

AN UNUSUAL AQUATIC SPHENODONTIAN (REPTILIA: DIAPSIDA) FROM THE TLAYUA FORMATION (ALBIAN), CENTRAL MEXICO

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ABSTRACT—The sphenodontian *Ankylosphenodon pachyostosus* new genus and species is the second unusual sphenodontian reported from the Albian deposits of the Tlayua Formation, near Tepexi de Rodríguez, Central Mexico. The skeleton is robust with pachyostotic ribs and vertebrae. Unique long teeth are ankylosed deep into the lower jaw extending close to the edge of the Meckelian canal. Long teeth with open roots, the lack of worn-out teeth, and the presence of posterior wear surfaces exhibiting dentine suggest that tooth growth was continuous. These features combined with a propalinal action of the deep lower jaw suggest herbivory. Herbivorous specializations of *Ankylosphenodon* are different from the laterally expanded teeth of *Toxolophosaurus* and *Eilenodon* and may have evolved to prevent total tooth loss, a feature which is observed in sapsheosaurs. A pachyostotic skeleton, a delay of the ossification of the epiphyses, and a solid structure of the vertebral column could be related to a none obligated aquatic behavior. These specializations differ greatly from those of other aquatic sphenodontians such as *Pleurosaurus* and *Palaeopleurosaurus*. A stout skeleton with swollen horizontal zygapophyses suggests affinities with sapsheosaurs; however, cladistic analysis support sister-group relationship with *Toxolophosaurus* and/or *Eilenodon* on the basis of shared propalinal jaw action and deep jaws. The presence of two unique sphenodontians in the Tlayua Quarry suggests the presence of an area for the diversification of lepidosaur reptiles. The late presence of sphenodontians in the Albian also suggests that this area was a refuge for archaic forms at the time.

INTRODUCTION

SPHENODONTIANS ARE a very well-known group of lepidosaur reptiles represented today by the single genus *Sphenodon*, which inhabits the coast of small islands around New Zealand. Since their exclusion from the Agamidae and the recognition that they belong to a different reptile “order” (Günther, 1867), they have been considered the ideal ancestral morphotype for lizardlike forms, thereby gaining status as living fossils (Broom, 1925; Romer, 1956). On the basis of current phylogenetic hypotheses, it is now known that *Sphenodon* is not primitive but a derived form in which the apparently primitive presence of a complete lower temporal bar was acquired secondarily within sphenodontian evolution (Whiteside, 1986; Wu, 1994; Reynoso, 1996). The fossil record of sphenodontians is patchy, and although more than 30 species are known, the number of taxa and specimens per geological period is limited. They are known from the Middle Triassic up to the Early Cretaceous but no fossils are known thereafter. The early rhynchocephalian *Gephyrosaurus* (Evans, 1980, 1981) and to a lesser degree the sphenodontian *Diphydontosaurus* (Whiteside, 1986) still show many primitive lepidosaur characters. The typical sphenodontian morphology, very similar to that of *Sphenodon*, was acquired by other Late Triassic genera. During the Jurassic, sphenodontians invaded different environments and evolved new morphologies. They modified their skeleton, altering the typical sphenodontian *Bauplan*, and became a relatively diverse group. Unfortunately, their limited fossil record prevents a complete understanding of these forms and their radiation, but a few good representatives show the broad spectrum of types. These included herbivores (Throckmorton et al., 1981; Rasmussen and Callison, 1981), and obligatorily aquatic forms such as pleurosaurs, which show an extreme example of body transformation (Fabre, 1974; Carroll, 1985a; Carroll and Wild, 1994). Such a wide range of behaviors is extremely rare in lepidosaurs (Pough 1973; Seymour, 1982).

The Albian deposits of Tepexi de Rodríguez have produced several reptiles including crocodiles, turtles (Espinosa-Arrubarena and Applegate, 1990), pterosaurs (Cabral and Applegate, 1993), and two lizards (Reynoso, 1998a; Reynoso and Callison, in press). Very recently, the “beaded” sphenodontian *Pamizinsaurus tlayuaensis* was described from these deposits (Reynoso, 1997). It has unusual rounded osteoscutes distributed along the

body, a possible specialization for protection in (dry) open environments. In this paper a second sphenodontian, showing a unique morphology possibly related to an aquatic mode of life and herbivory, is described. Its body shape is quite different from that of pleurosaurs, and the tooth morphology differs from all other known sphenodontians. Description of this sphenodontian will add new information about the degree of skeletal plasticity and morphological diversity among these lepidosaurs at the end of the Early Cretaceous.

Comparative material.—Redpath Museum, Montréal: *Sphenodon punctatus* RM 1135. Fossil specimens: Museum National de Histoire Naturelle, Paris: *Leptosaurus pulchelus* (type = *Kalimodon cerinesis*) CRN 77; *Leptosaurus cf. pulchelus* CN 572; *Sauranodon incisivus* (= *Sapsheosaurus thiollierei* No. 1548, cast); *Piocormus laticeps* (paratype, CNJ 72); *Leptosaurus pulchelus* (*Sapsheosaurus laticeps*, CNJ 68). Université Claude Bernard, Lyon: *Sapsheosaurus thiollierei* (no catalogue number). Carnegie Museum of Natural History: *Homoeosaurus maximiliani* C.M. 6438. Staatliches Museum für Naturkunde, Stuttgart: *Palaeopleurosaurus posidoniae* (no catalogue number).

SYSTEMATIC PALEONTOLOGY

Subclass LEPIDOSAURIA Dumeril and Bibron, 1839 (sensu Romer, 1956)
Order RHYNCHOCEPHALIA Günther, 1867
Suborder SPHENODONTIA Williston, 1925
Family SPHENODONTIDAE Cope, 1870 (sensu Reynoso, 1996)
Genus ANKYLOSPHENODON new genus

Type species.—*A. pachyostosus* new species.

Diagnosis.—As for the type and only known species.

Etymology.—Gr. from *ankylos* and *sphenodon*. In reference to the teeth ankylosed into the lower jaw, and to *Sphenodon*, the only surviving genus of the Sphenodontia.

ANKYLOSPHENODON PACHYOSTOSUS new species
Figures 1–8

Diagnosis.—Stout sphenodontian with postorbital skull region enlarged; upper temporal bar formed mainly by the squamosal; teeth attached deep within the lower jaw; continuous tooth growth; no dental regionalization; no flanges on dentary teeth; short retroarticular process; pachyostotic vertebrae with swollen

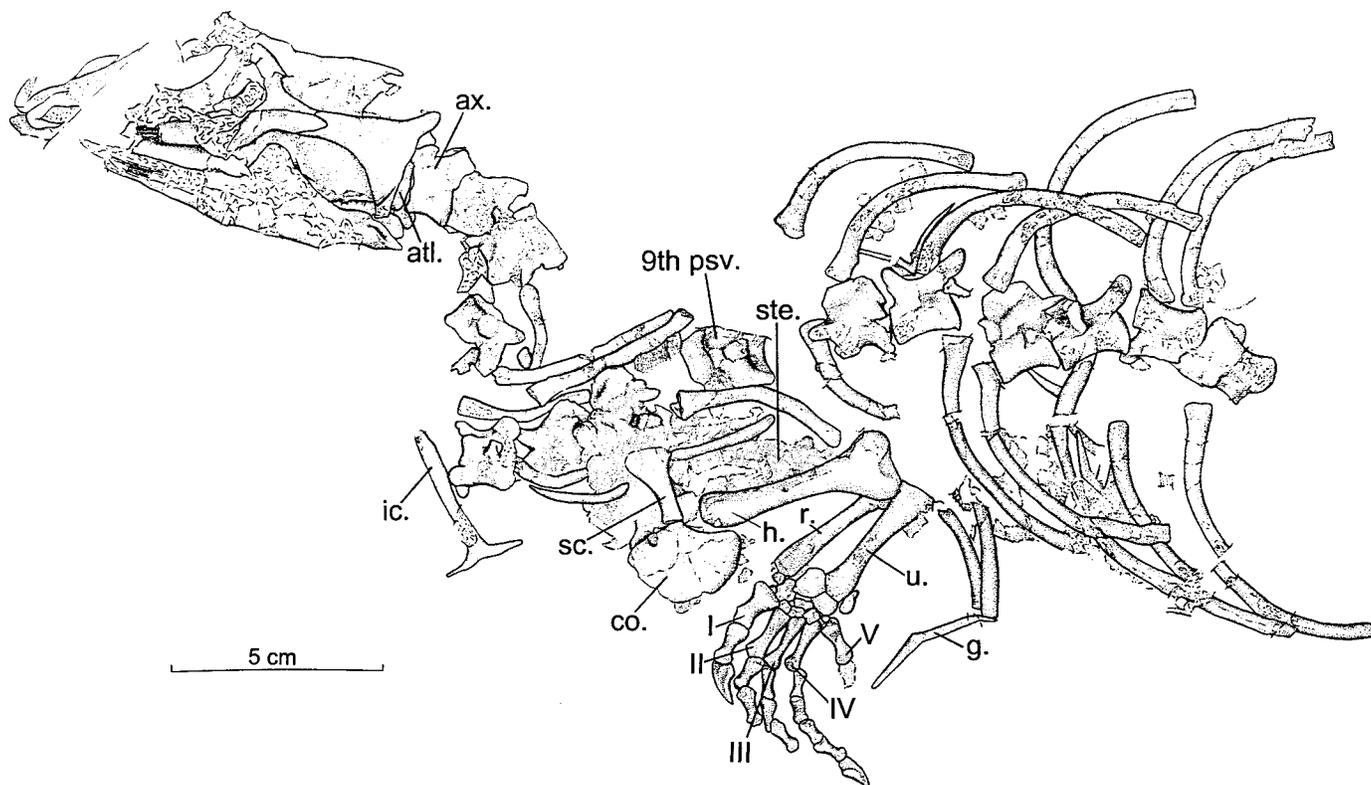


FIGURE 1—*Ankylosphenodon pachyostosus* n. gen. and sp. (IGM 7441). Skull, anterior portion of the presacral vertebral column, and left fore limb of the holotype as preserved. Abbreviations: *atl.*, atlas; *ax.*, axis; *co.*, coracoid; *g.*, gastralia; *h.*, humerus; *ic.*, interclavicle; *psv.*, presacral vertebrae; *r.*, radius; *sc.*, scapula; *ste.*, sternum; *u.*, ulna, Metacarpals in Roman numerals.

zygapophyses; zygapophyses with rounded articulating surfaces oriented in the horizontal plane; no thoracolumbar intercentra; pachyostotic thoracic ribs; second sacral rib with a broad posterior process; first digit distinctively broad with an enlarged ungual; short posterior process on ischium.

Description.—*Ankylosphenodon pachyostosus* is known from several partial skeletons exposed in bas relief on one surface of the block rock (Fig. 1), except one specimen that was extracted completely from the matrix. All skeletons are preserved in dorsal aspect, but a fragment of the thoracolumbar portion of a skeleton does give information about the ventral morphology. Although three of the seven partial skeletons have skulls, none of them shows anatomical detail. Of the three preserved skulls, one is split in half, other one is severely damaged, and the other one is crystallized.

General features.—Size and proportions of the skeletons are given in Table 1. The skull and limb proportions in relationship to the presacral vertebral column length cannot be established with certainty because no complete presacral series is preserved. The length of the presacral vertebral column (PSVCL) was reconstructed scaling the width of the distal end of the humerus and the length of the 19th vertebra, assuming the presence of 24 presacral vertebrae, the typical sphenodontian count (*Sphenodon*, *Homoeosaurus*, and *Sapheosaurus*). IGM 7442 is the largest specimen and IGM 7443 is the smallest. The only dimension in common in all the specimens is the width of the distal end of the humerus, which ranges from 13.1 to 19.2 mm. The holotype is about average size.

Skull and lower jaw.—The poor preservation of the skull prevents the establishment of skull proportions. By comparing the length of the lower jaw, assuming it to be equal to the skull

length (as in other sphenodontians), the upper temporal fenestra extends about half of the total skull length. The upper temporal arch is enlarged, much as in the aquatic genus *Sapheosaurus* (Fig. 2). It is formed primarily by a distinctively-broad squamosal that extends to the anterior half of the upper temporal fenestra, forming an anterior notch into which fits the posterior end of a long and slender jugal. The level of the dorsal margin of the jugal is indicated by an anterior notch in the squamosal and a faint suture with the postorbital. The postorbital extends posteriorly, almost reaching the posterior end of the jugal. The lower temporal bar is missing but might have been broken. In the holotype, the snout and skull table are missing, and, with exception of the premaxillae, only the internal bone is exposed. The premaxillae are separated but provide no information of the postnarial articulation or dental structure. There is no detail of the suspensorium. A suture delimits a small bone posterior to the quadrate process of the squamosal that is identified as a quadratojugal.

The lower jaw is typically sphenodontian in structure but robust in construction. It is dorsoventrally broadened on its medial portion and has an enlarged coronoid process that emerges straight dorsally from the posterior end of the tooth row. Anteriorly, the lower jaw becomes more slender, ending with an obliquely-oriented symphysis. The posterior process of the dentary extends beyond the coronoid bone, surrounding dorsally and laterally an enlarged surangular foramen. Other than the dentary, no detailed structure is preserved. The articular condyle is large and elongated anteroposteriorly, suggesting the possible presence of propalinal jaw action. Such action is also indicated by wear marks in the tooth and dentary surfaces (Fig. 3.2).

TABLE 1—Dimensions and proportions of different elements of the cranial and postcranial anatomy of *Ankylosphenodon pachyostosus* n. gen. and sp. Measurements in mm. Data in parentheses are approximated. Abbreviations. PSVCL = presacral vertebral column length.

Specimen	(Holotype)	IGM 7443	IGM 7442	IGM 7445	IGM 7446	IGM 7447
Skull length			(82.5)	(78.1)		
Postorbital skull length	22.4					
PSVCL						
from 1st to 19th vertebra	282.6					
from 20th to 24th vertebra		68.1				
from 1st to 13th vertebra	170.8					
from 14th to 24th vertebra		149.7			181.2	
19th vertebrae centrum length	19.4	14.0			15.7	
Estimation of the PSVCL						
Scaling 19th vertebrae	376.9	272.0			319.4	
Scaling humerus distal end	371.2	280.2	416.7	353.8		
Mean	374.0	276.1	410.6	348.6		
Mean			413.7	351.2	319.4	
Humerus length	49.3		55.8	52.0		50.9
Humerus shaft width	5.9		(7.5)	6.9		7.5
Humerus distal end width	17.1	13.1	19.2	16.3		16.5
Radius length		28.0	40.3			
Ulna length	32.8	27.2	40.0			
Femur length		56.1				
Tibia length		35.9				
Fibula length		35.2				
Skull/PSVCL			0.200	0.224		
Humerus/PSVCL	0.130		0.135	0.148		
Radius or ulna/PSVCL	0.086	0.100	0.097			
Femur/PSVCL		0.203				
Tibia/PSVCL		0.130				
Humerus:						
Shaft width/distal end width	0.345		0.391	0.423		0.455
Shaft width/total length	0.120		0.134	0.133		0.147
Distal end width/total length	0.347		0.344	0.313		0.324

Tooth structure.—External tooth morphology is only preserved on the posterior end of the dentary tooth row in IGM 7422 and at the tip of the dentary in IGM 7445 (Fig. 3.2, 3.3). Superficially, the teeth seem to be acrodont, but opportune longitudinal breakages of the holotype lower jaws and in IGM 7422 show that they extend deep into the dentary, as far as the upper margin of the Meckelian canal. This condition is unique for sphenodontians and resembles the ankylothecondont condition of rhynchosaurs (Benton, 1984). Fraser and Shelton (1988) have shown that some sphenodontians (e.g., *Planocephalosaurus*) have teeth enclosed in a shallow groove within the lower jaw. However, the condition in *Ankylosphenodon* is not similar to *Planocephalosaurus*, but rather the teeth are attached deep into the jaw to an extreme degree.

Although the erupted portion of the teeth look small and triangular, within the jaw teeth are long and laterally compressed. Each tooth extends anteroposteriorly overriding the following tooth to form an extensive, obliquely oriented tooth plate (Figs. 3, 4). Teeth are composed of an elongated sheath of hard, brownish enamel covering a white layer of dentine. The ventral part of each tooth is open, resting the dentine on the enamel surface of the posterior tooth, along the imbedded portion. The last tooth rests directly over the dentary. The tip of IGM 7442 and along the middle portion of the dentary in the holotype clearly shows that the tooth plate is completely enclosed within the dentary and not exposed medially, suggesting that only the tips of the teeth were used for food processing. In IGM 7442 the medial enamel surface is broadly exposed and shows some small microstriations, especially conspicuous at the anterior part of the jaw. On a major wear surface at the tip of the dentary, the anteroventral part of the most anterior tooth is also exposed in cross section and it could have been used for mastication all along its dorsal surface.

On the external portion of individual teeth, the enamel sheath covers each tooth except for the posterodorsal face, where the dentine is exposed. However, in the posterior teeth, known to be the last erupted of the tooth series in all sphenodontians (Harrison, 1901; Robinson, 1976), the posterior surface of the tooth is still covered with enamel. The lack of enamel on the posterior face of relatively older teeth suggests that it was already worn off. A major wear facet is present in the third tooth from the back of IGM 7442. Contrary to other sphenodontians, in which wear tends to reduce tooth size, the anterior teeth in *Ankylosphenodon* are always well exposed externally, remaining about the same size as the posterior teeth. The absence of reduction in the exposed tooth surface in anterior teeth can only be explained by the presence of continuous tooth growth. This also explains the sole exposure of dentine in the posterodorsal surface of the

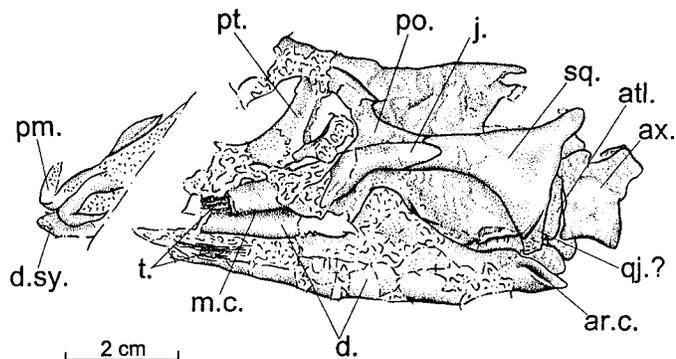


FIGURE 2—*Ankylosphenodon pachyostosus* n. gen. and sp. (IGM 7441). Detail of the skull of the holotype as preserved. Abbreviations as in Figure 1 plus: *ar.c.*, articular condyle; *d.*, dentary; *d.sy.*, dentary symphysis; *j.*, jugal; *m.c.*, meckelian canal; *pm.*, premaxilla; *po.*, postorbital; *pt.*, pterygoid; *qj.*, quadratojugal; *sq.*, squamosal; *t.*, teeth.

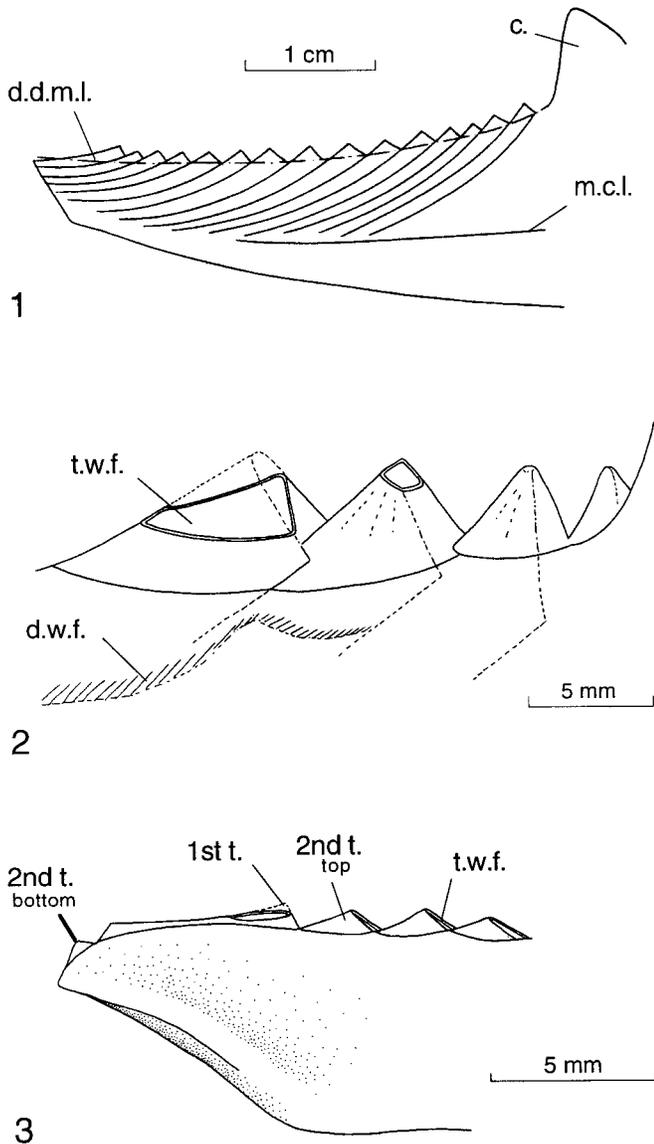


FIGURE 3—Diagrammatic reconstruction of the tooth series. 1, Lower jaw longitudinal section; 2, lateral view of the posterior part of the dental series showing wear marks on teeth and dentary; 3, symphyseal region of the dentary in medial view. 1 and 2 from IGM 7442 (2 is inverted), 3 from IGM 7445. Abbreviations: *d.d.m.l.*, level of the dorsal margin of the dentary; *d.w.f.*, dentary wear facet; *m.c.l.*, level of the meckelian canal; *t.*, teeth; *t.w.f.*, tooth wear facet.

tooth, so that the apex of individual teeth remains aligned at the same height in the tooth plate. Tooth growth has never been reported before in sphenodontians.

Anteroposteriorly-oriented tooth wear marks are present laterally on the posterior end of the jaw and associated teeth. Wear has degraded extensively the enamel on the lateral surface of the fourth most posterior tooth. The wear mark extends into the dentary bone, exposing a good portion of the enamel sheath of this tooth. This type of wear provide evidence for propalinal jaw action.

Axial skeleton.—The axial skeleton is pachyostotic (Figs. 1, 5, 6). Vertebrae are massive relatively to those of other sphenodontians. The enlargement of the vertebrae is caused by an

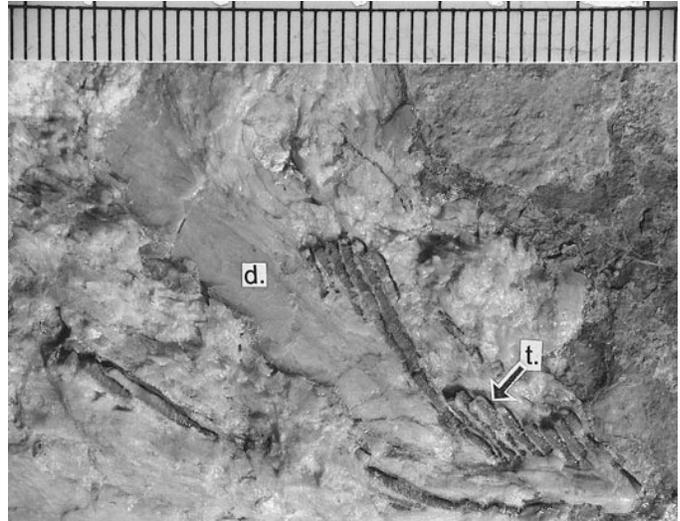


FIGURE 4—Detail of the internal structure of the tooth series as preserved in IGM 7442 of *Ankylosphenodon pachyostosus* n. gen. and sp. Scale in mm. Abbreviations as in previous figures.

increment of volume in the neural arches, zygapophyses, transverse processes, and neural spines. The thick neural arches are evident when comparing them with the reduced opening for the neural nerve. (Fig. 6). The ribs are as thick as the epipodials. Inside they are constituted by a soft, probably porous tissue, covered by a thick periosteal layer. In the skeleton the ribs give the appearance of being closely packed (Fig. 5), although not to the same degree as mesosaurs or nothosaurs.

The axial skeleton was reconstructed mostly from the holotype and from IGM 7443 (Figs. 2, 5). The total number of presacral vertebrae is unknown, even though all vertebrae are preserved between the two specimens. It was not possible to identify any point of reference to link the anterior and posterior counterparts from the two specimens, and the presence of 24 presacral vertebrae (the typical terrestrial sphenodontids count) was assumed. The length of the limb bones preserved in the several specimens were compared with an estimation of the presacral vertebral column length (Table 1). Relative differences suggest ontogenetic variation of limb length, in which limbs appear to be slightly shorter (between 5 and 10 percent) in larger specimens.

The holotype has 19 presacral vertebrae preserved, including a very small portion of the atlas, mostly hidden behind the squamosal. IGM 7443 has vertebrae 14 to 24 plus a small posterior portion of vertebra 13. The number of cervical vertebrae is difficult to establish. The orientation of the ribs may give some clue, since it could be associated with a different condition of their ventral attachment. In the holotype, some anterior ribs point forward, but all remaining ribs were preserved pointing backwards. The similar orientation of the posterior ribs was probably caused by the restriction imposed by their association with the sternum and gastralata. If so, the first posteriorly oriented rib is the ninth, suggesting that the eight anterior vertebrae were cervicals, which matches the number in *Sphenodon*.

The first well-exposed vertebra is the axis, but no particular detail is preserved. Vertebrae increase in size posteriorly, with the last presacral vertebra being the largest of the series. In articulated specimens, vertebrae are compressed dorsoventrally, obscuring the length of the neural spine. In isolated elements, the neural spine is large and square, extending all along the dorsal part of the neural arch (Fig. 6). Their bases are broad in

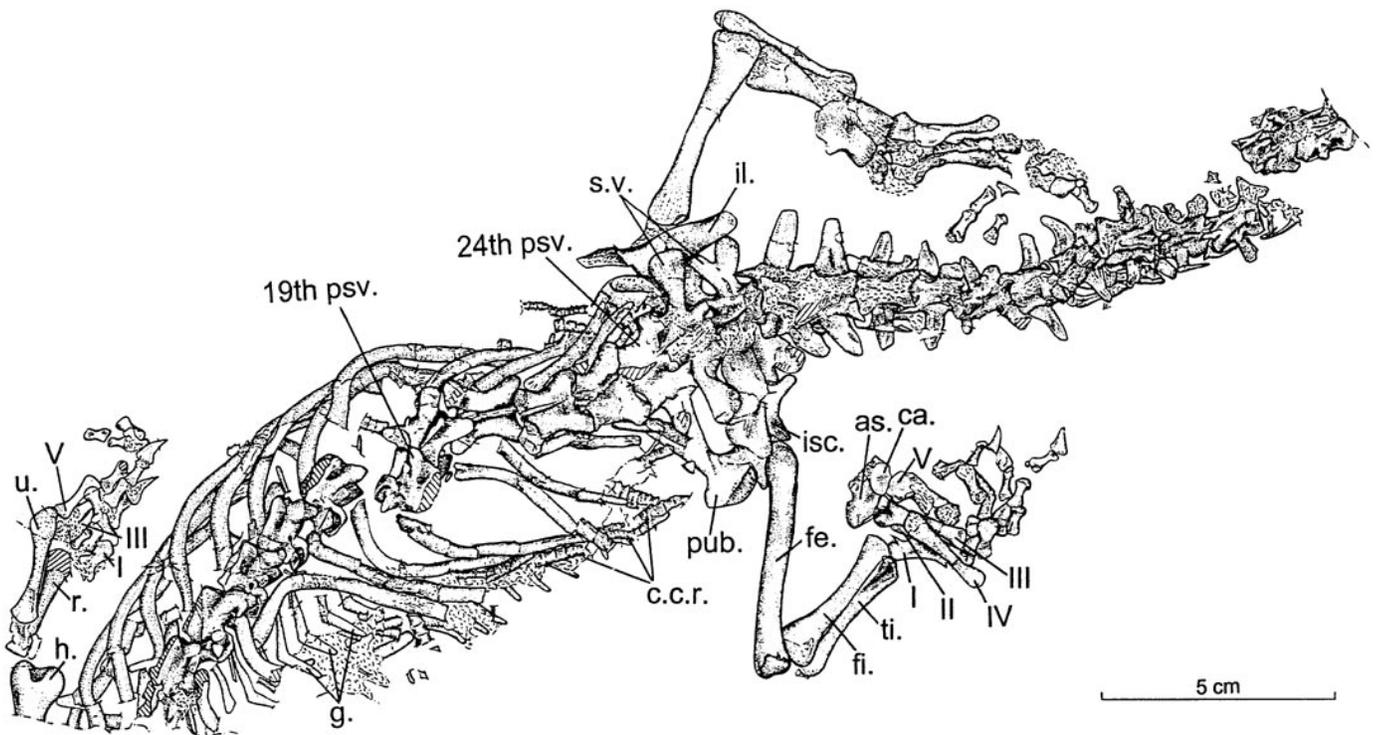
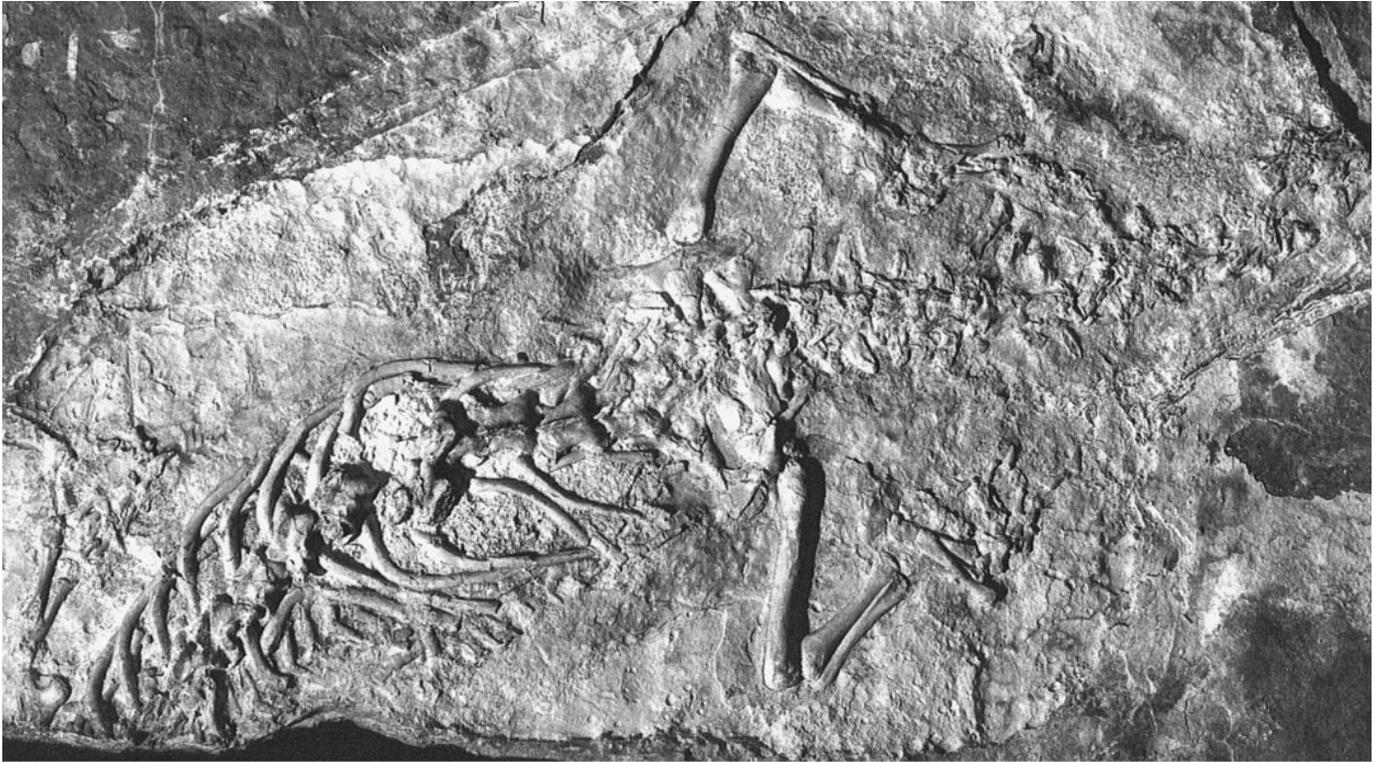


FIGURE 5—1, Photograph and 2, illustration of *Ankylosphenodon pachyostosus* n. gen. and sp. (IGM 7443). Posterior part of the presacral vertebral column, hind limbs and tail in a young specimen as preserved. Abbreviations as in Figure 1 plus: *as.*, astragalus; *ca.*, calcaneum; *c.c.r.*, cartilaginous costal ribs; *fe.*, femur; *il.*, ilium; *isc.*, ischium; *pub.*, pubis; *s.v.*, sacral vertebrae.

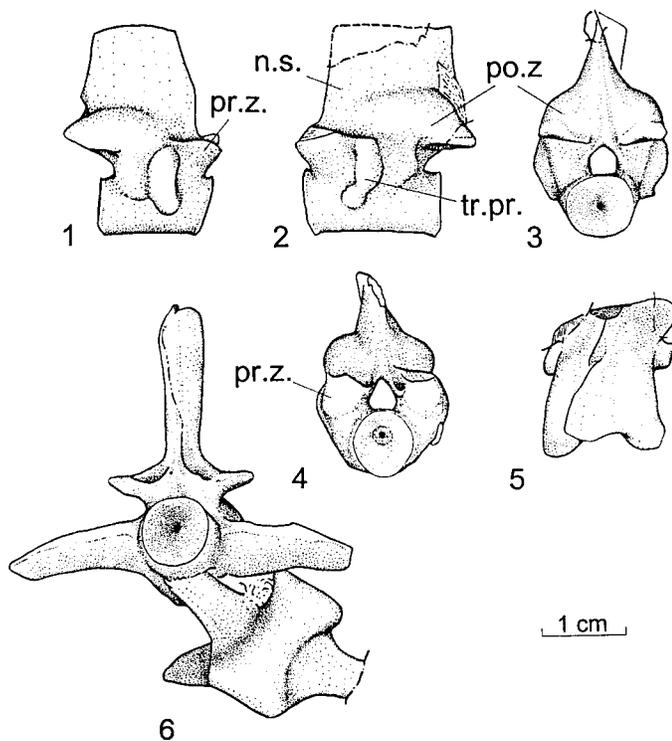


FIGURE 6—*Ankylosphenodon pachyostosus* n. gen. and sp. (IGM 7444). Detailed structure of isolated vertebra showing the swollen neural arches and horizontal zygapophyseal joints. 1, cervical vertebrae in lateral view; 2, posterior thoracic vertebrae in lateral view; 3, same in posterior view; 4, anterior thoracic vertebrae in posterior view; 5, same in dorsal view; 6, first and second caudal vertebrae in posterior and ventral view. Abbreviations: *n.s.*, neural spine; *po.z.*, postzygapophysis; *pr.z.*, prezygapophysis; *tr.pr.*, transversal process.

anterior view. The neural arches are completely fused to the centrum with no trace of a suture. The centrum is amphicoelous and notochordal, rounded and cylindrical in cross section. The notochordal canal is broad at the ends but restricted to a small perforation in the middle portion of the vertebra (Fig. 6.4). In dorsal vertebrae, the postzygapophysis forms a distinctive dorsal expansion that overrides the base of the neural spine and extends anteriorly beyond the level of the transverse process. The prezygapophysis expands in a similar fashion but extends onto the lateral surfaces of the centrum and merges with the transverse processes. Zygapophyseal articulation surfaces are rounded and oriented in the horizontal plane, restricting dorsoventral movements.

In IGM 7443, two sacral and 12 caudal vertebrae are preserved. Sacral vertebrae are stout and have sacral ribs completely fused to the centrum. The second sacral rib bears a pronounced posterior process that differs from that of sapsheosaurs in its greater width when compared to the rib. Caudal vertebrae are badly preserved and heavily crushed, but a disarticulated vertebra identified as the first caudal of IGM 7444 shows an enlarged neural spine (Fig. 6.6). Caudal vertebrae one to ten have well-developed transverse processes that become shorter and more slender posteriorly. The three most-anterior processes are oriented posterolaterally and the remainder point laterally. There are no traces of autotomous septa up to the tenth vertebra; however, on the 11th vertebra there is a faint midvertebral suture that could be an autotomous septum. This suture cannot be observed in the 12th vertebra, therefore the identification of this

structure as a true septum is dubious and may be an artifact of preservation.

No intercentral elements can be distinguished between thoracolumbar vertebrae and vertebral centra are articulated flatly bone to bone. The poor preservation of the cervical region makes it impossible to determine if cervical intercentra are present. In the caudal region, the dorsal preservation of IGM 7443 obscures the presence of caudal intercentra. Haemal arches are present after the sixth caudal.

Cervical ribs are present from the fifth vertebra to the tenth. The rib of the fifth vertebra is rather short but stout. The sixth rib is slightly larger than the fifth, and the seventh and eighth ribs are of equal size and just slightly smaller than sternal ribs. Thoracic ribs are all about the same length. All cervical ribs are holocephalous. There is no way to distinguish sternal ribs from other thoracolumbar ribs so the number attached to the sternum is unknown. Ribs from the 21st vertebra to the 23rd are free. They are smaller, thinner and have the distal ends rounded compared to the flat distal ends of thoracic ribs. The last presacral vertebra lack ribs.

Ventrally, as in other sphenodontids, there are gastralia. The central elements have a boomerang shape with an obtuse angulation. The degree of preparation of the specimen prevents examination of the gastral structure, but it seem to be arranged as in other sphenodontians. Gastral elements are preserved up to the level of the 22nd presacral vertebra and were probably absent after this point. Broad cartilaginous rib extensions, preserved as calcified tissue, connect the gastral elements to the thoracic ribs. The rib extensions are segmented in a regular pattern, much as is in *Palaeopleurosaurus* (Carroll, 1985a).

Limb elements.—Limb proportions are based on the assumption of the presence of 24 presacral vertebrae (Table 1). The humerus is only 63 percent of the femoral length. The rounded shape of the long bones, the lack of anatomical detail on the humerus, and the total absence of epiphyses suggest a delay in the ossification of limb elements.

Limb elements are well developed and heavily constructed (Figs. 7, 8). Their proportions relative to the presacral vertebral column are very similar to those of sapsheosaurs (Table 2; Fig. 9). The scapula and coracoid remain in position in the holotype, showing both bones entirely separated. The scapula is large and about the same length as the coracoid and the coracoid is rounded. The T-shaped interclavicle has relatively small lateral processes and a posterior process somewhat broadened distally.

The humerus is preserved in most specimens. It has a fully enclosed ectepicondylar foramen and an entepicondylar foramen perforates the ventral part of the humerus to the dorsal margin. The radius and ulna are subequal and about 66 percent of the humeral length. Both are stout elements with rounded distal and proximal ends and no trace of epiphyses.

All elements of the manus are present. The first digit and the intermedium are unusually large, and the lateral and medial centrale are very small and preserved displaced to the center of the manus. The medial centrale contacts the radiale, the second and probably the third distal tarsal. The lateral centrale contacts the fourth distal tarsal (and probably the third as well) and the ulnare laterally. The pisiform is enlarged and contacts the ulna extensively. The second, third, and fourth distal tarsals are subequal, the fifth is a little smaller, but the first is extremely reduced, probably associated with the enlargement of the first digit.

All metacarpals are of about the same length. The second, third, and fourth metacarpals are more slender than the first and fifth, with the first metacarpal being the broadest. Not all phalanges are preserved in the holotype, but the phalangeal count appears to conform with that of primitive lepidosaurs. Digit one has one robust phalanx plus an enlarged ungual. Digits two and

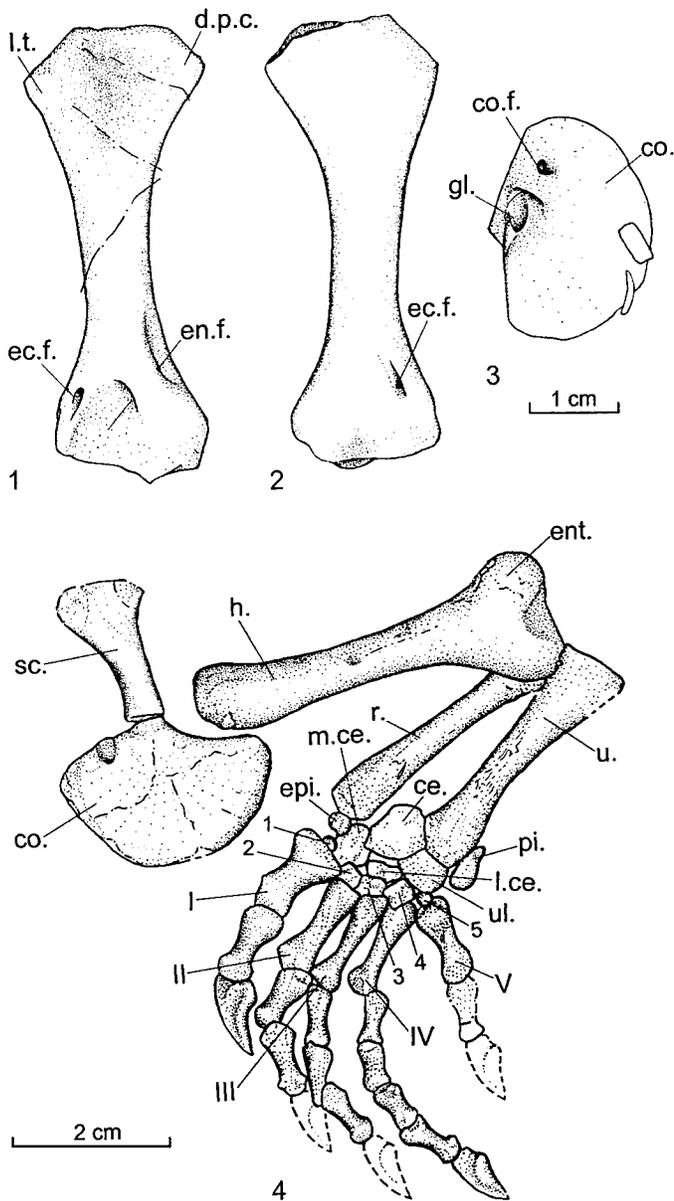


FIGURE 7—Forelimb of *Ankylosphenodon pachyostosus* n. gen. and sp. 1, Left humerus in ventral view; 2, left humerus dorsal view; 3, right coracoid in lateral view; 4, articulated left anterior limb as preserved in the holotype; 1-3 from IGM 7444, 4 from IGM 7441. Abbreviations as in Figure 1 plus: *ce.*, centrale; *co.f.*, coracoid foramen; *d.p.c.*, deltopectoral crest; *ec.f.*, ectepicondylar foramen; *en.f.*, entepicondylar foramen; *ent.*, entepicondyle; *epi.*, epiphysis; *gl.*, glenoid; *l.ce.*, lateral centrale; *l.t.*, lateral tuber; *m.ce.*, medial centrale; *pi.*, pisiform; *ul.*, ulnare. Distal carpals in Arabic numerals and metatarsals in Roman numerals.

three lack the unguis, but these elements are well preserved in IGM 7443. Digit four has five phalanges but the tip of the unguis is missing. Only the proximal portion of the first phalanx on the fifth digit is preserved.

The pelvic girdle of 7443 is preserved in dorsal view and mostly obscured by the last thoracic vertebrae and the sacra. The right ilium is preserved intact but the left is broken and bent onto the sacral region, covering the second sacral rib. The dorsal surface of the ilium is straight and shows traces of a dorsal iliac

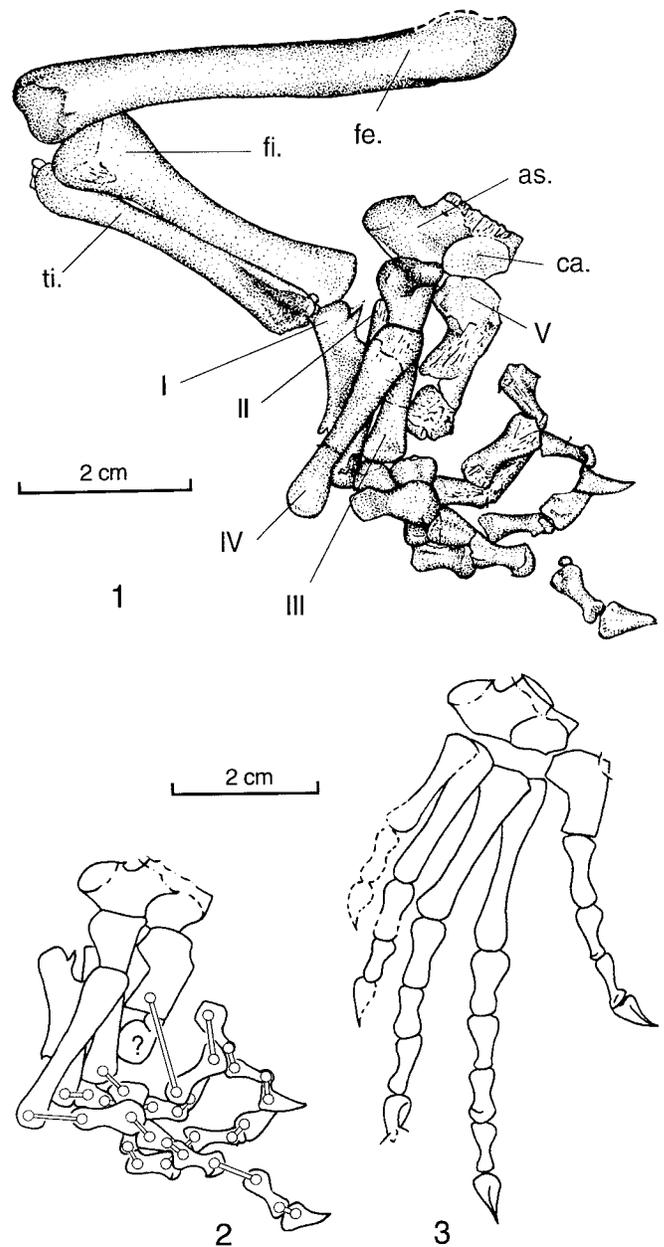
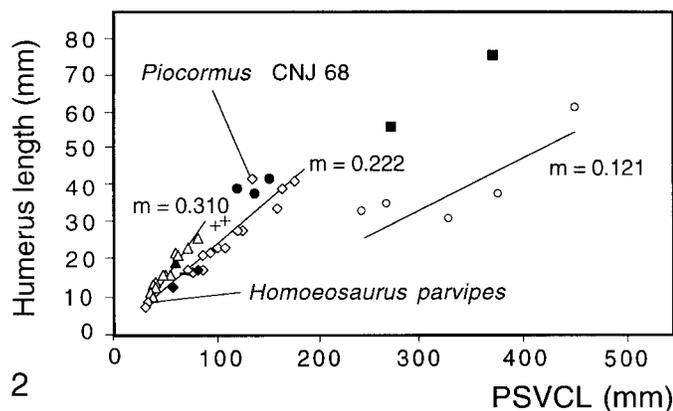
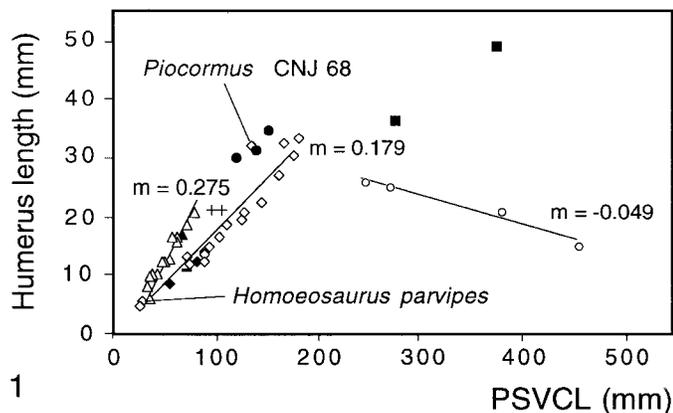


FIGURE 8—Hind limb of *Ankylosphenodon pachyostosus* n. gen. and sp. (IGM 7443). 1, Left hind limb as preserved; 2 and 3, reconstruction of the left pes. Abbreviations as in Figure 5. Metatarsals in Roman numerals.

tuber. The posterior end is broadened and does not taper posteriorly as in other sphenodontians. The overall shape of the ilium resembles that of *Palaeopleurosaurus*. Anteriorly, an enlarged flange extends onto a medial sulcus on the broadened dorsal head of the pubis, suggesting solid construction. The shape of the pubis resembles that of *Leptosaurus* and *Homoeosaurus*, in which the medial process is broadened medially but constricted close to the contact with the ilium. The ischium has a well developed posterior process but pointing slightly medially. No fusion of pelvic elements had occurred.

The femur is nearly 40 percent longer than the humerus (Table 1). The tibia and the fibula are subequal in length and both elements are about 35 percent of the femoral length. The tibia



- *Ankylosphenodon*
- ◆ *Brachyrhinodon*
- + *Clevosaurus*
- △ *Homoeosaurus*
- *Planocephalosaurus*
- *Pleurosaurs*
- ▲ *Polysphenodon*
- ◇ *Sapheosaurs*
- *Sphenodon*

FIGURE 9—Limb proportion relative to the presacral vertebrae column length (PSVCL) in different sphenodontians. 1, Humerus length vs. PSVCL; 2, femur length vs. PSVCL. Data from Table 2.

is about double the width of the fibula. As with the anterior limbs, they bear rounded ends with no ossified epiphyses. Pes elements are heavily crushed, making it difficult to reconstruct their shape and structure. The astragalus and calcaneum are fused but a suture is still evident. The fibular articulation is separated from the tibial articulation by a groove, as in *Sphenodon*. The first digit is not preserved, but, the phalangeal count seems to be typically reptilian (2? . 3. 4. 5. 4). In the left hind limb of IGM 7443, digit four is preserved sitting on top of all other digits, followed by digit three. The first and second metatarsals lie below other metapodial elements. Metatarsal fifth is hooked, but because it is preserved dorsally, the position of the ventral tubercles is not known. Phalanges of the fifth digit are relatively smaller and slender compared to the others.

Etymology.—In reference to the pachyostotic ribs and vertebrae.

Types.—Holotype: Instituto de Geología, Universidad Nacional Autónoma de México. Cat. No. IGM 7441 (Fig. 1), crushed, anterior portion of a complete skeleton. Paratypes: IGM 7442, skull and proximal elements of the right forelimb, split in

half and preserved in part and counterpart blocks; IGM 7443, almost complete postcranial skeleton; IGM 7444, disarticulated postcranial skeleton; IGM 7445, crystallized skull associated with some of the anterior portion of the postcranial skeleton; IGM 7446, presacral vertebra series associated with ribs. IGM 7447, disarticulated postcranial skeleton.

Occurrence.—Middle Member of the Tlayua Formation (Pantoja-Alor, 1992), Early Cretaceous, Middle or Late Albian (Seibertz and Buitrón, 1987). The Tlayua Formation is located on the Tlayua Quarry, 2 Km South East of the Colonia Morelos, near Tepexi de Rodríguez, Puebla, México. The holotype (IGM 7441) was collected in Locality No. IGM 2280-NSF#3; IGM 7443, IGM 7445, and IGM 7446 in Locality No. IGM 370 Cantera Tlayua-Aranguty; and IGM 7442, IGM 7444, and IGM 7447 in Locality No. IGM 2432-Cantera Tlayua-IGM (IGM 7444 in level Z-V and IGM 7447 in level Z-XXIII).

COMPARISON WITH OTHER SPHENODONTIANS AND PHYLOGENY

The lack of a well-preserved skull makes the establishment of the phylogenetic relationships of *Ankylosphenodon* n. gen. quite difficult. Sphenodontian phylogeny has been based largely on skull morphology, and postcranial elements have been considered secondary or unimportant (Fraser and Benton, 1989; Wu, 1994). Reynoso (1996, 1997) and Reynoso and Clark (1998) attempted to consider all available evidence in reconstructing phylogenetic relationships. However, in the published data matrix only a small percentage of the information deals with postcranial morphology.

Deeply-ankylosed teeth with possible continuous growth and a stout axial skeleton are unique characters that distinguish *Ankylosphenodon* from all other known sphenodontians and confirms its identity as a new taxon. The identity of *Ankylosphenodon* as a rhychocephalian is confirmed by the distinctive posterior process of the dentary extending far posterior to the coronoid process and bordering the ventral margin of the lower jaw. The presence of a posterior process on the second sacral vertebrae is shared with all sphenodontians, and an enlarged coronoid process is shared with sphenodontids (as defined by Reynoso, 1996) and *Planocephalosaurus*. *Ankylosphenodon* shares with all sphenodontids an upper temporal fenestra with a diameter greater than one-fourth of the skull length, and probably the modification of the premaxillae into a chisel-like structure. The presence of an enlarged posterior process of the ischium shared with *Homoeosaurus* and *Sapheosaurus*, may suggest close relationships of *Ankylosphenodon* to either taxa.

Limb proportions of different sphenodontians are listed in Table 2. Graphs of the length of the humerus or femur against the length of the presacral vertebrae column show three basic trends (Fig. 9). The first trend is described by *Homoeosaurus* and *Polysphenodon*, which have distinctly long legged-bodies compared to members describing the second trend (*Sapheosaurus*, *Leptosaurus*, *Kallimodon*, *Piocormus*, *Brachyrhinodon*, and *Planocephalosaurus*). The third trend includes the obligatorily-aquatic sphenodontians *Pleurosaurs* and *Palaeopleurosaurs* with very short limbs. In the first two trends, some overlap is observed between the smaller members of both lineages, probably correlated with typical limb disproportion observed in hatchling or juvenile stages. The position of *Clevosaurus* is ambiguous, since the humerus and femur fell in the sapheosaur and homoeosaur trends respectively. The limb proportions of *Ankylosphenodon*, especially in the femur, fit within the range of variation of sapheosaurs (second trend).

Ankylosphenodon is similar in much of the skeleton to sapheosaur sphenodontians. Sapheosaurs are an assemblage of

TABLE 2—Limb proportions in rhynchocephalians. For *Ankylosphenodon pachyostosus* n. gen. and sp., the humerus and femur length was calculated scaling the humerus of the holotype and the femur of IGM 7443 based on the 19th presacral vertebrae and the humerus distal end. Abbreviations: EM, l'Ecole de Mines; FSL, Centre des Sciences de la Terre Université Claude Bernard, Lyon; RPM, Redpath Museum, McGill University; KU, Kansas University. For other abbreviations refer to the original sources. Measurements in parentheses are average or approximate. * From several specimens.

Taxa	Catalogue number	PSVC length	Humerus length	Femur length	Humerus/PSVCL	Femur/PSVCL	Humerus/femur length	Source
<i>Ankylosphenodon pachyostosus</i>	Holotype	374.0	49.3	75.4	0.133	0.202	0.654	
	IGM 7443	276.1	36.5	56.1	0.132	0.203	0.651	
<i>Gephyrosaurus bridensis</i>	*		(16)	(22.5)			0.711	Evans, 1981
<i>Planocephalosaurus robinsonae</i>	*	(68)	(11)	(16)	0.162	0.235	0.688	Fraser and Walkden, 1984
<i>Polysphenodon mülleri</i>	MB R 1032	63	17	21.5	0.270	0.341	0.791	Fraser and Benton, 1989
<i>Brachyrhinodon taylora</i>	BMNH R 4776	81	13	18	0.160	0.222	0.722	Fraser and Benton, 1989
	BMNH R 4777	56	9	13	0.161	0.232	0.692	Fraser and Benton, 1989
<i>Clevosaurus hudsoni</i>	*	100	20	29	0.200	0.290	0.690	Fraser, 1988
	UMZC T1271	98	20	28	0.204	0.286	0.714	Fraser and Benton, 1989
<i>Pleurosaurus goldfussi</i>	no. 15640	380	21	38	0.055	0.100	0.553	Cocude-Michel, 1963
	no. 10339+40	330		31		0.094		Cocude-Michel, 1967a
<i>Pleurosaurus ginsburgi</i>	CNJ 67	454	15	(62)	0.033	0.137	0.242	Fabre, 1974
<i>Palaeopleurosaurus posidoniae</i>	no. 50722	242.2	26	33	0.107	0.136	0.788	Carroll, 1985a
	no. 50721	269.3	25	35	0.093	0.130	0.714	Carroll, 1985a
<i>Homoeosaurus maximilliani</i>	Munich	72	19	23	0.264	0.319	0.826	Cocude-Michel, 1963
	no. 1937-1-40	50	13	16.3	0.260	0.326	0.798	Cocude-Michel, 1963
	no. 414	46	13	16.3	0.283	0.354	0.798	Cocude-Michel, 1963
	no. Rhy 4	33	8.5	12	0.258	0.364	0.708	Cocude-Michel, 1963
	no. Rhy 5	62	16	21	0.258	0.339	0.762	Cocude-Michel, 1963
	RMc 1	36	10	13.4	0.278	0.372	0.746	Cocude-Michel, 1963
	RMc 2	37	10	13.4	0.270	0.362	0.746	Cocude-Michel, 1963
	RpM	37	10.1	13.5	0.273	0.365	0.748	Cocude-Michel, 1963
	no. 15675 Lyon	59	17.1	22	0.290	0.373	0.777	Cocude-Michel, 1963
	no. 3955	63	17	21.5	0.270	0.341	0.791	Cocude-Michel, 1967b
	Coll. Ghirardi	80	21	26	0.263	0.325	0.808	Fabre, 1973
<i>Homoeosaurus solnhofensis</i>	no. R4073	55	13.2	16.3	0.240	0.296	0.810	Cocude-Michel, 1963
<i>Homoeosaurus parvipes</i>	no. Rhy 1	36	6.5	10	0.181	0.278	0.650	Cocude-Michel, 1963
<i>Sapheosaurus thiollierei</i>	no. 15672	180	33.5		0.186			Cocude-Michel, 1963
	no. 15649	165	32.5	(40)	0.190	0.242	0.813	Cocude-Michel, 1963
	no. 15645	176	30.5	41	0.174	0.234	0.744	Cocude-Michel, 1963
	FSL (no number)	160	27	34	0.169	0.213	0.794	
<i>Kallimodon pulchellus</i>	no. 1887-VI-1	87.5	14.5	21	0.166	0.240	0.690	Cocude-Michel, 1963
	no. 1887-VI-2	75	12.4	17	0.165	0.227	0.729	Cocude-Michel, 1963
	no. 1911-I-34	87	14	18.2	0.161	0.209	0.769	Cocude-Michel, 1963
	no. 1922-I-15	87	12.5	18	0.144	0.207	0.694	Cocude-Michel, 1963
	no. Rhy 2	72	13.6	17.3	0.189	0.240	0.786	Cocude-Michel, 1963
	no. Rhy 3	102	17	23.3	0.167	0.228	0.730	Cocude-Michel, 1963
	no. 15671	144	23		0.160			Cocude-Michel, 1963
	nos. 15674+75	126.5	21	28	0.166	0.221	0.750	Cocude-Michel, 1963
	Sp.2 EM	123	20	28	0.163	0.228	0.714	Cocude-Michel, 1963
	CNJ 72	93	15.2	22	0.163	0.237	0.691	
<i>Piocormus laticeps</i>	(cast)	108	19	23	0.176	0.213	0.826	Cocude-Michel, 1963
	CNJ 68	135	32	42	0.237	0.311	0.762	
<i>Leptosaurus neptunius</i>	(no number)	27.6	5.8	7.7	0.212	0.279	0.753	Cocude-Michel, 1963
	no. R. 4108	31	6	8.6	0.194	0.277	0.698	Cocude-Michel, 1963
<i>Sphenodon</i>	(no number)	120	30	39	0.250	0.325	0.769	Fraser and Benton, 1989
	RPM	151.1	34.5	41.9	0.228	0.277	0.823	
	KU 98454	137.8	31.3	38.2	0.227	0.277	0.819	

species that are probably congeneric or even conspecific (Ahmad, 1993). The lack of well-prepared material and good descriptions makes their taxonomic status problematic. *Leptosaurus*, *Sapheosaurus*, *Piocormus*, and *Kallimodon* from the Upper Jurassic limestones of Bavaria (Germany) and Cerin and Canjuers (France) have been grouped within the Sapheosauridae (Hoffstetter, 1955; Kuhn, 1969; Gauthier et al., 1988a). Evans (1988) did not find any characters separating these taxa, but Wu (1994) and Reynoso (1996) have placed *Sapheosaurus* and *Kallimodon* in a paraphyletic position. Only small differences in snout length separate these genera. The range of ontogenetic and intraspecific variation of skull proportions have not been studied in sphenodontians, and characters associated with these features might be dubious.

Sapheosaurs are distinguished by the enlargement of the post-orbital skull region, which exceeds the length of the preorbital region. They also share an elongate but narrow upper temporal fenestra, a broad upper temporal arch, and laterally compressed vertebral centra (Cocude-Michel, 1963; Gauthier et al., 1988a).

As mentioned in the description, the skull of *Ankylosphenodon* is poorly known, although in the holotype the postorbital region of the skull is clearly longer than the preorbital region, as it is with sapheosaurs. This condition is also present in clevosaurus (Wu, 1994). However, on the base of current phylogenetic analysis, it is probably a convergent condition which in *Polysphenodon* and *Brachyrhinodon* is caused by an extensive reduction of the snout. Clevosaurus have a broad skull, but with very different appearance compared to sapheosaurs. The anteroposteriorly-enlarged skull of *Ankylosphenodon* resembles more the skull of sapheosaurs than that of clevosaurus. The width of the upper temporal fenestra is not known, as the holotype and only specimen in which this character might be established is preserved in lateral view. The enlarged upper temporal fenestra also resembles that of sapheosaurs. A similarly enlarged temporal fenestra is present in *Palaeopleurosaurus* (Carroll, 1985a), although the structure of the supratemporal arch is quite distinct. In *Palaeopleurosaurus* the postorbital extends far posteriorly onto the dorsal margin of the upper temporal fenestra, restricting

TABLE 3—Description of three different trends of limb proportions in sphenodontians. Values for (m) based on well represented taxa: Trend I in *Homoeosaurus*; trend II in sapsheosaurs for, and trend III in *Pleurosaurus* + *Palaeopleurosaurus*. Range includes all taxa belonging to each trend. *Piocormus laticeps* (CNJ 68) excluded from calculations; see text. Data from Table 2 and Figure 9.

Trend number	Taxa	Slope (m)	Range	Maximum	Minimum	Specimens overlapped with following trend	Minimum excluding overlapped specimen	Range between this and next trend	Estimated trend limits
<i>Humerus/PSVCL</i>									
I	<i>Homoeosaurus</i>	0.275	0.109	0.290	0.181	1	0.240	0.028	≤0.290, ≥0.226
II	<i>Polysphenodon</i> <i>Sapsheosaurs</i> <i>Brachyrhinodon</i>	0.179	0.068	0.212	0.144	—	—	0.037	≤0.225, ≥0.126
III	<i>Planocephalosaurus</i> <i>Pleurosaurus</i> <i>Palaeopleurosaurus</i>	0.049	0.074	0.107	0.033	—	—	?	≤0.125, ≥0.033
<i>Femur/PSVCL</i>									
I	<i>Homoeosaurus</i>	0.310	0.095	0.373	0.278	1	0.296	0.017	≤0.373, ≥0.288
II	<i>Polysphenodon</i> <i>Sapsheosaurs</i> <i>Brachyrhinodon</i>	0.222	0.072	0.279	0.207	—	—	0.070	≤0.287, ≥0.172
III	<i>Planocephalosaurus</i> <i>Pleurosaurus</i> <i>Palaeopleurosaurus</i>	0.121	0.043	0.137	0.094	—	—	?	≤0.171, ≥0.094

the squamosal to its very posterior margin. The primitive condition is retained in sapsheosaurs and *Ankylosphenodon* where the postorbital is shorter, and the squamosal extends anteriorly dorsal to the postorbital posterior process, close to the anterior half of the upper temporal fenestra. The postorbital process in *Ankylosphenodon* is shorter than in *Sapsheosaurus* and other sphenodontians. It does not extend beyond the anterior half of the upper temporal fenestra.

The presence of propalinal jaw action, indicated by the anteroposteriorly oriented tooth wear marks and the anteroposteriorly enlarged mandibular condyle, suggests affinities with *Zapatadon* (Reynoso and Clark, 1998), eilenodontines (Throckmorton et al., 1981; Rasmussen and Callison, 1981) and sphenodontines (Reynoso, 1996). However, the lack of other good synapomorphies makes affinities uncertain. The similarity with *Sapsheosaurus* plus the presence of propalinal jaw action may place *Ankylosphenodon* in an intermediate position between sapsheosaurs and sphenodontines.

A cladistic analysis using the branch and bound search algorithm of PAUP (Swofford, 1993) and Reynoso's (1996) data matrix with additional characters in subsequent papers (Reynoso, 1997; Reynoso and Clark, 1998) supports the sister-group relationships of *Ankylosphenodon* with *Eilenodon* and/or *Toxolophosaurus* (most parsimonious tree length = 129; consistency index = 0.643; retention index = 0.731). In this analysis *Prolacerta* was included as a third out-group, as a representative of basal archosauromorphs. *Clevoosaurus hudsoni*, *C. petilus*, *C. mcgilli*, and *C. bairdi* were merged into a single taxon, causing character 46 to become uninformative. Characters 22, 26, 29, 42, and 48 were modified and character 53 is new (Appendix). The primitive condition (0) of character 22 was modified to "mandibular foramen small or absent"; derived states 3 and 4, "thecodont" and "ankylothecodont" tooth implantation were added to character 26; derived state (2) "teeth transversely flattened" was added to character 29; character 42 was recoded according to the three different trends of limb proportions in Figure 9; and primitive state (0) "no contact between pterygoid bones" was added to character 48. In character 42, the lack of good sample size prevented the establishment of an accurate limit between limb trends (e.g., through the standard error). Then, the limits between character states were estimated by averaging the maximum value of a trend and the minimum value of the next trend, excluding highly discordant data (Table 3).

The strict consensus of 69 equally-parsimonious trees is unresolved within the Sphenodontidae (Fig. 10). This is primarily due to the almost complete lack of information for *Toxolophosaurus*, *Eilenodon*, *Cynosphenodon*, and *Ankylosphenodon*, the presence of several autapomorphic characters in *Ankylosphenodon* that cannot be satisfactorily applied to previously published transformation series, and the lack of good synapomorphies to support the inclusion of the new taxon in any other known group. The only synapomorphy that unambiguously joins *Ankylosphenodon* with eilenodontids is the presence of a high mandible. Four other synapomorphies listed in the Appendix define this node: propalinal jaw motion, short retroarticular process, wide marginal teeth, and swollen neural arches. Propalinal jaw motion is shared with *Zapatadon*, sphenodontines, and eilenodontines. As pointed out before, and in other published phylogenies (e.g., Fraser and Benton, 1989; Wu, 1994; Reynoso, 1996; Reynoso and Clark, 1988), this could be a synapomorphy grouping *Zapatadon*, *Toxolophosaurus*, *Eilenodon*, *Cynosphenodon*, *Sphenodon* and *Ankylosphenodon*. A short retroarticular process is shared with *Homoeosaurus*, *Pamizinsaurus*, *Eilenodon*, and *Sphenodon*, but this character may define a broader group. Wide marginal teeth are only present in eilenodontines and this condition is absent in *Ankylosphenodon*. In the data matrix it was coded as not applicable since none of the conditions describes precisely that of *Ankylosphenodon*. The presence of swollen neural arches cannot be established in eilenodontids, for which the vertebrae are unknown. If the *Ankylosphenodon*-eilenodontids sister-group relationships were accepted, similarities with sapsheosaurs would be convergent; i.e. a stout skeleton would have been acquired independently and the sapsheosaur robustness would not be transitional to the *Ankylosphenodon* condition. Unfortunately eilenodontines are only known from scattered material, and descriptions are based exclusively on their lower jaw. Although mandibles are very rich in characters, information about skull and postcranium is missing, and this last hypothesis of sister-group relationships should be considered as provisional until eilenodontids and/or *Ankylosphenodon* become better known.

MASTICATORY APPARATUS

Tooth structure and growth.—The peculiar dental morphology of *Ankylosphenodon pachyostosis* n. gen. and sp. deserves

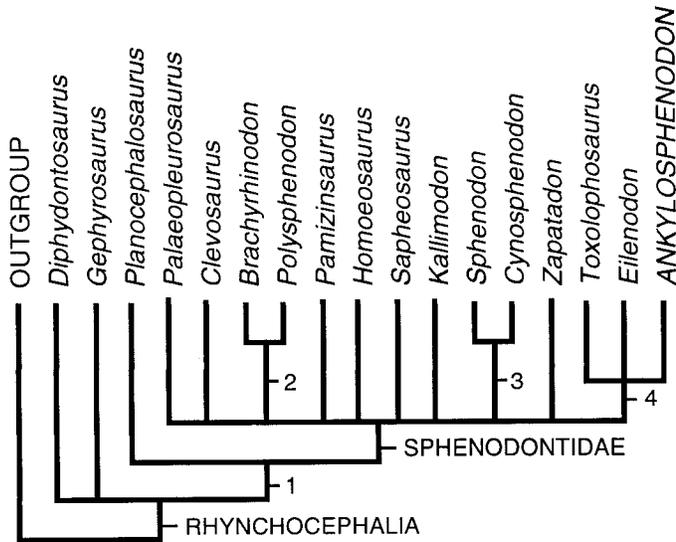


FIGURE 10—Strict consensus of 69 equally parsimonious trees (tree length = 129; consistency index = 0.643; retention index = 0.731) showing the sister-group relationships of *Ankylosphenodon*. Results obtained using the branch-and-bound search algorithm of PAUP and data from Reynoso (1996 and subsequent) with some modifications and one new character (Appendix). Apomorphy list (only unambiguous characters): RHYNCHOCEPHALIA: frontals fused, lower temporal bar bowed away beyond the limit of the abductor chamber, posterior process of the dentary ends posterior to coronoid process, supratemporal absent, small contact between pterygoid bones. NODE 1: lower temporal bar complete, broad mandibular symphysis, coronoid process pronounced, tooth added at the posterior part of the dental series, dental regionalization, three or less premaxillary teeth, posterior maxillary teeth with posteromedial flanges, dentary teeth with flanges, second sacral rib with pronounced posterior process, broad contact between pterygoids. SPHENODONTIDAE: length of supratemporal fenestra more than one fourth of skull length, broad posterior process of maxilla, frontals separated, narrow parietal table, parietal crest, posterior end of parietal slightly incurved, parietal foramen anterior to or level with anterior margin of supratemporal fenestra, pterygoid precluded from suborbital fenestra, enlarged mandibular foramen, well established lateral and medial wear facets on teeth, premaxilla forming a chisel-like structure, single lateral tooth row on palatines, orbital length less than one third of the skull length, enlarged quadrate-quadratojugal foramen. NODE 2: length of antorbital region of skull one fourth or less of skull length, broad parietal table, parietal crest absent, greatly incurved posterior edge of parietal, parietal foramen posterior to anterior margin of supratemporal fenestra, two rows of pterygoid teeth, small anterior contact between pterygoids. NODE 3, SPHENODONTINES: propalinal jaw action, anterior caniniform tooth on jaw and dentary. NODE 4: propalinal jaw action, deep mandible, retroarticular process reduced, marginal teeth expanded mediolaterally. A full description of the tree in the Appendix.

special attention. As mentioned above, the teeth are anterodorsally-oriented ridges deeply ankylosed to the jaw (Figs. 3, 4). Open dentine at the posterior end of worn teeth suggests the presence of continuous tooth growth, previously not reported in lepidosaurs. A unique feature of sphenodontians, including *Ankylosphenodon*, is the addition of new teeth at the posterior end of the jaw, while it grows (Harrison, 1901; Robinson, 1976). Older teeth occur anteriorly in the jaw and more recently-erupted teeth posteriorly. This permits the recognition of different ontogenetic stages and changes of tooth morphology due to wear in a single tooth series.

The wear pattern in other sphenodontids with propalinal jaw action responds to friction generated laterally and medially by

the maxillary and palatine tooth series (Robinson, 1976). In *Sphenodon*, as well as in *Toxolophosaurus* and *Cynosphenodon* (Throckmorton et al., 1981; Reynoso, 1996), the lateral and medial flanges of the tooth are the first structures to be worn out. After these are completely gone, the body of the tooth starts to be used as a chewing surface and continues to decrease in height until it disappears. Because anterior teeth were initially smaller and have been subjected to wear for a longer time, they are the first to disappear and are usually absent in mature individuals. The holotype of *Cynosphenodon huizachalensis* (Reynoso, 1996) shows extreme wear on the anterior teeth, but an even more extreme case is seen in the holotype of *Sappeosaurus thiollierei* in which all teeth on the dentary have been totally worn away (Cocude-Michel, 1963; Ahmad, 1993).

In tooth wear, *Ankylosphenodon* is similar to other sphenodontians. However, the final result is influenced by its unique tooth structure and morphology. As in other sphenodontians, recently-added teeth are triangular and entirely covered with enamel. As the tooth starts to be used, the enamel on the lateral surface is the first to be worn off, and because of the lack of lateral flanges the dentine is immediately exposed (Fig. 3.2). Subsequently, the medial surface becomes eroded as well. Because the dentine is softer than the enamel it will be worn rapidly, resulting in a slightly deeper dentine surface surrounded by the enamel sheath. This condition is observed in the anteriormost teeth (Fig. 3.3). The great difference between other sphenodontians and *Ankylosphenodon* is that teeth are never worn away, and in adult specimens even the smallest ones at the anterior end of the jaw preserve their triangular shape. Wear surfaces exposing dentine are displaced to the posterior part of the tooth, and recently erupted enamel covers the anterior and lateral sides of each tooth.

The internal structure of the dental series coupled with constant tooth growth seems to be responsible for the maintenance of teeth into adult stages, the preservation of the triangular shape, and the unexpected posterior orientation of the wear surface. Since the ankylosed portion of the teeth are anterodorsally oriented within the jaw, only the posterodorsal end of the elongated enamel sheath is exposed dorsally on the dentary. The triangular shape is outlined by the horizontal lateral and medial margins of the dentary. If the teeth were not overgrowing, the dentine would appear as an oval scar surrounded by enamel attached to the dorsal surface of the dentary. Instead of this, as soon as the tip of the exposed portion of the tooth becomes eroded, it is replaced by the eruption of a new oblique tooth portion pushing the wear surface to the posterior part of the tooth. The triangular shape will be maintained since the posterior end of the tooth is constituted mainly by soft dentine and would be eroded at a much faster rate than the newly erupted anterior enamel surface.

Feeding.—This particular tooth morphology undoubtedly prevents the complete loss of teeth as does happen in *Sappeosaurus*. Teeth with continuous growth, also present in some grazing mammals and in the incisors and cheek teeth of rodents, probably do prevent fast tooth erosion caused by highly abrasive substrate or food. Constant tooth growth may suggest a herbivorous diet in *Ankylosphenodon*. This feeding behavior is quite possible since the enlarged body size of *Ankylosphenodon* far exceeds the 300 g. required for a lepidosaur to afford herbivory (Pough, 1973). Within sphenodontians, only *Toxolophosaurus* and *Eilenodon* have been suggested as herbivores. Special anatomical features supporting herbivory are 1) the presence of an anteroposteriorly enlarged articular condyle of the mandible which permits grinder capacity for chewing; 2) the increase of the vertical dimensions of the mandible; 3) the close packing of dentary teeth; 4) the thickening of the enamel layer; and 5) the

widening of teeth to increase their shredding surface (Throckmorton et al., 1981; Rasmussen and Callison, 1981). Of all these features only the capacity for chewing (1) and the increase of the vertical dimensions of the jaw (2) are present in *Ankylosphenodon*.

The capacity for chewing in *Sphenodon* has been subject of several studies (Robinson, 1976; Throckmorton et al., 1981; Gorniak et al., 1982; Fraser, 1988). In this genus, an enlarged articulating condyle is associated with freedom to move the jaw anteriorly and posteriorly in a propalinal manner. Although *Sphenodon* shares this condition without being herbivorous, this only represents the primitive condition, suggesting that propalinal jaw action preceded herbivory in sphenodontian evolution. Chewing is necessary for optimal processing food, especially when consuming plant material. The mechanical shredding of plant material in the mouth will increase the amount of energy obtained from a given amount of food processed. A simple precision bite closure, present in most sphenodontians, would not be enough for processing plant food.

The absence in *Ankylosphenodon* of other expected herbivorous features present in eilenodontids suggests that the herbivorous specialization in *Ankylosphenodon* may be of a different nature. Instead of thickening the enamel for tooth durability, the teeth grew constantly, replacing worn surfaces with new enamel. The absence of laterally expanded teeth would be the only contradicting feature; however, in herbivorous squamates (e.g., *Iguana iguana* or *Amblyrhynchus cristatus*) there are no particular specializations in tooth morphology for grinding, although chewing capabilities are present. Contrary to supposedly primitive insectivorous sphenodontians, *Ankylosphenodon* does not show grasping or piercing teeth. As discussed above, the posterolateral wear surface of each tooth is broad and somewhat flattened. If the jaw is moved anteroposteriorly, as in *Sphenodon* or *Toxolophosaurus*, this surface would form an active grinding surface. Its grinding capabilities would not be as effective as the broad teeth of eilenodontids, but it seems that this advantage was exchanged in order to develop long-lasting, constantly-growing teeth. Contrasting tooth morphologies are also seen in artiodactyl and perissodactyl mammals (Young, 1975; Romer and Parsons, 1986). In the highly derived hypsodont horse dentition, the tooth crowns are larger and have more enamel plications than those of artiodactyls. This would enhance great grinding surface and long durability. In hypsodont dentition, however, the maximum tooth length is acquired in early stages of development, and teeth can be completely worn down in old organisms, resulting in starvation and death. In grazing ruminants, solenodont teeth may be not as durable as those of horses, but constant growth allows replacement of grinding surfaces throughout life.

MODE OF LIFE

Pachyostotic skeletons have long been associated with semi-aquatic behavior (Nopcsa, 1923; Nopcsa and Heidsieck, 1934) since they are not manifested in obligatory aquatic vertebrates. Pachyostotic skeletons are present in mesosaurs, nothosaurs, primitive mosasaurs, primitive snakes, chelonians, and champsosaurs (de Ricqlès, 1974), and among mammals in sirenians. The presence of stout ribs has been explained as a resistant structure to prevent lung collapse during diving (Nopcsa, 1923; Ginsburg, 1967) or to increase body weight to counteract the positive buoyancy that expanded lungs provide during apnea (Zangerl, 1935; Carroll, 1988). The persistence of cartilage within pachyostotic ribs has been observed in mesosaurs, suggesting that pachyostosis is a result of neoteny (de Ricqlès, 1974). Pachyostotic ribs are also correlated with a delay in the ossification in limb bones, carpus, and tarsus of aquatic organisms after

limbs are freed from support of body weight (Romer, 1956). Delay in the fusion of the neural arch and centra in nothosaurs and the sphenodontian *Palaeopleurosaurus* (Carroll, 1985a) have also been associated with the same phenomena. Pachyostotic ribs in *Ankylosphenodon* n. gen., although not as extreme as in mesosaurs and nothosaurs (e.g., *Pachypleurosaurus*), does suggest a partially-aquatic behavior. As in other partially-aquatic forms, the limbs of *Ankylosphenodon* are not fully ossified. The ends of the limb elements are somewhat rounded with no evidence of epiphyseal ossifications; however, the humerus still resemble those of fully-terrestrial sphenodontians. The lack of other aquatic modification such as dorsoventral expansion of the tail for propulsion and extreme reduction of limbs, as in other long bodied aquatic sphenodontids (Fabre, 1974; Carroll, 1985a), suggests that *Ankylosphenodon* was still dependent on terrestrial locomotion. All carpal elements are fully ossified and vertebral neural arches and centra are totally fused in the holotype. In the younger specimen (IGM 7443), there are no traces of the distal carpal elements, but the astragalus and calcaneum are already fused. The lack of carpal ossification in juveniles, associated with the presence of rounded distal ends on long bones may indicate that there is a certain delay in the ossification of *Ankylosphenodon*. The delay, however, is not comparable in degree to that of other more-obligated aquatic reptiles.

Contrary to the aquatic behavior suggested by the structure and degree of ossification of ribs and appendicular skeleton, the presence of strong intervertebral articulation, with well-developed horizontally-oriented zygapophyses, seems to indicate terrestriality. Swollen neural arches with horizontal zygapophyseal articulations are present in many terrestrial forms including some microsaurian amphibians, the seymouriamorph *Seymouria*, diadectomorphs, pareiasaurs, procolophonians, captorhinids, araeoscelidians, and the synapsid *Varanosaurus* (Carroll and Gaskill, 1978; Heaton, 1980; Sumida, 1990). Their presence in large captorhinids (e.g., *Labidosaurus*, *Kahneria*, and *Rothianiscus*) has been explained as preventing dorsoventral movement in order to support the rib cage and viscera in heavy organisms (Dilkes and Reisz, 1986). However, these structures do not seem to be size-related, since they are expressed in the small procolophonid *Owenetta* and in the giant pareiasaur *Sunctusaurus* (Heaton and Reisz, 1986; Reisz and Laurin, 1991).

Swollen neural arches with horizontal (or almost horizontal) zygapophyseal articulations are not unique to terrestrial environments and are present in a variety of aquatic forms such as the seymouriamorph *Kotlassia*, the early diapsid *Claudiosaurus* (Carroll, 1981), the nothosaurs [e.g., *Pachypleurosaurus* (Carroll and Gaskill, 1985), and *Serpianosaurus* (Rieppel, 1989)], and plesiosaurs [e.g., *Pistosaurus* (Meyer, 1855)]. In these organisms the structure of the vertebral column cannot be explained by the need for the support because of buoyancy. This structure has been interpreted as a primitive feature among amniotes, and it appears to be widely distributed in clades branching off basal to Sauria (Heaton and Reisz, 1986; Gauthier et al., 1988b); however, differences in many features of the vertebrae suggest that they arise convergently in several taxa (Carroll, 1988; Laurin and Reisz, 1995). Basal sphenodontians bear vertebrae with small and steeply-oriented zygapophyses (Evans, 1981), the primitive lepidosaurian condition. The swollen horizontal zygapophyses of *Ankylosphenodon* were then acquired secondarily, as in other amniote lineages. Swollen neural arches are also present in sapsheosaurs, suggesting that these structures were probably shared ancestrally in these two groups. The aquatic affinities of *Sapsheosaurus* were already suggested by Ahmad (1993) but without convincing arguments. However, the presence of swollen and horizontally-directed zygapophyses associated with pachyostotic ribs is shared convergently with some

aquatic genera and may have real functional implications. The less fully-developed swollen neural arches and the lack of pachyostotic ribs in *Sapheosaurus* would indicate a lesser degree of aquatic specialization compared to *Ankylosphenodon*. In *Sapheosaurus*, the orientation of the zygapophyseal articulation cannot be established because of the lack of a good lateral view of dorsal vertebrae and because of compression of dorsally-exposed vertebrae.

Carroll (1985b) pointed to the importance of body rigidity in aquatic organisms to reduce drag. Obligatory aquatic reptiles (Categories 1 and 2 of Carroll, 1985b), such as ichthyosaurs and plesiosaurs, have relatively-rigid bodies with large dorsal spines probably associated with well-developed interspinous ligaments that limit dorsoventral flexure of the trunk. Although the zygapophyses of ichthyosaurs and mosasaurs are reduced or totally lost, probably associated with an increase of the epaxial musculature (Carroll, 1988), the zygapophyses of *Claudiosaurus* and nothosaurs (Category 4 of Carroll, 1985b), are still an important element for the stiffening of the vertebral column. In *Pachypleurosaurus* and *Simosaurus* (Carroll and Gaskill, 1985; Rieppel, 1994), intraprezygapophyseal and intrapostzygapophyseal articulations (different from the zygosphenes and zygantrum articulations) give extra strength, and in *Dactylosaurus* and *Serpianosaurus* lateral movements are limited by peculiar intervertebral articulations in which the postzygapophysis fits in a groove on the prezygapophysis (Sues and Carroll, 1985; Rieppel, 1989).

Ankylosphenodon resembles closely Category 5 of aquatic reptiles (Carroll, 1985b). It still has long limbs effective for terrestrial locomotion. Crocodiles, and the marine iguana *Amblyrhynchus* belongs to this groups. In these reptiles, swimming is performed by lateral undulations of the tail (Mantel, 1940; Hobson, 1965). In crocodiles, lateral undulations of the body are not as important as the tail for propulsion. Lateral movements of the head and trunk are restricted to very narrow amplitude waves. These movements are probably caused secondarily by major lateral undulations of the tail which generates most of the propulsion (Mantel, 1940). The swimming patterns of *Amblyrhynchus* have not been properly studied and only some observations of its behavior have been reported and summarized by Dawson et al. (1977). From the photograph presented by Hobson (1965) it is clear that the mode of swimming is very similar to crocodiles. The body remains straight while the tail forms a broad arc, but the degree of lateral movements of the trunk related to the body is uncertain. In both the marine iguana and crocodiles the limbs are not important for swimming, and they are folded against the body to reduce drag.

Because of phylogenetic affinities (and possible historical constraints) it is expected that the swimming pattern of *Ankylosphenodon* may have been similar to that of *Amblyrhynchus*. In *Ankylosphenodon* the only ancestral anatomical feature that would strengthen the vertebral column is the pre-postzygapophysis complex. Their widely open position and large contact surfaces would have strongly resisted dorsoventral movement and the swollen dorsal surfaces of the zygapophyses must have increased their resistance to stress. The presence of enlarged and broad neural spines suggests a well-developed associated musculature and interspinous ligaments that may have played an important role in trunk vertebral column rigidity. The lack of structures that limit lateral movements suggest that they were possible. These movements may be a concession to terrestrial locomotion, but they may also be important for swimming by increasing the lateral body surface in contact with the water. Among lepidosaurs, snakes are the only organisms with similarly swollen, horizontally-oriented, broadly-open zygapophyses. These structures, associated with well-developed zygosphenes

and zygantrum accessory articulations, are obviously necessary to avoid dorsoventral flexure while providing lateral undulation, their only means of propulsion in either terrestrial or aquatic environments. The primitive Cenomanian marine snakelike lepidosaur *Pachyrhachis* (Haas, 1979), a probable intermediate morphotype between varanids and snakes, has similar vertebral structures, and is associated with pachyostotic ribs similar to those of *Ankylosphenodon*.

The sphenodontians *Pleurosaurus* and *Palaeopleurosaurus* have been classified with lizards as having a Category 3 locomotion system (Carroll, 1985b). The serpentine shape and the reduction of limbs is characteristic of this group, but the vertebral and rib specializations observed in *Ankylosphenodon* and other aquatic reptiles are not present (Cocude-Michael, 1963; Fabre, 1974; Carroll, 1985a). This suggests that pleurosaur sphenodontians were distinctly modified to aquatic life and were probably obligatorily aquatic.

BIOGEOGRAPHICAL AND PALEOECOLOGICAL SIGNIFICANCE

Ankylosphenodon pachyostotus n. gen. and sp. shows remarkable anatomical specializations never before described in sphenodontians. Its enlarged size relative to terrestrial sphenodontians, the presence of a pachyostotic skeleton with restricted dorsal movements but with limbs still functional for terrestrial displacement, and the presence of deep teeth with open roots for constant growth and jaw action for food grinding are features that collectively suggest simultaneous aquatic behavior and herbivory, rare among lepidosaurian reptiles (Pough, 1973; Seymour, 1982). *Ankylosphenodon* was collected in deposits in which most of the reported fauna consists of marine forms (Aplegate, 1996). The considerably larger number of specimens of the new genus recovered relative to other lepidosaurs suggests that they inhabited nearby areas and were probably co-habitants with the marine fauna. All these facts suggest that this sphenodontian may have had similar behavior to that of the marine iguanid *Amblyrhynchus cristatus* (Hobson, 1965; Carpenter, 1966; Dawson et al., 1977). According to Dawson et al., when compared to terrestrial iguanas, there are few if any special features in the marine iguana that allow it to inhabit a marine environment. Nevertheless, any special adaptation in marine iguanas must be unusual since there are no other known marine iguanas world wide. Dawson et al. suggest that the environmental features that lead to the evolution of *Amblyrhynchus* were unique, including a warm and equable terrestrial environment adjacent to cool upwelling marine waters that allowed the growth of a diverse flora of macrophytic algae, together with an isolated (i.e., insular) environment.

The depositional environment of the Tlayua Quarry may reflect similar conditions. Based on the presence of haematophagous dipteran and gymnosperms, Pantoja-Alor (1992) suggested a warm tropical terrestrial environment for the area that surrounded the Tlayua deposits. However, this argument is weakened because of the presence of these groups in cold climates. But, the presence of rounded osteoscutes in the sphenodontian *Pamizinsaurus* (Reynoso, 1997) convergent to those of the extant lizards *Heloderma*, can be associated with the influence of a hot environment at least on the terrestrial portion of the area, partially supporting Pantoja-Alor's hypothesis.

The association of *Ankylosphenodon* with other bizarre forms of lepidosaurs, including the sphenodontian *Pamizinsaurus* (Reynoso, 1997) and a rare basal squamate (Reynoso, 1998a), strongly suggest that the Tlayua deposits evolved in insular conditions. According to different models for speciation (Mayr, 1963; Gould and Eldredge, 1977; Wright, 1982) the easiest way for new highly specialized forms to succeed is by their evolution in small isolated populations. Within these conditions, newly

acquired characters can be randomly fixed through genetic drift as soon as the incipient population break genetic contact with their anatomically more-conservative ancestors.

The insular condition of the Tlayua fauna is also supported by the occurrence of forms that could be considered relicts in the deposits of the time. A fairly primitive basal squamate (Reynoso, 1998a) and a basal scinoid (Reynoso and Callison, in press) occur relatively late compared to their oldest, but more derived relatives (Evans, 1995). Sphenodontians and some Tlayua fishes (those more typical of older ages) rarely occur in the Early Cretaceous (Evans, 1995; L. Grande, personal commun., 1993) and have never been reported before into the Albian. Persistence of primitive forms is also a common phenomenon in isolated environments.

Geological evidence and data from marine invertebrate faunas is also consistent with the insular nature of the terrestrial fauna of Tlayua. Alencaster (1987) demonstrated that during the Albian the central-south portion of Mexico was flooded by the largest marine transgression of the Early Cretaceous. Marine invertebrates dating from this epoch were broadly distributed in the surroundings of the Tlayua quarry, denying the possibility of connections between the terrestrial portion of Tlayua and the emerged lands of North America (Reynoso, 1998b).

CONCLUSIONS

Ankylosphenodon pachyostosis n. gen. and sp. is the second sphenodontian reported from the Early Cretaceous deposits of Tlayua. Like the beaded sphenodontian *Pamizinsaurus tlayuaensis*, it has a unique morphology among sphenodontians. The presence of pachyostotic ribs, vertebrae with swollen neural arches, limb bones with rounded ends; and the lack of ossified epiphyses strongly suggest a partially aquatic behavior. On the other hand, the presence of teeth deeply-ankylosed to the jaw with apparent continuous growth is probably associated with herbivory. Aquatic specializations differ greatly from those of *Pleurosaurus* and *Palaeopleurosaurus*, whose long body with short limbs suggest a more-obligate aquatic behavior. In these genera the limbs have become so small that they could probably not function in terrestrial locomotion but relied on serpentine movements for aquatic locomotion. On the other hand, herbivorous specializations are also different from those of *Toxolophosaurus* and *Eilenodon*, which have laterally-expanded teeth and thickened enamel that increased grinding surface and durability. The anatomical specializations of *Ankylosphenodon* were previously unknown and give additional information as to the morphological diversification sphenodontians had achieved by the end of the Early Cretaceous. The late presence of sphenodontians in the Albian also supports the belief that this area was a refuge for archaic terrestrial forms.

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REFERENCES

- AHMAD, D. 1993. Un sphenodontien du Jurassique Supérieur de Cerin (France) et la question des "sapheosaures" (Diapsida, Sphenodontia). Unpublished Masters thesis, Université Paris 7, 28 p.
- ALENCASTER, G. 1987. Moluscos bentónicos de la mitad meridional de México durante el Cretácico. *Revista de la Sociedad Mexicana de Paleontología* 1:1–23.
- APPLEGATE, S. P. 1996. An overview of the Cretaceous fishes of the quarries near Tepic de Rodríguez, Puebla, México, p. 529–538. *In* C. Arratia and G. Viohl (ed.), *Mesozoic Fishes—Systematics and Paleoecology*. Dr. Friedrich Pfeil, Munich.
- BENTON, M. J. 1984. Tooth form, growth, and function in Triassic rhynchosaurs (Reptilia, Diapsida). *Palaeontology*, 27:737–776.
- BROOM, R. 1925. On the origin of lizards. *Proceedings of the Zoological Society of London*, 1925:1–16.
- CABRAL, M. A., AND S. P. APPLEGATE. 1993. Primer reporte del registro más austral de pterosaurios (Archosauria: Pterodactiloidea) del Cretácico de Norteamérica. Abstracts, IV Congreso Nacional de Paleontología, Sociedad Mexicana de Paleontología, México D.F., 24.
- CARPENTER, C. C. 1966. The marine iguana of the Galapagos Islands, its behavior and physiology. *Proceedings of the California Academy of Sciences*, 34:329–376.
- CARROLL, R. L. 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London*, 293:315–383.
- . 1985a. A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. *Palaeontographica, Abteilung A*, 189:1–28.
- . 1985b. Evolutionary constraints in aquatic diapsid reptiles. *Special Papers in Paleontology*, 33:145–155.
- . 1988. *Verebrate Paleontology and Evolution*. Freeman, New York, 698 p.
- , AND P. GASKILL. 1978. The Order Microsauria. *Memories of the American Philosophical Society*, 126:1–211.
- , AND ——. 1985. The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, 309:343–393.
- , AND R. WILD. 1994. Marine members of the sphenodontia, p. 70–83. *In* N. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge University Press, Cambridge and New York.
- COCUDE-MICHEL, M. 1963. Les rhynchocephales et les sauriens de calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 7:1–187.
- . 1967a. Revision des Rhynchocephales de la Collection du Musée Teyler de Haarlem (pays-Bas), I. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series B (Physical Sciences)* 34:538–546.
- . 1967b. Revision des Rhynchocephales de la Collection du Musée Teyler de Haarlem (pays-Bas), II. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series B (Physical Sciences)* 35:547–555.
- DAWSON, W. R., G. A. BARTHOLOMEW, AND A. F. BENNET. 1977. A reprisal of the aquatic specializations of the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Evolution*, 31: 891–897.

- DILKES, D. W., AND R. R. REISZ. 1986. The axial skeleton of the Early Permian reptile *Eocaptorhinus laticeps* (Williston). *Canadian Journal of Earth Sciences*, 23:1288–1296.
- ESPINOSA-ARRUBARRENA, L., AND S. P. APPLGATE. 1990. New finds from the Tlayua Quarry (Cretaceous, Albian) of reptiles and fish from Puebla, México. Abstracts of the 49th Annual Meeting of the Society of Vertebrate Paleontology. *Journal of Vertebrate Paleontology*, 9(3 suppl.):22A.
- EVANS, S. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society*, 70:203–264.
- . 1981. The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. *Zoological Journal of the Linnean Society*, 73:81–116.
- . 1988. The early history and relationships of the Diapsida, p. 221–260. In M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1, Amphibians, Reptiles, Birds*. Clarendon Press, Oxford.
- . 1995. Lizards: Evolution, early radiation and biogeography. *Short Papers 6th Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Beijing, 51–55.
- FABRE, J. 1973. Un squelette d'*Homoeosaurus aff. solnhofensis* (Rhynchocephalia) du Portlandien du Petit Plan de Canjuers (Var). *Comptes Rendus de l'Académie des Sciences, Paris*, 276:1139–1142.
- . 1974. Un squelette de *Pleurosaurus ginsburgi* nov. sp. (Rhynchocephalia) du Portlandien du Petit Plan de Canjuers (Var.). *Comptes Rendus de l'Académie des Sciences, Paris. Série D*, 278:2417–2420.
- FRASER, N. C. 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London, Series B*, 321:125–172.
- , AND M. J. BENTON. 1989. The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and relationships of the sphenodontids. *Zoological Journal of the Linnean Society*, 96:413–445.
- , AND C. G. SHELTON. 1988. Studies of tooth implantation in fossil tetrapods using high-resolution X-radiography. *Geological Magazine*, 125:117–122.
- , AND G. M. WALKDEN. 1984. The postcranial skeleton of the Upper Triassic sphenodontid *Planocephalosaurus robinsonae*. *Palaeontology*, 27:575–595.
- GAUTHIER, J. A., R. ESTES, AND K. D. QUEIROZ. 1988a. A phylogenetic analysis of Lepidosauromorpha, p. 15–98. In R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families*. Stanford University Press, Stanford.
- , A. G. KLUGE, AND T. ROWE. 1988b. Amniote phylogeny and the importance of fossils. *Cladistics*, 4:105–209.
- GINSBURG, L. 1967. Sur les affinités des Mésosaures et l'origine des Reptiles Euryapsides. *Comptes Rendus de l'Académie des Sciences, Paris, Séries D*, 264:244–246.
- GORNIK, G. C., H. I. ROSENBERG, AND C. GANS. 1982. Mastication in the Tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): Structure and activity of the motor system. *Journal of Morphology*, 171:321–353.
- GOULD, S. J., AND N. ELDREDGE. 1977. Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology*, 3:115–151.
- GÜNTHER, A. 1867. Contribution to the anatomy of *Hatteria* (*Rhynchocephalus*, Owen). *Philosophical Transactions of the Royal Society of London*, 157:595–629.
- HAAS, G. 1979. On a new snakelike reptile from the Lower Cenomanian of Ein Jabrid, near Jerusalem. *Muséum National d'Histoire Naturelle, Paris, Bulletin*, 4e Série, 1:51–64.
- HARRISON, H. S. 1901. *Hatteria punctata* its dentitions and its incubation period. *Anatomischer Anzeiger*, 20:145–158.
- HEATON, M. J. 1980. The Cotylosauria: a reconsideration of a group of archaic tetrapods, p. 491–551. In A. L. Panchen (ed.), *The Terrestrial Environment and the Origin of Land Vertebrates, Volume 15. Systematics Association, Special Symposium*.
- , AND R. R. REISZ. 1986. Phylogenetic relationships of captorhinomorph reptiles. *Canadian Journal of Earth Sciences* 23:402–418.
- HOBSON, E. S. 1965. Observations on diving in the Galapagos marine iguana, *Amblyrhynchus cristatus* (Bell). *Herpetological Notes*, 2:249–250.
- HOFFSTETTER, R. 1955. Rhynchocéphales, p. 556–576. In Piveteau, J. (ed.). *Traité de Paléontologie*. Masson et Cie, Paris.
- KUHN, O. 1969. Proganosauria, Bolosauria, Placodontia, Araeoscelidia, Triophosauria, Weigeltisauria, Millerosauria, Rhynchocephalia, Protorosauria. *Handbuch der Paläherpetologie*. Gustav Fischer Verlag, Stuttgart.
- LAURIN, M., AND R. R. REISZ. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, 113:165–223.
- MANTER, J. T. 1940. The mechanics of swimming in the alligator. *Journal of Experimental Zoology*, 83:345–358.
- MAYR, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, 797 p.
- MEYER, H. V. 1855. Briefliche Mitteilung an Prof. Bronn. *Neues Jahrbuch für Mineralogie und Geogn. Petrefaktenk.*, 1855:326–327.
- NOPCSA, F. V. 1923. Vorläufige Notiz über die Pachyostose und Osteosklerose einiger mariner Wirbeltiere. *Anatomischer Anzeiger*, 56:353–359.
- , AND E. HEIDSIECK. 1934. Ueber eine pachyostotische Rippe aus der Kreide Rügens. *Acta Zoologica*, 15:431–455.
- PANTOJA-ALOR, J. 1992. Geología y paleoambiente de la Cantera Tlayúa, Tepexi de Rodríguez, Estado de Puebla. *Universidad Nacional Autónoma de México, Instituto de Geología, Revista*, 9:156–169.
- POUGH, F. H. 1973. Lizard energetics and diet. *Ecology*, 54:837–844.
- RASMUSSEN, T. E., AND G. CALLISON. 1981. A new herbivorous sphenodontid (Rhynchocephalia: Reptilia) from the Jurassic of Colorado. *Journal of Paleontology*, 55:1109–1116.
- REISZ, R., AND M. LAURIN. 1991. *Owenetta* and the origin of turtles. *Nature*, 349:324–326.
- REYNOSO, V.-H. 1996. A Middle Jurassic *Sphenodon*-like sphenodontian (Diapsida: Lepidosauria) from Huizachal Canyon, Tamaulipas, Mexico. *Journal of Vertebrate Paleontology*, 16:210–221.
- . 1997. A “beaded” sphenodontian (Diapsida: Lepidosauria) from the Early Cretaceous of Central Mexico. *Journal of Vertebrate Paleontology*, 17:52–59.
- . 1998a. *Huehucuetzpalli mixtecus* gen. et sp. nov; a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México. *Philosophical Transactions of the Royal Society of London, Series B*, 353:477–500.
- . 1998b. Acatlántida y el origen insular de la fauna terrestre de Tlayúa. *Avances en Investigación: Paleontología de Vertebrados. Instituto de Investigaciones en Ciencias de la Tierra, Universidad Autónoma del Estado de Hidalgo, Publicación especial*, 1:4–11.
- , AND G. CALLISON. In press. A new scincomorph lizard from the Early Cretaceous of Puebla, México. *Zoological Journal of the Linnean Society*.
- , AND J. M. CLARK. 1998. A dwarf sphenodontian from the Huizachal Formation of Tamaulipas, Mexico. *Journal of Vertebrate Paleontology*, 18:333–339.
- RIEPPPEL, O. 1989. A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Philosophical Transactions of the Royal Society of London, Series B*, 323:1–73.
- . 1994. Osteology of *Simiosaurus gaillardoti* and the relationships of stem-group Sauropterygia. *Fieldiana, Geology*, 28:1–85.
- RIQLÈS, A. D. 1974. Recherches paléohistologiques sur les os longs des tétrapodes. V. Cotylosaures et mésosaures. *Annales de Paléontologie*, 60:13–48.
- ROBINSON, P. L. 1976. How *Sphenodon* and *Uromastix* grow their teeth and use them, p. 43–64. In A. d. A. Bellairs and C. B. Box (eds.), *Morphology and Biology of Reptiles*. Academic Press, London.
- ROMER, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, 772 p.
- , AND T. S. PARSONS. 1986. *The Vertebrate Body*. Saunders College Publishing, Philadelphia, New York, 679 p.
- SEIBERTZ, E., AND B. E. BUITRÓN. 1987. Paleontología y estratigrafía de los neohibolites del Albiano de Tepexi de Rodríguez, Edó. de Puebla (Cretácico Medio, México). *Sociedad Mexicana de Paleontología*, 1:285–299.
- SEYMOUR, R. S. 1982. Physiological adaptations to aquatic life, p. 1–51. In C. Gans and H. Pough (eds.), *Biology of the Reptilia, Volume 13*. Academic Press, New York.
- SUES, H.-D., AND R. L. CARROLL. 1985. The pachypleurosaurid *Dactylosaurus schroederi* (Diapsida Sauropterygia). *Canadian Journal of Earth Sciences*, 22:1602–1608.
- SUMIDA, S. S. 1990. Vertebral morphology, alternation of neural spine

- height, and structure in permo-carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. University of California Publications in Zoology, 122:1–129.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1.1. Computer program distributed by The Illinois Natural History Survey, Champaign.
- THROCKMORTON, G. S., J. A. HOPSON, AND P. PARKS. 1981. A redescription of *Toxolophosaurus claudi* Olson, a Lower Cretaceous herbivorous sphenodontid reptile. *Journal of Paleontology*, 55:586–597.
- WHITESIDE, D. I. 1986. The head skeleton of the rhaetian sphenodontid *Diphydontosaurus avonensis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London, Series B*, 312:379–430.
- WILLISTON, S. W. 1925. The osteology of reptiles. Cambridge. 300 p.
- WRIGHT, S. 1982. Character change, speciation, and the higher taxa. *Evolution*, 36:427–443.
- WU, X. 1994. Late Triassic-Early Jurassic sphenodontids (*Clevosaurus*) from China and the phylogeny of the Sphenodontida, p. 39–69. In N. C. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge University Press, Cambridge and New York.
- YOUNG, J. Z. 1975. *The Life of Mammals*. Clarendon Press, Oxford, 528 p.
- ZANGERL, R. 1935. *Pachypleurosaurus*, p. 1–80. In B. Peyer (ed.), *Trias Fauna der Tessinerkalkalpen*, X. Mémoires de la Société de Paléontologie Suisse, 56.

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APPENDIX

Data matrix.—Character 1–48 are from Reynoso (1996) and Reynoso (1997). Character 49–52 are from Reynoso and Clark (1998), and character 53 is new. *Prolacerta* was included as a third outgroup representative of a basal archosauromorph. Character 22, state (0) was modified to mandibular foramen small or absent; the foramen is absent in most squamates and *Prolacerta*. Character 26, state (3) “thecodont tooth implantation” and state (4) “ankylotheodont tooth implantation” were added; thecodont tooth implantation present in *Prolacerta* and ankylotheodont tooth implantation in *Ankylosphenodon*. Character 29, state (2) “teeth transversely flattened” added; present in *Eilenodon* and *Toxolophosaurus*. Character 42 was rewritten and recoded according to trends in limb proportions discussed in text (Fig. 9). Character 48, state (0) “no contact between pterygoids in the midline” added; no contact of pterygoids in *Youngina*, *Prolacerta*, and Squamata. Character 47 and 49 were recoded (1) for *Youngina*, and character 46 became uninformative (therefore ignored) after merging *Clevosaurus* species.

Modified characters:

22. Size of the mandibular foramen: small or absent (0); large (1).
26. Dental implantation: pleurodont (0), some degree of acrodonity (1), fully acrodon (2); thecodont (3); ankylotheodont (4).
29. Marginal teeth breadth: equal to length (0); mediolaterally expanded (2); transversely flattened (3).
42. Proportions of humerus and femur length related to presacral vertebral column length. Sapsheosaurs trend: humerus <0.225 , ≥ 0.126 ; femur ≥ 0.172 , <0.287 (0). *Homoeosaurus* trend: humerus ≥ 0.226 , <0.290 ; femur ≥ 0.288 , <0.373 (1). Pleurosaurus trend: humerus <0.125 , ≥ 0.033 ; femur <0.171 , ≥ 0.094 (2). Comment: Hatchling *Pamizinsaurus* has state (1); however its adult the condition is unknown; coded (?).
48. Contact between palatines in the midline: no contact (0); small contact (1); broad contact (2).

New character:

53. Dorsal shape of the zygapophyses: flat (0); swollen (1).

Data for modified and new characters. Abbreviations: 0 = primitive state; 1, 2, 3, 4 = derived conditions; ? = unknown; N = not applicable:

	22	26	29	42	48	53
<i>Youngina</i>	0	0	0	0	0	0
<i>Prolacerta</i>	0	3	0	0	0	0
Squamata	0	0	0	0	0	0
<i>Gephyrosaurus</i>	0	0	0	?	1	0
<i>Diphydontosaurus</i>	1	(0&1)	0	?	1	?
<i>Planocephalosaurus</i>	0	1	0	0	2	0
<i>Palaeopleurosaurus</i>	1	2	0	2	2	0
<i>Polysphenodon</i>	?	2	0	1	1	?
<i>Brachyrhinodon</i>	1	2	0	0	1	?
<i>Clevosaurus</i>	1	2	0	(0&1)	2	0
<i>Homoeosaurus</i>	1	2	0	1	2	0
<i>Kallimodon</i>	1	2	0	0	2	1
<i>Sapsheosaurus</i>	1	N	N	0	2	1
<i>Pamizinsaurus</i>	1	2	0	?	?	0
<i>Ankylosphenodon</i>	1	4	2	0	?	1
<i>Eilenodon</i>	1	2	1	?	?	?
<i>Toxolophosaurus</i>	1	2	1	?	?	?
<i>Zapatadon</i>	?	2	0	?	2	?
<i>Cynospheonon</i>	?	2	0	?	?	?
<i>Sphenodon</i>	1	2	0	0	2	0

Data for Ankylosphenodon.—? 1???? 1???? ????? ?111 11111 41120 0???? ?01 20???? ????? ?1

Data for Prolacerta (third outgroup).—00000 00000 00001 00000 00000 30000 00000 10001 10100 01010 000

Analysis and results.—Data matrix has 20 taxa and 53 characters. All characters are unordered. Characters 35 and 46 are uninformative and were ignored. Designated outgroup taxa: *Youngina*, *Prolacerta*, and Squamata.

Branch-and-bound search settings: Initial upper bound: unknown (compute via stepwise). Furthest addition sequence. Topological constraints not enforced. Multistate taxa interpreted as polymorphism.

Most parsimonious tree description: Number of trees retained = 69; tree length = 129; consistency index (CI) = 0.643; homoplasy index (HI) = 0.488; retention index (RI) = 0.731; rescaled consistency index (RC) = 0.470.

Consensus tree description: Strict consensus of 69 trees. Tree length = 163; CI = 0.509; HI = 0.595; RI = 0.532; RC = 0.271.

List of apomorphies (asterisk = ambiguous characters). Accelerated transformation (ACCTRAN) character-state optimization. Nodes correspond to those of Fig. 10:

RHYNCHOCEPHALIA: 6*, 8, 14, 23, 45, 48.

Gephyrosaurus: 6(0)*, 9.

Diphydontosaurus: 1, 22, 32.

Node 1: 15(0), 21, 24, 26*, 27, 30, 32(2), 34, 38*, 39, 40, 48(2).

Planocephalosaurus: 9, 52.

SPHENODONTIDAE: 1*, 2, 5, 7*, 8(0), 10, 11, 12, 13, 16*, 18, 22, 26(2)*, 28, 33, 36, 37*, 38(2)*, 41(2)*, 47(2)*, 49, 51.

Palaeopleurosaurus: 1(0)*, 5(0), 7(0)*, 9, 12(2), 13(0), 14(0), 15, 16(0)*, 17, 18(0), 34(2), 37(0)*, 41*, 42(2), 47, 52.

Node 2: 1(2), 3*, 4*, 10(0), 11(0), 12(0), 13(0), 16(0)*, 38, 48(0).

Polysphenodon: 2(0), 42, 49(0).

Clevosaurus: 3, 4, 11(0), 13(0), 34(2), 38, 41*, 43, 45(0), 47, 51(0).

Homoeosaurus: 1(0)*, 2(0), 7(0)*, 10(0), 11(0), 25, 34(2), 42, 47(0)*.

Kallimodon: 1(0)*, 34(2), 47(0)*, 53.

Sapsheosaurus: 7(0)*, 47(0)*, 53.

Pamizinsaurus: 17, 25, 43.

Node 3: 3*, 17*, 19, 25*, 31, 40(2)*, 41*, 50*.

Zapatadon: 2(0), 3, 5(0), 9, 16(0)*, 17, 18(0), 19, 44, 45(0), 49(0), 50.

Node 4: 19, 20, 25, 29, 53*.

Ankylosphenodon: 26(4), 29(2), 30(0), 39(0).