

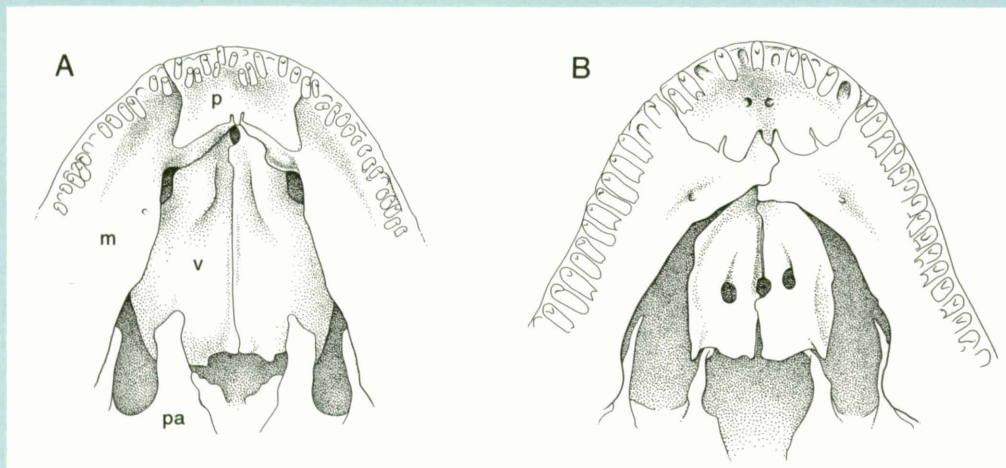
A REVIEW OF AFRICAN-MADAGASCAN GEKKONID LIZARD PHYLOGENY AND BIOGEOGRAPHY (SQUAMATA)

BY

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A Review of African-Madagascan Gekkonid Lizard Phylogeny and Biogeography (Squamata)

by

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ABSTRACT

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*, 183:1-20, 11 figs. The phylogenetic and biogeographic history of African-Madagascan gekkonid lizards is assessed with 34 morphological characters. The cladistic analysis employs 22 ingroup and seven outgroup genera as terminal taxa, and the best-fitting hypothesis leads to the following conclusions: (1) the ingroup forms a clade; (2) the generally recognized *Pachydactylus* assemblage of genera forms a clade, as do the northern and southern African subgroups, (*Geckonia*, *Tarentola*) and (*Chondrodactylus*, *Colopus*, *Pachydactylus*, *Palmatogecko*, *Rhoptropus*), respectively; (3) the Madagascan-Seychelles sample forms a historical entity, except for the ambiguously related *Geckolepis*; (4) the sample of Madagascan-Seychelles endemics is derived from African gekkos, and some of the African fauna has a Madagascan ancestry; (5) a *Lygodactylus-Phelsuma* clade (including *Rhoptropella*) is delimited; (6) *Blaesodactylus* and *Homopholis* are not sister taxa. Adding other "padded-toed" gekkos, *Gehyra*, *Gekko*, and *Hemidactylus*, to the ingroup leads to a substantially different set of phylogenetic and biogeographic conclusions, and reveals the tenuous nature of most of these conclusions. The close phylogenetic relationship between *Gehyra* and *Paragehyra* implied by Angel (1929) is not confirmed. It is clear that synapomorphies are more important than geographic proximity in recovering the history of gekkos. These results are largely at odds with Joger's (1985) and Bauer's (1990a) recent findings.

Key words: *Reptilia*, *Squamata*, *Gekkonidae*, *Africa*, *Madagascar*, *cladistics*, *biogeography*, *phylogeny*.

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INTRODUCTION

The most recent phylogenetic and biogeographic reviews of gekkonid lizards¹ from the Ethiopian Region by Joger (1985) and Bauer (1990a) did not include *Paragehyra*, a Madagascan endemic. The omission was understandable because that taxon was known only from the holotype of *P. petiti*. Recently, Nussbaum and Raxworthy (1994) collected several specimens of a new sister species of *P. petiti*, and the availability of that material has provided us with the opportunity to investigate the relationships of *Paragehyra*.

Joger's (1985) and Bauer's (1990a) studies were examined carefully for information that might be used to document the affinities of *Paragehyra*. Unfortunately, their phylogenetic propositions differ significantly (compare Figs. 1 and 2). Moreover, as the following review emphasizes, the questionable analytical methods and data they employed makes it difficult to judge the basis for their differences and to identify general agreement (Bauer, 1993: 251). Consequently, we found it necessary to re-examine the phylogenetic relationships of the Ethiopian Region gekko fauna, including *Paragehyra*.

RECENT RESEARCH ON THE PHYLOGENY OF GEKKONIDS FROM THE ETHIOPIAN REGION

Joger (1985) emphasized the immunological distances he obtained from precipitin tests because, as he asserted, such distances are "not subject to convergence or parallelism" (pp. 486-487) and therefore give the "correct phyletic branching order" (p. 480). However, Joger found it necessary to apply various "correction" factors to the distances (p. 481), in order to bring them in line with his assumption of a "clocklike behaviour of albumin in the evolutionary process" (p. 482). That he had to make those adjustments suggests this source of evidence for phylogenetic relationships may exhibit error. Further, Joger's immunological distances included only a few representatives of Ethiopian Region endemics, i.e., *Homopholis*, *Lygodactylus* (*L. gutturalis*, *L. picturatus*), *Pachydactylus*, *Palmatogecko*, *Phelsuma*, *Ptyodactylus*, *Rhoptropus*, *Stenodactylus*, and *Tarentola*. These taxa represent very few of the lineages usually assumed to have originated in that Region, and with the exception of *Phelsuma* (*P. dubia* from Madagascar and *P. v-nigra* from the Comoro Islands), all of his samples came from the African continent. Moreover, Joger provided only average values for one-way precipitin tests, and the assumption of constancy of evolutionary rate and the accuracy of the "correction factors" Joger employed cannot be critically evaluated in the absence of a complete, reciprocal matrix of distances. Perhaps most importantly, immunological distance data cannot be examined empirically to determine the specific independent evolutionary events responsible for alternative phylogenetic hypotheses, as is possible with character data when investigated in terms of character congruence (Kluge, 1989; Kluge and Wolf, 1993). In this sense, distance hypotheses are untestable propositions, and therefore are of no further interest in the present study.

Joger (1985) also attributed a wide variety of external and

internal morphological variation, including diploid chromosome number, to the aforementioned regional endemics, as well as *Gekkonina*. Unfortunately, none of this potential evidence was discussed in detail, and it is difficult to decipher several of Joger's characters (fig. 3, p. 487), such as "fusion of rostral halves," "characteristic pedal morphology," "distinct body proportions," and "blood proteins." Those putative synapomorphies that he referred to only as "other characters" (fig. 3, p. 487) are impossible to understand. In addition, much of the variation that Joger considered was sufficient only to distinguish subgroups of the aforementioned terminal taxa, not intergeneric relationships.

Joger's (1985: fig. 3) method of hypothesis formation must be questioned as well. He began with the pattern of relationships provided by the immunological distances, onto which he then mapped some of the character data in an attempt to realize confirmation and increased resolution (Fig. 1; his fig. 3). Such a protocol assumes the truth of the immunological distance topology, which prejudices the evaluation of the character data. For example, Joger necessarily had to claim the independent evolution of certain morphological character states such as hyperphalangy (Haacke, 1976) and the re-evolution of "adhesive pads" in *Ptyodactylus* (his fig. 4). Synapomorphies such as these can never be judged homologous with Joger's method, and it is not clear why he used any data other than immunological distances.

Thus, we conclude that Joger (1985) made only a limited contribution to our understanding of the history of the gekkonids from the Ethiopian Region. His sample of the endemic gekko fauna from the Region is small, and the amount and quality of the evidence and the analytical methods he employed are disputable. His analysis of only Ethiopian Region gekkos presumed a radiation of those endemics from a single most recent common ancestor, an assumption that is as yet unsupported by any data.

Bauer (1990a: 276) recognized five geographic kinds of African-Indian Ocean gekkonids: (a) southern outliers of primarily northern (tropical) radiations, (b) populations of pan-tropical species, (c) forms of broad distribution in the Indian Ocean region, (d) Indian Ocean (primarily Madagascan) endemics, and (e) southern African endemics. Bauer examined only those taxa of the last three types (c-e), and in doing so he presumed (like Joger) that the Ethiopian Region endemics evolved from a single most recent common ancestor. Bauer's data set consisted of 23 morphological characters observed on representatives of the following taxa (his appendix 1): *Afroedura*, *Ailuroonyx*, *Chondrodactylus*, *Colopus*, *Ebenavia*, *Geckolepis*, *Homopholis*, *Kaokogecko*, *Lygodactylus*, *Microscalabotes*, *Millotisaurus*, *Narudasia*, *Pachydactylus*, *Palmatogecko*, *Paroedura*, *Phelsuma*, *Phyllodactylus*, *Ptenopus*, *Rhoptropella*, *Rhoptropus*, *Urocotyledon*, and *Uroplatus*. Except for the claw reduction characters (see below), he seems to have included all of the decipherable and potentially informative characters employed by Joger. Although Bauer's character descriptions are brief, they are much more explicit than Joger's. No doubt, his failure to include Joger's diploid chromosome number character was simply a function of not being able to score most of the terminal taxa for that variable (King, 1987). Thus, we interpret Bauer's paper (as summarized in the data matrix in his appendix 1) to have included most of the relevant character evidence considered by Joger and, except for the

¹ Nomenclature follows that of Kluge (1987:39-40; 1993a).

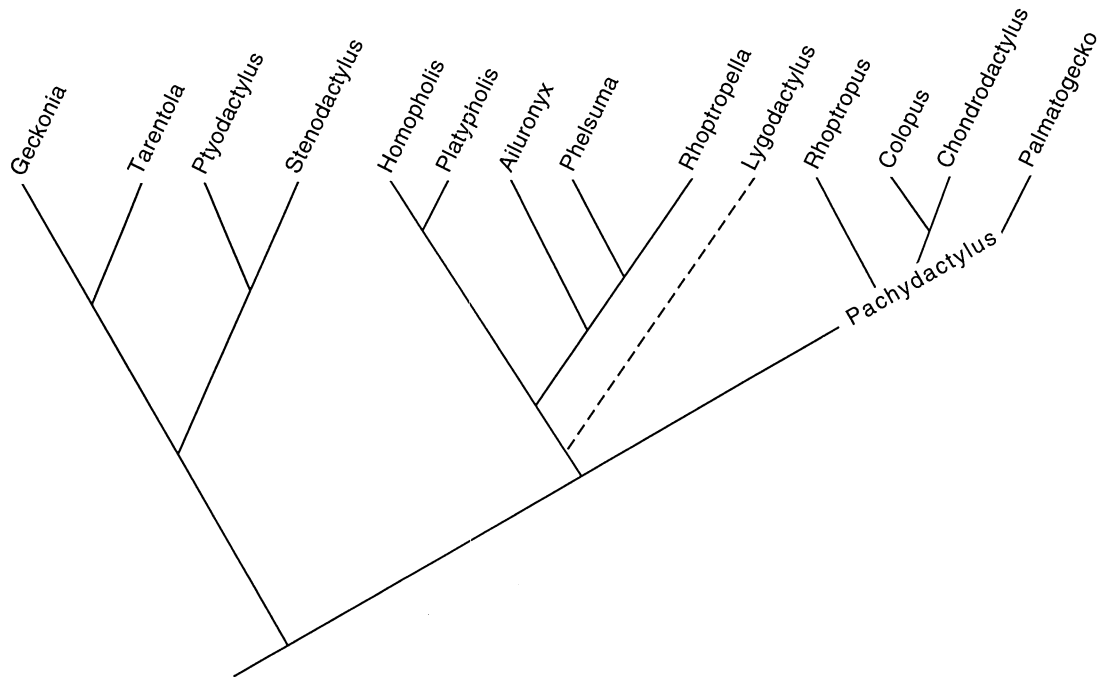


Fig. 1. A summary of Joger's (1985: fig. 3) hypothesis of phylogenetic relationships, in terms of those taxa investigated herein. Joger began with a topology based on immunological distances, onto which various character data were mapped in order to provide greater resolution and corroboration of the starting pattern (see text for further discussion). Joger considered the placement of *Lygodactylus* to be tentative, and he judged *Pachydactylus* to be paraphyletic, relative to *Colopus*, *Chondrodactylus*, *Palmatogecko*, and *Rhoptropus*.

omission of *Geckonia*, *Ptyodactylus*, *Stenodactylus*, and *Tarentola*, to have provided a more complete survey of the gekkonid taxa endemic to the Ethiopian Region.

Both Joger (1985) and Bauer (1990a) paid special attention to the presence/absence of the second ceratobranchial arch which Kluge (1983) advocated using in the higher classification of gekkonids. For example, Joger (p. 480) asserted that "a skeletal reduction like [the loss of the second ceratobranchial arch] is likely to occur more than once in groups like the geckos," and he then proceeded to ignore the arch variable in his analysis of African gekkonid relationships (Joger's fig. 3; see our Fig. 1).

Bauer (1990a: 276) referred to Kluge's (1983) work, as it related to Ethiopian Region gekkonids, as being the "least informative." Presumably, he reached that conclusion because Kluge used but a single (uncorroborated) synapomorphy, the loss of the second ceratobranchial arch, in diagnosing such a large group as Gekkonini. However, that Bauer claimed to have tested the "robustness" of the arch character and definitively rejected it deserves further comment. Bauer's mode of testing the arch variable (his character 7) was one of compatibility with another variable (Kluge, 1976), the presence/absence of the stapedial foramen in particular (Bauer's character 5). Indeed, those two characters are incompatible; however, all that can be concluded logically from such an outcome is that not both of the synapomorphies can be homologues—in fact, one or the other, or neither of two incongruent synapomorphies can mark the same part of phylogeny. Further, Kluge (1983) had already acknowledged that the loss of the second ceratobranchial arch could not be considered a *unique and unreversed state* (it was known to be incompatible with one or more other characters). Ironically, Bauer used the same arch character to delimit a major subgroup of the gekkonids he investigated, and within which

(in *Ebenavia* and *Paroedura*) the second ceratobranchial arch had to be interpreted as having re-evolved.

Böhme (1988: 160) did no better than Joger and Bauer in his evaluation of the ceratobranchial arch character. Indeed, that "*Ptyodactylus* is clearly linked by its hemipenis characters to the African Gekkoninae" does not necessarily disconfirm the arch character distinguishing Ptyodactylini from Gekkonini, because Böhme did not polarize the hemipenis variables he identified in gekkonids. We believe the level of taxonomic generality to which the arch apomorphy applies requires further study, and its phylogenetic informativeness remains an open question (see below).

The collection of endemic gekkos from the Ethiopian Region that Joger (1985) and Bauer (1990a) examined may not form a natural group, exclusive of gekkos from other geographic regions. In fact, Bauer (p. 277) alluded to just that possibility as regards his ingroup, as well as the terminal taxa he employed. Bauer did list the absence of preanal and/or femoral pores (character 22 in his fig. 1) as delimiting his ingroup (see also Fig. 2); however, that apomorphy is not a convincing diagnostic character state, because pores are present or absent among gekkonids outside the Ethiopian Region, and lacking a hypothesized outgroup hierarchy, which he did not provide, the history of that variation cannot be inferred. Further, that Bauer polarized his characters with the ROOT = ANCESTOR option in PAUP (Swofford, 1985) is taken to mean that he did not actually test the historical individuality of his study collection of Ethiopian Region terminal taxa (Clark and Curran, 1986; see also Nixon and Carpenter, 1993).

Our parsimony reanalysis of Bauer's evidence (1990a: appendix 1), exactly as he presented it, reveals that he failed to discover the best-fitting hypothesis for those data (Fig. 2; 100+ trees,

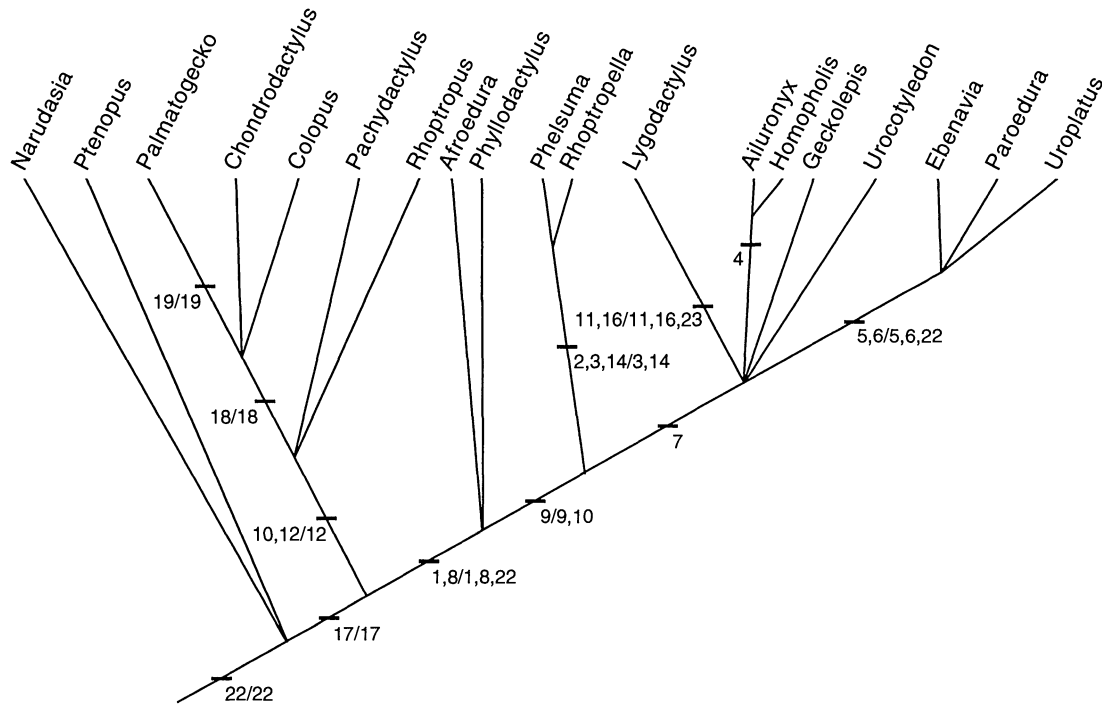


Fig. 2. A summary of Bauer's (1990a: fig. 1) hypothesis of phylogenetic relationships, in terms of the taxa investigated herein. *Palmatogecko* includes *Kaokogecko*, and *Lygodactylus* includes *Microscalabotes* and *Millotisaurus*. Bauer did not distinguish *Blaesodactylus* from *Homopholis*. The numbers refer to the characters Bauer considered to be evidence of group relationships. His interpretation as to the phylogenetic informativeness of those characters precedes the slash (/), and the correctly optimized, unambiguous, interpretation follows the slash.

$S = 44$, $CI = 0.55$). In fact, there are 42 cladograms one step shorter than he reported, the strict consensus of which is illustrated in Figure 3. Several taxa, in addition to those emphasized by Bauer (p. 278; *Geckolepis*, *Narudasia*, and *Ptenopus*), are responsible for the multiple equally parsimonious hypotheses he found. Bauer not only failed to find the best-fitting hypothesis(es), but he also did not present the most parsimonious distribution of character states on his published cladogram (see Fig. 2 for corrections). Nonetheless, it is noteworthy that both hypotheses based on Bauer's data (compare Figs. 2 and 3) delimited the *Pachydactylus* clade (see also Russell [1972], Haacke [1976], Joger [1985: fig. 3], and Kluge [1987: fig. 12]), as well as the (*Ailuronyx*, *Homopholis*), (*Lygodactylus*, *Microscalabotes*, *Millotisaurus*) and (*Paroedura*, *Ebenavia*, *Uroplatus*) groups, the latter being predicted by Bauer and Russell (1989a).

METHODS, INGROUP TAXA AND CHARACTERS

We used the outgroup rooting method and heuristic algorithms m^* and bb^* provided by Hennig86 (Farris, 1988) in our attempts to discover the best-fitting hypothesis of sister group relationships. The outgroup methodology not only establishes the globally most parsimonious description of the evidence, but tests the historical individuality of the ingroup (Clark and Curran, 1986; see also Nixon and Carpenter, 1993). Such a best-fitting cladistic hypothesis(es), in minimizing homoplasy, maximizes the explanatory power of the data (Kluge, 1993b). It is in this context that the homoplasy and taxonomic generality of each of the characters are judged. The large number of taxa

and the highly incongruent nature of the character states investigated forced us to use heuristic algorithms in our attempts to discover the most parsimonious cladogram, and under those circumstances the limited (m^*) and extended (bb^*) branch-swapping routines are generally recommended (Farris, 1988). *A posteriori* iterative weighting (the $xs w$ algorithm in Hennig86; Farris, 1988) was employed in choosing among two or more equally most parsimonious cladograms (the secondary cladograms of Kluge and Wolf, 1993). The combination of m^* , bb^* , and $xs w$ is iterated until the ensemble consistency (CI) and retention (RI) indices, metrics widely employed in phylogenetic inference to assess fit to data, do not change. Individual character consistency (ci) and retention (ri) indices are used to evaluate each variable's performance. The minimum number of steps a character can exhibit on a particular cladogram is s ; that number summed over all characters is S , or the total length of the cladistic hypothesis. A character's weight (w) is the product of its rescaled consistency and retention indices (times 10), where the smallest s is used. A more detailed discussion of this general approach can be found in Kluge (1993c).

The following Ethiopian Region endemics constitute the majority of the gekkonid ingroup terminal taxa surveyed: *Afroedura*, *Ailuronyx*, *Blaesodactylus*, *Chondrodactylus*, *Colopus*, *Ebenavia*, *Geckolepis*, *Geckonia*, *Homopholis*, *Lygodactylus*, *Pachydactylus*, *Palmatogecko*, *Paragehyra*, *Paroedura*, *Phelsuma*, *Phyllodactylus*, *Ptyodactylus*, *Rhothropella*, *Rhothropus*, *Tarentola*, *Urocotyledon*, *Uroplatus*. Three geographically widespread taxa, *Gehyra*, *Gekko*, and *Hemidactylus*, were added to the ingroup in a second analysis, in order to further test the historical individuality of the Ethiopian Region endemics and the robustness of their intergeneric

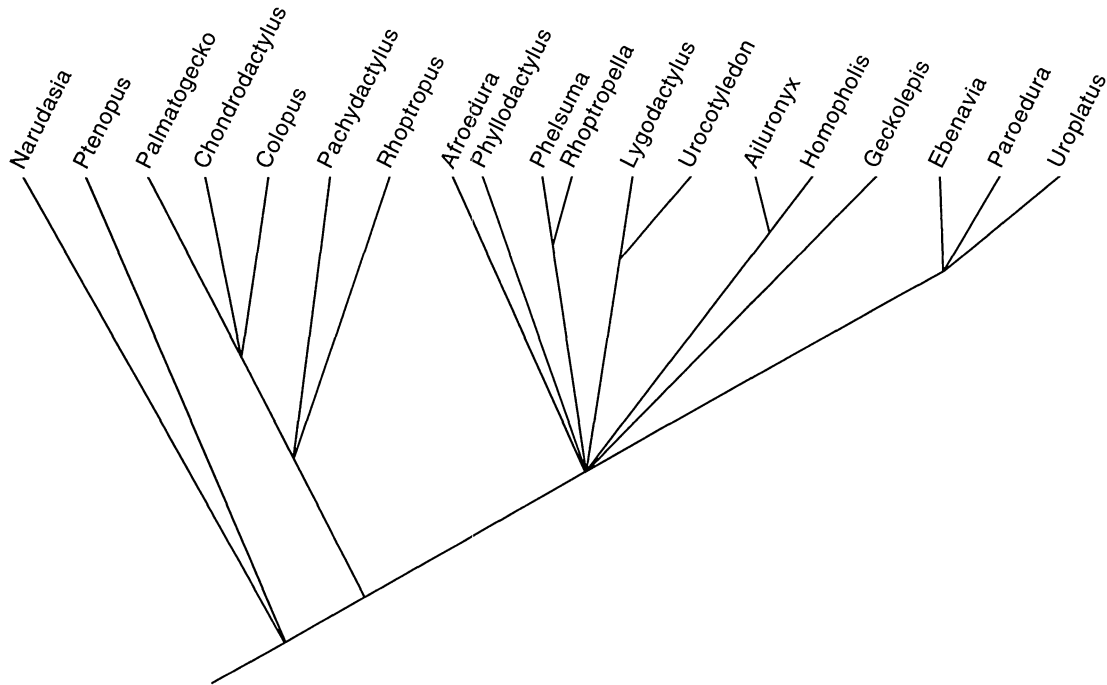


Fig. 3. A strict consensus of the 42 equally most parsimonious cladograms ($S = 43$, $CI = 0.55$, $RI = 0.78$) recovered from the data published by Bauer (1990a: appendix 1). Compare to Figure 2. Note the reduced resolution in this hypothesis, but *Urocotyledon*'s unambiguous sister group relationships.

relationships. All of the Ethiopian Region genera considered in detail by Joger (1985; Fig. 1) and Bauer (1990a; Fig. 2) are included as ingroup or outgroup taxa (see below). All of the terminal taxa analyzed in this study are represented by one or more specimens (see Appendix), and each terminal taxon is assumed to be monophyletic. With the exception of a large number of uncatalogued southern African *Phyllodactylus*, the species and skeletal material that we examined are listed in the Appendix, all of which are housed in the University of Michigan Museum of Zoology (UMMZ). Observations on very many species of *Phyllodactylus* were provided by James R. Dixon (pers. comm.), and are not based on specimens listed in the Appendix.

We believe Russell's (1978: 28) action of placing *Blaesodactylus* in the synonymy of *Homopholis* is unwarranted, because it was based on the "overall similarity between the types of the two nominal species (*Blaesodactylus boivini* and *Homopholis heterolepis* [= *B. sakalava*])." Further, Böhme and Meier (1980; see also Visser [1987] for diagnostic features) suggested that the African and Madagascan groups of species that Russell included in *Homopholis* be recognized as separate taxa. Thus, we employ *Blaesodactylus* for the Madagascan endemics (*B. antongilensis*, *B. boivini*, and *B. sakalava*) and *Homopholis* for the African species (*H. fasciata*, *H. mulleri*, and *H. walbergii*). We take this opportunity to synonymize *Kaokogecko* with *Palmatogecko*. The two monotypic genera are obviously sister taxa (see character descriptions below), and the use of a single generic taxon points to that affinity, whereas different names do not. There is little doubt that *Lygodactylus* (including *Domerguella*) is paraphyletic relative to *Microscalabotes* and *Millotisaurus*. Thus, we discuss intrageneric variation in terms of the four sets of species, but use *Lygodactylus* (sensu lato) as the single terminal taxon in our analyses of gekkonid relationships (Table 1). We leave the reclassification

of all *Lygodactylus* species to other investigators (e.g., Raxworthy, in progress). For the purposes of the present reanalysis, we follow Bauer (1990a; *contra* Russell, 1977a) in considering the monotypic *Rhoptropella* (*R. ocellata*) and *Phelsuma* as separate taxa. The former taxon is an Africa endemic, whereas the latter is very largely Madagascan, and their taxonomic separation in this study provides a basis for testing the relationships between those two biotas. The *Phyllodactylus* analyzed herein are southern African species only (*P. ansorgii*, *P. lineatus*, *P. microlepidotus*, *P. peringueyi*, and *P. porphyreus*), unless stated otherwise. Our research on southern African and Madagascan *Phyllodactylus*, with John Visser, will be published elsewhere. It is sufficient to note at this time that *P. brevipes* is almost certainly a Madagascan endemic and belongs to another part of the history of Gekkonini.

The present review of the phylogenetic relationships of Ethiopian Region gekkos is based largely on characters described by Russell (1972), Haacke (1976), Kluge, (1983; 1987), Joger (1985), and Bauer (1990a: 278). Their data are revised, wherever appropriate. Characters 1-23 follow exactly the order in which Bauer (1990a) listed them, and unless stated otherwise the reader can assume that Bauer considered state 0 to be plesiomorphic. Characters 25-28 were employed by Joger (1985), but omitted by Bauer (1990a). Neither Joger (1985) nor Bauer (1990a) used characters 24 and 29-34. Joger's (1985) chromosome character must be surveyed among many more gekkonids before its phylogenetic informativeness can be judged (see also Kluge, 1994).

OUTGROUP TAXA

Complete premaxilla bone fusion during ontogeny, egg shell mineralization and a relatively round egg shape characterize

Table 1 (cont.)

	<i>Ptyodactylus</i>	<i>Quedenfeldtia</i>	<i>Rhoptropella</i>	<i>Rhoptropus</i>	<i>Saurodactylus</i>	<i>Stenodactylus</i>	<i>Tarentola</i>	<i>Teratoscincus</i>	<i>Urocotyledon</i>	<i>Uroplatus</i>
1.	0	0	1	0	0	0	0	0	0/1	1
2.	0	0	1	0	1	0	0	0/1	0	0
3.	0	0	1	0	0	0	0	0	0	0
4.	0	0	0	0	0	0	0/1	0	0	0
5.	1	0	?	0	0	0	0	0	1	1
6.	0	0	0	0	0	0	0	0	1	1
7.	0	0	0	0	0	1	0	0	1	1
8.	0	0/1	1	0	0/1	0/1	0	0	1	0
9.	0	0	0	0	0	1	1	0/1	1	0
10.	1	1	0	0	1	0/1	1	1	0	0
11.	0	1	0	0	1	0	0	0	0	0
12.	0	0	0	1	0	0	1	0	0	0
13.	0	0	0	0	0	1	0	0	0	0
14.	0	0	1	0	0	0	0	0	0	0
15.	0	0	0	0	0	0	0	0	0	1
16.	0	0	1	0	0	0	0	0	0	0
17.	1	0	1	1	0	0	1	0	1	1
18.	0	0	0	0	0	1	0	1	0	0
19.	0	0	0	0	0	0/1	0	0	0	0
20.	0	0	0	0	0	0	0	0	0	0
21.	0	0	0	0	0	0	0	0	0	0
22.	1	1	0	0/1	1	0/1	1	1	1	1
23.	0	0	?	0	0	0	0	0	1	0
24.	0	1	0	0	1	0	0	0	0	0
25.	0	0	0	0	0	0	1	0	0	0
26.	0	0	1	1	0	0	1	0	0	0
27.	0	0	1	1	0	0	1	0	0	0
28.	0	0	1	1	0	0	0	0	0	0
29.	0	0	0	0	0	0	0	0	0	0
30.	0	0	1	0	1	0	0	0	1	1
31.	0	1	1	1	0/1	0	0	0	2	2
32.	0	0	0	0	0	1	0	1	0	0
33.	1	0	0	0	0	0	0	0	0	0
34.	1	1	1	1	1	1	1	0	1	1

Gekkonidae, and the monophyly of that taxon is accepted, in the absence of evidence to the contrary. Unfortunately, aside from the sphaerodactyl clade (Kluge, 1995), no other large subgroup of gekkonids has been distinguished unambiguously by two or more synapomorphies. Obviously, further research is required if we are to understand the history of this most speciose part of gekkotan phylogeny. Even the sister group relationships of much smaller taxa, like *Paragehyra*, are dependent on this more general hypothesis.

For the purposes of the present study, we assume the absence of a hyperextensive mechanism in the digits (*sensu* Russell, 1972), and being "naked-toed" (or "padless"), is plesiomorphic at the level of Gekkonidae. While the state of the digit cannot be optimized unambiguously for Pygopodidae, the mechanism is absent in Eublepharidae and *Teratoscincus*, and more generally in Squamata. Thus, the following "naked-toed" terminals are designated as outgroups: *Narudasia*, *Pristurus*, *Ptenopus*, *Quedenfeldtia*, *Saurodactylus*, *Stenodactylus*, and *Teratoscincus*. Likewise, Bauer (1990a) assumed the "naked-toed" condition to be plesiomorphic (his character 17), and the only two such taxa that he included in his study, *Narudasia* and *Ptenopus*, were judged to be sister lineages relative to all of the other terminals that he investigated on the basis of this single character (Figs. 2-3). Joger (1985) described the sister group relationships of only one "naked-toed" taxon, *Stenodactylus*; however, he postulated that it evolved from a "padded-toed" ancestor (Fig. 1). The aforementioned "naked-toed" outgroup taxa employed in our study are

from the Ethiopian Region, or are believed to be close relatives to those African lineages (Kluge, 1967a, 1987), and they include the taxa investigated by Joger and/or Bauer. The importance of considering additional "naked-toed" forms as outgroups (e.g., *Cnemaspis*, *Nactus* and *Tropicolotes*) requires further study; however, in terms of the characters we employed, their presence would probably not change our findings, because they are so similar to the outgroups we did include.

CHARACTER DESCRIPTIONS

1. Nasal bones paired (0) or fused (1). Both states are widely distributed among gekkonoids (Kluge, 1987; J. R. Dixon, pers. comm.), and we review that information because it provides the reader with a general sense of the conservativeness of the character (the same considerations apply to characters 4-8, 11, 13, 15, 20, 22-24, and 26). The fused condition is typical of *Afroedura* (Cogger, 1964), *Ailuroonyx*, *Aprasia* (all species, except *A. repens*), *Blaesodactylus*, *Christinus*, *Cnemaspis* (fused in *C. affinis*, *C. africana*, *C. boulengerii*, *C. kandiana*, *C. nigridius*, *C. quattuorseriata*, *C. siamensis*, and *C. wynadensis*; paired in *C. indica*, *C. kendallii*, and *C. ornata*; see Dring [1979] and Inger et al. [1984] for reviews of *Cnemaspis*), *Ebenavia*, *Hemiphyllodactylus*, *Lepidodactylus*, *Lygodactylus* (including *Domerguella*), *Microgecko* (*sensu* Kluge, 1983: 472; *contra* Leviton et al., 1992: 47), *Microscalabotes*, *Millotissaurus*, *Nactus*, *Paragehyra* (only paired posteriorly, like

Uroplatus), *Paroedura*, *Perochirus*, *Phelsuma* (fused in all species examined [see however, Bauer, 1990a], including *P. abbotti*, *P. astriata*, *P. barbouri*, *P. cepediana*, *P. comorensis*, *P. dubia*, *P. guentheri*, *P. guimbeaui*, *P. laticauda*, *P. lineata*, *P. madagascariensis*, *P. ornata*, and *P. sundbergi*), southern African *Phyllodactylus* (also fused in *P. riebeckii*, but not in other Old World species currently considered *Phyllodactylus*, such as *P. europaeus* and *P. siamensis*), *Pseudogekko*, *Rhohtropella*, some *Urocotyledon* (fused in *U. inexpectata* and *U. palmata*; paired in *U. wolterstorffi*; *U. weileri* to be determined), and *Uroplatus*. The nasals are fused throughout most or all of their length in all *Blaesodactylus* (*B. antongilensis*, *B. boivini*, and *B. sakalava*), whereas the supposedly closely related *Homopholis* (*H. fasciata*, *H. mulleri*, and *H. walbergii*) has paired elements. The paired nature of the nasals is even obvious in *P. fasciata*, which has the most extensive sculpturing of the bones of the snout of all six *Blaesodactylus*-*Homopholis* species.

2. Frontal bone single (0) or paired (1). The paired condition is present (Kluge, 1967a, 1987; see also Joger, 1985) in *Afroedura*, *Ailuroonyx* (the posterior 2/3 of the frontal), some *Geckolepis* (single in *G. maculata*, paired in *G. typica*), *Homopholis*, some *Lygodactylus*, some *Phelsuma*, *Rhohtropella*, *Saurodactylus*, and some *Teratascincus* (paired in *T. scincus*, single in *T. microlepis*, and one specimen of *T. przewalskii* has the posterior region of the bone paired, but the anterior portion is single). The variation observed in *Lygodactylus* and *Phelsuma* may be, at least in part, due to comparing specimens of different sizes and ages; however, that does not explain unambiguous cases of intraspecific variation where the specimens exhibiting the alternative conditions have nearly identical snout-vent lengths (e.g., in *L. klugei*, UMMZ 143389 exhibits the single state, whereas UMMZ 143390 has the paired condition). In contrast to *Blaesodactylus*, all adult *Homopholis* exhibit state 0. Only a subadult *P. fasciata* (UMMZ 127698) has the paired condition. The fact that the largest species of *Teratascincus* (*T. scincus*) exhibits the paired state and the smallest species (*T. microlepis*) the single condition indicates that, if this variation is to be interpreted as a heterochronic pattern, then it does not always accompany miniaturization (e.g., as in *Geckolepis*). As suggested by Kluge (1987: 34), the phylogenetic informativeness of this character is questionable, because of the extreme variation that occurs within some species. Stephenson (1962: fig. 5; see also Moffat, 1973) stated that *Pletholax* had a paired frontal; however, no such condition is evident in the specimens at hand (UMMZ 131215, 131232, 173966).

3. Frontal bone broadly participating in orbital rim (0), or excluded from orbital rim by pre- and postfrontal contact (1). The pre- and postfrontals are widely separated in almost all gekkonoids. In most pygopods, the contact is complete, or nearly so, and *Phelsuma* and *Rhohtropella* are also exceptions in that the frontal is excluded from the orbit by the union of the pre- and postfrontal bones.

4. Parietal bones paired (0) or single (1). This character varies little in gekkonoids. A single parietal is present only in some *Ailuroonyx*, *Chondrodactylus*, eublepharids, *Lepidoblepharis festae* (Parker, 1926), *Lialis*, some *Pachydactylus* (e.g., the *P. bibronii* complex), *Perochirus*, some *Phelsuma* (e.g., *P. guentheri*), and some *Tarentola*. The paired state may be obscured in the *Pachydactylus bibronii* complex by the deep sculpturing which covers the superficial postorbital bones. Also, the paired state is exhibited by all *Blaesodactylus* (*B. antongilensis*, UMMZ 192320; *B. boivini*,

UMMZ 201505; *B. sakalava*, UMMZ 192323) and *Homopholis walbergii* (UMMZ 127699). The fused state is typical of the remaining two *Homopholis* species (*H. fasciata* and *H. mulleri*), and is obviously correlated with the deep sculpturing that covers the parietals. Bauer (1990a: appendix 1) over-generalized the fused condition to all species in the *Blaesodactylus*-*Homopholis* complex.

5. Stapes perforate (0) or imperforate (1). According to Underwood (1971; see also Underwood, 1957), the facial artery passes behind the stapes in all lizards, except in gekkonoids and Dibamidae (*Anelytropsis* and *Dibamus*; Greer, 1976). The two conditions in gekkos and pygopods, both of which are considered derived, are (a) the stapes is imperforate, the artery passes anterior to the stapes, and (b) the artery passes through a foramen located distal to the footplate. The stapedia foramen is absent in the following gekkonoids (see also Kluge, 1987): *Ailuroonyx*, *Cnemaspis*, *Ebenavia*, *Geckonia*, *Gehyra*, *Gekko*, *Hemiphyllodactylus*, *Homonota*, *Lepidodactylus*, *Paroedura*, *Perochirus*, some southern African *Phyllodactylus* (foramen present in *P. ansorgii* and *P. lineatus*, but absent in *P. porphyreus*, according to J. R. Dixon, pers. comm.), *Ptenopus*, *Ptychozoon*, *Ptyodactylus*, Pygopodidae (both diplodactylines and pygopods), *Thecadactylus*, *Urocotyledon* (only *U. inexpectata* examined; contra Bauer, 1990a), and *Uroplatus*. Although Bauer (1990a) recorded *Rhohtropella* as having a perforate stapes, the single cleared and stained specimen of *R. ocellata* available to us (UMMZ 127760) has the imperforate condition. However, in that individual there is a conspicuous notch on the anterior side of the pedicel of the stapes, near the footplate, which suggests the artery passed within the developmental template of the stapes and that one of the foramen's enclosing walls failed to materialize. Thus, we score *Rhohtropella* as unknown.

6. Marginal tooth positions moderate in number (0) or many (1). Although Bauer (1990a: 278) employed this character, he did not specify a particular set of teeth (i.e., premaxillary, maxillary or dentary), nor did he precisely define the conditions "moderate" and "many." Fortunately in gekkonoids, the number of teeth on the maxilla and dentary are highly positively correlated, and likewise vary with age (body size) (e.g., Kluge, 1962). Thus, we have arbitrarily chosen the adult maxilla as the source of information on marginal tooth positions, and we infer those numbers from the states Bauer attributed to particular taxa. For example, he listed only *Ebenavia*, *Paroedura*, *Urocotyledon*, and *Uroplatus* as having state 1 (his appendix 1), and given that these taxa have 36 or more marginal maxillary tooth positions per side (see below) we will assume that range defines Bauer's state 1, and that 35 or less marginal teeth defines state 0. Our observations are summarized as follows, as modal or median values per side, determined on adults of as many species as are available, with exceptional material (those lying outside the narrow range exhibited by conspecifics and congeners) noted separately: *Afroedura* (27), *Ailuroonyx* (39), *Blaesodactylus* (39), *Chondrodactylus* (32), *Colopus* (25), *Ebenavia* (44), *Geckolepis* (33), *Geckonia* (24), *Gehyra* (29, except for one of three specimens of *G. oceanica* which has 36 [UMMZ 185913]), *Gekko* (33), *Hemidactylus* (29, except for *H. garnotii* and *H. giganteus* which have 37 and 36, respectively), *Homopholis* (*H. fasciata* has 25 [18 in subadult, UMMZ 127698], *H. walbergii* 35), *Lygodactylus* (17), *Millotiasaurus* (16), *Narudasia* (22), *Pachydactylus* (25), except *P. bibronii* complex which has 32), *Palmatogekko* (22), *Paragehyra* (38),

Paroedura (36), *Phelsuma* (25), southern African *Phyllodactylus* (30), *Pristurus* (20), *Ptenopus* (18), *Ptyodactylus* (30), *Quedenfeldtia* (18), *Rhothropella* (16), *Rhothropus* (27), *Saurodactylus* (24), *Stenodactylus* (26), *Tarentola* (30), *Teratoscincus* (29), *Urocotyledon* (36), and *Uroplatus* (56). Other studies, such as that of Kluge and Shea on pygopod phylogeny (in progress), suggest the above two-state representation of marginal tooth number variation underestimates the interspecific phylogenetic information present. Although future research on gekkonid relationships may score this variation as a multistate character, those additions will be problematic when it comes to coding the several states (Kluge and Shea, in progress). Observations on tooth numbers of other gekkonoids can be found in Bauer and Russell (1990), and Kluge and Shea (in progress).

7. Second ceratobranchial arch present (0) or absent (1). Kluge (1983; see also 1987) stated that this arch is completely absent, or nearly so, in the following gekkonoids: *Agamura*, *Ailuroonyx*, *Alsophylax*, *Aristelliger*, *Asiocolotes* (only *A. depressus* examined), *Blaesodactylus*, *Bogertia*, *Briba*, *Bunopus*, *Calodactylodes*, *Carinatogekko* (only *C. heteropholis* examined), *Cnemaspis*, *Cosymbotus*, *Crossobamon*, *Cyrtodactylus*, *Dravidogekko*, *Geckolepis*, *Gehyra*, *Gekko*, *Gymnodactylus*, *Hemidactylus*, *Hemiphyllodactylus*, *Heteronotia*, *Homopholis*, *Lepidodactylus*, *Luperosaurus*, *Lygodactylus*, *Millotissaurus*, *Perochirus*, *Phyllopezus*, some *Pristurus* (e.g., *P. carteri* and *P. crucifer*), *Pseudogekko*, *Ptychozoon*, *Stenodactylus*, *Teratolepis*, *Thecadactylus*, *Tropicolotes* (*sensu* Kluge, 1983), *Urocotyledon*, and *Uroplatus*. The arch is lacking in *Domerguella* species, and according to Bauer (1990a: appendix 1) it is also absent in *Microscalabotes*. Although a tiny portion of the second ceratobranchial arch remains in at least some *Blaesodactylus sakalava* and *Homopholis walbergii*, we scored the character state as 1 in those taxa.

8. Atlas paired (0) or fused (1) dorsally. Among diplodactylines, the fused condition occurs in a few specimens of *Diplodactylus* and *Rhyncoedura*, and perhaps all *Crenadactylus*. Also, state 1 seems to be consistently exhibited by adult *Christinus*, *Cnemaspis*, *Coleodactylus*, *Ebenavia*, *Gonatodes*, *Hemiphyllodactylus*, *Lepidoblepharis*, *Lepidodactylus*, *Lygodactylus*, *Millotissaurus*, some southern African *Phyllodactylus* (most Old World species, according to J. R. Dixon, pers. comm.; exceptions include *P. ansorgii*, *P. riebeckii*, *P. trachyrhinus*), *Pristurus*, *Pseudogonatodes*, some *Quedenfeldtia* (variable within *Q. moerens*), *Rhothropella*, *Saurodactylus* (single in *S. fasciatus*, paired in *S. mauritanicus*), *Sphaerodactylus*, some *Stenodactylus* (variable within *S. sthenodactylus*), and *Urocotyledon* (*U. inexpectata* and *U. palmata* examined; J. R. Dixon's pers. comm. that *U. wolterstorffi* is variable requires confirmation). Our conclusions concerning *Afroedura*, *Ailuroonyx*, *Blaesodactylus* (including *Homopholis*, only *H. walbergii* determined), *Phelsuma*, *Phyllodactylus*, and *Ptenopus* differ from Bauer's (1990a: appendix 1). The paired condition in some species of *Phelsuma* may be obscured by the prominent neural spine (ridge) on the anterior part of the atlas. There can be no doubt as to the fused state in *Rhothropella* because the neural arch is gently rounded on the dorsal midline and the width of the arch is uninterrupted in that region (there is no indentation anteriorly and/or posteriorly on the midline).

9. Ischiopubic fenestra as deep or deeper than wide (0) or much wider than deep (1). Bauer (1990a) used the term "chordate foramen of pelvis" for ischiopubic fenestra (a typographical error for cordiform foramen, according to A. M. Bauer, pers.

comm.). It appears that the depth and width of the fenestra were measured along (anteroposteriorly) and from (laterally) the midline, respectively. However, that characterization may not be accurate because in order for our quantitative assessment to be maximally consistent with Bauer's (1990a) observations we have to define (depth/width) states 0 and 1 as 1.17 or more and 1.16 or less, respectively. And, in any case, we disagree with Bauer (1990a: appendix 1) on the states he attributed to the following taxa: *Narudasia*, *Paroedura* (at least *P. pictus*), *Phelsuma*, *Rhothropus*, and *Urocotyledon*. Bauer (1990a) assumed a relatively wide fenestra (our state 1) to be plesiomorphic.

10. Hypoischium absent to moderately (0) or very (1) long. We consider the hypoischium to be very long (state 1) when it is longer than either the depth or the width of the ischiopubic fenestra (see character 9), otherwise it is state 0. Given this definition, we disagree with Bauer's observations concerning *Pachydactylus* and *Rhothropus*. The skeletal material at hand is not sufficiently well prepared to be able to confirm the condition Bauer (1990a) ascribed to *Homopholis* and *Paroedura*.

11. Cloacal bones present (0) or absent (1) in males. Cloacal bones and sacs (see cloacal sac character 24 below) appear to be diagnostic of gekkonoids, and their absence in that group has been interpreted as a loss (Kluge, 1982: 350). According to Kluge (1982), the following gekkonoids do not have cloacal bones: *Aristelliger* (ignoring the *os penis*), *Asaccus*, *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, most *Lygodactylus* (present in the *Domerguella* species group; Bastinck, 1986), *Millotissaurus*, *Narudasia*, some *Phyllodactylus* (e.g., *P. riebeckii* and *P. trachyrhinus*), *Pristurus*, *Pseudogonatodes*, *Quedenfeldtia*, *Saurodactylus*, and *Sphaerodactylus*. Bauer (1990a: appendix 1) incorrectly recorded *Lygodactylus* as invariable. We treat *Microscalabotes* as unknown. The fact that cloacal bones can be small and difficult to detect by external examination forces us to reject Bastinck's (1986: 216) inference that *Microscalabotes* does not have such elements. It is clear that at least males of the new species of *Paragehyra* described by Nussbaum and Raxworthy (1994) have well-developed cloacal bones (see Bastinck, 1986, for conjectures about the condition in *P. petiti*). Moffat's (1973) claim that cloacal bones are absent in *Pletholax* is incorrect (Kluge, 1982).

12. Digit I of manus and pes with two (0) or three (1) phalanges. The following gekkonoids exhibit the derived state (Kluge, 1983: fig. 12; see also Haacke, 1976): *Chondrodactylus*, *Colopus*, *Gekkonina*, *Pachydactylus*, *Palmatogekko*, *Rhothropus*, and *Tarentola*.

13. Digit IV of manus with five (0) or four (1) phalanges. The apparent loss (state 1) of a bony element in the fourth finger has been observed in the following gekkonoids (after Kluge [1967b, 1987], Russell [1972, 1979], Haacke [1976], Arnold [1977, 1980], Gasc [1977], Joger [1985], Perret [1986], Grismer [1988], and Bauer [1990b]): *Asaccus* (*A. elisae* and *A. gallagheri* require confirmation; Arnold, 1977:97), *Chondrodactylus*, *Cnemaspis occidentalis*, *C. petrodroma*, *C. spinicollis*, *Coleodactylus*, *Coleonyx brevis*, *Colopus*, *Diplodactylus stenodactylus*, *Hemitheconyx taylori*, *Nephruurus*, some Old World *Phyllodactylus* (e.g., *P. melanostictus* and *P. siamensis*; *P. riebeckii* requires confirmation), *Pseudogonatodes*, all pygopods, *Rhyncoedura*, and *Stenodactylus*. Some *Hemidactylus* (e.g., *H. albopunctatus*, *H. flaviviridis*, *H. frenatus*, and *H. mabouia*) have also been reported to have the reduced state; however, according to Russell (1977b: 335), "[t]he phalangeal formula of *Hemidactylus* is not reduced but instead exhibits a full phalangeal complement in both manus and pes.

Nonetheless, what is significant is the extreme state of modification of the antepenultimate phalanx of the third and fourth digit of the manus and third, fourth and fifth digit of the pes." Russell claimed to have found the same modification in *Bribo*, *Cosymbotus*, *Dravidogecko*, and *Teratolepis*. Indeed, the antepenultimate elements are extremely small in *Hemidactylus*, and might have been mistaken for phalangeal epiphyses, but an identical element is also present in the second finger and toe of a *Cosymbotus* (UMMZ 127624, but not UMMZ 13863). According to Russell's interpretation, it would be reasonable to postulate hyperphalangism for that specimen (manus: 24453; pes: 24454). Alternatively, if all such elements are phalangeal neomorphs then a hypothesis of reduction might apply to all the taxa in the complex (manus: 23343; pes: 23343). Further research is being undertaken to decide between these alternative interpretations.

14. Hypertrophied distal chondroepiphyses on antepenultimate and penultimate phalanges of digits two to five of both manus and pes absent (0) or present (1). We accept the claim of Russell and Bauer (1990; see also Joger, 1985) that chondroepiphyses are present only in *Phelsuma* and *Rhoptropella*.

15. Paraphalangeal elements absent (0) or present (1). The following are known to exhibit state 1 (Russell and Bauer, 1988): *Blaesodactylus*, *Bogertia*, *Bribo*, *Calodactylodes*, *Cosymbotus*, *Dravidogecko*, *Gehyra*, *Geckolepis*, *Hemidactylus*, *Hemiphyllodactylus*, *Homopholis*, *Lygodactylus*, *Palmatogecko* (absent in *P. vanzyli*; Bauer and Russell, 1991: 50), *Perochirus*, *Phyllopezus*, *Thecadactylus*, and *Uroplatus*. We also observed paraphalangeal elements in *Millotissaurus*. Bauer (1990a: 278, appendix 1) incorrectly scored only *Geckolepis* and *Blaesodactylus* (including *Homopholis*) as having a "paraphalangeal morphology."

16. Digit I long (0) or greatly reduced in length (1). Although the digit in question is short in *Homopholis sakalava*, it is scored as state 0 because, relatively speaking, it is not nearly as small as it is in *Lygodactylus* (including *Domerguella*), *Microscalabotes*, *Millotissaurus*, *Phelsuma*, and *Rhoptropella* (FitzSimons, 1943; *contra* Bauer, 1990a: appendix 1).

17. Hyperextensive mechanism absent (0) or present (1) in the digits (Russell, 1976, 1979). Bauer (1990a) observed that all gekkos without a hyperextensive mechanism also had padless digits, whereas those with the mechanism were either padded or padless secondarily. Russell (1976, 1979) also concluded that both setal loss and acquisition on the digits has occurred independently in gekkos.

18. Ventral digital scales smooth (0) or spinose (1). It is difficult to interpret Bauer's (1990a) meaning of "spinose," except for his having scored the occurrence of that state in only *Chondrodactylus*, *Colopus*, *Kaokogecko* and *Palmatogecko*. From this taxonomic distribution, we assume he was referring to the "peculiarly shaped palmar scales" mentioned by Haacke (1976: 81; see also Bauer and Russell, 1991) and illustrated by FitzSimons (1943: pl. 1) and Steyn and Haacke (1966: pl. 1). A similar condition may be found in *Stenodactylus* (Haas, 1957; see in particular *S. khobarensis*), *Teratoscincus* (Russell, 1972), and *Tropicolotes*.

19. Fleshy webs between digits absent (0) or present (1). Our synonymizing *Kaokogecko* with *Palmatogecko* effectively makes this character of Bauer's (1990a) an autapomorphy. Nonetheless, we retain the character in the present study for completeness. Extensive webbing has been observed in other ground dwelling gekkos (e.g., *Stenodactylus arabicus*; Arnold, 1980).

20. Skin rarely, if ever, (0) or frequently (1) torn. The skin of

gekkonoids appears to be torn more frequently than most other lizards, and the extreme specialization cited here (state 1) is confined to gekkos (Bauer, 1990a). The skin is readily torn in *Phelsuma breviceps* (R. A. Nussbaum, personal observations), perhaps more easily than in any other gekko. It is also torn frequently in at least some other species of *Phelsuma* (e.g., *P. madagascariensis*), although not in all congeners, and we treat the group as variable. According to Bauer et al. (1989: 80), state 1 is exhibited by all or most of the species of *Ailuronyx*, *Aristelliger*, *Geckolepis*, *Gehyra*, *Perochirus*, and *Teratoscincus*. The widespread nature of that condition in *Gehyra* and *Teratoscincus* requires documentation, and we have recorded those taxa as state 0. The supposedly fragile skin of *Pachydactylus namaquensis* (Greene, 1988; Bauer et al., 1993) and *P. scutatus* (A. M. Bauer, pers. comm.) are exceptional in *Pachydactylus*, and we score that genus as state 0.

21. Circumorbital scales unmodified (0) or with distinctive yellow pattern (1). Bauer (1990a:278) offered no further discussion of this character.

22. Preanal and/or femoral pores present (0) or absent (1). State 1 is exhibited by *Aprasia*, *Aristelliger*, *Blaesodactylus* (*B. antongilensis* and *B. sakalava* examined; *contra* Bauer, 1990a: appendix 1), *Bogertia*, *Calodactylodes*, *Chondrodactylus*, *Christinus*, some *Cnemaspis* (e.g., *C. boulengerii*, *C. kendallii*, some *C. nigridius*, some *C. siamensis*, and *C. timoriensis*; Dring, 1979), *Coleodactylus*, *Colopus*, *Delma*, *Diplodactylus* (rarely present; Kluge, 1967b), *Ebenavia*, *Geckolepis*, *Geckonia*, *Gonatodes*, *Goniurosaurus* (only *G. kuroiwae*), *Gymnodactylus*, some *Hemidactylus* (e.g., *H. aporus*, *H. forbesii*, *H. newtoni*, and *H. somalicus*; Loveridge, 1947), *Holodactylus*, *Homonota*, *Lepidoblepharis*, *Microgecko* (*sensu* Kluge, 1983), *Narudasia*, *Nephrurus*, *Ophidiocephalus*, most *Pachydactylus* (pores present in only two species, *P. telensis* and *P. tuberculatus*), *Palmatogecko*, *Paroedura*, some *Perochirus* (intraspecifically variable in *P. ateles*; Brown, 1976: 6), most *Phyllodactylus* (pores present in *P. lineatus*, *P. melanostictus*, and *P. siamensis*), *Phyllopezus*, *Phyllurus* (pores present in only *P. salebrosus*), *Pletholax*, *Pseudogonatodes*, *Pseudothecadactylus* (pores absent in only *P. cavaticus*), *Pristurus*, *Ptenopus*, *Ptyodactylus*, *Quedenfeldtia*, some *Rhoptropus* (Loveridge, 1947: 285; e.g., *R. afer* and *R. b. bradfieldi*), *Saurodactylus*, *Sphaerodactylus*, some *Stenodactylus* (see generic review by Arnold, 1980: 377), *Tarentola*, *Teratoscincus*, *Thecadactylus*, *Urocotyledon*, and *Uroplatus*.

23. Ventral surface of tip of tail without (0) or with (1) scansorial pad. The pilosity in question is difficult to see, often appearing only as a grayish tinge on the surface of a scale, and does not always occur on adjacent scales. Pilose subcaudal scales may or may not exhibit a midcaudal sulcus, which divides them into paired 'lamellae.' State 1 is believed to occur in *Bavayia*, *Eurydactylodes*, *Lygodactylus* (including *Domerguella*), *Microscalabotes*, *Millotissaurus*, some *Phelsuma* (*contra* Bauer, 1990a), *Phyllodactylus europeus*, *Pseudothecadactylus*, *Rhacodactylus*, and *Urocotyledon* (Mertens, 1964; van Eijsden, 1983; Kluge, 1983; Bauer, 1990b). Mertens (1964) implied that the scansorial pad is present in all *Phelsuma*. Although we agree that the caudal scales are obviously modified in some species (e.g., *P. madagascariensis*), we remain unconvinced that comparable pilose specializations occur in all other congeners (e.g., *P. lineata*). The condition in *Rhoptropella* remains to be determined.

24. Cloacal sacs present (0) or absent (1). As noted above, cloacal bones and sacs (see character 11) appear to be diagnos-

tic of gekkonoids, and their absence in parts of that group has been interpreted as one or more secondary losses (Kluge, 1982: 350). The presence/absence of cloacal bones and sacs are not perfectly correlated in *Thecadactylus* (Hoogmoed, 1973; Bastinck, 1986) and some pygopods (Kluge and Shea, in progress), and given such independent variation it seems reasonable to score them as separate characters. That we may infer subsequently from a particular hypothesis of phylogeny that bone and sac loss occurred together in the history of one or more clades does not decide the issue of non-independence of the two variables (*contra* Bastinck, 1986). Ordinarily, cladists interpret character congruence as a consequence of common ancestry, not dependent origin due to some other cause. Strong claims of character independence can rarely be made, particularly when the traits in question evolved in the distant past (Kluge and Wolf, 1993). The following gekkonoids do not have cloacal sacs (see Kluge, 1982): *Aprasia* (intraspecifically variable in females), *Aristelliger*, *Asaccus*, *Coleodactylus*, *Delma*, *Gonatodes*, *Lepidoblepharis*, *Lialis*, most *Lygodactylus* (present in the *Domerguella* species group; Pasteur, 1964; see also Bastinck, 1986), *Microscalabotes*, *Millotisaurus*, *Narudasia*, *Ophidiocephalus* (variable in both sexes), some *Phyllodactylus* (e.g., *P. riebeckii* and *P. trachyrhinus*), *Pletholax* (absent in females; however, may be variable in that sex), *Pristurus*, *Pseudogonatodes*, *Quedenfeldtia*, *Saurodactylus*, *Sphaerodactylus*, and some *Thecadactylus* (intraspecifically variable in both sexes of *T. rapicauda*; Hoogmoed, 1973; see also Bastinck, 1986).

25. Osteoderms absent (0) or present (1) in the supraorbital region. True osteoderms are located within the dermis, unlike "parafrenal bones" which are present below the dermis (Bauer and Russell, 1989b). According to Underwood (1970; see also 1957: 252) the orbit is roofed with osteoderms in various groups of lizards, and he pointed out that in gekkonoids that condition is found in *Aristelliger*, *Geckonia*, *Tarentola*, and *Teratoscincus*. We accept the distinction of Bauer and Russell (1989b) between true osteoderms and parafrenal bones, and also their claim that state 1 applies only to *Geckonia* and *Tarentola* (the ossifications in *Aristelliger* and *Teratoscincus* lie below the dermis). True supraor-

bital osteoderms may be continuous with those osteoderms overlying the frontal and other superficial cranial bones. *Paroedura* possesses cranial osteoderms, but these do not appear to occur in the supraorbital integument.

26. Claws are large (0) or small or absent (1) on digit I (manus and pes). Joger (1985:485) drew attention to the variable nature of claw size in African gekkonoids, and he also emphasized its sexually dimorphic nature in the following taxa ("vestigial claws present in all females, but practically never in males"): *Chondrodactylus*, *Colopus*, *Pachydactylus bibronii*, *Palmatogecko*, *Phelsuma madagascariensis*, *Rhoptropus barnardi*, and *Tarentola*. In order to maximize the informativeness of the size variation while minimizing possible non-independence, we have recognized three characters (26-28). We consider character 26 as inapplicable to *Millotisaurus* because it has lost digit I in the manus. According to Russell (1972), the first digit is clawless in most of the members of the *Gekko* group (*Gehyra* [variable], *Gekko*, *Hemiphyllodactylus* [absent in manus, present in pes], *Lepidodactylus*, *Luperosaurus*, *Perochirus*, *Pseudogekko*, *Ptychozoon*), and in *Bogertia* and *Briba*. We believe further survey work is necessary before the sexually dimorphic nature of claw size variation can be recorded as an additional character.

27. Claws are large (0) or small or absent (1) on digits II and III of the manus and pes. See character 26 above.

28. Claws are large (0) or small or absent (1) on digits IV and V of the manus and pes. See characters 26 above.

29. Maxillae separated or in narrow (0) or broad (1) contact posterior to the premaxilla. The peculiar condition of broad contact (Fig. 4) appears to be typical of only *Narudasia* and *Pristurus* (specimens of *P. carteri*, *P. crucifer*, *P. flavipunctatus*, *P. rupestris*, and *P. sokotranus* examined).

30. Lateral arms of interclavicle conspicuous (0) or inconspicuous (1). When the former condition is present, the interclavicle can be described as cruciform; when the latter applies it is more splint-like. These two states represent only the most obvious aspects of interclavicle variation (Fig. 5). For example, the cruciform state includes moderately long and wide

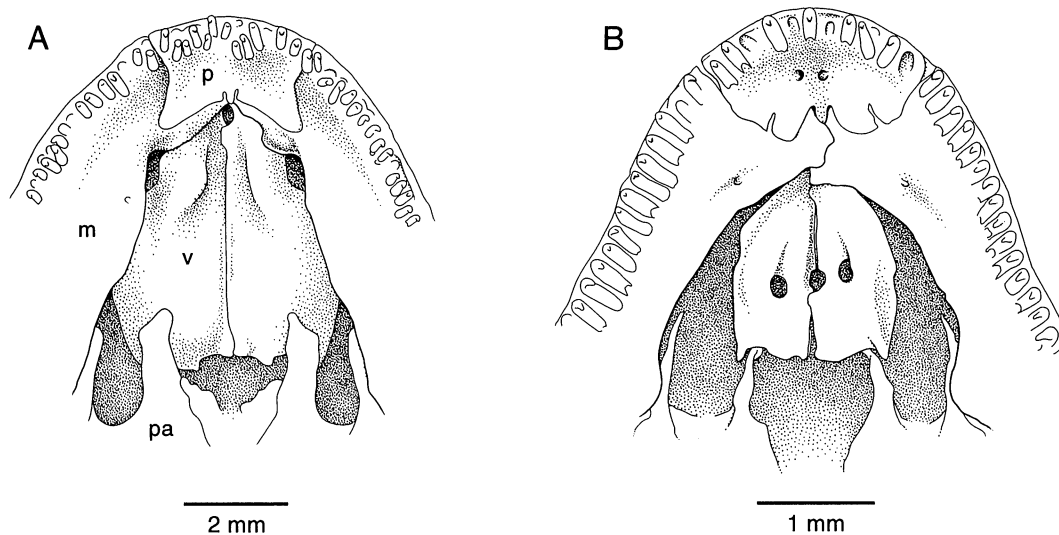


Fig. 4. Ventral view of the palate. A. The plesiomorphic condition in gekkos (Kluge, 1987: fig. 8). B. The apomorphic state, which is typical of *Narudasia* and *Pristurus* (Table 1). Abbreviations: m = maxilla; p = premaxilla; pa = palatine; v = vomer.

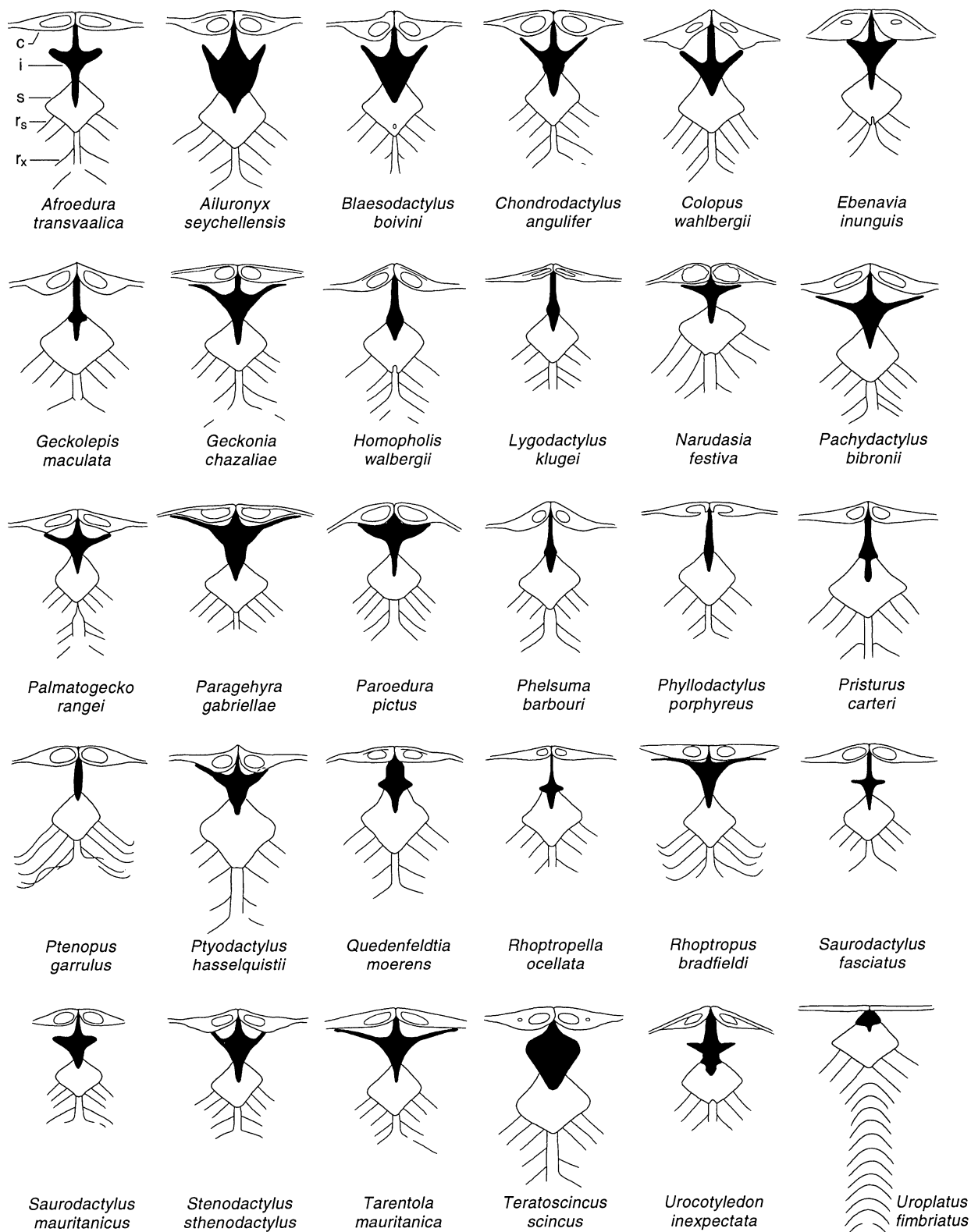


Fig. 5. Ventral view of the mid-ventral portion of the pectoral girdle of a representative of each terminal taxon investigated in detail in this study (not drawn to scale). For variation within genera (e.g., *Saurodactylus*) see text, character 30. Abbreviations: c = clavicle; i = interclavicle (black); rs = sternal rib; rx = xiphisternal rib; s = sternum.

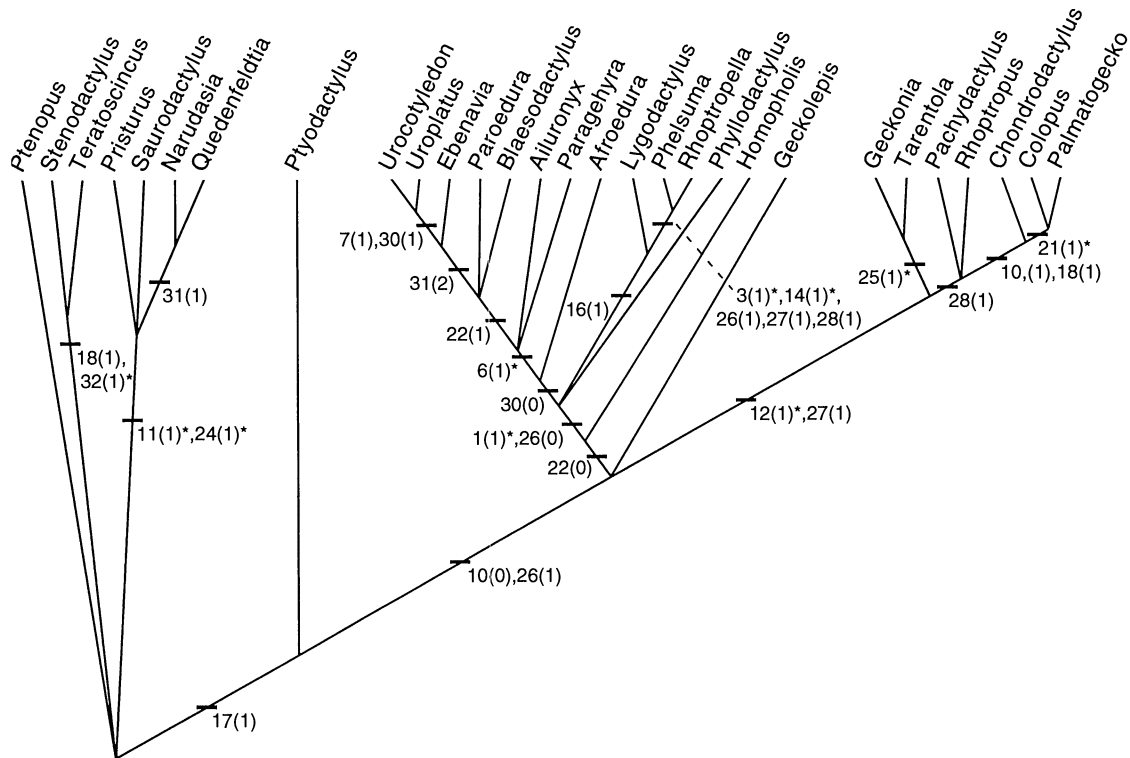


Fig. 6. Sister group relationships among the endemic Ethiopian Region ingroup taxa. The hypothesis is a strict consensus of the 72 equally most parsimonious cladograms ($S = 98$, $CI = 0.85$, $RI = 0.94$), after four iterations of differential character weighting. The length (S) of the consensus cladogram is 100. The “naked-toed” taxa, *Narudasia*, *Pristurus*, *Ptenopus*, *Quedenfeldtia*, *Saurodactylus*, *Stenodactylus*, and *Teratoscincus*, were designated outgroups. The raw data are listed in Table 1. The numbers refer to those characters and states (the latter in parentheses) which unambiguously delimit sister groups. Each asterisk denotes a unique and unreversed synapomorphy in this study (see text for further discussion). Compare to Figure 7.

to extremely long and narrow arms, the former lying some distance from the clavicles, whereas the latter make extensive contact with the clavicles. In state 1, the vertical body of the interclavicle can be narrow (almost rod-like) to extremely broad, (either oval to nearly triangular). Figure 5 summarizes the intergeneric variation observed in the taxa surveyed for this study (the two *Saurodactylus* illustrated, *S. fasciatus* and *S. mauritanicus*, document the high degree of variation that can occur among sister species). Although we scored *Phyllodactylus* as state 1, there is some notable variation. For example, *P. porphyreus* has no arms whatsoever, *P. lineatus* has short, but obvious, projections, and the condition in *P. europaeus* is intermediate between these extremes. We have no doubt that future research will make it possible to score additional phylogenetically informative descriptors, particularly identifying the dagger-shape variation which is intermediate between states 0 and 1.

31. Number of attached sternal and xiphisternal ribs 5-6 (0), 4 (1), or 3 (2). Only those ribs are counted which make a complete connection to the sternum and xiphisternum (Fig. 5). Although we assume this transformation to be additive, so that it is reasonable to apply a *posteriori* iterative weighting, that presumption has no effect on the phylogenetic hypothesis that is finally realized (Fig. 6).

32. Relatively few (0) or many (1) scleral ossicles. These data are taken from Kluge (1987: table 1). The only taxa that are judged to have state 1 in the present study are *Stenodactylus* and

Teratoscincus.

33. Splenial present (0) or absent (1). According to Kluge (1987), the splenial is present in all gekkonids, except *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, *Pristurus*, *Pseudogonatodes*, *Ptyodactylus*, and *Sphaerodactylus*.

34. Calcified postcranial endolymphatic sac absent (0) or present (1). Among those gekkonids surveyed herein, only *Teratoscincus* and “many” *Hemidactylus* (Simkiss, 1967) are said to exhibit state 0 (Kluge, 1987).

OTHER POTENTIAL EVIDENCE

Underwood (1954; 1970) emphasized the importance of pupil shape in the classification of gekkos. Although it is extremely difficult to accurately determine some of the different pupil types that he recognized (Kluge, 1967a: 14), certain of Underwood’s characterizations may eventually prove informative. For example, he referred to the *Rhoiptropus*-type (Underwood, 1954: 471) as occurring in *Chondrodactylus*, *Colopus*, *Palmatogecko*, *Ptenopus*, *Rhoiptropella*, and *Rhoiptropus*. In testing the generality of this synapomorphy, future investigators would be well advised to reexamine those taxa which Underwood listed as having straight-vertical and round pupils. Further, those tests should be made on living organisms under similar conditions (particularly light intensity).

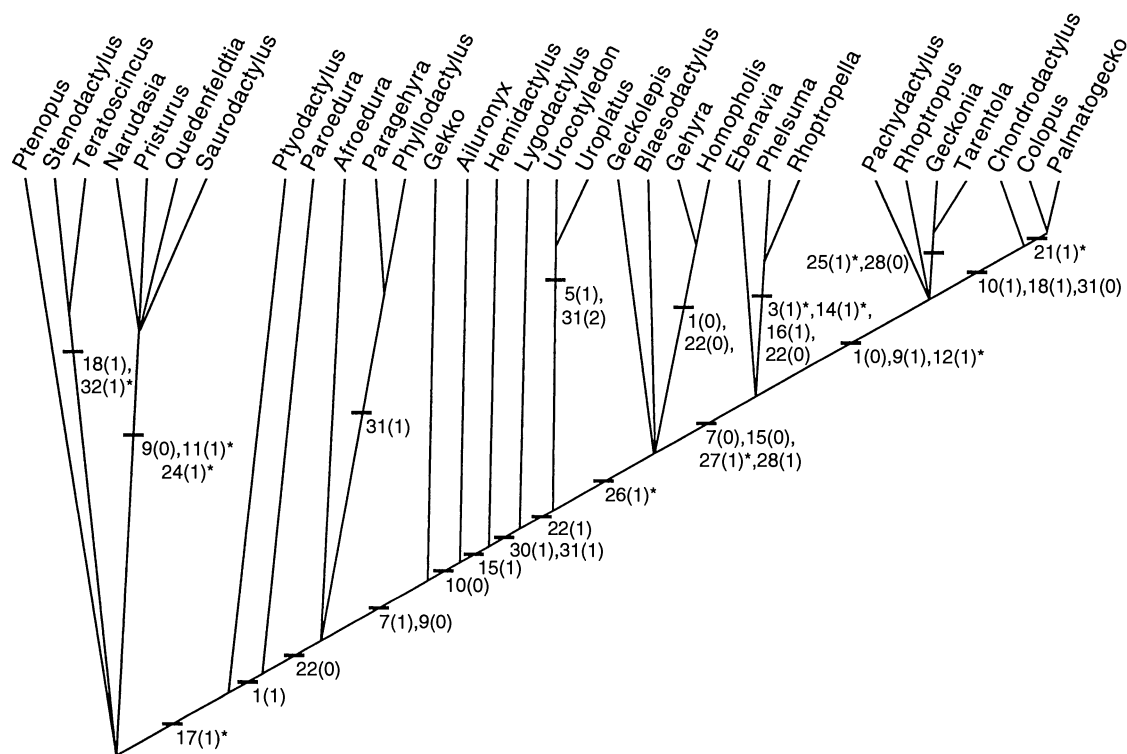


Fig. 7. Sister group relationships among the endemic Ethiopian Region (see Fig. 6) and extralimital ingroup taxa (*Gehyra*, *Gekko*, *Hemidactylus*). The hypothesis is a strict consensus of the 128 equally most parsimonious cladograms ($S = 101$, $CI = 0.82$, $RI = 0.93$), after four iterations of differential character weighting. The length (S) of the consensus cladogram is 103. The “naked-toed” taxa, *Narudasia*, *Pristurus*, *Ptenopus*, *Quedenfeldtia*, *Saurodactylus*, *Stenodactylus*, and *Teratoscincus*, were designated outgroups. The raw data are listed in Table 1. The numbers refer to those characters and states (the latter in parentheses) which unambiguously delimit sister groups. Each asterisk denotes a unique and unreversed synapomorphy in this study (see text for further discussion). Compare to Figure 6.

The variability Böhme (1988) described in the gekkonid hemipenis suggests another source of potentially informative characters. However, it is obvious that future research must provide more precise descriptions of that variability and survey many more taxa (Böhme, 1988: 67). Unfortunately, even the clearest of Böhme’s (1988: 160) conclusions, that “[t]he hemipenis ornamentation of *Uroplatus* is so unique that a higher categorial [sic] rank of this group seems justified,” is without merit in the context of the monophyletic taxonomy employed herein.

PHYLOGENETIC RESULTS

Our analysis of the relationships of the ingroup terminal taxa endemic to the Ethiopian Region (see p. xx above) involved four iterations (1: $CI = 0.39$, $RI = 0.66$; 2: $CI = 0.67$, $RI = 0.83$; 3: $CI = 0.74$, $RI = 0.88$; 4: $CI = 0.85$, $RI = 0.94$). Seventy-two equally most parsimonious secondary cladograms ($S = 98$) resulted from the **bb*** application in the last run, the strict consensus of which is illustrated in Figure 6 ($S = 100$). Several conclusions can be extracted from that conservative hypothesis: (1) relationships among the outgroups are unresolved, with the exception of *Narudasia*, *Pristurus*, *Quedenfeldtia* and *Saurodactylus* which form a clade (which also probably includes *sphaerodactyls*; Kluge, 1987; Kluge, in press)², and the sister taxa *Stenodactylus* and *Teratoscincus* (for an alternative opinion see Kluge, 1987); (2)

the historical individuality of the ingroup was confirmed, and *Ptyodactylus* is the sister lineage to all other parts of that clade; (3) the *Pachydactylus* group of Russell (1972; see also Haacke, 1976; Joger, 1985; Kluge, 1987; Bauer, 1990a) is delimited; (4) northern and southern African subgroups are identified within the *Pachydactylus* radiation (as per Russell, 1972; see also Joger, 1985); (5) no taxa known from Madagascar-Seychelles are included within the *Pachydactylus* clade, and the Madagascar-Seychelles assemblage forms a historical entity in its own right, except for the ambiguously placed *Geckolepis*; (6) a *Lygodactylus-Phelsuma* group (including *Rhoptropella*) is delimited; (7) *Paragehyra* is part of a highly derived assemblage, the components of which are restricted to Madagascar and nearby islands (the only exception is *Urocotyledon*); and (8) *Chondrodactylus* and *Colopus* are interpreted as being secondarily padless (see character 17; also Russell, 1972). Two of Bauer’s clades, (*Ailuronyx*, *Homopholis*) and (*Ebenavia*, *Paroedura*, *Uroplatus*) (1990a; see also Bauer and Russell, 1989a), are not supported, nor is the recent claim by Volobouev and Ineich (1994) that *Ailuronyx seychellensis* is more closely related to *Homopholis wahlbergii* than it is to *Phelsuma cepedianana* (Fig. 6; see also Fig. 7). *Geckonia* and *Tarentola* continue to be identified as sister taxa (Russell, 1972:95; Joger,

²*Sphaerodactyls* were excluded because they form a highly derived assemblage which does not affect the polarity decisions in this study.

1985), in spite of the "profound differences" Böhme (1988: 160) discovered between the hemipenes of these two taxa. Lastly, we do not agree with Böhme's (1988) conclusion that the unique hemipenis ornamentation of *Uroplatus* justifies a higher rank for that taxon alone, given the highly derived and consistent sister group relationship between *Urocotyledon* and *Uroplatus* that we discovered (Figs. 6-7).

Extreme caution must be exercised when the cladogram in Figure 6 is used in hypothesizing trends in character evolution and historical biogeographic events (see below). Although the cladistic hypothesis maximizes the explanatory power of the data at hand (Table 1), and "globally" so over in- and outgroups, it is sensitive to changes in characters and/or taxa.

It should be borne in mind that the proposition in Figure 6 is the result of three successive applications of character weighting (**xs w** iterations 2-4; see Table 2 for final weights). The strict consensus hypothesis from the first run is largely unresolved (there are 220 equally most parsimonious cladograms). Moreover, less than half (8/19) of the clades in the final result are corroborated by two or more synapomorphies (Fig. 6), and few of those phylogenetically informative characters can be interpreted as unique and unreversed (Table 2). Still further, the

data set is weaker than the individual character consistencies (**c**) might suggest (Table 2), because some independent evolution is ignored by coding polymorphic data as missing (Platnick et al., 1991). For example, the absence of cloacal bones (character 11, Table 2; see also cloacal sac, character 24) is reported as a unique and unreversed diagnostic feature of the (*Narudasia*, *Quedenfeldtia*, *Pristurus*, *Saurodactylus*) clade; however, the analysis does not take into account the absence of those bones (and sacs) in some *Lygodactylus* (Table 1).

The sensitivity of the cladogram illustrated in Figure 6 to taxonomic sampling is easily demonstrated by adding *Gehyra*, *Gekko*, and *Hemidactylus* to the ingroup of Ethiopian Region endemics and rerunning the analysis. Although only three iterations (**m***; **bb***; **xs w**) are required to achieve maximal fit to data (**S** = 101; **CI** = 0.82, **RI** = 0.93), the strict consensus of the resulting 128 equally most parsimonious secondary cladograms (**S** = 103) is substantially different from the ingroup of Ethiopian Region endemic taxa analyzed alone (compare Figs. 6 and 7). The three extralimital taxa are "padded-toed" (see character 17), and their addition substantially changes the relationships among the parts of the clade predominated by Madagascar forms (the sister group to the *Pachydactylus* radiation). Of particular interest is

Table 2. Individual character performances for hypothesis of figure 6. Abbreviations: **s** = number of steps; **ci** = consistency index; **ri** = retention index; **w** = weighting coefficient.

	1	2	3	4	5	6	7	8	9	10	11	
s	1	5	1	1	6	1	7	5	9	7	1	
ci	1.0	.20	1.0	1.0	.16	1.0	.14	.20	.11	.14	1.0	
ri	1.0	.00	1.0	1.0	.28	1.0	.14	.00	.33	.50	1.0	
w	10	0	10	10	0	10	0	0	0	0	10	
	12	13	14	15	16	17	18	19	20	21	22	
s	1	3	1	5	1	1	2	1	2	1	2	
ci	1.0	.33	1.0	.20	1.0	1.0	.50	1.0	.50	1.0	.50	
ri	1.0	.00	1.0	.00	1.0	1.0	.75	1.0	.00	1.0	.83	
w	10	0	10	0	10	10	3	10	0	10	4	
	23	24	25	26	27	28	29	30	31	32	33	34
s	2	1	1	5	3	3	2	6	9	1	2	1
ci	.50	1.0	1.0	.20	.33	.33	.50	.16	.22	1.0	.50	1.0
ri	.00	1.0	1.0	.66	.77	.71	.00	.50	.50	1.0	.00	1.0
w	0	10	10	1	2	2	0	1	1	10	0	10

Table 3. Individual character performances for hypothesis of Figure 7. Abbreviations: **s** = number of steps; **ci** = consistency index; **ri** = retention index; **w** = weighting coefficient.

	1	2	3	4	5	6	7	8	9	10	11	
s	6	5	1	1	9	6	3	5	8	4	1	
ci	.16	.20	1.0	1.0	.11	.16	.33	.20	.12	.25	1.0	
ri	.50	.00	1.0	1.0	.11	.16	.80	.00	.41	.76	1.0	
w	1	0	10	10	0	0	2	0	0	1	10	
	12	13	14	15	16	17	18	19	20	21	22	
s	1	3	1	3	2	1	2	1	2	1	4	
ci	1.0	.33	1.0	.33	.50	1.0	.50	1.0	.50	1.0	.25	
ri	1.0	.00	1.0	.66	.50	1.0	.75	1.0	.00	1.0	.62	
w	10	0	10	2	2	10	3	10	0	10	1	
	23	24	25	26	27	28	29	30	31	32	33	34
s	2	1	1	1	1	2	2	8	10	1	2	1
ci	.50	1.0	1.0	1.0	1.0	.50	.50	.12	.20	1.0	.50	1.0
ri	.00	1.0	1.0	1.0	1.0	.85	.00	.36	.46	1.0	.00	1.0
w	0	10	10	10	10	4	0	0	1	10	0	10

the unstable sister group affinities of *Paragehyra*. More generally, Figure 7 calls into question Bauer's assumption (1990a) that his ingroup terminal taxa form a natural group, and the addition of those three extralimital "padded-toed" taxa demonstrates the need for much more research on the higher classification of Gekkonidae. Bauer's claim (p. 277) that "the outgroups assigned are sufficiently broad to suggest that additions or deletions to or from the ingroup would not affect polarity assignments" remains to be tested. The consequences of adding other ingroup taxa must also be examined.

A general comparison of the diagnostic characters in Figures 6 and 7 (see also Tables 2-3) further serves to illustrate the weak nature of the data set at hand. More specifically, although both hypotheses may identify the same clade (e.g., *Phelsuma* + *Rhoptropella*), the discriminating evidence varies, because of ambiguity in character state optimization. Perhaps of greatest concern is the absence of a diagnostic feature supporting the historical individuality of the Ethiopian Region endemics (*contra* Joger, 1985; Bauer, 1990a: 279). The hyperextensive mechanism apomorphy (character 17) in Figure 6 must be corroborated with other synapomorphies. By itself, that character is simply not sufficient to exclude other "padded-toed" gekkonids, like *Gehyra*, *Gekko*, and *Hemidactylus*, and to avoid the significant effect they can have on the relationships of the ingroup of Ethiopian Region endemics.

A much revised history of the second ceratobranchial arch (character 7) is suggested by the phylogenetic hypothesis illustrated in Figure 6. In fact, the absence of the arch is hypothesized to have taken place seven times independently (only one of these unambiguously diagnoses a particular group). On the other hand, the hypothesized history of arch loss is much less complex according to Figure 7. On the latter cladogram, the number of independent evolutionary events has been reduced to four. Of these, two unambiguously diagnose groups: a loss, indicated by the character transformation 7(1), followed by a reversal, indicated by the transformation 7(0). Such a conjectured history of regaining the arch might be easily dismissed were it not for two factors. Firstly, the same major clade delimited by the re-evolved arch state is also unambiguously diagnosed by three other character states, the absence of paraphalangeal elements (character 15), claws small or absent on digits II and III of the manus and pes (character 27), and claws small or absent on digits IV and V of the manus and pes (character 28). Secondly, the re-evolution of the arch seems almost certain to have happened elsewhere in gekkonoids (e.g., *Gonatodes*, Kluge, 1987). In any case, the arch character cannot be dismissed as completely uninformative (*contra* Joger, 1985), and future studies of gekkonid relationships should include that variable.

BIOGEOGRAPHIC RESULTS

Joger (1985: 492) identified the existence of northern and southern African clades in his hypothesis of gekkonid relationships, and he further conjectured that the Madagascar fauna originated from within the southern African group (Fig. 1). Although Bauer (1990a: 280) did not investigate gekkos belonging to Joger's northern clade, he claimed to have confirmed the

Madagascar radiation (including that of the Comoros and Mascarenes) being derived from the southern gekkonid clade.

Although the available data do not support Bauer's (1990a: 280) conclusion that most of the Madagascar (including the Comoros and Mascarenes) gekkonid fauna (*Ailuronyx*³, *Blaesodactylus*, *Ebenavia*⁴, *Geckolepis*, *Paroedura* and *Uroplatus*) constitute "a single unit" (compare Figs. 2 and 3), corresponding area cladograms (Fig. 8 or 9) do suggest that the Madagascar fauna evolved subsequent to an African gekkonid radiation. Our analysis of the ingroup of Ethiopian Region endemics alone is also consistent with that biogeographic hypothesis (Fig. 10); however, even that minimal conclusion does not follow when *Gehyra*, *Gekko*, and *Hemidactylus* are added to the analysis (Fig. 7). The area cladogram for these data (Fig. 11) suggests a much more complex geographic history, perhaps one involving repeated dispersals between Africa and islands in the western Indian Ocean. That there is likely to have been such a complex history is also documented by those monophyletic taxa which are found on both the mainland and islands in the western Indian Ocean. Clearly, *Lygodactylus* and *Urocotyledon* have widespread African, and Madagascar and Seychelles distributions, respectively. *Phelsuma* must be cited as another example. Although all of the African records of *Phelsuma* occur along the east coast (Loveridge, 1947), and one African species (*P. dubia*) is considered to be conspecific with a Madagascar form, there exists the African endemic *P. parkeri* and the fact that the African *Rhoptropella* is consistently hypothesized to be the sister group to the largely Madagascar *Phelsuma* (Figs. 10-11). A recent phylogenetic study of chamaeleonines (Raxworthy and Nussbaum, in progress) also indicates a more complex history of dispersal between Africa and Madagascar than was previously recognized for that group.

STATUS OF *PARAGEHYRA*

Paragehyra was established by Angel (1929) on the basis of a single specimen, which he identified as a new species, *P. petiti*. Angel (p. 489) compared *Paragehyra* only to Madagascar gekkos that he believed had toe pads confined to the distal portion of the first segment of the toes and free, distal, claw-bearing phalanges, mainly *Gehyra* and *Hemidactylus*. Angel implied that *Paragehyra* is most closely related to *Gehyra* on the basis of shared, undivided toe pad lamellae (divided in *Hemidactylus*). Our research (Fig. 7) suggests this hypothesis is no longer tenable.

Russell (1972) included *Paragehyra* in his *Homopholis* group (*Blaesodactylus*, *Homopholis*, including *Platypholis*, and *Geckolepis*), but with reservations, because the only specimen of *Paragehyra* available was the holotype of *P. petiti*. Our research (Figs. 6-7) does not justify the recognition of a *Homopholis* group (*sensu* Russell, 1972). Further, our results indicate that *Paragehyra* does not exhibit a sister group relationship with any part of that group.

³*Ailuronyx* consists of two species, *A. seychellensis* and *A. trachygaster*. The former is restricted to the Seychelles; the latter is known only from the holotype, which was recorded as having been collected on Madagascar but without more specific location (Brygoo, 1990: 123).

⁴*Ebenavia* is known from Madagascar, Grande Comore and Mayotte (Comoro Islands) and Mauritius (Vinson and Vinson, 1969). Loveridge's (1957) record from Pemba Island, Tanzania, requires confirmation.

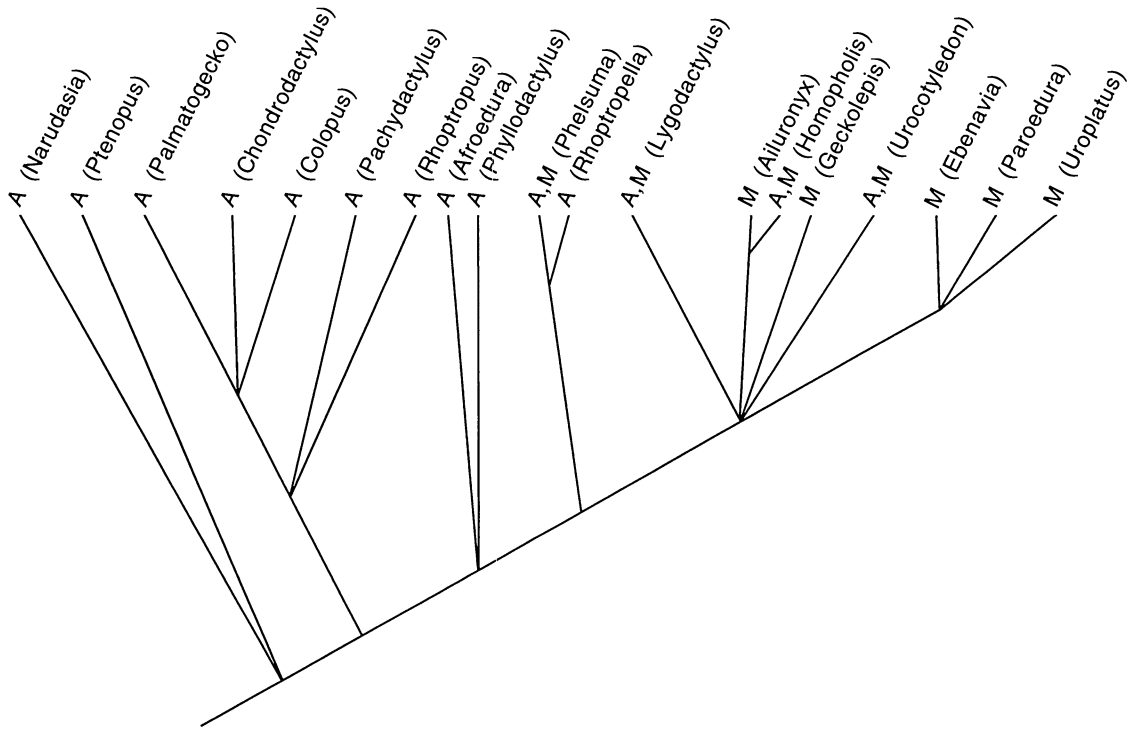


Fig. 8. An area cladogram based on the taxonomic relationships illustrated in Figure 2. Abbreviations: A = Africa (including the Arabian Peninsula); M = Madagascar (including Seychelles and other nearby islands in the western Indian Ocean).

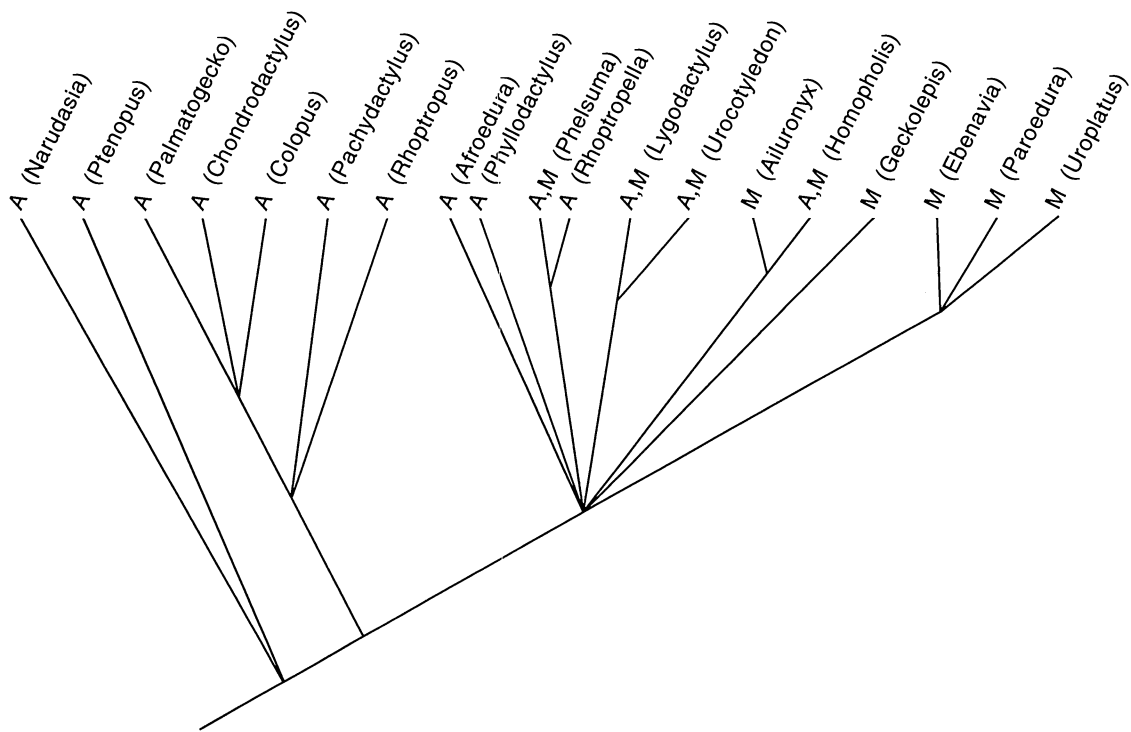


Fig. 9. An area cladogram based on the taxonomic relationships illustrated in Figure 3. Abbreviations: A = Africa (including the Arabian Peninsula); M = Madagascar (including Seychelles and other nearby islands in the Indian Ocean).

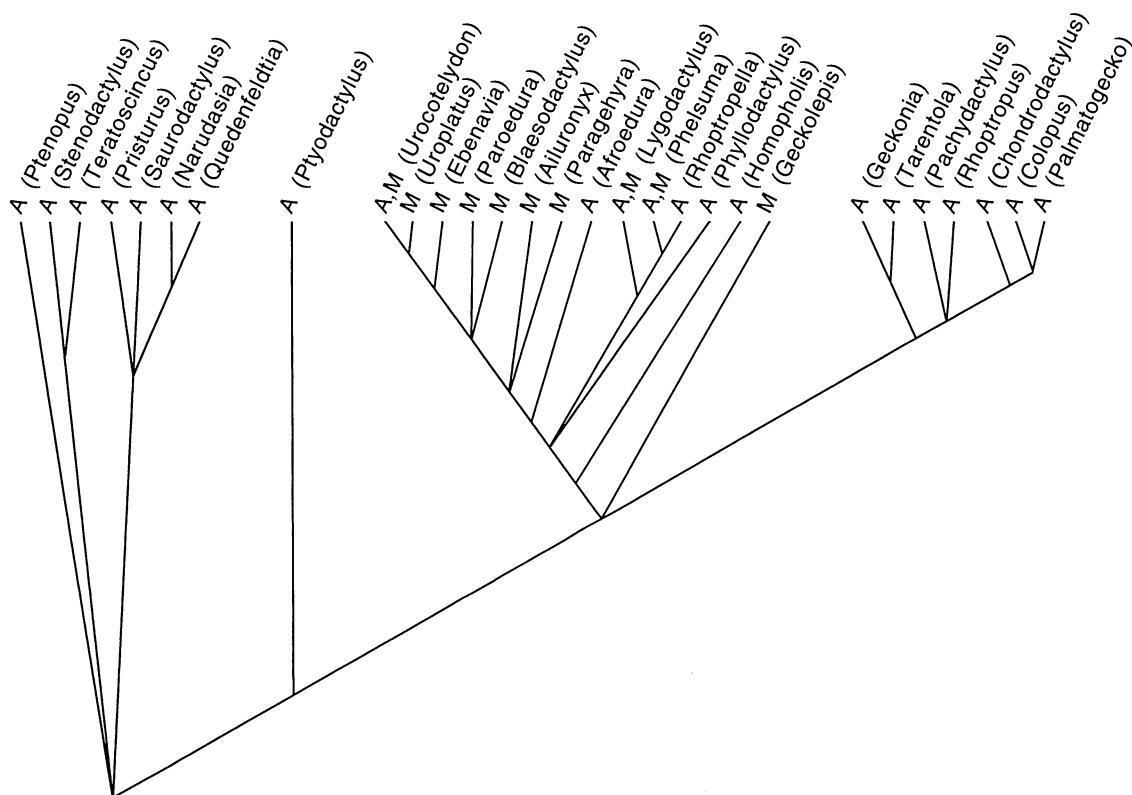


Fig. 10. An area cladogram based on the taxonomic relationships illustrated in Figure 6. Abbreviations: A = Africa (including the Arabian Peninsula); M = Madagascar (including Seychelles and other nearby islands in the Indian Ocean).

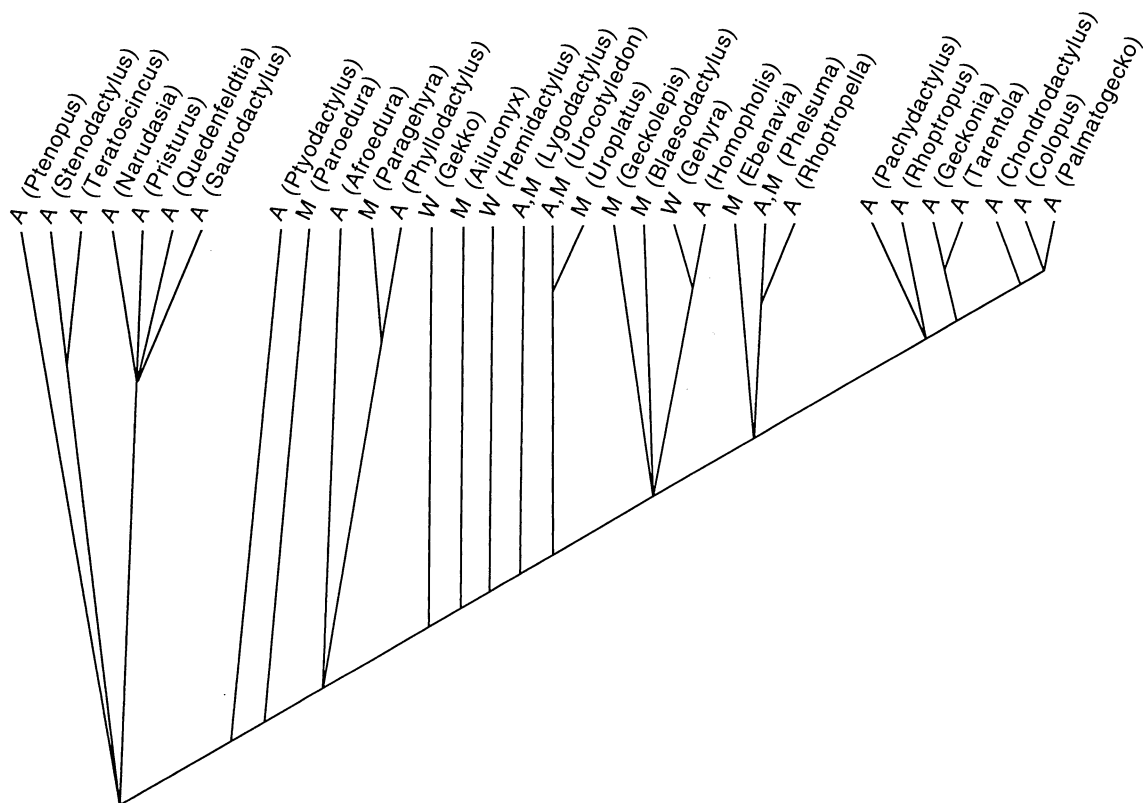


Fig. 11. An area cladogram based on the taxonomic relationships illustrated in Figure 7. Abbreviations: A = Africa (including the Arabian Peninsula); M = Madagascar (including Seychelles and other nearby islands in the Indian Ocean); W = geographically widespread.

The discovery of a second species of *Paragehyra* (*gabriellae*) in southeastern Madagascar represented by abundant material (Nussbaum and Raxworthy, 1994) allows the first opportunity to study the genus in detail. Nussbaum and Raxworthy (1994) identified a single derived character state shared by *P. gabriellae* and *P. petiti*. That state, a single distal, quadrangular lamella on digit I with an asymmetrically positioned (preaxial) claw, does not occur in other Afro-Madagascan gekkos, but it is similar to the condition observed in the New World *Aristelliger*. Our study, aimed at testing the hypotheses of Joger (1985) and Bauer (1990a), does not allow us to explore in detail the possibility of a close relationship between *Aristelliger* and *Paragehyra*, but given the results of our cladistic analyses (Figs. 6-7) a close relationship seems unlikely.

CONCLUSIONS

The need for additional research is obvious. The available character data, largely that of Joger (1985) and Bauer (1990a), are simply too meager and incongruent to support a hypothesis of historical individuality for gekkonids endemic to the Ethiopian Region. Even the sister group to *Paragehyra* cannot be judged unambiguously at this time. All biogeographic scenarios involving islands in the western Indian Ocean and the African mainland must be put on hold until more robust cladistic hypotheses are discovered. Only the African *Pachydactylus* clade identified by Russell (1972), consisting of *Chondrodactylus*, *Colopus*, *Geckonia*, *Pachydactylus*, *Palmatogekko*, *Rhopropus*, and *Tarentola*, appears to be well-founded. Above all else, it is clear that synapomorphies are more important than geographic proximity in recovering the history of gekkos.

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APPENDIX

GEKKOTAN SKELETAL MATERIAL EXAMINED

All of the following skeletal material is housed in the UMMZ. Each catalogue number represents one specimen, unless indicated otherwise in parentheses. Nomenclature follows Kluge (1993a).

Aeluroscalabotes felinus: 127494, 146749, 148898, 185901; *Afroedura pondolia* 127610; *A. transvaalica* 127611, 176624; *Agamura persica* 127612; *Ailuroonyx seychellensis* 127604, 148949, 186002; *Aprasia aurita* 131224; *A. parapulchella* 131157, 131193; *A. pseudopulchella* 131208, 131210; *A. pulchella* 131235; *A. repens* 129978-79, 137573, 173965; *A. striolata* 131176, 131180; *Aristelliger cochraniae* 127605, 172721, 185902; *A. georgeensis* 127606, 148117; *A. praesignis* 127607-609, 172722-23, 185924; *Bavayia cyclura* 127507; *Blaesodactylus boivini* 127614; *Briba brasiliiana* 127615; *Bunopus tuberculatus* 127613; *Calodactylodes aureus* 127616; *Carphodactylus laevis* 127508; *Chondrodactylus angulifer* 127617, 190381-82; *Christinus marmoratus* 127735-40, 173744-48; *Cnemaspis boulengerii* 127618; *C. kandiana* 127619; *C. kendallii* 127620; *C. quattuorseriata* 127621; *C. wynadensis* 127622; *Coleodactylus amazonicus* 127803 (2); *C. brachystoma* 144467; *C. meridionalis* 151498-99; *Coleonyx brevis* 127495 (6), 127496 (9), 176625, 185970; *C. elegans* 127497, 148118, 148901, 185981-85; *C. mitratus* 148902-903; *C. reticulatus* 132007; *C. switaki* 182010; *C. variegatus* 127498-502, 127514 (2), 127515-17, 127518 (4), 127519 (12), 127520 (3), 127521 (5), 127522, 148119, 176626; *Colopus wahlbergii* 127623; *Cosymbotus platyurus* 127624, 176627, 186003, 200294; *Crenodactylus ocellatus* 127509 (2), 127510 (3), 127511-13, 127523; *Crossobamon eversmanni* 127625; *C. orientalis* 127626 (2); *Cyrtodactylus annulatus* 127627; *C. louisianensis* 127628; *C. marmoratus* 127629; *C. peguensis* 176628; *Cyrtopodion kachhensis* 127631; *C. scaber* 127630; *Delma australis* 84309; *D. fraseri* 137576; *D. impar* 129982-83; *D. inornata* 131155, 131161; *D. nasuta* 130001, 131206; *D. tincta* 131237; *D. torquata* 137230; *Diplodactylus alboguttatus* 127524 (4), 127525; *D. byrnei* 127526; *D. conspicillatus* 127533-34; *D. damaeus* 127535 (12), 127536; *D. granariensis* 127563-65, 173728-29; *D. mairi* 127537-38, 127539 (2); *D. pulcher* 127542-44, 173730-32; *D. savagei* 127545; *D. squarrosus* 127547; *D. steindachneri* 127546; *D. stenodactylus* 127551-52, 127553 (6), 127554; *D. taenicauda* 127560 (3), 127561; *D. tessellatus* 127557-59; *D. vittatus* 127567; *D. sp.* 127562 (7), 127566; *Ebenavia inunguis* 127634; *Eublepharis hardwickii* 127503; *E. macularius* 127504-506, 128566, 148897, 172893-96, 176629 (2), 179332, 180354, 180389, 180452, 181812, 182130, 182273, 182281, 182446-47, 182519, 183507, 189455, 190401; *Geckoella nebulosus* 127632; *Geckolepis maculata* 127635; *Geckonia chazaliae* 127636; *Gehyra australis* 127637-38; *G. mutilata* 127639-42, 174615-20, 176630-32, 187470-71; *G. oceanica* 127643-44, 185913; *G. punctata* 127654-55, 127656 (2), 127657-58, 127659 (2), 127660 (4), 127661-63, 187472, 187476-80; *G. variegata* 127645-50, 127651 (3), 127652 (2), 127653, 173733-36; *Gekko geko* 127265, 127664, 128568, 148770-72, 155328-31, 176652, 183624, 187490-94; *G. tuberculatus* 176632, 187516; *G. vittatus* 127665, 127666 (2); *G. sp.* 148769; *Gonatodes albogularis* 127790-94, 148120, 151500, 172593-94, 183931, 185925; *G. annularis* 53894; *G. antillensis* 57325-26, 127795-96, 151501; *G. atricucullaris* 127797 (2), 127798; *G. humeralis* 127799-800, 128141; *G. ocellatus* 127801; *G. taniae* 151502; *G. vittatus* 54687, 54693, 127802 (2); *Goniurosaurus kuroiwuae* 182011; *Gymnodactylus gekoides* 127667; *Hemidactylus brookii* 127668 (2), 127669 (5), 127670-71, 128138-40, 149381 (10), 149382 (30), 176633 (2), 176634 (3); *H. flaviviridis* 127672; *H. frenatus* 127673 (3), 127674 (5), 127675, 127676 (2), 172595; *H. garnotii* 127677, 128567, 128834 (4); *H. giganteus* 127678; *H. karenorum* 127679 (4), 174614; *H. leschenaultii* 127680; *H. mabouia* 148773, 183508, 200176-78; *H. persicus* 127681; *H. triedrus* 128132-37, 142537; *H. turcicus* 127682, 127685, 148774; *Hemiphyllodactylus typus* 127683, 127684 (2), 176635; *Hemitheconyx caudicinctus* 132006, 148900, 190409; *Heteronotia binoei* 127686-90, 173737-42; *H. spelea* 127691; *Holodactylus africanus* 148899; *Homonota darwini* 127692 (2); *H.*

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