Syst. Biol. 49(2):233–256, 2000

Evaluating Trans-Tethys Migration: An Example Using Acrodont Lizard Phylogenetics

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Abstract.—A phylogenetic tree for acrodont lizards (Chamaeleonidae and Agamidae) is established based on 1434 bases (1041 informative) of aligned DNA positions from a 1685–1778 base pair region of the mitochondrial genome. Sequences from three protein-coding genes (*ND1, ND2,* and *COI*) are combined with sequences from eight intervening tRNA genes for samples of 70 acrodont taxa and two outgroups. Parsimony analysis of nucleotide sequences identifies eight major clades in the Acrodonta. Most agamid lizards are placed into three distinct clades. One clade is composed of all taxa occurring in Australia and New Guinea; *Physignathus cocincinus* from Southeast Asia is the sister taxon to the Australia–New Guinea clade. A second clade is composed of taxa occurring from Tibet and the Indian Subcontinent east through South and East Asia. A third clade is composed of taxa occurring from Africa east through Arabia and West Asia to Tibet and the Indian Subcontinent. These three clades contain all agamid lizards except *Uromastyx, Leiolepis,* and *Hydrosaurus,* which represent three additional clades of the Agamidae. The Chamaeleonidae forms another clade weakly supported as the sister taxon to the Agamidae. All eight clades of the Acrodonta contain members occurring on land masses derived from Gondwanaland. A hypothesis of agamid lizards rafting with Gondwanan plates is examined statistically. This hypothesis suggests that the African/West Asian clade is of African or Indian origin, and the South Asian clade is either of Indian or Southeast Asian origin. The shortest tree suggests a possible African origin for the former and an Indian origin for the latter, but this result is not statistically robust. The Australia–New Guinea clade rafted with the Australia–New Guinea plate and forms the sister group to a Southeast Asian taxon that occurs on plates that broke from northern Australia–New Guinea. Other acrodont taxa are inferred to be associated with the plates of Afro-Arabia and Madagascar (Chamaeleonidae), India (*Uromastyx*), or southeast Asia (*Hydrosaurus* and *Leiolepis*). Introduction of different biotic elements to Asia by way of separate Gondwanan plates may be a major theme of Asian biogeography. Three historical events may be responsible for the sharp faunal barrier between Southeast Asia and Australia–New Guinea, known as Wallace's line: (1) primary vicariance caused by plate separations; (2) secondary contact of Southeast Asian plates with Eurasia, leading to dispersal from Eurasia into Southeast Asia, and (3) dispersal of the Indian fauna (after collision of that subcontinent) to Southeast Asia. Acrodont lizards show the first and third of these biogeographic patterns and anguid lizards exhibit the second pattern. Modern faunal diversity may be influenced primarily by historical events such as tectonic collisions and land bridge connections, which are expected to promote episodic turnover of continental faunas by introducing new faunal elements into an area. Repeated tectonic collisions may be one of the most important phenomena promoting continental biodiversity. Phylogenetics is a powerful method for investigating these processes. {Acrodonta; Agamidae; Chamaeleonidae; Iguania; mitochondrial DNA; phylogenetics; plate tectonics; Reptilia; Sauria.}

Iguanian lizards form two monophyletic groups, the Acrodonta and Iguanidae, and are suggested to have had their origin in Gondwanaland during the Jurassic (Macey et al., 1997c; Moody, 1980). Whereas the Iguanidae occur in the New World, Madagascar, and Fiji, the Acrodonta are currently restricted to the Old World. Acrodont lizards, taxonomically recognized as the families Chamaeleonidae and Agamidae, occur mainly on land masses of Gondwanan origin (Madagascar, Seychelle Islands, Africa, Arabia, India, Southeast Asia, and Australia) but also occur in other re-

gions of Asia that are composed of Laurasian plates (Fig. 1).

The successive migration of land masses across the Tethys Sea from Gondwanaland to Laurasia provides an intriguing biogeographic situation. Taxa in Asia may have different histories based on the accretionary events of Gondwanan plates. Here, a study is conducted on acrodont lizards, a Gondwanan group, to illustrate how different Gondwanan origins of Asian species may be identified phylogenetically.

Acrodont lizards inhabit the following Gondwanan plates adjacent to or part of Asia (Fig. 1): Africa–Arabia, which connected with Asia 18 MYBP; India, which connected with Asia 50 MYBP; and Southeast Asia, which connected with Asia in three main accretionary events 120 MYBP or earlier (Indochinese blocks; Metcalfe, 1996; Richter and Fuller, 1996), 65 MYBP (small terranes to the south of Indochina; Metcalfe, 1996), and 10 MYBP (small island terranes as far north as Sulawesi; Hall, 1996). Acrodont lizards also occur in the following Gondwanan plates, which are not adjacent to Asia: Australia–New Guinea, Madagascar, and the Seychelle Islands. Other regions of Asia such as Turkey, Iran, Afghanistan, Tibet, and eastern China are composed of numerous blocks that accreted to Asia earlier, preceding the formation of the Acrodonta (Dercourt et al., 1986; Sengör, 1984; Sengör et al., 1988; Macey et al., 1997c); these regions make up the southern margin of the growing northern continental area termed Laurasia.

Taxa associated with a particular Gondwanan plate are expected to have deep divergences (endemic clade or basal paraphyletic group) associated with that Gondwanan plate and nested taxa in adja-

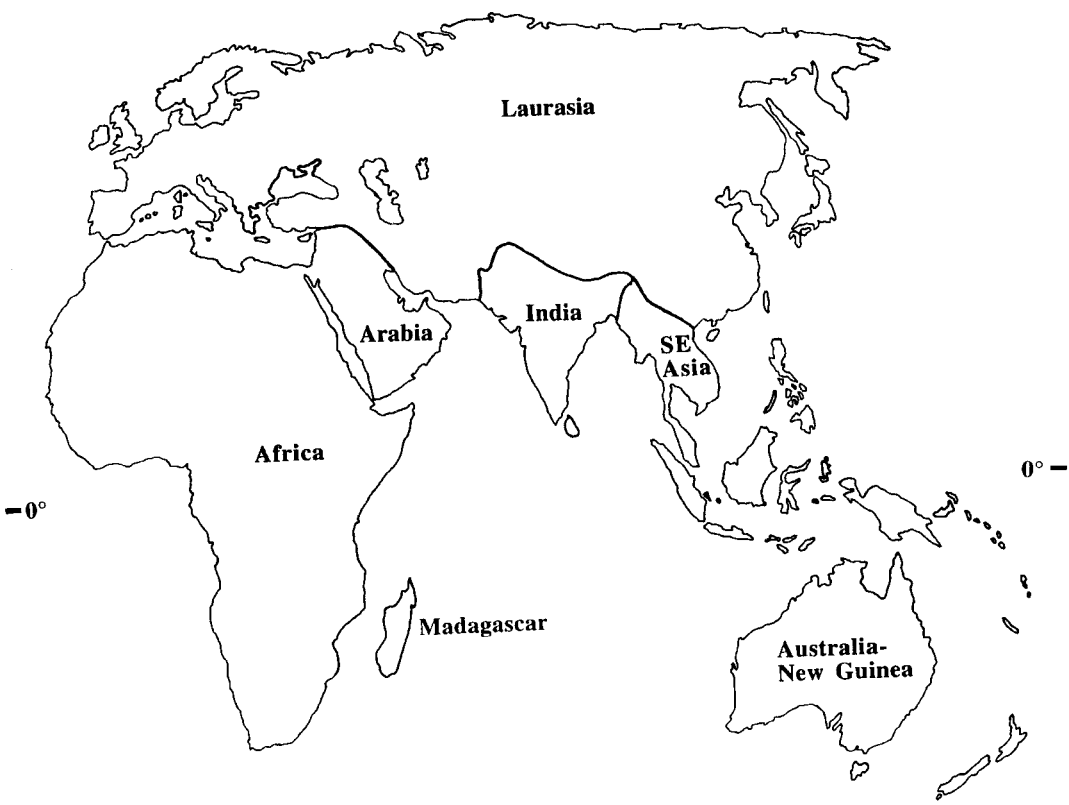


FIGURE 1. Major tectonic regions inhabited by the Acrodonta. The Eurasian portion of Laurasia is depicted as northern land masses that conglomerated prior to the collisions of Southeast Asia, India, and Arabia. The region shown as Southeast Asia is actually several plates. Africa and Arabia were previously connected, and Australia and New Guinea constitute a single plate. The small Gondwanan fragments of the Seychelle Islands (not shown) to the northeast of Madagascar are inhabited by species of the Chamaeleonidae not sampled for this study.

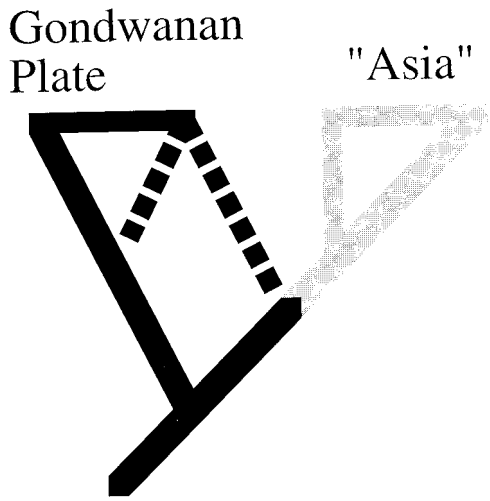


FIGURE 2. Expected phylogenetic topology for taxa originating on a Gondwanan plate. Taxa that have rafted with a particular Gondwanan plate are expected either to have deep divergences associated with that Gondwanan plate with nested taxa in adjacent regions of Asia, or at least to show a sister-group relationship between taxa on a particular Gondwanan plate and taxa in adjacent regions of Asia.

cent regions of Asia, or at least to show a sister-group relationship between taxa on a particular Gondwanan plate and taxa in adjacent regions of Asia (Fig. 2).

To assess phylogenetic relationships of acrodont lizards, we sequenced a 1685–1778 base pair segment of mitochondrial DNA from 70 ingroup species and two outgroup species (12 of these sequences were reported previously by Macey et al., 1997a, 1997c, 1998a). Our study focuses on the Agamidae. Our sampling represents 21% of the agamid species (68 of ~320) and 64% of the agamid genera (36 of 56); in addition, we include two representatives of the Chamaeleonidae. The region sequenced extends from the protein-coding gene *ND1* (subunit one of NADH dehydrogenase) through the genes encoding $tRNA^{Gln}$, $tRNA^{Ile}$, $tRNA^{Met}$, ND2, $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, to the protein-coding gene *COI* (subunit I of cytochrome *c* oxidase), (see Macey et al., 2000). Monophyly of the Acrodonta is extremely well supported by morphology (Frost and Etheridge, 1989) and mitochondrial DNA sequences (Macey et al. 1997c), including the unambiguous presence of a derived mitochondrial gene order (Macey et al., 1997a, 1997c, 1998a), a character that is highly unlikely to show parallelisms or reversals (Macey et al., 1997a, 2000). Outgroup structure is based on the phylogenetic hypothesis of Macey et al. (1997c). Two iguanid outgroups are used, *Basiliscus plumifrons* from the New World and *Oplurus cuvieri* from the Old World. These taxa are selected to cover a broad level of divergence within the acrodonts' sister taxon, the Iguanidae (Macey et al., 1997c).

MATERIALS AND METHODS

DNA Extraction and Sequencing

See the Appendix for museum numbers and localities for voucher specimens from which DNA was extracted and for the GenBank accession numbers.

Genomic DNA was extracted from liver by using the Qiagen QIAamp tissue kit. Genomic DNA was amplified by using denaturation at 94°C for 35 sec, annealing at 50–53°C for 35 sec, and extension at 70°C for 150 sec, with 4 sec added to the extension per cycle, for 30 cycles. Negative controls were run for all amplifications. Amplified products were purified on 2.5% Nusieve GTG agarose gels and reamplified under similar conditions. Reamplified double-stranded products were purified on 2.5% acrylamide gels (Maniatis et al., 1982). Template DNA was eluted from acrylamide passively over 3 days with Maniatis elution buffer (Maniatis et al., 1982). Cycle-sequencing reactions were run with the Promega fmol DNA sequencing system, using denaturation at 95°C for 35 sec, annealing at 45–60°C for 35 sec, and extension at 70°C for 1 min, for 30 cycles. Sequencing reactions were run on Long Ranger sequencing gels for 5–12 hr at 38–40°C.

Amplifications from genomic DNA were done with different primer combinations (Table 1). Most samples were amplified with L3878, L3881, L3887, L4160, or L4178b in combination with H4980. In addition, most samples were amplified with L4437 in combination with H5934. Other primers used for amplifications were as follows: L3002 in combination with H4419a, H4419b, H4419c, or H4629; L4160, L4178a, L4178b, or L4831 in combination with H5934; L4437 in combination with H5617a or H5617b;

TABLE 1. New primers used in this study. Primers are designated by their 3′ends which correspond to the position in the human mitochondrial genome (Anderson et al., 1981) by convention. H and L designate primers that extend the heavy and light strands, respectively. Positions with mixed bases are labeled with standard one-letter codes: R = G or A, Y = T or C, K = G or T, and N = any base.

Human position	Gene	Sequence
H4419b	$tRNA^{Met}$	5'-GGYATGGGCCCAACTGCTT-3'
H4419c	$tRNA^{Met}$	5'-GGTATGGGCCCAAKAGCTT-3'
H4629	ND2	5'-AAGTATTTTGTTGCGGCTTC-3'
L4882a	ND2	5'-TGACAAAAACTAGCCCC-3'
L4882b	ND2	5'-TGACAAAAAATTGCNCC-3'
L5550	$tRNA^{Trp}$	5'-AACCARAGGCCTTCAAAGC-3'
H5689	$tRNA^{Asn}$	5'-TTTAGGTAAATAGCTGTTAACTA-3'

and L5550 in combination with H6564. L3002 is from Macey et al. (1997a) and H6564 is from Macey et al. (1998a); these primers were not used for sequencing. Both strands were sequenced by using the primers listed in Table 1 and L3878 (Macey et al., 1998b), L3881, L3887, L4178a, L4178b, H4419a, L4645, L4831, H4980, L5002a, H5540, L5556, H5617a, H5617b, L5638a, L5638b, H5934, H5937 (all from Macey et al., 1997a), L4160 (Kumazawa and Nishida, 1993), L4437 (Macey et al., 1997c), and L5002b (Schulte et al., 1998).

Phylogenetic Analysis

Alignment of DNA sequences for phylogenetic inference in acrodont lizards was particularly difficult because of complex changes in major structural features of the mitochondrial genome (Macey et al., 2000). DNA sequences encoding part of ND1, all of ND2, and part of COI were aligned by amino acids with use of MacClade (Maddison and Maddison, 1992). Alignments of sequences encoding tRNAs were constructed manually, based on secondary structural models (Kumazawa and Nishida, 1993; Macey and Verma, 1997). Secondary structures of tRNAs were inferred from primary structures of the corresponding tRNA genes by using these models. Unalignable sequences from the three length-variable loop regions (D, T, and variable loops) of encoded tRNAs and some length-variable intergenic regions were excluded from phylogenetic analyses (see Results and supplemental information on the *Systematic Biology* Website: http:// www.utexas.edu/depts/systbiol).

Phylogenetic trees were estimated by PAUP* beta version 4.0b1 (Swofford, 1998), using 100 heuristic searches with random addition of sequences. Bootstrap resampling was applied to assess support for individual nodes by using 500 bootstrap replicates with 25 random additions per replicate. Decay indices (= "branch support" of Bremer, 1994) were calculated for all internal branches of the trees. To calculate decay indices, a phylogenetic topology containing the single node in question was constructed with MacClade (Maddison and Maddison, 1992) and analyzed as a constraint in PAUP* beta version 4.0b1 (Swofford, 1998) with 100 heuristic searches featuring random addition of sequences. These searches retained trees that violated the imposed constraint. The decay index was then tabulated as the difference in length between the shortest tree violating the constraint and the overall shortest tree.

The Wilcoxon signed-ranks test (Templeton, 1983; Felsenstein, 1985) was used to examine statistical significance of the overall equally shortest trees relative to alternative hypotheses. This test asks whether the most-parsimonious tree is significantly shorter than an alternative or whether their differences in length can be attributed to chance alone (Larson, 1998). Wilcoxon signed-ranks tests were conducted both as one and two-tailed tests. Felsenstein (1985) showed that one-tailed probabilities are close to the exact probabilities for this test but are not always conservative, whereas

the two-tailed test is always conservative. Tests were conducted with PAUP* beta version 4.0b1 (Swofford, 1998), which incorporates a correction for tied ranks.

Alternative phylogenetic hypotheses were tested by using the most-parsimonious phylogenetic topologies that were compatible with them. To find the most-parsimonious tree(s) compatible with a particular phylogenetic hypothesis, phylogenetic topologies were constructed by using MacClade (Maddison and Maddison, 1992) and analyzed as constraints in PAUP* beta version 4.0b1 (Swofford, 1998) with 100 heuristic searches and random addition of sequences.

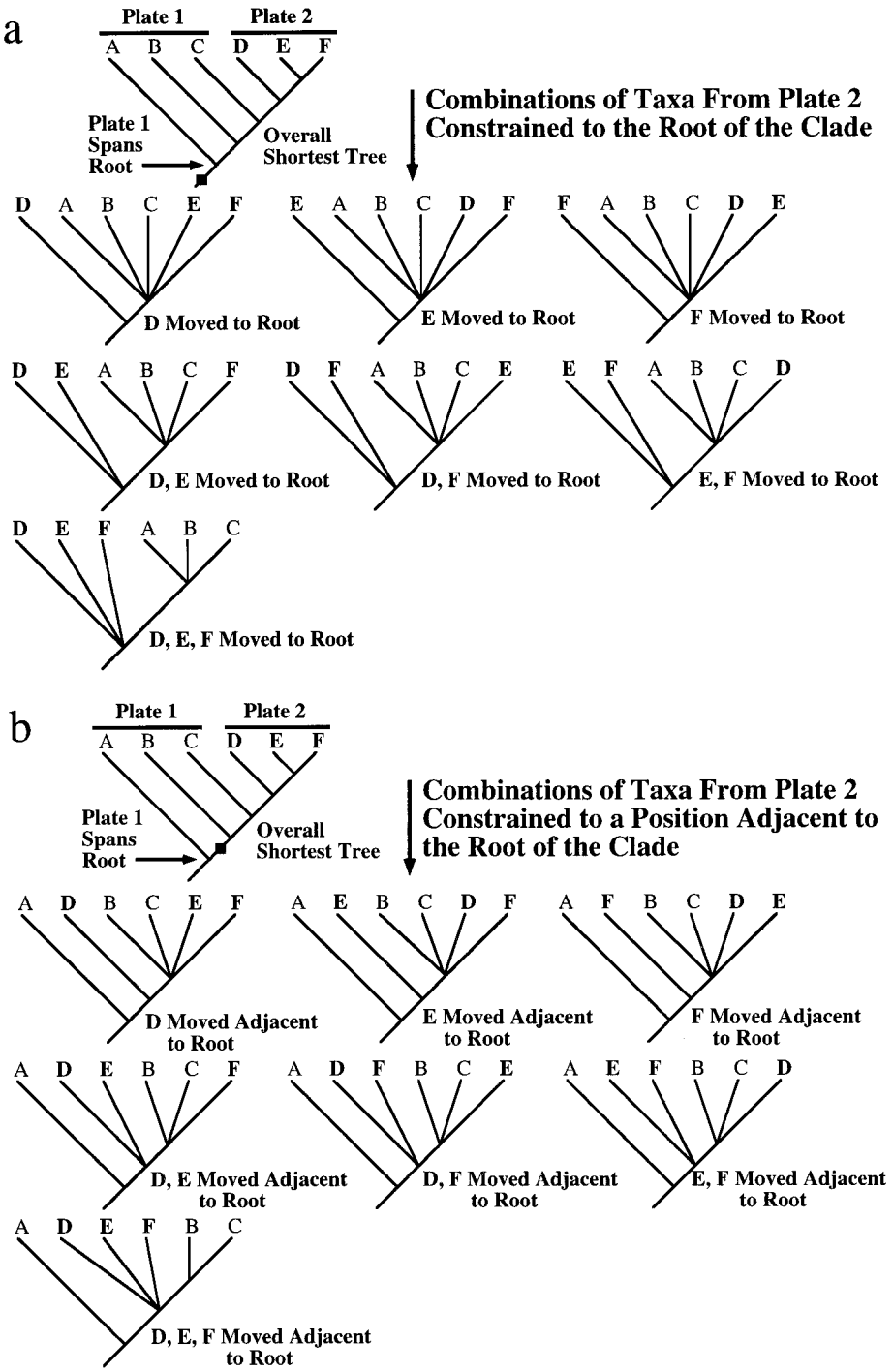
Evaluating the Tectonic Origin of Faunal Elements on Gondwanan Plates

We used the following procedure to identify an area cladogram and test it against alternatives with the Wilcoxon signed-ranks test (Templeton, 1983; Felsenstein, 1985).

1. Major clades. Identify clades that are potentially well supported by using bootstrap values and decay indices. Clades that are supported by at least 95% bootstrap value and a corresponding decay index of at least four (Felsenstein, 1985) should be considered potentially well supported.
2. Area cladogram. For each major clade revealed in step 1, identify association of each included species with one of the Gondwanan plates or with Laurasia. This step is equivalent to constructing an area cladogram by using tectonic plates as areas.
3. Monophyly tests. For each major clade, find the shortest alternative tree that disrupts the clade and use the Wilcoxon signed-ranks test (Templeton, 1983; Felsenstein, 1985) to determine whether the alternative tree is significantly less parsimonious than the overall most-parsimonious tree. Major clades that are supported statistically are examined for historical association with particular Gondwanan plates (see below).
4. Ancestral areas of clades. Identify the ancestral area for each major clade from steps 1 and 3. If all taxa in a clade are associated with the same tectonic plate, then that plate is considered the ancestral area of the clade. If more than one tectonic plate appears within a clade, the ancestral area is inferred to be the plate that spans the deepest phylogenetic divergence within the clade, provided that the shortest alternative topologies incompatible with this inference can be rejected statistically by the Wilcoxon signed-ranks test (Templeton, 1983; Felsenstein, 1985). If no single tectonic region spans the deepest divergence within a clade, the ancestral area cannot be identified unambiguously.
5. Statistical tests. Alternative hypotheses for the statistical tests identified in the previous paragraph are constructed as follows for each clade in which an ancestral area can be inferred. First, an alternative tree is found by constraining any species or group from a tectonic region other than the inferred ancestral region to be the sister taxon to the remaining species in the clade. This operation may produce a tree in which no single tectonic region spans the root of the clade under investigation. If this topology cannot be rejected as significantly less parsimonious than the overall shortest tree, the ancestral area for the clade cannot be inferred unambiguously. If this alternative topology is rejected, additional topologies that challenge the initial interpretation of ancestral area must be tested against the overall shortest tree.

Two approaches are used to identify the shortest alternative topologies for which species from an alternative tectonic region occur on both sides of the root within the clade under investigation, or in which no single tectonic region has species located on both sides of the root. These trees are then tested against the overall shortest tree to see if they are significantly less parsimonious (Fig. 3). The first approach examines all possible constraint trees (Fig. 3) that permit an alternative tectonic plate to be inferred as an equally or more likely region of origin for a clade under investigation. This approach is impractical if the number of taxa that must be constrained to specify alternative hypotheses exceeds six. Alternatively,

approximate constraints can be used. This approach differs from the more thorough approach by keeping intact the subgroups that are well supported in the overall shortest tree by high bootstrap values and decay indices. Because disruption of such subgroups would add many additional steps to the tree, this approach should be as accurate as the more-laborious approach, in which all different combinations of species



from an alternative tectonic plate are considered individually. Alternative trees are then found by using constraint trees as described in Figure 3.

RESULTS

DNA Sequences

The aligned sequences are deposited on the *Systematic Biology* Website. All phylogenetic topologies resulting from this study are deposited at the end of the NEXUS file.

Most protein-coding regions are alignable, but some regions are excluded from phylogenetic analyses (see the *Systematic Biology* Website for details of excluded regions). In the *ND2* gene, gaps are placed in the *Ctenophorus decresii* sequence at positions 632–634 and in the two *Leiolepis* sequences at positions 1109–1111 because of deleted amino-acid positions. Gaps are placed in all sequences (except the three *Agama* sequences) at positions 1184–1186 because of an inserted amino-acid position. In the *COI* gene, gaps are placed in the third amino-acid position for *Basiliscus, Oplurus,* both *Chamaeleo, Uromastyx,* and both *Leiolepis* (positions 1939–1941). The fourth amino-acid position is absent from *Acanthosaura capra,* and gaps are placed at positions 1942–1944.

Genes for $tRNA^{Ile}$ and $tRNA^{Gln}$ (positions 105–271) are switched in order in the two iguanid outgroup taxa to align with the acrodont ingroup taxa (see Macey et al., 1997c, for the actual gene order). The $tRNA^{Asn}$, $tRNA^{Cys}$, and $tRNA^{Tyr}$ genes encode tRNAs with unusual secondary structures in some taxa, which makes assessment of homologous sites difficult (Macey et al., 2000). The $tRNA^{Asn}$ gene encodes a tRNA with an unusual secondary structure in *Acanthosaura capra,* where three bases separate the D- and AA-stems instead of the expected two bases (Macey et al., 2000). This extra base appears to have resulted from an inserted base in the AA-stem at position 1739, and a gap was placed in all other taxa at this position. In addition, the $tRNA^{Asn}$ gene of *Physignathus cocincinus,* of all taxa sampled from Australia and New Guinea, and of the genus *Ceratophora* encodes a tRNA that has two bases between the D- and AC-stems instead of the expected single base (Macey et al., 2000). Therefore, a gap is placed in all other taxa at position 1716 between the D- and AC-stems.

In the $tRNA^{Tyr}$ gene, both *Acanthosaura* species sampled have a gene that encodes a tRNA with a truncated T-stem of three pairs instead of the usual five pairs (Macey et al., 2000). In addition, standard tRNAs have at least 11 bases in the T-stem and loop region. *Acanthosaura capra* has only 10 bases in the T-stem and loop region, and *Acanthosaura lepidogastra* has only nine bases. It is unclear which unpaired bases are deleted. Hence, unpaired bases of the T-loop for this tRNA gene are placed in the loop region excluded from phylogenetic analyses (positions 1902–1908).

Sequences range in length from 1685 to 1778 bases. The phylogenetic analyses are conducted by using 1434 alignable positions. The regions excluded from phylogenetic analyses correspond to 19% of the longest sequence (*Sitana ponticeriana*).

Several observations suggest that the DNA sequences reported are from the mito-

FIGURE 3. Constraint trees used to find the shortest alternative tree in which the inferred historical association of a clade with a particular tectonic plate is either different from the shortest overall tree or ambiguous. In this example, six taxa (taxa A–F) collectively occupy two different tectonic regions. In the overall shortest tree, the clade is inferred to have originated on plate 1 because only species from this plate occur on both sides of the root of the clade. To identify the shortest alternative tree compatible with the historical origin of the clade in plate 2, constraint trees are made with every combination of species from the alternative tectonic region (plate 2) moved to the root (a) or adjacent to the root (b) of the clade as shown by a box on the overall shortest tree. Assignment of an ancestral area to a clade is considered not strongly supported if any alternative tree cannot be rejected statistically. This example has seven possibilities (2^3-1), three combinations of one, three of two, and one of three species moved for each part a and b. As more taxa are considered, the number of different combinations of taxa that must be constrained rapidly increases. The number of constraint trees required is 2^n-1, where n is the number of taxa occurring on the alternative tectonic plate. An approximate procedure that is likely to produce the same results is to move well-supported groups as a unit. Groupings of taxa that receive good support from high decay indices and bootstrap values cost numerous steps to disrupt, and the shortest alternative tree is therefore expected to retain these groupings.

TABLE 2. Distribution of parsimony informative and variable positions (see the *Systematic Biology* Website for more detail of each genic region).

	Protein-coding codon positions			tRNA[a]			
Total	1st	2nd	3rd	Stem	Nonstem	Noncoding region[b]	All aligned sequence
Informative sites	248	195	324	213	60	1	1,041
Variable Sites	270	222	327	247	70	1	1,137

[a]Not including excluded positions, i.e., all of the $tRNA^{Cys}$ gene except the AC-stem and loop regions.
[b]One noncoding base position is informative and variable and is between the $tRNA^{Tyr}$ and COI genes.

chondrial genome and are not nuclear-integrated copies of mitochondrial genes (see Zhang and Hewitt, 1996). Protein-coding genes do not have premature stop codons, and tRNA genes appear to code for tRNAs with stable secondary structures, indicating functional genes. Strand bias further supports our conclusion that the 60 newly reported DNA sequences are from the mitochondrial genome. These sequences show strong strand bias against guanine on the light strand (G = 10.5–14.4%, A = 31.7–39.1%, T = 21.8–26.7%, and C = 25.2–32.9%), which is characteristic of the mitochondrial genome but not the nuclear genome. The 12 previously reported sequences analyzed here all show similar functional characteristics and strand bias (Macey et al., 1997a, 1997c, 1998a).

Genic Variation

Phylogenetically informative variation occurs among the three protein-coding genes, eight tRNA-coding genes, and one noncoding position (Table 2 and the *Systematic Biology* Website). Most of the variation and phylogenetically informative sites are from protein-coding regions (74% of informative sites). Interestingly, phylogenetically informative sites are in nearly equal proportion between first, second, and third codon positions and tRNA-encoding positions (24%, 19%, 31%, and 26% of informative sites, respectively). All eight tRNA genes contain phylogenetically informative positions in both stem and nonstem regions (20% and 6% of informative sites, respectively), and each protein-coding gene has phylogenetically informative sites in first-, second-, and third-codon positions. This observation suggests that no single class of characters is dominating the phylogenetic analysis.

Phylogenetic Relationships

Three equally most-parsimonious trees are produced from analysis of the 1434 aligned DNA sequences containing 1041 parsimony-informative base positions (Figs. 4–7 and Table 2; see also the *Systematic Biology* Website). Monophyly of the Acrodonta is well supported (bootstrap 100%, decay index 79). Within the Acrodonta, eight groups are distinguished: (1) *Chamaeleo,* (2) *Uromastyx,* (3) *Leiolepis,* (4) *Physignathus cocincinus,* (5) all Australian and New Guinean taxa, (6) *Hydrosaurus,* (7) a South Asian clade, and (8) an African–West Asian clade. Only single representatives of *Physignathus cocincinus Uromastyx* and *Hydrosaurus* were sampled, so monophyly was not assessed for these taxa.

Support for monophyly of the other five major groups is considerable (Fig. 4). The two species of *Chamaeleo* sampled form a well-supported clade (bootstrap 100%, decay index 64). The two species of *Leiolepis* sampled also form a clade that receives a high degree of support (bootstrap 100%, decay index 73). *Physignathus cocincinus* and all taxa sampled from Australia and New Guinea form a monophyletic group that receives strong support (bootstrap 100%, decay index 42), with *Physignathus cocincinus* being the sister taxon to a well-supported clade containing all taxa from Australia and New Guinea (bootstrap 95%, decay index 15). Monophyly of a group containing all South Asian taxa except *Leiolepis, Hydrosaurus,* and *Physignathus cocincinus* is well supported (bootstrap 100%, decay index 24). All taxa occurring in Africa and

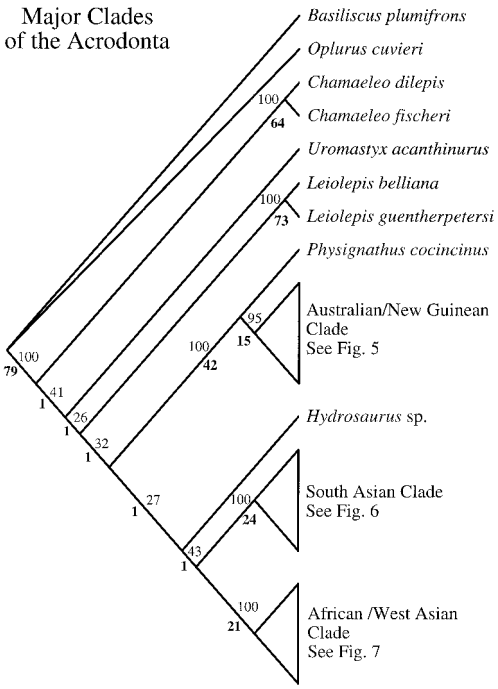


FIGURE 4. Phylogenetic relationships among the major clades of the Acrodonta. This figure depicts the more basal phylogenetic arrangements found in the strict consensus of the three equally most-parsimonious trees derived from analysis of the 1,041 informative DNA sequence characters. The tree (including Figs. 5, 6, and 7) has a length of 11,877 steps and a consistency index of 0.195. Bootstrap values are presented above the branches, and decay indices are shown in bold below the branches. Eight major branches can be recognized: (1) *Chamaeleo,* (2) *Uromastyx,* (3) *Leiolepis,* (4) *Physignathus cocincinus,* (5) an Australian–New Guinean clade, (6) *Hydrosaurus,* (7) a South Asian clade, and (8) an African–West Asian clade. In each case, when monophyly can be demonstrated (all except *Physignathus cocincinus, Uromastyx,* and *Hydrosaurus,* in which single representatives were sampled) considerable support is indicated from both bootstrap values of at least 95% and decay indices of 15 or higher. Among the major lineages, only the sister-group relationship between (4) *Physignathus cocincinus* and (5) an Australian–New Guinean clade is well resolved, with a bootstrap value of 100% and a decay index of 42.

West Asia (except *Chamaeleo* and *Uromastyx*) form a clade with substantial support (bootstrap 100%, decay index 21). There is little support for phylogenetic relationships among most major groups of the Acrodonta. The phylogenetic analysis places the Chamaeleonidae as the sister taxon to the Agamidae (decay index 1). Decay indices of 1 are reported also for nodes relating six major agamid lineages.

Phylogenetic resolution among Australian and New Guinean taxa is poor, with only a few exceptions (Fig. 5). *Amphibolurus* and *Chlamydosaurus* are sister taxa (bootstrap 98%, decay index 14), as are *Ctenophorus* and *Rankinia* (bootstrap 98%, decay index 13). A monophyletic grouping of *Caimanops, Diporiphora, Pogona,* and *Tympanocryptis* receives weak support (bootstrap 71%, decay index 7); however, *Caimanops* and *Diporiphora* are sister taxa (bootstrap 89%, decay index 10), and *Pogona* and *Tympanocryptis* also appear to be sister taxa (bootstrap 75%, decay index 8).

Within the South Asian agamid clade (Fig. 6), the genus *Draco,* wide-ranging on the Indian and Southeast Asian tectonic regions, is the sister taxon (bootstrap 99%, decay index 14) to a clade containing the Himalayan *Japalura variegata* and *Japalura tricarinata* of the Indian Subcontinent (boot-

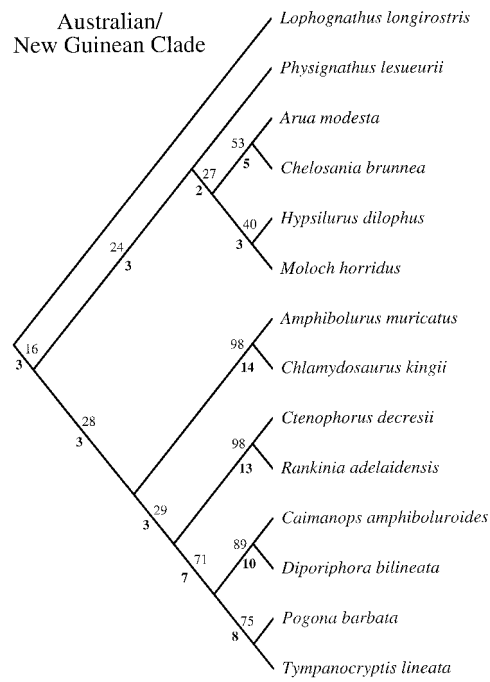


FIGURE 5. Phylogenetic relationships within the Australian–New Guinean clade of the Acrodonta. Bootstrap values are presented above branches, and decay indices are shown in bold below branches. Taxa occurring in New Guinea (*Arua* and *Hypsilurus*) appear not to form a monophyletic group with respect to Australian taxa.

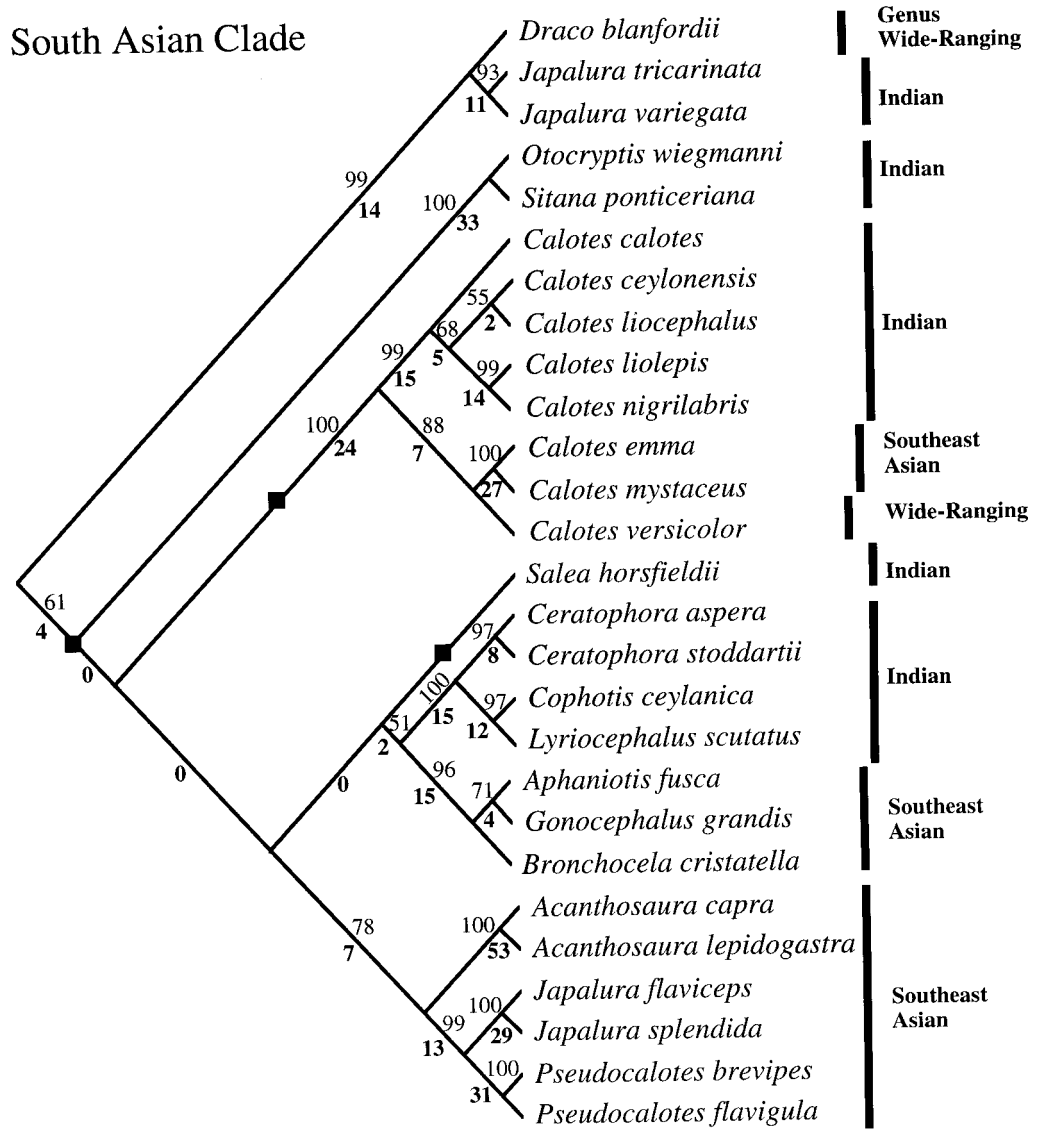


FIGURE 6. Phylogenetic relationships within the South Asian clade of the Acrodonta. This figure depicts one phylogenetic arrangement found in the three equally most-parsimonious trees derived from analysis of the 1,041 informative DNA sequence characters. Diamonds on branches denote the three alternative placements of the clade containing *Otocryptis wiegmanni* and *Sitana ponticeriana;* the position of this clade is the only difference in topology among the three shortest trees, and internal branches with a decay index of 0 produce a polytomy in the strict consensus tree. Bootstrap values are presented above branches, and decay indices are shown in bold below branches. Indian taxa span the root of the tree, and Southeast Asian taxa are nested within Indian taxa. Taxa that occur on the older accretionary block of East Asia (*Japalura flaviceps* and *Japalura splendida*) are highly nested on the tree.

strap 93%, decay index 11). The sister taxon to the clade containing *Draco* and Himalayan *Japalura* contains all remaining species (bootstrap 61%, decay index 4). The three most-parsimonious trees differ only in the placement of the Sri Lankan *Otocryptis* and *Sitana* (see Fig. 6). One tree groups these genera as the sister taxon to all remaining taxa except *Draco* and Himalayan *Japalura.* In a second tree, *Otocryptis* and *Sitana* appear to form the sister taxon to a monophyletic *Calotes* (bootstrap 100%, de-

cay index 24). Within *Calotes,* a monophyletic group of Sri Lankan species (*C. calotes, C. ceylonensis, C. liocephalus, C. liolepis,* and *C. nigrilabris*) is well supported (bootstrap 99%, decay index 15). Sri Lankan *Calotes* form the sister taxon to a clade (bootstrap 88%, decay index 7) composed of the wide-ranging *C. versicolor* and Southeast Asian *C. emma* and *C. mystaceus* (the latter two species being grouped with bootstrap 100%, decay index 27). The third most-parsimonious tree groups the Sri Lankan *Otocryptis* and *Sitana* as the sister taxon to the Indian *Salea. Salea* (or the clade composed of *Salea, Otocryptis,* and *Sitana*) is the sister taxon to a weakly supported clade (bootstrap 51%, decay index 2) composed of a Sri Lankan group (*Ceratophora, Cophotis,* and *Lyriocephalus;* bootstrap 100%, decay index 15), and a Southeast Asian group (*Aphaniotis, Gonocephalus,* and *Bronchocela;* bootstrap 96%, decay index 15). An additional clade is the sister taxon to the clade composed of *Salea* (possibly *Otocryptis* and *Sitana*), *Ceratophora, Cophotis, Lyriocephalus, Aphaniotis, Gonocephalus,* and *Bronchocela,* and includes Southeast Asian and East Asian species (*Acanthosaura, Japalura flaviceps, J. splendida,* and *Pseudocalotes;* bootstrap 78%, decay index 7). Monophyly of each of the genera *Acanthosaura, Japalura* (East Asian species), and *Pseudocalotes* is strongly supported (bootstrap 100%, decay index 53; bootstrap 100%, decay index 29; and bootstrap 100%, decay index 31; respectively). The East Asian species of the genus *Japalura* form the sister taxon to the Southeast Asian genus *Pseudocalotes* (bootstrap 99%, decay index 13), with the Southeast Asian genus *Acanthosaura* excluded. The phylogenetic distribution of taxa on the three most-parsimonious trees suggests an Indian origin for this clade, although a Southeast Asian origin is possible.

Within the African–West Asian clade, taxa are distributed on the Gondwanan plates of Afro-Arabia and the Indian Subcontinent (Fig. 7). The African genus *Agama* is monophyletic (bootstrap 100%, decay index 84), and *A. agama* and *A. atra* are sister taxa (bootstrap 82%, decay index 9). *Agama* forms the sister taxon to the remaining taxa in the African–West Asian clade with weak support (decay index 1). A clade composed of the Arabian *Pseudotrapelus* and *Trapelus* (decay index 1) forms the sister taxon to *Laudakia* and *Phrynocephalus* species (bootstrap 58%, decay index 3). Monophyly of *Trapelus* is well supported (bootstrap 100%, decay index 39), and *T. ruderatus,* which is wide ranging in North Africa, Arabia, and West Asia, is the sister taxon to other *Trapelus* (bootstrap 99%, decay index 16). Among the other four *Trapelus* (*T. agilis* of West Asia, *T. persicus* of Arabia, *T. sanguinolentus* of West Asia, and *T. savignii* of North Africa), relationships are not well supported. A clade of *Laudakia* (bootstrap 61%, decay index 3), potentially of Indian origin, forms the sister taxon to the other *Laudakia* species and *Phrynocephalus* (decay index 3). Within the potentially Indian clade of *Laudakia, L. sacra* of Tibet forms the sister taxon to a clade containing *L. nupta* (wide ranging from the northern margin of Arabia to the western margin of the Indian Subcontinent) and *L. tuberculata* of the Himalaya (bootstrap 56%, decay index 4). A clade composed of the wide-ranging (North Africa, Arabia, West Asia) *Laudakia stellio* and *Phrynocephalus* (decay index 3) is the sister taxon to a well-supported group of West Asian *Laudakia* (bootstrap 100%, decay index 19). Monophyly of *Phrynocephalus* (bootstrap 100%, decay index 40) is well supported, as is the sister-taxon relationship of *P. mystaceus* and *P. raddei* (bootstrap 100%, decay index 19). Among the West Asian clade of *Laudakia, L. lehmanni* of the lower Pamir forms the sister taxon to the other species (bootstrap 54%, decay index 2), and *L. himalayana* of the high Pamir and *L. stoliczkana* of the Sino-Mongolian deserts form a monophyletic group (bootstrap 78%, decay index 6). A clade containing Iranian Plateau species *L. microlepis, L. caucasia,* and *L. erythrogastra* receives some support (bootstrap 77%, decay index 5; although see Macey et al. {1998a} for a more detailed analysis). A monophyletic grouping of species occurring on the northern margin of the Iranian Plateau (*L. caucasia* and *L. erythrogastra*) is well supported (bootstrap 100%, decay index 38).

This phylogenetic estimate suggests an Afro-Arabian origin for the African–West Asian clade, although an Indian origin is possible. Note that taxa occurring exclu-

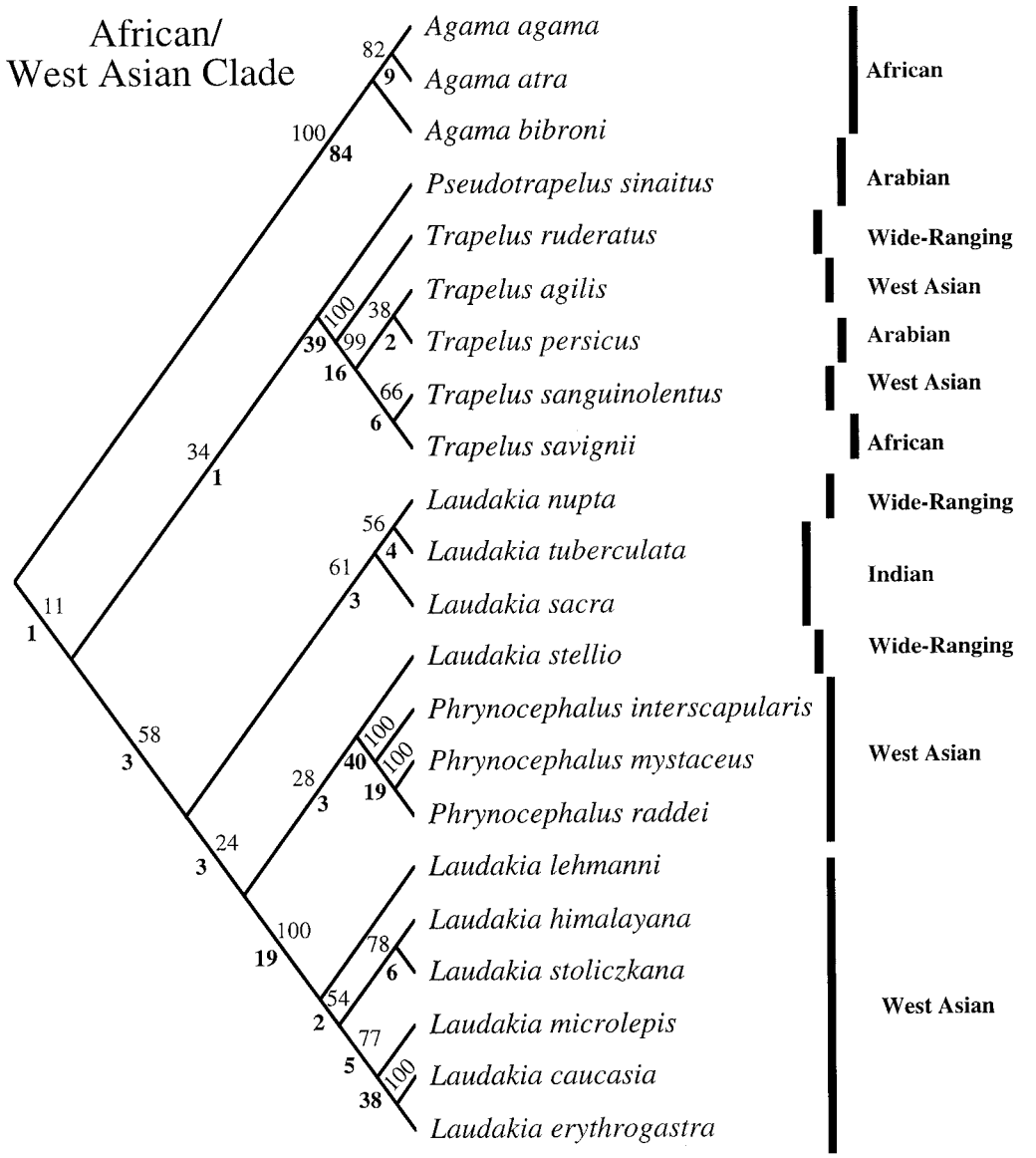


FIGURE 7. Phylogenetic relationships among the African–West Asian clade of the Acrodonta. Bootstrap values are presented above branches, and decay indices are shown in bold below branches. Taxa occurring on Afro-Arabia are in a basal position (*Agama, Pseudotrapelus, Trapelus savignii*, and *T. persicus*) with taxa occurring on the periphery of the Indian Subcontinent being in a nested position on the tree (*Laudakia sacra, L. nupta,* and *L. tuberculata*). *Trapelus ruderatus* and *Laudakia stellio* are wide ranging between Afro-Arabia and Laurasia, and *L. nupta* is wide ranging between the northern margin of Arabia through Laurasian plates to the western margin of the Indian Subcontinent. Among other taxa sampled, *Phrynocephalus* and other species of *Laudakia* and *Trapelus* occur on previously accreted land masses of Laurasia.

sively on the African (*Agama* and *Trapelus savignii*) and Arabian (*Pseudotrapelus* and *T. persicus*) plates are in a basal position on the tree. *Laudakia stellio* and *T. ruderatus* are wide ranging in the eastern Mediterranean region, occurring in northern Africa, northern Arabia, and Asia. The potentially Indian clade of *L. sacra, L. nupta* (wide ranging from Arabia to India), and *L. tuberculata* is nested on the tree.

Branch lengths obtained by using accelerated optimizations are shown in Figure 8.

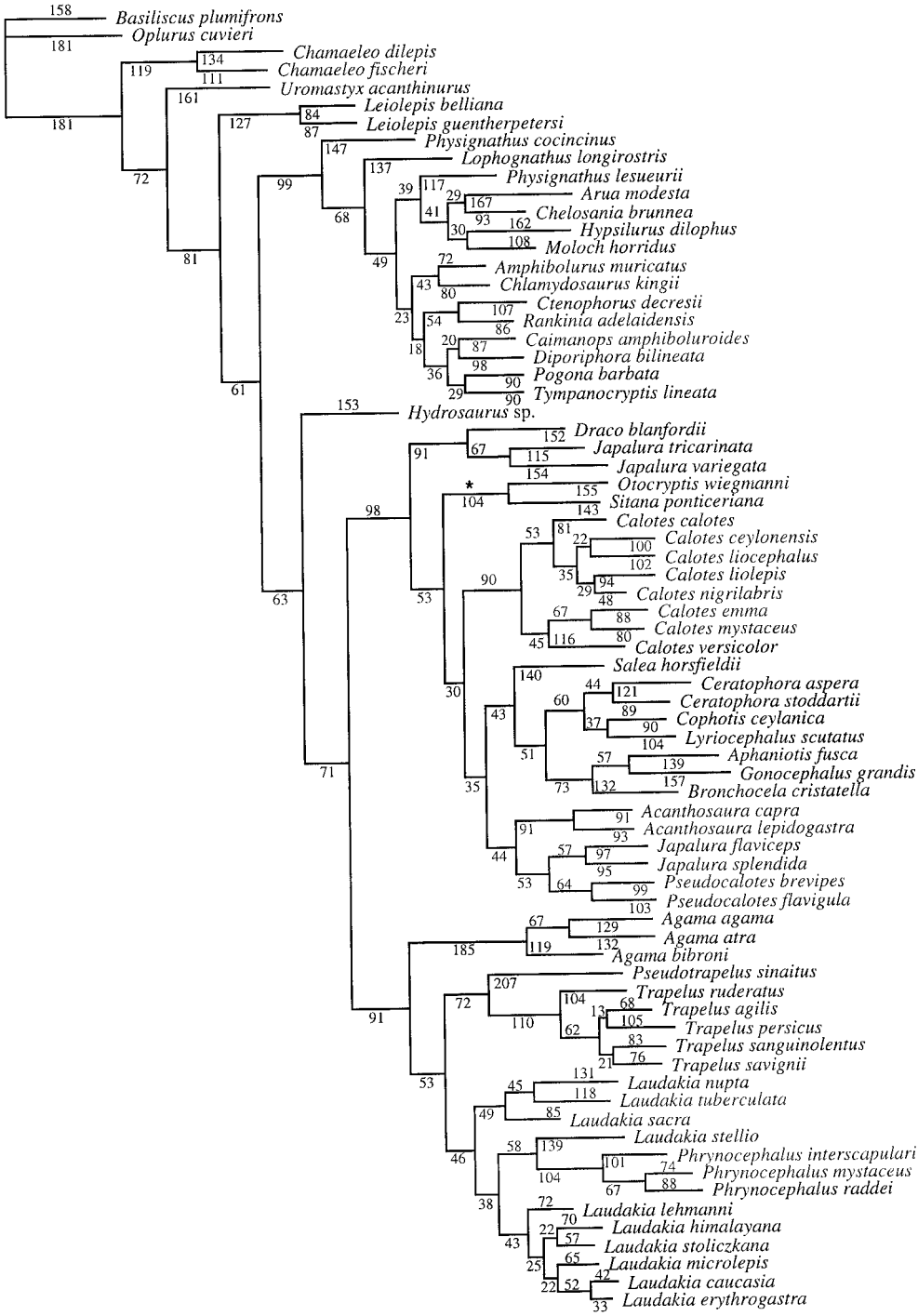


FIGURE 8. One of the three equally most parsimonious trees, illustrating relative branch lengths. Branch lengths are accelerated optimizations. The asterisk indicates the branch that is placed in two different places on the other two most-parsimonious trees (see Fig. 6). Note that branches relating most of the Acrodonta are relatively even in length.

Most of the Acrodonta shows surprisingly even branch lengths, suggesting substitutional rate uniformity across taxa through time. In addition, this optimization provides some level of confidence in the rooting of major clades, which are separated by long branches. If these clades were rooted in incorrect positions, exceptionally long branches would appear as an artifact of the incorrect rooting point.

The association of various monophyletic groups with different Gondwanan plates is as follows:

1. Both *Leiolepis* species occur on Southeast Asian plates of Gondwanan origin.
2. *Hydrosaurus* occurs primarily on Southeast Asian plates of Gondwanan origin (only one sample examined). In this study, the ancestral area of *Hydrosaurus* is inferred to be with Southeast Asian blocks that broke from Australia–New Guinea, although the genus is known to occur peripherally in western New Guinea.
3. *Physignathus cocincinus,* which is the sister group to all Australian and New Guinean taxa, occurs on Southeast Asian plates of Gondwanan origin, which broke from the northern margin of the Australia–New Guinea plate in successive phases.
4. Australian and New Guinean taxa collectively form a monophyletic group and occupy a separated Gondwanan plate.
5. The South Asian clade contains taxa occurring on the Indian Subcontinent, primarily in a basal position to those on Southeast Asian plates of Gondwanan origin; taxa occurring on Laurasian blocks in China are highly nested.
6. The African–West Asian clade has a topology suggestive of an Afro-Arabian origin but could have had an Indian origin.

Note that the Chamaeleonidae is monophyletic and occurs on the Gondwanan plates of Africa, Arabia, Madagascar, Seychelle Islands, and India. *Uromastyx* occurs on the Gondwanan plates of India, Arabia, and Africa, but more sampling is needed to test alternative biogeographic hypotheses for the Chamaeleonidae and *Uromastyx*.

The phylogenetic results provide an area cladogram for taxa occurring on Gondwanan plates. To assess support for the inferred origin of clades on separate Gondwanan plates, phylogenetic topologies representing alternative hypotheses of plate tectonic origins of taxa are tested statistically against the three overall most-parsimonious trees (Table 3). See the *Systematic Biology* Website for the three overall most-parsimonious trees and all alternative trees used in statistical tests.

Monophyly of Leiolepis.—The three overall most-parsimonious trees (A1–3), in which *Leiolepis* is monophyletic, are significantly shorter by the two-tailed Wilcoxon signed-ranks test than the most-parsimonious alternative trees having a nonmonophyletic *Leiolepis* (B1 and 2; test 1 in Table 3). This result supports an association of *Leiolepis* species with Southeast Asian plates of Gondwanan origin.

Hydrosaurus.—Hydrosaurus occurs primarily on the Southeast Asian plates of Gondwanan origin and only one sample was examined.

Clade containing Physignathus cocincinus *plus Australian and New Guinean taxa.*—The three overall most-parsimonious trees (A1–3), which group *Physignathus cocincinus* with the Australian and New Guinean taxa, are significantly more parsimonious than the shortest alternative trees separating *Physignathus cocincinus* from Australian and New Guinean taxa (C1–3) according to the two-tailed Wilcoxon signed-ranks test (test 2 in Table 3). This result suggests a vicariant split between the Southeast Asian *Physignathus cocincinus* and the clade containing the Australian and New Guinean taxa.

Australian–New Guinean clade.—When the three overall most-parsimonious trees (A1–3), which show a monophyletic Australian–New Guinean clade, are compared with the shortest alternative trees showing a nonmonophyletic Australian and New Guinean group (D1 and 2), this alternative is not rejected in favor of the overall shortest trees (test 3 in Table 3). The Australian–New Guinean clade receives considerable support, however, from the bootstrap analysis (95%) and has a decay index of 15.

TABLE 3. Results of the Wilcoxon signed-ranks test for the biogeographic analysis. Asterisks indicate a significant difference between the overall shortest tree and an alternative tree. One asterisk denotes significance in the one-tailed probability test and two asterisks denote significance in the two-tailed probability test. One-tailed probabilities (*P*) are shown; two-tailed probabilities are double these values. A significant result indicates that the hypothesis as stated is significantly more parsimonious than its alternative. All tree topologies are identified on the *Systematic Biology* web site.

Hypothesis and test no.	Trees	N^a	Z^b	P^c
1. Monophyly of	A1 vs. B1	228	4.47	0.001**
Leiolepis	A1 vs. B2	187	5.10	0.001**
	A2 vs. B1	233	4.34	0.001**
	A2 vs. B2	204	4.80	0.001**
	A3 vs. B1	204	4.86	0.001**
	A3 vs. B2	231	4.38	0.001**
2. *Physignathus*	A1 vs. C1	215	2.77	0.003**
cocincinus and the	A1 vs. C2	237	2.58	0.005**
Australian–New Guinean	A1 vs. C3	241	2.48	0.007**
taxa form a	A2 vs. C1	215	2.81	0.003**
monophyletic group	A2 vs. C2	239	2.60	0.005**
	A2 vs. C3	242	2.48	0.007**
	A3 vs. C1	227	2.59	0.005**
	A3 vs. C2	198	2.98	0.001**
	A3 vs. C3	200	2.89	0.002**
3. The	A1 vs. D1	226	0.95	0.170
Australian–New Guinean	A1 vs. D2	242	0.92	0.179
taxa form a	A2 vs. D1	240	0.93	0.177
monophyletic group	A2 vs. D2	240	0.93	0.177
	A3 vs. D1	275	0.74	0.229
	A3 vs. D2	264	0.82	0.207
4. South Asian	A1 vs. E1	130	2.06	0.020**
taxa form a	A1 vs. E2	142	1.97	0.024**
monophyletic group	A2 vs. E1	148	1.93	0.027*
	A2 vs. E2	153	1.89	0.030*
	A3 vs. E1	182	1.67	0.048*
	A3 vs. E2	189	1.62	0.053*
5. Root in the	A1 vs. F1	110	0.61	0.270
Indian Subcontinent	A1 vs. F2	120	0.58	0.280
for the South Asian	A2 vs. F1	121	0.58	0.282
Clade	A2 vs. F2	133	0.55	0.292
	A3 vs. F1	126	0.55	0.293
	A3 vs. F2	129	0.54	0.295
6. African–West Asian	A1 vs. G1	241	1.28	0.100
taxa form a	A1 vs. G2	254	1.24	0.108
monophyletic group	A1 vs. G3	214	1.39	0.082
	A1 vs. G4	228	1.34	0.090
	A2 vs. G1	257	1.25	0.107
	A2 vs. G2	267	1.21	0.114
	A2 vs. G3	234	1.34	0.091
	A2 vs. G4	245	1.29	0.098
	A3 vs. G1	249	1.28	0.100
	A3 vs. G2	259	1.24	0.108
	A3 vs. G3	227	1.35	0.089

TABLE 3. Continued

Hypothesis and test no.	Trees	N[a]	Z[b]	P[c]
	A3 vs. G4	238	1.31	0.096
7. Root in the Afro-	A1 vs. H1	316	0.08	0.468
Arabian plate for	A1 vs. H2	307	0.12	0.453
the African–West Asian	A1 vs. H3	309	0.07	0.472
clade	A2 vs. H1	312	0.14	0.444
	A2 vs. H2	302	0.13	0.450
	A2 vs. H3	306	0.13	0.450
	A3 vs. H1	295	0.180	0.429
	A3 vs. H2	278	0.173	0.431
	A3 vs. H3	284	0.170	0.432

[a]*N* = number of characters that differ in minimum number of evolutionary steps between the trees being compared.
[b]*Z* = normal approximation from the Wilcoxon signed-ranks test corrected for tied ranks.
[c]*P* = Probabilities <0.001 are not calculated exactly and are presented as 0.001.

South Asian clade.—The three overall most-parsimonious trees (A1–3), which show a monophyletic South Asian clade, are significantly more parsimonious than the shortest alternative trees showing a nonmonophyletic South Asian clade (E1 and 2) by the one-tailed Wilcoxon signed-ranks test (test 4 in Table 3). Hence, taxa in this clade appear to be associated with one of two Gondwanan regions, India or Southeast Asia.

To test whether the three overall shortest topologies (A1–3) suggesting a possible Indian origin could be distinguished from topologies suggesting a Southeast Asian origin, alternative trees were found by constraining Malaysian taxa (*Aphaniotis, Gonocephalus,* and *Bronchocela*) to be the sister group to the other taxa in this clade and finding the shortest alternatives under this constraint (F1 and 2). The alternative trees cannot be rejected as being significantly less parsimonious than the overall shortest trees (test 5 in Table 3). Hence, we cannot determine whether the South Asian clade is of Indian or Southeast Asian origin.

African–West Asian clade.—The three overall most-parsimonious trees (A1–3) showing an African–West Asian clade are not significantly shorter than the shortest alternative trees showing a nonmonophyletic African–West Asian group (G1–4) by the Wilcoxon signed-ranks test (test 6 in Table 3). This node appears strong in the bootstrap analysis (100%) and has a decay index of 21. Hence, taxa in this clade are associated with one of two Gondwanan plates, Afro-Arabia or India.

To eliminate the possibility that species located peripherally to the Indian subcontinent (*Laudakia sacra, L. nupta,* and *L. tuberculata*) might have been derived from the Indian plate, the three overall shortest topologies suggesting an Afro-Arabian origin were tested against the shortest alternative trees suggesting an Indian origin. To find the shortest alternative trees, all possible combinations of taxa were constrained to be the sister group to a clade containing the remaining species. These alternatives (H1–3), which place *L. sacra* as the sister taxon to all other taxa, and group *L. nupta* and *L. tuberculata* as the sister taxon to all remaining species, cannot be distinguished from the overall shortest trees (test 7 in Table 3). Therefore, we cannot determine whether the African–West Asian clade is of Afro-Arabian or Indian origin.

Taxonomy of the Acrodonta

Traditionally, two families have been recognized in the Acrodonta, the Chamaeleonidae and Agamidae. The Chamaeleonidae family is supported by morphological data, but the Agamidae* has little support for either monophyly or nonmonophyly (Macey et al., 1997c), so we continue to call it a metataxon (denoted with an asterisk), for which monophyly can be neither statistically confirmed nor rejected (Schulte et al., 1998). We have identified six

groups within the Agamidae that can be recognized as subfamilies. *Uromastyx* species can be recognized taxonomically as the Uromastycinae (Theobald, 1868). *Leiolepis* species can be recognized as the Leiolepidinae (Fitzinger, 1843). The clade composed of *Physignathus cocincinus* and all Australian and New Guinean taxa can be recognized as the Amphibolurinae (Wagler, 1830). *Hydrosaurus* species can be recognized as the Hydrosaurinae (Kaup, 1828). The South Asian clade can be recognized as the Draconinae (Fitzinger, 1826). The African–West Asian clade can be recognized as the Agaminae (von Spix, 1825).

Discussion

Tectonic Process for Assembly of a Continental Fauna

Our phylogenetic analysis identifies eight major acrodont lizard clades, each of which is associated with tectonic plates of Gondwanan origin. We suggest that the Acrodonta are of Gondwanan origin and that the fragmentation of Gondwanaland into separate tectonic plates contributed to early cladogenic events that led to these eight major clades. These major groups of the Acrodonta diverged from each other and diversified as their respective tectonic plates moved across the Tethys Sea and made contact at different points along the southern margin of Laurasia. The different acrodont lineages then entered Laurasia, assembling a complex Asian acrodont fauna. Because of the dispersal of acrodont lizards into Laurasia after the accretion of the Gondwanan plates, the major clades of the Acrodonta no longer exhibit endemism on their respective tectonic plates of origin; however, the deepest phylogenetic divergences within each clade trace to the clade's plate of origin.

The association of some taxa with a particular Gondwanan plate is straightforward, whereas other associations are more ambiguous. *Leiolepis* species occur only on the Southeast Asian blocks that broke from the northern margin of the Australia–New Guinea plate hundreds of MYBP and accreted to Asia 120 MYBP (Richter and Fuller, 1996) or earlier (Metcalfe, 1996). *Hydrosaurus* also occurs primarily on Southeast Asian blocks that could either be associated with an early phase (reaching completion as late as 120 or 65 MYBP) or a more recent phase (beginning 40 MYBP) of tectonic migration from the Australia–New Guinea plate to Southeast Asia.

The South Asian clade (Fig. 6) is identified as potentially being introduced into Asia by the Indian Subcontinent. The African–West Asian (Fig. 7) clade is identified as potentially being introduced into Asia by the Afro-Arabian Plate. In each case, alternative Gondwanan plates could have been used. For the South Asian clade, the Southeast Asian plates are possibly the source of Asian colonization. The African–West Asian clade may have originated from the Indian Subcontinent.

Strong debate has occurred over whether the Indian Plate had intermittent contact with Afro-Arabia during northward movement across the Tethys Sea between 148 and 50 MYBP (Sahni, 1984; Briggs, 1989; Patterson and Owen, 1991; Sahni, 1984; Thewissen and McKenna, 1992). The main point of contention has been the lack of an endemic fauna, past and present, in India. Thewissen and McKenna (1992) argue that Cretaceous fossil data from India do not establish a link to the Cretaceous African or Laurasian faunas, countering Briggs' (1989) argument that these faunas were in contact with India during its crossing of the Tethys Sea 148–50 MYBP. Our results suggest that Indian and Afro-Arabian acrodont lizards are basal groups of larger clades, some species of which have dispersed into adjacent tectonic regions after the collision of India (50 MYBP) and Afro-Arabia (18 MYBP) with Laurasia. Our findings therefore are consistent with Indian isolation during the crossing of the Tethys Sea.

The sister-group relationship discovered between *Physignathus cocincinus* and a clade of all the taxa occurring on the Australia–New Guinea plate is exactly what is predicted from a vicariant split between the Southeast Asian plates and the Australia–New Guinea plate. Alternatively, a dispersal event from Southeast Asia with a rapid recent radiation in Australia and New Guinea could be argued (Tyler, 1979; King 1990). Note that the Australia–New Guinea plate was far to the south of Asia until re-

cently, and such dispersal could not have predated 10 MYBP (Hall, 1996; Metcalfe, 1996). Also, taxa long considered to represent independent examples of dispersal from Southeast Asia to the Australia–New Guinea plate are not closely related (the two species of *Physignathus,* the Southeast Asian *Gonocephalus,* and the Australian–New Guinean *Hypsilurus*).

Sequence divergence between *Physignathus cocincinus* and taxa occurring on the Australia–New Guinea plate provides an additional line of evidence that a vicariant split caused the divergence of these taxa. The average DNA-sequence divergence between *Physignathus cocincinus* and taxa occurring on the Australia–New Guinea plate is 22.2% for the pair of lineages (average of 314 substitutions, range 289–341, within the 1434 aligned positions). This divergence is twice the amount expected for a split of 10 MYBP calculated from the same piece of DNA for *Laudakia* (Macey et al., 1998a), gekkonid lizards (Macey et al., 1999b), bufonid frogs (Macey et al. 1998b), and cyprinid fishes (Bermingham et al., 1997). Because saturation of mitochondrial sequences occurs past 10 MYBP (Moritz et al., 1987), this split is certainly much older. For example, the amount of sequence divergence observed between iguanid lizards in Madagascar and the New World, determined with sequences of the same segment of mitochondrial DNA with the same included regions (except no variable loop of the $tRNA^{Asn}$ gene; Macey et al., 1997c; Schulte et al., 1998) is 22.7% (average of 354 substitutions, range 275–354, within the 1405 aligned positions) and represents 160 million years of isolation (Rabinowitz et al., 1983; Chatterjee, 1992; Macey et al., 1997c). Therefore, we interpret the split between the Southeast Asian *Physignathus cocincinus* and the Australia–New Guinea clade to be within about the same time frame. In addition, *Physignathus cocincinus* occurs only on the southeast Asian blocks that broke from the northern margin of the Australia–New Guinea plate hundreds of MYBP and accreted to Asia 120 MYBP (Richter and Fuller, 1996) or earlier (Metcalfe, 1996); it is absent from more recent small tectonic fragments now distributed only as far north as Sulawesi.

Uromastyx species occur on both the Indian Subcontinent and Afro-Arabia. Immunological data of Joger (1986) suggest that all Afro-Arabian species form a monophyletic sister taxon to the Indian and Iranian species. This topology suggests an Indian origin for *Uromastyx,* but further work is needed to reject the hypothesis of an Afro-Arabian origin.

Members of the Chamaeleonidae certainly are associated with the Gondwanan plates of Africa, Madagascar, and the Seychelle islands, where most species are found. Further work is needed to examine Asian taxa occurring in Arabia and India, which are also of Gondwanan origin, to determine whether these taxa dispersed from Africa or were carried to their current locations by individual Gondwanan plates.

Figure 9 summarizes monophyletic groups that were introduced into Asia by different Gondwanan plates. Two clades (the African–West Asian clade, and *Uromastyx*) were introduced into Asia through either Afro-Arabia or India, and another clade (South Asian clade) was introduced to Asia either by India or Southeast Asian plates. The Southeast Asian plates introduced three additional acrodont groups to Asia (*Leiolepis, Hydrosaurus,* and *Physignathus*). The acrodont lizards in Asia therefore have different histories because of the complex tectonic evolution of land masses derived from Gondwanaland.

The pattern of clades associated with different Gondwanan plates now accreted to Asia may be a general one that could apply to additional components of the Asian flora and fauna. Detailed study using modern phylogenetic methodology is needed to test the hypothesis of a complex Gondwanan origin for other Asian taxa.

Tectonic Processes That Reinforce Wallace's Line

Wallace's line defines the division between the Australia–New Guinea fauna (Australian zoogeographic region) and that of southern Asia (Oriental zoogeographic region), with a few exceptions (for reviews see Briggs, 1987; van Oosterzee, 1997). The sharp faunal division now observed across Wallace's line (Fig. 10) results from three

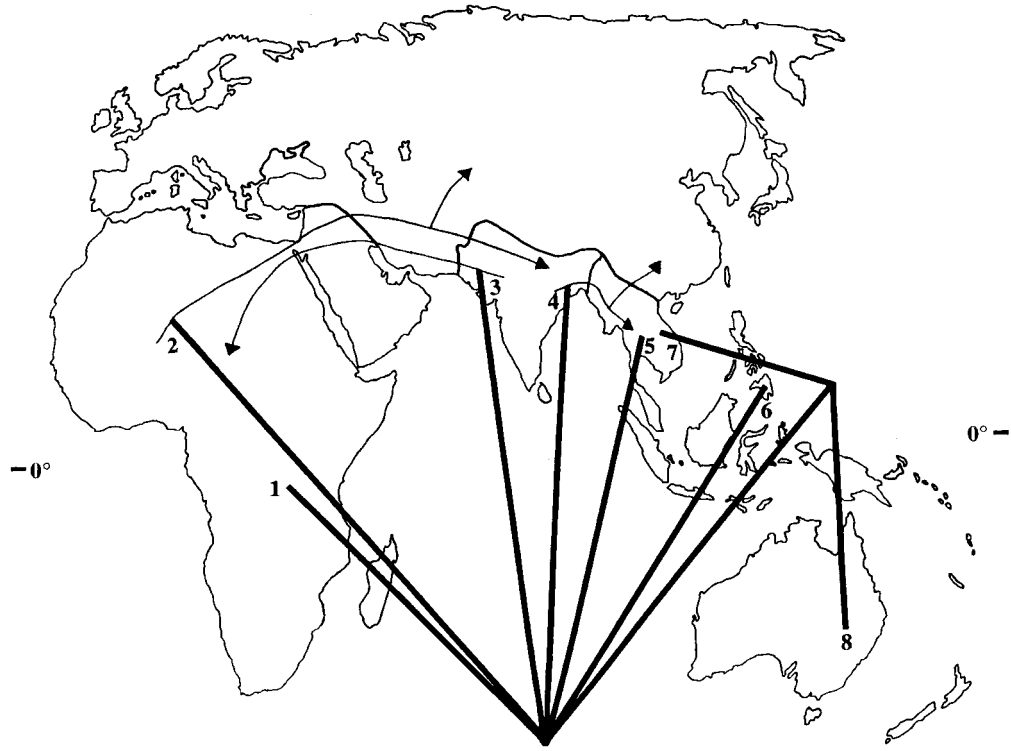


FIGURE 9. Area cladogram of Gondwanan plates that have introduced acrodont lizards into Asia. Acrodont lizards have been introduced to Asia by more that one accretionary event of Gondwanan tectonic plates. Numbers on branches refer to clades defined in the phylogenetic analysis (Figs. 4–7): 1 = *Chamaeleo;* 2 = African–West Asian clade; 3 = *Uromastyx;* 4 = South Asian clade; 5 = *Leiolepis;* 6 = *Hydrosaurus;* 7 = *Physignathus cocincinus;* and 8 = Australian–New Guinean clade. The shortest phylogenetic tree suggests that the African–West Asian clade is of Afro-Arabian origin and that the South Asian clade is of Indian origin, but alternative Gondwanan plates cannot be rejected as possible origins. Immunological data of Joger (1986) suggest an Indian origin for *Uromastyx,* but further work is needed to test the alternative hypothesis of an African origin.

major events. First, the tectonic split between the Southeast Asian blocks and the northern margin of the Australian–New Guinean plate hundreds of MYBP caused a primary division between the faunas. Second, accretion of these blocks to Eurasia 120 MYBP (or earlier) and 65 MYBP allowed dispersal of the Laurasian fauna to the Southeast Asian blocks, but deep oceanic barriers prevented faunal dispersal to the Australian–New Guinean plate, which at that time was far to the south. Third, the Indian collision (50 MYBP; Windley, 1988) brought to Asia an additional fauna that dispersed into the Southeast Asian blocks, but deep oceanic barriers again prevented dispersal to the Australian–New Guinean plate, still far to the south. A final minor step is the breaking of small fragments from the Australian–New Guinean plate 40 MYBP and the fusion of some of these plates to Sulawesi (10 MYBP), just to the east (Australian–New Guinean side) of Wallace's original line but to the west of Wallace's revised line of 1910 (see Briggs, 1987).

Acrodont lizards show evidence for two of these processes. First, the sister-taxon relationship between *Physignathus cocincinus* and taxa occurring on the Australian–New Guinean plate is evidence of the primary divergence between faunas. Second, dispersal of the South Asian clade from the Indian Subcontinent to the Southeast Asian blocks secondarily introduced faunal elements to the northeastern margin of the barrier.

Other reptiles provide evidence for this process. Phylogenetic results based on mi-

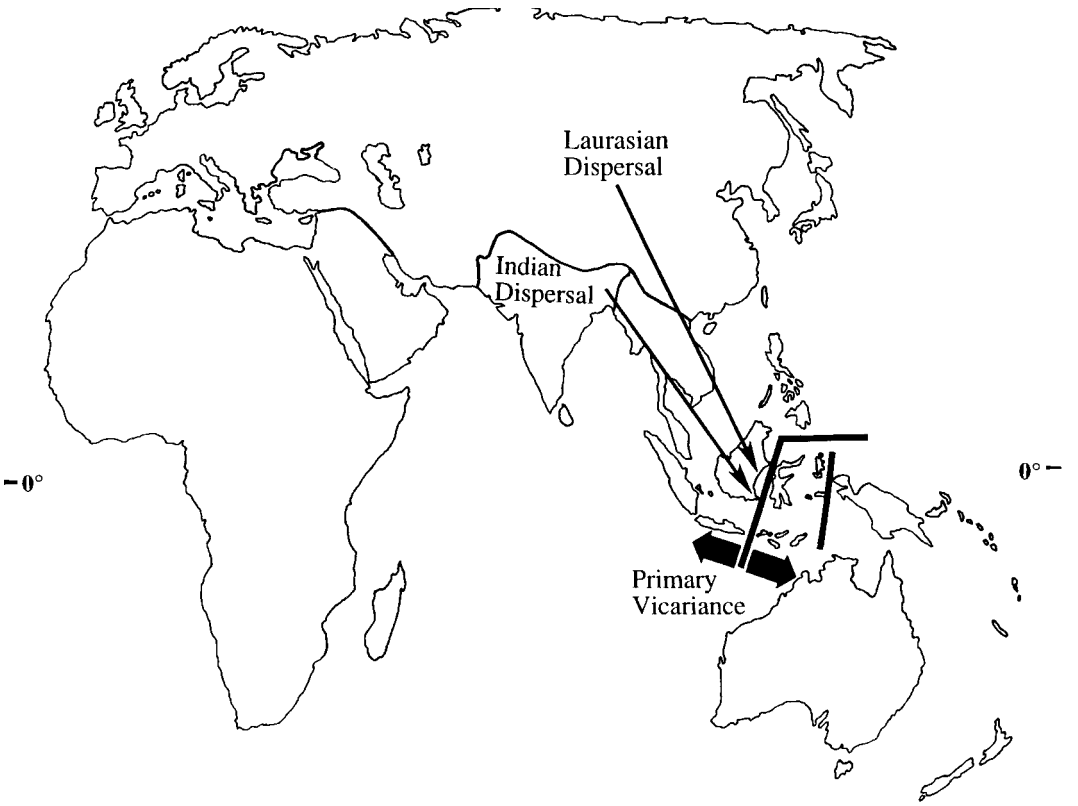


FIGURE 10. Three major events can be responsible for the sharp faunal division now observed across Wallace's line. First, the tectonic split of Southeast Asian blocks from the northern margin of the Australian—New Guinean plate hundreds of MYBP caused a primary division between the faunas. Second, accretion of these blocks to Eurasia 120 MYBP (or earlier) and 65 MYBP allowed dispersal of the Laurasian fauna to the Southeast Asian blocks, but deep oceanic barriers prevented dispersal to the Australian–New Guinean plate, which at that time was far to the south. Third, the Indian collision (50 MYBP, Windley, 1988) brought a new fauna that also dispersed into the Southeast Asian blocks, but deep oceanic barriers again prevented dispersal to the Australian–New Guinean plate, which was still far to the south. A final minor step is the breaking of small fragments from the Australian–New Guinean plate 40 MYBP and the fusion of some of these fragments to Sulawesi (10 MYBP), just to the east (Australian–New Guinean side) of Wallace's original line (bar with arrows) but to the west of Wallace's revised line (bar without arrows) of 1910 (see Briggs, 1987).

tochondrial DNA sequences of elapid snakes (Keogh, 1998) and varanid lizards (Fuller et al., 1998) both suggest a sister-group relationship between taxa on the Australian plate and taxa on the Southeast Asian blocks. Contrary to the original conclusions of both studies, these taxa may represent evidence for primary diversification between the two Gondwanan regions rather than more recent dispersal. One argument used against early vicariance is the presence of early fossils of varanids in Laurasia (see Fuller et al., 1998). However, this evidence can be explained easily by the continual accretion of Gondwanan fragments to the southern margin of Laurasia starting 300 MYBP (Sengör, 1984; Sengör et al., 1988; Feng et al., 1989; Kwon et al., 1989). In addition, not a single extant varanid species is endemic to Laurasian plates. Molecular phylogenetic analysis of anguid lizards shows evidence for a Laurasian taxon dispersing into Southeast Asian blocks (as far south as Borneo) but not crossing Wallace's line (Macey et al., 1999a). Hence, the dynamics of current biogeography in Asia are complex. Detailed study of numerous groups is needed to identify the different biogeographic histories of Asian faunal elements.

Tectonic Processes Stimulate Episodic Restructuring of Continental Faunas

Drifting microcontinents may introduce invasive faunal elements to megacontinents in the same way that "weed" species have invaded nonnative areas and continents. During collision of tectonic plates a microcontinental fauna may be eradicated by the megacontinental fauna, or alternatively, the microcontinental fauna penetrates the megacontinental fauna. If a microcontinental fauna is erased, it has no net effect on the megacontinent's faunal diversity. In contrast, if a microcontinental faunal element invades a megacontinental fauna, the biotic community may shift drastically, as has been observed in modern times with invasions of nonnative "weed species," which may cause major extinction events. Hence, the historical assembly of continental faunas may be dominated by periodic introductions involving plate tectonic collisions of microcontinents or land bridges that permit dispersal. This biogeographic hypothesis suggests episodic faunal turnover. During times of isolation, faunal diversity should be relatively stable with only gradual shifts. During times of contact between tectonic plates, rapid faunal turnover may result, including extinctions caused by niche overlap, as has been observed in the contact of North and South American mammals (Webb, 1991). The repeated accretion of different microcontinents with a particular megacontinent such as Asia may constitute a major source for the production of biodiversity. Conservation efforts perhaps should be concentrated in zones of tectonic collision because diversity there is expected to be high. Phylogenetics is a powerful tool that may be able to explain the complex faunal dynamics of global communities.

ACKNOWLEDGMENTS

This work was supported by grants from the National Science Foundation (predoctoral fellowship to J.R.M.; BSR-9106898 to A.L.; DEB-9318642 to J.B. Losos, K. de Queiroz, and A.L.; DEB-9726064 to A.L., J.R.M, and T.J.P.), National Geographic Society (4110–89 and 4872–93 to T.J.P. and J.R.M.; 4894–92 to I. S. Darevsky of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia), Russian Foundation of Basic Research (N 97–04–50093 to N.B.A.), the California Academy of Sciences and the Museum of Vertebrate Zoology. We thank E. Nick Arnold, Aaron M. Bauer, Carla Cicero, Steve Donnellan, Robert Drews, Jimmy A. McGuire, Eric R. Pianka, Jens Vindum, David B. Wake, and Yehudah L. Werner for tissue specimens. Mohomed Bahir, Zhili Fang, Nikolai Orlov, Sakhat M. Shammakov, Boris S. Tuniyev, and Ermi Zhao aided with field work. We also thank Patrick Couper, Steve Donnellan, Paul Horner, Ross Sadlier, and Laurie Smith for providing locality information of specimens from Australia and New Guinea. Richard Olmstead, Roderic D. M. Page, Mark Wilkinson, and an anonymous reviewer provided helpful comments on an earlier version of the manuscript. Robert Hall contributed useful information on the geologic history of Southeast Asia.

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Received 9 March 1998; accepted 28 July 1999
Associate Editor: R. Page

APPENDIX 1

Museum numbers and abbreviated localities for voucher specimens from which DNA was extracted, and GenBank accession numbers are presented below in phylogenetic order. More complete locality data are archived in GenBank accessions. The taxonomy used is after Macey et al. (1997c) and the results of the present study. The metataxon Agamidae*, for which monophyly has not been demonstrated or rejected statistically, is denoted with an asterisk. Acronyms are AMS, Australia Museum, Sydney, Australia; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; GNHM Re. ex., Göteborg Natural History Museum Reptilia Exotica, Göteborg, Sweden; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley; QM, Queensland Museum, Brisbane, Australia; SAMA, South Australia Museum, Adelaide, Australia; TNHC, Texas Memorial Museum, Austin; WAM, Western Australia Museum, Perth, Australia; WHT, Wildlife Heritage Trust, Colombo, Sri Lanka; and ZISP, Zoological Institute, St. Petersburg, Russia. BNHS-AMB represents a field number of Aaron M. Bauer for a specimen being deposited at the Bombay Natural History Society, Bombay, India. MVZ-RM represents field numbers of the first author for uncatalogued specimens being deposited at the Museum of Vertebrate Zoology, University of California at Berkeley. WAM-ERP represents a field number of Eric R. Pianka for uncatalogued specimens being deposited at the Western Australia Museum, Perth, Australia.

Iguanidae: 1.—*Basiliscus plumifrons,* Prov. Cartago, Costa Rica (MVZ 204068, U82680; Macey et al., 1997c); 2.—*Oplurus cuvieri,* Madagascar (MVZ-RM10468, U82685; Macey et al., 1997c).

Chamaeleonidae: 3.—*Chamaeleo dilepis,* Tanga Region, Tanzania (CAS 168922, AF128460); 4.—*Chamaeleo fischeri,* Tanga Region, Tanzania (CAS 168965, U82688; Macey et al., 1997c).

Agamidae*, Uromastycinae: 5.—*Uromastyx acanthinurus,* Ouarzazate Province, Morocco (MVZ 162567, U71325; Macey et al., 1997a, 1997b).

Agamidae*, Leiolepidinae: 6.—*Leiolepis belliana,* Phuket Province, Thailand (MVZ 215497, U82689; Macey et al., 1997c); 7.—*Leiolepis guentherpetersi,* Tri Thien Province, Vietnam (MVZ 222157, AF128461).

Agamidae*, Amphibolurinae (*Physignathus cocincinus,* and the Australian–New Guinean clade): 8.—*Physignathus cocincinus,* Gia-Lai Province, Vietnam (MVZ 222159, U82690; Macey et al., 1997c); 9.—*Lophognathus longirostris,* Western Australia, Australia (WAM-ERP-R29940, AF128462); 10.—*Physignathus lesueurii,* New South Wales, Australia (SAMA R33417, AF128463); 11.—*Arua modesta,* Southern Highlands Province, Papua New Guinea (AMS R122434, AF128464); 12.—*Chelosania brunnea,* Western Australia, Australia (AMS R140288, AF128465); 13.—*Hypsilurus dilophus,* Southern Highlands Province, Papua New Guinea (AMS R122449, AF128466); 14.—*Moloch horridus,* Northern Territory, Australia (SAMA R38770, AF128467); 15.—*Amphibolurus muricatus,* New South Wales, Australia (SAMA R34770, AF128468); 16.—*Chlamydosaurus kingii,* Queensland, Australia (SAMA R34531, AF128469); 17.—*Ctenophorus decresii,* South Australia, Australia (SAMA R31008, AF128470); 18.—*Rankinia adelaidensis,* South Australia, Australia (SAMA R40929, AF128471); 19.—*Caimanops amphiboluroides,* Western Australia, Australia (WAM R104419, AF128472); 20.—*Diporiphora bilineata,* Queensland, Australia (QM J46161, AF128473); 21.—*Pogona barbata,* South Australia, Australia (SAMA R41126, AF128474); 22.—*Tympanocryptis lineata,* Northern Territory, Australia (SAMA tissue collection R35B06, voucher may be lost, AF128475).

Agamidae*, Hydrosaurinae: 23.—*Hydrosaurus* sp., Western Samar Province, Samar Island, Philippines (TNHC 54902, AF128476). Note that this specimen is possibly a hybrid between *Hydrosaurus amboinensis* and *Hydrosaurus pustulatus* (J. A. McGuire, pers. comm.).

Agamidae*, Draconinae (South Asian clade): 24.—*Draco blanfordii,* Gia-Lai Province, Vietnam (MVZ 222156, AF128477); 25.—*Japalura tricarinata,* Xizang (Tibet) Autonomous Region, China (CAS 177397, AF128478); 26.—*Japalura variegata,* Sikkim (ZISP 20922, AF128479); 27.—*Otocryptis wiegmanni,* Sri Lanka (WHT 2262, AF128480); 28.—*Sitana ponticeriana,* Sri

Lanka (WHT 2060, AF128481); 29.—*Calotes calotes*, Sri Lanka (WHT 1679, AF128482); 30.—*Calotes ceylonensis,* Sri Lanka (WHT 1624, AF128483); 31.—*Calotes liocephalus,* Sri Lanka (WHT 1632, AF128484); 32.—*Calotes liolepis,* Sri Lanka (WHT 1808, AF128485); 33.—*Calotes nigrilabris,* Sri Lanka (WHT 1680, AF128486); 34.—*Calotes emma,* Dac Lac Province, Vietnam (MVZ 222144, AF128487); 35.—*Calotes mystaceus,* Mandalay Division, Myanmar (CAS 204848, AF128488); 36.—*Calotes versicolor,* Vinh Thu Province, Vietnam (MVZ 224102, AF128489); 37.—*Salea horsfieldii,* Tamil Nadu (in the Western Ghats), India (BNHS-AMB5739, AF128490); 38.—*Ceratophora aspera,* Sri Lanka (WHT 1825, AF128491); 39.—*Ceratophora stoddartii,* Sri Lanka (WHT 1512, AF128492); 40.—*Cophotis ceylanica,* Sri Lanka (WHT 2061, AF128493); 41.—*Lyriocephalus scutatus,* Sri Lanka (WHT 2196, AF128494); 42.—*Aphaniotis fusca,* Selangor, Malaysia (TNHC 57874, AF128495); 43.—*Gonocephalus grandis,* Selangor, Malaysia (TNHC 56500, AF128496); 44.—*Bronchocela cristatella,* Selangor, Malaysia (TNHC 57943, AF128497); 45.—*Acanthosaura capra,* Gia-Lai Province, Vietnam (MVZ 222130, AF128498); 46.—*Acanthosaura lepidogastra,* Vinh Thu Province, Vietnam (MVZ 224090, AF128499); 47.—*Japalura flaviceps,* Sichuan Province, China (MVZ 216622, AF128500); 48.—*Japalura splendida,* Sichuan Province, China (CAS 194476, AF128501); 49.—*Pseudocalotes brevipes,* Vinh Thu Province, Vietnam (MVZ 224106, AF128502); 50.—*Pseudocalotes flavigula,* Perak, Malaysia (TNHC 58040, AF128503; species-level identification of specimen 50 is tentative—it may be *P. floweri* or an undescribed species).

Agamidae*, Agaminae (African–West Asian Clade): 51.—*Agama agama,* Rift Valley Prov., Kenya (CAS 199007, AF128504); 52.—*Agama atra,* Cape Province, South Africa (CAS 193436, AF128505); 53.—*Agama bibroni,* Ar Rachidiya Province, Morocco (MVZ-FC 501201, voucher frozen whole, AF128506); 54.—*Pseudotrapelus sinaitus,* Fujeirah, United Arab Emirates (BMNH 1996.201, AF128507); 55.—*Trapelus ruderatus,* Kermanshahan Province, Iran (GNHM Re. ex. 5212, AF128508); 56.—*Trapelus agilis,* Kerman Province, Iran (GNHM Re. ex. 5210, AF128509); 57.—*Trapelus persicus,* Khuzistan Province, Iran (GNHM Re. ex. 5211, AF128510); 58.—*Trapelus sanguinolentus,* Ashkabad (Ashkhabad) Region, Turkmenistan (CAS 179758, AF128511); 59.—*Trapelus savignii,* Egypt (MVZ-RM10471, AF128512); 60.—*Laudakia nupta,* Markazi Province, Iran (GNHM Re. ex. 5209, AF128513); 61.—*Laudakia tuberculata,* Daman, Nepal (ZISP 20697.1, AF128514); 62.—*Laudakia sacra,* Xizang (Tibet) Autonomous Region, China (CAS 170554, AF128515); 63.—*Laudakia stellio,* Golan Heights, Israel (MVZ-RM10494, AF128516); 64.—*Phrynocephalus interscapularis,* Chardjou Region, Turkmenistan (CAS 179151, AF128517); 65.—*Phrynocephalus mystaceus,* Ashkabad (Ashkhabad) Region, Turkmenistan (CAS 179754, AF128518); 66.—*Phrynocephalus raddei,* Ashkabad (Ashkhabad) Region, Turkmenistan (CAS 179770, U82691; Macey et al., 1997c); 67.—*Laudakia lehmanni,* Tajikistan (CAS 183009, AF028677; Macey et al., 1998a); 68.—*Laudakia himalayana,* Tajikistan (CAS 183016, AF028676; Macey et al., 1998a); 69.—*Laudakia stoliczkana,* Xinjiang Uygur Autonomous Region, China (CAS 167878, AF128519); 70.—*Laudakia microlepis,* Kerman Province, Iran (GNHM Re. ex. 5135, AF028678; Macey et al., 1998a); 71.—*Laudakia caucasia,* Turkmenistan (CAS 184650, AF028683; Macey et al., 1998a); 72.—*Laudakia erythrogastra,* Turkmenistan (CAS 184400, AF028680; Macey et al., 1998a).