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

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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 1983*a*); 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 1994*a*) from Kirtlington, England (Bathonian), and *Changetisaurus estesi* (Fiederov & Nessov 1992) from Kyrgyztan, 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 *Paramacellodus*, *Becklesius*, *Saurillus* and *Saurillodon* (also known in Kirtlington; Evans 1995) have been reported from the Guimarota lignite mine (Oxfordian–Kimmeridgian) in Leira, Portugal (Seiffert 1973). *Dorsetisaurus* and *Paramacellodus* are also known from the Late Kimmeridgian and Early Tithonian deposits in Como Bluff, Wyoming (Prothero & Estes 1980; Chure 1992). The scincomorph *Sharovisaurus* was reported from the Kimmeridgian of Kazachstan, Central Asia (Hecht & Hecht 1984), and the skink *Mimobecklesisaurus* (Li 1985) from the Upper Jurassic of the Gansu province of China. *Euposaurus* from the Kimmeridgian of Cerin, France, long believed to be an iguanian (Cocude-Michel 1963; Estes 1983*b*), is now known to have been described on the basis of an assemblage of

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lepidosaurs from different taxa, and only the poorly preserved type can be assigned to the Squamata with uncertain relationships (Evans 1994*b*). Finally, the genera *Ardeosaurus*, *Eichstaettisaurus*, *Bavarisaurus* and *Palaeolacerta* were described from the lower Tithonian deposits of Solnhofen (Hoffstetter 1953, 1964, 1966; Cocude-Michel 1963, 1965; Ostrom 1978; Mateer 1982; Evans 1993, 1994*c*). The previously considered early lizard *Cteniogenys* from Como Bluff (Gilmore 1928; Prothero & Estes 1980) and Guimarota (Seiffert 1973), is now considered a choristodere (Evans 1989, 1990), and *Lisboasaurus*, also from Guimarota, is a small, unusual, archosaur (Buscalioni *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 *Yabeinosaurus* 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 *Ilerdaesaurus* (probably synonymous to *Meyasaurus*; Barbadillo & Evans 1995) was added to the Montsec collection (Hoffstetter 1965). *Parviraptor*, *Dorsetisaurus*, *Paramacellodus*, *Saurillus* and *Becklesius* all known from the late Jurassic are also found in the Berriasian deposits of Purbeck with two other scincomorphs: *Pseudosaurillus* and *Durotrigia* (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 *Ilerdaesaurus*, *Becklesius*, *Paramacellodus* and the new possibly anguimorph *Cuencasaurus* were found in the Late Barremian deposits of Uña and Galve, Spain (Richter 1991, 1994*a*,*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 *Paramacellodus* from the Berriasian (?) of Anoual, Morocco (Richter 1994*a*), and *Hoburogecko*, the earliest known gecko, from the Aptian–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 1983*a*; 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 (1994*b*) has recently demonstrated that *Euposaurus* 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 Rodríguez, Central Mexico, 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***
Lepidosauria Dumeril & Bibron, 1839
Possibly Squamata Oppel, 1811

(i) *Genus* Huehuecuetzpalli *gen. nov.*

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

Diagnosis. As for the type and only known species.

Type Species: Huehuecuetzpalli Mixtecus 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 4185 (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 Rodríguez, Puebla, México.

Horizon. Middle Member of the Tlayua Formation (Pantoja-Alor 1992). Early Cretaceous. Middle or Late Albian (Seibertz & 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

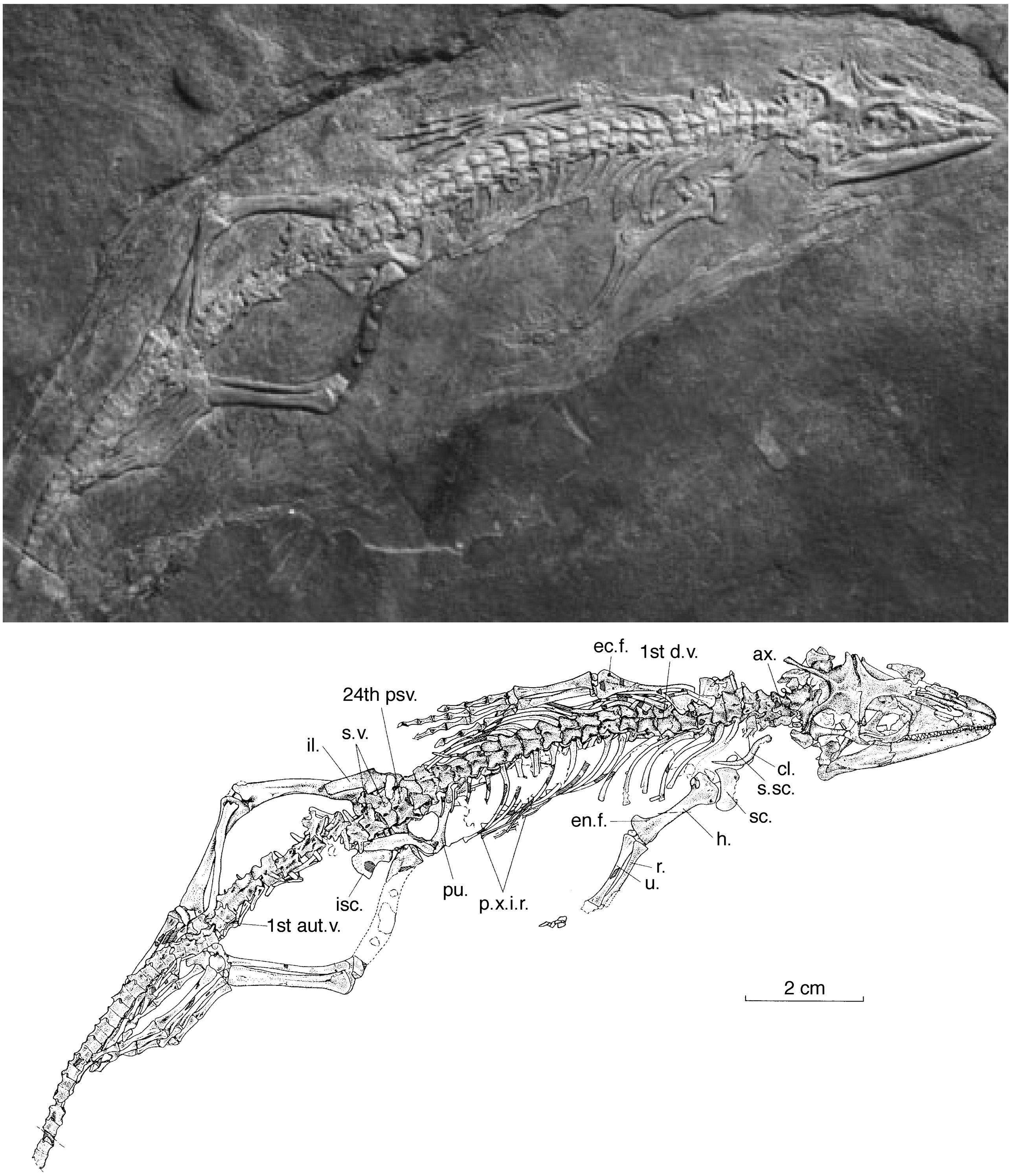

Figure 1. Skeleton of the holotype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 7389) as preserved on the block. Abbreviations are listed in Appendix 2.

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.

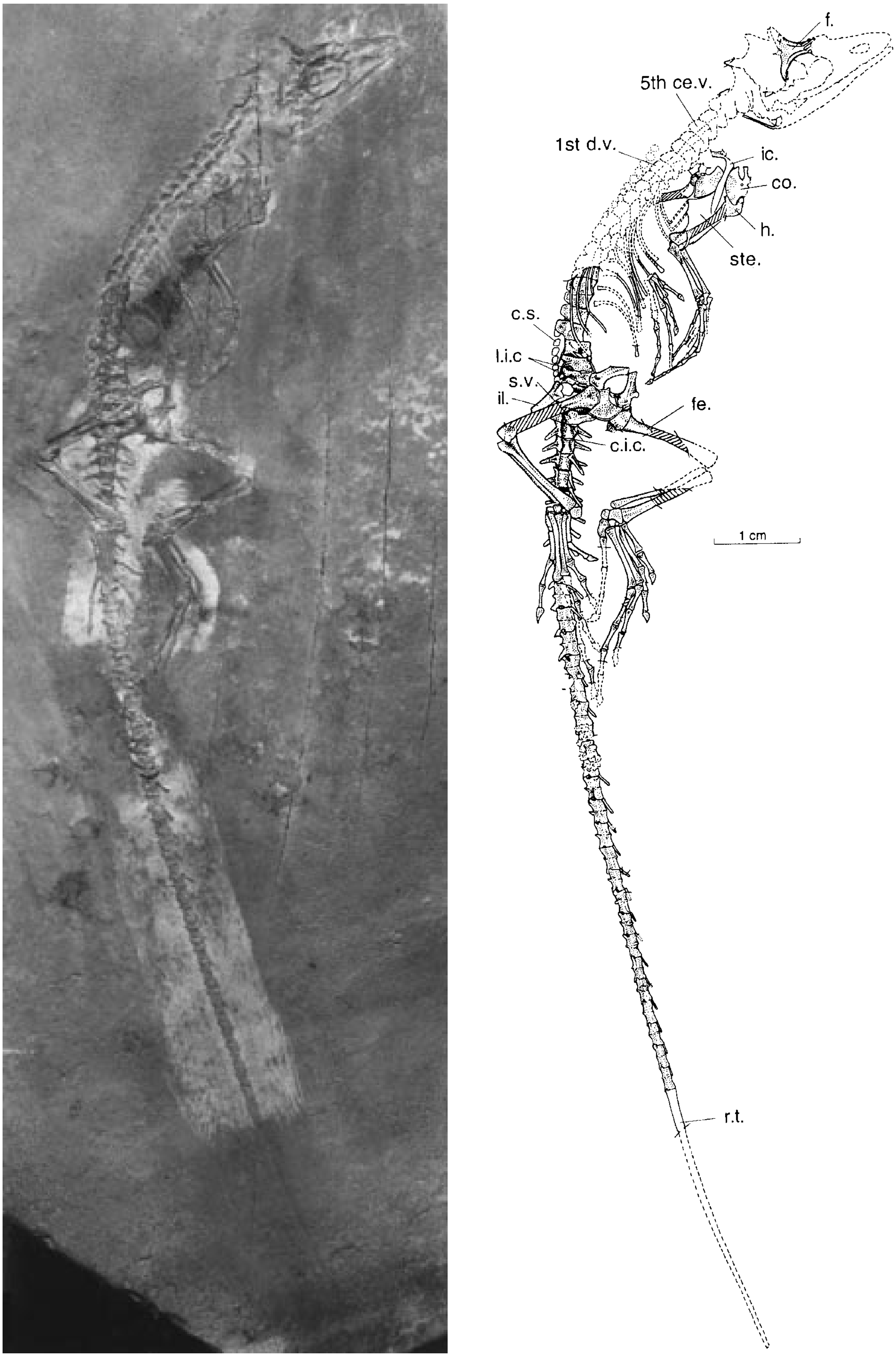

Figure 2. Skeleton of the paratype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 4185) as preserved on the block. Abbreviations are listed in Appendix 2.

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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.)

measurement	IGM 7389 (holotype) adult	IGM 4185 (paratype) juvenile	difference
total length	—	197.0	—
skull length	32.2	19.3	—
skull breadth at fronto-parietal suture	11.6	7.1	—
snout length	13.8	7.8	—
postorbital skull length	9.3	(5.0)	—
parietal table width	2.0	4.3	—
presacral vertebral column (PSVC) length	75.7	46.9	—
humerus	15.7	10.7	—
radius	12.9	(7.4)	—
ulna (without olecranon)	13.1	8.1	—
femur	(24.7)	15.2	—
tibia	20.7	12.7	—
fibula	20.3	13.6	—
metacarpal IV length	6.3	4.0	—
metatarsal IV length	12.9	8.6	—
manus 4th digit length	(19.0)	13.8	—
pes 4th digit length	(33.5)	24.5	—
tail length	—	126.6	—
replacement portion length	—	36.4	—
skull proportions			
skull length–PSVC length	0.425	0.412	0.013
skull breadth–skull length	0.360	0.368	−0.008
parietal table–skull length	0.062	0.223	−0.161
snout length–skull length	0.429	0.404	0.025
postorbital length–skull length	0.289	0.259	0.030
appendicular skeleton proportions			
humerus–PSVC length	0.207	0.243	−0.036
radius–PSVC length	0.170	0.158	0.012
ulna–PSVC length	0.173	0.173	0.000
femur–PSVC length	0.326	0.318	0.008
tibia–PSVC length	0.273	0.324	−0.051
fibula–PSVC length	0.268	0.292	−0.024
tail length–total length	—	0.643	—
replacement tip-tail length	—	0.288	—

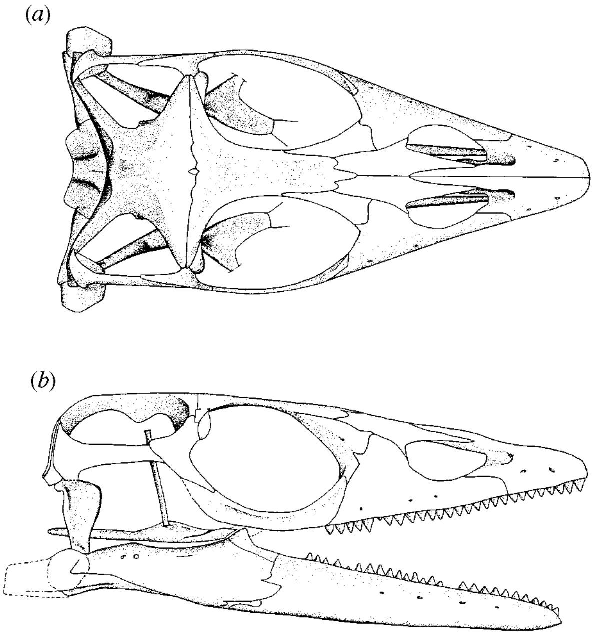

Figure 3. Reconstruction of the skull of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (*a*) Dorsal view; (*b*) lateral view. The lateral shape of the quadrate and pterygoid is unknown. The relation of the nasals and the narial process of the premaxillary is also obscure, however, the nasals might have been compressed down into the narial opening leaving the premaxillary narial processes exposed.

(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 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.

The dorsal process of the maxilla is short and contacts the nasals dorsally. In the juvenile, this process remains slightly separated from the rest of the maxilla suggesting that full ossification was not yet completed. The dental portion of the maxilla, however, is perfectly held by adjacent bones (premaxilla, jugal and prefrontal) permitting mastication. The infraorbital process of the maxilla is also short and extends just below the anterior margin of the orbit. A total of three sensory foramina aligned parallel to the dental series are present. The nasals are divided. In the

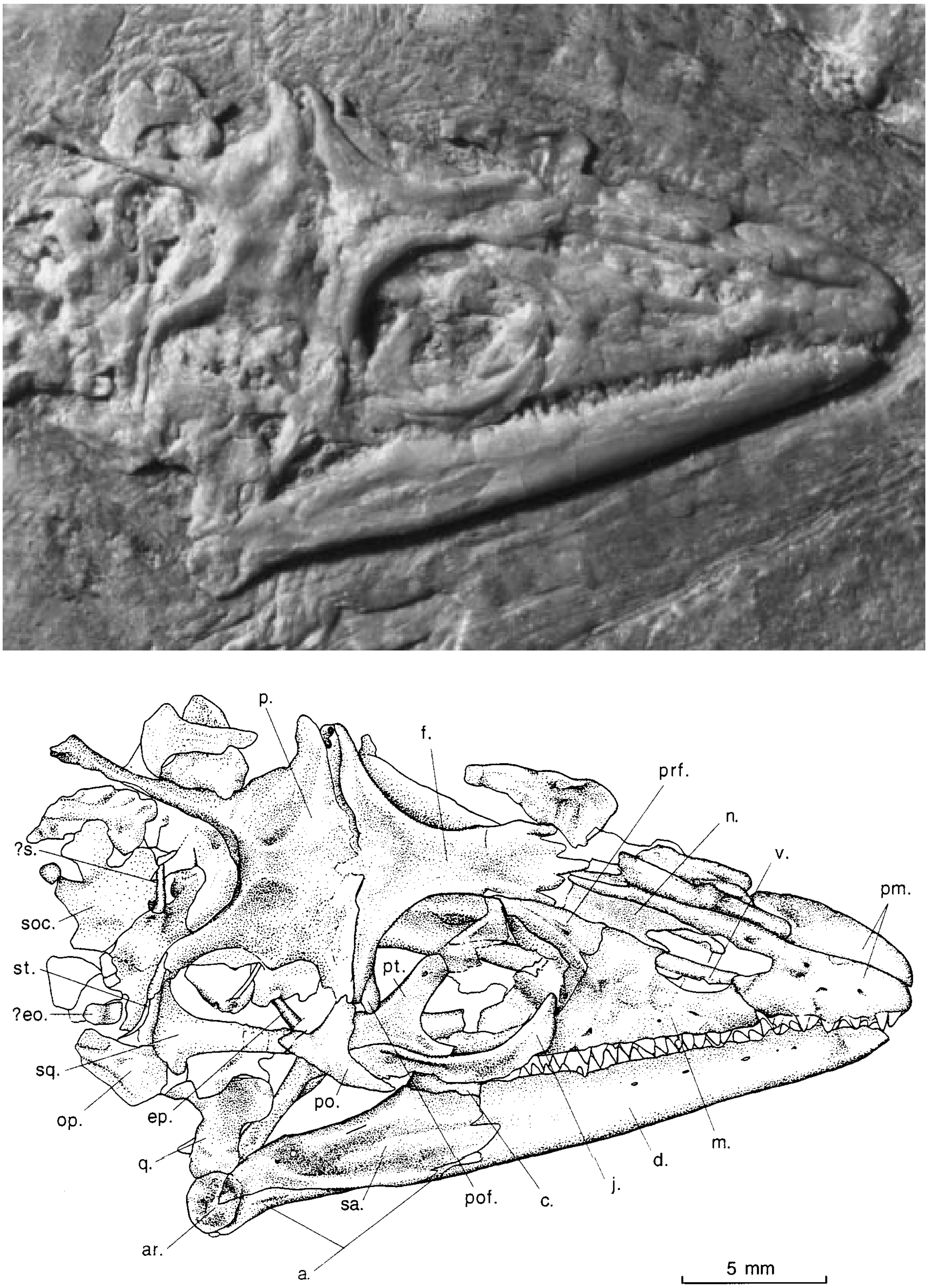

Figure 4. Skull of the holotype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 7389) as preserved on the block. Abbreviations are listed in Appendix 2.

holotype they are preserved crushed over the narial passageway exposing the narial processes of the premaxilla. As seen in the young specimen (figure 5*a*) 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

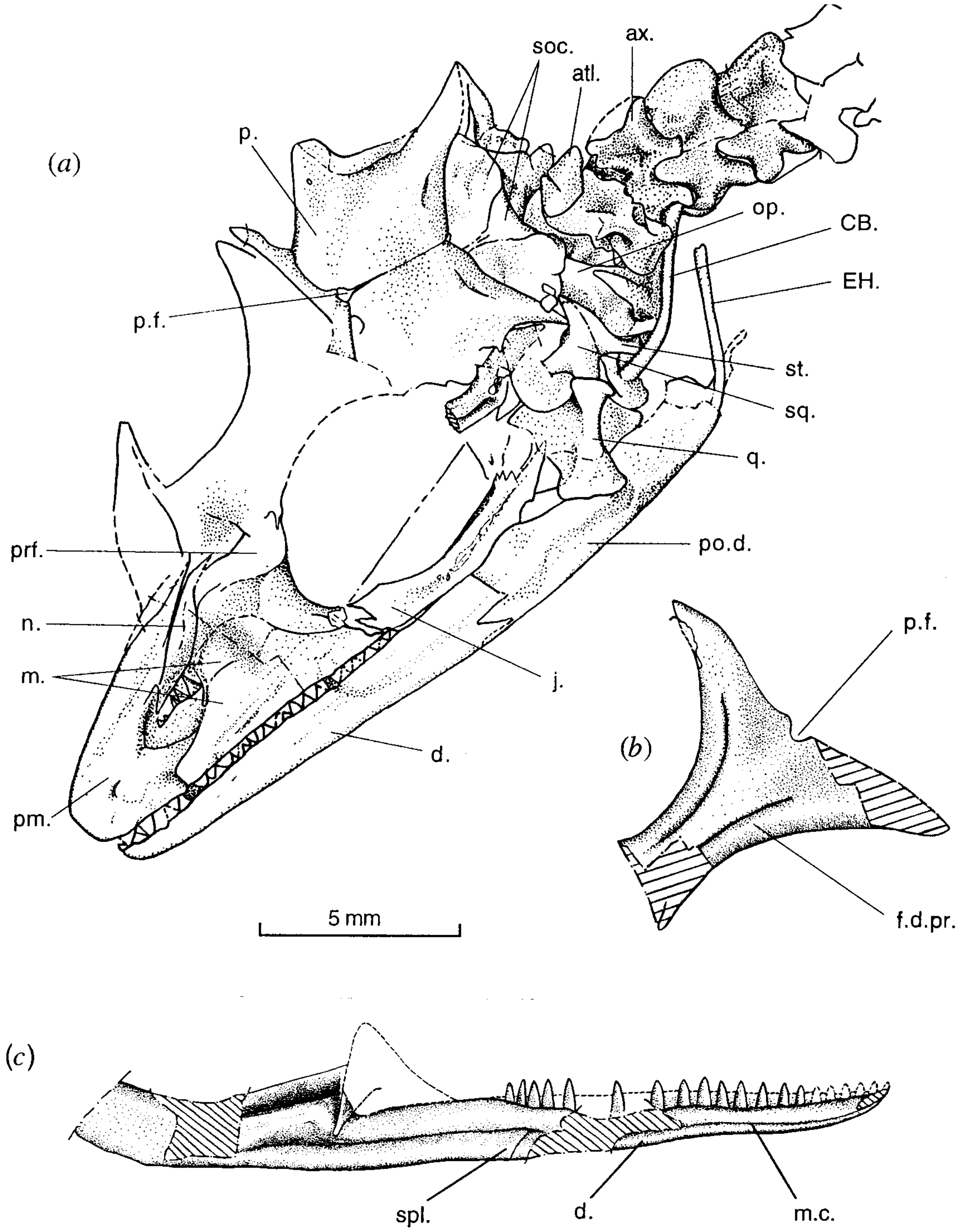

Figure 5. (*a*) Skull of the paratype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 4185), from fossil and latex cast as preserved on the block; (*b*) ventral view of the frontal; (*c*) reconstruction from a latex cast of the medial side of the lower jaw. Abbreviations are listed in Appendix 2.

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 5*a*). 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 5*b*).

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 5*a*). 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 quadrate 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 crest 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 quadrate 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 and the opisthotics are displaced far laterally. A small C-shaped bone lying medially to the right opisthotic resembles a disarticulated exoccipital. If this bone is correctly identified, the exoccipital was separated from the opisthotic in the adult. The possibility of the exoccipital being broken cannot be discarded, but judging from the similar way the exoccipital contacts are preserved in both opisthotics, it is hard to imagine that both bones followed simultaneously the same breakage pattern.

As a result of the posterior displacement of the supraoccipital, some traces of the right stape 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 epipterygoid contacting the alar process of the pro-otic 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 quadrate process.

(b) *Lower jaw*

The dentary comprises almost half of the total length of the slender jaw. The articulation between the dentary and postdentary 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 postdentary 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 *Huehuecuetzpalli* could have been hinged. In varanoids, however, the postdentary–dentary 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–dentary 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 5*c*). 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 postdentary 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 5*a*). 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 vertebral column is composed of 24 presacral vertebrae, two sacrals, and in the juvenile where the tail is complete, there are 32 caudal vertebrae plus a regenerated segment of about one-quarter of the total caudal

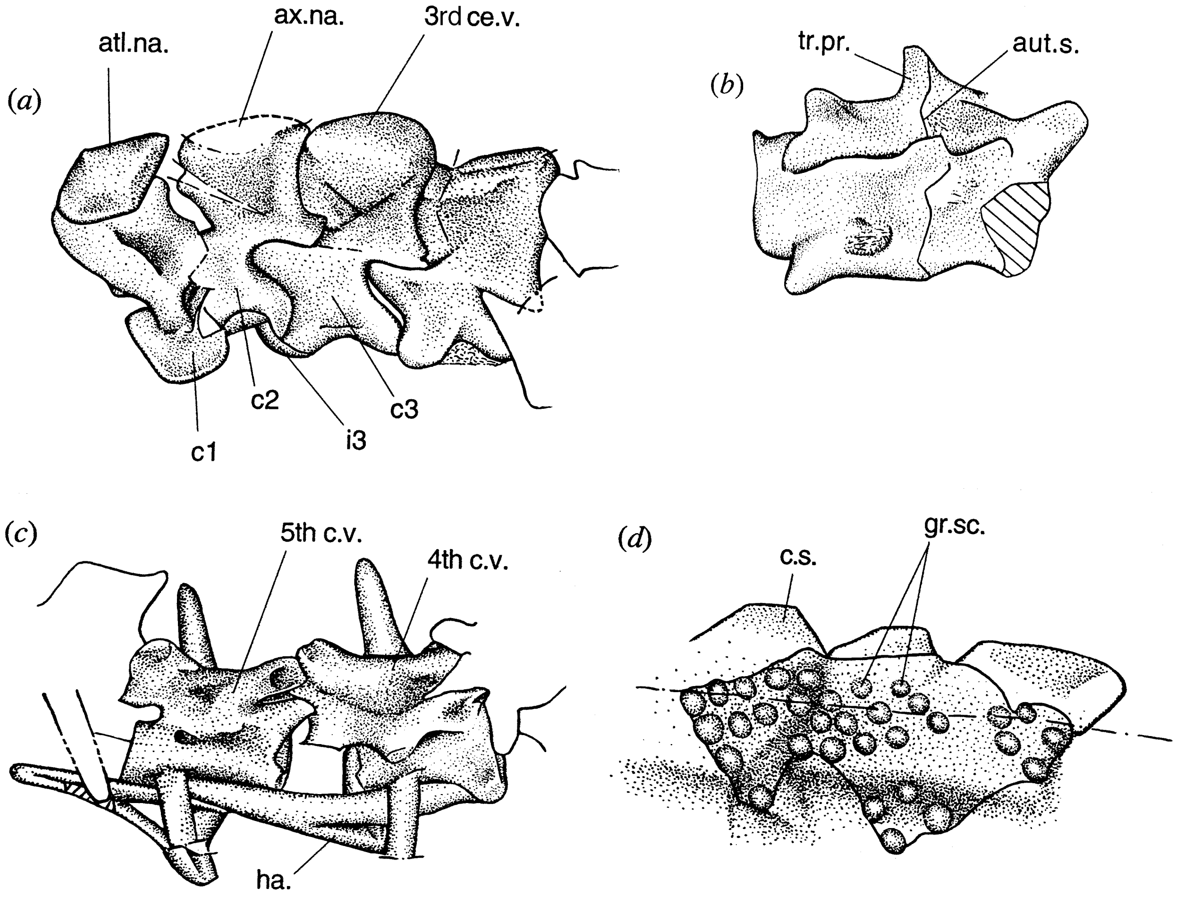

Figure 6. *Huehuecuetzpalli mixtecus* gen. et sp. nov. (*a*) Semireconstruction of the atlas–axis complex; (*b*) dorsal view of the third autotomous vertebrae; (*c*) lateral view of the fourth and fifth caudal vertebrae; (*d*) pattern of the epidermal scales preserved over the 13th and 14th presacrals. (*a*) and (*d*) from IGM 4185; (*b*) and (*c*) from IGM 7389. All scaled to about the same size. Abbreviations are listed in Appendix 2.

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 6*a*). 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 6*c*). 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 6*b*).

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 6*d*).

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 8*a*). The most posterior vertebrae have ribs of equal size to the sternal ribs and are associated with a series of postxiphisternal inscriptional ribs. In the juvenile, the inscriptional ribs are extremely thin, lying

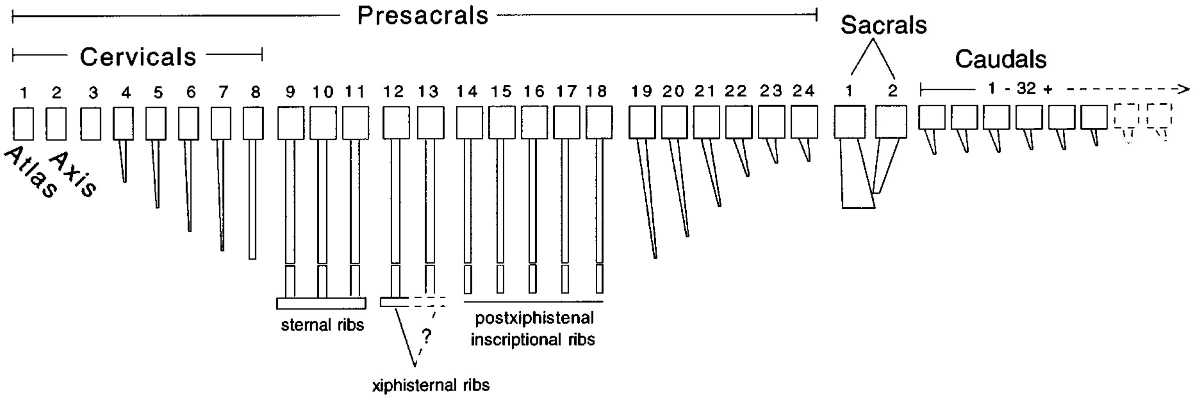

Figure 7. Schematical reconstruction of the vertebral column of *Huehuecuetzpalli mixtecus* gen. et sp. nov.

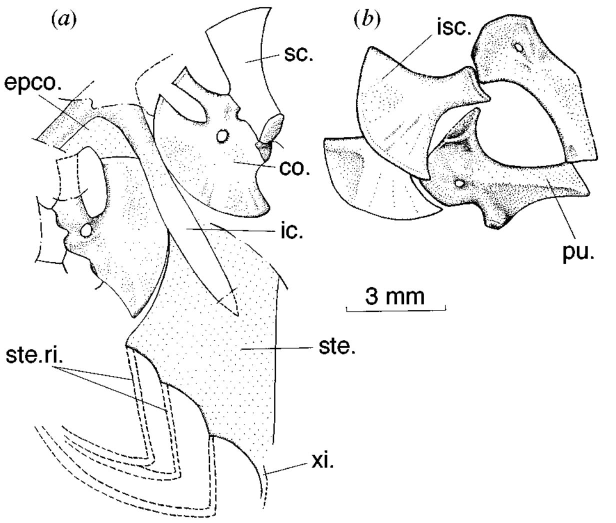

Figure 8. *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 4185). (*a*) Semi-reconstruction from cartilaginous remains, impressions, and latex casts of the shoulder girdle, sternum, and sternal ribs. Scapula reconstructed from its dorsal view in IGM 7389. (*b*) Ventral view of the pelvic girdle as preserved. Abbreviations are listed in Appendix 2.

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 inscriptional 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 8*a*). 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 unperforate 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 (Lécuru 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 intermedium, 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 8*b*). This orientation suggests a straight contact between the pubic bones, characteristic of the ventrally oriented symphysis of some 'iguanids' 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.

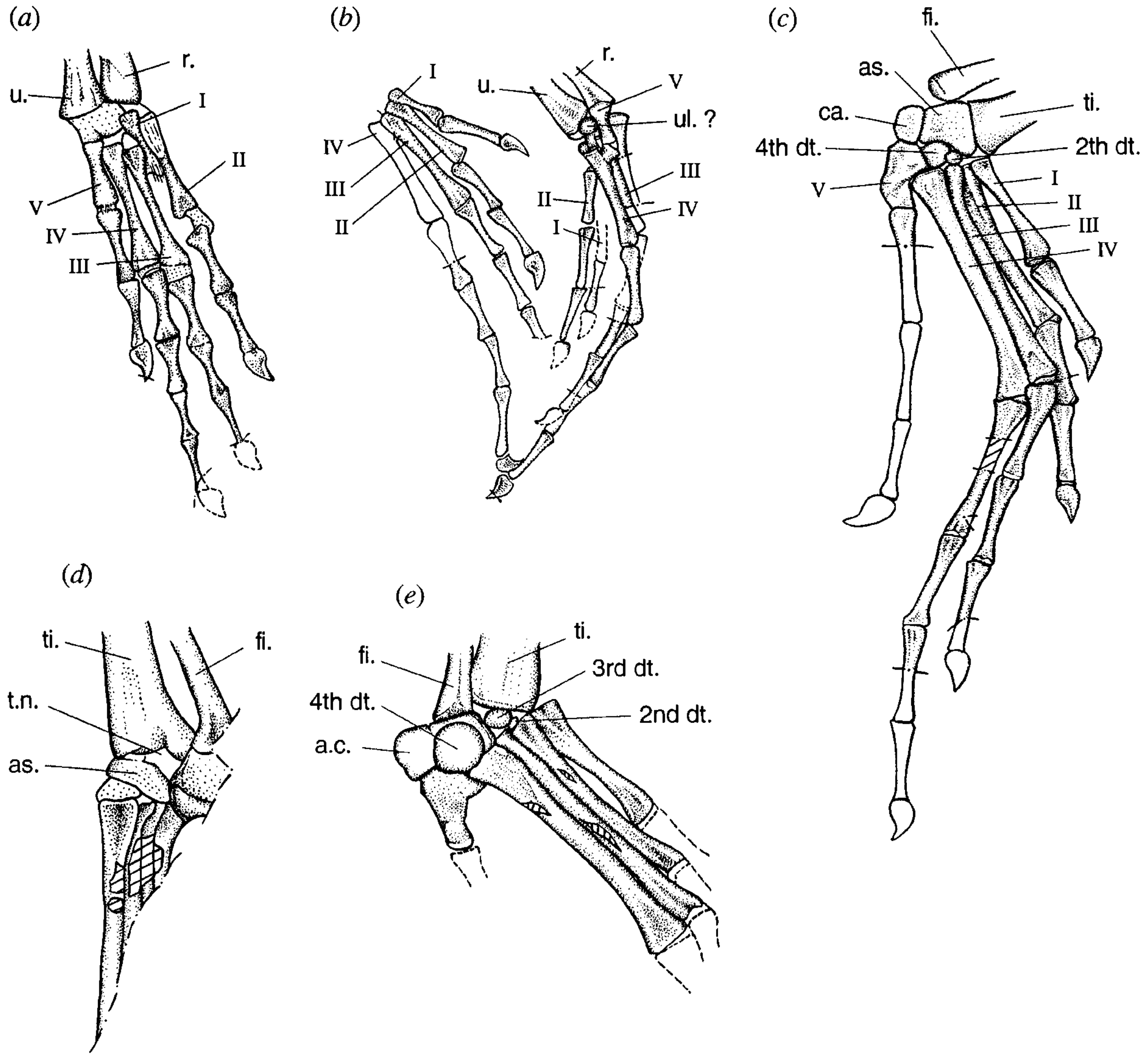

Figure 9. *Huehuecuetzpalli mixtecus* gen. et sp. nov. Manus and pes as preserved. (*a*) Left manus; (*b*) left and right manus, juvenile; (*c*) left pes on ventral view; (*d*) tibioastragalar articulation on left limb; (*e*) tarsal and metatarsal on the right pes of the adult. (*a*), (*d*), and (*e*) from IGM 7389; (*b*) and (*c*) from IGM 4185. All scaled to about the same size. Abbreviations are listed in Appendix 2.

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 9*d*). The astragalus and calcaneum are not fused but sutured in the juvenile specimen (figure 9*c*). 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 9*e*), 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*

(Rieppel 1994). The complete fusion of the frontal, however, shows that it is older than Rieppel's specimen number 18 and the hatchling of *Cyrtodactylus pubisulcus* (Gekkonidae) illustrated by Rieppel (1992*a*: 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-hatchling stages (Rieppel 1992*b*). 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 1′011′297 of *Lacerta vivipara* and almost reaches the stage of MBS 5625 (Rieppel 1992*b*). 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 prehatchling 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 1992*b*, 1994) and in the colubrid snake *Elaphe obsoleta* (Haluska & Alberch 1983), but not in chamaeleonines (Rieppel 1993). In *Lacerta* these two elements become fused in late prehatchling stages. In all known hatchling lizards, both ossification centres are ossified into a single maxillary bone. Among Squamata, only in boyeniid 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 hatchling lizards.

The presence of 'prehatchling' 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 *Palaeagama* and *Paliguana* 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 I) 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

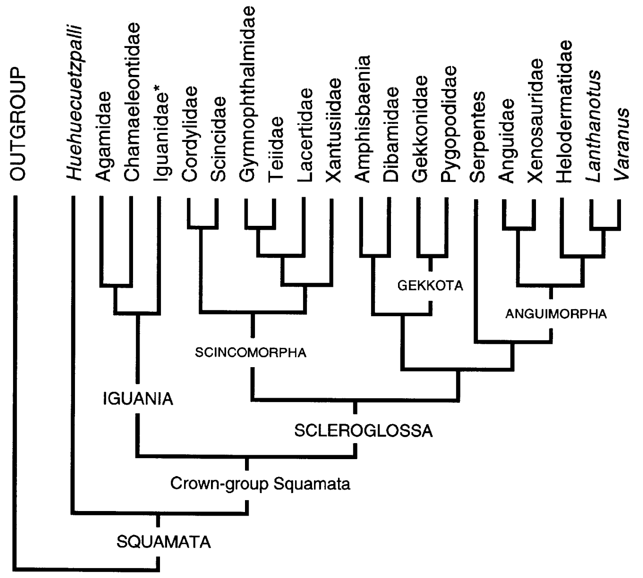

Figure 10. Most parsimonious tree showing the sister-group relationships of *Huehuecuetzpalli* with Squamata. Analysis was done by using an extended version of Estes *et al*.'s (1988) data matrix, as presented by Clark & Hernández (1994) with several additional modifications. List of modified characters 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 proximal head and tuber modified, anterior coracoid fenestra, gastralia absent. Crown-group Squamata: premaxilla paired, vertebrae centra procoelous, second distal tarsal absent. Iguania: frontal shelf broader than nasals, jugal contacts squamosal, tibia distal end gently convex. Scleroglossa: descending process of frontal contacts palatine, postfrontal forked medially, dorsal process of squamosal absent, large vomer, septomaxillae meet in midline, convex expanded septomaxilla, prominent choanal fossa of the palatine, long prootic alar process, large subdental shelf, cervical intercentra sutured or fused to preceding centra, 26 or more presacral vertebrae, clavicle strongly angulated, epiphyses fused before cranial fusion, muscle *rectus abdominis lateralis* present, mid-dorsal scale row absent. A full description of the tree is given in Appendix 1.

reported. 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 Anguimorpha, and dibamids and amphisbaenians 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 and parietals fused in the midline, straight frontoparietal suture broader than nasals, short parietal table not covering the occipital region posteriorly, squamosal with ventral peg for quadrate, lack of quadrate lappet of pterygoid, pterygoid enters the suborbital fenestra, broad interpterygoidal vacuity, paraoccipital process contacting suspensorium, angular ends anterior to articular condyle, cervical ribs single-headed, anterior coracoid fenestra, distinctly large thyroid fenestra in pelvic girdle with narrow pubis, hooked fifth metatarsal with modified plantar tuber, and gastralia absent. The primitive position of *Huehuecuetzpalli* relative to crown squamates is indicated by the unfused premaxillae, amphicoelous centra, entepicondylar foramen, and presence of a second distal tarsal, whereas derived states are synapomorphic for crown squamates. The presence of thoracolumbar intercentra and the possible persistence of the exoccipitals as separated elements after hatchling, are 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 assemblage excluding *Huehuecuetzpalli* in 68% of the trees in the 50% majority rule consensus tree, resulting when subjecting the data matrix to bootstrap (1000 replicas; see Appendix 1, part *d*). However, Bremer's branch support values (Bremer 1988, 1994) indicate that only two steps are necessary to collapse crown squamates into the Squamata (including *Huehuecuetzpalli*).

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 naris 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 *Bavarisaurus* (Evans 1994*c*), 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 tibial–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 paedomorphosis 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 1985; 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 plesiomorphic 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 plesiomorphic 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 intercentrum 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. *Bavarisaurus*, a possible scleroglossan, shows divided premaxilla, trunk intercentra, and presumably amphicoelous vertebrae (Ostrom 1978; Mateer 1982; Evans 1994*c*); *Eichstaettisaurus*, a possible gekkotan, has a divided premaxilla (other structures not known; Hoffstetter 1964); and *Parviraptor*, a possible anguimorph, preserves intervertebral notochordal canal (Evans 1994*a*). 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 perichordal sheath. In opposition with Evans' (1994*c*, p. 48) interpretation, the development of procoelous vertebrae in squamates does not pass through a morphogenic stage similar to that of

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).)

genus	humerus	femur	HRMc	FTMt	humerus/femur	HRMc/FTMt	behaviour
Huehuecuetzpalli							
adult	15.7	(24.7)	34.9	58.3	0.636	0.599	?
juvenile	10.7	15.2	22.1	36.5	0.704	0.605	?
Basiliscus MCZ 19490	25.3	42.4	49.5	97.8	0.597	0.506	bipedal
Heloderma RPM	33.0	35.0	65.6	69.7	0.943	0.941	fully terrestrial
Sphenodon RPM 1135	34.5	41.9	63.5	85.1	0.746	0.746	fully terrestrial
Cordylus MCZ 41881	15.3	18.4	28.5	40.2	0.832	0.709	terrestrial–climber
Gekko MCZ 173377	18.8	22.4	34.8	46.3	0.839	0.752	climber
Palaeopleurosaurus SMNS No. 50722	26.0	33.0	50.5	64.0	0.788	0.789	aquatic
Icarosaurus AMNH 2101	20.1	4.7	45.6	(63.1)	0.579	0.737	glider

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. 3*a*). In the case of *Parviraptor*, 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 sphaerodactylines, some diplodactylines, and pygopodid 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 (and possibly in *Ardeosaurus* and *Huehuecuetzpalli*) in which the vertebral ends are always broadly open and there is absolutely no trace of condyle formation and intervertebral notochord constriction. This last condition resembles more closely the centrum of *Sphenodon* (Howes & Swinnerton 1901; Werner 1971) and might well be a retained primitive character. The vertebral articulation of *Huehuecuetzpalli*, *Bavarisaurus*, and amphicoelous gekkonids is correlated with the presence of intercentra. The reversal of both structures to the primitive condition would be a complex process that requires the re-elaboration of intercentra.

The persistence of separated elements of the maxillae and supraoccipital through the juvenile stages of *Huehuecuetzpalli* can be explained either as a primitive feature among lizards in which the derived state will be the complete fusion of both elements in prehatchlings; or as the persistence through paedomorphosis of the prehatchling condition with separate elements retained into post-hatchling stages. No separated elements are present during the development of *Sphenodon* (Howes & Swinnerton 1901) indicating that the presence of a single ossification centre is primitive for lepidosaurs, and that the acquisition of separated centres of ossification in maxilla and supraoccipital is derived in squamates. This still leaves the question as to whether the late or early fusion of elements was the primitive condition within squamates. The presence of separated maxillary and supraoccipital ossification centres in *Huehuecuetzpalli* suggests that their fusion after the juvenile ontogenetic stage is primitive; however, because this condition is unknown in other lizards, it might be autapomorphic for *Huehuecuetzpalli*.

5. MODE OF LIFE

Huehuecuetzpalli mixtecus shows many characters associated with terrestriality. The body is rather short with well-developed limbs and a large tail. There are no obvious indicators of aquatic behaviour, although swimming capabilities cannot be discounted. The limbs are long and slender, with elongated digits on manus and pes. The forelimb is even shorter relative to the hind limb than it is in most other lizards. Although forelimb–hind limb indices do not provide accurate information about locomotion behaviour in lizards, some conclusions can be drawn. The limb proportions of *Huehuecuetzpalli* are intermediate between the bipedal lizard *Basiliscus* and some fully terrestrial forms (see table 2). This suggests that of 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 *Varanus* is adapted to catch relatively large and fast-moving prey (Rieppel 1979*a*). 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. *Huehuecuetzpalli* is the first basal squamate to be adequately documented and the only source of information in this regard.

Fossil lizards are known to date back as early as the Middle Jurassic of Europe (Evans 1995). *Huehuecuetzpalli* 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 (1983*a*) relatively primitive squamate taxa ('iguanids', 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 *Priscagama* 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 sphenodontians and lizards, with only the type specimen assignable to the Squamata, *Incerta sedis* (Evans 1994*b*). 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 'iguanids' 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. *Paramacellodus*, *Becklesius*, *Saurillus*, and *Pseudosaurillus* have enlarged replacement pits (Seiffert 1973; Hoffstetter 1967; Richter 1994*a*), and *Euposaurus* might be closely related to this group. The specific position of *Euposaurus*, however, cannot be established until new information becomes available.

7. CONCLUSIONS

Huehuecuetzpalli mixtecus is characterized by a combination of characters unlike those of any of the previously described Late Jurassic or Upper Cretaceous lizard. Its sister-group relationship with squamates is supported by 15 synapomorphies, but the presence of plesiomorphic characters rarely, if ever, seen in squamates, keeps it outside the crown squamates. It shares two characters with iguanians that may support affinities with this taxon.

Character congruence strongly supports the paedomorphic origin of a divided premaxilla, amphicoelous vertebrae, and thoracolumbar intercentra in geckos, but not in *Huehuecuetzpalli*. Their common presence in many early fossil squamates suggests that the derived features were present but not fixed until later in lizard evolution. Primitive amphicoelous vertebrae in some geckos may indicate that they branched off from squamate ancestors around this time period, preserving primitive features. The primitive condition of *Huehuecuetzpalli* indicates that it is the first known basal squamate providing information about character transformation during the early period of lizard evolution, although it is unexpectedly late in the fossil record.

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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.*'s 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, 68, 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 *Varanus*; in none of the specimens observed do the frontal downgrowths reach the palatines. Character 13 recoded (0, N) in Amphisbaenia, 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 (Rieppel 1980). Character 45 recoded (0) in Xantusiidae (Rieppel 1984). Character 50 variable (0, 1) in Anguidae, condition (1) present in *Diploglossus* and *Gerrhonotus* (Rieppel 1980). Character 51 variable (0, 1) in Lacertidae and Scincidae; exoccipitals are separated in *Podarcis* and in some late embryos of *Tiliqua* (Gauthier *et al.* 1988). Character 53 recoded (N) in Kuehneosauridae and rhynchocephalians; 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 *Paliguana* (Evans 1991). Character 90 variable (0, 1) in Teiidae; the second epibranchial 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. *Anopsibaenia*; 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 (1?) 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 95), 103, and 145, 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 prefrontals 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). Postorbital contribution to the posterior margin of the orbit: one half or more (0), less than one half (1), postorbital 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* (Rieppel 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 posterodorsal 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 amphisbaenians 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 1979*b*).

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 pol. rev.). Comment: State (0) of Estes *et al.* (1988: 102) was further divided into two states. The autotomous 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); Lécuru 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 tibia: 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 posteroventral process: absent (0); present, forming posterior margin of Jacobson's organ duct (1).

158 (G37). Septomaxilla extension: only on posteroventral edge of exonarinal 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). Coronoid process structure: coronoid medial and surangular lateral (0); formed primarily by coronoid (and dentary) (1).

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

167 (G79). Cervical vertebral intercentra 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 post-embryonic (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 fenestra broad pubic symphysis (1); large fenestra, narrow pubic symphysis (2).

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

180 (G125). Fibula–astragalocalcanear articulation size (0); small portion of fibula distal end (0); covers most of fibular distal end (1).

181 (G134). 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 (G132). Metatarsal 5: straight (0); hooked with medial and plantar tubercle (0); proximal head and medial plantar tubercle modified (2).

183 (G129). Distal tarsal 2: present (0); absent (1).

184 (G136). 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*

character number	2	4	7	14	17	18	19	25	28	58	60	71
Agamidae	0	0	1	N	0	1	0	1	0,2	0,1	0	0
Amphisbaenia	0	1	N	0,1,N	N	N	N	0,3	0,1	0,1	1,2,3	0
Anguidae	0	0,1	0,1,N	0,1	1,2	0	0,1	0	0	0	0,1	0,1
Chamaeleontidae	0,1	0,N	1,N	N	0	0,1	0	2,3	0,2	0,1	0	0
Cordylidae	0	0,1	0	0	1	0	1	0,3	0,2	2	1,2	1
Dibamidae	0	1	0	N	N	N	N	3	2	2	2	0
Gekkonidae	0	0,1	0	N	N	N	N	3	2	2	1	0
Gymnophthalmidae	0	0,1	0,1	0,1	1	0	0,1	3	0,1,2	0,2	1	0
Helodermatidae	0,1	0,2	N	N	N	N	N	3	0	1	1	0
Iguanidae*	0	0	0,1	0,N	0	1	0	0,1,2,3	0,2	0,1	1,3	0
Lacertidae	0	0	0,1	N	1	0	2	0,3	0	2	1	0
Lanthanotus	1	2	N	N	N	N	N	3	0	1	3	0
Pygopodidae	0	0,1	0,N	N	N	N	N	3	2?	2	1	0
Scincidae	0	0,1	0,N	0,1,N	2	1	2	0,3	0,2	2	1,2	0,1
Serpentes	0,1	0	0,N	0,N	0	N	N	3	2	2	1,2,3,N	0,N
Teiidae	0	0,1	0	0,1	1	0	0	0,1,3	0	2	1	0
Varanus	1	2	0	1	1	0	0	0	0	1	1	0
Xantusiidae	0	0,1	0	N	1	0	1	0,3	?	2	2	1
Xenosauridae	0	0	1	0,1	1	1	0	0	0	0	1,2	0
Rhynchocephalia	0	0	0,1	0	0	0,1	0	0	0,2	0,1	0	0
Kuehneosauride	0	0	0	0	0	?	0	1/3	0	0	N	N
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?
Youngingformes	0	0	0	0	0	0	0	0	0	?	N	?

character number	79	95	97	100	102	104	107	112	123	145
Agamidae	2	0	2	0	0,2	0,1	1	1,2	1	2
Amphisbaenia	2	0	1	2	0,3	2	N	0,N	N	2
Anguidae	1,2	0	1	0,2	0,1,2,3	2	0,1	1,N	2,N	2
Chamaeleontidae	2	0	0	0	0	0?,1	0	0	1	2
Cordylidae	1,2	0,1,2	0,1,2	0,1	2,3	0,2	0,1	1	2	2
Dibamidae	2	0	1	3	?	2	0	N	N	0
Gekkonidae	0,1,2	0	0	0	0,2	0,2	1	1,2	2	0,1
Gymnophthalmidae	1,2	1,2	2	1	3	0,2	1	2	2	2
Helodermatidae	2	0	1	0	0	2	1	0	2	2
Iguanidae*	1,2	0,1,2	0,1	0,1	0,1,2,3	0,1	1	1,2	1	2
Lacertidae	1,2	2	0,1,2	1	1,3	0,2	1	1	2	2
Lanthanotus	2	0	1	0	0	2	2	1	2	2
Pygopodidae	0,1,2	0	N	0	2	2	N	0,1,N	N	1
Scincidae	1,2	1	1	0,2,3	0,1,2,3	2	0,1	1,N	2,N	2
Serpentes	2	2	1	0	0	2	N	N	N	1
Teiidae	1	2	2	1	1,3	0,2	1	2	2	2
Varanus	0	0	1	0	0	2	2	2	2	2
Xantusiidae	1	0	0,2	0,1	1,2,3	2	1	1	2	2
Xenosauridae	1	0	1	0	0,1	2	1	1	2	2
Rhynchocephalia	0	0,1	0	0	1	0	0,1?	0	0	1?
Kuehneosauridae	?	0	N	0	0	0	?	0	?	0
Saurosternon	?	?	?	0	0	?	?	0	?	?
Younginiformes	?	0	0	0	0	0	?	0	0,1	0

(ii) *New characters*

character number	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166
Agamidae	1	1	1,N	1	1	1	0,1	1	1	1	1	2	1	1	1	1	1	1
Amphisbaenia	1	3	N	1	1	1	1	0	1	1	1	2	1,N	1	1	1,N	1	1
Anguidae	1	1	1,N	1,N	1,N	0,1,N	1	1	1	1	1	2	1	1	1	1	1	1
Chamaeleontidae	1	1	N	1	1	1	1	1	1	1	1	2	N	1	1	1	1	1
Cordylidae	1	0,1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
Dibamidae	1	1	N	1,N	1,N	1	1	0	1	1	1	2	1,N	1	1	N	1	1
Gekkonidae	1	1	1,N	1,N	1,N	1	1	1	1	1	1	2	1	1	1	1,N	1	1
Gymnophthalmidae	1	0,1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
Helodermatidae	1	1	1	1	1	1	1	0	1	1	1	2	1	1	1	1	1	1
Iguanidae*	1	1	1,N	1	1	1	1	0,1	1	1	1	2	1,N	1	1	0,1,N	1	1
Lacertidae	1	0,1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
Lanthanotus	1	1	1	1	1	1	1	0	1	1	1	2	1	1	1	1	1	1
Pygopodidae	1	1	N	1,N	1,N	1	1	0	1	1	1	2	1	1	1	1	1	1
Scincidae	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
Serpentes	1	2	1,N	N	N	1	1	1	1	1	1	2	N	1	0,1	1	1	1
Teiidae	1	1	1	1	1	1	0,1	1	1	1	1	2	0,1	1	1	0,1	1	1
Varanus	1	1	1	1	1	1	1	0	1	1	1	2	1	1	1	1	1	1
Xantusiidae	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	N	1	1
Xenosauridae	1	1	1	1	1	1	0,1	1	1	1	1	2	1	1	1	1	1	1
Rhynchocephalia	0,1	0	0	0	0	0,1	0	0	0	0	0	1	0	0	0	0	0	0
Kuehneosauridae	0	0	N	1	0	?	0	0	?	?	0	0	?	0	0	0	?	0
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Younginiformes	1	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0

character number	167	169	170	171	172	173	174	175	176	177	178	180	181	182	183	184	186	187
Agamidae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Amphisbaenia	1	1	1,N	2,N	1,N	1,N	1,N	0,N	1,N	1,N	N	N	N	N	N	1	1	1
Anguidae	1	1	1,N	2,N	1,N	1,N	1,N	1,N	1,N	1,N	2	1,N	2,N	2,N	1,N	1	0	0
Chamaeleontidae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Cordylidae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Dibamidae	1	1	1	N	N	N	N	N	N	N	N	N	N	N	N	1	1	0
Gekkonidae	1	1	0,1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Gymnophthalmidae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Helodermatidae	0	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	2	0
Iguanidae*	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Lacertidae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Lanthanotus	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	2	0
Pygopodidae	1	1	0,1,N	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0
Scincidae	1	1	1,N	2	1	1	1	1	1	1	2	1,N	2,N	2,N	1,N	1	0	0
Serpentes	1	1	1,N	N	N	N	N	N	N	N	N	N	N	N	N	1	0	1
Teiidae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Varanus	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	2	0
Xantusiidae	1	1	0,1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Xenosauridae	1	1	1	2	1	1	1	1	1	1	2	1	2	2	1	1	0	0
Rhynchocephalia	0	0	0	1,2	0	0	0	0	0	0	1	0	1	1	0	0	0	0
Kuehneosauridae	0	?	?	2	1	?	?	?	?	?	1	?	?	0	?	0	0	0
Saurosternon	?	?	?	0	0	?	?	1?	?	0	0	?	1	0	0	0	?	0
Younginiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(c) ***Data for Huehuecuetzpalli***

Symbols: X, excluded redundant characters; /, or.

00000 10?00 00001 00?0X 1??11 X11X0 10000 01??? 0???? 001?? ???00 ?00X1 ??1?1 ??X0X 000?? 0???0 0??0? 00?X? ?0001 X0X00 X1X0X X1X(1/2)? 01X?0 0100? 00200 0100? ????? ????? ????? ??011 111?? 1??1? ???11 1?X11 20??? ?12X1 ?201X 0?

(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, Kuehneosauridae, *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-bisection–reconnection (TBR) with MULPARS option

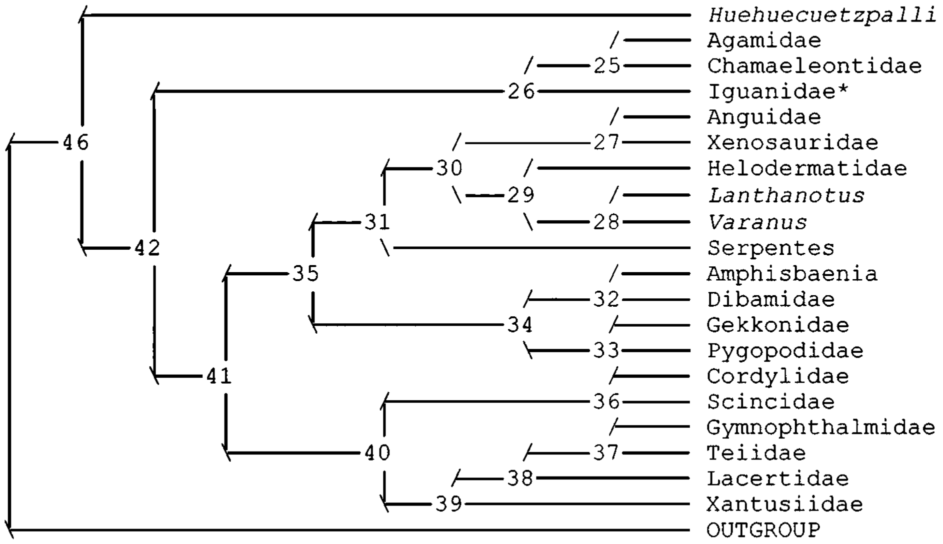

Figure 11. Most parsimonious tree rooted using outgroup method. Nodes are described in Appendix 1 (d)(ii).

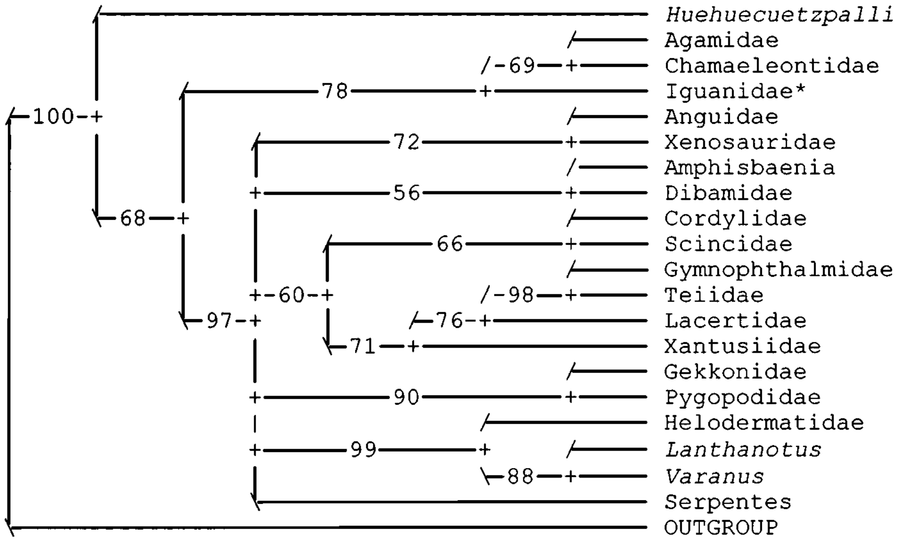

Figure 12. Bootstrap 50% majority-rule consensus tree.

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).

Node 46: 6, 15*, 21, 24, 37, 48, 51*, 82*, 83*, 112, 145(2)*, 150, 153, 155*, 156, 159, 160(2)*, 162*, 163*, 164, 166, 167*, 178(2), 182(2), 184.

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

Node 42: 1, 25(3)*, 93, 183.

Node 26: 7*, 8, 12*, 18, 65(2)*, 66*, 123, 143*.

Node 25: 60(0), 84.

Agamidae: 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)*, 67(0)*, 85, 88*, 114(0), 137(2).

Anguidae: 78, 124(2), 126, 147*.

Xenosauridae: 18, 75(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), 119, 129, 137(3), 143, 167(0).

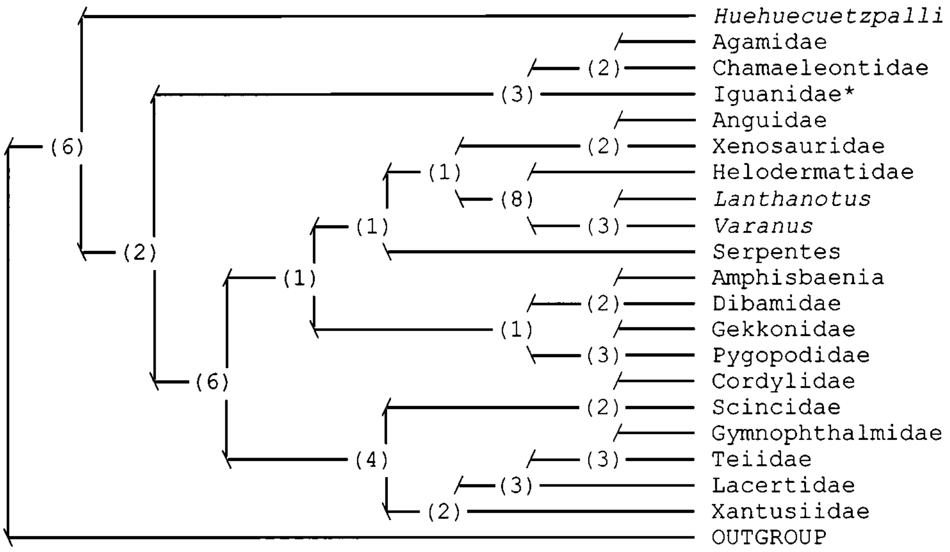

Figure 13. Branch support values obtained for the most parsimonious tree.

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), 78(0)*, 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), 135, 139, 140, 145.
Gekkonidae: 99(0), 109(1,0)*, 111, 118(0)*, 147(0)*, 156*.
Pygopodidae: 79(0), 133.
Node 40: 19*, 22*, 23, 54, 71*, 88*, 90(0)*, 91(0)*, 102(3), 114(0), 124(2)*, 129(2), 133, 138(2)*, 139*, 140(2), 144*.
Node 36: 76, 78*, 95*, 126, 127, 128, 148*.
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)*, 73(2), 90*, 112(2), 122, 137(4)*, 143.
Gymnophthalmidae: 11, 141.
Teiidae: 9(0), 45, 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; cl-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., epihyal; 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; l.i.c., lumbar intercentra; m., maxilla; m.c., Meckelian canal; n., nasal; op., opisthotic; p., parietal; p.f., parietal foramen; pm., premaxilla; po., postorbital; po.d., postdentary bones; pof., 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; soc., supraoccipital; spl., splenial; sq., squamosal; s.sc., suprascapula; st., supratemporal; ste., sternum; ste.ri., sternal ribs; s.v., sacral vertebras; ti., tibia; t.n., tibial distal notch; tr.pr, transverse process; u., ulna; ul., ulnare; v., vomer; xi., xiphisternum.

REFERENCES

Alifanov, V. R. 1989 The oldest gecko (Lacertilia: Gekkonidae) from the Lower Cretaceous of Mongolia. *Paleontol. J.* **23**, 128–131.

Barbadillo, J. & Evans, S. E. 1995 *Lizards (Reptilia: Squamata) from the Early Cretaceous of Las Hoyas, Spain*. Universidad Autónoma de Madrid, IInd International Symposium on Lithographic Limestones, Cuenca, pp. 27–28.

Bellairs, A. & Kamal, A. 1981 The chondrocranium and development of the skull in recent reptiles. In *Biology of the Reptilia*, vol. 11 (ed. C. Gans & T. Parsons), pp. 1–264. New York: Academic.

Borsuk-Bialnynicka, M. & Moody, S. M. 1984 Priscagamidae, a new subfamily of the Agamidae (Sauria) from the Cretaceous of the Gobi Desert. *Acta Palaeontol. Pol.* **29**, 51–81.

Bremer, K. 1988 The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**, 795–803.

Bremer, K. 1994 Branch support and tree stability. *Cladistics* **10**, 295–304.

Buscalioni, A. D., Ortega, F., Perez-Moreno, B. P. & Evans, S. E. 1996 The Upper Jurassic maniraptoran theropod *Lisboasaurus estesi* (Guimarota, Portugal) reinterpreted as a crocodylomorph. *J. Vert. Paleont.* **16**, 358–362.

Camp, C. L. 1923 Classification of the lizards. *Bull. Am. Mus. Nat. Hist.* **48**, 289–491.

Carroll, R. L. 1975 Permo-Triassic 'lizards' from the Karroo. *Palaeont. Afr.* **18**, 71–87.

Carroll, R. L. 1977 The origin of lizards. In *Problems in vertebrate evolution*, vol. 4 (ed. S. Mahala, R. S. Miles & A. D. Walker), pp. 359–396. *Linnaean Society Symposium Series.*

Carroll, R. L. 1985 A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. *Palaeontogr. Abt.* A **189**, 1–28.

Chure, D. J. 1992 Lepidosaurian reptiles from the Brushy Basin Member of the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah and Colorado, U.S.A. *J. Vert. Paleont.* **12** (3 suppl.), 24A.

Cifelli, R. L. & Nydam, R. L. 1995 Primitive, helodermatid-like platynotan from the Early Cretaceous of Utah. *Herpetologica* **51**, 286–291.

Clark, J. M. & Hernández, R. 1994 A new burrowing diapsid from the Jurassic La Boca Formation of Tamaulipas, Mexico. *J. Vert. Paleont.* **14**, 180–195.

Cocude-Michel, M. 1963 Les rhynchocephales et les sauriens de calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Nouv. Arch. Mus. Hist. Nat., Lyon* **7**, 1–187.

Cocude-Michel, M. 1965 Étude d'*Eichstättisaurus digitatellus* (=*Homoeosaurus digitatellus* Grier 1914), Saurien du Portlandien inférieur de Solnhofen. *Bull. Soc. Géol. France* **6**, 704–706.

Currie, P. J. & Carroll, R. L. 1984 Ontogenetic changes in the eosuchian reptile *Thadeosaurus*. *J. Vert. Paleont.* **4**, 68–84.

Endo, R. & Shikama, T. 1942 Mesozoic reptilian fauna in the Jehol Mountainland, Manchoukuo. *Bull. Cent. Nat. Mus., Manchoukuo* **3**, 1–19.

Ensom, P. C., Evans, S. E. & Milner, A. R. 1991 Amphibians and reptiles from the Purbeck Limestone Formation (Upper Jurassic) of Dorset. *Contrib. Paleont. Mus. Univ. Oslo* **364**, 19–20.

Estes, R. 1983*a* The fossil record and early distribution of lizards. In *Advances in herpetology and evolutionary biology* (ed. A. G. J. Rhodin & K. Miyata), pp. 365–398. Cambridge: Museum of Comparative Zoology.

Estes, R. 1983*b* *Sauria terrestria, Amphisbaenia*. Stuttgart: Gustav Fischer.

Estes, R. & Price, L. I. 1973 Iguanid of the Upper Cretaceous of Brazil. *Science* **180**, 748–751.

Estes, R., de-Queiroz, K. & Gauthier, J. A. 1988 Phylogenetic relationships within Squamata. In *Phylogenetic relationships of the lizard families* (ed. R. Estes & G. Pregill), pp. 119–282. Stanford University Press.

Etheridge, R. 1967 Lizard caudal vertebrae. *Copeia* **4**, 699–721.

Evans, S. E. 1989 New material of *Cteniogenys* (Reptilia: Diapsida; Jurassic) and a reassessment of the phylogenetic position of the genus. *N. Jb. Geol. Paläont., Mh.* **10**, 577–589.

Evans, S. E. 1990 The skull of *Cteniogenys*, a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire. *Zool. J. Linn. Soc.* **99**, 205–237.

Evans, S. E. 1991 A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of England. *Zool. J. Linn. Soc.* **103**, 391–412.

Evans, S. E. 1993 Jurassic lizard assemblages. *Rev. Paléobiol.* **7**, 55–65.

Evans, S. E. 1994*a* A new anguiomorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology* **37**, 33–49.

Evans, S. E. 1994*b* A re-evaluation of the Late Jurassic (Kimmeridgian) reptile *Euposaurus* (Reptilia: Lepidosauria) from Cerin, France. *Geobios* **27**, 621–631.

Evans, S. E. 1994*c* The Solnhofen (Jurassic: Tithonian) lizard genus *Bavarisaurus*: new skull material and reinterpretation. *N. Jb. Geol. Paläont., Abh.* **192**, 37–52.

Evans, S. E. 1995 Lizards: evolution, early radiation and biogeography. In *Sixth symposium on Mesozoic terrestrial ecosystems and biota, short papers*, pp. 51–55. Beijing: China Ocean Press.

Evans, S. E. & Barbadillo, J. 1996 An assemblage of lizards from the Early Cretaceous (Barremian) locality of Las Hoyas, Spain. *J. Vert. Paleont.* **16** (3 suppl.), 32A.

Evans, S. E. & Barbadillo, J. 1997 Early Cretaceous lizards from Las Hoyas, Spain. *Zool. J. Linn. Soc.* **119**, 23–49.

Evans, S. E. & Haubold, H. 1987 A review of the Upper Permian genera *Coelurusauravus*, *Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). *Zool. J. Linn. Soc.* **90**, 275–303.

Fiederov, P. V. & Nessov, L. A. 1992 Lizard from the Middle and Late Ferganian of the northwest coast (in Russian). *Univ. St Petersburg, News* **3**, 9–14.

Frazzetta, T. H. 1970 From hopeful monsters to bolyerine snakes? *Am. Nat.* **104**, 55–72.

Frost, D. R. & Etheridge, R. 1989 A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **81**, 1–65.

Gauthier, J. A. 1982 Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contrib. Paleontol. Univ. Wyoming* **21**, 7–64.

Gauthier, J. A., Estes, R. & de-Queiroz, K. 1988 A phylogenetic analysis of Lepidosauromorpha. In *Phylogenetic relationships of the lizard families* (ed. R. Estes & G. Pregill), pp. 15–98. Stanford University Press.

Gilmore, C. W. 1928 The fossil lizards of North America. *Mem. Natn. Acad. Sci.* **22**, 1–97.

Greer, A. 1970 A subfamilial classification of scincid lizards. *Bull. Mus. Comp. Zool. Harvard Univ.* **139**, 151–184.

Greer, A. 1985 The relationships of the lizard genera *Anelytropsis* and *Dibamus*. *J. Herpetol.* **19**, 116–156.

Haluska, F. & Alberch, P. 1983 The cranial development of *Elaphe obsoleta* (Ophidia, Colubridae). *J. Morphol.* **178**, 37–55.

Hecht, M. K. & Hecht, B. M. 1984 A new lizard from the Jurassic deposits of Middle Asia. *Paleontol. J.* **3**, 135–138.

Hoffstetter, R. 1953 Les sauriens anté-crétacés. *Bull. Mus., 2e série* **15**, 345–352.

Hoffstetter, R. 1964 Les sauria de Jurassique supérieur et spécialement les Gekkota de Baviere et de Manchourie. *Senck. Biol.* **45**, 281–324.

Hoffstetter, R. 1965 Les Sauria (=Lacertilia) du Jurassique Supérieur du Montsech (Espagne). *Bull. Soc. Géol. France, 7e série* **7**, 549–557.

Hoffstetter, R. 1966 A propos des genres *Ardeosaurus* et *Eichstaettisaurus* (Reptilia, Sauria, Gekkonoidea) du Jurassique Supérieur de Franconie. *Bull. Soc. Géol. France, 7e série* **8**, 592–595.

Hoffstetter, R. 1967 Coup d'oeil sur les sauriens (=Lacertiliens) des couches de Purbeck (Jurassique). *Prob. Act. Paléontol.* (*Évol. Vert.*) **163**, 349–371.

Hoffstetter, R. & Gasc, J.-P. 1969 Vertebrae and ribs of modern reptiles. In *Biology of the Reptilia,* vol. 1 (ed. C. Gans), pp. 201–310. London: Academic.

Howes, G. B. & Swinnerton, H. H. 1901 On the development of the skeleton of the Tuatara, *Sphenodon punctatus*; with remarks on the egg, hatching, and on the hatched young. *Trans. Zool. Soc. Lond.* **16**, 1–74.

Jollie, M. 1960 The head skeleton of the lizard. *A. Zool.* **41**, 1–64.

Kluge, A. G. 1982 Cloacal bones and sacs as evidence of gekkonid lizard relationships. *Herpetologica* **38**, 348–354.

Kluge, A. G. 1987 Cladistic relationships in the Gekkonoidea (Squamata, Sauria). *Misc. Publ. Mus. Zool. Univ. Michigan* **173**, 1–54.

Kluge, A. G. 1989 Progress in squamate classification. *Herpetologica* **45**, 368–379.

Kohring, R. 1991 Lizard egg shells from the Lower Cretaceous of Cuenca province, Spain. *Palaeontol*. **34**, 273–240.

Kuhn-Schnyder, E. 1962 Ein weiterer Schädel von *Macrocnemus basanii* Nopcsa aus der anisischen Stufe der Trias des Monte San Giorgio (Kt. Tessin, Schweiz). *Paläontol. Z.* **1962**, 110–133.

Lécuru, S. 1968 Remarques sur le scapulo-coracoide des lacertiliens. *Ann. Sci. Nat.* (*Zool.*) **10**, 475–510.

Li, J. 1985 A new lizard from Late Jurassic of Subei, Gansu. *Vertebr. PalAsiatica* **23**, 13–18.

Mateer, N. J. 1982 Osteology of the Jurassic lizard *Ardeosaurus brevipes* (Meyer). *Palaeontol*. **25**, 461–469.

Meszoely, C. A. M., Schaff, C. R. & Jenkins, F. A. 1987 Early Jurassic sphenodontids from North East Arizona. *J. Vert. Paleont.* **7** (3 suppl.), 21A.

Ostrom, J. H. 1963 Further comments on herbivorous lizards. *Evolution* **17**, 368–369.

Ostrom, J. H. 1978 The osteology of *Compsognathus longipes* Wagner. *Zitteliana* **4**, 73–118.

Pantoja-Alor, J. 1992 Geología y Paleoambiente de la Cantera Tlayúa, Tepexi de Rodrígez, Estado de Puebla. *Univ. Nac. Autón. Méx., Inst. Geol. Rev.* **9**, 156–169.

Pregill, G. K., Gauthier, J. A. & Greene, H. W. 1986 The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Trans. San Diego Soc. Nat. Hist.* **21**, 167–202.

Presch, W. 1988 Phylogenetic relationships of the Scincomorpha. In *Phylogenetic relationships of the lizard families* (ed. R. Estes & G. Pregill), pp.471–492. California: Stanford University Press.

Prothero, D. R. &. Estes, R. 1980 Late Jurassic Lizards from Como Bluff, Wyoming, and their paleoboiological significance. *Nature* **286**, 484–486.

Rage, J. C. 1992 Phylogénie et systématique des lepidosauriens. où en sommes-nous? *Bull. Soc. Herpetol. France* **62**, 19–36.

Rage, J. C. & Richter, A. 1994 A snake of the Lower Cretaceous (Barremian) of Spain: the oldest known snake. *N. Jb. Geol. Paläont., Mh.* **1994**, 561–565.

Reisz, R. R. 1981 A diapsid reptile from the Pennsylvanian of Kansas. *Spec. Publ. Mus. Nat. Hist. Univ. Kansas* **7**, 1–74.

Reynoso, V.-H. 1995 Lepidosaurian reptiles from the Cantera Tlayua (Albian), Tepexi de Rodríguez, Puebla, México. In *IInd International symposium on lithographic limestones, Lleida-Cuenca (Spain). Extended abstracts, pp. 131–132. Ediciones de la Universidad Autónoma de Madrid.*

Reynoso, V.-H. 1997 A 'beaded' sphenodontian (Diapsida: Lepidosauria) from the early Cretaceous of Central Mexico. *J. Vert. Paleont.* **17**, 52–59.

Richter, A. 1991 A new species of *Ilerdasaurus* and other lizards from Uña, Spain (Lower Cratecaeous). *Contribs Paleont. Mus. Univ. Oslo* **364**, 55–56.

Richter, A. 1994*a* Lacertilia aus der Unteren Kreide von Uña und Galve (Spanien) und Anoual (Marokko). *Berliner Geowiss. Abh.* **14**, 11–47.

Richter, A. 1994*b* Der problematische Lacertier *Ilerdasaurus* (Reptilia, Squamata) aus der Unter-Kreide von Uña und Galve (Spanien). *Berliner Geowiss. Abh.* **13**, 135–161.

Rieppel, O. 1979*a* A functional interpretation of the varanid dentition (Reptilia, Lacertilia Varanidae). *Gegen. morphol. Jb. Leipzig* **125**, 797–817.

Rieppel, O. 1979*b* A cladistic classification of primitive snakes based on skull structure. *Z. Zool. Syst. Evol.* **17**, 140–150.

Rieppel, O. 1980 The phylogeny of anguiomorph lizards. *Denk. Schweiz. Naturf. Gesell.* **94**, 1–85.

Rieppel, O. 1981 The skull and jaw adductor musculature in chamaeleons. *Rev. Suisse Zool.* **88**, 433–445.

Rieppel, O. 1984 The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zool. J. Linn. Soc.* **82**, 291–318.

Rieppel, O. 1987 The phylogenetic relationships within the Chamaeleonidae, with comments on some aspects of cladistic analysis. *Zool. J. Linn. Soc.* **89**, 41–62.

Rieppel, O. 1992*a* Studies in skeleton formation in reptiles. I. The postembryonic development of the skeleton in *Cyrtodactylus pubisulcus* (Reptilia, Gekkonidae). *J. Zool. Lond.* **227**, 87–100.

Rieppel, O. 1992*b* Studies in skeleton formation in reptiles. III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata). *Fieldiana* **68**, 1–25.

Rieppel, O. 1993 Studies in skeleton formation in reptiles. II. *Chamaeleo hoehnelii* (Squamata: Chamaeleoninae), with comments on the homology of carpal and tarsal bones. *Herpetologica* **49**, 66–78.

Rieppel, O. 1994 Studies in skeleton formation in reptiles. Patterns of ossification in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia, Squamata). *J. Herpetol.* **28**, 145–153.

Russell, D. A. 1967 Systematics and morphology of American mosasaurs (Reptilia, Sauria). *Bull. Peabody Mus. Nat. Hist.* **23**, 12–40.

Seibertz, E. & Buitron, B. E. 1987 Paleontología y estratigrafía de los neohibolites del Albiano de Tepexi de Rodríguez, Edo. de Puebla (Cretácico Medio, México). *Soc. Mex. Paleontol.* **1**, 285–299.

Seiffert, J. 1973 Upper Jurassic lizards from central Portugal. *Mem. Serv. Geol, Portugal* **22**, 1–85.

Swofford, D. L. 1993 *PAUP: phylogenetic analysis using parsimony, version 3.1.1.* Computer program. Champaign: The Illinois Natural History Survey.

Underwood, G. L. 1954 On the classification and evolution of geckos. *Proc. Zool. Soc. Lond.* **124**, 469–492.

Vidal, L. 1915 Nota geológica y paleontológica sobre el Jurásico superior de la Provincia de Lérida. *Bol. Inst. Geol. España* **36**, 17–55.

Waldman, M. & Evans, S. E. 1994 Lepidosauromorph reptiles from the Middle Jurassic of Skye. *Zool. J. Linn. Soc.* **112**, 135–150.

Werner, Y. L. 1971 The ontogenetic development of the vertebrae in some gekkonid lizards. *J. Morphol.* **133**, 41–92.

Wild, R. 1973 *Tanystropeus longbardicus* (Basani). In *Die Triasfauna der Tessiner Kalkalpen* (ed. E. Kuhn-Schnyder & B. Peyer). *Schweiz. Paläontol. Abh.* **95**, 11–62.

Winchester, L. & Bellairs, A. D. A. 1977 Aspects of vertebral development in lizard and snakes. *J. Zool.* **181**, 495–525.

Zangerl, R. 1945 Contribution to the osteology of the postcranial skeleton of amphisbaenians. *Am. Midl. Nat.* **33**, 764–780.