PHYLOGENETIC AND BIOGEOGRAPHIC PATTERNS OF BASILISCINE IGUANIANS
(Reptilia: Squamata: ‘‘Iguanidae’’)

BY
MATHIAS LANG

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EPIGRAPH

Sibilaque effundens cunctas terrentia pestes,
Ante venena nocens, late sibi submovet omne
Vulgus, et in vuca regnat Basiliscus arena.

But fiercely hissing through the poison'd air
The Basilisk exerts his deathfull glare:
At distance bids each vulgar pest remain,
And reigns sole monarch of his sultry plain.

Lucan (A.D. 39—65)

CONTENTS

ABSTRACT

As presently understood, the ''Iguanidae'' is composed of eight suprageneric, monophyletic clades, the interrelationships of which are unresolved. The phylogenetic relationships within one of these clades, the basiliscines, is investigated herein. Basiliscine ''iguanids'' comprise nine semiarboreal to arboreal species placed in three genera - *Basiliscus, Corytophanes,* and *Laemanctus* - which range from northwestern México, through Central America to Venezuela. The monophyly of the group is well substantiated within the context of ''Iguanidae''. Data for phylogenetic analysis are from osteological characters and soft anatomical features. Behavioral and ecological observations are included for all terminal taxa. The analysis was performed using a ''functional outgroup consensus approach'' in which the other seven ''iguanid'' clades were treated as unresolved functional outgroups. The results of the analysis indicate that each of the three genera is monophyletic, and that *Corytophanes* and *Laemanctus* are more closely related to one another than either is to *Basiliscus*. Within *Basiliscus*, the relationships are not completely resolved. *Basiliscus plumifrons* and *B. basiliscus* are one another's closest relatives and form a tritomy with *B. galeritus* and *B. vittatus*. Within *Corytophanes*, *C. percarinatus* and *C. cristatus* are each others closest relatives.

INTRODUCTION

Introduction to the ''Iguanidae''

''Iguanidae'' is the largest and most widespread family of non-ophidian squamates in the New World. Within extant squamates it is an early diverging taxon (Estes et al. 1988), comprising approximately 60 genera containing more than 600 species. Gauthier (1984), indicated that ''iguanids'' is a metataxon, i.e. a group for which there is no character evidence supporting either monophyly, paraphyly or polyphyly and used an asterisk following the taxon name. In this study the traditional quotation marks are used to indicate that this taxon is not a clear-cut monophyletic unit.

''Iguanids'' have a very extensive and curious geographic distribution. In the New World, ''iguanids'' range from southern Canada through North and Central America to Tierra del Fuego at the tip of South America. They also occur throughout the West Indies and Galápagos. They are found on Madagascar, the Comoro Islands, and on the islands of the Fiji-Tonga group in the South Pacific. This distribution poses some interesting zoogeographical questions (Renous 1979; Moody 1980; Blanc et al. 1983; Estes 1983a, 1983b; Grehan & Ainsworth 1985).

Members of this family are adapted to a broad spectrum of habitats. They can be found in temperate, tropical and subtropical areas and occur from extreme deserts to tropical rainforests, from sea level to above the tree line.

The fossil record of ''iguanids'' is scant at best (Estes 1983a) and most fossils referable to the ''iguanids'' are North American, and do not predate the Eocene (Estes & Price

1973; Estes 1983a, 1983b) except for an undescribed North American Paleocene ''iguanid'' (Estes, pers. comm.).

The basiliscines form a small group of semiarboreal and arboreal squamates, primarily centered in Middle America, but ranging from northwestern México to Ecuador and Venezuela. There are three genera that comprise this taxon: *Basiliscus* (4 species), *Corytophanes* (3 species) and *Laemanctus* (2 species).

One interesting question raised by the distribution of basiliscines pertains to the zoogeography of Central America and the origin and possible differentiation of the West Indian herpetofauna (Rosen 1975, 1978; Pregill 1981; Savage 1982; Buskirk 1985).

Basiliscines are moderately large lizards (150 to 240 mm snout-vent length, Ahl 1930), with a compressed body and a long, slender tail. The head of all adult basiliscines has a distinctive, vertical, blade-like process of the parietal bone that extends back over the neck. The development of the parietal blade is a unique derived character within the family that has been used repeatedly to diagnose basiliscines.

Laemanctus and *Corytophanes* remain moderately rare in collections, and little is known about their natural history. Both genera are inconspicuous and are essentially sit-and-wait predators, which also reflects their arboreal habits. *Basiliscus* is a more active predator, more conspicuous, has a more extensive range, and is therefore better represented in collections. There is a moderate amount of literature on the ecology and behavior of *Basiliscus*, particularly with respect to its terrestrial and aquatic bipedal locomotion (see section on diagnosis of taxa).

At the species level, the alpha taxonomy of basiliscines is reasonably well-known, although some authors still doubt the validity of certain species and subspecies (Peters 1967). Nevertheless, there has been no attempt to assess the phylogenetic relationship of basiliscines at the species level.

Historical Review of the Basiliscines

Attempts to sort out ''iguanids'' into subfamilies and suprageneric groupings have met with limited success (e.g. Wagler 1830; Duméril & Bibron 1837; Fitzinger 1843; Gray 1845; Boulenger 1885; Cope 1896, 1900; Smith 1946; Savage 1958; Etheridge 1959, 1964, Ethridge & de Queiroz 1988).

Boulenger (1885) listed the three basiliscine genera together apparently recognizing their affinity, but without proposing a formal taxonomic rank. Cope (1900) proposed a subfamily, the Basiliscinae, based upon the absence of both a left hepatopulmonary mesentery and inscriptional rib chevrons, and the presence of a perforated clavicle (looped clavicle of Cope). The lack of inscriptional ribs is hypothesized to be a primitive state and therefore cannot be used in defining monophyletic taxa. In addition, only *Basiliscus* and *Laemanctus* were included. Etheridge (1959) used the term ''basiliscine group'' and included *Basiliscus*, *Corytophanes* and *Laemanctus* as part of his Group II.

In a 1964 publication Etheridge used the term ''basiliscines'' without a definition or indication of which genera were included, but later (1967) listed all three genera under this term. Zug (1971), in an otherwise largely inconclusive study of arterial patterns in ''iguanids'', also concluded that *Basiliscus*, *Corytophanes* and *Laemanctus* form a phylogenetic unit.

In the most recent treatment, Etheridge & de Queiroz (1988) provided a detailed analysis of ''iguanids'', using 49 characters, primarily integumentary and osteological, representing 57 transformation series. They specified eight major groups of ''iguanids'' and listed thirteen synapomorphies for the basiliscines (Table 1).

In his review of the genus *Basiliscus*, Maturana (1962) recognized two units, based exclusively on external characteristics, such as scalation patterns and male secondary sex structures. A ''northern unit'' contained *B. vittatus* and the ''southern unit'' included the remaining three species of *Basiliscus*. The two groups were based on overall phenetic similarity and may therefore not represent natural groups.

McCoy (1968a) reviewed the genus *Laemanctus* and recognized two species: *L. longipes* with three subspecies and *L. serratus* with two subspecies. These two species differ in dorsal crest shape, casque shape, and arrangement of dorsal head scales. A third subspecies of *L. serratus* has recently been described by Pérez-Higareda and Vogt (1985).

The genus *Corytophanes* has not yet been revised, only descriptions of the three species have been offered (Gravenhorst 1833; Taylor 1956).

Goals and Problems of this Study

The goal of this study is to hypothesize a phylogeny of the currently recognized species and genera of basiliscines. This phylogeny is based primarily on osteological characters and characters from soft anatomy. Characters obtained from the literature such as modes of reproduction, karyotypes, genetic information, ecological data and physiological attributes are listed, but could not be used as systematic characters because an unequivocal interpretation of the polarity of characters states was not possible.

Three goals are stressed in this study. First, Etheridge & de Queiroz's (1988) characters are reexamined, using a larger sample size in order to corroborate or reject their character decisions and proposed phylogenetic relationships among the three genera of basiliscines. Second, basiliscine anatomy is described in more detail. Third, a diagnosis and description of the terminal taxa (=basiliscine species) is sought, to include monophyletic status, synapomorphies, geographical and ecological information.

Factors Important to the Development of this Study

An important factor in the present investigation is the availability of a superb series of systematic studies on diapsid reptiles analyzing successive internested taxa. Gauthier's (1984) cladistic analysis of higher categories of diapsid reptiles, together with the related study on lepidosauromorph reptiles (Gauthier et al. 1988) laid the foundation for Estes et al.'s (1988) analysis of the Squamata at the familial level. Etheridge & de Queiroz (1988), furthermore, analyzed the phylogenetic relationships within ''iguanids''. This present study then forms part of a continuum, analyzing the relationships of a monophyletic suprageneric taxon within the ''iguanids''.

Table 1: Basiliscine apomorphies shared with other suprageneric groups. Abbreviations listed in Table 6.

Caracter	Morun.	Oplur	Anol.	Iguan.	Scel.	Crot.	Trop.	Total
Parietal foramen # 2	X	X	X	*Sau* *Dip*	X	X	*Lei*	2
Parietal blade # 3	X	X	X	X	X	X	X	0
Osseous labyr # 8	X	*Chl*	ALL	*Dip*	ALL but *Pet Phr Scl*	ALL	*Urn* *Stn Oph*	6
Coronoid lat pr # 10	ALL(2)	X	Ans	ALL(2)	ALL(1)	ALL(1)	*Liogr* *Lei*	6
* Meck gr fused # 12	X	ALL	ALL	ALL	ALL	ALL	ALL	6
Palatal teeth # 17	ALL	ALL	All but *Pri Apt Chm*	ALL	ALL	X	ALL	6
* Clav fenest # 22	X	X	X	*Amb* *Con*	X	*Gam*	W*Trp* *Plc Urc*	3
* Clav lat mrg # 23	*Eny*	*Opl*	PAnl *Anl*	*Amb*	*Sclgr*	*Gam*	All but *Stn Plc Trp Plt*	7
Ribs 4th cerv # 28	X	*Opl*	Ans	ALL	Sand lzds	X	X	4
Caud Vert tr pr # 33	X	X	*Enu Pol*	X	X	X	*Oph*	2
Fem. pores lost # 41	X	ALL	All but *Pol*	X	X	X	ALL	3
Fr subocc scales # 47	ALL	X	Lios *Chm Anl*	All but *Ctn Dip Amb*	*Phr*	*Cro*	*Urn* *Plc Phy*	6
Dors shank musc # 49	ALL	ALL	ALL	X	*Scl* *Uro*	*Cro*	*Lio* *Phy Urn*	6
Total	5	7	10	9	8	7	11	57

BASILISCINE MONOPHYLY

Etheridge & de Queiroz (1988) listed thirteen synapomorphies supporting the monophyly of the basiliscines (Table 1). The posteriorly extended skull crest formed by the parietal bone, however, is the only unique, derived feature uniting the basiliscine clade within "iguanids".

Table 2: Character data matrix for eight superageneric clades of iguanids

	Character and description	Anol	Morun	Oplur	Trop	Iguan	Basil	Crot	Scel
2	Position of parietal foramen	0	0	0	0	0	1A	0	0
3	Adult parietal roof shape	0	0	0	0	0	3	0	0
5	Lacrimal foramen	0	1	0	0	0	0	0	0
6	Postfrontal bone	0	0	0	0	0	0	1	0
7	Surface of dermal roofing bones	2	1	0	0	0	0	0	0
8	Bony Labyrinth	2	0	0	0	0	1	1	0
9	Supratemporal position	0	0	0	0	2	0	0	0
10	Coronoid lateral process	0	2	0	0	2	1	1	1
11	Fusion of Meckel's groove	1	0	0	0	1	0	0	0
12	Closure of Meckel's groove	2	0	0	1	2	1	0	1
14	Splenial size	1	0	0	0	1	0	0	1
16	Posterior extent of dentary	0	1	2	1	0	0	1	1
17	Palatine teeth	0	1	0	1	1	1	0	1
18	Pterygoid teeth	0	0	0	0	0	0	0	1
19	Crowns of post. marginal teeth	0	2A	0	0	2A	0	0	0
21	Clavicle	0	0	0	0	0	0	0	1
22	Clavicular fenestra	0	0	0	0	0	1	0	0
23	Clavicular lateral margin	0	0	0	0	0	1B	0	0
25	Scapular fenestra	0	0	0	0	1	0	1	0
26	Posterior coracoid fenestra	0	0	0	0	0	0	1	0
27	Sternal fontanelle	0	0	0	2	0	0	0	1
28	Cervical ribs	0	1	1	0	2	2	0	1
30	Total # of presacral vertebrae	0	0	0	0	0	0	0	1A
32	Post-xiphist. inscript. rib pattern	1	1	2	0	0	0	0	0
33	Caudal vertebral types	0	0	0	0	1A	1B	0	0
35	Nuchal endolymphatic sacs	1	0	0	0	0	0	0	0
36	Scale organs	0	0	3	0	0	0	0	0
37	Subdigital scale surface microstr.	0	0	2	0	0	0	0	0
41	Femoral pores	0	0	1	1	0	1	0	0
44	Midorsal scale row	0	0	0	0	0	0	2	2
45	Interparietal scale	0	0	0	0	0	0	0	1A
46	Superciliary scales	1	2	0	0	0	0	1	0
47	Suboccular scales	0	2	0	0	0	2	0	0
48	Ulnar nerve pathway	0	0	1	0	0	0	1	0
49	Dorsal shank muscle innervation	1	1	1	0	0	1	0	0

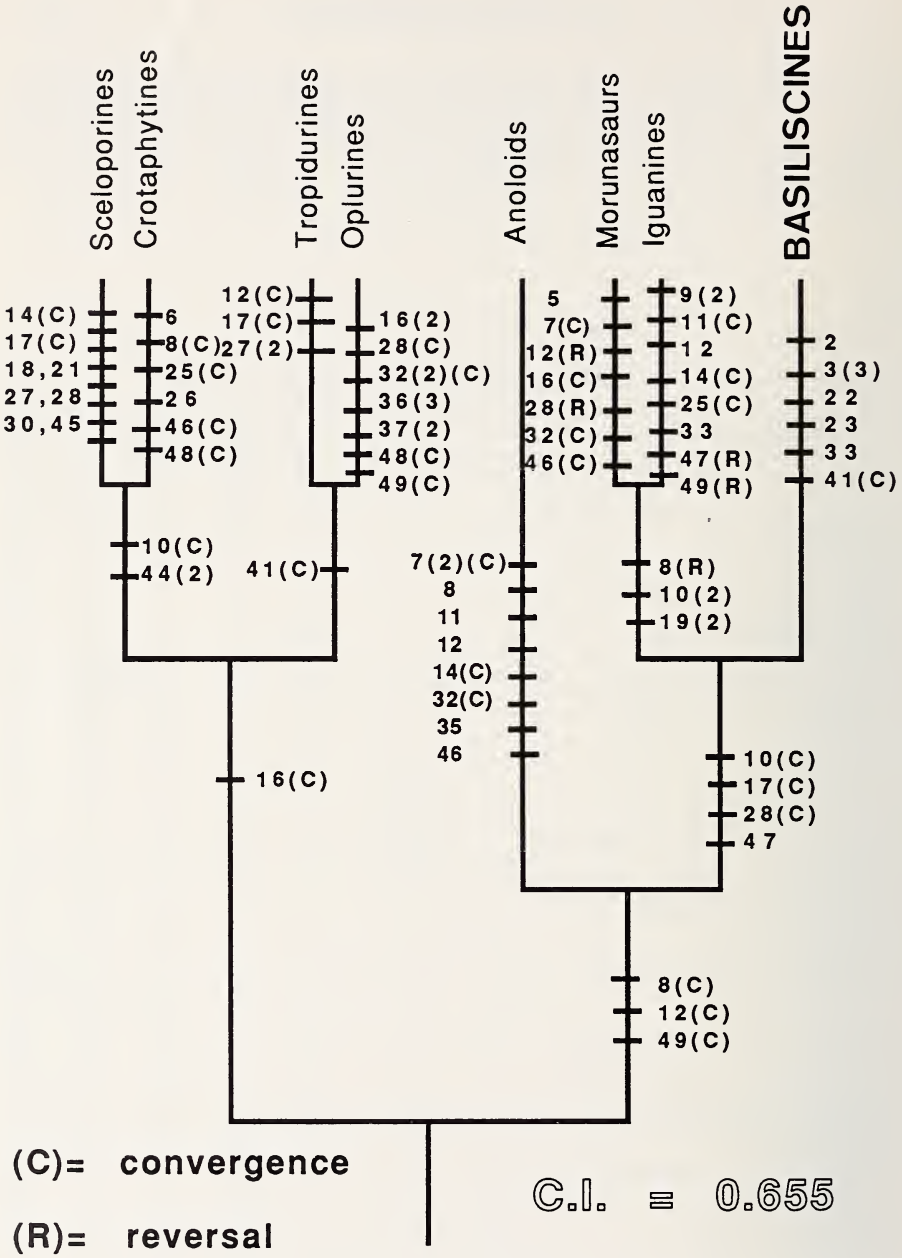

Fig. 1: Phylogenetic tree of the eight recognized suprageneric "iguanid" taxa. Characters are derived from Etheridge & de Queiroz (1988) and are listed in Table 2.

A data set including 36 of the 49 original characters, listed as apomorphies at the supra-generic level of Etheridge & de Queiroz's (1988) were reanalyzed (Table 2)[1]. The generated tree has a length of 84 and a consistency index of 0.655 (Fig. 1).

This tree indicates that there are 6 evolutionary events (5 non-homoplastic autapomorphies and 1 convergence) at the basiliscine node supporting the monophyly of this clade[2]. In addition to the expanded parietal blade, the following characters are antapomorphies for the basiliscines at the subfamilial/suprageneric level: the parietal foramen is located entirely within the frontal (with reversal to the primitive condition at the frontoparietal suture in *Laemanctus*); clavicular fenestration (secondarily lost in *Corytophanes*); lateral margins of clavicles are distinctly angular; caudal vertebrae are of the *Basiliscus*-type (Etheridge 1967); and femoral pores are lost (also lost in tropidurines and oplurines). Additional autapomorphies are: vertebrae have acquired zygosphene-zygantrum articulations (Etheridge 1964) and the postorbital bone is expanded dorsomedially over the dorsolateral portion of the supratemporal fossa (Etheridge & de Queiroz 1988) (Fig. 14, see section on the diagnosis of taxa).

The arrows in Fig. 2 indicate the instabilities[3] within the collapsed tree. The instabilities can be ascribed to homoplasies both between suprageneric clades and between terminal taxa (genera) and the suprageneric clades.

Crotaphytines share a common ancestry with sceloporines based on the presence of a small irregular process of the coronoid bone overlapping the posterolateral surface of the dentary and by the absence of a mid-dorsal scale row. This relationship is consistent with Gauthier's (1984) hypothesis. However, Gauthier's (1984) ''anoloid'' (= anoloids sensu Etheridge & de Queiroz (1988), morunasaurs and oplurines) clade is not supported by the collapsed cladogram at the suprageneric level. That oplurines are the sister taxon of tropidurines however, is based only on the absence of femoral pores, which are also absent in basiliscines and most anoloids. Morunasaurs on the other hand share a common ancestry with iguanines, based on the presence of a large blade-like process of the coronoid bone that descends over the posterolateral surface of the dentary, and expansion of the crowns of the posterior marginal teeth to become multicuspate.

The polarity of the coronoid character may be reversed (Etheridge & de Queiroz 1988). If the lack of a lateral process is derived, then there is some evidence for a tropidurine-oplurine clade, with convergence in anoloids. Furthermore, the morunasaur-iguanine clade would only be supported by multicuspate dentition.

The collapsed tree (Figs. 1—3) still demonstrates Etheridge & de Queiroz's (1988) basic conclusions: 1) there is good evidence for the monophyly of the eight suprageneric clades of ''iguanids'', and 2) the relationships among these eight taxa are to be regarded as unresolved.

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[1]) Characters used in this more restricted data set are characters at the suprageneric level. The character polarity at the basal node of each of the seven suprageneric clades does not necessarily reflect the condition for the less inclusive clades (iguanid genera).

[2]) The terms "synapomorphy" and "autapomorphy" follow the definitions of Ax (1984) (Fig. 6).

[3]) Instabilities are measured by the amount of homoplasies (= convergences and reversals) at a particular node.

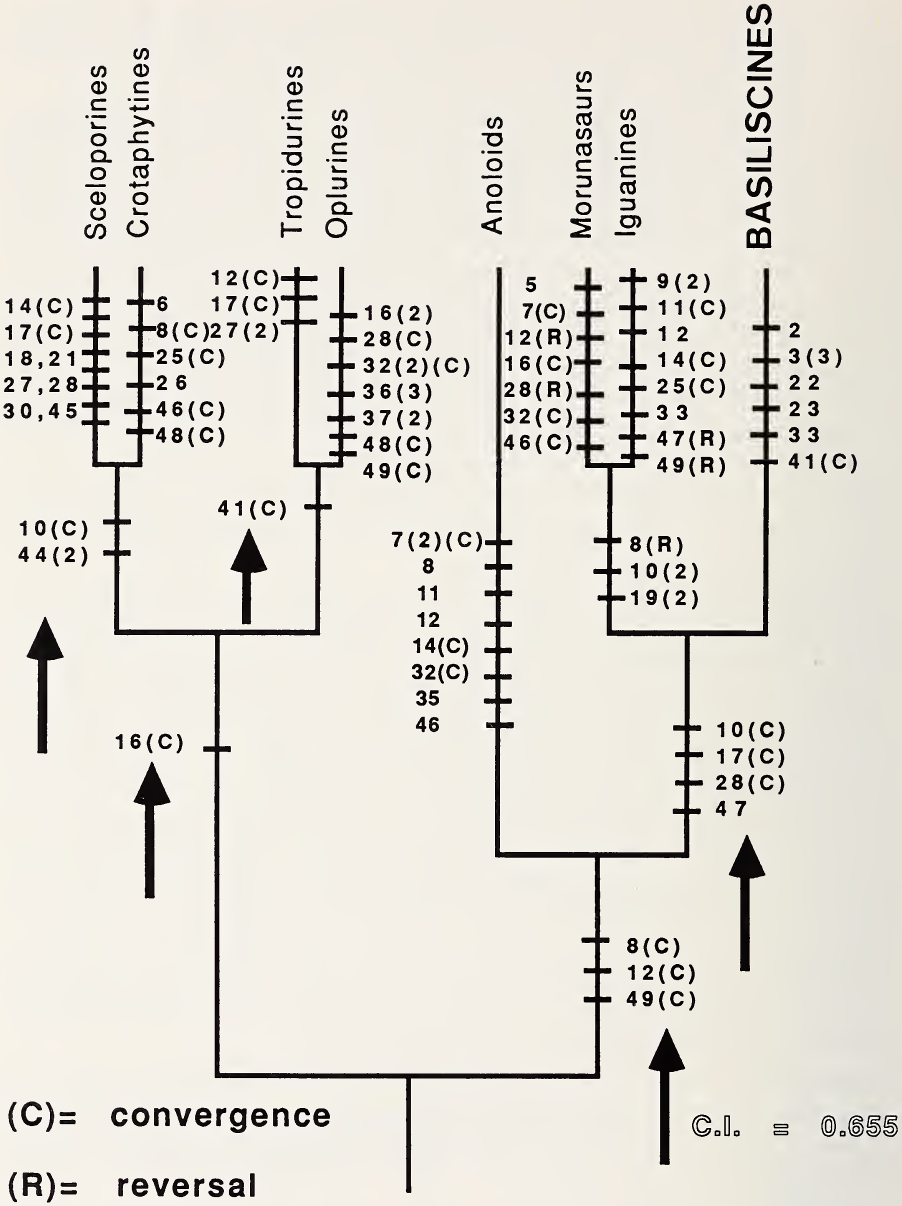


Fig. 2: Phylogenetic tree of the eight recognized suprageneric iguanid taxa. Characters are derived from Etheridge & de Queiroz (1988). Dark arrows indicate unstable nodes (i.e., nodes founded predominantly or exclusively on homoplasies).

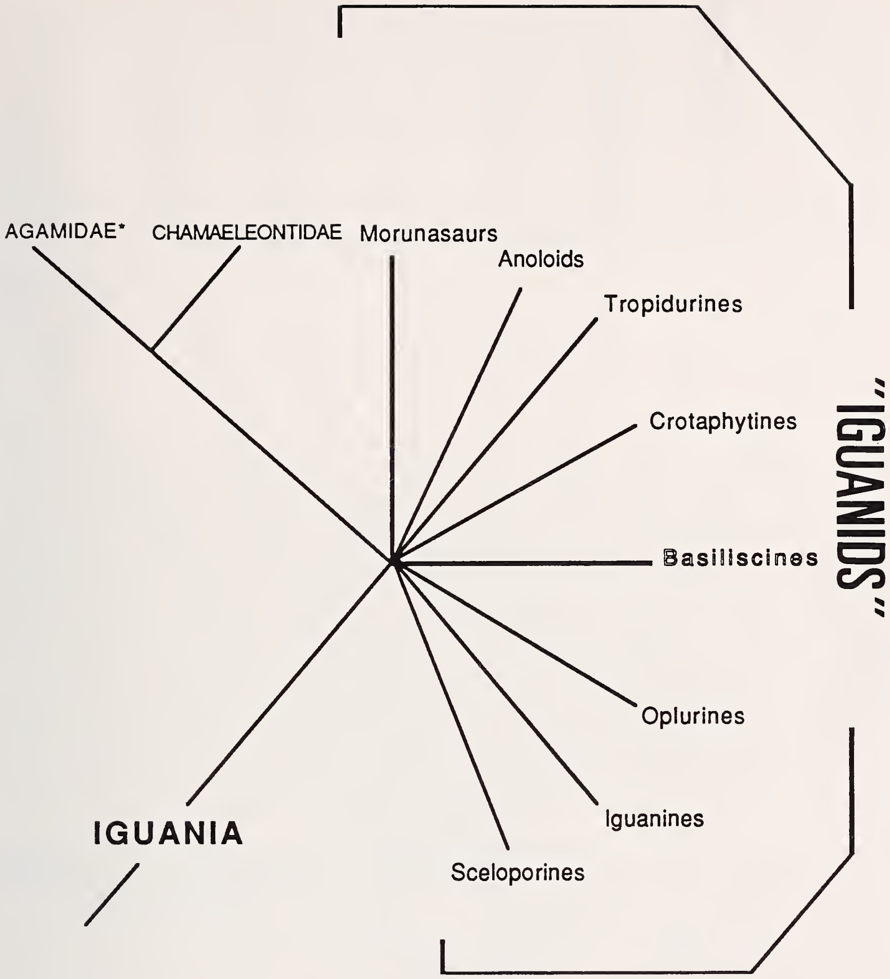


Fig. 3: A) Phylogenetic relationships within the Iguania. "Iguanidae" is a metataxon containing 8 suprageneric taxa of unresolved relationships. This cladogram is derived from Figs. 2 after collapsing of the unstable nodes.

The three basiliscine genera are also defined as distinct monophyletic taxa. *Basiliscus* is diagnosed by the dorsal expansion of the parietal crest above the plane formed by the edges of the parietal table, the acute angles formed by the articular surfaces of the caudal zygapophyses (Etheridge & de Queiroz 1988) and by the presence of free dermal margins on the pedal digits (Cope 1900). *Laemanctus* is diagnosed by the reduction of the number of keels on the subdigital scales to one (Boulenger 1885; Smith & Laufe 1945). *Corytophanes*, on the other hand, is highly modified and shows the best evidence for monophyly. The postemporal fossa is closed, the orbits are enlarged and the pre-

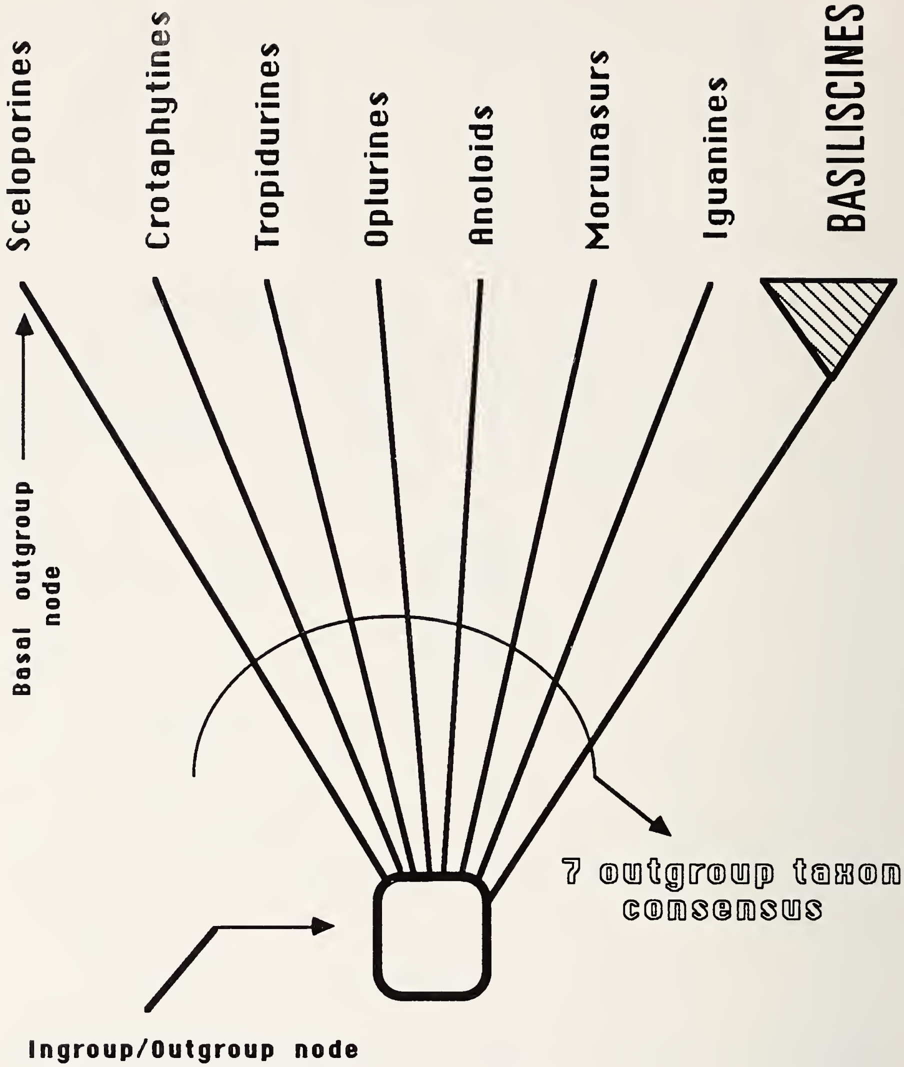


Fig. 3: B) Consensus cladogram showing the 7 functional outgroups and the ingroup/outgroup node (secondary level of analysis). The polarity at the ingroup/outgroup node is based on a 7 outgroup taxon consensus (see text for further discussion).

orbital portion of the skull is short. In addition, the roof of the nasal capsule is uncovered between the posteromedial portion of the nasals and the anteromedial portion of the frontal (Etheridge & de Queiroz 1988).

Corytophanes also shows a general trend towards arboreality in its skeletal structures, such as the lateral compression of its body and the elongation of the scapula. Some of the remaining autapomorphies indicative of monophyly are the development of a supraorbital process by the prefrontal and postorbital bones that underlie the superciliary ridges (also present in *Phrynosoma* and some *Polychrus*), the enlargement of the lateral shelves of the parietal crest to extend over the supratemporal fenestra (Etheridge 1959), and the further reduction and absence of the septomaxillae (Etheridge & de Queiroz 1988).

Etheridge & de Queiroz (1988) have thus presented good evidence for monophyletic status of the basiliscines within "iguanids", and for *Basiliscus*, *Corytophanes* and *Laemanctus*.

METHODS AND MATERIALS

Specimens

Specimens used in this study were either preserved in alcohol, cleared and stained, skeletons or radiographs. Most of the skeletal material used was prepared from preserved specimens in order to obtain a satisfactorily large series for observing possible skeletal variation and ontogenetic changes. Preparation of this material was done in two ways. The first technique involves removing the fleshy components of the specimens by handpicking and successively treating them with solutions of weak acid, ethylalcohol and water for short periods of time. This method, however, is somewhat laborious and may etch the bones, obliterating some suture lines. The second method involves the initial removal of the integument, viscera and major muscle mass. The specimen is then put into a waterbath for several days, changing the water on a regular basis until most of the preservatives are leached out. The specimen is then dried and cleaned by dermestid beetles.

Observations were made by direct examination or with the aid of a dissecting scope. Drawings and sketches were made with the aid of a camera lucida, or from photographs. Photographs were taken through an Olympus 35 mm SRL camera or a Polaroid, mounted on a Wild binocular dissecting microscope. Scanning electron micrographs were taken in the SEM lab at San Diego State University. Preparation of the specimens for the scanning electron microscope follows the techniques outlined in Peterson & Williams (1981). The specimens examined in this study are listed in Appendix A.

Outgroup Analysis

Hennig (1966) provided a method for reconstructing phylogenic histories. Although his Phylogenetic Systematics has been expanded and supplemented by four recent books (Eldredge & Cracraft 1980; Nelson & Platnick 1981; Wiley 1981; Ax 1984) and a multitude of papers, his basic method of analysis remains unchanged. As Hennig (1966) points out: only synapomorphies (= shared derived characters) contain information about the history of speciation (one line splitting in two). These synapomorphies are indicators of monophyletic taxa.

In order to discover synapomorphies, the polarity of a character transformation series must be known. Polarity is equivalent to which direction evolution of a particular character is thought to have proceeded. The primitive (plesiomorphic) condition is defined as the condition present in the ancestral species, and the derived (apomorphic) condition is the state present in the descendant group or taxon.

Many methods for assessing the polarity of characters have been proposed. The most commonly used ones include ingroup analysis, outgroup analysis, the ontogenetic method, and the paleontological method. These methods have been reviewed by Crisci & Steussy (1980), de Jong (1980), Stevens (1980), Arnold (1981), Nelson & Platnick (1981), Watrous & Wheeler (1981), Wiley (1981), Maddison et al. (1984) and others (see also literature cited therein). The ontogenetic and outgroup analysis methods have proven to be the most widely accepted today and are the only logically sufficient methods.

Outgroup analysis ensures that ingroup relationships are not only parsimonious internally, but that they are also consistent when considered in the context of related groups (Engelmann & Wiley 1977; Farris 1982).

When outgroup relationships are known, the ''global parsimony method'' as described by Maddison et al. (1984), seeks a simultaneous resolution of both the outgroups and ingroup with the data at hand. In addition, Arnold (1981) gives a theoretical foundation for estimating phylogenies at low taxonomic levels. However, there is still no method for the condition in which relationships within ingroups are to be resolved when relationships among outgroups are not fully resolved.

De Queiroz (1987) dealt with this problem in his analysis of the iguanines by limiting the outgroups to four taxa among the seven remaining unresolved suprageneric taxa of ''iguanids''. He hypothesized all possible outgroup relationships among the four outgroup taxa, rerooting those cladograms at the outgroup node (de Queiroz 1987, figs. 61-64). Polarity of character states were determined by the distribution of character states among the rerooted topologies of the outgroups. The choice of four among seven unresolved outgroups was arbitrary, because there is no evidence that the four outgroups chosen are more closely related to iguanines than either of the three remaining suprageneric clades are.

This study faces the exact same problem. At present no clear-cut sister-taxon of the basiliscines, or relationships among the suprageneric clades of ''iguanids'', can be inferred (Etheridge & de Queiroz 1988) (Figs. 1—3).

Basiliscines, iguanines, morunasaurs, oplurines, crotaphytines, some tropidurines and anoloids form the bulk of Etheridge's Group II lizards (Etheridge 1959:103). Etheridge (''old tree'' in: Paull et al. 1976) proposed the iguanines as closest relatives to the basliscines. Etheridge & de Queiroz (1988) however, showed that basiliscines also share a great number of their derived features not only with iguanines (9), but also with tropidurines (11), anoloids (10), sceloporines (8), crotaphytines (7), oplurines (7) and morunasaurs (5) (Table 1). In light of this and other facts, they proposed that the iguanine-basiliscine relationship is a hypothesis in need of further testing.

The morunasaurs share the greatest number of their derived features with basiliscines, one more than they do with either sceloporines, oplurines or anoloids (Etheridge & de Queiroz 1988). Morunasaurs are also considered by some as being an ancestral "iguanid" grouping (Etheridge "old tree", in: Paull et al. 1976).

Because there is no well-defined phylogeny for the eight suprageneric "iguanid" taxa, all seven non-basiliscine suprageneric taxa will be used as outgroups to determine polarities of character transformation series. It should be noted that because "iguanids" are a metataxon, Acrodonta ("Agamidae" + Chamaeleontidae) should also be included as the eighth functional outgroup. However, it is hypothesized that the addition of an eighth outgroup would not affect the polarity decision at the ingroup/outgroup node. I will therefore restrict the functional outgroups to include the seven proposed suprageneric clades of "iguanids".

Etheridge & de Queiroz (1988) listed synapomorphies of each of the eight major suprageneric groups of "iguanids" (Table 2). These apomorphies are presumed autapomorphies for the clade they represent, i.e., they are indicators of the character distributions at the basal nodes of those clades. Using this "collapsed" character data set (Table 2) a new phylogeny can be obtained (Fig. 1). An important criterion must be kept in mind when collapsing the initial terminal taxa (genera) at the basal node to the level of the eight suprageneric clades. Homoplasies are lost, as are synapomorphies between taxa below the suprageneric level ("iguanid" genera).

The new cladogram of "iguanid" suprageneric taxa (Figs. 1—3) accentuates Etheridge & de Queiroz's (1988) findings. First, there is good evidence for the monophyly of the eight suprageneric clades and second, evidence for relationships between these clades is rather weak. Fig. 2 indicates the nodes for which there is the least amount of support. The five nodes identified are based almost entirely on homoplasies (convergences or reversals). A more realistic approach is to remove the homoplaseous nodes and collapse this cladogram at the weak nodes (Figs. 3a & 3b).

Information content is lost in the two successive collapsing events, but the stability of the hypothesized phylogeny has increased. We now have seven functional outgroups to determine the polarity of character states at the ingroup/outgroup node.

Although relationships between the eight suprageneric taxa of "iguanids" have not been established, the relationships within the suprageneric taxa are better known (Etheridge & de Queiroz 1988) (Fig. 4). The phylogenies of these outgroups are used as the basis for determining the character state at the respective basal outgroup nodes.

Because the tropidurines and anoloids are quite large clades and contain many rare taxa for which material is not available, not all genera for these two groups are represented in this study. However, an acceptable compromise has been reached. Care was taken to represent each major clade within the tropidurines and anoloids by its earliest diverging member, and whenever possible, with taxa for which sufficient skeletal material was available to show ontogenetic changes. Those taxa closest to the outgroup node (earliest diverging taxa) will have the greatest effect (1/2 of the polarity decision) on the character state found at that outgroup node, whereas derived taxa that are phylogenetically further removed from the basal nodes will have the least amount of influence on the decision at the outgroup node (Maddison et al. 1984, rule 3). All genera of the remain-

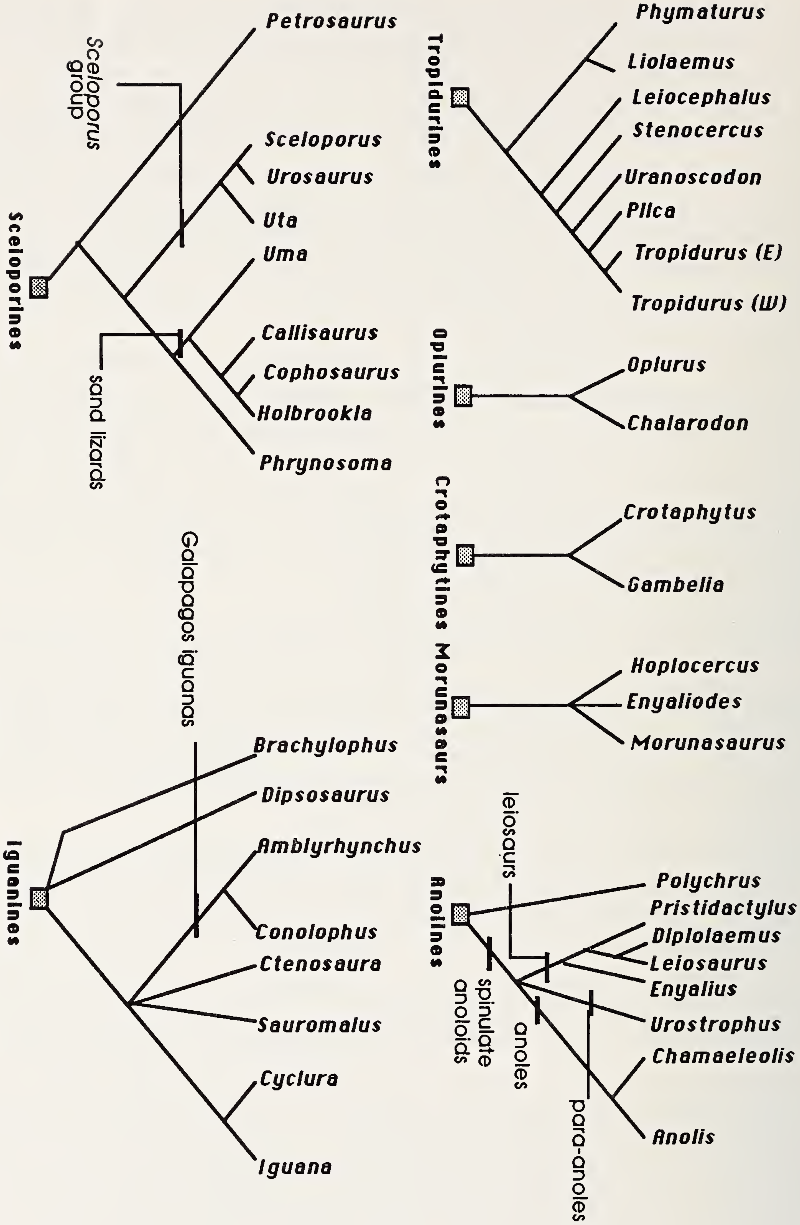


Fig. 4: Internal relationships within the 7 outgroup taxa (Etheridge & de Queiroz 1988). All genera are represented for 5 of the 7 suprageneric clades. For anolines and tropidurines the earliest diverging taxa for respective clades are represented. This topology is used throughout the study to determine the polarity at the basal outgroup nodes (primary level of analysis).

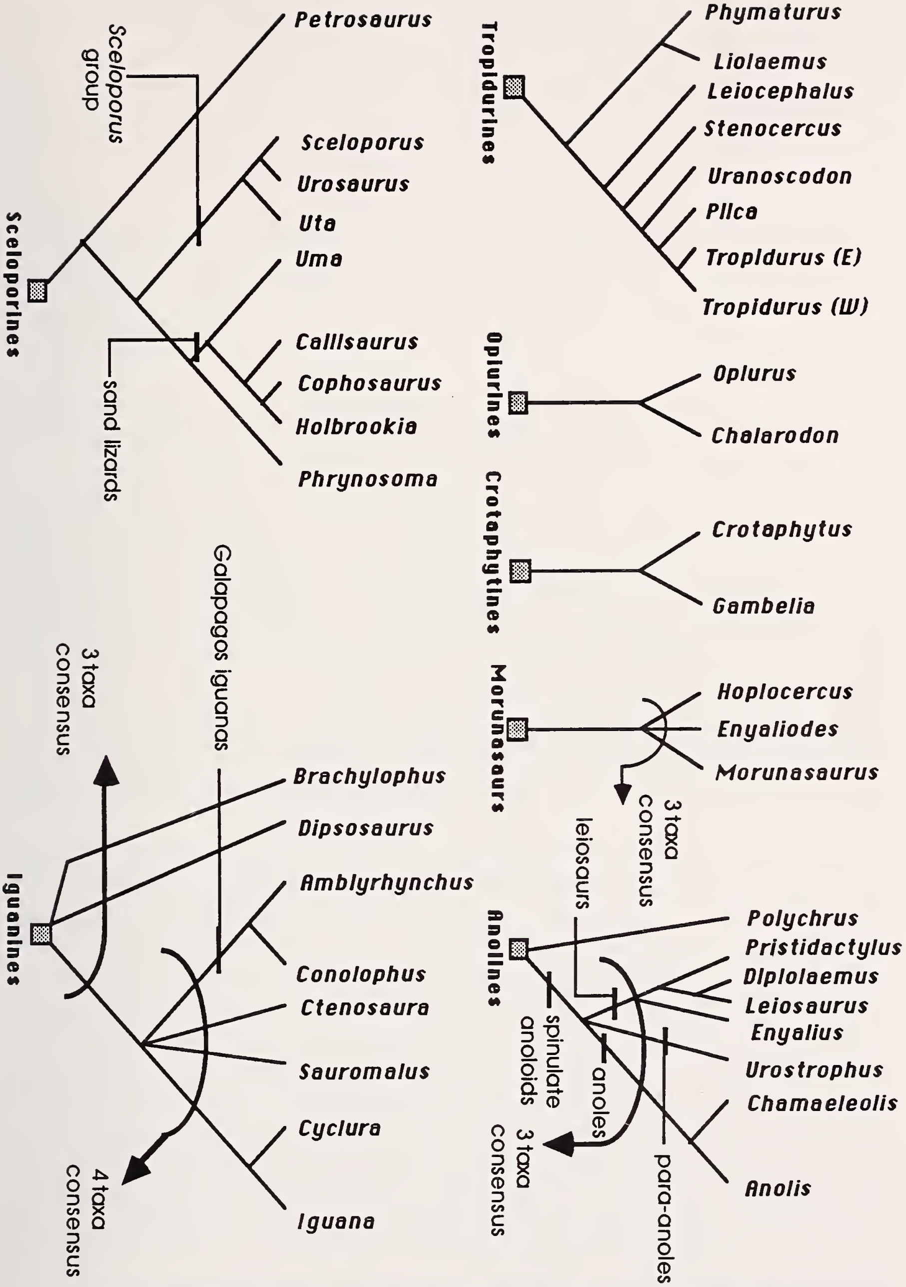


Fig. 5: Internal relationships of the 7 functional outgroups. Arrows indicate nodes at which consensus decisions are made (see text for discussion). Character states of dichotomous nodes are determined following Maddison et al. (1984) (see text and Fig. 7).

ing suprageneric clades (sceloporines, crotaphytines, oplurines, morunasaurs and iguanines) are represented (Fig. 4).

Within the tropidurines, *Phymaturus* (earliest diverging taxon) and *Liolaemus* represent the *Liolaemus*-group. The northern tropidurines are represented by *Leiocephalus* (earliest diverging taxon), *Stenocercus*, and the *Tropidurus*-group [*Uranoscodon, Plica*, Eastern and Western *Tropidurus*] (Etheridge & de Queiroz 1988) (Fig. 4).

Within the anoloids, *Polychrus* represents the earliest diverging taxon. The spinulate anoloids can be divided into three clades, the leiosaurs, the para-anoles and the anoles, that form a tritomy. The leiosaurs are represented by *Enyalius* (earliest diverging taxon), *Diplolaemus*, *Leiosaurus* and the paraphyletic *Pristidactylus*. The para-anoles are represented by *Urostrophus* and the anoles by *Chamaeleolis* and *Anolis* (Etheridge & de Queiroz 1988) (Fig. 4).

There are two levels of analysis in this study. The primary level of analysis determines the polarity at the basal outgroup nodes of the seven functional outgroups. The secondary level of analysis determines the polarity at the ingroup/outgroup node.

The polarity states at dichotomous nodes within the functional outgroups (primary level of analysis) are determined by the algorithm described by Maddison et al. (1984) (Fig. 7). However, Maddison et al.'s (1984) technique cannot be used at unresolved nodes. The ''consensus algorithm'' described below will be used at the four unresolved nodes within the ingroup to estimate character states at those nodes (Fig. 5). Polarities at the ingroup/outgroup node (secondary level of analysis) will also be determined using the consensus algorithm (Fig. 3).

Polarity decision of a binary character within the ingroup using a single outgroup involves the polarization of that character state within the ingroup that is also present in the outgroup as plesiomorphic. The alternate character state is polarized as apomorphic.

Considering two outgroups, the relationship of which are resolved or unresolved with respect to the ingroup, yields four possible patterns of character state distributions (A/A; A/B; A,B/A; A,B/A,B). The two resolved topologies can be rerooted at the ingroup/outgroup node giving identical topologies with respect to a single character distribution, i.e., the parsimonious assumption is made that the character does not alter character states between nodes. This ''rerooted topology'' is identical to the unresolved topology. The significant aspect for determining polarities at the ingroup node is the distribution pattern of character states among the outgroups and not the relationships among the outgroups. An equivocal polarity state (A,B) at a terminal node does not change the polarity decision and can therefore be removed from the analysis. Only two possible character state distribution patterns remain (Fig. 8). The first, (2:0 pattern) [A/A or B/B] results in an unequivocal polarity decision. The (1:1) [A/B] pattern results in an equivocal polarity decision. Each character showing a (1:1) distribution among two outgroups must be left unordered in the analysis.

The two topologies of an ingroup with three outgroups (Fig. 10) can be rerooted to a single topology (Fig. 9). Six character state distribution patterns among outgroup nodes can be identified, including equivocal character states (A,B). As previously mentioned,

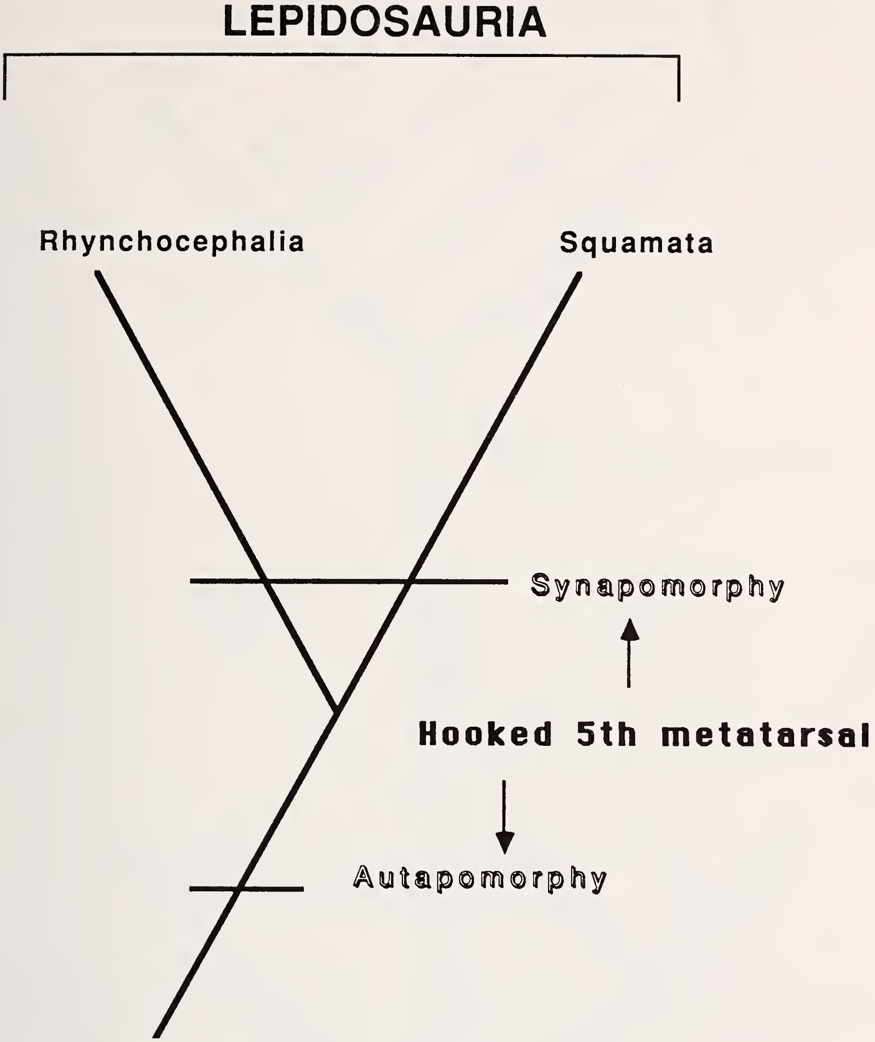


Fig. 6: Usage of the terms "synapomorphy" and "autapomorphy." Terminology follows that of Ax (1984).

equivocal character states at nodes do not alter the polarity decisions. For example a [A/A/A,B] character state distribution pattern with three outgroups can be reduced to [A/A] (2:0 pattern), resulting in an unequivocal polarity decision (Fig. 8). The [A/A,B/B] character state distribution pattern is reduced to [A/B] (1:1 pattern) resulting in an equivocal polarity decision.

After removing distribution patterns with equivocal character states only two distinct patterns remain (Fig. 9). For the (3:0) pattern an unequivocal decision is reached, in

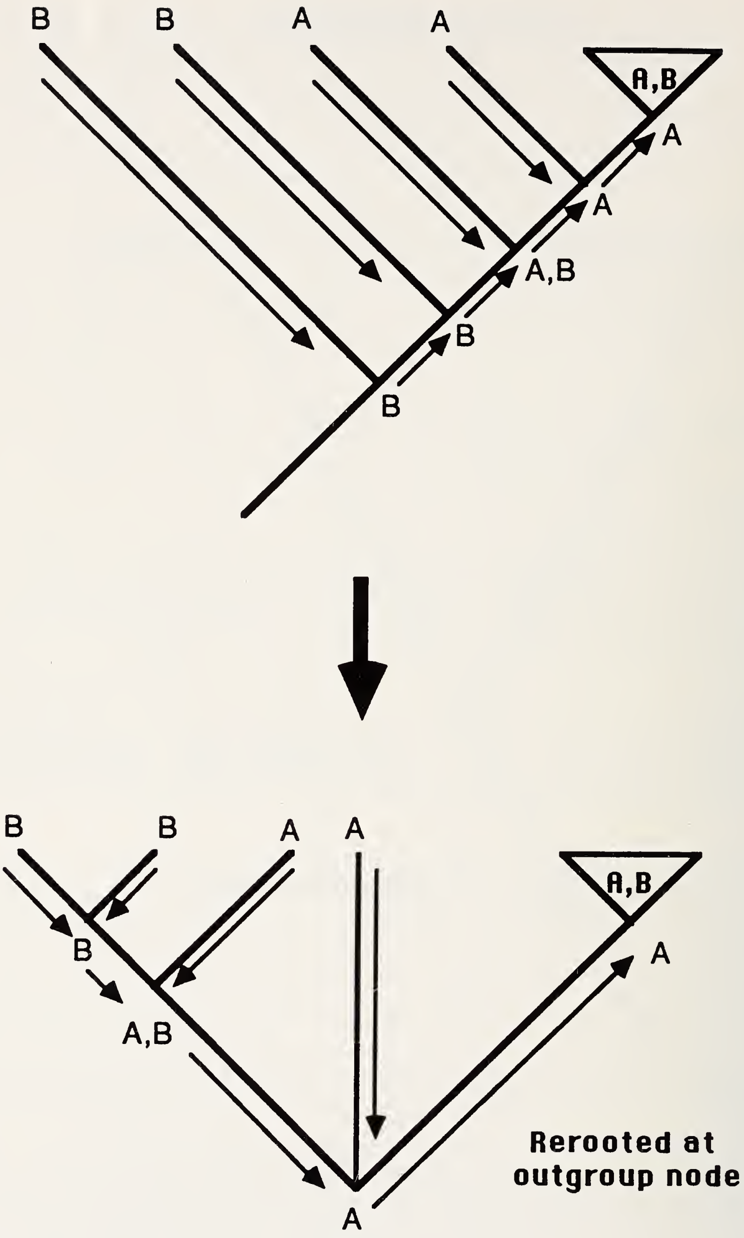


Fig. 7: Maddison et al's (1984) algorithm indicating the decision-making process of plesiomorphic character states at respective nodes (see text for further discussion).

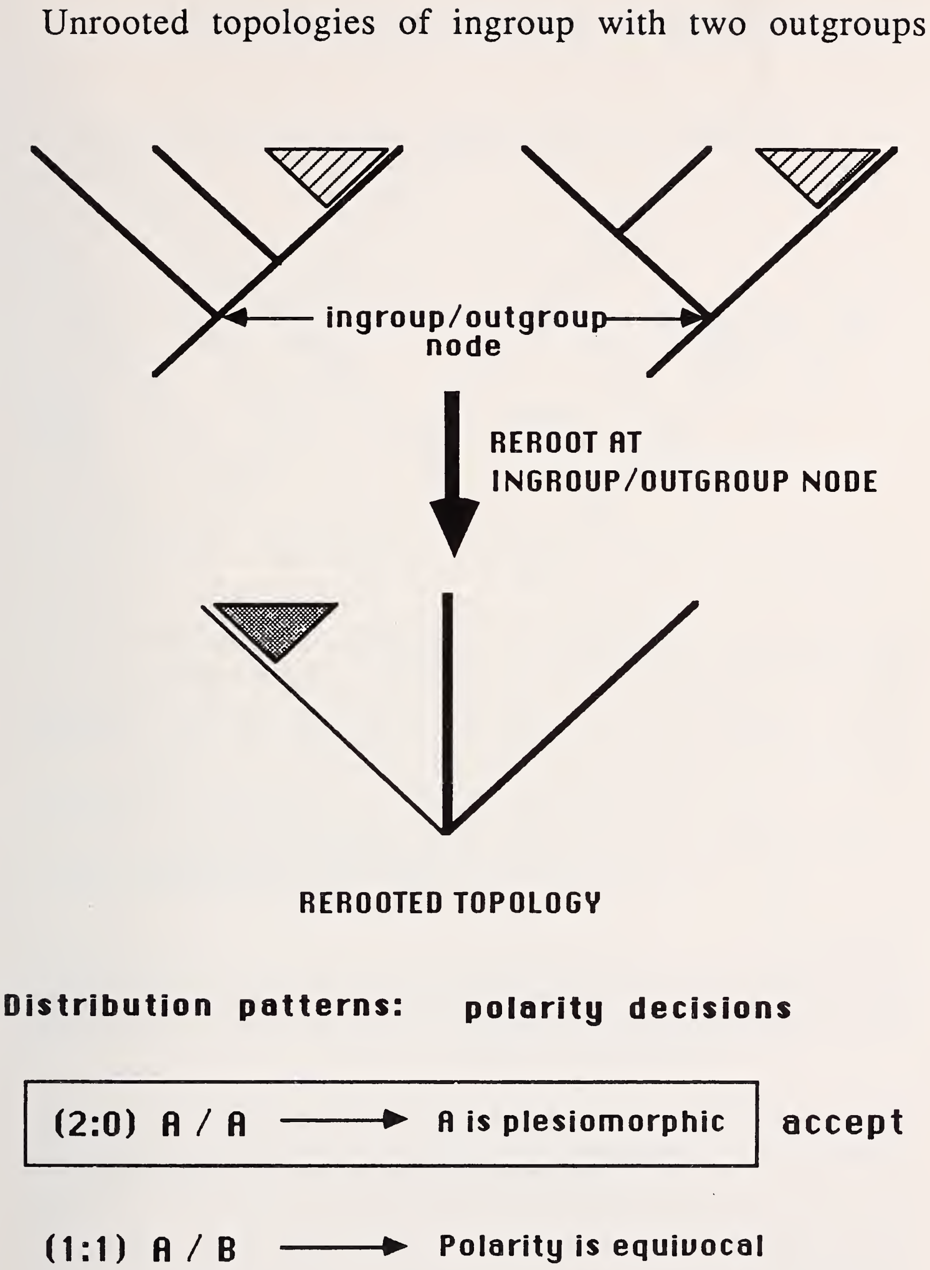
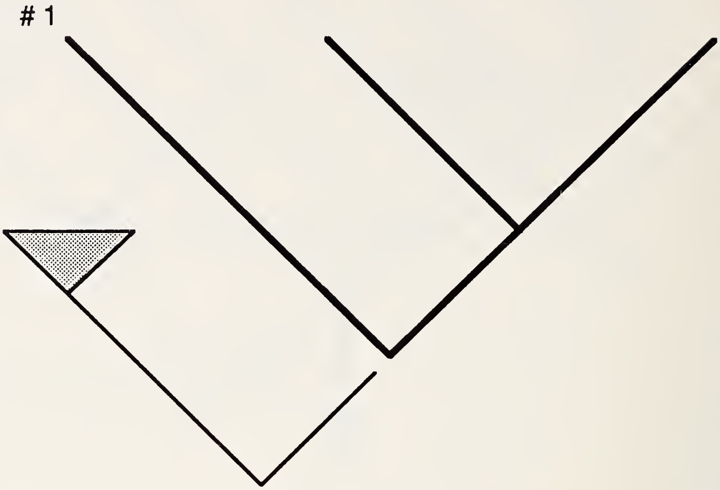


Fig. 8: Character state distribution patterns for two outgroups with resulting polarity decision at ingroup node. A single topology results when the 2 topologies are rerooted at the ingroup node.

REROOTED TOPOLOGY OF INGROUP WITH 3 OUTGROUPS:



Distribution patterns: polarity decisions

(3:0) A/A/A ⟶ A = PLESIOMORPHIC accept

(2:1) A/A/B ⟶ A = PLESIOMORPHIC
POLARITY EQUIVOCAL
(50 % occurrence)

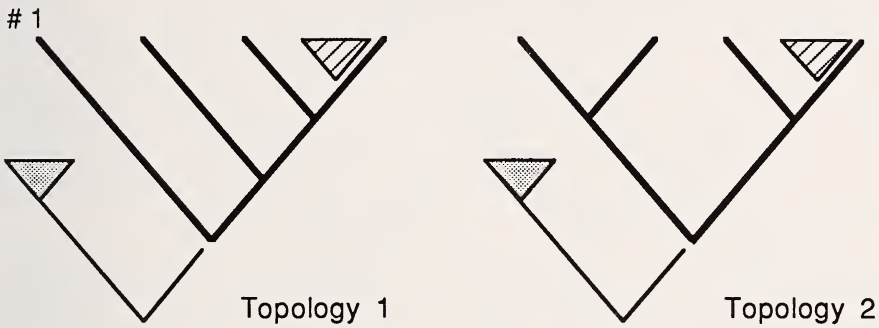
Fig. 9: Character distribution patterns and rerooted topology for an ingroup with three functional outgroups. The rerooted topology is derived from the 2 unrooted topologies of Fig. 10. This consensus algorithm is also used at the primary level of analysis to infer character states at tritomies.

which the widespread character state is the plesiomorphic condition at the ingroup/outgroup node. For a (2:1) pattern, an unequivocal polarity decision is reached if the widespread character state (e.g., ''A'') is found in the outgroup that is the closest sister-taxon to the ingroup (position 1 in Fig. 9). The polarity decision is equivocal if the alternate character state (e.g., ''B'') is found in that outgroup (1 position). The probability of this situation occurring is 50 %, allowing for equal probability of character distribution patterns and equal probability of occurrence of the two topologies. The less-common character state (e.g., ''B''), however, can never be the plesiomorphic condition at the ingroup/outgroup node. Each character showing a (2:1) character state distribution pat-

UNROOTED TOPOLOGIES OF INGROUP ▽ WITH 3 OUTGROUPS

AND

REROOTED TOPOLOGIES OF INGROUP ▽ WITH 4 OUTGROUPS:



Distribution patterns:	polarity decisions	
(4:0) A/A/A/A	A = PLESIOMORPHIC	accept
(3:1) A/A/A/B	A = PLESIOMORPHIC POLARITY EQUIVOCAL with B=#1 position of topology 1 (16.67 % occurrence)	
(2:2) A/A/B/B	A & B = PLESIOMORPHIC POLARITY IS EQUIVOCAL	

Fig. 10: Two unrooted topologies of an ingroup with 3 resolved functional outgroups (rerooted at the ingroup to a single topology Fig.9). The 2 unrooted topologies (IG and 3 OGs) are topographically identical to rerooted topologies of an IG with 4 OGs (Fig. 11). The consensus algorithm also infers character states at the basal node of a polytomy consisting of 4 unresolved clades.

tern among three unresolved outgroups should be left unordered in the analysis, because there is a 50 % chance of occurrence of a character distribution pattern that would result in an equivocal polarity decision.

Five taxa (four outgroups and one ingroup) under consideration result in three topographically different dichotomous cladograms depicting relationships among outgroups (Fig. 11). Rerooting at the ingroup node, two distinct topologies remain (Fig. 10). For any binary character, three character distribution patterns are possible, excluding equivocal characters (A,B) at terminal nodes. The (4:0) distribution pattern results in an unequivocal polarity decision. For a (3:1) distribution, a polarity decision is made, with the widespread condition being plesiomorphic. Only a single character state distribution pattern results in an equivocal polarity decision at the ingroup/outgroup node (''B'' in the 1 position of topology 1, Fig. 10). Assuming an equal probability of character state distribution patterns and an equal probability of obtaining either topology, the less-common character state in the 1 position of topology 1 has a 16.67 % chance of occurrence, which would result in an equivocal polarity decision.

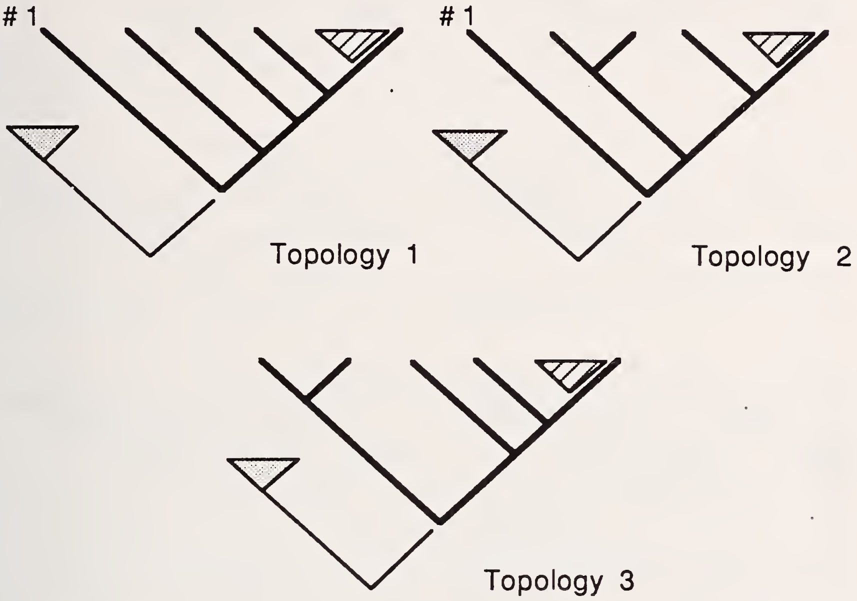
For an ingroup with five unresolved functional outgroups, six different topologies are possible (Fig. 12). When rerooted at the ingroup node, three distinct topologies remain with three character state distribution patterns. These three topologies are topographically identical to the three topologies involving 5 taxa (ingroup plus 4 outgroups) (Fig. 11). In the case of a (5:0) distribution pattern, the widespread character state is unequivocally the plesiomorphic condition at the ingroup/outgroup node. Considering a (4:1) distribution, there is a 75 % chance of occurrence of character states on topologies that result in an unequivocal polarity decision. This assumes that there is an equal probability of obtaining the three topologies and an equal probability of obtaining character state distribution patterns among these topologies. In a (4:1) distribution pattern, the less-common condition can never be hypothesized as being plesiomorphic. For this distribution pattern, the widespread character state should be accepted as the plesiomorphic condition at the ingroup/outgroup node considering the above mentioned criteria.

The eleven topologically different cladograms of an ingroup and six outgroups (Fig. 13A) can be rerooted at the ingroup node resulting in six dichotomous cladograms (Fig. 12). These six topologies are identical to the unrooted topologies of an ingroup with 5 outgroups. In this study, character state distribution patterns (6:0), (5:1) and (4:2) are polarized with the widespread condition being plesiomorphic at the ingroup/outgroup node. Characters with a (3:3) character state distribution pattern are left unordered. For a (5:1) pattern, a 13.06 % occurrence of character state distributions on topologies resulting in equivocal polarity decisions can be hypothesized (see Fig. 12 for cases). However, there is no condition for a (5:1) distribution in which the less-common character state (e.g., ''B'') can be considered plesiomorphic at the ingroup/outgroup node. In the case of a (4:2) pattern, there is only a hypothesized 4.85 % occurrence of character state distributions on topologies that could result in the less-common condition (e.g., ''B'') being the plesiomorphic state at the ingroup/outgroup node (Fig. 12). This is only the case when Maddison et al.'s (1984) ''doublet rule'' is in effect (e.g., ''B'' is in the 1 and

UNROOTED TOPOLOGIES OF INGROUP ▽ WITH 4 OUTGROUPS

AND

REROOTED TOPOLOGIES OF INGROUP ▽ WITH 5 OUTGROUPS:



Distribution patterns: **polarity decisions**

(5:0) A/A/A/A/A ⟶ A = PLESIOMORPHIC

(4:1) A/A/A/A/B ⟶ A = PLESIOMORPHIC
POLARITY EQUIVOCAL
with B=#1 position of top.1 & 2
(25 % occurrence)

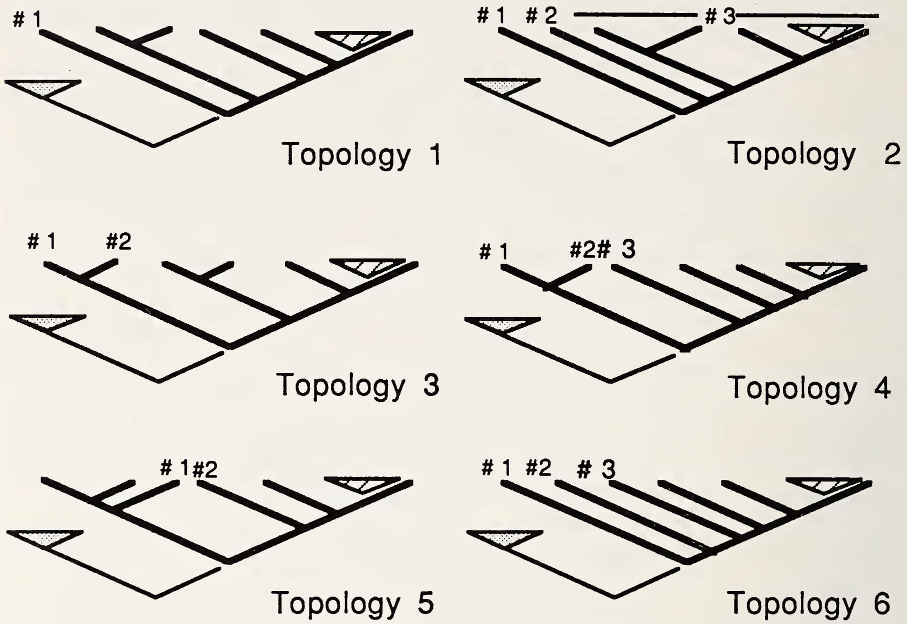
accept

(3:2) A/A/A/B/B ⟶ A = PLESIOMORPHIC
POLARITY IS EQUIVOCAL
B = PLESIOMORPHIC (Topology 1 only)

Fig. 11: Three unrooted topologies of an IG with 4 resolved functional OGs. The 3 topologies rerooted at the ingroup node result in the 2 topologies of Fig. 10. These topologies are topographically identical to rerooted topologies of an IG with 5 OGs (Fig. 12). The consensus algorithm with decisions also infers character state polarities at the basal node of a polytomy consisting of 5 unresolved clades.

UNROOTED TOPOLOGIES OF INGROUP ▽ WITH 5 OUTGROUPS

AND REROOTED TOPOLOGIES OF INGROUP ▽ WITH 6 OUTGROUPS:



Distribution patterns: **polarity decisions**

(6:0) A/A/A/A/A/A → A = PLESIOMORPHIC

(5:1) A/A/A/A/A/B → A = PLESIOMORPHIC
POLARITY EQUIVOCAL (13.06 % occ)
with B=#1 position of Top. 1, 2 & 6

(4:2) A/A/A/A/B/B → A = PLESIOMORPHIC
POLARITY IS EQUIVOCAL, when B is
#1 & #2 positions of Top. 3,4 & 5
#1 & #3 positions of Top. 2 (26.76 % occ)
#1 & any position of Top. 1
#1 & any position or #2 & #3 of Top. 6
B = PLESIOMORPHIC, when B is
#1 & #2 positions of Top. 2 & 6
(4.85 % occurrence)

accept

(3:3) A/A/A/B/B/B → A & B = PLESIOMORPHIC
POLARITY IS EQUIVOCAL

Fig. 12

2 positions of topologies 2 and 6). For a (3:3) pattern no unequivocal polarity decision can be reached.

An ingroup with seven functional outgroups results in eleven rerooted topologies at the ingroup node (Fig. 13A). In this study, characters with a (7:0), a (6:1) or a (5:2) distribution pattern will be polarized. In each case the widespread condition is the plesiomorphic condition at the ingroup node. In the case of a (5:2) character state distribution pattern there is a 2.47 % chance of occurrence of character states on topologies that would result in the less-common character state being plesiomorphic (Fig. 13B).

It must be reemphasized that an equivocal character state at a basal node does not affect the polarity decision at the ingroup/outgroup node and can be left out of the analysis. For example: the following character states for four outgroups (A/A/A/A,B) results in the same polarity decision as a (3:0) distribution for three outgroups (A/A/A) (Fig. 9). This is also true for multiple equivocal character states within a character set. The (A/A/A,B/A,B) character state combination for four outgroups results in the same polarity decision as case (2:0 pattern) for two outgroups (A/A) (Fig. 8).

The number of topologies increases as the number of functional outgroups used are increased. It is also true that with increasing numbers of outgroups it is more difficult to make unambiguous polarity decisions.

The algorithm described above differs from de Queiroz (1987) with respect to definition of the character states at the outgroup nodes. De Queiroz's (1987) algorithm assumes that the internal topology of the outgroups used to determine the polarity at the ingroup/outgroup node is not resolved. An "A,B" identified in de Queiroz's algorithm indicates that both character states are present within that outgroup, whereas "A,B" in this study signifies the condition found at the basal node of that clade. The indication of an "A" in de Queiroz's algorithm signifies that all taxa within that clade have the "A" condition. In this study "A" indicates the plesiomorphic condition found at the basal node of the outgroup taxon. For example, if *Phymaturus*, *Leiocephalus* and *Stenocercus* have the "A" condition and all other tropidurines have the alternate condition "B", the outgroup will be coded "A", because that is the plesiomorphic condition at the basal tropidurine node. Using de Queiroz's algorithm, the tropidurines would be coded "A,B" since both conditions are observed within the taxon.

For multistate characters the situation is more difficult. Nevertheless, the above mentioned criteria concerning polarity decisions remain unchanged. For example, a

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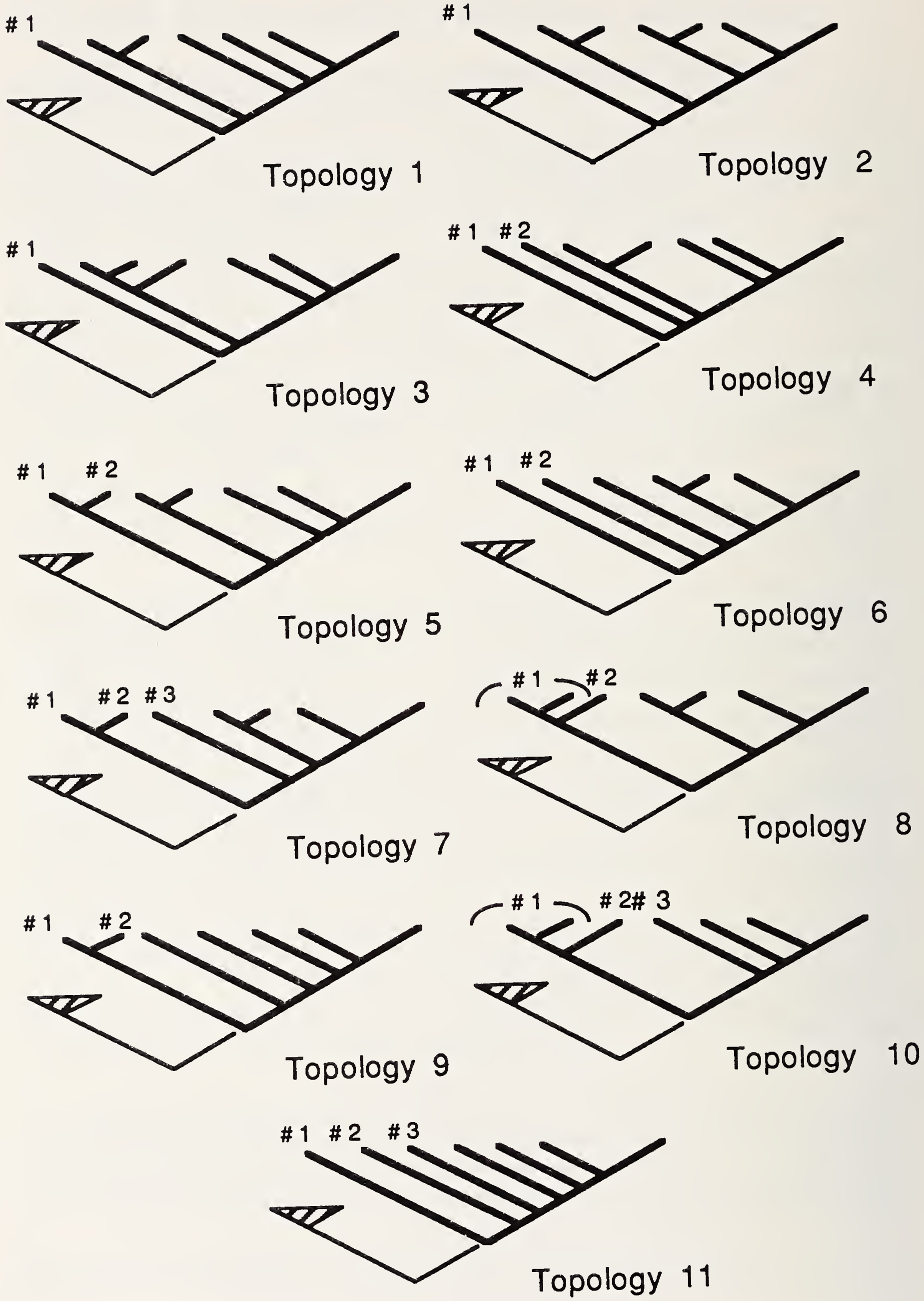
Fig. 12: Six unrooted topologies of an IG with 5 resolved functional OGs. The 6 topologies can be rerooted at the IG node and result in the 3 topologies of Fig. 11. The 6 topologies are topographically identical to the 11 rerooted topologies of an IG with 6 OGs (Fig. 13A). The consensus algorithm with decisions also infers character state polarities at the basal node of a polytomy consisting of 6 unresolved clades.

Fig. 13A: Eleven unrooted toplogies of an IG with 6 resolved functional OGs. The 11 topologies can be rerooted at the IG node and result in the 6 topologies of Fig. 12.

Fig. 13B: Inferred polarity decisions of IG with 6 resolved OGs. The consensus algorithm also infers character state polarities at the basal node of a polytomy consisting of 7 unresolved clades.



Topology 1

Topology 2

Topology 3

Topology 4

Topology 5

Topology 6

Topology 7

Topology 8

Topology 9

Topology 10

Topology 11

Fig. 13A

UNROOTED TOPOLOGIES OF INGROUP ▽ WITH 6 OUTGROUPS

AND

REROOTED TOPOLOGIES OF INGROUP ▼ WITH 7 OUTGROUPS

Distribution patterns: polarity decisions

(7:0) A/A/A/A/A/A/A → A = PLESIOMORPHIC

(6:1) A/A/A/A/A/A/B → A = PLESIOMORPHIC
POLARITY IS EQUIVOCAL; B is
#1 position of Top.
1, 2, 3, 4, 6 & 11
(13.49 % occurrence)

(5:2) A/A/A/A/A/B/B → A = PLESIOMORPHIC
POLARITY IS EQUIVOCAL; B is
#1 & #2 of Top. 5 & 8
#1 & any pos. of Top. 1, 2 & 3
#1 & any position but #2
of Top. 4 & 6
#1 & #2 or #1/#2 & #3
of Top. 7, 9 & 10
#1 & any position but 2 or
#2 & #3 of Top. 11
(26.59 % occurrence)
B = PLESIOMORPHIC, when B is
#1 & #2 of Top. 4, 6 & 11
(2.47 % occurrence)

accept

(4:3) A/A/A/A/B/B/B → A = PLESIOMORPHIC
POLARITY IS EQUIVOCAL
B = PLESIOMORPHIC
(not for Top. 5 & 8)

Fig. 13B

[A/A/A/A/B/C] (4:1:1) pattern results in the same polarity decision as a (4:2) pattern, in which the widespread condition is the plesiomorphic condition. In fact, in the above mentioned example, the less-common states (B or C) can never be considered to be the plesiomorphic condition at the basal node. For a (4:2) pattern the less-common state can be considered to be plesiomorphic at the basal node (Fig. 12). As an operational rule for multistate characters, the less-common states will be pooled and polarity decisions will then be inferred.

Character Definition

Characters were chosen that differ absolutely between the taxa, such as: the absence or presence of a structure; positional differences between structures that do not change during post-embryonic ontogeny; differences in shapes of structures; variation in the number of serial structures; variation in patterns between different taxa; and structures that vary under ontogenetic control for all members of a taxon (or taxa), but not for other taxa (de Queiroz 1985).

The following characters were omitted: 1) characters that do not vary between the basic taxa. 2) Characters of proportional differences, because they are often a reflection of ontogenetic change. 3) Characters whose variation within a basic taxon obscures the pattern of variation of that character between basic taxa (see discussion of variation below).

Although autapomorphies for terminal taxa do not contain any information about relationships between taxa, they will be included in the data matrix. This is an artifact of the algorithm used in this analysis. There is no à priori evidence that a character state unique to a single terminal taxon is to be regarded as an autapomorphy rather than a synapomorphy for all remaining terminal taxa. Autapomorphies are informative as indicators of monophyletic clades.

Characters are then represented as part of a linear unidirectional or bidirectional transformation series. Characters of a linear transformation series with a higher number indicate a direct transformation from a character state with the next lower number based on outgroup comparison (0 is used for the primitive state, 1 for the derived or intermediate state when a multistate character is used, and 2 is the most derived state in a three state character transformation series, etc.). A bi-directional transformation series on the other hand, implies a case of character evolution in two directions on either side of the plesiomorphic (ancestral) state. In this case the character has to be split into two uni-directional characters. Since cladograms are constructed on synapomorphies, this should not create any problems because a bi-directional transformation series can be considered as two ''uni-''directional transformation series in two different directions.

Each new or undescribed character examined, is followed by a description of its condition and variation within the basic taxa and the outgroups. Description of characters used from other studies are referenced and a brief description of the character states together with comments on discrepancies, ambiguities and/or conflicting ideas on polarity decisions are given. Each character used from an outside source has been checked on specimens to assure its accuracy, and personal observations or inconsistencies are noted. Characters and character states are re-evaluated when necessary. Additionally, a hypothesis of polarity will be established for each character transformation series using the outgroup consensus method described above.

The primary source of characters has been osteology, for several reasons: 1) When analyzing fossil taxa, characters of soft anatomy are not (or seldom) determinable. Consequently, when constructing a cladogram of extant taxa using primarily osteological characters, fossil taxa, when discovered, can be added to the cladogram quite readily. 2) It is more difficult to obtain a complete data set for characters of soft anatomy.

A data matrix (Table 5) was constructed after characters were identified and polarities indicated. This data matrix was then run on the PAUP (Phylogenetic Analysis Using Parsimony) program. A hypothetical phylogeny was then constructed showing sister taxa relationships among the basiliscines.

The term cladogram will be used throughout this study in place of phylogenetic tree, because no implication of ancestral taxa will be made.

Problems of Variation

Estes et al. (1988) gives an extensive discussion on the problems of variation within basic taxa involved in a cladistic analysis. The study used ''families'' of squamates as basic taxa. The basic taxon in this study is at the species level and, thus, the level of variation within terminal taxa is considerably less. Using less inclusive terminal taxa has been one of the solutions to the problems of variation discussed in the above mentioned study.

Variable characters as such are indicative of paraphyly. An additional point made by Estes et al. (1988) was that in previous systematic studies little or no comments on variation observed were reported. A conclusion may be that sample sizes were consistently too small to detect variation, or that information was deleted, which is contrary to the goal of science. I have made a conscious effort in this study to obtain adequate series of specimens as well as to emphazise ontogenetic series and sexual dimorphism. Every effort was also made to indicate observable variation within all basic taxa.

No solution to the problem of coding observable variable characters in terminal taxa can be proposed that does not have drawbacks. I will discuss three solutions to this problem, two of which are briefly discussed in the above mentioned studies.

In coding taxa with variable characters, Kluge & Farris (1969) split each taxon into two ''new'' taxa in order to maintain the information. For example, if one character is variable within taxon X; taxon X is split up into two taxa X1 and X2 each showing the exact same character states except for the variable character. If a taxon shows three variable conditions for a particular character, than the taxon will be split up into three ''new'' taxa, X1; X2; X3, each exhibiting a different variable state for that particular character. In the case in which two taxa have two variable characters, four ''new'' taxa have to be created to cover all possible combinations, unless all those specimens that show a variable condition for one character have the same variable condition for the other character, in which case only two ''new'' taxa are required. Nevertheless there will be an increase in the number of new taxa in two dimensions for each character in order to encompass all possible combinations. One increase occurs along the axis of ''number of variable states per character'' (linear growth), the other along the axis of ''number of variable characters per taxon'' (geometrical growth). The McClade program (Maddison & Maddison 1986) allows for polymorphisms within the data matrix and follows Kluge & Farris' (1969) operational method. However the same problem with numerous variations exist.

A second option is that all variable characters are deleted from the analysis and then later added to the cladogram, hypothesizing which state is most compatible with the other characters at hand. This is analogous to Le Quesne's (1979) method subsequently altered by Underwood (1982, pers. comm.), in which initially a character set is sought that is entirely compatible with itself, resulting in an initial cladogram with no homoplasies at all. The problem with this second option is that the initial cladogram may be constructed on a restricted data set and may not reveal the most parsimonious cladogram.

Estes et al.'s (1988) suggestion is that the plesiomorphic state based on morphological grounds, i.e., the condition that is found in outgroups, should be assigned to the taxa if a variable condition is observed. However, this practice amounts to asserting that the homoplasy is a convergence. If the morphologically ''derived'' condition is chosen for that taxon, the homoplasy then becomes a reversal. One therefore must arbitrarily choose a condition and later reevaluate the analysis and decide which state is most congruent with the other data at hand.

The problem seems to be one of how much variation is present in the data set itself, rather than deciding how to handle variation itself. Preferably, the Kluge & Farris (1969)/McClade (Maddison & Maddison 1986) methodology is used if few variable characters are present in the data set. On the other hand, Estes et al.'s (1988) method is preferred if numerous variable characters are present, rendering the Kluge & Farris/McClade method unmanageable.

DESCRIPTION OF CRANIAL SKELETON

Bones of the vertebrate skeleton can be divided into primary and secondary endoskeletal bones depending on their phylogenetic origin.

Most primary endoskeletal bones develop through endochondral ossification, which initially requires a hyaline cartilage model that is invaded by osteoblasts later in its development, replacing the cartilage with bone. Phylogenetically, primary endoskeletal bones always have been associated with the endoskeleton. Primary endoskeletal elements within the skull and lower jaws can be further categorized into neurocranium and splanchnocranium.

The neurocranium of squamates consists of the supraoccipital, exoccipitals, basioccipital, basisphenoid, prootics, scleral ossicles and septomaxillae. The main function of the neurocranial bones is to protect the brain and primary senses, such as olfaction (septomaxillae), vision (scleral ossicles) and hearing (prootic, exoccipitals and supraoccipitals).

The splanchnocranium of squamates consists of primary endoskeletal bones such as the epipterygoids, quadrate and articular, which function as gill supports in sarcopterygians, but have become associated with the skull and lower jaw of tetrapods.

Secondary endoskeletal bones (dermal bones) develop through intramembranous ossification and are phylogenetically part of the dermal exoskeleton of early sarcopterygians. In higher tetrapods these dermal bones become associated with the primary endoskeleton.

The dermal bones of the skull are collectively called the dermocranium, which include most of the skull and jaw bones except for the primary endoskeletal elements. The clavicle and interclavicle are part of the pectoral girdle and are the only remaining dermal bones of the post-axial skeleton.

In the following section are descriptions of the cranial skeleton of basiliscines. The characters are described as they pertain to the ingroup, and a brief indication of the condition within the remaining "iguanids" is also noted. Descriptions begin anteriorly and proceed posteriorly, regardless of phylogenetic origin or embryonic development. I do not consider it necessary to provide an elaborate discussion and description of the terminology of structures used, for that, the reader is referred to the excellent anatomical descriptions of Oelrich (1956) and Jollie (1960) for skull, jaws and hyoid apparatus, and Romer (1956) for postcranial elements. Their terminology will be used throughout this study except where indicted. Variation of described structures should be assumed to be consistent unless otherwise stated.

For convenience, the description of the cranial skeleton is subdivided into the following components arranged topographically: nasal capsule, palate, orbital region (including scleral ossicles), temporal region, posterior brain case and lower jaws (including the hyoid apparatus) and miscellaneous cranial characters.

Nasal Capsule

The anterior elements of the palate (premaxilla, maxilla and vomer) form the floor and part of the wall of the osseous nasal capsule. The nasal spine of the premaxilla, the nasals, lacrimals and the anteromedial portion of the prefrontals form the walls and the roof of the osseous nasal capsule. Imbedded within the nasal capsule is the septomaxilla.

Character 1: roof of nasal capsule (Figs. 14, 24). Analysis of ontogenetic series of *Basiliscus vittatus* indicates that during postembryonic growth, the anterior portion of the frontal bone grows anteriorly and is overlapped by the posterior aspect of the nasals. In juvenile *B. vittatus* the roof of the nasal capsule is uncovered and a fontanel is visible at the medial junction between the nasals and the frontal bone. In most adult "iguanids" examined, the posterior aspect of the nasals overlap the anterior aspect of the frontal bone and the roof of the nasal capsule is closed by bone.

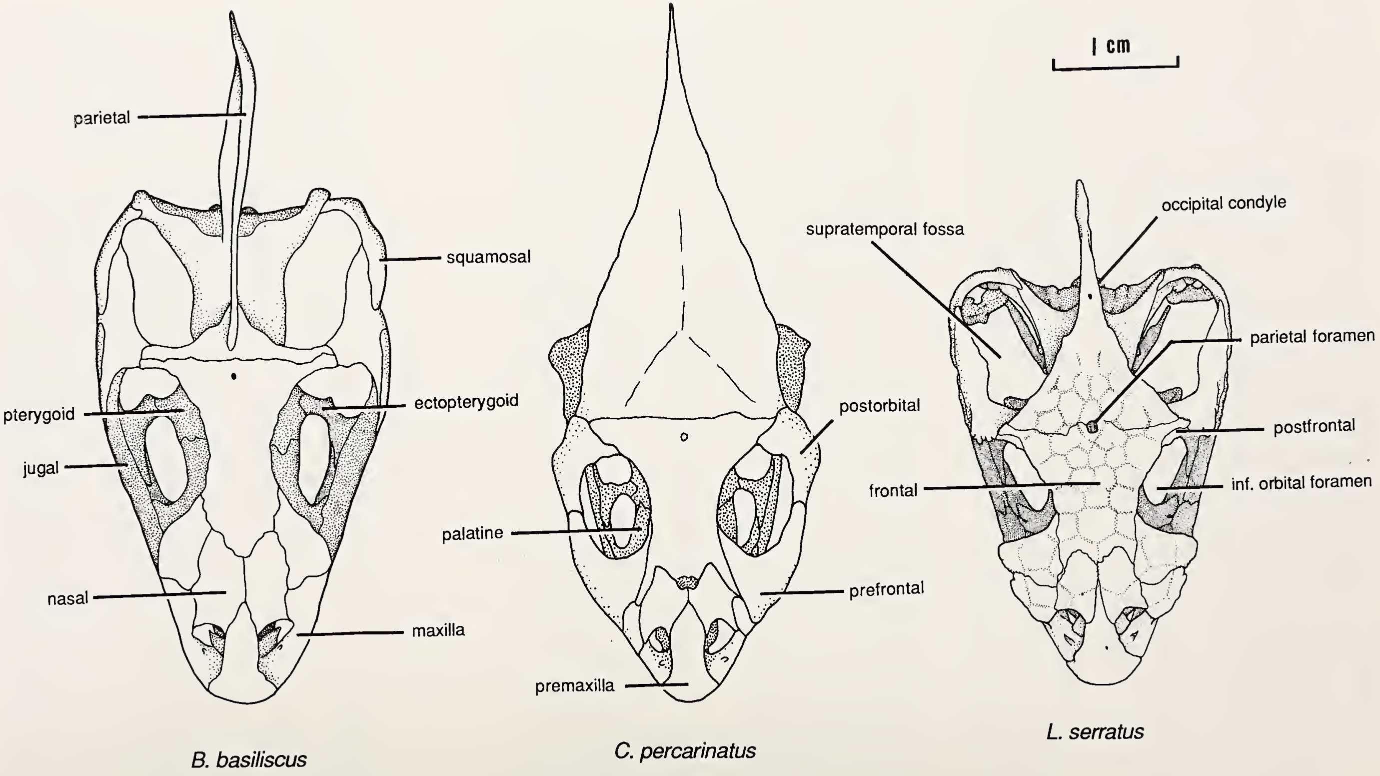


Fig. 14: Dorsal view of the skulls of *Basiliscus, Corytophanes* and *Laemanctus*. (Drawing of *Laemanctus* is by courtesy of K. de Queiroz).

In the morunasaurs *Enyalioides laticeps* and *Hoplocercus spinosus* a fontanel at the naso-frontal junction is present in juveniles that persists in adults. In the tropidurine genera *Uranoscodon* and *Strobilurus* an open nasal capsule roof is visible in adult specimens (G. Pregill, pers. comm.). Adult *Plica plica* also have nasal capsules that are not entirely roofed by bone. A small fontanelle is also present at the fronto-nasal suture in *Phrynosoma douglassii, P. orbiculare*, in some *P. modestum* (Presch 1969; pers. obs.) and in *Petrosaurus*. In all other "iguanids" examined, the anterior portion of the frontal bone was covered by the posterior overlap of the nasal bones, roofing the posterior aspect of the nasal cavity with bone.

Character state distribution at the basal nodes of the outgroups indicate that the bony nasal capsule roof in adults is the primitive condition in "iguanids" (6:0 consensus). The failure of the roof of the nasal capsule to close in adults is determined to be the derived condition[4].

In adult *Basiliscus* and *Laemanctus* the nasal capsule is roofed with bone, exhibiting the primitive "iguanid" condition. In *Corytophanes* a fontanel exists at the nasofrontal junction. The fontanel is proportionally larger in juvenile and smaller specimens but still remains in adult forms. In the largest specimens examined, a small fontanel is present located in a distinct indentation at the nasofrontal suture.

Septomaxillae (Fig. 15)

The septomaxilla is a thin, paired bone located anteriorly within the nasal capsule and separated by the nasal septum. The septomaxillae are held in place by cartilages within the nasal capsule, and lie on top of Jacobson's organ serving as a protective element for the anterior portion of the olfactory chamber.

Character 2: septomaxillae (Fig. 15). Three different conditions concerning the size and morphology of the septomaxillae exist in "iguanids". In iguanines, crotaphytines, oplurines and morunasaurs, the septomaxillae are bony elements that contact each other at the nasal septum. Occasionally, in some taxa (e.g. *Amblyrhynchus*) the horizontal plates curve dorsally and contact the ventral surface of the nasals (de Queiroz 1987). In all sceloporines, with the exception of *Cophosaurus, Holbrookia* and *Phrynosoma* the septomaxillae contact each other at the midline. In the latter three taxa the septomaxillae are reduced and are small horizontal platelets that do not contact at the midline. Septomaxillae contacting at the midline are found within the *Liolaemus*-group (e.g. *Liolaemus* and *Phymaturus*), and in *Stenocercus rosieventris* (Etheridge, pers. comm.). In most tropidurines the septomaxillae are small and do not contact each other at the midline. The character state at the tropidurine basal node is therefore equivocal.

In most anoloids examined, the septomaxillae are small, and are located in a horizontal plane not contacting at midline. In *Anolis marmoratus* the septomaxillae are in contact

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[4] In morunasaurs it is equally parsimonious to assume that the derived condition is a synapomorphy for that clade with reversals to the primitive condition in *Morunasaurus* and some species of *Enyalioides* as it is to consider the independant evolution of the uncovered nasal capsule roof in *Hoplocercus* and in some species of *Enyalioides*.

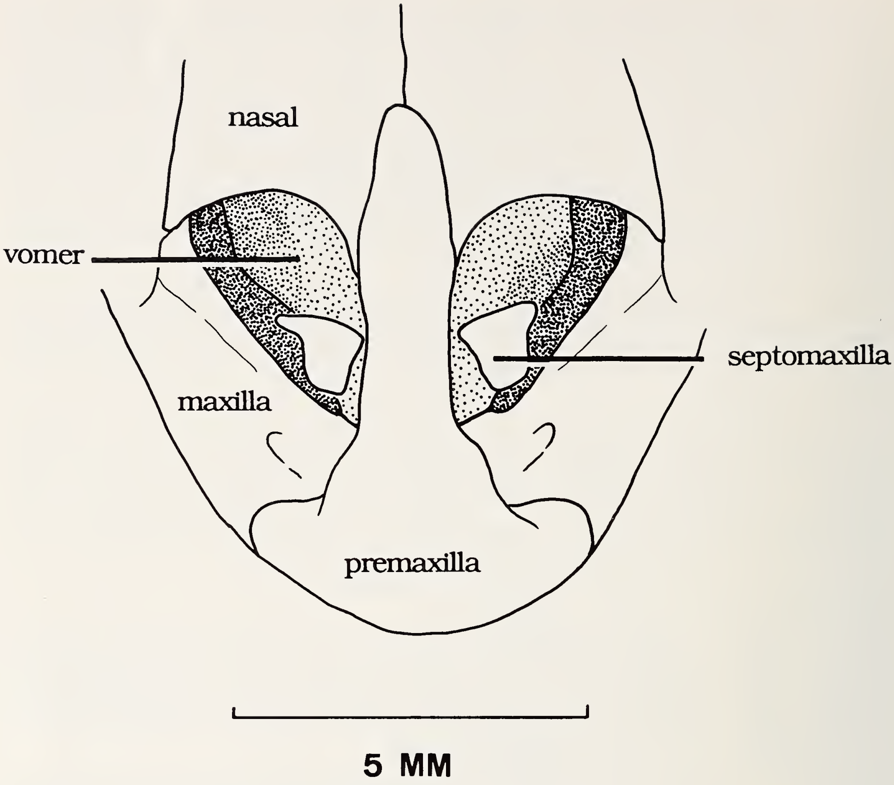


Fig. 15: Size and position of the septomaxillae *Laemanctus*.

(G. Pregill, pers. comm.). In *Leiosaurus belli* the septomaxillae were absent. During skeletal preparation the septomaxillae are sometimes inadvertently lost.

The septomaxillae in *Basiliscus* are small and triangular and separated at the midline by the nasal septum, when present. They are located on top of the vomers, but only slightly in contact with them. They are in contact with the maxillae along the anterior border. The posterior border curves dorsally, but lies free within the nasal capsule. In young specimens of *Basiliscus* the septomaxillae are proportionally larger and there is more extensive midline contact. No discernable variation within *Basiliscus* was observed.

In most specimens of *Corytophanes* species the septomaxillae are absent. Special attention was given to the anterior region of the snout during skeletal preparation to confirm the presence or absence of septomaxillae. When present in *Corytophanes*, the septomaxillae are slivers of thin, flat lamellar bone imbedded in connective tissue. Anteriorly they only slightly contact the maxillae at the anteromedial border but do not contact the underlying vomers. Posteriorly they do not curve dorsally as in *Basiliscus*.

The septomaxillae in *Laemanctus* are small and have a small contact zone with the maxillae anteromedially, but fail to reach the nasal septum or contact each other at the midline. Posteriorly the septomaxillae are straight, with no dorsal curvature (Fig. 15).

The distribution of character states among outgroups reveals a (5:1) consensus decision. Large septomaxillae contacting at the midline is the hypothesized plesiomorphic character state found at the ingroup/outgroup node.

Corytophanes and *Laemanctus* therefore show the apomorphic condition of the reduction (or loss) of the septomaxillae with loss of medial contact. This polarity decision contradicts that of Estes et al. (1988), in which septomaxillae not contacting at the midline (separated by a gap filled by the cartilaginous internarial septum) is considered to be plesiomorphic for squamates. Septomaxillae contacting each other at the midline is considered to be apomorphic. Estes et al. (1988) indicate that separated septomaxillae is the condition found in ''iguanids''. As indicated above, septomaxillae in contact is the widespread condition in ''iguanids'' suggesting a convergence with Scleroglossa (non-iguanian squamates).

Nasals (Figs. 14, 23)

The nasals are paired bones lying along the midline of the skull forming the roof of the nasal capsule. The nasals articulate with the nasal spine of the premaxilla, the frontal the prefrontals (occasionally) and with the ascending process of the maxilla. During ontogeny the frontal bone grows anteriorly underneath the nasal bones (see above), so that the posterior aspect lies within an excavation of the anterior portion of the frontal.

In *Basiliscus*, the dorsal aspect of the nasal and the nasal capsule is distinctly convex, being more pronounced in young (with no visible parietal crest) and subadults (with a small parietal crest) than in adults (with completely fused epiphyses). In both *Corytophanes* and *Laemanctus*, the dorsal aspect of the nasals is flat.

Character 3: nasal median contact (Figs. 14, 23). The medial contact zone between the two nasal bones varies considerably within ''iguanids''. In the sceloporines *Callisaurus, Holbrookia* and in *Hoplocercus* the nasals are separated for approximately 50% of their medial length by the nasal spine of the premaxilla. By contrast, in *Amblyrhynchus* and *Conolophus* there is essentially little or no medial separation of the nasals. The nasals cover the nasal spine posteriorly so that the posteriormost portion of the spine that is visible dorsally falls short of the transverse plane at the posterior end of bony external nares. *Brachylophus* and *Dipsosaurus* have about a 5% medial separation. The remaining iguanines (*Sauromalus, Ctenosaura* and *Iguana*) have the widespread ''iguanid'' condition of ca. 25% medial separation of the nasals by the nasal spine of the premaxilla. Some specimens of *Ctenosaura hemilopha*, and all specimens of *Sauromalus obesus*, have a separation of more than 50%. In *Leiosaurus belli* the nasals are completely separated. In the remaining outgroups, the nasals are separated anteriorly by the nasal spine by less than 50% of their median length. In oplurines there is very little anterior separation. In observed specimens of *Chalarodon madagascarensis* and *Oplurus cuvieri* the nasals are separated by approximately 20% of their entire median length. In *Leiocephalus* the amount of median contact varies ontogenetically (G. Pregill, pers. comm.). However, in all stages of ontogeny observed the median separation remained less than 50%.

Basiliscus and *Laemanctus* show the widespread "iguanid" condition (less than 50% nasal separation). In *Corytophanes hernandezi* and *C. percarinatus* the nasals are separated medially by more than 50% of their length (Fig. 14, 23). In all specimens of *C. cristatus* examined the nasals were almost always completely separated (Fig. 23). The nasal spine as such is not enlarged in *Corytophanes*, but rather the nasals are reduced and the anterior portions are oriented more laterally.

The distribution of character states at the outgroup basal nodes and the overall consensus cladogram suggests that the medial separation of the nasals by less than 50% of the total median length of the nasals is the primitive condition in "iguanids" (7:0 consensus), with a nasal separation of more than 50% being the intermediate condition (1). This character can be represented as a transformation series with the complete separation of the nasals in *C. cristatus* the apomorphic state (2).

Character 4: posterior margin of nasals. The posterior aspect of the nasals in basiliscines has three distinct shapes. In *Basiliscus* and *Laemanctus longipes*, the posterior margin of the nasals forms a smooth convex curve. In *Corytophanes*, the posterior margin of the nasals is pointed. In *L. serratus* the posterior aspect of the nasals is square.

Among the outgroups examined, all outgroups except crotaphytines, tropidurines and iguanines show the convex posterior margin as the unequivocal character state at respective basal nodes. Crotaphytines have pointed posterior margins similar to *Corytophanes*. In the tropidurines examined, the posterior margin of the nasals are also pointed as seen in *Corytophanes.*

Within the iguanine clade the polarization of the character state at the basal node is more problematic. *Brachylophus*, some *Ctenosaura* and *Iguana* show the convex posterior margin, whereas other *Ctenosaura, Sauromalus* and *Dipsosaurus* have pointed posterior processes. The Galapagos iguanas (*Amblyrhynchus* and *Conolophus*) have square posterior margins of the nasals similar to *Laemanctus*. The character state at the basal node of the iguanine clade is therefore equivocal.

The character state distribution at the basal nodes of the outgroups suggests that the convex posterior margin of the nasals is considered to be the plesiomorphic condition at the ingroup/outgroup node (4:2 consensus). The two alternate character states (nasals with pointed posterior processes and those with square posterior aspects) do not form a single transformation series, but are instead part of a bidirectional transformation series with the convex posterior margin as the plesiomorphic condition.

Prefrontals (Figs. 14, 23)

The prefrontals are triangular bones that form the anterodorsal aspect of the orbit and the posterodorsal aspect of the nasal capsule.

Character 5: prefrontal-nasal relationship (Figs. 14, 23). In all "iguanids" of the outgroups examined, except *Anolis* and *Petrosaurus*, the prefrontal exhibits a broad contact with the nasal medially. Although, the anterolateral aspects of the frontal separates the prefrontals from the nasals posteriorly (e.g., *Sceloporus jarrovi, Oplurus cuvieri, Morunasaurus annularis, Plica plica, Stenocercus guentheri* and others) the two bones are always in contact.

In *Anolis, Leiosaurus belli* and *Petrosaurus*, the maxilla separates the prefrontal and nasals anteriorly and the frontal separates these two bones posteriorly so that there is no contact between the prefrontals and the nasals.

The distribution of the character states at the basal nodes of the outgroups indicates that the widespread ''iguanid'' condition (broad contact between prefrontals and nasals with only partial posterior separation) is the plesiomorphic condition (7:0 consensus).

In *Corytophanes cristatus* the maxilla separates the prefrontal and the nasal anteriorly and contacts the anterolateral aspect of the frontal. In this case there is a complete separation between the prefrontal and nasal bones (as in *Anolis* and *Petrosaurus*). In *C. hernandezi* and *C. percarinatus* there is an anterior separation of the prefrontal and nasal by the maxilla and a posterior separation by the anterolateral aspects of the frontal so that only a small contact zone exists between these two bones. In *Basiliscus* there is only a posterior separation of the prefrontal from the nasal; otherwise these two bones are in broad contact (plesiomorphic condition).

This character can be interpreted as having a three state transformation series. In the plesiomorphic condition, there is a posterior separation of the prefrontal and nasal bones and a broad anterior contact between them. In the intermediate condition, the prefrontal and nasal are separated anteriorly by the maxilla in addition to being separated posteriorly by the anterolateral spine of the frontal, resulting in only a small contact zone between the prefrontal and the nasals. The apomorphic condition is a case in which the maxilla and the frontal contact each other resulting in a complete separation of the prefrontal and nasal bones.

Estes et al. (1988) have also used this character to resolve relationships among squamates. Their polarity decision and the one presented in this study coincide. The nasals are completely separated from the prefrontals in Dibamidae, Lacertidae, Xantusiidae and in Amphisbaenia.

Character 6: anterolateral spine of prefrontal (Figs. 14, 23). *Corytophanes* has a prominent anterolateral spine on the prefrontal that laterally overlaps the nasal process of the maxilla. This spine has not been observed in other taxa within the ingroup or outgroups examined. It is therefore an autapomorphy for *Corytophanes*.

Lacrimals

Lacrimals are small flat bones located in the anteroventral portion of the orbit, between prefrontals, nasal process of the maxilla, jugal and the palatine process of the prefrontals.

Character 7: groove at prefrontal-lacrimal junction (Fig. 16). *Basiliscus* and *Laemanctus* have a welldefined groove at the junction of the prefrontal and lacrimal bones in the anterolateral portion of the orbit. The functional significance of this groove has

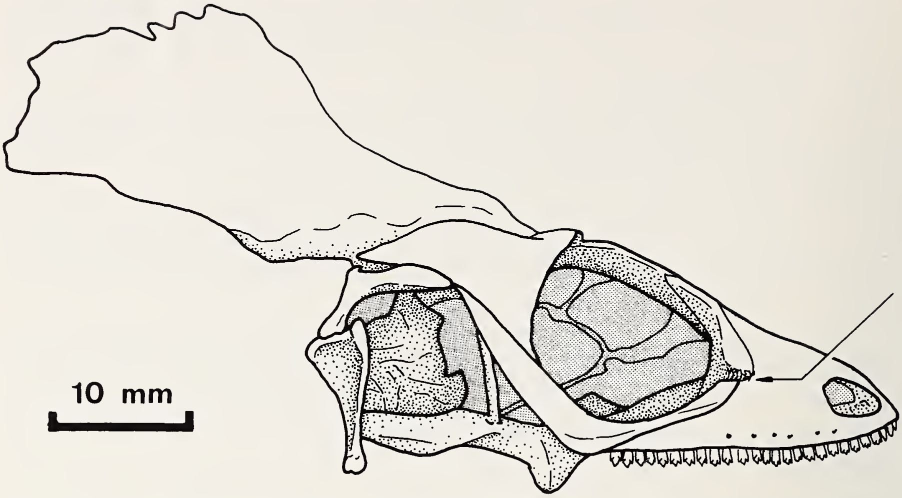


Fig. 16: Lateral view of the skull of *Basiliscus* showing the prominent groove at the prefrontal-lacrimal junction.

not been determined. *Corytophanes* lacks this groove, and the prefrontals have been highly modified (see character 16) such that the absence of the prefrontal-lacrimal groove may have been secondarily lost.

A prominent prefrontal-lacrimal groove was only observed in crotaphytines. All other outgroups lacked a groove. Therefore, the absence of the groove is considered to be the unequivocal plesiomorphic condition at the basal node of the ingroup (6:1 consensus).

Palate

The bony elements of the palate, beginning anteriorly, are the median premaxilla, paired maxillae, paired vomers, paired palatines, paired pterygoids and paired ectopterygoids.

Premaxilla

The premaxilla is a median triangular bone, with an anterior basilar portion (rostral body) that is expanded laterally. In basiliscines the rostral body usually contains seven to nine peg-like teeth with tapered crowns and no lateral cuspation.

Basiliscus shows considerable lateral expansion of the rostral body. In *Corytophanes* and *Laemanctus* this expansion is not as pronounced. It is difficult, however, to quantify any distinct difference in morphology between these three genera sufficient to warrant the description of a systematic character. Other "iguanids" that show a broad rostral body are *Amblyrhynchus, Crotaphytus, Iguana* and *Chalarodon*. Narrow rostral bodies are observed in *Enyalioides* and *Dipsosaurus*.

On the ventral portion of the rostral body, behind the teeth are foramina for the terminal portion of the maxillary arteries as in *Ctenosaura* (Oelrich 1956). The ventral aspect of the rostral body itself contacts the incisive process. The morphology of the incisive process varies considerably within basiliscines and among outgroups, from a very short single structure to a more elaborate and pronounced bilobed structure that may contact the vomers. Variation is so extensive as to eliminate this feature as a systematic character. De Queiroz (1987) indicated that most iguanines have a weak ventral crest that extends along the posterior edge of the premaxilla up onto the incisive process. Some *Basiliscus* have this welldeveloped crest, but in contrast to *Conolophus*, the foramina of the maxillary arteries do not pierce the crest. Other *Basiliscus*, *Corytophanes* and *Laemanctus* lack such a ridge. There is no consistent pattern of presence or absence of prominent crest within *Basiliscus* and its use as a systematic character is not warranted.

Maxilla

The maxillae are relatively large tooth bearing bones that form the anterolateral half of the skull; three distinct processes are present: premaxillary, nasal and posterior.

Vomer

The vomers are paired bones located posterior to the premaxilla in the anterior portion of the palate. Medially they are in contact with each other over their length. Anterolaterally they border the fenestra vomeronasalis externus, and the fenestra exochoanalis posteriorly.

The vomer, slightly constricted anteriorly, contacts the medial aspect of the premaxillary process of the maxilla. In some basiliscines, the anterior portion of the vomer is in direct contact with the ventral portion of the rostral body of the premaxilla. In others, the two anterior tips of the vomers do not contact the premaxilla, leaving a V-shaped excavation behind the incisive process that is occupied by the rostral part of the cartilaginous nasal septum. The extent of excavation is variable, and as mentioned above, is not always present.

Palatine

The palatines are medial bones of the palate that are separated from each other by the interpterygoid vacuity. They form the floor of the orbits, the ventral aspect of the posterior portion of the nasal capsule, and the roof of the central portion of the palate.

The infraorbital foramen is located at the lateral border of the maxillary process and shows considerable variation within certain outgroups, such as the iguanines. No consistent pattern with respect to variation of the infraorbital foramen was observed within basiliscines, however.

Character 8: palatine-ectopterygoid relationship (Fig. 17). In most "iguanids" the maxillary process of the palatine projects laterally to contact the maxilla, jugal, prefrontal and lacrimal bones. In all tropidurines, anoloids, crotaphytines, oplurines, morunasaurs, as in most other squamates, the maxillary process of the palatine does not contact the ectopterygoid. In some specimens of *Brachylophus, Amblyrhynchus* and in the sceloporine *Phrynosoma* the maxillary process of the palatine does contact the ectopterygoid, partially covering the medial aspect of the maxilla in dorsal view and excluding it from the suborbital fenestra. In the remaining "iguanid" taxa the maxillary process and the ectopterygoid approach one another but are not in contact.

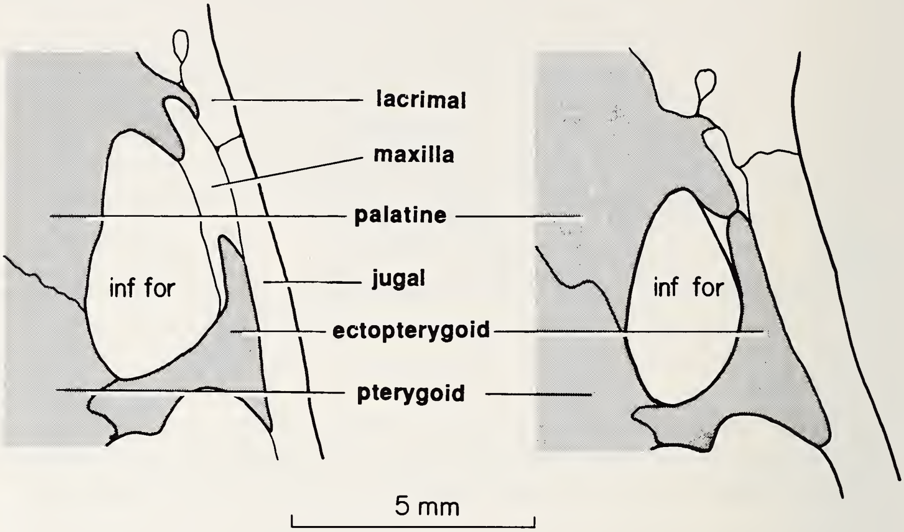


Fig. 17: Dorsal view of the inferior orbital rim and the infraorbital fenestra in *Laemanctus* (left) and *Basilicus* (right); inf for = infraorbital foramen

Basiliscus and *Laemanctus* do not have a palatine-ectopterygoid contact. In *Corytophanes* there is a general tendency of the maxillary process of the palatine to contact the ectopterygoid. However, only in *C. cristatus* is contact well-established.

The distribution of the character states suggests that dorsal separation between the maxillary process of the palatine and the ectopterygoid is the plesiomorphic condition for "iguanids" (7:0 consensus) and for squamates. The contact of the maxillary process of the palatine with the ectopterygoid has been independently derived in *Phrynosoma, Amblyrhynchus*, in some *Brachylophus* and in *Corytophanes cristatus*.

Pterygoid

The pterygoids are paired median bones that form the posterior portion of the palate. Three distinct processes are observable that extend anteriorly, laterally and posteriorly.

The palatine process sutures anteriorly with the palatine bone. There is an elevated portion on the ventral surface, at the base of the palatine process, which contains an arc of pterygoid teeth. Pteryoid teeth vary in shape, size and number, both inter- and intraspecifically. In *Basiliscus* there are four or five slightly recurved teeth parallel to the interpterygoid vacuity. In *Corytophanes*, up to ten teeth may be present that extend anteriorly past the transverse process. There are fewer teeth (3—5) in *Laemanctus*, which project medially towards the interpterygoid vacuity.

The number of pterygoid teeth and their morphology varies dramatically among outgroup taxa, such that a concise evaluation of character states is not possible. In morunasaurs, for example, *Enyalioides o'shaughnessyi* has one pterygoid tooth, whereas *E. laticeps* has from 11—13. *Morunasaurus* and *Hoplocercus* respectively contain 3—4 and 4—5 pterygoid teeth. A reduction in number of pterygoid teeth minimizes the gripping capacity of palatal dentition and therefore could be related to diet (Montanucci 1968).

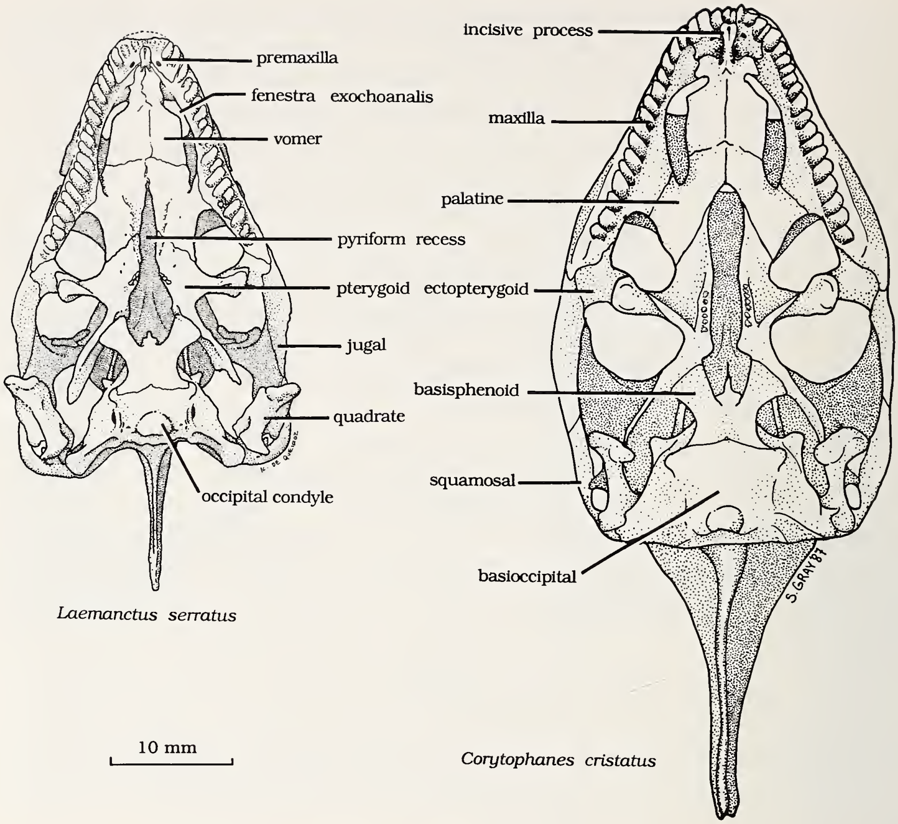
The transverse process forms a lateral, perpendicular plate that sutures to the ectopterygoid. Its dorsal surface is excavated and accommodates the body of the M. pseudotemporalis superficialis. The ventral border forms the posterior limit of the oral cavity and gives origin to the M. pterygomandibularis.

The quadrate process of the pterygoid (quadrate ramus of Robinson 1967) is flattened mediolaterally and extends caudolaterad to contact the ventromedial aspect of the quadrate. On the proximal portion of the dorsal border of the quadrate process is the columellar fossa (fossa pterygoidei), with which the ventral end of the epipterygoid articulates. The relative position of the columellar fossa is not under ontogenetic control. Medial to the columellar fossa is the pterygoid notch, into which the basipterygoid process of the basisphenoid is wedged. The position of the columellar fossa in basiliscines varies considerably from anterior to the pterygoid notch to locations posterior to the notch. No consistent pattern within the basal taxa was observed. At the laterodistal end of the quadrate process is a small facet which articulates with the quadrate. There are thus three moveable joints associated with the quadrate process; the columellar joint, the basipterygoid joint and the pterygoquadrate joint. The pterygo-palatine and pterygo-ectopterygoid joint are syndesmoses.

The shape of the interpterygoid vacuity varies within basiliscines. In *Basiliscus* it is constricted both anteriorly and at the base of the quadrate and transverse processes. In *Corytophanes* there are no constrictions, such that the sides of the interpterygoid vacuity are parallel. In *Laemanctus*, the posterior portion of the vacuity (at the base of the quadrate and transverse processes) is expanded. Although the patterns within the ingroup are consistent, the outgroups show too much variation to assess the polarity at the ingroup node.

Character 9: palatine process of pterygoid (Fig. 18). In all the outgroup taxa examined, except *Morunasaurus*, the palatine process of the pterygoid projects anteromedially to the level between the middle and the anterior aspect of the infraorbital foramen. In most sceloporines the anterior process of the palatine reaches the midpoint of the infraorbital foramen, but usually not beyond the midpoint of the infratemporal foramen. In *Morunasaurus*, the palatine process of the pterygoid projects medially past the anterior aspect of the infraorbital foramen.

Basiliscus and *Laemanctus* show the widespread "iguanid" condition in which the palatine process does not extend anteriorly past the anterior aspect of the infraorbital fora-



Laemanctus serratus

Corytophanes cristatus

Fig. 18: Palatal view of *Corytophanes* and *Laemanctus*. (Drawing on left courtesy of K. de Queiroz, Right courtesy of S. Gray).

men. In fact, the palatine process of *Basiliscus* and *Laemanctus* only reaches the midplane of the infraorbital foramen as in sceloporines.

Corytophanes shows the condition described for *Morunasaurus*, in which the palatine process projects anteromedially past the anterior aspect of the infraorbital foramen. This may actually be a result of the reduction of the preorbital region of *Corytophanes*, rather than an enlargement of the palatine process of the pterygoid as is suggested by other characters.

The distribution of the character states at the outgroup nodes indicates unequivocally that a palatine process not projecting past the anterior aspect of the infraorbital foramen is the plesiomorphic condition (6:0 consensus). The alternate condition, as seen in *Morunasaurs* and *Corytophanes* is derived.

Character 10: quadrate process of pterygoid (Fig. 19). Two distinct morphologies of the quadrate process of the pterygoid can been identified within "iguanids". First, the ventral and dorsal borders are parallel, except posteriorly where they taper before contacting the quadrate. However, in some specimens the terminal portion never reaches the level of the quadrate. In the alternate condition, the quadrate process is parallel anteriorly, but distinctly expanded posteriorly, and always forms a broad articulation with the quadrate.

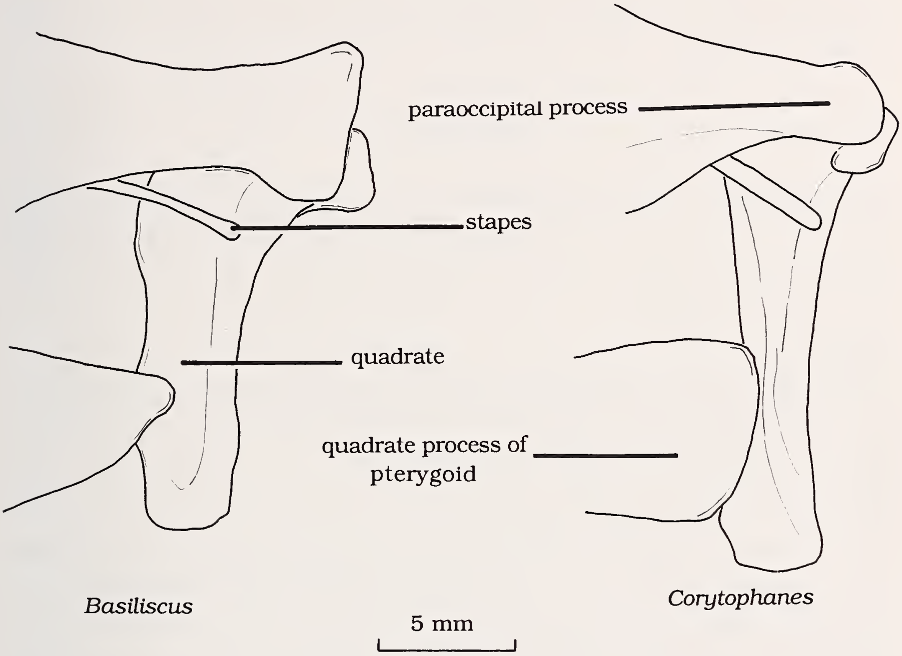


Fig. 19: Articulation of quadratic process of pterygoid and ventromedial aspect of quadrate of *Basiliscus* and *Corytophanes*.

Robinson (1967) indicated that streptostyly is increased by reducing the (terminal) width of the quadrate ramus of the pterygoid. Maximal streptostyly at the pterygoquadrate articulation is achieved when the pterygoid and quadrate are not in contact. On the other hand, streptostyly is minimal in the case of an expanded terminal quadrate process that is in broad contact with the quadrate.

Among the outgroups examined, all taxa except *Chamaeleolis* have a terminally tapered quadrate process of the pterygoid that is in narrow contact with the quadrate. *Chamaeleolis* has an expanded terminal portion of the quadrate process.

Among the basiliscines, *Basiliscus* and *Laemanctus* show the widespread "iguanid" condition of a tapered quadrate process, whereas in *Corytophanes* the alternate condition is present.

Outgroup comparison unequivocally demonstrates that a tapered quadrate process is the plesiomorphic condition at the basal node of the ingroup. An expanded quadrate process is considered to be a convergence between *Corytophanes* and *Chamaeleolis*, possibly being related to reduction of streptostyly as a result of feeding habits.

Ectopterygoid

A median vertical process articulates with the transverse process of the pterygoid in a tongue-and-groove articulation. A horizontal lateral process is sutured to the medial surface of the jugal.

Orbital Region

The following bones surround the orbital rim: lacrimal, prefrontal, frontal, postfrontal and jugal. The lacrimal and prefrontal form part of the nasal capsule and have been described in that section. Included in this section is the sclerotic ring, which is imbedded within the eye itself.

Frontal

The frontal is a median T-shaped bone forming the dorsal aspect of the orbit. Posteriorly it joins the parietal in a hinge suture. The anterior portion of the skull can thus be elevated and depressed in a perpendicular plane relative to the posterior portion of the skull (occipital region of Oelrich 1956). This movement has been termed kinetic (Bradley 1903) and metakinetic (Versluys 1912).

The middle portion of the frontal is constricted in *Basiliscus*, in most taxa of the outgroups examined, and in most non-ophidian squamates. The condition observed in *Chamaeleolis* is peculiar, in that the frontal is wide due to elaborate exostosis, obscuring the outlines of the frontal. Little or no constriction is present in some species of *Polychrus (e.g. gutturosus)* (Etheridge, pers. comm.) and *Phrynosoma. In Laemanctus* and *Corytophanes* the frontal is only slightly constricted in that the interorbital portion is as wide as the anterior portion.

Character 11: shape of midsagittal section of frontal. In the outgroup taxa, the frontal curves ventrally at the anterior and posterior ends to form a dome as viewed midsagittally. The two exceptions are *Sauromalus* and *Chamaeleolis*, in which the frontal bone is flat.

Within basiliscines, *Basiliscus* has the characteristic domed frontal. *Laemanctus* and *Corytophanes*, however, have a flat frontal bone. In addition, the posterior aspect of the frontal curves dorsally in *Corytophanes* to contact the lateral aspects of the parietal bone.

The distribution of character states among the outgroups indicates that a domed frontal bone is the unequivocal plesiomorphic condition at the ingroup/outgroup node (7:0 consensus). A flat frontal bone is therefore the apomorphic state, serving as a synapomorphy for a *Corytophanes-Laemanctus* clade. Hypothesizing a three state transformation series for this character, in which the domed frontal bone is the plesiomorphic state, a flat frontal the intermediate condition, and a flat frontal bone with upwardly curving posterolateral processes as the apomorphic condition, is unwarranted; i.e. it does not provide any information that would help resolve relationships among the nine basic taxa of the ingroup.

Postfrontal (Fig. 14).

The postfrontal is a small bone of the orbital rim found variably within the ''iguanids''. Etheridge & de Queiroz (1988) hypothesized that the presence of a postfrontal is a primitive character within the family because it is found in agamids, chamaeleons and other lepidosauromorphs in which the cranial morphology is well known. In non-iguanian squamates the postfrontal is absent in taxa with highly modified skulls (e.g. some snakes, some amphisbaenians and in *Dibamus* (Estes et al. 1988)). The absence of a discrete postfrontal, however, can occur either through loss of the ossification center itself; or by fusion with the frontal or postorbital.

Character 12: postfrontals (Fig. 14). Within basiliscines, *Basiliscus* and *Corytophanes* lack a postfrontal, whereas the postfrontal is present in *Laemanctus*. Character distribution at the outgroup basal nodes indicates a (4:2) character state distribution pattern. The presence of a postfrontal is therefore the plesiomorphic condition. This polarity decision also coincides with Estes et al. (1988) and Etheridge & de Queiroz (1988).

Jugal

The jugal is a flat, boomerang-shaped bone consisting of anterior and posterior (squamosal) rami of approximately equal length. The superior border of the jugal fits into the postorbital as a tongue and groove joint.

Medialy the jugal is in contact with the lateral process of the ectopterygoid. The posteroventral corner of the jugal and the posterior extent of the maxilla show two patterns in ''iguanids''. One condition exists in anoloids and in basiliscines, in which the posteroventral aspect of the jugal extends posteriorly past the ectopterygoid, such that the anterior ramus of the jugal contributes significantly to the maxillary arch, and excludes the lateral exposure of the ectopterygoid.

A second condition is observed in the remaining outgroups. In these, the posteroventral corner of the jugal does not extend past the ectopterygoid. In morunasaurs, sceloporines, tropidurines and oplurines examined, the posterior aspect of the maxilla extends completely beneath the anterior ramus of the jugal so that there is no lateral exposure of the ectopterygoid at the posterior aspect of the maxillary arch.

In crotaphytines and iguanines, however, the maxilla does not completely extend beneath the anterior ramus of the jugal. The ectopterygoid is exposed laterally such that the confluence of the ectopterygoid and the jugal form the posterior most aspect of the maxillary arch.

The two patterns can be used in an analysis at the suprageneric level, however, they are not used in this study because no variation occurs within the ingroup.

Character 13: squamosal process of jugal (Fig. 20). In most "iguanids", the squamosal process of the jugal tapers distally as it joins with the postorbital bone to form part of the supratemporal arch. In *Anolis equestris, Chamaeleolis* and *Phrynosoma*, the squamosal process of the jugal is broad.

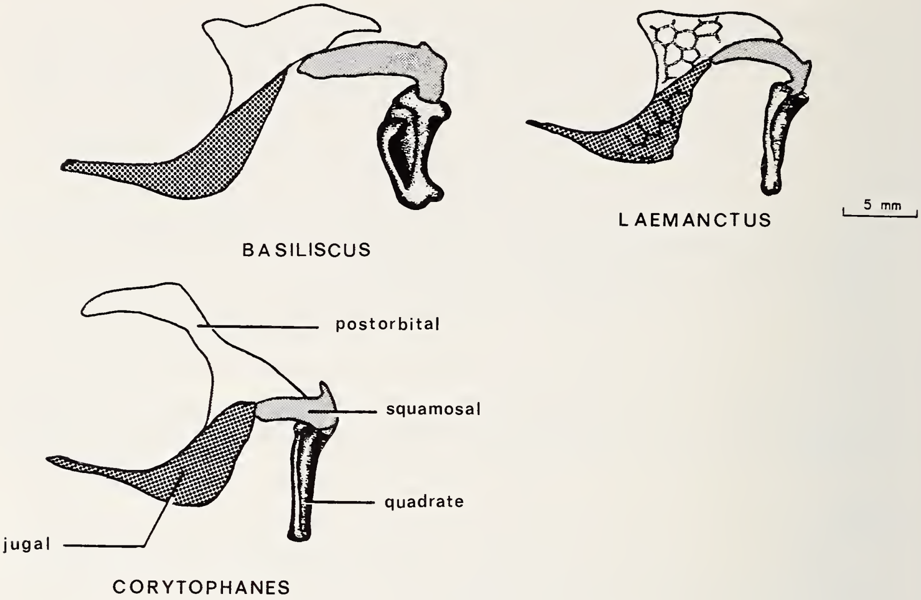


Fig. 20: Posterolateral aspect of skull of *Basiliscus*, *Corytophanes* and *Laeamanctus*, showing relative positions of jugal, squamosal, postorbital and quadrate.

Within the ingroup, *Basiliscus* and *Laemanctus* show the common "iguanid" pattern of a tapered squamosal process. In *Corytophanes* the squamosal process is expanded and broad similar to the condition seen in *Phrynosoma, Anolis equestris* and *Chamaeleolis*. This broad terminal expansion of the jugal includes a rigid tongue-and-groove joint between the postorbital bone and the jugal that supports the posterodorsal aspect of the orbit and the base of the supratemporal arch.

The distribution of character states indicates that a thin squamosal process of the jugal is the unequivocal plesiomorphic condition in "iguanids", and that a broad terminal portion of the jugal is the derived condition (7:0 consensus). Four independent origins for the derived character state are hypothesized.

Character 14: jugal-squamosal contact (Fig. 20). Three conditions of the squamosal-jugal relationship in "iguanids" are present: little or no contact between the squamosal process of the jugal and the anterior end of the squamosal; broad contact between the squamosal and jugal, which excludes the postorbital from the superior rim of the infratemporal fossa; and dorsal overlay of the anterior portion of the squamosal by the squamosal process of the jugal. Because the "overlaying" condition includes contact to an extended degree, only two conditions are recognized: contact or no contact between the squamosal and jugal. This feature is used as a systematic character because taxa with a tapering squamosal process (Character 13) can have broad contact (overlaying) with the squamosal. Therefore, characters 13 and 14 are exclusive of one another.

In morunasaurs and oplurines the squamosal process of the jugal and the anterior process of the squamosal are separated from each other or are only narrowly in contact on the inferior aspect of the supraorbital arch. In most sceloporines the two processes are separated, but there is narrow contact in *Uma, Holbrookia*, some *Callisaurus* and in some *Petrosaurus*. In *Phrynosoma*, there is a broad area of contact between the jugal and the squamosal.

All tropidurines with the exception of *Phymaturus* and *Liolaemus* have narrowly contacting or separated jugals and squamosals. In *Phymaturus* and *Liolaemus* the jugal and squamosal are in broad contact with some species (e.g., *Liolaemus kingii, Liolaemus fitzingeri, Phymaturus patagonicus*) showing some overlay.

In *Polychrus, Enyalius, Pristidactylus*, and the para-anoles the squamosals and jugals are separated. In most *Anolis* the squamosals are either completely separated from the jugals, or in narrow contact. In *Leiosaurus, Diplolaemus, A. equestris* and *Chamaeleolis* there is, however, a zone of broad contact between the jugal and squamosal on the inferior aspect of the supratemporal arch, with some instances of overlay. The condition observed in the derived anoloids does not affect the polarity decision at the anoloid basal node.

In all iguanines except *Dipsosaurus*, the squamosal and jugals are in narrow contact, or are completely separated. In *Dipsosaurus* the jugal overlays the anterior portion of the squamosal. Because *Dipsosaurus* forms part of a tritomy at the iguanine basal node (de Queiroz 1987; Fig. 4) no unequivocal character state can be determined at this outgroup node (2:1 consensus).

In crotaphytines the anterior portion of the squamosal is overlapped by the squamosal process of the jugal.

In *Basiliscus* and *Laemanctus* the squamosal and jugals are separated, or are in narrow contact. All three species of *Corytophanes* show a broad contact zone between the squamosal process of the jugal and the anterior process of the squamosal.

The distribution of character states at the basal outgroup nodes indicates that narrow or no contact between the jugal and the anterior aspect of the squamosal is plesiomorphic (4:1 consensus). A broad contact zone between the squamosal and jugal, which includes overlay, is the derived condition.

Character 15: posterior angle of jugal (Figs. 16, 20, 23). The posterior angle of the jugal in "iguanids" varies from an obtuse angle to 90 °.

In most "iguanids" the posteroventral aspect of the jugal forms an obtuse angle. The posteroventral corner is expanded and angular in the anoloids *Chamaeleolis* and *Ano-*

lis, in crotaphytines, some *Pristidactylus* (Etheridge, pers. comm.), and in *Petrosaurus*. In the above mentioned taxa, the squamosal process is triangular and the posterior margin is almost vertical. *Diplolaemus* and *Leiosaurus* have a peculiar condition in which the angle of the jugal has a posteriorly projecting spine.

In basiliscines, *Basiliscus* is variable with most specimens showing a ventrally rounded posteroventral edge with no indication of a posteroventral expansion. In *Corytophanes* and *Laemanctus* the posteroventral aspect of the jugal is distinctly angular and expanded posteriorly, such that the posterior aspect of the jugal forms a vertical margin.

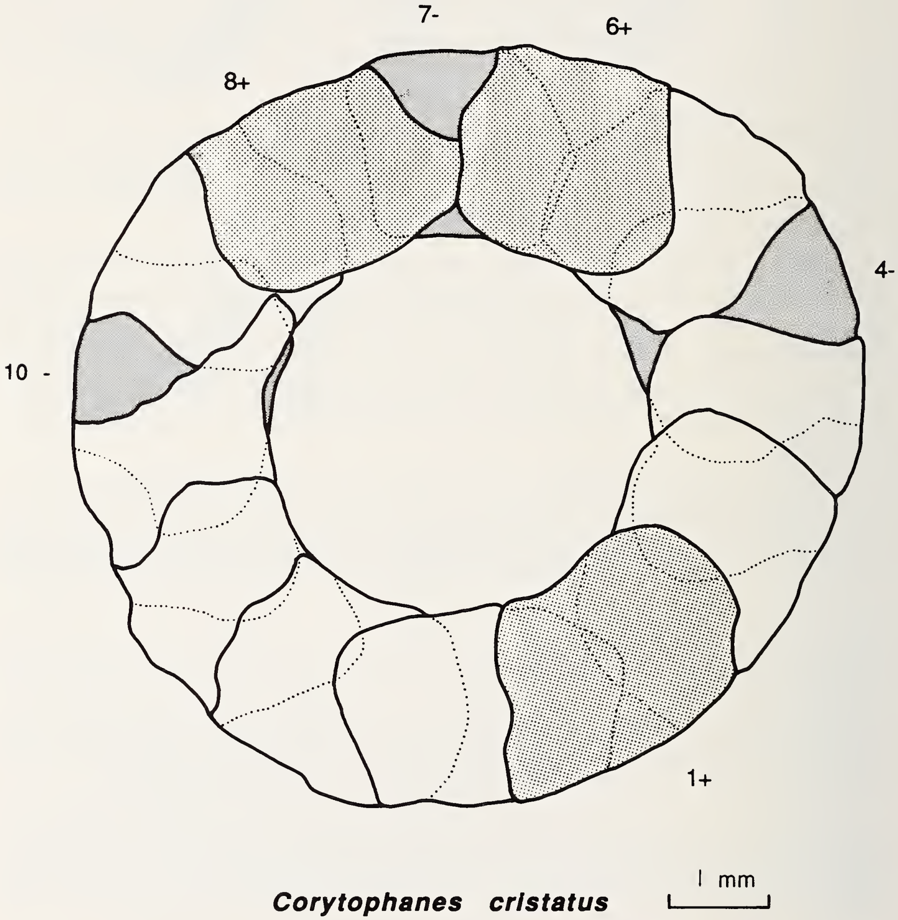


Fig. 21: Sclerotic ring showing "normal" pattern of overlap of the 14 scleral ossicles. The 1 ossicle is located at the posteroventral aspect of the eye. Subsequent numbering is caudodorsal. Symbols used are: i = imbricating, i.e. overlapping a single adjacent scleral ossicle; - = negative, i.e. scleral ossicle is overlapped by two adjacent ossicles; + = positive, i.e. scleral ossicle overlaps both adjacent ossicles.

The distribution of the character states at the basal outgroup nodes indicates that the rounded jugal is the unequivocal plesiomorphic condition in "iguanids" (5:1 consensus). An expanded right-angle jugal is the apomorphic condition.

Sclerotic Ring

The sclera of the eye contains a sclerotic ring that is made up of interlocking and overlapping thin bony platelets (scleral ossicles) (Fig. 21). Fourteen scleral ossicles with a consistent pattern of overlap between them is characteristic of the "iguanids" (Presch 1970; Underwood 1970, 1984; de Queiroz 1982). Scleral ossicles 1, 6 and 8 are defined as being positive (overlapping both immediately adjacent ossicles); 4 (temporal), 7 (dorsal) and 10 (nasal) are negative (overlapped by both neighboring ossicles); the remaining ossicles are imbricating (overlapped on one side and overlapping adjacent ossicle on the other side) (Underwood 1970, 1984; de Queiroz 1982).

Underwood (1970) reported 13 scleral ossicles for *Corytophanes* for the two eyes he examined, but no species was indicated. He indicted that a loss of scleral ossicle 9 (imbricating) would be the most parsimonious assumption involving but a single evolutionary shift from the presumed plesiomorphic "iguanid" condition. De Queiroz (1982) also examined *Corytophanes* and indicated that one of the eyes examined had 13 scleral ossicles rather than 14. It is not clear from his report from which species the variant pattern came. However, he suggets that it is through the loss of either scleral ossicle 5 or 6.

In this study all available scleral ossicles were examined. In *Corytophanes cristatus* and *C. hernandezi* the plesiomorphic "iguanid" condition was observed. In *Corytophanes percarinatus* most specimens had 13 scleral ossicles and considerable variation in pattern was observed. This fact leaves me to believe that the *Corytophanes* that Underwood (1970) examined is *C. percarinatus* and that the variant eye of de Queiroz (1982) was also from a *C. percarinatus* (listed as *Corytophanes sp.*).

Two points of interest should be stressed here. The *Corytophanes percarinatus* that show a reduction in number of scleral ossicles (13 vs. 14) with locality data were collec-

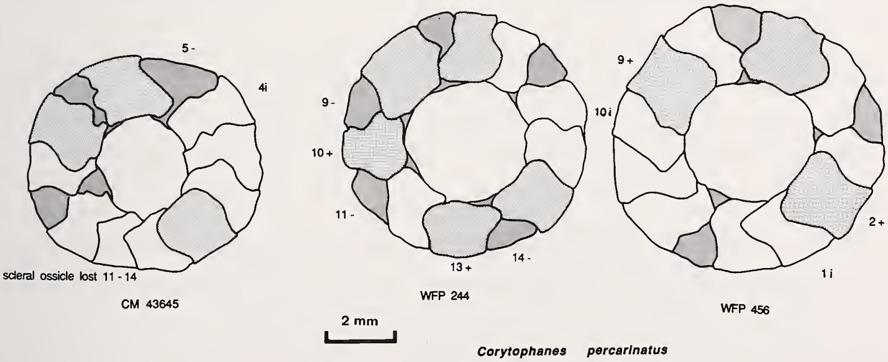


Fig. 22: Variations observed in sclerotic rings of *Corytophanes percarinatus*.

ted in the mountaneous regions of Guatemala. The second point is that asymmetry was common. All *C. percarinatus* showing reduction in one eye also showed reduction in the other eye. The pattern of overlap between the two eyes was quite different. Fig. 22 illustrates cases of variation observed in *Corytophanes*, with reduction and variable patterns of overlap.

Temporal Region

The bones discussed in this section are those that surround the two temporal and the postemporal fossae: postorbitals, parietal, squamosals, supratemporals, quadrates and epipterygoids.

Postorbital

The postorbital is a triangular bone that forms the posterodorsal aspect of the orbit and the anterolateral portion of the supratemporal fossa, and is the main support of the supratemporal arch. The postorbital may form part of the dorsal aspect of the infraorbital fossa when the ascending ramus of the jugal and the squamosal are not in contact (see character above).

Character 16: supraorbital process (Figs. 14, 23, 25, 33). In *Corytophanes* the postorbital bone has a spine projecting anteriorly that, with the posterior projecting spine of the prefrontal, forms a bony supraorbital arch. In *C. cristatus* and *C. percarinatus* the two spines are in contact and form a complete arch. In *C. hernandezi* the two spines do not meet and the supraorbital arch is thus incomplete. The distal ends of the two processes, however, are joined by connective tissue.

In Laemanctus the postorbital bone has a small anterior projection, but the posterior process of the prefrontal is absent. In *Basiliscus* neither process is present.

In *Phrynosoma* incomplete and complete supraorbital arches are present; *Anolis equestris* has an incomplete arch. In all other outgroup taxa examined the supraorbital arch is absent.

Using the outgroup consensus algorithm, the absence of a supraorbital arch is the unequivocal plesimorphic condition at the ingroup node (7:0 consensus). This character can be interpreted as a three-state transformation serie, wherein an incomplete arch is the intermediate state, and a complete bony supraorbital arch the apomorphic state.

Parietal

As mentioned above, the development of the parietal blade is the only character of the basiliscines that is not shared with any other "iguanid" genus. Therefore the description of this bone and its development deserve careful attention.

The parietal is a median unpaired quadrangular bone forming the roof of the cranial vault. The medial portion is constricted. The anterior portion forms a transverse suture with the frontal bone. The posterior supratemporal process overlies the supratemporal, and extends posterolaterally to contact the paraoccipital process of the exoccipital, the posterior aspect of the squamosal, and the dorsal portion of the quadrate at the intercalary cartilage. The posteromedial portion of the parietal articulates with the supraoccipital by means of the cartilaginous processus ascendens tecti synotici (Gaupp 1900;

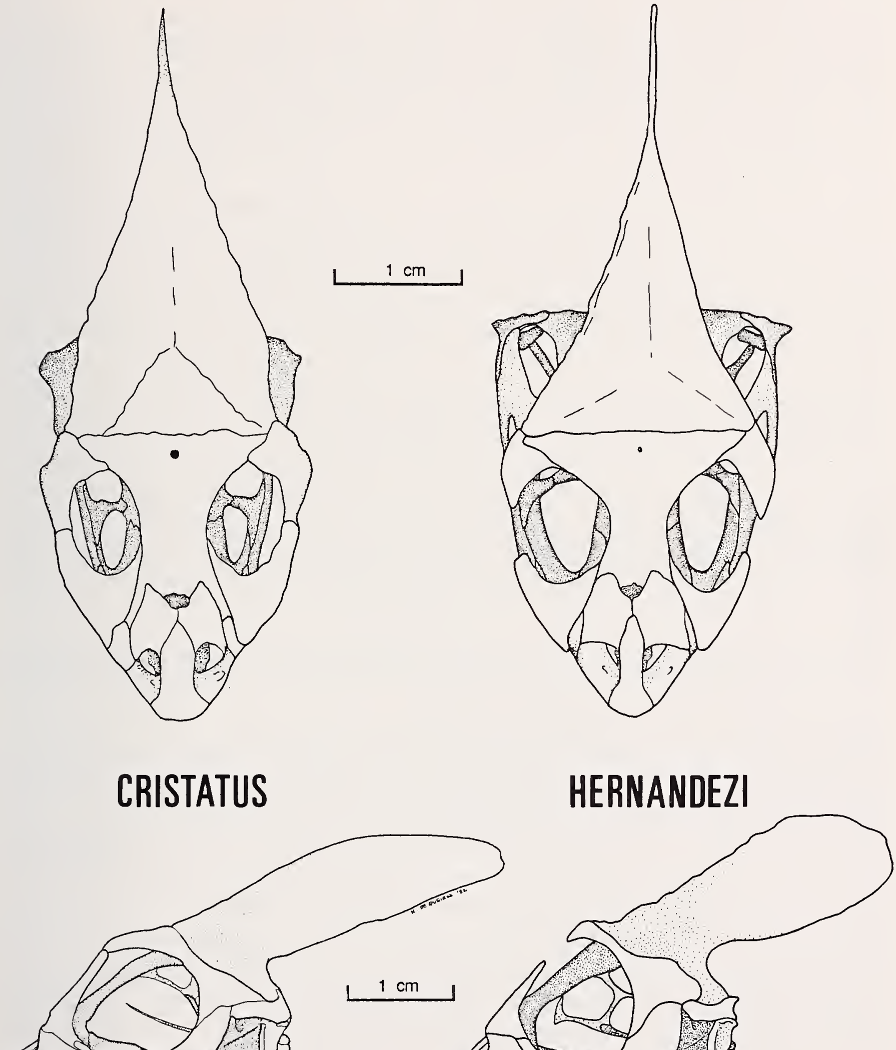


Fig. 23: Variation of bony supraorbital arc in *Corytophanes*. (Lateral view of *C. cristatus* is courtesy of K. de Queiroz).

de Beer 1937; Oelrich 1956). This process is the site of metakinesis between the occipital segment (posterior brain case) and the rest of the skull. Skull kinesis has not been investigated in basiliscines.

Five characters are discernable from the morphology and development of the parietal, with separate evolutionary histories (characters 18—22).

Character 17: parietal foramen position (Fig. 14). In "iguanids" the parietal foramen may be in one of three places on the skull. In most "iguanids" the parietal foramen is located at the frontoparietal suture. In some, the foramen lies more anteriorly, being entirely within the frontal bone, or it may lie posteriorly completely within the parietal (Boulenger 1890).

Estes et al. (1988) indicated that the parietal foramen, when present, is located within the parietal bone in most non-iguanian squamates (e.g., Agamidae, Lacertidae, Varanidae, Xenosauridae and *Sphenodon*) and polarized this condition as plesiomorphic for the Squamata, but considered its location at the frontoparietal suture to be a synapomorphy for Iguania. Etheridge & de Queiroz (1988) also considered the location of the parietal foramen at the frontoparietal suture as the plesiomorphic condition in Iguania. The parietal foramen located within the frontal or parietal were defined as being alternate apomorphic transformations. Loss of a parietal foramen was hypothesized as derived from the plesiomorphic condition, or from either apomorphy. This decision was based on the fact that among "iguanids" only some *Anolis* have a parietal foramen located entirely within the parietal bone. Given that anoles are monophyletic, reversing the polarity of this character (i.e the foramen within the parietal as the plesiomorphic condition, fide Estes et al. 1988) would be highly incongruent with many other characters.

The character state distributions at the basal outgroup nodes all indicate that the location of the parietal foramen at the frontoparietal suture is the plesiomorphic condition at the ingroup/outgroup node (6:0 consensus).

Within the basiliscines, *Basiliscus* and *Corytophanes* show the apomorphic condition, in which the parietal foramen is located entirely within the frontal bone. In *Laemanctus serratus* the parietal foramen is invariably found at the frontoparietal suture. In *L. longipes*, the position of the parietal foramen is highly variable: in some specimens the parietal foramen is clearly located within the frontal bone, whereas in others the foramen is close to the frontoparietal suture and in still others the foramen is located at the suture.

Using Estes et al.'s (1988) criterion for variation (see also discussion on variation), *Laemanctus longipes*, which shows both the plesiomorphic and apomorphic conditions should be coded as having the plesiomorphic condition.

In the context of "iguanids", the location of the parietal foramen within the frontal bone can be interpreted as an autapomorphy for the basiliscines, with a reversal in *Laemanctus serratus* and in some *L. longipes*. The presence of the parietal foramen within the frontal bone of *Dipsosaurus*, some *Sauromalus obesus* and in some *Leiocephalus* can be interpreted as convergence.

Character 18: lateral shelves of adductor crest (Figs. 14, 24). The insertion site of the adductor musculature on the top of the parietal can be raised to form a crest or crests. These are called adductor crests throughout this study. The adductor crests themselves can have shelves that project laterally to overlay the insertion of the adductor musculature.

Among the outgroups there are two conditions with respect to adductor crests. First, the adductor crests may lack lateral shelves, or when present, there are small lateral shelves that are confined to the anterolateral aspect of the adductor crests. Second, the two lateral adductor crests are prominent and are medially confluent at the posterior border of the parietal. The adductor crests in this case have distinct lateral shelves that extend the entire length of the crests. At the posterior aspect, the lateral shelves partially overlie the supratemporal opening.

The first condition was identified in most ''iguanids'', whereas the second condition was observed only in *Chamaeleolis, Phenacosaurus* (R. Etheridge, pers. comm.) and in some *Anolis*. Distribution at the outgroup basal nodes therefore show that the widespread ''iguanid'' condition is the plesiomorphic state, the alternate condition being apomorphic (7:0 consensus).

Within basiliscines, *Basiliscus* exhibits the plesiomorphic state in having small adductor crests with lateral shelves that are restricted to the anterolateral aspects of the crests. The adductor crests progress forward ontogenetically (see below) and the adductor crests and lateral shelves are lost.

Corytophanes exhibits the apomorphic condition. In addition, the two medial confluent crests continue as an enlarged posteriorly directed parietal blade. The lateral shelves are much expanded to completely overlie the supratemporal opening.

Laemanctus is intermediate: the lateral shelves of the adductor crests are prominent along their entire length, but they are not expanded posterolaterally to overlie the supratemporal opening.

The lateral shelves of the adductor crests in *Laemanctus* do not serve as the origin of any muscle, but simply cover the parietal blade origin of the m. pseudotemporalis superficialis. The posteriorly tapering shelves of *Corytophanes*, on the other hand, serve as an additional sites of origin for the m. pseudotemporalis superficialis (Costelli 1973; pers. observ.).

Character 19: parietal roof shape (Figs. 14, 24). The shape of the parietal roof in ''iguanids'' has been described by Etheridge (1959), and Etheridge & de Queiroz (1988). A trapezoidal parietal with widely separated lateral borders posteriorly is the primitive ''iguanid'' condition. Two intermediate evolutionary character states led to the apomorphic condition of the parietal bone, in which the median crests project posteriorly as a vertical blade.

Within the basiliscines, only the apomorphic condition is present; the adult parietal roof is Y-shaped with the posteriorly projecting blade a continuation of the two anterolateral adductor crests, confluent at the midline. Etheridge & de Queiroz's (1988) intermediate states therefore, do not apply, and only the primitive state with the absence of a parietal crest, and the apomorphic condition with a single median parietal blade, are used here.

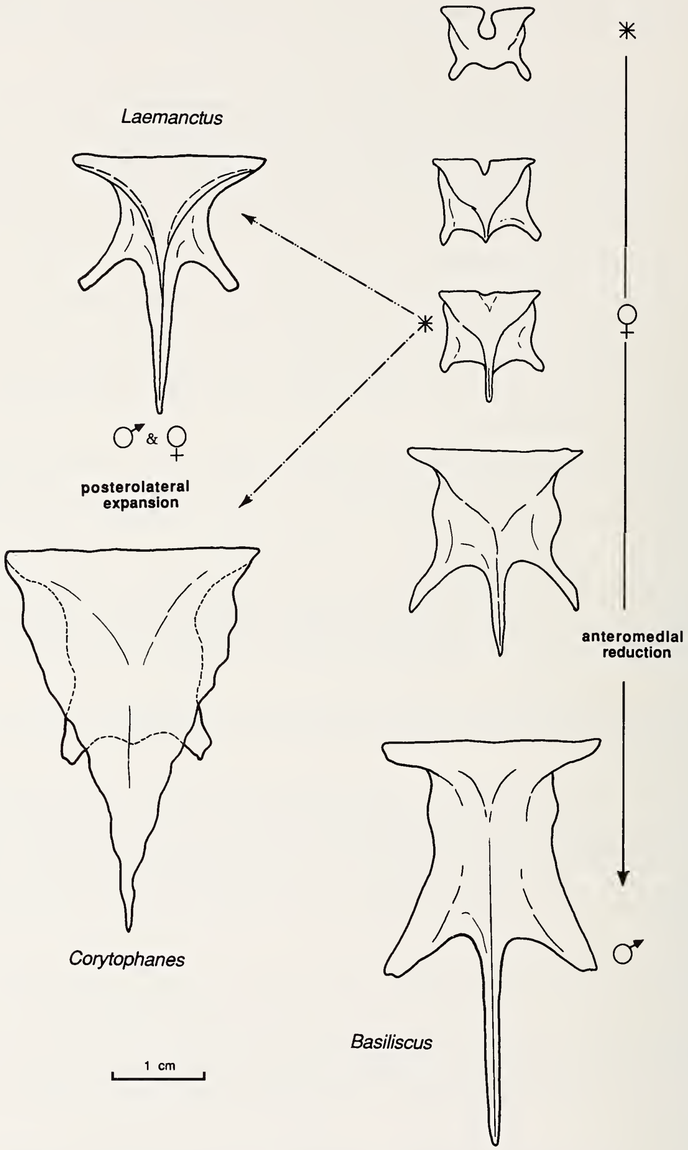


Fig. 24. Dorsal view of parietal bone in *Basiliscus, Corytophanes* and *Laemanctus*. Illustration shows different ontogenetic sequences, adductor ridge size differences, adult parietal roof shape, development of the parietal crest and parietal crest sexual dimorphism in basiliscines. The asterisk indicates stage at hatching for respective taxa (see text for further explanation).

Ontogenetic series of *Basiliscus* reveal that the two adductor crests diverge anteriorly, increasing the angle between them. In fully adult male *Basiliscus* the adductor crests meet at an angle of 180° that results in a single median parietal blade.

Ontogenetically, in *Laemanctus* and *Corytophanes* the adductor crests progress posteriorly, resulting in a posterior shift in the base of the parietal blade and a decrease in the angle between the two adductor crests. In fully adult *Laemanctus* an angle of about 60° is attained, whereas in adult *Corytophanes* the two adductor crests progress more posteriorly resulting in angles of approximately 30° to 45°.

I interpret this character as a bi-directional transformation series from the primitive "iguanid" condition (absence of a well-developed parietal blade). One direction, seen in *Basiliscus*, leads to the development of a median parietal blade with two anterolaterally projecting adductor crests. As these crests develop in an anteromedial direction, the angle between them increases, resulting in an anterior shift of the base of the median parietal blade.

In the other transformation from the primitive "iguanid" condition, there is a posterior progression of the adductor crests, which results in a decrease of the angle between them. Consequently, the base of the parietal blade shifts posteriorly. In adult *Laemanctus* the posterior shift is arrested when a 60° angle between the two anterior adductor crests is achieved. In *Corytophanes*, however, the posterior migration of the anterior adductor crests ceases at angles of 45° or less.

This character is coded as follows: outgroups posses the primitive condition (no median parietal crest), the *Basiliscus*-condition is coded as "1A"; the condition found in *Laemanctus* a "1B" and that of *Corytophanes* as "2B."

It is important to note that various outgroup taxa also possess an expanded median blade. *Chamaeleolis* and *Anolis equestris* have a blade similar to *Corytophanes-Laemanctus*. *Anolis garmani* and other large anoles have a distinctive median crest resulting from posterior confluency of the lateral adductor crests, with a *Basiliscus*-like anterior migration of these adductor crests (see also Etheridge 1959 and de Queiroz 1987 for comparable ontogenetic sequences in anoles and iguanines, respectively). Complete ontogenetic series of anoles and other "iguanids" are needed for further study of the development of the median crest. None of the above mentioned taxa, however, have well-developed parietal blades as seen in basiliscines.

Character 20: development of the parietal blade (Fig. 24). The developmental timing of the parietal blade is significantly different among the ingroup taxa.

In *Basiliscus* the parietal blade develops entirely postembryonically, whereas in *Corytophanes* and *Laemanctus* the median parietal blade is already well-developed at hatching.

Three alternative polarities can be hypothesized. The development of the parietal blade postembryonically is the apomorphic condition; the embryonic development of the parietal blade is the apomorphic condition, or both conditions are apomorphic and are part of a bi-directional transformation series from the plesiomorphic condition.

Embryonically, there may be deletion or retardation of certain developmental stages or the acceleration of developmental stages with respect to the postembryonic development of the parietal blade. Because deletion of non-terminal ontogenetic stages is unlikely, two alternatives remain: the acceleration of stages in *Corytophanes* and *Laemanctus*, or the retardation of ontogenetic stages in *Basiliscus*.

Among outgroup taxa (see above), the development of a median blade occurrs postembryonically. The hypothesized apomorphic condition is, therefore, an accelerated embryonic ontogeny of the median parietal blade in *Corytophanes* and *Laemanctus* with respect to *Basiliscus*.

Character 21: parietal blade sexual dimorphism (Fig. 24). The parietal blade in *Basiliscus* is only obtained by males, whereas both sexes of *Corytophanes* and *Laemanctus* have a well-developed parietal blade.

The parietal blade in adult male *Basiliscus* consists of a thin lamellar sheet of bone rising from a bony base. In adult female *Basiliscus* the bony base is present, but there is no vertical expansion.

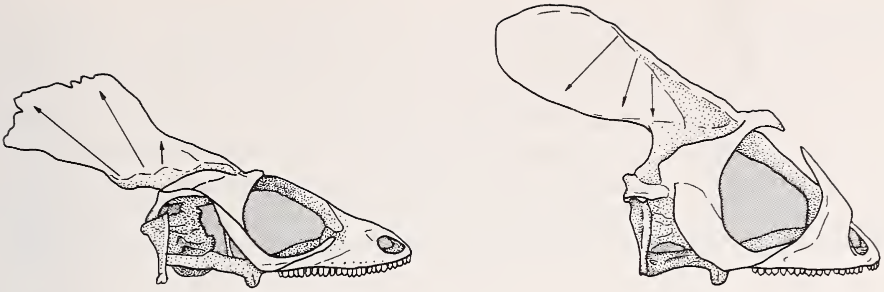
Outgroup data is of little help in resolving the polarity of this character, as the parietal blade is absent in most taxa. In those taxa (see above) that have a rudimentary parietal blade (median crest) there is insufficient skeletal material and information on the sex of the animal.

My observations on the developmental pattern of the parietal blade in *Basiliscus* show that subadults of both sexes have a ventral bony base, which is then elaborated in adult males. It is equally parsimonious to assume that the ancestral basiliscine was sexually dimorphic with respect to a well-developed blade than it is to accept the alternative condition, in which the ancestral basiliscine was not sexually dimorphic with regards to a well-developed blade. The former requires the the addition of a well-developed blade in female *Corytophanes & Laemanctus*, whereas the latter opts for the loss of a well-developed blade in female *Basiliscus*. Nonetheless, a survey of ''iguanids'' and other squamates suggests that sexual dimorphism in general seems to be the plesiomorphic condition, indicating that a sexually dimorphic blade is primitive for basiliscines.

Character 22: expansion of parietal blade (Fig. 25). As mentioned above, the parietal blade of *Basiliscus* consists of a ventral bony base with a vertically expanded blade of thin lamellar bone. In *Corytophanes* and *Laemanctus* the parietal blade is well ossified and is expanded ventrally.

The polarity of this character is again difficult to interpret because none of the taxa among the outgroups has a parietal crest. The two conditions of the parietal blade as described above are hypothesized to be part of a bi-directional transformation series. The plesiomorphic state is defined as the absence of a median parietal blade, with the dorsal expansion of the blade as one apomorphic condition, and the ventral expansion as the alternate apomorphic condition.

The parietal blade and associated characters are the only suite of attributes that are true autapomorphies for the basiliscines. The parietal blade itself most likely developed as a sexual dimorphic structure. It also has additional functional adaptations such as an expanded site of origin for the m. pseudotemporalis superficialis (see below). This is



B. VITTATUS C. HERNANDEZI

Fig. 25: Expansion of parietal blade in *Basiliscus* and *Corytophanes*.

in contrast to the only other "iguanids" with a parietal blade (*Chamaeleolis* and some *Anolis*), in which the parietal blade serves as both the site of origin for the m. pseudotemporalis superficialis and the dorsal head of the m. adductor medius. In *Basiliscus* the m. pseudotemporalis superficialis is restricted solely to the bony base of the parietal blade. In *Corytophanes* and *Laemanctus*, by contrast, this muscle has a broader origin, and originates from the laterally expanded adductor shelves in addition to most of the parietal blade.

Perhaps indirectly associated with the increased origin of the m. pseudotemporalis superficialis is the closure of the posttemporal fossa in *Corytophanes*. The dorsal head of the m. adductor mandibulae externus profundus is reduced greatly in *Laemanctus* and entirely absent in *Corytophanes*. In *Basiliscus* the dorsal head is well developed. The fibers of the dorsal head of the m. adductor mandibulae externus profundus run parallel to the fiber of the m. pseudotemporalis superficialis. Also, they both insert on the Bodenaponeurosis suggesting similar functions. The increased origin of the m. pseudotemporalis superficialis and therefore enlargement of this muscle in *Laemanctus* and *Corytophanes* may have resulted in the reduction (*Laemanctus*) and eventual loss (*Corytophanes*) of the dorsal head of the m. adductor mandibulae externus profundus. The loss of the dorsal head, which originates from the ventral surface of the parietal and runs through the posttemporal fossa may have led to the closure of this fossa. No experimental evidence can be provided to support this contention at this time, but the hypothesis seems plausible.

The timing of the development of the parietal blade in basiliscines is quite different. In *Basiliscus* the parietal blade develops entirely postembryonically. This is in contrast to the *Corytophanes-Laemanctus* clade in which the parietal blade is an embryonic development. It should also be noted that the parietal blade is sexually dimorphic for *Basiliscus*, but is well developed in both sexes in *Corytophanes* and *Laemanctus*. The suggestion is that the "ancestral" basiliscine was probably sexually dimorphic with respect to a parietal blade that developed postembryonically. The *Corytophanes-Laemanctus* clade is also the best supported node in the phylogeny showing no homoplasies.

Squamosal

The squamosal is an elongate, anchor-shaped bone forming the posterodorsal rim of the infratemporal fossa, and the posterolateral aspect of the supratemporal fossa.

Three processes may be present posteriorly: a dorsal process that articulates with the supratemporal process of the parietal, a condylar process, that articulates with the cephalic condyle of the quadrate, and a small distal process that projects medially into the intercalary cartilage. Robinson (1967) noted that in "lacertilians"[5] which retain the squamosal the dorsal process is much abbreviated or absent altogether. Within Iguania, the squamosal usually retains a much abbreviated dorsal process.

Character 23: dorsal process of squamosal (Fig. 20). The presence or absence of a dorsal process of the squamosal varies considerably within "iguanids". Among the tropidurines examined, *Liolaemus, Leiocephalus, Phymaturus, Plica* and some *Uranoscodon* posses a dorsal process that may or may not contact the supratemporal bone. In the eastern and western *Tropidurus, Stenocercus* and some *Uranoscodon* a dorsal process was absent. Character distribution for the tropidurines indicates that the presence of a dorsal hook is the condition found at the tropidurine basal node.

In anoloids, all specimens examined have a distinctive dorsal process of the squamosal, with an extreme case in *Chamaeleolis*. All sceloporines except *Uta, Urosaurus* and some specimens of *Petrosaurus* have a dorsal process. Both morunasaurs and oplurines lack a prominent dorsal process. All crotaphytines examined have a distinct dorsal process that contacts the supratemporal, in addition to a distinct distal process that articulates with the intercalary cartilage. In iguanines the absence of a dorsal process is the condition found at the basal node of that taxon, with a dorsal process of the squamosal present in *Sauromalus, Cyclura* and *Iguana*.

In *Basiliscus* no distinct dorsal, condylar or distal processes are apparent. In *Corytophanes* and *Laemanctus* a distinct dorsal process is present that contacts the posterolateral aspect of the supratemporal bone on the supratemporal process of the parietal.

The distribution of the character states yield an equivocal polarity decision at the ingroup/outgroup node (3:3 consensus). This character will therefore be left unordered in the data matrix.

Character 24: squamosal (Fig. 20). In all outgroups examined (except *Phrynosoma*), the squamosal is slightly convex dorsally and only contacts the cephalic condyle of the quadrate with the condylar process.

Within the ingroup, *Basiliscus*, *Laemanctus* and *Corytophanes cristatus* all have the condition described above, in which there is a single contact zone at the cephalic condyle of the quadrate between the squamosal and the quadrate. In *C. hernandezi* and *C. percarinatus* the anterior process of the squamosal is distinctly straight and overlaps the anterodorsal border of the lateral crest forming a "double articulation" with the quadrate. The ventral process of the squamosal forms a "peg and notch" articulation with the cephalic condyle of the quadrate as described by Robinson (1967). The former

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[5]) Quotes added to indicate this paraphyletic taxon.

articulation is a syndesmosis between the anterodorsal border of the quadrate and the medial aspect of the squmosal.

In *Phrynosoma* the anterior projection of the squamosal is straight and overlaps but does not contact the lateral anterodorsal aspect of the quadrate.

The distribution of character states among the outgroups indicates that the convex anterior projection of the squamosal (single articulation) is the unequivocal plesiomorphic condition within "iguanids" (7:0 consensus). The "double articulation" of the squamosal is a synapomorphy for *Corytophanes hernandezi* and *C. percarinatus* with a case of convergent evolution in *Phrynosoma*.

Supratemporal

The supratemporal is a small bone located on the ventral surface of the supratemporal process of the parietal bone. All basiliscines exhibit the primitive "iguanid" condition, with the supratemporal bone overlapping laterally the supratemporal process of the parietal.

Quadrate

The quadrate is an endochondral element that suspends the lower jaw at the back of the skull. The cephalic condyle of the quadrate articulates with the paraoccipital process medially, the supratemporal dorsally, and the squamosal laterally by means of an intercalary cartilage forming a synovial joint (Versluys 1912). In addition, a syndesmosis occurs between the slightly excavated articular facet, located above the ventral condyle and the quadrate process of the pterygoid (see description of character 10). The syndesmodial and synovial joints permit a certain degree of movement of the quadrate that, in conjunction with the loss of the quadratojugal, results in the squamate streptostylic skull (Robinson 1967). The ventral condyle of the quadrate articulates with the articular bone of the lower jaw.

Character 25: medial concha of quadrate. The quadrate of *Basiliscus* has a medially expanded concha which contacts the anterior portion of the paraoccipital process of the exoccipital bone. The quadrate of *Corytophanes* and *Laemanctus*, on the other hand, is not expanded medially beyond the cephalic and ventral condyles. This character can be interpreted as a three-state transformation, with an expanded medial concha that contacts the anterior portion of the paraoccipital process of the exoccipital bone as one state, an expanded medial concha as a second state (not contacting the paraoccipital process), and a constricted medial concha of the quadrate as a third character state. More conservatively this character is viewed as two states: the medial concha is either expanded or constricted. In species that have a medially expanded concha the amount of contact with the anterior portion of the paraoccipital process seems to be size related. But within the genera examined, the two state characterization is consistent.

Crotaphytines, morunasaurs, oplurines and all tropidurines have expanded medial concha, without exceptions. Within sceloporines all genera except *Callisaurus* and the ear-less lizards (*Cophosaurus* and *Holbrookia*) have expanded medial concha. Noteworthy is *Phrynosoma*, because the medial concha is extremely expanded dorsally. All iguanines except *Brachylophus* and *Amblyrhynchus* also have an expanded medial concha. In *Conolophus, Cyclura* and larger *Sauromalus* the expanded medial concha is supported by a bony strut that extends from the central portion of the quadrate to the mediodorsal aspect of the medial concha. The polarity at the iguanine basal node calls for an expanded medial concha to be the most parsimonious assumption (2:1 consensus). All anoloids examined except the leiosaurs have constricted medial concha.

The character state distribution at the outgroup nodes is a (6:1) consensus, with an expanded medial concha as the plesiomorphic condition at the ingroup/outgroup basal node.

Character 26: quadrate (Fig. 20). In all outgroup taxa, exclusive of the anoles, the quadrate has an anteriorly directed curvature. The stapes rests within this curvature. In anoles, however, the quadrate is straight and the cephalic condyle, the ventral condyle and the posterior crest all lie within a frontal plane, with the stapes contacting the posterior crest.

The distribution of character states at the outgroup basal nodes are all unequivocal and indicate that an anteriorly curving quadrate is the plesiomorphic condition at the ingroup/outgroup node (7:0 consensus).

Basiliscus shows the primitive "iguanid" condition with an anteriorly curving quadrate. *Corytophanes* and *Laemanctus* have the derived condition with a vertical posterior crest of the quadrate.

Epipterygoid

The epipterygoids are thin, cylindrical bones aligned vertically in the lateral aspect of the temporal region of the skull.

Character 27: epipterygoids. In *Basiliscus* and *Laemanctus* the epipterygoid shows the characteristic "iguanid" condition: the epipterygoid slopes forward and downward at an angle, and the dorsal end contacts the ventral portion of the parietal. In some specimens of *Basiliscus* and other "iguanids", a small vertical downgrowth of the parietal contacting the dorsal end of the epipterygoid can be observed. The ventral downgrowth, however, seems to be predominantly present in larger specimens.

In *Corytophanes* the epipterygoid is short, slants caudally and is never in contact with the ventral portion of the parietal bone. In *Corytophanes hernandezi* and *C. cristatus* the dorsal end of the epipterygoid is free and reaches the level of the supratrigeminal process. In these two taxa a ligamentous connection joins the head of the epipterygoid with the supratrigeminal process.

In *Corytophanes percarinatus* the epipterygoid also slants caudad, but is not free dorsally, and contacts with the alar process of the prootic.

In all outgroup taxa examined the dorsal end of the epipterygoid contacts the ventral aspect of the parietal. Presch (1969) reported the epipterygoid to be absent in *Phrynosoma solare*, but it is in fact present, but vistigal (Axtell 1986).

The distribution of character states at the outgroup nodes indicates that the epipterygoid contacting the ventral aspect of the parietal is the plesiomorphic condition at the ingroup/outgroup basal node (7:0 consensus).

The condition in *Corytophanes* is apomorphic, whereas the condition in both *Basiliscus* and *Laemanctus* are plesiomorphic.

Posterior Brain Case

The posterior brain case consists of the following neurocranial elements of endochondral origin: supraoccipital, exoccipitals, basioccipital, prootic and basisphenoid. These bones are tightly sutured or fused. The medulla and cerebellum are housed within these bones.

The anterior portion of the brain is not enclosed by bone, but is limited anteriorly by a double folded interorbital septum. The anterior cavity houses the hypothalamus, the optic lobes, the cerebral hemispheres, and the olfactory stalks.

Basisphenoid

The basisphenoid is a median bone forming part of the floor of the cranial cavity. It forms part of the basipterygoid joint, which is the major source of ventral kinesis between the posterior brain case and the rest of the skull (see also description of the pterygoid).

Character 28: crista ventrolateralis. The crista ventrolateralis (Säve-Söderbergh 1947) is located on the ventral portion of the basisphenoid and projects laterally, posterior to the basipterygoid process. The vidian canal is located dorsal to the crista ventrolateralis at the base of the basipterygoid process.

Within tropidurines, iguanines and sceloporines, the crista ventrolateralis is broad and expanded laterally to overly the vidian canal such that it is obscured in ventral view. A broad crista ventrolateralis also occurs in *Polychrus, Enyalius, Chamaeleolis, Anolis*, some *Enyalioides, Oplurus* and *Hoplocercus*.

In all remaining taxa of the outgroups, such as *Pristidactylus, Urostrophus,* crotaphytines, *Chalarodon, Morunasaurus* and some *Enyalioides*, the crista ventrolateralis is narrow and the vidian canal is visible in a ventral view.

The polarity at the ingroup/outgroup node is a (4:1) consensus decision, indicating that a broad crista ventrolateralis is the plesiomorphic condition. A narrow crista ventrolateralis with an exposed vidian canal (apomorphic condition) was only observed in *Basiliscus* within the ingroup.

Basioccipital

The basioccipital is a median neurocranial bone forming the floor of the posterior brain case and the median third of the occipital condyle. The dorsal aspect of the basioccipital is concave and protects the medulla oblongata.

Prootic & Orbitosphenoid

The prootic is a paired bone that forms the lateral walls of the cranial vault and is sutured to the other bones of the posterior brain case.

The lateral wall of the prootic has numerous crests for the attachment of aponeuroses. In most "iguanids" the medial wall is entirely covered with dura and the posterior aspect contains the tympanic bulla.

The supratrigeminal process of the prootic is prominent in *Basiliscus*, whereas it is small and sometimes absent in *Corytophanes* and *Laemanctus*. In addition, in *Corytophanes* there is connective tissue between the supratrigeminal process and the head of the epipterygoid, which is free (see also the description of the epipterygoid). The head of the epipterygoid contacts the pila antotica and is partially embedded within the prootic membrane. In *Basiliscus* and *Laemanctus*, the head of the epipterygoid contacts a ventral process of the parietal bone (see description of epipterygoid and character 27). Medially the epipterygoid contacts the pila antotica, but is completely excluded from the prootic membrane.

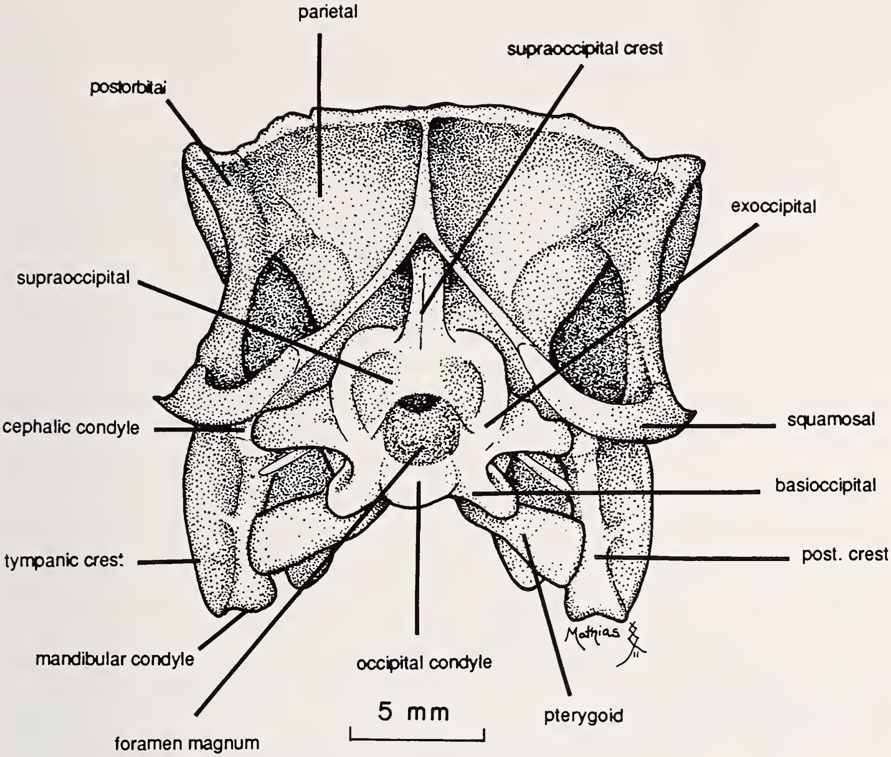
The orbitosphenoids are semicircular bones lying within the interorbital membranes. The orbitosphenoid is continuous with five orbital cartilages, one of which is the posteroventral pila antotica. During skeletal preparation, the orbitosphenoid and associated cartilages are frequently lost or damaged. Hence, large sample sizes of complete orbitosphenoids were not available for character evaluation.

Exoccipital

The exoccipital sutures dorsally with the supraoccipital, anteriorly with the prootic and ventrally with the basisphenoid. It consists of a central body, which houses the posterior half of the membranous labyrinth and the posterolaterally directed paraoccipital process.

Character 29: outlines of bony labyrinth (Fig. 26). Etheridge & de Queiroz (1988) used the amount of exposure of the superficial outlines of the osseous labyrinth of the inner ear as a systematic character. They recognized a three state character transformation: the superficial outlines of the osseous labyrinth are obscure (plesiomorphic condition); they are slightly raised above the occipital bones (intermediate condition) or they are very distinct, raised well above the surface of the occipital bones (apomorphic condition). Etheridge & de Queiroz's (1988) polarity decision is accepted here; non-exposure of the bony labyrinth above the occipital bone is widespread among the Scleroglossa and *Sphenodon*.

Among the outgroup taxa examined, the presumed apomorphic state occurs in several distantly related taxa. Well-defined outlines of the bony labyrinth are found in crotaphytines, most anoloids, *Petrosaurus, Urosaurus*, some *Enyalioides*, some *Oplurus* and in *Uranoscodon*. The presumed intermediate condition is widespread in sceloporines (except *Phrynosoma* and the above mentioned taxa), *Chalarodon, Hoplocercus, Leiocephalus* and in *Dipsosaurus*. The presumed plesiomorphic condition (superficial outlines of bony labyrinth obscure) is found in some anoloids, *Morunasaurus, Phrynoso-*



C. percarinatus

Fig. 26: Posterior view of skull of *Corytophanes percarinatus*. Dorsal expansion of bony labyrinth and limiting angles of parietal result in the closure of the postemporal fossa. Notice the broad contact of quadrate process of pterygoid with quadrate.

ma, all iguanines except *Dipsosaurus* and in tropidurines exclusive of *Uranoscodon* and *Leiocephalus*.

The distribution of the character states at the outgroup nodes shows a (2:1:1) consensus distribution. No unequivocal polarity decision at the ingroup/outgroup basal node can be made.

Within the ingroup, *Basiliscus* invariably shows the presumed intermediate condition (fide Etheridge & de Queiroz 1988). In *Corytophanes* and *Laemanctus* the bony labyrinth is elevated well above the occipital bones (presumed apomorphic condition).

Supraoccipital

The supraoccipital is a median bone that forms the dorsal rim of the foramen magnum. It roofs the dorsal aspect of the posterior brain case and contains the dorsal portion of the membranous labyrinth.

Character 30: posttemporal fenestra (Fig. 26). The supratemporal processes of the parietal in "iguanids" usually diverge at a 120° angle. In *Corytophanes*, however, they form an angle of less than 90°. Accordingly, in *Corytophanes* there is partial or complete closure of the postorbital fossa due to the dorsal projection of the bony labyrinth and the ventral expansion of the supratemporal process of the parietal.

In *Corytophanes hernandezi* the posttemporal fossa is partially closed, being restricted to a small area lateral to the bony labyrinth of the semicircular canals and dorsal to the paraoccipital process. In *C. percarinatus* and *C. cristatus* the paraoccipital process of the exoccipital is in broad contact with the squamosal process of the parietal, completely closing the posttemporal fossa.

The extensive contact of the prootic, supraoccipital and exoccipital bones with the parietal has resulted in the loss of the parietal-occipital joint, which is the seat of metakinesis in the squamate skull (as described by Jollie 1960). In *Corytophanes percarinatus* and *C. cristatus* there appears to be a complete loss of metakinesis. *Corytophanes hernandezi*, however, may or may not retain partial metakinesis. The dorsal head of the M. adductor mandibulae externus profundus, which passes through the posttemporal fossa in "iguanids" is lost in *Corytophanes* (Costelli 1973; see discussion of character 56).

To judge from ontogenetic series in *Basiliscus vittatus* and other well-represented "iguanids", the narrow angle of the supratemporal process of the parietal is a paedomorphic character. The posttemporal fossa is completely closed in some juveniles, but open in adults.

Among outgroups, the diverging supratemporal processes of the parietal form an angle of more than 90°, and a well-defined posttemporal fossa is present including a small contact zone at the parietal-occipital joint. The open posttemporal fossa is therefore the plesiomorphic condition (7:0 consensus). The partially closed fossa in *Corytophanes hernandezi* is considered to be the intermediate condition in this transformation series, and the closed condition in *C. percarinatus* and *cristatus* is apomorphic.

Lower Jaw and Hyoid

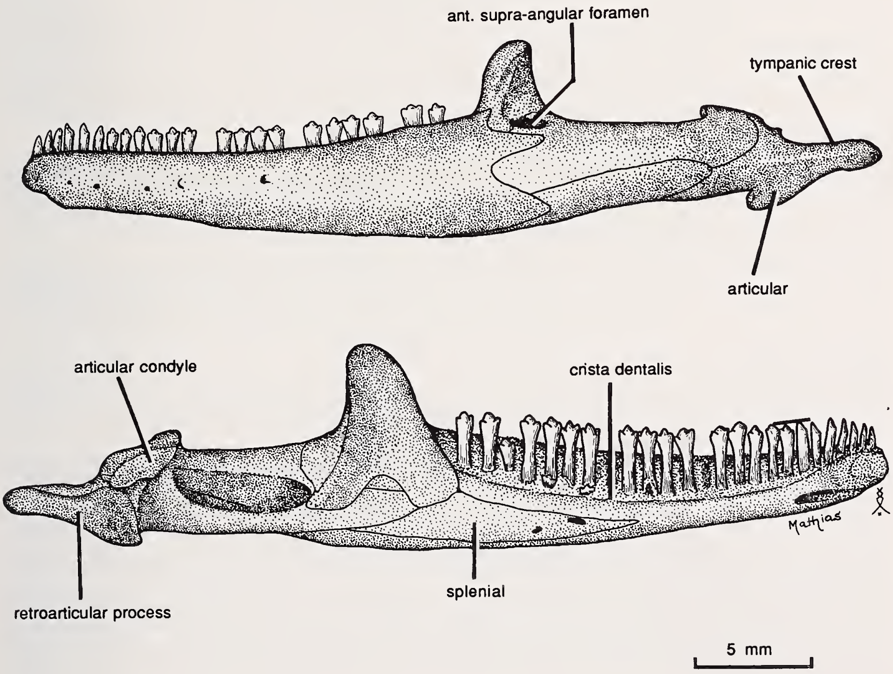
The lower jaws of squamates are united anteriorly at the mandibular symphysis by a band of dense connective tissue (syndesmosis). Posteriorly the jaws articulate with the quadrates (mandibular joint). The mandible is composed of six separate bones surrounding a central Meckel's cartilage: dentary, splenial, coronoid, angular, surangular and articular. I follow Oelrich's (1956) terminology in which the "articular" is a compound element that consists of the endochondral splanchnocranial articular that is fused to the intramembranous dermal prearticular.

The hyoid apparatus is located in the throat between the lower jaws, and serves as an attachment site for throat musculature and the tongue. Its description is included in this segment, although it is a separate element that is not a part of the lower jaw.

Dentary (Figs. 27—30)

The dentary is a hollow tooth-bearing bone surrounding Meckel's cartilage. It is rounded anteriorly where it meets the other dentary at the mandibular symphysis. Posteriorly the dentary surrounds the anterior aspect of other bones of the lower jaw.

Character 31: condition of Meckel's groove (Figs. 27—30). Etheridge & de Queiroz (1988) evaluated the condition of Meckel's groove as two characters: the fusion or nonfusion of Meckel's groove anterior to the splenial, and the extent of closure of the Meckel's groove anterior to the splenial. In this study I consider the state of Meckel's groove a binary transformation series: when fusion of the dentary on the lingual aspect of the lower jaw occurs, the open condition of the groove is affected and thus the two characters are interrelated.



Basiliscus galeritus

Fig. 27: Labial and lingual views of the lower jaws of *Basiliscus galeritus*.

The presumed primitive "iguanid" condition is for Meckel's groove to be entirely open from the anterior end of the splenial to the mandibular symphysis. From the presumed primitive condition, one part of the bi-directional transformation involves two states: an intermediate state in which Meckel's groove is closed half the distance or less from the splenial to the mandibular symphysis, and the presumed apomorphic condition in which Meckel's groove is closed for more than half the distance between the splenial and the symphysis. The other part of the bi-directional transformation involves the fusion of Meckel's groove for more than half the distance between the splenial and the mandibular symphysis. This character therefore has two bi-directional transformations, one involving closure (suturing), the other fusion.

The consensus algorithm indicates that the polarity state at the basal ingroup/outgroup node is equivocal (3:2:1 consensus). The character states are left unordered in the data matrix.

Accepting the polarity decision of Etheridge & de Queiroz (1988) results in a sutured Meckel's groove being a derived condition in sceloporines, some *Crotaphytus* and *Phymaturus*. A fused Meckel's groove for more than half the distance anterior to the splenial would be a derived condition found in all tropidurines (except *Phymaturus*, the recently extinct *Leiocephalus apertosulcus* (Etheridge 1965b), *Ctenoblepharis*, some *Liolaemus* (R. Etheridge, pers. comm.) and in *Leiocephalus anonymus* (Pregill 1984)), all anoloids, all iguanines, some *Oplurus* and *Chalarodon*. *Gambelia*, some *Crotaphytus*, some *Oplurus* and all morunasaurs have an open Meckel's groove. *Phrynosoma* is peculiar in that all character states are present.

In basiliscines, Meckel's groove is entirely open anterior to the splenial in *Laemanctus serratus* (Fig. 30) and sutured in *Basiliscus vittatus* (Fig. 28). In all other ingroup taxa, Meckel's groove is closed through fusion (i.e., no sutureline remains).

Reversing the polarity decision would result in the independent acquisition of an open Meckel's groove in *Basiliscus vittatus* and *Laemanctus serratus* within the ingroup.

Splenial (Figs. 27—30)

The splenial is a flat, plate-like bone located on the lingual surface of the lower jaw that covers the medial aspect of Meckel's cartilage.

Character 32: splenial size (Figs. 27—30). The anterior inferior alveolar foramen is located anteriorly in the splenial and serves as passage for the lingual branch of the inferior alveolar nerve in *Ctenosaura* (Oelrich 1956). The position of the anterior inferior alveolar foramen remains constant in most "iguanids" and is located below the penultimate or third to last posterior marginal tooth⁶. In most "iguanids" the splenial is short, extending forward only to the third or fourth posterior marginal tooth. In this condition, the anterior inferior alveolar foramen is located terminally or subterminally within the splenial.

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⁶) The position of the anterior inferior alveolar foramen is variable in *Leiocephalus* (G. Pregill, pers. comm.).

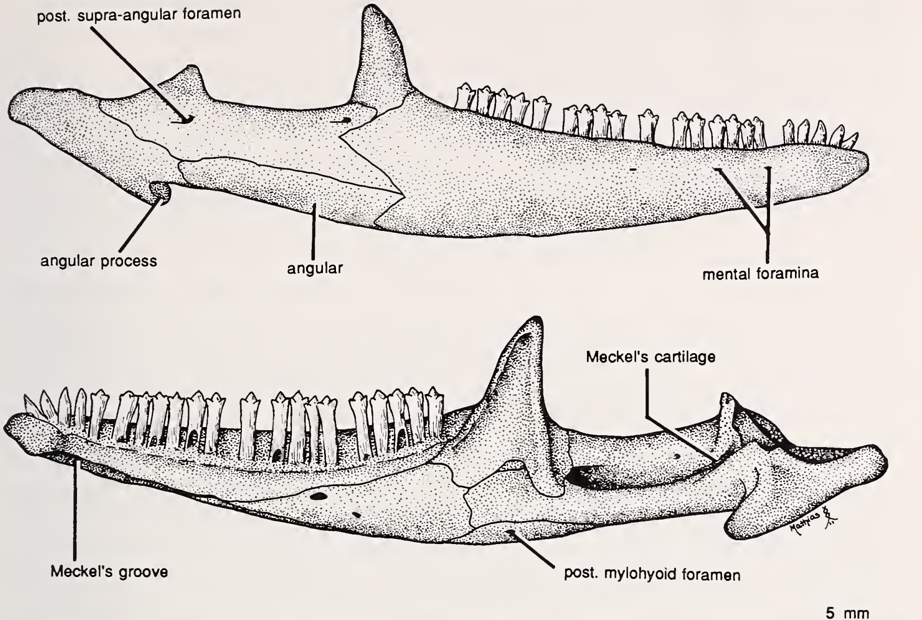

Fig. 28: Labial and lingual views of the lower jaw of *Basiliscus vittatus*.

In those "iguanid" genera that have an elongated splenial (past midpoint of dentary tooth row, the anterior inferior alveolar foramen is not located at the anterior end within the splenial, rather it is situated at the dentary-splenial suture. This condition occurs in *Phymaturus*, some *Liolaemus*, crotaphytines, most oplurines, morunasaurs, *Basiliscus* and *Laemanctus*.

In other "iguanids" with short splenials that do not reach the level of the anterior inferior alveolar foramen (e.g., *Anolis* and *Chamaeleolis*), the anterior inferior alveolar foramen is located between the coronoid and the dentary, entirely outside the splenial. This is also the case in taxa that have lost the splenial (e.g., some *Anolis*).

Within the basiliscines, *Basiliscus* and *Laemanctus* have a large splenial. *Corytophanes* on the other hand has a short splenial with a terminal anterior inferior alveolar foramen.

The character state distributions at the outgroup nodes indicates that a short splenial with a terminal or subterminal anterior inferior alveolar foramen is the consensus plesiomorphic condition (5:2 consensus). It should be noted, however, that within the broader context of the Squamata and Lepidosauria, an elongated splenial is considered to be the plesiomorphic condition (Romer 1956; Etheridge & de Queiroz 1988).

Coronoid (Figs. 27—30)

The coronoid is a triangular bone located approximately at the midpoint of the lower jaw. It has a prominent dorsal projection that serves for insertion of the M. adductor mandibularis externus and medius and the bodenaponerosis (see below). Ventrally, the coronoid has two anterior projections and a single posterior projection. The anterolabial projection is small in most basiliscines and articulates with the dentary and surangular on the labial aspect of the lower jaw. The anterolingual projection of the coronoid process extends half way down the lower jaw on the lingual side and articulates with the dentary, splenial and articular. The posteroventral projection is located on the lingual side of the lower jaw and forms the anterior rim of the mandibular foramen.

Character 33: coronoid lateral process (Figs. 27—30). This character has been described by Etheridge and de Queiroz (1988) as having three character states that are part of a transformation series. They hypothesized that the lack of a lateral process of the coronoid overlapping the posterolateral surface of the dentary is the plesiomorphic condition. A coronoid bone with a small, irregular process overlapping the posterolateral surface of the dentary is hypothesized to be the intermediate condition, and a coronoid with a large blade-like process descending over the posterolateral surface of the dentary is the presumed apomorphic condition.

Among tropidurines, a large blade-like process is the condition found at the basal node, but the *Tropidurus*-group in addition to *Stenocercus* lack a lateral process. All of the anoloids examined, except for *Chamaeleolis* and *Anolis*, and oplurines, have no coronoid lateral process. *Chamaeleolis* and *Anolis* have a blade-like process as do all iguanines and morunasaurs. Sceloporines and crotaphytines have a small irregular lateral process.

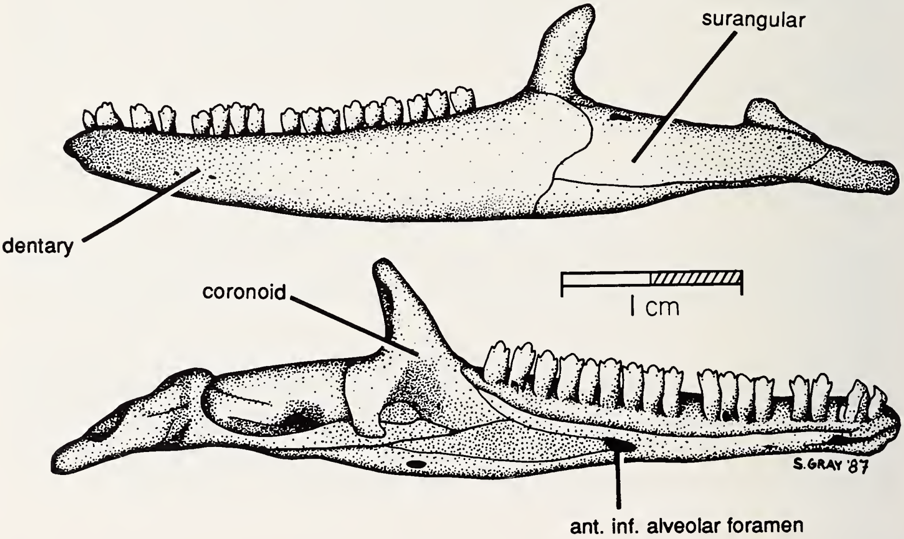

Fig. 29: Labial and lingual views of the lower jaw of *Corytophanes percarinatus*. (Drawing courtesy of S. Gray).

The distribution of the character states does not result in an unequivocal polarity decision (3:3:1 consensus).

Moreover, a fourth condition, not found within any outgroup, occurs within the ingroup. *Basiliscus*, *Corytophanes cristatus* and *C. percarinatus* have a small irregular lateral coronoid process that overlaps the posterolateral aspect of the dentary. *Corytophanes hernandezi* and both species of *Laemanctus*, on the other hand, have a small, hook-like process on the coronoid that projects posteriorly to overlap the posterodorsal aspect of the dentary.

Angular (Figs. 27—30)

The angular is an elongate bone that is primarily restricted to the ventral surface of the lower jaw. The posterior portion is slightly expanded and is visible on the labial surface. An anterior process extends on the ventral aspect of the lower jaw to contact the dentary.

Character 35: size of posterior aspect of angular (Figs. 27—30). The labial exposure of the posterior portion of the angular bone can be slight or extensive. In the latter condition the posterior portion of the angular bone is expanded and extends from a point below the coronoid process posteriorly to the articular fossa. In the former case there is only a sliver of the angular bone that is visible in labial view, and the posterior portion is not expanded.

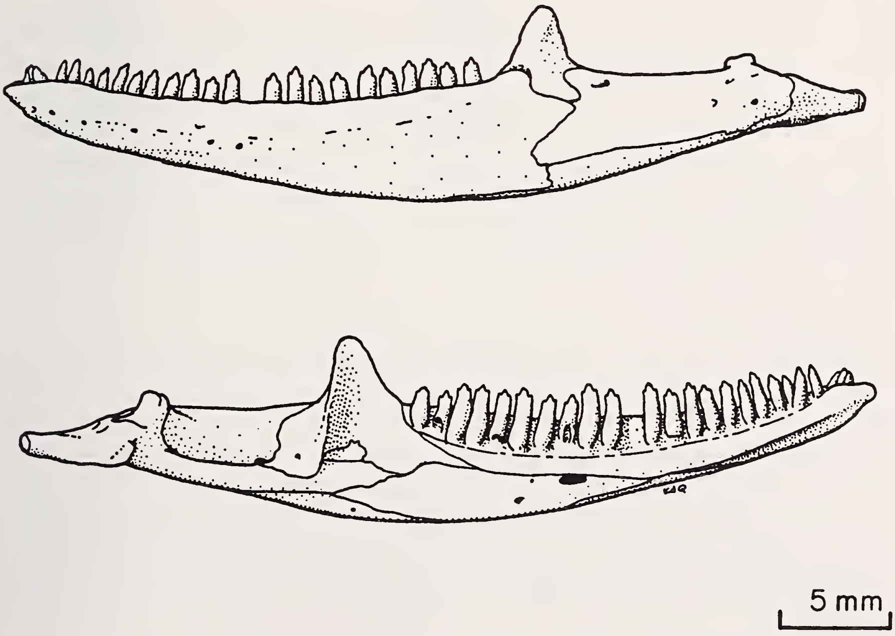

Fig. 30: Lingual and labial views of *Laemanctus serratus*. (Drawings courtesy of K. de Queiroz).

A pronounced labial exposure of the angular is found in *Pristidactylus,* all iguanines except *Sauromalus,* all sceloporines except *Petrosaurus,* crotaphytines, oplurines and morunasaurs. The alternate condition (a reduced labial exposure of the angular) is found in tropidurines, all anoloids except *Pristidactylus, Sauromalus* and *Petrosaurus.* A tiny angular is present on the lateral face of the mandible of *Chamaeleolis*. The angular may be absent in other anoles (Etheridge 1959).

At the basal outgroup nodes of iguanines, crotaphytines, oplurines and morunasaurs an expanded posterior portion of the angular is the unequivocal character state. In tropidurines and anoloids the alternate character state is the condition found at the basal node. The condition at the sceloporine basal node is equivocal. The distribution of the characters at the ingroup/outgroup basal outgroup nodes reveals a (4:2) consensus with an expanded posterior portion of the angular as the plesiomorphic condition at the ingroup / outgroup node.

Surangular (Figs. 27—30)

The surangular (supra-angular of Oelrich) forms the posterodorsal aspect of the labial side of the mandible. It forms the lateral wall of the mandibular foramen and together with the articular and angular bones contains the posterior portion of Meckel's canal. The dorsal aspect of the surangular is distinctly rounded and serves for insertion of the M. adductor mandibularis externus.

Articular (Figs. 27—30)

The articular bone consists of two main parts; a posterior condyle and a thin anterior ramus as indicated by Kingsley (1905). The condylar portion of the articular has a large labial condyle and a smaller lingual condyle that articulate with the ventral head of the quadrate to form the mandibular joint, an angular process and a retroarticular process.

Character 35: angular process size (Fig. 31). Two distinct patterns in the development of the angular process can be defined. First, in large adults of some taxa the angular process is about the same size relative to that of juveniles. Second, the angular process may be relatively small in hatchlings, but increases in size during ontogeny.

When characters are defined as ontogenetic transformations (e.g., increase in size vs. unchanged) rather than as instantaneous occurrences (e.g., large vs. small), there is no conflict between ontogeny and outgroups. Ontogenetic transformations themselves then can be used as systematic characters (de Queiroz 1985). Unfortunately, ontogenetic series for all taxa of the outgroups were not available for study. However, a juvenile with a relatively large angular process (instantaneous form) excludes the possibility of a transforming ontogeny. On the other hand, a taxon represented by a single adult with an enlarged angular process contains no information because the angular process may be part of either a transforming or non-transforming ontogeny. The only exception to be noted for this character is the case of *Amblyrhynchus,* in which the angular process is small in small specimens and does not enlarge during ontogeny (de Queiroz 1987, pers. obs.).

Among the outgroups examined, only *Leiocephalus, Phymaturus, Dipsosaurus*, some

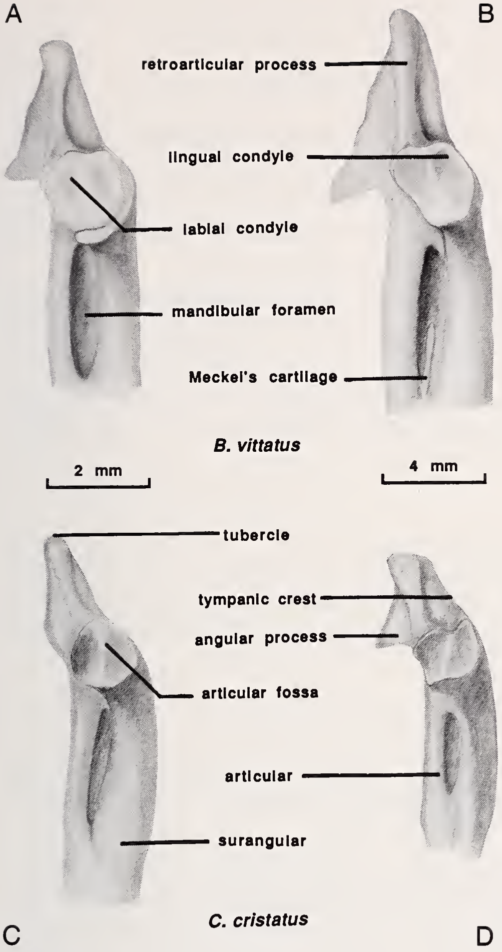

Fig. 31: Ontogenetic changes in size of the angular process in *Basiliscus* and *Corytophanes* A) Juvenile *B. vittatus* B) Adult *B. vittatus* C) Juvenile *C. cristatus* D) Adult *C. cristatus*.

Ctenosaura (de Queiroz 1987; pers. obs.) and *Petrosaurus* have angular processes that are part of a transforming ontogeny. All remaining taxa among outgroups have angular processes that are part of a non-transforming ontogeny.

The distribution of character states at the basal node of all outgroups except sceloporines, tropidurines and iguanines is unequivocal and calls for an angular process that is part of a non-transforming ontogeny as the plesiomorphic condition (4:0 consensus). The polarity at the basal node of the sceloporines, tropidurines and iguanines is equivocal, because of the character state observed in the respective earliest diverging taxa (*Petrosaurus, Phymaturus* and *Dipsosaurus*).

Within the basiliscines, juvenile *Basiliscus* have an enlarged angular process of the articular that is part of a non-transforming ontogeny (plesiomorphic condition). In *Cory-*

tophanes and *Laemanctus* the angular process is small in hatchlings and juveniles, but is large in adults, thus being part of a transforming ontogeny (apomorphic condition).

Character 36: angular process position. The angular process of "iguanids" is oriented in either of two ways relative to the long axis of the mandible: in an oblique plane or a horizontal plane. In tropidurines, anoloids, all iguanines except *Amblyrhynchus, Iguana* and some *Ctenosaura* and sceloporines the angular process is located in a horizontal plane parallel to the plane in which the articular process is located. In *Amblyrhynchus, Iguana* and some *Ctenosaura*, crotaphytines, oplurines and morunasaurs the angular process of the articular is oblique to the articular process.

The distribution of character states among the basal outgroup nodes shows a (4:3) consensus. This character cannot be polarized and is therefore left unordered in the data matrix.

Within the basiliscines, the angular process of *Corytophanes* and *Laemanctus* are located in a horizontal plane, whereas the angular process of *Basiliscus* is set at an oblique angle with respect to the plane of the lower jaw.

Meckel's cartilage (Figs. 27—30)

Meckel's cartilage originates from the articular bone and lies within Meckel's canal. Anteriorly Meckel's cartilage may be visible, or Meckel's groove may be sutured or fused and Meckel's cartilage may no longer be visible. Meckel's cartilage terminates anteriorly in the cutaneous tissue of the skin.

Hyoid apparatus (Fig. 32)

The hyoid apparatus and associated musculature has been treated in detail for a variety of squamates by Cope (1892), Camp (1923), Gnanamuthu (1937), Beebe (1944), Sondhi (1958) and Langebartel (1968).

The hyoid apparatus is a splanchnocranial element that is embryonically derived from an entoglossal structure (copula & hypohyal) and portions of three pharyngeal arches: the hyoid arch (basihyals & ceratohyals), and the first and second branchial arches (first and second ceratobranchials respectively) (Jollie 1960). It consists primarily of calcified cartilage and only two bony elements (first ceratobranchials).

The proximal portion of the ceratohyals in "iguanids" shows considerable variation, but two distinctive conditions persist: the proximal portion of the ceratohyals are either expanded or they are not expanded.

The proximal expansion itself varies considerably. Because the ceratohyals are cartilaginous elements, the proximal expansions are easily damaged during skeletal preparation. The proximal portion in some taxa is a simple expansion (e.g. *Crotaphytus, Conolophus, Ctenosaura, Sauromalus* etc.). In other taxa (e.g. *Basiliscus* and *Laemanctus*) the proximal portion of the ceratohyals is greatly expanded to form anteriorly or posteriorly projecting hooks (Romer 1956). Expansion of the proximal portion of the ceratohyals may be correlated with body size, with heavier bodied lizards having a more prominent proximal portion of the ceratohyals than slender bodied forms. This is certainly

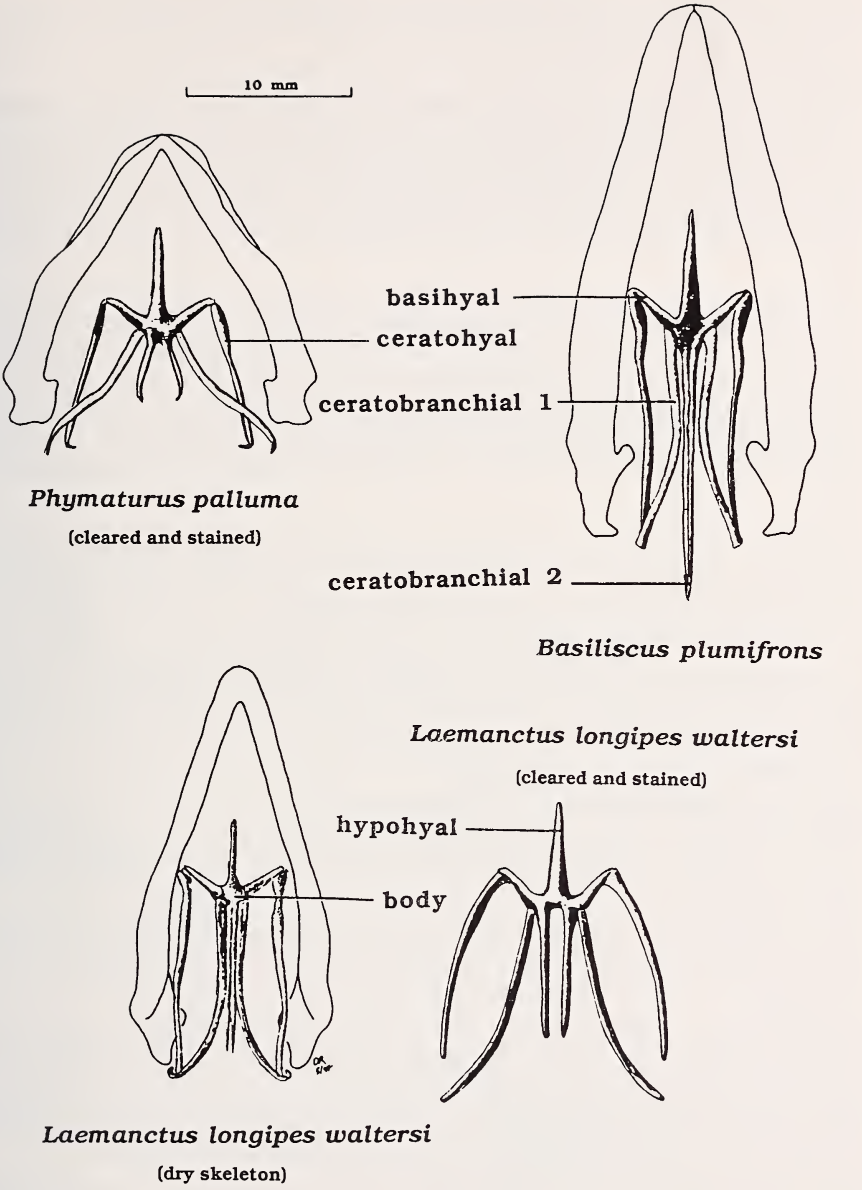

Fig. 32. Two different patterns of hyoid apparatus identified within the ingroup and among non-basiliscine "iguanids". *Phymaturus palluma* and *Laemanctus longipes* shows *X*-pattern in which the second ceratobranchials are the shortest posterior extending elements. *Basiliscus plumifrons* shows the *Z*-pattern with an elongated second ceratobranchial. Notice also the drying effect of skeletal elements in *Laemanctus longipes* with apparent fusion of the median second ceratobranchials. (Drawing courtesy of D. Rapp).

the case in iguanines, in which *Brachylophus* and *Dipsosaurus* have slender ceratohyals, by contrast to proximal expansions of the ceratohyals in *Conolophus, Amblyrhynchus* and *Ctenosaura*.

Examination of ontogenetic series of *Basiliscus* and *Laemanctus* reveals that expanded ceratohyals are present in hatchlings and do not change significantly relative to other hyoid elements. If an expanded ceratohyal is absolutely correlated with body size a distinct difference in degree of proximal expansion of the proximal portion of the ceratohyals would be expected. This, however, is not always the case in the outgroups examined.

Character 37: hyoid apparatus pattern (Fig. 32). Within "iguanids" two hyoid patterns can be identified. In this study the two patterns are identified as *X* and *Z*. In pattern *X* the median second ceratobranchial is the longest posterior hyoid element. The first ceratobranchials and the ceratohyals are usually equal in length. The posterior extent of the second ceratobranchial with respect to the other two elements varies considerably between taxa, but by definition is always the longest posteriorly extending element.

In pattern *Z*, the second ceratobranchials are the shortest posteriorly extending elements with respect to the first ceratobranchials and the ceratohyals. The ceratohyals and first ceratobranchials may be of equal length. Variation in this pattern is minimal.

The *X* pattern of posterior hyoid elements occurs in all anoloids, in *Leiocephalus* and in *Brachylophus*. All remaining taxa examined including all sceloporines, crotaphytines, oplurines, morunasaurs, tropidurines (exclusive of *Leiocephalus*) and iguanines (exclusive of *Brachylophus*) show the *Z* pattern in which the second ceratobranchial is the shortest element.

In most specimens that show the *Z* pattern, the ceratohyal and the first ceratobranchial have an equal posterior extension. In *Enyalioides, Morunasaurus* and *Tropidurus spinulosus* (Pregill, pers. comm.) the first ceratobranchial is the longest posteriorly extending hyoid element.

The distribution of the character states among the outgroups indicates that the *Z* pattern is the plesiomorphic condition at the ingroup/outgroup node, considering a (5:1) consensus.

Within the ingroup, the distribution of the hyoid patterns are somewhat random. *Basiliscus basiliscus, B. vittatus, Corytophanes* and *Laemanctus* show the *Z* pattern, with the first ceratobranchials the longest posteriorly extending hyoid element. In *Basiliscus plumifrons, Corytophanes cristatus* and *C. percarinatus* the hyoid apparatus shows the *X* pattern. No corresponding information for *B. galeritus* was available.

One note of caution should be added here, the lack of adequate material restricts the characterization of the various morphologies of the hyoid apparatus to generalities. For some of the outgroup taxa, only a single specimen was available for examination. The characterization of these two patterns may show more variation than suggested here. This argument is supported by the distribution and variation of character states within the ingroup for which many specimens were available.

Miscellaneous Cranial Characters

Character 38: rostral portion of skull (Fig. 16, 23, 25, 33). Among the outgroup taxa, two morphologies of the rostral portion of the skull are observed. A spatulate snout was observed in *Oplurus cuvieri* and all anoloids except *Enyalius* and *Pristidactylus*. Few tropidurines such as *Platynotus (Tapinurus) semitaeniatus, Ophryoessoides caducus* (Etheridge, pers. comm.) and *O. tricristatus* (Etheridge, pers. comm.) also show a spatulate rostrum. All other outgroup taxa have an arched anterior portion of the skull.

Using the algorithm for determining polarity at the basal node of the ingroup when outgroup relationships are unknown, indicates that the arched anterior portion of the skull is the plesiomorphic condition with a (5:1) consensus.

Basiliscus shows the common "iguanid" condition in which the rostral portion of the skull is rounded and arched. The premaxillary spine together with the nasals form part of this arch. In *Corytophanes* and *Laemanctus* on the other hand, the rostral portion

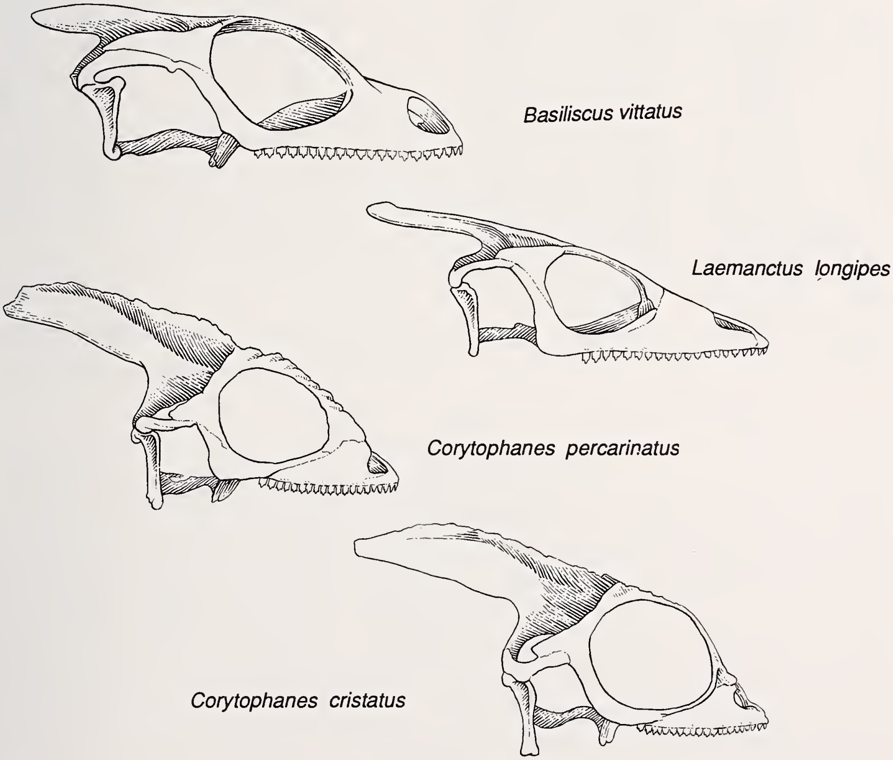

Fig. 33: Lateral view of *Basiliscus, Corytophanes* and *Laemanctus*. (Drawings by G. Christian).

is distinctly flat and spatulate. The premaxillary spine is flat as are the nasals and the remaining skull roof bones, such that the bones of the dorsal aspect of the skull are planar. The spatulate snout is therefore a synapomorphy for *Corytophanes-Laemanctus*, with homoplasy in the above mentioned taxa.

Character 39: crowns of posterior marginal teeth (Fig. 34). This character has been discussed by Etheridge & de Queiroz (1988). Although the outgroup evidence is equivocal for "iguanids", Etheridge & de Queiroz (1988) treat the tricuspid tooth crown as primitive. From the primitive condition two independent transformation series are hypothesized: one involves the broadening of the tooth crown and an increase in cuspation; the alternate transformation involves the reduction and eventual loss of accessory cusps. In order to asses the polarity of this character at the ingroup/outgroup node, this character is split into two characters, each representing alternate transformation series (Characters 39A and 39B).

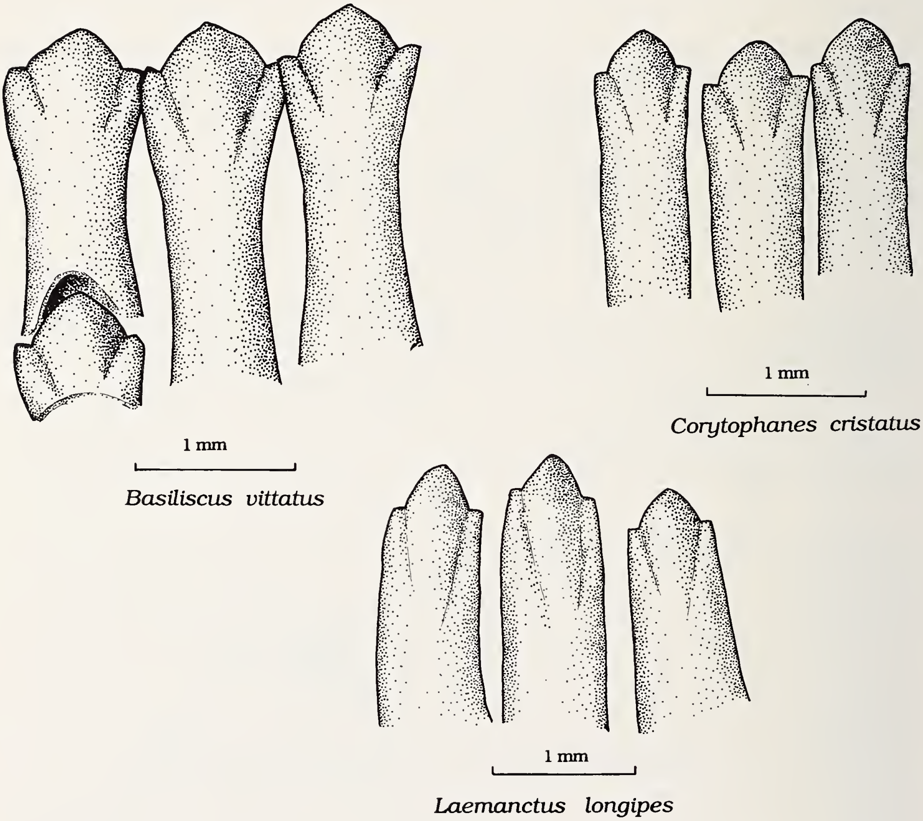

Fig. 34: Morphology of posterior marginal teeth of *Basiliscus, Corytophanes* and *Laemanctus*.

Expansion of the crown on the posterior marginal teeth (character 39A) occurs in *Phymaturus, Leiocephalus, Plica* and some *Liolaemus, Enyalioides*, some *Pristidactylus*, all iguanines, some *Sceloporus* and some *Oplurus*. All other outgroup taxa have a non-expanded crown, which also includes taxa with constricted crowns.

The basal nodes of the outgroup taxa indicate that a non-expanded tricuspid tooth crown with parallel sides is the plesiomorphic condition (4:2 consensus) at the ingroup/outgroup node.

With regard to the second transformation series (from tricuspid crown to tapered crown with small accessory cusps; Character 39B) the constriction of the crowns of the posterior marginal teeth occurs in some *Liolaemus*, some *Pristidactylus, Chamaeleolis*, and in all sceloporines except *Petrosaurus, Uta, Uma*, and *Sceloporus*. All outgroups except sceloporines indicate that the tricuspid crown is the character state found at the respective outgroup nodes. In sceloporines the decision at the basal node is equivocal.

The distribution of character states at the seven outgroup nodes indicates that the non-tapered crown is the plesiomorphic condition and a tapered crown the apomorphic condition at the ingroup/outgroup node (6:0 consensus).

Both bi-directional transformations have to be considered since the derived conditions of both transformations are observed within the ingroup. *Corytophanes* shows the primitive "iguanid" condition for both characters, with the crowns of the posterior marginal teeth having tricuspid crowns, more or less parallel-sided. *Basiliscus* on the other hand has posterior marginal teeth with distinctly expanded crowns (apomorphic condition of character 39A). Apparently, the teeth of *Basiliscus*, as with those of most non-ophidian squamates, are used for feeding upon various arthropods, their function being primarily that of gripping and breaking the exoskeleton of their prey (Montanucci 1968). The posterior marginal teeth of *Laemanctus* form part of the alternate transformation series, with very small secondary cusps (apomorphic condition of character 39B).

The distribution of the derived character states within the ingroup has no information content for resolving ingroup relationships.

Skull kinesis

Although no systematic character was designated, there are trenchant differences within the ingroup that merit some discussion. Even without experimental testing, the skull of *Basiliscus* shows signs of streptostyly in possessing a freely movable quadrate. As mentioned above, the quadrate is attached to the paraoccipital process and ventrally to the quadrate process of the pterygoid by a diarthrosis.

The kinetic maxillary segment is independent from the occipital segment except for three articulations. The basipterygoid joint is a synovial joint allowing anterior and posterior motion (see above). The second joint between the paraoccipital process of the exoccipital, the supratemporal and the parietal is a syndesmodial joint allowing only a small amount of movement. The third joint between the maxillary and occipital segments involves a highly flexible joint through the articulation of the taenia marginalis and the processus ascendens of the synoptic tectum. This is homologous to the conditions described by Oelrich (1956) for *Ctenosaura.*

Corytophanes has a short, high skull with a relatively short preorbital area and a longer postorbital region. The parietal blade is the most extensively developed in any basiliscine and is heavily ossified. Ventrally there is a broad articulation between the quadrate process of the pterygoid and the quadrate. In *Corytophanes*, the squamosal overlaps the posterolateral aspect of the quadrate, with a reversal in *C. cristatus* (Character 24). Both modifications result in reduced mobility of the quadrate with subsequent loss of streptostyly.

The three joints between the maxillary and occipital segments show a tendency to reduce the amount of movement resulting in a more rigid skull. The basipterygoid process is only narrowly expanded, resulting in a small articular surface. The posttemporal fossa is closed or partially closed, with the supraoccipital in close contact with the parietal (Character 30). The loss of this parietal-supraoccipital joint results in the loss of metakinesis. Furthermore, the frontal and parietal bones are in broad contact, with the parietal overlapping the frontal laterally. This condition further reduces kinesis within *Corytophanes*, in particular mesokinesis. The short epipterygoids that do not contact the parietal and the broad contact between the taenia marginalis is further evidence for the loss of skull kinesis in *Corytophanes.*

Laemanctus basically shows a condition intermediate between the kinetic skull of *Basiliscus* and the akinetic skull of *Corytophanes*. *Laemanctus* has short epipterygoids that do not reach the ventral aspect of the parietal, and a moderately expanded basipterygoid process. This is in contrast to the highly kinetic skull of *Basiliscus*, in which the epipterygoids are in contact with a parietal downgrowth, a broadly expanded basipterygoid process and a processus ascendens of the supraoccipital that fits into a socket on the posterior margin of the parietal.

Although it can be argued that a systematic character with three character states (kinetic, intermediate, akinetic skull) can be defined, Smith (1980) points out that electromyography, cineradiography and measurements of bone strain are necessary procedures if true kinesis is to be evaluated.

DESCRIPTION OF POSTCRANIAL SKELETON

The postcranial skeleton is described in this section and is subdivided into: 1) vertebral column, 2) ribs and rib articulation patterns, 3) pectoral girdle, including sternum and xiphisternum, 4) pelvic girdle and 5) appendicular skeleton.

Vertebral Column

"Iguanid" vertebrae are procoelous and articulate with the adjacent vertebrae through zygapophyses. The vertebral column can be grouped into three regions: presacral, sacral and caudal.

Presacral vertebrae

Twenty four presacral vertebrae is considered to be the primitive number in non-ophidian squamates (Hoffstetter & Gasc 1969). In "iguanids" this number may range from 21 to 26. The presacral vertebrae, excluding the atlas and axis, show little variation in morphology, except that the presacral vertebrae from the middle of the series tend to be larger than those found just posterior to the axis and anterior to the sacral vertebrae. The presacral vertebrae can however, be subdivided into: cervical vertebrae, which are those anterior to the first vertebra that has a costal connection to the sternum; thoracic vertebrae, those which have costal connections to the sternum directly or indirectly via the xiphisternum; and the lumbar vertebrae, which are presacral vertebrae posterior to the last thoracic vertebra that lack or have fused ribs.

Many structural peculiarities of the presacral region of *Basiliscus* are associated with bipedal locomotion (Snyder 1954). The presacral region is proportionally shortened and the neural spines are larger and more caudally inclined, particularly in the lumbar region. Shortening of the trunk moves the center of gravity closer to the areas of support (pelvis and hindlimbs) and enables bipeds to maintain more easily their upright posture. In male *B. basiliscus* and *B. plumifrons* the caudal inclination of the larger neural spines is carried to an extreme. The inclination, however, is also visible in adult females of all species of *Basiliscus*, and also in males of *B. vittatus* and *B. galeritus*.

Character 40: number of presacral vertebrae. The number of presacral vertebrae in lizards has been investigated by Hoffstetter & Gasc (1969) for lizards in general, and by Etheridge & de Queiroz (1988) for "iguanids".

Etheridge and de Queiroz hypothesized a bi-directional transformation series from the plesiomorphic condition (24 presacrals). One transformation series hypothesizes the increase in number of presacral vertebrae, whereas the other hypothesizes the reduction in number. Because all of the taxa of the ingroup form part of Etheridge and de Queiroz's "reduction" transformation series, taxa with 24 or more presacral vertebrae are coded as having the plesiomorphic condition (with respect to the reduction in number of presacral vertebrae). *Polychrus, Phymaturus*, some *Liolaemus* and some *Ctenosaura* are the only taxa that have more than 24 presacral vertebrae.

All anoloids, with the exception of some *Anolis*, have 24 presacral vertebrae. All tropidurines also possess 24 presacral vertebrae except for a specimen of *Liolaemus anomalus*, which has 23. Oplurines, iguanines, morunasaurs, and crotaphytines without exception have 24 presacral vertebrae.

Etheridge (1964) indicated that the usual number of presacral vertebrae in sceloporines is 23. *Phrynosoma* has a range of 22 to 24 presacral vertebrae according to Presch (1969). Etheridge (1962) found 23 presacral vertebrae in 68 *Sator grandaevus* and 22 in eight others. Among the remaining sceloporines, only some *Petrosaurus*, some *Sceloporus* and some *Uta* have 24 presacral vertebrae. Etheridge's (1964) contention is corroborated and 23 presacral vertebrae is the character state at the basal sceloporine node.

The consensus algorithm unequivocally supports Etheridge & de Queiroz's (1988) polarity decision, with a reduction of presacral vertebrae from the plesiomorphic condition (24) forming part of a transformation series.

All basiliscines except *Corytophanes percarinatus* have 24 presacral vertebrae. In *C. percarinatus*, however, there is a large degree of variation. Specimens of *percarinatus* from the highlands of Guatemala have a presacral vertebral count of 22, whereas specimens from lower elevations in Guatemala and El Salvador have 24 presacral vertebrae. Some specimens have 23 presacral vertebrae, but the locality data for these specimens is unknown. In addition specimens of *C. percarinatus* with a reduction in the number of presacral vertebrae, also show a consistent pattern of reduction in the number of scleral ossicles. Reduction in the number of scleral ossicles in *Corytophanes percarinatus* has been reported by Underwood (1970, 1984) and de Queiroz (1982) (see also description of scleral ossicles and Figs. 21, 22). Also of interest is the fact that in *C. percarinatus* there are consistently 16—17 maxillary teeth, whereas in *C. hernandezi* and *C. cristatus*, respectively, counts of 18 or 19 and 19 to 23 occur.

The reduction of skeletal elements that results from development in cold environments is a phenomenon in sarcopterygians known as "Jordan's rule" (Lindsey & Arnason 1981). Temperature controlled meristic variation in skeletal components has also been investigated in ambystomatid salamanders (Lindsey 1966) and in chickens (Lindsey & Moodie 1967). In squamates there has been some investigation on the effect of temperature on scutellation in the garter snake *Thamnophis* (Fox 1948; Fox et al. 1961) and on meristic characters in *Natrix fasciata* (Osgood 1968). A review of the literature has not revealed any references indicating occurance of this phenomenon in "iguanids".

If further investigations in fact indicate that the reduction in the number of presacral vertebrae (and other skeletal elements such as scleral ossicles) is positively correlated with cooler habitats, then this feature is no longer useful as a systematic character because its derivation is ecological rather than phylogenetic.

Character 41: lumbar ribs. Lumbar vertebrae have been defined by Etheridge & de Queiroz (1988) as postthoracic vertebrae with ribs fused or absent. They characterized lumbar vertebrae in terms of a bi-directional transformation. The hypothesized plesiomorphic condition is the absence of lumbar vertebrae (i.e., all postthoracic vertebrae have articulating ribs). Lumbar vertebrae with one or more ribs absent, or fused, are considered alternate apomorphic conditions. Because only loss of ribs is observed within the ingroup, this is the only transformation series of concern in this study. The fusion of lumbar ribs together with the presence of free-articulating ribs among the outgroups is coded as primitive with respect to the alternate transformation series (loss of lumbar ribs).

Loss of lumbar ribs was only observed in the following spinulate anoloids: some *Enyalius*, some *Urostrophus* and *Anolis*.

The condition at the basal node of all outgroups indicates that postthoracic vertebrae containing free articulating ribs or fused ribs is the plesiomorphic condition at the ingroup/outgroup node (7:0 consensus).

Within the ingroup, *Basiliscus* exhibits the plesiomorphic condition, in which all postthoracic vertebrae have free-articulating ribs. Both *Corytophanes* and *Laemanctus* have the apomorphic condition in which there is a lumbar vertebra without ribs. The loss of ribs is thus convergent between *Corytophanes-Laemanctus* and the above mentioned spinulate anoloids.

Sacral vertebrae

In tetrapodal squamates the sacrum consists of two vertebrae. Hoffstetter & Gasc (1969), indicate that these were the twenty-fifth and twenty-sixth vertebrae, such that in "iguanids" the sacrum still occurs in the plesiomorphic position. Asymmetrical sacra have been identified in various squamates by Hoffstetter & Gasc (1969), and also occur in basiliscines.

Caudal vertebrae

Etheridge (1959, 1967) investigated the linear differentiation in caudal vertebrae with respect to the orientation, position and shape of the transverse processes and the caudal fracture planes. Four types of caudal vertebrae were identified. All basiliscine genera are of the first type (Etheridge 1959:31), in which there is a short anterior series of non-autotomic vertebrae, each bearing a single pair of transverse processes. These are followed by a long second series of vertebrae without transverse processes. The proximal caudal vertebrae of the first series have long posterolaterally directed transverse processes (fused caudal ribs) that posteriorly become reduced in size and are directed laterally. In *Basiliscus*, the second series contains autotomous vertebrae, whereas caudal autotomy is entirely lacking in *Corytophanes* and *Laemanctus* (Table 3).

Complete hemal arches are found intercentrally, starting between the second and third, or third and fourth vertebrae. Hemal arches are prominent proximally, orientated posteroventrally, and have a bifurcated base. The arches decrease in size distally.

The number of caudal vertebrae varies considerably among the basiliscines, but is fairly constant within the genera (Table 3).

Character 42: caudal autotomy. *Basiliscus* possesses a modal number of nine caudal vertebrae in the first caudal series (= vertebrae with transverse processes counting posteriorly from the sacrum). The first vertebra with a fracture plane is consistently the tenth caudal vertebra (Table 3). Occasionally the first autotomic vertebrae (no. 10) has a small transverse process.

In *Corytophanes*, the modal number of caudal vertebrae with transverse processes is also nine, however, this number ranges from 8—12, with *Corytophanes percarinatus* showing the greatest amount of variation (see Table 3).

Laemanctus has a modal number of eleven caudal vertebrae with transverse processes, though some specimens have up to thirteen (Table 3).

Although *Corytophanes* and *Laemanctus* lack caudal autotomy, the caudal vertebrae still corresponds with the *Basiliscus*-type caudal vertebrae (Type I of Etheridge 1959, 1967).

Caudal autotomy has been lost independently in several "iguanid" taxa, for example *Uracentron, Polychrus*, some *Enyalius, Leiosaurus*, para-Anoles, *Iguana delicatissima*, some *Anolis, Brachylophus*, the Galapágos iguanines *Amblyrhynchus* and *Conolo-*

phus, Hoplocercus, Phrynosoma and *Crotaphytus* (Etheridge & de Queiroz 1988; pers. obs.).

Distribution of character states among the outgroups is a (4:0) consensus indicating that caudal autotomy is the plesiomorphic condition at the ingroup/outgroup node.

Character 43: ratio of number of neural spines to number of transverse processes in caudal vertebrae (Table 3). Proximally, the neural spines and transverse processes are distinct. Distally they become small with several transverse processes and neural spines being just small knobs. This makes counting the number of neural spines and transverse process on the caudal vertebrae subjective. Neural spines and transverse processes were counted as being present when they were larger than the caudal vertebral foramen on the respective vertebrae.

Table 3: Summary of caudal vertebrae counts

Taxa	# Neural spines (# of specimens)	# Transverse processes (# of specimens)	Total # caudal vertebrae
B. vittatus	21(8) 22(3) 23 (2)	9(11) 10(3)	55(2)
B. basiliscus	21(2) 23(2) 24(4) 25(1)	9(11) 10(1)	55(1)
B. plumifrons	21(4) 22(1)	9(8)	55(1)
B. galeritus	21(1)	9(1)	55(1)
C. cristatus	8(1) 9(2) 10(1)	8(1) 9(2) 10(1)	39(2)
C. hernandezi	9(3)	9(3)	40(1) 43(1)
C. percarinatus	9(4) 10(2) 12(1)	9(4) 10(2) 12(1)	40(3)
L. longipes	11(4) 13(1)	11(4) 13(1)	64(1)
L. serratus	10(1) 11(1) 12(1)	10(1) 11(1) 12(1)	60(1) 65(1)

In "iguanids" the relationship between the number of caudal vertebrae with neural spines and the number of caudal vertebrae with transverse processes comprises two patterns. A 1:1 ratio is the widespread "iguanid" condition, being found in all seven supra-generic non-basiliscine clades. For the most part, the 1:1 ratio is fairly consistent. In absolute numbers, there is considerable variation from a 9/9 situation in *Pristidactylus volcanensis* to a 31/31 condition in *Crotaphytus insularis*. Only two species of *Anolis* examined (*A. barahonensis* and *A. equestris)* showed a distinctive 2:1 ratio of number of neural spines to transverse processes on the caudal vertebrae.

The number of vertebrae with neural spines and transverse processes may vary ontogenetically with older (larger) individuals having more and better defined processes. The total number of caudal vertebrae is consistent within species for the limited number of specimens examined.

The distribution of the character states at the outgroup basal nodes indicates that a 1:1 ratio is the unequivocal plesiomorphic condition at the ingroup/outgroup basal node (7:0 consensus).

Within the ingroup, *Basiliscus* shows a 2:1 ratio (apomorphic condition, whereas *Corytophanes* and *Laemanctus* show the widespread plesiomorphic 1:1 ratio.

In contrast to the aforementioned, the next character is not restricted to any region of the vertebral column.

Character 44: neural spine height (Fig. 35). Three conditions of the neural spines can be identified in "iguanids". In the first condition, the neural spines are short, shorter than the vertebral body height. In this instance the anterior basal portion of the neural spine is made of thin lamellar bone and the spine itself is usually rounded. In the second condition, the neural spine is approximately the same height as the vertebral body. In this condition the lamellar bone is confined to a small region of the anterior base of the neural spine. The dorsal aspect of the neural spine is square. The third condition involves an extreme elongation of the neural spines to support a dorsal and caudal fin, as in male *Basiliscus basiliscus* and *Basiliscus plumifrons*.

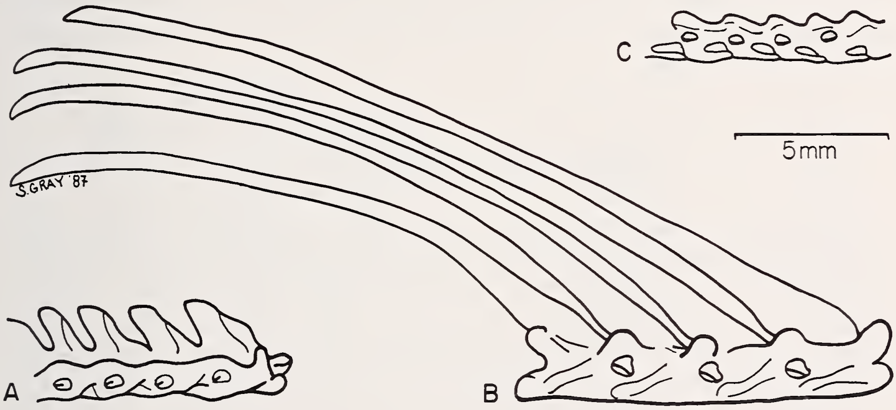

Fig. 35: Midbody vertebrae of basiliscines. A) *Corytophanes* B) *Basiliscus plumifrons* C) *Corytophanes*. (Drawing courtesy of S. Gray).

The extreme elongation of the neural spines in male *B. basiliscus* and *B. plumifrons* is an obvious apomorphic condition. There are two alternatives concerning the direction and interpretation of this character. First, this character can be interpreted as a single transformation with the short round neural spine as the primitive condition, the neural spine equal in size to the vertebral body as the intermediate condition, and the elongated neural spine the derived condition. Second, this character may be interpreted as a bi-directional transformation in which the neural spine equal in size to the vertebral body is the plesiomorphic condition and a short neural spine and an elongated neural spine being alternative apomorphic conditions.

Short neural spines are found in all sceloporines, crotaphytines, the leiosaurs *Pristidactylus, Leiosaurus*, and *Diplolaemus*, but not *Enyalius*, the para-anole *Urostrophus*, and in *Sauromalus*. All other "iguanids" of the outgroups have neural spines that are equal in size to the vertebral body.

The distribution of the character states among the outgroups reveals that the second hypothesis is the most parsimonious solution. Considering a (5:2) consensus, the polarity decision is unequivocal, with neural spines equal to the vertebral body being the plesiomorphic condition at the ingroup/outgroup node.

Corytophanes shows the plesiomorphic condition with neural spine length equal to that of the vertebral body. In *Laemanctus* the neural spines are short and rounded (apomorphic condition). In *Basiliscus*, all females exhibit the primitive condition with neural spines being the same size as the vertebral bodies. This is also the case for male *B. vittatus* and *B. galeritus*. In some large males of *B. vittatus* a zone of 4—5 large neural spines occur on the sixth to the tenth body vertebra.

As previously mentioned, the neural spines are extremely elongated in male *B. basiliscus* and *B. plumifrons*. The neural spines form an arc, with the highest neural spines in the midbody region. The neural spine on the last presacral, as well as those on the sacral vertebrae, are the same size as those of the vertebral body. The caudal vertebrae also have an arc of elongated neural spines with the high point approximately on the fifth or sixth caudal vertebra.

Ribs and Rib Articulation Patterns

All "iguanid" ribs consist of two parts: a bony dorsal component that attaches to the vertebral column, and a cartilaginous ventral portion (Etheridge 1965a). The length of the dorsal and ventral components vary considerably throughout the vertebral column.

Cervical ribs are identified as those anterior to the first vertebra bearing a costal connection to the sternum. Sternal ribs are defined as those ribs that have a direct individual connection to the sternum. Xiphisternal ribs are those that connect to the sternum via a xiphoid process. The xiphoid process (xiphisternum) are the paired cartilaginous rods that attach to the posterior portion of the sternum and serve as an attachment site for more than one rib. The xiphoid process has two, three and occasionally four rib attachments. In addition there are various other articulation patterns of postxiphisternal ribs in "iguanids", but these are not relevant to the ingroup.

In basiliscines, the bony dorsal ribs immediately behind those with cartilaginous extensions tied to the xiphisternum (postxiphisternal ribs), are characteristically as long as those immediately preceding them, but posteriorly the dorsal ribs gradually become much shorter. The ventral cartilaginous portion of the postxiphisternal ribs becomes reduced and terminates freely within the abdominal tissue, with the posterior ribs bearing only small cartilaginous knobs. The last few presacral vertebrae either have freely articulating ribs (*Basiliscus*) or they may lack ribs (*Corytophanes* and *Laemanctus*) (Character 41).

Hoffstetter & Gasc (1969) devised a simple convention for representing rib articulating patterns and presacral vertebrae in a serial fashion. The most common presacral formula in "iguanids" is 4+4+6(4+2)+10=24. The first number represents the number of cervical vertebrae without ribs, the second integer the number of cervical vertebrae bearing ribs. It can be deduced from the general formula of rib articulation that the fifth cervical vertebra is the first to bear any ribs at all. The third number (6) shows the number of thoracic vertebrae, followed in parentheses by the number of vertebrae that have costal connections to the sternum (4) and those vertebrae that have rib articulations with the xiphisternum (2). In other words, six ribs articulate with the sternum, four of which have a direct connection to the sternum (sternal ribs) and two connect to the sternum via the xiphisternum (xiphisternal ribs). The sixth number (10) represents the number of lumbar vertebrae. There is no distinction made in this formula between rib-bearing lumbar vertebrae and non rib-bearing vertebrae. The last number (24) indicates the total number of presacral vertebrae (See character no. 41).

Character 45: rib articulating patterns (Fig. 36A & 36B). As mentioned by Hoffstetter & Gasc (1969), the 6(4+2) condition is the most widespread condition in "iguanids". In this condition, the ribs on vertebrae 9—12 attach to the sternum, whereas the ribs of vertebrae 13 + 14 attach to the xiphisternum. Three alternative conditions occur

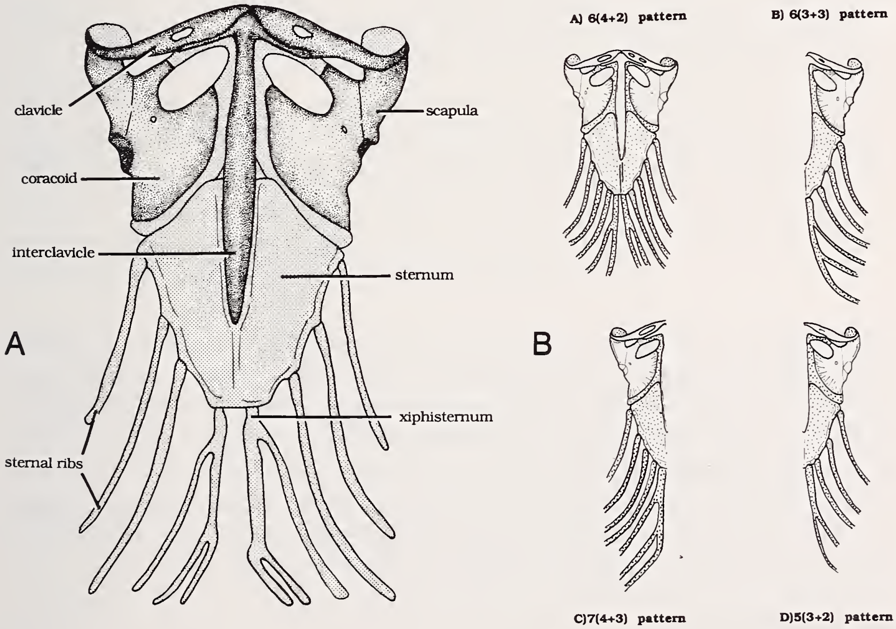

Fig. 36: A Ventral view of the pectoral girdle of *Laemanctus serratus* showing various skeletal elements. B: Ventral view of pectoral girdles of basiliscines showing variation in rib articulation patterns: A) 6(4+2) B) 6(3+3) C)7(4+3) D) 5(3+2).

within "iguanids": in the 7(4+3) condition, the rib of vertebrae 15 attaches to the xiphisternum resulting in a total of 3 xiphisternal ribs; the 6(3+3) condition results from the shift of the rib of vertebra 12 from the sternum onto the xiphisternum; the 5(3+2) condition results from the shift of the rib of vertebra 12 onto the xiphisternum and the loss of the xiphisternal connection of the rib of vertebra 14. This arithmetic notation assumes that the rib attachments are decoupled from the vertebrae, it is, however, a hypothesis in need of further testing.

Among the outgroup taxa examined, the 6(4+2) condition was observed in all iguanines, in crotaphytines, *Petrosaurus, Phymaturus*, some *Liolaemus* (R. Etheridge, pers. comm.), and some *Pristidactylus*. A 5(3+2) condition is present in *Uranoscodon*, eastern *Tropidurus*, *Leiocephalus*, some *Anolis* and the *Sceloporus*-group, exclusive of some *Urosaurus* and *Sceloporus*. The 7(4+3) condition is present in oplurines. The 6(3+3) was only identified within *Plica, Sceloporus* and some *Urosaurus*. All specimens of morunasaurs were damaged such that information about the xiphisternal pattern was lost.

Additional articulation patterns exist among the outgroup taxa such as a 5(2+3) pattern in *Anolis equestris*, 4(2+2) in *A. frenatus* and *Phrynosoma*.

Etheridge (1962, 1964) indicated that a high degree of intra- and interspecific variation in the pattern of xiphisternal rib attachments exists within sceloporines.

The distribution of character states at the outgroup basal nodes for this tri-state character is a (2:2:1) pattern. No polarity can therefore be determined for this character. The character will remain unordered in the initial data matrix.

Within the ingroup, *Basiliscus*, *Corytophanes cristatus* and *C. hernandezi* show the 6(4+2) pattern. *Corytophanes percarinatus* shows the 5(3+2) pattern. *Laemanctus longipes* as well as *L. serratus* have 6(3+3) and 7(4+3) conditions respectively (Fig 36B).

Pectoral Girdle

The "iguanid" pectoral girdle consists of the following elements: suprascapulae, scapulae, coracoids, (including procoracoids), epicoracoids and clavicles. The interclavicle and the sternum are part of the axial skeleton, but are described in this section because they form a functional anatomic unit in conjunction with the pectoral girdle. The clavicles and interclavicle are the only dermal elements in this section.

The only connection between the pectoral girdle and the vertebral column is through the sternum and the cartilaginous portion of the thoracic ribs. The pectoral girdle as such is maintained in position by the muscles that attach to it.

Suprascapulae (Fig. 37)

The suprascapulae are thin calcified cartilaginous elements that are fused to the scapulae and are usually expanded dorsally. The anterior border usually contains the acromial process to which the clavicle attaches.

Character 46: suprascapular cartilages. In all taxa of the outgroups examined, the suprascapular cartilages project dorsally and reach the level of the vertebral column. Because this latter condition was found at the basal node of the seven outgroups, the suprascapular cartilages reaching the level of the vertebrae is considered to be the plesiomorphic condition at the basal node of the ingroup (7:0 consensus).

All basiliscines except *Corytophanes cristatus* also show the widespread "iguanid" condition. In *C. cristatus*, however, the posterior portions of the suprascapular cartilages do not reach the level of the vertebral column. This, however, may be the result of a laterally-compressed body form, although the alternative condition was found in the laterally compressed *C. hernandezi* and *C. percarinatus*.

Scapulae (Figs. 36A, 37)

The scapulae are paired bones that fuse dorsally with the suprascapulae and ventrally with the coracoids. In juveniles and subadults the scapulocoracoid suture is very prominent, but when maximum size is reached the scapulae and the coracoids fuse together as a single functional unit and the suture is no longer visible.

Coracoids (Figs. 36A, 37)

The coracoids are attached to the ventral aspect of the scapulae at the scapulocoracoid suture. In addition to the scapulocoracoid fenestra, the anterior coracoid fenestra is located at the anterior border of the coracoid. Both fenestrae are bordered anteriorly by the epicoracoid. The procoracoid is located between the scapulocoracoid and the anterior coracoid fenestra.

Epicoracoid (Fig. 36A, 37)

The epicoracoid is a thin calcified cartilagenous element that attaches to the medial posteroventral and anterior portions of the coracoid and to the anterior portion of the scapula. Furthermore, it borders the fenestrae of the scapulocoracoid complex. Medially, the epicoracoids overlap each other dorsal to the sternum.

Clavicles

The clavicles are paired symmetrical bones that form the anterior margin of the pectoral girdle. The clavicles are dermal bones that usually curve dorsally. Ventrally the clavicles are supported by the anterior extremity of the interclavicle.

The shape of the clavicles varies considerably among "iguanids". Some "iguanid" clavicles are simple, whereas others have ventrally directed hooks (Etheridge 1964) and clavicular fenestrations (looped clavicle of Boulenger 1885).

Character 47: dorsal extent of clavicle (Fig. 37). The dorsal aspect of the clavicle of "iguanids" attaches at three locations. Commonly there is an articulation on the suprascapular cartilages dorsal to the junction of the suprascapula and the scapula, but occasionally the dorsal aspect of the clavicle articulates only with the suprascapula. In the least common condition, the dorsal aspect of the clavicle articulates with the scapula, and never reaches the level of the scapulo-suprascapular junction.

Because the distinction between the articulation being slightly above the scapulo-suprascapular junction and on the suprascapula itself varies interspecifically, these two character states are considered as one. In the alternative character state the clavicle does not contact the suprascapula.

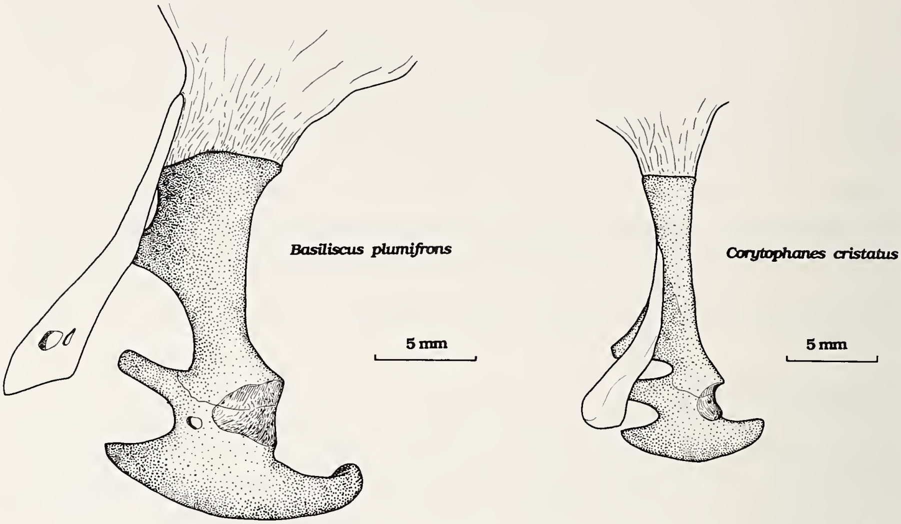

Fig. 37: Lateral view of pectoral girdles showing attachment sites of the dorsal aspect of the clavicle.

In tropidurines, iguanines, crotaphytines, sceloporines, oplurines, morunasaurs, *Pristidactylus, Leiosaurus, Diplolaemus, Urostrophus* and some *Anolis*, the clavicle reaches the suprascapula. In *Polychrus, Chamaeleolis* and some *Anolis* the clavicle clearly articulates on the scapula, and does not reach the suprascapula.

The distribution of character states at the basal outgroup nodes indicates that contact of the clavicle with the suprascapula is the plesiomorphic condition (6:1 consensus).

Within the basiliscines, the clavicle of *Basiliscus* and *Laemanctus* contacts the suprascapula (plesiomorphic condition). In *Corytophanes hernandezi* the clavicle also reaches the suprascapula, but in *C. cristatus* and *C. percarinatus* it does not.

Lécuru (1968a) indicated that the "iguanid" scapula is broad and short, but that on occasion it can become elongated and narrow. The result is a shift of the acromial process from the anterior border of the suprascapula (hypothesized primitive condition) to the anterior aspect of the scapula (derived condition). The position of the acromial process is displaced along the anterior border of the pectoral girdle and is a direct result of the change in shape of the scapula that varies with body form. As mentioned above, laterally-compressed arboreal "iguanids" show an elongated scapula, like that of chameleons.

The condition in some highly arboreal, laterally-compressed "iguanids", such as some *Anolis, Chamaeleolis, C. hernandezi*, and others, indicates that not all highly arboreal forms show a shift of the acromion process onto the scapula. This fact is regarded as evidence suggesting that the shift of the acromion onto the scapula may be a result of a laterally compressed body form.

Character 48: clavicular lateral margin. In the primitive "iguanid" condition, the shape of the lateral margin of the clavicle is irregular, or forms a smooth curve (Boulenger 1885). Although Etheridge and de Queiroz (1988) suggest a bi-directional transformation series from the plesiomorphic condition among "iguanids", only one transformation is considered in this study because only two alternative states of a single transformation occur among basiliscines. The two transformation series are the ventromedial expansion of the clavicle and the margin of the clavicle becoming angular.

Among the outgroup taxa examined, *Phymaturus*, some *Liolaemus*, some *Leiocephalus*, some *Uranoscodon*, all anoloids except *Polychrus*, some *Anolis, Chamaeleolis*, some *Enyalioides*, the *Sceloporus*-group lizards and *Gambelia* have clavicles with distinctly angular margins. All remaining outgroups examined do not have angular margins (this also includes taxa with ventromedially expanded clavicles).

The distribution of character states at the basal outgroup nodes is a (3:2) consensus. The polarity decision is therefore equivocal, and the character must be left unordered in the data matrix.

Within the basiliscines, *Corytophanes* shows a smooth irregular lateral margin of the clavicle. *Basiliscus* and *Laemanctus* on the other hand both have a distinctly angular lateral margin of the clavicle, with an acute projection at the apex of the angle.

Character 49: clavicular fenestration (Fig. 38). This character has been used by Etheridge & de Queiroz (1988) at the more inclusive level of the "iguanids". Among the taxa of the outgroups examined in this study, clavicular fenestrations were found only in the following taxa: some *Uranoscodon*, some *Plica*, western *Tropidurus* and some *Crotaphytus*. All other taxa of the outgroups examined lacked clavicular fenestration. The character states at the basal outgroup nodes suggests that the absence of a clavicular fenestration is the plesiomorphic condition at the ingroup/outgroup node, whereas a clavicular fenestration is unequivocally the apomorphic condition at the ingroup/outgroup node (7:0 consensus).

Among the basiliscines, clavicular fenestrations occur in *Basiliscus* and *Laemanctus*, but are absent in *Corytophanes*.

Clavicular fenestration is highly variable with respect to size and shape, and with respect to left and right clavicles. In fact, the exception is for both clavicles to exhibit the same pattern of fenestration. Because interspecific variation in addition to individual variation was widespread, no consistent pattern of fenestration was identified in *Basiliscus* (Fig. 38). In *Laemanctus*, however, both species are easily distinguished by the amount of fenestration. In *L. longipes* consistently there is a considerable amount of clavicular fenestration. In *L. serratus* there is very little fenestration, and on occasion none.

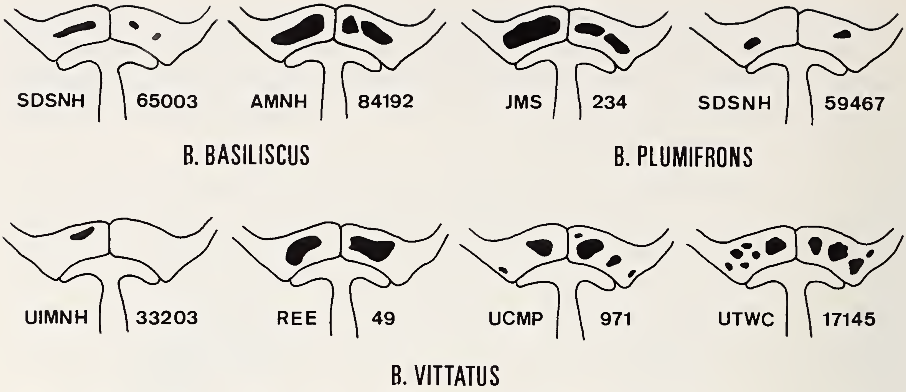

Fig. 38: Variation of clavicular fenestration observed in *Basiliscus.*

Fenestration seems to be size dependent. Larger specimens have less fenestration, and in the case of large specimens of *Basiliscus plumifrons* (largest species of *Basiliscus*) only a small slit is present. In addition, the clavicles of large male *B. plumifrons* are rotated into a vertical position with respect to increasing body size. A possible hypothesis for the reduction of fenestration of the clavicles with increased body size may be related to the increased attachment of muscles originating on the clavicle. The rotation of the clavicle may provide some additional mechanical advantage. This hypothesis, however, remains untested.

Although a high degree of variation exists within the terminal taxa of the ingroup, the use of this systematic character is warranted on the grounds that fenestration is consistently present or absent within terminal taxa.

Interclavicle

The interclavicle is a slender, rod-shaped median dermal bone on the ventral surface of the sternum. The interclavicle adheres medially to the external surface of the sternum (see below) and is always exposed. Anteriorly, the interclavicle has lateral processes that are either terminal or subterminal, and which vary considerably in shape and size in "iguanids". De Queiroz (1987) indicated that *Corytophanes hernandezi* and *Laemanctus serratus* have T-shaped interclavicles (defined as lateral processes forming an angle of more than 75° with the median element). However, the angle varies considerably within each taxon, from an arrow-shaped interclavicle (with an angle between the lateral processes and the median rod of less than 75°) to a T-shaped interclavicle.

The length of the interclavicle is also variable in "iguanids", with most interclavicles extending posteriorly 2/3 the length of the sternum.

Therefore, no systematic character was defined with respect to the angle of the lateral process, or the length of the interclavicle.

Sternum and Xiphisternum

Lécuru (1968b) indicated that the sternum can be subdivided into a presternum, mesosternum and a xiphisternum. The presternum is the highly developed anterior portion of the sternum. The mesosternum is the posteriormost portion of the sternum containing the xiphisterna. The distinction between mesosternum and xiphisternum is not clear and the two latter terms will be synonymized as xiphisternum. The presternum of Lécuru was referred to as the sternum above.

The sternum of "iguanids" is a centrally located skeletal element made of calcified cartilage. It is diamond-shaped of varying axial lengths, and articulates anterolaterally with the two epicoracoids and medially with the interclavicle.

The xiphisternum consists of two paired cartilaginous rods of approximately equal length that are attached to the posteromedial aspect of the sternum. These rods are partially supported by the xiphisternal ribs.

Pelvic Girdle

The "iguanid" pelvic girdle is characteristic of tetrapods in having a dorsal ilium that articulates with the sacral pleurapophyses, a posteroventral ischium, and an anteroventral pubis (Fig. 39).

Snyder (1954) indicated that the major differences between the pelvis of a quadruped (*Corytophanes*) and a biped (*Basiliscus* and *Laemanctus*) is the interacetabular width (= distance between the outer faces of the acetabulum), a longer ilium and a more extensive development of the preacetabular process. The greater extent of the preacetabular process in bipeds provides a more extensive attachment for the iliopubic ligament and the M. quadratus lumborum.

Character 50: preacetabular process (Fig. 39). This character has been used previously by de Queiroz (1987), who recognized two distinct conditions within iguanines: a large preacetabular (iliac) process and a small (reduced) preacetabular process. Among his outgroups examined, crotaphytines and oplurines, have a prominent preacetabular process, and morunasaurs have a reduced preacetabular process. Within his ingroup (iguanines) only *Sauromalus* has a reduced preacetabular process. He noted that within basiliscines both conditions were observed without noting which genera had which condition (de Queiroz 1987; pers. obs.)

All tropidurines exclusive of the *Liolaemus*-group and *Stenocercus* have a prominent preacetabular process. The sand lizards (*Uma, Uta, Callisaurus, Cophosaurus* and *Holbrookia*) and *Phrynosoma* have prominent preacetabular processes. The *Sceloporus*-group and *Petrosaurus* by contrast, have reduced preacetabular processes. Within anoloids only *Polychrus* has a reduced preacetabular process, whereas all the spinulate anoloids have a prominent preacetabular process.

Snyder's (1954) statement that bipedal lizards have an extensive development of the preacetabular process is certainly true. The well-known bipedal "iguanids" such as *Calli-*

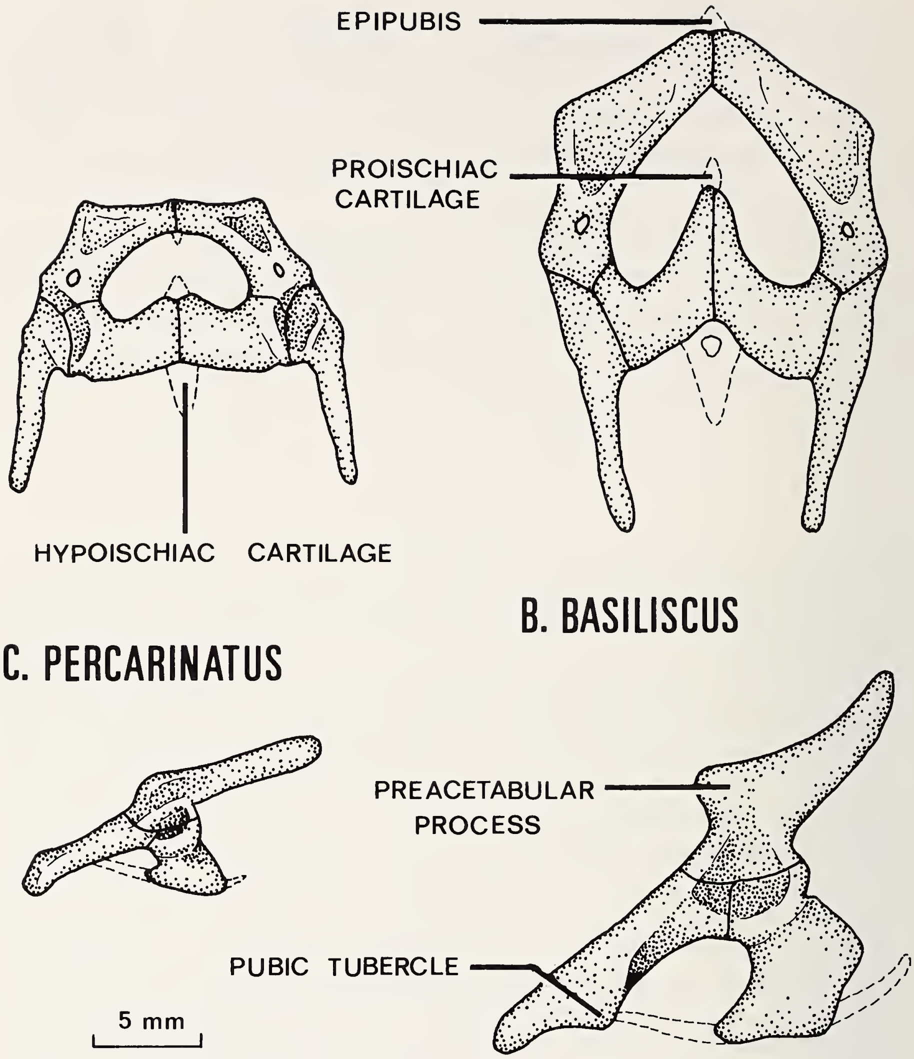

Fig. 39: Ventral and lateral views of pelvic girdle of *Basiliscus basiliscus* and *Corytophanes percarinatus*.

saurus, juvenile *Dipsosaurus*, *Crotaphytus* and *Basiliscus* have well developed preacetabular processes. In addition, most terrestrial, saxicolous and arenicolous "iguanids" have prominent preacetabular processes. In some cases the preacetabular process is as large as that of bipedal taxa. Notable exceptions are the terrestrial or saxicolous *Liolae-*

mus, Phymaturus, Stenocercus, Sauromalus, Morunasaurus and *Hoplocercus* which have reduced preacetabular processes or lack them altogether. The most arboreal ecomorphs (e.g. spinulate anoloids) also have prominent preacetabular processes. The arboreal *Enyalioides* also has a prominent preacetabular process. *Polychrus*, however, has a small preacetabular process. These exceptions, and the distribution pattern of character states among similar ecomorphs, falsify the notion that taxa sharing similar character states have ecomorphological similarities.

The distribution of the character states at the basal outgroup nodes is a (3:2) consensus resulting in an equivocal polarity decision at the ingroup/outgroup node. The consensus algorithm therefore does not corroborate de Queiroz's (1987) decision at his "lower level of analysis", that a large preacetabular process is the plesiomorphic state.

Basiliscus has a prominent preacetabular process, *Corytophanes* and *Laemanctus* have a reduced preacetabular process (Fig. 39).

Character 51: anterior extension of the symphysis pubis (Fig. 39). There are two conditions in "iguanids" with respect to the angle of the pubic symphysis. In the first condition there is almost no angle between the pubic rami, and the symphysis pubis does not extend anteriorly past the pubic tubercles. Alternatively, the rami of the pubic bones are at a discernible angle with one another and the symphysis extends anteriorly past the pubic tubercles.

In iguanines, morunasaurs, crotaphytines, *Oplurus, Phrynosoma*, all tropidurines except *Liolaemus, Leiocephalus* and *Uranoscodon*, and in all anoloids exclusive of *Polychrus* and *Anolis* the symphysis pubis does not extend anteriorly past the anterior pubic tubercles.

In sceloporines (exclusive of *Phrynosoma), Chalarodon, Liolaemus, Leiocephalus, Uranoscodon, Polychrus* and *Anolis* the two pubic rami are at angles with each other and the symphysis pubis extends anteriorly far beyond the pubic tubercles.

The distribution of character states at the basal outgroup nodes is a (4:1) consensus, hypothesizing that the symphysis pubis not extending anteriorly past the pubic tubercles is the plesiomorphic condition at the ingroup/outgroup basal node.

In basiliscines, *Corytophanes* and *Laemanctus* show the widespread "iguanid" condition with the symphysis pubis not extending past the pubic tubercles (plesiomorphic condition). In *Basiliscus* the rami are at angles with one another and the symphysis pubis extends anteriorly past the pubic tubercles (apomorphic condition). The derived condition has, therefore, independently evolved in *Liolaemus, Leiocephalus, Uranoscodon, Polychrus, Anolis*, sceloporines (with a reversal in *Phrynosoma), Chalarodon* and in *Basiliscus*.

Appendicular Skeleton

The appendicular skeleton can be subdivided into two main structural components: the skeleton of the forelimb and the skeleton of the hindlimb.

Forelimb

The forelimbs of basiliscines contain the following elements listed proximal to distal: humerus, radius + ulna, radiale, ulnare, pisiform, lateral centrale, five metacarpals and 17 phalanges. The forelimbs of "iguanids" tend to be very conservative, with little variation among the taxa and no limb reduction.

Hindlimb

The following skeletal components constitute the skeleton of the hindlimb: femur, tibia + fibula, astragalocalcaneum, two other tarsal bones, five metacarpals and 18 phalanges. As is the case with the forelimb, the hindlimb shows insufficient variation to warrant any systematic character definition.

DESCRIPTION OF INTERNAL ANATOMY

Myology

The M. adductor mandibulae externus is a large muscle mass that occupies the entire superficial portion of the infraorbital fossa in "iguanids". The muscles originate from the temporal bar and the posterior region of the temporal fossae. The M. adductor mandibulae externus inserts along the exterior Bodenaponeurosis, the coronoid and the surangular. The M. adductor mandibulae externus is divided into the levator anguli oris and the superficialis, medius, and profundus. Each of these muscles can be further subdivided. Superficially, the muscle mass is covered by the infratemporal fascia.

The following characters in this subsection have been taken from Costelli (1973). All terminal taxa used in this study were examined by Costelli (1973) except the following: *Petrosaurus, Urostrophus, Pristidactylus, Enyalius*, and *Diplolaemus*.

The missing information for the three leiosaur genera will be replaced by the condition observed in *Leiosaurus*. The condition in para-anoles and *Petrosaurus* (earliest diverging sceloporine) will be coded equivocal to minimize the effect on the polarity decisions at the basal outgroup nodes.

Character 52: infratemporal fascia. A sheet of fascia partially covers the infratemporal fossa in all "iguanids" (Oelrich 1956; Costelli 1973).

The expansion of the infratemporal fascia at the postero-dorsal corner of the infratemporal fossa is variable in "iguanids". Costelli (1973) identified six conditions, ranging from the presence of a small amount of fascia to fascia covering the entire muscle.

Because only two conditions were identified within the ingroup, only two character states are recognized: very little fascia present, and fascia covering variably from the postero-dorsal corner of the infratemporal fossa, to the entire muscle.

All "iguanids" examined by Costelli (1973) except *Phrynosoma* and the spinulate anoloids had extensive fascia present at the infratemporal fossa. This was also observed in

Basiliscus and *Corytophanes*. In the spinulate anoloids, in *Phrynosoma*, and *Laemanctus* there is little fascia present.

The distribution of the character states among the outgroup basal nodes suggests that the presence of fascia beyond the posterodorsal corner of the infratemporal fossa is the plesiomorphic condition at the ingroup/outgroup basal node (6:0 consensus).

Character 53: insertion of M. adductor mandibulae externus. The insertion of the M. adductor mandibulae externus onto the lower jaw varies among "iguanids"; it may insert from the top of the surangular to the ventral border of the mandible (Costelli 1973).

Costelli (1973) identified 5 character states for the ventral extent of this muscle, but with respect to the ingroup these five can be reduced to two: a) the externus extends only to the top of the surangular and b) the externus extends ventrally beyond the top of the surangular.

All taxa among the outgroups examined except the spinulate anoloids, together with *Basiliscus* and *Laemanctus*, show the latter condition. In *Corytophanes* and the spinulate anoloids the ventral extension of the M. adductor mandibulae externus only reaches the top of the surangular.

The distribution of the character states among the outgroup basal nodes is a (6:0) distribution pattern unequivocally indicating that the mandibular insertion of the M. adductor mandibulae externus projecting past the surangular is the plesiomorphic condition at the ingroup/outgroup node. The alternate state (mandibular insertion restricted to the surangular) is the apomorphic condition at the ingroup/outgroup basal node.

Character 54: M. levator anguli oris. The M. levator anguli oris is present in all "iguanids". Among the outgroup taxa, this muscle originates along the inferior border of the postorbital, the ventral aspect of the squamosal and the dorsal aspect of the tympanic crest of the quadrate. In those taxa that have a dorsally arched squamosal (see character 24), the origin of the M. levator anguli oris is restricted to the anterior part of the squamosal (not including the tympanic crest) and inserts on the dorsal aspect of the rictal plates (Costelli 1973).

A broad origin of the M. levator anguli oris occurs in *Basiliscus* and *Laemanctus*. In *Corytophanes*, however, the M. levator anguli oris originates at the junction of the jugal, postorbital and squamosal and does not include the tympanic crest. It then passes ventrad onto the superficial fascia, which covers the dorsal aspect of the infratemporal fossa anterior to the quadrate (Costelli 1973).

The distribution of the character states among the outgroup terminal taxa and outgroup basal nodes suggests that the broad origin of M. levator anguli oris including the tympanic crest of the quadrate is the plesiomorphic condition at the ingroup/outgroup basal node (7:0 consensus). The restricted origin of the M. levator anguli oris which does not include the tympanic crest of the quadrate, is the apomorphic condition found in *Corytophanes*.

Character 55: M. adductor mandibulae externus superficialis. The M. adductor mandibulae externus superficialis can be divided into two heads. When divided, the anterior head originates from the medial surface of the postorbital and inserts along the outer surface of the outer flap of the Bodenaponeurosis. The posterior head originates on the inferior surface of the squamosal, the dorsolateral surface of the quadrate, and the tympanic crest. These fibers insert on the Bodenaponeurosis and the lateral surface of the surangular (Costelli 1973).

The head of the M. adductor mandibulae externus superficialis is not separated in *Laemanctus*, oplurines, *Dipsosaurus, Enyaliosaurus*, the *Sceloporus*-group, the *Liolaemus*-group, all northern tropidurines except *Uranoscodon*, and in *Leiosaurus*. All other taxa among the outgroup have two heads of the M. adductor mandibulae externus superficialis.

Distribution of the character states among the outgroup basal nodes is a (3:2) pattern, for which no unequivocal polarity decision can be reached. This character will therefore be left unordered within the data matrix.

The distribution of the character states among representatives of other Scleroglossa using the phylogeny proposed by Estes et al. (1988) supports the notion that an M. adductor mandibulae externus superficialis with separate heads is indeed the plesiomorphic condition for "iguanids". Representative taxa of "Agamidae", Gekkota, Scincoidea and Anguiomorpha have two heads, whereas only chameleons and representative lacertoids have a single head.

Within basiliscines, *Basiliscus* and *Corytophanes* show the predicted plesiomorphic condition of a two-headed M. adductor mandibulae externus superficialis. *Laemanctus* on the other hand has only a single head.

Character 56: M. adductor mandibulae externus profundus. The M. adductor mandibulae externus profundus is the deepest segment of the M. adductor mandibulae externus muscle complex. The profundus can be divided into a ventral and dorsal head. The separation is roughly marked by the third branch of the mandibular ramus of the trigeminal nerve (Costelli 1973).

The ventral head of the profundus originates on the posterior process of the prootic and from the dorsal aspect of the pila antotica and inserts on the Bodenaponeurosis (Costelli 1973).

The dorsal head of the profundus originates from the ventral aspect of the parietal. Its fibers run medially through the posttemporal fossa and then pass anteroventrad to insert on the Bodenaponeurosis, dorsal to the ventral head of the profundus (Costelli 1973).

The dorsal head is well-developed among the outgroup taxa (with the exception of *Phrynosoma*) and in *Basiliscus*. In *Laemanctus* and *Phrynosoma* the dorsal head of the profundus is greatly reduced. In *Corytophanes*, which lacks a posttemporal fossa, the dorsal head of the profundus is entirely absent.

Costelli (1973) suggests that a reduction of the fossa would ultimately lead to the reduction or loss of the dorsal head of the profundus. However, this study suggests that the reverse scenario is more likely. Both *Laemanctus* and *Phrynosoma* have open posttemporal fossae but have an extremely reduced dorsal head of the profundus. The dorsal head is possibly entirely absent in *Phrynosoma*. This suggests that the reduction or loss of the dorsal head of the profundus may be reduced or lost independently of the condition of the posttemporal fossa. Instead, the hypothetical *Corytophanes-Laemanctus* ancestor may have reduced the dorsal head of the profundus with a subsequent loss of the dorsal head and the closure of the posttemporal fossa in *Corytophanes*, the condition being convergent in *Phrynosoma*, but without the closure of the posttemporal fossa.

This character can be defined as a three-state character, wherein distribution among outgroups suggests that a well-developed dorsal head of the profundus is the unequivocal plesiomorphic condition at the ingroup/outgroup node (7:0 consensus). A reduction of the dorsal head is the intermediate condition and the loss of the dorsal head the apomorphic condition.

Hemipenes

Cope (1886) was the first to investigate the hemipenial structure of "iguanids". In his pioneering study, he investigated 16 genera of "iguanids" including *Basiliscus* and *Corytophanes*. Unfortunately he did not indicate which species were examined. In Cope's systematic arrangement, *Corytophanes* is grouped with iguanines (exclusive of *Dipsosaurus*) and crotaphytines based on the presence of three welts (Stützsäume sensu Böhme 1988). *Basiliscus* on the other hand has no welts and is grouped together in Cope's scheme with the tropidurines *Uranoscodon, Uracentron* and *Tropidurus*.

Böhme (1988) in an excellent monographic study on saurian hemipenes within a morphologic and phylogenetic framework has taken a closer look at "iguanids". Although Böhme (1988) did not include all the genera required to make a polarity assessment in this study, his results are important. The reader is referred to Böhme (1988) for detailed morphological descriptions. He concludes that *Laemanctus* and *Basiliscus* are each others closest relatives based on the presence of an asulcate "medianer Zapfen" (= bulging on the median aspect of the asulcate side). This bulge is rather smooth (except in *B. plumifrons*). *Corytophanes* lacks the "medianer Zapfen".

Superimposing Böhme's findings on the cladogram based on other characters suggests that an asulcate "medianer Zapfen" can be considered as an autapomorphy for basiliscines with subsequent loss in *Corytophanes*.

DESCRIPTION OF EXTERNAL MORPHOLOGY

Squamation

Character 57: superciliary scales (Fig. 40). Etheridge & de Queiroz (1988) recognized three conditions of this character in "iguanids". The superciliary scales in "iguanids" characteristically form a row of elongated and broadly overlapping scales. Other "iguanids", however, have quadrangular, nonoverlapping superciliary scales. A third condition is intermediate between these two. Although evidence for polarizing this character is ambiguous, Etheridge & de Queiroz (1988), assigned the elongate and strongly overlapping superciliary scales as the plesiomorphic condition in "iguanids". Their decision was based on a comparable condition found in agamids. However, because the head scales of *Sphenodon*, chameleons and gekkonids exhibit little or no differentiation and are not strictly comparable, they were excluded when the polarity decision was made.

Basiliscus has elongate strongly overlapping superciliary scales, which are also found in *Dipsosaurus*, all sceloporines (exclusive of *Phrynosoma*), in some *Anolis*, oplurines and in all tropidurines examined except *Phymaturus* and *Uranoscodon*. The intermediate condition is found in *Corytophanes* in addition to crotaphytines, *Brachylophus,*

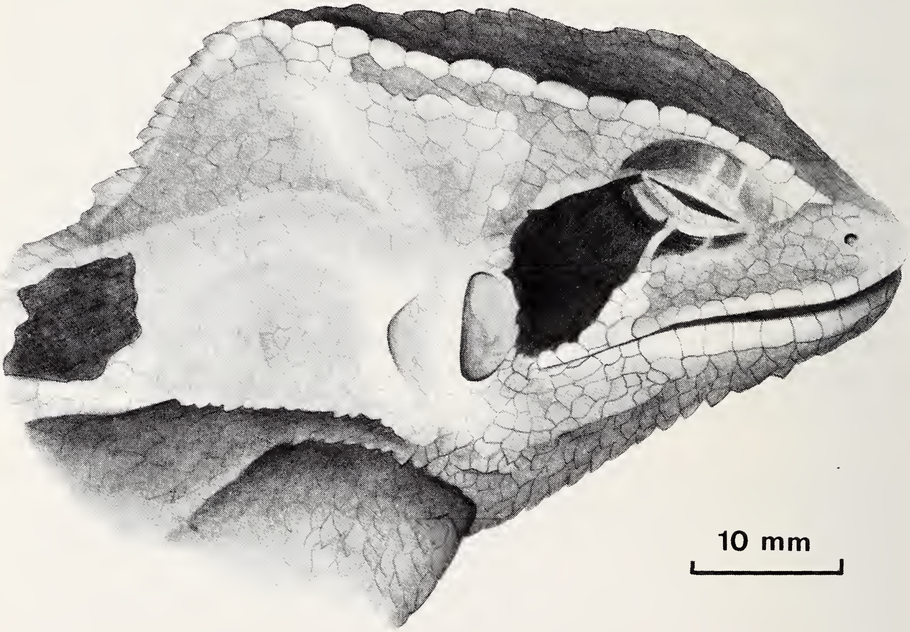

Fig. 40: Lateral view of head of *Corytophanes cristatus* showing pattern of supraciliary scales. (Drawing courtesy of S. Gray).

Conolophus, Ctenosaura, Cyclura, Iguana, Phrynosoma, leiosaurs, in some *Anolis, Phymaturus* and in *Uranoscodon*. Quadrangular, nonoverlapping superciliary scales are present in *Laemanctus* as well as *Amblyrhynchus, Sauromalus, Polychrus, Urostrophus* and morunasaurs (Etheridge & de Queiroz, 1988; pers. obs.).

Character state distribution at the basal nodes of the outgroups is a (3:2:1) pattern, for which no unequivocal polarity decision at the ingroup/outgroup node can be made. The option remains to accept Etheridge & de Queiroz's (1988) polarity decision. However, this character will be left unpolarized within the data matrix.

LIST OF SYSTEMATIC CHARACTERS

Included in this section is a list of systematic characters described in the previous section. For each character the polarities are given. For characters with unequivocal polarity decisions the polarization results are indicated.

1) Roof of nasal capsule: 0 → 1

(0) Nasal capsule entirely covered by frontal and nasals. (1) Nasal capsule uncovered at junction of frontal and nasals.

2) Septomaxillae: 0 → 1 → 2

(0) Present, contacting each other at midline, the maxillae anteriorly and lying on top of the vomers. (1) Present as small slivers of bone lying within the nasal cavity that do not contact each other at the midline. (2) Absent.

3) Nasal median contact: 0 → 1 → 2

(0) Separated by less than 50 % of their length. (1) Separated for more than 50 % of their length by nasal process of premaxilla. (2) Completely separated.

4) Posterior margin of nasals: 0 → 1A, 0 → 1B

(0) Posterior aspect of nasals form a smooth curve, with apex in the middle of the bone (0,0). (1A) Posterior aspect of nasals pointed (1,0). (1B) Posterior aspect of nasals are square (0,1).

5) Prefrontal-nasal relationship: 0 → 1 → 2

(0) Broad contact between prefrontals and nasals. (1) Small area of contact between prefrontals and nasals, with nasals separated anteriorly from prefrontals by prefrontal process of maxilla. (2) Prefrontals completely separated from nasals by prefrontal process of maxilla and antero-lateral process of frontal bone.

6) Anterolateral spine of prefrontal: 0 → 1

(0) Absent. (1) Present, projecting anteriorly over the premaxillary process of maxilla.

7) Groove at prefrontal-lacrimal junction: 0 → 1

(0) Absent. (1) Present.

8) Palatine-ectopterygoid relationship: 0 → 1

(0) No contact between ectopterygoids and palatines. (1) Ectopterygoids contact palatines; excluding maxillae from infraorbital foramen.

9) Palatine process of pterygoid: 0 → 1

(0) Does not project past the anteromost border of infraorbital foramen. (1) Extends anteriorly beyond the infraorbital foramen.

10) Quadrate process of pterygoid: 0 → 1

(0) Tapering posteriorly, or with parallel ventral and dorsal edges, but not expanded. (1) Quadrate process of pterygoid expanded terminally.

11) Shape of mid-sagittal section of frontal: 0 → 1

(0) Anterior and posterior aspects of frontal bone curve ventrally. (1) Frontal bone is flat in mid-sagittal sectional view, or anterior and posterior aspects of frontal bones curve dorsally.

12) Postfrontals: 0 → 1

(0) Present. (1) Absent.

13) Squamosal process of jugal: 0 → 1

(0) Thin squamosal process. (1) Broad squamosal process.

14) Jugal-squamosal contact: 0 → 1

(0) Separated or only narrowly in contact, but not overlapping. (1) Broad contact or overlapping.

15) Posterior angle of jugal: 0 → 1

(0) Not expanded postero-ventrally, rounded. (1) Expanded postero-ventrally, with postero-ventral aspect of jugal approaching the posterodorsal aspect.

16) Supraorbital process: 0 → 1 → 2

(0) Absent; postorbital and prefrontals lack processes. (1) Intermediate condition; prefrontals have posteriorly directed processes and postorbitals have anteriorly directed processes. (2) Postorbitals in contact with prefrontals via a supraorbital arch.

17) Parietal foramen position: 0 → 1

(0) At the frontoparietal suture. (1) Entirely within the frontal.

18) Lateral shelves of adductor crest: 0 → 1 → 2

(0) Absent or when present it is small and restricted to the anterolateral aspect of the adductor ridge. (1) Present along the lateral aspect of the parietal crest. (2) Large, expanded laterally to partially overlie the supratemporal opening.

19) Parietal roof shape: 0 → 1A; 0 → 1 B → 2B

(0) Parietal is trapezoidal with no median crest or parietal blade (0,0). (1A) Parietal is Y-shaped with a parietal blade. The lateral borders at the base of the parietal blade progress anteriorly with increased ontogeny to form a 180°angle in adults (1,0). (1B) Parietal is Y-shaped with the anterolateral borders at the base of the parietal crest progressing posteriorly with increased ontogeny to form a 60°angle in adults (0,1). (2B) Parietal is Y-shaped with the anterolateral borders at the base of the parietal blade progressing posteriorly with increased ontogeny to form a 30°angle in adults (0,2).

20) Development of the parietal blade: 0 → 1

(0) Post-embryonic development of median parietal blade. (1) Embryonic development of parietal blade.

21) Parietal blade sexual dimorphism: 0 → 1

(0) Parietal blade well-developed in males only. (1) Parietal blade well-developed in both sexes.

22) Expansion of parietal blade: 0 → 1A; 0 → 1B

(0) Absence of a parietal blade (0,0). (1A) Dorsal expansion (1,0). (1B) Ventral expansion (0,1).

23) Dorsal process of squamosal: (polarization: A=1 B=0)

(A) Prominent dorsal "hook" contacting the supratemporal. (B) No dorsal hook, i.e. ventral projection equals dorsal projection.

24) Squamosal: 0 → 1

(0) Curves dorsally, not contacting or overlapping the anterodorsal aspect of the quadrate (single articulation). (1) Straight, overlapping the anterodorsal border of lateral concha of quadrate, with sharp laterally pointed spine (double articulation).

25) Medial concha of quadrate: 0 → 1

(0) Expanded medially past the cephalic condyle. The medial concha may or may not contact the antero-lateral process of the paraoccipital process. (1) Not expanded, past the condyles (constricted).

26) Quadrate: 0 → 1

(0) Posterior crest arches anteriorly. (1) Posterior crest is vertical with no anterior curvature.

27) Epipterygoids: 0 → 1

(0) Contacting the ventral portion of parietal. (1) Free or contacting the alar process of prootic.

28) Crista ventrolateralis: 0 → 1

(0) Broad, expanded laterally obscuring the vidian canal. (1) Narrow, not expanded laterally.

29) Outlines of bony labyrinth: (polarization: A=NA B=1 C=0)

(A) (not present in ingroup) Superficial outlines of bony labyrinth obscure, not raised above the surface of the occipital bones. (B) Intermediate condition. (C) Superficial outlines very distinct, raised well above the surface of the occipital bones.

30) Posttemporal fenestra: 0 → 1 → 2

(0) Open, with the squamosal process at an angle of more than 90°. (1) Partially closed. (2) Closed, owing to the limiting angle of the squamosal process of parietal (less than 90°).

31) Condition of Meckel's groove: (polarization: A=1 B=NA C=0)

(A) Meckel's groove open between the anterior end of the splenial and the mandibular symphysis. (B) (Not present in ingroup) Meckel's groove partially open, sutured anterior to the splenial for half the distance between the anterior aspect of the splenial and the mandibular symphysis. (C) Meckel's groove closed and fused for more than half the distance between the anterior aspect of the splenial and the mandibular symphysis.

32) Splenial size: 0 → 1

(0) Splenial small, extending forward to a point between the dentary tooth row midpoint and the most posterior dentary tooth, with the anterior inferior alveolar foramen

located terminally at the anteromost aspect of the splenial. (1) Splenial large, extending forward to at least the midpoint of the dentary tooth row, with the anterior inferior alveolar foramen located dorsally, posterior to the anterior aspect of the splenial.

33) Coronoid lateral process: (polarization: A=1 B=0 C=NA)

(A) Coronoid bone with a small, irregular process overlapping the posterolateral surface of dentary. (B) A posteriorly directed curving process descends over the posterodorsal surface of the dentary. (C) (not present in ingroup) Coronoid bone without a process overlapping the postero-lateral surface of the dentary.

34) Size of posterior aspect of angular (labial view): 0 → 1

(0) Extends between coronoid process and articular fossa. (1) Lateral aspect reduced, does not extend between the coronoid process and the articular fossa.

35) Angular process size: 0 → 1

(0) Well defined, in juveniles and adults (non-transforming ontogeny). (1) Small in juveniles and well-defined only in large specimens (transforming ontogeny).

36) Angular process position: (polarization: A=1 B=0)

(A) Angular processes positioned in a horizontal plane. (B) Positioned in an oblique plane.

37) Hyoid apparatus pattern: 0 → 1

(0) Z-pattern in which the second ceratobranchial is the shortest posterior element, the first ceratobranchial and the ceratohyal being of equal length. (1) X-pattern; the second ceratobranchial is the longest element, the first ceratobranchial and the ceratohyal may or may not be equal in length.

38) Rostral portion of skull: 0 → 1

(0) Arched dorsally. (1) Rostral portion of skull is pointed or keel-shaped (spatulate).

39) Crowns of posterior marginal teeth: 0 → 1A; 0 → 1B

(0) Tricuspid, with more or less parallel sides (0,0). (1A) Tricuspid, with distinctly expanded crowns (1,0). (1B) Tricuspid, with distinctly tapered crowns and very small secondary cusps (0,1).

40) Number of presacral vertebrae: 0 → 1 → 2

(0) 24. (1) 23. (2) 22.

41) Lumbar ribs: 0 → 1

(0) All with free articulating ribs. (1) One or more with ribs absent.

42) Caudal autotomy: 0 → 1

(0) Present. (1) Absent.

43) Ratio of no. of neural spines to no. of transverse processes in caudal vertebrae: 0 → 1

(0) 1/1 ratio. (1) 2/1 ratio.

44) Neural spine height: 0 → 1A; 0 → 1B

(0) Neural spines same size as vertebral body (0,0). (1A) Neural spines enlarged in thoracic, lumbar and caudal regions in males (1,0). (1B) Neural spines reduced; shorter than height of vertebral body (0,1).

45) Rib articulation patterns: (polarization: A=0 B=2A C=1B D=1A)

(A) 6(4+2) (0,0). (B) 7(4+3) (2,0). (C) 5(3+2) (0,1). (D) 6(3+3) (1,0).

46) Suprascapular cartilages: 0 → 1

(0) Project dorsally to the level of the vertebrae, sometimes meet above neural spines. (1) Suprascapular cartilages do not reach the level of the vertebral column.

47) Dorsal extent of clavicle: 0 → 1

(0) Clavicle reaches the suprascapular cartilages, with the acromion process located on suprascapular cartilage or at the scapulo-suprascapular junction. (1) Clavicle does not reach the suprascapular cartilage, with acromion process located on anterior aspect of scapula.

48) Clavicular lateral margin: (polarization: A=1 B=0)

(A) Lateral margin of clavicle irregular, or forming a smooth curve. (B) Lateral margin of clavicle distinctly angular, with an acute projection at the apex of the angle.

49) Clavicular fenestrae: 0 → 1

(0) Absent. (1) Present.

50) Preacetabular process: (polarization: A=1 B=0)

(A) Prominent. (B) Reduced.

51) Anterior extension of symphysis pubis: 0 → 1

(0) Symphysis pubis does not extend anteriorly past the pubic tubercles. (1) Symphysis pubis extends anteriorly past pubic tubercles with pubic rami join together forming an acute angle.

52) Infratemporal fascia: 0 → 1

(0) Fascia present, variably covering the posterodorsal aspect of the infratemporal fossa to the entire M. adductor mandibulae externus. (1) Little fascia present at posterodorsal corner of infratemporal fossa.

53) Insertion of M. adductor mandibulae externus: 0 → 1

(0) Mandibular insertion projects past the surangular. (1) Mandibular insertion restricted to the surangular.

54) M. levator anguli oris: 0 → 1

(0) Origin includes the tympanic crest of the quadrate. (1) Does not originate from the tympanic crest of the quadrate.

55) M. adductor mandibulae externus superficialis: (polarization: A=1 B=0)

(A) Single dorsal head. (B) Two separate dorsal heads.

56) M. adductor mandibulae externus profundus: 0 → 1 → 2

(0) Dorsal head well developed. (1) Dorsal head reduced. (2) Dorsal head is absent.

57) Superciliary scales: (polarization: A=1A B=2B C=1B)

(A) Elongate and strongly overlapping (1,0). (B) Intermediate (0,2). (C) Quadrangular, nonoverlapping (0,1).

Table 4: Distribution of character states among outgroups with polarity decisons.

Description	Trop	Anol	Iguan	Scel	Crot	Oplur	Morunasaurs	Polarity
01. Roof of nasal capsule	A	A	A	A	A	A	A,B(1:1)	A = 0 B = 1 (6:0)
02. Septomaxillae	A,B	B	A	A	A	A	A	A = 0 B = 1 (5:1)
03. Nasal median contact	B	B	B	B	B	B	B	A = 1 B = 0 (7:0)
04. Posterior margin of nasals	A	B	A,B,C	B	A	B	B	A = 1a B = 0 C = 1b (4:2)
05. Prefrontal-nasal relationship	C	C	C	C	C	C	C	A = 2 B = 1 C = 0 (7:0)
06. Antero-lateral spine of prefrontal	B	B	B	B	B	B	B	A = 1 B = 0 (7:0)
07. Groove at prefrontal-lacrimal junction	B	B	B	B	A	B	B	A = 1 B = 0 (6:1)
08. Platine-ectopterygoid relationship	B	B	B	B	B	B	B	A = 1 B = 0 (7:0)
09. Palatine process of pterygoid	B	B	B	B	B	B	A,B (2:1)	A = 1 B = 0 (6:0)
10. Quadrate process of pterygoid	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
11. Shape of mid-sagtital section of frontal	B	B	B	B	B	B	B	A = 1 B = 0 (7:0)
12. Postfrontals	B	A,B	B	B	A	A	B	A = 1 B = 0 (4:2)
13. Squamosal process of jugal	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
14. Jugal-squamosal contact	A,B,C	A	A,B (2:1)	A	C	A	A	A = 0 B = 1 C = 2 (4:1)
15. Posterior angle of jugal	A	A	A	A,B	B	A	A	A = 0 B = 1 (5:1)
16. Supraorbital process	B	B	B	B	B	B	B	A = 1 B = 0 C = 2 (7:0)
17. Parietal foramen position	A	A	A,B (2:1)	A	A	A	A	A = 0 B = 1 (6:0)
18. Lateral shelves of adductor crest	A	A	A	A	A	A	A	A = 0 B = 1 C = 2 (7:0)
19. Parietal roof shape	A	A	A	A	A	A	A	A = 0 B = 1a C = 1b D = 2b (7:0)
20. Development of parietal blade	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
21. Parietal blade sexual dimorphism	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
22. Expansion of parietal blade	A	A	A	A	A	A	A	A = 0 B = 1a C = 1b (7:0)
23. Dorsal process of squamosal	A	A	B	A,B	A	B	B	equivocal (3:3)
24. Squamosal	B	B	B (2:1)	B	B	B	B	A = 1 B = 0 (7:0)
25. Medial concha of quadrate	A	B	A (2:1)	A	A	A	A	A = 0 B = 1 (6:1)
26. Quadrate	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
27. Epipterygoids	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
28. Crista ventrolateralis	B	B	B	B	A	A,B	A,B (1:1)	A = 1 B = 0 (4:1)
29. Qutlines of bony labyrinth	A	C	A,B (2:1)	A,B	B	A,B	A	equivocal (2:1:1)

30. Posttemporal fenestra	A	A	A	A	A	A	A	A = 0 B = 1 C = 2 (7:0)
31. Condition of Meckel's groove	B,C	C	C	B	A	C	A	equivocal (3:2:1)
32. Splenial size	B	B	B	B	A	B	A	A = 1 B = 0 (5:2)
33. Coronoid lateral process	C	B	C	B	B	A	C	equivocal (3:3:1)
34. Size of posterior aspect of angular	B	B	A	A,B	A	A	A	A = 0 B = 1 (4:2)
35. Angular process size	A,B	A	A,B (2:1)	A,B	A	A	A	A = 0 B = 1 (4:0)
36. Angular process position	A	A	A	A	B	B	B	equivocal (4:3)
37. Hyoid apparatus pattern	Z	X	X,Z (2:1)	Z	Z	Z	Z	Z = 0 X = 1 (5:1)
38. Rostral Portion of Skull	A	B	A	A	A	A,B	A	A = 0 B = 1 (5:1)
39A. Crowns of posterior marginal teeth	B	A	B	A	A	A	A,B (2:1)	A = 0 B = 1 (4:2)
39B. Crowns of posterior marginal teeth	A	A	A	A,B	A	A	A	A = 0 B = 1 (6:0)
40. Number of presacral vertebrae	A	A	A	B	A	A	A	A = 0 B = 1 (6:1)
41. Lumber ribs	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
42. Caudal autotomy	A	A,B	A,B (2:1)	A	A,B	A	A	A = 0 B = 1 (4:0)
43. Ratio of ns to tp in caudals	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
44. Neural spine height	A	A	A	B	B	A	A	A = 0 B = 1 (5:2)
45. Rib articualting patterns	B	B	A	A,B	A	C	?	equivocal (2:2:1)
46. Suprascapular cartilages	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
47. Dorsal extent of clavicle	B	A	B	B	B	B	B	A = 1 B = 0 (6:1)
48. Clavicular lateral margin	A,B	B	A	B	A,B	A	A (2:0)	equivocal (3:2)
49. Clavicular fenestration	B	B	B	B	B	B	B	A = 1 B = 0 (7:0)
50. Preacetabular process	A,B	A,B	A	B	A	A	B	equivocal (3:2)
51. Anterior extension of symphysis pubis	B	A,B	B	A	B	A,B	B	A = 1 B = 0 (4:1)
52. Infratemporal fascia	A	A,B	A	A	A	A	A	A = 0 B = 1 (6:0)
53. Insertion of m. add. mand. ext.	B	A,	B	B	B	B	B	A = 0 B = 1 (6:0)
54. M. levator anguli oris	A	A	A	A	A	A	A	A = 0 B = 1 (7:0)
55. M. add. mand. ext. superficialis	A,B	B	B	A,B	B	A	A	equivocal (3:2)
56. M. add. mand. ext. profundus	A	A	A	A	A	A	A	A = 0 B = 1 C = 2 (7:0)
57. Superciliary scales	A	C	A,B	A	B	A	C	equivocal (3:2:1)

T a b l e 5 : Character data matrix of ingroup with polarization results of equivocal characters.

Description	vitt	basil	plum	galer	christ	hern	perc	long	serr	Polarization
01. Roof of nasal capsule	0	0	0	0	1	1	1	0	0	
02. Septomaxillae	0	0	0	0	1	1	1,2	1	1	
03. Nasal median contact	0	0	0	0	2	1	1	0	0	
04. Posterior margin of nasals	0	0	0	0	1a	1a	1a	0	1b	
05. Prefrontal-nasal relationship	0	0	0	0	2	1	1	0	0	
06. Antero-lateral spine of prefrontal	0	0	0	0	1	1	1	0	0	
07. Groove at prefrontal-lacrimal junction	1	1	1	1	0	0	0	1	1	
08. Platine-ectopterygoid relationship	0	0	0	0	1	0	0	0	0	
09. Palatine process of pterygoid	0	0	0	0	1	1	1	0	0	
10. Quadrate process of pterygoid	0	0	0	0	1	1	1	0	0	
11. Shape of mid-sagtital section of frontal	0	0	0	0	1	1	1	1	1	
12. Postfrontals	1	1	1	1	1	1	1	0	0	
13. Squamosal process of jugal	0	0	0	0	1	1	1	0	0	
14. Jugal-squamosal contact	0	0	0	0	1	1	1	0	0	
15. Posterior angle of jugal	0	0	0	0	1	1	1	1	1	
16. Supraorbital process	0	0	0	0	2	1	2	0	0	
17. Parietal foramen position	1	1	1	1	1	1	1	0	0	
18. Lateral shelves of adductor crest	0	0	0	0	2	2	2	1	1	
19. Parietal roof shape	1a	1a	1a	1a	2b	2b	2b	1b	1b	
20. Development of parietal blade	0	0	0	0	1	1	1	1	1	
21. Parietal blade sexual dimorphism	0	0	0	0	1	1	1	1	1	
22. Expansion of parietal blade	1a	1a	1a	1a	1b	1b	1b	1b	1b	
23. Dorsal process of squamosal	B	B	B	B	A	A	A	A	A	[A = 1 B = 0]
24. Squamosal	0	0	0	0	0	1	1	0	0	
25. Medial concha of quadrate	0	0	0	0	1	1	1	1	1	
26. Quadrate	0	0	0	0	1	1	1	1	1	
27. Epipterygoids	0	0	0	0	1	1	1	0	0	
28. Crista ventrolateralis	1	1	1	1	0	0	0	0	0	
29. Qutlines of bony labyrinth	B	B	B	B	C	C	C	C	C	[A = NA B = 1 C = 0]

30. Posttemporal fenestra	0	0	0	0	2	1	2	0	0	
31. Condition of Meckel's groove	A	C	C	C	C	C	C	C	A	[A = 1 B = NA C = 0]
32. Splenial size	1	1	1	1	0	0	0	0	0	
33. Coronoid lateral process	A	A	A	A	A	B	A	B	B	[A = 1 B = 0]
34. Size of posterior aspect of angular	0	0	0	0	1	1	1	0	0	
35. Angular process size	0	0	0	0	1	1	1	1	1	
36. Angular process position	B	B	B	B	A	A	A	A	A	[A = 1 B = 0]
37. Hyoid apparatus pattern	0	0	1	?	1	0	1	0	0	
38. Rostral Portion of Skull	0	0	0	0	1	1	1	1	1	
39A. Crowns of posterior marginal teeth	1	1	1	1	0	0	0	0	0	
39B. Crowns of posterior marginal teeth	0	0	0	0	0	0	0	1	1	
40. Number of presacral vertebrae	0	0	0	0	0	0	0,1	0	0	
41. Lumber ribs	0	0	0	0	1	1	1	1	1	
42. Caudal autotomy	0	0	0	0	1	1	1	1	1	
43. Ratio of ns to tp in caudals	1	1	1	1	0	0	0	0	0	
44. Neural spine height	0	1a	1a	0	0	0	0	1b	1b	
45. Rib articualting patterns	A	A	A	A	A	A	C	B	D	[A = 0 B = 2a C = 1b D = 1a]
46. Suprascapular cartilages	0	0	0	0	1	0	0	0	0	
47. Dorsal extent of clavicle	0	0	0	0	1	0	1	0	0	
48. Clavicular lateral margin	B	B	B	B	A	A	A	B	B	[A = 1 B = 0]
49. Clavicular fenestration	1	1	1	1	0	0	0	1	1	
50. Preacetabular process	A	A	A	A	B	B	B	B	B	[A = 1 B = 0]
51. Anterior extension of symphysis pubis	1	1	1	1	0	0	0	0	0	
52. Infratemporal fascia	0	0	0	0	0	0	0	1	1	
53. Insertion of m. add. mand. ext.	0	0	0	0	1	1	1	0	0	
54. M. levator anguli oris	0	0	0	0	1	1	1	0	0	
55. M. add. mand. ext. superficialis	B	B	B	B	B	B	B	A	A	[A = 1 B = 0]
56. M. add. mand. ext. profundus	0	0	0	0	2	2	2	1	1	
57. Superciliary scales	A	A	A	A	B	B	B	C	C	[A = 1a B = 2b C = 1b]

Table 6: List of abbreviations used in previous tables.

ADD. = adductor
All = all members of clade
Amb = *Amblyrhynchus*
ANOL = anoloids
Anl = *Anolis*
Ans = anoles
Apt = *Aptycholaemus*
caud = *caudal*
cerv = *cervical*
Chl = *Chalarodon*
Chm = *Chamaeleolis*
Clav = clavicular
Con = *Conolophus*
Cro = *Crotaphytus*
Crot. = crotaphytines
Ctn = *Ctenosaura*
Dip = *Dipsosaurus*
Dors = dorsal
Enu = *Enyalius*
Eny = *Enyalioides*
Equiv. = equivocal
ext. = externus
Fem. = femoral
fenest = fenestra
Fr = fragmented
Gam = *Gamelia*
gr = groove
Iguan. = iguanines
labyr = labyrinth
lat = lateral
Lei = *Leiocephalus*
Lio = *Liolaemus*
*Lio*gr = *Liolaemus* group
Lios = liosaurs
M. = musculo
mand. = mandibulae
Meck = Meckel's
Morun. = morunasaurs
mrg = margin
musc = musculature
NS = neural spines
Oph = *Ophryoessoides*
Opl = *Oplurus*
Oplur. = oplurines
PAnl = para-anoles
Pet = *Petrosaurus*
Phr = *Phrynosoma*
Phy = *Phymaturus*
Plc = *Plica*
Plt = *Platynotus*
Pol = *Polychrus*
pr = process
Pri = *Pristidactylus*
Sand lzds = sand lizards
Sau = *Sauromalus*
Scel. = sceloporines
Scl = *Sceloporus*
*Scl*gr = *Sceloporus* group
Stn = *Stenocercus*
subocc = suboccular
TP = transverse processes
tr = transverse
Trop. = tropidurines
Trp = *Tropidurus*
Urc = *Uracentron*
Urn = *Uranoscodon*
Uro = *Urosaurus*
Vert = vertebrae
W*Trp* = western *Tropidurus*

X = character not expressed in this clade.

(1) / (2) = apomorphic states within a character transformation series.

DISCUSSION

Phylogeny

The character data matrix containing 10 unpolarized characters (Table 5) was run on the PAUP program (Phylogenetic Analysis Using Parsimony, Version 2.4; Swofford

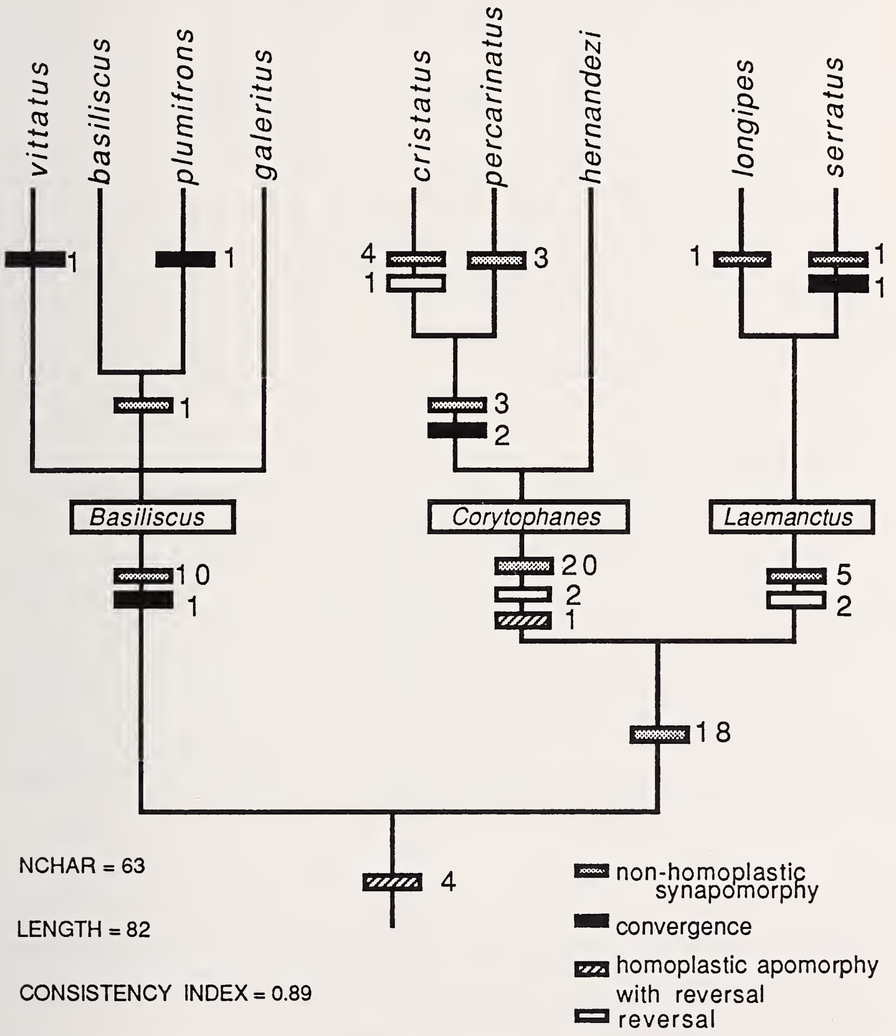

Fig. 41: Reconstructed phylogeny of basiliscine iguanians. The numbers indicate the number of characters supporting each node. A non-homoplatic synapomorphy is a character that neither reverses nor is a convergence at any level.

1985) using the mulpars and global swapping options. In this initial run the unordered characters were polarized with respect to the rest of the data set. Subsequently all unordered characters were substituted by the polarized value, resulting in a cladogram with a length of 82 (C.I. = 0.89) for 63 coded characters (Fig. 41)[7]. Fig.42 shows the distribution of homoplasies.

The proposed phylogeny supports the monophyly of the three basiliscine genera. *Corytophanes* and *Laemanctus* form a natural grouping supported by a large number of non-homoplastic autapomorphies and *Basiliscus* is the earliest diverging taxon. At the species-level the proposed phylogeny is not well-supported (Fig. 41). Within *Basiliscus*, *plumifrons* and *basiliscus* are sister taxa and form a tritomy with *vittatus* and *galeritus*. Within *Corytophanes*, *C. hernandezi* is the earliest diverging taxon with few autapomorphies. The *percarinatus-cristatus* clade is well-supported (Fig. 41).

In addition to the 10 unordered characters, several others might be polarized erroneously (4:2 and 5:2 consensus patterns; Fig. 12 & 13). The polarities of these characters should be reversed if Maddison et al.'s (1984) "doublet rule" applies to the less common character state (Fig. 12 & 13). The following six characters show possible erroneous polarity decisions: Posterior margins of nasals [Character 4, (4:2 consensus): less common condition occurs in crotaphytines and tropidurines]; Postfrontals [Character 12, (4:2 consensus): less common condition found in crotaphytines and oplurines]; Splenial size [Character 32, (5:2 consensus): less common condition in crotaphytines and morunasaurs]; Size of posterior aspect of angular [Character 34, (4:2 consensus): less common condition in tropidurines and anoles]; Crowns of posterior marginal teeth [Character 39A, (4:2 consensus): less common condition in iguanines and tropidurines]; and Neural spine height [Character 44, (5:2 consensus): less common condition in sceloporines and crotaphytines].

It is interesting to note that none of these six characters show the same pair of outgroup taxa with the less-common character state. This means that at most only a single polarity decision can be erroneous. For example, if crotaphytines and tropidurines were to form a clade with basiliscines, in which the basiliscines were more closely related to either crotaphytines or tropidurines, than either of these two taxa are to each other, then the polarity for character 4 should be reversed. This would exclude any other polarity decision from being erroneous. In addition to the erroneous polarity decisions for the ten unordered characters[8], at most only one additional polarity reversal can be made for the (4:2) and (5:2) characters within the context of "iguanids".

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[7]) The consistency index (C.I.) does not give a measure of the stability of the cladogram, but gives an estimate of the "best-fit" of characters on a particular topology. An ideal character data set (i.e. perfect fit with no characters showing homoplaies) has a C.I. = 1. The resulting cladogram may or may not be fully resolved showing polytomies and unsupported nodes. On the other hand, a fully resolved cladogram may show a low consistency index.

[8]) Not all of the unordered characters can have erroneous polarity decisions, because the same conditions apply as in the case of a (4:2) and (5:2) pattern. The polarity reversal of one unordered character in a partricular situation can exclude the reversal in all others.

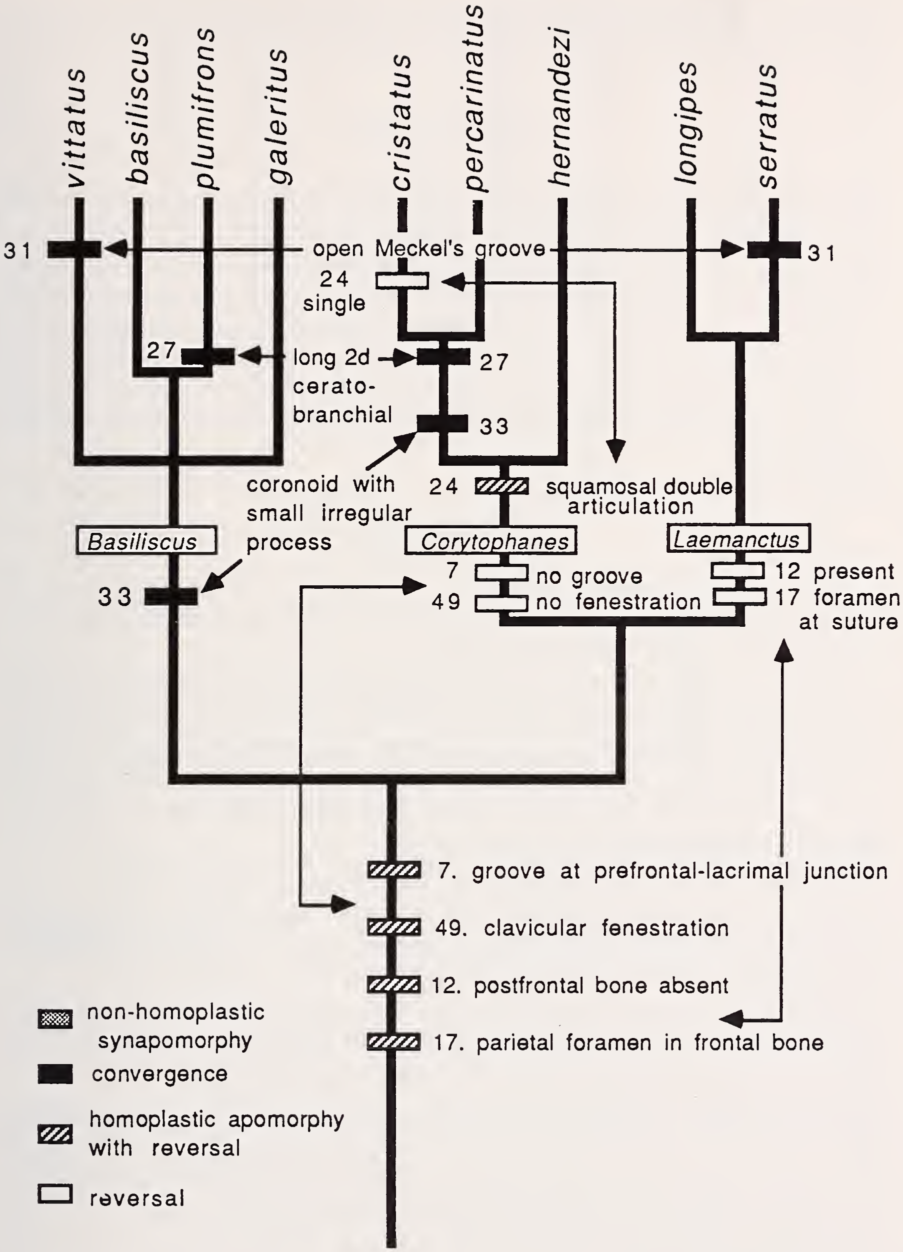


Fig. 42: Distribution of homoplastic characters on the phylogeny of basiliscines.

Therefore, a maximum predicted eleven erroneous polarity decisions can be made using the consensus approach. A minimum of no erroneous polarirty decisions is possible.

Diagnosis of Taxa

The monophyly of the basiliscines with respect to other iguanine suprageneric clades is well substantiated (see discussion on basiliscine monophyly).

This section includes the diagnoses for the monophyletic taxa within the basiliscines. For each taxon the following information is provided: 1) a list of synonyms and/or descriptions; 2) etymology; 3) distribution; 4) a diagnosis (phylogenetic definition of the respective taxa sensu Gauthier et al. (1988), including apomorphies (non-homoplastic autapomorphies and homoplasies)); 5) description of taxon; 6) ecological and life history data (for terminal taxa only); 7) fossil record, if any, and; 8) karyotypes, if available.

BASILISCINES

Etymology: From the greek *basiliskos* meaning small king, in reference to the expanded parietal blade symbolic of a crown.

Diagnosis: Heretofore basiliscines have been given an informal taxonomic recognition (Etheridge 1964). Strong evidence is presented in this study for the designation of a formal subfamilial taxonomic name Basiliscinae Cope. However, the primary emphasis, has been on resolving relationship between basal taxa within the basiliscines, and no formal taxonomic change will be made. The following characters are autapomorphies at the basiliscine basal node (Fig. 41—43):

1) expanded, well-developed parietal blade (Etheridge & de Queiroz 1988).

2) parietal foramen located entirely within the frontal (with reversal to the primitive condition at the frontoparietal suture in *Laemanctus*, Fig. 42). Also found in *Dipsosaurus, Sauromalus*, and some *Leiocephalus* (character 14).

3) clavicular fenestration (secondarily lost in *Corytophanes*, Fig. 42). Clavicular fenestration is also present in the Galapágos iguanas (*Amblyrhynchus, Conolophus), Gambelia*, the western *Tropidurus, Plica* and *Uracentron* (Character 49).

4) caudal vertebrae of *Basiliscus*-type. Also in *Enyalius, Polychrus and Ophryoessoides*.

5) femoral pores lost (also in tropidurines, oplurines and all anoloids except *Polychrus*).

6) vertebrae with zygosphene-zyganthrum articulations (Etheridge 1967).

7) expansion of postorbital bone dorsomedially over dorsolateral portion of the supratemporal fossa.

8) prominent groove at prefrontal-lacrimal junction (lost in *Corytophanes*, Fig. 42). Prominent groove is also found in crotaphytines (Character 7).

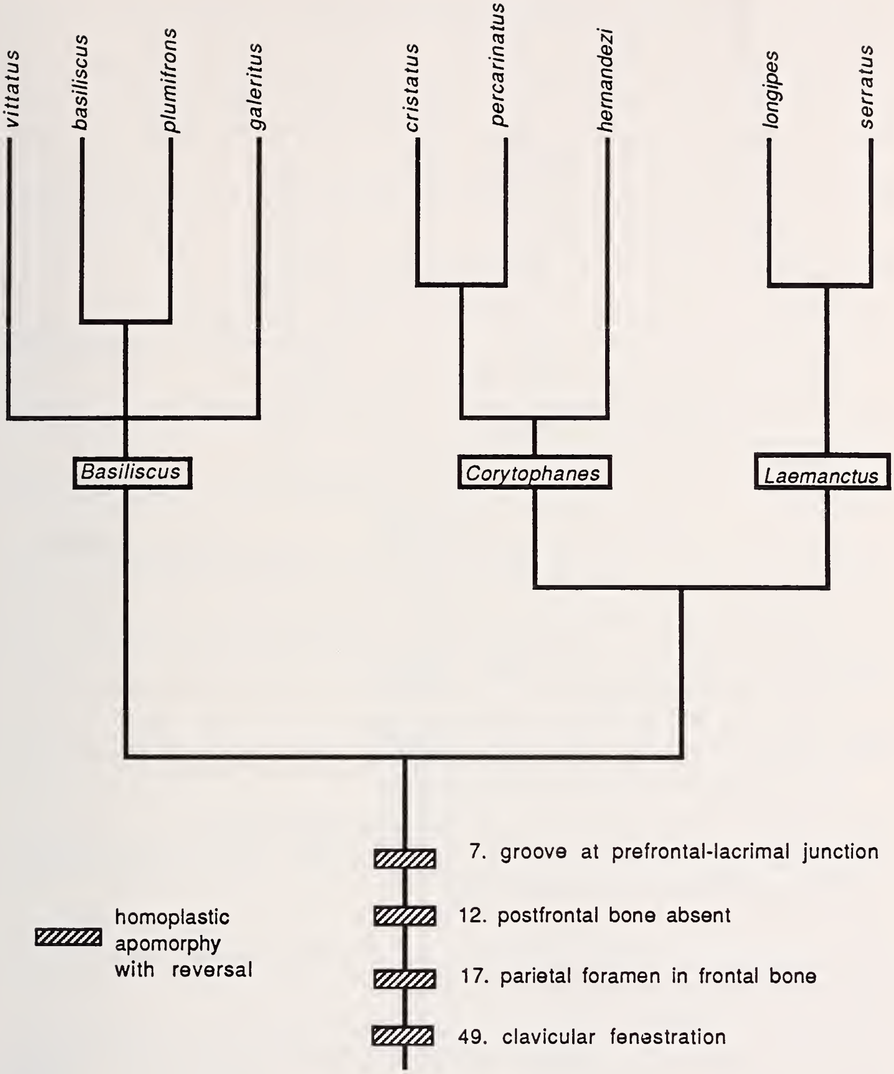


Fig. 43: Homoplastic characters in support of the basiliscine basal node. A complete list of apomorphies is given in the diagnoses section.

9) postfrontal bone absent (present in *Laemanctus*, Fig. 42). The postfrontal bone is absent in most oplurines, *Polychrus, Leiosaurs, Chamelinorops*, sand lizards and *Phrynosoma*, crotaphytines, and some *Phymaturus* (Character 12).

Basiliscus Laurenti, 1768

1768 *Basiliscus* Laurenti, Synop. Rept., Wien, 50. - Type species: (by monotypy): *Basiliscus americanus* Laurenti, 1768 = *Lacerta basiliscus* Linnaeus, 1758.

1828 *Corythaeolus* Kaup, Isis von Oken, Leipzig, 21: 1147. - Type species (by monotypy): *Basiliscus vittatus* Wiegmann, 1828.

1830 *Oedicoryphus* Wagler, Natür. Syst. Amph., München, 148. - Type species: *Basiliscus vittatus* Wiegmann, 1828.

1843 *Basiliscus (Basiliscus)* — Fitzinger, Syst. Rept., Wien, 1:53.

1843 *Basiliscus (Corythaeolus)* — Fitzinger, Syst. Rep., Wien 1:53.

1845 *Thysanodactylus* Gray, Cat. Spec. Liz. Coll. brit. Mus., London, 193. - Type species (by monotypy): *Ophryessa bilineata* Gray, 1839.

1852 *Lophosaura* Gray, Ann. Mag. nat. Hist., London, (2) 10: 438. - Type species (by monotypy): *Lophosaura goodridgii* Gray, 1852.

1852 *Ptenosaura* Gray, Ann. Mag. nat. Hist., London, (2) 10: 438. - Type species (by monotypy): *Ptenosaura seemanni* Gray, 1852.

1852 *Cristasaura* Gray, Ann. Mag. nat. Hist., London, (2) 10: 439. - Type species (by monotypy): *Cristasaura mitrella* Gray, 1852.

1854 *Craneosaura* Gray in Richardson, Zool. Voy. Herald, Vert., London, 148. - Type species: *Ptenosaura seemanni* Gray, 1852.

1860 *Daconura* Hallowell, Proc. Acad. nat. Sci. Philad., 12: 482 - Type species (by monotypy): *Daconura bivittata* Hallowell, 1860.

1862 *Paraloma* Cope, Proc. Acad. nat. Sci. Philad., 14: 181. - Type species (by monotypy): *Daconura bivittata* Hallowell, 1860.

1885 *Basiliscus* — Boulenger, Cat. Liz. brit. Mus., London, 2:106.

1893 *Dactylocalotes* Werner, Zool. Anz., Leipzig., 16: 361. - Type species (by monotypy): *Dactylocalotes elisa* Werner, 1893.

Etymology: Derived from the Greek *basiliskos* meaning small king in reference to the expanded parietal blade symbolic of a crown.

Distribution (Figs. 45—48): Low to moderate elevations of Jalisco (western México) and Tamaulipas (eastern México) through Central America to the pacific coast of Ecuador, Colombia and northwestern Venezuela.

Description: Nostrils are oriented laterally. Head covered with small flat rather keeled uniform scales. Eye-opening large. Six or seven large upper and lower labial shields. External ear opening is oval, located above the level of the mouth. The occiput is elongated and narrow behind with a small parietal blade in adult females and a large blade in adult males. The throat has a slight pouch with a well marked gular fold that is confluent with the antehumeral fold.

Elongated body with long laterally compressed tail and well-developed limbs. Scales of back are small and rhombic either smooth or keeled. Ventral scales larger, square;

smooth or keeled. Superior surface of the limbs covered by rhomboid keeled scales. No femoral or preanal pores. Toes elongated, compressed, unequal with a series of broad

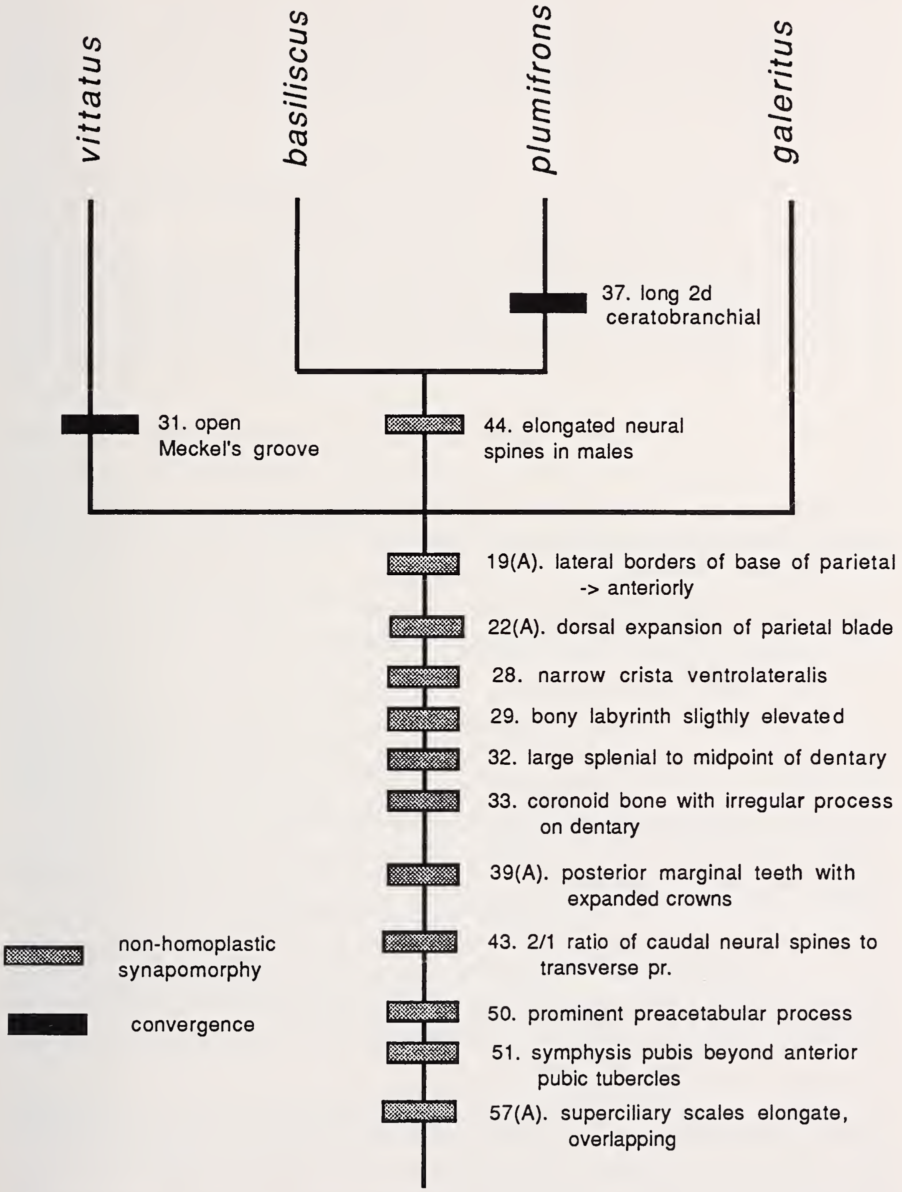


Fig. 44: Reconstructed phylogeny of *Basiliscus*.

scales above and a series of convex square plates beneath with central carinated ridges. The adpressed hind limb reaches the tip of the snout or a little beyond. The toes of the hind limbs have prominent lateral toe fringes. Caudal scales keeled much enlarged inferiorly.

Diagnosis: The following is a list of apomorphies diagnostic of *Basiliscus* (Fig. 44).
1) Parietal Y-shaped to form a posteriorly directed blade. Lateral borders at the base of the parietal blade progress anteriorly with increased ontogeny to form a 180° angle in adults (Character 19A).

2) Parietal blade expanded dorsally. (Character 22B).

3) Crista ventrolateralis narrow, not obscuring the vidian canal (Character 28).

4) Outlines of bony labyrinth slightly elevated (Character 29).

5) Splenial large, extending anteriorly to midpoint of dentary tooth row (Character 32).

6) Coronoid bone with small irregular process overlapping the posterolateral surface of the dentary (convergence with *cristatus-percarinatus* clade, Fig. 42) (Character 33).

7) Crowns of posterior marginal teeth tricuspid, with expanded crowns (Character 39A).

8) 2/1 ratio of neural spines to transverse processes in the caudal vertebrae. (Character 43).

9) Prominent preacetabular process (Character 50).

10) Symphysis pubis extends anterior to the pubic tubercles and pubic rami join together forming an acute angle. (Character 51).

11) Superciliary scales elongate and strongly overlapping (Character 58).

12) Free flaps of skin on the pedal digits (Cope 1875).

13) Aquatic bipedalism.

Ecology & Life History: Riparian habitats for this genus have been observed by many authors (e.g., Allee and Schmidt 1952; Fitch 1973 and literature cited therein). Cope (1875), was one of the first to describe *Basiliscus* running in an upright position over water. Lydekker et al. (1912:95) discussed bipedalism in both recent and fossil Archosaurs and correctly inferred that this mode of locomotion had developed independently in Archosaurs and Lepidosaurs. Barbour (1926) correctly pointed out that *Basiliscus* did not use its tail for swimming and never dove into the water. This phenomenon has subsequently been termed "aquatic bipedalism" (Von Wettstein 1934; Ditmars 1936; Verril 1937; Laerm 1973, 1974, and others). Using anatomy and cinematography, Snyder (1949, 1954) and Laerm (1973, 1974) extensively investigated the morphological constraints and functional adaptations to bipedal locomotion. Bellairs (1969) measured peak bipedal locomotion at 10.9 km/hr.

Snyder (1949) summarized findings on bipedal locomotion and listed two categories: bipedal and partially bipedal. Within the "iguanids", *Crotaphytus, Callisaurus* and *Basiliscus* showed a bipedal gait, with *Dipsosaurus* and *Uma* being partially bipedal. Bipedal locomotion has, therefore, been independently acquired in at least three suprageneric groups of "iguanids".

Although there has been no published observation of aquatic bipedalism in *Basiliscus galeritus*, we can assume that they have the capability. *Basiliscus galeritus* has the two elements identified by Snyder (op. cit.) that are required for aquatic bipedalism: expanded lateral digital lamellae and a heavy tail (as counterbalance). Laerm (1973) discussed the functional significance of toe fringes and demonstrated that the lateral toe fringes are not necessary for aquatic bipedalism, as had been suggested by previous authors. The presence of lateral toe fringes however, does increase the efficiency of running on water. Aquatic bipedalism has also evolved as a predator avoidance mechanism for both terrestrial and aquatic predators (Laerm 1973).

Aquatic bipedalism, apparently does not occur in any other squamate taxon and therefore may serve as an autapomorphy in support of the monophyly of *Basiliscus*.

Barden (1943a) examined stomach contents of Panamanian basilisks and stated that a wide variety of food is consumed. Approximately 78% of the total volume of food uptake involves animal material, whereas the remaining 22% is plant material. The conclusions reached by Barden indicates that *Basiliscus* eats virtually all animal foods, supplementing its diet with plant material.

Basiliscus vittatus Wiegmann, 1828

1828 *Basiliscus vittatus* Wiegmann, Isis von Oken, Leipzig, 21: 373. - Type locality: not given (Syntypes: ZMB 549-551). - Restricted type locality (Smith & Taylor 1950): "Veracruz, Veracruz".

1828 *Corythaeolus vittatus* — Kaup, Isis von Oken, Leipzig, 21: 1147.

1830 *Oedicoryphus vittatus* — Wagler, Natür. Syst. Amph., München, 148.

1837 *Basiliscus vittatus* — Duméril & Bibron, Erpét. gén., Paris, 4: 187.

1843 *Basiliscus (Corythaeolus) vittatus* —Fitzinger, Syst. Rept., Wien, 1: 53.

1845 *Corythaeolus vittatus* — Gray, Cat. Spec. Liz. Coll. brit. Mus., London, 193.

1852 *Cristasaura mitrella* Gray (syn. fide Boulenger 1885), Ann. Mag. nat. Hist., London, (2) 10: 439. - Type locality: "Honduras" (Holotype: BM 1946.8.9.16)).

1860 Daconura bivittata Hallowell (syn. fide Boulenger 1885), Proc. Acad. nat. Sci. Philad., 12: 482. - Type locality: "Nicaragua" (Holotype: USNM 6056). - Restricted type locality (Smith & Taylor 1950): "Greytown".

1862 *Paraloma bivittata* — Cope, Proc. Acad. nat. Sci. Philad., 14: 181.

1862 *Basiliscus (Cristasaura) nuchalis* Cope (syn. fide Boulenger 1885), Proc. Acad. nat. Sci. Philad., 14: 181. Type locality: "near Greytown, Nicaragua" (Holotype: USNM 5845).

1885 *Basiliscus vittatus* — Boulenger, Cat. Liz. brit. Mus., London, 2: 109.

1893 *Dactylocalotes elisa* Werner (syn. fide Peters & Donoso-Baros 1970), Zool. Anz., Leipzig, 16: 361. - Type locality: "Sumatra" (Holotype: not located).

1956 *Basiliscus vittatus* — Taylor, Kans. Univ. Sci. Bull., Lawrence, 38 1: 171; Fig. 47, 48.

Etymology: Derived from the Latin *vittatus* meaning decorated or bound with a ribbon. This is in reference to the parietal blade of male *vittatus*, which takes on the form of a thin ribbon.

Distribution: (Fig. 45). Along the coasts of southern México from Jalisco and southern Tamaulipas, through the Isthmus of Tehuántepec southward into northwestern Colombia. Recorded by Boulenger (1885) from Ecuador.

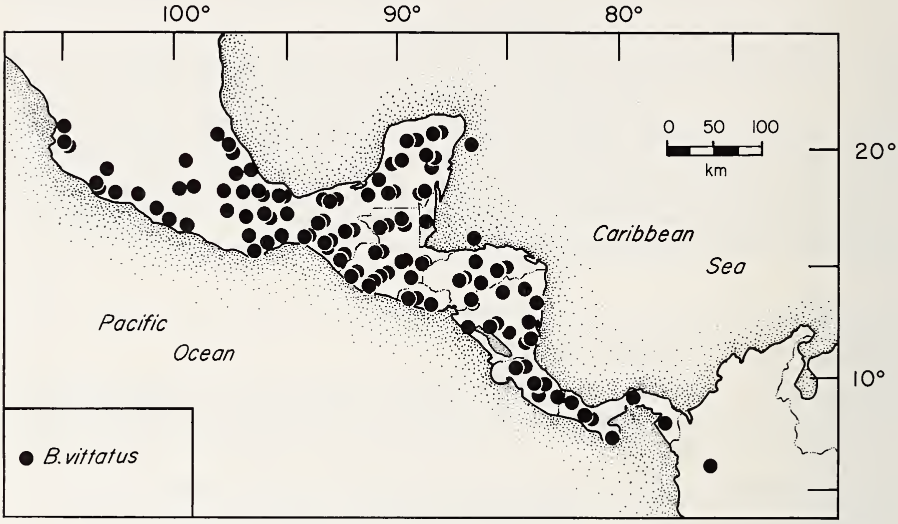


Fig. 45: Distribution map of *Basiliscus vittatus*. Symbols represent localities of examined specimens.

Description: Parietal blade is triangular in males projecting posteriorly. A dorsal crest is slightly elevated in males and the tail crest is simple and serrated. Ventral scales keeled.

Dorsum is brown green with two longitudinal yellow stripes are on either side of the body originating from the head. The superior stripe originates from the corner of the eye transverses the base of the parietal blade and continues the length of the trunk taking on a copper tint. This stripe may be interrupted in the head region. Black cross bands span between the two superior longitudinal strips in the neck and anterior back. In adults however this pattern is less distinct and somewhat disrupted. The inferior stripe originates from the external nares passes below the eye along the inferior aspect of the shoulder and terminates ordinarily on the flanks. Underside yellowish with throat slightly orange. Limbs and tail transversed by brown bands.

Diagnosis: Within basiliscines, *Basiliscus vittatus* is diagnosed by the presence of an open Meckel's groove between the anterior end of the splenial and the mandibular symphysis (Fig. 28, 43). This character was designated by Etheridge & de Queiroz (1988) as being plesiomorphic. The character polarity was equivocal at the basiliscine basal node using the consensus algorithm. This character was then polarized with respect to the other characters suggesting that within the basiliscines the open Meckel's groove is the derived condition. An open Meckel's groove is also found in *Laemanctus serratus* and indicates a convergence between these two taxa.

Ecology&Life History: *Basiliscus vittatus* occurs from sea level to 1200 m and is found most frequently near water in open situations, both in tropical and subtropical wet and dry forest. In the Yucatán peninsula of México, which lacks streams and rivers, *B. vittatus* is found near ceñotes (sinkholes) with open vegetation (pers. obs.). *Basiliscus vittatus* is also reported to be common around irrigation ditches and water holes, and rarely far from water (Hartweg 1940). Echelle et al. (1972) reported juvenile *B. vittatus* catching fish.

Sexual maturity is reached at a snout-vent length of 90—100 mm (Gaige et al. 1937) and under 1 year of age (Hirth 1963). The reproductive season is year-round with peak activity occurring from the end of April to the beginning of May. Clutches have up to 18 eggs (Ahl 1930; Fitch 1970). Average clutch size is 4.2 eggs per clutch (Hirth 1963), with gestation periods from 50 to 55 days (Ahl 1930). Eggs have an average length of 16.96 mm, a width of 11.04 mm, and a weight of 1.18 g (Conant & Downs 1940).

Recorded maximal life span in captivity is 5 years and 11 months (Conant & Hudson 1949). However, only ten % of the hatchlings reach 1 year of age and only 2 % survives to 2 years (Conant & Downs 1940).

Brattstrom (1965) measured nocturnal body temperatures of sleeping *Basiliscus vittatus*, ranging from 22.5 °C — 26.0 °C. This is in contrast to mean diurnal body temperatures ranging from 32.6 °C — 37.5 °C (Hirth 1965). Body temperatures were only slightly less than air temperatures. Maintenance of body temperatures below ambient are a result of open-mouth panting. Overall temperature reduction as well as temperature gradients between head (2.46 °C below ambient) and body core temperature (0.71 °C below ambient) can be directly correlated with the increased evaporation from the buccal cavity (Crawford et al. 1977).

Fossil Record: Langebartel (1953) reported a nearly complete right maxilla with 22 teeth from cave deposits at Actun Spukil, Yucatán, México.

Karyotype: 2n=36; 12 metacentric macrochromosomes and 24 acrocentric microchromosomes (Gorman et al. 1967)

Basiliscus galeritus Duméril, 1851

1851 *B.[asiliscus] Galeritus* Duméril in Duméril & Duméril, Cat. Méth. Coll. Rept. Mus. Paris, 61. - Type locality: "N.-Grande" (Syntypes: MHNP 2130-2131).

1852 *Ptenosaura Seemanni* Gray (syn. fide Boulenger 1885), Ann. Mag. nat. Hist., London, (2) 10: 438. - Type locality: "Quibo, on west coast of America" (Holotype: not located).

1854 *Craneosaura Seemanni* — Gray in Richardson, Zool. Voy. Herald, Vert., London, 148; Pl. 25.

1860 *Basiliscus seemanni* — Günther, Proc. zool. soc. Lond., 234.
1885 *Basiliscus galeritus* — Boulenger, Cat. Liz. brit. Mus., London, 2: 110.
1956 *Basiliscus galeritus* — Taylor, Kans. Univ. Sci. Bull., Lawrence, 38 1: 177.

Etymology: Derived from the Latin *galeritus* meaning wearing a hood.

Distribution (Figs. 46, 48): Pacific coast of Costa Rica to pacific slopes of Colombia and Ecuador. The presence of *Basiliscus galeritus* in Costa Rica has been disputed (Taylor 1956). In an ecogeographical analysis of the lizards of Costa Rica by Wake (1964), *Basiliscus galeritus* also was not reported. In a more recent publication on the

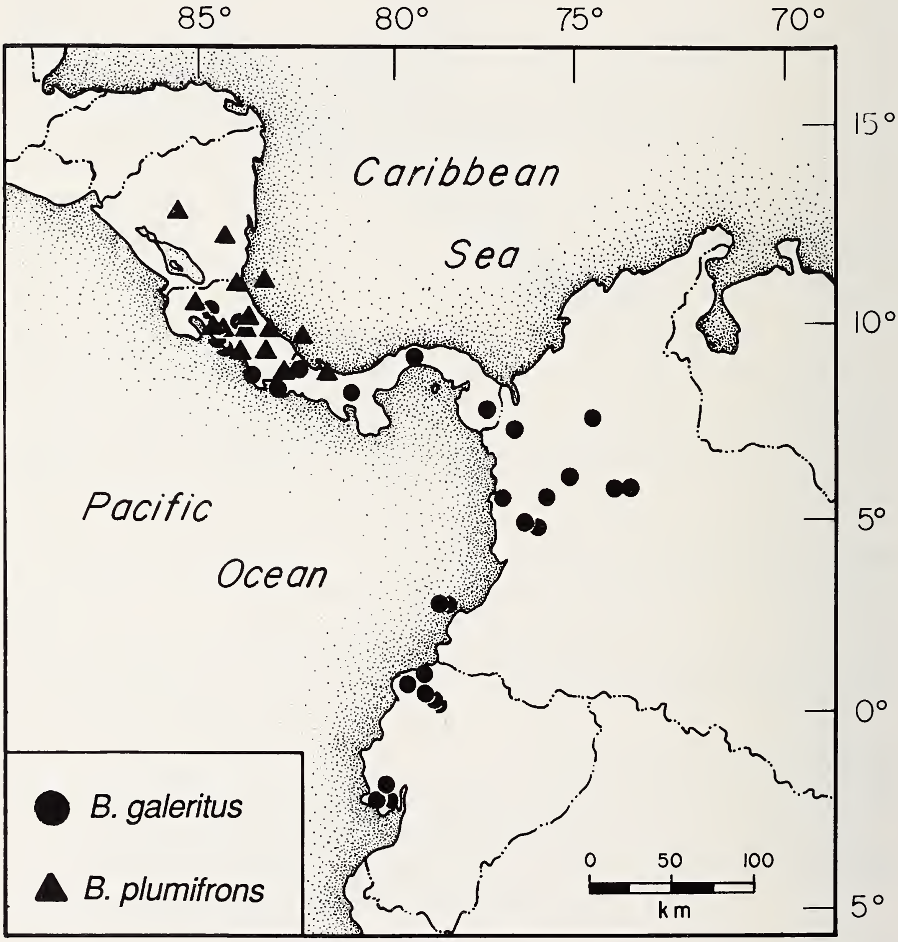


Fig. 46: Distribution map of *Basiliscus galeritus* and *Basiliscus plumifrons*. Symbols represent localities of specimens examined in this study.

herpetofauna of Costa Rica by Savage & Villa (1986), *Basiliscus galeritus* also was absent from Costa Rica. Numerous specimens have been examined from Costa Rica in this study, and locality data are included on Fig. 48.

Diagnosis: *Basiliscus galeritus* lacks a well-defined crista tuberalis, a character difficult to evaluate and rather subjective. It was therefore not included in the analysis. Maturana (1962) listed various autapomorphies for this species such as a midorsal scale row consisting of three small scales followed by a single enlarged scale.

Description: Males possess a parietal crest that is rounded with a prominent fleshy base. Two folds of skin attach to the inferior aspect of the parietal crest and anteriorly to the tympanum. Distinctive neck.

Middorsal scale row of dorsum posterior to the shoulders and the anterior aspect of the tail consists of large triangular scales separated at regular intervals by two to four small intervening scales. Ventral body scales are smooth. Tail three times as long as body.

Inferior labials grayish-green. Throat yellow. A yellow stripe originates below the eye passes under the tympanum and disappears on the side of the neck. Another stripe is located on the anterior aspect of the flanks. Dorsum is olive-green and tail has brown spots. Limbs and tail transversed by semicircular black rings.

Ecology & Life History: No ecological or life history data have been reported for this taxon.

Fossil Record: none.

Karyotype: no information available.

Clade: *B. basiliscus* - *B. plumifrons*

Diagnosis: This clade is diagnosed by the elongation of the neural spines in the thoracic, lumbar and caudal regions in males (Character 44) (Fig. 44).

Basiliscus basiliscus (Linnaeus, 1758)

1758 *Lacerta basiliscus* Linnaeus, Syst. Naturae, Ed. 10, 1: 206 - Type locality: "America australi" (Holotype: based upon Seba 1734, vol. 1, Pl. 100, Fig. 1, which was based (fide Taylor 1956) upon MHNP 780).

1768 *Basiliscus americanus* Laurenti (substitute name for *Lacerta basiliscus* Linnaeus, 1758), Synop. Rept., Wien, 50.

1802 *Iguana Basiliscus* — Latreille in Sonnini & Latreille, Hist. nat. Rept., Paris, 1: 258.

1802 *Basiliscus mitratus* Daudin (substitute name for *Lacerta basiliscus* Linnaeus, 1758), Hist. nat. Rept., Paris, 3: 310; Pl. 62.

1830 *Basiliscus basiliscus* — Wagler, Natür. Syst. Amph., München, 148.

1839 *Ophyessa bilineata* Gray (syn. fide Boulenger 1885), Zool. Beechy's Voyage, Rept., London, 94. - Type locality: "coast of South America, Fernando de Noronha" (questioned by Boulenger, Cat. Liz. brit. Mus, 2, 1885, 108) (Holotype: BM unnumbered).

1845 *Basiliscus Americanus* — Gray, Cat. Spec. Liz. Coll. brit. Mus., London, 192.

1845 *Thysanodactylus bilineatus* — Gray, Cat. Spec. Liz. Coll. brit. Mus., London, 194.

1852 *Lophosaura Goodridgii* Gray (syn. fide Boulenger 1885), Ann. Mag. nat. Hist., London, (2) 10: 438. - Type locality: "Quibo" (Holotype: not located).

1876 *Basiliscus guttulatus* Cope (syn. fide Boulenger 1885), J. Acad. nat. Sci. Philad., (2) 8: 156. - Type locality: "Camp at Buhio Soldado, Panama" (Holotype: USNM 25164).

1876 *Basiliscus mitratus* — Cope, J. Acad. nat. Sci. Philad., (2) 8: 125; Pl. 25, fig. 2.

1885 *Basiliscus americanus* — Boulenger, Cat. Liz. brit. Mus., London, 2: 108.

1956 *Basiliscus basiliscus* — Taylor, Kans. Univ. Sci. Bull., Lawrence, 38 1: 175.

Basiliscus basiliscus basiliscus (Linnaeus, 1758)

1962 *Basiliscus basiliscus basiliscus* — Maturana, Bull. Mus. comp. Zool. Harv., Cambridge (Massachusetts), 128 1: 20.

Basiliscus basiliscus barbouri Ruthven, 1914

1914 *Basiliscus barbouri* Ruthven, Proc. biol. Soc. Wash., 27: 9; Fig. 1,2. - Type locality: "Gaira River at Minca, San Lorenzo, Santa Marta Mountains, Colombia (altitude 2200 ft)" (Holotype: UMMZ 45411).

1962 *Basiliscus basiliscus barbouri* — Maturana, Bull. Mus. comp. Zool. Harv., Cambridge (Massachusetts), 128 1: 20.

Etymology: (See *Basiliscus) Basiliscus basiliscus barbouri* was named by Ruthven (1914) in honor of Thomas Barbour, herpetologist in the Museum of Comparative Zoology.

Distribution (Figs. 47, 48): *Basiliscus b. basiliscus* ranges from the southwestern coast of Nicaragua through Costa Rica and Panama into northwestern Colombia. *Basiliscus b. barbouri* is found in northern Colombia and the Santa Marta mountains of northwestern Venezuela.

Diagnosis: Within the basiliscines, Zug (1971) indicated that the coeliac artery is absent in *Basiliscus basiliscus*, whereas it is present in all other *Basiliscus, Corytophanes hernandezi* and in *Laemanctus longipes*. The superior mesenteric arteries have completely taken over the function of the coeliac in *B. basiliscus* (Zug 1971). Within the basiliscines the absence of the coeliac artery is an autapomorphy diagnosing *B. basiliscus*.

Description: Snout region covered by polygonal scales. Parietal blade is triangular or round in males and projects posteriorly past the neck. In females and juveniles the parietal blade is small with only a slight dorsal projection. Dorsal and caudal crests of males are well-developed, supported by the extension of neural spines. The dorsal crest starts at the neck and terminates in the lumbar region with the anterior neural spines

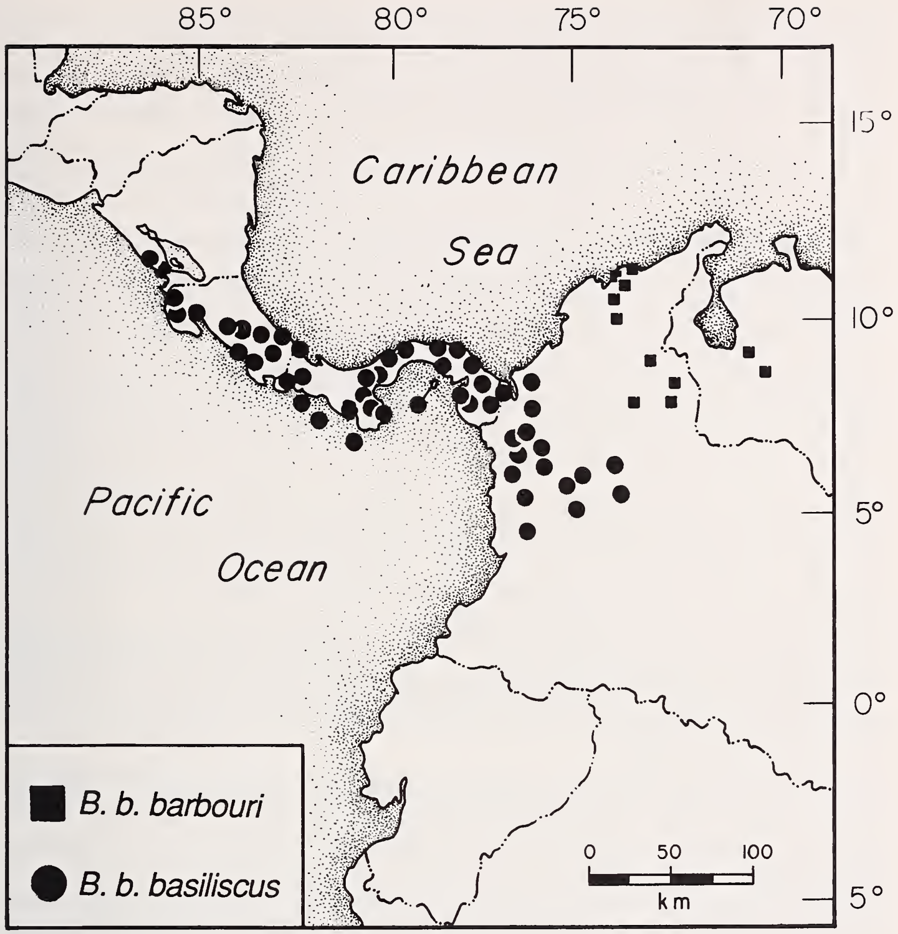


Fig. 47: Distribution of *Basiliscus b. basiliscus* and *B. b. barbouri*. Symbols represent localities of examined specimens.

being shorter than the posterior ones. The greatest height is approximately the same size as the body. Seventeen or eighteen neural spines support the dorsal crest. The caudal crest is supported by 23 neural spines and originates in the sacral region just posterior to the dorsal crest. The caudal crest is short at first and becomes longer towards the middle of the tail to become shorter again. The two crests are distinct with the free border serrated. The dorsal crest itself is covered with thin hexagonal or pentagonal scales arranged in longitudinal rows parallel to the neural spines. In females a mid-dorsal scale row is low and slightly serrated. In males the caudal crest is restricted to the anterior 2/3 of the tail. The scales of the anterior portion of the tail are square and distinctly keeled, posteriorly they become hexagonal. The scales of the terminal portion of the tail are imbricated and show the strongest keeling. Ventral scales smooth. The tail is compressed and is three times as long as the body. The dorsum is brownish-green. A yellow longitudinal band originates from the posterior aspect of the eye and disappears in the neck region. Another stripe of the same color, slightly broader is located inferior and originates from the external nares and passes below the eye to terminate on the shoulder. Diffuse black bands are located on top of the back and in the neck region. Underside is yellow-green, with the throat slightly grayish.

Basiliscus basiliscus barbouri differs from *Basiliscus b. basiliscus* mainly, if not exclusively by the shape of the head crest. Ruthven (1914) described *barbouri* as "having a single (parietal) crest, not erect but pendant on the side of the neck, ribbon-like narrowing rapidly from its base ... to form a narrow lobe."

Ecology & Life History: Ahl (1930) reported maximal snout-vent length of 240 mm for *Basiliscus basiliscus*. Reproduction season is short and restricted to July with clutches of up to 11 eggs (Ahl 1930; Fitch 1970). This is in distinct contrast to *Basiliscus vittatus*, which breeds all year, with peak reproductive activity in late spring and early summer (Fitch 1970, see above). The nest of *Basiliscus basiliscus* consists of a funnel 102 mm in depth and 91 mm at the mouth cavity, exiting at a 60° angle to the surface. Incubation periods vary from 55—60 days (Lieberman 1980). Van Devender (1979) analyzed the growth ecology of *Basiliscus basiliscus* from two study sites in Costa Rica. Female growth rates were sensitive to both seasonal and annual differences in rainfall, varying inversely with reproductive activity. Male growth rates were dependent on the social structure of the population, with highest asymptotic growth at sites with larger, more dominant males. Densities were measured between 200—400 individuals per hectare (Van Devender 1983).

Basiliscus basiliscus is diurnal and inhabits riparian habitats along small, forested streams, with shady, rocky areas being their prefered habitat. Escape behavior involves the typical basilisk habit of dashing across the stream and disappearing in the undergrowth (Evans 1947).

A study of *Basiliscus b. basiliscus* on Barro Colorado Island by Barden (1943b) indicated that the lizards were restricted primarily to 15—20 ft along the shoreline. There were minimal displacements, with 105 ft being the greatest distance travelled, and average distances travelled being 15—20 ft. The surprising find of Barden's (1943b) observations was that no evidence was found to assume territoriality. This would indicate that the expanded parietal blade and the elongated neural spines act primarily for sexual attraction and not territoriality display. However, Fitch (1981) mentioned that territoriality is highly developed in *Basiliscus*, with males fighting fiercely at times.

Fleet & Fitch's (1974) observations of *Basiliscus basiliscus* in Costa Rica indicates that there is an ontogenetic shift in diet from predatory habits to increased herbivory. This coincides with Pough's (1971) findings that most lizards over 200 grams are herbivorous. However, Fleet & Fitch (1974) indicate that *B. basiliscus* is to be considered an opportunistic predator as an adult. This is perhaps best demonstrated by the reported feeding association between *B. basiliscus* and the Mantled Howler Monkeys (*Alouatta palliata* Gray). *Basiliscus basiliscus* were feeding on the fruits of *Anacardium excelsum* dropped by the Howler Monkeys (Glander 1979). In addition, Bennett (1962) lists *B. basiliscus* as commensals in Bayano cuna indian houses in eastern Panamá, and Rand & Robinson (1969) report on predation of *Iguana iguana* nests on Barro Colorado Island by *B. basiliscus*. Echelle et al. (1972) reported juvenile *B. basiliscus* and *B. vittatus* catching fish.

Body temperatures were measured by Brattstrom (1965) for *Basiliscus basiliscus* at 26 °C (air temperature of 26.2 °C).

Böhme (1975) provided evidence for a parthenogenic population of *B. b. barbouri* from the San Gil de Soatá region in Colombia. Evidence for parthenogenesis was based on a collection of four females that ovopositioned after a considerable time of isolation from other males in captivity. All offspring where again females. The breeding group was subsequently infested and died without the evaluation of karyotypes (Böhme, pers. comm.). Even without direct evidence, there is still good evidence of parthenogenesis in this population. This would also be the first reported case of parthenogenesis within "iguanids".

Fossil Record: None.

Karyotype: 2n=36; 12 metacentric macrochromosomes and 24 acrocentric microchromosomes (Paull et al. 1976).

Basiliscus plumifrons Cope, 1876

1876 *Basiliscus plumifrons* Cope, J. Acad. nat. Sci. Philad., (2) 8: 125; Pl. 25, Fig. 1, 1a. - Type locality: "Sipurio, Costa Rica" (Syntypes: USNM 32622-32626; UIMNH 40735).

1956 *Basiliscus plumifrons* — Taylor, Kans. Univ. Sci. Bull., Lawrence, 38 1: 167; Fig. 46.

Etymology: This specific epithet is a compound name derived from the latin words *pluma* (feather) and *frons* (forepart). This is in reference to a small feather-like blade anterior to the larger posterior parietal blade.

Distribution: (Figs. 46, 48). Central Nicaragua south to low and moderate elevations of Atlantic versant of Costa Rica to northwestern Panamá.

Diagnosis: This clade is diagnosed by the *X*-pattern of the hyoid apparatus, in which the second ceratobranchial is elongated (Character 37) (Fig. 44). The long second ceratobranchial was also identified in the *cristatus percarinatus* clade (Fig. 42) and is interpreted as a convergence.

Description: Head crests of males are bi-lobed, consisting of a principal posterior portion and an accessory anterior portion. The parietal crests are covered with large smooth scales, and the borders are acute. The top of the head is covered with small scales, which are weakly or not at all keeled. The dorsal scales are smaller than the ventral, but a little larger than the lateral, and faintly keeled. The dorsal crest of males is highest behind the middle; its elevation exceeds that of the body by one-third. The crest is supported by fifteen rays and covered by smooth scales. Ventral scales are smooth,

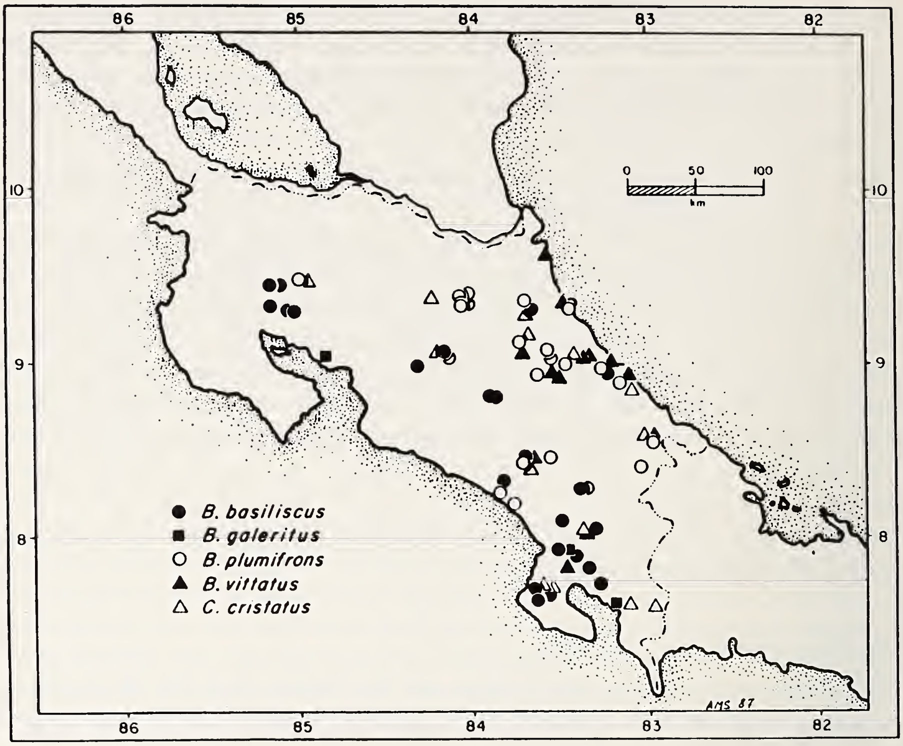


Fig. 48: Localities of examined and reported specimens of basiliscines in Costa Rica. (Drawing courtesy of A. Simons).

with scales of the upper surface of the limbs equally large. The caudal crest is also elevated, and includes fifteen rays; it is covered by thin subequal scales, of which there are eight in a vertical row. Scales of the tail are strongly keeled below, weakly keeled elsewhere. Color dark green, becoming blue. No longitudinal or transverse bands on the head, body or throat, but rather a row of white-yellow spots from the axilla to the groin, and a similar row along the upper side of the back, which is lacking in some specimens. Three vertical pale-bordered black spots on the dorsal crest, which may be obsolete in some individuals. Crested part of the tail is green, the remainder yellowish, with brown rings on the proximal part.

Ecology & Life History: *Basiliscus plumifrons* is known from below 100 m in tropical moist forest. As with the other species of this genus, it is semi-arboreal and semi-aquatic, occupying shaded or closed forest situations.

Hirth (1962) examined *Basiliscus plumifrons* from Tortuguero beach in Costa Rica. His findings with regard to ecological attributes are consistent with the findings of the other species of this genus. No vegetation was consumed by specimens with snout-vent lengths of less than 135 mm. Juveniles are primarily insectivorous whereas subadults and adults have a mixed diet. The presence of crustaceans in stomachs reflect riparian habits.

Fossil Record: None.

Karyotype: Information not available.

Clade: *Corytophanes-Laemanctus*

The *Corytophanes-Laemanctus* node is supported by eighteen non-homoplastic autapomorphies clade (Fig. 49):

1) Septomaxillae are small slivers of bone lying within the nasal cavity, not contacting at midline (character 2).

2) Frontal bone flat in mid-sagittal view (*Laemanctus*), or anterior and posterior aspects of frontal bones curve dorsally (*Corytophanes*) (character 11).

3) Posterior angle of jugal expanded posteroventrally, with posteroventral aspect of jugal approaching posterodorsal aspect (character 15).

4) Lateral shelves of adductor crest extend along lateral aspect of parietal (character 18).

5) Parietal Y-shaped with anterolateral borders at base of parietal blade progressing posteriorly with increasing size to form a 60° angle in adults (character 19B).

6) Parietal blade develops embryonically (character 20).

7) The parietal blade well developed in both sexes (character 21).

8) Parietal blade expanded ventrally from a dorsal bony base (character 22B).

9) Dorsal process of the squamosal with prominent dorsal "hook" that contacts the supratemporal (character 23).

10) Medial concha of quadrate is constricted (character 25).

11) Posterior crest of the quadrate is vertical with no anterior curvature (character 26).

12) Angular process of the articular small in juveniles and well-defined only in large individuals (well-defined transforming ontogeny from small process to large one) (character 35).

13) Angular process in a horizontal plane (character 36).

14) Rostral portion of skull spatulate or keel-shaped (character 39).

15) One or more presacral vertebrae lacking ribs, i.e., presence of lumbar vertebrae (character 41).

16) Caudal autotomy lost (character 42).

17) Dorsal head of M. adductor mandibulae externus profundus reduced (character 56).

18) Superciliary scales show the intermediate condition (character 57B).

In addition, Etheridge & de Queiroz (1988) list the following characters indicative of the monophyly of this clade: presence of a sharp canthal ridge (Fig. 40) and the ventrally compressed and expanded hemal arches (Etheridge & de Queiroz 1988).

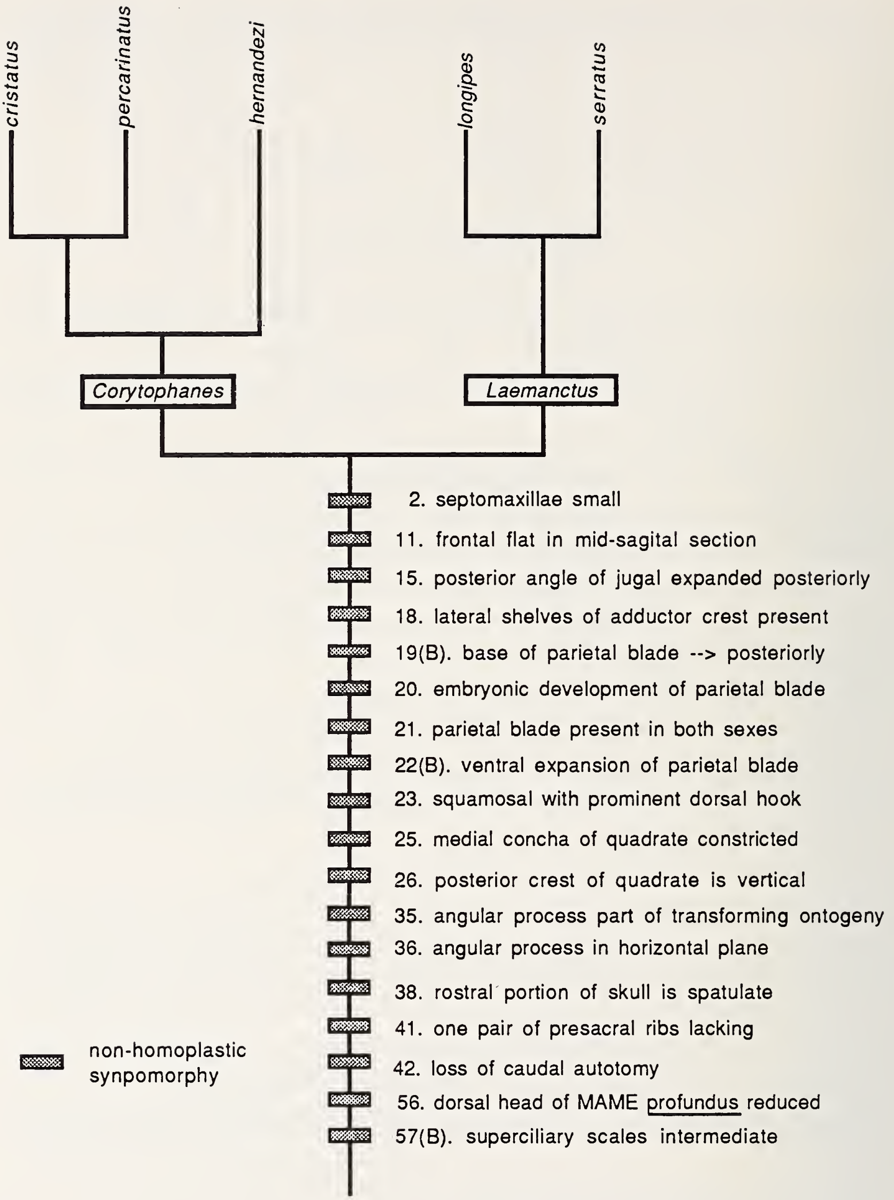


Fig. 49: Reconstructed phylogeny of *Corytophanes-Laemanctus* node. This clade is supported entirely by non-homoplastic synapomorphies.

Corytophanes Boie, 1827

1827 *Corytophanes* Boie in Schlegel, Isis von Oken, Jenna, (1826) 20: 290. - Type species (by monotypy): *Agama cristata* Merrem, 1821.

1830 *Corythophanes* Wagler (invalid emendation of *Corytophanes* Boie, 1827), Natür. Syst. Amph., München, 151.

1830 *Chamaeleopsis* Deppe, Preis-Verzeich. Sauget., Vög., Amph., Fische u. Krebse, Berlin, 3. - Type species (subsequent designation by Fitzinger 1843): *Chamaeleopsis hernandesii* Deppe, 1830.

1831 *Chamoeleopsis* - Wiegmann (emendation of *Chamaeleopsis* Deppe, 1830), in Gray in Cuvier edit. Griffith, Anim. Kingd., London, 9: 45.

1843 *Corythophanes (Chamaeleopsis*) - Fitzinger, Syst. Rept., Wien, 1: 16.

1843 *Corythophanes (Corytophanes*) - Fitzinger, Syst. Rept., Wien, 1: 16.

1885 *Corythophanes* — Boulenger, Cat. Liz. brit. Mus., London, 2: 101.

Etymology: Derived from the Greek *Korus*, genetive *korythos* meaning helmet and *phaino* meaning conspicuous, in reference to the conspicuous parietal blade. Although there was a spelling error in the original description by Boie, the spelling of *Corytophanes* is only indicated once in the original description. Therefore Wagler's emendation to *Corythophanes* is not valid. The orthography of this genus is somewhat puzzling. The greek word korystes means "one armed with a helmet." Wagler's emendation perhaps should therefore have been *Corystophanes* rather than *Corythophanes*.

Distribution: (Figs. 48, 51). Central Veracruz and San Luis Potosí, México to northwestern Colombia.

Diagnosis: This clade is the best supported node in the cladogram, and is defined by the following 21 non-homoplastic autapomorphies, together with two reversals (Fig. 50).

1) Roof of the nasal capsule consistently uncovered at junction of frontal and nasals (character 1).

2) Nasals separated for more than 50 % of their length by the premaxilla (character 3).

3) Posterior aspect of nasals pointed (character 4).

4) Small area of contact between prefrontals and nasals, with nasals separated anteriorly from prefrontals by nasal process of maxilla (character 5).

5) Anterolateral spines present on prefrontals that project anteriorly over nasal process of maxilla (character 6).

6) Groove at prefrontal-lacrimal junction lost. This represents a reversal to the plesiomorphic condition (character 7) (Fig. 42).

7) Palatine process of the pterygoid extends anteriorly beyond the infraorbital foramen (character 9).

8) Quadrate process of pterygoid expanded terminally (character 10).

9) Squamosal process of the jugal broad (character 13).

10) Jugals and squamosals in broad contact or overlapping (character 14).

11) Supraorbital processes show intermediate condition, in which prefrontals have posteriorly directed processes and the postorbitals have anteriorly directed processes that do not meet (Character 16).

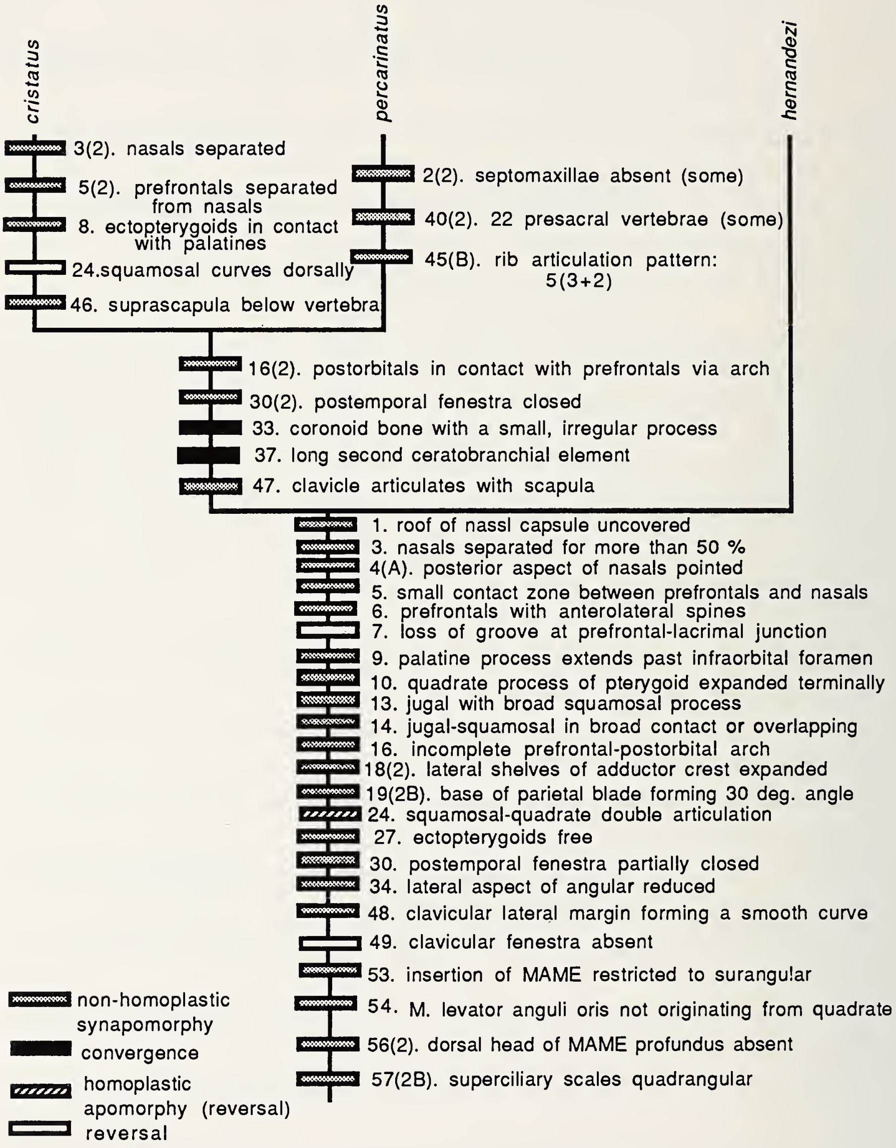


Fig. 50: Reconstructed phylogeny of *Corytophanes*.

12) Lateral shelves of adductor crest large, expanded laterally to partially overlie the supratemporal opening (character 18).

13) Parietal Y-shaped with anterolateral borders at base of parietal blade progressing posteriorly with increased size to form a 30° angle in adults (character 19B).

14) Squamosal straight overlapping anterodorsal border of lateral flange of quadrate, creating a double articulation (character 24).

15) Dorsal aspect of the epipterygoids free (character 27).

16) Posttemporal fenestrae partially closed due to limiting angles of squamosal processes of parietal and dorsal expansion of bony labyrinth (character 30).

17) Lateral aspect of angular reduced, not extending between coronoid process and articular fossa (character 34).

18) Lateral margin of clavicle irregular or forming a smooth curve. The polarity decision of this character is contrary to that of Etheridge & de Queiroz (1988), but it is the most parsimonious assumption considering the ingroup topology (character 48).

19) Clavicular fenestration lost. This is a reversal to the plesiomorphic condition (character 49) (Fig. 42).

20) Mandibular insertion of the M. adductor mandibulae externus restricted to surangular (character 53).

21) M. levator anguli oris does not originate from tympanic crest of the quadrate (character 54).

22) Dorsal head of the M. adductor mandibulae externus profundus lost (character 56).

23) Superciliary scales show intermediate condition as defined by Etheridge & de Queiroz (1988) (character 57-2B).

In addition, the reduction, of the preorbital portion of the skull is listed by Etheridge & de Queiroz as an autapomorphy for this clade. This is hypothesized as being a paedomorphic character. The uncovered roof of the nasal capsule and the closure of the postemporal fossa, are further evidence that *Corytophanes* is paedomorphic. Both are found in many juvenile "iguanids".

Description: Nostrils oriented posterolaterally. Parietal crest consisting of two sharp lateral ridges that unite posteriorly. Bony supraorbital arch formed by pre- and postfrontal. The nuchal crest small or large, connecting the posterior aspect of the parietal crest with a low dorsal crest. Tympanum distinct. Gular fold is confluent with antehumeral fold. Body laterally compressed, covered with imbricate smooth or keeled scales. A more or less distinct lateral fold along each side of the body. No femoral or preanal pores. Tail long, feebly compressed. Elongated limbs covered with large keeled scales.

Corytophanes hernandezi (Deppe, 1830)

1830 *Chamaeleopsis Hernandesii* Deppe, Preis-Verzeich. Sauget., Vög., Amph., Fische u. Krebse, Berlin, 3. - Type locality: "Mexico" (Syntypes: ZMB 545 (3)). - Restricted type locality (Smith & Taylor 1950): "Jalapa, Veracruz".

1834 *Ch.[amaeleopsis] Hernandesii* — Wiegmann, Herp. Mex., Saur. Spec., Berlin, 1: 38; Pl. 6.

1837 *Corythophanes chamaeleopsis* Duméril & Bibron (substitute names for *Chamaeleopsis Hernandesii* Wiegmann, 1834), Erpét. gén., Paris, 4: 176.

1843 *Corythophanes (Chamaeleopsis) Hernandesii* — Fitzinger, Syst. Rept., Wien, 1:52.

1845 *Chamaeleopsis Hernandesii* — Gray, Cat. Spec. Liz. Coll. brit. Mus., London, 194.

1856 *Corythophanes Hernandezii* — Lichtenstein, Nom. Rept. et Amph. Mus. Zool. Berol., Berlin, 8.

1874 *Corythophanes mexicanus* Bocourt (substitute name for *Chamaelopsis Hernandesii* Wiegmann, 1834), Miss. Sci. Mex., Rept.: 122, pl. 17; fig. 1.

1885 *Corythophanes hernandesii* — Boulenger, Cat. Liz. brit. Mus., London, 2: 103.

1960 *Corythophanes hernandezii* — Alvarez Del Toro, Rept. Chiapas, Tuxtla Gutiérrez, 84; unnumb. figs.

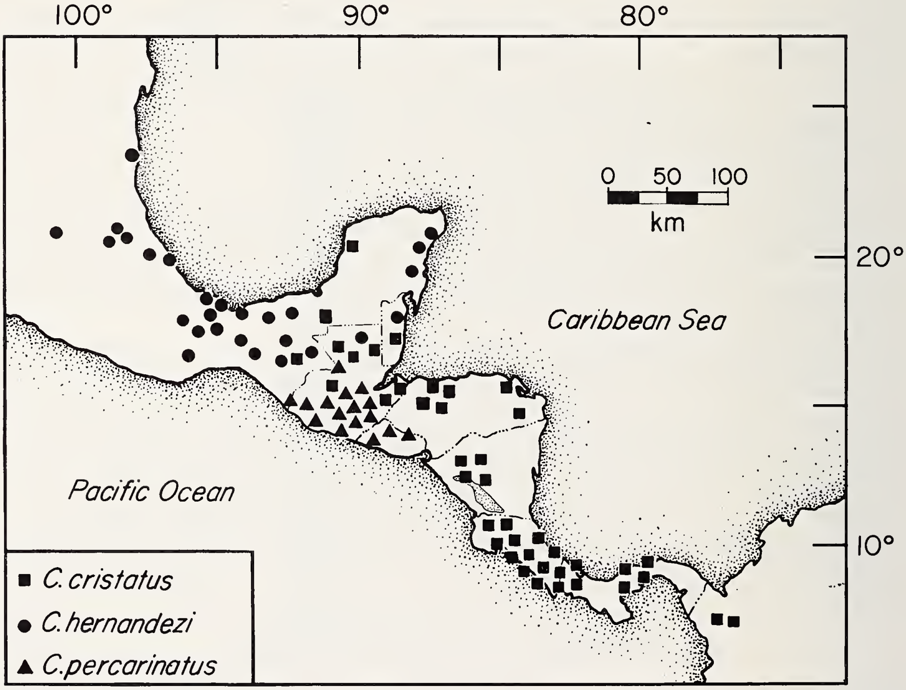


Fig. 51: Geographical distribution of *Corytophanes*. Symbols represent localities of examined specimens.

Etymology: This species was named by Deppe (1830) in honor of Francisco Hernandez.

Distribution: (Fig. 51). Caribbean versant of central Veracruz, México southward to northern Guatemala.

Diagnosis: *Corytophanes hernandezi* is diagnosed by the presence of a single round scale organ at the posterior edge of the supralabial scales (Lang, in prep.).

Description: Upper head scales keeled or striated. A large bony spine (squamosal spine) above the tympanum. Gular scales elongate, strongly keeled, forming longitudinal series separated by granules. Nuchal crest small, following the contour of the bony parietal blade and not continuous with the low dorsal crest. Ventral scales large, strongly keeled. Caudal scales strongly keeled.

Dorsum olive-brown with irregular blackish brown spots or cross bands. Venter brownish with darker spots.

Ecology & Life History: Very little ecological information is available for this species. *C. hernandezi* is highly arboreal and occurs from sea level to approximately 1300 m in tropical and subtropical wet forests. The reproductive season is in September with a gestation period of 67 days. A single clutch size of seven eggs is reported by Pérez-Higareda (1981).

Fossil Record: None.

Karyotype: 2n=36; 12 metacentric macrochromosomes and 24 acrocentric microchromosomes (Schwenk et al. 1982).

Clade: *cristatus-percarinatus.*

Diagnosis: The *cristatus-percarinatus* sister-taxon relationship is supported by the following three non-homoplastic autapomorphies, with two convergences (Fig. 50):

1) Bony supraorbital process complete forming an arch overlying the dorsolateral aspect of the eyes (character 16).

2) Posttemporal fossa entirely closed (character 30).

3) Coronoid bone with a small irregular process overlapping the posterolateral surface of dentary (character 33). This is considered a convergence with *Basiliscus* (Fig. 42).

4) Hyoid apparatus of the *X*-type with long second ceratobranchial (character 37). This is convergent with *Basiliscus plumifrons* (Fig. 42).

5) Dorsal aspect of clavicle articulates with scapula (character 47).

Corytophanes percarinatus Duméril, 1856

1856 *Corythophanes percarinatus* Duméril, Arch. Mus. hist. Nat., Paris, 8: 518; Pl. 20, Fig. 3,3a. - Type locality: “Ascuintla dans l’Amer. centrale” = Escuintla, Guatemala, according to Stuart, Misc. Publ. Mus. Zool. Univ. Mich., 122, 1963: 67. (Holotype: MHNP 2117).

1873 *Corythophanes percarinatus* — Bocourt in Duméril & Bocourt, Miss. Sci. Mex., Rept., Paris, 3: 120; Pl. 17, Fig. 2.

1952 *Corythophanes percarinatus* — Mertens, Abh. senckenb. Naturforsch. Ges., Frankfurt a. M., 487: 46; Pl. 12, Fig. 71.

Etymology: The name *percarinatus* is derived from the latin word *carina* (= keeled; carinate), in reference to the carinate head scales.

Distribution: (Fig. 51). Pacific versant of Southern México from the Isthmus of Tehuántepec through Guatemala to El Salvador on the pacific coast.

Diagnosis: This taxon is diagnosed by a single autapomorphy (Fig. 50). *Corytophanes percarinatus* has only three true ribs connected to the sternum, plus two xiphisternal ribs [5(3+2) pattern]. In some individuals the septomaxilla is absent and others have only 22 presacral vertebrae (see above).

Description: Upper headscales keeled or striated. A short series of enlarged keeled scales is present from the orbit to above the tympanum. A large bony spine (squamosal spine) above the tympanum. Gular scales elongate, strongly keeled, forming longitudinal series separated by granules. Short nuchal crest with serrated dorsal ridge. Ventral scales large strongly keeled. Caudal scales strongly keeled.

Dorsum olive-brown, with irregular blackish-brown spots or cross bands. Broad black bands radiating from the eye, not extending beyond the orbit. Venter whitish olive.

Ecology & Life History: *Corytophanes percarinatus* is viviparous, a condition that has evolved as an adaptation to the relative cold climates in the mountains of Guatemala. Other "iguanid" genera including *Sceloporus, Phrynosoma* and *Liolaemus* have viviparous species living in high-latitude or high-altitude environments (McCoy 1968b). In Alta Verapaz, México, it only occurs in the pine and pine-savanna lands (Stuart 1948).

Little is known about the reproductive cycles and reproductive strategies of this species. Females do not reach sexual maturity or breed until the second year, with an average single annual reproductive potential of 7.1 eggs per clutch (McCoy 1968b; Fitch 1970).

Fossil Record: None.

Karyotype: No information available.

Corytophanes cristatus (Merrem, 1821)

1821 *Agama cristata* Merrem, Tent. Syst. Amph., Marburg, 49. - Type locality: "Ceylona" (Holotype: based upon Seba 1734, 1: 147; Pl. 94, Fig. 4). - Restricted type locality (Smith & Taylor 1950): "Orizaba, Veracruz."

1827 *Corytophanes cristatus* — Boie (by inference) in Schlegel, Isis von Oken, Jena, (1826) 20: 290.

1833 *Corythophanus cristatus* — Gravenhorst, Nova Acta Akad. Caesar. Leop.-carol., Halle, 16: 938; Pl. 65, Fig. 6—10.

1843 *Corythophanes (Corythophanes) cristatus* — Fitzinger, Syst. Rept., Wien, 1: 52.

1885 *Corythophanes cristatus* — Boulenger, Cat. Liz. brit. Mus., London, 2: 101.

1956 *Corythophanes cristatus* — Taylor, Kans. Univ. Sci. Bull., Lawrence, 38 1: 161; Fig. 45.

Etymology: The term *cristatus* is derived from the Latin *crista* meaning tufted or crested.

Distribution: (Figs. 48, 51). Central Vera Cruz and the west coast of the Yucatán peninsula through Costa Rica to northwestern Colombia.

Diagnosis: *Corytophanes cristatus* is defined by the following four non-homoplastic autapomorphies, in addition to a single reversal (Fig. 50):

1) Nasals completely separated by premaxilla (character 3).

2) Prefrontals are completely separated from the nasals, with frontals and maxillae in contact (character 5).

3) Palatines in contact with ectopterygoids below orbits, excluding maxillae from infraorbital foramen (character 8).

4) Anterior aspect of squamosal curves dorsally and does not contact or overlap anterodorsal aspect of the quadrate. This is a reversal to the plesiomorphic condition (character 24) (Fig. 42).

5) Suprascapular cartilages do not reach the level of vertebral column (character 46).

Description: Upper head scales smooth and small, irregular, no enlarged occipital scales. Gular region with longitudinal series of small scales separated by granules. Nuchal crest with serrated edge. Ventral scales moderately large, strongly keeled imbricate, arranged in transverse series. Tail more than twice as long as the body.

Dorsum olive- or reddish brown, with irregular blackish-brown spots or cross bands. A white spot is present on the elbow and at the base of the arm. Blackish streaks radiate from the eye extending down to the lower lip. Venter pale brown with a few dark spots.

Ecology & Life History: *C. cristatus* is arboreal and occurs in tropical and subtropical wet forests from sea level to 1300 m. Maximal reported longevity was 2 years and 5 months for a captive specimen (Altman & Ditmer 1962). There are two reports on clutch size of six (Ream 1965) and five eggs (Bock 1987). Bock (1987) reported a nest measuring 50 mm in diameter and 95 mm in depth. The top egg in the clutch mass was 20 mm in length. Bock (1987) suggested that female *Corytophanes cristatus* use the top of their head to excavate the nests.

Corytophanes cristatus is an extreme sit-and-wait predator that usually perches in an upright position. Stomach content analyses suggest that *cristatus* ordinarily feeds infrequently, perhaps not even daily and is selecting primarily large arthropods (Andrews 1979). Barbour (1923) indicated that *C. cristatus* "... (its) actions (are) singularly chameleon-like." *Corytophanes cristatus* is also a good example of catalepsy or passive concealment. This animal remains inconspicuous among the branches and foliage of an arboreal environment by eliminating all minor movements not directly associated with a change of position (Davis 1936).

In the threat display *Corytophanes cristatus* orients itself lateral to the threat. It increases its appearance by straigtening its limbs, flattening its body, opening its mouth and by holding its head straight to stretch the nuchal membrane (Davis 1936; Mertens 1946).

Fossil Record: None.

Karyotype: 2n=36; 12 metacentric macrochromosomes and 24 acrocentric microchromosomes (Schwenk et al. 1982).

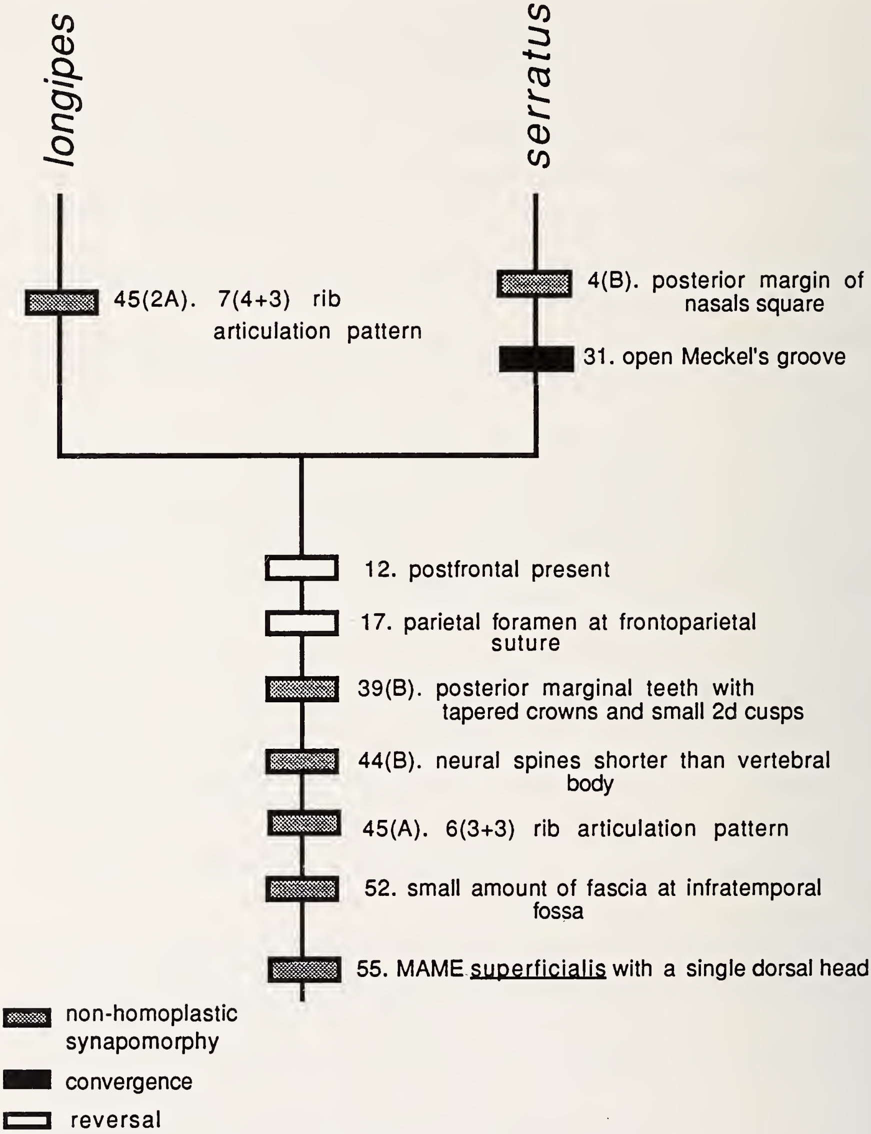


Fig. 52: Reconstructed phylogeny of *Laemanctus*.

Laemanctus Wiegmann, 1834

1834 *Laemanctus* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 16. - Type species (subsequent designation by Fitzinger 1843): *Laemanctus longipes* Wiegmann, 1834.

1843 *Laemanctus (Laemanctus)* — Fitzinger, Syst. Rept., Wien, 1:63.

Etymology: Wiegmann named *Laemanctus* from the greek words *laimos* (neck) and *ancho* (compressed) in reference to the tapered crowns of the marginal teeth.

Distribution: (Figs 54 & 55). This genus occurs from central Tamaulipas southward through the Yucatán peninsula into Guatemala and northwestern Honduras.

Diagnosis: This study reveals the following characters supporting the monophyly of this taxon (5 non-homoplastic autapomorphies and 2 reversals) (Fig. 52):

1) Presence of free postfrontals (character 12). This is a reversal from the apomorphic condition found at the basiliscine basal node (Fig. 42).

2) Parietal foramen located at frontoparietal suture. This is a reversal from the apomorphic condition, in which the foramen was located entirely within the frontal bone (character 17) (Fig. 42).

3) Crowns of the posterior marginal teeth tricuspid, with tapered crowns and reduced lateral cusps (character 39B).

4) Neural spines shorter than height of vertebral body (character 44B).

5) 6(3+3) rib articulation pattern (character 45A).

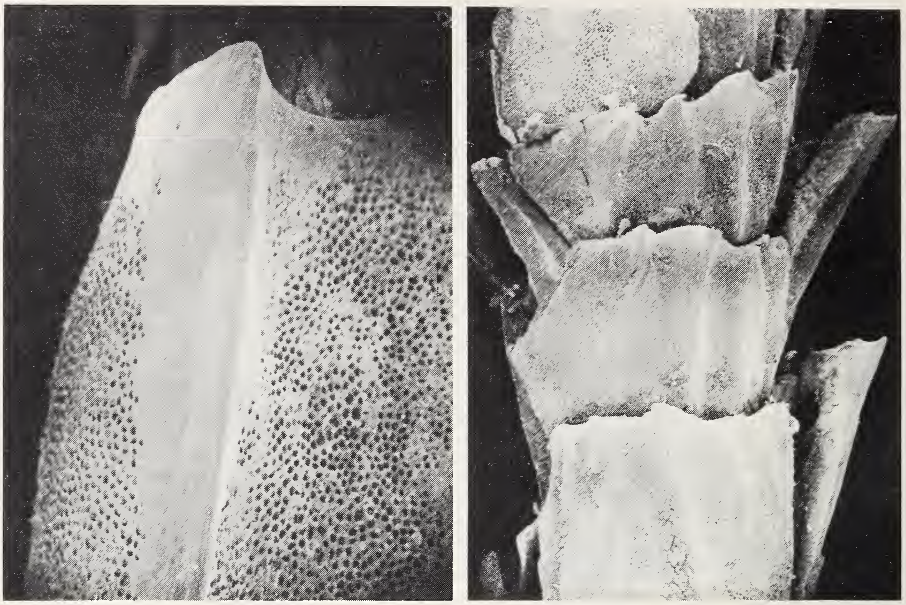
6) Small amount of fascia present at posterodorsal corner of infratemporal fossa (character 53).

7) M. adductor mandibulae externus superficialis with a single dorsal head (character 55).

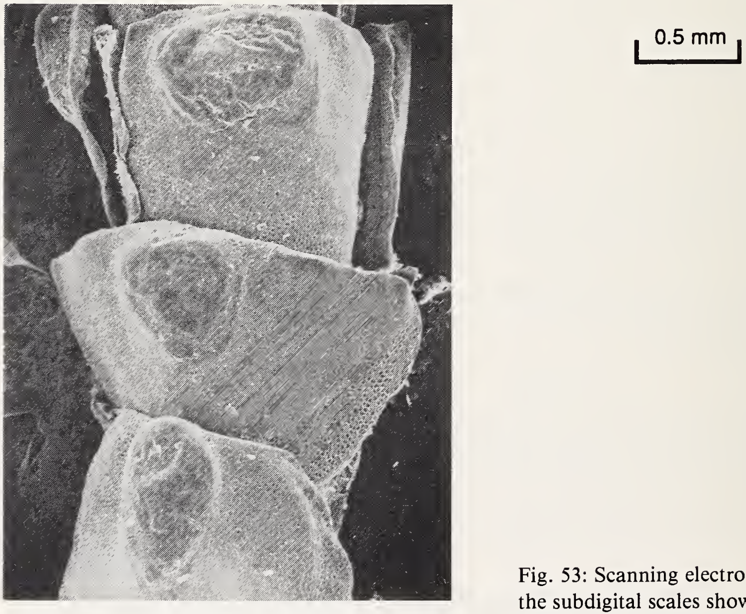
In addition, Boulenger (1885), Smith (1944) and Etheridge & de Queiroz (1988) mention the reduction of the number of keels on the subdigital scales in this taxon to one. Smith & Laufe (1945) also indicates that the presence of distinct keratinized knobs on the plantar surface of the pedal digits (Fig. 53). Etheridge & de Queiroz (1988) indicate that the extensive development of scale impressions on the head of *Laemanctus* is indicative of its monophyletic status.

Description: Both males and females have a flat-topped parietal region (casque) projecting over the neck. The gular fold may be absent or present, but there is no gular pouch. Laterally-compressed body, extremely long round tail, legs and toes. The adpressed hind limbs reach beyond the tip of the snout. Infradigital lamellae with a median tubercle-like keel. Ventral scales keeled and imbricating. No femoral or preanal pores.

In preservatives the green colors usually change to purple, with some of the older specimens turning light pink.



Basiliscus galeritus *Corytophanes percarinatus*



Laemanctus serratus

Fig. 53: Scanning electron micrograph of the subdigital scales showing plantar surface.

Laemanctus longipes **Wiegmann, 1834**

1834 *L.[aemanctus] longipes* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46; Pl. 4. - Type locality: "Jalapam" (Holotype: ZMB 494).

1843 *Laemanctus (Laemanctus) longipes* — Fitzinger, Syst. Rept., Wien, 1: 63.

1877 *Laemanctus longipes* — Boulenger, Bull. soc. Zool. Fr., Paris, 2: 464; Pl. 7, Fig. 2, 2a.

1885 *Laemanctus longipes* — Boulenger, Cat. Liz. brit. Mus., London, 2: 105.

1968 *Laemanctus longipes* — McCoy, Copeia, 4: 666.

Laemanctus longipes longipes **Wiegmann, 1834**

1968 *Laemanctus longipes longipes* — McCoy, Copeia, 4: 667.

Laemanctus longipes deborrei **Boulenger, 1877**

1877 *Laemanctus de Borrei* Boulenger, Bull. soc. Zool. Fr., Paris, 2: 465; Pl. 7, Fig. 1a—b. - Type locality: "Tabasco (Méxique)" (Syntypes: IRSNB 2.003—4).

1885 *Laemanctus deborrii* — Boulenger, Cat. Liz. brit. Mus., London, 2: 106.

1887 *Laemanctus deborrei* — Cope, Bull. U. S. natn. Mus., Washington, 32: 33.

1968 *Laemanctus longipes deborrei* — McCoy, Copeia, 4: 668; Fig. 2.

Laemanctus longipes waltersi **Schmidt, 1933**

1933 *Laemanctus waltersi* Schmidt, Publs. Field Mus. nat. Hist., zool. Ser., Chicago, 20: 20. - Type locality: "Lake Ticamaya, east of San Pedro, between the Chamelecon and Ulua Rivers, Honduras" (Holotype: FMNH 5213)

1968 *Laemanctus longipes waltersi* — McCoy, Copeia, 4: 670.

Etymology: The species name *longipes* is in reference to the elongated feet. *Laemanctus longipes waltersi* was named by Schmidt in honor of Leon L. Walters with whom he collected the type specimen. *Laemanctus longipes deborrei* was named by Boulenger in honor of M. Preudhomme de Borre, curator at the Royal Belgian Museum of Natural History.

Distribution: (Fig. 54). *Laemanctus l. longipes* ranges from the eastern side of the Plateau of México to the Isthmus of Tehuántepec. *Laemanctus longipes deborrei* ranges from the foothills on the south side of the Isthmus of Tehuántepec, across the base of the Yucatán peninsula southward into Guatemala. *Laemanctus longipes waltersi* is restricted to northern slopes of Sierra de Pija, Honduras.

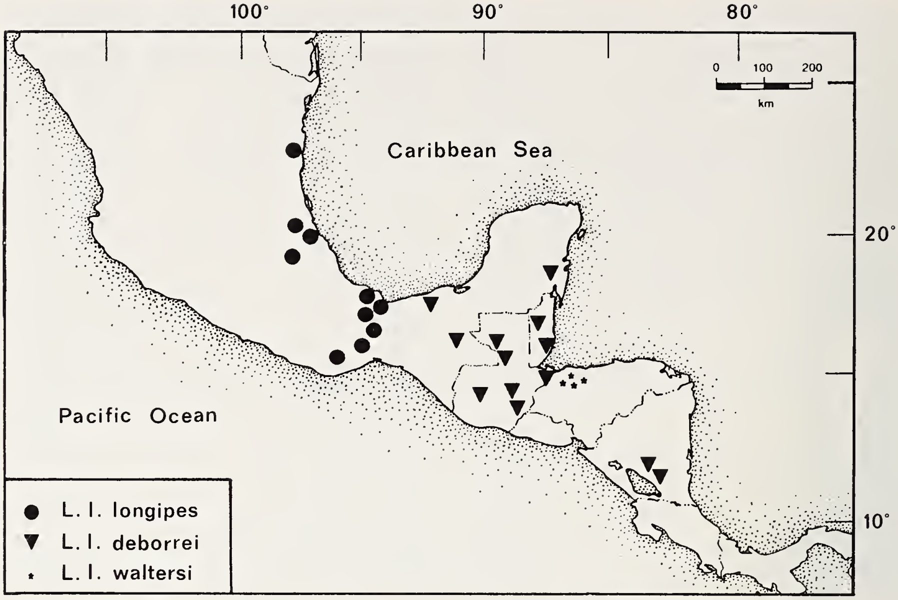


Fig. 54: Geographical distribution of *Laemanctus longipes*. Symbols represent localities of examined specimens.

Diagnosis: There is only a single apomorphic feature that defines this taxon (Fig. 52). All specimens examined have a 7(4 + 3) sternal rib articulating pattern (character 45A).

Description: The head scales are slightly carinated. The gular scales have more than one keel. Antehumeral fold poorly developed. Ventral scales sharply keeled, dorsal scales smooth. Dorsum bright green crossed by five or six bars of dark green sometimes outlined in black, which continue on the tail as bands of dark rings. The top of the head is yellow-green. The edge of the casque is outlined by black markings. A light yellow-white stripe passes from eye to foreleg bordered superiorly by a brown band. A yellow streak from the axilla to the groin is sometimes broken up. A yellow spot is present on each side of base of tail. The venter is light green. *Laemanctus l. longipes*, has a complete gular fold and small body scales (50—59 around mid-body). *Laemanctus l. deborrei* are moderate sized lizards characterized by medium sized body scales (42—47 scales around mid-body). The gular fold is well-developed and continuous. *Laemanctus l. waltersi* is smaller in size than the other two subspecies of *Laemanctus longipes*. It is characterized by very large body scales (30—32 scales around mid-body). Gular fold absent or interrupted.

Ecology & Life History: *Laemanctus longipes* occurs from sea level to about 600 m in tropical moist and dry forest (Martin 1958; Stuart 1966). It is arboreal and diurnal. Maximal reported snout vent length for this species is 150 mm (Ahl 1930).

Laemanctus longipes is oviparous. Duellman (1963) reported finding a nest of *L. l. deborrei* in late June, with an average egg size of 24.2 by 15.4 mm. McCarthy (1982) reported average dimensions for the eggs: 25.4 mm length x 14.2 mm width with an average of 2.4 grams per egg. Only a single report of clutch sizes of four and five exist (Duellman 1963).

Both species of *Laemanctus* seem to replace each other geographically particularly in the Yucatán Peninsula (Figs. 54 & 55). This was cited as an example of competitive exclusion by Lee (1980).

Vaillant (1896) was the first to report on coloration changes in *Laemanctus longipes.* Stuart (1948), Reyst (1954) and Klinghöffer & Scherpner (1957) have also reported on metachrosis in *Laemanctus.*

Some confusion remains concerning the terrestrial locomotion of *Laemanctus.* McCoy (1968a) has given the best summary of the ecology of this genus and his field observations indicate that *Laemanctus* is capable of bipedal locomotion. This supports the reports of Martin (1958). Snyder (1954; see above) also regarded *Laemanctus* as bipedal based on its general similarity to *Basiliscus.* Duellman (1963; 1965) collected both species of *Laemanctus* from bushes. The retention of a cylindrical body form and the articulation of the clavicle on the suprascapular cartilages, suggest that *Laemanctus* is not truly arboreal, but rather semi-arboreal.

Fossil Record: None.

Karyotype: No information available.

Laemanctus serratus Cope, 1864

1864 *Laemanctus serratus* Cope, Proc. Acad. nat. Sci. Philad., 16: 176. - Type locality: “Orizaba Valley, México” (Holotype: RMNH 2845).

1877 *Laemanctus serratus* — Boulenger, Bull. soc. Zool. Fr., Paris, 2: 463; Pl. 7, Fig. 3.

1885 *Laemanctus serratus* — Boulenger, Cat. Liz. brit. Mus., London, 2: 104.

1968 *Laemanctus serratus* — McCoy, Copeia, 4: 671.

Laemanctus serratus serratus Cope, 1864

1968 *Laemanctus serratus serratus* McCoy, Copeia, 4: 672; Fig. 4.

Laemanctus serratus alticoronatus Cope, 1865

1865 *Laemanctus alticoronatus* Cope, Proc. Acad. nat. Sci. Philad., 17: 192. - Type locality: “Yucatan, near Merida” (Holotype: USNM 12283).

1885 *Laemanctus alticoronatus* — Boulenger, Cat. Liz. brit. Mus., London, 2: 105.

1968 *Laemanctus serratus alticoronatus* — McCoy, Copeia, 4:674.

Laemanctus serratus mccoyi Pérez-Higareda & Vogt, 1985

1985 *Laemanctus serratus mccoyi* Pérez-Higareda & Vogt, Bull. Maryland Herp. Soc. 21: 140. - Type locality: El Acuyal, municipality of Catemaco, Veracruz, México (Holotype: Univ. Nac. Auton. de Méx. - Los Tuxtlas No. 1326).

Etymology: Both *serratus* and *alticoronatus* (from the latin *alter* and *corona)* are named in reference to the serrated posterior aspect of the head in this species. *Laemanctus serratus mccoyi* was named in honor of Dr. Clarence J. McCoy of the Carnegie Museum.

Distribution: (Fig. 55). The distribution of *L. serratus* appears to be correlated with the distribution of dry tropical forests. It ranges from extreme northeastern Guanajuato along the lowlands south around the gulf of México into Yucatán. *Laemanctus serratus serratus* is found in the Atlantic lowlands of México. It occurs from the Rio Soto le Marina in Central Tamaulipas, southward through San Luis Potosí, Veracruz, Oaxaca and Chiapas, eastern México. *Laemanctus serratus mccoyi* is only known from its type locality. *Laemanctus serratus alticoronatus* is found in the northwestern third of the Yucatán peninsula.

Diagnosis: This taxon is diagnosed by a single non-homoplastic apomorphy together with a convergence (Fig. 52):

1) Posterior margin of nasal bones distinctly square (character 4B).

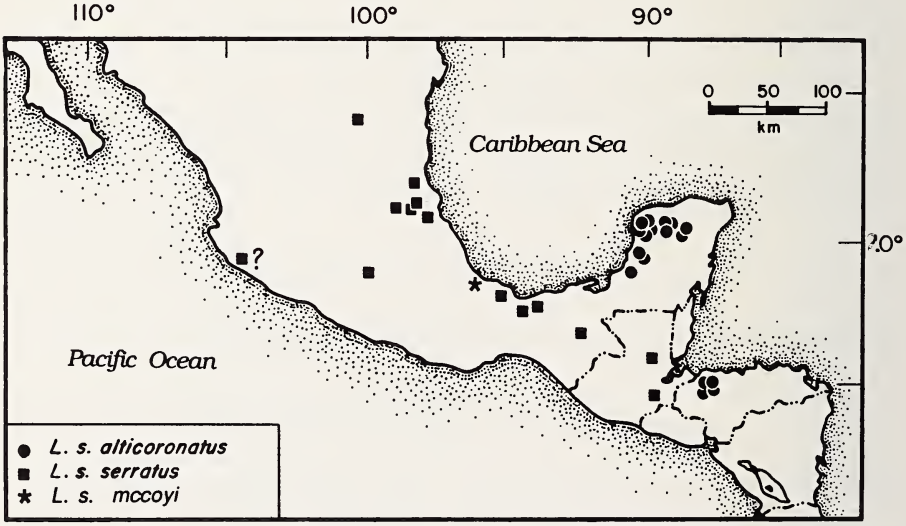


Fig. 55: Distribution map of *Laemanctus serratus*. Symbols represent localities of examined specimens.

2) Meckel's groove open between anterior end of splenial and mandibular symphysis (character 31). This is convergent with *Basiliscus vittatus* (Fig. 42).

Description: Nasals single, with nostril centrally located. Twelve infralabials with 14—15 supralabial scales. The anterior head scales are 4 to 5 times larger than the posterior head scales and consist of 3 to 4 pairs of enlarged scales between the rostral and the orbits. A large azygous scale is variably present. Parietal eye not distinct in a small scale. Dorsal head scales are strongly rugose or tubercular. The posterior aspect of the head consists of triangular shaped scales forming a distinct serration. The scales of the posterior head serration are striate. Gular fold continuous but shallow. Antehumeral fold absent.

Middorsal scale row forming a projecting serrated crest of triangular scales. Dorsal and ventral scales are keeled.

The color pattern of *Laemanctus serratus* is highly variable. The dorsal aspect of the head is bright green with most of the dorsal head scales outlined in black. The dorsum is bright green with 5—7 transverse black bars separated by spaces twice the width of the crossbars. A bright white lateral stripe extends from eye to shoulders, bordered above by a broad dark line that narrows posteriorly. A ventrolateral white line extends from axilla to the groin area. The venter is light green. A white thigh spot if found on either side of the thigh as well as over each ear and on each side of the neck above the ventrolateral stripe (McCoy 1968a). The tail is ringed with diffuse brown bands.

Laemanctus s. serratus is characterized by small body scales (average 59 at midbody); higher number of casque scales (average more than 22); more numerous fourth toe subdigital lamellae (average more than 75); azygous scale usually present (72%) (McCoy 1968a). *Laemanctus serratus alticoronatus* is characterized by slightly larger body scales (average 53 at midbody); lower number of casque scales (average 21); less numerous fourth toe subdigital lamellae (average less than 74); usually no azygous scale (76%). *Laemanctus serratus mccoyi* has scale counts averaging 51 around midbody, and few forth toe subdigital lamellae (average around 66). There are usually no azygous scales (75%) (Pérez-Higareda & Vogt 1985).

Ecology & Life History: Ecological data of *Laemanctus serratus* are roughly equivalent to those of *L. longipes*; some additional data is included in this section.

Maximal reported snout-vent length for this species is 190 mm (Ahl 1930). The upper altitudinal limit for *Laemanctus serratus* probably lies above 800m. Tropical deciduous forests of lower mountainous slopes are the characteristic habitats (Martin 1958). The reproductive season is correlated with the beginning of the summer rains (Holdridge 1957).

Laemanctus serratus is oviparous. Martin (1958) reported observations of nest digging in Tamaulipas in mid June. Recorded egg sizes were 23 by 12 mm. A gestation period of ten months is reported for *L. serratus* by Klinghöffer & Scherpner (1957). Martin (1958) reported snails, insects and a lizard (*Anolis*) among the stomach contents in this species.

This species has also been observed running bipedally across a road just south of Tamaulipas (R. Etheridge, pers. comm.). Also noted is a coloration change in this species when disturbed (see above).

Fossil Record: Langebartel (1953) tentatively identified an incomplete left dentary from a cave deposit in Actun Lara, Yucatán, México.

Karyotype: Information not available.

Biogeography

The geological history of Central America during the Early Tertiary allows for two biogeographical interpretations of the early evolutionary history of basiliscines. Within this framework, I review the present distributions of basiliscines with respect to major faunal units.

Basiliscus vittatus occurs in open habitats of the lowlands to elevations of 1500 m in México from Jalisco and southern Tamaulipas, through the Isthmus of Tehuántepec southward through Central America into northwestern Colombia (Fig. 45). Müller (1973) listed *Basiliscus vittatus* as a faunal element of the Central American Rain Forest Center defined to include southeastern México (except dry regions of Yucatán), northern Guatemala and Central Honduras. The limits of these faunal elements are determined by three primary factors: a) the course of the 1500 m contour, b) the occurrence of pine forest in Honduras and Nicaragua, and c) the presence of open, unforested areas. However, within this Center, *Basiliscus vittatus* occurs in open areas and clearings. Although the center of distribution appears to be located within this Center, this species also extends further north along the Pacific and Atlantic lowlands and the Yucatán Peninsula of México, and southward through Central America into extreme northwestern Colombia.

Although much of the distribution of *Basiliscus vittatus* coincides with Müller's Central American Rain Forest Center and is listed as a faunal element thereof, the occurrence of *B. vittatus* in more xeric areas should be noted. A north and southward dispersal is probably correlated with the general habits of this species and association with cleared forested areas (Van Devender 1979).

The Colombian Pacific Center (Müller 1973) is correlated with the limits of the lowland rain forests, which extend from Western Ecuador in the south to the southern outliers of the mountains of Darién, Panamá in the north. The distribution of *Basiliscus galeritus* along the Pacific coast of Costa Rica to pacific slopes of Colombia and Ecuador coincides exactly with Müller's Colombian Pacific Center (Fig. 46). This Center can be subdivided into two Subcenters, the Chocó and Nechi. The Chocó Subcenter is defined as west of the Cordillera Occidental of the Andes and is the one of interest to this study.

Basiliscus b. basiliscus, a characteristic Costa Rican Center faunal element, ranges from the southwestern coast of Nicaragua through Costa Rica and Panamá into northwestern Colombia (Fig. 47). As defined by Reinig (1950; see also Müller 1973), the Costa Rican Center is divided into the Mosquito Subcenter north, and the Chiriqui Subcenter south of the Cordillera de Talamanca. *Basiliscus b. basiliscus* is not an endemic Costa

Rican Center faunal element, but extends southward into the northern aspect of the Chocó Subcenter.

Basiliscus basiliscus barbouri is found in the Santa Marta mountains of northern Colombia and in northwestern Venezuela, and is associated with the montane forests of the Sierra Nevada Center, and the isolated lowland rain forests at the foot of the Sierra de Santa Marta of the Santa Marta Center to the south (Müller 1973). The Santa Marta Center, in contrast to the Sierra Nevada Center has many more endemics such as *Anolis gaigei, A. solifer*, and *A. solitarius*. The Santa Marta and Sierra Nevada Centers are separated from the Colombian Pacific Center by the dry areas south and southwest of the Sierra de Santa Marta.

Basiliscus plumifrons occurs in forested habitats of moderate elevations from Central Nicaragua south along the atlantic versant of Costa Rica into northwestern Panamá (Fig. 46). *Basiliscus plumifrons* is also a Costa Rican Center faunal element (Müller 1973). In contrast to *B. basiliscus, B. plumifrons* is an endemic Costa Rican Center faunal element.

All four species of *Basiliscus* occur in Costa Rica (Fig. 48). *Basiliscus vittatus* is found along the Caribbean versant of Costa Rica in the Mosquito Subcenter. *Basiliscus galeritus*, which is a Colombian Pacific Center faunal element, is found along the Pacific versant of the Chiriqui Subcenter where it is sympatric with *B. basiliscus* and *B. plumifrons*.

Corytophanes hernandezi, occurs along the Atlantic versant of central Veracruz, México southward to northern Guatemala, with a disjunct population in Belize and the east coast of the Yucatán Peninsula (Fig. 51). *Corytophanes cristatus* ranges from central Veracruz and the west coast of the Yucatán Peninsula through Costa Rica to northwestern Colombia (Fig. 51). Both species are considered to be Central American Rain Forest Center faunal elements.

Corytophanes percarinatus, occurs along the Pacific versant of Southern México from the Isthmus of Tehuántepec through the highlands of Guatemala to El Salvador (Fig. 51). Müller's (1973) definition of the Guatemalan Montane Subcenter (northern part of the Central American Montane Forest Center) corresponds approximately with the Guatemalan Highland province of Savage (1966). The faunal elements of this Center are restricted to montane forests above 1500 m.

Laemanctus longipes is a southern Central American Rain Forest element. *Laemanctus l. longipes* is distributed throughout the Isthmus of Tehuántepec (Fig. 54). *Laemanctus l. deborrei* is found from the base of the Yucatán Peninsula southward into Guatemala, with a disjunct population in central Nicaragua (Fig. 54). *Laemanctus l. waltersi* is restricted to the northern slopes of the Sierra de Piju in Honduras (Fig 54).

Laemanctus serratus serratus, on the other hand, is a northern Central American Rain Forest element. It ranges from the Río Soto le Marina in central Tamaulipas southward through San Luis Potosí into Chiapas. *Laemanctus serratus mccoyi* is located within the range of *L. s. serratus* and is only known from its type locality (Fig. 55). *Laemanctus s. alticoronatus* is clearly a member of the Yucatán Center faunal element. It is predominantly found in the northwestern third of the Yucatán peninsula, but also occurs at the base of the peninsula and in extreme northwestern Honduras (Fig. 55). This species is adapted to the dry, thornbrush savanna of the Yucatán. Müller (1973) indicated that in the area between Flores (Guatemala) and Xcalak (México) there is a zone of interdigitation of elements belonging to the Yucatán Center and the Central American Rain Forest Center. *Laemanctus s. alticoronatus* has successfully colonized this transition zone.

The entire *Corytophanes-Laemanctus* clade, with the exception of *C. percarinatus* (Guatemalan Montane Forest Subcenter element) and *L. s. alticoronatus* (Yucatán Center) is composed of Central American Rain Forest elements.

The center of origin[9] of *Basiliscus* (earliest diverging taxon within the basiliscines) is located in present-day Costa Rica were all four species occur (Fig. 48). This area corresponds with Early Cenozoic Middle American volcanic islands or the Chortis block (Smith 1985). The presumed center of origin of the *Corytophanes-Laemanctus* clade is located at the base of the present-day Yucatán peninsula. In this region the ranges of all five species of this clade either contact or overlap.

Three alternatives exist as to the origin of basiliscines: 1) the basiliscines are North American in origin and spread into Central and South America, 2) they are South American in origin and invaded Central America by dispersal or 3) the basiliscines are Central American in origin and have evolved in situ.

Estes (1983b) suggested that "iguanids" occupied at least the southern portions of Gondwana by the Early Cretaceous. His scenario predicts that by the Late Cretaceous, non-oplurine "iguanids" had begun to diversify as represented by *Pristiguana* from the Late Cretaceous of Brazil. To continue this line of reasoning, the basiliscines may represent an Early Cenozoic radiation of this early "iguanid" stock into Central America with a subsequent diversification in situ.

Savage (1966, 1982) stated that the basiliscines represent a product of a rather limited northward dispersal from South America across volcanic islands probably beginning in the Late Cretaceous and continuing into the Early Tertiary. This statement is further supported by Estes & Báez (1985). A Central American origin seems to be the most plausible hypothesis because of the relatively old age of this clade, as indicated by the relatively high number of apomorphies. Therefore, attention must be focused on geological and possible vicariant events in Central America during the Early Tertiary.

As summarized by Smith (1985), there are many excellent reconstructions of the Cenozoic tectonic history of Central America and the Caribbean that have been proposed (e.g. Malfait & Dinkleman 1972; Pindell & Dewey 1982; Wadge & Burke 1984). Some commonalities exist among these various models, but none of them are completely compatible. Therefore, different biogeographical patterns result from interpreting these various geological models.

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[9] The center of origin of Müller (1973) is static, and is based on present distributional patterns, with minimal historical considerations. Hennig's (1966) "progression rule" postulates that the earliest diverging taxon is located within the center of origin of that monophyletic taxon.

Five models of Middle American tectonic events are discussed here. Malfait & Dinkleman's (1972) model opts for the presence of oceanic lithosphere on the Caribbean plate between North and South America (Smith 1985: Fig. 18). Perfit & Heezen's (1978) model also allows for oceanic islands; however, these are not part of the Caribbean plate. In contrast, Wadge & Burke (1983) locate Central America (= Chortis block) west of the South México continental margin. Central America subsequently slid south of the Motagua Fault Zone to its present day location during the period 30—0 Ma (E. Oligocene-present; Smith 1985: Fig. 19). The Miocene configuration of tectonic boundaries is similar to that presented by Malfait & Dinkleman (1972) (Smith 1985; fig. 20). Pindell & Dewey's (1982) model contrasts with that of Wadge & Burke (1983) by having an outright connection between the Chortis Block and Central America. For biogeographical purposes, these latter two models are comparable during the Early Eocene. The Panamanian link between Central and South America occurred only in the last 10 Ma (Pliocene; Smith 1985; fig. 21).

Two main biogeographical scenarios of the early biogeographical history of basiliscines can be deduced from these geological models. The "Oceanic Island" hypothesis is based on the models of Malfait & Dinkleman (1972) and Perfit & Heezen (1978). For this scenario, the ancestral basiliscine stock dispersed from South America onto oceanic islands located between North and Central America. The *Corytophanes-Laemanctus* stock subsequently dispersed and diversified on the Mesoamerican block, whereas *Basiliscus* evolved in situ on the islands (Fig. 56).

The "Chortis-block" scenario postulates an ancestral basiliscine stock dispersal onto the Chortis block from South America (= "East Pacific Plate" of Sykes et al. 1982) (Fig. 56). As with the oceanic island scenario, the ancestral *Corytophanes-Laemanctus* stock dispersed onto Mesoamerica and speciated further. *Basiliscus* is derived from the ancestral population on the Chortis block. The dispersion onto the Mesoamerican block was either a land dispersion across a transform fault (model of Pindell & Dewey 1982), across the Cayman Trough (Wadge & Burke 1983) or perhaps by waif dispersal across 1400 km of ocean (Sykes et al. 1982). The problem with the second biogeographical interpretation is that the transform fault of Pindell & Dewey (1982) may not be a sufficient isolating barrier, whereas the separation of the "East-Pacific plate" of Sykes et al. (1982) may be too much of a barrier. These two biogeographical scenarios are based primarily on the centers of origin of these taxa.

The notion that the *Corytophanes-Laemanctus* center of origin is north of the *Basiliscus* center further supports the hypothesis of a northward vicariance or dispersal of the basiliscines onto the southern aspect of the Mesoamerican block.

Superimposing these biogeographical data on the proposed phylogeny, we can hypothesize biogeographical trends within basiliscines. The *Corytophanes-Laemanctus* clade, for the most part, is a Central American Rain Forest component. As previously hypothesized, this clade dispersed onto the southern aspect of the Mesoamerican block from either the Chortis block or Central American volcanic islands. From the phylogenetic center of origin *C. hernandezi* represents a northward dispersal, *C.*

cristatus a southward dispersal and *C. percarinatus* a population that has become separated from *C. cristatus* by the uplifting of the Guatemalan Highlands.

Corytophanes cristatus and *C. percarinatus* are allopatric. Müller (1973) believed that about 11—12,000 years ago the Guatemalan Montane Forest biome extended farther down to lower altitudes than at present and that montane species lived partly in what is now part of the lowlands. These two species may have occurred in sympatry. As temperatures began to rise, the altitudinal range of the montane forest shifted to a higher elevation, leading to a further isolation of the Guatemalan Montane Forest biome.

Laemanctus serratus shows a northward dispersal from the presumed phylogenetic center of origin, whereas *L. longipes* has dispersed to the south. No obvious geological event can be invoked to postulate the allopatric speciation of these two genera.

In the northern part of the Chocó Subcenter *B. galeritus* is found sympatrically with *B. b. basiliscus*. In light of the proposed phylogeny, *B. galeritus* reached the northern Chocó Subcenter first, with subsequent further invasion of the southern Chocó Subcenter. The first invasion of Chocó Subcenter (*B. galeritus*) happened during perhaps the Miocene to Pliocene (see above). The second invasion of the northern Chocó Subcenter by *B. basiliscus* occurred more recently after the isthmus link. *Basiliscus basiliscus* invading the Chocó encountered a reproductively isolated population. *Basiliscus basiliscus barbouri* has subsequently been further isolated with a parthenogenic population being present in the Sierra Nevada de Santa Marta.

Basiliscus basiliscus and *B. plumifrons* are clearly Costa Rican faunal elements and each others closest relatives.

The biogeographical interpretation of *Basiliscus vittatus* is problematic. The range of this species coincides with the range of the genus, except for *B. b. barbouri* and *B. galeritus* in the southern Chocó region. Therefore, numerous biogeographical interpretations can be given with regard to its distribution. The simplest interpretation postulates a northward dispersion along the Atlantic and Pacific coastal lowlands of México.

That neither of the three basiliscine genera are present in the Antilles, and in particular the Greater Antilles, seems to refute Rosen's (1975), Savage's (1982), and Guyer & Savage's (1986) model of Caribbean biogeography. The basiliscines, which most certainly predate the Eocene, were in place when the hypothesized "proto-Antilles" (Rosen (1975), based on a model proposed by Malfait & Dinkleman (1972)), are suggested to have been located between North and South America before their northeastern movement to their present-day location.

The complete absence in the Caribbean of this prime "iguanid" candidate is only construed negative evidence to falsify Rosen's (1975) hypothesis. However, it does suggest that alternate interpretations of Middle and Central American biogeography must be considered. In particular, either the interpretation of Caribbean biogeography proposed by Pregill (1981), and based on a model by Perfit & Heezen (1978), or the three above-mentioned models hypothesizing a Chortis block, explain the absence of basiliscines from the Caribbean. These models are supported further by the distributional patterns of a large number of terrestrial vertebrates. In particular, the Pregill/Perfit &

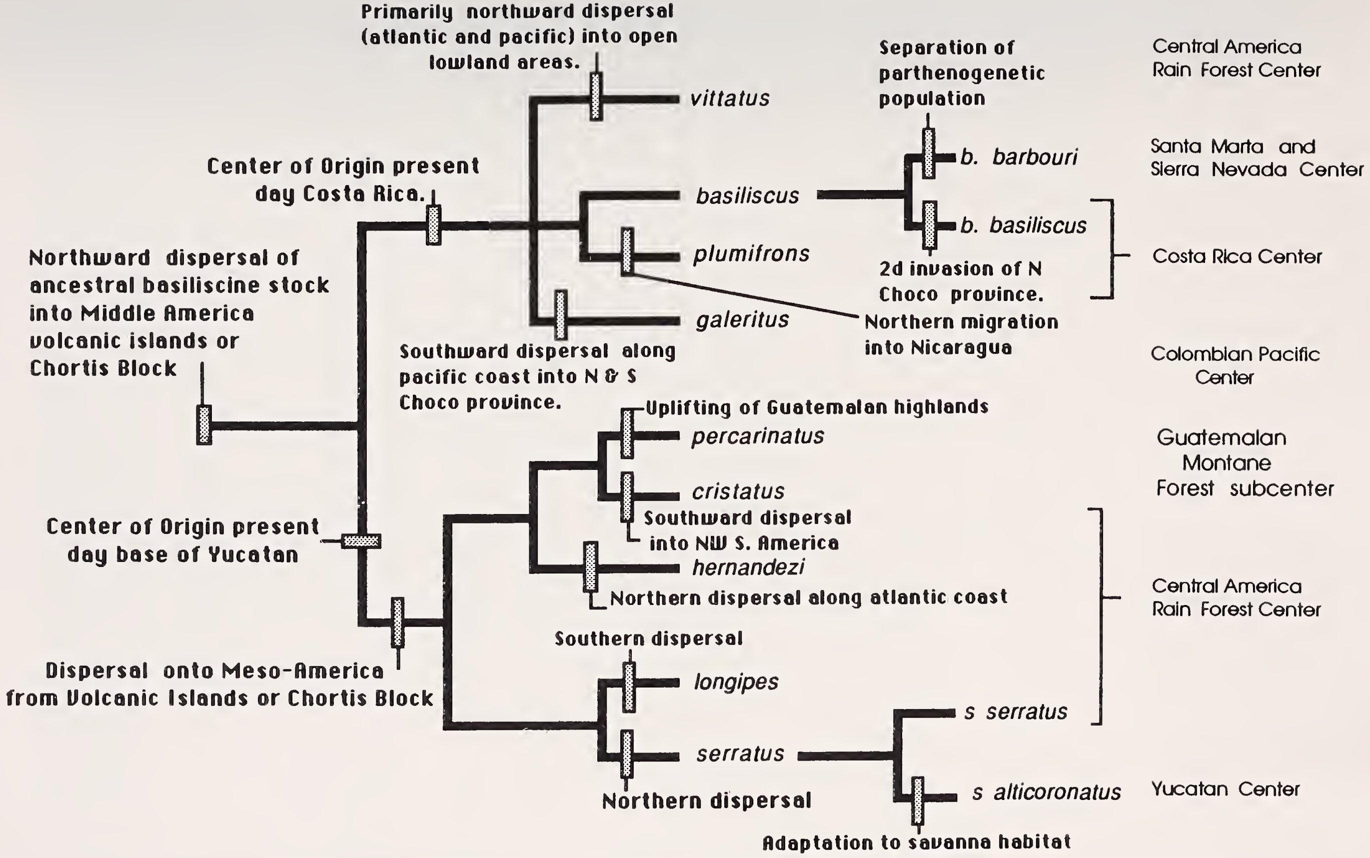

Fig. 56: Proposed biogeographical patterns superimposed on the phylogeny. See text for further discusion.

Heezen hypothesis indicates that the Greater Antilles evolved as a mid-Caribbean archipelago from subduction of oceanic lithosphere that began in the Late Cretaceous. Pregill (1981), therefore, suggested that the Antilles were in their approximate present-day position at the time that Malfait & Dinkleman's (1972) "proto-Antilles" were located between North and South America, an area coinciding with basiliscine distribution. Certainly Pregill's (1981) model better explains the absence of basiliscines from the Greater Antilles, whereas Rosen's (1975) model would predict their presence in the Antilles.

Briggs (1984) also postulated that the Antilles were created in situ with no land connection among the islands, or between the islands and the mainland. His conclusions coincide with those of Pregill (1981) in that the Antilles are to be regarded as oceanic islands that have gradually accumulated their terrestrial and freshwater biota by means of overseas dispersal.

Another proponent of the in situ development of the Antilles is Rivas (1958, 1986). However, Rivas subscribed to the notion of a former land connection of the Antilles with Central America, with overland colonization to explain biogeographical patterns of freshwater fishes in the Antilles. This hypothesis is not supported by recent geological evidence.

Several notes of caution should be added here. First, there is no good evidence that the above-defined faunal Centers are real entities. In addition, Müller's (1973) center of origin concept does not take many historical concepts into account. Secondly, because only a single example (taxon) is used here, with no degrees of freedom, no general statement can be made concerning the relationships among these faunal Centers. In essence the cladogram of faunal and geographical areas is simply an example of possible relationships between faunal districts for a single clade.

Figure 56 shows the hypothesized vicariant, dispersal and geological events superimposed on the phylogeny. Various faunal assemblages can be related to one another. For example the Santa Marta Center shows affinities the Costa Rican Center and the Central American Rain Forest Center shows affinities with the Guatemalan Montane Forest Subcenter.

Based on the proposed phylogeny, the Guatemalan Montane Forest Subcenter shows affinities with the Central American Rain Forest Center. This is in contrast to Müller's (1973) statement that the Central American Rain Forest Center has close affinities with the Costa Rican Center.

Phylogenetic Affinities with other "Iguanids"

Although the initial focus of this study has been the resolution of relationship within the basiliscine clade, it has been necessary to look at all other "iguanid" clades as functional outgroups. Still no clear-cut sister taxon to the basiliscines can be hypothesized. Following is a summary of possible sister taxa relationships with comments on the evidence.

First taxonomic outgroup

Although not entirely convincing, the data show best evidence for an anoloid-basiliscine clade. This clade is supported by five synapomorphies. All anoloids and basiliscines show extensive rugosities of the skull that are not only restricted to the frontal, but are also found on the prefrontals and sometimes the nasal bones. The osseous labyrinth within this clade is very prominent (reversal in *Basiliscus*). All members of this clade, with the exception of *Polychrus* lack a scapular fenestra. Scapular fenestra are however also absent in the *Liolaemus*-group and in some *Sceloporus*-group members. Within the anoloid-basiliscine clade, caudal autotomy has been lost in the arboreal species of basiliscines (*Corytophanes* and *Laemanctus*), in *Phenacosaurus, Chamaelinorops, Chamaeleolis* and the mainland Alpha *Anolis*, all of which are arboreal; other arboreal *Anolis* however retain it (R. Etheridge, pers. comm.; pers. obs.). In the leiosaurs, *Enyalius, Pristidactylus,* and *Diplolaemus* retain autotomy; *Leiosaurus* has lost it. Many other iguanids outside this clade (e. g., *Brachylophus, Amblyrhynchus, Crotaphytus, Uracentron* and the Acrodonta) have lost caudal autotomy, with no correlation to arboreality or terrestriality. A flat, spatulate rostral portion of the snout is another derived character in support of this taxon (with an arched premaxillary spine present in leiosaurs and *Basiliscus*). A spatulate rostrum, however, is also characteristic of *Oplurus, Enyalioides*, arenicolous sceloporines and tropidurines.

Noticeable also is the fact that expanded parietal crests are restricted to these two clades although the two types of crests are not homologous (see description of parietal blade).

Böhme's (1988) hemipenial investigations suggest that the simple stump-like hemipenis is the plesiomorphic condition found in iguanines, oplurines, morunasaurs, sceloporines and crotaphytines. Basiliscines, anoles and para-anoles show the intermediate condition of a slightly bifurcated intromittent organ. In *Polychrus*, leiosaurs and tropidurines the derived condition of a completely bifurcated hemipenes is observed. These findings may further support an anoloid-basiliscine relationship, with a bifurcated hemipenes being convergent between *Polychrus*, leiosaurs and tropidurines.

Alternate contenders for the first taxonomic outgroup position are crotaphytines and iguanines. The evidence for either of these hypotheses is rather weak.

Crotaphytines and basiliscines have a prominent lateral groove at the prefrontal-lacrimal junction. This groove has been lost in *Corytophanes*, possibly owing to the development of a bony supraorbital arch. Bipedal locomotion can also be regarded as a character uniting these two taxa. However, bipedal locomotion requires the possession of strong hind legs, short fore limbs, a shortening of the presacral region and the possession of an elongated or heavy tail to act as a counterbalance (Snyder 1954). Common possession of these musculoskeletal specializations does not necessarily predict common ancestry, but certainly doesn't exclude that possibility. Regarding this character as having phylogenetic affinities requires the convergence of many other characters.

A basiliscine-iguanine clade can only be supported by the presence of five cervical vertebrae (Hoffstetter & Gasc 1969). This character is not unique to basiliscines and iguanines. Five cervical vertebrae are found in anoles, sand lizards plus *Phrynosoma*, and in *Oplurus*.

Second taxonomic outgroup

The choice of a second taxonomic outgroup to the basiliscines becomes increasingly speculative. Etheridge & de Queiroz (1988), prefer a morunasaur-oplurine-anoloid clade based on the *Oplurus*-type of postxiphisternal inscriptional rib pattern. In light of the proposed anoloid-basiliscine relationship, the *Oplurus*-type rib pattern could be a synapomorphy for a morunasaur-oplurine-anoloid-basiliscine clade, with subsequent loss of terminal cartilages on the postxiphisternal ribs in *Basiliscus*. Unfortunately there are no other characters that support this contention.

An iguanine-anoloid-basiliscine clade is supported solely by the possession of a medial constricted concha of the quadrate. Within this clade the medial concha has become expanded in large iguanines and in *Basiliscus*.

The loss of femoral pores is a character supporting a tropidurine-oplurine-anoloid-basiliscine clade. Within this clade the assumption of reacquisition of femoral pores in *Polychrus* must be made.

Additional characters such as the presence or absence of the postfrontal and palatine teeth, the condition of Meckel's groove, septomaxillae and the preacetabular process, the pattern of subocular and superciliary scales, the dorsal shank muscle innervation, and the posterior extent of the jugal are all characters that reveal various combination of clades none of which shows overwhelming support.

The anoloids show the best evidence of being closely related to basiliscines. The evidence for relationship to that clade remains equivocal and is therefore presented as a hypothesis to be further supported.

SUMMARY AND CONCLUSIONS

Etheridge & de Queiroz's (1988) phylogenetic study of the "Iguanidae" has established the recognition of eight suprageneric monophyletic taxa. Their analysis did not hypothesize any sister taxon relationship between the basiliscines and any other of the non-basiliscine "iguanids".

In order to resolve the relationships among members of the ingroup, it was necessary to use all seven non-basiliscine "iguanids" as functional outgroups. Because "Iguanidae" itself is a metataxon, with no evidence of monophyly within the Iguania, the Acrodonta ("Agamidae" and Chamaeleontidae) should be considered as the eighth functional outgroup. Yet the addition of an eighth outgroup will not substantially affect the polarity at the ingroup/outgroup node.

The outgroup consensus algorithm used in this study allows for polarization of character states at basal nodes of polytomies of up to seven taxa or at the ingroup/outgroup node of an ingroup with up to seven unresolved taxa. Estimation of possible erroneous polarity assumptions are presented and unequivocal polarity decisions are made when the evidence of making an erroneous polarity decision was minimal or non existent.

The resulting phylogeny after replacement of unpolarized characters by polarized characters is well supported at several nodes. The monophyly of each of the three ingroup taxa is well supported. The evidence at the alpha level is, however, less convincing, suggesting that the species are rather conservative (i.e., few evolutionary divergences determinable) with respect to the generic level. The *Corytophanes-Laemanctus* clade forms a natural group and *Basiliscus* is the earliest diverging taxon within the basiliscines.

The hypothesized phylogeny suggests that the ancestral basiliscine was very *Basiliscus*-like, with a groove at the prefrontal-lacrimal junction, the absence of a postfrontal bone, the parietal foramen located in the frontal bone, clavicular fenestration, sharp canthal ridges and no femoral pores, to name a few characters. The ancestral basiliscine was presumably also terrestrial and bipedal with some semiarboreal (i.e., tree trunk) tendencies as seen in *Basiliscus* and *Laemanctus*. Therefore, *Corytophanes* has become secondarily arboreal.

To conclude, the proposed basiliscine phylogeny is based primarily on cranial osteological features and is therefore presented as a hypothesis to be further tested. In particular, more non-osteological characters are needed to further corroborate the proposed phylogeny. In addition, behavioral, ecological and genetic information are needed to complete a representative data set.

However, the problem of outgroup analysis in which the ingroup forms part of a large polytomy, and in which none of the ingroup taxa can be used as functional outgroups (ingroups with three taxa), remains the biggest problem. The consensus algorithm presented in this study was used to obtain a best estimate for the direction (polarity) of character transformations. This best approach for resolving relationships for "iguanids" still remains the resolution and determination of relationships within Iguania, which in this and previous studies has not been possible.

RESUMEN

Actualmente son reconocidos ocho taxa monofiléticos supragenéricos en la familia "Iguanidae". Uno de estos taxa, los basiliscínidos, está representado por los géneros *Basiliscus*, *Corytophanes* y *Laemanctus*. La monofilia de los basiliscínidos se basa sólo en una característica sinapomórfica (el desarrollo de una cresta parietal ósea que se proyecta atrás), además de una combinación única de otras características derivadas que comparten con otros clados de iguánidos. La filogenía de los basiliscínidos fué construida usando una aproximación de "consenso de grupo externo y funcional" considerando al resto de los "iguanidos" como grupos funcionales. El volumen del conjunto de datos característicos son: características osteológicas además de las características de partes blandas, la microestructura de la escama, el comportamiento y la ecología. Los resultados obtenidos indican monofilía para los tres géneros, estando más fuertemente relacionados *Corytophanes* y *Laemanctus* entre ellos que con *Basiliscus*.

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APPENDIX A

List of specimens examined

The following is a listing of preserved and skeletal material (including radiographs) examined in this study.

Preserved material examined

Many preserved specimens of both in- and outgroup taxa were examined in this study. Rather than to give an extensive listing of all the specimens examined, a complete list of institututions from which material was borrowed and examined follows. Institutional abbreviations follow those of Leviton et al. (1985) in addition to some acronyms of private collections. The same acronyms are used for the skeletal material.

American Museum of Natural History [AMNH]

The Academy of Natural Sciences of Philadelphia [ASNP]

The University of California at Berkeley, Museum of Vertebrate Zoology [MVZ]

British Museum (Natural History) [BMNH]

California Academy of Sciences [CAS]

Carnegie Museum of Natural History [CM]

Collection of J.F. Copp (La Jolla, Ca.)

Collection of Dr. Richard E. Etheridge (San Diego State University) [REE]

Field Museum of Natural History, Chicago [FMNH]

Harvard University, Museum of Comparative Zoology [MCZ]

University of Illinois, Museum of Natural History [UIMNH]

The University of Kansas, Museum of Natural History [KU]

Koninklijk Belgisch Instituut Voor Natuur Wetenschappen (Brussels) [IRSNB]

Los Angeles County Museum of Natural History [LACM]

Collection of Dr. Gregory Pregill (San Diego Natural History Museum) [GKP]

Collection of Dr. W. Presch (California State University at Fullerton) [WP]

San Diego Natural History Museum [SDSNH]

National Museum of Natural History, Smithsonian Institution [USNM]

Texas A & M University, College Station, Tx. [TCWC]

The University of Texas at Arlington, Collection of Vertebrates [UTACV]

University of California, Berkeley, Museum of Paleontology [UCMP]

Collection of Dr. J.M. Savage, University of Miami [JMS]

The University of Michigan, Museum of Zoology [UMMZ]

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn [ZFMK]

Skeletal material

Museum numbers are listed for the ingroup only. For all outgroups a list of examined species is followed by the number of specimens examined. Radiographs from the collection of Darrel Frost [The University of Kansas] are indicted by (R). Museum acronyms are listed above.

BASILISCINES

Basiliscus basiliscus (including *Basiliscus b. basiliscus* and *Basiliscus b. barbouri*): AMNH 57769, 74615, 84192; KU 84956, 93452, 93453, 93454, 93455; MVZ 199579, 13765; REE 2015; MCZ 2001, 6565, 101409; JMS 1420, 1543, 1581; WP 183, 194, 199, 200, 201, 208, 231, 251, 257, 260, 270, 311, 374, 609.

Basiliscus galeritus: MCZ 165713

Basiliscus plumifrons: REE 427, 2014; MCZ 19490; JMS 234; WP (uncat.); SDSNH 57098, 57099, 57100, 59467, 60430, 60431.

Basiliscus vittatus: MVZ 40654, 78381, 78382, 95988, 95989; UCMP (uncat.), UCMP 971 (JAS 3362), 972 (JAS 3364), 973 (JAS 3365), 975 (JAS 3367), 993 (JAS 3368), 995 (JAS 33668); BMNH 62.1.17.4; CAS (uncat.); REE 49, 555, 637, 1601, 1729, 1757, 1759; IRSNB 3344, 3345; UIMNH 33203, 33204; KU 93451, 96174, 96175; JMS 365; UMMZ 150207, 150215, 150219, 150229, 150258, 150266, 150376, 150319, 150326, 150339; WP 64, 68, 87, 114; SDSNH 60432, 65003, 65004; TCWC 17145, 17149.

Corytophanes cristatus: IRSNB 3346; UCMP 118941; CAS 145217; FMNH 211939; MCZ 133981; SDSNH 62345, 63108, 64060, 64543; (R).

Corytophanes hernandezi: BMNH 1913.7.19.63; CAS 5845, 74348; CM 57586, 57587; REE 1176, 1800; UTACV R-3215 (skull and mandibles).

Corytophanes percarinatus: UCMP 113057; CM 43644, 43645; KU 93456, 190773; WP 244, 384, 456, 491; (R).

Laemanctus longipes (including *Laemanctus l. longipes*; *L. l. deborrei* and *L. l. waltersi*): MCZ 137673; CAS 18334, 18335; FMNH 213398; KU 74910, 187739 (R); WP 518, 3 specimens (uncat.); SDSNH 62914, 64059, 64542; USNM 12227; UTACV R-10060.

Laemanctus serratus (including *Laemanctus s. alticoronatus* and *L. s. serratus*): AMNH 44982; REE 619; KU 74910, 70265 (R), 75532 (R); USNM 83435.

ANOLES

Polychrus acutirostris (2); *marmoratus* (R).

* Spinulate Anoloids

— Leiosaurs:

Pristidactylus achalensis (3 + R); *scapulatus* (2); *volcanensis* (3).

Enyalius bilineatus (2); *braziliensis* (1); *catenatus* (1).

Diplolaemus bibroni (2); *darwinii* (1+R).
Leiosaurus belli (1); *catamarcensis* (3); *paronae* (1).

— Para Anoles
Urostrophus vautieri (1+R).

— Anoloids
Chamaeleolis chamaelioniodes (3).
Anolis barahonae (3); *bimaculatus* (3); *carolinensis* (4+R); *chlorocyanus* (2); *coelestinus* (3); *cristatellus* (10+R); *cybotes* (3); *distichus* (3); *equestris* (5+R); *frenatus* (3+R); *garmani* (3); *gingivinus* (3); *lemurinus* (R); *limifrons* (3); *lineatopus* (3); *lividus* (3); *marmoratus* (2); *opalinus* (2); *pentaprion* (R); *petersi* (4+R); *pulchellus* (1); *punctatus* (R); *sagrai* (3); *stratulus* (3); *townsendi* (1); *wattsi* (3); *sp.* (3).

TROPIDURINES

Phymaturus palluma (2+R); *patagonicus* (5); *punae* (2).
Liolaemus anomalus (3); *boulengeri* (2+R); *darwini* (4); *elongatus* (1+R); *fitzingerii* (2+R); *kingii* (3+R); *lineomaculatus* (3); *iridescens* (1); *multiformis* (2+R); *nigroventris* (2); *pictus* (2+R).
Ophryoessoides tricristatus (1).
Leiocephalus barahonensis (2); *carinatus* (5); *greenwayi* (2); *lunatus* (2); *loxogrammus* (5); *melanochlorus* (R); *personatus* (2); *punctatus* (5); *schreibersi* (3+R); *semilineatus* (3).
Stenocercus apurimacus (2); *crassicaudatus* (2); *empetrus* (2); *formosus* (1); *guentheri* (1+R); *humeralis* (2); *ochoai* (1); *ornatissimus* (2); *praeornatus* (1); *rhodomelas* (1); *rosieventris (R); variabilis* (2); *varius* (1+R).
Uranoscodon superciliosa (3+R).
Plica plica (4+R); *umbra* (4+R).
Tapinurus semitaeniatus (2).
Uracentron azurem (R); *flaviceps* (2).
Strobilurus torquatus (2).

*Eastern *Tropidurus*:
Tropidurus albemarlensis (5); *bivittatus* (3); *delanonis* (2); *duncanensis* (1); *habelii* (1); *koepckeorum* (1); *occipitalis* (1); *peruvianus* (5+R); *stolzmanni* (1); *tigris* (3).

*Western *Tropidurus*:
Tropidurus bogerti (1); *etheridgei* (2); *hispidus* (5+R); *hygomi* (1); *melanopleurus* (3); *spinulosus* (2+R); *torquatus* (2).

IGUANINES

Brachylophus fasciatus (8).
Dipsosaurus dorsalis (15+R).

Amblyrhynchus cristatus (10)
Conolophus phallidus (3); *subcristatus* (4).
Ctenosaura acanthura (5); *hemilopha* (14); *pectinata* (6); *similis* (10).
Sauromalus ater (2); *hispidus* (7); *obesus* (13); *slevini (2); varius* (7).
Cyclura carinata (1); *cornuta* (5); *cychlura* (1); *nubila* (5).
Iguana delicatissima (1); *iguana* (12).

SCELOPORINES

Petrosaurus mearnsi (3 + R); *thalassinus* (3 + R).

* *Sceloporus*-group:
Uta stansburiana (6); *palmeri* (R).
Sceloporus clarki (10); *cyanogenys* (4); *formosus* (1 + R); *graciosus* (5); *grammicus* (4); *jarrovi* (6); *magister* (3); *malachiticus* (4); *merriami* (2); *occidentalis* (5); *olivaceus* (7); *orcutti* (4); *poinsettii* (3); *scalaris* (4); *spinosus* (3); *torquatus* (2 + R); *undulatus* (5); *utiformis* (R); *variabilis* (3 + R).
Urosaurus bicarinatus (2); *gadovi* (1); *nigricauda* (1); *ornatus* (5).

*Sand lizards:
Uma inornata (7); *notata* (5); *scoparia* (3).
Cophosaurus texanus (5 + R).
Holbrookia maculata (10 + R); *propinqua* (8).
Callisaurus draconoides (6 + R).
Phrynosoma asio (2); *cornutum* (11); *coronatum* (3); *douglassii* (3); *m'callii* (3); *modestum* (3); *orbiculare* (3); *platyrhinos* (2); *solare* (2).

CROTAPHTINES

Crotaphytus collaris (20 + R); insularis (3); *reticulatus* (10 + R).
Gambelia silus (10); *wislizenii* (5 + R).

OPLURINES

Oplurus cuvieri (2 + R); *fierensis* (1 + R); *quadrimaculatus* (1).
Chalarodon madagascarensis (4 + R).

MORUNASAURS

Enyalioides heterolepis (R); *laticeps* (3 + R); *o'shaughnessyi* (1).
Hoplocercus spinosus (2).
Morunasaurus annularis (2 + R).

Appendix B

Key to species of Basiliscus

1a. Ventral scales keeled; 1—2 chin shields contact an infralabial. Head crest of adult male and large juvenile males single, triangular in outline. Ground color brown to olive, often with a distinct reddish to yellow dorsolateral stripe from eye to shoulder or beyond .... *Basiliscus vittatus*

1b. Ventral scales smooth; 3—4 chinshields almost always contacting infralabials. Head crest of adult males rounded in outline or with a posteriorly directed lobe. Ground color often bright to dull green 2

2a. Middorsal scale row consisting of an alternation of a large and small scales (2—4); adult males without prominent dorsal and caudal crest .... *Basiliscus galeritus*

2b. Middorsal scale row of females and juveniles uniform in size; adult males with prominent dorsal and caudal crests supported by elongated neural spines 3

3a. Head crest single in adult and large juvenile males. Throat of juveniles with three distinct longitudinal lateral stripes. Ground color of adults brown, olive or bronze. Juveniles are pale green, lacking the series of distinct large light spots along sides. Two pairs of lateral stripes usually present .... *Basiliscus basiliscus*

3b. Head crest of adult males and large juveniles comprised of two lobes; a small anterior lobe and a pronounced posterior lobe. Adult females and juveniles have only a single small parietal extension. Throat of adults and juveniles uniform, usually dark. Ground color of adults dark bluish-green, with one or two series of large light spots along sides. Dorsum of juvenile bright green .... *Basiliscus plumifrons*

Key to species of *Corytophanes*

1a. Nuchal crest interrupted, not continuous with dorsal crest, but following the outline of the parietal blade. Supraorbital semicircles with a distinct lateral keel. The adpressed hind limb reaches considerably beyond the tip of the snout *Corytophanes hernandezi*

1b. Nuchal crest continuous with dorsal crest. Supraorbital semicircles lacking longitudinal keels. The adpressed hind limb reaches the tip of the snout or a little beyond 2

2a. Upper head scales distinctly keeled or rugose, prominent lateral squamosal spine .... *Corytophanes percarinatus*

2b. Upper head scales smooth, no lateral squamosal spine . *Corytophanes cristatus*

Key to species of *Laemanctus*

1a. Anterior dorsal head scales large and regular, consisting of paired or both paired and azygous scales. Posterior edge of head serrated, consisting of a series of conical scales. Middorsal scale row forming a serrated crest .... *Laemanctus serratus*

1b. Anterior dorsal head scales small and irregular. Posterior edge of head smooth lacking serration. No distinct middorsal scale row .... *Laemanctus longipes*

Authors's address:
Mathias Lang, Department of Herpetology, San Diego Natural History Museum & Department of Biology, San Diego State University. San Diego, California, USA
Present address: Zoologisches Forschungsinstitut und Museum A. Koenig, Adenauerallee 150—164, 5300 Bonn 1.

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