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EARLY CRETACEOUS LEPIDOSAURS (REPTILIA: DIAPSIDA) FROM CENTRAL MÉXICO AND THE PHYLOGENY OF LEPIDOSAUROMORPHS

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PREFACE

This thesis presents results on the study of four new lepidosaur reptiles from the Early Cretaceous of México. It is divided into five chapters. In the first chapter, a general introduction to the subject and detailed information about locality, materials used for study and comparison, and methods are given. Four new genera and species of lepidosaur reptiles are described and illustrated in the next four chapters. Their detailed anatomy provides information to clarify some aspects in the phylogeny of the rhynchocephalians and squamates. The last chapter is dedicated to a broad study of the phylogenetic relationships of the Lepidosauromorpha in the view of understanding the early evolution of lizards. In chapter 2 and 3, the sphenodontians *Pamizinsaurus tlayuaensis* and *Ankylosphenodon pachyostoseus* are described. Particular characters permit one to draw conclusions as to their ontogeny, behavior, and were useful for reconstruction of the paleoenvironment of the locality. In chapters 4 and 5 the lizards *Huehuecuetzpalli mixtecus* and *Tepexisaurus tepexii* are described and illustrated. Detailed anatomical information enables one to establish their phylogenetic position and to review the phylogeny of the Squamata. The primitive condition of *Huehuecuetzpalli* required a major analysis of the Lepidosauromorpha, presented in chapter six. In this new phylogeny, obscure lizard-like taxa occupy a phylogenetic position that permitted tracing the evolution of characters towards the modern lizard body plan. In this analysis, rigorous principles of character coding are applied in order to organize character information in a reasonable manner and to make character coding repeatable -a major problem in phylogenetic studies. The resultant phylogenetic hypothesis was compared with other published hypothesis.

All illustrations, descriptions, and conclusions are original except where indicated on text or figure captions. Figure 1 was redrawn from an unpublished masters thesis (González-Rodríguez, 1989: p. 10, fig. 3); figure 2 was taken from Pantoja-Alor (1992: p. 167, fig. 14), and figure 38 was redrawn from cladograms published by Evans (1991: p. 408, fig. 16) and Clark and Hernández (1994: p. 190, fig. 6). The thesis is presented as separated papers ready for submission, therefore some information may appear repetitive. Chapter 2 is already accepted and in press. Part of the data matrix presented on Chapter 2 is from Reynoso (1996). Some data on Chapter 3 are from a paper submitted with Dr. James Clark (George Washington University, USA). Chapter 5 will be co-authored with Dr. George Callison (San Diego University, USA). His contributions to the paper were a rough draft describing the specimen and the elaboration of Table 10.

Original contribution to knowledge includes:

a) Description of two previously unknown genera of sphenodontians
b) Recognition of these sphenodontians as the latest fossil record of this group, extending its geological range from the Late Triassic to the Albian.
c) Recognition of unique morphological features in both new sphenodontians that indicates the great morphological diversification sphenodontians achieve before their nearly complete extinction.
d) Revision of the phylogeny of the Rhynchocephalia in the view of new evidence. In this analysis several characters were recoded according to new principles and the thesis provides a complete data matrix.
e) Description of two previously unknown genera of squamates.
f) Recognition of *Huehuecuetzpalli mixtecus* as the only known sister-taxon of crown-group squamates, which permits the polarization of several characters within squamate phylogeny and the understanding of character distribution at the base of the Squamata.
g) The revision of characters and character states useful in the phylogenetic analysis of the Squamata, in which information of the diagnostic characters of the Squamata were newly coded.
h) The recognition of *Tepexisaurus* as the first documented pre-scincoid lizard giving information about the early transformation of characters towards the scincoid morphology.

i) The first review of the status of paramacellodid lizards based on a cladistic hypothesis in which the Paramacellodidae is recognized as a paraphyletic assemblage since some genera may be placed within Scincoidea and another as their sister-group.

j) Recognition of the Tlayua deposits as an insular deposit in which sphenodontians and archaic forms of lizards survived late in the fossil record. Unique features departing from original primitive pattern of sphenodontians and lizards, suggest that their evolution occurred in isolation.

k) Elaboration of the first cladistic analysis of the Lepidosauromorpha including all "families" of extant lizard and early fossils. This permits a new understanding of taxa and character distribution within basal lepidosauromorphs.

l) Incorporation of the Middle Jurassic lepidosauromorphs *Marmoretta* and *Tamaulipasaurus* within the Lepidosauria at the base of the branch leading to lizards.

m) Recognition of the Middle Jurassic lizard *Bavarisaurus* as part of the Ardeosauridae and this group excluded from the Squamata.

n) The thesis provide newly reviewed data sets that are useful in the phylogenetic analysis of the Rhynchocephalia, Squamata, and Lepidosauromorpha as a whole.

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Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow clear and precise judgment to be made of the importance of originality of the research reported in the thesis.

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ACKNOWLEDGMENTS

I am particularly indebted to the Aranguty family and to all the workers of the Tlayua Quarry who have found these specimens and preserved them for Science; to Dr. Shelton Applegate and M. Sc. Luis Espinosa who made the specimens available for study, and to Dr. María del Carmen Perrillat who arranged the loan of the material. I especially thank my advisor Dr. Robert Carroll for reading several drafts of the thesis and for discussion of the specimens. His great knowledge in anatomy made me explore areas that I would otherwise have ignored. I extend my sincere thanks to my teacher and guide Dr. Marisol Montellano for long distance support and help throughout my studies, and Dr. George Callison who loaned the specimen of *Tepexisaurus* and contributed in its description. I appreciate the patience of Dr. Robert Holmes who proofread my drafts. His comments undoubtedly improved my thesis manuscript. I also thank Drs. David Dilkes, Susan Evans, David Green, Marisol Montellano, and Nick Fraser for help with particular chapters. I appreciate discussion and tips about lizard anatomy and systematics from Drs. Susan Evans, Gao Keqin, Oliver Rieppel, and Kevin de Queiroz. I thank Dr. Javier Barbadillo for giving me access to unpublished information about Las Hoyas lizards. Dr. Pierre -Ives Gagnier introduced me to PAUP, and Dr. David Dilkes to cladistic branch support analyses. I sincerely appreciate David's discussions on character coding, character distribution in early diapsids, and his constant support throughout my work. Kate Holmes introduced me to the use of EXEL statistics program. I thank Dr. Dirk Meckert for discussion of obscure features in some specimens, to my good friend Ernesto Vega for suggesting the generic name of *Pamizinsaurus*, and Mrs. Alice Carroll for transporting several specimens of *Ankylosphenodon* from California. Dr. Mark Norrell gave me access to the collection of fossil lepidosaurs in the American Museum of Natural History and Dr. Jim Clark to the holotype of *Tamaulipasaurus morenoi* temporarily in the George Washington University. I sincerely thanks all the help provided by Jim. Dr. Bernard Battail permitted me to examine sphenodontian specimens in the Museum de Histoire Naturelle, Paris, and Dr. Jean Claude Rage (Université Pierre et Marie Curie, Paris) of a superb specimen of *Sapheosaurus* now in the Universté Claude Bernard, Lyon. Dr. John Cradle kindly loaned several specimens of extant squamates from the collection of the Museum of Zoology, Harvard University. Dr. Robert Evander introduced me to resin/acid preparation techniques, Mr. Jesús Alvarez helped me to acid-prepare the holotype of *Ankylosphenodon*, and Mr. Gerardo Alvarado cast the specimens donated to the Redpath Museum. Photographic work was done by McGill Image Center and Mr. Hector Hernández to whom I extend my thanks. My friends Martin Dubreuil and Michael Chartier translated the abstract into French.

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ABSTRACT

Four new lepidosaurs from the Early Cretaceous deposits of the Tlayua Quarry, Central México are described, establishing their phylogenetic relationships using cladistic methodology. These lepidosaurs have unique characters never present in related forms suggesting that they have evolved in isolated environments far from immediate ancestors, indicating the insular nature of the quarry. The sphenodontid *Pamizinsaurus tlayuaensis* is covered with unique rows of small rounded osteoderms that could have protected it against predation in open environments. *Ankylosphenodon pachyostoseus* has unusual teeth ankylosed deep into the dentary with probable continuous growth, which combined with propalinal action of a deep lower jaw suggest herbivory. Unique pachyostotic ribs and vertebrae, delay in the ossification of the epiphyses, and zygapophyses horizontally oriented to stiffen the vertebral column could be related to aquatic behavior. The unique morphology of *Pamizinsaurus* and *Ankylosphenodon* argue against the concept of low morphological diversification of sphenodontians.

The lizard *Huehuecuetzpalli mixtecus* shows most iguanian features, but still retains a divided premaxilla, amphicoelous vertebrae, thoracolumbar intercentra, and the second distal tarsal, supporting a phylogenetic position as sister-group of squamates. Although late in the fossil record, *Huehuecuetzpalli* provides important information on early transformation of characters in lizard evolution. *Tepexisaurus tepexii* is an early scincomorph relatively more primitive to all known scincoids. The lack of osteoderms indicates that *Tepexisaurus* and some paramacellodids are not scincoids, suggesting that the Paramacellodidae is not monophyletic. The relative primitive morphology of *Tepexisaurus* in Albian deposits can be correlated with the late presence of sphenodontians and the relictual nature of *Huehuecuetzpalli* in Tlayua. This suggests that Tlayua was a refuge for archaic terrestrial forms.

Character transformation at the origin of the Squamata was explored through a phylogenetic analysis including basal lepidosauromorphs, the best known early squamates, and extant squamate "families". Results using a rigorously reviewed data set, show that many

characters suggested to be squamate autapomorphies are certainly along a lineage basal to the Squamata, which includes *Marmoretta*, *Tamaulipasaurus*, the Ardeosauridae (redefined to include *Bavarisaurus*), and *Huehuecuetzpalli*. The name Squamatoidea to group all taxa basal to Squamata + squamates is suggested. The Total Branch Support index obtained falls between values of other published phylogenies. The low values seem to be affected by the inclusion of several fossil taxa with incomplete information and the redistribution of a limited number of characters in a greater number of branches.

RÉSUMÉ

Quatre nouveaux lépidosaures provenant des dépôts du Crétacé inférieur de la carrière de Tlayua, située dans le centre du Mexique, sont décrits et leurs relations phylogénétiques sont établies grâce à la méthode cladiste. Ces lépidosaures possèdent des caractères uniques qui ne se retrouvent jamais chez les formes apparentées, ce qui suggère qu'ils auraient évolués dans des environnements isolés, loin de leurs ancêtres immédiats, et qui indique la nature insulaire du site. Le sphénodontidé *Pamizinsaurus tlayuaensis* est couvert de rangées de petits ostéodermes arrondis, un caractère unique, qui pourraient l'avoir protégé contre la prédation dans des environnements découverts. *Ankylosphenodon pachyostoseus* possède des dents inusitées, ankylosées profondément dans le dentaire et dont la croissance était probablement continue. Ceci, combiné au mouvement propalinéal d'une mandibule profonde, suggère l'herbivorie. Des caractères uniques, tels des côtes et des vertèbres pachyostosées, une ossification tardive des épiphyses et des zygapophyses orientées horizontalement pour rigidifier la colonne vertébrale, pourraient indiquer des habitudes aquatiques. Les morphologies uniques de *Pamizinsaurus* et d'*Ankylosphenodon* militent à l'encontre de l'idée d'une diversification morphologique modeste chez les sphénodontes.

Le lézard *Huehuecuetzpalli mixtecus* arbore la plupart des traits iguaniens mais il conserve encore un prémaxillaire divisé, des vertèbres amphicoeles, des intercentrums thoraco-lombaires et le deuxième tarse distal, ce qui milite en faveur d'une position phylogénétique en tant que groupe-frère des squamates. Bien que tardif dans le registre fossile, *Huehuecuetzpalli* fournit d'importants renseignements sur les transformations anciennes de caractères dans l'évolution des lézards. *Tepexisaurus tepexii* est un ancien scincomorphe relativement plus primitif que tous les scincoïdes connus. L'absence d'ostéodermes indique que *Tepexisaurus* et quelques uns des paramacellodidés ne sont pas des scincoïdes, et sugère aussi que le Paramacellodidae ne représente pas en fait un assemblage monophylétique. La morphologie relativement primitive de *Tepexisaurus* dans

l'Albien peut être corrélée avec la présence tardive de sphénodontes et la nature relictuelle de *Huehuecuetzpalli* dans Tlayua. Ceci sugère que Tlayua constituait un refuge pour des formes terrestres archaïques.

Les transformations de caractères à l'origine de Squamata ont été explorées au moyen d'une analyse phylogénétique qui incluait les lépidosauromorphes basals, les squamates anciens les mieux connus et les "familles" de squamates actuels. Grâce à l'usage d'un ensemble de données rigoureusement révisé, les résultats montrent que plusieurs caractères proposés comme étant des autapomorphies squamates se situent en fait le long d'une lignée basale à Squamata, et qui inclut *Marmoretta*, *Tamaulipasaurus*, les Ardeosauridae (redéfinis afin d'inclure *Bavarisaurus*) et *Huehuecuetzpalli*. Le terme Squamatoidea est proposé afin de grouper tous les taxons qui sont basals aux Squamata + les squamates. L'index de Support de Branche Total (Total Branch Support index) obtenu se situe entre les valeures calculées pour les autres phylogénies publiées. Les valeurs faibles obtenues ici semblent être affectées par l'inclusion de nombreux taxons fossiles desquels on obtient une information incomplète et par la redistribution d'une quantité limitée de caractères à l'intérieur d'un plus grand nombre de branches.

CHAPTER 1

GENERAL REMARKS

GENERAL REMARKS

INTRODUCTION

The Lepidosauria is a very diverse group with world wide distribution. Its extant members includes lizards, snakes, and amphisbaenians, grouped within the Squamata (Estes 1983a), and two species of rhynchocephalians: *Sphenodon punctatus* and *S. guntheri*, from the islands of New Zealand (Daugherty 1990). Rhynchocephalians, squamates, and some other relatively more primitive lizard-like fossil forms have been grouped within the Lepidosauromorpha (Gauthier et al. 1988a); one of the two major groups of diapsid reptiles. Archosauromorphs, which includes crocodiles, dinosaurs, and birds is the other one.

Despite their abundance, the fossil record of lepidosaurian lizards is not well documented. The rhynchocephalians are known from complete or nearly complete specimens from several Old World Late Triassic to Early Cretaceous deposits (Table 1). Almost 30 different species have been described from European lithographic limestone (Huene 1910; Cocude-Michel 1963, 1967a, b; Fabre 1973, 1974; Carroll 1985a, Ahmad 1993; Renesto 1995), from the British fissure fillings (Evans 1980, 1981, 1992; Fraser 1982, 1986, 1988; Fraser and Benton 1989; Whiteside 1986; Evans and Fraser 1992) and from China (Sun et al. 1992; Wu 1994). Without considering a single dentary that was once considered the earliest known rhynchocephalian (Broom 1905), only scattered fossil fragments have been collected from Africa (Gow and Raath 1977; Rich et al. 1983; Sues and Reisz 1995; Evans pers. com. 1995), and there is absolutely no record in South America or Australia. In North America only a few fragmentary fossils have been recognized as rhynchocephalians (Gilmore 1909; Simpson 1926; Throckmorton et al. 1981; Rasmussen and Callison 1981; Meszoley et al. 1987; Sues and Baird 1993; Reynoso 1992, 1995, in press, and work in progress; Fraser and Wu in press). Until now, no complete

TABLE 1. General information of fossil rhynchocephalians reported in literature, outlined according to results presented on this thesis.

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
LEPIDOSAURIA Duméril & Bibron, 1839			
RHYNCHOCEPHALIA Günther, 1869			
Gephyrosaurus bridensis Evans, 1980	Lower Jurassic (Hettagian or Sinemurian)	Bridgend, S.Glamorgan Wales, UK	St Brides & Pant-y-ffynnon fissure infills in Dinantian Limestones
SPHENODONTIA Williston, 1925			
Diphydontosaurus avonis Whiteside, 1986	Upper Triassic (Lower Rhaetian)	Gloucestershire, SW Britain, UK	Tyntherington & Cromhall quarries, fissures infills in Dinantian Limestones
	(Norian)	North Itally	Calcare di Zorzino of Cene
Planocephalosaurus robinsonae Fraser, 1982	Upper Triassic (Upper Rhaetian)	Gloucestershire, SW Britain, UK	Cromhall & Tyntherington quarries; fissure infills in Dinantian Limestone
SPHENODONTIDAE Cope, 1870			
Pleurosauridae Lyddeker, 1880			
Pleurosaurus goldfussi Meyer, 1831 (= *Anguisaurus bipes*; *A. münsteri*, *A. minor*, *Saurophidium münsteri*, *Pleurosaurus münsteri*, *P. minor*, ? *P. lorteti*)	Upper Jurassic	Monheim,Solnhofen, Eichtätt, Sappenfeld, Daiting & Wintershoft, Bavaria, Germany Cerin (Ain),	Solnhofen Limestone France Calcaire Lithographique

(Table 1, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
-*P. ginsburgi* Fabre, 1974	Upper Jurassic (Portlandien)	Canjuers (Var), France	Calcaire Lithographique
Acrosaurus frischmanni Meyer, 1854	Upper Jurassic	Eichtätt & Schrandel Bavaria, Germany	Solnhofen Limestone
Palaeopleurosaurus posidoniae Carroll, 1985	Lower Jurassic (Upper Liassic)	Holzmaden, Germany	Posidonienschiefer
Clevosaurs (Wu, 1994)			
Polysphenodon mülleri Jaekel, 1911	Upper Triassic (Carnian)	Hannover, Germany	Middle Keuper beds
Brachyrhinodon taylori Huene, 1910 (=*Telerpeton*)	Upper Triassic (Norian)	N.E. Scotland, UK	Lossiemouth Sandstone Fm
Clevosaurus hudsoni Swinton, 1939	Upper Triassic	Gloucestershire	Cromhall, Tyntherington,
	(Upper Rhaetian)	SW Britain. UK	Pant-y-ffynnon, Highcroft, quarries; fissures infills in Dinantian Limestones
-*C. minor* Fraser, 1988	Upper Triassic (Upper Rhaetian)	Gloucestershire SW Britain. UK	Cromhall quarry fissures infills in Dinantian Limestones
-*C. mcgilli* Wu, 1994 (= *Rarojugalosaurus mcgilli*)	Lower Jurassic SW Chine	Lufeng Co., Yunan, Upper Dark Red beds	Lower Lufeng Fm

(Table I, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
-*C. petilus* Wu, 1994 (= *Dianosaurus petilus,*	Upper Triassic ?	Lufeng Co., Yunan, SW Chine	Lower Lufeng Fm Upper Dull Purplish beds
Asiacephalosaurus wangi, *C. wangi*)	Lower Jurassic		Lower Lufeng Fm Upper Dark Red beds
-*C. bairdi* Sues, Shubin & Olsen, 1994	Lower Jurassic (Hettangian)	Cumberlain Co. Nova Scotia; Canada	McCoy Brook Fm
-*C. sp.* Sues & Reiz, 1995	Lower Jurassic	South Africa	Elliott or Clarens Fm
Homoeosaurus Meyer, 1845			
Homoeosaurus maximiliani Meyer, 1845 (=*H. jourdani* Lortet)	Upper Jurassic (Lower Tithonian- Kimmeridgian)	Kelheim, Solnhofen & Eichtätt, Bavaria, Ger.	Solnhofen Limestone
		Isle of Purbeck, UK	Purbeck Fm
		Cerin (Ain). France	Calcaire lithographique
-*H. solnhofensis* Cocude-Michel, 1963	Upper Jurassic	Solnhofen, Bavaria Germany	Solnhofen Limestone
	(Portlandien)	Canjuers (Var.) France	Calcarie Lithographique
-*H. parvipes* Cocude-Michel, 1963	Upper Jurassic	Germany; unknown	Lithographic Limestones,
Sapheosauridae Bau, 1825			
Leptosaurus neptunius Goldfuss, 1831 (= *Lacerta neptunia*; *Homoeosaurus neptunius*; *H. maximilliani*)	Upper Jurassic	Monheim, Frankfort Bavaria, Germany	Solnhofen Limestone

(Table 1, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
Sapheosaurus thiollierei Meyer, 1852 (=*Piocormus thiolierei* *Sauranodon incisivus* *Sapheosaurus thiollierei*)	Upper Jurassic (Kimmeridgian)	Cerin (Ain), Fra.	Calcaire Lithographique
Piocormus laticeps Wagner, 1852 (=*Sapheosaurus laticeps*)	Upper Jurassic (Lower Portlandien)	Kelheim, Bavaria Germany	Solnhofen Limestone
Kallimodon pulchellus Zittel, 1887 (= *Homoeosaurus pulchellus*; *H. brevipes*	Upper Jurassic	Kelheim, Painten, & Kapfelberg, Bavaria Germany	Solnhofen Limestone
-*K. cerinesis* Cocude-Michel, 1963 (=*Saurandon incisivus*, *Homoeosaurus rhodani*, *Stelliosaurus* 2a. sp.)	Upper Jurassic (Kimmeridgian)	Cerin (Ain), Fra.	Calcaire Lithographique
Eilenodontidae Rasmussen & Callison, 1981			
Toxolophosaurus cloudi Olson, 1960	Lower Cretaceous (Barremian)	Bow Co., Montana. USA	Kootenai Fm
Eilenodon robustus Rasmussen & Callison, 1981	Upper Jurassic (Tithonian)	Fruita Mesa Co., Col. USA	Morrison Fm

(Table 1, continued)

Species	Age Range	Locality	Quarry, Formation, Level
Sphenodontinae Cope, 1869			
Opisthias rarus Gilmore, 1909	Upper Jurassic (Tithonian)	Como Bluff, Wyo. USA Dorset, England, UK Algoa Basin, S.Afr	Morrison Fm, Quarry 9 Purbeck Limestone Fm Kirkwood Fm
Theretairus antiquus Simpson, 1926	Upper Jurassic (Tithonian)	Como Bluff, Wyo. USA	Morrison Fm, Quarry 9
Cynosphenodon huizachalensis Reynoso, 1992	Middle Jurassic (Upper Bathonian)	Huizachal Canyon, Mex. Oxfordshire, UK	La Boca Fm Forest Marble Fm
Sphenodontidae ***incerta sedis***			
Monjurosuchus splendens Endo, 1940	Upper Jurassic	Liaoning Province	Jiufotang Fm
Sigmala sigmala Fraser, 1986	Upper Triassic (Upper Rhaetian)	S. Gloucestershire England, UK	Cromhall quarry fissures infills in Dinantian Limestones
Pelecymala robustus Fraser, 1986	Upper Triassic (Upper Rhaetian)	S. Gloucestershire England, UK	Cromhall quarry fissures infills in Dinantian Limestones
unnamed sp. Gow & Raath, 1977	Upper Triassic	Chitake River, Zambezi	Forest Sandstone Valley, Rhodesia
unnamed sp. Sues & Baird, 1993	Upper Triassic (Norian)	Hartford bassin Connecticut, USA	New Heaven Arkose Fm, Newark Supergroup

specimen other than a Lower Jurassic clevosaur from Nova Scotia (Sues et al. 1994) has been reported from North America.

The early fossil record of squamates is even less complete (Table 2). The earliest forms are known from isolated jaws and maxillas, some skull roof bones, and isolated vertebrae from Middle Jurassic deposits of Central Asia and England (Nesov 1992; Evans 1993, 1994a). Only a few complete skeletons have been recovered from the Upper Jurassic Limestones of Germany, France, and China (Wagner 1852; Meyer 1860; Grier 1915; Broili 1938; Hoffstetter 1953, 1964, 1966; Cocude-Michel 1961, 1965; Endo and Shikama 1942; Evans 1994b, c; Lortet 1892; Ostrom 1978; Mateer 1982). Other material of this age is only known from disarticulated remains from Portugal (Seiffert 1973), and England (Ensom et al. 1991). Lower Cretaceous lizards have been known only from scattered remains in Italy and Spain (Vidal 1915; Brame 1967, 1973; Hoffstetter et al. 1965; Hoffstetter 1965); however, many new localities are providing information about lizard diversity from this time interval. These includes scattered material from Russia (Nesov 1985) and very well preserved material from Uña, Galve, and Las Hoyas, Spain (Richter 1991, 1994a, b; Barbadillo and Evans 1995). The locality of Uña is particularly important because it has produced the earliest snake remains (Rage and Richter 1994). New data has established an Early Cretaceous age of the Purbeck deposits (Evans 1995) with abundant taxa of lizards (Hoffstetter 1967). As with sphenodontians, early fossil lizards are practically unknown in Africa and South America. In North America only very incomplete remains have been reported from the Upper Jurassic deposits of the Morrison Formation (Prothero and Estes 1980; Chure 1992) and from the Early Cretaceous of Utah (Cifelli and Nydam 1995).

The most complete lepidosaurs are known primarily from lithographic limestone deposits (see Tables 1 and 2). The fine grained sediments associated with special depositional conditions are ideal for the preservation of small terrestrial vertebrates (Barthel 1970). Unfortunately such sediments (*Lagerstätten, sensu* Gould 1989) are not abundant

TABLE 2. General information of squamatoids and early fossil squamates reported in literature, outlined according to results presented on this thesis.

Species	Age range	Locality	Quarry, formation, level
LEPIDOSAURIA Duméril & Bibron, 1839			
SQUAMATOIDEA new taxon			
Marmoretta oxoniensis Evans, 1991	Middle Jurassic (Upper Bathonian)	Kirtlington, Oxfordshire, U.K	Old Cement Works Quarry
Tamaulipasaurus morenoi Clark & Hernández, 1994	Middle Jurassic	Huizachal Canyon, Tamaulipas, México	La Boca Fm
Ardeosauridae Camp, 1923			
Ardeosaurus brevipes Meyer, 1855 (=*A. digitalellus*)	Upper Jurassic	Eichstätt, Bavaria, Germany	Solnhofen Limestone
Eichstaettisaurus schroederi Broili, 1938 (=*Broliosaurus schroederi)*	Upper Jurassic	Wintershof & Eichstätt Bavaria, Germany	Solnhofen Limestone
Bavarisaurus macrodactylus Wagner, 1852	Upper Jurassic	Keilheim, Bavaria, Germany	Solnhofen Limestone

(Table 2, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
SQUAMATA Merrem, 1820			
SCINCOMORPHA Camp, 1923			
Meyasaurus fauray Vidal, 1915	Lower Cretaceous (Berrassian-Valenginian)	Montsec, Catalonya, Spain	Pedrera de Rubies
-*M.crusafronti* Hoffstetter, 1965	"	"	"
-*M. unaensis* Richter, 1991	Lower Cretaceous (Upper Barremian)	Uña, Cuenca, Spain	Limnic Lignite Wealden Facies
-*Meyasaurus* new sp Barbadillo & Evans, 1995	Lower Cretaceous (Barremian)	Cuenca, Spain	Las Hoyas
-M. sp. Richter, 1994	Lower Cretaceous (Lower Barremian)	Galve, Teruel, Spain	
Teiidae Gray, 1827			
Buckantaus crassidens Nesov, 1985	Lower Cretaceous (Albian)	Khadzhakul, USSR	

(Table 2, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
"Paramacellodidae" Estes, 1983			
Paramacellodus oweni Hoffstetter, 1967 (=*Saurillus robustidens*; *Becklesisaurus scincoides*)	Upper Jurassic	Dorset, England, UK	Purbek Limestone Fm
-*P. sinuosus* Richter, 1994	Lower Cretaceous (Upper Barremian)	Uña, Cuenca, Spain	Limnic Lignite Wealden Facies
-*P. marocensis* Richter1994	Lower Cretaceous (Berriasian-Aptian)	Anoual, Talsinnt, Morocco	Anoual sinclinal, B-sequence of "Couches rouges"
-P. sp Prothero & Estes, 1980	Upper Jurassic	Wyoming, USA	Morrison Fm
Ensom et al., 1991	"	Dorset, England, UK	Purbek Limestone Fm
Richter, 1994	Lower Cretaceous (Lower Barremian)	Galve, Teruel, Spain	
Becklesius hoffstetteri Seiffert, 1973 (=*Macellodus brodiei* Hoffstetter, 1967 but **no** *M. broidei* Owen, 1854; *Becklesisaurius hoffstetteri*)	Upper Jurassic Portugal	Leira & Porto Pinheiro,	Guimarota lignite Mine
-*B. cataphractus* Richter, 1994	Lower Cretaceous (Upper Barremian)	Uña, Cuenca, Spain	Limnic Lignite Wealden Facies
-*Becklesius* sp. Ensom et al., 1991	Upper Jurassic	Dorset, England, UK	Purbek Limestone Fm
Richter, 1994b	Lower Cretaceous (Upper Barremian)	Uña, Cuenca, Spain	Limnic Lignite Wealden Facies

(Table 2, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
Pseudosaurillus becklesi Hoffstetter, 1967	Upper Jurassic	Dorset, England, UK	Purbek Limestone Fm
-*P. sp* (=*Saurillus obstusus* Hoffstetter, 1967; **no** *S. obtusus* Owen, 1854)	Upper Jurassic	Dorset, England, UK	Purbek Limestone Fm
Saurillodon proraformis Seiffert, 1973	Upper Jurassic	Leira, Portugal	Guimarota lignite Mine
-*S. henkeli* Seiffert, 1973	Upper Jurassic	Leira, Portugal	Guimarota lignite Mine
Saurillus obtusus Owen, 1854	Upper Jurassic (Portlandian-Kimmeridgian)	Dorset, England, UK Leira, Portugal	Purbek Limestone Fm Guimarota lignite Mine
Mimboblecklesisaurus gansuensis Li, 1985	Upper Jurassic	Subei, Gansu, China	Chijinbu group
Sharovisaurus karatuensis Hecht & Hecht, 1984	Upper Jurassic	Karatau, Kazakh	Karabastau Fm
unnamed sp. Chure, 1992	Upper Jurassic (Kimmeridgian-Tithonian)	Dinosaur National Monument, Utah USA	Morrison Fm
ANGUIMORPHA Fubinger, 1900			
Dorsetisauridae Hoffstetter, 1967			
Dorsetisaurus purbeckensis Hoffetstter, 1967 (=*Introrsisaurus pollicidens)*	Upper Jurassic, (Portlandian-Kimmeridgian)	Dorset, England, UK Leira, Portugal	Purbek Limestone Fm Guimarota lignite Mine

(Table 2, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
-*Dorsetisaurus hebetidens* Hoffstetter, 1967	Upper Jurassic, (Portlandian)	Dorset, England, UK	Purbek Limestone Fm
-*D. sp* Prothero & Estes, 1980 Ensom et al., 1991	Upper Jurassic	Wyoming, USA Dorset, England, UK	Morrison Fm Purbek Limestone Fm
Changetisaurus estesi Nesov, 1992	Middle/Upper Jurassic (Callovian)	Kyrzstan	
Parviraptor estesi Evans, 1994	Middle Jurassic-Lower Cretaceous (Bathonian-Berriasian)	Kirtlington & Dorset, UK Leira, Portugal	Old Cement Works Purbek Limestone Fm Guimarota mine
Helodermatidae Gray, 1837			
unnamed sp. Cifelli & Nydam, 1995	Lower Cretaceous	Emery Co. Utah, USA	Cedar Mountain Fm
SERPENTES Linneaus, 1766			
unnamed sp. Rage & Richter, 1994	Lower Cretaceous (Lower Barremian)	Uña, Cuenca, Spain	Limnic Lignite Wealden Facies

(Table 2, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
SQUAMATA *INCERTA SEDIS*			
Euposauridae Camp, 1923			
Euposaurus thiollierei Lortet, 1892	Upper Jurassic (Kimmeridgian)	Cerin (Ain), France	Calcaire Lithographique
Anguimorphs ?			
Cuencasaurus estesi Richter, 1994	Lower Cretaceous (Upper Barremian)	Uña, Cuenca, Spain	Limnic Lignite Wealden Facies
Scincomorphs ?			
Conicodontosaurus djadochtaensis Gilmore, 1943	Upper Cretaceous	Mongolian Peoples Republic	Djadokhta Fm
-*C. kanhsiensis* Young, 1973	Upper Jurassic or Lower Cretaceous	Kanhsien, Kiangsi, China	
Lacertoid ?			
Durotrigia triconodens Hoffstetter, 1966	Upper Jurassic	Dorset, England, UK	Purbek Limestone Fm
-D. sp Ensom et al., 1991	Upper Jurassic	Dorset, England, UK	Purbek Limestone Fm

(Table 2, continued)

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
Unknown			
Yabeinosaurus tenuis Endo & Shikama, 1942	Upper Jurassic	Tsaotzushan Manchuria, China	Tsaotzushan
-*Y. youngi* Hoffsteter, 1964	Upper Jurassic	Ketzutung, Lyngyuan Hsien, Lianong, China	
Palaeolacerta bavarica Cocude-Michel, 1961	Upper Jurassic	Bavaria, Germany	Solnhofen Limestone
Teilhardosaurus carbonairus Shikama, 1947	Lower Cretaceous	Wafangatun, South Manchuria, China	Husin coal mine
Costasaurus rusconi Costa, 1851	Lower Cretaceous	Pietraroia, Italy	
Dicarlesia incognita Huene, 1931	Lower Cretaceous	Tres Cruzes, Jujuy, Argentina	
Hodzhakulia magna Nesov, 1985	Lower Cretaceous (Albian)	Khadzhakul, ex USSR	
Oxia karakalpakensis Nesov, 1985	Lower Cretaceous (Albian)	Khadzhakul, ex USSR	

in North America. Today, only two Early Cretaceous deposits with this quality of preservation are known in the New World: The Santana Formation in Brazil (Massey 1990), and the Tlayua Formation in México (Applegate et al. 1984; Martill 1989). The Santana Formation has produced numerous fish, pterosaurs, and other reptiles, but no lizards or rhynchocephalians have ever been reported. The Tlayua Formation, in contrast, has produced several lepidosaurs that, although they are not abundant, are beautifully preserved and represent the only complete Early Cretaceous forms known in North America.

Two rhynchocephalians represent the latest fossil record of these forms before their near extinction in the Late Cretaceous. Their unique morphology demonstrates that although rhynchocephalians are generally considered of conservative anatomy, the group is capable of evolving highly modified forms. Their derived condition provides information for the reconstruction of character transformation to the extant genus *Sphenodon*. Two lizards, represent contrasting degrees of evolution preserved in the same locality. The more derived one adds information about the evolution of anatomical characters within the Scincomorpha, one of the major clades of the Squamata; while the other one, notable for its primitive construction, provides information about early character transformation in lizards after branching off from lepidosaur ancestors.

Late Permian-Late Triassic lizard-like forms (Table 3) were initially considered true lizards (i.e. squamates) by Robinson (1962), Colbert (1966, 1970), and Carroll (1975). Because of the lack of derived features present in either squamates or rhynchocephalians, they are now thought to be basal lepidosauromorphs or even more primitive forms (Benton 1985; Gauthier et al. 1988a; Evans 1988). The presence of transitory forms from basal lepidosauromorphs to rhynchocephalians (Evans 1980, Whiteside 1986) permits the reconstruction of the evolution of the group throughout the Triassic up to the Cretaceous and Recent. For squamates, the story is different since there is a gap between the latest well known basal lepidosauromorph, *Kuehneosaurus* from the Late Triassic of England

TABLE 3. General information of basal lepidosauromorphs reported in literature, outlined according to results presented on this thesis.

Species	**Age Range**	**Locality**	**Quarry, Formation, Level**
LEPIDOSAUROMORPHA Benton 1983			
Lepidosauriformes Gauthier et al 1988			
Saurosternon bainii Huxley 1868	Upper Permian	Styl Krantz Sneeuwberg South Africa	*Cistecephalus* or *Daptocephalus* Zone
Kuehneosauridae Robinson 1967			
Kuehneosaurus latus Robinson 1962	Upper Triassic	Mendip Hills England, UK	Emborough Quarry
Icarosaurus siefkeri Colbert 1966	Upper Triassic	Bergen Co. New Jersey, USA	Granton Lockatong Fm
Kuehnosuchus latissimus Robinson 1967	Upper Triassic	Mendip Hills England, UK	Batscombe Fm
Not lepidosauromorphs			
Palaeagama vielhaueri Broom 1926	Lower Triassic or Upper Permian	Kinira, Mount Frere South Africa	*Lystrosaurus* or *Daptocephalus* Zone
Paliguana whitei Broom 1903	Lower Triassic or Upper Permian	Donnybrooke South Africa	"

and North America (Robinson 1962; Colbert 1970), and the earliest well known squamates: *Ardeosaurus*, *Bavarisaurus*, and *Eichstaettisaurus* from the Upper Jurassic of Germany (Hoffstetter 1966; Evans 1993, 1994c). Although several squamates are known between these horizons, all can be accommodated within extant groups and no transitional forms have ever been reported. The middle Jurassic amphisbaenian-like *Tamaulipasaurus* is the only taxon suggested to be sister-group of crown squamates (Clark and Hernández 1994) but its relationships are still unclear. The Tlayua quarry is therefore extremely important because the discovery of a possible lepidosaur-squamate transitional form, although in somewhat later deposits.

The characterization of the rhynchocephalians and lizards of the Albian deposits of the Tlayua Formation in Tepexi de Rodríguez, Central Mexico is the main goal of this thesis. Their morphology will be compared to other known forms and a broad phylogenetic hypothesis for both lepidosaur main lineages is generated including well known fossil forms. This study is performed to establish character transformation in sphenodontians and squamates, in the light of understanding of character change in the lepidosaur-squamate transition. The stratigraphic and biogeographic importance of each lepidosaur and the fauna as a whole is evaluated and their relevance to paleoenvironmental reconstruction of the Tlayua deposits is considered.

THE TLAYUA QUARRY

Tlayua Formation is the formal name given to a series of laminated limestone deposits near Tepexi de Rodríguez, Puebla, México (Pantoja-Alor 1992). The Tlayua Quarry is located in the middle portion of this Formation. It is world famous because of its well preserved fishes, however, it has more recently been recognized as a source of complete skeletons of previously unknown terrestrial lepidosaurs (Reynoso 1995).

The Tlayua quarry was started by a local family in 1959 to extract limestone for construction (Pantoja-Alor 1992). The first fossils were collected soon after the quarry was opened. The paleontological importance of the locality was noticed later by a Mexican scout, who noted its significance in an article in a tourism magazine (Moller 1980). Soon after, the Instituto de Geología of the Universidad Autónoma de México began to investigate the locality, but it was not until 1982 that the findings were shown to the international scientific community (Applegate and Espinosa-Arrubarrena 1982).

After recognizing the scientific importance of the fossils, the family running the quarry became interested in their recovery and preservation. The Instituto de Geología and the family agreed that the fossils would be kept in the University of Mexico, and in exchange, a small local museum to exhibit some of the fossils and casts of important specimens was constructed. The subsequent development of the site produced benefits for the local economy, establishing much interest amongst the local population, and ensured the successful recovery of the new material. Although the commercial sale of fossils is illegal in México, it is a common practice, and its prevention it is one of the most important goals of Mexican paleontologists.

Since 1981, the Instituto de Geología had carried out an extensive paleontological and geological research program in Tlayua. This has been supported by the National Geographic Society (1982-1983), Natural Science Foundation (1985), Consejo Nacional de Ciencia y Tecnología (1989-today) and Consejo Nacional de la Biodiversidad. The Instituto de Geología and the local people have developed an interesting work system. Today, the quarry is worked in two sections: the commercial quarrying section where the fossils are randomly found; and a Scientific quarry ("CONACyT quarry") where the fossils are searched layer by layer from top to bottom, with strict stratigraphic control. Since none of the workers were familiar with fossiliferous structures, a training program was given, and now all of them are capable to identify any biotic remain or print. Every find is kept to be later identified by a specialist. The commercial quarry is still owned and managed by the family, who receive all economic benefits. Operation of the CONACyT quarry is financed by the University, and the quarrying benefits go to the family as well.

The family also receives benefits for assisting researchers and visitors to the locality and museum.

Locality

The Tlayua Quarry is located in the province of Tlaxiaco in the area known as the High Mixteca (97° 54' W; 18° 35' N), 92 km south east of the City of Puebla (González-Rodríguez 1989). It is accessed through the federal highway 150 Puebla-Tehuacán, taking the road 455 to San Juan Ixcaquixtla in "La Colorada". The quarry is located at the end of a dirt road, 2 km southeast of the Colonia Morelos situated on km 42 of road 455, 3 km North of Tepexi de Rodríguez (Applegate et al. 1984; Fig. 1).

Stratigraphic relationships

The Tlayua Formation is a series of white and reddish limestones 300 m thick (Pantoja-Alor 1992) composed of three members (Fig. 2). The lower member is incomplete and rests discordantly over the Early Paleozoic metamorphic schist of the Acatlán Complex (Ortega 1978). The Tlayua Quarry is located in the nearly 50 m thick middle member, and is overlaid by a thinner and weathered superior member. The Tlayua Formation is covered discordantly by the Plio-Pleistocene sediments of the "Pie de Vaca" and "Agua de Luna" Formations (Pantoja-Alor et al. 1988).

Lithology

The upper member is composed by two different microfacies: one with dolomite crystals, interclasts, and abundant milioloid foraminifera; and the other with dolomite crystals within a micritic matrix (Malpica-Cruz et al. 1988). In this member the carbonates were transformed secondarily to dolomite in a marine to fresh water transition. The lower member is a micritic limestone with abundant interclasts and milioloid foraminifera. It is

Fig. 1. Map showing the locality of the Tlayua Quarry, Tepexi de Rodríguez, México (from González-Rodríguez 1989).

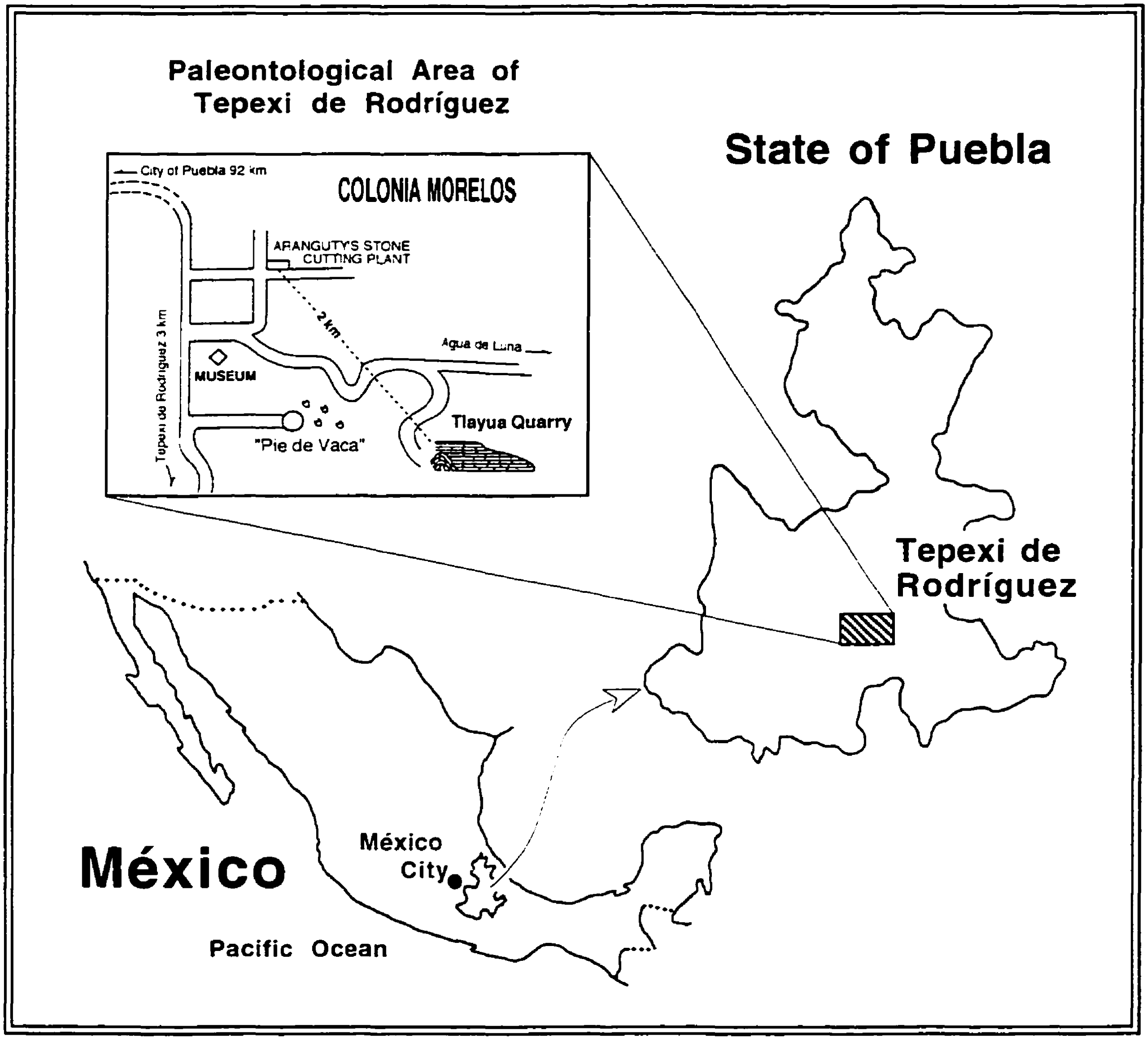
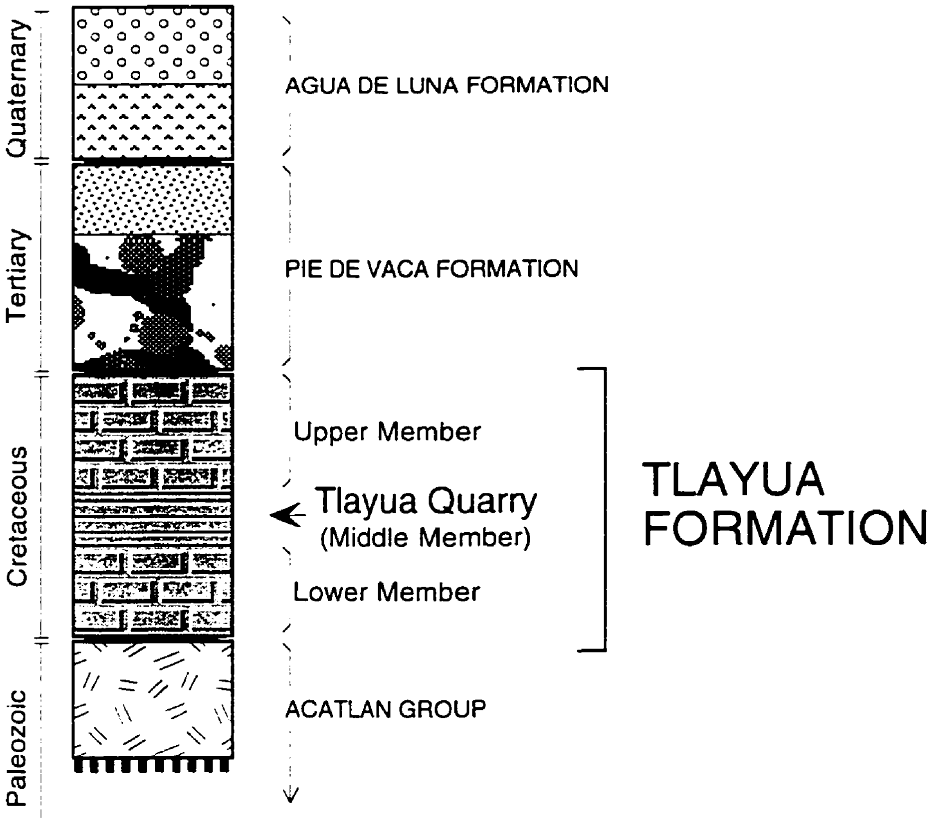

Paleontological Area of Tepexi de Rodríguez
City of Puebla 92 km
COLONIA MORELOS
ARANGUTY'S STONE CUTTING PLANT
2 km
Agua de Luna
MUSEUM
Tepexi de Rodríguez 3 km
"Pie de Vaca"
Tlayua Quarry
State of Puebla
Tepexi de Rodríguez
México
México City
Pacific Ocean

Fig. 2. Stratigraphic relationships of the Tlayua Quarry within the Tlayua Formation and other geological deposits in the Tepexi de Rodríguez area (from Applegate et al. 1984 and Pantoja-Alor et al. 1988).


Quaternary
Tertiary
Cretaceous
Paleozoic
AGUA DE LUNA FORMATION
PIE DE VACA FORMATION
Upper Member
Tlayua Quarry
(Middle Member)
Lower Member
ACATLAN GROUP
TLAYUA FORMATION

characterized by its massive stratification and the presence of biostromes 20 to 50 cm thick composed of the rudiste *Toucasia polygira* (Alencaster 1973).

The middle member, from which the deposits of the quarry originate, is also a micritic limestone with similar proportion of micrite or microcrystallized calcite to the Solnhofen limestones (Applegate et al. 1984, Applegate 1987). In contrast to the lower member, it exhibits microstratification, with layers that can vary from millimeters to centimeters. Bioturbation, organic matter, and clasts other than coccolitophorid shell fragments are almost completely absent. Some layers exhibit desiccation marks, sole or rain drop marks, and intercalated strata of volcanic origin. The sediments are undulated throughout the quarry and they can be strongly deformed in some places due to the Laramidic events during the Tertiary. Most well preserved fossils are found in characteristic, soft red microstrata formed diagenetically, either by biotic precipitation of ferric hydroxide (Applegate et al. 1984), or exposure of sediments to short periods of oxidation at the surface (Pantoja-Alor 1992).

Age

The age of the quarry is still uncertain. According to Alencaster (1973) rudistes suggest Albian age for the Lower Member. Based on the index fossil foraminifera *Dicyclina schlumbergeri* the Upper Member was dated as Cenomanian to Late Albian (Fernández-Becerra 1985).

The age of the middle member has been estimated from different evidence: belemnites of the genus *Neohibolites* (Seibertz and Buitrón 1987) and ammonites of the genus *Morticeras* (Cantú-Chapa 1987) suggest a mid to late Albian age. However, other stratigraphic information suggests that it may be as old as Late Aptian (Padilla in Applegate et al. 1984). The fish fauna, however, includes genera that range from the Upper Jurassic to the Lowermost Cretaceous (Grande pers. com. 1992). Palinological evidence supports an Albian age (Mártinez pers. com. 1996).

Depositional environment

The most striking feature of the Tlayua fossils is their extremely good preservation. The fauna includes soft bodied organisms such as terrestrial spiders, holothuroids, and polychaetes (Buitrón and Malpica-Cruz 1987; Applegate pers. com. 1996). Some fishes have preserved soft anatomy such as crystalline lenses of the eye and stomach contents (Applegate and Espinosa-Arrubarrena 1982). In the lizards, some soft body parts are also preserved. The preservational qualities of the Tlayua limestones qualify it as a *Lagerstätten*, a paleontological deposit with exceptional preservation. Because of that, special attention has been paid to the depositional conditions.

Two main hypotheses have been suggested. The first, based mainly on biotic data, suggests that the sediments were deposited in an anaerobic marine environment, 10 to 50 m deep. In this kind of environment bacterial decay can be retarded, permitting soft tissue to be calcified (Applegate et al. 1984; Applegate 1987). This hypothesis is supported by the lack of bioturbation in the sediments and little evidence of postmortem activity. Applegate et al. (1984) and Applegate (1987) suggest that the organisms are alloctonous to the depositional environment and were washed in from many different places. The presence of scales and fishes aligned in particular orientations, as well as some disarticulated fish suggest the presence of deep water low speed currents.

An alternate hypothesis, based mainly on stratigraphic evidence, proposes a well oxygenated shallow water environment (Malpica-Cruz et al. 1988; Pantoja-Alor 1992). This model suggests that the alloctonous fauna was trapped in an intertidal zone or within surface pools, and was then rapidly covered by sediments carried by low energy water currents and subjected to short periods of desiccation (Fig. 3). The microstratification suggests laminated currents such as waves produced in shallow water (i.e. near the beach). These conditions are also supported by the lack of bioturbation, lack of organic matter and the fine sediment granulometry. The layers with desiccation marks, sole marks, and rain drop marks support the exposure at the surface and a concomitantly highly oxygenated environment (Pantoja-Alor 1992).

Paleoecology, environmental and geographical setting

The fossils preserved in the Tlayua deposits come from different environments. There are shallow water elopids, surface clupeids, coral reef picnodonts, benthonic echinoderms, mollusks, decapods, and terrestrial reptiles, arthropods and plants. From this evidence plus the geological features described above, several conclusions about the surrounding environment can be reached. Two alternative settings have been proposed. The first hypothesis suggest a marine basin surrounded by the mainland and a coral or rudistes reef (Applegate et al. 1984). The presence of pelagic species suggests that this basin was open to the ocean. Applegate (1987) found a number of similarities in conditions of deposition and fauna between the Tlayua quarry and the Solnhofen limestones (Barthel 1970), and concluding that the two environments must have been similar. In the Tlayua Formation, however, no concrete evidence of a reef has been discovered.

The second hypothesis suggest that all organisms were carried onto a large terrestrial platform subjected to periodical inundations (Fig. 3). This hypothesis requires the presence of lowland areas forming littoral lagoons that occasionally open to the ocean (Pantoja-Alor 1992). Pantoja-Alor also concludes that the presence of gymnosperms and a dipteran (haematophagous) suggest a warm and humid terrestrial environment, however, the presence of dipterans and gymnosperms common to cold climates does not support this hypothesis.

Associated Fauna

The total number of species preserved in the Tlayua deposits is still unknown. Applegate et al. (1984) and González-Rodríguez (1989, 1990) lists most of the recognized taxa from which many are new.

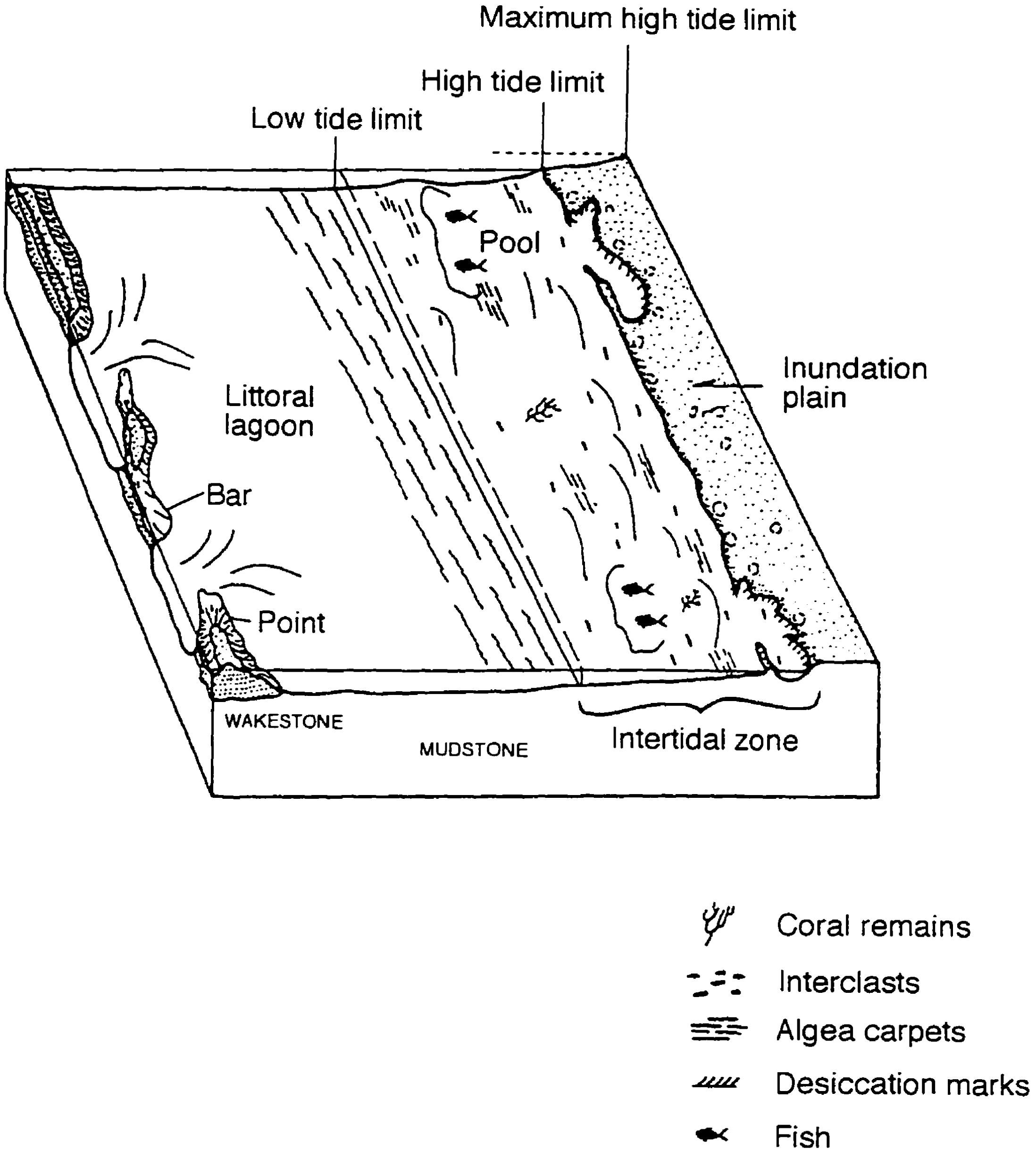

Maximum high tide limit
High tide limit
Low tide limit
Pool
Inundation plain
Littoral lagoon
Bar
Point
WAKESTONE
MUDSTONE
Intertidal zone
Coral remains
Interclasts
Algea carpets
Desiccation marks
Fish

Fig. 3. Reconstruction of the depositional environment and geographic-ecological setting of the Tlayua Quarry during the Early Cretaceous, according to Malpica-Cruz et al. (1988) and Pantoja-Alor (1992).

Bone and organic impressions are the two most common fossil elements within the quarry. The fossils are cream-white and contrast strongly with the red sediments of the matrix, although some picnodont teeth can be brownish or black.

All taxa registered or described up to now are listed on the Appendix 1.1. The benthic taxa includes: coccolitophorid algaes, miliolid foraminifera, hydrozoas, a polychaete, belemnites, ostreids, gastropods, crinoids, sea urchins, star fishes, ophiuroids, sea cucumbers, decapods and isopods. The coral reef fauna is represented by the picnodont fish. The pelagic biota includes pelagic ammonites, elasmobranchs, holostean fishes (Semiodontidae, Macrosemiidae, Amiidae, Ophiopsidae, Aspidorhynchidae, Caturidae, Heterodontidae and Hibodontidae), teleostean fishes (Chirocentridae, Pholidophoridae, Ichthyodectidae, Elopidae, Plethodontidae and Clupeidae). And, finally, the terrestrial biota includes: a gymnosperm leaf, two arachnids, and a dipteran insect.

Among reptiles, almost 80 specimens of mostly isolated or partially articulated reptile bones have been collected since the early years of excavation. Several partial or complete skeletons have also been collected (Espinosa-Arrubarrena and Applegate 1990). These includes plesiosaur teeth, and pterosaur fragments, very well preserved complete terrestrial and aquatic turtles, two crocodiles of apparently the same species and four new types of lepidosaurs. These lepidosaurs are subject of this paper.

MATERIAL

Studied material

Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México (IGM).

Pamizinsaurus tlayuaensis

IGM 6854 (Holotype). Almost complete juvenile skeleton preserved in part and counterpart blocks.

Ankylosphenodon pachyostoseus

IGM 7441 (Holotype). Anterior portion of a complete skeleton.

IGM 7442. Skull and proximal elements of the right forelimb split in half preserved in part and counterpart blocks.

IGM 7443. Almost complete postcranial skeleton

IGM 7444. Disarticulated postcranial skeleton.

IGM 7445. Crystallized skull associated with some of the anterior portion of the postcranial skeleton.

IGM 7446. Presacral vertebrae series associated with ribs.

Huehuecuetzpalli mixtecus

IGM 7389 (Holotype). Complete skeleton.

IGM 4185 (Paratype). Complete juvenile skeleton preserved in part and counterpart blocks.

Tepexisaurus tepexii

IGM 7466 (Holotype). Complete skeleton.

Comparative Material

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

Squamata- Museum of Comparative Zoology, Harvard University: *Basiliscus plumifrons* MCZ-R-19490 CS; *Agama agama* MCZ-R-173366 CS; *Draco sp.* MCZ-R-1548340 CS; *Uromastix acanthurinus werneri* MCZ-R-27382 CS; *Dibamus taylori* MCZ-R-27067 CS (Paratype); *Bipes biporcatus* MCZ-R-83227 CS; *Amphisbaena alba* MCZ-R-54299 CS; *Eublepharis maculatus* MCZ-R-79778 CS; *Gekko gekko* MCZ-R-173377 CS; *Phelsuma lineata* MCZ-R-11688 CS; *Uroplatus fimbriatus* MCZ-R-180529 CS; *Pygopus lepidopus* MCZ-R-10287 CS; *Lacerta jacksoni* MCZ-R-131783 CS; *Ameiva a. ameiva* MCZ-R-131787 CS; *Tupinambis rufesens* MCZ-R-74091 CS; *Chalcides oceolatus* MCZ-R-9828 CS; *Eumeces inexpectatus* MCZ-R-173375 CS; *Tiliquia nigrolutea* MCZ-R-1077 CS; *Cordylus warreni* MCZ-R-41881 CS; *Anguis fragilis* MCZ-R-37174 CS; *Diploglossuss costatus* MCZ-R-59688 CS; *Gerrhonotus liocephalus loweryi* MCZ-R-24514 CS; *Xenosaurus grandis rackhami* MCZ-R-54315 *CS*. Museum National of Canada: *Varanus sp.* Redpath Museum, Montréal: *Mabuya striata* RM 1015; *Chamaleo chamaleo* RM 11; *Chamaleo sp*, RM 1095; *Boa* RM 1128, RM 1129, RM 1125; Viper snake (no label) RM 1117. Unnumbered material from the Redpath Museum: *Iguana sp.* (several skulls); *Agama sp.*; *Scelophorus undulatus*; *Lacerta sp.*; *Varanus bengaliensis* (complete skeletons and several articulated and disarticulated skulls; *Gekko sp.*; *Gerrhonotus multicarinatus*; *Heloderma sp.*; banded gecko (no label); *Anolis carolinensis* (several skeletons); *Crotaphytus sp.*; *Lacerta agilis*. Fossil specimens: *Eichstaettisaurus schroederi* plaster cast. Carnegie Museum of Natural History: *Ardeosaurus digitalellus* CMNH 4026.

Lepidosauromorphs- American Museum of Natural History: *Icarosaurus siefkeri* AMNH 2101; *Kuehneosaurus sp.* (disarticulated remains AMNH); Instituto de Geología, Universidad Nacional Autónoma de México: *Tamaulipasaurus morenoi* IGM 6620, IGM 6621, IGM 6623.

METHODS

Preparation and casting

To remove the matrix, both mechanical and chemical means were used. Well sharpened carbide needles and a dentist drill were used to remove the sediments. Acetic acid (15%) was sometimes applied locally with a brush to soften the matrix, washing the fossil thoroughly every night during the preparation period. More intensive acid preparation was accomplished by embedding the specimen in plasticine exposing only the part to be prepared and bathing it in acetic acid for 24 hours. The specimen was then immersed in water to remove the acid for 24 hours, and then allowing it to dry. This cycle was repeated until the specimen was clearly exposed. A thick layer of Glyptal was applied in areas already cleared to prevent overpreparation. To remove all remaining acid, the fossils were washed thoroughly for three days in running water at the end of the preparation.

High fidelity latex casts were made to replicate the shapes of lost bones preserved as impressions. Additional information was gained by drawing the impressions directly.

Phylogenetic analysis

Phylogenetic analysis was executed using PAUP 3.1.1 (Swofford 1993) and McClade 3.05 (Maddison and Maddison 1995). Maximum parsimony trees stability was estimated using bootstrap analysis (Felsestein 1985). The Bremer's branch support and total support indices (Bremer 1988, 1994) were estimated for resultant trees and compared to other published phylogenies. Detailed procedures are outlined in each chapter.

Appendix to chapter 1

Appendix 1.1

Diversity in the Tlayua Quarry

PLANTS: Algae: coccolitophorids

Gymnosperma: Podozamites, (Weber in Pantoja-Alor 1992)

Frenolepsis (Martill 1989)

MICROINVERTEBRATES:

Foraminifera: Benthic miliolids

INVERTEBRATES:

Celenterata: hydrozoas

Polychaeta: *Ophiomorpha granulosa* (impressions; Buitrón and Malpica-Cruz 1987)

Mollusca:

Pelagic ammonites (Cantú-Chapa 1987)

Morticeras sp.

Hysteroceros sp.

Anisoceras sp.

Belemnites:

Neohibolites (Seiberts and Buitrón 1987)

Bivalves: desarticulated Ostreids

Gasteropoda:*Casiopides* (Buitrón and Malpica-Cruz 1987)

Echinodermata:

Crinoidea

Echinoidea: *Pseudocharis* (Applegate et al. 1982)

Asteridea

Ophiuroidea (Buitrón and Malpica-Cruz 1987)

Holoturoidea: five different kind (Applegate 1987; in prep.)

Arthropoda:

Aracnida: Terrestrial spiders

Crusteacea: Decapoda

Isopoda (Applegate 1987)

Copepoda (González-Rodríguez and Vega 1993)

Insecta: Diptera: Tipulidae (Popov 1991, in Pantoja-Alor 1992)

Unidentified radules (Applegate et al. 1984)

Tracks of soft body invertebrates

VERTEBRATES: (50 taxa+)

Elasmobranchians

Holosteans: 9 families (Applegate et al. 1984; González 1989)

Semiodontidae: *Lepidotes*

Picnodontidae 4 sp, 3 gen, 2 Fam (Applegate and Espinosa-Arrubarrena 1992)

Tepexichthys arangutthyorum (Applegate 1992)

Amiidae: 3 or 4, includes *Vialamia*

Macrosemiidae: 5 kinds; includes *Macroseniocotzus* and one new genus and species (González-Rodríguez 1989, González-Rodríguez and Applegate 1991)

Ophiopsidae: *Teoichthys kallistos* (Applegate 1988)

Aspidorhynchidae: *Belonostomus*: (2th most abundant Holostean)

Hibodontidae

Heterodontidae

Caturidae

Teleosteans: 5 families (Applegate et al. 1984, González-Rodríguez 1989 and González-Rodríguez 1990)

- Clupeidae: most abundant fish; 4 kinds, includes*Clupeus*
- Chirocentridae: 2 or 3 kinds.
- Pholidophoridae
- Ichthyodectidae
- Elopidae
- Plethodontidae

Reptiles: (Applegate et al. 1984, Espinosa-Arrubarrena and Applegate 1990)

- Chelonia: five turtle skeletons
- Archosauria:
    - Crocodylia: two specimens
    - Pterodactyla isolated bones (Applegate 1987; Cabral and Applegate 1993)
- Euryapsida: plesiosaur teeth
- Rhynchocephalia:
    - *Pamizinsaurus tlayuaensis* gen. et sp. nov. (Chapter 2 this thesis)
    - *Ankylosphenodon pachyostoseus* gen et sp. nov. (Chapter 3 this thesis)
- Squamatoidea (new taxon):
    - *Huehuecuetzpalli mixtecus* gen. et sp. nov. (Chapter 4 this thesis)
- Squamata:
    - *Tepexisaurus tepexii* gen. et sp. nov. (Chapter 5 this thesis)

CHAPTER 2

A BEADED SPHENODONTIAN (DIAPSIDA: LEPIDOSAURIA) FROM THE EARLY CRETACEOUS OF CENTRAL MEXICO

A BEADED SPHENODONTIAN (DIAPSIDA: LEPIDOSAURIA) FROM THE EARLY CRETACEOUS OF CENTRAL MEXICO

INTRODUCTION

The fossil record of sphenodontians is well known from Late Triassic to Early Cretaceous deposits of Europe, China, and North America (Gilmore 1909; Simpson 1926; Huene 1952; Cocude-Michel 1963; Fabre 1973, 1974; Throckmorton et al. 1981; Rasmussen and Callison 1981; Fraser 1982, 1986, 1988; Carroll 1985a; Fraser and Benton 1989; Whiteside 1986; Sues and Baird 1993; Wu 1994; Sues et al. 1994, Reynoso, in press). The present distribution of *Sphenodon* and recent fossil discoveries show that the sphenodontians once had a world wide distribution (Sues and Reisz 1995). In spite of their abundance, sphenodontians are generally viewed as primitive reptiles showing little diversity since their first appearance (Romer 1956; Porter 1972; Dawbin 1982; Zug 1993). However, more recently Carroll and Wild (1994) argued that different morphological patterns have been successful in sphenodontian evolution, and that *Sphenodon* is significantly different from Triassic sphenodontians. Most Triassic sphenodontians depart little from the original type. However, towards the Late Jurassic, new dental and postcranial specializations were acquired: chewing apparatus in sphenodontines, plant grinding teeth in eilenodontines, long legs in terrestrial homoeosaurs, and stout skeletons in aquatic sapheosaurs. Carroll and Wild (1994) have contrasted the bizarre shape of the slim, short limbed and long bodied marine pleurosaurs with the terrestrial *Sphenodon*.

In 1989, a single sphenodontian specimen with an *Heloderma*-like dermal armor was collected by workers at the Tlayua Quarry, north Tepexi de Rodríguez, Puebla, Mexico. This is the first documented evidence of such specialization in sphenodontians.

SYSTEMATIC PALEONTOLOGY

LEPIDOSAURIA Dumeril et Bibron, 1839

RHYNCHOCEPHALIA Günther, 1869

SPHENODONTIA Williston, 1925

SPHENODONTIDAE Cope, 1869

Genus *PAMIZINSAURUS* gen. nov.

Type Species- *P. tlayuaensis*

Etymology- From *pamizintli* (with corn on top), Náhuatl; and *saurus*: "Lizard covered with corn". In reference to the bead-like osteoscutes covering the body. A testimony to "corn", the basic food in Mesoamerican native cultures.

Diagnosis- As for the type species

Species *PAMIZINSAURUS TLAYUAENSIS* sp. nov.

Figs. 4, 5, and 6

Holotype- Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, México. IGM 6854. A severely crushed skeleton of a juvenile sphenodontian preserved in part and counterpart blocks. The skull is badly preserved and most of the anterior limb elements are lacking.

Etymology- from *tlayua* (= place of darkness), Náhuatl. In reference to the name of the quarry where the skeleton was found.

Locality- Tlayua Quarry, Locality No. 2432 Cantera Tlayua-IGM, level Z/X. Middle Member of the Tlayua Formation (Pantoja-Alor 1992). 2 Km South East of the Colonia Morelos, near Tepexi de Rodríguez, Puebla, México.

Age- Early Cretaceous. Middle or Late Albian (Seibertz and Buitrón 1987).

Diagnosis- Sphenodontian with small rounded osteoscutes aligned in transversely oriented rows; relatively few hatchling teeth with well developed ridges, symphysial end of the dentary tapered anterodorsally with the ventral process of the symphysis displaced posteriorly in early ontogeny, small posteromedial processes of the pterygoids close to the midline almost closing the interpterygoid vacuity, short tail covered with osteoderms arranged in rings.

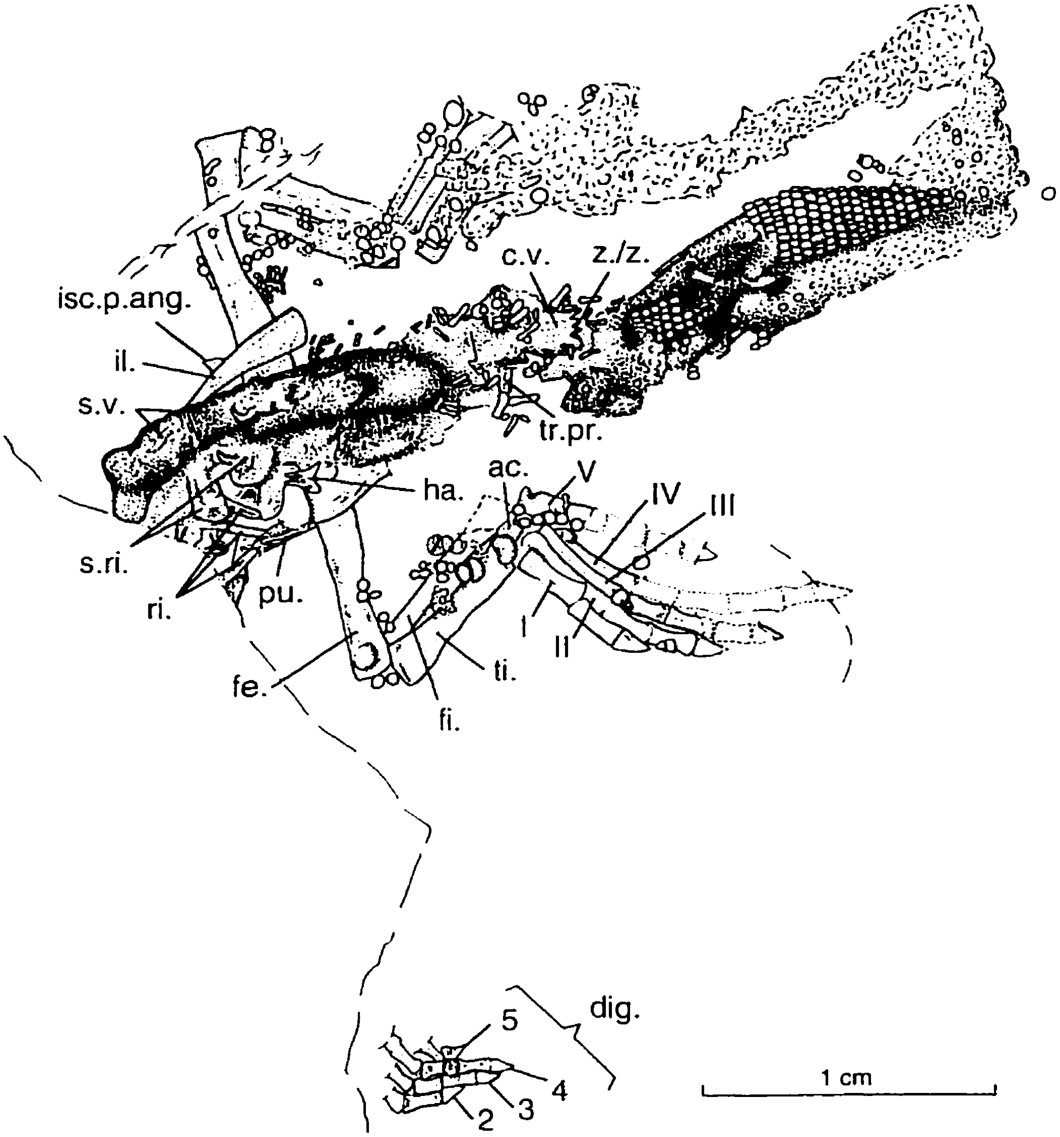
DESCRIPTION

The holotype and only known specimen is preserved in part and counterpart blocks (Figs. 4 and 5). In one block, the skull and anterior portion of the body are in ventrolateral view, and in the other, the posterior part of the presacral vertebral column, left hand, the pelvic girdle, posterior limbs, and tail are visible in dorsal view. Carelessness in preliminary preparation damaged considerably the specimen. The distal portion of both right and left toes were removed, and portions of the skull, in particular the premaxilla and maxilla, were over-prepared.

Most of the skeleton is covered by remnants of calcified body tissue and small osteoscutes, obscuring detail of the vertebral column and head. Other elements, such as the palate, lower jaws, and posterior limbs and girdle, are free and completely exposed.

The holotype of *Pamizinsaurus* is a post-hatchling sphenodontian. It is very small with a relatively large head and a short tail. The skull length from the tip of the premaxilla to the occipital condyle is 16 mm, the presacral vertebral column is 36 mm; and the tail is 25 mm. The femur is 8.8 mm, the tibia 5.7 mm, and the fibula 6.4 mm. Proportions relative to presacral vertebral column length are as follow: head=0.44; tail=0.69; femur=0.32; tibia=0.21; fibula=0.23.

Fig. 4. *Pamizinsaurus tlayuaensis* gen. et sp. nov. (IGM 6854). Block with head and anterior region of the body.


c.v.
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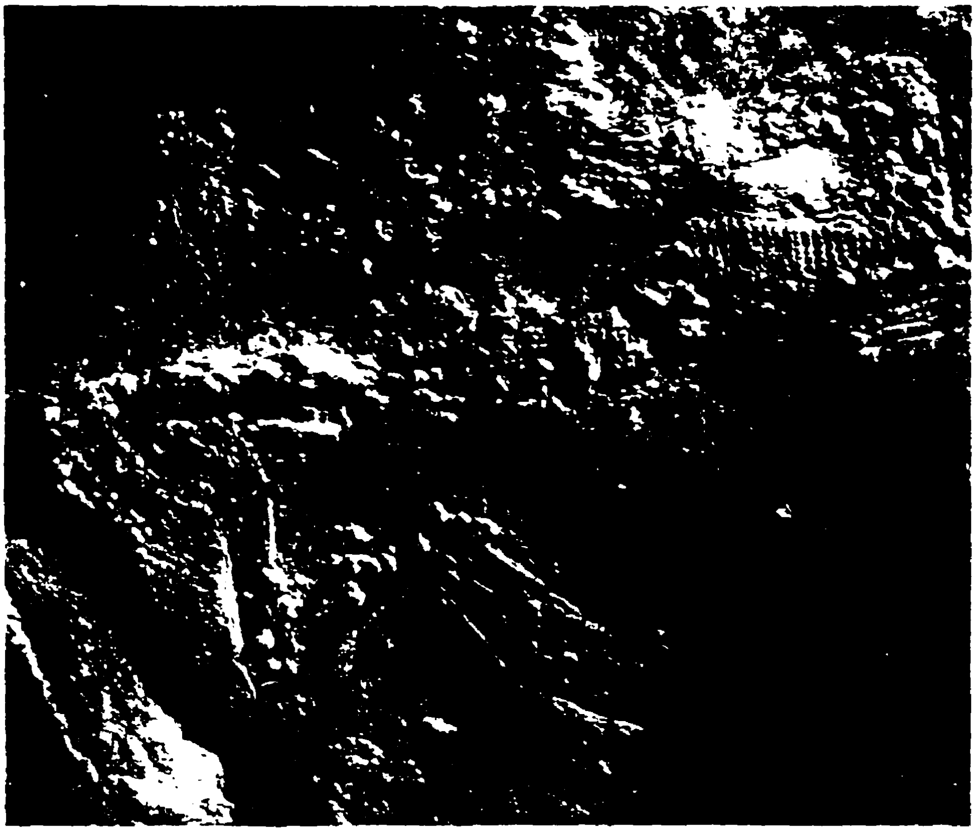
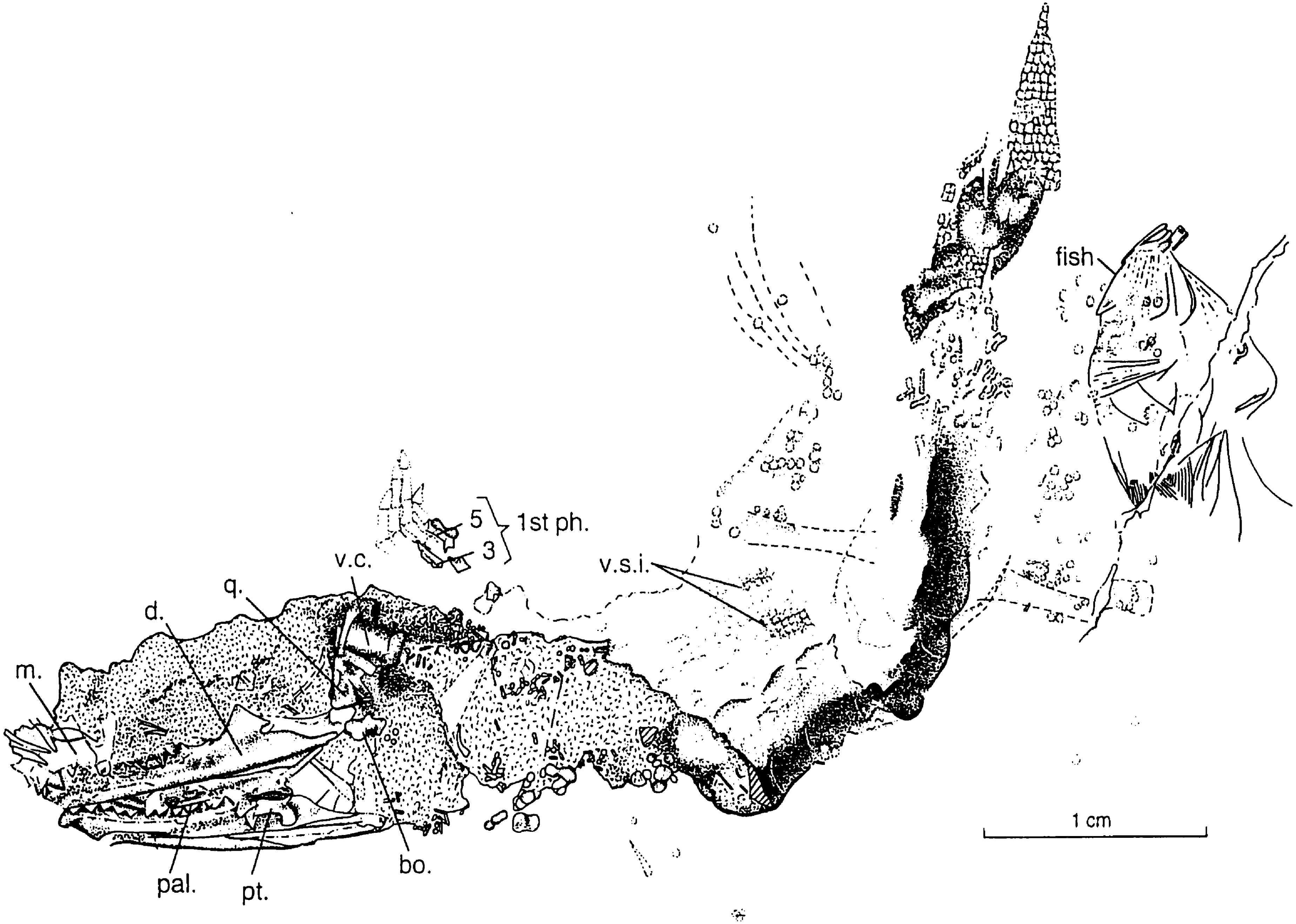


Fig. 5. *Pamizinsaurus tlayuaensis* gen. et sp. nov. (IGM 6854). **A**. Photograph and **B**. illustration of counterpart block with posterior part of the vertebral column, pelvic girdle, limbs, and tail. Digits indicated in Arabic numerals and metatarsals in Roman numerals.


fish
5
3
1st ph.
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1 cm

Skull

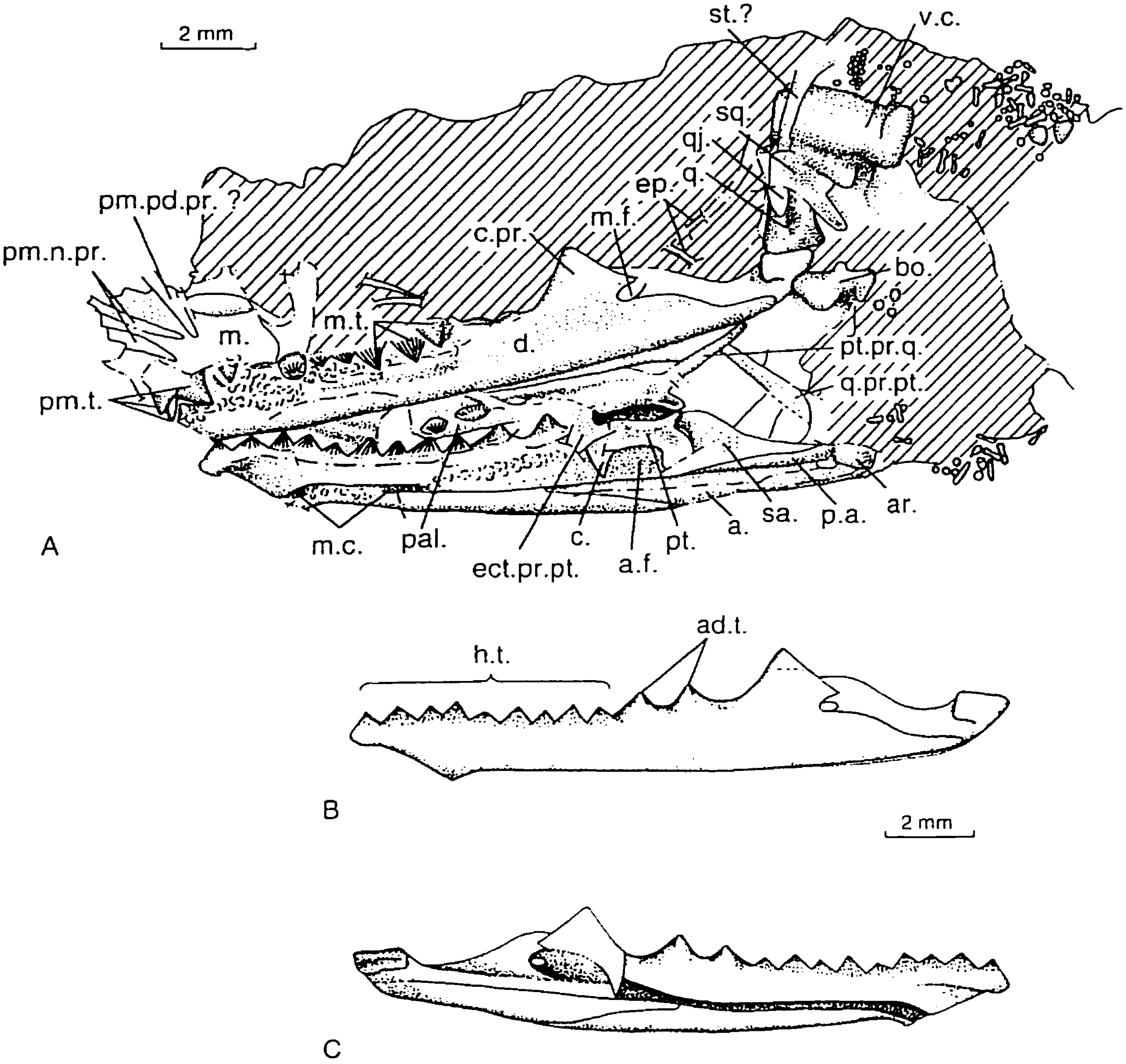
Only the lower jaws, still articulated with the quadrate and occluded within a well defined maxillary-palatine groove are well preserved (Fig. 6A). The premaxilla, maxillary teeth, quadrate/quadratojugal, basioccipital and the epipterygoid and the supratemporal process of the squamosal can barely be identified. The quadrate is exposed laterally and a well developed lateral emargination is present. A small rounded quadratojugal is attached to its lateral surface but its original position is uncertain. The ventral projection of the squamosal extends close to the ventral end of the quadrate. Its end is rounded suggesting that the lower temporal bar was not in contact. A slender supratemporal (or supratemporal process of the squamosal) lies dorsal to the quadrate.

The anterior end of the premaxilla is broken. Only the left and right nasal processes can be recognized. Posterior to the latter, an isolated structure resembling the posterodorsal process of the premaxilla of *Clevosaurus* (Fraser 1988; Sues et al. 1994; Wu 1994) is present, but its positive identification is impossible. The premaxilla bears three discrete large, triangular, acrodont teeth. The typical sphenodontian chisel-like structure does not appear to be developed. The lateral tooth is the largest of the series and is brightly polished. The maxilla bears five large conical teeth with well developed striations from tip to base. The tooth series exhibits a size alternation pattern with the second and fourth teeth slightly smaller than the rest.

The dentaries obscure most of the palatines and pterygoids leaving only two large palatine teeth visible. As in *Sphenodon*, the central region between the three rami of the pterygoid is elongated anteroposteriorly, the pterygoids are slightly curved medially in a concave manner, and posteriorly, the interpterygoid vacuity is almost closed by the pterygoid posteromedial processes. The quadrate and ectopterygoid processes of the pterygoid are slender.

The long and slender lower jaws are preserved with the left in lateral and the right in medial views (Fig. 6 B, C). The dentary presents a broad symphysis with the ventral

Fig. 6. *Pamizinsaurus tlayuaensis* gen. et sp. nov. (IGM 6854). **A**. Detail of the head as preserved. **B** and **C**. Reconstruction of the lateral and medial view of the lower jaw.



2 mm
st.?
v.c.
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qj.
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pm.pd.pr. ?
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2 mm
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projection placed in an unusual posterior position, giving the appearance that the anterior end of the dentary tapers distally. The coronoid, surangular, angular, prearticular, and articular closely resemble those of other sphenodontians. Laterally, the posterior process of the dentary projects far back beyond a high coronoid process, and a large mandibular foramen is enclosed by the dentary and surangular. The Meckelian canal opens medially along the entire length of the jaw. The articular condyle is short anteroposteriorly and the retroarticular process is absent.

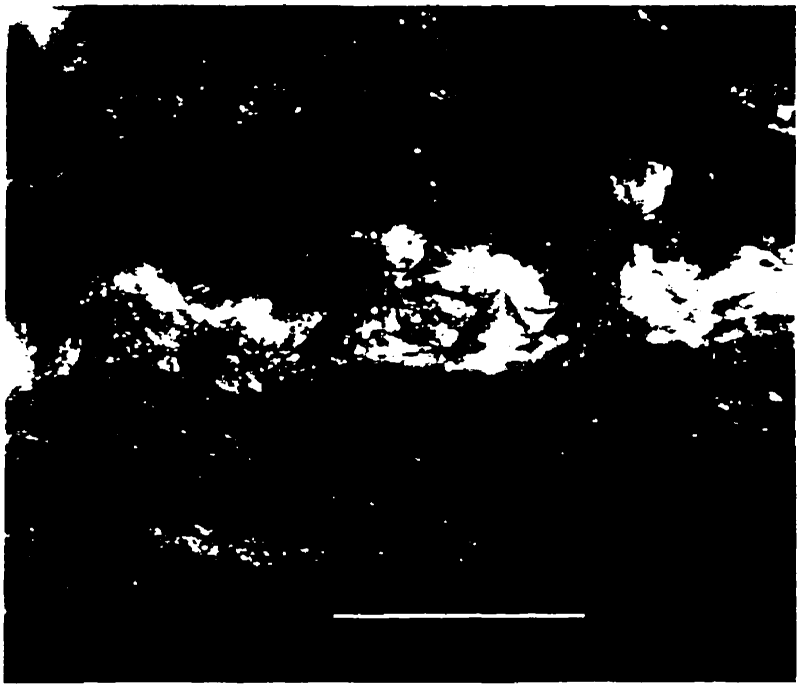
The dentition of the right dentary is completely preserved. The teeth alternate in size. Of the eleven teeth present, the first nine correspond to the second and third generation of the hatchling dentition (Harrison 1901), and the last two correspond to the first and second additional teeth (Robinson 1976). The hatchling teeth have prominent striations similar to those of the maxillary teeth (Fig. 7). In contrast, the additional teeth are superficially smooth, each bearing a prominent posterolateral flange. All teeth are triangular in laterally view, but the tip of each additional tooth is placed just posterior to the mid-length of the tooth. No bite marks or smooth wear surfaces are evident on either teeth or jaws. However, the presence of a very short articular condyle may suggest that this sphenodontid had orthal jaw closure.

Postcranium

Most vertebrae are covered with osteoderms and calcified body tissue making it difficult to establish their limits. The numbers and general shape are unknown. Only some information can be gained from exposed segments of the caudal vertebrae.

The neural spines are not evident and probably were compressed onto the centra. The zygapophyses are well developed and the zygosphene and zygantrum accessory articulations are present but weak. The presacral ribs are slender and slightly curved, becoming shorter caudally. The presence of ribs on the last three presacral vertebrae suggest that ribs were distributed all along the trunk region. The sacral ribs are broader

Fig. 7. *Pamizinsaurus tlayuaensis* gen. et sp. nov. (IGM 6854). Tooth microstructure on the medial side of the right hatchling tooth series. Arrow pointing at tooth number six. Scale bar equals 1 mm.



than the presacrals but as long as the last presacral rib. A very short laterally oriented rib appears to be is unfused to the fifth caudal vertebra.

The iliac blade is thin with a very broad distal end. The dorsal edge is straight and lacks the dorsal tuber, probably still unossified. Postmortem compression of the posterior limbs and toes has artificially increased the width of the elements. The femur is almost straight. Its proximal head is not exposed and the distal head ends flat with no evidence of epiphyses. The tibia is thicker than the fibula, but the fibula is longer. A single bone, probably a fused astragalocalcaneum, is found in the pes region. The phalangeal count is 2, 3, 4, 5, 4. The first metatarsal is slightly broader than the second and third (condition not clear on the fourth). The fifth metatarsal is hooked, shorter than other metatarsals, and bears a prominent outer process.

Only the more distal phalanges of the left hand are preserved. They are more slender than those of the toes. It is not possible to establish the exact phalangeal count, but it may be similar to that of other sphenodontians. Digit 2 has two preserved phalanges: digit 3, has four plus the distal end of the metatarsal; digit 4, only shows four and digit 5, three.

Osteoderms

Dermal osteoscutes are preserved all over the body. Their external appearance and color is very different from that of the bony elements. These structures are hard and appear to be ossified. The surface of each osteoscute is smooth and lacks ornamentation. Two kinds can be identified: most are hexagonal, slightly enlarged anteroposteriorly and with rounded corners; others less common are dumbbell-shaped with rounded ends. Both can be of various sizes. Mid-size rounded osteoscutes can be found on the presacral region, limbs, and tail. Larger osteoscutes are present on the limbs, and the smallest ones are on the neck region. The most conspicuous dumbbell-shaped osteoscutes are distributed around the proximal end of the tail, very near to where the cloaca was probably located.

Smaller dumbbell-shaped osteoscutes are present on the limbs, and especially in the neck region.

Over the distal and medial parts of the tail the rounded osteoscutes alternate and are arranged in rings (Fig. 8 A, B). The number of osteoscutes reduces regularly to the end of the tail, where a single osteoscute is present. There is no suggestion of a mid-dorsal longitudinal row. In the presacral region the osteoscutes are preserved as natural molds. They are also transversally oriented, but slightly oblique (Fig. 8C). In the remaining areas of the body the osteoscutes are disarticulated.

DISCUSSION

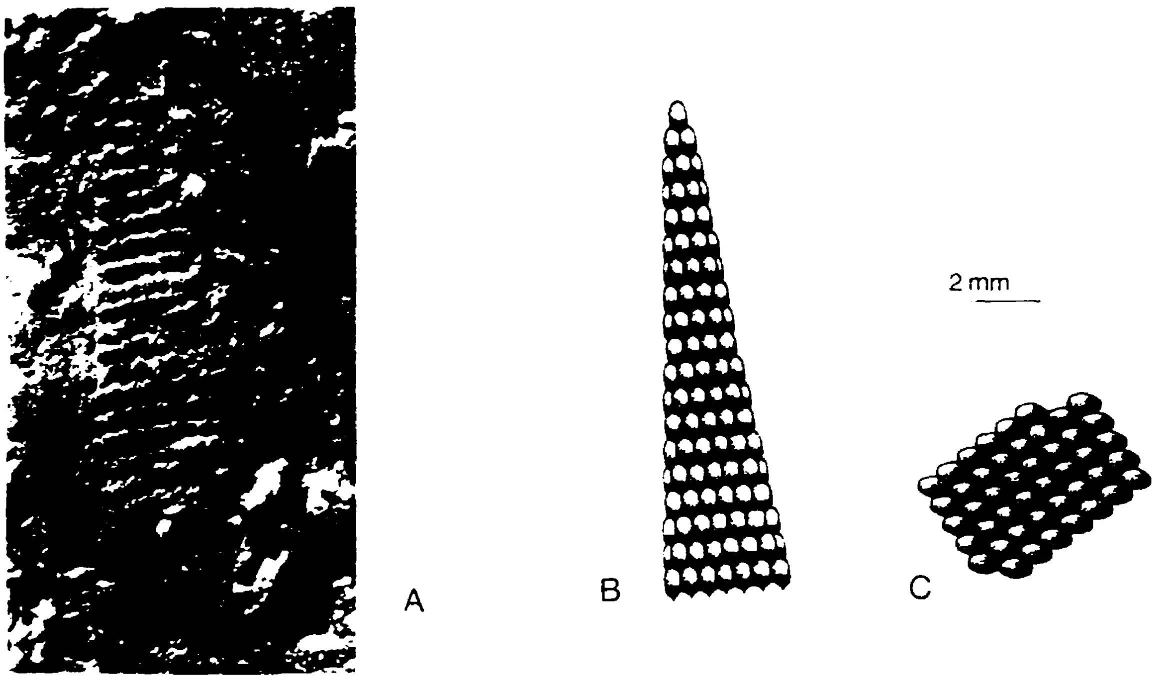
Since the holotype, and only known specimen of *Pamizinsaurus tlayuaensis* is a very immature individual, it is difficult to compare with other sphenodontians. Most known fossil sphenodontians are adults, and only small fragments of juvenile sphenodontians, represented primarily by lower jaws, have been described. Since *Sphenodon* is the only sphenodontian for which ontogeny is well known, it is the most useful source of comparison.

Ontogeny

The size of *P. tlayuaensis* is similar to that of prehatched (stage S II) *Sphenodon* (=75 mm; Howes and Swinnerton 1901). However, its skull length (measured from the tip of the premaxilla to the occipital condyle=16mm) is larger than Harrison's (1901) and Rieppel's (1992a) stage S specimens (skull length=13.5 and 12.5 respectively), but smaller to Harrison's (1901) stage T ("few weeks after hatchling") specimen (skull length=19 mm; see also Robinson 1976).

In spite of its relatively smaller size, the age of the holotype of *P. tlayuaensis* is estimated to be older than stage T of *Sphenodon*. In stages S and T of *Sphenodon*, the hatchling teeth are weakly attached to the jaw and the additional teeth are not yet erupted

Fig. 8. *Pamizinsaurus tlayuaensis* gen. et sp. nov. (IGM 6854). **A**. Osteoscutes on the distal portion of the tail. **B** and **C**. Reconstruction of the scutellation pattern of the tail and presacral region.


A
B
C
2 mm

(Harrison 1901; Rieppel 1992a). The firmly attached hatchling dentition and the presence of two additional teeth on the posterior end of the dental series suggest that *P. tlayuaensis* had reached at least the stage T2 "a few months after hatchling" (Harrison 1901; Robinson 1976, fig. 3). The fact that in *Sphenodon*, the first additional teeth emerge little before reaching the stage T2 (Robinson 1976; skull length not given by Harrison,1901 but expected to be larger than in stage T), suggest that *Pamizinsaurus* was smaller than *Sphenodon* in a given ontogenetic stage.

The holotype of *P. tlayuaensis* has fewer hatchling teeth than *Sphenodon* at stage T2. *Sphenodon* bears up to 11 hatchling teeth in the last month of incubation (Harrison 1901) and up to 16 hatchling teeth at stages T to T3 (at stage T2 three teeth are replaced by a successional tooth), whereas hatchling *Pamizinsaurus* has only 9. As stated by Rieppel (1992a), in *Sphenodon*, the first additional tooth is not added at the posterior end of the hatchling series (as suggested Robinson 1976) but replaces the last hatchling teeth, shortening the hatchling tooth series. This same pattern might have occurred in *Pamizinsaurus*, where some hatchling teeth were probably replaced by one or two additional teeth. The number of teeth on the hatchling series, however, will still be less than in *Sphenodon* after replacement. Early stages of *Clevosaurus hudsoni* and the Middle Jurassic sphenodontine *Cynosphenodon* (Reynoso 1992; 1996) have 12 hatchling teeth similar to *Sphenodon*. At post-stage T2 the hatchling series is reduced to eight or less hatchling teeth (Fraser 1988). The reduction of the hatchling tooth row in these sphenodontians, however, is caused by the replacement of the first four to five hatchling teeth by anterior successional teeth, completely absent in *Pamizinsaurus*.

A unique feature of the hatchling dentition of *Pamizinsaurus* is the presence of well established ridges. Hatchling teeth of *Sphenodon*, *Clevosaurus*, and *Cynosphenodon* seems to lack dental ridges (Rieppel 1992a, fig. 3; Fraser 1988; Reynoso 1992) and they are not evident in any other juvenile sphenodontian. Well developed ridges present in additional teeth of some adult forms such as *Opisthias* and *Kallimodon* (Cocude-Michel

1963) are not homologous to those of the hatchling series. Each hatchling tooth in *Clevosaurus hudsoni* exhibits anterior and posterior razor-like flanges (Fraser 1988) not well developed in *Pamizinsaurus*. Morphology of additional teeth, however, are very similar in both taxa.

The presence of three unfused premaxillary teeth is also a juvenile character. As in *Sphenodon*, the lateral tooth is the largest. The second tooth must belong to the second generation of successional teeth, and the first and third, to the third; no replacement seems to have occurred yet, although the first and second teeth might have been close to being shed. In *Sphenodon* three premaxillary teeth are present before stage S and the second tooth is shed after stage T2.

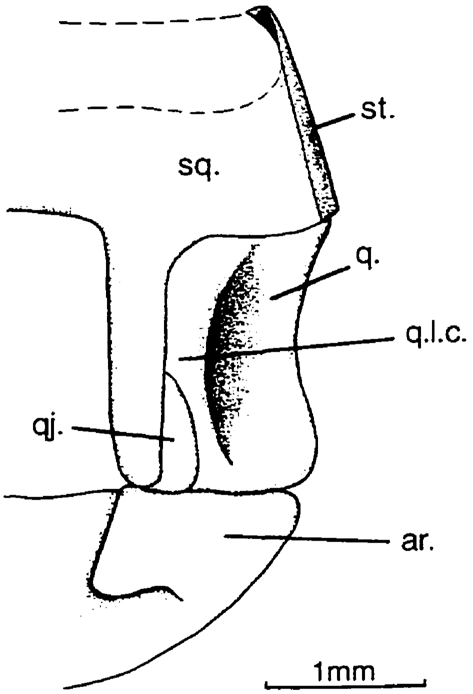
Unusual characters of the lower jaw are the peculiar shape of the symphysial region and the lack of retroarticular process. The ventral projection of the mandibular symphysis, present in all sphenodontians, is placed more posteriorly giving a tapered shape to the anterior end of the dentary. In most sphenodontians, the anterior edge of the symphysis forms an angle of close to 125° in relation to the ventral edge of the jaw. In *Pamizinsaurus*, as well as in *Palaeopleurosaurus* (Carroll 1985a), and *Toxolophosaurus* (Throckmorton et al. 1981) the angle is greater. This character apparently is not correlated with ontogeny. In hatchling *Sphenodon*, *Clevosaurus* and *Cynosphenodon* (Rieppel 1992a; Fraser 1988; Reynoso 1995), the anterior end of the jaw shows an inverse pattern. Initially the angle is close to 90°, increasing gradually during development. The condition present in *Pamizinsaurus* is only observed in late adult forms. Although the absence of the retroarticular process could also be interpreted as an early ontogenetic character, there is no evidence that supports its enlargement with age. In the juvenile *Diphydontosaurus* the process is already present (Renesto 1995), and in *Sphenodon* the process is absent throughout its ontogeny. This latter condition could have been expressed in *Pamizinsaurus*.

Postcranial elements are too poorly preserved to be compared with known hatchling sphenodontians, although two unique features can be recognized: The iliac blade is posteriorly broad, and it lacks a dorsal tuber. This condition parallels stage T of *Sphenodon* (Howes and Swinnerton 1901, Plate 6, fig. 9), and differs from most adult sphenodontians, in which the dorsal tuber of the ilium is present and the iliac blade tapers distally. A distinctive iliac dorsal tuber is present in squamates and sphenodontians but absent in other lepidosauromorphs. The absence of this structure is plesiomorphic to the Lepidosauria and its absence in hatchling stages corroborates its polarity ontogenetically. It is interesting to notice, however, that hatchling features are present in adult *Palaeopleurosaurus* (as reconstructed by Carroll 1985a). The conditions exhibited by *Palaeopleurosaurus* may be retained primitive characters.

Comparison with other sphenodontians

The configuration of the temporal region (Fig. 9) differs considerably from *Sphenodon* and resembles that of primitive sphenodontians (Whiteside 1986): the lower temporal bar is incomplete, the squamosal ventral ramus is ventrally oriented, the quadrate is well exposed laterally bearing a well developed lateral emargination, and the quadratojugal is reduced, resting on the lateral surface of the quadrate. An isolated element placed dorsal to the suspensorium resembles the supratemporal of the hatchling *Sphenodon* (Rieppel 1992a). Disruption of this region, however, makes it impossible to determine whether it was a separated element as in *Clevosaurus hudsoni* or *C. bairdi* (Fraser 1988; Sues et al. 1994), or fused to the squamosal as in other sphenodontians. The ventral extension of the squamosal reaching the ventral end of the quadrate resembles that of *Clevosaurus* and differs from primitive sphenodontians where the quadrate is longer. The lack of a facet for the quadratojugal on the quadrate prevents the establishment of the actual position of the quadratojugal. Figure 6 was reconstructed conservatively.

Fig. 9. *Pamizinsaurus tlayuaensis* gen. et sp. nov. (IGM 6854). Reconstruction of the postemporal region. The position of the quadratojugal is uncertain.


st.
sq.
q.
q.l.c.
qj.
ar.
1mm

The structure of the pterygoids of *Pamizinsaurus* resembles *Sphenodon* more than any other sphenodontian. In both genera, the central region of the pterygoid between the pterygoidal rami is elongated, the edges bordering the pterygoidal vacuity are concave, and the small posteromedial processes are almost closing the interpterygoid vacuity. A similar, but less obvious configuration is present in *Palaeopleurosaurus* (Carroll 1985a). In the latter, the interpterygoid opening is relatively more closed than in other sphenodontids, although its posterior opening is as wide as the widest section of the vacuity. In *C. petilus*, the central region between the rami is also elongated (Wu 1994).

Osteoscutes distributed along the body have never been reported in any sphenodontian. Although the preservation of loosely attached structures is unlikely in some depositional environments, *Homoeosaurus*, *Kallimodon*, *Sapheosaurus*, *Pleurosaurus*, *Palaeopleurosaurus*, *Polysphenodon*, and *Clevosaurus*, (Cocude-Michel 1963; Carroll 1985a; Fraser 1988; Sues et al. 1994) have been collected from environments in which there is a very good possibility to preserve osteoderms *in situ*, if present. In none of these sphenodontians, however, have traces of such structures been reported. This unambiguous feature undoubtedly justifies the recognition of *Pamizinsaurus tlayuaensis* as a new species.

PHYLOGENETIC RELATIONSHIPS

The presence of a small lateral palatine tooth row, separated premaxillary teeth and supratemporal, and the absence of teeth and jaw wear facets, can be interpreted as either primitive or juvenile features, and makes it difficult to establish the sister-group relationships of *Pamizinsaurus*. The lack of information on many other characters makes phylogeny even more problematic. A main palatine tooth row parallel to the maxillary tooth row separated by a groove where the dentary fits, a well developed coronoid and postdentary process, a broad mandibular symphysis, fully acrodont dentition with flanges, three or less premaxillary teeth, and the presence of anterior juvenile teeth, are synapomorphies shared by *Pamizinsaurus* with all crown sphenodontians

(*Diphydontosaurus* and *Planocephalosaurus* excluded), but more accurate relationships are uncertain.

A branch and bound analysis using a modified version of Reynoso's (1996) data matrix (Appendix 2.1, Table 4) suggests that *Pamizinsaurus* is the sister-taxon of the clade sphenodontines + eilenodontines (Fig. 10; Appendix 2.2). Characters 1, 4, 9, and 33 of Sues et al. (1994) and two new characters were included in the analysis. Three synapomorphies support the sister-group relationships of *Pamizinsaurus* : a long central region of the pterygoid, the narrowing of the posterior end of the interpterygoid vacuity, and a small or absent retroarticular process (the first two characters not known in eilenodontines). The long central region of the pterygoid in *Palaeopleurosaurus*, the narrow posterior end of the interpterygoid vacuity in *Brachyrhinodon* and *Polysphenodon*, and the small retroarticular process in *Homoeosaurus* are interpreted as convergence or parallelism.

Pamizinsaurus may have a posterodorsal process of the premaxilla, although the actual connection of the process to the bone is not known, leaving the character dubious. This feature has been considered to be a very important synapomorphic (and diagnostic) character for *Clevosaurus* (Wu 1994). If present, *Pamizinsaurus* might be placed within this genus. In spite of this, an extra analysis coding the posteromedial process of the maxilla as present (state 1), gave identical results to those described above (Appendix 2.2), and the inclusion of *Pamizinsaurus* within *Clevosaurus* is not supported. According to this hypothesis, the posterodorsal process of the premaxilla is convergent in the two taxa.

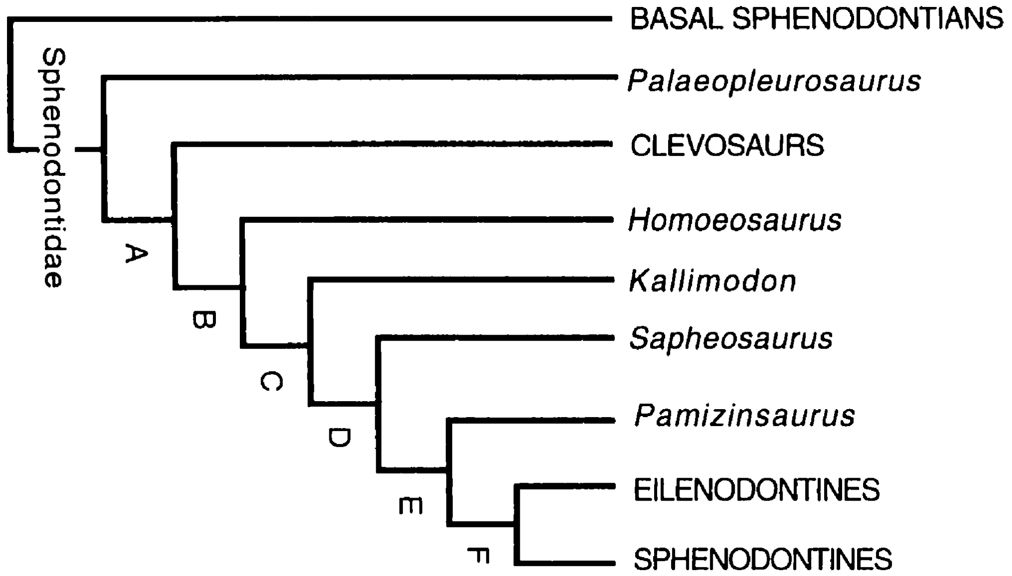
PALEOECOLOGICAL SIGNIFICANCE

The presence of osteoscutes is an unique feature among sphenodontians. Its pattern is strikingly similar to the dermal osteoscutes of helodermatids. In both taxa, osteoscutes are rounded, anteroposteriorly elongated, and aligned in transversal rows (somewhat diagonal on the lateral presacral region). The osteoscutes of the neck region are small and

TABLE 4. Character states for rhynchocephalians. Abbreviations: 0 = primitive; 1 and 2 = derived states; ? = unknown; N = not applicable; V= variable (0 & 1).

Character	5	10	15	20	25	30	35	40	45	
Youngina	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Squamata	00V00	0V000	00001	00000	00000	00000	0000N	NN200	10000	00N
Gephyrosaurus	00000	00110	00011	00000	00100	00000	00001	00000	??001	000
Diphydontosaurus	10000	10100	00011	00000	01100	VV000	01001	0000?	1?001	000
Planocephalosaurus	00000	10110	00010	00000	10110	11001	02011	00111	10001	001
Palaeopleurosaurus	01000	10011	12001	01000	11110	21101	02121	10211	10001	011
Polysphenodon	20??1	11000	00010	0?100	??1?0	21101	?2111	1?1??	?1?0?	020
Brachyrhinodon	21111	11000	00010	00?00	11110	21101	02111	1?1??	?000?	020
Clevosaurus hudsoni	11111	11001	00010	00100	11110	21101	02121	11111	10100	111
C. bairdi	21111	11001	00011	00100	11110	2110?	02121	1?111	??110	1??
C. petilus	11111	110?0	0001?	01100	11110	2110?	?2?21	1111?	??100	111
C. mcgilli	21111	110?0	0101?	10100	11110	21101	02121	1111?	??110	111
Homoeosaurus	00001	10000	0V110	10100	11111	21101	02121	1?211	21001	001
Kallimodon	010?1	1?001	11110	10100	11110	21101	02121	1?211	20001	001
Sapheosaurus	11001	?0001	11110	10??0	11110	NNNNN	0N1NN	?NNN1	2?0?1	001
Eilenodon	?????	?????	?????	??11	?1111	2111?	??11	???1?	?????	???
Toxolophosaurus	?????	?????	?????	???11	1111?	21111	0??11	???1?	?????	???
Cynosphenodon	?????	?????	?????	???10	1?11?	21101	121?1	???1?	?????	???
Sphenodon	11101	11001	11110	11110	11111	21101	12111	11212	10001	021
Pamizinsaurus	?????	?????	?????	?1?00	11111	21?01	02??1	1??1?	?????	?2?

Fig. 10. Hypothesis of sister-group relationships of *Pamizinsaurus tlayuaensis* obtained by using the branch-and-bound search algorithm of PAUP (Swofford 1993) and the data matrix of Reynoso (1996; see Appendix 2.1). All characters are unordered. Tree description: tree length = 91; consistency index = 0.648; retention index = 0.787. Apomorphy list (only unambiguous characters): **Sphenodontidae**: broad mandibular symphysis, pronounced coronoid process, dental regionalization, flanges on dentary teeth, broad anterior contact between pterygoid bones. **A**: broad posterior process of the maxilla, pterygoid precluded from the suborbital fenestra, flanges on palatine tooth row. **B**: parietal foramen anterior to or level with anterior margin of supratemporal, palatine wide posteriorly, prominent posterior process of ischium. **C**: narrow parietal table, parietal crest absent. **D**: length of antorbital region between one fourth and one third of skull length. **E**: elongate central region of pterygoid, reduced retroarticular process, greately constricted posterior passageway of interpterygoidal vacuity. **F**: propalinal jaw motion. **Clevosaurs**: length of antorbital region one fourth or less of skull length, length of lower temporal fenestra more than one fourth of skull length, reduced premaxillary process of maxilla, narrow and elongated dorsal process of jugal. A full description of the tree is given in Appendix 2.3.



BASAL SPHENODONTIANS
Palaeopleurosaurus
CLEVOSAURS
Homoeosaurus
Kallimodon
Sapheosaurus
Pamizinsaurus
EILENODONTINES
SPHENODONTINES
Sphenodontidae
A
B
C
D
E
F

they are irregularly enlarged on the limbs (Bogert and Martín del Campo 1956). Obvious differences are the presence of small irregular granular scales between the bead-like scales (not preserved in *Pamizinsaurus*), and the absence of dumbbell-shape scales in *Heloderma*. No other known lizard shares a similar scutellation pattern or beaded scales.

No function other than protection has been given for the dermal armor of *Heloderma*. Arrington (1930) stated that the thick armor of *Heloderma* prevents the penetration of the fangs of rattlesnakes. Its efficiency against other larger predators. however, is not well documented. Several observations by Bogert and Martín del Campo (1956) describes the defensive reaction of the "gila monsters" after being attacked and bitten by dogs, but the injury caused by their teeth is not detailed. Birds of prey, coyotes and badgers are possible, but undocumented, predators of helodermatids.

The interaction of *Pamizinsaurus* with poisonous snakes is very improbable. Although snakes were already present in the Early Cretaceous, (Cuny et al. 1990; Rage and Richter 1994), colubroids did not make their appearance until the Eocene (Rage et al. 1992). In spite of this, *Pamizinsaurus* might have had interacted with other poisonous animals, and a solid armor could have played a similar role against small predators as in *Heloderma*.

Convergent patterns of dermal armor may also indicate similar habitats. *Heloderma* inhabits mainly semi-arid lands with scattered vegetation or areas with marked seasonality of rainfall. Even though there is not an obvious correlation between having a thick protection and a dry environment, there is certainly more risk of predation in open habitats. The armor in *Pamizinsaurus* could have been necessary for survival if it were affected by similar environmental conditions as *Heloderma*.

The fauna of the Tlayua Quarry bears fishes representatives of several different environments: shallow water elopids; surface clupeids; coral reef pycnodonts; and benthonic echinoderms, mollusks, and decapods. The presence of *Pamizinsaurus* undoubtedly introduces a fully terrestrial organism to the system. It was presumably washed out from the terrestrial platform into an aquatic deposit. This does not contradict any depositional environment setting proposed (Applegate et al. 1984; Pantoja-Alor 1992). However, the dermal structure of *Pamizinsaurus* supports a relatively dry terrestrial climate with seasonal rain that contrast with the warm and humid climate suggested by Pantoja-Alor (1992).

STRATIGRAPHICAL SIGNIFICANCE

Fossil sphenodontians are known from the Late Triassic to the Early Cretaceous. Before the discovery of *Pamizinsaurus*, the latest known fossil sphenodontian was *Toxolophosaurus cloudi* from the Kootenai Formation (Barremian) Silver Bow County, Montana, of North America (Olson 1960). *Pamizinsaurus* is now the latest known fossil sphenodontian extending the fossil record into the Albian. No other sphenodontians are known between *Pamizinsaurus* and the extant *Sphenodon* except for the subfossil referred as *Sphenodon diversum* (Colenso 1886) from the North Island of New Zealand.

CONCLUSIONS

The fossil record of sphenodontians is still very incomplete, and much remains to be learned. The morphology of the sphenodontians was very conservative during the Late Triassic. However, it is clear that in the Late Jurassic and Early Cretaceous a now well documented radiation occurred. Sphenodontians inhabiting different environments diverged from the primitive sphenodontian type, and produced several distinct body morphologies. Long bodied sphenodontians appeared by the early Jurassic (Carroll 1985a) and continued to evolve up to the end of the Jurassic. Terrestrial herbivorous sphenodontians with a complex chewing apparatus and stout marine sphenodontians appeared in the Late Jurassic. From the Early Cretaceous a beaded sphenodontian is now known. The lack of fossils after the Early Cretaceous may indicate the end of this remarkable diversification.

Appendix to chapter 2

Appendix 2.1

List of Characters

Character 1-42 corresponds to those of Reynoso (1996). Character 43, 44, 45, and 46 correspond to characters 1, 4, 9, and 33 of Sues et al. (1994) respectively. Character 33 of Sues et al. (1994): suborbital fenestra enclosed by more than two bones (0), enclosed only by the ectopterygoid and palatine (1), was rephrased as: Maxilla included in suborbital fenestra (0); excluded (1). As previously written Sues et al.'s character 32 becomes redundant. The number or bones entering into the suborbital fenestrae (character 33), includes the pterygoid to which character 32 makes reference. Characters 47 and 48 are new. In the analysis, *Cynosphenodon* was merged with *Sphenodon* (sphenodontines), and *Eilenodon* with *Toxolophosaurus* (eilenodontines) becoming characters 20, 29, 31, and 35 uninformative, therefore ignored. Characters used in rhynchocephalian phylogeny are:

1.- Antorbital region /skull length: one-third or more (0), between one-fourth and one-third (1), one fourth or less (2)
2.- Supratemporal fenestra /skull length: one-fourth or less (0), more than one-fourth (1)
3.- Lower temporal fenestra/skull length: one-fourth or less (0), more than one-fourth (1)
4.- Premaxillary process of maxilla: elongate (0), reduced (1)
5.- Posterior portion of maxilla: gradually tapering off or very narrow (0), broad (1)
6.- Lacrimal: present (0), absent (1)
7.- Dorsal process jugal: broad and short (0), narrow and elongated (1)
8.- Frontals: separated (0), fused (1)
9.- Parietals: separated (0), fused (1)

10.- Parietal width between supratemporal passages: broader than interorbital width (0), narrower (1)

11.- Parietal crest: absent (0), present (1)

12.- Posterior edge of parietal: greatly incurved (0), slightly incurved (1) or convex (2)

13.- Parietal foramen position: posterior to the anterior margin of supratemporal fenestra (0), at level or anterior (1)

14.- Lower temporal bar: aligned with the maxillary tooth row (0), bowed away beyond the limit of the abductor chamber (1)

15.- Lower temporal bar: complete (0), incomplete (1)

16.- Palatine: tapers posteriorly (0), becomes relatively wide (1)

17.- Central region of pterygoid between three rami: short (0), elongate (1)

18.- Pterygoid: borders suborbital fenestra (0), precluded from the suborbital fenestra (1)

19.- Jaw motion: orthal (0), propalinal (1)

20.- Mandible: narrow (0), deep (1)

21.- Mandibular symphysis breadth: slender (0), broad (1)

22.- Mandibular foramen small (0), big (1)

23.- Posterior process of dentary: ends anterior to coronoid process (0), ends posteriorly (1)

24.- Coronoid process: absent or weak (0), pronounced (1)

25.- Retroarticular process size: pronounced (0), reduced (1)

26.- Dental implantation: pleurodont (0), a degree of acrodont (1), fully acrodont (2)

27.- Tooth replacement: alternate (0), addition of teeth at the back of the jaw (1)

28.- Lateral and medial wear facets on marginal teeth: absent or poorly developed (0), well established (1)

29.- Marginal teeth breadth: equal to length (0), mediolaterally expanded (1)

30.- Dental regionalization with small juvenile teeth at anterior end of maxilla and dentary: absent (0), present (1)

31.- Anterior caniniform tooth on dentary and maxilla: absent (0), present (1)

32.- Number of premaxillary teeth: more than seven (0), seven to four (1), three or less (2)

33.- Premaxillary teeth: separated (0), forming a chisel-like structure in mature (1)

34.- Posterior maxillary tooth shape: simple cones (0), with posteromedial flanges in at least one tooth (1), with extensive flanges (2)

35.- Lateral palatine tooth row: small (0), enlarged (1)

36.- Number of palatine tooth rows: more than one (0), a single lateral tooth row (1)

37.- Flanges on palatal tooth row: absent (0), present on some (1)

38.- Number of pterygoid tooth rows: three or more (0), two rows (1), one or absent (2)

39.-Anterolateral flanges on dentary teeth: absent (0), present on at least one tooth (1)

40.- Posterior process of second sacral rib: small (0), prominent (1), absent (2)

41.- Ischium: uninterrupted posterior edge extending from the acetabulum to the median symphysis (0), posterior process on posterior margin (1), prominent posterior process present (2)

42.- Limb proportions with respect to the presacral column: humerus ≤ 0.20, tibia ≤ 0.25, femur < 0.30, radius < 0.15 (0); all measures greater than these values (1)

43.- Premaxilla posterodorsal process: absent (0), present (1)

44.- Prefrontal-jugal contact: absent (0), present (1)

45.- Supratemporal: present as a separated element (0), absent or fused to the squamosal (1)

46.- Suborbital fenestra lateral margin: maxilla on margin of suborbital fenestra (0) ectopterygoid contact palatine excluding the maxilla from the suborbital fenestra (1)

New characters

47.- Posteromedial processes of pterygoid separated one from the other, leaving the interpterygoid vacuity widely open posteriorly (0), posterior opening of the interpterygoid vacuity as wide as the vacuity (1), vacuity almost closed by the posteromedial processes of the pterygoids (2).

State (1) in *Palaeopleurosaurus*, and *clevosaurs*; further transformed in *Polysphenodon* and *Brachyrhinodon*. Unknown in *Clevosaurus bairdi*, Eilenodontines, and *Cynosphenodon*.

48.- Anterior contact between pterygoid bones: small or absent (0); broad contact (1). Derived condition in *Planocephalosaurus*, *Palaeopleurosaurus*, *Clevosaurus*, *Homoeosaurus*, *Kallimodon*, *Sapheosaurus*, and *Sphenodon*. Unknown in *Clevosaurus bairdi*, Eilenodontines, and *Cynosphenodon*.

Appendix 2.2

Analysis and Results

ANALYSIS 1.- Posteromedial process of premaxilla coded as (?)

```
Data matrix has 18 taxa, 48 characters
All uninformative characters ignored
Valid character-state symbols: 012
Missing data identified by '?'
All characters unordered

Designated outgroup taxa:
   Youngina
   Squamata

Current status of all characters:
    Characters 20, 29, 31,  and 35 are uninformative (ignored)

Branch-and-bound search settings:
   Initial upper bound: unknown (compute via stepwise)
   Addition sequence: furthest
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

Branch-and-bound search completed:

   Shortest tree found = 91
   Number of trees retained = 2

Tree description:

   Unrooted tree(s) rooted using outgroup method
   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree length = 91
Consistency index (CI) = 0.648
Homoplasy index (HI) = 0.418
Retention index (RI) = 0.787
Rescaled consistency index (RC) = 0.510

Consensus tree description:

Tree length = 92
Consistency index (CI) = 0.630
Homoplasy index (HI) = 0.424
Retention index (RI) = 0.776
Rescaled consistency index (RC) = 0.489
```

```
/----------------------------------------------------- OUTGROUP
|     /----------------------------------------------- Gephyrosaurus
|     +----------------------------------------------- Diphydontosaurus
|     |    /------------------------------------------ Planocephalosaurus
\----32    |    /------------------------------------- Palaeopleurosaurus
      |    |    |                               /----- Polysphenodon
      \---31    |                    /---------19----- Brachyrhinodon
           |    |                    |          /----- Clevosaurus hudsoni
           \---30    /--------------23    /----20----- C. petilus
                |    |               \---22     /----- C. bairdi
                |    |                    \----21----- C. mcgilli
                \---29     /-------------------------- Homoeosaurus
                     |     |    /--------------------- Kallimodon
                     \----28    |    /---------------- Sapheosaurus
                           \---27    |          /----- Eilenodontines
                                \---26    /----24----- Sphenodontines
                                     \---25----------- Pamizinsaurus

Statistics derived from consensus tree:

     Component information (consensus fork) = 15 (normalized = 0.938)
     Nelson-Platnick term information = 93
     Nelson-Platnick total information = 108
     Mickevich's consensus information = 0.611
     Colless weighted consensus fork (proportion max. information) = 0.711
     Schuh-Farris levels sum = 550 (normalized = 0.674)
     Rohlf's CI(1) = 0.869
     Rohlf's -ln CI(2) = 42.194 (CI(2) = 4.74e-19)

Apomorphy lists: (*Ambiguous characters)

Node 32: 6*, 8, 9*, 14, 23, 45
Gephyrosaurus: 6(0)*
Diphydontosaurus: 1, 9(0)*, 22, 32
Node 31: 15(0)*, 21, 24, 26*, 27, 30, 32(2), 34*, 38*, 39, 40, 48
Node 30: 2, 8(0), 22, 26(2)*, 28, 33, 34(2)*, 36, 38(2)*, 47*
Palaeopleurosaurus: 10, 11, 12(2), 14(0), 15*, 17
Node 29: 5, 9(0)*, 18, 37
Node 23: 1(2), 3, 4, 7, 38*, 45(0)*, 46*
Node 19: 34, 47(2)*, 48(0)
Polysphenodon: 2(0), 42
Node 22: 43
Node 20: 1
Clevosaurus hudsoni: 10
C. petilus: 17
Node 21: 15*, 44
C. bairdi: 10
C. mcgilli: 12, 16
Node 28: 12*, 13, 16, 41(2), 47(0)*
Homoeosaurus: 2(0), 25, 42
Node 27: 10, 11
Node 26: 1, 34*
Node 25: 3*, 7*, 17, 25, 40(2)*, 41*, 47(2)
Node 24: 19
```

ANALYSIS 2.- Posteromedial process of premaxilla coded as (1)

```
   Shortest tree found = 92
   Number of trees retained = 2

Tree description:
   Unrooted tree(s) rooted using outgroup method
   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree length = 92
Consistency index (CI) = 0.641
Homoplasy index (HI) = 0.424
Retention index (RI) = 0.781
Rescaled consistency index (RC) = 0.501

Strict consensus of 2 trees:

/---------------------------------------------------- OUTGROUP
|     /---------------------------------------------- Gephyrosaurus
+     +---------------------------------------------- Diphydontosaurus
|     |    /----------------------------------------- Planocephalosaurus
\-----+    |    /------------------------------------ Palaeopleurosaurus
      |    |    |                              /----- Polysphenodon
      \----+    |                    /---------+----- Brachyrhinodon
           |    |                    |         /----- Clevosaurus hudsoni
           \----+    /---------------+    /----+----- C. petilus
                |    |               \----+    /----- C. bairdi
                |    |                    \----+----- C. mcgilli
                \----+     /------------------------- Homoeosaurus
                     |     |    /-------------------- Kallimodon
                     \-----+    |    /--------------- Sapheosaurus
                           \----+    |         /----- Eilenodontines
                                \----+    /----+----- Sphenodontines
                                     \----+---------- Pamizinsaurus
```

CHAPTER 3

AN UNUSUAL AQUATIC SPHENODONTIAN FROM THE TLAYUA FORMATION (ALBIAN), CENTRAL MÉXICO

AN UNUSUAL AQUATIC SPHENODONTIAN FROM THE TLAYUA FORMATION (ALBIAN), CENTRAL MÉXICO

INTRODUCTION

Sphenodontians are a very well known group of lepidosaur reptiles today represented by the single genus *Sphenodon*, inhabiting the coast of small islands around New Zealand. Since their exclusion from the Agamidae and the recognition that they belong to a different reptile "Order" (Günther 1867), they have been considered the perfect ancestral morphotype for lizard-like forms, thereby gaining their status as living fossils (Broom 1925; Romer 1956). On the base of current phylogenetic hypotheses, it is now known that *Sphenodon* is not primitive but a derived form in which the apparently primitive presence of a complete lower temporal bar was acquired secondarily within sphenodontian evolution (Whiteside 1986; Wu 1994; Reynoso 1996). The fossil record of sphenodontians is patchy, and although more than 30 species are known, the number of representatives and specimens per geological period is limited. They are known from the Middle Triassic up to the Early Cretaceous but no fossils are known from that time until the Recent. The early rhynchocephalian *Gephyrosaurus* (Evans 1980, 1981) and to a lesser degree the sphenodontian *Diphydontosaurus* (Whiteside 1986) still show many primitive lepidosaur characters. The typical sphenodontian morphology, very similar to that of *Sphenodon*, was acquired by other Late Triassic genera. During the Jurassic, sphenodontians invaded different environments and evolved new morphologies. They modified their skeleton, altering the typical sphenodontian *Bauplan* and become a relatively diverse group. Unfortunately, their limited fossil record prevents a complete understanding of these forms and their radiation, but a few good representatives show the broad spectrum of types. These included herbivores (Throckmorton et al. 1981; Rasmussen and Callison 1981), and obligatorily aquatic forms such as pleurosaurs which show in an extreme example of body transformation (Fabre 1974; Carroll 1985a; Carroll and Wild 1995). Such a wide range of behaviors is extremely rare in lepidosaurs (Szarski 1963; Ostrom 1963; Seymour 1982).

The Albian deposits of Tepexi de Rodríguez have produced a good number of reptiles including crocodiles, turtles (Espinosa-Arrubarrena and Applegate 1990), pterosaurs (Cabral and Applegate 1993), and two lizards (see Chapters 4 and 5). Very recently, the beaded-sphenodontian *Pamizinsaurus tlayuaensis* was described from these deposits (Chapter 2; Reynoso, in press). It shows unique rounded osteoscutes distributed along the body, a possible specialization for protection in (dry) open environments. In this chapter, a second sphenodontian, showing a unique morphology possibly related to an aquatic mode of life and herbivory, is described. Its body shape is quite different from that of pleurosaurs and the tooth morphology differs from all other known sphenodontians. Knowledge of this sphenodontian will add new information about the degree of skeletal plasticity and morphological diversity gained among these lepidosaurs by the end of the Early Cretaceous.

SYSTEMATIC PALEONTOLOGY

SPHENODONTIA Williston 1925

SPHENODONTIDAE Cope 1870

Genus ANKYLOSPHENODON, gen. nov.

Type species- *A. pachyostoseus*

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

Diagnosis- As for the type and only known species.

ANKYLOSPHENODON PACHYOSTOSEUS, sp. nov.

Figs. 11-18

Holotype- Instituto de Geología, Universidad Nacional Autónoma de México. Cat. No. IGM 7441 (Fig. 11). Crushed, anterior portion of a complete skeleton.

Referred material- IGM 7442: Skull and proximal elements of the right forelimb split in half and preserved in part and counterpart blocks; IGM 7443: Almost complete postcranial skeleton; IGM 7444: Disarticulated postcranial skeleton; IGM 7445: Crystallized skull associated with some of the anterior portion of the postcranial skeleton; IGM 7446: Presacral vertebrae series associated with ribs. IGM 7447: Disarticulated postcranial skeleton.

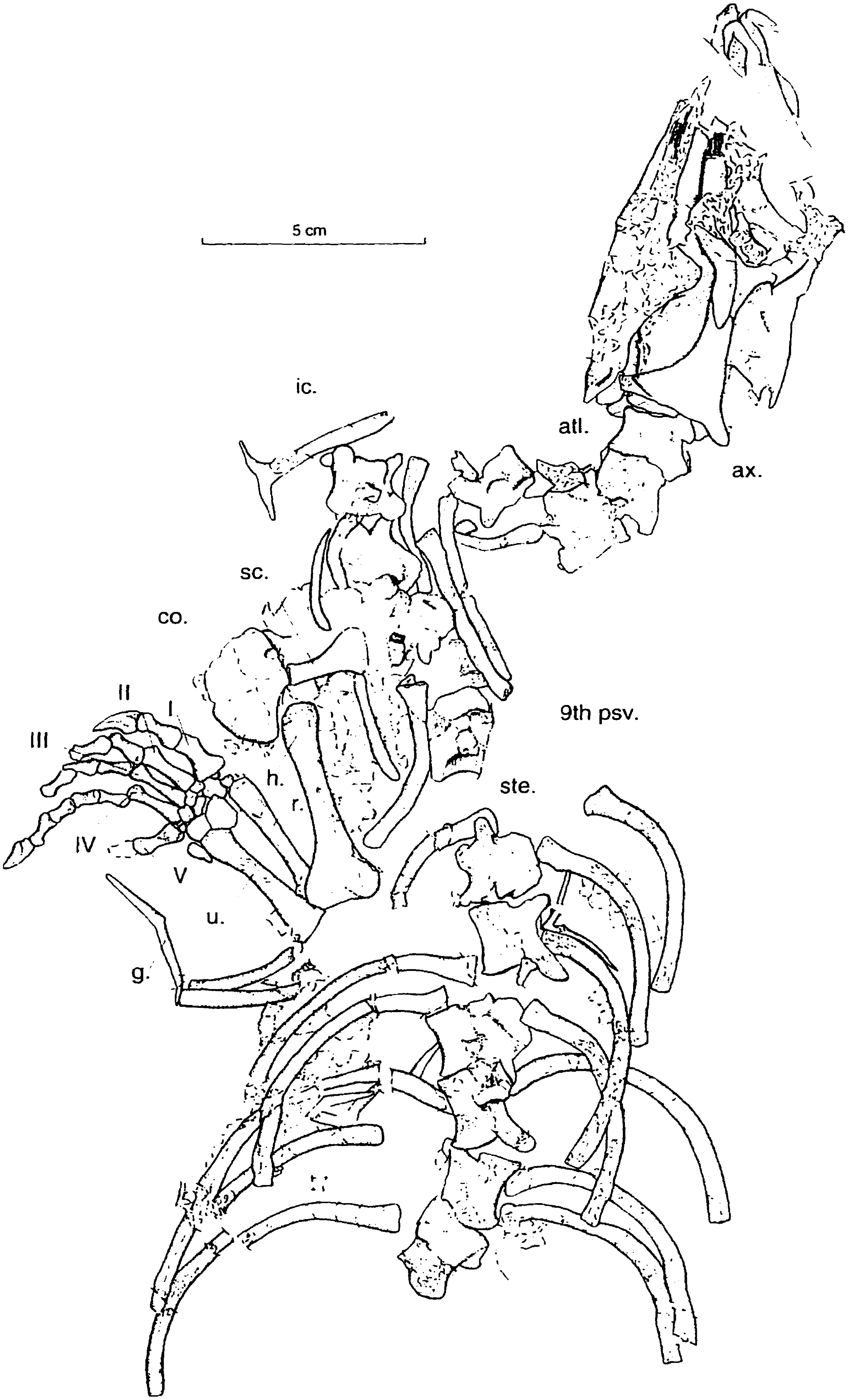
Etymology- In reference to the pachyostotic ribs and vertebrae.

Locality- Tlayua Quarry, 2 Km South East of the Colonia Morelos, near Tepexi de Rodríguez, Puebla, México. The Holotype (IGM 7441) was collected in Loc. No. IGM 2280-NSF#3; IGM 7443, IGM 7445, and IGM 7446 in Loc. No. IGM 370 Cantera Tlayua-Aranguty; and IGM 7442, IGM 7444, and IGM 7447 in Loc. No. IGM 2432-Cantera Tlayua-IGM (IGM 7444 in level Z-V and IGM 7447 in level Z-XXIII).

Horizon- Middle Member of the Tlayua Formation (Pantoja-Alor 1992). Early Cretaceous. Middle or Late Albian (Seibertz and Buitrón 1987).

Diagnosis- Stoutly constructed sphenodontian with postorbital skull region enlarged; upper temporal bar formed mainly by the squamosal; teeth attached deep within the lower jaw; continuous tooth growth; no dental regionalization; no flanges on dentary teeth; short retroarticular process; pachyostotic vertebrae with swollen zygapophyses; zygapophyses with rounded articulating surfaces oriented in the horizontal plane; no thoracolumbar intercentra; no autotomous septum in caudal vertebrae; pachyostotic thoracic ribs; second sacral rib with a broad posterior process; first digit distinctively broad with an enlarged ungual; short posterior process on ischium.

Fig. 11. *Ankylosphenodon pachyostoseus* gen. et sp. nov. (IGM 7441). Skull, anterior portion of the presacral vertebral column, and left fore limb of the holotype of as preserved.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DESCRIPTION

Ankylosphenodon pachyostoseus is known from several partial skeletons exposed in bas relief on one surface of the block rock, as well as one specimen that was extracted completely from the matrix. All skeletons are preserved in dorsal aspect but there is a fragment of the thoracolumbar portion of a skeleton that does give information about the ventral morphology. Unfortunately, no skull is in good condition. Although three of the seven partial skeletons have skulls, none of them show anatomical detail. This is very unfortunate since the establishment of the phylogenetic relationships of sphenodontians is based primarily on cranial morphology. Of the three skulls preserved, one is split in half, other one is severely damaged, and the last one is crystallized. In spite of this, very interesting anatomical information can be obtained.

Size and proportions of the skeletons are given in Table 5. The skull and limb proportions in relationship to the presacral vertebral column length cannot be established with certainty because no complete presacral series is preserved. The length of the presacral vertebrae column (PSVC) was reconstructed scaling the width of the distal end of the humerus and the length of the 19th vertebrae, assuming the presence of 24 presacral vertebrae, the typical sphenodontian vertebral number as indicated by *Sphenodon*, *Homoeosaurus*, and *Sapheosaurus*. IGM 7442 is the largest specimen and IGM 7443 is the smallest. The only dimension in common in all the specimens is the width of the distal end of the humerus which ranges from 13.1 mm to 19.2 mm. The holotype is about average size.

Skull and lower jaw

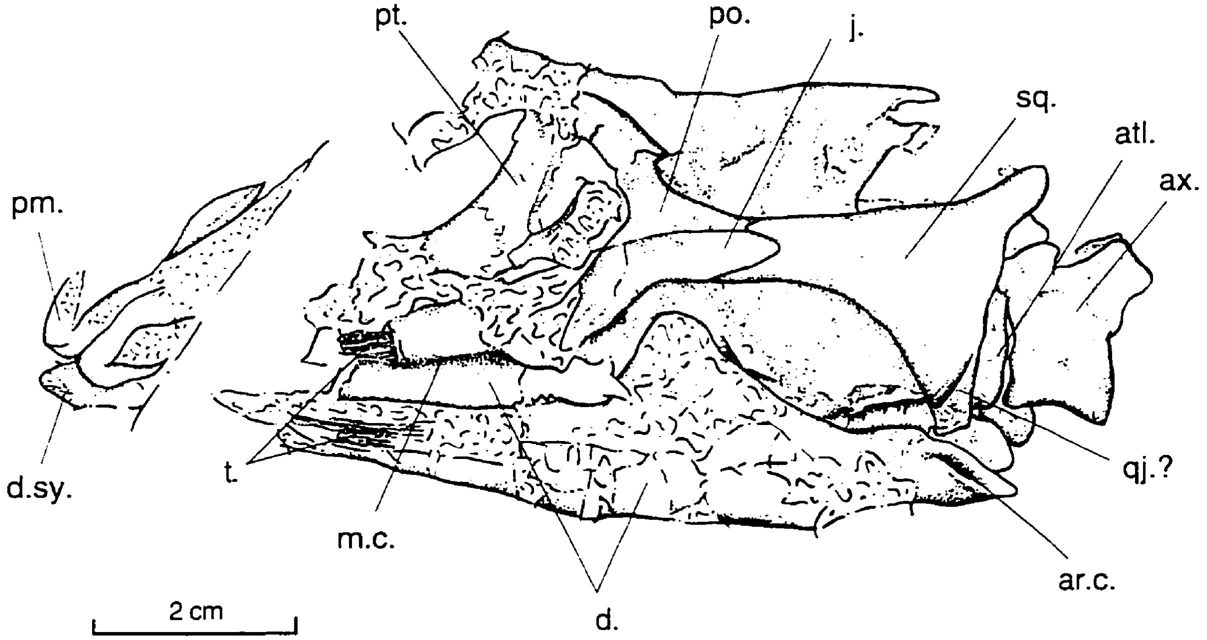
The poor preservation of the skull prevents the establishment of skull proportion. By comparing the length of the lower jaw, assuming it to be equal to the skull length (as in other sphenodontians), the upper temporal fenestra extends about half of the total skull length. The upper temporal arch is enlarged much as in the aquatic genus *Sapheosaurs* (Fig. 12). It is formed primarily by a distinctively broad squamosal that extends to the anterior half of the upper temporal fenestra, forming an anterior notch into which the posterior end of a long and slender jugal fits. The level of the dorsal margin of the jugal is indicated by an anterior notch in the squamosal and a faint suture with the postorbital. The postorbital extends posteriorly, almost reaching the posterior end of the jugal. The lower temporal bar is missing but might be broken. In the holotype, the snout and skull table are missing and only the internal bone exposed. The separated premaxillae are the only elements distinguished but provide no information of the postnarial articulation or dental structure. There is no detail of the suspensorium. A suture delimits a small bone posterior to the quadrate process of the squamosal that is identified as a quadratojugal.

The lower jaw is typical sphenodontian but robustely constructed. It is dorsoventrally broadened on its medial portion and has an enlarged coronoid process that emerges straight dorsally from the posterior end of the tooth series. Anteriorly, the lower jaw becomes more slender, ending with an obliquely oriented symphysis. The posterior process of the dentary extends beyond the coronoid bone, surrounding dorsally and laterally an enlarged surangular foramen. Other than the dentary, no detailed structure is preserved. The articular condyle is large and elongated anteroposteriorly suggesting the possible presence of propalinal jaw action, also indicated by wear marks in the tooth and dentary surfaces (Fig. 13B).

Dentition

External tooth morphology is only preserved on the posterior end of the dentary tooth row in IGM 7422 and at the tip of the dentary in IGM 7445 (Figs. 13B, C). Superficially, the teeth seems to be acrodont, but an opportune longitudinal breakage of lower jaws of the holotype and IGM 7422 shows that they extends deep into the dentary as far as the upper margin of the Meckelian canal. This condition is unique for

Fig. 12. *Ankylosphenodon pachyostoseus* gen. et sp. nov. (IGM 7441). Detail of the skull of the holotype of as preserved.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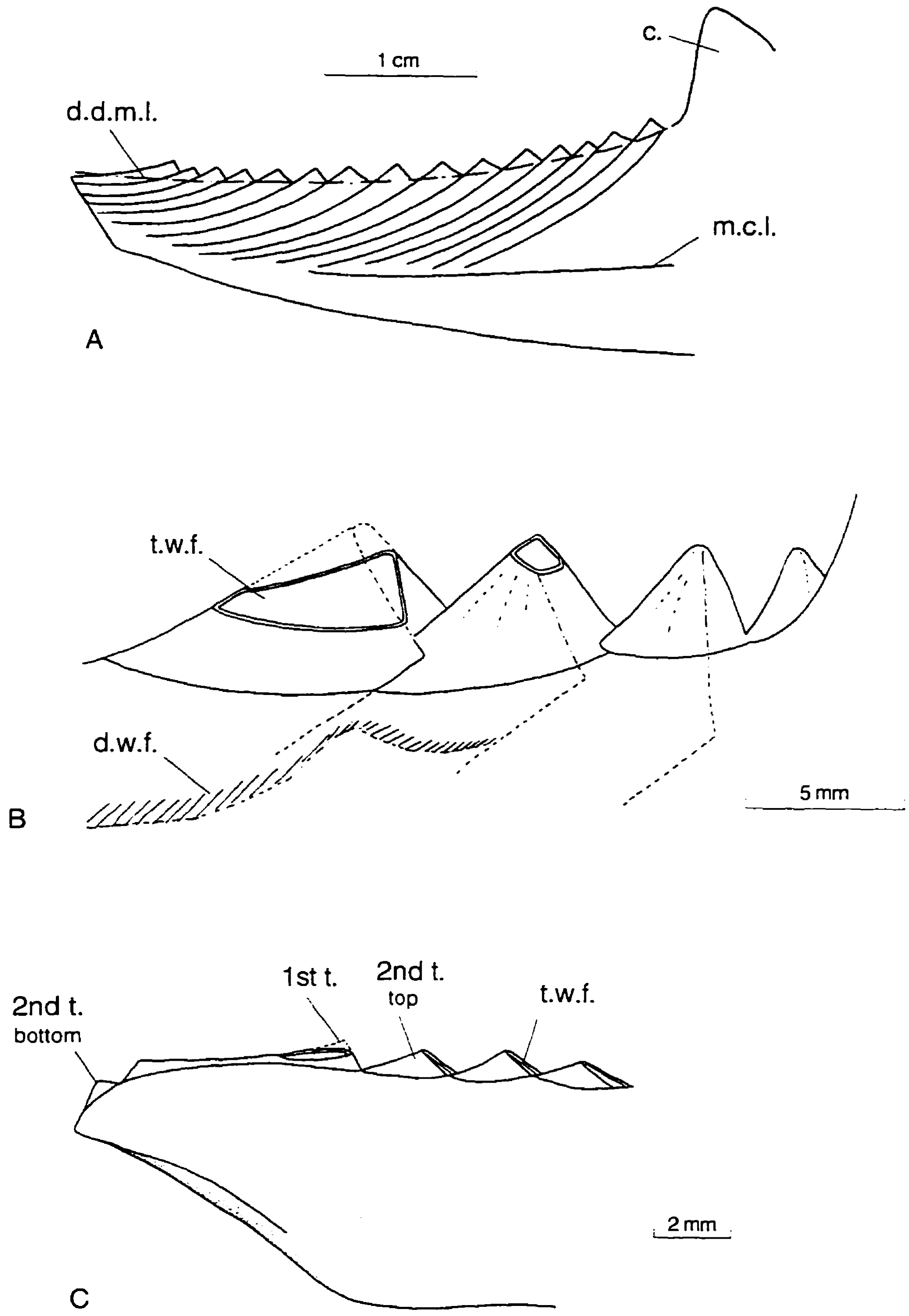
ar.c.
2 cm

Fig. 13. Diagrammatic reconstruction of the tooth series. **A.** Lower jaw longitudinal section. **B**. Lateral view of the posterior part of the dental series showing wear marks on teeth and dentary. **C**. Symphysial region of the dentary in medial view. A. and B from IGM 7442; C. from IGM 7445. Figure B is inverted.

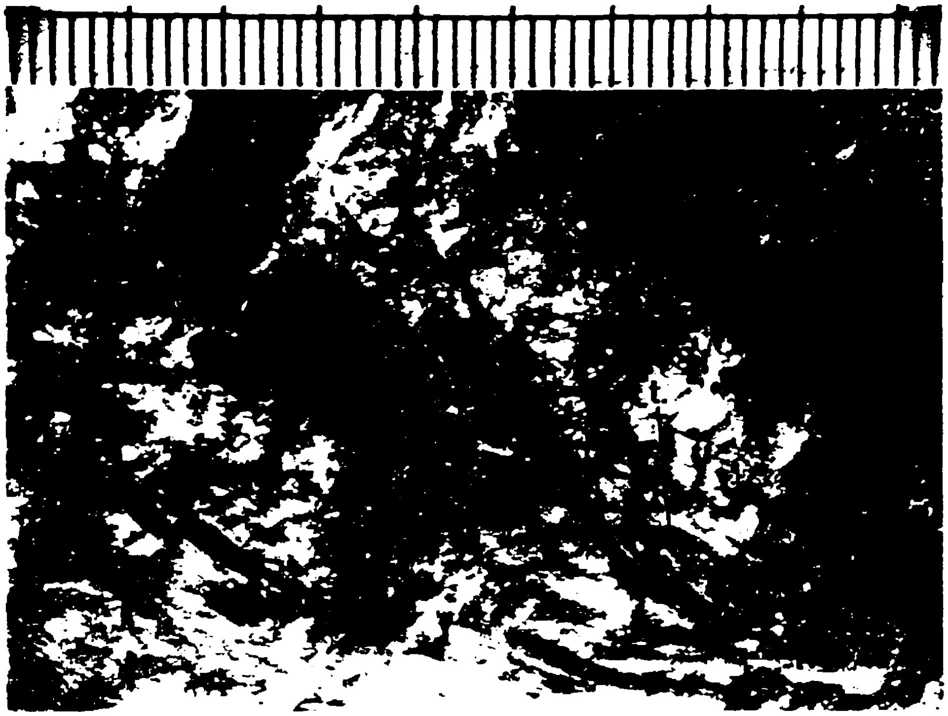

c.
1 cm
d.d.m.l.
m.c.l.
A
t.w.f.
d.w.f.
B
5 mm
2nd t.
bottom
1st t.
2nd t.
top
t.w.f.
2 mm
C

sphenodontians and resembles the ankylothecodont condition of rhynchosaurs (Benton 1984a). Fraser and Shelton (1988) have shown that some sphenodontians (e.g. *Planocephalosaurus*), have teeth enclosed in a shallow groove within the lower jaw. However, the condition in *Ankylosphenodon* is not similar to *Planocephalosaurus*, but rather the teeth are ankylosed to the jaw to an extreme degree.

The structure of the teeth is unique among sphenodontians. Externally, they look like triangular, rather small teeth; but internally, each tooth extends anteroventrally as laterally compressed cylinders overriding the following tooth and forming an extensive, obliquely oriented tooth plate (Figs. 13, 14). Each tooth is composed of an inverted canal of hard brownish enamel surrounding a white layer of dentine. The ventral part of the teeth is open and each tooth rest on the surface of the following one along the imbedded portion. The last tooth rest directly over the dentary bone. At the tip of IGM 7442 and middle portion of the dentary in the holotype, it is clear that the tooth plate is completely included within the dentary and that it is not exposed medially, suggesting that only the tips of the teeth were used for mastication. In IGM 7442 the medial enamel surface is broadly exposed and show some small microestriations, more conspicuous at the anterior part of the jaw. On a major wear surface at the tip of the dentary, the anteroventral part of the most anterior tooth is also exposed in cross section and it could have been used for mastication all along its dorsal surface.

On the external portion of individual teeth, the enamel sheath surrounds each tooth except for the posterodorsal face in which the dentine is exposed. However, in the posterior teeth, known to be the last erupted of the tooth series in all sphenodontians (Harrison 1901; Robinson 1976), the posterior surface of the tooth is still covered with enamel. The lack of enamel on the posterior face of relatively older teeth suggest that it was already worn out. A major wear facet is present in the third tooth from the back of IGM 7442. Contrary to other sphenodontians in which wear tends to reduces tooth size, anterior teeth are always well exposed externally, remaining about the size of the posterior teeth.

Fig. 14. Detail of the internal structure of the tooth series as preserved in IGM 7442 of *Ankylosphenodon pachyostoseus* gen. et sp. nov. Scale in mm.



The absence of reduction in the exposed tooth surface in anterior teeth only can be explained by the existence of continuous tooth growth. This also explains the sole exposure of dentine in the posterodorsal surface of the tooth, so that the apex of individual teeth remains aligned at the same height in the tooth plate. Tooth growth has never been reported before in sphenodontians.

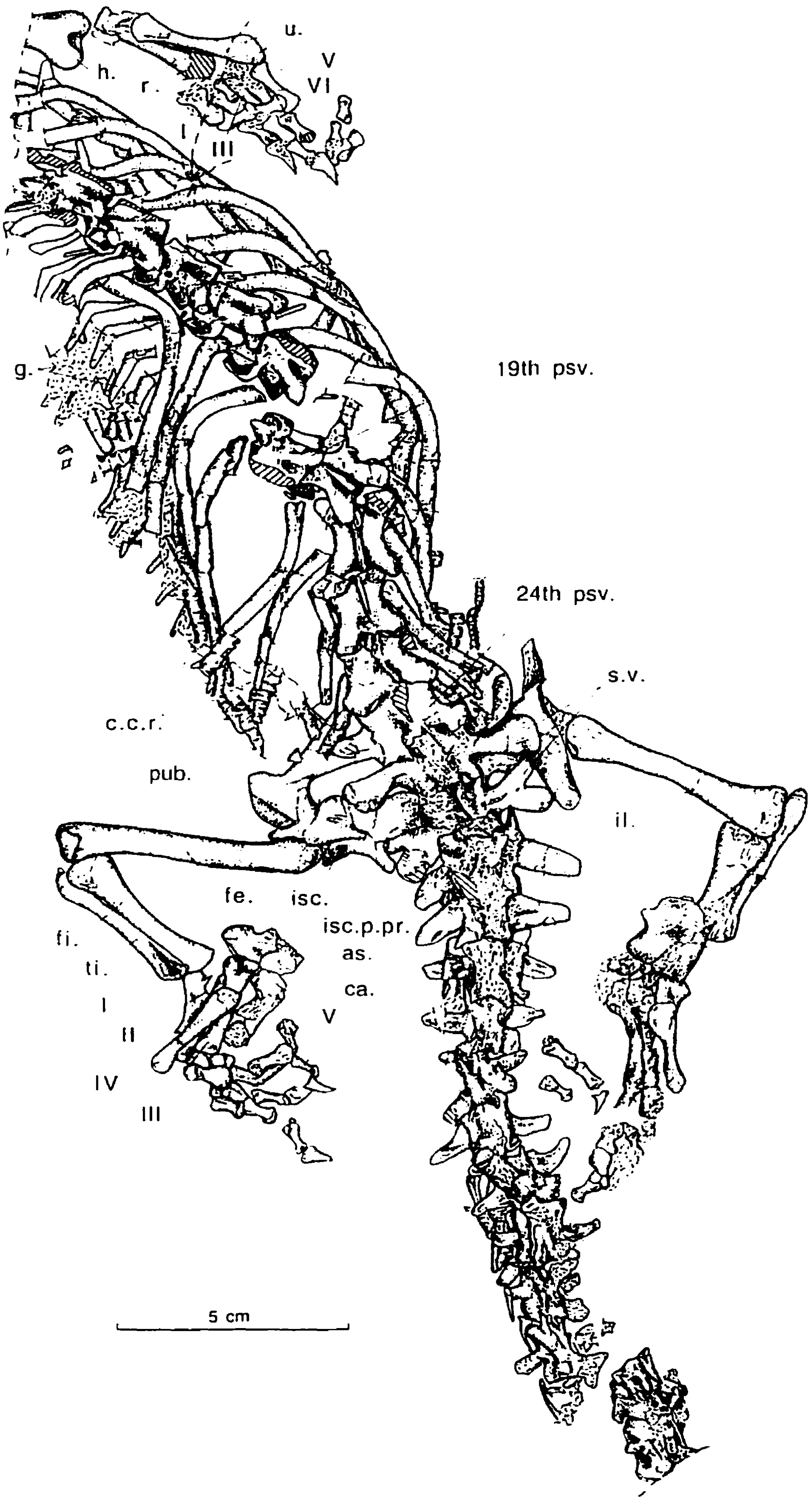
Anteroposteriorly oriented tooth wear marks are present laterally on the posterior end of the jaw and associated teeth. Wear has degraded extensively the enamel on the lateral surface of the fourth most posterior tooth. The wear mark extends into the dentary bone, exposing a good portion of the enamel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

Postcranial axial skeleton

The axial skeleton was reconstructed mostly from the holotype and IGM 7433 (Figs. 12 and 15). The total number of presacral vertebrae is unknown, even though all vertebrae are preserved between the two specimens. Because it is not possible to identify any point of reference to link the anterior and posterior counterparts from two different specimens, the presence of 24 presacral vertebrae was assumed according to the typical terrestrial sphenodontids count. In the overall reconstruction, the difference in size of the two specimens was compared through the width of the distal end of the humerus, and the length of the 19th vertebral centrum. The radius, ulna, and first metacarpal are other identifiable elements in common. However, they did not provide a consistent basis of comparison of the relative size. The extremely different values obtained by estimating the vertebral column length suggests the possibility of variation in limb length during ontogeny.

The holotype has 19 presacral vertebrae preserved, including a very small portion of the atlas mostly hidden behind the squamosal. IGM 7443 has vertebrae 14 to 24 plus a small posterior portion of vertebra 13. The number of cervical vertebrae is difficult to

Fig. 15. *Ankylosphenodon pachyostoseus* gen. et sp. nov. (IGM 7443). Posterior part of the presacral vertebral column, hind limbs and tail in a young specimen as preserved.


u.
V
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I
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24th psv.
s.v.
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isc.p.pr.
fi.
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I
II
V
IV
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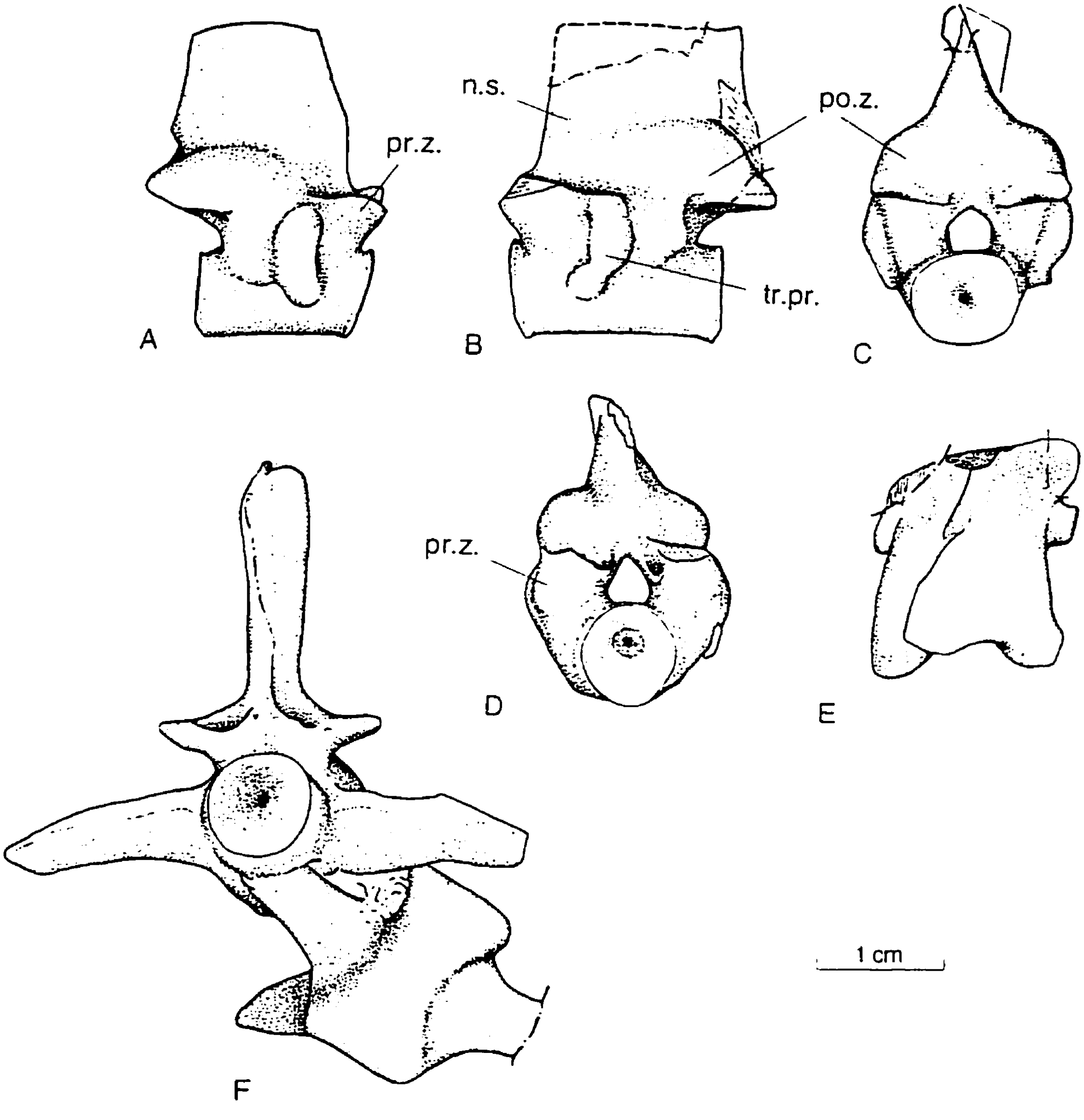
5 cm

establish. The orientation of the ribs can give some clue since it could be associated with a different condition of their ventral attachment. In the holotype, some anterior ribs point forward, but all remaining ribs were preserved pointing backwards. The similar orientation of the posterior ribs was probably caused by the restriction imposed by their association with the sternum and gastralia. If so, the first posteriorly oriented rib is the ninth suggesting that the eight anterior vertebrae were cervicals. This matches the number in *Sphenodon*.

The first well exposed vertebra is the robust axis, but no particular detail is preserved. In common with the axis, all cervical and thoracic vertebrae are remarkably massive. They increase in size posteriorly with the last presacral vertebrae being the largest of the series. In articulated specimens, vertebrae are compressed dorsoventrally obscuring the length of the neural spine. In isolated elements, the neural spine is large and square, extending all along the dorsal part of the neural arch (Fig. 16). Their bases are broad in anterior view. The neural arches are completely fused to the centrum with no trace of a suture. The centrum is amphicoelous and notochordal. It is rounded and cylindrical in cross section; the notochord canal is broad at the ends but restricted to a small perforation in the middle portion of the vertebrae (Fig. 16D). The massiveness of the vertebrae is caused primarily by the presence of uniquely enlarged zygapophyses. In dorsal vertebrae, the postzygapophysis forms a distinctive dorsal expansion that overrides the base of the neural spine and extends anteriorly beyond the level of the transverse process. The prezygapophysis expands in a similar fashion, but extending onto the lateral surfaces of the centrum and merges with the lateral processes. Zygapophyseal articulation surfaces are rounded and oriented in the horizontal plane, restricting dorsoventral movements.

In IGM 7443, two sacral and 12 caudal vertebrae are preserved. Sacral vertebrae are stout and have sacral ribs completely fused to the centrum. The second sacral rib bears a pronounced posterior process but differs from that of sapheosaurs in that the width of the posterior process is greater than the rib itself. Caudal vertebrae are badly preserved and

Fig. 16. *Ankylosphenodon pachyostoseus* gen. et sp. nov. (IGM 7444). Detailed structure of isolated vertebra showing the swollen neural arches and horizontal zygapophyseal joints. **A.** Cervical vertebrae lateral view. Posterior thoracic vertebrae in (**B**) lateral, and (**C**) posterior view. Anterior thoracic vertebrae in (**D**) posterior, and (**E**) dorsal view. **F**. First and second caudal vertebrae in posterior and ventral view.


pr.z.
n.s.
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A
B
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pr.z.
D
E
F
1 cm

heavily crushed, but a disarticulated vertebra identified as the first caudal of IGM 7444 shows an enlarged neural spine (Fig. 16F). Caudal vertebrae one to ten have well developed transverse processes that become shorter and more slender posteriorly. The three most anterior processes are oriented posterolaterally and the remainder point laterally. There is no traces of autotomous septum up to the tenth vertebra. On the 11th vertebra, however, there is a faint midvertebral suture that could be an autotomous septum. This suture cannot be observed in the 12th vertebra, therefore the identification of this structure as a true septum is dubious and may be an artifact of preservation.

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

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

Ventrally, as in other sphenodontids, there are gastralia. The central elements have a boomerang shape with an obtuse angulation. The degree of preparation of the specimen prevents all aspects of gastral structure from being seen, but the gastralia seem to be arranged as in other sphenodontians. Gastral elements are preserved up to the level of the 22nd presacral vertebra and were probably absent after this point. Broad cartilaginous rib extensions, preserved as calcified tissue, connect the gastral elements to the thoracic ribs.

The rib extensions are segmented in a regular pattern, much as is in *Palaeopleurosaurus* (Carroll 1985a).

Appendicular skeleton

Limb proportions are based on the assumption of the presence of 24 presacral vertebrae (Table 5). The humerus is only 63% of the femoral length. The rounded shape of the long bones, the lack of anatomical detail on the humerus, and the total absence of epiphyses suggest a delay in the ossification of limbs elements.

Limb elements are well developed and heavily constructed (Figs. 17, 18). Their proportions relative to the presacral vertebral column are very similar to those of sapheosaurs (Table 6; Fig. 19). The scapula and coracoid remain in position in the holotype, showing both bones entirely separated. The scapula is large and about the same length as the coracoid and the coracoid is rounded. The T-shaped interclavicle has relatively small lateral processes and a posterior process somewhat broadened distally.

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

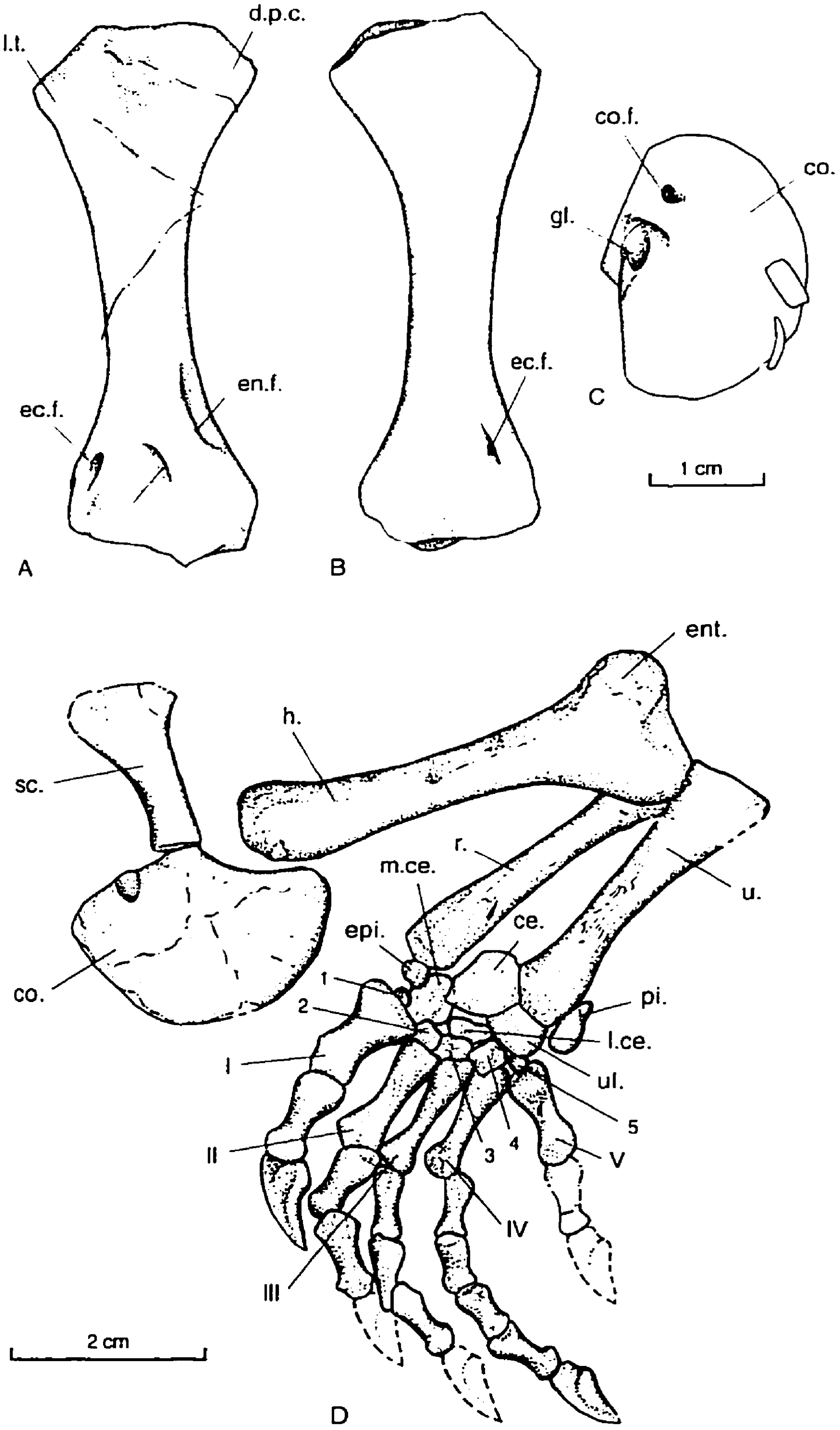
All elements of the manus are present but disproportionate in relation to other sphenodontians. The first digit and the intermedium are unusually large and the lateral and medial centrale are very small and preserved displaced to the center of the manus. The medial centrale contacts the radiale, the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

TABLE 5. Dimensions and proportions of different elements of the cranial and postcranial anatomy of *Ankylosphenodon pachystoseous*. Measurements in mm. Data in parenthesis are approximated. Abbreviations. PSVCL = presacral vertebral column length.

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

Fig. 17. Forelimb of *Ankylosphenodon pachyostoseus* gen. et sp. nov. **A**. Left humerus in ventral view. **B**. Left humerus dorsal view. **C**. Right coracoid in lateral view. **D**. Articulated left anterior limb as preserved in the holotype. A-C. IGM 7444; D. IGM 7441.

Fig. 18. Hind limb of *Ankylosphenodon pachyostoseus* gen. et sp. nov. (IGM 7443). **A.** Left hind limb as preserved. **B.** Right femur in posterior view. **C** and **D**. Reconstruction of the left pes.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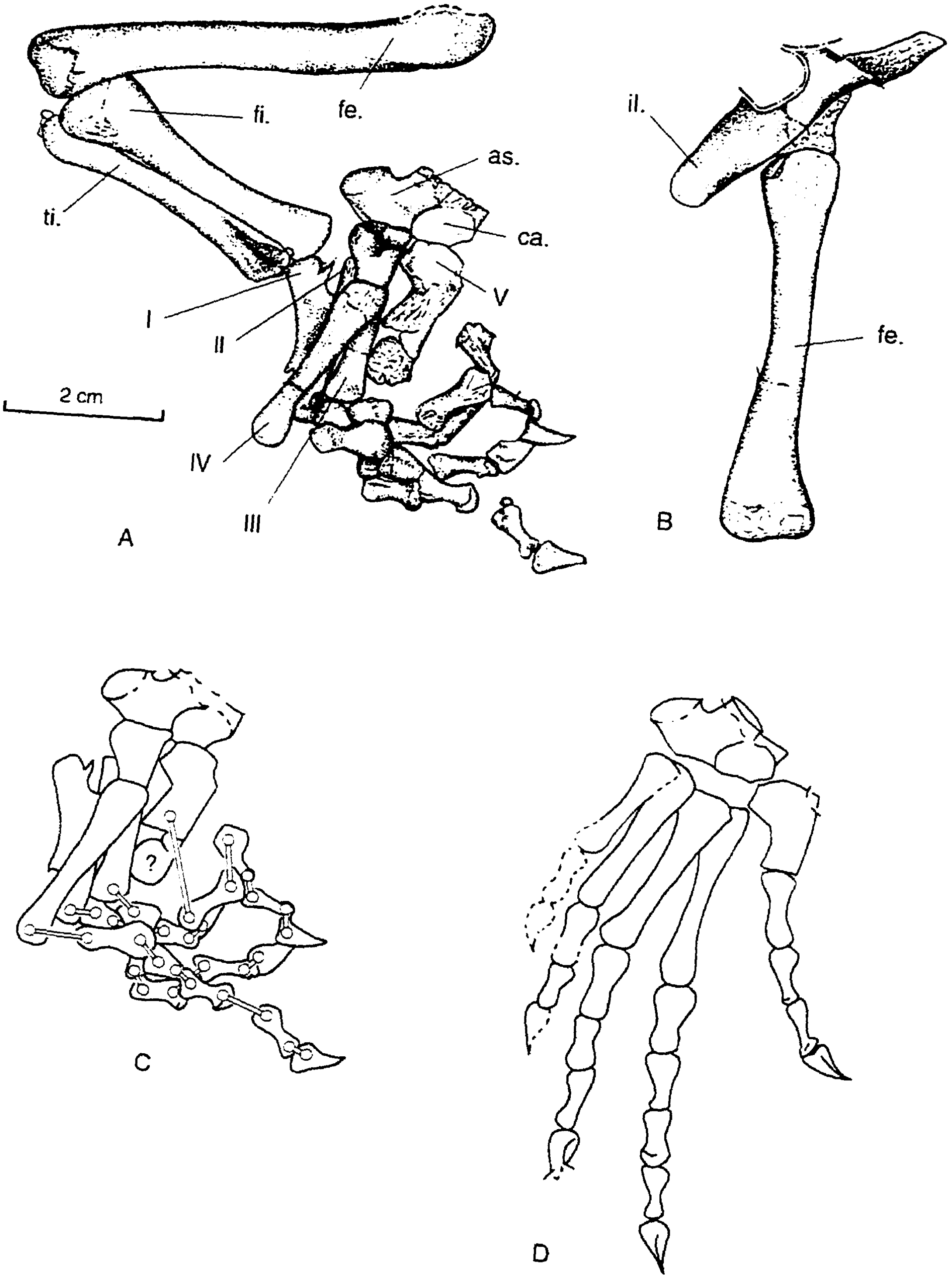
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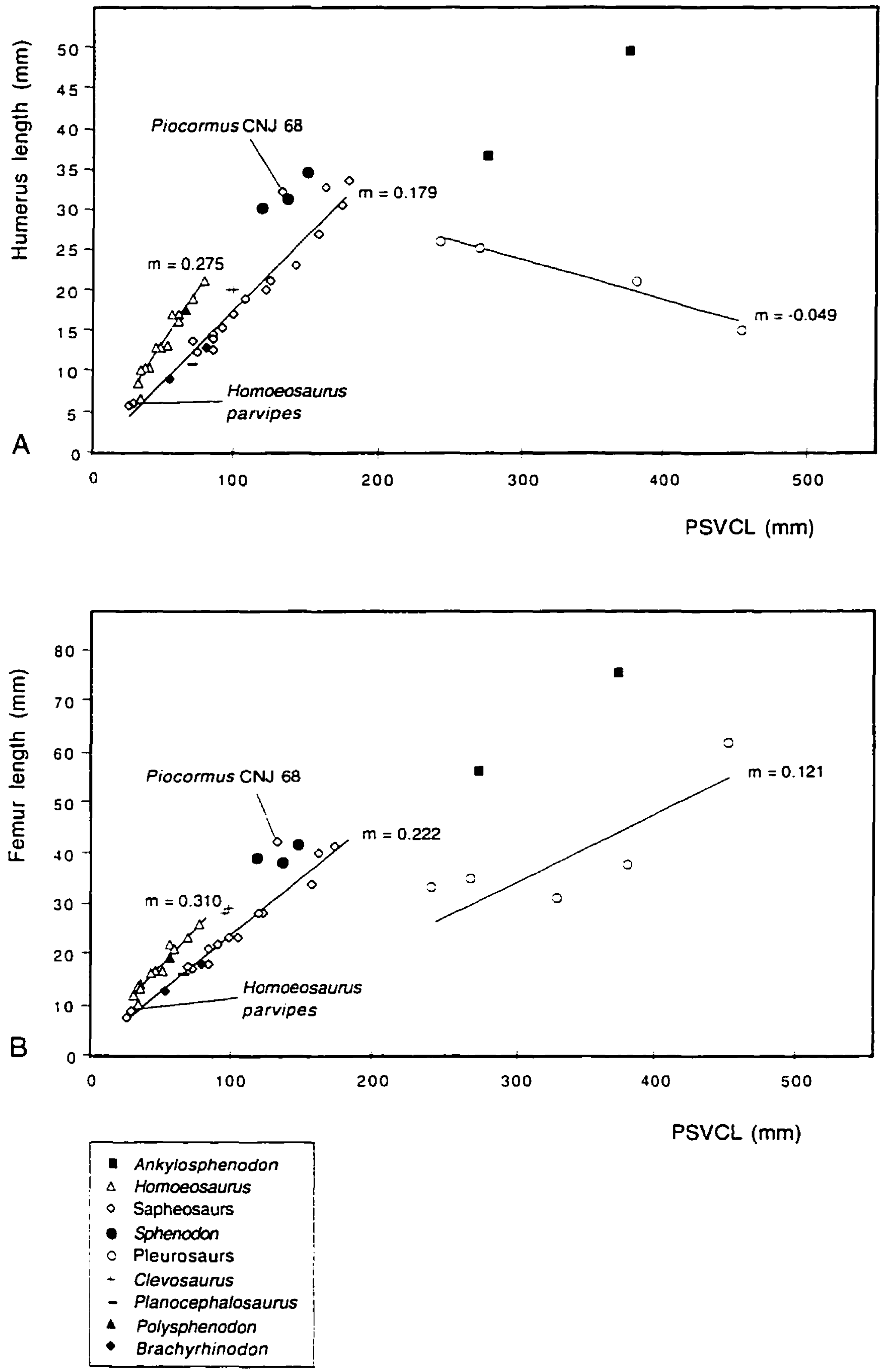
TABLE 6. Limb proportions in rhynchocephalians. For *Ankylosphenodon*, the humerus and femur length was calculated scaling the humerus of the holotype and the femur of IGM 7443 based on the 19th presacral vertebrae and the humerus distal end. Abbreviations: EM, l'Ecole de Mines; FSL, Centre des Sciences de la Terre Université Claude Bernard, Lyon; RPM, Redpath Museum, McGill University; KU, Kansas University. For other abbreviations refer to the original sources. Measurements in parenthesis are average or approximate. * From several specimens.

TAXA	**Catalogue number**	**PSVC length**	**Humerus length**	**Femur length**	**Humerus/ PSVCL**	**Femur/ PSVCL**	**Humerus / Femur length**	**Source**
Ankylosphenodon pachyostoseus	Holotype	374.0	49.3	75.4	0.133	0.202	0.654	
	IGM 7443	276.1	36.5	56.1	0.132	0.203	0.651	
Gephyrosaurus bridensis	*		(16)	(22.5)			0.711	Evans, 1981
Planocephalosaurus robinsonae	*	(68)	(11)	(16)	0.162	0.235	0.688	Fraser and Walkden, 1984
Polysphenodon mülleri	MB R 1032	63	17	21.5	0.270	0.341	0.791	Fraser and Benton, 1989
Brachyrhinodon taylori	BMNH R 4776	81	13	18	0.160	0.222	0.722	"
	BMNH R 4777	56	9	13	0.161	0.232	0.692	"
Clevosaurus hudsoni	*	100	20	29	0.200	0.290	0.690	Fraser, 1988
	UMZC T1271	98	20	28	0.204	0.286	0.714	Fraser and Benton, 1989
Pleurosaurus goldfussi	no. 15640	380	21	38	0.055	0.100	0.553	Cocude-Michel, 1963
	no. 10339+40	330		31		0.094		Cocude-Michel, 1967a
P. ginsburgi	CNJ 67	454	15	(62)	0.033	0.137	0.242	Fabre, 1974
Palaeopleurosaurus posidoniae	no. 50722	242.2	26	33	0.107	0.136	0.788	Carroll, 1985a
	no. 50721	269.3	25	35	0.093	0.130	0.714	"
Homoeosaurus maximilliani	Munich	72	19	23	0.264	0.319	0.826	Cocude-Michel, 1963
	no. 1937-1-40	50	13	16.3	0.260	0.326	0.798	"
	no. 414	46	13	16.3	0.283	0.354	0.798	"
	no. Rhy 4	33	8.5	12	0.258	0.364	0.708	"
	no. Rhy 5	62	16	21	0.258	0.339	0.762	"
	RMc 1	36	10	13.4	0.278	0.372	0.746	"
	RMc 2	37	10	13.4	0.270	0.362	0.746	"
	RpM	37	10.1	13.5	0.273	0.365	0.748	"
	no. 15675 Lyon	59	17.1	22	0.290	0.373	0.777	"
	no. 3955	63	17	21.5	0.270	0.341	0.791	Cocude-Michel 1967b
	Coll. Ghirardi	80	21	26	0.263	0.325	0.808	Fabre, 1973

(Table 6, continued)

TAXA	**Catalogue number**	**PSVC length**	**Humerus length**	**Femur length**	**Humerus/ PSVC**	**Femur/ PSVC**	**Humerus/ Femur length**	**Source**
Homoeosaurus solnhofensis	no. R4073	55	13.2	16.3	0.240	0.296	0.810	Cocude-Michel, 1963
H. parvipes	no. Rhy 1	36	6.5	10	0.181	0.278	0.650	"
Sapheosaurus thiollierei	no. 15672	180	33.5		0.186			Cocude-Michel, 1963
	no. 15649	165	32.5	(40)	0.190	0.242	0.813	"
	no. 15645	175	30.5	41	0.174	0.234	0.744	"
	FSL (no number)	160	27	34	0.169	0.213	0.794	
Kallimodon pulchellus	no. 1887-VI-1	87.5	14.5	21	0.166	0.240	0.690	Cocude-Michel, 1963
	no. 1887-VI-2	75	12.4	17	0.165	0.227	0.729	"
	no. 1911-I-34	87	14	18.2	0.161	0.209	0.769	"
	no. 1922-I-15	87	12.5	18	0.144	0.207	0.694	"
	no. Rhy 2	72	13.6	17.3	0.189	0.240	0.786	"
	no. Rhy 3	102	17	23.3	0.167	0.228	0.730	"
	no. 15671	144	23		0.160			"
	nos. 15674+75	126.5	21	28	0.166	0.221	0.750	"
	Sp.2 EM	123	20	28	0.163	0.228	0.714	"
	CNJ 72	93	15.2	22	0.163	0.237	0.691	
Piocormus laticeps	(moulage)	108	19	23	0.176	0.213	0.826	"
	CNJ 68	135	32	42	0.237	0.311	0.762	
Leptosaurus neptunius	(no number)	27.6	5.8	7.7	0.212	0.279	0.753	"
	no. R. 4108	31	6	8.6	0.194	0.277	0.698	"
Sphenodon	(no number)	120	30	39	0.250	0.325	0.769	Fraser and Benton 1989
	RPM	151.1	34.5	41.9	0.228	0.277	0.823	
	KU 98454	137.8	31.3	38.2	0.227	0.277	0.819	

Fig. 19. Limb proportion relative to the presacral vertebrae column length (PSVCL) in different sphenodontians. **A**. Humerus length vs. PSVCL. **B**. Femur length vs. PSVCL. Data from Table 6.


A
Humerus length (mm)
0
5
10
15
20
25
30
35
40
45
50
Piocormus CNJ 68
m = 0.179
m = 0.275
m = -0.049
Homoeosaurus
parvipes
0
100
200
300
400
500
PSVCL (mm)
B
Femur length (mm)
0
10
20
30
40
50
60
70
80
Piocormus CNJ 68
m = 0.222
m = 0.310
m = 0.121
Homoeosaurus
parvipes
0
100
200
300
400
500
PSVCL (mm)
■ Ankylosphenodon
△ Homoeosaurus
◇ Sapheosaurs
● Sphenodon
○ Pleurosaurs
+ Clevosaurus
- Planocephalosaurus
▲ Polysphenodon
◆ Brachyrhinodon

All metacarpals are of about the same length. The second, third, and fourth metacarpals are more slender than the first and fifth, with the first metacarpal the broadest. Not all phalanges are preserved in the holotype, but the phalangeal count appears to conform with that of primitive lepidosaurs. Digit one has one robust phalanx plus an enlarged ungual. Digits two and three lack the ungual, but these elements are well preserved in IGM 7443. Digit four has five phalanges but the tip of the ungual is missing. Only the proximal portion of the first phalanx on the fifth digit is preserved.

The pelvic girdle, preserved in dorsal view, is mostly obscured by the last thoracic vertebrae and the sacrals. The right ilium is preserved intact but the left is broken and bent onto the sacral region, covering the second sacral rib. The dorsal surface of the ilium is straight and shows traces of a dorsal iliac tuber. The posterior end is broadened and does not tapers posteriorly as in other sphenodontians. The overall shape of the ilium resembles that of *Palaeopleurosaurus*. Anteriorly, an enlarged flange extends onto a medial sulcus on the broadened dorsal head of the pubis, suggesting solid construction. The shape of the pubis resembles that of *Leptosaurus* and *Homoeosaurus* in which the medial process is broadened medially but constricted close to the ilium contact. The ischium has a well developed posterior process but pointing slightly medially. No fusion of pelvic elements had occurred.

The femur is nearly 40% longer than the humerus (Table 5). The tibia and the fibula are subequal in length and both elements are about 35% of the femoral length. The tibia is about double the width of the fibula. As with the anterior limbs, they bear rounded ends with no ossified epiphyses. Pes elements are heavily crushed making it difficult to reconstruct their shape and structure. The astragalus and calcaneum are fused but a suture is still evident. The radial articulation is separated from the tibial articulation by a groove as in *Sphenodon*. The first digit is not preserved, otherwise, the phalangeal count seems to be typical reptilian (2?, 3, 4, 5, 4). In the left hind limb of IGM 7443, digit four is preserved sitting on top of all other digits, followed by digit three. The first and second metatarsal lie below other metapodial elements. Metacarpal fifth is hooked, but because it is preserved dorsally, the position of the ventral tubercles is not known. Phalanges of the fifth digit are relatively smaller and slender compared to the others.

COMPARISON WITH OTHER SPHENODONTIANS AND PHYLOGENY

The lack of a well preserved skull and the presence of many unique derived features make the establishment of the phylogenetic relationships of *Ankylosphenodon* quite difficult. Sphenodontian phylogeny has been based largely on skull morphology and postcranial elements have been considered secondary or unimportant (Fraser and Benton 1989, Wu 1994). Reynoso (1996 and subsequently) attempted to consider all available evidence in reconstructing phylogenetic hypotheses. However, in the published data matrix only a small percentage of the information deals with postcranial morphology.

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

Limb proportions of different sphenodontians are listed in Table 6. There are three basic trends in which the length of the humerus or femur are graphed against the length of the presacral vertebrate column (Fig. 19). *Homoeosaurus* and *Polysphenodon* have distinctly long-legged bodies compared to sapheosaurs (*Sapheosaurus*, *Leptosaurus*, *Kallimodon*, *Piocormus*), *Brachyrhinodon*, and *Planocephalosaurus*. A third trend is expressed by the obligatorily aquatic sphenodontians *Pleurosaurus* and *Palaeopleurosaurus*. In the first two trends some overlap is observed between the smaller members of both lineages, probably correlated with limb disproportions typical of hatchling or juvenile stages. The limb proportions of *Ankylosphenodon*, especially in the femur, fit within the range of variation of sapheosaurs. The position of *Clevosaurus* is ambiguous since the humerus and femur fell respectively in the sapheosaurs and homoeosaurs trends.

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

Sapheosaurs are distinguished by the enlargement of the postorbital skull region, while exceeds the length of the preorbital region, with an elongate but narrow upper temporal fenestra, a broad upper temporal arch, and laterally compressed vertebral centra (Cocude-Michel 1963; Gauthier et al. 1988a). As mentioned before, the skull of *Ankylosphenodon* is in very bad condition, but as in sapheosaurs, the postorbital region of the skull is larger than the preorbital region. This condition is also present in clevosaurs (Wu 1994), however, on the base of current phylogenetic analysis, it is probably a convergent condition which in *Polysphenodon* and *Brachyrhinodon* is caused by an extensive reduction of the snout. Clevosaurs have a broad skull, but with very different appearance compared to sapheosaurs. The anteroposteriorly enlarged skull of *Ankylosphenodon* resembles more the skull of sapheosaurs than that of clevosaurs. The width of the upper temporal fenestra is not known, as the holotype and only specimen in which this character might be established, is preserved in lateral view. The enlarged upper temporal fenestra also resembles that of sapheosaurs. A similarly enlarged temporal fenestra is present in *Palaeopleurosaurus*, (Carroll 1985a), although the structure of the supratemporal arch is quite distinct. In *Palaeopleurosaurus*, the postorbital extends far posteriorly onto the dorsal margin of the upper temporal fenestra, restricting the squamosal very much to its posterior margin. The primitive condition is retained in sapheosaurs and *Ankylosphenodon* where the postorbital is shorter and the squamosal extends anteriorly dorsal to the postorbital posterior process close the anterior half of the upper temporal fenestra. The postorbital process in *Ankylosphenodon* is shorter than in *Sapheosaurus* and other sphenodontians. It does not extend beyond the first half of the upper temporal fenestra.

The presence of propalinal jaw action indicated by the anteroposteriorly oriented tooth wear marks and the anteroposteriorly enlarged mandibular condyle, suggest affinities with the clade that includes an unnamed genera from the Huizachal Canyon, North East Mexico (Reynoso and Clark submitted), eilenodontines (Throckmorton et al. 1981; Rasmussen and Callison 1981) and sphenodontines (Reynoso 1996). However, the lack of other good synapomorphies makes the position within this clade uncertain. The similarity with *Sapheosaurus* plus the presence of propalinal jaw action may place *Ankylosphenodon* in an intermedium position between these groups.

A cladistic analysis using the branch and bound search algorithm of PAUP (Swofford 1993) and Reynoso's (1996) data matrix with additional characters in subsequent papers (Reynoso, in press; Reynoso and Clark submitted; see Appendix to

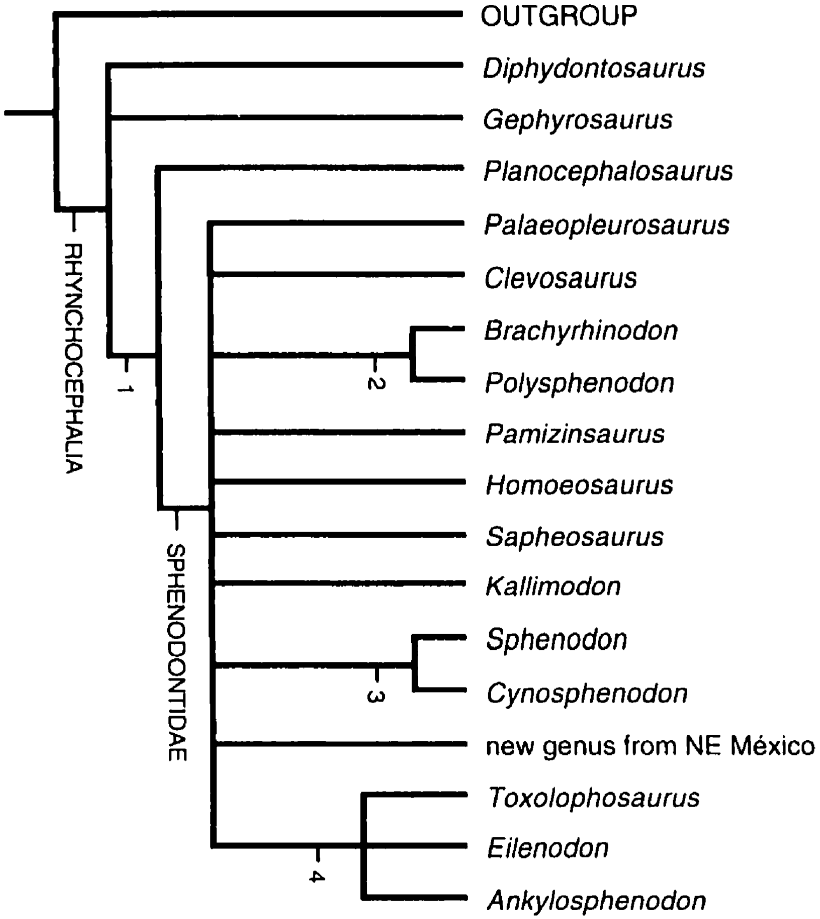
Chapter 2) support the sister-group relationships of *Ankylosphenodon* with eilenodontids (Tree length = 120; Consistency index = 0.658; Retention index = 0.725; see Appendix 3.2). Characters 26 and 42 were modified (Appendix 3.1). The derived state "ankylothecodont teeth" was added to the character "tooth implantation" (26); and character 42 was recoded according to the three different trends of limb proportions found (Fig. 19). The lack of good sample size prevented the establishment of an accurate limit between each character state (e.g. through the standard deviation). Then, the limits between two trends were calculated by adding the mid-distance value between the lowermost and the uppermost data in the range of variation of a trend and the following one, excluding highly discordant data (Table 7). *Clevosaurus hudsoni. C. petilus*, *C. mcgilli*, and *C. bairdi* were merged into a single taxon causing characters 35 and 46 to become uninformative.

The strict consensus of 93 equally parsimonious trees is unresolved within the Sphenodontidae (Fig. 20). This is primarily due to the almost complete lack of information for *Ankylosphenodon*, the presence of characters that cannot be satisfactorily applied to previously published transformation series, and the lack of good synapomorphic characters to support its inclusion in any other known group. The only synapomorphy that unambiguously joins *Ankylosphenodon* with eilenodontids is the presence of a high mandible. In Appendix 3.2 four other synapomorphies define this node: propalinal jaw motion, short retroarticular process, wide marginal teeth, and swollen neural arches. Propalinal jaw motion is shared with sphenodontines and eilenodontines as well as with the new genus of the Huizachal Canyon (Reynoso and Clark submitted). As pointed before and in other published phylogenies (e.g. Fraser and Benton 1989; Wu 1994; Reynoso 1996; Reynoso and Clark submitted) this could be a more exclusive synapomorphy grouping all mentioned taxa and *Ankylosphenodon*. A short retroarticular process is shared with *Homoeosaurus*, *Pamizinsaurus*, *Eilenodon*, and *Sphenodon* but this character may also define a more exclusive group. Wide marginal teeth are only present in eilenodontines and this condition is absent in *Ankylosphenodon*. In the data matrix it was coded as not

TABLE 7. Description of three different trends of limb proportions in sphenodontians. Values for (m) based on well represented taxa: Trend I in *Homoeosaurus*; trend II in *Sapheosaurus* for, and trend III in *Pleurosaurus* + *Palaeopleurosaurus*. Range includes all taxa belonging to each trend. *Piocormus laticeps* (CNJ 68) excluded from calculations; see text. Data from Table 6 and Fig. 19.

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

Fig. 20. Strict consensus of 69 equally parsimonious trees (tree length = 121; consistency index = 0.661; retention index = 0.727) showing the sister-group relationships of *Ankylosphenodon*.. Results obtained using the branch-and-bound search algorithm of PAUP and data fom Reynoso (1996 and subsequent) with some modifications and one new character (Appendix 2.1). Apomorphy list (only unambiguous characters): **Rhynchocephalia**: frontals fused, lower temporal bar bowed away beyond the limit of the abductor chamber, posterior process of the dentary ends posterior to coronoid process, supratemporal absent. **Node 1**: lower temporal bar complete, broad mandibular symphysis, coronoid process pronounced, tooth added at the posterior part of the dental series, dental regionalization, three or less premaxillary teeth, posterior maxillary teeth with posteromedial flanges, dentary teeth with flanges, second sacral rib with pronounced posterior process, broad contact between pterygoids. **Sphenodontidae**: length of supratemporal fenestra more than one fourth of skull length, broad posterior process of maxilla, frontals separated, narrow parietal table, parietal crest, posterior end of parietal slightly incurved, parietal foramen anterior to or level with anterior margin of supratemporal fenestra, pterygoid precluded from suborbital fenestra, enlarged mandibular foramen, well established lateral and medial wear facets on teeth, premaxilla forming a chisel-like structure, single lateral tooth row on palatines, orbital length less than one third of the skull length, enlarged quadrate-quadratojugal foramen. **Node 2**: length of antorbital region of skull one fourth or less of skull length, broad parietal table, parietal crest absent, greatly incurved posterior edge of parietal, parietal foramen posterior to anterior margin of supratemporal fenestra, two rows of pterygoid teeth, anterior contact between pterygoids small or absent. **Node 3, Sphenodontines**: propalinal jaw action, anterior caniniform tooth on jaw and dentary. **Node 4**: propalinal jaw action, deep mandible, retroarticular process reduced, marginal teeth expanded mediolaterally. A full description of the tree in Appendix 3.2.


OUTGROUP
Diphydontosaurus
Gephyrosaurus
Planocephalosaurus
Palaeopleurosaurus
Clevosaurus
Brachyrhinodon
Polysphenodon
Pamizinsaurus
Homoeosaurus
Sapheosaurus
Kallimodon
Sphenodon
Cynosphenodon
new genus from NE México
Toxolophosaurus
Eilenodon
Ankylosphenodon
RHYNCHOCEPHALIA
SPHENODONTIDAE
1
2
3
4

applicable since none of the conditions perfectly describes the condition present in *Ankylosphenodon*. The presence of swollen neural arches cannot be established in eilenodontids, for which the vertebrae are unknown. If the *Ankylosphenodon*-eilenodontids sister-group relationships is accepted, this would mean that similarities with sapheosaurs are convergent; i.e. a stout skeleton was acquired independently and the sapheosaur robustness is not transitional to the *Ankylosphenodon* condition. Unfortunately eilenodontines are only known from scattered material and descriptions are based exclusively on their lower jaw. Although mandibles are very rich in characters, information about skull and postcranial is missing and this last hypothesis of sister-group relationships should be considered as provisional until eilenodontids and/or *Ankylosphenodon* become better known.

TOOTH STRUCTURE, GROWTH AND FEEDING

The peculiar dental morphology of *Ankylosphenodon* deserves special attention. As mentioned above, the teeth are anterodorsally-oriented ridges deeply ankylosed to the jaw (Figs. 13, 14). Open dentine at the posterior end of worn teeth suggests the presence of continuous tooth growth, never reported in other lepidosaurs. A unique feature of sphenodontians, including *Ankylosphenodon*, is the addition of new teeth at the posterior end of the jaw while it grows (Harrison 1901; Robinson 1976). Older teeth occur anteriorly in the jaw and more recently erupted teeth posteriorly. This permits the recognition of different ontogenetical stages and changes of tooth morphology due to wear in a single tooth series.

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

In tooth wear, *Ankylosphenodon* is similar to other sphenodontians. However, the final result is influenced by the unique tooth structure and morphology. As in other sphenodontians, recently added teeth are triangular and entirely covered with enamel. As the tooth starts to be used, the enamel of the lateral surface is the first to be worn out, and because of the lack of lateral flanges, the dentine is immediately exposed (Fig. 13B). Subsequently the medial surface become eroded as well. Because the dentine is softer than the enamel, this will be worn rapidly resulting in a slightly deeper dentine surface surrounded by the enamel sheath. This condition is observed in the anteriormost teeth (Fig. 13C). The great difference between other sphenodontians and *Ankylosphenodon* is that these are never worn away, and even the smallest teeth at the anterior end of the jaw preserve their triangular shape in adult specimens. Wear surfaces exposing dentine are displaced to the posterior part of the tooth, and recently erupted enamel covers the anterior and lateral sides of each tooth.

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

This particular tooth morphology undoubtedly prevent the complete loss of teeth as does happen in *Sapheosaurus*. Teeth with continuous growth are also present in some grazing mammals and in the incisors and cheek teeth of rodents to prevent fast tooth erosion caused by highly abrasive substrate or food. Constant tooth growth may suggests herbivorous diet in *Ankylosphenodon*. This feeding behavior is quite possible since the enlarged body size of *Ankylosphenodon* far exceeds the 300 gr. minimum limit require for a lepidosaurs to afford herbivory (Pough 1973; Troyer 1983, Jaksic and Schwenk 1983). Within sphenodontians, only *Toxolophosaurus* and *Eilenodon* have been suggested as herbivores. Special anatomical features supporting herbivory are the presence of an anteroposteriorly enlarged articular condyle of the mandible which permits grinder capacity for chewing, the increase of the vertical dimensions of the mandible, the close packing of dentary teeth, the thickening of the enamel layer, and the widening of teeth to increase their shredding surface (Throckmorton et al. 1981; Rasmussen and Callison 1981). Of all these features only the capacity for chewing and the increase of the vertical dimensions of the jaw are present in *Ankylosphenodon*.

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

The absence in *Ankylosphenodon* of other expected herbivorous features present in eilenodontids suggests that the herbivorous specialization in *Ankylosphenodon* may be of a different nature. Instead of thickening the enamel for tooth durability, the teeth grew constantly, replacing worn surfaces with new enamel. The absence of laterally expanded teeth would be the only issue contradicting herbivory; however, in other herbivorous lizards (e.g. *Iguana iguana* or *Amblyrhynchus cristatus*) there are not particular specializations in tooth morphology for grinding, although chewing capabilities are present. Contrary to supposedly primitive insectivorous sphenodontians, *Ankylosphenodon* does not show grasping or piercing teeth. As discussed above, the posterolateral wear surface of each tooth is broader and somewhat flattened. If the jaw is moved anteroposteriorly as in *Sphenodon* or *Toxolophosaurus*, this surface would form an active grinding surface. Its grinding capabilities would not be as effective as the broad teeth of eilenodontids, but it seems that this advantage was exchanged in order to develop long lasting, constantly growing teeth. Contrasting tooth morphologies are also seen in artiodactyl and perissodactyl mammals (Young 1975; Romer and Parson 1986). In the highly derived hypsodont horse dentition, the tooth crowns are larger and have more enamel plications than those of artiodactyls. This would achieve great grinding surface and long durability. In hypsodont dentition, however, the maximum tooth length is acquired in early stages of development and teeth can be completely worn down in old organisms (Reynoso and Montellano 1994) resulting in starvation and death. In grazing ruminants, solenodont teeth may be not as durable as those as horses, but constant growth allow replacement of grinding surfaces throughout life.

MODE OF LIFE

Pachyostotic skeletons have long been associated with semiaquatic behavior (Nopcsa 1923; Nopcsa and Heidsisck 1934) since are not manifested in fully aquatic vertebrates. Pachyostotic skeletons are present in mesosaurs, nothosaurs, primitive mosasaurs, primitive snakes, cholophidians, and champsosaurs (de Ricqlès 1974), and in sirenians among mammals. The presence of stout ribs has been explained as a resistant structure to prevent lung collapse during diving (Nopcsa 1923, Ginsburg 1967) or to increase body weight to counter act the positive buoyancy provided by expanded lungs during apnea (Zangerl 1935; Carroll 1988a). The persistence of cartilage within pachyostotic ribs has recently been observed in mesosaurs, suggesting that pachyostosis is a result of neoteny (de Ricqlès 1974). Pachyostotic ribs are also correlated with a delay in the ossification in limb bones, carpus, and tarsus of aquatic organisms after limbs are freed from support of body weight (Romer 1956). Delay in the fusion of the neural arch and centra in nothosaurs and the sphenodontian *Palaeopleurosaurus* (Carroll 1985a) have also been associated with the same phenomena. Pachyostotic ribs in *Ankylosphenodon*, although not as extreme as in mesosaurs and nothosaurs (e.g. *Pachypleurosaurs*), does suggest a partially aquatic behavior. As in other partially aquatic forms, the limbs of *Ankylosphenodon* are not fully ossified. Although the ends of the limb elements are somewhat rounded, there is no evidence of epiphyseal ossifications, and the humerus lack anatomical detail, they otherwise closely resemble limbs of terrestrial sphenodontians. The lack of other aquatic modification such as dorsoventral expansion of the tail for propulsion and reduction of limbs as in other long bodied aquatic sphenodontids (Fabre 1974; Carroll 1985a) suggests that *Ankylosphenodon* was still dependent on terrestrial locomotion. All carpal elements are fully ossified and vertebral neural arches and centra are totally fused in the holotype. In the younger specimen (IGM 7443), there are no traces of the distal carpal elements, but the astragalus and calcaneum are already fused. This, associated with the presence of rounded distal ends on long bones may indicates that there is a certain delay in the ossification of *Ankylosphenodon*. The delay, however, is not comparable to the degree of other more obligated aquatic reptiles that would explain the less extensively pachyostotic ribs.

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

Swollen neural arches with horizontal (or almost horizontal) zygapophyseal articulations are not unique to terrestrial environments and are present in a variety of aquatic forms: the seymouriamorph *Kotlassia*; the early diapsid *Claudiosaurus* (Carroll 1981); the nothosaurs (e.g. *Pachypleurosaurus*; Carroll and Gaskill 1985; and *Serpianosaurus*, Rieppel 1989); and plesiosaurs (e.g. *Pistosaurus*, Meyer 1855). In these organisms the structure of the vertebral column cannot be explained by the need for the support, because of the virtual lack of weight in water. This structure has been interpreted as a primitive feature among amniotes and it appears to be widely distributed in clades branching off basal to Sauria (Heaton and Reisz 1986; Gauthier et al. 1988b); however, differences in many features of the vertebrae suggest that they have arouse convergently in several taxa (Carroll 1988a). Primitive sphenodontians bear vertebrae with small and steeply oriented zygapophyses (Evans 1981), the primitive lepidosaurian condition. The swollen horizontal zygapophyses of *Ankylosphenodon* were then acquired secondarily, as in other amniote lineages. Swollen neural arches are also present in sapheosaurs, suggesting that these structures were probably shared ancestrally in these two groups. The aquatic affinities of *Sapheosaurus* were already suggested by Ahmad (1993) but without convincing arguments. However, the presence of swollen and horizontally directed zygapophyses associated with pachyostotic ribs is shared convergently with some aquatic genera and may have real functional implications. The less fully developed swollen neural arches and the lack of pachyostotic ribs in *Sapheosaurus* would indicates a lesser degree of aquatic specialization compared to *Ankylosphenodon*. In *Sapheosaurus*, the orientation of the zygapophyseal articulation cannot be established because of the lack of a good lateral view of dorsal vertebrae and because of compression of dorsally exposed vertebrae.

Carroll (1985b) pointed to the importance of body rigidity in aquatic organisms to reduce drag. Obligatory aquatic reptiles (Categories 1 and 2 of Carroll 1985b) such as ichthyosaurs and plesiosaurs, have relatively rigid bodies with large dorsal spines probably associated with well developed interspinous ligaments which limit dorsoventral flexure of the trunk. Although the zygapophyses of ichthyosaurs and mosasaurs are reduced or totally lost, probably associated with an increase of the epaxial musculature (Carroll 1988a), the zygapophyses of *Claudiosaurus* and nothosaurs (Category 4 of Carroll 1985b) are still an important element for the stiffening of the vertebral column. In *Pachypleurosaurus* and *Simosaurus* (Carroll and Gaskill 1985; Rieppel 1994a) intraprezygapophyseal and intrapostzygapophyseal articulations (different from the zygosphene and zygantrum articulations) give extra strength, and in *Dactylosaurus* and *Serpianosaurus* lateral movements are limited by a peculiar intervertebral articulation in which the postzygapophysis fits in a groove on the prezygapophysis (Sues and Carroll 1985; Rieppel 1989). *Ankylosphenodon* resembles closely Category 5 of aquatic reptiles (Carroll 1985b). It still has long limbs effective for terrestrial locomotion. Crocodiles, and the marine iguana *Amblyrhynchus* belongs to this groups. In these reptiles, swimming is performed by lateral undulations of the tail (Manter 1940; Hobson 1965). In crocodiles. lateral undulations of the body are not as important as the tail for propulsion. Lateral movements of the head and trunk are restricted to very narrow amplitude waves. These movements are probably caused secondarily by major lateral undulations of the tail which generates most of the propulsion (Manter 1940). The swimming patterns of *Amblyrhynchus* have not been properly studied and only some observations of its behavior have been reported and summarized by Dawson et al. (1977). From the photograph presented by Hobson (1965) it is clear that the mode of swimming is very similar to crocodiles. The body remains straight while the tail forms a broad arc, but the degree of lateral movements of the trunk related to the body is uncertain. In both the marine iguana and crocodiles the limbs are not important for swimming and they are placed against the body to reduce drag.

Because of phylogenetic affinities (and possible historical constraints), it is expected that the swimming pattern of *Ankylosphenodon* may be similar to that of *Amblyrhynchus*. In *Ankylosphenodon*, the only ancestral anatomical feature that strength the vertebral column is the pre-postzygapophysis complex. Their widely open position and large contact surfaces strongly resisted dorsoventral movement and the swollen dorsal surfaces of the zygapophyses must have increased their resistance to stress. The presence of enlarged and broad neural spines suggests a well developed associated musculature and interspinous ligaments that may have played an important role in trunk vertebral column rigidity. The lack of structures that limit lateral movements suggest that lateral movements were still possible. These movements may be a concession to terrestrial locomotion, but they may also be important for swimming by increasing the lateral body surface in contact with the water. Snakes, among lepidosaurs, are the only organisms with similar swollen, horizontally oriented, and broadly open zygapophyses. These structures, associated with well developed zygosphene and zygantrum accessory articulations, are obviously necessary to avoid dorsoventral flexure while providing lateral undulation, as their only means of propulsion in either terrestrial or aquatic environments. The primitive Cenomanian marine snake-like lepidosaurs *Pachyrhachis* and *Estesius*, probable intermediate forms between varanids and snakes (Haas 1979, 1980), have similar vertebral structures but associated with pachyostotic ribs similar to those of *Ankylosphenodon*.

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

BIOGEOGRAPHICAL AND PALEOECOLOGICAL SIGNIFICANCE

Ankylosphenodon pachyostoseus shows remarkable anatomical specializations never observed in previously described sphenodontians. Its enlarged size relative to terrestrial sphenodontians, the presence of a pachyostotic skeleton with restricted dorsal movements but with still functional limbs for terrestrial displacement, and the presence of deep teeth with open roots for constant grow and jaw action for food grinding, are a combination of features that suggest simultaneous aquatic behavior and herbivory, rare among lepidosaurian reptiles (Ostrom 1963; Seymour 1982). *Ankylosphenodon* was collected in deposits in which most of the fauna reported consist of marine forms (see Appendix to Chapter 1). The considerably larger number of specimen of this genus recovered relative to other lepidosaurs suggests that they inhabit nearby areas and were probably co-habitants with the marine fauna. All this facts suggest that this sphenodontian may have had similar behavior to that of the marine iguanid *Amblyrhynchus cristatus* (Hobson 1965; Carpenter 1966; Dawson et al. 1977). According to Dawson et al. there are few if any special features in the marine iguana, when compared to terrestrial iguanas, that allow it to inhabit marine environment. In spite of this, they point to the unusual nature of this phenomenon in that there are no other marine iguanas. Dawson et al. suggest that the environmental features that lead to the evolution of *Amblyrhynchus* were unique. These include a warm and equable terrestrial environment with cool upwelling waters that allow the growth of diverse flora of macrophytic algae, together with an isolated (i.e. insular) environment.

The Tlayua quarry may reflect similar conditions. Based on the presence of haematophagous dipterans and gymnosperms, Pantoja-Alor (1992) suggested a warm tropical terrestrial environment for the area surrounding the Tlayua deposits. Although this argument is weakened because of the presence of some members of these groups in cold climates, the presence of rounded osteoscutes in *Pamizinsaurus*, convergent to the extant lizards *Heloderma*, is possibly related to hot and open environments (Chapter 2), partially supporting Pantoja-Alor's hypothesis.

On the other hand, the association of several bizarre forms of lepidosaurs, including the sphenodontians *Pamizinsaurus* and *Ankylosphenodon*, and the "lizard" *Huehuecuetzpalli* (see Chapters 2 and 4; Reynoso 1995) strongly suggest that the Tlayua deposits were insular. According to evolutionary theory, the easiest way highly specialized forms can succeed is by their evolution in small isolated populations in which the new acquired characters can be randomly fixed through genetic drift (Mayr 1963; Gould and Eldredge 1977; Wright 1982). Continuous genetic contact with anatomically more conservative ancestors would have to be lost. The insular condition of the Tlayua fauna is furthermore supported by the occurrence of forms that could be considered relict in the deposits of the time. *Huehuecuetzpalli* is a fairly primitive lizard found in a relatively late deposit in relationship to the oldest known lizards, which otherwise belong to know groups (Chapter 4, Evans 1995). Sphenodontians, and some Tlayua fishes, which are more typical of the Upper Jurassic, rarely occur in the Early Cretaceous (Throckmorton et al.

1981, Rasmussen and Callison 1981, Grande pers. com. 1993), and never in the Albian. Although biological information supports the insular nature of the Tlayua deposits, more evidence needs to come from the geology of the site and surrounding areas before drawing definitive conclusions.

CONCLUSIONS

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

Appendix to chapter 3

Appendix 3.1

Data Matrix

Character 1-48 are from Reynoso (1996) and Reynoso (in press; see Appendix to Chapter 2). Character 49-52 are from Reynoso and Clark (submitted), and character 53 is new. State 3 "ankylothecodont tooth implantation" was added to character 26; and state 2 " teeth transversely flattened to character 29. Character 42 was rewritten and recoded according to trends in limb proportions discussed in text (Fig. 19). Characters 35 and 46 become uninformative (therefore ignored) after merging *Clevosaurus* species. Abbreviations: 0 = primitive state; 1, 2, 3 = derived conditions; ? = unknown; N = not applicable. Modified characters read:

26. Dental implantation: pleurodont (0), some degree of acrodonty (1), fully acrodont (2); ankylothecodont (3). *Planocephalosaurus* (1); *Palaeopleurosaurus*, *Polysphenodon*, *Brachyrhinodon*, *Clevosaurus*, *Homoeosaurus*, *Kallimodon*, *Pamizinsaurus*, *Eilenodon*, *Toxolophosaurus*, *Opisthias*, *Cynosphenodon*, *Sphenodon*, and the new genus from Huizachal (2); *Ankylosphenodon* (3); *Diphydontosaurus* (0 and 1); *Sapheosaurus*, not applicable. *Polysphenodon* and *Brachyrhinodon* unknown.
29. Marginal teeth breath: equal to length (0); mediolaterally expanded (2); transversely flattened (3). (1) *Eilenodon* and *Toxolophosaurus*; (2) *Ankylosphenodon*. *Sapheosaurus*, not applicable.
42. Proportions of humerus and femur length related to presacral vertebral column length. Sapheosaurs trend: humerus <0.225, ≥0.126; femur ≥ 0.172, <0.287 (0). *Homoeosaurus* trend: humerus ≥0.226, <0.290; femur ≥0.288, <0.373 (1). Pleurosaurs trend: humerus <0.125, ≥0.033; femur <0.171,_≥0.094 (2). *Homoeosaurus* and *Polysphenodon* (1); *Palaeopleurosaurus* (2); *Clevosaurus* (0,1);

Eilenodon, *Toxolophosaurus*, *Cynosphenodon* and the new genus from Huizachal unknown. *Planocephalosaurus* coded (0?) and *Polysphenodon* (1?). Hatchling *Pamizinsaurus* has state (1); however its adult the condition is unknown; coded (?).

Characters from Reynoso and Clark (submitted):

49. Orbit one third of the skull total length or greater (0); less than one third of the skull length (1).
50. Quadrate-quadratojugal emargination pronounced (0); reduced (1). This character was proposed by Evans (1988: Character K 23) and has been included in several analysis (Fraser and Benton 1989; Wu 1994; and Sues et al. 1994) when it was autapomorphic to *Sphenodon* and not informative.
51. Quadrate-quadratojugal foramen small (0); enlarged (1).
52. Quadrate-quadratojugal foramen between the quadrate and the quadratojugal (0); within the quadrate (1).

New character:

53. Dorsal shape of the zygapophyses: Flat (0); swollen (1). Kallimodon, Sapheosaurus, and Sapheosaurus (1); *Diphydontosaurus*, *Polysphenodon*, *Brachyrhinodon*, *Eilenodon*, *Toxolophosaurus*, *Cynosphenodon* and the new genus from Huizachal unknown.

Data for *Ankylosphenodon*:

?1??? ?1??? ????? ???11 11111 31120 0???? ???01 20??? ????? ??1

Appendix 3.2

Analysis and Results

```
Data matrix has 19 taxa, 53 characters
All uninformative characters ignored
Valid character-state symbols: 0123
Missing data identified by '?'
Gaps identified by '-', treated as "missing"
All characters unordered

Designated outgroup taxa:
   Youngina
   Squamata

Current status of all characters:
    Characters 35 and 46 are uninformative (ignored)

Branch-and-bound search settings:
   Initial upper bound: unknown (compute via stepwise)
   Addition sequence: furthest
   Initial MAXTREES setting = 200
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

Branch-and-bound search completed:
   Shortest tree found = 121
   Number of trees retained = 69

Most parsimonious tree description:

Tree length = 121
Consistency index (CI) = 0.661
Homoplasy index (HI) = 0.479
Retention index (RI) = 0.727
Rescaled consistency index (RC) = 0.480

Strict consensus of 69 trees:
                                      /---------- Ankylosphenodon
                             /-------26---------- Eilenodon
                             |        \---------- Toxolophosaurus
                             +------------------- Palaeopleurosaurus
                             |        /---------- Polysphenodon
                             +--------23--------- Brachyrhinodon
                             +------------------- Clevosaurus
                   /--------25------------------- Homoeosaurus
                   |         +------------------- Kallimodon
                   |         +------------------- Sapheosaurus
                   |         +------------------- Pamizinsaurus
         /--------22         +------------------- gen.nov.NE Mexico
         |         |         |        /---------- Cynosphenodon
         |         |         \-------24---------- Sphenodon
/-------21         \----------------------------- Planocephalosaurus
|        +--------------------------------------- Gephyrosaurus
|        \--------------------------------------- Diphydontosaurus
\------------------------------------------------ OUTGROUP
```

```
Statistics derived from consensus tree:

     Component information (consensus fork) = 7 (normalized = 0.412)
     Nelson-Platnick term information = 64
     Nelson-Platnick total information = 71
     Mickevich's consensus information = 0.198
     Colless weighted consensus fork (proportion max. information) = 0.418
     Schuh-Farris levels sum = 490 (normalized = 0.506)
     Rohlf's CI(1) = 0.435
     Rohlf's -ln CI(2) = 27.295 (CI(2) = 1.40e-12)

Consensus tree description:

Tree length = 155
Consistency index (CI) = 0.516
Homoplasy index (HI) = 0.594
Retention index (RI) = 0.500
Rescaled consistency index (RC) = 0.258

Apomorphy lists: (*Ambiguous characters)

Node 21: 6*, 8, 14, 23, 45
Node 22: 15(0), 21, 24, 26*, 27, 30, 32(2), 34, 38*, 39, 40, 48
Node 25: 1*, 2, 5, 7*, 8(0), 10, 11, 12, 13, 16*, 18, 22, 26(2)*, 28,
      33, 36, 37*, 38(2)*, 41(2)*, 47(2)*, 49, 51
Node 26: 19, 20, 25, 29, 53*
Ankylosphenodon: 26(3), 29(2), 30(0), 39(0)
Palaeopleurosaurus: 1(0)*, 5(0), 7(0)*, 9, 12(2), 13(0), 14(0), 15,
      16(0)*, 17, 18(0), 34(2), 37(0)*, 41*, 42(2), 47, 52,
Node 23: 1(2), 3*, 4*, 10(0), 11(0), 12(0), 13(0), 16(0)*, 38, 48(0)
Polysphenodon: 2(0), 42, 49(0)
Clevosaurus: 3, 4, 11(0), 13(0), 34(2), 38, 41*, 43, 45(0), 47, 51(0)
Homoeosaurus: 1(0)*, 2(0), 7(0)*, 10(0), 11(0), 25, 34(2), 42, 47(0)*
Kallimodon: 1(0)*, 34(2), 47(0)*, 53
Sapheosaurus: 7(0)*, 47(0)*
Pamizinsaurus: 17, 25, 43
gen.nov.NE Mexico: 2(0), 3, 5(0), 9, 16(0)*, 17, 18(0), 19, 44, 45(0),
      49(0), 50
Node 24: 3*, 17*, 19, 25*, 31, 40(2)*, 41*, 50*
Planocephalosaurus: 9, 52
Gephyrosaurus: 6(0)*, 9
Diphydontosaurus: 1, 22, 32
```

CHAPTER 4

HUEHUECUETZPALLI MIXTECUS GEN. ET SP.NOV; A PRIMITIVE LIZARD FROM THE EARLY CRETACEOUS LIMESTONES OF TEPEXI DE RODRÍGUEZ, CENTRAL MÉXICO

HUEHUECUETZPALLI MIXTECUS GEN. ET SP. NOV; A PRIMITIVE LIZARD FROM THE EARLY CRETACEOUS LIMESTONES OF TEPEXI DE RODRÍGUEZ, CENTRAL MÉXICO

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 close to 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 1983b); however, the earliest known squamates are from the Middle Jurassic of Britain. They consist of scattered material of very distinctive lizard elements that can be assigned to crown squamate taxa (Evans 1993; Waldman and Evans 1994). Early Jurassic lizards were reported by Meszoley et al. (1987), however, their specific affinities are uncertain and they may be basal lepidosauromorph taxa rather than lizards (Meszoley, pers. com. 1995). The earliest well documented squamates are the middle Jurassic anguimorphs *Parviraptor estesi* (Evans 1994a) from Kirtlington, England (Bathonian), and *Changetisaurus estesi* (Nesov 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 (Table 2). 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 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 and Estes 1980; Chure 1992). The scincomorph *Sharovisaurus* was reported from the Kimmeridgian of Kazachstan, Central Asia (Hecht and Hecht 1984), and the skink *Mimbobecklesisaurus* (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 1983a), now is known to have been described on the basis of an assemblage of lepidosaurs from different taxa, and only the badly preserved type can be assigned to the Squamata with uncertain relationships (Evans 1994b). 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, 1994c). The previously considered early lizard *Ctenogenys* from Como Bluff (Gilmore 1928; Prothero and Estes 1980) and Guimarota (Seiffert 1973), is now considered a choristodere (Evan 1989, 1990), and *Lisboasaurus*, also from Guimarota, is a small theropod (Milner and Evans 1991).

The fossil record of lizards during the Early Cretaceous was poor, leaving a big 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 and Evans 1995); and *Yabeinosaurus* from Berriasian? deposits of North-Eastern China (Endo and Shikama 1942). Very recently, a number of new localities have yielded numerous specimens some of which are superbly preserved. The scincomorph *Ilerdaesaurus* (probable synonymous to *Meyasaurus*; Barbadillo and 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; Ensom et al. 1991; Evans 1995). Remains of the earliest snake (Rage and 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 Late Barremian deposits of Uña and Galve, Spain (Richter 1991, 1994a, b). Deposits of similar age in Las Hoyas, Spain yield a new assemblage of lizards to be described (Barbadillo and Evans 1995, pers. com. 1995). Outside Europe, only a new species of *Paramacellodus* from the ?Berriasian of Anoual Morocco (Richter 1994a), 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 and 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 1983b; Estes et al. 1988) in which iguanians are the first mayor offshoot of the cladistic tree, implying that earlier representatives to be expected. Evans (1994b) has recently demonstrated that *Euposaurus* is not an iguanian but a pleurodont lizard with uncertain relationships. Although *Tamaulipasaurus*, from the Middle Jurassic of north east México (Clark and 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 one of the most superbly preserved fossil lizards world wide (Reynoso 1995). Skeletons are fully articulated but heavily compressed. Fortunately, their oblique preservation provides full view of the organisms, facilitating reconstruction and providing almost all possible information. The lizard here described, even though somewhat late in the fossil record, shows many features of a relict of an earlier stage of squamate evolution, and provides evidence of early character transformation within squamates.

SYSTEMATIC PALEONTOLOGY

LEPIDOSAUROMORPHA Benton 1983

LEPIDOSAURIA Dumeril and Bibron, 1839

HUEHUECUETZPALLI gen. nov.

Type species- *H. mixtecus* sp. nov.

Etymology- From *huéhuetl* (ancient) and *cuetzpalli* (lizard), Náhuatl.

Diagnosis- As for the type and only known species.

HUEHUECUETZPALLI MIXTECUS sp. nov.

(Figs. 21-29)

Holotype- Instituto de Geología, Universidad Nacional Autónoma de México. Cat. No. IGM 7389 (Figs. 22, 23). Crushed, but beautifully preserved complete skeleton.

Paratype- Cat. No. IGM 4185 (Figs. 24, 25). 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 tissue 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 and Buitrón 1987). IGM 7389 was collected in locality IGM-1995-NSF #2, level H, quadrant 1/5; and IGM 4185 in IGM-1971-NSF#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; distal end of ulna gently convex; distal end of the tibia notched; fourth distal tarsal very large; second distal tarsal present; middorsal row of osteoderms.

DESCRIPTION

Huehuecuetzpalli mixtecus is only known from two articulated skeletons. IGM 7389 is an adult. Its skull measures 32.2 mm in length and the presacral vertebral column 75.5 mm (Table 8). 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. 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 is based on IGM 4185.

TABLE 8. Dimensions, proportions, and comparisons of different skeletal elements in the adult and juvenile specimens of *Huehuecuetzpalli mixtecus*. Measurements in mm. Data in parenthesis are approximated.

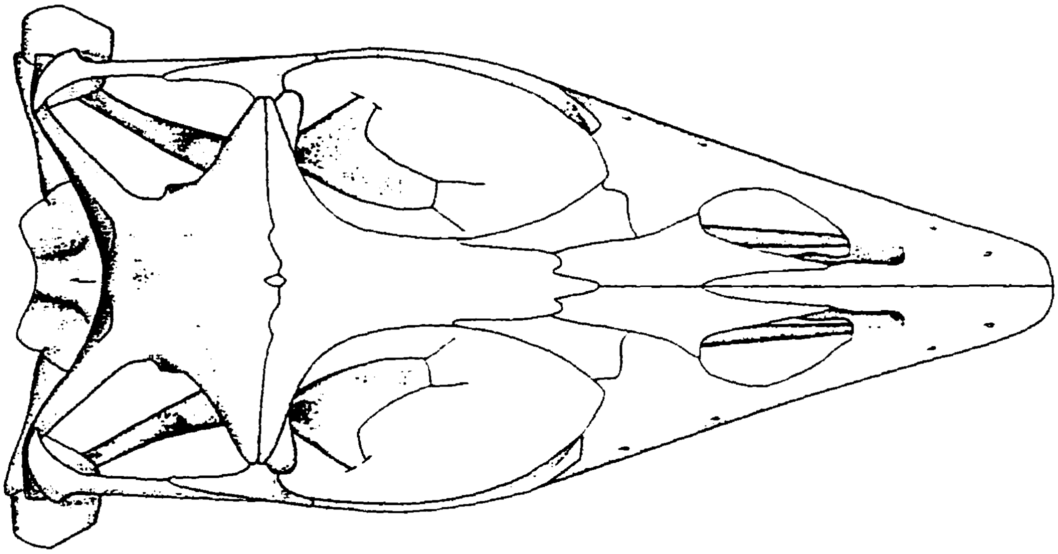
Specimen	**IGM 7389 (Holotype)**	**IGM 4185 (Paratype)**	
Age	Adult	Juvenile	
Total length	---	197.0	
Skull length	32.2	19.3	
Skull breath at fronto-parietal suture	11.6	7.1	
Snout length	13.8	7.8	
Postorbital skull length	9.3	(5.0)	
Parietal table width	2.0	4.3	
Presacral vertebral column (PSVC) length	75.7	46.9	
Humerus	15.7	10.7	
Radius	12.9	(7.4)	
Ulna (without oleacranon)	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			**Difference**
Skull length/PSVC length	0.425	0.412	0.013
Skull breath/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	

Skull

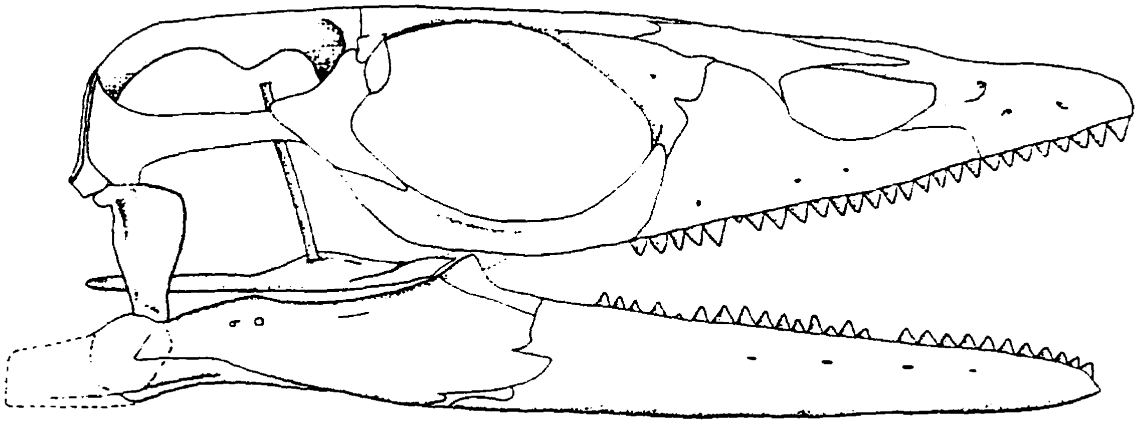
The skull is narrow with a long and slender snout (Fig. 21). In general appearance, it resembles that of *Varanus*, but the postorbital region is primitively constructed showing some iguanian features. The total length of the skull is twice the width at the frontoparietal suture, and the snout is almost 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 boarder 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 and Hawbold 1987). In *Huehuecuetzpalli*, however, the very long frontal process of the premaxillae extends well posteriorly, reaching the frontals as in squamates (Fig. 22). 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 loose contact with the maxilla and prefrontal. In varanids no infranarial processes of the premaxilla is 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 remain separated from the rest of the maxilla suggesting that full skull ossification was not yet completed. The infraorbital process is short as well and extends just below the anterior margin of the orbit. Three sensory foramina aligned parallel to the dental series are present. The nasals are divided but contact each other on the midline

Fig. 21. 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.

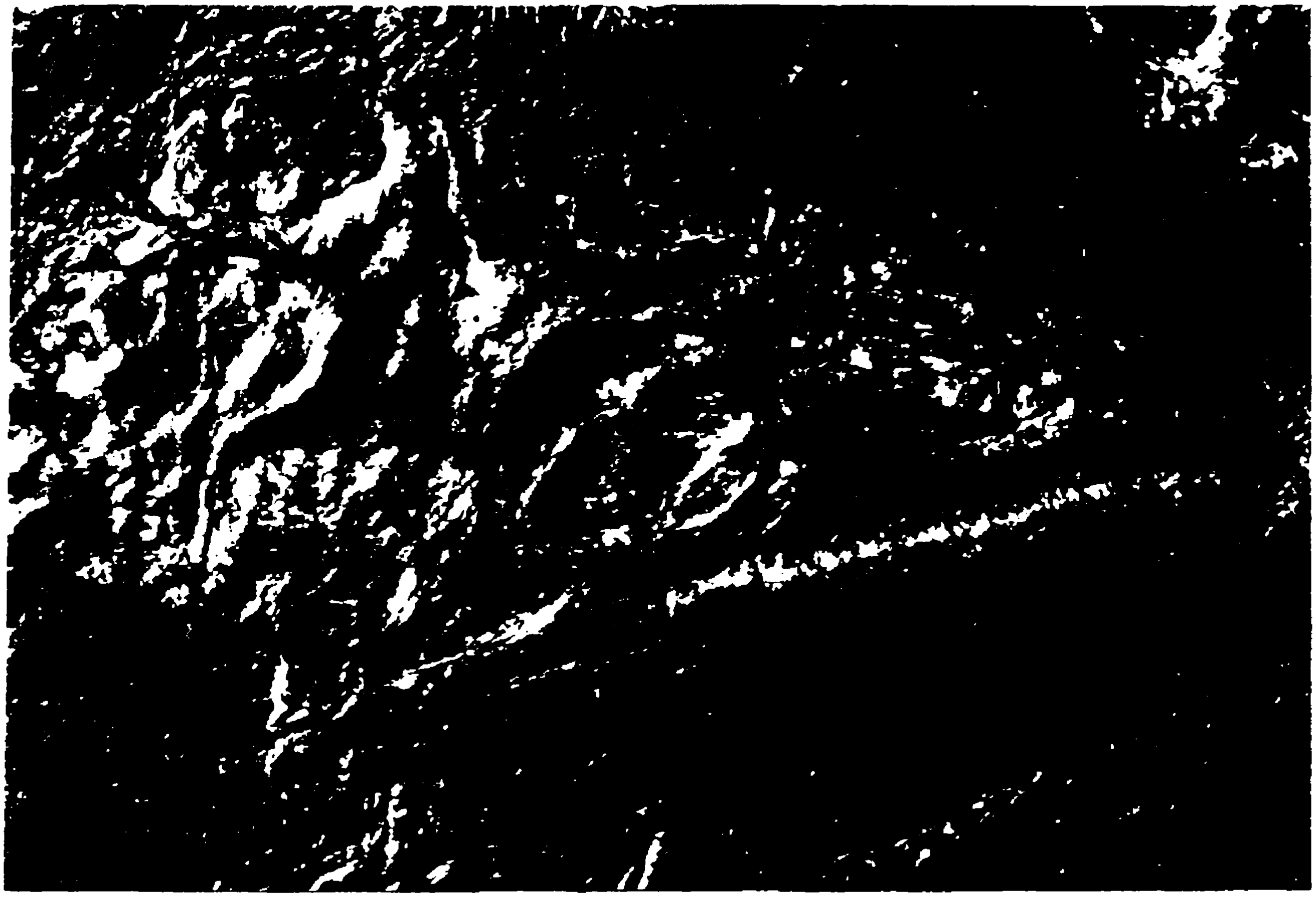


A



B

Fig. 22. Skull of the holotype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 7389) as preserved on the block.



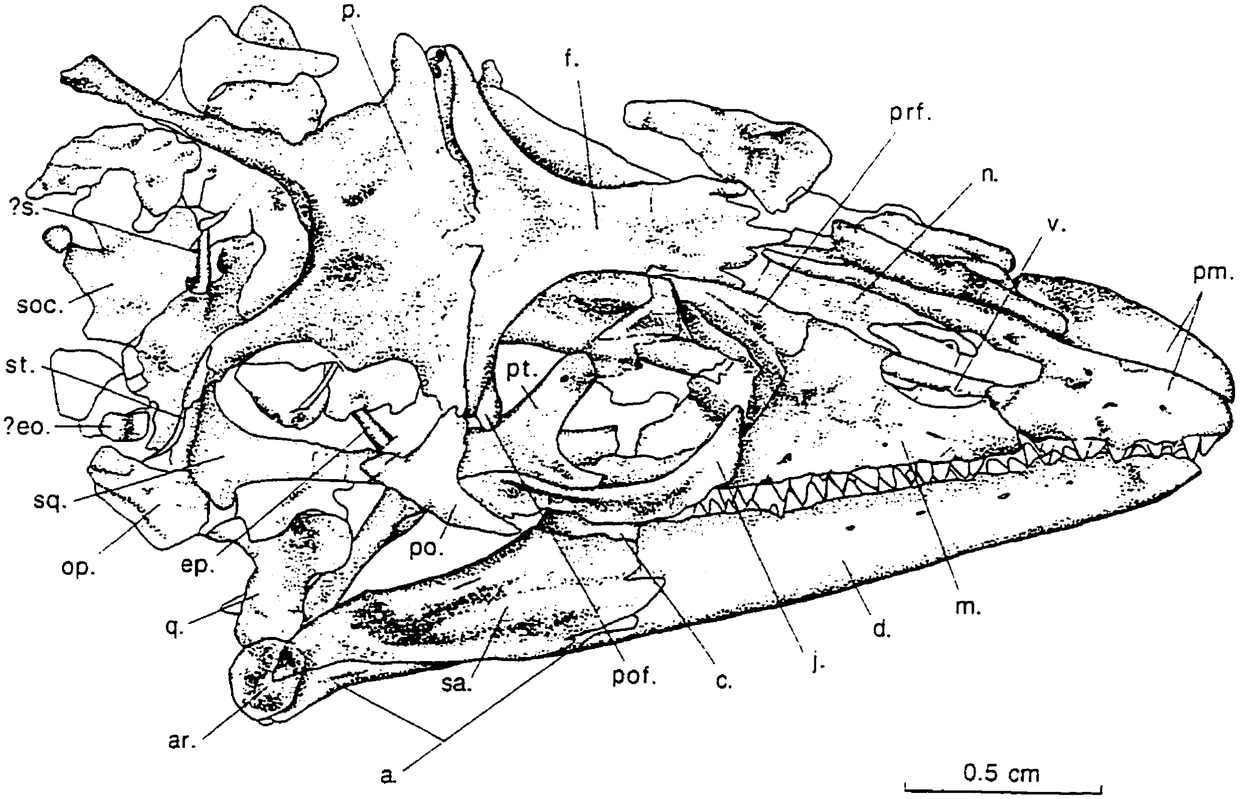

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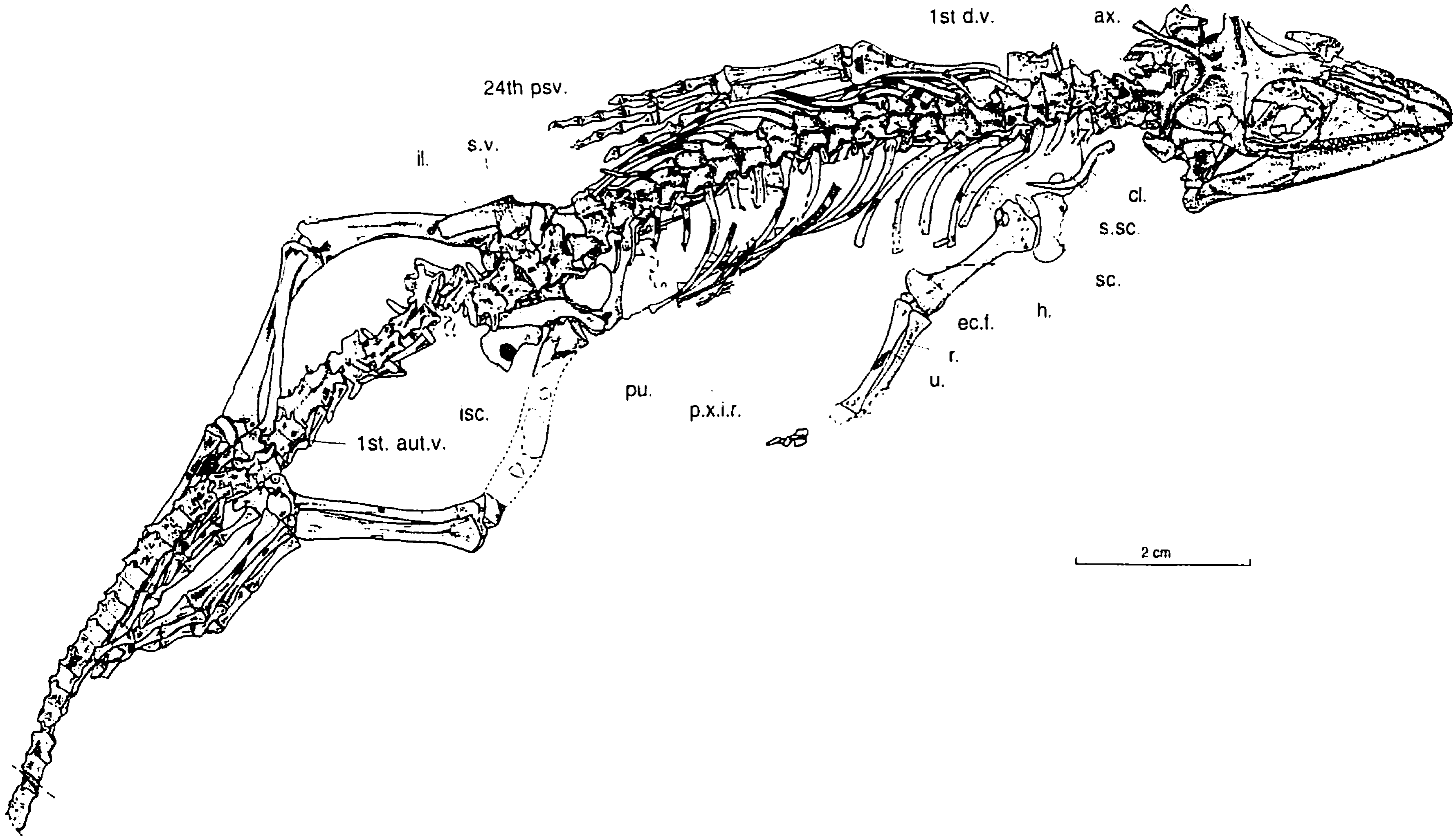
Fig. 23. Skeleton of the holotype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 7389) as preserved on the block.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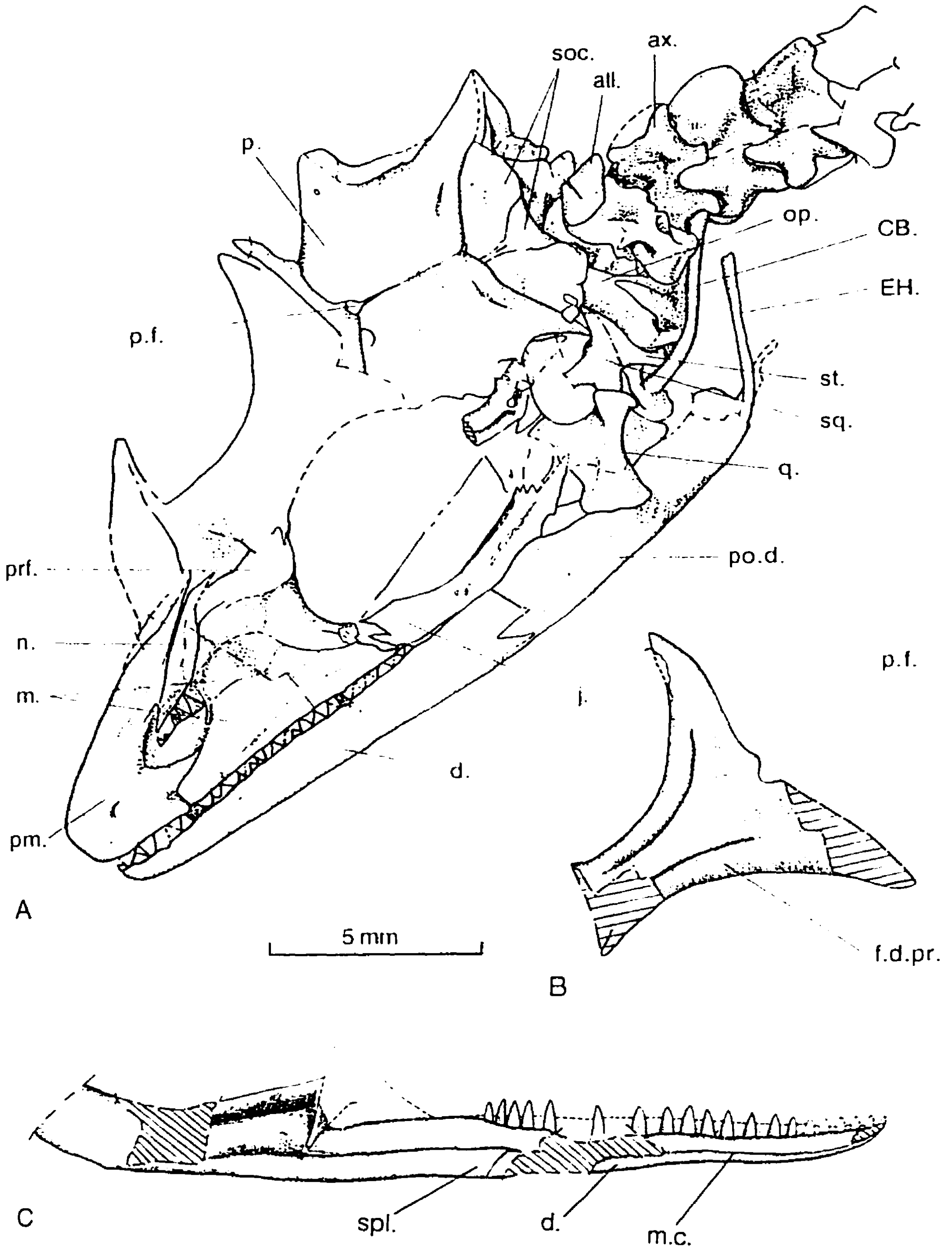
2 cm

covering the premaxillary narial process. However, in the holotype the nasals are crushed over the narial passageway exposing the narial processes of the premaxilla. The anterior margin of each nasal is strongly emarginated, placing the posterior margin of the external naris far back in the snout. A lacrimal could not be identified, but a small posterior process of the maxilla extending over the prefrontal might indicate the dorsal limit of this bone, suggesting that it has fused to the prefrontal. Only one lacrimal foramen penetrating the maxilla is evident. The jugal forms the entire ventral edge of a fully encircled orbit. Its posterior end is obscured by the postorbital, so it is uncertain whether it reach 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 two bones 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 slightly. separated anteriorly and a slight suture remain posteriorly (Fig. 24). 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 parallel between the orbits. Ventrally the descending process for the olfactory tract are very short (Fig. 24B).

Extensive lateroventral flanges on the lateral margins of the parietal indicate that the lower jaw adductor musculature originated on its dorsal surface. The short parietal table does not cover the anterior part of the occipital region. The lateral process is long and has a reduced supratemporal attached posteriorly. The parietal foramen is on the fronto-parietal suture as indicated in the juvenile specimen (Fig. 24A). In the adult, its presence cannot be established because this part of the skull is crushed.

Fig. 24. **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.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A
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B
C
spl.
d.
m.c.

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 to most squamates and similar in size and proportions to geckos and the Early Cretaceous lizard *Meyasaurus* (Evans and Barbadillo, in press). An enlarged somewhat curved posterior crest suggest that the quadrate was bowed outward. The different position in which the quadrate was preserved in the adult and juvenile skulls (compare Figs. 22 and 24), 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 centers 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.

As a result of the posterior displacement of the supraoccipital, some traces of the right stape are exposed in the holotype (Fig. 22). 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 sutured to the alar process of the prootic is visible through the upper temporal fenestra.

Little of the palate can be seen. Only the anterior margin of the pterygoid is well exposed through the orbit (Fig. 22). It broadly borders the posterior margin of a wide suborbital fenestra and has a long slender quadrate process.

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 since 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 condyle. 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 since 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 extends 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 retroarticular 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 impression on the counterpart block of the juvenile specimen (Fig. 24C). 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 center 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.

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 22, 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 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 determinated.

Hyoid apparatus

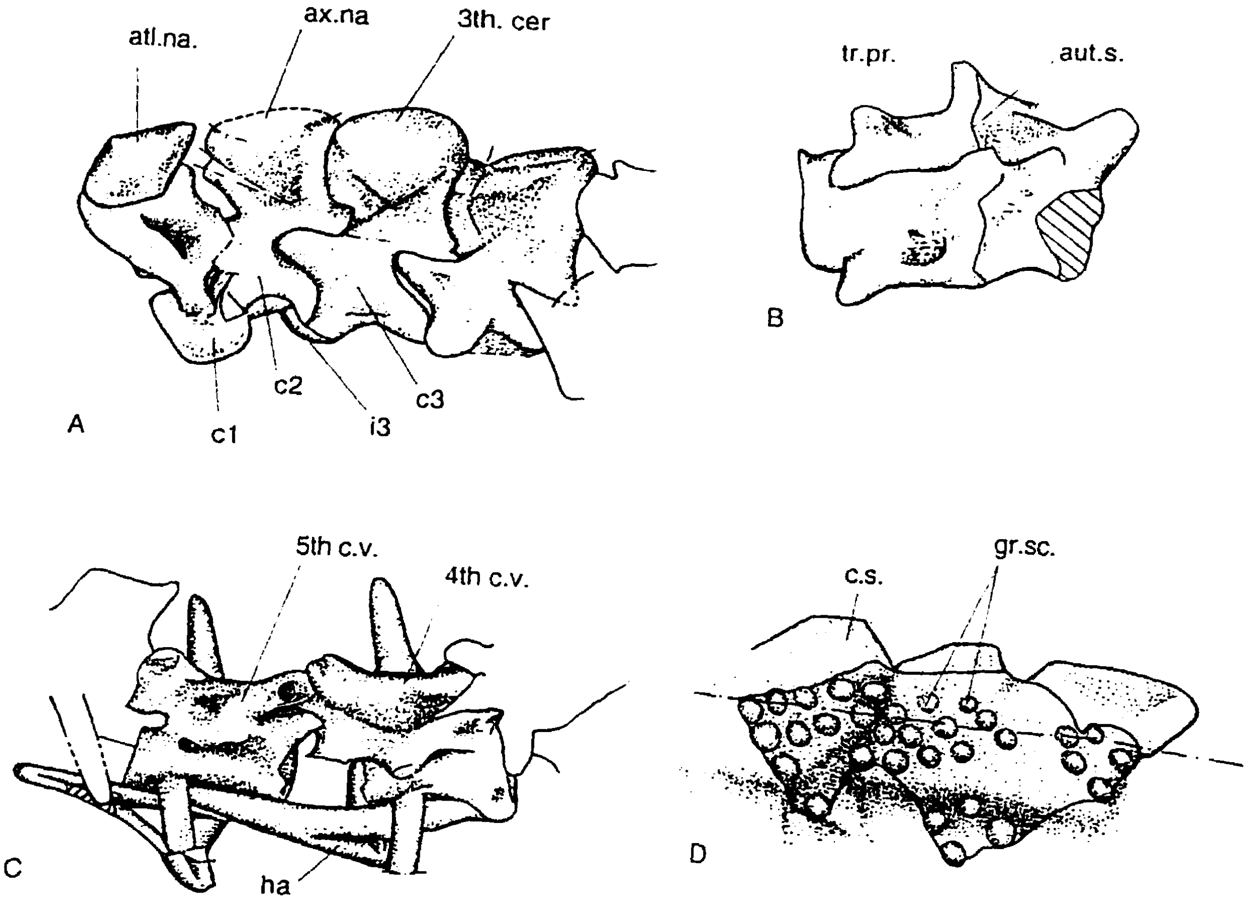
Some bones of the hyoid apparatus are preserved in the juvenile specimen (Fig. 24). According to their position the anterior was identified as the first ceratobranchial and posterior as the epihyal. The latter one, however, may be the hyoid cornu.

Postcranial axial skeleton

The vertebral column is composed by 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 fourth of the total caudal length (Fig. 25). 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 (Fig. 26B). 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

Fig. 25. Skeleton of the paratype of *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 4185) as preserved on the block.

Fig. 26. *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 (IGM 4185); B and C (IGM 7389). All scaled to about the same size.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category of Hoffstetter and 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 remain 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 (Fig. 26C). 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 to the posterior end and almost disappear at the level of the first autotomous vertebra. The lateral processes of the first six vertebrae projects slightly backwards, but by the seventh vertebrae they begin to point anteriorly. Autotomous 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; Fig. 26B).

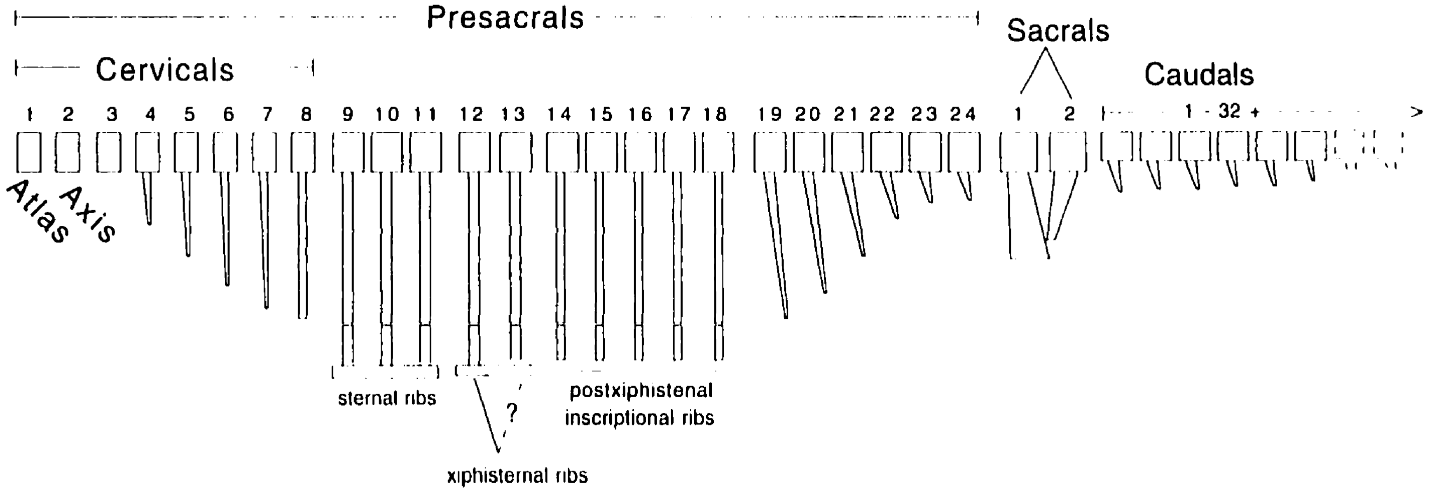
In the juvenile specimen, the thirty-second caudal vertebra is broken through the autotomous septa, and a regeneration segment, preserved as calcified cartilage, replace most or all of the original length of the tail. Regeneration tails are presented in the "paramacellodid" lizards *Tepexisaurus* from this same locality (Chapter 5) and in a scincomorph from Las Hoyas, in Spain (Evans pers. com. 1995). 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 (Fig. 26D).

Holocephalous cervical ribs are present from the fourth or fifth cervical vertebrae to the eighth (Fig. 27). The next three ribs are connected to the sternal plate via calcified cartilage, and another pair is attached to a mesosternum (Fig. 28A). 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 disorganized in the abdominal region; in the adult, they are broader and remain aligned with the ribs (Fig. 23). 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 reduce in size towards the sacral region. The sacral ribs are fully ossified to the sacral vertebrae and there is no posterior process or bifurcation of the second sacral rib. Dark material within the abdominal region may be remnants of stomachal contents, but no biotic morphology can be discerned.

Appendicular skeleton

In the juvenile, the junction between the coracoid and scapula is marked by a distinct suture (Fig. 28A). 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, but the timing of fusion in relation to the fusion of the metatarsal bones 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 partially preserved as calcified cartilage and an area of impression. It is a single unperforated plate, retaining the primitive lizard rhomboidal shape where the coracoid articulation is slightly shorter than the rib bearing

Fig. 27. Schematical reconstruction of the vertebral column of *Huehuecuetzpalli mixtecus* gen. et sp. nov.


Presacrals
Cervicals
Sacrals
Caudals
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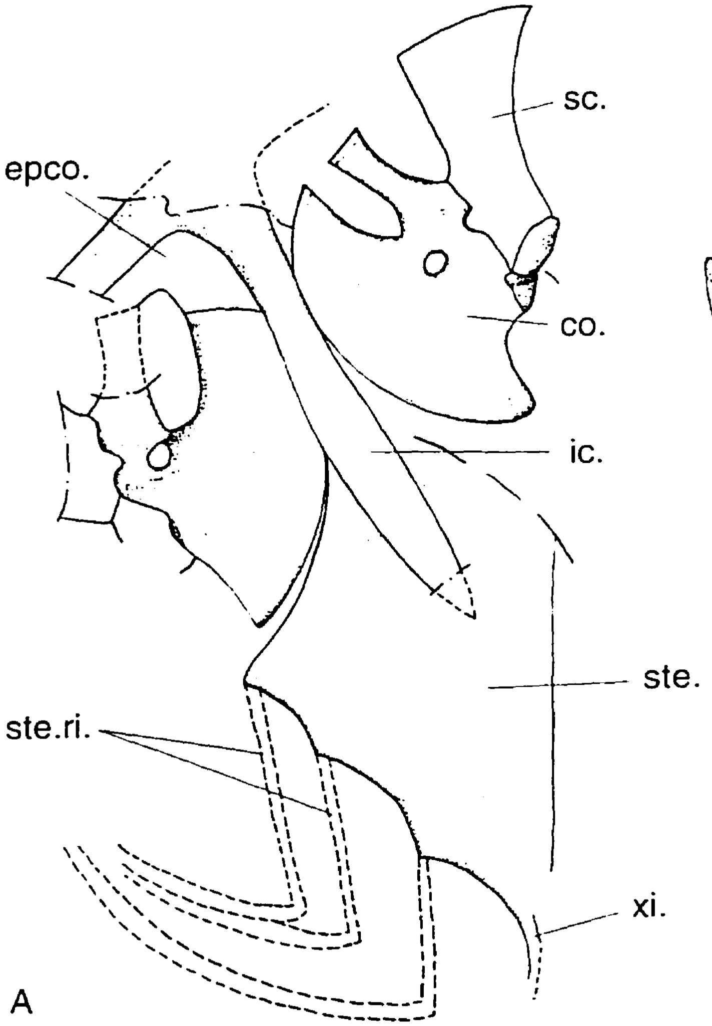
1 2
1 - 32 +
Atlas
Axis
sternal ribs
?
xiphisternal ribs
postxiphistenal inscriptional ribs

Fig. 28. *Huehuecuetzpalli mixtecus* gen. et sp. nov. (IGM 4185). **A**. Semireconstruction 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.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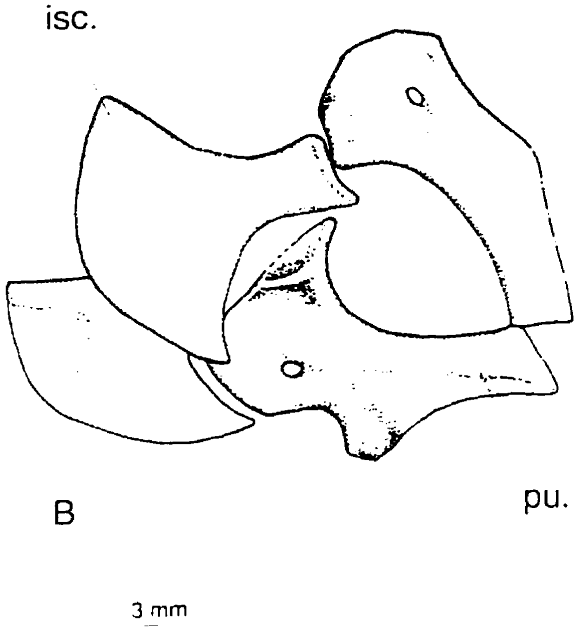
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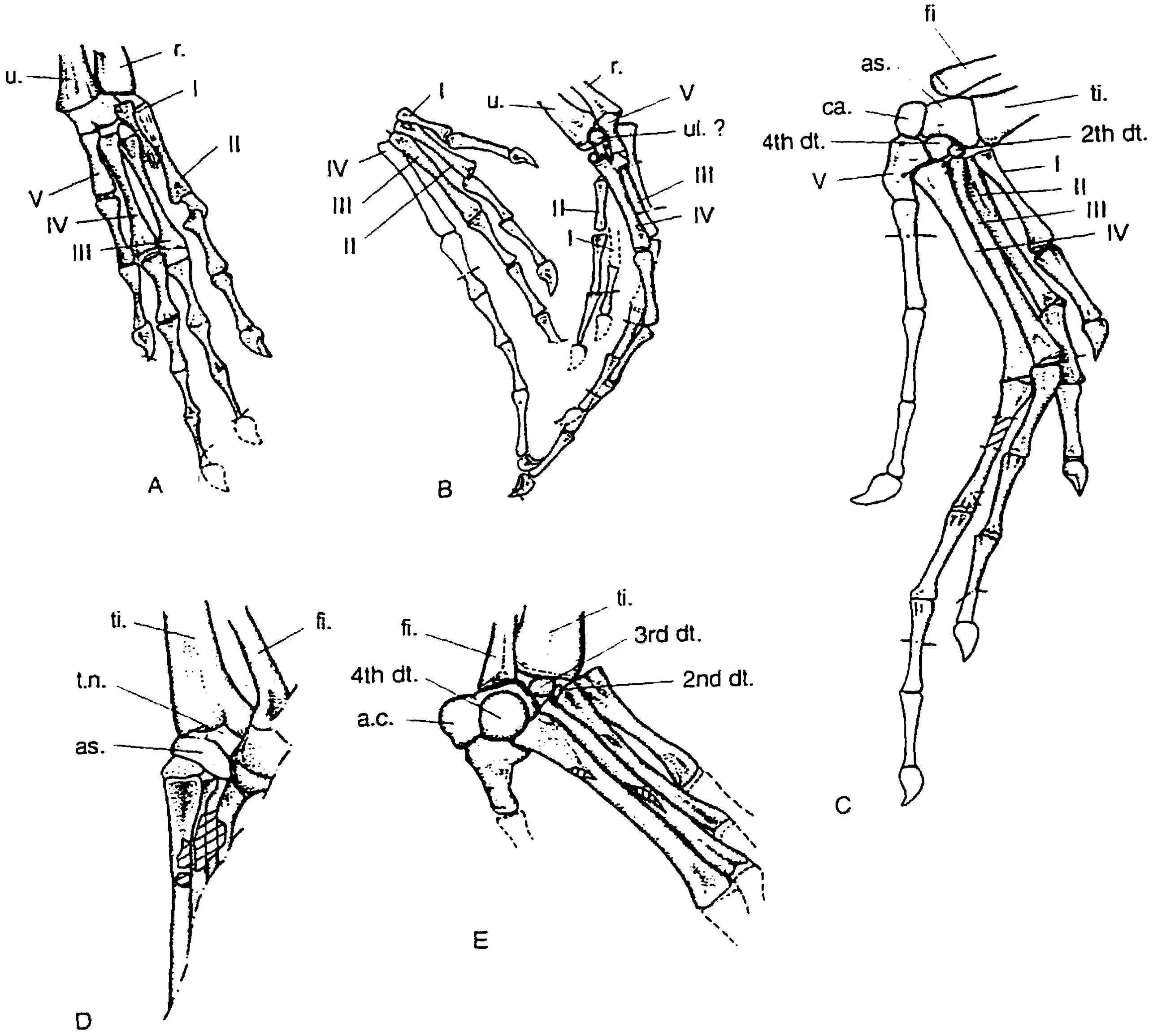
portion. The clavicles are rod-shaped and slightly curved. The lack of an acromial process on the scapula suggest that the clavicle was attached to the suprascapula (Lécuru 1968). The position of the clavicle as preserved on the adult specimen leads to the same conclusion.

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, relatively shorter than the femur (Table 8) and has a fully enclosed ectepicondylar foramen. The ulna and radius are subequal in breath and length. A rounded epiphyseal precursor of the olecranon remains free between the ulna and the humerus. A similar rounded element in the type specimen of *Bavarisaurus macrodactylus* (Hoffstetter 1964) is instead the condyle radiale. The carpal elements are badly preserved and cannot be described (Fig. 29). In the juvenile specimen the intermedium, fourth distal carpal, a structure that can be the ulnare or the fifth distal carpal, and another that can be the ulna epiphysis or the pisiform are preserved. The manus has long digits with a primitive squamate phalangeal count (3, 5, 4, 3, 2).

The symphysis of the pubis is short and flat, oriented perpendicularly (Fig. 28B). 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 this species. The ischium is distinctly rounded distally with a relative slender shaft.

The femur is long, straight, and has a distal lateral recess in which the fibula 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 (Fig. 29D). The astragalus and calcaneum are not fused but sutured in the juvenile specimen (Fig. 29C). The condition in the adult is

Fig. 29. *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**. Tibio/astragalar articulation on left limb. **E**. Tarsal and metatarsal on the right pes of the adult. A, D, and E (IGM 7389); B and C (IGM 4185). All scaled to about the same size.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unknown since the unusually enlarged fourth distal carpal obscures the proximal tarsals. A further primitive feature is the presence of a small second distal tarsal (Fig 29E), 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 and 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).

DISCUSSION

Ontogeny

With only two specimens it is impossible to trace a complete developmental series in *Huehuecuetzpalli*. However, changes in its early ontogeny may are of interest and may have 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 posthatchling stage when compared to the degree of ossification of *Lacerta agilis* (Rieppel 1994b). The complete fusion of the frontal, however, shows that it is older than Rieppel's specimen #18 and the hatchling of *Cyrtodactylus pubisulcus* (Gekkonidae) illustrated by Rieppel (1992b: fig. 1). The high degree of ossification indicates that it 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 to 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 relatively to the presacral vertebral column do not shows significant differences between the juvenile and adult specimens (Table 8), although these features usually change in ontogeny. This suggest that adult proportions were already acquired at the ontogenetic stage of the juvenile specimen in spite of its relatively smaller size.

The parietals, maxilla, and supraoccipital are not fully ossified. One third of the interparietal suture 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 determinated. However, the fact that the frontal and the parietal were easily separated and preserved separated in the counterpart blocks with no traces 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 the interparietal region ossify in the lates recognized post-hatchling stages (Rieppel 1992c). The closure of the frontoparietal suture precedes the total closure of the parietals at the midline, and the parietals are the last to fill the interparietal space behind the frontoparietal suture. The developmental stage of the smaller specimen of *Huehuecuetzpalli* is more advanced than the developmental stage of NMBE 1'011'297 of *Lacerta vivipara* and almost reaches the stage of MBS 5625 (Rieppel 1992c). In the later, 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 notice 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 by two ossification centers (Haluska and Alberch 1983). The dorsal part will become the ascending process of the maxillary while the ventral portion the support for the dentition. This two distinct ossification elements are present in very early stages of ossification in *Lacerta* (Rieppel 1992c; 1994b) and in the colubrid snake *Elaphe obsoleta* (Haluska and Alberch 1983), but not in chamaeleonines (Rieppel 1993). In *Lacerta* this two elements become fused in late prehatchling stages. In all known hatchling lizards, both ossifications centers are ossified into a single maxillary bone. Only in boyeniid snakes, among Squamata, do these bones remain separated until adulthood is reached (Frazzeta 1970). In *Huehuecuetzpalli* they remain separated after hatchling 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 center on the dorsal aspect of each otic capsule that fuses to a smaller supraoccipital precursor has been described in some lizards (Jollie 1960; Bellairs and 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 centers become fully fused into a single supraoccipital in hatchling lizards.

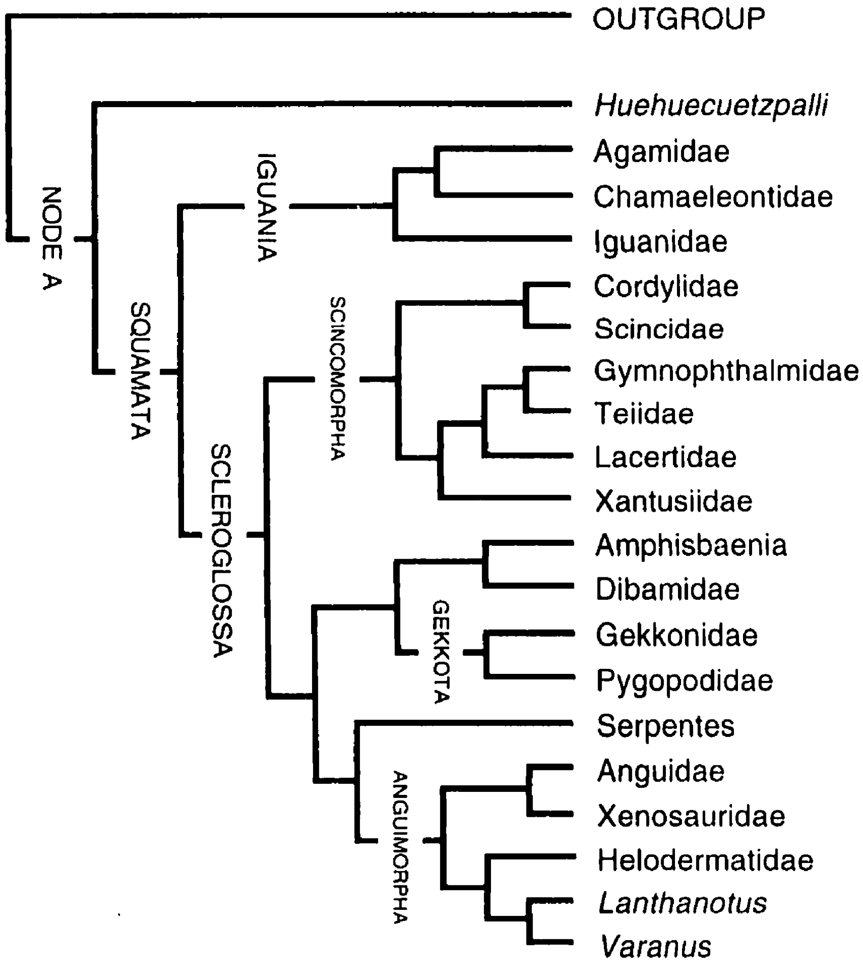
The presence of "prehatchling" features in an early fossil lizard can either be explained as a primitive condition later incorporated to the early development in modern lizards, or as being acquired secondarily through paedomorphosis in *Huehuecuetzpalli*. A final conclusion depends on the phylogenetic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

Phylogeny

To establish the phylogenetic position of *Huehuecuetzpalli* in the context of the Squamata, a cladistic analysis was carried out using a modified version of Estes et al.'s (1988, appendix table 1) data matrix. The single most parsimonious tree was obtained 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 ignored. Instead of using an average outgroup, younginiforms, *Saurosternon*, kuehneosaurids, and rhynchocephalians were used as a multiple outgroup. To reduce the number of resultant trees the incompletely known 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 1-36) listed by Estes et al. (1988, p. 186-187). To consider all available evidence, characters 185-187 of Clark and Hernández (1994) were included with some modifications. Character states for the diagnostic characters of the Squamata were taken from Gauthier et al. (1988a: 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 Appendix 4.1. Respective data matrices are presented separately for modified characters and new characters in Appendix 4.2. In data for *Huehuecuetzpalli*, "X" indicates gaps created in the data matrix after character combination.

The single most parsimonious hypothesis (Fig. 30) suggests that *Huehuecuetzpalli* is the sister-group of the Squamata (tree length 819, CI = 0.791, RI = 0.663; Appendix 4.3). 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

Fig. 30. Most parsimonious tree showing the sister-group relationships of *Huehuecuetzpalli* with Squamata. Analysis performed using an extended version of Estes et al. (1988) data matrix as presented by Clark and Hernández (1994) with several additional modifications. List of modified characters and character states is presented in Appendix 4.1, and data for *Huehuecuetzpalli* and other squamates is in Appendix 4.2. All characters are unordered and multistate characters are interpreted as polymorphism. Tree description: Tree length = 819, consistency index = 0.788, retention index = 0.661. Apomorphy list (only unambiguous characters): **Node A**: 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. **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 prior to cranial fusion, muscle rectus abdominis lateralis present, mid-dorsal scale row absent. A full description of the tree is given in Appendix 4.3.


OUTGROUP
NODE A
Huehuecuetzpalli
SQUAMATA
IGUANIA
Agamidae
Chamaeleontidae
Iguanidae
SCLEROGLOSSA
SCINCOMORPHA
Cordylidae
Scincidae
Gymnophthalmidae
Teiidae
Lacertidae
Xantusiidae
Amphisbaenia
Dibamidae
GEKKOTA
Gekkonidae
Pygopodidae
Serpentes
ANGUIMORPHA
Anguidae
Xenosauridae
Helodermatidae
Lanthanotus
Varanus

taxa (Estes et al. 1988: fig. 5, p. 136; Kluge 1989; Clark and Hernández 1994). Snakes came out as the sister-group of Anguimorpha, dibamids and amphisbaenians are sister-groups, branching off together as sister-taxa of gekkotans. As in 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) indicating the weakness of their results and diagnosis due to several flaws in their analysis (Kluge 1989). As an example, Autarchoglossa was defined by three characters: 1. no contact between jugal and squamosal; 2. dermal rugosities on skull; and 3. muscle *rectus abdominis lateralis* present. Of them, the first character is certainly primitive for Squamata; the second one 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. In contrast, unambiguous characters for Autarchoglossa in results here presented (Fig. 30) are completely different: 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 reorganization of the information in the basal nodes expands the transformation series beyond the limits of the Squamata. This possibility is explored further in Chapter 6.

The sister-group relationship of *Huehuecuetzpalli* with the clade comprising all crown squamates is supported by 15 synapomorphies: fused parietals and frontals, 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, squamate hooked fifth metatarsal, and gastralia absent. The primitive position of *Huehuecuetzpalli* relative to crown squamates is indicated by the unfused premaxillae, amphicoelous centra, and presence of a second distal tarsal, while derived states are synapomorphic for crown squamates. The presence of thoracolumbar intercentra and the possibly persistence of the exoccipitals as separated elements after hatchling are other characters rarely if ever present within Squamata. The position of *Huehuecuetzpalli* outside Squamata is well supported since Squamata appeares as a monophyletic assamblage excluding *Huehuecuetzpalli* in 70% of the trees in the 50% majority rule consensus tree resulting from subjecting the data matrix to bootstrap analysis (100 replicas; see Appendix 4. 3). Bremer's branch support values (Bremer 1988, 1994) indicates that only two steps are necessary to collapse squamates into the clade comprising Squamata + *Huehuecuetzpalli.*

In order to keep all crown squamates grouped together according to the definition given by Estes et al. (1988), *Huehuecuetzpalli* cannot be assigned to the Squamata in spite of the great number of characters shared by both taxa. By adopting this procedure the number of characters diagnosing the Squamata will drop considerably (Fig. 30).

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 due to 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 1994c) and it could easily be explained as convergent. The structure of the lower jaw is quite different in *Huehuecuetzpalli* in which the hinge is formed by the angular extending between the dentary and surangular, and not by a projection of the ventral part of the surangular between the dentary and the splenial.

A notch on the distal end of the tibia was considered a scleroglossan synapomorphy by Estes et al. (1988); however, the polarity of this character at the base of the Squamata is unknown since iguanians have a gently convex tibial distal end, while *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 base of results here presented, the presence of a tibial notch is better interpreted as 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. 1988a), and the presence of amphicoelous vertebrae in geckos 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 favored on the base of character congruence in current phylogenetic hypotheses (Kluge 1987; Gauthier et al. 1988a; Estes et al. 1988). The inclusion of gekkonids within Scleroglossa, the best supported clade in squamate phylogeny, is indicated by several characters (Fig. 30).

Explaining the evolution of these characters in *Huehuecuetzpalli* is more complicated since 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. According to the most parsimonious cladogram, the presence of these characters in *Huehuecuetzpalli* is better explained as primitive, with further transformation in crown squamates. However, if they are paedomorphic in *Huehuecuetzpalli*, the position of this genus in the cladogram might be incorrect.

Two alternative hypotheses of character transformation are suggested. Drawing an alternative scenario in which the presence of a divided premaxilla, amphicoelous vertebrae, and thoracolumbar intercentra are of paedomorphic origin in squamates and *Huehuecuetzpalli*, 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 these taxa. 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 suggests that paired premaxillae, amphicoelous notochordal vertebrae, and trunk intercentrum are reversed within many taxa, their condition as retained primitive characters is still a possibility since 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 1994c); *Eichstaettisaurus*, a possible gekkotan, has a divided premaxilla (other structures not known; Hoffstetter 1964); and *Parviraptor* (a possible anguimorph) preserves intervertebral notochordal canal (Evans 1994a). In addition, a second distal tarsal is present in some Early Cretaceous lizards from Las Hoyas (Evans pers. com. 1995). 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 fixed at the time when the major Squamata clades originated.

The morphology of the intervertebral articulation has receive 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 and 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 prearticular surface, which is covered by an extension of the perichordal sheath. In contrast with Evans (1994c, p. 48) interpretation, the development of procoelous vertebrae in squamates does not pass through a morphogenic stage similar to that of the amphicoelous vertebrae of the adult *Sphenodon*. In adult *Sphenodon*, the notochord is constricted only in the middle portion of the vertebrae (Howes and 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 and Bellairs 1976: fig. 3a). 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 not likely 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 and 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 reelaboration of intercentra.

The persistence of separated elements of the maxillae and supraoccipital through the juvenile stages of *Huehuecuetzpalli* can be explain 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 the adult stages. No separated elements are present during the development of *Sphenodon* (Howes and Swinnerton 1901) indicating that the presence of a single ossification center is primitive for lepidosaurs, and that the acquisition of separated centers of ossification in maxilla and supraoccipital is derived in squamates. This still leaves the question as to weather the late or early fusion of elements was the primitive condition within squamates. The presence of separated maxillary and supraoccipital ossification centers in *Huehuecuetzpalli* suggests that their fusion after juvenile ontogenetic stage is primitive; however, because this condition is unknown in other lizards, might be autapomorphic for *Huehuecuetzpalli.*

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 behavior, 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 that it is in most other lizards. Although forelimb/hind limb indices do not provide accurate information about locomotion behavior in lizards, some conclusions can be drawn. The limb proportions of *Huehuecuetzpalli* are intermediate between the bipedal lizard *Basiliscus* and some fully terrestrial forms (Table 9). This suggests that of one of these behavior or a combination of both was present. 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 behavior. The jaw structure of *Varanus* is adapted to catch relatively large and fast-moving prey (Rieppel 1979a). The varanoid's large, pointed, blade-like teeth are not present in the new genus, suggesting the preference for small prey (of insect size). Herbivory, limited to about a dozen lizard species (Ostrom 1963), is highly unlikely. The lack of biotic structures in the remnants of stomach contents in the juvenile specimen of *Huehuecuetzpalli* gives no indication about their diet; however, a more elaborate analysis of the contents might give additional information.

BIOGEOGRAPHY AND STRATIGRAPHIC SIGNIFICANCE

When reviewing the fossil record of squamates, it is interesting to notice 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 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 as a relict of an earlier lineage and new specimens in older deposits are expected to be discovered. As pointed out by Estes (1983b) relatively primitive squamate taxa (iguanids, chamaeleontids, agamids) could have had a Gondwanaland origin and diversification, based on their modern distribution and current phylogenetic hypotheses.

TABLE 9. 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 (1985a).

Genera	**Humerus**	**Femur**	**HRMc**	**FTMt**	**Humerus/ Femur**	**HRMc/ FTMt**	**behavior**
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	33	50.5	64.0	0.788	0.789	aquatic
Icarosaurus AMNH 2101	20.1	34.7	45.60	(63.1)	0.579	0.737	glider

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 definitive conclusions.

If 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 and Price 1973) and *Priscagama* from Mongolia (Borsuk-Bialynicka and Moody 1984). Although *Euposaurus* from the Late Jurassic of France was long time considered 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 1994b). Of the few character 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 two taxa. It is important to notice 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 1994a) and *Euposaurus* might be assigned to this group. The specific position of *Euposaurus*, however, cannot be established until new information becomes available.

SUMMARY AND 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 relationships with squamates is supported by 15 synapomorphies, but the presence of plesiomorphic characters rarely if ever seen in squamates, keep 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* indicate 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.

Appendix to Chapter 4

Appendix 4.1

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. (1988a; Appendix I; see below), and characters 185-187 are from Clark and Hernández (1994). Several characters were modified: Characters 19-20; 25-26; 28-29; 58-59; 60, 68, 70-71 (partially); 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 and Hernández 1994) is redundant to character 107 and was excluded; character 31 (character 179 of Clark and Hernández 1994) was combined with character 123. Character 185 of Clark and Hernández (1994) was combined with character 150 (Gauthier et al.'s 1988a character 3), and character 186 was modified.

Clark and Hernández (1994) modifications of states in Estes et al. (1988) data matrix were considered. All other characters were coded as presented by Estes et al. (1988) with exception of: Character 4 was recoded not applicable (N) in cases where the postfrontal or postorbital is absent. Character 7 was fully recoded since 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, since 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 *Tiliquia* (Gauthier et al. 1988a). 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 and Gasc 1969). Character 111 recoded (N) in Chamaeleontidae, the scapular fenestra of chamaeleontids might not be homologous to that of other lizards (Frost and Etheridge 1989). Character 115 and 118 recoded (N) in snakes and dibamids. The lack of clavicle and interclavicle in these forms is due to the loss of the shoulder girdle, a different condition from that of (e.g.) chamaeleontids. Character 115 was recoded and (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*; Zangerl 1945) lack clavicles but does have 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*. Polarity of characters 95-96 (here character 95), 103, and 145, was reverted.

Abbreviations: 0 = primitive conditions; 1, 2, 3, 4, 5 = derived states; ? = unknown; N = not applicable; X = excluded. In brackets: CH = Clark and Hernández (1994); E = Estes et al. (1988); FE = Frost and Etheridge (1989); G = Gauthier et al.

(1988a); 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.

Modifications to Estes et al. (1988) characters:

2 (rewritten). Nasal/maxilla structure: in contact (0), separated by external nares (1); [R11][PGG3, 4][P61]. Comment: External nares are considered retracted only if the nasals and the maxilla loss 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 frontal contact 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 *Chamaleo* (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][FE5].

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); [FE16][P70][PGG45]. Comments: Estes' et al. (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, 1979b).

71 (divided). Structure of the coronoid/surangular articulation: surangular restricted to the lateroventral margin of the coronoid process (0), surangular overlaping 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. Here are considered together since both belong to the same transformation series.

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 *Xantusiia* (Hoffstetter and 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). 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 and 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).

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 deep (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, usually imperforated (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: continuos (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). Merged to character 107. See Appendix 4.1

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). Intermedium size/contact: large, contacts ulna (0); small, absent, does not contact ulna (1)

176 (G102). Lateral centrale/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). Combined to character 123. This Appendix.

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-groove articulation (2)

182 (G132). 132.- 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). Merged to character 150. This Appendix.

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)

Appendix 4.2
Data matrix

Data for Estes et al. (1988) 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
Kuehneosauridae	0	0	0	0	0	?	0	1/3	0	0	N	N
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?
Younginiformes	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

New incorporated 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

Data for *Huehuecuetzpalli*: (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 21??? ?12X1 ?201X 0?

Appendix 4.3

Analysis and results

```
Data matrix has 24 taxa, 187(-18=169) characters
All uninformative characters ignored
Valid character-state symbols: 012345
Missing data identified by '?'
Not Applicable identified by 'N', treated as "missing"

Designated outgroup taxa:
   Rhynchocephalia
   Kuehneosauridae
   Saurosternon
   Younginiformes

Current status of all characters:
    All character 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:
   Addition sequence: random
      Number of replicates = 100
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

   Shortest tree found at replicate number 2

Tree description:
   Unrooted tree(s) rooted using outgroup method
   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree length = 819
Consistency index (CI) = 0.791
Homoplasy index (HI) = 0.744
Retention index (RI) = 0.663
Rescaled consistency index (RC) = 0.525
```

```
Tree number 1:

     /------------------------------------------ Huehuecuetzpalli
     |                                    /----- Agamidae
     |                              /----25----- Chamaeleontidae
     |    /------------------------26----------- Iguanidae
     |    |                               /----- Anguidae
/---46    |                    /---------27----- Xenosauridae
|    |    |               /---30    /----------- Helodermatidae
|    |    |               |    \---29     /----- Lanthanotus
|    |    |          /---31         \----28----- Varanus
|    \---42          |    \--------------------- Serpentes
|         |    /----35                    /----- Amphisbaenia
|         |    |     |              /----32----- Dibamidae
|         |    |     \-------------34     /----- Gekkonidae
|         |    |                    \----33----- Pygopodidae
|         \---41                          /----- Cordylidae
|              |          /--------------36----- Scincidae
|              |          |               /----- Gymnophthalmidae
|              \---------40         /----37----- Teiidae
|                         |    /---38----------- Lacertidae
|                         \---39---------------- Xantusiidae
\----------------------------------------------- OUTGROUP

Apomorphy lists: (* = ambiguous characters)

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
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)
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

Bootstrap:

```
Bootstrap method with heuristic search:
   Starting seed = 1
   Number of bootstrap replicates = 100
   Bootstrap sampling over non-excluded/non-ignored characters only
   Addition sequence: random
      Number of replicates = 5
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 200
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

Bootstrap 50% majority-rule consensus tree

     /-------------------------------------- Huehuecuetzpalli(1)
     |                                /----- Agamidae(2)
     |                          /-67--+----- Chamaeleontidae(5)
     |     /---------81---------+----------- Iguanidae(11)
/100-+     |                          /----- Anguidae(3)
|    |     |    /---------70----------+----- Xenosauridae(20)
|    |     |    |                     /----- Amphisbaenia(4)
|    |     |    +---------60----------+----- Dibamidae(7)
|    \-70--+    |                     /----- Cordylidae(6)
|          |    |    /-------60-------+----- Scincidae(15)
|          |    |    |                /----- Gymnophthalmidae(9)
|          |    +-68-+          /-97--+----- Teiidae(17)
|          \-96-+    |     /-70-+----------- Lacertidae(12)
|               |    \-81--+---------------- Xantusiidae(19)
|               |                     /----- Gekkonidae(8)
|               +---------88----------+----- Pygopodidae(14)
|               |               /----------- Helodermatidae(10)
|               +------100------+     /----- Lanthanotus(13)
|               |               \-85--+----- Varanus(18)
|               \--------------------------- Serpentes(16)
\------------------------------------------- OUTGROUP
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CHAPTER 5

A NEW SCINCOMORPH LIZARD FROM THE EARLY CRETACEOUS OF PUEBLA, MÉXICO

A NEW SCINCOMORPH LIZARD FROM THE EARLY CRETACEOUS OF PUEBLA, MÉXICO

INTRODUCTION

Scincomorphs are among the earliest known fossil lizards. Scattered material and isolated diagnostic elements have been collected in the Middle Jurassic deposits of Britain (Evan 1993; in press). Early scincomorphs have been included within the Paramacellodidae (Estes 1983a), a cordyloid-like assemblage that resembles extant cordylids in the presence of compound ventral osteoscutes and weakly keeled, non-compound, rectangular dorsal osteoscutes that cover the body in overlapping series. These characters are only known in the genus *Paramacellodus* from the Early Cretaceous of Purbeck, England (Hoffstetter 1967) and in *Sharovisaurus* from Kazachstan (Hecht and Hecht 1984) in which the scuttelation pattern is similar to that of the Cordylinae. Other taxa referred to Paramacellodidae share only a similar lower jaw structure that does not differ greatly from modern cordylids. Osteoscutes are not known for these taxa, making their identity as paramacellodids dubious. In Europe, *Paramacellodus*, *Becklesius*, *Saurillus*, *Pseudosaurillus*, and *Saurillodon* have been described from the Oxfordian/Kimmeridgian deposits of Guimarota, in Portugal and from Purbeck (Seiffert 1973; Estes 1983a; Ensom et al. 1991; Evans 1993). Prothero and Estes (1980) reported *Paramacellodus* from the Late Jurassic of Wyoming, USA, but the earliest appearance of the family can now be extended to the Bathonian where *Saurillodon*, a lizard with possibly reduced limbs, and two other unnamed genera were reported from the deposits of Kirtlington (Evans 1993). Other early scincomorphs include *Ardeosaurus* reviewed recently by Evans (1994c) who removed it from the Gekkota (Hoffstetter 1964) and placed it in Scincomorpha (more probably just Scleroglossa) based on the structure of the temporal region. *Mimbobecklesisaurus* was described from skeletal fragments from the Upper Jurassic of the Gansu province of China (Li 1985), and another complete xantusiid-like scincomorph was reported from the Late Jurassic of the Morrison Formation (Chure 1992, Evans 1995).

The Albian deposits of the Tlayua formation, Tepexi de Rodríguez, Puebla, have yielded an interesting assemblage of superbly preserved lepidosaurs that includes an unusual beaded sphenodontian (Reynoso in press; Chapter 2), an equally unusual aquatic sphenodontian with ankylosed teeth and pachyostotic skeleton (Chapter 3), and a primitive lizard with varanid-like skull (Chapter 4). A complete skeleton of a new scincomorph relatively more primitive to scincoid lizards is here described. Its exquisite preservation adds significant information to the pre-scincoid morphology and clarifies the phylogenetic position of early scincomorphs in relation to modern lizards.

SYSTEMATIC PALEONTOLOGY

LEPIDOSAURIA Dumeril and Bibron, 1839

SQUAMATA Oppel, 1811

SCINCOMORPHA Camp, 1923

TEPEXISAURUS gen. nov.

Type species- *T. tepexii*

Etymology- From *tepexi* (Náhuatl), red stone; and *sauros* (Greek) lizard. Lizard of the red stones, in allusion to the red color of the Tlayua deposits.

Diagnosis- As for the type and only known species

TEPEXISAURUS TEPEXII sp. nov.

(Fig. 31)

Holotype- Instituto de Geología, Universidad Nacional Autónoma de México, Cat. No. IGM 7466 (Fig. 31). Well preserved skeleton with the head separated from the body and part of the tail missing. The skull, atlas and axis are visible in ventral view, and the postcranial skeleton in dorsal view.

Etymology- For Tepexi de Rodríguez municipality where the Tlayua Quarry (the type locality) is located.

Locality- Tlayua Quarry, Loc. No. IGM-370 Cantera Tlayua Aranguty. No level specified. The Tlayua Quarry is located 2 Km South East of the Colonia Morelos, near Tepexi de Rodríguez, Puebla, México.

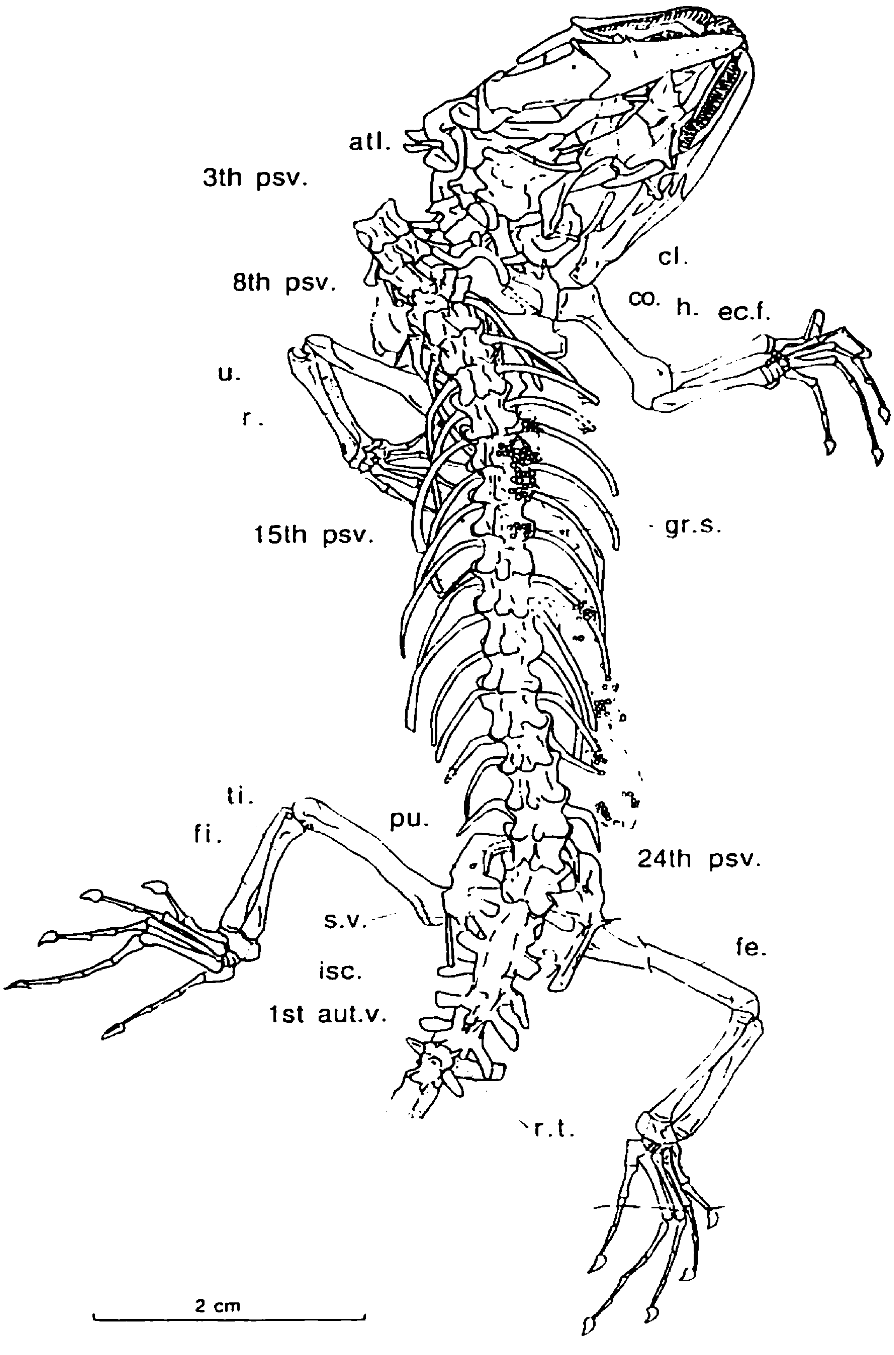
Horizon- Middle Member of the Tlayua Formation (Pantoja-Alor 1992). Early Cretaceous, Middle or Late Albian (Seibertz and Buitrón 1987).

Diagnosis- Scincomorph lizard with 29 small maxillary teeth packed closely and the coronoid overlapped strongly by the dentary and surangular. Differs from other scincomorphs in the presence of 23 presacral vertebrae (shared with *Ardeosaurus*), scapular emargination, epipterygoid ventrally expanded, and cervical intercentra ventrally flat. Shares with scincoids the presence of a small medial flange on the retroarticular process and weak zygosphene and zygantrum articulations, but lack dorsal and ventral osteoderms.

DESCRIPTION

The holotype and only known specimen of *Tepexisaurus tepexii* is exquisitely preserved but crushed (Fig. 31). The head, atlas-axis complex and clavicles are visible in ventral view, and the rest of the postcranial skeleton is exposed in dorsal view. The specimen is fully articulated and lacks the ilia and the end of the tail. The ilia presumably remain attached to the counterpart block that unfortunately was not collected. Some damage is observed on the dorsal surface of the sacral region and first caudal vertebrae. As in other Tlayua lizards, there is no significantly breakage of the bones despite of the

Fig. 31. Skeleton of *Tepexisaurus tepexii* gen. et sp. nov. (IGM 7466) as preserved on the block.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flattening of the skeleton into a single plane. Palatal bones are deformed following the contour of the elements beneath, and the head was compressed in a manner to expose simultaneously the left and right lower jaw in medial and lateral view, respectively. The left side of the palate and the braincase are well exposed providing a great deal of information. Some details of the dermatocranium can be observed through the empty spaces of the palate and lower temporal fenestra. Remnants of dermal scales and soft tissue are preserved on some vertebrae and ribs. The complete ossification of all tarsals and carpals, the fusion of the astragalocalcaneum, scapula and coracoid, and the olecranon process to the ulna suggest that the specimen is an adult.

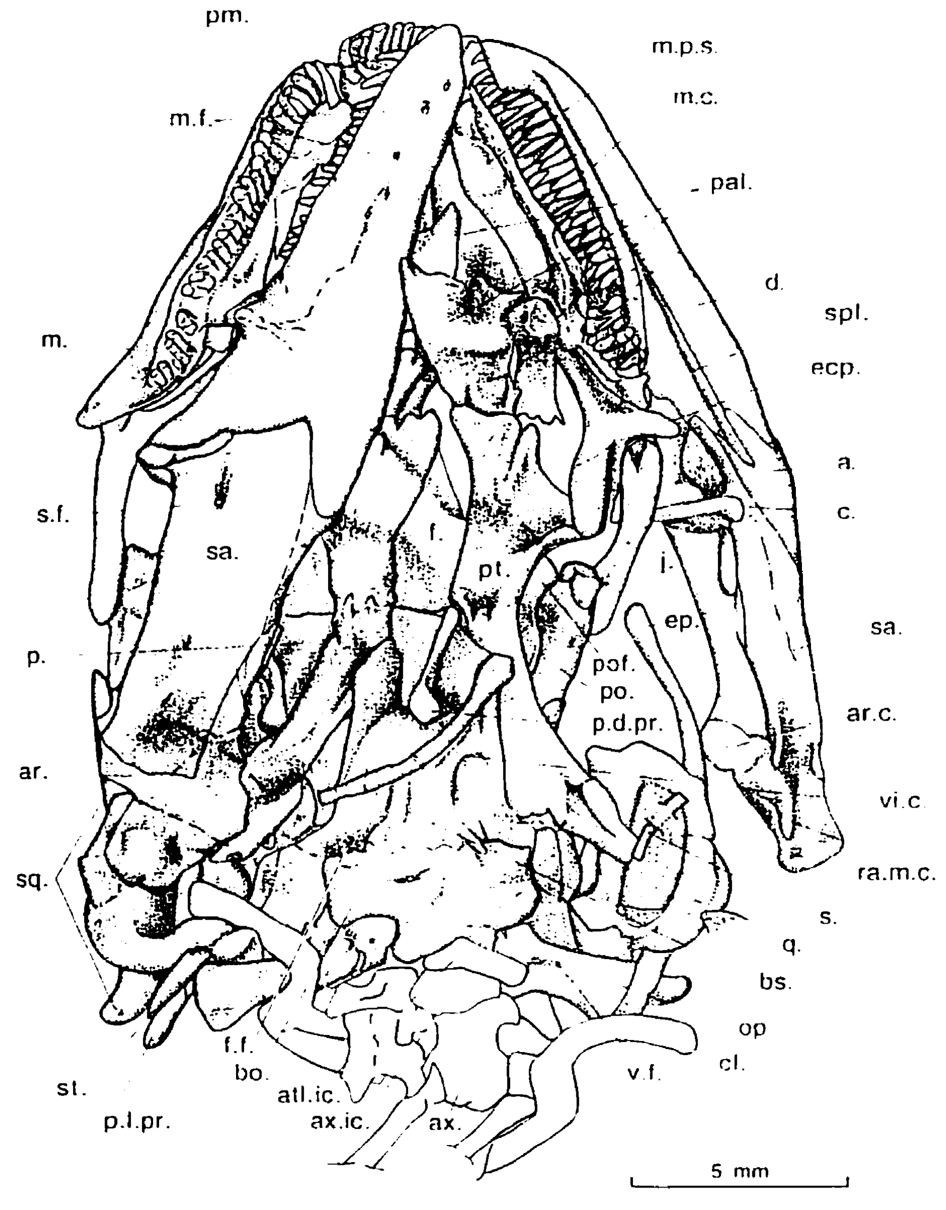
Skull

The skull is large and broad with a short snout that measures about one third of the skull length (Fig. 32). Its total length, measured from the tip of the premaxilla to the occipital condyle, is about 30% of the presacral vertebral column (Table 10). The right mandible is laying on top of the right side of skull obscuring details of anterior portion of the palate.

Little except the dentition can be observed on the premaxilla. Only 11 teeth are exposed, but the lower jaw appears to be covering at least two extra ones giving a total count of 13. The teeth are conical and slightly curved with sharpened tips. Whether or not the premaxillary bones are fused is not known.

The right maxillae is preserved in ventral view and the left in medial view. In ventral aspect, a wide shelf extends medially from the base of the tooth series. The maxilla retains approximately the same width throughout most of its length except posteriorly where it tapers. The tooth series terminates posteriorly slightly beyond the anterior end of the orbit, but the maxilla continues posteriorly as a postero-lateral directed process to about the mid point of the orbit. A cup-shaped depression on the margin of the last third of the maxilla is the facet for the palatine. The contact is relatively slender and comparable to that

Fig. 32. Skull of *Tepexisaurus tepexii* gen. et sp. nov. (IGM 7466) as preserved on the block.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of lacertids and anguids. A longitudinally oriented facet for the reception of the anterior process of the ectopterygoid is also present a short distance posterior to the articulation with the palatine, suggesting that the maxilla was almost excluded from the suborbital fenestra.

The pleurodont teeth are covered extensively by the labial margin of the maxilla. They are cylindrical, unicuspate, and although somewhat recurved anteriorly, they become straight caudally. Their shape is similar to those of *Becklesius* (Richter 1994a). The tips of the teeth also tend to change shape from nearly conical anteriorly to more laterally compressed posteriorly. The posterior teeth of the right maxilla appear to have blunt tips. Comparison with the sharply pointed teeth on the posterior left maxilla shows this condition was caused by compression. Twenty-nine tooth positions can be counted on both sides. The mode of replacement is obscure. Small posterolingual pits typical of scincomorphs are not obvious but they might be not preserved. The lack of enlarged replacement pits at the base of the teeth suggest that the iguanian-type replacement (Edmund 1960) was not present. In the right maxilla a small replacing tooth appears adjacent and slightly posterior to tooth number five. Similar teeth are present on positions 11, 17, 20, and 25 of the left side, but the older teeth were already shed.

Only small areas of the frontal are visible on this specimen. A short length of the left lateral margin shows the location of part of the left orbit. The strong ventral cristae cranii can be traced alongside this margin under the deformed overlying palatal bones. Both ridges begin medial to the posterolateral corners of the frontal and converge anteriorly. The contact between the paired descending processes of the frontal is uncertain, since the deformed area of the left pterygoid appears to outline the wall of the aerial groove. Whether the frontals were paired or fused cannot be determined. A straight, transversely oriented fronto-parietal suture can be observed on either side of the right pterygoid. .

Projecting ventrally from the parietal are a pair of narrow, elongated crest-like processes that partially wall the lateral part of the braincase. Swollen ends very similar to those of the cordylids (e.g. *Cordylus campbelli*) articulate with the epipterygoids as in most scincomorphs, although in the holotype the epipterygoids are disarticulated. The presence of a parietal foramen and the paired or fused condition of the parietals cannot be confirmed because the right pterygoid and sphenoid obscure this region. Neither parietal tabs underlying the frontals nor a fossa for the reception of these tabs on the ventral surface of the frontal are present, as they are in gymnophthalmids. The medial position of parietal downgrowths and the structure of the postorbital bones (see below) suggest that the adductor musculature was attached to the ventral surface of the skull roof. The tip of a long and slender supratemporal process of the parietal is exposed posterior to the suspensorium.

The prefrontals are covered by the left and right palatines and the dentary, but deformation of the palatal elements as they were crushed down onto the skull table provides a rough outline of these bones. In most lizards the prefrontals are thick bones with medially expanded projections that form the anterior wall of the orbit. The posterior ends of the masses beneath the deformed palatine delimit the anterior boundaries of the orbits but no other details can be discerned.

Both sturdy jugals are present. The right jugal is exposed in ventral aspect and the left in medial. In ventral view, the jugal is straight along the postorbital region. It tapers dorsally, lapping under the ventrolateral edge of the postorbital. A small foramen pierces the posteroventral margin close to the most posterior contact with the maxilla. The maxillary process of the jugal extends under the orbit, but the contact with the prefrontal is unknown. In medial view, the jugal is slightly curved and somehow constricted behind the orbital rim. Near the ventral-most end is the facet for the ectopterygoid. The jugal does not contact the postfrontal, but abuts very close to it and does not approach the squamosal.

The postfrontal and postorbital are better seen on the left side of the temporal region. Both bones remain in articulation and are not fused together. They extend caudally and board the lateral edge of the parietal. The upper temporal fenestra is closed at least to the level of the anterior tip of the squamosal, but whether it is closed throughout the remainder of its length is unknown.

The postorbital is flat and mainly horizontal, forming part of the skull roof. A jugal process is very small or absent. The postfrontal is a broad element, of about the same width as the postorbital. In spite of its total width in ventral aspect, the bone might be only exposed slightly in dorsal view, as in cordylids.

The suspensorium is supported by the squamosal, the supratemporal and the paraoccipital process. Only the anterior and posterior tips of both squamosals are exposed. The posterior ends are sharply curved suggesting the presence of the typical scleroglossan J-shaped squamosal, although the presence or absence of the squamosal dorsal process is uncertain. The supratemporal lies deep between the posterior end of the squamosal, parietal, and paraoccipital process.

Most of the vomerine region of the palate is obscured by the right dentary and the vomerian process of an anterolaterally displaced right palatine. Only a very small portion of the lateral concave emargination that boarders the internal naris of the right vomer is exposed. Laterally, the internal naris parallels the straight medial margin of the maxilla, and medially is concave, following the lateral expansion of the vomer. The posterior boundary of the internal naris is located slightly posterior to the palatine/maxilla contact.

The outline of the palatine is trapezoidal. Anteriorly, the vomerine process of the palatine projects more anteriorly than the maxillary process and the area between these processes is vaulted dorsally to form the posterior and lateral walls of the naris. The maxillary process is preserved with the articulation facet facing ventrally. The vomerine process of the palatine seems to end freely without a superficial ventral contact with the vomers. This is suggested by the way the vomerine process of the left palatine is preserved, overriding the body of the right palatine and dentary, and by the way the right palatine has become similarly displaced over the vomers. The flange formed anteriorly by the vomerine process might have provided a secondary passage for the choana, extending the narial passageway further back into the mouth. The articulation with the pterygoid is extensive, almost transversally oriented, and interdigitated. Interdigitations are small and rounded, probably forming a kinetic hinge (Frazzetta 1962). Depending on how much spreading distortion is allowed in the postmortem flattening of the skull, the palatines may be restored as just touching or separated at the midline. The lack of a facet on their medial margin suggest that the palatines were most probably separated.

The ectopterygoid is triradiate. The lateral process is elongated and fits into a medial articulating facet of the jugal. The anterior process extends forward, almost reaching the maxilla/palatine contact, therefore almost excluding the maxilla from the suborbital fenestra. The entire anterolateral surface forms a flange that fits into a groove on the maxillary posteromedial edge. The pterygoidal process is broad and crushed flat as is the rest of the skull. An originally more vertical position is suggested by the decoupling of the ectopterygoid from the articulation facet of the pterygoid.

The pterygoid lacks teeth on its ventral surface. The palatine process is broad, with its medial part projected more anteriorly. The lack of medial facets on either anterior tip suggests that the pterygoids were separated by a broad interpterygoidal vacuity. The ectopterygoid process bears an enlarged and ventrally oriented transverse flange that runs from the ectopterygoid contact to the central body of the pterygoid, broadening medially. The central body is broad and somewhat short anteroposteriorly. It lacks the medial process for the basipterygoid. The basipterygoid facet, is located posterior to the point where the quadrate process diverges from the central plate. The quadrate process of the pterygoid is long and slender in ventral view. At its posterior end, the process curves laterally and tapers distally to form a lateral facet where the quadrate abuts. The quadrate process maintains a primitive condition and is broadened distinctively dorsoventrally as in most iguanians.

The long, slender epipterygoids are displaced the right on top of the braincase and the left covered partially by the quadrate. The ventral end is swollen to almost twice the diameter of the shaft and rounded at its articulation with the pterygoid. The dorsal end has approximately the same diameter as the shaft. Both epipterygoids are bowed equally with the convexity facing posteriorly, suggesting that this is their natural shape.

The left quadrate is preserved in posterior aspect, and the right is crushed and twisted to expose the cephalic condyle. In posterior view, the quadrate is D-shaped and imperforate. The tympanic crest is broad throughout its length. A thick crest boarding the lateral edge of the quadrate emargination is apparently formed by the compressed lateral margins of the quadrate lateral conch suggesting that the lateral conch was not only wide but also distinctively deep. On the medial side of the quadrate there is a small crest that extends from the cephalic condyle to the mandibular condyle. The ventral portion of the medial crest seems not to be modified as a lappet for the pterygoid, but this condition is uncertain since this part is obscured by the overlying quadrate process of the pterygoid. The conspicuous posterior curvature of the posterior quadrate crest suggests a strongly bowed quadrate in lateral view. The cephalic condyles are smooth surfaces separated by a medial groove. They probably contacted the posterior end of the temporal arch and the paraoccipital process, permitting a great amount of streptostyly. The mandibular articulations are also smooth and separated by a groove. The groove suggest the presence of a ridge on the mandibular counterpart. A broken medial portion of a slender stape, similar to the stapes of other squamates, lies on top of the quadrate lateral conch.

Although the braincase region is heavily compressed and distorted, several important features can be discerned. The suture between the basisphenoid and the basioccipital is faint, but clearly interdigitated. Anteriorly, the basipterygoid processes are elongated, but do not seem to be very broad in the condylar region. The parasphenoid process is either not preserved or is bent backwards and obscured by the left parietal downgrowth. The basisphenoid is transversely narrow on its central portion. Wide lateral wings represent a recessus jugularis and not an expanded crista lateralis. Two small parallel ridges delimit the lateral edges of the medial region of the basipterygoid. This portion has been flattened exposing the lateral margins. On the left side, the crista prootica (also out turned because of compression) marks the most lateral margin of the braincase. A small depression on the anterior region indicates the position of the posterior opening of the vidian canal, but the perforation itself is not evident. More posteriorly, on the paraoccipital process and close to the midline is a small foramen facialis. The position of the suture between the prootic and basisphenoid is uncertain, so it cannot be said which bone is pierced by the jugular vein, although it is clearly enclosed by the crista prootica. If the suture in Figure 32 is correctly identified, then the vidian canal traverses the suture between both bones as in some skinks and cordylids. The distorted basioccipital shows a well developed sphenooccipital tubercle. The occipital condyle is mostly obscured by the atlantal hypocentrum.

Under the lateral margins of the crista prootica and parallel to the sphenooccipital tubercles are two heavily compressed lateral processes that resemble the alar process of the prootic in lacertids. At the posterior part of the skull, a fused opisthotic-exoccipital is turned anteriorly leaving only the posterior face exposed. As in other squamates, they are oriented slightly backwards, and the broad distal ends contact mainly the quadrate. A pair of vagal foramina are exposed on the dorsal surface close to the occipital condyle.

Mandible

The structure of the lower jaw is similar to that of scincoids and xantusiids. The robust dentary is distinctly wider in the region around the postdentary articulation (Fig. 32). The anterior end of the dentary is less robust and tapers close to the end. Five or six foramina mentalia pierce the anterior half of the bone. The posterior end is notched to receive a similarly robust surangular. A lateral process extends dorsally, overlaying laterally the coronoid, almost covering it up to the apex. The posterior process of the dentary extends dorsally to almost level the tip of the coronoid. Ventrally, the dentary extends posteriorly to fit in an anterior notch of the angular.

A centered and fully open Meckelian canal occupies the medial surface of the lower jaw from the mental symphysis to the posterior end of the splenial. Thirty closely spaced mandibular teeth are present, a similar number to that of the maxilla. Teeth number 2-3, 5, 8, 13, 18, 24, and 26 are missing. The teeth are long and peg-like with recurved tips, and sit on a broad subdental shelf. About two-thirds of the tooth length is overlapped laterally by the dentary labial margin leaving exposed only a relatively short tooth portion. As in the maxilla, mode of tooth replacement is not clear, and no lingual or posterolingual replacement pits are evident.

The surangular covers most of the lateral surface of the postdentary region, restricting the angular to the ventral border of the mandible. It overlaps tightly the posterior margin of the coronoid to restrict the lateral exposure of the coronoid to a small antero-ventrally directed ridge as in cordylids and xantusiids. The posterior end of the surangular does not reach the articular condyle. An enlarged anterior surangular foramen pierces the lateral surface of the surangular, forming a deep groove that extends anteriorly to the ventral end of the coronoid. On the posterior half of the surangular, a posterior surangular foramen and an additional unnamed foramen are aligned posteriorly, at the same level of the surangular foramen.

Although the angular is almost completely fused to the articular and surangular, a faint suture permits delineation of their limits. The angular is exposed primarily on the medial side of the jaw. Anteriorly it forks, bearing a ventral notch for the reception of the dentary and a dorsal notch for the reception of the splenial. Posteriorly it is reduced, and extending only as far as the middle portion of the postdentary region.

The splenial is a small triangular bone. It extends anteriorly to the level of the last third of the tooth bearing portion of the dentary, and posteriorly to the level of the coronoid process. The Meckelian canal passes throughout its ventral margin. The anterior process of the fused prearticular-articular prevents contact of the splenial with the surangular below the coronoid.

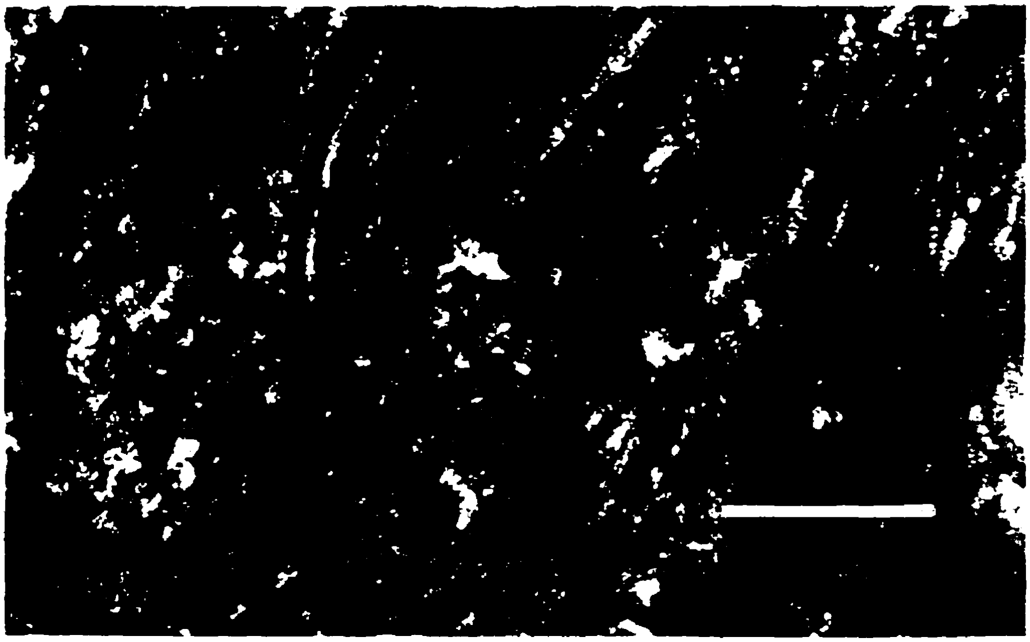
The articular condyle is formed only by the articular. Posterior to the articular surface a rather short and broad retroarticular process is present. On the right mandible the process was overturned and flattened to the level of the lateral surface of the dentary. Nevertheless, the process shows a slight twist and a medial inflection of the process is presumed. On the left mandible, the process does not appear to be as wide. This condition, however, might be an artifact of compression. As in most scincoids, a medial flange is present on the retroarticular process.

Postcranial skeleton

The majority of the postcranial skeleton is exposed in dorsal aspect (Fig. 31). It was separated by a very short distance from the cranium prior to fossilization. The preservation is particularly remarkable not only for its completeness but also for showing remnants of soft tissue in a regenerated tail and what appears to be patches of granular integumentary scales (Fig. 33).

A complete presacral column of 23 vertebrae and 2 sacral vertebrae are preserved, but only 6 proximal caudals remain. The last vertebra was autotomized and a small section of a regenerated tail remains attached to its end. Another small portion of regenerated tail was displaced transversally beneath more anterior vertebrae. The atlas-axis remains attached to the skull. Both neural arches are smashed to the right side, but they preserve some details. The atlas is about one third the length of the axis. Their respective intercentra and the axis centra are exposed in ventral aspect. Ventrally, the atlantal centrum contacts extensively the second intercentrum leaving only a very reduced contact with the first intercentrum. The axis appears to be procoelous, but this condition is uncertain. If so, then the posterior cotyle is not very pronounced. The neural arch is enlarged and bears a broad neural spine that is somewhat extended posteriorly. The anterior part of the third vertebral neural arch remains articulated to the axis.

Fig. 33. Detail of the granular scale remains preserved on top of the vertebral column in the holotype of *Tepexisaurus tepexii* gen. et sp. nov. (IGM 7466). Scale bar = 2 mm.



The arrangement of the cervical intercentra resembles the primitive lacertilian type (type I intercentra of Hoffstetter and Gasc 1969) in which the atlas intercentrum contacts the ventral margin of the occipital condyle, and the axis intercentrum is placed in an intervertebral position, contacting the atlas intercentrum anteriorly and the axis centrum posteriorly. Both intercentra lack ventral keels as in primitive lepidosaurs.

It is difficult to determinate the number of cervical vertebrae based on the number of rib attached to the sternum. Small flattened ribs are present from the third to fifth cervicals. All more posterior ribs are enlarged to about the same length. The ribs of the seventh vertebrae (and probably the sixth as well) have rounded ends suggesting that they were free ribs. A small portion of a sternal rib shows between the eighth and nine right ribs. It seems to contact the anteriormost sternal rib emargination, immediately posterior to the coracoid articulation. The distal end, however, is obscured by the eight and nine ribs, and it is not clear with which of these two ribs it was associated. In either case, *Tepexisaurus* could not have less than seven cervical vertebrae. It is interesting to note that ribs nine to twelve are oriented in the same way, suggesting that only these ribs were attached to the sternum. Thus, the formula for the cervical ribs would be two ribless vertebrae + three vertebrae bearing short distally widened ribs + two (or three) long slender vertebrae (Hoffstetter and Gasc 1969).

Trunk vertebrae are short anteroposteriorly. The neural spines are short and the zygapophyses well developed. On some vertebrae, traces of weak zygosphene/zygantra articulations can be discerned, but in most vertebrae compression of the neural arches obscures this region. In the last presacral vertebra the post-zygapophyses are distinctly closer to one other compared to anterior vertebrae. All trunk vertebrae bear ribs except the last one. Trunk ribs remain of the same size from the first sternal rib (either eighth or ninth) to rib number 16, after which they decrease in size. The posteriormost presacral ribs are strongly angulated.

The area around the anteroposterior axis of the two sacrals and first three caudals is heavily crushed. The shape and length of the impression on top of these vertebrae suggest that an unpreserved ilium covered them. Each sacral and caudal vertebra bears a single rib fused to the centrum. In the caudal vertebrae they are oriented slightly posteriorly. Only five caudal vertebrae remain complete since the sixth was autotomized and has a replacement tail attached posteriorly. The first autotomous vertebrae is the fifth. Although the septum is clearly preserved, the slight displacement of the transverse processes prevents the establishment of the position of the autotomous septa relative to the processes. The lack of transverse processes in the anterior portion of the autotomized vertebrae suggest that it was split anterior to the transverse processes (vertebrae type 3 of Etheridge 1967). This type of vertebrae occurs in the Upper Jurassic genus *Paramacellodus* (Hoffstetter 1967).

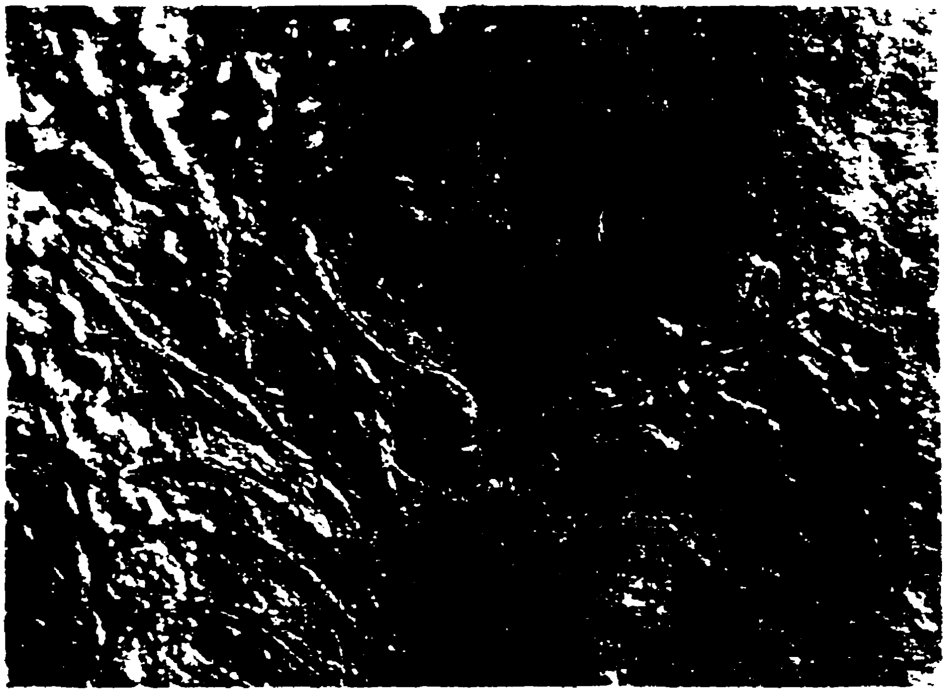
Appendicular skeleton

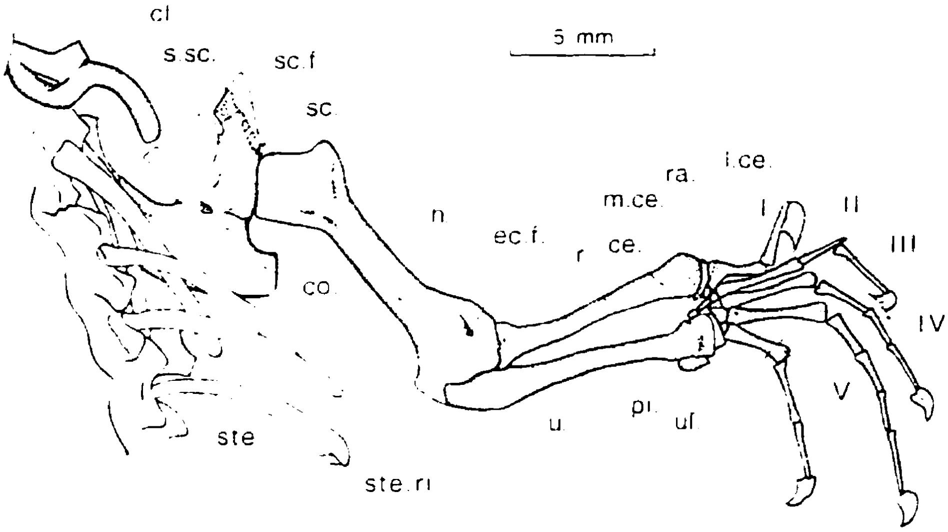
Both clavicles are preserved in ventral view and displaced on either side of the atlas-axis complex (Fig. 32). They are S-shaped, but strongly angulated. On the proximal end, a modest expansion lies in the frontal plane. Partial division of the main body of the clavicle suggests the presence of a clavicular fenestra.

The sternum is visible faintly below the eighth to tenth right ribs (Fig. 34). As exposed, it has three lateral extensions for the sternal ribs, suggesting that at least three ribs were attached (possibly ribs nine to 11). There are no signs of fenestration, but this region is covered by the dorsal vertebrae. A small portion of a thin interclavicle is observed to the right of the seventh vertebra. No other details of this bone can be discerned. Fragments of secondary ribs at the ends of some trunk vertebrae are mostly likely from postxiphisternal inscriptional ribs.

The scapula and coracoid are covered partially by remnants of soft tissue, probably the cartilaginous suprascapula. Both bones are preserved in articulation, but a faint suture indicates that are not co-ossified. The scapulocoracoid, anterior coracoid, and a small

Fig. 34. Detail of the right shoulder girdle and forelimb of *Tepexisaurus tepexii* gen. et sp. nov. (IGM 7466) as preserved.

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scapular fenestrae are present. The scapular dorsal process is expanded posteriorly, and the postero-ventral process of the coracoid terminates abruptly in a squared, angular extension similarly to cordylids and paramacellodids (Hoffstetter 1964, Prothero and Estes 1980). Traces of the epicoracoid cartilage are preserved anterior to the coracoid.

The front limbs are typically squamate with co-ossified epiphyses. Measurements and proportions are given in Table 10. The right humerus was compressed, exposing both ventral and medial faces at the same plane. As in the other long bones of the holotype, the shaft has been broadened because of compression. An ectepicondylar foramen is present.

The radius and ulna are subequal in length. The ulna has a co-ossified olecranon, a deep sigmoid notch, and an almost hemispherical distal end. The manus is preserved in detail. The dorsal aspect is shown on the right manus and the ventral on the left. The carpal elements identified are the radiale, ulnare, intermedium, medial centrale, lateral centrale, pisiform, and distal carpals two to five (interpretation of medial carpal elements from Carroll 1977). The broadening of the proximal end of the first metacarpal suggests that the first distal carpal was fused to the epiphysis. In general, the structure and arrangement of the carpal bones are consistent with extant lizards. The intermedium is about the size of the lateral centrale and does not contact the ulna. The medial centrale is similar in size to the intermedium and lateral centrale and is excluded from the medial border of the manus. The pisiform sits high (mostly above the ulnare) as in the scincomorphs *Lepidophima* and *Xantusiia* (Xantusiidae) and in the skink *Macroscincus* (Renous-Lécuru 1973).

The manus of *Tepexisaurus* retains the plesiomorphic lepidosaurian phalangeal formula 2-3-4-5-3. A short, curved, and dorsoventrally expanded, but distally pointed ungual terminates each digit. The ungual of the first digit is considerably larger that the other ones.

Neither ilium is well preserved. Parts of them were lost on an uncollected counterpart block, or were overprepared. As pointed out before, a long imprint about the

TABLE 10. Measurements of the holotype of *Tepexisaurus tepexii* (in millimeters).

Total Specimen Length	186*ca*
Presacral Vertebral Column Length (PSVC)	58.4
PVCL plus Skull Length = Presacral Length (PSL)	81.7
Skull Length (tip of the premaxilla to occipital condyle)	23.3
A-P Diameter of Orbit	4.7
Quadrate Height	5.2
Mandible Length	20.8
Mandible Height at dorsal tip of Coronoid	5.1
Dorsal tip of Coronoid to center of articulation facet	7.8
Mentis to dorsal tip of Coronoid	12.2

(SKULL LENGTH/PSL) = 29%

Forelimb:

Total length from proximal humerus to tip of longest digit	33*ca.*
Humerus Length (=H)	11.4
H/PS X 100 = 14%	
H/F X 100 = 80%	
Ulna Length	9.4
Radius Length (=R)	8.3
R/H X 100 = 73%	

Digit	Metacarpal length	Phalanx length				
		1	2	3	4	5
I	2.2	2.4	1.6	.	.	.
II	3.2	1.9	2.4	1.4	.	.
III	3.8	2.0	2.0	2.5	1.5	.
IV	3.6	1.9	1.8	1.7	2.5	1.2
V	2.4	2.1	2.5	1.4	.	.

METACARPAL III/H X 100 = 33%

Hind limb:

Total Length from proximal femur to tip of longest digit	42.4*ca.*
Femur Length (=F)	14.2
F/PS X 100 = 17%	
Tibia Length (=T)	10.7
T/F X 100 = 75%	
H+R/F+T X 100 = 79%	
Fibula Length	9.9
R/H X 100 = 73%	

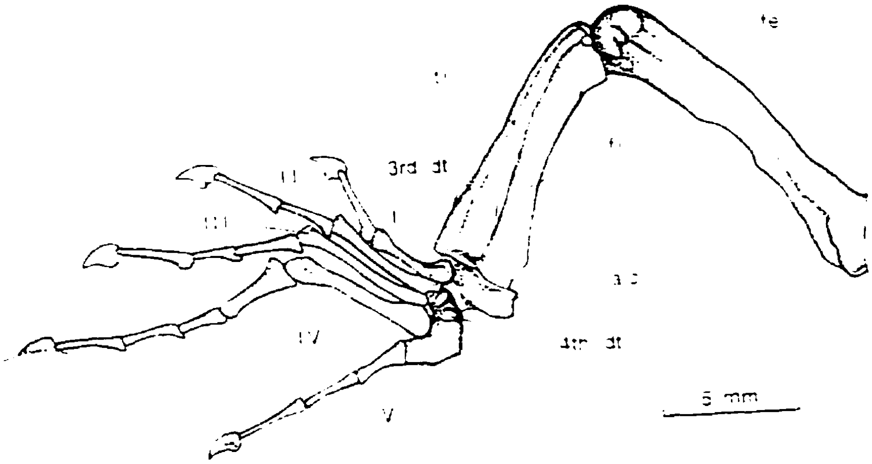
Digit	Metacarpal length	Phalanx length				
		1	2	3	4	5
I	3.5	3.0	1.3	.	.	.
II	4.8	2.3	2.7	1.1	.	.
III	5.8	2.3	2.1	2.7	1.0	.
IV	6.0	2.9	2.1	2.2	2.2	1.1
V	2.0	2.5	2.6	2.7	1.6	.

METATARSAL IV/F X 100 = 42%
METATARSAL V/METATARSAL IV X 100 = 33%

size expected of the left ilium is deforming the dorsal surface on the sacral and first caudal vertebrae. Other than the length, no other feature of the ilium is evident. The anterior margin of the right ischium is preserved. Its unusually broad contact with the pubis, shown by a well defined puboischial suture, reduces the size of the pelvic thyroid fenestra. The posterior edge of the left ischium is exposed lateral to the first caudal vertebrae, but no details are preserved. The robust pubis is quite wide proximal to the acetabulum and is penetrated by a moderately large obturator foramen. The short ventral extension of the pubis resembles the primitive squamate condition (Estes et al. 1988: fig. 8d).

Posterior limbs are preserved in dorsal aspect (Fig. 35). Their dimensions and proportions are reported in Table 10. The tibia is subequal in length to the fibula and bears a distal notch for the articulation of the astragalus as seen on the left limb. The right and left tarsi are fully ossified. The astragalus and calcaneum are fused, but a faint suture is still visible. The astragalus is considerably larger, bearing wide articulations for both the tibia and fibula. Only a very small part of the medial end of the fibula contacts the calcaneum. A perforation in the right astragalus appears to be an artifact and is probably damage caused by preparation. An enlarged fourth distal tarsal has approximately equal areas of articular surface for the astragalocalcaneum and the fifth metatarsal. On the right pes the fourth distal tarsal was fortunately overturned to show the complex tongue-in-groove articulation with the astragalocalcaneum (Brinkmann 1980). The third distal tarsal is much smaller than the fourth. No other tarsal bones can be identified. The fifth metatarsal is hooked. Both are preserved with only their dorsal sides exposed and the location of the plantar tubers is uncertain. The phalangeal formula of the pes is the primitive count (2-3-4-5-4). As in the manus each digit is terminated by a short, claw-supporting phalanx.

Fig. 35. Detail of the left hind limb of *Tepexisaurus tepexii* gen. et sp. nov. (IGM 7466) as preserved.


fe
ti
fi
3rd dt
II
I
III
a c
IV
4th dt
V
5 mm

DISCUSSION

Phylogenetic position

The sister-group relationships of *Tepexisaurus* were established using PAUP 3.1.1 (Swofford 1993) and a modified version of Estes et al.'s (1988) data matrix presented in Chapter 4. The analysis was performed through an heuristic search using the random-additional-sequence algorithm with 100 repetitions. The procedures were the same as those discussed in Chapter 4. All characters were unordered, multistate characters treated as polymorphism, and uninformative characters were ignored. The outgroup was composed by younginiforms, *Saurosternon*, Kuehneosauridae and Rhynchocephalia. With the exclusion of *Huehuecuetzpalli*, character 15 becomes uninformative. A small, rounded postorbital is autapomorphic for iguanids. Characters 157 and 158 are uninformative.

The five most parsimonious trees (tree length = 821, CI = 0.792, RI = 0.660, Appendix 5.1) were obtained at replicate number two, giving a good margin of security that all of the most parsimonious trees were found in the search. The strict consensus suggests that *Tepexisaurus* is the sister-group of scincoids (Fig. 36). The tree topology agrees in some aspects with results and discussion presented by Estes et al. (1988), since the position of snakes, gekkotans, and the clade amphisbaenians + dibamids is uncertain. Whatever the position of these taxa in the cladogram, it does not significantly influence the character distribution in the lineage leading to *Tepexisaurus*. Against results presented in Chapter 4, derived from the same data matrix, the Autarchoglossa is only supported in one of the most parsimonious hypothesis (Fig. 37D).

In each of the five hypotheses, the inclusion of *Tepexisaurus* in Squamata is supported by the absence of the ventromedial quadrate lappet of the pterygoid, broad interpterygoidal vacuity, absence of palatal and pterygoid teeth, procoelous vertebrae, anterior coracoid emargination, broad straight frontoparietal suture, ventral peg of the squamosal for the articulation of the quadrate, vomer and pterygoid separated by palatine, pterygoid in suborbital fenestra, paraoccipital process contacts suspensorium, pin-like

Fig. 36. Strict consensus of 5 equally parsimonious trees showing the sister-group relationships of *Tepexisaurus tepexii* with scincoids. The tree is the result of 100 replicas of a random additional sequence heuristic search using PAUP (Swofford 1993). The data matrix used is that of Estes et al. (1988) as modified in Chapter 4 (Appendix 4.1, 4.2). Characters for *Tepexisaurus* are in Appendix 5.1. Tree description: Tree length = 821; consistency index = 0.792; retention index = 0.660, rescaled consistency index = 0.523. Apomorphy list (only unambiguous characters present in all trees): **Squamata**: premaxillae fused, parietals fused, straight frontoparietal suture broader than nasofrontal suture, short parietal table with occipital region exposeddorsally, squamosal with ventral peg for quadrate, quadrate lappet of pterygoid absent, opisthotic and exoccipital fused, palatine teeth absent, pterygoid teeth absent, broad interpterygoidal vacuity, pterygoid and vomer separated, paraoccipital process contact suspensorium, angular ends anterior to articular condyle, vidian canal fully enclosed by bone, subdivided metotic fissure, pin-like stapes, stapedial artery posterior to stapes, procoelous vertebrae, keeled cervical intercentra, cervical ribs single headed, large thyroid fenestra in pelvic girdle, hooked fifth metatarsal with proximal head and tuber modified, gastralia absent. **Scleroglossa**: descending process of frontal contacts palatine, vomer extends posterior to midpoint of maxillary tooth row, septomaxillae meet in midline, convex expanded septomaxilla, prominent choanal fossa of the palatine, 26 or more presacral vertebrae, epiphyses fused prior to cranial fusion, rectus abdominis lateralis muscle present, mid-dorsal scale row absent.

(Fig. 36. continued)

Iguania: broad frontal shelf below nasals, jugal and squamosal in contact above lower temporal fenestra. **Node 1**: posteromedial flange or tuber on retroarticular process, weak zygosphene and zygantrum intervertebral articulations. **Anguimorpha**: posterior opening of the vidian canal at the basisphenoid prootic suture, well developed intramandibular septum, Meckelian groove open ventrally or with anterior alveolar foramen, posterolateral notches on dentary for surangular and coronoid, dorsal osteoderms. **Scincomorpha**: parietal downgrowths, dermal rugosities vermiculated. **Lacertoidea**: prearticular crest, adductor mandibulae muscle extends far into the Meckelian groove, origin pseudotemporalis superficialis muscle extends posteriorly. **Node 2**: posterior process of maxilla extends anterior to orbit, posteroventral opening of Jacobson's organ is closed by bone, enlarged anterior premaxillary teeth. **Scincoidea**: ventral osteoderms, dorsal osteoderms. A full description of the tree is given in Appendix 5.1.

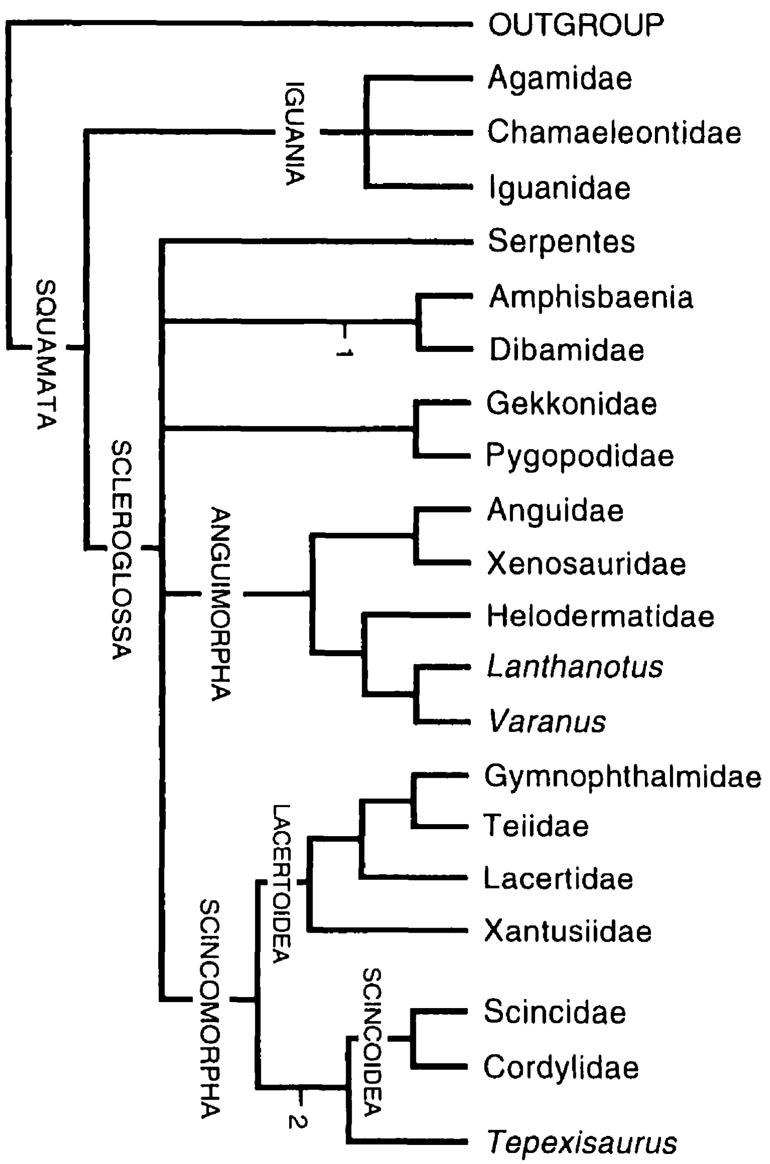
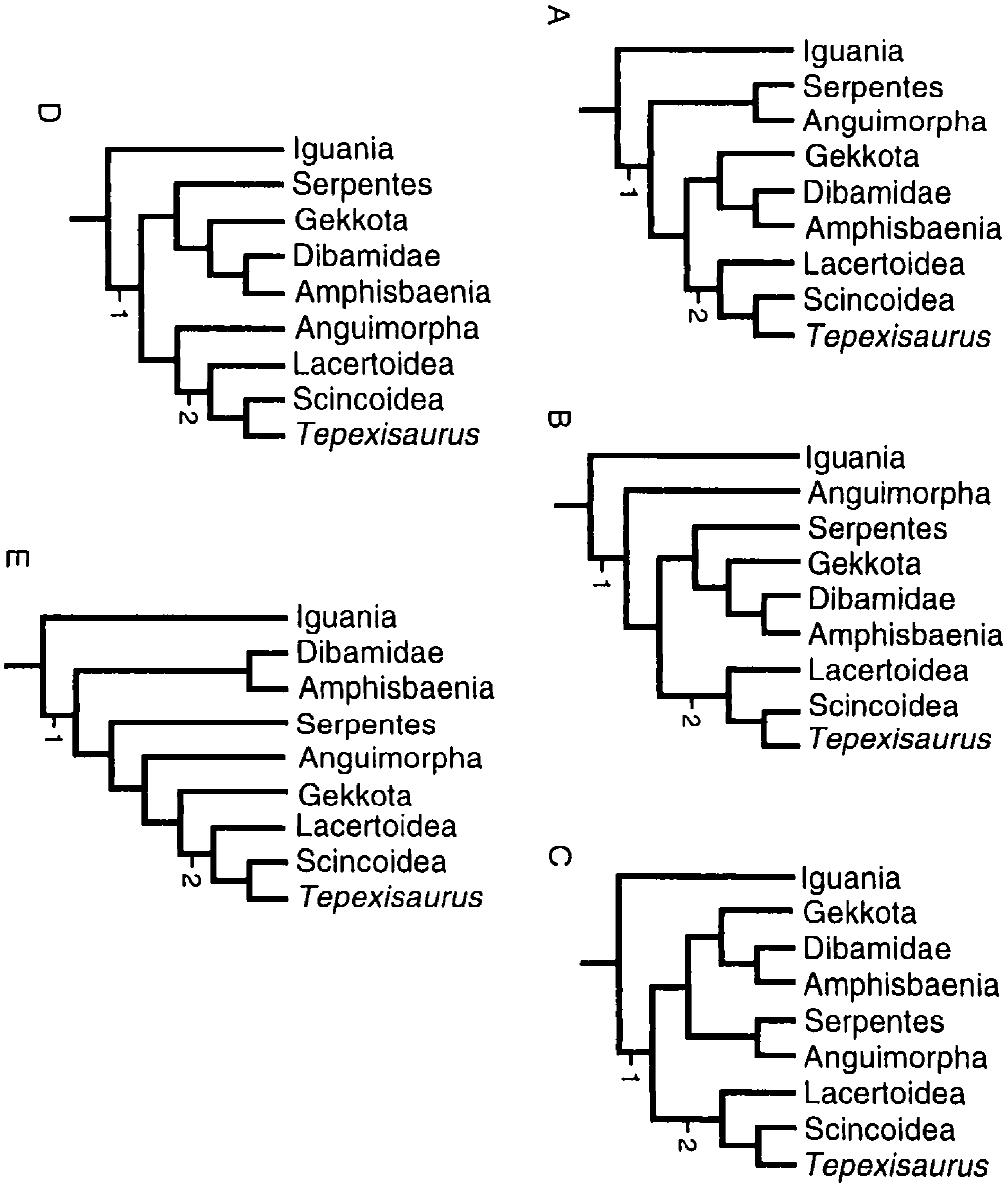

OUTGROUP
Agamidae
Chamaeleontidae
Iguanidae
IGUANIA
Serpentes
Amphisbaenia
Dibamidae
1
Gekkonidae
Pygopodidae
SQUAMATA
SCLEROGLOSSA
Anguidae
Xenosauridae
Helodermatidae
Lanthanotus
Varanus
ANGUIMORPHA
Gymnophthalmidae
Teiidae
Lacertidae
Xantusiidae
LACERTOIDEA
Scincidae
Cordylidae
Tepexisaurus
SCINCOIDEA
2
SCINCOMORPHA

Fig. 37. Five most parsimonious trees showing different hypothesis of sister-group relationships of scleroglossans basal to scincomorphs. A-E corresponds respectively to hypotheses 1-5 in the text. Node 1 = Scleroglossa. Node 2 = Scincomorpha.


A
Iguania
Serpentes
Anguimorpha
Gekkota
Dibamidae
Amphisbaenia
Lacertoidea
Scincoidea
Tepexisaurus
1
2
B
Iguania
Anguimorpha
Serpentes
Gekkota
Dibamidae
Amphisbaenia
Lacertoidea
Scincoidea
Tepexisaurus
1
2
C
Iguania
Gekkota
Dibamidae
Amphisbaenia
Serpentes
Anguimorpha
Lacertoidea
Scincoidea
Tepexisaurus
1
2
D
Iguania
Serpentes
Gekkota
Dibamidae
Amphisbaenia
Anguimorpha
Lacertoidea
Scincoidea
Tepexisaurus
1
2
E
Iguania
Dibamidae
Amphisbaenia
Serpentes
Anguimorpha
Gekkota
Lacertoidea
Scincoidea
Tepexisaurus
1
2

stapes, vidian canal enclosed by bone, short angular, all cervical ribs single headed, large thyroid fenestra, hooked fifth metatarsal, the absence of the gastralia. The condition of the plantar tuber of the fifth metacarpal is unknown, and the presence of keeled cervical intercentra is an unambiguous synapomorphy of squamates that is reversed in *Tepexisaurus*. In the fifth hypothesis (Fig. 37E), the presence of an anterior emargination of the coracoid and the pterygoid entering the margin of the suborbital fenestra do not support unambiguously the Squamata. An anteriorly emarginated coracoid ambiguously diagnoses the clade Anguimorpha + Scincomorpha + Gekkota, and the pterygoid entering the supratemporal fenestra may be interpreted as diagnostic of Squamata or convergent in iguanians and scleroglossans (excluding dibamids and amphisbaenians).

The inclusion of *Tepexisaurus* in Scleroglossa is supported by three unambiguous synapomorphies present in the five most parsimonious hypothesis: vomer extended posterior to the middle of the maxillary tooth row, prominent palatine choanal fossa, and strongly angulated clavicle. In the third hypothesis, a large subdental shelf is an additional synapomorphy supporting this clade (Fig. 37C); however, in the second hypothesis this character supports the clade Scincomorpha + Dibamidae + Amphisbaenia + Gekkota + Serpentes. A strongly angulated clavicle does not support the Scleroglossa in the fifth hypothesis, but is rather an ambiguous character defining Anguimorpha + Scincomorpha + Gekkota. The presence of 26 or more presacral vertebrae is diagnostic to scleroglossans. The reduction of the presacrals count to 23 vertebrae is a unique condition of *Tepexisaurus* among scleroglossans, but convergent with some agamids, chamaeleontids, and iguanids. A long slender pubis and the cervical intercentrum sutured or fused to the preceding centrum diagnose scleroglossans in different trees of the five most parsimonious hypotheses. In *Tepexisaurus*, both characters are reversed to the primitive conditions -short pubis and intervertebral cervical intercentrum. The possible presence of a forked postfrontal, coded as unknown in the analysis because the bone is obscured by the pterygoid, would support further the inclusion of *Tepexisaurus* within Scleroglossa. A distal tibial epiphyseal notch is an ambiguous character that defines scleroglossans. Its presence in *Huehuecuetzpalli* suggests that it may diagnose a more exclusive clade (Chapter 4).

A postorbital that contributes to less than half of the posterior margin of the orbit supports the inclusion of *Tepexisaurus* in the Autarchoglossa (hypothesis 4) or Autarchoglossa + Gekkota (hypothesis 5). In the other three hypotheses this condition is explained as an ambiguous synapomorphy joining Scincomorpha and Anguimorpha with other inclusive clades, or acquired independently in these two taxa.

The characters supporting Scincomorpha vary considerably from hypothesis to hypothesis in the five most parsimonious trees. With the exception of the presence of the parietal downgrowths and presence of dermal rugosities, no other character is consistent in all five hypotheses. Parietal downgrowths would be the only synapomorphy supporting the inclusion of *Tepexisaurus* in the Scincomorpha, since the presence of dermal rugosities is not known. An autotomous septum splitting the caudal vertebrae anterior to the transverse process is suggested as a synapomorphy of Scleroglossa in the second to fourth hypotheses. This character is variable in all terminal taxa of the Scincomorpha except Gymnophthalmidae. In *Tepexisaurus* the condition is uncertain since the position of the autotomous septum (that is certainly present) could be anterior to the transverse process or pass through them.

The sister-group relationships of *Tepexisaurus* with scincoids is supported by the presence of a broad retroarticular process with a posteromedial flange and weak zygosphene and zygantrum accessory articulations. The presence of a broad retroarticular process is only supported unambiguously in hypothesis 2, 3, and 4, but defines ambiguously this clade or a more exclusive node in hypotheses one and five. The lack of ventral and dorsal osteoderms and the presence of a splenial extending posterior to the apex of the coronoid place *Tepexisaurus* in a primitive position in relation to skinks and cordylids.

Although the five most parsimonious hypotheses agree in the position of *Tepexisaurus* as sister-group of scincoids (supported by three characters in most of the trees) the branch does not appears to be stable. The clade collapse after 100 bootstrap replicas using the random additional sequence algorithm of PAUP (Swofford 1993; Appendix 5.1). The branch support values (Bremer 1988, 1994) were calculated using the converse constraint option of PAUP, and it was found that only one additional step is required to collapse it. The branch instability is caused mainly by the amount of unknown information of *Tepexisaurus* in the data matrix as well as the frequency of convergence in all lineages. In light of the relative instability of the branch supporting its sister relationships with scincoids, *Tepexisaurus* is referred only to the Scincomorpha.

Comparison with other early lizards

The Late Jurassic genus *Ardeosaurus* and the Late Jurassic-Early Cretaceous Paramacellodidae are early fossil lizards anatomically similar to *Tepexisaurus*. Paramacellodids have been typically referred as "cordyloid" scincomorphs (Estes 1983a), but the position of *Ardeosaurus* in the cladogram is controversial (Evans 1993, Chapter 6). Although *Ardeosaurus* might not be a scincomorph, comparison with *Tepexisaurus* is necessary in order to establish the new genus as a distinct taxon.

Comparison of *Tepexisaurus* with *Ardeosaurus* is difficult because the skull in the best preserved specimen of *Ardeosaurus* is exposed only in dorsal aspect (Mateer 1982) while the holotype of *T. tepexii* is visible in ventral view. Most of the characters listed by Evans (1993) when comparing *Ardeosaurus* with *Eichstaettisaurus* are not known in *Tepexisaurus* (Table 11). Characters shared by *Ardeosaurus* and *Tepexisaurus* are: a narrow interpterygoid vacuity, the lack of contact between the jugal and squamosal, an upper temporal fenestra closed or nearly closed, and 23 presacral vertebrae. The lack of a jugal-squamosal contact is shared by most scleroglossans, and a restricted or close upper temporal fenestra is a synapomorphy of scincomorphs. Both characters are distributed

TABLE 11. Comparison between *Ardeosaurus*, *Eichstaettisaurus*, and *Tepexisaurus* based on characters listed by Evans (1993).

	Ardeosaurus	***Eichstaettisaurus***	***Tepexisaurus***
Skull sculpture	present	absent	-
Head scale pattern	present	absent	-
Parietals	fused	paired	-
Frontals	paired	fused	-
Semicircular canals	prominent	no prominent	-
Snout	pointed	rounded	rounded
Supratemporal	behind parietal	lateral to parietal	lateral to parietal
Prefrontals	emarginated	does not encroach on frontal	-
Frontoparietal suture	interdigitated	smooth	smooth
Pterygopalatine contact	broad	narrow	narrow
Interpterygoid vacuity	narrow	broad	narrow
Epipterygoid	with kink	columnar	bowed
Jugal/squamosal contact	absent	present	absent
Upper temporal fenestra	nearly closed	open	closed
Presacral vertebrae number	23	31	23

broadly within Scincomorpha and uninformative to establish more specific relationships within the group. Although the interpterygoid vacuities of *Ardeosaurus* and *Tepexisaurus* are narrower compared to that of *Eichstaettisaurus*, the condition in the former genera does not differ significantly from most squamates. This character is also distributed broadly and uninformative. The presence of 23 presacral vertebrae may be the only derived character shared by *Ardeosaurus* and *Tepexisaurus.* This feature is rare among squamates found otherwise only in some iguanians, indicating that it must have evolved independently within scincomorphs. Differences in the shape of the snout, position of the supratemporal, shape of the frontoparietal suture, relative extension of the pterygopalatine contact, and shape of the epipterygoid indicate clearly that *Ardeosaurus* and *Tepexisaurus* are distinct (Table 11). Although *Ardeosaurus* has been classified as a scincomorph (Evans 1993), results in Chapter 6 suggest that this genus is not a squamate, but a basal squamate. Since the position of *Tepexisaurus* remains within Scincomorpha, the similarity between *Ardeosaurus* and *Tepexisaurus* is explained better as convergence.

The several genera referred to Paramacellodidae are known from scattered material from different localities in Europe and North America. Their descriptions are based mainly on lower jaws. The structure of the lower jaw of *Tepexisaurus* is the same as that of all known paramacellodid lizards. The coronoid bone is restricted anteriorly and posteriorly by the dentary and surangular, and only a small lateral ridge is exposed. This condition is known for *Paramacellodus*, *Becklesius*, and *Pseudosaurillus*, but is not very clear in *Saurillus* and *Saurillodon*, although it might be present (Estes 1983a). A medial flange on the retroarticular process is unknown in most paramacellodids because the retroarticular process is usually broken in specimens referred to this family.

Unfortunately no paramacellodid lizard is known well enough to be considered in a broader phylogenetic analysis including *Tepexisaurus* and other extant squamates. Estes (1983a), however, has suggested a close relationship of paramacellodid lizards with cordylids (grouped as cordyloids) on the basis of similar rectangular osteoderms. Skinks, on the other hand, also have osteoderms although they are predominantly cycloid in shape. The presence of compound osteoderms is a major synapomorphy supporting the monophyly of Scincoidea (cordylids + skinks). According to the phylogenetic hypothesis presented above, *Tepexisaurus* is excluded from the Scincoidea because of the lack of dorsal and ventral osteoderms. Therefore, it cannot be referred to either Scincidae, Cordylidae or Paramacellodidae. Similarity of *Tepexisaurus* with members of these groups is based only on primitive characters.

The presence of osteoderms in some members of the Paramacellodidae (e.g. *Paramacellodus*, *Sharovisaurus*, and probably *Mimbobecklesisaurus*) may suggest their inclusion within Scincoidea. However, there are no shared derived characters in those paramacellodids lacking osteoderms (e.g. *Pseudosaurillus* and *Saurillodon*) that could indicate that they are scincoids. The possible inclusion of *Paramacellodus* and *Sharovisaurus* within the Scincoidea, and *Pseudosaurillus* and *Saurillodon* together with *Tepexisaurus* as sister-group of this taxon indicates that the Paramacellodidae as described by Estes (1983a) is a paraphyletic assemblage.

Tepexisaurus shares with *Pseudosaurillus* the presence of about 30 closely packed teeth, a condition never present in other paramacellodids. This feature might indicate affinity between both taxa. Some characters that distinguish *Tepexisaurus* as a different taxon from *Pseudosaurillus* are the almost complete overlap of the coronoid process by a broad posterodorsal process of the dentary that extends near to the tip of the coronoid bone, the posterior overriding of the coronoid bone by a secondary small dorsal process of the surangular that hides most of the coronoid laterally, a medially open Meckelian groove showing the primitive squamate pattern, and the angular restricted laterally to the ventral edge on the jaw, while the surangular is widely exposed. On the other hand, *Saurillodon* differs from both *Tepexisaurus* and *Pseudosaurillus* in the presence of less than 15 blunt conical teeth.

The evolution of rectangular compound osteoderms within scincoids can be explained in two different ways if "armored paramacellodids" are considered sister-group of scincoids or of cordylids. If they are the sister-group of cordylids + skinks, rectangular osteoderms will be synapomorphic of Scincoidea with further transformation to cycloid osteoscutes in skinks. If paramacellodids are the sister-group of cordylids, the presence of rectangular osteoderms will be synapomorphic of Cordyloidea, but the term Cordyloidea should be limited to include only those paramacellodids with osteoderms, and cordylids. Whatever the position the assemblage of "armored paramacellodids" might have, the lack of unique derived characters supporting the monophyly of the group indicates that it should be treated as a metataxon until new evidence becomes available.

STRATIGRAPHY AND BIOGEOGRAPHY

Early scincomorphs, represented mainly by paramacellodid lizards, are distributed broadly in space and time. They have been reported from the Bathonian to the Berriasian (Evans 1995). Geographically, they are known primarily from Europe but some remains have been found in the Late Jurassic of North America (Prothero and Estes 1980) and Africa (Richter 1994a). Hypotheses of early distribution and radiation of lizards suggest that major groups originated following the breakup of Pangea (Estes 1983b). Iguanians radiated within the Gondwanaland continents and scleroglossan lizards in the Laurasian continents, subsequently exchanging their faunistic elements. *Huehuecuetzpalli mixtecus* from the Tlayua deposits of Tepexi de Rodríguez is a primitive lizard that may have iguanian affinities. With *Tepexisaurus*, a scincomorph is added to the fauna. The association of *Huehuecuetzpalli* and *Tepexisaurus* is the earliest evidence of both iguanians and scleroglossans in the same deposit. This association indicates that the intercontinental lizard exchange started as early as the Albian. The area surrounding the deposits of the Tlayua quarry was apparently an area of contact between the two megacontinents.

The primitive position of *Tepexisaurus* in the phylogenetic tree does not match with its stratigraphic position. It was collected from Albian deposits while relatively more derived "paramacellodid" lizards are known since the Bathonian (42 ma before). The primitive condition of *Tepexisaurus* represented in late deposits suggest that a lizard with primitive scincoid morphology survived as late as the Albian. The late presence of a lizard relatively primitive to paramacellodids can be correlated with the similarly late presence of *Huehuecuetzpalli*, a primitive iguanian-like squamate, and late presence of sphenodontians in the Tlayua deposits (Chapter 2 and 3). This is the fourth example of a relict taxon present in Tlayua and gives additional evidence supporting the hypothesis that the locality was a refuge for archaic terrestrial forms during the Albian.

CONCLUSIONS

Paramacellodidae is a poorly known cordyloid-like assemblage of Late Jurassic and Early Cretaceous lizards. The discovery of a complete skeleton with a relatively more primitive morphology has clarify some aspects of the phylogeny of this group. The absence of osteoscutes places *Tepexisaurus*, *Saurillodon*, and *Pseudosaurillus* in a more primitive position relative to other paramacellodids which can be more reliably included within scincoids or cordyloids. This indicates that Paramacellodidae as it has been constituted is a paraphyletic assemblage. Future work should assign paramacellodid genera to well established monophyletic groups.

The presence of a primitive iguanian-like lizard *Huehuecuetzpalli mixtecus* and the scincomorph *Tepexisaurus tepexii* in the Tlayua deposits, is the earliest known fauna composed by Gondwanaland and Laurasian squamate elements, suggesting that intercontinental lizard exchange happened as early as the Albian. The presence of *Tepexisaurus* as a relict taxa in Tlayua, supports the hypothesis that the area around these deposits was a refuge for ancient terrestrial lepidosaurs.

Appendix to Chapter 5

Appendix 5.1

Analysis and Results

```
Data matrix has 24 taxa, 187(-18= 169) characters
All uninformative characters ignored
Warning. PAUP does not support MSTAXA = VARIABLE; UNCERTAIN used
instead.
Valid character-state symbols: 012345
Missing data identified by '?'
Gaps identified by '-', treated as "missing"

No taxa have been deleted.

Designated outgroup taxa:
   Rhynchocephalia
   Kuehneosauridae
   Saurosternon
   Younginiformes

Current status of all characters:
    All character 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 15, 157, and 158 are uninformative (ignored)

Data for Tepexisaurus: (X = excluded redundant characters; / = or)
????0 ?0??? ?0?00 0102X ??1?? X0?X? ?00?0 ?1?1? ??010 001?? ???10 ?02X2
??000 10X0X 100?? 101?0 0110(1/2) 00?X? ??1?1 X0X?0 X(1/3)X1X X0X(2/3)?
11X?0 1?0?? ?020? 00??? ????? ????? ????? ??0?1 11111 1??12 0?111 10X11
21111 112X1 2(2/3)11X 00

Heuristic search settings:
   Addition sequence: random
      Number of replicates = 100
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

    5th shortest tree found at replicate number 2

Heuristic search completed
   Total number of rearrangements tried = 1220929
   Length of shortest tree(s) found = 821
   Number of trees retained = 5

Tree description:
   Unrooted tree(s) rooted using outgroup method
   Character-state optimization: Accelerated transformation (ACCTRAN)
```

```
Most parsimonious trees description:

Tree length = 821
Consistency index (CI) = 0.792
Homoplasy index (HI) = 0.745
Retention index (RI) = 0.660
Rescaled consistency index (RC) = 0.523


Strict consensus of 5 trees:

Consensus tree description:

Tree length = 831
Consistency index (CI) = 0.782
Homoplasy index (HI) = 0.748
Retention index (RI) = 0.640
Rescaled consistency index (RC) = 0.501

                                /------------- Tepexisaurus
                   /-----------42      /------ Cordylidae
                   |            \-----41------ Scincidae
                   |                   /------ Gymnophthalmidae
             /----40            /-----37------ Teiidae
             |     |      /----38------------- Lacertidae
             |     \-----39------------------- Xantusiidae
             |                         /------ Anguidae
             |            /-----------30------ Xenosauridae
             +-----------33     /------------- Helodermatidae
      /-----36            \----32      /------ Lanthanotus
      |      |                  \-----31------ Varanus
      |      |                         /------ Amphisbaenia
      |      +------------------------34------ Dibamidae
/----29      |                         /------ Gekkonidae
|     |      +------------------------35------ Pygopodidae
|     |      \-------------------------------- Serpentes
|     |                                /------ Agamidae
|     \-------------------------------25------ Chamaeleontidae
|                                      \------ Iguanidae
\--------------------------------------------- OUTGROUP

Statistics derived from consensus tree:

     Component information (consensus fork) = 18 (normalized = 0.818)
     Nelson-Platnick term information = 105
     Nelson-Platnick total information = 123
     Mickevich's consensus information = 0.326
     Colless weighted consensus fork (proportion max. information) = 0.447
     Schuh-Farris levels sum = 845 (normalized = 0.417)
     Rohlf's CI(1) = 0.724
     Rohlf's -ln CI(2) = 59.651 (CI(2) = 1.24e-26)

Apomorphy lists:

Node 29: 1, 21, 24, 37, 48, 51, 65(2)*, 82, 83, 93, 112, 145(2), 150,
      153, 155, 156, 159, 160(2), 162, 163, 164, 166, 167, 178(2),
      182(2), 184
Node 36: 9, 10*, 13, 17*, 34, 39, 40, 41, 44, 49, 58(2), 60, 74, 75, 79,
      97, 104(2), 116, 123(2)*, 124, 130, 134, 138, 146, 147*
```

Node 40: 6*, 10(0)*, 19(2)*, 22*, 23, 54, 60(2)*, 65(0)*, 71*, 88*, 90(0), 91(0)*, 102(3), 114(0), 124(2), 129(2), 133, 138(2), 139*, 140(2), 144*
Node 42: 76, 78, 95, 107(0)*, 128*
Tepexisaurus: 85(1/2), 97(0), 104, 109(2/3), 111, 124(0), 161(0), 167(0)
Node 41: 66(0), 126, 127, 148*
Cordylidae: 19, 139(0,2)*
Scincidae:17(2), 18, 43, 141, 144(0)*
Node 39: 12*, 24(0)*, 73, 74(0), 75(0), 79(0), 97(2), 100*, 121*, 131, 132
Node 38: 37(0), 48(0)*, 60*, 66(0), 71(0)*, 81, 87, 95(2), 137(3)*, 140, 142*
Node 37: 12(0)*, 19(0)*, 24*, 54(0)*, 73(2), 90*, 112(2), 122, 137(4)*, 143
Gymnophthalmidae: 11, 141
Teiidae: 9(0), 45, 46, 124
Lacertidae: 23(0), 36, 53, 114, 128, 139(2)
Xantusiidae: 19, 27, 31(0), 38, 46, 52, 55(2), 65, 72, 125
Node 33: 14*, 53, 56, 57, 58(0)*, 63, 65(0)*, 85*, 127, 128, 133, 136, 137(2)*, 147(0)*
Node 30: 7*, 10(0)*, 25(0), 36, 66(0), 88*, 114(0)
Anguidae: 78, 124(2), 126, 147*
Xenosauridae: 18, 75(0), 129(2)
Node 32: 2*, 4(2)*, 5*, 16*, 27, 45, 58*, 61*, 64, 67, 69, 85(2)*, 86, 92, 137(3)*, 142, 156(0), 186(2)
Helodermatidae: 37(0), 54, 65, 90(0), 112(0), 119, 129, 143, 167(0)
Node 31: 3, 30, 61(2)*, 62, 63(2), 94, 107(2), 109(2)*, 137(4)*
Lanthanotus: 10(0)*, 60(3), 66(2), 83(0), 109(3)*
Varanus: 5(0)*, 9(0), 16(0)*, 25(0), 32, 36, 42, 53(0), 88(0), 112(2), 124(0), 132, 137(5)*
Node 34: 4, 16*, 22*, 27, 32*, 35, 42, 45*, 53(2)*, 55(2)*, 60(2)*, 72*, 75(0), 85, 100(2)*, 107(0)*, 109(3), 112(0)*, 118*, 122*, 137(0)*, 156(0), 175(0)*, 186
Amphisbaenia: 5, 13(0), 34(0), 58(0,1), 137(4)*, 138(2), 141, 150(3), 187
Dibamidae:10(0)*, 28(2), 43, 49(0), 51(0), 78, 100(3)*, 110, 139(2), 145(0), 148
Node 35: 16, 28(2), 31(0)*, 32, 35*, 38*, 52*, 54, 55(2), 66(0), 77, 78, 91(0)*, 97(0)*, 102(2)*, 125*, 134(0), 135, 139, 140, 141, 145
Gekkonidae: 99(0), 111, 147(0)*
Pygopodidae: 79(0), 109(3), 118, 133, 156(0)
Serpentes: 13(0), 17(0)*, 28(2), 33, 47, 64, 65, 66(2), 67, 85(2), 95(2), 136, 137(5), 145, 150(2), 187
Node 25: 6, 7, 8, 12, 18, 84*, 143
Agamidae: 25, 80, 97(2)
Chamaeleontidae: 38, 47, 107(0), 109(3), 110, 112(0), 115, 118, 122, 137(0), 142
Iguanidae: 60(1,3), 84(0)*

Bootstrap:

```
Bootstrap method with heuristic search:
   Starting seed = 1
   Number of bootstrap replicates = 100
   Bootstrap sampling over non-excluded/non-ignored characters only
   Addition sequence: random
      Number of replicates = 5
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

Bootstrap 50% majority-rule consensus tree

                  /------------------------ Tepexisaurus(1)
                  |                 /------ Cordylidae(6)
                  +-------64--------+------ Scincidae(15)
            /-56--+                 /------ Gymnophthalmidae(9)
            |     |           /-100-+------ Teiidae(17)
            |     |     /-74--+------------ Lacertidae(12)
            |     \-59--+------------------ Xantusiidae(19)
            |                       /------ Anguidae(3)
            +----------76-----------+------ Xenosauridae(20)
            |                       /------ Amphisbaenia(4)
      /-100-+----------58-----------+------ Dibamidae(7)
      |     |                       /------ Gekkonidae(8)
      |     +----------95-----------+------ Pygopodidae(14)
      |     |                 /------------ Helodermatidae(10)
/-100-+     +-------100-------+     /------ Lanthanotus(13)
|     |     |                 \-83--+------ Varanus(18)
|     |     \------------------------------ Serpentes(16)
|     |                             /------ Agamidae(2)
|     \-------------86--------------+------ Chamaeleontidae(5)
|                                   \------ Iguanidae(11)
\------------------------------------------ OUTGROUP
```

CHAPTER 6

PHYLOGENETIC POSITION OF LATE JURASSIC AND EARLY CRETACEOUS LIZARDS: CROSSING THE LEPIDOSAURIA/SQUAMATA BOUNDARY

PHYLOGENETIC POSITION OF LATE JURASSIC AND EARLY CRETACEOUS LIZARDS: CROSSING THE LEPIDOSAURIA/SQUAMATA BOUNDARY

INTRODUCTION

Among papers attempting to establish a robust cladistic hypothesis of the lepidosauromorph and squamate phylogeny, contributions of Gauthier et al. (1988a) and Estes et al. (1988) are particularly important. They made the first efforts to include as much of the available evidence as possible. Gauthier et al. (1988a) concluded that the "Paliguanidae" (Carroll 1975, 1977) is a paraphyletic assemblage within which *Palaeagama* formed a polytomy with Younginiformes, while *Paliguana* and *Saurosternon* diverged at the next node. *Kuehneosaurus* (Robinson 1962, 1967) is not a squamate but a basal Lepidosauromorph; *Gephyrosaurus* (Evans 1980, 1981) is sister-group of sphenodontians, and that the Squamata is a monophyletic assemblage including snakes, amphisbaenians and dibamids. Estes et al. (1988) concluded that "Lacertilia" and Camp's (1923) Ascalabota (Gekkonidae + Iguania) are not monophyletic and that Gekkota (Gekkonidae + Pygopodidae) should be included with anguimorphs and scincomorphs in a monophyletic assemblage called Scleroglossa. The phylogenetic position of dibamids, amphisbaenians and snakes remained uncertain, but were included within their Scleroglossa.

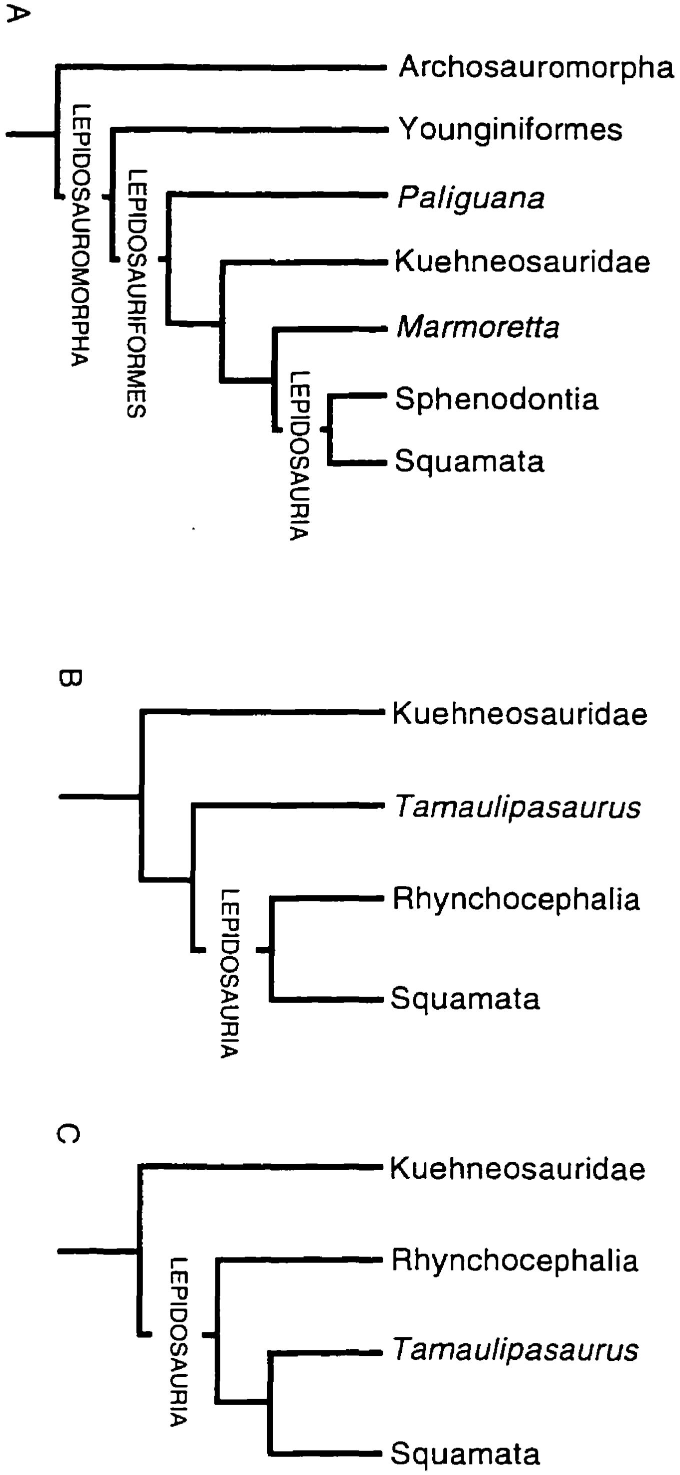
Some problems with the procedure of these analyses were pointed by the original authors and by Kluge (1989): Multistate characters were ordered; character change directional; the same characters were divided in two or more transformation series increasing the amount of redundant information; the ignorance of limbless characters to avoid an apodan taxon; and the use of an all zero or an average outgroup arbitrarily scored. Another problem in Estes et al.'s (1988) analysis is the exclusion of some characters shown explicitly or implicitly to be polymorphic within Squamata by Gauthier et al. (1988a).

A common practice in the study of Lepidosaurian and squamate relationship is the separation of information into different data sets. Phylogenetic studies of the Lepidosauromorpha, Lepidosauria or even larger categories, have lumped squamates, reducing all information into a single taxon, usually ignoring its variance (Benton 1984b, 1985; Evans 1984, 1988; Gauthier et al. 1988a; Laurin 1991). On the other hand, squamates have been analyzed independently from any other lepidosauromorphs, only using basal taxa or sphenodontians to establish character polarity. As with squamates, all taxa are usually merged into an average outgroup (Estes et al. 1988; Kluge 1989; Clark and Hernández 1994) assuming that there is no character transformation before the divergence of the Squamata.

Using these procedures, the discovery of intermediate forms between rhynchocephalians (as defined by Gauthier et al. 1988a) and squamates is impossible and all other lepidosauromorphs are forced to branch off the cladogram either outside Lepidosauria or within the Squamata. An extreme example is the case of *Marmoretta* (Evans 1991) which was assumed to be primitive in relation to the Lepidosauria before verifying the broader context of its phylogenetic position. To establish its sister-group relationships, rhynchocephalians and squamates were lumped into the Lepidosauria, excluding the possibility of *Marmoretta* branching off within the Lepidosauria (Fig. 38A).

An analogous problem occurs when analyzing assumed squamate fossil taxa in a data matrix built up with characters phylogenetically useful for extant squamates (e.g. Estes et al.'s 1988 data matrix). Fossil taxa can be forced to become part of any of the major group of squamates since diagnostic characters for the Squamata, uninformative for ingroup analysis, are excluded. When a fossil taxon lacks any of the diagnostic features of the Squamata, it will pass unadvertised, preventing them the possibility to branch off outside the Squamata. This is the case of the Early Cretaceous lizard *Huehuecuetzpalli mixtecus* (Chapter 4). Although it possesses most squamate synapomorphies, it lacks some of the features diagnostic for the Squamata. Preliminary cladistic analysis using the

Fig. 38. Sister-group relationships of Middle Jurassic lepidosauromorphs. **A.** Cladogram showing the sister-group relationships of the *Marmoretta* as presented by Evans (1991). **B** and **C.** Two alternative equally parsimonious hypothesis of the sister-group relationships of *Tamaulipasaurus* as presented by Clark and Hernández (1994).

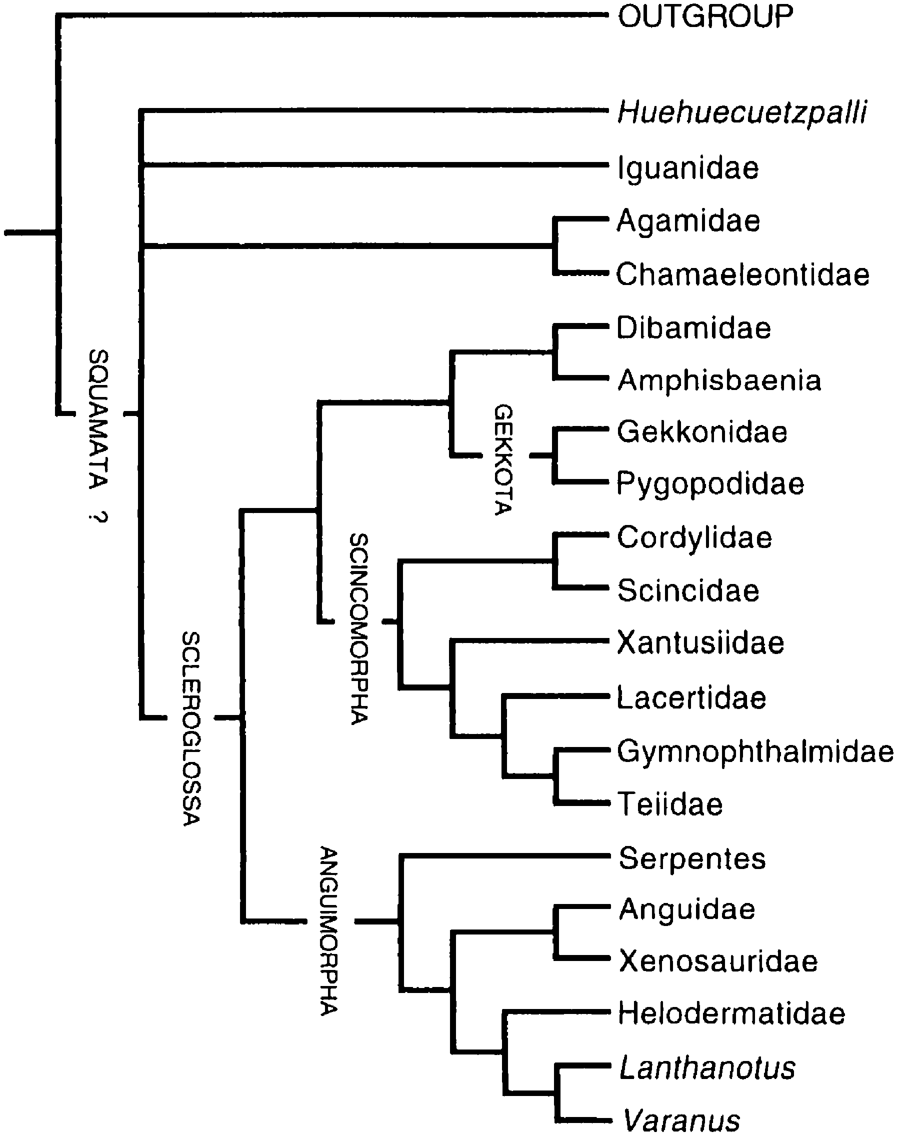

A
Archosauromorpha
Younginiformes
Paliguana
Kuehneosauridae
Marmoretta
Sphenodontia
Squamata
LEPIDOSAUROMORPHA
LEPIDOSAURIFORMES
LEPIDOSAURIA
B
Kuehneosauridae
Tamaulipasaurus
Rhynchocephalia
Squamata
LEPIDOSAURIA
C
Kuehneosauridae
Rhynchocephalia
Tamaulipasaurus
Squamata
LEPIDOSAURIA

data matrix of Gauthier et al. (1988a) for the Lepidosauromorpha shows *Huehuecuetzpalli* to be the sister-group of squamates. However, in the strict consensus tree using the data matrix of Estes' et al. (1988) for the Squamata, it appears to form a polytomy with iguanians and scleroglossans at the base of the cladogram (Fig. 39). The distribution of characters used in the analysis remained obscure at this node. The hypothesis suggesting *Huehuecuetzpalli* as sister-group of squamates was only possible until when all diagnostic characters of the Squamata were included (Chapter 4).

Clark and Hernández (1994) presented a similar case when analyzing the phylogenetic position of the Middle Jurassic burrowing diapsid *Tamaulipasaurus morenoi*. Their conclusions suggest that *Tamaulipasaurus* was sister-group of either lepidosaurs or squamates (Fig. 38B). They explored the phylogenetic position of this fossil using two separate data sets, one for lepidosauromorphs and another for squamates. When conducting their analysis within squamates, they did search beyond Estes et al.'s (1988) data matrix by adding some diagnostic characters for the Squamata, but they did not explore further in a broader data set as would have been advisable since they were dealing with an even more primitive form. When analyzing *Tamaulipasaurus* in the context of the Lepidosauromorpha, all of its characters that were known to change within the Squamata were ignored. Therefore, the hypothesis suggesting that *Tamaulipasaurus* is the sister-group of lepidosaurs was misleading because of the uncertain distribution of characters crossing the Squamate/Lepidosauria boundary.

The current chapter attempts to review the phylogeny of the Lepidosauromorpha in a broader context while making use of the new information provided by the newly described taxa. The redistribution of derived characters crossing the Squamata/Lepidosauria boundary and their effect in squamate phylogeny is evaluated. Particular attention is given to the position of Late Jurassic and Early Cretaceous lizard-like forms in order to reconstruct the early evolution of lizards. The phylogenetic position of

Fig. 39. Strict consensus tree obtained by analyzing the Early Cretaceous lizard *Huehuecuetzpalli mixtecus* in the data matrix of Estes et al. (1988) as is, showing an unresolved polytomy at the base of the Squamata. Tree length 765; consistency index = 0.762; retention index = 0.623.


OUTGROUP
Huehuecuetzpalli
Iguanidae
Agamidae
Chamaeleontidae
Dibamidae
Amphisbaenia
Gekkonidae
Pygopodidae
Cordylidae
Scincidae
Xantusiidae
Lacertidae
Gymnophthalmidae
Teiidae
Serpentes
Anguidae
Xenosauridae
Helodermatidae
Lanthanotus
Varanus
SQUAMATA ?
SCLEROGLOSSA
GEKKOTA
SCINCOMORPHA
ANGUIMORPHA

taxa sometimes considered problematic, namely snakes, amphisbaenians, and dibamids, is also analyzed.

THE PROCEDURE

The analysis was performed using a combined data matrix from Estes et al. (1988), Gauthier et al. (1988a) and Evans (1991). New characters used by Clark and Hernández (1994) were also considered. All published characters were used in order to keep all available evidence, although some characters of Evans (1991) may be dubious. Special care was taken to avoid ambiguities and redundant information in both characters and character states. When redundant characters were found they were merged or combined; when two characters or two character states were described within a single character, they were coded separately. Many characters were rewritten according to the following convention:

All characters (Wiley et al's 1991 transformation series) must be composed of three elements: the anatomical part, a descriptive noun describing the anatomical part, and the possible homologous states the character can achieve (character states). The anatomical part is the structure that is being modified in the transformation series and can be as fine in the anatomy as necessary (e.g. skull, skull table, parietal, parietal downgrowths, etc.); the descriptive noun must be explicitly written for every particular anatomical part or structural complex (e.g. skull length, skull table proportions, etc.); and the character states are adjectives, stating all the possible conditions the anatomical part can achieve (e.g. skull length: long (0), short (1), etc.). The character states must be described in full and not just denying the alternative condition (e.g. shape of the anterior margin of the coracoid: smooth (0), fenestrated (1); *not*, coracoid anterior margin: not fenestrated (0), fenestrated (1)). Presence/absence characters only apply to the loss of whole bones and not to the detailed anatomical part since the alternative condition can be described in most of the cases (e.g. shape of the medial surface of the retroarticular process: smooth (0), with lateral flange (1);

not, flange of the retroarticular process: absent (0); present (1)). Presence/absence was sometimes applied where it was difficult to describe the alternative condition (e.g. to describe presence/absence of foramina). A number of characters states where the part described is lacking were rescored as not applicable (N). Redundant characters where "absent" condition is involved can only be combined with characters related to size if a tendency towards disappearance is noticed (e.g. size of the postorbital: large (0), small (1), absent (2)). If the lack of a structure is observed within a more inclusive anatomical part or is involved within an entirely different character, not applicable (N) was used instead (e.g. the lack of contact between the jugal and squamosal cannot be scored if the jugal or squamosal is missing). Absence cannot be applied as a derived condition if the character describes shape, length, width etc. and "N" should be used instead (e.g. absence of the postfrontal is not a derived condition for the character "postfrontal shape"). Although these statements may appear to be obvious to most systematists, mistakes were frequently found in many of the data matrices used for this study. Most characters of Estes et al. (1988) match these conditions but some problems were found when redundant characters are combined, specially those coming from two distinct data matrices. This procedure was necessary to keep information organized in a consistent manner and was particularly useful in finding redundancies and new character states. A full description of the characters used is presented in Appendix 6.1. Modifications of Estes et al.'s (1988), Gauthier et al.'s (1988a) and Evans' (1991) characters are made explicit when necessary and broadly compared with other published information. Modifications to original Estes et al.'s (1988) data sets made in Chapter 4 were considered.

Characters 7, 18, 31, 46, 50, 54, 55, 56, 57, 71, 81, 85, 89, 94, 96, 106, 108, 109, 110, 111, 112, 113, 118, 119, 122, 131, 137, and 138 of Gauthier et al. (1988a) are uninformative and were excluded (see Appendix 6.2). Although I agree with Kluge (1989) in including all available evidence on phylogenetic analysis, soft anatomy characters 139, 141-161, 163-167, and 169 of Gauthier et al. (1988a) were excluded. These characters are only known in extant squamates and the rhynchocephalian *Sphenodon* and might force sister-group relationships between squamates and rhynchocephalians. Because the variability within crown squamates was not established, these characters turn into constant and do not provide any information to solve relation within basal lepidosauromorphs or squamates. In spite of this, characters 141-159, and 169 will support squamate monophyly and characters 161, 163-167 support the rhynchocephalian-squamate sister relationship. The inclusion of these characters, properly coded within the Squamata, is imperative for further work.

Because of limitations in PAUP algorithms, a multistate character where a not applicable condition (N) is involved is assumed to have evolved within the terminal taxon. PAUP ignores "?" and "N" if combined with another states, using only the alternative polymorphic state(s) in the analysis. This problem was repeatedly found in taxa with limbless members (such as anguids and skinks). Multistate characters were treated as polymorphism. In cases where a character is coded but uncertain (any state followed by a question mark), the expected primitive or derived condition (or conditions if multistate) was applied by PAUP.

All characters were scored for the extant squamate "families" (*sensu* Estes et al. 1988): the Middle Jurassic and Early Cretaceous lizards *Ardeosaurus brevipes*, *Eichstaettisaurus schroederi* and *Bavarisaurus macrodactylus* (Cocude-Michel, (1963; Hoffstetter 1964, 1966; Ostrom 1978; Mateer 1982; Evans 1993, 1994c, 1995); *Parviraptor estesi* (Evans 1994a); the Tlayua forms *Huehuecuetzpalli mixtecus* and *Tepexisaurus tepexii* (Chapter 4 and 5); the lepidosauromorphs *Tamaulipasaurus morenoi* (Clark and Hernández 1994), *Marmoretta oxiniensis* (Evans 1991; Waldman and Evans 1994), and the Kuehneosauridae -*Kuehneosaurus latus* (Robinson 1962, 1967) + *Icarosaurus siefkeri* (Colbert 1966, 1970); *Saurosternon bainii*, *Paliguana whitei*, *Palaeagama vielhaueri* (Carroll 1975). The rhynchocephalians *Gephyrosaurus bridensis* (Evans 1980, 1981), *Clevosaurus hudsoni* (Fraser 1988), *Planocephalosaurus robinsonae*

(Fraser 1982; Fraser and Waldman 1984), *Sapheosaurus thiollierei* (Cocude-Michel 1963), *Homoeosaurus maximilliani* (Cocude-Michel 1963, Wu 1994), and *Sphenodon punctatus* were first coded and then merged to reduce the number of taxa in the analysis, but keeping all possible variations within the clade. The selected outgroup were *Prolacerta broomi* (Gow 1975) chosen to represent the Archosauromorpha because of its primitive condition within the clade; and the Younginiformes (Currie 1982), the immediate outgroup of Sauria (Laurin 1991). In many characters the primitive condition is not "0" because the polarity was extended back to early diapsids (Vaugh 1955; Reisz 1977, 1981; Reisz et al. 1984).

Comments on squamate terminal taxa discussed by Kluge (1989) were accepted as valid pending revision. The problems regarding the monophyly of the Agamidae, Iguanidae and Gekkonidae are recognized. The solution of these problems is beyond the goals of the current paper but should be considered in further investigations. These metataxa were used in the same manner as in Estes et al. (1988). Some other problems with monophyletic taxa were noted: Agamidae is monophyletic if *Priscagama* is not included (Frost and Etheridge 1989); "clevosaurs" as treated by Gauthier et al. (1988a) do not include *Planocephalosaurus* (Wu 1994, Reynoso 1996); and Sphenodontinae (as defined by Reynoso 1996 and similar to "sphenodonts" of Gauthier et al. 1988a) does not include *Opisthias*, which proved to lack a caniniform tooth (Evans and Fraser 1992).

The data matrix is constituted by 34 taxa and 225 characters (Appendix 6.3). This matrix is far from being complete. In the course of its elaboration about 100 additional characters relevant to squamate phylogeny were found. A full analysis, including this new information and all terminal taxa of the rhynchocephalians is in progress. The current data matrix was limited in order to show how distribution of taxa in the cladogram may vary simply by removing the effect of the separation of information into independent data matrices, without changing significantly the actual data.

Standard procedures of the analysis were heuristic searches using the random additional sequence algorithm of PAUP (Swofford 1993), with 100 repetitions and seed prompted to 1 so that the results can be exactly replicated (Appendix 6.4). An experimental branch and bound search with all taxa was attempted, but stopped after 400+ hours with no results. Random additional sequence with 1000 repetitions was tried, but because all most parsimonious trees were found within the first five repetitions, a prolonged analysis was deemed unnecessary. All characters were treated as unordered. In the first analysis younginiforms were the only outgroup (Laurin 1991) and *Prolacerta* was left as an in-group to evaluate the uncertain position of *Paliguana* and *Palaeagama* within the Sauria. For a simple analysis of character distribution, a second PAUP analysis was performed excluding *Palaeagama* and *Paliguana* after verifying that their exclusion does not affected the topology and character distribution of the consensus tree (Wilkinson 1995). Characters 138, 139, 156, and 173 became uninformative after the taxa exclusion. To explain character distribution ACCTRAN optimization was preferred over DELTRAN, however, ACCTRAN will extend the origin of a character to the most basal node possible, even if the character is not known in taxa branching off at this position. In such cases a delayed transformation was preferred so that the character will describe the node at its first known appearance on the cladogram.

Selection of the outgroup

To polarize characters, Younginiforms and *Prolacerta* were selected as outgroup taxa. The Younginiformes is constituted by *Youngina capensis*, *Acerodontosaurus piveteaui*, *Kenyasaurus mariakaniensis*, *Thadeosaurus colcanapi*, *Tangasaurus menelli*, and *Hovasaurus boulei* (Gow 1975; Currie 1980, 1981, 1982; Harris and Carroll 1977; Carroll 1981; Currie and Carroll 1984). Younginiforms (characterized primarily by *Youngina capensis*) and *Prolacerta* are particularly important not only because they are the closest sister-groups of Lepidosauromorphs, but because of their historical importance in assessing the origin of lizards.

Youngina capensis was described by Broom (1914) as an Eosuchian thecodontian, and placed as a primitive generalized representative of the line giving rise to lizards (Broom 1925). Since then it has been considered as the primitive model of lizard evolution and ancestral type of both lizards and sphenodontians (Romer 1956). In recent studies, the position of Younginiformes in the cladogram remained controversial. Gauthier (1984), Benton (1984b; 1985), Evans (1984; 1988), and Gauthier et al. (1988a), placed this clade as branching off at the base of the Lepidosauromorpha; however, a recent analysis, has shown that *Youngina* lacks most saurian and lepidosauromorph synapomorphies (Laurin 1991: characters E 1-14 and J 1-9) falling outside Sauria as immediate sister-group of Lepidosauromorpha and Archosauromorpha (see also Gaffney 1980).

Prolacerta was described by Parrington (1935). The lack of an incomplete temporal bar was believed to indicate that it was immediate ancestor of lizards (Kuhn-Schnyder 1954; Robinson 1962, 1967); This same argument has been used to group other prolacertiforms (e.g. *Tanystropheus*) within Squamata (Wild 1973, 1980). Gow (1975) and Carroll (1977), have questioned the close relationship of *Prolacerta* with lepidosaurs or Squamates. Gow (1975) suggested that *Prolacerta* is more closely related to proterosuchian thecodontians than to lizards, and that it could be a perfect ancestor for *Macrocnemus* and *Tanystropheus*. Carroll (1977) and Wild (1980), on the other hand, have suggested that either *Prolacerta* is a specialized member of a basically primitive assemblage that gave rise to lizards or pertain to a completely different radiation. Recent cladistic analysis has definitively placed *Prolacerta* within the Archosauromorpha (Benton 1984b, 1985; Evans 1984, 1988; Laurin 1991). Laurin (1991) lists ten synapomorphies showing that *Prolacerta* is undoubtedly an archosauromorph. According to this hypothesis *Prolacerta* (and prolacertiforms) would be the first taxon to branch off the cladogram within the Archosauromorpha and therefore as the closest sister-group of lepidosauromorphs.

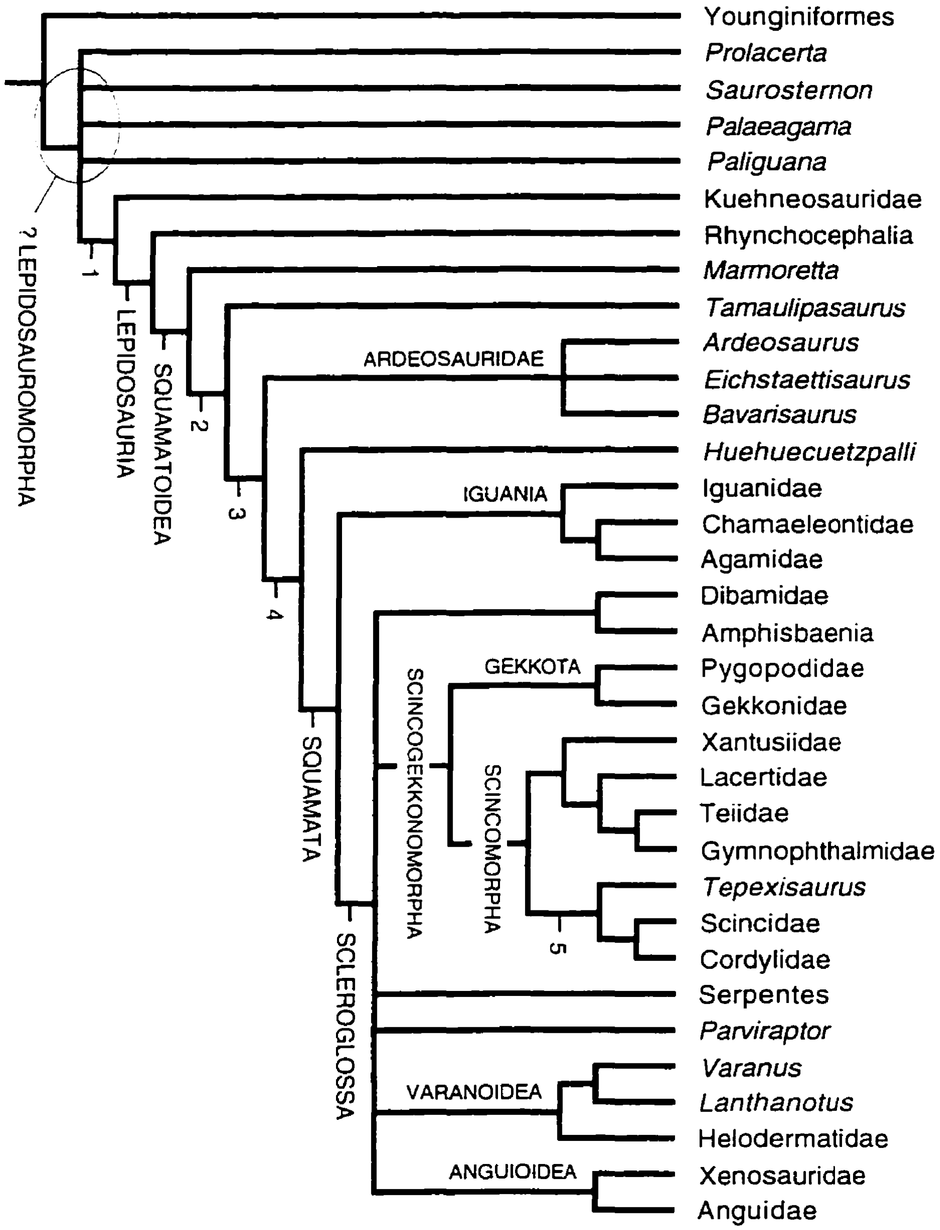
Recently Rieppel (1994a) suggested that sauropterygians are the closest sister-group of Lepidosauromorpha. However, this hypothesis depends on the position of turtles within

Sauria, assuming a monophyletic Reptilia (Gauthier et al. 1988b). If turtles are left aside (Rieppel 1994a; fig. 69), sauropterygians will be certainly included within neodiapsids but branching off as a polytomy with lepidosauromorphs and rhynchosaurs, prolacertiforms, *Trilophosaurus* and Choristidera. Although sauropterygians could be included as outgroup in the current analysis, it was preferred to leave them outside until their position in the cladogram is established by a broader analysis in the context of the Reptilia.

RESULTS

A strict consensus of 100 equally parsimonious trees including all lepidosauromorph taxa is presented in Figure 40. The cladogram requires 1128 steps with a high Consistency Index (= 0.715) but a rather low Rescaled Consistency Index (= 0.447) which indicates that homoplastic characters are abundant. The tree topology is substantially different from previously phylogenetic hypotheses, particularly in the basal nodes. The relationships of *Palaeagama* and *Paliguana* are uncertain and their inclusion within Lepidosauromorpha is dubious. *Marmoretta* (Evans 1991) branches off the cladogram within Lepidosauria followed next by *Tamaulipasaurus* (Clark and Hernández 1994). The exclusion of the Solnhofen lizards from the Squamata is particularly striking. *Ardeosaurus*, *Eichstaettisaurus* and *Bavarisaurus* branch off the cladogram as sister-groups of *Huehuecuetzpalli* + Squamata, forming a monophyletic assemblage. Within the Squamata, the topology is more or less conservative but a major change is the sister-group relationships of Gekkota and Scincomorpha. Dibamids and amphisbaenians always appear as sister-taxa, but the position in the cladogram of the clade formed by these two taxa is uncertain. Precise sister-group relationship of snakes is also uncertain but they are related in some combination with the clade amphisbaenians + dibamids, varanoids, anguioids or *Parviraptor*. The sister-group relationships of *Huehuecuetzpalli* with Squamata and *Tepexisaurus* with Scincoidea are still supported as presented in the chapters 4 and 5. A

Fig. 40. Strict consensus of 100 equally parsimonious trees showing the sister-group relationships of basal lepidosauromorphs and early lizards resulted from 100 replicas of heuristic search using the Random Additional Sequence algorithm of PAUP (Swofford 1993). Tree length = 1128; consistency index = 0.715; retention index = 0.625, rescaled consistency Index = 0.447.


Younginiformes
Prolacerta
Saurosternon
Palaeagama
Paliguana
Kuehneosauridae
Rhynchocephalia
Marmoretta
Tamaulipasaurus
ARDEOSAURIDAE
Ardeosaurus
Eichstaettisaurus
Bavarisaurus
Huehuecuetzpalli
IGUANIA
Iguanidae
Chamaeleontidae
Agamidae
Dibamidae
Amphisbaenia
GEKKOTA
Pygopodidae
Gekkonidae
Xantusiidae
Lacertidae
Teiidae
Gymnophthalmidae
Tepexisaurus
Scincidae
Cordylidae
Serpentes
Parviraptor
VARANOIDEA
Varanus
Lanthanotus
Helodermatidae
ANGUIOIDEA
Xenosauridae
Anguidae
? LEPIDOSAUROMORPHA
1
LEPIDOSAURIA
SQUAMATOIDEA
2
3
4
SQUAMATA
SCLEROGLOSSA
SCINCOGEKKONOMORPHA
SCINCOMORPHA
5

detail description of the results and a full list of apomorphies is presented in Appendix 6.4. In the text, characters in brackets always refers to characters published by previous authors.

TREE DESCRIPTION AND TAXONOMY

LEPIDOSAUROMORPHA Benton, 1983

New definition: The most recent common ancestor of *Saurosternon*, *Kuehneosaurus*, and Lepidosauria, and all of its descendants.

Preliminary remarks: *Saurosternon*, *Paliguana*, and *Palaeagama* have been long considered good ancestral types for lizard evolution (Broom 1925, Carroll 1975, 1977, 1988b). *Paliguana* was first described as an iguanian (Broom 1903, Camp 1923, Huene 1956), but because the presence of a quadratojugal it was later placed within the Eosuchia (allied to *Youngina*) as a rhynchocephaloid-near-to-lizards form (Broom 1925). *Palaeagama* was described as an eosuchian but grouped with *Paliguana* in the new family Paliguanidae (Broom 1926). In the same paper, Broom pointed out similarities between *Palaeagama* and *Saurosternon* which was subsequently also included in the Paliguanidae (Romer 1956). The "paliguanids" were restudied by Carroll (1975) who reassessed their lizard affinities, pointing out a number of similarities between *Kuehneosaurus* and lizards. He removed them from Younginiforms and placed them in the Lacertilia and provisionally within the Eolacertilia of Romer (1966).

Estes (1983a), noted that there are no derived features in *Palaeagama* or *Saurosternon* to certify their inclusion in Paliguanidae; and Gauthier et al. (1988a), have demonstrated that paliguanids is not monophyletic but a paraphyletic assemblage. In most recent cladistic analyses *Palaeagama* and *Saurosternon*, have been excluded because so few characters are known that their position in the cladogram is very poorly established, however, their inclusion within Lepidosauromorpha has been granted (Benton 1985, Laurin 1991, Evans 1991). Current analysis indicates that *Paliguana* and *Palaeagama* cannot be assigned with certainty to the Lepidosauromorpha. The Lepidosauromorpha can be diagnosed by three unambiguous and 14 ambiguous characters.

Unambiguous synapomorphies:

106.- Ectepicondylar groove closes into a foramen during ontogeny. Further transformation in Ardeosauridae (as here defined), chamaeleontids, teoiids, and amphisbaenians.

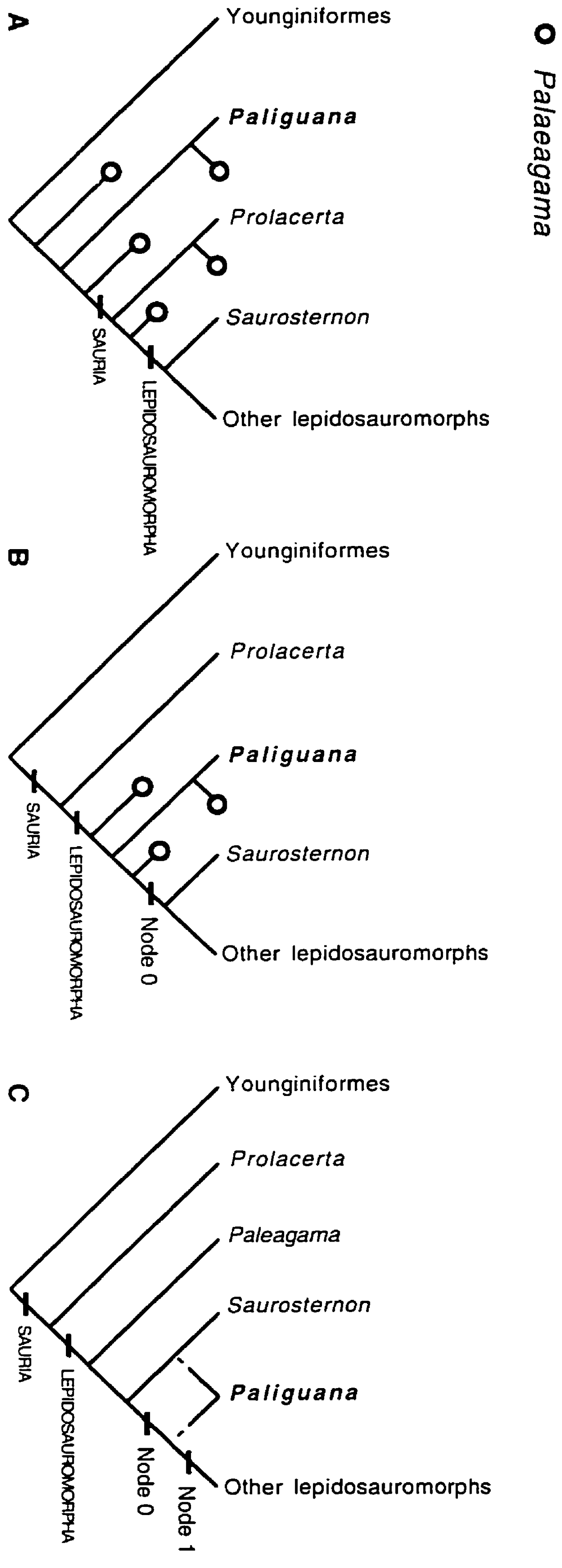
190.- Gracile interclavicle. Invariant.

214.- Process of fourth distal tarsal projects below astragalus. Further transformation in Node 3.

Comments: From Laurin's (1991) diagnosis only the presence of a lateral conch on the quadrate to support the tympanum is an ambiguous lepidosauromorph character. An incomplete lower temporal bar, the lack of postparietal, and a small lateral exposure of angular are present in *Prolacerta* and are probably saurian synapomorphies. The presence of a prominent retroarticular process formed by the prearticular bone is an invalid character since the retroarticular process in lepidosauromorphs is formed mainly by the articular with a small contribution of the prearticular in sphenodontians and mosasaurs (Romer 1956). An enlarged retroarticular process is also present in *Prolacerta* and it is probably a saurian synapomorphy. A fenestrated pelvic girdle defines a more inclusive group since *Saurosternon* lack the thyroid fenestra. See (Laurin 1991) for comments on lepidosauromorph characters used by Gauthier et al. (1988a).

Figure 41 shows all most parsimonious hypotheses resolving the polytomy of *Paliguana*, *Palaeagama*, *Saurosternon* and *Prolacerta* shown in Figure 40. Neither *Paliguana* or *Palaeagama* are clearly Lepidosauromorphs. These two taxa can either fall within Lepidosauromorpha or outside this clade; and further more, *Palaeagama* can even be considered sister-group of *Prolacerta*, i.e. of archosauromorphs!. The multiplicity of solutions is due to the fact that there are no unambiguous characters supporting the sister-

Fig. 41 . Ten possible solutions of the sister-group relationships of *Palaeagama* (represented with circles on the cladograms) and *Paliguana*. **A.** If *Paliguana* is outside Lepidosauromorpha then no synapomorphies support any sister-group hypothesis of either *Paliguana* or *Palaeagama*. **Tree description** (only unambiguous characters): **Sauria**: no postparietal, no tabulars, anterolaterally divergent prefrontal-nasal suture. **Lepidosauromorpha**: ectepicondylar foramen close in ontogeny, gracile interclavicle, tongue and groove articulation between fourth distal tarsal and astragalocalcaneum. If *Palaeagama* is sister-group of Sauria, then Sauria is undefined. Characters defining Lepidosauromorpha may vary depending the position of *Palaeagama* within Sauria. All other clades are unsupported. **B**. *Paliguana* and *Palaeagama* are within Lepidosauromorpha: **Lepidosauromorpha**: broad snout, enlarge head of the quadrate. If *Paliguana* and *Palaeagama* are sister-groups, then the presence of a lateral expansion on the quadrate for the support of the tympanum should be added. **Node 0**: enclosure of the ectepicondylar groove into a foramen. **C**. Two final hypotheses of sister-group relationships of *Paliguana*, both of which are unsupported. If *Paliguana* is sister-group of *Saurosternon*, then the presence of a strong maxillary dorsal process and an anteroventral margin of the orbit formed by maxilla and jugal should be added to diagnosis of Node 1 (Fig. 42 and text). If *Paliguana* branches off the cladogram after *Saurosternon*, then only the two newly added conditions support this node.


A
Younginiformes
Paliguana
Prolacerta
Saurosternon
Other lepidosauromorphs
SAURIA
LEPIDOSAUROMORPHA
B
Younginiformes
Prolacerta
Paliguana
Saurosternon
Other lepidosauromorphs
SAURIA
LEPIDOSAUROMORPHA
Node 0
C
Younginiformes
Prolacerta
Paleagama
Saurosternon
Paliguana
Other lepidosauromorphs
SAURIA
LEPIDOSAUROMORPHA
Node 0
Node 1
○ Palaeagama

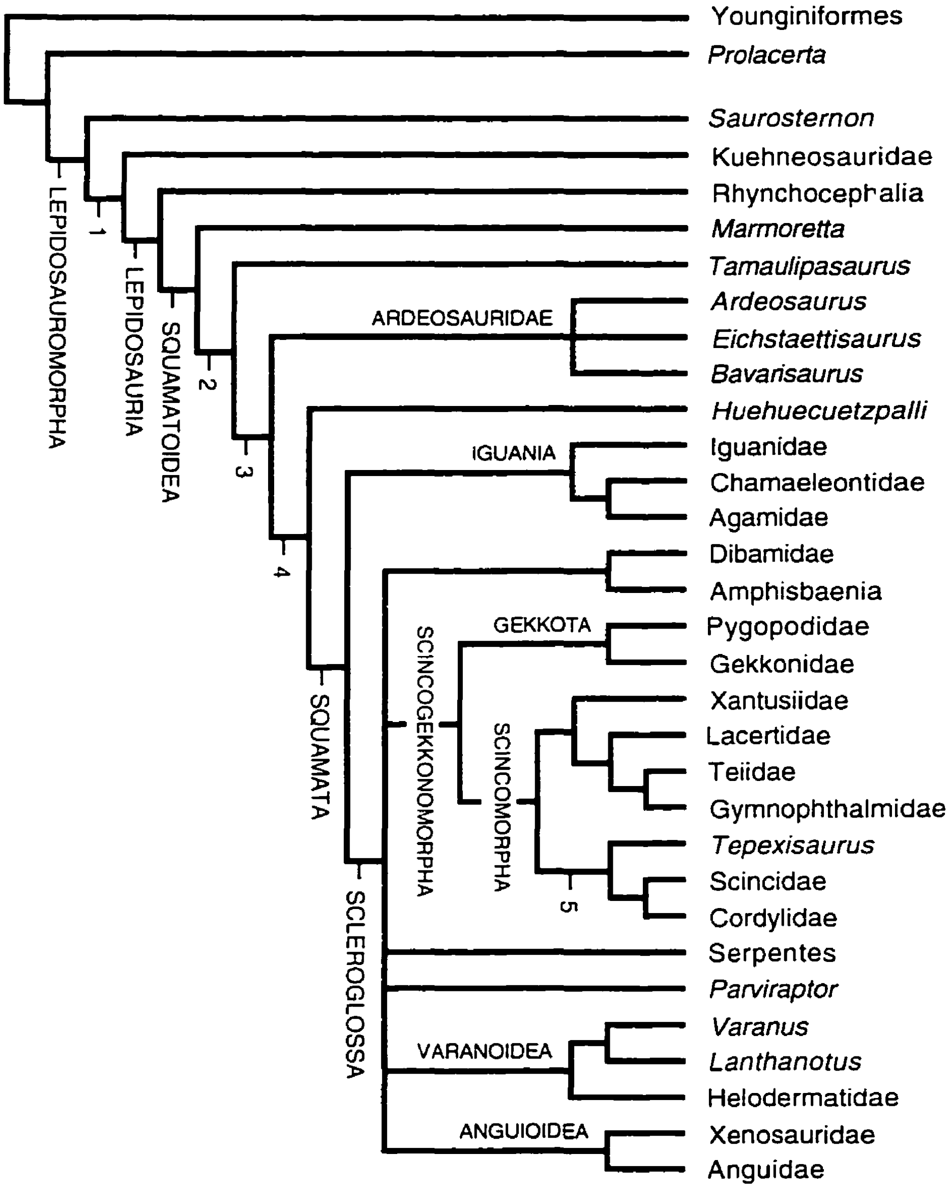
group relationships of either *Palaeagama* or *Paliguana* in any of the hypothesis presented. If *Paliguana* and *Palaeagama* are outside Lepidosauromorpha (Fig. 41A), only a few nodes are unambiguously supported. Figure 41B shows a series of solutions considering *Paliguana* and *Palaeagama* within Lepidosauromorpha but branching off the cladogram in any combination before *Saurosternon*. In these hypotheses, the Lepidosauromorpha is supported by the presence of a broad snout and an enlarged head of the quadrate; but if *Paliguana* and *Palaeagama* are sister-groups, the presence of a lateral expansion on the quadrate to support the tympanum should be added to the diagnosis. *Saurosternon* will be grouped within the Lepidosauriformes (Gauthier et al. 1988a), unambiguously diagnosed by the enclosure of the ectepicondylar groove into a foramen. A final possibility suggests that *Palaeagama* is a lepidosauromorph and *Paliguana* is a lepidosauriform either the sister-group of *Saurosternon* or the sister-group of all other lepidosauriforms except *Saurosternon* (Gauthier et al.'s 1988a results); however, none of these hypotheses are supported by unambiguous characters (Fig. 41C).

Congruent results in all parsimonious cladograms are that *Prolacerta* always branches off at the base, and that *Saurosternon* remains the sister-group of *Kuehneosaurus* + Lepidosauria. Variation in tree topology at the base of the tree is caused by the ten different ways *Palaeagama* and *Paliguana* can be sorted. With the removal of *Paliguana* and *Palaeagama*, the analysis yields only ten equally parsimonious hypotheses with the same tree topology and character distribution as when these taxa were considered. This indicates that the excluded taxa do not contribute in the generation of the tree topology. They can therefore be safely excluded from the analysis to reduce the number of equally parsimonious hypotheses, making phylogeny more easy to analyze (Wilkinson and Benton 1995). In the reduced consensus, *Saurosternon* branches off the cladogram at the base of Lepidosauromorpha, with *Prolacerta* its closest sister-group (Fig. 42). By accepting this procedure, the clade Lepidosauromorpha can only be defined by excluding *Palaeagama* and *Paliguana*. Lepidosauriformes becomes synonymous with Lepidosauromorpha (Gauthier

Fig. 42. Reduced consensus that is the result of the removal of *Palaeagama* and *Paliguana* from the analysis and resolution of the sister-group relationships at the base of the Lepidosauromorpha. The analysis is the same as that shown in Fig. 40, but excluding four uninformative characters. Tree description: Number of trees = 2; tree length = 604; consistency index = 0.460; retention index = 0.607; rescaled consistency index = 0.279. Apomorphies list (only unambiguous characters). **Lepidosauromorpha**: closed entepicondylar groove, gracile interclavicle, tongue and groove articulation between the fourth distal tarsal and the astragalocalcaneum. **Node 1**: thickness of humerus reduced, small thyroid fenestra. **Lepidosauria**: no teeth on transverse flange of pterygoid, small lacrimal, thick metacarpals I and IV, preorbital region equal to or longer than postorbital region, steeply inclined ilium with pubic flange, pelvic bones fused in adults. **Squamatoidea** (new taxon): no median contact between palatine and vomer, pterygoid included in suborbital fenestra, coronoid process formed primary by coronoid bone, sacral and caudal ribs fused in embryo, no contact between quadrate and epipterygoid. **Node 2**: lacrimal absent, anteroventral margin of orbit formed by jugal, opisthotic and exoccipitals fused in embryo, no quadrate foramen. **Node 3:** occipital region not covered by parietals, coronoid clasp dentary, narrow nasals, no quadratojugal, peg for quadrate notch on squamosal. **Node 4, Ardeosauridae** (new definition): postfrontal forked medially, parietal foramen within parietals, no dorsal process of squamosal, 23 or fewer presacral vertebrae, ectepicondylar foramen or groove absent, postfrontal enters margin of upper temporal fenestra. **Node 5**: eight cervical vertebrae, clavicle articulates with suprascapula. **Squamata**: fused premaxillae, no thoracolumbar intercentra, second distal tarsal absent. **Iguania**: broad frontal shelf below nasals, no contact of jugal and squamosal over lower temporal fenestra, gently convex tibial distal end. **Scleroglossa**: frontal

(Fig. 42. continued)

descending process of frontal contacts palatine, postfrontal forked medially, postorbital contributing less than half of the posterior part of the orbital rim, no dorsal process of squamosal, convex septomaxillae contact medially along a raised crest, anterodorsally oriented prootic alar process, retroarticular process without dorsal pit, retroarticular process inflected medially, 26 or more presacral vertebrae, strongly angulated clavicles, long narrow pubis, epiphyses fused prior to cranial fusion, anterior head of pseudotemporalis profundus muscle present, wide tongue, no modification of middorsal scale row, only posterior tongue keratinized. **Scincogekkonomorpha** (new definition): lateral flange of parietal for ventral insertion of adductor musculature, large subdental shelf, tongue plicate. **Gekkota**: descending processes of frontal in contact medially, no postorbital, postorbital bar incomplete by reduction or absence of jugal, Meckelian groove close and fused, retroarticular process offset, m. extracollumelaris, no quadrate process of stapes, stapedial artery passes anterior to stapes. **Scincomorpha**: parietal downgrowths, very large symphysial process of pubis, vermiculated dermal rugosities on skull table, mushroom shape tongue in cross section, all tongue keratinized. **Anguioidea**: palpebral ossifications, splenial extends posterior to or is at level of apex of coronoid, 10-20% of tongue notched. **Platynota**: nasal and maxilla separated by external nares, splenial-dentary suture supported with connective tissue, narrow elongated upper temporal fenestra that is constricted posteriorly. **Varanoidea**: maxillary posterior process ends below antorbital region, maxilla excluded from suborbital fenestra, plicidentine, strongly oblique vertebral condyles, no caudal autotomy septa, pterygoid excluded from suborbital fenestra. A full description of the tree is given in Appendix 6.4.


Younginiformes
Prolacerta
Saurosternon
Kuehneosauridae
Rhynchocephalia
Marmoretta
Tamaulipasaurus
Ardeosaurus
Eichstaettisaurus
Bavarisaurus
Huehuecuetzpalli
Iguanidae
Chamaeleontidae
Agamidae
Dibamidae
Amphisbaenia
Pygopodidae
Gekkonidae
Xantusiidae
Lacertidae
Teiidae
Gymnophthalmidae
Tepexisaurus
Scincidae
Cordylidae
Serpentes
Parviraptor
Varanus
Lanthanotus
Helodermatidae
Xenosauridae
Anguidae
LEPIDOSAUROMORPHA
1
LEPIDOSAURIA
SQUAMATOIDEA
2
3
4
ARDEOSAURIDAE
IGUANIA
SQUAMATA
SCLEROGLOSSA
SCINCOGEKKONOMORPHA
GEKKOTA
SCINCOMORPHA
5
VARANOIDEA
ANGUIOIDEA

et al. 1988a). Because Lepidosauromorpha has priority over Lepidosauriformes, the latter term would become invalid.

Although the inclusion of *Palaeagama* and *Paliguana* within the Lepidosauromorpha is supported by two (or three) synapomorphies, phylogenetic analysis involves working with the most economical way of distributing overall evidence in the cladogram. Consequently, none of the ten resulting hypotheses is more plausible than any other. The lack of parietals and postparietals and the presence of an anteroventrally divergent prefrontal-nasal suture vindicates the inclusion of *Palaeagama* within Sauria and should be classified as Sauria *incerta sedis* until new evidence becomes available. The case of *Paliguana* is more complex. All three unambiguously derived features defining Sauria (see also Laurin 1991) are lacking. Although the presence of a broad snout and a quadrate with an enlarged head and with lateral conch are clearly lepidosauromorph features, the presence of tabulars and postparietals, a prefrontal nasal suture parallel to the midline and the lack of contact between paraoccipital process of opisthotic with suspensorium, suggest that *Paliguana* falls outside Sauria. *Paliguana* should be classified as a Neodapsida *incerta sedis*. The same conclusion was reached by Evans (1988).

With the exclusion of *Paliguana* from the Lepidosauromorpha and the Sauria, the Neodiapsida (Benton 1985, Laurin 1991) can be defined as -the most recent common ancestor of Younginiformes, *Paliguana*, and Sauria, and all of its descendants. Laurin (1991) lists 4 synapomorphies supporting this clade:

[D1].- Ventromedial flange of parietal for dorsal attachment of jaw adductor muscles present.

[D2].- Narrow anteroventral process of squamosal

[D3].- Trunk ribs holocephalous

[D4].- Ends of humerus robust

Paliguana certainly has dorsal attachment of the jaw adductor musculature and a narrow anteroventral process of squamosal if compared to *Petrolacosaurus* (Reisz 1981).

The presence of several lepidosauromorph characters, however, may lead to a redistribution of characters in the younginiforms/saurians boundary. The analysis did not extend to all neodiapsids and a broader analysis is needed to clarify this point.

With the exclusion of *Palaeagama* from the Lepidosauromorpha, Sauria can be defined as -the most recent common ancestor of *Palaeagama*, Lepidosauromorpha, and Archosauromorpha, and all of its descendants. Characters supporting this node are invariant within Lepidosauromorpha:

138.- Postparietals absent.

139.- Tabulars absent.

173.- Anterolateral divergent prefrontal-nasal suture.

In addition, Laurin (1991) listed eleven additional synapomorphies: squamosal confined to dorsal portion of skull, a strong, broad contact between paraoccipital process and cheek, cleithrum absent, lateral centrale in manus small or absent. All are constant within the Lepidosauromorpha. Five other synapomorphies show reversals within Lepidosauromorpha: An emarginated quadrate (reversed in *Marmoretta*, chamaeleontids, amphisbaenians, some rhynchocephalians, and some snakes); slender stapes with no stapedial foramen (reversed in *Kuehneosaurus*), a large retroarticular process (reversed in dibamids and *Sphenodon*), and the absence of the fifth tarsal (reversed in *Saurosternon*).

The last two characters might be better explained as synapomorphies of more inclusive groups of Lepidosauromorpha: lack of teeth on the transverse flange of pterygoid (present in Kuehneosauridae (Evans 1991) and some rhynchocephalians) and the fifth metatarsal hooked (not so in *Saurosternon* and *Kuehneosaurus*) are lepidosaur synapomorphies.

NODE 1: Kuehneosauridae + Lepidosauria (= unnamed taxon of Gauthier et al. 1988a).

Preliminary remarks: The Kuehneosauridae is a highly specialized group of gliding reptiles composed by *Kuehneosaurus latus*, *K. lattisimus* (Robinson 1962) and *Icarosaurus* *siefkeri* (Colbert 1966, 1970) from the late Triassic of England and North America. These taxa were grouped in the monophyletic assemblage Kuehneosauridae by Romer (1966). Initially Robinson (1962) classified them within the Squamata on the basis of the lack of a lower temporal fenestra and the presence of a streptostylic quadrate. Later the Kuehneosauridae were removed from the Squamata and grouped within the Eolacertilia (Robinson 1967), a paraphyletic assemblage containing primitive lizards, but were considered relatively more evolved than sphenodontians (Carroll 1988b). Works by Gauthier et al. (1988a) and Evans (1991) agree that Kuehneosauridae is a basal lepidosauromorph clade branching off as sister-group of Lepidosauria (Node 1 in Fig. 42). Two unambiguous characters plus seven ambiguous characters support this relationship.

Unambiguous synapomorphies for node 1:

191.- Thickness of humerus reduced. Reversed within rhynchocephalians.

204.- Small thyroid fenestra. Further transformation in squamatoids (new taxon; see below).

Comments: From Gauthier et al. (1988a), only the presence of a metacarpal IV subequal or slightly shorter than metacarpal III can be explained as an unambiguous synapomorphy of node 1 if the transition from subequal metacarpals to slightly shorter metacarpal IV is ordered. Subequal metacarpals III and IV is autapomorphic for Kuehneosauridae. An anterolaterally oriented prefrontal nasal suture, loss of tabulars and postparietals, paraoccipital process of opisthotic contacting quadrate (reversed in *Paliguana* if included in Lepidosauromorpha) and an angular reduced on lateral view of mandible, are saurian synapomorphies. The loss of teeth on the transverse flange of the pterygoid is synapomorphic of a more inclusive node (see above). From Evans (1991) the surangular contributing only to the articular rim is an ambiguous synapomorphy of node 1. The quadrate condyle extending well below the occipital condyle and a anterolaterally oriented nasal-prefrontal suture are saurian synapomorphies.

After the exclusion of *Palaeagama* and *Paliguana*, character distribution in this node is modified. If *Paliguana* is sister-group of *Saurosternon* (Fig. 41C), the presence of a strong maxillary dorsal process and an anteroventral margin of the orbit formed by maxilla and jugal will be two other unambiguous characters supporting node 1; but, if *Paliguana* branches off the cladogram after *Saurosternon*, only these last characters will support node 1, and the presence of a more slender humerus and a small thyroid fenestra will become ambiguous characters supporting either this node or defining the Lepidosauriformes.

LEPIDOSAURIA Haeckel, 1868 (as redefined by Romer 1956).

Definition: The most recent common ancestor of rhynchocephalians (as defined by Gauthier et al. 1988a) and squamatoids (new taxon), and all of its descendants.

Preliminary remarks: Since the removal of *Sphenodon* from Squamates (Günther 1869), the rhynchocephalians have been considered the closest lizard relatives (Romer 1956) and an important key in the understanding character evolution towards the lizard morphology. The presence of a lower temporal bar was considered enough to designate them the primitive ancestral type. The recent discovery that primitive sphenodontians lack this bar (Robinson 1973, Evans 1980, Whiteside 1986), overturned the importance of this character in the origin of squamates (Rieppel and Gronowsky 1981). This aspect of the skull of *Sphenodon* is thus considered a derived structure within rhynchocephalians (Whiteside 1986). With the exclusion of the "eolacertilians" (*Paliguana*, *Palaeagama*, *Saurosternon*, and the kuehneosaurids) from an intermediate position between rhynchocephalians and squamates, the sister-group relationship of both taxa is well supported (Benton 1985, Evans 1988, Gauthier et al. 1988a, Estes et al. 1988; this study). Lepidosauria is supported by seven unambiguous and 14 ambiguous characters.

Unambiguous synapomorphies (all are invariant in more inclusive groups):

76.- No teeth on transverse flange of pterygoid.

135.- Small lacrimal on orbital rim.

198.- Metacarpals I and V thicker than II, III, and IV.

166.- Preorbital region equal or longer than postorbital region.

202.- Steeply inclined ilium.

203.- Pubic flange on ilium.

205.- Pelvic bones fused in adults.

In addition to the unambiguous character listed, six soft anatomy characters mentioned by Gauthier et al. (1988a: characters 161, and 163-167) support the Lepidosauria and can be added to the diagnosis (see Appendix 6.2).

Comments: From characters listed by Gauthier et al. (1988a), the imperforate stapes, complete abducens canal and well developed dorsum sellae, teeth attached superficially to jaw, sternal plates fused in embryo, caudal autotomy septa, lepidosaur knee joint, lateral centrale of pes fused to astragalus in embryo; first distal tarsal lost, and the presence of a hooked fifth metatarsal are ambiguous lepidosaurian characters or character better explained to originate in this node. Neither rhynchocephalians nor squamatoids (new taxon) have imperforate stapes. The course of the stapedial artery in rhynchocephalians as shown by *Sphenodon*, is anterior to the stapes. This character is autapomorphic to rhynchocephalians (convergent in gekkotans and snakes). An imperforate stapes will be synapomorphic to lepidosaurs only if alternative courses of the stapedial artery are proven to describe an ordered transformation series. Similarly, the presence of a hooked metatarsal with a broad lateral plantar tuber and a medial plantar tuber restricted to the proximal portion of the bone, is autapomorphic to rhynchocephalians. The presence of a hooked fifth metatarsal would be a lepidosaurian synapomorphy only if the sphenodontian type is proven to precede the squamate type in an ordered transformation series.

An analogous problem arises with respect of the mode of tooth implantation. Gauthier et al. (1988a) and Evans (1991) have lumped together the presence of acrodont and pleurodont dentition as a derived condition. If treated separately acrodont dentition would have evolved separately within rhynchocephalians and acrodont squamates, being autapomorphic in each case. Pleurodont dentition is better explained as a lepidosaur synapomorphy since this condition is primitive within rhynchocephalians (Evans 1980) and squamates. The ordered transformation of pleurodont to acrodont dentition is well supported (Whiteside 1986). The use of a combined condition "teeth attached to the margin of the teeth" is not justified.

Sternal plates fused in embryo, presence of the lepidosaur knee joint, and the pes lateral centrale fused to astragalus in embryo appear as Kuehneosauridae + Lepidosauria synapomorphies. However, these characters are not known in kuehneosaurids and are better explained as lepidosaurian synapomorphies. The mandibular condyle formed only by articular bone is an ambiguous Kuehneosauridae + Lepidosauria synapomorphy (Evans 1991). The ectepicondylar groove closing into a foramen in adult and the ilium forming 80-85% of surface area of acetabulum are respectively a lepidosauromorph synapomorphy and an ambiguous lepidosauromorph synapomorphy (reversed in kuehneosaurids). The anterior portion of the pubis outturned medially and the absence of the fifth distal tarsal are possible saurian synapomorphies. Within lepidosauromorphs, parasphenoid teeth are only present in kuehneosaurids and should be considered as autapomorphic or a retained primitive character of this taxon. The lack of teeth on the parasphenoid is a Neodiapsida synapomorphy (Benton 1985).

The presence of accessory intervertebral articulations has a complex distribution. It is better explained as an ambiguous Node 2 synapomorphy reversed in Squamata and acquired independently within the Rhynchocephalia. A long anterior process of the squamosal contacting the jugal over the lower temporal fenestra is only present in some Rhynchocephalians, *Eichstaettisaurus*, most iguanians, skinks and xenosaurids. Either optimization method suggests that it was acquired independently in each of these taxa. The lack of xiphisternum is unique for rhynchocephalians and this character should be considered autapomorphic for this clade in the context of the Lepidosauromorpha. A reduced xiphisternum is an ambiguous synapomorphy in more inclusive clades within squamatoids (new taxon).

Finally, the presence of secondary ossification centers, the calcification of several soft anatomy elements, and bone composed of dense lamellar avascular bone are lepidosaur synapomorphies not known in any fossil forms. These character were excluded from the analysis (see Appendix 6.2).

Evans (1991) mentioned two other characters: A large head of the quadrate is either a lepidosauromorph synapomorphy (if *Paliguana* and *Palaeagama* are included), or a *Kuehneosaurus* + Lepidosauria synapomorphy, reversed in *Marmoretta*; nasals narrower than nares is a Node 3 synapomorphy.

SQUAMATOIDEA new taxon

Definition: The most recent common ancestor of *Marmoretta*, *Tamaulipasaurus*, the Bavarisauridae (as here defined), *Huehuecuetzpalli*, Squamata, and all of its descendants.

Preliminary remarks: Basal members of the Squamatoidea have been considered either sister-groups of the Lepidosauria or to be included within the Squamata. As mentioned before, these results are expected if basal lepidosauromorphs are analyzed lumping squamates into a single terminal taxa and if Squamata is analyzed assuming that all fossil squamate-like forms belong to one or another of the so called "major groups of Squamata". In the literature, no name grouping stem and crown squamates was found, so the new name Squamatoidea is suggested. It was considered convenient to name only the root of this clade until new information of more inclusive clades becomes available, and to keep the name Squamata for the crown group squamates only, avoiding redefinition of that taxon. Eolacertilia (Romer 1966), erected to group ancestral lizard-like forms, could have been redefined and used; however, this taxon groups *Kuehneosaurus*, *Palaeagama*, *Paliguana* and *Saurosternon*, which are certainly a paraphyletic assemblage of stem lepidosauromorphs. Sukhanov (1976) uses the name Prolacertilia to indicate ancestral lizards. This name, however was not properly established and its use is unfortunate because it can be confused with Prolacertilia of Huene (1956) which includes prolacertids, askeptosaurs, thalattosaurs, and clariziids. Camp (1923) used the term Sauria to group all squamates including their ancestors, but Sauria has been redefined by Gauthier (1984) and Laurin (1991) as the most recent ancestor of archosauromorphs and lepidosauromorphs, closer to its original usage.

The Middle Jurassic lepidosauromorph *Marmoretta* is the most basal squamatoid to branch off the cladogram. It was described by Evans (1991) and Waldman and Evans (1994) as the sister-group of Lepidosauria; however, Waldman and Evans (1994) pointed out the presence of several lepidosaur synapomorphies. Squamatoidea is diagnosed by five unambiguous and 22 ambiguous characters (see Appendix 6.4). Because fossil taxa lack data for many of the ambiguous characters they might be better explained as originating within a more inclusive group.

Unambiguous synapomorphies:

150.- Palatine-vomer median contact lost. Reversed within Agamidae, Teiidae, Polyglyphanodontines, and *Shinisaurus*.

162.- Pterygoid contact margin of suborbital fenestra. Reversed in some large iguanines, pygopods, varanoids, amphisbaenians and dibamids.

177.- Coronoid process formed primarily by coronoid. Invariant.

185.- Sacral and caudal ribs fused in embryo. This character was coded in fossil taxa as far as our knowledge permits. Invariant.

224.- Quadrate-epipterygoid contact lost. Invariant.

Comments: Evans (1991) found four synapomorphies that support the position of *Marmoretta* as sister-group of lepidosaurs. The lack of teeth on the pterygoid flange, reduced lacrimal mostly limited to the orbital rim, and teeth superficially attached are unambiguous or ambiguous lepidosaur synapomorphies. The absence of teeth on the parasphenoid is an invalid character since the alternative state "teeth present" is autapomorphic for *Kuehneosaurus*. All characters indicating the sister-group relationship of *Marmoretta* and lepidosaurs would also apply if *Marmoretta* were placed within the Lepidosauria, but become lepidosaur synapomorphies instead. The lack in rhynchocephalians of the five unambiguous synapomorphies diagnosing squamatoids strongly support the conclusion that *Marmoretta* branches off the cladogram after the node defining Lepidosauria. The exclusion of many taxa, the merging of rhynchocephalians and squamates into a single terminal taxon, and the use of only a small sample of characters from which almost 30% are uninformative for lepidosauromorph relationships, makes Evans' (1991) conclusions dubious.

The presence of median contact of vomers and palatines is uncertain in *Marmoretta*. This character was coded (1?) from the reconstruction of the palatal region given by Evans (1991). If rescored as not known (?), the tree topology does not change, and the contact between vomers and palatines will diagnose ambiguously the following node.

NODE 2: Unnamed taxon: *Tamaulipasaurus*, the Ardeosauridae (as here defined) *Huehuecuetzpalli*, and the Squamata.

Preliminary remarks: *Tamaulipasaurus* is a small burrowing diapsid described by Clark and Hernández (1994) from the Middle Jurassic deposits from México. It was classified as a Sauria *incerta sedis* because its identity within Archosauromorpha was possible but not explored. However, the presence of several characters discussed in previous node description, some of which are unique to lepidosauromorphs, strongly suggest its inclusion within this group. Of the conflictive characters mentioned by Clark and Hernández (1994), only the nares close to the midline and the enlarged L-shape quadratojugal are not documented within lepidosauromorphs and may suggest archosauromorph affinities. Other characters mentioned are dubious since they are variable within the Lepidosauromorpha: an enlarged premaxilla separating the maxilla from the nares is present in clevosaur sphenodontians (Wu 1994, Sues et al. 1994); a reduced parietal foramen is present in kuehneosaurids and some squamates; and the notochordal canal is absent in all procoelous lepidosauromorphs (except some geckos and xantusiids) and in the platycoelous vertebrae of *Kuehneosaurus* (Evans 1991).

Equally parsimonious hypothesis presented by Clark and Hernández (1994) suggested that *Tamaulipasaurus* is either the sister-group of lepidosaurs or squamates. As pointed out before, the different hypotheses of sister-group relationships of *Tamaulipasaurus* resulted since its position in the cladogram is in the borderline between the phylogeny of basal lepidosauromorphs and squamates. Results were obtained by analyzing data for this genus in Gauthier et al.'s (1988a) data matrix for Lepidosauromorphs and in Estes et al.'s (1988) data matrix for squamates independently. These analysis did not avoid the usual problem of merging all squamates into a single taxon in the analysis of lepidosauromorphs. The exclusion of basal lepidosauromorphs in the analysis for the Squamata precluded understanding character distribution at the base of the Squamata. Results of the current analysis supports the inclusion of *Tamaulipasaurus* within Squamatoidea on the basis of four unambiguous and eight ambiguous characters.

Unambiguous synapomorphies for Node 2:

26.- Lacrimal absent. The distribution of this character is rather complex. The lacrimal is an independent bone in scincomorphs, anguimorphs but might be fused to the prefrontal secondarily within several squamate terminal taxa. Within basal squamatoids the character probably reverted in *Bavarisaurus* (if the lacrimal is certainly present).

28.- Anteroventral margin of orbit formed by jugal. The maxilla enters the anteroventral margin of the orbit in gekkotans, xantusiids and in *Parviraptor*. The character is polymorphic within several terminal squamate taxa.

48.- Opisthotic and exoccipitals fused in embryo. This character was coded in fossil forms as far as our knowledge. The reversed condition "opisthotic and exoccipitals separated", is present in dibamids, in the lacertid *Podarcis*, and probably in *Huehuecuetzpalli*.

148.- Quadrate foramen lost. The lack of a quadrate foramen is constant within this clade. *Kuehneosaurus* lack the foramen as well but this character may have been acquired independently.

NODE 3, unnamed taxon: Ardeosauridae (as here defined), *Huehuecuetzpalli*, and Squamata.

Preliminary remarks: The taxonomic position of *Ardeosaurus*, *Eichstaettisaurus* and *Bavarisaurus* has been very controversial. *Ardeosaurus* was described as a rhynchocephalian (Meyer 1855, Grier 1914) and classified as such by Lydekker (1888) and Zittel (1889) but was called a scincoid by Nopcsa (1908). Camp (1923) classified it as a gekkotan, position followed by Hoffstetter (1964, 1967), Mateer (1982), and Estes (1983a); but Mateer pointed at some scincomorph features. Scincomorph affinities of *Ardeosaurus* have been suggested by Robinson (1967) and Evans (1993, 1995).

Eichstaettisaurus was described as *Ardeosaurus* ? by Broili (1938) but then separated in the new genera *Broiliosaurus* by Hoffstetter (1953) and renamed *Eichstaettisaurus* by Kuhn (1958). Cocude-Michel (1963, 1965) synonymised it with *Ardeosaurus digitalellus*, but later Hoffstetter (1964; 1967) again separated the two genera but grouped them in the Ardeosauridae of Camp (1923). This position was followed by Estes (1983a) but questioned by Evans (1993, 1995). There is near consensus that *Eichstaettisaurus* is a gekkotan (Hoffstetter 1964, 1967; Robinson 1967; Estes 1983a); but Evans (1993) has some doubts.

Bavarisaurus was described as a rhynchocephalian by Wagner (1852) and placed within lizards by Huene (1955). It has been suggested to be an early iguanian (Hoffstetter 1955; Kuhn 1961; Cocude Michel (1961); but Hoffstetter (1964), Estes (1983a), Kluge

(1987) and Estes et al. (1988) considered it a gecko. Recently Evans (1993) placed it as a probable anguimorph scleroglossan lizard.

The redistribution of squamate characters along basal squamatoid nodes shows five unambiguous and six ambiguous characters supporting the position of the Ardeosauridae (as here defined) as the sister-group of *Huehuecuetzpalli* and all squamates.

Unambiguous synapomorphies for Node 3:

23.- Occipital region not covered by parietals. Reversed in Lacertoidea and within chamaeleontids, cordylids and xenosaurids. Convergent within Rhynchocephalia.

64.- Coronoid clasps dentary laterally and medially. Reversed in Acrodonta. Further transformation of this character in scincomorphs, amphisbaenians, dibamids, snakes, and *Lanthanotus*.

136.- Narrow nasals. Invariant.

142.- Quadratojugal lost. Invariant.

145.- Peg for quadrate notch on squamosal. Invariant.

ARDEOSAURIDAE Camp, 1923. New definition (Node 4 in Fig. 42).

New definition: The most recent common ancestor of *Ardeosaurus*, *Eichstaettisaurus*, *Bavarisaurus*, and all of its descendants.

Preliminary remarks: The taxonomic history of *Ardeosaurus*, *Eichstaettisaurus* and *Bavarisaurus* was reviewed above. The Ardeosauridae was constituted by Camp (1923) to include Ardeosaurus; later Hoffstetter (1953, 1964, 1967) placed *Eichstaettisaurus* and *Yabeinosaurus* (Endo and Shikama 1942) within this group. Although *Yabeinosaurus* has been ignored in current analysis because of the lack of a good description, its inclusion is necessary in future work. *Bavarisaurus* has always been considered apart from Ardeosauridae, but all three genera have been grouped within the Gekkota (Estes 1983a). Estes (1983a), Kluge (1967, 1987), and Evans (1993, 1995) have pointed out the lack of characters to support sister-group relationships of *Ardeosaurus* and *Eichstaettisaurus*, and

Evans (1993) has listed a number of differences between both taxa, considering Ardeosauridae polyphyletic. These conclusions are not supported on the basis of the current analysis. Six unambiguous and five ambiguous synapomorphies supports the monophyly of Ardeosauridae.

Unambiguous synapomorphies:

13.- Postfrontal forked medially. Convergent in Scleroglossa with further reversed in amphisbaenians, snakes, and within teiids.

24.- Parietal foramen within parietals. Reversed in anguimorphs and within several terminal scincomorph and in iguanian taxa.

31.- Dorsal process of squamosal lost. Convergent in Scleroglossa with further reversed in amphisbaenians (Clark and Hernández 1994) and within xenosaurids and teiids.

93.- 23 or fewer presacral vertebrae. Convergent with *Tepexisaurus* and within terminal iguanian taxa.

106.- Ectepicondylar foramen or groove absent. Not known in *Ardeosaurus* (see below). Convergent in chamaeleontids, teiioids and amphisbaenians.

163.- Postfrontal on margin of upper temporal fenestra. Convergent in rhynchocephalians, teoiids, skinks, and within some anguimorph terminal taxa.

Comments: Characters 13 and 31 would suggest scleroglossan affinities of ardeosaurids. Although placing the Ardeosauridae within this groups is a feasible hypothesis, the position of ardeosaurids outside Squamata is the most parsimonious hypothesis on the base of current knowledge. If *Bavarisaurus* is forced to be the sister-group of Gekkota, and the Ardeosauridae as previously defined (*Eichstaettisaurus* + *Ardeosaurus*) is forced to be the sister-group of both Gekkota and *Bavarisaurus* (hypothesis of Estes 1983a, and Kluge 1987), the tree length will increase by 13 steps. On the other hand, if *Eichstaettisaurus* is forced to be sister-group of Gekkota, *Ardeosaurus* of Scincomorpha and *Bavarisaurus* of Anguimorpha (hypothesis of Evans 1993), the tree will increase by 16 steps. If the members of Ardeosauridae are to be included within Squamata, the best hypothesis would be to place the whole assemblage as here defined as sister-group of Scleroglossa. This hypothesis requires only five additional steps. More synapomorphies uniting ardeosaurids with gekkotan, scincomorph, anguimorph, or scleroglossan squamates are needed to support cladistically any of these hypotheses.

The polytomy within Ardeosauridae can be solved either by placing *Bavarisaurus* as the sister-group of *Eichstaettisaurus* or *Ardeosaurus* (Fig. 43). No hypothesis supports the sister-group relationship of *Ardeosaurus* and *Eichstaettisaurus* as suggested by Hoffstetter (1964, 1967), so Ardeosauridae cannot be defined without including *Bavarisaurus*. Unambiguous characters supporting the two possible solutions are:

Hypothesis 1: *Bavarisaurus* and *Eichstaettisaurus* are sister-groups (Fig. 43A; Node i)

7.- Frontals constricted between orbits.

20.- Unfused parietals.

Hypothesis 2: *Bavarisaurus* and *Ardeosaurus* are sister-groups (Fig. 43B; Node ii)

4.- Maxilla contact frontal.

43.- Broad ectopterygoid restricting suborbital fenestra.

If *Bavarisaurus* and *Ardeosaurus* are considered sister-groups, the lost of the ectepicondylar foramen (character 106, state 2) should be added to the diagnosis of the Ardeosauridae.

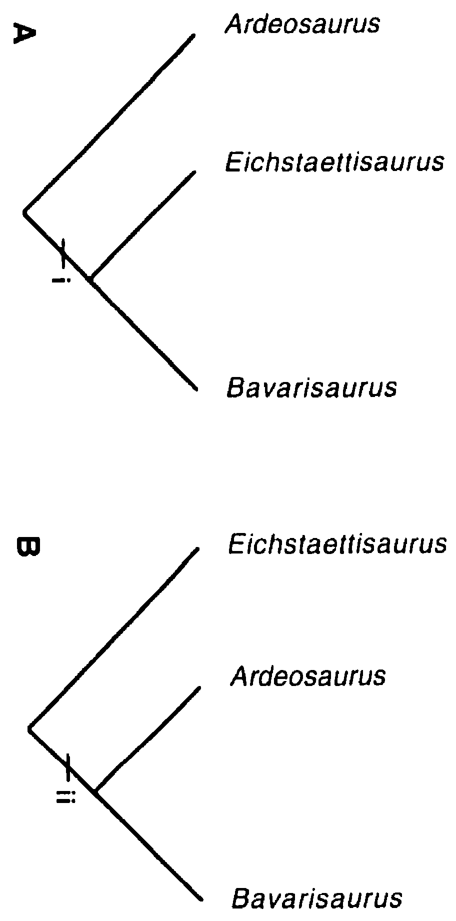
NODE 5, unnamed taxon: *Huehuecuetzpalli* and Squamata.

Preliminary remarks: Results of the current analysis support conclusions discussed in Chapter 4. The node is supported by two unambiguous and six ambiguous synapomorphies.

Unambiguous synapomorphies for Node 5:

94.- Eight cervical vertebrae. Reversed in chamaeleontids, *Tepexisaurus*, within scincoid terminal taxa, dibamids and within anguids. Convergent within Rhynchocephalia and further transformation in varanids.

Fig. 43. Two equally parsimonious hypotheses of sister-group relationships within the Ardeosauridae. **A**. **Node i:** frontals constricted between orbits, separated parietals. **B**. **Node ii**: maxilla contacts frontal, broad ectopterygoid that restrictes suborbital fenestra. The sister-group relationship of *Ardeosaurus* + *Eichstaettisaurus* (Ardeosauridae as defined by Camp 1923; Estes 1983a) is not supported. If *Bavarisaurus* is sister-group of *Ardeosaurus*, then the absence of the ectepicondylar foramen should be added to the diagnosis of the Ardeosauridae as defined here (cf. Fig. 42: Node 4).


A
Ardeosaurus
Eichstaettisaurus
i
Bavarisaurus
B
Eichstaettisaurus
Ardeosaurus
ii
Bavarisaurus

102.- Clavicle articulates with suprascapula. Reversed within agamids, iguanids, and gekkonids.

SQUAMATA Oppel, 1811.

Definition: The most recent common ancestor of Iguania and Scleroglossa and all of its descendants (Estes et al. 1988).

Preliminary remarks: Snakes and amphisbaenians have long been considered separated groups from Lacertilia (Romer 1956; Underwood 1957, 1970; Sukhanov 1976; Northcutt 1978; Rieppel 1978; Rage 1982; Estes 1983a). Contrary to this view, Gauthier et al. (1988a) and Estes et al. (1988), gave a list of 84 synapomorphies supporting their inclusion within major lacertilian groups, turning Lacertilia into a paraphyletic assemblage. The taxonomic composition of Squamata has been complex and groups such as prolacertids (Wild 1973, 1980), kuehneosaurids (Robinson 1962, 1967), and "the Paliguanidae" (Carroll 1977, 1988b) were once included. All these groups, however, now are known to be either basal lepidosauromorphs or dubiously referred to this group. Squamata is supported by only three unambiguous and two ambiguous synapomorphies.

Unambiguous synapomorphies:

1.- Fused premaxilla. Reversed within gekkonids and skinks.

89.- No thoracolumbar intercentra. Reversed in gekkonids and within xantusiids. Convergent in *Kuehneosaurus*.

211.- No second distal tarsal. Invariant. Convergent in *Bavarisaurus*.

Comments: Of characters listed by Estes et al. (1988), soft anatomy characters that support squamate monophyly but were not included in the analysis (characters [38-66], but see Appendix 6.2) are better explained as ambiguous squamate synapomorphies. Those soft anatomy characters diagnosing ambiguously the Squamatoidea are also better explained as ambiguous squamate synapomorphies since these are not known in fossil forms and they could have been originated at any nodes within the basal squamatoids. Septomaxilla with ventral projection forming posterior margin of the duct of Jacobson's organ, large vestibule of septomaxilla, fissura metotica divided, vidian canal fully enclosed posterolaterally, pin-like stapes, cervical intercentra with prominent hypapophyses, nearly hemispherical distal end of the ulna, lateral centrale in contact with the second distal carpal, less than 10% of the tongue notched, and the stapedial artery passing posterior to stapes, diagnose other squamatoid basal nodes, but are not known in correspondent with basal forms. These are therefore better explained as ambiguous squamate synapomorphies. The loss of vomerian teeth is better explained as a squamate synapomorphy with independent lost within rhynchocephalians because the presence of vomerian teeth in primitive rhynchocephalians. Fourteen scleral ossicles and the presence of preanal pores are better explained as scincogekkonomorph synapomorphies. Less than 14 scleral ossicles would be the primitive condition for squamates (contra Estes et al. 1988). The lack of zygosphene and zygantrum accessory articulations is difficult to explain since the condition is not known in ardeosaurids. It may be an ambiguous squamate synapomorphy or a primitive saurian synapomorphy in which accessory articulations were independently developed in *Huehuecuetzpalli*, *Tamaulipasaurus* and within Squamata.

Other characters listed as diagnostic characters or ambiguous synapomorphies are better explained as appearing in less inclusive groups: Eight cervical vertebrae, pterygoid lappet of quadrate absent, anterior coracoid fenestra present, and clavicle articulating suprascapula are Node 5 synapomorphies or ambiguous characters better explained as appearing at this node. Narrow nasals, transversally oriented frontoparietal suture, deep supratemporal, squamosal articulation of quadrate notched or fenestrated, angular not reaching mandibular condyle, styloid process on radius fitting on groove in radiale, first metacarpal contacting medial centrale and second distal carpal, enlarged thyroid fenestra, most distal end of tibia forms part of astragalocalcanear joint, complex tongue-in-groove astragalocalcanear/fourth distal tarsal joint, squamate hooked fifth metatarsal, loss of gastralia, braincase broadly exposed dorsally, broad interpterygoidal vacuity, coronoid lateral process as lappet of dentary, are Node 3 synapomorphies or ambiguous character better explained as appearing at this node. A gently convex tibial distal end and the presence of a distal tibial notch fitting to the astragalus ridge are derived conditions when the ridge and trough articulation in the tibio-astragalar joint are lost. A notched tibia (synapomorphy of unnamed taxon 3) is the primitive condition for Squamata, and the gently convex tibial distal end is a synapomorphy of iguanians (Chapter 4, contra Estes et al. 1988).

A columelliform epipterygoid with a narrow base, anteroventral border of orbit formed by jugal, and opisthotic fused to exoccipital in embryo are Node 2 synapomorphies or ambiguous characters better explained as appearing at this node. The pterygoids separated from vomers and included in the suborbital fenestra, coronoid formed mainly by coronoid bone, and sacral and caudal ribs fused in embryo are squamatoid synapomorphies or ambiguous characters better explained to appear in this node. The loss of the ventral ramus of squamosal and presence of gracile limbs are Node 1 synapomorphies or ambiguous characters better explained as appearing at this node. The presence of a ventral ramus of squamosal is autapomorphic for rhynchocephalians, and the presence of stout limbs in rhynchocephalians is better interpreted as a reversal. Because the parietals are fused and palatine teeth are present primitively in rhynchocephalians these characters are better explained as ambiguous lepidosaur synapomorphies. The fusion of neural arches to the centra in the embryo, loss of entepicondylar foramen in humerus, and the carpal intermedium small or absent are ambiguous saurian synapomorphies. Finally, the paraoccipital process contacting suspensorium is an ambiguous neodiapsid synapomorphy. The paraoccipital process ends freely only in *Paliguana*. The modification of the paraoccipital process to take part in the support of the quadrate (not included in the analysis) would be an unnamed taxon 2 synapomorphy since this state is already present in *Tamaulipasaurus*.

IGUANIA Cuvier 1817

Definition: The most common ancestor of Iguanidae, Agamidae, and Chamaeleontidae and all its descendants.

Preliminary remarks: The Iguanidae was originally considered to include Agamidae and Iguanidae (Camp 1923); and chamaeleontids were later added (McDowell and Bogert 1954; Romer 1956; Underwood 1971, Moody 1980; Estes 1983a; Frost and Etheridge 1989). *Sphenodon* was first included within the Agamidae (Gray 1831) before Günther (1869) pointed at differences from squamates and placed it in a distinct order. Camp (1923) classified paliguanids within iguanians. The Late Jurassic lizard *Euposaurus* (Cocude-Michel 1963, Hoffstetter 1964, Estes 1983a), once thought to be an iguanian (but see Camp 1923), is now considered to be a squamate of uncertain relationships (Evans 1993).

Unambiguous synapomorphies:

8.- Broad frontal shelf below nasals. Invariant.

18.- No contact between jugal and squamosal over lower temporal fenestra. Reversed within chamaeleontids, convergent with *Eichstaettisaurus*, skinks and xenosaurids.

107.- Gently convex distal end of tibia. Invariant, probably convergent with *Eichstaettisaurus*.

Comments: From characters mentioned by Estes et al. (1988; see also Etheridge and Frost 1989), the frontals constricted between orbits and the presence of a parietal foramen on frontoparietal suture are ambiguous iguanian characters. Postfrontal reduced is an invalid synapomorphy since this bone is never present in chamaeleontids and agamids. The parietal foramen on the frontoparietal suture and a small postfrontal are convergent in *Huehuecuetzpalli* and can be explained as synapomorphies of Node 5 with reversal in scleroglossans. Frontals fused in embryo is an ambiguous lepidosaur synapomorphy; the presence of a finger-like angular process and the caudal autotomy septum posterior to the vertebral transverse process are explained as being acquired independently in Gekkota and within several Squamata terminal taxa as accelerated or delayed transformations.

Dracomorph brain, loss of m. intercostalis ventralis, and tongue with serous and sero-mucous mucocites were not included in the analysis but are also considered to diagnose Iguania by Etheridge and Frost (1989). Metacromatism is only present in some iguanids and reticulate papillae on posterior limbs of tongue is an Acrodonta synapomorphy with independent evolution in anoles (Schwenk 1988).

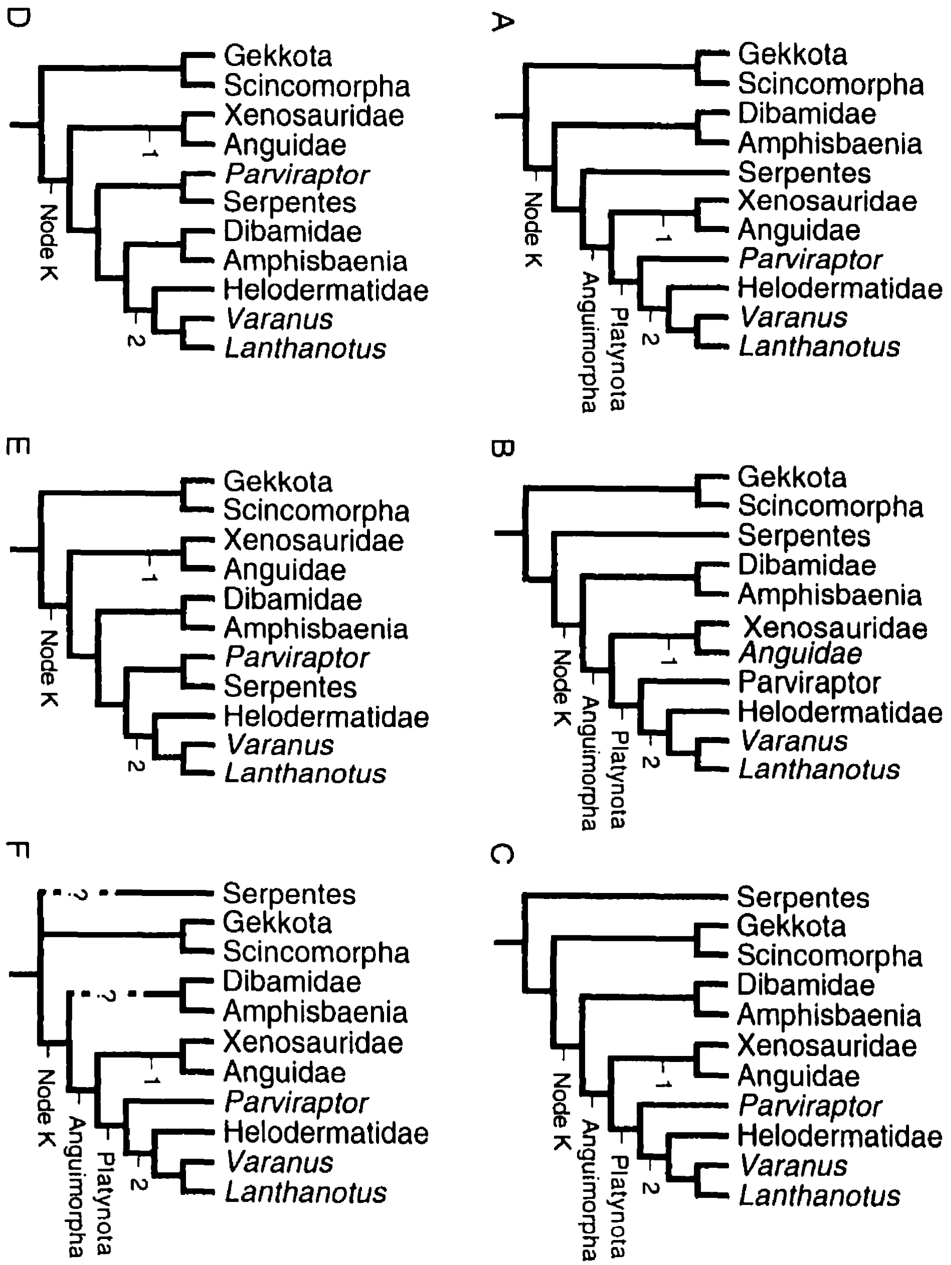
SCLEROGLOSSA Estes, Gauthier and de Queiroz, 1988

Definition: The most common ancestor of Gekkota, Scincomorpha, Anguimorpha, Amphisbaenia, Dibamidae and Serpentes and all its descendants.

Preliminary remarks: The clade Scleroglossa was originally defined to group Gekkota, Autarchoglossa, Amphisbaenia, Dibamidae and Serpentes. Since the sister-group relationship between gekkotans and scincomorphs is better supported, the Autarchoglossa is considered a paraphyletic assemblage. According to Estes et al. (1988) the name Scleroglossa is preferred over Sukhanov's Scincogekkonomorpha because, contrary to Kluge's (1989) arguments, the Scincogekkonomorpha does not include amphisbaenians, dibamids and snakes. Here the name Scincogekkonomorpha Sukhanov is redefined for a more inclusive group (see below).

In the strict consensus (Fig. 42) the sister-group relationships within the Scleroglossa are not fully resolved. Figure 44 A-E show five equally parsimonious hypotheses of interrelationships of ingroup taxa. Although the strict consensus is collapsed in most of the clades, differences in the five trees are only caused by the uncertain placement of snakes and the clade composed of dibamids and amphisbaenians. All other taxa remain in a constant position when these "problematic taxa" are removed (Fig. 44F). In all hypotheses, snakes are included within Scleroglossa; but contrary to Estes et al.'s results (1988: fig. 6), the sister-group relationships of dibamids and amphisbaenians is well supported and the position of the clade formed by these taxa is placed in a more inclusive position either as the sister-group of anguimorphs or included within this taxon (Node K).

Fig. 44. **A-E.** Five equally parsimonious hypotheses showing the possible sister-group relationships of snakes and the clade composed by amphisbaenians and dibamids. **F.** Consensus tree compatible with all five hypotheses. Snakes have an uncertain relationship within Scleroglossa, and the clade formed by dibamids and amphisbaenians is of uncertain relationship within Node K. *Parviraptor* is consistently the sister-group of varanoids. Apomorphy list: **Node K**: frontals separated, replaced teeth added posterolingually, cervical centra attached to preceding centra, more than 40% of tongue notched, small triangular posterior process of jugal, well developed intramandibular septum. **Anguimorpha**: intramandibular septum located posteriorly in the dentary, anteroventral alveolar foramen of Meckelian groove, dentary with posterior surangular and coronoid notches, dorsal osteoderms, cephalic osteoderms, retractile foretongue. Node 1 = Anguioidea; Node 2 = Varanoidea.

A
Gekkota
Scincomorpha
Dibamidae
Amphisbaenia
Serpentes
Xenosauridae
Anguidae
Parviraptor
Helodermatidae
Varanus
Lanthanotus
Node K
Anguimorpha
Platynota
1
2
B
Gekkota
Scincomorpha
Serpentes
Dibamidae
Amphisbaenia
Xenosauridae
Anguidae
Parviraptor
Helodermatidae
Varanus
Lanthanotus
Node K
Anguimorpha
Platynota
1
2
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Serpentes
Gekkota
Scincomorpha
Dibamidae
Amphisbaenia
Xenosauridae
Anguidae
Parviraptor
Helodermatidae
Varanus
Lanthanotus
Node K
Anguimorpha
Platynota
1
2
D
Gekkota
Scincomorpha
Xenosauridae
Anguidae
Parviraptor
Serpentes
Dibamidae
Amphisbaenia
Helodermatidae
Varanus
Lanthanotus
Node K
1
2
E
Gekkota
Scincomorpha
Xenosauridae
Anguidae
Dibamidae
Amphisbaenia
Parviraptor
Serpentes
Helodermatidae
Varanus
Lanthanotus
Node K
1
2
F
Serpentes
Gekkota
Scincomorpha
Dibamidae
Amphisbaenia
Xenosauridae
Anguidae
Parviraptor
Helodermatidae
Varanus
Lanthanotus
?
?
Node K
Anguimorpha
Platynota
1
2

The node descriptions vary in each hypothesis. To simplify tree description, the diagnosis of subsequent clades are based on the same most parsimonious trees, but removing snakes and the clade dibamids + amphisbaenians (Fig. 44F). Character distribution of all hypotheses is presented in full in Appendix 6.4. Scleroglossa is the best supported clade within the lepidosauromorph phylogeny.

Unambiguous synapomorphies:

9.- Descending process of frontal contacts palatine. Reversed in *Varanus* and teiids.

13.- Postfrontal forked medially. Reversed within teiids, convergent in ardeosaurids.

17.- Postorbital contributing less than half of the posterior part of the orbital rim. Further transformation in skinks and within anguids.

31.- Squamosal dorsal process lost. Reversed in amphisbaenians and within teiids and xenosaurids

37.- Septomaxillae contact medially in raised crest. Invariant.

38.- Convex expanded septomaxillae. Invariant.

46.- Anterodorsally oriented prootic alar process. Reversed in dibamids.

67.- Retroarticular process without dorsal pit. Reversed in lacertiforms and within cordylids. Convergent with some iguanids.

93.- 26 or more presacral vertebrae. Reversed in *Tepexisaurus* and within several scincogekkonomorphs, Convergent with *Eichstaettisaurus* and *Bavarisaurus*.

102.- Strongly angulated clavicles. Reversed within cordylids and varanids.

108.- Long narrow pubis. Further transformation in scincomorphs and anguids, reversed in *Varanus*.

114.- Epiphyses fused prior to cranial fusion. Invariant.

117.- Anterior head of muscle pseudotemporalis profundus present. Reversed in gekkonids and within anguids

122.- Wide tongue. Further transformation in scincomorphs and amphisbaenians.

130.- No modification of middorsal scale row. Invariant. Convergent with some agamids and iguanids.

223.- Posterior part of tongue keratinized. Further transformation in scincomorphs and amphisbaenians.

Comments: Vomers not extending beyond the middle of the maxillary tooth row, prominent choanal fossa of palatines, posterior border of retroarticular process obliquely twisted, and non-prehensile tongue are scleroglossan synapomorphies listed by Estes et al. (1988) here considered ambiguous. The adductor musculature attached ventrally on parietal is a Scincogekkonomorpha (as here defined) synapomorphy acquired independently in helodermatids and within anguioid terminal taxa and iguanians. Enlarged cephalic scales is a scincogekkonomorph synapomorphy convergent in anguids. The lack of subdental shelf is a platynotan synapomorphy; and the presence of oscillatory chemiosensory tongue protrusion can be explained either as an anguimorph or a anguimorph + snakes synapomorphy. A large anterior process of the interclavicle is an ambiguous Node 4 or squamate synapomorphy. Four sternal ribs and a notched distal tibial epiphysis are present in *Huehuecuetzpalli*. These are therefore ambiguous synapomorphies of Node 5.

The loss of glandular epithelium on foretongue is redundant to the keratinzation of the tongue. Only the last character is a scleroglossan synapomorphy.

SCINCOGEKKONOMORPHA Sukhanov (1976) new definition:

New definition: The most recent common ancestor of Gekkota, and Scincomorpha and all its descendants.

Fürbringer (1900), on the basis of shoulder musculature, suggested the close relationships of geckos and skinks (Sukhanov 1976). This hypothesis, however, never gained wide acceptance since Camp's (1923) alternative view which suggested that geckos are closely related to iguanians (grouped in the Ascalabota) became more popular. Estes et al. (1988) demonstrated that Gekkota and Iguania are not closely related, concluding that gekkotans were included in the very well supported assemblage Scleroglossa.

While the position of gekkotans is basal in the Scleroglossa, anguimorphs and scincomorphs were grouped in the Autarchoglossa. Estes et al. (1988), however, recognize that the Autarchoglossa is supported only by three dubious characters. In several attempts to reconstruct squamate phylogeny using the original data matrix of Estes et al. (1988), the clade Autarchoglossa was always the first to collapse. The present analysis can no longer sustain the Autarchoglossa, since the sister-group relationship of Gekkota and Scincomorpha are better supported.

The name Scincogekkonomorpha (Sukhanov 1976) was redefined to group only Gekkota and Scincomorpha (Anguimorpha excluded). This new definition is in accordance to Sukhanov's conclusions since he never included any anguimorph taxa in his research or discussion.

Unambiguous synapomorphies:

51.- Lateral flange of the parietal for ventral insertion of adductor musculature. Reversed in teiids and within gymnophthalmids. Convergent in helodermatids, *Ardeosaurus*, and *Eichstaettisaurus*, and within anguioids and iguanians.

55.- Large subdental shelf. Reversed within gymnophthalmids.

123.- Posterior part of the tongue plicate. Further transformation in lacertids. Equivocal distribution in cordylids.

The splenial extended posteriorly to or beyond the level the coronoid process is an unambiguous synapomorphy in hypotheses A, B, and C (Fig. 44), and the presence of the second ceratobranchial is an additional synapomorphy suggested in hypothesis C only. These characters become ambiguous in other hypotheses.

Other ambiguous characters are: suborbital fenestra restricted or closed by postfrontal, retroarticular process broadened posteriorly, 14 scleral ossicles, second epibranchial present, epicoracoid cartilage contacts suprascapula and mesoscapula, femoral and preanal pores present, and a broad upper temporal arch. Many of these characters, however, cannot be coded for gekkotans or shows polymorphism within several scincogekkonomorph terminal taxa.

Comments: Presch (1988) and Swenk (1988) support Gekkota and Scincomorpha sister-group relationships as well. The exclusion of dibamids and snakes, the ignorance of variation within terminal taxa, the use of only *Sphenodon* as an outgroup, and the miscoding of several characters are flaws found in Presch's (1988) analysis. The exclusion of dibamids is particularly questionable when they have been considered traditionally scincomorphs, the subject of his study. Schwenk's (1988) results are not comparable since they were based exclusively in tongue structure. Presch (1988) and Schwenk (1988) give several additional characters not included in Estes et al.'s (1988) data matrix and their inclusion might strengthen the Scincogekkonomorpha. Characters supporting this clade are good no-ambiguous synapomorphies if compared with those supporting Autarchoglossa in Estes et al. (1988).

GEKKOTA Cuvier, 1817

Definition: The most recent common ancestor of Gekkonidae, Pygopodidae, and all of its descendants.

Preliminary remarks: For preliminary remarks see papers of Rieppel (1984), Kluge (1987), Grismer (1988) and Estes et al. (1988).

Unambiguous synapomorphies:

10.- Descending processes of the frontal in contact medially. Convergent in *Varanus*, helodermatids, and within anguids, gymnophthalmids, and xantusiids.

16.- No postorbital. Convergent in dibamids, platynotans, *Tamaulipasaurus*, and within skinks and amphisbaenians,

29.- Postorbital bar incomplete because of reduction or absence of jugal. Convergent in dibamids and *Varanus* and within skinks, amphisbaenians and snakes.

52.- Meckelian groove closed and fused. Convergent in xenosaurids and dibamids, and within iguanids, skinks, gymnophthalmids, and amphisbaenians.

70.- Medial offset of retroarticular process. Invariable

119.- M. extracollumelaris. Invariable

125.- Quadrate process of stapes absent. Convergent in skinks, gymnophthalmids, amphisbaenians and within xantusiids and anguids.

129.- Stapedial artery anterior to stapes. Reversed within gekkonids. Convergent in rhynchocephalians and snakes.

Other unique characters are: paired dentinal egg-teeth present, large wing-like hyoid cornu present, spindle body present in tectorial membrane, elongated cochlear duct and basiliar membrane, cochlear limbus extremely large, sublingual glands diffusely scattered across floor of mouth (Kluge 1987; Wever 1978; Estes et al. 1988).

Comments: In addition, Estes et al. (1988) gives the following synapomorphies: Bony canal for lateral head vein on crista prootica, autotomy septa posterior to a single pair of transverse process, postcloacal bones, carpal intermedium lost, and a ciliary restrain system for hair cells with combined tectorial and sallet system, are ambiguous gekkotan synapomorphies. The retroarticular process broadened posteriorly is an ambiguous scincogekkonomorph synapomorphy. Parietal foramen lost, and retroarticular process inflected medially are ambiguous scleroglossan synapomorphies. The splenial not extending anteriorly beyond the midpoint of the tooth row is an ambiguous squamate synapomorphy. Absence of pterygoid teeth and lacrimal are ambiguous synapomorphies defining Node 3 and 2 respectively. The ontogenetic fusion of frontals is a lepidosaur synapomorphy.

SCINCOMORPHA Camp, 1923

Definition: The most recent common ancestor of Scincidae, Cordylidae, Xantusiidae, Lacertidae, Teiidae, and Gymnophthalmidae and all of its descendants.

Preliminary remarks: See preliminary remarks in Camp (1923), Estes et al. (1988), and Presch et al. (1988).

Unambiguous synapomorphies:

22.- Parietal downgrowths. Reversed in lacertids and within skinks.

108.- Very large symphysial process of pubis. Reversed in teiids and *Tepexisaurus*. Convergent in anguids.

113.- Vermiculated dermal rugosities on skull table. Reversed within skinks, gymnophthalmids, teiids and xantusiids. Convergent in *Ardeosaurus*, xenosaurids, and within Amphisbaenia.

122.- Mushroom shape tongue in cross section. Reversed within cordylids, convergent in amphisbaenians.

223.- All tongue keratinized. Reversed within cordylids, convergent in amphisbaenians.

Comments: Estes et al. (1988) also mentioned the following synapomorphies: lateral process of coronoid overlapped anteriorly by dentary and posteriorly by surangular is an ambiguous scincomorph synapomorphy. Ciliary restrain system for hair cell includes a combined tectorial and sallet system is a lacertiform synapomorphy. The loss of nasal-prefrontal contact, is a convergent character within scincomorph terminal taxa as shown by accelerated or delayed optimization.

The position of the Early Cretaceous lizard *Tepexisaurus* agrees with results presented in Chapter 5. The presence of parietal downgrowths supports its inclusion in Scincomorpha, and the presence of a small flange on the medial margin of the retroarticular process and weak zygosphene and zygantrum accessory articulations indicate its sister-group relationships with scincoids (Fig. 42, Node 5).

Node K, Unnamed (Fig. 44F): Amphisbaenia, Dibamidae, and Anguimorpha

Preliminary remarks: The positions of amphisbaenians and dibamids have been very controversial. There is agreement on the monophyly of Dibamidae (Rieppel 1984), which traditionally has been considered within the Scincomorpha. Cope (1900) and Fürbringer (1900) placed *Anelythropsis* and *Dibamus* in different families within Leptoglossa (= Scincomorpha). Gadow (1901) restricted dibamid relations to skinks, gerrhosaurids and lacertids. Camp (1923) placed them within Scincoidea, but later Underwood (1957) suggested that they should be classified with Gekkota. Gasc (1968) and Gasc and Renous (1979) concluded that the similarities with gekkotans are convergent and dibamids lay outside Squamata and should be of same hierarchical rank as Sauria (= Squamata). Rieppel (1984) supported sister-group relationships of dibamids with Acontinae but noted that the position of these two groups among other skinks is debatable. Rieppel argues against Senn and Northcutt's (1973) hypothesis of snake-dibamid relationships pointing out that they only share one character against the many shared by dibamids with lizards. This conclusion, however, is based on the assumption that snakes are outside Lacertilia. Greer (1985) showed that dibamids share most of the derived characters with amphisbaenians and then with snakes.

Cope (1900) placed Amphisbaenia with Annulati (Aniella, Amphisbaenia, Euchrirotheidae, Trogonophidae) but Fürbringer (1900) elevated Amphisbaenia to same ordinal rank to Lacertilia (see also Gans 1978). Camp (1923) placed them within Scincomorpha and Gadow (1901) allied them specifically with xantusiids and teiids. Bogert (1964) related them to burrowing teiids and Rage (1982) suggested sister-group relationships with snakes.

Estes et al. (1988; fig. 5A) in a broad analysis including all limbless squamates concluded that dibamids and amphisbaenians form a monophyletic group branching off the cladogram as sister-taxa of Anguimorpha + Serpentes. In spite of this, they to placed dibamids and amphisbaenians as separated taxa with uncertain relationships on the basis of their results when excluding limbless forms. Results of the current analysis agree with Estes et al.'s (1988) most parsimonious tree. dibamids and amphisbaenians form a monophyletic assemblage but branched off the cladogram either as the sister-group of Anguimorpha or within that group.

Unambiguous synapomorphies:

6.- Frontals separated. Reversed within amphisbaenians, anguids, and xenosaurids.

78.- Replacement teeth added posterolingually. Invariant

88.- Cervical vertebrae intercentra attached to preceding centra. Further transformation in *Parviraptor*, convergent in scincoids.

121.- More than 40% of tongue notched. Reversed in dibamids, anguioids, and helodermatids. Further transformation in *Varanus*. Convergent in teiioids.

141.- Small triangular posterior process of jugal. Reversed within anguids, and varanids. Convergent in agamids, cordylids, and lacertids.

221.- Well developed intramandibular septum in Meckelian groove. Reversed in *Parviraptor*.

Comments:

The sister-group relationships of Amphisbaenia and Dibamidae are very well supported but the number of characters vary from eight to three unambiguous characters in each hypothesis. Of these possible synapomorphies, only the absence of the supratemporal and the posterior enclosure of the Jacobson's Organ are consistent in all five hypotheses. The other characters define other nodes or become ambiguous according to the particular character distribution of each hypothesis.

The position of the clade composed of dibamids and amphisbaenians is uncertain. There are four different possibilities of interrelationships (Fig. 44). The sister-group relationships of Dibamidae + Amphisbaenia with the clade Anguimorpha + snakes is supported by characters 6, 88, and 141; sister-group relationships with anguimorphs only is supported by characters 78, 141, 121, 221. The postorbital absent, short posterior extension of the maxilla, and the maxilla and pterygoid excluded from the suborbital fenestra support the sister-group relationships with Varanoidea. The medial contact of the descending processes of the frontal, subdental shelf absent, fewer than 14 scleral ossicles, elongated, constricted posteriorly upper temporal fenestra, posterior extension of dentary ends anterior to coronoid process support sister-group relationships with snakes and platynotans (Varanoidea + *Parviraptor*).

On the basis of current knowledge, the conclusion of Estes et al. (1988; fig. 6) in considering dibamids and amphisbaenians of uncertain relationships at the base of the Scleroglossa is incorrect. Dibamids + amphisbaenians branching off as sister-group of Scincogekkonomorpha, snakes, or scincogekkonomorphs + anguimorphs is not shown in any of the most parsimonious trees. Then dibamids and amphisbaenians should be considered *incerta sedis* in a clade more inclusive than Scleroglossa (i.e. Node K).

ANGUIMORPHA Fürbringer, 1900

Diagnosis: The most common ancestor of Anguioids and Platynota and all of its descendants.

Preliminary remarks: See preliminary remarks in Rieppel (1980), Gauthier (1982), and Estes et al. (1988).

Unambiguous synapomorphies:

53.- Posterior intramandibular septum. Convergent within chamaeleontids and rhynchocephalians.

54.- Anteroventral alveolar foramen of Meckelian groove. Convergent within chamaeleontids.

58.- Dentary with posterior surangular and coronoid notches. Further transformation in varanids.

111.- Dorsal osteoderms. Reversed within Varanus, convergent in Scincoids, *Huehuecuetzpalli* and within gekkotans.

112.- Cephalic osteoderms. Reversed within *Varanus*, convergent in scincoids and lacertids.

120.- Retractile foretongue. Invariant.

Comments: Lacrimal a separate element, posterior opening of vidian canal at basisphenoid-prootic suture, splenial extends anteriorly beyond the middle of the dentary tooth row, and presence of the anterior head of the muscle pseudotemporalis profundus are also unambiguous synapomorphies if snakes are the sister-group of Anguimorpha.

Of the characters presented by Estes et al. (1988), presence of palpebral ossifications is an anguioid synapomorphy with convergent in *Varanus*; 10-20% of tongue free part notched is an anguioid autapomorphy; posterolingual tooth replacement with small pits and cervical intercentra sutured to the posterior part of preceding centrum is a Node K synapomorphy; more than 26 presacral vertebrae is a scleroglossan synapomorphy; second ceratobranchial absent is an ambiguous squamate synapomorphy; and absence of femoral pores is a saurian or even more primitive condition.

Neither Gauthier (1982) nor Estes et al. (1988) found synapomorphies to support the Anguioidea (McDowell and Bogert 1954). On the base of this study the Anguioidea is supported by the presence of palpebral ossifications.

Scleroglossa *incerta sedis*.

SERPENTES Linnaeus, 1766

Preliminary remarks: As with dibamids and amphisbaenians, the positions of Serpentes have been very controversial. Snakes appear to be a monophyletic assemblage (Rieppel 1988a, b; but see McDowell and Bogert 1954). In earlier classifications snakes have always been considered a higher ranking category within squamates (Cope 1900; Gadow 1901; Romer 1956) equal to lacertilians. On the other hand, snakes have been suggested to be outside Squamata or branching off early in squamate evolution (Cope, 1869; Hoffstetter 1955; Underwood 1970, 1971; Kochva 1978; Rieppel 1988b; Schwenk 1988; and Rage 1982). Nopcsa (1908), Camp (1923), McDowell and Bogert (1954), McDowell (1972) and Bellairs (1972) suggested varanoid or platynotan (Aigialosauridae, Dolichosauridae included) relationships; but Rieppel (1983) showed that there are no similarities between *Lanthanotus* and primitive snakes, except the platyblastic skull. Brock (1941; see also Blanc 1981) related them to scincomorphs. Rage (1982) supported the view that snakes are the sister-group of amphisbaenians; and Senn and Northcutt (1973) related them to *Dibamus*. Gasc and Renous (1979) argue against this last hypothesis suggesting that similarities are due to convergence.

This work support Estes et al.'s (1988) conclusion that Serpentes are within Scleroglossa but with uncertain relationships. However, its position as sister-taxon of Anguimorpha is present in only one of the four most parsimonious hypothesis. Serpentes may be the sister-group of scincogekkonomorphs + dibamids + amphisbaenians + anguimorphs; of dibamids + amphisbaenians + anguimorphs; of anguimorphs alone; or be included within anguimorphs as sister taxon of *Parviraptor*. When including Serpentes in the tree description, character distribution is modified in other nodes. The first hypothesis is supported by a postfrontal forked medially and the short contribution of the postorbital to the posterior rim of the orbit; the second by the frontals separated and cervical intercentrum attached to preceding centra; the third by the loss of foretongue retractility; and the sister-group with *Parviraptor* by a U-shaped frontoparietal suture and a weak maxillary dorsal process.

FEASIBILITY TEST AND DISCUSSION

Tree robustness was estimated by analyzing the data matrix developed here using the Bootstrap method (Felsestein 1985) and by calculating branch support values and the tree total branch support index (Bremer 1989). Results were compared to bootstraps on previously published data matrices and branch support indexes of resultant strict consensus trees (Appendix 6.5; Tables 12 and 13). Data matrices and strict consensus trees for comparison includes Gauthier et al. (1988a), Estes et al. (1988), Evans (1991), Clark and

TABLE 12. Bremer's branch support values (b) for different clades in previously published hypothesis. Abbreviations [E1] Estes et al. (1988) analysis, all taxa included, [E2] Estes et al. (1988) analysis with Dibamidae, Amphisbaenia, and Serpentes excluded; [R1] *Huehuecuetzpalli* analyzed in the data matrix of Estes et al (1988) as is (Fig. 39); [R2] *Huehuecuetzpalli* analysis presented in Chapter 4; [R3] *Tepexisaurus* analysis presented in Chapter 5; [CH1] Clark and Hernández's (1994) analysis of squamates; [G] Gauthier et al.'s (1988a) analysis; [CH2] Clark and Hernández's (1994) analysis of lepidosauromorph; [Ev] Evans (1991) analysis. The plus symbol (+) after a taxon name indicates an unnamed node including the taxon plus all taxa branching off after this node. ~ Taxon excluding dibamids, amphisbaenians, and snakes. ^ Taxon including *Tamaulipasaurus*. * Taxon including *Marmoretta*. Values of Lepidosauromorpha includes *Paliguana*, *Palaeagama*, Younginiforms and Rhynchosaurs (see text). Other abbreviations: Amp, Amphisbaenia; Ang, Anguimorpha; Dib, Dibamidae; Gek, Gekkota; Hom, *Homoeosaurus*; Lep, Lepidosauria; Mar, *Marmoretta*; Pal, *Paliguana*; Sap, sapheosaurs; Sci, Scincomorpha; Ser, Serpentes; Sph, *Sphenodon*; You, *Youngina*.

Clade	This Chapter	[E1]	[E2]	[R1]	[R2]	[R3]	[CH1]	[G]	[CH2]	[Ev]
Iguania	2	3	2	-	3	1	3	-	-	-
Acrodonta	2	1	1	1	2	-	-	-	-	-
Anguimorpha	-	-	7	3	1	2	1	-	-	-
Anguioidea	2	1	1	3	2	2	1	-	-	-
Varanoidea	4	5	10	7	8	8	4	-	-	-
Varanidae	4	6	6	5	3	4	5	-	-	-
Ang-Ser	-	-	-	1	1	-	-	-	-	-
Scincomorpha	3	2	1	2	4	1	2	-	-	-
Scincoidea	3	1	2	2	2	2	1	-	-	-
Tepexisaurus...+	2	-	-	-	-	1	-	-	-	-
Lacertoidea	2	2	2	2	2	1	4	-	-	-
Lacertiformes	3	4	4	3	3	2	4	-	-	-
Teiioidea	3	5	5	4	3	4	5	-	-	-
Autarchoglossa	-	-	-	-	1	-	-	-	-	-
Sci-Gek	1	-	1	-	-	-	-	-	-	-
Sci-Gek-Dib-Amp	-	-	-	1	-	-	-	-	-	-
Gekkota	3	3	9	4	3	3	2	-	-	-
Gek-Dib	-	1	-	-	-	-	-	-	-	-
Gek-Dib-Amp	-	-	-	1	1	-	-	-	-	-
Dib-Amp	2	-	-	1	2	1	-	-	-	-
Scleroglossa	1	12	6~	4	6	7	-	-	-	-
Squamata	1	-	-	-	2	11	-	-	-	-
Huehuecuetzpalli..+	1	-	-	2	7	-	-	-	-	-
Ardeosauridae	1	-	-	-	-	-	-	-	-	-
Ardeosauridae......+	3	-	-	-	-	-	-	-	-	-
Tamaulipasaurus...+	1	-	-	-	-	-	-	-	-	-
Marmoretta..........+	1	-	-	-	-	-	-	-	-	-
Rhynchocephalia	-	-	-	-	-	-	-	-	4	6
Hom-Sap	-	-	-	-	-	-	-	2	2	-
Hom-Sap-Sph	-	-	-	-	-	-	-	12	10	-
Sphenodontia	-	-	-	-	-	-	-	7	6	-
Lepidosauria	2	-	-	-	-	-	-	5	4^	-
Lep-Mar	-	-	-	-	-	-	-	-	-	3
Kuehneosauridae....+	2	-	-	-	-	-	-	3	3^	1*
Lepidosauromorpha	1	-	-	-	-	-	-	-	-	1*
Younginoidea	-	-	-	-	-	-	-	3	4	-
You-Pal	-	-	-	-	-	-	-	-	-	1
Total support (Σ b)	50	46	57	46	56	50	32	36	35	6

TABLE 13. Descriptive indices in previous published lepidosauromorph and squamate phylogenies. Abbreviations as in Table 12. Uninformative characters on this paper are after the removal of *Paliguana* and *Palaeagama* from the analysis. Number of shortest trees in parenthesis is the value excluding different topologies in the outgroup.

	This paper	[E1]	[E2]	[R1]	[R2]	[R3]	[CH1]	[G]	[CH2]	[Ev]
Characters in Data Matrix	225	148	148	148	169	169	187	171	165	35
Uninformative Characters	4	14	26	0	2	3	43	77	82	3
(%)	1.8	9.5	17.6	0.0	1.2	1.8	23.0	45.0	49.7	8.6
No. Informative Characters	221	134	122	148	167	166	144	94	81	32
Number of taxa (ingroup)	30	19	16	20	20	20	20	13	14	5
No. of shortest trees	10	4	1	8(4)	1	5	13	27	54	2
Tree length	1120	712	561	765	819	821	750	134	143	64
Consistency index	0.716	0.756	0.800	0.762	0.791	0.792	0.736	0.821	0.783	0.688
Rescaled consistency index	0.438	0.463	0.553	0.475	0.525	0.523	0.437	0.730	0.673	0.344
Retention index	0.611	0.613	0.691	0.623	0.663	0.660	0.596	0.889	0.860	0.500
Total support index	0.045	0.065	0.102	0.060	0.068	0.061	0.043	0.269	0.245	0.094

Hernández (1994) and those presented for chapters 4 and 5 including independently *Huehuecuetzpalli* and *Tepexisaurus*.

Standard procedures on bootstrap method are 100 bootstrap replicas using heuristic search algorithm with the Random Additional Sequence option (five replicates) and starting seed prompted to 1. The five replicas of the random additional sequence were established after running several preliminary searches and noticing that all shortest trees are obtained at replicate number three at the most.

The branch support values and total branch support indexes were calculated for all clades of different previously trees (Table 12). All data matrices were reanalyzed following as close as possible the procedures specified on their respective texts in an attempt to reproduce the published trees. To standardize the computerization of branch support in all analyses, and make comparisons even easier, in every case multistate characters were treated as polymorphism and strict consensus was always used (e.g. instead of the Adam's consensus used by Gauthier et al. 1988a). In Clark and Hernández's (1994) analysis for the Squamata, data for characters 149-184 of extant lizards and the outgroup were not specified; then, characters were coded according to the data matrix presented in Chapter 4, (Appendix 4.2) and the average outgroup was established by merging states of all outgroup taxa. Branch support values were calculated for each node by searching for all shortest trees that do not have the clade to test, using the Converse Constraint option of PAUP and heuristic search with the Random Additional Sequence option (10 replicates). Branch and bound search was used when possible.

Strict consensus of trees generated for each analysis are presented in Appendix 6.5. Some trees differ from published cladograms. For Gauthier et al. (1988a) Lepidosauriformes is not supported and *Acerodontosaurus* fall outside Younginiformes forming a polytomy with *Youngina* + tangasaurs, *Paliguana*, *Palaeagama*, *Saurosternon* and the clade kuehneosaurids + Lepidosauria. For Estes et al. (1988) the most parsimonious tree (p. 136; fig. 5) was replicated (see also Kluge 1989) but it was impossible to generate the "conservative cladogram" from which they based their classification. The clade Autarchoglossa was never recreated even when including or excluding amphisbaenians, dibamids and snakes. For Evans (1991) the ingroup is not monophyletic since Rhynchosauria falls within the Lepidosauromorpha. Branch support values for each node for the different analyses is presented in Table 12, and tree statistics and total branch support indexes in Table 13. Branch support values for results in this chapter are based on the reduced consensus tree obtained after excluding *Paliguana* and *Palaeagama* (Fig. 42).

Bootstrap analysis shows that the phylogeny of the Lepidosauromorpha presented in this chapter is well supported in its basal clades. Only the very basal node including *Saurosternon* cannot be supported in more of the 50% of the resampled trees. The position of *Marmoretta* and *Tamaulipasaurus* within the Lepidosauria, branching off the lineage leading to squamates does not collapse, strongly supporting the newly proposed clade Squamatoidea.

The situation of more derived taxa contrasts with basal nodes. The clade comprising Ardeosauridae, *Huehuecuetzpalli*, and Squamata, as well as many clades within the squamates collapsed into a single polytomy (see Appendix 6.4). Iguania, Acrodonta, Anguioidea, Scincoidea, Scincoidea + *Tepexisaurus*, Gekkota, Lacertoidea, Lacertiformes, Teiioidea, Varanoidea, and Varanidae are stable clades and their validity cannot be questioned. Strikely, neither Anguimorpha, Scincomorpha or the well supported clade Scleroglossa survived the bootstrap analysis. As expected, problematic taxa amphisbaenians, dibamids and snakes collapsed as well. The clade *Tepexisaurus* + scincoids that collapsed after bootstrap in Chapter 5, here survived in 57 % of the saved trees. *Parviraptor* which its inclusion in Anguimorpha appeared to be well supported (Evans 1994a) did collapse.

It is interesting to notice that all fossil squamatoids included in the analysis collapsed into the polytomy except, *Tamaulipasaurus*, *Marmoretta*, and *Tepexisaurus*. The collapse of all fossil taxa into the polytomy seems to be more an artifact of the resampling technique than to real data. As the Bootstrap method works upon the resampling of characters from the original data matrix, is expected that taxa with several gaps will be more strongly affected if compared against taxa with complete data sets. Every time a derived character known in the fossil forms is excluded from the newly generated data matrix, it will result in the misplacement or collapse of one or several taxa in the resultant tree. This will favored the generation of small changes in tree branching in each search which will result on the complete collapse of the tree when computing the average 50% majority rule consensus. This effect is increased even more when several taxa with missing information are analyzed together, as observed. When bootstrapping the data matrix of Estes et al. (1988) including only extant forms, the clades suffer a lesser degree of collapsing after random resampling. In this case, Scincomorpha and Anguimorpha are present respectively in 51 and 63 % of the trees, and Scleroglossa in 97%. When *Tepexisaurus* is included alone, Scleroglossa is supported in 100% of the trees, Scincomorpha in 56%, but Anguimorpha did not survived.

The collapse of well supported clades within the Squamata when fossil taxa are included in the analysis is difficult to explain. The effect of missing information of fossil taxa exposed above, combined with the uncertain position of problematic taxa within the cladogram are the two major factors affecting the final tree topology. The uncertain position of snakes may pay a major role in the collapse of the Scleroglossa and the Anguimorpha, while the uncertain position of gekkotans and the clade composed by dibamids and amphisbaenians may contribute to the collapse of the Anguimorpha and the Scincomorpha. Different hypotheses of interrelationships indicate that snakes can fell outside Scleroglossa, within Anguimorpha, or even be sister-group of *Parviraptor.* The most parsimonious tree presented by Estes et al. (1988: fig. 5A) suggests that gekkotans are the sister-group of scincomorphs, and that dibamids and amphisbaenians fell within Anguimorpha. In the analysis for *Huehuecuetzpalli* (Chapter 4) amphisbaenians and dibamids are the sister-group of gekkotans and all three taxa are in turn the sister-group of Anguimorpha and snakes. In the analysis of *Tepexisaurus* (Chapter 5), the position of these taxa is totally uncertain and in the strict consensus appear in a polytomy within Scleroglossa. With the incorporation of *Parviraptor* (this chapter) there are five possible hypothesis of sister-group relationships of this taxa completely different to those resultant in the analysis of *Tepexisaurus* (compare Figs. 37 and 44). The simultaneous incorporation of several fossil taxa, permeated with the character resampling of bootstrap analysis, may generate a good number of hypotheses of interrelationship of problematic taxa. The great number of generated hypothesis will reduce the probability of one to be present preferentially in more than 50% of the resultant trees, collapsing the node.

The inclusion of *Huehuecuetzpalli* does not seem to affect the position of gekkotans, dibamids, and amphisbaenian since this genus is branches off in a very basal position. However, the incorporation of fossil taxa branching off within Scleroglossa, particularly *Parviraptor*, seem to create further difficulty in defining the sister-group relationships of these problematic taxa, weakening even further the phylogenetic conclusions. In future research, it is expected that when more fossil taxa are included in the analysis, results would be even more uncertain. Although the position of a fossil taxon in a cladogram is usually based on very few characters, this does not mean that few characters indicate low probability of interrelationship. The quality of the character itself (depending on its consistency index, for example) is very important and could be significant.

The collapse of the Squamata with some squamatoid basal taxa seems to respond to a different cause than taxa within Scleroglossa. Ardeosaurids and *Huehuecuetzpalli* also collapse with other squamates in the polytomy. This may be due because to the several scleroglossan characters that ardeosaurids show in their cranial anatomy and the similar features that *Huehuecuetzpalli* shares with iguanians. This permits the establishment of an alternative phylogenetic hypothesis in which *Huehuecuetzpalli* is placed within or as sister-group of iguanians, and ardeosaurids might be placed within Scleroglossa (as suggested by

Evans 1993, 1995). Although the most parsimonious hypothesis do not support this view because the lack of several apomorphic characters diagnostic for squamates in either ardeosaurids and *Huehuecuetzpalli*, a resampling of characters can lead to the alternative hypothesis that seems to be an easy step with the available evidence. If a consensus tree is computed between the most parsimonious tree (Fig. 42) and trees of the theoretical alternative hypothesis suggested above, the Scleroglossa and the clades basal to squamate will collapse, similarly to what the 50% majority rule consensus tree shows when all fossil taxa are included. The different factors collapsing clades within the Scleroglossa and basal to Squamata in a single polytomy are due to an ascending and descending effect of weakly supported fossil taxa and problematic clades.

Branch support values are consistent with results gained from bootstrap analysis. The best supported clades are Ardeosauridae, Scincomorpha, Gekkota, Lacertiformes, Teiioidea, Varanoidea, and Varanidae. This clades are also the best supported in other hypotheses. However, the number of steps necessary to collapse some of them are considerably lower when fossil taxa are included than when only extant taxa are included.

The significance of branch support values in the phylogenetic hypotheses seem to be dubious. It is clear that branch support values as well as total support indexes will depend on the number of taxa and characters included in the analysis. Table 12 shows how the number of steps necessary to collapse a branch decrease considerably when the number of taxa included is increased. The case of Scleroglossa is extreme. In the Estes et al. (1988) analysis for example, 12 steps are necessary to collapse this clade; seven if only *Tepexisaurus* is included; four characters if only *Huehuecuetzpalli* is included; and one characters if all fossil taxa are included. As mention before, the position of *Huehuecuetzpalli* close to the root of squamates will have a greater ascending effect in character distribution around this area, affected even more by ardeosaurids which branch off at a more basal position.

The total branch support indexes of every published trees is quite low (Table 13). Although it is not possible to estimate within confident limits what is a "good" or a "bad" tree, in relation to previous published trees, the total branch support index of the cladogram here presented is just slightly lower (*ti* = 0.045) than those presented by Estes et al. (1988), and in Chapter 4 and 5, but higher than Clark and Hernández's (1994) results for the Squamata (*ti* = 0.043). Higher indexes are present in trees of Gauthier et al. (1988a) and Clark and Hernández (1994) for lepidosauromorph phylogeny (0.269 and 0.245), however, the inclusion of many different taxa make results difficult to compare.

A final remark is on the number of additional steps necessary to collapse the whole tree. Twelve additional steps are necessary to collapse Estes et al.'s (1988) and Gauthier et al.'s (1988a) strict consensus trees while only four steps are necessary to collapse the tree here presented. The difference between these results is serious, even more when the inputted information is virtually the same and only reorganized. This effect can be due to two factors: a) the use of a large amount of redundant information by Estes et al. (1988) in which two characters (virtually the same) outweigh support for a given node; and b) the increase in the number of branches in the tree here presented because the inclusion of more taxa limits number of character that define each node.

CONCLUSIONS

The most parsimonious hypothesis of the phylogeny of the Lepidosauromorpha indicates that *Paliguana* and *Palaeagama* are not Lepidosauromorphs, *Tamaulipasaurus* and *Marmoretta* are basal lepidosaurs included in the new clade Squamatoidea, *Bavarisaurus* is an ardeosaurid and the whole clade Ardeosauridae does not belong to the Squamata but is a basal squamatoid branching off the cladogram after *Tamaulipasaurus*, *Huehuecuetzpalli* is certainly primitive relative to Squamata; and the position of *Tepexisaurus* and *Parviraptor* as scincomorph and anguimorph lizards respectively is corroborated.

This analysis shows that tree topology and character distribution may differ greatly from expected results when data matrices are merged, dissolving limits imposed by researchers assuming monophyletic entities, and if fossil taxa are included. Most of the characters said to appear at the moment squamates diverged from lepidosaur ancestors appear to be distributed along the branches of a previously unknown lineage of lizard-like forms basal to crown squamates. Of the 36 osteological synapomorphies of the Squamata listed by Estes et al. (1988), fourteen scleral ossicles and the presence of preanal pores are better explained to originate in a more inclusive clade. Other characters listed as diagnostic of the Squamata are better explained as appearing in less inclusive groups: eight cervical vertebrae, pterygoid lappet of quadrate absent, anterior coracoid fenestra , and clavicle articulating suprascapula diagnose Node 5; narrow nasals, transversally oriented frontoparietal suture, deep supratemporal, squamosal articulation of quadrate notched or fenestrated, angular not reaching mandibular condyle, styloid process on radius fitting on groove in radiale, first metacarpal contacting medial centrale and second distal carpal, enlarged thyroid fenestra, most distal end of tibia forms part of astragalocalcanear joint, complex tongue-in-groove astragalocalcanear/fourth distal tarsal joint, squamate hooked fifth metatarsal, loss of gastralia, braincase broadly exposed dorsally, broad interpterygoidal vacuity, coronoid lateral process as lappet of dentary diagnose Node 3; a columelliform epipterygoid with a narrow base, anteroventral border of orbit formed by jugal, and opisthotic fused to exoccipital in embryo diagnose Node 2; and the pterygoids included in the suborbital fenestra and separated from the vomers, coronoid formed mainly by coronoid bone, and sacral and caudal ribs fused in embryo are squamatoid synapomorphies. A notched tibia is synapomorphic for Node 3 and not of the Scleroglossa. The gently convex tibial distal end is not a primitive character for squamates but an autapomorphy of iguanians.

Although the results here presented appear to be weakly supported as demonstrated by the ease of node collapse with bootstrap resampling and the presence of low branch support values, the protocol for its construction is much more rigorous than that followed by Estes et al. (1988), Gauthier et al. (1988a); Evans (1991); and Clark and Hernández (1994). In addition to that, the total support index is just slightly lower than that of Estes et al.'s (1988) analysis, a broadly accepted hypothesis in spite of its numerous flaws (Kluge 1989). Branch collapse seems to be due to a major susceptibility to character resampling of fossil taxa with missing information compared with extant taxa with complete data sets, and a combination of this effect with the uncertain position of problematic taxa, such as snakes, dibamids, and amphisbaenians. Low branch support values, on the other hand, are due to the redistribution of a limited number of characters in several additional branches, reducing the total number of characters supporting each node.

Improvement to previous published analyses includes: the merging of redundant information in multistate characters, the inclusion of all available character states instead of grouping them *a priori* in assumed evolutionary units, the division of characters involving character states describing different anatomical parts, but assumed to be part of the same transformation series, the incorporation of all available evidence including characters considered "bad" according to the point of view of previous researchers; the inclusion of fossil taxa in spite of extensive missing data, and by analyzing information with a rigorous and stable protocol that includes unordered change in transformation series and results described through a strict consensus tree. Results here presented, might be falsified in exactly the same terms as presented.

Current discussion of phylogeny has focused on the search for new methods to estimate confidence in the results of cladograms. The importance of character coding has been omitted from discussion. This issue is particularly important because results are largely based on the way characters are selected and how character states are coded. This is the basic substance in which cladistic systems work. It is important to govern the conditions by which a character is established and the limits that will permit the coding of one character state or the other. Frequently these limits are not clearly discerned, particularly when working with continuous change, and when the selection of one or the other character state is an arbitrary decision. It should be possible to code characters and characters states repeatedly, independent of individual biases. This matter deserves much more attention in subsequent studies of phylogeny.

Appendix to Chapter 6

Appendix 6.1

List of Characters

Characters 1-132 are from Estes et al. (1988); 133 and 134 from Clark and Hernández (1994); 135-216 from Gauthier et al. (1988a); and 217-221 from Evans (1991). All other characters are new or resulted from the division of previous characters. Modifications to characters and character states presented in Chapter 4 (Appendix 4.1) were considered. Full descriptions of most characters are presented in referred papers. [R] refers to Rieppel (1980); [PGG] to Pregill et al. (1986); [E] to Estes et al. (1988); [G] to Gauthier et al. (1988a); [P] to Presch (1988); [Ev'88] to Evans (1988); [FE] to Frost and Etheridge (1989); [Ev] to Evans (1991); [L] to Laurin, (1991); and [C&H] to Clark and Hernández (1994). Other abbreviations: *co* = combined; *div* = divided; *pol.rev* = polarity reversed, *mod* = modified.

1. Premaxillae association: paired (0), fused (1); [E1] [G62]
2. Nasal/maxilla structure: in contact (0), separated by external naris (1); [E2] [R11] [PGG 3,4] [P61]. Comment: External naris is considered retracted only if the nasal and the maxilla lose contact and if the frontal contacts the naris (see character 4). Pregill et al. (1988) divide the state (1) in little contact (Helodermatidae) or no contact. Little contact is considered contact present.
3. Nasals association: paired (0), fused (1); [R10 *pol.rev*] [PGG1] [E3] [P41].
4. Nasal/prefrontal contact: broad contact (0), separated by maxilla/frontal contact (1), separated by external naris (2); [R18 *pol.rev*] [PGG2] [E4 state 2 added] [P56]. Comment: In state (2) Frontal contacts naris.

5. 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*] [PGG10] [E5] [P62].

6. Frontals association: paired (0), fused (1); [R13 *pol.rev*] [E6] [G65] [Ev17] [P42].

7. Shape of the lateral borders of the frontals: parallel (0), constricted between orbits (1); [E7]. Comment: If frontal does not contacts the orbit rim, then the character does not apply.

8. Shape of the anterior margin of the frontal: even at contact with nasal (0), broad shelf extends below nasal (1); [E8]

9. Descending process of frontal /palatine contact: absent (0), frontal reaches palatine (1); [E9]

10. Median contact of frontal descending process: absent (0), descending processes in contact ventrally (1): McDowell and Bogert (1954); [R16] [PGG7] [E10] [P53]. Comment: Pregill et al. (1986) includes in state (1) the extension of the frontal descending processes. Well developed processes are not always in contact.

11.- Shape of the posterior margin of the frontal: ends even at parietal contact (0), frontal tabs project posteriorly onto parietal dorsal surface (1); [E11].

12.- Postfrontal: present or fused (0), absent (1); [E12] [FE9 *mod*]. Comment: Very small postfrontal counts as present.

13.- Postfrontal shape: subtriangular (0), semilunate, forked medially (1); [E13] [P63].

14.- Postfrontal/postorbital structure: sutured (0); fused (1); [R20] [E14]. Comment: Not applicable if postfrontal or postorbital is missing.

15.- Postfrontal size: extensive (0), reduced (1); [E15] [G48]. Comment: Greatly enlarged postfrontal is considered an additional state by Gauthier et al. (1988a) that is only present in some rhynchocephalians. This condition is grouped in state (0). This character could be combined with character 12. It is treated separated because it is difficult to determinate size when the postfrontal is fused with the postorbital.

16.- Postorbital: present (0), absent (1); [PGG12] [E16] [P50]

17.- Postorbital contribution to the posterior margin of the orbit: one half or more of the posterior orbital margin (0), less than one half (1), postorbital excluded from the orbital rim (2); [R21-E17 *co*] [P55].

18.- Jugal/squamosal contact over the lower temporal fenestra: absent (0) both bones in contact (1); [E18 *mod*] [G8] [P67] [FE8]. Comment: The ambiguous condition of jugal "very near" to the squamosal [E18; state 1] is ignored. Structurally both bones are either in contact or separated.

19.- Supratemporal fenestra restriction: supratemporal fenestra open widely (0), restricted or closed by the postorbital (1), restricted or closed by the postfrontal (2). [E 19-20 *co*].

20.- Parietals association: paired (0), fused (1); [E21] [G63] [Ev18 = Ev'88:L1] [P43].

21.- Shape of the anteroventral margin of the parietal: even at contact with frontal (0), tab of parietal projects below the frontal (1); [E22].

22.- Parietal ventral downgrowths: absent (0), present (1); [E23].

23.- Posterior length of the parietal table: extends over the occipital region (0), ends anterior to occipital region (1); [E24] [P76 *pol.rev*] Might be redundant with G46 (here excluded).

24.- Parietal foramen position: within parietal (0), on frontoparietal suture (1), within frontal (2); absent (3); [E 25-26 *co*] [R30 *pol.rev*] [PGG11] [G4] [P64] [FE11] [Ev'88:G2] [L:G3] [Ev31].

25.- Extension of the posterior process of the maxilla; extends well below orbit (0), extends only anteriorly (1); [E27] [FE3 *mod*]. Comment: The state of a process that is extended posterior to the frontoparietal suture (Frost and Etheridge 1989: 3 state 1) is included in state (0).

26.- Lacrimal structure: a separated element (0), fused to the prefrontal (1), absent (2); [E 28-29 *co*] [P44] [FE5].

27.- Number of lacrimal foramina: one (0), two (1); [R25 *pol.rev*] [PGG22] [E30] [P45].

28.- Anterior extent of the jugal: ends anterior to orbit (0), extends below the anteroventral border of the orbit (1). [E31] [P83 *pol.rev*].

29.- Dorsal extension of the jugal: contacts the postorbital or postfrontal (0), short, postorbital bar incomplete (1); [R26 *pol.rev*] [E32] [P84].

30.- Squamosal: present (0), absent (1); [E33] [P46]

31.- Shape of the dorsal margin of the squamosal: dorsal process present (0) gently curved, jockey stick shape (1); Robinson (1967), [E34] [P47 *pol.rev*].

32.- Supratemporal: present (0), absent (1); [E35] [G13]. Comment: the apparent absence of the supratemporal in some taxa (e.g. in the Rhynchocephalia; Rieppel 1992a) might be due to its fusion to another element.

33.- Palpebral ossifications: absent (0); present (1); Underwood (1970), [PGG78 *pol.rev*] [E36] [P48].

34.- Quadrate/pterygoid structure: sutured (0), fixed by connective tissue (1), secondary lappet of quadrate present (2); [E37-G20 *co*].

35.- Vomers association: separated (0), fused (1); [E38]

36.- Posterior extension of the vomer: short (0), extended posterior to one half of the maxillary tooth row (1); [PGG31] [E39]. Comment: Pregill et al. (1986: 31) compare the extension of the vomer with the palatine instead of the maxilla. The character is not comparable with Estes et al. (1988: 39) but is still the same.

37.- Median contact of the septomaxilla: separated by a cartilaginous gap (0), meet on midline along a raised crest (1); [E40].

38.- Dorsal shape of the septomaxilla: flat or concave (0), expanded and convex (1); [E41]

39.- Posteroventral opening of Jacobson's organ: not closed by bone (0), closed by median contact of maxilla and vomer (1); [R42 *pol.rev*] [E42].

40.- Medial extension of the palatine: absent (0), forms a bony secondary palate (1); [E43]

41.- Size of the palatine choana fossa: no fossa (0), small (1); enlarged (2); [R44 *pol.rev*] [E44-G60 *co*].

42.- Ectopterygoid/palatine anterolateral contact: no contact, maxilla included in the suborbital fenestra (0), both bones in contact excluding maxilla from the suborbital fenestra (1); [R9 *pol.rev*] [PGG36] [E45] [P81].

43.- Ectopterygoid size: slender (0), enlarged, restricting suborbital fenestra (1); [E46].

44.- Epipterygoid: present (0), absent (1); [E47].

45.- Interpterygoidal vacuity width: narrow (0), broad (1); [E48].

46.- Shape of the alar process of prootic: short directed dorsally (0), large, narrow, directed anterodorsally (1); Gauthier (1982); [E49] [P73]

47.- Length of the supratrigeminal process of prootic: feebly developed or absent (0); long finger-like projection (1); [R60] [E50]

48.- Opisthotic/exoccipital structure: fused late in adult (0), fused in embryo (1); [E51] [G64]

49.- Lateral head vein/crista prootica structure: free lateral head vein (0), enclosed in a bony canal of the crista prootica (1); [E52]

50.- Position of the posterior opening of the vidian canal: within the basisphenoid (0), at the basisphenoid-prootic suture (1), within the prootic (2); [E53]

51.- Lateral extensions of the parietal roof: large lateral flange for the ventral attachment of the adductor musculature present (0), parietal roof not extended laterally (1); [PGG14] [E54 *pol.rev*] [L:D1].

52.- Enclosure of the Meckelian groove: open groove (0), closed, but suture remains (1), groove closed and fused (2); Gauthier (1982); [E55] [G68] [Ev20] [P86] [FE20].

53.- Position of the intramandibular septum of the Meckelian groove: anterior in the dentary. (0); near to the posterior end of the dentary tooth row (1); Gauthier (1982); [E56 *div*]. Comment: Estes et al. (1988: 56) found that the size of the posterior process is correlated with its position and was included in the same character. In *Parviraptor* however, a feebly developed septum is placed posterior in the dentary.

54.- Position of the Meckelian groove: open medially (0); open ventrally (1); [E57].

55.- Subdental shelf size: small (0), shelf absent (1), large (2); [E 58-59 *co*].

56.- Shape of the anterior end of the surangular disarticulated: tapers anteriorly (0); forms a broad almost vertical edge (1); [PGG39] [E61 *div*]. Comment: Estes et al.'s (1988: 61, state 2) includes the extent of the anterior end of the surangular. This state is part of another character and is, therefore ignored (see character 175).

57.- Anteromedial extension of the prearticular disarticulated: near to the anterior end of the surangular (0); shorter, remains near to the coronoid bone (1); [E62].

58.- Posterolateral shape of the dentary: straight (0), surangular and coronoid notches present (1), notches reduced (2); [E63]

59.- Structure of the dentary/postdentary articulation: extensive tongue and groove articulation (0); overlap reduced (1); McDowell and Bogert (1954); [PGG37] [E64] [P36].

60.- Anterior extension of the splenial: anterior to midpoint of the dentary tooth row (0), shorter (1); [E65 *div*] [FE21] [Ev19 *div*]. Comment: Estes et al. (1988) included the additional state "splenial absent". Since the size of the splenial is affected by its anterior and posterior extension, it cannot be combined into a single transformation series where the absence of the splenial can be combined. If the absence of the splenial is included in this and next characters, it will become redundant, therefore it was preferred to keep the state separated in a different transformation series (see character 176).

61.- Posterior extension of the splenial: extends to or beyond the level of the apex of the coronoid (0), extends close to the level of the apex of the coronoid (1), very small overlap with postdentary bones (2); [R62 *pol.rev*] [PGG42] [E66] [FE22 *mod*]. Comment: Frost and Etheridge (1989: 22) compared the position of the posterior end of the splenial relatively to the adductor fossa, dividing state (0) further.

62.- Structure of the splenial/dentary articulation: extensive bone to bone contact (0), reduced contact separated by connective tissue (1); [PGG43] [E67].

63.- Shape of the anterior margin of the coronoid: curves smoothly into dentary (0), long low horizontal anterodorsal extension (1); [E69].

64.- Structure of the coronoid/dentary articulation: dentary overlaps most of the lateral surface of the coronoid (0), coronoid clasps dentary (1), coronoid overlapped anteriorly by a small posterodorsal process of the dentary (2), coronoid and dentary meet with no overlap (3); [E 60, 68, 70, 71 *div*-FE16 *co, pol.mod*] [P70] [PGG45 *div*]. 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 E71 is divided (see character 222).

65.- Angular: present or fused (0), absent (1); [E72] [P77]

66.- Lateral surface on the prearticular region: smooth (0), prearticular crest present (1), prominent crest with embedded angular process (2); [E73].

67.- Shape of the dorsal surface of the retroarticular process: with sulcus or pit (0), flat surface; [E74].

68.- Orientation of the retroarticular process: aligned to the dentary (0), inflected medially (1); [E75]

69.- Shape of the medial margin of the retroarticular process: smooth (0), with a posteromedial flange or tuber (1); [E76].

70.- Retroarticular process offset: absent (0), present (1); [E77]

71.- Posterior breath of the retroarticular process: tapers distally or sides parallel (0), broad posteriorly (1); [E78].

72.- Retroarticular process torsion: not twisted posteriorly (0), posterior border obliquely twisted (1); [R70] [E79]. Comment: The condition strongly twisted (Rieppel 1980: 70, state 0) is included in state 1.

73.- Finger-like angular process: absent (0), present (1); [E80]

74.- Size of the adductor fossa: small to moderate (0), widely expanded and inflated (1); [E81].

75.- Palatine teeth: present (0), only enlarged lateral row present (1), absent (2); [R51 *pol.rev*] [PGG34] [E82-G23,25 *co*] [P39] [FE27]

76.- Pterygoid teeth: present (0), only on the median surface of the pterygoid (1), absent (2); [R52 *pol.rev*] [PGG35] [E83-G24 *co*] [P38] [FE28] [L:E5] [Ev13; Ev'88:J5].

77.- Tooth implantation: subpleurodont or subthecodont (0), pleurodont (1), acrodont (2); Edmund (1960); [E84-G75 *co*] [P14] [FE26 *div*] [Ev16; Ev'88: J13)]. Comment: Frost and Etheridge (1989) combined tooth replacement with this character. The character is independent and should be treated separately.

78.- Marginal tooth replacement: tooth developed lingually with large resorption pits (0), developed posterolingually with small pits (1), developed posterolingually with no pits (2), no replacement present (3). Edmund (1960); [PGG26] [E85-FE26 *div, co*] [P15].

79.- Marginal tooth microstructure: absent (0), striations present at the base of the tooth (1). [PGG24] [E86].

80.- Maxillary teeth alignment: all teeth placed at the same level (0); posterior maxillary tooth offset due to the enlargement of the anterior teeth (1). [E87]

81.- Number of scleral ossicles: more than 14 (0), 14 (1), less than 14 (2); [PGG79 *mod*] [E 88-89 *co*].

82.- Second epibranchials: present (0), absent (1); Camp (1923); [PGG77] [E90] [P37] [G135].

83.- Second ceratobranchials: present (0), absent (1); Camp (1923); [E91] [P13] [G135].

84.- Orientation of the intervertebral articulation: meet vertical or almost vertical (0), meet strongly oblique (1); [E92].

85.- Shape of the centrum articulation: amphicoelous (0), procoelous (1); [E93] [G84].

86.- Shape of the centrum body: cylindrical (0), constricted anterior to condyles (1). [E94]

87.- Size of the zygosphene and zygantrum accessory articulations: articulations absent (0), weakly developed (1), strong (0); Hoffstetter and Gasc (1969); [E 95-96 *co, pol.rev*] [G78] [P33]

88.- Attachment of the cervical intercentrum: intervertebral (0), sutured or fused to preceding centra (1), sutured or fused to next centra (2); [R72] [E 97-98 *co, mod*]. Comment: Estes et al. (1988: 97, 98) separated the conditions "sutured" and "fused" in different character states. These conditions are considered together because both belong to the same transformation series.

89.- Thoracolumbar intercentra: present (0), absent (1); Hoffstetter and Gasc (1969); [E99] [G83] [P34 *pol.rev*].

90.- Structure of the transverse processes on caudal vertebrae: one pair of transverse processes (0), two pair diverging (1), two pair converging (2), anterior part of transverse process absent (3); [E 100-101 *co*].

91.- Position of the autotomy septa in caudal vertebrae: splits transverse process (0), posterior to transverse process (1), anterior to transverse process (2); Hoffstetter and Gasc (1969); [E102-P31 *pol.rev, co*]. Comment: State (0) of Estes et al. (1988: 102) is divided further into two states. In Chapters 4 and 5, this character was combined with character 92; however, the position of the autotomy septum in fossil forms is obscure even when the septum is certainly present. In *Parviraptor* the septum is present, but the position cannot be determined because the transverse processes are not known.

92.- Autotomy septa in caudal vertebrae: absent (0), present (1); Etheridge (1967); [PGG52 *pol.rev*] [E103 *pol.rev*] [G80] [P30 *pol.rev*] [FE41 *pol.rev*]

93.- Number of presacral vertebrae: 24-25 (0), 23 or fewer (1); 26 or more (2); [PGG51] [E 104-105-106 *co*].

94.- Number of cervical vertebrae: seven or less (0), eight (1), nine or more (2); McDowell and Bogert (1954); [PGG49] [E 107-108 *co*] [G171] [P32].

95.- Number of sternal ribs: five (0) four (1), three (2), two or fewer (3); [PGG61] [E109] [FE39]

96.- Number of postxiphisternal inscriptional ribs connected midventrally: none (0), at least one (2); [E110] [FE40]. Comment: Frost and Etheridge (1989) also consider the state "free ribs not attached either ventrally or dorsally" this is present only in some iguanids.

97.- Shape of the dorsal margin of the scapula: straight or smoothly curved (0), fenestrated (1); Lécuru (1968); [E111] [P58] [FE35 *pol.rev*]. Comment: Chameleons have an enlarged notch on the scapula that might not be homologous to the fenestration of other squamates (Frost and Etheridge 1989).

98.- Shape of the anteroventral margin of the coracoid: smoothly curved (0), anterior coracoid fenestra present (1); anterior and posterior fenestrae present (2); Lécuru (1968); [PGG56, 57, *pol.rev*] [E 112-113 *co*] [P 59, 60] [FE36 *pol.rev*]. Comment: Frost and Etheridge (1989) consider the "presence of a weak posterior fenestra" an additional state here included in state (2).

99.- Extension of the epicoracoid cartilage: reaches mesoscapula and suprascapula (0), fails to contact either (1); [PGG55] [E114].

100.- Clavicles: present (0), absent (1); [E 115]. Comment: The clavicle is present in all limbed squamates with the exception of chamaeleontids. In dibamids and snakes the character is not applicable since the lack of the clavicle obey to the loss of the shoulder girdle.

101.- Clavicle shape: simple rod contouring scapulocoracoid (0); strongly angulated and curve anteriorly away from scapulocoracoid (1); [E116].

102.- Clavicle dorsal articulation: with scapula (0), with suprascapula (1); [E117] [G95]

103.- Interclavicles: present (0), absent (1); [E118]. Comments: The character is coded (N) in dibamids and snakes since the absence of the interclavicle is due to the loss of the shoulder girdle. This condition is not the same as for chamaeleontids and *Bipes* among amphisbaenians in which the interclavicle is absent and the shoulder girdle is present.

104.- Interclavicle shape: T or anchor-shape (0), cruciform with anterior process well developed (1); lateral processes absent (2); two anterior processes (3); Camp (1923); Lécuru (1968); [E 119-120 *co*] [P 65-66 *co*] [PGG59 *pol.rev*].

105.- Sternal plate perforation: solid plate (0), sternal fontanelle present (1); Lécuru (1968); [E121] [P79] [FE37 *div*].

106.- Ectepicondyle groove enclosure: groove present throughout ontogeny (0), groove close to form a foramen (1); foramen or groove absent (2); [E122-G114 *co*] [L:J7 *pol.rev*]. Comment: As it is difficult to establish if a groove will become a foramen in most fossil taxa, the character is coded as far as our knowledge permits.

107.- 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); [E123-G133 *co*].

108.- Length of the symphysial process of the pubis: short (0); longer (1); very long (2): [E124]

109.- Postcloacal bones: absent (0), present (1); [E125] [P78].

110.- Ventral osteoderms: absent (0), present (1); [E126].

111.- Dorsal osteoderms: absent (0), present (1); [E127] [G140].

112.- Cephalic osteoderms: absent (0), present (1); [E128].

113.- Texture of the skull roof: smooth (0), with rugosities reflecting overlaying scale pattern (1), vermiculated rugosities (2); [E129] [FE7 *mod*]. Comment: Frost and Etheridge (1989) combine the lack of rugosities and their presence on the frontal in the same state. The presence of rugosities on the frontals should be considered as rugosities present.

114.- Epiphyses/diaphyses structure: separated (0) fused (1); [E130].

115.- Ventral extension of the m. adductor mandibulae posterior: does not reach the Meckelian groove (0); extends far into the Meckelian groove (1): Rieppel (1980); [E131] [P80].

116.- Origin of the m. pseudotemporalis superficialis: only extends anteriorly along the mesial margin of the temporal fossa (0), extends posteriorly (1); Rieppel (1980); [E132] [P82].

117.- Anterior head of m. pseudotemporalis profundus: absent (0), present (1); Rieppel (1980); [E133] [P27 *pol.rev*].

118.- M. rectus abdominis lateralis: absent (0), present (1); Camp (1923); [E134] [P88].

119.- M. extracolumellaris: absent (0), present (1); Wever (1978); [E135] [P5].

120.- Foretongue retractility: no retractility (0), foretongue retracts into the posterior part of the tongue (1); McDowell and Bogert (1954); [E136] [P11].

121.- Proportion of tongue notched expressed as percentage of the length of the tongue: notch absent (0), notch less than 10% (1); between 10 and 20% (2), between 20 and 40% (3), between 40 and 50% (4), more than 50% (5); [PGG71,72] [E137] [G162].

122.- Shape of the cross-section of the anterior part of the tongue: rounded (0), much wider than tall (1), mushroom-shaped (2). Camp (1923); [E138 *div*] [P12]. Comment: Estes et al.'s (1988) treated character "tongue texture" (Camp 1923) within this character. Both characters are not the same and should not be combined.

123.- Tongue plication: entire tongue scaly or papillose (0), posterior tongue plicate (1), entire tongue plicate (2); [E139].

124.- Ciliary restraint system for hair cells: tectorial system (0), combined tectorial and sallet system (1), sallet system only (2); Wever (1978); [E140] [P1].

125.- Quadrate process of stapes: present (0), absent (1); [E141].

126.- Position of the ulna nerve in the forelimb: superficial (0), deep (1); [E142] [PGG76] [FE58].

127.- Innervation of the dorsal muscles of the lower leg: peroneal nerve (0), interosseous nerve (1); [E143].

128.- Femoral or preanal organs: absent (0), present (1); McDowell and Bogert (1954); [E144] [G170] [P35 *pol.rev*] [FE48 *pol.rev*].

129.- Course of the stapedial artery: stapes perforated (0), anterior to stapes (1), posterior to stapes (2); [E145 *pol.mod*] [G35 *div*] [L:E 9] [Ev28; Ev'88:J11].

130.- Shape of the middorsal scale row: similar to other body scales (0), modified (1); [E146] [G168 *pol.rev*] [FE46].

131.- Size of the cephalic scales: relatively small (0) enlarged (1); [E147].

132.- Shape of the body scales: non overlapping granular scales (0); deeply overlapping cycloid scales (1); [E148].

133.- Size of the premaxillary teeth: same size as posterior maxillary teeth (0), enlarged (1), abruptly small (2); [PGG23-C&H 186 *co*].

134.- Structure of the anterior end of the braincase: closed only by cartilage (0) closed by bone (1); [C&H 187].

135.- Lacrimal size: large (0); small restricted to orbital rim (1); [G1 *div*] [Ev14; Ev'88: J12]. Comments: State (2), "lacrimal absent" of Gauthier et al. (1988a: character 1) was deleted because it is already expressed in character 27.

136.- Width of nasals: greater than width external naris (0), narrower (1); [G2] [Ev25].

137.- Frontoparietal suture shape: w-shaped and as broad as the nasofrontal suture (0), straight and broader than nasofrontal suture (1), U shaped (2), interdigitated (3); [G3-C&H 185 *co*].

138.- Postparietals: present (0), absent (1); [G5] [L:G5, J2] [Ev8; Ev'88:J4].

139.- Tabulars: present (0), absent (1); [G6] [L:E3] [Ev7; Ev'88:J3].

140.- Quadratojugal anteroventral shape: rounded and not projecting anteriorly (0), with enlarged anterior process (1); [G9] [Ev9; Ev'88:J2].

141.- Extension of the jugal posterior process: reaches the suspensorium (0); midway below the lower temporal fenestra (1); small triangular process (2); process absent (3); [R27-G10,11 *co*] [Ev32, *pol.rev*; Ev'88:G3, *pol.rev*]. Comment: The extension of the jugal before and after the lower temporal fenestra midpoint (Evans 1991: 32) is ambiguous and difficult to estimate since it depends on the shape and length of the lower temporal fenestra.

142.- Quadratojugal: separate element (0), never present separately or absent (1); [G12] [Ev27].

143.- Supratemporal position: superficial on supratemporal process of the parietal (0), deep but mostly on the lateral surface of the supratemporal process (1), deep but mostly on the medial surface of the supratemporal process (2); [G14-FE12 *co*]. Comment: In chameleons, the supratemporal is on the posteromedial surface of the squamosal and not on the supratemporal process. This condition is not applicable.

144.- Size of the anteroventral process of the squamosal: broads covering most of the quadrate laterally (0), tapers distally bordering the anterior margin of the quadrate (1), process absent (2); [G 15,40-L:D2 *co*] [L:B5 *div*, L:E4 *div*].

145.- Structure of the squamosal/quadrate articulation: squamosal hollowed ventrally to cap the quadrate (0), squamosal with a ventral peg that fits in a notch or socket on the quadrate (1); [G16].

146.- Ventral extension of the quadrate: does not reach occipital condyle (0), extends well beyond occipital condyle (1); [G17] [Ev17]. Comment: This character was ignored by Clark and Hernández (1994), but is considered to be phylogenetically informative.

147.- Width of the quadrate in posterior view: narrow (0), expanded laterally forming a conch that supports the tympanum (1); [G19] [L:J3] [Ev2 *div*] Comment: Evans (1991) added the state "conch formed by a combination of quadrate and quadratojugal" as part of this transformation series. However, this state, is not concerned with the homologous anatomical part described in the character (i.e. the quadrate), but with the conch itself and cannot be considered here (see character 225).

148.- Quadrate foramen: present (0), absent (1); [G21].

149.- Vomerian teeth: present (0), absent (1); [G22].

150.- Pterygoid/vomer association: in contact medially (0), separated (1); [G26] [P85].

151.- Length of the pterygoid process of quadrate: extended to the spheno-occipital tuber (0), does not reach it (1); [G27].

152.- Shape of the ventral end of the epipterygoid: expanded ventrally (0), collumeliform (1); [G28 *div*]. Gauthier et al. (1988a) consider the presence of a broad epipterygoid to be correlated with the contact of the epipterygoid to the quadrate. In *Marmoretta*, and some squamates, the epipterygoid is wide, but does not contact the quadrate. The character is divided.

153.- Structure of the abducens canals: canals absent or incomplete (0), complete (1); [G29] [Ev26; Ev'88:J14].

154.- Vidian canal enclosure: open groove (0), fully enclosed by bone (1); [G30].

155.- Structure of the metotic fissure: continuous (0), subdivided (1); [G32].

156.- Lateral extension of the paraoccipital process: ends freely (0), contacts suspensorium (1); [G33] [L:A4] [Ev10; Ev'88:J6].

157.- Width of the distal end of the paraoccipital process: as wide as the proximal end (0), expanded (1); [G34] [L:E6].

158.-Stapes width: thick (0), thinner (1), pin-like (2); [G35 *div*] [L:E8]. Comment: Gauthier et al. (1988a: 35) combined this character with "presence of stapedial foramen", a character that is clearly uncorrelated. Laurin (1991) is correct to consider separately these characters. Perforation of the stapes is already considered in character 129.

159.- Quadrate shape in lateral view: straight (0), bowed (1); [G36] [L:E7] [Ev3].

160.- Extension of the septomaxilla: limited to the posteroventral edge of the external nares (0), roofs Jacobson's organ dorsally (1); [G37].

161.- Extension of the posteroventral process of the septomaxilla: process absent (0), process extends to form posterior margin of the duct of Jacobson's organ; [G38].

162.-Palatine-ectopterygoid posteromedial contact: both bones in contact excluding pterygoid from suborbital fenestra (0), separated (1); [G39].

163.- Association of the parietal and postorbital on dorsal surface of the skull: in contact excluding postfrontal from the margin of the upper temporal fenestra (0), separated (1); [G41-Ev1 *co*] [P57] [Ev'88:M1] [L:B3]. Comment: The inclusion of the prefrontal in the upper temporal fenestra does not assure lack of contact between the parietal and the postorbital. Both bones might still be in contact on the ventrally. Informative character that was ignored by Clark and Hernández (1994).

164.- Length of the posterior process of the postorbital: does reach end of upper temporal fenestra (0), goes beyond end of upper temporal fenestra (1), process absent (2); Cope (1900); [R35] [G42] [L:I1] [P22].

165.- Size and shape of the upper temporal fenestra: broad and oval (0), narrow elongated constricted posteriorly (1), very small or close (2); [G 43-53 *co*].

166.- Preorbital/postorbital skull proportion: preorbital region shorter (0), preorbital region equal or longer than postorbital region (1); [G44].

167.- Width of the upper temporal arch: slender (0), broad (1); [G45].

168.- Width of parietal table in adults: broad (0), narrow (1); [G47].

169.- Extension of the palatine over the suborbital fenestra: no extension, palatine narrow (0); palatine laterally enlarged restricting suborbital fenestra (1); [G49].

170.- Caniniform tooth: present (0), absent (1); [G51 *pol.rev*] [L:B1].

171.- Marginal tooth row distribution: no gap between maxillary and premaxillary tooth row (0); edentulous region between these tooth series (1); [G52]

172.- Posterior contact of the posterior process of the jugal below the lower temporal fenestra: only contacts the quadratojugal (0), also or only the quadrate (1), ends free (2); [G58 *mod*]. Comment: The lack of a posterior process of the jugal does not account for a free ending posterior process. If the squamosal, the jugal or its posterior process are absent, then the character is not applicable.

173.- Orientation of the prefrontal/nasal suture: parasagital (0), divergent anterolaterally (1); [G59] [L:E1] [Ev6].

174.- Snout proportions: snout short and broad (0), large and narrow (1); [PGG21 *pol.rev*] [G61].

175.- Posterior extension of the dentary: no further than the coronoid process (0), extends beyond the coronoid process (1), ends anterior to process (2); [R61-G66 *co*] [FE17] [= R65]. Comment: The anterior extension of the surangular (Rieppel 1980: 65) is correlated to the posterior extension of the dentary.

176.- Splenial: present (0), absent (1); [G67] [Ev19 *div*] [P54].

177.- Structure of the coronoid process: coronoid bone supported laterally by the surangular (0), coronoid eminence formed primarily by the coronoid bone (1); [G69] [Ev21].

178.- Posterior extension of the angular: beyond articular condyle (0), does not reach the articular condyle (1).

179.- Size of the retroarticular process: small (0), large (1), absent (2); [G 72-73 *co*] [L:E10, LB6 *pol.rev*] [Ev4].

180.- Contribution of the surangular to the articular condyle: one third to one half of the articular surface (0), only on the outer rim (1); [G74] [Ev12].

181.- Neural arch/centra association: fused in post-embryo (0); fused in embryo (1); [G77].

182.- Ventral shape of the cervical vertebrae intercentra: flat (0), with hypapophyses (1); [G79].

183.- Shape of the caudal vertebrae centra: round or oval (0), compressed laterally (1); [G82].

184.- Number of heads on the cervical ribs: two heads in one or more cervical ribs (0), all single headed (1), all dicephalous (2); [G86-L:F4 *co*].

185.- Sacral and caudal rib relation to respective vertebrae centra: fused in post-embryo (0), fused in embryo (1); [G87].

186.- Shape of the second sacral rib: single lateral projection (0), well developed posterior process present (1); [G88].

187.- Xiphisternum size: large (0), small (1), absent (2); [PGG60 *mod*] [G90].

188.- Sternal plate structure: two paired plates separated in post-embryo (0), plates fused in embryo (1); [G91]. Comment: Informative character ignored by Clark and Hernández (1994).

189.- Structure of the scapulocoracoid anterior contact; both anterior margins in contact (0), anterior margins separated by a scapulocoracoid fenestra (1); [G92].

190.- Interclavicle size: robust (0), gracile (1); [G93] [L:J6].

191.- Humerus shaft thickness; robust (0), gracile (1); [G97].

192.- Humerus entepicondyle foramen: present (0), absent (1); [G98] [L:F6].

193.- Shape of the radial distal epiphysis: with prominent posteromedial process (0), epiphysis ends evenly (1); [G99].

194.- Shape of the ulna distal end: gently convex (0), nearly hemispherical (1); [G100].

195.- Intermedium size: enlarged reaching the ulna (0), small restricted to the carpal region (1), absent (0); [G101].

196.- Relation of the lateral centrale with the second distal carpal: separated (0), in contact (1); [G102].

197.- Relation of the first distal carpal with the metacarpal I: separated (0), fused (1); [G103].

198.- Width of metacarpal elements: metacarpals II, III, and IV, wider than I and V (0), metacarpals I and V wider (1); [G104].

199.- Length of metacarpal IV: longer than metacarpal III; both subequal (1), metacarpal III longer (2); [G105].

200.- Size of the olecranon and sigmoid notch: well developed in adults (0); poorly developed in adults (1); [G107-L:C2 *co*]. Comment: Informative character ignored by Clark and Hernández (1994).

201.- Contribution of ilium to the acetabulum: 80-85% of the acetabulum (0), 60-65% of the acetabulum (1); [G116].

202.- Shape of the dorsal margin of the ilium: straight (0), ilium pubic flange present (1); [G117].

203.- Ilium orientation: almost horizontal (0), more steeply inclined (1); [G120].

204.- Structure of the ischiopubic contact: both bones fused in continuous plate (0), margins separated by a small thyroid fenestra (1), broad fenestration between bones narrowing the pubic symphysis (2); [G121] [L:J8].

205.- Pelvic bones association: separated in adults (0), fused (1); [G123].

206.- Shape of the femur/fibula articulation: fibula sits at anterior end of femur (0), fibula sits on femoral lateral recess (1); [G124].

207.- Fibular/astragalocalcaneal articulation structure: astragalocalcaneum sits on a small portion of the distal end of the fibula (0), entire fibular distal end articulates with astragalocalcaneum (1); [G125].

208.- Astragalus/calcaneum association: sutured (0) fused before the fusion of the scapula and coracoid (1); [G126].

209.- Lateral centrale on pes: present as a distinct element (0), fused to astragalus in embryo (1); [G127].

210.- First distal tarsal: present (0), absent (1); [G128].

211.- Second distal tarsal: present (0), absent (1); [G129]

212.- Fifth distal tarsal: present as a separated element (0), absent or fused in embryo (1); [G130] [L:E13].

213.- Shape of the metatarsal V: straight (0), simple hook (1), hooked but with medial and plantar tuber present (2), hooked but proximal head of the plantar tuber modified (3); Robinson (1976); [G132] [L:E14].

214.- Shape of the fourth distal tarsal/astragalocalcaneal articulation: both bones meet evenly (0), process of the fourth distal tarsal projects under the astragalocalcaneum (1), complex tongue and groove articulation (2); [G134] [L:J9].

215.- Gastralia: present (0), absent (1); [G136].

216.- Shape of the maxillary dorsal process: weak, only a smooth curve (0), strongly pronounced (1); [Ev22].

217.- Size of the quadrate head: small (0), enlarged (1); [Ev24].

218.- Structure of the premaxilla/maxilla contact: maxilla extends below external nares to contact premaxilla (0), the posterior end of the premaxilla projects dorsally excluding the maxilla from margin of external nares (1); [Ev'88:G1] [L:F1] [Ev30].

219.- Ratio of length nasal/frontal: nasal shorter than frontals (0), longer (1); [Ev33; Ev'88:H4].

220.- Posterior length of the dentary tooth row: reaches posterior end of maxillary tooth row (0), shorter (1); [Ev35; Ev'88:H5].

221.- Size of the intramandibular septum in the Meckelian groove: poorly developed septum (0), septum enlarged (1); New, from [E56].

222.- Structure of the coronoid/surangular articulation: surangular restricted to the lateroventral margin of the coronoid process (0), surangular overlapping the coronoid process posteriorly (1); New, from [E71].

223.- Tongue texture: with papillae and glandular (0), posterior part keratinized (1), all tongue keratinized (2); New, from Camp (1923); [= E138], [= P12]).

224.- Ventral end of the epipterygoid/quadrate relation: in contact (0), separated (1); New, from [G28].

225.- Structure of the posterior margin of the quadratojugal: sutures wide the quadrate (0) modified to support tympanum: (1). New from [Ev2]

Appendix 6.2

Excluded Characters

Characters 7, 18, 31, 46, 50, 54, 55, 56, 57, 71, 81, 85, 89, 94, 96, 106, 108, 109, 110, 111, 112, 113, 118, 119, 122, 131, 137, and 138 of Gauthier et al. (1988a) are uninformative and were excluded. Abbreviations: G followed by a number stands for Gauthier et al. (1988a) and the character number; ch. = character; ≈ = similar.

G7. Postfrontal overlain by post orbital is present only in the Rhynchocephalia. Taxa lacking either the postfrontal or the postorbital were recoded as not applicable. Not known in *Bavarisaurus*, *Parviraptor*, *Paliguana*, *Saurosternon* and *Prolacerta*. Not applicable in *Tamaulipasaurus*.

G18 = Evans (1991: ch. 29) ≈ Laurin (1991: ch F2). Nares are associated only in Kuehneosauridae. Evans (1991: ch. 29) coded nares separated (state 0) for *Paliguana*, but the condition is unknown (Carroll 1975). In Laurin (1991), character F2 "narial confluence" is mixed with "premaxillary narial process width" and should be considered as two characters. Not known in *Paliguana*, *Palaeagama*, and *Saurosternon*.

G31 = Evans (1991: ch. 15). Parasphenoid teeth are present only in Kuehneosauridae. Not known in *Bavarisaurus*, *Eichstaettisaurus*, *Ardeosaurus*, *Parviraptor*, *Paliguana*, *Palaeagama*, and *Saurosternon*.

G46. Might be redundant with Evans (1991: ch. 24). A short lateral process of the parietal that contacts a large dorsal process of the squamosal is present only in rhynchocephalians that lack a separated supratemporal. Squamates without a dorsal process of the squamosal were coded as not applicable. Not known in *Palaeagama*, *Paliguana*, and *Saurosternon*.

G50 ≈ Laurin (1991: ch. F2), see comment on G18. A broad nasal process of the premaxilla is present only in rhynchocephalians. Not known for *Parviraptor*, *Paliguana*, *Palaeagama*, and *Saurosternon*.

G54. Large quadrate foramen is present only in *Sphenodon*. If the foramen is absent is coded as not applicable. Not known in *Bavarisaurus*, *Ardeosaurus*, *Parviraptor*, *Paliguana*, *Palaeagama*, and *Saurosternon*.

G55. A premaxilla forming a chisel-like structure is present only in the Sphenodontia. Not known in *Parviraptor*, *Paliguana*, *Palaeagama*, and *Saurosternon*.

G56. Flanges on teeth are present only in Sphenodontidae. Not known in *Parviraptor* and *Saurosternon*.

G57. Enlarged posterior maxillary teeth are present only in sphenodontian. Character not known in *Paliguana*, *Palaeagama*, and *Saurosternon*.

G71 = Laurin (1991: ch. J4) and Evans (1991: ch. 11). A small exposure of the angular on the lateral surface of the lower jaw is present in all saurian. Character not known in *Eichstaettisaurus*, *Ardeosaurus*, *Parviraptor*, *Paliguana*, *Palaeagama*, *Saurosternon*, and *Tamaulipasaurus*.

G76. The presence of long or equally wide and long articular condyle on the lower jaw with an anteroposterior ridge is present only on rhynchocephalians. The character is unknown in all fossil forms except *Tamaulipasaurus* and *Prolacerta* which has the primitive condition.

G81. Accessory articulations between trunk vertebrae neural spines are present only in Younginiformes. Not known in *Paliguana* and *Tamaulipasaurus*.

G85 modified to Laurin (1991: ch. F5) by adding the state "moderately enlarged trunk vertebrae transverse process". Long transverse processes of the trunk vertebrae are present only in Kuehneosauridae. Moderately developed processes are present in *Prolacerta*. Not known in *Paliguana* and *Tamaulipasaurus*.

G89. Distal aliform outgrowths on ribs are present only in few sphenodontids. Not known in *Bavarisaurus*, *Parviraptor*, Kuehneosauridae, *Paliguana*, *Palaeagama*, *Saurosternon*, *Tamaulipasaurus*, and *Prolacerta*.

G94 = Laurin (1991: ch. E11). The cleithrum is absent in all saurians. Not known in *Parviraptor*, Kuehneosauridae, *Paliguana*, *Palaeagama*, *Marmoretta* and *Tamaulipasaurus*.

G96 = Laurin (1991: ch. I3). A twisted radius is present only in *Acerodontosaurus*. Not applicable in limbless taxa. Not known in *Parviraptor*, *Paliguana*, *Saurosternon*, *Marmoretta*, *Tamaulipasaurus*, and *Prolacerta*.

G106 ≈ Laurin (1991: ch. E12). A medial centrale of twice the size of the lateral centrale is present in all saurians. This character is unknown in *Prolacerta* (contra Laurin, 1991). Gow's reconstruction of carpus of *Prolacerta* (Gow 1975, fig. 23c) is based upon disarticulated remains and the relationships between bones are uncertain. Not applicable in limbless taxa. Character not known in *Bavarisaurus*, *Eichstaettisaurus*, *Ardeosaurus*, *Parviraptor*, Kuehneosauridae, *Paliguana*, *Palaeagama*, *Marmoretta*, *Tamaulipasaurus*, and *Prolacerta*.

G108. Radius shaft longer than ulna is present only in *Youngina* and Tangasauridae. Not applicable coded in limbless taxa. Not known in *Parviraptor*, *Paliguana*, *Marmoretta*, and *Tamaulipasaurus*.

G109 = Laurin (1991: ch. L I2). Strong developed entepicondyle is present only in Younginiforms. Laurin's (1991) character D4 is redundant. The ratio of the humerus distal head width /shaft length depends on the width of the ectepicondyle here considered. Limbless taxa coded not applicable. Not known in *Parviraptor*, *Paliguana*, *Marmoretta*, *Tamaulipasaurus*.

G110 polarity reverted = Laurin (1991: ch. C3). A humerus shorter than the femur is present in all saurians, *Youngina*, and *Acerodontosaurus*. Limbless taxa were coded not applicable. Not known in *Parviraptor*, *Paliguana*, *Marmoretta*, *Tamaulipasaurus*.

G111. A medial centrale contacting the third distal carpal instead of the fourth distal carpal is present only in the Tangasauridae. Limbless taxa were coded not applicable. Not known in *Huehuecuetzpalli*, *Bavarisaurus*, *Eichstaettisaurus*, *Ardeosaurus*, *Parviraptor*, Kuehneosauridae, *Paliguana*, *Palaeagama*, *Saurosternon*, *Marmoretta*, *Tamaulipasaurus*, and *Prolacerta*.

G112. Subequal in size, ventrally placed scapula and coracoid is present in some tangasaurs. Limbless taxa were coded not applicable. Not known in *Bavarisaurus*, *Parviraptor*, *Paliguana*, *Palaeagama*, *Marmoretta*, and *Tamaulipasaurus*.

G113 polarity reverted = Laurin (1991: ch. A6 and H7). A radius that is 70 to 90 % of the humerus length is present in all saurians, *Youngina*, and *Acerodontosaurus*. Limbless taxa were coded not applicable. Not known in *Parviraptor*, *Paliguana*, *Marmoretta*, and *Tamaulipasaurus*.

G118. A short iliac blade is present only in *Youngina*. Limbless taxa were coded not applicable. Not known in *Bavarisaurus*, *Parviraptor*, *Paliguana*, *Palaeagama*, *Saurosternon*, *Marmoretta*, and *Tamaulipasaurus*.

G119. An outturned pubis is present in all lepidosaurs and *Prolacerta*. Limbless taxa were coded not applicable. Not known in *Bavarisaurus*, *Eichstaettisaurus*, *Ardeosaurus*, *Parviraptor*, Kuehneosauridae, *Paliguana*, *Palaeagama*, *Saurosternon*, *Marmoretta*, and *Tamaulipasaurus*.

G122. Long ischial tuber is present only in sphenodontians. Limbless taxa were coded not applicable. Not known in *Bavarisaurus*, *Ardeosaurus*, *Parviraptor*, *Paliguana*, *Marmoretta*, *Tamaulipasaurus*.

G131. Character excluded. No information about the ontogenetic fusion of fourth and fifth distal tarsal is available for most groups.

G137. Bony epiphyses are known to be present in all lepidosaurs. Limbless taxa were coded not applicable. Character not known in *Parviraptor*, Kuehneosauridae, *Paliguana*, *Palaeagama*, *Saurosternon*, *Marmoretta*, *Tamaulipasaurus*, and *Prolacerta*.

G138. Constant character. A dense lamellar avascular bone is present in all known Squamates and in *Sphenodon*. Not known in all fossil forms.

Excluded soft anatomy characters:

All soft anatomy characters were included except characters 139,141-161, 163-167, and 169 of Gauthier et al. (1988a). These characters are only known in extant squamates and the rhynchocephalian *Sphenodon*. Variability within Squamata was not established and their inclusion might force the monophyly of the Squamata or the Rhynchocephalian / Squamata sister-group relationships.

The calcification of most connective tissue, a transverse cloacal slit, kidney with sexual segment, tongue used to secure pray, small ciliary process, tendon of m. nictitans attached to m. retractor bulbi muscle and interorbital septum, regular shading of skin, and cartilaginous disk in lower eyelid, still should be considered synapomorphies of Lepidosauria. Other synapomorphies of Squamata should be: the lack of pars tuberalis of adenohypophyses, cochlear duct facing laterally, perilymphatic sacs within recessus scalae tympani present, reduction of the anterior cartilage of the braincase, caruncle absent, pallets on the ventral surface of tongue tip, Jacobson's organ separated from the nasal capsule, extensive sensory epithelium on the Jacobson's organ, Jacobson's organ duct open ventrally into organ cavity, large lateral nasal gland enclosed in the cavum conchale, lacrimal duct extended anteriorly to the region of the Jacobson's organ duct, ligamentous interhyal, saccullar ovaries, multiple interdigitations of the m. intermandibularis and mandibulohyoideus, m. intermandibularis innervated only by the mylohyoid nerve, m. depressor mandibulae and episternocleidomastoideus completely separated, at least some fibers of the m. clavodeltoideus extends onto the ventral surface of the clavicle, meniscus of knee joint formed by a single plate that is pierced by cruciate ligament, paired evertible hemipenes in males, lateral division of the m. retractor bulbi becomes the m. bursalis.

Appendix 6.3

Data Matrix

Most characters were coded as presented by Estes et al. (1988), Gauthier et al. (1988a), Evans (1991) and Clark and Hernández (1994). States for *Prolacerta*, *Marmoretta*, Rhynchocephalians, *Ardeosaurus*, *Eichstaettisaurus*, *Bavarisaurus*, and *Parviraptor* are original and were coded annotating their variability. Modifications presented in Chapter 4 (Appendix 4.1) were considered. Several other modifications and comments to characters are listed below. Character number refers to those of Appendix 6.1. Abbreviations: ch. = character; / = or; 0 = primitive condition; 1, 2, 3, etc. = derived states; N = not applicable; ? = unknown data.

Priscagama was not considered within Agamidae because its inclusion in the group is uncertain (Frost and Etheridge 1989). Otherwise the primitive condition of characters 60, 76, and 175 should be included in future research. Character 61 (see also 176) is variable in Chamaeleontidae; *Brookesia*, *Rhampholeon*, and all *Chamaleo* do have a splenial (Rieppel 1987) with a short anterior process (Frost and Etheridge 1989). In the iguanids *Liolaemus* and *Ctenoblepharys* the supratemporal is placed in a ventral groove below the supratemporal process, thus character 143 is not applicable to these taxa. Contrary to Rieppel (1980), the lateral margins of the frontal are straight in *Varanus*, and the number of scleral ossicles are 15 (Underwood 1970; vs. 14 coded by Pregill et al. (1986). The splenial is absent in some xantusiids (Estes 1983; ch. 60 coded 1, N). Contrary to Rieppel (1980: ch. 61) the posterior extension of the dentary in *Shinisaurus* is not considerably shorter than in other xenosaurids.

In *Bavarisaurus*, the nasals are paired Wagner (1852; ch. 3, state 0). The frontals might be paired (Evans 1994c), however, there is no evidence of a suture (ch. 6 uncertain coded 1?). There are no hypapophyses in the cervical region (Hoffstetter 1964), and the intercentra are almost flat with a small ventral ridge (ch. 182 state 0). In *Eichstaettisaurus*, the articulation of the lateral centrale with the distal carpal cannot be coded because the lateral centrale is either unossified or lacking (ch. 196 coded ?). In *Ardeosaurus*, the fifth metatarsal is hooked, but is preserved in dorsal view and the position of the plantar tubers is unknown (ch. 213 coded 2/3). The number of presacral vertebrae have been reported to be of variable numbers (e.g. 25 by Hoffstetter 1964; 24 by Cocude Michel 1963), but Mateer (1982) and Evans (1993) agree in 23 presacrals.

In *Parviraptor*, the nasal/prefrontal contact is not known. From the reconstruction given by Evans (1994a) both bones might be separated by the maxilla (ch. 4 coded 1?). The descending processes of the frontal are pronounced and almost in contact medially. The contact itself, however, is not preserved (ch. 10 coded ?). The occipital region is not preserved so it cannot be discerned if it is covered by the parietal. The posterior shape of the parietal suggests that the parietal was not extended above the occipital region (ch. 23 code 1?). The splenial facet on the dentary suggests a loose suture between the dentary and splenial (ch. 62 coded 1) although the splenial is not preserved. The type of tooth replacement is uncertain; however, there are no enlarged resorption pits on the lingual side of the teeth (ch. 78 coded 1/2). Vertebrae centrum are procoelous (notochordal) in adult. No condition can be applied. (ch. 85 coded N). The position of the autotomy septum in caudal vertebrae cannot be determined because the transverse processes are absent (ch. 91 coded N).

In *Marmoretta*, the Meckelian groove is closed and sutured in adults, but remains open in juveniles. Character 52 was coded (1) giving preference to the adult condition. The presence of the splenial and its anterior length, the tabulars, and postparietals cannot be inferred from the available material and are unknown (recoded ? contra Evans 1991: ch. 7, 8, and 19). Also contrary to Evans (1991: ch. 9) the presence of the quadratojugal can be inferred from the articulating facets on the quadrate, but its shape and size is unknown. The quadrate is more likely to be straight in lateral view if compared to the squamate condition (ch. 159 coded 0). In *Tamaulipasaurus*, characters 146, 163, 164, 188 and 200 excluded by Clark and Hernández (1994) were reintroduced and rescored. The postfrontal is absent, therefore its size cannot be estimated (contra Clark and Hernández 1994: ch. 15). The stapes are not perforated and the course of the stapedial artery is unknown (ch. 129 coded 1/2).

In rhynchocephalians, the vidian canal is not fully ossified so the position of a posterior opening is indeterminate. In Kuehneosauridae, the parietal foramen is absent (Robinson 1962; Colbert 1970; Evans 1991) or if present is on the frontoparietal suture (ch. 24 coded 1/3). Teeth on the transverse flange of the pterygoid are present (Evans, 1991; contra Gauthier et al. 1988a: ch. 24), and vomerian teeth seem to be present since the position of the vomers in the dorsal view of *Icarosaurus* (Colbert 1970) dorsal view correspond to a palatal area with denticles on the ventral side. The anterior part of the enlarged palatine mentioned by Colbert (1970) well may be undifferentiated vomers (compare figs. 6 and 9 in Colbert 1970). The surangular does form part of the coronoid process and it is not included in the articular condyle of the lower jaw (Evans 1991). As in rhynchocephalians the position of a posterior opening of the vidian canal is indeterminate.

In *Paliguana*, the presence of a separated quadratojugal is uncertain (Carroll 1975; contra Evans 1991: ch. 27). The postorbital length of the skull is certainly shorter than the preorbital region (ch. 166 coded 0). In *Palaeagama*, the postorbital is certainly shorter than the preorbital region (ch. 166 coded 0). Contrary to Gauthier et al. (1988a: ch. 95) whether the clavicle articulates the scapula or suprascapula in *Saurosternon* is unknown (Carroll 1975). In *Prolacerta* the presence or absence of the parietal foramen is variable (Gow 1975; contra Evans 1991; 31). Contrary to Laurin (1991: ch. J2) the postparietals are absent. Laurin (1991) includes this character twice in his data matrix with contradictory information. According to Gow (1975), the surangular does form part of the articular condyle of the lower jaw as opposed to Evans (1991: ch. 12) data. All characters related to the structure of carpus and tarsus are not known since Gow's (1975) reconstruction was done from disarticulated remains (D. Dilkes pers. com., but see Colbert 1987).

Data Matrix Table 1

Taxa\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Agamidae	1	0	0	0	0	1	1	1	0	0	0	1	N	N	N
Amphisbaenia	1	0	0	1	1&N	0&1	N	0	1	1	0	0?&1	0&N	0&1&N	0&N
Anguidae	1	0	0	0&1	0&1	0&1	0&1&N	0	1	0&1	0	0	1	0&1	0
Cordylidae	1	0	0	0&1	0	0&1	0	0	1	0	0	0	1?	0	0
Chamaeleontidae	1	0&1	0&1	0&N	0&1	1&N	1&N	1	0	0	0&1	1	N	N	N
Dibamidae	1	0	0	1	0&N	0	0	0	1	0	0	0&1	1&N	N	0&N
Gekkonidae	0&1	0	0&1	0&1	0	0&1	0	0	1	1	0	0	1	N	0
Gymnophthalmidae	1	0	0	0&1	0	1	0&1	0	1	0&1	1	0	1	0&1	0
Helodermatidae	1	0&1	0	0&2	1	0	N	0	1	1	0	0	1	N	0
Iguanidae	1	0	0	0	0	1	0&1	1	0&1	0	0	0&1	0	0&N	1&N
Lacertidae	1	0	0	0	0	0&1	0&1	0	1	0	0	1?	N	N	N
Lanthanotus	1	1	1	2	1	0	N	0	1	0	0	0	1	N	0
Pygopodidae	1	0	0&1	0&1	0&1	0&1	0&N	0	1	1	0	0	1	N	0
Scincidae	0&1	0	0&1	0&1	0&1	0&1	0&N	0	1	0	0	0	1	0&1&N	0
Serpentes	1	0&1	0&1	0	0&1&N	0	0&N	0	1	1	0	0&1	0&N	0&N	0&N
Teiidae	1	0	0	0&1	0	0&1	0	0	0	0	0	0	0&1	0&1	0
Varanus	1	1	1	2	0	0	0	0	0	1	0	0	1	1	0
Xantusiidae	1	0	0	0&1	0	0&1	0	0	1	0&1	0	1?	N	N	N
Xenosauridae	1	0	0	0	0	0&1	1	0	1	0	0	0	1	0&1	0
Huehuecuetzpalli	0	0	0	0	0	1	0	?	0	0	0	0	0	0	1
Tepexisaurus	?	?	?	?	0	?	0	?	?	0?	?	0	1	0	0
Bavarisaurus	0	0	0?	1?	0	1	1	?	?	0?	0	0	1	0	0
Eichstaettisaurus	0	0	0	0	0	1	1	?	?	?	0	0	1	0	0
Ardeosaurus	0	0	0	1	0	0	0	?	?	?	0	0	1	0	0
Parviraptor	?	1	?	1?	0	0	0	?	?	?	0	0	1	?	0
Rhynchocephalia	0	0	0	0	0	0&1	0&1	0	0	0	0&1	0	0&1	0	0
Kuehneosauridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paliguana	?	?	0?	0	0	0	0	?	0?	0?	0	0	0	0	0
Palaeagama	?	?	0	0	0	0	0	?	0?	0?	0?	0	0	0	0
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	?	1	?	1	0	1	0	0	0	0	0	0	0	0	0
Tamaulipasaurus	0	0	0	0	N	0	0	?	?	?	?	1	N	N	N
Prolacerta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Younginiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Agamidae	0	0	1	0	1	0&1	0	1	1	0	0&2	0	0&1	0	0
Amphisbaenia	0&1	?&N	N	N	1	?	N	1	0&3	1	0&1	0	1	0&1	0
Anguidae	0	1&2	0	0&1	1	0	0	1	0	0&1	0	0	1	0&1	0&1
Cordylidae	0	1	0	1	1	0&1	1	0&1	0&3	0	0&2	0	0&1	0	0
Chamaeleontidae	0	0	0&1	0	1	0&1	0	0&1	2&3	0	0&2	0	0&1	0	0
Dibamidae	1	N	N	N	1	1	N	1	3	1	2	N	N	1	0&1
Gekkonidae	1	N	N	N	0&1	0	0	1	3	0	2	N	0&1&N	1	0&1
Gymnophthalmidae	0	1	0	0&1	1	1	1	1	3	0	0&1&2	0	1	0	0
Helodermatidae	1	N	N	N	1	0	0	1	3	1	0	0	1	0	0
Iguanidae	0	0	1	0	1	0&1	0	1	0&1&2&3	0	0&2	0	1	0	0
Lacertidae	0	1	0	2	1	1	0	0	0&3	0	0	0	0&1	0	0
Lanthanotus	1	N	N	N	1	0	0	1	3	1	0	1	1	0	0
Pygopodidae	1	N	N	N	0&1	0	0	1	3	0	2?	0	0&N	1	0&1
Scincidae	0&1	2	1	2&N	1	0&1	0&1	1	0&3	0	0&2	0	0&1&N	0&1	0
Serpentes	0	0	N	N	1	0	N	1	3	0	2	0	N	0&1	1
Teiidae	0	1	0	0	1	1	1	1	0&1&3	0	0	0	1	0	0
Varanus	0	1	0	0	1	0	0	1	0	1	0	1	1	1	0
Xantusiidae	0	1	0	1	0&1	1	1	0	0&3	1	?	0	0	0	0
Xenosauridae	0	1	1	0	1	0	0	0&1	0	0	0	0	1	0	0
Huehuecuetzpalli	0	0	?	0	1	?	0	1	1	1	1	0	1	0	0
Tepexisaurus	0	1	0	2	?	0	1	?	?	0	?	?	1	0	0
Bavarisaurus	0	0	0?	0	0	?	?	1	0	1	0?	?	1	0	0
Eichstaettisaurus	0	0	1	0	0	0	?	1	0	0	2?	?	1	0	0
Ardeosaurus	0	0	0	0	1	0	?	1	0	0	2?	?	1	0	0
Parviraptor	?	?	?	0	0	0	0	1?	0	0	?	?	0	?	0
Rhynchocephalia	0	0	0&1	0	0&1	0&1	0	0&1	0	0	0&2	0	0	0	0
Kuehneosauridae	0	0	?	0	0	?	0	0	1/3	0	0	?	0	0	0
Paliguana	0	0	0	0	0	?	?	0	0	0	0	?	1	0	0
Palaeagama	0	0	0?	0	0	?	?	0	0	?	0	?	1	0	0
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	0	0	0?	0	1	1	0	0	3	0	0	?	0	0	1?
Tamaulipasaurus	1	N	0	N	1	?	N	0	3	1	2	N	1	0	0
Prolacerta	0	0	0	0	0	?	0	0	0&3	0	0	1	1	0	0
Younginiformes	0	0	0	0	0	?	0?	0	0	0	0	1	1	0	0

(Data matrix table 1 continued)

Taxa\Character	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Agamidae	0	0&1	0	1	0	0	0	0	0	0	1	0	0	0	0&1
Amphisbaenia	0	1?	0	1	0	1	1	1	1	0	2	0&1	0	0&1	1
Anguidae	1	0&1?	1	1	0	1	1	1	0&1	0	2	0&1	0	0	1
Cordylidae	1	0	0&1	1	0	1	1	1	0	0	2	0	0	0	1
Chamaeleontidae	0	0	0	1	1	0	N	N	0	0	1	0	0	1	1
Dibamidae	1&N	1	0	1	0	1?	1	1	1&N	1	2	1	0	0&1	1
Gekkonidae	1	0&1	0	1	0&1	1	1	1	0	0	2	0&1	0	0	1
Gymnophthalmidae	1	0	0	2	0&1	1	1	1	0&1	0	2	0	0	0	0&1
Helodermatidae	1	0	0	2	0	1	1	1	0	0	2	1	0	0	1
Iguanidae	0	0	0	1&2	0	0	0	0	0	0	1	0	0	0&1	0&1
Lacertidae	1	0	1	2	0	1	1	1	0	0	2	0	0	0	0&1
Lanthanotus	1	0	0	1	0	1	1	1	0	0	2	1	0	0	1
Pygopodidae	1	1?	0	1	1	1	1	1	0&1	0	2	0&1	0	0	1
Scincidae	1	0	0&1	1	0&1	1	1	1	0&1	1	2	0	0	0	1
Serpentes	N	0&1	0	1	0	1&N	1	1	N	0	2	0	0	1	1&N
Teiidae	0&1	0	0	2	0	1	1	1	0	0	2	1	1	0	0
Varanus	1	0	1	1	0	1	1	1	1	0	2	1	0	0	1
Xantusiidae	1	0	0	1	1	1	1	1	0&1	0	2	0	1	0	1
Xenosauridae	0&1	0	1	1	0	0&1	1	1	0&1	0	2	0	0	0	1
Huehuecuetzpalli	0	0	0	1	?	?	?	?	?	?	?	?	?	0	?
Tepexisaurus	?	?	?	1	?	0	?	?	0	0	2	1	0	0	1
Bavarisaurus	1	0	0	?	?	?	?	?	?	?	?	?	1?	?	?
Eichstaettisaurus	1	0	0	?	?	?	?	?	?	?	?	0	0	0	1
Ardeosaurus	1	0	0	?	?	?	?	?	?	?	?	1	1	0	1
Parviraptor	1	?	?	?	?	1	?	?	0	0	2	0	?	?	?
Rhynchocephalia	0	0&1	0	0&1	0	0&1	0	0	0	0	0	0	0	0	0&1
Kuehneosauridae	0	1	0?	0	?	0?	?	?	?	0	0	0	0	?	0?
Paliguana	0	0?	0?	0	?	?	?	?	?	?	?	?	?	?	?
Palaeagama	0?	0?	0?	?	?	?	?	?	?	?	?	?	?	?	?
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	?	?	0?	0	?	?	?	?	?	?	0?	0	0	0	0
Tamaulipasaurus	0	1	0	0	?	?	?	?	?	0	0	?	?	?	?
Prolacerta	0	0	0	0	0	1	0	?	0	0	0	0	0	0	?
Younginiformes	0	0	0?	0	0	1	?	?	?	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Agamidae	0	0&1	1	0	0	0&1	0	0	0	0&1	0	0	0	0	1&N
Amphisbaenia	1	0	1	0	?	1	0&1&2	N	N	0&1	0	N	0	0	1&N
Anguidae	1	0&1	1	0	1	0&1	0	1	1	0	0	0	1	0	0&1
Cordylidae	1	0	1	0	0&1	0	0&1	0	0	2	0	0	0	0	0
Chamaeleontidae	0	0	1	0	0	0&1	0	0&1	0&1	0&1	0	0	0	0	1&N
Dibamidae	0?	0	0	0	2&N	1	2	?	N	2	0	0	0	0	N
Gekkonidae	1	0	1	0&1	0	0	2	0	N	2	0	0	0	0	1&N
Gymnophthalmidae	1	0	1	0&1	0	0&1	0&2	0	0	0&2	0	0	0	0	0&1
Helodermatidae	1	0	1	0	1	0	0	1	1	1	1	0	1	1	1
Iguanidae	0&1	0&1	1	0	0	0&1	0&1&2	0	0	0&1	0	0	0	0	0&1&N
Lacertidae	1	0	0&1	0	1	0	0	0	0	2	0	0	0	0	0
Lanthanotus	1	0	1	0	1	1	0	1	1	1	1	1	2	1	0
Pygopodidae	1	0	1	1	0	0	2	?	N	2	0	0	0	0	1&N
Scincidae	1	0	0&1	0	0&1	0	0&1&2	0	0	2	0	0	0	0	0&1
Serpentes	N?	0	1	0	0	1	0	0	0	2	0	0&1	0	1	1
Teiidae	1	0	1	0	0	1	0&1	0	0	2	0	0	0	0	0
Varanus	1	0	1	0	0	1	0	1	1	1	1	1	2	1	0
Xantusiidae	1	0	1	1	0&1	0	2	0	N	2	0	0	0	0	1&N
Xenosauridae	1	0	1	0	0&1	0&1	0	1	1	0	0	0	1	0	0
Huehuecuetzpalli	?	?	?	?	?	1	0	?	0	0	?	?	0	0	?
Tepexisaurus	?	?	0	?	?	0	0	?	0	2	?	?	0	0	1
Bavarisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Eichstaettisaurus	?	?	1?	?	?	0	?	?	?	?	?	?	?	?	?
Ardeosaurus	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?
Parviraptor	?	?	?	?	?	1	0	1	1	1	?	?	?	?	0
Rhynchocephalia	0	0	0	0	N	1	0&1	0&1	0	0&1	0&1	1	0	0	N
Kuehneosauridae	?	?	0	?	N	1	0	?	0	0	0	?	0?	?	0
Paliguana	?	?	0	?	?	1	?	?	?	?	?	?	?	?	?
Palaeagama	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	?	?	0	?	1	1	1	0	0	0	1	?	?	?	?
Tamaulipasaurus	0	0	1	0	?	1	1	?	0	1	?	?	0	0	?
Prolacerta	0	0	0	0	N	1	0	?	1	0	?	0	0?	?	0
Younginiformes	0	0	0	0	N	1	0	?	?	?	?	?	?	?	0

(Data matrix table 1 continued)

Taxa\Character	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Agamidae	1	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Amphisbaenia	1	0	0	1&2&3	0&1	0	1	0	0	0	0	1	0	0	2
Anguidae	0	0	0	0&1	0	0	1	1	0	0	1	1	0	0	0&2
Cordylidae	0	0	0	1&2	0	0	0&1	1	1	0	0&1	1	0	0	2
Chamaeleontidae	0	N	0	0	0	0	N	0	0	0	0	0	0	0	2
Dibamidae	N	N	0	2	1?	0	1	0	0	0	1	1	0	0	2
Gekkonidae	0	0	0	1	0&1	0	1	1	0	1	1	1	0	0	2
Gymnophthalmidae	0&1?	0	0	1	0	2	0&1	0	0	0	0	0	0	1	2
Helodermatidae	1	1	1	1	0	0	1	1	0	0	0	1	0	0	0&2
Iguanidae	0&1	0	0	1&3	0&1	0	0&1	0	0	0	0	0	0&1	0	0&2
Lacertidae	0	0	0	1	0	1	0	0	0	0	0	0	0	1	2
Lanthanotus	2	1	1	3	0	0	1	1	0	0	0	1	0	0	2
Pygopodidae	0	0	0	1	0&1	0	1	1	0	1	1	0	0	0	2
Scincidae	0	0	0	1&2	0&1	0	1	1	1	0	1	1	0	0&1	2
Serpentes	2	1	0&N	1&2&3&N	0&1	0	1&N	1&N	0&N	0&N	0&N	1&N	0	0	0&2
Teiidae	0	0	0	1	0	2	0	0	0	0	0	0	0&1	1	2
Varanus	1	1	1	1	0	0	1	1	0	0	0	1	0	0	2
Xantusiidae	1	N	0	2	1	1	0	0	0	0	0	0	0	0	2
Xenosauridae	0	0	0	1&2	0	0	1	0	0	0	0	1	0	0	2
Huehuecuetzpalli	1/2	?	0	1	0	?	?	?	0?	0	0	?	0	0	?
Tepexisaurus	0	0	0	2	0	0	1	?	1	0	1	?	0	0	2
Bavarisaurus	?	?	0	1	0	0	?	?	?	?	1	0	?	?	?
Eichstaettisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ardeosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Parviraptor	?	1	?	?	?	?	?	?	?	?	?	?	?	?	2
Rhynchocephalia	N	N	0	0	0	0	0&N	0&1&N	0&1&N	0&N	0&N	0&N	0&N	0	1&2
Kuehneosauridae	?	?	N	N	0	0&?	0&?	0	0?	0	1	0?	0?	0	0
Paliguana	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Palaeagama	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	?	?	0	0	0	?	?	?	?	?	?	?	?	?	0
Tamaulipasaurus	?	?	?	0	?	?	N	N	N	N	N	N	?	?	2
Prolacerta	1	0	0	N	0	0	0	0	1	0	0	0	0	0	0
Younginiformes	?	?	?	N	?	?	?	?	?	?	?	?	?	?	0

(Data matrix table 1 continued)

Taxa\Character	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Agamidae	2	2	3	0	0	2	0&1	0&1	0	1	0&1	0	2	1	0
Amphisbaenia	2	1&2	1&2&N	0	0	2	1	0&1	0	1	0	0	1	1	2
Anguidae	1&2	1	1	0&1?	0	1&2	0&1	1	0	1	0	0	1	1	0&2
Cordylidae	1&2	1	0	0	0	1&2	0	0&1	0	1	0	0&1&2	0&1&2	1	0&1
Chamaeleontidae	2	2	3	0	0	2	1	1	0	1	0	0	0	1	0
Dibamidae	2	1	1	0	0	2	1	1	0	1	0	0	1	1	3
Gekkonidae	2	1	0	0	0	0&1&2	0&1	0&1	0&N	0&1	0&N	0	0	0	0
Gymnophthalmidae	1&2	1	0&1	0	1	1&2	1	0&1	0	1	0	1&2	2	1	1
Helodermatidae	1&2	1	2	1	0	2	0	1	1	1	0	0	1	1	0
Iguanidae	1&2	1	0	0	0&1	1&2	0&1	0&1	0	1	0	0&1&2	0&1	1	0&1
Lacertidae	1&2	1	0	0	1	1&2	0	0	0	1	0	2	0&1&2	1	1
Lanthanotus	1	1	2	1	0	2	1	1	1	1	1	0	1	1	0
Pygopodidae	2	1	0	0	0	0&1&2	0&1	0	0	1	0	0	N	1	0
Scincidae	1&2	1	0&1	0	0	1&2	0&1	0&1	0	1	0	1	1	1	0&2&3
Serpentes	1&2	1	2	0	0	2	1	1	0	1	0&1	2	1	?	0
Teiidae	1&2	1	0&1	0	1	1	0&1	0&1	0	1	0&1	2	2	1	1
Varanus	2	1	2	1	0	0	1	1	1	1	1	0	1	1	0
Xantusiidae	2	1	0	0	0	1	0	0	0	0&1	0	0	0&2	0&1	0&1
Xenosauridae	1&2	1	1	0	0	1	1	1	0	1	0	0	1	1	0
Huehuecuetzpalli	?	1	?	0	0	?	?	?	N	0	N	1	0	0	0
Tepexisaurus	2	1	1/2	0	0	?	?	?	?	?	?	1	0	?	0
Bavarisaurus	2	?	?	?	?	?	?	?	0	0?	N	?	0	0	0
Eichstaettisaurus	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0
Ardeosaurus	?	?	?	?	?	?	?	?	?	1	0	?	?	?	0
Parviraptor	?	1	1/2	0	0	?	?	?	0	N	0	1	2	?	0
Rhynchocephalia	1&2	0&1&2	0&3	0	0	0	0	0	0	0	N	0&1	0	0	0
Kuehneosauridae	0	0	0	0?	0	?	?	?	N	0	N	0	N	1	0
Paliguana	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeagama	?	?	?	0?	?	?	?	?	N	0	N	?	?	0	0
Saurosternon	?	?	?	?	?	?	?	?	N	0	N	?	?	0	0
Marmoretta	1	1	0	0	0	?	?	?	0	0	N	0?	?	?	0
Tamaulipasaurus	?	1	?	0	0	?	?	?	0	1	0	1	N	?	?
Prolacerta	0	0	0	0	0	1	0	?	0	0	N	0	0	0	0
Younginiformes	0	0	?	?	0	?	?	?	N	0	N	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
Agamidae	N	0&1	0&1	1	0&1&2	0	0	1&2	0&1	0	0	0&1	0	0&1	0&1
Amphisbaenia	2&N	0&1	2	N	3&N	0	0&N	0&N	1?&N	0&1&N	N	1	1	N	0&N
Anguidae	0&1&2	0&1	2	0&1	1&2&N	0	0&1&N	1&N	0	0	1	1	0&1	1&N	0
Cordylidae	1&2	1	0&2	0&1	0&1	0&1	0	1	0	0	0&1	1	0	1	0
Chamaeleontidae	N	0	0?&1	0	3	1	N	0	1	1	N	N	1	N	0&1
Dibamidae	?	1	2	0	3	1	N	N	N	N	N	N	N	N	0
Gekkonidae	1&N	0&1	0&2	1	1&2	0&1	1	1&2	0&1	0	1	0&1	0	1&2	0&1
Gymnophthalmidae	2	1	0&2	1	1&3	0&1	0	2	0	0	1	1	0	1&2	1
Helodermatidae	N	0	2	1	1	0	0	0	1	0	1	1	0	2	0
Iguanidae	0&1&2&N	0&1	0&1	1	0&1&2&3	0&1	0&1	1&2	0&1	0	0	0&1	0	0&1	0&1
Lacertidae	0&2	1	0&2	1	0&1	0&1	0	1	1	0	1	1	0	1	0&1
Lanthanotus	N	0	2	2	3	0	0	1	1	0	1	1	0	3	0
Pygopodidae	1	1	2	N	3	0	0&N	0&1&N	N	0	1&N	1	1	N	0
Scincidae	0&1&2&N	0&1	2	0&1	1&3	0&1	0&1&N	1&N	0	0	1	1	0&1	1&N	0&1
Serpentes	N	0	2	N	N	0	N	N	N	N	N	N	N	N	N
Teiidae	0&2	1	0&2	1	1	0	0&1	2	0	0	1	1	0	1	1
Varanus	N	0	2	2	2	0	0	2	1	0	0&1	1	0	0&1	0&1
Xantusiidae	0&1&2	1	2	1	1&2	0	0	1	0	0	1	1	0	1	0&1
Xenosauridae	0&N	0&1	2	1	1	0	0	1	0	0	1	1	0	0&1	0
Huehuecuetzpalli	0	1	0	1	2	?	0	1	?	0	0	1	0	0/1	0
Tepexisaurus	0/2	1	1	0	1/2	?	1	1	?	0	1	1	0	?	?
Bavarisaurus	0	1	1	?	?	?	?	?	?	0	?	0	0	0	?
Eichstaettisaurus	?	1	2	?	?	?	1	?	?	0	?	?	?	?	0
Ardeosaurus	?	1	1	0	?	?	0	?	?	0	?	?	?	?	?
Parviraptor	N	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchocephalia	0	1	0	0&1?	0&1&2	0	0	0	0	0	0	0	0	0	0
Kuehneosauridae	N	0	0	?	?	?	0	0	?	?	?	?	?	?	?
Paliguana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeagama	?	?	0?	?	?	?	?	?	?	?	?	?	?	?	?
Saurosternon	N	0	?	?	?	?	0	0	?	0	0	0	0	0	0?
Marmoretta	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Tamaulipasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Prolacerta	N	0	0	0	?	?	0	0	?	0	0	?	0	0	?
Younginiformes	N	0	0	?	0?	?	0	0	?	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Agamidae	1	1	0	0	0	0	0	0&1	0	0&1	0	0	0	0	0
Amphisbaenia	2&N	N	N	0	0	0	0	0&2	1	0	0	0	1	0	0
Anguidae	1&N	2&N	2	0	1	1	1	0&1	1&N	0	0	0&1	1	0	1
Cordylidae	1	2	2	0	1	1	1	2	1	0	0	1	1	0	0
Chamaeleontidae	2	1	0	0	0	0	0	0&1	0	0	0	0	0	0	0
Dibamidae	N	N	N	0	0	0	0	0	N	0	0	0	1	0	0
Gekkonidae	1	2	1	0&1	0	0&1	0	0	1	0	0	0	0	1	0
Gymnophthalmidae	2	2	2	0	0	0	0	0&2	1	1	1	1	1	0	0
Helodermatidae	1	2	1	0	0	1	1	1	1	0	0	1	1	0	1
Iguanidae	1	1	0	0	0	0	0&1	0&1	0	0	0	0	0	0	0
Lacertidae	1	2	2	0	0	0	1	2	1	1	1	1	1	0	0
Lanthanotus	1	2	1	0	0	1	1	0	1	0	0	1	?	0	1
Pygopodidae	N	N	N	1	0	0	0	0	N	0	0	1	0	1	0
Scincidae	1	2&N	2	0	1	1	1	0&2	1&N	0	0	1	1	0	0
Serpentes	N	N	N	0	0	0	0	0	N	0	0	0	1	0	1
Teiidae	2	2	1	0	0	0	0	0&2	1	1	1	1	1	0	0&1
Varanus	1	2	0	0	0	0&1	0&1	0&1?	1	0	1	1	1	0	1
Xantusiidae	1	2	2	1	0	0	0	0&2	1	1	1	1	1	0	0
Xenosauridae	1	2	1	0	0	1	1	2	1	0	0	1	1	0	1
Huehuecuetzpalli	1	2	0	0?	0	1	0	0	0	?	?	?	?	?	?
Tepexisaurus	1	2	0	?	0	0	?	?	1	?	?	?	?	?	?
Bavarisaurus	2	2	?	?	0	0	0	0	?	?	?	?	?	?	?
Eichstaettisaurus	2	1	?	?	?	0	0	0	0	?	?	?	?	?	?
Ardeosaurus	?	?	?	?	?	0	0	2	?	?	?	?	?	?	?
Parviraptor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchocephalia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kuehneosauridae	1	?	0	0?	0	0	0	0	?	?	?	?	?	?	?
Paliguana	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
Palaeagama	0	?	0?	0?	0	0?	0?	0	?	?	?	?	?	?	?
Saurosternon	1	?	0?	0?	1	0?	?	?	?	?	?	?	?	?	?
Marmoretta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tamaulipasaurus	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
Prolacerta	0	?	0	?	?	?	0	0	?	?	?	?	?	?	?
Younginiformes	0&1	0&1	0	0?	0	0&1	0	0	N	?	?	?	?	?	?

(Data matrix table 1 continued)

Taxa\Character	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
Agamidae	1	0	0	0	0	0	1	0&1	2	0&1	0	0	0	0	1&N
Amphisbaenia	4	2	0	0	1	0&N	N	0&1	2	1	1	0	1	1	1&N
Anguidae	2	1	0	0	0&1	0	0	0	2	1	1	0&1	0	0	1
Cordylidae	1	1&2	0&2	2	0	0	0&1	1	2	1	1	0&1	0	0	1&N
Chamaeleontidae	0	0	0	0	N	1	1	0	2	0	0	0	0	0	1&N
Dibamidae	0	1	2?	?	0	N	N	0	0	1	1	1	1	0	N
Gekkonidae	1	1	1	1	1	0	0	0&1	0&1	1	0	0&1	0	0	N
Gymnophthalmidae	4	2	1	1	1	1	1	0&1	2	1	1	0&1	0	0	1&N
Helodermatidae	3	1	0	0	0	1	1	0	2	1	0	0	2	0	1
Iguanidae	1	0	0	0	0	0&1	0&1	0&1	2	0&1	0&1	0	0	0	1&N
Lacertidae	3	2	2	1	0	0&1	0	0&1	2	1	1	0	0	0	1
Lanthanotus	4	1	0	0	0	1	0	0	2	1	0	0	2	0	1
Pygopodidae	1	1	1	1	1	N	0	0&1	1	1	1	0&1	0	0	N
Scincidae	1	2	1	2	1	0	0	0	2	1	1	1	0	0	1&N
Serpentes	5	1	N	0	0	N	N	0	1	1	0&1	0&1	0	1	N
Teiidae	4	2	1	1	0	1	1	0&1	2	1	1	0	0	0	1
Varanus	5	1	N	0	0	1	0	0	2	1	0	0	2	0	1
Xantusiidae	1	2	1	2	0&1	0	0	1	2	1	1	0	0	0	N
Xenosauridae	2	1	0	0	0	0	0	0	2	1	0	0	0	0	1
Huehuecuetzpalli	?	?	?	?	?	?	?	?	?	?	?	0	0	?	N
Tepexisaurus	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?
Bavarisaurus	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1?
Eichstaettisaurus	?	?	?	?	?	?	?	?	?	?	?	?	0	?	N
Ardeosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	N
Parviraptor	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Rhynchocephalia	0	0	0	0	0	0	0	0	1?	0	0	0	0	0	1
Kuehneosauridae	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0
Paliguana	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0
Palaeagama	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?
Marmoretta	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1
Tamaulipasaurus	?	?	?	?	?	?	?	?	1/2	?	?	?	1	1	N
Prolacerta	?	?	?	?	?	?	?	?	1/2	?	?	?	0	0	0
Younginiformes	?	?	?	?	?	?	?	?	0	?	?	1	0	0	0

(Data matrix table 1 continued)

Taxa\Character	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Agamidae	1	1	1	1	N	2	1	1&N	2	1	1	1	1	1	0&1
Amphisbaenia	1	3	1	1	N	2&N	1	N	2	1	1	1	1	1	1
Anguidae	1	1	1	1	N	2&3	1	1&N	2&N	1&N	1	1	1	0&1	1
Cordylidae	1	0&1	1	1	N	2	1	1	2	1	1	1	1	1	1
Chamaeleontidae	1	1	1	1	N	3	1	N	2	1	1	0	1	1	1
Dibamidae	1	1	1	1	N	N	1	N	2&N	1&N	1	1	1	1	1
Gekkonidae	1	1	1	1	N	3	1	1&N	2&N	1&N	1	1	1	1	1
Gymnophthalmidae	1	0&1	1	1	N	3	1	1	2	1	1	1	1	1	1
Helodermatidae	1	1	1	1	N	2	1	1	2	1	1	1	1	1	1
Iguanidae	1	1	1	1	N	3	1	1&2&N	2	1	1	1	1	1	1
Lacertidae	1	0&1	1	1	N	2	1	1	2	1	1	1	1	1	1
Lanthanotus	1	1	1	1	N	3	1	1	2	1	1	1	1	1	1
Pygopodidae	1	1	1	1	N	3	1	N	2&N	1&N	1	1	1	1	1
Scincidae	1	1	1	1	N	3	1	1	2	1	1	1	1	1	1
Serpentes	1	2	1	1	N	2&3&N	1	1&N	N	N	1	1	1	1	1
Teiidae	1	1	1	1	N	3	1	1	2	1	1	1	1	1	0&1
Varanus	1	1	1	1	N	3	1	1	2	1	1	1	1	1	1
Xantusiidae	1	1	1	1	N	3	1	1	2	1	1	1	1	1	1
Xenosauridae	1	1	1	1	N	2	1	1	2	1	1	1	1	1	0&1
Huehuecuetzpalli	1	1	1	1	N	3	1	1	2	1	1	1	1	?	?
Tepexisaurus	?	1	?	?	N	3	1	1	2	1	?	1	1	1	1
Bavarisaurus	1	0	?	?	N	3	?	1	2	1	?	?	?	?	?
Eichstaettisaurus	1	1	1	1	N	3	1	1	2	1	?	1	?	?	?
Ardeosaurus	1	1	1	1	N	3	1	1	2	1	?	1	?	?	?
Parviraptor	?	2	?	?	?	?	?	?	2	1	?	?	?	?	1
Rhynchocephalia	0&1	0	1	1	0&1	0&1	0	0	1	0	0&1	0&1	0	0&1	0
Kuehneosauridae	0	0	1	1	N	3	1	N	2	0	1	1	1	0	0
Paliguana	0	0	0	0	?	1	?	?	2	0	1	1	?	?	?
Palaeagama	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	0?	2	?	?	?	3	0	?	?	0?	?	0	0	?	1?
Tamaulipasaurus	0	3	1	1	0	1	0	N	2	0	1	1	1	?	?
Prolacerta	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0
Younginiformes	1	0	0	0	0	0&1	0	0	0	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
Agamidae	0	1	1	1	1	1	1	2	1	1	1	1	0	0	0
Amphisbaenia	0	1&N	0	1	1	1	1	2	0	1	1	0	N	N	N
Anguidae	0	1	1	1	1	1	1	2	1	1	1	1	0&1	1	2
Cordylidae	0	1	1	1	1	1	1	2	1	1	1	1	0	1	2
Chamaeleontidae	0	N	1	1	1	1	1	2	0	1	1	1	0	0	0
Dibamidae	0	1&N	1	1	1	1	1	2	1	1	1	0	N	N	N
Gekkonidae	0	1	1	1	1	1	1	2	1	1	1	1	0	N	N
Gymnophthalmidae	0	1	1	1	1	1	1	2	1	1	1	1	1	0	2
Helodermatidae	0	1	1	1	1	1	1	2	1	1	1	0	1	N	N
Iguanidae	0	1&N	1	1	1	1	1	2	1	1	1	0&1	0&N	0	0
Lacertidae	0	1	1	1	1	1	1	2	1	1	1	1	0	1	2
Lanthanotus	0	1	1	1	1	1	1	2	1	1	1	0	0	N	N
Pygopodidae	0	1	1	1	1	1	1	2	1	1	1	0	0	N	N
Scincidae	0	1	1	1	1	1	1	2	1	1	1	1	1&N	1&N	2
Serpentes	0	N	0&1	0&1	1	1	1	2	0&1	1	1	1	0	2&N	N
Teiidae	0	0&1	1	1	1	1	1	2	1	1	1	1	0&1	0	0
Varanus	0	1	1	1	1	1	1	2	1	1	1	0	0	0	1
Xantusiidae	0	1	1	1	1	1	1	2	1	1	1	1	0	0	2
Xenosauridae	0	1	1	1	1	1	1	2	1	1	1	1	0	0	0
Huehuecuetzpalli	0	?	?	?	?	?	1	?	1	?	?	1	0	0	0
Tepexisaurus	0	0	1	1	?	1	1	2	1	?	?	1	?	0	2
Bavarisaurus	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?
Eichstaettisaurus	?	1	?	?	?	?	?	?	?	?	?	1	1	0	?
Ardeosaurus	?	1	?	?	?	?	?	?	?	?	?	1	1	0	?
Parviraptor	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1
Rhynchocephalia	1	0	1	0	0	1	0	1	0&1	0	0	0	1	0	0&2
Kuehneosauridae	0	?	0	0	0	1	0	0	1	?	?	0	0	0	0
Paliguana	0	?	?	?	?	0	0	?	1	?	?	?	0	0	0
Palaeagama	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Saurosternon	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Marmoretta	0	0	0	0	?	?	?	?	0	?	?	1	0	0	0
Tamaulipasaurus	1	?	?	?	?	1	0	1	1	?	?	?	N	N	N
Prolacerta	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0
Younginiformes	0	0	0	0	0	0&1	0	0	0	?	?	0	1	1	0

(Data matrix table 1 continued)

Taxa\Character	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Agamidae	1	0	0	0	0	0	N	1	0	1	0&1	1	1	1	1
Amphisbaenia	N	N	0	0	1	0	N	N	0	1	0&1	1	1&N	2	1
Anguidae	1	0	0	0	1	0	N	1&N	0	0&2	0	1	1	1	1
Cordylidae	1	1	0	0	1	0	N	1&N	0	0	0	1	1	1	1
Chamaeleontidae	1	0	0	0	1	0	N	1&N	0	1	0&1	1	1	1	1
Dibamidae	1	N	0	0	1	0	N	N	0	1	1	1	N	0	1
Gekkonidae	1	N	0	0	1	0	N	1&N	0	0	0&1	1	1&N	1	1
Gymnophthalmidae	1	0	0	0	1	0	N	1&N	0	0	0	1	1	1	1
Helodermatidae	1	N	0	0	1	0	N	1&N	0	2	0	1	1	1	1
Iguanidae	1	0	0	0	1	0	N	1	0	0&1	0&1	1	0&1&N	1	1
Lacertidae	1	1	0	0	1	0	N	1	0	0	0	1	1	1	1
Lanthanotus	1	N	0	0	1	0	N	N	0	2	0	1	1	1	1
Pygopodidae	1	N	0	0	1	0	N	1&N	0	1	0&1	1	1&N	1	1
Scincidae	1	1	0	0	1	0	N	1&N	0	0	0	1	1&N	1	1
Serpentes	1&N	N	0	0	0&1	0	N	1	0	2	0	1&N	1&N	0&1&2	1
Teiidae	0	0	0	0	1	0	N	1&N	0	2	0	1	0&1	1	1
Varanus	0	0	0	0	1	0	N	N	1	2	0	1	1	1	1
Xantusiidae	1	1	0	0	1	0	N	1&N	0	0	0&1	1	N	1	1
Xenosauridae	1	0&1	0	0	1	0	N	1	0	0	0	1	1	1	1
Huehuecuetzpalli	0	0	0	0	1	0	N	1	1	0	?	1	1	1	?
Tepexisaurus	1	1	0	0	1	0	N	?	0	0	0	1	1	1	1
Bavarisaurus	0	0	0	?	1	0	N	N	0	0	?	?	1	1	?
Eichstaettisaurus	1	0	0	0	1	0	N	1	0	?	?	?	?	?	?
Ardeosaurus	1	0	0	0	?	?	N	N	0	?	?	?	?	?	?
Parviraptor	1	?	0	0	1	?	?	N	1	?	0	?	?	?	?
Rhynchocephalia	0&1	0&1	0&1	1&2&3	0&1	0&1	1&2	1	0	1	1	0	0	0&1&2	1
Kuehneosauridae	0	0	0	0	1	0	N	1	0	0	0	0	0	1	1
Paliguana	0	0	0	?	?	?	?	0	0	0	?	?	?	1	?
Palaeagama	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?
Saurosternon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Marmoretta	1	0	1	0	1	0	N	N	0	0	?	1	?	?	1
Tamaulipasaurus	1	N	0	?	1	1	0	1	0	0	?	?	?	2	?
Prolacerta	1	0	0	1	1	0	2	1	1	2	0	0	0	1	0
Younginiformes	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
Agamidae	1	1	0	1	1	0&1	1	1	1	1	1	1	1	1	1&2
Amphisbaenia	1	1	0	1	1	N	1&2	1&N	1&N	N	1&N	1&N	1&N	1&N	0&N
Anguidae	1	1	0	1	1	1	1&2	1&N	1&N	1&N	1&N	1&N	1&N	1&N	1&N
Cordylidae	1	1	0	1	1	0&1	1	1	1	1	1	1	1	1	1
Chamaeleontidae	1	1	0	1	1	1	1	1	1	N	1	1	1	1	2
Dibamidae	1	1	0	1	1	1	1	1	N	N	N	N	N	N	N
Gekkonidae	0&1	1	0	1	1	0&1	1	1	1	1	1	1	1	1	2
Gymnophthalmidae	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Helodermatidae	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Iguanidae	1	1	0	1	1	0&1	1	1	1	1	1	1	1	1	1&2
Lacertidae	1	1	0	1	1	0&1	1	1	1	1	1	1	1	1	1
Lanthanotus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Pygopodidae	0&1	1	0	1	1	1	1	1	1&N	N	N	N	N	N	N
Scincidae	1	1	0	1	1	1	1	1	1&N	1&N	1	1	1	1	1&2
Serpentes	1	1	0	1	1	N	N	N	N	N	N	N	N	N	N
Teiidae	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1&2
Varanus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	2
Xantusiidae	0&1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Xenosauridae	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Huehuecuetzpalli	1	?	0	1	1	1	1	1?	1	1	1	1	?	?	?
Tepexisaurus	1	0	?	1	1	1	?	1	1	1	1	1	1	1	1
Bavarisaurus	1	0?	?	?	1	1	?	?	?	1	1	0	?	?	?
Eichstaettisaurus	1	?	?	1	1	1	?	?	1	?	1	1	0	0?	1
Ardeosaurus	1	?	?	1	1	1	?	?	1	?	1	1	?	?	?
Parviraptor	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchocephalia	0&1	0	0&1	0	0	0&1	2	1	0	1	0&1	0	0	0	0
Kuehneosauridae	?	0	0	0	?	1	?	?	0	?	1	1	?	?	?
Paliguana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeagama	?	?	0	?	0	?	?	?	?	?	0	?	?	?	?
Saurosternon	?	?	0	?	?	?	?	0	0	1	0	0	?	?	1?
Marmoretta	1	?	0	?	1	?	?	?	?	?	?	?	?	?	?
Tamaulipasaurus	?	N	?	1	?	?	?	?	?	?	?	?	?	?	?
Prolacerta	1	0	?	2	?	0	?	?	0	0	0	1	?	0	1
Younginiformes	0	0	0&1	0	0	0&1	?	0	0	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
Agamidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Amphisbaenia	1&N	1&N	1&N	2&N	0&N	N	N	N	N	N	N	N	N	N	N
Anguidae	1&N	1&N	1&N	2&N	0&N	1	1	1	2	1	1&N	1&N	1&N	1&N	1&N
Cordylidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Chamaeleontidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Dibamidae	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Gekkonidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Gymnophthalmidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Helodermatidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Iguanidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Lacertidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Lanthanotus	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Pygopodidae	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Scincidae	1	1	1	2	0	1	1	1	2	1	1&N	1&N	1&N	1&N	1&N
Serpentes	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Teiidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Varanus	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Xantusiidae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Xenosauridae	1	1	1	2	0	1	1	1	2	1	1	1	1	1	1
Huehuecuetzpalli	?	1	1	2	0	?	1	?	2	1	1	1	1	1	1
Tepexisaurus	1	1	1	2	0	?	?	?	2	?	1	1	?	1	1
Bavarisaurus	?	?	1	2	0	?	?	?	2	1	1	1	1	1	1
Eichstaettisaurus	?	1	1	1	0	?	1	?	2	1	1	1	1	1	1
Ardeosaurus	?	?	?	?	?	?	?	?	2	?	?	?	0?	?	?
Parviraptor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhynchocephalia	0	0	1	2	0	1	1	1	1	1	1	0	1	1	1
Kuehneosauridae	?	?	0	1	?	0	0	0	1	0?	?	?	?	?	?
Paliguana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeagama	?	?	0	0	?	?	?	?	0	?	?	?	?	?	?
Saurosternon	?	0	0	0	?	?	?	?	0	?	?	?	0	0	0
Marmoretta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tamaulipasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Prolacerta	?	?	1	0	1	1	0	0	0	0	0	0	0	0	0
Younginiformes	0	0	0	0&2	1	0	0	0	0	0	0	0	0	0	0

(Data matrix table 1 continued)

Taxa\Character	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225
Agamidae	1	1	3	2	1	1	1	0	0	0	0	0	0	1	N
Amphisbaenia	N	N	N	N	1	1	1	0	0/1	0	1	0	2	1	N
Anguidae	1&N	1&N	3&N	2&N	1	1	1	0	0	0	1	0&1	1	1	N
Cordylidae	1	1	3	2	1	1	1	0	0	0	0	1	1&2	1	N
Chamaeleontidae	1	1	3	2	1	1	1	0	0	0	0&1	0	0	N	N
Dibamidae	N	N	N	N	1	1	1	0	1	0	?	0	1	1	N
Gekkonidae	1	1	3	2	1	1	1	0	0	0	0	0	1	1	N
Gymnophthalmidae	1	1	3	2	1	1	1	0	0	0	0	0	2	1	N
Helodermatidae	1	1	3	2	1	1	1	0	0	0	1	0	1	1	N
Iguanidae	1	1	3	2	1	1	1	0	0	0	0	0	0	1	N
Lacertidae	1	1	3	2	1	1	1	0	0	0	0	0	2	1	N
Lanthanotus	1	1	3	2	1	1	1	0	0	0	1	0	1	1	N
Pygopodidae	N	N	N	N	1	1	1	0	0	0	?	0	1	1	N
Scincidae	1&N	1&N	3&N	2&N	1	1	1	0	0	0	0	0&1	2	1	N
Serpentes	N	N	N	N	1	0	1	0	0&1	0&1	0	0&N	1	N	N
Teiidae	1	1	3	2	1	1	1	0	0	0	0	0	2	1	N
Varanus	1	1	3	2	1	1	1	0	0	0	1	0	1	1	N
Xantusiidae	1	1	3	2	1	1	1	0	0	0	0	1	2	1	N
Xenosauridae	1	1	3	2	1	1	1	0	0	0	1	0	1	1	N
Huehuecuetzpalli	0	1	3	?	1	1	1	0	0	0	?	0	?	?	N
Tepexisaurus	1	1	2/3	2	1	?	1	?	?	0	?	1	?	1	N
Bavarisaurus	1	1	3	2	1	1	?	0	0	0	?	0	?	?	?
Eichstaettisaurus	0	1	3	?	1	1	1	0	0	?	?	?	?	1	N
Ardeosaurus	?	?	2/3	?	1	1	1?	0	0	?	?	?	?	1	?
Parviraptor	?	?	?	?	?	0	?	?	?	?	0	?	?	?	?
Rhynchocephalia	0	1	2	1	0	1	0&1	0&1	0&1	0&1	0	0	0	0	0&1
Kuehneosauridae	?	?	0	?	0	1	1	1	0	0	?	N	?	?	N
Paliguana	?	?	?	?	?	0	1	0	0	0	?	?	?	?	N
Palaeagama	?	?	?	?	0	0	1	?	0	?	?	?	?	?	N
Saurosternon	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?
Marmoretta	?	?	?	?	0	0	0	0	0	0	0	0	?	1	1
Tamaulipasaurus	?	?	?	?	?	1	1	0	0	?	?	?	?	?	0
Prolacerta	0	1	1	0	?	0	0	1	1	0&1	?	0	?	0	1
Younginiformes	0	0&1	0	0	0	0	0	0	0	0	?	?	?	0	0

Appendix 6.4

Analysis and Results

Analysis 1: All taxa included; defined outgroup Younginiformes

```
Data matrix has 34 taxa, 225 characters
Valid character-state symbols: 012345
Missing data identified by '?'
Gaps identified by '-', treated as "missing"

No taxa are deleted

Designated outgroup taxa:
   Younginiformes

All characters are informative
All characters are unordered

Heuristic search settings:
   Addition sequence: random
      Number of replicates = 100
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

   Random-addition-sequence replicate 1 (seed = 1):
     0 trees in memory at start of replicate
       60 trees found (length=1128)
   Random-addition-sequence replicate 2 (seed = 1999765965):
     60 trees in memory at start of replicate
       40 additional trees found (length=1128)

   100th shortest tree found at replicate number 3

Heuristic search completed
   Total number of rearrangements tried = 9635198
   Length of shortest tree(s) found = 1128
   Number of trees retained = 100
   Time used = 00:25:45.6

Tree description:
   Unrooted tree(s) rooted using outgroup method
   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree length = 1128
Consistency index (CI) = 0.715
Homoplasy index (HI) = 0.748
Retention index (RI) = 0.625
Rescaled consistency index (RC) = 0.447
```

```
Strict consensus of 100 trees:

                                                      /---- Agamidae
                                                  /---+---- Chamaeleontidae
                               /------------------+-------- Iguanidae
                               |                      /---- Amphisbaenia
                               |   /------------------+---- Dibamidae
                               |   |                  /---- Anguidae
                               |   +------------------+---- Xenosauridae
                           /---+   |                  /---- Cordylidae
                           |   |   |              /---+---- Scincidae
                           |   |   |       /------+-------- Tepexisaurus
                           |   |   |       |          /---- Gymnophthalmidae
                           |   |   |   /---+      /---+---- Teiidae
                           |   \---+   |   |  /---+-------- Lacertidae
                           |       +---+   \--+------------ Xantusiidae
                       /---+       |   |              /---- Gekkonidae
                       |   |       |   \--------------+---- Pygopodidae
                       |   |       |              /-------- Helodermatidae
                       |   |       +--------------+   /---- Lanthanotus
                       |   |       |              \---+---- Varanus
                   /---+   |       +----------------------- Serpentes
                   |   |   |       \----------------------- Parviraptor
                   |   |   \------------------------------- Huehuecuetzpalli
               /---+   |                              /---- Bavarisaurus
               |   |   \------------------------------+---- Eichstaettisaurus
            /--+   |                                  \---- Ardeosaurus
            |  |   \--------------------------------------- Tamaulipasaurus
        /---+  \------------------------------------------- Marmoretta
    /---+   \---------------------------------------------- Rhynchocephalia
    |   \-------------------------------------------------- Kuehneosauridae
    +------------------------------------------------------ Paliguana
/---+------------------------------------------------------ Palaeagama
|   +------------------------------------------------------ Saurosternon
|   \------------------------------------------------------ Prolacerta
\---------------------------------------------------------- Younginiformes

Statistics derived from consensus tree:

     Component information (consensus fork) = 24 (normalized = 0.750)
     Nelson-Platnick term information = 254
     Nelson-Platnick total information = 278
     Mickevich's consensus information = 0.408
     Colless weighted consensus fork (proportion max. information) = 0.496
     Schuh-Farris levels sum = 2967 (normalized = 0.496)
     Rohlf's CI(1) = 0.635
     Rohlf's -ln CI(2) = 93.000 (CI(2) = 4.08e-41)
```

Ten hypotheses of character distribution at the base of the Lepidosauromorpha:

Trees number 1, 2, 3, 4, 10, 16, 65, 74, 82, 91:

```
            /-58------ Other lepidosauromorphs
         /-57
      /-56  \--------- Paliguana
   /-55  \------------ Saurosternon
/-54  \--------------- Palaeagama
|  \------------------ Prolacerta
\--------------------- Younginiformes
```

Apomorphy lists:

```
Node 54: 95*, 129*, 136(0), 138*, 139*, 144*, 146, 158*, 159, 163(0), 164(0),
            172(2)*, 173*, 179, 181, 192*, 195, 201*, 225*
Node 55: 27(0)*, 36(0)*, 144(2)*, 147*, 174(0), 180*, 186*, 190*, 200(0)*,
            206*, 214*, 217
Node 56: 106
Node 57: 132(0)*, 188*, 191*, 199*, 204*, 208*, 209*, 210*
Node 58: 24(3)*, 28(0), 32*, 141(3)*, 216
Paliguana: 138(0)*, 139(0)*, 156(0), 173(0)*
Saurosternon: 110, 192(0)*, 212(0)
Prolacerta: 54*, 69*, 81*, 140, 157, 162, 166, 169, 175(2), 184(2), 198, 213,
                  218, 219
```

Trees number 5, 11, 17, 22, 31, 40, 69, 78, 86, 95:

```
            /-58------ Other lepidosauromorphs
         /-57
      /-56  \--------- Saurosternon
   /-55  \------------ Paliguana
/-54  \--------------- Palaeagama
|  \------------------ Prolacerta
\--------------------- Younginiformes
```

Apomorphy lists:

```
Node 54: 95*, 129*, 136(0), 138*, 139*, 144*, 146, 158*, 159, 163(0), 164(0),
            172(2)*, 173*, 179, 181, 192*, 195, 201*, 225*
Node 55: 27(0)*, 36(0)*, 144(2)*, 147*, 174(0), 180*, 186*, 190*, 200(0)*,
            206*, 214*, 217
Node 56: 106*
Node 57: 24(3)*, 28(0)*, 32*, 141(3)*, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Paliguana: 138(0)*, 139(0)*, 156(0), 173(0)*
Prolacerta: 54*, 69*, 81*, 140, 157, 162, 166, 169, 175(2), 184(2), 198, 213,
            218, 219
```

Trees number 6, 12, 18, 23, 32, 41, 61, 62, 63, 72:

```
          /-58-------- Other lepidosauromorphs
      /--57
      |   \----------- Saurosternon
   /-56           /--- Paliguana
/-55  \----------54--- Palaeagama
|  \------------------ Prolacerta
\--------------------- Younginiformes
```

Apomorphy lists:

```
Node 55: 95*, 129*, 136(0), 138*, 139*, 144*, 146, 158*, 159, 163(0), 164(0),
            172(2)*, 173*, 179, 181, 192*, 195, 201*, 225*
Node 56: 27(0)*, 36(0)*, 144(2)*, 147, 174(0), 180*, 186*, 190*, 200(0)*, 206*,
            214*, 217
Node 57: 24(3)*, 28(0)*, 32*, 106, 141(3)*, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Node 54: 138(0)*, 139(0)*, 156(0)*, 173(0)*
Prolacerta: 54*, 69*, 81*, 140, 157, 162, 166, 169, 175(2), 184(2), 198, 213,
            218, 219
```

Trees number 7, 13, 19, 24, 33, 42, 68, 77, 85, 94:

```
            /-58------ Other lepidosauromorphs
         /-57
      /-56  \--------- Saurosternon
   /-55  \------------ Palaeagama
/-54  \--------------- Paliguana
|  \------------------ Prolacerta
\--------------------- Younginiformes
```

Apomorphy lists:

```
Node 54: 95*, 129*, 136(0), 138*, 139*, 144*, 146, 158*, 159, 163(0), 164(0),
            172(2)*, 173*, 179, 181, 192*, 195, 201*, 225*
Node 55: 27(0)*, 36(0)*, 144(2)*, 147, 174(0), 180*, 186*, 190*, 200(0)*, 206*,
            214*, 217
Node 56: 141(3)*
Node 57: 24(3)*, 28(0)*, 32*, 106, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Paliguana: 138(0)*, 139(0)*, 156(0), 173(0)*
Prolacerta: 54*, 69*, 81*, 140, 157, 162, 166, 169, 175(2), 184(2), 198, 213,
            218, 219
```

Trees number 8, 14, 20, 25, 34, 43, 66, 75, 83, 92:

```
            /-58------ Other lepidosauromorphs
         /-57
      /-56  \--------- Saurosternon
   /-55  \------------ Palaeagama
/-54  \--------------- Prolacerta
|  \------------------ Paliguana
\--------------------- Younginiformes
```

```
Apomorphy lists:

Node 54: 95*, 129*, 136(0), 144(2), 146, 147*, 158*, 159, 163(0), 164(0),
            172(2)*, 174(0)*, 179, 181*, 192*, 195*, 201*, 217*, 225*
Node 55: 138, 139, 156*, 173, 218*
Node 56: 27(0)*, 36(0)*, 141(3)*, 180*, 186*, 190*, 200(0)*, 206*, 214*
Node 57: 24(3)*, 28(0)*, 32*, 106, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Prolacerta: 54*, 69*, 81*, 140, 144, 147(0)*, 157, 162, 166, 169, 174*, 175(2),
            184(2), 198, 213, 217(0)*, 219


Trees number 9, 15, 21, 26, 35, 44, 67, 76, 84, 93:

          /-58-------- Other lepidosauromorphs
      /--57       /--- Paliguana
   /-56    \------54--- Saurosternon
/-55  \--------------- Palaeagama
|  \------------------ Prolacerta
\--------------------- Younginiformes

Apomorphy lists:

Node 55: 95*, 129*, 136(0), 138*, 139*, 144*, 146, 158*, 159, 163(0), 164(0),
            172(2)*, 173*, 179, 181, 192*, 195, 201*, 225*
Node 56: 27(0)*, 36(0)*, 144(2)*, 147*, 174(0), 180*, 186*, 190*, 200(0)*,
            206*, 214*, 217
Node 57: 106
Node 58: 24(3)*, 28(0), 32*, 132(0)*, 141(3)*, 188*, 191, 199*, 204, 208*,
            209*, 210*, 216
Node 54: 110*, 138(0)*, 139(0)*, 156(0)*, 173(0)*, 192(0)*, 212(0)*
Prolacerta: 54*, 69*, 81*, 140, 157, 162, 166, 169, 175(2), 184(2), 198, 213,
            218, 219


Trees number 27, 36, 45, 49, 53, 57, 64, 73, 81, 90:

          /-58-------- Other lepidosauromorphs
      /--57
   /-56    \----------- Saurosternon
   |  \--------------- Prolacerta
/-55               /--- Paliguana
|  \-------------54--- Palaeagama
\--------------------- Younginiformes

Apomorphy lists:

Node 55: 95*, 129*, 136(0), 144(2), 146, 147*, 158*, 159, 163(0), 164(0),
            172(2)*, 174(0)*, 179, 181*, 192*, 195*, 201*, 217*, 225*
Node 56: 24(3)*, 138, 139, 156*, 166*, 173, 218*
Node 57: 27(0)*, 28(0)*, 32*, 36(0)*, 106, 141(3)*, 180*, 186*, 190, 200(0)*,
            206*, 214, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Prolacerta: 54*, 69*, 81*, 140, 144, 147(0)*, 157, 162, 169, 174*, 175(2),
            184(2), 198, 213, 217(0)*, 219
```

```
Trees number 28, 37, 46, 50, 54, 58, 71, 80, 88, 97:

            /-58------ Other lepidosauromorphs
         /-57
      /-56  \--------- Saurosternon
   /-55  \------------ Prolacerta
/-54  \--------------- Paliguana
|  \------------------ Palaeagama
\--------------------- Younginiformes

Apomorphy lists:

Node 54: 95*, 129*, 136(0)*, 144(2), 146*, 147*, 158*, 159*, 163(0), 164(0)*,
            172(2)*, 174(0), 179*, 181*, 192*, 195*, 201*, 217, 225*
Node 56: 24(3)*, 138, 139, 156*, 166*, 173, 218*
Node 57: 27(0)*, 28(0)*, 32*, 36(0)*, 106, 141(3)*, 180*, 186*, 190, 200(0)*,
            206*, 214, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Prolacerta: 54*, 69*, 81*, 140, 144, 147(0)*, 157, 162, 169, 174, 175(2),
            184(2), 198, 213, 217(0), 219


Trees number 29, 38, 47, 51, 55, 59, 89, 98, 99, 100:


          /-58-------- Other lepidosauromorphs
      /--57
      |   \----------- Saurosternon
   /-56           /--- Palaeagama
/-54  \----------55--- Prolacerta
|  \------------------ Paliguana
\--------------------- Younginiformes

Apomorphy lists:

Node 54: 95*, 129*, 136(0), 144(2), 146, 147*, 158*, 159, 163(0), 164(0),
            172(2)*, 174(0), 179, 181*, 192*, 195*, 201*, 217, 225*
Node 56: 138, 139, 156*, 173, 218*
Node 57: 24(3)*, 27(0)*, 28(0)*, 32*, 36(0)*, 106*, 141(3)*, 180*, 186*, 190,
            200(0)*, 206*, 214, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Node 55: 54*, 69*, 81*, 140*, 147(0)*, 157*, 162*, 169*, 175(2)*, 184(2)*, 213*
Prolacerta: 144, 166, 174, 198, 217(0), 219


Trees number 30, 39, 48, 52, 56, 60, 70, 79, 87, 96:

            /-58------ Other lepidosauromorphs
         /-57
      /-56  \--------- Saurosternon
   /-55  \------------ Prolacerta
/-54  \--------------- Palaeagama
|  \------------------ Paliguana
\--------------------- Younginiformes
```

```
Apomorphy lists:

Node 54: 95*, 129*, 136(0), 144(2), 146, 147*, 158*, 159, 163(0), 164(0),
            172(2)*, 174(0), 179, 181*, 192*, 195*, 201*, 217, 225*
Node 55: 138*, 139*, 156*, 173*, 218*
Node 56: 24(3)*, 166*
Node 57: 27(0)*, 28(0)*, 32*, 36(0)*, 106, 141(3)*, 180*, 186*, 190, 200(0)*,
            206*, 214, 216*
Node 58: 132(0)*, 188*, 191, 199*, 204, 208*, 209*, 210*
Saurosternon: 110, 192(0)*, 212(0)
Prolacerta: 54*, 69*, 81*, 140, 144, 147(0)*, 157, 162, 169, 174, 175(2),
              184(2), 198, 213, 217(0), 219
```

Analysis 2: *Palaeagama* and *Paliguana* excluded; designated outgroup: Younginiformes and *Prolacerta*)

```
Data matrix has 34 taxa, 225 characters
All uninformative characters ignored
Valid character-state symbols: 012345
Missing data identified by '?'
Gaps identified by '-', treated as "missing"

The following taxa have been deleted:
   Paliguana
   Palaeagama

Designated outgroup taxa:
   Prolacerta
   Younginiformes

Current status of all characters:
   Characters 138,139, 156, and 173 are uninformative (ignored)

Heuristic search settings:
   Addition sequence: random
      Number of replicates = 100
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

   Random-addition-sequence replicate 1 (seed = 1):
     0 trees in memory at start of replicate
       6 trees found (length=1120)
   Random-addition-sequence replicate 2 (seed = 1564144539):
     6 trees in memory at start of replicate
       minimal tree (length=1120) identical to tree #1,
         skipping to next replicate
   Random-addition-sequence replicate 3 (seed = 737371389):
     6 trees in memory at start of replicate
       4 additional trees found (length=1120)

     10th shortest tree found at replicate number 3
```

```
Heuristic search completed
   Total number of rearrangements tried = 5667169
   Length of shortest tree(s) found = 1120
   Number of trees retained = 10

Tree description:
   Unrooted tree(s) rooted using outgroup method
   Character-state optimization: Accelerated transformation (ACCTRAN)

Tree length = 1120
Consistency index (CI) = 0.716
Homoplasy index (HI) = 0.750
Retention index (RI) = 0.611
Rescaled consistency index (RC) = 0.438

Strict consensus of 10 trees:

                                                  /---- Agamidae
                                               /-57---- Chamaeleontidae
                             /----------------56------- Iguanidae
                             |                    /---- Amphisbaenia
                             |  /----------------33---- Dibamidae
                             |  |                  ---- Anguidae
                             |  +----------------34---- Xenosauridae
                          --55  |                 /---- Cordylidae
                         |   |  |              /-35---- Scincidae
                         |   |  |      /------36------- Tepexisaurus
                         |   |  |      |           ---- Gymnophthalmidae
                         |   |  |   /-40       /-37---- Teiidae
                         |   \-45   |  |   /--38------- Lacertidae
                         |      +--42  \--39----------- Xantusiidae
                     /--54      |   |             /---- Gekkonidae
                     |   |      |   \------------41---- Pygopodidae
                     |   |      |              /------- Helodermatidae
                     |   |      +-------------44  /---- Lanthanotus
                     |   |      |              \-43---- Varanus
                  /-53   |      +---------------------- Serpentes
                  |  |   |      \---------------------- Parviraptor
                  |  |   \----------------------------- Huehuecuetzpalli
              /--52  |                            /---- Bavarisaurus
              |   |  \---------------------------46---- Eichstaettisaurus
          /--51   |                               \---- Ardeosaurus
          |   |   \------------------------------------ Tamaulipasaurus
       /-50   \---------------------------------------- Marmoretta
   /--49  \-------------------------------------------- Rhynchocephalia
/-48   \----------------------------------------------- Kuehneosauridae
|  \--------------------------------------------------- Saurosternon
\------------------------------------------------------ OUTGROUP

Statistics derived from consensus tree:

     Component information (consensus fork) = 25 (normalized = 0.833)
     Nelson-Platnick term information = 281
     Nelson-Platnick total information = 306
     Mickevich's consensus information = 0.404
     Colless weighted consensus fork (proportion max. information) = 0.618
     Schuh-Farris levels sum = 3339 (normalized = 0.673)
     Rohlf's CI(1) = 0.834
     Rohlf's -ln CI(2) = 89.337 (CI(2) = 1.59e-39)
```

```
Consensus tree description:

Tree length = 1144
Consistency index (CI) = 0.701
Homoplasy index (HI) = 0.755
Retention index (RI) = 0.582
Rescaled consistency index (RC) = 0.408

Apomorphy lists:

Node 48: 24(3)*, 27(0)*, 28(0)*, 32*, 36(0)*, 95*, 141(3)*, 144(2)*, 147*,
       174(0)*, 180*, 190, 200(0)*, 206*, 214, 216*, 217*
Node 49: 132(0)*, 188*, 191, 192*, 199*, 204, 208*, 209*, 210*
Node 50: 6*, 20*, 52*, 60*, 75(2)*, 76, 77*, 92*, 129*, 135, 149*, 153*, 158*,
       166*, 198, 199(2)*, 201*, 202, 203, 205, 213(2)*
Node 51: 81(2)*, 82*, 83*, 98*, 99*, 107(2)*, 121*, 129(2)*, 137*, 143*, 150,
       155*, 160*, 161*, 162, 177, 178*, 184*, 185, 189*, 196*, 197*, 204(2)*,
       207*, 213(3)*, 214(2)*, 224
Node 52: 26(2)*, 28, 45*, 48, 55*, 76(2)*, 85*, 87*, 148, 152*, 154*, 215*
Node 53: 23, 32(0)*, 34*, 41*, 52(0)*, 64, 136, 142, 145, 157*, 158(2)*
Node 54: 15*, 26(0)*, 94, 102, 104*, 182*, 193*, 194*
Node 55: 1, 87(0)*, 89, 91(2)*, 211
Node 56: 7*, 8, 12*, 18, 92(0)*, 107, 127*, 175*, 195(2)*
Node 57: 64(0), 77(2), 78(3)
Agamidae: 24, 73, 88(2), 141(2), 170(0)
Chamaeleontidae: 35, 44, 61(0), 94(0), 95(3), 96, 98(0), 100, 103, 106(2),
       121(0)*, 126, 147(0), 159(0)
Node 45: 6(0), 9, 10*, 13, 15(0)*, 17, 31, 36*, 37, 38, 41(2)*, 46, 53*, 54*,
       67, 68, 72, 78, 88, 93(2), 101, 108, 114, 117*, 118, 120*, 121(4)*, 122,
       130, 131*, 141(2)*, 165*, 223
Node 33: 4, 16*, 21*, 25, 29*, 32, 39, 42*, 50(2)*, 52(2)*, 64(2)*, 65*, 68(0),
       90(2)*, 94(0)*, 95(3), 98(0)*, 103*, 106(2)*, 117(0)*, 120(0)*, 133,
       162(0), 175, 176*, 179(0)*, 195(0)*, 219*, 221*
Amphisbaenia: 5, 13(0), 31(0), 122(2), 125, 134, 137(3), 153(0), 159(0),
       179(2)*, 223(2)
Dibamidae: 10(0)*, 26(2)*, 40, 46(0), 48(0), 55(2)*, 71, 90(3)*, 96, 121(0)*,
       123(2), 129(0), 132
Node 34: 7*, 10(0)*, 24(0), 33, 50*, 55(0)*, 58, 60(0)*, 61(0), 81*, 91(0)*,
       99(0)*, 111, 112, 121(2), 165(0)*, 221
Anguidae: 71, 108(2), 110, 164, 165(2)*
Xenosauridae: 18, 68(0), 113(2), 131(0)*
Node 42: 6*, 19(2)*, 51(0), 53(0)*, 54(0)*, 55(2)*, 61(0), 71*, 78(0), 81*,
       82(0)*, 83(0), 88(0)*, 99(0)*, 120(0)*, 121*, 123, 124*, 128*, 141(3)*,
       165(2)*, 167*
Node 40: 10(0)*, 22, 64(2)*, 108(2), 113(2), 122(2), 124(2)*, 222*, 223(2)
Node 36: 69, 87, 94(0)*, 112*
Node 35: 60(0)*, 88*, 110, 111, 132*, 164
Cordylidae: 19, 123(0,2)2, 141(2)
Scincidae: 17(2), 18, 40, 125, 128(0)*, 163
Tepexisaurus: 36(0), 42, 48(0), 78(1,2), 93, 97, 108(0), 152(0), 182(0)
Node 39: 12*, 21, 23(0)*, 66, 67(0), 68(0), 71(0)*, 72(0), 88(2)*, 90*, 105*,
       115, 116
Node 38: 34(2), 45(0)*, 60(0), 64*, 74, 80, 87(2), 121(3)*, 124*, 126*, 222(0)*
Node 37: 12(0)*, 19(0)*, 23*, 51*, 66(2), 82*, 98(2), 106(2), 121(4)*, 127,
       163*, 167(0)
Gymnophthalmidae: 11, 125
Teiidae: 9(0), 42, 43, 108, 165(0), 166(0), 175(2)
Lacertidae: 22(0), 33, 50*, 99, 112, 123(2), 141(2), 164
```

Xantusiidae: 19, 25, 28(0), 35, 43, 49, 52(2), 61, 65, 109
Node 41: 16, 26(2)*, 28(0)*, 29, 32*, 35*, 49*, 52(2), 70, 91*, 109*, 118(0), 119, 125, 129, 195(2)*
Gekkonidae: 89(0), 97, 117(0)*, 131(0)*
Pygopodidae: 72(0), 95(3), 103, 162(0), 175
Node 44: 2*, 4(2)*, 5*, 14*, 16*, 25, 42, 50*, 56, 58*, 59, 62, 63, 78(2)*, 79, 84, 92(0), 111, 112, 126, 131(0)*, 133(2), 162(0), 175(2), 221
Helodermatidae: 34(2), 51(0), 82(0), 98(0), 104(2), 113, 121(3)*, 127, 163, 182(0)
Node 43: 3, 27, 57, 58(2)*, 60(0), 86, 94(2), 95(2)*, 141(3)*
Lanthanotus: 10(0)*, 61(2), 64(3), 76, 95(3)*, 104(3)
Varanus: 5(0)*, 9(0), 16(0)*, 24(0), 29, 33, 39, 50(0)*, 81(0), 98(2), 108(0), 116, 121(5)*, 166(0), 174, 195(2)
Serpentes: 13(0), 17(0), 26(2)*, 30, 44, 53(0)*, 54(0)*, 55(2)*, 59, 61(2), 62, 78(2)*, 87(2), 92(0), 117(0)*, 121(5)*, 129, 134, 137(2), 164(2), 175(2), 216(0)
Parviraptor: 2, 4, 20(0), 24(0), 28(0), 60(0), 62, 87, 88(2), 137(2), 163, 174, 181(0), 216(0)
Huehuecuetzpalli: 24, 25, 26*, 55(0)*, 85(0)*, 95(2)*, 111, 166(0), 174
Node 46: 4*, 7*, 13, 20(0)*, 24(0), 31, 43*, 71*, 93, 106(2), 163
Bavarisaurus: 25, 26(0)*, 85(0)*, 133(2), 137(0), 166(0), 192(0), 211
Eichstaettisaurus: 4(0)*, 18, 43(0)*, 51(0), 93(2), 97, 107, 199
Ardeosaurus: 6(0), 7(0)*, 20*, 42, 113(2), 208(0)
Tamaulipasaurus: 6(0)*, 12, 16, 25, 133, 134, 137(3)*, 141*, 151, 171, 179(2)
Marmoretta: 2, 4, 21*, 30, 50*, 56, 75(0)*, 92(0)*, 137(2)*, 147(0)*, 153(0)*, 159(0), 168, 216(0), 217(0)*, 225*
Rhynchocephalia: 24(0)*, 57, 141(0,1)*, 144*, 151, 163, 169(1,2,3), 172(1,2)*, 175, 176, 187(2)*, 192(0)*, 195(0)
Kuehneosauridae: 71, 89, 142, 148, 218*
Saurosternon: 110, 212(0)

Two hypothesis of character distribution within Ardeosauridae:

Trees number 1, 2, 3, 7, 8

```
      /--- Bavarisaurus
  /--50--- Eichstaettisaurus
-51------- Ardeosaurus
```

Apomorphy lists:

Node 51: 4*, 13, 24(0), 31, 43*, 71*, 93, 106(2)*,163

Node 50: 7, 20(0), 51(0)*, 85(0)*, 97*
Bavarisaurus: 25, 26(0), 133(2), 137(0), 166(0), 192(0), 211
Eichstaettisaurus: 4(0)*, 18, 43(0)*, 93(2), 107, 199
Ardeosaurus: 6(0)*, 42, 113(2), 208(0)

Trees number 4, 5, 6, 9, 10

```
      /--- Bavarisaurus
  /--50--- Ardeosaurus
-51------- Eichstaettisaurus
```

Apomorphy lists:

Node 51: 7*, 13, 20(0)*, 24(0), 31, 71*, 93*, 106(2), 163
Node 50: 4, 42*, 43, 133(2)*, 211*
Bavarisaurus: 25, 26(0), 85(0)*, 137(0), 166(0), 192(0)
Ardeosaurus: 6(0), 7(0)*, 20*, 113(2), 208(0)
Eichstaettisaurus: 18

Five hypothesis of character distribution within Scleroglossa:

Trees number 1 and 4:

```
                        /--- Amphisbaenia
      /---------------33--- Dibamidae
  /--40      /-------------- Anguioidea
  |    ¦  /-38   /---------- Varanoidea
  |    \-39  \--37---------- Parviraptor
-49        \---------------- Serpentes
  |
  \------------------------ Scincogekkonomorpha
```

Trees number 1 and 4:

Apomorphy list:

Node 49: 9, 10*, 13*, 15(0)*, 17*, 31, 36*, 37, 38, 41(2)*, 46, 55(2)*, 67,
68*, 72*, 93(2), 101, 108, 114, 118*, 122, 130, 131*, 165(2)*, 223
Node 40: 6(0), 78*, 88, 121(0)*, 141(2), 221*
Node 33: 4, 16*, 21*, 25, 29*, 32, 39, 42*, 50(2)*, 52(2)*, 64(2)*, 65*,
68(0)*, 90(2)*, 94(0)*, 95(3), 98(0)*, 103*, 106(2)*, 133, 162(0),
176*, 179(0)*, 195(0)*, 219*
Amphisbaenia: 5, 13(0)*, 26(0,1), 31(0), 55(0,1)*, 121(4)*, 122(2), 125, 134,
137(3), 153(0), 159(0), 179(2)*, 223(2)
Dibamidae: 10(0)*, 40, 46(0), 48(0), 71, 90(3)*, 96, 123(2), 129(0), 132
Node 39: 59*, 62*, 78(2)*, 91(0)*, 92(0)*, 120, 121(5)*, 131(0)*, 175(2)*
Node 38: 14*, 24(0)*, 26(0), 50, 53, 54, 55(0)*, 58, 60(0), 111, 112, 117
Anguioidea: 7*, 10(0)*, 33, 59(0)*, 61(0), 62(0)*, 78*, 81*, 99(0)*, 121(2),
175(0)*
Node 37: 2, 4*, 16*, 55*, 56*, 63*, 126*, 133(2)*, 163*, 165
Varanoidea: 4(2)*, 5*, 24(3)*, 25, 42, 79, 84, 162(0)
Parviraptor: 20(0), 28(0), 87, 88(2), 92*, 137(2), 174, 181(0), 216(0), 221(0)*
Serpentes: 13(0)*, 17(0)*, 30, 44, 61(2), 87(2), 129, 134, 137(2), 164(2),
216(0), 221(0)*
Scincogekkonomorpha: 19(2)*, 51(0), 61(0), 71*, 81*, 82(0)*, 83(0)*, 99(0)*,
117*, 123, 124*, 128*, 167*, 175(0)*

Trees number 2 and 5:

```
                         /--- Amphisbaenia
          /------------33--- Dibamidae
      /-39  /-------------- Anguioidea
      |  \-38   /---------- Varanoidea
  /--40     \--37---------- Parviraptor
  |   \-------------------- Serpentes
-49
  \------------------------ Scincogekkonomorpha
```

Apomorphy lists:

Node 49: 9, 10*, 13*, 15(0)*, 17*, 31, 36*, 37, 38, 41(2)*, 46, 55(2)*, 67, 68, 72*, 93(2), 101, 108, 114, 118*, 122, 130, 131*, 165(2)*, 223
Node 40: 6(0), 78*, 88, 120*, 121(4)*, 141(2)*, 175(2)*
Node 39: 4*, 14*, 16*, 26(0)*, 50*, 53*, 54*, 55(0)*, 221
Node 33: 21*, 25, 29*, 32, 39, 42*, 50(2)*, 52(2)*, 64(2)*, 65*, 68(0), 90(2)*, 94(0)*, 95(3), 98(0)*, 103*, 106(2)*, 120(0)*, 133, 162(0), 175, 176*, 179(0)*, 195(0)*, 219*
Amphisbaenia: 5, 13(0)*, 31(0), 122(2), 125, 134, 137(3), 153(0), 159(0), 179(2)*, 223(2)
Dibamidae: 10(0)*, 26(2)*, 40, 46(0), 48(0), 55(2)*, 71, 90(3)*, 96, 121(0)*, 123(2), 129(0), 132
Node 38: 24(0)*, 58, 60(0), 91(0)*, 111, 112, 117, 131(0)*
Anguioidea: 4(0)*, 7*, 10(0)*, 16(0)*, 33, 61(0), 81*, 99(0)*, 121(2), 175(0)*
Node 37: 2, 55*, 56*, 59*, 62, 63*, 78(2)*, 126*, 133(2)*, 163*, 165
Varanoidea: 4(2)*, 5*, 24(3)*, 25, 42, 79, 84, 92(0), 162(0)
Parviraptor: 20(0), 28(0), 87, 88(2), 137(2), 174, 181(0), 216(0), 221(0)
Serpentes: 13(0)*, 17(0)*, 30, 44, 59, 61(2), 62, 78(2)*, 87(2), 92(0), 121(5)*, 129*, 134, 137(2), 164(2), 216(0)
Scincogekkonomorpha: 19(2)*, 51(0), 61(0), 71*, 81*, 82(0)*, 83(0)*, 99(0)*, 117*, 123, 124*, 128*, 167*

Trees number 3 and 6:

```
                        /--- Amphisbaenia
      /-39------------33--- Dibamidae
      |   \-38-------------- Anguioidea
      |       \--37---------- Varanoidea
  /--48           \---------- Parviraptor
  |   |
-49   \-------------------- Scincogekkonomorpha
  |
  \------------------------ Serpentes
```

Apomorphy lists:

Node 49: 6(0)*, 9, 10*, 15(0)*, 31*, 36*, 37, 38, 41(2)*, 46*, 55(2)*, 67, 68, 72, 88*, 93(2), 101*, 108*, 114*, 118, 122, 130, 131*, 165(2)*, 223
Node 48: 13, 16*, 17, 26(0)*, 92*, 117*
Node 39: 4*, 14*, 50*, 53*, 54*, 55(0)*, 78, 121(4), 141(2), 221
Node 33: 21*, 25, 29*, 32, 39, 42*, 50(2)*, 52(2)*, 64(2)*, 65*, 68(0), 90(2)*, 94(0)*, 95(3), 98(0)*, 103*, 106(2)*, 117(0)*, 133, 162(0), 175, 176*, 179(0)*, 195(0)*, 219*
Amphisbaenia: 5, 13(0), 31(0), 122(2), 125, 134, 137(3), 153(0), 159(0), 179(2)*, 223(2)
Dibamidae: 10(0)*, 26(2)*, 40, 46(0), 48(0), 55(2)*, 71, 90(3)*, 96, 121(0), 123(2), 129(0), 132
Node 38: 24(0)*, 58, 60(0), 91(0)*, 111, 112, 120, 131(0)*
Anguioidea : 4(0)*, 7*, 10(0)*, 16(0)*, 33, 61(0), 81*, 99(0)*, 121(2)
Node 37: 2, 55*, 56*, 59*, 62, 63*, 78(2)*, 126*, 133(2)*, 163*, 165, 175(2)*
Varanoidea: 4(2)*, 5*, 24(3)*, 25, 42, 79, 84, 92(0), 162(0)
Parviraptor: 20(0), 28(0), 87, 88(2), 137(2), 174, 181(0), 216(0), 221(0)
Scincogekkonomorpha: 6*, 19(2)*, 51(0), 61(0), 71*, 81*, 82(0)*, 83(0), 88(0)*, 99(0)*, 123, 124*, 128*, 167*
Serpentes: 30, 44, 59, 61(2), 62, 78(2), 87(2), 120, 121(5), 129*, 134, 137(2), 164(2), 175(2), 216(0)

Trees number 7 and 9:

```
                      /---- Amphisbaenia
               /-----33---- Dibamidae
          /--36------------ Varanoidea
       /-38           /---- Serpentes
  /--40   \----------37---- Parviraptor
  |   \-------------------- Anguioidea
-49
  \------------------------ Scincogekkonomorpha
```

Apomorphy lists:

Node 49: 9, 13, 15(0)*, 17, 31, 36*, 37, 38, 41(2)*, 46, 67, 68, 72*, 93(2), 101, 108, 114, 117*, 118*, 122, 130, 131*, 165(2)*, 223
Node 40: 6(0)*, 50*, 53, 54, 78*, 88, 120, 121(2)*, 141(2), 221*
Node 38: 2*, 4*, 10, 55, 59*, 61*, 62*, 78(2)*, 81(2), 95(3)*, 98(0)*, 99*, 117(0)*, 121(4)*, 165, 175(2)
Node 36: 5*, 14*, 16, 25, 42, 133*, 162(0)
Node 33: 2(0)*, 21*, 29*, 32, 39, 50(2)*, 52(2)*, 59(0)*, 62(0)*, 64(2)*, 65*, 68(0), 78*, 90(2)*, 94(0)*, 103*, 106(2)*, 120(0), 175, 176*, 179(0)*, 195(0)*, 219*
Amphisbaenia: 13(0), 31(0), 122(2), 125, 134, 137(3), 153(0), 159(0), 179(2)*, 223(2)
Dibamidae: 5(0)*, 10(0), 26(2)*, 40, 46(0), 48(0), 55(2), 71, 90(3)*, 96, 121(0)*, 123(2), 129(0), 132
Varanoidea: 4(2)*, 56, 58*, 63, 79, 84, 92(0), 111, 112, 117*, 126, 131(0)*, 133(2)*
Node 37: 17(0)*, 26(2)*, 28(0)*, 44*, 50(0)*, 61(2)*, 87*, 121(5)*, 129*, 137(2), 164(2)*, 216(0), 221(0)*
Serpentes: 4(0)*, 13(0), 30, 53(0), 54(0), 55(2), 87(2)*, 92(0), 134
Parviraptor: 20(0), 24(0), 60(0), 88(2), 163, 174, 181(0)
Anguioidea: 7*, 24(0), 33, 58, 60(0)*, 91(0)*, 111, 112
Scincogekkonomorpha: 19(2)*, 51(0), 55(2), 71*, 82(0)*, 83(0)*, 123, 124*, 128*, 167*

Trees number 8 and 10:

```
                      /---- Amphisbaenia
          /----------33---- Dibamidae
       /-38   /------------ Varanoidea
       |  \--37       /---- Serpentes
  /--40       \------36---- Parviraptor
  |   \-------------------- Anguioidea
-49
  \------------------------ Scincogekkonomorpha
```

Trees number 8 and 10:

Apomorphy lists:

Node 49: 9, 13, 15(0)*, 17, 31, 36*, 37, 38, 41(2)*, 46, 67, 68*, 72*, 93(2), 101, 108, 114, 117*, 118*, 122, 130, 131*, 165(2)*, 223
Node 40: 6(0)*, 50*, 53, 54, 78, 88, 120*, 121(0)*, 141(2), 221
Node 38: 4*, 10*, 16*, 25*, 42*, 55*, 61*, 81(2), 95(3)*, 98(0)*, 99, 117(0)*, 162(0)*, 165*, 175*
Node 33: 21*, 29*, 32, 39, 50(2)*, 52(2)*, 64(2)*, 65*, 68(0)*, 90(2)*, 94(0)*, 103*, 106(2)*, 120(0)*, 133, 176*, 179(0)*, 195(0)*, 219*

```
Amphisbaenia: 5, 13(0), 31(0), 121(4)*, 122(2), 125, 134, 137(3), 153(0),
            159(0), 179(2)*, 223(2)
Dibamidae: 10(0)*, 26(2)*, 40, 46(0), 48(0), 55(2), 71, 90(3)*, 96, 123(2),
            129(0), 132
Node 37: 2, 59, 62, 78(2), 92(0)*, 121(5)*, 126*, 131(0)*, 175(2)*
Varanoidea: 4(2)*, 5*, 14*, 56, 58*, 63, 79, 84, 111, 112, 117*, 133(2)
Node 36: 16(0)*, 17(0)*, 25(0)*, 26(2)*, 28(0)*, 42(0)*, 44*, 50(0)*, 61(2)*,
            87*, 129*, 137(2), 162*, 164(2)*, 216(0), 221(0)
Serpentes: 4(0)*, 13(0), 30, 53(0), 54(0), 55(2), 87(2)*, 134
Parviraptor: 20(0), 24(0), 60(0), 88(2), 92*, 163, 174, 181(0)
Anguioidea: 7*, 24(0), 33, 58, 60(0)*, 91(0)*, 111, 112, 121(2)*
Scincogekkonomorpha: 19(2)*, 51(0), 55(2), 71*, 82(0)*, 83(0)*, 123, 124*,
            128*, 167*
```

Bootstrap analysis:

```
Bootstrap method with heuristic search:
   Starting seed = 1
   Number of bootstrap replicates = 100
   Bootstrap sampling over non-excluded/non-ignored characters only
   Addition sequence: random
      Number of replicates = 5
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 1000
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism

Warning. Tree can not be rooted such that specified ingroup is monophyletic.
```

```
Bootstrap 50% majority-rule consensus tree

                                                 /----- Agamidae(1)
                                           /-84--+----- Chamaeleontidae(5)
                                /----84----+----------- Iguanidae(10)
                                +---------------------- Amphisbaenia(2)
                                |                /----- Anguidae(3)
                                +-------67-------+----- Xenosauridae(19)
                                |                /----- Cordylidae(4)
                                |          /-75--+----- Scincidae(14)
                                +----57----+----------- Tepexisaurus(21)
                                +---------------------- Dibamidae(6)
                                |                /----- Gekkonidae(7)
                                +-------86-------+----- Pygopodidae(13)
                                |                /----- Gymnophthalmidae(8)
                           /-68-+          /-95--+----- Teiidae(16)
                           |    |     /-69-+----------- Lacertidae(11)
                           |    +-66--+---------------- Xantusiidae(18)
                           |    |          /----------- Helodermatidae(9)
                           |    +----97----+     /----- Lanthanotus(12)
                           |    |          \-87--+----- Varanus(17)
                      /-73-+    +---------------------- Serpentes(15)
                      |    |    +---------------------- Huehuecuetzpalli(20)
                      |    |    +---------------------- Bavarisaurus(22)
                      |    |    +---------------------- Eichstaettisaurus(23)
                /-58--+    |    +---------------------- Ardeosaurus(24)
                |     |    |    \---------------------- Parviraptor(25)
           /-54-+     |    \--------------------------- Tamaulipasaurus(30)
           |    |     \-------------------------------- Marmoretta(29)
     /-58--+    \-------------------------------------- Rhynchocephalia(26)
     |     \------------------------------------------- Kuehneosauridae(27)
/----+------------------------------------------------- Saurosternon(28)
|    \------------------------------------------------- Younginiformes(32)
\------------------------------------------------------ Prolacerta(31)
```

Appendix 6.5

Analysis of previously published data matrices

General procedures:

For Estes et al. (1988) and Clark and Hernández (1994) analysis for the Squamata:

```
Heuristic search
   Settings:
   Addition sequence: random
      Number of replicates = 100
      Starting seed = 1
   Tree-bisection-reconnection (TBR) branch-swapping performed
   MULPARS option in effect
   Steepest descent option not in effect
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism
   All uninformative characters ignored
```

For Gauthier et al (1988a), Evans (1991), and Clark and Hernández (1994) analysis within basal lepidosauromorphs:

```
Branch-and-bound search
   Settings:
   Initial upper bound: unknown (compute via stepwise)
   Addition sequence: furthest
   Initial MAXTREES setting = 100
   Branches having maximum length zero collapsed to yield polytomies
   Topological constraints not enforced
   Trees are unrooted
   Multi-state taxa interpreted as polymorphism
   All uninformative characters ignored
```

Estes et al. (1988):

Analysis 1: All taxa included

```
Data matrix has 29 taxa, 148 characters

Designated outgroup taxa: Estes et al.' average outgroup

Current status of all characters: Characters are ordered
      Character 1, 11, 14, 15, 21, 29, 33, 50, 80, 93, 104, 117, 119,
            and 125 are uninformative (ignored)

Tree description:
      Tree length = 712
      Consistency index (CI) = 0.756
      Homoplasy index (HI) = 0.779
      Retention index (RI) = 0.613
      Rescaled consistency index (RC) = 0.463
```

```
Strict consensus of 4 trees:
                                                  /-------- Agamidae
                                         /--------+-------- Chamaeleontidae
        /--------------------------------+----------------- Iguanidae
        |                                         /-------- Anguidae
        |        /--------------------------------+-------- Xenosauridae
        |        |                                /-------- Cordylidae
        |        |        /-----------------------+-------- Scincidae
/-------+        |        |                       /-------- Gymnophthalmidae
|       |        +--------+              /--------+-------- Teiidae
|       |        |        |      /-------+----------------- Lacertidae
|       |        |        \------+------------------------- Xantusiidae
|       \--------+                       /----------------- Dibamidae
|                +-----------------------+        /-------- Gekkonidae
|                |                       \--------+-------- Pygopodidae
|                |                       /----------------- Helodermatidae
|                +-----------------------+        /-------- Lanthanotus
|                |                       \--------+-------- Varanus
|                +----------------------------------------- Amphisbaenia
|                \----------------------------------------- Serpentes
\---------------------------------------------------------- Average Outgroup
```

Analysis 2: Dibamidae, Amphisbaenia. and Serpentes deleted

```
Data matrix has 26 taxa, 148 characters

Designated outgroup taxa: Estes et al.'s average outgroup

Current status of all characters: Characters are ordered
      Characters 1, 4, 11, 14, 15, 21, 29, 33, 35, 43, 47, 50, 51, 70,
            72, 80, 93, 101, 104, 107, 110, 115, 117, 119, 125, and 148
            are uninformative (ignored)

Tree description:
      Tree length = 561
      Consistency index (CI) = 0.800
      Homoplasy index (HI) = 0.745
      Retention index (RI) = 0.691
      Rescaled consistency index (RC) = 0.553
                                                   /------- Agamidae
                                           /-------+------- Chamaeleontidae
       /-----------------------------------+--------------- Iguanidae
       |                                           /------- Anguidae
       |                            /--------------+------- Xenosauridae
       |      /---------------------+      /--------------- Helodermatidae
/------+      |                     \------+       /------- Lanthanotus
|      |      |                            \-------+------- Varanus
|      |      |                                    /------- Cordylidae
|      \------+              /---------------------+------- Scincidae
|             |              |                     /------- Gymnophthalmidae
|             |       /------+             /-------+------- Teiidae
|             |       |      |      /------+--------------- Lacertidae
|             \-------+      \------+---------------------- Xantusiidae
|                     |                            /------- Gekkonidae
|                     \----------------------------+------- Pygopodidae
\---------------------------------------------------------- Average Outgroup
```

Gauthier et al. (1988a):

```
Data matrix has 14 taxa, 171 characters

Designated outgroup taxa: All zero outgroup

Current status of all characters: Characters are ordered
   Characters 3, 14, 16, 18, 20, 26, 28, 30, 32, 34, 35, 37, 38, 39, 43,
      44, 45, 50, 51, 52, 53, 54, 57, 60, 62, 64, 69, 70, 79, 84, 85,
      86, 87, 90, 92, 95, 96, 99, 100, 102, 103, 106, 110, 111, 112,
      113, 114, 118, 125, 129, 131, 133, 135, 136, 138, 139, 140, 141,
      142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154,
      155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167,
      168, 169, and 170 are uninformative (ignored)

Tree description:
      Tree length = 134
      Consistency index (CI) = 0.821
      Homoplasy index (HI) = 0.276
      Retention index (RI) = 0.889
      Rescaled consistency index (RC) = 0.730

Strict consensus of 27 trees:
                                                   /------- Tangasaurs
       /-------------------------------------------+------- Youngina
       +--------------------------------------------------- Acerodontosaurus
       +--------------------------------------------------- Paliguana
       +--------------------------------------------------- Palaeagama
/------+--------------------------------------------------- Saurosternon
|      |      /-------------------------------------------- Kuehneosaurs
|      |      |                            /--------------- Sphenodonts
|      |      |                     /------+       /------- Homoeosaurs
|      \------+              /------+      \-------+------- Sapheosaurs
|             |       /------+      \---------------------- Clevosaurs
|             \-------+      \----------------------------- Gephyrosaurus
|                     \------------------------------------ Squamates
\---------------------------------------------------------- OUTGROUP
```

Evans (1991):

```
Data matrix has 8 taxa, 35 characters

Designated outgroup taxa:
   Cteniogenys
   Rhynchosauria
   Prolacertiformes

Current status of all characters: All characters are unordered
      Characters 4, 15, and 25 are uninformative

Tree description:
      Tree length = 64
      Consistency index (CI) = 0.688
      Homoplasy index (HI) = 0.469
      Retention index (RI) = 0.500
      Rescaled consistency index (RC) = 0.344
```

```
Strict consensus of 2 trees:
                                              /------------ Youngina
                       /----------------------+------------ Paliguana
                       |           /----------------------- Kuehneosauridae
            /----------+-----------+          /------------ Marmoretta
            |          |           \----------+------------ Lepidosauria
/-----------+          \----------------------------------- Rhynchosauria
|           \---------------------------------------------- Prolacertiformes
\---------------------------------------------------------- Cteniogenys
```

Clark and Hernández (1994):

Analysis within Squamata:

```
Data matrix has 21 taxa, 187 characters

Designated outgroup taxa:
   Kluge's (1989) outgroup

Current status of all characters:
      All characters are ordered
      Characters 11, 14, 15, 21, 29, 33, 50, 80, 93, 104, 117, 119, 125,
            149, 151, 152, 154, 155, 157, 158, 159, 161, 162, 163, 164,
            165, 166, 169, 170, 171, 172, 173, 174, 175, 176, 177, 178,
            179, 180, 181, 182, 183, and 184 are uninformative (ignored)

Tree description:
      Tree length = 750
      Consistency index (CI) = 0.736
      Homoplasy index (HI) = 0.777
      Retention index (RI) = 0.593
      Rescaled consistency index (RC) = 0.437

Strict consensus of 13 trees:
                                                /---------- Agamidae
          /-------------------------------------+---------- Chamaeleontidae
          |                                     \---------- Iguanidae
          |                                     /---------- Anguidae
          |                  /------------------+---------- Xenosauridae
          +------------------+         /------------------- Helodermatidae
          |                  \---------+        /---------- Lanthanotus
          |                            \--------+---------- Varanus
          |                                     /---------- Cordylidae
          |        /----------------------------+---------- Scincidae
/---------+        |                            /---------- Gymnophthalmidae
|         +--------+                   /--------+---------- Teiidae
|         |        |         /---------+------------------- Lacertidae
|         |        \---------+----------------------------- Xantusiidae
|         +------------------------------------------------ Dibamidae
|         |                                     /---------- Gekkonidae
|         +-------------------------------------+---------- Pygopodidae
|         +------------------------------------------------ Amphisbaenia
|         +------------------------------------------------ Serpentes
|         \------------------------------------------------ Tamaulipasaurus
\---------------------------------------------------------- Kluge's Outgroup
```

Analysis within basal Lepidosauromorpha:

```
Data matrix has 15 taxa, 165 characters

Designated outgroup taxa: All zero outgroup


Current status of all characters: All characters are ordered
      Characters 3, 14, 16, 17, 19, 25, 27, 29, 31, 33, 36, 37, 38, 42,
            47, 48, 51, 54, 57, 59, 61, 62, 65, 66, 67, 76, 79, 80, 81,
            82, 84, 88, 91, 92, 95, 96, 98, 99, 105, 106, 107, 108, 112,
            119, 123, 125, 127, 129, 130, 132, 133, 134, 135, 136, 137,
            138, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149,
            150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161,
            162, 163, and 164 are uninformative (ignored)

Tree description:

Tree length = 143
Consistency index (CI) = 0.783
Homoplasy index (HI) = 0.315
Retention index (RI) = 0.860
Rescaled consistency index (RC) = 0.673

Strict consensus of 54 trees:

                                                   /------- Tangasaurs
       /-------------------------------------------+------- Youngina
       +--------------------------------------------------- Acerodontosaurus
       +--------------------------------------------------- Paliguana
       +--------------------------------------------------- Palaeagama
/------+--------------------------------------------------- Saurosternon
|      |      /-------------------------------------------- Kuehneosaurs
|      |      |                            /--------------- Sphenodonts
|      |      |                     /------+       /------- Homoeosaurs
|      \------+              /------+      \-------+------- Sapheosaurs
|             |       /------+      \---------------------- Clevosaurs
|             |       |      \----------------------------- Gephyrosaurus
|             \-------+------------------------------------ Squamates
|                     \------------------------------------ Tamaulipasaurus
\---------------------------------------------------------- OUTGROUP
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SUMMARY AND FINAL CONCLUSIONS

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The Early Cretaceous (Albian) deposits of the Cantera Tlayua, in Central México show a unique ensemble of archaic lepidosaurian forms. The holotype of the sphenodontian *Pamizinsaurus tlayuaensis* gen. et sp. nov. is a posthatchling characterized by a body covered with rows of small rounded osteoderms transversally oriented, relatively few hatchling teeth with well developed ridges, and a posteriorly displaced ventral process of the mandibular symphysis at an early ontogenetic stage. A small retroarticular process, long central region of the pterygoid, and the constriction of the posterior end of the interpterygoid vacuity suggest sister-group relationships with sphenodontines + eilenodontines. The conspicuous dermal skeleton suggest that it could have protected against predation in open environments.

The sphenodontian *Ankylosphenodon pachyostoseus* gen. et sp. nov. is a robust sphenodontian with unusual teeth ankylosed deep into the lower jaw and pachyostotic ribs and vertebrae unique among sphenodontians. The teeth are large inverted canals of enamel resting obliquely one to another and extending far down to the edge of the Meckelian canal. Open tooth roots, the lack of worn out teeth, and posterior wear surfaces exhibiting dentine, suggest that tooth grow was continuous. These feature combined with a propalinal action of a deep lower jaw suggest herbivory. Herbivorous specializations of *Ankylosphenodon* are different from those of other sphenodontians. *Toxolophosaurus* and *Eilenodon*, have instead laterally expanded teeth with thickened enamel that increased grinding surface and durability. Continuously growing teeth may have evolve to prevent total tooth loss which is observed in sapheosaurs. On the other hand, pachyostotic skeleton, delay on the ossification of the epiphyses, and a solid structure of the vertebral column could be related to a none obligatory aquatic behavior. These specializations also differ greatly from those of other aquatic sphenodontians. *Pleurosaurus* and *Palaeopleurosaurus* have long body with short limbs that indicates a more obligate aquatic behavior since limbs have become so small that they could probably not function in terrestrial locomotion. A stout skeleton with swollen zygapophyses horizontally oriented suggest affinities of *Ankylosphenodon* with sapheosaurs: however, the presence of propalinal jaw action and a deep jaw may support an eilenodontine sister-group relationship.

The fossil record of sphenodontians is still very incomplete, and much remains to be learned. The morphology of the sphenodontians was very conservative during the Late Triassic. However, it is clear that in the Late Jurassic and Early Cretaceous a now well documented radiation occurred. Sphenodontians inhabiting different environments diverged from the primitive sphenodontian type, and produced several distinct body morphologies. Aquatic long bodied sphenodontians appeared by the early Jurassic and continued to evolve up to the end of the Jurassic. Terrestrial herbivorous sphenodontians with a complex chewing apparatus and stout marine sphenodontians appeared in the Late Jurassic. From the Early Cretaceous an armored sphenodontian and a stoutly constructed herbivorous aquatic sphenodontian are now known. The unique anatomical specializations of *Pamizinsaurus* and *Ankylosphenodon* give additional information as to the great diversity that sphenodontians had achieve by the end of the Early Cretaceous. This new evidence argue against the common idea of low morphological diversification of sphenodontians. The presence of two unique sphenodontians in the Tlayua quarry suggests the presence of an area of high diversification for lepidosaur reptiles. The late presence of sphenodontians in the Albian also suggest that this area was a refuge for archaic forms at the time. They are the latest known sphenodontians in the fossil record. The lack of fossils after the Early Cretaceous may indicate the end of this remarkable diversification.

Huehuecuetzpalli mixtecus gen. et sp. nov. is a primitive lizard known by a juvenile and an adult specimen. It is characterized by a combination of characters unlike those of any of the previously described Late Jurassic or Early Cretaceous lizards. *Huehuecuetzpalli* has most of the synapomorphies common to modern squamate groups, but still retains primitive features rare in living Squamata. A premaxillae anteriorly elongated resulting in the elongation of the snout and the apparent retraction of the external nares are autapomorphic characters that resemble varanids. A small rounded postfrontal and a parietal foramen on the frontoparietal suture suggest iguanian affinities, but a divided premaxilla, amphicoelous vertebrae, thoracolumbar intercentra, and the presence of the second distal tarsal, suggest a more primitive position supporting a sister-group relationship with squamates. The presence of many of this characters individually in some modern squamates question their importance as primitive features because might be of paedomorphic origin; however, their presence in *Huehuecuetzpalli* and other early lizards suggest that derived states might have been fixed later to the branch off the Squamata, in lizard evolution. Although late in the fossil record *Huehuecuetzpalli* provides important information of early transformation of characters in lizards. *Huehuecuetzpalli* shares two characters with iguanians that may support affinities with this taxon. If it is interpreted as an early iguanian, it would be the earliest known iguanian, extending the range of this lineage into the Albian.

Tepexisaurus tepexii gen. et sp. nov. is the best preserved early scincomorph and the first known taxon that is morphologically primitive to scincoids and paramacellodid lizards. The presence of parietal downgrowths, the coronoid overlapped anteriorly and posteriorly by the dentary and surangular, a small medial flange on the retroarticular process, and weak zygosphene and zygantrum articulations suggest scincoid relationships, but the absence of osteoscutes place *Tepexisaurus* as sister-group of this taxon. It shares the presence of ±30 closely packed teeth with the poorly known Upper Jurassic genus *Pseudosaurillus*, but differences in the coronoid structure, Meckelian groove and jaw proportions indicate that both taxa are distinct. Similar to *Tepexisaurus*, the absence of osteoscutes in *Pseudosaurillus* and *Saurillodon* place these taxa in a more primitive position relative to other paramacellodids which can be more reliably included within Scincoidea. Thus, Paramacellodidae is a paraphyletic assemblage.

The late presence of a pre-scincoid lizard in the Albian deposits of Tlayua can be correlated with the late presence of sphenodontians and the relictual nature of *Huehuecuetzpalli mixtecus*. It gives additional evidence to support the hypothesis that Tlayua was a refuge for terrestrial archaic forms during the Albian. The co-existence of a scincomorph and an iguanian-like lizard in Tlayua is the earliest known example of a fauna composed of squamates from Gondwanaland and Laurasian and suggests that intercontinental lizard exchange happened as early as the Albian.

A phylogenetic analysis to explore the early history of characters transformation towards the modern squamate anatomy, always obscure in other phylogenetic hypotheses, was performed in the light of new evidence. All basal lepidosauromorphs, the best known early squamates, and extant squamate families were included. Improvements to previous data matrices includes: the merging of redundant information in multistate characters, the inclusion of all available character states instead of grouping them *a priori* in assumed evolutionary units, the division of characters involving character states describing different anatomical parts, but assumed to be part of the same transformation series, the incorporation of all available evidence including characters considered "bad" according to the point of view of previous researchers; the inclusion of fossil taxa in spite of extensive missing data, and by analyzing information with a rigorous and stable protocol that includes unordered change in transformation series and results described through a strict consensus tree. The final cladistic analysis shows that tree topology and character distribution may differ greatly from expected results when data matrices are merged dissolving limits imposed by researchers assuming monophyletic entities. Several characters previously considered autapomorphic for squamates are certainly distributed along a previously unknown lineage of lizard-like forms basal to the Squamata. This lineage includes *Parviraptor*, *Tamaulipasaurus*, the monophyletic assemblage composed by *Eichstaettisaurus-Ardeosaurus-Bavarisaurus*, and *Huehuecuetzpalli*. The name Squamatoidea is suggested to group all non rhynchocephalian lepidosaurs basal to

Squamata + squamates; Ardeosauridae is extended to include *Bavarisaurus*; and Scincogekkonomorpha is redefined to include Gekkota and Scincomorpha. *Paliguana* and *Palaeagama* are not lepidosauromorphs. Although the most parsimonious hypothesis seems to be weakly supported, the Total Branch Support index are not different from values obtained in other published phylogenies of the Squamata. Branch collapse seems to be due more to a susceptibility of fossil taxa with missing information to character resampling compared with extant taxa with complete data sets, and a combination of this effect with the uncertain position of problematic taxa. Low branch support values, on the other hand, are due to the redistribution of a limited number of characters in several additional branches, reducing the total number of characters supporting each node.

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LIST OF ABBREVIATIONS

1-5	distal carpals/tarsals
I-V	metacarpals/metatarsals
a.	angular
a.c.	astragalocalcaneum
ad.t.	additional teeth
a.f.	adductor fossa
ar.	articular
ar.c.	articular condyle
as.	astragalus
atl.	atlas
atl.ic.	atlantal intercentrum
atl.na.	atlantal neural arch
aut.s.	autotomous septum
aut.v.	autotomous vertebrae
ax.	axis
ax.ic.	axial intercentrum
ax. na.	axial neural arch
bo.	basioccipital
bs.	basisphenoid
c.	coronoid
c1-c3	vertebral centra
ca.	calcaneum
CB.	ceratobranchial
c.c.r.	cartilagenous costal ribs
ce.	centrale

ce.v.	cervical vertebrae
c.i.c.	caudal intercentra
cl.	clavicle
co.	coracoid
co.f.	coracoid foramen
c.pr.	coronoid process
c.s.	calcified scutes
c.v.	caudal vertebrae
d.	dentary
d.d.m.l.	level of the dorsal margin of the dentary
dig.	digits
d.p.c.	deltopectoral crest
d.sy	symphysis of dentary
dt.	distal tarsal
d.v.	dorsal vertebrae
d.w.f.	dentary wear facet
ec.f.	ectepicondylar foramen
ecp.	ectopterygoid
ect.pr.pt.	ectopterygoid process of pterygoid
EH.	epihyal
ent.	entepicondyle
ent.f.	entepicondylar foramen
eo.	exoccipital
ep.	epipterygoid
epco.	epicoracoid cartilage
epi.	epiphysis
f.	frontal

f.d.pr.	descending process of frontal
fe.	femur
f.f.	foramen facialis
fi.	fibula
g.	gastralia
gl.	glenoid
gr.sc.	granular scales
h.	humerus
ha.	haemal arch
h.t.	hatchling teeth
i3	third intercentrum
ic.	interclavicle
il.	ilium
isc.	ischium
isc.p.ang.	ischium posterior angulation
isc.p.pr.	ischium posterior process
j.	jugal
l.ce.	lateral centrale
l.i.c.	lumbar intercentra
l.t.	lateral tuber
m.	maxilla
m.c.	Meckelian canal
m.ce.	medial centrale
m.c.l.	level of the Meckelian canal
m.f.	mandibular foramen
m.p.s.	maxillary palatal shelf
m.t.	maxillary teeth

mt.	metatarsals
n.	nasal
n.a.	neural arch
n.s.	neural spine
op.	opisthotic
p.	parietal
p.a.	prearticular
pal.	palatine
p.d.pr.	parietal descending process
p.f.	parietal foramen
ph.	phalanges
pi.	pisiform
p.l.pr.	parietal lateral process
pm.	premaxilla
pm.n.pr.	premaxillary nasal process
pm.pd.pr.	premaxillary posterodorsal process
pm.t.	premaxillary teeth
po.	postorbital
po.d.	postdentary bones
pof.	postfrontal
po.z.	postzygapophysis
prf.	prefrontal
pr.z.	prezygapophysis
psv.	presacral vertebrae
pt.	pterygoid
pt.pr.q.	pterygoid process of quadrate
pu.	pubis

p.x.i.r.	postxiphisternal inscriptional ribs
q.	quadrate
qj.	quadratojugal
q.l.e.	quadrate lateral expansion
q.pr.pt.	quadrate process of pterygoid
r.	radius
ra.	radiale
ra.m.c.	retroarticular medial crest
ri.	ribs
r.t.	replacement tail
s.	stapes
sa.	surangular
sc.	scapula
sc.f.	scapular fenestra
s.f.	surangular foramen
soc.	supraoccipital
spl.	splenial
sq.	squamosal
s.ri.	sacral ribs
s.sc.	suprascapula
st.	supratemporal
ste.	sternum
ste.ri.	sternal ribs
s.v.	sacral vertebras
t.	teeth, tooth
ti.	tibia
t.n.	tibial distal notch

tr.pr	transverse process
t.w.f.	tooth wear facet
u.	ulna
ul.	ulnare
v.	vomer
v.c.	vertebrate column
v.f.	vagus foramen
vi.c.	vidian canal
v.s.i.	ventral skin impression
xi.	xiphisternum
z/z.	zygosphene and zygantrum accessory articulation

IMAGE EVALUATION
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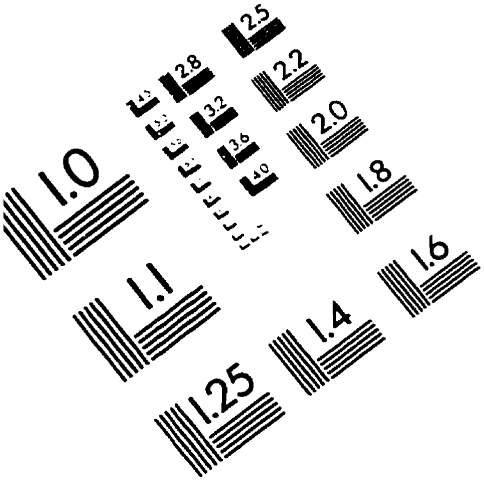

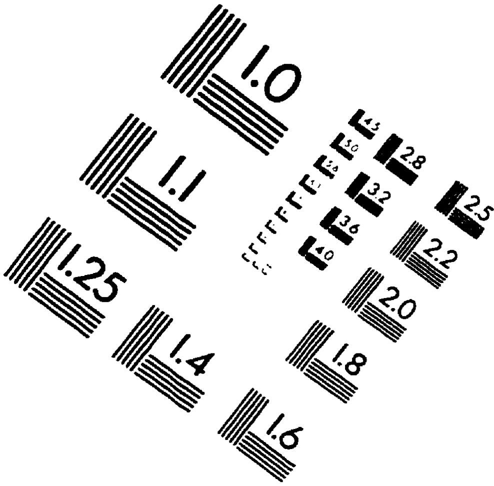

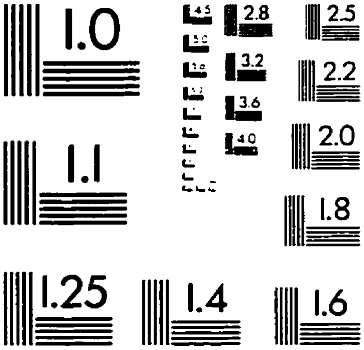

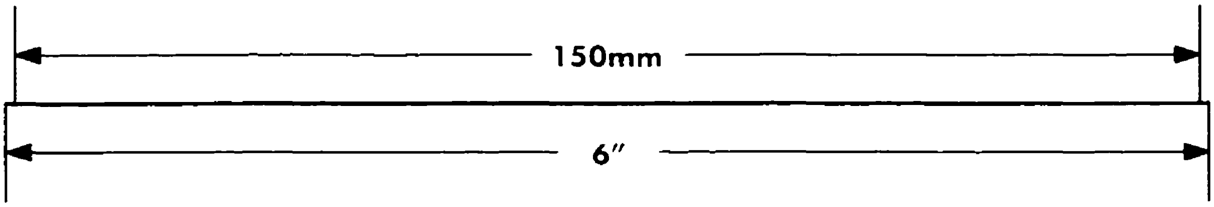

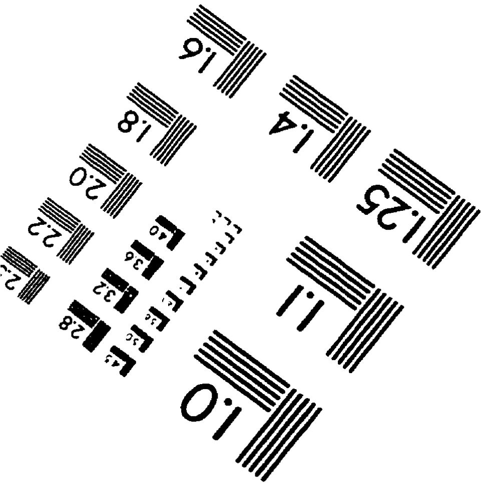

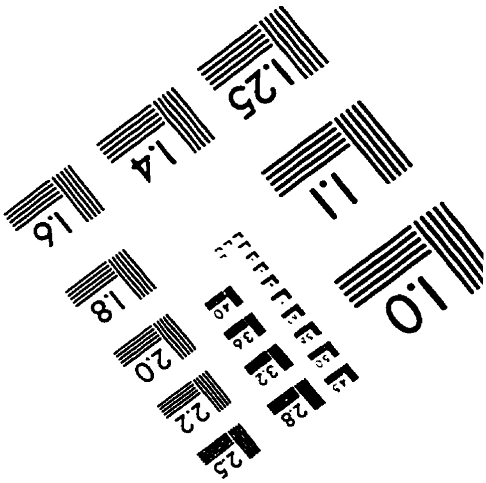

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