

AN ENIGMATIC NEW DIAPSID REPTILE FROM THE UPPER PERMIAN OF EASTERN EUROPE

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INTRODUCTION

Diapsid reptiles were the most common and/or conspicuous vertebrates of land, sea, and air environments of the Mesozoic. However, these reptiles were only minor components of terrestrial faunas during the preceding late Paleozoic. The oldest known diapsids are araeoscelidians, which first appeared during the Late Carboniferous (Reisz, 1977; deBraga and Reisz, 1995), but did not last beyond the Early Permian (e.g., Reisz et al., 1984). The other Permian diapsids are all thought to be more crownward taxa, which have been referred to as either “neo-diapsids” (Gauthier et al., 1988) or “eosuchians” (Laurin, 1991). These include the younginiforms, most of which are known only from the uppermost Permian of Madagascar and southern Africa (Gow, 1975; Currie, 1980, 1981).

We describe here a new specimen from uppermost Permian strata near Mezen in northwestern Russia. This area is host to numerous fossil localities, which have produced a wide range of synapsid and reptilian taxa. The subject of this report comes from the Glyadnaya Shchelya locality, which has also produced specimens of the parareptiles *Nyctiphruetus*, *Bashkyroleter*, and *Macroleter*, indeterminate therapsid material, and specimens of the basal synapsid *Mesenosaurus*. The new specimen was catalogued as a referred specimen of *Mesenosaurus* following its initial preparation by M. F. Ivakhnenko, but closer inspection reveals that it is a diapsid reptile. This discovery is particularly significant because the specimen represents the oldest known diapsid to be recovered from the vast continental deposits of the Russian Platform, which is famous for its diverse Late Permian faunal assemblages. The new diapsid specimen is described here as a new genus and species, which, interestingly, exhibits features that are suggestive of a crown-group diapsid identity.

**Institutional Abbreviations**—MCZ, Museum of Comparative Zoology of Harvard University, Cambridge; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow.

MATERIAL AND METHODS

The specimen comprises a partial skull and a few axial fragments. Most of the left side of the skull and the posterior part of the skull table were lost to erosion before collection, and small portions of bone from the remainder of the skull and mandible have been weathered away and only their impressions remain. The matrix investing the posterior region of the skull is haematitic, which has made preparation very difficult and

necessitated limited exposure of the bones (which appear to be disarticulated axial elements for the most part). Prior to preparation, the left side of the specimen was embedded in a resinous material, which filled in the natural impressions, and then the specimen was prepared mechanically from the right side.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768

DIAPSIDA Osborn, 1903

*LANTHANOLANIA IVAKHNENKOI*, gen. et sp. nov.

**Holotype**—PIN 162/56, a skull preserving the snout, circumorbital elements, partial braincase, right mandibular ramus, and partial left dentary.

**Diagnosis**—A diapsid reptile characterized by a dorsoventrally low maxilla, the presence of an anteriorly facing pit on the neck of the basiptyergoid process, and a small, splint-like coronoid.

**Locality and Horizon**—Glyadnaya Shchelya, a fossil locality on the banks of the Mezen River in Mesen District, Arkhangel'sk Province, Russia. Uppermost Kazanian or lowermost Tatarian, Upper Permian (Ivakhnenko et al., 1997).

**Etymology**—The generic name is from the Greek word *lathanos*, which means “forgotten” or “overlooked,” and the Latin word *lanius*, which means “butcher” or “ripper.” The prefix refers to the fact that the holotype was originally accessioned into the collections of the PIN as a basal synapsid, and the suffix alludes to the presumed faunivory of this reptile. The gender is feminine. The specific epithet honours M. F. Ivakhnenko for his contributions to the study of the early amniotes of Russia.

DESCRIPTION

The entire specimen as preserved (Fig. 1) is approximately 30 mm in length. The well-preserved surfaces of the roofing elements are smoothly finished for the most part; the various kinds of furrows and pits that ornament the skulls of parareptiles and many other basal reptiles are clearly absent. A reconstruction of the skull in lateral view is shown in Figure 2.

The premaxilla is represented by several fragments lying at the anterior end of the snout, pieces that appear to include both left and right elements. Apart from a curved piece of bone at the anteriormost tip of the skull, which may be the remains of the alveolar portion of the left premaxilla in dorsal view, little can be made of these fragments.

The maxilla reaches its greatest dorsoventral height just posterior to the external narial opening, and then descends gradually to a greatly attenuated tip. The maxilla contacts the nasal dorsally and so broadly excludes the lacrimal from the external narial opening. Posterior to the contact with the nasal, the dorsal

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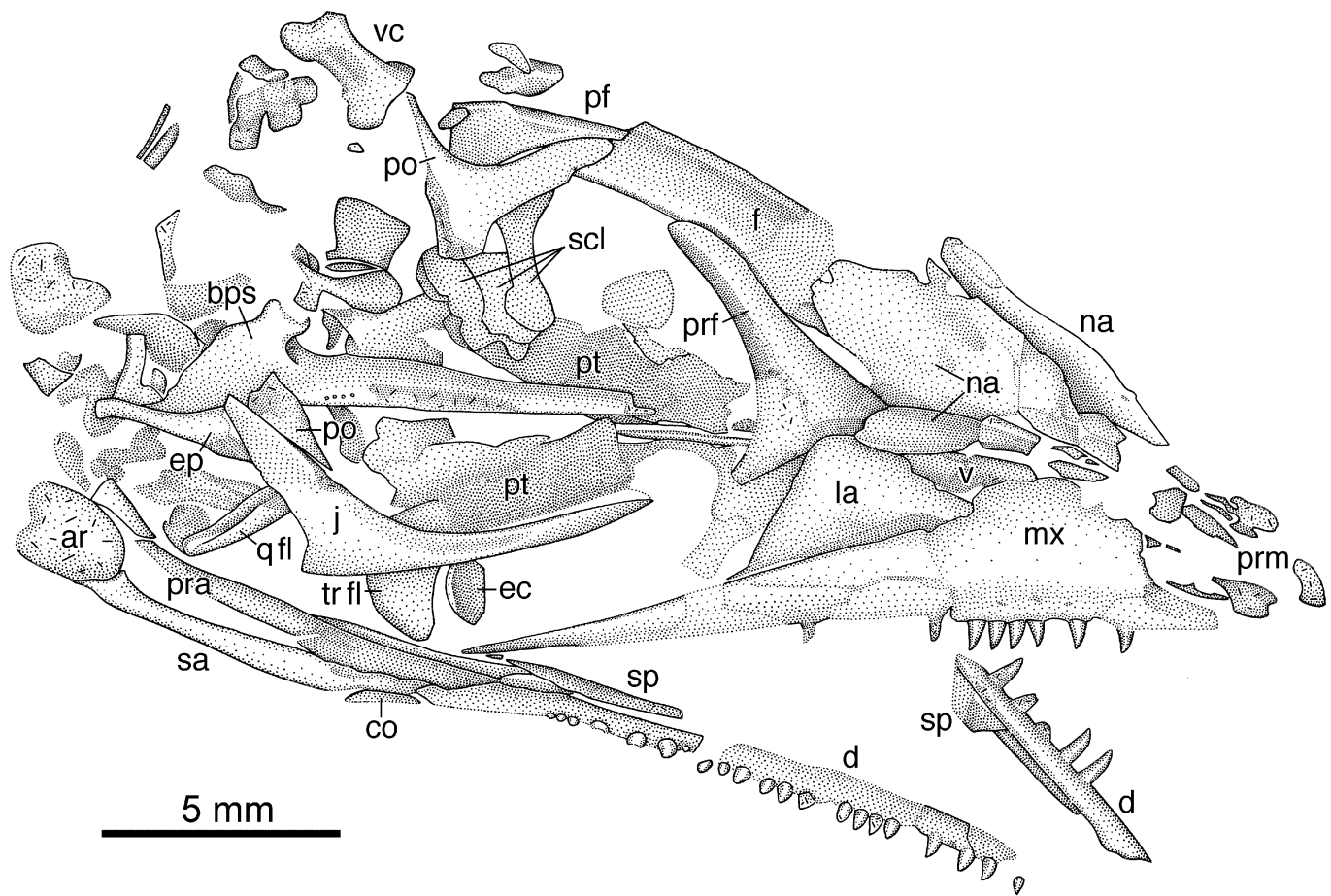


FIGURE 1. *Lanthanolania ivakhnenkoi*, gen. et sp. nov., PIN 162/56, holotype. Skull in right lateral view and right mandibular ramus in dorsal view. **Abbreviations:** ar, articular; bps, basiparaspheoid; co, coronoid; d, dentary; ec, ectopterygoid; ep, epipterygoid; f, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; pf, postfrontal; po, postorbital; pra, prearticular; prf, prefrontal; prm, premaxilla; pt, pterygoid; q fl, quadrate flang of pterygoid; sa, surangular; scl, scleral ossicles; sp, splenial; tr fl, transverse flange of pterygoid; v, vomer; vc, vertebral centrum.

margin of the maxilla had broad contacts for both the lacrimal and the jugal. The lateral surface bears a few supralabial foramina of approximately the same size. What is preserved of the dentition indicates that the teeth were both homodont and isodont. Teeth supported by areas that are now preserved as impressions are barely discernible as faint ridges in the supporting resin. Their margins are difficult to delineate from the surrounding resin, and consequently these teeth are not illustrated in the figure, but they do indicate that the dentition occupied most of the ventral margin of the maxilla; only the posterior 1 mm or so of the maxilla appears to have been edentulous.

Lithostatic crushing has collapsed the right nasal into two long fragments that are "hinged" along a crack, which runs forward from a point adjacent to the anterior tip of the prefrontal (Fig. 1). It appears that, in life, the nasal was a large, curved sheet of bone that spanned the dorsal and lateral surfaces of the snout (Fig. 2). Ventrally, the nasal appears to have had an extensive contact with the dorsal lamella of the maxilla, thereby restricting the lacrimal from the external naris. Laterally, the nasal formed sutures with the lacrimal and the prefrontal, although the exact proportions of these contacts are difficult to determine. More posteromedially, the nasal shares an overlapping suture with the frontal.

The lacrimal has the outline of an isocetes triangle, with the longest edge being overlapped broadly by the maxilla. The dorsal margin of the lacrimal is well preserved; it forms an acute

angle with the elongate sutural surface receiving the maxilla, suggesting strongly that the lacrimal terminated anteriorly close to the most rostral portion of the lacrimal that is visible in lateral view. The slightly convex posterior margin of the lacrimal forms the anteroventral corner of the orbit, but it is unclear whether the posteroventral process of the lacrimal made contact with the jugal. Dorsally the lacrimal lay broadly over the prefrontal and contacted the lateral margin of the nasal. No openings for the lacrimal ducts are visible.

The prefrontal is characterized by a long and narrow posterodorsal process, a morphology for that process that is strongly reminiscent of that seen in *Youngina* (Reisz et al., 2000). Ventrrolaterally the prefrontal was covered by the lacrimal, as evidenced by the presence of a well-marked, dorsoventrally low sutural surface for the latter bone. The antorbital surface is set at a sharp angle to the superficial surface of the bone.

The frontal appears to have been a long and rectangular element, although the determination of its exact length is impossible because of the overlying postfrontal and postorbital. The free, lateral edge that contributes to the orbital margin parallels the medial margin, but anteriorly the frontal becomes expanded slightly beyond the slight overlapping contact with the posterodorsal process of the prefrontal. The dorsal surface of the frontal is devoid of ornament or striations, but a broad furrow is formed between the slightly raised medial and lateral margins.

Immediately posterior to the frontal is a slightly obscured L-

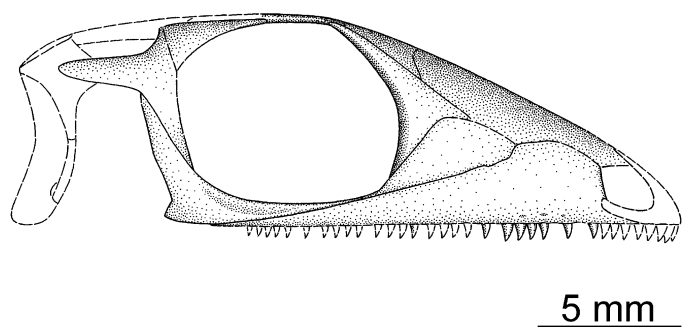


FIGURE 2. Reconstruction of the skull of *Lanthanolania ivakhnenkoi* in lateral view.

shaped element that appears to be the postfrontal. The medial portion is the thickest portion of the bone, and the sutural surface for the frontal can be seen to occupy at least the anterior two-thirds of the medial margin. The dorsal surface of the postfrontal drops from the raised medial edge, giving the impression that bone thins laterally from the contact with the frontal. Although the exact outline of the lateral corner of the postfrontal is indeterminate because of the overlying postorbital, the manner in which the posterior and lateral margins of the postfrontal approach each other conforms closely with what is known for *Youngina* (Reisz et al., 2000).

The slender jugal resembles those of various crown-group diapsids in that the subtemporal process ends freely. The subtemporal process is short and roughly triangular in outline, and its outline resembles most closely that which has been illustrated for the basal lepidosauromorph *Paliguana* (Carroll, 1975). There is no possibility that the shortness of the process is an artifact, because the free margin of the process is undamaged and supported by a narrow fringe of matrix. The suborbital process of the jugal extends anteriorly from the central region of the bone and attenuates to a sharp tip. A blade-like posterodorsal process extends dorsally and slightly posteriorly to support the postorbital bone, a fragment of which lies in its presumed natural position along the orbital margin of the jugal.

The postorbital is preserved in close association with the postfrontal, but one process is absent; the missing portion appears to be the triangular fragment that remains in contact with the jugal. Thus, the right postorbital is entirely present, but its two components are associated more closely with their respective neighboring elements than with each other. If this interpretation is correct, then the posterior process of the postorbital was the longest and most substantial of the three rami. The dorsomedial process is the shortest of the three, and it is narrower and its base thicker than that of the other two processes. In these features the dorsomedial process resembles very closely those of *Youngina* (Reisz et al., 2000) and *Prolacerta* (Gow, 1975). This observation suggests that, as in those diapsid taxa, the postorbital plesiomorphically retained a narrow contact with the parietal to exclude the postfrontal from the upper temporal opening.

Most of the palate appears to be present, but details of its constituent elements are obscured by weathering and underlying roofing bones. The right pterygoid lies in its expected position with respect to the parasphenoid and the roofing elements, but only its transverse flange and quadrate processes are readily visible. The transverse flange is a robust, slightly quadrangular projection, whereas the quadrate flange is a dorsoventrally low tongue of bone that bears an equally narrow medial process. This is the tympanic or arcuate flange, and it resembles very closely those of *Youngina* and *Prolacerta*. A crescentic bone

just anterior to the transverse flange of the pterygoid probably represents the ectopterygoid.

Only the parasphenoid and the basisphenoid are discernible from among the many bones and fragments that litter the posterior region of the skull, and they are fused together indistinguishably. The parasphenoid portion includes a long and robust cultriform process that narrows gradually as it extends anteriorly. Its distal tip is missing but it seems likely that it would have reached at least as far as the level of the antorbital region, and its base houses the roots of several tiny teeth or denticles. The line of teeth does not extend posteriorly onto the body of the bone, which is flat and featureless and lacks the deep median excavation that characterizes the parasphenoids of other diapsids. Little of the basisphenoid is visible except the right basiptyergoid process, which takes the form of a simple, button-like projection. A distinguishing feature of the process is a conspicuous pit that occupies the anterior surface of the neck region. The basiptyergoid process thus resembles those of squamate diapsids in which the vidian canal opens anteriorly at the base of the basiptyergoid process. However, the small size of the specimen and the fragility of the bone precludes exploratory mechanical preparation in order to determine whether the pit is the egress of a vidian canal or if it ends blindly. In support of the former interpretation is the observation that there is no entrance for the internal carotid artery at the ventral juncture between the basiptyergoid process and the main body of the parasphenoid. The apparent absence of such a foramen suggests that the internal carotid must have entered the braincase higher on the lateral side of the basiparasphenoid complex, presumably with the vidian branch of the facial nerve, and thus passed through a vidian canal. The presence of a vidian canal is a synapomorphy of lizards (Rieppel, 1993), but vidian canals are present also in parareptiles (Gow, 1972; Kemp, 1974; Spencer, 2000).

Only the right mandibular ramus is well preserved and it is visible only in dorsomedial aspect. The right dentary is preserved half as bone and half as impression. It accommodates 21 teeth and has empty alveoli for an additional 4 or 5 teeth. A missing portion may have borne a further 4 teeth, which would bring the dentary dentition to approximately 30 tooth positions in total. There is no clear separation between the alveolar portions of either dentary and the tooth crowns, which suggests strongly that bone of attachment is serving to ankylose the teeth to the bone. The teeth are virtually identical to those of the maxilla. There are no resorption pits associated with any of the teeth on the lingual surface of the dentary. The surangular and the dentary contact one another medially and exclude the coronoid from both the adductor fossa and from contact with the prearticular. The coronoid is a small splint of bone positioned atop the low coronoid eminence.

Numerous bones and fragments are preserved in a broad arc that runs from the posterior end of the right mandibular ramus over to the right postfrontal and postorbital. Most of these bits are unidentifiable and no diagnostic features are visible, although it is likely that a few of the larger, more robust elements are braincase elements.

## DISCUSSION

The diapsid nature of *Lanthanolania ivakhnenkoi* is established clearly by the triradiate organization of both the postorbital and the jugal. The contact between the nasal and the maxilla, the anteroposteriorly short lacrimal, and the isodont marginal dentition suggest that the phylogenetic position of *Lanthanolania* is more crownwards than Araeoscelidia. The flat ventral surface of the parasphenoid is shared with millerettids (Gow, 1972), but *Lanthanolania* displays none of the synapomorphies listed by Laurin and Reisz (1995) for Millerettidae.

Taking this into consideration with the triradiate nature of both the jugal and the postorbital, it is highly unlikely that *Lanthanolania* is a millerettid parareptile.

The broadest review of the interrelationships of Paleozoic diapsids is that of Laurin (1991), who identified four stem-group diapsid lineages. The basalmost diapsids belong to the clade Araeoscelidia. The genus *Coelurosauravus* is the most basal taxon of the araeoscelidian sister group. *Apsisaurus witteri* is the next crownward diapsid taxon. Lastly, Younginiformes was identified by Laurin (1991) as the sister group of the diapsid crown clade ("Sauria" sensu Gauthier et al., 1988; Laurin, 1991). Laurin (1991) did not include *Claudiosaurus germaini* (Carroll, 1981), from the Madagascan Permian, but this species has been identified as a stem diapsid (more basal than Younginiformes) in analyses published by Rieppel (1994) and Rieppel and Reisz (1999).

The addition of *Lanthanolania* to the data matrix of Laurin (1991) and a rerunning of this augmented matrix in PAUP\* 4.0b10 (Swofford, 2002) results in 5 equally parsimonious trees (each of 101 steps). Four of the trees position *Lanthanolania* within the diapsid crown group ("Sauria" sensu Gauthier et al., 1988) as a lepidosauromorph; the fifth tree identifies *Lanthanolania* as the sister taxon of the crown group. Strict and majority-rule consensus trees of the five trees are shown in Figure 3. The available evidence seems to suggest that the new diapsid is either a member of the diapsid crown group or it is a very close relative. However, if a single step is added to the most parsimonious trees (i.e., in trees 102 steps long), *Lanthanolania* forms a sister-group relationship with *Coelurosauravus*. In trees of 103 steps, *Lanthanolania* can be placed at various positions on the diapsid tree, but an extra 5 steps are required to place *Lanthanolania* in a clade with araeoscelidians. The level of uncertainty in the phylogenetic position of *Lanthanolania* among diapsids exclusive of Araeoscelidia is due clearly to the fact that we could code it for only 12 of the 69 characters (or 17%). Notably, the observation that 5 extra steps are required to make *Lanthanolania* form a clade with *Petrolacosaurus* and *Araeoscelis* suggests that it is unlikely that the new taxon is an araeoscelidian.

It would be ideal to conduct a new phylogenetic analysis of basal diapsids, but such an investigation would be premature before pivotal, poorly known diapsid taxa such as *Youngina* and *Coelurosauravus* can be restudied in detail. New material of *Coelurosauravus* (Frey et al., 1997) will provide badly needed data on the structure of the skull of that diapsid genus, and planned reappraisals of the genera *Claudiosaurus* and *Youngina* by the first author will help to clarify the relationships of these taxa with respect to other basal neodiapsids. Until such work is published, with new information that could very well result in a thorough overhaul of the current understanding of early diapsid diversification, the evolutionary implications of *Lanthanolania* as a diapsid reptile will continue to be difficult to evaluate. Once new information appears on stem diapsids such as the younginiforms, a more rigorous picture of diapsid evolution during the late Paleozoic should emerge.

## CONCLUSIONS

*Lanthanolania ivakhnenkoi* is a new genus and species of diapsid reptile from the Upper Permian of the Mezen River Basin, northern Russia. The localities of the Mezen River Basin are either uppermost Kazanian or lowermost Tatarian, making *Lanthanolania* the oldest diapsid from the vast continental deposits of the Russian Platform, and only the second diapsid to be described from the Russian Permian after *Archosaurus rossicus*. All previously described Late Permian diapsids are known from middle through to uppermost Tatarian strata (Munk and Sues, 1993; Rubidge et al., 1995; Sues and Munk, 1996;

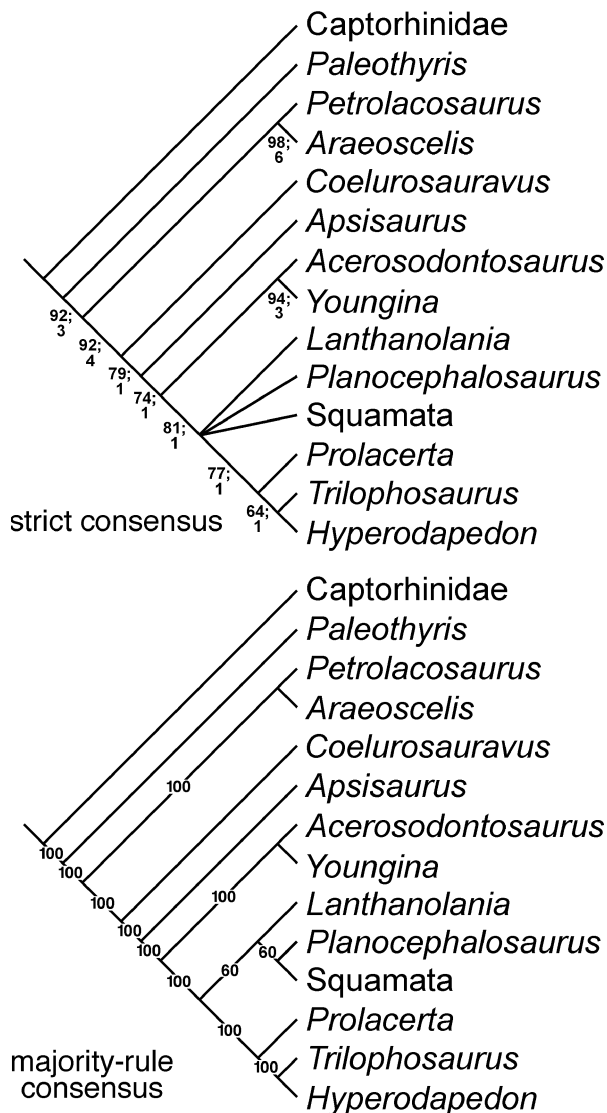


FIGURE 3. Strict and majority-rule consensus trees of 5 equally parsimonious trees discovered in a PAUP\* 4.0b10 analysis of an augmented and slightly modified version of the data matrix in Laurin (1991). Tree length = 101, consistency index (excluding uninformative characters) = 0.68, rescaled consistency index = 0.55. Following new information on the postorbital of *Youngina* (Reisz et al., 2000), this taxon is recoded as "0" for character B3 in the Laurin (1991) matrix. *Lanthanolania* is coded for the 69 characters of Laurin (1991) as follows: 11???? 1101???? ??? ??? 1???????????? 0???????? ???? 0?????? 0?? 1????????

Dilkes, 1998), thereby making *Lanthanolania ivakhnenkoi* the oldest of the Late Permian diapsids.

The presence of a single diapsid among hundreds of amniote specimens that have been collected from the Mezen River basin underscores the rarity of this group of reptiles in the Upper Permian. This disparity is not a reflection of small size, as numerous small parareptiles and synapsids have been recovered from the basin, including complete skulls of *Macroleter* and *Nyctiphruetus* that are less than 2 cm in length. Clearly, diapsids in general and crown-group diapsids in particular were very rare components of the Late Permian faunal assemblages of the Russian Platform (Modesto and Rybczynski, 2000).

The same pattern prevails in other highly fossiliferous Upper Permian localities. For example, only a handful of crown-clade

diapsid specimens have been collected from the Upper Permian strata of the Karoo Basin in South Africa, which is renowned for thousands of synapsid and parareptilian specimens. Although diapsid phylogeny indicates that both archosauromorphs and lepidosauromorphs originated during the Late Permian (Dilkes, 1998), the spectacular diversification of diapsids during the Mesozoic is poorly reflected in the late Paleozoic.

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