REFLECTIONS ON SOME RUSSIAN EOTHERIODONTS (REPTILIA, SYNAPSIDA, THERAPSIDA)

by

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CONTENTS

Palæovertebrata, Montpellier, **5** : 79-109, 29 fig.

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ABSTRACT

A la suite de l'enrichissement par l'un de nous (P.K.T.) du matériel d'Eothériodontes, ceux-ci (essentiellement *Biarmosuchus* et *Eotitanosuchus*) sont réexaminés et figurés. Une réévaluation de leurs particularités conduit à adopter la distinction en deux familles, pour lesquelles de nouvelles diagnoses sont proposées. Ceci nous amène à discuter des affinités de ces deux familles, d'une part avec les Sphénacodontes, d'autre part avec les Thériodontes primitifs sud-africains (Gorgonopsidés et Ictidorhinidés). Ces considérations appellent à leur tour des conséquences paléogéographiques qui sont abordées en conclusion.

As a result of the enrichment of eotheriodont material by one of us (P.K.T.), these specimens (essentially *Biarmosuchus* and *Eotitanosuchus*) are reexamined and refigured. A reevaluation of their particularities supports the distinction of two families, for which new diagnoses are proposed. This leads us to discuss the affinities of these families, with respect to the sphenacodonts on one hand, and to the South African primitive theriodonts on the other (gorgonopsids and ictidorhinids). This study contains inherent paleogeographic consequences which are considered in conclusion.

Infolge von Neuaufsammlungen von Eotheriodontiden durch einen von uns (P.K.T.) wurden diese (hauptsächlich *Biarmosuchus* und *Eotitanosuchus*) revidiert und abgebildet. Eine Neuabwägung ihrer Besonderheiten führt zur Unterscheidung zweier Familien, für die neue Diagnosen vorgeschlagen werden. Dies führt zur Erörterung der Beziehungen diese beiden Familien zu den Sphenacodontiden einerseits und zu den primitiven Theriodontiden Südafrikas (Gorgonopsidae und Ictidorhinidae) anderseits. Diese Betrachtungen haben palaegeographische Konsequenzen zur Folge, die in der Schlussbetrachtung angestellt werden.

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INTRODUCTION

This short study has as its only aim the presentation of some new elements as a base for reflection on animals which are probably related, even though often widely separated in time and space. It appears that though the meshes of the interrelational net are indeed getting tighter, there remains enormous gaps, and it is always too tempting to think that the specimens one has on hand are " the " links.

The presence of vertebrate tetrapods in beds dating from early in the late Permian of the U.S.S.R., has been known for nearly a century. But, as concerns the group studied here, this knowledge remained for a long time limited to a mandible (*Phthinosaurus*) figured and discussed by Seeley (1894), Efremov (1940) and Watson (1942). Then in 1954 Efremov made known a skull fragment (*Phthinosuchus*) which he considered related to the preceding mandible; both specimens he grouped in the new family Phthinosuchidae. Several years later, excavations made in the U.S.S.R. on one hand and in the United States on the other, brought to light a whole fauna of an exceptional interest, since it is composed of elements morphologically intermediary between pelycosaurs and primitive theriodonts. It is then that Olson, in his comparative study of the Permian faunas of the two continents (1962), created for these forms the infra-order Eotheriodonta (1). In the U.S.S.R. the eotheriodonts comprised (if one excepts the brithopodids) five genera, *Phthinosaurus, Phthinosuchus, Eotitanosuchus, Biarmosuchus* and *Biarmosaurus*, the last three each being represented by a skull and by several fragments of the skeleton. Further excavations have yielded nothing more of the genera *Phthinosaurus* and *Phthinosuchus* (2) and but little eotitanosuchid material, but several skulls and skeletons of *Biarmosuchus* (*sensu lato*). It thus became necessary to present these new acquisitions and to reevaluate the generic and familial distinctions. This doing, we have been lead to compile a brief comparison between these forms and the pelycosaurs on one hand, and with primitive gorgonopsians on the other. We have evoked, in conclusion, the paleogeographic problems brought up by these comparisons.

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(1) Term not utilized in the classification of Kalandadze *et al.* (1968).

(2) This is the reason why we have ignored them here, the type-elements being too incomplete for their entering usefully in our comparisons.

DESCRIPTIONS

Biarmosuchus tener TCHUDINOV, 1960

BIBLIOGRAPHY :

Tchudinov, 1960, pp. 84-85, fig. 2;
Olson, 1962, pp. 56-57, fig. 25 A-G, pl. 13 A; pp. 183-184;
Tchudinov, 1964, p. 92, fig. 2;
Tchudinov, 1965, pp. 120-121;
Kalandadze *et al.*, 1968, p. 83.

LIST OF MATERIAL : type-specimen PIN 1758/2 (3) — skull completed prepared, except ventrally (fig. 1-3-5). It has been flattened during fossilization, which resulted in the right side being stretched and the left side, especially at the rear, being pushed in. The left part of the occiput is preserved, but the temporal fossa of the same side is practically suppressed. On the right side the posterior border of the temporal fossa has been destroyed. Preserved with the skull were : the cervical vertebrae, the eroded thoracic vertebrae, some ribs, the pectoral girdle, the complete right anterior limb and the damaged left anterior one (fig. 7-10).

PIN 1758/8 — a big skull in a rather poor state of preservation and flattened dorso-ventrally. The palate is accessible, since practically nothing of the mandible is preserved. A complete skeleton was associated with the skull in a single block (fig. 11-14); the only parts missing were the left anterior and posterior limbs.

PIN 1758/19 — posterior part of a skull limited anteriorly by the pineal foramen (fig. 4); associated here were a few vertebrae and ribs (Tchudinov, 1964).

PIN 1758/255 — skull lacking the anterior part of the snout, and very compressed laterally. Few bones are preserved (fig. 6), but their impressions are present. The lower jaw is in place.

(3) All the Eotheriodonts considered here come from the Ezhovo locality, upper Kazanien age, U.S.S.R., and are kept in the Paleontological Museum of the U.S.S.R., Moscow.

Discussion : The maximum length of the type-skull would be from 152 to 160 mm, that of the snout 99 mm (measured between the anterior border of the snout and that of the orbits). Tchudinov (1960) has given a short description of the skull, and a lateral view of it. A few modifications to details of the interpretation can be suggested, mainly due to the fact that in 1960 the author of the genus had at his disposal only one specimen; we know now four specimens, although they are more or less incomplete. The varied deformations suffered by the skulls are sufficient to account for the slight differences in proportions that one of us (D.S.) has attributed to the diverse parts, compared with the original figures. However, the temporal fossa seems definitely a little wider than it was originally thought; and Tchudinov thinks now that their dorsal border, which is slightly indented anteriorly, is only slightly lower than that of the orbits. On PIN 1758/19 the right orbit is relatively smaller than on the other specimens, but it might be a result of the crushing. The slope towards the front and ventrally of the occiput, though difficult to estimate, seems to be more accentuated than previously drawn, and hence reversed relative to the sphenacodont stage.

Details of the bones to be noted (still on the lateral side) are the existence of a well developped transverse process of the septomaxilla, the situation of the premaxillary-maxillary suture in front of the last incisor, the length of the prefrontals, that of the lacrymals (these bones may be not as

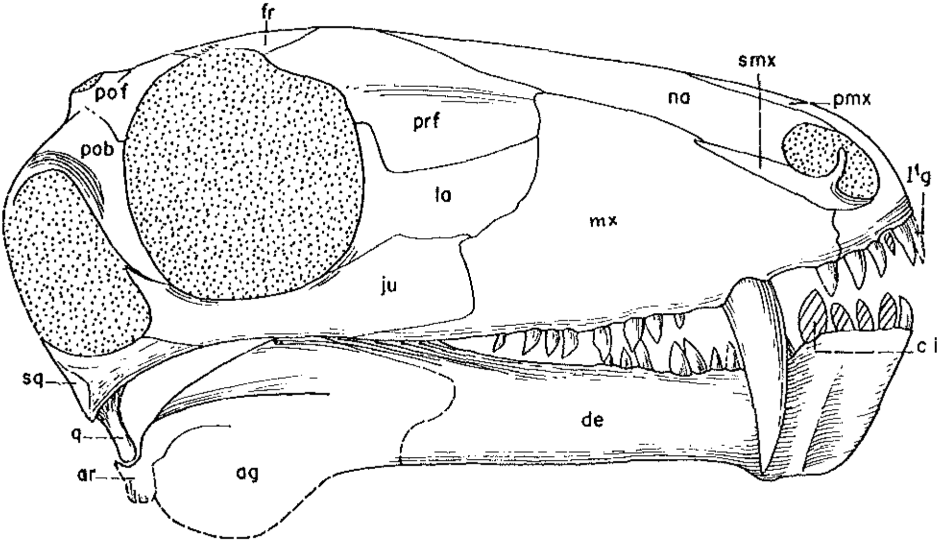

Fig. 1. — *Biarmosuchus tener,* type-specimen PIN 1758/2. Skull, slightly restored, lateral view. X 3/4.

ag : angular; ar : articular; c i : lower canine; de : dentary; fr : frontal; I^1 g : first left upper incisor; ju : jugal; la : lacrymal; mx : maxillary; na : nasal; pmx : premaxillary; pof : postfrontal; pob : postorbital; prf : prefrontal; q : quadrate; smx : septomaxillary; sq : squamosal.

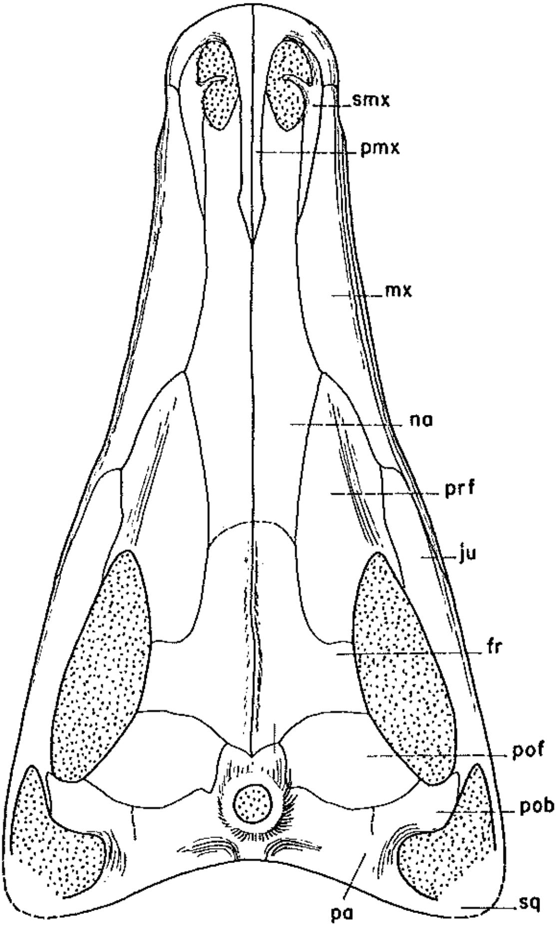

FIG. 2. — *Biarmosuchus tener*, type-specimen PIN 1758/2. Skull, slightly restored, dorsal view. × 3/4.
pa : parietal. Other abreviations as in fig. 1.

high as previously drawn), the modest height of the maxilla and the shortness of the lateral postorbitals. Lastly, the ventral border of the quadrate presents a condyloid articular surface.

On the dorsal surface, a crest emphasizes the median suture between the frontals and that between the parietals. To this character and others already stressed by the creator of the genus, one can add the great interorbital width, the still greater intertemporal width, the large size of the postfrontals, the important participation of the frontals in the supraorbital border, and the length of the premaxillary between the nasals; this last character is difficult to account for with respect to a sphenacodontid origin or to a theriodont ancestry.

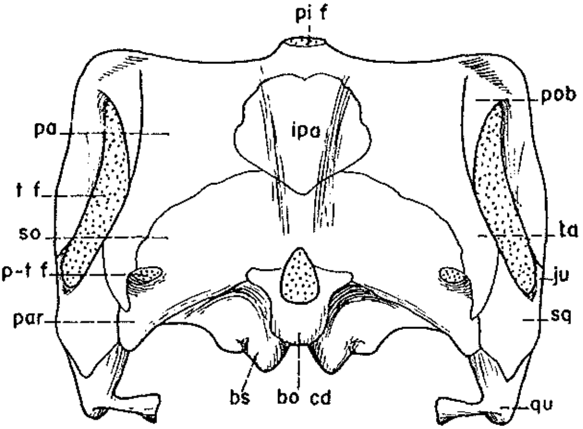

FIG. 3. — *Biarmosuchus tener*, type-specimen PIN 1758/2. Skull, slightly restored, posterior view. × 3/4.

bo cd : basioccipital condyle; bs : basisphenoid; ipa : interparietal; ju : jugal; pa : parietal; par : paroccipital process; pi f : pineal foramen; pob : postorbital; p-t f : post-temporal fossa; qu : quadrate; so : susoccipital; sq : squamosal; ta : tabular; t f; temporal fossa.

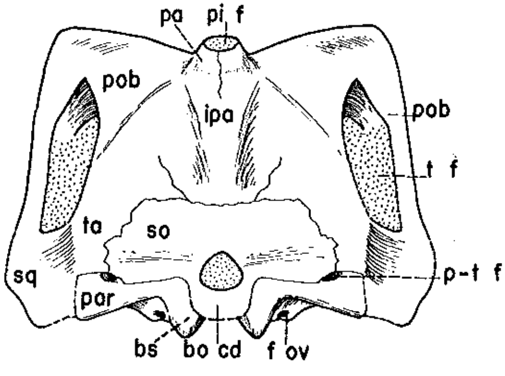

FIG. 4. — *Biarmosuchus tener*, PIN 1758/19. Skull, slightly restored, posterior view. × 1/2.

f ov : fenestra ovalis. Other abreviations as in fig. 3.

We have noted that the occiput is inclined antero-ventrally. The interparietal is particularly small and the supraoccipital particularly large. The opisthotics appear to be slender and the post-temporal fossa as well as the occipital foramen apparently very small. The quadrate must have extended notably ventrally beyond the squamosal, but its principal orientation (transverse or longitudinal) cannot be determined. On the specimen PIN 1758/19 the anterior surface of the occipital plate is visible; the overlapping of the supraoccipital by the interparietal can here be clearly recognized.

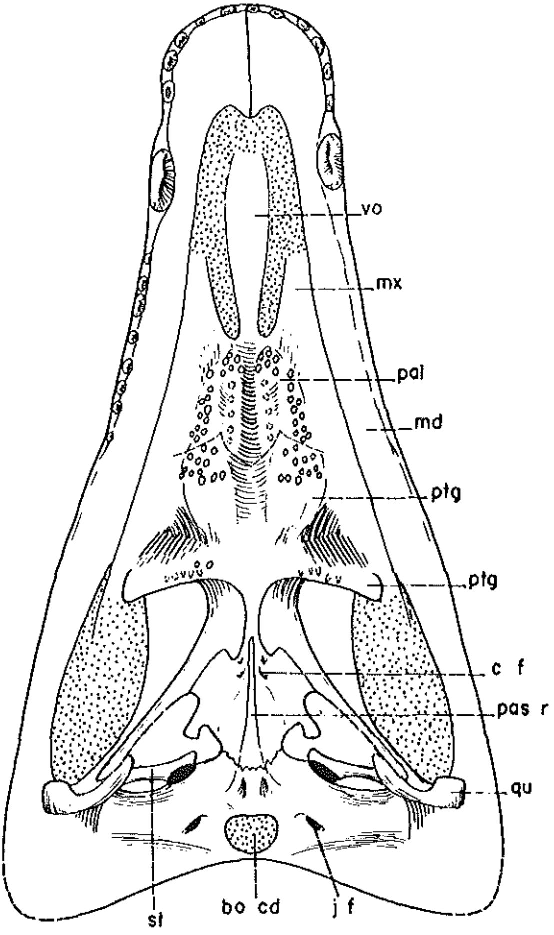

FIG. 5. — *Biarmosuchus tener*, specimen-type PIN 1758/2. Skull, slightly restored, ventral view. × 3/4.

bo cd : basioccipital condyle; c f : carotid foramen; j f : jugular foramen; md : mandible; mx : maxillary; pal : palatine; pas r : parasphenoidal rostrum; ptg : pterygoid; qu : quadrate; st : stapes; vo : vomer.

Concerning the ventral view, the vomer is not accessible on the type; but from other specimens, it seems to be a single bone, deeply situated, widening at mid-length; the details of its relief are not known. The palatal tuberosities (palatine as well as pterygoid) are long. The relative position of the pterygoid transverse apophyses varies somewhat with the specimens (between the midpoint and the posterior limit of the orbit); these apophyses are very high and slightly curved (they are straight in Pelycosauria). Behind the transverse apophyses, the basicranium remains short; noteworthy is the obliquity of the quadrate rami and their anterior width, the anterior position

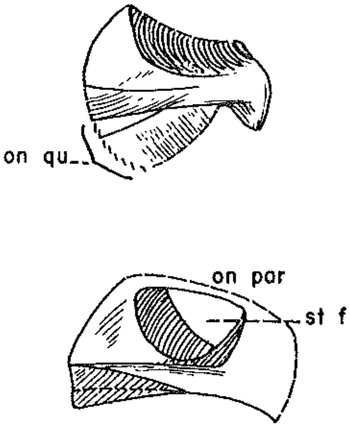

Fig. 6. — *Biarmosuchus tener*, PIN 1758/255. Left stapes. × 1.
on par : paroccipital side; on qu : quadrate side; st f : stapedial foramen.

of the occipital condyle as well as that of the quadrate. The stapes (PIN 1758/255) is perforated (fig. 6).

The lower jaw is perhaps less slender than previously figured; the dentary lacks a coronoid apophysis.

The question of tooth indentification and number remains uncertain. Previously Tchudinov counted three incisors and three precanines *sensu stricto*. The type-specimen presents eleven upper teeth anteriorly : five on the right side, five on the left plus one situated medianly and a little on the left. This might be a replacing tooth; the other possibility would be that the sixth right incisor is missing, since the diastema 1^5 — C = 3,5 on the left, 7,5 on the right; but further preparation did not lead to any trace of it. However, the skull PIN 1758/8 certainly seems to have twelve anterior teeth. Now, in order to know if the last ones are true precanines, we should know the precise situation of the ventral premaxillary-maxillary suture, which we do not. But we know it on *Biarmosaurus* cf. *tener* PIN 1758/18 (cf. p. 93), and like in that case, we must have here no real precanines. Anyway, there exists only eight lower incisors. These teeth are provided with serrations, at least on their anterior border. The creator of the genus drew one single canine, but on the skull PIN 1758/255, two canines are certain; of course there might be a replacement tooth, but the youngest one seems to be the most laterally situated, which is the opposite that one would expect of a replacement tooth. The eight postcanines have a convex anterior border and a straight or concave posterior border with serrations; a constriction at the base of the crown is indicated.

The intermeshing of the anterior teeth is uncertain; on the type, the lower incisors come in front of the posterior, but this is artificial. However, on PIN 1758/8, I_2 and I_3 almost intermesh with the uppers; I_4 on the

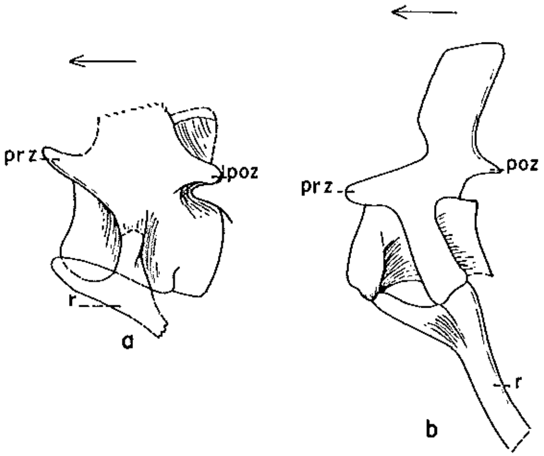

FIG. 7. — *Biarmosuchus tener,* type-specimen PIN 1758/2. Fifth (a) and seventh (b) cervical vertebrae, lateral view. × 3/4.

poz : postzygapophysis; prz : prezygapophysis; r : rib.

contrary is clearly lingual to I^4 and I^5. The other specimens have no lower dentition preserved.

Tchudinov (1960) did not describe the postcranial elements; he only published (1964) a drawing of the ilium of PIN 1758/8. But in 1962 Olson gave the main characteristics of these elements : their slenderness, resemblance with brithopodids in the interclavicula and the scapula, and the large size of the claws. We shall distinguish the information given by the type from that given by PIN 1758/8.

Concerning the first specimen, the cervical vertebrae are moderately slender, with neural apophyses incomplete but certainly low and quite wide; however C 7 has a higher and narrower neural apophysis than the anterior cervicals. Ribs were present, bicephalous, at least from C 5. No intercentrum is preserved.

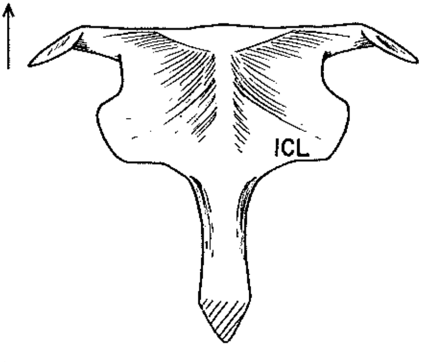

FIG. 8. — *Biarmosuchus tener,* type-specimen PIN 1758/2. Interclavicula, (right side restored), ventral view. × 1/2.

The pectoral girdle is incomplete; the size and shape of the interclavicula are remarkable (it is reminiscent of that of *Varanops* but is more massive). It presents anteriorly not only a wide coracobrachial insertion, but also a clavicular process.

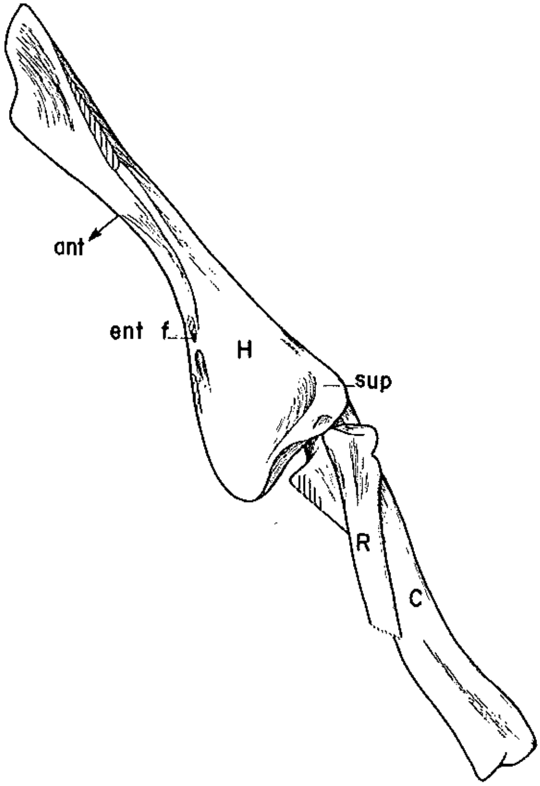

FIG. 9. — *Biarmosuchus tener*, type-specimen PIN 1758/2. Left anterior limb, ventro-mesial view. × 1/2.

C : cubitus; H : humerus; R : radius; ent f : entepicondylar foramen.

The humerus presents a long, narrow diaphysis, with distal and proximal epiphyses quite expanded; the bone is considerably twisted. There exists only the entepicondylar foramen, situated high on the bone. The coracobrachial fossa is well indicated and the deltopectoral crest protruding, while that of the supinator is thin.

In the hand, two centralia are present, but the carpals 4 and 5 are already fused. Finally, the claws appear to have been quite powerful. The digital formula is 2, 3, 4, —,—.

On PIN 1758/8, the cervical vertebrae are more stocky, and the neural apophyses particularly short and wide. No intercentrum is preserved here either. The last dorsal vertebrae have high and narrow neural apophyses. The sacral vertebrae have well developed transverse apophyses.

The scapula is very slender; the well developed procoracoid contrasts with the small coracoid. The humeral diaphysis appears to have been less slender than that of the type.

FIG. 10. — *Biarmosuchus tener*, type-specimen PIN 1758/2. Left hand, mesio-ventral view. × 3/4.

c : centrale; i : intermedium; r : radiale; u : ulnare.

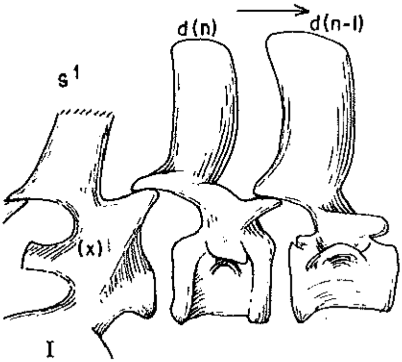

FIG. 11. — *Biarmosuchus tener*, PIN 1758/8. Last two dorsal vertebrae (d) and first sacral (s). × 3/4.

x : point of fusion between the transverse apophysis and the central rib.
I : Ilium

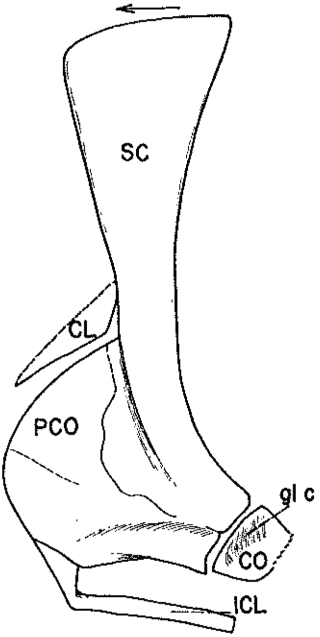

FIG. 12. — *Biarmosuchus tener,* PIN 1758/8. Left scapular girdle, specimen still in the block. × 1/2.

CL : clavicula; CO : posterior coracoid; ICL : interclavicula; PCO : anterior coracoid; SC : scapula.
gl c : glenoid cavity.

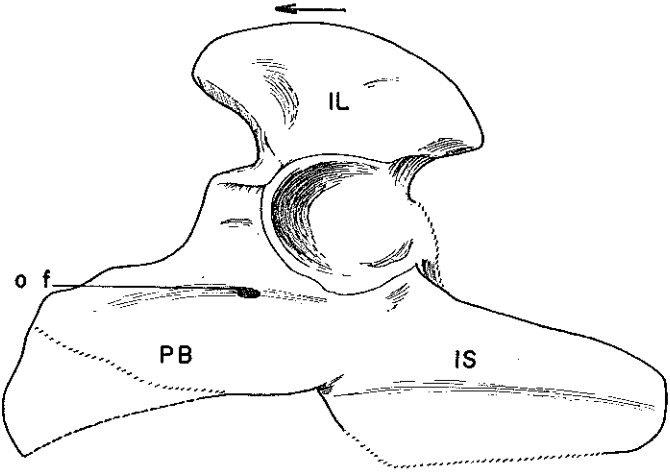

FIG. 13. — *Biarmosuchus tener,* PIN 1758/8. Left pelvic girdle, slightly restored, lateral view. × 1/2.

IL : ilium; IS : ischium; PB : pubis.
o f : obturator foramen.

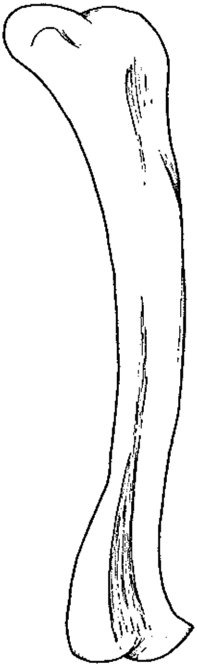

FIG. 14. — *Biarmosuchus tener*, PIN 1758/8. Right femur, mesio-ventral view. × 1/2.

The pelvic girdle is that figured by Tchudinov (1964), but the pubis has been secondarily pushed in. The femur, also very slender, presents a well formed head, and the curvature of the bone remains weak.

Biarmosuchus **cf.** ***tener***

(*Biarmosaurus antecessor* TCHUDINOV 1964)

BIBLIOGRAPHY :

Tchudinov, 1964, pp. 91-93, fig. 1.
Olson, 1962, p. 57, fig. 25 H.
Kalandadze *et al.*, 1968, p. 83.

LIST OF MATERIAL : PIN 1758/7 — a skull crushed laterally (fig. 15-17); often the bones are represented only by their imprints. The posterior part of the skull (temporal fossa, occiput) has been completely pushed in. The lower jaw is more complete on the left side than on the right. A few vertebrae still cling to the occiput (fig. 18). Part of the skeleton was associated (fig. 19).

PIN 1758/18 — a skull laterally crushed on the left side; nothing is preserved behind the orbit on the right side, and on the left side the temporal fossa is represented only by its lower half. The palate has been partially prepared and the occiput as well as the mandibular articulation are illegible. Half of the sclerotic ring persists in the left orbit. Three cervical vertebrae adhere to the occiput.

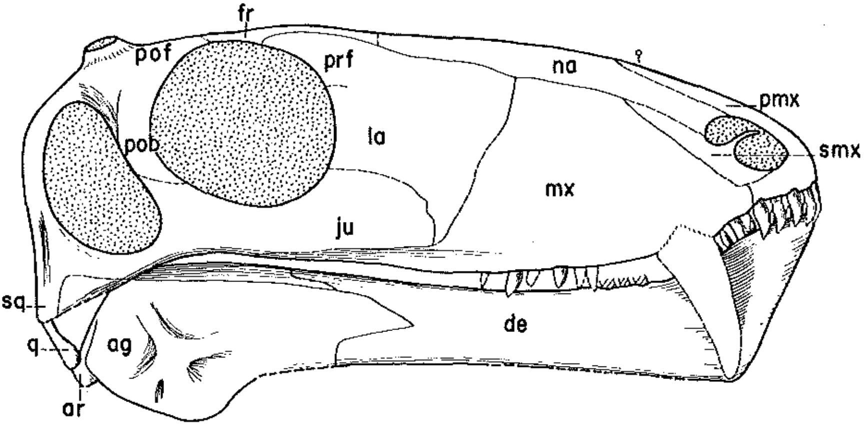

FIG. 15. — *Biarmosuchus* cf. *tener*, PIN 1758/7. Skull, slightly restored, lateral view. × 1/2. ag : angular; ar : articular; de : dentary; fr : frontal; ju : jugal; la : lacrymal; mx : maxillary; na : nasal; pmx : premaxillary; pob : postorbital; pof : postfrontal; prf : prefrontal; q : quadrate; smx : septomaxillary; sq : squamosal.

DISCUSSION : The type-skull of "*Biarmosaurus antecessor*" is bigger (208 to 210 mm) than that of *B. tener*, but this is not so marked with PIN 1758/18; the snout is relatively longer (128 to 130 mm) but perhaps this is due to an older age of the individual. Also, the orbits are here relatively smaller (especially on PIN 1758/18); in the opinion of Tchudinov, they are more round. In details, the prefrontal is longer relative to the maxillary. Ventrally, the transverse apophyses are situated more anteriorly, at least on the type, which does not agree with an older age. Finally, the incisors (12) are smaller (4), while the canines are stronger (although this is not so clear on PIN 1758/18) and correlatively the "chin" is more pronounced. Tchudinov finds that the maxillary step is more accentuated, that the pineal boss is more developed and the canine more recurved; but these differences remain slight.

On the other hand, one finds the same profile with an interorbital sulcus, a suborbital crest, the same narrow septomaxillary, long dorsal premaxillaries, long lacrymals and long supraorbital frontals, the same small interparietal, the same short postorbital bone, the same shape of the jugal posteriorly. Ventrally, the palatal sulcus is equally narrow and the dentigerous ridges were probably similar, the vomer is at least equally deep, the quadrate bone

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(4) All situated in the premaxillaries, hence all incisors.

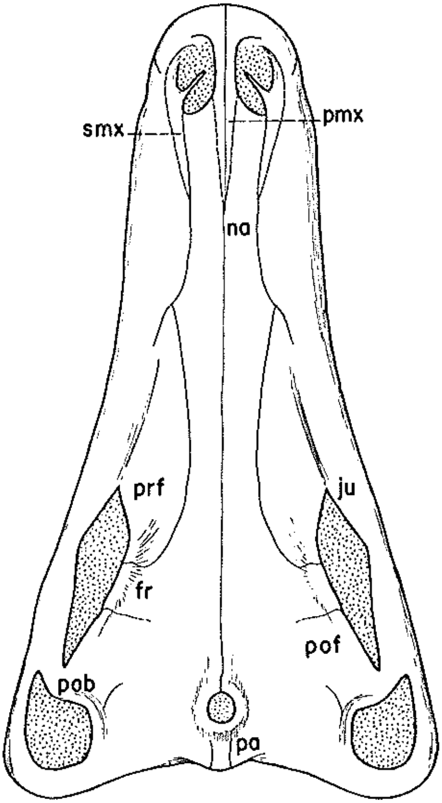

FIG. 16. — *Biarmosuchus* cf. *tener,* PIN 1758/7. Skull, slightly restored, dorsal view. × 1/2. fr : frontal; ju : jugal; na : nasal; pa : parietal; pmx : premaxillary; pob : postorbital; pof : postfrontal : prf : prefrontal; smx : septomaxillary.

goes as far below the squamosal, and the lower jaw has the same slenderness, absence of a coronoid process, and a large angular.

In the postcranial skeleton, one notices that one of the last cervical vertebrae (or one of the first dorsals) recalls the last cervical of *B. tener* with its high and narrow neural arch, perhaps even higher and narrower here. The presacral vertebrae show the same slenderness.

The scapula seems wider at its proximal extremity than in the previous type-specimen.

The original drawing of the pelvic girdle by Tchudinov (1964) might have to undergo a slight correction in that the iliac blade would extend a little further forward (1/3 the length of the ischion) and the pubis has been a little flattened. This girdle is very similar to that of the preceding type-specimen, but Tchudinov considered that it was shorter and wider and that the cotyloid cavity was shallower and not bordered with an anterior rim.

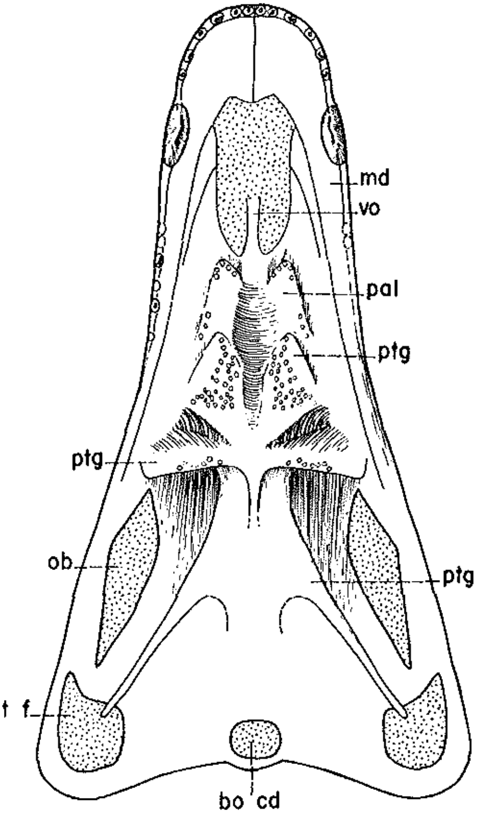

FIG. 17. — *Biarmosuchus* cf. *tener,* PIN 1758/7. Skull, slightly restored, ventral view. × 1/2. bo cd : basioccipital condyle; md : mandibule; ob : orbit; pal : palatine; ptg : pterygoid; t f : temporal fossa; vo : vomer.

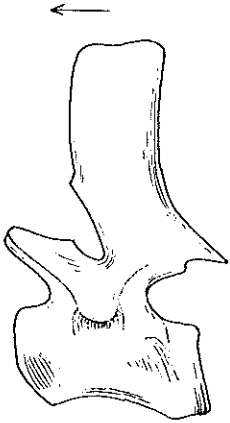

FIG. 18. — *Biarmosuchus* cf. *tener,* PIN 1758/7. Last cervical or first dorsal vertebra, lateral view. × 3/4.

The femoral head is perhaps here a little less well indicated. Lastly, the claws of the foot seem less voluminous than those of the hand of *Biarmosuchus tener*, even though the specimen is here bigger. The digital formula is — —4 5 —.

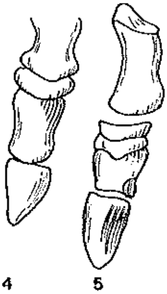

FIG. 19. — *Biarmosuchus* cf. *tener*, PIN 1758/7. Left foot, digits 4 and 5, dorsal view. × 3/4.

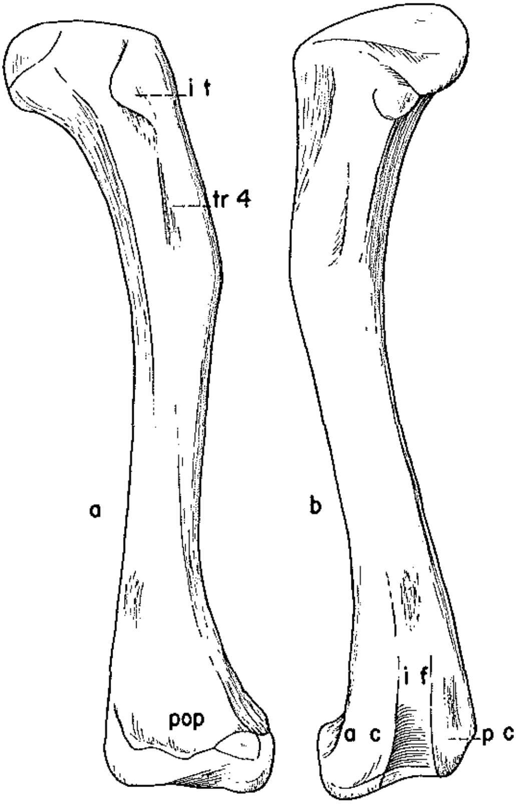

FIG. 20. — Biarmosuchidae, gen. indet., PIN 1758/86. Femur: a, ventral view; b, dorsal view.
a c: anterior condyle; i f: patellar sulcus; i t: internal trochanter; p c: posterior condyle; pop: popliteal space; tr 4: fourth trochanter.

FIG. 21. — Biarmosuchidae, gen. indet., PIN 1758/320. Left foot, ventral view. × 3/4.

It does seem, as suggested by Olson (1962) and Tchudinov (personal communication, 1968) that we are concerned with a single genus. And Tchudinov even favors now the opinion that most of the differences could well be attributed to individual variation, stage of growth, sexual dimorphism, etc.; however, altogether they might also correspond to a specific individuality distinct from that of *Biarmosuchus tener.*

It might be of some interest to give as an appendix some information on the skeleton of three specimens identified as Biarmosuchidae :

PIN 1758/86 — the front part of a skull, with a complete skeleton included in a block (fig. 20);
PIN 1758/320 — posterior and anterior feet (fig. 21-23);
PIN 1758/260 — the distal part of the humerus.

The first is well preserved, but its elements have not been cleared from the block in which they are included. The femur is especially remarkable by its slenderness, the presence of a head more distinct than that in the preceding example and forming an angle with the diaphysis; the muscular insertions appear less strong than on the humerus. The patella is very large. The tibia is slender.

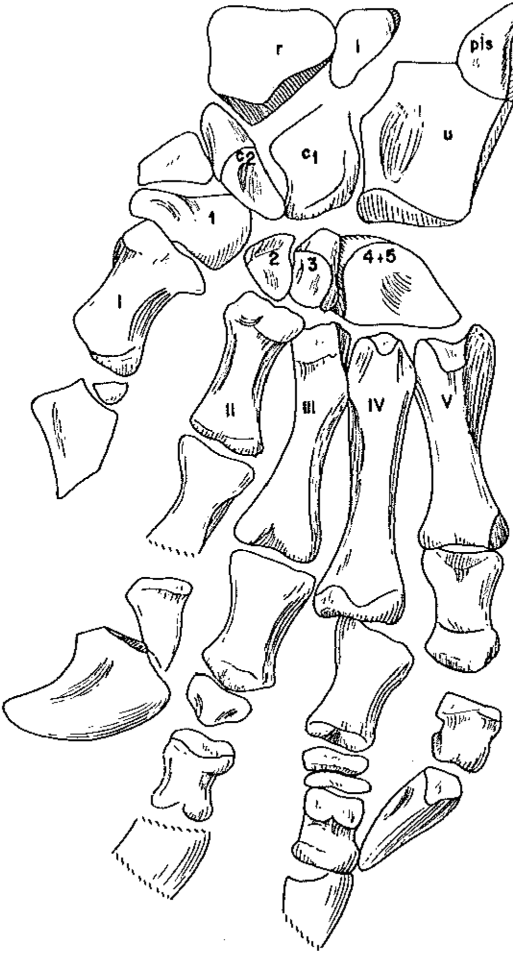

FIG. 22. — Biarmosuchidae, gen. indet., PIN 1758/320. Left hand, dorsal view. × 3/4. c : centrale; i : intermedium; pis : pisiform; r : radiale; u : ulnare.

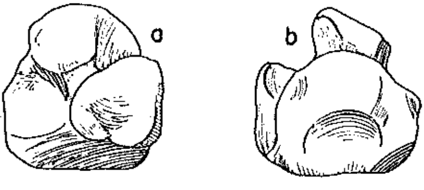

FIG. 23. — Biarmosuchidae, gen. indet., PIN 1758/320. Astragalus : a, dorsal view; b, ventral view. × 3/4.

In the second specimen, the fore- and hind feet are almost complete, the hand is slightly more stocky than that of the type of *Biarmosuchus tener,* but the claws have the same proportions; one is able to complete the palangeal formula : 2 3 4 5 3. In the foot the astragalus presents three well indicated articular surfaces. It is the fifth metatarsal which is the widest and the longest (the 4th in the hand). The cuneiforms 4 and 5 are fused. The phalangeal formula must have been 2 3 4 5 4. Again, claws might be a little stronger in the hand than in the foot.

In the third specimen, the lower extremity of the humerus is somewhat different from that of the type of *B. tener.*

Eotitanosuchus olsoni TCHUDINOV 1960

BIBLIOGRAPHY :

Tchudinov, 1960, pp. 82-83, fig. 1;
Olson, 1962, pp. 49-52, fig. 19, pl. 12 A, p. 182;
Tchudinov, 1965, p. 121, fig. 2;
Kalandadze *et al.*, 1968, p. 83.

LIST OF MATERIAL : Type-specimen PIN 1758/1 — a skull very crushed laterally (with uplifting of the left posterior part and a downward shift of the right side). The three left arcades are missing, and the base of the skull as well as the transverse apophyses have been truncated; the dentition was damaged. The skull has been well prepared and the sutures have been drawn on it (fig. 24-26, 28).

PIN 1758/85 — several skull fragments (fig. 27);
PIN 1758/292 — a maxillary;
PIN 1758/229 — atlas and axis of an eotitanosuchid (fig. 29).

DISCUSSION : The authors mentionned above have sufficiently described the particularities of this form; we shall not linger upon them, except where they intervene in the comparison with *Biarmosuchus.* This skull, with a long snout, had certainly more circular orbits than they are now preserved; but they are relatively much smaller than in *Biarmosuchus.* On the other hand, the temporal fossae are somewhat larger in size relative to the last genus. The crushing that the orbits have undergone has at the same time depressed the interparietal region and stretched the occiput towards the rear. As in *Biarmosuchus* (*sensu lato*) there exists an indentation of the anterior part of the supratemporal border. The ventral border of the skull is much more sinuous than in *Biarmosuchus,* recalling almost *Dimetrodon.* The postorbital bar is here also slightly twisted. The pineal foramen is particularly wide. The parietal bones are very short as in *Biarmosuchus* and the sphenacodonts. There was no

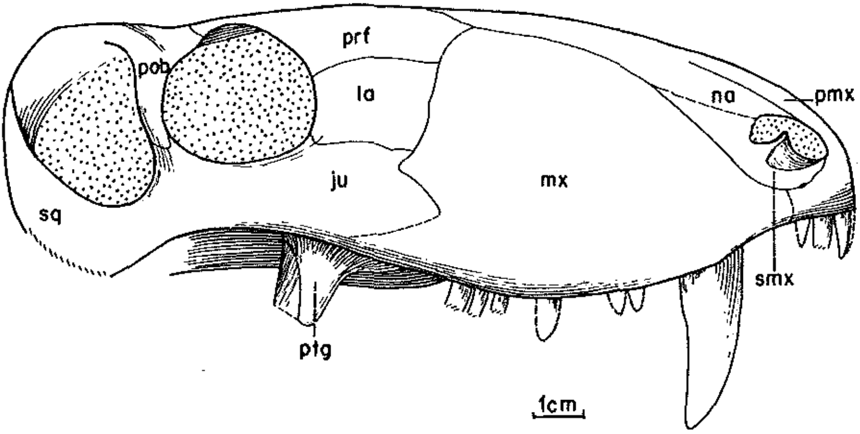

FIG. 24. — *Eotitanosuchus olsoni,* type-specimen PIN 1758/1. Skull, slightly restored, lateral view. × 1/3 ca.

ju : jugal; la : lacrymal; mx : maxillary; na : nasal; pmx : premaxillary; pob : postorbital; prf : prefrontal; ptg : pterygoid; smx : septomaxillary; sq : squamosal.

preparietal. The premaxillaries, very low anteriorly, probably extended a long way between the nasals, in the same way as in *Biarmosuchus.*

Laterally, abundant pits occur in the maxillary. The intraorbital lacrymal is perforated with two foramina (there is only one in pelycosaurs; the situation is unknown in *Biarmosuchus*). Lastly, the septomaxillary probably sent out a facial transversal lamina as in *Biarmosuchus.*

In the occiput, the existence of a supratemporal is uncertain. The interparietal is much more developed than in *Biarmosuchus.* There still exists a wide opisthotic- quadrate contact.

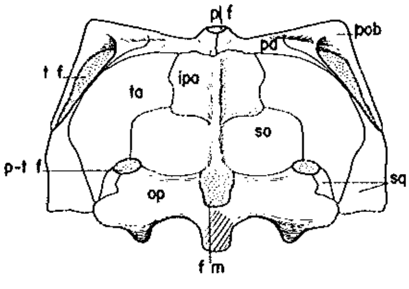

FIG. 25. — *Eotitanosuchus olsoni,* type-specimen PIN 1758/1. Skull, slightly restored, occipital view. × 1/4 ca.

f m : foramen magnum; ipa : interparietal; op : opisthotic; pa : parietal; pi f : pineal foramen; pob : postorbital; p-t f : post-temporal fossa; sq : squamosal; ta : tabular; t f : temporal fossa.

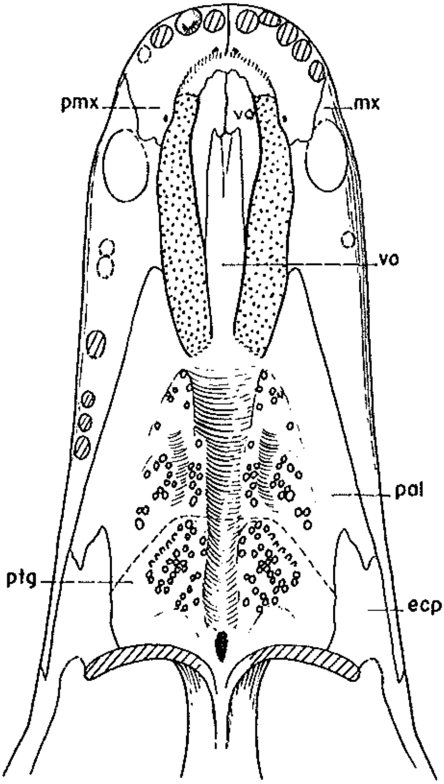

FIG. 26. — *Eotitanosuchus olsoni,* type-specimen PIN 1758/1. Skull, slightly restored, ventral view. × 1/3 ca.

ecp : ectopterygoid; mx : maxillary; pal : palatine; pmx : premaxillary; ptg : pterygoid; vo : vomer.

FIG. 27. — *Eotitanosuchus* sp., PIN 1758/85. Vomer, ventral view. × 1/4 ca.

Ventrally, the most interesting element is the vomer, deeply situated as in *Biarmosuchus;* on the type-specimen of *Eotitanosuchus,* a possible suture divides the vomer anteriorly (on the specimen PIN 1758/85 the anterior suture is more distinct); it is then interrupted, to appear again but less clearly at the posterior part of the bone; but this « suture » is superficial and does not go through the thickness of the bone. The mesial edge of the palatines forms a sharp crest; the dentigerous tuberosities, doubtlessly separated from their symetrical counterparts by a palatal sulcus, are very similar to those of *Biarmosuchus.* The ectopterygoid is very narrow but perhaps not, as long as previously drawn. The shortness of the basioccipital evokes the situation found in the sphenacodonts, as in *Biarmosuchus.* Finally, there would be, just in front of the carotid foramina, an interpterygoid vacuity which, according to Tatarinov (oral comm. 1968), bars *Eotitanosuchus* from the gorgonopsid ancestry.

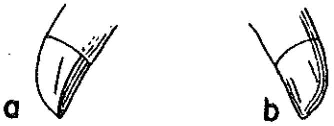

FIG. 28. — *Eotitanosuchus olsoni,* type-specimen PIN 1758/1. Right upper I^2; a, labial side; b, lingual side. × 1/3.

The dentition consists of 4 to 5 upper incisors, but it does not seem that there is any true precanine. On the right side, I^4 —C measures 24 mm; on the left, it measures only 14 mm; C — Pc^1 is practically equal on both sides (13 mm on the right, 15 on the left). It then seems that the left " I^4 " is actually an I^5 and that this tooth is missing on the right. No more than in the case of *Biarmosuchus* do we know whether there was one or two upper canines : on the specimen PIN 1758/85 an obscure zone follows the functional canine, a zone which might correspond to a resorbed canine; lastly the maxillary PIN 1758/292 carries two distinct canines, but we do not know whether this is a replacement phenomenon. There would be eight postcanines.

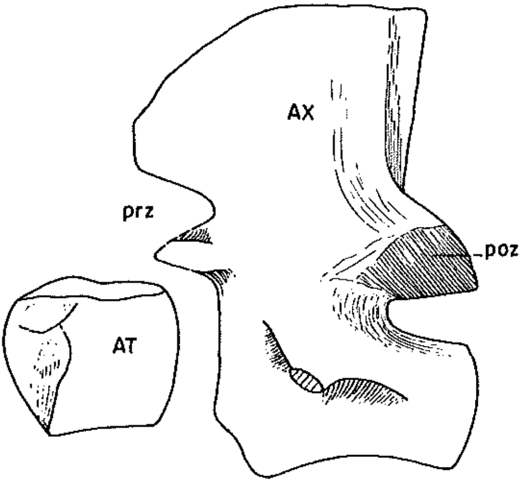

FIG. 29. — Eotitanosuchid ? PIN 1758/229. Atlas and axis, lateral view. × 2/3.
AT : atlas; AX : axis.
prz : prezygapophysis; poz : postzygapophysis.

COMPARISONS

First, as far as the generic distinction of *Eotitanosuchus* from *Biarmosuchus* is concerned, Tchudinov (1964) cites the following characters : the situation of the pineal foramen, nearer to the nuchal crest in *Eotitanosuchus* (though it is not certain that this character is specifically variable, or even individually during growth); the pterygoid tranverse apophyses are in the latter form more curved towards the back; there would not be here any palatal sulcus (but this is clearly due to compression); lastly, the upper canine is directed more vertically (but it was already somewhat more vertical in the type of *Biarmosuchus tener* than on that of "*Biarmosaurus antecessor*").

Nevertheless these differences are supported by a few others : the lacrymal is shorter in *Eotitanosuchus* and correlatively the maxillary is longer; the interparietal is much more developed; the infraorbital and zygomatic arches are less slender; all these differences correspond to a more evolved state. Finally the alveolar border of the maxillary is more convex; the canine is stronger. The generic distinction seems indisputable in the face of this ensemble of characters.

Tchudinov (1960), Boonstra (1963), Kalandadze *et al.* (1968), unite *Eotitanosuchus* with *Biarmosuchus* in the family Eotitanosuchidae. Olson (1962) places them in two distinct families. A reconsideration of the situation leads us to Olson's conclusion. The characters which, in *Biarmosuchus,* seem to have a supra-generic value, are :

1 — the length of the snout;
2 — the large size of the orbits, and the correlative angulation of the dorsal profile of the skull;
3 — the small size of the temporal fossa;
4 — the beginning of an intertemporal indentation;
5 — the indication of a twist of the postorbital bar;
6 — the very slight sinuosity of the ventral border of the skull;
7 — the facial position of the transverse lamina of the septomaxillary;
8 — the feeble height of the premaxillary under the nares;
9 — the situation of the nares, more dorsal than anterior;
10 — the shortness of the parietals;
11 — the shortness of the basioccipital;
12 — the deep situation of the vomer;
13 — the absence of a coronoid process of the dentary;
14 — the posterior extension of the reflected lamina of the angular;
15 — the possible intermeshing of the anterior incisors ?
16 — the long dorsal premaxillaries;
17 — the existence of a parasphenoidal rostrum.

Characters	biarmosuchids	*Eotitanosuchus*	ictidorhinids
1	+	+	s(5)
2	+	0	+
3	+	0	+
4	+	+	s
5	+	+	0
6	+	0	s
7	+	+	+
8	+	+	+
9	+	+	s
10	+	+	+
11	+	+	+
12	+	+	s
13	+	?	+
14	+	?	+
15	+	?	s
16	+	+	s
17	+	+	0

(5) s : present in certain genera.

Among these seventeen characters, eleven (1, 4, 5, 7, 8, 9, 10, 11, 12, 16, 17) are present in *Eotitanosuchus*, three (2, 3, 6) are absent and three (13, 14, 15) are unknown. Among the common eleven, four (8, 9, 10, 11) exist also in at least primitive sphenacodonts and are consequently a common ancestral heritage (6). Three (7, 12, 17) are common to most primitive theriodonts and correspond thus to a post-sphenacodont stage. Finally, the last four (1, 4, 5 and 16) exist perhaps already in specialized sphenacodonts, and become more developed in the brithopodids. These last four constitute then the strongest indication of a relationship of the two genera, but they are strongly counterbalanced by at least two of the diverging characters (2, 3); the two others (loss of precanines and stronger ventral sinuosity) represent, the first a step

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(6) Admittedly, this qualification of « primitive » or « evolved » characters can be very disputable; for instance, the great length of the snout can be considered primitive if one refers to sphenacodonts, evolved if one refers to early pelycosaurs.

ahead of *Biarmosuchus* in a theriodont direction, the second a step "backwards", that is, a slight desynchronization in their evolution.

In order to interpret this situation, we must remember that we are, with these genera, near to the origin of major systematic subdivisions, and consequently that the resemblances between them must be more numerous than the differences; but it is the existence of the latter that we must take into account if we want to discover the origin of these subdivisions. At the origin of mammals, for exemple, and even quite late, certain specimens appear sometimes quite difficult to place even at the ordinal level, and if we did not know the subsequent developments, we would group them together; we have here the same situation and the same difficulty. And it would seem that in this view, *Eotitanosuchus* and *Biarmosuchus* belong to the same infra-order, *but to two different families, both being recently detached from a common* stock which leads more or less directly to Brithopodidae. We have then to give a new diagnosis of the two families, Eotitanosuchidae and Biarmosuchidae.

Biarmosuchidae. — Dorsal profile of the skull very convex; ventral profile barely sinuous. Interorbital roof narrow, intertemporal roof wide; large orbits; small temporal fossae, with their dorsal border lower than that of the orbits. Vomer deep; palatine and pterygoid dentigerous tuberosities long. High parasphenoidal ventral rostrum. No coronoid process of the dentary; lower jaw articulation situated low and slightly pushed forwards; reflected lamina of the angular reaches backwards close to the mandibular articulation. Postcanines moderately small and numerous. Stapes perforated.

Eotitanosuchidae. — Dorsal profile of the skull slightly convex; ventral profile sinuous. Interorbital roof wider than in *Biarmosuchus;* intertemporal roof narrower, relatively. Orbits smaller in surface than the temporal fossae. Vomer deep; dentigerous palatine tuberosities long; pterygoid tuberosities shorter. Interpterygoid vacuity present. Postcanines moderately small and numerous.

In the next paragraph, the affinities of the Biarmosuchidae will be taken up. As for *Eotitanosuchus,* its affinities are usually taken to be with gorgonopsids; Tatarinov, however, sees an opposition to this view, particularly in the presence of an interpterygoid vacuity in the former; but such a vacuity is not uncommon in gorgonopsids. However, we must recognize that the characters 4, 5 (if really present) and 16, speak in favor of Tatarinov's view; and it cannot be excluded that eotitanosuchids would be the ecological predecessors of gorgonopsians, and as such would present a similarity merely due to an adaptation to the same environment. But the other possibility — that *Eotitanosuchus* is a member of the group which gave rise to Gorgonopsidae — appears more attractive than previously stated (Sigogneau 1970).

Biarmosuchidae-Ictidorhinidae. — It does seem that the orbital and temporal specializations preclude the biarmosuchids from the gorgonopsid (*sensu stricto*) ancestry. But these same specializations evoke strongly the ictidorhinids.

The cranial morphology of the Ictidorhinidae will not be redescribed here, this having been done already a number of times (Sigogneau 1970, and in press). But before undertaking their comparison with the Biarmosuchidae, let us keep in mind that these forms come from the upper Permian of South Africa and even, with the exception of one genus, from the top of the upper Permian, while the Biarmosuchidae come from what could be considered as the "middle" Permian of the northern hemisphere : a considerable geological and geographical gap thus separates these two groups. However, if one goes back to the list of the seventeen characters utilized in the preceding comparison, one finds that eight of them (2, 3, 7, 8, 10, 11, 13, 14) are constantly present in the Ictidorhinidae, seven (1, 4, 6, 9, 12, 15, 16) are known in certain genera, and only two (5, 17) are constantly lacking.

A more precise analysis shows that among these common characters appears a slight majority of primitive ones (7) : 1, 8, 9, 10, 11, 13, 14, 16; the other seven are specializations.

Among the two absent characters in ictidorhinids, one (5) was considered as constituting a specialization common to Eotitanosuchidae and Biarmosuchidae. Concerning the character 17, its absence represents a more evolved state. This discrepancy is accentuated by the presence, in the Ictidorhinidae, of a preparietal. In the limbs, apart from a common gracility and a common primitivity of the pelvic girdle, there is not much resemblance between the two families.

But altogether the Ictidorhinidae share with the Biarmosuchidae more specializations than the latter share with the Eotitanosuchidae. How should this be interpreted ? Should one see in the Ictidorhinidae a continuation of the biarmosuchids ? In this process, there would have been, as in the hypothetical lineage eotitanosuchids-gorgonopsids, loss of character 5 at least, and acquisition of a preparietal (8). This opinion, refuted in Sigogneau 1970 seems more appealing now that ictidorhinids appear more and more distinct from gorgonopsids (Sigogneau, in press).

Biarmosuchidae-Sphenacodontidae. — If we must look in the Sphenacodontidae for the ancestry of the Biarmosuchidae, as they are the only known pelycosaurs to possess a reflected lamina of the angular — and this condition being so far considered as obligatory —, we note that it is in *Haptodus s.l.* (9) that the orbits are the widest, which thus present the most ancestral-like aspect to the Biarmosuchidae. The forms belonging to this genus are small, with only a slight ventral sinuosity of the skull and a lowly situated mandibular articulation, as in biarmosuchids.

On the other hand, the face is short, the postorbital shows no trace of twisting, the lacrymal reaches the nares, the dorsal premaxillary remains short (as in all Sphenacodontinae and in contrast to the ophiacodonts); there

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(7) See footnote p. 104.

(8) The independant appearance of the preparietal in the two lines should not constitute an insurmontable obstacle to this hypothesis. It is to be remembered that this bone was individualized also in dicynodonts; in fact, the preparietal of the ictidorhinids shows more resemblance to that of the dicynodonts than to that of the gorgonopsids.

(9) However we must insist on the fact that, according to Romer himself (Romer and Price, 1940, p. 300), the reflected lamina of the angular is, in *Haptodus,* only « suggested ».

are numerous precanines and postcanines, and the lower canine is not differentiated. These primitive characters the leave door open for many eventual developments.

If, however, one considers the big orbits of the Biarmosuchidae as having appeared later, then one might look towards other genera of sphenacodontids for ancestry. But *Neosaurus, Oxyodon, Bathygnathus, Thrausmosaurus,* and *Macromerion* are too poorly known for use in phylogenetic considerations, and *Secodontosaurus* has a somewhat aberrant plan of cranial structure and already long neural apophyses as had *Sphenacodon* and *Ctenospondylus*. As for *Dimetrodon,* it can only represent the end of a phylum including the above genera. In contrast, the supposed distribution of *Haptodus* in Western Europe is favorable to a possible affiliation with the eotheriodonts; it might well be, as suggested by Romer and Price in 1940, that with *Haptodus,* we are near to the origin of the Russian eotherapsids, that is, of the line common to the brithopodids and the eotheriodonts and thus, to the true therapsids.

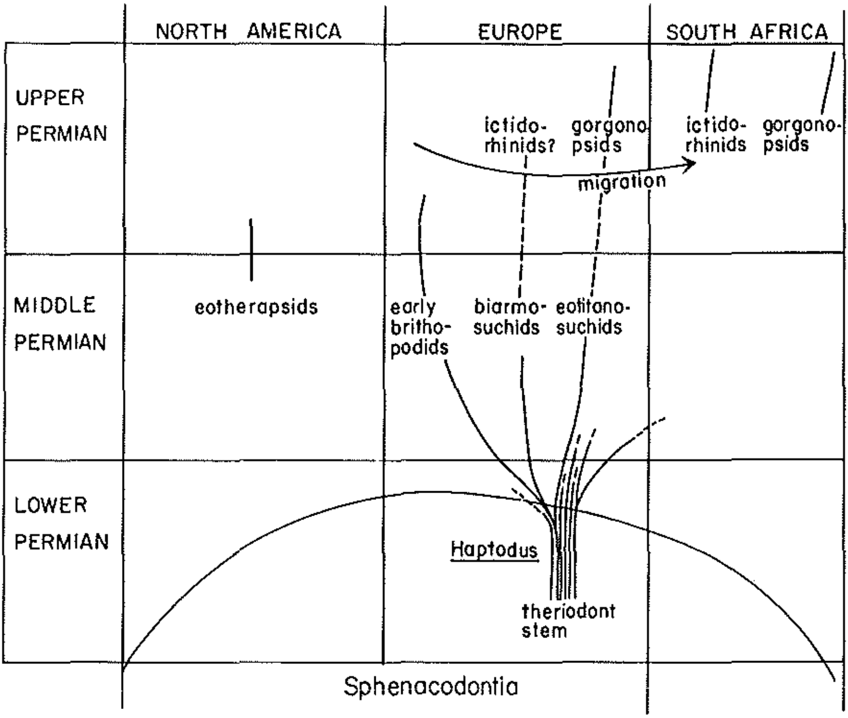
If then *Haptodus* appears as the most acceptable ancestral genus, there remains however quite a considerable gap, geologic, geographic and morphologic, between the two ensembles, biarmosuchids and sphenacodontids. Of course, it must be remembered also that *Haptodus* remains quite unsatisfactorily known.

CONCLUSION

The preceding study poses an interesting problem of paleogeography. Let us recall the facts : there exist sphenacodonts, ophiacodonts and edaphosaurs in North America and in Europe, all of them in the upper Carboniferous and lower Permian, and then possible sphenacodonts in the upper Permian of South Africa. Eotherapsids are found in the " middle " Permian, in North America as in Russia. And before the end of the late Permian, in Russia and South Africa, appear the therapsids. Among them the gorgonopsids, being very similar in the northern and southern hemispheres,, must have had a single origin.

In other words, available data seem to indicate that the South African therapsids are not indigenous, but result from a migration of elements coming from the northern hemisphere. This migration must have had occured rather late (early in the upper Permian), since one does not have, in South Africa, brithopodids which, in Russia appear at the same time as the eotheriodonts but continue later into the upper Permian.

Thus ictidorhinids and gorgonopsids would have been born in Europe, the absence of the first in the Russian strata being only due to their rarity : they are quite rare in South Africa also, compared to the abundance of gorgonopsids. The relations of the groups involved would seem at present to be as in the following scheme.



It does remain that, in spite of the additional knowledge acquired in recent years, one does not yet detect very clearly the origin of the therapsids, and especially of the theriodonts; the Russian eotheriodonts known at present are already too specialized, and too close in some ways to brithopodids. Nevertheless, Nopcsa's opinion (1928, p. 20) that "it is in Russia that we may hope to discover all those types that are necessary to bridge over the gap observable between the types known from Texas and those known from the Karro " remains probably in large part valid.

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BIBLIOGRAPHIE

BOONSTRA L. D., 1963. — Early dichotomies in the therapsids. *S. African Jour. Sci.* **LIX**, n° 5, pp. 176-195, 12 fig.

EFREMOV I.A., 1940. — [Description préléminaire des nouveaux Tétrapodes permiens et triasiques d'U.R.S.S.] *Trudy Inst. Paleont. Akad. Nauk S.S.S.R.*, **X**, n° 2, pp. 1-140, 25 fig., 14 pl. (en russe).

EFREMOV I. A., 1954. — Une faune de vertébrés terrestres dans les grès cuprifères permiens de l'ouest de la région pré-ouralienne. *Trudy Inst. Paleont. Akad. Nauk S.S.S.R.*, **LIV**, pp. 1-146, 82 fig., 33 pl. (traduction B.R.G.M., n° 2565).

KALANDADZE N.N., OTCHEV V.G., TATARINOV L.P., TCHUDINOV P.K., SHISHKIN M.A., 1968 — [Catalogue des Tétrapodes permiens et triasiques d'U.R.S.S. *In Amphi*biens et Reptiles du Paléozoïque supérieur et du Mésozoique d'U.R.S.S. Academie des Sciences d'U.R.S.S., section de Biologie générale, Moscou]. P. 72-91 (en russe).

NOPCSA F., 1928. — Paleontological notes on reptiles. *Geol. Hungarica,* ser. Pal., **I**, fasc. 1, p. 1-84, 14 fig., 9 pl.

OLSON E. C., 1962. — Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. *Trans. Amer. Phil. Soc.*, n.s., **52**, pt. 2, 224 p., 69 fig., 19 pl.

ROMER A. S. and PRICE L.W., 1940. — Review of the Pelycosauria. *Geol. Soc. Amer., Spec. Papers,* n° 28, X + 538 p., 71 fig., 46 pl.

SEELEY H.G., 1894. — Researches on the structure, organization and classification of the fossil Reptilia. VIII. Further evidences of *Deuterosaurus* and *Rhopalodon* from the Permian rocks of Russia. *Phil. Trans. Roy. Soc. London,* ser. B, **CLXXXV**, p. 663-717, 14 fig., pl. 60-63.

SIGOGNEAU D., 1970. — Révision systématique des Gorgonopsiens sud-africains. *Cahier de Paléontologie,* éd. C.N.R.S., Paris, 417 pp., 243 fig., 93 pl.

SIGOGNEAU D., 1970. — Contribution à la connaissance des Ictidorhinidae (Gorgonopsia). *Pal. Afr.*, **13**, p. 25-38, 7 fig., 3 pl.

TCHUDINOV P.K., 1960. — [Thérapsides du Permien supérieur de la localité d'Ezhovo]. *Paleont. Zh. Akad. Nauk S.S.S.R.*, n° 4, p. 81-94, 5 fig. (en russe).

TCHUDINOV P. K., 1964. — [Connaissance des Dinocéphales d'U.R.S.S.]. *Paleont. Zh. Akad. Nauk S.S.S.R.*, n° 2, p. 85-98, 5 fig. (en russe).

TCHUDINOV P. K., 1965. — New facts about the upper Permian of the U.S.S.R. *Jour. Geol.*, **73**, n° 1, p. 117-130, 5 fig.

WATSON D. M. S., 1942. — On Permian and Triassic tetrapods. *Geol. Mag.*, **79**, p. 81-116, 5 fig.