

Euconcordia nom. nov., a replacement name for the captorhinid eureptile *Concordia* Müller and Reisz, 2005 (non Kingsley, 1880), with new data on its dentition

Robert R. Reisz^{*,1}, Yara Haridy¹, and Johannes Müller²

¹Department of Biology, University of Toronto Mississauga, 3359 Mississauga Rd. N., Mississauga, ON L5L 1C6, Canada, robert.reisz@utoronto.ca, yara.haridy@mail.utoronto.ca

²Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany, johannes.mueller@mfn-berlin.de

Abstract: The oldest known captorhinid reptile, and the only Carboniferous representative of this important clade of early eureptiles was named *Concordia cunninghami*. This was done on the basis of the cranial material from two specimens, but the name is preoccupied by an extant hippolytid crustacean. We therefore coined the new name, *Euconcordia*, as a replacement name for this taxon, and the new combination is *Euconcordia cunninghami*. In addition, the recent significant increases in our understanding of dental anatomy in early amniotes in general, and captorhinid reptiles in particular, has allowed us to reinterpret the anatomy of the marginal and palatal teeth of this taxon.

<http://zoobank.org/urn:lsid:zoobank.org:pub:E31E05A9-C673-426E-A024-F5335BDBC6CB>

Key Words: Carboniferous; Kansas; Pennsylvanian

INTRODUCTION

Müller and Reisz (2005) described a new taxon of captorhinid reptile (*Concordia cunninghami*) from the Hamilton Quarry, a Pennsylvanian Lagerstätte in Greenwood County, Kansas (Schultze 1996). *Concordia cunninghami* is the earliest-known member of Captorhinidae and remains the only Carboniferous record of this important, otherwise Permian clade. This small reptile is particularly important because its discovery has allowed palaeontologists to follow the evolutionary history of this clade, as it gradually transitioned from small insectivorous and carnivorous amniotes to omnivores (as seen in basal captorhinids) and eventually the highly derived herbivores (moradisaurine captorhinids) that we see in the Late Permian. There is convincing evidence that captorhinids are the first group of eureptiles to diversify significantly during the initial stages of amniote evolution (LeBlanc et al. 2015; Modesto et al. 2014).

Unfortunately, the name *Concordia* is preoccupied by an extant hippolytid crustacean, *Concordia* Kingsley, 1880. The hippolytid *Concordia* is currently considered a junior synonym of *Latreutes* Stimpson, 1860, with the sole species *Concordia gibberosus* Kingsley, 1880 in the synonymy

*corresponding author

Published November 9, 2016. © 2016 by the authors submitted Sept. 22, 2016; accepted with revisions Oct. 17, 2016; revisions received Nov. 4 2016. Handling editor: Robert Holmes. DOI 10.18435/B53W22

of *Latreutes parvulus* (Stimpson, 1871) (Ledoyer 1986). Although *Concordia* Kingsley, 1880 is not currently considered a valid genus, the name nevertheless remains unavailable, necessitating the establishment of a replacement name for the captorhinid *C. cunninghami*.

SYSTEMATIC PALAEONTOLOGY

EUREPTILIA Olson, 1947
CAPTORHINIDAE Case, 1911
Euconcordia nom. nov.

Concordia Müller and Reisz, 2005, non Kingsley, 1880

Type Species: *Concordia cunninghami* Müller and Reisz, 2005.

Holotype: KUVV 87102a & b, (Fig. 1 A, B) dorsally preserved skull and its counterpart, a partial, ventrally preserved braincase (originally erroneously indicated as KUVV 8702a & b).

Referred Specimens: KUVV 96164a & b, (Fig. 2 A, B) skull preserved in palatal view, and its counterpart, a partial skull roof preserved in dorsal view (originally erroneously indicated as KUVV 96/64).

Horizon and Locality: Calhoun Shale, Shawnee Group, Virgilian Series, Upper Pennsylvanian; Hamilton Quarry near Hamilton, Greenwood County, Kansas, USA.

Emended Diagnosis: Small captorhinid eureptile characterized by the presence of teeth on the medial and lateral edges of the vomer, and an extensive field of teeth on the cultriform process of the parasphenoid. In addition, there is

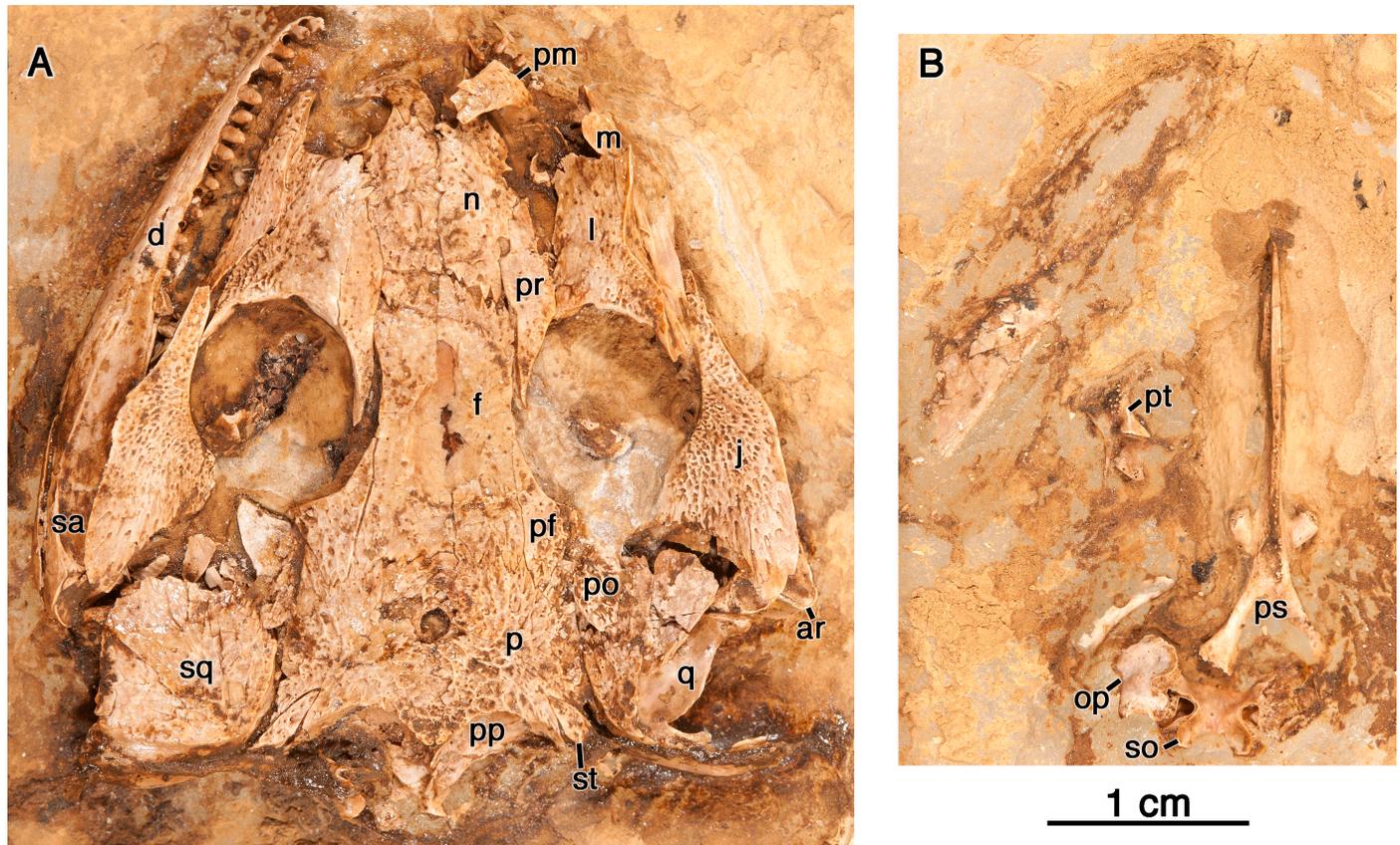


Figure 1. *Euconcordia cunninghami*, holotype, KUV 87102a & b. A, skull roof exposed in dorsal view, with left mandible partially exposed and moved anterolaterally, with quadrate bone still partly in articulation with the articular bone. B, its counterpart, a partial, ventrally exposed braincase (This specimen was originally erroneously identified as KUV 8702a & b). Abbreviations used in figures: ar, articular; bo, basioccipital; d, dentary; f, frontal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pal, palatine; pm, premaxilla; po, postorbital; pp, postparietal; ps, parasphenoid; pt, pterygoid; q, quadrate; s, stapes; sa, surangular; so, suprapccipital; sq, squamosal; st, supratemporal; v, vomer. Scale bars = 1cm

a longitudinal ridge on the mandible along the dorsal edge of the sculptured lateral surface of the dentary and surangular bones. On the pterygoid, the large fields of palatal teeth covering the transverse flange of the pterygoid and the anterior palatal process of the bone are separated by a narrow edentulous groove. Differs from all other captorhinids in having posteriorly embayed parietals, reduced heterodonty, lacking a downturned premaxilla with enlarged anterior teeth, lack of a retroarticular process, and absence of a medial alary process on the jugal.

Etymology: An alteration of the previous name *Concordia*, by adding the prefix *Eu*, meaning true.

NEW COMPARATIVE ANATOMICAL INFORMATION

Recent studies of dental development and evolution among captorhinid eureptiles and Early Permian parareptiles (LeBlanc and Reisz 2015) have now allowed us to reinterpret the dental anatomy of this basal captorhinid. We therefore take this opportunity to reexamine the dental

morphology of *Euconcordia cunninghami*, and also provide more complete visual information on the remarkable cranial remains of this taxon.

The marginal dentition was originally described as pointed, conical teeth, with places for up to five small teeth on the premaxilla, and up to 18 places on the maxilla, with no true caniniform. The four anterior-most teeth are distinctly more elongated than the more posterior members of the series. The dentary has places for 17 teeth, uniform in shape, slender with recurved apices. Our interpretation, based on careful reexamination of the marginal dentition, differs from the original description in a number of impactful ways.

The right premaxillary teeth (Fig. 3A) exposed in medial view are indeed slender, but are quite long, extending nearly the same distance above the alveolar shelf of the bone as the anterior maxillary teeth. In addition, the first premaxillary tooth appears to be slightly longer than the fifth tooth, based on the distance between the tip of the tooth and the edge of the alveolar shelf. Apically, the teeth curve slightly medially, have a delicate lingual ridge that extends to the central apex, and on either side of the tip, there are delicate carinae.

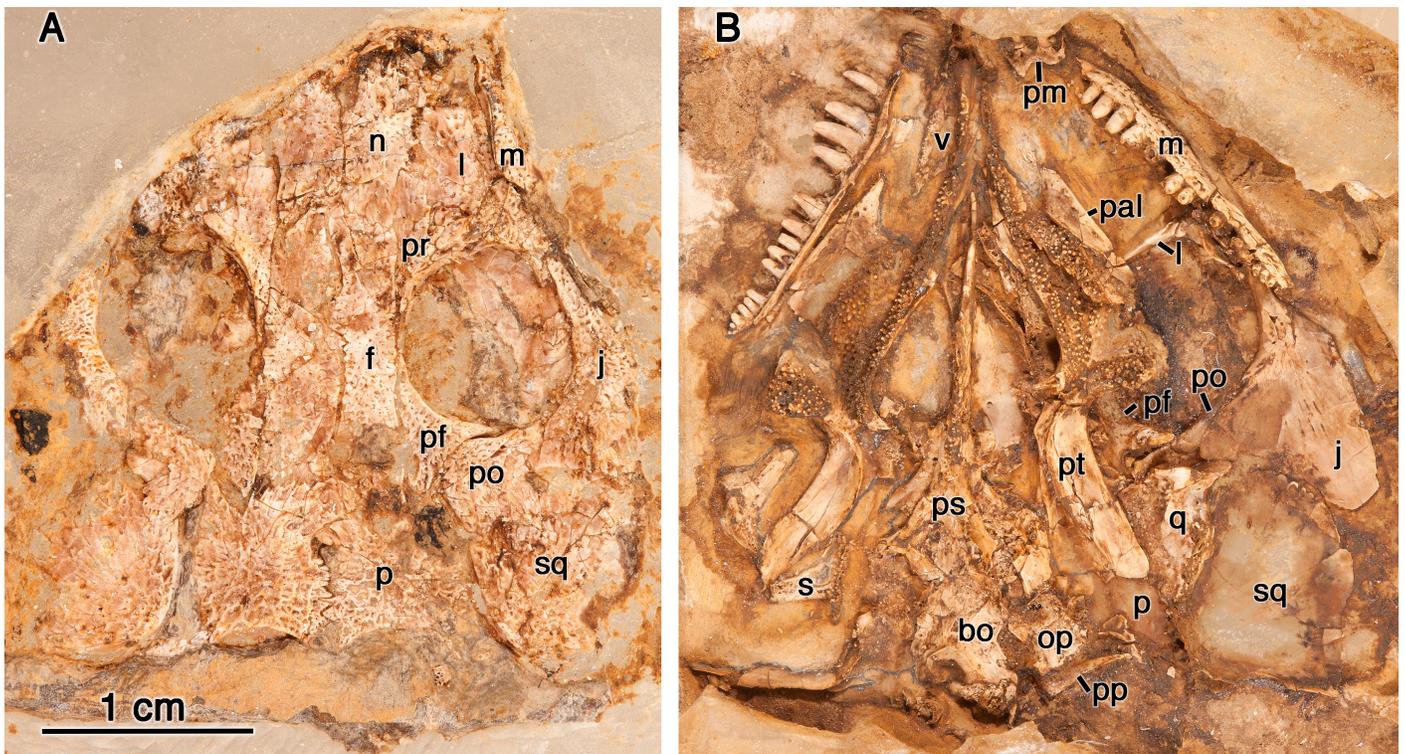


Figure 2. *Euconcordia cunninghami*, referred specimen KUV 96164a & b. A, the skull roof preserved in dorsal view. B, its counterpart, skull preserved in palatal view. This specimen was originally erroneously labeled as KUV 96/64 (Müller and Reisz 2005). Abbreviations as in Figure 1. Scale bars = 1cm

The outline of the maxillary teeth (Fig. 3A, B) also differs from their original description. The teeth are not simple cones, but are slightly bulbous at the base, with crowns that are not conically pointed but rather are more complex, with anterior and posterior carinae restricted to the apex of the tooth and forming an obtuse triangular cutting blade. The crown portion of each tooth is covered by enamel and curves gently medially, and slightly posteriorly, although it lacks the distinct recurvature that characterizes basal eureptiles (Carroll 1964). The posterior maxillary teeth are not conical either, but exhibit a slightly bulbous base or with parallel sides, and the relatively broad crowns of these teeth display delicate apical carinae. These teeth are reminiscent of the marginal teeth of other basal captorhinids (Modesto 1996), including *Captorhinus laticeps*, and differ from the teeth in the basal eureptiles *Hylonomus*, *Paleothyris*, *Thuringothyris*, and *Protorothyris*. Their teeth have a simple conical outline with recurved tips, and lack apical carinae (pers. obs. RRR). It is generally agreed that this morphology is associated with faunivory, feeding on arthropods and small tetrapods. It is likely that the dental morphology that is present in these four eureptiles represents the primitive condition for amniotes. Thus, we can argue that some the dental modifications towards omnivory and eventually high fiber herbivory that characterize later captorhinids are already present in *Euconcordia*. In particular the slightly

bulbous dentition in combination with the carinae may have been ideally suited for feeding on a wider variety of foods than basal eureptiles. However, based on size and body shape, it is unlikely that *Euconcordia* and other early single tooth-rowed captorhinids were high fiber herbivores. That feeding behavior is most likely present in the moradisaurine captorhinids (Reisz and Fröbisch 2014).

The dentary teeth (Fig. 3C) are plesiomorphic in being less heterodont than the maxillary teeth, and lack the typical captorhinid condition of greatly enlarged first and second teeth. In fact, the first tooth of the dentary is comparatively small, and the space for the second tooth suggests that the tooth occupying it would also have to be small. The largest teeth of the dentary are located in the mid-region of the tooth row, occupying tooth positions 8 through 12. They are clearly bulbous in lateral outline, and each possesses carinae on either side of the central apex. The teeth are slightly recurved at the tip, but this is because each tip points posterodorsally, and the curvature of the anterior carina is more pronounced than the posterior carina. It should also be noted that the most posterior teeth seem to lose this recurvature entirely, whilst maintaining their bulbous base.

Like most other Paleozoic reptiles, *Euconcordia* possesses dentition on several elements of the palate. Although previously referred to as ‘denticles’, we prefer to restrict that



Figure 3. Marginal dentition of *Euconcordia cunninghami*. A, KUV 96164a, right premaxilla and maxilla exposed in lingual view. B, KUV 96164a, left maxilla exposed in partial lateroventral view. C, KUV 87102a, dentition on left dentary, exposed in partial lateral view. Scale bar = 1 cm

term to the structures that are present along the cutting edges in teeth of theropod or prosauropod dinosaurs (Brink and Reisz 2014; Sues et al. 2004), or the crowns of iguanid squamates. We therefore use a different dental terminology, referring to the palatal dentition using the term teeth, rather than ‘denticles’, as is the convention in extant anatomical descriptions (Mahler and Kearney 2006). This is done in order to emphasize the similarities between the dentition on the palatal and marginal bones of the skull. Anatomically, the palatal teeth of Palaeozoic amniotes appear to be indistinguishable from their marginal teeth, and are characterized by the presence of enamel, dentine, and pulp cavity. It is therefore likely that they developed the same way as marginal teeth, and are therefore developmentally homologous with them.

The vomer was originally described as possessing two rows of ‘denticles’, with the lateral row being considered to be autapomorphic. Our interpretation differs from the

original description in recognizing that the vomerine dentition is not arranged into single lateral and medial rows, but rather in two patternless fields of teeth (Fig. 2B). The teeth making up the field running along the lateral edge of the vomer are smaller than the teeth of the medial field, as well as those in other palatal fields. This is in stark contrast with other captorhinids, where the vomer is completely edentulous and exhibits well developed longitudinal ridges where the lateral and medial fields of teeth are located in *Euconcordia cunninghami*.

The palatine bone has a large field of teeth covering the medial half of the bone (Fig. 2B), and is more extensive than in any other captorhinid or basal eureptile. This field of palatine teeth is confluent with that on the pterygoid. Three fields of teeth are present on the pterygoid. The first and longest is located on a broad ridge that extends anteriorly from the basicranial articulation to the vomer, along the medial edge of palatal ramus. The second field covers the

ventral surface of the transverse flange. The third field spans the ventral surface of the bone between the other two fields, meets the first, medial field at the level of the basicranial articulation. However, these conjoined fields are separated from that on the transverse flange by an acute angled edentulous groove with an apex that points towards the basicranial articulation. As is the case for the palatine, the fields of teeth on the pterygoid are more extensive and cover a greater area of the bone than in any other Early Permian eureptile, and significantly more than in any other captorhinid.

The cultriform process of the parabasisphenoid is edentulous only in the area that is overlain by the palate, whereas posteriorly it bears an extended field of teeth where it is exposed ventrally in the region of the interpterygoid vacuity (Figs. 1B, 2B). This field is transversely expanded in the region of the tubera, extending a short distance posteriorly onto the main body of the parabasisphenoid, and reminiscent of the condition seen in the early eureptiles *Hylonomus* (Carroll 1964) and *Paleothyris* (Carroll 1969), but contrary to the edentulous parasphenoid of *Thuringothyris* (Müller et al. 2006).

We can therefore conclude that in contrast to other captorhinids, the palatal dentition is much more extensive in *Euconcordia cunninghami*, and much of the palatal surface is covered by fields of small teeth. These small teeth do not increase in size posteriorly on the transverse flange of the pterygoid, as it commonly occurs in other reptiles (Reisz et al. 2014).

Two interesting anatomical features of *Euconcordia cunninghami* are relevant to studies of captorhinid evolution, and worthy of discussion. All captorhinid reptile specimens that have the appropriate region of the skull preserved show the presence of a well developed, medially projecting alary process on the jugal. This stout process forms a rugose sutural contact with the base of the transverse flange of the pterygoid. The ectopterygoid bone that usually resides in this region of the palate in other reptiles is absent in captorhinids. The absence of the alary process in *E. cunninghami* (Fig. 2B) does raise the possibility that an ectopterygoid may have been present, because the alary process of the jugal normally takes on the function of bracing the cheek against the pterygoid bone in the region where the ectopterygoid is usually located in other reptiles. It is not possible to determine with confidence if the bone was present or absent in *E. cunninghami* because this region of the palate is incompletely preserved. This region of the skull is also not preserved well in *Thuringothyris*, the generally accepted sister taxon to *E. cunninghami* and all other captorhinids, but the presence of an ectopterygoid was reported in that taxon (Boy and Martens 1991; Müller et al. 2006). The absence of an alary process on the jugal of *Eucondordia*, suggests that the ectopterygoid may have been also present in *E. cunninghami*.

The second unusual feature of *E. cunninghami* is the presence of a sharp ridge that separates the lateral, ornamented surface of the dentary and surangular bones, from their smooth dorsal surface (Fig. 1A). The latter smooth surface is presumed to be for the insertion of the large jaw adductor musculature, and is widely present in other captorhinids. Interestingly, this smooth surface complements the laterally expanded temporal region of the skull, where the jugal extends ventrally and laterally beyond the maxillary tooth row. The dorsal smooth shelf is particularly large in the moradisaurine captorhinids (Reisz et al. 2010), but is also well developed in *Captorhinus* (Heaton 1979), *Labidosaurus* (Modesto et al. 2005), and *Rhiodenticulatus* (Berman and Reisz 1989). However, in these captorhinids the separation between these two areas of the lower jaw is not sharply demarcated by a ridge as is seen in *E. cunninghami*.

ACKNOWLEDGMENTS

We thank Christian F. Kammerer (Museum für Naturkunde, Berlin) for bringing this homonymy to our attention and for taxonomic assistance, and Diane Scott for photography of the specimens. This research was supported by grants from NSERC (Discovery Grant), Canada, and University of Toronto to RRR.

LITERATURE CITED

- Boy, J. A. and Martens, T. 1991. Ein neues captorhinomorphes Reptil aus dem thüringischen Rotliegend (Unter-Perm; Ost-Deutschland). *Paläontologische Zeitschrift* 65:363–389. DOI 10.1007/BF02989852
- Brink, K.S., R.R. Reisz, A.R.H. LeBlanc, R.S. Chang, Y.C. Lee, C.C. Chiang, T. Huang, and D.C. Evans. 2015. Developmental and evolutionary novelty of the serrated teeth of theropod dinosaurs. *Scientific Reports* 5 (12338). DOI 10.1038/srep12338
- Carroll, R.L. 1964. The earliest reptiles. *Zoological Journal of the Linnean Society* 45:61–83. DOI 10.1111/j.1096-3642.1964.tb00488.x
- Carroll, R.L. 1969. A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology* 43:151–170.
- Case, E.C. 1911. A revision of the Cotylosauria of North America. Carnegie Institution of Washington Publication 145:1–122.
- Heaton, M.J., and R.R. Reisz. 1980. A skeletal reconstruction of the Early Permian captorhinid reptile *Eocaptorhinus laticeps* (Williston). *Journal of Paleontology* 54:136–143.
- Kingsley, J.S. 1880 [for 1879]. On a collection of Crustacea from Virginia, North Carolina, and Florida, with a revision of the genera of Crangonidae and Palæmonidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 31:383–427.
- LeBlanc, A.R.H., and R.R. Reisz 2015. Patterns of tooth development and replacement in captorhinid reptiles: A com-

- parative approach for understanding the origin of multiple tooth rows. *Journal of Vertebrate Paleontology* e919928. DOI 10.1080/02724634.2014.919928
- LeBlanc, A.R.H., A.K. Brar, W. May, and R.R. Reisz. 2015. Multiple tooth-rowed captorhinids from the Early Permian fissure fills of the Bally Mountain Locality of Oklahoma. *Vertebrate Anatomy Morphology Palaeontology* 1:35–49. DOI 10.18435/B5RP4N
- Ledoyer, M. 1986. Faune mobile des herbiers de phanérogames marines (Halodule et Thalassia) de La Laguna de Términos (Mexique, Campêche). I. Les Caridea (Crustacea Decapoda) et aperçu sur la faune globale. *Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México* 13:147–170.
- Mahler D.L., and M. Kearny 2006. The palatal dentition in squamate reptiles: Morphology, development, attachment, and replacement. *Fieldiana Zoology* 108:1–61.
- Modesto, S.P. 1996. A basal captorhinid reptile from the Fort Sill fissures, Lower Permian of Oklahoma. *Oklahoma Geology Notes* 56:4–14.
- Modesto, S.P., and R.M.H. Smith 2001. A new Late Permian captorhinid reptile: a first record from the South African Karoo. *Journal of Vertebrate Paleontology* 21:405–409. DOI 10.1671/0272-4634(2001)021[0405:ANLPCR]2.0.CO;2
- Modesto, S.P., D.M. Scott, D.S. Berman, J. Muller, and R.R. Reisz. 2007. The skull and the palaeoecological significance of *Labidosaurus hamatus*, a captorhinid reptile from the Lower Permian of Texas. *Zoological Journal of the Linnean Society* 149:237–262. DOI 10.1111/j.1096-3642.2007.00242.x
- Modesto, S.P., A.J. Lamb, and R.R. Reisz. 2014. The captorhinid reptile *Captorhinikos valensis* from the Lower Permian Vale Formation of Texas, and the evolution of herbivory in eureptiles. *Journal of Vertebrate Paleontology* 34:291–302. DOI 10.1080/02724634.2013.809358
- Müller, J., and R.R. Reisz. 2005. An early captorhinid reptile (Amniota, Eureptilia) from the Upper Carboniferous of Hamilton, Kansas. *Journal of Vertebrate Paleontology* 25:561–568. DOI 10.1671/0272-4634(2005)025%5B0561:AECRAE%5D2.0.CO;2
- Müller, J., D.S. Berman, A.C. Henrici, T. Martens, and S.S. Sumida. 2006. The basal reptile *Thuringothyris mahlendorffae* (Amniota: Eureptilia) from the Lower Permian of Germany. *Journal of Palaeontology* 80:726–739.
- Olson, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana (Geology)* 11:1–53.
- Pearson, M.R., R.B.J. Benson, P. Upchurch, J. Fröbisch, and C.F. Kammerer. 2013. Reconstructing the diversity of early terrestrial herbivorous tetrapods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372:42–49. DOI 10.1016/j.palaeo.2012.11.008
- Reisz, R.R., and J. Fröbisch. 2014. The oldest caseid synapsid from the Late Pennsylvanian of Kansas, and the evolution of herbivory in terrestrial vertebrates. *PlosOne* 9: e94518. DOI 10.1371/journal.pone.0094518
- Reisz, R. R., J. Liu, J. Li, and J. Müller. 2011. A new captorhinid reptile, *Gansurhinus qingtoushanensis* gen. et sp. nov., from the Permian of China. *Naturwissenschaften* 98:435–441. DOI 10.1007/s00114-011-0793-0
- Reisz, R. R., A.R.H. LeBlanc, and M. J. MacDougall (2014) A new species of the parareptile *Delorhynchus*, based on articulated skeletal remains from Richards Spur, Lower Permian of Oklahoma. *Journal of Vertebrate Paleontology* 34:1033–1043. DOI 10.1080/02724634.2013.829844
- Ricqlès, A.J., and P. Taquet. 1982. La faune de vertébrés de Permien Supérieur du Niger. I. Le captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria) – le crane. *Annales de Paléontologie* 68:33–106.
- Schultze, H-P. 1996. Terrestrial biota in coastal marine deposits: fossil-Lagerstätten in the Pennsylvanian of Kansas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 119 (3): 255–273. DOI 10.1016/0031-0182(95)00011-9
- Stimpson, W. 1860. Prodrömus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladore Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII, Crustacea Macrura. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1860:22–47.
- Stimpson, W. 1871. Notes on North American Crustacea in the museum of the Smithsonian Institution. No. III. *Annals of the Lyceum of Natural History in New York* 10:119–163.
- Sues, H-D., R. R. Reisz, S. Hinnic, and M. Raath. 2004. On the skull of *Massospondylus carinatus* Owen, 1854 (Dinosauria: Sauropodomorpha) from the Elliot and Clarens formations (Lower Jurassic) of South Africa. *Annals of the Carnegie Museum* 73:239–258.