BIOLOGY 622 – FALL 2014
BASAL AMNIOTA - STRUCTURE AND PHYLOGENY

WEEK – 4
REPTILIA AND BASAL EUPRETILIA

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INTRODUCTION

To acquire an appreciation of the significance of the term "Reptilia", it is worth a bit of historical perspective.

Reptilia was originally erected as a class by Laurenti in 1768 to accept all tetrapods that were neither birds nor mammals.

Owen (1854, 1859) therefore included amphibians in the group.

Haekel (1866) recognized the reproductive similarity of Reptiles, birds, and mammals – amniotes, and thus removed extant amphibians from the Reptilia.

One of the better known of vertebrate paleontologists to have worked on the problem of the origin of reptiles was Robert Carroll. Most of his initial work was done outside of the cladistics paradigm, and became something of a self-fulfilling prophecy of animals being more and more primitive as ancestors.

In the late 1960s Carroll's work nonetheless held sway, and to his credit, he did have a number of the proper groups in play:

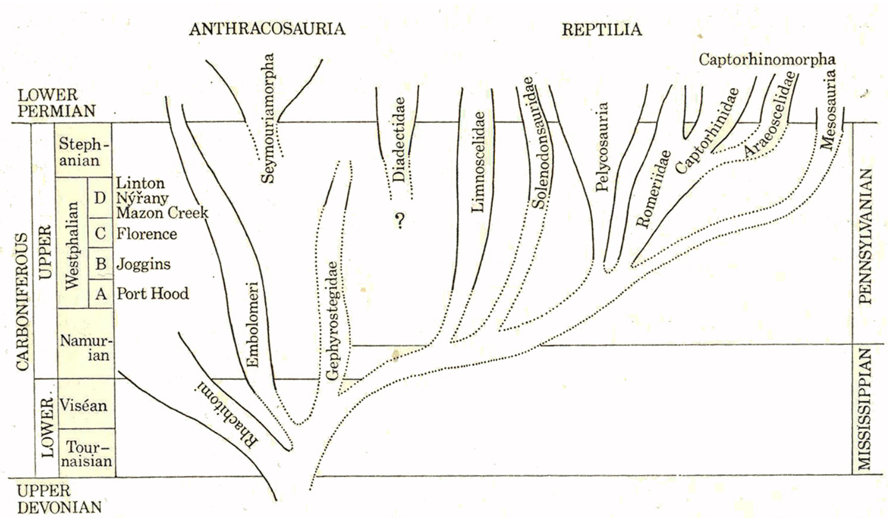


FIGURE 20. Phylogeny of Paleozoic reptiles and anthracosaurs. Relative age of pertinent fossil localities and geological subdivisions indicated.

Early workers had no problem with a paraphyletic Reptilia, and so basal synapsids (“pelycosaurs”) were included as well. But this essentially became a “search for ancestors” as opposed to a search for origins, so those ancestors went farther and farther back, and became less and less reptilian.

Carroll suggested that all other amniotes could be derived from a primitive family of reptiles he dubbed the family Romeriidae. The basis of this family was the genus *Romeria*, based on two species found in north-central Texas – *Romeria prima*, and *R. texensis*. (For our purposes, we will consider them together, just referring to *Romeria*. The family also included a number of other small, insectivorous, lizard-sized/shaped taxa that Carroll suggested demonstrated the generalized condition expected of primitive reptiles, and amniotes in general. They included taxa such as *Paleothyris*, *Protorothyris*, and others – taxa we will return to next week.

From the Romeriidae Carroll derived the Captorhinidae, the Pelycosauria, and all other groups of basal amniotes.

Now remember, Carroll was working in an environment that had not yet adopted cladistics. Willi Hennig had already proposed the concept in Germany, but the only people who had adopted the strategy at this point were entomologists. To give credit where credit is due, note that in Carroll’s scenario, most of the major players are in place, even if their exact placement is not what we accept today:

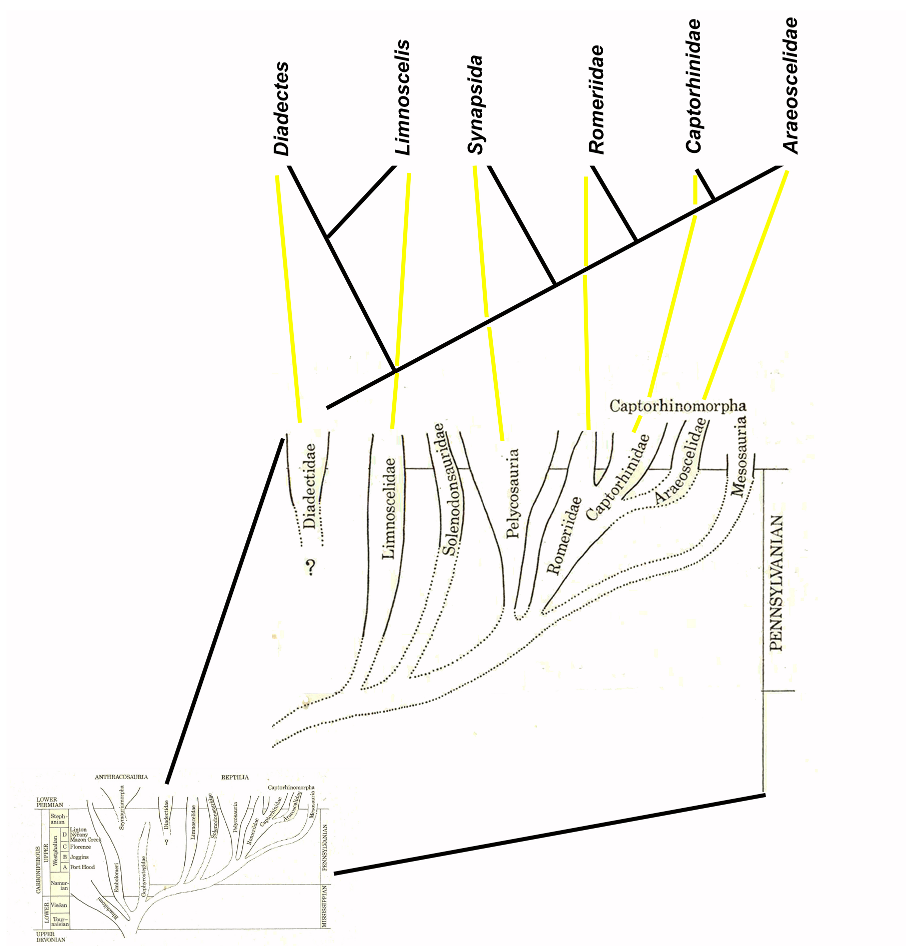


FIGURE 20. Phylogeny of Paleozoic reptiles and anthracosaurs. Relative age of pertinent fossil localities and geological subdivisions indicated.

In the mid to later 1970s. careful cladistics work showed that in fact *Romeria* was more closely related to Captorhnidae than – well – other romeriids. Heaton (1979) ultimately removed *Romeria* from the Romeriidae, placing it as a primitive member of Captorhinidae. This left us with the problematic situation of a family without its patronym namesake. Technically, you can't name a group after a taxon that is a member of another group. So the taxon name "Romeriidae" was invalidated.

This left the group to be renamed. Carroll grudgingly called it the "Protothyridae".

But technically it is supposed to be called the PROTOROTHYRIDIDAE. (Which is the term we'll use.)

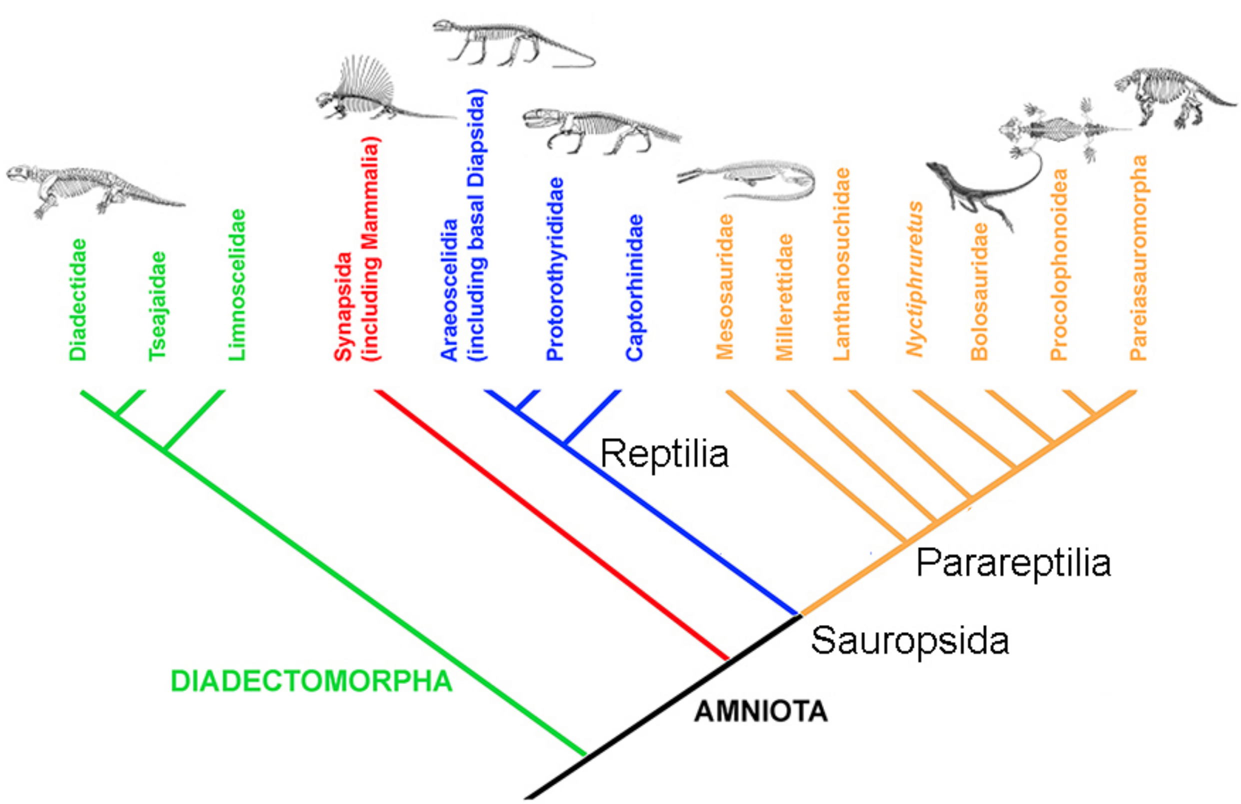
More recent workers have:

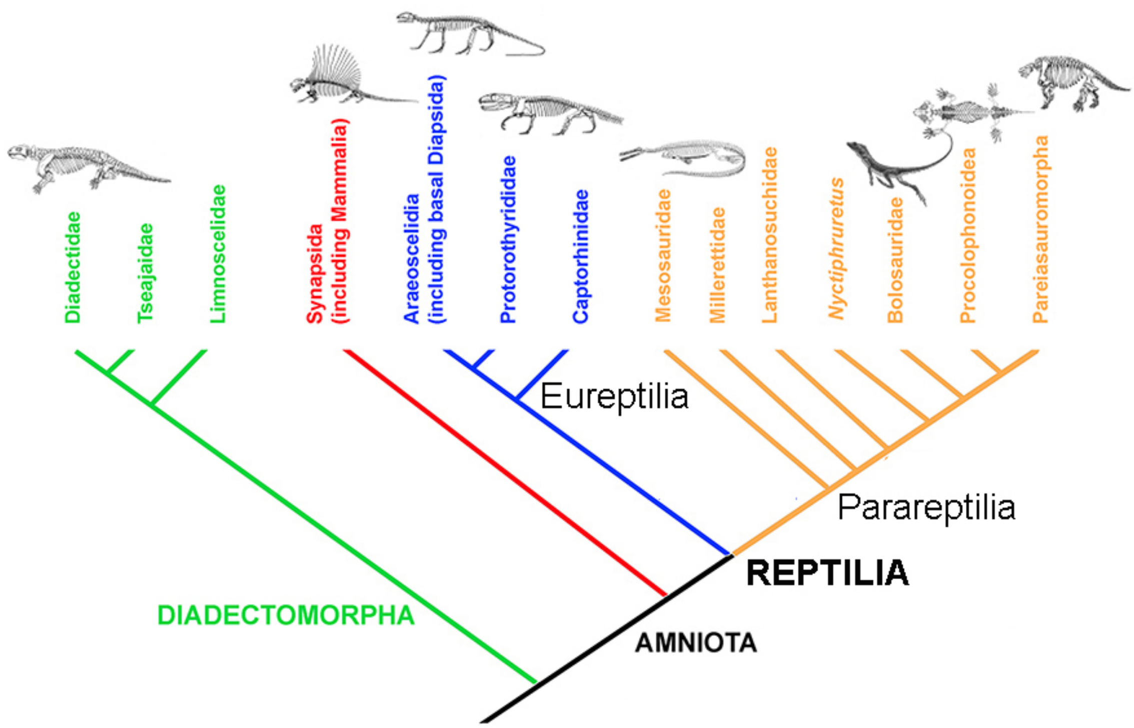
Began to employ the rules of cladidstics / phylogenetic systematics wherein groups are determined by unique features, and the interrelationships of groups determined by shared, derived features.

Recognized the fundamental distinction between Synapsida, and other amniotes, began to recognize that a group distinct from Synapsida needed recognition. This group included living and extinct taxa traditionally considered reptiles.

But, just because the cladograms (i.e phylogenetic trees) are the product of newly rigorous methodology, it doesn't mean every hypothesis of relationships has been identical.

In one case, all non-synapsid amniotes have been referred to as reptiles, and in others as "Sauropsids". Note the following alternative designations:

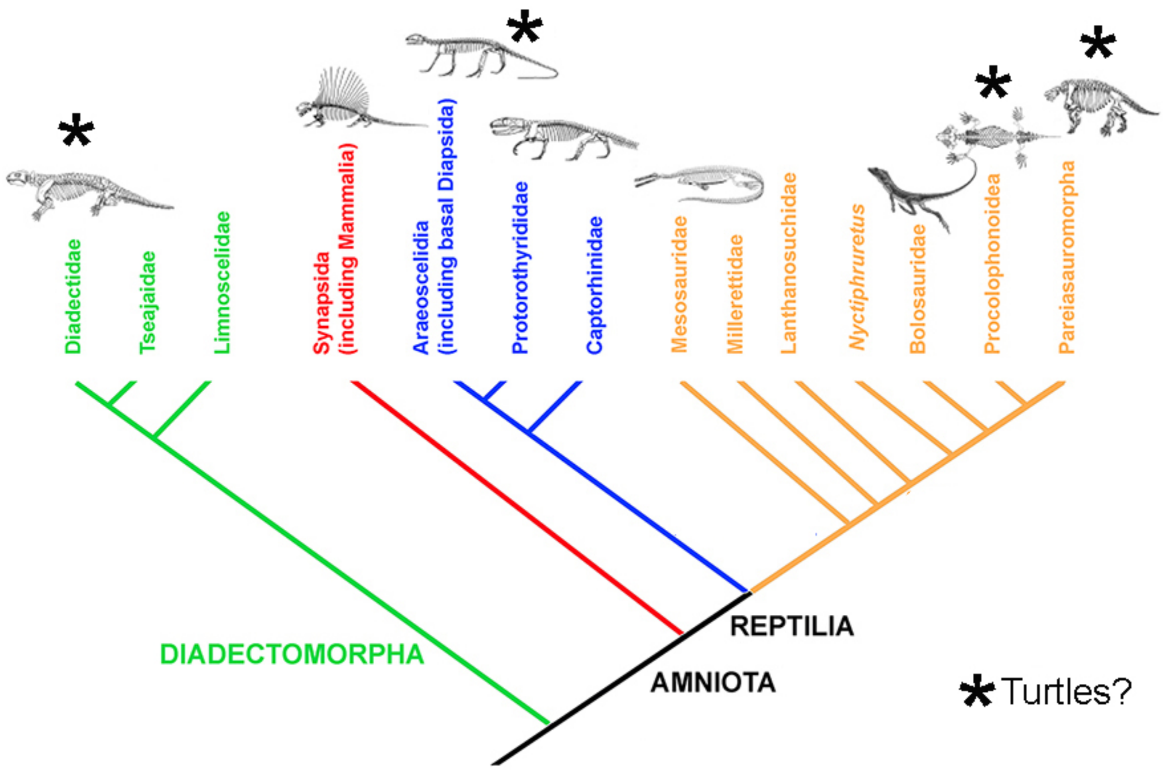




THE VARIETY OF GROUPS HYPOTHESIZED TO HAVE GIVEN RISE TO TURTLES

Most workers have recognized that extant reptiles, including crocodilomorphs, squamates, and turtles must be included in a grouping that would be considered reptilian, but the frequently contentious placement of turtles over the years resulted in some impressive phylogenetic gymnastics as they were considered to be related to any number of different groups. These have included diadectomorphs, pareiasaurs, procolophonids, and even diapsids.

This demonstrates the issue of crown-based versus node-based taxon definitions. Because turtles are amniotes, using a crown-based strategy means whatever group to which they belong must also be part of crown-group Amniota. Note the implications of amniote definitions if they wound up being closely related to, or part of, Diadectomorpha. If turtles were proven part of Diadectomorpha, then Diadectomorpha would be part of crown-group Amniota. If not, then we would have to argue for a node-based definition of Amniota if we wanted to include them.



The taxonomic scheme we have adopted for this course includes both traditionally defined "true" reptiles and parareptiles as members of the Reptilia. For our purposes Reptilia is divided into two great groups, the Eureptilia (or "true reptiles"), and the Parareptilia.

Subsequent work has made it clear that the protorothyridids are not necessarily primitive by virtue of their small size and insectivorous nature. In fact close relatives like basal synapsids and all diadectomorphs are rather robust to say the least.

So, it seems to make sense that members of the family Captorhinidae are the basal-most member of Reptilia, and the Protorothyrididae are more closely related to the similarly gracile Araeoscelidia. We will hear about those groups next week.

REPTILIA

Eureptilia
(Family) Captorhinidae
Romeriida
“Protorothyrididae”
Araeoscelidia (including Diapsida)

Parareptilia
Mesosauria
Milleritidae
Lanthanosuchidae
Nyctiphruretus
Bolosauridae
Procolophonoidea
Pareiasauromorpha

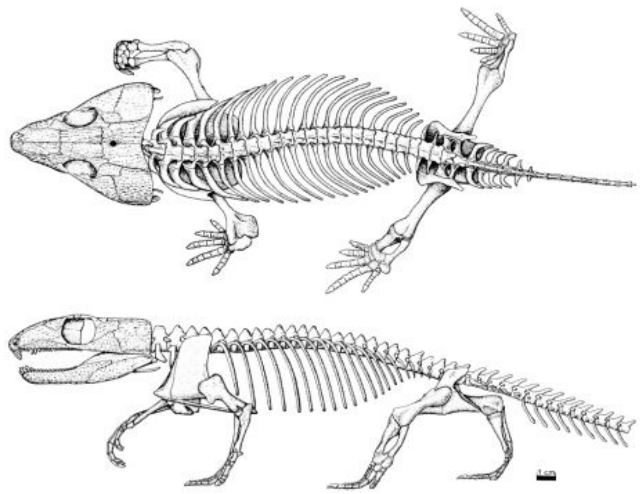
Features that define true reptiles and - the reptilian subset that retains extant reptiles – will be discussed today.

CHARACTERISTICS OF REPTILIA AND EUREPTILIA

Previously, anatomical features used to “define” reptiles used to be simply those we used to define amniotes in general. However, with the recognition that Synasida and Reptilia represent distinct lineages of Amniota, we must now come up with a new set of synapomorphies to define Reptilia as a subset of Amniota.

The family Captorhinidae is amongst the basal-most of all reptilian clades, so it is logical to choose a member of this family to demonstrate features of both Reptilia as well as Eureptilia. The well-known genus *Captorhinus* will be a model. (We will return to it in the review of diversity and distribution of this important family.) Here we will use the reconstructions done by Heaton (1979).

Captorhinus (next page left) was a small to moderate sized reptile, approximately the size of the local southern Californian “chuckwalla” (*Sauromalus obesus*) (next page right).



REPTILIA

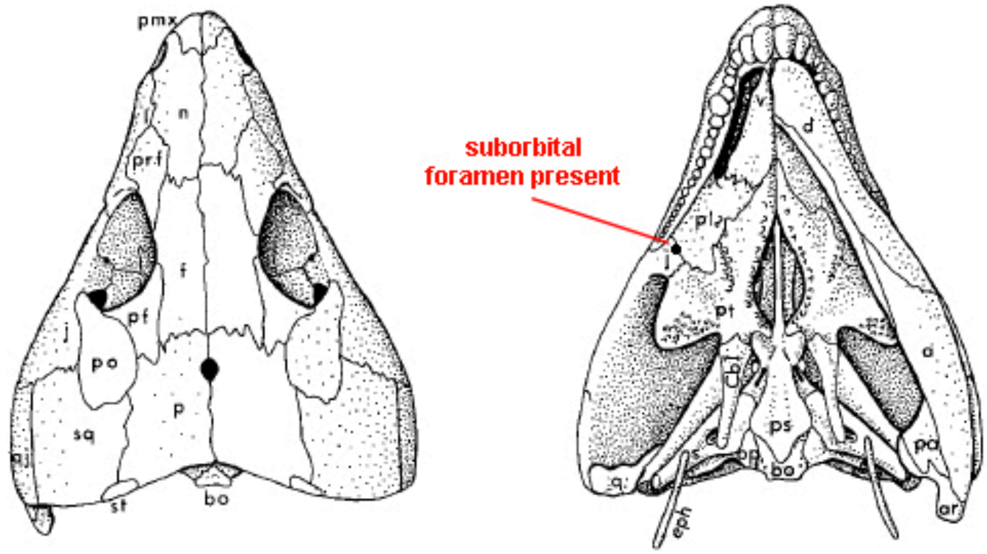
Reptiles and parareptiles together comprise the complete Reptilia. These two groups offer a moderately high degree of diversity in body sizes and shapes; thus the features that characterize the group tend to be size-independent characters.

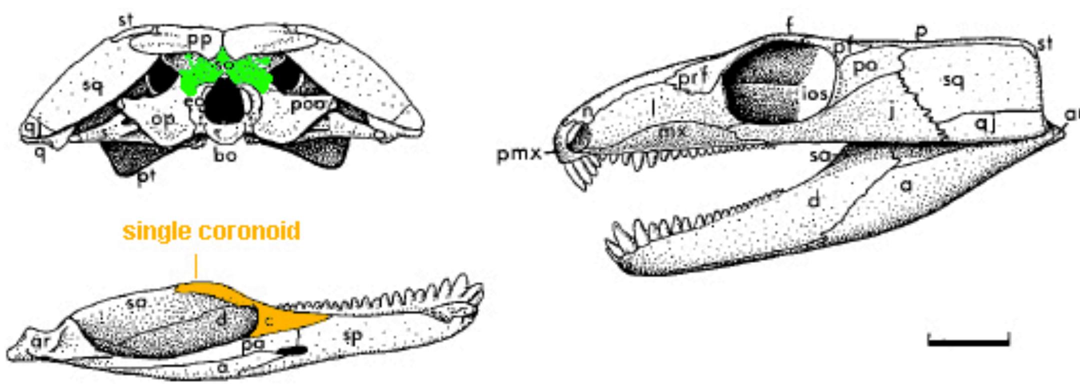
It has been suggested that the following features are synapomorphies of Reptilia:

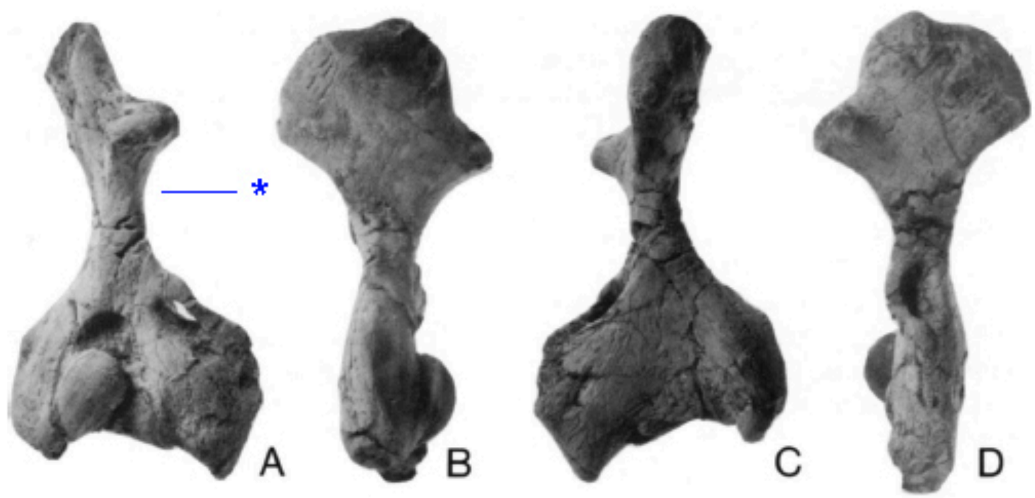
1. Presence of a single coronoid. (Synapsids and diadectomorphs have two coronoid elements.)
2. Supinator process parallel to humeral shaft and separated from it by a groove.
3. Presence of a single pedal centrale. (Two centralia were present in the tarsus (ankle) of synapsids and diadectomorphs.)
4. Tabular small. (The tabular is missing in captorhinids.)
5. Suborbital foramen present. The suborbital foramen is a small hole near the lateral edge of the palate, between the pterygoid, palatine, and ectopterygoid (or jugal, when the ectopterygoid is absent).
6. Supraoccipital anterior crista present. (The supraoccipital of reptiles has a paired anterior parasagittal flange called an anterior crista.)
7. Supraoccipital plate narrow.

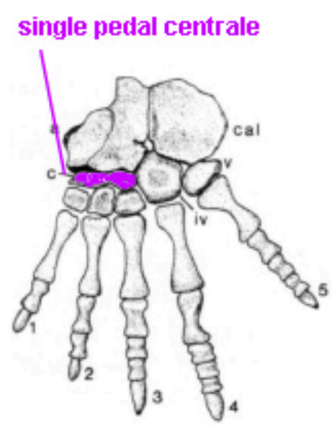
In the image following:

- The skull is from *Captorhinus* (Heaton, 1979).
- The photos of humeri are from *Labidosaurus* , a larger member of the family (Sumida, 1989).
- The illustration of the foot is also from *Labidosaurus* (Sumida, 1989).









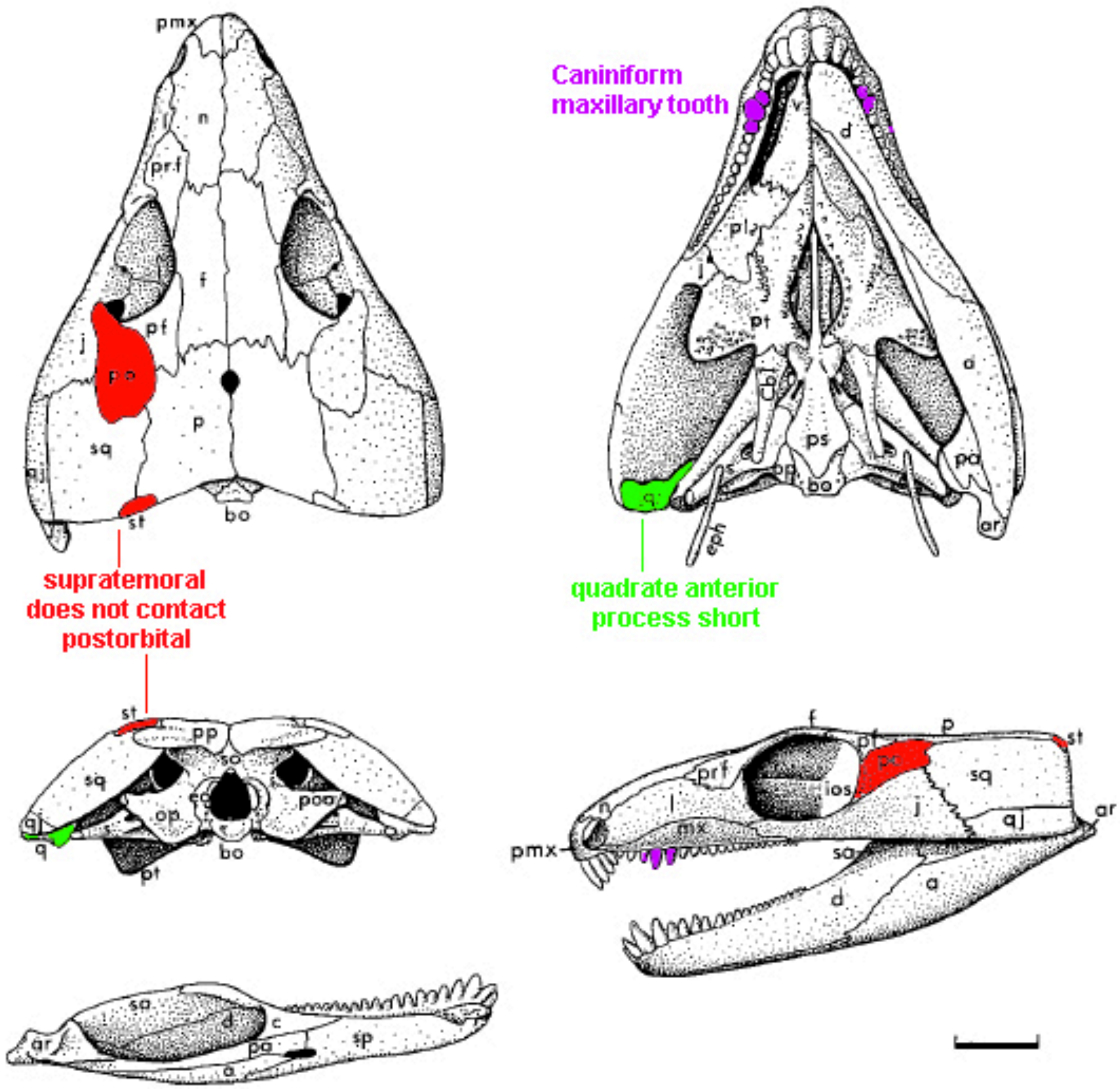
1 cm

*supinator process not perpendicular to humeral shaft

EUREPTILIA

Whereas the taxon Reptilia is characterized by cranial characters exclusively, Eureptilia is characterized by a mixture of cranial and postcranial features. These include:

1. Supratemporal small. (The supratemporal is large in most other groups of amniotes.)
2. Supratemporal does not contact the postorbital.
3. Caniniform maxillary tooth present. (Most other early amniotes have a relatively homodont dentition and no anterior maxillary tooth is much larger than the other teeth.)
4. Quadrate anterior process short. (The anterior process of the quadrate extends anteriorly along more than 55% of the quadrate ramus of the pterygoid in most other amniotes.)
5. Ventrolateral constriction of vertebral centra. (Vertebral central are "hourglass" shaped.)
6. Narrow blade of the ilium. See below on this page.


Caniniform
maxillary tooth
supratemoral
does not contact
postorbital
quadrate anterior
process short
pmx
n
prf
f
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qj
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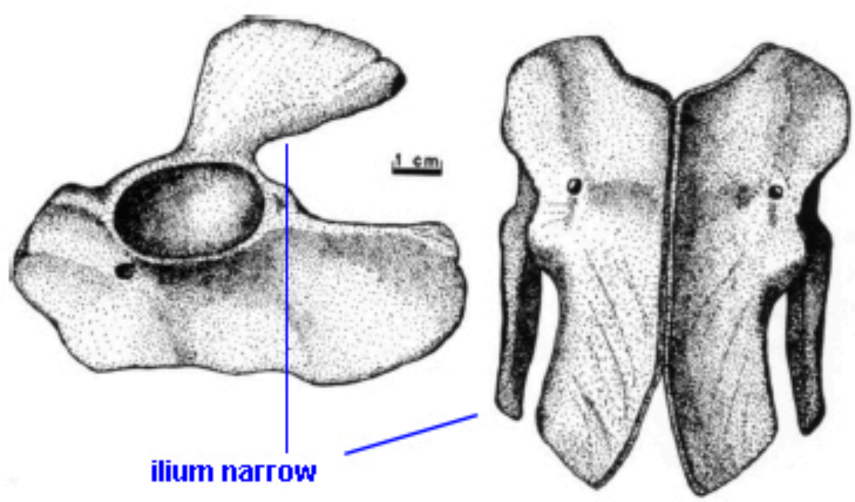
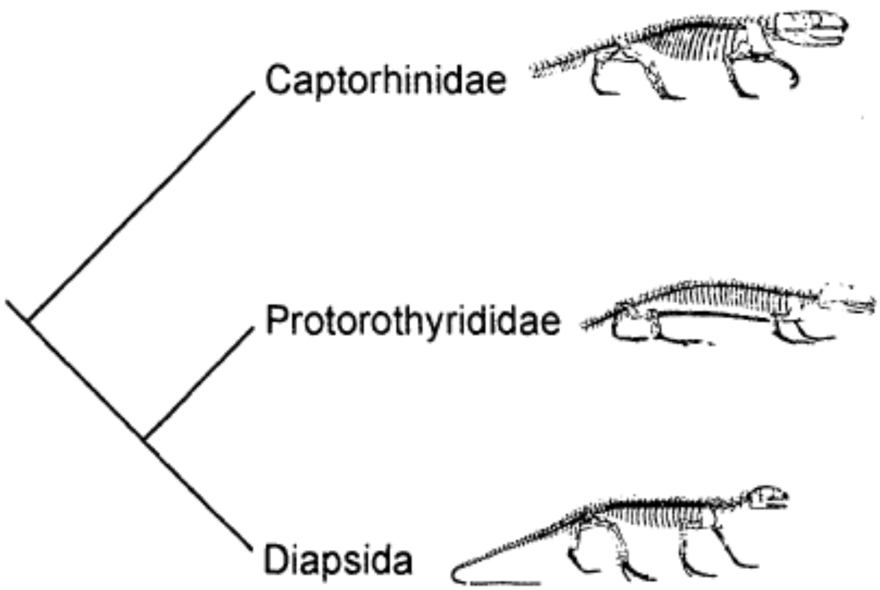

1 cm
ilium narrow

FAMILY CAPTORHINIDAE

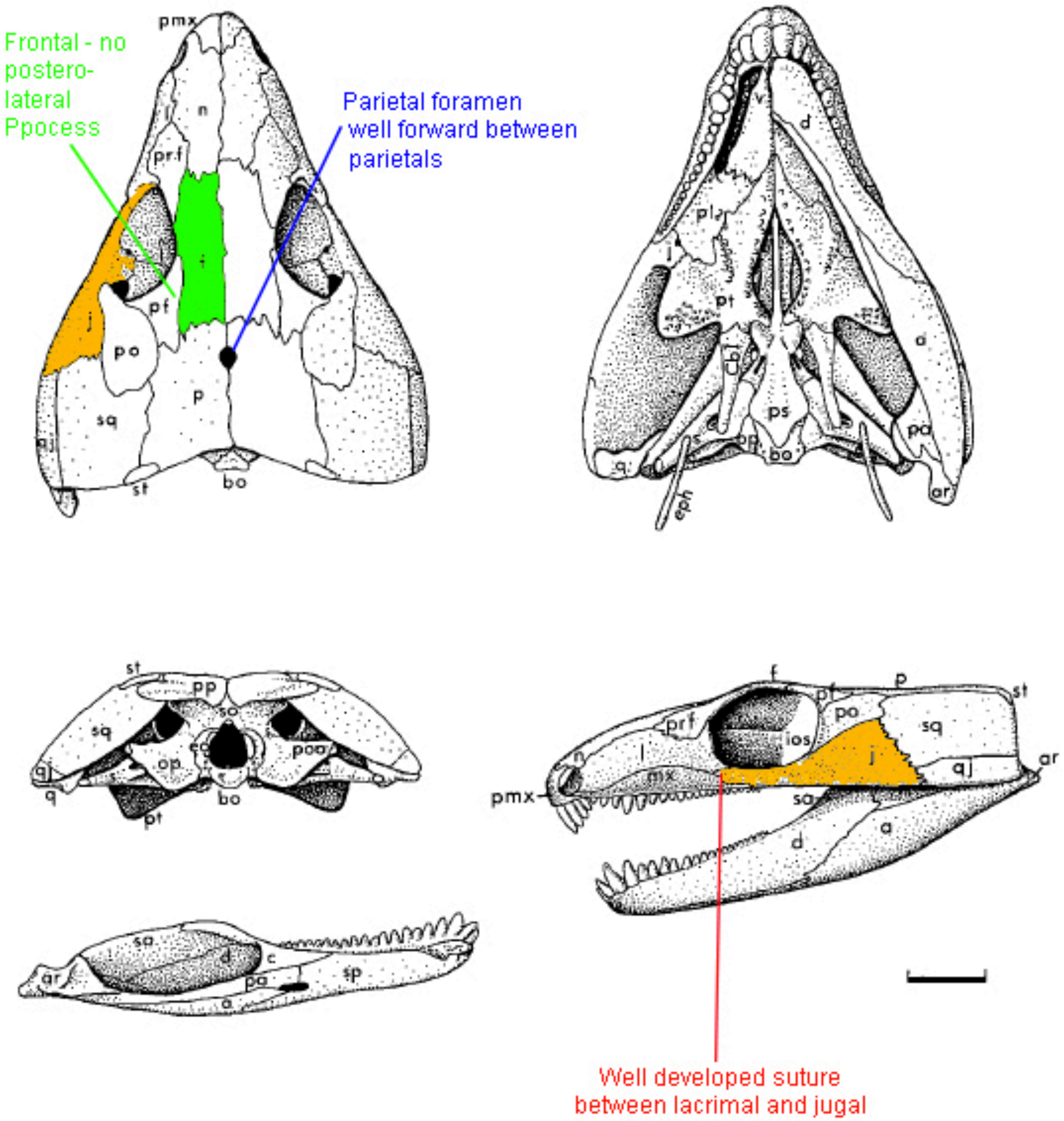
It was long thought that the smallest, generalized members of Amniota also represented the model of a primitive reptile. Robert Carroll championed this idea, referring to the group s the “Protorothyridae”. However, more recent work has suggested that these animals, properly named Protorothyrididae, are most closely related to basal Diapsida, leaving Captorhinidae as the most basal of Eureptilia:



The reptilian family Captorhinidae was long characterized as a generalized group that was very conservative in nature. However recent discoveries have indicated that it is in fact a globally distributed family with a wide temporal distribution – from Late Pennsylvanian to Late Permian.

Morphologically, the features unique to, and defining of, the Captorhinidae are the following [somewhat esoteric] skeletal features:

1. a well developed suture between lacrimal and jugal
2. the pineal foramen is place relatively far forward between the parietals
3. absence of posterolateral frontal processes
4. the jugal extends anteriorly/rostrally beyond the anterior orbital margin



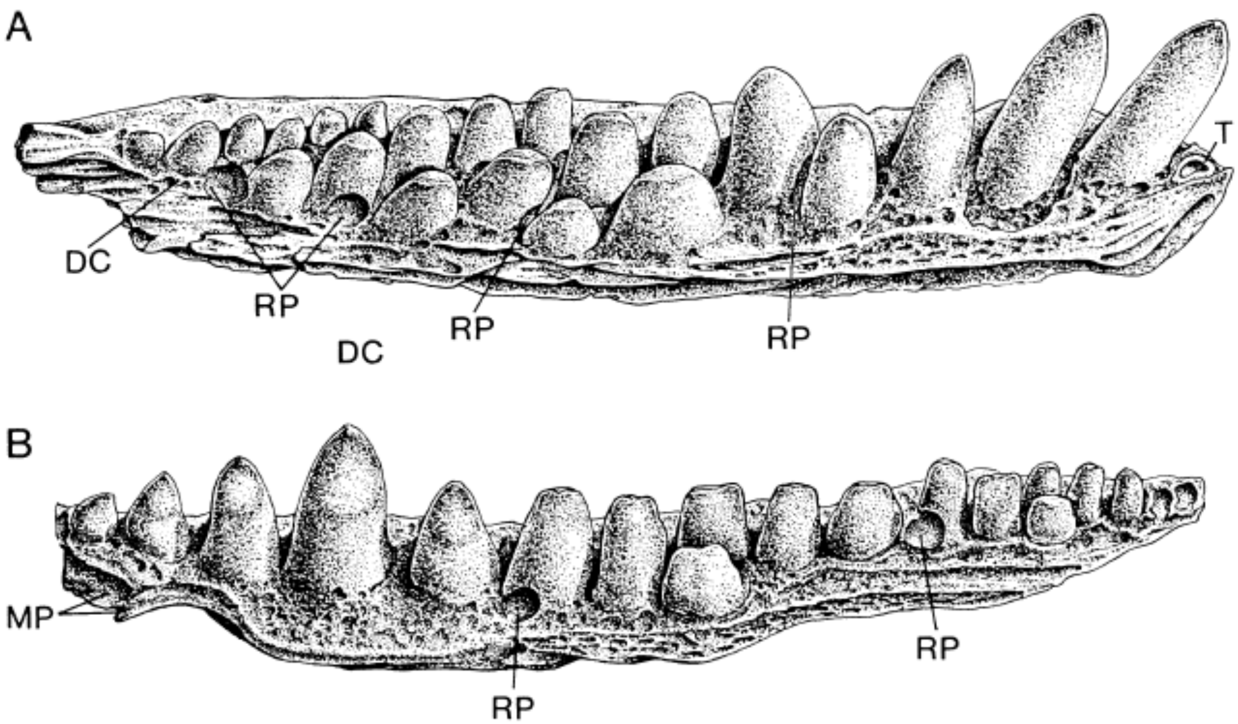
The basal eureptilian family Captorhinidae was long characterized as a fairly conservative, generalized family that didn't change much through time. The one exception to this has been the development of multiple tooth rows in some members of the family. It is a feature for which the family is perhaps best known, however because it is not present in all members, it can't be a defining feature of the family.

Initial work on this feature by well know workers such as Everett Olson and Armand de Ricqlés proposed that captorhinids with single maxillary and dentary tooth rows were more primitive (and usually smaller), whereas multiple tooth rows tended to be fond in later (i.e. younger, more recent), larger, more advanced taxa.

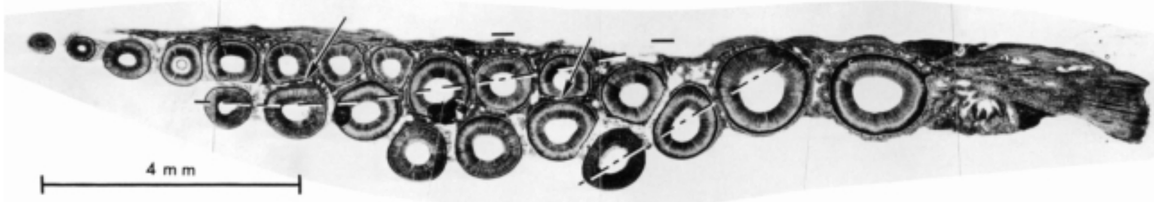
Examples of a captorhinid with single maxillary and dentary tooth rows may be seen in the examples of *Captorhinus* that are being used to illustrate the features of Reptilia, Eureptilia, and Captorhinidae above.

However work by Modesto and colleagues and our lab over the past ten years now suggests that the family is a model of multiple instances of parallel evolution. Multiple tooth rows may have evolved as many as three times in the family and large size is found in a least two different lineages of the family as well.

Following is a closeup of an isolated left dentary and maxilla of *Captorhinus*. Note the multiple tooth row that run at approximately angles to the long axis of the element.



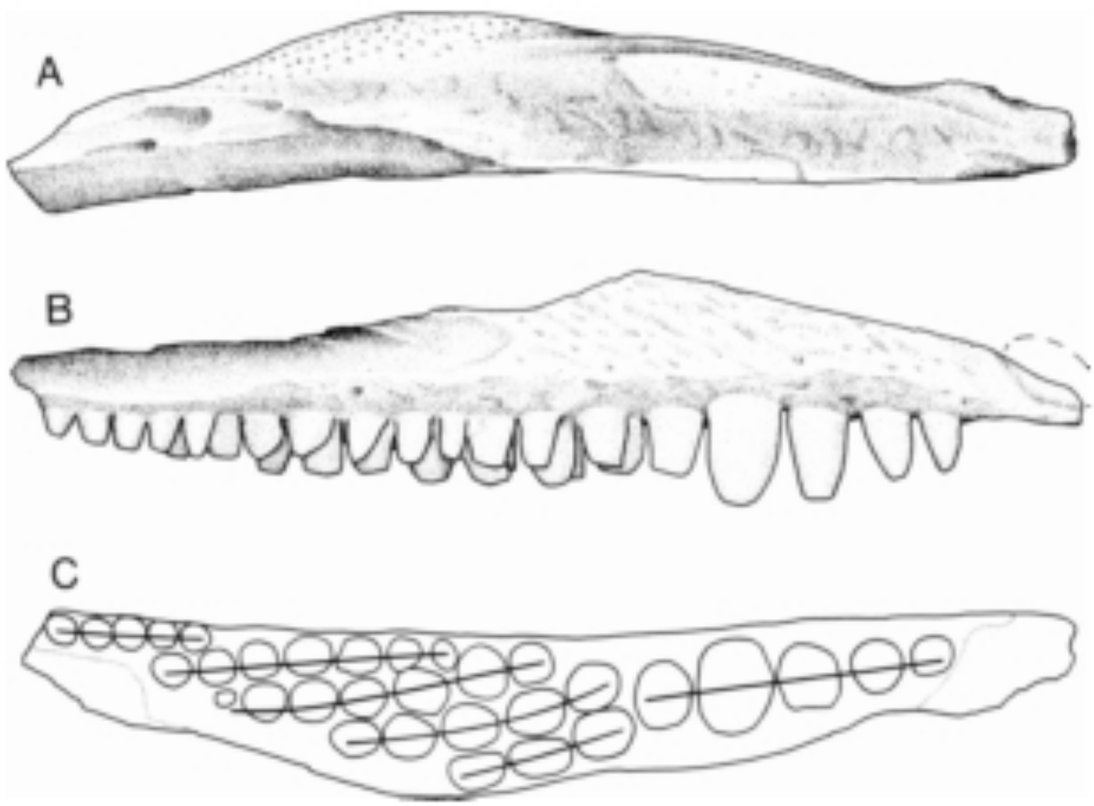
Next is a histological section of a *Captorhinus* jaw, demonstrating clearly the lines of teeth knows as Zahnreihen.

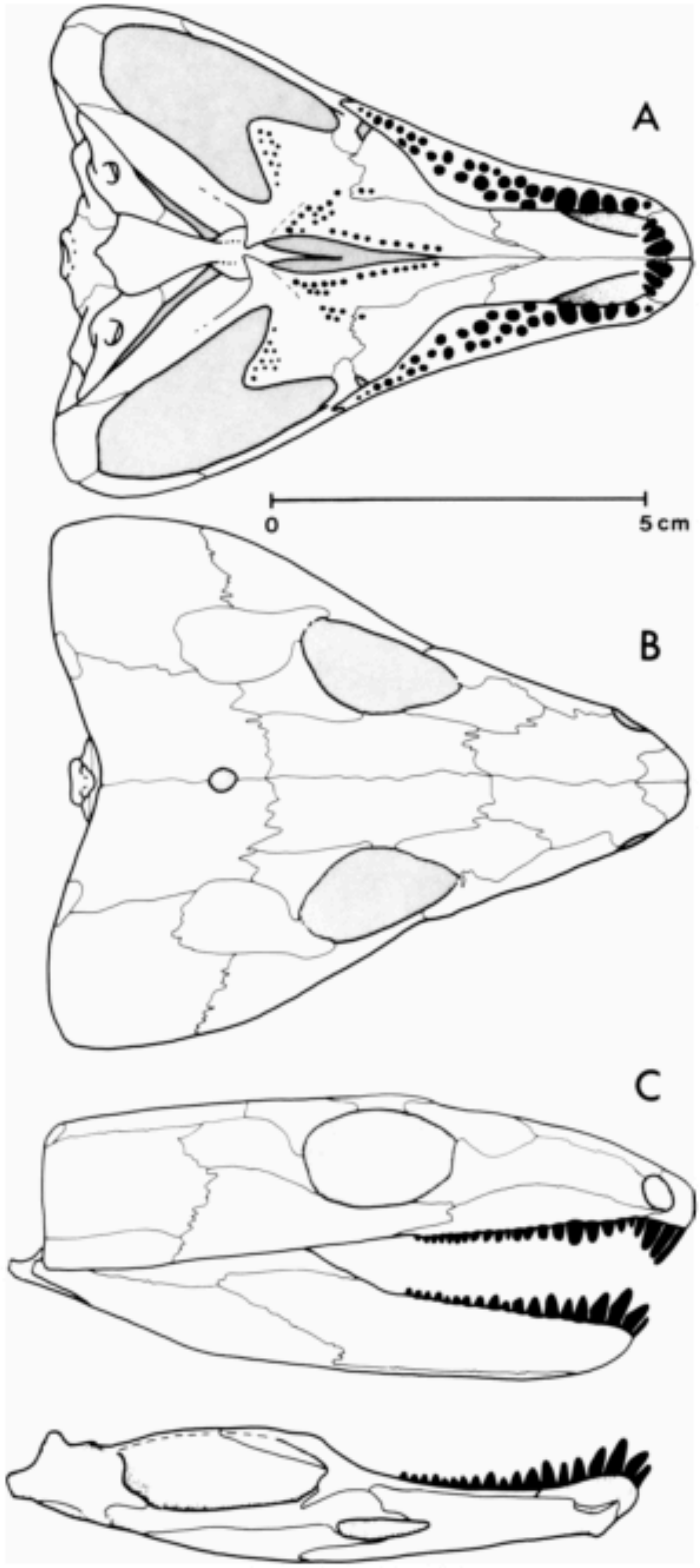


Zahnreihen is a German-derived word that refers to the theory that throughout the life of animals that have constantly replacing teeth:

- Impulses pass along the jaws from front-to-back at regular invervals, stimulating the development of teeth at each successive tooth locus.
- Bolt and DeMar (1975) and Ricqlés and Bolt (1983) hypothesized that there were multiple Zahnreihen in the jaws of reptiles like *Captorhinus*.

In the illustration below, you can see them interpreting as many as five to six waves or Zahnreihen in *Captorhinus*.



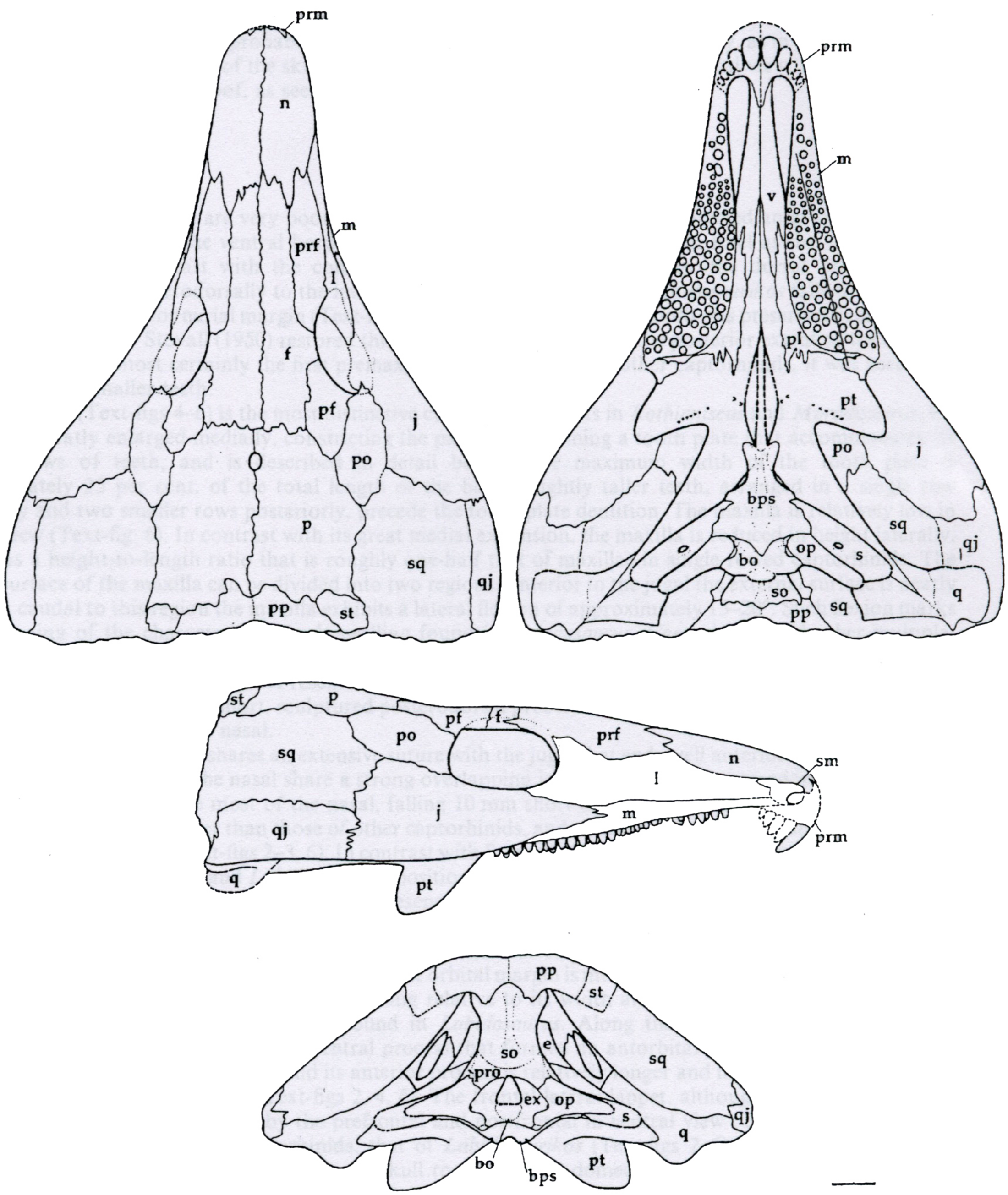


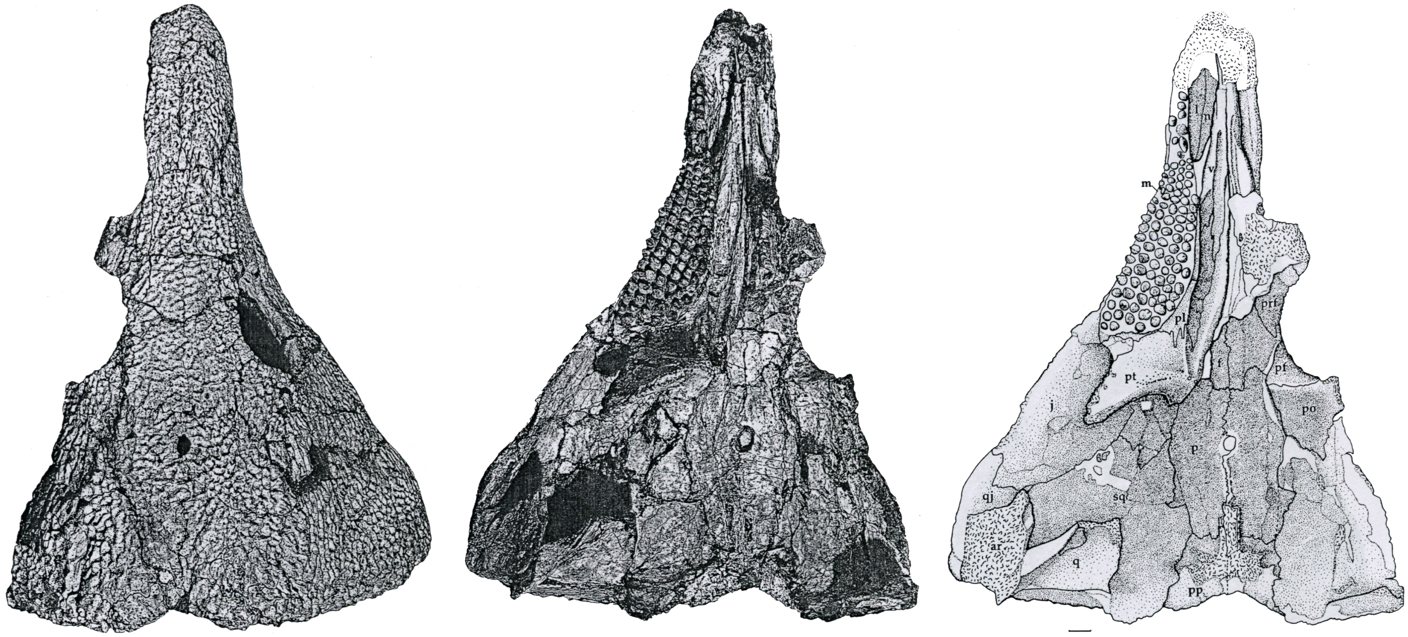
Captorhinus is moderately small member of the family.

Captorhinid Subfamily
MORADISAURINAE

Much larger, more derived members of the family have been united into the subfamily Moradisaurinae. Moradisaurinae is defined as larger captorhinid reptiles with multiple rows of maxillary and dentary teeth with the rows arranged in parallel with one another. Some taxa have as many as seven rows of teeth on each side.

Following are illustrations of the moradisaurine captorhinid *Labidosaurikos* from the Early Permian of Oklahoma to demonstrate the pattern of parallel tooth rows.

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