BIOLOGY 622 – FALL 2014
BASAL AMNIOTA - STRUCTURE AND PHYLOGENY

WEEK – I
INTRODUCTION
ANATOMICAL DEFINITION OF AMNIOTA
DIADECTOMORPHA

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INTRODUCTION

Students in BIOL 622 (2014) are expected to have a thorough understanding of basic vertebrate structure, particularly skeletal structure. If any of the terms used in this course are unfamiliar, you should take immediate note of them and make sure you understand them from your standard vertebrate anatomy texts.

BRIEF OVERVIEW OF BASAL AMNIOTA
DEFINITION, PHYLOGENY, AND STRUCTURE

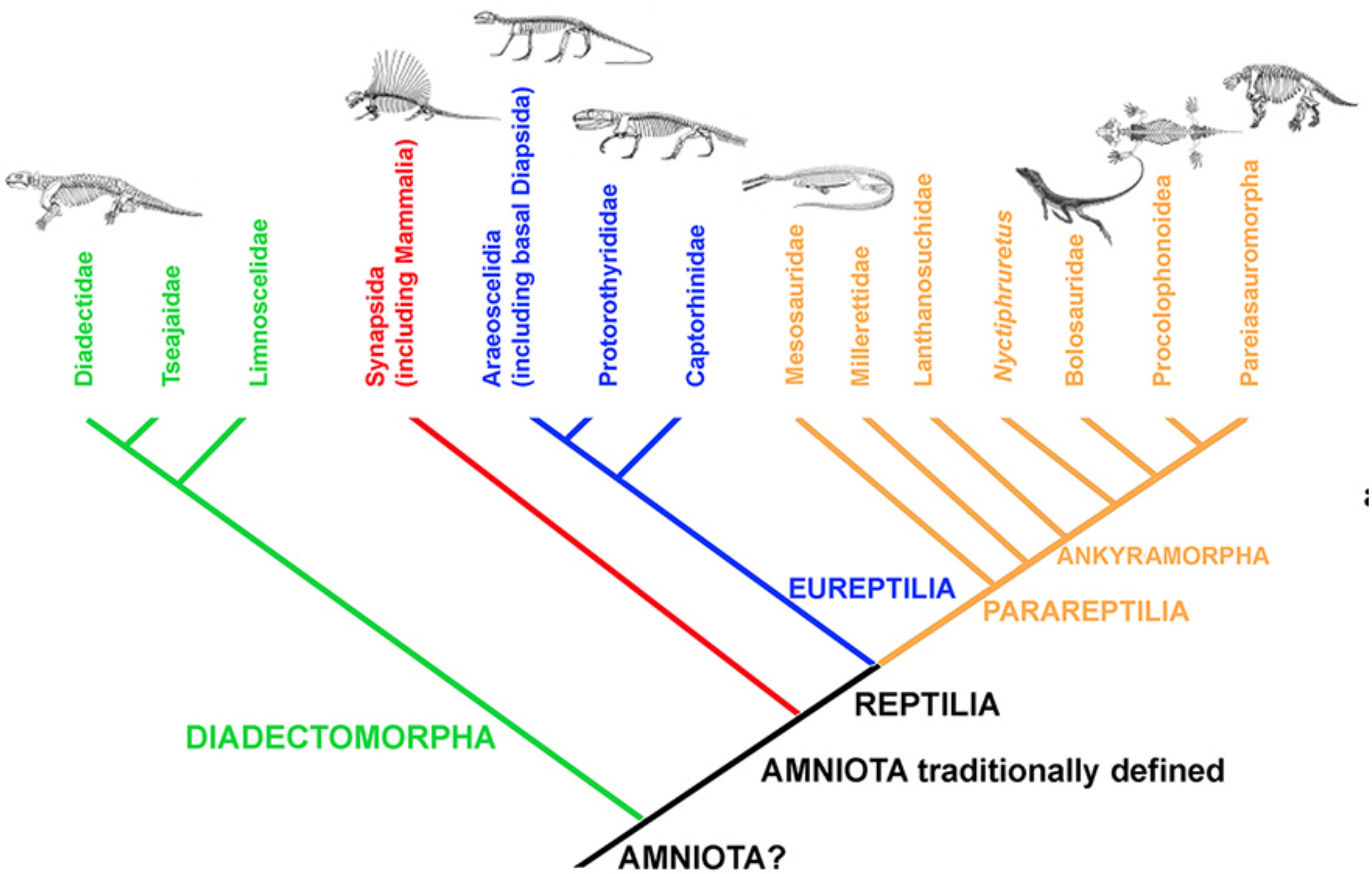
The old-fashioned and out-of-date characterization of Amniota is one that is still unfortunately still clung to in many introductory biology texts. Notably, these texts often have molecular advances in place within a few years (very quick for textbooks), but textbook definitions of Amniota (comprised of extant Reptila, Mammalia, and Aves) are in may cases a third of a century out of date.

"Classic" – i.e. out of date – characterizations of Amniota often go something like this:

    Class Amphibia
Superclass Amniota
    Class Reptilia
    Class Mammalia
    Class Aves

This encourages the misunderstanding that each of these groups is phylogenetically equivalent. In fact, Aves is a subset of Reptilia, having evolved from theropod saurischian dinosaurs. Further, it doesn't reflect the diversity of basal reptiles. This seminar class will not deal with the origin of birds, but will address the two major lineages of Amniota, Reptilia and the lineage that ultimately lead to mammals, the Synapsida. Within Reptilia it will review the diversity of early reptiles, which encapsulates two major reptilian groups: the Eureptilia ("true reptiles") and the lesser known but extremely diverse Parareptilia. Finally, it will also briefly address the relationship of Diadectomorpha to basal Amniota, as the former is minimally a very close (extinct) relative of Amniota, or may actually be amniotes themselves.

This class will use as its scaffolding the most reasonable composite phylogeny that can be compiled using the most recent publications on the interrelationships of basal amniotes. Many of these primary references are listed in your reading for the course. The phylogeny is part of the course homepage, your syllabus and is reproduced here:



SYNAPOMORPHIES OF AMNIOTA

There are dozens of defining features of Amniota. Most are based on extant amniotes, and a crown-group approach to phylogenetic systematics allows the use of embryological characters. Note the following features gathered from numerous references. All characters marked by the symbol * would generally be considered features that cannot be tested in [potentially] fossil amniotes.

Embryological Structures*
- Amnion*
- Chorion*
- Allantois*
- (Chorioallantoic membrane)*

Integumentary system
- Complete loss of lateral line system *
- Waterproof skin*
- Horny Nails
- Claws

Respiratory/Disgestive Systems
- Relatively enlarged lungs*
- Costal (negative pressure) breathing

Nervous System*
- Paired Spinal Accessory (XI) Nerves*
- Paired Hypoglossal (XII) Nerves*

Skeletal System - Axial
- Atlantal pleurocentrum excluded from ventral margin of vertebral column by axial intercentrum
- Alternation of neural spine height in presacral vertebrae
- Two pairs of sacral ribs

Skeletal System - Appendicular
- Screw-shaped glenoid
- Ectepicondyle of humerus well developed.
- Highly developed olecranon process of ulna
- Pisiform (neomorph)
- Only two manual Centralia
- Manual phalangeal formula: 2-3-4-5-3
- Calcaneus (derived from fibulare)
- Astragalus (fused from tibiale, intermedium and proximal central elements.
- Only one pedal central
- Pedal phalangeal formula: 2-3-4-5-4

Skeletal System - Skull
- Loss of intertemporal bone.
- Postparietals on occipital surface of skull
- Ossified spraoccipital
- Post-temporal foramen lateral to supraoccipital

Skeletal System – Lower Jaw
- Single splenial bone of lower jaw

- Single coronoid bone of lower jaw
- Development of retroarticular process

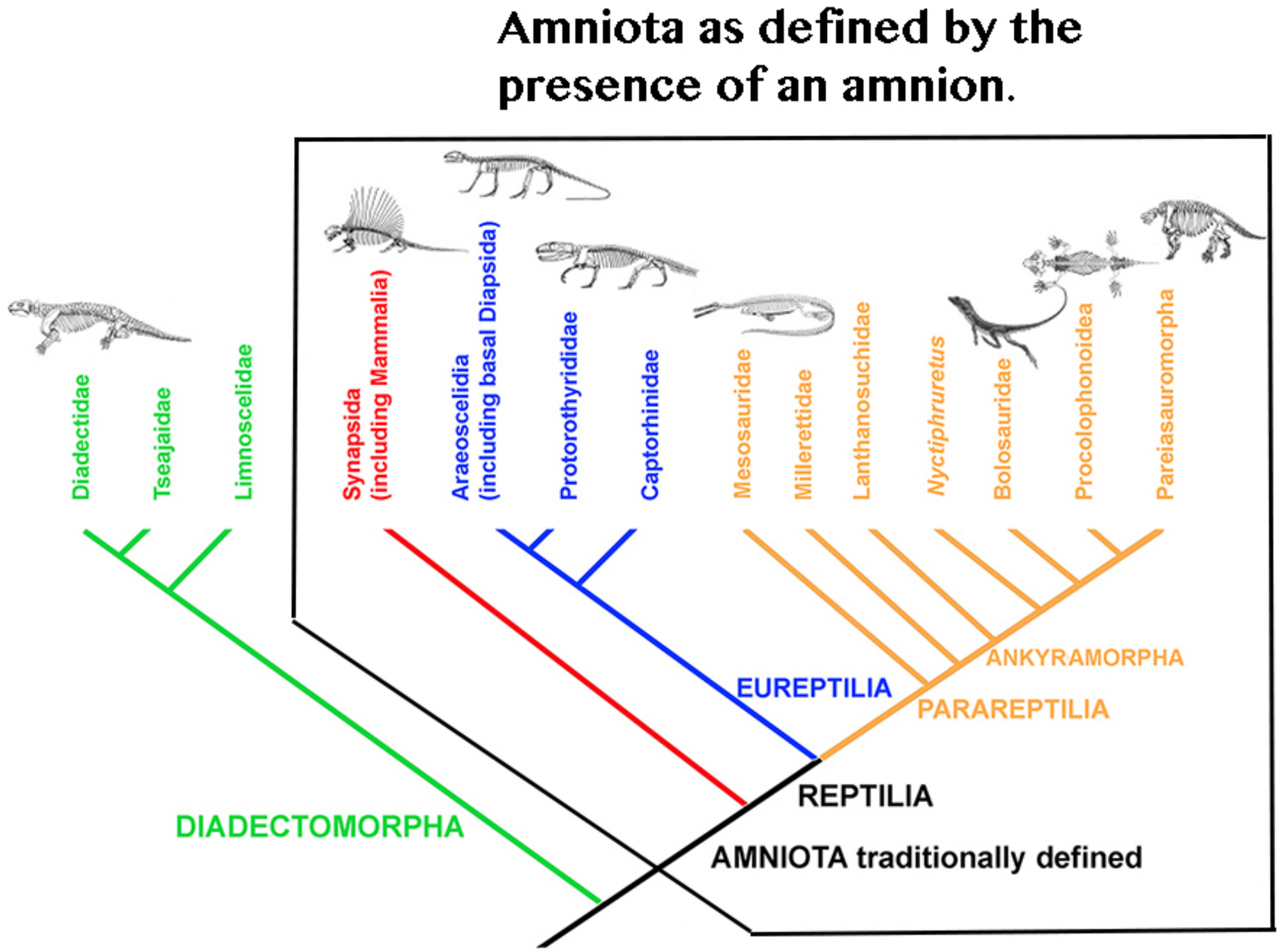
Of course this course is dealing with the fossil animals that are at the base of the amniote radiation, ranging in age from about 300 to 250 million years old. Thus we are restricted to skeletal structures or those that can be inferred from skeletal structures:

1. Horny Nails
2. Claws
3. Costal (negative pressure) breathing
4. Atlantal pleurocentrum excluded from ventral margin of vertebral column by axial intercentrum
5. Alternation of neural spine height in presacral vertebrae
6. Two pairs of sacral ribs
7. Screw-shaped glenoid
8. Ectepicondyle of humerus well developed.
9. Highly developed olecranon process of ulna
10. Pisiform (neomorph)
11. Only two manual Centralia
12. Manual phalangeal formula: 2-3-4-5-3
13. Calcaneus (derived from fibulare)
14. Astragalus (fused from tibiale, intermedium and proximal central elements).
15. Only one pedal central
16. Pedal phalangeal formula: 2-3-4-5-4
17. Loss of intertemporal bone.
18. Postparietals on occipital surface of skull
19. Ossified supraoccipital
20. Post-temporal foramen lateral to supraoccipital
21. Single splenial bone of lower jaw
22. Single coronoid bone of lower jaw
23. Development of retroarticular process

Of course there could be more, but this is a good start. All the taxa at the base of Amniota, [Synapsida + Reptilia] posses these features, and each of the groups we discuss will then have additional features characteristic for themselves.

What then of Diadectomorpha?

Technically, if the possession of an amnion (as well as chorion and allantois) is the fundamental feature of Amniota, then the crown-group definition of Amniota is that taxon that includes all extant taxa that possess an amnion (Reptiles including Aves, and Mammalia) and their most recent common ancestor. This would then mean Amniota as strictly defined includes the common ancestor of Reptilia + Synapsida. Therefore see where that node would be on the phylogeny that is the basis of this class:



DIADECTOMORPHA

But here's the deal. Of the twenty-three skeletal synapomorphies of listed above, Diadectomorpha have all of them with the exception of character #10 , the pisiform. And that is primarily because we do not yet know if it might have been a cartilaginous structure in the group.

IF Amniota is defined on the basis skeletal structures only, Diadectomorpha, Snapsida, and Reptilia become an unresolved trichotomy. Inclusion of embryological features, features for which we have data one way or the other, then Amniota as traditionally defined is distinguished as above.

There is no way to know if diadectomorphs had an amnion or not. What we can say is that even without knowledge of the presence/absence of an amnion, Diadectomorpha is the sistergroup to Amniota *sensu stricto.*

If we use the skeletal features discussed above, then Diadectomorpha might logically be considered as amniotes and it would be inferred that they most likely possessed an amnion. This is known as a "node-based" approach to phylogenetic reconstruction.

Side Note: Following will be an example of the organization of the manner of presentation for all other groups for the remainder of the term:

PART I – Sumida

- Introduction to group discussed
- Synapomorphies, defining features of group. Definition of group. Its place within basal Amniota.

PART II – Presenting class member

- Diversity of group discussed, including major subdivisions of group and review of all genera of that group.
- Biogeography/Geographic Distribution of group (and how that may bear on major subdivisons)
- Temporal Distribution of group (and how that may bear on major subdivisons)

INTRODUCTION TO DIADECTOMORPHA

Diadectomorpha includes three families:

Diadectomorpha
- Family Limnoscelidae
- Family Tseajaiidae
- Family Diadectidae

Limnoscelidae used to have a number of genera assigned to it, but the work of Natalia Wideman revealed that all but one genus was valid. Thus it is known as a monogeneric Family. There are two recognized species of Limnoscelidae: *Limnoscelis paludis*, and *L. dynatis*.

Tseajaiidae is, and has been since its initial description, a monogeneric Family. It is also monospecific, consisting of a single taxon: *Tseajaia campi*.

Diadectidae has had numerous taxa assigned to it over the past century. Everett Olson declared a number of these taxa invalid. Admittedly, many were named prior to the advent of the more rigorous methodology currently demanded by present-day phylogenetic systematics.

SYNAPOMORPHIES OF DIADECTOMORPHA

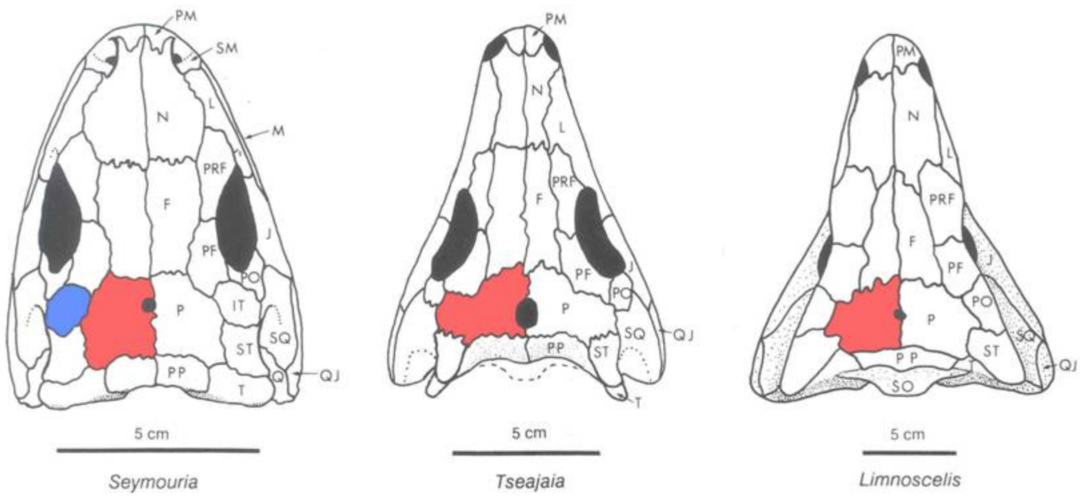
Diadectomorphs possess all of those defining amniote features discussed above, but also have a number of features unique to the group. These include:

- Loss of intertemporal bone with intertemporal becoming incorporated into parietal as a lateral wing of the parietal bone.
- Supraoccipital extending beyond margin of the otic capsule.
- Anteriorly directed processes of atlantal intercentrum and axial intercentrum fit into ventral grooves on basioccipital and atlantal intercentrum respectively.

- Extremely robust adductor crest of ventral surface of the femur.

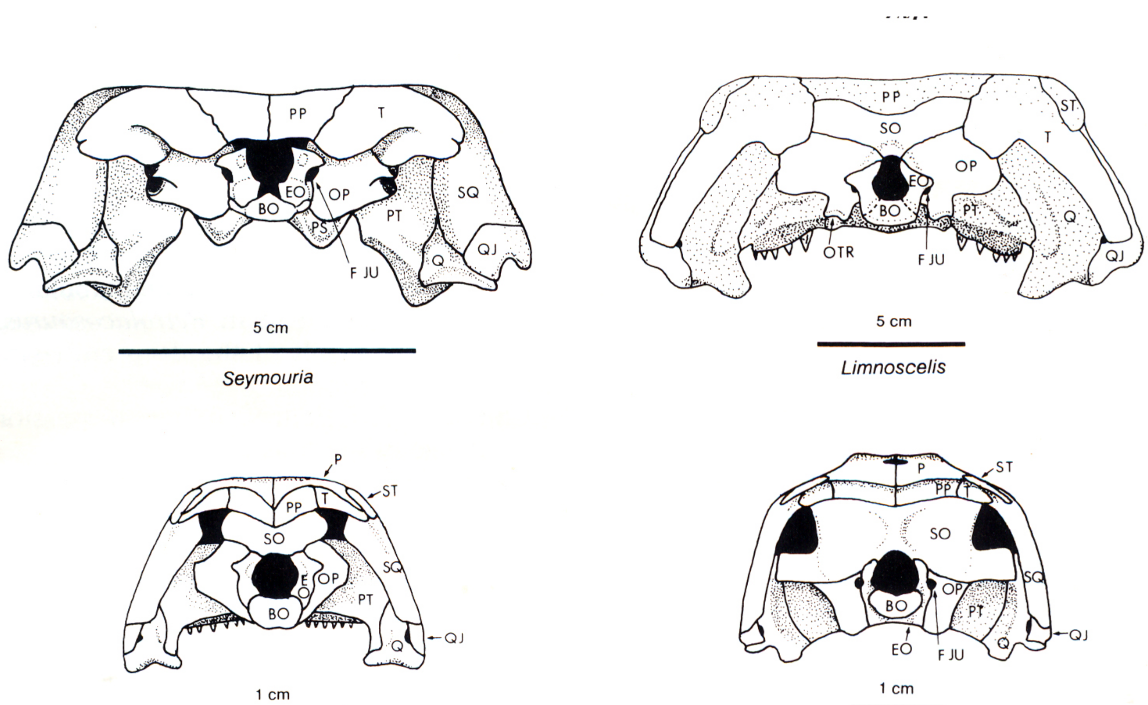
Loss of intertemporal bone with intertemporal becoming incorporated into parietal as a lateral wing of the parietal bone:

Note the presence of an intertemporal bone in the amphibian *Seymouria*, below left. However, note how it is incorporated into the parietal as a lateral flange in the diadectomorphs *Tseajaia* and *Limnoscelis* middle and below right respectively



Supraoccipital extending beyond margin of the otic capsule:

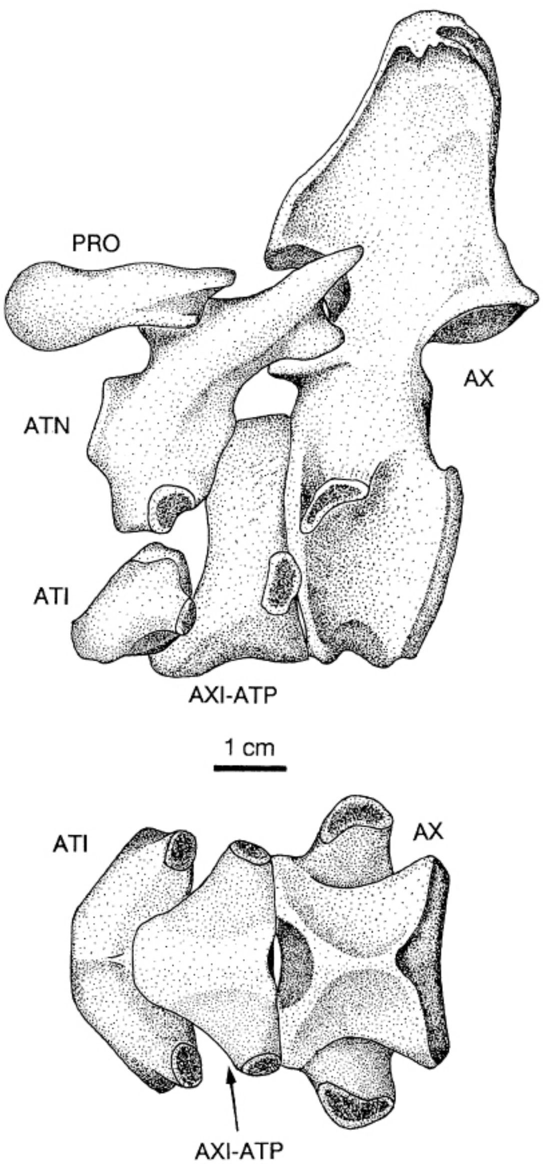
For example below: *Seymouria* is an amphibian with no ossified supraoccipital. Notice how in the diadectomorph limnosclid *Limnoscelis* the wide extent of the suporaoccipital (SO).

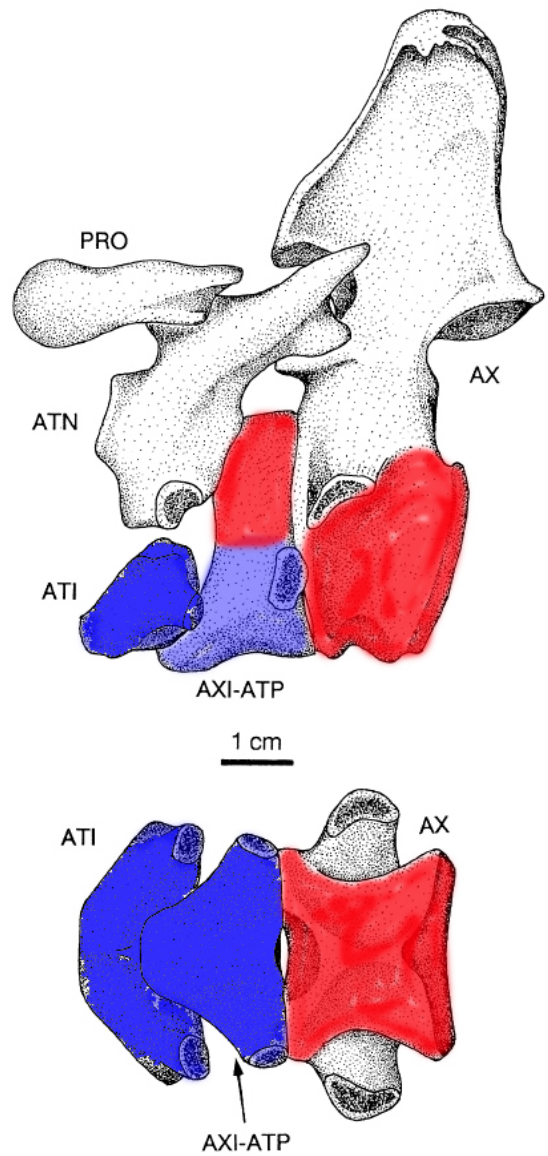


Anteriorly directed processes of atlantal intercentrum and axial intercentrum fit into ventral grooves on basioccipital and atlantal intercentrum respectively:

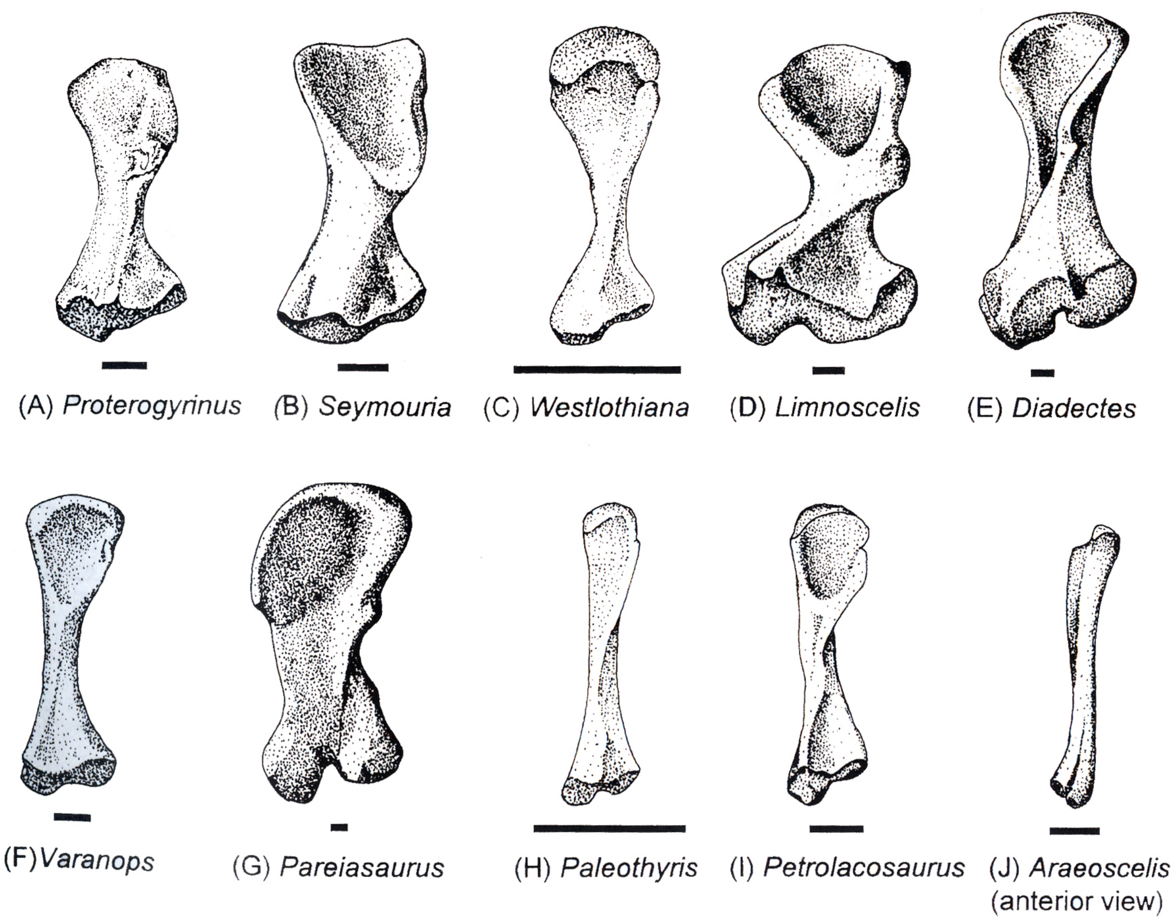
The example below is the diadectomorph diadectid *Diaderctes*. Note:

Atlantal intercentrum is an independent structure.
Right and left atlantal neural arches are independent structures, and do not fuse in the dorsal midline.
The axial intercentrum comes to underlie the atlantal pleurocentrum – excluding the axial pleurocenrum from ventral exposure on the underside of the vertebral column.
A small right and left proatlas provide articulation for the atlantal neural arches with the occipital region of the skull
The axis is very robust, as is the very large neural spine.





Extremely robust adductor crest of ventral surface of the femur: Note how robust in *Limnoscelis* and *Diadectes* below:



DIVERSITY
BIOGEOGRAPHIC AND TEMPORAL DISTRIBUTION OF DIADECTOMORPHA

As mentioned above, Limnoscelidae and Tseajaiidae are monogeneric families. There are two known valid species of *Limnoscelis*, and only one for *Tseajaia*.

If you search on diadecteds, you will find lots of genera. Of them, only a few are well known.

DIADECTOMORPHA

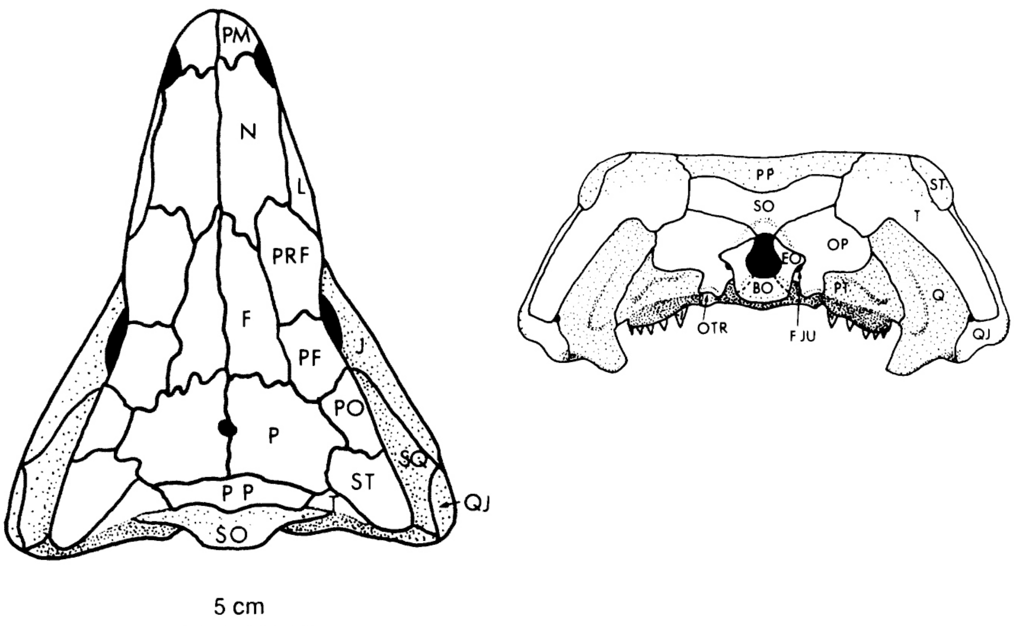
Family Limnoscelidae		
Genus *Limnoscelis*		
	L. paludis	Late Pennsylvanian; north-central New Mexico (southeastern Utah?)
	L. dynatis	Late Pennsylvanian; central Colorado
Family Tseajaiidae		
Genus *Tseajaia*		
	T. campi	Early Permian, southeastern Utah; Late Pennsylvanian/Early Permian north-central New Mexico
Family Diadectidae		
Genus *Ambedus*		
	A. pusillus	Early Permian; central Ohio
Genus *Desmatodon*		
	D. hesperis	Late Pennsylvanian; central Colorado
	D. hollandi	Late Pennsylvanian; Pennsylvania
Genus *Diadectes*		
	D. absitus	Early Permian; central Germany
	D. sanmiguelensis	Early Permian; central Colorado
	D. sideropelicus	Early Permian; Texas, Oklahoma, Ohio(?), southeastern Utah, Pennsylvania
	D. tenuitectes	Early Permian; northcentral Texas
Genus *Diasparactus*		
	D. zenos	Late Pennsylvanian/Early Permian; northern New Mexico
Genus *Orobates*		
	O. pabsti	Early Permian; Thuringia, central Germany
Genus *Phanerosaurus*		
	P. naumanni	Early Permian; Saxony, Germany
Genus *Stephanospondylus*		
	S. pungnax	Early Permian; Saxony, Germany

Of the diadectids, *Ambedus* is known from only a fragmentary dentary and maxilla. *Phanerosaurus* and *Stepahospondylus* are known only from fragmentary vertebral materials from Europe. The specimens have since been lost (probably during World War II).

The generic names "Oradectes" and "Silvadectes" have been proposed by one worker, but he never published his work in a refereed journal and are thus not considered valid taxonomic terms (despite his attempting to place them in Wikipedia).

Limnoscelidae: *Limnoscelis*

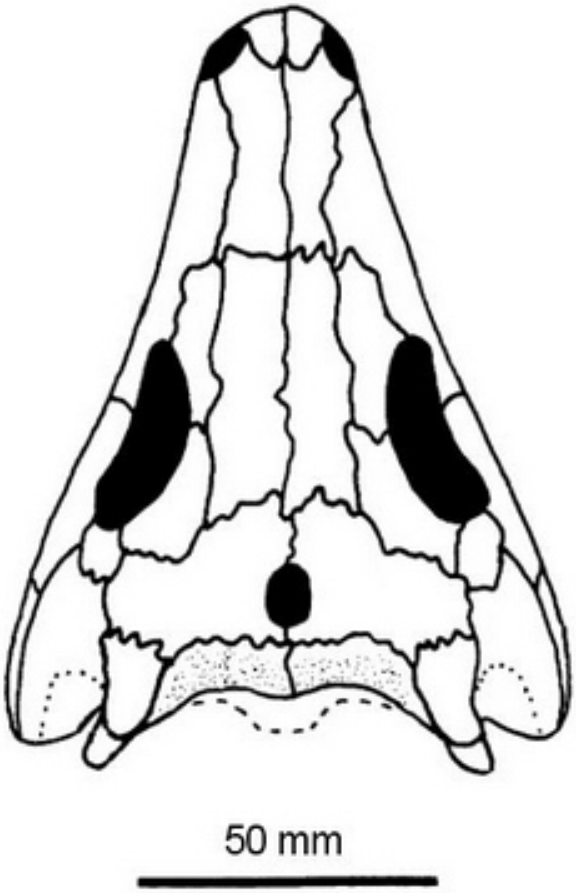
Limnoscelis is known from one complete skeleton from the Late Pennsylvanian north-central New Mexico, and a scattered bunch of elements of [probably] a single individual from the Late Pennsylvanian of central Colorado. It is known by its large caniniform teeth, and almost small alligator like size.

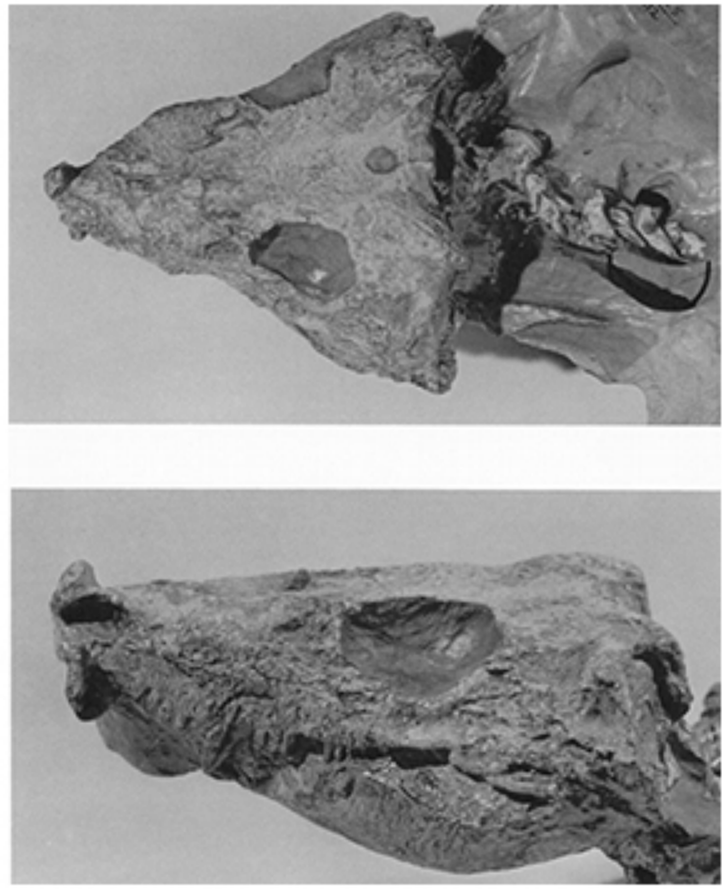


Limnoscelis

Tseajaiidae: *Tseajaia*

Tseajaia is a rare but unique diadectomorph known from the U.S. desert southwest four-corners region. It is known from one complete skeleton and another isolated skull. This has allowed reasonable reconstruction of the skull.

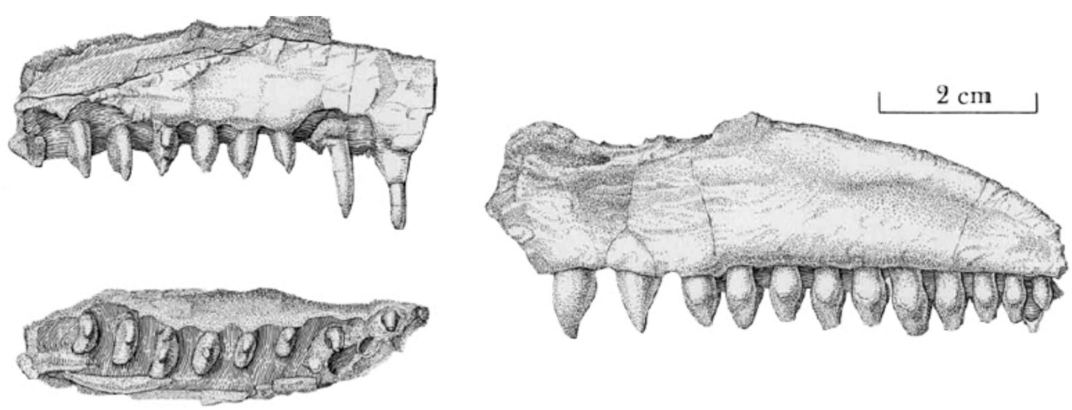




Diadectidae:

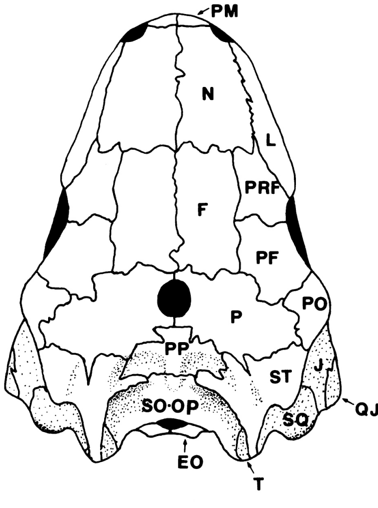
The diadectids are well known for being extremely robust, often very large. Highly terrestrially adapted, and amongst the earliest of high-fiber herbivores.

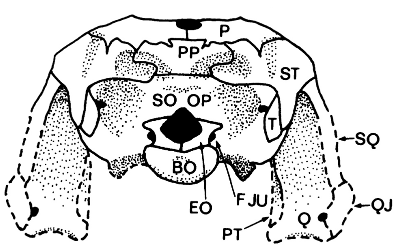
Desmatodon: *Desmatodon* is known from partial material, mostly jaw material. See the isolated maxilla from the Late Pennsylvanian of Colorado below.



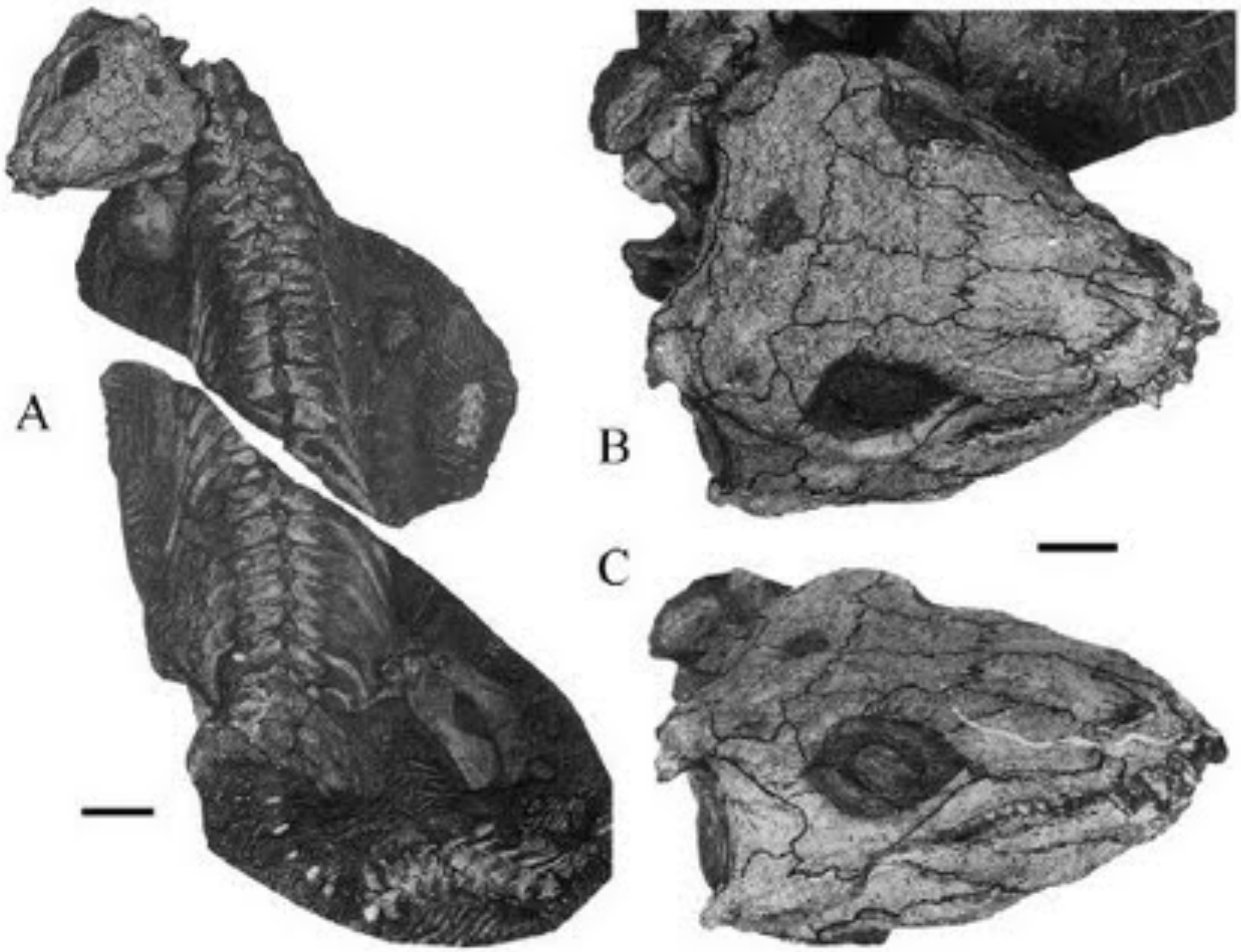
Diasparactus: *Diasparactus* is known only from one partial skeleton, but it has unique vertebral structure with very tall neural spines. The specimen shown below is mostly made of plaster, but the vertebrae and their long spines are actually real.

Diadectes: *Diadectes* is the best known and represented of the diadectids. It is particularly well known for very large specimens from North America, but they generally fuse the skull bones to the point that they are not useful phylogenetically. Juvenile specimens from New Mexico (not fused yet) and mature specimens from German (just plain beautifully preserved) have helped us to determine structure in the diadectids much more clearly.



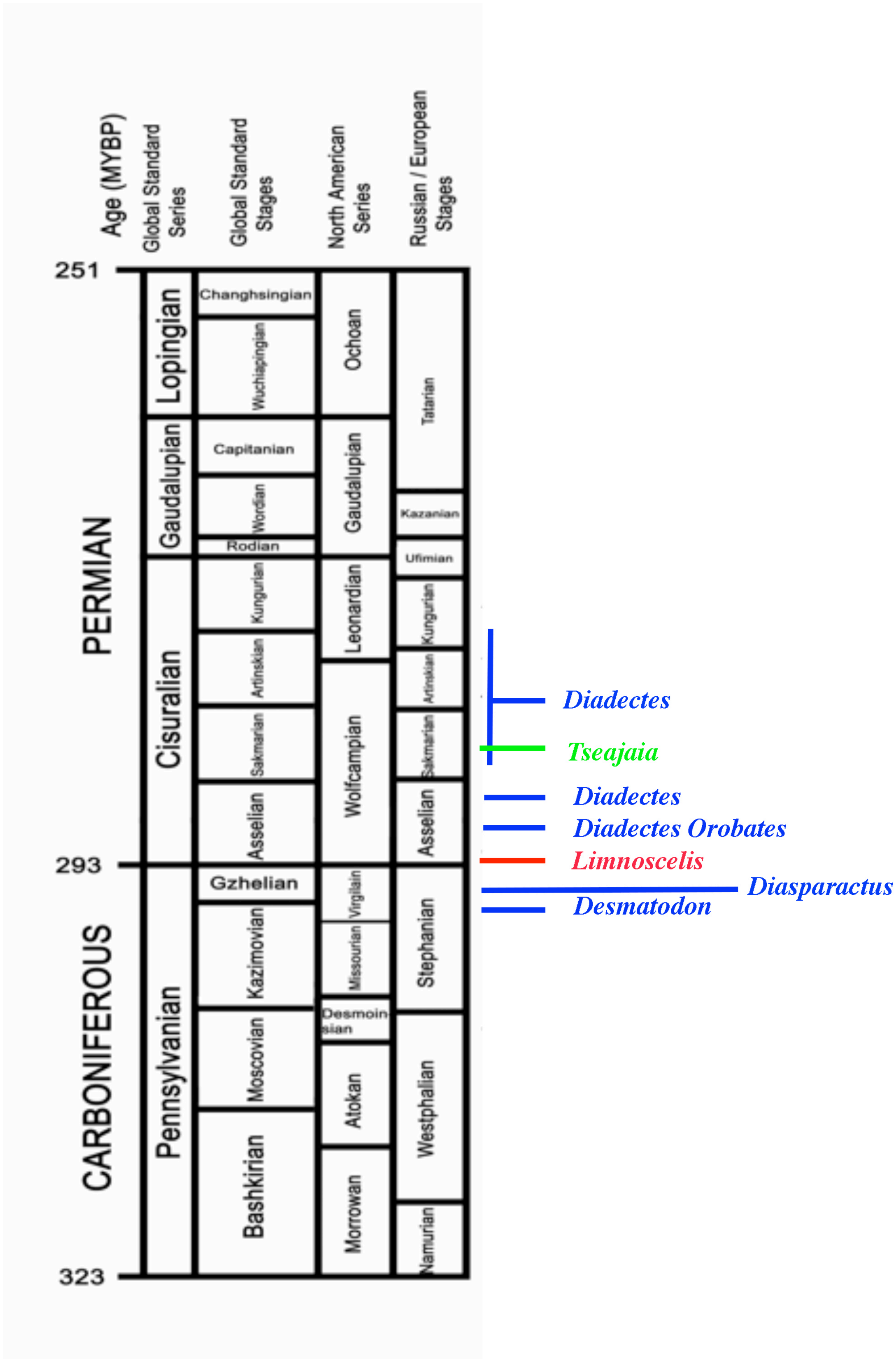


Superbly preserved *Diadectes* from the Early Permian of central Germany:



Orobates: *Orobates* is one of the most completely preserved and best known of diadectids. It is slightly more primitive than *Diadectes* (also known from that locality), but still retains the herbivorous features typical of diadectids.

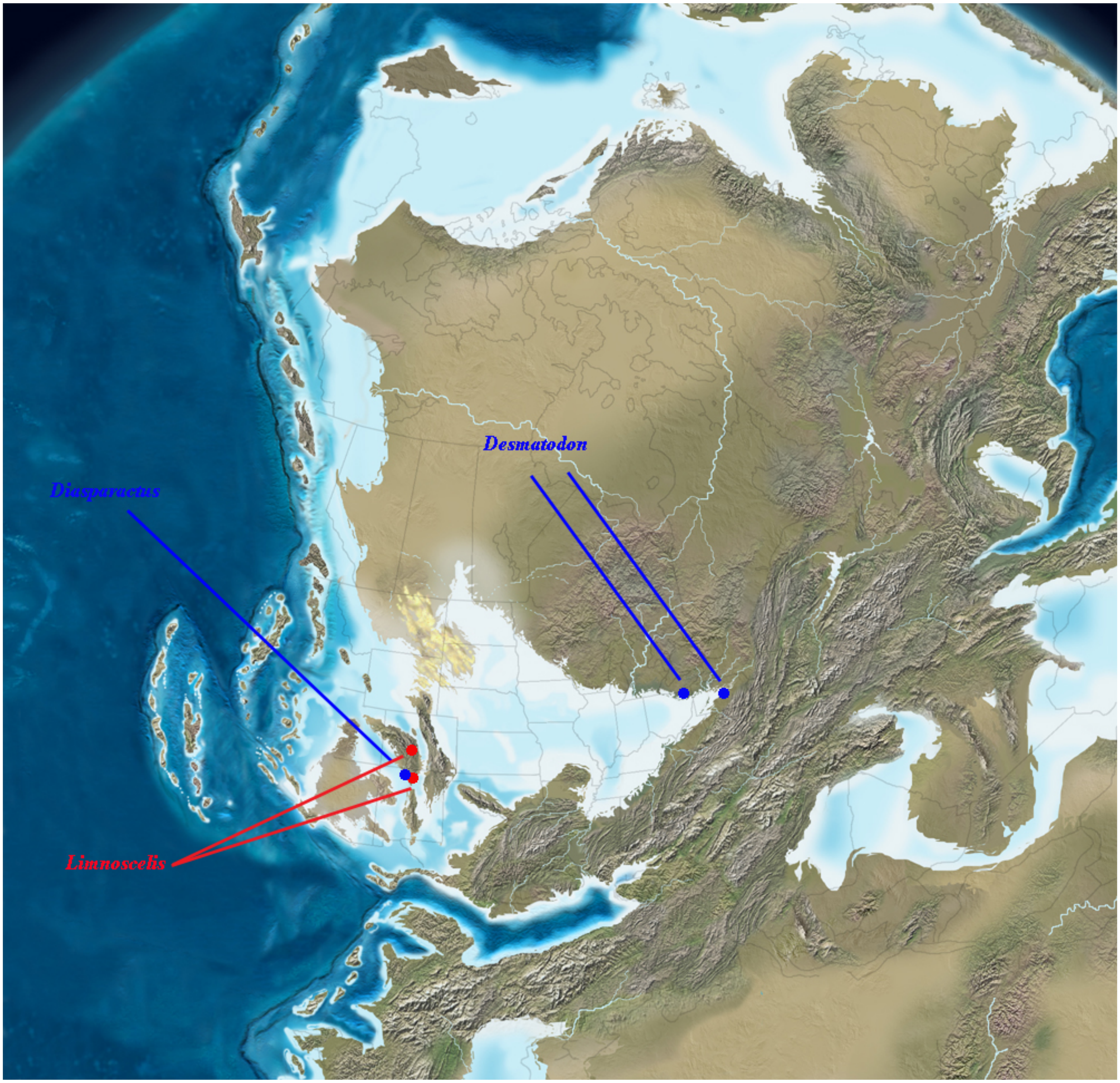
PALEO-BIOGEOGRAPHIC DISTRIBUTION OF DIADECTOMORPHS



Late Pennsylvanian

Limnoscelis (two species) is generally considered as the most basal of the Diadectomorpha, and they are known from Late Pennsylvanian age sediments of northcentral New Mexico, central Colorado, and southeastern Utah. See the red dots below.

The earliest known diadectids are found from the Late Pennsylvanian as well, *Diasparactus* from north-central New Mexico, and *Desmatodon* from the Tri-state area of Ohio/Pennsylvania/West Virginia.

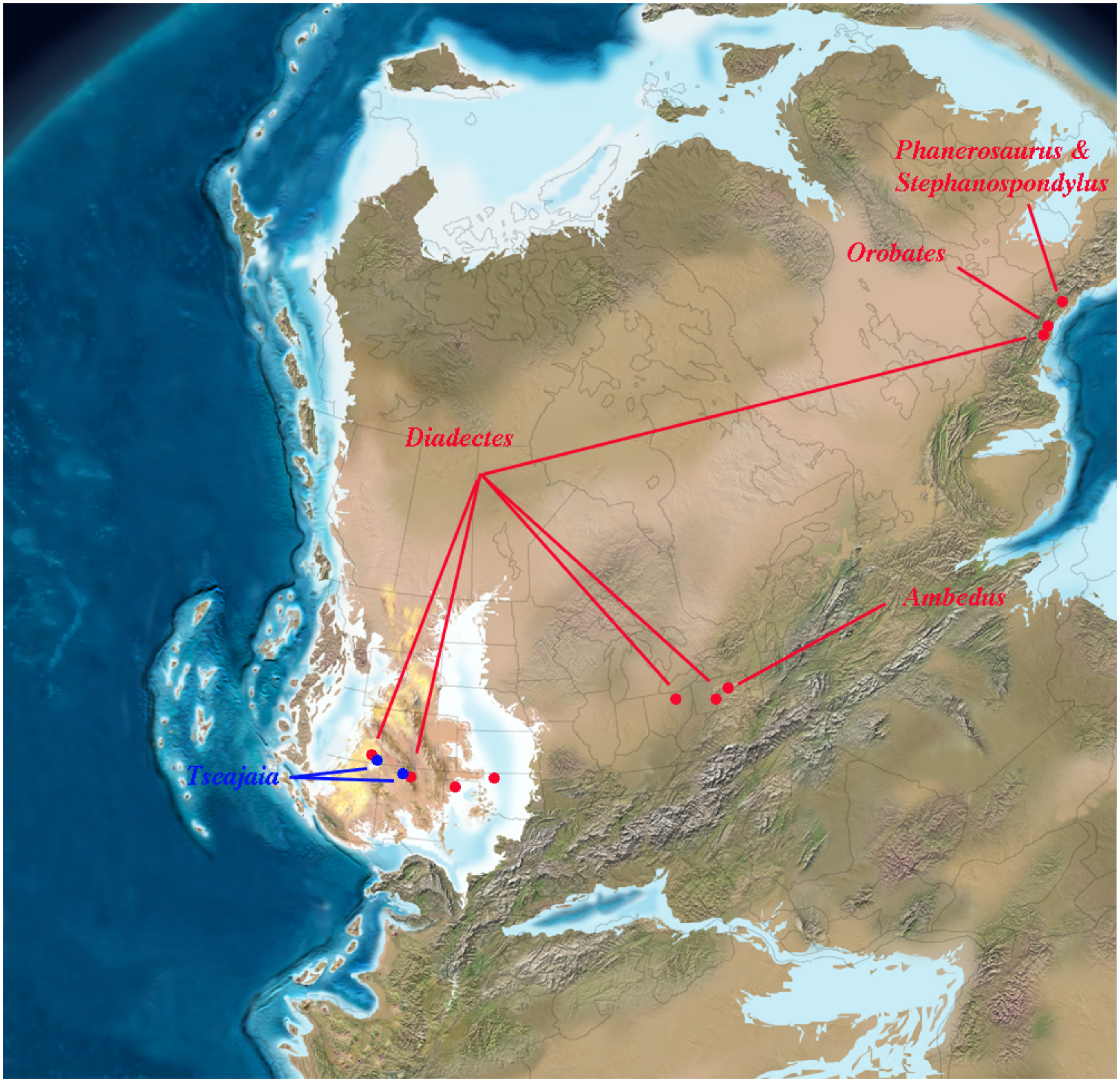


Early Permian

Whether the Diadectomorpha diversified in the Early Permian, or whether we have just had better luck finding them from Early Permian sediments, we do not know. However, numerous diadectids are known from the Early Permian, as well as the unique form *Tseajaia* known from southeastern Utah and north-central New Mexico.

Diadectes is the most common of the diadectids, found in many regions of Pangea. Numerous other taxa (*Ambedus, Phanerosaurus, Stephanospondylus*) are known from much more fragmentary materials. Notably, *Orobates* is found only in central Germany, but is represented by numerous complete specimens.

It is reasonable to say that diadectids have a distribution through northern Pangea.



APPENDIX – SKULL STURCTURES FOR STUDENTS THAT REQUIRE REVIEW

The dermal bones of the skull roof include:

MIDLINE OR MEDIAN SERIES: from rostral to caudal: nasal, frontal parietal, postparietal*.

MARGINAL TOOTH-LAERAL TOOTH-BEARING BONES: premaxilla, maxilla, septomaxilla* (though some include this in the circumorbital series)

CIRCUMORBITAL SERIES (BONES CURROUNDING THE ORBIT): septomaxilla* (though some include this in the marginal toothed series, lacrimal, prefrontal*, postfrontal*, postorbital*, jugal.

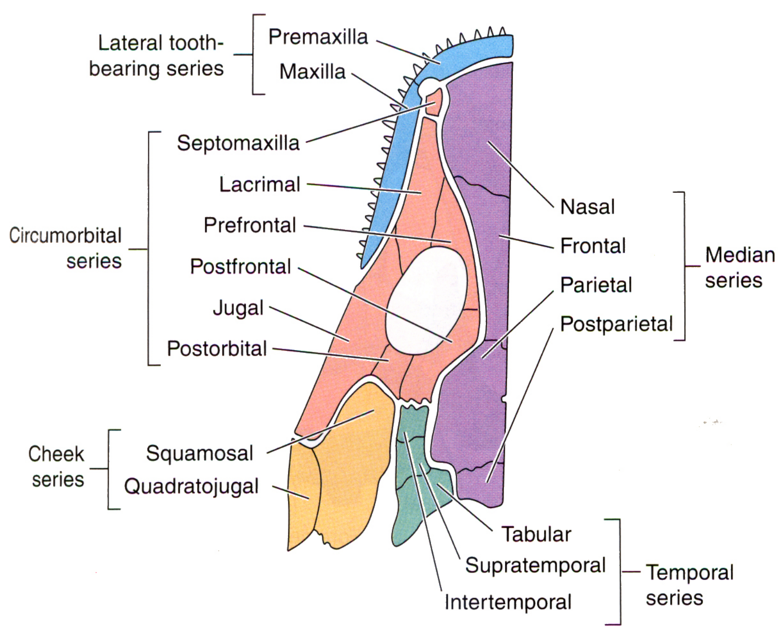
CHEEK: squamosal*, quadratojugal*.

TEMPORAL SERIES: intertemporal*, supratemporal*, tabular*.

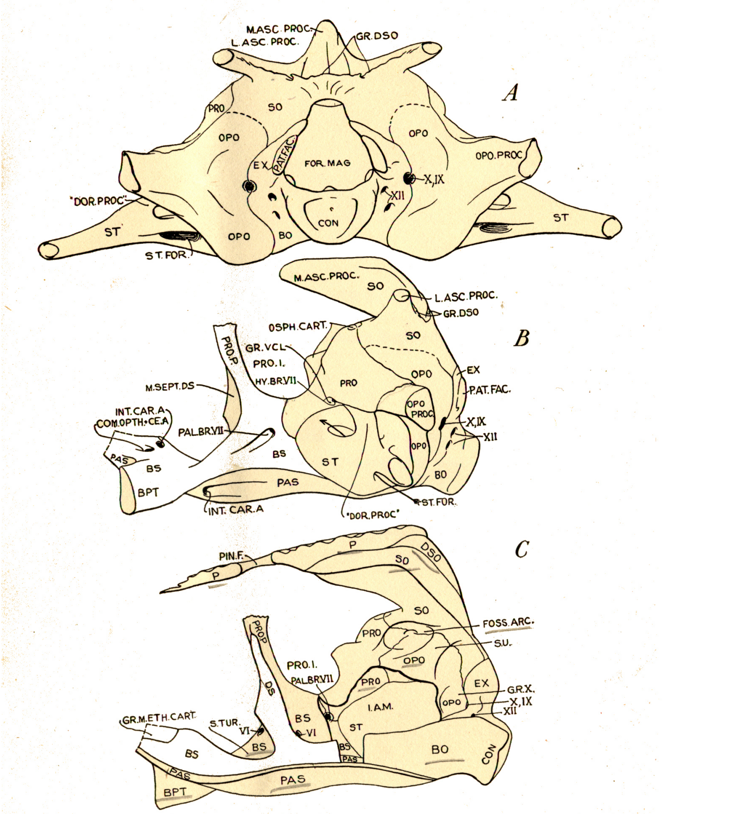
The dermal bones of the palate include:

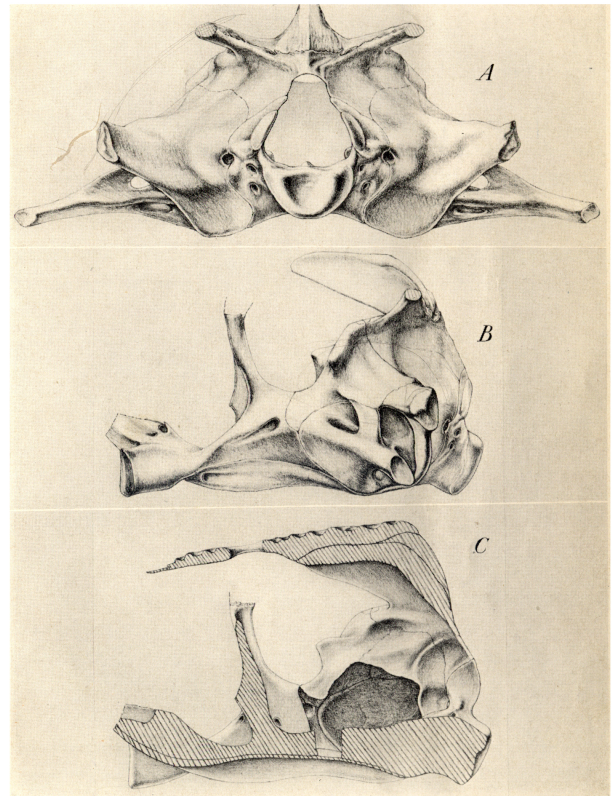
MIDLINE SERIES: Vomer, pterygoid

LATERAL SERIES: palatine, ectopterygoid

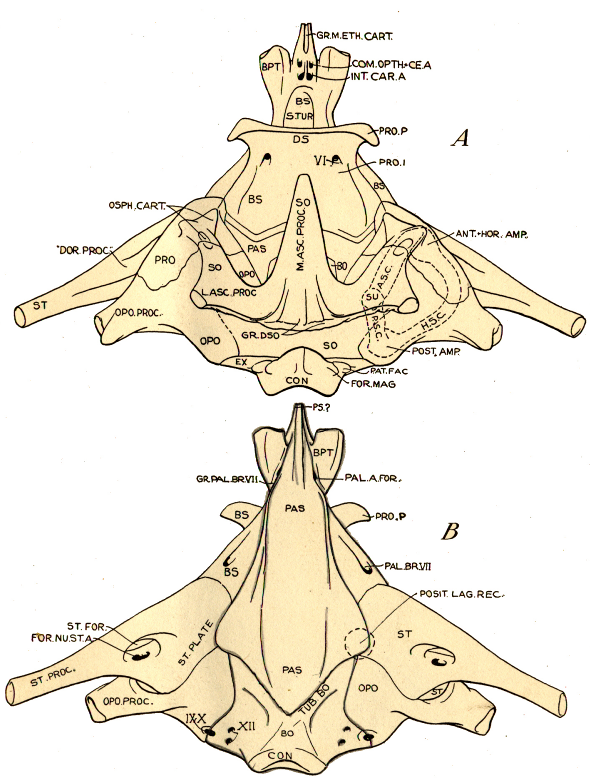


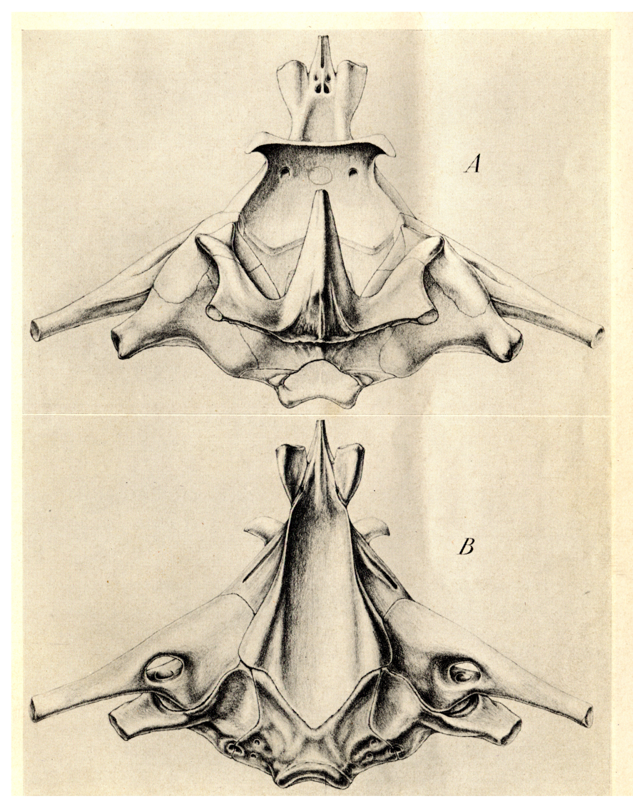
Below: the braincase of the basal reptile *Captorhinus*. (A) occipital view; (B) left lateral view; (C) sagittal view.



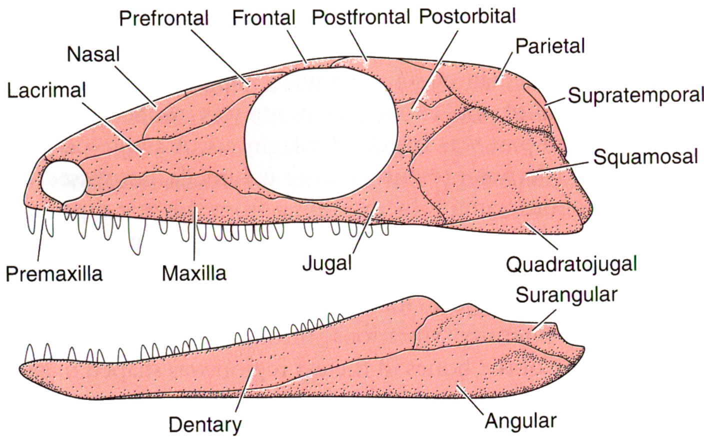


Below: the braincase of the basal reptile *Captorhinus*. (A) dorsal view; (B) ventral view.

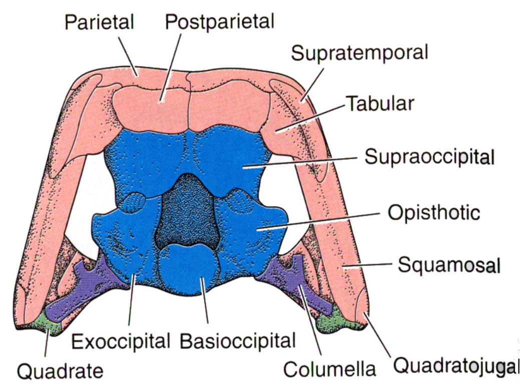




In the images that follow, note the braincase is color-coded blue.

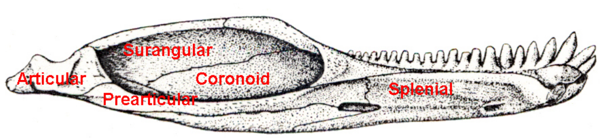


Lateral view of †*Paleothyris*

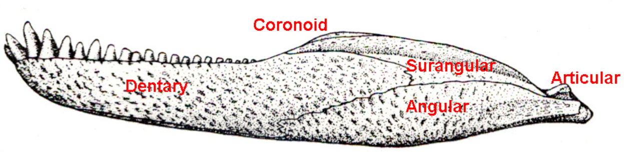


Posterior view of †*Paleothyris*

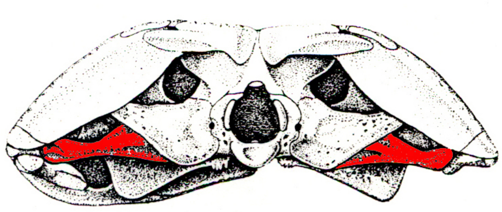
Structures of the splanchnocranium of the Lower Permian basal reptile *Captorhinus*. Mandibular arch - Jaw and Hyoid arch - Stapes (in red)

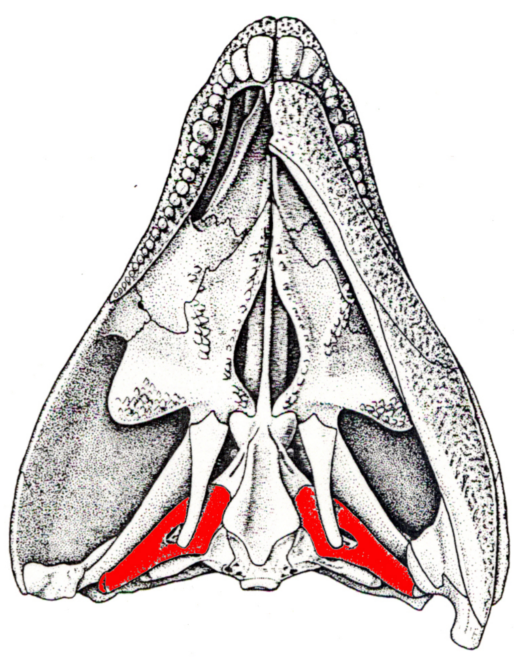


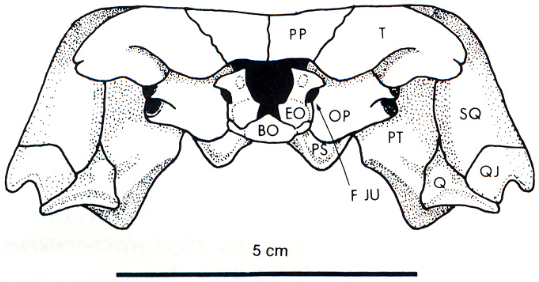
Internal (lingual) view



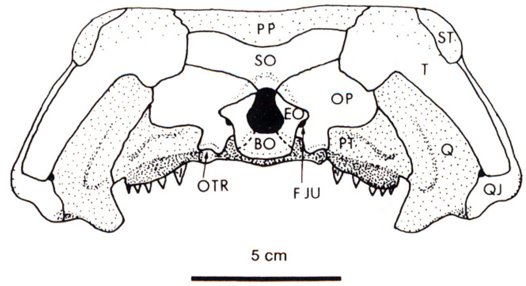
External (labial) view



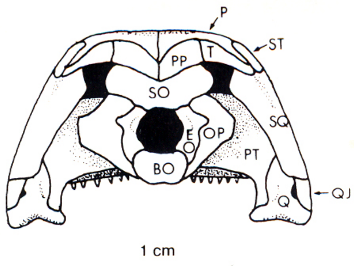


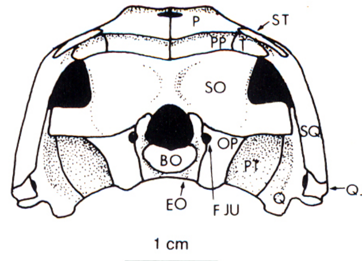


Seymouria



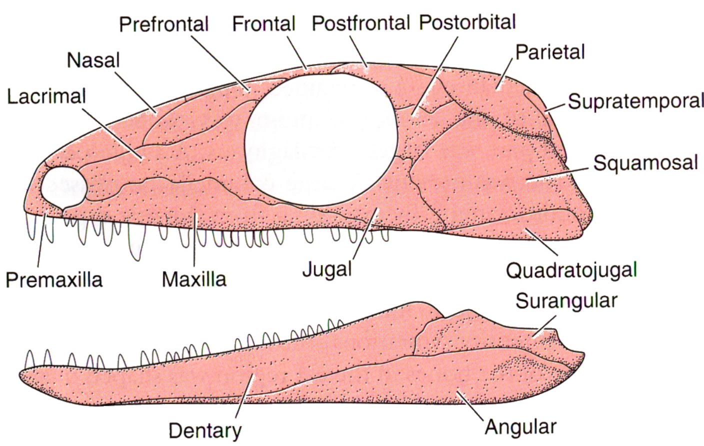
Limnoscelis



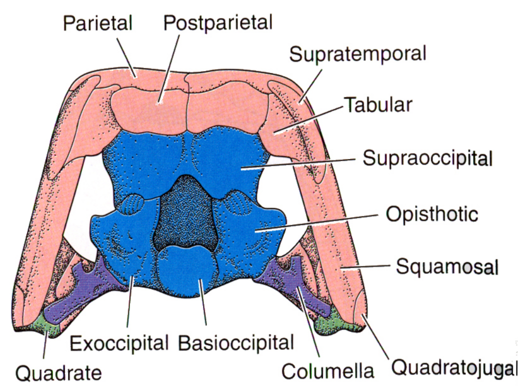


DERMAL ELEMENTS IN BASAL AMNIOTES

Basal amniotes retain almost all of the roofing and dermal elements seen in earlier non-amniote tetrapods. Notably, the proportions of some may change, and with that the postparietals are often pushed to having only an occipital exposure. Following is an illustration of the primitive reptile *Paleothyris*. Note how the stapes (a splanchnocranial element) acts as a strut, bracing the cheek region of the dermal roof relative to the braincase.



Lateral view of †*Paleothyris*



Posterior view of †*Paleothyris*