

Polymorphism Versus Species Richness—Systematics of Large *Dendrobates* from the Eastern Guiana Shield (Amphibia: Dendrobatidae)

KATHARINA C. WOLLENBERG, MICHAEL VEITH, BRICE P. NOONAN, AND STEFAN LÖTTERS

A molecular phylogeny based on a fragment of the mitochondrial 16 S rRNA gene and morphological comparisons suggests that only one polymorphic species of large *Dendrobates*, commonly assigned to *D. tinctorius*, occurs on the eastern Guiana Shield and its vicinities. The oldest available name for this taxon is *D. tinctorius* (Schneider, 1799). We place *D. azureus* Hoogmoed, 1969 as its junior synonym. Data for *D. machadoi* Bokermann, 1958 are not available, but we suspect that this name has to be treated in the same way. *Dendrobates tinctorius* exhibits numerous variants differing in color and pattern.

THE Neotropical poison frogs (Dendrobatidae) comprise a monophyletic unit of more than 230 species in various genera (Santos et al., 2003; Vences et al., 2003). Roughly one-fourth of these species display aposomatic coloration, accompanied by potent skin alkaloids. The occurrence of intraspecific phenotypic polymorphism within the Dendrobatidae has been well documented (Symula et al., 2001; Summers et al., 2003; Lötters et al., in press) and poses serious problems to taxonomic study in the group.

Among the five species of *Dendrobates* known from the eastern Guiana Shield and its vicinities are three large ones with adult size > 34 mm: *Dendrobates azureus* Hoogmoed, 1969, *D. machadoi* Bokermann, 1958, and *D. tinctorius* (Schneider, 1799). In a taxonomic revision, Silverstone (1975) suggested that *D. tinctorius* represents a wide-spread, polymorphic species, with *D. machadoi* as a junior synonym. He considered *D. azureus*, known from a single locality within the geographic range of *D. tinctorius*, a valid taxon. According to Hoogmoed (1969) and Silverstone (1975), *D. azureus* differs from *D. tinctorius* by having most parts of the black dorsum with close-set blue (in preservative bluish gray) reticulation (vs. close-set blue reticulation reduced, or dorsum with whitish, yellowish, or greenish pattern), a hunchbacked (vs. straight) posture, and a relatively small, oval (vs. relatively large, round) tympanum.

Silverstone (1975) included both nominal species in a phenetic *D. tinctorius* species group along with: *Dendrobates auratus* (Girard, 1854), trans-Andean; *D. galactonotus* Fitzinger, 1864, southeastern Amazonia; *D. truncatus* (Cope, 1860), Andean. In addition, *D. leucomelas* Fitzinger, 1864 from the western Guiana Shield and *D. nubeculosus* Jungfer and Böhme, 2004, from the eastern Guiana Shield have been added to the *D. tinctorius* group (see Jungfer and Böhme, 2004). Subsequent to Silverstone (1975), more geo-

graphically restricted color variants of large *Dendrobates* have been recognized from the eastern Guiana Shield. A large proportion of these recently recognized variants have been discovered through the activities of the live animal trade. Numerous trivial names have been suggested for them (see Table 1); scientifically, variants have been assigned to *D. tinctorius* (Walls, 1994; Lötters et al., in press).

Molecular phylogenies (Vences et al., 2003; Noonan and Wray, 2006) have demonstrated that, apart from *D. galactonotus*, the *D. tinctorius* group represents a monophyletic unit (no data are currently available for *D. nubeculosus* and *D. truncatus*). However, sampling of *D. tinctorius* in these studies has been limited to a few representatives and has overlooked the potential diversity suggested by the phenotypic variation present in this taxon. Morphological variation among populations of *D. tinctorius* is remarkable, especially in terms of color and pattern (Silverstone, 1975; Lötters et al., in press). Additional geographic variants with close-set blue reticulation (similar to *D. azureus*) have been identified; some variants even exhibit a hunchbacked posture, and tympanum sizes have been found to vary considerably (SL, unpubl. obs.). Consequently, some doubt has arisen about the distinctness of *D. azureus*, or, alternatively, about the conspecificity of variants assigned to *D. tinctorius*. The purpose of this paper is to reassess the taxonomic status of large *Dendrobates* from the eastern Guiana Shield and to test whether previously mentioned diagnostic morphological characters are in fact suitable for taxon distinction when subjected to a statistical analysis.

MATERIALS AND METHODS

Molecular phylogeny.—Tissue samples from 38 specimens of 23 phenotypic variants assigned to *Dendrobates tinctorius*, four topotypic specimens of

TABLE 1. VARIANTS ASSIGNED TO *Dendrobates tinctorius* (LISTED BY THEIR TRIVIAL NAMES; CF. LÖTTERS ET AL., IN PRESS) AND OTHER *Dendrobates*, EITHER CAPTIVE-BRED OR WILD-CAUGHT (CB, WC), USED FOR THE MOLECULAR PHYLOGENY, AND THEIR HAPLOTYPE ALLOCATION (SEE TEXT). Material taken from GenBank is indicated by asterisks.

Name	Locality	Origin	Voucher (ZFMK)	GenBank accession number	Haplotype
Alanis	Suriname: Tafelberg	CB	83993	DQ768783	1
Alanis	Suriname: Tafelberg	CB		DQ768777	1
Amatopo	French Guiana: Amatopo, near Lucie River	WC		DQ768762	1
Amatopo	French Guiana: Amatopo, near Lucie River	WC	83991	DQ768778	1
Amatopo	French Guiana: Amatopo, near Lucie River	CB		DQ768763	1
Bakhuis	Guyana/Suriname: Bakhuis Mountains.	CB		DQ768776	2
Boulanger	French Guiana: near Cacao	WC		DQ768767	2
Brazil	Brazil: Serra do Navio	CB		DQ768756	2
Brazil	Brazil: Serra do Navio	CB		DQ768770	2
Brazil	Brazil: Serra do Navio	CB		DQ768771	2
Cacao	French Guiana: near Cacao	WC		DQ768774	4
Cayenne	French Guiana: Matoury	CB		DQ768793	1
Citronella	Suriname: Kasikasima Mountains.	WC		DQ768785	1
Greyspot	Suriname: Eilerts de Haan Mountains	CB		DQ768784	3
Greyspot	Suriname: Eilerts de Haan Mountains	CB		DQ768791	3
Kaysers Mountains	Suriname: Kaysers Mountains	WC		DQ768760	3
Lorenzo	Brazil: Amapá	CB		DQ768766	2
Mont Matoury	French Guiana: Matoury	CB		DQ768779	1
New River	Suriname/Guyana: New River	CB		DQ768781	1
New River	Suriname/Guiana: New River	WC		DQ768782	1
Nikita	French Guiana: unknown locality	CB	83995	DQ768788	1
Nominat	French Guiana: Kaw Mountains area	WC	83990	DQ768786	1
Oranje Gebergte	Suriname: Tafelberg	CB	83992	DQ768758	3
Oranje Gebergte	Suriname: Tafelberg	CB		DQ768790	3
Oyapock	French Guiana: Oyapock River	CB		DQ768780	1
Oyapock	French Guiana: Oyapock River	WC		DQ768789	1
Patricia	Suriname: Lucie River	CB		DQ768761	1
Patricia	Suriname: Lucie River	CB		DQ768792	1
Regina	French Guiana: south of Regina	CB		DQ768755	1
Regina	French Guiana: Mount Bauge	WC	83994	DQ768787	1
Sipaliwini Blue	Suriname: southern Sipaliwini	CB		DQ768768	1
Sipaliwini Green	Suriname: southern Sipaliwini	CB		DQ768764	3
Sipaliwini Green	Suriname: southern Sipaliwini	CB		DQ768765	3
Sipaliwini Green	Suriname: southern Sipaliwini	CB		DQ768775	3
Suriname Cobalt	Suriname: southeastern Tafelberg	WC		DQ768772	1
Suriname Cobalt	Suriname: southeastern Tafelberg	WC		DQ768773	1
Te Poe	Suriname: Te Poe	WC		DQ768757	3
Te Poe	Suriname: Te Poe	WC		DQ768769	3
<i>D. auratus</i>	Costa Rica: unknown	WC		DQ768798	—
<i>D. auratus</i>	Panama: Nusagandi	WC		AF_128601*	—
<i>D. auratus</i>	Unknown (pet trade)	WC	66710	AF_124115*	—
<i>D. azureus</i>	Suriname: Mt. Vier Gebroeders	CB	83974	DQ768794	1
<i>D. azureus</i>	Suriname: Mt. Vier Gebroeders	CB	83975	DQ768795	1
<i>D. azureus</i>	Suriname: Mt. Vier Gebroeders	CB	83976	DQ768796	1
<i>D. azureus</i>	Suriname: Mt. Vier Gebroeders	WC	83977	DQ768797	1
<i>D. imitator</i>	Peru: Tarapoto	WC		AF_124118*	—
<i>D. leucomelas</i>	Venezuela: unknown	WC	66711	AF_124119*	—
<i>D. pumilio</i>	Panama: Isla Bastimentos	WC		DQ768799	—
<i>D. sp. aff. azureus</i>	Brazil: Alto Rio Trombetas?	WC		AY_263250*	—
<i>D. sylvaticus</i>	Ecuador: Santo Domingo	WC		AF_128616*	—

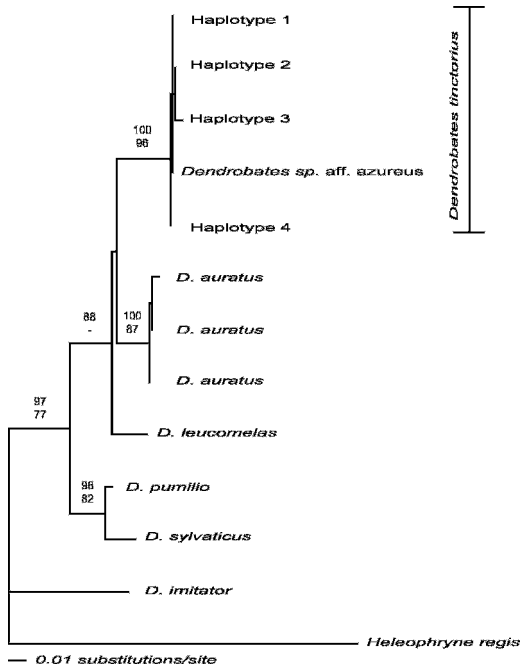


Fig. 1. Maximum likelihood phylogram with MP (upper) and ML (lower) support values. The data suggest that *Dendrobates tinctorius* is a polymorphic species (with *D. azureus* as a junior synonym, see text), in which four haplotypes can be identified. For allocation of haplotypes to variants assigned to *D. tinctorius* and to the nominal *D. azureus* see Table 1, and for inclusion of *Dendrobates* "sp. aff. *azureus*" see text.

D. azureus, and one each of two other *Dendrobates* species were obtained (Table 1). Samples consisted of clipped toes of adults or tail tips of tadpoles from captive-bred or wild-caught individuals, as well as ethanol-preserved muscle tissue. Few vouchers could be maintained, as most tissue originated from living specimens (Table 1). Tissue samples were preserved in 98% ethanol.

DNA was isolated using a Roche High Pure Template Preparation Kit; polymerase chain reaction (PCR) was performed with Amersham PureTaq ReadyToGo™ PCR Beads to amplify a 561-bp fragment of the mitochondrial 16 S rRNA gene. Oligonucleotide primers were 16sar-L (for) 5'-CGC CTG TTT ATC AAA AAC AT-3' (Palumbi et al., 1991) and 16 s-BH (rev) 5'-CCG GTC TGA ACT CAG ATC ACG-3' (modified from Palumbi et al., 1991). Thermocycling profile was as follows: initial denaturation (90 s at 94 C), followed by 30 cycles of denaturation (30 s at 94 C), primer annealing (30 s at 55 C), and elongation (45 s at 72 C). Purification of PCR products was performed with a Roche High Pure

Product Purification Kit. Single-stranded DNA fragments were sequenced in one direction (forward) with an automatic sequencer (ABI Prism 377).

All obtained sequences were verified as dendrobatid DNA by standard nucleotide-nucleotide BLAST search. Sequences were subsequently grouped into haplotypes. Additional sequences of other *Dendrobates* and of *Heleophryne regis* (Heleophrynidae) obtained from GenBank were included in the data set (Table 1, Fig. 1). For the investigated gene, the best-fit model of evolution was computed with MODELTEST 3.06 for ingroup taxa only, using the Akaike Information Criterion (Posada and Crandall, 1998; Posada and Buckley, 2004). Phylograms were computed with PAUP*, Version 4b10 (D. L. Swofford, PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), Sinauer, Sunderland, 2001).

Maximum likelihood (ML) analysis was performed with quartet puzzling (100,000 replicates). Heuristic searches were performed applying the maximum parsimony (MP) algorithm, with 2000 non-parametric bootstrap replicates (Felsenstein, 1985). Characters in MP searches were treated as unordered with equal weight. Gaps were treated as "missing;" multistate characters were interpreted as "uncertain." Trees were computed with random stepwise addition of taxa, and branch swapping was performed with the TBR (Tree-Bisection-Reconnection) algorithm. The consistency index (CI) was computed to test for the level of homoplasy (Kluge and Farris, 1969).

Morphology.—A total of 39 specimens from 15 localities assigned to *Dendrobates tinctorius* and 34 *D. azureus* (including 29 of the 42 type specimens) were examined (see Table 2 and Material Examined; collection abbreviations follow Leviton et al., 1985). Close-set bluish gray reticulation on dorsum (not on extremities) was coded as present or absent. The following measurements (in mm), in accordance with previous authors (Hoogmoed, 1969; Silverstone, 1975), were taken with dial calipers to nearest 0.1: snout-vent length (SVL), vertical and horizontal tympanum diameter (TDv, TDh), horizontal eye diameter (ED). Only frogs with SVL > 34.0 mm (assumed to represent adults) were included in the analysis. To adjust for overall body size effects, we computed residuals of TDv, TDh, and ED to SVL. Via discriminant analysis, specimens assigned to *D. tinctorius* and *D. azureus* were reclassified to show if specimens could be correctly assigned to their respective taxon using morphometry alone.

RESULTS

Molecular phylogeny.—A total of 561 base pairs of the 16 S rRNA gene were obtained for all haplotypes. MODELTEST computed the GTR + I model of base substitution as the best-fit model of evolution using the Akaike Information Criterion ($-\ln L = 1461.3853$, $AIC = 2940.7705$), with base frequencies $\pi_A = 0.2967$, $\pi_C = 0.2259$, $\pi_G = 0.1956$, $\pi_T = 0.2817$; substitution rates were $[A-C] = 1.7402$, $[A-G] = 3.3249$, $[A-T] = 2.3754$, $[C-G] = 0.0000$, $[C-T] = 10.3856$, and $[G-T] = 1.0000$; proportion of invariable sites was $I = 0.6271$. The C-G rate was set to 0.0001 in PAUP* to compute phylograms. Out of 561 characters, 85 were parsimony-informative. The PAUP* alignment was submitted to TreeBase.

The MP analysis recovered three equally parsimonious trees (222 steps; not shown). The ML search recovered a single best tree ($-\ln L = 1785.5196$, Fig. 1). The arrangement of *D. auratus* and *D. leucomelas* within the *D. tinctorius* group was not well resolved: ML placed *D. auratus* as the sister group to variants assigned to *D. tinctorius* plus *D. azureus*, whereas MP placed *D. leucomelas* as their sister group (not shown). This indicates a high degree of genetic similarity of the members of the *D. tinctorius* group studied. However, the monophyly of the *D. tinctorius* group with respect to other *Dendrobates* was recovered in all MP and ML analyses and was strongly supported in the bootstrap and quartet puzzling analysis (Fig. 1). Moreover, all samples assigned to *D. tinctorius* and *D. azureus* clustered together with high statistical support (Fig. 1). Average genetic distances (calculated on the basis of the uncorrected p substitution model) between *D. auratus* and variants assigned to *D. tinctorius* plus *D. azureus* were 5.97%, and between *D. leucomelas* and *D. tinctorius* plus *D. azureus* were 5.61%, respectively. Average genetic distances among investigated variants assigned to *D. tinctorius* ranged between 0 and 0.48% (including *D. azureus*). As a consequence, these results suggest that color variants assigned to *D. tinctorius* and *D. azureus* all represent a single species.

All analyzed variants assigned to *D. tinctorius* and *D. azureus* exhibited one of four 16 S haplotypes (Fig. 1; Table 1). The specimen of Vences et al. (2003) designated as *Dendrobates* "sp. aff. *azureus*" showed no differences from haplotype 1 (in which all other *D. azureus* were grouped). However, it was not included in haplotype 1 due to its higher content of unresolved base positions (N; Fig. 1). Consistency Index of the ML topology excluding the outgroup *Heleophryne regis* (128 variable characters)

was 0.87, indicating low levels of homoplasy. No homoplasies were detected in the placement of the four *D. tinctorius*-haplotypes, as CI was 1.0 for them.

Morphology.—Morphometrics of the measured traits are provided in Table 2. Through PCA, three factors were extracted with eigenvalues always close to 1.0. Each factor contained significant factor loadings of only one measurement, so covariation among the three variables was low (Table 3). Analysis was therefore continued with the computed residuals. Residuals of all specimens (i.e., involving those of *Dendrobates azureus*) largely overlapped (Fig. 2). Different proportions of tympanum and eye diameter between *D. azureus* and other large *Dendrobates* from the eastern Guiana Shield and vicinities, as claimed by previous authors, were not supported. Discriminant analysis failed to reclassify about one-third of the measured specimens assigned to *D. tinctorius* and *D. azureus* to their respective nominal species. The percentages of correctly classified specimens (67.64% *D. azureus* and 66.66% *D. tinctorius*) were statistically not supported ($P = 0.466$ for *D. azureus*; $P = 0.534$ for *D. tinctorius*).

Presence or absence of close-set bluish gray reticulation on dorsum revealed that all *D. azureus* individuals and one specimen assigned to *D. tinctorius* (i.e., the New River variant; Material Examined) displayed this character. These data neither support nor reject conspecific status of *D. azureus* and variants assigned to *D. tinctorius*.

DISCUSSION

Our results indicate that the large *Dendrobates* of the eastern Guiana Shield and its vicinities exhibit limited genetic divergence equivalent to intraspecific levels observed in other dendrobatid frogs (Santos et al., 2003; Vences et al., 2003). Morphometric characters previously used to define *D. azureus* are shown to represent variable traits among populations of a single species. Studies suggesting these characters to be useful to distinguish different taxa did not involve statistical analysis (Hoogmoed, 1969; Silverstone, 1975). But even if *D. azureus* and *D. tinctorius* had shown stronger morphometric divergence, in the light of the pronounced fixed color pattern variation among *D. tinctorius* populations, this could only be seen as another morphological trait with pronounced differences among genetically similar populations of the same evolutionary lineage.

TABLE 2. MORPHOMETRICS (IN MM) OF SPECIMENS ASSIGNED TO *Dendrobates tinctorius* FROM 15 KNOWN LOCALITIES AND TWO UNKNOWN LOCALITIES, AND OF *D. azureus* (AND INCLUDING TYPE SPECIMENS), INDICATED BY AN ASTERISK. FOR ABBREVIATIONS SEE TEXT. WHEN MORE THAN ONE SPECIMEN WAS AVAILABLE, THE MEAN IS GIVEN, FOLLOWED BY ONE STANDARD DEVIATION AND THE RANGE IN PARENTHESES. FOR SPECIMENS EXAMINED SEE MATERIAL EXAMINED.

Locality	<i>n</i>	SVL	TDv	TDh	ED
Brazil: Amapá, Serra do Navio	4	34.9 ± 4.7 (31–41.8)	2.2 ± 0.4 (1.9–2.7)	2.2 ± 0.4 (1.7–2.7)	4.0 ± 0.1 (3.8–4.3)
French Guiana: Approuague-Kaw, Mts. Bauge	1	37.4	2.1	2.2	3.9
French Guiana: Approuague-Kaw, Mts. Kaw	1	22.7	1.5	1.1	3.0
French Guiana: Mts. Atachi Bakka	3	40.0 ± 2.7 (36.9–42.0)	2.1 ± 0.4 (1.8–2.5)	2.2 ± 0.2 (2.0–2.4)	4.3 ± 0.6 (3.9–5.0)
French Guiana: Maripasoula, Saül	1	42.4	2.4	2.5	4.2
French Guiana: unknown locality	2	37.5 ± 0.8 (36.9–38.0)	2.3 ± 0.6 (1.9–2.7)	1.9 ± 0.1 (1.8–2.0)	3.9 ± 0.1 (3.9–4.0)
French Guiana: unknown locality	1	33.8	2.0	2.0	3.9
Suriname: Nickerie, Boetoe, near Lucie River	2	45.3 ± 2.7 (43.4–47.2)	2.3 ± 0.4 (2.0–2.5)	1.8 ± 0.1 (1.7–1.8)	4.6 ± 0.5 (4.6–4.7)
Suriname: rechter Kabalebo River	1	37.4	2.0	1.7	4.0
Suriname: Toekoemotoe Creek	1	40.7	2.4	2.0	4.4
Suriname: Sipaliwini, Kabalebo, Kamp Kayzer	1	36.8	2.0	1.3	3.6
Suriname: Sipaliwini, Mt. Kassikassima	1	34.0	2.2	1.6	3.1
Suriname: Sipaliwini, Sipaliwini River, Koeroni Creek	2	45.8 ± 4.2 (42.8–48.7)	2.4 ± 0.2 (2.3–2.5)	1.9 ± 0.1 (1.8–2.0)	5.2 ± 0.4 (4.9–5.5)
Suriname: Sipaliwini, Tafelberg, airstrip	1	50.8	2.8	5.0	1.7
Suriname: Sipaliwini, Tafelberg	6	40.9 ± 2.6 (37.2–44.1)	2.2 ± 0.3 (1.9–2.6)	2.0 ± 0.4 (1.3–2.5)	3.9 ± 0.2 (3.7–4.2)
Suriname: Sipaliwini, Mt. Teboe near van Loon Mts	10	43.3 ± 2.6 (39.6–46.6)	2.4 ± 0.6 (1.9–3.8)	2.1 ± 0.3 (1.6–2.5)	4.4 ± 0.5 (3.8–5.3)
Suriname: Sipaliwini, Wilhelmina Gebergte, linker Coppename River	1	46.8	2.0	1.5	4.5
Suriname: Sipaliwini, forest island on western slope Vier Gebroeders Mountain*	34	39.8 ± 2.0 (36.1–43.0)	2.1 ± 0.3 (1.6–2.8)	1.6 ± 0.2 (1.2–2.3)	4.3 ± 0.3 (3.8–4.8)

Coloration in life varies among large *Dendrobates* in the eastern Guiana Shield and its vicinities (Lötters et al., in press). These variants are here shown to represent a single, widespread, polymorphic species based on molecular and morphometric data. Since coloration is highly variable within other *Dendrobates* species as well (Lötters et al., 1999; Symula et al., 2001; Summers et al., 2003), we suggest that this character be

employed with caution for taxonomic purposes in *Dendrobates*.

The utility of relative posture in life to distinguish *D. azureus* from other large *Dendrobates* from the eastern Guiana Shield and its vicinities was not examined here, as this character is, at best, difficult to quantify (see Hoogmoed, 1969; Silverstone, 1975). Moreover, as mentioned above, our observations suggest that some variants assigned to *D. tinctorius* show

TABLE 3. FACTOR LOADINGS OF PRINCIPAL COMPONENT ANALYSIS (ASTERISKS INDICATE VALUES > 0.7); FOR ABBREVIATIONS IN FIRST COLUMN SEE TEXT.

	Factor 1	Factor 2	Factor 3
ED/SVL	0.049	0.994*	0.097
TDv/SVL	-0.99*	-0.049	-0.134
TDh/SVL	-0.135	-0.1	-0.986*
Explained variance	1.0	1.001	0.999
Proportion of total variance	0.333	0.334	0.333

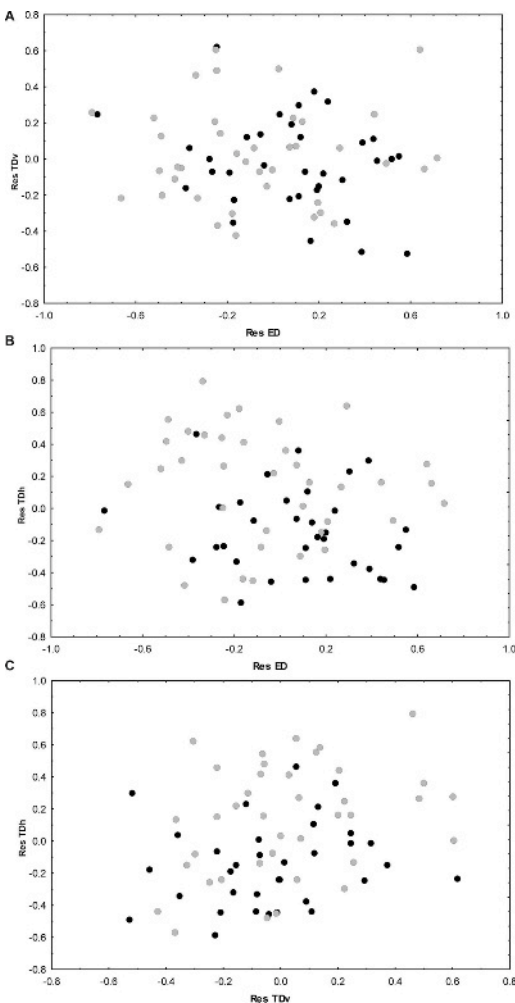


Fig. 2. Scatter plots for all combinations of residuals of the variables TDv, TDh, and ED to SVL for specimen of large *Dendrobates* from the eastern Guiana Shield and its vicinities (filled circles: type specimens and topotypic material of the nominal species *Dendrobates azureus*).

a hunchbacked posture in life (see illustrations in Lötters et al., in press).

Our results suggest that the variants assigned to *D. tinctorius* and *D. azureus* represent one evolutionary lineage, to which we assign joint species status. In principle, we herein follow the evolutionary species concept (cf. Simpson, 1961; Wiley, 1981), which defines species as evolutionary lineages over time. However, the studied populations of *D. tinctorius* and *D. azureus* also form a homogeneous segment of population-level lineages and therefore match the definition of a species under the general lineage concept of species (de Queiroz, 1998). Congruence of morphological and molecular data in merging both taxa into a single lineage makes assignment of joint species applicable under the operational view of the genealogical concordance concept (Avice and Ball, 1990).

The oldest available name for this taxon is *D. tinctorius*. Apart from the fact that none of the many trivial names is available under the ICZN code, none of the names treated here refers to variants that merit specific status. *Dendrobates azureus* should be treated as a junior synonym and thus simply as another variant of *D. tinctorius*. Our samples of *D. tinctorius* represent variants from all over the eastern portion of the Guiana Shield. Since no other large species of *Dendrobates* is known to occur in this region and based on the findings of Silverstone (1975), we suspect that *D. machadoi* also is a junior synonym of *D. tinctorius*, although neither type specimen nor topotypic material of this taxon was included in this analysis.

MATERIAL EXAMINED

Dendrobates azureus.—Suriname: Sipaliwini, forest island on western slope Vier Gebroeders Mountain, RMNH 13837a–i, 13838–13839d, 13840c–13843b, 13843d–f, 13848h–i (29 specimens of type series including holotype), ZFMK 83974–980. Specimens assigned to *Dendrobates tinctorius*: Brazil: Amapa, Serra do Navio, ZFMK 54375–76, 54436, 57254, 83989. French Guiana: Approuague-Kaw, Mts. Bauge/Mts. Kaw ZFMK 83990, 83994; Amatopo, near Lucie River, ZFMK 83988, 83991; Maripasoula, Mts. Atachi Bakka, ZFMK 83981–983; Maripasoula, Saül, ZFMK 83984; unknown locality, ZFMK 40687, 40689, 83995. Suriname: Nickerie, Boetoe, near Lucie River, RMNH 37090–91; Nickerie, rechter Kabaleboriver, RMNH 37092; Saramacca, Toekoemoetoe Creek, RMNH 13848; Sipaliwini, Kabalebo, Kamp Kayzer, RMNH 37089; Sipaliwini, Mt. Kassikas-sima, ZFMK 83985; Sipaliwini, Sipaliwini River, Koeroni Creek, RMNH 1355a–b; Sipaliwini, Tafelberg, Airstrip, RMNH 37093; Sipaliwini, Tafel-

berg, RMNH 40691–95, 48582, ZFMK 83992–993; Sipaliwini, Mt. Teboe near van Loon Mts., ZFMK 83986–987, 67164–71; Sipaliwini, Wilhelmina Gebergte, linker Coppename River, RMNH 13849a.

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- (KCW) ZOOLOGY DEPARTMENT, MAINZ UNIVERSITY, 55099 MAINZ, GERMANY; (BPN) DEPARTMENT OF INTEGRATIVE BIOLOGY, BRIGHAM YOUNG UNIVERSITY, 501 WIDB, PROVO, UTAH 84602; AND (MV, SL) INSTITUTE FOR BIODIVERSITY AND ECOSYSTEM DYNAMICS, UNIVERSITY OF AMSTERDAM, KRUISLAAN 318, 1098 SM AMSTERDAM, THE NETHERLANDS. E-mail: (SL) lotters@science.uva.nl. Send reprint requests to SL. Submitted: 24 Jan. 2005. Accepted: 8 Aug. 2006. Section editor: J. M. Quattro.