

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3139, 23 pp., 11 figures, 3 tables
June 29, 1995

Cladistic Relationships of Sphaerodactyl Lizards

ARNOLD G. KLUGE¹

CONTENTS

Abstract	2
Introduction	2
Acknowledgments	2
Materials and Methods	3
Ingroup Terminal Taxa	3
Outgroups	7
Sources of Specimens	7
Sources of Data	8
Hypothesis Formulation	8
Characters	9
Other Observations	13
Cladistic Results	13
Homonymy-Heteronymy, Individual Variants, and the Evolution of the Ungual Sheath	14
A Gekko in Amber	18
References	20
Appendix. Cleared and Stained Specimens Examined	22

¹ Curator and Professor, Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, Michigan 48109.

ABSTRACT

A cladistic analysis of 25 internal and external morphological synapomorphies results in the following most parsimonious hypothesis of sphaerodactyl lizard relationships: (*Gonatodes* (*Lepidoblepharis* (*Sphaerodactylus* (*Coleodactylus*, *Pseudogonatodes*))))). The value of the ungual sheath in diagnosing the (*Lepidoblepharis*, *Sphaerodac-*

tylus, *Coleodactylus*, *Pseudogonatodes*) clade is judged in terms of the homonymy and heteronymy relations of the individual scales of the digits. An Oligo-Miocene gekko in amber from the Dominican Republic is almost certainly a *Sphaerodactylus*.

INTRODUCTION

The historical relationships of the major clades of gekkonoid lizards continue to be reexamined and reformulated with the discovery of new synapomorphies and the reinterpretation of characters employed in earlier studies (Kluge, 1967, 1987, 1994; Bauer, 1990; Kluge and Nussbaum, 1995). The taxonomy of these family-group categories has also been altered with the application of a strictly monophyletic nomenclature (Kluge, 1987). However, some major groups of gekkos have received relatively little review in recent years and are ripe for further study. For example, there is the New World Sphaerodactylidae of Underwood (1954), which now consists of approximately 132 species (table 1) in five genera, *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, *Pseudogonatodes*, and *Sphaerodactylus* (Kluge, 1993). Sphaerodactyls, as I will informally refer to this group of New World endemics, account for approximately 14% of all gekkonoid species recognized currently (including pygopods), with *Sphaerodactylus* being the most speciose genus-group of all gekkos (Kluge, 1993).² Although the monophyly of each sphaerodactyl genus appears to be well corroborated (Parker, 1926; Vanzolini, 1968a; Huey and Dix-

on, 1970; Russell, 1972; Hoogmoed, 1985), the interrelationships of these taxa remain poorly understood, as indicated by competing hypotheses of affinities. The following propositions of sister-group relationships, in parenthetical notation, illustrate some of those different propositions: (*Gonatodes* (*Lepidoblepharis* (*Pseudogonatodes*, *Sphaerodactylus*))) after Noble (1921: fig. 8); (*Gonatodes* (*Lepidoblepharis*, *Pseudogonatodes* (*Coleodactylus*, *Sphaerodactylus*))) after Parker (1926)³; (*Gonatodes* (*Lepidoblepharis* (*Pseudogonatodes* (*Coleodactylus*, *Sphaerodactylus*)))) after Vanzolini (1968b); (*Gonatodes* ((*Lepidoblepharis*, *Pseudogonatodes*) (*Coleodactylus*, *Sphaerodactylus*))) after Russell (1972). The present paper begins with a re-examination of the cladistic affinities among the five genera, including the hypothesis that the New World radiation is monophyletic. Such a historical accounting is then used to assess the evolution of certain details of digit scalation in the sphaerodactyl clade, and to classify a gekko preserved in Oligo-Miocene amber from the Dominican Republic.

ACKNOWLEDGMENTS

I wish to thank Darrel Frost for his counsel on the correct identification of *Sphaerodactylus dommeli*. David A. Grimaldi generously gave me the opportunity to report on the American Museum of Natural History *Sphaerodactylus* in Dominican amber, and it was his preliminary description of the specimen which provided the basis for my further investigation. Wolfgang Böhme and Dieter

² My use of sphaerodactyl is not to be confused with Russell's (1972) *Sphaerodactylus* Group, which excluded *Gonatodes*. Currently, 90 species of *Sphaerodactylus* are recognized. Other species-rich gekkonoid genera include *Cyrtodactylus* (sensu stricto; 62 species), *Hemidactylus* (75), *Lygodactylus* (51), and *Phyllodactylus* (56). The total number of genera and species of gekkonoids listed by Kluge (1993) is 102 and 962, respectively. These numbers represent approximately 12 and 29% increases in the recognized genus and species group taxa in the past 30 years, since Wermuth (1965).

³ Actually, Parker (1926: 301) implied that *Lepidoblepharis* and *Coleodactylus* are paraphyletic.

TABLE 1
Cleared and Stained Sphaerodactyls Examined

Genera recognized	Species recognized	Species sampled	Specimens examined
<i>Coleodactylus</i>	5	3	5
<i>Gonatodes</i>	17	14	35
<i>Lepidoblepharis</i>	16	4	11
<i>Pseudogonatodes</i>	5	3	9
<i>Sphaerodactylus</i>	90	47	111
Totals:	133	71	171

Schlee provided information on the original material of *S. dommeli*. Carlos Rivero-Blanco generously provided information from his doctoral thesis on *Gonatodes* systematics. The late Albert Schwartz was especially helpful in obtaining material of sphaerodactyls for clearing and staining. Others contributing material included Richard Zweifel, American Museum of Natural History; Jens Vindum, California Academy of Sciences; Jay M. Savage, private collection; Pedro Ruiz, Instituto de Ciencias Naturales Renovables y del Ambiente, Bogotá; William E. Duellman, Museum of Natural History, University of Kansas; John Wright, Los Angeles County Museum of Natural History; Doug Rossman, Louisiana State University, Museum of Zoology; Carlos Rivero-Blanco, Museo de Ciencias Naturales, Caracas; Ernest E. Williams, Museum of Comparative Zoology, Harvard University; David B. Wake, Museum of Vertebrate Zoology, University of California, Berkeley; José Ayarzagüena, Museo de Historia Natural La Salle, Caracas; Richard Thomas, private collection; James R. Dixon, Texas A&M University; Walter Auffenburg, University of Florida, Florida State Museum; Tom Uzzell, University of Illinois, Natural History Museum; George Zug, United States National Museum. L. Lee Grismer and Greg K. Pregill reviewed the penultimate draft of this paper, and the manuscript was improved considerably as the result of their efforts.

MATERIALS AND METHODS

INGROUP TERMINAL TAXA

The following five sphaerodactyl genera, which contain 5, 17, 16, 5, and 90 recognized

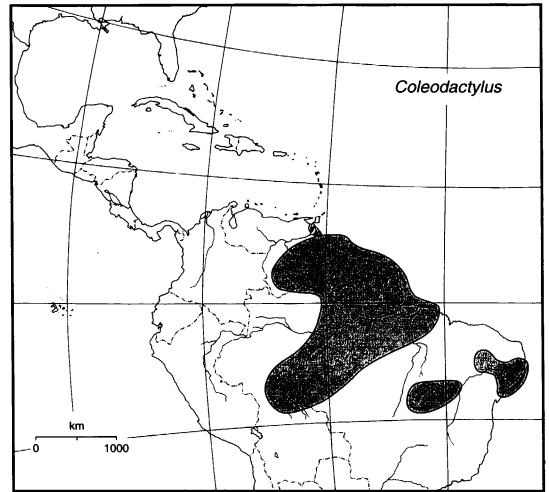


Fig. 1. Geographic range of *Coleodactylus*.

species, respectively, constitute the ingroup terminal taxa employed in this study. Junior synonyms are placed in parentheses (currently recognized subspecies are indicated with an asterisk). The accompanying i.e. and n.n. notations specify an invalid emendation (e.g., *lapsus calami* or substitute name) and nomen nudum, respectively. Complete citations to taxonomic authorship can be found in Kluge (1993).

Coleodactylus Parker (1926a)

Species content (and synonymy): 1. *amazonicus* Andersson, 1918 (*zernyi* Wettstein, 1928); 2. *brachystoma* Amaral, 1935 (*pfimeri* Miranda-Ribeiro, 1937); 3. *guimaraesi* Vanzolini, 1957; 4. *meridionalis* Boulenger, 1888b; 5. *septentrionalis* Vanzolini, 1980.

Geographic distribution (fig. 1): Most of the species are now known from several geographically close localities (Vanzolini, 1980; Hoogmoed, 1985). The remaining disjunct species distributions may not be due to lack of collecting.

Gonatodes Fitzinger (1843)

Species content (and synonymy): 1. *albogularis* A. M. C. Duméril and Bibron, 1836 (*albicularis* [i.e.] Fitzinger, 1843; *fuscus** Hal- lowell, 1855; *varius* A. H. A. Duméril, 1856; *notatus** Reinhardt and Lütken, 1862; *ma-*

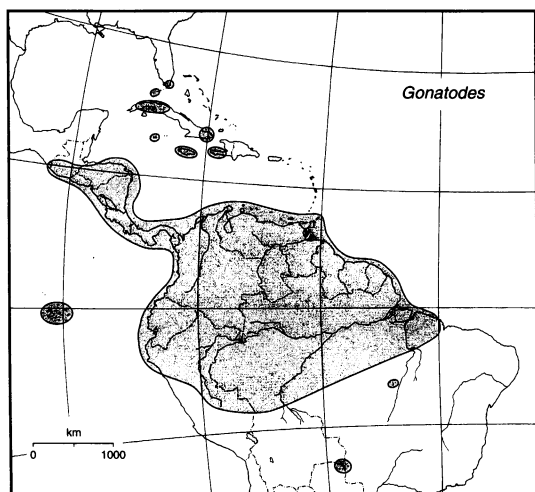


Fig. 2. Geographic range of *Gonatodes*.

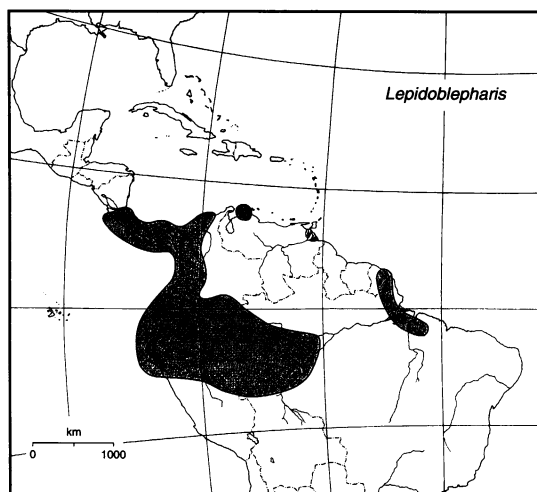


Fig. 3. Geographic range of *Lepidoblepharis*.

culatus Steindachner, 1867; *braconnieri* O'Shaughnessy, 1875; *bodinii** Rivero-Blanco, 1964); 2. *annularis* Boulenger, 1887a (*annularis* Boulenger, 1887b; *boonii* Lidth de Jeude, 1904; *beebei* Noble, 1923a); 3. *antillensis* Lidth de Jeude, 1887; 4. *atricucularis* Noble, 1921a; 5. *caudiscutatus* Günther, 1859b (*collaris* Garman, 1892); 6. *ceciliae* Donoso-Barros, 1965a; 7. *concinatus* O'Shaughnessy, 1881 (*buckleyi* O'Shaughnessy, 1881; *ligiae* Donoso-Barros, 1967); 8. *eladioi* Nascimento, Avila-Pires and Cunha, 1987; 9. *falconensis* Shreve, 1947; 10. *hasemani* Griffin, 1917 (*spinulosus* Amarál, 1932); 11. *humeralis* Guichenot, 1855 (*ferrugineus* Cope, 1864 [1863]; *incertus* W. Peters, 1872a [1871]; *sulcatus* O'Shaughnessy, 1875); 12. *ocellatus* Gray, 1831a (*condifentatis* [n.n.] Marcuzzi, 1950); 13. *petersi* Donoso-Barros, 1967; 14. *seigliiei* Donoso-Barros, 1965a; 15. *taniae* Roze, 1963; 16. *tapajonicus* Rodrigues, 1980; 17. *vittatus* Wiegmann, 1856 (*gillii* Cope, 1864 [1863]; *roquensis** Roze, 1956).

Geographic distribution (fig. 2): Venezuela and the Dutch West Indies represent the area of greatest species diversity (Rivero-Blanco, 1979). Although *Gonatodes* is present on Trinidad and Tobago, representatives are otherwise absent from the Lesser Antilles, and much of the Greater Antilles. The Florida distribution (mainland and Keys) probably

represents recent human introductions. Specimens from the Cayman Islands, Jamaica, and Haiti are considered representative of an endemic subspecies (*notatus*) of the widespread *G. a. albogularis*. The coastal Cuban records of *G. a. fuscus* may represent human introductions; however, that interpretation does not seem to apply to interior localities (Schwartz and Henderson, 1988). The Galapagos material is believed to represent a mainland South American species, *G. caudiscutatus*, which probably represents one or more accidental introductions by humans. The two disjunct South America records are referable to the widespread and otherwise continuously distributed *G. humeralis* to the north (Vanzolini, 1968a, 1968b; Rivero-Blanco, 1979).

Lepidoblepharis Peracca (1897b)

Genus synonymy: *Lathrogecko* Ruthven, 1916.

Species content (and synonymy): 1. *buchwaldi* Werner, 1910b; 2. *colombianus* Mechler, 1968; 3. *duolepis* Ayala and Castro, 1983; 4. *festae* Peracca, 1897b; 5. *grandis* Miyata, 1985; 6. *heyerorum* Vanzolini, 1978a; 7. *intermedius* Boulenger, 1914a; 8. *miyatai* Lamar, 1985; 9. *microlepis* Noble, 1923b; 10. *montecanoensis* Marquezich and Taphorn, 1994; 11. *oxycephalus* Werner, 1894; 12. *per-*

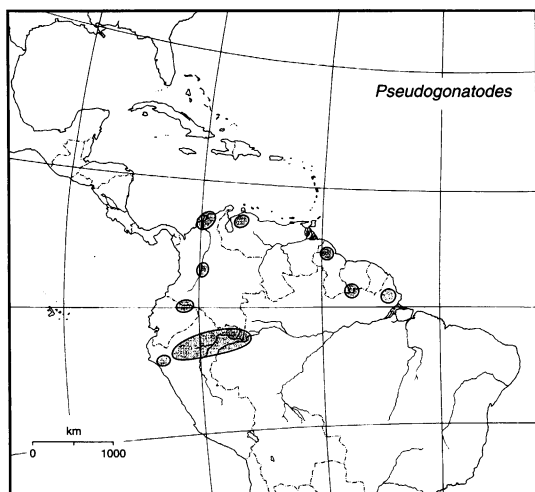


Fig. 4. Geographic range of *Pseudogonatodes*.

accae Boulenger, 1908; 13. *ruthveni* Parker, 1926a; 14. *sanctaemartae* Ruthven, 1916 (*fugax* Ruthven, 1928); 15. *williamsi* Ayala and Serna, 1986; 16. *xanthostigma* Noble, 1916.

Geographic distribution (fig. 3): The disjunct part of the range at the mouth of the Amazon River represents *L. heyerorum*, and that which occurs in Venezuela is *L. montecanoensis*. All species of *Lepidoblepharis*, other than *L. festae* and *L. heyerorum*, are found outside the Amazon Basin, the majority of which are from Colombia (Mechler, 1968).

Pseudogonatodes Ruthven (1915)

Species content (and synonymy): 1. *barbouri* Noble, 1921a; 2. *furvus* Ruthven, 1915; 3. *guianensis* Parker, 1935a (*amazonicus** Vanzolini, 1967); 4. *lunulatus* Roux, 1927; 5. *peruvianus* Huey and Dixon, 1970.

Geographic distribution (fig. 4): The species are allopatric (Huey and Dixon, 1970), and lack of collecting probably does not explain entirely the highly fragmented distribution.

Sphaerodactylus Wagler (1830)

Genus synonymy: *Sphaeriodactylus* Gray, 1831a.

Species content (and synonymy): 1. *alta-velensis* Noble and Hassler, 1933 (*breviros-*

*tratus** Shreve, 1968; *enriquilloensis** Shreve, 1968; *lucioi** R. Thomas and Schwartz, 1983b); 2. *argivus* Garman, 1888 (*bartschi** Cochran, 1934; *lewisii** Grant, 1941 [1940]); 3. *argus* Gosse, 1850 (*henriquesi* Grant, 1940; *andresensis** Dunn and Saxe, 1950); 4. *armasi* Schwartz and Garrido, 1974; 5. *armstrongi* Noble and Hassler, 1933 (*hypsinephes** R. Thomas and Schwartz, 1983a); 6. *asterulus* Schwartz and Graham, 1980; 7. *beattyi* Grant, 1937 (*seamani** R. Thomas and Schwartz, 1966a); 8. *becki* K. P. Schmidt, 1919b; 9. *bromeliarum* G. Peters and Schwartz, 1972; 10. *caicosensis* Cochran, 1934; 11. *callocricus* Schwartz, 1976; 12. *celicara* Garrido and Schwartz, 1982; 13. *cinereus* Wagler, 1830 (*stejnegeri** Cochran, 1931); 14. *clenchi* Shreve, 1968 (*apocoptus** Schwartz, 1983); 15. *cochranae* Ruibal, 1946; 16. *copei* Steindachner, 1867 (*anthracinus* Cope, 1862a [1861]; *picturatus** Garman, 1887; *asper* Garman, 1888; *cataplexis** Schwartz and R. Thomas, 1965 [1964]; *enochrus** Schwartz and R. Thomas, 1965 [1964]; *polyommatus** R. Thomas, 1968; *astreptus** Schwartz, 1975; *pelates** Schwartz, 1975; *websteri** Schwartz, 1975; *deuterus** Schwartz, 1975); 17. *corticola* Garman, 1888 (*aporrox** Schwartz, 1968a; *campter** Schwartz, 1968a; *soter** Schwartz, 1968a); 18. *cricoderus* R. Thomas, Hedges and Garrido, 1992; 19. *cryptius* R. Thomas and Schwartz, 1977; 20. *darlingtoni* Shreve, 1968 (*noblei** Shreve, 1968; *bobilini** R. Thomas and Schwartz, 1983a; *mekistus** R. Thomas and Schwartz, 1983a); 21. *difficilis* Barbour, 1914a (*lycauges** Schwartz, 1983; *euopter** Schwartz, 1983; *typhlopous** Schwartz, 1983; *peratus** Schwartz, 1983; *diolenius** Schwartz, 1983; *anthracomus** Schwartz, 1983); 22. *dunni* K. P. Schmidt, 1936; 23. *elasmorhynchus* R. Thomas, 1966; 24. *elegans* MacLeay, 1834 (*punctatissimus** A. M. C. Duméril and Bibron, 1836; *alopex* Cope, 1862a [1861]); 25. *elegantulus* Barbour, 1917; 26. *epiurus* R. Thomas and Hedges, 1993; 27. *epizemius* Garrido and Jaume, 1984 (*docimus* Schwartz and Garrido, 1985); 28. *fantasticus* Cuvier, 1836 (*ligniservulus** W. King, 1962b; *anidrotus** R. Thomas, 1964; *fuga** R. Thomas, 1964; *hippomanes** R. Thomas, 1964; *karukera** R. Thomas, 1964; *orescius** R. Thomas, 1964; *phyzacinus** R. Thomas, 1964;

- tartaropylorus** R. Thomas, 1964); 29. *gai-geae* Grant, 1932; 30. *gilvitorques* Cope, 1862a (1861); 31. *glaucus* Cope, 1866 (1865) (*inornatus* W. Peters, 1873; *torquatus* Strauch, 1887); 32. *goniorhynchus* Cope, 1895 (1894); 33. *graptolaemus* Harris and Kluge, 1984; 34. *heliconiae* Harris, 1982; 35. *homolepis* Cope, 1886 (*carinatus* Andersson, 1916; *imbricatus* Andersson, 1916; *mertensi* Wermuth, 1965); 36. *inaguae* Noble and Klingel, 1932; 37. *intermedius* Barbour and Ramsden, 1919 (*drapetiscus* Schwartz, 1958); 38. *klauberi* Grant, 1931a; 39. *ladae* R. Thomas and Hedges, 1988; 40. *lazelli* Shreve, 1968; 41. *leucaster* Schwartz, 1973; 42. *levinsi* Heatwole, 1968; 43. *lineolatus* Lichtenstein and von Martens, 1856 (*casicolus* Cope, 1862a [1861]); 44. *macrolepis* Günther, 1859a (*imbricatus* Fischer, 1881; *grandisquamis** Stejneger, 1904 [1903]; *danforthi* Grant, 1931a; *parvus** W. King, 1962b; *ateles** R. Thomas and Schwartz, 1966a; *guarionex** R. Thomas and Schwartz, 1966a; *inigo** R. Thomas and Schwartz, 1966a; *mimetes** R. Thomas and Schwartz, 1966a; *phoberus** R. Thomas and Schwartz, 1966a; *spanius** R. Thomas and Schwartz, 1966a; *stibarus** R. Thomas and Schwartz, 1966a); 45. *mariguanae* Cochran, 1934; 46. *microlepis* Reinhardt and Lütken, 1862 (*melanospilus* A. H. A. Duméril, 1873; *thomasi** Schwartz, 1965); 47. *micropithecus* Schwartz, 1977b; 48. *millipunctatus* Hallowell, 1861 (1860) (*continentalis* Werner, 1896d); 49. *molei* Boettger, 1894b (*buergeri* Werner, 1900b; *venezuelanus* Roux, 1927; *boettgeri* [n.n.] Donoso Barros, 1968); 50. *monensis* Meerwarth, 1901; 51. *nicholsi* Grant, 1931a; 52. *nigropunctatus* Gray, 1845a (*decoratus** Garman, 1888; *flavicaudus** Barbour, 1904; *gibbus** Barbour, 1921; *alayo** Grant, 1959a; *atessares* R. Thomas and Schwartz, 1966b; *granti** R. Thomas and Schwartz, 1966b; *lisodesmus** R. Thomas and Schwartz, 1966b; *ocujal** R. Thomas and Schwartz, 1966b; *strategus** R. Thomas and Schwartz, 1966b; *porrasi** Schwartz, 1972); 53. *notatus* Baird, 1859 (1858) (*exsul** Barbour, 1914a; *amaurus** Schwartz, 1966 [1965]; *atactus** Schwartz, 1966 [1965]; *peltastes** Schwartz, 1966 [1965]); 54. *nycteropus* R. Thomas and Schwartz, 1977; 55. *ocoae* Schwartz and R. Thomas, 1977; 56. *oliveri* Grant, 1944; 57. *omoglaux* R. Thomas, 1982; 58. *oxyrhinus* Gosse, 1850 (*dacnicolor** Barbour, 1910); 59. *pacificus* Stejneger, 1903; 60. *parkeri* Grant, 1939; 61. *parthenopion* R. Thomas, 1965; 62. *perissodactylus* R. Thomas and Hedges, 1988; 63. *plummeri* R. Thomas and Hedges, 1992; 64. *ramsdeni* Ruibal, 1959; 65. *randi* Shreve, 1968 (*methorius** Schwartz, 1977a; *strahmi** Schwartz, 1977a); 66. *rhaddotus* Schwartz, 1970; 67. *richardi* Hedges and Garrido, 1993; 68. *richardsonii* Gray, 1845a (*gossesi** Grant, 1939); 69. *roosevelti* Grant, 1931a; 70. *rosaurae* Parker, 1940; 71. *ruibali* Grant, 1959b; 72. *sabanus* Cochran, 1938; 73. *samanensis* Cochran, 1932; 74. *savagei* Shreve, 1968 (*juanilloensis** Shreve, 1968); 75. *scaber* Barbour and Ramsden, 1919; 76. *scapularis* Boulenger, 1902; 77. *schwartzi* R. Thomas, Hedges and Garrido, 1992; 78. *semasiops* R. Thomas, 1975; 79. *shrevei* Lazell, 1961; 80. *sommeri* Graham, 1981; 81. *sputator* Sparrman, 1784 (*pictus* Garman, 1887); 82. *storeyae* Grant, 1944; 83. *streptophorus* R. Thomas and Schwartz, 1977 (*sphenophanes** R. Thomas and Schwartz, 1983a); 84. *thompsoni* Schwartz and Franz, 1976; 85. *torrei* Barbour, 1914a (*spielmani** Grant, 1958); 86. *townsendi* Grant, 1931a; 87. *underwoodi* Schwartz, 1968a; 88. *vincenti* Boulenger, 1891 (*festus** Barbour, 1915; *monilifer** Barbour, 1921; *adamus** Schwartz, 1964; *diamesus** Schwartz, 1964; *josephinae** Schwartz, 1964; *pheristus** Schwartz, 1964; *psammus** Schwartz, 1964; *ronaldi** Schwartz, 1964); 89. *williamsi* R. Thomas and Schwartz, 1983b; 90. *zygaena* Schwartz and R. Thomas, 1977.

Geographic distribution (fig. 5): Only one species, *S. molei*, occurs on Trinidad and Tobago, and that taxon is also widely distributed on mainland South America (Harris, 1982: fig. 5). No *Sphaerodactylus* occurs in the Dutch West Indies, or the Grenadines and Grenada, which is similar to the geographical distribution of *Gonatodes*. Two radiations of *Sphaerodactylus*, West Indian and mainland groups of species, have been mentioned in recent research (Hass, 1991); however, synapomorphies have yet to be discovered which diagnose the latter group of endemics (Harris and Kluge, 1984). Although *S. pacificus*, which is endemic to Cocos Island, is quite likely to be part of the mainland radiation, other species geographically close to the mainland do not appear to be part of

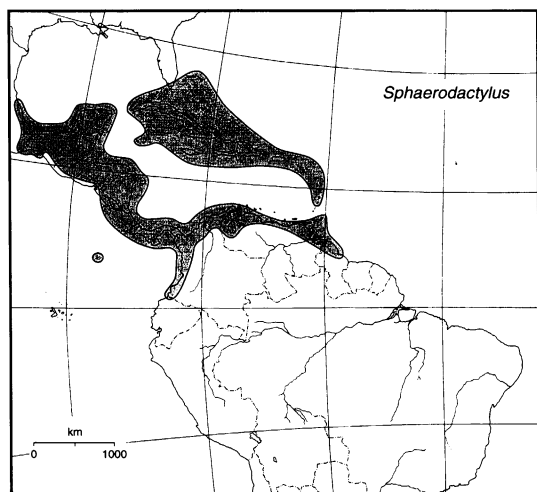


Fig. 5. Geographic range of *Sphaerodactylus*.

that history. For example, *S. argus* is thought to be part of the Antillean radiation (Hass, 1991), but that species is present on Corn Island, Honduras, and Isla San Andres, Colombia. The former location probably represents a human introduction, whereas the latter may not (Schwartz and Henderson, 1988). The Swan Islands records for *S. notatus* also indicate a species that is considered part of the West Indian radiation, and has probably dispersed toward the mainland.

Sphaerodactylus and *Anolis* (sensu lato) exhibit certain geographic similarities. The numbers of species of each taxon found on West Indian islands are highly correlated⁴. In addition, the three most widespread *Anolis* species (*A. carolinensis*, *A. distichus*, and *A. sagrei*) have geographic ranges very similar to the three most widespread *Sphaerodactylus* species (*S. argus*, *S. copei*, and *S. notatus*).

OUTGROUPS

The sister-group relationships of the sphærodactyl lineage to the northeast African-

southwest Asian *Pristurus* was delimited by six synapomorphies, including absence of the splenial bone, and the individuality of that assemblage was formally recognized by placing all six taxa in Sphaerodactylini (Kluge, 1987). A recent review of African-Madagascan gekko relationships (Kluge and Nussbaum, 1995) suggested that *Pristurus* belongs to a clade of African gekkos, which includes *Narudasia*, *Quedenfeldtia*, and *Saurodactylus*. The absence of cloacal sacs and bones was found to be diagnostic of that group, which would also include sphærodactyls (Kluge and Nussbaum, 1995; their characters 11 and 24, respectively). Also, the absence of preanal and/or femoral pores is characteristic of that assemblage (Parker, 1926; see also Kluge and Nussbaum, 1995; their character 22). Further, Russell (1972) suggested that *Gonatodes* is similar, if not closely related, to *Cnemaspis*, particularly the Indian-Oriental species-group, and therefore I have also included the latter taxon as an outgroup. Thus, I have expanded the outgroups in this study, to include *Cnemaspis*, *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus*, in order to render the ingroup character polarity hypotheses more globally parsimonious, and to more generally test the individuality of the ingroup (Clark and Curran, 1986; Nixon and Carpenter, 1993; Kluge, 1994). The fact that Kluge and Nussbaum's (1995: figs. 6,7) analyses led to different sister-group hypotheses for *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus*, which also differed from those delimited herein, strongly suggests the need for further research on those outgroup taxa.

SOURCES OF SPECIMENS

The skeletons of more than half of the currently recognized species of sphærodactyls were examined (table 1; Appendix). The repository abbreviations for that material are as follows: AMNH, American Museum of Natural History; AS and ASFS, Albert Schwartz private collection (now KU); CAS, California Academy of Sciences; CR, Costa Rica Collection, Jay M. Savage private collection, currently housed at the University of Miami; ICN, Instituto de Ciencias Naturales Renovables y del Ambiente, Bogotá; KU,

⁴ $r = 0.846$, $df = 390$; the data were taken from Maclean et al. (1977). Only those islands that had at least one species of either genus were scored. The islands south of St. Vincent, including those in close proximity to the mainland of South America, were not sampled.

TABLE 2^a
Data Matrix: Character by Taxon

	A	B	C	D	E	F	G	H	I	J
1.	0	0	0	0	1	1	0	0	0	0
2.	0	1	1	1	0	0	1	0	0	1
3.	0	1	1	1	0	0	1	0	0	1
4.	0	1	1	1	0	1	1	0	0	1
5.	0	1	0	0	0	0	1	0	0	1
6.	0/1	1	1	1	0	1	1	0/1	0/1	1
7.	0	0	0	0/1	0	0	0	0	0	1
8.	1	0	0	0	0	1	0	0	0	0
9.	0	1	0	1	0	0	1	0	0	1
10.	0	1	1	1	1	0	1	1	0/1	1
11.	0	2	0	0	0	0	2	0	0	1
12.	0	2	0	0	0	0	1	0	0	1
13.	0	1	1	1	0	0	1	0	0	0/1
14.	0	1	0	1	0	1	1	1	0	0/1
15.	0	1	1	1	0	0	1	0	0	1
16.	0	1	1	1	0	1	1	0	0	1
17.	0	1	1	1	0	1	1	1	?	1
18.	0	0	1	1	?	1	0	1	?	1
19.	0	1	1	1	0	0	1	0	0	1
20.	0	0	1	0/1	0	0	0	0	1	1
21.	0	1	0	1	0	0	1	0	0	0
22.	0	1	0	1	0	0	1	0	0	1
23.	0	1	0	0	0	0	1	0	0	0
24.	0	1	0	0	0	0	0	0	0	1
25.	1	1	1	1	0	1	1	1	1	1

^a The taxa, by columns, are A = *Cnemaspis*, B = *Coelodactylus*, C = *Gonatodes*, D = *Lepidoblepharis*, E = *Narudasia*, F = *Pristurus*, G = *Pseudogonatodes*, H = *Quedenfeldtia*, I = *Saurodactylus*, and J = *Sphaerodactylus*. Data are analyzed as missing when they appear in the matrix as ? (unknown) and 0/1 (variable).

Museum of Natural History, University of Kansas; LACM, Los Angeles County Museum of Natural History; LSUMZ, Louisiana State University, Museum of Zoology; MCNC, Museo de Ciencias Naturales, Caracas; MCZ, Museum of Comparative Zoology, Harvard University; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; MHNLS, Museo de Historia Natural La Salle, Caracas; RT, Richard Thomas private collection; TCWC, Texas A&M University; UF, University of Florida, Florida State Museum; UINHM, University of Illinois, Natural History Museum; UMMZ, University of Michigan, Museum of Zoology; USNM, United States National Museum. The skeletal material for the outgroups is listed in Kluge and Nussbaum (1995).

SOURCES OF DATA

The vast majority of the characters used have been mentioned in other research on sphaerodactyl relationships (Noble, 1921; Parker, 1926; Underwood, 1954; Kluge, 1967, 1982, 1983, 1987; Vanzolini, 1968a, 1968b; Russell, 1972), or in studies on other gekkos (e.g., Bauer, 1990; Kluge and Nussbaum, 1995). Some of the evidence cited most often comes from the scalation and shape of the digits, particularly the ungual sheath. Unfortunately, an inconsistent terminology and several arbitrary systems of letter and number labels for those scales have been employed over the years (Noble, 1921; Parker, 1926, Mechler, 1968; Vanzolini, 1968a, 1968b; Russell, 1972; Hoogmoed, 1985). I believe our understanding of the evolution of sphaerodactyl digits will improve substantially by adopting a standardized nomenclature. Further, a simple system of names and labels based strictly on anatomical location, rather than presumed homology, is to be preferred because topological similarity is important in determining which variants are scored as shared apomorphies. Thus, I apply the following terms and labels in my discussions of the sphaerodactyl ungual sheath:

(1) Dorsals (labeled d in the illustrations employed herein). These scales form one or two (rarely) proximal- to distal-oriented rows on the dorsal midline of the digit. Dorsals are usually larger than laterals.

(2) Ventrals (labeled v). Often termed subdigital or inferior lamellae in the literature on squamates. These scales form one or two (rarely) proximal- to distal-oriented rows on the ventral midline of the digit. They are almost always wider than the adjacent scales.

(3) Laterals (labeled l). These scales form two or more proximal- to distal-oriented rows between the dorsals and ventrals.

The scale (or series) adjacent to the dorsals is referred to as superolateral(s), whereas inferolateral(s) applies to that scale (or series) adjacent to the ventrals. The terms pre- and postaxial, or lateral and median, refer to the side of the digit on which the lateral scale occurs.

HYPOTHESIS FORMULATION

The best-fitting hypothesis of sphaerodactyl relationships was determined with the ie

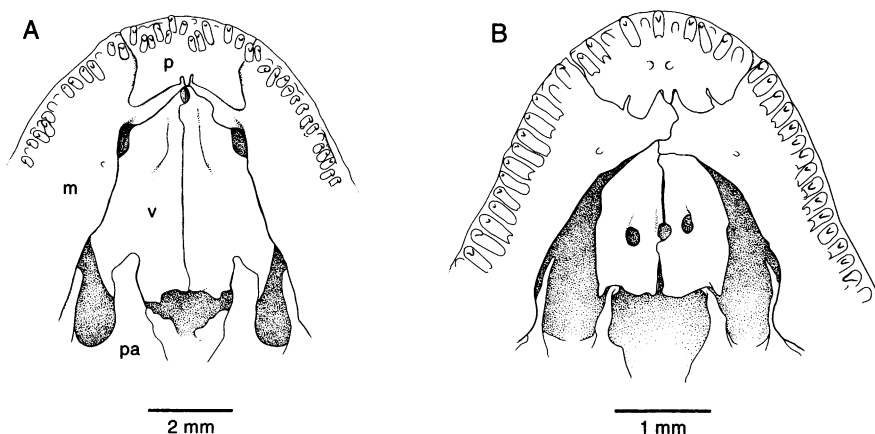


Fig. 6. Ventral view of the palate (reproduced from Kluge and Nussbaum, 1995). A. The plesiomorphic condition in gekkos. B. The apomorphic state, which is typical of *Narudasia* and *Pristurus*. m = maxilla; p = premaxilla; pa = palatine; v = vomer.

(implicit enumeration) command in Hennig86 (Farris, 1988). Fit to data is assessed in terms of consistency and retention indices. Character consistency, c , is defined as m/s , where s is the minimum number of steps a character can exhibit on a given tree hypothesis, and m is the minimum number of steps that character can show on any tree hypothesis (Kluge and Farris, 1969). Character retention, r , is defined as $(g-s)/(g-m)$, where g is the greatest number of steps a character can have on any tree (Farris, 1989). The ensemble consistency, C , and ensemble retention, R , indices used to choose among alternative phylogenetic hypotheses are simply the quantities for a single character, m , g and s , summed over all characters in the matrix, thereby providing corresponding totals, M , G and S . Thus, $C = M/S$, and $R = (G-S)/(G-M)$.

Polarity was realized with the outgroup option in Hennig86 (Farris, 1988); *Cnemaspis*, *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus* were designated as outgroups to the sphaerodactyl ingroup. The two multistate characters, 11, 12, were treated as additive. Table 2 summarizes which character states have been attributed to the terminal taxa.

CHARACTERS

1. Maxillae separated or in narrow (0) or broad (1) contact posterior to premaxilla. Ac-

cording to Kluge and Nussbaum (1995; their character 29), the apomorphic state is restricted to *Narudasia* and *Pristurus* (fig. 6). The plesiomorphic condition was illustrated originally by Kluge (1987: fig. 8).

2. Maxillary process of palatine long (0) or short or absent (1). A long maxillary process, state 0, is similar in length to the vomerine process of the palatine.

3. The choanal canal on the ventral surface of the palatine is short and shallow (0) or long and deep (1). Russell (1972) referred to the similar palates of sphaerodactyls, and he considered *Gonatodes* to be a part of that New World radiation largely because of that similarity. Unfortunately, Russell did not specify the exact nature of the palatal similarity; however, the size and shape of the choanal canal seem to have been a part of his assessment.

4. Splenial present (0) or absent (1). According to Kluge (1967, 1987), the splenial is present in most lizards, including all gekkonids, except *Pristurus*, *Ptyodactylus*, and sphaerodactyls. This is character 33 in Kluge and Nussbaum (1995). Hecht and Edwards (1976) used the absence of the splenial as evidence for sphaerodactyl common ancestry; however, they overlooked that same state in *Pristurus* and *Ptyodactylus*, and the pygopod *Aprasia* (Kluge, 1976). The two gekkonids do not seem to share any derived states (Kluge and Nussbaum, 1995), besides the ab-

sence of the splenial, that could be used as evidence of their common ancestry, and there can be little doubt that *Aprasia* is part of an independent line of evolution. The loss of the splenial in sphaerodactyls and *Pristurus* may not be convergent; however, that interpretation will be judged later in this study, in the context of the analysis of all of the relevant available evidence and character congruence.

5. Coronoid tall (0) or short (1). The size of the coronoid is assessed relative to the general contour of the mandible, when viewed laterally. The tall state much exceeds that contour, whereas the short condition is hardly elevated above that outline.

6. Neural arch of atlas paired (0) or fused (1). Kluge and Nussbaum (1995) observed (their character 8) that the fused condition occurs in all sphaerodactyls, *Pristurus*, some *Quedenfeldtia* (variable in *Q. moerens*), and some *Saurodactylus* (single in *S. fasciatus*, paired in *S. mauritanicus*). The arch is single in almost all *Cnemaspis* (*C. affinus*, *C. africana*, *C. indica*, *C. kandiana*, *C. nigridia*, *C. ornata*, *C. quatturoseriata*, *C. siamensis*, and *C. wynadensis*). The paired state was observed only in *C. boulengerii*, and possibly one individual of *C. kendallii*. Thus, I have scored *Cnemaspis* as variable. The arch is paired in *Narudasia*.

7. Lateral projection of hyoid cornu present (0) or absent (1). The projection is well developed in *Cnemaspis*, *Coleodactylus*, *Gonatodes* (absent in one of three specimens of *G. humeralis* examined), *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus*. It is variable in *Lepidoblepharis*—absent in one of three *L. microlepis* (UMMZ 131865) and all three *L. s. sanctaemartae* examined (the projection is well developed in both *L. s. fugax* available). It is recorded as present in *Pseudogonatodes*; however, it is not always well developed. It is uniformly absent in *Sphaerodactylus*.

8. Second ceratobranchial arch present (0) or absent (1). According to Kluge and Nussbaum (1995; their character 7), the arch is typical of all of the taxa included in this study, except *Cnemaspis* and *Pristurus*. Noble (1921) appears to have been the first to call attention to the presence of the second ceratobranchial arch in *Sphaerodactylus*, as well as its absence in such taxa as *Cnemaspis*.

9. Vertebrae amphicoelous (0) or procoelous (1). The apomorphic state is actually defined as well developed procoely (see Kluge, 1987: fig. 5). Noble (1921: fig. 1) briefly discussed the procoelous nature of some sphaerodactyls, and Underwood (1954: 476) implied that *Gonatodes* was strictly procoelous.

10. Number of attached sternal and xiphisternal ribs more than four (0) or less than five (1). According to Kluge and Nussbaum (1995; their character 31), *Narudasia* and *Quedenfeldtia* exhibit state 1, *Pristurus* state 0, and *Saurodactylus* is variable (0/1). All sphaerodactyls are recorded as state 1 (see also Noble, 1921: figs. 4,5); however, the following individual variation was observed: one of the three *Gonatodes albogularis fuscus* specimens examined exhibited both states (UMMZ 127793); the one *G. caudiscutatus* examined had both states; one of two *G. taniae* examined possessed state 0 (UMMZ 124303); one of four *G. v. vittatus* specimens had state 0 (CR 453); the one *Sphaerodactylus altavelensis enriqueilloensis* studied exhibited both states; two of seven *S. a. argus* investigated possessed state 0 (UMMZ 127809, USNM 40510); the one specimen of *S. becki* and *S. corticola soter* had both states; one of three *S. klauberi* exhibited both states (RT 3902); one of two *S. lineolatus* possessed state 0 (UMMZ 63739); one of five *S. milnepunctatus* had both states (UMMZ 152733); one of eight *S. molei* exhibited state 0 (RT 1191); one of three *S. oxyrhinus* possessed both states (UMMZ 85911); one of two *S. roosevelti* had state 0 (RT 4107); both *S. ro-saurae* exhibited state 0.

11. Fourth phalangeal element in fourth finger long (0), short (1) or absent (2). I treat this transformation series as additive (see fig. 7). The apomorphic condition in the forefoot of *Pseudogonatodes* appears to have been reported first by Gasc (1976: 22).

12. Fourth phalangeal element in fourth toe long (0), short (1), or absent (2). I also treat this transformation series as additive (see fig. 7).

13. One or more large fenestrae present (0) or absent (1) in clavicle. Noble (1921: figs. 4,5; see also Parker, 1926) appears to have been the first to draw attention to this variation in sphaerodactyls. All *Coleodactylus* and *Pseudogonatodes* studied have no conspicuous fenestrae (tiny openings may be present).

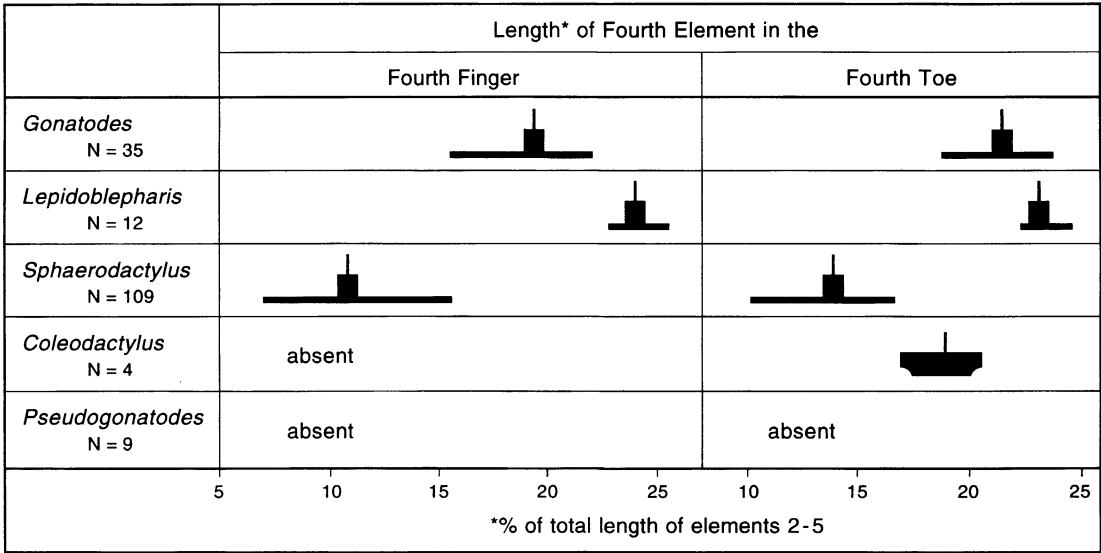


Fig. 7. The length of the fourth phalangeal element in the fourth digit of the fore- and hindfoot of sphaerodactyls. The horizontal line is the observed range of variation; the vertical line is the mean; the dark rectangle is one standard deviation. N = sample size.

All of the representatives of *Gonatodes* and *Lepidoblepharis* examined have no discernible fenestrae, except for two of five *G. antillensis* (UMMZ 127795a,b) and the single *L. buchwaldi* and *L. intermedius* examined, which have one or more tiny openings. While the vast majority of *Sphaerodactylus* observed have state 0, like the outgroups, there are several exceptions which cause me to record that taxon as variable (0/1). With the exception of the single *S. corticola soter* and one of the 13 *S. n. notatus* examined (UMMZ 95583), almost all of this variation occurs among mainland endemics (Harris and Kluge, 1984). For example, although all *S. glaucus* (8 specimens) and *S. heliconiae* (1) have state 0, *S. dunni* (1), *S. homolepis* (2 of 2), *S. millepunctatus* (5 of 6; UMMZ 152733 is the exception), and *S. molei* (5 of 8; AMNH 15617-8 and RT 1191 are the exceptions) are usually state 1. Also, although the size of the fenestrae in both representatives of *S. lineolatus* and *S. pacificus* studied is not tiny or absent, the opening is much smaller than is typical of most *Sphaerodactylus* species.

14. Interclavicle shape cruciform (0) or more daggerlike (1). The focus is on the lateral margin of the interclavicle, which lies approximately halfway between the clavicles

and the sternum (Noble, 1921: figs. 4,5). Long and short (or none) “arms” describe the two states, 0 and 1, respectively. Some gekkos have nearly straight interclavicles, which expand considerably at or posterior to their insertion into the sternum (e.g., *Pristurus*). These examples are recorded as state 1. Although I have scored *Coleodactylus*, *Lepidoblepharis*, and *Pseudogonatodes* as state 1, the lateral margins of the interclavicle exhibit a noticeable projection. Like the previous character, there is obvious variation in *Sphaerodactylus*, which forced me to record that taxon as variable (0/1). Moreover, almost all of the exceptional taxa are again mainland endemics. For example, all *S. dunni* and *S. molei* clearly exhibit state 1, and the interclavicle arms in *S. homolepis* are nearly equally short. All other mainland endemics, including *S. millepunctatus*, have much more cruciform-shaped interclavicles.

15. Hypoischium long (0) or short or absent (1). Noble (1921: fig. 6) appears to have been the first to draw attention to the much reduced hypoischium in sphaerodactyls.

16. Meatal closure muscle L- (0) or O- (1) shaped. The muscle borders the posterior and ventral margins of the external auditory meatus in state 0, whereas the muscle encircles

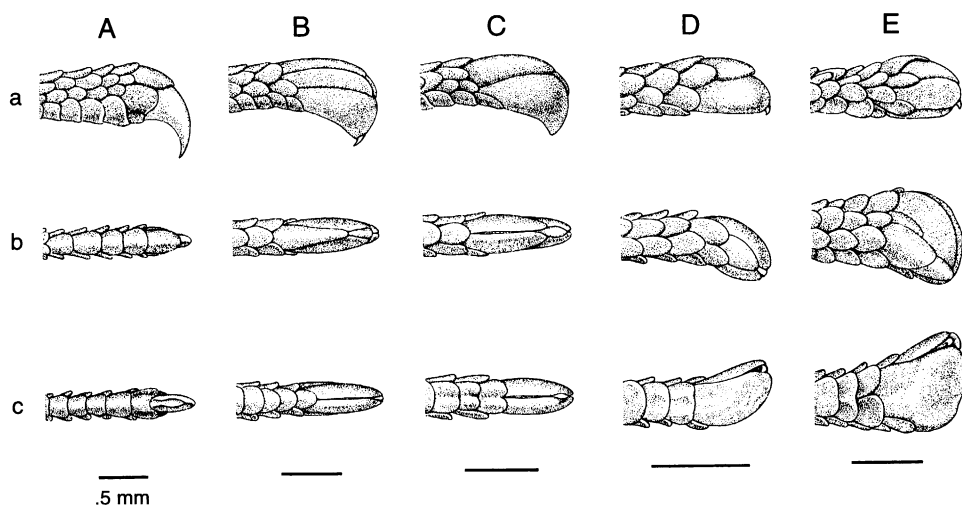


Fig. 8. Lateral (a), dorsal (b), and ventral (c) views of the fourth toe of representative sphaerodactyls. A. *Gonatodes*. B. *Lepidoblepharis*. C. *Pseudogonatodes*. D. *Coleodactylus*. E. *Sphaerodactylus*.

entirely, or nearly completely, that opening in state 1. According to Kluge (1987: fig. 6; after Weaver, 1973, 1974, 1978), state 1 applies to *Pristurus* and sphaerodactyls.

17. Clutch size two or more (0) or one (1). Even though the modal values are obviously two and one for states 0 and 1, respectively, there is some variation (see Kluge, 1987).

18. Escutcheon generation glands absent (0) or present (1). Escutcheon glands are found in most sphaerodactyls (Maderson, 1972; Menchel and Maderson, 1971), and similar holocrine epidermal modifications in the pre-anal region have been observed in some (*Coleonyx brevis*, *C. variegatus*, and *Hemitheconyx taylori*), but not all, eublepharine gekkos. If Maderson's (1972) conclusion is correct, that the escutcheon scale types in sphaerodactyls and eublepharine gekkos are not homologous, then this epidermal modification provides additional evidence that sphaerodactyls form a natural group (Kluge, 1983, 1987; his character 33). However, the weight of the generation gland evidence for monophyly also depends on how the absence of an escutcheon (state 0; Vanzolini, 1968b) in *Coleodactylus* and *Pseudogonatodes* is interpreted, as plesiomorphic or an evolutionary reversal. I have recorded state 1 for *Gonatodes*, *Lepidoblepharis*, *Pristurus*, and *Sphaerodactylus* (Harris and Kluge, 1984: fig. 15). I tentatively accept Russell's (1972: 182)

conclusion that similarly modified scales are present in *Quedenfeldtia*. The type of generation gland has yet to be determined for *Pristurus*. If that gland is of the B type (see Arnold, 1976: pl. 2) then there is additional evidence for relating *Pristurus* to the sphaerodactyl group.

19. Beta generation glands present (0) or absent (1). This character was reviewed by Kluge (1983; see also Kluge, 1987; his character 32).

20. Supraciliary spine absent (0) or present (1). Parker (1926: 298; see also Russell, 1972: 241) apparently was the first to emphasize the possible phylogenetic informativeness of this character when he stated that the absence of a "supraciliary spine" distinguished *Coleodactylus* from *Sphaerodactylus*. Indeed, the spine is extremely large in almost all *Sphaerodactylus* (e.g., Harris and Kluge, 1984: fig. 3); however, smaller projections are generally present in *Gonatodes* and some *Lepidoblepharis*. Spines appear to be absent in both *Coleodactylus* and *Pseudogonatodes*. Single spines also seem to be absent in all of the outgroups, except *Saurodactylus* (Bons and Pasteur, 1957a: fig. 2). Although the entire margin of the eyelid is spinose in *Quedenfeldtia*, I have recorded that taxon as state 0, because no single projection is particularly long, as it is in sphaerodactyls.

21. Supraciliary plate(s) absent (0) or pres-

ent (1). Vanzolini (1968b: 86) described some sphaerodactyls as having "the anterior granules . . . [of the eyelid] . . . enlarged into flat scales." Although such plates occur in most sphaerodactyls, there is considerable variation among species of *Gonatodes* and *Sphaerodactylus*, and they are never particularly large in any case. However, those plates are especially noticeable in all other sphaerodactyls (see figures in Mechler, 1968), and I have recorded only these species as having state 1.

22. Ungual sheath of digit absent (0) or present (1). Russell (1972) stated that the sheath is present only in *Coleodactylus*, *Lepidoblepharis*, *Pseudogonatodes*, and *Sphaerodactylus*, and Noble (1921) and Parker (1926) also commented on the importance of the unguis in diagnosing that subgroup of sphaerodactyls (fig. 8). Noble (1921) claimed the sheath merely represents an enlargement of the distalmost scales of the digit, such that they nearly completely surround the claw.

23. Distalmost superolateral scales in digit separated by dorsal scale (0) or in contact (1). This character applies generally to the fourth toe (fig. 8).

24. Tip of fourth toe straight (0) or bent laterally (1). State 1 is also obvious in terms of the asymmetrical size and distribution of the scales which make up the unguis (fig. 8).

25. Pupil narrowly elliptical and conspicuously emarginate (0) or more nearly circular and straight (1). Underwood (1954; see also Parker, 1926) referred to the former state as the gekko-type. State 1 does include an oval pupil with slightly "puckered" margins (e.g., *S. parkeri*, Underwood, 1954: 487; *Saurodactylus*, Bons and Pasteur, 1957a, 1957b). Other observations on pupil shape come from Underwood (1970: 20), Werner (1977), Frankenberg (1979), and Thomas (1982).

OTHER OBSERVATIONS

Several other characteristics have been used in previous discussions of sphaerodactyl monophyly or intergeneric relationships; however, I have not employed them in this study because they are (1) plesiomorphic, (2) too variable, (3) unknown for many taxa, and/or (4) have not passed the preliminary

tests of homology (Rieppel, 1980a; see also Patterson, 1982). The omitted characters include several of those mentioned by Noble (1921: fig. 6), Underwood (1954: 470, 476, 480, 488; 1970; see also Vanzolini, 1968b), and Kluge (1967). These characters are: (1) true eyelids absent, spectacle covering eye; (2) parietals paired; (3) absence of vocalization; (4) presence of sexual dichromatism; (5) temporal fovea present; (6) presence of oil droplets in visual cells; (7) premaxilla develops from single center of ossification, paired condition absent from adults; (8) calcified endolymphatic sacs present in postcranial region; (9) supratemporal absent; (10) scleral ossicles approximately 14 per eyeball; (11) angular absent; (12) frontal single; (13) nasals paired; (14) squamosal rarely absent; (15) pectineal process of the pelvic girdle well developed.

CLADISTIC RESULTS

There are three equally most parsimonious, best-fitting, hypotheses of sister-group relationships for the characters summarized in table 2 ($S = 36$; $C = 0.75$; $R = 0.83$), with *Cnemaspis*, *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus* included as outgroups. All of the variable relationships occur among three outgroup taxa, *Cnemaspis*, *Narudasia*, and *Saurodactylus*, and a strict consensus topology of those results is shown in figure 9. A posteriori iterative weighting did not improve the resolution.

Each resolved clade is corroborated by two or more characters assumed to be independent pieces of evidence (fig. 9). Further, the individual character consistency and retention indices summarized in table 3 indicate that most of the diagnostic variables have had unique and unreversed histories on the best-fitting hypothesis of sphaerodactyl relationships. The following diagnosis summarizes the evidence: (*Pristurus*, sphaerodactyls): splenial absent, meatal closure muscle O-shaped; (sphaerodactyls): maxillary process of palatine short or absent, choanal canal on ventral surface of palatine long and deep, fenestra absent in clavicle, hypochium short or absent, beta generation glands absent; (*Lepidoblepharis*, *Sphaerodactylus*,

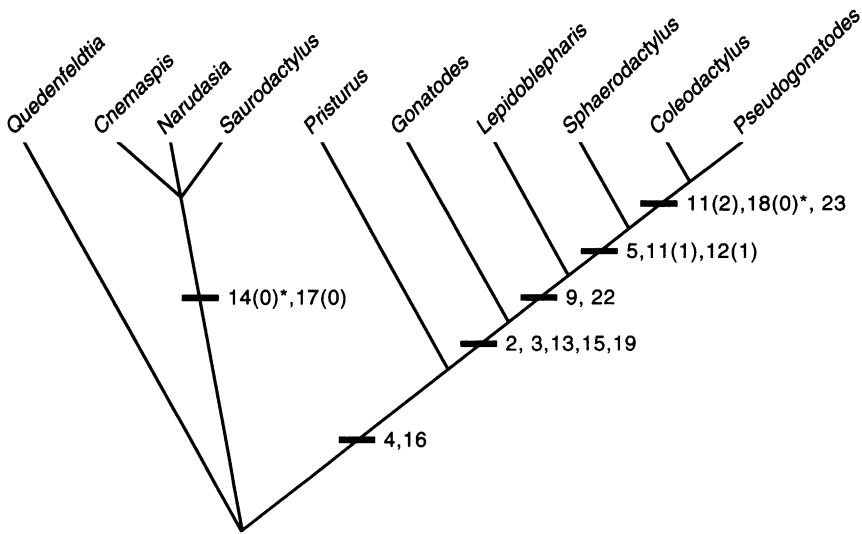


Fig. 9. A strict consensus of the three equally most parsimonious cladograms for the data summarized in table 2 ($S = 36$, $C = 0.75$, $R = 0.83$). All of the variation in relationships occurs among the outgroups. The numbers refer to the diagnostic characters discussed in the text; state 1 can be assumed unless indicated otherwise in parentheses. The asterisk refers to a homoplastic state.

Coleodactylus, *Pseudogonatodes*): procoelous vertebrae, ungual sheath present; (*Sphaerodactylus*, *Coleodactylus*, *Pseudogonatodes*): coronoid short, fourth phalangeal element in fourth finger relatively short, fourth phalangeal element in fourth toe relatively short; (*Coleodactylus*, *Pseudogonatodes*): fourth phalangeal element in fourth finger absent, escutcheon generation glands absent, distal-most superolateral digit scales in contact.

HOMONOMY-HETERONOMY, INDIVIDUAL VARIANTS, AND THE EVOLUTION OF THE UNGUAL SHEATH

The presence of the ungual sheath has long been recognized as diagnostic of a large group of sphaerodactyls, *Coleodactylus*, *Lepidoblepharis*, *Pseudogonatodes*, and *Sphaerodactylus* (fig. 8). The sheath is believed to be absent only in *Gonatodes*. Further, numerous authors have used the general shape of the digits and the terminal toe pad scalation to delimit each sphaerodactyl genus. These characteristics of the digits have also been

employed as evidence of intergeneric relationships. For example, based on toe pad scalation, Noble (1921) hypothesized a single line of progression from *Gonatodes* to *Lepidoblepharis* to *Pseudogonatodes* to *Sphaerodactylus* (the two *Coleodactylus* species recognized at that time, *C. amazonicus* and *C. meridionalis*, were included in *Sphaerodactylus*), whereas Parker (1926) derived *Pseudogonatodes* from *Lepidoblepharis* and, independently, *Sphaerodactylus* from *Lepidoblepharis* by way of a common ancestor with *Coleodactylus* (see also Vanzolini, 1968a).

My reinterpretation of the evolution of the individual scales of the ungual sheath, which is to follow, assumes that the scalation throughout much of the length of the free digit, including those epidermal modifications covering the ultimate phalangeal bone and the claw, form a homonomous series. My references to homonomy are simply observational and have nothing to do with speculations about possible underlying developmental mechanisms for the iterated parts (Riedel, 1978; Roth, 1984, 1988; Wagner, 1989a, 1989b). I use the similarity of a re-

TABLE 3^a
Individual Character Performances According to Figure 9

	1	2	3	4	5	6	7	8	9	10	11
s	2	1	1	1	1	1	1	2	1	2	2
c	.50	1.0	1.0	1.0	1.0	1.0	1.0	.50	1.0	.50	1.0
r	.00	1.0	1.0	1.0	1.0	1.0	1.0	.00	1.0	.00	1.0
	12	13	14	15	16	17	18	19	20	21	22
s	2	1	2	1	1	1	2	1	3	2	1
c	1.0	1.0	.50	1.0	1.0	1.0	.50	1.0	.33	.50	1.0
r	1.0	1.0	.66	1.0	1.0	1.0	.55	1.0	.00	.50	1.0
	23	24	25								
s	1	2	1								
c	1.0	.50	1.0								
r	1.0	.00	1.0								

^a s = number of steps; c = consistency index; r = retention index.

peated series of elements, proximal to distal oriented rows of digit scales in this study, as part of my preliminary test of similarity of particular scales in the unguis sheath (Rieppel, 1980a; Patterson, 1982). My use of homonymy might be considered a special case of two of Remane's (1952) similarity criteria—similarity in relative position, and similarity of transitional form. The basic idea in my application is that the similarity of highly differentiated repeated parts among organisms can be judged in terms of the less- or undifferentiated parts of the comparable series. It is the *homonymy* (the identity of repeated parts within and among organisms) that serves as the basis in similarity for saying that *heteronomous* conditions or organisms are part of the "same" synapomorphy relation. Thus, similarity of highly modified unguis sheath scales in different sphaerodactyls is not only assessed in terms of the similarity of the particular scales, but the series of which they are assumed to be a part (fig. 8). I believe this basis for assessing similarity will be even more important once the developmental basis for digital scale patterning is understood (Hinchliffe and Johnson, 1980; Raynaud, 1985; Rosenberg et al., 1992).

My reinterpretation of the evolution of the individual scales of the unguis sheath also takes advantage of previously overlooked in-

trageneric and individual variation. Lastly, my reinterpretations conform to the pattern of sister-group relationships provided by the best-fitting hypothesis (fig. 10). The following remarks pertain to the fourth toe, unless stated otherwise; the terminology was outlined under Material And Methods.

Gonatodes (Figs. 8, 10) exhibits little interspecific variation in toe shape and scalation. The digits are long, angulate, and compressed throughout their length. The claw is well developed and exposed—the unguis sheath is said to be absent (Russell, 1972). There are single well defined rows of dorsals and ventrals, between which are located two or three rows of smaller and more variably shaped laterals. Of the 10 species surveyed, only *G. ceciliae* and *G. taniae* are characterized by three pairs of laterals (see Rivero-Blanco, 1979, for additional details). The claw in *Gonatodes* is almost always surrounded by two scales. I hypothesize the upper scale to be a dorsal, at least in part, on the basis of similar anatomical position and shape of the scute, relative to the homonomous dorsals immediately proximate to it. The relatively larger size of the terminal dorsal may indicate that it includes part of each distalmost superolateral; however, I have no other observations to corroborate that proposition. The ventrally located scale surrounding the claw

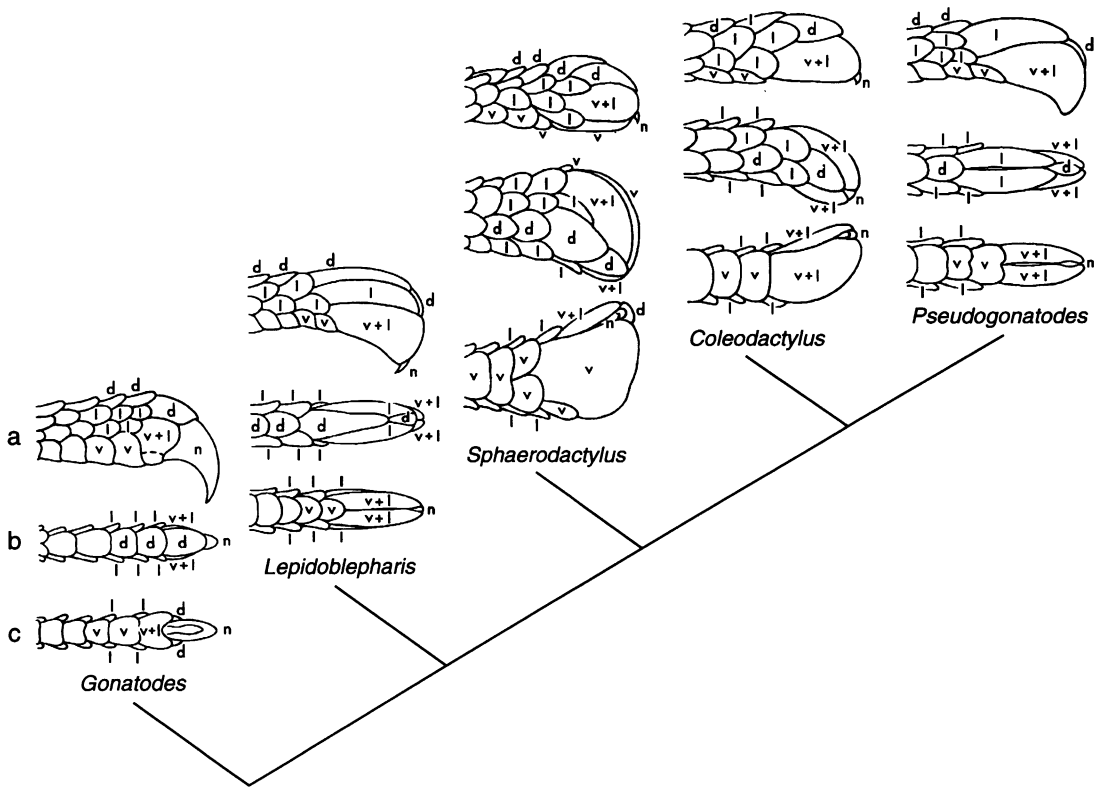


Fig. 10. Sphaerodactyl sister-group relationships (see fig. 8), with dorsal, lateral, and ventral views of the scalation of the fourth toe (see fig. 8). d = dorsal; l = lateral; n = claw (nail); v = ventral.

is much taller than the homonomous ventrals immediately proximal to it. The additional height on each side is approximately that of an inferolateral. Rarely observed adult variants with partial or complete lateroventral division of the most distal ventral supports the hypothesis that the more ventrally located scale surrounding the claw is a composite (ventral + inferolaterals). Also, the distal-most ventral is frequently notched anteriorly, and occasionally that ventral is completely divided into two symmetrical scales. These individual adult variants may also suggest that the more ventrally located scale surrounding the claw includes more than one ventral (see discussion below).

Lepidoblepharis (figs. 8, 10) species have undilated digits like *Gonatodes*; however, they tend to be much more round in cross section. Short-toed congeners, like *L. sanctaemartae*

and *L. xanthostigma*, have less angulate digits. Much of the claw in *Lepidoblepharis* is hidden between two pairs of enlarged scales, which I assume to be laterals (at least in part), and a row of two dorsals, the distalmost being tiny. The ungual sheath of *Lepidoblepharis* does not include a separate ventral. The inferolaterals contact each other distal and proximal to the claw, and their extreme depth may indicate that they have had ventrals fused to them during ontogeny. The individual variation observed in *Gonatodes* (see discussion immediately above) also supports my contention that the inferolateral of the ungual sheath is a composite. The fact that two dorsals in a row form the ungual sheath may indicate that the claw is covered laterally by two fused supero- and inferolaterals per side. The single alcoholic specimen of *L. intermedius* examined (UMMZ 127205) did not

have a single well defined row of dorsals proximate to the unguis sheath. Mechler (1968: fig. 17) illustrated *L. colombianus* as having two small rows of dorsals.

The remaining sphaerodactyl genus with undilated digits, *Pseudogonatodes* (figs. 8, 10), is much more similar to *Lepidoblepharis* than it is to *Gonatodes*. The digits of *Pseudogonatodes* tend to be even shorter, stockier, and less angulate than those of *Lepidoblepharis*. The claw of *Pseudogonatodes* may be entirely hidden. The unguis sheath consists of a pair of large supero- and inferolaterals (probably a composite of ventral + inferolateral) and a single tiny dorsal distal to the claw. Unlike the unguis sheath of *Lepidoblepharis* and *Sphaerodactylus*, the more posteriorly located dorsal is absent in *Pseudogonatodes*. There is no evidence that the lack of a dorsal is a result of fusion with the superolaterals. There is considerable variation in *Pseudogonatodes* in number of laterals proximal to the unguis sheath: one or two pairs were observed in *P. barbouri*, two in *P. lunulatus*, and three in *P. furvus*. Moreover, the latter species did not have a single well defined row of dorsals. Huey and Dixon (1970) apparently overlooked these interspecific differences.

Coleodactylus and *Sphaerodactylus* (figs. 8, 10) resemble each other in terms of the dilation and asymmetry of their unguis sheaths. However, the best-fitting hypothesis of sister-group sphaerodactyl relationships suggests (optimization of the characters in question is ambiguous) that those two features of size and shape might have evolved independently. A detailed comparison of the individual scales of *Coleodactylus*, *Pseudogonatodes*, and *Sphaerodactylus* adds support to the homoplasy hypothesis.

The unguis sheath of at least some species of *Coleodactylus* (*C. meridionalis* and *C. septentrionalis*; Vanzolini, 1968a: fig. 3, and Hoogmoed, 1985: fig. 2, respectively) consists of five scales, which nearly cover the entire claw. I interpret these to be a single dorsal and two pairs of laterals. This pattern is the same as that observed in *Pseudogonatodes*—the more proximate dorsal of the sheath is assumed to be absent, while the more distal dorsal is present. However, the small size of the superolateral in *Coleodac-*

tylus is more like that in *Sphaerodactylus*. Given the same arguments that I used for *Lepidoblepharis* and *Pseudogonatodes*, I hypothesize that the inferolaterals of the sheath in *Coleodactylus* are a composite, including one or two ventrals. The enlarged, pilose scale in the sheath of *Coleodactylus* is almost certainly the postaxial ventral + inferolateral, and the asymmetry of the digit appears to be a simple function of the larger size of that member of the pair. The number of specimens is not sufficient to evaluate Vanzolini's (1957) scenario of digit evolution in the genus, beyond concluding that the presence of four scales in the unguis sheath of some *Coleodactylus* species (Vanzolini, 1968a: fig. 4) is apomorphic.

Most *Sphaerodactylus* species have a greater number of scales of various sizes and shapes forming the unguis sheath than do other sphaerodactyls. In addition, the size of the sheath in most *Sphaerodactylus* is much larger and more markedly asymmetrical. These species have made it particularly difficult to identify the homonymy and heteronymy relations to the unguis sheath scales, which in turn makes individual scale comparisons between representatives of different sphaerodactyl genera even more problematical. In order to minimize the effects of extreme differentiation, I have relied mostly on species, like *S. klauberi*, which have relatively straight and undilated digits. I assume that these taxa are plesiomorphic relative to those with markedly bent and terminally wide digits.

Usually, the unguis sheath of *Sphaerodactylus* consists of an extremely large pad, a row of two dorsals (Noble, 1921, claimed the more proximal dorsal was a lateral; however see Parker, 1926: 300), and two or three rows of laterals. The superolateral scale in the sheath is much shorter than the inferolateral, which I assume is a developmental composite (including a ventral; see previous arguments for *Lepidoblepharis* and *Pseudogonatodes*). The preaxially located composite is nearly vertical, with its median counterpart almost horizontal. At least in some species of *Sphaerodactylus*, such as *S. klauberi*, the horizontal plate appears to cover another equally large scale completely; this second horizontal scute is pilose and forms the conspicuous pad of

the unguis sheath. This interpretation applies most obviously to species like *S. klauberi* where there is relatively little asymmetry. Moreover, in species like *S. klauberi*, there is a small scale without pilosity located at the postaxial, proximal border of the pad, which I interpret to be the counterpart to the larger ventral. Thus, I am not only hypothesizing that the pilose pad of *Sphaerodactylus* is a ventral, but that the pad is the preaxial ventral. This scenario of the asymmetrical evolution of the pilose pad in *Sphaerodactylus* is consistent with the other less proximate homonomous ventrals being either notched or completely divided. Such a subdivision of the ventral has also been observed in *Gonatodes*, *Lepidoblepharis*, and *Pseudogonatodes*. I hypothesize that all other small scales at the proximal pre- and postaxial margins of the pilose ventral in *Sphaerodactylus* are inferolaterals. Variation in the rows of scales proximal to the unguis sheath (4–6, mode of 5; see also Parker, 1926) and the absence of a well defined row of dorsals at the base of the unguis sheath make this proposition highly speculative. The study of ontogenetic series may provide the evidence necessary to test this hypothesis because *Sphaerodactylus* is known to undergo considerable transformation of digital shape during ontogeny (Werner, 1971). In summary, I propose that the pilose pad is a modified preaxial ventral in *Sphaerodactylus*, whereas the pilose part of the sheath is assumed to be the postaxial ventral + inferolateral in *Coleodactylus*. If this interpretation is correct, then there is additional evidence for the independent evolution of the dilation and asymmetry of the digit in *Coleodactylus* and *Sphaerodactylus* (fig. 10).

A GEKKO IN AMBER

A dark, clear yellow piece of amber was forwarded to David A. Grimaldi, American Museum of Natural History, by Ms. Susan Hendrickson, who acquired it in the Dominican Republic. It is a slightly asymmetrical tear-shaped piece, 53 mm long by 11 mm wide at the broadest point, with some deep longitudinal scratches. The piece contains an entire specimen of a tiny lizard, SVL about

14.0 mm, tail length about 13.6 mm. The specimen is mostly cleared, and is entirely surrounded by a reddish "halo," which is typical of some Dominican amber, particularly those with pyritized inclusions. The lizard itself is not pyritized. The piece had originally been cracked and appears to have been repaired with glue. The fracture extends through the specimen, from just behind the left foreleg to the base of the right foreleg.

The right side of the head is occluded by some fractures and by black and white granular debris, perhaps a product of decomposition. The left side of the head is most visible (fig. 11). A small part of the tongue protrudes from the base of the left side of the mouth, with a small drop "hanging" from the tip. A small bubble protrudes from the tip of the mouth. The eyes are very large, partly sunken, and point forward. The face and nose are short; the cranial portion of the head just behind the eyes is high and dome-shaped. Scallation on the throat is observable, but the whitish granular substance (presumably decayed tissue) on the remainder of the head obscures the scalation.

The trunk, abdomen, legs, tail, and feet are mostly cleared, some small portions with tissue debris in them. One can see scalation over most of the body when properly reflected and transmitted fiber-optic light is employed. The dorsal body scales are small and only slightly imbricate. Curiously, there is no evidence of bone in the parts that are most transparent (e.g., feet, legs, tail). Perhaps this is a juvenile specimen, with little ossification, and the soft bones decayed with the other tissues. The right foreleg and foot are bent back against the trunk; the left foreleg is forward, with the foot flat and the toes splayed. Both hind legs stick out from the body. The toes are clearly visible. The trunk and tail are filled with a pocket of air, but the posterior third of the tail is not so obscured. The tail is complete, and covered below with enlarged ventrals. Air pockets occur at the tips of some toes; however, details of foot scalation are evident (fig. 11). There is an unguis sheath and the tip of each digit is obviously asymmetrical in shape (figs. 8, 10). There are approximately 13 ventrals covering the fourth toe, two of which are paired at the origin of digit.

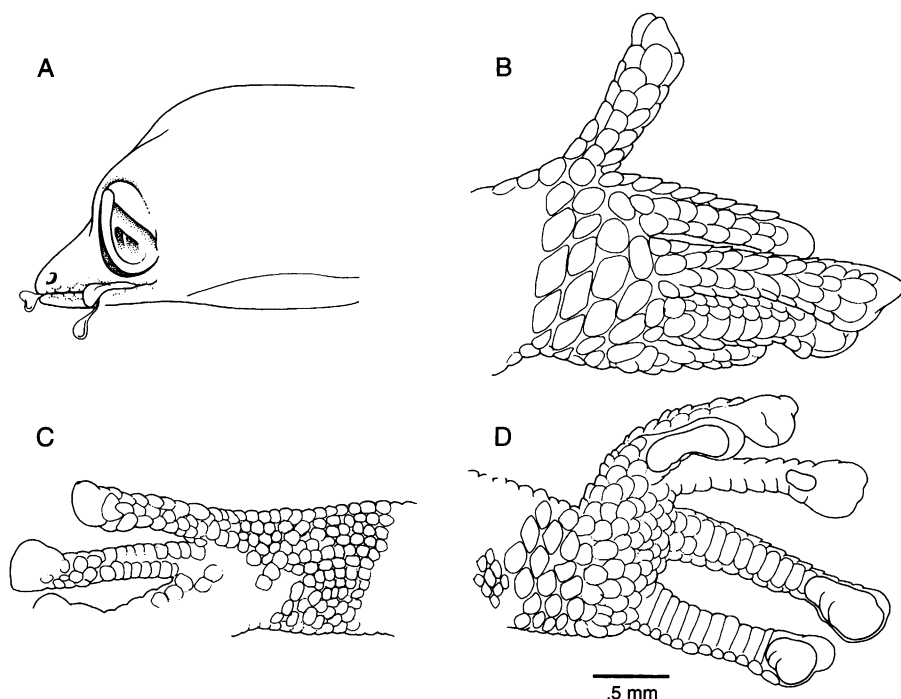


Fig. 11. Illustrations of AMNH lizard preserved in Oligo-Miocene Dominican amber (provided by D. A. Grimaldi). A. Left lateral view of the head. B. Dorsal view of right forefoot. C. Ventral view of left forefoot. D. Ventral view of left hindfoot.

Given the presence of a conspicuously asymmetrical ungual sheath (fig. 11), there can be little doubt that the AMNH gekko in amber is a *Sphaerodactylus*. The small size of the dorsal body scales, and their slightly imbricate nature, are conditions similar to those of other Hispaniolan *Sphaerodactylus*, such as *S. callocricus*, *S. cinereus*, *S. elegans*, and *S. samanensis* (Henderson and Schwartz, 1984). Unfortunately, I cannot be certain that the fossil exhibits any autapomorphies, and therefore I cannot determine whether it represents a new species. That it is a highly derived form is suggested by its similarity to species in the *cinereus* species-group (Hass, 1991). That such a derived *Sphaerodactylus* fossil is believed to be of Oligo-Miocene age (23–30 mybp; Grimaldi, 1995) seems to indicate that Hass' (1991: 547; see also Hedges et al., 1992) albumin clock estimates for times of origin for sister lineages *Lepidoblepharis* and *Sphaerodactylus*, and *Gonatodes* (*Lepi-*

doblepharis and *Sphaerodactylus*), 27 and 37 mybp, respectively, are too low. This discrepancy may be due to the evolutionary saturation of the genes responsible for the clock.

Judging from the description of *Sphaerodactylus dommeli* (Böhme, 1984), also known only from Dominican amber, the AMNH specimen is certainly representative of a different species. In fact, the general habitus (proportions of limbs, shape of head) of *S. dommeli* suggests that it is probably an anoline lizard (Darrel Frost, personal commun.). The better photograph of *S. dommeli* (of the paratype specimen in the Staatliches Museum in Stuttgart, Schlee, 1980; 1990) also corroborates this tentative placement. The type material of "*Sphaerodactylus*" *dommeli* must be reexamined in order to correctly reclassify the species; comparison with Rieppel's (1980b) green anole from Dominican amber is essential.

REFERENCES

- Arnold, E. N.
1976. Little-known geckoes (Reptilia: Gekkonidae) from Arabia with descriptions of two new species form the Sultanate of Oman. *J. Oman Studies, Spec. Report* 1975: 81–110.
- Bauer, A.
1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonner Zool. Monogr.* 30: 218 pp.
- Böhme, W.
1984. Erstfund eines fossilen Kugelfingergeckos (Sauria: Gekkonidae: Sphaerodactylinae) aus Dominikanischem Bernstein (Oligozän von Hispaniola, Antillen). *Salamandra* 20: 212–220.
- Bons, J., and G. Pasteur
1957a. Récentes captures de *Saurodactylus fasciatus* Werner, et nouvelles observations sur le genre *Saurodactylus* (Gekkonidés). *Bull. Soc. Sci. Nat. Phys. Maroc* 37: 57–65.
1957b. Nouvelles remarques sur les saurodactyles, avec description de *Saurodactylus mauritanicus brosetti* n. subsp. *Bull. Soc. Nat. Phys. Maroc* 37: 175–195.
- Clark, C., and D. J. Curran
1986. Outgroup analysis, homoplasy, and global parsimony: a response to Maddison, Donoghue, and Maddison. *Syst. Zool.* 35: 422–426.
- Farris, J. S.
1988. Hennig86 Software, Version 1.5, and Hennig: Hennig86 Reference. Distributed by the author.
1989. The retention index and the rescaled consistency index. *Cladistics* 5: 417–419.
- Frankenberg, E.
1979. Pupillary response to light in gekkonid lizards having various times of daily activity. *Vision Res.* 19: 235–245.
- Gasc, J.-P.
1976 (1975). Contribution à la connaissance des squamates (Reptilia) de la Guyane Française. Nouvelles localités pour les sauriens. *C. R. Soc. Biogéogr.* 454: 17–36.
- Grimaldi, D.
1995. On the age of Dominican amber. In K. B. Anderson and J. C. Crelling (eds.), *Amber and resinites*. Am. Chem. Soc. Symp. Vol. pp. 1–11. Washington, D.C.
- Harris, D. M.
1982. The *Sphaerodactylus* (Sauria: Gekkonidae) of South America. *Occas. Pap. Mus. Zool. Univ. Michigan* 704: 31 pp.
- Harris, D. M., and A. G. Kluge
1984. The *Sphaerodactylus* (Sauria: Gekkonidae) of Middle America. *Occas. Pap. Mus. Zool. Univ. Michigan* 706: 59 pp.
- Hass, C. A.
1991. Evolution and biogeography of West Indian *Sphaerodactylus* (Sauria: Gekkonidae): a molecular approach. *J. Zool. (London)* 225: 525–561.
- Hecht, M. K.
1976. Phylogenetic inference and methodology as applied to the vertebrate record. *Evol. Biol.* 9: 335–363.
- Hecht, M. K., and J. L. Edwards
1976. The methodology of phylogenetic inference above the species level. In M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), *Major patterns of vertebrate evolution*, pp. 3–51. New York: Plenum Press.
- Hedges, S. B., C. A. Hass, and L. R. Maxson
1992. Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proc. Natl. Acad. Sci.* 89: 1909–1913.
- Henderson, R. W., and A. Schwartz
1984. A guide to the identification of the amphibians and reptiles of Hispaniola. *Milwaukee Public Mus. Spec. Publ. Biol. Geol.* 4: 70 pp.
- Hinchliffe, J. R., and D. R. Johnson
1980. The development of the vertebrate limb: an approach through experiment, genetics, and evolution. Oxford: Clarendon Press.
- Hoogmoed, M. S.
1985. *Coleodactylus septentrionalis* Vanzolini, a lizard new for the Surinamese fauna (Sauria: Gekkonidae).—Notes on the herpetofauna of Suriname X. *Zool. Meded.* 59: 229–238.
- Huey, R. B., and J. R. Dixon
1970. A new *Pseudogonatodes* from Peru with remarks on other species of the genus. *Copeia* 3: 538–542.
- Kluge, A. G.
1967. Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Am. Mus. Nat. Hist.* 135: 60 pp.
1976. Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of the theory, methods and data. *Misc. Publ. Mus. Zool. Univ. Michigan* 152: 72 pp.

1982. Cloacal sacs and bones as evidence of gekkonoid lizard relationships. *Herpetologica* 38: 348–355.
1983. Epidermal gland evolution in gekkonoid lizards. *J. Herpetol.* 17: 89–90.
1987. Cladistic relationships in the Gekkonoidae (Squamata, Sauria). *Misc. Publ. Mus. Zool. Univ. Michigan* 173: 54 pp.
1993. Gekkonoid lizard taxonomy. *Dactylus*, Spec. Publ. 245 pp.
1994. Principles of phylogenetic systematics and the informativeness of the karyotype in documenting gekkotan lizard relationships. *Herpetologica* 50: 210–221.
- Kluge, A. G., and J. S. Farris
1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18: 32 pp.
- Kluge, A. G., and R. A. Nussbaum
1995. A review of African-Madagascan gekkonid lizard phylogeny and biogeography (Squamata). *Misc. Publ. Mus. Zool. Univ. Michigan*, in press.
- Maclean, W. P., R. Kellner, and H. Dennis
1977. Island lists of West Indian amphibians and reptiles. *Smithson. Herpetol. Inf. Serv.* 40: 47 pp.
- Maderson, P. F. A.
1972. The structure and evolution of holocrine epidermal glands in sphaerodactyline and eublepharine gekkonid lizards. *Copeia* 4: 559–571.
- Mechler, B.
1968. Les Geckonidés de la Colombie. *Rev. Suisse Zool.* 75: 305–371.
- Menchel, S., and P. F. A. Maderson
1971. Some observations on the pattern of development of the escutcheon in sphaerodactyline gekkonids. *Am. Zool.* 11: 706.
- Nixon, K. C., and J. M. Carpenter
1993. On outgroups. *Cladistics* 9: 413–426.
- Noble, G. K.
1921. The bony structure and phyletic relations of *Sphaerodactylus* and allied lacertilian genera, with the description of a new genus. *Am. Mus. Novitates* 4: 16 pp.
- Parker, H. W.
1926. The Neotropical lizards of the genera *Lepidoblepharis*, *Pseudogonatodes*, *Lathrogecko*, and *Sphaerodactylus*, with the description of a new genus. *Ann. Mag. Nat. Hist.* 17: 291–301.
- Patterson, C.
1982. Morphological characters and homology. In K. A. Joysey and A. E. Friday (eds.), *Problems in phylogenetic reconstruction*, pp. 21–74. New York: Acad. Press.
- Raynaud, A.
1985. Development of limbs and embryonic limb reduction. In C. Gans and F. Billett (eds.), *Biology of the Reptilia*, Vol. 15, Development B, pp. 59–148. New York: Wiley.
- Remane, A.
1952. Die Grundlagen des natürlichen Systems der vergleichenden Anatomie und der Phylogenetik. Leipzig: Geest and Portig.
- Riedel, R.
1978. Order in living organisms. New York: Wiley.
- Rieppel, O.
1980a. Homology, a deductive concept? *Z. Zool. Syst. Evolutionsforsch.* 18: 315–319.
1980b. Green anole in Dominican amber. *Nature* 286: 486–487.
- Rivero-Blanco, C. V.
1979. The Neotropical lizard genus *Gonatodes* Fitzinger (Sauria: Sphaerodactylinae). Ph.D. thesis, Texas A&M Univ. Univ. Microfilms International.
- Rosenberg, H. I., A. P. Russell, and M. J. Cavey
1992. Development of the subdigital adhesive pads of *Ptyodactylus guttatus* (Reptilia: Gekkonidae). *J. Morphol.* 211: 243–258.
- Roth, V. L.
1984. On homology. *Biol. J. Linn. Soc.* 22: 13–29.
1988. The biological basis of homology. In C. J. Humphries (ed.), *Ontogeny and systematics*, 26 pp. New York: Columbia Univ. Press.
- Russell, A. P.
1972. The foot of gekkonid lizards: a study in comparative and functional anatomy. Ph.D. Thesis, Univ. London.
1979. Parallelism and integrated design in the foot structure of gekkonine and dipodactyline geckos. *Copeia* 1: 21 pp.
- Schlee, D.
1980. Bernstein-Raritäten. Farben, Strukturen, Fossilien, Handwerk. Stuttgart.
1990. Das Bernstein-Kabinett. Stuttg. Beitr. Naturkd. Ser. C 28: 100 pp.
- Schwartz, A., and R. W. Henderson
1988. West Indian amphibians and reptiles: a check-list. *Milwaukee Public Mus., Contrib. Biol. Geol.* 74: 264 pp.
- Thomas, B. W.
1982. New Zealand Gekkonidae: evolution trends and taxa. In D. G. Newman (ed.), *New Zealand herpetology*, pp. 333–339. Occas. Publ. New Zealand Wildlife Service 2.

- Underwood, G.
 1954. On the classification and evolution of geckos. *Proc. Zool. Soc. London* 124: 469–492.
 1955. Classification of geckos. *Nature* 175: 1089.
 1970. The eye. In C. Gans and T. S. Parsons (eds.), *Biology of the Reptilia*. Vol. 2, 97 pp. New York: Acad. Press.
 1976. Comments on phyletic analysis of gekkotan lizards. In M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), *Major patterns in vertebrate evolution*, pp. 53–55. New York: Plenum Press.
- Vanzolini, P. E.
 1957. O genero *Coleodactylus* (Sauria, Gekkonidae). *Pap. Avulsos Dep. Zool. (São Paulo)* 13: 17 pp.
 1968a. Lagartos Brasileiros da família Gekkonidae (Sauria). *Arq. Zool. (São Paulo)* 17: 84 pp.
 1968b. Geography of the South American Gekkonidae (Sauria). *Arq. Zool. (São Paulo)* 17: 85–112.
 1980. *Coleodactylus septentrionalis*, sp. n., with notes on the distribution of the genus (Sauria, Gekkonidae). *Pap. Avulsos Dep. Zool. (São Paulo)* 34: 9 pp.
- Wagner, G. P.
 1989a. The origin of morphological characters and the biological basis of homology. *Evolution* 43: 1157–1171.
 1989b. The biological homology concept. *Annu. Rev. Ecol. Syst.* 20: 51–69.
- Weaver, E. G.
 1973. Closure muscles of the external auditory meatus in Gekkonidae. *J. Herpetol.* 7: 323–329.
 1974. The ear of *Lialis burtonis* (Sauria: Pygopodidae): its structure and function. *Copeia* 2: 297–305.
 1978. The reptile ear: its structure and function. Princeton, NJ: Princeton Univ. Press.
- Wermuth, H.
 1965. Liste der rezenten amphibien und reptilien. Gekkonidae, Pygopodidae, Xantusiidae. *Das Tierreich* 80: 246 pp.
- Werner, Y. L.
 1971. The ontogenetic development of the vertebrae in some gekkonoid lizards. *J. Morphol.* 133: 41–92.
 1977. Ecological comments on some gekkonid lizards of the Namib Desert, South West Africa. *Madoqua* 10: 157–245.

APPENDIX

Cleared and Stained Specimens Examined

- Coleodactylus amazonicus* (UMMZ 127803a,b); *C. brachystoma* (UMMZ 144467); *C. meridionalis* (UMMZ 103051a,b).
Gonatodes albogularis albogularis (CR 538, UMMZ 127790a,b); *G. a. fuscus* (UMMZ 127792,3, 148120); *G. a. notatus* (UMMZ 127794); *G. annularis* (UMMZ 53894); *G. antillensis* (MHNLS 2231, UMMZ 57325,6, 127795a,b); *G. atricucullaris* (TCWC 28333, UMMZ 127797a,b, 127798); *G. caudiscutatus* (MCZ 74175); *G. ceciliae* (MCZ 79808); *G. concinnatus* (CR 1949, MCZ 77390); *G. hasemani* (MCZ 119418); *G. humeralis* (CR 1096, UMMZ 127800, 128141); *G. ocellatus* (UMMZ 127801); *G. seigliei* (CR 1001); *G. taniae* (CR 900, UMMZ 124303); *G. vittatus vittatus* (CR 453, UMMZ 54687, 54893, 127802a,b); *G. sp. nov.* (MCN 3740).
Lepidoblepharis buchwaldi (MCZ 145149); *L. festae* (LACM 44678); *L. intermedius* (CAS 13260); *L. microlepis* (UMMZ 127804,5, 131865,6); *L. sanctaemartae* (UMMZ 125043, 125045, 127806a,b).
Pseudogonatodes barbouri (UMMZ 127807,8); *P. guianensis guianensis* (KU 121951, TCWC 41231,2); *P. lunulatus* (MCZ 48894, UMMZ 124312); *P. peruvianus* (LSUMZ 27359, MVZ 82137).
Sphaerodactylus altavelensis brevirostratus (ASFS 44073); *S. a. enriquilloensis* (RT 771); *S. argivus argivus* (UMMZ 143257); *S. argus argus* (KU 157180, UMMZ 127809a–c, USNM 40510, 192526); *S. armstrongi* (AS 30444); *S. beattyi beattyi* (UMMZ 143256); *S. becki* (AS 6277); *S. caicosensis* (UMMZ 143263); *S. callocricus* (UF 21559, USNM 41252); *S. cinereus cinereus* (AMNH 49566, RT 4108, UMMZ 95582a–j, 127810,11); *S. clenchi* (AS 34334); *S. copei cataplexis* (UMMZ 143260); *S. corticola soter* (UMMZ 143259); *S. darlingtoni noblei* (AS 28627); *S. difficilis* (RT 1418); *S. dunni* (LACM 47302); *S. elegantulus* (UMMZ 143255); *S. fantasticus fantasticus* (AS X5385); *S. gaigeae* (UMMZ 73606, 143254); *S. glaucus* (UMMZ 70448, 143261, 151524, 151529–32, USNM 113126); *S. gonior-*

hynchus (UMMZ 127812, USNM 42054); *S. heliconiae* (ICN 3217, 3226, UMMZ 171649) *S. homolepis* (UF 31305, 37188, UMMZ 127818); *S. inaguae* (UMMZ 127815); *S. klauberi* (RT 3902, UMMZ 73594, 143252); *S. lineolatus* (UMMZ 63738,9); *S. macrolepis macrolepis* (UMMZ 127816a,b); *S. mariguanae* (UMMZ 127817, 148123); *S. microlepis microlepis* (UMMZ 143250); *S. millepunctatus* (KU 157110, LACM 47784, UMMZ 117873, 143262, 151525, 151527, 152733); *S. molei* (AMNH 15616–21, RT 1191, UMMZ 65168); *S. monensis* (UMMZ 143253); *S. nicholsi* (UMMZ 143251); *S. nigropunctatus alayoi* (UINHM 44223); *S. n. gibbus* (UMMZ 127823, 117018); *S. notatus notatus* (UMMZ 95583a–j, 148121); *S. n. exsul* (USNM 23361–3, 23358); *S. oxyrhinus oxyrhinus* (ASFS 20050, UMMZ 85911, 143258); *S. pacificus* (UMMZ 127819a,b); *S. parkeri* (UMMZ 127820,1); *S. randi randi* (ASF V39837); *S. roosevelti* (ASFS 4290, RT 4107); *S. rosaurae* (LSUMZ 22385, UF 28557); *S. sabanus* (ASFS 19776); *S. savagei savagei* (ASFS 35019, USNM 40973,4); *S. sputator* (ASFS 19956); *S. streptophorus streptophorus* (ASFS 42503); *S. torrei torrei* (AS V15725); *S. underwoodi* (ASFS 10934); *S. vincenti vincenti* (ASFS 18139).

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org