

ON THE SYSTEMATICS OF THE GEKKONID GENUS *TERATOLEPIS* GÜNTHER, 1869: ANOTHER ONE BITES THE DUST

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(with two text-figures)

ABSTRACT.— A molecular phylogenetic analysis (cyt *b*, ND4, RAG-1 and PDC genes) of the two recognized species (*fasciata* and *albofasciata*) of *Teratolepis* and representatives of all major clades of *Hemidactylus* reveals that *Teratolepis* is embedded within the Tropical Asian clade of the latter genus. Its closest relatives are the other small terrestrial South Asian species, *H. reticulatus* and *H. gracilis*. The monophyly of Tropical Asian *Hemidactylus* as a whole is not supported, but the terrestrial clade including *Teratolepis* is well supported as the sister-group to *H. brookii* among the taxa sampled. *Hemidactylus anamallensis* and *H. scabriceps* are likely members of this clade as well. Synonymization of *Teratolepis* with *Hemidactylus* follows earlier actions sinking other small (*Cosymbotus*) or monotypic (*Dravidogecko*, *Briba*) genera that rendered *Hemidactylus* paraphyletic. This action necessitates a new specific epithet for *Hemidactylus fasciatus* (Blyth, 1853) which is a junior secondary homonym of *Hemidactylus fasciatus* Gray 1842, a widespread and common West African gecko. We therefore here erect the replacement name *Hemidactylus imbricatus* nomen novum.

KEY WORDS. – Gekkonidae, *Hemidactylus*, *Teratolepis*, molecular phylogeny, taxonomy.

INTRODUCTION

The ‘*Hemidactylus* group’ of geckos (*Hemidactylus*, *Briba*, *Cosymbotus*, *Dravidogecko*, *Teratolepis*) was identified by Russell (1972, 1976, 1979) on the basis of internal digital anatomy. Bauer and Russell (1995) formally synonymized the monotypic peninsular Indian genus *Dravidogecko* with *Hemidactylus* based on a more detailed consideration of pedal anatomy. A recent species level phylogeny of *Hemidactylus* based on the mitochondrial genes cytochrome *b* and 12S (Carranza and Arnold, 2006) revealed that two other members of the *Hemidactylus* group-*Cosymbotus* (two species, tropical Asia) and

Briba (monotypic, Brazil)- were in fact embedded deeply within it, rendering *Hemidactylus* paraphyletic and consequently requiring taxonomic action. Although Carranza and Arnold (2006) did not take this action themselves, Zug et al. (2007) formally included the species previously allocated to *Cosymbotus* in *Hemidactylus* and similar action is required in the case of *Briba*. Until now the phylogenetic position of the remaining small genus in the group, *Teratolepis* (two species, India and Pakistan), has not been formally assessed.

The taxonomic history of *Teratolepis* is disproportionately convoluted and complex,

given that only two species, *T. fasciata* (Blyth, 1853) and *T. albofasciata* (Grandison and Soman, 1963) are presently recognized (Rösler, 2000; Kluge, 2001). Although the latter is poorly known, the former is fairly common in the pet trade (Mudrack, 1977, 1986; Girard, 1993; Klarsfeld, 2001; Pouliček, 2002; Henkel and Schmidt, 2003).

Teratolepis fasciata (Blyth, 1853) was originally described as *Homonota fasciata* from an unstated locality in British India. Blyth's (1853) allocation to *Homonota*, however, was inconsistent with Gray's (1845) generic diagnosis of that genus, and Günther (1869) subsequently erected the new genus *Teratolepis* to accommodate the species, emphasizing its bizarre scalation (relatively large, flat, weakly imbricate polygonal scales on the dorsum and very large imbricate scales on tail, which is typically swollen basally).

Kluge (1964), in revising the genus *Homonota*, now restricted to South America, moved *Gymnodactylus fasciatus* Duméril and Bibron, 1836 into *Homonota*, creating the new combination *H. fasciata* — a junior secondary homonym of Blyth's (1853) name. Kluge (1964) was aware of the earlier name and indicated “[non] *Homonota fasciata*: Jerdon [sic], 1853, p. 468” in his account of this species. Wermuth (1965) subsequently provided a replacement name for *G. fasciatus*, *G. pasteuri*, in order to deal with another instance of secondary homonymy, that between *G. fasciatus* Duméril and Bibron, 1836 and *Uromastix fasciatus* Ménériès, 1832, a junior subjective synonym of *Gymnodactylus caspius* Eichwald, 1831 (now *Tenuidactylus caspius*). In an addendum to the same work, Wermuth (1965) incorporated Kluge's (1964) generic reallocations and transferred *G. fasciata* Duméril and Bibron, 1836 to *Homonota*, as *Homonota pasteuri* (nomen novum). Although neither name was cited extensively in the following decades, Vanzolini (1968) and Cei (1978) used Wermuth's replacement name, whereas Kluge (1991, 1993) continued to use *H. fasciata*. Abdala and Lavilla (1993) provided further evidence to support Kluge's usage and subsequently, most authors (e.g., Abdala, 1993, 1998; Dirksen and de la Riva, 1999; Rösler, 2000; Kluge, 2001) have employed this name. Abdala and Lavilla (1993) based their argu-

ment on the fact that the removal of *H. fasciata* to *Teratolepis* by Günther (1869) obviated the need for a replacement name.

Annandale (1906) described a second species, *Teratolepis scabriceps* from Rámanád [= Ramnad], Madura [= Madurai] District, Tamil Nadu but this species, which has subsequently been collected in Sri Lanka as well (Maricukatti [= Marichchukkaddi], Northern Province), was removed to a new genus, *Lophopholis*, by Smith and Deraniyagala (1934) on the basis that it possessed the imbricate scales, but not the undivided scansors of *T. fasciata*. Smith (1935) also reported the locality Adiyar [= Adayar] near Madras [= Chennai] for this species. Deraniyagala (1953) recognized the affinity of *Lophopholis* to *Hemidactylus* by including both genera (along with the dissimilar *Calodactylodes*) in his subfamily Hemidactylinae and most subsequent authors have allocated *L. scabriceps* to the genus *Hemidactylus* (e.g., Loveridge, 1947; Kluge, 1991, 1993, 2001; Das and Andrews, 1997; de Silva, 1996, 1998; Rösler, 2000; Das and de Silva, 2005) although it has been retained as a separate genus by some workers (e.g., Murthy, 1990; Tikader and Sharma, 1992).

Grandison and Soman (1963) described the small terrestrial gecko *Hemidactylus albofasciatus* from the villages of Dorle, Dabhill and Gavkhadi in the Ratnagiri District of Maharashtra. This species has only partly divided subdigital scansors and imbricate scales on the tail. Grandison and Soman (1963) suggested that the affinities of *H. albofasciatus* were with *H. reticulatus*, another small terrestrial *Hemidactylus* with undivided proximal subdigital lamellae. More recently Murthy (1990) suggested a close relationship to another Indian endemic, *H. prashadi*, although the basis for this is unclear as the two taxa exhibit size, colour, scansor, and body and tail scalation features that are greatly dissimilar to one another. Kluge (1967) first transferred *H. albofasciatus* to *Teratolepis* based on a personal communication from Jerry A. Anderson. Subsequent workers have either retained *albofasciatus* in *Hemidactylus* (Murthy, 1990; Tikader and Sharma, 1992; Sharma, 2002), or removed it to *Teratolepis* (e.g., Das et al., 1998; Das, 2001; Rösler, 2000; Kluge, 2001), although none have presented explicit justifications for their allocations.

The recent taxonomic history of both *T. albofasciata* and *H. scabriceps* thus suggests that *Teratolepis* and *Hemidactylus* are closely allied. Indeed, as early as 1876 Theobald noted the similarity of *Teratolepis* to *Hemidactylus* spp., especially with respect to head scalation. The close relationship of these two genera was recently confirmed by Han et al. (2004) and Feng et al. (2007), who found that *Hemidactylus* and *Teratolepis* shared, along with *Agamura*, *Crosobamon*, *Cyrtodactylus* and *Geckoella*, a 9 bp insertion and a 21 bp deletion in the nuclear gene *c-mos*. Unfortunately, however, this analysis used only generic exemplars and an even more recent species-level phylogeny of *Hemidactylus* based on mitochondrial genes (Carranza and Arnold, 2006) did not include any specimens of *Teratolepis* spp., nor any other endemic South Asian taxa.

The recent rediscovery of *Teratolepis albofasciata* by one of us (VG) at Dorle village provided genetic material to assess the relationships of this taxon and precipitated a reinvestigation of the status of *Teratolepis* and its affinities with respect to *Hemidactylus*.

Materials and methods

Based on preliminary results from a broad scale phylogenetic analysis of all gekkotan lizards (Bauer, Jackman and Greenbaum, unpublished) the affinities of *Teratolepis* with *Hemidactylus* (Han et al., 2004; Feng et al., 2007) were confirmed. For this study, we thus included in our ingroup the two species currently assigned to *Teratolepis*, as well as representatives of Carranza and Arnold's (2006) five major clades, as well as the West African species *H. fasciatus*, which they sampled but did not include in any of their named clades. As geographic proximity suggested that affinities of *Teratolepis* would most likely be with Carranza and Arnold's "Tropical Asian Clade", we included representatives of all of the constituent taxa reported on by Carranza and Arnold (2006), as well as the Indian endemics *H. reticulatus* and *H. gracilis*. These two species have been proposed to be closely allied to one another (Bauer et al., 2005) and the former species had previously been predicted to be allied to *Teratolepis albofasciata* (Grandison and Soman, 1963). We used three representatives of the chiefly southeast Asian/Indo-Australian

genus *Cyrtodactylus* as outgroup taxa based on the results of Han et al. (2004) and Feng et al. (2007). Specimens sampled and their associated clade membership based on Carranza and Arnold (2006) are listed in Table 1.

Genomic DNA was isolated from 95–100% ethanol-preserved tail or liver samples with the Qiagen DNeasy tissue kit (Valencia, CA, USA). We used double-stranded PCR to amplify 3733 aligned bases of mitochondrial (ND2, ND4, *cyt b*) and nuclear (RAG1, PDC) gene sequence data with five different pairs of published primers (Table 2). For some key taxa, not all five genes could be sequenced: ND2, ND4 and RAG1 lacking for *Hemidactylus reticulatus*; *cyt b*, ND4, RAG-1 and PDC lacking for *H. gracilis* and *Teratolepis albofasciata*.

Amplification of 25 μ l PCR reactions was executed on an Eppendorf Mastercycler gradient thermocycler. Amplification of genomic DNA occurred with an initial denaturation step of 95°C for 2 min, followed by denaturation at 95°C for 35 s, annealing at 50°C for 35 s, and extension at 72°C for 95 s with 4 seconds added to the extension per cycle for 32 cycles for mitochondrial DNA and 34 cycles for nuclear DNA. When necessary, annealing temperatures were adjusted to increase or decrease specificity on a case by case basis, and products were visualized with 1.5% agarose gel electrophoresis. Target products were purified with AMPure magnetic bead solution (Agencourt Bioscience) and sequenced with either the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) or the DYEnamic™ ET Dye Terminator Kit (GE Healthcare). Sequencing reactions were purified with CleanSeq magnetic bead solution (Agencourt Bioscience) and analyzed with an ABI 3700 automated sequencer. The accuracy of sequences was ensured by incorporating negative controls and sequencing complementary strands. Sequences were aligned by eye in the computer program SeqMan, and protein-coding genes were translated to amino acids with MacClade (Maddison and Maddison, 1992) to confirm conservation of the amino acid reading frame and check for premature stop codons.

Phylogenetic relationships among the samples were assessed with maximum parsimony and Bayesian optimality criteria. Based on the missing data indicated above, three datasets

were analyzed: RAG1, PDC, ND2, ND4 and *cyt b* (all taxa except *T. albofasciata*, *H. reticulatus* and *H. gracilis*), PDC and *cyt b* (all taxa except *T. albofasciata* and *H. gracilis*), and ND2 alone (all taxa except *H. reticulatus*).

Maximum parsimony (MP) analyses were conducted in PAUP*4.0b10 (Swofford, 2002). The heuristic search algorithm was used with the following conditions: 25 random-addition replicates, accelerated character transformation (ACCTRAN), tree bisection-reconnection (TBR) branch swapping, zero-length branches collapsed to yield polytomies, and gaps treated as missing data. Each base position was treated as an unordered character with four alternate states. We used nonparametric bootstraps (1000 pseudoreplicates) to assess node support in resulting topologies.

The Akaike Information Criterion (AIC) in ModelTest 3.06 (Posada and Crandall, 1998) was used to find the model of evolution that best fit the data for subsequent Bayesian inference (BI) analyses. The GTR + γ + I model was used with the most parsimonious tree to estimate the parameters, and the same conditions as the parsimony search were used to find the Bayesian trees with the best likelihood scores.

Partitioned Bayesian analyses were conducted with MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) with default priors. Separate models for each gene and codon position of protein-coding genes were estimated (Brandley et al., 2005). A total of 10 partitions were made: RAG1, 3 codons; PDC, 3 codons, ND2, ND4 and *cyt b*, 3 codon positions; and mitochondrial tRNAs. Analyses were initiated with random starting trees and run for 2,000,000 generations; Markov chains were sampled every 100 generations. Convergence was checked by plotting likelihood scores against generation, and 125 trees were discarded as "burn in." Two separate analyses with two independent chains were executed to check for convergence of log-likelihoods in stationarity (Huelsenbeck and Ronquist, 2001). Both analyses ended with the standard deviation of split frequencies less than 0.01.

RESULTS

The dataset based on all genes yielded a Bayesian tree (Fig. 1) in which each of Carranza and Arnold's (2006) clades except the 'Tropical

Asian Clade' were monophyletic with posterior probabilities of 1.0. The *H. angulatus* clade was sister to the remaining members of the genus, which were themselves divided into two weakly supported clades ($pp < 0.90$): one consisting of *H. fasciatus* as the sister group of a subset of the Tropical Asian clade comprising *H. garnotii*, *H. karenorum*, *H. bowringii* and *H. platyurus* (we here follow Zug et al., 2007 in formally allocating the members of the genus *Cosymbotus* to *Hemidactylus*), and another with the remaining Tropical Asian forms as the sister group to the Arid clade plus the African-Atlantic and *H. mabouia* clades. Support for interclade relationships was generally weak, with only the union of *H. mabouia* with the African-Atlantic clade receiving strong support ($pp = 1.0$). Within the Tropical Asian species, all relationships in both clades, except the sister group relationship of *H. garnotii* and *H. bowringii* were supported by posterior probabilities of 1.0. In this analysis, *Teratolepis fasciata* was strongly supported as the sister species of *H. brookii*, with *H. frenatus* and *H. flaviviridis* as sequentially more distant relatives.

In the Bayesian analysis of ND2 alone, all of Carranza and Arnold's (2006) clades were monophyletic, although the Tropical Asian clade had no significant support ($pp = 0.62$). All other interclade relationships were well-supported, but the tree topology differed greatly from that of the previous analysis: Arid clade ((*H. mabouia*, African-Atlantic clade) ((*H. fasciatus*, *H. angulatus* clade) Tropical Asian clade)). Within the Tropical Asian clade, the same two groupings revealed by the larger data set were recovered, but in this case *H. karenorum* was weakly supported as the sister of *H. garnotii* ($pp = 0.60$). In the *H. brookii* subclade, relationships among the species dealt with in the previous analysis were identical. The added taxa, *Teratolepis albofasciata* and *H. gracilis* were strongly supported as sequential sister taxa to *Teratolepis fasciata*, with all three taxa sister to *H. brookii* (Fig. 2A).

In the PDC and *cyt b* analyses, all higher order relationships, except the monophyly of *Hemidactylus* sensu lato and the union of *H. mabouia* with the African-Atlantic clade ($pp = 1.0$), received weak support and were different from both previous analyses: *H. angulatus* clade (Arid clade (*H. fasciatus* (*H. mabouia*,

African-Atlantic clade) Tropical Asian clade))). Relationships also differed within the Tropical Asian clade, with *H. flaviviridis* more closely related to the *H. bowringii* group than to the *H. brookii* group. However, the remaining relationships within the *H. brookii* group were identical to both other analyses with respect to shared taxa (Fig. 2B). The additional taxon for which only PDC and *cyt b* were available, *H. reticulatus*, was strongly supported as the sister to *T. fasciata*.

Maximum parsimony analyses of the same datasets yielded less well-resolved trees that were, however, fully consistent with the Bayesian analyses. Parsimony bootstrap support was high (> 90%) for all clades that also had high posterior probabilities (Fig. 1). In the ND2 and PDC + *cyt b* analyses, *H. gracilis* and *Teratolepis albofasciata*, and *H. reticulatus*, respectively, were likewise strongly supported as constituting a monophyletic group with *T. fasciata* (Fig. 2).

DISCUSSION

Phylogeny.— With respect to the monophyly of each of the clades identified by Carranza and Arnold (2006), our results are consistent with these authors' own findings of moderate to high support values. On the other hand, our different analyses yielded different patterns of relationship among these clades, an unsurprising result, given that Carranza and Arnold (2006) reported no significant support values for inter-clade relationships in their analyses. However, our data did yield consistent support for the sister group relationship of *H. mabouia* and the African-Atlantic clade. The position of *H. fasciatus* remains problematic, grouping weakly with the *bowringii* group of the Tropical Asian clade (all genes) or the *H. mabouia*/African-Atlantic clade + all Tropical Asian taxa (PDC and *cyt b*), or strongly with the *H. angulatus* clade (ND2).

Patterns within the Tropical Asian clade are more consistent. The two clades reflected in Carranza and Arnold's (2006) results, the *H. bowringii* and *H. brookii* groups, are always retrieved, although in the PDC/*cyt b* tree, *H. flaviviridis* clustered weakly with the *H. bowringii* group, rather than with the *H. brookii* group. Patterns within the *H. bowringii* group varied slightly between analyses and from

those reported by Carranza and Arnold (2006). However, patterns within the *H. brookii* group were consistent and in the five-gene analysis, *Teratolepis fasciata* was the sister group to *H. brookii*. Based on the ND2 data, the two species of *Teratolepis* are each other's sister species and are nested deep within the *Hemidactylus* tree, closer to *H. gracilis* than to *H. brookii*. Although we lack ND2 data for *H. reticulatus*, this species is strongly supported as the sister group to *Teratolepis* by *cyt b* data (lacking for *H. gracilis* and *T. albofasciata*). With the available data, it is not possible to resolve the relationships of *H. gracilis*, *H. reticulatus* and *Teratolepis* to one another, but it is clear that all four are members of a single, well-supported clade.

Teratolepis is just one of several small genera of geckos that have long been recognized as allied to *Hemidactylus*, but which have been segregated because of their possession of one or more recognizable features, which although diagnostic, are probably best regarded as autapomorphic and not indicative of higher relationships. Parker (1942), who studied the speciose and morphologically diverse *Hemidactylus* of the Horn of Africa, considered generic arrangements that partitioned *Hemidactylus*-like genera into different groups to be largely arbitrary. However, prevailing systematic views of the period favored the recognition of morphologically distinctive groups, even if this rendered other groups paraphyletic.

The strongly supported inclusion of *Teratolepis* within *Hemidactylus* is not surprising. Earlier authors (Grandison and Soman, 1963; Murthy, 1990) hypothesized close relationships between *T. albofasciata* and South Asian *Hemidactylus*, and Anderson (1964) noted similarities in the vocalizations of *T. fasciata* in the Indus Delta plain to those of sympatric *Hemidactylus*. Russell (1972, 1976, 1979), who argued that internal digital anatomy was a more reliable indicator of homology and affinity than external form, defined a '*Hemidactylus* group' of geckos (*Hemidactylus*, *Briba*, *Cosymbotus*, *Dravidogecko*, *Teratolepis*) based on a series of apparently derived internal digital structures: dorsal interossei muscles robust — with fleshy bellies extending as far as the digital inflection, tendinous insertion of dorsal interossei muscles onto distal margin of each scansor, and anteped-

Table 1. List of samples used in this study and their membership in the clades of *Hemidactylus* identified by Carranza and Arnold (2006). Collection abbreviations: AMB = Aaron M. Bauer field series, BNHS = Bombay Natural History Society, CAS = California Academy of Sciences, FK = Fred Kraus field series, FMNH = Field Museum of Natural History, ID = Indraneil Das field series, JFBM = James Ford Bell Museum, University of Minnesota, St. Paul, JS = Jay Sommers (Kansas City), KU = University of Kansas Natural History Museum, LLLG = L. Lee Grismer field series, LSUMZ = Louisiana State University Museum of Natural Sciences, MCZ = Museum of Comparative Zoology, Harvard University, MVZ = Museum of Vertebrate Zoology, University of California, Berkeley, MZUSP = Museu de Zoologia da Universidade de São Paulo, WRB = William R. Branch field series.

Sample	Clade Membership (Carranza & Arnold, 2006)	Museum No.	Locality	GenBank Accession Numbers						
				cyt b	ND2	ND4	RAG-1	PDC		
<i>Cyrtodactylus ayeaewandensis</i>	—/outgroup	CAS 216446	Myanmar, Rakhine State, vic. Kanthaya Beach	EU268380	EU268348	EU268411	EU268287	EU268317		
<i>Cyrtodactylus consobrinus</i>	—/outgroup	LLG 4062	Malaysia, Sarawak, Niah Cave	EU268381	EU268349	EU268412	EU268288	EU268318		
<i>Cyrtodactylus loriae</i>	—/outgroup	FK 7709	Papua New Guinea, Milne Bay Province, Bumisi, N slope of Mt. Simpson	EU268382	EU268350	EU268413	EU268289	EU268319		
<i>Hemidactylus cf. angulatus</i>	H. angulatus	MVZ 245438	Nigeria, Togo Hills, Nkwanta	EU268399	EU268367	EU268430	EU268306	EU268336		
<i>Hemidactylus bowringii</i> 1	Tropical Asian	CAS 206649	Myanmar, Sagaing Division, Alaungdau Kathapa Natl. Park	EU268405	EU268373	EU268436	EU268312	EU268342		
<i>Hemidactylus bowringii</i> 2	Tropical Asian	CAS 228109	China, Yunnan Province, Nujang District, Liuku	EU268406	EU268374	EU268437	EU268313	EU268343		
<i>Hemidactylus brasiliensis</i>	African-Atlantic	MZUSP 92493	Brazil, Piauí, Parque Nacional Serra das Confusões	EU268383	EU268351	EU268414	EU268290	EU268320		
<i>Hemidactylus brookii</i> 1	Tropical Asian	LLG 6755	Malaysia, Pulau Pinang, Empanggon Air Hitam	EU268398	EU268366	EU268429	EU268305	EU268335		
<i>Hemidactylus brookii</i> 2	Tropical Asian	LLG 6754	Malaysia, Pulau Pinang, Empanggon Air Hitam	EU268397	EU268365	EU268428	EU268304	EU268334		
<i>Hemidactylus brookii</i> 3	Tropical Asian	CAS 206638	Myanmar, Mandalay Division	EU268407	EU268375	EU268438	EU268314	EU268344		
<i>Hemidactylus fasciatus</i> 1	not placed in clade	WRB no number	Gabon, Rabi	EU268402	EU268370	EU268433	EU268309	EU268339		
<i>Hemidactylus fasciatus</i> 2	not placed in clade	CAS 207777	Equatorial Guinea, Bioko Island, 3.6 km N of Luba	EU268403	EU268371	EU268434	EU268310	EU268340		
<i>Hemidactylus flaviviridis</i> 1	Tropical Asian	FMNH 245515	Pakistan, Punjab Province	EU268387	EU268355	EU268418	EU268294	EU268324		
<i>Hemidactylus flaviviridis</i> 2	Tropical Asian	ID 7626	India, Rajasthan, Kuldhara	EU268388	EU268356	EU268419	EU268295	EU268325		

<i>Hemidactylus frenatus</i> 1	Tropical Asian	LLG 6745	Malaysia, Pulau Pinang, Empangon Air Hitam	EU268390	EU268358	EU268421	EU268297	EU268327
<i>Hemidactylus frenatus</i> 2	Tropical Asian	AMB 7411	Sri Lanka, Pidipitya	EU268389	EU268357	EU268420	EU268296	EU268326
<i>Hemidactylus frenatus</i> 3	Tropical Asian	AMB 7420	Sri Lanka, Rathgala	EU268391	EU268359	EU268422	EU268298	EU268328
<i>Hemidactylus garnotii</i> 1	Tropical Asian	CAS 223286	Myanmar, Rakhine State, Taung Gok Township, Ma Ei Ywa Ma Village	EU268395	EU268363	EU268426	EU268302	EU268332
<i>Hemidactylus garnotii</i> 2	Tropical Asian	CAS 222276	Myanmar, Mon State, Kyaihto Township, Kyait Hti Yo Wildlife Sanctuary	EU268396	EU268364	EU268427	EU268303	EU268333
<i>Hemidactylus gracilis</i>	not included	BNHS 1592	India, Maharashtra, Pune	—	EU268379	—	—	—
<i>Hemidactylus greeffii</i>	African-Atlantic	CAS 219044	São Tome and Principe, São Tome Island, Praia da Mutamba	EU268401	EU268369	EU268432	EU268308	EU268338
<i>Hemidactylus hatitanius</i>	H. angulatus	CAS 198442	Dominican Republic, Nacional Dist., near Santo Domingo	EU268404	EU268372	EU268435	EU268311	EU268341
<i>Hemidactylus karenorum</i>	Tropical Asian	CAS 210670	Myanmar, Mandalay Division, Kyaukpadaung Township, Popa Mt. Park	EU268394	EU268362	EU268425	EU268301	EU268331
<i>Hemidactylus mabouia</i>	H. mabouia	MCZ R-184446	South Africa, Limpopo Province	EU268393	EU268361	EU268424	EU268300	EU268330
<i>Hemidactylus palaichthus</i>	African-Atlantic	LSUMZ H-12421	Brazil, Roraima State	EU268400	EU268368	EU268431	EU268307	EU268337
<i>Hemidactylus persicus</i>	Arid	CAS 227612	Oman, Wilayat Nazwa, 4.5 km N. of Tanuf, Wadi Tanuf	EU268409	EU268377	EU268440	EU268316	EU268346
<i>Hemidactylus platyurus</i>	Tropical Asian	KU 304111	Philippines, Lubang	EU268384	EU268352	EU268415	EU268291	EU268321
<i>Hemidactylus reticulatus</i>	not included	AMB 5730	India, Tamil Nadu, Vellore	EU268410	—	—	—	EU268347
<i>Hemidactylus robustus</i>	Arid	MVZ 248437	Pakistan, Thatta District, 40 km S of Mipur Sakro	EU268408	EU268376	EU268439	EU268315	EU268345
<i>Hemidactylus turcicus</i>	Arid	LSUMZ H-1981	USA, Louisiana, Baton Rouge	EU268392	EU268360	EU268423	EU268299	EU268329
<i>Teratolepis albofasciata</i>	not included	BNHS 1579	India, Maharashtra, Ratnagiri District, Dorle Village	—	EU268378	—	—	—
<i>Teratolepis fasciata</i>	not included	JS 11	Pakistan (captive specimen)	EU268385	EU268353	EU268416	EU268292	EU268322
<i>Teratolepis fasciata</i>	not included	JFBM 2	Pakistan (captive specimen)	EU268386	EU268354	EU268417	EU268293	EU268323

Table 2. Primers used in this study.

Primer	Gene	Reference	Sequence
ND4f11	ND4	Jackman et al. (2008)	5'-GCAAATACAAACTAYGAACG-3'
Laur1	Leu tRNA	Arevalo et al. (1994)	5'-CATTACTTTTTACTTGGATTGACCA-3'
PHOF2	PDC	Bauer et al. (2007)	5'-AGATGAGCATGCAGGAGTATGA-3'
PHOR1	PDC	Bauer et al. (2007)	5'-TCCACATCCACAGCAAAAACTCCT-3'
L4437b	Met tRNA	Macey et al. (1997)	5'-AAGCAGTTGGGCCCATACC-3'
L5002	ND2	Macey et al. (1997)	5'-AACCAAAACCAACTACGAAAAAT-3'
ND2f101	ND2	Greenbaum et al. (2007)	5'-CAAACACAAACCCGRAAAAT-3'
ND2r102	ND2	Greenbaum et al. (2007)	5'-CAGCCTAGGTGGGCGAATTG-3'
Trpr3a	Trp tRNA	Greenbaum et al. (2007)	5'-TTTAGGGCTTTGAAGGC-3'
H5934a	COI	Macey et al. (1997)	5'-AGRGTGCCAATGTCTTTGTGRIT-3'
R13	RAG1	Groth and Barrowclough (1999)	5'-TCTGAATGGAAATCAAGCTGTT-3'
R18	RAG1	Groth and Barrowclough (1999)	5'-GATGCTGCCTCGGTCGGCCACCTTT-3'
RAG1 F700	RAG1	Bauer et al. (2007)	5'-GGAGACATGGACACAATCCATCCTAC-3'
RAG1 R700	RAG1	Bauer et al. (2007)	5'-TTTGACTGAGATGGATCTTTTGCA-3'

multimate phalanx on digits III and IV of manus and III-V of pes short and erect. In addition, all members of this group that have paraphalanges possess the *Hemidactylus* type, lying within the lateral digital tendons (Russell and Bauer, 1988).

Subsequent phylogenetic work has borne out the evolutionary reality of this cluster of genera; Carranza and Arnold (2006) demonstrated that both *Cosymbotus* and *Briba* were embedded within major clades of *Hemidactylus* — a fact corroborated here. Both of these groups have typical *Hemidactylus*-type divided subdigital scansors and are arboreal.

The two *Hemidactylus* that are particularly closely related to *Teratolepis*, *H. gracilis* and *H. reticulatus* are poorly known, but both are primarily terrestrial (Sanyal et al., 1993; Murthy, 1990; Bauer et al., 2005) as are the *Teratolepis* species (Grandison and Soman, 1963; Anderson, 1964; Minton, 1966). As early as 1912 Annandale suggested that *H. gracilis* (as *H. platyceps*) was most closely related to *H. reticulatus*, and in 1972, Russell had identified a group within *Hemidactylus* that shared a distinctive pattern of digital anatomy — this comprised *H. albofasciatus*, *H. gracilis* and *H. reticulatus*, as well as the Socotran species *H. pumilo*, which is also terrestrial (Rösler and Wranik, 2000, 2003). The remaining member of Russell's *Hemidactylus* group, *Dravidogecko anamallensis*, is also chiefly terrestrial or rupicolous (Gvoždik and Veselý, 1998; Henkel and Schmidt, 2003). All of these taxa share a number of morphological

features in common with each other that are associated with their terrestrial habitus. Bauer and Russell (1995) demonstrated that undivided subdigital scansors were shared by *T. fasciata*, *H. reticulatus* and *Dravidogecko anamallensis* and that an intermediate pattern of divided distalmost scansors occurred in *T. albofasciata*, as well as a few *Hemidactylus* sensu stricto, such as *H. bouvieri* and *H. somalicus*. Based on the continuum between divided and undivided scansors, the fact that at least one *Hemidactylus* has completely undivided scansors, and their shared internal digital anatomy, Bauer and Russell (1995) synonymized *Dravidogecko* with *Hemidactylus*. Although they did not explicitly address the taxonomic status of *Teratolepis*, identical arguments could be made for its synonymization with *Hemidactylus*. Unfortunately, we lacked tissue samples of *Hemidactylus* (formerly *Dravidogecko*) *anamallensis* and are unable to assess whether it is also a member of the *Teratolepis* clade or if its undivided scansors represent a convergent morphology within the Tropical Asian clade of *Hemidactylus*, although on biogeographic grounds, we suspect the former interpretation. Bauer and Russell (1995) concluded that *H. anamallensis* was a relatively primitive *Hemidactylus*, but if we are correct in our conjecture, it represents part of a highly derived lineage that has undergone secondary loss of some scansorial features. *Hemidactylus scabriceps* may well also be a member of this radiation as it shares imbricate scalation with *Teratolepis* spp. This taxon is particularly poor-

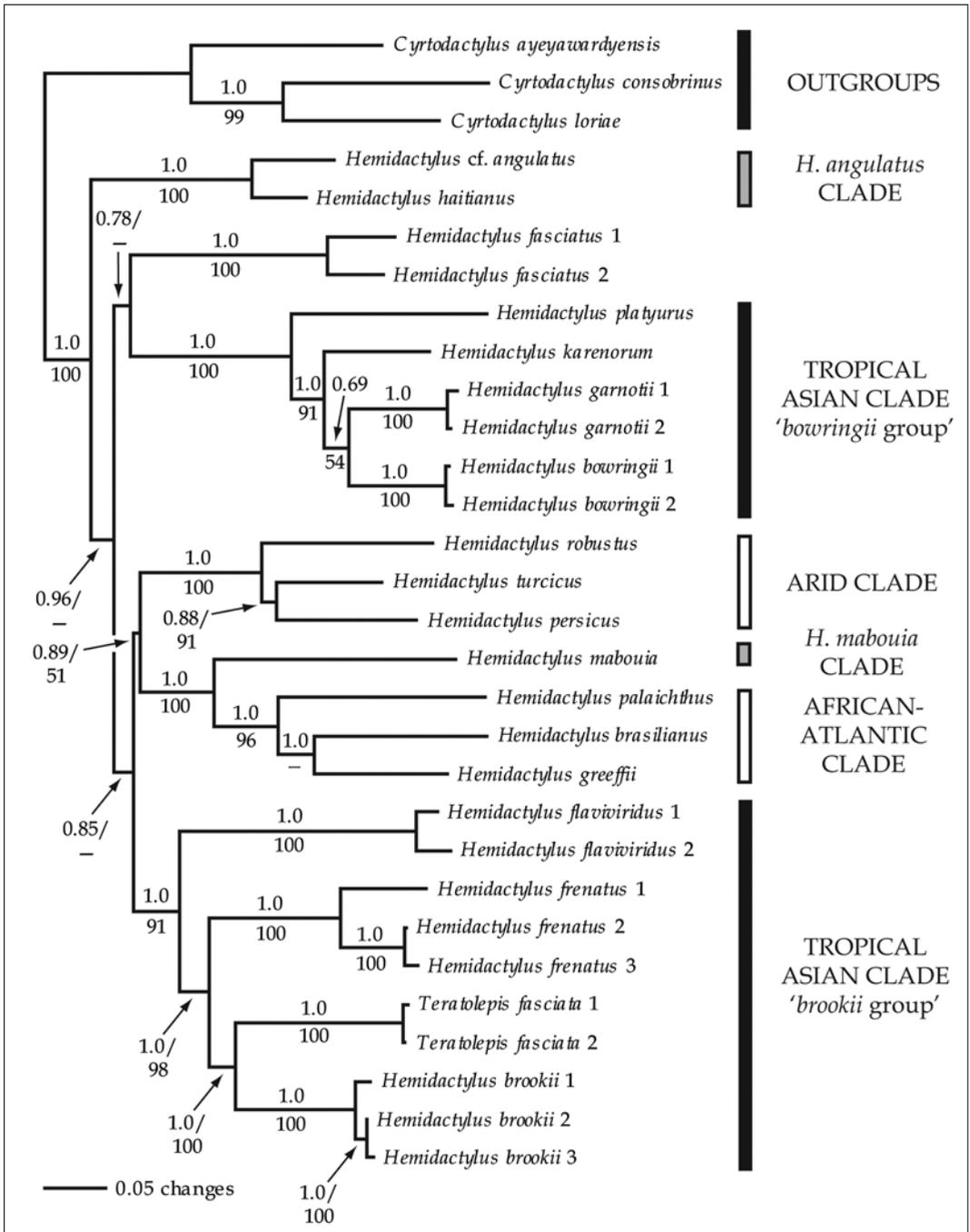


Figure 1. Phylogenetic relationships among *Teratolepis fasciata* and representative species of *Hemidactylus* based on the combined analysis of the mitochondrial genes ND2, ND4 and *cyt b*, and the nuclear genes RAG1 and PDC. Bayesian inference tree with branch lengths corresponding to those of tree with best likelihood score. Bayesian posterior probabilities indicated above the branches and maximum parsimony bootstraps indicated below. Bars at right indicate membership in the main clades of *Hemidactylus* identified by Carranza and Arnold (2006). Note the lack of support for a monophyletic Tropical Asian Clade and the strong support for the inclusion of *Teratolepis fasciata* within the *brookii* group.

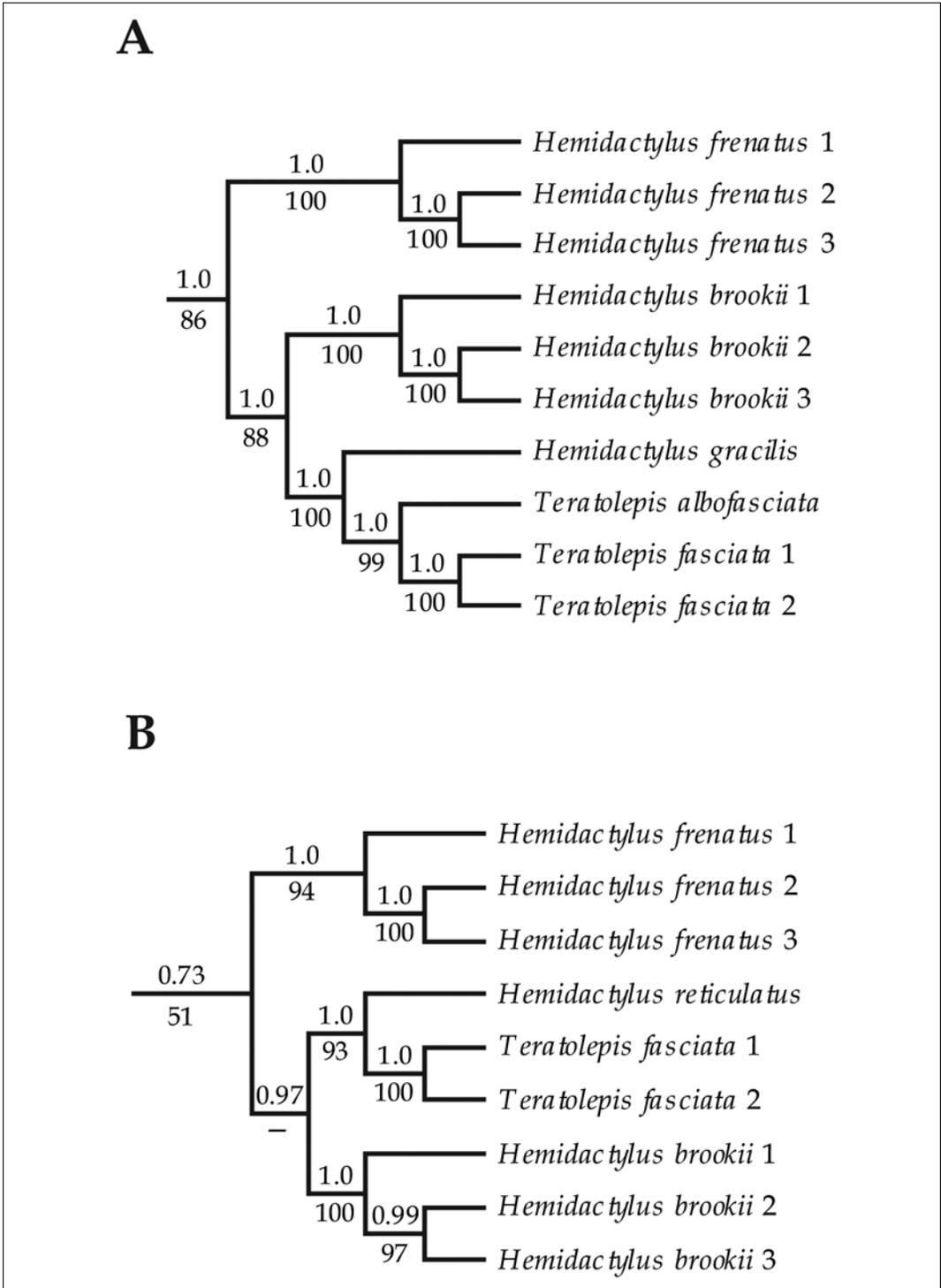


Figure 2. Phylogenetic relationships among members of the *Hemidactylus brookii* group based on ND2 alone (A) and *cyt b* and PDC alone (B). The analyses of these particular partitions permitted the inclusion of key taxa for which complete data were lacking: *H. gracilis* and *Teratolepis albofasciata* (A) and *H. reticulatus* (B). Results of the phylogenetic analyses of all taxa sampled are presented in the text. Topologies depicted are from the Bayesian tree and do not show likelihood branch lengths. Bayesian posterior probabilities indicated above the branches and maximum parsimony bootstraps indicated below. The added taxa are strongly supported as members of the *brookii* group and as close relatives of *Teratolepis fasciata* in particular.

ly known, with no new specimens having been recorded since Smith (1935). Indeed, the validity of the Sri Lankan record, dating from 1933, is questionable and relatively intense search efforts by several groups of researchers (e.g., Manamendra-Arachchi, 1997) have yielded no additional specimens. It has been considered extirpated by some authors (Somaweera and Wickramasinghe, 2006).

Taxonomic Implications.— Regardless of the precise pattern of relationships among the members of the *Teratolepis* group, it is clear that maintenance of monophyletic groupings requires their collective inclusion into *Hemidactylus*. While this poses no problem in the case of *T. albofasciata*, which reverts to the genus within which it was initially described, it has more far-reaching taxonomic implications for *Teratolepis fasciata* which becomes *Hemidactylus fasciatus* (Blyth, 1853), a secondary junior homonym of *Hemidactylus fasciatus* Gray, 1842, a common and widespread species of West African gecko. There are no junior synonyms available for *T. fasciata* (see synonymies in Smith 1935; Wermuth 1965; Rösler 2000; Kluge 2001) so a replacement name is required. We, therefore, propose *Hemidactylus imbricatus* Bauer, Giri, Greenbaum, Jackman, Dharne & Shouche as a *nomen novum* for *Hemidactylus fasciatus* (Blyth, 1853) in order to prevent secondary homonymy. The specific epithet refers to the imbricate scales of the dorsum, and particularly the tail of this species.

Comments on original description and distribution of *Hemidactylus imbricatus*, nom. nov.— Blyth's description of *Homonota fasciata* has been cited as Blyth or Blyth in Jerdon "1854 (1853)" by several recent authors (e.g., Das et al., 1998; Kluge, 2001) and many modern authors (e.g., Hoge and Romano Hoge, 1981; Golay et al., 1993; McDiarmid et al., 1999; David and Ineich, 1999) have given the date of 1854 to species described by Jerdon in the same paper. The 1854 date is almost certainly based on that on the title page of the entire volume in which the paper appeared. However, the original wrappers on the specific part of the journal containing this paper (Volume 22[VI] = issue CCXXXVII) are dated 1853 and in the absence of information to the contrary, we follow Bauer (2003) and accept this date as correct.

Although Blyth (1853) did not specify the origin of the types of *Homonota fasciata*, Theobald (1876) subsequently stated that the type locality was "Jaulnah," Hyderabad Province [= Jalna, Maharashtra]. It is unclear from the description if there was more than one type specimen, but ZSI 5981, now in terrible condition, has been regarded as the holotype. Das et al. (1998), however, noted that BMNH 69.8.28.32, presented by Dr. A. H. Leith from Sind, might be a syntype. This assertion was based on a penciled note in the BMNH loose-leaf catalogue, but is not substantiated by any other data (C. J. McCarthy in litt. April 2007). Indeed, it is clear that this specimen is that examined and discussed by Günther (1869).

Boulenger (1890) and Annandale (1905) considered *T. fasciata* to be distributed in Sind and the Deccan — the latter based solely on Theobald's (1876) Jalna record. The populations in Pakistan are well documented. Smith (1935), Anderson (1964), Minton (1962, 1966), Mertens (1969), and Khan (2002, 2004) reported *T. fasciata* from the Indus Delta of Sind and Minton (1966) considered it restricted to the Tatta and Hyderabad districts of the province. Khan (1999) characterized its habitat as tropical thorn forest and sand dunes in semi-desert areas of the Thar Desert and later (Khan, 2006) as *Salsola* and grass-dominated areas of desert scrub vegetation on silt. Although some of the reported localities to the east of the Indus River approach the Indian border quite closely, there have been no records from adjacent Rajasthan.

Aside from the Jalna record, the only locality in the current territory of the Republic of India is that reported by Smith (1935) from Shillong in the Khasi Hills of north-eastern India. Both Indian localities were considered erroneous by Minton (1966) and Khan and Mirza (1977), and Das (2001) considered only Pakistani records to be valid. Nonetheless, *Teratolepis fasciata* has continued to be listed as part of the Indian fauna by many subsequent authors (e.g., Daniel, 1983, 2002; Murthy, 1990; Tikader and Sharma, 1992; Mathew, 1995; Sharma, 2002). Tikader and Sharma (1992) added an unspecified record from Tamil Nadu and also incorrectly included Sri Lanka in the range of the species. All these records are almost certainly incorrect. However, one of the authors (VBG) has recently discov-

ered a new species of *Hemidactylus* clearly allied to *H. imbricatus* from Maharashtra (to be described elsewhere) and it is possible that this species (or *H. albofasciatus* or *H. scabriceps*) might have been responsible for at least the doubtful peninsular localities, particularly if identification was based on the imbricating caudal scalation shared by all of these taxa.

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