Huehuecuetzpalli mixtecus gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México

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Huehuecuetzpalli mixtecus gen. et sp. nov. is characterized by a combination of characters unlike those of any of the previously described Late Jurassic or Early Cretaceous lizards. It has most of the synapomorphies common to modern squamates, but still retains primitive features rare in living taxa. Autapomorphic characters include an anteroposteriorly elongated premaxilla that results in the elongation of the snout and the apparent retraction of the external nares. A small rounded postfrontal and a parietal foramen on the frontoparietal suture suggest affinities with iguanians, but the retention of divided premaxillae, amphicoelous vertebrae, thoracolumbar intercentra, entepicondylar foramen, and a second distal tarsal supports the hypothesis that Huehuecuetzpalli has a more basal position relative to the extant squamates. Although its appearance is late in the fossil record of lizards, Huehuecuetzpalli is the first report of a basal squamate. It provides important information on early transformation of characters in lizard evolution. Many primitive characters present in some modern squamates are usually explained by paedomorphosis; however, these characters are common in early lizards suggesting that derived states may have been fixed later in lizard evolution. If Huehuecuetzpalli is an iguanian, then it would be the earliest known representative of this lineage and extends their fossil record into the Albian. This paper presents an extensive review of the characters and character states used in previously published cladistic analyses of the Squamata.

Keywords: Lepidosauria; Squamata; Iguanidae; cladistics; biogeography; Tlayua Quarry

1. INTRODUCTION

The Squamata is a group of highly diversified diapsid reptiles with a world-wide distribution, yet very little is known about their origin, early evolution, and diversification. The Squamata is divided in six major taxa: iguanians, anguimorphs, scincomorphs, gekkotans, snakes and amphisbaenians. The vernacular term ‘lizard’ is applied to the first four taxa. Squamates are grouped together with sphenodontians in the Lepidosauria, which in turn is included with some other primitive forms in the Lepidosauromorpha, one of the two major branches of diapsid evolution. To date almost 3300 species of lizards, 2300 of snakes, and 130 of amphisbaenians have been described (Rage 1992).

The history of the Lepidosauromorpha can be extended to the Upper Permian (Carroll 1975, 1977; Estes 1983a); however, the earliest known squamates are from the Middle Jurassic of Britain (Evans 1993; Waldman & Evans 1994). They consist of scattered material of very distinctive lizard elements that can be assigned to crown squamate taxa. Early Jurassic lizards were reported by Meszoely et al. (1987), however, their specific affinities are uncertain and they may be basal lepidosauromorph taxa rather than lizards (C. A. M. Meszoely, personal communication). The earliest well-documented squamates are the middle Jurassic anguimorphs Parviraptor estesi (Evans 1994a) from Kirtlington, England (Bathonian), and Changetsisaurus estesi (Fiedler & Nesov 1992) from Kyrgyzstan, Central Asia (Callovian). Towards the Late Jurassic, the squamate fossil record is better known, but still from a very small number specimens, most of them restricted to localities in Europe and North America. In most localities the remains are very fragmentary and consist mostly of disarticulated material. Parviraptor the anguimorph Dorsetisaurus, and the scincomorphs Paramacel- lodus, Becklesius, Saurillus and Saurillodon (also known in Kirtlington; Evans 1995) have been reported from the Guimarota lignite mine (Oxfordian–Kimmeridgian) in Leiria, Portugal (Seiñer 1973). Dorsetisaurus and Paramacellodus are also known from the Late Kimmeridgian and Early Tithonian deposits in Como Bluff, Wyoming (Prothero & Estes 1986; Chure 1992). The scincomorph Shanweisaurus was reported from the Kimmeridgian of Kazachstan, Central Asia (Hecht & Hecht 1984), and the skink Mimobecklesiurus (Li 1985) from the Upper Jurassic of the Gansu province of China. Eunosaurus from the Kimmeridgian of Cerin, France, long believed to be an iguanian (Cocudé-Michel 1963; Estes 1983a), is now known to have been described on the basis of an assemblage of...
lepidosaurs from different taxa, and only the poorly preserved type can be assigned to the Squamata with uncertain relationships (Evans 1994b). Finally, the genera Adrosaurus, Eichstaettisaurus, Basavisiisaurus and Palaeoacerta were described from the Lower Tithonian deposits of Solnhofen (Hoffstetter 1953, 1964, 1965; Cocude-Michel 1963, 1965; Ostrom 1978; Matear 1982; Evans 1993, 1994a). The previously considered early lizard Ctenognathus from Gomo Bluff (Gilmore 1928; Prothero & Estes 1980) and Guimarota (Seiffert 1973), is now considered a choristodere (Evans 1989, 1990), and Lisboaia, also from Guimarota, is a small, unusual, archosaur (Bascaldi et al. 1996).

The fossil record of lizards during the Early Cretaceous was poor, leaving a large gap in our understanding of early lizard evolution. For many years, only two genera were known: Meyasaurus from the Berriasian-Valanginian deposits in Montsec, Spain (Vidal 1915; Barbadillo & Evans 1995); and Labeosaurus from Berriasian (?) deposits of northeastern China (Endo & Shikama 1942). Very recently, a number of new localities have yielded numerous specimens some of which are superbly preserved. The scincomorph Herdeaesaurus (probably synonymous to Meyasaurus; Barbadillo & Evans 1995) was added to the Montsec collection (Hoffstetter 1965). Pairisinopterus, Donetsisaurus, Paramacelodus, Saruillas and Becklesius all known from the late Jurassic are also found in the Berriasian deposits of Purbeck with two other scincomorphs: Pseudosaurus and Duroteria (Hoffstetter 1967; Seiffert 1973; Ensom et al. 1991; Evans 1995). Remains of the earliest snake (Rage & Richter 1994), eggshells of the possibly earliest gecko (Kohring 1991), additional specimens of Herdeaesaurus, Becklesius, Paramacelodus and the new possibly anguimorph Cuencasaurus were found in the Late Barremian deposits of Uña and Galve, Spain (Richter 1991, 1994a,b). Deposits of similar age in Las Hoyas, Spain yield a new assemblage of lizards to be described (Barbadillo & Evans 1995; Evans & Barbadillo 1996). Outside Europe, only a new species of Paramacelodus from the Berriasian (?) of Anoual, Morocco (Richter 1994a), and Hohwugecko, the earliest known gecko, from the Aaptian-Albian of Mongolia (Alifanov 1989), have been described. In North America, Early Cretaceous squamates are even more scarce. A single primitive helodermatid maxillary fragment was reported from the Albian of Utah, USA (Cifelli & Nydam 1995).

Although some Late Jurassic and Early Cretaceous squamates are represented by well-preserved specimens, very few contribute to our understanding of the early evolution of the Squamata. As noted by Evans (1995), most early squamates can be referred to one of the major squamate crown groups. It is particularly striking that no iguanians or taxa basal to the Squamata have ever been collected. This particular distribution within the fossil record does not match the most recent hypotheses of squamate phylogeny and biogeography (Estes 1983a; Estes et al. 1988), in which iguanians are the first major offshoot of the cladistic tree, implying that earlier representatives are to be expected. Evans (1994b) has recently demonstrated that Euphausaurus is not an iguanian but a pleurodont lizard with uncertain relationships. Although Tamaulipasaurus, from the Middle Jurassic of northeast México (Clark & Hernández 1994), might be the only squamate sister-group reported, particular burrowing specializations make it far from the expected primitive squamate type.

The Albian deposits of Tepexi de Rodriguez, Central México, bear some of the most superbly preserved fossil lepidosaurs world-wide (Reynoso 1995, 1997). Skeletons are fully articulated, but heavily compressed. Fortunately, their oblique preservation provides full view of the organisms, facilitating reconstruction and giving a good amount of information. The lizard described here, even though somewhat late in the fossil record, shows many features of an earlier stage of squamate evolution and provides evidence of early character transformation within squamates.

2. SYSTEMATIC PALAEONTOLOGY

(a) Lepidosauromorpha Benton, 1983

Lepidosaurus Dumeril & Bibron, 1839

Possibly Squamata Oppel, 1811

(i) Genus Huehuecuetzpalli gen. nov.

Etymology. From huehue (the ancient) and cuetzpalli (lizard), Náhuatl.

Diagnosis. As for the type and only known species.

Type Species: Huehuecuetzpalli Mixteca sp. nov.

Holotype. Instituto de Geología, Universidad Nacional Autónoma de México. Catalogue no. IGM 7389 (figure 1). Crushed, but beautifully preserved complete skeleton.

Paratype. Catalogue no. IGM 4183 (see figure 2). Crushed but beautifully preserved skeleton of a juvenile lizard preserved in part and counterpart blocks. Limbs, girdles and the posterior part of the vertebral column are preserved in ventral view in one of the blocks; the broken head and the anterior part of the vertebral column are visible in dorsal view on the other. Some cartilaginous and soft tissues are preserved.

Etymology. For La Mixteca, the native name given to the broad geographical area were the Tlayua Quarry is located.

Locality. Tlayua Quarry, 2 km south-east of the Colonia Morelos, near Tepexi de Rodriguez, Puebla, México.

Horizon. Middle Member of the Tlayua Formation (Pantoja-Alor 1992). Early Cretaceous. Middle or Late Albian (Schultz & Buitrón 1987). IGM 7389 was collected in locality IGM-1995-NSF number 2, level H, quadrant 1/5; and IGM 4185 in IGM-1971-NSF number 1, level Z/10, quadrant 16/5.

Diagnosis. Paired premaxillae elongated anteriorly, showing the apparent retraction of the external nares and the elongation of the snout; posterior process of maxilla ends below anterior part of orbit; short descending processes of frontals; parietal foramen on the frontoparietal suture; small rounded postfrontal; triradiate squamosal; cervical intercentra sutured to following centra; amphicoelous vertebrae in adult; 24 presacral vertebrae; weak zygosphene and zygantrum articulations; thoracolumbar intercentra; clavicle a simple rod; short pubis; entepicondylar foramen in humerus, distal end of ulna gently convex; distal end of the tibia...
notched; fourth distal tarsal very large; second distal tarsal present; middorsal row of osteoderms.

3. DESCRIPTION

_Huehuecuetzpalli mixtecus_ is only known from two articulated skeletons. IGM 7389 is an adult (figure 1). Its skull measures 32.2 mm in length and the presacral vertebral column 75.5 mm (see table 1). Other than the distal part of the tail, the right femur, and distal elements of the right forelimb, the skeleton is complete. IGM 4185 is a juvenile (figure 2). Its skull measures 19.3 mm in length, the presacral vertebral column 46.9 cm, and the tail length almost doubles the snout–vent length. Unfortunately some bones on the skull table were lost when the block was split in the field; however, imprints of these bones are preserved on the counterpart block and some details were obtained through high fidelity latex casts. The description of the dorsal aspect of the skeleton is mainly based on IGM 7389. The ventral side, girdles, and medial side of the jaw description is based on IGM 4185.

Figure 1. Skeleton of the holotype of _Huehuecuetzpalli mixtecus_ gen. et sp. nov. (IGM 7389) as preserved on the block. Abbreviations are listed in Appendix 2.
Figure 2. Skeleton of the paratype of *Huehuecuetzpalli mixteca* gen. et sp. nov. (IGM 4185) as preserved on the block. Abbreviations are listed in Appendix 2.
The skull is narrow with a long and slender snout (see figure 3). In general appearance, it resembles that of *Varanus*, but the postorbital region is primitively constructed showing some iguanian features. The total length of the skull is twice the width at the frontoparietal suture, and the snout is almost half of the total skull length. The premaxillae are unfused and unusually long. Their anterior end is extended far forward relative to other lizards, and the infranarial process of the premaxilla extends far posteriorly to border the external naris ventrally. This peculiar snout structure is associated with its elongation and the concomitant retracted appearance of the external nares. This condition is emphasized even more by the anterior emargination of the nasals (see below). The structure of the snout resembles superficially that of other non-lepidosaurian diapsids, such as some Prolacertiformes (Kuhn-Schnyder 1962; Wild 1973) or *Coelurosauravus* (Evans & Haubold 1987). In *Huehuecuetzpalli*, however, the very long frontal process of the premaxilla extends posteriorly below the nasals, reaching the frontals as in squamates (figure 4). This unusual complex of characters is not present in any other lepidosauromorph and diagnoses the new genus. Retracted nares are also present in varanids, but with a very different structure. The retraction of the nares results from the reduction of the lateral edge of the nasals which lose contact with the maxilla and prefrontal. In varanids no infranarial processes of the premaxilla are present and the anterior tip of this bone is short as in other squamates. The elongation of the snout in varanids is the result of the anterior projection of the maxilla and narrowing of the snout. In *Huehuecuetzpalli*, as in varanids, the premaxilla extends into the naris to form a shelf, but an enlarged concave septomaxilla is not evident.

### Table 1. Dimensions, proportions, and comparisons of different skeletal elements in the adult and juvenile specimens of *Huehuecuetzpalli mixtecus* (Measurements in millimetres. Data in parentheses are approximated.)

<table>
<thead>
<tr>
<th>Measurement</th>
<th>IGM 7389 (holotype)</th>
<th>IGM 4185 (paratype)</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>total length</td>
<td>197.0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>skull length</td>
<td>32.2</td>
<td>19.3</td>
<td>—</td>
</tr>
<tr>
<td>skull breadth at fronto-parietal suture</td>
<td>11.6</td>
<td>7.1</td>
<td>—</td>
</tr>
<tr>
<td>snout length</td>
<td>13.8</td>
<td>7.8</td>
<td>—</td>
</tr>
<tr>
<td>postorbital skull length</td>
<td>9.3</td>
<td>(5.0)</td>
<td>—</td>
</tr>
<tr>
<td>parietal table width</td>
<td>2.0</td>
<td>4.3</td>
<td>—</td>
</tr>
<tr>
<td>presacral vertebral column (PSVC) length</td>
<td>75.7</td>
<td>46.9</td>
<td>—</td>
</tr>
<tr>
<td>humerus</td>
<td>15.7</td>
<td>10.7</td>
<td>—</td>
</tr>
<tr>
<td>radius</td>
<td>12.9</td>
<td>(7.4)</td>
<td>—</td>
</tr>
<tr>
<td>ulna (without olecranon)</td>
<td>13.1</td>
<td>8.1</td>
<td>—</td>
</tr>
<tr>
<td>femur</td>
<td>(24.7)</td>
<td>15.2</td>
<td>—</td>
</tr>
<tr>
<td>tibia</td>
<td>20.7</td>
<td>12.7</td>
<td>—</td>
</tr>
<tr>
<td>fibula</td>
<td>20.3</td>
<td>13.6</td>
<td>—</td>
</tr>
<tr>
<td>metacarpal IV length</td>
<td>6.3</td>
<td>4.0</td>
<td>—</td>
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<tr>
<td>metatarsal IV length</td>
<td>12.9</td>
<td>8.6</td>
<td>—</td>
</tr>
<tr>
<td>manus 4th digit length</td>
<td>(19.0)</td>
<td>13.8</td>
<td>—</td>
</tr>
<tr>
<td>pes 4th digit length</td>
<td>(33.5)</td>
<td>24.5</td>
<td>—</td>
</tr>
<tr>
<td>tail length</td>
<td>—</td>
<td>126.6</td>
<td>—</td>
</tr>
<tr>
<td>replacement portion length</td>
<td>—</td>
<td>36.4</td>
<td>—</td>
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<tr>
<td>skull proportions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>skull length–PSVC length</td>
<td>0.425</td>
<td>0.412</td>
<td>0.013</td>
</tr>
<tr>
<td>skull breadth–skull length</td>
<td>0.360</td>
<td>0.368</td>
<td>−0.008</td>
</tr>
<tr>
<td>parietal table–skull length</td>
<td>0.062</td>
<td>0.223</td>
<td>−0.161</td>
</tr>
<tr>
<td>snout length–skull length</td>
<td>0.429</td>
<td>0.404</td>
<td>0.025</td>
</tr>
<tr>
<td>postorbital length–skull</td>
<td>0.289</td>
<td>0.259</td>
<td>0.030</td>
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</tbody>
</table>

### Appendicular skeleton proportions

<table>
<thead>
<tr>
<th>Measurement</th>
<th>IGM 7389 (holotype)</th>
<th>IGM 4185 (paratype)</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>humerus–PSVC length</td>
<td>0.207</td>
<td>0.243</td>
<td>−0.036</td>
</tr>
<tr>
<td>radius–PSVC length</td>
<td>0.170</td>
<td>0.156</td>
<td>0.012</td>
</tr>
<tr>
<td>ulna–PSVC length</td>
<td>0.173</td>
<td>0.173</td>
<td>0.000</td>
</tr>
<tr>
<td>femur–PSVC length</td>
<td>0.326</td>
<td>0.318</td>
<td>0.008</td>
</tr>
<tr>
<td>tibia–PSVC length</td>
<td>0.273</td>
<td>0.324</td>
<td>−0.051</td>
</tr>
<tr>
<td>fibula–PSVC length</td>
<td>0.268</td>
<td>0.292</td>
<td>−0.024</td>
</tr>
<tr>
<td>tail length–total length</td>
<td>—</td>
<td>0.643</td>
<td>—</td>
</tr>
<tr>
<td>replacement tip-tail length</td>
<td>—</td>
<td>0.288</td>
<td>—</td>
</tr>
</tbody>
</table>

(a) **Skull**

The skull is narrow with a long and slender snout (see figure 3). In general appearance, it resembles that of *Varanus*, but the postorbital region is primitively constructed showing some iguanian features. The total length of the skull is twice the width at the frontoparietal suture, and the snout is almost half of the total skull length. The premaxillae are unfused and unusually long. Their anterior end is extended far forward relative to other lizards, and the infranarial process of the premaxilla extends far posteriorly to border the external nares.
holotype they are preserved crushed over the narial passageway exposing the narial processes of the premaxilla. As seen in the young specimen (figure 5a) the nasals contacted each other on the midline covering the premaxillary narial process, as in other squamates. The anterior border of each nasal is strongly emarginated, placing the posterior margin of the external naris far back in the snout. A separated lacrimal could not be
identified, but a small posterior process of the maxilla extending over the prefrontal indicates the position where the lacrimal–prefrontal suture should be. This suggests that the lacrimal was fused to the prefrontal. A single lacrimal foramen penetrating the maxilla is evident. The jugal forms the entire ventral edge of an orbit fully encircled by bone. Its dorsal end is obscured by the postorbital, so it is uncertain whether it reached the squamosal or not. A slight bending of the ventral margin of the postorbital might indicate the posteriormost position of the jugal suture, suggesting that the jugal and squamosal were not in contact. The short postorbital is triangular in shape and its posterior process does not reach the posterior margin of the upper temporal fenestra. Dorsally it contacts a small rounded prefrontal and the anterolateral process of the parietal. As in ‘iguanids’, the small prefrontal is restricted to the orbital rim.

The skull table is wide, particularly in the juvenile. Both frontals and parietals are fused medially in the adult, but in the younger specimen the parietals are still separated anteriorly and a slight suture remains posteriorly (figure 5a). The fronto-parietal suture is straight and hinged, and considerably broader than the fronto-nasal contact. The frontal enters the orbital margin and
its lateral borders are not constricted between the orbits. Ventrally, the descending processes for the olfactory tract are very short (see figure 5b).

Extensive lateroventral flanges on the lateral margins of the parietal indicate that the jaw adductor musculature originated on its dorsal surface. The short parietal table does not cover the anterior part of the occipital region. The lateral processes of the parietals are long and have a reduced supratemporal attached posteriorly. The parietal foramen is located on the fronto-parietal suture as indicated in the juvenile specimen (figure 5a). In the adult, its presence cannot be established because this part of the skull is crushed.

The upper temporal arch is formed mostly by an anteriorly enlarged, laterally facing squamosal similar to that of iguanians and teiids. A well developed dorsal process extends onto the parietal supratemporal process and a peg for the quadratojugal projects ventrally.

The quadrate is preserved in posterior view in the juvenile specimen. Its ventral end is relatively more slender than the dorsal, and it has well developed lateral and medial crests. The tympanic process is relatively large compared with most squamates, but similar in size and proportions to geckos and the Early Cretaceous lizard *Meyasaurus* (Evans & Barbadillo 1997). An enlarged, somewhat curved posterior crest suggests that the quadrate was bowed outward. The different positions in which the quadrate was preserved in the adult and juvenile skulls (compare figures 4 and 5), show the presence of a high degree of streptostyly. Ventromedially, the quadrate touches the quadratojugal process of the pterygoid, but there is no ventromedial projection or lappet to receive it.

The supraoccipital is a short, laterally expanded bone. In the juvenile, the lateral extensions remain separated from the medial body suggesting the presence of an axial and two lateral centres of ossification. The opisthotic has well-developed, distally expanded lateral processes; because of distortion their orientation cannot be established. In the adult specimen the supraoccipital is displaced posteriorly (figure 4). It borders broadly the posterior margin of a wide margin of the pterygoid is well exposed through the orbit.

As a result of the posterior displacement of the supraoccipital, some traces of the right stapes are exposed in the holotype (see figure 4). It is not as slender as in extant squamates and more closely resembles the stapes of *Sphenodon*. The dorsal portion of a thin columnar epityrsygyroid contacting the alar process of the prootic is visible through the upper temporal fenestra.

Little of the palate can be seen. Only the anterior margin of the pterygoid is well exposed through the orbit (figure 4). It borders broadly the posterior margin of a wide suborbital fenestra and has a long slender quadratojugal process.

(b) Lower jaw

The dentary comprises almost half of the total length of the slender jaw. The articulation between the dentary and postdental bones (Gauthier 1982) cannot be described because the opposing surfaces are in contact. The surangular, angular and articular are distinct elements. The surangular occupies most of the lateral surface of the postdental and extends well posteriorly to form part of the articular facet. It extends anteriorly to overlap the dentary. The angular is only exposed on its anterior end. It forms a complex tongue-and-groove articulation between the ventral contact of the dentary and surangular. This articulation resembles the hinged articulation of varanoids suggesting that the jaw of *Huahuastephus* could have been hinged. In varanoids, however, the postdental–dental articulation is structurally different as the hinge is formed by projection of the ventral part of the surangular between the dentary and the splenial.

An anteroposteriorly short coronoid caps the posterior end of the dentary, but does not extend far anteriorly or clasp the dentary laterally. This type of contact is present ancestrally in lizards and resembles the coronoid–dental structure in agamids and chamaeleontids. The posterior part of the lower jaw seems to be twisted medially, but, because of the compression of the specimen, this condition is uncertain. No trace of a retro-articular process is evident, although it might be broken in both specimens.

The medial side of the jaw was reconstructed from a latex cast taken from an impression on the counterpart block of the juvenile specimen (figure 5a). Although it lacks detail, some features can be discerned. The coronoid is well developed and the adductor fossa is deep. A completely open Meckelian groove extends down the centre of the ramus from below the coronoid process to the tip of the jaw. A short splenial is faintly visible. It does not reach the middle part of the tooth-bearing portion of the dentary. The straight articulation with the postdental bones gives another indication that the lower jaw is hinged. The subdental shelf is either weakly developed or absent.

(c) Dentition

Teeth in both the maxilla and premaxilla are pleurodont, peg-like, closely packed, and of similar size all along the tooth series. In figure 4, the tooth bases appear to be somewhat broadened, but this shape is probably an effect of the compression. Each premaxilla bears six teeth, and the maxilla has 13. The dentary has 24 teeth in the large specimen and 19 in the juvenile. The tooth replacement is alternating, to judge from small, recently erupted teeth. The position of the replacement teeth or presence of pits cannot be determined.

(d) Hyoid apparatus

Some bones of the hyoid apparatus are preserved in the juvenile specimen (see figure 5a). According to their position, the anterior element was identified as the first ceratobranchial and the posterior element as the epihyal. The latter one, however, may be the hyoid cornu.

(e) Postcranial axial skeleton

The ventral column is composed of 24 presacral vertebrae, two sacras, and in the juvenile where the tail is complete, there are 32 caudal vertebrae plus a regenerative segment of about one-quarter of the total caudal
length (figure 2). The first eight vertebrae lack rib contact with the sternal plate and are identified as cervicals. In the juvenile specimen the atlas and axis are beautifully preserved in dorsolateral aspect (figure 6a). The atlas is large and ring-shaped with the dorsal contact of the neural arches separated. The neural spine of the axis is anteroposteriorly expanded and straight on its dorsal edge. Its centrum is of similar size to the other cervical vertebrae. The intercentral arrangement falls into the type A category of Hoffstetter & Gasc (1969). The first and second intercentrum are obscured by the left side of the atlas centrum; but, a single large ventral articulation surface for an unfused first intercentrum suggests that only this element was sutured ventrally. The third intercentrum remains as a separate element lying between the axis and the third cervical vertebra.

As observed in a disarticulated area on the caudal region, the vertebrae centra are amphicoelous (figure 6c). The dorsal vertebrae are short anteroposteriorly with weakly developed neural spines. In ventral view they are cylindrical, with straight articulation surfaces between the centra. Thoracolumbar intercentra are observed in at least the last three presacrals, and intercentral chevron bones are present anterior to the first and second caudals. Beginning with the third caudal intercentra, all bear haemal arches. Weak zygosphene–zygantrum articulations are evident between some presacral vertebrae. The transverse processes of the proximal caudal vertebrae are simple, well-developed, and already fused in the juvenile. They become gradually smaller towards the posterior end and almost disappear at the level of the first autotomous vertebra. The lateral processes of the first six vertebrae project slightly backwards, but by the seventh vertebrae they begin to point anteriorly. Autotomy septa are present posterior to the eighth caudal vertebra. The septum passes transversally near the mid-length of the vertebrae, slightly dividing the transverse process anteriorly (type 3 of Etheridge 1967; figure 6b).

In the juvenile specimen the 32nd caudal vertebra is broken through the autotomy septum, and a regeneration segment, preserved as calcified cartilage, replaces most or all of the original length of the tail. Regenerated tails are presented in a primitive scincomorph from the same locality (V.-H. Reynoso and G. Callison, unpublished data), and in a scincomorph from Las Hoyas, in Spain (Evans & Barbadillo 1997). In the juvenile specimen, a row of calcified osteoderms are observed parallel to the presacral vertebral column from the ninth to the last dorsal. Calcified granular scales are also preserved over the neural arches of the 13th–15th presacrals (figure 6d).

Holocephalous cervical ribs are present from the fourth or fifth cervical vertebrae to the eighth (see figure 7). The next three ribs are connected to the sternal plate via calcified cartilage, and another pair is attached to a mesosternum (figure 8a). The most posterior vertebrae have ribs of equal size to the sternal ribs and are associated with a series of postxiphisternal inscriptive ribs. In the juvenile, the inscriptive ribs are extremely thin, lying
disorganized in the abdominal region; but, in the adult, they are broader and remain aligned with the ribs (figure 1). Damage caused to the abdominal region in previous preparation of the adult specimen obscures the morphology of the inscriptive ribs. The last five presacral vertebrae bear free ribs that are reduced in size towards the sacral region. The sacral ribs are fully co-ossified with the sacral vertebrae and there is no posterior process or bifurcation of the second sacral rib. Dark material within the abdominal region of the juvenile specimen may be remnants of stomach contents, but no biotic morphology can be discerned.

(f) **Appendicular skeleton**

In the juvenile, the junction between the coracoid and scapula is marked by a distinct suture (figure 1). Damage caused to the abdominal region in previous preparation of the adult specimen obscures the morphology of the inscriptive ribs. The last five presacral vertebrae bear free ribs that are reduced in size towards the sacral region. The sacral ribs are fully co-ossified with the sacral vertebrae and there is no posterior process or bifurcation of the second sacral rib. Dark material within the abdominal region of the juvenile specimen may be remnants of stomach contents, but no biotic morphology can be discerned.

In the adult specimen, the junction between the coracoid and scapula is marked by a distinct suture (figure 8a). In the adult specimen, an isolated scapula lying anterior to the rib cage shows a smooth contact surface for the coracoid. This suggests that the scapula and coracoid remained separated into adulthood. Whether these bones fully co-ossify at some point is unknown. A well-developed scapulocoracoid fenestra intercepts the anterior border of both girdle elements. The coracoid is fenestrated anteriorly, and its medial margin articulated with a T-shaped interclavicle that projects posteriorly just beyond the first sternal rib attachment. Some calcified remains of cartilaginous tissue separating the coracoid from the interclavicle may represent the epicoracoid cartilage. The lateral processes of the interclavicle are incomplete, so their extent cannot be estimated. The sternum is partly preserved as calcified cartilage and an area of impression. It is a single unperforated plate, retaining the primitive lizard rhomboidal shape where the coracoid articulation is slightly shorter than the rib-bearing portion. The clavicles are rod-shaped and slightly curved. The lack of an acromial process on the scapula suggests that the clavicle was attached to the suprascapula (Lécure 1968). The position of the clavicle as preserved on the adult specimen leads to the same conclusion.

The limbs are gracile and well-ossified. In the adult specimen, bony epiphyses are preserved and most of them are already fused to the diaphyses. The humerus is slender and relatively shorter than the femur (table 1). It retains the primitive entepicondylar foramen and has a fully enclosed ectepicondylar foramen. The ulna and radius are subequal in breadth and length. A rounded epiphyseal precursor of the olecranon remains free between the ulna and the humerus. A similar rounded structure in the type specimen of *Bavarisaurus macrodactylus* (Hoffstetter 1964) is instead the radial condyle of the humerus. The carpal elements are badly preserved and cannot be described (figure 9). In the juvenile specimen the intermediate, fourth distal carpal, a structure that could be the ulnare or the fifth distal carpal, and another that could be the ulna epiphysis or the pisiform, are preserved. The manus has long digits with the primitive squamate phalangeal count 3, 5, 4, 3, 2.

The symphysis of the pubis is short, flat, and oriented perpendicularly (figure 8b). This orientation suggests a straight contact between the pubic bones, characteristic of the ventrally oriented symphysis of some ‘iguaniids’ and *Varanus*. Although the orientation of the pubic tubercle cannot be established, a ventrally oriented symphysis appears to be associated with a more anteriorly oriented tubercle (Estes et al. 1988). This condition is assumed to pertain to the new species. The ischium is distinctly rounded distally with a relative slender shaft.
The femur is long, straight, and has a distal lateral recess in which the fibula once sat. The tibia and fibula are subequal in length. The left tibia, preserved in medial view, has an enlarged distal notch into which a ridge on the proximal end of the astragalus fits, as is common to scleroglossan squamates (figure 9d). The astragalus and calcaneum are not fused but sutured in the juvenile specimen (figure 9c). The condition in the adult is unknown because the unusually enlarged fourth distal tarsal obscures the proximal tarsals. A further primitive feature is the presence of a small, second distal tarsal (figure 9e), always absent in extant squamates. In the juvenile specimen, the second distal tarsal cannot be observed, probably because it was still unossified. As pointed out by Currie & Carroll (1984) in primitive lepidosaurs, the ossification of the second distal tarsal occurs after the ossification of the fourth and third distal tarsals was completed. The fifth metatarsal is hooked with lateral and medial plantar tubercles. Similar to the manus, the pes has enlarged digits with a complete phalangeal count (2, 3, 4, 5, 4).

4. DISCUSSION
(a) Ontogeny
With only two specimens it is impossible to trace a complete developmental series in Huehuecuetzpalli. However, changes in its early ontogeny may be of interest and of phylogenetic importance.

The complete fusion of the cranial elements suggests that the larger specimen is of postjuvenile age, and probably an adult condition was already acquired. The olecranon process of the ulna, however, is not completely ossified and attached to the ulna, and only a ball of hard tissue (calcified cartilage or bone) is preserved. It was impossible to find information in the literature about the time when the precursor of the olecranon process become fused to the ulna.

The age of the smaller specimen is more difficult to establish. The complete ossification of the fourth distal tarsal and the still separated astragalus and calcaneum undoubtedly suggest a post-hatchling stage when compared with the degree of ossification of Lacerta agilis.
The complete fusion of the frontal, however, shows that it is older than Rieppel's specimen number 18 and the hatching of Cryptodactylus pabulosus (Gekkonidae) illustrated by Rieppel (1992; fig. 1). The high degree of ossification indicates that it is close to the latest stages of development preceding complete ossification. Juvenile skull characters are the presence of a broader parietal table with short lateral processes. Compared with the adult skull, the juvenile parietal table is more than 15% broader on the narrower section excluding the ventrolateral flanges for the dorsal attachment of the jaw adductor musculature. The relative length of the snout, and the proportions of the skull and limbs relative to the presacral vertebral column, do not show significant differences between the juvenile and adult specimens (see table 1), although these features usually change in ontogeny. This suggests that adult proportions were already acquired at the ontogenetic stage of the younger specimen in spite of its relatively smaller size.

In this same specimen, the parietals, maxilla, and supraoccipital are not fully ossified. A total of one-third of the suture between parietals is still open, when the rest is already in contact showing only a slight trace of a suture. The degree of closure of the frontoparietal suture cannot be determined. However, the fact that the frontal and the parietal were easily separated and were preserved separately in the counterpart blocks, with no trace of breakage, may suggest that the suture was not yet closed and a fontanelle was still present. In Lacerta, the fontanelle formed by the opening of the skull table on the frontoparietal suture and between the parietals, ossify until the latest recognized post-hatching stages (Rieppel 1992c). The closure of the frontoparietal suture precedes the total closure of the parietals at the midline, and the parietals are the last to fill the interparietal space behind the frontoparietal suture. The developmental stage of the smaller specimen of Huehuecuetzpalli is more advanced than the developmental stage of NMBE 1011297 of Lacerta vivipara and almost reaches the stage of MBS 5625 (Rieppel 1992b). In the latter, the parietals are already in contact posteriorly but remain open anteriorly, similar to the juvenile specimen of Huehuecuetzpalli.

Specific comparisons of delay in the ossification of the maxilla and supraoccipital can be made with modern lizards. It is interesting to note that in the juvenile specimen of Huehuecuetzpalli certain features do not match with the age estimated for the specimen. The preservation of two separated elements on the maxilla and three on the supraoccipital deserve particular attention.

The maxilla of prehatching lizards is composed of two ossification centres (Haluska & Alberch 1983). The dorsal part will become the ascending process of the maxillary whereas the ventral portion will become the support for the dentition. These two distinct ossification elements are present in very early stages of ossification in Lacerta (Rieppel 1992b, 1994) and in the colubrid snake Elaphe obsota (Haluska & Alberch 1983), but not in chamaeleonines (Rieppel 1993). In Lacerta these two elements become fused in late hatching stages. In all known hatching lizards, both ossification centres are ossified into a single maxillary bone. Among Squamata, only in boenidae snakes these bones remain separate until adulthood (Frazzeta 1970). In Huehuecuetzpalli they remain separate after hatching, but do become fused in the adult. The position of the suture between the two maxillary elements in the juvenile of Huehuecuetzpalli is distinctly high on the dorsal process of the maxilla. This condition contrasts with that of Lacerta in which the dorsal element constitutes most of the maxilla, and the ventral portion is restricted to support of the dentition.

On the supraoccipital, the presence of a distinct epiotic centre on the dorsal aspect of each otic capsule that fuses to a smaller supraoccipital precursor has been described in some lizards (Jollie 1960; Bellairs & Kamal 1981). However, the ossification pattern and distribution of this feature among lizards is still obscure. As for the maxilla, the supraoccipital and epiotic ossification centres become fully fused into a single supraoccipital in hatching lizards.

The presence of ‘prehatching’ features in an early fossil lizard can be explained either as a primitive condition later incorporated into the early development in modern lizards, or as being acquired secondarily through paedomorphosis. A final conclusion depends on the phylogenetic position of the new lizard.

(b) Phylogeny

To establish the phylogenetic position of Huehuecuetzpalli in the context of the Squamata, a cladistic analysis was done by using a modified version of Estes et al.'s (1988, appendix table 1) data matrix. The single most parsimonious tree was obtained by implementing the heuristic search option using the Random Additional Sequence algorithm of PAUP (Swofford 1993) with 100 repetitions. All characters were unordered, multistate taxa interpreted as polymorphism, and uninformative characters 157 and 158 were ignored (see Appendix 1). Instead of polarizing the characters by using a single average outgroup created with the modal character states of the outgroup members (see, for example, Estes et al. 1988; Kluge 1989), younginiforms, Saurosternon, kuehneosaurids, and rhynchocephalians were used as a multiple outgroup. To reduce the number of resultant trees the incompletely known outgroup taxa Palasagama and Poliguana were excluded from the analysis. Because of the primitive condition of Huehuecuetzpalli, the data matrix was extended to include the osteological characters diagnostic for the Squamata (characters 136) listed by Estes et al. (1988, pp. 186–187). To consider all available evidence, characters 185–187 of Clark & Hernández (1994) were included with some modifications. Character states for the diagnostic characters of the Squamata were taken from Gauthier et al. (1988; appendix 1) some of which were also modified. Character modification includes the combination of characters to avoid redundant information, the rewriting of characters or character states considered ambiguous, and the inclusion of new or previously ignored information. To avoid reproducing the list of characters and data matrices of Estes et al. (1988), their character numeration was retained and only modified, and new characters are described in part (a) of Appendix 1. Respective data matrices are presented separately for modified characters and new characters in part (b) of Appendix 1. In data for Huehuecuetzpalli (Appendix 1, part c). ‘X’ indicates gaps created in the data matrix after character combination. Character distribution on trees was explored by using either ACCTRAN or DELTRAN character optimization, although in part (d) of Appendix 1 only ACCTRAN is
Figure 10. Most parsimonious tree showing the sister-group relationships of *Huehuecuetzpalli* with Squamata. Analysis was done by using an extended version of Estes et al.’s (1988) data matrix, as presented by Clark & Hernández (1994) with several additional modifications. List of modified characters and character states and data for *Huehuecuetzpalli* and other squamates is presented in Appendix 1. All characters are unordered and multistate characters are interpreted as polymorphism. Tree description: tree length, 820; consistency index, CI=0.790; retention index, RI=0.662. Apomorphy list (only unambiguous characters): Squamata: frontals fused, parietals fused, straight frontoparietal suture broader than nasofrontal suture, short parietal table exposing occipital region dorsally, squamosal with ventral peg for quadrate, quadrate lappet of pterygoid absent, pterygoid in suborbital fenestra, broad interpterygoidal vacuity, paraoccipital process contacts suspensorium, angular ends anterior to articular condyle, cervical ribs single headed, large thyroid fenestra in pelvic girdle, hooked fifth metatarsal with modiﬁed plantar tuber, and other characters rarely, if ever, present within crown squamates. The position of *Huehuecuetzpalli* outside crown squamates is well supported because crown squamates appears as a monophyletic clade comprising all crown squamates is supported by 15 synapomorphies: frontals fused, parietals fused, mid-dorsal scale row absent. A full description of the tree is given in Appendix 1.

Discussion about character distribution and ontogeny, however, is based only on unambiguous characters except when otherwise indicated. The single most parsimonious hypothesis (see figure 10) suggests that *Huehuecuetzpalli* is the sister-group of the Squamata (tree length, 820; consistency index, CI=0.790; retention index, RI=0.662; Appendix 1, part d). Curiously, the resultant tree is compatible with Estes et al.’s (1988: fig. 6) squamate phylogeny, but differs greatly with their most parsimonious hypothesis when including all taxa (Estes et al. 1988: fig. 5, p. 136; Kluge 1989; Clark & Hernández 1994). Snakes came out as the sister-group of Anguimorphs, and dibamids and amphibaenians become sister-taxa, branching oﬀ together as a sister-group of gekkotans. As in the results of Estes et al. (1988), the Scleroglossa is well-supported, but by only seven unambiguous characters, and Autarchoglossa by two. The characters diagnosing each node diﬀer considerably from those listed by Estes et al. (1988). For example, Autarchoglossa was deﬁned by three characters: (i) no contact between jugal and squamosal; (ii) dermal rugosities on skull; and (iii) muscle *rectus abdominis lateralis* present. Of these, the ﬁrst character is unambiguously primitive for Squamata; the second character is a generalization of the dermal rugosities of both anguimorphs and scincomorphs, but corresponds to diﬀerent and not necessarily ordered characters; and the third character does support the clade, but ambiguously, only when implementing ACCTRAN character optimization. In contrast, unambiguous characters for Autarchoglossa in my results (see ﬁgure 10) are frontal paired, and descending process of the frontals in contact below narial passageway. The reorganization of characters in the tree is caused, in part, because the reorganization of the information in the basal nodes expands the transformation series beyond the limits of the Squamata. This possibility is being explored further in a broader analysis of the Lepidosauromorpha (V.-H. Reynoso, unpublished data).

The sister-group relationship of *Huehuecuetzpalli* with the clade comprising all crown squamates is supported by 15 synapomorphies: frontals fused, parietals fused, mid-dorsal scale row absent. Of those listed by Estes et al. (1988), the ﬁrst character is unambiguously primitive for Scleroglossa is well-supported, but by only seven unambiguous characters, and Autarchoglossa by two. The character diagnosing each node diﬀer considerably from those listed by Estes et al. (1988). For example, Autarchoglossa was deﬁned by three characters: (i) no contact between jugal and squamosal; (ii) dermal rugosities on skull; and (iii) muscle *rectus abdominis lateralis* present. Of these, the ﬁrst character is unambiguously primitive for Squamata; the second character is a generalization of the dermal rugosities of both anguimorphs and scincomorphs, but corresponds to diﬀerent and not necessarily ordered characters; and the third character does support the clade, but ambiguously, only when implementing ACCTRAN character optimization. In contrast, unambiguous characters for Autarchoglossa in my results (see ﬁgure 10) are frontal paired, and descending process of the frontals in contact below narial passageway. The reorganization of characters in the tree is caused, in part, because the reorganization of the information in the basal nodes expands the transformation series beyond the limits of the Squamata. This possibility is being explored further in a broader analysis of the Lepidosauromorpha (V.-H. Reynoso, unpublished data).

Whether *Huehuecuetzpalli* is a true squamate or not is difficult to establish as it depends on how the group is deﬁned. The great number of characters supporting the sister-group relationships of *Huehuecuetzpalli* with crown squamates might suggest its inclusion in the Squamata;
however, if the term Squamata is only applied to crown members of the clade, *Huehuecuetzpalli* will fall outside. To avoid the creation of a new name grouping the new genus with crown squamates, *Huehuecuetzpalli* is referred tentatively to the Squamata.

The shape of the skull and mandible are very similar to varanids, and in outline resemble the primitive hypothetical mosasaur illustrated by Russell (1967, p. 201). Marked differences in the detailed anatomy and the lack of practically all scleroglossan synapomorphies, suggest that these similarities are convergent. The similar skull pattern of *Huehuecuetzpalli* and *Varanus* is only superficial and is an striking example of convergence in lizard evolution. As pointed out before, the enlargement of the snout in *Huehuecuetzpalli* is caused by the anteroposterior enlargement of the premaxillary region, placing the nares posteriorly on the skull, further emphasized by a slight emargination of the nasals posterior to the nares. In varanids, the enlargement of the snout is caused by the enlargement of the maxilla, and the retracted appearance of the nares is only the effect of the reduction of the nasals. *Huehuecuetzpalli* does share with varanids the short posterior process of the maxilla extending anterior to the orbit and the possible presence of a hinged lower jaw. The posterior process of the maxilla is also short in xantusiids and in the Late Jurassic lizard *Baurusaurus* (Evans 1994c), and it could easily be explained as convergent. The structure of the lower jaw is quite different in *Huehuecuetzpalli*, in which the hinge is formed by the angular extending between the dentary and surangular, and not by a projection of the ventral part of the surangular between the dentary and the splenial.

A notch on the distal end of the tibia was considered a scleroglossan synapomorphy by Estes *et al.* (1988); however, the polarity of this character at the base of the Squamata is unknown as iguanians have a gently convex tibia—distal end, whereas *Sphenodon* and other outgroup members still present the primitive locked tibio-astragalar joint (Reisz 1981). Estes *et al.* (1988) assumed the convex distal head to be primitive over a notched tibia within squamates, but on the basis of results here reported, the presence of a tibial notch is the primitive condition in Squamata, with further transformation in iguanians to a gently convex condition.

Most of the characters indicating the primitive condition of *Huehuecuetzpalli* relative to crown squamates have been interpreted as acquired secondarily (reversals) through paedomorphism in several of the derived squamates lineages. Paired premaxillae have been said to be paedomorphic in skinks and gekkonids (Greer 1970; Kluge 1987); as have separate exoccipitals in dibamids (Greer 1983; Gauthier *et al.* 1988); and the presence of amphicoelous vertebrae in gekkonids and xantusiids (Underwood 1954; Kluge 1987).

Particular attention has been given to the presence of a paired premaxillae and amphicoelous vertebrae in some gekkonids. Their presence in gekkonids has been very controversial. However a paedomorphic origin rather than the retention of the primitive condition has been favoured on the base of character congruence in current phylogenetic hypotheses (Kluge 1987; Estes *et al.* 1988; Gauthier *et al.* 1988). The inclusion of gekkonids within Scleroglossa, the best supported clade in squamate phylogeny, is indicated by several unambiguous characters (see figure 10; Appendix 1, part d).

Understanding the presence of primitive characters in *Huehuecuetzpalli* might be more complicated as this genus branches off the cladogram at the root of the tree. Contrary to gekkonids, it cannot be included in any of the major groups of the Squamata and the pleisiomorphic or paedomorphic (reversal) presence of a divided premaxilla, amphicoelous vertebrae, and thoracolumbar intercentra cannot be granted. According to the most parsimonious cladogram these characters are pleisiomorphic for crown squamates, but if they were paedomorphic for *Huehuecuetzpalli* (as are interpreted in geckos) the position of this genus in the cladogram might be incorrect.

An alternative hypotheses of character transformation might be suggested. Drawing a scenario in which the presence of a divided premaxilla, amphicoelous vertebrae, and thoracolumbar intercentra are of paedomorphic origin in *Huehuecuetzpalli*, they would become autapomorphic for the new genus, and the alternative derived states would be primitive for the Squamata as a whole. Then, the presence of two unique derived characters of iguanians: a small rounded postfrontal restricted to the orbital rim and the parietal foramen on the frontoparietal suture, would support sister-group relationships between *Huehuecuetzpalli* and iguanians. The lack of a separated postfrontal in agamids and chamaeleontids, however, indicates that the presence of a small rounded postfrontal could restrict the sister-group relationships to 'iguanids' only.

Although scleroglossan synapomorphies suggest that paired premaxillae, amphicoelous notochordal vertebrae, and trunk intercentra are reversed within some taxa, their condition as retained primitive characters is still a possibility because they are widely distributed in early fossil forms assigned to several of the major groups of the Squamata, but in a basal position. *Baurusaurus*, a possible scleroglossan, shows divided premaxilla, trunk intercentra, and presumably amphicoelous vertebrae (Ostrom 1978; Mateer 1982; Evans 1994c); *Eichstaettsaurus*, a possible gekkotan, has a divided premaxilla (other structures not known; Hoffstetter 1964); and *Parviraptor*, a possible anguimorph, preserves intervertebral notochordal canal (Evans 1994a). In addition, a second distal tarsal is present in some Early Cretaceous lizards from Las Hoyas (S. E. Evans, personal communication). Although character congruence suggests that the derived condition of these characters was present in crown squamates ancestrally, their broad distribution in early fossil forms may indicate that these characters were not completely canalized in the developmental pathways at the time when the major Squamata clades originated.

The morphology of the intervertebral articulation has received considerable attention. As pointed by Kluge (1987), intervertebral articulations have two aspects: the shape of the condyle and the presence of a notochordal canal. Each is associated with different developmental processes. As described by Winchester & Bellairs (1971), the condyle develops as an outgrowth of cartilaginous tissue from the back of the centrum, later replaced by endochondral bone, and the cotyle is formed by proliferation of cartilaginous tissue around the rim of the pre-articular surface, which is covered by an extension of the perichondral sheath. In opposition with Evans' (1994c, p. 48) interpretation, the development of procoelous vertebrae in squamates does not pass through a morphogenic stage similar to that of...
Icarosaurus

Gekko

Cordylus

Heloderma

Basiliscus

genus humerus femur HRMc FTMt humerus/femur HRMc/FTMt behaviour

Table 2. Forelimb and hind limb proportion and locomotion system in different saurians

(Institutional abbreviations: AMNH, American Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; RPM, Redpath Museum, McGill University; SMNS, Staatliches Museum für Naturkunde, Stuttgart. Other abbreviations: HRMc, humerus + radius + fourth metacarpal lengths; FTMt, femur + tibia + fourth metatarsal lengths. Data for Palaeopleurosaurus from Carroll (1985).)

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the amphicoelous vertebrae of the adult Sphenodon. In adult Sphenodon, the notochord is constricted only in the middle portion of the vertebrae (Howes & Swinnerton 1901) and articulating surfaces remain perforated through life. By contrast, in squamates, constriction starts at the articulating surfaces after condyle formation, and a notochordal remnant is an important part of intravertebral structure after hatching (Winchester & Bellairs 1976: fig. 3a). In the case of Paractonger, as in Anguis and Natrix, the notochordal canal is preserved, but within a clearly procoelous intervertebral condition. This is the same for xantusiids and eublepharines, most gekkotans (Kluge 1987). In these taxa, the retention of a notochordal canal is the result of a delay in the constriction of the notochord after condyle formation. This condition is unlikely to be the same as that of gekkonines and most diplodactylines (Howes & Swinnerton 1901) and might well be a retained primitive character. The limb proportions of Huehuecuetzpalli are intermediate between the bipedal lizard Basiliscus and some fully terrestrial forms (see table 2). This suggests that one of these habits or a combined behaviour was probable. The enlarged tail, similar in proportions to Basiliscus, supports bipedal locomotion as well. Arboreal lizards have higher forelimb–hind limb ratios.

The similarity between the skulls of Huehuecuetzpalli and varanids may suggest that they share similar jaw mechanics, possibly associated with similar foraging behaviour. The jaw structure of Vaurus is adapted to catch relatively large and fast-moving prey (Rieppel 1979a). The varanoid’s large, pointed, blade-like teeth are not present in the new genus, suggesting the preference for small prey (of insect size). Herbivory, limited to about a dozen lizard species (Ostrom 1963), is highly unlikely. The lack of biotic structures in the remnants of stomach contents in the juvenile specimen of Huehuecuetzpalli gives no indication about their diet; however, a more elaborate analysis of the contents might give additional information.

6. BIOGEOGRAPHY AND STRATIGRAPHIC SIGNIFICANCE

When reviewing the fossil record of squamates, it is interesting to note that all fossil forms have been assigned
to one of the major clades of the Squamata (Evans 1995). No basal members of squamates or early representatives of the iguanians, the first major offshoot in squamate phylogeny, have ever been documented. The rarity of basal squamates and early iguanians obscures the early evolution of the Squamata. *Euposaurus* was found in late Early Cretaceous deposits of Central Mexico and is somewhat late for documenting the early evolution and diversification of lizards. It can be considered a relict of an earlier lineage and new specimens in older deposits are expected to be discovered. As pointed out by Estes (1983a) relatively primitive squamate taxa (*‘iguaniids’, agamids, and chamaeleontids*) could have had a Gondwanaland origin and diversification based on their modern distribution and current phylogenetic hypotheses. This would explain their absence in the Jurassic and Early Cretaceous of Europe and North America. The localization of the Tlayua Quarry in southern Laurasia could explain the finding of a basal squamate in modern North America. However, the geographical position of the quarry in relation to northern or southern land masses has not been established and more knowledge of the fauna and its interrelationships, as well as the geological correlation of the area to other places in North or South America, is needed before drawing definite conclusions.

If the iguanian affinities of *Huehuecuetzpalli* are supported, it will extend the fossil record of iguanians back into the Albian and might suggest the presence of Gondwanaland elements in the Tlayua deposits. The earliest known true iguanians are the Late Cretaceous *Pristiguana* of Brazil (Estes & Price 1973) and *Prissagama* from Mongolia (Borsuk-Bialynicka & Moody 1984). Although *Euposaurus* from the Late Jurassic of France was for a long time considered to be the earliest iguanian (Cocude-Michel 1963), assigned specimens are considered to represent an assemblage of pheno-dontians and lizards, with only the type specimen assignable to the Squamata, *Incerta sedis* (Evans 1994b). Of the few characters described for *Euposaurus*, slender slightly angulated clavicles is primitive for iguanians and squamates as a whole. Although this is a primitive character and cannot be used to establish relationships, the combination of fully pleurodont dentition, enlarged replacement pits, and simple rod-shaped clavicles, is unique to *iguaniids* and some cordylids, restricting the possible affinities of *Euposaurus* to one of these taxa. It is important to note that cordylids are possibly related to paramacellodid lizards: a successful group during the Late Jurassic.

APPENDIX 1

Abbreviations: 0, primitive conditions; 1, 2, 3, 4, 5, derived states; ? unknown; N not applicable; X excluded. In brackets: CH, Clark & Hernández (1994); E, Estes et al. (1988); FE, Frost & Etheridge (1989); G, Gauthier et al. (1988); P, Presch (1988); PGG, Pregill et al. (1986); R, Rieppel (1980); pol. rev., polarity reverted.

The number following the initial refers to the character number in their respective data matrix. Taxa followed by an asterisk (*) indicate metataxa.
(a) Modified and new characters

Characters 1–148 are from Estes et al. (1988), characters 149–184 are characters 1–36 from the ‘Diagnosis of the Squamata’ (Estes et al. 1988, p. 186–187) following Gauthier et al. (1988; appendix I; see below), and characters 185–187 are from Clark & Hernández (1994). Several characters were modified: characters 19–20, 25–26, 28–29, 58–59, 60, 67, 70–71 (partly); 88–89; 95–96; 97–98; 100–101; 102–103; 104–106; 107–108; and 112–113 were combined to reduce redundant information. Characters 2, 4, 5, 18, 71, and 123, were rewritten or modified to avoid ambiguity. Of Estes et al.’s ‘Diagnosis of the Squamate’, character 20 (character 168 of Clark & Hernández 1994) is redundant to character 107 and was excluded; character 31 (character 179 of Clark & Hernández 1994) was combined with character 123. Character 185 of Clark & Hernández (1994) was combined with character 150 (character 3 of Gauthier et al. 1988), and character 186 was modified.

Clark & Hernández’s (1994) modifications of states in Estes et al.’s (1988) data matrix were considered. All other characters were coded as presented by Estes et al. (1988) with the exception of the following. Character 4 was recoded as not applicable (N) in cases where the postfrontal or postorbital is absent. Character 7 was fully recoded as the shape of the orbital margins of the frontals cannot be scored if the postorbital and prefrontal are in contact. Character 9 recoded (0) in Vananas; in none of the specimens observed do the frontal downgrowths reach the palatines. Character 13 recoded (0, N) in Amphisbaenians, as the postfrontal is absent in some. Character 26 recoded (1) in Kuehneosauridae, Evans (1991). Character 42 recoded (0) in Lanthanotus and variable (1, 0) in Xenosauridae. Lanthanotus is palaeochoanate and among xenosaurids only Shinisaurus is palaeochoanate (Riek 1980). Character 45 recoded (0) in Xantusiidae (Riek 1984). Character 50 variable (0, 1) in Anguidae, condition (1) present in Diploglossus and Gerrhonotus (Riek 1980). Character 51 variable (0, 1) in Lacertidae and Scincidae; exocephalials are separated in Podarcis and in some late embryos of Tiliguana (Gauthier et al. 1988). Character 53 recoded (N) in Kuehneosauridae and rhynochephalians; the absence of a complete closure of the vidian canal makes the position of its posterior opening indeterminate. Character 55 recoded (0) in Kuehneosauridae (Evans 1991); character 82 recoded (1) in Lanthanotus; palatine teeth are absent; character 83 variable (0, 1) in Helodermatidae. Character 84 recoded (0) in Poliguanus (Evans 1991). Character 90 variable (0, 1) in Teiidae; the second ephibranchial is absent in Bachia (Camp 1923). Character 102 variable (0, 1) in Agamidae; some Uromastix do have autotomy septum (Hoffstetter & Gasc 1969). Character 111 recoded (N) in Chamaeleontidae, the scapular fenestra of chamaeleontids might not be homologous to that of other lizards (Frost & Etheridge 1989). Character 115 and 118 recoded (N) in snakes and dibamids. The lack of clavicle and interclavicle in these forms results from the loss of the shoulder girdle; a different condition from that of (for example) chamaeleontids. Character 115 was recoded (0, 1, N) in amphisbaenians; although most amphisbaenians lack the clavicles because the loss of the shoulder girdle (not applicable condition), some amphisbaenians (e.g. Amphisbaena; see Zangerl 1945) lack clavicles but do have a vestigial shoulder girdle (state 1).

Character 120 variable (0, 1) in Iguanidae; Leiocephalus presents an anterior process. Character 125 recoded (17) in Xantusiidae; postcloacal bones are present but probably not homologous to those of gekkonids (Kluge 1982). Data not available for Estes et al. (1988) and were recoded as suggested by Presch (1988); character 133 recoded (0) in amphisbaenians and dibamids, character 135 recoded (0) in Gymnophthalmidae and Lanthanotus, and character 140 recoded (1) in Gymnophthalmidae and (0) in Lanthanotus. The polarity of characters 95–96 (here character 93), 103, and 143, was reverted.

(i) Modifications to Estes et al. (1988) characters

2 (rewritten). Nasal–maxilla structure: in contact (0), separated by external nares (1); (R11) (PGG 3, 4)/(P61). Comment: external nares are considered to be retracted only if the nasals and the maxilla lose contact and if frontals contact naris, see character 4. Pregill et al. (1988) divides the state (1) in small contact (Helodermatidae) or no contact. Small contact is considered contact present.

4 (modified, state 2 added). Nasal–prefrontal contact: broad contact (0), separated by maxilla–frontal contact (1), separated by external nares (2); (R18 pol. rev.) (PGG 2)/(P56). Comment: in state (2) the frontals contact the nares. Although in Lanthanotus the nasals and frontals are barely touching each other, the state ‘bones separated by external nares’ is preferred.

5 (rewritten). Structure of the dorsal margin of the orbit: composed by frontal (0), prefrontal contacts postfrontal or postorbital excluding frontal from the margin (1); (R19, 14 pol. rev.) (PGG 10)/(P62).

17 (modified, state 2 added). Postorial contribution to the posterior margin of the orbit: one half or more (0, less than one half (1), postorial excluded from the orbital rim (2); (R21) (P55).

18 (rewritten). Jugal–squamosal contact over the lower temporal fenestra: absent (0), both bones in contact (1); (G8) (P67)/(FE 8). Comment: the ambiguous condition jugal ‘very near’ to the squamosal (state 1) was ignored. Structurally both bones are in contact or not. The jugal and squamosal are not in contact in Bradypodion, most Rhampholeon, Brookesia, and some Chamaeleo (Riek 1981, 1987). In teiids the jugal and squamosal are near but clearly separated.

19 (19, 20 combined). Supratemporal fenestra restriction; supratemporal fenestra widely open (0), restricted or closed by the postorbital (1), restricted or closed by the postfrontal (2).

25 (25, 26 combined). Parietal foramen position: on parietal (0); on frontoparietal suture (1); on frontal (2); absent (3).

28 (28, 29 combined). Lacrimal structure: a separated element (0), fused to prefrontal (1), absent (2); (P44)/(FE 5). 58 (58, 59 combined). Subdental shelf size: small (0), shelf absent (1), large (2).

60 (60, 68, 70, and 71 divided, combined). Structure of the coronoid–dentary articulation: dentary overlaps most coronoid lateral surface (0), coronoid clasp dentary (1), coronoid overlapped anteriorly by a small posterooral process of the dentary (2), coronoid and dentary meet with no overlap (3); (FE 16)/(P70)/(PGG 45). Comments: Estes et al.’s (1988) character 60 and 71 are redundant. In
dibamids and amphibiaeanians the coronoid is overlapped anteriorly by the dentary but not posteriorly by the surangular, therefore character 71 was divided. In the snake Anilius the coronoid is overlapped anteriorly by a small dentary dorsal process (Rieppel 1979b).

71 (divided). Structure of the coronoid–surangular articulation: surangular restricted to the lateroventral margin of the coronoid process (0), surangular overlapping the coronoid process posteriorly (1).

88 (88, 89 combined). Number of scleral ossicles: more than 14 (0), 14 (1), less than 14 (2); (PGG 79).

95 (95, 96 combined). Size of the zygosphene and zygantrum accessory articulations: articulations absent (0), weakly developed (1), strong (0); (G78)(P33).

97 (97, 98 combined). Attachment of the cervical intercentrum: intervertebral (0), sutured or fused to preceding centra (1), sutured or fused to next centra (2); (R72). Comment: Estes et al. (1988: characters 97, 98) separated the conditions 'sutured' and 'fused' in different character states. As both belong to the same transformation series they are considered together.

100 (100, 101 combined). Number of transverse processes on caudal vertebrae: one pair (0), two pair diverging (1), two pair converging (2), anterior part of transverse process absent (3).

102 (102, 103 combined and modified). Position of the autotomy septa in caudal vertebrae: autotomy septa absent (0) splits transverse process (1), posterior to transverse process (2), anterior to transverse process (3); (P31). Comment: Etheridge (1989) considered the 'presence of a weak septum' an additional state here included in character 71. In the snake Anilius the septum passes posterior to the transverse process in Xantusia (Hoffstetter & Gasc 1969).

104 (104–106 combined). Number of presacral vertebrae: 24–25 (0), 23 or fewer (1); 26 or more (2); (PGG 51).

107 (107, 108 combined). Number of cervical vertebrae: seven or less (0), eight (1), nine or more (2); (PGG 49)(G171)(P32).

112 (112, 113 combined). Shape of the anteroventral margin of the coracoid: smoothly curved (0), anterior coracoid fenestra present (1); anterior and posterior fenestrae present (2); Lécureu 1968; (PGG 56, 57, pol. rev) (P 59, 60)(FE 36 pol. rev). Comment: Frost & Etheridge (1989) considered the 'presence of a weak posterior fenestra' an additional state here included in state (2).

123 (combined with G133) Shape of the distal end of the ulna: with a ridge in the astragalocalcaneal articulation (0), gently convex (1), notched to fit astragalocalcaneum ridge (2).

(ii) New characters (characters 149–187)

149 (G2). Nasals width: greater than nares (0); less than nares (1).

150 (G3 modified; combined with CH 185). Frontal–parietal suture shape and size: W-shape, equal to nasofrontal suture (0); straight, broader than nasofrontal suture (1).

151 (G14). Supratemporal position: superficial (0); wrapping ventral supratemporal process (1).

152 (G15). Squamosal ventral process: present (0); absent (1).

153 (G16). Squamosal ventral surface shape: hollow, caps quadrate (0); peg fits on quadrate notch (1).

154 (G22). Vomerine teeth: numerous (0); absent or few (1).

155 (G26). Pterygoid–vomer medial contact: present (0); absent (1).

156 (G39). Palatine posterior process: contact ectopterygoid excluding pterygoid of suborbital fenestra (0); reduced, pterygoid in suborbital fenestra (1).

157 (G38). Septomaxilla posteriorventral process: absent (0); present, forming posterior margin of Jacobson's organ duct (1).

158 (G37). Septomaxilla extension: only on posteroventral edge of exornarial fenestra (0); form Jacobson's organ vestibule to nasal capsule floor (1).

159 (G34). Paraoccipital process: not expanded distally (0); expanded distally (1).

160 (G35 rewritten). Stapes size: thick (0); thinner (1); pin-like (2). Comment: perforated condition of stapes already considered in character 145.

161 (G28). Epipterygoid ventral expansion: wide, contacts quadrate (0); columelliform, does not contact quadrate (1).

162 (G32). Metotic fissure: continuous (0); subdivided (1).

163 (G30). Vidian canal: open posteriorly (0); fully enclosed by bone (1).

164 (G70). Angular posterior extension: beyond articular condyle (0); less than articular condyle (1).

165 (G69). Coronoïd process structure: coronoïd medial and surangular lateral (0); formed primarily by coronoïd (and dentary) (1).

166 (G86). Cervical rib head numbers: two in one or more (0); all single-headed (1).

167 (G79). Cervical vertebral intercentrum shape: flat ventrally (0); keeled ventrally (hypapophysis present) (1).

168 (Excluded). G171 merged to character 107 (see above).

169 (G87). Sacral and caudal rib–centrum fusion: fused in post-embryo (0); fused in embryo (1).

170 (G77). Neural arch–centrum fusion: fused in postembryonic (0); fused in embryo (1).

171 (G97). Humerus shaft: thick, robust (0); thickness reduced, robust (1); gracile (2).

172 (G98). Humerus entepicondylar foramen: present (0); absent (1).

173 (G100). Ulna distal end shape: gently convex (0); nearly hemispherical (1).

174 (G99). Radius distal epiphysis: with prominent posteromedial process (0); process absent (1).

175 (G101). Intermediate size–contact: large, contacts ulna (0); small, absent, does not contact ulna (1).

176 (G102). Lateral central–distal carpal 2 relation: separated (0); in contact (1).

177 (G103). Distal carpal 1–metacarpal 1 association: different elements (0); fused (1).

178 (G121). Pelvic girdle shape: solid plate, no thyroid fenestra (0); small fenestrae broad pubic symphysis (1); large fenestrae, narrow pubic symphysis (2).

179 (Excluded). G133 combined to character 123 (see above).

180 (G125). Fibula–astragalocalcaneal articulation size (0); small portion of fibula distal end (0); covers most of fibular distal end (1).
181 (GI34). Distal tarsal 4–astragalocalcaneal articulation: no tongue-and-groove articulation (0); process of distal tarsal 4 under astragalus (1); complex tongue-and-groove articulation (2).

182 (GI32). Metatarsal 5: straight (0); hooked with medial and plantar tubercle (0); proximal head and medial plantar tubercle modified (2).

183 (GI29). Distal tarsal 2: present (0); absent (1).

184 (GI36). Gastralia: present (0); absent (1).

185 (Excluded). CH 185 merged to character 150 (see above).

186 (CH 186 modified; combined with PGG 23). Size of the premaxillary teeth: same size as posterior maxillary teeth (0), enlarged (1), abruptly small (2).

187 (CH 187). Anteroventral structure of the braincase: close only by cartilage (1), closed by bone (0).

(b) Data matrices

(i) Data for Estes et al. (1988). Only modified characters

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(c) Data for Huehuetzcuatzalli
Symbols: X, excluded redundant characters; ?, or.
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(d) Analysis and results
Data matrix has 24 taxa, 187 (−18=169) characters. All uninformative characters ignored. Valid character-state symbols: 0, 1, 2, 3, 4, and 5. Missing data identified by ‘?’. Not Applicable identified by ‘N’, treated as ‘missing’. Designated outgroup taxa: Rhynchocephalia, Kuehnesauridae, Saurosternon, and Younginiformes. All characters unordered; characters 20, 26, 29, 59, 68, 70, 89, 96, 98, 101, 103, 105, 106, 108, 113, 168, 179, and 185 have no character assigned (excluded); characters 157 and 158 are uninformative (ignored).

Heuristic search settings: random addition sequence, 100 replicates, starting seed is 1. Branch-swapping: tree-reconnection (TBR) with MULPARS option.
in effect. Branches having maximum length zero collapsed to yield polytomies. Topological constraints not enforced. Trees are unrooted and multi-state taxa are interpreted as polymorphism.

(i) Description of most parsimonious tree
Shortest tree found at replicate number 2. Tree length = 820, consistency index (CI) = 0.790, homoplasy index (HI) = 0.744, retention index (RI) = 0.662, rescaled consistency index (RC) = 0.523.

(ii) Apomorphy list. Node numbers correspond to those of figure 11 (* denotes ambiguous characters)
Tree described using accelerated transformation (ACCTRAN).


Huehuecuetzpalli: 27, 28, 63, 65, 95, 99(0)*, 102, 127, 172(0).

Node 42: 1, 25(3)*, 93, 183.
Node 26: 2*, 8, 12*, 10, 63(2)*, 66*, 123, 143*.
Node 25: 80, 97(2).

Anguidae: 25*, 80, 97(2).
Chamaeleontidae: 38, 47, 107(0), 109(3), 110, 112(0), 115, 118, 122, 137(0), 142.
Node 41: 9, 13, 15(0)*, 17*, 34, 39, 40, 41, 44, 49, 58(2), 74*, 75*, 79*, 97, 104(2), 116, 124*, 130, 134, 138*, 146, 147*.
Node 35: 6(0), 10, 28(2)*.

Node 31: 64*, 67*, 85(2), 136, 137(5), 147(0)*.
Node 30: 14*, 28(0)*, 53, 56, 57, 58(0)*, 63, 127, 128, 133.

Node 27: 7*, 10(0)*, 25(0), 36, 64(0)*, 66(0)*, 85, 88*, 114(0), 137(2).

Anguidae: 78, 124(2), 126, 147*.
Chamaeleontidae: 18, 27(0), 129(2).
Node 29: 2*, 4(2)*, 5*, 16*, 27, 45, 58*, 61*, 66*, 69, 86, 92, 142, 156(0), 186(2).

Helodermatidae: 37(0), 54, 65, 90(0), 112(0), 118, 129, 137(3), 143, 167(0).

Figure 11. Most parsimonious tree rooted using outgroup method. Nodes are described in Appendix 1 (d)(ii).

Figure 12. Bootstrap 50% majority-rule consensus tree.
Node 28: 3, 30, 61(2)*, 62, 63(2), 94, 107(2), 109(2)*.
Lanthanotus: 10(0), 60(3), 66(2), 83(0), 109(3)*, 137(4).
Varanus: 5(0)*, 9(0), 16(0)*, 25(0), 32, 36, 42, 53(0), 88(0), 112(2), 124(0), 132.
Serpentes: 13(0), 17(0)*, 33, 47, 65, 66(2), 95(2), 145, 150(2), 187.
Node 34: 4*, 16, 32, 35, 45*, 55(2), 65(2), 72*, 78*, 109(3)*, 118*, 141*, 156(0)*.
Node 32: 22*, 27, 42, 53(2)*, 60(2)*, 66*, 75(0)*, 85, 100(2)*, 107(0)*, 112(0)*, 122*, 137(0)*, 175(0)*, 186.
Amphisbaenia: 5, 13(0), 28(0,1)*, 34(0), 58(0,1), 137(4)*, 138(2), 150(3), 187.
Dibamidae: 10(0), 43, 49(0), 51(0), 100(3)*, 110, 139(2), 141(0)*, 145(0), 148.
Node 33: 31(0)*, 38*, 52*, 54, 77, 91(0)*, 97(0)*, 102(2)*, 125*, 134(0), 139, 140, 145.
Gekkonidae: 99(0), 109(1,0)*, 111, 118(0)*, 147(0)*, 156*.
Pygopodidae: 79(0), 80, 112(0)*, 129(0), 132, 144(0)*, 145*.
Cordylidae: 139(0,2)*.
Scincidae: 17(2), 18, 19(2)*, 43, 141, 144(0)*.
Node 39: 12*, 24(0)*, 73, 74(0)*, 75(0)*, 79(0)*, 97(2), 100*, 121*, 131, 132.
Node 38: 19(0)*, 37(0), 48(0)*, 71(0)*, 81, 87, 95(2), 137(3)*, 140, 142*.
Node 37: 12(0)*, 24*, 54(0)*, 75(2), 90*, 112(2), 122, 137(4)*, 143.
Gymnophthalmidae: 11, 141.
Triidae: 9(0), 43, 46, 124.
Lacertidae: 19(2)*, 23(0), 36, 53, 114, 128, 139(2).
Xantusiidae: 27, 31(0), 38, 46, 52, 55(2), 60(2), 65, 66*, 72, 125.

(iii) Bootstrap analysis
A total of 1000 bootstrap replicates with ten replicates of random addition sequence heuristic search. Starting seed is 1. Branch-swapping with tree-bisection–reconnection (TBR) and MULPARS option in effect. Branches having maximum length zero collapsed to yield polytomies. Topological constraints are not enforced. Trees are unrooted and multi-state taxa are interpreted as polymorphism.

(iv) Bremer’s branch support values
Calculated using the converse constrain option and random addition sequence with ten replicates. Starting seed is 1. Branch-swapping with tree-bisection–reconnection (TBR) and MULPARS option in effect. Branches having maximum length zero collapsed to yield polytomies. Topological constraints are not enforced. Trees are unrooted and multi-state taxa are interpreted as polymorphism.

APPENDIX 2
I-V, metacarpals/metatarsals; a., angular; a.c., astragalocalcaneum; ar., articular; as., astragalus; atl., atlas; atl.na., atlantal neural arch; aut.s., autotomous septum; aut.r., autotomous vertebrae; ax., axis; ax.na., axis neural arch; c., coronoid; c1-c3, vertebral centra; ca., calcaneum; CB., ceratobranchial; ce.v., cervical vertebrae; c.i.c., caudal intercentra; cl., clavicle; co., coracoid; c.s., calcified scutes; c.v., caudal vertebrae; d., dentary; dt., distal tarsal; d.v., dorsal vertebrae; ec.f., ectepicondylar foramen; EH., ephyal; en.f., entepicondylar foramen; eo., exoccipital; ep., epipterygoid; epco., epicoracoid cartilage; f., frontal; f.d.pr., descending process of frontal; fe., femur; fi., fibula; gr.sc., granular scales; h., humerus; ha., haemal arch; i3, third intercentrum; ic., interclavicle; il., ilium; isc., ischium; j., jugal; i.l., ilmbrar intercentra; m., maxilla; m.c., Meckelian canal; n., nasal; op., opisthotic; p., parietal; p.f., parietal foramen; pm., premaxilla; po., postorbital; po.d., postdental bones; po.p., postfrontal; prf., prefrontal; psv., presacral vertebrae; pt., pterygoid; pu., pubis; p.x.i.r., postxiphisternal inscriptional ribs; q., quadrate; r., radius; s., stapes; sa., surangular; sc., scapula; sc., supraoccipital; spl., splenial; sq., squamosal; s.s., suprascapula; st., supratemporal; st., sternum; ste., sternum ribs; s.v., sacral vertebrae; t., tibia; t.n., tibial distal notch; tr.pr, transverse process; u., ulna; ul., ulnare; v., vomer; xi., xiphisternum.
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