On the labyrinthodonts of the USSR.

II. Permian labyrinthodonts of the former Government of Viatka

by I. A. Efremov [= Efremoff][*]

1. A new description of the labyrinthodont *Platyops stuckenbergi* Trautschold from the Late Permian deposits of the Kityak River, a confluent of the the Viatka River.

The skull of *Platyops stuckenbergi*, which was described by Trautschold (16)[†] in the seventies of the last century, is the only preserved type of all the labyrinthodonts that have been described in Russia up to the eighties. The description of Trautschold, who has not prepared his object, does not answer the demands of present-day paleontology, and as a result it was necessary to re-work his material. Thanks to the kindness of the late Prof. Noinsky, Director of the Geological Division of Kazan University, where Trautschold's material is kept, I have succeed in obtaining the *Platyops* cranium for the purpose of preparation and examination. I had at my disposal together with the type—an incomplete skull that was pictured by Trautschold under No. 1 in plate I (see Fig. 20)—several fragments pictured in this place under Nos. 2, 3, 4, 5, 6, 7, 14, and 16.

The locality of all the remains is known with sufficient certainty. The entire material was collected by Prof. Stuckenberg in an abandoned copper mine near the village of Akbatyrova on the Kityak River (the right confluent of the Viatka River), in the Malmysh district of the former Viatka Government. The layer containing the bones represents a lens of compact cuprous marl that is somewhat bituminous and undoubtedly belongs to a continental facies. This marl, petrographically and genetically, shows great similarity to the cuprous marls of the Kargalin mines in southwestern Cisuralia[**] (9).

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[†] Numbers referring to works cited in the catalogue.

[**] Cisuralia = lands on western slope of Ural chain.

Fig. 1. *Platyops stuckenbergi*. Dorsal cranial aspect. 2/3 nat. size. Prf. – prefrontal; Mx. – maxilla; Ju. – jugal; Fr. – frontal; Par. – parietal; Prf. – postfrontal; porb. – postorbital; Sq. – squamosal; St. – supratemporal; Dsoc. – dermosupraoccipital; Tab. – tabular.

The stratigraphic position of the Kityak strata is not fully explained. We probably have here a continental facies of the shell-bearing horizon of the Kazan stage, which, as we shall see later, seems to agree with the evolutionary stage of the described form.

The incomplete skull (Trautschold, Pl. 1, fig. 1), which is of the greatest interest, was prepared to the utmost detail. The skull, in spite of the general good preservation of the bones, is very incomplete. The whole anterior portion of the snout cavities is broken off together with the anterior margin of the interpterygoid. On the occipital surface both mandibular condyles are broken, the occipital condyles were knocked off. The left mandibular condyle, which Trautschold pictures as partially preserved, has been lost. From the dorsal surface the whole left half of the dorsal bones on the cranial roof and a portion of the quadratojugal are knocked off. On the ventral surface the palatine ramus of the pterygoid is corroded by crystallization of calcite.

Fig. 2. *Archegosaurus decheni*; Dorsal aspect of the cranium
1/2 nat. size (accord. to Herman v. Meyer.)
Dorsal surface of the cranium.
(pl. IX, fig. 1 and fig. 1 in text).

The triangular skull, with its narrow elongated snout, belongs to an old individual. The dermal bones of the cranial roof attain considerable thickness, their sutures were not determined by Trautschold due to coalescence. We have tried to clean the surface of the bones by means circular brushes of a boring [p. 119] machine, moistening the bones with alcohol and subsequently macerating them in hydrochloric acid. As a result of this, all the sutures became plainly visible.

The substance in the sutures was smeared with India ink under a binocular microscope [p. 120] and the sutures became thus visible even to the inexperienced observer.

The skull is somewhat deformed. However, the tangential deformation is so small that the general relations of the formative cranial elements are not changed. The skull is relatively high, which is in contradiction of the generic name (*Platyops* – flat face). The orbits are fairly large, ovally elongate, and laterally situated. The longitudinal axes of the orbits are placed diagonally and spread out toward the anterior portion of the skull. The surfaces of the frontal section of the orbits are inclined toward the front, so that the orbits are oriented partially to the front and partly laterally. The inner margins of the orbits are elevated whereas the interorbital strip is concave, although to a lesser degree than in *Benthosaurus*. A large parietal foramen some 15 mm behind the line joining the posterior margins of the orbit is situated precisely at the midline of the cranium. As we shall see further, the orbits of *Platyops* cannot be considered as being situated posteriorly; on the contrary—they are placed near the center of the cranium. The auditory excisions are sharply expressed, deep, and narrow. In our object only the right auditory fossa, partly broken in the rear, has been preserved.

The structure of the roof elements of cranium shows a remarkable similarity with *Archegosaurus* (fig. 2) (14).

The frontals, in the form of long narrow stripe, do not participate in the border of the orbits, and only their posterior half has been preserved. Of the prefrontals, the posteromedial extensions have been preserved, which form the anterior margins of the orbits. All remaining elements composing the cranial roof have been preserved only on the right half, which is sufficient for the reconstruction of the whole cranium, according to the law of symmetry.

The long, sickle-like postfrontal is joined to the prefrontal at the anterior corner of the orbit, whose whole medial margin is formed by it. It also articulates through the inner margin with the frontal and with the whole outer margin of the anterior half of the parietal. The posterior margin of the postfrontal is joined on the outer side with the supratemporal and the postorbital. The broad and wedge-like postorbital forms the whole posterior margin of the orbits and with its posterior end is wedged far between the supratemporal and the squamosal, a very characteristic feature for *Archegosaurus*. The jugal is a large bone that is extended on a deep suture with the squamosal to half of the whole postorbital part of the cranium. This bone bounds the whole outside of the cranium and is in contact with the posterior end of the very long maxilla by its diagonal serrated suture. The quadratojugal is absent from both cranial sides, but judging from its impression and the mutual relationship with the squamosal it was [p. 121] very long and narrow. The squamosal is a broad, trapezoid-like bone that forms the whole external and anterior margins of the auditory excision. The whole lower end of it is broken off in our object. The inner margin of the squamosal bears a sharp elevation approximately in the middle of the bone, in the vicinity of a suture joining that bone to the supratemporal. The suture between the squamosal and the supratemporal is very wide in spite of its serrated edges, and is not tightly pressed together. This points to the absence of an intimate connection between these bones. This fact must be considered as a sign of primitiveness that has been retained by our form. In the Embolomeri this suture forms the "table" delimitation of the skull. In the Crossopterygii a simple ligament is found instead of this bone (20).

The narrow and very long supratemporal forms by its posterolateral corner a component of the inner margin of the auditory excision. The large dermosupraoccipital has sinuous outlines that, however, are almost square. Their posterior margins form an oblique surface that descends to the occipital surface of the skull. In the occipital section the dermosupraoccipital reveals a considerable expansion, pushing the tabular to the side.

The wedge-like tabular is very small on the dorsal surface, expanding, however, considerably under the dermosupraoccipital. The end of the free extension of the tabular is broken off, however we can discern plainly that the posterior horn of the tabular was small and ended in the form of an obtuse triangle, without extending backward very far. The posterior margin of dorsal surface is sharply bent, however not in a posterior direction, whereby the dorsal surface forms both of the dermosupraoccipitals in one broken line, from which each one extends in a straight line.

Due to the great age of the individual, the sculpture is expressed very sharply. The mucose canals are weakly developed but the nasofrontal canal is particularly well developed.

The ventral surface of the skull.
(Plate IX, fig. 3, and fig. 3 in the text).

The ventral surface of the skull shows a very interesting shape. The interpterygoids are relatively small and narrow, the infratemporal cavities being on the contrary well developed, deep, and broad.

The parasphenoid has a very peculiar shape in the form of a high equilateral trapezoid. The parasphenoid body is very narrow from the front, expanding evenly and strongly toward the back. Only the anterior narrow section of it is in direct contact with the basal portions of the pterygoids. The remaining larger portion of the parasphenoid body extends freely backward between [p. 122] the quadrate rami of the pterygoid. The margins of the parasphenoid body form laterally cylindrical folds, then they bend in a dorsal direction and surround the massive lower surfaces of the exoccipitals. The bones thus greatly resemble a spade. The parasphenoid bears anteriorly a long and narrow cultriform process that expands somewhat at the distal end and reaches the anterior end of the interpterygoid cavities. A little to the front of the base, the cultriform process has two small symmetrical extensions, the role of which is not clear.

Fig. 3. *Platyops stuckenbergi*. Ventral aspect of the cranium
1/3 nat. size. Anterior portion restored. Mx – maxilla, ecpt. – ectopterygoid (transversum), pt. – pterygoid, prsph. – parasphenoid.

The anterior portion of the parasphenoid body articulating with the pterygoids reveals a shagreen dentition. The articulation of the parasphenoid with the pterygoids is effected by means of a simple superimposition of the fine lamina of the parasphenoid body upon a special step that has formed under the covered basal portion of the pterygoids. In such a structure the massive basicranial portion reveals itself as being suspended between the infratemporal cavities, its supporting point being in the front in the articulation of the pterygoids and in the occipital extensions. This structure is not conducive, during burial of the animal, to preservation of the basicranial portions, and the frequent absence of the occipital portion in *Archegosaurus* resulted in the faulty supposition that this portion was not ossified. The basicranial portion was preserved only in old animals with massive bones or during burial in stagnant waters (in marls).

The pterygoids are very broad and massive. The palatine rami are connected by a deep suture to the ectopterygoids and bear a shagreen dentition while being extended widely to the front. The anterior portion of the palatine rami are broken off; their small anterior extensions completely surrounded the whole outer [p. 123] margin of the interpterygoid cavities, probably reaching the prevomers. The quadrate rami of the pterygoids are long and well developed. The ascending laminae are very broad and thin, whereby the infratemporal cavities attain very large dimensions. The palatine rami of the pterygoids are bent sharply downward, and as a result the palate has acquired a convex form. The parasphenoid is bent inward into the skull and lies in a depression between the pterygoids. The postorbital portion of the cranium is thereby very high but flattened suddenly toward the front; the preorbital portion has the flat configuration usual with stegocephalians (Pl. 1, Fig. 2). There is no doubt that such a structure caused a deepening of the infratemporal cavities, which are necessary for attachment of the numerous muscles of the very long lower jaw and particularly the masticatory muscles.

The ectopterygoid (ectopterygoid) is a long, narrow bone that, having its inception at the anterior margin of the infratemporal cavity, is enclosed between the palatal ramus of the pterygoid and the posterior margin of the maxilla.

Only the right portion of the maxilla has been preserved; the posterior end remains in the form of a narrow strip that has reached the anterior edge of the infratemporal cavity.

The maxilla bears a row of fairly large teeth, the first order of which extend to the end of the bone. As has been mentioned above, both mandibular condyles are fractured, but the lines of the supposed continuation of the bones indicate that they did not extend much beyond the line of the occipital condyles. However, when we envisage the whole free portion of them, we realize that their length must have been much greater.

The occipital surface of the skull, and the neurocranium.
(Pl. X, fig. l, and figs. 4, 5 and 6 in text.).

The occipital surface of the neurocranium extends from the cranial roof between the very high ascendant laminae of the quadrate rami.

In fig. 4, which represents a reconstruction of the posterior cranium of *P. stuckenbergi*, we can observe, as a result of precise measurement of bone interrelations, that the quadrate rami descend below the neurocranium and form a continuous bony wall for the masticatory muscles. Otherwise the outer margin of the cranial roof, which is formed by the maxilla and the quadratojugal, is much higher than the surface of the lower margin of the quadrate rami. This circumstance induced me to give to the reconstructed mandibular condyles a scalar (step-like) form. Another surmise is that the quadrate occupied a very inclined position; this however, [p. 124] is less probable. We have a good example of this structure in *Palaeogyrinus decorus* Watson from the Carboniferous Period (20). All the bones of the occipital portion are very massive. Both occipital condyles are broken; thanks to this circumstance the massive basioccipital with its deep longitudinal fossa for the chorda in the middle is made plainly visible. The basioccipital, as it seems, participated to a certain extent in the building of the occipital condyles, which must have represented a transition from tripartite to one of two parts.

Fig. 4. *Platyops stuckenbergi*. Posterior aspect
5/7 nat. size. Tab. – tabular, Parocc. – paroccipital, Sq. – squamosal, St. – stapes, Dsoc. – dermosupraoccipital, Exocc. – exoccipital, Condocc. – occipital condyle, Boc. – basioccipital, Rqpt. – quadrate ramus of the pterygoid, X. – foramen for the vagus nerve.

The exoccipital is a massive columnar bone with complicated branching. It has coalesced firmly at its lower end with the basioccipital, separating it thus through its diagonal extension from the cavity of the medulla oblongata. The exterior side of the lower end of the exoccipital forms in the front the posterior margin of the fenestra ovalis. The lower contour of the fenestra is limited by the parasphenoid which bends upward around the lower part of the exoccipital (fig. 5). The superior ascending processes of the exoccipital bone, which leads to the dermosupraoccipital as well as the paraotic process, are not developed. The suture joining the exoccipital with the descending process of the dermasupraoccipital originates on the upper basal margin of the supraoccipital process of the exoccipital bone, which separates the small cartilaginous supraoccipital from the medulla oblongata. The upper portion of the exoccipital and the outer surface of the supraoccipital are inclined forward, which is characteristic for the old Rachitomi.

Fig. 5. *P. stuckenbergi*. Neurocranium viewed from the left with a longitudinal section through the dermal bones of the cranium. 3/4 nat. size. Orb. – orbits, for. par. – parietal foremen, fen. ov. – fenestra ovalis, fbpt. – basal portion of the left pterygoid, ept. – epipterygoid, dashes – delimitation of basisphenoid and basioccipital, Long bars – petrified alluvium.

Fig. 6. *Palaeogyrinus decorus* Wats. Left aspect of the neurocranium. 5/6 nat. size (acc. to D. M. S. Watson). SpEth – sphenethmoid, pr. Ot. prootic, Proc. Bpt. – basiopterygoid process, Ps. Fen. Ov. – pseudo fenestra ovalis, Par. Sp. – parasphenoid, B.oc. – basioccipital, Exo. – Exoccipital, X. – foramen for the vagus nerve.

Somewhat below the insertion of the lower edge of the paroccipital the exoccipital is pierced by a fairly large foramen for the 10th nerve. Below this foramen and very close to the base of the occipital condyle is situated another small foramen for the 12th nerve. Upon our specimen the surface of the bone at this place is chipped off so that there is visible only the inner continuation of this foramen directed toward the foramen of the vagus nerve. [p. 126]

Fig. 7. *Platyops stuckenbergi*. Bony braincase anteriorly. nat. size; dc. – dermal roof of the cranium, largpt. – ascending lamina of quadrate ramus, ept. – epipterygoid, palpt. – palatine ramus of the pterygoid, parsph. – parasphenoid, bsp. – cartilaginous basisphenoid, fbpt. – a facet on the basal portion of the pterygoid for the basisphenoid. Back portion is the brain cavity.

The paroccipital appears exceptionally well developed. It has its inception very close to the foramen for the vagus nerve and extends upward, thus forming the whole paraotic crest; i.e., the whole lower margin of the posttemporal fenestra. The upper portion of the paroccipital is strongly expanded and, extending forward and onward, forms the whole superior portion of the wall of the braincase (Fig. 5). Its anterior margin could not, unfortunately, be prepared without damaging the cranium, but is most likely that it coalesces anteriorly with the prootic. Anteriorly, the paroccipital forms an obliquely descending continuation, thus surrounding the fenestra ovalis from above and from the front. This cranial structure represents a retained primitive character. In fig. 7 the bony braincase of *Platyops* is pictured. It is noteworthy that here the pterygoids are fastened by means of the non-ossified basisphenoid instead of the parasphenoid. The basal portions of the pterygoids, appearing here in the form of massive thick columns, have peculiar symmetrical quadratic projections that apparently were intended for the cartilaginous basisphenoid. Upon the lower surfaces of these projections firmly reposes the thin concave anterior portion of the parasphenoid body. Judging from the articulatory facets, the thickness of the cartilaginous basisphenoid exceeded the thickness of the parasphenoid by several times. The *Platyops* viewed here shows an interesting transitional stage in the substitution of the basisphenoid due to the development of the parasphenoid in the cranial base, exactly as indicated by Prof. Watson and Academician P. P. Suskin (15, 20, 21). On the anterior surface of the articulatory facets of the pterygoid, at the juncture of the parasphenoid with the basisphenoid, is the minute, bent epipterygoid. Both epipterygoids have been symmetrically preserved on both sides; however, in view of their small size and the bad state of preservation, their structural minutiae are indistinct. There is a thin and relatively long ascending process. The otic process has apparently not developed at all. Noteworthy is the exceedingly minute size of the epipterygoid, finding its plausible explanation in its scanty stage of ossification. The tympanic cavity is very narrow, due to the extension of ascending quadrate laminae so close to the neurocranium.

The stapes is a long, thin, and bent bone (fig. 8) in the right portion of the skull. It was found perfectly preserved and in its natural position. Thanks to the narrow tympanic cavity the upper 2/3 of the stapes is directed almost vertically and lies very close to the wall of the braincase. The lower end of the stapes is expanded considerably and is separated into two condyles by a deep sulcus. On the upper end of the expanded stapes is found a round stapedial foramen. Above this opening this bone bends obliquely upward. Right above this stapedial foramen a comb-like projection extends obliquely and upward from the inner margin of the bone and diagonally over its posterior surface. This projection ends at the external margin of the stapes with a minute delicate process that is directed toward the ascending lamina of the quadrate ramus. Above this process the stapes has customary round diameter. The presence of this small process points [p. 128] to an old characteristic—the connection of the stapes with the quadrate (15). In the occipital region, the parasphenoid surrounds the lower surfaces of both exoccipitals and almost reaches the base of the condyles.

The ascending laminae of the quadrate ramus are connected with the descending edges of the squamosals. Outside the tympanic cavity on the external surface of the mandible between the quadrate ramus of the pterygoid and the squamosal bone is a narrow cleft that passes posteriorly into the ordinary

[missing page]

decidedly do not belong to the above-named fragments and are derived from a much smaller individual.

Fragment No. 13 is a jugal portion of the cranium that almost equals the lower jaw of skull No. l in size. The exterior margin of the right orbit is preserved.

Fragment No. 14 is a segment of the right pterygoid-ectopterygoid complex of the cranium.

Fragment No. 16 (Pl. XI, fig. 8) is the articular end of a small left lower jaw. Only a small portion of the bone has been preserved. On account of its weak development the retroarticular process is of interest.

Fragments 13 and 14 have not contributed any information concerning the genus *Platyops* and are therefore not pictured. [p. 129]

In fragments Nos. 2 and 3 the palatal and dental surfaces were cleaned of encrustations.

After correcting the displacements of the bone as found in the matrix, we succeeded in joining together fragments 5, 6, and 7 and the lower jaws, which were separated from Nos. 2 and 3, a complete anterior end of the lower jaw, and to partially restore it (Pl. X, fig. 2). Fragments Nos. 2 and 3 were also glued together (Pl. X, figs. 3 and 4).

The united fragments Nos. 2 and 3 show the preorbital portion of the snout which is broken off in the back near the anterior end of the interpterygoid fossae, and in the front—a little ahead of the choanae. The palatal bones are poorly preserved, and their sutures are not distinguishable.

The prevomers are broad and very long; they bear moderately dense arrangement of "canines" which are placed in a checkerboard arrangement parallel with the main tooth row on the maxillae. On the anterior end of the fragment are long and narrow and relatively large choanae. They are close to each other and are separated by a strongly elevated portion of the prevomers. When compared with the complete skull, the position of the choanae in our fragment shows that they were placed rather far toward the back. Behind the choanae is an aperture mentioned by Trautschold, which apparently lodged the large post-choanal teeth.

The lower jaw is very interesting. In the proximal third of the interspace between the choanae and the interpterygoid cavities, both branches of the lower jaw enter into a long symphysis and thereby become sharply reduced. From this point the mandible extends forward as a narrow, massive, and semi-round bone. Its component parts have coalesced here so firmly that it is impossible to distinguish the sutures. The lower jaw bears a row of numerous teeth that are rather small, of the same length, and somewhat bent posteriorly. The teeth increase in width at the expanded anterior end and at the beginning of the constriction of the mandible in front of the round expansion. The teeth in our specimen have not been preserved, but their dimensions can be determined from the sizes of the alveoli. The lower mandible is covered by fossa-like furrowed sculpture.

Fragment No. 4 is badly preserved and deformed.

It was found through preparation that the upper portion of this fragment represents a portion of the rostrum (pl. 11, fig. 4). It is difficult to assign it to skull No. 1. The upper maxilla of the fragment bears rather small teeth, whereas the lower jaw (pl. XI, fig. 3) has very large teeth in the anterior end of the fragment. These are somewhat bent, and surround the rostrum where its sudden reduction to the front begins. The number of the teeth is three on each side;—

two of almost the same size and a smaller one, which plays the role of a supplementary tooth. These fluctuations in tooth size in *Platyops* are very remarkable and recall a similar structure in Recent gavials.

The position of the nares could not even approximately be established the *Platyops*. In all probability they were situated far ahead of the choanae.

While preparing skull No. l several postcranial bones were found in the stony mass surrounding the ventral surface of the skull, which probably belonged to the same individual.

l. Vertebra (pl. XI, fig . 6). A typical rhachitomous cervical vertebra consisting of 3 elements and having large pleurocentra. The neural arch is distinguished by well developed pre- and postzygapophyses, and a relatively low spinal process that is bent somewhat posteriorly. There is a hypocentrum of the second vertebra in situ. The hypocentra are deeply excised for the chord and do not show any high degree of ossification, which is characteristic for [p. 131] later Rhachitomi.

2. Hypocentrum (pl. XI, fig. 7) of the same type, but with only partially preserved haemal arch, which belonged to the caudal section.

3. Rib (Pl. XIII, fig. 5) with a very fine, strongly expanded, and somewhat damaged head. This rib is thin, and the sharp incline in its outer surface indicates that *Platyops* had a relatively narrow and high torso. In addition to these bones, two hypocentra and the upper part of a poorly preserved scapula were found within the interpterygoid cavities of skull No. l; these had to be destroyed in order to prepare the basicranial section.

The above-described facts enable us to form a fairly accurate representation concerning the structure of *Platyops*. It represents a typical rhachitomous form in the series of long-headed labyrinthodonts, one that has retained many of the primitive characteristics; the loose suture of the supratemporal and squamosal, an indication of the stapes joining with the quadrate, the structure of the braincase and the basicranial section. The structural details revealed during the study of *Platyops* were proved for the first time as belonging to a series of long-headed labyrinthodonts. They demonstrated that this series has retained more primitive characteristics than any other form of other series that were coeval with the representatives of the above-mentioned series.

Fig. 9. *Archegosaurus decheni*. Palatal aspect of the cranium (acc. to Watson). 1/6

nat. size.

The comparison of *Platyops stuckenbergi* with known representatives of the superorder of labyrinthodonts shows an immediate relationship to *Archegosaurus*. The form and interrelationship of the dermal bones in the cranial roof are very similar in *Platyops* and *Archegosaurus* (figs. 1 and 2). Their palatal structures in their general arrangement are not distinguishable (fig. 9). The basicranial portion of *Archegosaurus* is unfortunately little known and furnishes no criterion for comparison. The manner of suspension of the cranial base is however the same in *Platyops*, but thanks to the absence of ossification of the basisphenoid and the reduction of the basipterygoid process, it has attained a higher degree of evolution. [p. 132]

For this reason it is probable that *Platyops* represents a special form of an old group of Archegosauridae that were distributed throughout Eurasia. The essential peculiarities of *Platyops* consist in the progressive adaptation together with the sharp elongation of the rostrum, in the expansion of the infratemporal cavities and the resulting convexity of the forehead. It is possible that the same transmutations will be proved in their embryonic stages in old longirostral individuals of *Archegosaurus*, in case we should find their well-preserved remains. An indication of the preservation of the "table" also takes place in *Archegosaurus*, as can be plainly seen from the figures of Burmeister (4). It is very interesting that in such an old individual as indicated by the skull of *Platyops stuckenbergi*, no traces of ossification of the sphenoid are observable, in contradistinction from *Archegosaurus*. There are likewise differences in the disposition of the orbits, which are placed more laterally and forward in *Platyops*. When we turn to the primitively organized longicranial forms of labyrinthodonts, we find in the Lower Carboniferous an embolomerous form such as *Pholidogaster* (figs. 10 and 11). This form is very old in comparison with the one described above, but it shows several characteristics that allow it to be viewed as the common progenitor of a series of longicranial forms (23). Most remarkable is the structure of the basisphenoid with its shape of a high trapezoid that extends freely backward from the ventral side of the long quadrate ramus. The general structure of *Pholidogaster* shows that its evolutionary development takes a different direction than that of the other coeval forms, e.g. *Loxomna*, i.e. in the direction of parvicranial structure as a result of an active mode of life. Another embolomerous form, *Palaeogyrinus decorus* Wats., likewise from the Carboniferous of England, greatly recalls *Platyops* both in the construction of the neurocranium, as well as in the expansion of the quadrate ramus. I present here a figure of a neurocranium of *Palaeogyrinus* (fig. 6), upon which is observable a very characteristic looping of the basicranial portions by the parasphenoid and a considerable anterior expansion of the paroccipital. Simultaneously the braincase of *Platyops* is distinguishable by a considerable expansion of the cranial base and lesser ossification. It is probable that the bone designated as a basisphenoid in *Pholidogaster* by Prof. D. M. S. Watson represents mostly the parasphenoid which surrounds the cranial base in the form of a thin sheet. [p. 133]

Another interesting common characteristic of *Palaeogyrinus* and *Platyops* is the structure of the ascending lamina of the quadrate ramus of the pterygoid. The ventral margin of the quadrate ramus descends far under the surface of the cranial base thus giving rise to a step-like disposition of the condyles behind, while the masticating muscles are separated from the buccal cavity by a continuous bony wall. Such an old form of Embolomeri must be differentiated from so late a representative of Rhachitomi as *Platyops*, at least by its very primitive character.

Fig. 10. *Pholidogaster pisciformis*. Dorsal surface of the cranium (acc. to Watson). 3/7 nat. size. Tem. – intertemporal, Pt. Fr. – postfrontal.

Fig. 11. *Pholidogaster pisciformis*. Ventral surface of cranium. (acc. to Watson). 3/7 nat. size. Proc. B. Pt. – basipterygoid process, Bsp. – basisphenoid, Ec.pt. – ectopterygoid, Pv. – prevomer, Pal. – palatine.

However, such common characteristics point to the possibility of parallel retention of similar anatomical peculiarities even in very primitive forms and are useful in testing the correctness of the data received.

It would be of the highest importance to examine *Cricotus* which stands in the same series of longirostral forms with high and narrow crania (fig. 12). This form is very interesting as a representative of Lower Permian Embolomeri. Unfortunately, the structure of the occipital, basicranial, and auditory portions [p. 134] of *Cricotus* is unknown. Because fairly complete skulls are available, this must be ascribed to insufficient investigation and faulty preparation (3 and 12). There is no doubt that a thorough examination of *Cricotus*, *Chenoprosopus*, *Cricotillus*, and *Archegosaurus* could furnish much information concerning the evolution of the long-headed series that originated and developed in Laurasia. That continent shows altogether different centers of form development than the other great continent of that age, Gondwana. It is possible that the examination of a series of long-headed forms will eventually reveal a gradual transition from Embolomeri to Rhachitomi. On the basis of an observed existence of a series of long skulls, I propose widening out the concept of the family Archegosauridae—because *Archegosaurus* is a member of the series that was established first—and to assign to this family the rank of superfamily.

In such case the diagnosis of *Platyops stuckenbergi* Trautschold may acquire the following form:

Superorder Labyrinthodontia, order Rhachitomi, superfamily Archegosaura, family Archegosauridae, subfamily Platyopsidae, genus *Platyops*, species *stuckenbergi*.

Fig. 12. *Cricotus crassidiscus*, skull from above (acc. to R. Broom). 4/9 nat. size.
Ssq. (suprasquamosal), St – supratemporal.

The skull is of triangular form, relatively high with a long and narrow rostrum. The orbits are fairly large, oval in form, and their longitudinal axes are obliquely disposed. The orbital surfaces are directed anterolaterally. In relation to component elements of the cranial roof, the orbits are situated almost in the middle of the skull, somewhat close together with their inner margins slightly lifted and with the interorbital strip somewhat concave. The preorbital region of the skull is strongly elongate. The choanae are placed forward of the back. The lower jaws have coalesced into a large symphysis in front of the interpterygoid cavities and have round expansions at their end; in all probability the end of the rostrum was also expanded in a similar manner. The interpterygoid cavities are relatively narrow, the infratemporal foramina are exceedingly large and deep. The parasphenoid is trapezoidal in form, narrowed anteriorly with margins bent upward and forming cylinder-like folds laterally. The attachment with the basal portion of the pterygoids is brought about by the simple superposition on the most anterior portion of the parasphenoid body; the basicranial section is freely suspended between the quadrate ramus of the pterygoids.

The cultriform process is relatively narrow, expanding somewhat toward the front. The palatal rami of the pterygoids reach the anterior end of the interpterygoid cavities, reveal a shagreen dentition, and are very broad. They are bent downward, which results in the convexity of the palate. The ascending laminae of the quadrate ramus are strongly expanded and form a continuous bony wall for the masticatory muscles. The mandibular condyles do not reach far beyond the condylar section of the occiput, and reveal a step-like structure. The paroccipital is well developed and directed to the front, thus building the supra-posterior part of the lateral wall of the braincase, and surrounding the fenestra ovalis from the front and above. The stapes bears a minute lateral process. A well-ossified basioccipital and a small epipterygoid are present. The supraoccipital, sphenethmoid, and basisphenoid were not completely ossified. It must be mentioned that the supratemporal takes part in building the auditory meatus. [p. 135]

Biologically *Platyops* converges, without any doubt, with Recent gavials, on account of its narrow and long rostrum, characteristic distal expansion, dental system, and posterior position of the choanae. However, the rostral elongation is not so great as indicated by Trautschold or as in the case of the gavial, but its role in adaptation is the same.

The low spinal processes of the vertebrae, which are directed posteriorly, the broad heads of the obliquely descending ribs, and the features of the appendicular system as represented by Trautschold, indicate that *Platyops* possesses a narrow, high trunk, probably a long tail, and relatively small but strong limbs that were suited to rapid swimming.

2. Fauna of the labyrinthodonts *Platyops* from the lime rocks of Chirki-Shikhovo on the Viatka River.

History of the Expedition.

The village of Chirki-Shikhovo is situated on the right shore of the Viatka River, some 24 km above the city of Viatka. The Late Permian lime deposits in the Chirki-Shikhovo stone quarries have been known for a long time on account of a rich fauna of Permian fishes. The remains of stegocephalians found there were either not examined at all, or considered to be those of fishes.

In the years 1923–1924 A. W. Chabakov, acting under the orders of Prof. A. Rjabinin, brought hence a number of indubitable stegocephalian remains. Although incomplete, these remains indicated the presence of labyrinthodonts with a narrow and long rostrum in the lime strata of Chirki-Shikhovo. They were established by Prof. Rjabinin as the remnants of *Platyops*, without any precise description of the data, however, since even the description of the generic type as furnished by Trautschold was very indistinct. [p. 136]

The work of A. W. Chabakov on the fishes of Chirki-Shikhovo is now finished, and according to his kind communication these fishes are represented by the genera *Platysomus*, *Amblypterus*, *Acrolepis*, *Palaeoniscus*, and *Atherstonia*.

In 1928, on my return trip from the Sharenga expedition organized by the Academy of Sciences of the USSR, whose leader I was, I visited the College of Chirki-Shikhovo. In spite of the short sojourn there, I succeeded in gathering a considerable number of remains of both labyrinthodonts and fishes, and establishing the circumstances of their burial and geologic position (8). In the quarries of Chirki-Shikhovo is a series of multicolored marly limes some 25 m in thickness.

The limestone strata are not dislodged and contain no filler of marl or gypsum. The coloration of limestones varies from dark gray to pure white. In the upper portion of the series the limestone layers are thinner, the deposits of marl much heavier, and finally the whole series passes over into marls with thin layers, upon whose surface lies the loamy high-terraced alluvium of the Viatka River. The limestone strata are considerably thicker toward the middle of the deposits, which generally are oriented in a NE–SW direction. They contain more marl or even sand toward their edges and show a gradual reduction in thickness toward the center. The site represents without doubt the deposits of a small water basin of the estuary type, in which has taken place first the deposition of carbonates which ended with that of pelites. The details of sedimentation were not established by us. It is possible that the limestones of the mentioned site represent only a cyclic variation in the littoral of the basin. The labyrinthodonts occur in only one stratum of limestone and in the marly interstratum that covers this limestone layer. Counting from above, it is the 23rd layer (according to G. Fredericks) which contains a white marl-bearing limestone and is named by the local inhabitants "Belyak" and which, lying in the lowest portions of the laminates series, emits the smell of H_2S when struck. The whole laminated series was opened in 5 places, but only in cut No. 1 (in the northeast portion of location) are the remains of labyrinthodonts and fishes found in such abundance that the whole layer is filled by them. The bones are dark in color, very friable, much deformed, and sharply contrasting from the white limestone. The remains of stegocephalians and fishes are scattered without any order through the layer. The elements of the postcranial skeleton are generally [p. 137] separated, which induces the supposition that burial took place when the macerated corpses were washed down by constant streams which emptied into the estuary.

The collected material contains 11 incomplete skulls and cranial fragments of labyrinthodonts, as well as numerous poorly preserved bones of the postcranial skeleton. The limestone from which the material was collected was broken up in winter and has cracked up badly under the influence of frost. This, together with the great friability of the bones and their bad state of preservation, has rendered preparation very difficult.

The whole material is not yet prepared in view of the poor preservation of the remains and strong intermixture of bones of different specimens. Supplementary material is needed. After a reexamination of the genotype of *Platyops*, *Platyops stuckenbergi*—the labyrinthodont fauna of Chirki-Shikhovo could be established with certainty.

Description of the remains.

Skull No .1 (No. 8/2250 Palaeoz. Inst.) (pl. XII, fig. 3) presents the ventral surface and is covered by a thin lamina of limestone. The cranium is strongly fractured in the dorsoventral direction, which makes it difficult to prepare its dorsal surface. There is a sharp coarctation of the cranium toward the end of the interpterygoid cavities. Its entire left portion is broken off. Likewise the hole left infratemporal foramen with the surrounding bones is missing and the posterior margin of the cranial base is broken off. The occipital portion is broken off and is not preserved. The interpterygoid cavities are relatively narrow and the infratemporal foramina are very big. The parasphenoid has the form of a high trapeze, it is connected with the pterygoids only by its anterior portion and extends itself freely backward between the quadrate ramus. Its lateral margins are bent upward and form in a lateral direction 2 cylindrical folds. In front the parasphenoid bears the narrow cultriform process. The fairly wide palatine rami of the pterygoids reveal shagreen dentition. The anterior margins of the interpterygoid cavities have been completely preserved; unfortunately the sutures between the bones are not distinguishable. In general, the palatal structure does not show any essential differences from *Platyops stuckenbergi*. There are a few intimations of evolutionary transformations which are revealed in the development of a firmer and broader connection of the parasphenoid body, and the basal portion of the pterygoids in the greater coarctation of the cultriform process and it appears, in a certain enlargement of the interpterygoid cavities. It is possible that in the occipital portion which has not been preserved the same insignificant transformations have taken place.

Skull No. 2 (No. 1/2250) (pl. XIII, fig. 2) represents the complete nasal portion of a small young specimen with its postorbital part broken off. The skull is badly preserved. All the bones of the cranial roof are completely broken off so that in the nasal region of the skull are exposed the much-damaged endocranial bones, and in the orbital region the endocranium is likewise destroyed. The skull is of interest because a strong elongation of the preorbital elements is not observable, due probably to the youth of the individual. There was preserved an impression of the left orbit which shows an oval form, oblique position, and a raised inner margin.

The impression of the skull No. 3 (Nos. 18 and l8a/2250) (Cast pl. XIII, fig. 3) has been preserved very imperfectly and has a complete nasal portion that furnishes the basis for a precise reconstruction. A portion of matrix in the middle of the rostrum is broken off. The occipital margin and its whole left post-lateral cranial contour are broken off. On the cast that is pictured [p. 138] in our photographic figures, the sutures of the cranial roof are discernible in all their details and agree in all respects with those of *P. stuckenbergi*. The right orbit and the inner margin of the left orbit are intact. There is a round parietal foramen that lies at a certain distance behind the orbits, as in *P. stuckenbergi*. At the end of the rostrum a weakly expressed roundish expansion is indicated.

The impression of cranium No. 4 (Nos. 15 and 15a/2250) (Cast pl. XIII, fig. 1) shows the deformed cranial roof of a large individual. The rostrum and the right occipitolateral margin are broken off. We succeeded in establishing the sutures of the cranial elements. The contours of the bones are identical with those of skull No. 3 and therefore the following description applies equally to skull No. 3.

The parietals are well developed and narrowed toward the front, the fairly large parietal foramen is situated at the beginning of the coarctation. The postfrontal is large, sickle-like, and unites with the prefrontal in front at the beginning of the anterior margin of the orbit, forcing the latter in to the the interorbital strip. The large postorbital is triangular, elongate, and wedged between portions of the supratemporal and squamosal. The large dermosupraoccipital is strongly expanded in the occipital region. The preserved left auditory excision is fairly deep, the posterior horn of the tabular does not extend far back. In the auditory passage is the impression of a stapes that is displaced toward the back due to deformation.

The squamosal has a small lump on the suture with the supratemporal ahead of the auditory passage, which is characteristic for *Platyops*. The orbits are rather large with oval contours and convex inner margins. In spite of deformation we perceive that the orbital axes, especially the right, are obliquely oriented. In the preorbital region the cranium has a rather sharp coarctation, and the lateral indicates a parallel course.

The roof of cranium No. 5 (No. 6/2250) (pl. XI, fig. 2) represents the almost entirely preserved postorbital region of an average-sized cranial roof that is somewhat deformed dorsoventrally. In the anterior portion of the fragment the posterior margins of the orbits are preserved.

The endocranium is not preserved. The orbits are oval and obliquely [p. 139] oriented. A small parietal foramen is found in back of the orbits. The sutures of the cranial roof are hard to distinguish as a result of the bad preservation of the specimen. The suture between the supratemporal and squamosal seems to be narrowed more than in the genotype. There is an elevation extending infero-anteriorly from the auditory incision. The tabulars are not large on their dorsal surfaces, their posterior ends are rather short. The posterior contour of the supratemporal touches the auditory excision between the tabular and the squamosal. The mandibular condyles do not extend far back; they are partially damaged and crushed. The occipital margin of the skull bends strongly toward the front in the form of an arc with a small radius.

Cranial impression No. 6 (Nos. 19 and 19a/2250). The cast of it (pl. XI, fig. 1) shows the roof of a small cranium with the preorbital region lacking. The skull is strongly deformed, the sutures having disappeared; however we are able to form a clear representation of its shape and the shortness of its mandibular condyles, as well as of the short processes of the tabulars.

Cranial fragment No. 7 (No. 2/2250), which represents the orbital region of a large skull, shows the oblique placements of the orbits, the broad palatine rami of the pterygoids, and the anterior expansion of the narrow cultriform process.

Fragment No. 8 (No. 20/2250) (Pl. IX, fig. 4) represents the middle of an average-sized skull. It was prepared from the ventral side. In spite of its extremely bad preservation, the fragment is worthy of notice. It shows the anterior portion of the interpterygoid fossae, the narrow cultriform process, and the nasal region with its long and narrow choanae. It is plainly visible that a very noticeable coarctation takes place near the anterior border of the interpterygoid fossae. This narrowing is less pronounced in the rostral direction up to the choanae [p. 140], whence the lateral margins of the cranium run parallel. The fragment recalls in its general appearance the identical regions in the longirostral labyrinthodonts *Aphaneramma* and *Lonchorhynchus* from Spitsbergen (26 and 27).

Thanks to the greater narrowing of the preorbital region, the choanae approach each other even more than in the case of *Platyops stuckenbergi*.

Skull No. 9 (No. 4/2250) (pl. XI, fig. 5) represents the left half of a small skull that is much compressed dorsoventrally and does not show the nasal region. Only the left orbit, the left auditory excision, and the left mandibular condyle are complete. The skull, belonging to a young individual, is particularly interesting. It possesses characteristics that distinguish it from the adults—a relatively broad and abbreviated cranium, abbreviated mandibular condyles, and elongated tabular processes. The last characteristics must be partly ascribed to deformation, which has pushed the auditory fossa apart and shoved the tabular toward the back and under. The sutures are not distinguishable due to the poor preservation of the bones.

Skull No. 10 (No. 3/2250) (pl. XII, fig. 4) belongs likewise to a very young individual. It is almost the same size as No. 9 and shows the same peculiarities. In contradistinction to skull No. 9, the right postorbital half and a small part of the preorbital half are preserved. In addition to the bad state of preservation, skull No. 10 is crushed more together than skull No. 9.

Besides the described remains, there is in the collection a series of uncertain fragments that cannot contribute anything substantial to the completion of the results obtained. There are poorly preserved nasal regions that allow us to infer that in large individuals the extension and narrowing of the preorbital cranial region was considerable (No. 14/2250).

Of the numerous remains of the postcranial skeleton, the following bone can be attributed with certainty to *Platyops*:

1. The neural arch (No. 22/2250) of a rhachitomous lumbar vertebra. It is on account of the low spinous process, bent strongly backward, the massiveness, and the structure of the transverse process. The neural canal is very narrow and the zygapophyses are not developed (pl. XI, fig. 9).

2. The fragment of a right scapula (No. 23/2250) though badly preserved shows however the central portion of the delicate and narrow scapula (with a remnant supraglenoid foramen?).

[p. 141]

3. An interclavicle (No. 24/2250) (pl. XIII, fig. 6) belongs to a small individual. This delicate and poorly preserved bone of an abbreviated rhomboid shape is covered by striated

sculpture. The upper portion of the bone is broken off; according to all appearances it extended upward in the form of a corner so that its general aspect was of that of 2 different triangles put together. The lower triangle was isosceles with a large top angle, the upper triangle was acute with a sharp apex. On the right side of the bone (left on the skeleton) the facet for the clavicle is partially preserved. The center of sculptured striae is in the geometric bone center.

4. A left clavicle (No. 25/2250) (pl. XIII, fig. 4) was very poorly preserved. The inner anterior and posterior margins and the suprascapular process are broken off. The bone shows considerable thickness, well-expressed grooved sculpture, and belonged indubitably to a large individual. Its inner margin is very delicate; this indicates that it has broken off probably very close to the true margin of the bone.

The clavicle undoubtedly was long and narrow, thus indicating that it belonged to an active animal.

The humeri No. 26/2250 and No. 27/2250 are very badly preserved, greatly deformed, and belonged to animals of different sizes. Through examination of both bones we can conclude that the humerus was a thin, slender, and relatively long bone that possessed the usual screw-like twisting of the epiphyses, but did not have the large unciform processes for the attachment of muscles as is the case with continental forms of labyrinthodonts.

The ilium (No. 28/2250) (pl. XI, fig. 10) is fairly interesting in spite of its preservation. It is a relatively small and thin bone. Its upper end is hardly enlarged at all, bent somewhat in an anterior direction, and has elevated anterior and posterior margins with traces of muscle and ligament attachments. In the region of the acetabulum is a characteristic hump. The lower end of the bone is crushed, which gives it a strongly expanded appearance. Its anterior and posterior margins were originally bent outward and the expansion was somewhat smaller. This ilium in its form is distinguishable from the short, expanded, and massive ilia of later Rhachitomi and is characteristic of the active, aquatic longicranial labyrinthodonts.

There is, besides the described bones, a poorly preserved hypocentrum (No. 21/2250) (pl. XIII, fig. 7).

Among the unprepared remains in the collection were numerous ill-preserved hypocentra that do not show any peculiar shape and are typical of the usual rhachitomous vertebrae. The remaining elements of the postcranial skeleton [p. 142] are very badly preserved and, being found mixed together in the multiform fauna of Chirki-Shikhovo, require the greatest circumspection in their determination. There are 4 gastrocentral vertebrae fused together, which must have belonged to the same reptile.

Together with above-described skulls was found a cranial fragment that must have belonged to a labyrinthodont of another type. I deem it necessary to give a brief description of it (although it is impossible to classify it exactly) in order to record the presence of such forms in Chirki-Shikhovo. The skull (No. 5/2250) (Pl. XII, figs. 1 and 2) is greatly compressed dorsoventrally and so badly crushed that its thickness (height) does not exceed 1 cm. In spite of this circumstance, and the fact that the matrix had a tendency to crack, it was dexterously prepared from its dorsal and ventral surfaces by F. Kuzmin of the Palaeozoological Institute.

The skull represents the left half of the preorbital portion of a large brevirostral labyrinthodont. The postorbital portion is entirely broken off, the left orbit is perfectly preserved. The bones of the cranial roof are partly broken off and their sutures cannot be traced. The orbit is relatively small, of an irregularly rounded form. Judging from the length of the individual preorbital elements of the cranial roof, the orbits must have been located in the posterior half of the cranium. The right half of the rostral end has been partially preserved. The rostrum is blunt and rounded, but is narrow when compared with the broad postorbital region. The small, longitudinally oval nasal apertures are placed laterally at the posterior end of the anterior rostral third. The strong deformation is plainly visible on its ventral surface (pl. XII, fig.2). The right half of the rostral end is displaced to the front and under. The palatine ramus of the pterygoid is torn off from the palatine and ectopterygoid bones, shoved forward and inward, and broken in two. The margins of the left choana are broken off, giving the latter an enormous appearance.

The palatine ramus of the pterygoid is very long and reaches the prevomers anteriorly; its narrow anterior portion and its entire external margin are covered by grooved, ray-like sculpture, the remaining portion reveals a shagreen dentition.

The palatine is long and narrow and forms the posterior margins of the choanae. It bears two very large postchoanal teeth and a second row of small teeth. The ectopterygoid is partially preserved; it is broad and bears a row of teeth that are the continuation of those found on the palatine. The maxilla is massive and commences at the anterior margin of the choana; it is broken off at the posterior end of the fragment. It bears a row of teeth along its entire length.

The premaxilla is strongly developed and forms the entire anterior end of the skull; it bears on its margin large teeth of the first order. In place of the anterior palatal openings are deep fossae that do not communicate with nasal cavity. The anterior or palatal openings probably pierced the [p. 143] premaxillae; however, the absence of this feature on our fragment can be explained by the strong deformation, and the poor preservation of the bone.

Of the parasphenoid there was preserved only the anterior end of the very narrow cultriform process.

The broad prevomers bound the choanae from the inner margins in the middle portion; they bear likewise shagreen teeth. The postmedial ends of the bones are elongated into a pointed process that meets the cultriform process of the parasphenoid.

The exceedingly long palatine ramus of the pterygoid enables us to draw the inference that the cranium belongs to a representative of the Rhachitomi. The small cultriform process points to a possible relationship of the animal to the family Rhinesuchidae, although the length of the pterygoid, the size of the choanae, and the narrow structure of the anterior palatal portion, which in typical Rhinesuchidae is expanded diagonally, contradict this. In its general configuration and in the narrowing of the jugal region it resembles greatly the skull of *Melosaurus*. The type skull of *Melosaurus* (the only specimen) has been unfortunately very imperfectly described by H. v. Meyer (13). In consideration of the contradictory features, I assign the skull No. 5/2250 provisionally to ?*Melosaurus* sp., classifying it simultaneously as "incertae sedis." The new discovery in Chirki-Shikhovo must furnish, without doubt, more complete and more easily determinable material concerning this interesting, and as it appears, transitional form.

All the above described skulls Nos. 1–10 greatly resemble *Platyops stuckenbergi* Trautschold both in general aspect and in cranial structure, as well as in the structural details of the endo- and basicranial regions. On the grounds of the above-mentioned facts, I have determined their generic designation as *Platyops* and assign them to the family Archegosauridae. However, all the representatives of the genus *Platyops* from Chirki-Shikhovo show insignificant differentiating characteristics when compared with the genotype, *Platyops stuckenbergi* being of a somewhat higher evolutionary grade. These differentiating characteristics are as follows: [p. 144]

1. Further elongation of the preorbital cranial region which is connected with the cultriform process of the parasphenoid.

2. The development of a more solid connection between the anterior portion of the

parasphenoid body and the basal portions of the pterygoids.

3. A firm connection between the supratemporal and the squamosal.

4. A certain abbreviation of the mandibular condyles. These characters permit us to enter the *Platyops* from Chirki-Shikhovo as a special species that is very closely related to *Platyops stuckenbergi* and which shows a further differentiation in its evolution and adaptation.

I propose to name this species in honor of the renowned English palaeontologist Prof. D. M. S. Watson, who was the first to establish the laws of evolutionary mutations in the labyrinthodonts, *Platyops watsoni*.

As has been mentioned above, we observe a gradual transition from *Archegosaurus* through *Platyops stuckenbergi* to *Platyops watsoni* and notice certain "advances" of labyrinthodonts that have been established by Prof. D. S. Watson and by Academician P. P. Suskin. Through the continuation of these mutations we arrive at a type that finds its expression in the Spitzbergen labyrinthodonts *Lonchorhynchus* and *Aphaneramma*. Both these labyrinthodonts are distinguishable from *Platyops watsoni* by the following features:

1. Through further elongation of the preorbital region and through the very narrow cultriform process.

2. Through the development of a very long suture between the parasphenoid and pterygoids.

3. Through considerable reduction of the mandibular condyles.

4. Through the transposition of eyes somewhat more anterolaterally.

In addition they are distinguished by the following features, which are characteristic for later labyrinthodonts—the Stereospondyli.

(a) By the reduction of the basioccipital, basisphenoid, and palatine ramus of the pterygoid.

(b) By the probable reduction of the paroccipital bone (not firmly established, however).

Fig. 13 shows a reconstruction of the dorsal surface of cranium of *Platyops watsoni*, which has been drawn on the basis of the 10 skulls at hand. In fig. 14 is presented the reconstruction of the dorsal surface of *Lonchorhynchus* according to Abel (1). Both figures show a very convincing similarity and their relationship is like that of descendant to progenitor. I have changed Abel's along the dotted line which outlines the anterior end of the snout.

Fig. 13. *Platyops watsoni*, n. sp.
2/3 nat. size.
Qj. – Quadratojugal
Lac. – Lacrimal
Na. – Nasal
Pmx. – Premaxilla
(Cranial roof restored)

Fig. 14. *Lonchorhynchus obergi*
Cranial roof. Reconstructed
according to O. Abel.
The end of snout has been
rounded off by us.

[p. 146] This rounded rostral outline is identical with that in *Platyops*. Fig. 15 shows the occiput of *Lonchorhynchus* in Abel's reconstruction and next to it our interpretation of the same form. It is very probable that the downward bend (as pictured by Abel) represents cylindrical folds of the parasphenoid which are very characteristic of *Platyops*. The presence of an ossified basioccipital in the occiput of *Lonchorhynchus* is very characteristic for those forms of the longicranial series that have retained the greatest primitiveness. This primitiveness can be explained by life in an extensive freshwater basin, i.e. it was developed through constant facial conditions and through the active exploration of the principal food—fishes. This circumstance has conditioned the influence of external factors upon the longicranial series and its rapid geographic distribution. Its great resemblance to the *Platyops watsoni* corroborates the opinion of D. M. S. Watson concerning the probable descent of the Spitzbergen longirostral labyrinthodonts from a series of different type than the family Trematosauridae. The external narrowing of the cultriform process of the parasphenoid is a modification that is observable simultaneously in several series and finds its clearest expression in the series *Eryops* – *Rhinesuchus* – *Benthosaurus* – *Trematosaurus*. These circumstances make it obligatory to reexamine the taxonomic position of *Lonchorhynchus* and *Aphaneramma* through detailed study of their endocranial portions. It is possible that these two forms will have to be excluded from the family Trematosauridae and that they have descended directly from the Archegosauridae.

Geological conclusions.

The stratigraphic position of the cupriferous continental deposits where *Platyops stuckenbergi* was found is not precisely established. The discovery of the fairly primitive rachitomous *Platyops*, which is relatively close to the Lower Permian *Archegosaurus*, indicates that these deposits are related to the cupriferous stratum P_2r of Kargalin and to the ore-bearing layer P_2. It should be yet mentioned that *Platyops rickardi* Twelvetrees was found in the marly lens of the Roshdestvenski mine in the Kargalin district, which served Trautschold as a basis for his description. This original has been lost, however it has been insufficiently studied because it represented only a fragment of the endocranium. For this reason I have left it out of consideration in my redescription of the genus *Platyops*, although I have retained the generic nomenclature of Twelvetrees without being able to judge the material.

The stratigraphic position of the limestone layers of Chirki-Shikhovo must be higher than the position of the cupriferous layer of Kityak. This was the opinion until the present time, and is corroborated by the fact that such a geological deduction agrees with the correct palaeontological investigations.

The inferences of geologist Mazarovich as to whether some of the horizons of the continental deposits of the Viatka belong to the Triassic, because the remains of *Platyops* were found in them, are erroneous because the genus *Platyops* is Permian. The limestones of Chirki-Shikhovo correspond most probably to the upper portions of the Kazan horizon and thus to the lower portions of the Tatar horizon if we accept the deposit of gypsum for the end of the cycle of Kazan deposition and the deposits of limestones and marl as forming the base of [p. 147] the Tatar stage. Thus the *Platyops* fauna existed for a considerable period on the Permian continent of Cisuralia, during which time it greatly increased and evolved.

Final Conclusions.

All labyrinthodonts can present multitudinous structural variations in the dermal roof of the cranium in connection with the plastic metamorphosis of its separate elements. Otherwise the basal construction of the endocranium is extremely typical and constant in all series, particularly the Rhachitomi and Stereospondyli.

We want to describe now a few principal types of structure of the cranial roof. In fig. 16 the most typical forms of the different series are schematically represented. As I have already mentioned in my work on *Benthosaurus* (7), the orbits, through their modified position in the cranial roof, plastically change the form of individual dermal bones. Through displacement in the rostrum, the nares also modify the dermal elements. In all cases the parietal foramen is retained as an immovable center. This is due to the fact that the parietal foramen is connected with the basisphenoid and is always situated above the sella turcica, that is to say, the mechanical center of the cranium.

In the forms with orbits displaced backward and close together, such as the series of *Capitosaurus* skulls (fig. 16, B), the postorbital elements are closely pressed together and abbreviated, while the preorbital ones are considerably elongated. The expansion of the skull, particularly the snout, is accompanied by the expansion of the preorbital and lateral dermal elements. The parietal foramen approaches the line connecting the posterior borders of the orbits. The opposite is observed in forms with anteriorly displaced orbits (*Metoposaurus*, fig. D). The postorbital dermal bones are strongly elongated and dominate, by their size, the compressed and small preorbital bones. The parietal foramen lies far back from the line of the posterior orbital margins. Fig. C, representing schematically *Platyops* or *Archegosaurus*, shows that the line of the posterior orbital margins is situated far in front of the parietal foramen. This harmonizes with the postorbital dermal elements, which are so elongated as if the orbits were situated in the middle of the skull. Therefore we must regard this structure of the cranial roof as a form whose orbits lie closely to the cranial center and which reveals a disproportionally elongated preorbital cranial region as an adaptive modification. All young individuals of *Archegosaurus*, as well as of *Platyops*, actually reveal a strong elongation of the nasal region, which increases gradually with age. We see in fig. F, which represents a later brachyopid, how the dermal cranial roof stretches forth diagonally while all the individual dermal bones are completely closed. The pre- and postorbital elements are extremely narrow longitudinally and widen out diagonally. The enormous orbits are likewise very close together, while the interorbital bones are narrowed down. Simultaneously all the lateral elements are extremely large and so strongly expanded that they appear oriented diagonally. The parietal foramen lies between posterior margins of the orbits. The very young forms of labyrinthodonts—a young *Archegosaurus*, *Eryops anatinus*, and a very small skull of *Benthosaurus* from my excavations on the Sharshenga River—show the following interesting peculiarities:

1. The mandibular condyles lie in the plane of the condylar section of the occiput. [p. 149]

2. The orbits are relatively large and situated. in the middle of the cranium.

Fig. 16. The forms of the dermal elements in the crania of labyrinthodonts

(greatly schematized). A. – Embolomerous type; B. – *Eryops* type; C – *Platyops* type; D. – *Metoposaurus* type; E. – a larva or very young type; F. – Brachyopidae type; G. – *Diceratosaurus*; H. – *Pelosaurus*.

3. The parietal foramen lies very close to the posterior margins of the orbits; and still oftener between the posterior margins.

4. The otic incisures are not sharply indicated.

The young and larval forms that are known in the series of parabolic skulls, namely the groups Brachyopidae—*Platyceps wilkinsoni* Steph. and partly the young *Dvinosarus* which has been described by W. P. Amalizky (No. 33 Am) as *Dvinosaurus primus*—have a relatively narrower skull than adult individuals. In "*Dvinosaurus primus*" the skull is almost triangular and the orbits are nearer to the cranial center than in older individuals. The outer orifice of the parietal foramen in Dvinosauridae is not known.

The schematic interrelations of the elements of cranial roof in a young form are pictured in fig. 16, E. It can be demonstrated that they resemble those of the old form of Embolomeri which is represented in fig. 16, A.

The representatives of the remaining divisions of the old amphibians—the Lepospondyli and Phyllospondyli—are pictured in figs. G and H. In *Diceratosaurus* (fig. G), the orbits are placed far to the front, the parietal foramen being closer to the orbits and farther from the occipital region than is the case in the Labyrinthodontia.

Pelosaurus, one of the most typical branchiosaurids (fig. 4), has similarly developed pre- and postorbital elements. Its great orbits lie approximately in the middle of the skull. However, the parietal foramen lies far from the occipital margins on the hindermost margins of the orbits. We also encounter characteristics in *Pelosaurus* that correspond to the young—and larval forms—of labyrinthodonts.

In *Diceratosaurus* the occipital portion of the cranial roof is apparently better developed and extends farther back than in labyrinthodonts, whereas the line of its occipital section is inclined backward. In *Pelosaurus*, which recalls labyrinthodont larvae, we observe, as it seems, a different stem of cranial development than in labyrinthodonts. The extreme abbreviation and the transposition of mandibular condyles to the fore was brought about much earlier in *Pelosaurus* than in labyrinthodonts.

The oldest skull, which served as an initial type for all the cranial series, had apparently an almost triangular high shape, possessed an equal development of the pre- and postorbital elements, and centrally located orbits. The parietal foramen, due to its constant connection with the basisphenoid, remained stationary in all the modifications of the cranial roof, which had as its result its gradual reduction. Through the powerful structural dynamics of labyrinthodonts, the forced statics of the parietal foramen became uncomfortable. On the basis of [p. 151] what has been stated above, it appears probable that both eyes of the oldest skull, belonging perhaps to an ancestor still living on dry land, were situated laterally in the skull, namely in its marginal elements, which have shown a proportionally equal development with the "table." The parietal foramen, which was large in comparison with its known reduced forms, was situated between the orbits on a line with the orbital centers. By its immutable connection with the basisphenoid, we can surmise that the latter was situated farther to the front than is the case in the present forms. We shall see the corroboration of the inference below.

Fig. 17. Evolution and reduction of the supraoccipital (schematized). A. – Old Embolomeri (Lower Carboniferous); B. – Old Rhachitomi (Lower Permian); C. – Old Stereospondyli (Lower Triassic); SO – supraoccipital: black markings – osseous portion; dotted markings – cartilaginous.

During the continued evolution of the labyrinthodonts a development and progressive enlargement of the skull has taken place at the expense of the central and preorbital dermal elements, with a simultaneous impingement on that wall which had its origin in the confines of the last occipital segment. Such a course in cranial growth harmonizes with the entire evolution of labyrinthodonts, which is expressed in the loss of several occipital segments and the absolute predominance of the orbit-nasal region.

Very interesting in the evolution of the labyrinthodonts is the gradual reduction of the supraoccipital, which is represented in fig. 17. In the remaining Embolomeri (fig. A), the large supraoccipital forms a portion of the cranial roof at a somewhat inclined plane, and articulates with the dermosupraoccipital by means of the oblique cut of the dorsal surface. In the reciprocal relation of the supraoccipital and the basioccipital we may observe certain resultant symmetry of the brain capsule.

In older Rhachitomi (fig. B) the supraoccipital is much more reduced [p. 152] and inclined. The dermosupraoccipital acquired an oblique orientation, descending suddenly to the occipital surface, under which reposes the supraoccipital. The upper portion of the exoccipital likewise incline forward. Thus the occipital portion of the neurocranium emerges somewhat to the rear of the margin on the cranial roof, while the entire occipital surface is inclined toward the front. Distinct examples of such structure are observable in *Eryops*, *Platyops*, and many others.

Fig. C represents a stage in the final reduction of the supraoccipital that may be observed in old Stereospondyli and in later Rhachitomi. The occipital surface again acquired a vertical position, and the supraoccipital lies entirely under the dermal crania1 roof. In the position of the strongly reduced basi- and supraoccipital, a secondary symmetry is observable. The entire series of these transformations is accompanied by a progressive development of the parasphenoid, so that in the final evolutionary stage, the remnants of the occipital region of the primitive neurocranium lie almost parallel to each other between the dermal cranial base and the cranial roof of the flat skull. An analogous transposition of the supraoccipital under the dermal cranial roof is observable in *Pareiasaurus* (15). In labyrinthodonts however, the supraoccipital becomes unnecessary and disappears entirely, due to the vertical development of the exoccipital and the descending process of the dermosupraoccipital, which play the role of the supraoccipital in *Pareiasaurus*.

Another very characteristic transformation in the evolution of the dermal cranium of labyrinthodonts is the transmutation of the otic incisure, which harmonizes fully with the progressive expansion and flattening of the skull. With the exception of a few forms in different series representing evolutionary deviations, and whose otic incisures are obliterated, the otic incisure in the evolution of the Embolomeri into the Stereospondyli is unchangeably transposed in a posterolateral direction upon the dorsal surface of the skull. In fig. 18 A B C are found the 4 types of otic incisures in Embolomeri, Rhachitomi, and Stereospondyli. In the oldest Embolomeri (*Pholidogaster*, fig. A) the auditory fossa is a direct product of an incomplete conjunction of the "table" with the lateral elements of the cranial roof. In the Embolomeri of the Upper Carboniferous (*Baphetes*, fig. B), the otic incisure consists of a small portion of the posteromedial margin of the tabular, the largest portion of the supratemporal from the inside and the front, and the squamosal from the outside. In old Rhachitomi (*Eryops*, fig. C) the supratemporal becomes gradually dislodged through the developing tabular and the posterointernal medial corner in the medial portion of the squamosal, and participates in [p. 153] building a small portion of the anterior margin of the otic incisure. In Stereospondyli and later

Rhachitomi (*Benthosaurus*, fig. D), a special process of the squamosal is developed that, meeting the expanded tabular, entirely dislodges the supratemporal from the otic incisure. Finally the tabular and squamosal in later Stereospondyli push the supratemporal far to the front. A good transitional stage between stages C and D is *Platyops* whose otic incisure is made up solely of the end of the pointed supratemporal.

This series of transformations is fairly typical and furnishes a new supporting point for the determination of indistinct fragments. An exception to this rule is found in the Lower Permian *Trimerorhachis* which displays an otic incisure of the progressive D type (fig. 18).

Fig. 18. Evolution of the otic incisures from Embolomeri to Stereospondyli. A. – Embolomeri, *Pholidogaster* (Lower Carboniferous); B. – Embolomeri, *Baphetes* (Upper Carboniferous); C. – *Eryops* (Lower Permian); D. – *Benthosaurus* (Permo-Triassic).

Otherwise *Trimerorhachis* has a flat and broad skull, which reveals numerous progressive peculiarities. Therefore it should be regarded as a form of an early specialized branch; in this connection the arrangement of the otic incisure becomes intelligible. Most interesting is a representative of the Rhachitomi from the ?Lower Triassic—*Micropholis* *stowi*, which has been exhaustively described by Prof. D. M. S. Watson (18).

In the anterior portion of the otic incisure of *Micropholis* lies a small supratemporal wedged between the temporal and squamosal, whereby the intertemporal becomes large and well developed. If the fact established by Watson really exists, it is possible that we may observe a gradual reduction of the supratemporal and its replacement by the intertemporal in the series of evolutionary mutations of labyrinthodonts. In such a case that process of the squamosal which is in contact with the tabular represents the remains of the supratemporal, and the supratemporal of Stereospondyli is in reality the intertemporal. This supposition still requires a careful reexamination of more abundant material: it must however be [p. 154] taken into consideration when the cranial sutures of the dorsal surface have been determined.

In conclusion it should be mentioned that in the evolutionary modifications of the labyrinthodonts two series of transformations are noticed which are in need of reexamination.

1. The Embolomeri and many old Rhachitomi have a large, well ossified sphenethmoid that occurs in forms of various ages. The rest of the later Rhachitomi and, as *Platyops* reveals no

traces of such ossification, either later Rhinesuchidae or transitional forms—the Benthosauridae. On the other hand, a very large, massive and well ossified sphenethmoid is present in the Stereospondyli, as for instance *Trematosaurus* and *Capitosaurus*. Lack of material temporarily precludes determination of whether in this case in the Embolomeri there takes place an early divergence in the series or an imperfect homology of the sphenoid.

2. The position of the mandibular condyles is a primitive characteristic that also agrees with the young forms of labyrinthodonts.

Agreeing with the data of all the authors who have investigated the oldest Tetrapoda, such a position of the mandibular condyles should be observed in the putative ancestors of all three classes of land vertebrates. In the Embolomeri the mandibular condyles advance posteriorly and attain maximum elongation in some of the old Rhachitomi. In later Rhachitomi the reduction of the quadrate rami of the pterygoids begins, which attain their maximum in the latest Stereospondyli, and the transposition of mandibular condyles to the front again. This series of changes is one of the positive evolutional transformations that were established by Prof. D. M. Watson.

The representatives of the group Osteolepidae of the piscine forms Crossopterygii, which are nearest to the oldest Tetrapoda so well investigated by Watson, are distinguished particularly by the position of the basisphenoid and the basal portions of the pterygoids which extend far to the front. For this reason the quadrate rami of the pterygoids are extremely long, and the basioccipital whose posterior surface lies almost in the line of mandibular condyles is segregated from the basisphenoid by a considerable unossified fissure, which might be possibly connected with the pituitary tube.

In comparing the various evolutionary stages of the cranium in labyrinthodonts, the course of cranial evolution as pictured in fig. 19 (A, B, C, D) should be considered as probable.

[p. 155]

Fig. 19. Evolution of the neurocranium of labyrinthodonts. A. – Pisces, Osteolepidae, *Eusthenopteron* (Devon.); B. – Hypothetical form – The ancestor of labyrinthodonts (Upper Devon.); C. – a form of Embolomeri – *Pholidogaster* (Lower Carboniferous); D. – rhachitomous labyrinthodont – *Eryops* (Lower Permian); E and F – Hypothetical forms – the beginning of the mammalo–reptilian stem. Black coloration – Neurocranium.

[p. 156]

With the transition to dry land there commences the evolution of the non-ossified portion in the cranial base of bones covering the parasphenoid, which connects the separated portions of basioccipital and basisphenoid. Thus there results a form with a large, long cranial base that extends far backward between the long quadrate ramus of the pterygoid—the hypothetical form B. The point of juncture between the basisphenoid and pterygoid lies far to the front in the middle of the skull, and the parietal foramen must be placed between the orbits, which are situated in the middle of the skull. Then there begins the gradual displacement of the basioccipital to the front, with the exclusion of a portion of the occipital segment, which results in a considerable abbreviation of the basicranial portion. This stage is pictured in fig. C, and can be observed in the Embolomeri and in the longicranial series in *Archegosaurus* and *Platyops*. The next stage (*Eryops*, fig. D) shows already a strong reduction of this freely suspended portion of the cranial base. The nodosities of the mandibular articulation would be transposed far backward due to the great length of the quadrate ramus and the reduction of the freely suspended cranial base.

From stage D there begins the reduction of the quadrate ramus and the transposition of mandibular articular process nodosities to the front (besides the inclusion of one occipital segment), as has been so clearly proved by Prof. Watson. It is interesting that there exists in the labyrinthodonts either a certain interspace between the basioccipital and the basisphenoid (it is not known whether this is the case with the Embolomeri) or no connection is noticeable between these bones. This circumstance corroborates the above-expressed supposition and points to the relationship of labyrinthodonts to another stem, which separated very early from the mammalo-reptilian one. The strong compression of the neurocranium through the intensive development of the infratemporal foramina, so clearly expressed in old Embolomeri and preserved in early Rhachitomi, is worth notice. In the Rhachitomi in addition, the cranial base is elevated to the cranial roof and lies far above the horizontal surface of both quadrates, in contradistinction to the mammalo-reptilian stem in which the cranial base sinks far down. Both characters mentioned disappear only in later labyrinthodonts as a result of cranial flattening and further cranial alterations in the two-dimensional plane. In others the reduction of the old neurocranium takes place, thanks to the development of lateral and dermal bones and the expansion of the dermal base, and has as its result that the stapes, which has assumed a vertical position only by the compression of the neurocranium, lapses again into an oblique one.

[p. 157] In fig. 19, E and F are presented the schematic neurocrania of the hypothetical mammalian and reptilian ancestors. Here we may observe the cranial development not in the enlargement of the nasal region, but of the occipital, and the expansion of the cranial base at the expense of the infratemporal foramina, which may be reduced or even disappear. The neurocranium is equally expanded in the vertical direction whereby it is situated lower than the quadrates. This is for the development of the brain and requires the retention of many occipital segments, by which reptiles and especially mammals are signaled. This diagram agrees with evolution of the auditory apparatus in old Tetrapoda, which has been described by Academician P. P. Suskin. It is possible that some data for the establishment of the number of occipital segments in old Tetrapoda can be obtained by means of the structure of the spinal column. We can e.g. obtain from the embolomerous type of spinal column the gastrocentral type of first (and second) vertebrae if we include the basal elements of the skull and reconstruct the spinal column according to the structure of the first vertebra.

An exhaustive exploration of the voluminous material will require several studies. The task of the present article is only the presentation of several interesting questions.

When we examine the facts deposited, we come to the following deductions:

1. The longicranial series is peculiar, and shows the retention of primitive characters as a result of its capacity to resist the influences of external medium.

2. The series of labyrinthodonts, as projected by Prof. D. M. S. Watson, must have really existed, and been of the degree of evolutionary development.

3. The labyrinthodont skull is very plastic in reference to diverse modifications, and the dermal elements of its roof have very great affinity.

For this reason the alterations in cranial form, in the appearance of the dorsal and ventral surfaces, the position of the nasal apertures and orbits, etc., are of relatively little value in their significance for evolution; they could have developed in a very short period, and a very great number of genera might have been the result. The labyrinthodonts form a group having a great capacity for evolution thanks to their extreme primitiveness, which facilitates the development of different branches of this group on account of the simplicity with which morphological changes can be effected. Therefore the species arising due to this evolution are not of the same significance as species that arise through the rapid and slight modifications in the form of the plastic skull.

4. The parietal foramen functions as an immovable cranial center, which gives a starting point for establishing the original contours of the modified skull.

5. A very essential character of the evolutionary stage in the dorsal surface of labyrinthodont skull is the position of the otic incisure among the elements surrounding it in the cranial roof.

The deviating character and developmental plan of the labyrinthodont skull indicates the independence of the common stem of mammals and reptiles; we must assume that this stem has branched off already in the Devonian, or that it has originated much later independently.

Fig. 20. A photograph of Pl. I, from the works of Trautschold.

7. The great extent of modifications due to age indicates a very great longevity among labyrinthodonts and requires a reexamination of a series of taxonomic data where young forms were described as modifications. I shall attempt to elaborate this thought in my future work on the Benthosauridae with corresponding material.

8. The examination of the neurocranium of the Seymouriamorpha can furnish interesting data, because it is possible to regard these as the representatives of the common stem of reptiles and mammals, which has evolved in parallel with the stem of labyrinthodonts.