

PSEUDOSUCHIANS OF THE U.S.S.R.*

by

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1. REVISION OF THE PSEUDOSUCHIANS OF THE U.S.S.R.

Pseudosuchia were first described from Soviet territory by Huene⁽²²⁾ in 1940. From the very incomplete remains found in Lower Triassic deposits in the north of the European part of the U.S.S.R. and the southern maritime territory, he erected two genera, *Chasmatosuchus* Huene and *Dongusia* Huene.

For a long time the forms described by Huene were the only Pseudosuchia known from the Soviet Union, and only lately, with the discovery of a wealth of new material, has the list been considerably extended. In all, seven species of Pseudosuchia belonging to five genera and three or four families, have now been described in the U.S.S.R. Data on all these forms are given in Table I. In addition, indeterminate remains of Pseudosuchia are known from certain other deposits of the Lower and part of the Middle Triassic^(2, 4).

In the light of all the known Pseudosuchia material from Soviet territory (in the collection of the Paleontologischeskii Institut, AN SSSR [Institute of Paleontology, USSR Academy of Sciences, PIN], and partly in that of Saratov State University), the author has been able to substantially modify this list. The results of the revision are set out below.

Genus *Vjuschkovia* Huene, 1960

In the course of excavations in 1953 and 1954, members of the Institute staff recovered fairly complete remains of large pseudosuchians from the Rossypnoe site, Orenburg Province. The site was discovered by Garyainov⁽¹⁾, who assigned the enclosing deposits to the Romashkino suite. The material collected contained remains of five individuals, of various sizes, including the greater part of the skeleton of one specimen.

Huene, having familiarized himself with this material during his stay in Moscow in autumn, 1957, described the Rossypnoe pseudosuchian under the name *Vjuschkovia triplicostata* Huene, 1960⁽²⁶⁾. He pointed out that in regard to skull structure the new form was close to the family Ornithosuchidae, but that the structure of the limbs was similar to that of the Erythrosuchidae; he therefore thought it advisable to erect a separate family for the Rossypnoe pseudosuchian, Vjuschkoviidae, from which the

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Ornithosuchidae originated. He did not, however, supply a formal diagnosis of the new family.

Certain inaccuracies, however, had crept into Huene's description and affected his conclusions regarding the systematic position of *Vjuschkovia*. Closer acquaintance with the material in the Institute of Paleontology has revealed a profound similarity between that genus and the South African *Erythrosuchus* Broom, 1905^(12, 13). The structure of the braincase in *Vjuschkovia triplicostata* is very similar to that of the specimen of *Erythrosuchus africanus* Broom, 1905, described by Brink⁽⁹⁾ (Figs. 1 and 2). In both forms there is a deep fossa in the posterior part of the braincase, in the region of the parietal and adjacent parts of the frontals. In both forms the prefrontals, tapering anteriorly, overlap the frontals and are wedged into the nasals at the back (Huene did not notice the sutures between the braincase bones and mistook the prefrontals for the frontals). The frontals form the orbital margin for only a very short distance, the orbit being deeply wedged up between the prefrontals and the superior part of the postorbital arch of bones. In both forms the prefrontals form a laterally protruding crest and send out a process that descends along the anterior margin of the orbit. The postorbital forms a lateral crest, with a deep fossa in its descending process. In both forms there is conspicuous thickening in the region where the postorbital articulates with the postfrontal (Huene did not notice the postfrontal at all and attributed it entirely to the postorbital). Both forms have a deep fossa in the ventral surface of the braincase, in the region where the postorbital arch is articulated with the adjacent parts of the frontal and parietal. In the Rossypnoe pseudosuchian this fossa is occupied by the superior end of the prootic (Fig. 3). Were it not for Brink's reference to the presence of a postparietal in *Erythrosuchus africanus*, his description of that skull would be applicable in every detail to the Rossypnoe form; but in the latter, the postparietal hardly exists at all as an independent formation. One gets the impression that the main difference between the two "genera" is one of size alone: the length of the *E. africanus* skull described by Brink is 75 cm, whereas the *V. triplicostata* skull is 40–60 cm long.

Table 1.

Species	Family	Range	Age
<i>Archosaurus rossicus</i> Tatarinov, 1960 ⁽⁶⁾	Proterosuchidae ⁽⁶⁾	Vladimir Province	P ₂ , top of Tatarian stage (zone IV)
<i>Chasmatosuchus rossicus</i> Huene, 1940 ⁽²²⁾	Proterosuchidae ⁽²⁴⁾	Vologda Province	T ₁ , Vetluga series (zone V)
<i>Chasmatosuchus parvus</i> Huene, 1940 ⁽²²⁾	Proterosuchidae ⁽²⁴⁾	Vologda Province	T ₁ , Vetluga series (zone V)
<i>Chasmatosuchus</i> sp. ⁽²²⁾	Proterosuchidae ⁽²⁴⁾	Vologda Province and Komi ASSR	T ₁ , Vetluga series (zone V)
<i>Chasmatosuchus</i> <i>vjuschkovi</i> Otschev, 1961 ⁽⁵⁾	Proterosuchidae ⁽⁴⁾	Orenburg Province	T ₁ , Buzuluk suite (zone V)
<i>Garjainia prima</i> Otschev,	Garjainidae ⁽³⁾	Orenburg Province	T ₁ , Buzuluk suite (zone V)

1956⁽³⁾

<i>Dongusia colorata</i> Huene, 1940 ⁽²²⁾	Proterosuchidae ⁽²⁴⁾ or Euparkeriidae ⁽²⁶⁾	Orenburg Province	T ₁ , Tananyk suite (zone VI)
<i>Vjuschkovia triplicostata</i> Huene, 1960 ⁽²⁶⁾	Vjuschkoviidae ⁽²⁶⁾	Orenburg Province	T ₁ or T ₂ , Romashkino suite (zone VI or VII)

Comparison of *V. triplicostata* with the largest specimen of *E. africanus* (length of skull 95 cm) described by Huene⁽²⁰⁾ reveals further similarities between the two animals. Both forms possess a similarly constructed premaxilla, bearing five teeth and, together with the nasal, bordering the terminally situated naris; the only difference is that the *E. africanus* premaxilla is more massive. The shape of the squamosal (not described by Huene), quadratojugal, and jugal in *V. triplicostata*, all of which are exactly similar to the equivalent bones in *E. africanus*, permits the conclusion that the posterior margin of the lateral inferior) temporal fenestra in *V. triplicostata* did not have the forward bend reconstructed by Huene⁽²⁶⁾. As in the specimen of *E. africanus* described by him, *V. triplicostata* has a conical process protruding backward from the posterior margin of the parietals. Huene at first regarded this process in *E. africanus* as paired and formed by the two parietals⁽²⁰⁾, but later maintained that it was formed by the unpaired postparietal^(21, 24). In *V. triplicostata* this projection was probably formed by the unpaired postparietal, but was very indistinctly demarcated from the parietals. However that may be, the postparietals in *V. triplicostata* do not overlap the temporal surface of the parietal posterolateral process, as Huene shows them, but are either wanting or form the above-mentioned conical projection. Lastly, the structure of the prootic, which is closely adnate to the opisthotic and exoccipital, is very similar in both forms.

Essentially, the *E. africanus* skull described by Huene differs from the *V. triplicostata* skull in only three characters. In the African animal the postorbital enters the margin of the superior temporal fenestra, there is a large (about 1 cm in diameter) parietal foramen, and there is no lateral foramen in the lower jaw. In the Rossypnoe form the postfrontal does not reach the margin of the superior temporal fenestra, the parietal foramen, if present, was very small (the corresponding part of the braincase in both *V. triplicostata* specimens in the PIN collection is attenuated and collapsed), while in the lower jaw there is a well-formed lateral foramen. The first two characters distinguish Huene's specimen of *E. africanus* not only from *V. triplicostata*, but also from the other specimen of *E. africanus* described by Brink, which is completely similar in these characters to the Rossypnoe pseudosuchian. In regard to the lateral foramen in the lower jaw, it must be noted that in Huene's specimen the corresponding part of the lower jaw has been lost and there is no basis whatsoever for his assertion that the foramen was wanting. Moreover, the shape of the angular and surangular in *E. africanus* makes it more likely than not that the lateral foramen was present. No other specimens of the *E. africanus* lower jaw are known.

The strong resemblance in structure between *V. triplicostata* and *E. africanus* extends to the limb skeleton, which differ only in secondary details^(13, 20, 26). The only clear distinction between the two forms lies in the shape of the vertebral centra, which are conspicuously abbreviate in *E. africanus* and moderately elongate in *V. triplicostata*⁽²⁶⁾. The smaller *E. africanus* individual described by Broom⁽¹³⁾, however, has somewhat

more elongate vertebrae, whereas in *V. triplicostata* the vertebrae became more flattened with the growth of the animal. In all other respects, however — the high position of the transverse processes on the dorsal vertebrae, the presence of crests joining the diapophyses to the zygapophyses and parapophyses, the lateral constriction of the vertebral centra, equipped with a ventral carina, and the shape of the neural canal, which is high and laterally compressed — the vertebrae of the African pseudosuchian are very similar to those of *V. triplicostata*. Between the latter's vertebrae are well-developed intercentra, which Huene⁽²⁰⁾ assumed to exist in *E. africanus* on the basis of the shape of the vertebral centra. All this allows us to regard *V. triplicostata* as a form extremely close to *E. africanus*, and leaves no foundation whatsoever for distinguishing it as a separate family. Nor are there sufficient grounds for erecting a separate genus for the Rossypnoe pseudosuchian, for in the main it is distinguished from *E. africanus* by nothing more than its smaller dimensions and the more convex margins of its prefrontals; the latter character, incidentally, is conspicuously variable in both species. At first glance, *V. triplicostata* is sharply distinguished from all other pseudosuchians by its tricapitulate anterior body ribs⁽²⁶⁾, but, as I shall show below, this character occurred widely in primitive pseudosuchians and, in all probability, was also present in *E. africanus*. I therefore regard the appellation *Vjuschkovia* Huene, 1960 as a synonym of *Erythrosuchus* Broom, 1905, and shall henceforth call the Rossypnoe pseudosuchian *Erythrosuchus triplicostatus* (Huene), 1960. The braincases depicted in Huene's work⁽²⁶⁾ and kept in the PIN collection under No. 952/59 (Fig. 2) should be regarded as the lectotype of this species (not holotype).

Genus *Garjainia* Otschev, 1958 and Family Garjainidae

In 1958 V. G. Ochev (= Otschev) described a large, new pseudosuchian, *Garjainia prima*, from the Buzuluk suite of the Lower Triassic (Andreevka site, Orenburg Prov.) and erected a separate family for it. Ochev regarded *G. prima* as a form relatively near to the Proterosuchidae and justified according it family rank on the grounds that it possessed a number of progressive characters: it was thecodont and lacked palatal teeth, an interparietal, parietal foramen, and intercentra between the vertebrae(3). In Ochev's opinion, it stood closest to such proterosuchids as *Elaphrosuchus* Broom, 1948, which it resembled in having only a slight downward bend of the snout.

Ochev kindly gave me an opportunity for studying the *G. prima* material directly, and as a result I am convinced of the profound similarity between this form and the genus *Erythrosuchus*, particularly *E. triplicostatus*, which was not described until after Ochev's work had been published. *G. prima* is sharply differentiated from members of the Proterosuchidae by its comparatively high skull, the shape of the orbits and temporal fenestrae, and the abrupt expansion of the prootic along the ventral surface of the braincase. In skull structure *G. prima* is distinguished from *E. africanus* mainly by its smaller dimensions (length of skull 43 cm) and relatively lower skull. In these characters it turns out to be entirely similar to *E. triplicostatus*. Further preparation revealed the presence of a very small parietal foramen (less than 1 mm in diameter) in *G. prima*, and the probability that the posttemporal had been retained (it has probably been lost from the specimen, but the characteristic sutural surface of the posterior margin of the supraoccipital, which stands well away from the posterior margin of the parietals,

suggests that it existed. In regard to all the structural characters of the skull that have been compared, the details of its relief, with the characteristic fossa in the posterior part of the braincase, the excrescence on the postorbitals, the horizontal crest on the prefrontals, and other features, *G. prima* fully resembles *E. triplicostatus*. The base of the skull (not known for *E. africanus*) is identically constructed in both forms and is characterized by close fusion of the basioccipital with the basisphenoid, both bones being almost vertical, and by the presence of two horizontal crests on their occipital surface. The *G. prima* premaxilla bears five teeth, and the lower Jaw possesses a lateral foramen placed partly as in *E. triplicostatus*. The vertebrae in both *G. prima* and *E. triplicostatus* are somewhat elongate and identically constructed; among the *G. prima* material is a single intercentrum, not recognized by Ochev. It should be noted, however, that there is still no proof that the anterior body ribs were still tricapitulate in *G. prima*, because only the 2nd–5th cervical and the 4th posterior dorsal vertebrae have been preserved. The two forms are very similar also in regard to the structure of the shoulder girdle. All this means that there is no justification for erecting the family Garjainidae.

It would seem that only one character substantially distinguishes *G. prima* from the African *E. africanus* and the Rossynoe *E. triplicostatus*: the *G. prima* snout has a clearly expressed downward bend, whereas Huene depicts the snout of the other two forms as completely straight^(20, 26). Yet the left jaw bone of *E. triplicostatus*, which has been almost fully preserved, has a clearly expressed upward bend of its anterior part, such as is characteristic also of *G. prima* and constitutes reliable evidence that there was a notch between the maxilla and premaxilla. In this section the *E. triplicostatus* maxilla, like that of *G. prima*, bore three comparatively short teeth. The complete similarity of the maxilla and premaxilla in the two forms indicates that the snout was just as much downcurved in *E. triplicostatus* as in *G. prima*. In the case of *E. africanus* only a small fragment of the anterior part of the left maxilla is depicted, with the anterior alveolus situated clearly above the level of the rest⁽²⁰⁾. The last three teeth of the *E. africanus* maxilla are abbreviate⁽⁹⁾. All this obliges us to regard the moderately expressed downward bend of the snout as characteristic not only of *G. prima*, but also of the two species of *Erythrosuchus*. All these forms are similar also in regard to the total number of teeth in the jaw bone — 11 in *E. africanus*⁽⁹⁾, 13–14 in *E. triplicostatus*, 15 in *G. prima*.

It seems to me quite clear that the genera *Garjainia* and *Erythrosuchus* are synonyms. Only *G. prima* can be regarded as a separate species, differing from *E. triplicostatus* in certain secondary characters (the margin of the prefrontal protrudes outward more sharply than in *E. triplicostatus*, and the outward spread of the parietal along the anterior margin of the superior temporal fenestra is more marked). The generic appellation *Garjainia* Otschev, 1958 should be reduced to a synonym of *Erythrosuchus* Broom, 1905 and *G. prima* should henceforth be named *Erythrosuchus primus* (Otschev), 1958. This species is very close to *Erythrosuchus triplicostatus*.

Genus *Dongusia* Huene, 1940

The genus *Dongusia* was created by Huene on the basis of a single vertebra, which he regarded as an anterior dorsal. He regarded the characteristic features of this genus as the presence of a moderately expressed hyposphene, the position of the

diapophyses above the level of the neural canal and of the parapophyses at the height of the latter, and the presence of four crests, the first running from the diapophyses toward the prezygapophyses, the second toward the postzygapophyses, the third toward the posterior margin of the vertebra, and the fourth toward the parapophyses. The centrum of the vertebra is laterally compressed and bears a longitudinal carina on its ventral surface⁽²²⁾. No new material of *Dongusia* has been described since the original description, and this genus is still known solely on the basis of the species *D. colorata* Huene, 1940.

Comparison of the material has revealed a remarkable similarity between the *D. colorata* vertebra and the posterior dorsal vertebrae of *E. triplicostatus* and *E. primus*. The latter has similarly situated transverse processes, with four identically situated crests running from the topmost of them. On both sides of the crest joining the diapophyses to the parapophyses both forms have deep fossae. The third fossa is situated above the crests joining the diapophyses to the prezygapophyses. Both in *E. triplicostatus* and in *E. primus* the vertebral centra are laterally compressed and usually bear a longitudinal ventral carina. The proportions of the vertebrae too are similar in both forms (Figs. 4 and 5). All this suggests that the genera *Dongusia* and *Erythrosuchus* are related and also that *D. colorata* was described from a posterior, not an anterior, dorsal vertebra.

Of the characters cited by Huene, only the presence of the hyposphene distinguishes the *D. colorata* vertebra from the vertebrae of either of our species of *Erythrosuchus*. The structure on the *D. colorata* vertebra, however, described by Huene as a hyposphene, is wrongly depicted in his work⁽²²⁾ and can be called only a rudimentary hyposphene. In reality the *D. colorata* “hyposphene” is a paired structure divided by a median cleft. Each of its halves is formed by a plate that bends downward from the inner margin of the postzygapophysis. The two plates come close together but remain divided by the median cleft. Ventrally they are joined to the roof of the neural canal (Fig. 6, b). In the drawing in Huene’s work⁽²²⁾, the “hyposphene” is depicted as unpaired and somewhat hypertrophied and its connection with the postzygapophyses is shown very indistinctly (Fig. 6, a).

In the vertebra of both our species of *Erythrosuchus* (*E. triplicostatus* and *E. primus*), there is also a structure corresponding to the *D. colorata* “hyposphene”. This consists of downcurved projections of the inner margin of the postzygapophyses, articulated with small platforms situated on the inner surface of the prezygapophyses (the latter have been destroyed in the *D. colorata* vertebra). These projections must have restricted the mobility of the vertebrae when the body was bending sideways. The expression of this structure varies somewhat from one vertebra to another, but it is usually less well-developed than in *D. colorata*. The impression created is that the width of the cleft dividing the processes of the postzygapophysis depends largely on the deformation of the vertebrae, which became laterally depressed, so that the processes come close together and the whole formation becomes practically indistinguishable from the *D. colorata* “hyposphene” (Fig. 6, c).

The remarkable similarity of vertebral structure between *D. colorata* and both our species of *Erythrosuchus* suggests generic identity of all these forms. The variable degree to which the “hyposphene” is expressed in *E. triplicostatus* means that we cannot attach particular significance to its somewhat greater development in the *D. colorata* vertebra. All this allows us to regard the genus *Dongusia* Huene, 1940 as a synonym of

Erythrosuchus Broom, 1905. The name *D. colorata* Huene, 1940 should be replaced by *E. coloratus* (Huene) 1940. Among the characters distinguishing *E. coloratus* from *E. triplicostatus* we may mention the somewhat greater expression of the “hyosphene” and the presence of a median crest, jutting out backward from the margin of the neural spine, in the fossa above the postzygapophyses. It should be noted that in particular cases the characters of such a crest are observed also in the vertebrae of our other two species of *Erythrosuchus*. The paucity of material from Donguz makes it impossible to give a clear diagnosis of *E. coloratus*, the independence of which therefore remains for the moment not definitely proven.

Genus *Chasmatosuchus* Huene, 1940

This genus was also described by Huene⁽²²⁾ on the basis of very incomplete material, but its independence is not in doubt. *Chasmatosuchus* is distinguished from other pseudosuchians by the structure of the teeth, which have triangular crowns abruptly compressed at the sides.

Study of the originals has made it possible to correct Huene’s description in important respects. First it must be noted that *Chasmatosuchus*, like *E. triplicostatus*, possessed tricapitulate anterior dorsal ribs. The two articulated vertebrae that form the lectotype of the type species *Ch. rossicus* Huene, 1940 (holotype not distinguished by Huene) belong to the anterior dorsal ribs and bear three areas for articulation with the rib, corresponding to the parapophysis and the divided diapophysis. The “inferior” diapophysis looks like a crest, still unseparated from the “superior”, but terminating in a completely independent articular surface. In this respect there is complete analogy between the anterior dorsal vertebrae of *Ch. rossicus* and of *E. triplicostatus*. All these three facets are depicted in Huene’s work, but he regarded the “inferior” diapophysis as a simple crest unrelated to articulation with a rib. It is interesting that the division of the diapophysis and the triple articular surfaces for the rib are expressed also in the very small vertebra that served Huene as the holotype for his description of another species, *Chasmatosuchus* (?) *parvus*. This vertebra should also be assigned to the anterior dorsal and not to the cervical, as Huene thought.

Further, Huene was wrong in calling the *Chasmatosuchus* teeth acrodont teeth seated in a deep furrow. In reality each tooth is situated in an independent alveolus, but the root part of the old teeth is closely adnate to the alveolar walls, and the outer teeth begin to resemble acrodont teeth. The crowns of the young teeth are triangular, greatly compressed laterally, and serrated not only along the posterior margin, as Huene shows them, but also along the anterior margin. The old teeth are greatly worn down, become outwardly more rounded, and the serrations of their anterior margin have been completely abraded.

Huene classified all the *Chasmatosuchus* remains into three groups according to size, assigning the largest to the type species *Ch. rossicus*, the very small vertebra mentioned above to *Ch. (?) parvus*; the rest, intermediate in size, he describes as *Chasmatosuchus* sp.

Such a principle of species classification inevitably raises doubts. I should have thought it more correct to retain only one of the two species described by Huene, the type species *Ch. rossicus*. The *Ch. (?) parvus* vertebra differs from the *Ch. rossicus* vertebrae

mainly in size and elongation. Comparison with the *Erythrosuchus triplicostatus* vertebrae suggests that these differences relate to the age of the animal.

Since Huene's work⁽²²⁾ was published, other *Chasmatosuchus* remains have been recovered from Lower Triassic deposits in the northeast of the European part of the USSR — from the River Fedorovka (Kirov Province) and the village of Spasskoe (Gor'kii Province). On one of the Spasskoe vertebrae the division of the diapophysis into two parts and the tricapitulation of the articular facets for the ribs are well expressed. Another interesting feature is the very low height of the neural spine on this vertebra. In all the remaining *Chasmatosuchus* vertebrae the apices of the neural spines have been lost, but it is possible that their short length may turn out to be a diagnostic character for the genus. The fragment of skull base from Spasskoe somewhat resembles the base of the *E. triplicostatus* skull and differs chiefly in its miniature character. The skull base in *Chasmatosuchus* was less high, and *Chasmatosuchus* had only one of the two transverse crests characteristic of *E. triplicostatus*. The *Chasmatosuchus* remains from Spasskoe (*Phaantosaurus* and *Tupilacosaurus* beds) and Fedorovka (*Tichvinskia* beds) came from different stratigraphic horizons and possibly relate to different species, but until we have more complete material we must refrain from erecting species based on certain differences observable in the *Chasmatosuchus* remains from different sites; apart from the type species, we shall describe them as *Chasmatosuchus* sp.

Ochev provisionally assigned the premaxilla of a very small pseudosuchian that he found in the Buzuluk suite, along with *Erythrosuchus primus* (Andreevka site, Orenburg Prov.) to the genus *Chasmatosuchus*. The *Ch. (?) vjuschkovi* premaxilla has a clearly expressed downward bend and bears only five teeth in all. These teeth differ sharply from those of *Chasmatosuchus* from the northeast of the European part of the USSR: their crowns are acuminate and bend conspicuously backward. The short nasal passage, opening in a deep incision of the premaxilla, and the total absence of a bony internasal septum, sharply distinguishes *Ch. (?) vjuschkovi* from *Archosaurus rossicus*; but these characters, like the number of teeth, give it a resemblance to *Erythrosuchus*. I do not think that it can be assigned to the same genus as *Ch. rossicus*. It could be that the *Ch. (?) vjuschkovi* premaxilla really belongs to a very young individual of *Erythrosuchus primus*, but this question cannot be finally settled until further material has been studied.

COMPOSITION OF THE PSEUDOSUCHIAN FAUNA OF THE U.S.S.R.

I have thus come to the conclusion that all the large pseudosuchians described from the Soviet Triassic belong to *Erythrosuchus*. This genus has hitherto been known only from the type species and has been regarded as characteristic of the top of the Lower Triassic (*Cynognathus* Zone) in South Africa. Various species of *Erythrosuchus* have turned out to be common occurrences in the continental Triassic of South Cisuralia, where their stratigraphic range is very wide, from the Buzuluk suite (*E. primus*) to the Romashkino (*E. triplicostatus*). The great similarity of these species is evidence against there being a great difference in the age of the enclosing deposits and makes me inclined to date the Romashkino suite as Lower Triassic. Most geologists support this view. Garyainov and Chalyshev, who assign the whole Romashkino suite⁽¹⁾ or at least its Rossypnoe beds to the Middle Triassic, regarded the form of the pseudosuchians they

found in it as one of the main arguments in favor of so dating the suite. With the discovery of the systematic position of *E. triplicostatus* this argument loses force.

The only consideration to hold us back from categorically dating the Rossypnoe beds as Lower Triassic is the extent of the stratigraphic range of *Erythrosuchus*. The surangular lower-jaw bone from the Koltaevo site, which, according to its fauna, belongs to the Middle Triassic (I. A. Efremov's zone VII) may possibly belong to the same genus.

In the north of the European part of the U.S.S.R., where no *Erythrosuchus* remains have yet been found, another pseudosuchian genus occurs widely in the Lower Triassic. This is *Chasmatosuchus*, which in general characterizes the somewhat older deposits of the Vetluga series. *Chasmatosuchus* has hitherto been known only from very incomplete remains and has therefore been difficult to study. In its vertebral structure this genus is very similar to *Chasmatosaurus*, characteristic of the very bottom of the Triassic (*Lystrosaurus* Zone) in South Africa, India, and China, but the structure of the teeth seems to allow the two genera to be distinguished. The *Chasmatosuchus* remains in the PIN may well belong to different species, but until we have new material we must refrain from distinguishing them.

Table 2.

Species	Family	Range	Age
<i>Archosaurus rossicus</i> Tatarinov, 1960	Proterosuchidae	Vladimir Province	P ₂ , top of Tatarian stage (zone IV)
<i>Chasmatosuchus rossicus</i> Huene, 1940	Proterosuchidae	Vologda Province	T ₁ , Vetluga series (zone V)
<i>Chasmatosuchus</i> sp.	Proterosuchidae	Gor'kii Province, Vologda Province, and Komi ASSR	T ₁ , Vetluga series (zone V)
<i>Erythrosuchus primus</i> (Otschev), 1958 (? = <i>Chasmatosuchus? vjuschkovi</i> Otschev, 1961)	Erythrosuchidae	Orenburg Province	T ₁ , Buzuluk suite (zone V)
<i>Erythrosuchus coloratus</i> (Huene), 1940	Erythrosuchidae	Orenburg Province	T ₁ , Tananyk suite (zone VI)
<i>Erythrosuchus triplicostatus</i> (Huene), 1960	Erythrosuchidae	Orenburg Province	T ₁ , Romashkino suite (zone VI)

Table 2 shows a revised list of the pseudosuchians known at present in Soviet territory. It is interesting that all these forms belong to the most primitive group of pseudosuchians, the superfamily Proterosuchoidea. I am inclined to regard the form described by Ochev as *Chasmatosaurus* (?) *vjuschkovi* as a young individual of *Erythrosuchus primus*, and I provisionally place it among the synonyms of the latter.

STRUCTURE OF THE PROTEROSUCHIAN VERTEBRAL COLUMN

Huene⁽²⁶⁾ mentioned a remarkable feature of the axial skeleton of *Erythrosuchus triplicostatus*, namely tricapitulation of the anterior dorsal ribs, to which the animal owes its specific name. According to Huene's observations, an additional facet for articulation with a rib appears on the first dorsal vertebra of *E. triplicostatus*, situated between the diapophysis and the parapophysis, on a crest running from the diapophysis. This additional facet disappears in the sixth and subsequent dorsal vertebrae, and the ribs again become bicapitular.

The additional facet formed, in my opinion, through division of the diapophysis. It appears at the base of the neural arch and on the first dorsal vertebra is practically unseparated from the diapophysis. Inspection of a series of dorsal vertebrae, however, does not bear out Huene's conclusion regarding the disappearance of the additional facet on the posterior dorsal vertebrae. On the fifth dorsal vertebra the tricapitulation of the articular facets for the ribs is very well expressed. The "superior" diapophysis is situated high on the neural arch, running off from it above the level of the neural canal, while the "inferior" diapophysis is situated at the ventral margin of the neural arch, below the neural canal, and the parapophysis is situated in the middle of the vertebral centrum, at the latter's inferior margin. Both the facets retained on the sixth and subsequent dorsal vertebrae are situated on the neural arch and correspond in position to the "superior" and "inferior" diapophyses. The impression thus created is that the parapophysis disappears on the posterior dorsal vertebrae and that the bicapitular posterior dorsal ribs in *E. triplicostatus* are articulated to a divided diapophysis, instead of to the diapophysis and parapophysis. Then both heads of the posterior dorsal ribs in *E. triplicostatus* will correspond to a divided tuberculum, instead of to the capitulum and tuberculum in the strict sense of the word.

The bicapitular ribs of caudate amphibians are probably of a similar nature, except that in them the neoformal, secondary diapophysis is situated above, instead of below, the primary one⁽¹⁷⁾. Incidentally, according to certain new data, only the proximal part of the parapophysis is reduced in caudate amphibians, while the distal part is adnate to the diapophysis, so that the bicapitular ribs of caudate amphibians are of the usual nature⁽⁸⁾.

There are grounds for asserting that the tricapitulation of the anterior dorsal ribs characterized not only *E. triplicostatus*, but also many or even all proterosuchians (Proterosuchidae and Erythrosuchidae). We have already noted the triple character of the rib facets on the anterior dorsal vertebrae of *Chasmatosuchus*. It is possible that the anterior dorsal ribs in *E. africanus* were also tricapitular. The *E. africanus* vertebra described by Huene⁽²⁰⁾ as a cervical was in all probability the first dorsal vertebra. Its neural spine slopes forward and is greatly dilated at the end, as is characteristic of the first dorsal vertebra in *E. triplicostatus*⁽²⁶⁾. The centrum of the *E. africanus* vertebra described is abruptly flattened (height-length ratio of its centrum 2.18); the first dorsal vertebra in *E. triplicostatus* is also usually somewhat flattened (1.40–1.66). On the centrum of the *E. africanus* vertebra described there was a well-formed parapophysis and a diapophysis, corresponding in position to the "inferior" diapophysis in *E. triplicostatus*. In the drawing in Huene's work^(26, Plate V, 3c) a broad crest can be seen above this diapophysis, comparable in position with the "superior" diapophysis of *E. triplicostatus*. The triple character of the rib facets on the *E. africanus* vertebra is obscured by the fact that the ends of the "superior" diapophysis seem to have been broken off. Such a defect

often occurs also on the anterior dorsal vertebrae of *E. triplicostatus*. It thus looks probable that the anterior dorsal ribs in *E. africanus* were also tricapitular. On the posterior dorsal vertebrae of *E. africanus*, however, the rib facets were arranged in exactly the same way as in *E. triplicostatus*^(12, 13, 20).

The dorsal vertebrae of the remaining proterosuchians are known only in the case of *Chasmatosaurus*^(23, 30); on one of the *Ch. indicus* vertebrae illustrated in Huene's work⁽²³⁾ distinct characters of triple rib facets can be seen, connected with the development of a crest running from the diapophysis ("superior") to the anterior margin of the vertebra. Although this tripling was not even mentioned by Huene, comparison of his drawing with the *Erythrosuchus* and *Chasmatosuchus* vertebrae leaves little room for doubting its existence. On the other hand, the rib facets on the posterior dorsal vertebrae of *Chasmatosaurus yuani*⁽³⁰⁾ are situated in the same way as in *Erythrosuchus*.

The tricapitulation of the anterior dorsal ribs can thus be regarded as a character widespread among proterosuchians or even common to all of them. The true parapophysis disappears on the posterior dorsal vertebrae in proterosuchians and the two transverse processes correspond to a divided diapophysis. This raises the question of homology in relation to the rib articulations in the remaining archosaurians. The archosaurian ribs, of course, were bicapitular, both heads of the dorsal ribs adjoining the neural arch. It is usually thought that this displacement had been brought about by a shift of the parapophysis onto the neural arch and the structure of the vertebrae from the region transitional between the cervical and dorsal vertebrae seems to support this contention^(17, 27); but in the light of the above data on the vertebral structure of proterosuchians — the most primitive of archosaurians — it is possible that the two transverse processes of the archosaurian dorsal vertebrae corresponded to a divided diapophysis. The proterosuchians would then be less sharply differentiated from the remaining archosaurians in regard to their rib articulations. In this case the structure of the typical archosaurian vertebra could be derived from the proterosuchian type, as a result of the disappearance of the parapophysis even on the first dorsal vertebra.

3. SOME COMMENTS ON PROTEROSUCHIAN CLASSIFICATION AND ECOLOGY

All the pseudosuchians hitherto described from the USSR belong to the proterosuchians (superfamily Proterosuchoidea), which included the most primitive archosaurs. It is usually held that the archosaurs originally possessed some ability for bipedal locomotion^(19, 27), but the proterosuchians do not permit so definite a conclusion. Apart from isolated fragments, the limbs have hitherto been known only for two proterosuchian genera, *Chasmatosaurus*^(14, 30) and *Erythrosuchus*^(20, 26). Members of both genera were four-legged animals, without any sign of adaptation to bipedal locomotion. The proximal head of the femur in *Erythrosuchus* ran not inward but upward, while the fourth trochanter was very poorly expressed; the assembly of proximal ossicles in the *Chasmatosaurus* pes is unusually complete for archosaurs. Only the considerable length of the hind limbs suggests that they may have had a more important function in locomotion.

Proterosuchians are usually divided into two families, Proterosuchidae Huene, 1908 and Erythrosuchidae Watson, 1914. The degree of morphological differences

between them, however, has been greatly exaggerated. It is usually thought that the proterosuchids are distinguished from the erythrosuchids by their acrodont teeth⁽²⁴⁾; in both groups, however, the teeth are situated in well-formed alveoli, and only their close connection with the alveolar walls has given rise to the widespread opinion that they proterosuchid teeth were acrodont. The premaxilla has the same degree of downward recurvature in both groups. The skull was metakinetic, and the quadrate was freely articulated with the squamosal (character observed by me in *Erythrosuchus triplicostatus*). In the majority of proterosuchians the parietal foramen was retained. The base of the skull, too, has turned out to be fairly similar in *Chasmatosaurus* and *Erythrosuchus*. Small intercentra were probably retained between the vertebrae in proterosuchians, and the anterior dorsal ribs were tricapitulate in them. So considerable a morphological similarity justifies regarding all proterosuchians as members of one family. The Proterosuchidae and the Erythrosuchidae can be kept as subfamilies, but must not be distinguished by the characters that have been proposed in the past.

The subfamily Proterosuchinae comprises comparatively small animals (length of skull under 40 cm) with a very low skull. The premaxilla is long, bearing up to eight teeth and having a distinct downward recurvature. The orbits are circular. The metakinetic character of the skull is very well expressed. Palatal teeth are retained^(10, 11). I include the following forms in this subfamily: *Archosaurus rossicus* Tatarinov, 1960 (P₂, Upper Tatarian substage of the European part of the USSR); *Chasmatosaurus vanhoepeni* Houghton, 1924 (T₁, *Lystrosaurus* zone, South Africa); *Ch. indicus* (Lydekker), 1867 (T₁, *Lystrosaurus* zone, India); *Ch. yuani* Young, 1936 (T₁, *Lystrosaurus* zone, China^(30, 31)); *Elaphrosuchus rubidgei* Broom, 1946 (T₁, *Lystrosaurus* zone, South Africa); *Chasmatosuchus rossicus* Huene, 1940 (T₁, Vetluga series, European part of the USSR); *Proterosuchus fergusi* Broom, 1903 (T₁, *Procolophon* zone, South Africa). Huene assigns to this group also *Seemannia palaeotriadica* Huene, 1958, known from an isolated tooth found in the Upper Buntsandstein of Germany⁽²⁵⁾. This form, however, was described without diagnosis and was given generic rank only because no pseudosuchian remains had previously been found in the Lower Triassic of western Europe. Teeth indistinguishable in the essential characters from the tooth illustrated in Huene's work⁽²⁵⁾ can be found among those of *Chasmatosuchus* sp. and even of *Erythrosuchus triplicostatus*. All this obliges us to regard *Seemannia palaeotriadica* Huene, 1958 as a nomen nudum. All that its discovery means is that we can speak of some kind of proterosuchians in western Europe.

The subfamily Erythrosuchinae comprises very large animals (length of skull up to 1 m) with a comparatively high skull and elongate, very narrow facial part. The alveolar margin of the premaxilla in them is abbreviate and bears only five teeth. The premaxilla is separated from the maxilla by a deep incision and bends slightly downward. The orbits are not round but dorsoventrally elongate. Kineticism of the skull is less strongly expressed, owing to the development of the superior margin of the prootic along the ventral surface of the braincase. The prefrontals are elongate, with a convex outer margin, and almost exclude the frontal from the orbital margin. The palatal teeth have been lost. The base of the skull is massive and bears a pair of horizontal crests.

The only genus I assign to the Erythrosuchinae is *Erythrosuchus* Broom, 1905, known from the Lower Triassic of Cisuralia and South Africa. Nevertheless, certain data do suggest that the group had a wider range. In 1948 Rusconi⁽²⁸⁾ described the skull of a

new brachyopoid labyrinthodont, *Chigutisaurus tunuyanensis*, from the Lower Triassic of Argentina. In 1951 he assigned to this species (with a question mark) a very complete postcranial skeleton from the same bed⁽²⁹⁾. According to the characters taken into account, this postcranial skeleton belongs to a small erythrosuchian. The anterior dorsal vertebrae of this form possess triple facets for ribs (illustrated, but not mentioned by Rusconi) and abruptly dilated neural spines, just like the corresponding vertebrae of *Erythrosuchus triplicostatus*. Both transverse processes of the posterior dorsal vertebrae in the South American form are situated on the neural arch, as in *Erythrosuchus*. The vertebra described by Rusconi as the sacral is indistinguishable from the second sacral vertebra of *E. triplicostatus*. The girdles, particularly the pelvic girdle, bear none of the characteristic labyrinthodont characters and turn out to be similar to the corresponding bones in *Erythrosuchus* (except that the bone described by Rusconi as the clavicle was in all probability wrongly determined by him). The scapula at first assigned by Rusconi to *Ch. tunuyanensis*⁽²⁸⁾ possibly belongs to an erythrosuchian, as does the bone later described by him, together with a fragment of labyrinthodont jaw bone, as that of a new trematosaur, *Icanosaurus rectifrons*⁽²⁹⁾. In the reconstruction of *Ch. tunuyanensis* given by Rusconi⁽²⁹⁾, the skull of the brachyopoid labyrinthodont has been mounted with the postcranial skeleton of an erythrosuchid, with the result that such unaccustomed characters in labyrinthodonts as the presence of seven cervical vertebrae and so forth are here represented. It seems to me beyond dispute that these remains belong to an erythrosuchian and until new material is available I include them in the following list, under the name *Erythrosuchus?* sp. 1. The fragment of lower jaw belonging to a large pseudosuchian from the Middle Triassic deposits assigned to the Yushatyr suite (Koltaevo III site) can also be provisionally assigned to *Erythrosuchus*. With these forms the complete list of members or the subfamily Erythrosuchinae known to date appears as follows: *Erythrosuchus primus* (Otschev), 1958 (P₁, Buzuluk suite, Cisuralia); *E. coloratus* (Huene), 1940 (T₁, Tananyk suite, Cisuralia); *E. triplicostatus* (Huene), 1960 (T₁, Romashkino suite, Cisuralia); *E. africanus* Broom, 1905 (T₁, *Cynognathus* zone, South Africa); *Erythrosuchus?* sp. 1 (= *Chigutisaurus? tunuyanensis* Rusconi, 1948) (T₁, Limense beds, Argentina); *Erythrosuchus?* sp. 2 (T₂, Yushatyr suite, Cisuralia).

The main differences between the Erythrosuchinae and the Proterosuchinae are connected with the transition of the former to an actively predaceous mode of life. The Proterosuchinae probably fed on small animals. They probably included crocodyloid, ichthyophagous forms of the *Chasmatosaurus* type, with a hook at the end of the snout. Smaller Proterosuchinae of the *Chasmatosuchus* type, which had the teeth dilated in the anteroposterior direction, presumably fed on invertebrates. The Erythrosuchinae, however, went over to feeding on large prey that offered active resistance to the predator. Like the predaceous crocodiles, the Erythrosuchinae would turn the victim over with sharp jerks of the head. This was most probably the reason for the reduced kineticism of the skull, which increased its mechanical stability, an important factor in such movements. I further associate with this mode of feeding the strengthening of the skull base, an indication of the force of the cervical musculature, and also the development of the rudimentary "hyposphenes", which improved the animal's stability as the body bent sideways. In connection with this hypothesis of an actively predaceous mode of life in the Erythrosuchinae, it is interesting that the *E. triplicostatus* remains bear numerous traces of injuries sustained in the animal's lifetime. Among these we may mention the

infraction of the lower jaw in one specimen, an infraction in the region of the second and third cervical vertebrae, producing anomalous concrescence of these vertebrae, two cases of fracture of the tibia, and two cases of fracture of the clavicle.

Ecologically the Erythrosuchinae were in all probability close to the relatively terrestrial sebecosuchian-type crocodiles⁽¹⁶⁾. Like the erythrosuchi, the latter had an incision between the premaxilla and the maxilla, although it was less pronounced; an enlarged mandibular tooth ran into this incision. The anterior teeth in the Sebecosuchidae were prehensile, somewhat circular in cross-section, although the differentiation of the teeth was much less pronounced. The *Erythrosuchus* lower jaw was abbreviate and extended only slightly beyond the level of the incision between the maxilla and premaxilla, but the anterior lower jaw teeth ran obliquely upward and, together with the premaxillary teeth, were used for holding the prey. Unlike the Sebecosuchidae, however, the snout was very narrow in *Erythrosuchus*, and there was no enlarged canine in the lower jaw. These differences were probably partially due to the different origin of the animals (*Erythrosuchus* originating from the very narrow-snouted Proterosuchidae, and Sebecosuchidae from crocodiles with a snout that was usually dilated at the end). The erythrosuchi were in all probability more terrestrial animals than the Sebecosuchidae, but the general proportions of their body, with the relatively massive head and short limbs, indicates that these animals too had some association with water.

REFERENCES

(Not listed.)

FIGURE CAPTIONS

Fig. 1. *Erythrosuchus africanus* Broom, braincase (after A. Brink) (9).

Fig. 2. *Vjuschkovia triplicostata* Huene, braincase; lectotype, PIN No. 951-59.

Fig. 3. *Vjuschkovia triplicostata* Huene, braincase and prootics, ventral view; PIN No. 951-60.

Fig. 4. *Dongusia colorata* Huene, vertebra, lateral view; PIN No. 268-2.

Fig. 5. Posterior dorsal vertebra of *Erythrosuchus triplicostatus* (Huene), lateral view; PIN No. 951-65.

Fig. 6. Vertebrae: a – *Dongusia colorata* Huene (22); b – *Dongusia colorata* Huene (from specimen), PIN No. 268-2; c – cervical vertebra of *Erythrosuchus triplicostatus* (Huene), PIN No. 951-65.