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 PENN-SYLVANIAN 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)

pal

91





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 manimal-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.

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

(j)

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.





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



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.



Figure 10-6. VERTEBRAE OF PRIMITIVE AMNIOTES AND AN-THRACOSAURS. (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.



"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 PROTO-ROTHYRIS, A PRIMITIVE AMNIOTE FROM THE LOWER PER-MIAN. Abbreviations as in Figure 8-3, plus: smf, submeckelian fossa. From Clark and Carroll, 1973.

Ancho del arco neural:



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 AN-THRACOSAURS. (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.



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.)

Vuelve el escapulo-coracoide!

3 centros de osificacion (2 coracoides)

Interclavicula forma de "T"

Origen del astragalo (tibiale + carpales)

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).



Fig. 3. Morphology and models of homology between the tares of animatics and annihile intropols, based in part on Peabody (1961). Actedonus is a temperatury, an amphibian grade totrapod, and its tarene is thought to represent the primitive condition from which the annihile tareas evolved. Capterforms is a captarbinist careptile. The arrows with large numbers represent models of subject the annihile tareas evolved. Capterforms is a captarbinist careptile. The arrows with large numbers represent models of subject the operation, the one-center model of Bioppel (1991), the three-center model of Peabody (1981) and later asilters, and the fear-center model (this study). Four outflexities is Acheloses are color-coded in the parts of the reptilian astronalises each is thought to represent under each model minimum on the time, yellow, etc. green, ct. transp. A. astronation, to-observe the tare in the subject of the reptilian astronada 1–4, cr. in, references, finalary, dt1–5, distal taread 1–7, f. Shula, is, Redare, to, intermediant, to, totals.



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.



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

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.

Nomenclatura de fenestras temporales en amniotos

(d)





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.



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.

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

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 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.

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.





SC

Figure 10-15. SKULL OF THE MILLEROSAUR MILLEROSAUR RUS, $\times 2$. (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.



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 OPEN-INGS. 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, $\times \frac{1}{3}$. 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



gi de la construction de la cons

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, $\times 1$. From Ivachnenko, 1979. (e) The Upper Triassic genus Hypsognathus, $\times \frac{1}{3}$ From Colbert, 1946. Courtesy of the Library Services Department, American Museum of Natural History. Abbreviations as in Figure 8-3.

(a)

(b)



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.



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.





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).















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-



Figure 10-14. REPRESENTATIVES OF THE FAMILY CAPTOR-HINIDAE. (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.

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



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 PENN-SYLVANIAN 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 llium angosto

Brazos y piernas de = longitud



Araeoscelis



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



Verdaderos Diápsidos (corona), tb llamados SAURIA Descendientes del ACMR de cocodrilos y lagartijas

-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.



AND NON

d

articular

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

surangular,





sa

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

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

-lleon expandido, mayores musculos de la pierna

-Condylos femorales simetricos







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)





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 \leq humeral length, length of metatarsal IV \leq length of metatarsal III, length of pedal phalanx IV–1 \leq 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), *Drepanosaurus unguicaudatus* (modified from Pinna 1984) and pelves of (left to right) *Hypuronector limnaios* (modified from Colbert & Olsen 2001), *Drepanosaurus unguicaudatus* (modified 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 $\geq 3 \times$ longer than associated vertebrae, vertical orientation of iliac blade, tibial length $\leq 0.65 \times$ femoral length, calcaneal tuber. **D**, Tail of *Drepanosaurus unguicaudatus* (modified from Pinna 1984), 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 AF-RICA. (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

genus Thadeosaurus (Figure 11-10). In this genus and all other early lepidosauromorphs, the neck and the distal limb elements are much shorter than those of Petrolacosaurus. However, aside from these particular features, most skeletal characters of the early lepidosauromorphs can be directly derived from those of Petrolacosaurus. Thadeosaurus has five cervical vertebrae; the centra are recessed at both ends (a condition termed amphicoelous); intercentra are present throughout the trunk and continue for two or three segments beyond the sacrum. The transverse processes that support the ribs in the trunk region are very short, in sharp contrast with those of many early archosauromorphs. Unlike primitive diapsids, the caudal ribs are fused to the centra and extend directly laterally. This feature has evolved convergently in many groups of late Permian amniotes.



Figure 11-10. THADEOSAURUS, AN EOSUCHIAN REPTILE FROM THE UPPER PERMIAN OF MADAGASCAR. The pattern of the skeleton is almost ideal for an ancestor of the modern lepidosaurs. Length of skeleton without tail about 20 centimeters. From Currie and Carroll, 1984. In the adult, the scapulocoracoid appears as a single unit, without a trace of suture. However, early growth stages show that it forms from two centers of ossification, with only a single coracoid element. This element seems

Younginiformes

Hovasaurus



- 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







1 cm

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

Como crown diapsida: Ilium extenso Femur gracil 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.


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 SWITZER-LAND. 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.

Icthyopterygia (condición euryapsida)



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 [HUPEHSU-CHUS]. 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.





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. (c) Schematic cross section of snout. All approximately life size.

"Nanchangosauridae" heptadáctilo! Otra semejanza con Ichthyosauria: Unicos tetrápodos corona q presentan más de 5 dedos! (verdaderos)





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



describe a basal ichthyosauriform from the upper Lower Triassic (about 248 million years ago) of China, whose primitive skeleton indicates possible amphibious habits. It is smaller than ichthyopterygians and had unusually large flippers that probably allowed limited terrestrial locomotion. It also retained characteristics of terrestrial diapsid reptiles, including a short snout and body trunk². Unlike more-derived ichthyosauriforms³, it was probably a suction feeder. The new species supports the sister-group relationships between ichthyosauriforms and Hupehsuchia⁴, the two forming the Ichthyosauromorpha. Basal



Figure 2 | The holotype of *Cartorhynchus lenticarpus* gen. et sp. nov. a, Whole specimen. b, Close-up of ribs. c, Ribs of *Chaohusaurus* (AGM CH-628-16) for comparison. d, Skull and shoulder elements. e, Skull of a newborn *Chaohusaurus*²⁰ drawn to the same scale as d for comparison. f, Right forelimb. g, Right hindlimb. a, angular; as, astragalus; ca, calcaneum; cbi, first ceratobranchial; cl, clavicle; d, dentary; f, frontal; Fe, femur; Fi, fibula; H, humerus; i, intermedium; icl, interclavicle; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pm, prefrontal; po, postorbital; prf, prefrontal; pf, postfrontal; q, quadrate; qj, quadratojugal; R, radius; r, radiale; sa, surangular; sc, scapula; scl, scleral ossicles; sp, splenial; sq, squamosal; st, supratemporal; Ti, tibia; U, ulna; u, ulnare; i–v (in g), metapodials. Scale bars, 1 cm.





Figure 4 | Phylogenetic hypotheses of *Cartorhynchus*. a, Position of *Cartorhynchus* among Diapsida, with aquatic adaptations excluded.
b, As in a but with aquatic adaptations included. c, Relationships of basal ichthyosauriforms. Analyses are based on most recent phylogenetic data sets

for marine reptile relationships⁴ and ichthyopterygian phylogeny (C. Ji *et al.*, manuscript in preparation), respectively (Supplementary Information). All trees were abbreviated from more complete topologies (Extended Data Figs 1–3).



Utatsusaurus del Triásico de Japón





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



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*





Chaohusaurus

Grippia, del triásico de alemania, presenta una órbita grande, una nariz retraída respecto a la punta del hocico.

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



Chaohusaurus gelshanesis 0,5 a 0,7 metros. Vivió hace 245 millones de años (Triásico inferior)

Mixosaurus cornalianus 0,5 a 1 metro. Vivió hace 235 millones de años (Triásico medio) palatine les.



Ophthalmosaurus icenicus 3 a 4 metros. Vivió desde hace 165 hasta hace 150 millones de años (Jurásico medio o superior)

ALETA DORSAL

ALETA CAUDAL EN FORMA DE MEDIA LUNA



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



Latipinados: Con cuatro carpales Distales y cuatro dígitos

Longipinados:

Principales

Con tres carpales

distales y tres dígitos

Longipinados Latipinados Figure 12-30. DIFFERENT PATTERNS OF THE FRONT LIMBS ICHTHYOSAURS. (a) Utatsusaurus (Lower Triassic). From Shikan 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 longin 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. La alta especialización acuática se corresponde con la presencia de reproducción vivípara



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 OPHTHAL-MOSAURUS FROM THE UPPER JURASSIC. (a) Skeleton, approximately 3½ meters long. From Andrews, 1910. (b) Restoration. From McGowan, 1983.





Opthalmosauria: Platypterygius









FIGURA 1. Distribución geográfica de las localidades de donde han sido documentados resto de ictiosaurios en Chile: 1) Quebrada Sajasa, Región de Antofagasta (21°46'S; 68°15'W). 2) Cerritos Bayos, Región de Antofagasta (22°30'S; 69°05'W). 3) Placilla de Caracoles, Región de Antofagasta (23°02'S; 59'W). 4) Quebrada Incahuasi, Región de Antofagasta (25°38'S; 69°15'W). 5) Pingo Quemado, Región de Antofagasta (24°31'S; 69°15'W). 6) Quebrada Punta del Viento, Región de Antofagasta (25° 05'S; 69° 15'W). 7) Sierra de Varas, Región de Antofagasta (24°49'S; 69°11'W). 8) Quebrada Doña Inés Chica, Región de Atacama (26°07'S; 69°20'W). 9) Pan de Azúcar, Región de Atacama (26°03'S; 70°30'O). 10) Potrerillos, Región de Atacama (26°03'S; 70°02'W). 11) Cerro Blanco, Región de Atacama (28°02'S; 70°08'W). 12) Quebrada La Iglesia, Región de Atacama (28°08'S; 69°53'W). 13)
Quebrada Tres Cruces, Región de Coquimbo (29°58'S; 70°29'W). 14) Río Colina, Región Metropolitana (31°52'S; 70°00'W). 15) Río de Los Hielos, Región de Magallanes y Antártica Chilena (51°05'S; 73°18'W).



FIGURA 3. Ichthyosauria indet. Seis centros vertebrales asociados, de un mismo individuo. MPC.1605; MPC.1606; MPC.1607; MPC.1608: Centros caudales. A1, B1, C1, D1) Vistas laterales. A2, B2, C2, D2) Vistas articulares.
MPC.1609. Centro dorsal. E1) Vista lateral. E2) Vista articular. MPC.1610. Centro dorsal mal preservado. F) Vista articular. Quebrada Pan de Azúcar, Región de Atacama, NE Parque Nacional Pan de Azúcar, Región de Atacama,

Formación Pan de Azúcar, Hettangiano. Barra de escala = 50 mm.



FIGURA 4. Ichthyosauria indet. Manflas, Región de Atacama, Formación Lautaro, Bajociano medio. T.342: A) Porción proximal del rostro en vista lateral, B) vista anterior y C) vista dorsal. T.337; T.338: D, E) Bloques conteniendo fragmentos de costillas. T.332: F) Vértebra torácica incompleta en vista anterior. T.331: G) Vértebra torácica en vista anterior. Modificado de Tavera, 1981. Barra de escala = 10 mm.

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FIGURA 6. Ichthyosauria indet. Río de Los Hielos, Parque Nacional Torres del Paine. Formación Tobífera o Zapata, Jurásico Medio - Cretácico Inferior. A) Montaje de los tres fragmentos del bloque (modificado de Schultz *et al.* 2003).
B) Aspecto *in situ* de la misma pieza, mostrando el detalle de las vértebras anficélicas en sección longitudinal debido a la erosión del bloque. Barra de escala en A = 50 mm.

122



FIGURA 7. TY11: *?Platypterygius hauthali* A-B) Aspecto *in situ* del individuo y dibujo a escala del espécimen *in situ* con la descripción anatómica de la imagen anterior. Escala = 800 mm.



FIGURA 8. TY11: A) Detalle del cráneo B) Dibujo del contorno de los elementos del rostro y basicranium identificados. Escala = 0.1 m. C) Detalle del basioccipital. D) Descripción anatómica del elemento. Escala = 50 mm.
E) Detalle del supraoccipital. F) Descripción de las secciones identificadas en el elemento Escala = 50 mm.





FIGURA 10. A) Detalle del miembro anterior de TY11. El color gris oscuro indica la ubicación relativa de los dígitos pre- y postaxiales. B-E) Dibujo a escala de *Platypterygius hauthali* von Huene: B) Húmero del holotipo (MLP 79-I-30-1) en vista dorsal. C) Sección distal del húmero del holotipo. D) Fragmento de aleta anterior (especimen MLP 79-I-30-2). E) Fragmento de aleta anterior del holotipo (MLP 79-I-30-1).

127



В



FIGURA 11. TY17: Ophthalmosauridae indet. A) Aspecto *in situ* del individuo. Escala = 2 m. B) Dibujo a escala del espécimen *in situ* con la descripción anatómica de la imagen anterior. Barra de escala= 100 mm.



FIGURA 12. TY17: A) Detalle del íleon *in situ*. Escala = 50 mm. B) Dibujo esquemático de la imagen anterior. C) Aleta posterior derecha e izquierda. D) Descripción anatómica de las aletas posteriores Escala = 50 mm.



FIGURA 13. Comparación de las aletas posteriores de TY17 (A) con la de diferentes oftalmosáuridos. B) Aleta posterior derecha de *Platypterygius australis* (modificado de Zammit *et al.* 2010). C) Fémur derecho de *Platypterygius hercynicus* (modificado de Kolb y Sander 2009) las líneas indican la articulación distal del fémur con la fibula, tibia y extrazeugopodial. D) Sección distal del fémur derecho de *Platypterygius hercynicus* (modificado de Kolb y Sander 2009). E) Aleta posterior izquierda de *Sveltonectes insolitus* (Fischer *et al.* 2011b). F) Aleta posterior derecha de *Aegirosaurus leptospondylus* (modificado de Fernández 2007). G) Aleta posterior derecha de *Caypullisaurus bonapartei* (modificado de Fernández 2007). H) Fémur izquierdo de *Platypterygius americanus* (modificado de Maxwell y Kear 2010). I) Sección distal del fémur izquierdo de *Platypterygius americanus* (modificado de Maxwell y Kear 2010).











FIGURA 14. TY25: Ophthalmosauridae indet. A) Aspecto *in situ* del individuo. Escala = 1 m. B) Dibujo a escala del espécimen *in situ* con la descripción anatómica de la imagen anterior. Escala = 100 mm. C) Detalle de una porción de la columna vertebral (ultimas dorsales, primeras caudales). D) Dibujo del mismo indicando la ubicación de la parapófisis, diapófisis y las facetas para la articulación de los arcos neurales. E) Detalle de la sección caudal de la columna vertebral. F) Descripción anatómica de la imagen anterior. G) Detalle de los arcos y espinas neurales H) Dibujo interpretativo y descripción anatómica de la figura anterior


FIGURA 15. TY25: A) Aletas posterior derecha e izquierda B) Descripción anatómica de la imagen anterior.
Escala = 50 mm. Comparación con aletas posteriores de otros oftalmosáuridos: C) Sección distal del fémur derecho de *Arthropterygius chrisorum* (modificado de Maxwell 2010). D) Fémur derecho de *Arthropterygius chrisorum* (modificado de Maxwell 2010). E) Aleta posterior izquierda de *Cryopterygius kristiansenae* (modificado de Druckenmiller *et al.* 2012). F) Aleta posterior izquierda de *Sveltonectes insolitus* (Fischer *et al.* 2011b). G) Aleta posterior derecha de *Aegirosaurus leptospondylus* (modificado de Fernández 2007). H) Aleta posterior derecha de *Caypullisaurus bonapartei* (modificado de Fernández 2007). I) Aleta posterior izquierda de *Ophthalmosaurus icenicus* (modificado de Fernández 2007).







FIGURA 16. TY03: Ophthalmosauridae indet. A) Aspecto *in situ* del individuo. Escala = 800 mm. B) Descripción anatómica de la imagen anterior. Escala = 10 mm. C) Detalle de la organización de las espinas neurales. D)
Dibujo interpretativo y descripción anatómica de C. E) Detalle de la sección proximal de una costilla. F) Dibujo interpretativo y descripción anatómica de E.



FIGURA 17. Esquema paleogeográfico del límite Jurásico - Cretácico: A) Jurásico superior (150 Ma. aprox.). Hacia fines del Titoniano o Berriasiano temprano el Corredor Hispánico habría conectado a las faunas del hemisferio norte con el sur. El corredor de Sudáfrica y Rocas Verdes ('South African / Rocas Verdes Corridor') en el hemisferio sur ya habría comenzado a formarse, pero no habría sido completamente efectivo aún. El aislamiento producido en el hemisferio sur habría permitido la especialización del grupo. B) Cretácico temprano (120 Ma. aprox.). Ictiosaurios del hemisferio sur se conectarían con fauna del Tethys oriental a través del ya efectivo corredor de Sudáfrica y Rocas Verdes ('South African /Rocas Verdes Corridor'), mientras que el Corredor Hispánico pudo haber continuado actuando como paso para fauna marina en el hemisferio norte. Estrellas indican localidades donde han sido encontrados ictiosaurios ophthalmosauridos. La estrella blanca indica *P. hauthali* en la Cuenca Neuquina y de Rocas Verdes. Líneas punteadas oscuras indican las posibles rutas de dispersión de ophthalmosauridos. Imagen modificada de Riccardi (1991).

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



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

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.





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









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).