

The reptile *Macroleter*: First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia

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ABSTRACT

The spectacular evolutionary history of terrestrial vertebrates is uncharacteristically poorly documented between the Paleozoic sub-equatorial exposures of the Permo–Carboniferous of North America and Europe, and the much higher latitude, Upper Permian deposits of central Russia and southern Africa. We report here that the discovery of the reptile *Macroleter* in Oklahoma provides the first direct vertebrate evidence of biochronological correlation between continental sediments from the Upper Permian of North America and Russia. The presence of the reptile *Macroleter*, a member of a major group of Upper Permian amniotes known previously only from central Russia, in North America improves dramatically our understanding of this early phase of amniote evolution, and also provides evidence of terrestrial tetrapod faunal interchange between North America and Russia in Late Permian time.

Keywords: paleobiogeography, paleontology, Permian, terrestrial reptile.

INTRODUCTION

The geographic and climatic distribution of Paleozoic fossiliferous sediments is strongly biased, creating a major gap in the evolutionary history of early terrestrial vertebrates. Carboniferous and Early Permian tetrapods are known primarily from North America and Western Europe, which were at that time located near the equator (Scotese and McKerrow, 1990). For the Late Permian, these areas have few fossiliferous continental sediments, but diverse Late Permian amniote assemblages (Amniota is a group of higher vertebrates that includes reptiles, birds, and mammals, and their fossil relatives) are known from exposures in Russia and South Africa, which were located at high northern and southern latitudes (about 40°N and 60°S, respectively).

There are significant faunal differences between Early and Late Permian terrestrial vertebrate assemblages: In the Early Permian, terrestrial vertebrates are represented by numerous anamniote stegoce-

phalians (temnospondyls, embolomeres, seymouriamorphs, lepospondyls), and amniotes. By the Late Permian, anamniotes (tetrapods that fall outside the amniote group, colloquially also called amphibians) were rare and almost entirely aquatic, whereas amniotes had increased in abundance and diversity.

Among amniotes (Fig 1, A), synapsids (mammals and their extinct relatives) are the most diverse (Fig. 1, B), and are represented during the Early Permian by six basal families, eothyridids, caseids, varanopseids, ophiacodontids, edaphosaurids, and sphenacodontoids (Reisz, 1986), and only a single therapsid (Laurin and Reisz, 1996) is known. By the Late Permian, most synapsids were therapsids (Kemp, 1982), and only two varanopseids and one caseid have been found in Upper Permian sediments of Russia or South Africa (Reisz et al. 1998). A similar succession can be seen in the second major group of amniotes, the group that includes captorhinids, protorothyridids, and diapsids (Fig. 1, E). In the Early Permian, this group was represented by numerous captorhinids and protorothyridids (Clark and Carroll, 1973), and a few diapsids (Reisz et al., 1984; Laurin, 1991, deBraga and Reisz 1996). By the Late Permian, captorhinids were rare (Ricqlès and Taquet, 1982), and this group is represented mainly by neodiapsids (Carroll 1987).

The faunal succession among the third major group of amniotes (Fig. 1, D) is poorly understood because this group is represented in the Early Permian by only a few taxa (deBraga and Reisz, 1996, Modesto, 1999, Berman et al., 2000). By the Late Permian, members of this group were both abundant and diverse. They include bolosaurids, lanthanosuchids, nyctiphruetids, and *Macroleter* in Russia (Ivachnenko, 1987), *eumotosaurids*, millerettids, and procolophonoids in South Africa (Modesto, 2000), and pareiasaurs in both areas (Boonstra, 1934; Ivachnenko, 1987).

Previous studies have attempted to bridge these faunal discontinuities and to present evidence for biochronological correlations between North American and Russian Permian strata, but the evidence was unconvincing (Sidor and Hopson 1995). Most notable among these were the studies by Olson (1962) and Chudinov (1983). Evidence for stratigraphic correlations came from comparisons of faunal complexes that apparently had a similar composition at the suprageneric level. These provided evidence for similarities in the vertebrate trophic structure, but not for accurate correlations because of the longevity of the compared suprageneric taxa. The general problem has been compounded by the description of numerous new taxa, mainly new genera, which

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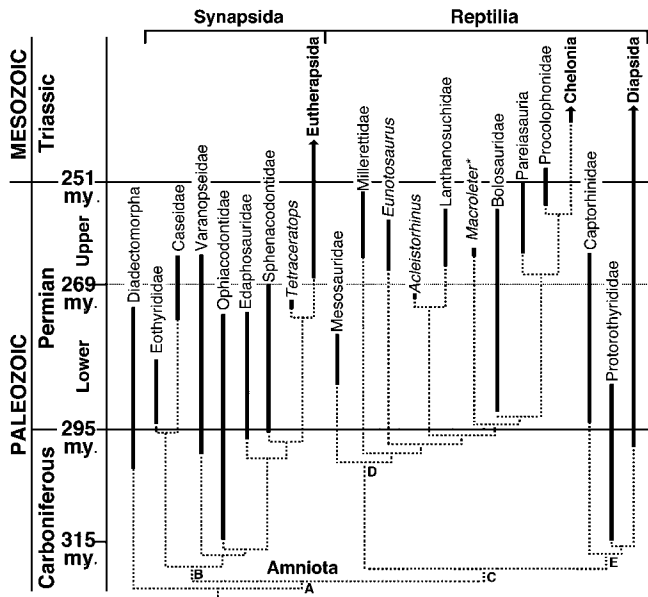


Figure 1. Amniote phylogeny, redrawn and modified from Sues and Reisz (1998). In order to keep the phylogeny as clear as possible, some taxonomic designations have not been included (Modesto, 1999, 2000). The basic dichotomy of amniotes (A) into synapsids (B) and reptiles (C) is indicated, but the controversial taxonomic designations of the two groups of parareptiles or anapsids (D) and eureptiles (E) have not been included. Instead we used capital letters A–E for the sake of simplicity and clarity. The relationships of Chelonia also remain highly controversial. Dashed lines indicate hypothesized patterns of relationships and currently unrecorded ranges of lineages. Solid lines indicate temporal ranges of lineages as documented by the fossil record. Terminal arrows indicate that the named groups continue into the Mesozoic, and also include extant taxa. Thus, Eutherapsida includes mammals, Chelonia includes extant turtles, and Diapsida includes dinosaurs, birds, crocodiles, and squamates. Note that among basal synapsids Caseidae, and Varanopseidae extend into the Upper Permian, and together with *Macroleter* are the only taxa that are present in both northern Russia and Oklahoma.

tended to emphasize differences rather than similarities (Olson, 1962). These new taxa are based on very poorly preserved, fragmentary specimens. Therefore, the recent conclusion that the first proposed affinities of these taxa as therapsids was wrong (Sidor and Hopson, 1995) is not surprising. The recent reappraisal of these poorly known taxa withdraws most of the previously available evidence about the stratigraphic correlations between continental Ufimian and Kazanian formations in Russia and the presumed contemporary continental formations in North America.

In this article, we provide evidence that the holotype of *Seymouria agilis* (Olson, 1980), a nearly complete skeleton from the Chickasha Formation of Oklahoma, is a misinterpreted reptile (parareptile sensu Laurin and Reisz, 1995), and that it belongs to *Macroleter*, a genus previously known only from the Upper Permian sedimentary strata of Russia. This identification has important implications for biochronological correlations because it provides the first evidence of congeneric forms being present in lower Upper Permian continental strata of Russia and North America, and it also provides important new data for

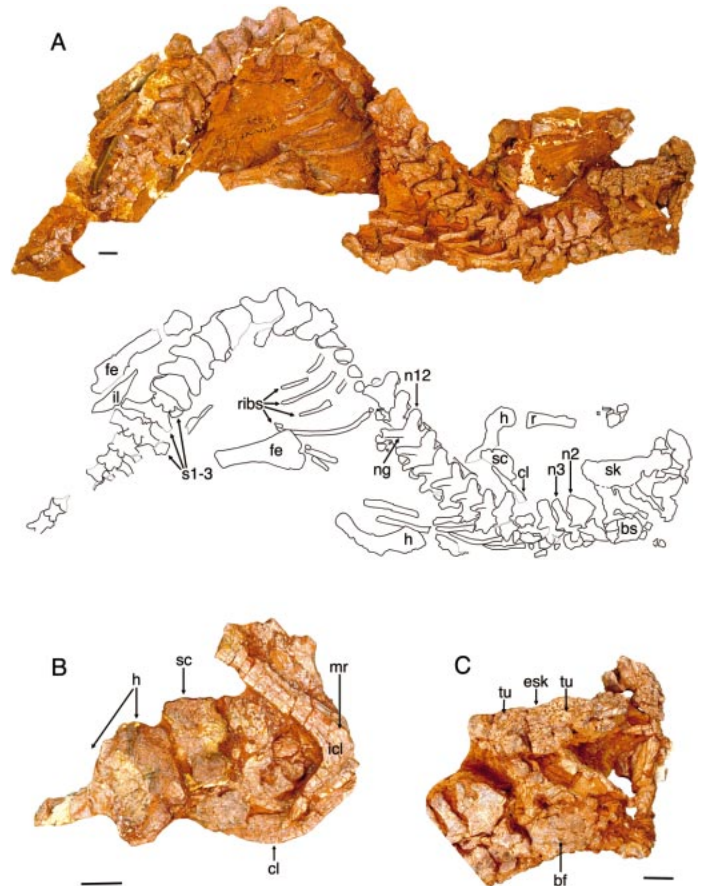


Figure 2. Photographs of *Macroleter*. (A) Photograph and outline of the holotype skeleton and only known specimen of *Macroleter agilis* (new combination). Fragment of skull roof and the cervical vertebrae are exposed in right lateral view, whereas the rest of the skeleton is visible in dorsal view. (B) Enlarged part of shoulder girdle and proximal part of humerus of *Macroleter agilis* in ventral view, exposed on the underside of specimen. (C) Enlarged part of skull region and first three vertebrae of *Macroleter agilis* in same view as A. Abbreviations: bf—basisphenoid foramen; bs—basisphenoid; cl—clavicle; esk—edge of skull table; fe—femur; h—humerus; icl—interclavicle; il—ilium; mr—median ridge of interclavicle; n2-n12—neural arches and spine of cervical and dorsal vertebrae; ng—neural arch groove; r—radius; s1-3—sacral vertebrae 1-3; sc—scapulocoracoid; sk—fragment of the skull roof; tu—tuberosities on postorbital and supratemporal bones, located near the edge of the skull roof, and next to typical deep, circular pits that are present on the skull table. Scales = 1 cm.

studies of terrestrial amniote dispersals during the early evolutionary history of this group.

DESCRIPTION AND COMPARISON

The holotype and only known specimen (Fig. 2A) of *Seymouria agilis* (UCMP 143 277) consists of a fragmentary skull, a string of vertebrae extending from the atlas to proximal caudals, the girdles, and some limb elements (Olson, 1980).

Contrary to the original description and interpretation of this form

(Olson, 1980), the identity of UCMP 143 277 as an amniote is unquestionable, because all skeletal autapomorphies of amniotes are present in this specimen (Laurin and Reisz, 1995, Appendix 3). In addition, affinities of UCMP 143 277 to the reptiles found in the Upper Permian sediments of Russia are supported by overwhelming evidence. The synapomorphies that support this interpretation include (1) the narrow, tall, cervical neural arches associated with swollen dorsals (n2 and n12 in Fig. 2A); (2) the anterior groove on the postzygapophyseal buttress (ng in Fig. 2A); (3) the three sacral ribs (s1–3 in Fig. 2A); (4) the T-shaped interclavicle with a deep anterior groove into which the narrow clavicular head fits (cl in Fig. 2B); (5) the tall, narrow scapulo-locoracoid (sc in Fig. 2B); (6) the antero-posteriorly expanded, tall iliac blade (il in Fig. 2A); and (7) the expanded humeral proximal head (h in Fig. 2B). All other known morphological features of UCMP 143 277 are entirely consistent with reptilian affinities.

The assignment of UCMP 143 277 to *Macroleter* is also well supported on the basis of cranial similarities (Ivachnenko, 1987), although the fragmentary nature of the specimen and the lack of published detailed anatomical postcranial descriptions of *Macroleter* have hampered detailed comparisons until recently. Several articulated skeletons of *Macroleter poezicus* have been collected from the Mezen River Basin in northern Russia, and the best specimens were prepared recently, making direct detailed comparisons possible (Ivachnenko et al., 1997, Pls. 41 and 42). The synapomorphies linking UCMP 143 277 with *Macroleter* (to the exclusion of other reptiles) include (1) the peculiar pattern of dermal sculpturing, consisting of deep circular pits separated by broad, flat areas, and widely spaced tuberosities (tu in Fig. 2C); (2) the elongate basisphenoid (bs in Fig. 2A) that bears a broad, shallow, paired pit on either side of its dorsal sagittal ridge (bf in Fig. 2C); (3) the prominent median ridge on the parasternal process of the interclavicle (mr in Fig. 2B); (4) the horizontal dorsal edge of the expanded iliac blade (il in Fig. 2A); (5) the long, slender humeral shaft (h in Fig. 2B). In fact, UCMP 143 277 is almost indistinguishable from *M. poezicus* on the basis of its morphology. Detailed comparisons between the North American and Russian specimens reveal a remarkable level of similarity; the only distinguishing feature is the large size of the third sacral rib (s3), which is slightly broader than the second (s2) in UCMP 143 277 (Fig. 2A). This is in contrast to *M. poezicus*, which shows in PIN 4543/3 the primitive condition for reptiles, the third sacral rib being the smallest of the series.

The former classification of this specimen in the genus *Seymouria* is not supported by any synapomorphy, or even by any detailed, unpolarized anatomical character that is not also present in *Macroleter*. This evidence leads us to reassign UCMP 143 277 to the genus *Macroleter*, tentatively retaining the specific designation of *M. agilis* on the basis of the single recognizable autapomorphy of the large size of the third sacral rib. We therefore propose the new combination *Macroleter agilis* for this reptile from North America.

Olson's misinterpretation of the North American *Macroleter* is understandable because at the time of the original description of this specimen, little was known about the anatomy of small Late Permian Russian reptiles, and the genotype of *Macroleter* was undescribed (Tverdokhlebova and Ivachnenko, 1984). There are a few superficial similarities between *Seymouria* and *Macroleter*, which seem to have misled Olson in his original description of the new species (Olson, 1980), including the presence of well-developed sculpturing on the skull roof, and swollen neural arches in the dorsal region. However, with the discovery of *Macroleter* in Russia, we can recognize that these features are quite distinct in the two taxa; a special anterior groove on the neural arch and tuberosities on the sculptured skull roof are present

in *Macroleter* (Ivachnenko et al., 1997, Pls. 41, 2B, and 42 E). These features are not present in any seymouriamorph.

DISCUSSION

Biochronological Significance

Very few studies have dealt with the age of the Chickasha Formation. The most widely used biostratigraphic markers, such as conodonts, mollusks, or arthropods, are not found in this formation because it is continental. Palynological evidence could be useful, and it may, in the future, enable other scientists to test our conclusions, but unfortunately, "The Permian deposits of the United States have been neglected by plant micropaleontologists" (Wilson, 1962, p. 5). Therefore, the evidence presented above is especially critical to assessing the age of the Chickasha Formation.

Paleogeographic Significance

The group of early tetrapods often known as "parareptiles" has long posed a difficult taxonomic and phylogenetic problem. Olson (1947), who erected the taxon Parareptilia, placed in it Seymouriamorpha, Diadectomorpha, Procolophonina, Pareiasauria, and Chelonia, and Ivachnenko (1987) retained a similar concept of Parareptilia. The inclusion in this group of animals (such as seymouriamorphs) known to have retained a reproductive cycle similar to that of extant amphibians suggested that this group achieved an amniote status independently of other reptiles, hence the name "parareptiles" (Olson, 1947; Ivachnenko, 1987). Recent studies of this group (Lee, 1995; deBraga and Reisz, 1996; Laurin and Reisz, 1995, 1997) have resolved their phylogeny and have resulted in the removal of seymouriamorphs and diadectomorphs from this group. These taxa are now believed to be stem-tetrapods (seymouriamorphs) and stem-amniotes (diadectomorphs). Thus, parareptiles are now considered to be a group of amniotes (millerettids, lanthanosuchids, *Macroleter*, etc.) that many authors believe to also include turtles (Fig. 1).

The fossil record of this branch of reptiles (Fig. 1E) appears to indicate that they lived from the Early Permian to at least the Late Triassic (and even to recent time, if turtles belong to this group). Only two Early Permian representatives of this group (*Acleistorhinus* and *Bolosaurus*) are known from North America (deBraga and Reisz, 1996; Berman et al., 2000), whereas information about the diverse reptile fauna of the Late Permian comes mainly from Russia (Ivachnenko et al., 1997) and South Africa (Boonstra, 1934). By the Triassic, this group had a nearly worldwide distribution, as shown by the presence of procolophonids on most continents (Colbert and Kitching, 1975; Li, 1989).

The reinterpretation of UCMP 143 277 as *Macroleter*, a form otherwise known only from the Upper Permian of northern Russia, provides the strongest known evidence that the Chickasha Formation of north-central Oklahoma belongs to the Guadalupian, and that it is equivalent in age to the late Kazanian, or early Tatarian of the Russian platform. This conclusion is further strengthened by the fact that *Macroleter poezicus* does not appear until late in the Kazanian, even though localities preserving older Kazanian terrestrial communities are known (Ivachnenko et al., 1997). Olson (1965) had reached similar conclusions, but problems with the identity of much of Olson's material from the North American Guadalupian had raised doubts about the validity of his proposed stratigraphic correlations with the Kazanian (Sidor and Hopson, 1995).

Comparisons between the faunal assemblages of the Mezen River basin of northern Russia, which straddles the Kazanian-Tatarian boundary, and the Chickasha exposures (locality BC-8) near Hitchcock, Blaine County, Oklahoma (Olson, 1965) reveal startling similarities. Recent, extensive collecting programs in the Mezen River basin have yielded a rich assemblage of amniotes that includes both reptiles and synapsids. In addition to synapsids restricted to the Late Permian, such as *Niaftasuchus* and *Biarmosuchus*, the Mezen River basin fauna includes the caseid *Ennatosaurus* and the varanopseid *Mesenosaurus* (Ivachnenko et al., 1997). Reptiles are represented by the small *Nictiphruetus* and *Nycteroleter*, as well as by the larger form *Macroleter*. It is interesting to note that *Macroleter* is the second most commonly found fossil at Mezen (23 specimens collected in the years 1998–2000), and in contrast to the other two taxa that are also found in other, younger regions of the Russian platform, *Macroleter* is restricted to the Mezen basin. The Chickasha locality near Hitchcock, Oklahoma, includes caseid remains, together with a single skeleton of the varanopseid *Varanodon*, as well as the only known skeleton of *Macroleter agilis* (new combination). Thus, both faunal assemblages have caseid and varanopseid synapsids, normal members of the Early Permian fauna of North America, but also include *Macroleter*, a member of the Late Permian evolutionary radiation of reptiles. Contrary to Olson's interpretation (1965, p. 68), the Chickasha fauna of Oklahoma does appear to contain elements of the faunal assemblage that characterizes the late Kazanian of Russia.

The Chickasha fauna also includes a number of poorly preserved, fragmentary specimens of uncertain identity (Olson, 1965). This includes two fragmentary skeletons of the poorly known temnospondyl *Fayella chickashaensis* (Olson, 1965), and a partial skull and parts of the skeleton of a nectridean amphibian *Diplocaulus parvus* (Olson, 1972). Olson believed that *Fayella* was a dissorophid, a group that ranges from the Pennsylvanian to the Upper Permian (Gubin, 1980). However, we could find no dissorophid autapomorphies in the published descriptions of *Fayella chickashaensis*. Therefore, we consider this taxon a *Temnospondyli inserta sedis*. Considering that temnospondyls are known from the Mississippian to the Lower Cretaceous, the presence of *Fayella* in the Chickasha Formation is not stratigraphically informative. *Diplocaulus* is known mostly from Lower Permian strata, but it also occurs in poorly dated Moroccan strata that may be Lower or Upper Permian (Dutuit, 1976). Finally, both species are endemic to this faunal complex, so they are not incompatible with a Late Permian age of the Chickasha Formation.

Paleogeographic History of Reptiles

Although the closest known relatives of *Macroleter* are from Russian sediments, the presence in North America (deBraga and Reisz, 1996) of the oldest known members of this group (*Acleistorhinus* and *Bolosaurus*) suggests that this group may have originated in North America. The discovery of *Macroleter* reported here raises the possibility that the group continued to evolve in North America in the Late Permian. Its previous absence on this continent in the post-Leonardian Permian has been explained by the hypothesis that the group had locally disappeared after having invaded Russia and Africa (where they are represented by an abundant Late Permian fauna). In this scenario, the discovery of *Macroleter agilis* in North America provides evidence for a precocious, rapid evolutionary radiation of this group and that these reptiles (parareptiles) either invaded or reinvaded North America in the Late Permian and became fairly numerous and diverse there by the early Mesozoic. An alternative interpretation is that these reptiles never

became extinct in North America, but have not yet been found on that continent in sufficient numbers to support a hypothesis of continued evolutionary radiation. Recent anatomical studies of *Eunotosaurus africanus* (Modesto, 2000) and phylogenetic analysis of *Sterosternum tumidum* (Modesto, 1999) have shown not only that these enigmatic South African reptiles are part of this reptilian group, but also that the early evolutionary diversification of this group very likely occurred in Gondwana. The latter conclusion supports the hypothesis that their Laurasian evolutionary diversification (which includes *Macroleter*) in the Late Permian represents a secondary dispersal.

Identification of UCMP 143 277 as a reptile and, more specifically, a member of the genus *Macroleter* appears to constitute the first evidence from fossil amniotes that supports established ideas that North America was connected to Europe in the Late Permian (Scotese and McKerrow, 1990). Milner (1993) identified two Late Permian tetrapod faunal provinces: a northern Dvinosaurid-Chroniosuchid province known only from parts of Euramerica (from Russia to Kashmir), and a southern Rhinesuchid province, known from southern and eastern Africa, Madagascar, India, and Australia. Milner (1993) thought that these faunal provinces were differentiated only by their nonamniote fauna because many amniote groups were common to both provinces (Pareiasauridae, Coelurosauravidae, Rubidgeidae, Procynosuchidae, and Anteosauridae). However, the recent reinterpretation of *Macroleter*, lanthanosuchids and nictiphruetids (all restricted to the Dvinosaurid-Chroniosuchid province) as amniotes (deBraga and Reisz, 1996) suggests that some amniotes shared the same pattern of endemism. Amniotes have also been found in Upper Permian strata of South Africa (in the Rhinesuchid province), but they belong to other groups (Millerettidae, Pareiasauridae, and Procolophonoidea).

The identification of UCMP 143 277 as a specimen of *Macroleter* constitutes the first evidence of the northern Dvinosaurid-Chroniosuchid province in North America, and thus the first direct evidence of tetrapod faunal interchange between North America and Russia in the Late Permian. The lack of any other evidence for the existence of this faunal province in North America is probably a result of the very poor fossil record of terrestrial vertebrates on this continent in the Late Permian (Olson, 1962).

CONCLUSIONS

The startling discovery of a reptile previously known only from the Upper Permian of Russia in North American Permian continental sediments allows us to propose that these exposures are Late Permian in age. The presence of synapsids, such as varanopseids and caseids, in the Chickasha Formation of Oklahoma and on the Russian platform is compatible with this conclusion because among synapsids, only these two groups and therapsids are known to have extended into the Late Permian (Tatarian). Other groups of synapsids that were common in Lower Permian exposures but not represented in well-known Upper Permian sedimentary strata are also absent in the Chickasha Formation. Although correlations between continental strata in North America, central Russia, and South Africa remain highly problematic, we hope that this report will attract the attention of geologists who will be interested in testing this hypothesis, possibly by using paleomagnetic, paleosol, palynological, or other types of data.

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REFERENCES CITED

- Berman, D.S., Reisz, R.R., Scott, D., Henrici, A.C., Sumida, S.S., and Martens, T., 2000, Early Permian bipedal reptile: *Science*, v. 290, p. 969–972.
- Boonstra, L.D., 1934, Pareiasaurian studies, Part IX, The cranial osteology: *South African Museum Annals*, v. 31, p. 1–38.
- Carroll, R.L., 1987, *Heleosuchus*: An enigmatic diapsid reptile from the Late Permian or Early Triassic of southern Africa: *Canadian Journal of Earth Sciences*, v. 24, p. 664–667.
- Chudinov, P.K., 1983, Early therapsids: *Paleontologicheskovo Institut, Trudy*, v. 202, p. 1–227 (in Russian).
- Clark, J., and Carroll, R.L., 1973, Romeriid reptiles from the Lower Permian: *Museum of Comparative Zoology Bulletin*, v. 144, p. 353–407.
- Colbert, E.H., and Kitching, J.W., 1975, The Triassic reptile *Procolophon* in Antarctica: *American Museum Novitates*, v. 2566, p. 1–23.
- deBraga, M., and Reisz, R.R., 1996, The Early Permian reptile *Acleistorhinus pteroticus* and its phylogenetic position: *Journal of Vertebrate Paleontology*, v. 16, p. 384–395.
- Dutuit, J.-M., 1976, Découverte d'amphibiens Lépospondyles dans la série inférieure de la formation rouge d'Argana (Atlas Occidental Marocain): *Académie des Sciences de Paris Comptes Rendus*, v. 283, p. 1733–1734.
- Gubin, J.M., 1980, New Permian dissorophids from the Preurals: *Paleontologicheskii Zhurnal*, v. 1980, p. 82–90.
- Ivachnenko, M.F., 1987, Permian parareptiles of U.S.S.R.: *Trudy Paleontologicheskogo Instituta* v. 223, 159 p. (in Russian).
- Ivachnenko, M.F., Golubev, V.K., Gubin, Y.M., Kalandadze, N.N., Novikov, I.V., Sennikov, A.G., and Rautian, A.S., 1997, Permian and Triassic tetrapods of Eastern Europe: *Moscow, GEOS*, 216 p. (in Russian).
- Kemp, T.S., 1982, Mammal-like reptiles and the origin of mammals: *New York, Academic Press*, 363 p.
- Laurin, M., 1991, The osteology of a Lower Permian eousuchian from Texas and a review of diapsid phylogeny: *Linnean Society Zoological Journal*, v. 101, p. 59–95.
- Laurin, M., and Reisz, R.R., 1995, A reevaluation of early amniote phylogeny: *Linnean Society Zoological Journal*, v. 113, p. 165–223.
- Laurin, M., and Reisz, R.R., 1996, The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid: *Journal of Vertebrate Paleontology*, v. 16, p. 95–102.
- Laurin, M., and Reisz, R.R., 1997, A new perspective on tetrapod phylogeny, in Sumida, S., and Martin, K., eds., *Amniote Origins—Completing the Transition to Land*, London, Academic Press, p. 9–59.
- Lee, M.S.Y., 1995, Historical burden in systematics and the interrelationships of 'Parareptiles': *Cambridge Philosophical Society Biological Reviews*, v. 70, p. 459–547.
- Li, J.L., 1989, A new genus of Procolophonidae from Lower Triassic of Shaanxi, China: *Vertebrata Palasiatica*, v. 27, p. 248–267.
- Milner, A.R., 1993, Biogeography of Palaeozoic tetrapods, in Long, J.A., ed., *Paleozoic vertebrate biostratigraphy and biogeography*: London, Belhaven Press, p. 325–353.
- Modesto, S.P., 1999, Observations on the structure of the Early Permian reptile *Stereos-ternum tumidum* Cope: *Palaeontologica Africana*, v. 35, p. 7–19.
- Modesto, S.P., 2000, *Eumotosaurus africanus* and the Gondwanan ancestry of anapsid reptiles: *Palaeontologica Africana*, v. 36, p. 1–7.
- Olson, E.C., 1947, The family Diadectidae and its bearing on the classification of reptiles: *Fieldiana Geology*, v. 11, 53 p.
- Olson, E.C., 1962, Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R.: *American Philosophical Society Transactions*, new ser., v. 52, 224 p.
- Olson, E.C., 1965, New Permian vertebrates from the Chickasha Formation in Oklahoma: *Oklahoma Geological Survey Circular* v. 70, 70 p.
- Olson, E.C., 1972, *Diplocaulus parvus*, n. sp. (Amphibia, Nectridea) from the Chickasha Formation (Permian: Guadalupian) of Oklahoma: *Journal of Paleontology*, v. 46, p. 656–659.
- Olson, E.C., 1980, The North American Seymouriidae, in Jacobs, L.L., ed., *Aspects of vertebrate history*: Flagstaff, Museum of Northern Arizona Press, p. 137–152.
- Reisz, R.R., 1986, Pelycosauria, in Wellnhofer, P., ed., *Encyclopedia of paleoherpetology*, 17A: Stuttgart, Gustav Fischer Verlag, 102 p.
- Reisz, R.R., Berman, D.S., and Scott, D., 1984, The anatomy and relationships of the Lower Permian reptile *Araeoscelis*: *Journal of Vertebrate Paleontology*, v. 4, p. 57–67.
- Reisz, R.R., Dilkes, W.D., and Berman, D.S., 1998, Anatomy and relationships of *Elliotsmithia longiceps* Broom, a small synapsid (Eupelycosauria: Varanopseidae) from the Late Permian of South Africa: *Journal of Vertebrate Paleontology*, v. 18, p. 602–611.
- Ricqlès, A.d., and Taquet, P., 1982, La faune de vertébrés du Permien Supérieur du Niger I. Le captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria)—Le crâne: *Annales de Paléontologie*, v. 68, p. 33–106.
- Scotese, C.R., and McKerrow, W.S., 1990, Revised world maps and introduction, in McKerrow, W.S., and Scotese, C.R., eds., *Palaeozoic palaeogeography and biogeography*: London, Geological Society, p. 1–21.
- Sidor, C.A., and Hopson, J.A., 1995, The taxonomic status of the Upper Permian eotheriodont therapsids of the San Angelo Formation (Guadalupian), Texas: *Journal of Vertebrate Paleontology*, v. 15, p. 53A.
- Sues, H.-D., and Reisz, R.R., 1998, Origin and early evolution of herbivory in terrestrial tetrapods: *Trends in Ecology and Evolution*, v. 18, p. 142–145.
- Tverdokhlebova, G.I., and Ivachnenko, M.F., 1984, Nykteroleteriids from the Upper Permian of Eastern Europe: *Paleontologicheskii Zhurnal*, v. 1984 (3), p. 98–111 (in Russian).
- Wilson, L.R., 1962, Permian plant microfossils from the Flowerpot Formation, Greer County, Oklahoma: *Oklahoma Geological Survey Circular*, v. 49, 50 p.

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