

Phylogenetic relationships of geckos of the genus *Nactus* and their relatives (Squamata: Gekkonidae)

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Abstract. We employed nuclear and mitochondrial DNA sequence data to investigate relationships within the gekkonid genus *Nactus* and between *Nactus* and other gekkonid genera. Nuclear (RAG-1, PDC) and mitochondrial (ND2) data provide strong support for conflicting patterns of relationship among bisexual New Guinean species of *Nactus* and the unisexual oceanic form *N. pelagicus*. This may be explained by an ancient mitochondrial introgression event between *N. sphaerodactyloides* and *N. vankampeni*, a recent selective sweep of mitochondrial DNA throughout *N. vankampeni*, and gene conflict stemming from the hybrid event that gave rise to *N. pelagicus*. Strong support from all data partitions is obtained for the sister group relationship of *Nactus* to a clade consisting of the Australian *Heteronotia* and the Southeast Asian *Dixonius*. Putative synapomorphies of the *Nactus/Heteronotia/Dixonius* clade include the reduction of the second phalanx of digit IV of the manus and the presence of regular rows of keeled (sometimes multicarinate) dorsal tubercles on the dorsum. *Nactus* and *Heteronotia* both include parthenogenetic species formed via hybridogenesis. This is rare among geckos, and vertebrates in general, and at some level may also be synapomorphic. *Dixonius* is not known to have any all-female species, but "*D. siamensis*" consists of multiple chromosome "races" that mirror morphologically cryptic, but karyotypically distinct, species in the other two genera. The strong support for the *Nactus/Heteronotia/Dixonius* clade demonstrates that the leaf-toed digital morphology of *Dixonius* has evolved multiple times within the Gekkonidae and suggests that superficial digital morphology may be misleading with respect to gekkonid suprageneric relationships.

Keywords. Gekkonidae, *Nactus*, *Heteronotia*, *Dixonius*, molecular phylogeny, convergence, parthenogenesis, digital morphology.

INTRODUCTION

Geckos and pygopods comprise the Gekkota, a relatively basal lineage among squamates (Townsend et al., 2004; Vidal and Hedges, 2005) and the only major lineage of pri-

marily nocturnal lizards (Pianka and Vitt, 2003). Current estimates of gekkotan diversity recognize approximately 1135 species in 108 genera (Kluge, 2001; Bauer, 2002; Han et al., 2004). The diversity of gekkotans, their great age (165-225 Myr; Kluge, 1987; Vitt et al., 2003; Vidal and Hedges, 2005; Kumazawa, 2007), and broad distribution, as well as their ecological significance and possession of many morphological, physiological, and behavioral autapomorphies (Pianka and Vitt, 2003) should make them model organisms for study. However, this has been hindered by a lack of a well-corroborated hypothesis of relationship among gekkotan taxa.

The composition and interrelationships of higher order gekkotan clades are generally well established (Kluge, 1967, 1987; Donnellan et al., 1999; Harris et al., 1999, 2001; Han et al., 2004; Townsend et al., 2004), as are species level phylogenies for some of the less diverse basal clades (e.g., Pygopodidae – Jennings et al., 2003; Carphodactylidae – Hoskin et al., 2003; Schneider, 2004). However, relationships between genera in the most speciose clade of gekkotans, the Gekkonidae, have never been resolved. Previous morphological studies have recognized the (often digital) autapomorphies of particular genera or clusters of genera, but have been unable to identify relationships between such clusters (Loveridge, 1947; Russell, 1972, 1976; Kluge, 1983). Further, extensive homoplasy with respect to digital characters has been both predicted *a priori* (Russell, 1976, 1979) and implied by non-congruence with other data sets (Han et al., 2004; Gamble et al., 2008). Until now mitochondrial DNA studies have likewise proved to be incapable of resolving many gekkonid intrageneric relationships as they suffer from both a lack of sampling across all taxa and limitations in the depth of phylogenetic divergences that can reliably be reconstructed (Ota et al., 1999).

As part of a broader study of gekkotan relationships we are currently examining both inter- and intrageneric level relationships among all recognized genera of gekkonids. Although several clusters of genera, such as those comprising the “*Gekko* Group” and the “*Pachydactylus* Group” have received consistent support from both morphological (Kluge, 1968; Russell, 1972; Haacke, 1976; Bauer, 1990; Kluge and Nussbaum, 1995) and molecular studies (Han et al., 2004; Bauer and Lamb, 2005; Lamb and Bauer, 2006), relationships among most gecko genera remain poorly resolved at best. This is especially true of those taxa that lack the adhesive subdigital mechanism for which many climbing geckos are known. Russell (1972, 1979), for example, established many intergeneric morphotypic groupings for “padded” geckos, but included all “padless” forms except *Cyrtodactylus*, *Stenodactylus* and *Teratoscincus* into a single cluster.

One padless genus that has received recent taxonomic attention is *Nactus*, a group of ten currently recognized species, as well as an uncertain number of undescribed forms in New Guinea (Donnellan and Moritz, 1995; Zug and Moon, 1995; Zug, 1998; Kraus, 2005; Rösler et al., 2005). Species of *Nactus* are chiefly terrestrial and are represented by bisexual species in the Mascarene Islands (*N. serpensinsula*, *N. coindemirensis*), in northern Australia (*N. eboracensis*, *N. galgajuga*, *N. cheverti*), New Guinea (*N. vankampeni*, *N. acutus*, *N. sphaerodactylodes*), and the southern Solomon Islands and northern and central Vanuatu (*N. multincarinatus*). In southern Vanuatu, New Caledonia, Fiji, Polynesia, and Micronesia a unisexual form, *N. pelagicus*, occurs (Moritz, 1987; Zug, 1989; Bauer and Henle, 1994; Zug and Moon, 1995; Kraus, 2005; Rösler et al., 2005).

The genus *Nactus* was erected by Kluge (1983) to accommodate certain species of geckos that were, at the time, assigned to the large, chiefly tropical Asian genus *Cyrto-*

dactylus. Kluge divided *Cyrtodactylus* on the basis of the condition of the second ceratobranchial arch. Whereas most members of the genus possessed the presumed derived condition of loss of this structure, a small cluster of species retained the primitive state and were thus allocated to Kluge's paraphyletic "Ptyodactylini." In addition to the hyoid arch condition, Kluge (1983) considered *Nactus* diagnosable on the basis of several external features including: regular rows of enlarged dorsal tubercles (absent in *N. coindemirensis*), multicarinate dorsal tubercles and carinate ventral scales (absent in *N. galgajuga*), and fused nasal bones (Kluge, 1983; Bullock et al., 1985). Among these features, multicarinate tubercles are autapomorphic (Kluge, 1983; Kraus, 2005), but fused nasals are widespread among diverse genera (Bauer, 1990; Kluge and Nussbaum, 1995). Bullock et al. (1985) redefined the genus, adding the lack of a radially directed portion on the ventralmost of the 14 scleral ossicles as a derived character of *Nactus*.

Kluge (1963) suggested that *Nactus* (then considered part of *Cyrtodactylus*) might be related to the Australian *Heteronotia*, but no explicit support for this was provided. Russell (1972: 171) subsequently stated "It is clear from the study of digital structure that *C. pelagicus* should be referred to *Heteronotia*" but no taxonomic action was taken. Ulber and Gericke (1988) hypothesized that *Nactus* was the sister group of *Cyrtodactylus* plus the genera of Palearctic naked-toed geckos (recognized by them as *Mediodactylus*, *Cyrtopodion*, *Tenuidactylus*, *Agamura*, *Bunopus*, *Alsophylax*, *Carinatogekko* and *Altiphylax*) and Macey et al. (2000) found weak support for *Nactus* as the sister group to *Cyrtopodion* based on allozymes, but their sampling included only six genera of geckos. Greer (1989), on the other hand, considered the affinities of *Nactus* to be unknown and in the absence of any explicit, well-supported higher order patterns of relationship including *Nactus*, Kraus (2005) included a diversity of potential outgroups in a phylogenetic analysis of *Nactus* based on 23 morphological characters. He used five different sets of outgroups: 1) "Gekkonini" with naked toes – *Alsophylax*, *Bunopus*, *Cyrtodactylus*, *Cyrtopodion*, *Mediodactylus*, *Tenuidactylus*; 2) "Ptyodactylini" with naked toes – *Paroedura* [sic!; this genus has distal subdigital scansors], *Pristurus*, *Quedenfeldtia*; 3) "Ptyodactylini" with fused nasals – *Ebenavia*, *Paragehyra*, *Paroedura*; 4) Austro-papuan gekkonids – *Cyrtodactylus*, *Gehyra*, *Gekko*, *Hemidactylus*, *Hemiphyllodactylus*, *Heteronotia*, *Lepidodactylus*; and 5) a combination of all 17 outgroup genera. Kraus (2005) found no evidence for the monophyly of *Nactus*, as the species lacking multicarinate tubercles (*N. galgajuga* and *N. coindemirensis*) consistently clustered with outgroup genera or as part of a basal polytomy involving the outgroups and an otherwise monophyletic *Nactus*.

Although it can be argued that some of the morphological characters employed by Kraus (2005) might be prone to homoplasy, at least in part the lack of evidence for the monophyly of *Nactus* may be due to the choice of outgroup taxa. We here present data on both the inter- and intrageneric relationships of *Nactus* in order to provide an appropriate basis for future phylogenetic studies within this genus and its nearest relatives and to identify evolutionary questions within this group that will require further study. Our findings indicate conflict between nuclear and mitochondrial data sets with respect to intrageneric relationships, but strongly support a pattern of intergeneric relationships that imply that traditional views regarding the phylogenetic value of digital morphology may be misleading.

MATERIAL AND METHODS

Eight samples of *Nactus* representing the parthenogenetic *N. pelagicus* and four New Guinean species were included in a broad multi-locus study of gekkotan relationships (Bauer A.M., Jackman T.R. and Greenbaum E., unpubl. data) that incorporated representatives of 467 species in 97 genera, including all gekkonid genera except one from South America (*Bogertia*) and representatives of the Palearctic Asian taxa *Alsophylax*, *Altigecko*, *Siwaligecko* and *Indogecko*, all of which are probably members of a larger clade of Palearctic bent-toed geckos which was represented by other taxa in our sampling. As a result, a strongly supported clade with long branch length including *Nactus* was identified as a member of a more inclusive group comprising the majority of Old World gekkonids exclusive of a small number of chiefly Palearctic genera (Gamble et al., 2008). For the present study, *Nactus* and the other members of its clade identified in the broader study (*Heteronotia* and *Dixonius*) were treated as ingroup taxa and representatives of two other well-supported lineages in the main gekkonid clade were chosen as outgroups (*Hemidactylus robustus* and *Gekko gecko*) (Table 1). Results of the broader study of gekkonid relationships will be presented elsewhere.

Genomic DNA was isolated from the tail or liver tissue samples preserved in 95-100% ethanol with the Qiagen DNeasy tissue kit (Valencia, CA, USA). We used double-stranded PCR to amplify 2,971 aligned bases of six mitochondrial (ND2 and five tRNAs – 1,484 bases) and two nuclear (1,068 bases of RAG-1 and 419 bases of PDC [phosducin]) genes using the primers listed in Table 2 (see Jackman et al., 2007 for details regarding the phosducin gene). All nuclear sequence data was protein coding.

Amplification of 25 μ l PCR reactions were executed on an Eppendorf Mastercycler gradient thermocycler. Amplification of genomic DNA began with an initial denaturation for 2 minutes at 95 °C followed by 95 °C for 35 s, annealing at 50 °C for 35 s, and extension at 72 °C for 150 s with 4 s added to the extension per cycle for 32 cycles for mitochondrial DNA and 34 cycles for nuclear DNA. When needed, annealing temperatures were adjusted to increase or decrease specificity on a case by case basis. Products were visualized with 1.5% agarose gel electrophoresis. Target products were purified with AMPure magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) and sequenced with either the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) or the DYEnamic™ ET Dye Terminator Kit (GE Healthcare, Piscataway, NJ, USA). Sequencing reactions were purified with CleanSeq magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) 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 Pro (DNASTAR Inc., Madison, WI, USA), and all four protein-coding genes were translated to amino acids with MacClade (Madison 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 parsimony, likelihood, and Bayesian optimality criteria. 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 (1,000 pseudoreplicates unless stated otherwise) to assess node support in resulting topologies with TBR branch swapping and 5 random addition replicates per pseudoreplicate. Strict consensus trees were calculated when several equally parsimonious trees resulted from MP searches.

We used the Akaike Information Criterion (AIC) in ModelTest 3.06 (Posada and Crandall, 1998) to find the model of evolution that best fit the data for subsequent maximum likelihood (ML) and Bayesian inference (BI) analyses. All genes were pooled to determine the best model for ML analyses, but separate models for each gene were run for BI. Separate models for each gene and

Table 1. List of samples used in this study giving sample locality, museum voucher specimen or collector's field number, and GenBank accession numbers for each gene. Collection abbreviations: AMB = Aaron M. Bauer, ASW = Alison Swindle Whiting, BPBM = Bernice P. Bishop Museum, CAS = California Academy of Sciences, FF = Frank Fast, FK = Fred Kraus, FMNH = Field Museum of Natural History, LLG = L. Lee Grismer.

Sample	Museum No.	Locality	GenBank Accession Numbers		
			ND2	RAG-1	PDC
<i>Dixonius siamensis</i>	LLG 7328	Phom Aural, Pursat Province, Cambodia	EU054299	EU054283	EU054267
<i>Dixonius siamensis</i>	LLG 7378	Phom Aural, Pursat Province, Cambodia	EU054298	EU054282	EU054266
<i>Dixonius vietnamensis</i>	FMNH 263003	Keo Seima district, Mondolkiri Province, Cambodia	EU054297	EU054281	EU054265
<i>Gekko gekko</i>	CAS 204952	Vic. Mwe Hauk Village, Ayeyarwardy Division, Myanmar (16°16'39.2"N, 94°45'37.5"E)	EU054288	EU054272	EU054256
<i>Hemidactylus robustus</i>	FMNH 245519	Makran District, Gwadar Division, Baluchistan Province, Pakistan	EU054287	EU054271	EU054255
<i>Heteronotia binoei</i>	AMS 151170	Fort Grey Tip, Sturt National Park, New South Wales, Australia	EU054301	EU054285	EU054269
<i>Heteronotia binoei</i>	AMS 159893	Limestone Caves, Ashford, New South Wales, Australia	EU054302	EU054286	EU054270
<i>Heteronotia planiceps</i>	AMS 140331	23.3 km NNW of junction of Tunnel Creek Road with Great Northern Hwy., Western Australia, Australia	EU054300	EU054284	EU054268
<i>Nactus</i> sp.	ASW 510	Tekadu, Lakekamu River basin, Morobe Province, Papua New Guinea (7°41'S, 135°33'E)	EU054292	EU054276	EU054260
<i>Nactus</i> sp.	ASW 666	Tekadu, Lakekamu River basin, Morobe Province, Papua New Guinea (7°41'S, 135°33'E)	EU054294	EU054278	EU054262
<i>Nactus acutus</i>	BPBM 20755	Rossel Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea	EU054289	EU054273	EU054257
<i>Nactus pelagicus</i>	AMB 7287	Mt. Gouémba, Province Sud, New Caledonia (22°10'00"S, 166°56'27"E)	EU054291	EU054275	EU054259
<i>Nactus pelagicus</i>	FF6	Ile des Pins, Province Sud, New Caledonia	EU054290	EU054274	EU054258
<i>Nactus sphaerodactylodes</i>	BPBM 20759	Sudest Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea	EU054293	EU054277	EU054261
<i>Nactus vankampeni</i>	FK 11384	Wewak, East Sepik Province, Papua New Guinea	EU054295	EU054279	EU054263
<i>Nactus vankampeni</i>	BPBM 18671	Mt. Shungol, Morobe Province, Papua New Guinea	EU054296	EU054280	EU054264

Table 2. Primers used in this study.

Primer	Gene	Reference	Sequence
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'-AACCAAACCCAACACTCGAAAAAT-3'
ND2f101	ND2	Greenbaum et al. (2007)	5'-CAAACACAAACCCGRAAAAT-3'
ND2r102	ND2	Greenbaum et al. (2007)	5'-CAGCCTAGGTGGGCGATTG-3'
Trpr3a	Trp tRNA	Greenbaum et al. (2007)	5'-TTTAGGGCTTTGAAGGC-3'
H5934a	COI	Arevalo et al. (1994)	5'-AGRGTGCCAATGTCTTTGTGRTT-3'
R13	RAG-1	Groth and Barrowclough (1999)	5'-TCTGAATGGAAATTC AAGCTGTT-3'
R18	RAG-1	Groth and Barrowclough (1999)	5'-GATGCTGCCTCGGTCGGCCACCTTT-3'
RAG1 F700	RAG-1	Bauer et al. (2007)	5'-GGAGACATGGACACAATCCATCCTAC-3'
RAG1 R700	RAG-1	Bauer et al. (2007)	5'-TTTGTACTGAGATGGATCTTTTGTGCA-3'

codon position of protein-coding genes were estimated (Brandley et al., 2005). ML analyses with empirical base frequencies (obtained in ModelTest) were performed in PAUP* with a neighbor-joining starting tree. As with MP, the nonparametric bootstrap was used to assess the stability of internal nodes in the resulting phylogenies.

Partitioned Bayesian analyses were conducted with MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) with default priors. Analyses were initiated with random starting trees and run for 1,000,000 generations; Markov chains were sampled every 1,000 generations. Convergence was checked by plotting likelihood scores against generation, and 25 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).

Maximum likelihood Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa, 1999) were used using PAUP*4.0b10 (Swofford, 2002). To compare the nuclear and mitochondrial data sets. Parameters for the test were estimated using the alternative topology with a GTR + Gamma + invariant model. The test was performed using RELL bootstrap (one tailed) and 1,000 bootstrap replicates. Parsimony estimates of incongruence between data sets were performed using an incongruence-length difference (ILD) test (Farris et al., 1995) as implemented in PAUP*4.0b10 (Swofford, 2002) as the partition homogeneity test. For this test, 10,000 replicates were made to generate the null distribution to test the significance of the observed sum of tree lengths for the data sets.

RESULTS

The combined data set had 2,971 characters and 1,264 variable characters, 904 of which were parsimony-informative. The mitochondrial data set had 687 informative characters, and the RAG1 and PDC had 147 and 70 informative characters respectively. One most parsimonious tree of 2,728 steps was found. The likelihood score of the optimal ML tree was $-\ln L$ 16115.19.

Members of the genus *Nactus* included in our study formed a well-supported monophyletic group in all analyses performed. *Nactus* is the sister group to another well-supported clade including the genera *Heteronotia* and *Dixonius*. Each of the three genera, as well as the clade as a whole, and that comprising *Heteronotia* plus *Dixonius* are supported by MP and ML bootstrap values of 100% and Bayesian posterior probabilities (Pp) of 1.0 (Fig. 1).

Intraspecific relationships within *Nactus* were poorly supported as a result of strong conflict between the data partitions. In a combined analysis of all genes, except for the grouping of *Nactus sphaerodactylodes* and *N. vankampeni* ($Pp = 0.97$), all branches received weak support in the Bayesian analysis (Fig. 1). The combined nuclear and mitochondrial MP tree had the same topology as the ND2 tree (undoubtedly reflecting the

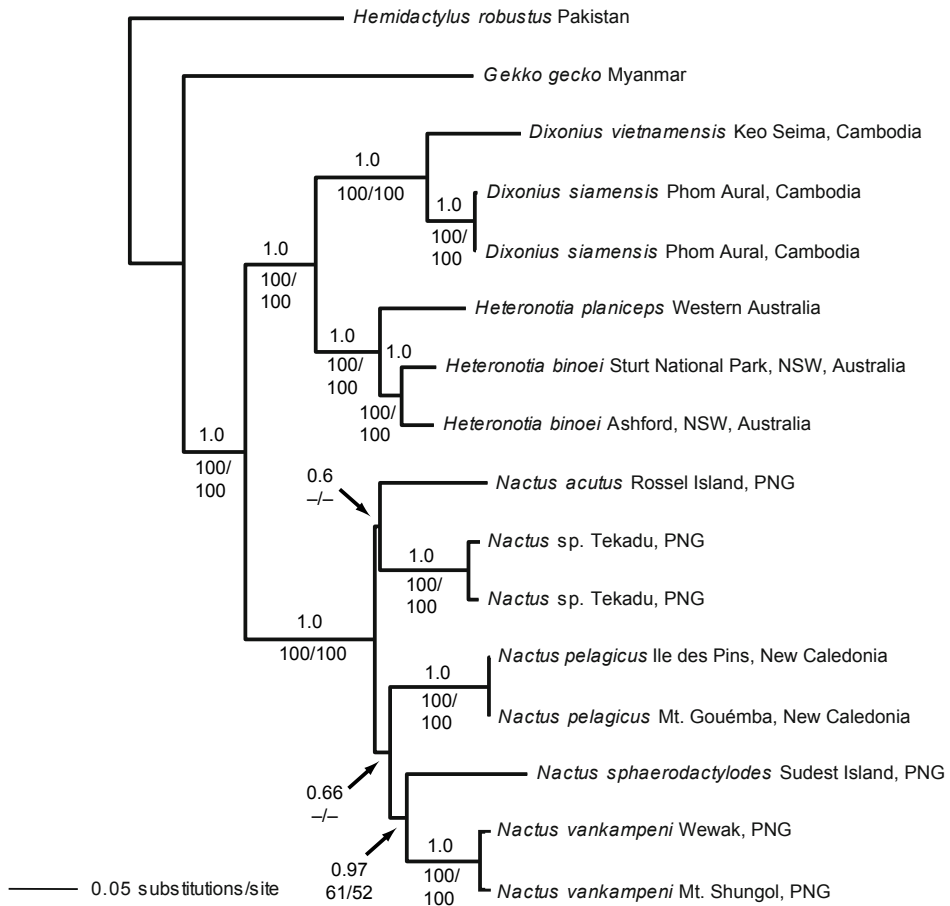
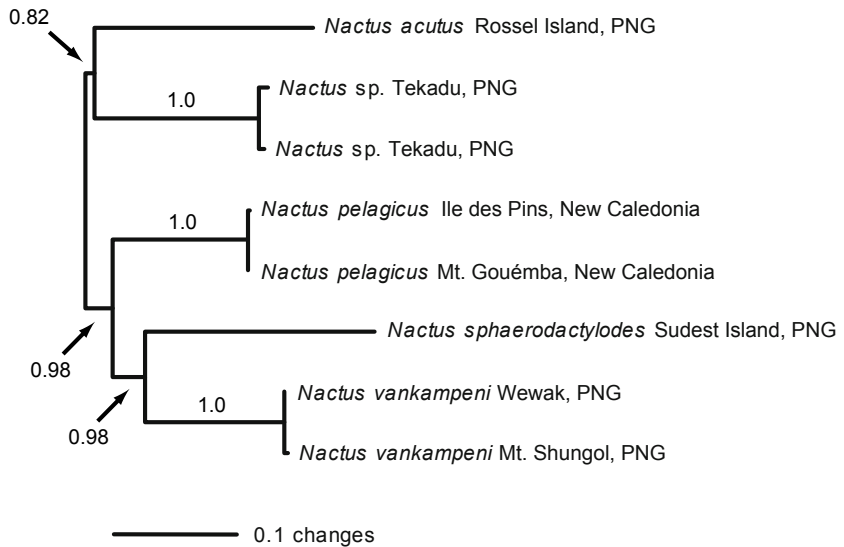


Fig. 1. Bayesian tree with maximum likelihood branch lengths of *Nactus* and its closest relatives based on the combined RAG-1, Phosducin (PDC) and ND2 data sets. Bayesian inference posterior probabilities are shown above the branches and maximum likelihood/maximum parsimony bootstrap values below. The relationships between the species of *Nactus* exactly match those of the mtDNA alone, but the low support values between the species reflect a conflict with the nuclear data (see text).

A



B

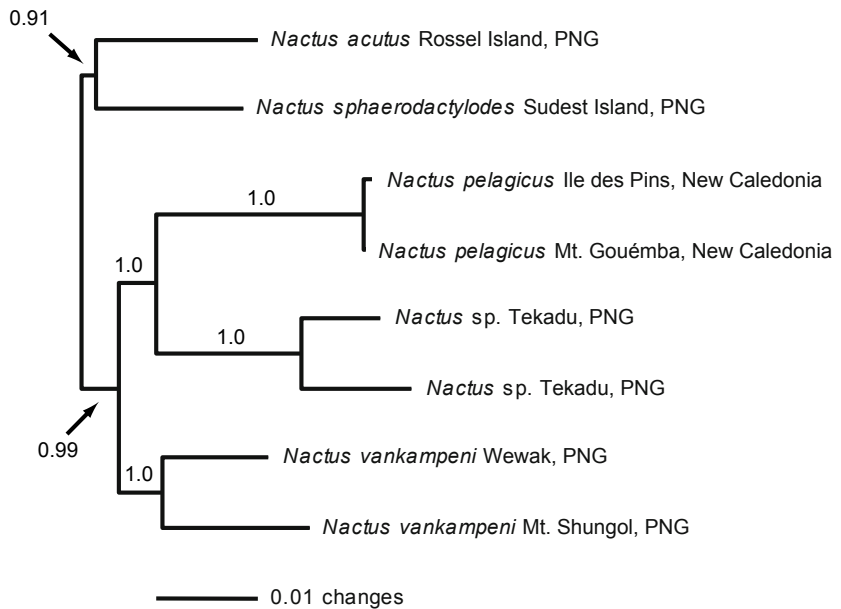


Fig. 2. Bayesian trees showing hypotheses of relationship within *Nactus* based on A) ND2 mitochondrial DNA and B) combined RAG-1 and PDC nuclear DNA data. Values indicated are Bayesian inference posterior probabilities.

greater number of parsimony informative characters for this gene relative to the nuclear markers), but all interspecific bootstrap values were low. The nuclear data (PDC and RAG-1) were combined and the resultant tree (Fig. 2B) was compared to the tree based on mitochondrial DNA (ND2) alone (Fig. 2A). The topologies of the two trees differ significantly with respect to inferred relationships within *Nactus*, and both have relatively high support values for these conflicting relationships. In the mitochondrial tree the clade *pelagicus* (*sphaerodactyloides* plus *vankampeni*) received strong support, whereas in the nuclear tree the relationships: *vankampeni* (*pelagicus* plus sp.) were supported by posterior probabilities of 1.0. In addition, although nuclear genes suggest a deep divergence between the two sampled populations of *N. vankampeni*, they are nearly identical with respect to ND2 sequence. Based on the SH test, the ND2 data set rejects the nuclear DNA topology as significantly different from the ND2 topology ($P = 0.024$) and the nuclear data set rejects the ND2 topology as significantly different as well ($P = 0.022$). In addition, the ILD test revealed significant incongruence between the nuclear and mitochondrial data sets ($P = 0.045$), but no significant conflict between the two nuclear DNA data sets ($P = 0.344$).

DISCUSSION

It is clear from the SH and ILD tests that the low support values for relationships in the combined analyses of the genus *Nactus* are the result of character conflict between the nuclear and mitochondrial data sets. Although several scenarios may be posited, this strong conflict can be hypothesized to have been generated by three historical events. First, the relationship of *N. sphaerodactyloides* and *N. vankampeni* (Fig. 2A), which is well supported by mitochondrial DNA, can be explained as an ancient mitochondrial introgression event between the two species as has been described recently in phrynosomatid lizards (Leaché and McGuire, 2006). Second, the nearly identical mtDNA but deeply divergent nuclear DNA of the two *N. vankampeni* samples (Figs. 2A, 2B) may be the result of a recent selective sweep of mitochondrial DNA throughout *N. vankampeni*. Third, the well-supported relationship of *N. pelagicus* and *Nactus* sp. based on nuclear but not mitochondrial DNA may be a consequence of the origin of *N. pelagicus* from bisexual parental species of two different lineages – the gene conflict representing these disparate lineages. It has been hypothesized that the bisexual species that gave rise to *N. pelagicus* would have had $2N = 42$ and $2N = 28$ chromosomes, respectively (Moritz, 1987). Remaining conflicts in the nuclear and mitochondrial trees are not well supported in one or both trees. Increased sampling of the species of *Nactus* may help to further clarify the source of conflict between mitochondrial and nuclear genes in this genus.

Our analyses of the nuclear data alone are similar to those of Kraus (2005) in that *N. acutus* and *N. sphaerodactyloides*, which were identical with respect to Kraus's morphological characters, are sister species, albeit with weak support ($Pp = 0.91$). However, Kraus (2005) found support for the affinities of this species pair to *N. vankampeni*. This is inconsistent with our nuclear data, whereas our ND2 and combined analyses support the close relationship of only *N. sphaerodactyloides* with *N. vankampeni*.

Morphological data would link *Nactus* sp. with *N. pelagicus*, as do the nuclear data. Donnellan and Moritz (1995) identified a minimum of three bisexual lineages among New

Guinea "*N. pelagicus*" based on allozyme data. Our bisexual "*pelagicus*" specimens are from Tekadu, Lakekamu River basin, Morobe Province, Papua New Guinea, geographically intermediate between the nearest confirmed localities of all three forms. Morphologically, they are most similar to Form D, one of four putative taxa identified by Rösler et al. (2005). The resolution of specific identity of all of the New Guinea bisexual forms is hindered by an incomplete knowledge of the distribution of the different allozyme and morphological forms, and by the complicating fact that several names currently in the synonymy of *N. pelagicus* may apply to one or more of these (Bauer and Henle, 1994; Donnellan and Moritz, 1995; Zug and Moon, 1995; Zug, 1998). George Zug (pers. comm.) is currently conducting a comprehensive analysis of New Guinea "*N. pelagicus*," which include at least five distinct taxa, and specific allocation of our bisexual *N. pelagicus* will have to wait until this is completed.

Kraus (2005) found that the species lacking multicarinate tubercles (*N. galgajuga* and *N. coindemirensis*) consistently clustered with outgroup genera or as part of a basal polytomy involving his outgroups and an otherwise monophyletic *Nactus*. The polyphyly of the Mascarene taxa had earlier been proposed by Bullock et al. (1985), who considered *N. coindemirensis* as basal in the genus, but Ulber and Gericke (1988) assumed a sister group relationship between Mascarene taxa (for which they erected the subgenus *Mascarenogecko*) and Pacific *Nactus*, and more recently Austin and Arnold (2006) have suggested that Mascarene *Nactus* are derived from Australasia, having dispersed over water via the prevailing currents and winds. Kraus's (2005) placement of *N. galgajuga* outside of the clade including the other Australian species (*N. eboracensis*, *N. cheverti*) contradicts the conclusions of Zug (1998), who considered the shared smooth subcaudals of all three Australian species as evidence of their probable monophyly. Our sampling included no Australian or Mascarene species, however, so we are unable to evaluate Kraus's (2005) placement of the problematic species *N. galgajuga* and *N. coindemirensis*.

The inclusion of *Nactus* and *Heteronotia* in a single, well-supported clade (although not as sister taxa) corroborates the work of Kluge (1963) and Russell (1972), both of whom suggested that the two were closely related. Indeed, the external similarity of *Heteronotia* and *Nactus* is evident in the fact that Macleay's (1878) descriptions of the species now assigned to *N. eboracensis* and *N. cheverti* placed them in the genus *Heteronota* (subsequently changed to *Heteronotia* owing to its preoccupation). Boulenger (1885) subsequently transferred one species (*N. cheverti*), but not the other, into *Gymnodactylus* (then including taxa now assigned to *Cyrtodactylus* and *Nactus*), despite the great morphological similarity between the two forms (Zug, 1998). Loveridge (1934) likewise synonymized *H. eboracensis* with *H. binoei*.

Heteronotia currently includes three named and recognized species, *H. binoei*, *H. spelea* and *H. planiceps* (Storr, 1989). However, there are three bisexual chromosome races and two genetically diverse parthenogenetic lineages resulting from multiple hybridization events between two of the bisexual races currently subsumed under the name *H. binoei* (Moritz, 1983, 1993; Moritz et al., 1989a, b, 1990; Moritz and Heideman, 1993; Strasburg and Kearney, 2005; Kearney et al., 2006). Our two samples are nearly identical to one another and represent the same bisexual cytotype (EA6 *vide* Moritz, 1991). Patterns of relationship among the various bisexual and unisexual groups still subsumed within *Heteronotia binoei* are well resolved, with initial diversification of the sexual races estimated

to have occurred approximately 6 million years ago and the origin of the two recognized clonal lineages having occurred in the Pleistocene, perhaps within the last 300,000 years (Strasburg and Kearney, 2005; Kearney et al., 2006).

While the affinities of *Heteronotia* to *Nactus* are not particularly surprising, those of *Dixonius* are. *Dixonius* Bauer et al., 1997 was erected to accommodate southeast Asian leaf-toed geckos previously assigned to the polyphyletic and nearly cosmopolitan *Phyllodactylus*. Four species of *Dixonius* are currently recognized (Bauer et al., 2004; Das, 2004). *Dixonius siamensis* has the broadest range, occurring from Songkhla (7° N), south of the Isthmus of Kra (Taylor, 1963), north to at least Chiang Mai (19° N) (Grossmann et al., 1996; Manthey and Grossmann, 1997) and from southern Myanmar (Annandale, 1905a, b) to the Lao Peoples Democratic Republic (Stuart, 1999) and Vietnam (Smith, 1935; Bourret, 1939; Szczerbak and Nekrasova, 1994). This broad distribution, along with obvious geographic variation in color pattern (Taylor, 1963) suggests that *D. siamensis*, as presently construed, may actually represent a complex of similar species. This hypothesis is supported by Ota et al. (2001), who demonstrated that a minimum of two chromosome forms ($2N = 40$ and $2N = 42$) exist among Thai populations of *D. siamensis*. The remaining species have more limited distributions – *D. melanostictus* occurs in Sara Buri and Nakhon Ratchasima provinces in central Thailand (Taylor, 1962, 1963; Chan-Ard et al., 1999), *D. hangseesom* is known only from Kanchanaburi Province, western Thailand, and *D. vietnamensis* has been found in southern Vietnam and Cambodia (Bobrov, 1992; Das, 2004; Stuart et al., 2006).

The phylogenetic affinities of *Dixonius* to other gekkonids had not been previously investigated, but allozyme data and morphology did not suggest that it was especially closely related to other clades of leaf-toed geckos (Bauer et al., 1997). The possible generic distinctness of the group was first noted by Annandale (1905b), who considered the presence of preloacal pores as highly distinctive within *Phyllodactylus*. Dixon (1964) subsequently noted that *D. siamensis* exhibited a reduced manual phalangeal formula of 2:3:4:4:3. Russell (1972) demonstrated that there was in fact no phalangeal loss in digit IV of the manus, but identified a unique reduction in size of phalanx II of this digit. Bauer et al. (1997) subsequently diagnosed *Dixonius* relative to other leaf-toed geckos on the basis of these preloacal pore and digital characters, as well as the tuberculate condition of the dorsum and the proximal bifurcation of the hypoischium.

In retrospect it is possible to identify known morphological and biological characters that support the monophyly of the *Nactus/Heteronotia/Dixonius* clade. Russell (1972) noted that *Nactus pelagicus* and *Heteronotia binoei* share a nearly identical phalangeal pattern, with a long slender first phalanx and short second and third phalanges. Species now allocated to *Dixonius* were distinguished by Russell (1972) from all other *Phyllodactylus* by their extremely short second phalanx on digit IV of the manus. The reduced second phalanx in all three forms may be considered a putative synapomorphy of the group as a whole. Dorsal scalation serves as another potential feature uniting members of this clade. *Heteronotia* and *Nactus* have the derived condition of multicarinate dorsal tubercles (keeled but unicarinate in *Dixonius*), and all three genera have very regularly arranged rows of dorsal tubercles (lost in some *Nactus*).

A third putative synapomorphy is parthenogenesis, or at least the existence of nearly morphologically identical cryptic species with differing chromosomal complements that

establish the basis for the hybrid origin of such unisexuals. Parthenogenesis is rare in nature, with only 0.1% of species exhibiting this reproductive strategy (White, 1978). The infrequency of parthenogenesis in nature is assumed to be related to the deleterious effects of parthenogenesis on fitness (Kearney and Shine, 2004). All known unisexual vertebrates exhibit a clonal mode of parthenogenesis associated with a hybrid origin (Vrijenhoek et al., 1989), which results in high levels of heterozygosity. Heterozygosity levels are also increased in the case of allopolyploids (Kearney and Shine, 2004). It has been suggested that this increased heterozygosity may lead to increased developmental stability and success (Vrijenhoek and Lerman, 1982; Wetherington et al., 1987). Specifically, Kearney and Shine (2004) suggested that parthenogenetic *Heteronotia binoei* might be buffered against effects of temperature during development. It has been suggested that parthenogens of hybrid and polyploidy origin capture and “freeze” the diversity of parental sexual forms and that this, as well as non-additive interactions among the genomes of hybrid polyploids might provide a means of introducing diverse phenotypes that could diversify into and exploit ecological vacuums. Kearney (2003) suggested that *H. binoei* might represent such a case in the Australian desert, and one might consider the nocturnal terrestrial niche for lizards in much of the Pacific a similar vacuum that may have provided an equivalent opportunity for *Nactus pelagicus*. No parthenogens have been identified within *Dixonius*, but the chromosome variation identified in *D. siamensis* by Ota et al. (2001), sets up the possibility for hybridogenesis.

The strong support for the *Nactus/Heteronotia/Dixonius* clade demonstrates that sub-digital scansors, and in particular, the leaf-like terminal scansors of *Dixonius*, have evolved multiple times within the Gekkonidae. Such scansors occur in a variety of other strongly supported gekkonid clades including the group comprising *Phyllodactylus*, *Haemodracon*, *Asaccus* and their relatives (Gamble et al., in press), and at least two separate Afro-Malagasy clades: *Uroplatus* and its relatives (Greenbaum et al., 2007) and *Paroedura* and its relatives (Jackman et al., 2008.). Russell (1979) highlighted convergence in digital structure between diplodactylid and gekkonid geckos and suggested that similar convergence might occur within gekkonids themselves (Russell, 1976). Extensive digital variability within single lineages, especially that involving the secondarily derived loss of scansorial morphology, has subsequently been demonstrated in several gekkonid lineages (Carrillo de Espinoza et al., 1990; Lamb and Bauer, 2006). Our results suggest that digital structure may be even more labile than previously proposed and, at least at the superficial level it has been interpreted by most authors (e.g., Loveridge, 1947), may be positively misleading with respect to phylogenetic relationships.

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