Journal of Vertebrate Paleontology 25(3):561–568, September 2005

AN EARLY CAPTORHINID REPTILE (AMNIOTA, EUREPTILIA) FROM THE UPPER CARBONIFEROUS OF HAMILTON, KANSAS

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ABSTRACT—A new eureptile, *Concordia cunninghami*, gen. et sp. nov., is described from the Upper Pennsylvanian Hamilton-Fossillagerstätte, Kansas, U.S.A. The new taxon is currently known on the basis of two well-preserved skulls. A phylogenetic analysis groups *Concordia* consistently with captorhinids; the holotype, therefore, can be regarded as the oldest record of a captorhinid reptile, and the first one from the Carboniferous. *Concordia* reduces to a notable extent the stratigraphic gap between captorhinids and the first appearance of other eureptiles. Furthermore, the new taxon is the third known amniote representative from the Hamilton fauna, improving our knowledge of Late Carboniferous terrestrial communities.

INTRODUCTION

In recent years, significant new information has emerged on the evolutionary history of Carboniferous amniotes. However, we still lack a considerable amount of knowledge about the timing of the origin (Reisz, 1997; Reisz and Müller, 2004) and initial stages of amniote diversification. The Upper Pennsylvanian Fossillagerstätte near Hamilton, Kansas, and another locality near Garnett, Kansas, U.S.A., have recently provided most of the evidence about the initial stages of amniote diversification, only about 10 million years after the first appearance of amniotes in the fossil record (Kissel and Reisz, 2004). In particular, the Hamilton site has yielded a diverse fauna that includes one of the oldest known diapsids, *Spinoequalis* (DeBraga and Reisz, 1995), and the oldest known varanopid synapsid *Archaeovenator* (Reisz and Dilkes, 2003). Here we report on a new eureptile from this locality, one that can be confidently assigned to the Captorhinidae as the oldest known member of that clade. As the first group of reptiles to show a significant level of taxonomic diversification and geographic dispersal, captorhinids provide important new insights into the biogeography and the dispersal pattern of early amniotes.

MATERIAL AND METHODS

The referred material consists of two skulls housed at the Vertebrate Paleontology Collection of the University of Kansas, Lawrence (KUVP). Both skulls were discovered by splitting of shale, and were therefore embedded in resin in order to protect the delicate bones, as well as to permit exposure of bone surfaces. This was undertaken by acid preparation before we received these specimens for study. The skull roof of KUVP 8702a was similarly prepared by Ms. Akiko Shinya. Drawings were made with a Wild stereomicroscope equipped with a camera lucida. Although the process of embedding was necessary in this case, permitting the viewing of some features that would not be otherwise observable, illustration of some structures located deeply in the resin was not possible.

SYSTEMATIC PALEONTOLOGY
EUREPTILIA Olson, 1947
CAPTORHINIDAE Case, 1911
CONCORDIA, gen. nov.
CONCORDIA CUNNINGHAMI, sp. nov.

Etymology—The generic name is based on the Latin word 'concordia,' meaning 'unity, agreement, harmony' referring to the fact that the taxon finally corroborates the long held assumption that captorhinids must also have existed in the Late Carboniferous. The specific name is in honor of Christopher R. Cunningham, who studied this form as part of his PhD thesis on the Hamilton Quarry.

Holotype—KUVP 8702a & b, dorsally preserved skull along with its counterpart, a partial, ventrally preserved braincase.

Referred Specimen—KUVP 96/95, ventrally preserved skull and a thin, poorly preserved dorsal counterpart.

Horizon and Locality—Calhouns Shale, Shawnee Group, Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; Hamilton Quarry near Hamilton, Greenwood County, Kansas, U.S.A.

Diagnosis—Small captorhinid eureptile characterized by the presence of two rows of vomerine teeth, and a longitudinal, keel-like ridge on the dorsolateral surface of the mandible; differing from all other captorhinids in lacking a downturned premaxilla, development of a true caniniform, and a retroarticular process on the mandible; also differing from other captorhinids in having each parietal posteriorly embayed, all palatal bones and parabasisphenoid with denticles, and a short stapes.

Description

Skull Roof and Cheek—The two skulls and the braincase are preserved in dorsal and ventral views, respectively (Figs. 1–3). The quadratojugal is missing in both skulls, but this is doubtlessly a result of preservation, because the straight ventral edge of the squamosal and the posteroventral tip of the jugal indicate the original presence of a quadratojugal. The dermal skull roof shows a distinct pattern of sculpturing, similar to that seen in small captorhinids, even though it appears less well developed than in other well-known forms such as *Captorhinus* (Fox and Bowman, 1966; Heaton, 1979). The degree of ossification suggests it was a mature animal.

The paired premaxilla is short. Even though it is slightly crushed and dislocated from the nasal and the maxilla, it is obvious that it was vertically oriented and did not overlap the mandible anteroventrally. This is indicated by the overall slenderness of the bone as compared to that of other early captorhinids with a definitely down-turned rostrum, and with premaxillae usually having a massive ventral base. It is somewhat difficult to determine the exact number of teeth present on each element, because KUVP 8702a (Fig. 1) shows only two teeth on the right premaxilla, while KUVP 96/95 (Fig. 3) shows remnants of five

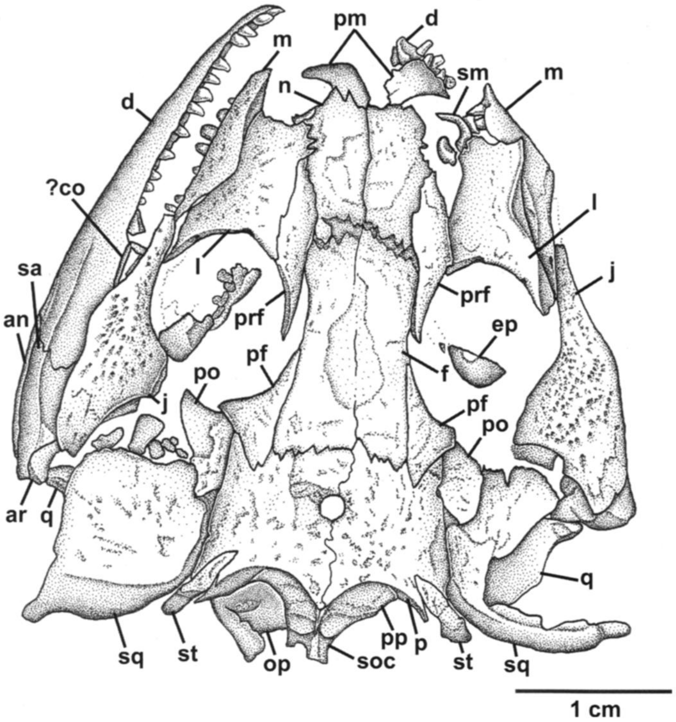

FIGURE 1. *Concordia cunninghami*, holotype (KUVP 8702a). **Abbreviations**: **an**, angular; **ar**, articular; **co**, coronoid; **d**, dentary; **ep**, epipterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **q**, quadrate; **sa**, surangular; **sm**, septomaxilla; **soc**, supraoccipital; **sq**, squamosal; **st**, supratemporal.

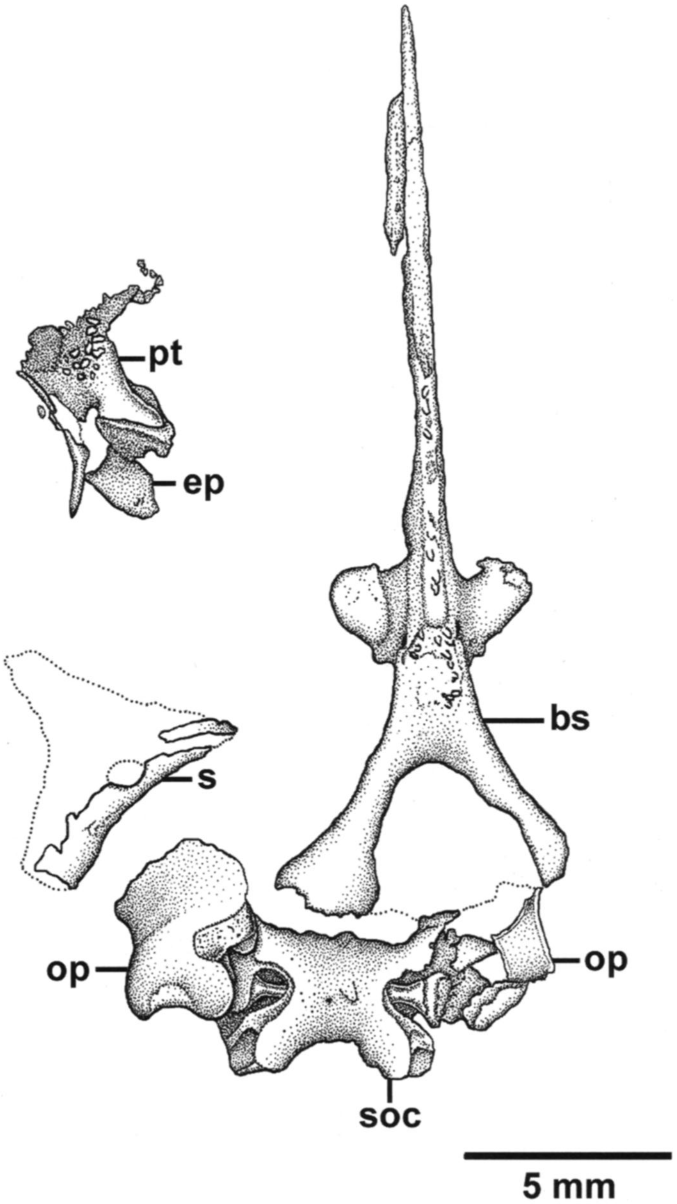

FIGURE 2. *Concordia cunninghami* (KUVP 8702b), associated braincase in ventral view. **Additional abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **pt**, pterygoid; **s**, stapes.

teeth on its left half. However, it is reasonable to assume that these premaxillae had places for five teeth. The teeth are small, closely spaced, and have pointed apices. In most early amniotes the premaxilla has three processes, a palatal process, a lateral maxillary process, and a dorsal nasal process. Only the dorsal process is preserved sufficiently in *Concordia* for comparative purposes, being a fairly broad structure that forms a two-pronged suture with the nasal. Thus, the dorsal process of the premaxilla nearly matches in width the anterior process of the nasal above the narial opening.

The maxilla is slender and elongate. As it is typically seen in other small captorhinids, the maxilla is very low and shows only a very modest dorsal lamina in its central portion, extending only slightly above the alveolar shelf. Anteriorly, the maxilla forms the ventral border of the naris, and posteriorly it terminates in a thin projection at the anterior level of the orbit. KUVP 8702a also shows parts of the internal (medial) side of the maxilla in its right half. There is a well-developed horizontal lamina that presents a prominent expansion anteromedially. Posteriorly, the lamina becomes more slender. Almost at the caudal end of the maxilla, the medial side shows a small foramen that may be related to the passage of the alveolar nerve. There is only a single row of teeth, which can be well seen in both maxillae of KUVP 96/95. KUVP 8702a has 11 teeth on the left maxilla, whereas KUVP 96/95 has 14 teeth on the right maxilla and 16 on the left. However, the maximum number of teeth can be estimated to be 18, as indicated by the spaces and sockets between the preserved teeth. There is not a true caniniform, but at least the 4 anterior-most teeth are distinctly more elongated than the more posterior members of the series. The dorsal lamina of the maxilla reaches its maximum height immediately posterior to the slightly enlarged teeth, and is therefore not related to the size of the teeth. There is no distinct broadening or expansion of any tooth. In the central part of the bone, the teeth are distinctly lower and their height slightly decreases posteriorly. The posterior-most 4 teeth are very low, with the last one being developed only as a small knob.

The septomaxilla is only poorly preserved, but some parts of it are visible in the nasal openings of KUVP 8702a. It was apparently a small, rounded element close to the posterior border of the naris, as in *Captorhinus*. This is in contrast to the condition seen in synapsids and diadectomorphs where the septomaxilla is always pillar-like. However, due the fragmentary nature of this element in *Concordia*, a more thorough description is not possible. Similarly, the poor preservation of this element in most early amniotes prevents a wider comparison.

The paired nasal is a broad, elongate plate, with a gently curved dorsal surface both anteroposteriorly and mediolaterally. The anterior portion of the nasal matches closely the posterior

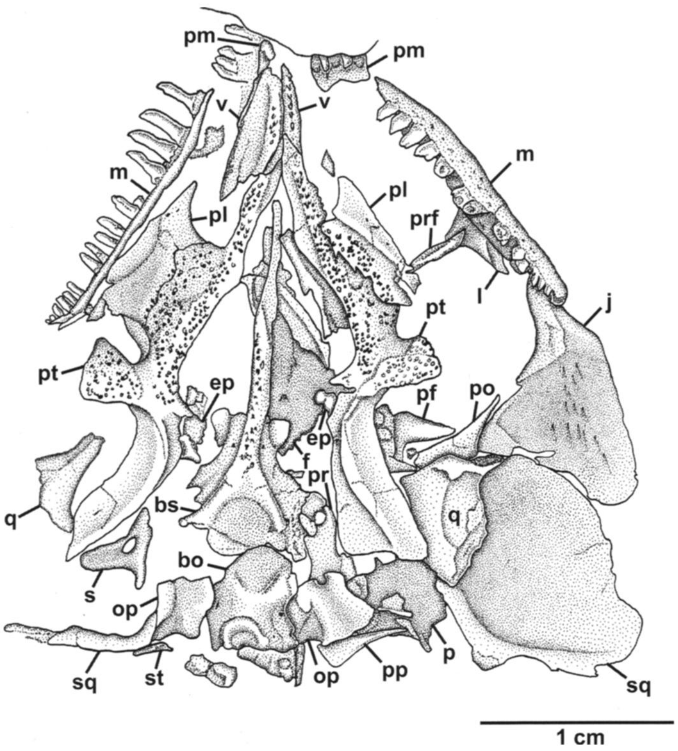

FIGURE 3. *Concordia cunninghami*, referred specimen (KUVP 96/95). **Additional abbreviations**: **pl**, palatine; **v**, vomer.

width of the premaxilla, and is only slightly narrower than its posterior suture with the frontals.

The lacrimal is an unusually large element that forms much of the transverse curvature of the snout, following smoothly the curvature of the nasal anterolaterally, and bridging the dorsal surface and the lateral surfaces of the snout in the antorbital region. It reaches far dorsally along the anterior margin of the orbit, and its shape and outline appear comparable to those of the lacrimal of *Rhiodenticulatus* (Berman and Reisz, 1986). Anteriorly, where the lacrimal contributes to the formation of the posterior border of the naris, the bone was possibly in contact with the septomaxilla, but this determination must remain equivocal. Unfortunately, the anterior opening of the lacrimal duct could not be detected. On the posterior (orbital) edge of the lacrimal, however, the duct opens through two foramina, one being situated relatively far dorsally, close to the prefrontal, the other being more ventrally positioned. Anterolaterally, the bone shows a strongly interdigitating contact with the nasal, whereas the contact with the prefrontal is straight. Posteroventrally, the lacrimal shows a well-developed projection that forms the anteroventral orbital margin, and makes an elongate contact with the jugal. The lacrimal achieves its greatest height along the antorbital margin, and probably made contact with the palatine.

The prefrontal is long and slender in dorsal view, but also has a well-developed ventral process. Anteriorly, the bone terminates in a sharp tip and forms a significant portion of the lateral border with the nasal, approximately equal in length to its suture with the frontal. This is in contrast to the condition in *Captorhinus* and *Labidosaurus,* where the prefrontal-nasal suture is significantly shorter than the postfrontal-frontal suture. In addition, the prefrontal is wedged deeply into the posterior part of the nasal in the latter taxa, whereas in *Concordia*, this suture curves gently towards the nasal-lacrimal contact. Posteriorly, it is very elongated, tapers increasingly, almost reaching the anterior tip of the postfrontal. It therefore contributes significantly to the dorsal border of the orbit. The large ventral process of the prefrontal is laterally covered by the lacrimal, but it is possible to discern that the process is still well developed and reaches far downwards at least to the level of the dorsal foramen of the lacrimal duct in KUVP 8702a, and well beyond that, nearly to the base of the lacrimal bone in KUVP 96/95.

The paired frontal has a rectangular outline and forms the bulk of the supraorbital area. Its overall shape and proportions relative to the other elements of the skull are nearly identical to those in *Captorhinus.* Although it is the longest mid-line element of the skull roof, being significantly longer than the nasal and slightly longer than the parietal, its contribution to the orbital margin is short, as in other captorhinids. Posteriorly it is slightly expanded at the level of the posterior orbital margins, where it contacts the large parietal in a nearly transverse, strongly serrated suture.

The postfrontal is roughly triradiate. Anteriorly, it terminates in a slender, sharp tip. Posteriorly, there is a much shorter and broader process that is almost fully embraced by the parietal, but extends only slightly beyond the posterior edge of the frontal bone. Laterally, the postfrontal forms the posterodorsal margin of the orbit and contacts the postorbital along an anteroventrally sloping suture.

The postorbital is relatively stout but short. Although the holotype skull has incompletely preserved postorbitals, and it is not clear how far the ventral process extended along the posterior margin of the orbit, the paratype shows in ventral view that this process formed approximately the upper half of the posterior orbital margin. The contact between postorbital and postfrontal is reduced significantly by a distinct anterolateral extension of the parietal that projects extensively between the two bones. Posteriorly, the postorbital extends only a short distance between the parietal and the squamosal bones, as in other captorhinids.

The paired parietal is broad but relatively short. Each parietal is notably embayed at its posterior margin, forming a well-developed median posterior process. As already noted above, there is a distinct anterolateral projection extending between postorbital and postfrontal. Posterolaterally, there was a well-developed, anteromedially directed facet for the slender, superficial supratemporal. A well-developed occipital flange of the parietal extends from the midline to the medial edge of the supratemporal, and underlies the paired postparietal. The relatively small pineal foramen, similar in relative size to those in small captorhinids, is located anteriorly along the median, moderately interdigitated parietal suture.

The paired postparietal is a well-developed, semi-lunar element that overlies the occipital flange of the parietal. Thus, the postparietal is situated on the occipital surface of the skull, posterior and slightly ventral to the skull table, and lacks any dermal ornamentation or sculpturing. The two postparietals fully meet each other medially, and the suture between the two bones is developed as a sharp crest that continues ventrally on the supraoccipital. As in other captorhinids, there is no trace of a tabular such as is normally located lateral to the postparietal in other amniotes.

The supratemporal is a small sliver of bone that is embedded in the posterolateral wing of the parietal. The anterior tip of the supratemporal is relatively slender and pointed, whereas its posterior part is slightly broader. The anterior portion of the bone occupies the posterolateral corner of the skull table and is slightly sculptured, whereas its posterior part curves ventrally onto the occiput, has a smooth surface, and probably overlaid the occipital flange of the squamosal.

The squamosal is large, as it is typically seen in most early tetrapods, occupying most of the temporal region of the skull roof. At its gently curved posterior edge is a distinct occipital flange. This flange is not completely vertically oriented; rather, it slopes posteroventrally, and forms the gently convex posterior edge of the skull in the temporal region. The temporal part of the squamosal is gently sculptured, and is separated from the smooth surface of the occipital flange by a distinct subvertical ridge.

The jugal is large, bridges the snout with the temporal region, and forms most of the suborbital region of the skull roof. Although disarticulated in both specimens, fortuitous exposure in both lateral (KUVP 8702a, Fig. 1) and medial views (KUVP 96/95, Fig. 3) makes it possible to describe the jugal in detail. The jugal can be divided readily into three regions: a long slender anterior process, a short postorbital dorsal process, and a broad, flat temporal flange. The slender anterior process forms the anteroventral border of the orbit and extends anteriorly between the lacrimal and the maxilla as a tongue-like process. The dorsal process of the jugal is broad, relatively low, and supports the ventral process of the postorbital along its anterior edge. The posterior flange is sheet-like, forms the ventral part of the temporal region beneath the squamosal, and extends slightly posteriorly beneath the squamosal, probably to make contact with the quadratojugal. In most respects the jugal is indistinguishable from that seen in *Rhiodenticulatus*. However, two features of this bone merit particular attention. (1) The anterior process decreases gradually in height as it extends anteriorly beyond the anterior edge of the orbit, and terminates as a slender acuminate wedge between the lacrimal and maxilla. In contrast, this process has a relatively broad anterior end in *Captorhinus* and other captorhinids where this area is well preserved. (2) The exposure of the medial surface of the jugal has allowed us to determine that there was no medial process, a feature that is present in *Captorhinus, Rhiodenticulatus*, and other captorhinids where this can be examined. In these two features, the jugal of *Concordia* shows the primitive eureptilian condition.

Perhaps the most significant feature of the jugal is well represented in both medial and lateral views: the ventral edge of the anterior process is not in line with the ventral edge of the posterior half of the bone, a condition seen in captorhinids. Although disarticulated, we can determine that this represents at least a modest development of a posterior process or a lateral expansion of this region of the skull, similar to that in *Rhiodenticulatus* (Berman and Reisz, 1986), and further developed in other, larger captorhinids.

The quadrate is exposed on the left side of KUVP 96/95 and is also partially exposed on the right side of the holotype KUVP 8702a. It appears to have been relatively broad in medial view, with a well-developed, tall, dorsal process. The condyle for the articulation with the lower jaw has the typical amniote configuration, with two convex, slightly elongate tuberosities whose long axes are probably at a slight angle to the long axis of the skull. These two elements of the condyle are separated by a shallow, broad groove. The medial tuberosity of the condyle is broader than the lateral one, is located more posteriorly, and extends well beyond the dorsal process of the bone. The posterior edge of the quadrate is emarginated between the condyle and the dorsal process, probably for the passage of the quadrate foramen.

Palate—The vomer is relatively small. Like all the other palatal bones (Fig. 3), the vomer possesses denticles. Preservation is not perfect in that area, but it is likely that two rows must have been present originally, situated in the medial and lateral areas, both rows being very narrow. The medial row of denticles represents a continuation of the medial row on the pterygoid, whereas the presence of lateral denticles may be considered to be an autapomorphy of *Concordia* because no other early eureptile currently known shows a lateral row of denticles on the vomer.

The palatine is a broad plate with a distinct, anterolateral, sharp elongation that is wedged between the maxilla and the internal naris. The medial part of the ventral surface of this bone bears the field of denticles that is continued on the pterygoid.

The pterygoid has the typical amniote division into three parts, the large palatal surface anteriorly, a well-developed quadrate ramus posteriorly, and a prominent transverse flange that is clearly offset from the remaining parts of the bone. The counterpart of KUVP 96/95 indicates that the pterygoid replaces the ectopterygoid in front of the transverse flange, but unfortunately it is not possible to illustrate this area properly. This is because the area is deeply concave, and is represented in the ventral view of the palate by a deep emargination between the palatal ramus and the transverse flange. The missing part of the pterygoid is visible in the counterpart embedded in plexiglass.

The anterior palatal process of the pterygoid extends far anteriorly, is wedged between the vomers, its anterior tip terminating at about the level of the first or second maxillary tooth. Nearly half of the palatal process of the pterygoid meets its mate at the midline, but its posterior half has a concave medial edge that forms the large interpterygoid vacuity. The transverse flange is well developed and has a broad lateral edge. Slightly posterior to the level of the flange, the pterygoid has a sharp medial indentation for the basicranial articulation and the ventral process of the epipterygoid, which fits into it and forms the articulation proper. The quadrate process is composed of two flanges: the arcuate flange and the dorsal flange. The former is a broadly curving, nearly horizontal plate that extends between the base of the transverse flange and the ventromedial side of the quadrate ramus, running along the latter, probably to the level of the condyle. The dorsal flange extends from the basicranial articulation to the dorsal process of the quadrate, and supports the flat, elongate base of the epipterygoid. The same pattern can be observed in some other early amniotes, e.g., ophiacodontid synapsids (Reisz 1986), or stem-amniotes such as the diadectomorph *Limnoscelis* (pers. obs.), suggesting it may be a feature that is plesiomorphic for amniotes. Moradisaurine captorhinid taxa, for example, no longer appear to possess the same arrangement.

Three areas of denticles are distributed on the pterygoid, the longest extending along the medial edge of the palatal ramus, a second field on the transverse flange covering much of its ventral surface, and a third running diagonally from the basicranial articulation and extending onto the palatine. The medial and diagonal rows converge posteriorly into a single row, immediately anterior to the basicranial articulation.

Braincase—The basioccipital is well exposed in ventral view in KUVP 96/95 (Fig. 3). As in other captorhinids, it is distinctly longer than broad and is generally a prominent element. Posteriorly, it forms part of the occipital condyle; anterolaterally it shows relatively well-developed basituberal projections.

The supraoccipital is well preserved in internal view (KUVP 8702b, Fig. 2), showing a distinct butterfly-shaped outline because of almost equally developed dorsolateral and ventrolateral processes, surrounded by prominent, dorsally directed flanges. The semicircular canals are situated between the two projections. KUVP 8702a (Fig. 1) shows parts of the dorsal surface of the bone, bearing a median crest as a posteroventral continuation of the crest formed between the postparietals. This crest probably served for the attachment of tendons of the neck musculature.

The opisthotic is comparatively stout and compact. It does not possess lateral elongations that are present in other captorhinids where they normally extend to the cheeks and form the paroccipital processes. Instead, the bone is very short. The lateral part of the ventral surface is noticeably depressed and might have served as a groove receiving the medial portion of the stapes.

The stapes is relatively short, with a poorly developed shaft. The stapedial foramen is large. The medial part of the stapes is somewhat difficult to interpret because a clear separation between the footplate and the dorsal process cannot be discerned. Instead, there seems to be a single large medial expansion of the stapes. As seen in the best-preserved stapes, the right element in

KUVP 96/95, the anteriorly directed part of the enlarged medial head may represent the footplate proper, whereas the slender posterior process may represent the dorsal process that would have attached to the opisthotic.

As typically observed in many reptiles, the para- and basisphenoid are indistinguishably fused. Anteriorly, this compound element presents a slender, sharp, elongate cultriform process. The basipterygoid processes are anterolaterally directed and relatively stout. Medial to them, the sulcus for the passage of the internal carotids is embedded in a slight groove that runs along the posterolateral edge of the bone. Posteriorly, the ventral part of the parabasisphenoid is smooth but laterally expanded and has two projections on each side. The first process is situated posterodorsally, whereas the second is ventrally positioned, extends farther posteriorly, and probably would have contacted the basituberal projections of the basioccipital when in articulation. The cultriform process and its posterior extension between the basipterygoid processes bear irregularly distributed denticles.

Remnants of the prootic are visible in the left side of KUVP 96/95, right next to the main body of the parabasisphenoid. In fact, only the relatively low anterolateral part of the prootic can be seen, showing that there was an emargination in the anterior edge of the bone that served for the passage of the trigeminal nerve.

Mandible—The lower jaw (Figs. 1, 2) is not completely exposed in either specimen, but at least parts of the lateral surface can be described. Unlike many other captorhinids, most of the external surface of the mandible is smooth and lacks extensive dermal sculpturing, a condition that is not due to preparation.

The dentary is the largest element of the mandible, making up more than three quarters of the overall jaw length. The outline of the bone indicates that the mandible was relatively straight in both lateral and occlusal views, and only in the symphyseal area is the bone distinctly curved medially. A notable feature is the development of a lateral crest-like ridge, starting at the beginning of the posterior third of the bone, extending beyond its border onto the surangular, and terminating at the level of the articular. This type of ridge, not seen in early amniotes, usually serves in modern lizards as an attachment for tendons and muscles of the external jaw adductor (Müller, 2002), and the same may be assumed for the taxon described here. Because a comparable structure is not known in other captorhinids or early eureptiles, it is likely that the visible prominence of this feature is an autapomorphy of *Concordia*.

The left dentary of KUVP 8702a bears 13 teeth, whereas the maximum tooth number was probably 17. The teeth are rather uniform in shape, relatively small, slender, and with recurved apices. Only the symphyseal and the posterior-most teeth are slightly smaller than the others, in contrast to the condition seen in more derived captorhinids, where the anterior teeth of the dentary are distinctly larger than the rest of the dentition on the mandible.

Some remnants of the splenial can be seen in KUVP 8702a, lying below or somewhat medial to the dentary, are only visible from an angle that makes them impossible to include in the drawing. The bone accompanies the dentary along most of its extension, with the exception of the anterior-most and posterior-most portions, and therefore does not contribute to the symphysis. A slender, rather nondescript piece of bone that can be tentatively attributed to the coronoid can be seen posterior to the tooth-bearing portion of the dentary. The surangular forms the posterodorsal part of the mandible. As already mentioned, the lateral ridge described above extends onto this bone, where it becomes almost crest-like. The angular covers the posteroventral area of the mandible. It represents a flat plate with slightly rounded corners. The articular, partly exposed in lateral view, consists of a small lens of bone situated at the posterior end of the mandible above the surangular. There is no retroarticular process. The prearticular is unfortunately not visible.

PHYLOGENETIC ANALYSIS

In order to determine the relationships of *Concordia*, a phylogenetic analysis was performed, including 12 ingroup taxa *(Petrolacosaurus, Palaeothyris, Protorothyris, Thuringothyris, Concordia, Romeria texana, Rhiodenticulatus, Labidosaurus, Labidosaurikos, Captorhinus aguti, C. laticeps*), and two outgroup representatives (caseids, millerosaurs). The data matrix is based on a previous analysis of captorhinid relationships (Dodick and Modesto, 1995), but several character definitions were modified to make them informative for this investigation. Furthermore, nine new characters were added to the data set (see the Appendix for further information). Additionally, the number of included taxa was increased as a result of the inclusion of *Concordia, Paleothyris, Petrolacosaurus*, caseids, and millerosaurs. Moreover, *Romeria texana* was entered instead of *Romeria* as a whole, because a re-investigation of this genus, along with an evaluation of its monophyletic status, appears necessary in the opinion of the authors. Dodick and Modesto (1995) used *Protorothyris* as an outgroup taxon, but this was considered insufficient in the present study because we did not focus only on captorhinid ingroup relationships.

Using the branch-and-bound search option of PAUP*4.0b10 (Swofford, 2002), nine equally parsimonious trees were obtained (TL = 86, CI = 0.6207, HI = 0.3793, RI = 0.7556, RC = 0.4690). Lack of resolution affects the base of the tree, but *Concordia* always falls with captorhinids as their basal-most taxon (Fig. 4). The monophyly of captorhinids and *Concordia* is supported by four unequivocal synapomorphies: (1) anterior position of the pineal foramen (#13[1]); (2) loss of the tabular (#15[1], ci = 1); (3) absence of the ectopterygoid (#17[1], ci = 1); and (4) reduction of the maxillary tooth number (#34[1]). Unequivocal autapomorphies of *Concordia* are the short posterior extent of the maxilla, terminating well anterior to the level of the posterior margin of the orbit (#3[1]), and the dorsal expansion of the lacrimal (#40[1]).

It is interesting that due to the high number of plesiomorphic traits and as a result of character incongruence the statistical support for the present result is comparatively weak: bootstrap support (1000 replicates) for the monophyly of *Concordia* and captorhinids is only 72%. It takes three additional steps to move *Concordia* from its position, but even then it shows up as the sister-taxon of captorhinids in 95% of 359 trees.

DISCUSSION

Despite the equivocal statistical support, *Concordia* can be reasonably assigned to the Captorhinidae, especially in view of the unambiguous (ci = 1) synapomorphies that unite this taxon with all other captorhinids. In particular, the loss of the tabular and the ectopterygoid are very typical for the Captorhinidae, and can only rarely be found in other amniotes. It should be noted, however, that the manner in which the ectopterygoid was lost in captorhinids is still unclear. In *Concordia*, it appears that the pterygoid replaces it, whereas in *Captorhinus*, for example, it looks as though the ectopterygoid is replaced by a medial extension of the jugal. Unfortunately, no detailed investigations on this topic have been performed so far, which is why we treat in this study the absence of the ectopterygoid and the presence of a medial process of the jugal as independent characters.

In conclusion, we unite *Concordia* with all other captorhinids on the basis of a stem-based taxon definition: Captorhinidae are the clade consisting of *Concordia* and all organisms or species that share a more recent common ancestor with *Concordia* than with any other eureptile. Our results also differ from previous cladistic analyses of captorhinid relationships (Dodick and

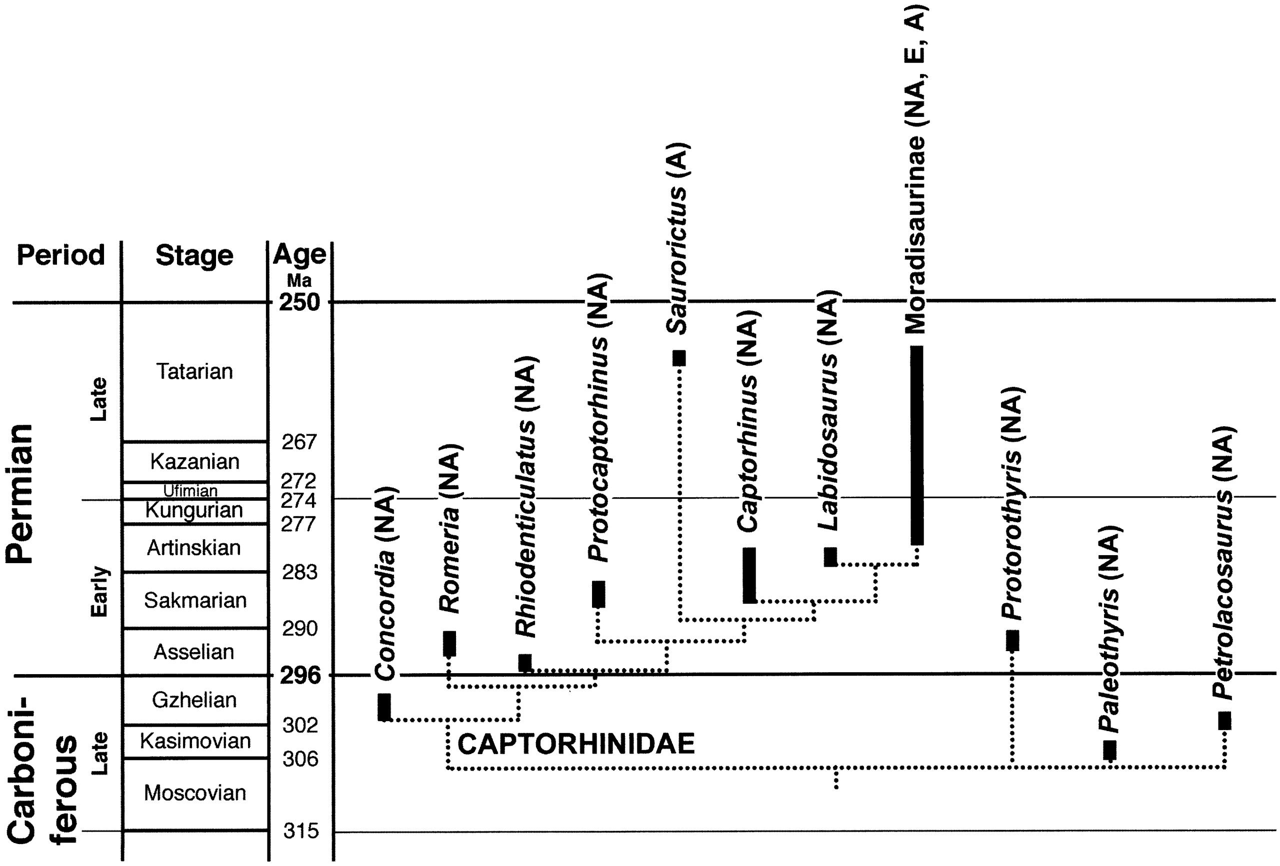

FIGURE 4. Consensus tree of eureptilian relationships as obtained from the cladistic analysis (outgroup taxa excluded), also showing the temporal occurrence of the major taxa. **Abbreviations**: **A**, Africa; **E**, Europe; **NA**, North America.

Modesto, 1995; Modesto and Smith, 2001) in that *Protocaptorhinus* and *Rhiodenticulatus* have switched positions in the cladogram, which means that the latter taxon is now more basally positioned. The new topology, however, has a better fit with the stratigraphic occurrence of the respective taxa, resulting in shorter ghost lineages.

The oldest known eureptile is the fragmentarily preserved 'protorothyridid' *Hylonomus* from the Upper Pennsylvanian of Joggins, Nova Scotia (Carroll, 1964), having an approximate age of 313–316 Ma (Menning et al., 2000). Hamilton, on the other hand, has an age of 295–300 Ma, a difference of at least 13 Ma. This means that even though *Concordia* reduces the stratigraphic gap between captorhinids and their closest relatives to a significant extent, a prominent ghost lineage still must be postulated. It should be noted that Wideman and Sumida (2004) presented recently a re-investigation of the "limnoscelid" *Limnostygis* from the Middle Pennsylvanian of Florence, Nova Scotia (Carroll 1967), stating that at least parts of the vertebrae assigned to this taxon could indeed belong to a captorhinid reptile. If this assumption were correct, then the fossil material from Florence would represent the oldest record of captorhinids. In our opinion, however, additional fossil evidence is needed, because affinities to other 'cotylosaurs' can currently not be excluded on the basis of the available material.

Another important aspect of the analysis is the paraphyletic status of all remaining eureptiles. Although the monophyly of the Protorothyrididae has already been questioned previously (e.g. Boy and Martens, 1991), the present investigation is the first computer-assisted cladistic analysis in which not only *Paleothyris* or *Protorothyris* have been entered exclusively. It is certainly possible that further investigations will resurrect the monophyletic status of this family, but the analysis shows that it is necessary to re-evaluate many early eureptilian taxa with regard to their anatomy and their phylogenetic position.

The phylogeny of captorhinids points to a strong diversification of this group in the region of North America within the Early Permian. It is not until the Middle Permian that captorhinids appear in Eastern Europe (Ivachnenko et al., 1997), and not until the Late Permian that they appear in Gondwana, the African (Gaffney and McKenna, 1979; de Ricqlès and Tacquet, 1982; Gow, 2000; Modesto and Smith, 2001) and Indian regions of Pangaea (Kutty, 1972). These Eastern European and Gondwanan taxa are all positioned higher in the captorhinid tree, providing good correspondence between the temporal and phylogenetic data. In fact, the tree topology indicates that captorhinids originated sometime during the Late Carboniferous in the equatorial regions of North America, being initially relatively small, probably insectivorous forms with a lizard-like appearance. Later during captorhinid evolution, several representatives of this clade became larger and, in part, also developed more specific adaptations, such as multiple tooth rows. Apparently, it was not until this later stage of captorhinid evolution that some taxa also spread towards Eastern Europe, and also into the southern regions of Pangaea. In particular, the evolutionary history of this clade indicates that there must have been at least two invasions of the southern continents, one by small, single-tooth-rowed taxa such as *Saurorictus*, and another one by the large, multiple-tooth-rowed moradisaurines (Fig. 5). The latter, however, are only known from Russia and the northern part of Africa, so that it appears that only the smaller taxa migrated farther south. It should be noted that another multiple-tooth-rowed captorhinid has been described from the Late Permian of Zambia

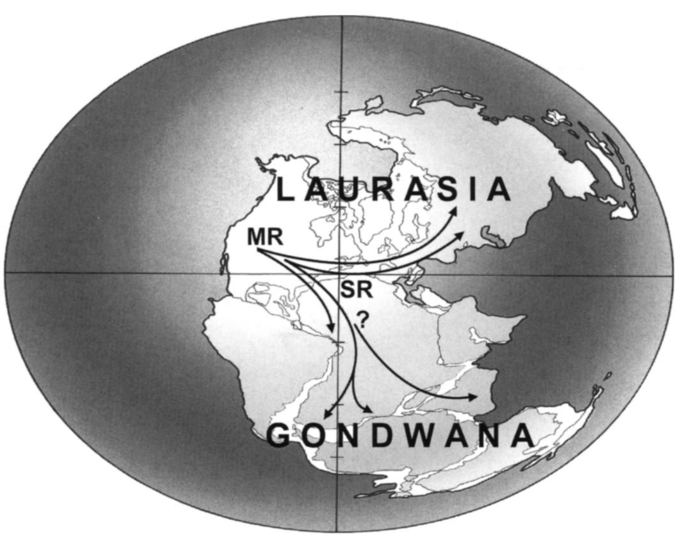

FIGURE 5. The proposed biogeographic pattern of the Captorhinidae. **Abbreviations**: **SR**, single tooth-rowed taxa; **MR**, multiple tooth-rowed taxa.

(Gow, 2000), and was assigned to the genus *Captorhinus*. However, the material is poorly preserved, and new findings are necessary to evaluate if this was either another Gondwanan invasion of captorhinids or if those specimens belong to one of the two radiations mentioned above. The same might be true for an unnamed captorhinid from India (Kutty, 1972).

ACKNOWLEDGMENTS

We thank Drs. C. Cunningham, H.-P. Schultze, and J. A. Boy, Ms. A. Shinya, K. Folinsbee, and D. Scott for their assistance during various phases of this project. JM and RR were financially supported by the Deutsche Forschungsgemeinschaft (MU 1760/2-1), and NSERC Canada, respectively.

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APPENDIX 1

Character list for the phylogenetic analysis of captorhinids. Character definitions marked with an asterisk are new. All characters are treated as unordered.

(1) Premaxilla: ventral margin aligned antero-posteriorly (0) or antero-ventrally (1) in lateral view.
(2) Maxilla: relatively straight (0) or posterior end flexed laterally (1).
(3) Maxilla: posteriormost tooth positioned at level of posterior margin of orbit (0) or positioned more anteriorly (1). (Character definition modified.)
(4) Lacrimal: suture with jugal small (0) or well developed (1).
(5) Snout: broad, equal to or greater than 35% of skull length (0) or narrow, equal to or less than 25% of skull length (1).
(6) Prefrontal: anterior process short and tall, approximately equal to posterodorsal process in antero-posterior length (0) or long and narrow, approximately twice antero-posterior length of posterodorsal process (1).
(7) Frontal: anterior process short, less than 40% of frontal sagittal length (0) or long, approximately 55% of frontal sagittal length (1).
(8) Jugal: alary process absent (0), present and positioned no higher than midpoint of suborbital process of jugal and distinct from orbital margin (1), or positioned dorsally on medial surface of jugal and flush with orbital margin (2).
(9) Quadratojugal: antero-posteriorly elongate (0) or short, not extending anteriorly beyond midpoint of postorbital margin (1).
(10) Quadratojugal: acuminate (0) or square-tipped (1) anteriorly.
(11) Postorbital cheek: relatively straight (0) or expanded laterally (1).
(12) Supratemporal: contact with postparietal tenuous or absent (0) or well developed (1). (Character definition modified.)
(13) Pineal foramen: positioned at (0) or anterior to (1) midpoint of interparietal suture.

(14) Postparietal: contacting mate fully along height (0) or dorsally only, postparietals separated slightly ventrally by supraoccipital (1).

(15) Postparietal: transversely short with tabular present (0) or transversely elongate with tabular absent (1).

(16) Skull table occipital margin: embayed bilaterally (0), straight (1), or with single median embayment (2).

(17) Ectopterygoid: present (0) or absent (1).

(18) Pterygoid: transverse flange broad-based and distinctly angular (0) or narrow and tongue-like (1) in ventral view.

(19) Parasphenoid: deep ventral groove absent (0) or present (1) between cristae ventrolateralis.

(20) Cultriform process: extending anteriorly (0), extending slightly dorsally at roughly 15 degrees to basal plane (1), or extending anterodorsally at more than 45 degrees to basal plane (2).

(21) Supraoccipital: sloping anterodorsally (0), or vertically or rather posterodorsally (1). (Character definition modified.)

(22) Supraoccipital: lateral ascending processes accounting for half or less (0) or two-thirds or more (1) of height of the bone.

(23) Occipital condyle: at level of (0) or immediately anterior to (1) quadrate condyles.

(24) Paroccipital process: short (0) or rod-like (1).

(25) Sculpturing: consisting of small honeycombing pits and grooves (0) or of pits and grooves with notably larger, randomly positioned pits on posterior skull table (1).

(26) Mandibular ramus: relatively straight (0) or sigmoidal (1) in ventral view.

(27) Mandibular ramus: narrow, 8% or less of total jaw length (0) or broad, no less than 14% of total jaw length (1).

(28) Mandibular ramus: posterior end rectilinear (0) or acuminate (1) in lateral view.

(29) Mandibular ramus: lateral shelf absent (0) or present (1) below coronoid process.

(30) Coronoid: anterior process short (0) or elongate (1).

(31) Meckelian foramen: small, antero-posterior length roughly 9% or less of total jaw length (0) or large, antero-posterior length greater than or equal to 14% of total jaw length (1).

(32) Coronoid posterodorsal process: slender, forming dorsal-most quarter of lateral wall of adductor fossa (0) or deep, forming dorsal-most third of lateral wall of adductor fossa (1).

(33) Retroarticular process: absent (0), present and broader transversely than long (1), or present and longer antero-posteriorly than broad (2).

(34) Maxillary dentition: tooth stations numbering 30 or more (0) or 25 or fewer (1); for multiple-rowed taxa, only those teeth with unobstructed profiles when viewed laterally are considered.

(35) Maxillary caniniform teeth: present (0) or absent (1).

(36) Multiple tooth rows: absent (0) or present (1).

(37) Marginal dentition: "cheek" teeth conical (0) or chisel-shaped (1).

(38) Dentary: teeth isodont (0), caniniform region present anteriorly (1), or caniniform tooth present anteriorly with caniniform region absent (2).

(39) Dentary: first tooth oriented mainly vertically (0) or leaning strongly anteriorly (1).

(40) Antorbital area: mainly formed by lacrimal and prefrontal (0) or mostly by lacrimal due to strong dorsal expansion of the bone (1).*

(41) Orientation of supratemporal: obliquely oriented into anteromedial direction, thereby lying within facet of parietal (0) or positioned mediolaterally at posterior edge of parietal (1).*

(42) Parasphenoid: with (0) or without (1) teeth.*

(43) Vomer: with (0) or without (1) teeth.*

(44) Palatine: with (0) or without (1) teeth.*

(45) Parietal: not strongly projecting between postfrontal and postorbital (0) or distinct anterolateral process partially separating postfrontal and postorbital from each other (1).*

(46) Stapes: distal process short (0) or elongate (1).*

(47) Supratemporal: large (0) or small (1).*

(48) Posterolateral corner of skull roof: mainly formed by supratemporal (0) or by parietal (1).*

(49) Squamosal contribution to posttemporal fenestra: absent (0), present (1).*

APPENDIX II

Character-taxon matrix used for phylogenetic analysis.

Caseidae
1000000000 0010?00000 0001000001 000110?000 000000000

Millerettidae
0010000011 0000020000 000000000 0011100000 000010000

Protorothyris
0000000000 0?00000000 0?00000000 0000000000 010010111

Romeria texana
110?010?10 001010?000 0?0??0000? ??01000100 0?1011111

Protocaptorhinus
1101000110 001111?000 000100000? ??11000?00 1???01111

Rhiodenticulatus
1101010101 0011111000 ?00??00001 ???1000101 ?1?111111

C. laticeps
1111000201 1011121111 0000000101 0021001110 111011111

C. aguti
1111000201 1011121111 0000000101 0021011110 111011111

Labidosaurus
1111111101 1111121112 1111111111 1111101200 1???01111

Labidosaurikos
1111111101 1111121112 1111111110 1111111200 111101111

Concordia
001101000? 0010101000 000000000? ??01000001 000010111

Paleothyris
0000010000 0000000000 000000000? ??00000000 001000111

Petrolacosaurus
000110000? 000000011? 0001000001 0000000000 000010111

Saurorictus
?111000?01 0?011????? 0???00???? ???1000100 ????0??11