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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 173

**Cladistic Relationships in the  
Gekkonoidea  
(Squamata, Sauria)**

by

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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
April 3, 1987

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## ABSTRACT

Kluge, Arnold G. 1987. *Cladistic Relationships in the Gekkonoidea (Squamata, Sauria)*. *Misc. Publ. Mus. Zool. Univ. Michigan*, 173:1-54, figs. 1-12.—The phylogenetic relationships among gekko and pygopod lizards are investigated. The most parsimonious hypothesis contains several well-corroborated clades. Twenty-seven synapomorphies characterize the group gekkos + pygopods. Eublepharines represent the most primitive lineage, and its sister-group is diagnosed by four shared derived features. Thus, gekkos are no longer considered a monophyletic assemblage. The sister-group relationship between diplodactylines and pygopods is based on a single apomorphy, a meatal closure muscle that encircles or nearly encircles the external auditory meatus. The majority of gekkos—gekkonines and sphaerodactylines—form an assemblage diagnosed by four apomorphies, with the genus *Teratoscincus* being the sister-lineage to all others. Sphaerodactylines and the genus *Pristurus* constitute a group which is set apart by six synapomorphies. *Pristurus* and *Gonatodes* are sister-taxa, in that order, to the remaining sphaerodactylines. The absence of the second ceratobranchial arch diagnoses a large group of gekkonines, mostly African in distribution. A strictly monophyletic classification is proposed, and the phylogenetic hypothesis on which it is founded is consistent with several major events in the breakup of Pangea.

Key words: *Biogeography, cladistics, Eublepharidae, Gekkonidae, gekkos, phylogeny, Pygopodidae, pygopods.*

## CONTENTS

	PAGE
INTRODUCTION.....	1
METHODS AND MATERIALS .....	6
ANCIENT GEKKOTANS .....	10
CHARACTER ANALYSES.....	11
Informative Characters .....	11
Questionable Evidence .....	33
CONCLUSIONS .....	36
Most Parsimonious Cladogram .....	36
Character Evolution.....	36
Evidence For Sister-Group Relationships .....	38
Classification .....	39
Biogeography.....	40
ACKNOWLEDGMENTS .....	42
LITERATURE CITED .....	47
APPENDIX I: Centrum Shape Of Adult Trunk Vertebrae .....	54
APPENDIX II: Diplodactylines Examined For Vertebral Processes .....	54

## ILLUSTRATIONS

FIGURE		PAGE
1	Recently proposed phylogenetic hypotheses of the major groups of gekkonoids .....	3
2	Ground-plan divergence diagram .....	4
3	Cladogram illustrating the concept of synapomorphy .....	7
4	Cladogram illustrating character congruence and homoplasy .....	7
5	Graph of condyle development in sphaerodactylines .....	15
6	Character-state tree of meatal muscle transformation series .....	20
7	Paired premaxillae of day-old pygopods .....	22
8	Ventral views of palate .....	26
9	Graph of variation in numbers of scleral ossicles .....	27
10	Skull and endolymphatic sacs of <i>Phyllodactylus europaeus</i> .....	32
11	Cladogram of gekkonoids (based on evidence summarized in Table 3).....	37
12	Cladogram of relationships among certain "ptyodactylines" .....	41

## TABLES

TABLE		PAGE
1	Number of scleral ossicles per eyeball.....	43
2	X-ray diffraction analysis of gekkonoid egg shell and "calcium milk".....	45
3	Gekkonoid data matrix .....	46

## INTRODUCTION

More than 25% of all living genera and species of lizards are placed in the Gekkonoidea,<sup>1</sup> and much has been written in the last 30 years about their phylogenetic relationships. Underwood's seminal papers on gekkos were based largely on eye characters (1951, 1954, 1955). Hecht (1976) and Russell (1979) inferred three principal lines of evolution from Underwood's Linnean classification (1954): Eublepharidae, Sphaerodactylidae and Gekkonidae. The latter was subdivided into Gekkoninae and Diplodactylinae on the basis of differences in pupil shape. In 1957, Underwood documented a sister-group relationship of the cosmopolitan gekkos with the snake-like pygopods of Australia and New Guinea (Fig. 1J; see also McDowell and Bogert [1954]). Werner (1961) accepted Underwood's (1954) major terminal taxa of gekkos, but proposed an alternative phylogenetic interpretation (Fig. 1F; Yehudah Werner, pers. comm.).

I concluded that the pupil-shape evidence emphasized by Underwood was more variable than he recorded (Kluge, 1967a). Further, I examined his hypothesis of gekko relationships for congruence with a different data set of 18 characters, mostly taken from the skeletal system (Kluge, 1967a). Wagner's (1961) ground-plan divergence method of phylogenetic inference was used to analyze those data. My major conclusions (Figs. 1A, 2) were: (1) The five eublepharine genera were relatively more primitive than all other living gekkos. However, I was unable to discover evidence that the five shared a more recent common ancestor than the one that gave rise to the remaining gekkos. (2) The Diplodactylinae + Gekkoninae + Sphaerodactylinae group shared a common ancestor; those gekkos had certain derived states in common which were not shared with the eublepharines. (3) The Gekkoninae + Sphaerodactylinae was also delimited by shared derived features, and, presumably, formed a natural assemblage. (4) Likewise, there was evidence that the five sphaerodactyline genera constituted a historical entity. (5) No shared derived features were discovered that provided unambiguous evidence for either of the two largest groups of gekkos, Diplodactylinae and Gekkoninae. Furthermore, I altered much of the generic composition of Underwood's Diplodactylinae and Gekkoninae in my analyses (contrary to the claims of Hecht [1976], and Hecht and Edwards [1977]), the former subfamily being restricted to the 13 genera endemic to the Australian Region (Table 1).

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<sup>1</sup>Popularly referred to as gekkos and pygopods (flap-footed lizards), they account for over 90 genera and 850 species (Table 1). In all sections of this paper, except Classification and Biogeography (pp. 39-42), I use current nomenclature, unless stated otherwise. Thus, the present character analyses can be more efficiently summarized and readily related to the data and interpretations of previous authors. Gekkota refers to both gekkonoids and Jurassic bavarisaurs. The taxonomic composition of the other higher taxa follows Kluge (1967a; 1974). While I endorse Wiley's (1981a) proposal that undiagnosed taxa be placed in shutter quotes, I have not employed that convention when citing previous research in order to simplify the presentation.

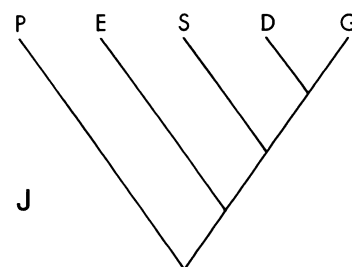
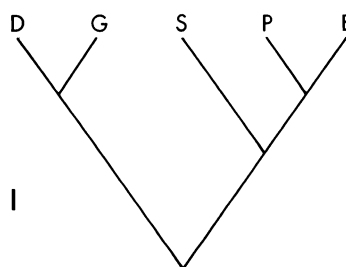
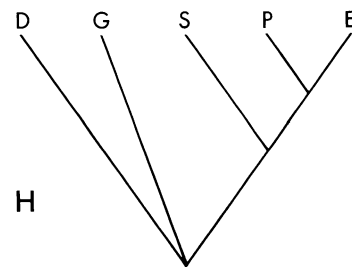
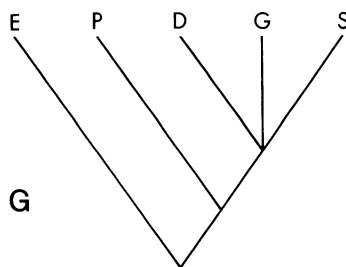
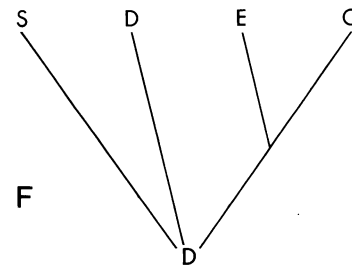
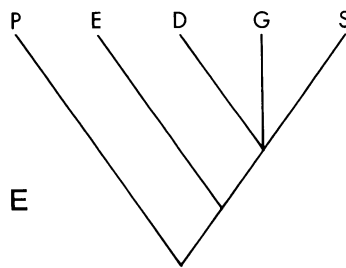
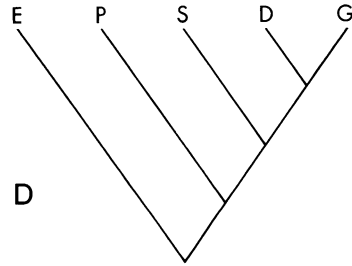
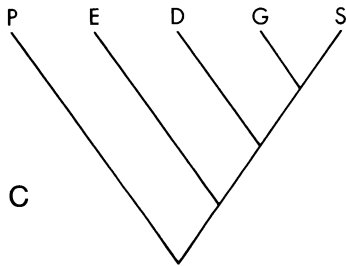
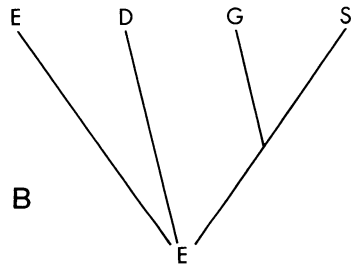
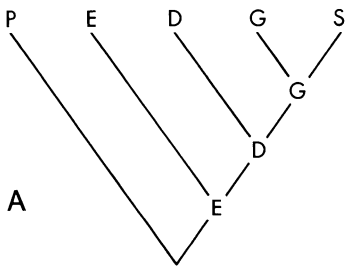
My Linnean classification was not totally consistent with, nor fully informative of, the phylogenetic hypothesis on which it was based (Kluge, 1967a; see also Wiley, 1981a,b). According to my 1967a data, neither Eublepharinae, Diplodactylinae nor Gekkoninae were diagnosed, and, thus, there was no evidential basis for the monophyly implied by those sub-familial names. I acknowledged the paraphyly of the Gekkoninae when I hypothesized a sister-group relationship between *Pristurus*, a gekkonine, and the Sphaerodactylinae. Further, I did not recognize formal taxonomic categories that would identify the hypothesized common ancestry of Diplodactylinae + Gekkoninae + Sphaerodactylinae, nor that of Gekkoninae + Sphaerodactylinae. The primary purpose of this paper is to derive a strictly monophyletic classification for a hypothesis of phylogenetic relationships of the Gekkonoidea (pp. 39-40).

Also in 1967 (Kluge, 1967b), I delineated two major genealogical lineages of diplodactylines, Carphodactylini (9 genera) and Diplodactylini (4 genera). The former group was described in terms of a novel patch of preanal pores, the latter by several osteological synapomorphies. Subsequently, I studied the taxonomy (Kluge, 1974) and cladistics (Kluge, 1976a) among pygopods, and I accepted Underwood's opinion (1957; see also Rieppel, 1984) that they are the sister-group to gekkos. More recently (Kluge, 1983a), I used the absence of the second ceratobranchial to diagnose the Gekkonini (35 genera, plus three assigned tentatively). The remaining 24, largely African, gekkonine genera did not share a novelty, and, as a paraphyletic assemblage, they were referred to as "Ptyodactylini."

Joger (1985) used molecular data to assess relationships among certain African gekkos. He assumed (p. 480) that his immunological distance measurements gave the "correct phyletic branching order; genetic distances... are not subject to convergent [evolution, and they] show a good correlation with the geological time passed since the separation of the phyletic branches..." The assumption of constant rate of evolution was not upheld by his own data; he had to employ a variable correction factor in certain comparisons because those distances "were constantly lower than those of the other antisera used (p. 481)." A similar finding might also follow from the relationships he identified between *Pachydactylus* and *Palmatogecko*. He concluded that *Palmatogecko* is much closer to some species of *Pachydactylus* than it is to others, and this can be interpreted as either (1) the latter genus is paraphyletic, or (2) the constant rate assumption is false.

FIG. 1. Recently proposed phylogenetic hypotheses of the major groups of gekkonoids (D = diplodactylines, E = eublepharines, G = gekkonines, P = pygopods, S = sphaerodactylines). A. After Kluge (1967a; redrawn from Fig. 2, except for placement of the pygopods which Kluge [1976a] considered the sister-group of gekkonoids). B. Attributed to Kluge (1967a) by Russell (1976). C. Attributed to Kluge (1967a) by Hecht (1976). D. After Hecht (1976: fig. 1C). Also, attributed to Moffat (1973a) by Russell (1979). E. Moffat's (1973a: fig. 1A) preferred hypothesis. F. After Werner (1961; also pers. comm.). G. After Moffat (1973a: fig. 1B). H. After Hecht (1976: fig. 1D). I. Attributed to Hecht (1976) by Russell (1979). J. Attributed to Underwood (1954, 1957) by Hecht (1976) and Russell (1979). Also attributed to Moffat (1973a) by Russell (1979).





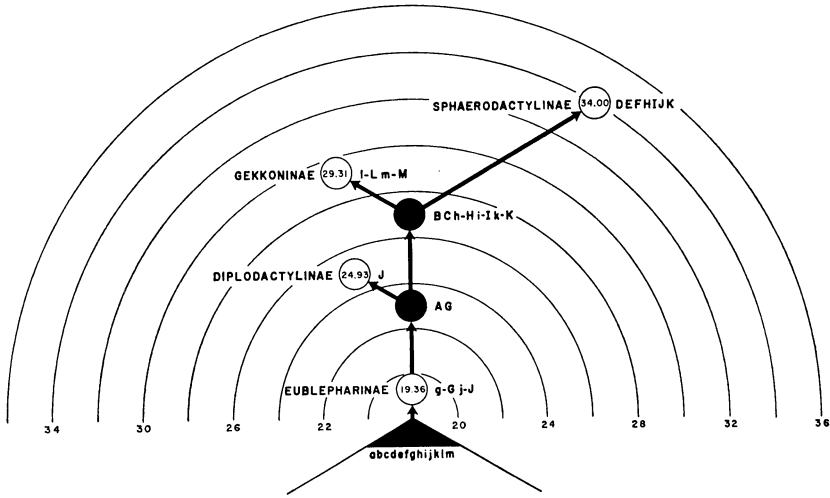


FIG. 2. The ground-plan divergence diagram published by Kluge (1967a:fig. 8). Open circles indicate the then recognized subfamilies, Diplodactylinae, Eublepharinae, Gekkoninae, and Sphaerodactylinae; closed circles are hypothetical intermediate nodes. The fractional numbers refer to the total divergence from the common ancestor over all 18 characters analyzed. Isolated letter symbols denote characters, lower case primitive, upper case derived. Once the character-state transition is plotted (e.g., a → A) the reader can assume that all derived clades also exhibit the apomorphic condition (e.g., A).

There is a large literature critical of genetic distances (e.g., Farris, 1981, 1985; Farris *et al.*, 1979, 1982a), and it is clear that Joger was mistaken when he asserted that immunological distances are not subject to convergent evolution. Other problems with Joger's paper include: an incomplete distance matrix; averaging distances over congeners; and not specifying which algorithm he used to cluster the data. The latter is especially critical because Joger claimed to have discovered the most parsimonious cladogram (his fig. 3). This is impossible, because fitting distances is a statistical problem, whereas only character data are judged in terms of parsimony. He incorrectly interpreted synapomorphy as unique and unreversed (Farris and Kluge, 1985, 1986), which underscores his poor understanding of phylogenetic inference.

Most of Joger's (1985) systematic conclusions are unconvincing and also invite criticism. He recognized three geographically coherent groups, northern Africa (*Geckonia*, *Ptyodactylus*, *Stenodactylus*, *Tarentola*), Afro-Madagascar (*Ailuronyx*, *Homopholis*, *Lygodactylus*, *Phelsuma*), and southern Africa (*Chondrodactylus*, *Colopus*, *Kaokogecko*, *Pachydactylus* [incl. *Elastmodactylus*], *Palmatogecko*, *Rhoptropus*), and he concluded that the latter two radiations were sister-taxa. This pattern of relationships leads to a relatively unparsimonious interpretation of the synapomorphies recognized by Haacke (1976) and Kluge (1983a); at least three independent losses and/or gains of hyperphalangeal first fingers and toes and elaborate cloacal spurs (see Fig. 12) and at least four cases of independent losses and/or gains of the

second ceratobranchial have to be postulated. Joger also attempted to account for some other morphological evidence in terms of his genetic distance hypothesis of relationships, but he failed partly because he overlooked significant variation. For example, he diagnosed the Afro-Madagascar assemblage as having fused nasals and paired frontals. However, this group is not convincingly supported by those characters, because one or both vary interspecifically in *Homopholis*, *Lygodactylus* and *Phelsuma*. *Homopholis* is particularly noteworthy, because *H. boivini* (UMMZ 127614) exhibits fused nasals and frontals, whereas both are paired in *H. fasciata* (UMMZ 127698) and *H. walbergi* (UMMZ 127699). Thus, I do not concur with Joger's conclusions.

Moffat (1973a) has also examined gekkonoid relationships. Limb reduction and presence/absence of the *rectus abdominis superficialis* muscle and sacral pleurapophyseal processes were used as evidence, in addition to 14 of the characters that I had analyzed (13 skeletal, plus the eyelid-spectacle transformation; Kluge, 1967a). She discarded four of my characters (vocal ability, clutch size, epidermal glands, endolymphatic system). Moffat treated each of the four major taxonomic groups of gekkonids that I recognized as if they were diagnosable and monophyletic. She accepted my hypothesis that Diplodactylinae + Gekkoninae + Sphaerodactylinae is a natural assemblage; however, she rejected the common ancestry that I proposed for Gekkoninae + Sphaerodactylinae. Her preferred hypothesis (Fig. 1E; see also 1G), with pygopods and gekkos as sister-lineages, was based on the assumption that flap-footed lizards possessed the *rectus abdominis superficialis* muscle, a presumed primitive condition, whereas gekkos had lost it. Subsequently, I was unable to locate that muscle in any gekkonoid and I treated the character as uninformative with respect to the relationships among gekkos and pygopods (Kluge, 1976b).

Hecht (1976), and Hecht and Edwards (1977), reexamined some of the data and hypotheses in Kluge (1967a) and Moffat (1973a). Hecht's, and Hecht and Edwards', modified data sets included the eyelid-spectacle transformation but only 10 of the skeletal features I had studied in detail; the nasal, hyoid arch, and squamosal characters were ignored. The three characters contributed by Moffat were analyzed, and they also added one of their own, the extreme development of the cochlear limbus. However, the limbus character is uninformative regarding gekko and pygopod relationships, because it is symplesiomorphic in the Gekkonioidea. Like Moffat (1973a), they treated the four subfamilies as if they were well-documented "natural groups" (Hecht, 1976:354). Even though Hecht, and Hecht and Edwards, seemed to accept Moffat's use of shared primitive traits as evidence of common ancestry, her inappropriate outgroup comparisons, and most of her data analyses (see section on Methods and Materials below), they rejected her preferred hypothesis of relationships. Instead, they endorsed the phylogeny illustrated in Figure 1D (see also Fig. 1H), which was influenced by their reinterpretation of intervertebral articulation, as well as by differential character weighting.

In considering intergeneric relationships within Diplodactylinae and Gekkoninae, Russell (1976, 1979) rediagrammed the hypotheses of Underwood, Kluge, Moffat, and Hecht. Unfortunately, most of his renderings misrepresented the original authors' opinions (Figs. 1B, D, I, J). Hecht (1976) committed a similar diagramming error (Fig. 1C). Given the substantial number of hypotheses, intended or misrepresented, that have appeared over the past 30 years (Fig. 1), discovery of new characters, and reinterpretation of some of the old data, I believe it is appropriate once again to review gekkonoid phylogenetic relationships and classification.

### METHODS AND MATERIALS

Only shared derived features, synapomorphies (Fig. 3), provide evidence of genealogical relatedness. Novelty hypothesized to have evolved but once are the most convincing basis for a proposition of common ancestry; traits hypothesized to have evolved more than once in the study group tend to be more ambiguous, especially if the instances of homoplasy are close on the cladogram. While one synapomorphy is sufficient, corroborated shared derived features are more compelling, and especially when those data are obtained from different sources (*e.g.*, skeleton and chromosomes [Kluge, 1983b]; Fig. 4). Synapomorphies are topographically, compositionally and ontogenetically similar (Patterson, 1982). A claim of putative homology is examined *in the context* of a particular hypothesis of relationships. For example (Fig. 3), the condition shared by (A+B+C) may be a relevant synapomorphy at that taxonomic level, but it is a symplesiomorphy, and uninformative, relative to (A+B).

Not all synapomorphies are congruent, which is to acknowledge that well-founded alternative genealogical hypotheses exist (Fig. 4), or that homoplasy exists and was not identified and eliminated in the pretesting stage of analysis (Patterson, 1982). The impasse created by contradictory evidence can be escaped by choosing the hypothesis supported by the most evidence. In effect, this is the simplest (most parsimonious) proposition, because the number of *ad hoc* singular hypotheses, such as homoplasy, are minimized. The most parsimonious explanation pertains to *all* character data provided in a given study (Kluge, 1984). If common ancestry is inferable from homologues and each synapomorphy is separately considered a putative homologue then the cladist can do no better than to use parsimony. To do otherwise is simply illogical and counterproductive to one's goals. I adopt the parsimony approach in reaching my conclusions of historical relationships among gekkonoids.

Estimating which of two or more similar attributes is derived (apomorphic) or primitive (plesiomorphic) is crucial to all phylogenetic systematic methods, and outgroup and ontogenetic criteria are widely used in those assessments. "Parsimonious outgroup analysis is accomplished by attaching an outgroup to the (undirected) most parsimonious tree for the group

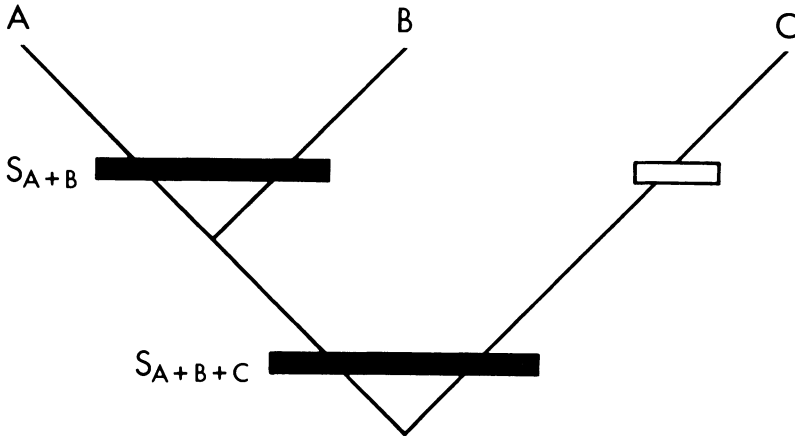


FIG. 3. Synapomorphy  $S_{(A+B)}$  (solid bar) supports the hypothesis that taxon (A+B) is a natural group, when the comparable condition in taxon C (open bar) is plesiomorphic. Should the apomorphic condition be found in C then the synapomorphy no longer provides evidence for (A+B), but it may provide evidence at a more inclusive level, such as (A+B+C).

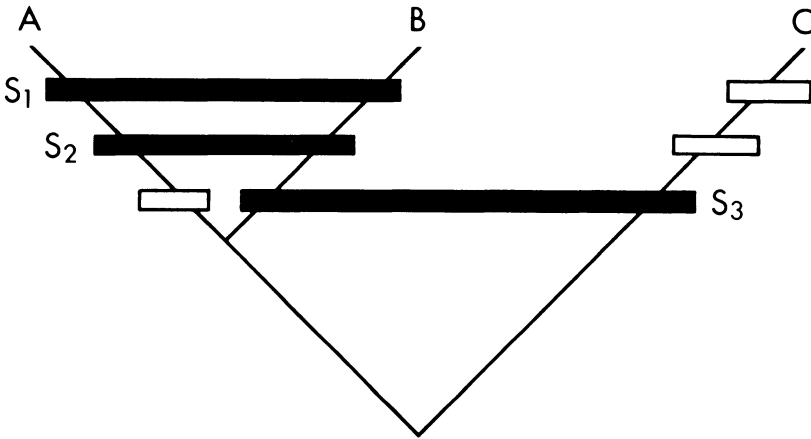


FIG. 4. Two synapomorphies  $S_1$  and  $S_2$  support the recognition of the (A+B) group, whereas synapomorphy  $S_3$  is evidence for another hypothesis of sister-group relationships (B+C). Under these circumstances of contradictory evidence,  $S_3$  is said to be incongruent with  $S_1$  and  $S_2$ . Having chosen the simplest hypothesis of relationships (A+B),  $S_3$  is interpreted as homoplastic.

analyzed so as to minimize the number of origins of features needed to account for observed properties of taxa" (Farris, 1982:329). The number of outgroups that need be considered to effect a maximally parsimonious hypothesis is related to the homogeneity of character-states in the outgroups, and the resolution of the relationships of the outgroups (Maddison *et al.*, 1984). The ontogeny criterion has been interpreted in either of two ways:

ontogenetic precedence, i.e., the state appearing earlier in a transformation series is plesiomorphic; or generality, i.e., the more common state in two or more ontogenies is primitive (Kluge, 1985; Kluge and Strauss, 1985). The outgroup criterion is preferred over the ontogeny criterion for three reasons. It is capable of detecting deleted and inserted stages in ontogeny, of testing Nelson's law pertaining to parallelism between ontogeny and phylogeny (Nelson, 1978), and of establishing the best fit to data at *all* levels of taxonomic universality, *viz.*, minimizing the number of *ad hoc* hypotheses (Farris, 1982; Kluge, 1985; Kluge and Strauss, 1985). In the present study, I use both outgroup and ontogeny criteria whenever possible. The few ontogenetic data available predicted the same polarity as the outgroup criterion. My review of the ancient gekkotans (see below) leads me to believe that Jurassic bavarisaurids are the immediate sister-group(s) of gekkonoids, and I employ these fossils in my outgroup analysis whenever they exhibit the character in question. I accept Camp's (1923:333) conclusion that *Autarchoglossa* (*sensu stricto*: Scincomorpha and Anguimorpha) and *Gekkota* are sister-groups (Estes, 1983b; Gauthier, 1982), and I include the former assemblages in my outgroup analyses as well. I consider *all* other lizards (Iguania included) when inferring plesiomorphy in particularly variable characters. Xantusiids, once thought to be gekkotans (McDowell and Bogert, 1954; Savage, 1963), are considered scincomorphs (Estes, 1983b; Moffat, 1973a).

A difference of opinion exists as to how knowledge is derived from phylogenetic hypotheses. Some view synapomorphy schemes as falsifiable, *sensu* the Popperian hypothetico-deductive method (*e.g.*, Gaffney, 1979). However, others, including myself, regard them as individual statements, not universals, and, thus, neither verifiable or falsifiable. They represent unique parts of the genealogy. Whereas paraphyletic groups can be viewed as classes (they are spatiotemporally unbounded things, timeless and eternal), cladists avoid recognizing them, because evidence for their historical reality cannot be obtained (they are not diagnosable, because they do not share a unique historical origin), and they would exhibit peculiar biological properties, such as never becoming extinct or becoming extinct by definition only. Some systematists regard the application of the rule of parsimony as a Popperian test (*sensu* falsification); however, I agree with Patterson (1978: 221) that "it belongs to the pretesting stage of the competition between two [or more] hypotheses, when each is checked for internal consistency." Similarly, evaluating the level of generality of an apomorphy (Fig. 3) does not seem to fit Popper's (1963) notion of conjecture and refutation, because a "preferred hypothesis" can always be saved with *ad hoc* propositions (Hull, 1983). Compositional and topographic similarity and ontogenetic origin of character-states also appear to be more a part of the pretesting stage of research. To be sure, we learn from our mistaken perceptions but this does not constitute the quality of discovery associated with testing a scientific hypothesis, where the consequent clause of the synthetic statement is potentially falsifiable. As I see it, the major contribution that Popper made

to phylogenetic systematics is not falsifiability, but insistence on presenting knowledge claims in their most exposed form so that they can be critically examined. Phylogenetic systematics may be preferred over other systematic philosophies, because its methodology is simple and clearly presented, data are treated explicitly, *ad hoc* hypotheses are minimized, and it is capable of discovering highly corroborated patterns of relationships (see summary in Kluge, 1983b).

Alternative phylogenetic hypotheses can be deduced from different data sets (Kluge, 1983b), but they also result from using different systematic methods. For example, Kluge's (1967a; Figs. 1A, 2) and Moffat's (1973a; Fig. 1E, G; see also Hecht [1976; Fig. 1D, H], and Hecht and Edwards [1977]) conclusions of sister-group relationships are at odds. The alternatives are probably due to different philosophies, because the data bases are nearly identical (pp. 1 - 6). The ground-plan divergence method of phylogenetic inference I employed (Fig. 2) was the forerunner of the now widely used parsimony approach of quantitative phylogenetic systematics, which I employ in this study (Kluge and Farris, 1969; Farris, 1970; Farris, *et al.*, 1970). [Swofford's (1985) "alltrees" option was used to find the best-fitting hypothesis.] Both methods assume putative homologous states are ordered according to their relative primitiveness, and both use shared derived states as evidence of recency of common ancestry (*i.e.*, the synapomorphy concept of Hennig [1966]). Furthermore, the two methods seek the branching diagram (or diagrams) that best fits all given polarized characters, and this is the most parsimonious hypothesis. The outgroup criterion, as applied to both fossils and living taxa, was the principal argument that I used in 1967 to deduce character-state primitiveness (Kluge, 1967a). Hecht (1976:350-351) and Hecht and Edwards (1977:41) claimed that I also employed a simplified weighting system and Darlington's concept of zoogeography in polarizing my characters. This is erroneous; perhaps they meant to direct these criticisms to Underwood (1954).

Moffat (1973a) misunderstands the outgroup criterion (Kluge, 1976a), and misapplication of this criterion might be responsible for her different systematic conclusions. For example, Moffat (1973a) often deduced the gekkonoid plesiomorphic state from the presence of that condition in nonsquamates (*e.g.*, cotylosaurs, eosuchians, archosaurs, pelycosaurs, ichthyosaurs and rhynchocephalians). She was also strongly influenced by the Triassic kuehneosaurs. The latter are not lepidosaurs (Benton, 1985; Evans, 1984). Elsewhere, Moffat even showed (p. 279) a preference for the questionable "common equals primitive," or ingroup, criterion (see also Estabrook [1977]): "The determination of the primitiveness of character-states in living organisms from a comparison of these organisms with one another is based on the following assumption: if the same character-state occurs in two or more species or groups of species (genera, families, etc.) of living organisms it is assumed to have been inherited from a common ancestor unless there is evidence to show that it has arisen independently in these taxa as a result of parallel evolution." She overlooked the possibility that the shared state may be derived, not primitive (*e.g.*,  $S_{A+B}$  in Fig. 3).

Moffat (1973a) rightly emphasized unique character-states as evidence of common ancestry. Unfortunately, she also emphasized plesiomorphic states as evidence. That Moffat's research on gekkonoid relationships relied on symplesiomorphies can be concluded from her following statements: "If an advanced character-state can be shown to have arisen only once within the Gekkota so that it is unique within this group, *it is as important as the primitive state of the character for determining gekkotan relationships inter se*" (p. 286; my italics). "The greater the antiquity of a character-state . . . the greater is the probability that it is in fact unique. . . . A character-state which was present in the earliest reptiles, was inherited by eosuchians and later by the earliest known squamates and rhynchocephalians and is also present in geckos is almost certainly unique and is therefore of considerable importance in establishing the phylogenetic relationships of the Gekkonidae, not only *inter se*, but with other lizards as well. . . . The term unique can be used, not in its strict, absolute sense, but in a relative sense to describe a character-state which has arisen only once, within a particular taxon. Such a unique advanced state within that taxon will be a primitive state in all smaller groups possessing it within the taxon concerned" (p. 279).

I review 56 sources of evidence, those most often used in the recent literature on gekkonoid phylogeny, and 44 of the least variable of these characters are included in the final analysis. More lengthy character descriptions and illustrations can be found in the references provided. An array of newly discovered synapomorphies will be published separately, because they require more detailed and lengthy descriptions. I have lumped most genera into higher taxa in order to simplify my presentation and discussion of the evidence and the final conclusions. Only *Gonatodes*, *Pristurus* and *Teratoscincus* are recognized separately, because they exhibit corroborated sister-group relationships with more diverse clades. The following abbreviations are used in referring to the repository of specimens: FMNH (Field Museum of Natural History, Chicago), MCZ (Museum of Comparative Zoology, Harvard), NMV (National Museum of Victoria, Melbourne), RT (Richard Thomas, personal collection), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), USNM (United States National Museum, Washington, D.C.), WAM (Western Australian Museum, Perth).

#### ANCIENT GEKKOTANS

Two groups of Upper Jurassic lizards have been assigned for many years to the Gekkota (Hoffstetter, 1964; Estes, 1983a,b). One of these, Ardeosauridae, consists of three genera, *Ardeosaurus* and *Eichstaettisaurus* from Germany, and *Yabeinosaurus* from Manchuria; while the other family, Bavarisauridae, consists of two genera from Germany, *Bavarisaurus* and *Palaeolacerta*. Neither assemblage can be convincingly diagnosed (Kluge, 1967a:12), and the relationship of the former group to gekkonoids is not well-documented (Estes, 1983a,b). For example, the similarity of maxillary



and vertebral shape, and the presence of paired premaxillae, many small teeth, and intercentra might be used to relate ardeosaurs to gekkotans (Estes, 1983b; R. Estes, pers. comm.); however, those same conditions are also found among a wide variety of other lizards. Moreover, *Ardeosaurus* exhibits extensive dermal rugosities and much enlarged epidermal scutes, and the latter are like those peculiar to the Autarchoglossa (Gauthier, 1982; Mateer, 1982). The absence of any indisputable gekkotan synapomorphies, coupled with the similarity of the size and shape of their cranial scutes, suggests that ardeosaurs might be more closely related to the autarchoglossan clade. The absence of a pineal foramen (Gundy and Wurst, 1976) and the presence of amphicoelous centra, both derived states among lizards, are found in bavarisaurus and gekkonoids, and those synapomorphies appear to provide somewhat better evidence of their common ancestry (Hoffstetter, 1964). Thus, I treat *Bavarisaurus* and *Paleolacerta* as sister-taxa to gekkonoids; however, I withhold judgment on ardeosaur classification. Ostrom (1978: 113) concluded that *Bavarisaurus macrodactylus* was "a very fast-running, predominantly ground-dwelling lizard, perhaps similar to the living species of *Cnemidophorus*." If this interpretation is correct, it would have been similar to *Pristurus*, which has atypical habits among gekkonoids.

## CHARACTER ANALYSES

### INFORMATIVE CHARACTERS<sup>2</sup>

1-2. INTERVERTEBRAL ARTICULATION.—Adult squamate vertebrae are often referred to as being either amphicoelous or procoelous (Hoffstetter and Gasc, 1969). Traditionally, the salient parameter in this dichotomy has been simply the shape of the intervertebral surface of each centrum: biconcave in amphicoelous vertebrae, concave anteriorly and convex posteriorly in procoelous vertebrae. Considerable controversy exists concerning the usefulness of this character in reptilian systematics, especially when employed as evidence of phylogenetic relationships among gekkos and pygopods (Hecht, 1976; Hecht and Edwards, 1977; Hoffstetter and Gasc, 1969; Kluge, 1967a; Moffat, 1973a; Underwood, 1954, 1955, 1977). Before reconsidering this character as evidence of gekkonoid relationships, it is necessary to summarize Winchester and Bellairs' (1977) excellent study of the developmental history of squamate centra. I believe their observations help to settle the controversy surrounding the definition of the shape of the intervertebral surfaces in gekkotans and to put the question of homology on a much firmer foundation (Patterson, 1982). The following remarks pertain only to trunk vertebrae, because of considerable regional variation (Holder, 1960; see also

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<sup>2</sup>The characters are discussed in the approximate order in which their synapomorphies resolve the different levels of gekkonoid common ancestry (Fig. 11). They are numbered in order to simplify the conclusions and their presentation in Table 3.

below). The atlas-axis, sacral, and caudal vertebrae with autotomy are the most highly modified segments of the vertebral column and their morphology is not discussed.

According to Winchester and Bellairs (1977), development of a mid-trunk centrum is relatively simple and similar in all snakes and lizards, including *gekkos*. Initially, a condensed mass of mesenchyme, the perichordal tube, forms around the notochord. The definitive intersegmental pattern of vertebral position becomes evident when intersclerotomic fissures disappear, postsclerotomite and presclerotomite masses fuse, and the perichordal tube thickens ventral to that fusion. Chondrification begins within the perichordal tube on each side of the notochord. Perichondral ossification then takes place midway along the centrum on its ventral and ventrolateral margins. A thin tube of perichondral bone exists at birth or hatching. Endochondral bone formation occurs during postnatal life and is usually completed at sexual maturity. Replacement of cartilage with bone, constriction of the notochord, and disappearance of the notochordal sheath takes place earlier in the centrum than it does in the intervertebral joint. A labyrinth of marrow spaces usually occupies much of the body of the adult centrum. These spaces are easy to confuse with the notochordal canal, which may persist in adults as a continuous tube, except where interrupted by the midvertebral chordal cartilage (Holder, 1960).

The vertebrae remain continuous until chondrification and perichordal thickenings give rise to intervertebral joints (Winchester and Bellairs, 1977). The condyle of a procoelous vertebra is an outgrowth of the centrum. It begins as a slightly chondrified ring of tissue around the outer margin of the centrum. The condyle grows into a nearly solid ball with further cartilage formation, rounding outward posteriorly and filling internally. The anterior end of the centrum also chondrifies first around the rim; however, additional development is limited to a narrow zone covering the concave surface of the centrum. The notochord is constricted, both posteriorly and anteriorly, where the ball and socket joints form. A continuous, only slightly constricted, notochord may remain in adults, particularly in amphicoelous *gekkos* (Holder, 1960). The pad between the ball and socket of successive vertebrae develops from perichordal thickening, and a synovial cavity may be found therein in some squamates.

Hoffstetter and Gasc (1969) and Werner (1971) contended that there is a basic difference in the mode of condyle formation between procoelous *gekkos* and other procoelous squamates. These claims are unfounded according to the research of Winchester and Bellairs (1977).

Some authors (*e.g.*, Holder [1960] and Moffat [1973a]) have modified the definition of the procoely-amphicoely character in squamates to include the persistence of the notochord in the adult and the presence or absence of an intercentrum. Moffat (1973b) complicated matters further by recognizing two "mechanically" different joints between centra, diarthroses and amphiarthroses. According to Le Gros Clark (1939:136), however, "one may recognize immovable joints or *synarthroses*, freely moveable joints or

*diarthroses*, and, as an intermediate category, *amphiarthroses* or partially moveable joints. All diarthroses are formed by cartilage-covered articular surfaces, separated by a joint cavity which is lined by a synovial membrane. In synarthroses and amphiarthroses on the other hand, the articulating bones are united by fibrous tissue or cartilage." Moffat (1973b) stated that notochord tissue is resorbed during development in diarthrotic vertebrae whereas joints are usually traversed by a persistent notochord in amphiarthrotic vertebrae. She concluded that the non-synovial type of articulation characterizes the Gekkota and *Xantusia vigilis*. Apparently, this complex and confusing characterization led Hecht (1976; see also Hecht and Edwards [1977]) to assume that Moffat (1973a; see also Holder [1960]) had actually identified four character-states: true amphicoely (Gekkoninae and Diploctylinae), partial amphicoely (Sphaerodactylinae), non-synovial procoely (Eublepharinae and pygopods), and synovial procoely (all other modern lizards). According to A. d'A. Bellairs (pers. comm.) and Winchester and Bellairs (1977), the type of joint present in squamates is not always dictated by presence or absence of the notochord. For example, neonate *Anguis* and *Natrix* have a somewhat constricted notochord that passes through the synovial cavity and articular cartilages (Winchester and Bellairs, 1977:fig. 3). Furthermore, intervertebral joints in *Lacerta* are amphiarthroses, without synovial cavities, and indistinguishable from those of procoelous gekkonoids. Thus, I conclude that the type of joint does not provide unambiguous evidence of gekkotan common ancestry, and, further, recognizing such conditions does not help to delimit centrum shape more accurately among squamates.

I suspect that adding the conditions of the notochord and presence or absence of intercentrum to the shape character has unnecessarily confused matters. I have reanalyzed these three variables as if they were independent. If they are found to be perfectly congruent on the best-fitting phylogenetic hypothesis, then one of the three characters, or some combination, might be considered sufficient to describe the diversity in the gekkotan intervertebral articulation. If the three are incongruent then there is good reason to continue to treat them as separate characters.

*Intervertebral Articulation* (Character 1). Among the reproductively mature (adult) gekkonoid skeletons examined (see Appendix I for generic survey), only the following possessed a well-developed condyle, and they may be viewed as procoelous: all eublepharines, pygopods, and sphaerodactylines, except *Gonatodes* (Noble, 1921; Holder, 1960), and only *Ebenavia* among gekkonines (Kluge, 1967a). A few *Gonatodes* approached procoely; however, the vast majority were decidedly different from all other sphaerodactylinae genera (Fig. 5). Hecht (1976:355) and Hecht and Edwards (1977) implied that a "single species" of *Pristurus* was procoelous; they probably meant to cite *Ebenavia*. I examined several cleared and stained adult *Pristurus*, representing two species groups (Kluge, 1983b), and found no mid-trunk centra that were definitely procoelous (*P. carteri*, UMMZ 127747; *P. crucifer*, UMMZ 127748a-b; *P. flavipunctatus*, UMMZ 127749, 127750a-b;

*P. sokotranus*, UMMZ 127751). On the other hand, a few diplodactylines possessed vertebrae that were more procoelous than amphicoelous (*Carphodactylus laevis*, UMMZ 127508; *Crenadactylus ocellatus*, UMMZ 127509a-b, 127510a-c, 127511-12, 127523; *Diplodactylus vittatus*, UMMZ 127563-65; *Oedura marmorata*, UMMZ 127583; *Phyllurus milii*, UMMZ 127591a-b; *Rhynchoedura ornata*, UMMZ 127602), although most species and genera in this group were typically amphicoelous. The extensive variation in the Diplodactylinae was confirmed by Moffat (1973a:285), but was overlooked by Hecht (1976) and Hecht and Edwards (1977).

*Notochord* (Character 2). According to Holder (1960; see also Werner [1971]), the notochordal canal persists throughout the centrum, except for chordal cartilage interruption, in adult diplodactylines, gekkonines and sphaerodactylines. The canal remains large in the intervertebral joint in amphicoelous gekkos. The effect of procoelous condylar development on canal diameter appeared slight in *Sphaerodactylus*, and was hardly evident in *Phyllurus milii*. Similarly, there was little notochordal constriction in the adult *Ebenavia inunguis* examined (SVL = 40 mm; UMMZ 127634).

Moffat (1973a:table 3) reported notochordal centra for adult eublepharines, and my study of a large series of cleared and stained *Eublepharis macularius* and *Coleonyx variegatus* has largely confirmed her statement. For example, juvenile *E. macularius* (SVL = 56-67 mm; UMMZ 172894-96) exhibited little or no evidence of procoely and the notochord was large intervertebrally. A subadult *E. macularius* (SVL = 74 mm; UMMZ 172893) had weakly developed condyles, but notochord size appeared little affected within intervertebral joints. Procoely was well-developed in adults (SVL = 116-134 mm; UMMZ 127504-505) and notochord diameter was greatly reduced within the ossified cartilaginous ball. According to Moffat (1973a), the canal persisted throughout the centrum. This adult state is reminiscent of the condition reported by Winchester and Bellairs (1977:fig. 3) for neonate *Anguis*, *Lacerta*, and *Natrix*, which are considered procoelous squamates. *Coleonyx* was similar to *Eublepharis*. Adult *C. variegatus* (e.g., UMMZ 127519, 127521) possessed a tiny, but persistent, notochord; it was slightly larger at the concave end of the centrum. The presence of an open notochordal canal in adult eublepharines can be inferred from the small depression located at the condyle apex, without actually having to section the centrum. An adult *Aeluroscalabotes felinus* (SVL = 92 mm; UMMZ 127494) exhibited no such canal, when viewed in mid-sagittal section. Thus, not all eublepharines retain a notochord throughout life, contrary to Moffat's statement (1973a). The interior of the condyle, as well as the core of the centrum proper, consisted of spongy bone; however, it appeared to be much denser than in other adult eublepharines.

The observations on pygopods were similar to those described above for eublepharines. The notochord, while reduced in diameter in adults, usually persisted intervertebrally as a tiny canal, although it was obliterated entirely in some especially large specimens. For example, adult *Aprasia* and *Delma* possessed a large notochordal canal (*A. repens*, SVL = 99.5 mm, UMMZ

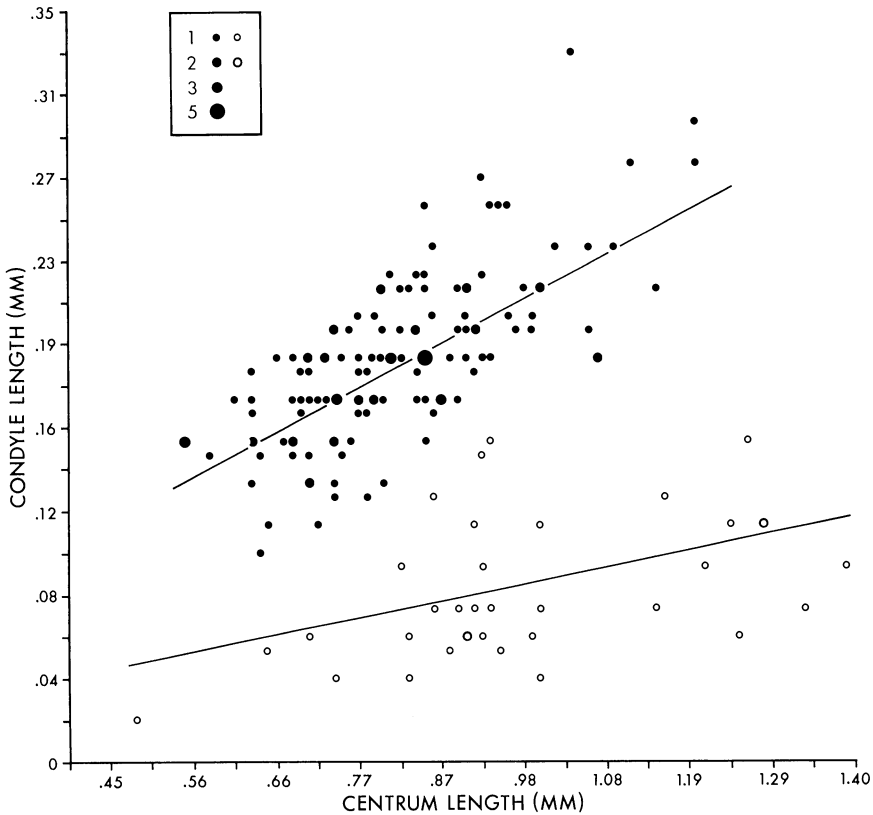


FIG. 5. The degree of condyle development in sphaerodactylines. Open circles are individuals of 14 species of *Gonatodes*. Closed circles are individuals of *Coleodactylus* (3 species), *Lepidoblepharis* (5 species), *Pseudogonatodes* (4 species), and *Sphaerodactylus* (47 species). Size of symbols indicates number of superimposed observations (see legend). Solid lines are derived from least squares regression analysis of the two sets of data (open and closed circles).

137573; *D. australis*, SVL = 59.5 mm, UMMZ 84309). However, an adult *Pygopus nigriceps* (SVL = 163.0 mm, UMMZ 129980) exhibited no evidence of a canal at either end of any of its trunk vertebrae.

I conclude that the notochordal canal usually persists throughout life in gekkonoids, although it is constricted in procoelous eublepharines and pygopods, especially intervertebrally. The failure to obliterate the notochordal canal during ontogeny may be considered a gekkonoid synapomorphy (Holder, 1960; Winchester and Bellairs, 1977). Eventually, that persistence may be found to predate the origin of the Gekkonoidea, as inferred from the presence of well-developed amphicoely in the Jurassic bavarisaurus (Estes, 1983a).

*Intercentrum.* There is considerable difference of opinion regarding the distribution of the gekkonoid intercentrum. For example, Noble (1921) maintained that the intercentrum is gradually lost, with increasing procoely,

in sphaerodactylines (*Gonatodes* to *Lepidoblepharis* to *Sphaerodactylus*). Camp (1923) stated that these tiny crescent-shaped bones fuse with the condyles of procoelous vertebrae, whereas Holder (1960:300) claimed that "intercentra typically persist throughout the [vertebral] column in both amphicoelous and procoelous" forms. While I basically agree with Holder that the intercentrum is usually present, there is considerable variation both regionally and taxonomically. When intercentra were observed, those in postcervical segments were smaller than in cervical segments and sometimes absent. Postcervical intercentra could not be identified with certainty in *Aprasia*, *Delma*, or *Pletholax*; however, they were present in *Lialis* and *Pygopus* (for list of specimens examined see Kluge [1976a]). In *Pygopus*, the bone was intraspecifically variable (in both *P. lepidopodus* and *P. nigriceps*): in some individuals it existed in all body segments, whereas in others it was present only in the anteriormost few. All *Lialis* (*L. burtonis* and *L. jicari*) had well-developed intercentra throughout the vertebral column, although those in anterior segments were much larger; those in the lumbar region were smaller and often divided into two pieces.

Among 170 cleared and stained sphaerodactylines, representing all genera and the majority of the species, only seven species appeared to show loss of mid-trunk intercentra. The bone was absent in both *Coleodactylus amazonicus* specimens examined (UMMZ 127803a-b), and in the only specimen of *S. inaguae* available (UMMZ 127815). Intraspecific variation was observed in *Pseudogonatodes lunulatus* (absent, MCZ 48894; present, UMMZ 124312), *Sphaerodactylus argus* (absent, USNM 192526; present, KU 157110, UMMZ 127809a-c, USNM 40510), *S. cinereus* (absent, UMMZ 127810; present, RT 4108, UMMZ 127811), *S. klauberi* (absent, UMMZ 143252; present, RT 3902, UMMZ 73594), and *S. parkeri* (absent, UMMZ 127821; present, UMMZ 127820). No doubt the smallness of the bone, its regional variation, and obscure position intervertebrally have contributed to a certain amount of error in observation and difference of opinion among authors. For example, Noble's (1921) conjecture that the intercentrum is reduced in size as a function of increasing procoely cannot be supported, because the width of intercentrum was not correlated with length of condyle in sphaerodactylines (for *Coleodactylus*, *Lepidoblepharis*, *Pseudogonatodes* and *Sphaerodactylus*,  $n = 133$ ,  $r = .375$ ,  $P > .01$ ; for *Gonatodes*,  $n = 35$ ,  $r = .684$ ,  $P > .01$ ).

*Summary.* The more complex definitions of procoely and amphicoely advocated by Holder (1960; see also Moffat [1973b]) seem to have led to questionable interpretations of relative primitiveness of the two intervertebral articulation states in gekkonoids. For example, adult *Sphenodon* are amphicoelous and retain a well-developed notochord and intercentrum. Amphicoelous gekkos also retain a notochord and possess an intercentrum. The implication is that because all three parameters of the definition are the same in *Sphenodon* and certain gekkos, each of the states in the latter (especially shape of the intervertebral articulation) is more likely to be primitive. This is tantamount to assuming the phenotype is incapable of undergoing differential evolution. Alternatively, a well-developed condyle

(classical procoely) might be considered plesiomorphic in the Gekkonoidea, because that shape is widespread among all other lizards (see Kluge [1967a] and Gauthier [1981, 1982] for explicit uses of the outgroup criterion). However, existence of amphicoely in a radiation of Jurassic gekkotans (bavarisaurus) could be considered evidence that amphicoely is primitive in the Gekkonoidea, as I will further discuss below (pp. 36-38). Moffat's (1973a:300-301) argument for amphicoely being primitive is not compelling, especially since she used cotylosaurs, pelycosaurs, ichthyosaurs, eosuchians and rhynchocephalians as outgroups to the Gekkonoidea. Underwood (1954, 1955) reversed his opinion as to plesiomorphic state, from procoely to amphicoely, because he considered the Triassic kuehneosaurs to be definitive lizards (see also Hoffstetter and Gasc [1969], and Carroll [1977]); Moffat (1973a:278) was similarly influenced by the Triassic material. These fossils are no longer believed to be lizards (Benton, 1985; Estes, 1983a; Evans, 1982, 1984), and, thus, are an inappropriate outgroup to gekkonoids (Kluge, 1967a). Underwood's most recent opinion (1977), that procoely is plesiomorphic, was based on a within-group parsimony argument. Gauthier's (1981) preference for procoely as the primitive gekkonoid centrum shape led him to conclude that amphicoely was acquired secondarily through paedomorphosis.

3. STAPEDIAL FORAMEN.—The stapedia (facial) artery passes through the stapes in primitive amniotes; however, the stapedia foramen is absent in *Sphenodon* and most squamates (Greer, 1976). The squamate exceptions are the dibamids *Anelytropis* and *Dibamus*, and a wide variety of gekkonoids. The outgroup criterion suggests an imperforate stapes is the primitive state among gekkonoids. All eublepharine and sphaerodactylina genera listed in Table 1 have a stapedia foramen. An imperforate stapes in one *Coleodactylus amazonicus* (UMMZ 127803), one *Lepidoblepharis microlepis* (UMMZ 127804) and one *Pseudogonatodes barbouri* (UMMZ 127808), out of 255 sphaerodactylines examined, documents minor individual variation. All pygopod and diplodactylina genera, except *Eurydactylodes*, lack a stapedia foramen. Gekkonines are variable, as the following list indicates: Foramen absent - *Ailuronyx*, *Cnemaspis*, *Ebenavia*, *Gekkonina*, *Gehyra*, *Gekko*, *Hemiphyllodactylus*, *Homonota*, *Lepidodactylus*, *Perochirus*, *Phyllodactylus*, *Ptenopus*, *Ptychozoon*, *Ptyodactylus*, *Thecadactylus*, *Urocotyledon*, and *Uroplatus*. Foramen present - *Afroedura*, *Aristelliger*, *Bunopus*, *Calodactylodes*, *Chondrodactylus*, *Cosymbotus*, *Cyrtopodium*, *Geckolepis*, *Gonydactylus*, *Hemidactylus*, *Heteronotia*, *Homopholis*, *Lygodactylus*, *Pachydactylus*, *Palmatogekko*, *Phelsuma*, *Phyllodactylus*, *Pristurus*, *Quedenfeldtia*, *Rhoptropus*, *Saurodactylus*, *Stenodactylus*, *Tarentola*, *Teratoscincus*, and *Tropicolotes*. A more extensive survey of gekkonines is being compiled, and it will be published separately.

According to Rieppel (1984), the stapedia artery passes through the stapedia foramen or in front of the stapes in all gekkos and pygopods. I am reluctant to accept Rieppel's conclusion that this is evidence for the historical reality of the Gekkonoidea, because a combination of character-states is involved (Farris *et al.*, 1982b).

4. EXTRACOLUMELLA.—Gekkos and pygopods are exceptional among lizards in not having an internal process on the extracolumella (Wever, 1978). I accept Rieppel's (1984) opinion that this state is a synapomorphy of gekkonoids.

5. EXTRACOLUMELLA MUSCLE.—Gekkonoids have an extracolumella muscle, which is found in no other lizards according to Wever (1978). Although only a single pygopod species has been examined (*Lialis burtonis*), presence of this muscle is tentatively treated as a synapomorphy of the Gekkonioidea (see also Rieppel, 1984).

6. SPINDLE BODY.—The tectorial membrane, near its origin from the cochlear limbic lip, has a prominent thickening called the spindle body (Wever, 1978:80). This structure has been found only in gekkos and pygopods, and is considered a synapomorphy of the Gekkonioidea.

7. AUDITORY PAPILLA.—Gekkonoids have a peculiar pattern of hair cells along the auditory papilla (Wever, 1965, 1978). The "papilla is segmented, with a dorsal portion containing hair cells whose ciliary tufts are attached to a tectorial membrane and a ventral portion divided longitudinally so that the hair cells on one side continue to tectorial attachments whereas those on the other side are surmounted by a line of sallets that make the ciliary connections" (Wever, 1978:467). I interpret this arrangement to be a gekkonoid synapomorphy.

8. COCHLEAR DUCT AND BASILAR MEMBRANE.—Shute and Bellairs (1953; see also Wever [1978]) drew attention to the elongation of the gekkonid cochlear duct and basilar membrane. The lengths of these structures appear not to be exceeded in any other lizard, with the exception of pygopods (Wever, 1978:587). Thus, the elongate state is considered a gekkonoid synapomorphy.

9. QUADRATE SUSPENSION.—Rieppel (1984:297, 305, 309) recognized a type of quadrate suspension peculiar to gekkonoids, which he called "paroccipital abutting." The dorsomedial end of the quadrate articulates relatively loosely with a small but conspicuous facet on the anteroventral surface of the paroccipital process of the opisthotic (Kluge, 1962). Neither the supratemporal or squamosal seem to play a major role in keeping the head of the quadrate in place against the process. According to Rieppel, a ligament usually extends between the quadrate head and the squamosal and performs that function. The suspension is especially delicate in those species that have lost the squamosal (see below).

10-11. CLOACAL BONES AND SACS.—Typically, gekkonoids possess one or two pairs of postcloacal bones and a pair of associated postcloacal sacs (Kluge, 1967a). These structures appear to be unique, and are considered synapomorphies of the Gekkonioidea. Loss of these bones and sacs "may have occurred as many as six times independently" (Kluge, 1982:354). Such a high degree of variation means that their absences do not provide especially good evidence of relationships. Hecht and Edwards (1977) did not mention that variation, and Moffat (1973a) incorrectly stated that male pygopods of the genus *Pletholax* have no postcloacal bones (Kluge, 1982). I cannot



imagine a reasonable causal basis for Russell's (1972:244) claim that "the loss of cloacal sacs and bones is intimately associated with diurnality."

12. MEATAL CLOSURE MUSCLE.—Versluys (1898) discovered the meatal closure muscle in gekkonids, and Wever (1973, 1974, 1978) described in detail its taxonomic distribution, structure, and function. A tiny posteriorly located meatal muscle, also a specialized derivative of the *constrictor colli*, is present in a few anguids, but its anatomy does not suggest a closure function (Wever, 1978). The muscle is well-developed and widespread among gekkonoids, where it appears to close the external auditory meatus (Wever, 1978). I assume the closure function to be a gekkonoid synapomorphy (Fig. 6).

Among gekkonoids, the muscle takes two extreme forms: (1) L-shaped, bordering the posterior and ventral meatal margins, and (2) O-shaped, entirely or nearly completely encircling the meatus. I consider the O-shaped condition apomorphic, the L-shaped state being anatomically more like the assumed primitive ventral position. My assumption is based on the ventral position of the *constrictor colli*, from which the closure muscle fibers originate. The L-shaped state is found in all eublepharines investigated and all, except a few diurnal, gekkonines. The O-shaped condition characterizes diplodactylines + pygopods. The muscle completely encircled the external auditory meatus in *Pseudothecadactylus* (UMMZ 127150), nearly encircled it in *Hoplodactylus* (UMMZ 127158), and was more open and C-shaped in *Naultinus* (UMMZ 129352). In *Carphodactylus laevis* (UMMZ 131419), the muscle seemed to be confined to the posterior meatal margin. The quadrate is exceptionally well-developed in this species, and its bony lateral margin contacted the dorsal, anterior, and ventral meatal rim. Such contact appears to make impossible any closure function in these areas. Thus, I consider the *Carphodactylus* condition to be a specialized form of the O-shaped state.

The meatal muscle is absent in all sphaerodactylines, *Pristurus* (*P. crucifer* and *P. phillipsi* were examined [MCZ 71910, 72013]), and in occasional gekkonines (*Phelsuma dubia*, *P. madagascariensis*, and *Lygodactylus*). I assume absence to be a loss, an apomorphic condition (Fig. 6), because that state occurs in highly derived taxa. For example, the muscle was well-developed in most *Cyrtopodion* species, but only a few fibers existed on one side, and none on the other, in some but not all individuals of *C. kotschy orientalis*. Such variation suggests the loss of the muscle has been achieved independently, perhaps several times among gekkonines.

13. EYE-LICKING.—Moffat (1973a) recorded eye-licking behavior among all major gekkonoid lineages and treated such behavior as a synapomorphy of the group. That hypothesis is adopted here, although Gauthier's (pers. comm.) observations of similar behavior among xantusiids may cast doubt on this feature being diagnostic of gekkonoids. In any case, the evolution of eye-licking behavior must be considered independent of the gekkonoid spectacle because the behavior also occurs in eublepharines whereas the spectacle does not (Bustard, 1963, 1965; Moffat, 1973a).

14. QUADRATE APONEUROSIS.—Rieppel (1984) stated that the aponeurosis lying in the external adductor muscle, immediately anterior to the quadrate,

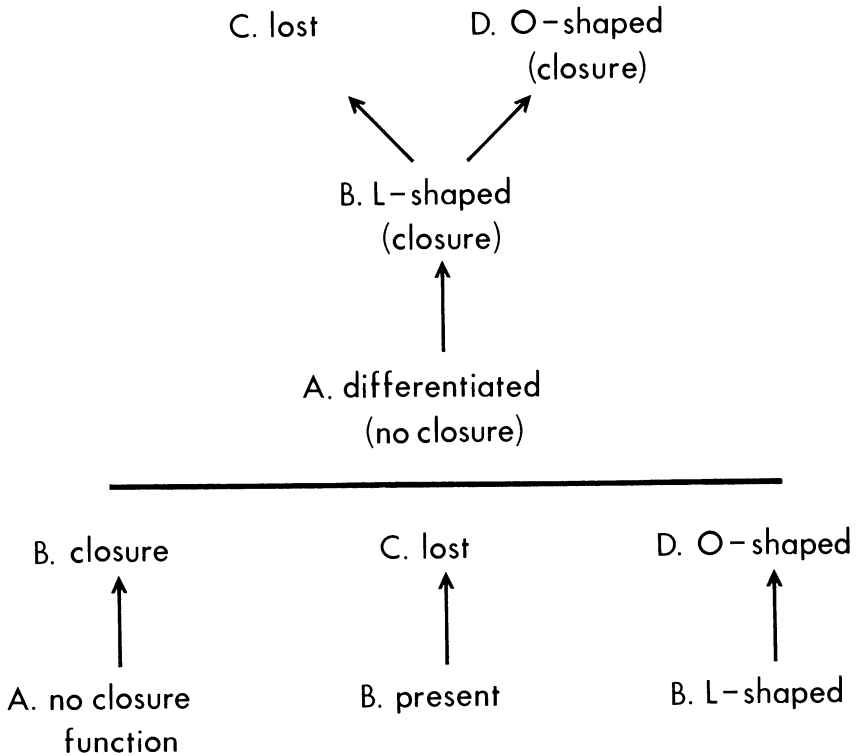


FIG. 6. The meatal muscle transformation series adopted in this paper. The complex character-state hypothesis is diagrammed above the horizontal line, the single-step transformations below.

is present in pygopods but absent in gekkos. If the aponeurosis is widespread among autarchoglossan lizards, as Rieppel stated, then there is evidence for gekkos being a natural entity, excluding pygopods. However, I have been unable to locate the aponeurosis in primitive pygopods, *Delma* and *Pygopus* (Kluge, 1976a), and I believe the loss of that sheet of connective tissue to be diagnostic of the Gekkonoidea. Rieppel examined several of the more derived pygopods, including *Aprasia*, *Lialis*, and *Pletholax*, but only one *Pygopus*.

15. EGG-TEETH.—A pair of dentinal egg-teeth was observed in all gekkos, except ovoviviparous diplodactylines, and I interpreted these teeth as a mark of gekko common ancestry (Kluge, 1967a). The paired condition has also been found in pygopods (*Lialis burtonis*, NMV D57183-84; *Pygopus lepidopodus*, UMMZ 175937-38; see Fig. 7), which provides further evidence that gekkos + pygopods is a natural group. The single dentinal egg-tooth exhibited by other squamates and *Sphenodon* is considered primitive. The epidermal caruncle found in turtles and crocodylians serves a similar purpose, but it does not belong to the same transformation series as the squamate egg-tooth. Woerdeman (1919, 1921) claimed that the paired egg-

teeth of gekkonids belongs to a different and later generation of teeth than the single median tooth of other lizards (see De Beer [1949] for an alternative opinion, and Smith *et al.* [1953] for a more complete discussion).

16. MIDBRAIN.—Evidence for gekkonoid monophyly can be found in the midbrain. Northcutt (1978:46) pointed out that pygopods and gekkos share a unique periventricular tectal lamina.

17. VISUAL CELLS.—Underwood (pers. comm.) examined the retinas of several gekkos (*Aristelliger* — two species; *Coleonyx*; *Gehyra*; *Gekko*; *Gonatodes* — three species; *Hemidactylus*; *Hoplodactylus*; *Naultinus*; *Phelsuma* — two species; *Phyllodactylus*; *Sphaerodactylus* — two species; *Tarentola*; and *Thecadactylus*) and two pygopods (*Aprasia* and *Lialis*). Underwood (1970; pers. comm.) concluded that the type C double visual cells present in gekkos are unique among squamates. They have straight horizontal rows of alternating doubles, with type A singles and type C doubles between them. Type C doubles have not been observed in pygopods (Underwood, 1957), and the horizontal rows are straighter than in lizards generally. The relatively primitive *Delma* and *Pygopus* must be examined for type C doubles before Underwood's conclusion that the pygopod retina is plesiomorphic relative to gekkos can be accepted. According to Underwood (pers. comm.), gekko type C doubles could fail to "pair off"; such failure would result in the pygopod condition. This interpretation of process assumes prior knowledge of a phylogenetic pattern. In the absence of that knowledge, I am forced to consider the pygopod state primitive (see pp. 6-10). However, many more observations are required before this character's congruence with other characters can be accurately assessed among the gekkonoids.

18. OLFACTORY CANAL.—Typically in lizards, the *crista cranii* of the frontal bone (Oelrich, 1956) are only weakly developed and partially surround the olfactory lobe of the brain (McDowell and Bogert, 1954:fig. 35). The *crista cranii* closely approach each other below the olfactory lobe only in a few autarchoglossans. They meet but do not fuse in some anguimorphs (*e.g.*, *Heloderma* and *Varanus*), and in some adult gymnophthalmines they appear to fuse (MacLean, 1974). Gekkonoids, with few exceptions (*e.g.*, *Aprasia*, *Pristurus*, and *Saurodactylus*), exhibited a completely enclosed olfactory canal and fused *crista cranii*, which I interpret as a synapomorphy of the group (see also Rieppel, 1984). The condition in *Aprasia* was exceptional in that a much enlarged and ossified *trabecula communis* completed the bony floor to the canal (Bellairs and Kamal, 1981:fig. 30). In adult *Saurodactylus*, the *crista cranii* met on the ventral midline but remained unfused throughout their length, or were only partially fused. At least some species of *Pristurus* (*e.g.*, *P. carteri* and *P. flavipunctatus*) had a completely open olfactory canal; the *crista cranii* formed walls to the canal but did not curve inward toward the midline. The frontal downgrowth condition remains to be determined in Jurassic gekkotans.

19. KARYOTYPE.—Paull, *et al.* (1976) argued that a karyotype of 12 metacentric macrochromosomes and 24 microchromosomes is probably

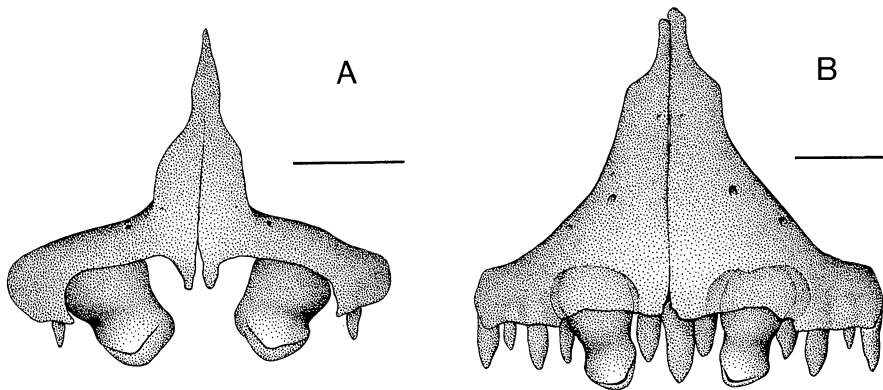


FIG. 7. Anterior views of the paired premaxillae of day-old pygopods. A. *Lialis burtonis* (NMV D57183, SVL = 86.0 mm). B. *Pygopus lepidopodus* (UMMZ 175938, SVL = 86.5 mm). Note the massive paired egg-teeth. The horizontal line equals 0.5 mm.

primitive for lizards. According to Gorman (1973:354), gekkonoids can be diagnosed as having "primarily... a graded series of acrocentric chromosomes, without a distinct break between macrochromosomes and microchromosomes. Large metacentric elements are not frequent and the majority of the two armed chromosomes, when they occur, appear to have subterminal centromeres" (see also De Smet, 1981). Diploid numbers are 28-46 (Gilboa, 1975; Hardy, 1975; McBee, *et al.*, 1984). The karyotype of *Coleonyx switaki* described by Murphy (1974), and confirmed by Fritts, *et al.* (1982), does not agree with any of these criteria. However, the reduced diploid complement of 24 in *C. switaki*, consisting of a graded series of 22 metacentric and two acrocentrics, can be explained simply as a unique case of Robertsonian fusion, derived from a primitive state like that proposed by Gorman (1973; see also King [1979]). The same interpretation can be applied to the  $2n = 28$  of *Diplodactylus tessellatus* (King, 1973).

20. CLUTCH SIZE.—Clutch size varies from 1-4 among gekkonoids (Fitch, 1970; Sabath, 1981; Schwaner, 1980); however, each species thus far investigated with large sample sizes has a pronounced modal value of one or two eggs. Moffat's (1973a:299) conclusion that clutch size is simply related to adult body size, and, thus, of "*no phylogenetic significance*" (my italics; see also Russell [1972:245]), appears to be much too sweeping a generalization. The only suggestion of a correlation between intraspecific body size (SVL) and clutch size that I am aware of occurs in *Gehyra oceanica* (Schwaner, 1980:fig. 3F), and it is not a statistically significant correlation ( $r_s = .323$ ,  $n = 18$ ). One might also claim that there is a tendency for smaller species to lay but one egg. However, all small gekkonines do not do so, as is well-illustrated by the tiny *Lygodactylus picturatus* (SVL = 28-34 mm) and *L. somalicus* (SVL = 25-27 mm), which lay two (Greer, 1967).

More than two eggs per clutch is common among lizards (Fitch, 1970), and I consider a reduced number a gekkonoid synapomorphy. Further, I hypothesize one egg to be apomorphic relative to two. The Sphaerodactylinae appear to be uniformly characterized by a clutch of one (Duellman, 1978; Dixon and Soini, 1975; Fitch, 1970; Hoogmoed, 1973; Werner, 1972), in spite of their modest adult sizes (e.g., *Gonatodes* and *Pseudogonatodes*, SVL > 50 mm). Beebe (1944:155) observed a *Sphaerodactylus molei* with two oviducal eggs, however, that individual was exceptional; four others seen by that author had single eggs. Such a reduction (mode/species) has been only rarely observed elsewhere among gekkonines (e.g., *Aristelliger barbouri*, Noble and Klingel, 1932; *Gehyra variegata*, Bustard, 1965; *Microgecko helenae*, Minton, 1966; *Phyllodactylus galapagensis*, Kushlan, 1981; *Pristurus rupestris*, Arnold and Gallagher, 1977; *Tropiocolotes steudneri*, Werner, 1972). Congeners of some of these exceptional species are known to lay the usual two eggs (*Aristelliger*, Lynn and Grant, 1940; *Gehyra*, Schwaner, 1980; *Phyllodactylus*, Alvarez del Toro, 1960), and the simplest explanation is that these are independently evolved reductions in clutch size. I assume the reduced number in *Pristurus rupestris* is true of all congeners (Table 3).

21. SUPRATEMPORAL ARCH.—A complete supratemporal arch, as well as an open supratemporal fenestra, is characteristic of most lizards, including the Jurassic gekkotans (Hoffstetter, 1964; McDowell and Bogert, 1954; Romer, 1956). Even though several families of fossorial lizards lack the arch, I still consider gekkonoids to be diagnosed by absence of this bony arcade (Estes, 1983a).

22. JUGAL.—A jugal with a large ascending postorbital process, usually contacting the postorbital and squamosal, is characteristic of most lizards, including Jurassic gekkotans (Romer, 1956). The gekkonoid condition consists of a reduced jugal and, thus, an incomplete postorbital arch, which I consider apomorphic. The entire loss of the jugal is extremely rare among gekkonoids (e.g., *Lialis burtonis* [Kluge, 1976a]).

23. RECTUS ABDOMINIS LATERALIS.—Moffat (1973a:282) accepted Camp's (1923) contention that the *rectus abdominis superficialis* (= *rectus abdominis lateralis*; for new terminology see Moody [1983]) is present in pygopods. Thus, she and others (Hecht, 1976; Hecht and Edwards, 1977; Underwood, 1957) considered pygopods and gekkos sister-taxa. However, I showed that the muscle is absent in flap-footed lizards, as it is in gekkos, and pointed out that, if hypothesized as a loss, it may merely provide evidence for gekkonoid common ancestry (Kluge, 1976b). Alternatively, the muscle's absence may be even more simply interpreted as primitive, with its origin limited to the common ancestor of the Autarchoglossa. The latter hypothesis does not depend on the historical reality of Camp's (1923) Ascalabota (Iguania + Gekkota), and it provides evidence against Xantusiidae being transferred from Autarchoglossa to Gekkota. Our current understanding of the phylogenetic usefulness of the *rectus abdominis lateralis* would no doubt have been reached much earlier had Camp's opinions concerning homology and functional significance been tested rather than merely assumed to be true

(Moffat, 1973a:283, 286-7). Only a broad systematic study of squamates will provide a rational basis for polarizing the *rectus abdominis lateralis* transformation series. Until such a study is undertaken, I hypothesize that the gekkonoid state is apomorphic.

24. HYOID ARCH.—I identified two transformation series in the hyoid arch in 1967: modification of the hyoid cornu and its effect on the hypohyal-ceratohyal union, and presence/absence of the inner, proximal ceratohyal projection (Kluge, 1967a). The cornu is large and wing-like in all eublepharines, diplodactylines, gekkonines (except *Tropiocolotes*), and sphaerodactylines (except some mainland *Sphaerodactylus*, and *Coleodactylus* and *Pseudogonatodes*). Among pygopods, the cornu is large and the hypohyal-ceratohyal robust in *Delma*, *Paradelma*, *Pletholax* and *Pygopus*. The arch is discontinuous and the cornu small to absent in *Aprasia*, *Lialis* and *Ophidiocephalus*. A continuous hyoid arch, without a prominent hyoid cornu, is characteristic of most other lizards (Camp, 1923; Tanner and Avery, 1982). Thus, I infer that the presence of a large wing-like hyoid cornu is a gekkonoid synapomorphy and that interruption of the hypohyal-ceratohyal and associated reduction of the cornu are derived states.

The inner ceratohyal projection is absent in all eublepharines and pygopods, many gekkonines, most diplodactylines, and, among sphaerodactylines, in *Coleodactylus*, *Pseudogonatodes*, and some mainland *Sphaerodactylus* (Kluge, 1967a). The projection is conspicuous in other gekkonoids. The inner margin of the ceratohyal is smooth in iguanians and autarchoglossans (Camp, 1923; Tanner and Avery, 1982), and I interpret the prominence found in certain gekkonoids to be derived. Its exact taxonomic distribution remains to be determined in gekkonoids, because the character is difficult to see in most skeletal preparations, and I have not employed it in the present phylogenetic analysis.

25. COCHLEAR LIMBUS.—Hecht (1976; see also Hecht and Edwards [1977]) contended that extreme development of the cochlear limbus is diagnostic of the Gekkota. The condition is tentatively treated herein as a gekkonoid synapomorphy; however, it is observed elsewhere among squamates. For example, Wever (1978) documented that extreme form of cochlear development in certain autarchoglossans (*e.g.*, Teiidae).

26. TECTUM SYNOTICUM.—Typically among lizards, as well as in *Sphenodon*, the tectum synoticum has a prominent midline process projecting anterodorsally; the process is usually ossified and makes extensive contact with the underside of the parietal(s) in adults (Bellairs and Kamal, 1981:fig. 19). According to Rieppel (1984), the ascending process is absent in gekkonoids, and he interpreted that condition as a synapomorphy. I agree that the anterior margin of the supraoccipital usually has an even border in adult gekkos and pygopods, with the parietals being supported by the otic capsules alone; however, the parietals did contact a sizeable mid-dorsal pedicel of bone in a few taxa. The exceptions appeared to be associated with different specializations, such as an elevated cranial vault (*Gekko*) or postorbital elongation of the skull, so that the parietal body was some

distance from the occipital arcade (e.g., *Lialis* and *Pygopus*). Tentatively, I assume these states to be convergent with the ascending process of other lizards.

27. RECESSUS SCALAE TYMPANI.—According to Rieppel (1984), the medial aperture within the *recessus scalae tympani* is divided into two foramina in gekkonoids, whereas it is single in other lizards. Rieppel listed the subdivision as a gekkonoid synapomorphy and I concur, and he stated that *Aprasia* might be exceptional in having only a single medial aperture. The pygopod condition is usually difficult to determine because the foramina in the *recessus* are tiny, narrow openings.

28. PREMAXILLA-VOMER.—The premaxilla and vomer are in broad contact in most lizards. According to Rieppel (1984), the anteromedial shelf of the maxilla tends to separate the two bones in a few families, such as agamids, chamaeleonids and gekkos, but not in pygopods. This was one of three characters Rieppel used as evidence for the Gekkonioidea being a natural group, excluding pygopods (see immediately below). I have been able to confirm the plesiomorphic condition in more derived pygopods (e.g., *Aprasia*, *Lialis*, *Pletholax*; Kluge, 1976a); however, the gekkonid condition was observed in the more primitive genera (*Delma*, *Pygopus*; see Fig. 8). While the extent of this variation requires further study (to be published elsewhere), it seems more accurate to characterize both the Gekkonidae and Pygopodidae as having the apomorphic state.

29. PSEUDOTEMPORALIS MUSCLE.—Rieppel (1984) noted that the pygopod pseudotemporalis muscle inserts on the parietal anterior to the epipterygoid. He interpreted this condition as primitive, whereas lack of contact in gekkos was inferred to be apomorphic. I have confirmed Rieppel's observations, but I do not believe the pygopod state is plesiomorphic. Typically among lizards (e.g., xantusiids; see Rieppel, 1984:fig. 15), the pseudotemporalis is divided into two major slips, the profundus associated with the epipterygoid, which does not insert on the parietal, and the more anterior superficialis, which broadly inserts on that covering bone. In pygopods, the epipterygoid and parietal are in much closer proximity than in gekkos, often in contact, and the pseudotemporalis is a continuous sheet of fibers that insert on the markedly developed lateral wall of the parietal, which is at best only weakly expressed in gekkos. Thus, the pygopod condition is not the same as in other lizards, and I have coded gekkos and pygopods as having different apomorphic states.

30. SCLERAL OSSICLES.—I agree with Moffat (1973a) that a low number of scleral ossicles (probably about 14 per eyeball) is the most likely primitive state in the Gekkonioidea (Table 1; Fig. 9), in contrast to "the low- to mid-twenties" state that I suggested previously (Kluge, 1967a). I am swayed by the impressive set of data taken from many outgroup taxa, including iguanians, autarchoglossans and *Sphenodon*, the majority of which possess 14 ossicles (De Queiroz, 1982). Also persuasive is the fact that only those gekkos with 14 ossicles show the exact pattern of plate overlap that is so widespread among other lizards (seven families; Underwood, 1970); gekkos with higher numbers of ossicles never exhibit that pattern.

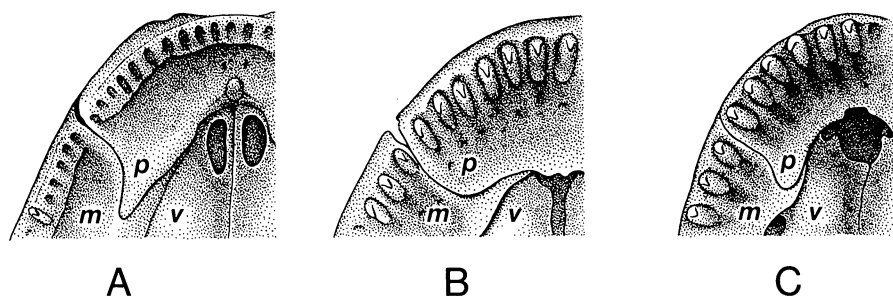


FIG. 8. Ventral views of the palate illustrating the nature of the separation of the premaxilla (p) from the vomer (v) by the anteromedial shelf of the maxilla (m). A. *Aeluroscalabotes felinus* (UMMZ 146749). B. *Pygopus nigriceps* (UMMZ 137574). C. *Delma inornata* (UMMZ 131161).

Moffat (1973a:285) described the variation in gekkonoids as “c. 14 scleral ossicles per eye,” or not, while Hecht altered it to circa 14 scleral ossicles, or a reduced number. As Table 1 and Figure 9 show, Moffat (1973a), Hecht (1976), and Hecht and Edwards (1977) misrepresented the information on ossicle number that I summarized in 1967 (Kluge, 1967a). If a low ossicle number is primitive in the Gekkonoida then an increased number provides some evidence for the Eublepharinae being a natural group (Fig. 9). The same conclusion would apply to the Diplodactylinae, according to my final phylogenetic hypothesis, which is presented below.

31. SPECTACLE.—The spectacle (brille of some authors) is a fixed transparent outer covering of the eye, formed by fusion of the eyelids (Bellairs and Boyd, 1947). Moffat (1973a) tended to emphasize “loss” of eyelids, rather than their modification into a spectacle, in her treatment of gekkonoid relationships.

The spectacle is also found in other groups of lizards (Underwood, 1970), and it is generally presumed to have evolved independently more than once. Among gekkonoids, the spectacle is present in all non-eublepharines (Bellairs, 1948; Hecht and Edwards, 1977; Moffat, 1973a; Underwood, 1957). In those gekkonoids with a spectacle, the *depressor palpebralis inferior* is absent (Underwood, 1970). The *depressor* is probably necessarily lost with modification of the eyelids into a spectacle, and, thus, I have not scored it as an additional character. The spectacle, and/or absence of the *depressor*, is considered characteristic of the non-eublepharine radiation of gekkonoids. I have confirmed that *Teratoscincus* has a spectacle.

32. BETA GENERATION GLANDS.—Beta generation glands appear to be restricted to diplodactylines and gekkonines (Bons and Pasteur, 1977), and I treated these holocrine specializations as a synapomorphy and evidence that the two lineages form a natural group (Kluge, 1983c). Pygopods remain to be thoroughly investigated; however, P. Maderson (pers. comm.) would not expect generation glands of any form to be retained in limbless taxa because of their constant belly-substrate contact.



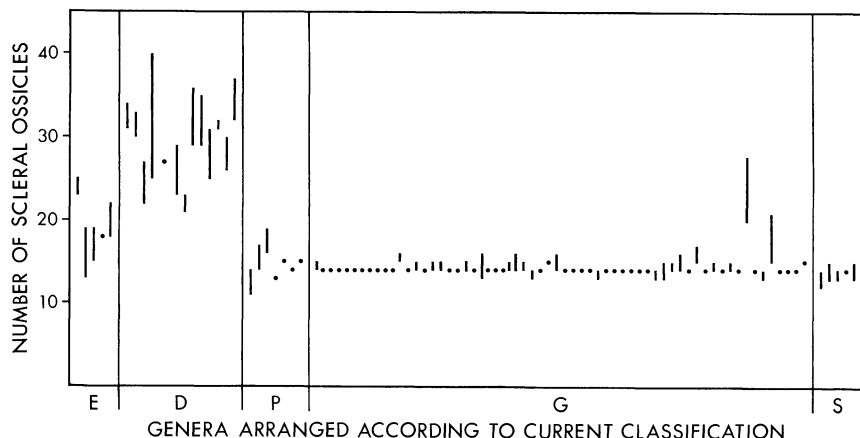


FIG. 9. The ranges of variation in number of scleral ossicles (per eyeball). The data are arranged according to the taxonomic order in Table 1. E = Eublepharinae, D = Diplodactylinae, P = Pygopodidae, G = Gekkonidae, S = Sphaerodactylinae.

33. ESCUTCHEON GENERATION GLANDS.—Maderson (1972) concluded that the escutcheon type of generation gland found in a few eublepharines and in the Sphaerodactylinae evolved independently. I argued that the escutcheon type marked Sphaerodactylinae as a historical entity (Kluge, 1967a). He also pointed out that the state in *Coleodactylus* and *Pseudogonatodes* could be interpreted as vestigial, and, as such, indicative of their common ancestry (Kluge, 1983c). The escutcheon may be present in *Pristurus*, as evidenced by the hypertrophied abdominal scales found in *P. celerrimus* (Arnold, 1977). Taylor and Leonard's (1956:1023) claim that *Tarentola* "may have some special glandular scales such as occur in Sphaerodactylidae" cannot be confirmed. According to Russell (1972:182), *Quedenfeldtia* "males bear preanal and femoral patches of callose, pitted, brown scales which resemble an escutcheon in their position;" however, the similarity of the two conditions requires further study. Moffat (1973a:299) would have been able to differentiate the Sphaerodactylinae from the gekkonines (Fig. 1A, E, G) had she emphasized shared derived character-states, rather than symplesiomorphies, and had she not arbitrarily discarded this character.

34. PARIETAL.—The adult lizard parietal bone is usually azygous (McDowell and Bogert, 1954; Romer, 1956). The fused condition uniformly characterizes eublepharines (Kluge, 1967a) and all Jurassic gekkotans (Estes, 1983a). The parietals are not fused in the Diplodactylinae or Sphaerodactylinae. Only *Lialis* exhibits the fused state among pygopods (Kluge, 1976a), and, with few exceptions, the parietal is paired throughout the Gekkoninae. Unlike Moffat (1973a:300), I hypothesize the paired state to be derived, based on the common occurrence of the azygous condition in non-gekkonoids.

35. SUPRATEMPORAL.—The supratemporal is absent in all diplodactylines, gekkonines and sphaerodactylines (Kluge, 1967a). Also, it was not observed in pygopods (Kluge, 1976a). The bone is present in some eublepharines (*Aeluroscalabotes felinus*, *Eublepharis macularius*, *E. kuroiwae*, *Holodactylus africanus*), but not others (*E. harwickii*, *Hemitheconyx caudicinctus*, *H. taylori*, all *Coleonyx* species). Hecht and Edwards (1977) did not report this variation among eublepharines. The supratemporal and squamosal were both present as separate centers of ossification in hatchling *Eublepharis*; however, only the larger squamosal was evident in similar developmental stages of *Gonatodes*, *Hemidactylus*, *Naultinus*, and *Phelsuma*. The loss of the supratemporal seems unlikely to have occurred only once in the Gekkonioidea, given the variation observed among eublepharines. If the Eublepharinae is considered a natural group, the loss of the supratemporal may be construed as a synapomorphy diagnostic of all other gekkonoids.

36. ANGULAR.—The angular is a prominent bone in the lower jaw of most lizards (Romer, 1956; McDowell and Bogert, 1954). It is present among all eublepharines (Kluge, 1967a), except the highly derived *Coleonyx brevis*, *C. reticulatus*, and *C. variegatus* (Kluge, 1975). The bone also occurs in the gekkonine genus *Teratoscincus* (Arnold, 1977). I assume its absence in all other gekkonids is the apomorphic state.

37. TECTORIAL MEMBRANE.—According to Wever (1978:511), diplodactylines are peculiar in that the tectorial membrane of the ear has a greatly thickened mid-portion, which is not to be confused with the spindle body. A similar condition has been observed elsewhere only in one gekkonine (*Thecadactylus rapicauda*), and this membrane novelty is tentatively accepted as a synapomorphy of the Diplodactylinae.

38. LIMBS.—Moffat (1973a:table 2) used reduced limbs in classifying the Gekkota. However, the character is largely uninformative as to gekkonoid relationships because that apomorphy only corroborates the already well-documented cohesiveness of pygopods (see also Hecht [1976], and Hecht and Edwards [1977]).

39. PREMAXILLA.—I identified two patterns of premaxilla ontogeny in gekkonoids (Kluge, 1967a). Further, I noted the distinction between them was most evident at the egg-tooth stage of development, one state being paired, the other azygous. The paired condition was confined to the Eublepharinae (*Holodactylus* requires determination) and Diplodactylinae (*Rhynchoedura* requires further study), and the condition was identifiable in adults as a persistent notch or split in the dorsal margin of the nasal process. The alternative condition was found in gekkonines (Bellairs and Kamal, 1981:fig. 29) and sphaerodactylines, in which only one center of ossification was present at the inception of bone formation. Moffat (1973a:285) was incorrect in citing the paired premaxillae-state as *absent* in some eublepharines. Hecht's reference to this character (1976:table 1; see also Hecht and Edwards [1977]), in terms of only the adult condition, is an over-simplification, because the distinction between the two states is most apparent early in

ontogeny. I hypothesized the azygous state to be apomorphic, because Jurassic gekkotans possessed a paired premaxilla (Kluge, 1967a).

The enigmatic *Teratoscincus* exhibited no indication of the paired state in very young specimens (e.g., FMNH 200199, *T. scincus*, SVL = 44.0 mm). I have been able to determine unequivocally that the pygopod condition is paired. Day-old *Lialis burtonis* (NMV D57183 [cleared and stained] and D57184, SVL = 86.0 and 88.5 mm, respectively) exhibited a nearly completely paired premaxilla, with an egg-tooth still firmly ankylosed to each half (Fig. 7). The premaxilla was completely paired in day-old *Pygopus lepidopodus* (UMMZ 175937 and 175938 [cleared and stained], SVL = 83.0 and 86.5 mm, respectively; Fig. 7). Cleared and stained juvenile (UMMZ 137573) and adult (UMMZ 129978-79) *Aprasia repens* also showed a distinct separation of the nasal processes, and dissections of other young individuals corroborated that finding for pygopods generally: completely paired, *A. pulchella* (WAM R36456; SVL = 46.2 mm); paired nasal processes, *Delma australis* (WAM R53462; SVL = 37.7 mm); notched mid-dorsal surface of nasal process, *Aclys concinna* (WAM R59132; SVL = 38.5 mm), *D. fraseri* (WAM R30705; SVL = 32.5 mm), *Lialis burtonis* (WAM R14772; SVL = 88.5 mm).

Moffat (1973a:300) pointed out that the paired state of the premaxilla "may represent a persistent ancestral condition in some forms and a secondarily derived condition in others." (She also argued the same for frontals, nasals and parietals.) This was an appeal to a particular process, i.e., truncation of ontogeny, as a way of explaining away an apparent case of independent evolution. Moffat seemed unaware that "some phylogenetic context, however crude, is a fundamental prerequisite for a hypothesis of heterochrony" (Fink, 1982:255; Kluge and Strauss, 1985). Further, as Patterson (1982) has argued, only character congruence is capable of distinguishing plesiomorphy from truncated ontogeny.

The azygous premaxilla is cladistically congruent with the presence of a calcareous egg shell, and a functional correlation may exist between the two characters. I believe it is reasonable to assume that a single premaxilla is much more rigid than the paired state. Thus, the single premaxilla may allow the egg-teeth anchored to its ventral margin to more readily pierce the calcareous shell, and assure freeing the young. In spite of this possible functional relationship, I tentatively treat the two characters as independent evidence of phylogenetic relationships in gekkonoids.

40. EGG SHELL.—Gekkonines and sphaerodactylines are exceptional among all lizards (except *Dibamus*; Boulenger, 1912; Smith, 1935) in laying a pliable egg which becomes hardened on exposure to air (Werner, 1972; Underwood, 1977). The leathery-shelled eggs of eublepharines, diplodactylines, and pygopods remain relatively pliable until hatching, like those of other squamates, and this state is considered plesiomorphic (Bustard, 1965, 1967, 1968, 1970; Kluge, 1974; Underwood, 1977). *Teratoscincus* has a calcareous-shelled egg (Minton, 1966), although it appears to be much thinner than that of most gekkonines and sphaerodactylines (Michael Miller, pers. comm.).

X-ray diffraction analysis of gekkonoid egg shells better documents the nature of that biomineralization (Table 2). Single representatives of gekkonines (*Hemidactylus mabouia*) and sphaerodactylines (*Gonatodes fuscus*) exhibited a well-developed diffraction pattern characteristic of calcite. The shell of a eublepharine (*Coleonyx variegatus*) had a very weak calcite profile, whereas a diplodactyline (*Diplodactylus conspicillatus*) showed no evidence of mineralization. All four gekkos studied possessed a large organic, non-crystalline, component.

Dunson (1982) and Dunson and Bramham (1981) have clearly shown that calcareous-shelled eggs of gekkonines and sphaerodactylines are much more resistant to desiccation than leathery-shelled eggs of other lizards. They have even lower water vapor conductance and shell permeability than do avian eggs. Brown and Alcalá (1957) also demonstrated that calcareous-shelled eggs of gekkos can withstand long periods of exposure to sea water and remain viable, whereas the leathery type of squamate egg does not.

Ovoviviparity is known in three diplodactyline genera, *Rhacodactylus* of New Caledonia and *Hoplodactylus* and *Naultinus* of New Zealand (Bartmann, 1979; Boyd, 1942). That specialized condition is assumed to be derived, relative to the leathery state. This interpretation is conditional on loss of the outer organic covering of the egg (Bauchot, 1965).

41. EGG SHAPE.—Egg ellipticity (ratio of width to length) varies from 0.42 to 0.70 in Eublepharinae and Diplodactylinae and 0.60 to 1.00 in Gekkoninae (including *Teratoscincus* [Miller, 1982; fig. 2]) and Sphaerodactylinae (Werner and Carmel, 1977; Werner, 1972). Freshly laid eggs of pygopods *Aprasia parapulchella* and *Delma tincta* varied from 0.23 to 0.32 and from 0.43 to 0.49, respectively (Kluge, 1974). A single *Pygopus lepidopodus* egg was 0.42 (Fitzgerald, 1983). The exceptional narrowness of *Aprasia*'s eggs was correlated with the marked slenderness of the adult. I hypothesize that the more nearly round condition in gekkonines and sphaerodactylines is apomorphic. While there is considerable variation in egg shape among lizards, the more elongate form seems to predominate among non-gekkotans (Fitch, 1970; Kopstein, 1938; Schwaner, 1980; Vitt, 1981).

42. ENDOLYMPHATIC SYSTEM.—The endolymphatic system of lizards is usually confined to the skull and cranial vault. In a few iguanid and agamid genera, in chamaeleons, and commonly in gekkonines and sphaerodactylines, the system is expanded into a large sac, the cervical extension, on each side of the neck (Kluge, 1967a; see Fig. 10). Recent reviews by Dacke (1979) and Simkiss (1967) emphasized the earlier conclusion of Ruth (1918) that the post-cranial projection swells with "calcium milk," especially in females, during the reproductive season. The endolymph consisted of a highly concentrated solution of calcium carbonate. An x-ray diffraction profile of this material in a preserved *Gekko gekko* (Table 2) suggested that it is stored in the form of aragonite. Leavell (1972) found strontium, calcium carbonate, potassium, nickel, chloride and sodium in the endolymph of *Phyllodactylus xanti*.

The existence of a large cervical extension of the endolymphatic system

filled with calcium carbonate has never been observed in eublepharines, diplodactylines, or pygopods. I interpret this state to be plesiomorphic among gekkonoids. The presence of the post-cranial projection filled with calcium carbonate is tentatively treated as a synapomorphy of the Gekkoninae + Sphaerodactylinae. *Teratoscincus* (Arnold, 1977; E. N. Arnold, pers. comm.) and "many" *Hemidactylus* (Simkiss, 1967:225) are thought to lack the reservoir, while several other genera remain to be investigated (Kluge, 1967a). Probably the simplest explanation for the few iguanid, agamid and chamaeleon examples is independent evolution.

Bustard (1968) speculated that calcified endolymphatic sacs in gekkos may provide calcium for egg-shell formation. Leavell (1972) has clearly shown that the cervical extension is larger and more seasonally variable in size in female than male *Phyllodactylus xanti*. As calcium carbonate increased in the sacs, the ovarian eggs were enlarging and approaching the time of ovulation. As the cervical sacs sharply decreased in size, the egg-shell began to form. The sacs may also function as a calcium store before and during times of exceptional bone growth (e.g., shortly after hatching, as in *Phelsuma* sp.).

43. SPLENIAL.—I noted that the splenial was present in all gekkonids, except the Sphaerodactylinae and those gekkonines belonging to the genera *Pristurus* and *Ptyodactylus* (Kluge, 1967a). The absence in sphaerodactylines and *Pristurus* was considered a synapomorphy. I was unable to corroborate Russell's (1972) claims that *Quedenfeldtia* lacks the splenial, while *Pristurus* possesses one. All pygopods examined possess a splenial, except *Aprasia* (Kluge, 1976a). Hecht and Edwards (1977) did not mention this variation.

44. SECOND CERATOBANCHIAL ARCH.—I considered the absence of the second ceratobranchial arch to be a synapomorphy of some gekkonines (Kluge, 1983b). That newly diagnosed tribe, Gekkonini, consists of the following genera: *Agamura*, *Ailuronyx*, *Alsophylax*, *Aristelliger*, *Bogertia*, *Briba*, *Bunopus*, *Calodactylodes*, *Carinatogekko*, *Cnemaspis*, *Cosymbotus*, *Crossobamon*, *Cyrtopodion*, *Dravidogekko*, *Geckolepis*, *Gehyra*, *Gekko*, *Gonydactylus*, *Gymnodactylus*, *Hemidactylus*, *Hemiphyllocladactylus*, *Heteronotia*, *Homopholis*, *Lepidodactylus*, *Luperosaurus*, *Lygodactylus*, *Milotisaurus*, *Perochirus*, *Phyllopezus*, *Pseudogekko*, *Ptychozoon*, *Stenodactylus*, *Teratolepis*, *Thecadactylus*, *Tropicolotes*, *Urocotyledon*, and *Uroplatus*. The presence or absence of the second ceratobranchial was not checked in *Garzoniella*, *Microscalabotes* and *Paragehyra*. However, they were tentatively referred to the Gekkonini because of their close relationship to genera which did exhibit the diagnostic feature of the tribe. The arch appears to have been lost independently in the most derived species group in *Pristurus*, a genus Kluge (1983b) referred to the "Ptyodactylini."

The completely continuous second branchial arches observed in *Coleonyx* and some *Gonatodes* (Camp, 1923) have been reinterpreted as independently evolved apomorphies (Kluge, 1983b), rather than plesiomorphic states (Kluge, 1967a; Hecht, 1976; Hecht and Edwards, 1977). I could not corroborate (Kluge, 1983b) the complete three arch condition recorded for

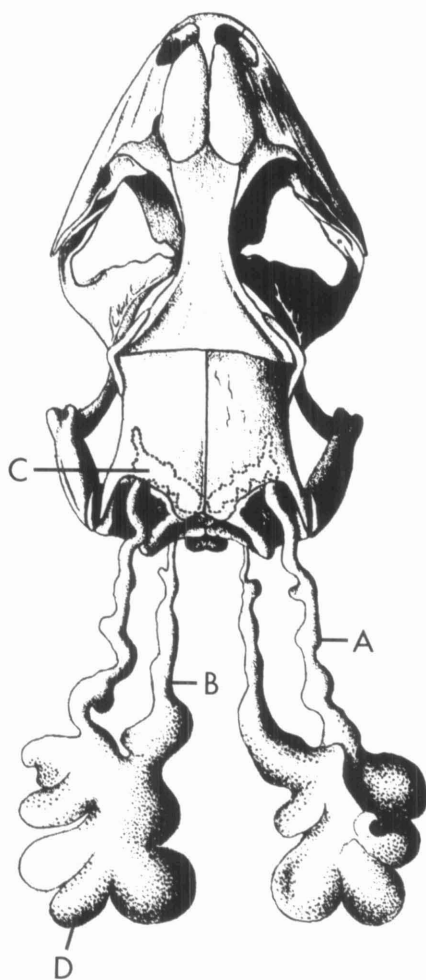


FIG. 10. Dorsal view of the skull and endolymphatic sacs of *Phyllodactylus europaeus* (reproduced from Wiedersheim [1875:fig. 4]). Ducts (A-B) connect larger endolymphatic spaces in the cranial vault (C) with those alongside the neck (D).

*Nautilinus elegans* by Stephenson and Stephenson (1956; see also Moffat [1973a]). Thus, the continuity of the epibranchial-ceratobranchial rods of the second arch do not appear to provide evidence of common ancestry at higher taxonomic levels among gekkonoids (see alternative views by Hecht [1976], and Hecht and Edwards [1977]).

## QUESTIONABLE EVIDENCE

VOCALIZATION.—Male, female, and juvenile gekkonoid lizards vocalize (Frankenberg, 1978, 1982; Marcellini, 1974). They are like most other tetrapods in that they make distress, fright or release calls (Frankenberg and Werner, 1984; Milton and Jenssen, 1979; Weber and Werner, 1977). Ordinarily, such sounds are emitted when an individual is confronted and/or attacked by a predator or conspecific. This type of vocal response is widespread among non-gekkotan lizards (Bowker, 1980), and I assume it is the plesiomorphic state in the Gekkonioidea. However, certain gekkos have long been recognized for their ability to emit complex sounds termed multiple chirps (Marcellini, 1978) or clicks (Werner, *et al.*, 1978). This class of sounds may be modulated, and they are thought to convey intraspecific messages over "long distances" (Gans and Maderson, 1973; Werner, *et al.*, 1978). These sounds are usually associated with establishing and maintaining a territory and attracting mates (Bustard, 1970; Cloudsley-Thompson, 1972). Unfortunately, these types of calls are well-documented only for a few gekkonids. According to Marcellini (1978), species in the following gekkonine genera are known to produce the more complicated chirps: *Aristelliger*, *Cyrtopodion*, *Gekko*, *Hemidactylus*, *Phyllodactylus*, *Ptenopus*, *Ptychozoon*, *Ptyodactylus*, and *Thecadactylus*. Remarks by Bustard (1970), Robb (1980), and Thomas (1982) imply that at least a few diplodactylines possess the same ability. Eublepharines (Marcellini, 1978) and sphaerodactylines (Dale Marcellini, Al Schwartz, and Richard Thomas, pers. comm.), while known to make distress calls, seem incapable of producing multiple chirps (see, however, Underwood [1954:480]). Pygopods readily vocalize under duress (Cogger, 1967; Sonneman, 1974; Weber and Werner, 1977), and it is clear that some (*Delma impar*, *D. inornata*, *Lialis burtonis*) also emit more complex social signals (Annable, 1983).

The earlier descriptions of gekkonoid vocalizations rarely recorded the social context or type of sound produced and, therefore, such references are of no value in relating the more complex calls to genealogical groups. Identifying structural and functional correlates of the novel form of vocalization, in either the laryngeal apparatus (Paulsen, 1967; Wiedersheim, 1875) or auditory system (Wever, 1978), remains to be fully explored. Future research in this area might also attempt to correlate the ability to produce complex calls with whether or not the species is predominantly nocturnal or diurnal. Assuming gekkonoids to be primitively nocturnal, and diurnality to have evolved independently (Underwood, 1970), provides a working hypothesis for why some gekkonines and the Sphaerodactylinae do not emit more social types of calls. It seems best not to attribute any phylogenetic significance to vocalization in gekkonoids until variation in the communication system is much better documented. No doubt, the social significance attributed to certain lacertid vocalizations (Böhme, 1981) represents convergent evolution.

OCCIPITAL CONDYLE.—A bipartite occipital condyle forms when the exoccipitals extend posteriorly beyond the basioccipital. Rieppel (1984) cited

Gardiner (1982) as the source for his claim that such a condition is characteristic of gekkonoids. I can find nothing in Gardiner's paper that leads me to that position. Further, I doubt that any gekko or pygopod has a bipartite occipital condyle like that in lissamphibians. It is true that the exoccipitals are usually slightly longer than the basioccipital early in ontogeny, but in adult gekkonoids that differential, if it remains at all, is obscured by a continuous thick pad of cartilage that actually forms the articular surfaces of the condyle. The easiest way to assess the nature of the occipital condyle(s) is to examine the cranial facets on the atlas. At least in adult gekkos and pygopods it appears to be a single, U-shaped articular surface, not two as Rieppel claimed.

FRONTAL.—I reviewed the distribution of single and paired frontal bones among the Gekkonidae in 1967 (Kluge, 1967a). I concluded that the variation was uninformative with respect to characterizing sister-group relationships among the major lineages, because only six of 51 gekkonine genera (with one of those being intragenerically variable) exhibited the paired state (Kluge, 1967a). The presence of paired frontals in one of five pygopod genera (Moffat, 1973a) further supports my contention. Even bavarisaurids are variable in this regard (Estes, 1983a). Hecht (1976) and Hecht and Edwards (1977) were unaware that gekkonines and pygopods exhibit *both* states; their tables listed these groups as invariably paired. They treated the paired state as primitive (see also Moffat [1973a]), and the condition of fused frontals as a synapomorphy uniting all eublepharines, diplodactylines and sphaerodactylines. Unfortunately, they gave the impression that the evolution of an azygous frontal in gekkonoids was a unique event. I continue to reject this character in my studies of major gekkotan relationships, because the variability does not appear to be corroborated by other synapomorphies.

SQUAMOSAL.—The squamosal is absent in the gekkonine genera *Lygodactylus*, *Saurodactylus* (absent in *S. mauritanicus* but present in *S. fasciatus*), and *Teratoscincus*, and the sphaerodactyline genus *Coleodactylus* (Kluge, 1967a). The bone is also absent in a pygopod, *Aprasia repens* (Kluge, 1976a). Given the absence of corroborating synapomorphies, I believe many, if not all, of these are most simply explained as homoplasious losses (see also Kluge [1967a]). Moffat (1973a:286) also discounted this character as evidence of gekkonoid relationships; however, her reason for doing so carries no weight, because it was based on the widespread nature of the primitive state, *i.e.*, presence of the squamosal.

NASALS.—Nasal bones are usually paired in gekkonoids, as they are in almost all other lizards. The gekkotan azygous state, which I considered derived (Kluge, 1967a), occurs only in the following gekkonines: *Afroedura*, *Ailuroonyx*, *Cnemaspis* (in part), *Ebenavia*, *Hemiphyllodactylus*, *Homopholis* (in part), *Lepidodactylus*, *Lygodactylus*, *Microgecko*, *Nactus*, *Paroedura*, *Perochirus*, *Phelsuma*, Old World *Phyllodactylus* (in part), *Pseudogekko*, *Uroplatus* (see also Kluge, 1983b). Moffat (1973a) listed paired nasals for all pygopods except *Aprasia*, in which she claimed that they are partially fused. My review (Kluge, 1976a) of the flap-footed lizards agreed with her



conclusions, except that *A. repens* exhibited the primitive state and the azygous condition appeared to be complete in adults of other *Aprasia* species.

It is obvious that the apomorphic condition of the nasals is uninformative with respect to higher classification of gekkonoids. Nevertheless, it may provide evidence of certain intergeneric relationships (*e.g.*, common ancestry of *Hemiphyllocladylus*, *Lepidodactylus*, *Pseudogekko*, and possibly *Perochirus*; Kluge, 1968).

**LATERAL HEAD VEIN CANAL.**—Rieppel (1984:310) stated "the partial or complete bony enclosure of the passage of the lateral head (internal jugular) vein across the basiptyergoid process" is diagnostic of the group Gekkonoida + Pygopodidae. He cited Estes (1983a) as the source for his claim, but that attribution appears to be erroneous. Estes (p. 122) reviewed the braincase evidence for xantusiids being the sister-group of gekkonoids, and he concluded that variation in the closure of the canal in teiids, lacertids and scincids was too great to consider the character diagnostic of the group Xantusiidae + Gekkonoida. The variation among gekkonoids, from open to complete closure, further negates Rieppel's use of that character.

**HEAD SCALATION.**—Large head scales are typical of autarchoglossans, and therefore one might conclude that the small scales of gekkonids are derived (Friederich, 1978:table 1). The condition in pygopods is complicated because small- and large-scaled species are present, although the more primitive genera all exhibit the former state (*Delma*, *Paradelma* and *Pygopus*; Kluge, 1974, 1976a). Inferring the direction of evolution in the size of gekkonoid head scales is made even more difficult by the fact that almost all iguanians and *Sphenodon* possess small scales. Moreover, the difficulty of identifying comparable individual scales, especially in the prefrontal and parietal regions, leads me to conclude that there has been considerable independent evolution (Friederich, 1978).

**SACRAL PLEURAPOPHYSES.**—Moffat (1973a; see also Cogger [1964] and Holder [1960]) found a triangular process on the posterior edge of pleurapophyses of the second sacral vertebra in the Eublepharinae, Gekkoninae and Sphaerodactylinae, but it was not observed in the Pygopodidae or Diplodactylinae. The process was also present in non-gekkotan lizards (Hoffstetter and Gasc, 1969). Moffat, therefore, hypothesized that their presence in the Gekkonoida is primitive. Moffat (1973a) did not use *Sphenodon*, which lacks such processes (Hoffstetter and Gasc, 1969:fig. 30), as her outgroup in this instance, although she had employed that taxon in deciding several other character-state polarities of gekkonoids.

Several cleared and stained UMMZ diplodactylines had pronounced processes on their sacral pleurapophyses. The usefulness of this character in establishing relationships among gekkonoids is further brought into question by the variation that exists among pygopods. Hecht's (1976:354; see also Hecht and Edwards [1977]) assertion that the process "is totally absent in the Pygopodidae because of limb loss" is false. A second sacral vertebra with moderately developed pleurapophyses exists in some species. I have ex-

amined cleared and stained material of all pygopod genera except *Ophidiocephalus*, and many specimens had a triangular process on the posterior edge of the pleurapophysis of the second sacral vertebra. These protuberances were not present in all species, nor did they always occur on both right and left pleurapophyses in an individual. The process was best developed in *Lialis jicari* (UMMZ 131189), *Pygopus nigriceps* (UMMZ 129984), *Aprasia aurita* (UMMZ 131157), *A. parapulchella* (UMMZ 131157), and *A. striolata* (UMMZ 131176). Thus, while I accept Moffat's conclusion that presence of the process is primitive, I believe loss of this character-state has limited value in establishing relationships among major groups of gekkonoids because of extensive individual variation in diplodactylines and pygopods. The character is also variable in other lizards, although the process is generally absent in higher Autarchoglossa.

## CONCLUSIONS

### MOST PARSIMONIOUS CLADOGRAM

The single, most parsimonious cladistic hypothesis for the evidence summarized in Table 3 is illustrated in Figure 11. The consistency index (*c*) of Kluge and Farris (1969) and the F-value of Farris (1981) provide indices to how well the cladogram fits all of the data (*c* = 0.797; F = 1.511; F (normalized) = 0.099). Discounting the three autapomorphies (characters 37, 38 and 44), *c* = 0.786 (44/56). All sister group relationships are resolved except for the Gekkonini, "Ptyodactylini," and *Pristurus* + sphaerodactylinae polytomy.

### CHARACTER EVOLUTION

Character evolution is hypothesized in terms of the cladogram shown in Figure 11. The following synapomorphies, as coded in Table 3, are unique and unreversed: 2, 4-9, 13-16, 19-29, 31, 33-35, 37-44. Characters 1-3, 10-12, 18, 20, 24, 27-28, 33-37, and 42-44 exhibit some homoplasy within the recognized terminal taxa (see distribution of superscript *a* in Table 3). Thus, the simplest explanation of homology applies to the synapomorphies in characters 4-9, 13-16, 19, 21-23, 25-26, 29, 31 and 38-41. Seventeen percent of the homoplasy recorded in the most parsimonious cladogram is unambiguously interpreted as convergence, 83% as reversal. This striking difference is consistent with the thesis that gekkonoids are largely pedomorphic. While the numbers of characters are small, there is no conspicuous bias of loss characters (e.g., reduction of a bony element or process) being more prone to homoplasy than characters which suggest the acquisition of some feature. This is an empirical test which provides evidence counter to Hecht's (1976) proposition that loss characters are less informative of common ancestry, and should be discounted *a priori*.

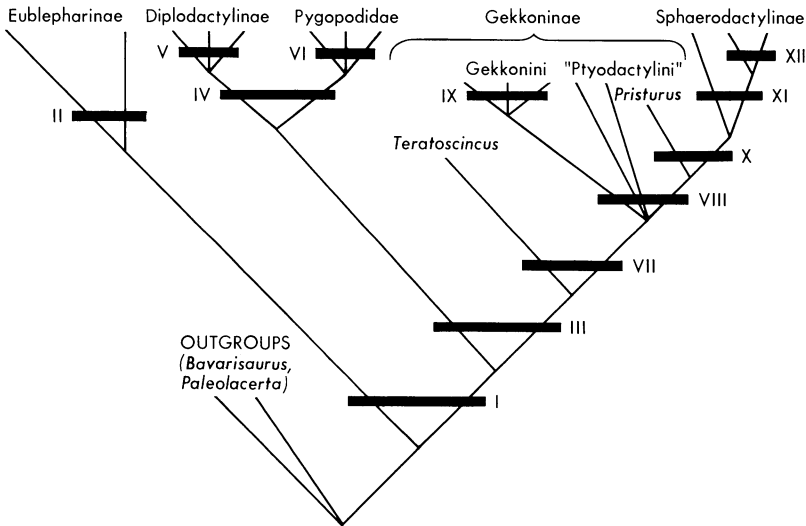


FIG. 11. Twelve (I-XII) gekkonoid sister-groups obtained from a parsimony analysis of the evidence summarized in Table 3. The nomenclature follows Kluge (1967a; 1976a; 1983b). See text (pp. 11-32) for summary of synapomorphies at each level of universality.

The congruence-parsimony test (*sensu* Fig. 11; Patterson, 1982) leads to a reinterpretation of some of the evidence summarized in Table 3. For example, procoely (character 1) is hypothesized to have evolved independently in eublepharids, pygopods and the four sphaerodactyline genera denoted by the term Sphaero (see Table 3). *Ebenavia*, a "ptyodactylin," also exhibits that convergent state, and several diplodactylines and *Gonatodes* (Fig. 5) tend toward procoely. Perhaps the polarity of the character has been misjudged; however, to consider procoely the primitive gekkotan condition leads to a far less simple description of that character's evolutionary history. Thus, I am forced to conclude that the primitive squamate state of procoely has been attained several times among gekkonoids. An amphicoelous centrum with a continuous notochordal canal (character 2) may have been achieved by paedomorphosis in early gekkotans (Gauthier, 1981).

The congruence-parsimony test also indicates independent evolution of the stapelial foramen (character 3). The simplest interpretation requires a secondary loss of the foramen in the diplodactyline + pygopod clade, as well as at least two losses among the Gekkonini and "Ptyodactylini" and individual variance in this feature among a few Sphaero genera. Altering the polarity would lead to a less parsimonious interpretation. The absence of cloacal sacs and bones (characters 10-11) hypothesized in the lineage leading to *Pristurus* + sphaerodactylines is almost certainly secondary. Even though there are additional absences among the Gekkonini and "Ptyodactylini," changing the polarity of these transformation series leads to a description of

character evolution that requires even more *ad hoc* explanations. Interpreting the absence of the meatal closure muscle (character 12) as a loss in the *Pristurus* + Sphaerodactylinae clade, as well as in the Gekkonini and "Ptyodactylini," also seems to be the simplest explanation.

The nature of the visual cells (character 17) in pygopods requires restudy, as I suggested earlier, before the hypothesized reversal can be considered justified. There seems to be little doubt that the bony floor to the olfactory canal (character 18) has been lost secondarily in *Pristurus* as well as in the "Ptyodactylini" and at least one pygopod. Characters 20 (clutch size) and 24 (hyoid cornu) have been reduced independently several times—in the Gekkonini, among "ptyodactylins," and in the *Pristurus* + sphaerodactylinae clade. The broad contact between the premaxilla and vomer (character 28) observed in the more derived pygopods (Table 3) is most simply interpreted as an evolutionary reversal. The number of scleral ossicles (character 30) appears to involve considerable homoplasy. Only by treating this character as a multistate variable will a more accurate estimation of the homoplasy be obtained. There appears to be little doubt that the beta generation gland (character 32) has been lost independently in sphaerodactylines. The simplest interpretation for the escutcheon generation gland (character 33) is that it evolved at least twice independently: some eublepharines, and *Pristurus* (?) + sphaerodactylines.

The parietals (character 34) are almost certainly secondarily fused in the pygopod clade and in a few Gekkonini and "Ptyodactylini." Other research (Kluge, 1967a, 1975) indicated that the supratemporal (character 35) has been lost independently in non-eublepharine gekkos and at least once among eublepharines. Similarly, the angular (character 36) has probably been lost independently in non-eublepharine gekkos and in the Eublepharinae. It is equally parsimonious to consider an angular-like bone to have been regained in *Teratoscincus* or lost independently in the diplodactylinae + pygopod group. The absence of the extracranial endolymphatic system (character 42) in the Gekkonini, and possibly among the "Ptyodactylini," is almost certainly a secondary loss. A much more complete survey than is presently available is required to better estimate the degree of homoplasy in this character. The absence of the splenial (character 43) in *Ptyodactylus* is very likely convergent to its absence in the *Pristurus* + sphaerodactylinae clade.

#### EVIDENCE FOR SISTER-GROUP RELATIONSHIPS

The most parsimonious phylogenetic hypothesis for gekkonoids (Fig. 11) contains 12 clades. This pattern of relationships is consistent (*sensu* Wiley, 1981b) with my previous hypothesis (Fig. 2). The following list summarizes the range of numbers of synapomorphies, in parentheses, diagnostic of each major clade: I (27-29), II (1-3), III (4-5), IV (1-3), V (1-2), VI (4-5), VII (3-4), VIII (1-3), IX (1), X (6), XI (1), XII (1). Variation in diagnostic information is due to different optimizations of ambiguous characters. *Pristurus* and

*Teratoscincus* are diagnosed by (1) and (0-2) characters, respectively. These numbers and the nature of that evidence (unique in the Gekkota, a reversal or a convergence) are the bases for the confidence that I attribute to the different clades. It is obvious that clade I is exceptionally well corroborated, whereas IX, XI and XII require further study. The 12 levels of common ancestry, and the *minimum* character evidence for their historical reality, in parentheses and numbered as in the CHARACTERS section, are:

- I. Gekkonoidea (2, 4-29).
- II. Eublepharinae (1).
- III. "non-eublepharine" gekkonoids (31-32, 34-35).
- IV. Diplodactylinae + Pygopodidae (12).
- V. Diplodactylinae (37).
- VI. Pygopodidae (1, 17, 29, 38).
- VII. Gekkoninae + Sphaerodactylinae (39-41).
- VIII. Gekkoninae + Sphaerodactylinae, excluding *Teratoscincus* (42).
- IX. Gekkonini (44).
- X. *Pristurus* + Sphaerodactylinae (10-12, 20, 33, 43).
- XI. Sphaerodactylinae (32).
- XII. Sphaerodactylinae, excluding *Gonatodes* (1).

Three characters, 3, 30, and 36, provide additional evidence for sister-group relationships; however, there is no single optimal parsimony distribution for them. For example, character 3 diagnoses clades I or III; 30 diagnoses clades I, III, IV, VII, or Pygopodidae; 36 diagnoses III, VII, or *Teratoscincus*.

#### CLASSIFICATION

The previously published classifications of gekkonoids and their Jurassic relatives are inconsistent with the cladogram presented in Figure 11, and a new taxonomy isomorphic with that phylogenetic hypothesis is:

- Infraorder Gekkonomorpha Fürbringer, 1900
  - Plesion "Bavarisauridae" Cocude-Michel, 1961; Kuhn, 1961
    - Genus *Bavarisaurus* Hoffstetter, 1953
    - Genus *Palaeolacerta* Cocude-Michel, 1961
  - Microorder Gekkota Cuvier, 1817
    - Superfamily Eublepharoidea Boulenger, 1883, new rank
      - Family Eublepharidae Boulenger, 1883
    - Superfamily Gekkonoidea Gray, 1825
      - Family Gekkonidae Gray, 1825
        - Subfamily Gekkoninae Gray, 1825
          - Gekkoninae, *incertae sedis*: "Ptyodactylinae" Kluge, 1983b, new rank
        - Tribe Gekkonini Gray, 1825

- Tribe Sphaerodactylini Underwood, 1954, new rank
- Subfamily Teratoscincinae, new subfamily
- Family Pygopodidae Boulenger, 1884
- Subfamily Diplodactylinae Underwood, 1954
- Tribe Carphodactylini Kluge, 1967b
- Tribe Diplodactylini Underwood, 1954
- Subfamily Pygopodinae Boulenger, 1884, new rank

Eublepharoidea and Teratoscincinae are redundant with Eublepharidae and *Teratoscincus*, respectively. The former names can be eliminated without perturbing the isometry of the cladogram (Fig. 11) and Linnean classification.

Some major groups appear to be well-founded among the "ptyodactylines" (Figure 12); however, many genera cannot be related at this time. The Sphaerodactylini includes *Pristurus*, not *Phyllodactylus* as per Russell (1972:245-46), and a review of the relationships of the genera referred to this tribe will be published elsewhere (Kluge, ms.). The previous classification of pygopods (Kluge, 1976a) must be adjusted to their new subfamily status. Moreover, pygopods and Diplodactylini genera *Crenadactylus*, *Diplodactylus*, *Oedura* and *Rhynchoedura* share several cranial modifications, which may indicate that flap-footed lizards are cladistically even more derived than shown in Figure 11.

#### BIOGEOGRAPHY

My earlier phylogenetic analysis of gekkotans was followed with a biogeographic scenario that assumed fixed continents, existence of land-bridges, and frequent trans-oceanic dispersal (Kluge, 1967a). My principal conjecture was that the Diplodactylinae evolved during the Late Mesozoic from a primitive gekko, like the eublepharid *Aeluroscalabotes*, located in southeast Asia. Since that review, plate tectonics has become generally accepted, and it is now commonplace to recognize mobile continents as responsible for lineage splitting (Humphries, 1981). Moreover, as Cracraft (1975) pointed out, according to the theory of plate tectonics, Australia and New Zealand lay far to the south throughout the Mesozoic (see Owen [1976] for an alternative view), as a part of Gondwanaland, and overwater dispersal of gekkos from Asia to Australia was less likely than previously thought. Given such glaring inconsistencies with my earlier biogeographic thesis, and in view of the cladistic hypothesis summarized in Figure 11, I will reconsider some major features of gekkotan geographic history. In the present review I attempt to discover only those congruences between the breakup of Pangaea and the hypothesized genealogy of gekkotans. In effect, this is a test of Presch's (1983:198) conclusion that "The breakup and movement of the plates does not appear to have been the major vicariant force acting on the evolution of the lizard family-subfamily taxa . . ." There are many hypothesized past positions, connections and times of separation

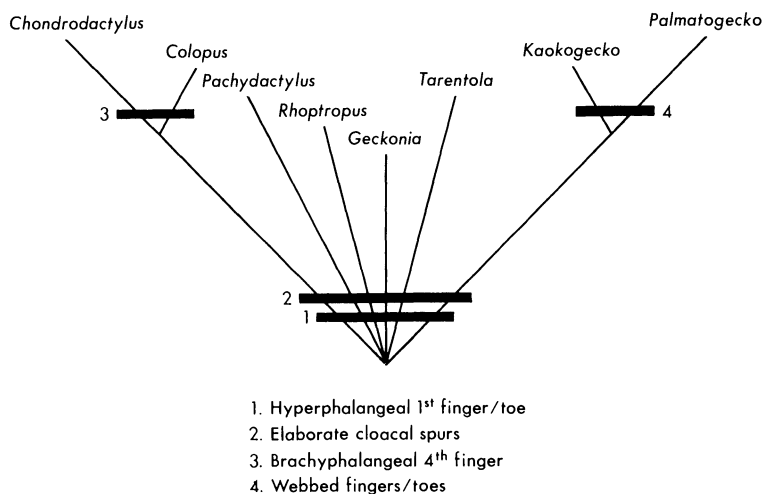


FIG. 12. Synapomorphies (1-4) suggesting sister-group relationships among certain "ptyodactylines" (after Haacke [1976] and Russell [1972]).

of Gondwanan landmasses (Moody, 1980; Owen, 1976). I have accepted that set endorsed by biogeographers (see for example, Cracraft, 1973, 1974).

I hypothesize the breakup of Pangaea into Laurasia and Gondwanaland about 180 mybp was the vicariance responsible for divergence of gekkotans into Eublepharidae and Gekkonidae. I assume eublepharids are Laurasian in origin, even though some taxa included in that family are found today on landmasses derived from Gondwanaland (*e.g.*, *Hemitheconyx* and *Holodactylus* in northern Africa). The extra-Laurasian distributions must therefore be considered more recent secondary dispersals. The widespread Laurasian distribution of relatively primitive *Eublepharis* (eastern Iraq to India, southern Turkmenia, Norway and Hainan Islands, Gulf of Tonkin, and Okinawa and Ryukyu Islands) and the German and Manchurian locations of Jurassic bavarisaurids, the sister-groups to gekkotans, are the bases for this assumption.

If Gekkonidae is the southern vicariant then at least some of the gekkonid + pygopodid diversity might be due to the breakup of Gondwanaland. For example, the Africa-India and Australia-New Zealand separation (Rosen, 1978) about 85 mybp is congruent with the postulated divergence of Gekkonidae and Pygopodidae (Fig. 11). In turn, separation of India from Africa about 60 mybp could account for the origin of the Gekkonini; however, the uncorroborated common ancestry of that lineage and its unresolved relationship to the "ptyodactylines" and the Sphaerodactylini makes this portion of my interpretation highly speculative. One of the major monophyletic groups of "ptyodactylines" (Fig. 12) consists almost entirely of African taxa, which might represent the genealogical counterpart to the Gekkonini. No doubt, dispersal was responsible for much of the remainder

of the Gekkonini origins, because many of the genera are widespread and sympatric (e.g., *Cyrtopodion*, *Gonydactylus*, *Hemidactylus*, *Lygodactylus*, and *Phyllodactylus*). The Ethiopian-Neotropical track indicated by the distribution of the Sphaerodactylini may have involved trans-Atlantic dispersal, like that postulated for *Hemidactylus*, *Lygodactylus*, and *Tarentola* (Kluge, 1969; Bons and Pasteur, 1977).

The Australian Region endemic, Pygopodidae (Fig. 11), provides one of the most interesting divergences to be interpreted. The initial split leading to the pygopodid radiation is consistent with the separation of Africa-India and Australia-New Zealand (Rosen, 1978; Cracraft, 1980). However, the relationship of the principal lineages, Pygopodinae and Diplodactylinae, does not fit the Australia-New Zealand vicariance especially well. The Australia-New Zealand separation would be consistent if pygopods were the sister-group to the *Crenadactylus* + *Diplodactylus* + *Oedura* + *Rhynchoedura* lineage of Kluge (1967b). Under such a hypothesis, the remaining Diplodactylinae, the Carphodactylini, would have dispersed from New Zealand to New Caledonia, as well as to Australia, perhaps by way of the Lord Howe Rise (Tyler, 1979). Cracraft (1980) recognized a similar pattern among gruiforme birds. In contrast to Presch (1983), I conclude that much of the biogeographic history of gekkotans is consistent with a vicariance hypothesis involving the breakup and movement of the Pangaeon plates. My interpretation is also inconsistent with Estes' (1983b) opinions that Antarctica was never occupied by gekkonoids, and that Southeast Asia was the center of gekkotan evolution.

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TABLE 1  
NUMBER OF SCLERAL OSSICLES PER EYEBALL

Taxon (recognized genera-species-subspecies) <sup>a</sup>	Range
Eublepharinae (5-19-14)	
<i>Aeluroscalabotes</i>	23-25
<i>Coleonyx</i>	13-19
<i>Eublepharis</i>	15-19
<i>Hemitheconyx</i>	18
<i>Holodactylus</i>	18-22
Diplodactylinae (13-84-10)	
<i>Bavayia</i>	31-34
<i>Carphodactylus</i>	30-33
<i>Crenodactylus</i>	22-27
<i>Diplodactylus</i>	25-40
<i>Eurydactylodes</i>	27
<i>Hoplodactylus</i>	23-29
<i>Naultinus</i>	21-23
<i>Nephrurus</i>	29-36
<i>Oedura</i>	29-35
<i>Phyllurus</i>	25-31
<i>Pseudothecadactylus</i>	31-32
<i>Rhacodactylus</i>	26-30
<i>Rhynchoedura</i>	32-37
Pygopodidae (7-31-2) <sup>b</sup>	
<i>Aprasia</i>	11-14
<i>Delma</i>	14-17
<i>Lialis</i>	16-19
<i>Ophidiocephalus</i>	13
<i>Paradelma</i>	15
<i>Pletholax</i>	14
<i>Pygopus</i>	15
Gekkonidae (63-607-206) <sup>c</sup>	
<i>Afroedura</i>	14-15
<i>Agamura</i>	14
<i>Ailuronyx</i>	14
<i>Alsophylax</i>	14
<i>Aristelliger</i>	14
<i>Asaccus</i>	14 <sup>d</sup>
<i>Bogertia</i>	14
<i>Briba</i>	14
<i>Bunopus</i>	14
<i>Calodactylodes</i>	14
<i>Carinatogekko</i>	14 <sup>d</sup>
<i>Chondrodactylus</i>	15-16
<i>Cnemaspis</i>	14
<i>Colopus</i>	14-15
<i>Cosymbotus</i>	14
<i>Crossobamon</i>	14-15
<i>Cyrtopodion</i>	14-15
<i>Dravidogekko</i>	14

TABLE 1 Continued

Taxon (recognized genera-species-subspecies) <sup>a</sup>	Range
<i>Ebenavia</i>	14
<i>Geckolepis</i>	14-15
<i>Geckonia</i>	14
<i>Gehyra</i>	13-16
<i>Gekko</i>	14
<i>Gonydactylus</i>	14-15
<i>Gymnodactylus</i>	14
<i>Hemidactylus</i>	14-15
<i>Hemiphyllodactylus</i>	14-16
<i>Heteronota</i>	14-15
<i>Homonota</i>	13-14
<i>Homopholis</i>	14
<i>Kaoko Gecko</i>	15 <sup>d</sup>
<i>Lepidodactylus</i>	14-16
<i>Luperosaurus</i>	14
<i>Lygodactylus</i>	14
<i>Microgecko</i>	14
<i>Millotissaurus</i>	14
<i>Nactus</i>	13-14
<i>Narudasia</i>	14
<i>Pachydactylus</i>	14
<i>Palmatogecko</i>	14
<i>Paragehyra</i>	14
<i>Paroedura</i>	14 <sup>d</sup>
<i>Perochirus</i>	14
<i>Phelsuma</i>	13-14
<i>Phyllodactylus</i>	13-15
<i>Phyllopezus</i>	14-15
<i>Pristurus</i>	14-16
<i>Pseudogecko</i>	14
<i>Ptenopus</i>	15-17
<i>Ptychozoon</i>	14
<i>Ptyodactylus</i>	14-15
<i>Quedenfeldtia</i>	14
<i>Rhoptropus</i>	14-15
<i>Saurodactylus</i>	14
<i>Stenodactylus</i>	20-28
<i>Tarentola</i>	14
<i>Teratolepis</i>	13-14
<i>Teratoscincus</i>	15-21
<i>Thecadactylus</i>	14
<i>Tropiocolotes</i>	14
<i>Urocotyledon</i>	14
<i>Uroplatus</i>	15

TABLE 1 Continued

Taxon (recognized genera-species-subspecies) <sup>a</sup> Range	
Sphaerodactylinae (5-120-79)	
<i>Coleodactylus</i>	12-14
<i>Gonatodes</i>	13-15
<i>Lepidoblepharis</i>	13-14
<i>Pseudogonatodes</i>	14
<i>Sphaerodactylus</i>	13-15

<sup>a</sup> Extracted from Kluge (1967a:table 1), Kluge (1976a:table 1), and Underwood (1970:table 1).

<sup>b</sup> Largely estimated from the modal values presented by Kluge (1976a).

<sup>c</sup> Among all of the currently recognized gekkonoid genera, only *Microscalabotes* was not sampled.

<sup>d</sup> New observations (not according to footnote a).

TABLE 2  
X-RAY DIFFRACTION ANALYSIS OF GEKKONOID EGG SHELL AND "CALCIUM MILK"

Egg Shell						"Calcium Milk"					
<i>Coleonyx variegatus</i>			<i>Hemidactylus mabouia</i>			<i>Gonatodes fuscus</i>			<i>Gekko gekko</i>		
relative intensity (%)	$^{\circ}2\theta^a$	$d^b$	relative intensity (%)	$^{\circ}2\theta$	d	relative intensity (%)	$^{\circ}2\theta$	d	relative intensity (%)	$^{\circ}2\theta$	d
100	29.7	3.01	100	29.7	3.01	100	29.8	3.00	100	26.4	3.37
			20	36.3	2.48	30	36.4	2.47	60	27.4	3.25
10	39.5	2.28	30	39.7	2.27	30	39.9	2.26	50	33.3	2.69
7	43.4	2.09	15	43.5	2.08	30	43.6	2.08	40	36.3	2.47
			50	47.8	1.90	60	47.9	1.90			
			40	48.8	1.87	45	48.9	1.36			

<sup>a</sup> degrees two theta is a relative measure of the diffracted x-ray beam.

<sup>b</sup> d is the spacing between atoms from which x-rays are diffracted.

TABLE 3  
GEKKONOID DATA MATRIX

Character	Ancestor	Eublepharinae	Diplodactylinae	Pygopodidae	<i>Teratoscincus</i>	Gekkonini	"Pyodactylini"	<i>Pristurus</i>	<i>Gonatodes</i>	Sphaero <sup>c</sup>
1	0	1	0 <sup>a</sup>	1	0	0	0 <sup>a</sup>	0	0 <sup>a</sup>	1
2	0	1 <sup>a</sup>	1	1 <sup>a</sup>	1	1	1	1	1	1
3	0	1	0	0	1	1 <sup>a</sup>	1 <sup>a</sup>	1	1	1 <sup>a</sup>
4	0	1	1	1	1	1	1	1	1	1
5	0	1	1	1	1	1	1	1	1	1
6	0	1	1	1	1	1	1	1	1	1
7	0	1	1	1	1	1	1	1	1	1
8	0	1	1	1	1	1	1	1	1	1
9	0	1	1	1	1	1	1	1	1	1
10	0	1	1	1	1	1 <sup>a</sup>	1 <sup>a</sup>	0	0	0
11	0	1	1	1 <sup>a</sup>	1	1 <sup>a</sup>	1 <sup>a</sup>	0	0	0
12	0	1	2 <sup>a</sup>	2	1	1 <sup>a</sup>	1 <sup>a</sup>	0	0	0
13	0	1	1	1	1	1	1	1	1	1
14	0	1	1	1	1	1	1	1	1	1
15	0	1	1	1	1	1	1	1	1	1
16	0	1	1	1	1	1	1	1	1	1
17	0	1	1	0	1	1	1	1	1	1
18	0	1	1	1 <sup>a</sup>	1	1	1 <sup>a</sup>	0	1	1
19	0	1	1	1	1	1	1	1	1	1
20	0	1	1	1	1	1 <sup>a</sup>	1 <sup>a</sup>	2	2	2
21	0	1	1	1	1	1	1	1	1	1
22	0	1	1	1	1	1	1	1	1	1
23	0	1	1	1	1	1	1	1	1	1
24	0	1	1	1	1	1 <sup>a</sup>	1	1	1	1 <sup>a</sup>
25	0	1	1	1	1	1	1	1	1	1
26	0	1	1	1	1	1	1	1	1	1
27	0	1	1	1 <sup>a</sup>	1	1	1	1	1	1
28	0	1	1	1 <sup>a</sup>	1	1	1	1	1	1
29	0	1	1	2	1	1	1	1	1	1
30 <sup>b</sup>	0	1	1	0	1	0	0	0	0	0
31	0	0	1	1	1	1	1	1	1	1
32	0	0	1	?	1	1	1	1	0	0
33	0	0 <sup>a</sup>	0	0	0	0	0	1	1	1
34	0	0	1	1 <sup>a</sup>	1	1 <sup>a</sup>	1 <sup>a</sup>	1	1	1
35	0	0 <sup>a</sup>	1	1	1	1	1	1	1	1
36	0	0 <sup>a</sup>	1	1	0	1	1	1	1	1
37	0	0	1	0	0	0 <sup>a</sup>	0	0	0	0
38	0	0	0	1	0	0	0	0	0	0
39	0	0	0	0	1	1	1	1	1	1
40	0	0	0	0	1	1	1	1	1	1
41	0	0	0	0	1	1	1	1	1	1
42	0	0	0	0	0	1 <sup>a</sup>	1	1	1	1
43	0	0	0	0 <sup>a</sup>	0	0	0 <sup>a</sup>	1	1	1
44	0	0	0	0	0	1	0	0 <sup>a</sup>	0	0

<sup>a</sup> One or a few exceptions, or variants that might be interpreted as exceptions.

<sup>b</sup> Dividing this character into 14 or more ossicles obscures much variation (see Fig. 9).

<sup>c</sup> *Coleodactylus*, *Lepidoblepharis*, *Pseudogonatodes*, *Sphaerodactylus*.

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## APPENDIX I

## CENTRUM SHAPE OF ADULT TRUNK VERTEBRAE

The centrum shape of an adult trunk vertebra was determined for one or more species of the following gekkonoid genera. Eublepharinae: *Aeluroscalabotes*; *Coleonyx* (incl. *Anarbylus*); *Eublepharis*; *Hemitheconyx*; *Holodactylus*. Diplodactylinae: *Bavayia*; *Carphodactylus*; *Crenadactylus*; *Diplodactylus* (incl. *Lucasium*); *Hoplodactylus*; *Naultinus*; *Nephrurus*; *Oedura*; *Phyllurus*; *Pseudothecadactylus*; *Rhacodactylus*; *Rhynchoedura*. Gekkoniinae: *Afroedura*; *Agamura*; *Ailuronyx*; *Alsophylax*; *Aristelliger*; *Asaccus*; *Briba*; *Bunopus*; *Calodactylodes*; *Chondrodactylus*; *Cnemaspis*; *Colopus*; *Cosymbotus*; *Cyrtopodion*; *Ebenavia*; *Geckolepis*; *Geckonia*; *Gehyra*; *Gekko*; *Gonydactylus*; *Gymnodactylus*; *Hemidactylus*; *Hemiphyllodactylus*; *Heteronotia*; *Homonota*; *Homopholis* (incl. *Blaesodactylus*); *Lepidodactylus*; *Lygodactylus*; *Microgecko*; *Millotisaurus*; *Narudasia*; *Pachydactylus*; *Palmatogecko*; *Perochirus*; *Phelsuma* (incl. *Rhoptropella*); *Phyllodactylus*; *Phyllopezus*; *Pristurus*; *Ptenopus*; *Ptyodactylus*; *Ptychozoon*; *Quedenfeldtia*; *Rhoptropus*; *Saurodactylus*; *Stenodactylus*; *Tarentola*; *Teratolepis*; *Teratoscincus*; *Thecadactylus*; *Tropiocolotes*; *Uroplatus*. Pygopodidae: *Aclys*; *Aprasia*; *Delma*; *Lialis*; *Ophidiocephalus*; *Paradelma*; *Pletholax*; *Pygopus*. Sphaerodactylinae: *Coleodactylus*; *Gonatodes*; *Lepidoblepharis*; *Pseudogonatodes*; *Sphaerodactylus*.

## APPENDIX II

## DIPLODACTYLINES EXAMINED FOR VERTEBRAL PROCESSES

The following cleared and stained UMMZ diplodactylines were examined for presence of a process on the posterior edge of the pleurapophysis of the second sacral vertebra. The number of asterisks indicates the degree of development of the process; those without a process are not marked with an asterisk. *Bavayia cyclura* (127507), *Carphodactylus laevis* (127508), *Crenadactylus ocellatus* (127509a-b, 127510a-b, 127510c\*, 127511-12, 127523), *Diplodactylus vittatus* (127563a, 127563b\*\*, 127564\*\*, 127565a-b), *Hoplodactylus pacificus* (127574a-b, 127575), *Naultinus elegans* (127576a-b), *Nephrurus levis* (127581a-b), *Oedura marmorata* (127583), *Phyllurus milii* (127591a-b), *Pseudothecadactylus australis* (127598\*\*), *Rhacodactylus auriculatus* (127599), *Rhynchoedura ornata* (127600, 127601\*\*, 127602a, 127602b\*\*).







