadrat foramen; X – vagus nerve foramen; XII – hypoglossal nerve foramen; for. – squamosal foramen; cdoc. – occipital condyles.]

Behind these foramina, closer to the margins of the condyles, are also situated other minute foramina serving probably for the passage of the XIIth pair of nerves. The parotic process of the exoccipital is probably connected to the descending process of the tabular by means of a deep serrated suture, and leaves not a trace of a paroccipital on the outside.

There are ridges on both sides of the foramen magnum upon the inner side of the exoccipitals that are directed upward and forward along the foramen magnum, probably supporting the cartilaginous supraoccipital (fig. 4, psex.).

Less strongly expressed are the lower diagonal processes of the both exoccipitals (fig.
4 pbex.), which converging below the foramen magnum [p. 765] separate the cephalic canal from the cartilaginous basioccipital. The ascending superior processes of the exoccipitals are joined by their strong sutures with the laterally directed processes of the dermosupraoccipitals. On the right side of the exoccipital is a deep sulcus whose genesis may be considered abnormal. The posttemporal fenestrae are deep and wedge-shaped.

The quadratojugal articulation of the pterygoid articulates above with the laterally directed margins of the squamosals, forming long sutures. Their distal ends are fairly thickened and are joined by the inner sides of the quadratojugal bones.

The thickened portions of the quadratojugal form round ridges that bend gradually in the front toward the bottom of the tympanic cavity. Above, the quadratojugal form thin laminae that reach to the cranial roof and form the external and anterior walls of the tympanic cavity. The bottom of the tympanic cavity (fig. 4 cvt.) is formed by the pterygoid and partly by the parasphenoid. The inner walls of the tympanic cavity and the fenestra ovalis remain unossified. In our individual the stapes has not been preserved. There is also no trace of an epipterygoid nor of the prootic bone, which were probably not ossified due to the youth of our specimen.

There is a large quadratojugal occupying one-half of the quadratojugal. Above this aperture in the descending crest of the squamosal is a large and upward-directed nutrient foramen. The descending crest of the squamosal is bend inward and, together with the crest of the quadratojugal of the pterygoid, forms a fossa for the powerful depressar his mandibuli muscle. On the margins of the otic incisure is a hardly noticeable sulcus—the place where the tympanic membrane was secured.

The basioccipital, supraoccipital, basisphenoid, and sphenethmoid were not completely ossified.

**Measurements of the cranium.**

- Cranial length from the end of muzzle to the middle of occipital incisor: 140 mm
- Maxim. breadth in the region of mandibular articulation: 111 mm
- Distance of the orbital centers from the middle of cranial length: 25 mm
- Distance between orbits: 20 mm
- Length of orbits: 22 mm
- Breadth of orbits: 16 mm
- Distance from the center of nasal apertures to the end of the rostrum: 23 mm
Comparative diagnosis.

When we compare our form with the well-known representatives of *Rhachitomi* and *Stereospondyli*, we see that the families of the highest labyrinthodonts—Rhinesuchidae of *Rhachitomi*, and Mastodonsauridae and Trematosauridae of *Stereospondyli*—are closest to it.

The basal construction of the skull of these three families shows several similar characteristics (fig. 5, 6, 7.).

*Rhinesuchus* shows in the similarity of the general cranial structure an indubitably greater primitiveness—the presence of an osseous basisooccipital and basisphenoid, the presence of a paroccipital on the external side of the occipital region, and the great length of the quadrate rami of the pterygoid. The smaller development of

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<td>Distance between the nasal apertures</td>
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<tr>
<td>Length of nasal apertures</td>
<td>15 mm</td>
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<tr>
<td>Length of choanae</td>
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<td>Breadth of choanae</td>
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<td>Distance between dermosupraoccipital and parasphenoid</td>
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<td>Breadth of mandibular articulation</td>
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<td>Distance between occipital condyles</td>
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<td>Distance between otic incisures</td>
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<td>Depth of otic incisures</td>
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<td>Breadth of palatine ramus in the middle of palatal ramus</td>
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<td>Breadth of parasphenoid body between the pterygoids</td>
<td>26 mm</td>
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[Fig. 5. Ventral cranial aspect of *Rhinesuchus whaitsi*, accord. to D. M. S. Watson (3/20 nat. size).]

the parasphenoid body, the great length of the palatal ramus of the pterygoid, and the substantial size of the postlateral corners of the prevomers strengthen this deduction. Beside these general characteristics, there are yet special features to distinguish, such as the different form of cranium, special grouping of the shagreen and teeth in the palate, and the absolutely different construction of the ventral surface in the anterior part of the snout. Turning to *Stereospondyli*, it is interesting to note that the two families which resemble our form, Mastodonsauridae and Trematosauridae, are also very close to each other. The
Mastodonsauridae resemble our form through the general position and shape of the components of the cranial roof, orbital structure, identical form of the mucous canals, and the small cultriform process of the parasphenoid. Equally identical is the structure of the pterygoid-ectopterygoid palatine complex of the palatal surface. However, the differences of *Mastodonsaurus* from our form are greater than the similarities. The frontal of *Mastodonsaurus* takes part in the orbital structure, the anterior palatal foramina are very peculiar and open onto the dorsal surface of the cranium. The cultriform processes parallels the prevomers for some distance from below. The sculpture and shagreen are entirely absent from parasphenoid and pterygoid. The quadrate rami of the pterygoid are strongly abbreviated so that the mandibular articulations of *Mastodonsaurus* lie in front of the occipital condyles. The skull itself is much more flattened.

The ectopterygoid-palatine tooth row does not reach the margin of the infratemporal cavity by far. The position, form, and size of the choanae and teeth in the prevomers are totally different from our form. The form of the occipital condyles is also totally different. The Trematosauridae resemble our form only in the general construction of the dorsal and ventral surface of the cranium, and the narrow cultriform process.

[Fig. 6. Dorsal and ventral cranial aspect of *Mastodonsaurus acuminatus* and *M. giganteus* accord. to Fr. von Huene (approx. 3/15 and 3/40 nat. size).]

The Trematosauridae are distinguishable from our form in equal degree (fig. 7, 8). The skull itself is incomparably much higher. Pointing to an active mode of life in a predatory animal, the orbits of the Trematosauria are small and placed laterally in the cranium. As a result of this, the components of the cranial roof are in different relationship to one another.

[p. 768] The reduction of the palate and the quadrate rami of the pterygoid are very great.

The parasphenoid body is strongly developed, and its free posterior margin almost covers the occipital condyles from below.

[Fig. 7. Ventral cranial aspect of *Trematosaurus brauni* acc. to D. M. S. Watson, 1/2 nat. size.]
The exoccipital is not visible on the ventral surface. The cultriform process is wedged between the posterior extensions of the prevomer and extends to the margin of the interpterygoid fossa. The lateral palatal cavities are placed more laterally and separated by a broad septum.

[Fig. 8. Posterior aspect of the skull of *Trematosaurus brauni*, acc. to D. M. S. Watson (5/12 nat. size). The same denotations as in the previous figures.]

A second supplemental tooth row is lacking in the prevomers. The shagreen on the pterygoids is very weakly expressed. The occipital region of *Trematosaurus* (fig. 8.) is much differentiated from our form (fig. 4.), and represents, as indicated by Watson, a greater progressive specialization. It should be noted that according to the structure of the palate and that occipital region our form resembles *Capitosaurus* more than any other family of labyrinthodonts. Thus our form possesses several similar features with the above-named groups. Although more primitive than *Mastodonsaurus* and *Trematosaurus* on account of the development of the parasphenoid, the quadrate rami, and palatal branches of the pterygoid (et. cet.), our form has advanced farther than *Rhinesuchus* in the evolutionary course that is common to all labyrinthodonts.

[p. 769] Judging from the absence of osseous basioccipitals, and basisphenoid, as well as paroccipitals, and from the reduction of the palatine rami of the pterygoid, our form represents a fairly advanced stereospondyl. However, in the entire material found together with it there is no sign of stereospondylosous vertebrae, while many hypocentra and neural arches of rhachitomous type are present. Neither were pleurocentra encountered. This circumstance convinces us that our form possessed a rhachitomous spine. The absence of pleurocentra points to its strong reduction, which is perfectly plausible in the transition of the rhachitomous spine into a stage that is very close to the stereospondylosous type. Watson overlooked the presence of rhachitomous elements in the spinal column of *Mastodonsaurus*.

All these facts present the possibility of assuming that our form stands upon the boundary between Rhachitomi and Stereospondyli, but already possesses the characteristic cranial structure of the Stereospondyli. The geological age of our form—Permo-Triassic,
agrees with this assumption. The circumstance that it bears the common characteristics of the various groups of Stereospondyli corroborates this view.

The deduction.

Due to the considerations enumerated above, I enter this new form into a special genus for which I propose the name *Benthosaurus*, in view of its clearly indicated adaptation to life in deep water. The specific denomination *Benthosaurus sushkini* is given in honor of my teacher, the late Academician P. P. Sushkin, who laid the foundation for an exact morphological study of the Paleozoic fauna of the terrestrial vertebrates of the USSR. Because the *Benthosaurus* is apparently an intermediate form, I refrain for the time being from referring it to any particular family of labyrinthodonts. As a result of a detailed study of the morphological peculiarities of *Benthosaurus*, and due to the abundance of recent material from the same excavations, it must in all probability be placed in a special family.

I shall yet remark that my faunal study of Russian stegocephalians embraces a series of forms that indicate a transitional character either in the direction of *Gondwanosaurus*—or into the *Benthosaurus* type.

[p. 770] Biologically *Benthosaurus* clearly shows an adaptation to a life in from the position of the orbits and the flatness of the skull. However, in its general cranial configuration and the position and nasal aperture it reminds one of a mobile form.

The *Benthosaurus* is probably a branch of the stem of the aquatic rhinesuchid-like ancestors, which were more active than known rhinesuchids. Due to the transition in the Late Permian and Permo-Triassic into a desert climate, the great freshwater basin diminished greatly in size, and *Benthosaurus* adjusted itself to the new conditions by means of an adaptation to a benthonic mode of life.

**Diagnosis.**

*Benthosaurus sushkini*, gen. et. sp. nov.

The skull is of a regular triangular form. The orbits are situated in the posterior half of the skull, close to each other. The pterygoid adjoins the palatine bone. A supplementary wedge-like tooth row on the prevomer. Cultriform process very narrow and articulating with the extended ends of prevomer. The pterygoids are sculptured and bearing shagreen teeth, like
the parasphenoid body. The parasphenoid is leaf-like in shape, narrowed in posterior direction. The exoccipitals are visible from the ventral side of the cranium. The mandibular articulation is behind the occipital condyles, which are paired. A foramen for the XII nerve pair is present. The paroccipital is not visible from the outside of the posterior cranium. The basisphenoid and sphenethmoid not ossified. The spinal column is of a progressive rhachitomous type.

Geological Museum of the Academy of Sciences,
Leningrad.