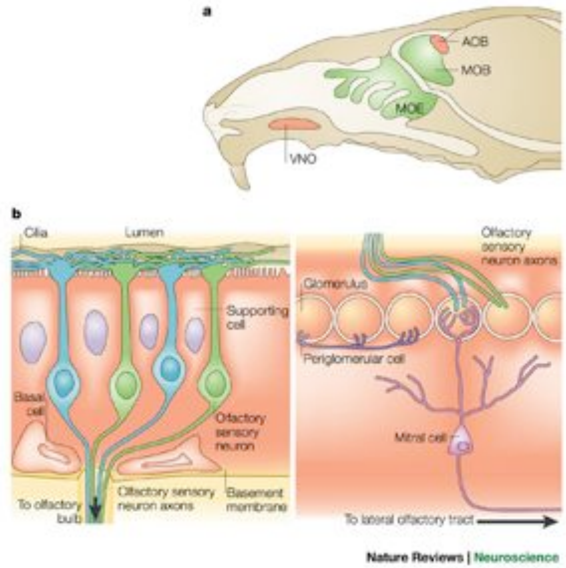
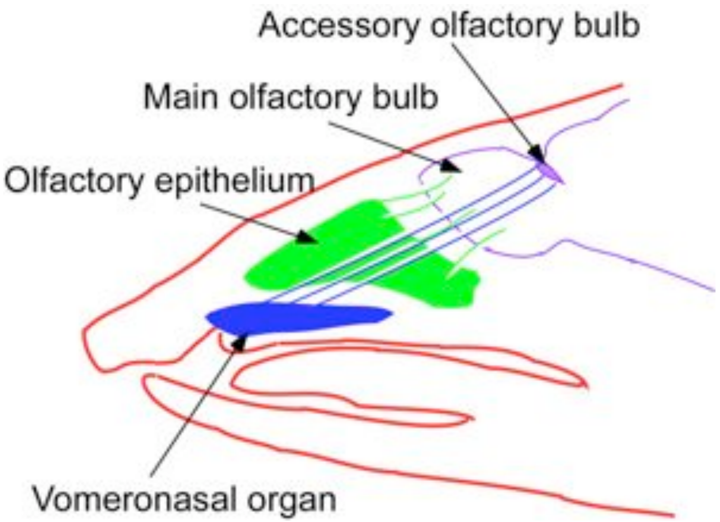
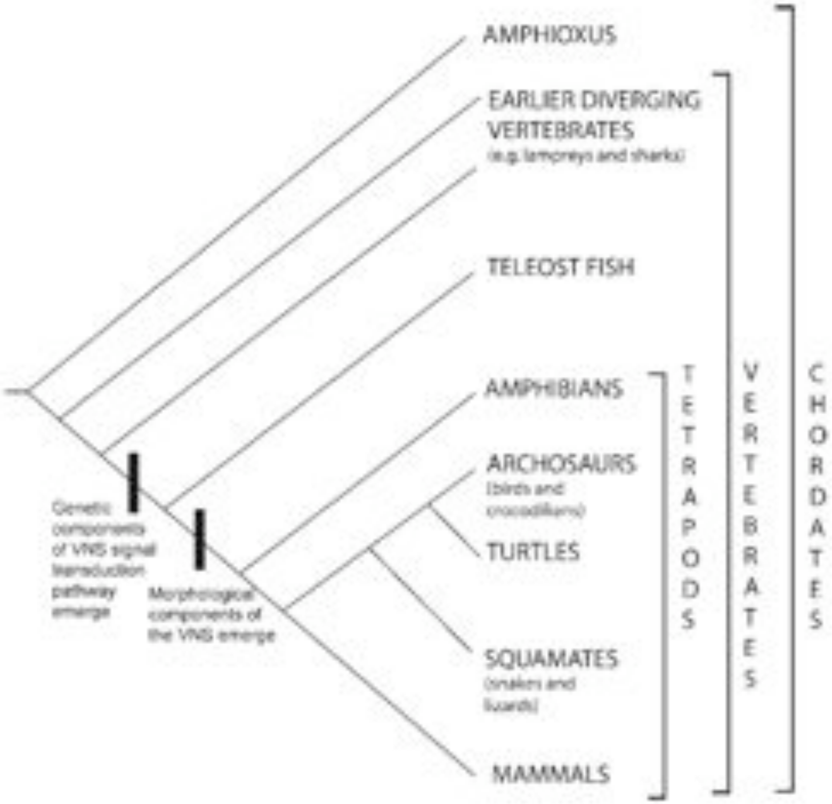
Órgano Vomeronasal: presente en los principales linajes de tetrápodos vivientes







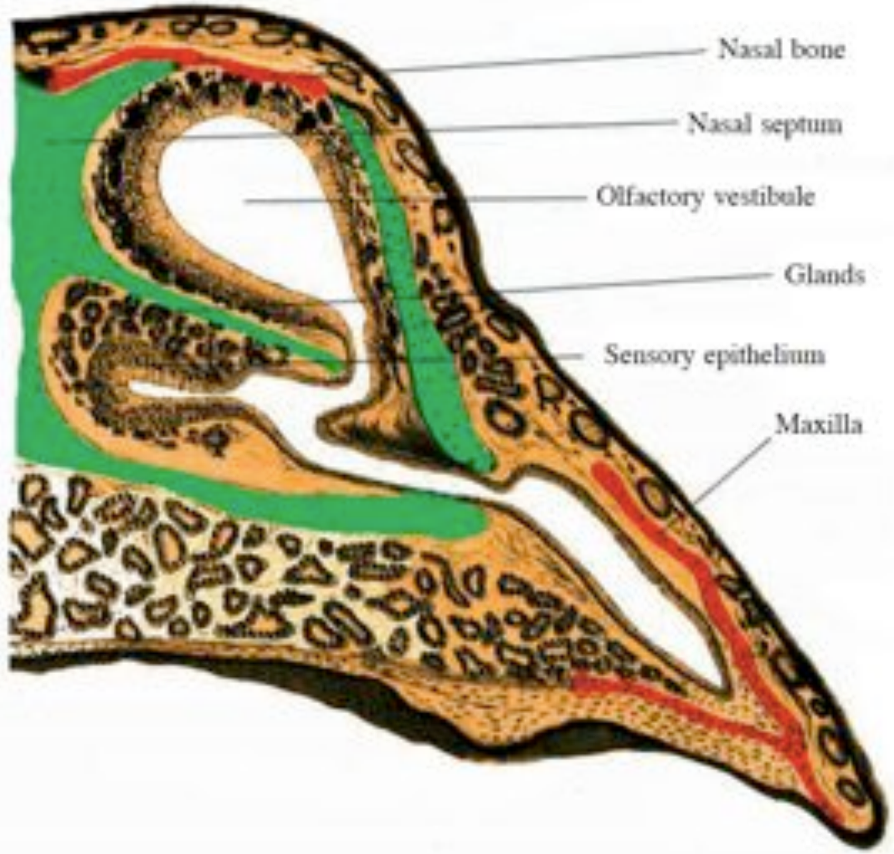


Fig. 5. Cross section of a head of the frog, *Hyla arborea*, made just posterior to the anterior naris. The vomeronasal organ is found beneath the olfactory vestibule, which lies anterior to the eminentia olfactoria of the main olfactory organ. A series of grooves runs from the anterior naris to the sensory epithelium of the vomeronasal organ. Water is transported along these grooves from the environment to the vomeronasal organ and out *via* the maxillary recess and the posterior naris. From von Mihalkovics (1899).

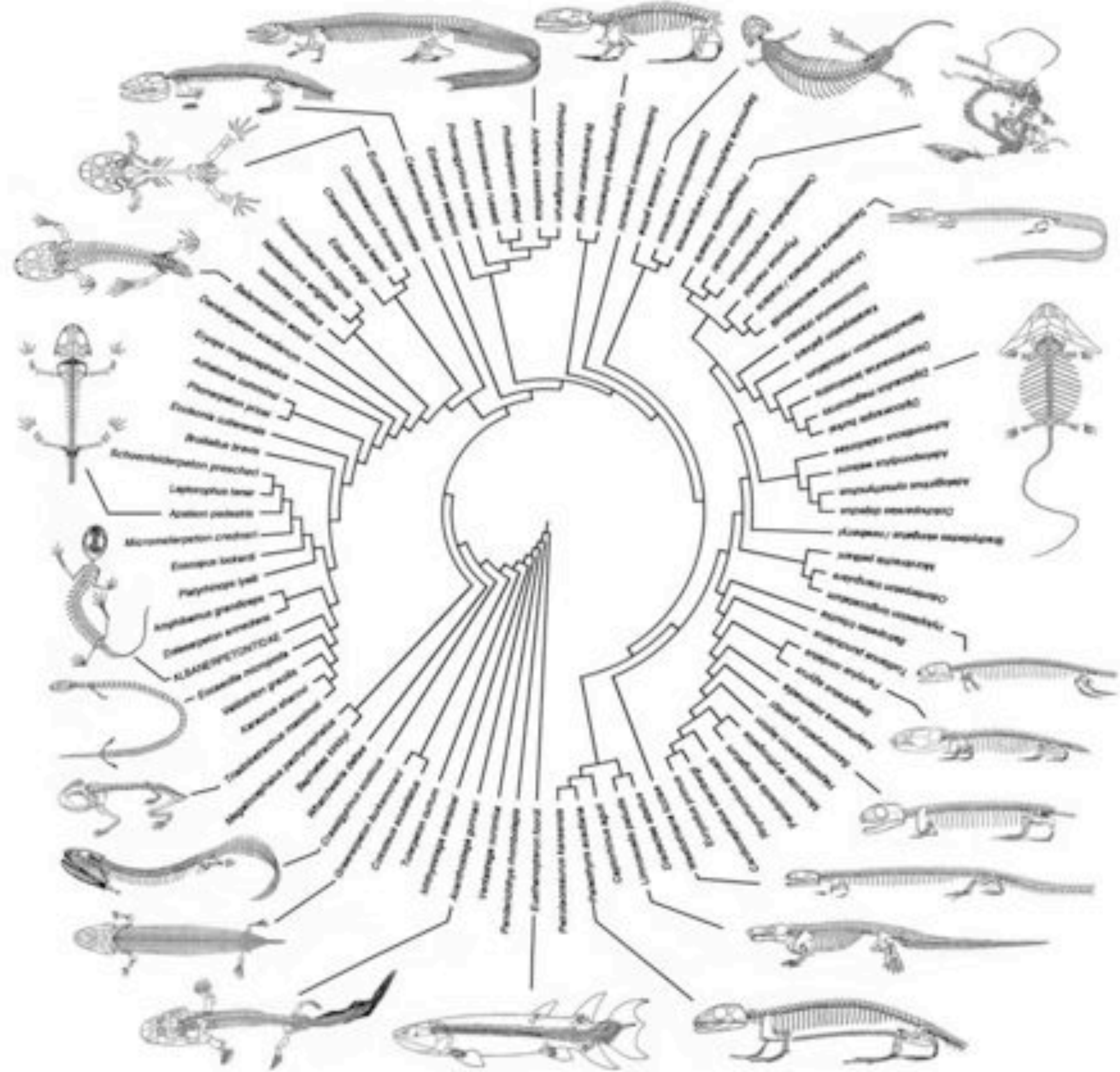
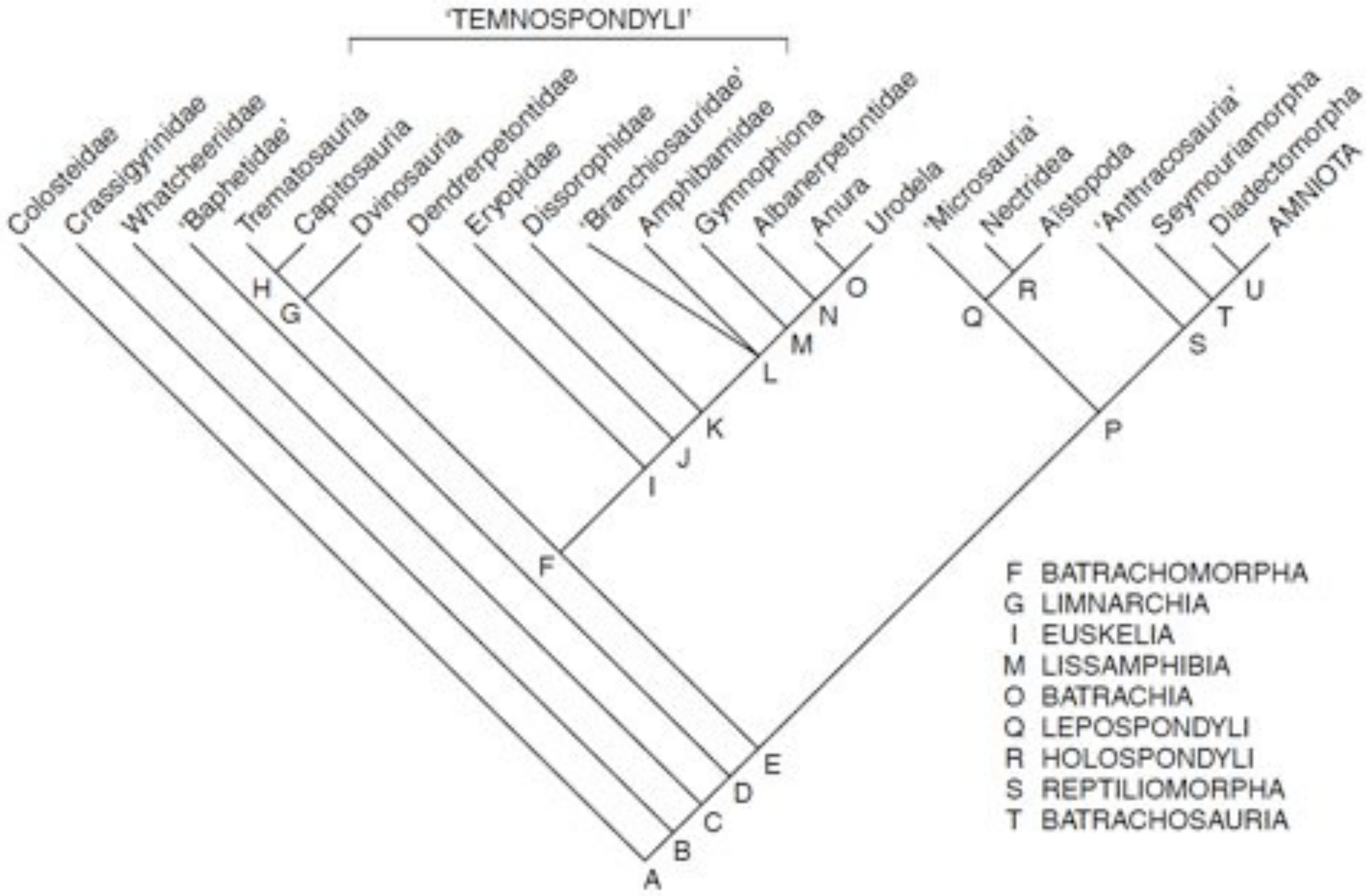
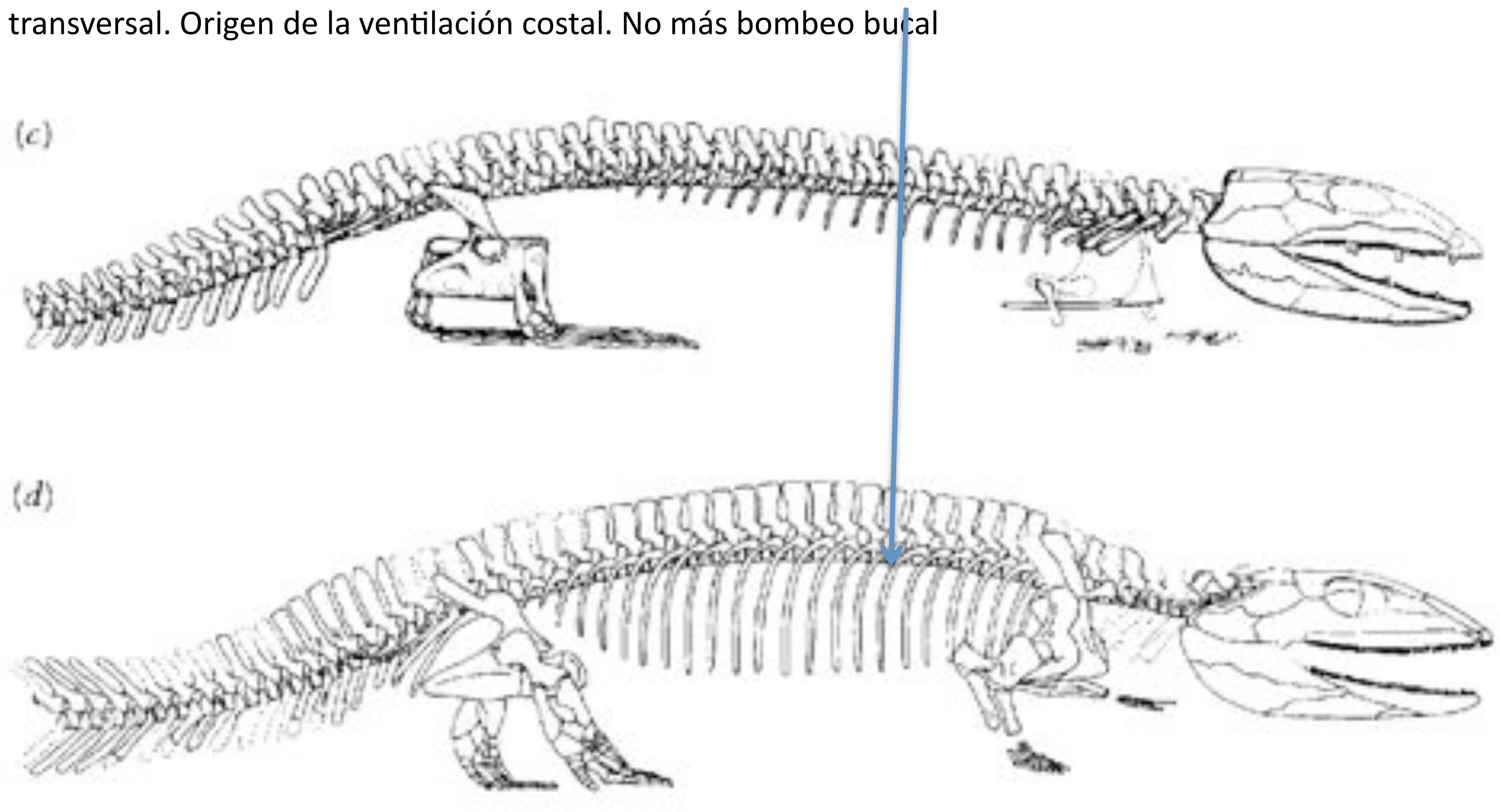


Fig. 6. Circular dendrogram of tetrapod interrelationships using the branching sequence shown in Fig. 5. Selected taxa illustrated as indicators of morphological diversity (figures not drawn to the same scale).



'TEMNOSPONDYLI'
Colosteidae
Crassigyrinidae
Whatcheeriidae
'Baphetidae'
Trematosauria
Capitosauria
Dvinosauria
Dendrerpetontidae
Eryopidae
Dissorophidae
'Branchiosauridae'
Amphibamidae
Gymnophiona
Albanerpetontidae
Anura
Urodela
'Microsauria'
Nectridea
Aïstopoda
'Anthracosauria'
Seymouriamorpha
Diadectomorpha
AMNIOTA
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
F BATRACHOMORPHA
G LIMNARCHIA
I EUSKELIA
M LISSAMPHIBIA
O BATRACHIA
Q LEPOSPONDYLI
R HOLOSPONDYLI
S REPTILIOMORPHA
T BATRACHOSAURIA

Reptiliomorpha (“anthracosauria”): Aparecen costillas más desarrolladas, que enmarcan el contorno del pecho en vista transversal. Origen de la ventilación costal. No más bombeo bucal



Upper Mississippian of West Virginia. Length about 1.5 meters. *From Godfrey, 1986.* (*c*) *Caerorhachis*, a terrestrial temnospondyl from the Upper Mississippian of Scotland. Approximately 30 cm long. *From Holmes and Carroll, 1977.* (*d*) *Proterogyrinus*, a primitive anthracosaur from the Upper Mississippian of West Virginia. Approximately 1 meter long. *From Holmes, 1984.*

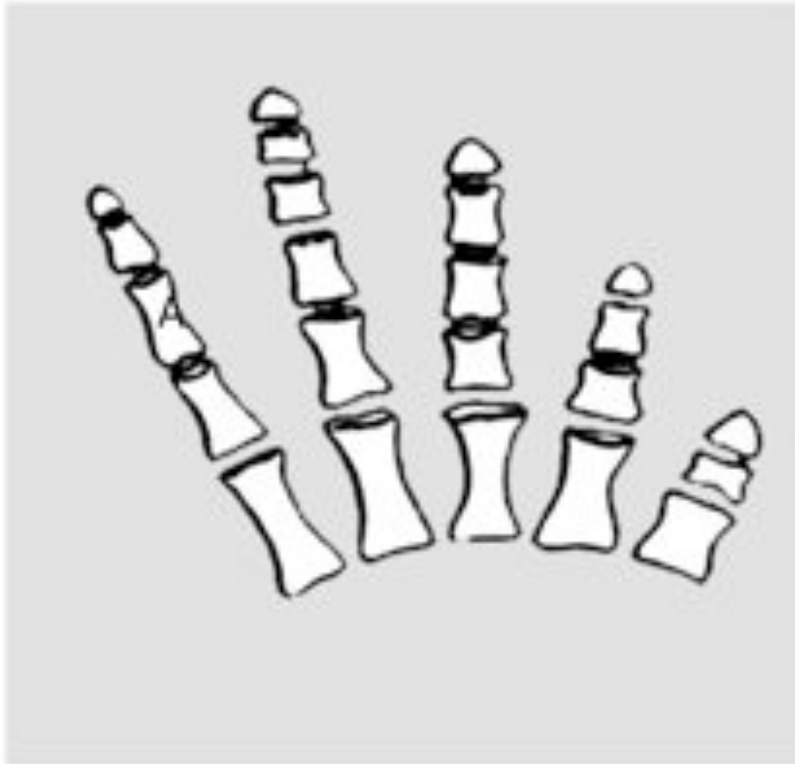
The postcranial skeleton of *Proterogyrinus* is typical of terrestrial animals with well-developed limbs and a relatively short trunk. There are 32 presacral vertebrae,

Among Paleozoic amphibians, only the anthracosaurs share significant derived characters with early amniotes. These features include contact between the tabular and parietal and the dominance of the pleurocentrum. Although a multipartite atlas-axis complex is a feature of primitive labyrinthodonts, only in anthracosaurs is the pleurocentrum the major element that supports the atlas and axis arches as it does in early amniotes.

anterior

P

Manus



Pes

~~En cambio~~, los tetrápodos mas cercanos a los amniotos que a los anfibios modernos ("anthracosaurios" o reptiliomorphos) como *Seymouria* retuvieron la pentadactilia ancestral en la mano y presentan un numero especifico de falanges en cada dígito: 2-3-4-5-3 en la mano, y 2-3-4-5-4 en el pie

Intertemporal aún presente (ausente en amniotos)

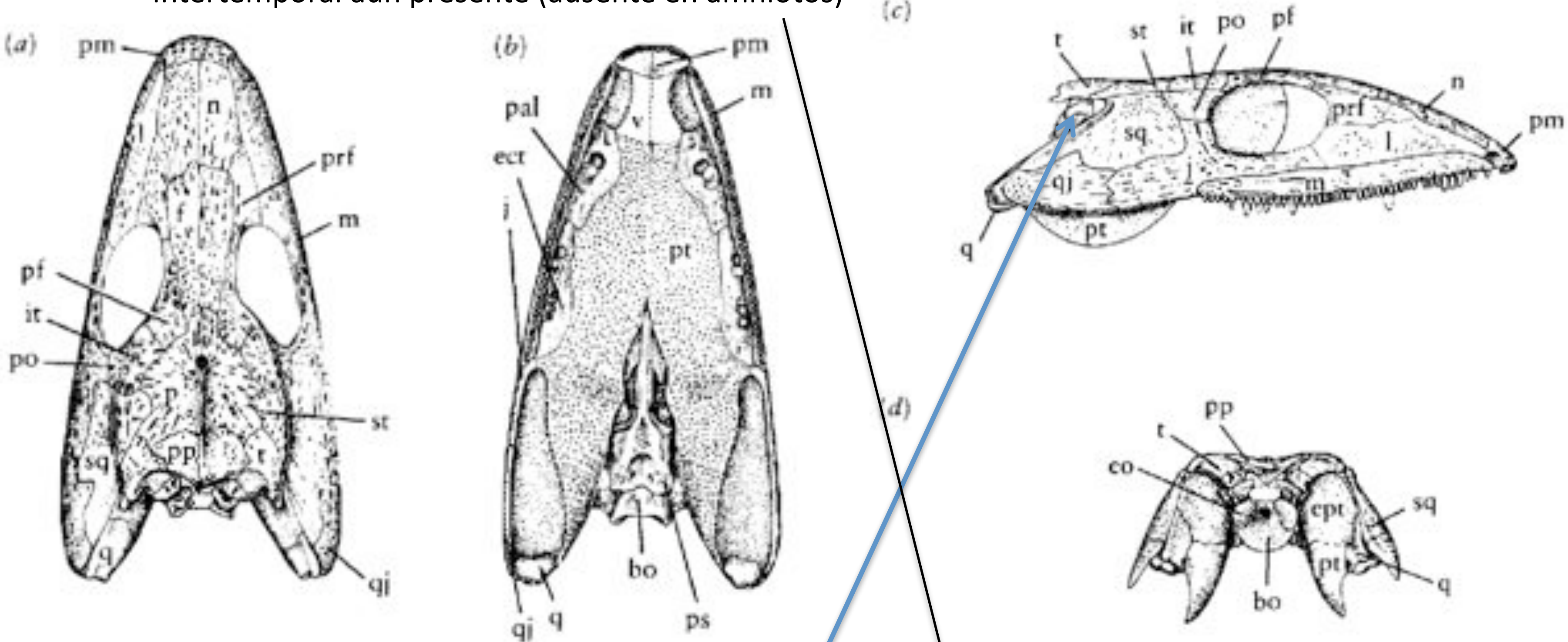
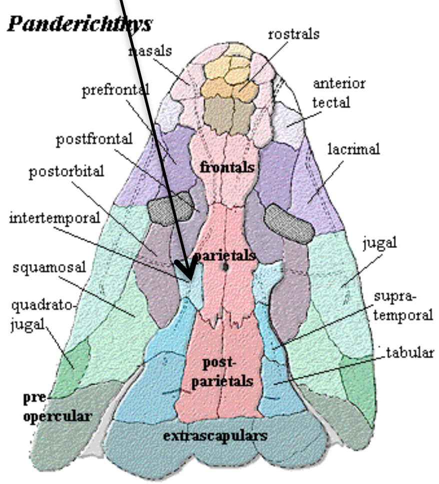
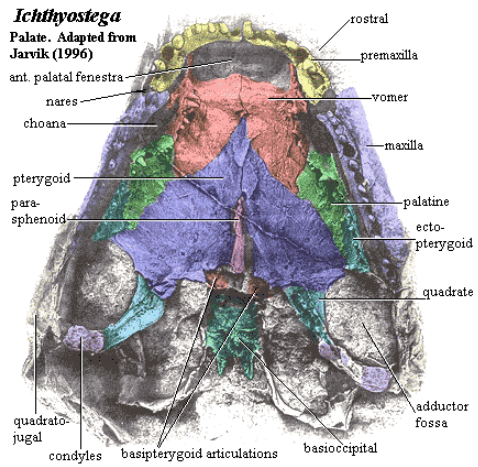


Figure 9-20. SKULL OF *PROTEROGYRINUS*. (*a*) Dorsal, (*b*) palatal, (*c*) lateral, (*d*) occipital views. Original about 20 centimeters long. Abbreviations as in Figure 8-3. *From Holmes, 1984.*

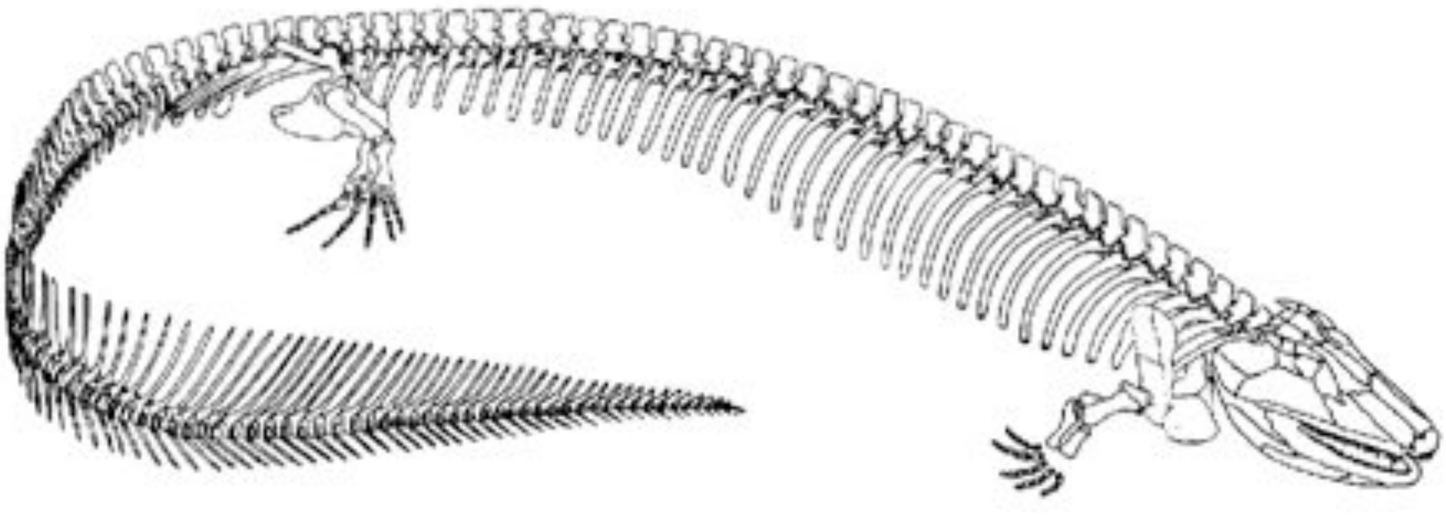
skull is primitive in retaining a line of weakness between the cheek and the skull table, and the palate is closed (Figure 9-20). The skull table is advanced in the forward extension of the tabular to the parietal. The braincase is solidly fixed to the skull roof, with the otic capsule attached to the underside of the tabular. From their first appearance in the fossil record, the anthracosaurs have an embayment in the posterior margin of the cheek that was generally considered to have supported a tympanum. Clack (1983) described a large, bladelike stapes in early genera that is quite different from the narrow rodlike structure usually found in animals known to have an impedance matching ear.



Skull in dorsal view. After Vorobyeva & Schultz (1991).

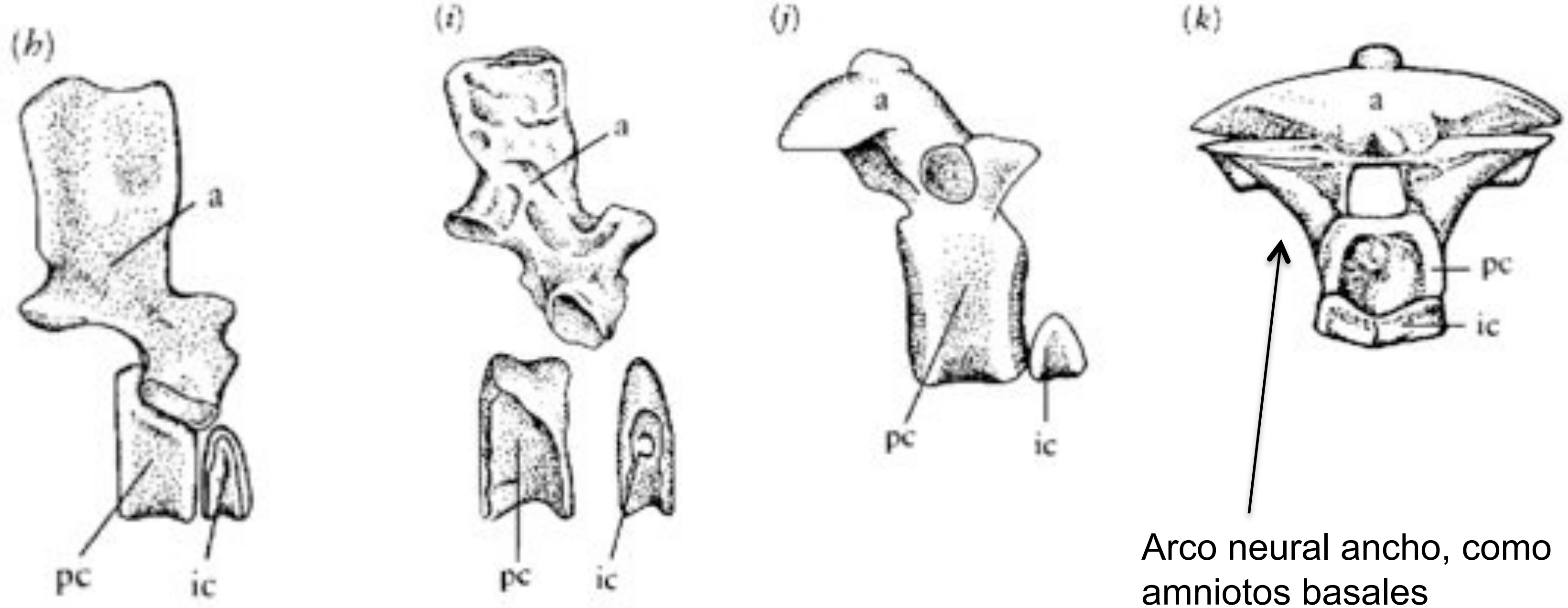


(a)



The best known anthracosaurs are the embolomeres, reviewed by Panchen (1970). They became specialized for aquatic locomotion by elongation of the trunk region, with approximately 40 presacral vertebrae (Figure 9-21).

(Romer, 1957a). Some genera reevolved a dorsal caudal fin. The embolomeres are best represented in the Carboniferous of Great Britain, where they apparently inhabited fairly deep bodies of water. However, in the Lower Permian, their remains are restricted to deltaic deposits in southwestern North America. The group did not survive beyond the Lower Permian.



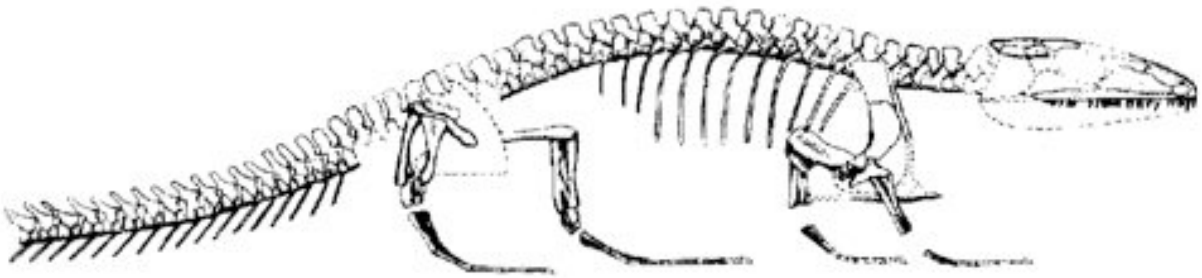
Arco neural ancho, como amniotos basales

The postcranial skeleton of *Proterogyrinus* is typical of terrestrial animals with well-developed limbs and a relatively short trunk. There are 32 presacral vertebrae, each consisting of a crescentic intercentrum and a large horseshoe-shaped pleurocentrum supporting the neural arch (see Figure 9-13*b*). This condition is clearly advanced over typical temnospondyls. We may assume that the pleurocentra, which were paired in rhipidistians and primitive temnospondyls, have grown ventrally to meet at the

1980. (*b*) *Proterogyrinus*, a primitive anthracosaur; pleurocentra and intercentra are both crescentic. *From Holmes and Carroll, 1977.* (*i*) The embolomere *Eogyrinus;* both intercentra and pleurocentra are complete cylinders. *From Panchen, 1966. By permission of the Zoological Society of London.* (*j* and *k*) *Seymouria* in lateral and anterior views. Note the widely expanded neural arches. *From Panchen, 1967, and Gregory, 1951, respectively. Courtesy of the Library Services Department, American Museum of Natural History.* Abbreviations as follows: a, arch; ic, intercentrum; pc, pleurocentrum.

The intercentrum and the pleurocentrum of each vertebra (see Figure 9-13*i*) were elaborated as subequal cylinders, which probably permitted a great deal of flexibility in the column and facilitated undulatory swimming. However, Otrs anthracosauria basales, posibles ancestros de amniotos:

Bruktererpeton (gephyrostegid), Eoherpeton



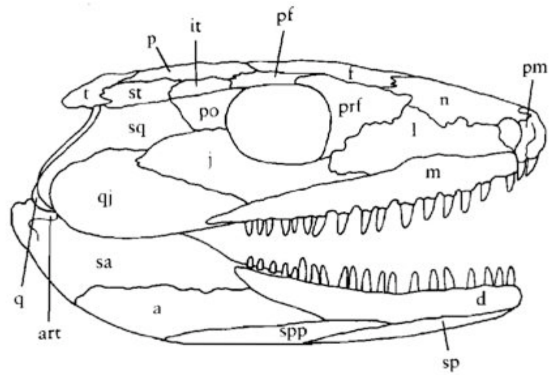
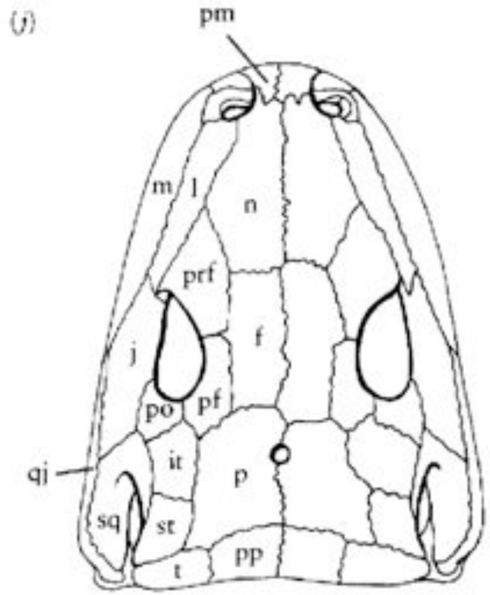


Figure 9-23. *Eoherpeton*, a primitive anthracosaur; lateral view of the skull. Abbreviations as in Figure 8-3. A slightly modified illustration of *Eoherpeton* is presented by Smithson (1985) in a new description of this genus. *From Panchen, 1980b.*

Seymouriamorfos: Ya no hay flexibilidad de la zona de la mejilla respecto al techo craneal



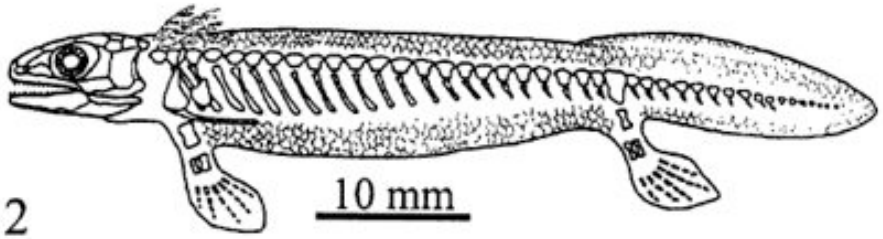
Seymouria: skull roof solidly attached to the cheek

given rise to the seymouriamorphs of the Permian. Unlike other anthracosaurs (but like temnospondyls), the skull and cheek region are solidly attached and the dermal bones are marked by distinct pits and grooves. The otic notch is very deep and the stapes is reduced to a narrow rod.

Seymouriidae, los seymouriamofos más terrestres

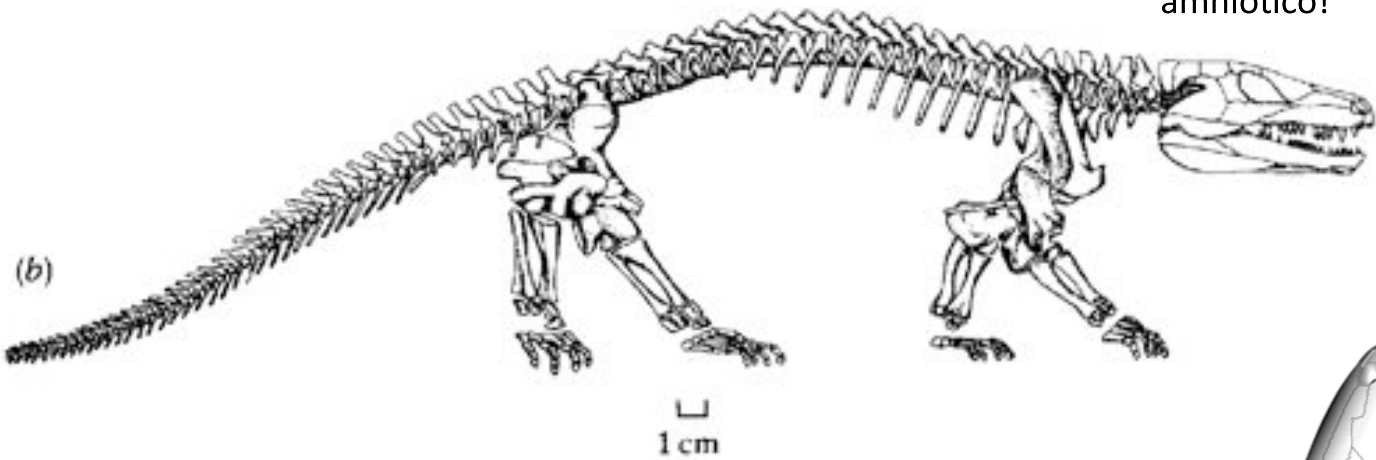
The Seymouriidae, Discosauriscidae, and Kotlassiidae (Figures 9-22 and 9-24) apparently belong to a single assemblage with relatively consistent skeletal patterns but different ways of life. The seymouriids are primarily North American, with questionably assigned material from Russia. Their limb proportions indicate they were the most terrestrial of anthracosaurs. Discosauriscids, from central

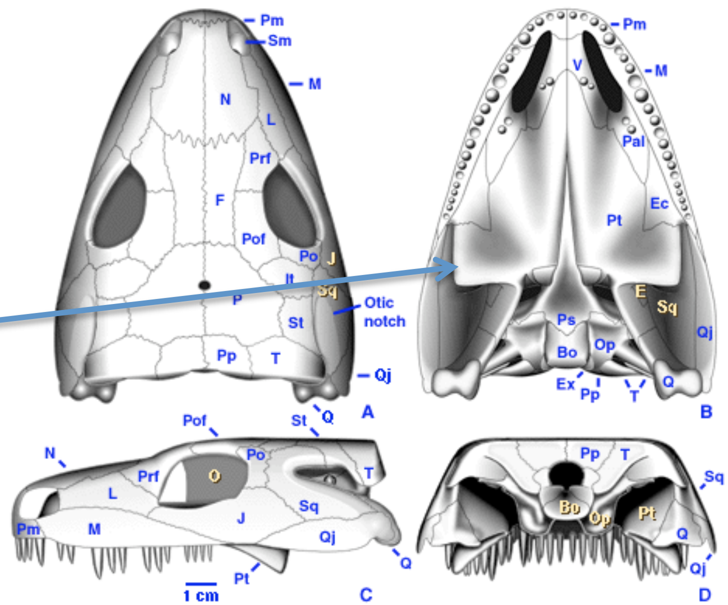
2



Hay larva: Falta aún para el huevo amniótico!

(b)





Proceso transverso del pterygoideo: synapomorfía con amniotos

Aún hay intertemporal

Seymouriamorfos acuáticos

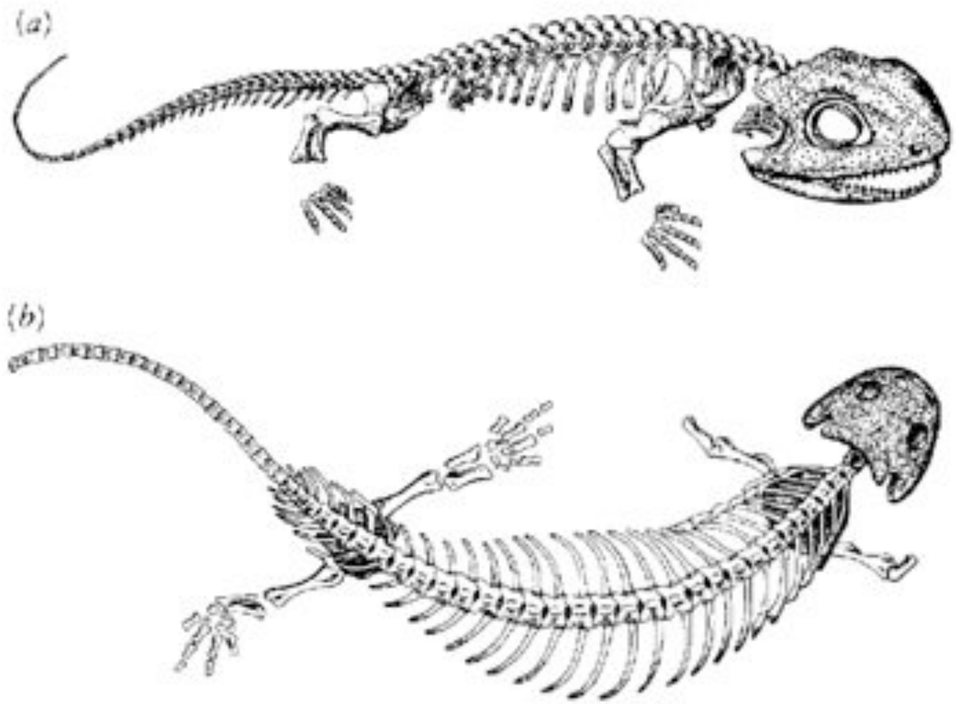


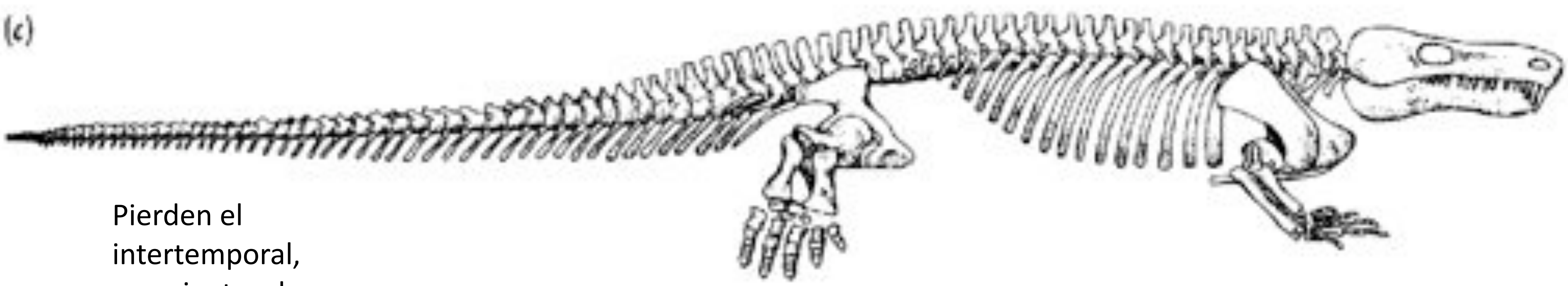
Figure 9-24. AQUATIC ANTHRACOSAURS. (*a*) *Discosauriscus*, a small early Permian seymouriamorph, slightly less than natural size. *From Spinar, 1952.* (*b*) The skeleton of the Upper Permian seymouriamorph *Kotlassia*, × 1/2. The manus is unknown. *From Bystrow, 1944.*

terrestrial of anthracosaurs. Discosauriscids, from central and eastern Europe and recently reported in China (Zhang, Li, and Wang, 1984) are known only from larval or neotenic forms. The kotlassiids, known only from the Upper Permian of Russia, reverted to an aquatic way of life, like the terminal temnospondyls. In common with some dissorophids and plagiosaurs, they developed dermal armor covering the trunk region.

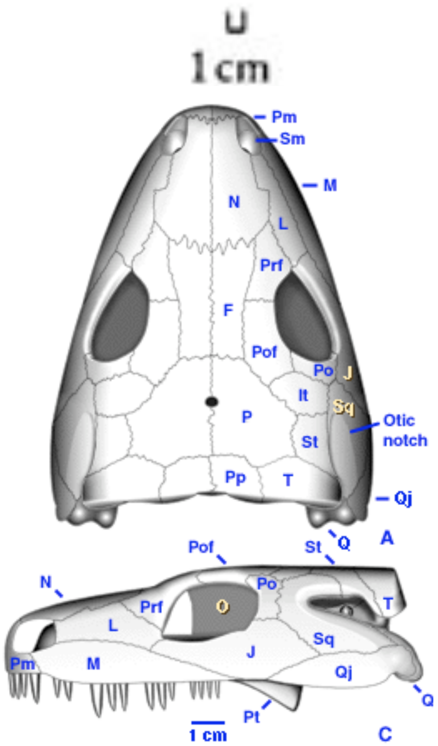
Members of the Limnoscelidae (see Figure 9-22*c*), Solenodonsauridae, and Tseajaiidae may not be particularly closely related to one another, but all have an otic notch and a primitive configuration of the occiput and temporal region. All are relatively large, and their skeleton suggests that they were primarily terrestrial, at least as adults.

these groups share with primitive amniotes is the transverse flange of the pterygoid. *Limnoscelis* has lost the intertemporal bone, but the postorbital rather than the parietal has grown into the area it once occupied.

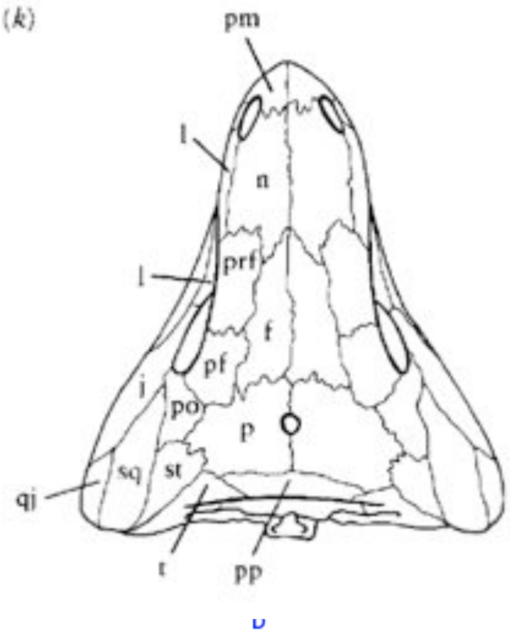
(c)



Pierden el intertemporal, semejante a lo ocurrido en Lepospondylos y Temnospondylos derivados



(k)



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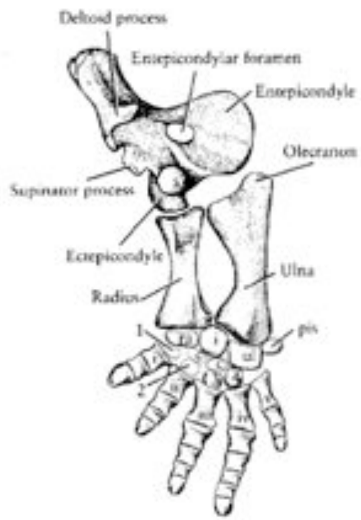
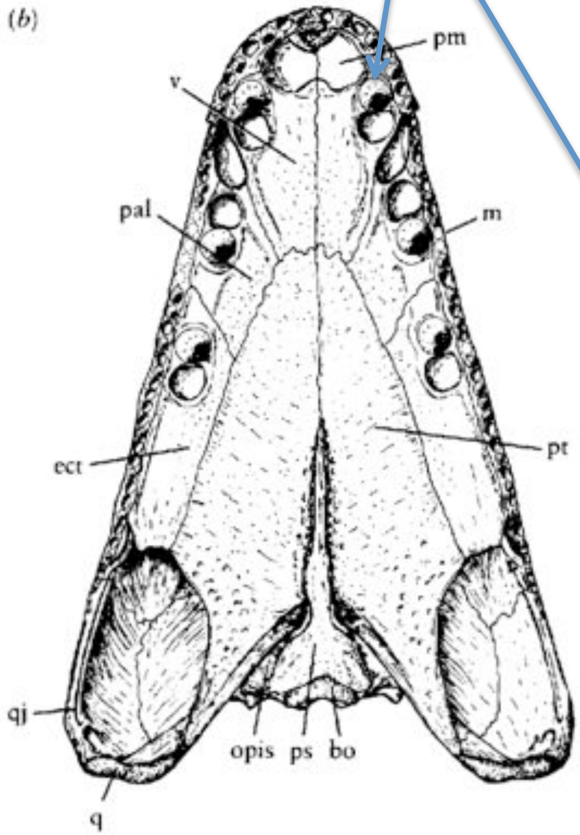
m-

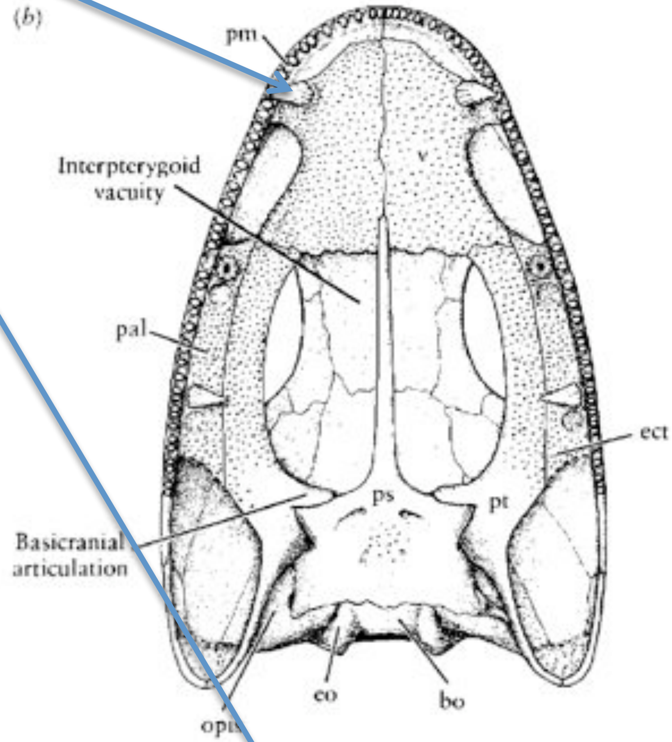
(a)



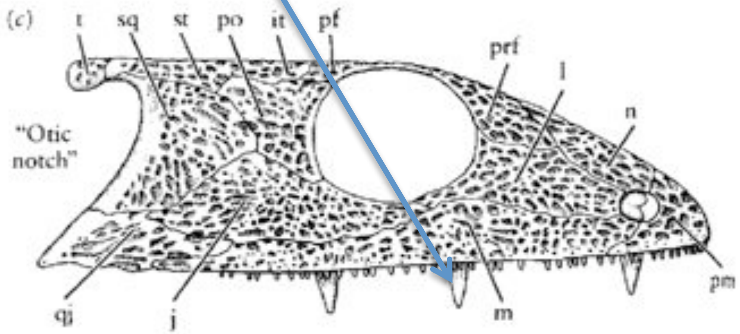
Grandes colmillos del paladar: Desaparecen en Limnoscelidae

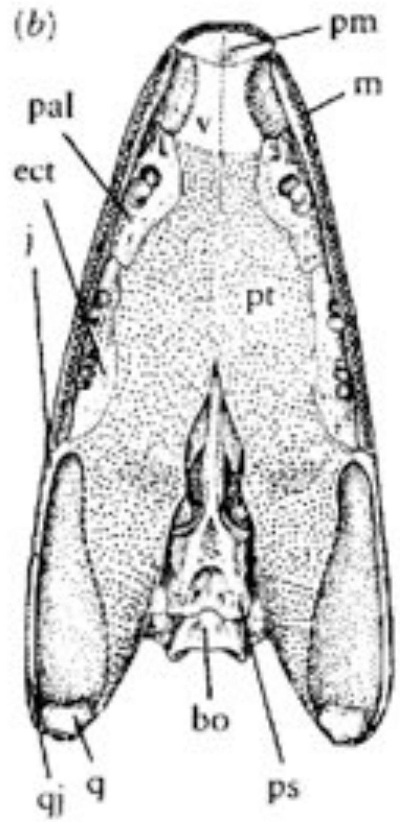


Megalocephalus (stem neotetrapoda)



Dendreerpeton (temnospondyl)





Proterogyrinus ("anthracosaur")

DIADECTOMORPHA

DOS vertebras sacrales en vez de 1 sola!

A diferencia de Seymouriamorfa, no hay trazas de linea lateral

Presencia de GARRAS (excavador?)

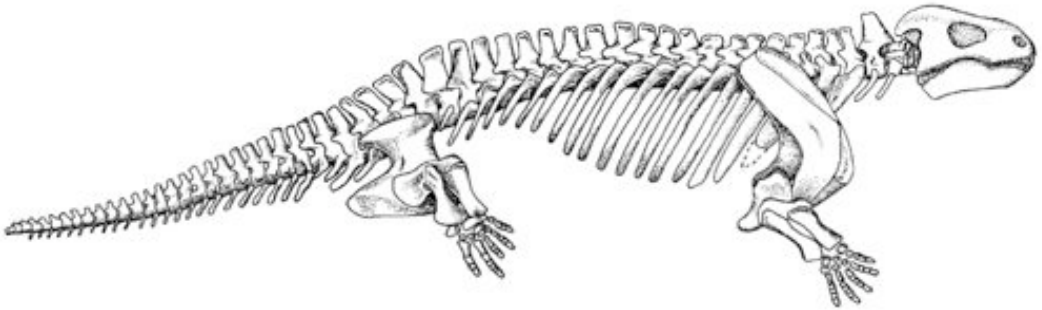


Figure 10-9. RESTORATION OF THE SKELETON OF *DIADECTES*, A PRIMITIVE TETRAPOD OF UNCERTAIN AFFINITIES (about 3 meters long). Most of the postcranial skeleton resembles that of primitive amniotes if adjustment is made for its great size. *From Carroll, 1969c.*

Expansión del supraoccipital, como en amniotos basales

advanced amniotes, not by the squamosal, as in amphibians. The presence of a large supraoccipital in the early diadectids suggests that they evolved from the base of the same lineage that gave rise to the protorothyrids, but they may have evolved separately from the primitive anthracosaurs.

The term Cotylosauria, which is commonly used in reference to the primitive reptilian stock, was originally coined for the genus *Diadectes*. It became associated with a wide range of primitive tetrapods, including the seymouriamorphs and other terrestrial anthracosaurs as well as a host of primitive amniotes. The presence of swollen neural arches was one of the most conspicuous features by which this group was recognized (Heaton, 1980). Since the term cotylosaur has been used to include both amphibians and reptiles and because the phylogenetic position of the Diadectidae remains contentious, an alternate name, Captorhinida, is used here for the order that includes the most primitive amniotes.

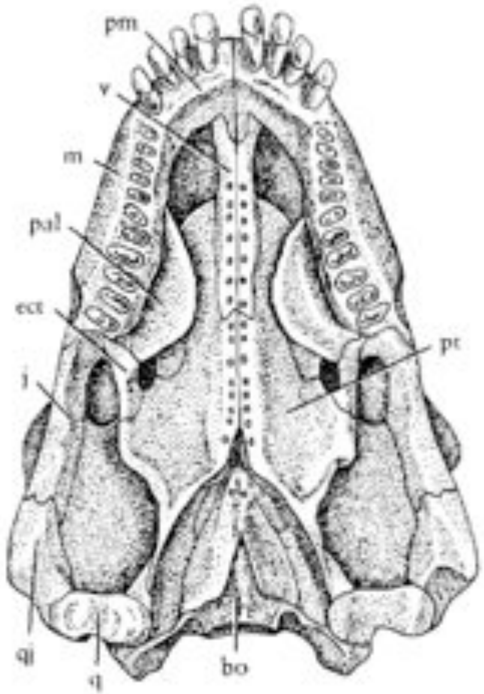
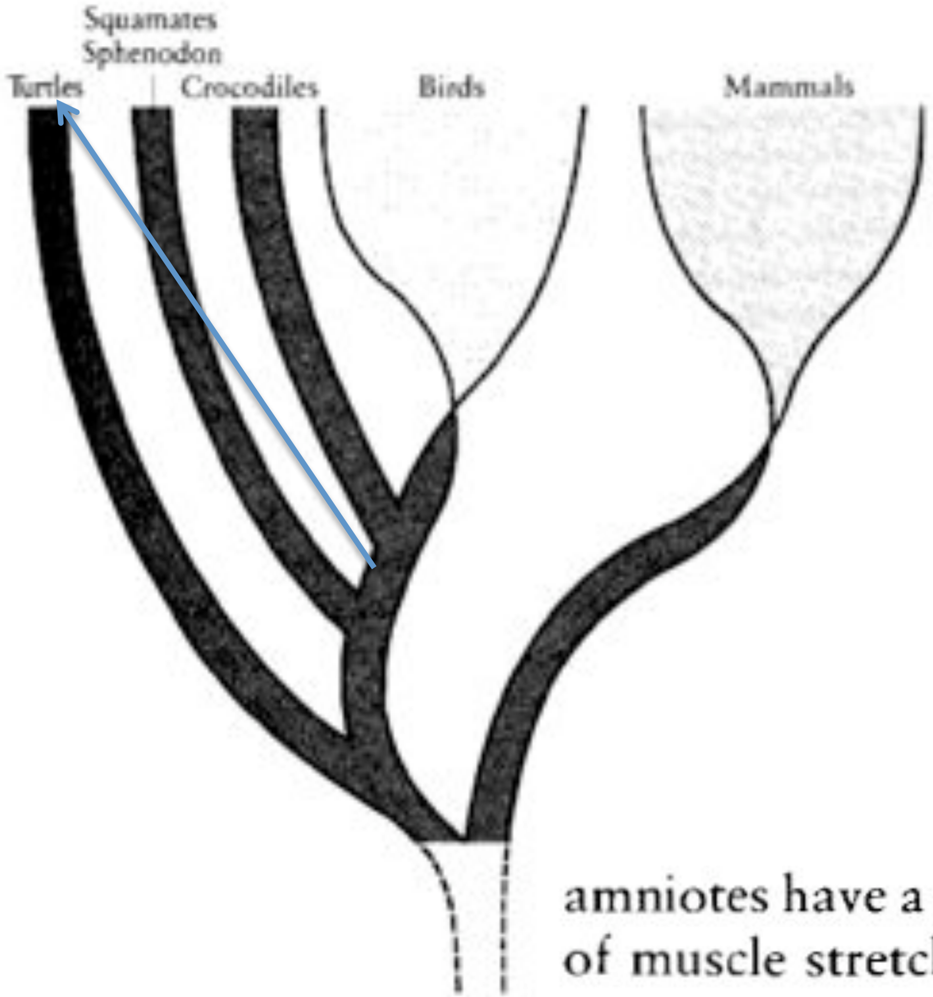


Figure 10-10. THE PALATE OF *DIADECTES*. The cheek teeth are expanded transversely to form a large crushing area. The palatine bone forms a partial secondary palate. The skull roof is formed of thick spongy bone, unlike that of other early tetrapods. Abbreviations as in Figure 8-3. *From Carroll, 1969c.*

Noción parafilética



We may use the term reptile to refer informally to turtles, crocodiles, lepidosaurs, and primitive amniotes, but we cannot define the Reptilia rigorously except as amniotes that are not birds or mammals.

In sharp contrast with the fossil record of amphibians, modern amniotes are linked to their Paleozoic ancestors by a relatively complete sequence of intermediate forms. The earliest known amniotes are immediately recognizable as members of this assemblage because of the similarities of their skeleton to those of primitive living lizards.

amniotes have a much more complete and effective system of muscle stretch receptors than do amphibians. An ad-

Figure 10-1. SIMPLIFIED PHYLOGENY OF AMNIOTES. The class Reptilia, as customarily defined, includes all the darkly stippled lineages. Reptiles have a common ancestry but are considered paraphyletic since they do not include all their descendants. Birds and mammals can each be defined on the basis of unique, shared derived characters. Reptiles can be defined as amniotes that lack the specialized characters of birds and mammals.

Los amniotos presentan reproducción en tierra por fecundación interna
El huevo cleidoico es semipermeable y permite la ovoposición fuera del agua. Existe desarrollo directo sin etapa larval libre.
El huevo provee su propio charco (“Asimilación del medio”)

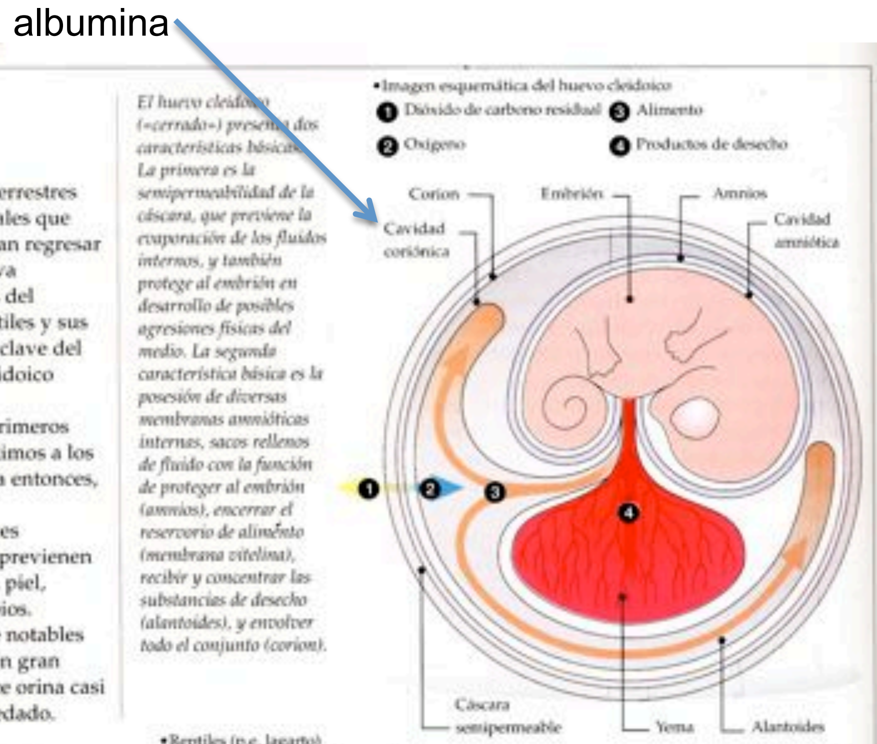
fresh water. If the egg is laid on damp ground, water is drawn into the allantois by osmosis. In modern reptiles such as many lizards and turtles that have permeable egg shells, the water content within the egg may more than double during development because of absorption into the allantois.

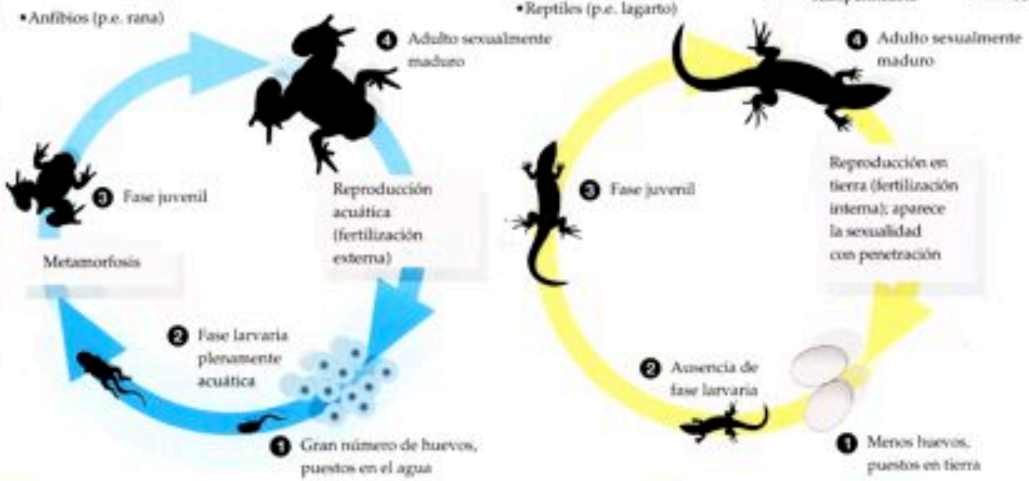
LOS AMNIOTAS Y EL HUEVO CLEIDOICO

Los primeros tetrápodos —animales terrestres de cuatro patas— eran anfibios, animales que vivían sobre tierra pero que necesitaban regresar al agua para reproducirse. La definitiva separación del agua llegó a principios del Carbonífero con los amniotas (los reptiles y sus descendientes, aves y mamíferos). La clave del éxito de los amniotas fue el huevo cleidoico (derecha).

El huevo cleidoico permitió a los primeros reptiles alejarse de los territorios próximos a los cursos de agua en los que vivían hasta entonces, y colonizar regiones más áridas. El recubrimiento cutáneo de los reptiles es escamoso e impermeable, con lo cual previenen la evaporación del agua a través de la piel, proceso que sí tiene lugar en los anfibios. Muchos reptiles disponen también de notables adaptaciones para retener líquidos. Un gran número de ellos, por ejemplo, produce orina casi sólida, un rasgo que las aves han heredado.

El huevo cleidoico («cerrado») presenta dos características básicas. La primera es la semipermeabilidad de la cáscara, que previene la evaporación de los fluidos internos, y también protege al embrión en desarrollo de posibles agresiones físicas del medio. La segunda característica básica es la posesión de diversas membranas amnióticas internas, sacos rellenos de fluido con la función de proteger al embrión (amnios), encerrar el reservorio de alimento (membrana vitelina), recibir y concentrar las substancias de desecho (alantoides), y envolver todo el conjunto (corion).





Los anfibios retienen una modalidad reproductiva parecida a la de los peces: ponen gran cantidad de huevos de pequeño tamaño, cuya temprana eclosión produce formas larvarias (renacuajos), que más tarde se metamorfosean en adultos. Los reptiles ponen menos huevos, no presentan fase larvaria, y su fertilización es interna. La de los peces y anfibios, en cambio, es externa: el macho libera los espermatozoides al agua mientras la hembra pone los huevos.

The largest plethodontid salamanders that undergo direct development on land are no more than 100 millimeters long from their snout to the base of the tail. Lizards of this body length lay eggs that are similar in size to those of the larger plethodontids.

By analogy, one can argue that the origin of amniotes proceeded via a stage in which nonamniotic eggs were laid on land and development was direct. Prior to the evolution of extraembryonic membranes, adult size would have been restricted as it was in plethodontids, so that the largest eggs that could develop without extra support and protection would contain enough nutrients for the young to develop fully before hatching. Very large am-

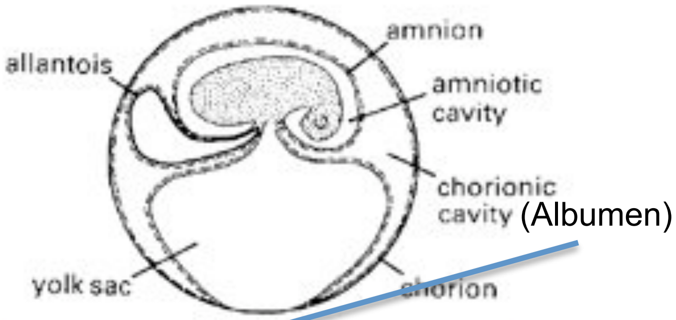
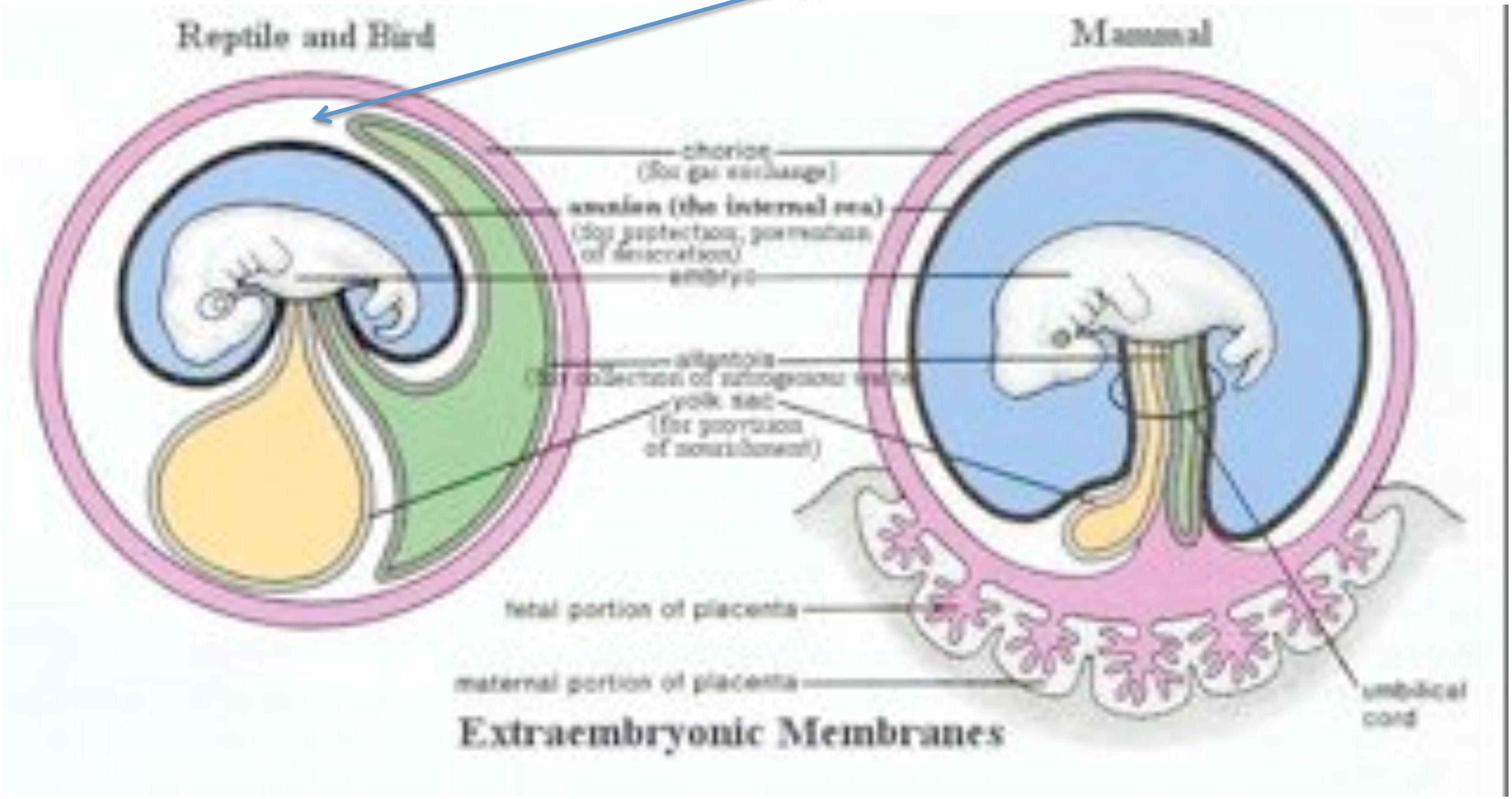
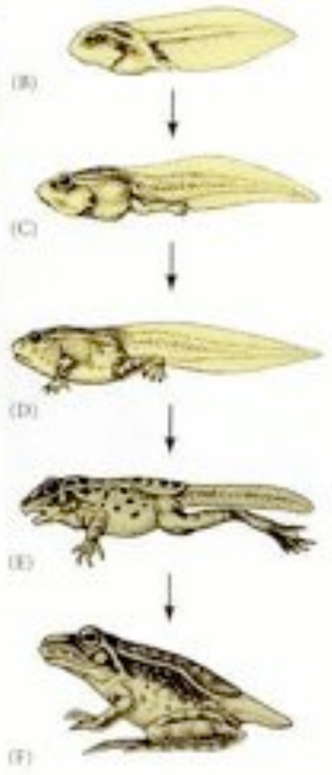
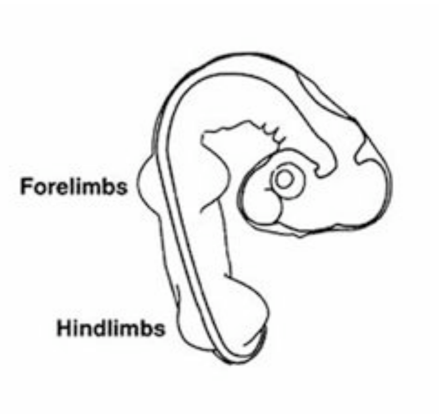


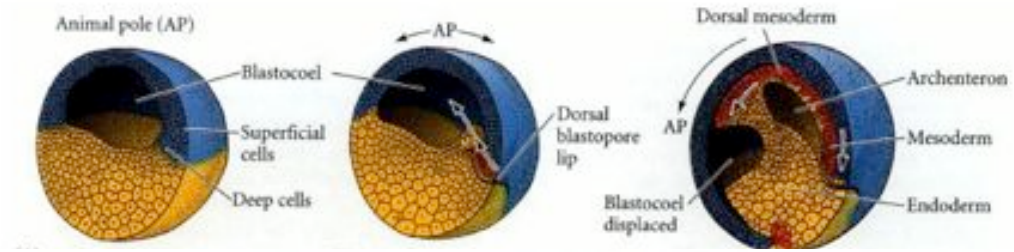
Fig. 5.4 The cleidoic egg, showing the semipermeable shell and the extraembryonic membranes.



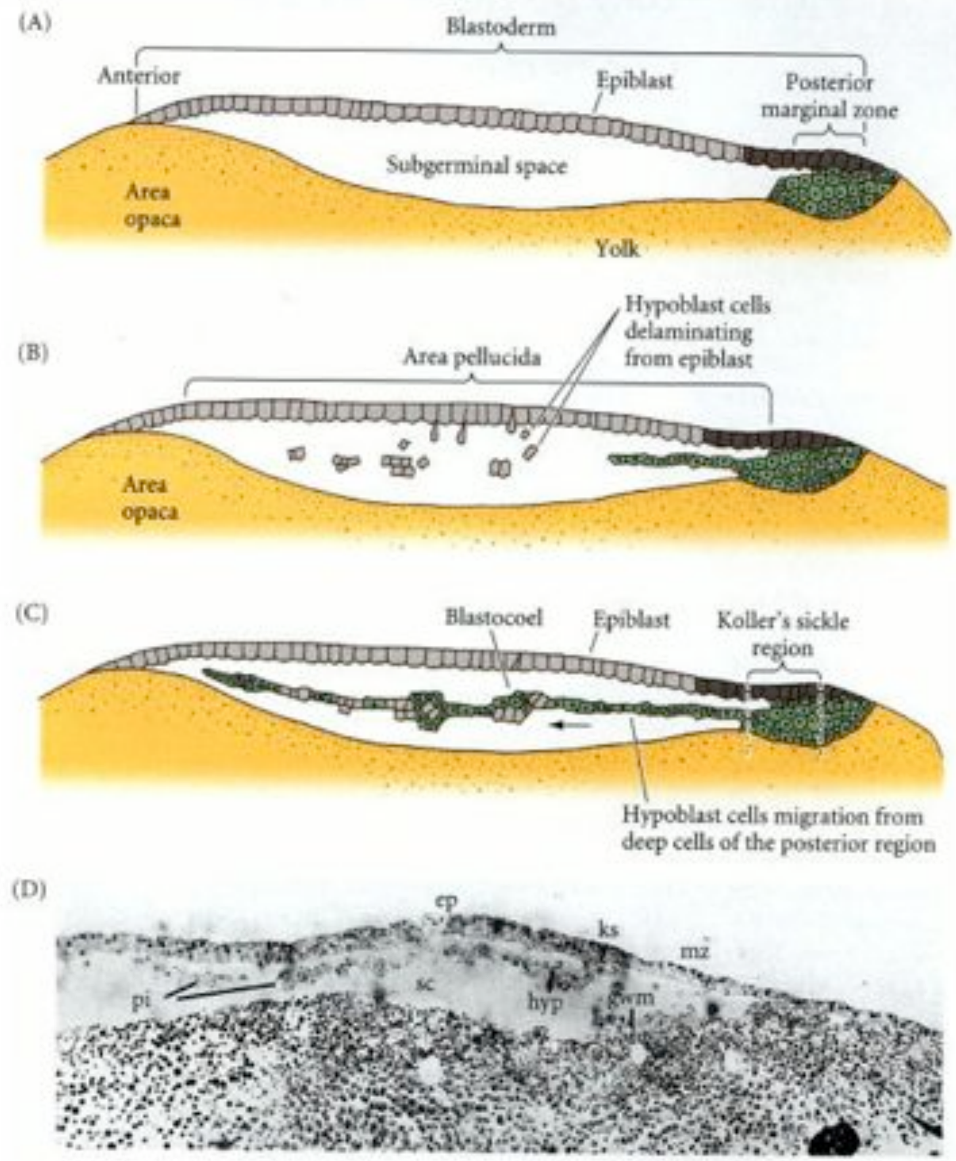
En amniotos, el desarrollo de las extremidades ocurre notablemente más temprano que en anfibios (en anfibios es un evento tardío asociado a metamorfosis, no embriogénesis)
(Tarea: y en pletodontidos?)







Anfibios

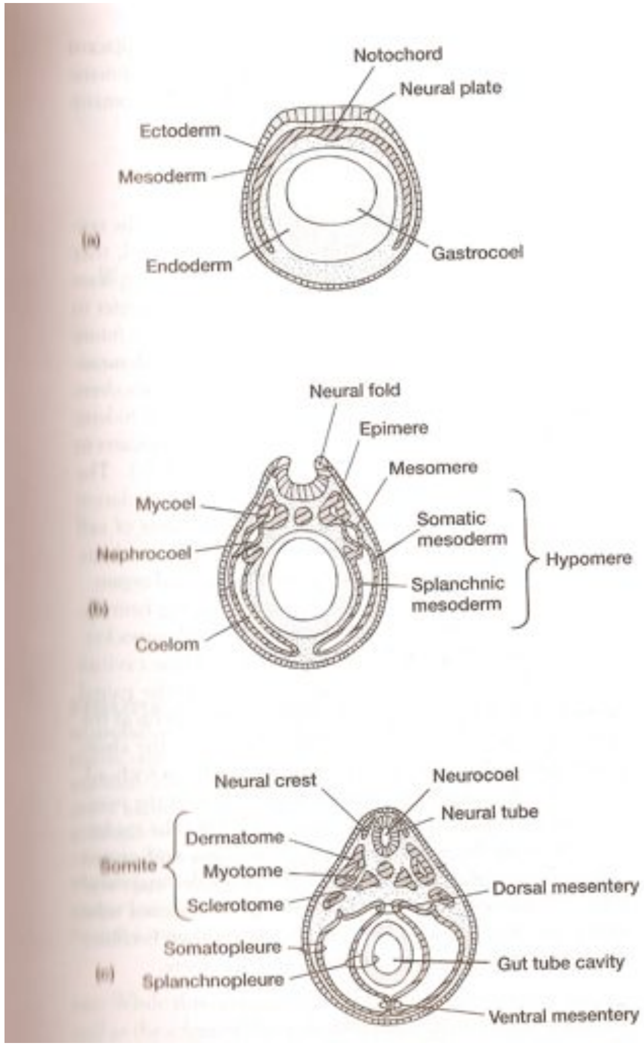


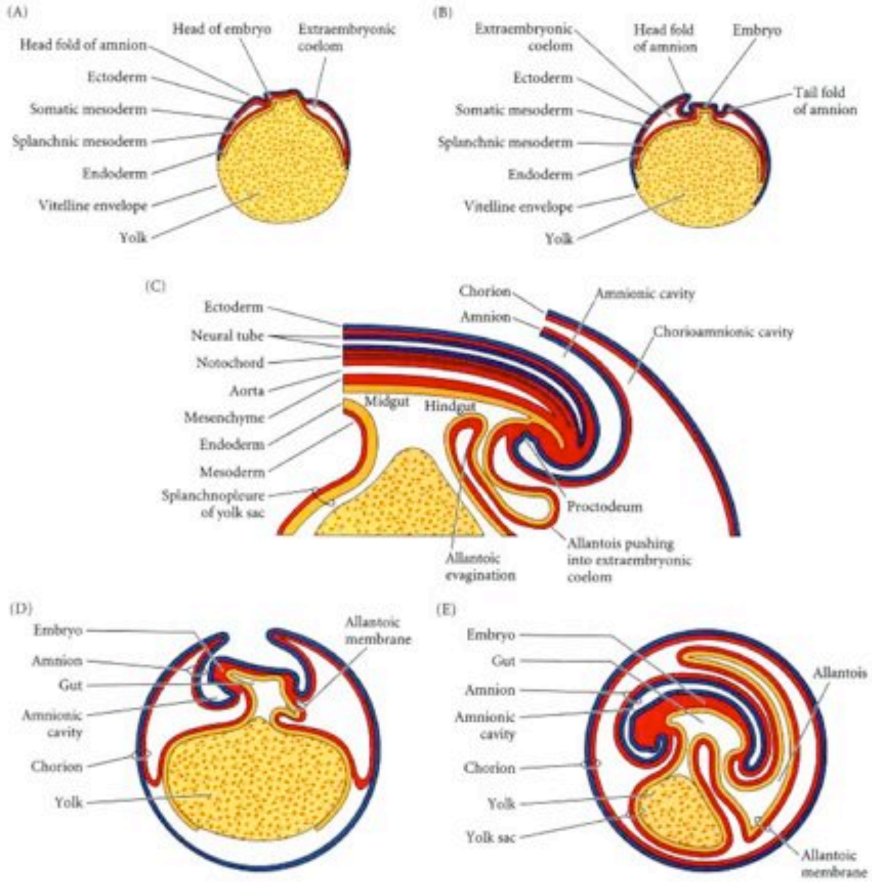
Amnioto: huevo telolecítico

Formación secundaria del blastocele.

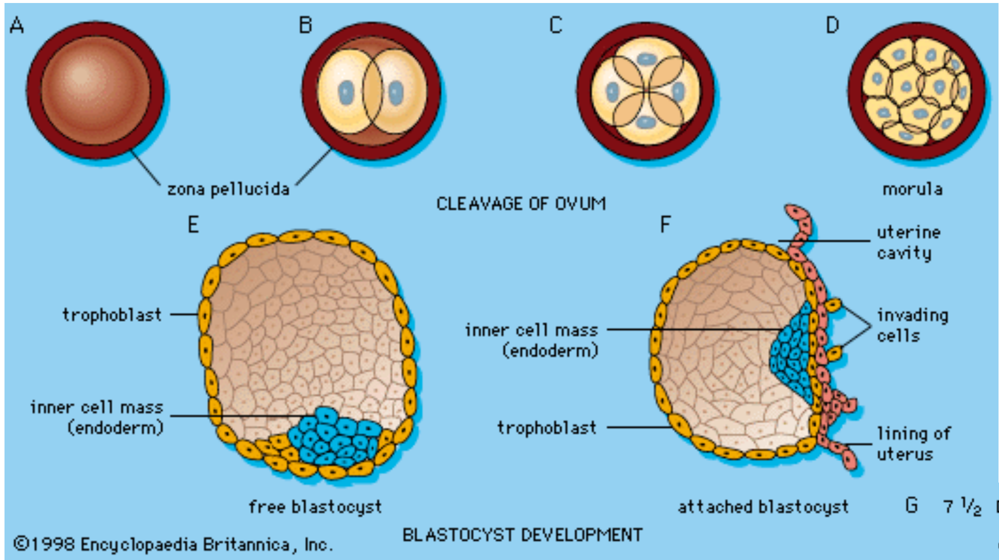
En aves, reptiles, y monotremas el mesodermo somático (de la somatopleura) se extiende por encima del embrión generando la cavidad amniótica. La esplacnopleura genera un divertículo que junto al endodermo forma el alantoides

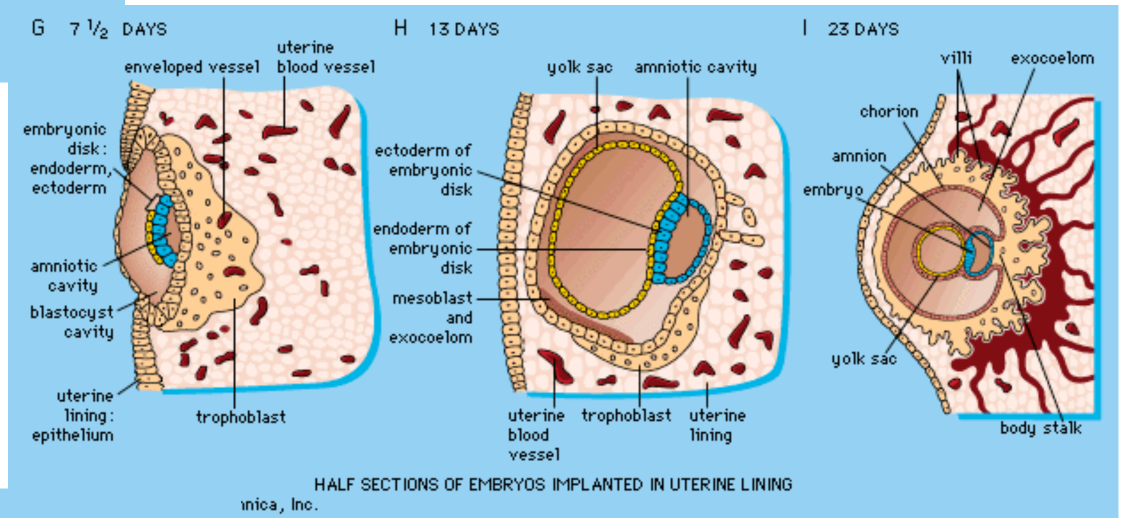
Extraembryonic membranes develop in a similar way in all three living groups of amniotes. It is more parsimonious to assume that their common ancestor had already developed this feature than to propose that it had evolved separately two or three times. The small size of the early fossils also suggests that they may already have achieved a pattern of reproduction approaching that of modern amniotes.

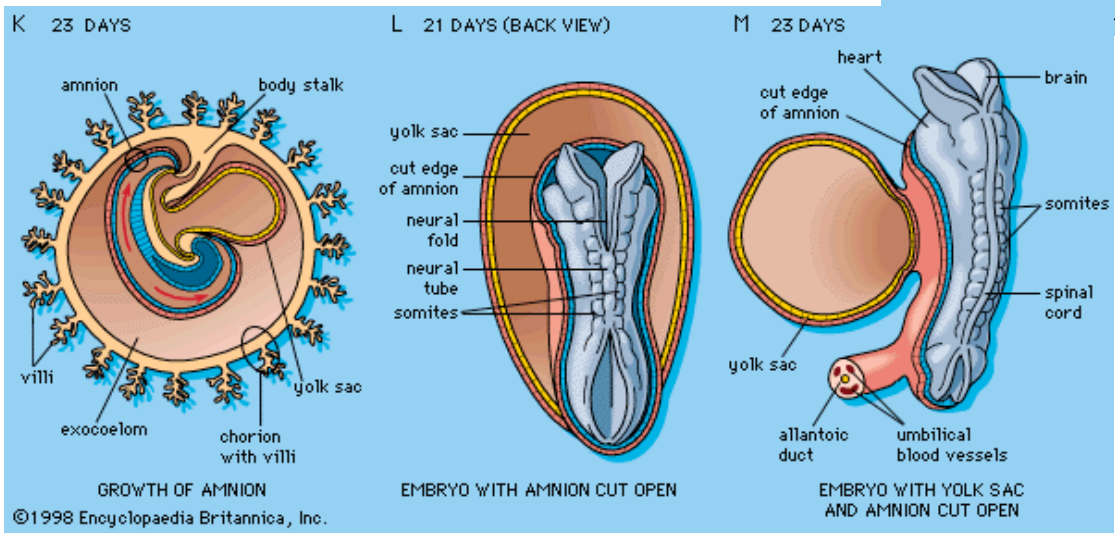


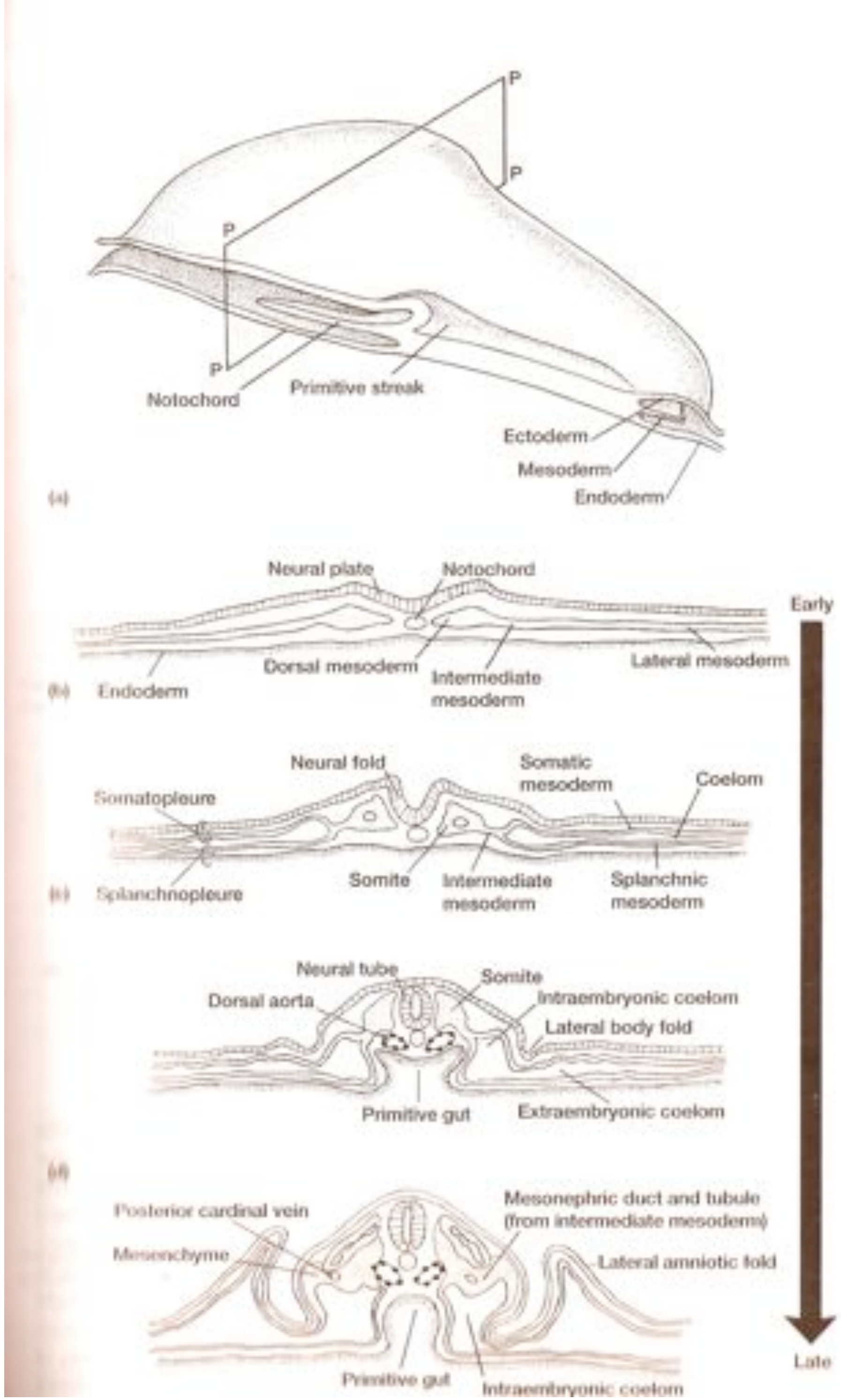


Euterios: desarrollo temprano de la futura cavidad amniótica



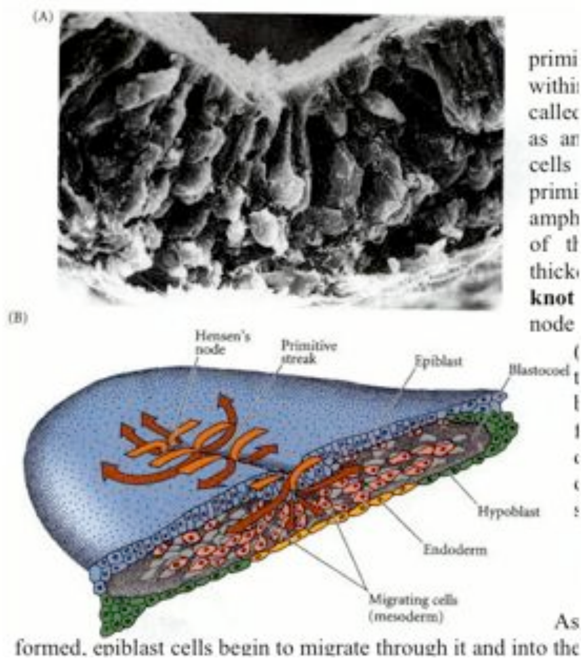




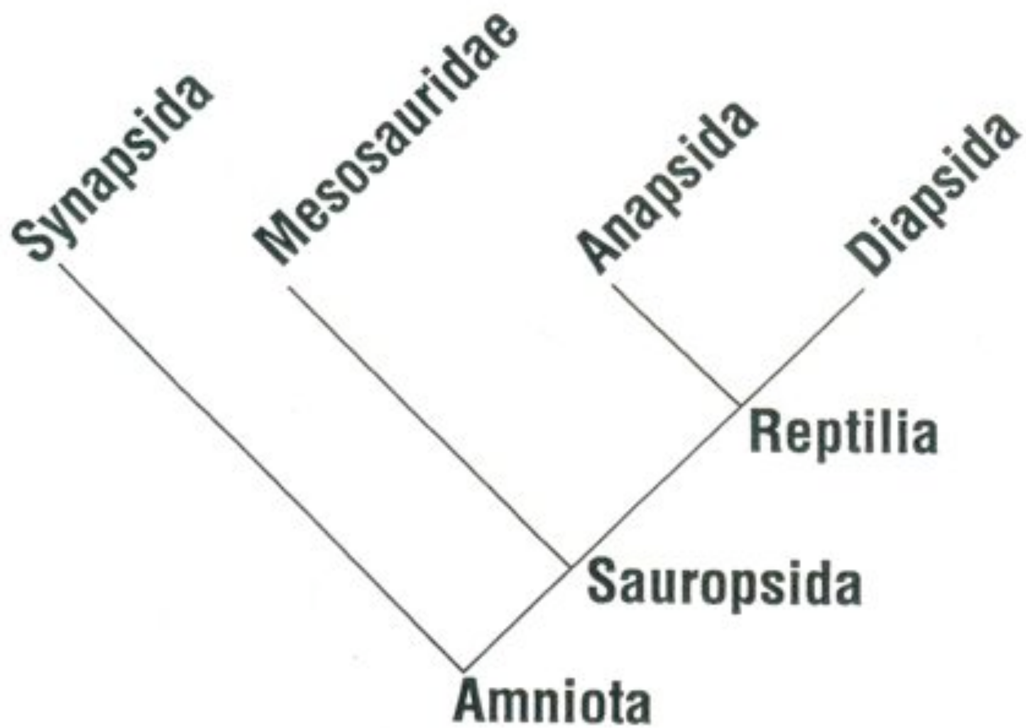


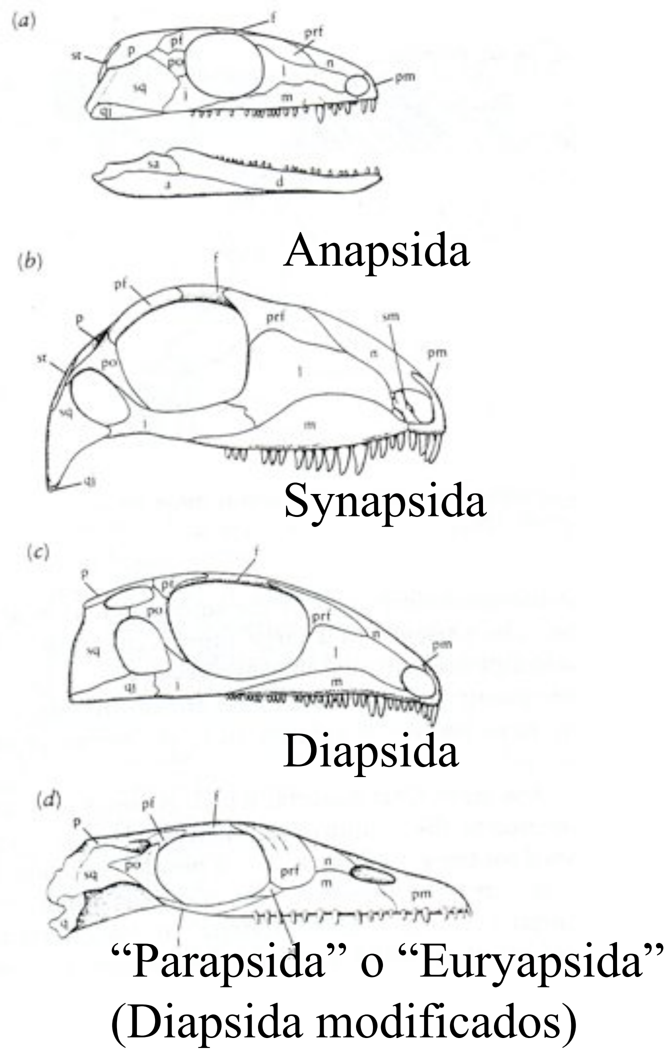
Gastrulación en Aves y Reptiles

Hay un blastodisco en que se forma un surco primitivo por el cual ingresan celulas que se extienden hacia anterior y hacia los lados. Las primeras celulas en ingresar hacia anterior conforman la cabeza del embrión. Las células endodérmicas que ingresan desplazan las del hipoblasto hacia los lados. Juntas, conforman el saco vitelino.



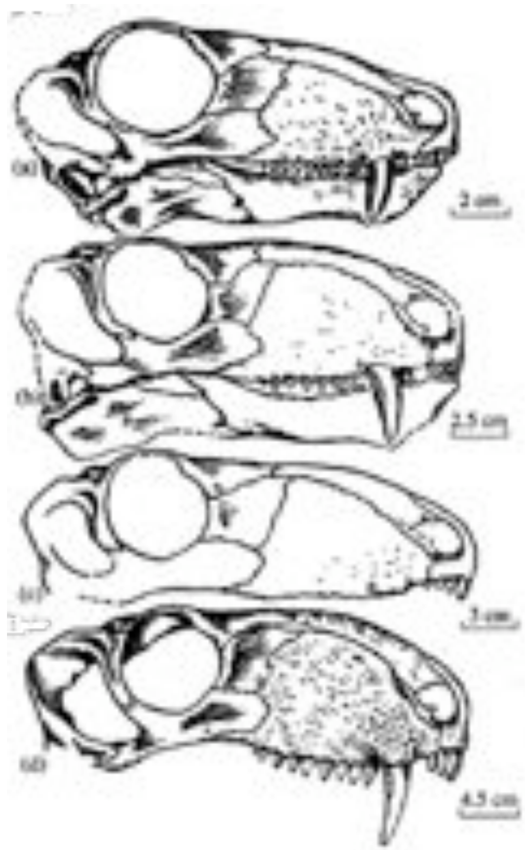
Los amniotos pueden dividirse en dos líneas principales: Los synapsidos (de quienes provienen los mamíferos) y los Sauropsidos (de quienes provienen "reptiles" y aves).
Los Synápsidos poseen una apertura (fenestra) en el cráneo, detrás del ojo, debajo de la unión entre los huesos postorbital y escamoso. Comparten un ancestro en común más reciente con un mamífero que con una lagartija. Filogenéticamente, no pertenecen a reptilia, pero a la mayoría se les conoce como "reptiles semejantes a mamíferos"

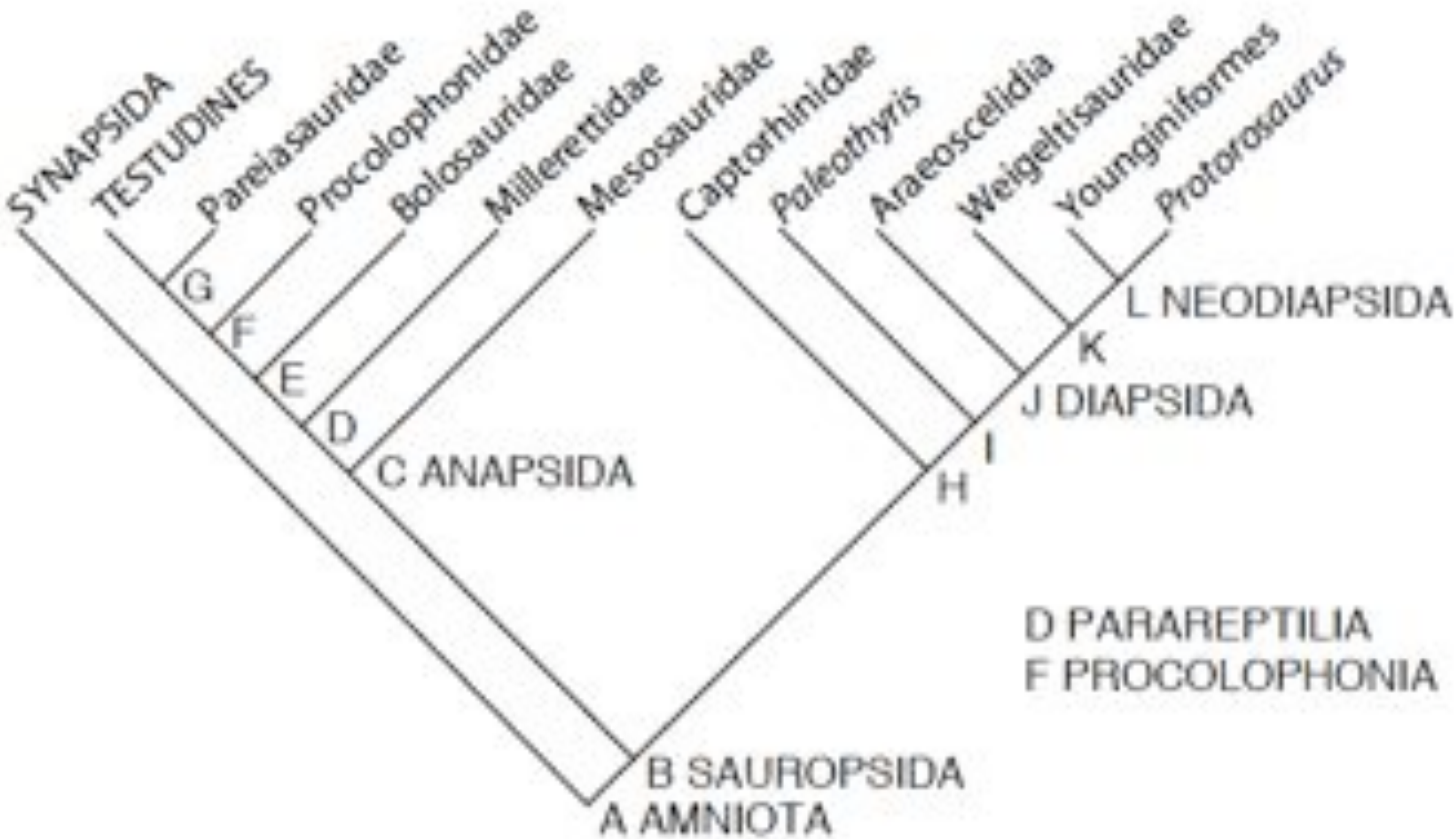




SYNAPSIDOS:

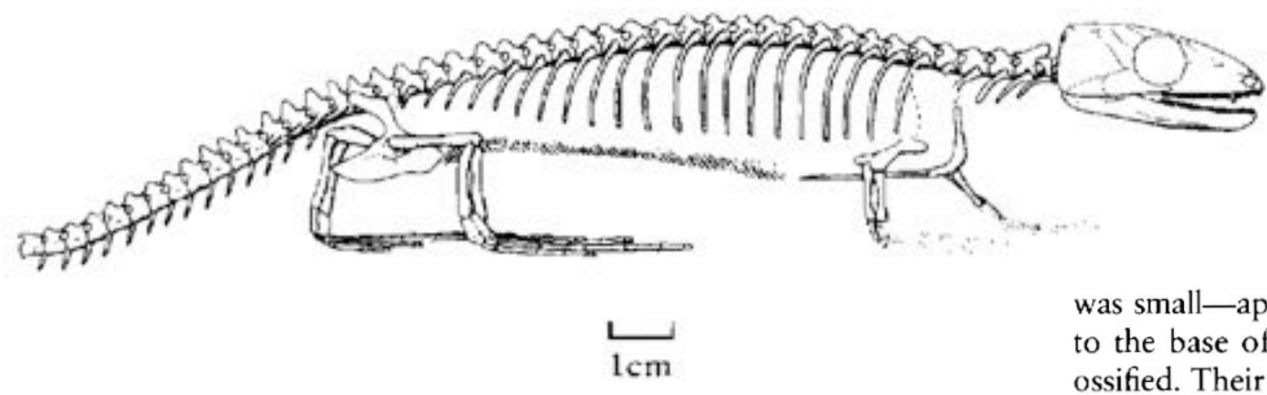
VOLVEREMOS A ELLOS!




SYNAPSIDA
TESTUDINES
Pareiasauridae
Procolophonidae
Bolosauridae
Millerettidae
Mesosauridae
Captorhinidae
Paleothyris
Araeoscelidia
Weigeltisauridae
Younginiformes
Protorosaurus
G
F
E
D
C ANAPSIDA
L NEODIAPSIDA
K
J DIAPSIDA
I
H
B SAUROPSIDA
A AMNIOTA
D PARAREPTILIA
F PROCOLOPHONIA

Los amniotos mas antiguos conocidos ya tienen afinidad especificamente con los reptilia, indicando que ya habian aparecido todos los atributos generales de amniotos modernos (corona)

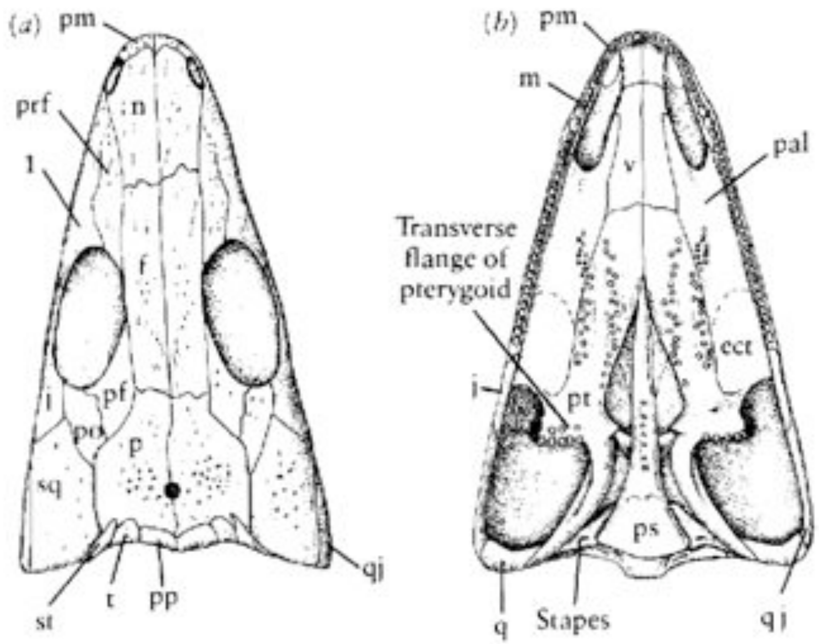
The best-known primitive amniotes from the early Pennsylvanian are *Hylonomus* (Figure 10-2) and *Paleothyris* (Figure 10-3). We include these genera and other genera from the later Pennsylvanian (Carroll and Baird, 1972) and Lower Permian (Clark and Carroll, 1973) within the family Protorothyridae (Romeriidae) in the order Captorhinida.



was small—approximately 100 millimeters from the snout to the base of the tail—and the skeleton was very well ossified. Their general appearance would have closely resembled that of modern lizards.

Figure 10-2. SKELETON OF ONE OF THE EARLIEST KNOWN AMNIOTES, *HYLONOMUS LYELLI* FROM THE EARLY PENNSYLVANIAN OF JOGGINS, NOVA SCOTIA. The remains were found within the upright stump of the giant lycopod *Sigillaria*. *From Carroll and Baird, 1972.*

EXPANSION DEL SUPRAOCCIPITAL (desde diadectomorpha)



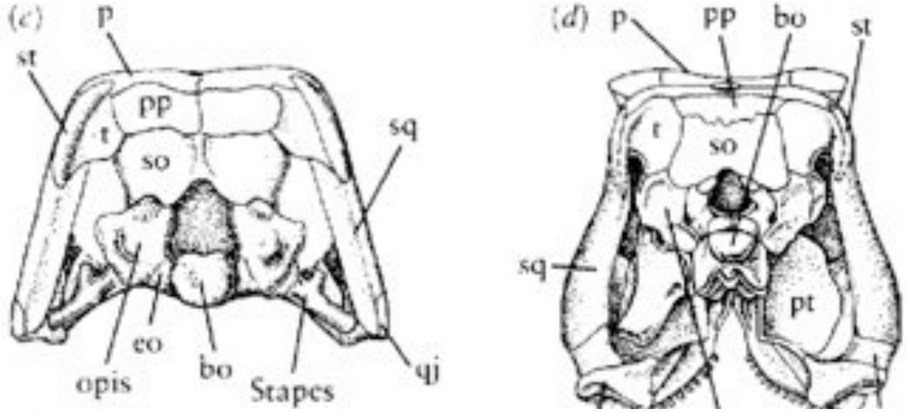
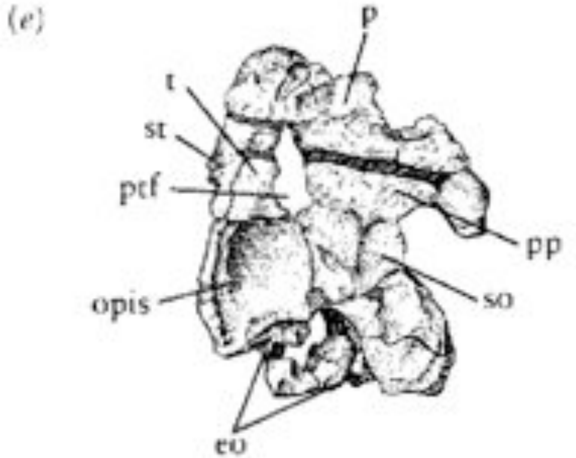


Figure 10-3. THE SKULL OF PRIMITIVE AMNIOTES. The skull of *Paleothyris* in (*a*) dorsal, (*b*) palatal, and (*c*) occipital views. *From Carroll and Baird, 1972.* (*d*) Occiput of the primitive mammal-like reptile *Ophiacodon. From Romer and Price, 1940. With permission of the Geological Society of America.* (*e*) Occiput of an immature specimen of *Desmatodon*, a carboniferous relative of *Diadectes. From Vaughn, 1972.* In all these skulls the supraoccipital is a broad plate of bone that links the exoccipitals and otic capsules with the dermal bones at the back of the skull table. (*f*) The stapes of *Hylonomus*, which is characteristic of primitive amniotes. *From Carroll, 1969b.* Abbreviations as in Figure 8-3.

Hyomandibular (estribo) robusto

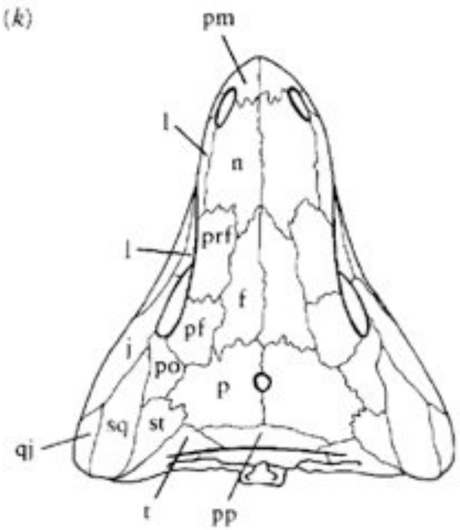


paroccipital processes, which extend from the otic capsules to the quadrates in modern lizards, were poorly developed and did not link the braincase to the cheek.

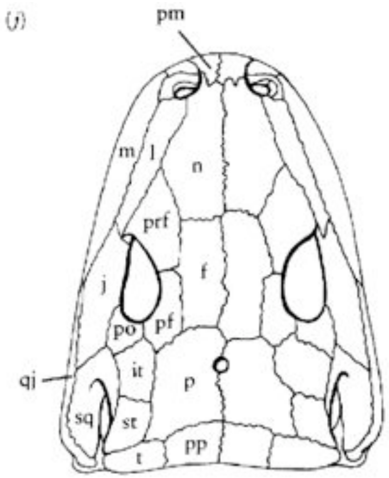
a, angular; ano, anocleithrum; art, articular; at, anterior tectal; bo, basioccipital; bs, basisphenoid; cl, clavicle; clei, cleithrum; cor, coronoid; d, dentary; ect, ectopterygoid; eo, exoccipital; ept, epipterygoid; esl, lateral extrascapular; esm, medial extrascapular; f, frontal; gul, gular plate; ina, internasal; inf, interfrontal; it, intertemporal; j, jugal; l, lacrimal; lr, lateral rostral; m, maxilla; n, nasal; o, opercular; opis, opisthotic; p, parietal; pal, palatine; part, prearticular; pf, postfrontal; pm, premaxilla; po, postorbital; pop, preopercular; pos, postspiracular; pot, posttemporal; pp, postparietal; prf, prefrontal; pro, proötic; ps, parasphenoid; pt, pterygoid; ptf, posttemporal fossa; q, quadrate; qj, quadratojugal; sa, surangular; sclei, supracleithrum; sm, septomaxilla; so, supraoccipital; sop, subopercular; sp, splenial; sph, sphenethmoid; spp, postsplenial; sq, squamosal; st, supratemporal; subm, submandibular (includes also the more anterior plates in this series); t, tabular; v, vomer; I–XII, cranial nerves. *From Moy-Thomas and Miles, 1971, after Jarvik. By permission from Chapman and Hall, Ltd.*

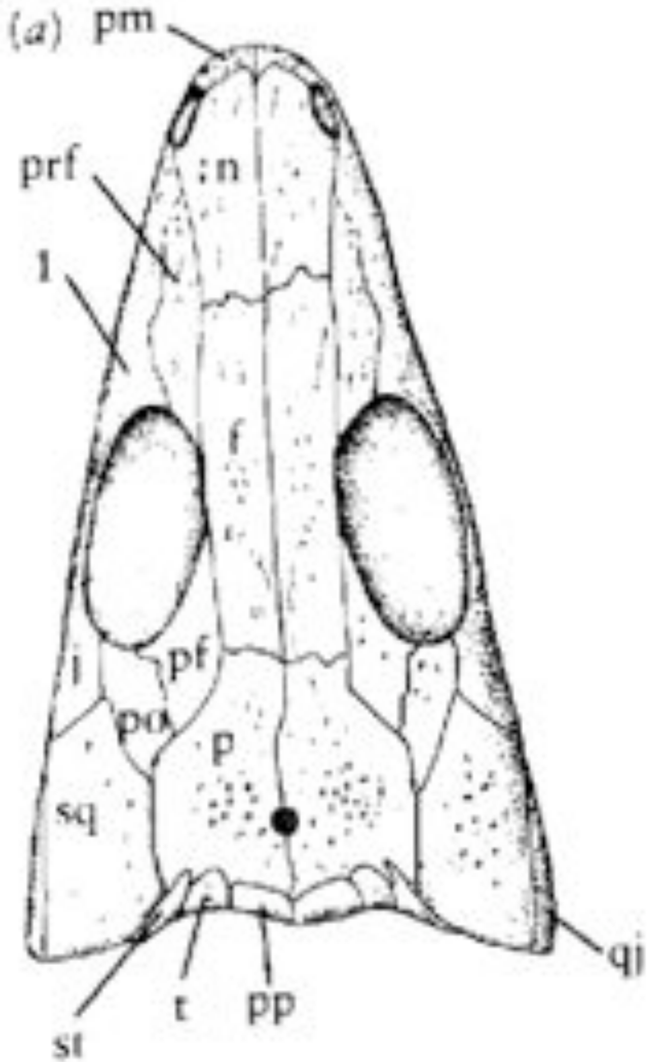
Pérdida del intertemporal, expansion lateral del parietal

The skull roof, like that of Paleozoic amphibians, forms a nearly complete dermal covering, with openings for the eyes, pineal, and nostrils. The pattern of the bones resembles that of small anthracosaurs such as the gephyrostegids, except for the absence of an otic notch and the intertemporal bone. The area that was occupied by that bone in primitive amphibians appears to have been taken over by the extensive parietal, which separates the postorbital from the supratemporal. The postparietal, tabular, and supratemporal are reduced in size and their exposure is limited to the occipital surface.



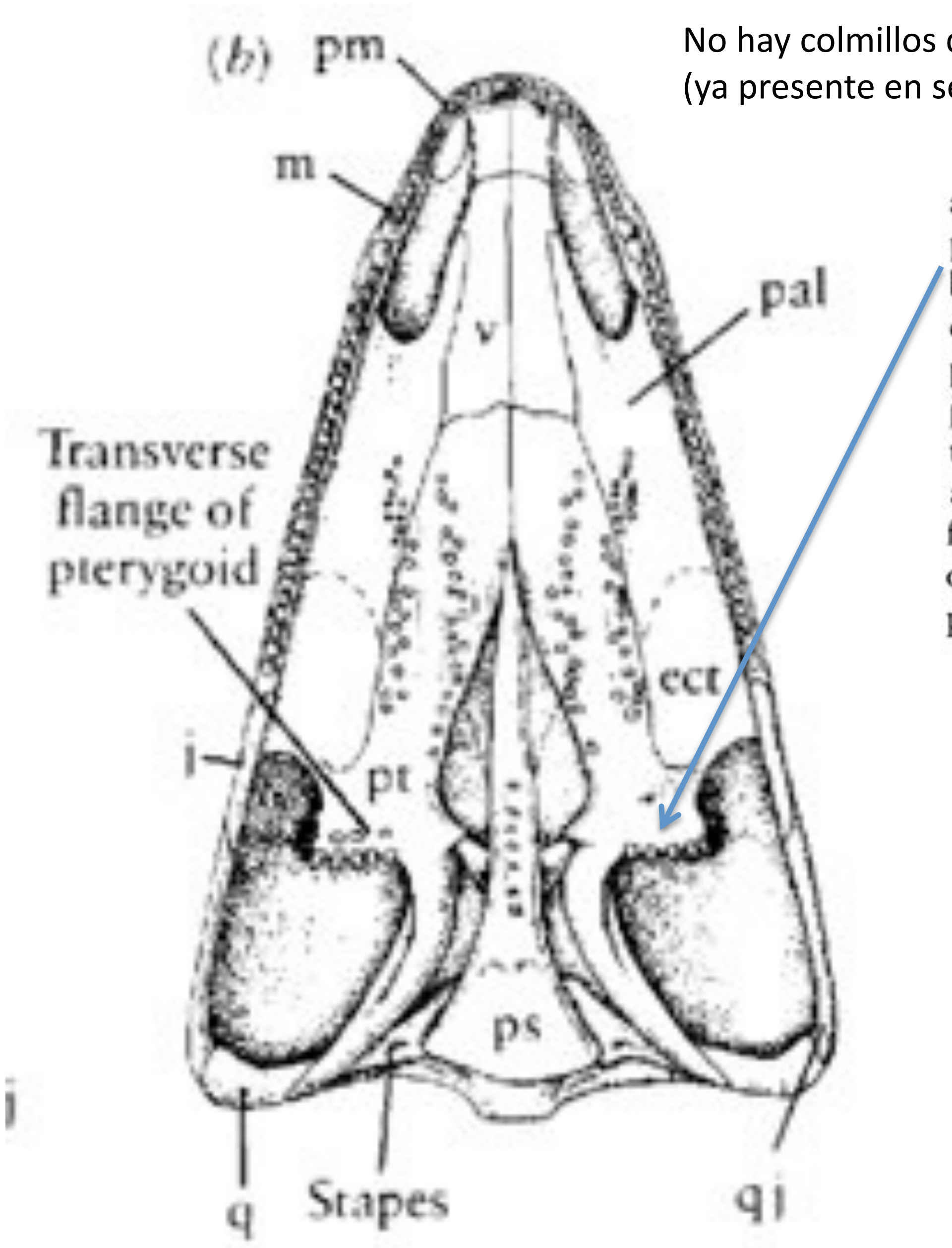
Limnoscelis





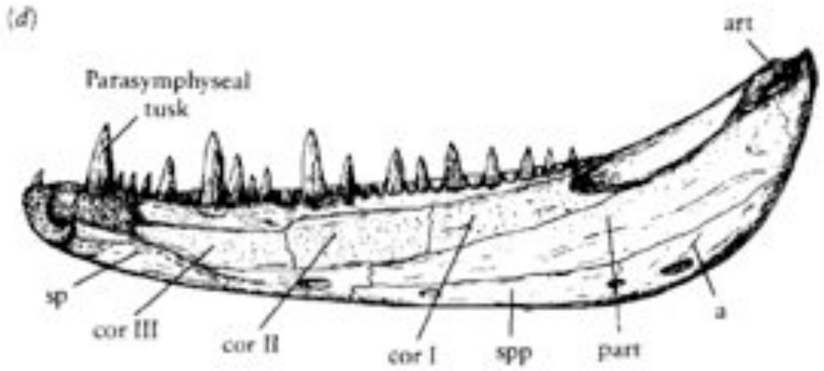
a, angular; ano, anocleithrum; art, articular; at, anterior tectal; bo, basioccipital; bs, basisphenoid; cl, clavicle; clei, cleithrum; cor, coronoid; d, dentary; ect, ectopterygoid; eo, exoccipital; ept, epipterygoid; esl, lateral extrascapular; esm, medial extrascapular; f, frontal; gul, gular plate; ina, internasal; inf, interfrontal; it, intertemporal; j, jugal; l, lacrimal; lr, lateral rostral; m, maxilla; n, nasal; o, opercular; opis, opisthotic; p, parietal; pal, palatine; part, prearticular; pf, postfrontal; pm, premaxilla; po, postorbital; pop, preopercular; pos, postspiracular; pot, posttemporal; pp, postparietal; prf, prefrontal; pro, proötic; ps, parasphenoid; pt, pterygoid; ptf, posttemporal fossa; q, quadrate; qj, quadratojugal; sa, surangular; sclei, supracleithrum; sm, septomaxilla; so, supraoccipital; sop, subopercular; sp, splenial; sph, sphenethmoid; spp, postsplenial; sq, squamosal; st, supratemporal; subm, submandibular (includes also the more anterior plates in this series); t, tabular; v, vomer; I–XII, cranial nerves. *From Moy-Thomas and Miles, 1971, after Jarvik. By permission from Chapman and Hall, Ltd.*

No hay colmillos del paladar: "aleta" transversal del pterygoideo (ya presente en seymouria)



The most significant feature of the palate in early amniotes is the presence of a transverse flange on the pterygoid. The portion of this bone that is lateral to the basicranial articulation is angled ventrally into the mouth cavity. In modern lizards, the transverse flange of the pterygoid serves as the origin of one of the largest of the jaw-closing muscles, the pterygoideus. The orientation of this muscle, which is at nearly right angles to the other adductor jaw muscles, enables it to exert its maximum force when the jaws are wide open. There is little evidence of the existence of a large pterygoideus muscle in any primitive amphibian.

In contrast with labyrinthodonts, the palate of primitive amniotes does not have large fangs. In most genera there are three rows of denticles, one on the transverse flange of the pterygoid, a second along the margin of the small interpterygoid vacuities, and a third extending across the palatine bone. Some early amniotes with large marginal teeth show a trace of labyrinthine infolding, but this infolding is absent in most genera. Many early amniotes have two pairs of large marginal teeth near the anterior end of the maxilla that are broadly comparable with the mammalian canine teeth.



“laberintodonte” temprano Megalocephalus (Baphetidae)

The lower jaw (Figure 10-5) lacks parasymphyseal tusks, which are present in early labyrinthodonts, and has one or two coronoids and a splenial. Otherwise, the elements resemble those of most primitive amphibians.

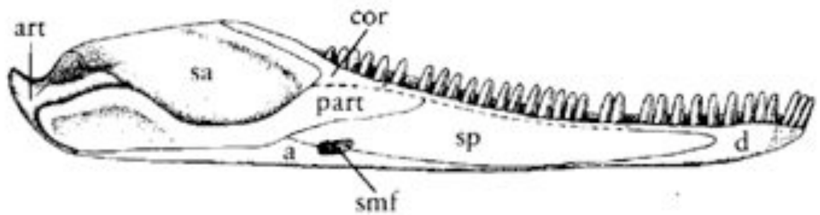
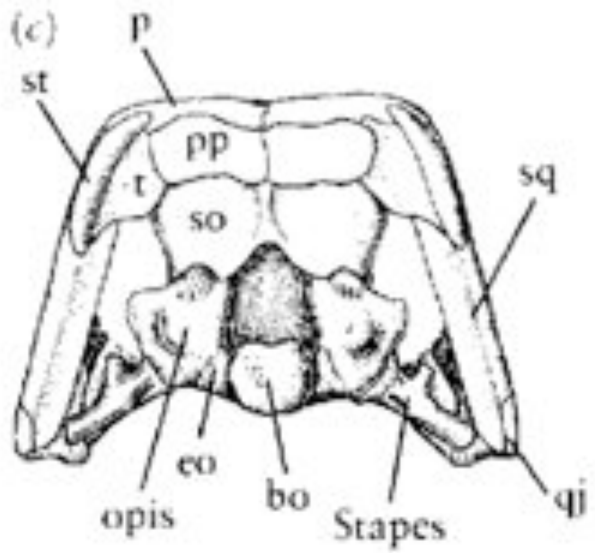


Figure 10-5. MEDIAL VIEW OF THE LOWER JAW OF *PROTOROTHYRIS*, A PRIMITIVE AMNIOTE FROM THE LOWER PERMIAN. Abbreviations as in Figure 8-3, plus: smf, submeckelian fossa. *From Clark and Carroll, 1973.*



Because the back of the braincase was initially not firmly attached to either the skull roof or the cheek, the stapes retained an important role in its support. The stapes is a large element, with an expanded foot plate, a thick shaft that extends obliquely and ventrolaterally toward the quadrate, and a short dorsal process that articulates with the otic capsule. The large size of the stapes and particularly its broad foot plate precludes its effective participation in an impedance-matching system such as was described previously in Chapter 9. However, a fenestra ovalis is present.

It was long assumed that early amniotes had a tympanum, but they lack an otic notch and a tympanum would have had to be very large to activate a stapes of this size. In later amniotes, either the squamosal, quadrate, or angular became specialized to support a large tympanum. Hearing in early amniotes may have occurred by bone conduction, as in salamanders, caecilians, and those modern reptiles without a tympanum. In these groups, hearing is limited to relatively low-frequency, high-intensity sounds (Wever, 1978).

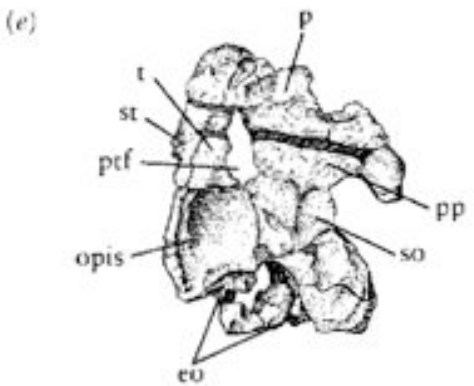
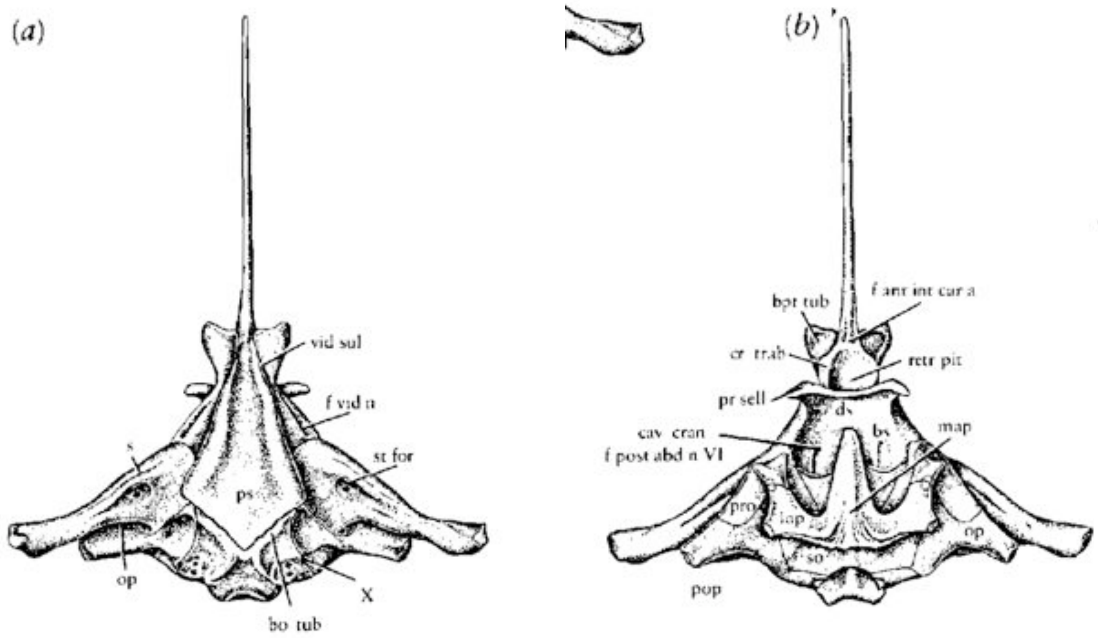
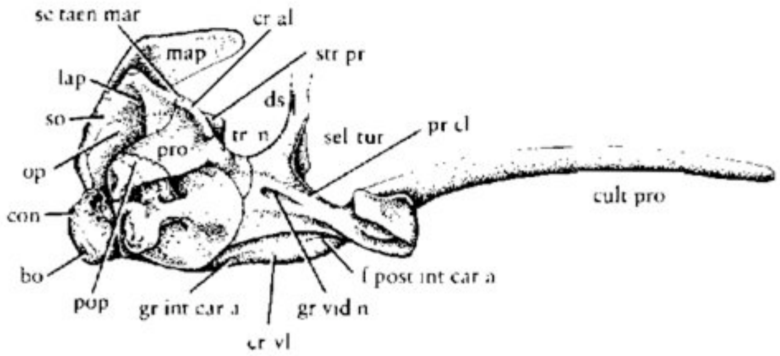


Figure 10-3. THE SKULL OF PRIMITIVE AMNIOTES. The skull of *Paleothyris* in (*a*) dorsal, (*b*) palatal, and (*c*) occipital views. *From Carroll and Baird, 1972.* (*d*) Occiput of the primitive mammal-like reptile *Ophiacodon*. *From Romer and Price, 1940. With permission of the Geological Society of America.* (*e*) Occiput of an immature specimen of *Desmatodon*, a carboniferous relative of *Diadectes*. *From Vaughn, 1972.* In all these skulls the supraoccipital is a broad plate of bone that links the exoccipitals and otic capsules with the dermal bones at the back of the skull table. (*f*) The stapes of *Hylonomus*, which is characteristic of primitive amniotes. *From Carroll, 1969b.* Abbreviations as in Figure 8-3.





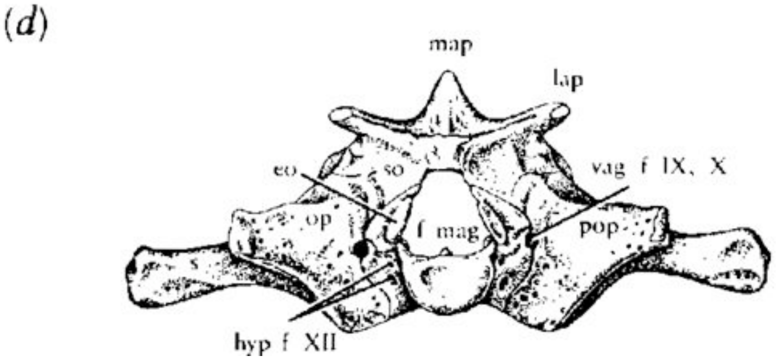


Figure 10-4. BRAINCASE OF PRIMITIVE AMNIOTES. (*a*) Ventral, (*b*) dorsal, (*c*) lateral, and (*d*) occipital views of the captorhinid *Eocaptorhinus*. Abbreviations as follows: bo tub, basioccipital tubercle; bpt tub, basipterygoid tubercle; bs, basisphenoid; cav cran, cavum cranii; con, occipital condyle; cr al, crista alaris; cr trab, crista trabecularis; cr vl, crista ventrolateralis; cult pro, cultriform process; ds, dorsum sella, f ant int car a, foramen anterior for internal carotid artery canal; f mag, foramen magnum; f post abd n VI, foramen posterior of abducens (VI) nerve canal; f post int car a, foramen posterior of internal carotid artery canal; f vid n, foramen for vidian (VII) nerve; gr int car a, groove for internal carotid artery; gr vid n, groove for vidian (VII) nerve; hyp f XII, hypoglossal (XII) nerve foramina; lap, lateral ascending process of supraoccipital; map, median ascending process; op, opisthotic; pop, paroccipital process; pr cl processus clinoideus; pro, proötic; pr sell, processus sellaris; ps, parasphenoid; retr pit, retractor pit; s, stapes sc taen mar, scar for attachment of taenia marginalis; sel tur, sella turcica; so, supraoccipital; st for, stapedial foramen; str pr, supratrigeminal process; tr n, trigeminal notch; vag f IX, X, vagus foramen (IX, X); vid sul, vidian sulcus. *From Heaton, 1979.*

The general structure of the braincase of early amniotes resembles that of modern lizards (Figure 10-4). The occipital plate and otic capsule are well ossified, but the more anterior portion is largely cartilaginous, in contrast with the condition in most labyrinthodonts. The area os-

The basioccipital and base of the exoccipitals form a prominent medial occipital condyle that fits into a ring formed by the intercentrum and the arches of the atlas vertebra like the ball of a ball-and-socket joint. The otic capsule consists of a posterior opisthotic and anterior proötic. Together with the supraoccipital, they enclose the semicircular canals.

In early amniotes, the elements of the palatoquadrate, which are still extensive in primitive amphibians, are reduced to the relatively small epipterygoid and the quadrate. The epipterygoid has a wide base that is in contact with the upper surface of the pterygoid and forms the basicranial articulation with the basisphenoid. Dorsally,

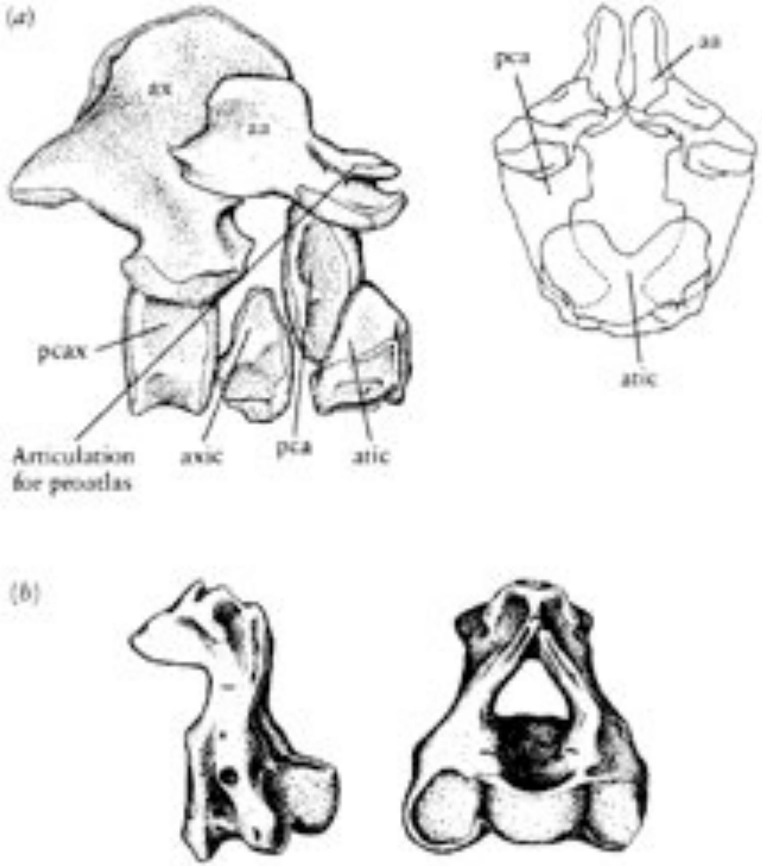


Figure 9-12. (*a*) Atlas-axis complex of the early anthracosaur *Proterogyrinus* showing the multipartite structure common to most labyrinthodonts; lateral and anterior views, × 2. A further small paired element, the proatlas, links the atlas arch with the exoccipital. *From Holmes, 1984.* (*b*) First cervical vertebra of the microsaur *Euryodus* showing pattern common to lepospondyls, in which the first vertebra is a unitary structure, × 4.5. The articulating surface with the skull is very broad, limiting lateral movement of the head. *From Carroll and Gaskill, 1978.* Abbreviations as follows: aa, atlas arch; ax, axis arch; atic, atlas intercentrum; axic, axis intercentrum; pca, pleurocentrum of atlas; pcax, pleurocentrum of axis.

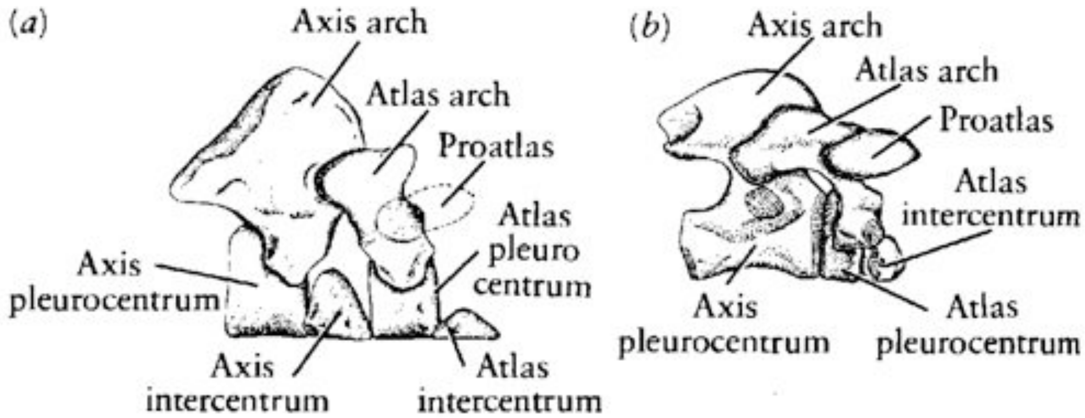
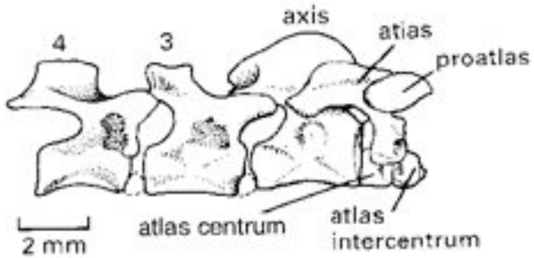


Figure 10-6. VERTEBRAE OF PRIMITIVE AMNIOTES AND ANTHRACOSAURS. (*a*) Atlas-axis complex of the anthracosaur *Gephyrostegus. From Carroll, 1970.* (*b*) Atlas-axis of the protorothyrid *Paleothyris. From Carroll, 1969b.* (*c* and *d*) Trunk vertebra of a primitive

trunk vertebrae. The elements of the atlas-axis complex are basically similar to those of primitive anthracosaurs, except for the greater degree of consolidation, with the axis arch and centrum fused.

Ancho del arco neural: discusión



The postcranial skeleton of early amniotes generally resembles that of the primitive living reptile *Sphenodon*. The vertebral centra consist of large spool-shaped pleurocentra, with deep recesses at both ends for the notochord, and small crescentic intercentra. In the primitive state, the neural arches are narrow and the zygapophyses are close to the midline (Figure 10-6). A suture between the neural arch and the pleurocentrum may remain in the

axis arch and centrum fused. The earliest amniote in which an accurate count can be made has 32 presacral vertebrae, but other early genera have 24 or 25. Most early amniotes have two sacral vertebrae and a very long tail. Ribs are present throughout the trunk and at the base of the tail.

Tseajaia and limnoscelids both have greatly expanded neural arches, a feature that is also observed among some Permian amniotes (see Figure 10-6). This specialization was once thought to be a primitive character of amniotes. However, it is not present in the earliest amniote groups and may have evolved convergently within several later lineages in association with large body size.

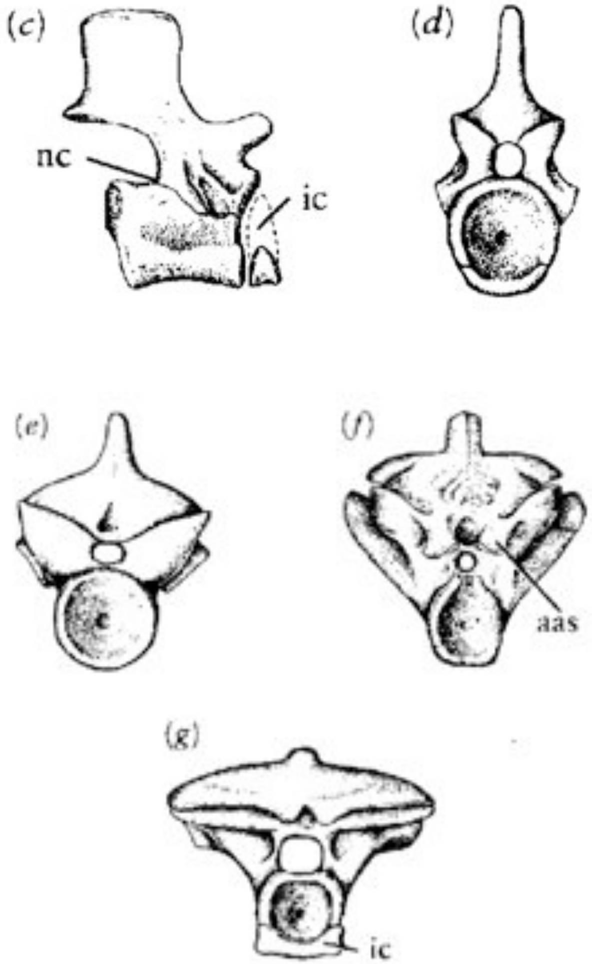


Figure 10-6. VERTEBRAE OF PRIMITIVE AMNIOTES AND ANTHRACOSAURS. (*a*) Atlas-axis complex of the anthracosaur *Gephyrostegus*. *From Carroll, 1970*. (*b*) Atlas-axis of the protorothyrid *Paleothyris*. *From Carroll, 1969b*. (*c* and *d*) Trunk vertebra of a primitive amniote based on the Carboniferous specimen number 1901.1378 from the Humboldt Museum, Berlin. (*c*) *From Carroll, 1970*. Anterior views of three primitive tetrapods with laterally expanded neural arches: (*e*) the limnoscelid *Limnostygis*, (*f*) *Diadectes*, and (*g*) *Seymouria*. Abbreviations as follows: aas, accessory articulating surfaces; ic, intercentra; nc, neurocentral suture.

Vuelve el escapulo-coracoide!

3 centros de osificacion (2 coracoides)

Interclavicula forma de “T”

Origen del astragalo (tibiale + carpales)

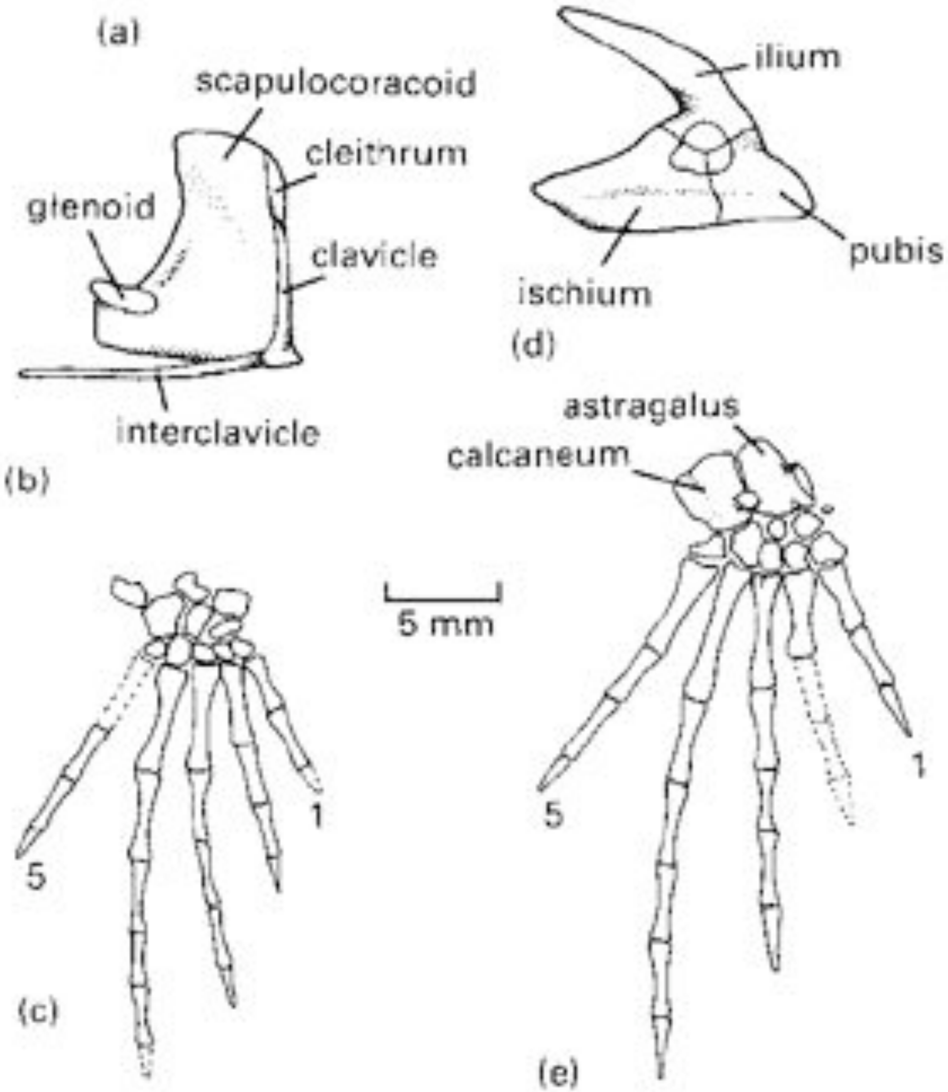


Fig. 5.2 Vertebrae and limbs of the earliest amniotes (a–c, e) *Paleothyris* and (d) *Hylonomus*: (a) cervical vertebrae 1–4; (b) pectoral girdle; (c) hand; (d) pelvic girdle; (e) foot. (After Carroll, 1969a.)

10-8). The size of the clavicles and cleithra is reduced, and the interclavicle has a distinctive *T* shape. In the primitive state, the adult scapulocoracoid is ossified as a single unit with a screw-shaped glenoid. In immature specimens, we can see that it is formed from three centers of ossification: the vertical scapula and separate anterior and posterior coracoids. The humerus has a relatively long narrow shaft from which the extremities are expanded at right angles to one another. As in many primitive Paleozoic amphibians, there is an entepicondylar foramen. A supinator process, which is proximal to the ectepicondyle, may be a primitive feature for amniotes. The carpus has 11 well-ossified, tightly fitting elements, including a pisiform (Figure 10-8). The tarsus is specialized over that of most Paleozoic amphibians in having the tibiale, intermedium, and proximal centrale fused into a single bone, the astragalus. Peabody (1951) documented this fusion ontogenetically. The fibulare is enlarged and is now termed the calcaneum. As in anthracosaurs, the phalangeal count of the manus is 2, 3, 4, 5, 3 and that of the pes is 2, 3, 4, 5, 4. Based on the similarity of the joints of the girdles and limbs and the evidence of foot prints, we assume that the general pattern of locomotion in early amniotes probably was broadly similar to that of primitive amphibians and has been little altered in primitive living lizards (Holmes, 1977).

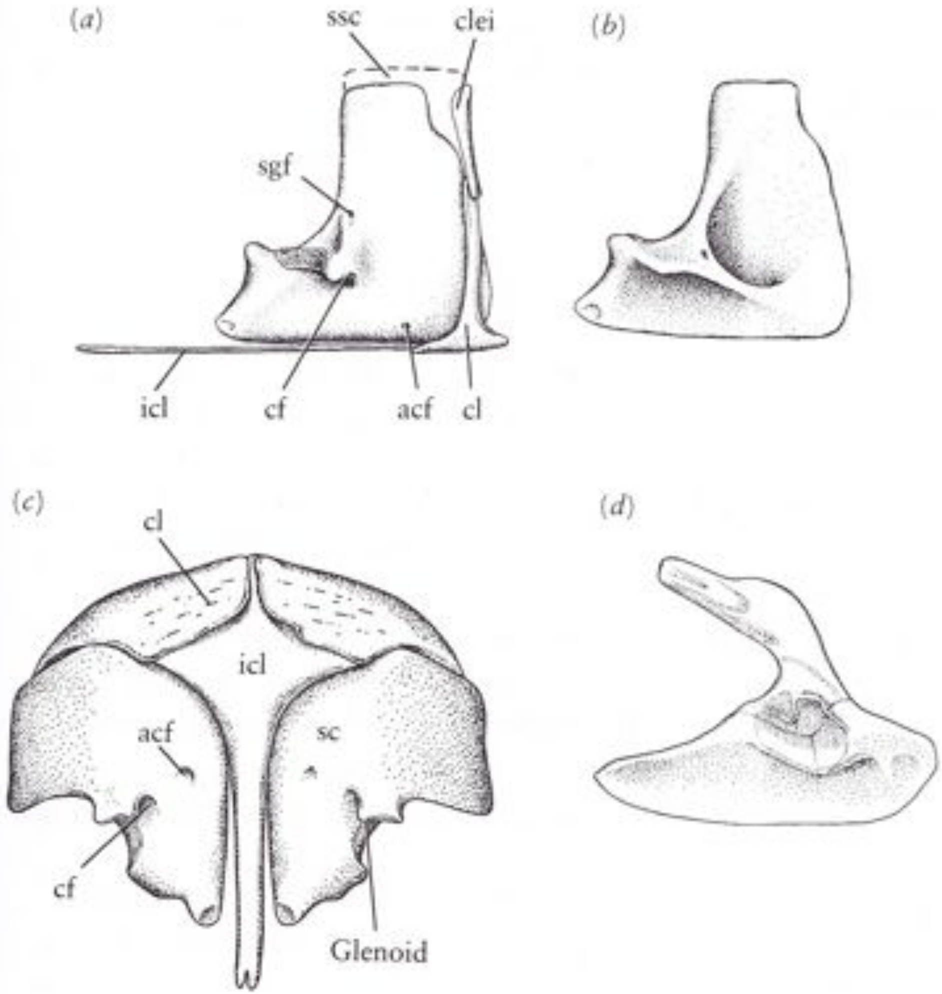


Figure 10-7. GIRDLES OF PRIMITIVE AMNIOTES. Pectoral girdle of *Protorothyris* in (*a*) lateral, (*b*) medial, and (*c*) ventral views. *From Clark and Carroll, 1973.* (*d*) Lateral view of the pelvis of *Hylonomus*. *From Carroll, 1969a. With permission of Cambridge University Press.* Abbreviations as follows: acf, anterior coracoid foramen; cf, coracoid foramen; cl, clavicle; clei, cleithrum; icl, interclavicle; sc, scapula; sgf, supraglenoid foramen; ssc, suprascapular cartilage.

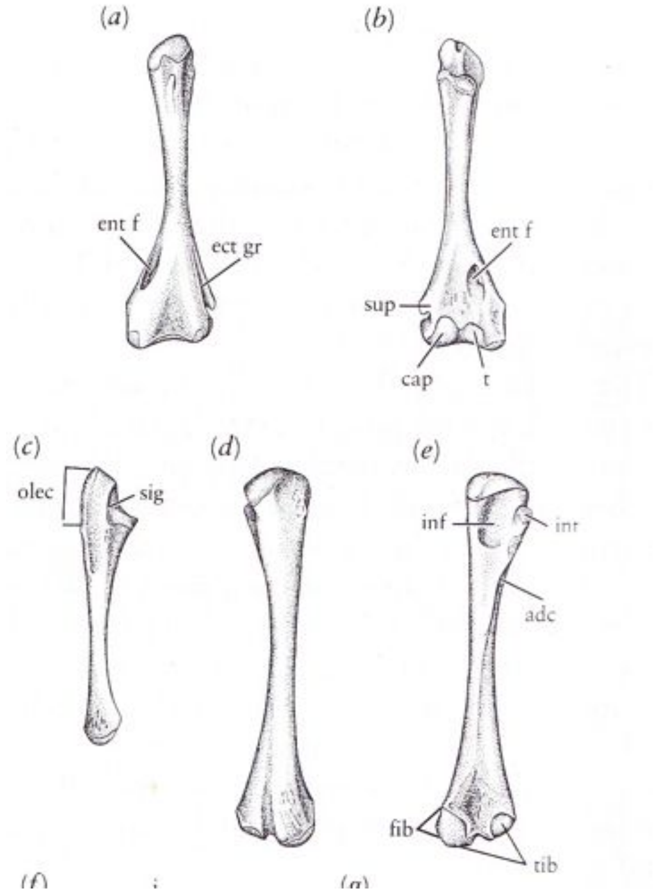


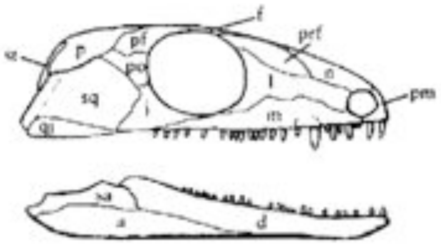
Figure 10-8. LIMB BONES OF PRIMITIVE AMNIOTES. Humerus in (*a*) dorsal and (*b*) ventral views. (*c*) Ulna in anterior view. Femur in (*d*) dorsal and (*e*) ventral views, based on a protorothyrid from the Lower Permian, $\times 1\frac{1}{2}$. *From Reisz, 1980.* (*f*) Carpus and manus of *Paleothyris. From Carroll, 1969a.* (*g*) Lower limbs, tarsus and pes of *Paleothyris*, $\times 1\frac{1}{2}$. *From Carroll, 1969a.* (*d* and *e*) *With permission of Cambridge University Press.* Abbreviations as in Figure 9-10 plus: adc, adductor crest; cap, capitellum; ect gr, ectepicondylar groove; ent f, entepicondylar foramen; fib, condyle for fibula; in f, intertrochanteric fossa; in t, internal trochanter; olec, olecranon; sig, sigmoid notch; sup, supinator process; t, trochlea; tib, condyle for tibula.

terior coracoids. The humerus has a relatively long narrow shaft from which the extremities are expanded at right angles to one another. As in many primitive Paleozoic amphibians, there is an entepicondylar foramen. A supinator process, which is proximal to the ectepicondyle, may be a primitive feature for amniotes. The carpus has

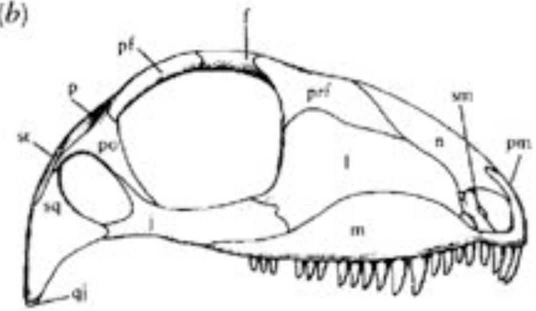
Nomenclatura de fenestras temporales en amniotos

The diapsids are so diverse that it is convenient to recognize two major subgroups: the Lepidosauromorphs, which are represented in the modern fauna by sphenodontids, lizards, and snakes, and the Archosauromorphs, which include the dinosaurs and their kin as well as the living crocodiles.

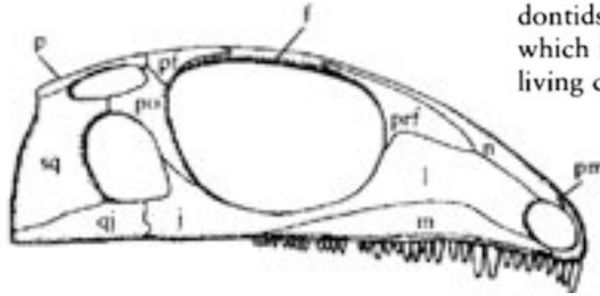
(a)



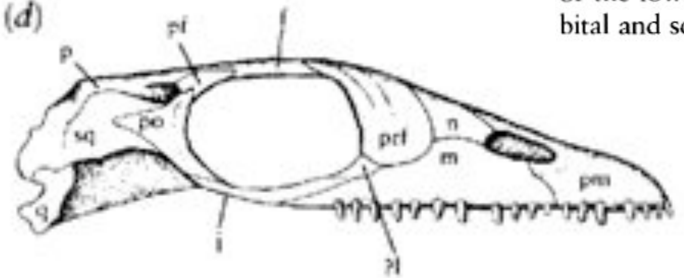
(b)



(c)



(d)



an anapsid configuration. The pattern seen in plesiosaurs can be derived from that of early diapsids by elimination of the lower temporal bar and thickening of the postorbital and squamosal (Carroll, 1981). An intermediate stage

Figure 10-11. SKULLS OF EARLY AMNIOTES SHOWING THE PATTERN OF TEMPORAL OPENINGS THAT DISTINGUISH THE MAJOR GROUPS. (*a*) The anapsid condition, illustrated by the protorothyrid *Paleothyris*. (*b*) The synapsid condition, exemplified by the early mammal-like reptile *Haptodus*. (*c*) The diapsid condition, shown by *Petrolacosaurus*. (*d*) The nothosaur *Neusticosaurus*, illustrating the parapsid or euryapsid condition. The diapsid and synapsid configurations are thought to have evolved separately from the anapsid condition. The euryapsid pattern has evolved from the diapsid pattern by loss of the lower temporal bar. Abbreviations as in Figure 8-3.

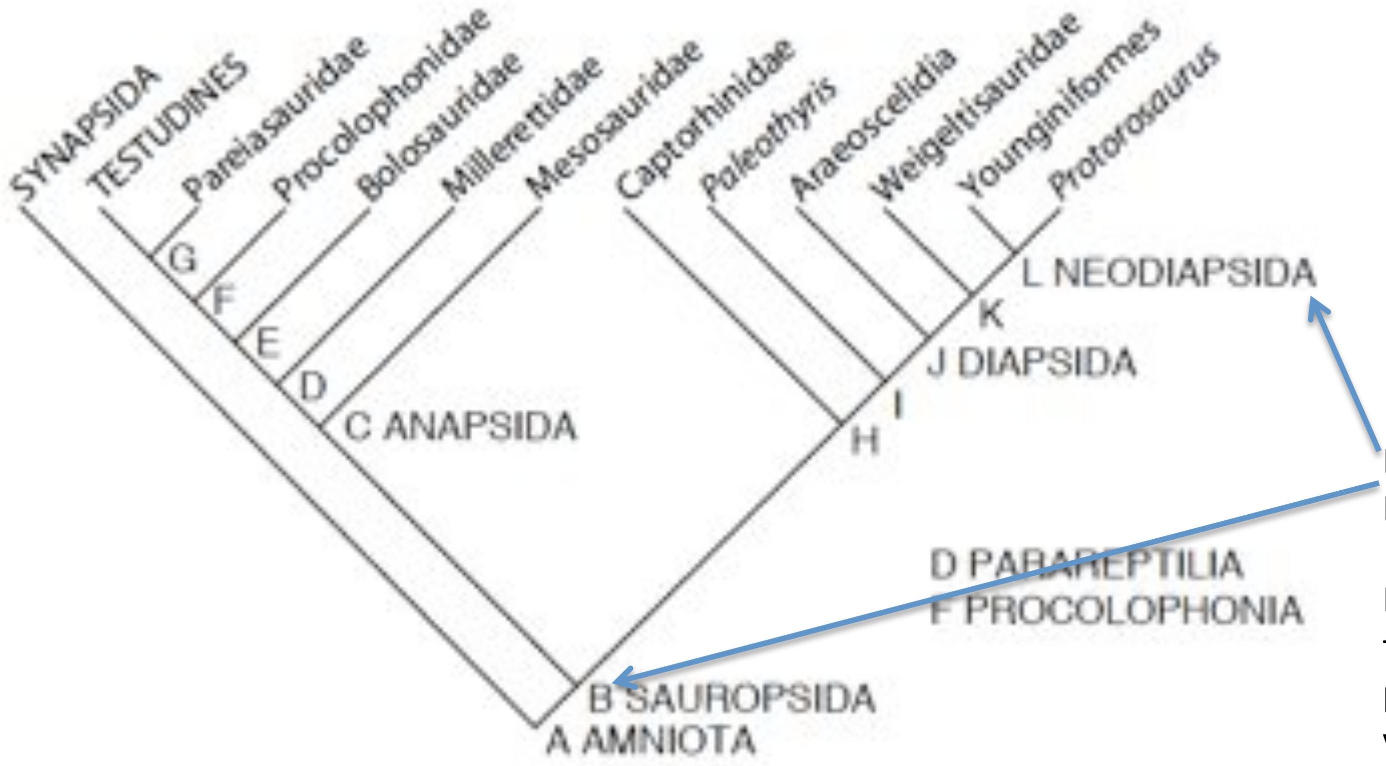
Development of temporal openings was not limited to these major subclasses but also occurred among several minor groups that are included among the Anapsida on the basis of their otherwise conservative anatomy. The nature of the temporal openings nevertheless provides a practical basis for distinguishing the major groups of amniotes. Surprisingly, the reasons for their initial development are still not adequately established. When fully elaborated, their configuration can be related to particular patterns of the adductor jaw musculature, but this function does not account for their initiation as small openings in the otherwise relatively smooth skull roof.

niotes. Surprisingly, the reasons for their initial development are still not adequately established. When fully elaborated, their configuration can be related to particular patterns of the adductor jaw musculature, but this function does not account for their initiation as small openings in the otherwise relatively smooth skull roof.

The development of temporal openings may be attributed to two major factors: differential concentration of mechanical stress in the skull and concentration of areas of muscle attachment. From studies of living vertebrates, we know that during growth bone is deposited most thickly along lines of stress; between areas of stress the bone may be thin or absent altogether. The particular shape and proportions of the skull in primitive amniotes determine where stress was concentrated. The fact that muscles can be more strongly attached to ridges and edges of bone than to flat surfaces would account for the concentration of muscle origins along the thickened areas. The forces applied by the muscles would result in further thickening.

Very thin areas of bone between the thickened ridges are subject to cracking, especially where they are crossed by sutures, such as the area of the cheek in primitive amniotes where the squamosal, postorbital, and jugal join. During feeding, force is concentrated on the sutures. This stress could be dissipated by the development of a larger opening with rounded margins in which the force is distributed around the periphery. (In metal work and bone surgery, rounded openings may be made to dissipate force concentrated by sharp cracks, see Frost, 1967). This factor may account for the initial fenestration seen in synapsids and early diapsids. The different proportions of the skull

PARAREPTILIA / CROWN REPTILIA: conceptos variables



Dos posibles posiciones para Reptilia (grupo corona)

Mientras no se resuelva, todos menos el nodo k pueden ser stem-reptiles en vez de reptiles

Salvo el nodo j, y algunas excepciones (milleretidae, bolosauridae) , todos en este arbol no tienen fenestras temporales: es la condición plesiomórfica.

Anapsida = Parareptilia ("at the side of reptiles") a subclass or clade of reptiles which are variously defined as an extinct group of primitive anapsids, or a more cladistically correct alternative to Anapsida. Whether the term is valid depends on the phylogenetic position of turtles, the relationships of which to other reptilian groups are still uncertain.

Reptilia: Crown-group

Grupos vivientes:
-Testudinata (tortugas)

Los diápsidos (seguros):
-Arcosauria (Cocodrilos + aves).
-Lepidosauria (lagartijas, incluyendo las serpientes)

Synapomorfías:
-Fundamentalmente diurnos (no como anfibios y dipnoi)
-Excelente vision de colores, varias rhopdopsinas. (dentro de sarcopterygia, sólo los monos, además de ellos)
-Foco rápido: Células estriadas se insertan en el cristalino en un diagnóstico anillo ecuatorial
-Fibras estriadas en el iris , respuesta rápida a cambios en niveles de luz
-Membrana nictitante altamente móvil, 3er párpado

Resisten desecación

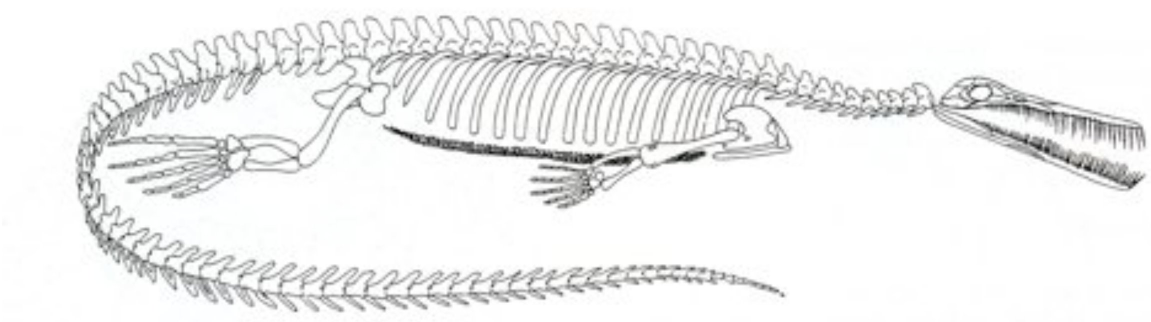
-Sintetizan ácido úrico en el hígado. Puede ser excretado con muy poco líquido (ej. Aves). Los riñones permiten el paso de grandes cristales de urea. Poseen un sistema especial, altamente eficiente de recuperación de sales.

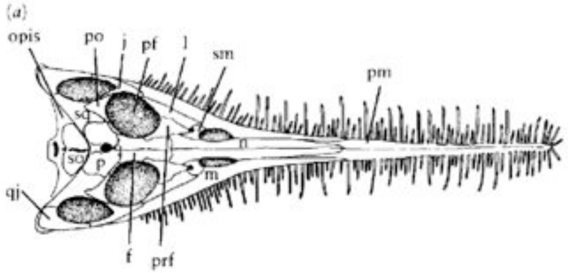
-Piel altamente queratinizada, menos glandular que mamíferos y anfibios. Presencia de Phi-queratinas

Los Mesosauridae eran marinos y constituyen el registro más temprano de la reversión de un amnioto a vivir en el agua. Sus fósiles se han encontrado en el carbonífero tardío y pérmico temprano

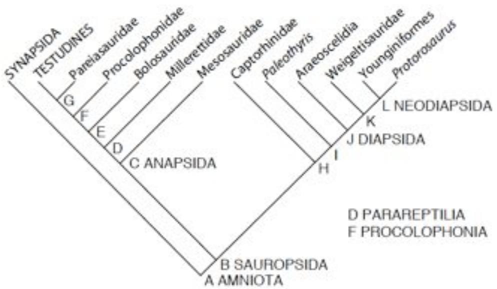
The long and laterally compressed tail probably served for aquatic propulsion. The ribs at the base of the tail are fused to the caudal vertebrae, unlike those of more primitive amniotes, to permit more solid attachment of the muscles. Surprisingly, the more posterior vertebrae show evidence of caudal autotomy like those of the terrestrial captorhinids.

The neural arches of the trunk are widely expanded, which limited twisting of the column but facilitated lateral bending. The trunk ribs are thickened, approaching the shape of bananas, in contrast with the slim ribs of most primitive amniotes. The same pattern is seen in modern sirenians, which show a similar degree of aquatic adaptation. Thickening of the ribs and an increase in their internal ossification, a condition termed **pachyostosis,** would have increased the weight of the animals so that they could stay submerged without muscular effort.





The girdles are somewhat smaller than their counterparts in protorothyrids and captorhinids, and the blade of the scapula is notably shorter. The ulna and radius and the tibia and fibula are shorter relative to the humerus and femur. The rear foot is a large, paddle-shaped structure, with the fifth toe more elongated than in other early amniotes.



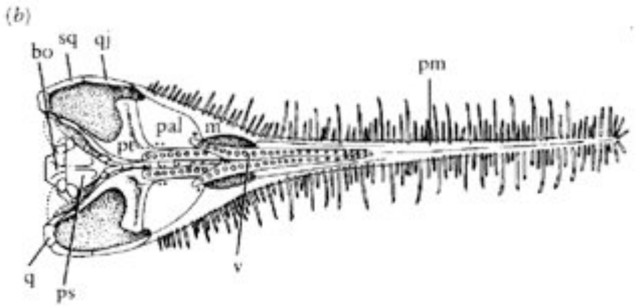


Figure 10-21. SKULL OF *MESOSAURUS*. (*a*) Dorsal and (*b*) palatal view. Recent work indicates that the cheek was solidly ossified, without a lateral temporal opening. Abbreviations as in Figure 8-3. *From von Huene, 1941.*

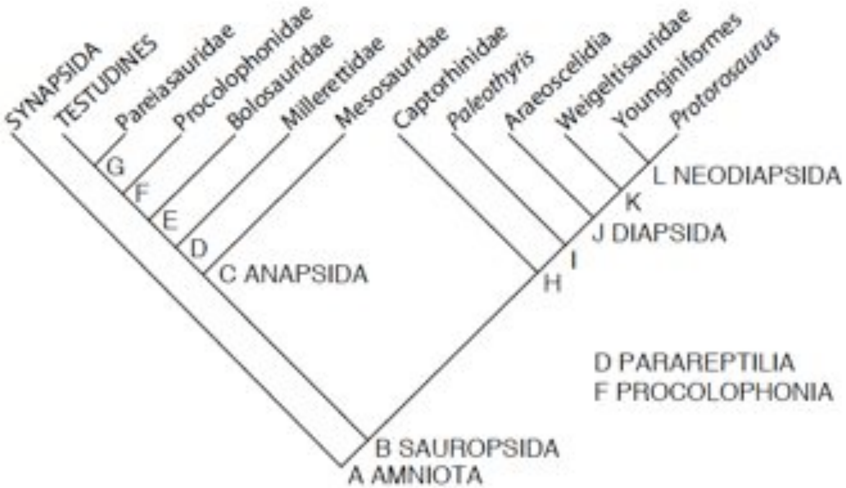
Los Reptilia incluye a todos los descendientes del ancestro común más reciente de los reptiles vivientes. Comprende tres grupos vivientes claramente distinguibles: Testudines (tortugas), Lepidosauria (lagartos y serpientes) y Archosauria (crocodylia+aves).

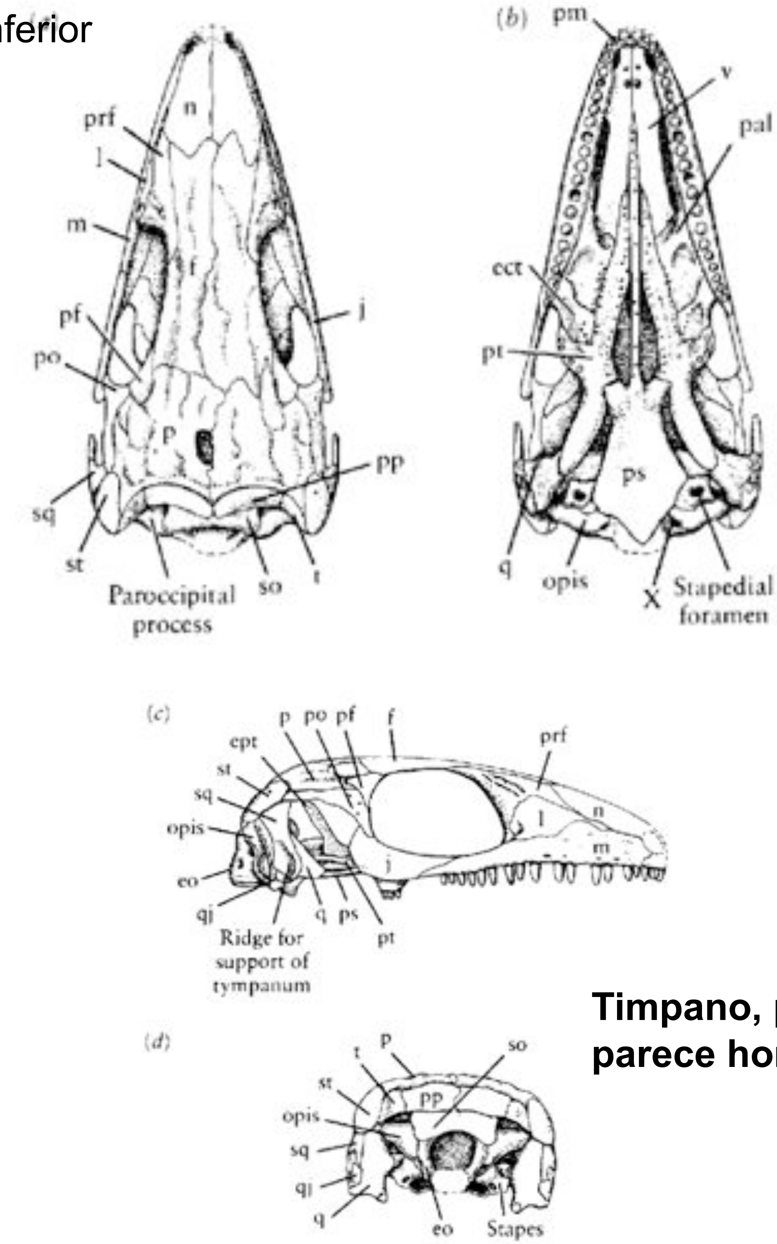
MILLERETIDAE: Reduccion/perdida barra temporal inferior

scribed, the skull roof is primitive in the retention of large postparietals, tabulars, and supratemporals, but other cranial features are significantly specialized. There is typically (but not always) a lateral temporal opening; the lower temporal bar may not be complete, and the quad-

directly laterally. The squamosal and quadratojugal are embayed posteriorly like an otic notch to support a tympanum. This pattern is expected for the structure of an impedance matching ear and is apparently the first manifestation of such a structure in amniotes. Most advanced diapsids and turtles support the tympanum by the quadrate. In millerosaurs, the quadrate retains the primitive configuration seen in captorhinomorphs.

The millerosaurs were succeeded in time by true lizards, which probably were more successful in exploiting the same general way of life. Some authors have suggested that millerosaurs were ancestral to lizards, but it is now clear that lizards (as discussed in the next chapter) evolved from primitive diapsids with a dorsal as well as a lateral temporal opening.





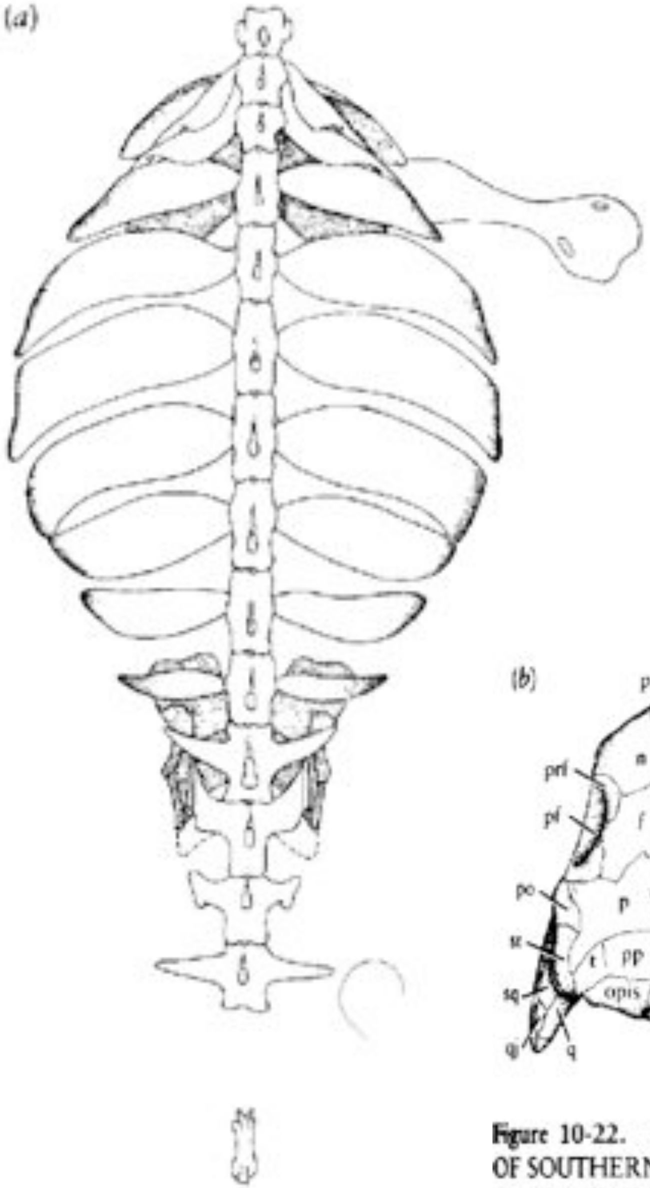
Timpano, pero no parece homologo

Figure 10-15. SKULL OF THE MILLEROSAUR *MILLEROSAURUS*, ×2. (*a*) Dorsal view. (*b*) Palatal view. (*c*) Lateral view. (*d*) Occipital view. Abbreviations as in Figure 8-3. *Based on specimens in the Bernard Price Institute, University of Witwatersrand, South Africa.*

greatly elongate centra (Figure 10-22). The ilium is very high and attached by only a single sacral rib. In other features of the postcranial skeleton, *Eunotosaurus* remains primitive. There is no trace of dermal armor, and the blade of the scapula is external to the ribs. What is known of the limbs resembles the pattern of captorhinomorphs.

Until recently, very little was known of the skull. Keyser and Gow (1981) demonstrate that *Eunotosaurus* shares no important derived features of the cranium with turtles. The presence of a platelike occiput, which is formed by very large postparietals that reach the opisthotic would appear to preclude development of the pattern of the adductor jaw musculature that is characteristic of all Chelonia. In turtles, the musculature extends posteriorly through the occiput via the posttemporal fossae. The cheek of *Eunotosaurus* is deeply emarginated ventrally, with the quadrate and quadratojugal being separated from the jugal. There is a normal marginal dentition.

Eunotosaurus is classified in a distinct suborder of the Captorhinida but has no obvious affinities with other members of this group.



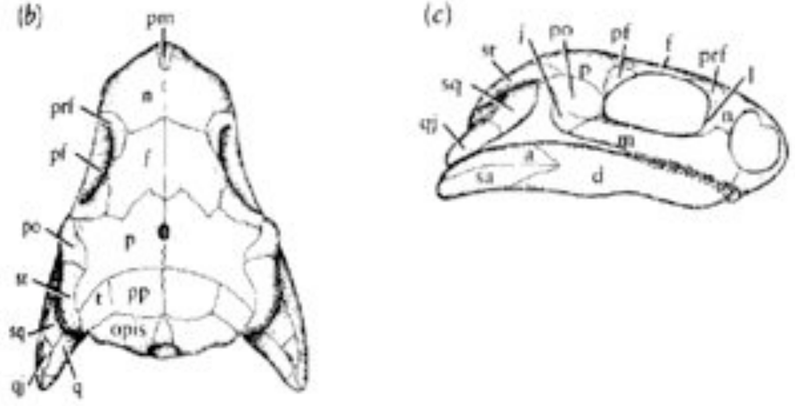
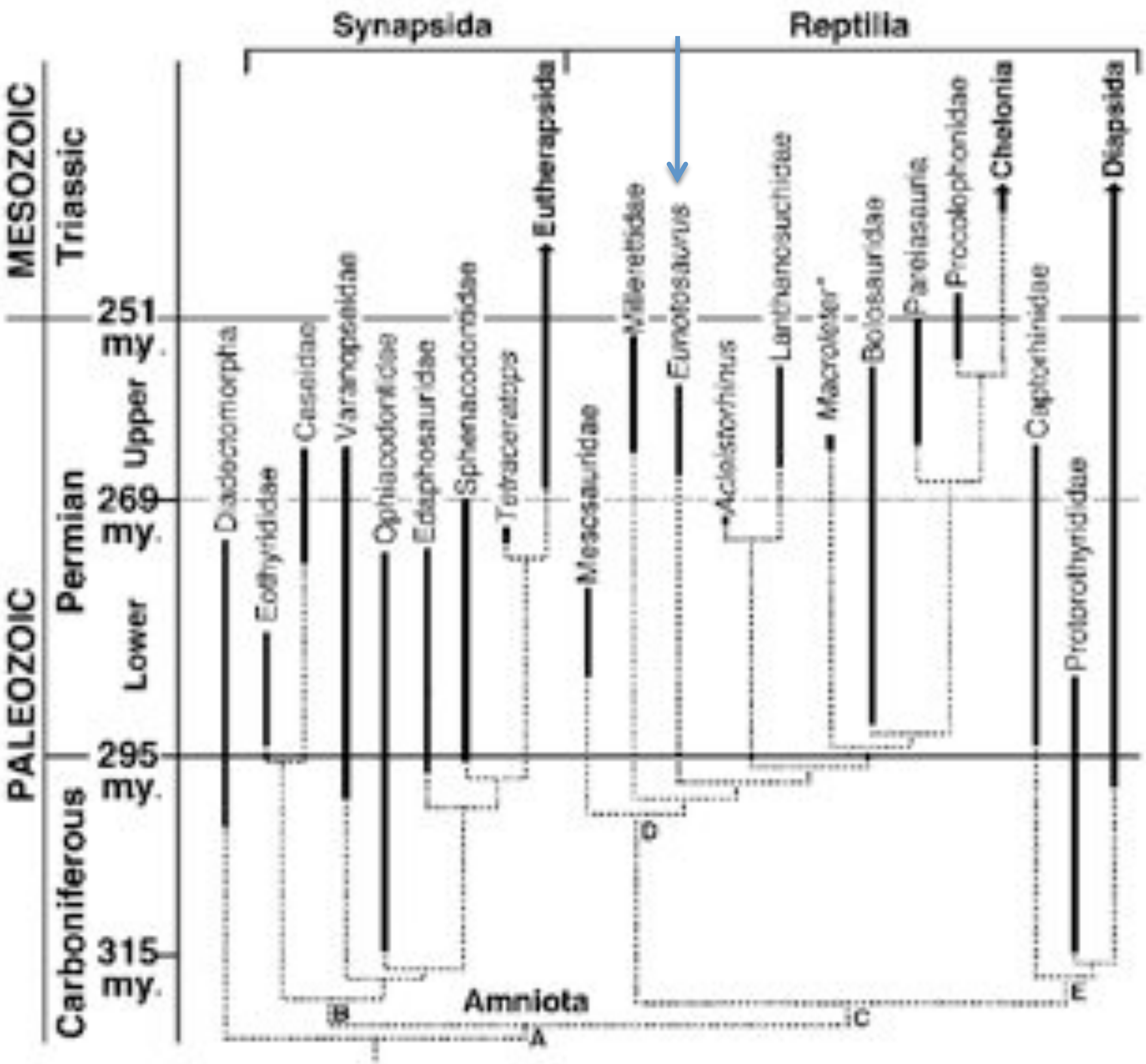
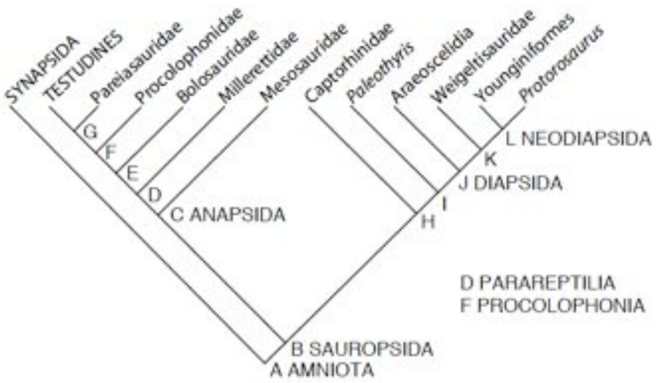


Figure 10-22. *EUNOTOSAURUS* FROM THE UPPER PERMIAN OF SOUTHERN AFRICA. (*a*) Postcranial skeleton. *From Cox, 1969.* (*b* and *c*) Skull. The pattern of the trunk and ribs is similar to that of turtles, but the skull shows no evidence of affinities with that group. *From Keyser and Gow, 1981.* Abbreviations as in Figure 8-3.


Synapsida
Reptilia
MESOZOIC
Triassic
PALEOZOIC
Permian
Upper
Lower
Carboniferous
251 my.
269 my.
295 my.
315 my.
Diadectomorpha
Eothyrididae
Caseidae
Varanopseidae
Ophiacodontidae
Edaphosauridae
Sphenacodontidae
Tetraceratops
Eutherapsida
Mesosauridae
Millerettidae
Eunotosaurus
Acleistorhinus
Lanthanosuchidae
Macroleter
Bolosauridae
Pareiasauria
Procolophonidae
Chelonia
Captorhinidae
Protorothyrididae
Diapsida
Amniota
A
B
C
D
E



The Acleistorhinidae and Bolosauridae are among the minor groups that are recognized as distinct families (Figure 10-13). Both have lower temporal openings but show no other similarities with the synapsids. *Bolosaurus* has molariform cheek teeth with a specific occlusal pattern. The coronoid process of the lower jaw is elevated to provide a more powerful bite.

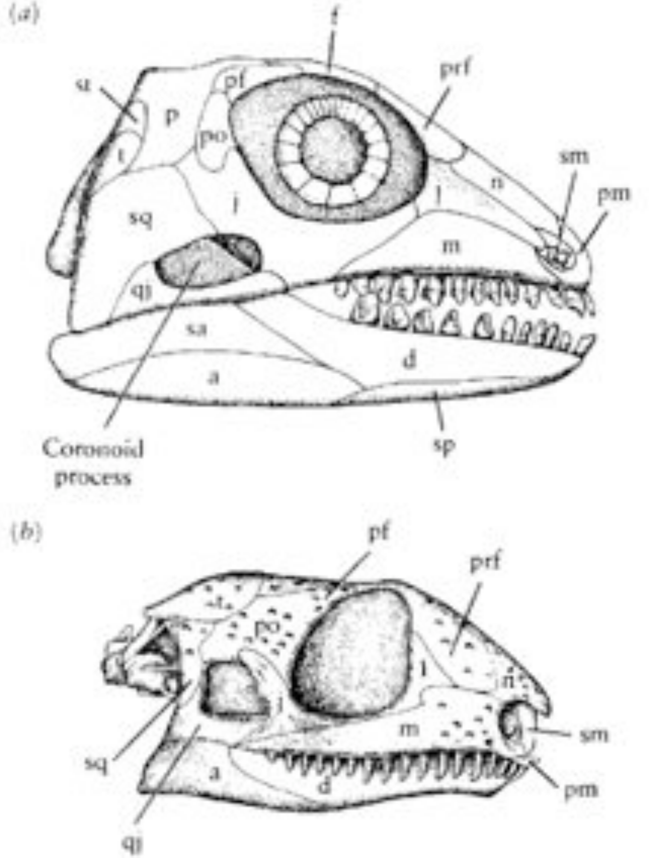
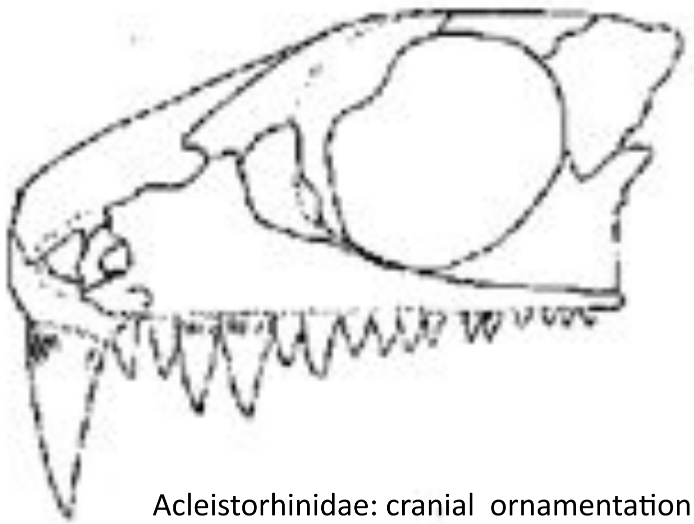


Figure 10-13. SKULLS OF TWO PRIMITIVE AMNIOTES FROM THE LOWER PERMIAN SHOWING LATERAL TEMPORAL OPENINGS. They show no close affinities with other groups. (*a*) *Bolosaurus*, in which the cheek teeth are expanded and show precise occlusion; note also the high coronoid process. (*b*) *Acleistorhinus*. Abbreviations as in Figure 8-3. *From Daly, 1969.*



Acleistorhinidae: cranial ornamentation consists of sparse and shallow circular dimples.[2]

Procolophonoids retain what appears to be a very primitive pattern of the postcranial skeleton. Like protorothyrids, but in contrast to all other reptiles from beds above the Lower Permian, the caudal ribs are not fused to the centra and extend posteriorly to parallel the axis of the tail. Within the group (and like the larger captor-

sprawling posture. The endochondral shoulder girdle is ossified in three units that are distinct in the adults: the dorsal scapula and the anterior and posterior coracoids. These elements are evident in immature specimens of captorhinids and pelycosaurs and may be primitive for amniotes, but in most early genera they coossify at an early stage so that they are indistinguishable in the adult. The attachment of the pelvic girdle is enhanced in all procolophonoids by the incorporation of a third sacral rib.

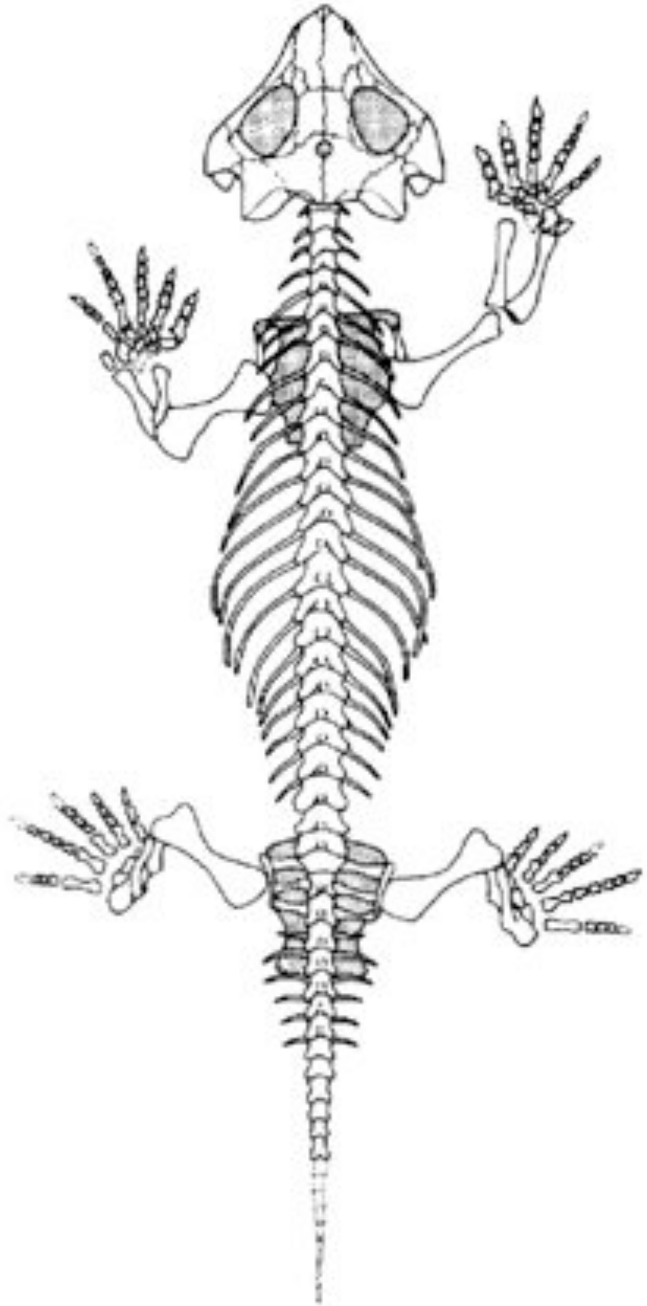
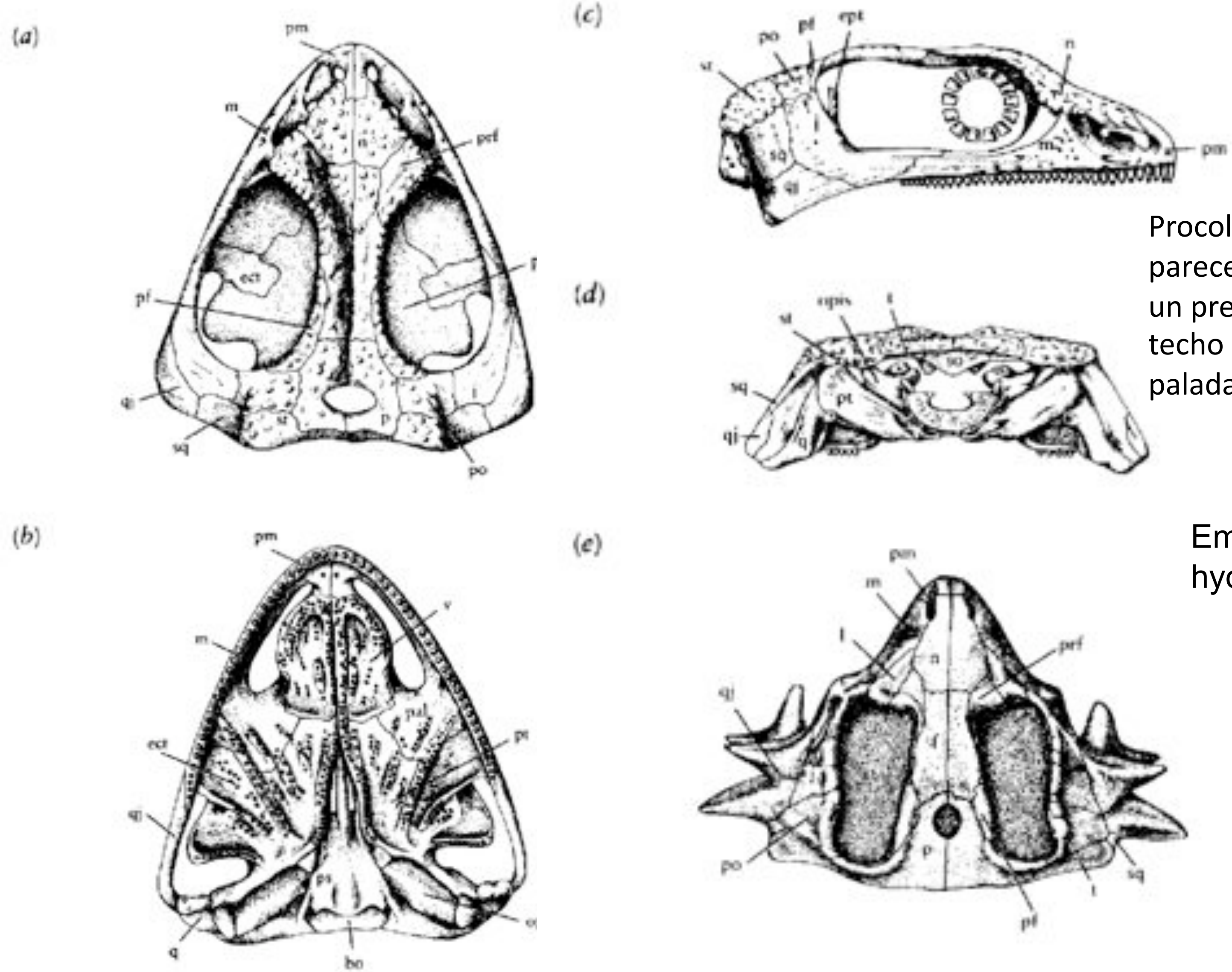


Figure 10-16. Skeleton of the Lower Triassic procolophonoid *Procolophon*, ×⅓. *From Colbert and Kitching, 1975. Courtesy of the Library Services Department, American Museum of Natural History.*

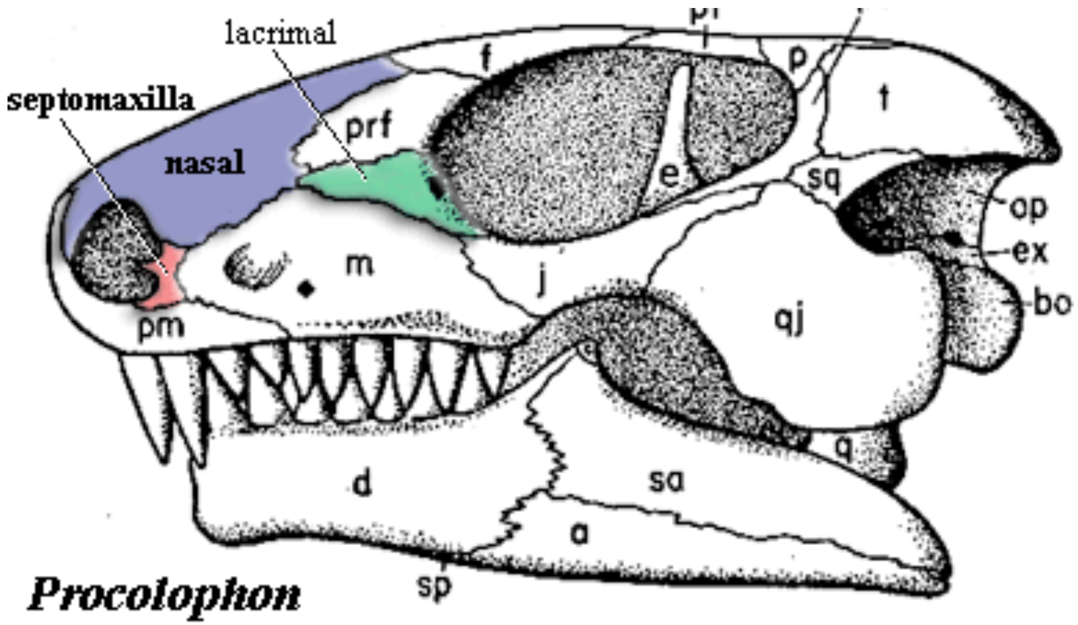


Procolofonidos y Pareiasaurios se parecen a tortugas en la presencia de un prefrontal robusto apoyando el techo del craneo anterior sobre el paladar

Emarginacion del cuadrado, hyoides grácil: timpano

The skull of procolophonoids is specialized in having the orbital margin embayed posteriorly to expose the area of the jaw musculature as a pseudotemporal opening. As in millerosaurs, the jaw articulation is anterior to the occipital condyle and there is a narrow, laterally directed stapes that probably participated in an impedance-matching system. As in millerosaurs, the tympanum would have been supported by the squamosal rather than by the quadrate, as was the case in most diapsids and turtles.

Figure 10-17. PROCOLOPHONOID SKULLS. Skull of the Upper Permian procolophonoid *Nyctiphruretus* in (*a*) dorsal, (*b*) palatal, (*c*) lateral, and (*d*) occipital view, ×1. *From Ivachnenko, 1979.* (*e*) The Upper Triassic genus *Hypsognathus*, ×⅓ *From Colbert, 1946. Courtesy of the Library Services Department, American Museum of Natural History.* Abbreviations as in Figure 8-3.



Septomaxillae of two reptilomorphs from Romer (1956)

The dentition of early procolophonoids from the Upper Permian of Russia, Madagascar, and South Africa is primitive. It consists of a large number of small, peglike teeth. The skull roof is thin and fragile. In the widespread and diverse Triassic procolophonoids, the number of teeth is much reduced and each is a bulbous, transversely expanded structure that was possibly associated with a herbivorous diet. The skull is enlarged and the bones variably thickened (Colbert, 1946; Carroll and Lindsay, 1985).

more upright pose than in other primitive amniotes to support the massive trunk. The scapula is much longer than in other primitive tetrapods, and the pelvis has an almost mammalian configuration, with the pubis and ischium small and rotated posteriorly behind the elongate ilium. This configuration may have helped accommodate muscles that moved the rear limbs in a manner approaching the fore and aft gait of mammals. The feet were short, had a reduced number of phalanges, and faced anteriorly.

The origin of Pareiasaurs remains speculative

osteodermos

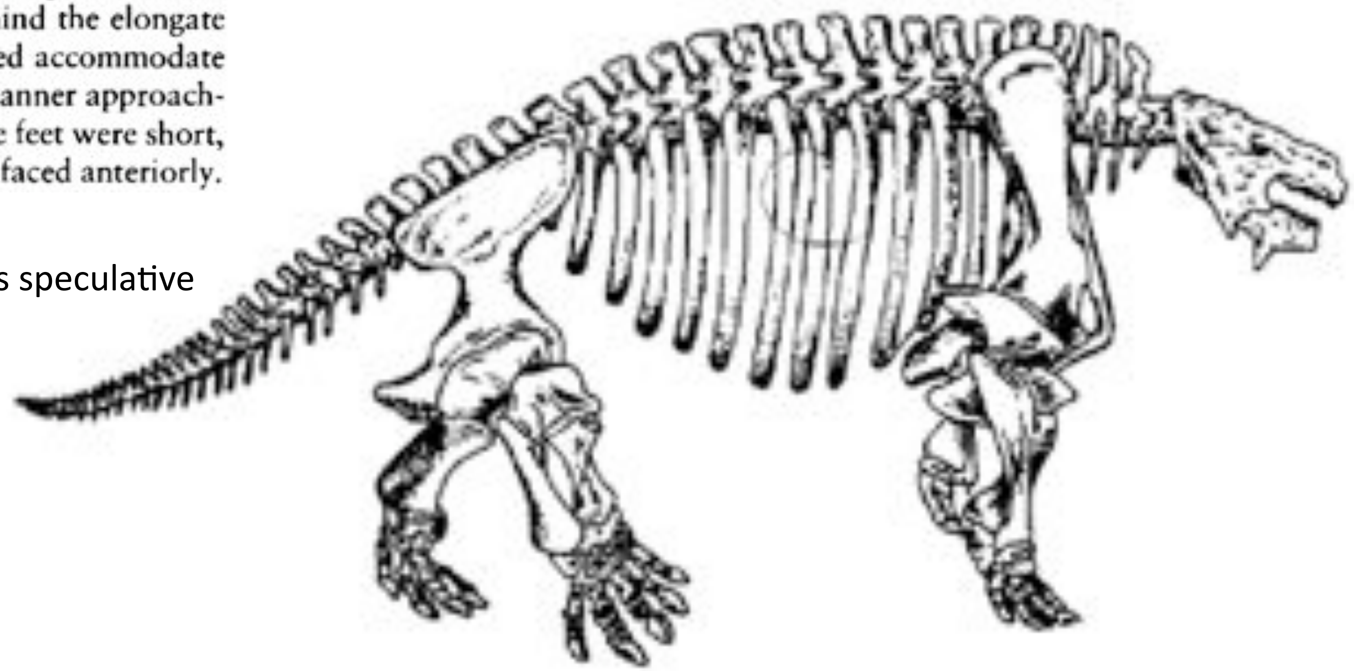
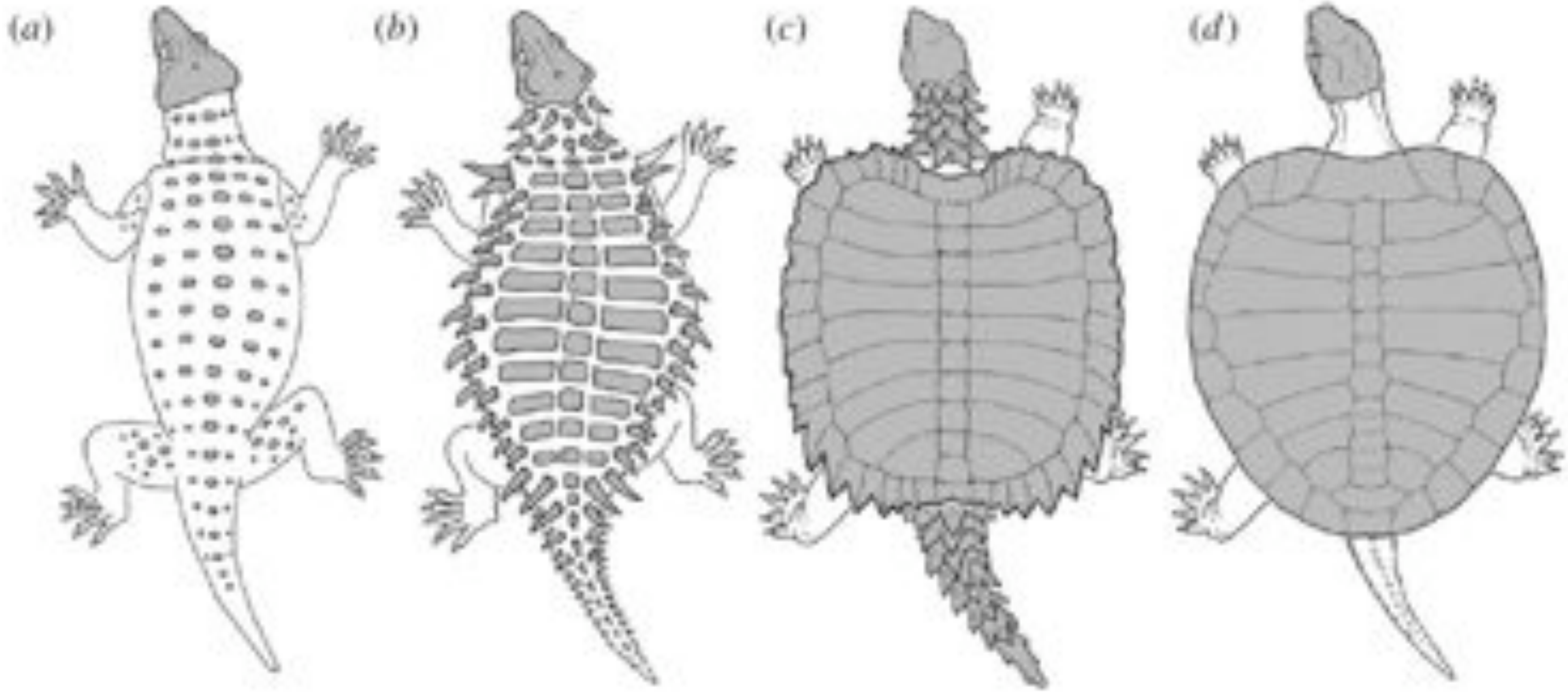
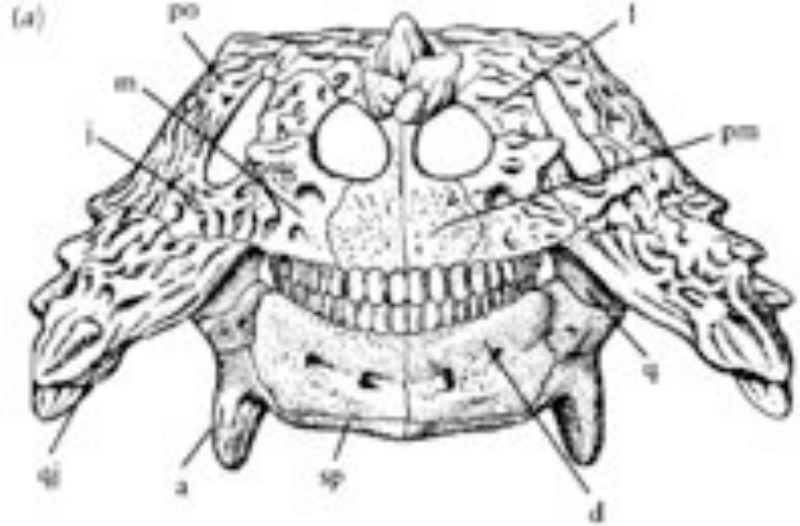


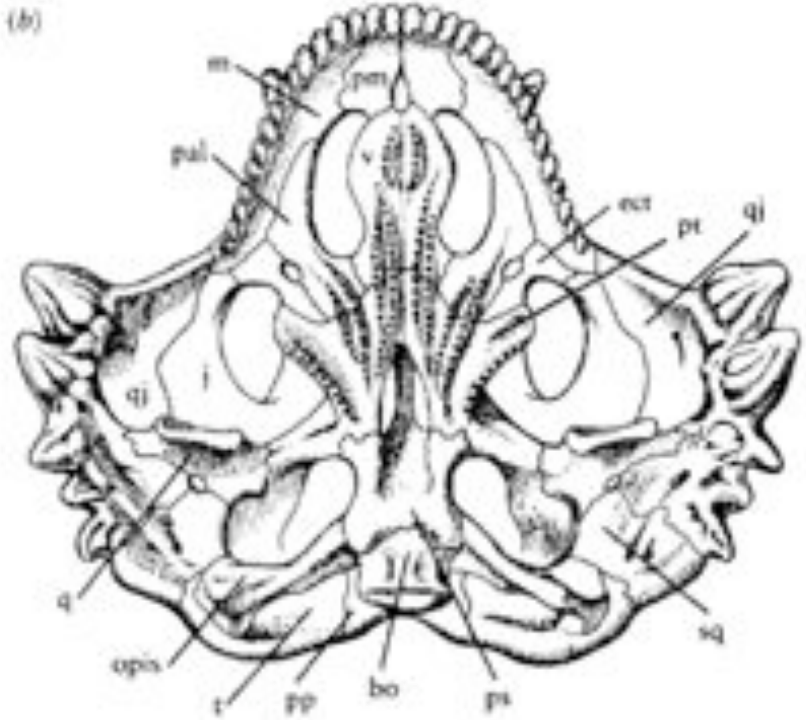
Figure 10-18. THE PAREIASAUR *SCUTOSAURUS* FROM THE LATE PERMIAN OF RUSSIA; ORIGINAL 2 METERS LONG. *From Gregory, 1951. Courtesy of the Library Services Department, American Museum of Natural History.*


(a)
(b)
(c)
(d)

Hyoides grácil: tímpano

The skulls are short, massive, and laterally expanded. The jaw articulation is well anterior to the occipital condyle, which increased the mechanical advantage of the jaw musculature while decreasing the gape. The palate is strongly integrated with the base of the braincase and the margins of the skull. The teeth have laterally compressed leaf-shaped crowns that are similar in shape to the teeth of modern herbivorous lizards. Together with the massive trunk region, they suggest that the pareiasaurs had a herbivorous diet. Most genera had small bony plates embedded in the skin of the trunk region.





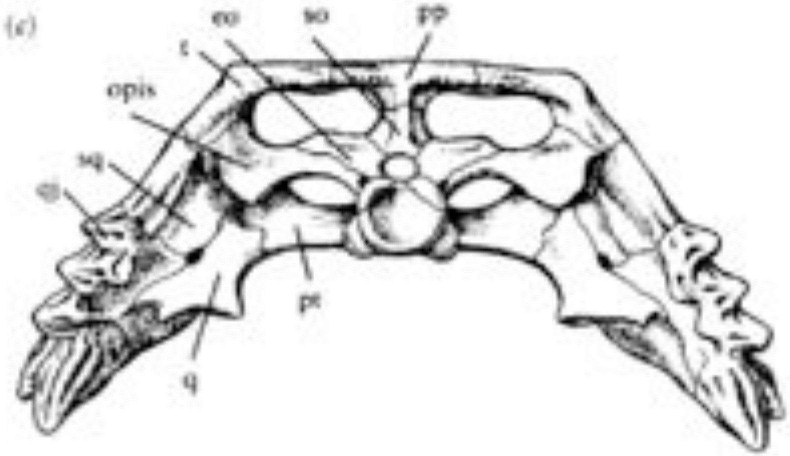


Figure 10-19. SKULL OF THE PAREIASAUR *SCUTOSAURUS*. (*a*) Anterior, (*b*) palatal, and (*c*) occipital views. Specimen is from the Upper Permian of Russia. Width about 50 centimeters. Abbreviations as in Figure 8-3. *From Kuhn, 1969.*

Tienne hyoides delgado, sugiriendo la presencia de timpano

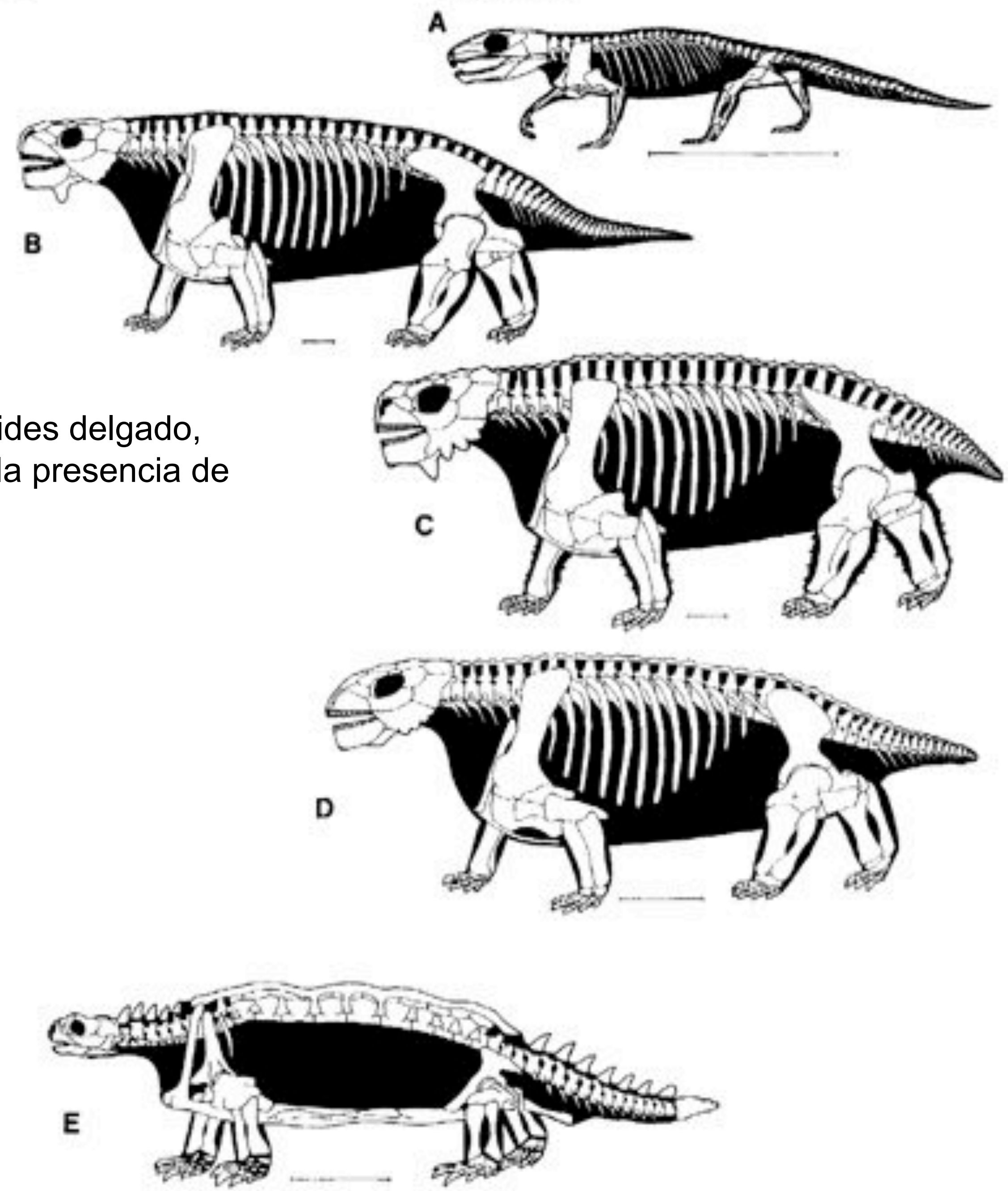
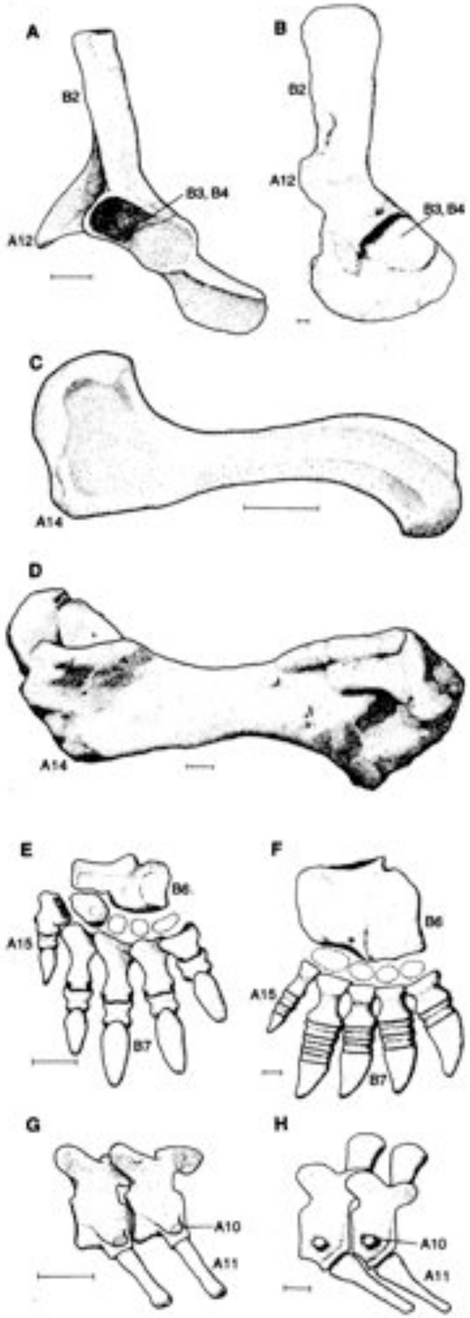
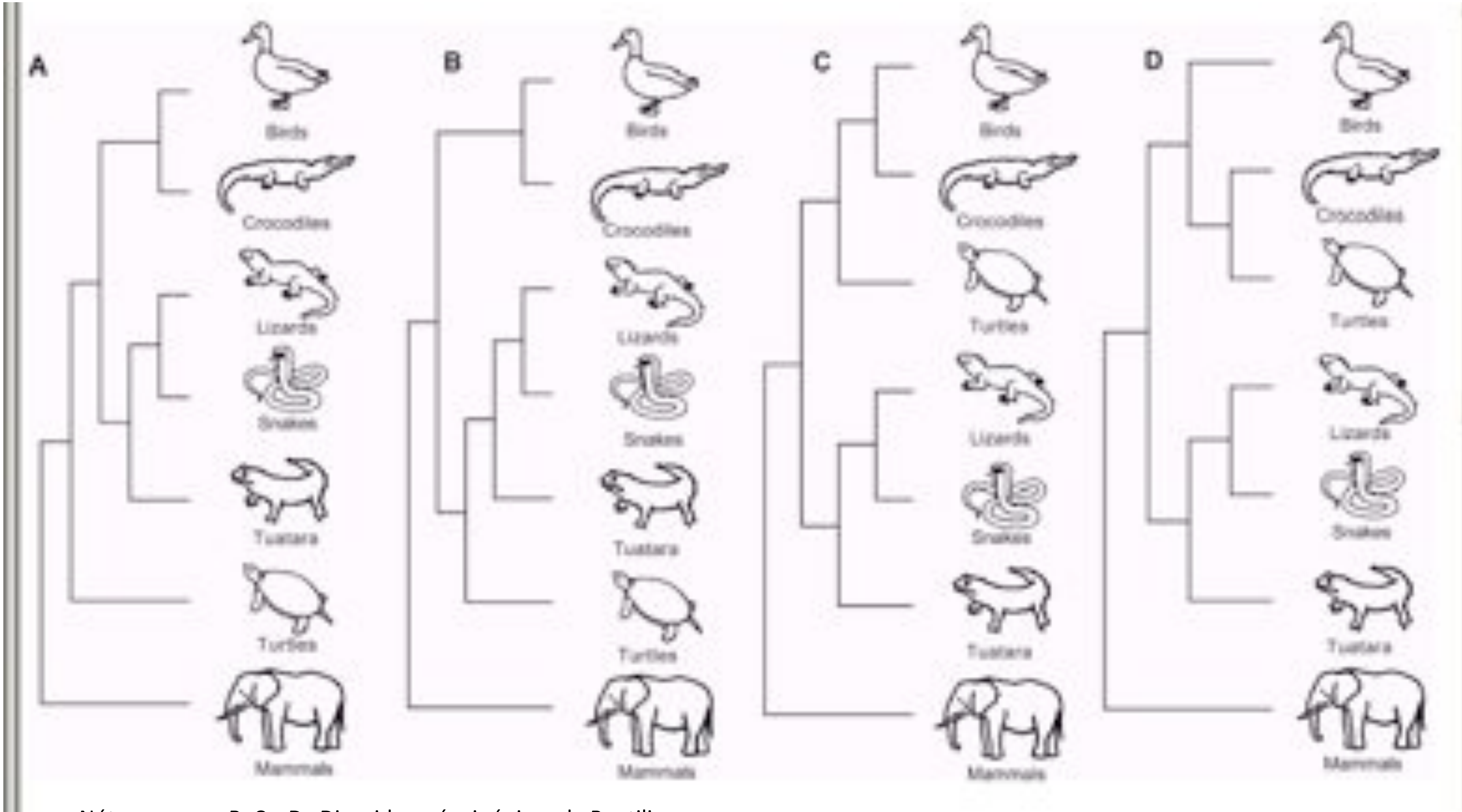


Figure 2. Outline skeletal reconstructions of various basal amniotes. A, *Captorhinus*. B, *Bradysaurus*. C, *Scutosaurus*. D, *Anthodon*. E, *Proganochelys*. (A) after Heaton and Reisz (1986), (B) after BMNH R1971, (C) after PIN 1005/1532, (D) after BPI 1/548 and SAM 10074, (E) after Gaffney (1990).


A
B2
B3, B4
A12
B
B2
A12
B3, B4
C
A14
D
A14
E
B6
A15
B7
F
B6
A15
B7
G
A10
A11
H
A10
A11

Sin embargo, existe controversia sobre la posición basal de las tortugas (representada en el árbol "A"). Podrían ser diápsidos que secundariamente perdieron sus aperturas craneales. Algunos estudios morfológicos consideran que son diápsidos cercanos a los Lepidosauria (arbol B), mientras que la evidencia molecular repetidamente ha señalado que son diápsidos cercanas a los Archosauria (árboles C y D, últimamente sólo C)



Nótese que en B, C y D, Diapsida sería sinónimo de Reptilia

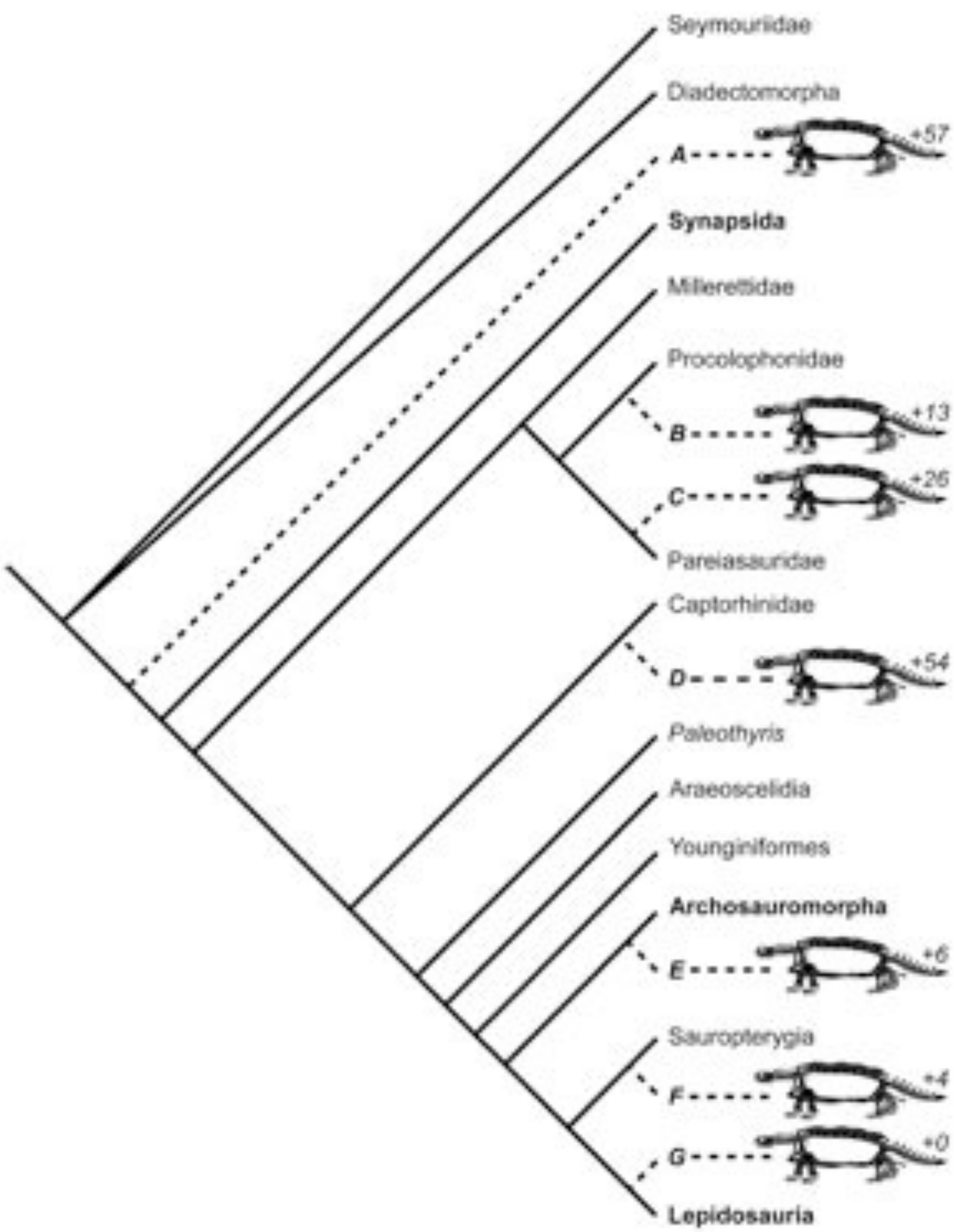
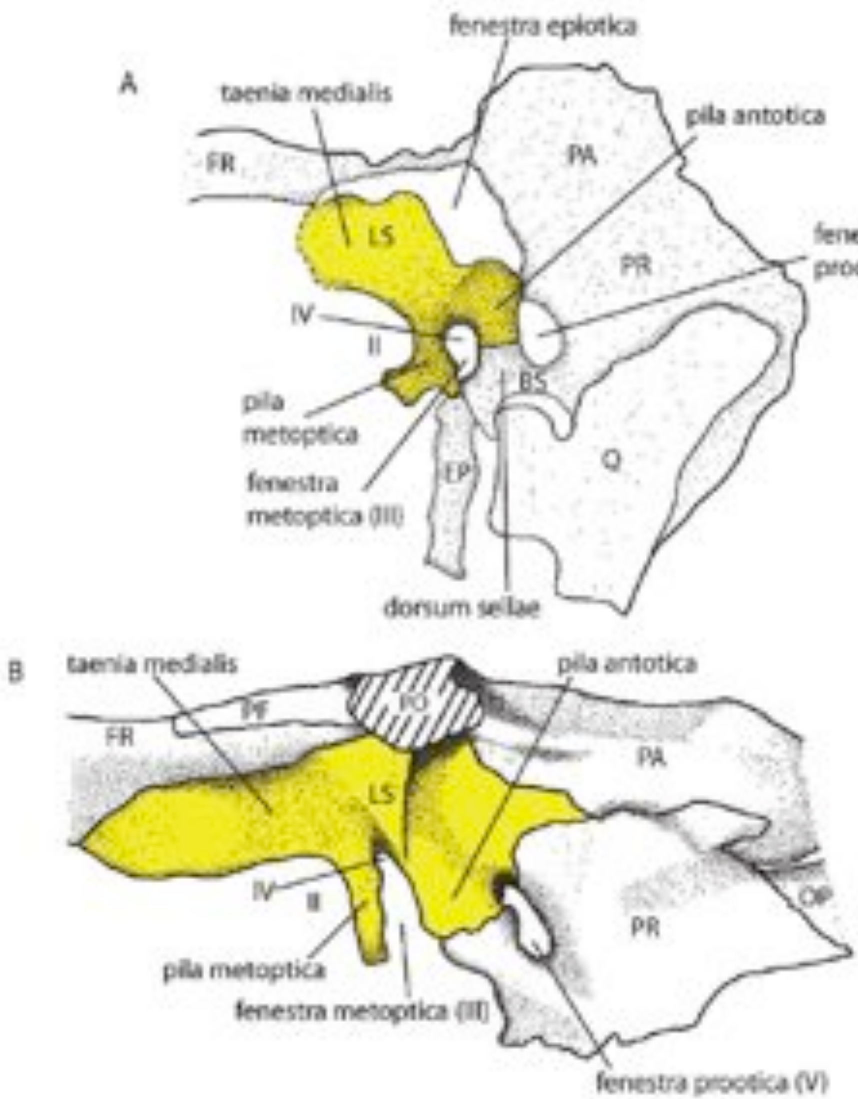


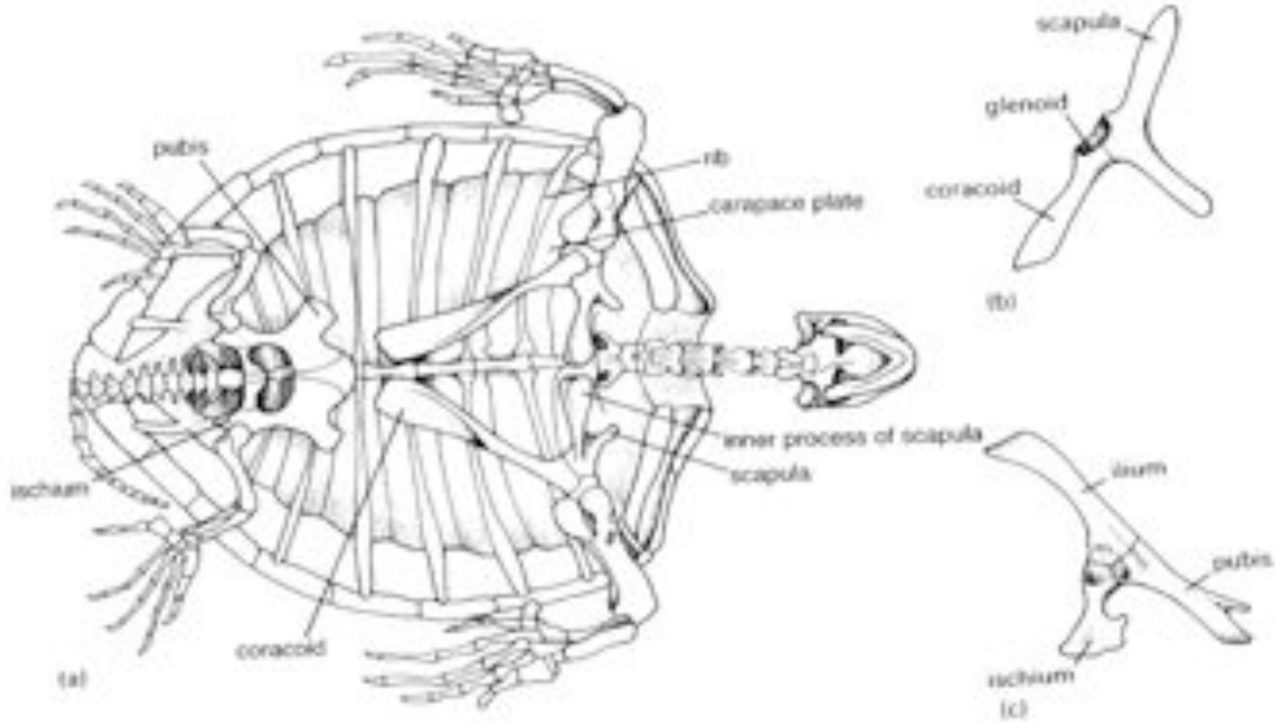
FIGURE 1. Summary of alternative hypotheses explaining the phylogenetic position of turtles (Testudines) among Amniota. A, Turtles are the sister taxon to all other amniotes (Gaffney, 1980); B, turtles are parareptiles most closely related to procolophonids (Laurin and Reisz, 1995); C, turtles are parareptiles most closely related to (or nested within) pareiasaurs (Gregory, 1946; Lee, 1993, 1997a); D, turtles are the sister taxon to captorhinids (Gauthier et al., 1988a, 1988b); E, turtles are derived diapsids that have secondarily lost their temporal fenestrae, and are most closely allied with archosauromorphs (Merck, 1997; Zardoya and Meyer, 1998; Kumazawa and Nishida, 1999; Hedges and Poling, 1999; Mannen and Li, 1999; Cao et al., 2000); F, turtles are derived diapsids most closely related to sauropterygians (Rieppel and deBraga, 1996; deBraga and Rieppel, 1997; Rieppel and Reisz, 1999); G, turtles are derived diapsids most closely related to lepidosaurs (this study). Number of additional evolutionary steps required for each alternative hypothesis indicated in *italics*; see text for discussion. Taxa that include extant members indicated in **bold**. Skeletal reconstructions of the oldest known turtle, *Proganochelys*, modified from Lee (1997a).

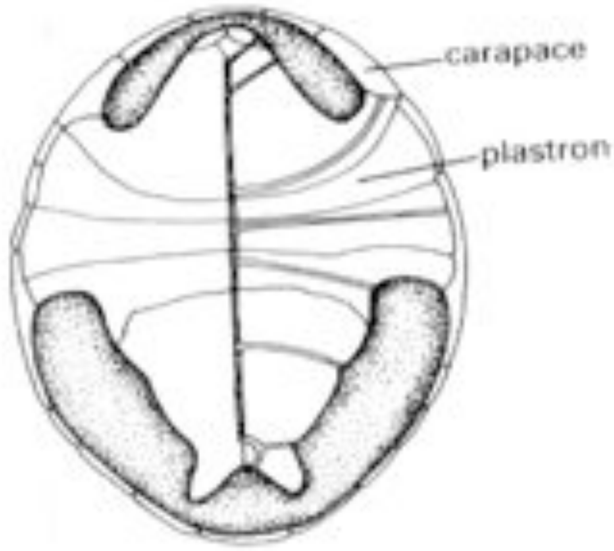


Abstract. Turtles are placed with increasing consistency by molecular phylogenetic studies within Diapsida as sister to Archosauria, but published gross morphology–based phylogenetic analyses do not recover this position. Here, we present a previously unrecognized unique morphological character offering support for this hypothesis: the presence in stem turtles of a laterosphenoid ossification identical to that in Archosauriformes. The laterosphenoid is a tripartite chondrocranial ossification, consisting of an ossified pila antotica, pila metoptica, and taenia medialis + planum supraseptale. It forms the anterior border of the exit for the trigeminal nerve (V) and partially encloses the exits for cranial nerves III, IV, and II. This ossification is unique to turtles and Archosauriformes within Vertebrata. It has been mistakenly dismissed as anatomically dissimilar in these two groups in the past, so we provide a complete description and detailed analysis of correspondence between turtles and Archosauriformes in each of its embryologically distinct components. A preliminary phylogenetic analysis suggests other potential synapomorphies of turtles and archosaurs, including a row or rows of mid-dorsal dermal ossifications.

Figure 1. (A) Left laterosphenoid of *Proganochelys quenstedti* SMNS 15759 in lateral view, after Gaffney (1990). (B) Right laterosphenoid of *Proterosuchus fergusi* NMQR 1484 in lateral view, reflected, after Clark et al. (1993). (C) Chondrocranium of *Crocodylus porosus* after ref 1 with region ossified as laterosphenoid filled in. **BS**, basisphenoid; **FR**, frontal; **EP**, epipterygoid; **LS**, laterosphenoid; **OP**, opisthotic; **PA**, parietal; **PF**, postfrontal; **PO**, postorbital; **PR**, prootic; **Q**, quadrate.

Las Testudines (tortugas) poseen un amplio registro fósil, a partir del Triásico. Presentan un caparazón dorsal fusionado a las costillas y un plastron ventral. La cintura pectoral (escapula, coracoide) se ubica debajo de las costillas y tiene dos “aristas” que dan una apariencia triradiada al cinturón pectoral. La cintura pélvica también tiene apariencia triradiada. El rostro posee un pico córneo anterior





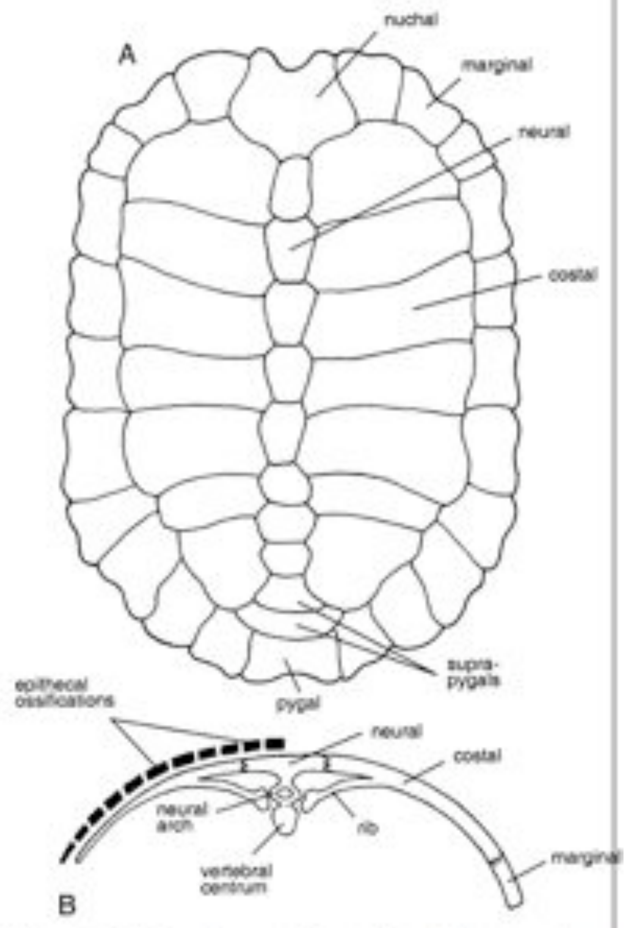


Figure 1. Schematic representation of the turtle carapace in dorsal view (A) and in a transverse section (B) (A: after A.F. Carr, Handbook of Turtles, Cornell University Press, 1952, Fig. 2c).

Figure 2. The carapace of a marine turtle (*Caretta caretta*) in ventral view, showing the close association of the ribs with the costal plates.

turtles, but the ribs of turtles are unique among vertebrates in that they chondrify within the deep layers of the thickened dermis of the carapacial disk. Perichondral ossification starts at the point of entry of the rib into the dermis, and from there spreads laterally. Once the whole cartilage of the embryonic rib is surrounded by perichondral bone, trabecular bone starts to spread from the rib through the dermis of the carapacial disk, and the costal plate is formed. In a similar pattern, the cartilaginous tips of the neural spines of the dorsal vertebrae pierce the deep layers of the dermis of the carapacial disk. Following their perichondral ossification, trabecular bone spreads from them through the dermis to form the neural plates.

Por ventral, los nueve huesos el plastron tiene un origen embriológico totalmente distinto, a partir de células de la cresta neural del *tronco* (único tetrápodo en que se conoce hueso de cresta troncal)

Son huesos membarnosos, posiblemente homólogos a gastralia (costillas ventrales)

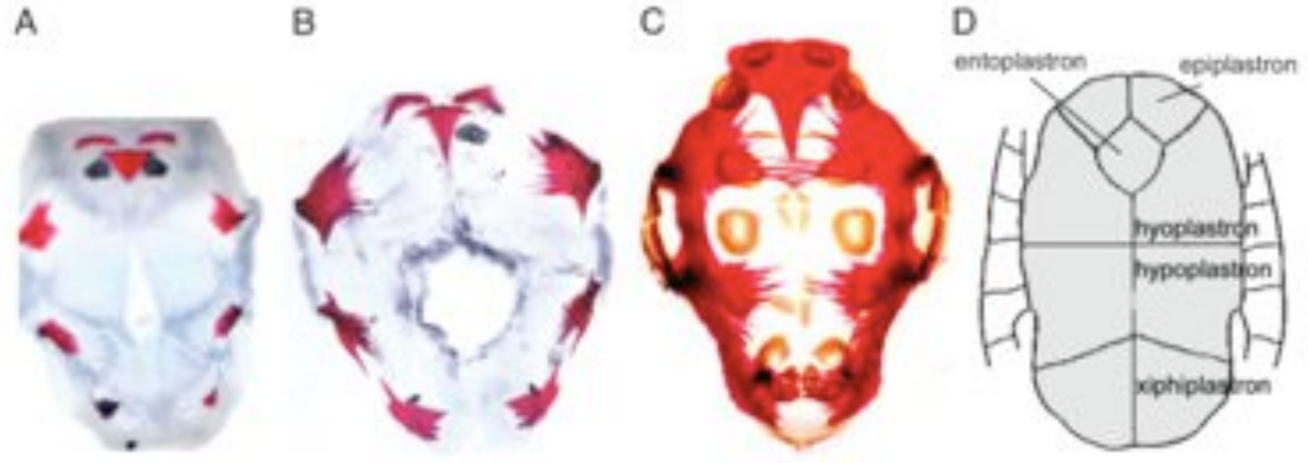


Fig. 1. Intramembranous ossification of the plastron. (A–C) Three stages of plastron development stained with alcian blue (cartilage) and alizarin red (bone). The turtle embryos used in this report were in this size range. (A) A 1 cm long embryo, showing the three anterior centers of ossification and the three laterally paired ossification centers (the blue staining is from girdle cartilage). (B) A 2.2 cm turtle, showing spicules radiating from ossification centers. (C) A 2.7 cm turtle showing fusion of the anterior ossification centers. (D) Plastron nomenclature in a mature *Trachemys scripta* (after Gilbert et al. 2001).

La forma en que esconden la cabeza define los dos grupos vivientes principales: Pleurodira (retraen la cabeza lateralmente) y Cryptodira (retraen la cabeza verticalmente). Ambos grupos también se diferencian por la musculatura de las mandíbulas (con una troclea (polea) a partir de un proceso de la capsula ótica, pleurodira; o del pterygoideo, cryptodira) Los Casichelydia presentan además el desarrollo de un a cámara ótica alrededor del oído medio.

TESTUDINATA: Tortugas modernas (corona), son todos los descendientes del ACMR de Pleurodiras y Cryptodiras

Proganochelys: no tiene uno ni lo otro (polaridad?)

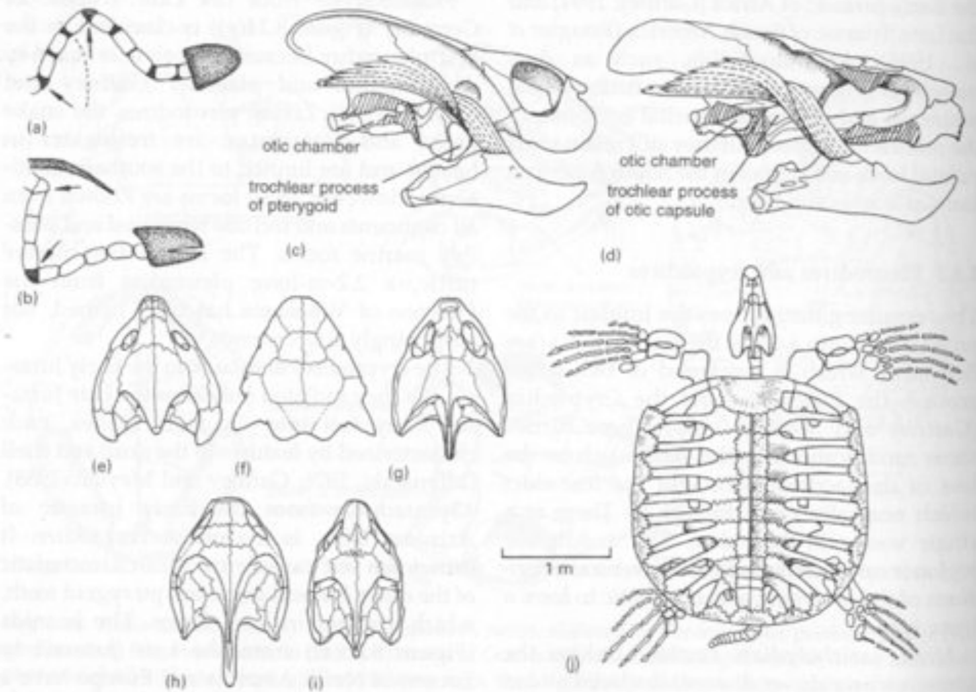
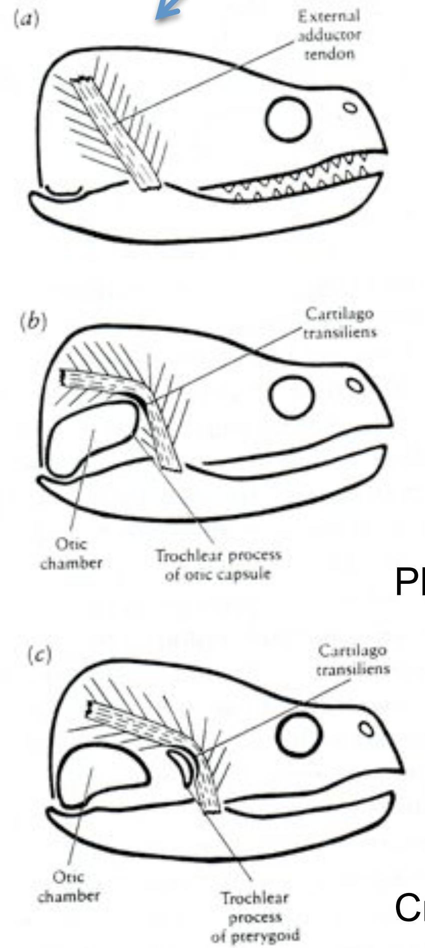


Fig. 8.25 Turtle classification and diversity: mode of neck folding in (a) a typical pleurodire in dorsal view, and (b) a cryptodire in ventral view; course of main jaw adductor muscle mass in *Emydura*, a pleurodire (c) and *Chelydra*, a cryptodire (d); (e–i) the diversity of turtle skulls, all in dorsal view: (e) *Eubaena*, a baenid; (f) *Meiolania*, a meiolanid; (g) *Toxochelys*, a chelonioid; (h) *Adocus*, a trionychoid; (i) *Mauremys*, a testudinoid; (j) the giant Cretaceous marine turtle *Archelon* in dorsal view. [Figures (a, b) after Mlynarski, 1976; (c–i) after Gaffney and Meylan, 1988; (j) after Wieland, 1909.]



Pleuro

Crypto

Kayentachelys muestra el arreglo de musculatura cryptodira, indicando que ésta es la condición ancestral, que fue modificada en pleurodira

(contra la típica suposición de que cada arreglo apareció por separado: lección sobre homología!!)

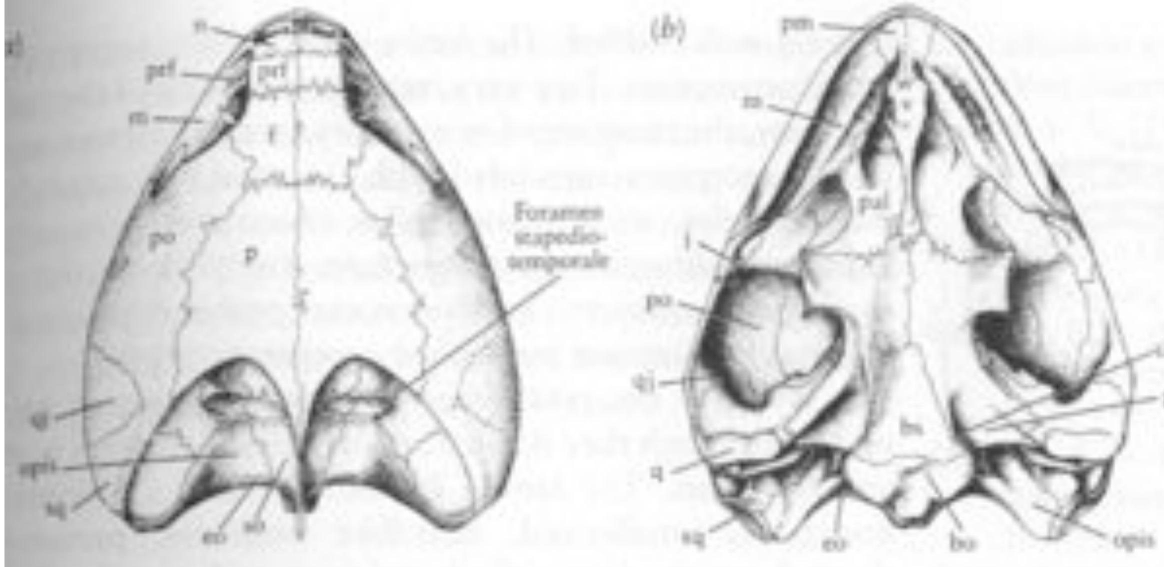
Pleurodira

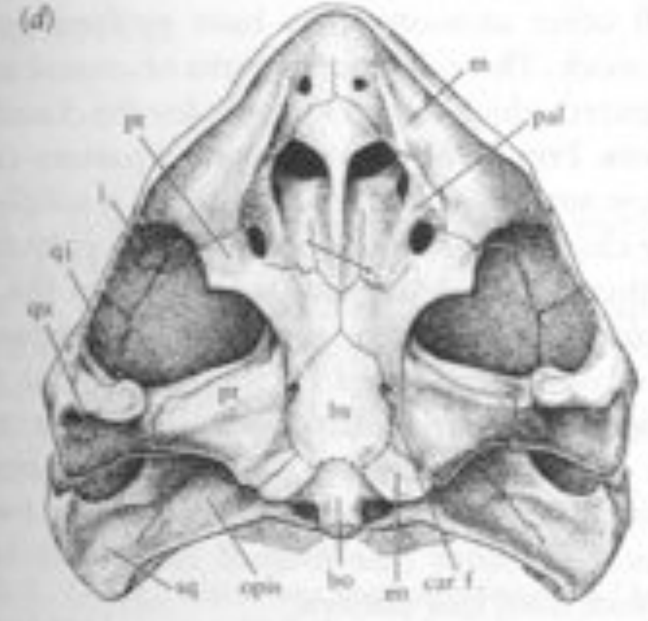
Vivientes:

-Pelomedusidae (3 generos)
-Chelidae (12 generos)

Cryptodira

Vivientes:
Testudinoidea (incluye terrestres)
Chelonoidea (tortugas marinas)
Trionychidae (caparazón blando)





En tortugas, el prefrontal comunica el techo del cráneo con el paladar

Figure 10-28. SKULL OF ONE OF THE EARLIEST KNOWN CRYPTODIRES, *PLESIOCHELYS*. A member of the superfamily Chelonoidea from the Upper Jurassic of Switzerland. (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views. Note position of foramen for carotid artery at the rear of the suture between the pterygoid and basisphenoid. *From Gaffney, 1979.* (*d*) *Baena*, an Eocene baenid cryptodire. Palate showing opening for carotid artery (cart f) midway in length of pterygoid-basisphenoid suture. *From Gaffney, 1972. Courtesy of the Library Services Department, American Museum of Natural History.* Abbreviations as in Figure 8-3.

Proganochelys por mucho tiempo fue la tortuga más antigua y basal conocida

Pan-Testudinata (Apo-Clado): todos los descendientes del ACMR de tortugas con la primera forma que presenta caparazón (Proganochelys)

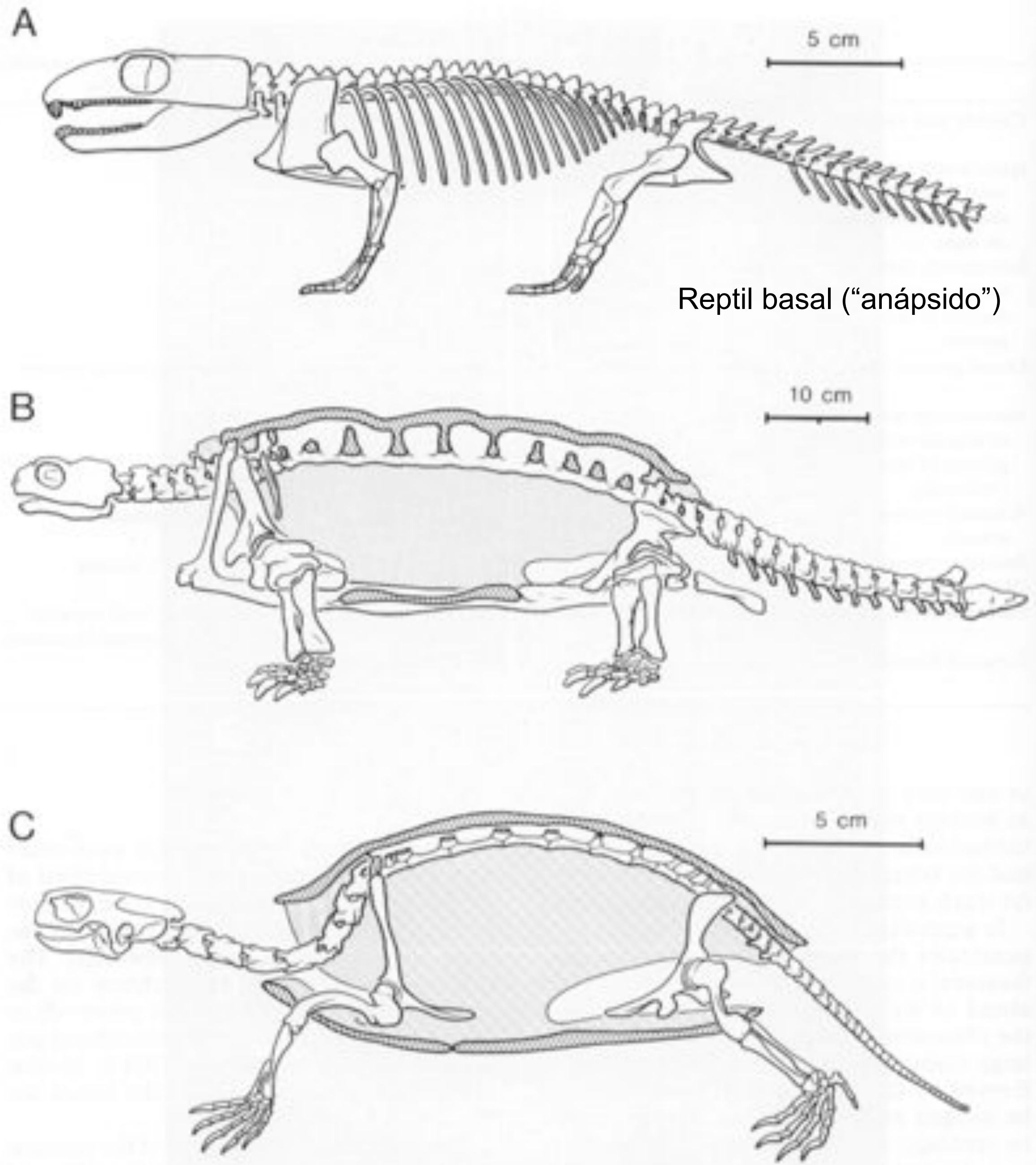


Fig. 133. Comparison of turtles and a primitive amniote. The two turtles have the shell (but no other skeletal elements) sectioned parasagittally, just to the left of the midline. **A**, *Captorhinus* sp., Early Permian, from Heaton and Reisz (1980), distal portion of tail deleted. **B**, *Proganochelys quenstedti*, SMNS 16980, Late Triassic. **C**, *Emys orbicularis*, from Bojanus (1819) and specimens, Recent.

Entre los rasgos primitivos de *Proganochelys* se encuentra la presencia de una cola alargada y un paladar con dientes unido "laxamente" al neurocráneo. En tortugas más derivadas el paladar se encuentra fusionado firmemente a la base del neurocráneo. Otras tortugas primitivas son las Australochelidae, de África y Sudamérica, que presentan colas largas. *Proganochelys* y las Austrochelidae además no podían esconder la cabeza dentro del caparazón.

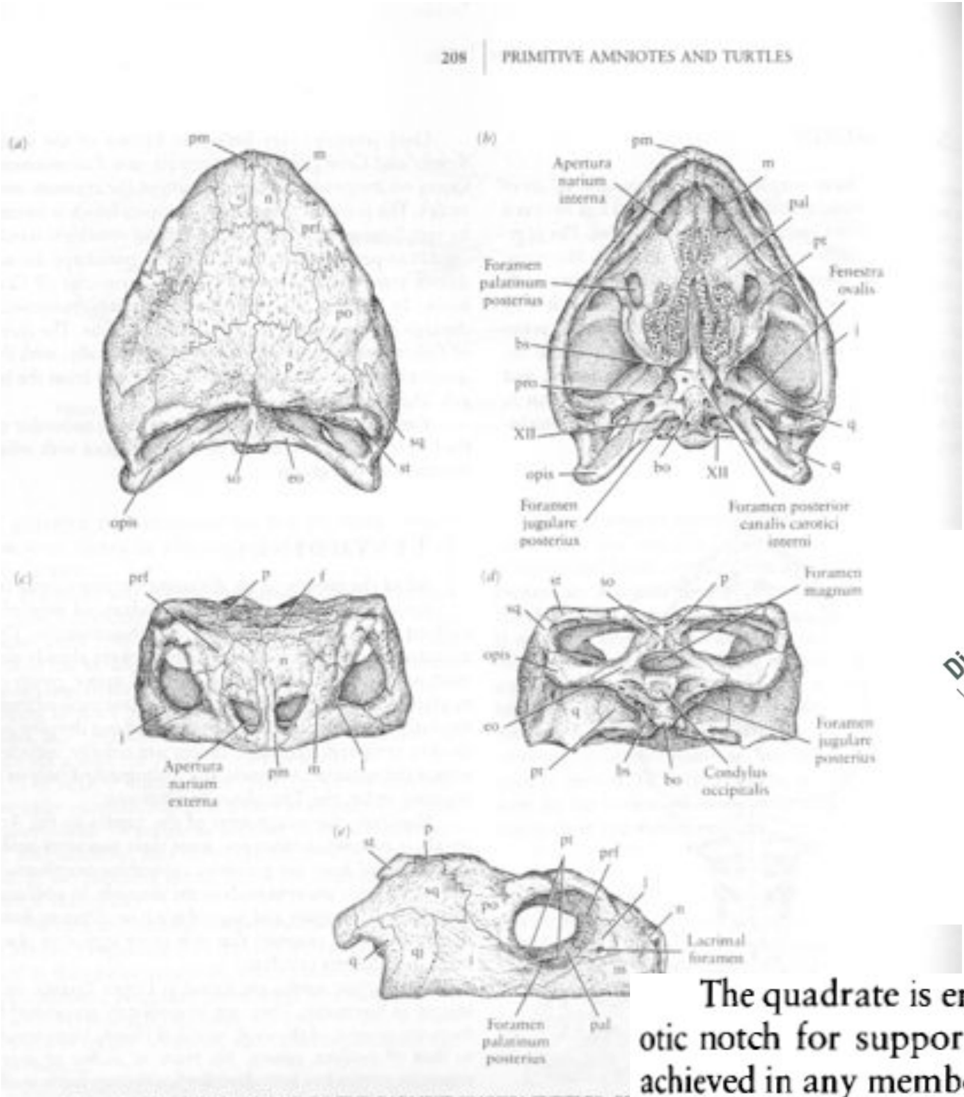
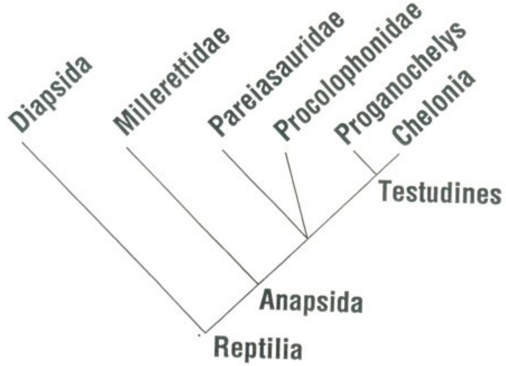
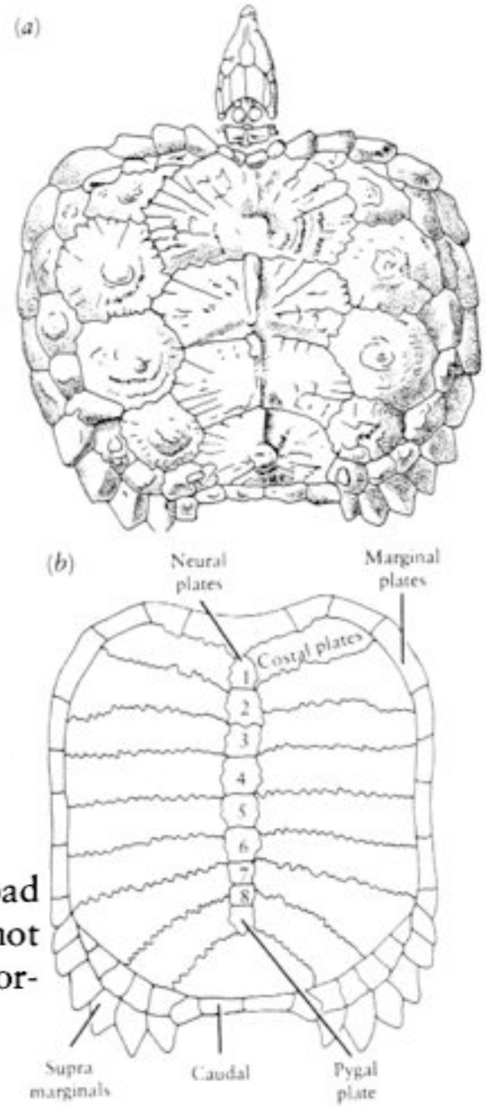
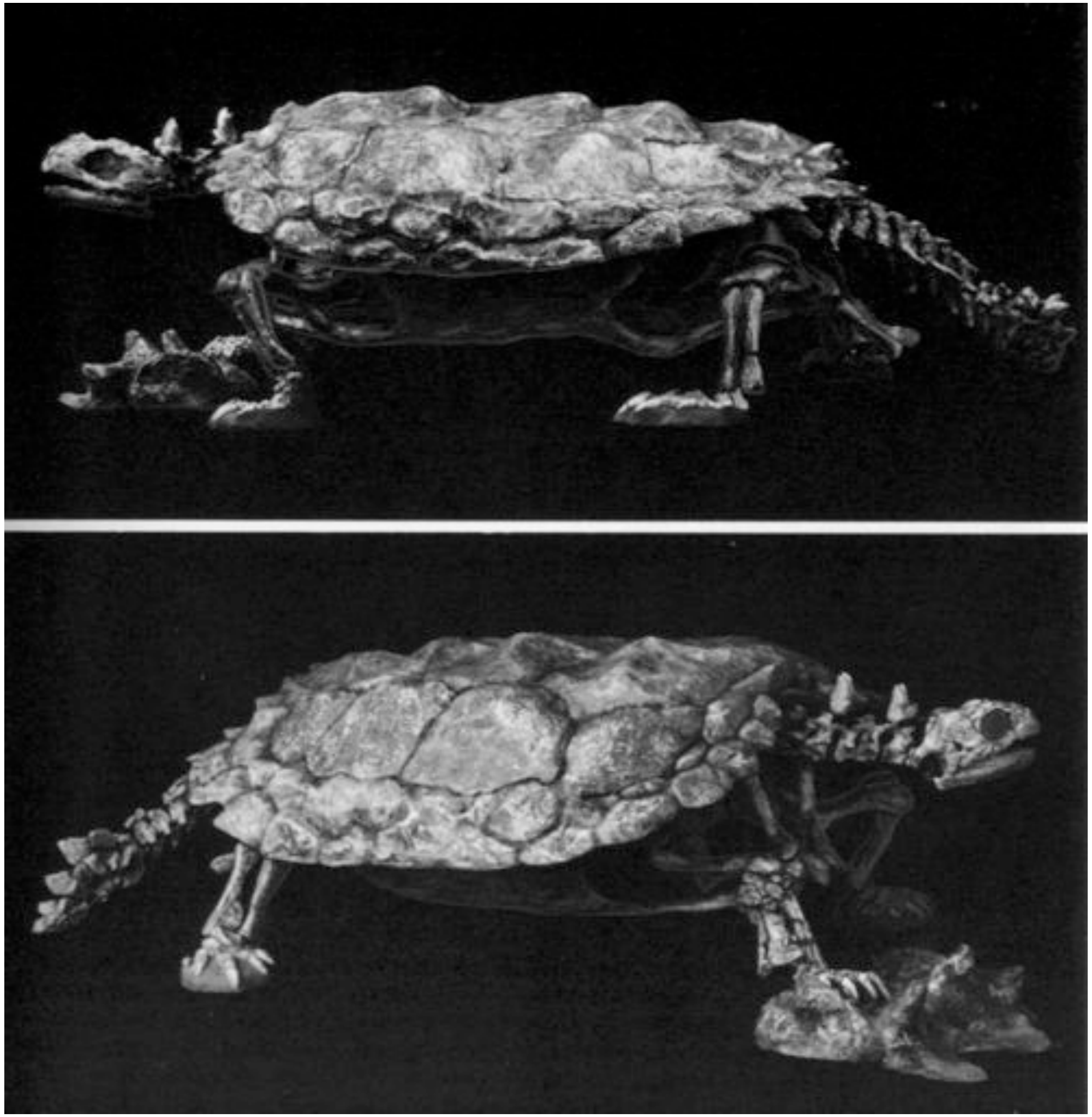


Figure 10-23. SKULL OF ONE OF THE EARLIEST KNOWN TURTLES, PR... TRIASSIC OF GERMANY. × ½ (a) Dorsal view. (b) Palatal view. (c) Anterior view. (d) Occipital view. (e) Lateral view. Abbreviations as in Figure 8-3. *From Gaffney and Meeker, 1983.*



The quadrate is embayed posteriorly to form a broad otic notch for support of a tympanum, a condition not achieved in any members of the Captorhinomorpha. Dor-





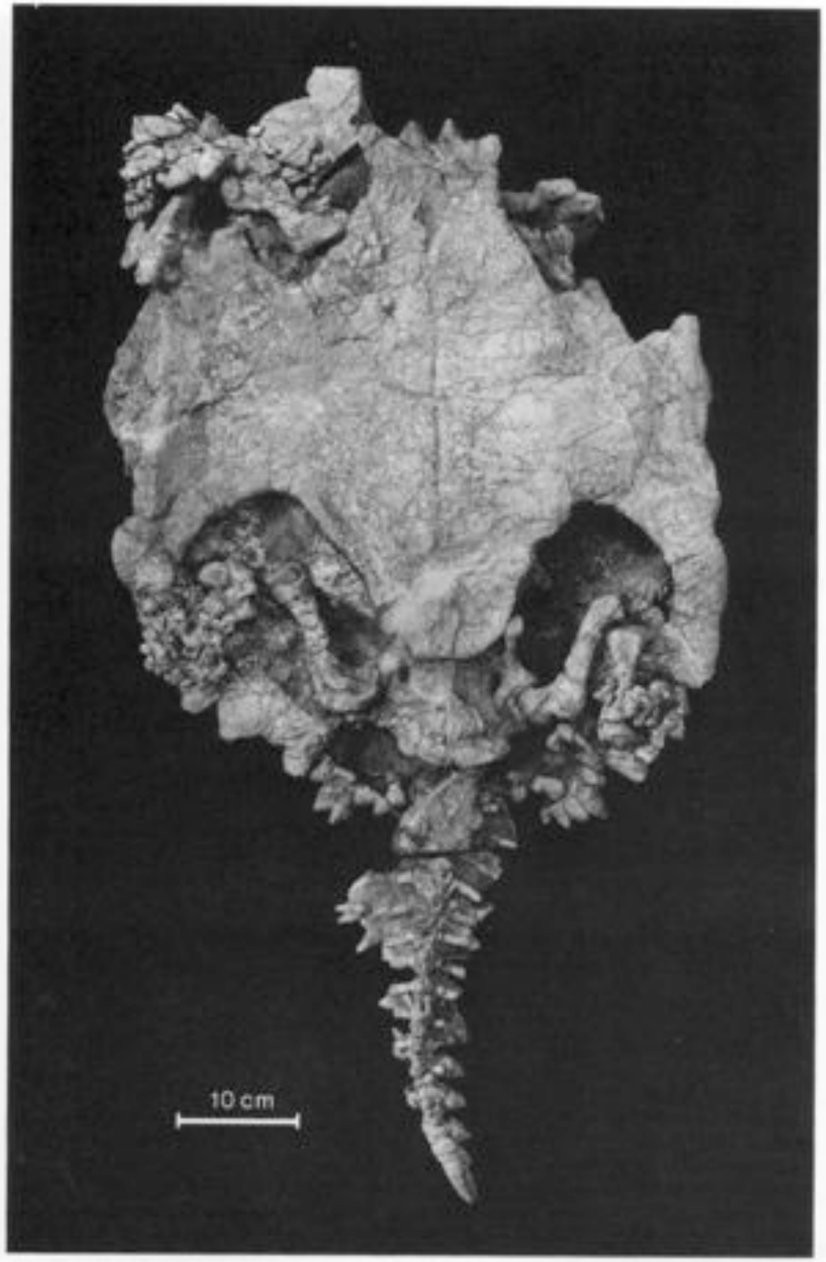


Fig. 87. *Proganochelys quenstedti*. SMNS 17204. Ventral view of shell and associated elements. From Gaffney (1985a).

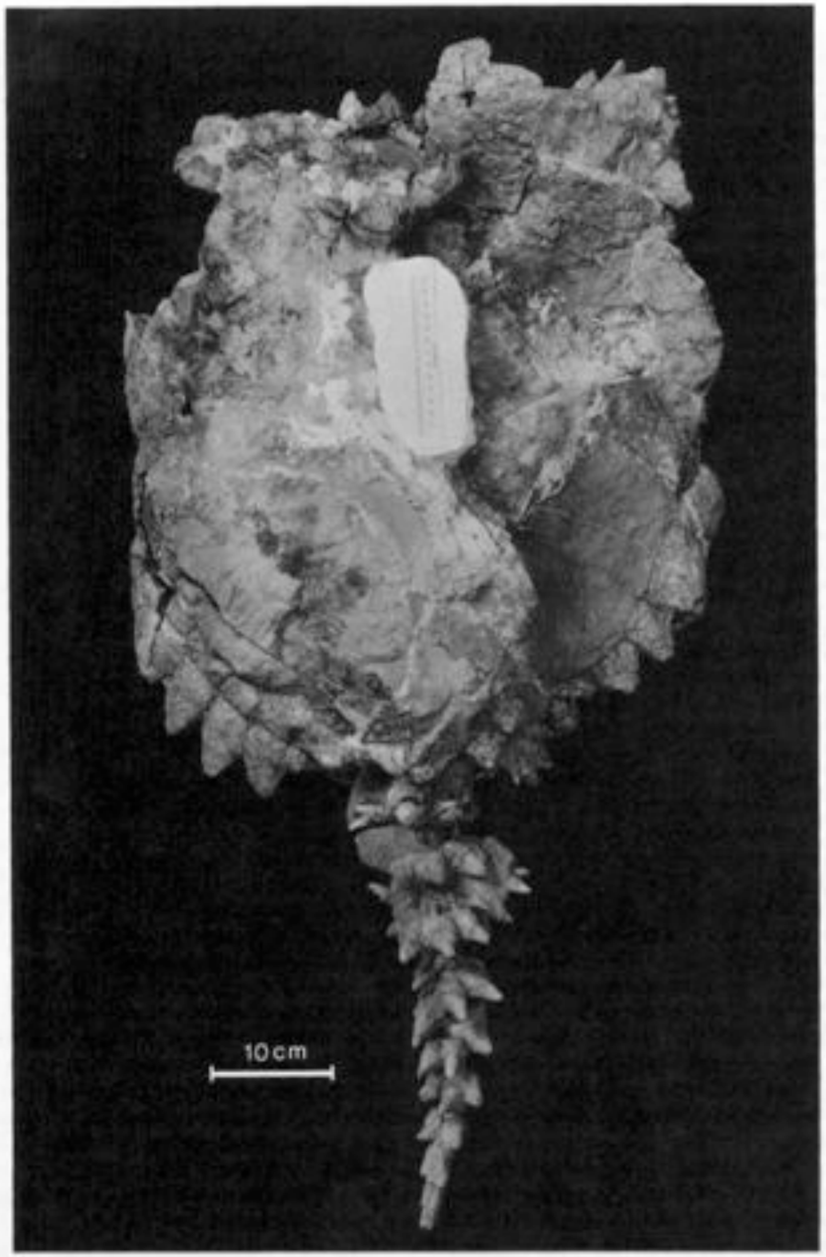


Fig. 85. *Proganochelys quenstedti*. SMNS 17204. Dorsal view of shell and associated elements.

Proganochelys también posee una cintura pectoral que retiene la presencia de la clavícula e interclavícula. \

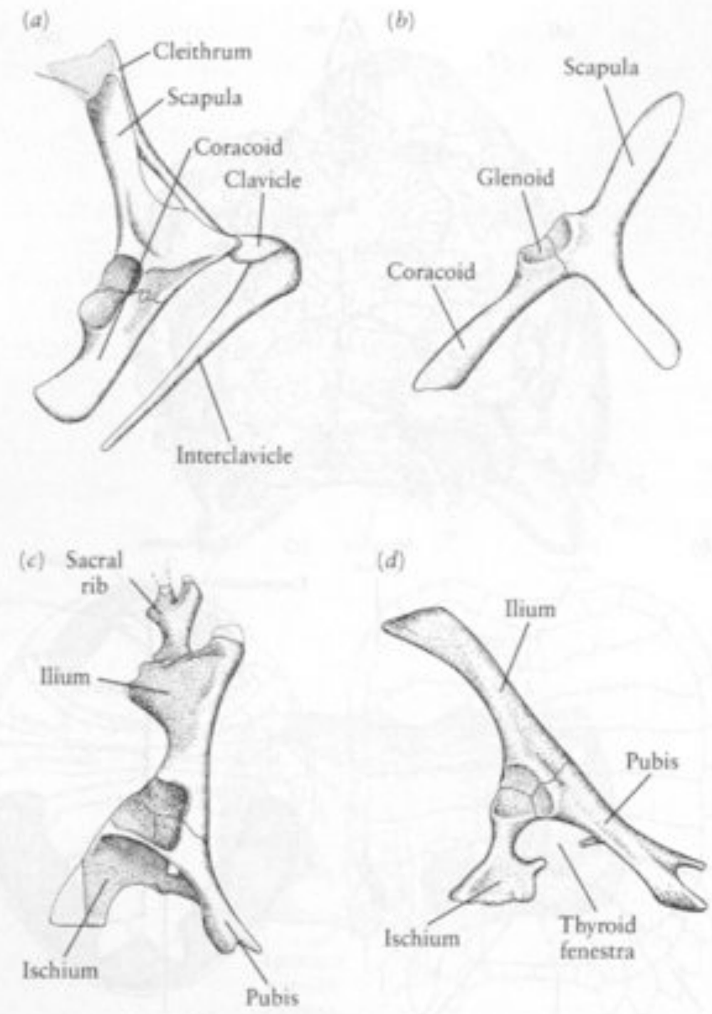
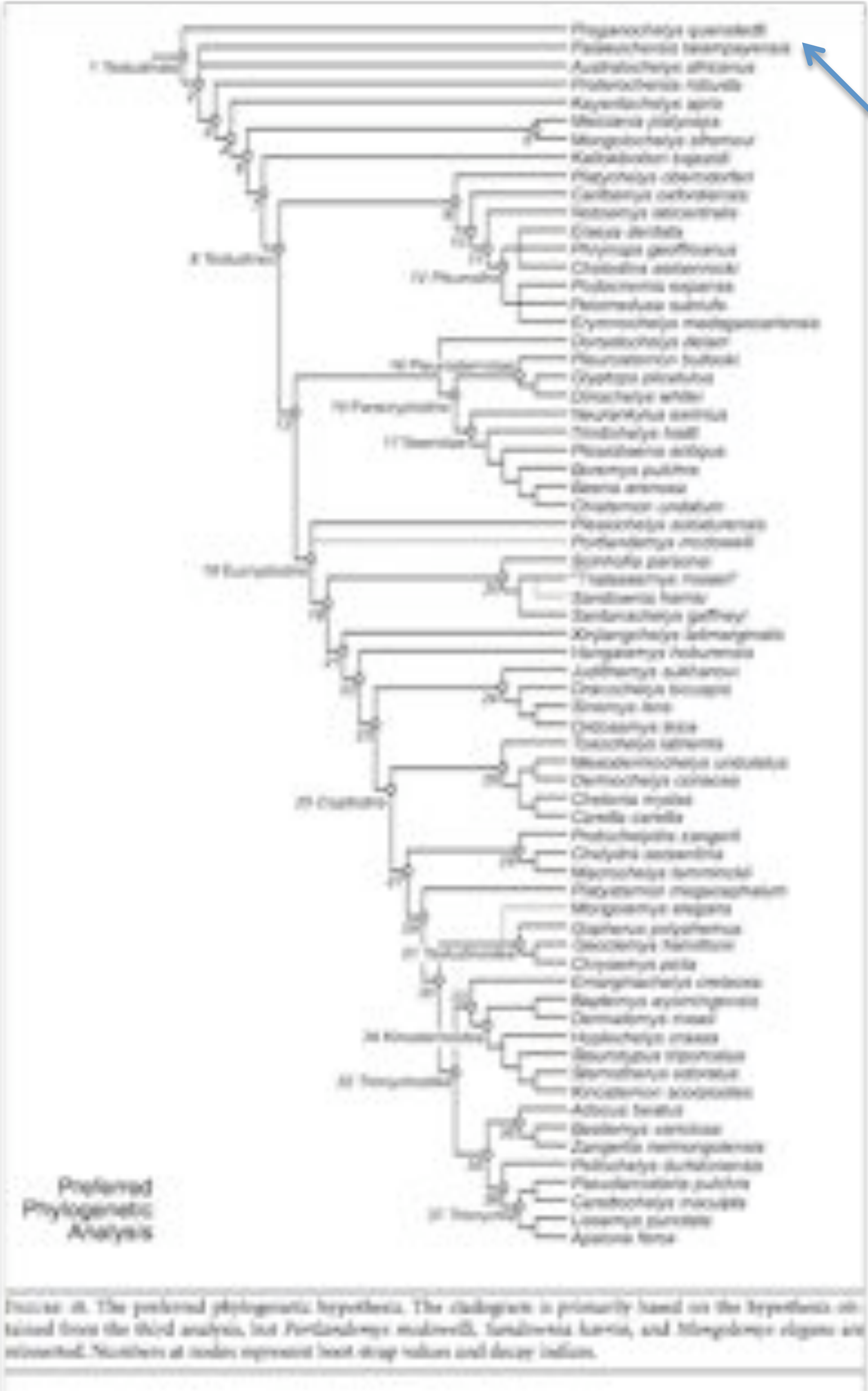
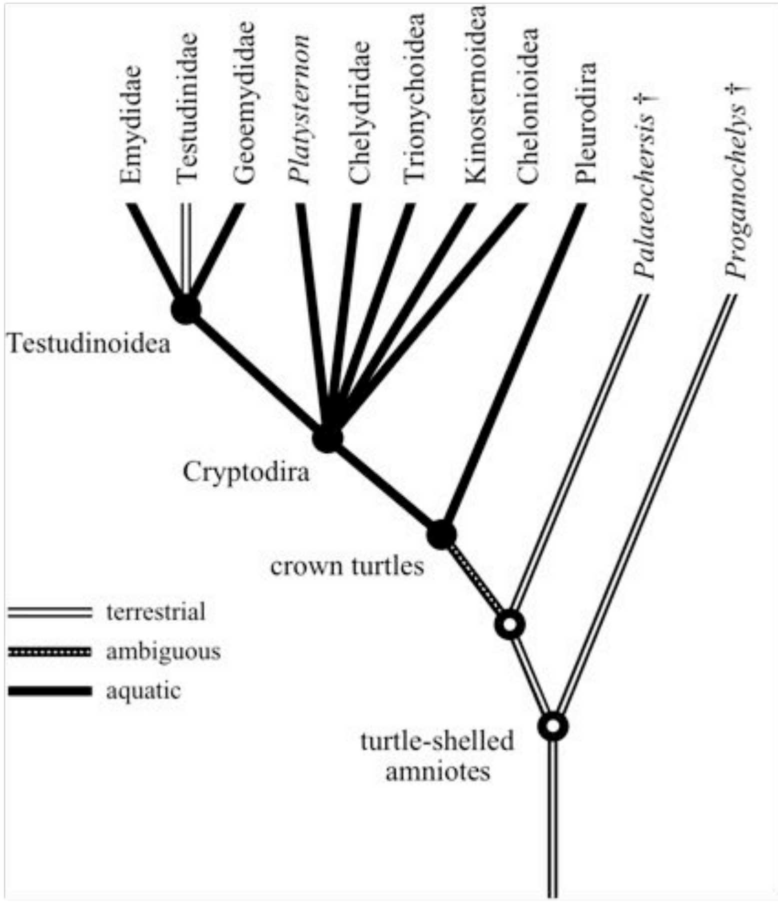


Figure 10-25. PECTORAL AND PELVIC GIRDLES OF TURTLES. (*a* and *c*) *Proganochelys. From Jaekel, 1915–1916.* (*b* and *d*) A modern turtle.



Las tortugas corona descienden de formas acuáticas, sin embargo, los pan-testudinos terrestres sugieren un previo paso por la vida terrestre.

Nadadoras: manos largas
Terrestres: manos cortas



Teoría gradualista: Origen del caparazón a partir de integración de osteodermos dérmicos, posterior incorporación de las costillas al caparazón

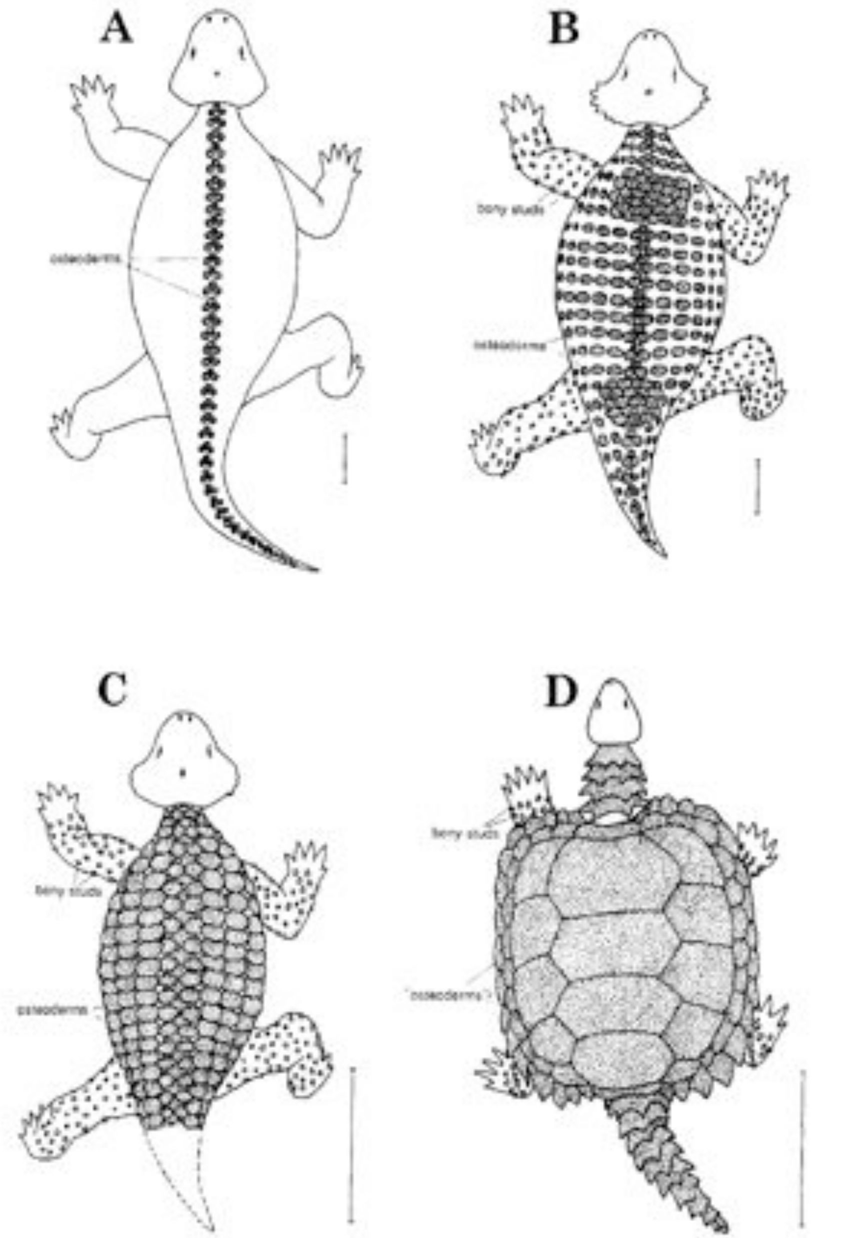


Figure 19. Dorsal views of reconstructions of (A) *Bradysaurus*, (B) *Scutosaurus*, (C) *Anthodon* and (D) *Proganochelys*, showing dorsal dermal armour and bony studs over limbs in (B) and (C), as well as overall similarity in body proportions. (A) after BPI 1/4195, (B) and BPI 1/6 and 1/548, (C) after Gaffney (1990).

However:

the fact that the earliest fossil turtle (*Proganochelys*)[9] from the Upper Triassic of Europe (215 Mio years) has a complete theca. Furthermore, epithecal ossifications appear later than ossifications of the theca in development and, in modern turtles, epithecal ossifications tend to form in evolutionarily relatively advanced forms only.

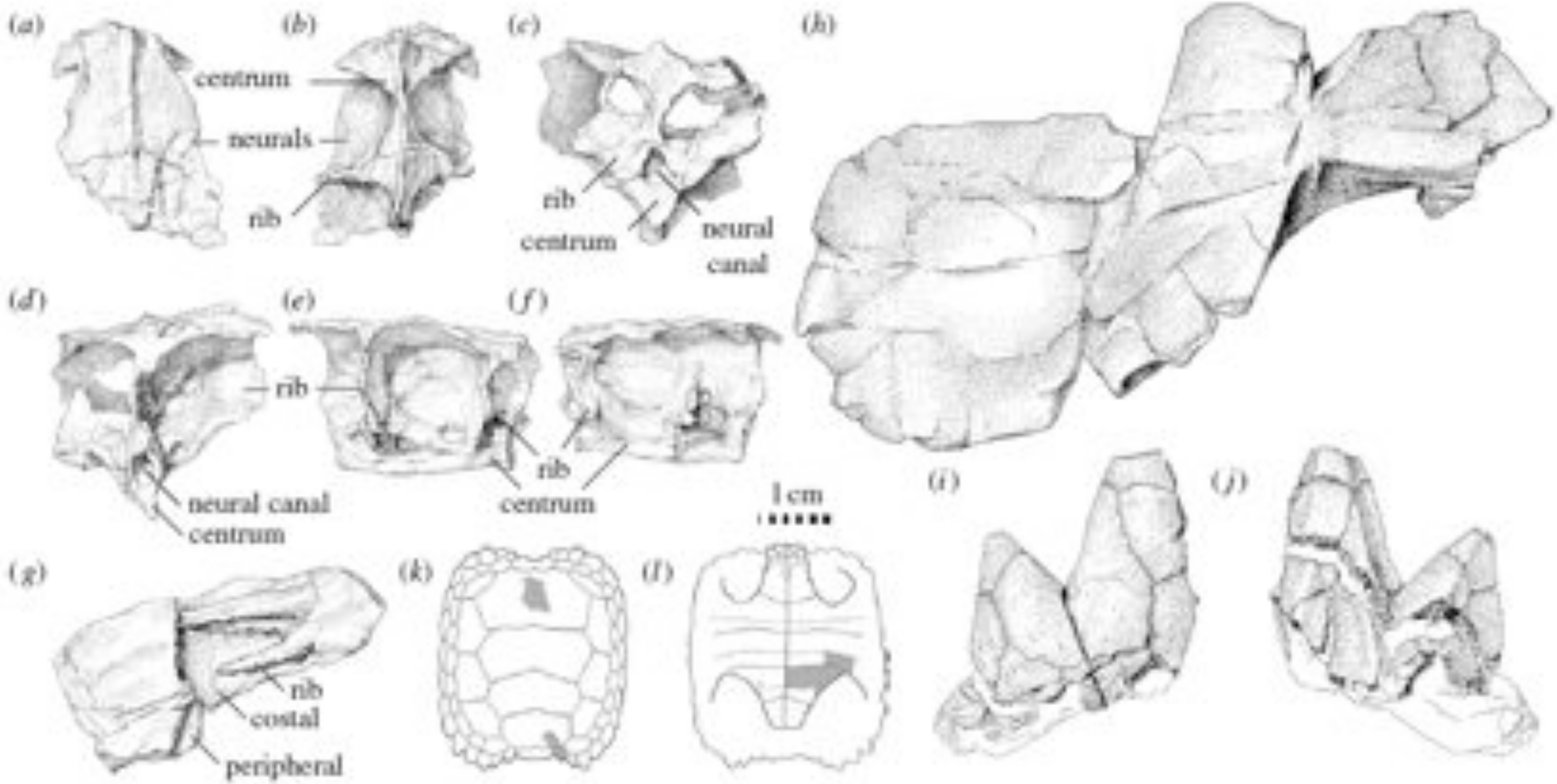


Figure 1. Illustrations of *C. tenertesta*, NMMNH P-16697. (*a*) Dorsal, (*b*) ventral, (*c*) anterior, (*d*) posterior, (*e*) right lateral and (*f*) left lateral views of a portion of the central carapace with the associated dorsal vertebrae and ribs. (*g*) Ventral view of a posterior carapacial fragment, consisting of two right costals, two ribs and some peripherals. Note how the ribs run superficially along the visceral surface of the overlying osteoderms. (*h*) Ventral view of partial left hypoplastron. (*i*) Anterior and (*j*) posterior views, respectively, of the neck spine consisting of multiple osteoderms. Approximate location of illustrated shell fragments within the (*k*) carapace and (*l*) plastron of the better known basal turtle *Proganochelys quenstedti* (redrawn from Gaffney (1990) and Joyce (2007)).

Chinlechelys

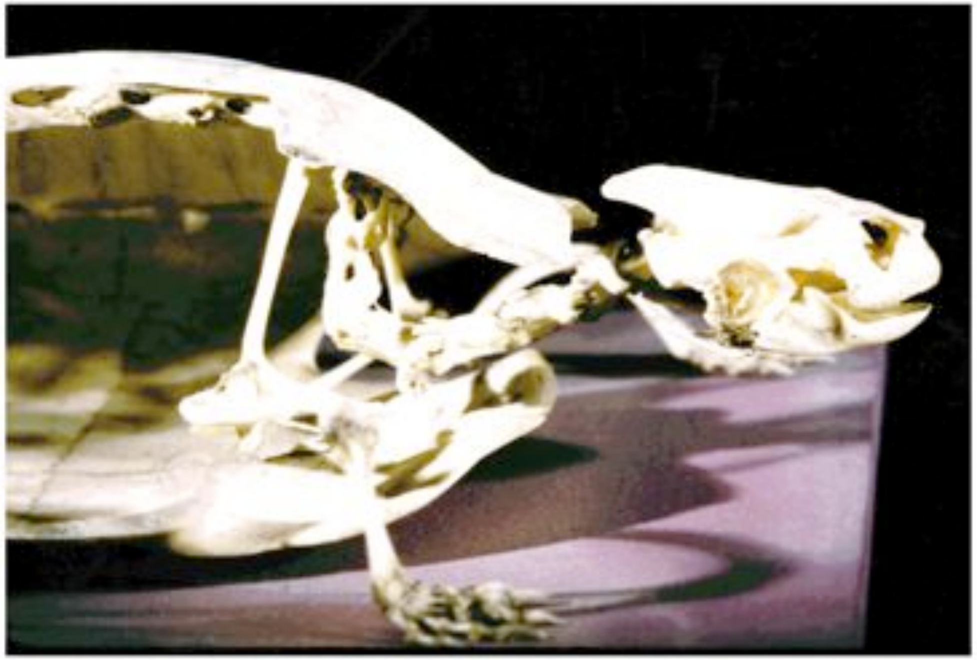
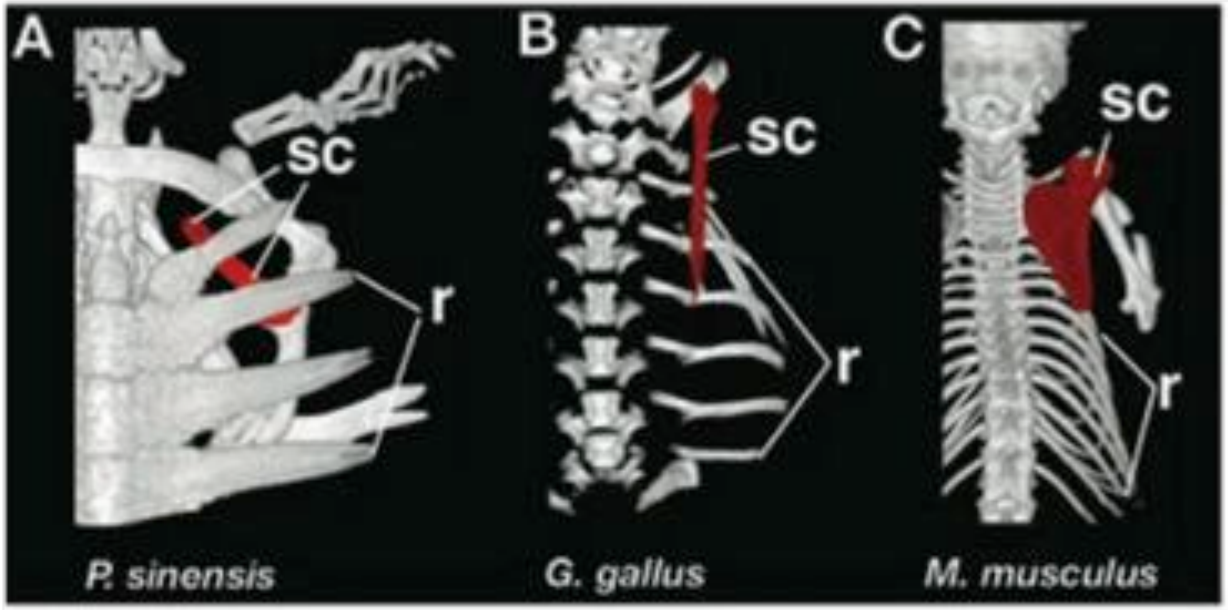


Figure 3. The relationship of the shoulder blade to the carapace in turtles (*Graptemys geographica*).

In support of a gradual evolution of the turtle body plan, some authors tried to explain this position of the scapula by a backwards shift of the pectoral girdle in turtles. A recent theory



As a turtle embryo grows and develops, the contours of the future carapace are soon mapped out by an accelerated growth and a thickening of the skin on its back. The carapacial disk is formed. The margin of the carapacial disk shares histological and chemical properties with the marginal apical ridge of the early limb bud, a region that was long known to be an important site for inductive tissue interaction in the formation of the limb skeleton. Somite extirpation experiments confirmed a somitic origin for those cells that form the ribs as well as the thickened dermis of the carapacial disk in the snapping turtle.[14] Extirpation experiments performed on the margin of the carapacial disk, referred to as carapacial ridge, confirmed its role in the deflection of rib growth to a more superficial position in turtles.[13]

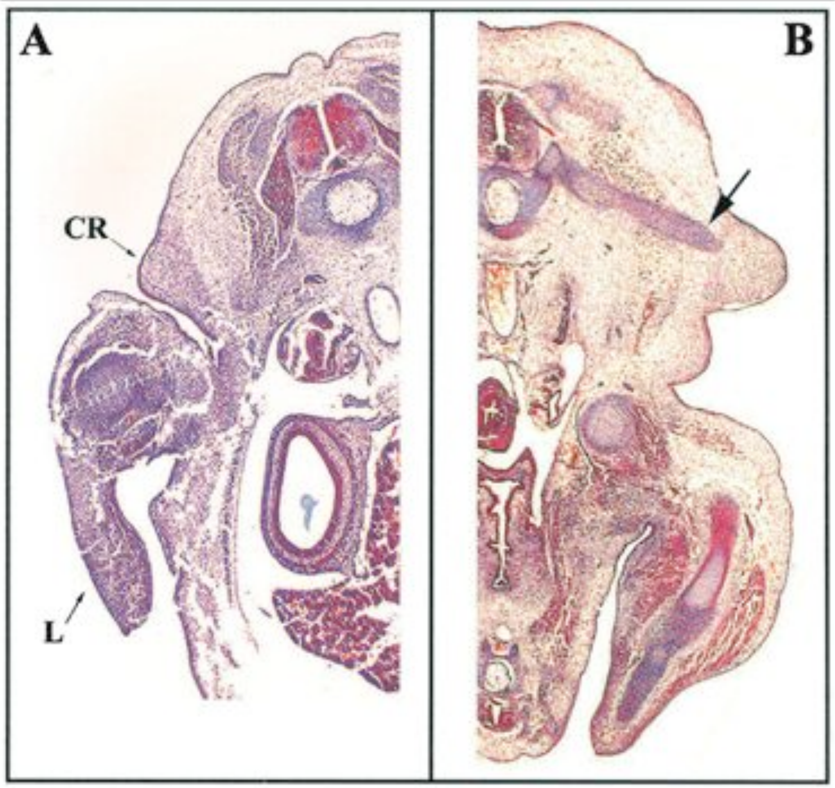
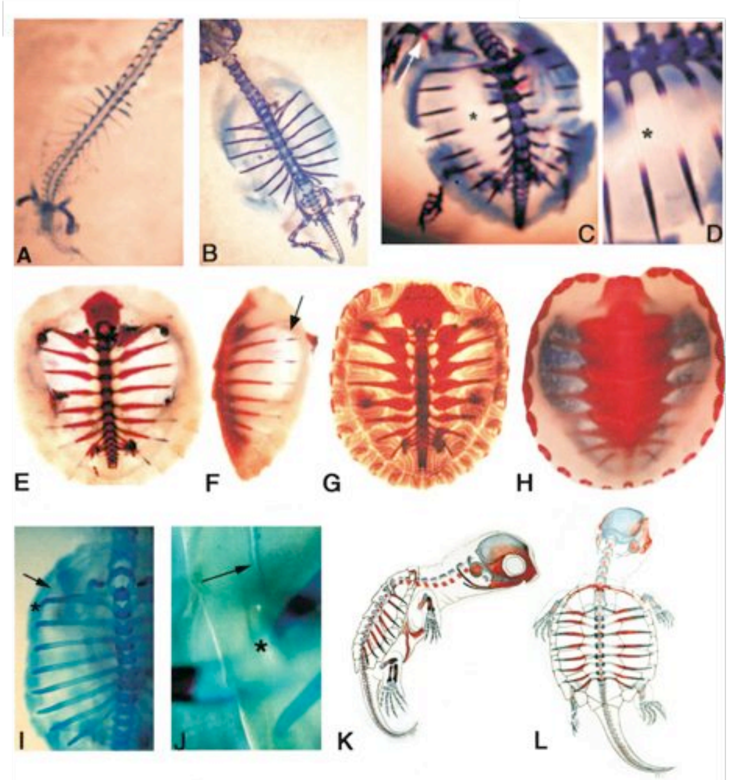


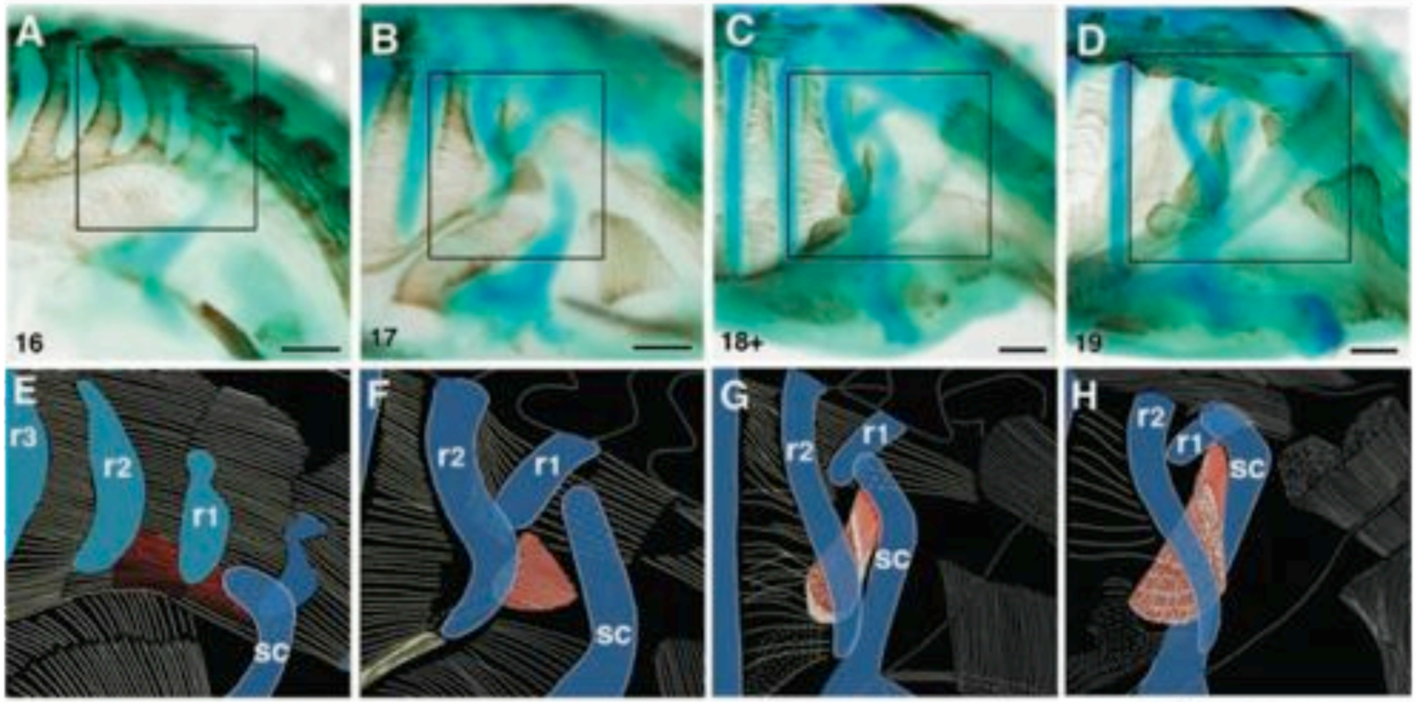
Fig. 2. Carapace ridge and rib entry into the CR of *Trachemys scripta.* Mallory's triple stain of embryos sectioned serially on (A) day 23 and (B) day 29 of incubation. The CR has formed by day 23, but rib entry (arrow in (B)) is not seen until a few days later. The sections are taken through extended limb buds (L) that can be seen for comparison.



Experimento de injerto de costilla de pollo en dermis de pollo: induce osificación en la dermis

TEORIA PARACRINA del origen del caparazón (saltacionista)

Costillas y caparazón: from anterior to under. Posterior shift?



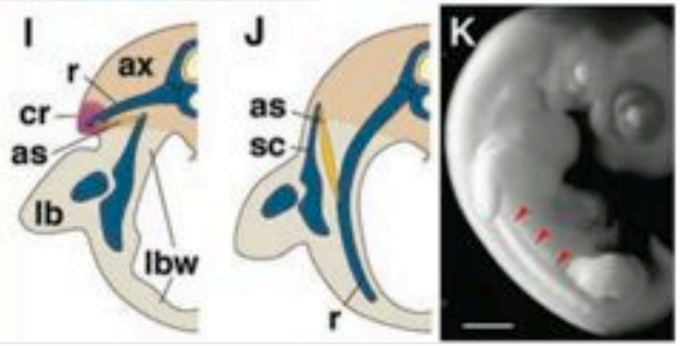


Fig. 2. Developmental twisting of AS muscle in *P. sinensis*. (**A** to **H**) Cartilages were stained with alcian blue and muscles were immunochemically stained with MF20, in whole mounts of stages 16 to 19 *P. sinensis* embryos. The boxes in the top row of photos are magnified to show schematically the relationships between the AS muscle (red), the scapula, and the ribs (r1 to r3) in the middle row. (**I** and **J**) Schematic transverse views to compare the topography of ribs, body wall (lbw), and forelimb bud (lb) with shoulder girdle between the embryos of turtles (I) and generalized amniotes (J). Generally, the amniote ribs grow ventrally into the lateral body wall, whereas in the turtle, they are arrested in the axial part (ax), growing toward the CR. (**K**) The CR (arrowheads) in stage 14 *P. sinensis* embryo. Scale bars, 500 μm for (A) to (D), 1 mm for (K).

Dato Evo-Devo con olor a saltacionismo:

The amniote vertebra is composed of two parts that originally develop independently, but most of the time fuse in the adult (Fig. 1B). One part is the centrum, which replaces the embryonic notochord. Above the centrum develops the neural arch, which together with the centrum forms the neural canal for the spinal cord. In turtles, the neural arches of the dorsal vertebrae shift forward by half a segment, carrying the ribs with them, again a unique condition in amniotes.[15] The neural arches of successive vertebrae consequently meet each other above the midpoint of the centrum, whereas the ribs come to lie lateral to the no longer functional intervertebral joints. The myomeric and neuromeric segmentation is thus secondarily established in the dorsal region of turtles,[16] as was already the case in *Proganochelys*.[9] The functional reason for this anterior shift of the neural arches is not clear, other than that it may contribute to the mechanical strength of the carapace, as the neural plates come to alternate with the costal plates (Fig. 1A).

Odontochelys: La más antigua tortuga, basal, con dientes aún!

-Sin caparazón! Sólo hay placas neurales
-costillas dorsales expandidas (“abiertas”, extendidas hacia lateral)

-Depósitos marinos!

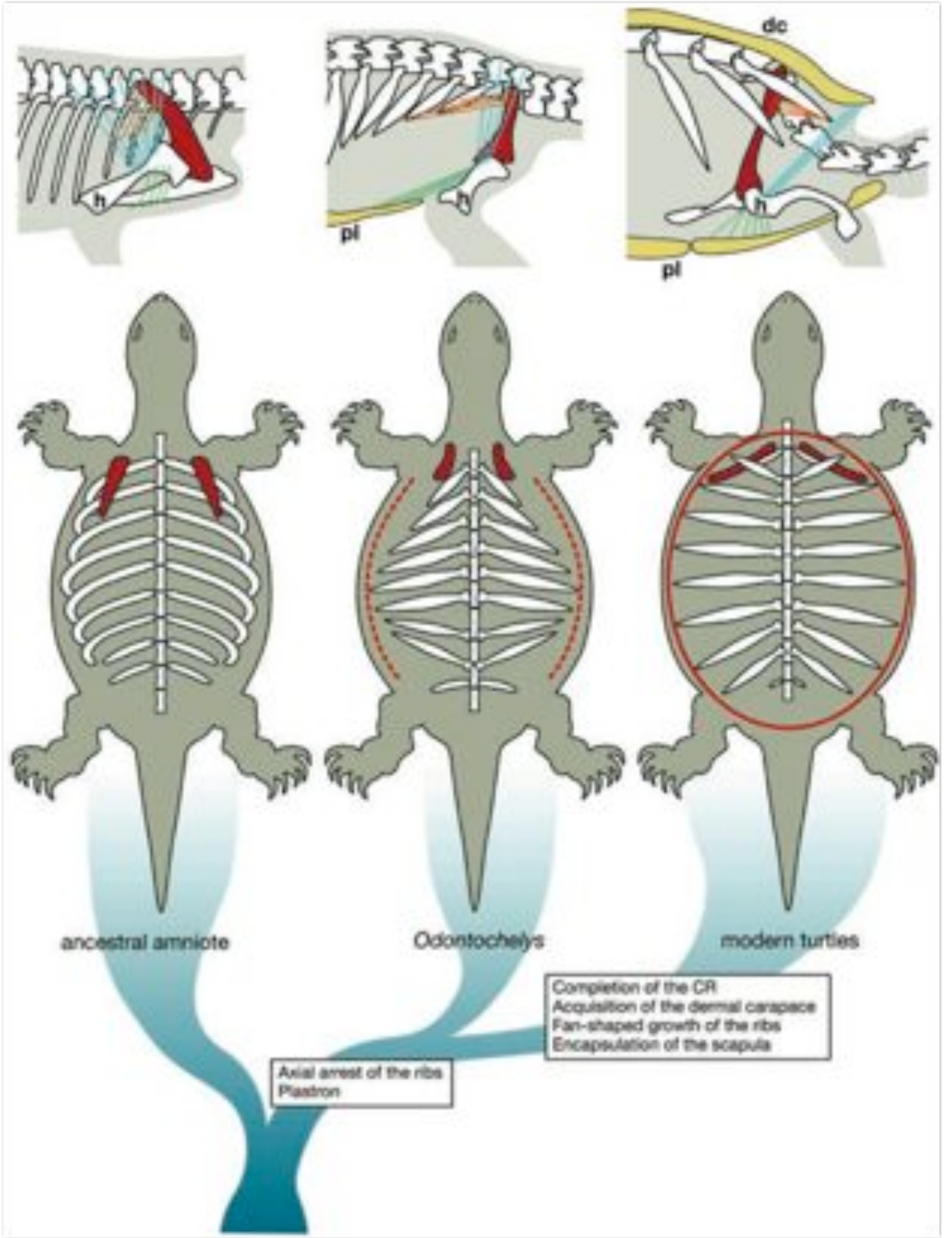
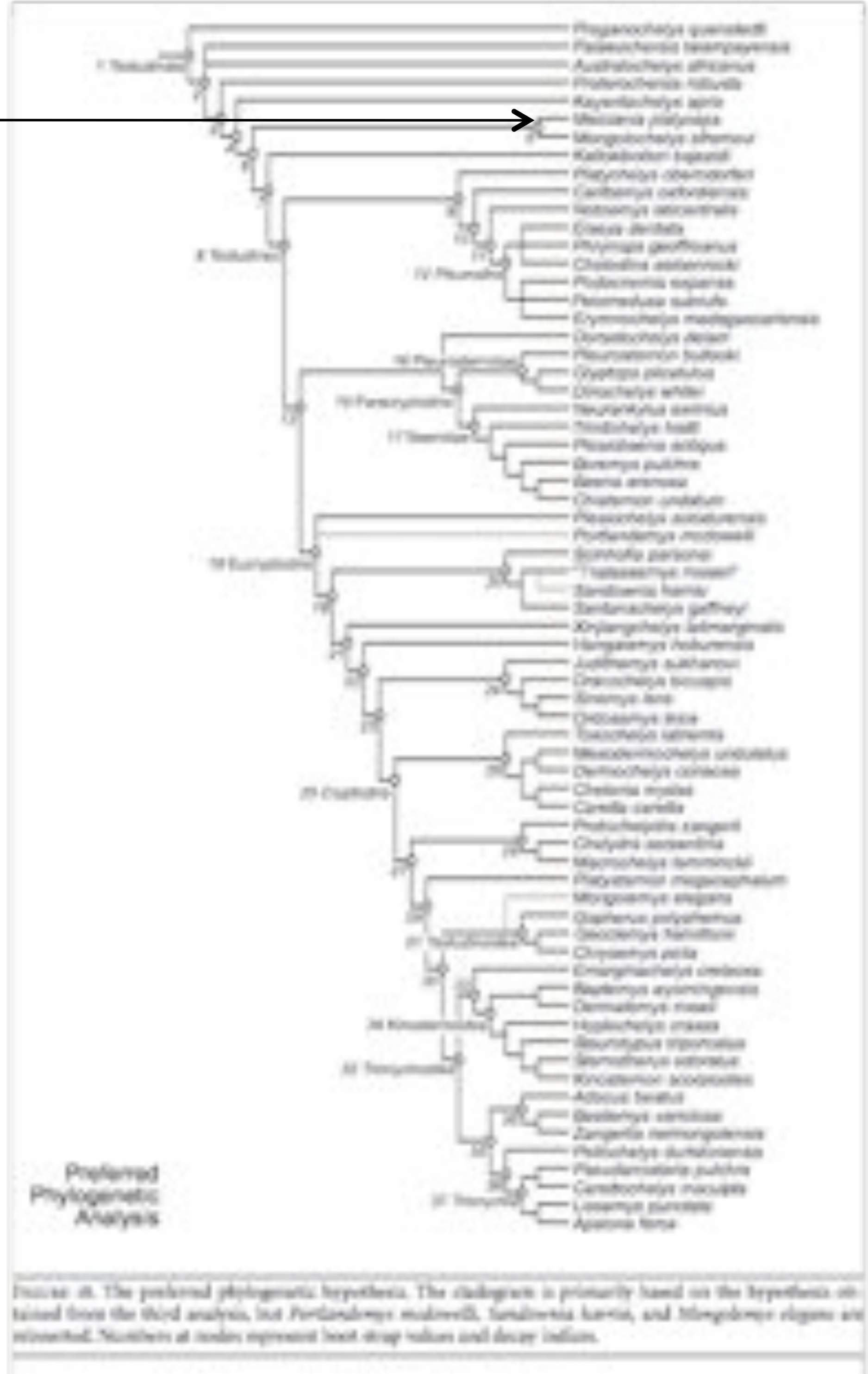
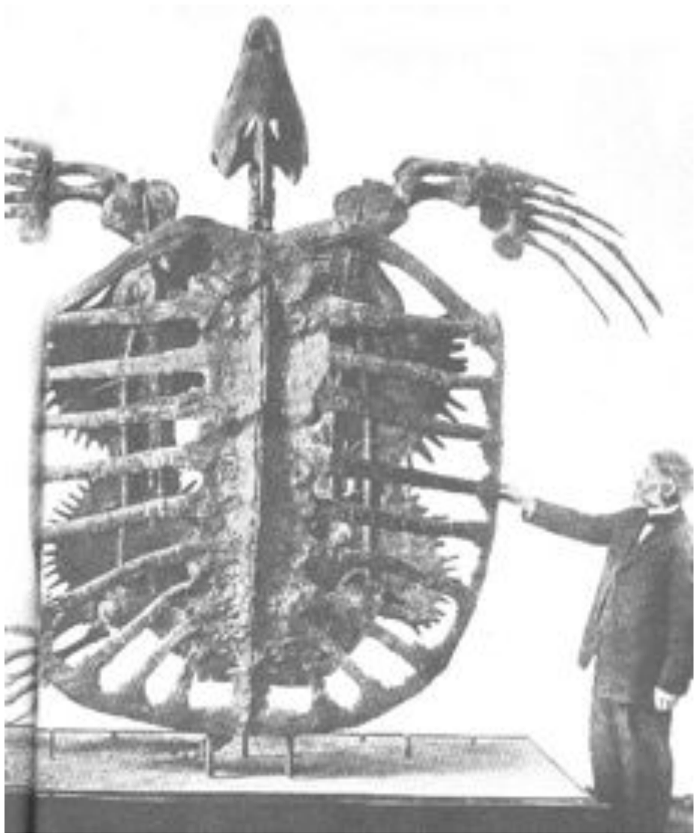


Fig. 4. Evolution of the turtle body plan. (**Top**) A hypothetical sequence of changes in musculoskeletal connectivities. The scapula is red, AS muscle orange, latissimus dorsi blue, and pectoralis green. In *Odontochelys*, the AS would have connected the scapula and distal tips of anterior ribs antero-posteriorly. The pectoralis would have connected the humerus and the plastron (pl). (**Bottom**) A phylogenetic consideration. In *Odontochelys*, the CR (red broken line) may have developed only temporarily and incompletely in the embryo. In the modern turtle, the CR (red solid line) forms a complete circle, inducing the fan-shaped growth of the ribs. dc,

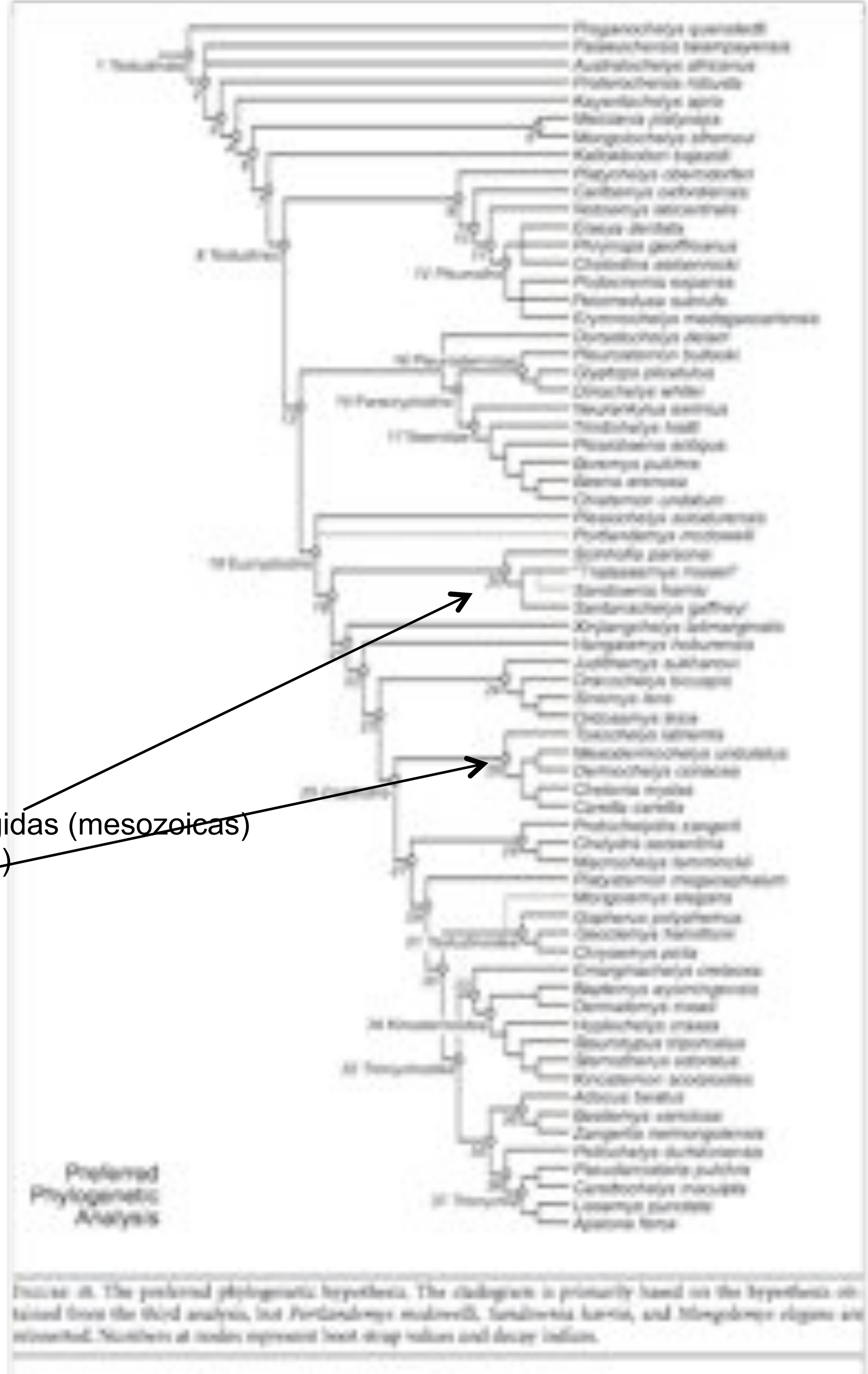
Meiolania platyceps

Nueva Caledonia
Oligoceno-Holoceno
2.5 M

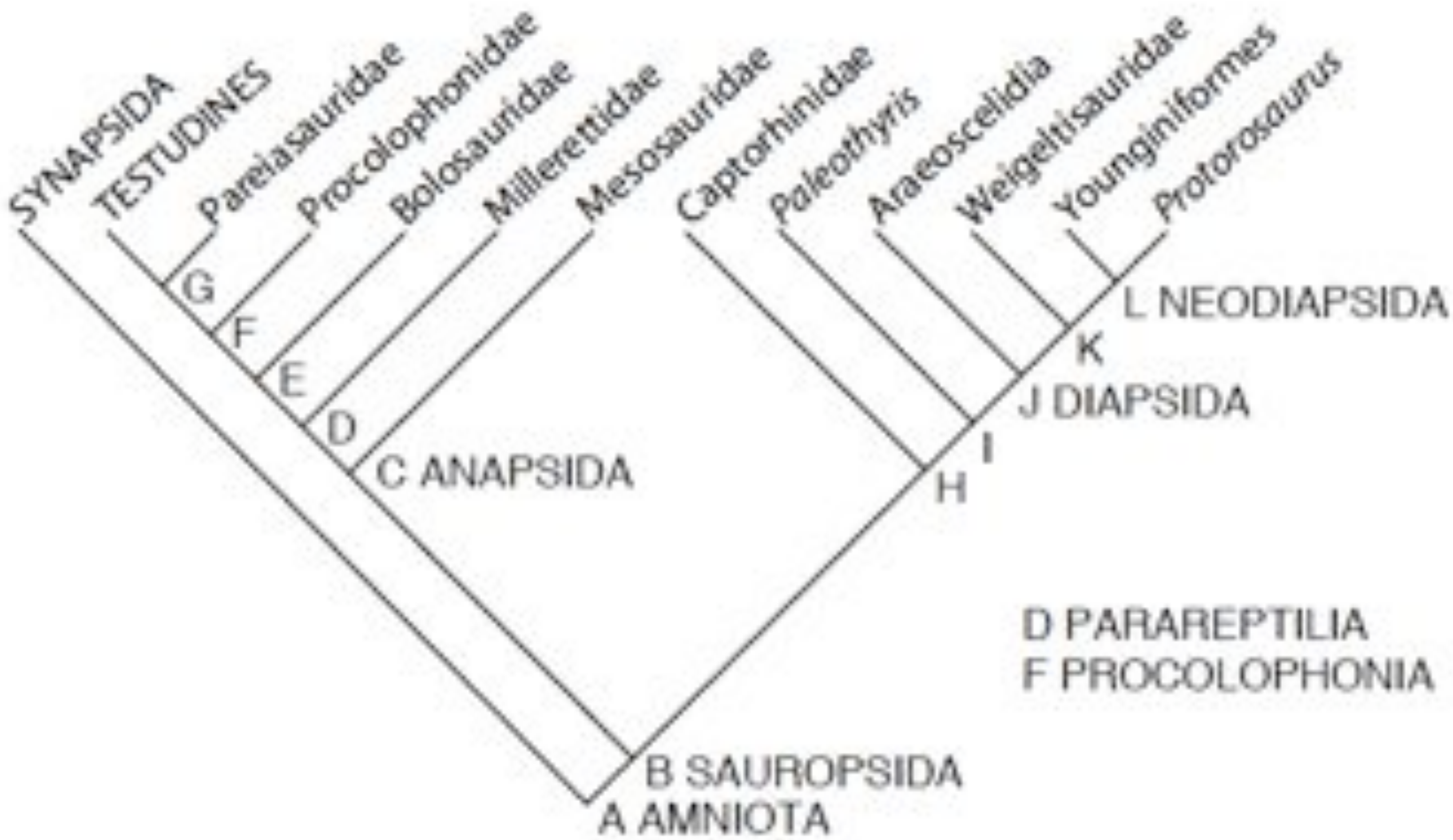




Tortugas marinas Protostegidas (mesozoicas)
y Chelonioideas (modernas)

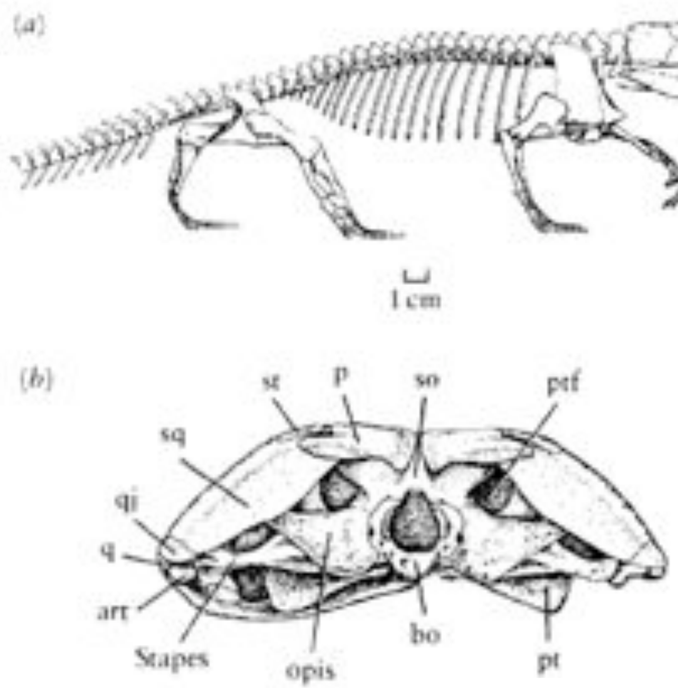


Continuemos con nuestro paseo: abandonamos los anápsidos y nos acercamos a los diápsidos (arcosaurios + lepidosaurios)



Captorhinidae
;

H, postorbital does not reach supratemporal, supratemporal small, caniniform maxillary tooth, quadrate anterior process is short;



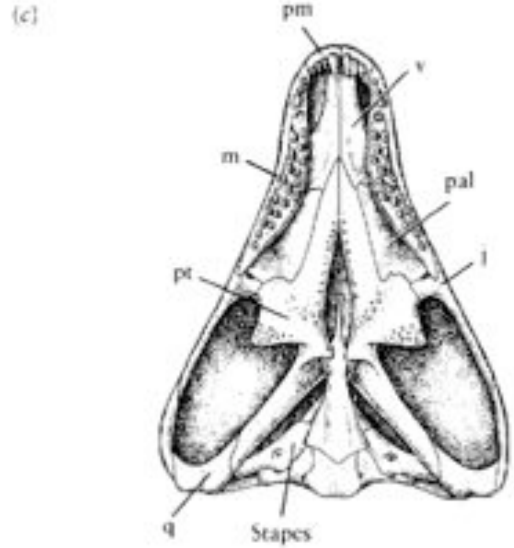
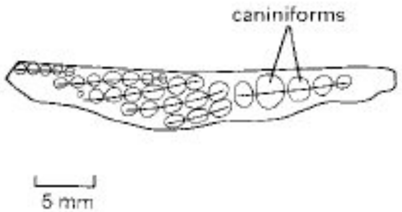


Figure 10-14. REPRESENTATIVES OF THE FAMILY CAPTORHINIDAE. (*a*) Reconstruction of the skeleton of *Eocaptorhinus*. *From Heaton and Reisz, 1980.* (*b*) Occipital view of *Eocaptorhinus*. *From Heaton, 1979.* Note the massive stapes and large posttemporal fossa. (*c*) Palate of *Captorhinus*, showing multiple tooth row. The ectopterygoid bone is missing; its position is replaced by a medial process of the jugal. *From Clark and Carroll, 1973.* Abbreviations as in Figure 8-3.



have multiple rows of marginal teeth. This may have come about by a delay in tooth loss at the time new teeth were added. As many as 12 rows were functional at a time, with the earlier tooth rows "drifting" laterally across the jaw surface (de Ricqlès and Bolt, 1983). Such a dentition might have been an adaptation to feeding on plant ma-

su

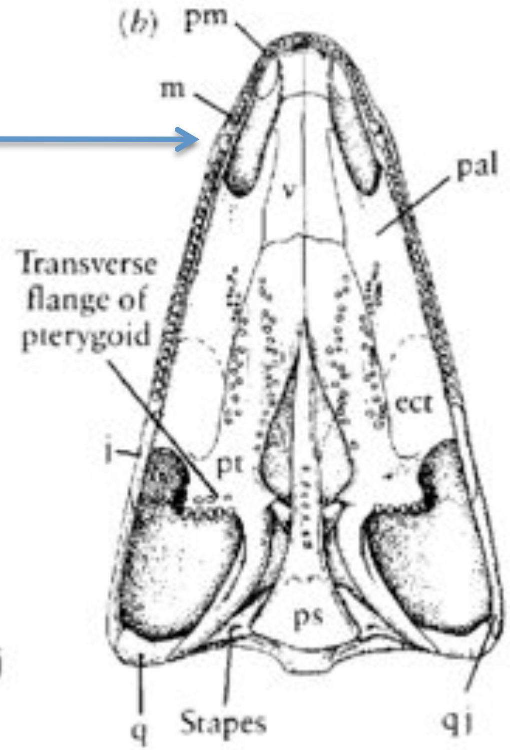
pratemporals are reduced and later lost, and the tabulars are missing. In advanced genera, the braincase is supported by the paroccipital processes of the otic capsules, which extend to the cheek. The early members of the

In relation to their large size, the neural arches are swollen and the zygapophyses laterally placed, like those of diadectids, seymouriamorphs, and limnoscelids. Captorhinids are not known to survive the Permian, but early members of the group show some characteristics that are expected in the ancestors of turtles, including the loss of the ectopterygoid bone (Gaffney and McKenna, 1979).

tabular separate from opisthotic, ventral keel on anterior vertebral centra, carpus and tarsus long and slender, metatarsals and metacarpals overlap;

Protorothyridae

Par de caniniformes!



The best-known primitive amniotes from the early Pennsylvanian are *Hylonomus* (Figure 10-2) and *Paleothyris* (Figure 10-3). We include these genera and other genera from the later Pennsylvanian (Carroll and Baird, 1972) and Lower Permian (Clark and Carroll, 1973) within the family Protorothyridae (Romeriidae) in the order Captorhinida.

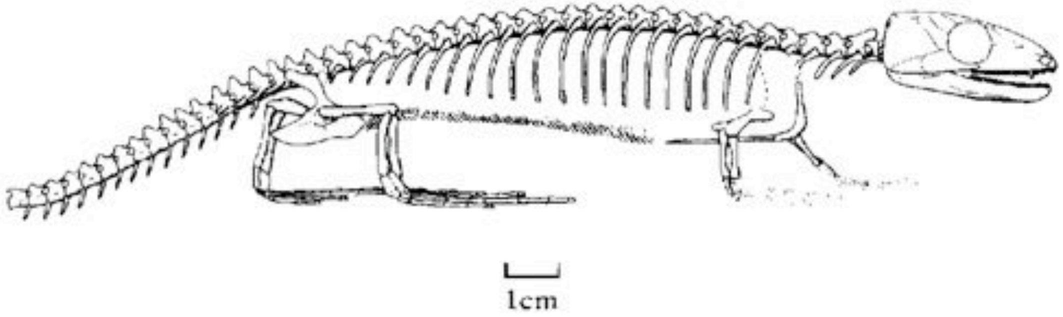
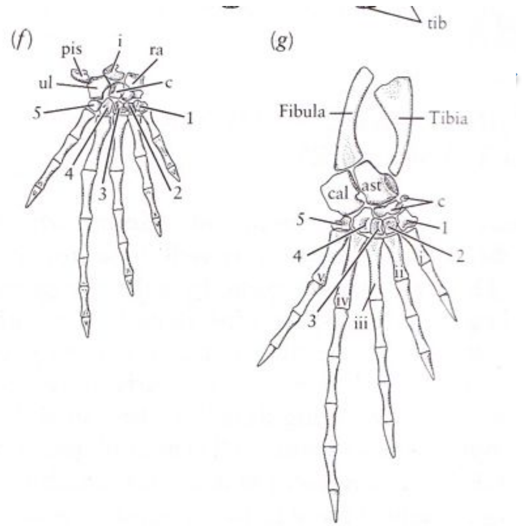


Figure 10-2. SKELETON OF ONE OF THE EARLIEST KNOWN AMNIOTES, *HYLONOMUS LYELLI* FROM THE EARLY PENNSYLVANIAN OF JOGGINS, NOVA SCOTIA. The remains were found within the upright stump of the giant lycopod *Sigillaria*. *From Carroll and Baird, 1972.*



APO-DIAPSIDA todos los descendintes del ACMR compartido por diapsidos actuales con la forma más antigua en que aparezca la configuración temporal diápsida (actualmente, Aeroscelidia)
Los Araeoscelidia incluyen las formas más antiguas conocidas de diápsidos como *Petrolacosaurus*, en el que se hacen evidentes las dos aperturas postorbitales. Poseen extremidades más largas que los "Protorothyridae"

Aeroscelidia : Synapomorfías de apo-diapsida con diapsida corona

-Dos fenestras temporales (reorganizacion de la musculatura mandibular)
-Foramen suborbital
-Extremidades largas y esbeltas
-Esternon mineralizado

Rasgos primitivos (plesiomorfias ausentes en corona)

Gran escamoso cubre el cuadrado
Jugal robusto
Caninos
Lacrimal se extiende a naris externa
No hay proceso retroarticular en la mandibula inferior
Dos coracoides
Femur robusto con extremos desiguales, tobillo desalineado
Ilium angosto
Brazos y piernas de = longitud

The Permian World 111

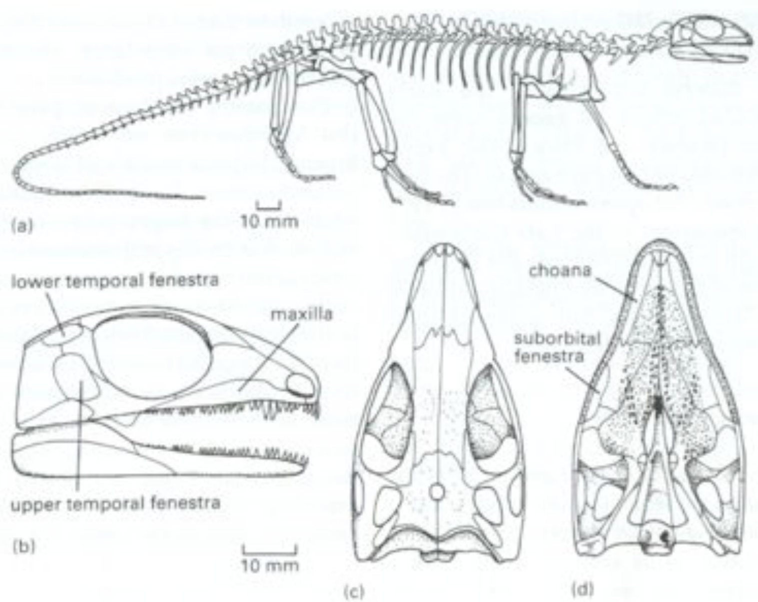
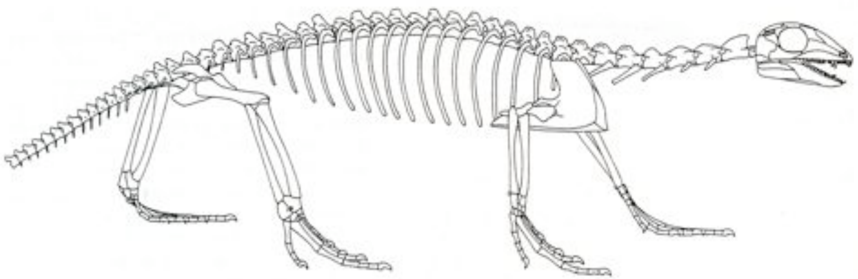
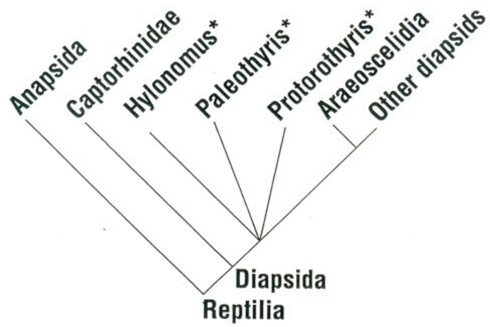


Fig. 5.4 The first diapsid, *Petrolacosaurus*: (a) skeleton; (b–d) skull in lateral, dorsal, and ventral views. (After Reisz, 1981.)



Araeoscelis

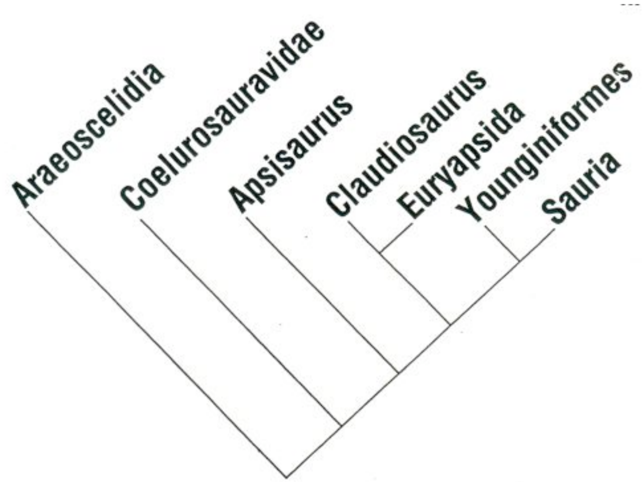


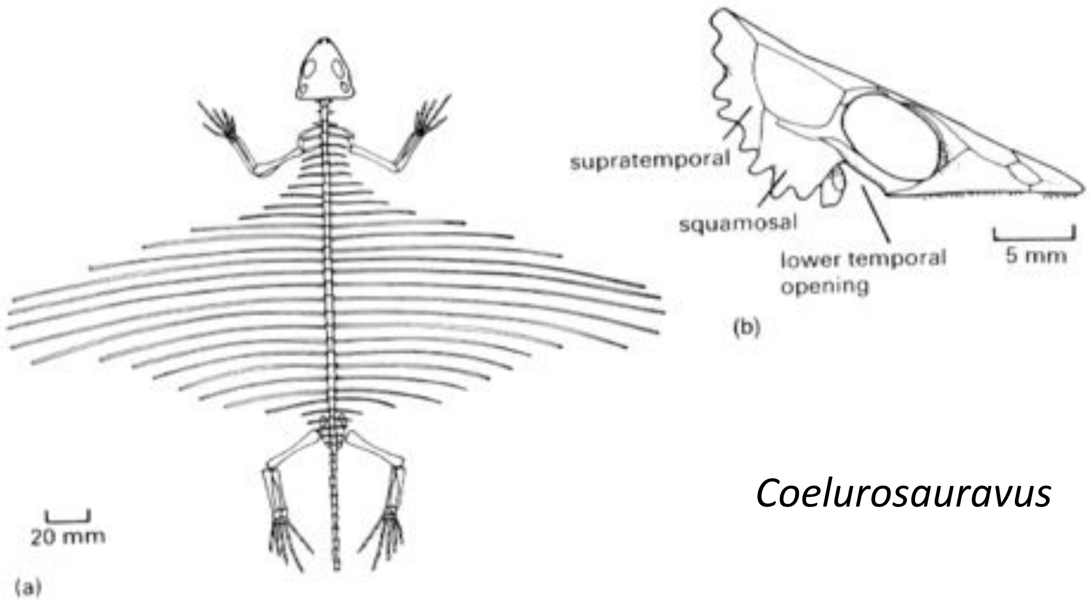
Los apodiápsidos incluyen
las primeros fósiles de vertebrados voladores, los Coelurosauravidae (tambien conocidos como Weigeltisauridae) del pérmico de europa y madagascar.

-Ileon expandido, mayores musculos de la pierna

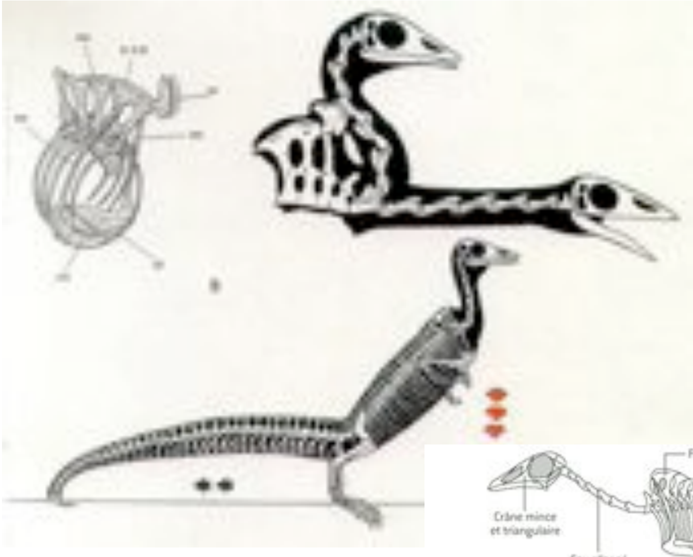
-Condylos femorales simetricos

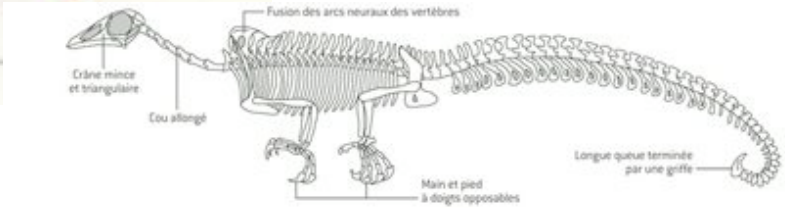
Propuesta Nueva: AVICEPHALA
incluye además los problemáticos Megalancosaurus, Longisquama
(clado mayor, Avicephala)

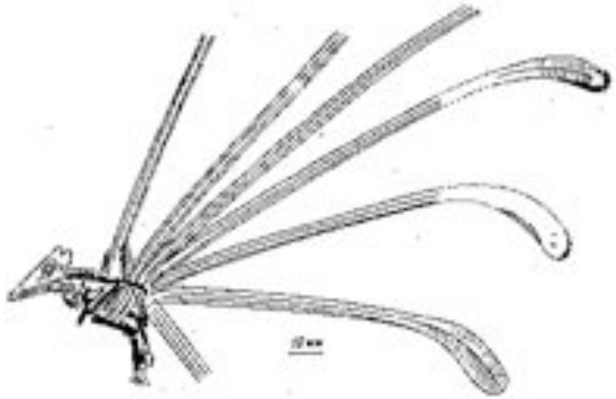




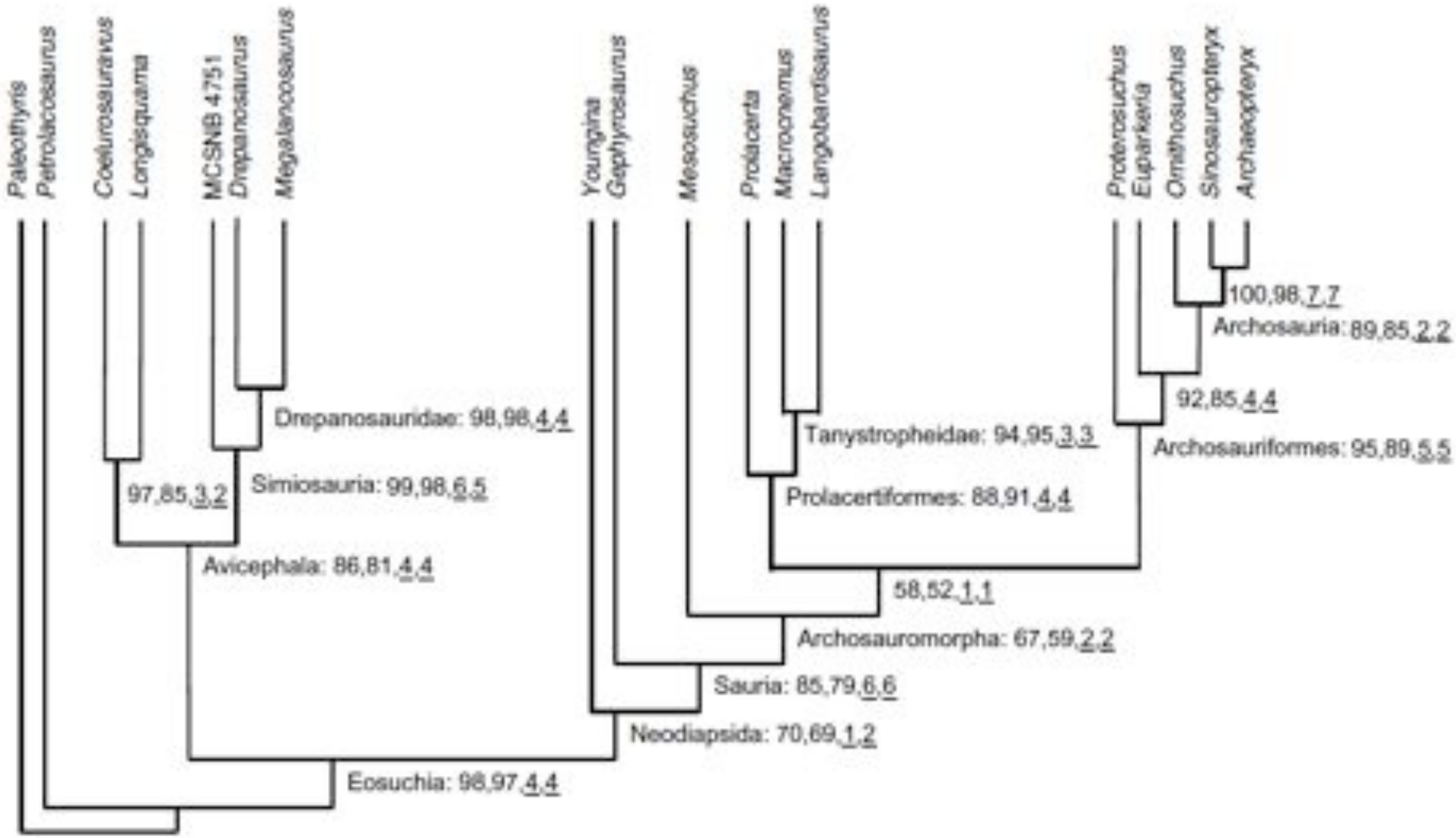
Coelurosauravus







También se ha sugerido que son pan-arcosaurios, pero la evidencia es débil y se reconocen gralmente "plesiomórficos" (consistente con la idea de que son stem-diapsids)



Paleothyris
Petrolacosaurus
Coelurosauravus
Longisquama
MCSNB 4751
Drepanosaurus
Megalancosaurus
Youngina
Gephyrosaurus
Mesosuchus
Prolacerta
Macrocnemus
Langobardisaurus
Proterosuchus
Euparkeria
Ornithosuchus
Sinosauropteryx
Archaeopteryx
100,98,7,7
Archosauria: 89,85,2,2
92,85,4,4
Archosauriformes: 95,89,5,5
Drepanosauridae: 98,98,4,4
Tanystropheidae: 94,95,3,3
97,85,3,2
Simiosauria: 99,98,6,5
Prolacertiformes: 88,91,4,4
Avicephala: 86,81,4,4
58,52,1,1
Archosauromorpha: 67,59,2,2
Sauria: 85,79,6,6
Neodiapsida: 70,69,1,2
Eosuchia: 98,97,4,4

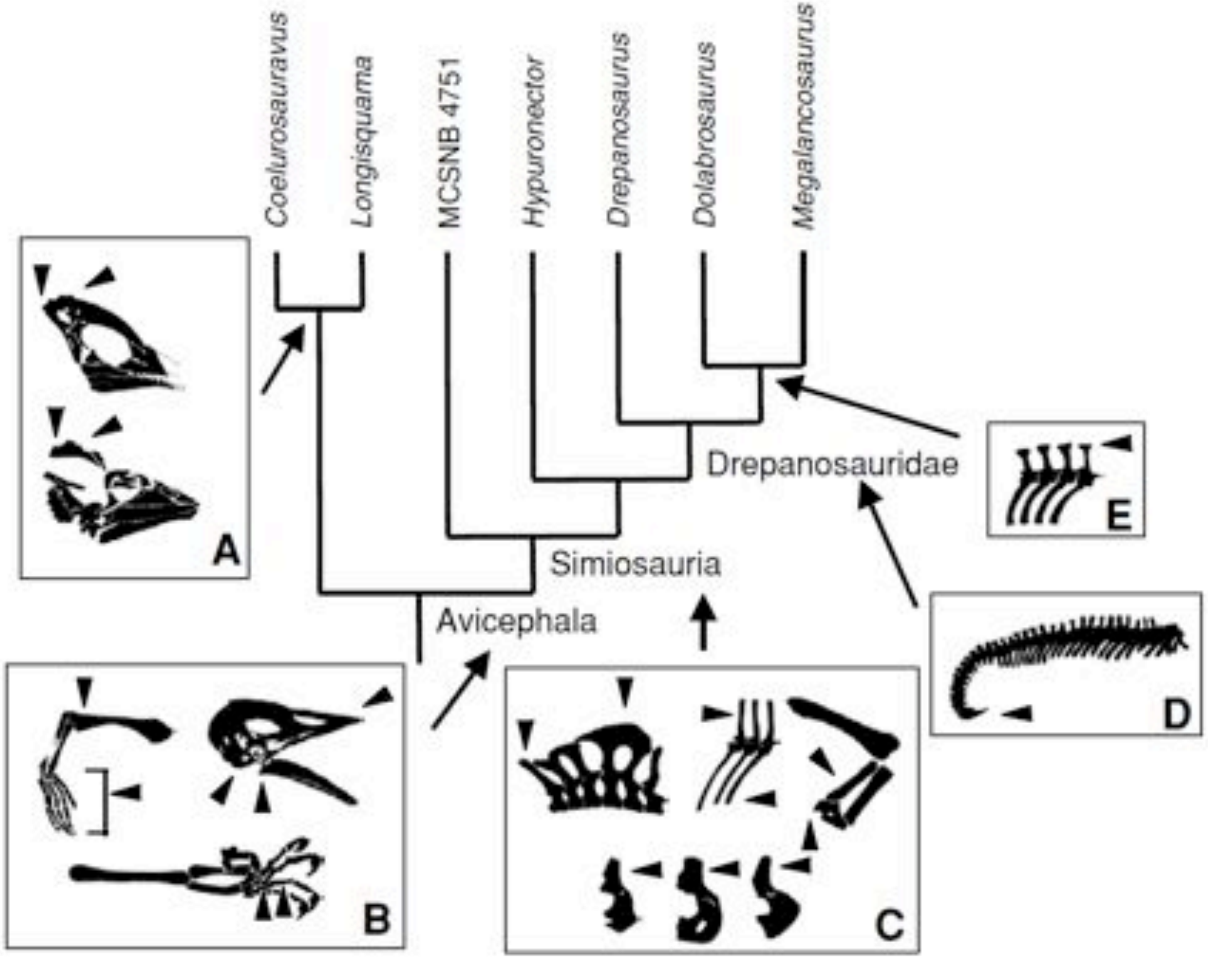
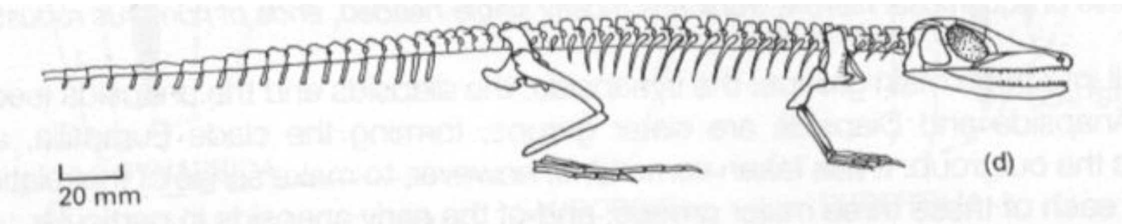


Figure 4 Select synapomorphies of Avicephala and its sub-clades. Drawings not to scale. Anterior is to the right in all cranial, axial and pelvic drawings. **A**, Skulls of *Longisquama insignis* (PIN 2584/4) and *Coelurosauravus jaekeli* (modified from Evans 1987), showing synapomorphies of *Longisquama* + *Coelurosauravus*: parietals upswept, parietal rim ornamented with bumps. **B**, Skull (MFSN 1769) and hindlimb (MBSN 26) of *Megalancosaurus preonensis*, together with forelimb of *Coelurosauravus jaekeli* (modified from Evans 1987), showing synapomorphies of Avicephala: sharply pointed snout, craniomandibular joint ventral to posterior extremity of orbit, strong posterior inclination of posterior border of skull, reduction in distal humeral width, manual length ≤ humeral length, length of metatarsal IV ≤ length of metatarsal III, length of pedal phalanx IV–1 ≤ length of pedal phalanx III–1. **C**, Anterior dorsal vertebrae of *Megalancosaurus preonensis* (modified from Renesto 1994*b*), portion of caudal series of *Hypuronector limnaios* (modified from Colbert & Olsen 2001), hindlimb of *Drepanosaurus unguicaudatus* (modifed from Pinna 1984) and pelves of (left to right) *Hypuronector limnaios* (modified from Colbert & Olsen 2001), *Drepanosaurus unguicaudatus* (modifed from Pinna 1984) and *Megalancosaurus preonensis* (MBSN 26), showing synapomorphies of Drepanosauroidea: high dorsal neural spines, distal expansions and fusion of anterior dorsal neural spines, elongate mid-caudal neural spines, anterior hemal arches ≥ 3 × longer than associated vertebrae, vertical orientation of iliac blade, tibial length ≤ 0.65 × femoral length, calcaneal tuber. **D**, Tail of *Drepanosaurus unguicaudatus* (modifed from Pinna 1984), showing a synapomorphy of Drepanosauridae: terminal caudal claw. **E**, Portion of caudal series of *Dolabrosaurus aquatilis* (Berman & Reisz 1992), showing a synapomorphy of *Dolabrosaurus* + *Megalancosaurus*: mid-caudal neural spines T-shaped.

Younginiformes: **“Eosuquio”**, término parafilético para cercanos a los diapsidos corona

Pequeños depredadores ecológicamente semejantes a las lagartijas, con piernas marcadamente más largas que los brazos y fenestras del cráneo expandidas. Incluye formas acuáticas de cola profunda
Han sido considerados posibles ancestros de los Euryapsidos marinos

Rasgos más cercanos a diapsida (corona):
Cuadrado expuesto lateralmente, pero sin espacio para oido medio
Mayor largo de las piernas q los brazos
Rasgo primitivo: Hyoides robusto



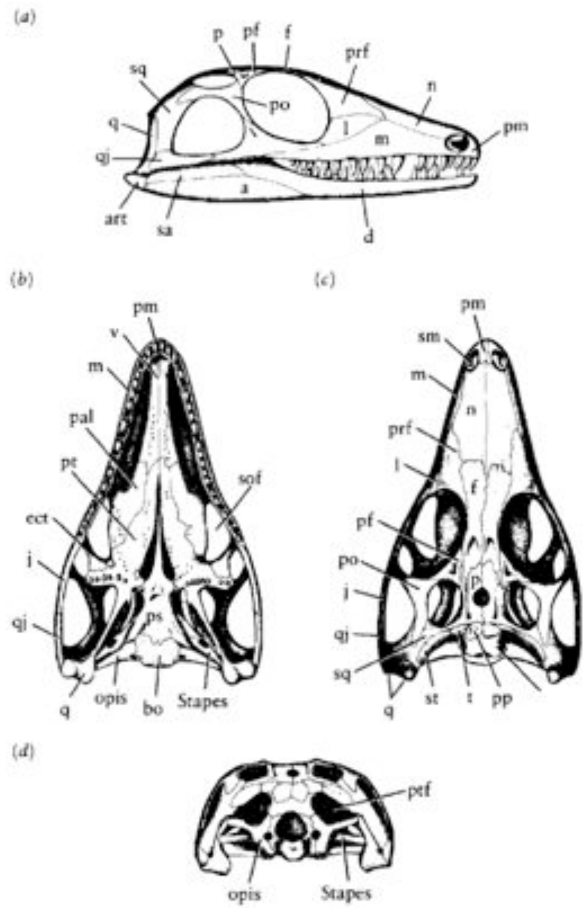
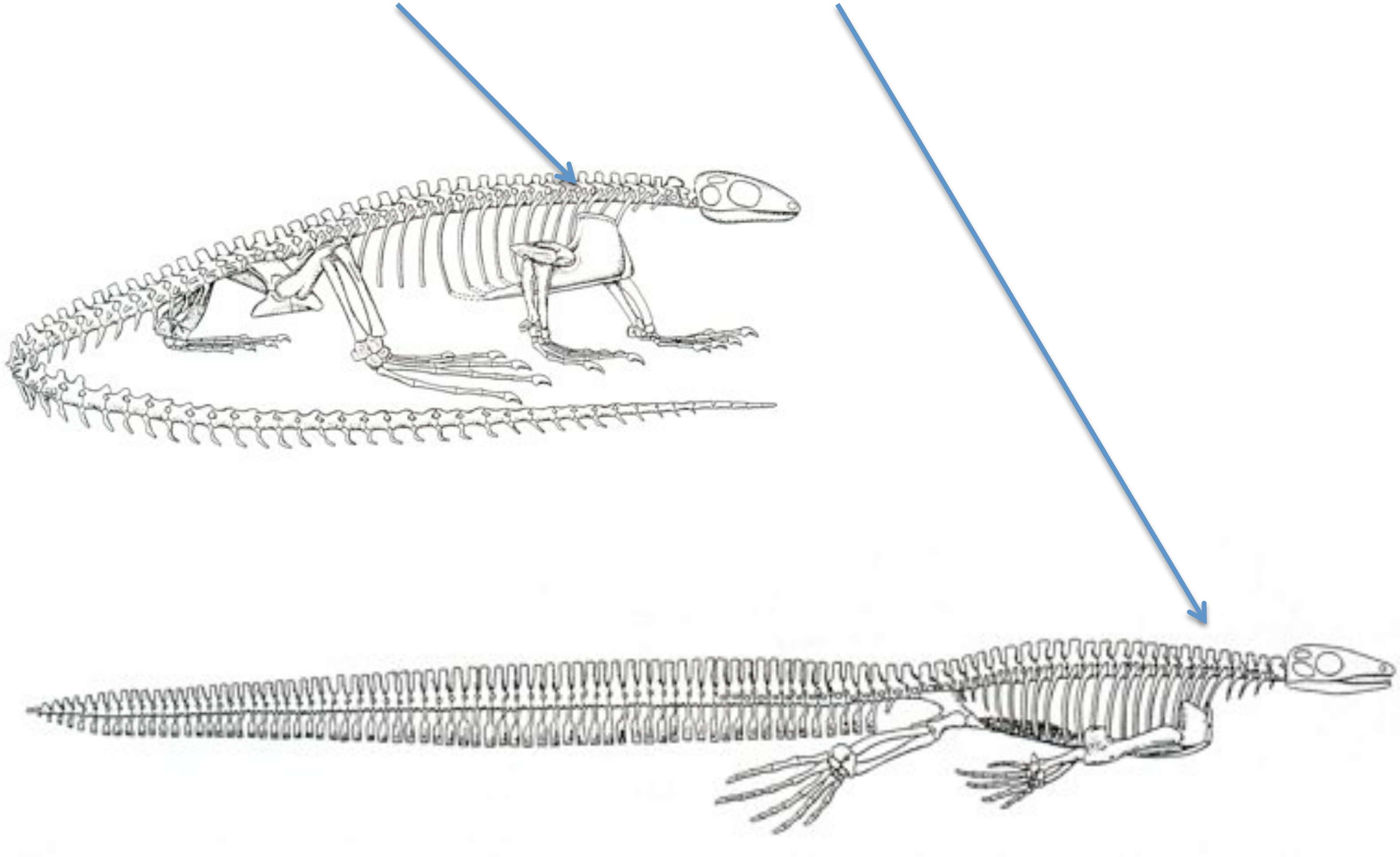


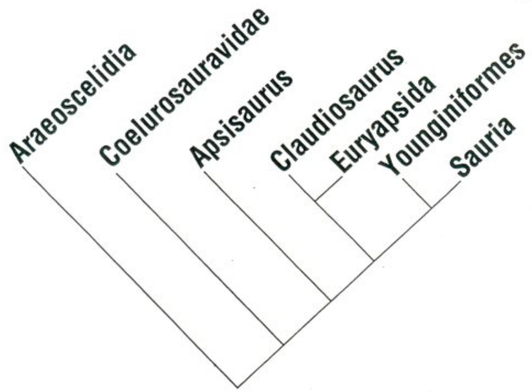
Figure 11-9. SKULL OF THE CHARACTERISTIC EOSUCHIAN *YOUNGINA* FROM THE UPPER PERMIAN OF SOUTHERN AFRICA. (*a*) Lateral, (*b*) palatal, (*c*) dorsal, and (*d*) occipital views. The quadrate is exposed laterally, but there is no embayment for support of a tympanum. The stapes is massive and oriented obliquely to the surface of the skull. There is no evidence that it participated in an impedance-matching mechanism at this stage in diapsid evolution. Approximately natural size. Abbreviations as in Figure 8-3, plus: sof suborbital fenestra. *From Carroll, 1981.*

Youngina, pérmico tardío de alemania

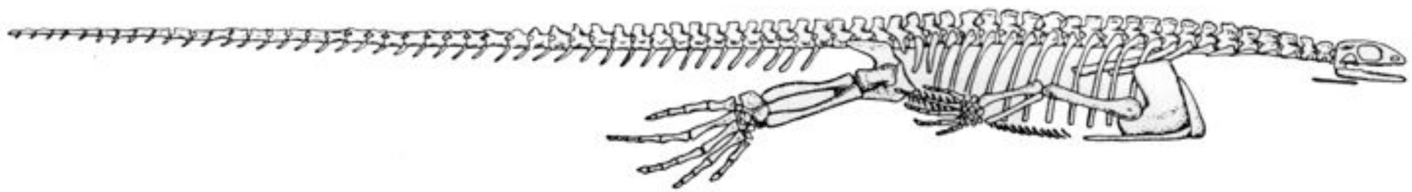
Otros Younginiformes: Thadeosaurus (younginiforme) y Hovasaurus (acuático)

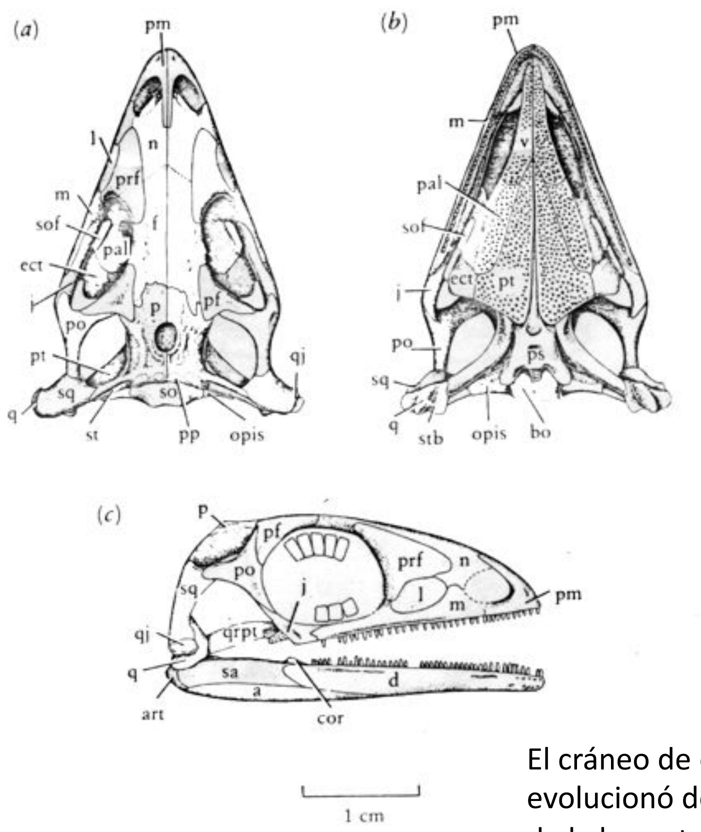


- *Claudiosaurus* del Pérmico Superior de Madagascar, es un reptil marino que se destaca por el desarrollo de un cuello largo que puede ser descrito como resultado del desplazamiento hacia posterior de la cintura pectoral. Un rasgo primitivo(? para sauropterygia) es el mayor desarrollo de las piernas
- Posible Sauropterygio basal



Claudiosaurus





Como Sauropterygia (Euryapdsida):
No hay esternon oseo
perdida barra temporal inferior

Como crown diapsida:
Ilium extenso
Femur gracil
Rodilla y tobillo alineados (simetricos)
Perdida de caniniformes
Lacrimal no abarca naris externa

Rasgos primitivos:
No hay proceso retroarticular (timpano)
Gran foramen parietal

El cráneo de *Claudiosaurus* revela que condición euryapsida evolucionó desde los primitivos diápsidos mediante la pérdida de la barra temporal inferior.

Verdaderos Diápsidos (corona), tb llamados SAURIA

-Oído que iguala la impedancia, permite oir a alta frecuencia sonidos llevados por el aire. Esto lo indica la evidencia clara para un tímpano: cuadrado curvado para cavidad del oído medio, hyoides (estribo) delgado, y proceso retroarticular.

-Disparidad de pierna, más larga que el brazo. Bipedismo facultativo.

Synapsida:
P.R. convergente

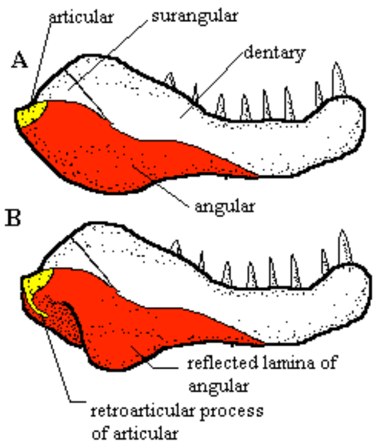
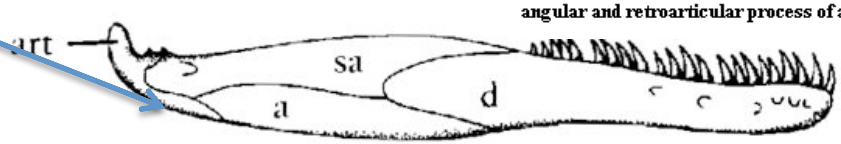
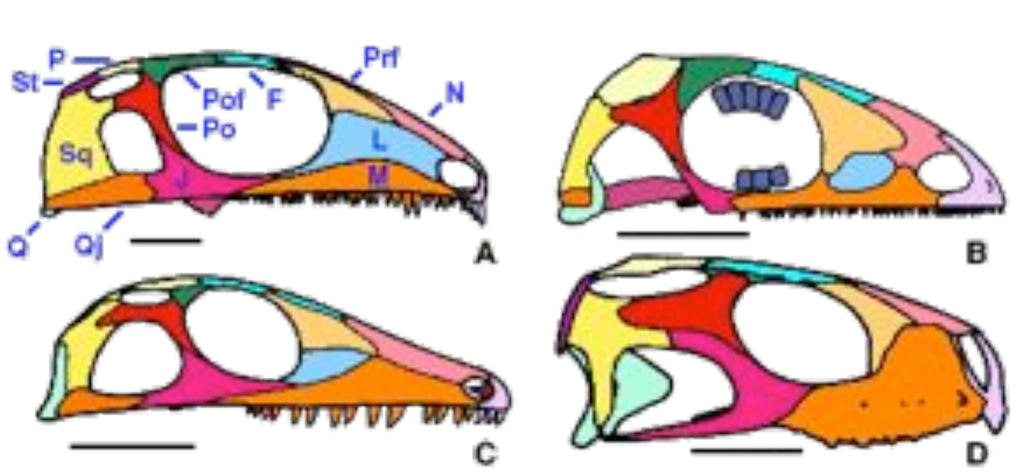
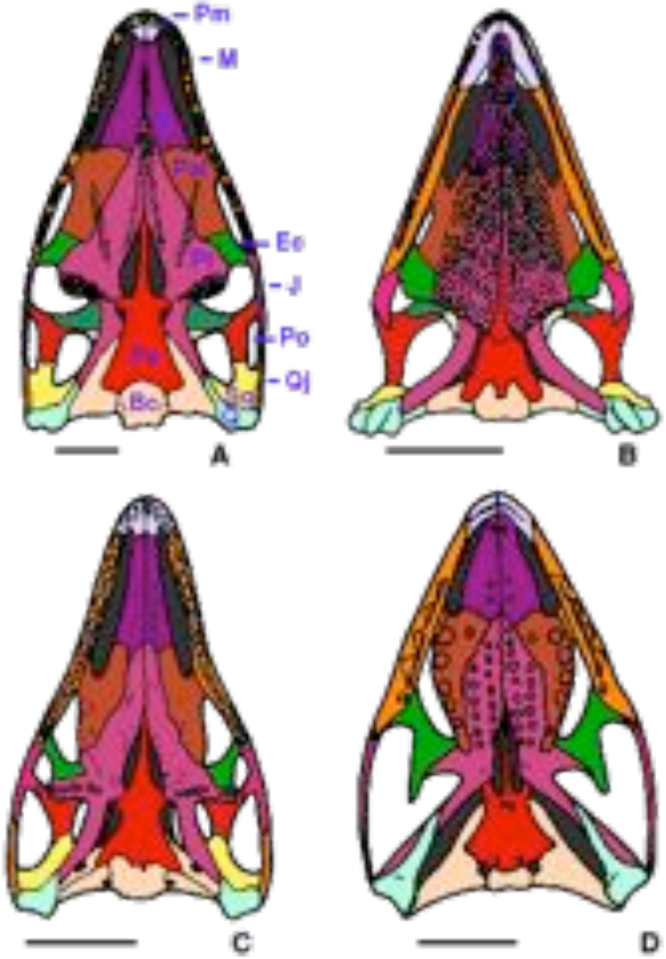
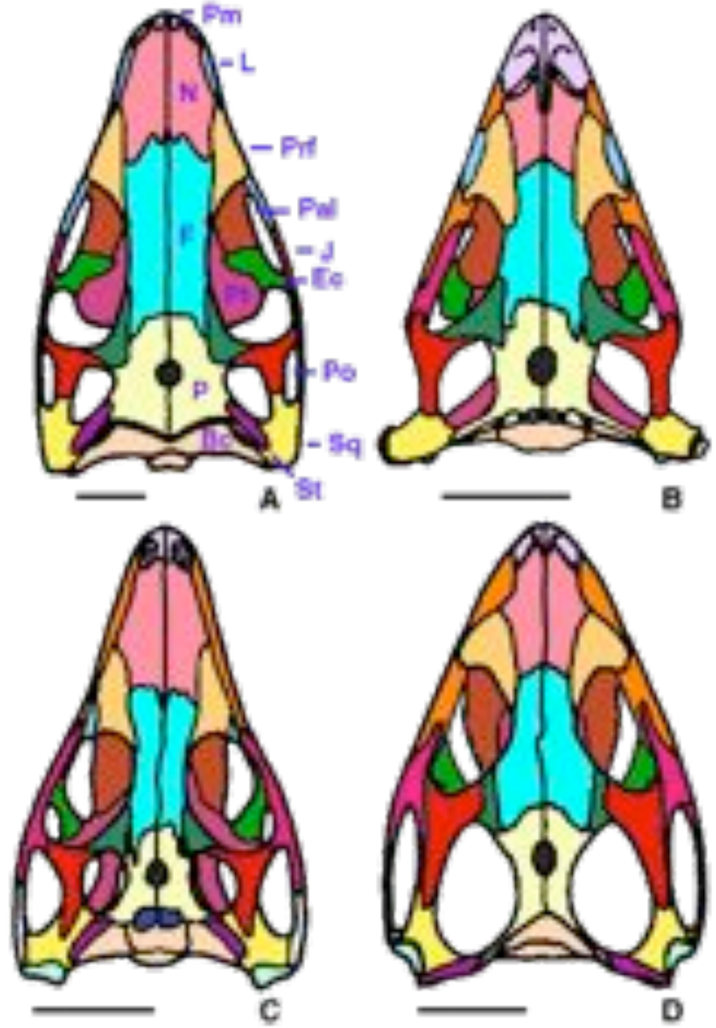


Fig. 1. Synapsid right mandible in right lateral view, with and without reflected lamina of angular and retroarticular process of articular





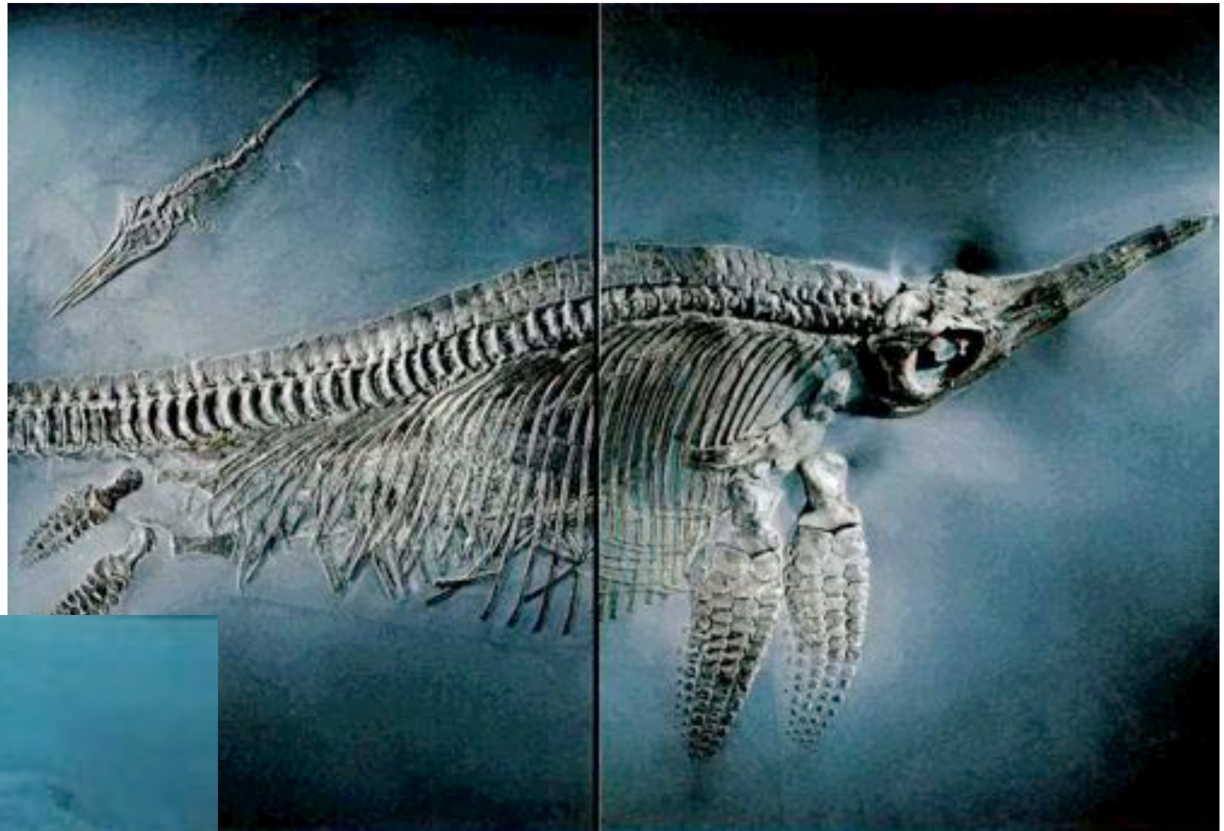


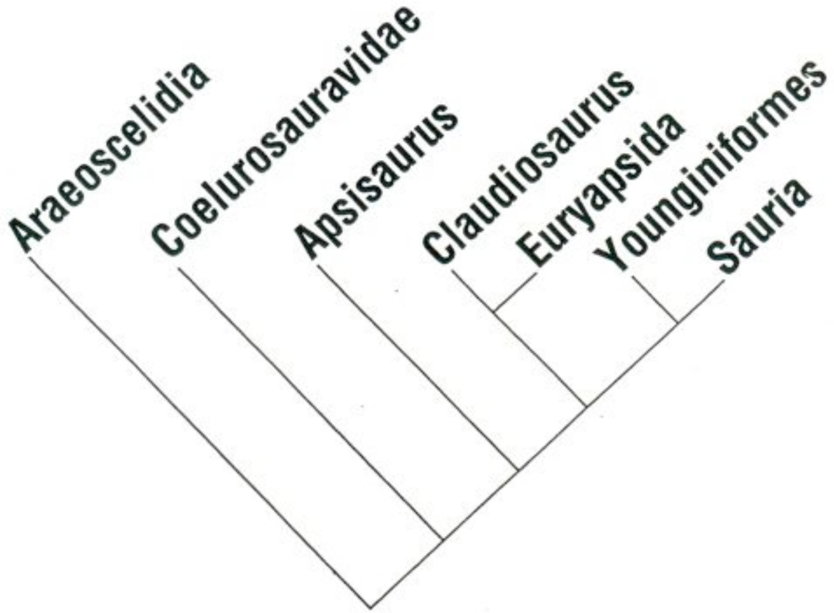


A, Petrolacosaurus, a Pennsylvanian araeoscelidian; B, Claudiosaurus, an Upper Permian neodiapsid; C, Youngina, an Upper Permian younginiform; D, Clevosaurus, a Late Triassic sphenodontid (a saurian).

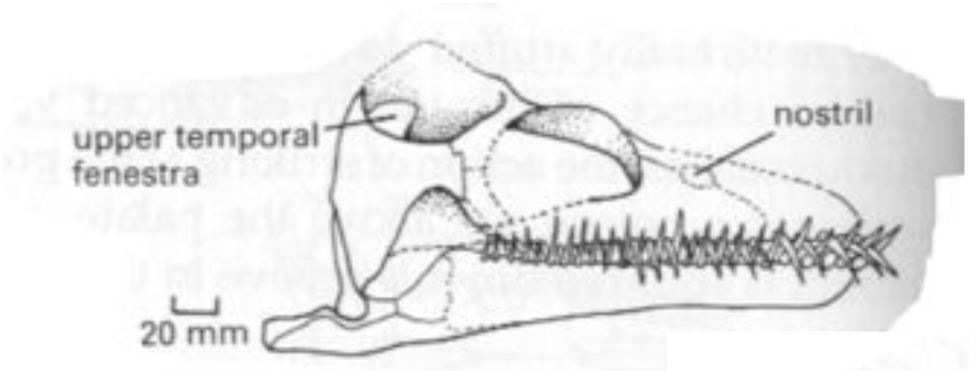
Antes de pasar a los verdaderos diapsida, hacemos un alto para los reptiles marinos Euryapsida, de afinidades inciertas, pero reconocidos como diapsidos, quizás cercanos al origen de los sauria ("eosuquios")

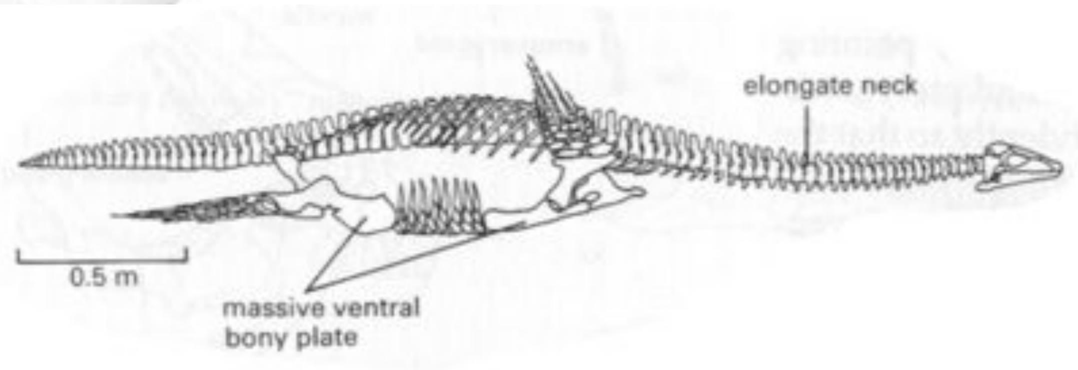
Sauropterygia e Icthyopterygia

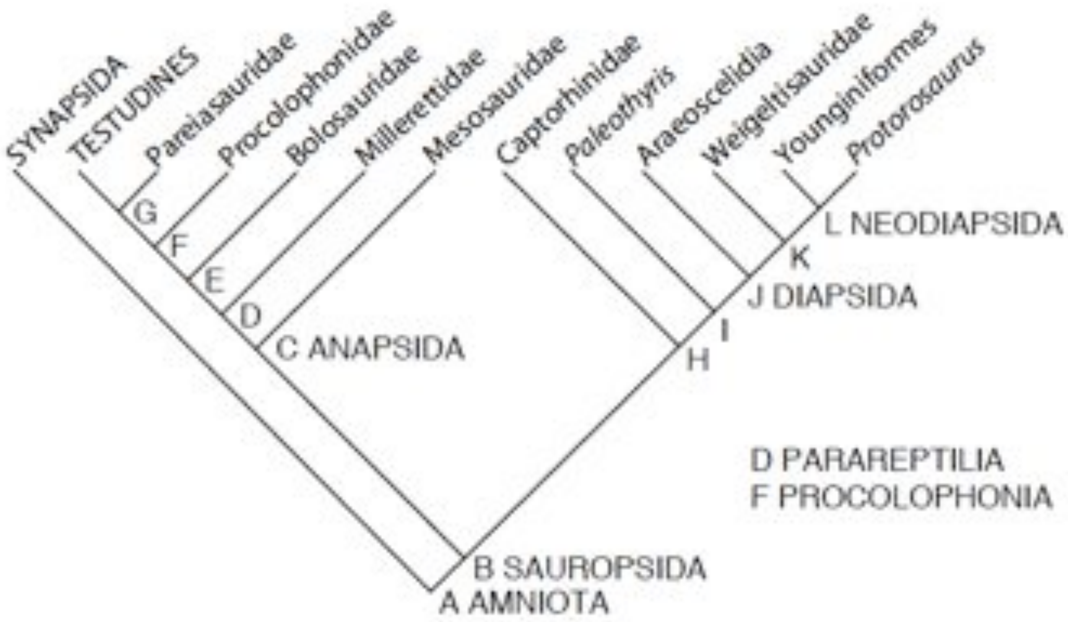




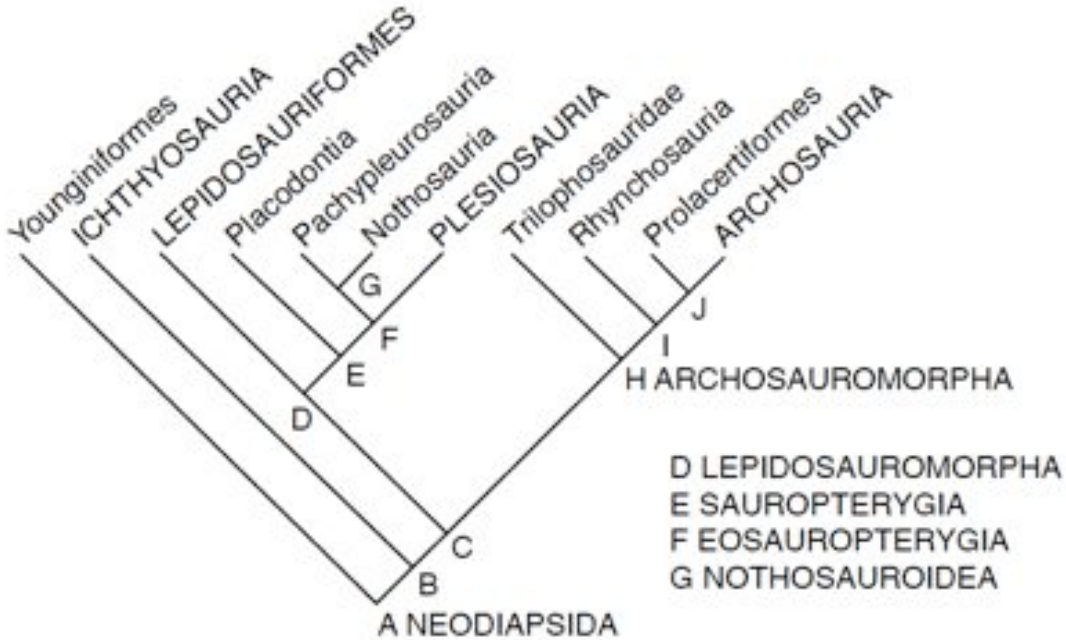
En el pérmico hace su aparición un grupo importante de reptiles marinos mesozoicos, de afinidades debatidas. La mayoría de estas formas marinas poseen un cráneo de condición euryapsida (parapsida), caracterizado por la presencia de un fenestra única sobre el puente postorbital- escamoso





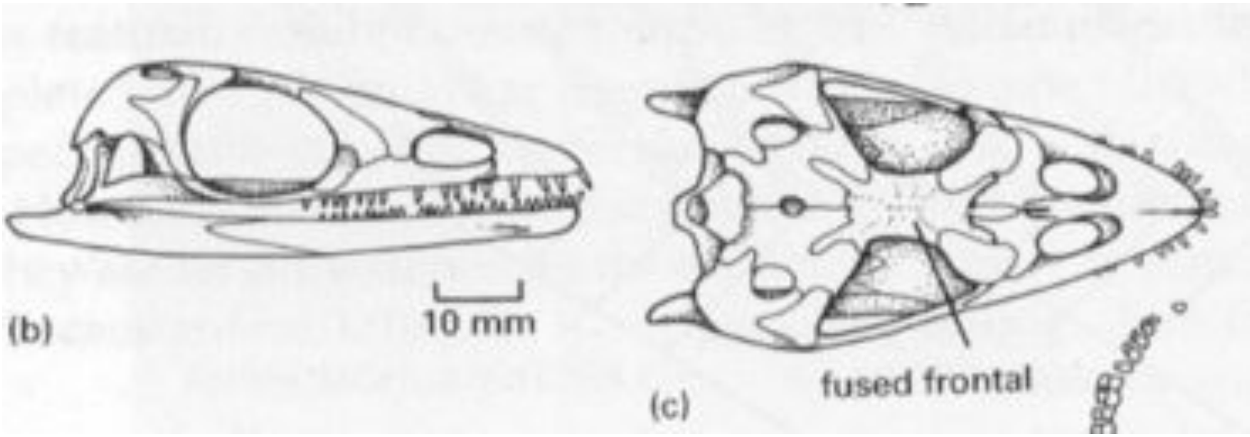


La posición de los Ichthyosauria es particularmente Incierta
(acá, euryapsida es parafilético!)



John Merck, tesis doctoral no publicada:
Dentro de diapsidos corona, los euryapsidos pueden ser más cercanos a los arcosauria (croc y aves) que a lepidosauria (lagartijas), llevando a la sugerencia del término Pan-arcosauria (incluyendo a sauropterygia)

Synapomorfías posibles: Hocico largo, articulación mandibular por detrás del occipital (para comerte mejor)



Sauropterygio

Pachypleurosaurus

Quianosuchus, arcosaurio marino del triásico

Thalattosauria

Diápsidos marinos de afinidades inciertas. Según John Merck, junto a Sauropterygia e Ichthyosauria, constituyen un sólo clado de Pan-Arcosaurios marinos. Los tres grupos poseen rostro alargado y fosas nasales posteriomente desplazadas (más cerca de los ojos)

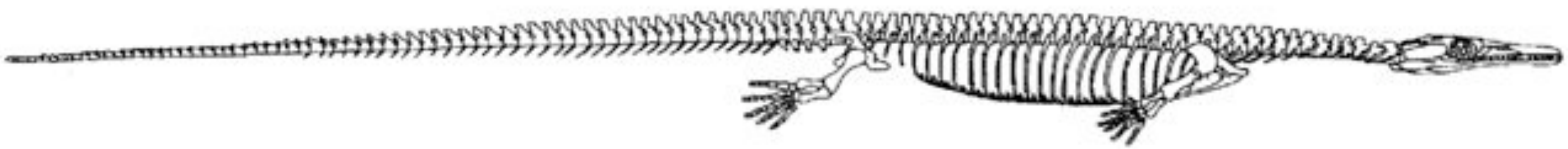
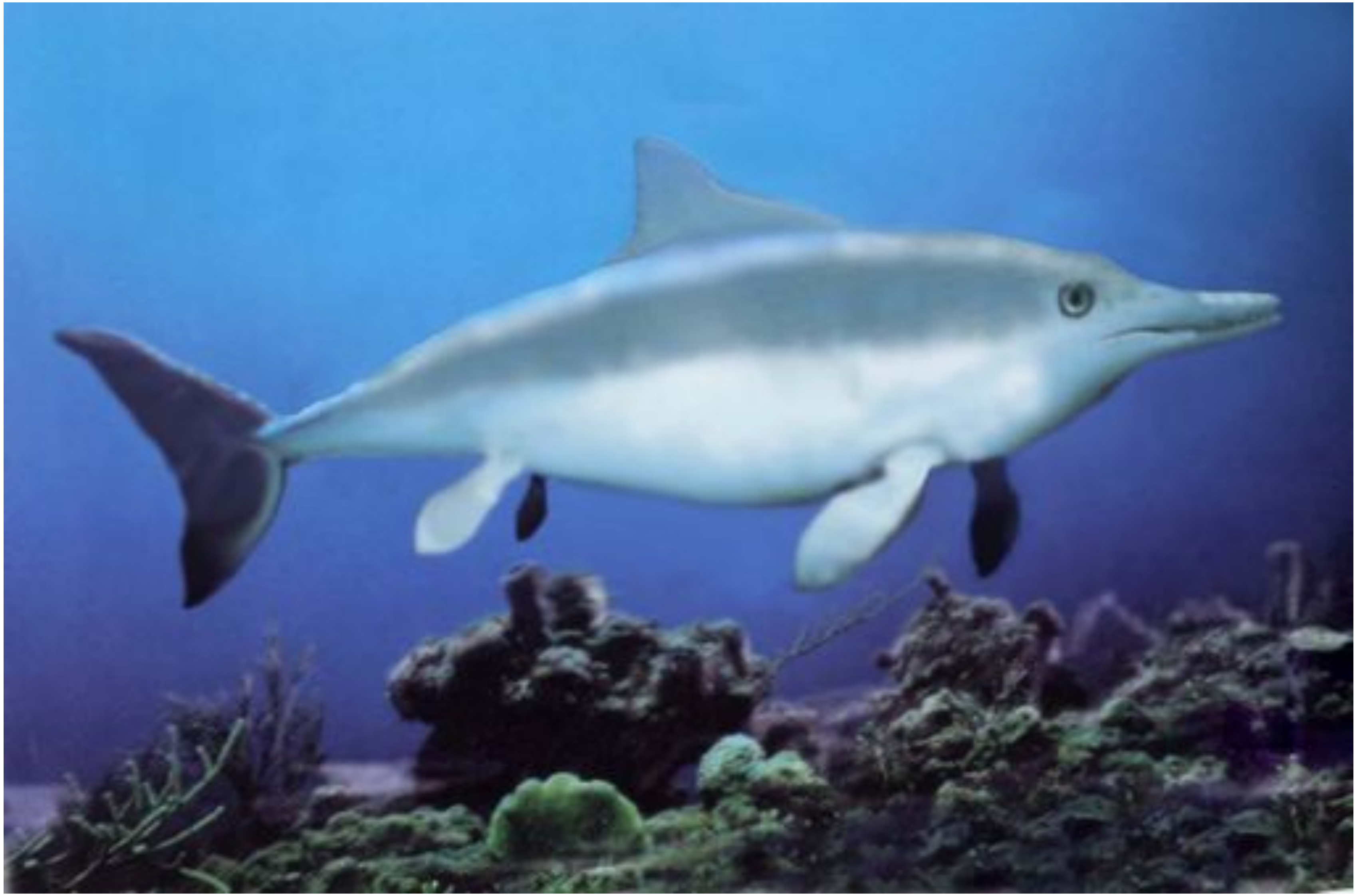


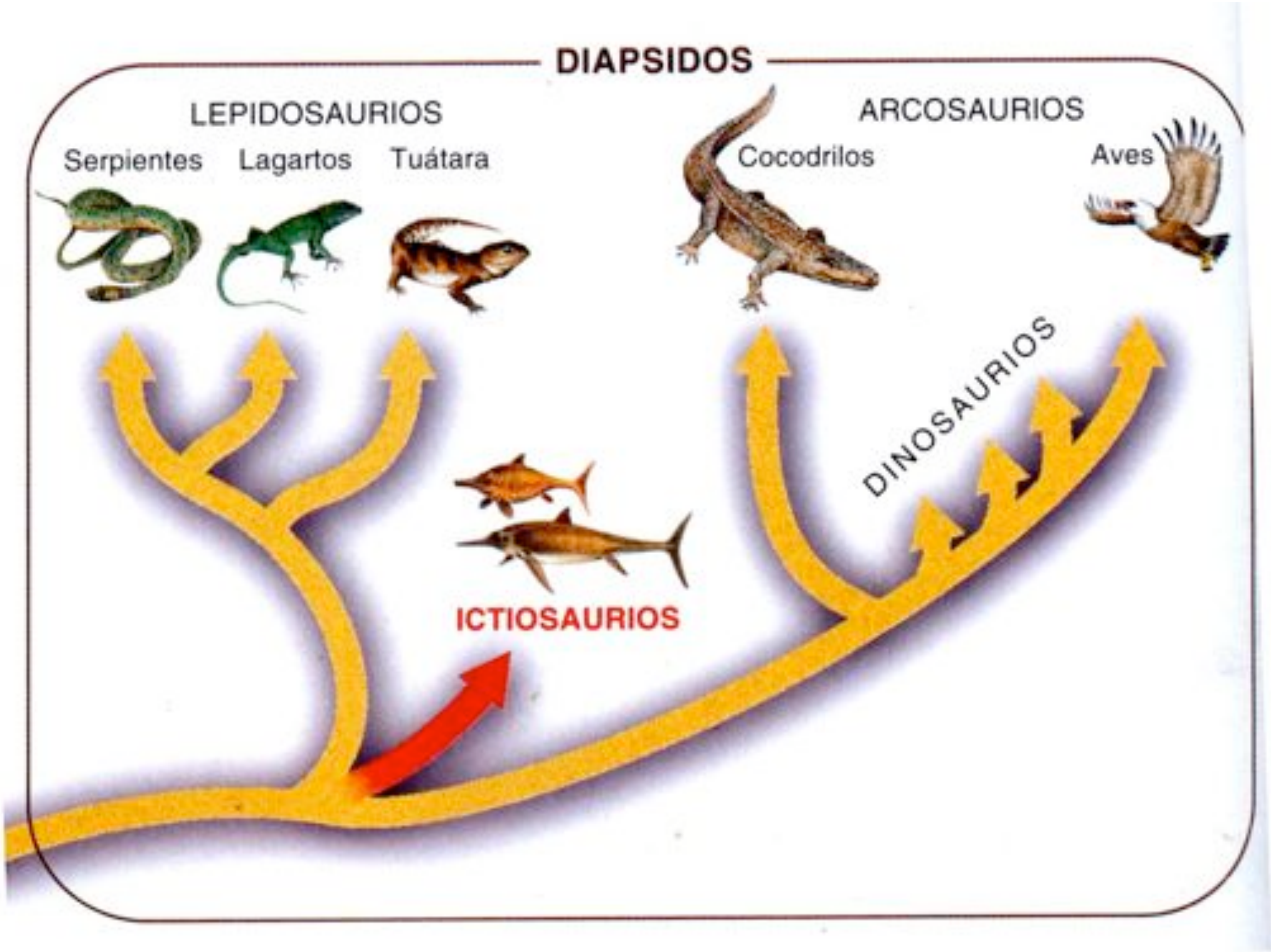
Figure 11-6. *ASKEPTOSAURUS*, A PRIMITIVE AQUATIC DIAPSID FROM THE MIDDLE TRIASSIC OF SWITZERLAND. Approximately 2 meters long. *From Kuhn-Schnyder, 1974.*

neck and trunk are greatly elongated, as in many aquatic groups, and the nostrils are set well back on the long snout. The limbs are short but not specialized as paddles.

Icthyosauria (“lagarto pez”)



La posición filogenética de los ictiosaurios es poco clara, debatiéndose incluso si comparten un ancestro en común más reciente con los cocodrilos (Archosauromorpha) que las lagartijas (Lepidosauromorpha)



Un candidato a ancestro son los Hupehsuchia, diápsidos de afinidades inciertas. La armadura dérmica y la presencia de una apertura anteorbital sugiere afinidades con los archosauria

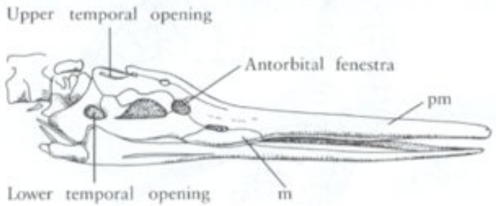
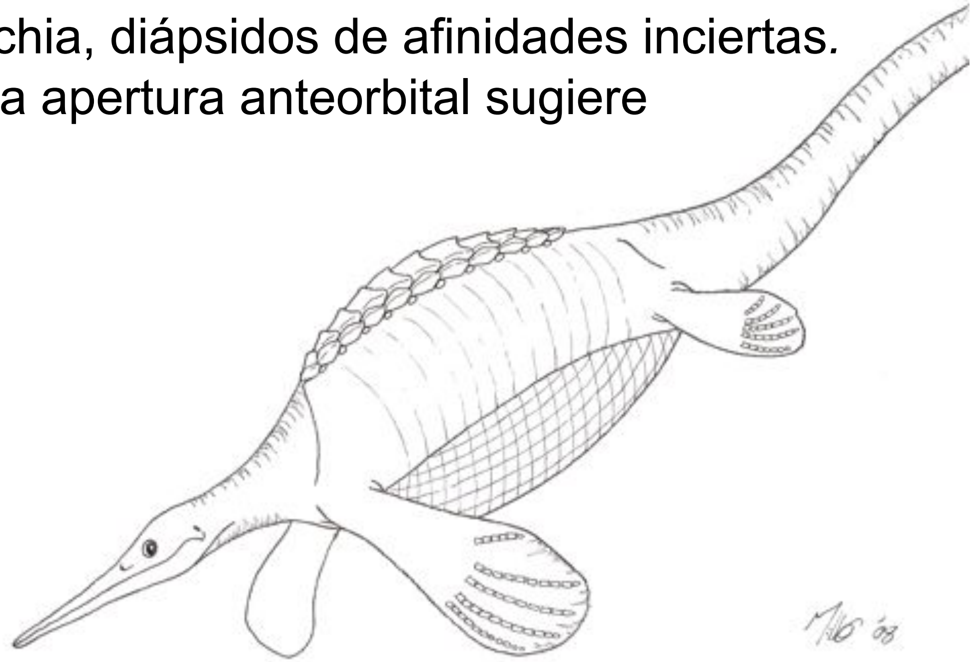
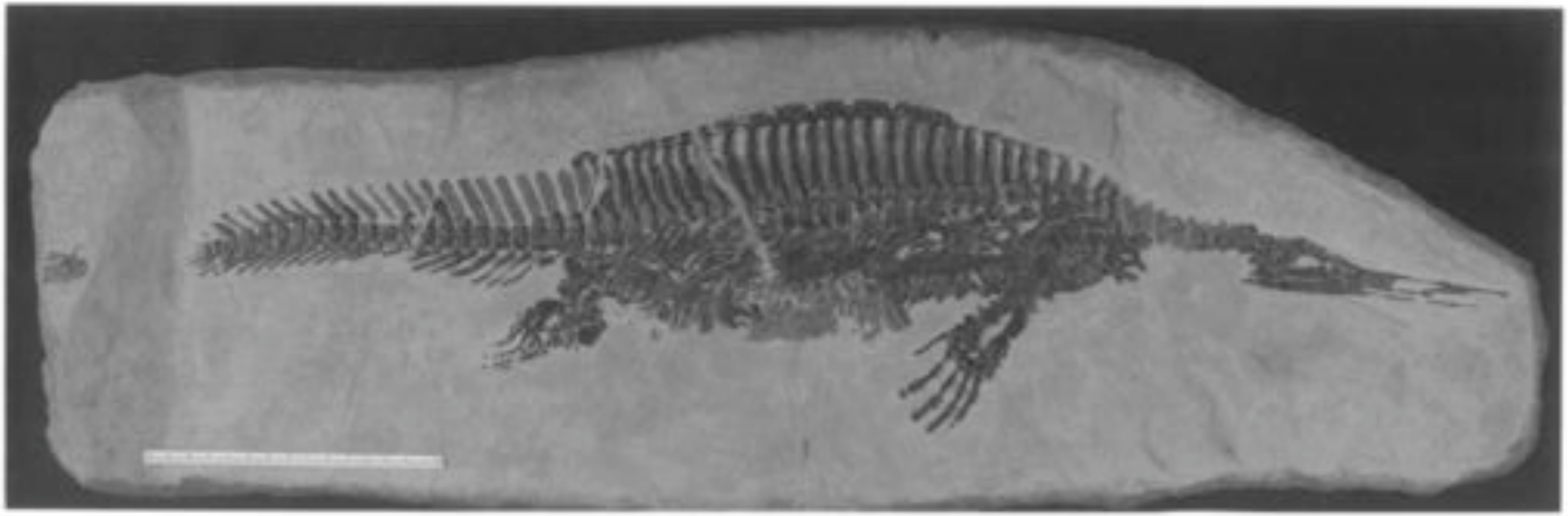


Figure 12-25. SKULL OF *NANCHANGOSAURUS* [*HUPEHSUCHUS*]. The presence of an antorbital fenestra is a feature it shares with archosaurs. In contrast with all orthodox ichthyosaurs, there is also a lateral temporal opening. The taxonomic position of this genus is uncertain. It may be an ichthyosaurlike archosaur or a link between primitive archosaurs and ichthyosaurs. Abbreviations as in Figure 8-3. *From Young and Dong, 1972.*





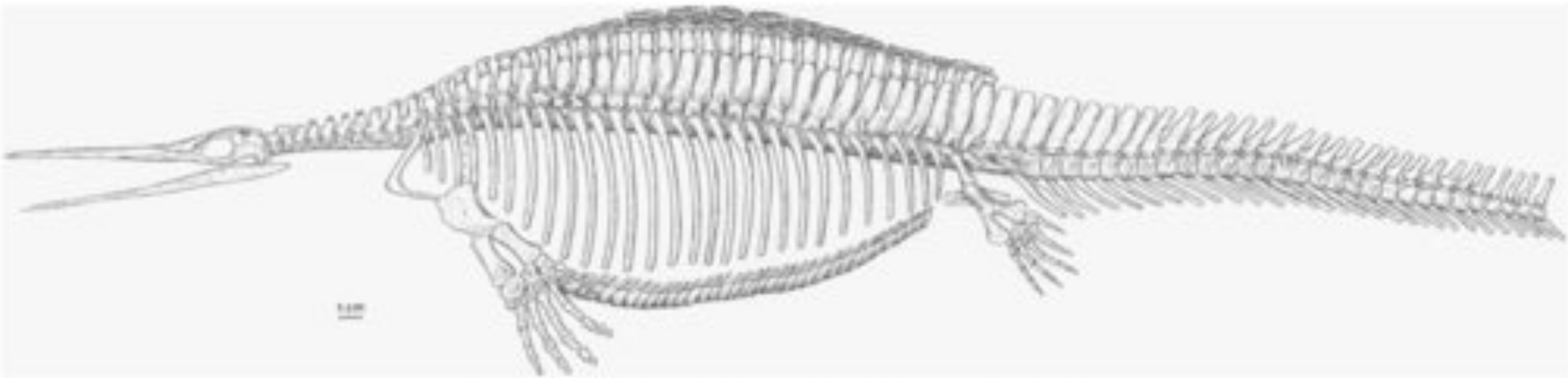
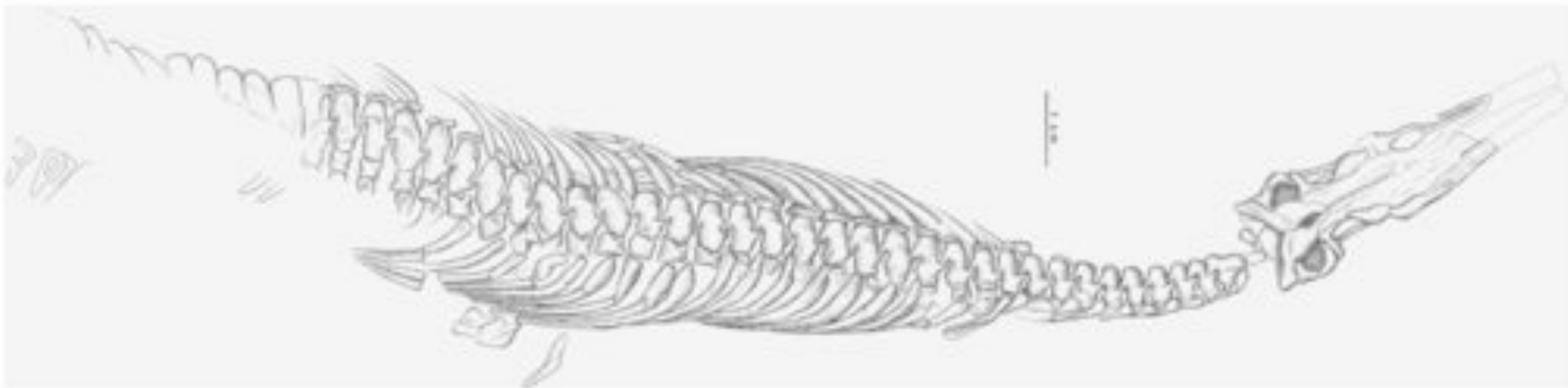


Figure 5. *Hupehsuchus*, skeletal reconstruction based primarily on the holotype.



Nanchangosaurus

The fossils of *Hupehsuchus* and *Nanchangosaurus* provide knowledge of a previously unrecognized assemblage of Triassic aquatic reptiles. Most features of *Hupehsuchus* demonstrate a high degree of adaptation for rapid swimming. The function of the multiple rows of dermal plates above the neural spines remains enigmatic. The Hupehsuchia are definitely members of the Diapsida, but their specific affinities to other groups of primitive diapsids remain unknown. The great degree of convergence shown by secondarily aquatic reptiles makes it very difficult to apply cladistic methodology to establish their phylogenetic position. The extensive gap in the fossil record of the neodiapsids during their period of initial radiation makes it difficult to discover synapomorphies that unite the major groups. The mode of swimming by lateral undulation and the reduction of the transverse processes suggest the possibility that ichthyosaurs and the Hupehsuchia might share a common aquatic ancestry, but this is not firmly established.

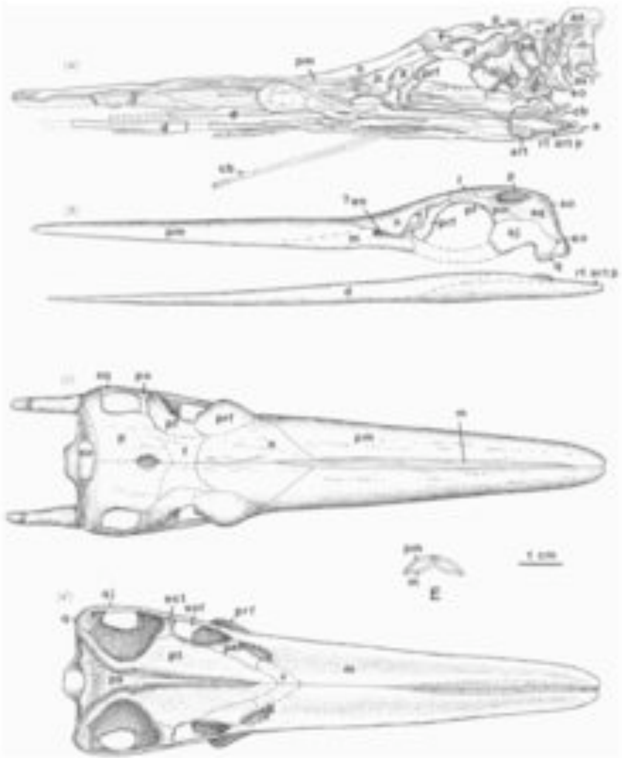
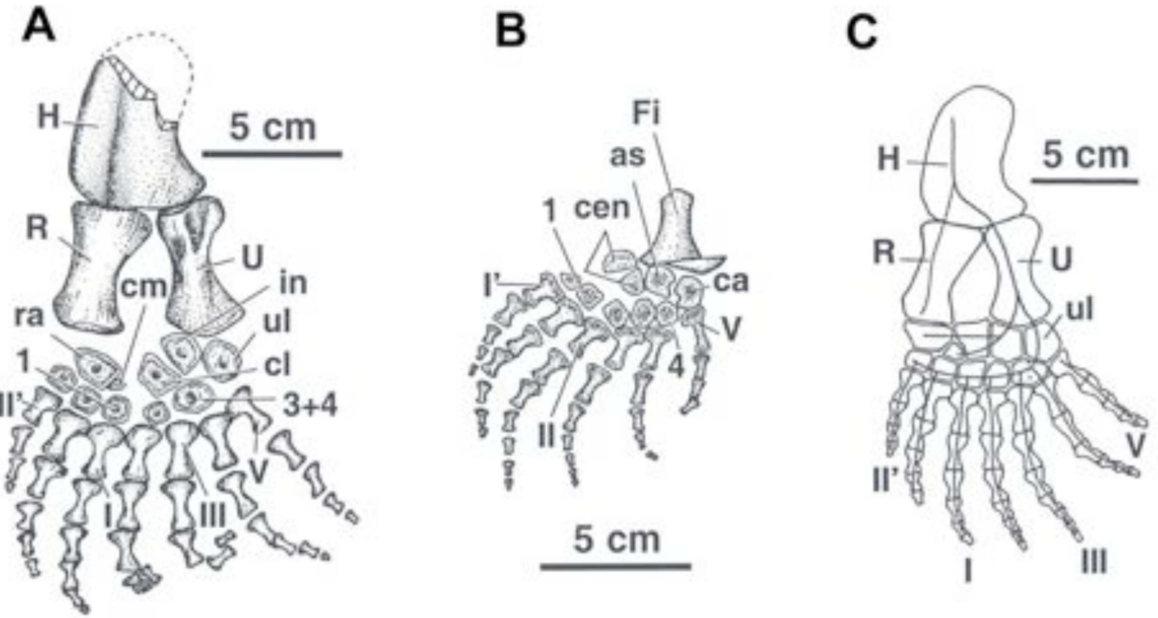
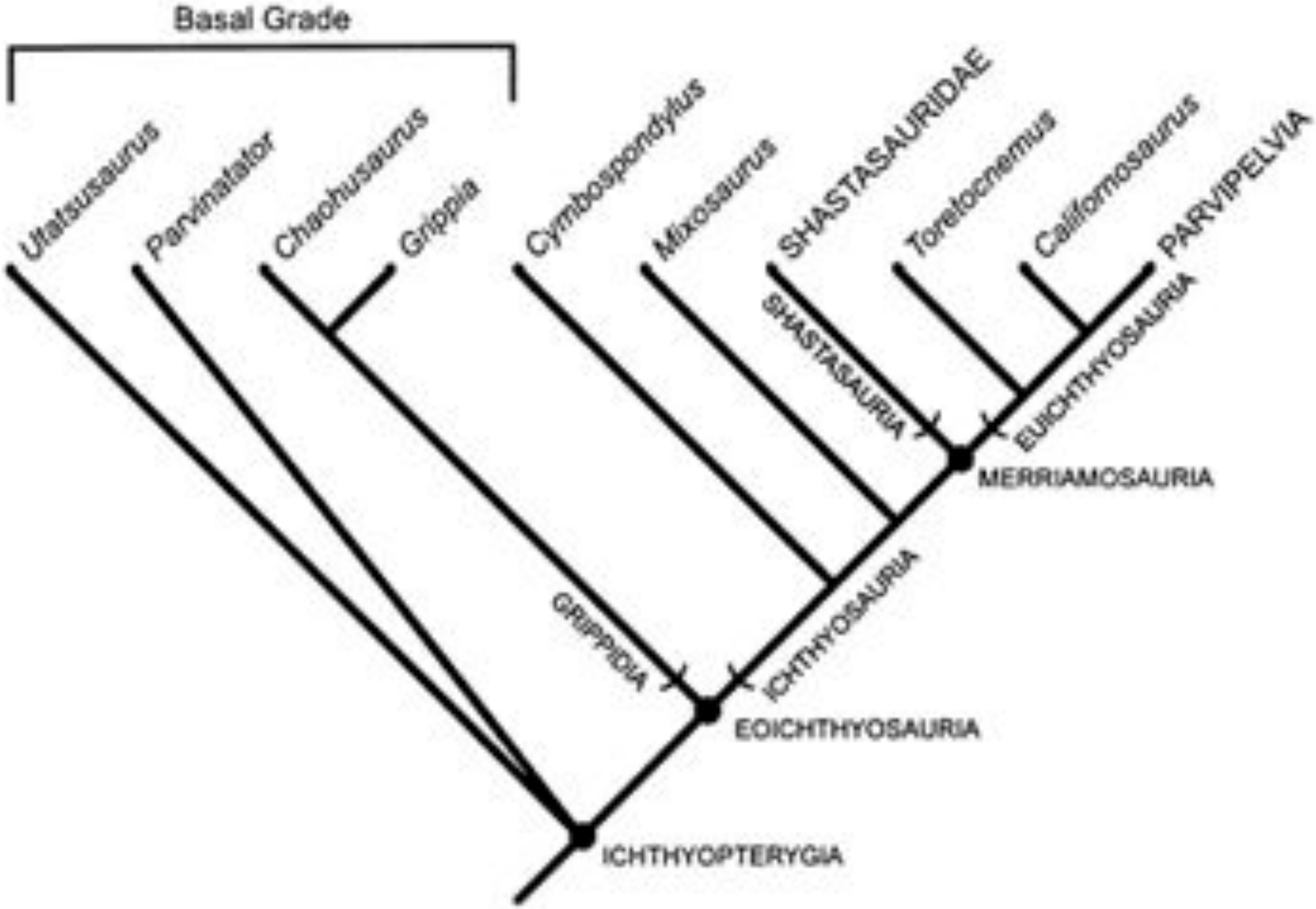


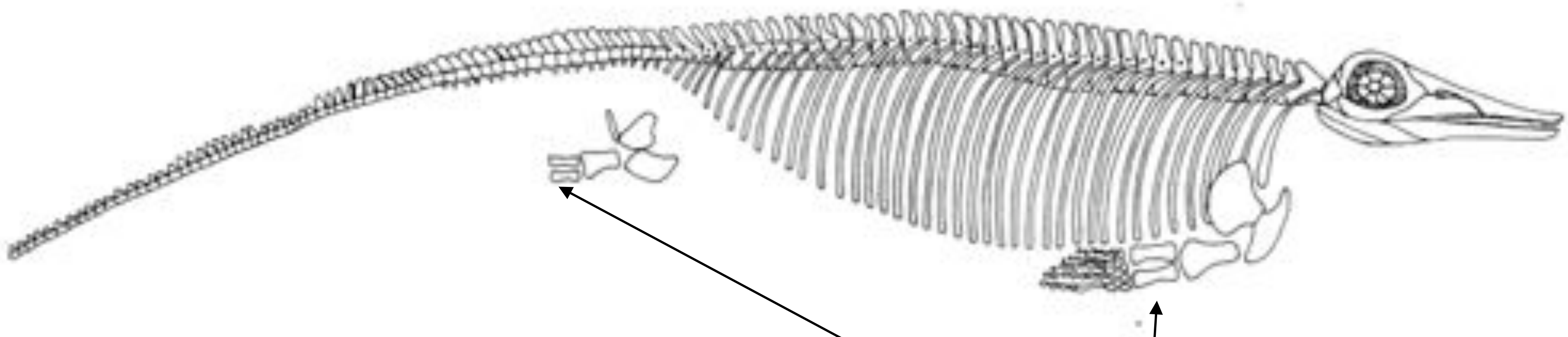
Figure 9. Skull of *Hupehsuchus*. (a) Drawing of skull of holotype, seen primarily in lateral view. X shows position of opening referred to as an antorbital fenestra by Young and Dong. Guide to other abbreviations at end of text. (b–d) Restoration of skull in lateral, dorsal and palatal views, based on the type and V4068. (e) Schematic cross section of snout. All approximately life size.

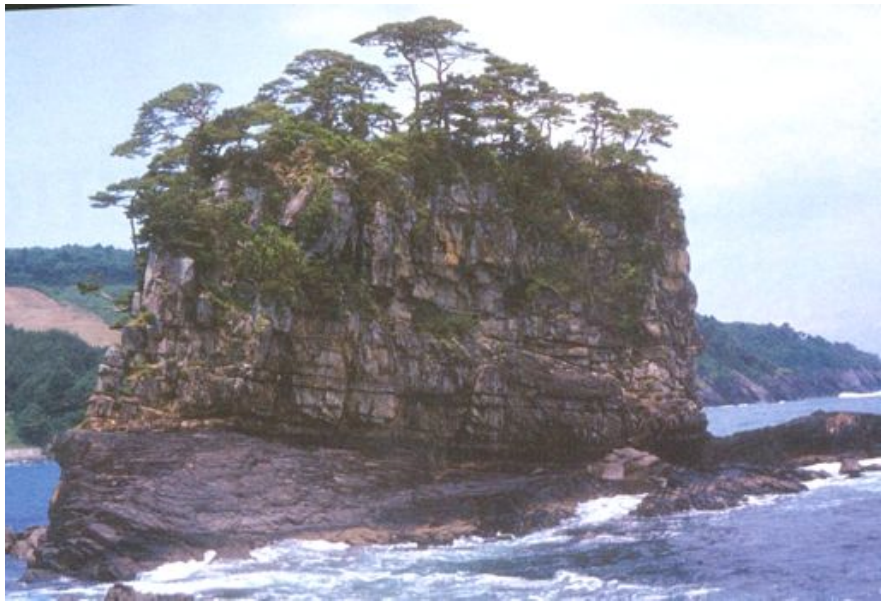
“Nanchangosauridae” heptadáctilo! Otra posible synapomorfía con Ichthyosauria: Unicos tetrápodos corona q presentan más de 5 dedos! (verdaderos)




Basal Grade
Utatsusaurus
Parvinatator
Chaohusaurus
Grippia
Cymbospondylus
Mixosaurus
SHASTASAURIDAE
Toretocnemus
Californosaurus
PARVIPELVIA
SHASTASAURIA
EUICHTHYOSAURIA
MERRIAMOSAURIA
ICHTHYOSAURIA
GRIPPIDIA
EOICHTHYOSAURIA
ICHTHYOPTERYGIA

Utatsusaurus del Triásico de Japón





Utatsusaurus

Su aletas son primitivas:
Posee “antebrazos” y “pantorrillas”, (zeugopodos) alargados. Presenta metacarpales alargados

Figure 12-26. THE ICHTHYOSAUR *CYMBOSPONDYLUS*. Skeleton is from the Middle Triassic of Nevada, approximately 10 meters long. *From Merriam, 1908.*

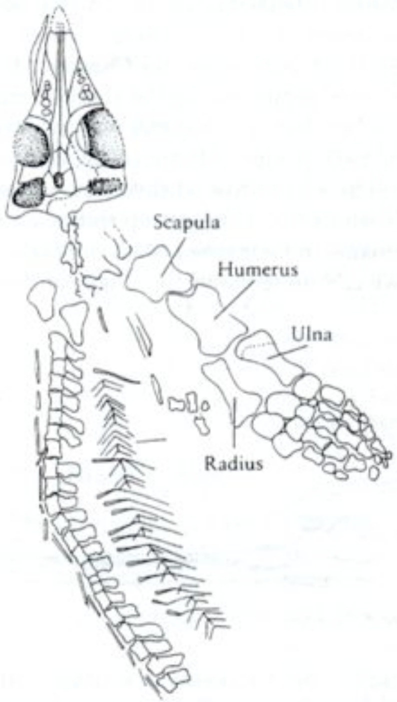
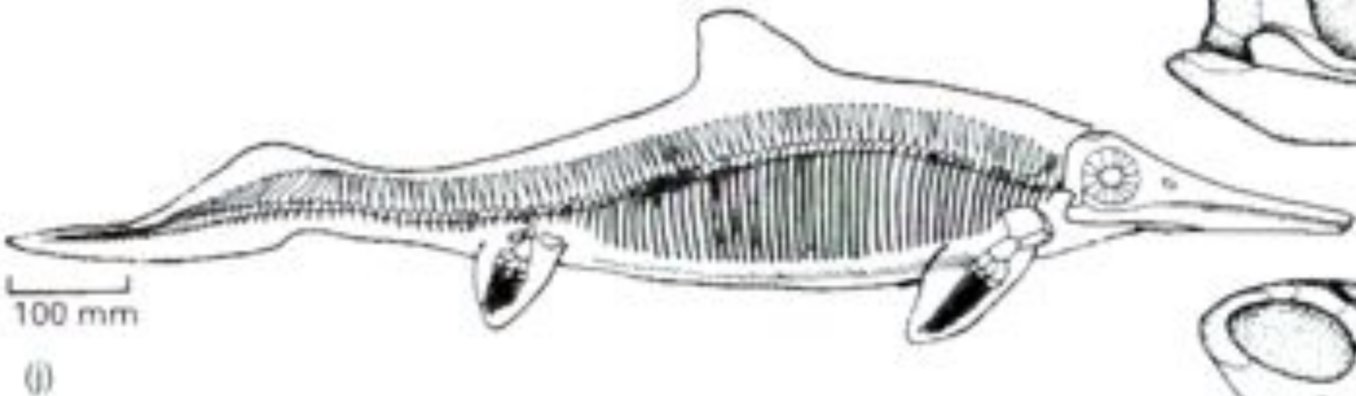


Figure 12-23. THE PRIMITIVE ICHTHYOSAUR *CHAOHUSAURUS* FROM THE BASE OF THE TRIASSIC SEQUENCE IN CHINA. Approximately 1 meter long. The pectoral limb is much larger than that of *Utatsusaurus*. *From Young and Dong, 1972.*

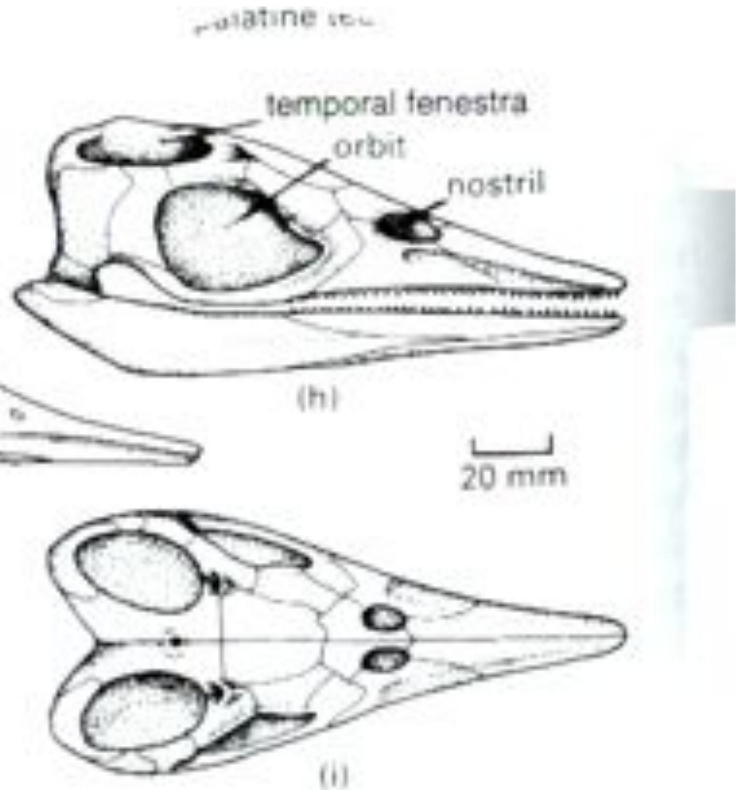
Otros Ichthyosauria primitivos. Nótese que el extremo distal de la cola no está fuertemente doblado hacia abajo como en las formas derivadas en las que conforma el lóbulo inferior de la cola Heterocerca. Nótese zeugopodo alargado en *Chaohusaurus*

Los ichtyosauria más antiguos y primitivos conocidos son ya muy especializados en la vida marina. *Grippia*, del triásico de alemania, presenta una órbita grande, una nariz retraída respecto a la punta del hocico.

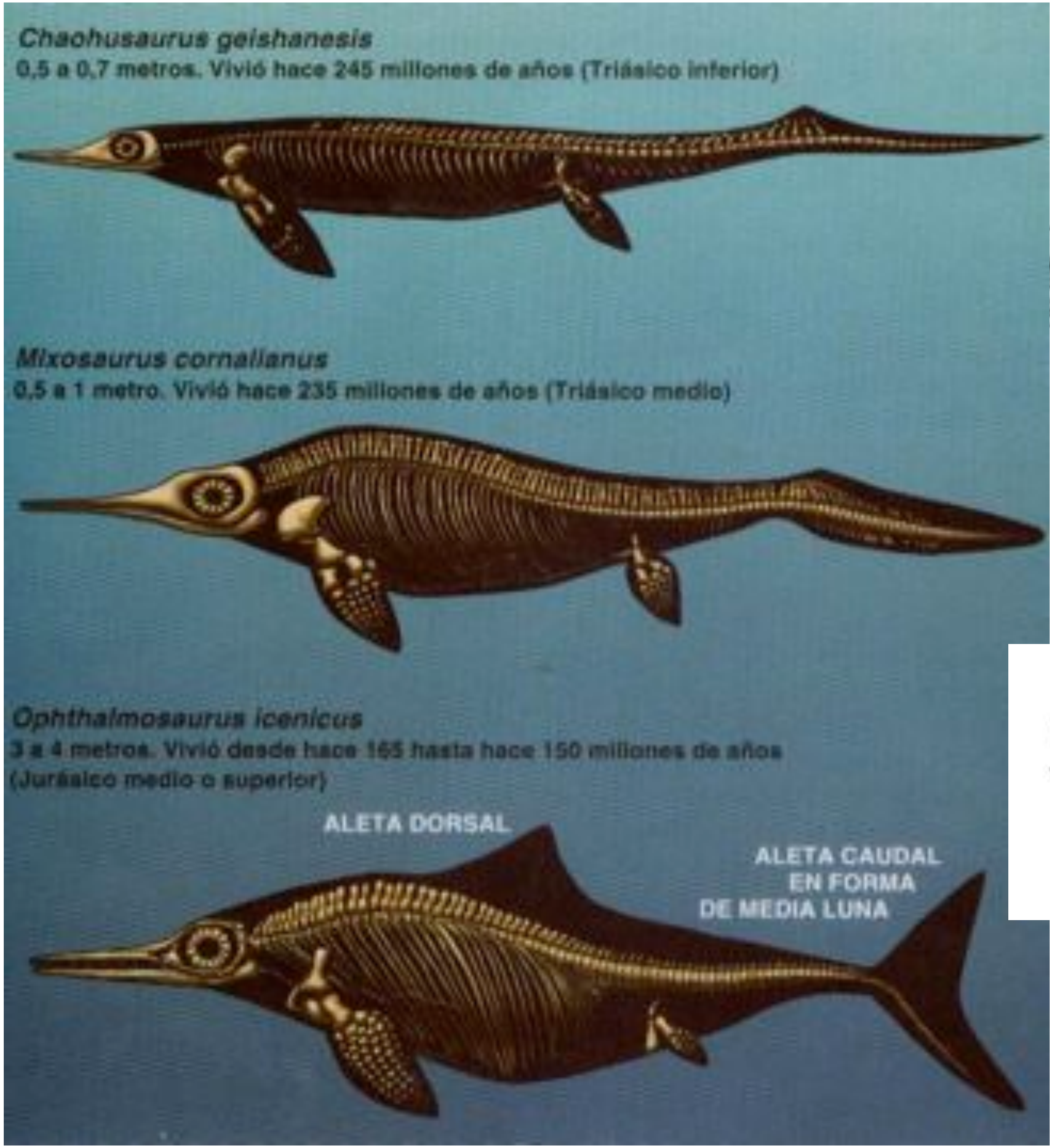
Mixosaurus, del triásico, presenta aletas ya muy avanzadas, con hiperfalangia, y una cola ligeramente más dirigida hacia abajo en la aleta

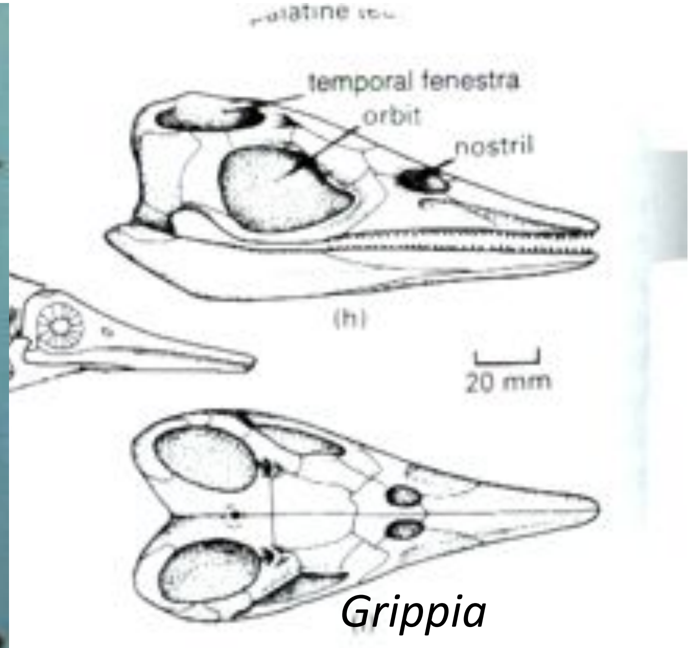


Mixosaurus

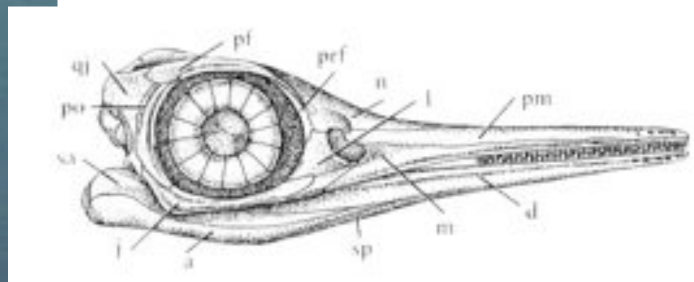


Grippia



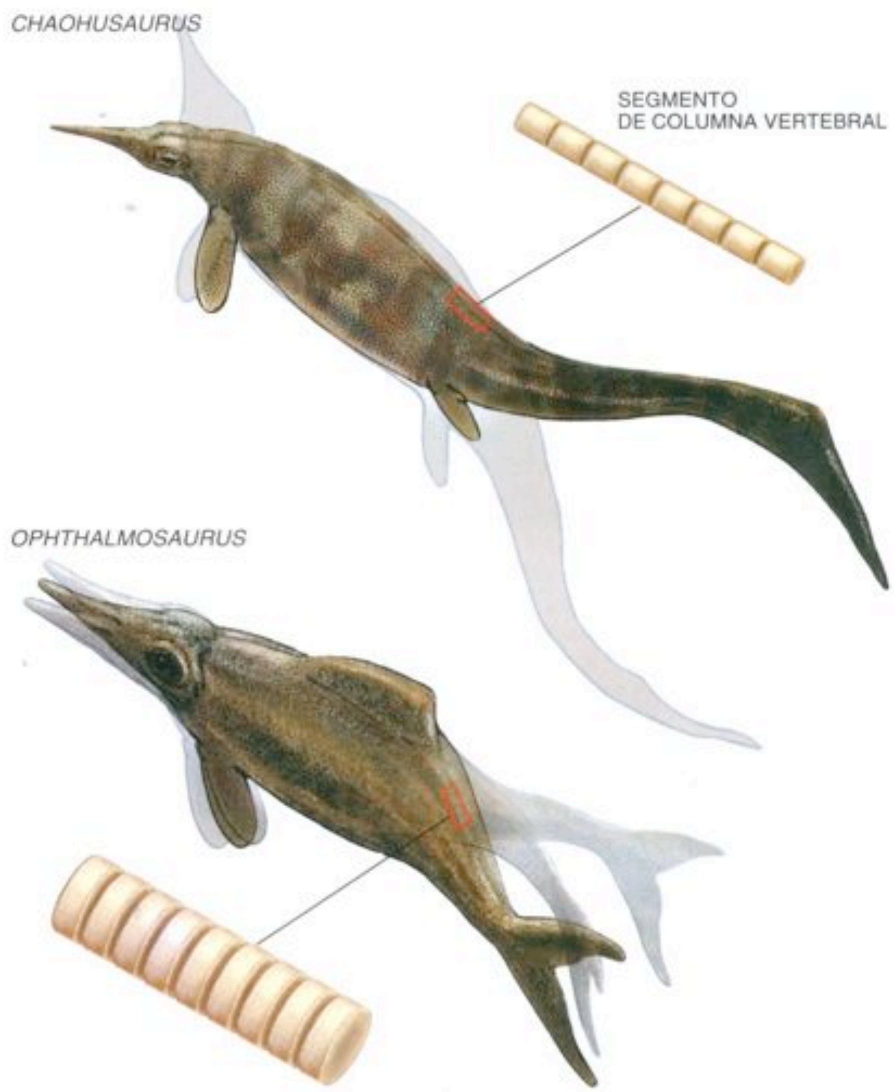


Grippia



Opthalmosaurus

- Los cambios morfológicos experimentados por las vértebras de ictiosaurios entre el Triásico y Jurásico determinaron un importante innovación en el tipo desplazamiento dentro del medio acuático.
- La natación ondulatoria de los ictiosaurios primitivos como *Chaohusaurus* requería la flexión lateral generalizada del cuerpo.
- En *Ophthalmosaurus* y otros ictiosaurios más avanzados el cuerpo se hace extremadamente rígido y adquiere una forma fusiforme que le permite al animal ser propulsado por una muy bien desarrollada aleta caudal. Los restos fósiles de Ictiosaurios pos-triásicos también evidencian la existencia de una aleta dorsal como se observa en los cetáceos actuales.



Algunos ictiosaurios del triásico tardío llegaron atener 15m (*Shonisaurus*).

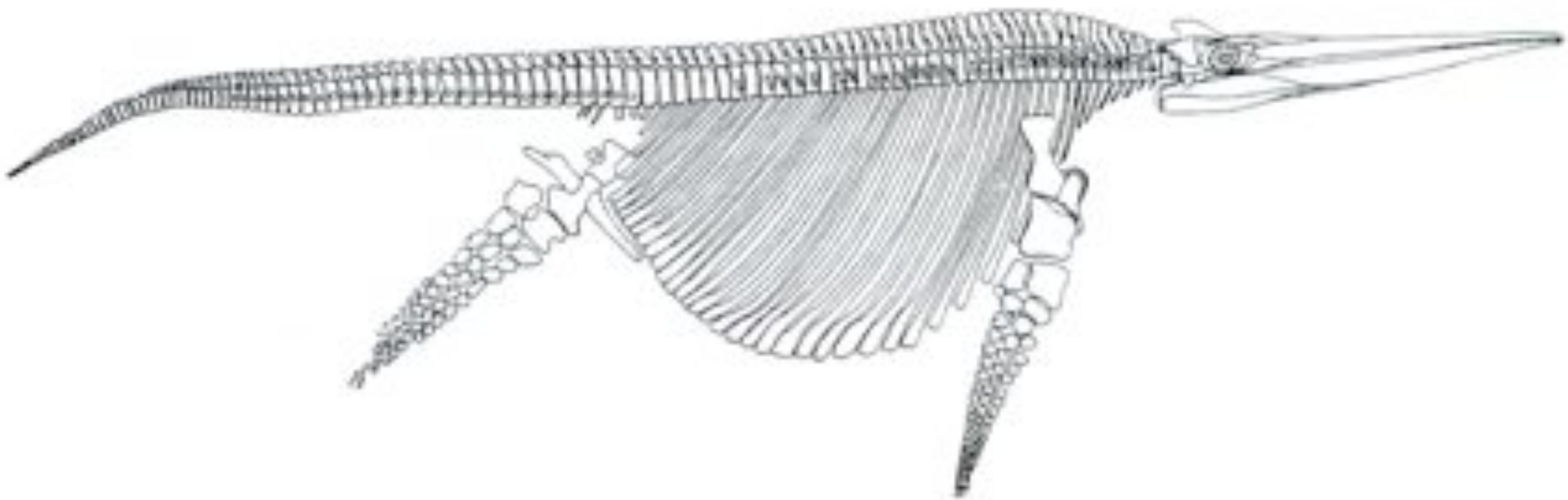


Figure 12-29. THE UPPER TRIASSIC ICHTHYOSAUR *SHONISAURUS* WHICH REACHED A LENGTH 15 METERS. The heads of the ribs are not drawn, in order to show the articulating surfaces of the vertebrae. *From Camp, 1980.*

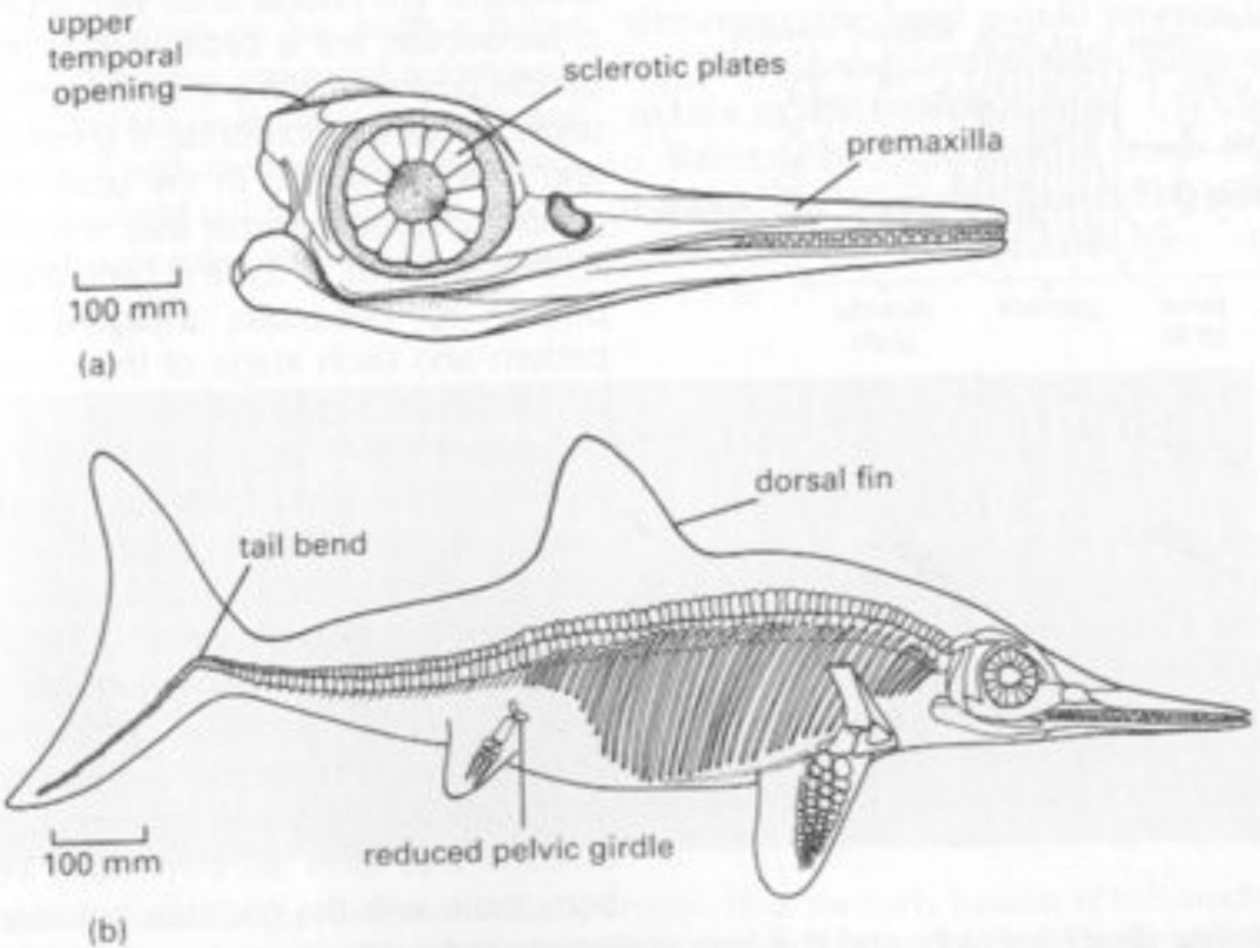
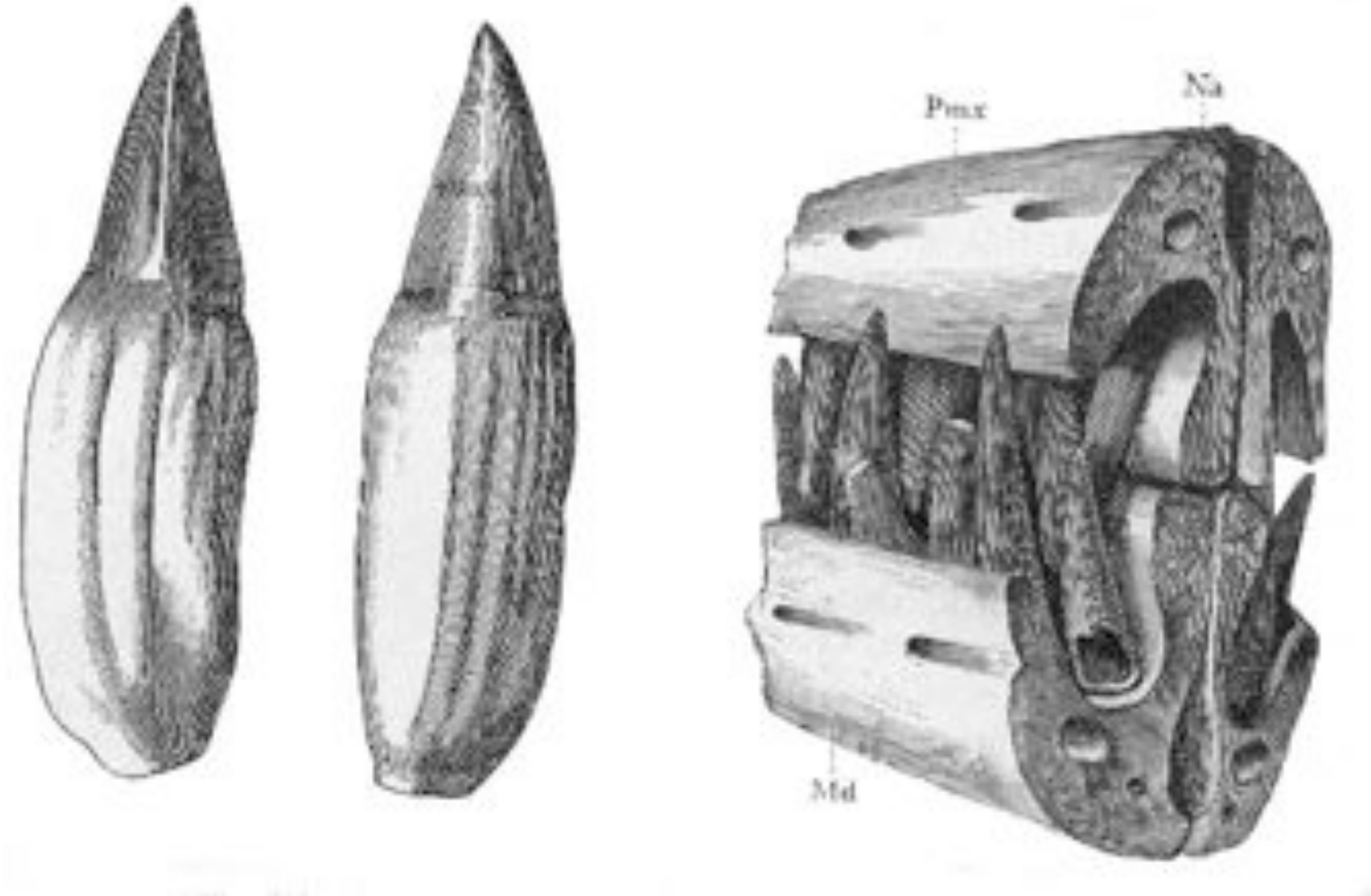


Fig. 8.31 The ichthyosaurs: (a) skull, and (b) skeleton of the Early Jurassic *Ichthyosaurus*; the body outline is based on skin impressions preserved with some European material. (After Andrews, 1910.)

En los icthyosauria más derivados del jurásico y cretácico, únicos supervivientes de una diversidad de formas triásicas, los dientes se insertan en la mandíbula al interior de una especie de “canaleta” común más bien que al interior de alvéolos individuales. Las costillas a los largo de todo el cuerpo presentan dos “cabezas”



Los ictiosaurios derivados poseen una interclavícula en forma de “T” y la pelvis se encuentra reducida en distintos grados

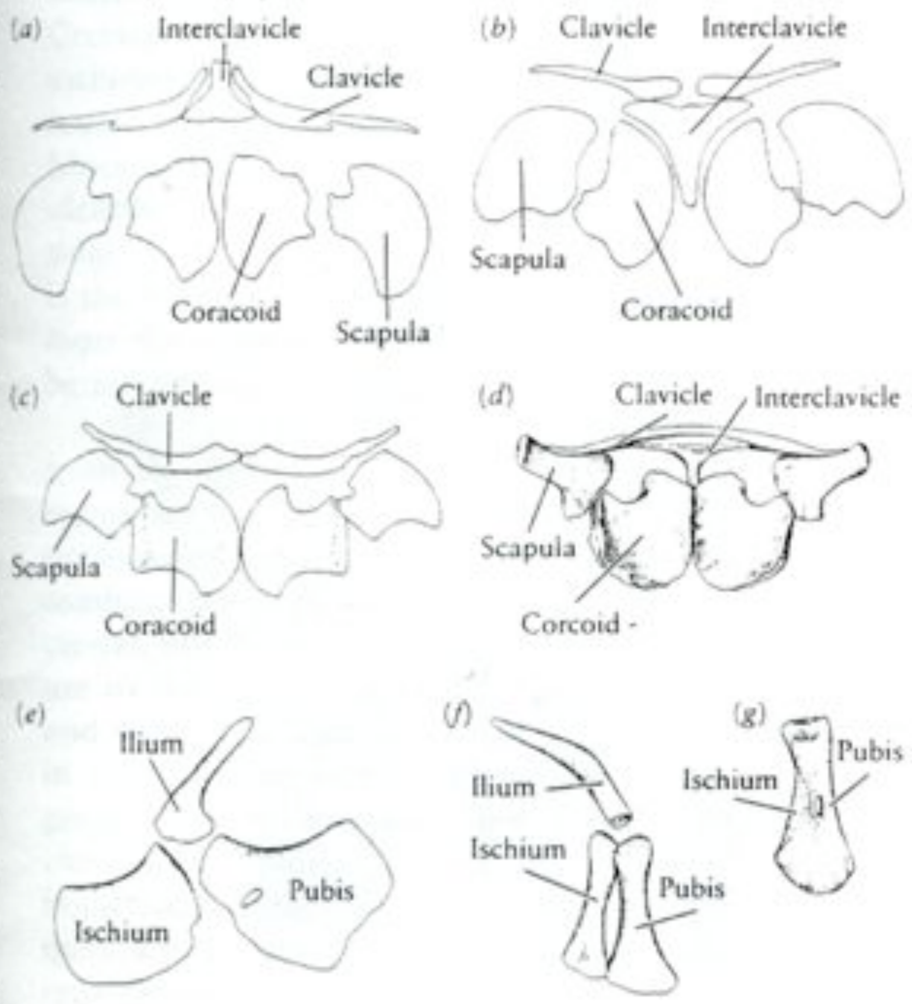


Figure 12-28. CHANGING PATTERN OF THE PECTORAL AND PELVIC GIRDLES AMONG ICHTHYOSAURS. (*a, b, c,* and *d*) Pectoral girdles of *Utatsusaurus* (Lower Triassic), *Mixosaurus* (Middle Triassic), *Shastasaurus* (Upper Triassic), and *Ophtalmosaurus* (Upper Jurassic). (*e, f,* and *g*) Pelvic girdles of *Cymbospondylus* (Middle Triassic), *Ichthyosaurus* (Lower Jurassic), and *Ophthalmosaurus* (Upper Jurassic). *(a) From Shikama, Kamei, and Murata, 1972, restored on the basis of the specimen drawing. (b, c, e, and f) From Merriam, 1908. (d and g) From Andrews, 1910.*

Ictiosaurios primitivos.
Hay elementos más alargados que en los derivados

Longipinados:
Con tres carpales distales y tres dígitos Principales

Latipinados:
Con cuatro carpales Distales y cuatro dígitos

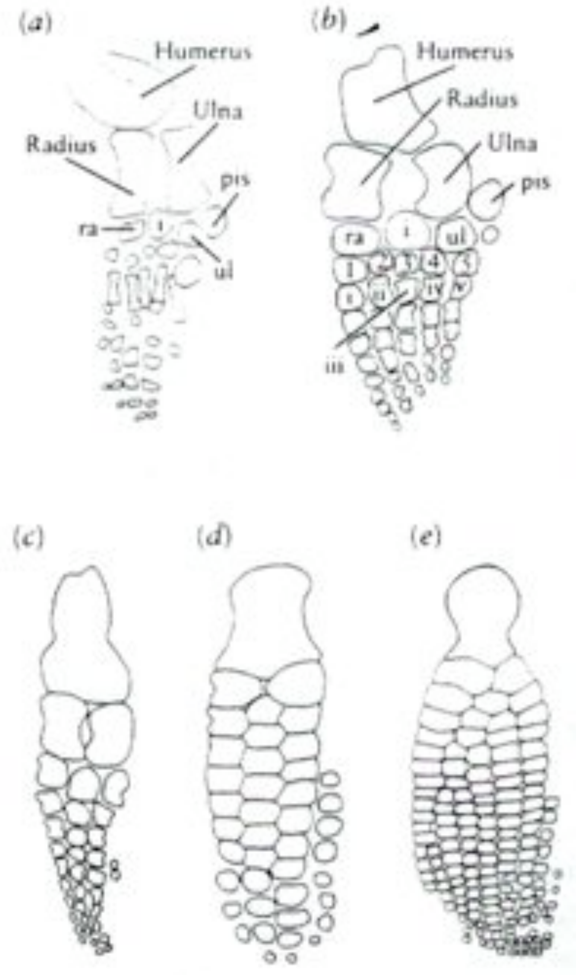


Figure 12-30. DIFFERENT PATTERNS OF THE FRONT LIMBS ICHTHYOSAURS. (*a*) *Utatsusaurus* (Lower Triassic). *From Shikar Kamei, and Murata, 1978.* (*b*) *Mixosaurus* (Middle Triassic). *Fr McGowan, 1972.* (*c*) *Merriamia* (Upper Triassic). *From McGowan, 19* (*d*) *Proteosaurus*, showing the pattern that is characteristic of longip nates (Lower Jurassic) *From McGowan, 1972.* (*e*) *Ichthyosaurus co munis*, showing the pattern of latipinnates (Lower Jurassic). *Fr McGowan, 1972.* Abbreviations as follows: i, intermedium; pis, p form; ul, ulnare; 1–5, distal carpals; i–v, metacarpals. (*b–e*) *By p mission of The Royal Ontario Museum.*

Un Icthyosaurio muy derivado: Opthalmosaurus, sin dientes y provisto de una órbita ocular gigantesca.
Los Icthyosauria se extinguieron antes del cretácico tardío, mucho antes de la gran extinción cretácico terciaria

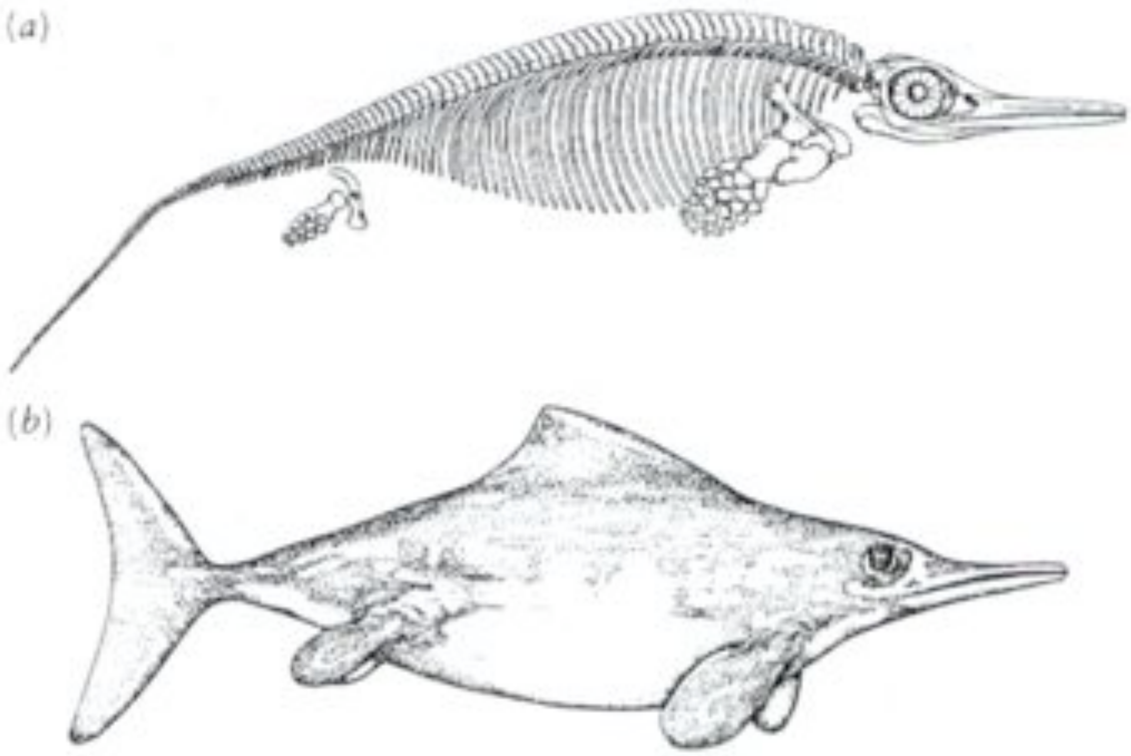


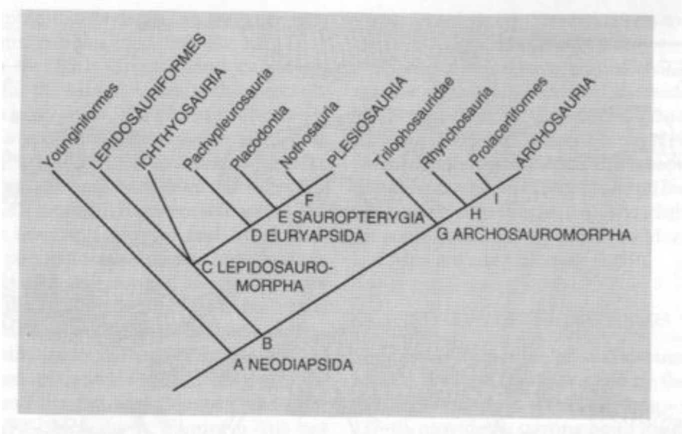
Figure 12-20. THE ADVANCED ICHTHYOSAUR *OPHTHALMOSAURUS* FROM THE UPPER JURASSIC. (*a*) Skeleton, approximately 3½ meters long. *From Andrews, 1910.* (*b*) Restoration. *From McGowan, 1983.*

La alta especialización acuática se corresponde con la presencia de reproducción vivípara

EURYAPSIDA.

Los pachypleurosaria se diferencian de *Claudiosaurus* en que los miembros se han reducido. No se aprecian demasiado modificados para propulsión acuática. En ***Pachypleurosaurus*** las espinas neurales y hemales ubicadas cerca de la base de la cola se expanden dorsalmente y ventralmente formando una superficie para propulsión.

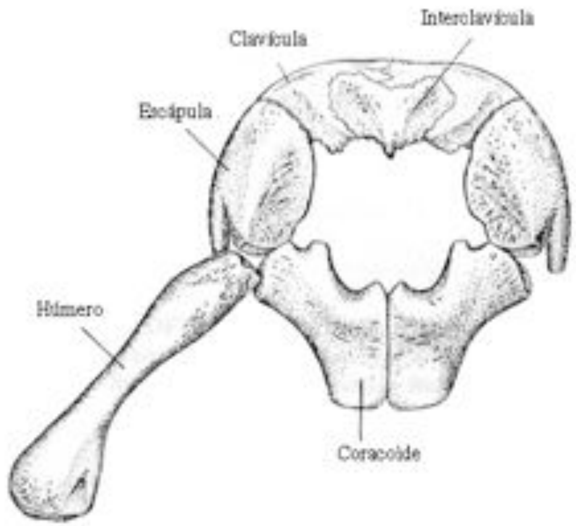
Pachypleurosaurus



Coracoides contactados medialmente

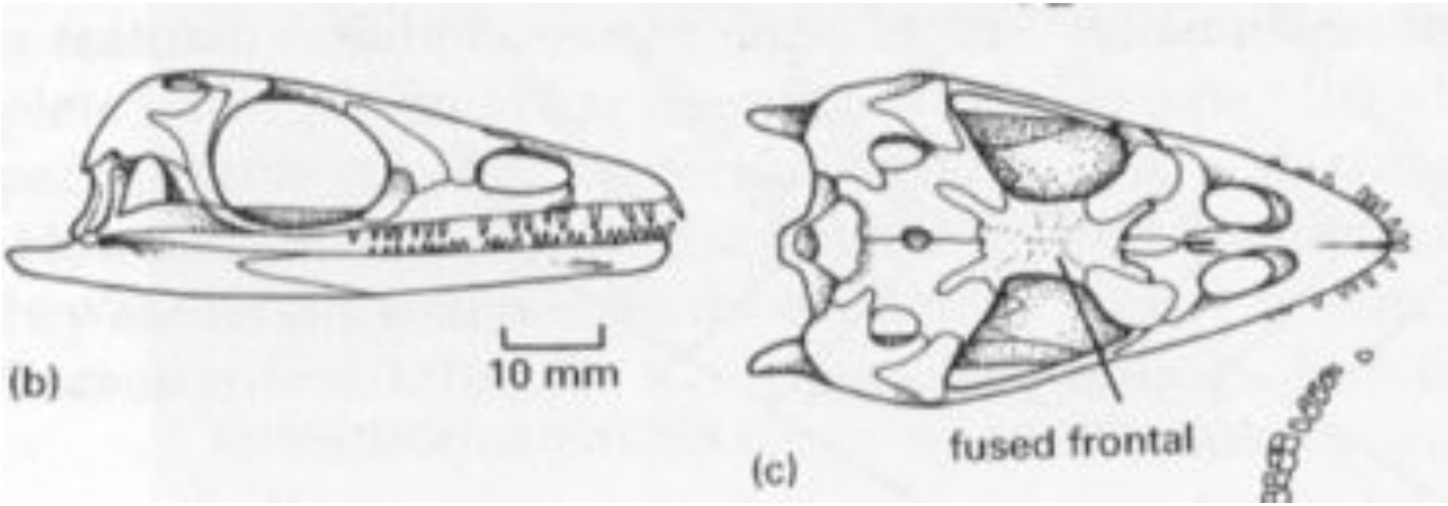
Costillas paquiostoticas

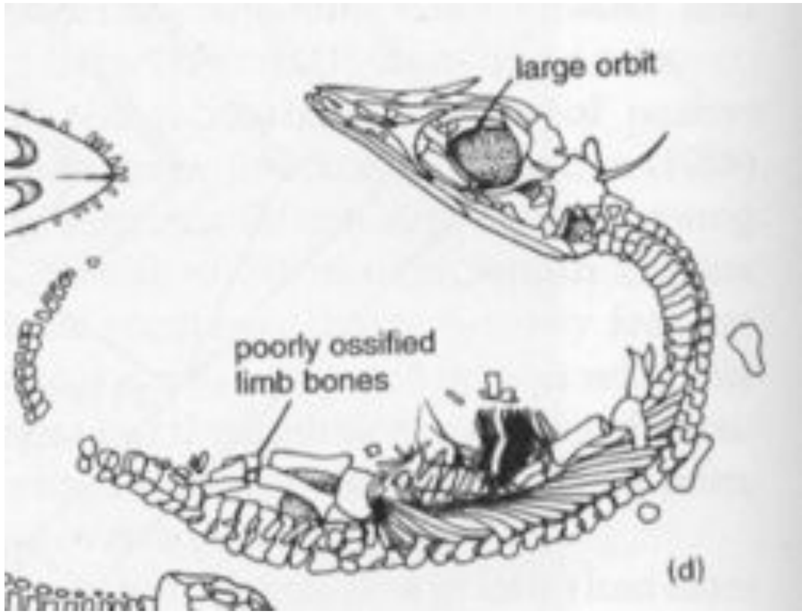
Ausencia de esternon osificado



La osificación de cinturas, carpales y tarsales ha sido grandemente reducida y las articulaciones no muestran rasgos que facilitan movimiento en tierra.

El cráneo de pachypleurosaurus es alargado y ligero, con gran órbita y apertura nasal, pero una pequeña fenestra temporal. Los dientes son espaciados y proyectados hacia delante. Presentan proceso retroarticular, hyomandibular delgado lo cual sugiere homología del timpano con el de Sauria.





Embrión o recién nacido de un Pachypleurosauria

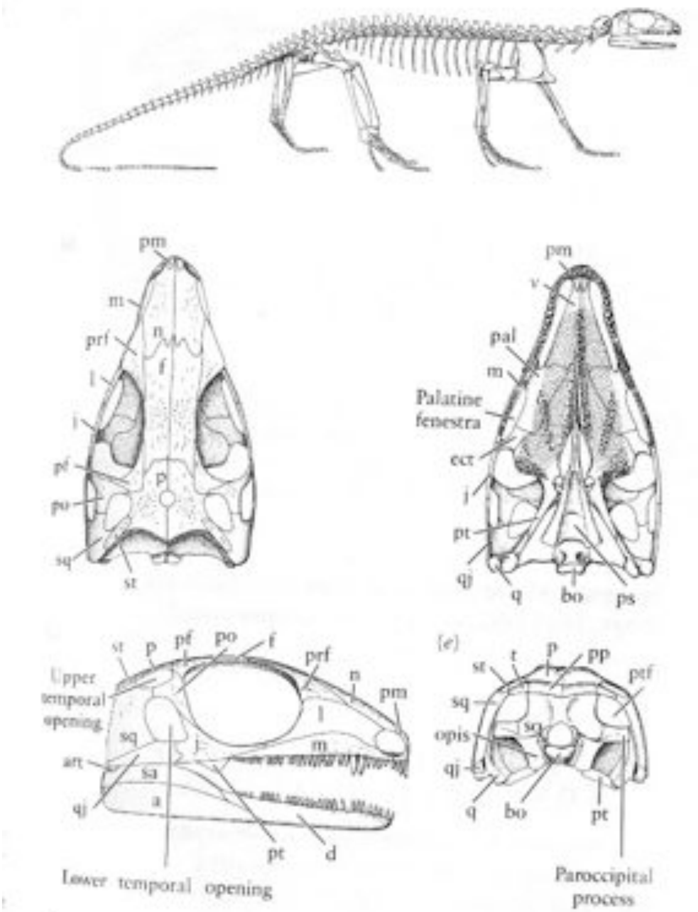
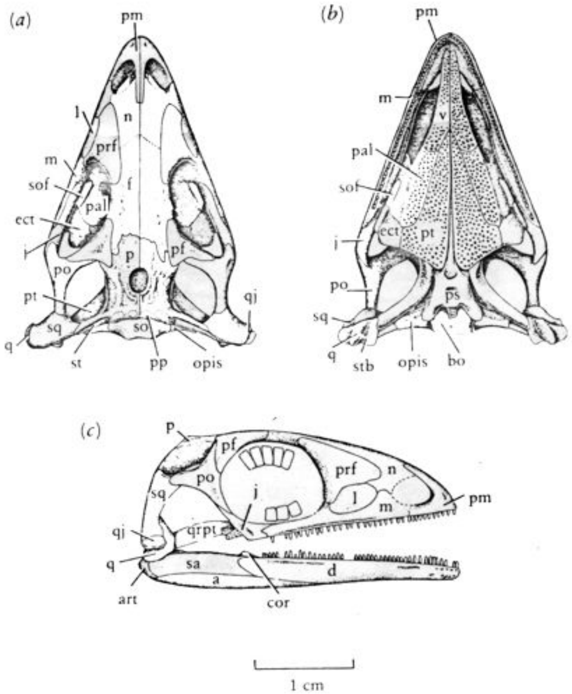
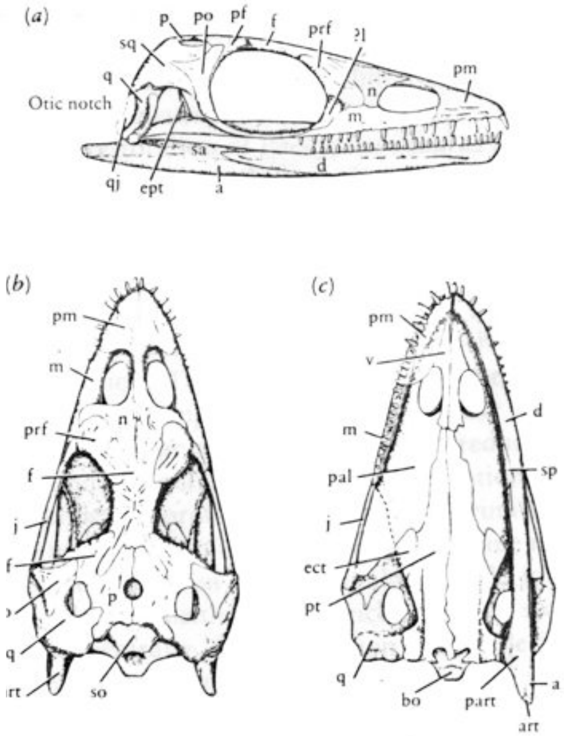


Figure 11-2. THE EARLIEST AND MOST PRIMITIVE KNOWN DIAPSID, *PETROLACOSAURUS* FROM THE UPPER CARBONIFEROUS OF KANSAS. (*a*) Skeleton, about 20 centimeters long, not including the tail. Skull in (*b*) dorsal, (*c*) palatal, (*d*) lateral, and (*e*) occipital views. Approximately × ⅔. Abbreviations as in Figure 8-3. *From* Reisz, 1981.

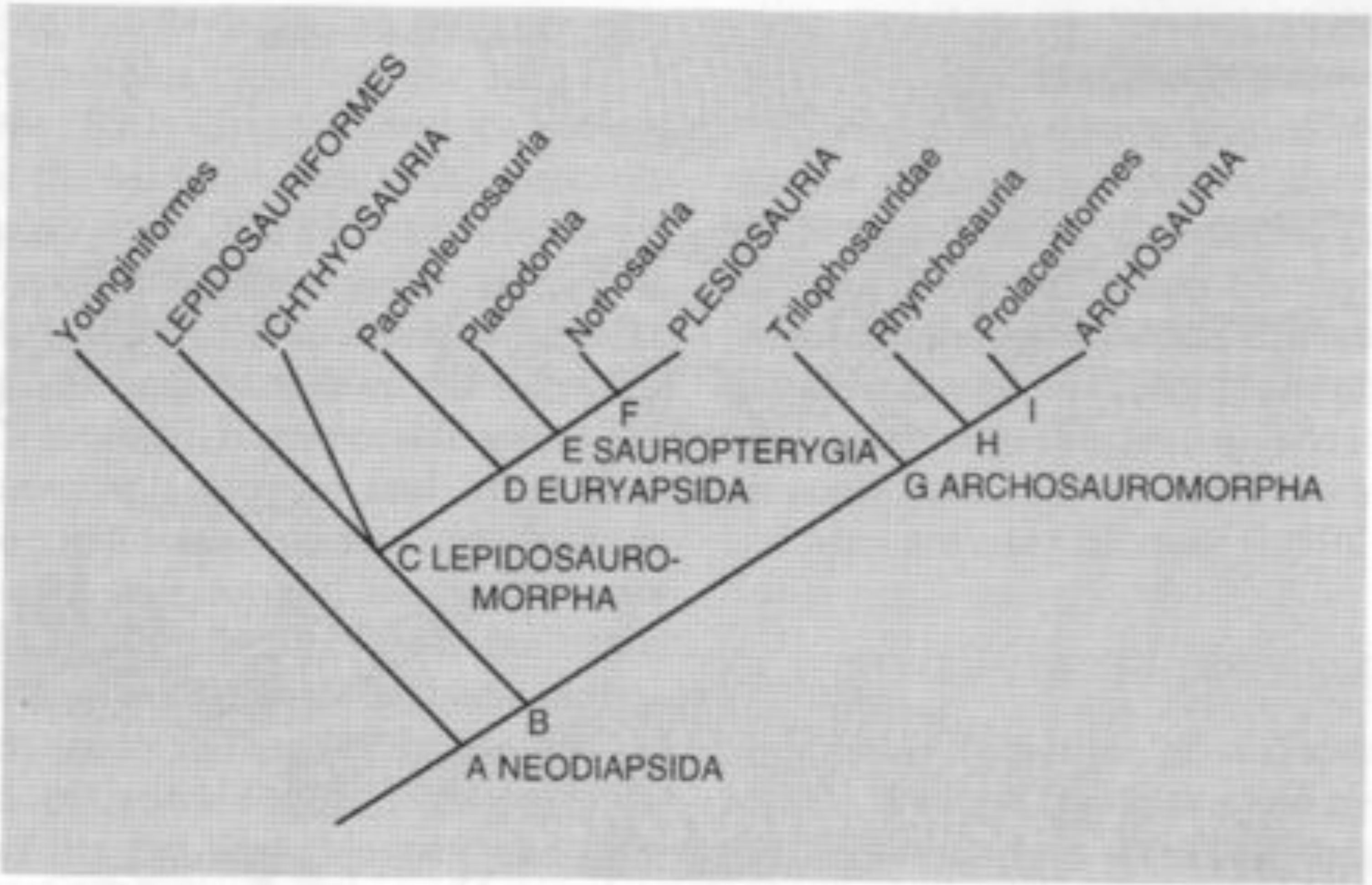


Claudiosaurus



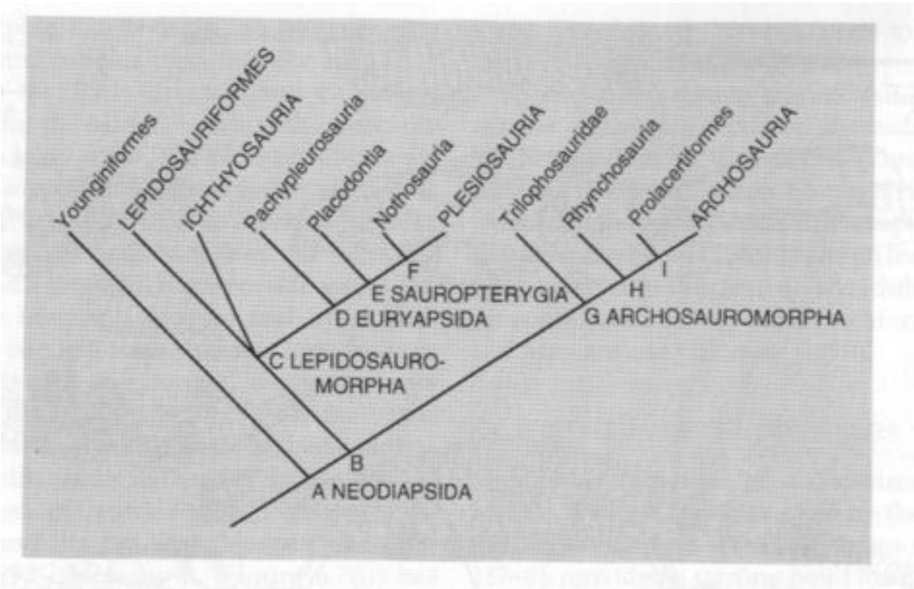
Pachypleurosaurus

En Pachypleurosauridae y los Nothosauria, la vacuidad interpterygoidea ha desaparecido por completo y los pterygoideos están firmemente unidos


Younginiformes
LEPIDOSAURIFORMES
ICHTHYOSAURIA
Pachypleurosauria
Placodontia
Nothosauria
PLESIOSAURIA
Trilophosauridae
Rhynchosauria
Prolacertiformes
ARCHOSAURIA
F
E SAUROPTERYGIA
H
I
D EURYAPSIDA
G ARCHOSAUROMORPHA
C LEPIDOSAURO-
MORPHA
B
A NEODIAPSIDA

Nothosauria

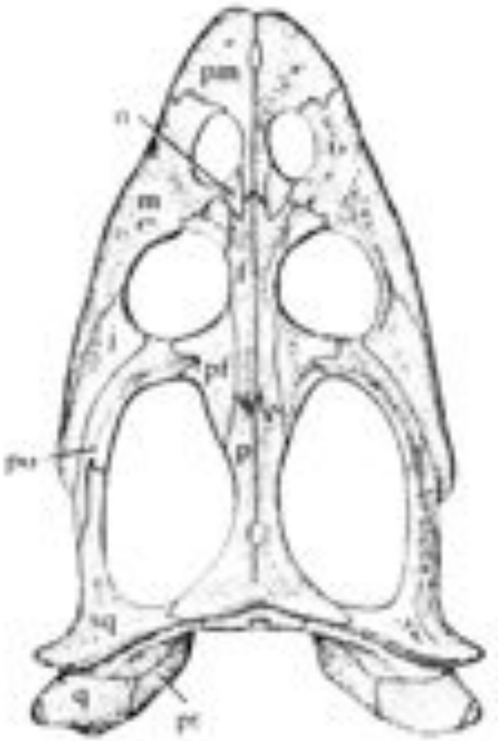
- Los notosaurios son conocidos principalmente desde el Triásico Medio de Europa y China, son de mayor tamaño (1-4 m) y presentan una mayor especialización en el estilo de vida acuático.



- En muchos Notosaurios las costillas y vértebras son paquiostóticas es decir, más gruesas y pesadas, condición posibilitada por el hábito marino y que aumentaría la gravedad específica, posibilitando el sumergirse con un mínimo de esfuerzo. Esta característica incluso es evidente en los más pequeños géneros como ***Neusticosaurus*.**

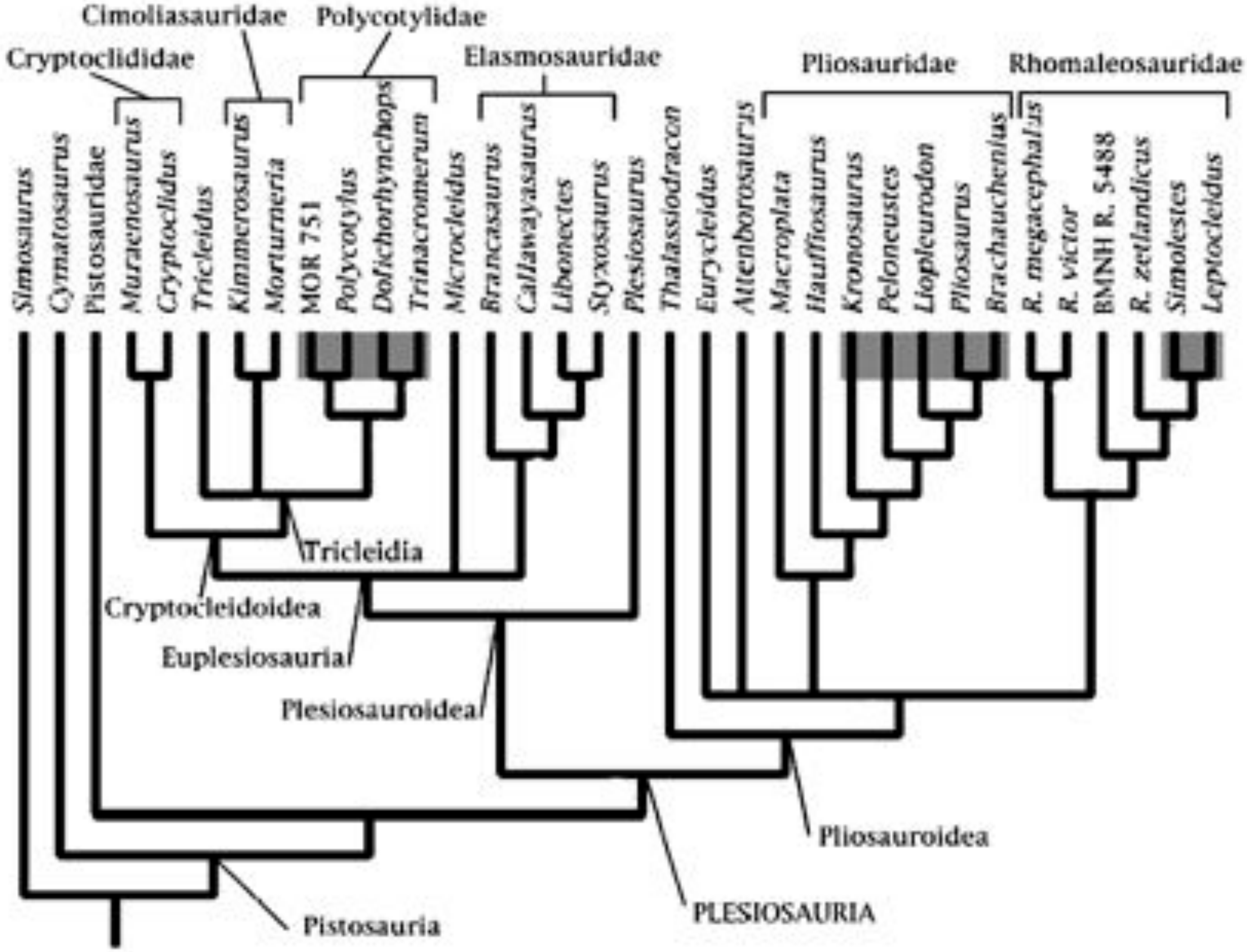
  A diferencia de pachypleurosauria, la cola no es lateralmente aplanada, y es de corta longitud, indicando el desplazamiento por locomoción paraxial (movimiento de las extremidades en vez de la columna). Es posible notar un mayor desarrollo de las extremidades anteriores probablemente relacionada a su mayor importancia en la locomoción

Ceriosaurus del Triásico



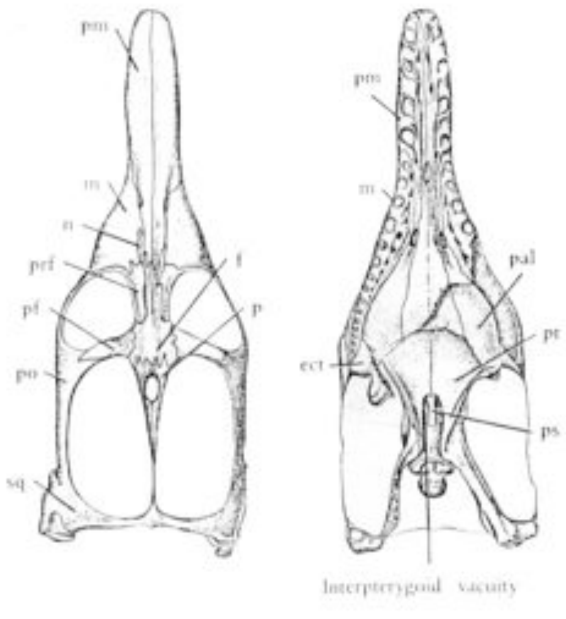
- El género ***Nothosaurus*** superaba los 4 metros de largo y su cráneo es mucho más ancho posteriormente. Los Nothosauria presentan aperturas supratemporales mucho más grandes que en Pachypleurosauridae

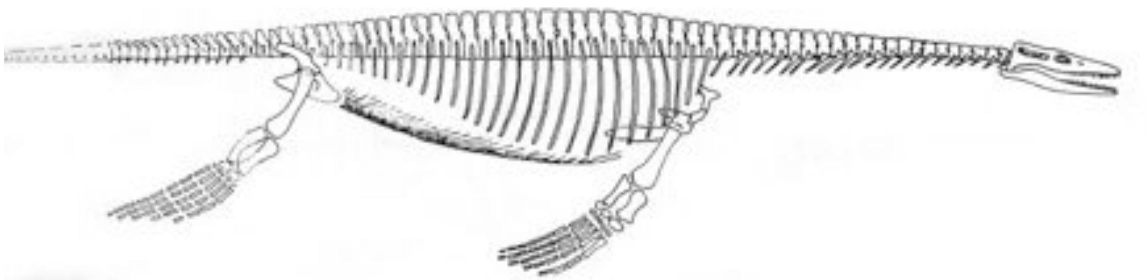
  Nothosaurus tiene espinas neurales muy altas y estrechos arcos neurales sugiriendo un tronco más rígido.


Cryptoclididae
Cimoliasauridae
Polycotylidae
Elasmosauridae
Pliosauridae
Rhomaleosauridae
Simosaurus
Cymatosaurus
Pistosauridae
Muraenosaurus
Cryptoclidus
Tricleidus
Kimmerosaurus
Morturneria
MOR 751
Polycotylus
Dolichorhynchops
Trinacromerum
Microcleidus
Brancasaurus
Callawayasaurus
Libonectes
Styxosaurus
Plesiosaurus
Thalassiodracon
Eurycleidus
Attenborosaurus
Macroplata
Hauffiosaurus
Kronosaurus
Peloneustes
Liopleurodon
Pliosaurus
Brachauchenius
R. megacephalus
R. victor
BMNH R. 5488
R. zetlandicus
Simolestes
Leptocleidus
Tricleidia
Cryptocleidoidea
Euplesiosauria
Plesiosauroidea
Pliosauroidea
PLESIOSAURIA
Pistosauria

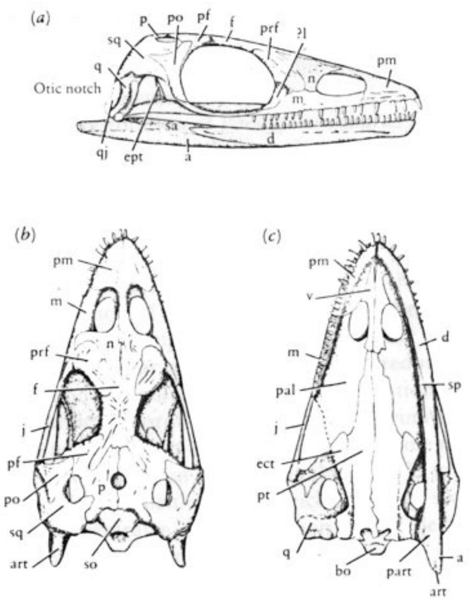
Pistosauridae

- Un género del Triásico Medio, *Pistosaurus,* presenta evidente mayor rigidez del trono y mayor desarrollo de las extremidades especializadas en aletas. El nado ha sido transferido desde el movimiento del cuerpo (axial) hacia la locomoción paraxial. El cuerpo en general es semejante a nothosauria. Puede considerarse como grupo hermano de los plesiosaurios. Presenta aperturas nasales de posición retraída
- El cráneo retiene la presencia de los huesos nasales, los que se han perdido en plesiosaurios.





A diferencia de los Nothosauria y pachypleurosauridae, Pistosaurus y los Plesiosauria presentan una vacuidad interpterygoidea, como en los primeros diápsidos.



Pachypleurosaurs

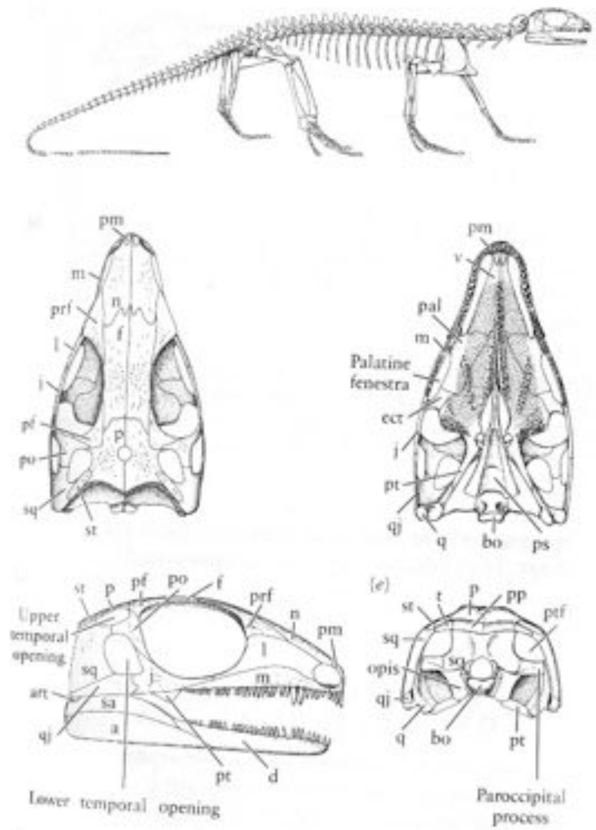
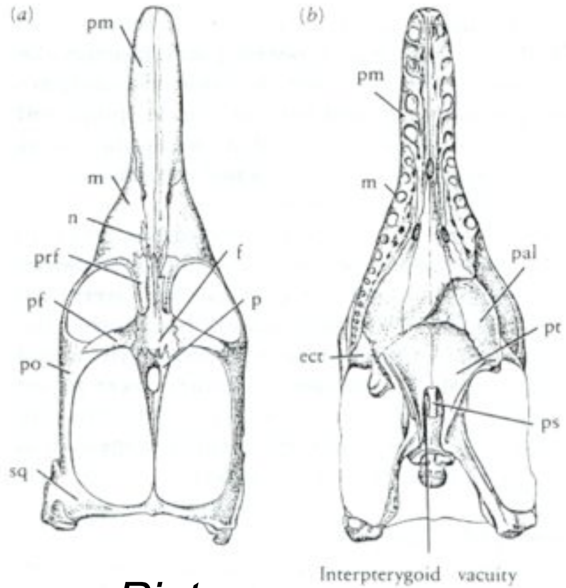
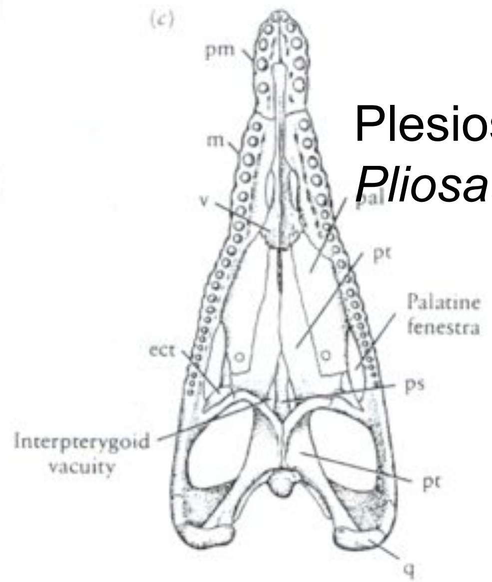


Figure 11-2. THE EARLIEST AND MOST PRIMITIVE KNOWN DIAPSID, *PETROLACOSAURUS* FROM THE UPPER CARBONIFEROUS OF KANSAS. (*a*) Skeleton, about 20 centimeters long, not including the tail. Skull in (*b*) dorsal, (*c*) palatal, (*d*) lateral, and (*e*) occipital views. Approximately × [illegible]. Abbreviations as in Figure 8-3. *From Reisz, 1981.*

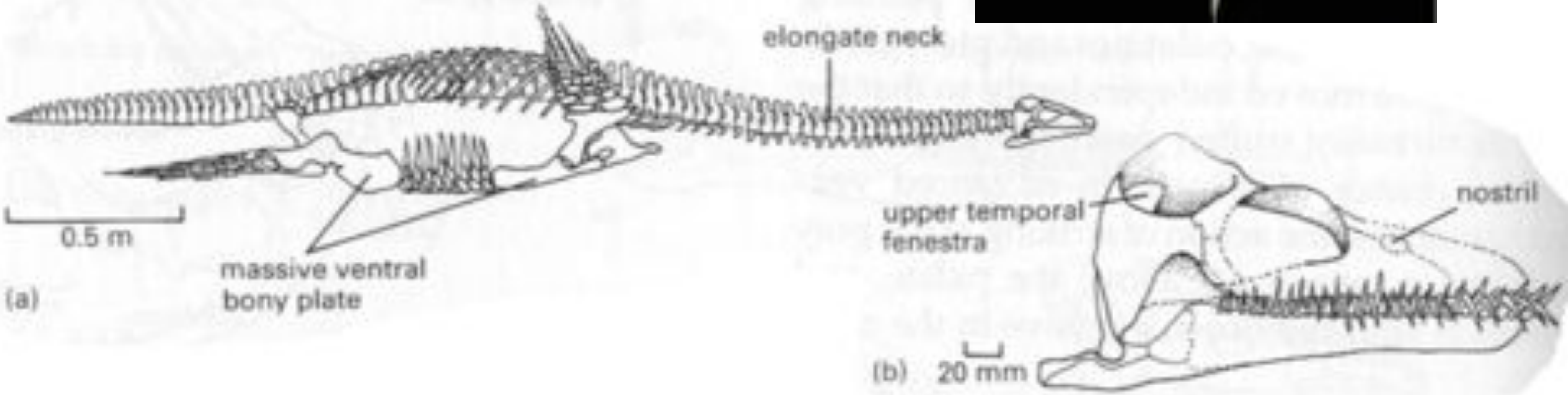


Pistosaurus

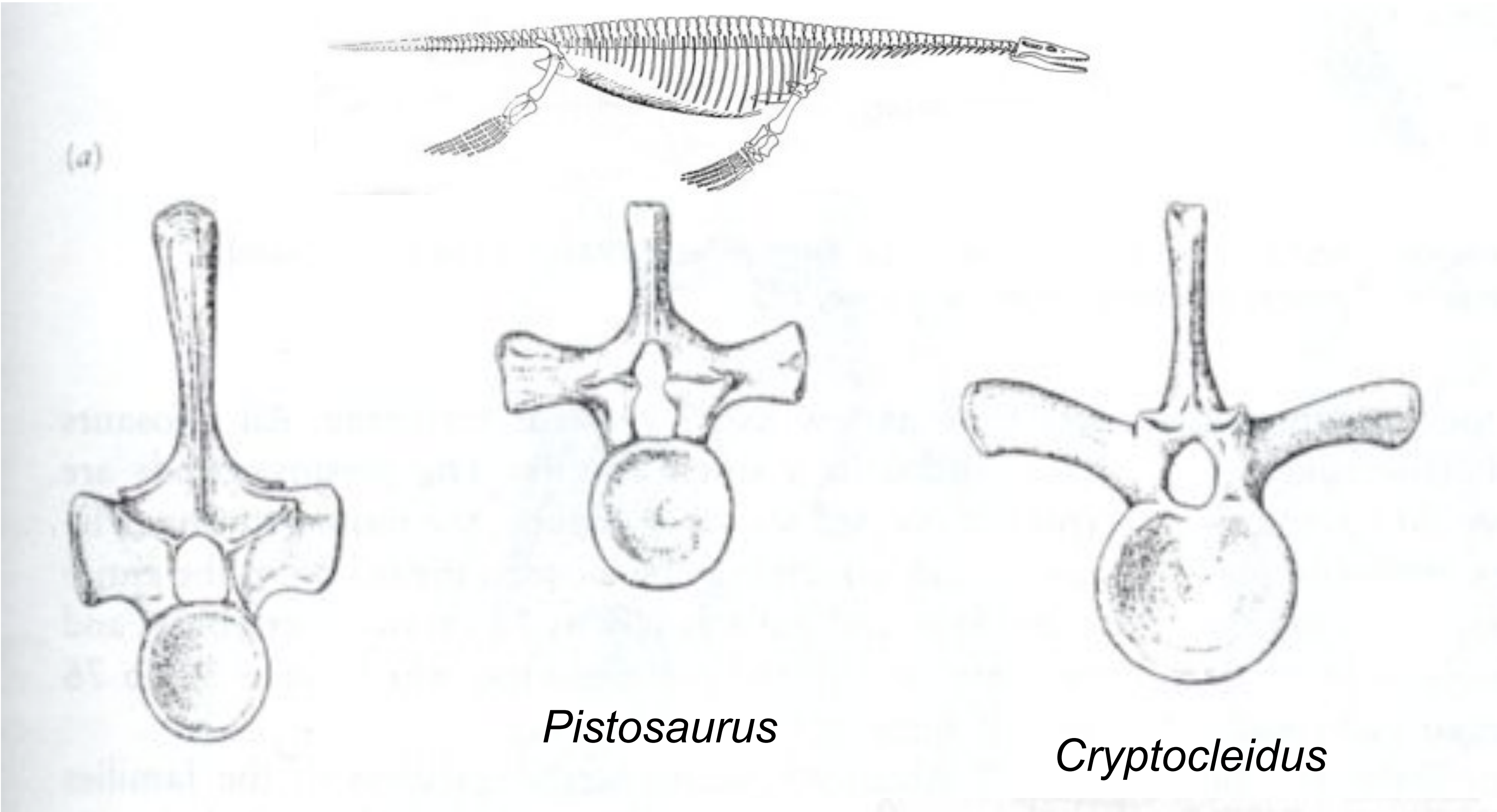


Plesiosauria: *Pliosaurus*

Los **Plesiosauria** estaban altamente capacitados para la locomoción submarina, con poderosas aletas y cinturones pélvicos y pectorales pesadamente reforzados.
Los **Cryptoclididae** presentan una articulación de la mandíbula por debajo de la línea de los dientes.



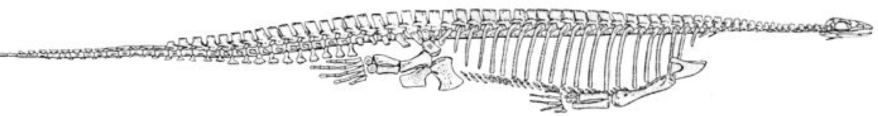
Se redujo el tamaño de las articulaciones entre vértebras y aumentó el tamaño de los procesos transversales en las vértebras del tronco de los Plesiosauria.

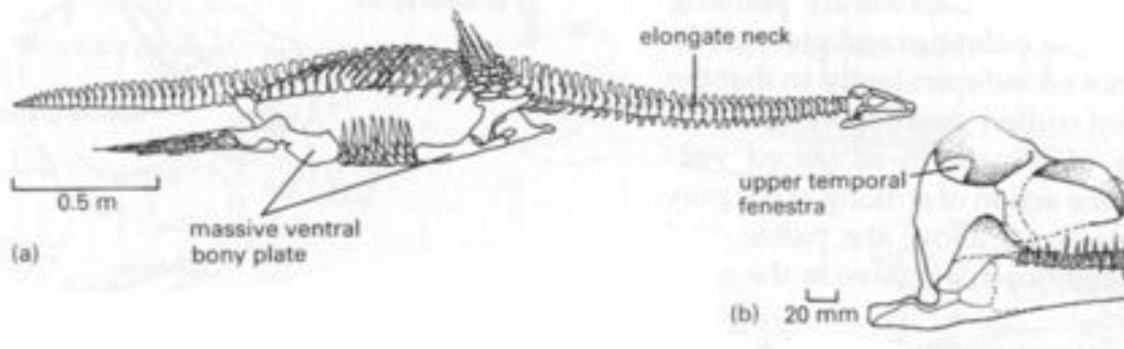


Pistosaurus

Cryptocleidus

Pachypleurosaurus

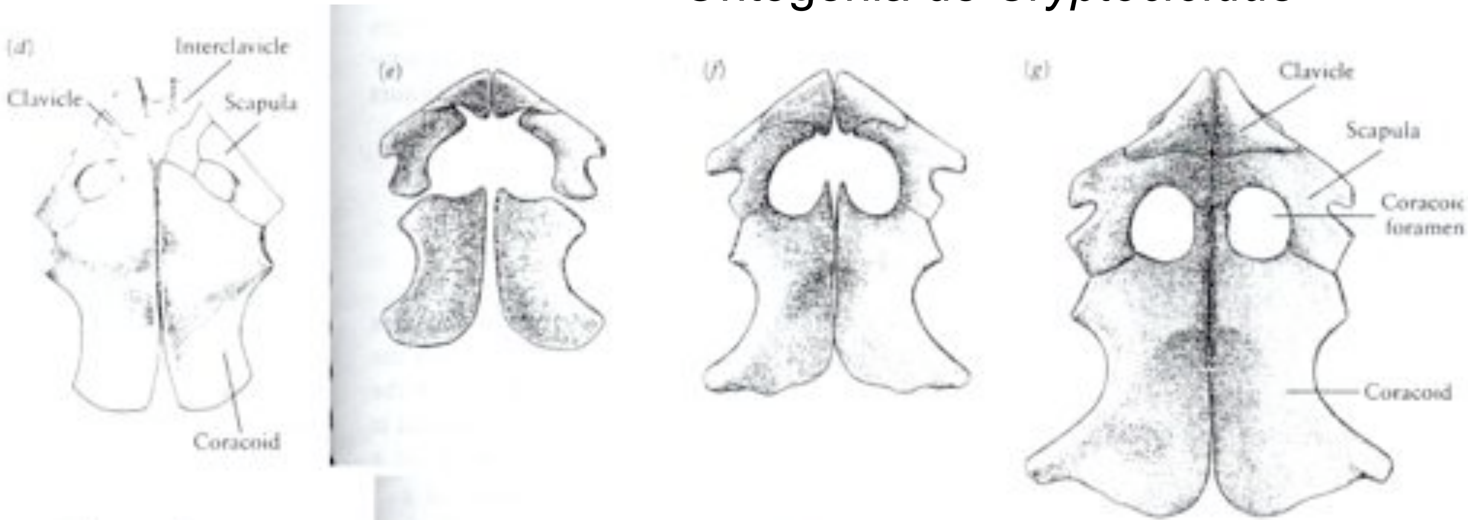




Cinturones pectorales : recapitulación ontogenética en el proceso de extensión hacia medial de las escápulas

Plesiosaurus

Ontogenia de *Cryptocleidus*



Húmeros

Pistosaurus

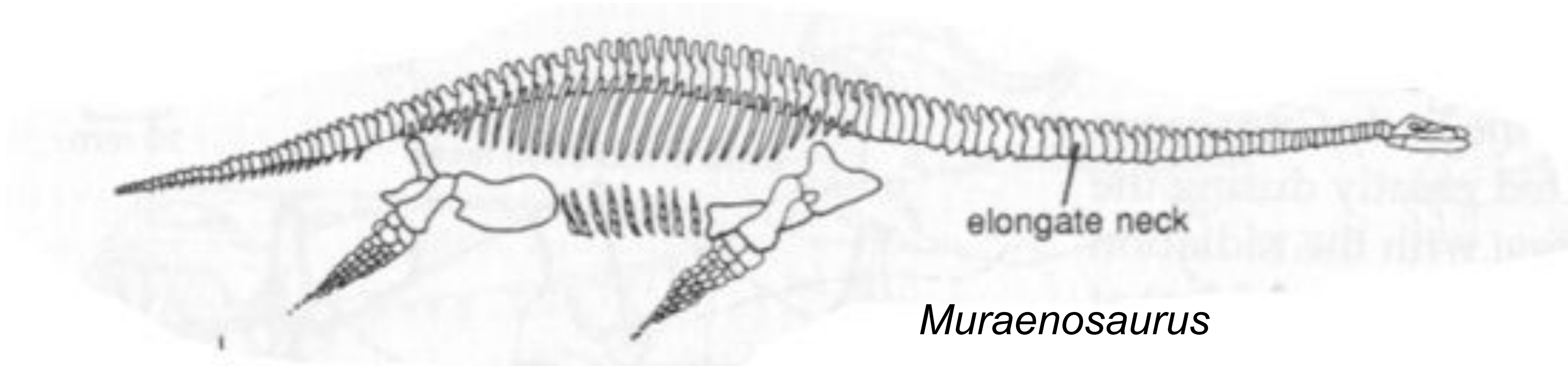
Plesiosaurus

Muraenosaurs

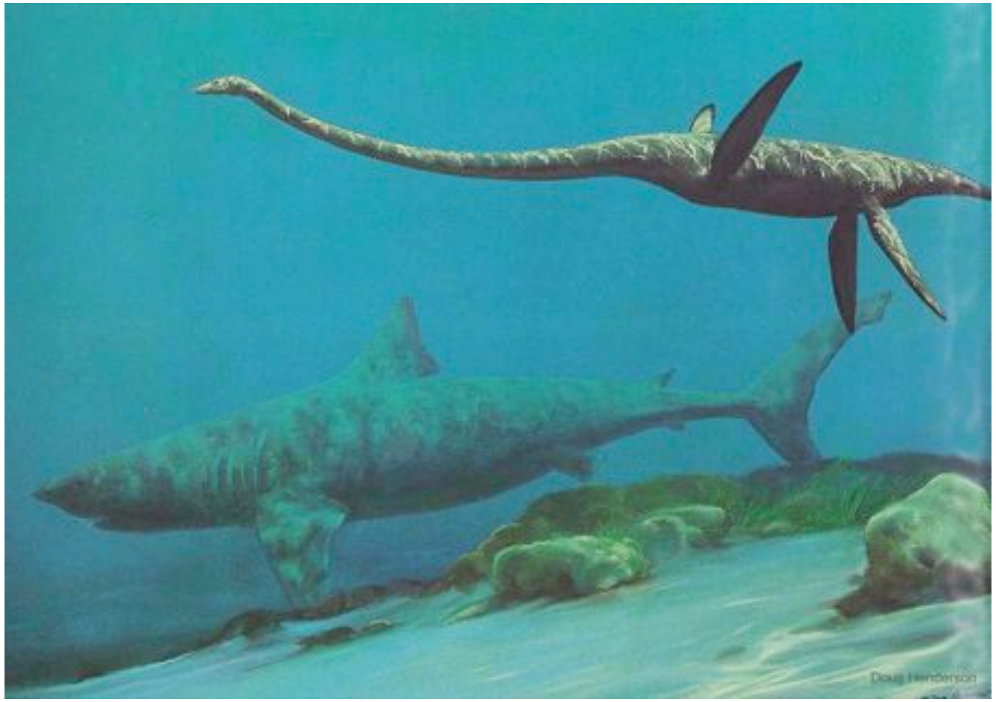
Expansión del extremo distal

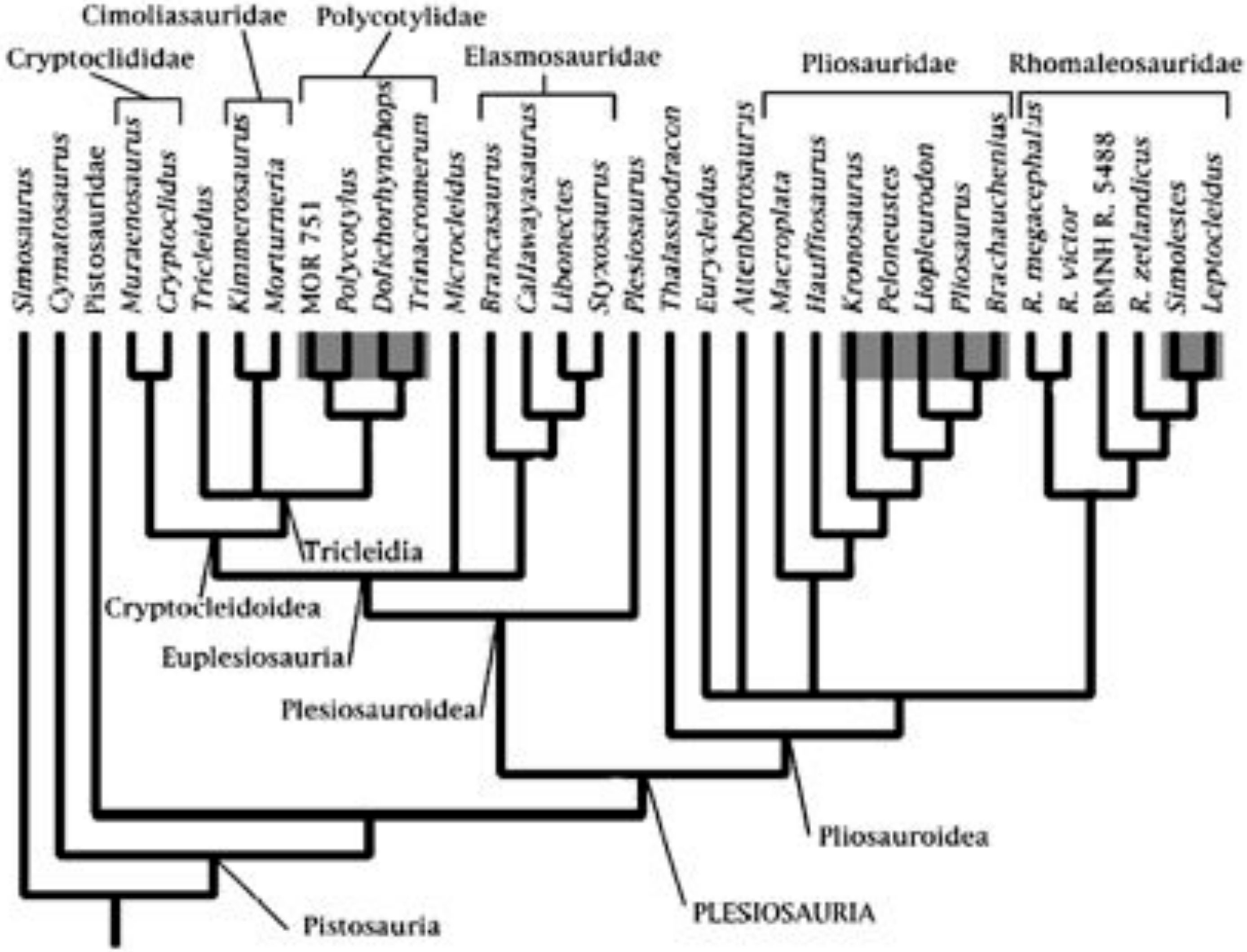
Plesiosauria: Elasmosauridae

Los elasmosauridae presentan cuellos extremadamente alargados, con hasta 76 vértebras



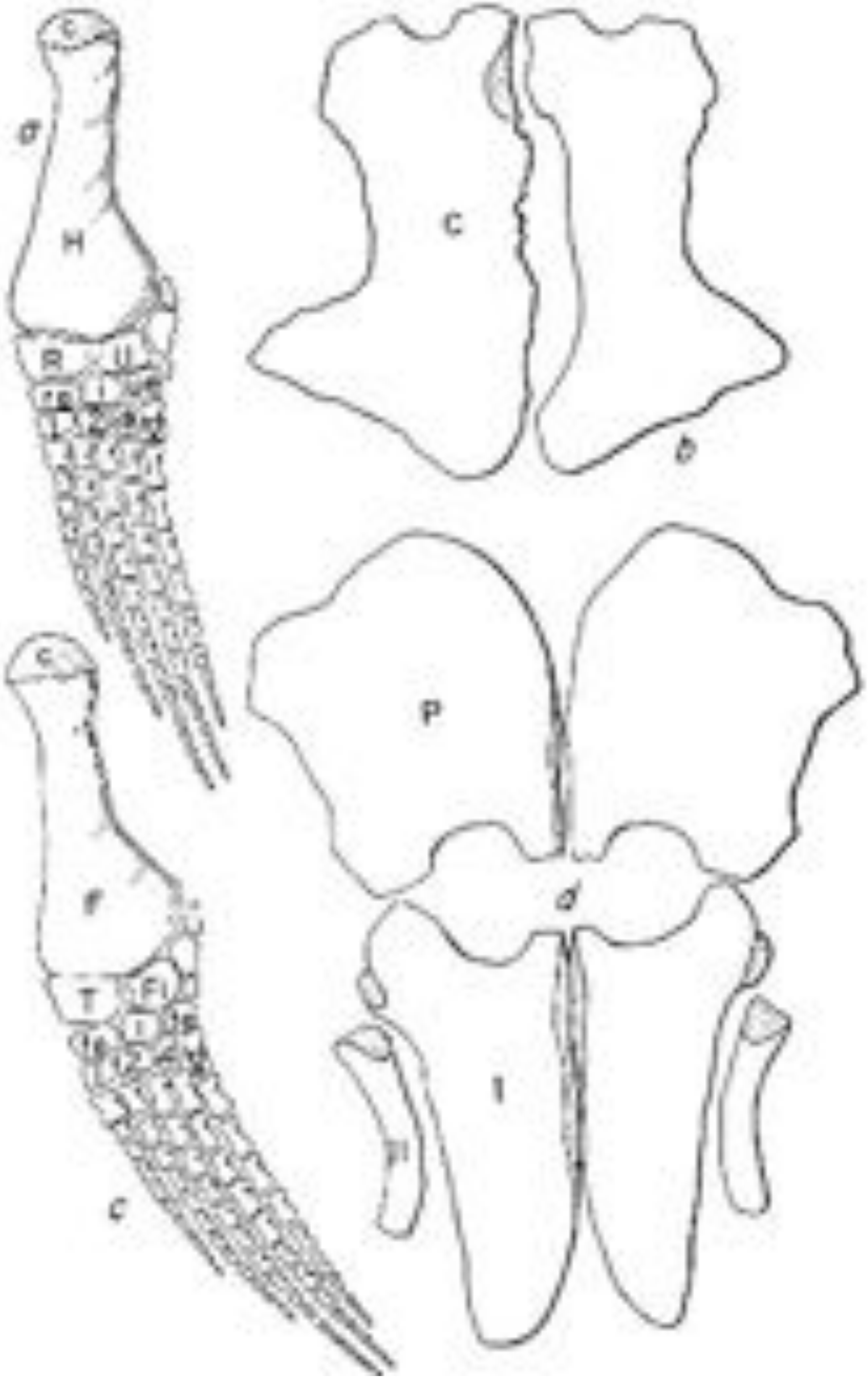
Muraenosaurus

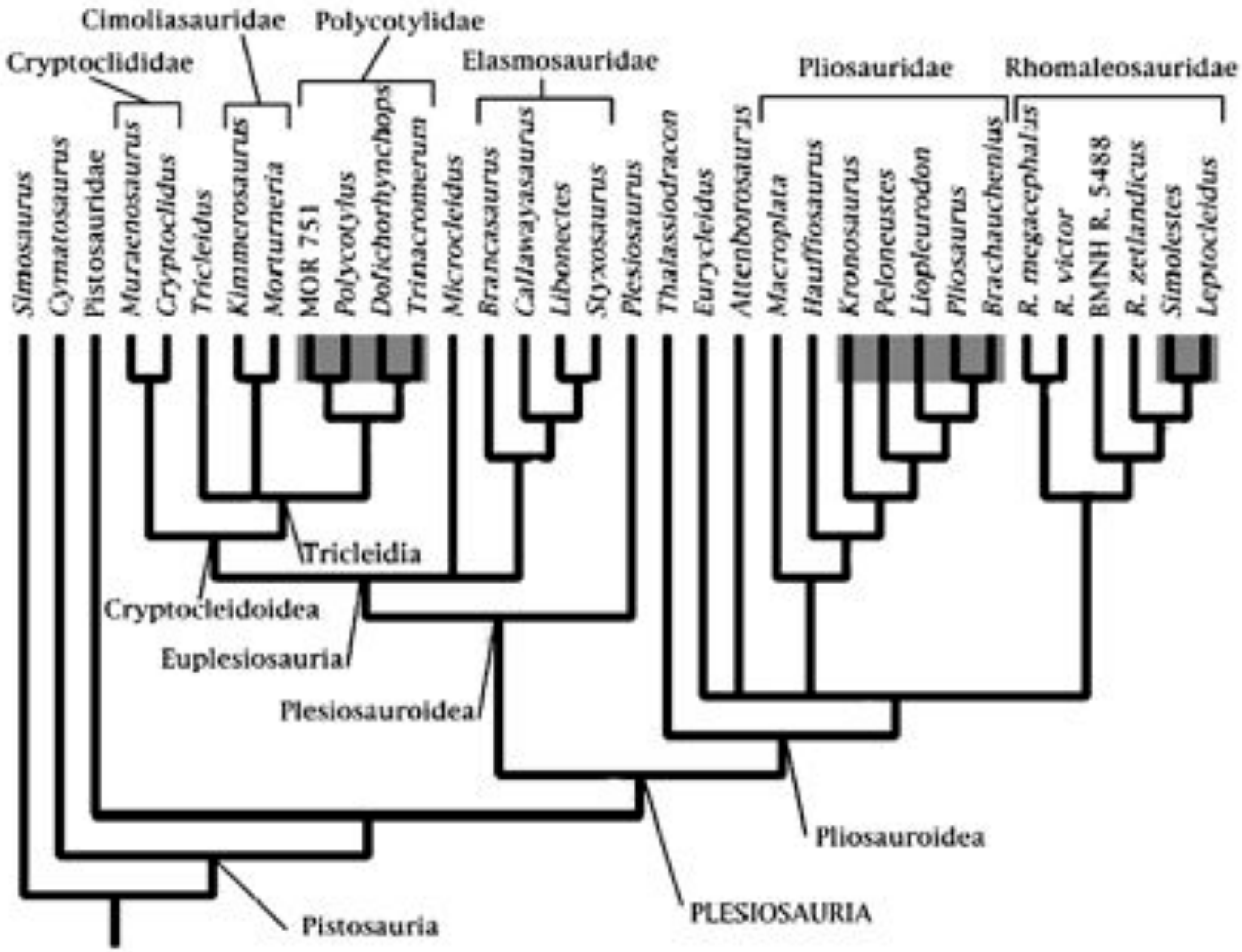



Cimoliasauridae
Polycotylidae
Cryptoclididae
Elasmosauridae
Pliosauridae
Rhomaleosauridae
Simosaurus
Cymatosaurus
Pistosauridae
Muraenosaurus
Cryptoclidus
Tricleidus
Kimmerosaurus
Morturneria
MOR 751
Polycotylus
Dolichorhynchops
Trinacromerum
Microcleidus
Brancasaurus
Callawayasaurus
Libonectes
Styxosaurus
Plesiosaurus
Thalassiodracon
Eurycleidus
Attenborosaurus
Macroplata
Hauffiosaurus
Kronosaurus
Peloneustes
Liopleurodon
Pliosaurus
Brachauchenius
R. megacephalus
R. victor
BMNH R. 5488
R. zetlandicus
Simolestes
Leptocleidus
Tricleidia
Cryptocleidoidea
Euplesiosauria
Plesiosauroidea
Pliosauroidea
PLESIOSAURIA
Pistosauria

Familia Polycotylidae
Dolichorhynchops osborni

Dolichorhynchops



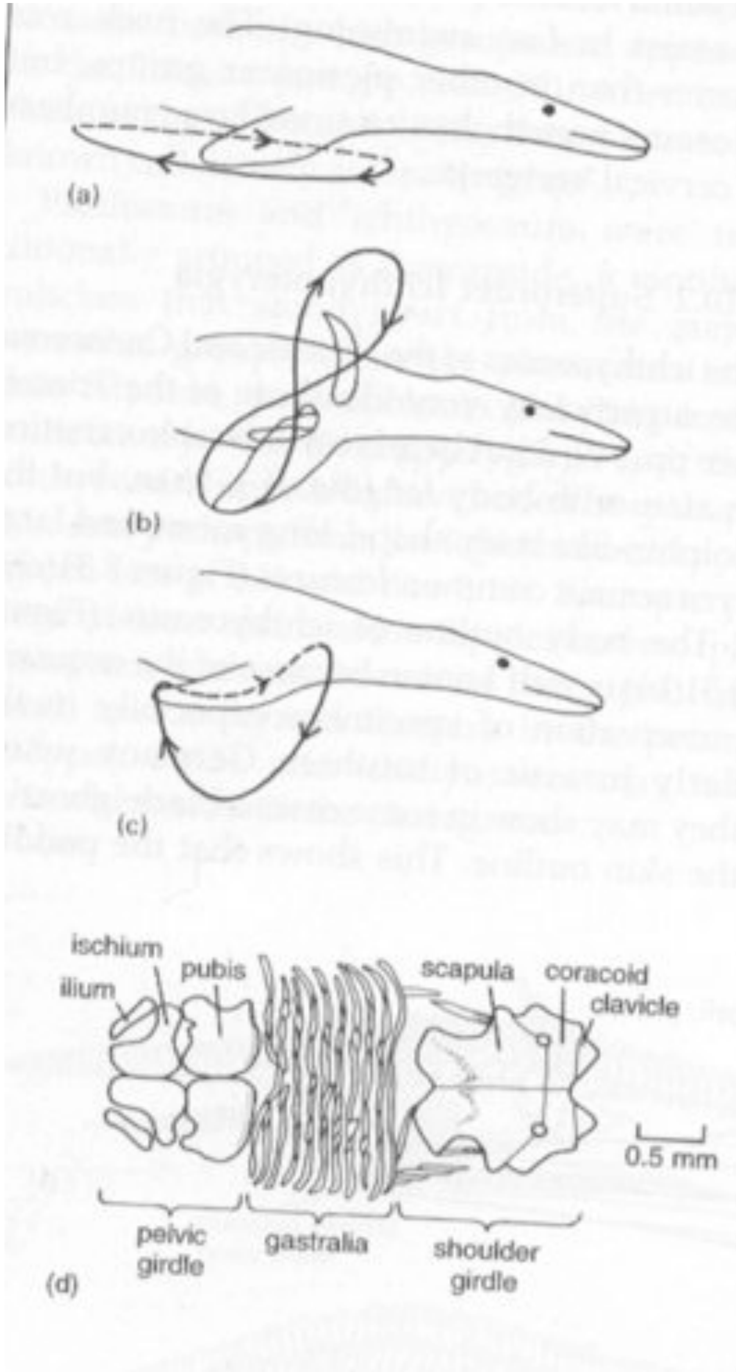


Cimoliasauridae
Polycotylidae
Cryptoclididae
Elasmosauridae
Pliosauridae
Rhomaleosauridae
Simosaurus
Cymatosaurus
Pistosauridae
Muraenosaurus
Cryptoclidus
Tricleidus
Kimmerosaurus
Morturneria
MOR 751
Polycotylus
Dolichorhynchops
Trinacromerum
Microcleidus
Brancasaurus
Callawayasaurus
Libonectes
Styxosaurus
Plesiosaurus
Thalassiodracon
Eurycleidus
Attenborosaurus
Macroplata
Hauffiosaurus
Kronosaurus
Peloneustes
Liopleurodon
Pliosaurus
Brachauchenius
R. megacephalus
R. victor
BMNH R. 5488
R. zetlandicus
Simolestes
Leptocleidus
Tricleidia
Cryptocleidoidea
Euplesiosauria
Plesiosauroidea
Pliosauroidea
PLESIOSAURIA
Pistosauria

Pliosauridae

Kronosaurus

Los pliosauridae poseían cabezas gigantescas (hasta 3m), cuellos más cortos (hasta tan sólo 13 vértebras). La unión de las ramas mandibulares (symphisis) es muy extensa.



“Remar bajo el agua”, como los patos

“volar bajo el agua”, como los pingüinos

“Estilo intermedio”, León marino

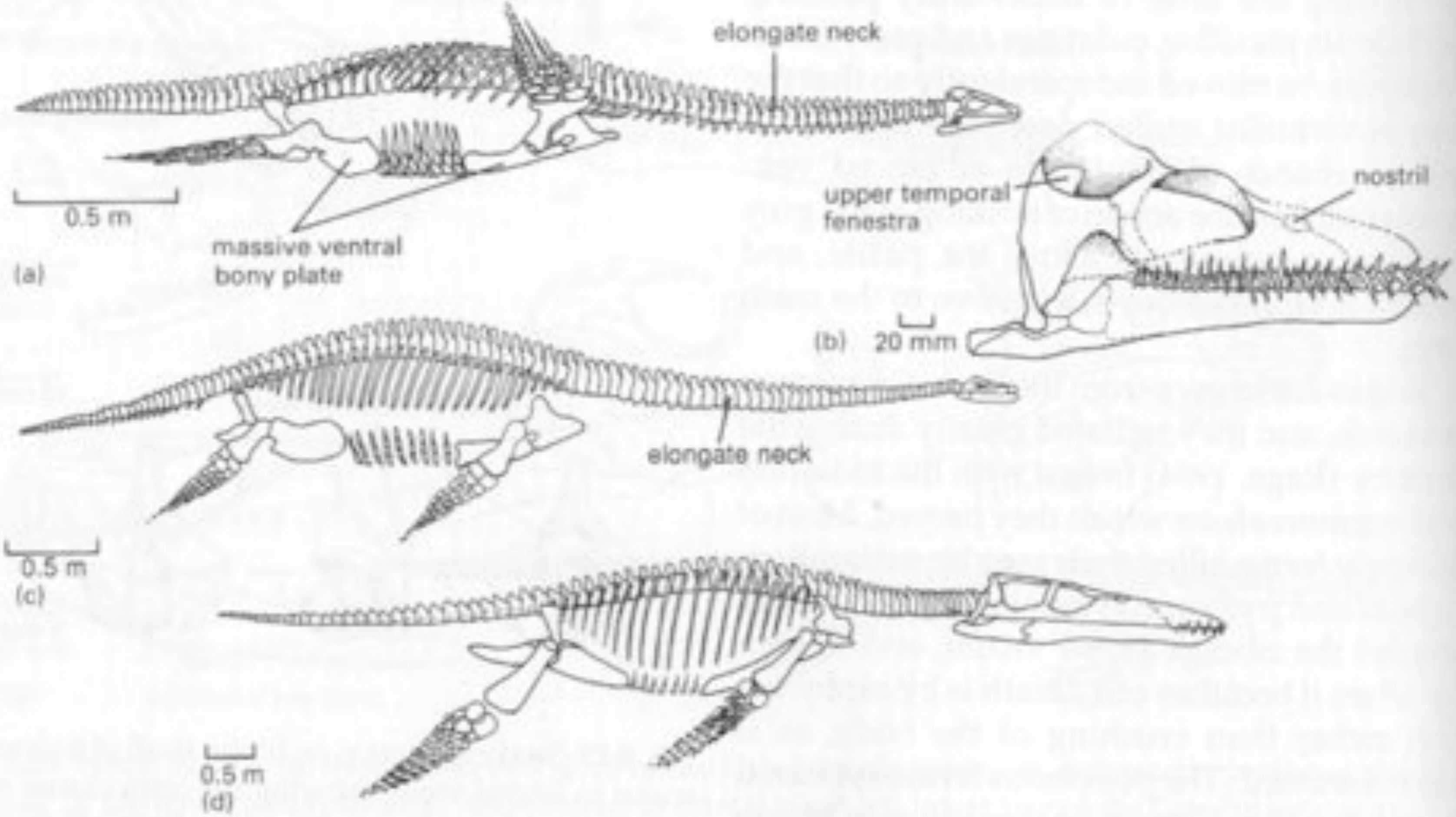
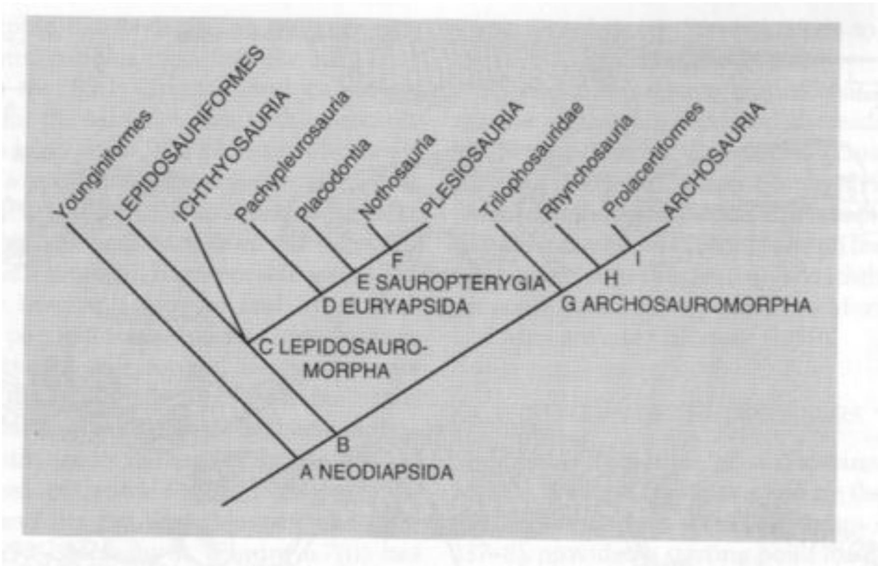
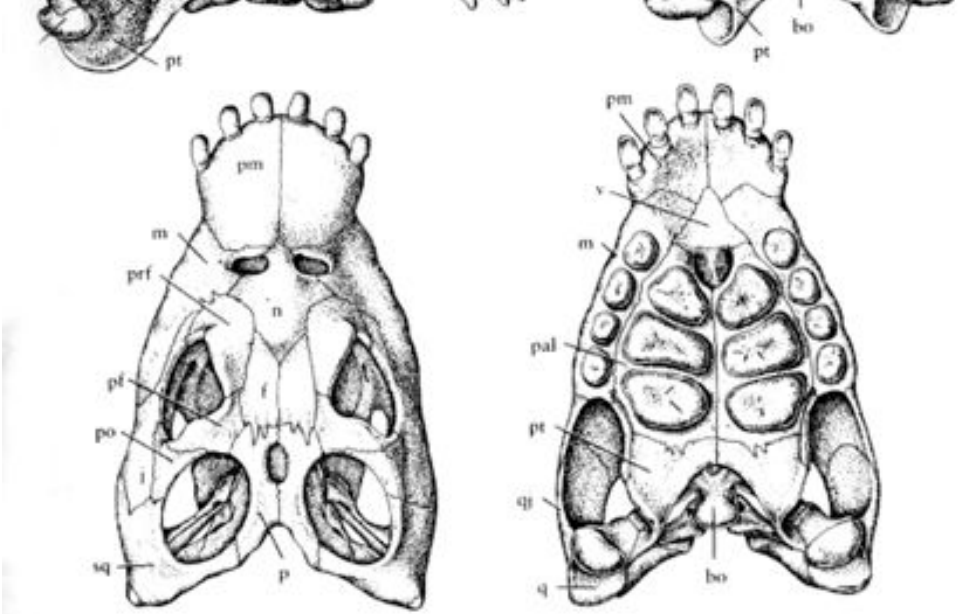


Fig. 8.30 The plesiosaurs: (a, b) the Late Jurassic cryptoclidid *Cryptoclidus*, skeleton in swimming pose and skull in lateral view; (c) the Late Jurassic elasmosaur *Muraenosaurus*; (d) the Late Jurassic pliosaur *Liopleurodon*. [Figures (a, b) after Brown, 1981; (c, d) after Robinson, 1975.]



•Los placodontes son conocidos en el Triásico Medio y Superior de Europa, áfrica del Norte y Medio Oriente. El cuerpo es robusto y si bien no presenta grandes adaptaciones para la vida acuática la reducción de la osificación de cinturas y articulaciones revela la disminución de la locomoción terrestre. En el género *Henodus* el cuerpo se encuentra protegido por una armadura dérmica. Los placodontes fueron malacófagos según se desprende de su particular dentición.



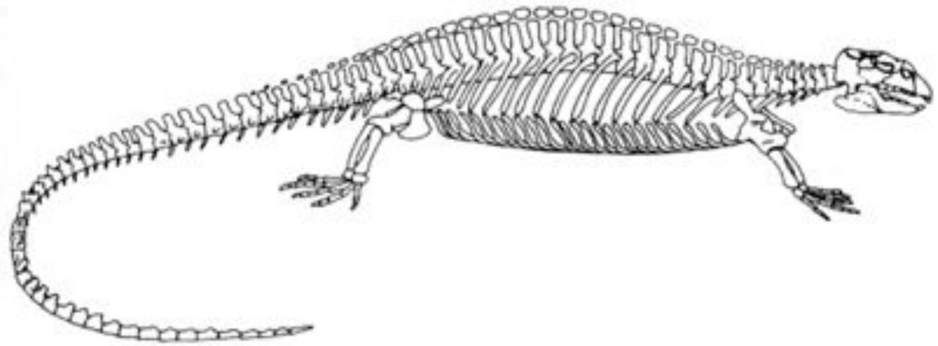


Figure 12-19. *HELVETICOSAURUS*, A PRIMITIVE PLACODONT IN WHICH THE MARGINAL TEETH ARE NOT CRUSHING PLATES. There is no trace of dermal armor. The specimen is approximately 2 meters long. *From Peyer, 1955.*

Algunos placodontes evolucionaron caparazones protectoras

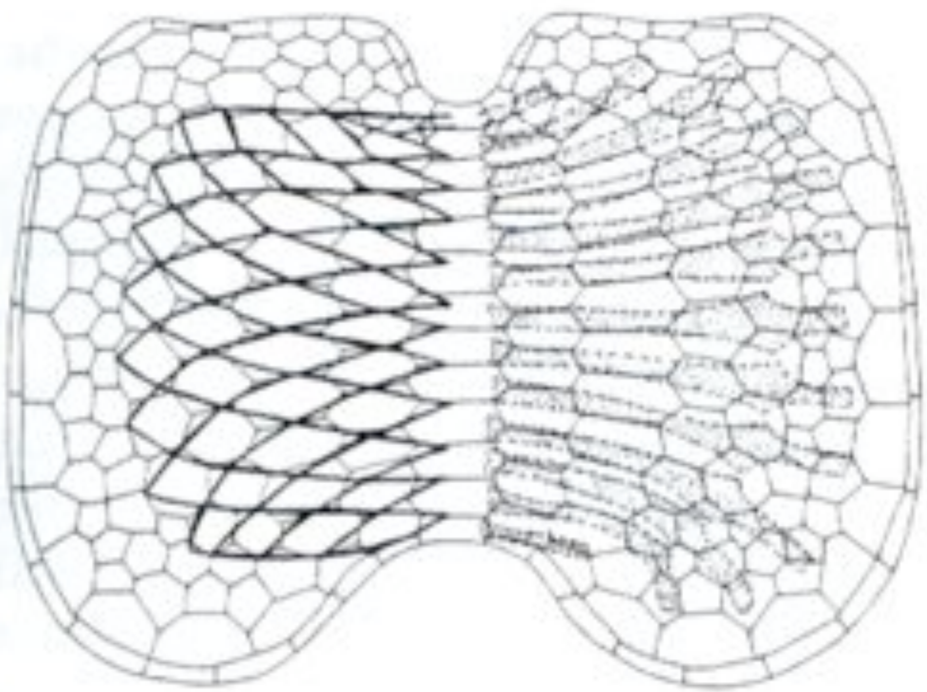
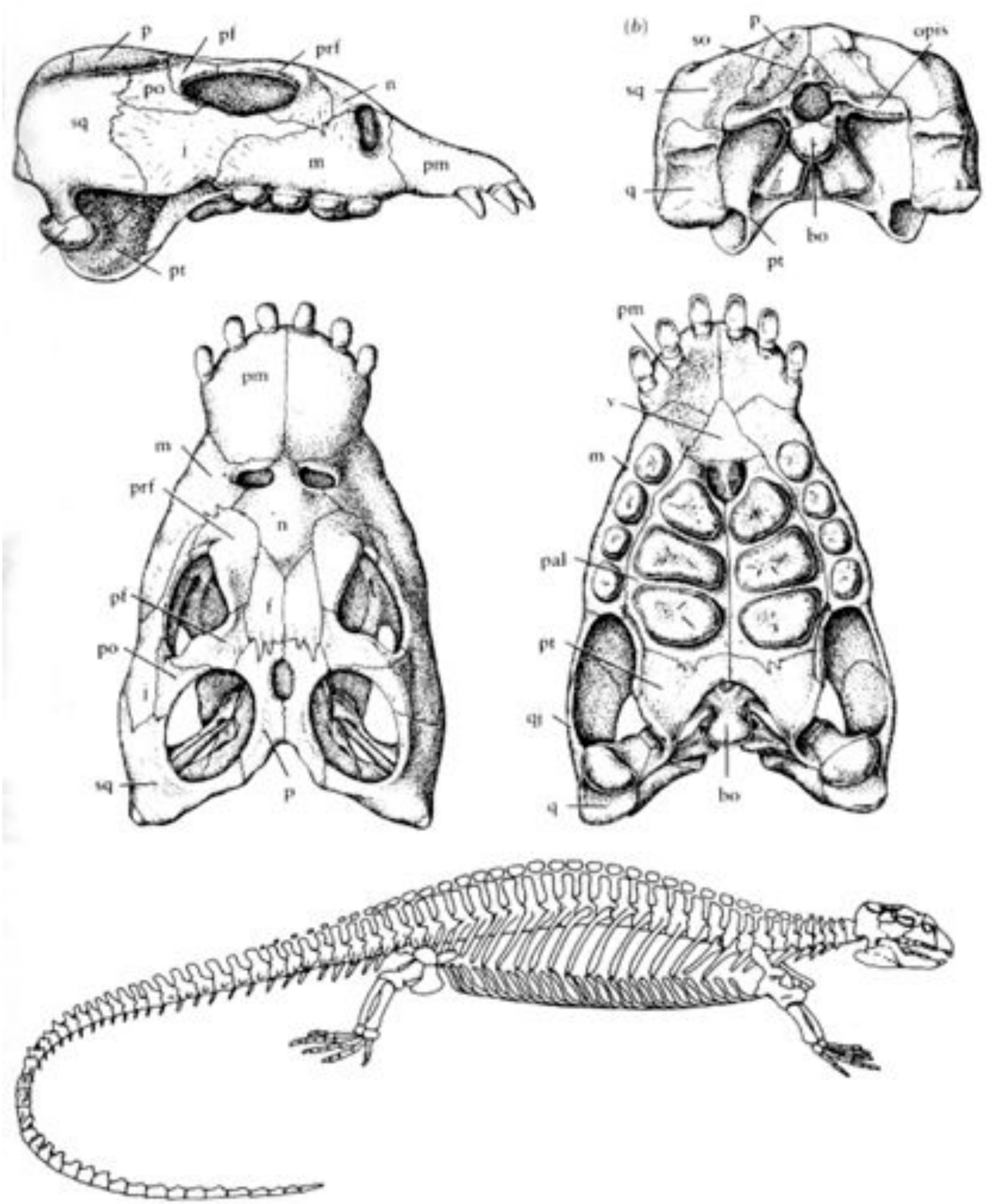


Figure 12-18. DORSAL ARMOR OF THE PLACODONT *HENODUS*. Irregular polygons show the pattern of the dermal armor. Heavier lines on the left show the pattern of overlying epidermal scutes. Stippled bars on the right represent the underlying ribs. The carapace reached approximately 1 meter in width. *Redrawn from Westphal, 1976.*

Los placodontes son exclusivamente triásicos y abundan en el triásico medio de Europa. Sus restos se encuentran en depósitos marinos de baja profundidad. Un arreglo de gastralia muy pesadas se ubica ventralmente, al igual que en Nothosauria y Pachypleurosauria.
La dentadura presenta incisivos espatulados, y pesados y durísimos dientes globulares en el palatino, maxilar y dentario. El dentario presenta un proceso ascendente y la mandíbula presenta una configuración de “cascanueces” con la línea de los dientes ubicada por debajo de la articulación con el cráneo



Los placodontes se caracterizan por tener vértebras anficélicas con largos procesos transversales

propulsion.

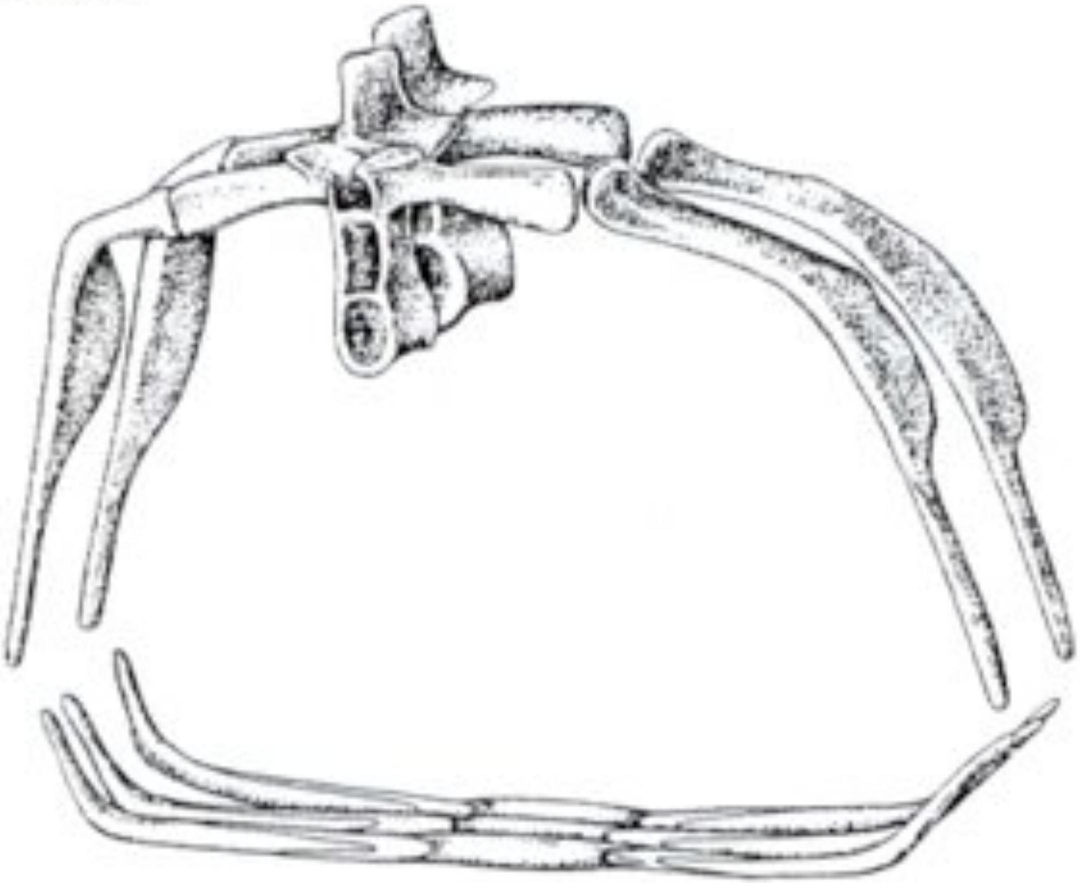


Figure 12-16. VERTEBRAE, RIBS, AND GASTRALIA OF THE PLACODONT *PARAPLACODUS*. This genus shows the long transverse processes and deeply amphicoelous centra that are characteristic of this group. *From Peyer, 1935.*

Las cinturas de las extremidades presentan articulaciones poco desarrolladas (profundas) de acuerdo a una locomoción más acuática que terrestre.

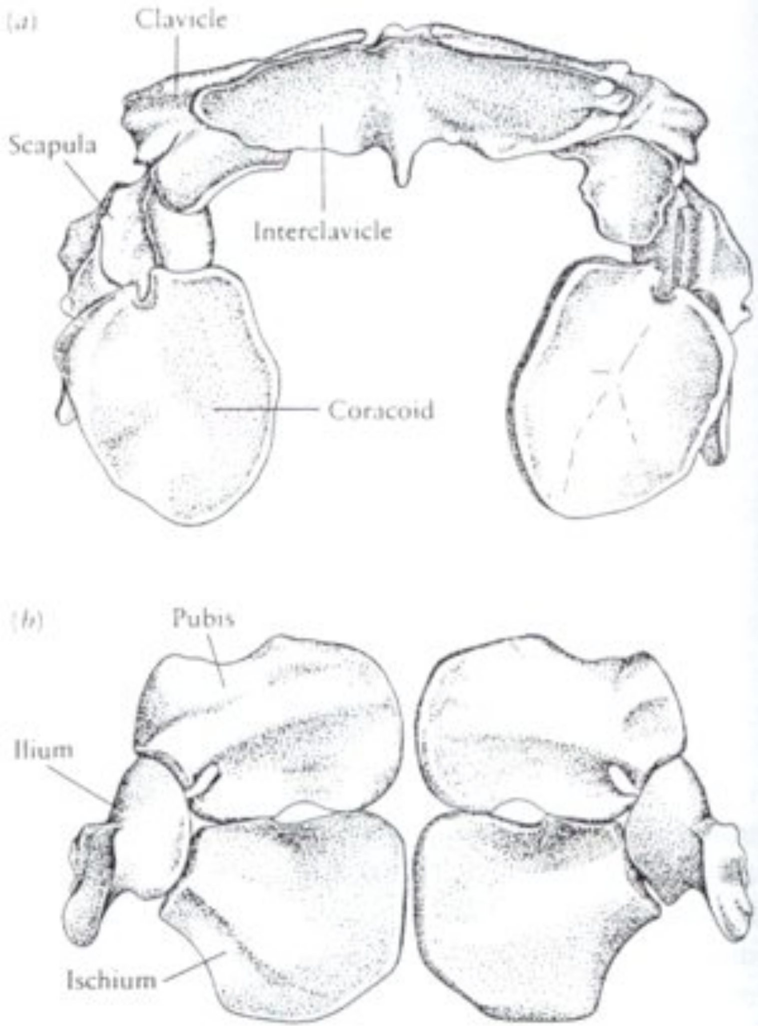
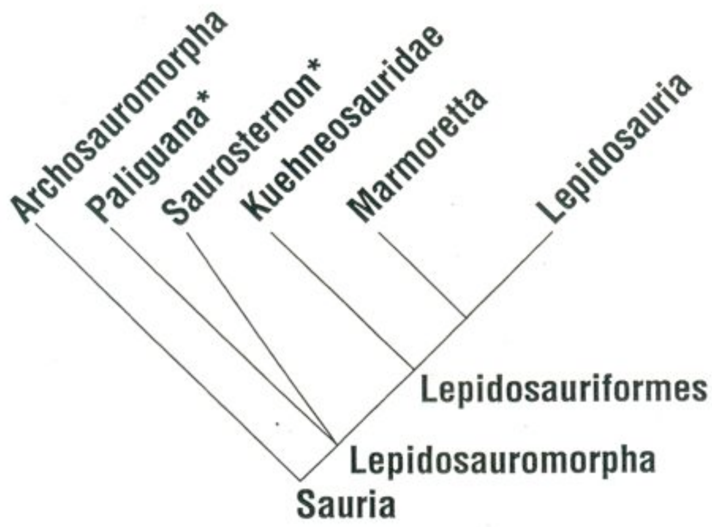


Figure 12-17. (*a*) Pectoral girdle of *Placodus* in ventral view. As in nothosaurs, the interclavicle broadly underlies the clavicle. (*b*) Pelvic girdle in dorsal view. It is primitive in lacking large thyroid fenestrae. *From Peyer and Kuhn-Schnyder, 1955.*

Verdaderos Diápsidos (corona), tb llamados SAURIA

-Tímpano proceso retroarticular.

-Disparidad de pierna, más larga que el brazo. Bipedismo facultativo.

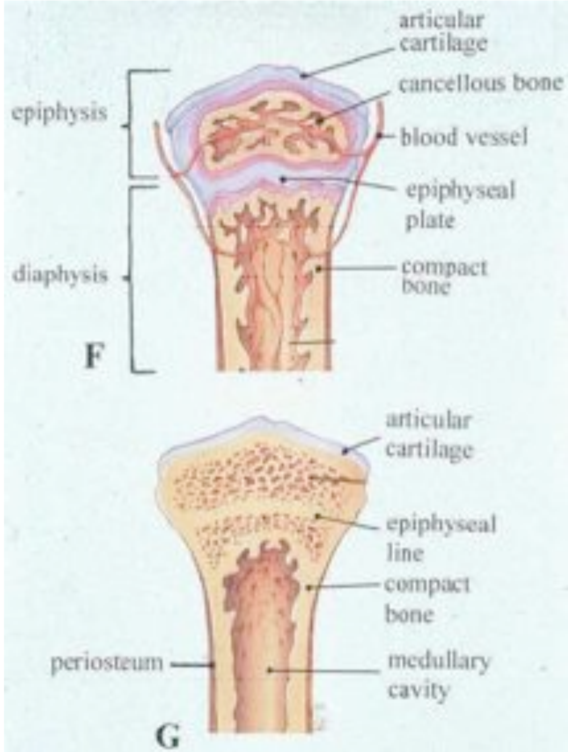


Los Diápsidos modernos (Sauria) se dividen en Archosauromorfa (cocodrilos y aves) y Lepidosauromorfa (lagartos y serpientes). Los
Lepidosauromorfos: Más cercanos a Lepidosauria que a Arcosauria
Arcosauromorfos: Más cercanos a Arcosauria que a Lepidosauria

Lepidosauria (corona): descendientes del ACMR del Tuatara y serpientes (u otro squamata)

Lepidosauromorpha

Stem Lepidosauria: *Paliguana, Saurosternon*. Pérdida de la barra temporal inferior
Cuadrado modificado para timpano.
En *Saurosternon* aparecen las EPIFISIS, centros de osificacion secundarias en los extremos de los huesos largos (convergentemente adquiridos por mamiferos y lepidosauria)



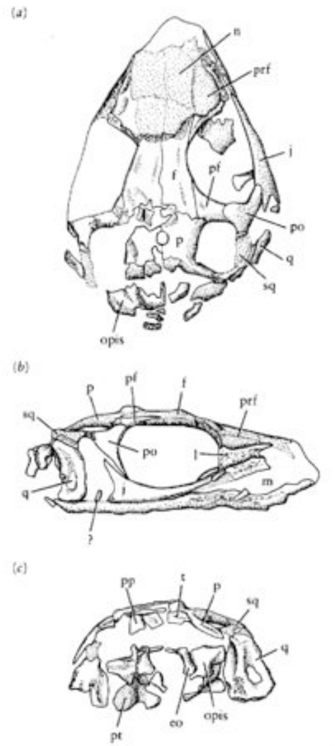
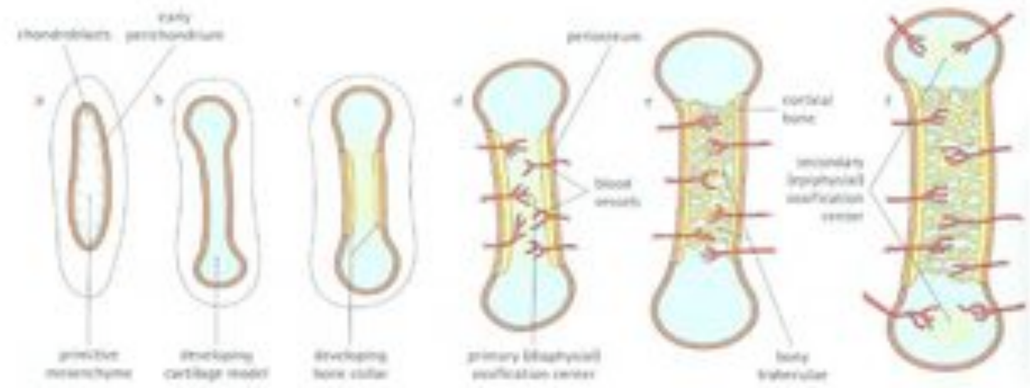
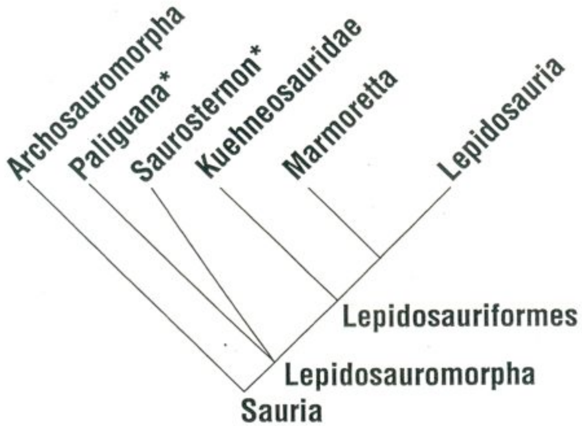
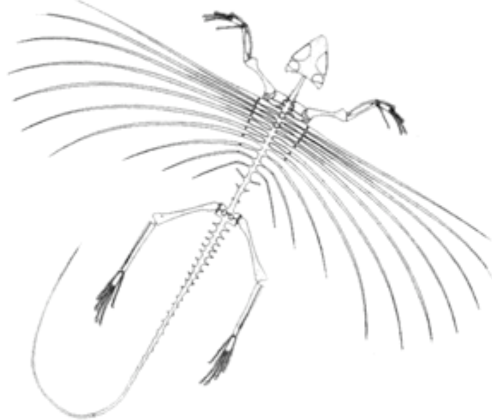


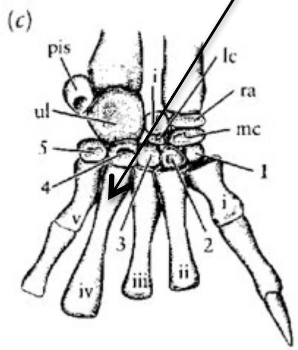
Figure 11-22. SKULL OF THE EARLIEST KNOWN LIZARD *PALIGUANA*. From the Upper Permian of southern Africa. (*a*) Dorsal, (*b*) lateral, and (*c*) occipital views, ×2. Abbreviations as in Figure 8-3. *From Carroll, 1977.*



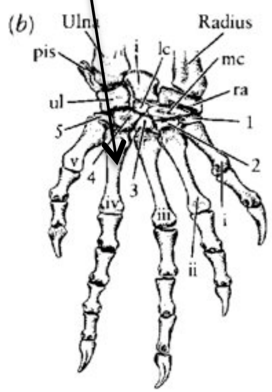




Lepidosauriformes: Los KUEHENEOSAURIDAE planeadores!:
-acortamiento metacarpo 4 (mano más simétrica)
-fenestra pélvica ("thyroidea")
-prefontral conecta el techo del cráneo con el paladar (tb en tortugas! convergencia)
-maxilar forma parte del margen de la órbita



Saurosternon



Tuatara

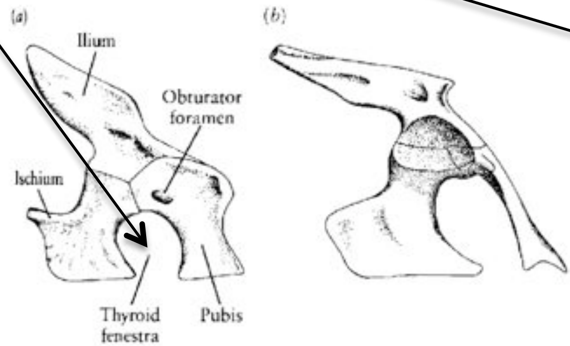


Figure 11-15. PELVES OF LEPIDOSAURS. (*a*) Pelvis of the Upper Triassic sphenodontid *Planocephalosaurus. From Fraser and Walkden, 1984.* (*b*) Pelvis of *Iguana*. In both sphenodontids and modern lizards, there is a large opening ventrally between the pubes and ischia, the thyroid fenestra. This opening may have evolved in the common ancestor of these two groups or independently after their divergence. A thyroid fenestra evolves separately in several other groups of diapsid reptiles.

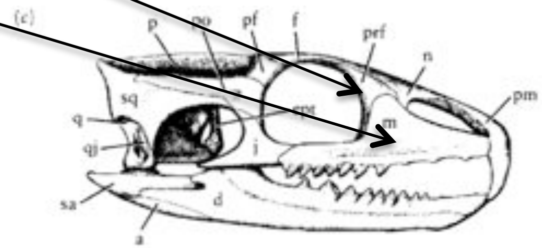
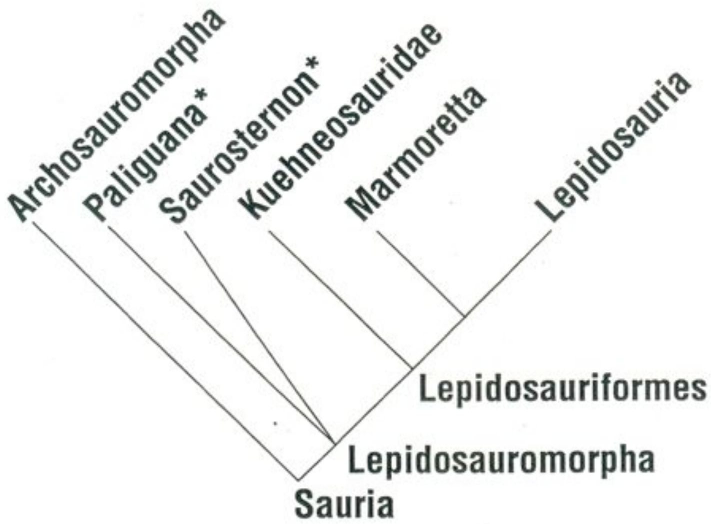


Figure 11-20. SKULL OF THE PRIMITIVE PLEUROSAUR *PALEO-PLEUROSAURUS*. (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views. Note similarity to *Sphenodon* (see Figure 11-17). Abbreviations as in Figure 8-3. *From Carroll, 1985.*

Lepidosaurio
(tuatara marina)

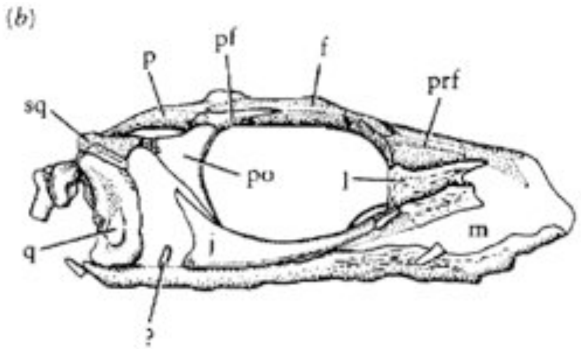


MARMORETTA: más Lepidosauriano aún!

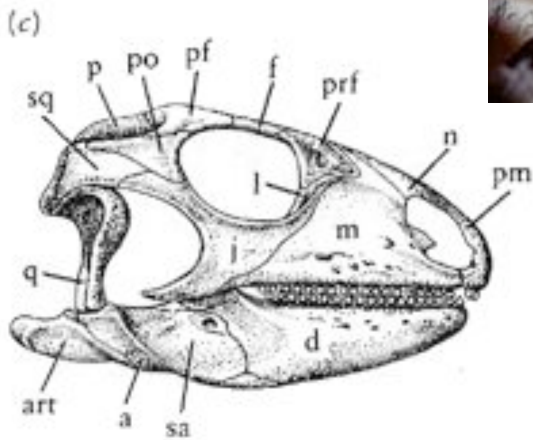
-Perdida de los dientes en el proceso transversal del pterygoide
-Lacrimal confinado a la orbita

-Dientes de implantación pleurodonta

Figure 1. Five major types of tooth implantation, and several variations of them, are recognized in amniotes. After Romer (1956) and Edmund (1960).



Paliguana



Teiidae (squamata)

LEPIDOSAURIA

7000 ESPECIES, ½ son serpientes Caenophidias (los “teleosteos” de Lepidosauria)

Frecuentemente considerados como “aproximación” a ancestro de mamíferos. Obviamente falso.

Ej. Evolución de la articulación dentario-escamosa de mamíferos sería imposible, ya que en Lepidosauria sólo hay articulacion cuadrado-articular.

Esto es una especialización de Lepidosauria: la condición plesiomórfica (presente en tortugas y ancestros de los mamíferos) tiene articulación doble en la mandíbula (Lado interno, aticular, lado externo, surangular) por lo que la articulación cuadrado-articular pudo perderse manteniendo la funcionalidad (los mamíferos elaboraron la articulacion externa, mientras que los huesos internos pasaron al oido medio).

Algunas synapomorfías:

-Tajo cloacal transvero (en vez de longitudinal)
-El riñon es postcloacal (base de la cola) y la galndula adrenal se ubica en el mesenterio gonadal
-reambio completo de la piel (en vez de continuo desgaste/generacion)
-Cola frágil, regenerable
-Fila de espinas mediales sobre el dorso
-Captura de presas pequeñas usando la lengua

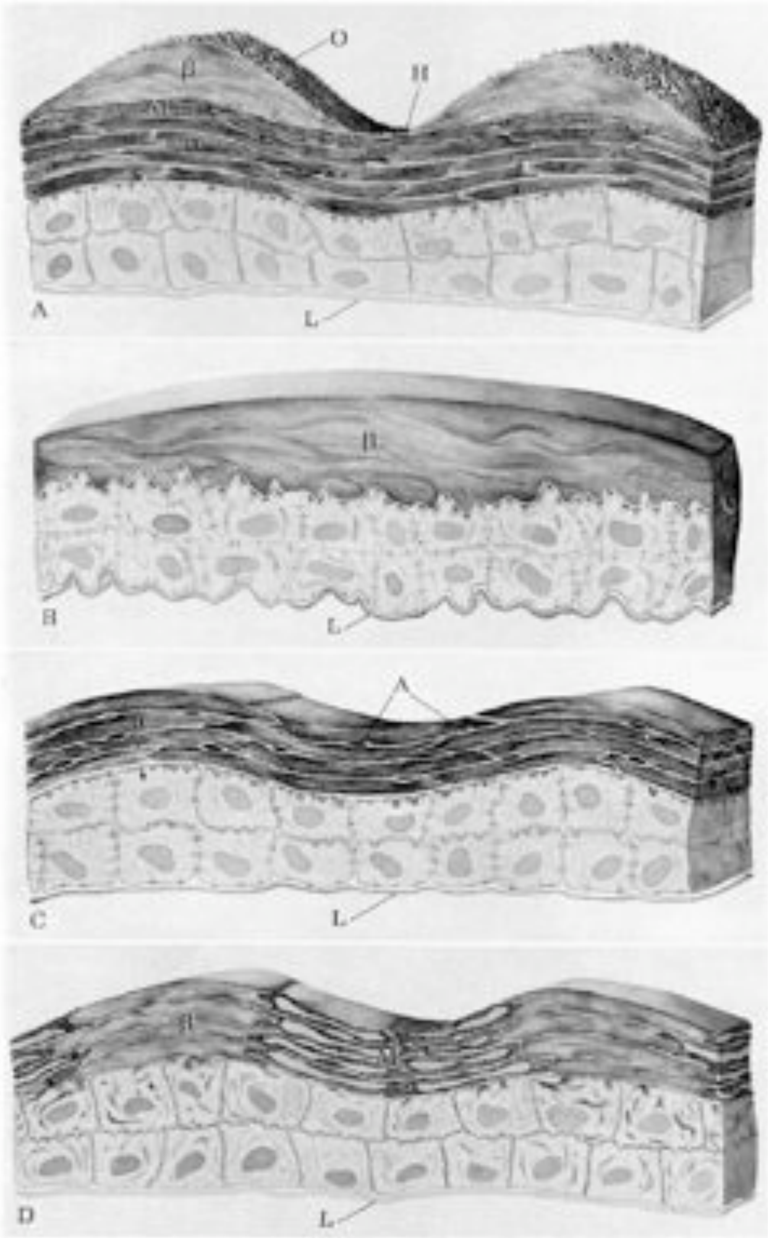
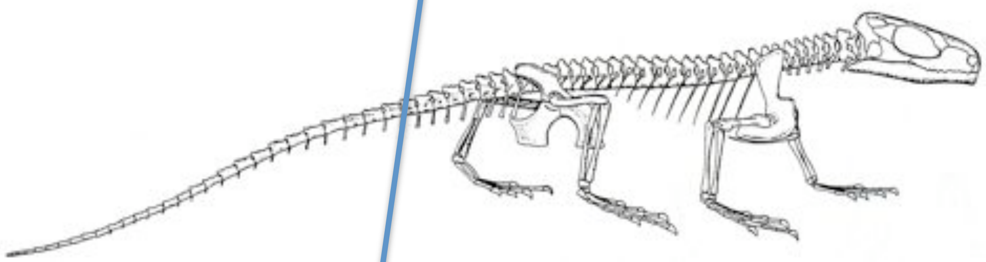


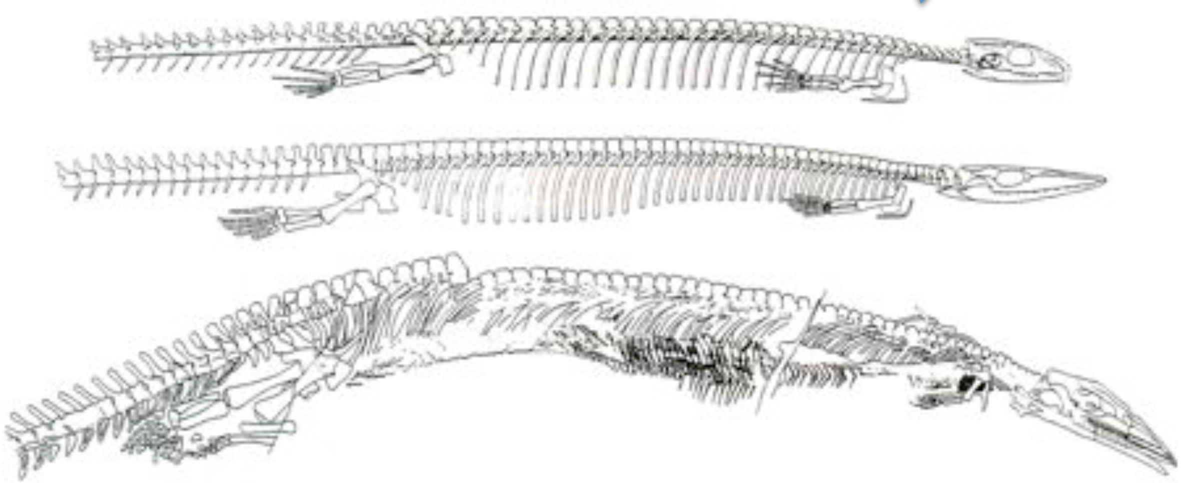
Fig. 1A—D

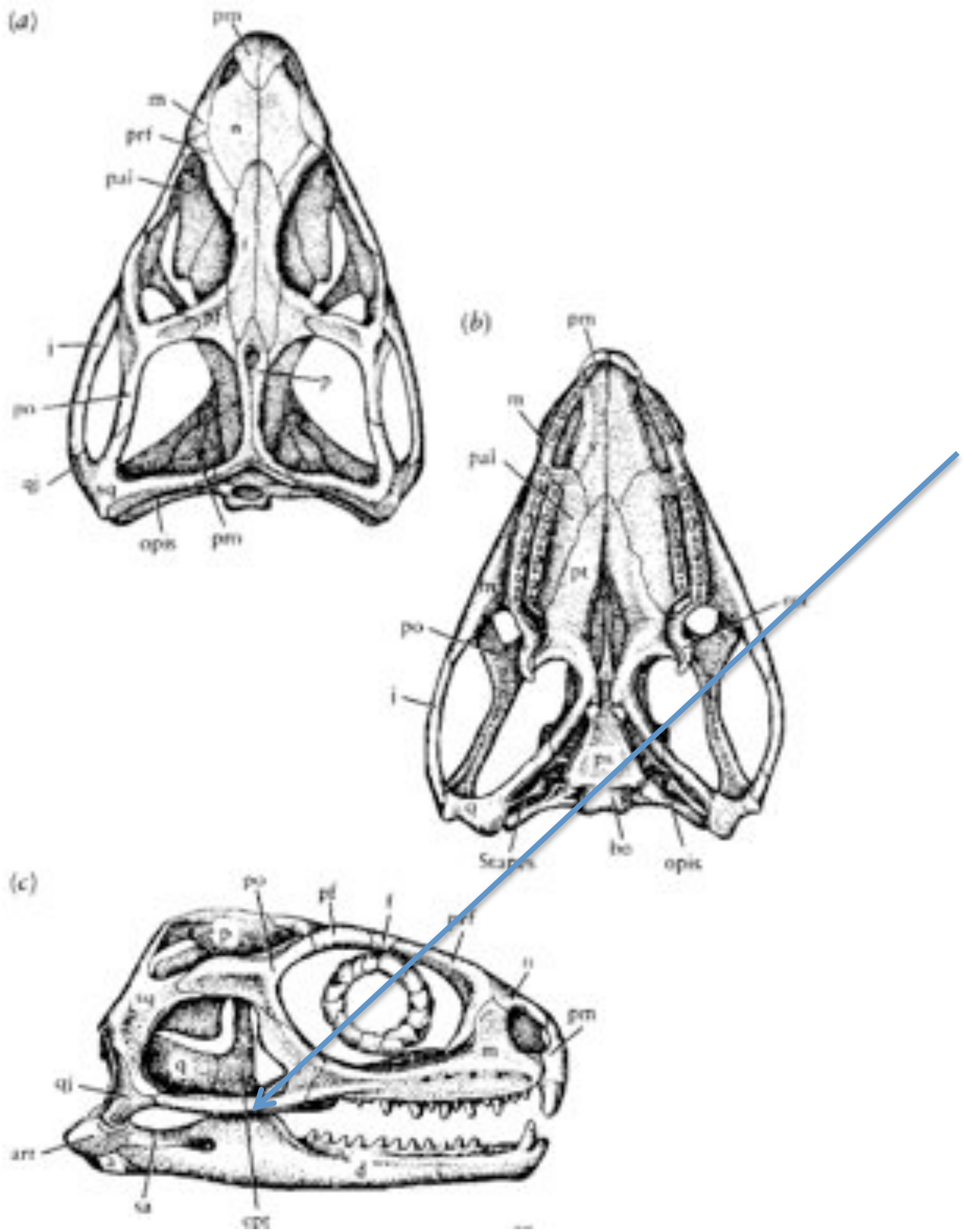
-En Lepidosauria, la epidermis de las escamas presenta capas sobrepuestas de beta queratinas sobre alfa queratinas. En otros reptiles se encuentran alternadas.

Fig. 1 A—D. Diagram of the types of epidermis found in the different orders of reptiles. A. The skin of Squamates is composed of a series of layers. The spinule covered surface, called the Oberhäutchen (*O*), rests upon a thick compacted β layer (β) that disappears in the hinge regions (*H*). Beneath the β layer is a thin layer of flattened cells called the mesos (*M*), which rests upon the α layer (α). Cellular outlines are not apparent in the β layer but are in the α layer. The living stratum beneath, in all groups, consists of cell layers which overlie a basal lamina (*L*). B. The shell of turtles is composed of only a β layer (β) which is firmly attached by means of desmosomes to the underlying living cells. C. The neck and leg skin of turtles is composed only of an α layer (α). Interspersed with desmosomal remnants are extracellular accumulations of PAS-positive material (*A*). D. The epidermis of crocodilians varies in composition with the center of the scale having the characteristics of a β layer (β) and the hinge region appearing much like a mesos layer (*M*), having characteristics of both α and β keratin. Crocodilians are unique among reptiles in possessing a granular layer which is particularly evident in the hinge region

Los Lepidosauria incluyen a Rhynchocephalia (Sphenodontidae, único representante viviente: el Tuatara de Nueva Zelandia) y Squamata (Lagartos y serpientes).
Los Rhynchocephalia fueron comunes del triasico tardio al jurasico (solo persistieron en el cretácico de sudamerica) evolucionaron una familia de formas acuáticas llamadas Pleurosauridae, que vivieron entre el jurásico temprano y el cretácico temprano. Ecologicamente diversas, con formas marinas: Pleurosauridae. Tras su declive, se diversifican los Squamata.







Rasgo posiblemente primitivo: aún presentan la barra temporal inferior.

Hilera de dientes mandibulares encaja entre dos hileras de dientes superiores.

La mandíbulas “serruchan” presas => pérdida del tímpano

SQUAMATA:

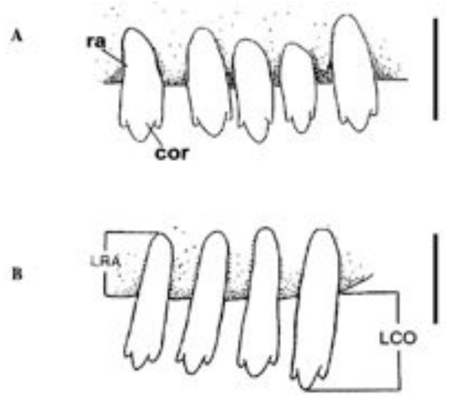
Los Squamata se dividen en Iguania y Scleroglossae.

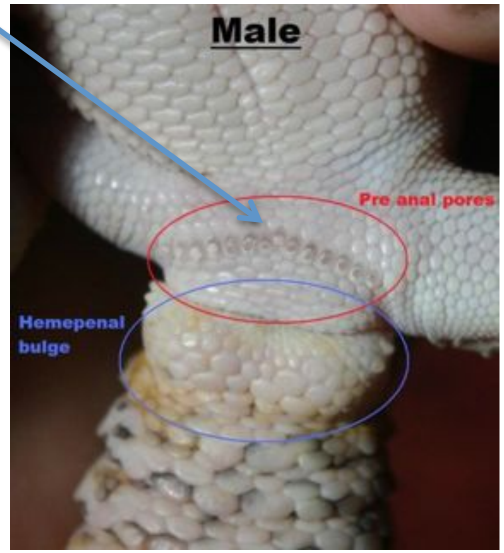
Iguania: todos los mas cercanos a una iguana que a una serpiente

Scleroglossae: todos los más cercanos a la serpiente a la iguana

Fig. 1. Representative squamates: top row (left to right), *Sphaerodactylus cinereus* (Sphaerodactylidae); *Cricosaura typica* (Xantusiidae); *Ameiva lineolata* (Teiidae); middle row, *Typhlops anousius* (Typhlopidae); *Anolis noblei* (Iguanidae); *Tropidophis maculatus* (Tropidophiidae); bottom row, *Epicrates angulifer* (Boidae); *Cadea blanoides* (Cadeidae); and *Uromacer oxyrhynchus* (Dipsadidae). Photos by S.B. Hedges.

SQUAMATA:
Hemipenes pareados evertibles
Dientes tricuspides
Poros femorales y preanales
Musculos de la garganta interdigitantes





Elaboración del vomeronasal:
-Cuerpos fungiformes, llenos de epitelio sensorial
-Rotado 90 grados respecto a Tuatara: el ducto del VN se proyecta hacia bajo en vez de hacia el lado para conectarse con el surco coanal. Se recapitula en la ontogenia
-dos “palllets” (?) bajo la punta “muescada’ de la lengua, usada en muestreo con la lengua.

SQUAMATA: Metakinesis y Streptostylia.

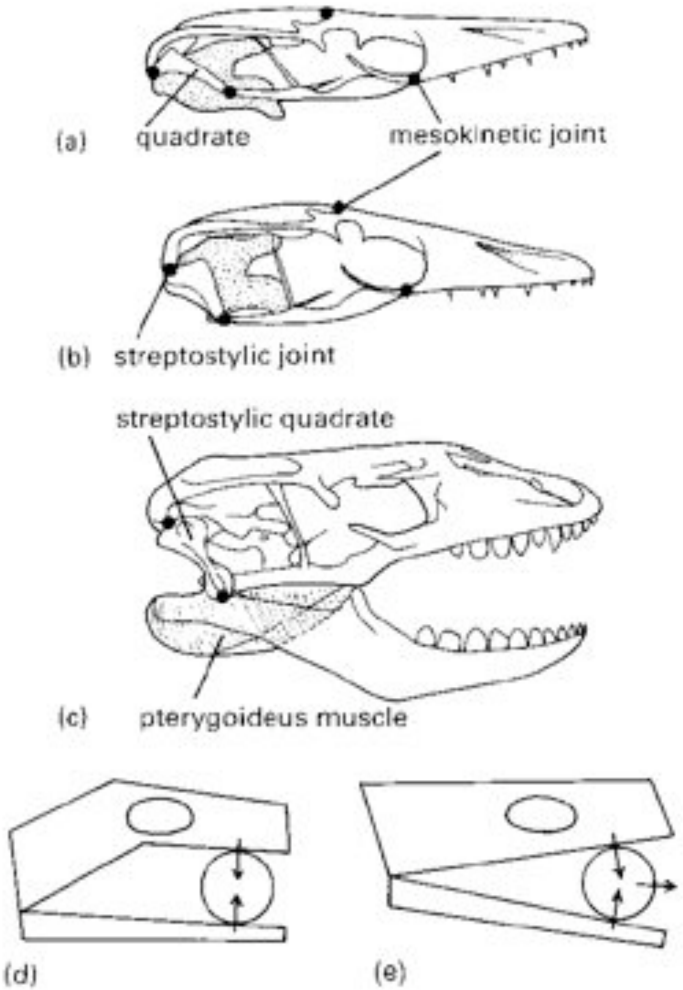
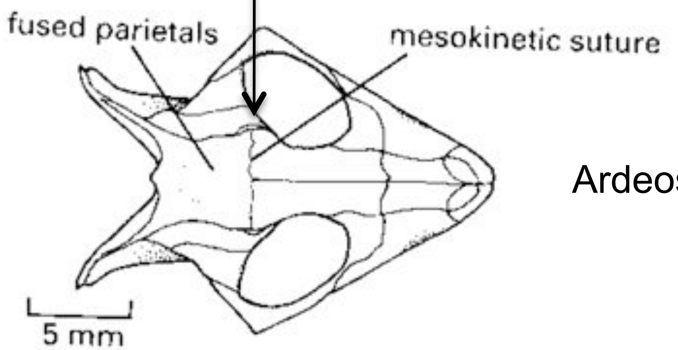


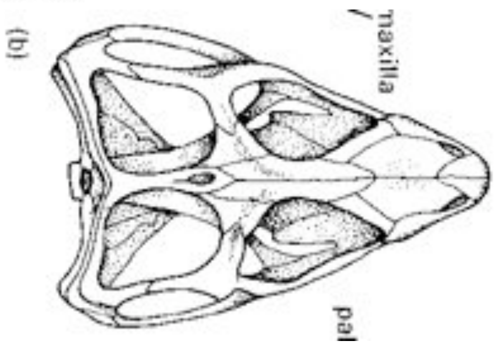
Fig. 8.32 Lizard jaw mechanics: (a, b) skull of *Varanus*, showing the skull flexed up (a) and (b) down; (c) lizard skull with the jaws open and the streptostylic quadrate swung back so that the pterygoideus jaw muscles have their maximum effect; (d, e) diagrammatic lizard skulls showing the advantages of kinesis in holding a food particle (left) that would otherwise be forced out by the bite in a non-mobile skull (right). [Figures (a, b) after Alexander, 1975, courtesy of the Cambridge University Press; (c) after Smith, 1980, copyright © 1980 Macmillan Magazines Ltd; (d, e) after Frazzetta, 1986.]

1 between the frontal and parietal in the skull roof and a matching joint in the palate, the **mesokinetic joints;**
2 between the braincase and the skull (parietal, supratemporal, quadrate and pterygoid), the **metakinetic joints;**
3 between the quadrate (supratemporal + squamosal + paroccipital process) at the top, and the quadrate and pterygoid at the bottom, the **streptostylic joints.**

Sutura frontoparietal recta, flexible



Ardeosaurus (gecko)



Tuatara
(sin metakinesis)

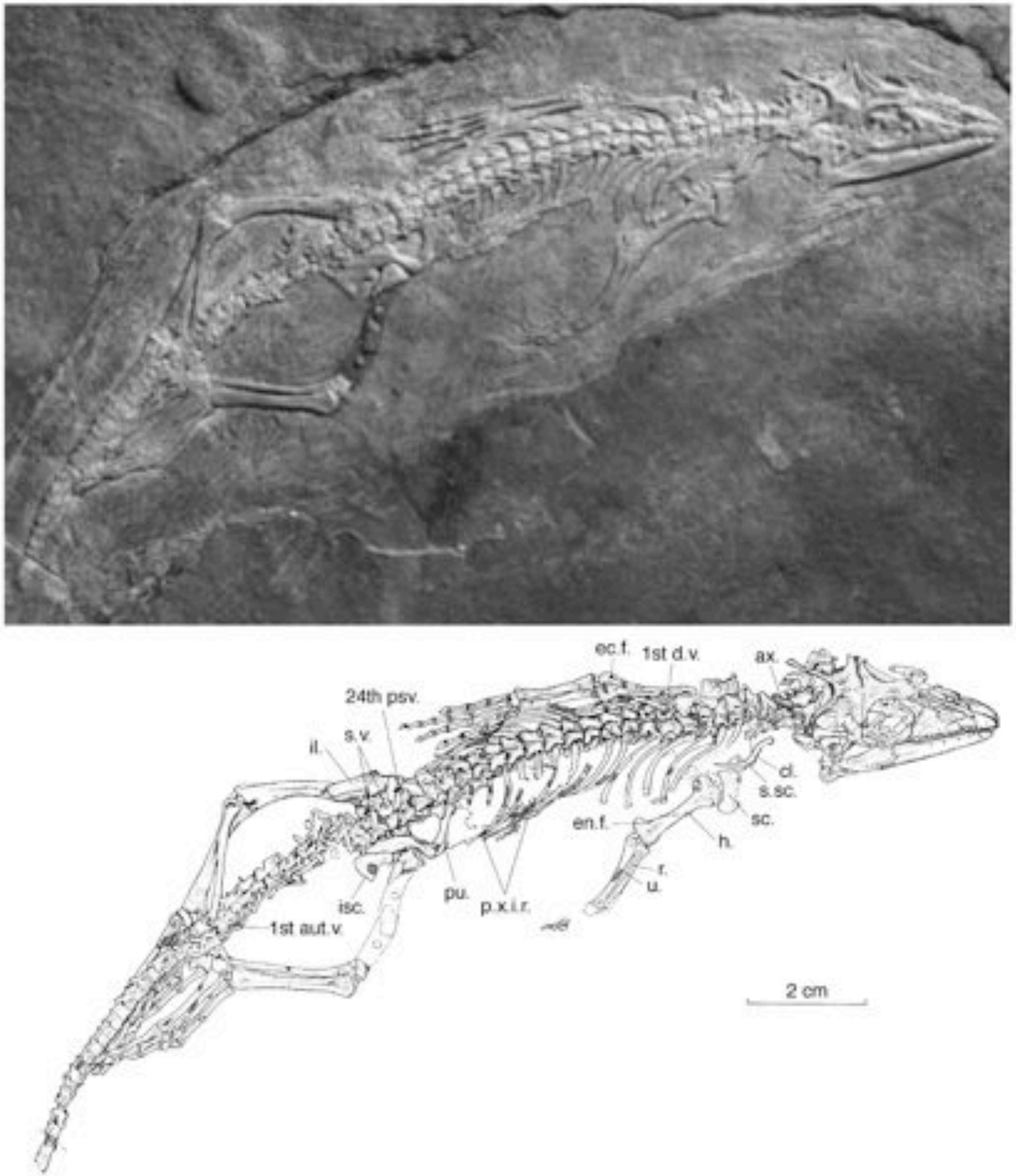


Figure 1. Skeleton of the holotype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 7389) as preserved on the block. Abbreviations are listed in Appendix 2.

Huehuecuetzpalli

"archaeopteryx of lizards"
Stem squamata

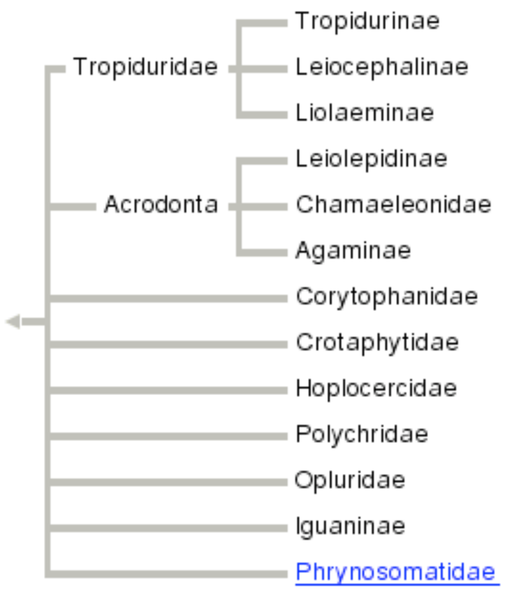
-Como tuatara, tiene escamas dorsales granulares, y la fila medial de escamas

-Sutura fronto partietal es ancha, pero aún hay sobreposición del frontal sobre parietal

-cuadrado streptostilico, pero sin modificaciones correspondientes de la barra temporal superior

Supratemporal grande en la apertura temporal superior (reducido en squamata corona, y ausente en todos los demás tetrápodos vivientes)

Los Iguania incluyen a las Iguanas y Camaleones



Phrynosomatidae:
Iguania basales?

Tropiduridae

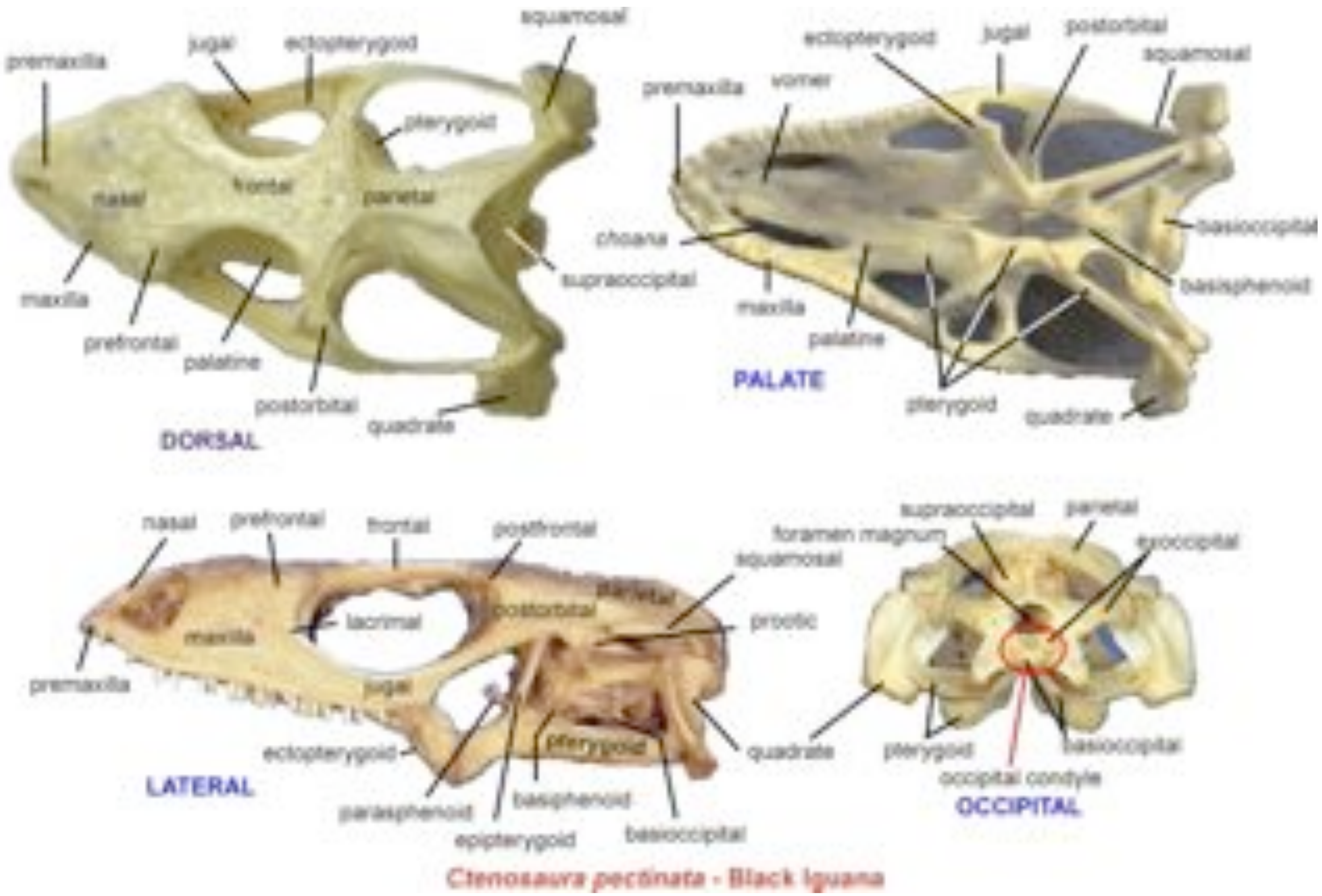
Chamaleonidae

Iguaninae


A
Brookesia
Rhampholeon
Physignathus
Agama
Uromastyx
Phrynosomimus †
Priscagama †
Mimeosaurus †
Isodontosaurus †
Enyalioides
Hoplocercus
Morunasaurus
Anolis vermiculatus
A. occultus
A. heterodermus
amber anole †
FMNH PR2379 †
ANISOLEPINAE
LEIOSAURINAE
Polychrus guttosus
P. marmoratus
P. femoralis
CORYTOPHANIDAE
IGUANIDAE
CROTAPHYTIDAE
IGM 3/858 †
Ctenomastax †
Temujinia †
Zapsosaurus †
Anchaurosaurus †
Oplurus AMNH R71452
Oplurus cyclurus
Oplurus AMNH R47944
Chalarodon
TROPIDURINAE
Stenocercus
Liolaemus
Leiocephalus
Igua †
Polrussia †
PHRYNOSOMATIDAE
Hoyalacerta †
Huehuecuetzpalli †
SCINCOGEKKONOMORPHA
GEKKONOMORPHA
LACERTOIDEA
CORDYLOIDEA
SCINCOIDEA
CARUSIOIDEA
ANGUIDAE
SHINISAURIA
MONSTERSAURIA
VARANIFORMES
MOSASAURIA

IGUANIA:

Familai fósil



Unico hueso frontal, en forma de reloj de arena

Foramen parietal sobre la sutura frontoparietal

Postfrontal pequeño, postorbital se extiende por debajo de la sutura frontoparietal

Nasales cortos

Acrodonta

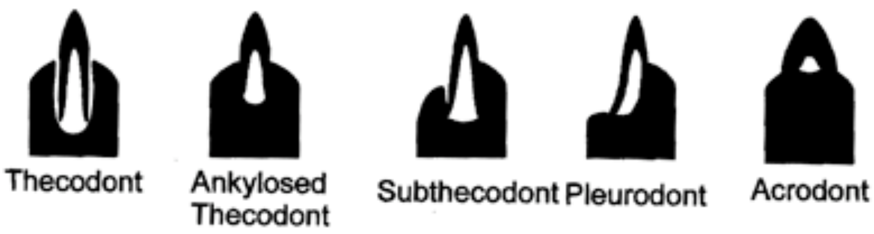
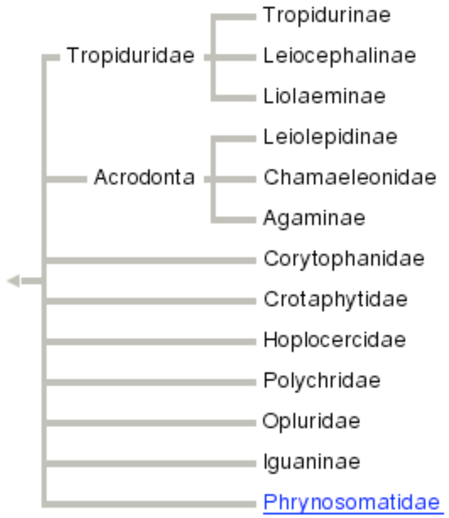


Figure 1. Five major types of tooth implantation, and several variations of them, are recognized in amniotes. After Romer (1956) and Edmund (1960).

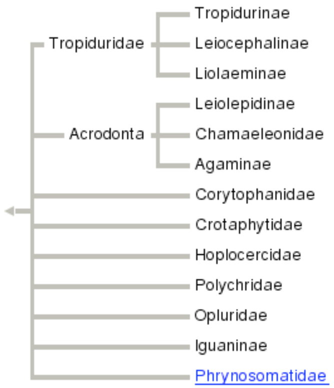


Lengua especialmente protrusible (ej. Camaleones)

Agaminae

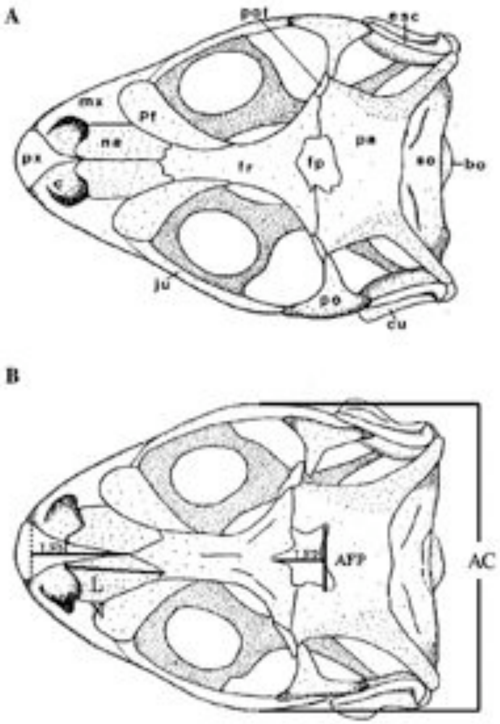
Their tails cannot be shed and regenerated like those of geckoes, though a certain amount of regeneration is observed in some. Well-developed, strong legs

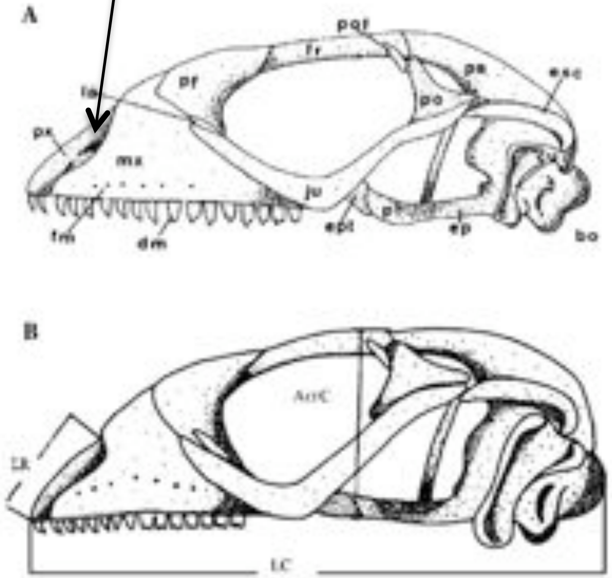
Fig. 48. *Uromastyx dispar maliensis* (= *Uromastyx maliensis* ... (A) Broad view of the body except the tail tip. (B) Detail of ... (compare with fig. 51) and 300(1) (compare with fig. 50), among ... housed at Dickerson Park Zoo in Springfield, Missouri. Photo by R. M. Shearman.



“Tropiduridae”

Margen profundamente inclinado del proceso nasal del maxilar





Microlophus

Scleroglossae:

- -Lengua plana y queratinizada
- -Vomeronasal grande
- -Union yugal-postorbital es una articulacion movil
- -los musculos temporales se insertan en “tabla” del parietal
- -vomer grande
- -proceso alar del prootico
- -perdida de proceso ascendiente del escamoso
- -Proceso facial amplio del maxilar
- -26 en vez de 24 vertebras pre-sacrales
- -interclavicula en forma de cruz (no de “T”)

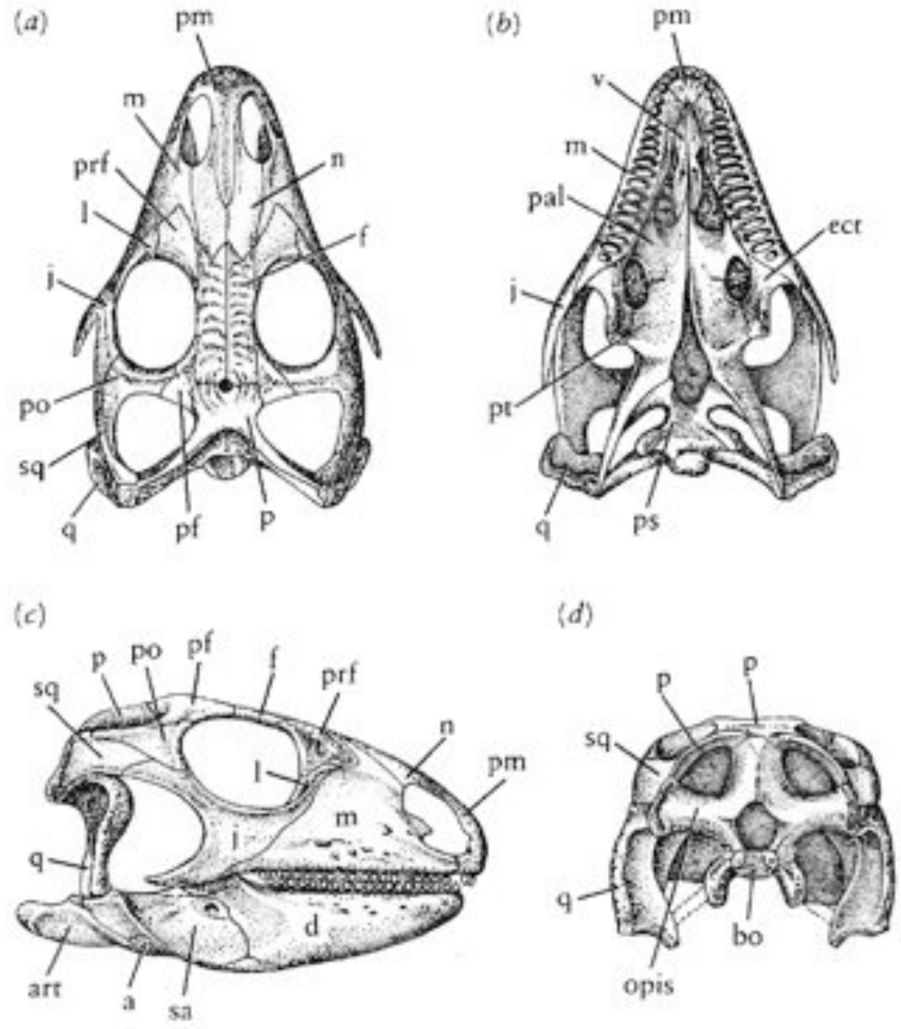
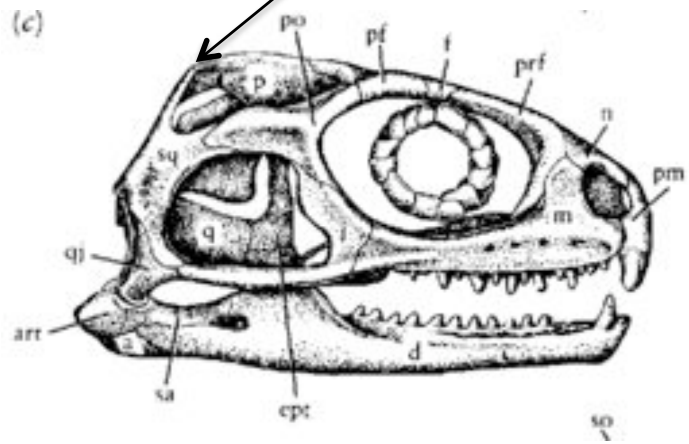
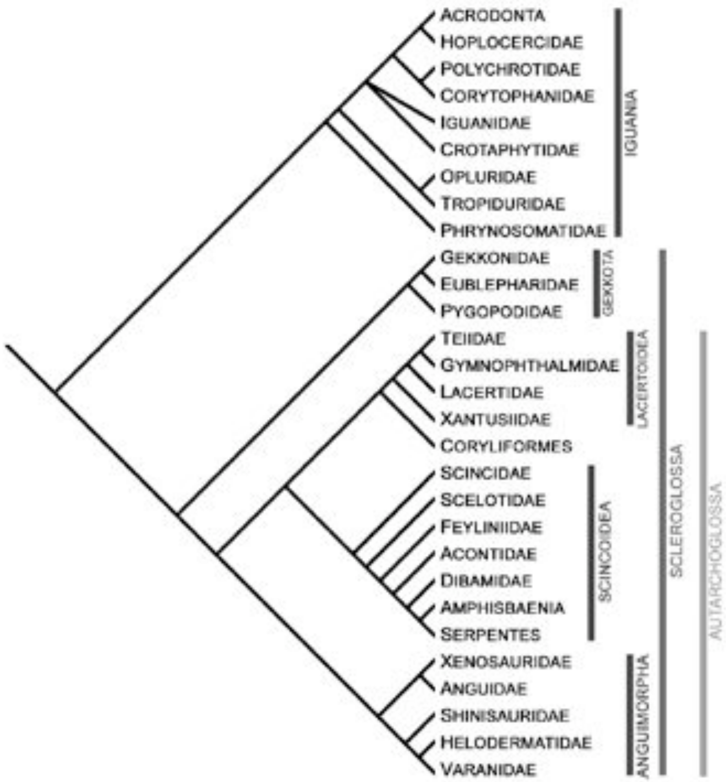


Figure 11-27. THE UPPER CRETACEOUS TEIID LIZARD *POLYGLYPHANODON*. (*a*) Dorsal, (*b*) palatal, (*c*) lateral, and (*d*) occipital views, × ½. The pattern of the skull root is typical of modern lizards. A transverse suture separates the frontals and parietals, which permits raising the snout in some genera. The pineal opening lies along this suture rather than further posteriorly as in more primitive lepidosaurs. The parietal and premaxilla are both fused at the midline. Abbreviations as in Figure 8-3. *From Gilmore, 1942. By permission of Smithsonian Institution Press.*



Tuatara (no-scleroglossae)



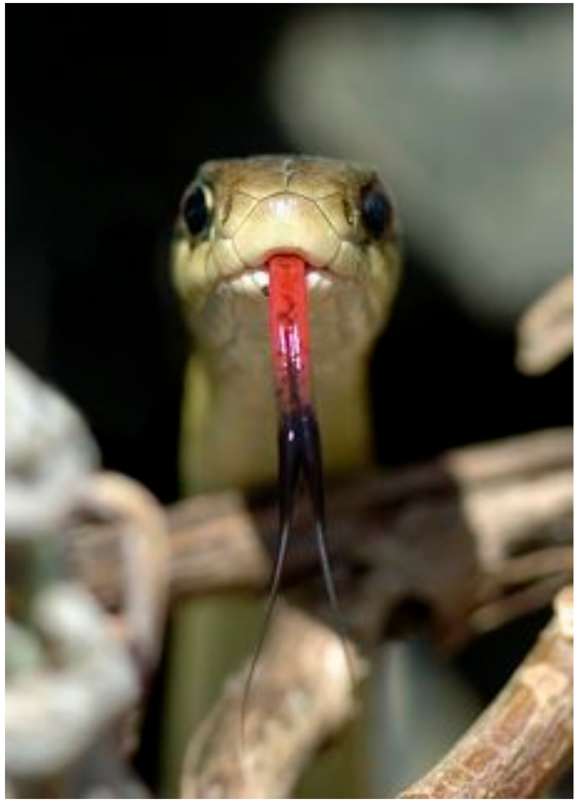


Fig. 61. The current phylogenetic hypothesis (Adams consensus) reduced to display only the major extant squamate clades. The accompanying higher taxonomy (in shades of gray along the right side of the cladogram) demonstrates that the taxonomy proposed here would create minimal disturbance for herpetologists and other neontologists.

Gekkota:
-Esfíncter muscular del oido
-importante vocalizacion
-nocturnos
-lengua modificada para humedecer ojo
-1 ó 2 huevos
-excepto eublepharidos basales, escamas filiformes en dedos

Fosiles en el jurasico

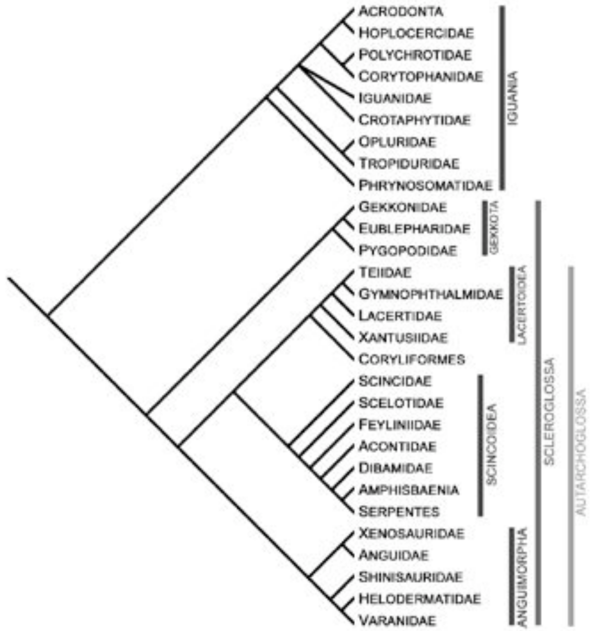
Pygopodidae: gekos sin piernas

Autarchoglossa

-Organo vomeronasal encerrado

-Músculo rectus abdominus unido a la piel en intersticios entre grandes filas transversales de escamas ventrales

-Escamas cefálicas grandes, regulares, como placas firmemente unidas al cráneo



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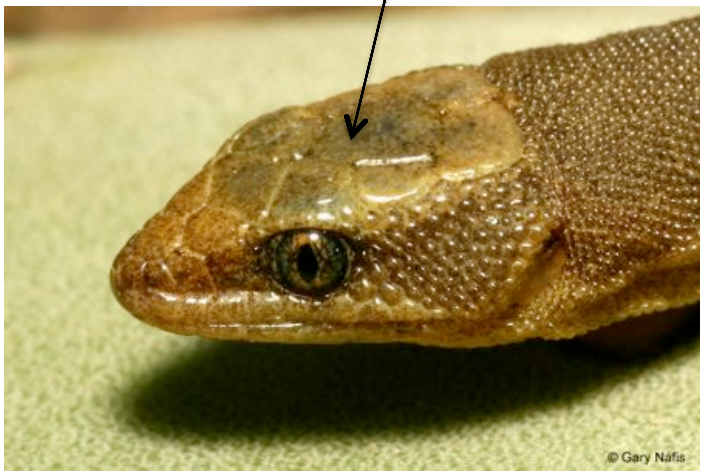
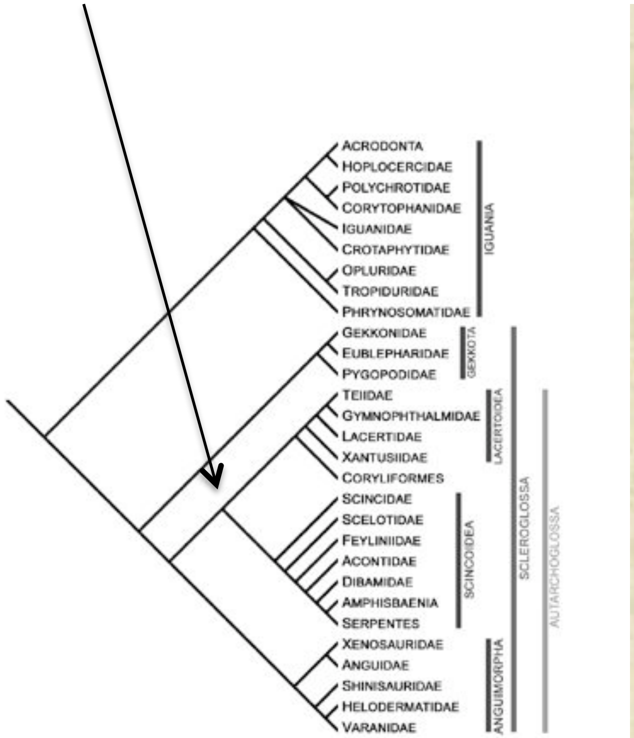


Xantusia

serpiente

Scincomorpha: Scincoidea (puede o no incluir: Amphisbamidae, Dibamidae, Serpentes!), Lacertoides, Xantusidae



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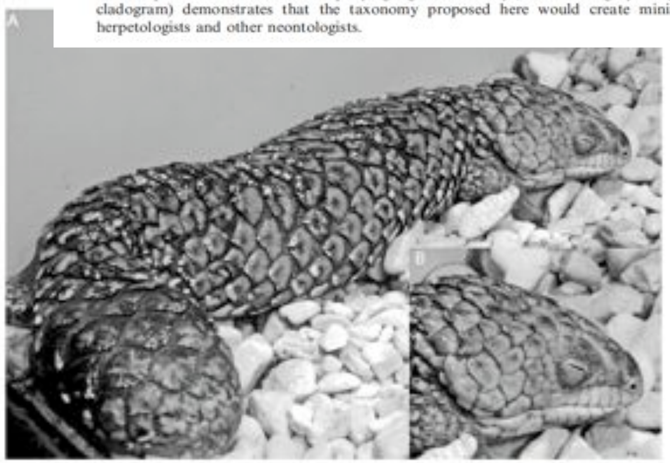


Fig. 51. *Tiliqua rugosa asper* (sensu Shea 1988; =*Trachydosaurus rugosus*). (A) Broad view of the body. (B) Detail of the head. Note the presence of character states 298(2), 305(1), 306(1), 307(1), 308(1), and 314(0). Specimen housed at the San Diego Zoo in Balboa Park, California. Photo by R. M. Shearman.

-Lengua escamosa!
-Osteodermos compuestos (varios forman uno). Ej. Paramacellodus, jurasico de afganistan

Aconthias (scincoidea)

Dibamidae: “serpientes” ciegas

Cráneo rigidamente fusionado
No hay pterygoideo
No hay oido externo
Ojo reducido, cubierto con una escama
Machos con vestigios de piernas
Huevos calcificados

Scincoidea

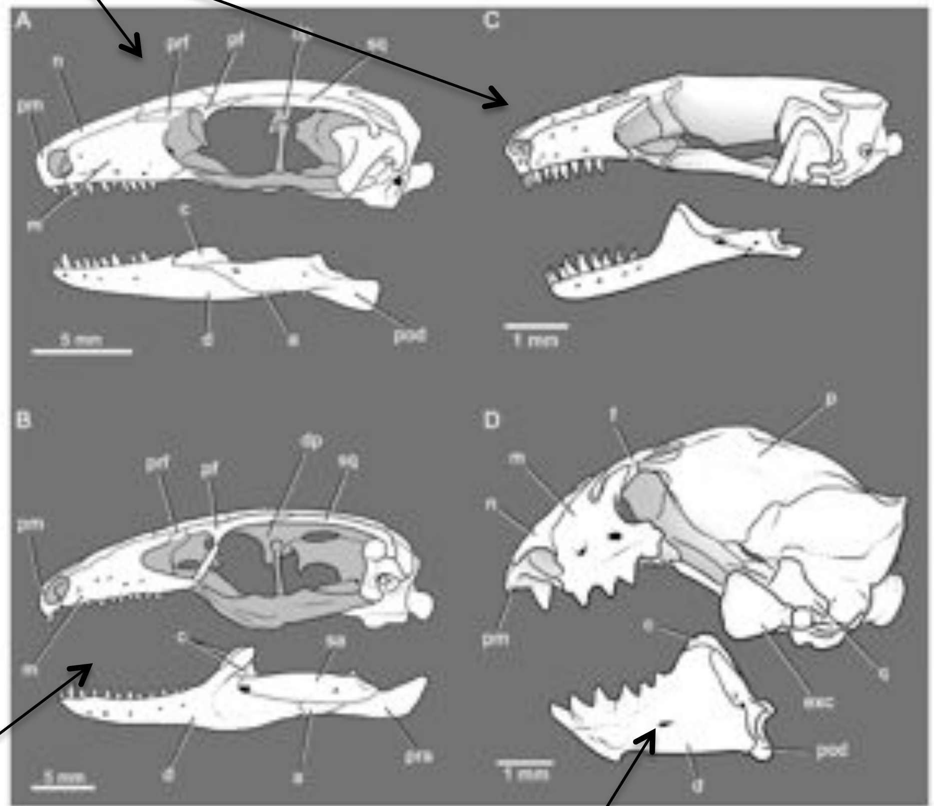


Fig. 57. The skulls of some representative, nonsnake scincophidians in left lateral view. (A) *Feylinia elegans*, (B) *Acontias plumbeus*, (C) *Dibamus novaeguineae*, and (D) *Diplometopon zarudnyi*. Note the progressive development of the descending processes of the frontals, descending processes of the parietals, and coronoid process of the dentary. Modified after (A–B) Rieppel, 1981a, (C) Rieppel (1984b) and Greer (1985), and (D) Maisano et al. (2005; 2006).

Amphisbaenia

Amphisbaenia. Completamente fosoriales y ciegas.
Gusto y olfato muy agudos, lengua bifida con “air flicking” (no solo substrate-licking, como en lacertoides)

Bipes

OPHIDIA (serpentes). Afinidades debatidas

No hay parpados ni timpanos.
Cuerpo y organos alargados.
Vomeronasal gigante
No hay cuello (salvo atlas/axis. Expresión amplia deHoxC-6, -8)

Dinilysia, Najash. Serpientes del cretácico, con piernas vestigiales, sacro en Najash

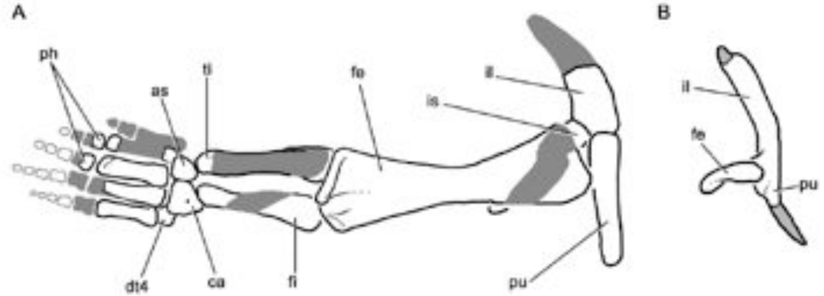
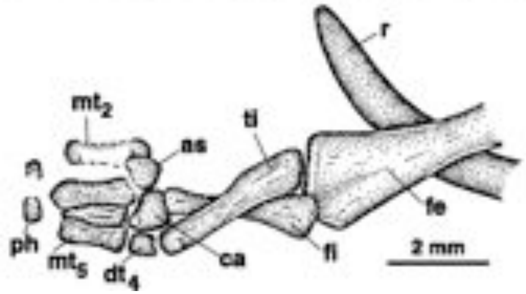
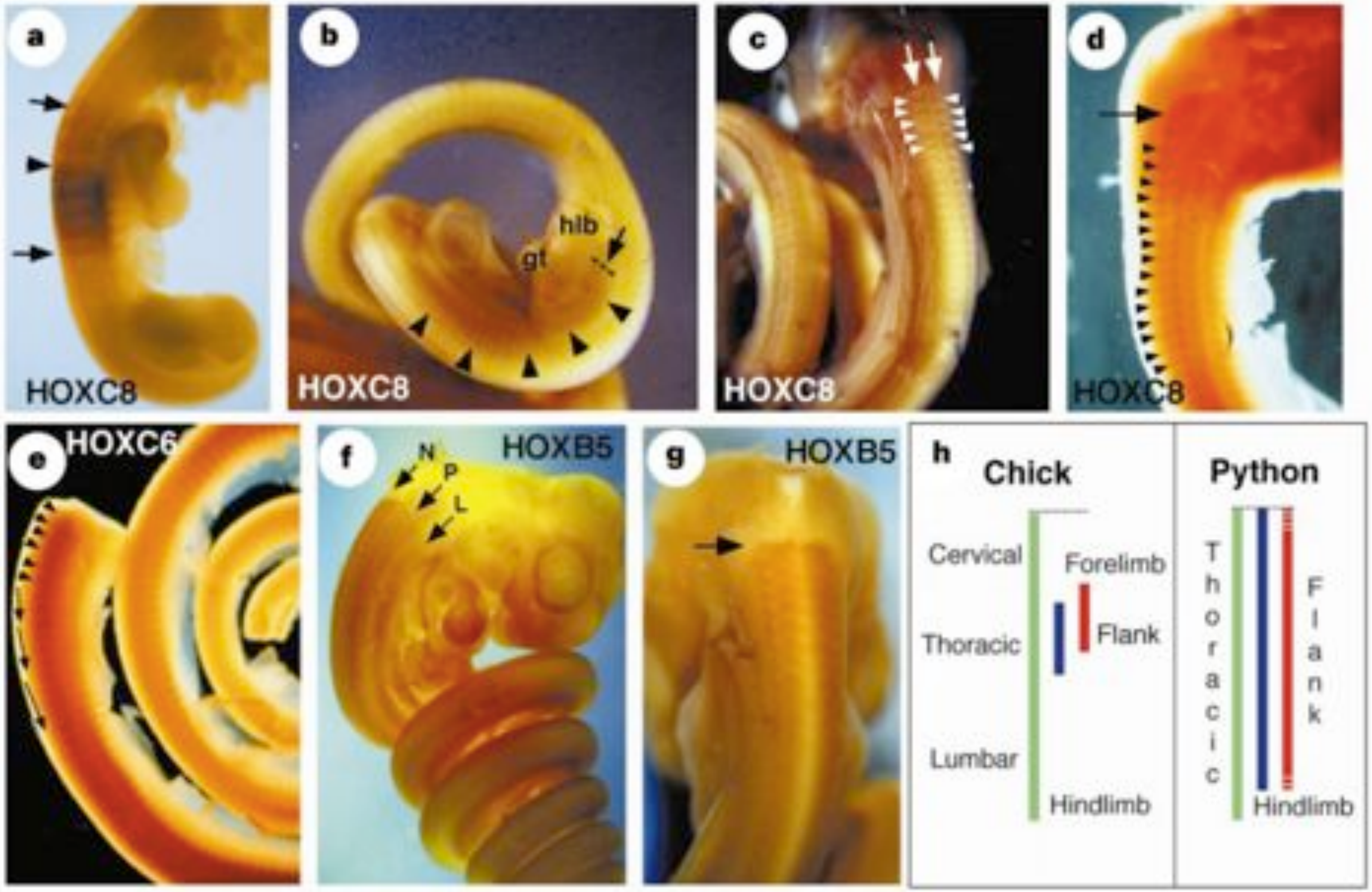


Fig. 47. Hind limbs (A) *Haasiophis terrasanctus* and (B) *Blanus cinereus*. The hind limb of *Haasiophis terrasanctus*, a snake is well developed with tarsals, metatarsals, and phalanges [character state 290(0)]. The hind limb of *Blanus* is composed only of a femur without distal elements such as a pes [an exemplar of character state 290(1)]. Note that the dark gray represents unknown or heavily reconstructed portions and the light gray (in B) represents cartilaginous elements. The gray outlines represent portions that are hypothesized to have originally been present, but for which there is not direct evidence. Modified after (A) Tchernov et al. (2000) and Rieppel et al. (2003), and (B) Kearney (2002).

Las primera serpientes como *Haasiophis* y Pachyrhachis del cretácico temprano presentan pequeñas piernas incluso con elementos del arco digital, y han sido recuperadas de hábitats marinos. Por lo tanto, es posible que las serpientes perdieran las extremidades en el medio marino, y después hayan "recolonizado" el medio terrestre. Se ha argumentado que las serpientes descendieron de autarchoglosos marinos cercanos a los Varanidae, los Mosasauridae




a
HOXC8
b
hlb
gt
HOXC8
c
HOXC8
d
HOXC8
e
HOXC6
f
N
P
L
HOXB5
g
HOXB5
h
Chick
Cervical
Forelimb
Thoracic
Flank
Lumbar
Hindlimb
Python
Thoracic
Flank
Hindlimb

Sin embargo, las serpientes marinas actuales son derivadas. La rama más basal de serpientes son las Scolecophidia: Serpientes ciegas, diminutas, fosoriales, semejantes a scincomorfos como dibamidae y amohisbaenidae

Posible origen fosorial de las serpientes… o convergencia?

Ojo re-constituido?

Anguimorpha

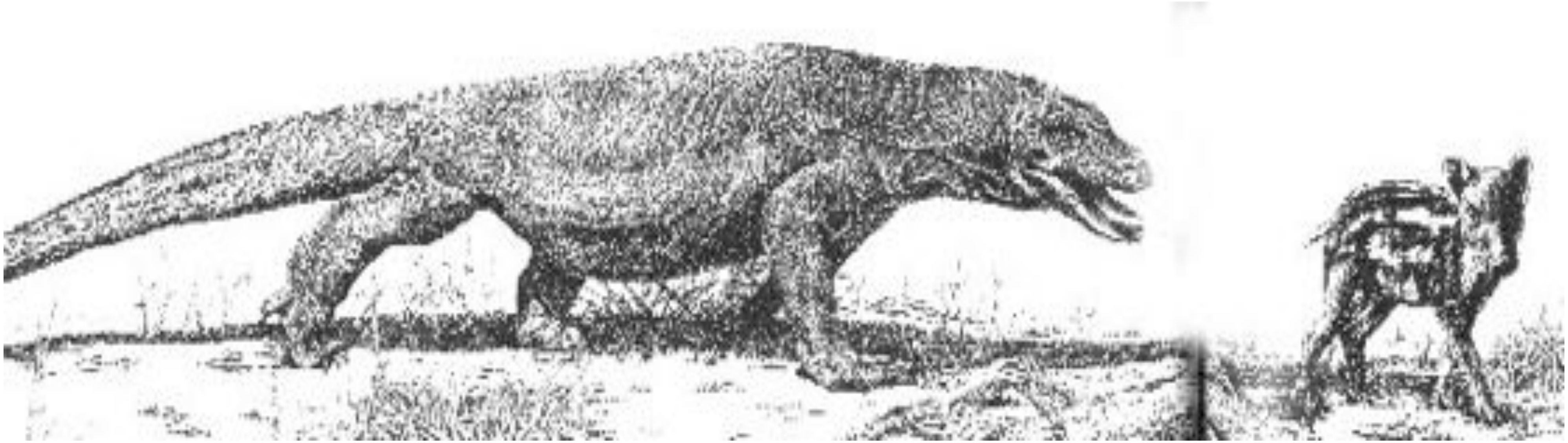
Lengua bifida, cuerpos largos con al menos 28 vertebras presacrales.
Bases de los dientes presentan repliegues (laberintodontes)
Articulación intra-mandibular

Frecuentemente considerados posibles parientes de las serpientes

Anguidae: muchas formas semejantes a serpientes

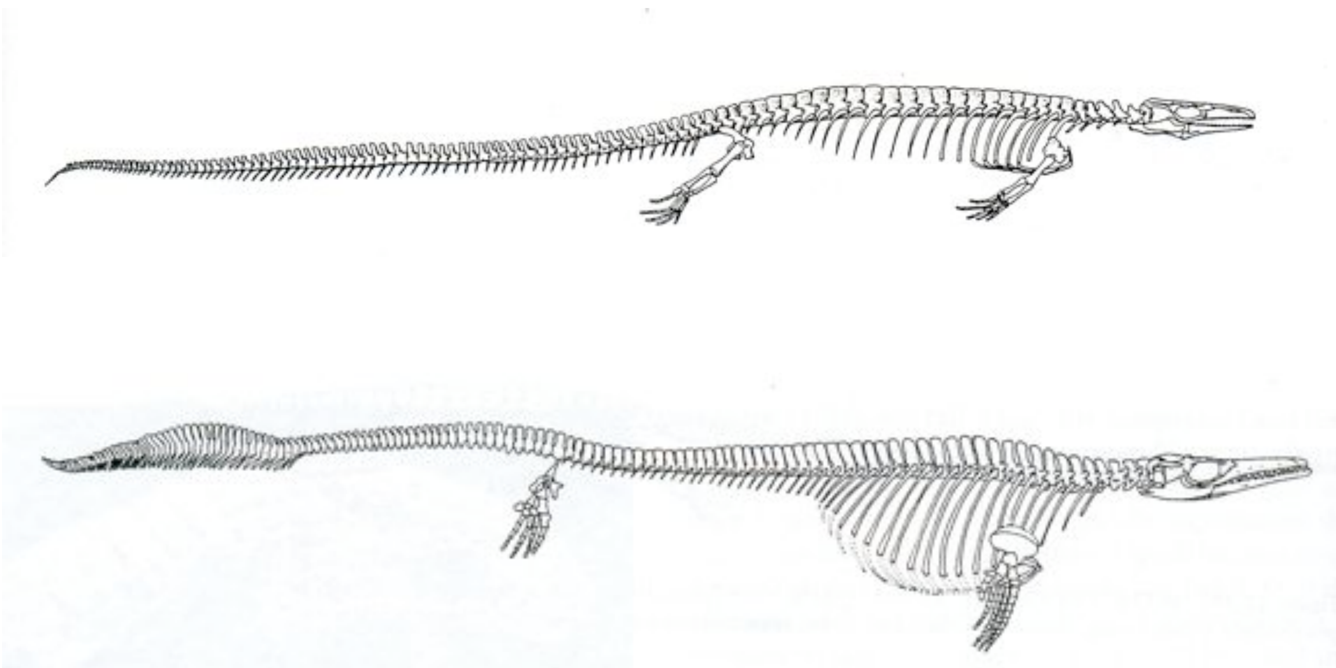
Varanoidea: macrocarnivoros como el dragon de Komodo (varanidae), formas venenosas como Helodermatidae (monstruo de gila)

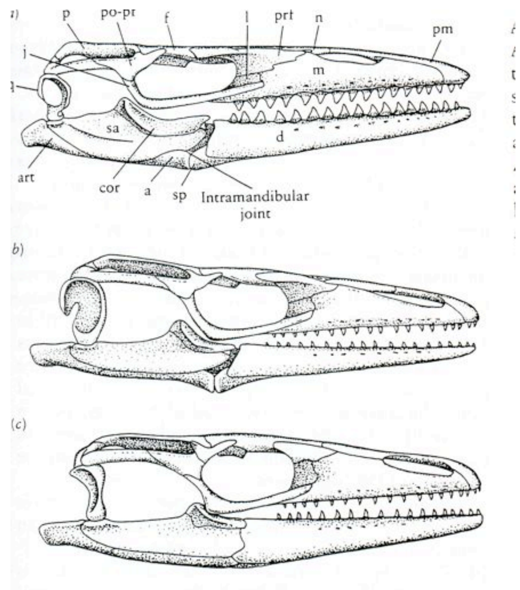
Varanus
(Dragon de Komodo)

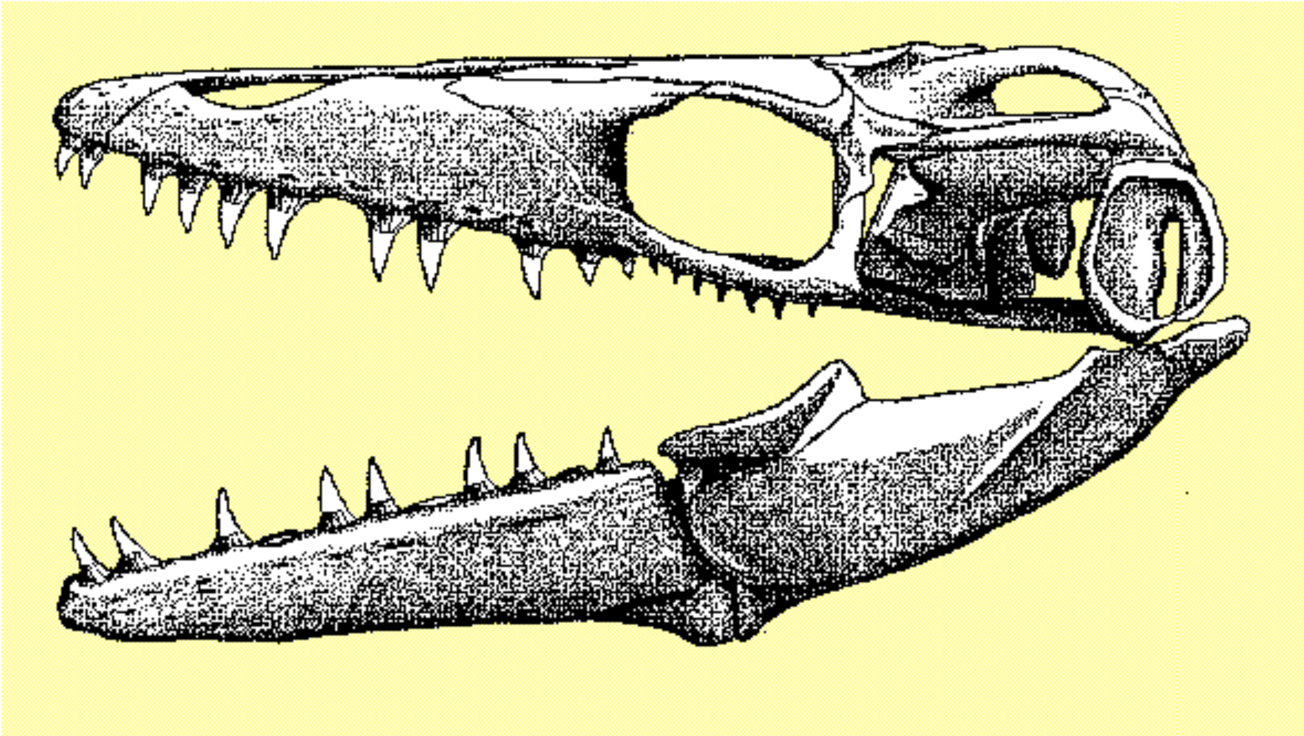


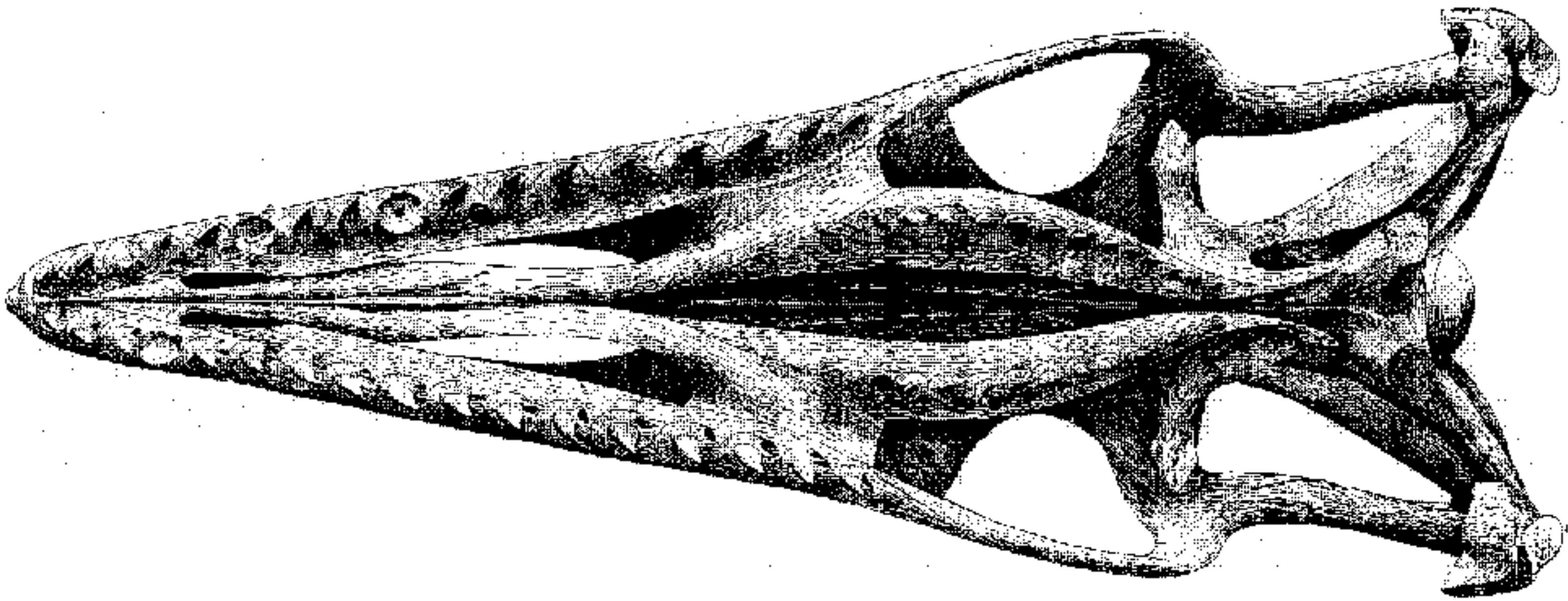
Repetidamente se ha señalado la cercanía de Varanoidea a Mosasauridae. El descubrimiento de los mosasauridae por Georges Cuvier hacia comienzos del siglo XIX permitió reconocer el hecho de la extinción y da inicio formal a la ciencia paleontológica

Dentro de los Squamata, los mayores tamaños ocurrieron en
los varanoidea, quienes evolucionaron gigantescas formas acuáticas,
los Mosasauridae









Análisis recientes confirman que los Mosasauria pertenecen dentro de Varanoidea

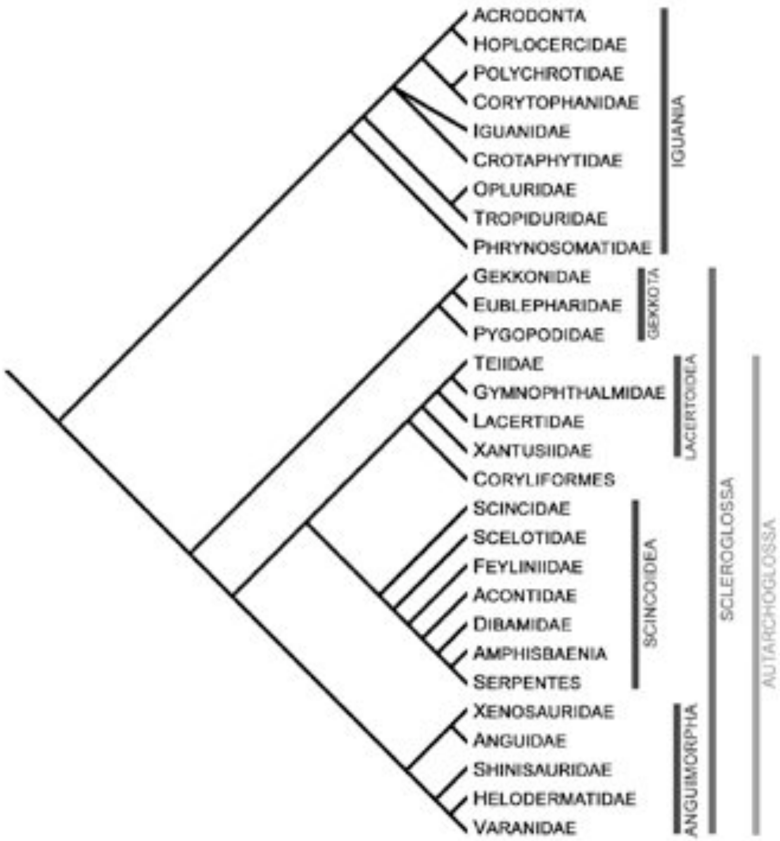


Fig. 61. The current phylogenetic hypothesis (Adams consensus) reduced to display only the major extant squamate clades. The accompanying higher taxonomy (in shades of gray along the right side of the cladogram) demonstrates that the taxonomy proposed here would create minimal disturbance for herpetologists and other neontologists.

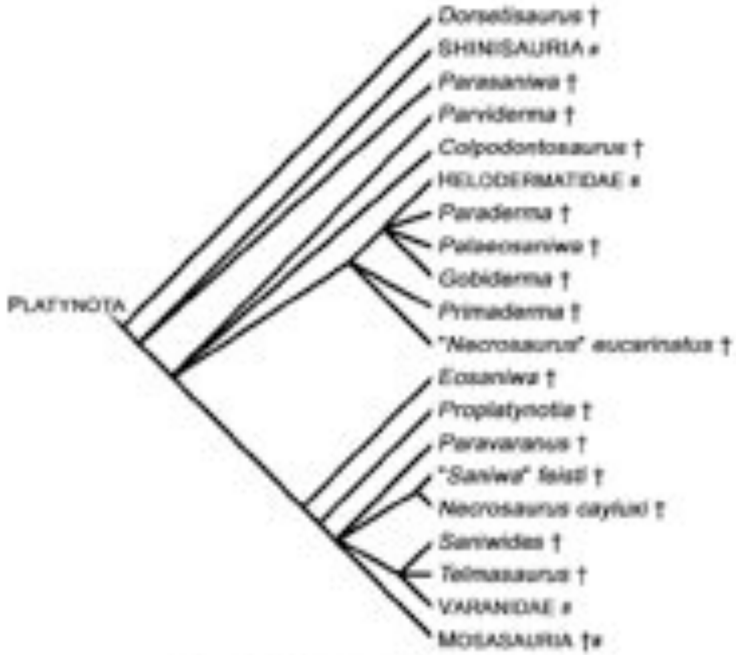
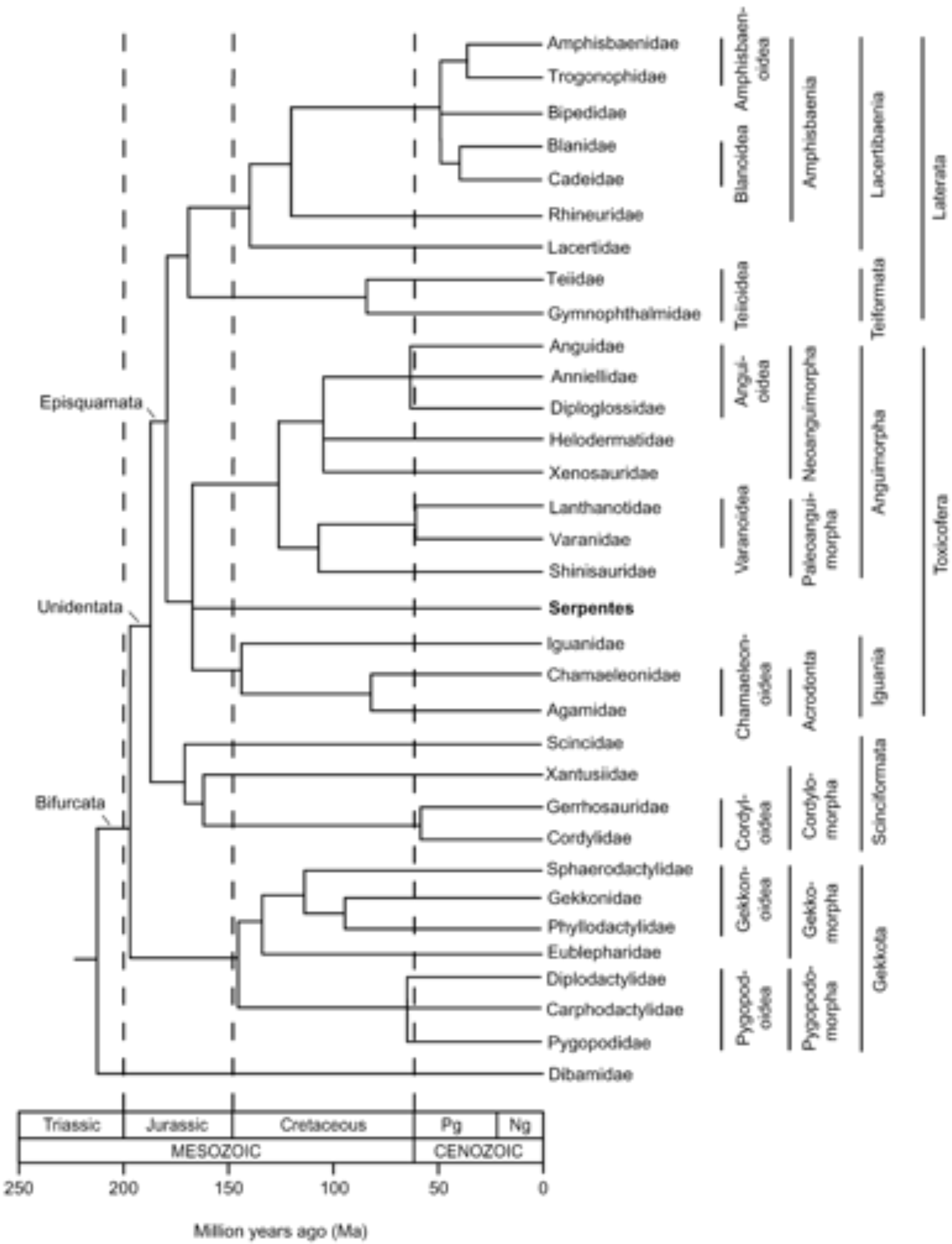


Fig. 60. Continued.



La filogenia molecular (2009!) contiene contradicciones con la morfológica en los clivajes más basales, como colocar a los Iguania al medio de un montón de Scleroglossae

(Este muestreo de Iguania es MUUUUY MALOOOO!!! Sólo 3 grupos!!)

Whaaaaaaat????
No Phrynosomatidae??????

Filogenia morfologica, 2008