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Rafael O. de Sá
University of Richmond, rdesa@richmond.edu

W. Ronald Heyer

Arley Camargo

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A PHYLOGENETIC ANALYSIS OF *VANZOLINIUS* HEYER, 1974
(AMPHIBIA, ANURA, LEPTODACTYLIDAE):
TAXONOMIC AND LIFE HISTORY IMPLICATIONS ¹

(With 1 figure)

RAFAEL O. DE SÁ²
W. RONALD HEYER³
ARLEY CAMARGO⁴

ABSTRACT: The validity of the monotypic leptodactylid frog genus *Vanzolinius* Heyer, 1974 has been questioned recently. We explore the relationships of *Vanzolinius discodactylus* within the cluster of closely related genera *Adenomera*, *Leptodactylus*, and *Lithodytes* with both morphological and molecular data sets. Morphological and combined morphological and molecular data were analyzed using maximum parsimony; molecular data sets were analyzed with maximum likelihood methods. The resultant relationships are unambiguous in *Vanzolinius* being imbedded within *Leptodactylus*. In order to maintain *Leptodactylus* as a monophyletic genus, *Vanzolinius* is placed in the synonymy of *Leptodactylus* Fitzinger, 1826. The implications of relationships analyzed in this study are discussed in terms of both nomenclature and life-history evolution.

Key words: *Leptodactylus*. *Vanzolinius*. Phylogenetic relationships. Life history evolution.

RESUMO: Análise filogenética de *Vanzolinius* Heyer, 1974 (Amphibia, Anura, Leptodactylidae): implicações taxonômicas e sobre a história de vida.

A validade do gênero monotípico de leptodactilídeo *Vanzolinius* Heyer, 1974, tem sido questionada recentemente. Neste estudo exploramos as relações de *Vanzolinius discodactylus* dentro do agrupamento de gêneros proximamente relacionados *Adenomera*, *Leptodactylus* e *Lithodytes* por meio de dados morfológicos e moleculares. Dados morfológicos e dados morfológicos e moleculares combinados foram analisados por parcimônia máxima, dados moleculares foram analisados por máxima verossimilhança. As relações resultantes são inequívocas em *Vanzolinius* ter que ser incluído em *Leptodactylus*. Para manter *Leptodactylus* como um gênero monofilético, *Vanzolinius* Heyer 1974, é colocado na sinonímia de *Leptodactylus* Fitzinger, 1826. As implicações dos relacionamentos analisados neste estudo são discutidas em termos de nomenclatura e evolução dos modos reprodutivos.

Palavras-chave: *Leptodactylus*. *Vanzolinius*. Relações filogenéticas. Evolução da história de vida.

INTRODUCTION

The frog genera *Adenomera* Fitzinger, 1867, *Lithodytes* Fitzinger, 1843, and *Vanzolinius* Heyer, 1974 have, at one time or another, been included in the genus *Leptodactylus*. BOULENGER (1883) described the currently recognized monotypic *Vanzolinius* as *Leptodactylus discodactylus*. HEYER (1970) associated this taxon with the *Leptodactylus melanonotus* species group. Later, HEYER (1974a) placed the taxon within *Lithodytes* commenting on its possible distinctiveness and subsequently created the genus *Vanzolinius* to accommodate this species

(HEYER, 1974b). The most recent morphological analysis indicated that *Vanzolinius* shared distinctive characteristics with *Leptodactylus diedrus* (HEYER, 1998). Previous analyses of relationships agreed that within the subfamily Leptodactylinae the genera *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Vanzolinius* formed a monophyletic clade and that the genus *Physalaemus* Fitzinger, 1826, was more distantly related to this clade (HEYER, 1974a, 1975; LYNCH, 1971).

It is necessary to establish convincingly whether the genus *Leptodactylus* as currently understood is monophyletic, if we wish to understand the

¹ Submitted on February 28, 2005. Accepted on June 17, 2005.

² University of Richmond, Department of Biology, Richmond, VA 23173, USA. E-mail: rdesa@richmond.edu.

³ National Museum of Natural History, Amphibians & Reptiles, MRC 162, PO Box 37012, Smithsonian Institution, Washington, DC 20013-7012, USA.

⁴ Universidad de la República, Facultad de Ciencias, Sección Zoología Vertebrados. 4225 Iguá, Montevideo 11400, Uruguay.

evolution of life history variation in *Leptodactylus*. In this paper, we are particularly interested in determining the phylogenetic relationships of *Vanzolinius*. Preliminary findings on relationships of previously proposed monophyletic clades in the *Leptodactylus* cluster (*Adenomera*, *Leptodactylus*, *Lithodytes*, *Vanzolinius*) are also presented in this paper, and we discuss the implications of our results for understanding aspects of life history evolution in this cluster.

MATERIAL AND METHODS

Taxon sampling – Species groups within *Leptodactylus* were previously recognized on the basis of morphological and life history characters (HEYER, 1969). We included samples from each of the four species groups to sample the morphological diversity within *Leptodactylus*. *Leptodactylus riveroi* Heyer & Pyburn, 1983, a species of uncertain species group affinity, and *L. silvanimbus* McCranie *et al.*, 1980, a species recently suggested as basal within the genus (HEYER, DE SÁ & MULLER, 2005), were also included. *Physalaemus* has been shown to function well as an outgroup for *Leptodactylus* using both morphological and molecular data (HEYER, 1998; HEYER, DE SÁ & MULLER, 2005); herein *Physalaemus gracilis* (Boulenger, 1883) was the outgroup taxon.

The taxa analyzed in this study are: *Leptodactylus bufonius* Boulenger, 1894, *L. fuscus* (Schneider, 1799) (*fuscus* species group); *L. leptodactyloides* (Andersson, 1945), *L. melanonotus* (Hallowell, 1861) (*melanonotus* species group); *L. chaquensis* Cei, 1950, *L. insularum* Barbour, 1906 (*ocellatus* species group); *L. pentadactylus* (Laurenti, 1768) (*pentadactylus* species group); *L. diedrus* Heyer, 1994, *L. riveroi*, *L. silvanimbus* (*Leptodactylus* of unclear species group affinity); *Adenomera hylaedactyla* (Cope, 1868), *Lithodytes lineatus* (Schneider, 1799), *Vanzolinius discodactylus* (Boulenger, 1883); and *Physalaemus gracilis* (as the outgroup). For both the morphological and molecular data, the data for *L. pentadactylus* are from Middle American specimens. See Tissue Voucher Specimens section at the end of this paper for specimen data used for molecular analyses. Museum abbreviations follow LEVITON *et al.* (1985).

Morphological data set – The morphological matrix is provided in Appendix 1. The character state descriptions and ordering information are the same as those published in HEYER (1998) with the

following exceptions. We had no tissue samples for *Adenomera marmorata* and *Physalaemus pustulosus*, two of the taxa used in HEYER (1998), so we used morphological data for *Adenomera hylaedactyla* and *Physalaemus gracilis*, for which we do have molecular data. Data taken for *A. hylaedactyla* and *P. gracilis* were taken from HEYER (1974a), HEYER, DE SÁ & MULLER (2005), USNM 292477 (cleared-and-stained *A. hylaedactyla*) and RdS 511 (larval *P. gracilis* from Uruguay, Canelones, Balneario Atlantida, Rafael de Sá field number). These two species have a few states that differ from their congeners, and require recoding of states and/or redefinition of states as follows.

Character 7, toe webbing. *Physalaemus pustulosus* was coded as having a unique state in the data set of HEYER (1998), toes with weak basal fringes and webbing. *Physalaemus gracilis* has toes without web or fringes, a condition found in other taxa in the data set. The new definitions are: State 0 – toes without web or fringes; State 1 – toes with fringes extending length of toes except for tips; State 2 – females with weakly developed lateral toe fringes and males either with ridges or weakly developed fringes. The state ordering is 0-1-2.

Character 15, depressor mandibulae muscles. The depressor mandibulae may have one to three slips of origin, from the dorsal fascia (df), the zygomatic and/or otic ramus of the squamosal (sq), and the tympanic annulus (at) (following the terminology defined by STARRETT, 1968). Lower case indicates small slips of the muscle, upper case indicates large slips. *Physalaemus pustulosus* has the dfSQat condition, whereas *P. gracilis* has DFSQat. The DFSQat condition is state 0 in our data matrix.

Character 18, anterior petrohyoideus muscle. *Adenomera hylaedactyla* has a state not found in the data set of HEYER (1998). The new definitions are: State 0 – the anterior petrohyoideus muscle inserts entirely on the edge of the hyoid apparatus; State 1 – the muscle inserts on the edge of the hyoid and on the ventral body of the hyoid in part; State 2 – the muscle inserts entirely on the ventral surface of the hyoid body. The state ordering is 0-1-2.

Character 24, sartorius muscle. The condition in *P. gracilis* does not differ from some other taxa in the data set, in contrast to the condition found in *P. pustulosus*. The new definitions are: State 0 – muscle moderate; State 1 – intermediate condition between States 0 and 2; State 2 – muscle broad. The state ordering is 0-1-2.

Character 32, sacral diapophyses. *Physalaemus gracilis* does not differ in this character from other taxa. Thus characters 32-37 in our data set equal characters 33-38 in the HEYER (1998) data set.

Molecular methodology – DNA extraction followed HILLIS *et al.* (1996). Two segments of the mitochondrial genome were amplified using the polymerase chain reaction (PCR). A segment of the 12S r RNA of ~ 900 nucleotides and a segment of the 16S r RNA of ~ 700 nucleotides were amplified. Double-stranded (DS) PCR amplifications were performed in a final volume of 50µl containing 0.4µl of each primer, 1.0µl of each dNTP, 3.0µl of 25mM MgCl₂, and 1.25 units of *Taq* (*Thermus aquaticus*) DNA polymerase; the reaction was overlaid with 50µl of mineral oil. PCR conditions were as follows: 94°C for 60s, 57°C for 60s, and 72°C for 60s, with 25 cycles for the 12S amplification and 30 cycles for the 16S amplification. Amplified product was purified using Wizard® PCR Preps Kit (Promega). Of the purified DS fragment, 0.5µl were mixed with 1.5µl of a single IRD-labeled primer, 7.2µl of Sequencing Buffer, 1.0µl of Sequitherm Excel™II (Epicentre Technologies Co.) DNA polymerase, and 6.8µl of dH₂O. Subsequently, 4.0µl of this mix was added to each of 4 tubes containing 2µl of each nucleotide respectively. PCR conditions were as follows (30 cycles): 92°C for 30s, 55°C for 30s, and 70°C for 30s. SS amplified and IR labeled fragments were sequenced in a LI-COR 4200 IR DNA Sequencer on 6% acrylamide gels. A total of 839 12S and 648 16S nucleotide positions were aligned unambiguously using Clustal X and positions of ambiguous alignments were not used in the phylogenetic analyses. GenBank accession numbers for the sequence data are AY943217–242. The alignment matrix is provided in Appendix 2.

Phylogenetic Analysis – Maximum Parsimony (MP) analysis using PAUP* 4.0 (SWOFFORD, 2002) was used for both the morphological data set and the combined morphological and molecular data set. Molecular data sets were analyzed with maximum likelihood (ML) in PAUP* under the GTR+I+G model recommended by both the Hierarchical Likelihood Ratio Test and the Akaike Information Criterion used by Modeltest 3.04 (POSADA & CRANDALL, 1998). We obtained a total of 37 morphological characters and 1486 base pairs (bp) for each taxon (839 bp corresponding to the 12S rDNA gene and 647 bp to the 16S rDNA gene). Sequences were aligned using Clustal X (THOMPSON, HIGGINS & GIBSON, 1994). We ran individual analyses for each of the

data sets (i.e., morphology, 12S, and 16S data sets) as well as combined analyses (i.e., 12S+16S matrix, morphology+12S+16S matrix). In combined analyses gaps were alternatively considered as missing or as 5th characters; we also evaluated the effect of the substitution bias in the analysis of the combined data matrix using MP by down-weighting transitions to transversions 5:1.

RESULTS

There is modest variation in the 12S, 16S, and 12S+16S data sets (Tabs.1-3). The maximum sequence divergences between pairs of taxa are 21% for the 12S data, 16% for the 16S data, and 18% for the 12S+16S data.

The results of all cladistic analyses are almost identical; consequently we present the maximum parsimony combined data set results and point out where the analyses differ (Fig.1). The parsimony analysis of the combined data matrix results in a single tree (length=1430, consistency index=0.56) in which *Vanzolinius* exhibits a sister taxa relationship with *L. diedrus*. This relationship is also recovered in the analyses of the combined molecular data partitions as well as in all analyses of the 12S data partition. The analyses of the 16S data partition position *Vanzolinius* in the following clade (*L. diedrus* (*L. leptodactyloides*+*Vanzolinius*)). The distance data matrices show that the close relationship of *L. diedrus* with *Vanzolinius* is unambiguous in the 12S data (Tab.1), but not at all clear in the 16S data, where *L. diedrus* and *Vanzolinius* have lower sequence distance values with *L. silvanimbus* and several members of the *L. fuscus*, *L. melanonotus*, and *L. ocellatus* group members than with each other (Tab.2). The morphological data set demonstrates strong support for a *L. diedrus*–*V. discodactylus* sister species relationship with 100% bootstrap support.

DISCUSSION

Phylogenetic conclusions – The following conclusions are supported by the analyses performed on our data.

First, *Vanzolinius* always clusters within *Leptodactylus*. The data are very clear and convincing for this conclusion. There are two nomenclatural options to resolve the phylogenetic conclusion that *Vanzolinius* is imbedded within *Leptodactylus*: *Vanzolinius* could be synonymized with *Leptodactylus*; or one or more clades within

Leptodactylus could be raised to generic status. Current (unpublished) data are inconclusive regarding the phylogenetic relationships among *Leptodactylus* species, and rule out elevating certain clades within *Leptodactylus* to generic status at this time. However, we think there are compelling arguments for placing *Vanzolinius* in the synonymy of *Leptodactylus*. The previous actions on generic placement of the species *discodactylus* were all based on morphological and karyotype data. The strongest support for generic recognition of *Vanzolinius* as a genus distinct from *Leptodactylus* involved two morphological features of the toes: the toe tips of *V. discodactylus* are expanded into small disks with longitudinal grooves on the dorsal surface and the terminal phalanges are T-shaped (HEYER, 1974b). With the discovery of *Leptodactylus diedrus*, the morphological distinctiveness between *Leptodactylus* and *Vanzolinius* was bridged to a large extent (HEYER, 1998). Thus, the morphological data used to define *Vanzolinius* as a genus distinct from *Leptodactylus* are seriously compromised by inclusion of the data for *L. diedrus* and the molecular data strongly support synonymizing *Vanzolinius* with *Leptodactylus*. Consequently, we hereby synonymize the genus *Vanzolinius* Heyer, 1974 with the genus *Leptodactylus* Fitzinger, 1826.

Second, the genera *Adenomera* and *Lithodytes* may share a sister-group relationship and our data provide support that both are evolutionarily distinct from *Leptodactylus* (including *Vanzolinius*).

Third, the previously recognized “traditional” species groups may not all be monophyletic, although the two members of the *L. fuscus* group form a well-supported clade in this study.

Fourth, a sister-group relationship between *L. discodactylus* and *L. diedrus*, previously suggested by HEYER (1998), is reasonably well supported by the morphological and combined molecular data sets.

Finally, *Leptodactylus riveroi*, a taxon of uncertain relationships, exhibits suggestive affinities to the *L. melanonotus* species group.

Life history implications – All members of the subfamily Leptodactylinae (except *Limnomedusa*), place their eggs in foam nests (LANGONE, 1995). Within the *Leptodactylus* cluster, however, there is variation regarding where the foam nests are deposited and considerable variation occurs in other life history aspects. Two examples illustrate how an understanding of phylogenetic relationships in this group is critical to deciphering life history evolution in the genus *Leptodactylus*.

Table 1. 12S sequence differences between taxon pairs included in study using General Time Reversible (GTR) parameter values.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>L. diedrus</i>	-													
2 <i>L. riveroi</i>	0.148	-												
3 <i>L. silvanimbus</i>	0.126	0.137	-											
4 <i>L. bufontius</i>	0.139	0.144	0.115	-										
5 <i>L. fuscus</i>	0.136	0.165	0.135	0.077	-									
6 <i>L. chaquensis</i>	0.128	0.119	0.078	0.095	0.097	-								
7 <i>L. insularum</i>	0.123	0.133	0.094	0.094	0.096	0.065	-							
8 <i>L. leptodactyloides</i>	0.131	0.135	0.086	0.107	0.116	0.042	0.087	-						
9 <i>L. melanonotus</i>	0.137	0.146	0.101	0.105	0.117	0.087	0.088	0.097	-					
10 <i>L. pentadactylus</i>	0.144	0.160	0.116	0.118	0.118	0.107	0.113	0.115	0.131	-				
11 <i>V. discodactylus</i>	0.113	0.166	0.141	0.136	0.129	0.126	0.116	0.130	0.136	0.134	-			
12 <i>A. hylaedactyla</i>	0.177	0.197	0.177	0.156	0.157	0.145	0.151	0.156	0.174	0.161	0.168	-		
13 <i>Lith. lineatus</i>	0.207	0.203	0.175	0.168	0.173	0.175	0.187	0.178	0.182	0.165	0.190	0.161	-	
14 <i>P. gracilis</i>	0.185	0.212	0.167	0.151	0.156	0.161	0.164	0.162	0.164	0.171	0.182	0.160	0.174	-

Table 2. 16S sequence differences between taxon pairs included in study using General Time Reversible (GTR) parameter values.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>L. diedrus</i>	-													
2 <i>L. riveroi</i>	0.129	-												
3 <i>L. silvanimbus</i>	0.099	0.111	-											
4 <i>L. bufonius</i>	0.118	0.136	0.101	-										
5 <i>L. fuscus</i>	0.096	0.132	0.099	0.053	-									
6 <i>L. chaquensis</i>	0.085	0.105	0.072	0.093	0.079	-								
7 <i>L. insularum</i>	0.088	0.098	0.060	0.088	0.072	0.039	-							
8 <i>L. leptodactyloides</i>	0.092	0.124	0.109	0.117	0.116	0.085	0.092	-						
9 <i>L. melanonotus</i>	0.083	0.100	0.079	0.097	0.091	0.060	0.063	0.084	-					
10 <i>L. pentadactylus</i>	0.108	0.128	0.099	0.096	0.082	0.086	0.074	0.117	0.080	-				
11 <i>V. discodactylus</i>	0.104	0.118	0.125	0.132	0.114	0.099	0.094	0.087	0.100	0.114	-			
12 <i>A. hylaeodactyla</i>	0.135	0.136	0.128	0.144	0.133	0.128	0.124	0.131	0.111	0.128	0.147	-		
13 <i>Lith. lineatus</i>	0.155	0.146	0.116	0.138	0.125	0.125	0.120	0.156	0.121	0.131	0.160	0.105	-	
14 <i>P. gracilis</i>	0.160	0.163	0.126	0.150	0.139	0.126	0.124	0.148	0.145	0.145	0.165	0.143	0.133	-

Table 3. Combined 12S & 16S sequence differences between taxon pairs included in study using General Time Reversible (GTR) parameter values.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>L. diedrus</i>	-													
2 <i>L. riveroi</i>	0.140	-												
3 <i>L. silvanimbus</i>	0.114	0.125	-											
4 <i>L. bufonius</i>	0.130	0.140	0.109	-										
5 <i>L. fuscus</i>	0.118	0.150	0.118	0.066	-									
6 <i>L. chaquensis</i>	0.109	0.113	0.075	0.094	0.089	-								
7 <i>L. insularum</i>	0.108	0.118	0.079	0.092	0.085	0.054	-							
8 <i>L. leptodactyloides</i>	0.114	0.130	0.096	0.111	0.116	0.060	0.089	-						
9 <i>L. melanonotus</i>	0.113	0.126	0.092	0.101	0.106	0.075	0.077	0.091	-					
10 <i>L. pentadactylus</i>	0.128	0.146	0.109	0.108	0.102	0.098	0.096	0.116	0.108	-				
11 <i>V. discodactylus</i>	0.109	0.144	0.134	0.134	0.123	0.114	0.106	0.111	0.120	0.125	-			
12 <i>A. hylaeodactyla</i>	0.158	0.170	0.155	0.151	0.147	0.138	0.139	0.145	0.146	0.146	0.159	-		
13 <i>Lith. lineatus</i>	0.184	0.178	0.148	0.155	0.152	0.153	0.157	0.168	0.154	0.150	0.177	0.136	-	
14 <i>P. gracilis</i>	0.174	0.190	0.149	0.150	0.149	0.145	0.147	0.156	0.155	0.160	0.175	0.152	0.156	-

First, two clades (*Adenomera* and the *L. fuscus* species group) within Leptodactylinae share the same pattern of males constructing a terrestrial subsurface chamber, attracting females to the chamber acoustically, and depositing the foam nest in the chamber where at least embryonic and early larval development take place (see KOKUBUM & GIARETTA, 2005 and references cited therein). Our data indicate that this complex life history pattern was independently derived in both clades and is not the result of shared ancestral adaptations. Also, at least some members of the *L. pentadactylus* group use pre-existing terrestrial burrows in which they deposit their foam nest (see GIBSON & BULEY, 2004 and references cited therein). Additional taxon sampling is required to determine whether this pattern served as a precursor to the actual construction of terrestrial incubating chambers in the *L. fuscus* group. Our preliminary data suggest support for this scenario.

Second, there is considerable variation in female attendance of foam nests and larvae, whether attending females communicate with their larvae, and how females communicate with their larvae (VAZ-FERREIRA & GEHRAU, 1975; WELLS & BARD, 1988). As far as is known, parental care does not occur in any species of the *L. fuscus* group. Our preliminary data indicate that intensive taxon sampling with additional data is required to resolve relationships among the *Leptodactylus* species that demonstrate female attendance and communication with their offspring in order to understand the evolution of parental care in *Leptodactylus*.

More intensive taxon sampling and the sequencing of nuclear and more slowly evolving genes should provide a well-supported phylogeny for *Leptodactylus* at the species level that will allow a better understanding of the evolution of life history variation in the *Leptodactylus* cluster.

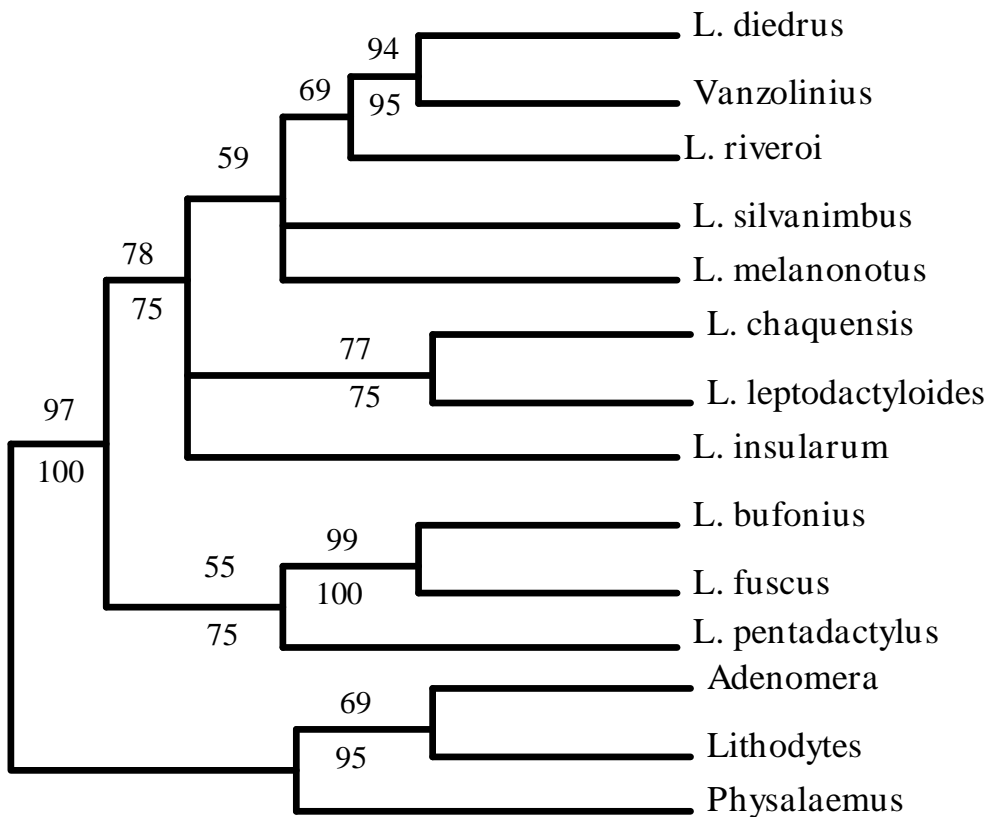


Fig.1- Maximum Parsimony Tree of combined (morphological and molecular) data sets. Gaps were considered as a fifth character. Numbers above branches correspond to bootstrap support in parsimony analysis; numbers below branches are bootstrap support values from Maximum Likelihood analysis of the combined molecular data set.

TISSUE VOUCHER SPECIMENS

Adenomera hylaedactyla – BRAZIL: PARÁ: Alter do Chão (MZUSP 70958)

Leptodactylus bufonius – ARGENTINA: SALTA: 54 km NE of Joaquín V. González on provincial route 41 (USNM field number 175816, deposited in FML).

Leptodactylus chaquensis – ARGENTINA: TUCUMÁN: ca 40 km SE San Miguel de Tucumán at km post 1253 on International Route 9 (USNM 319708).

Leptodactylus diedrus – VENEZUELA: AMAZONAS: Río Negro, near Neblina base camp on left bank of Río Baria (= Río Mawarinuma) (USNM 30715).

Leptodactylus discodactylus – ECUADOR (QCAZ 16788).

Leptodactylus fuscus – BRAZIL: RORAIMA: Caracaranã, near Normandia (MZUSP 67073).

Leptodactylus insularum – PANAMA: PANAMA: Río Indio, camino hacia Las Minas (CH 4956).

Leptodactylus leptodactyloides – BRAZIL: PARÁ: Serra de Kokoinhokren (MZUSP 70969).

Leptodactylus melanonotus – BELIZE: CAYO: between San Jacinto and Spanish Lookout road on Webster Highway, Caesar's Hotel (USNM 535964).

Leptodactylus ocellatus – BRAZIL: SANTA CATARINA: Campeche (MZUSP 68993).

Leptodactylus "pentadactylus" – PANAMA: BOCAS DEL TORO: Isla Popa (USNM 347153).

Leptodactylus riveroi – VENEZUELA: AMAZONAS: Río Negro, Neblina base camp on left bank of Río Baria (= Río Mawarinuma) (USNM 562029).

Leptodactylus silvanimbus – HONDURAS: OCOTEPEQUE; Belén Gualcho (USNM 348631).

Lithodytes lineatus – BRAZIL: MATO GROSSO: Apiacás (MZUSP 80874).

Physalaemus gracilis – URUGUAY: SALTO: Espinillar (RdS 788 field number).

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APPENDIX 1

Morphological (primarily) data matrix used for phylogenetic analysis

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	34	35	36	37	
<i>L. bufonius</i>	3	0	0	0	0	0	3	4	0	3	0	1	1	1	1	0	2	0	0	0	2	1	0	0
<i>L. fuscus</i>	3	0	0	3	0	0	3	4	0	3	0	1	1	1	1	0	1	0	1	0	2	1	0	0
<i>L. leptodaactyloides</i>	1	0	2	1	1	0	1	0	3&5	0	2	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>L. melanotus</i>	1	0	2	0	0	0	1	1	5	0	2	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>L. chaquensis</i>	2	0	2	3	0	0	1	2	2	0	2	0	0	0	1	0	0	0	0	0	2	2	0	0
<i>L. insularum</i>	1	0	2	2	0	0	1	1	3	0	2	0	0	0	1	0	0	0	1	0	3	3	0	0
<i>L. pentadactylus</i>	1	0	1	2	0	0	0	2	4	0	3	1	0	0	1	0	0	0	0	0	1&3	2	1	1
<i>L. diedrus</i>	1	0	2	0	2	0	1	?	?	?	?	?	1	?	1	0	0&1	0	0	0	2	0	0	0
<i>L. riveroi</i>	0	0	2	2	0	0	1	0	4	0	2	0	?	?	1	0	0	0	0	0	1&2	1	1	1
<i>L. sivanimbubus</i>	1	0	2	0	0	0	2	0	5	0	2	0	0	?	1	0	0	0	0	0	3	3	0	0
<i>A. hylaedactyla</i>	1	0	0	0	1	0	0	?	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	1
<i>Lith. lineatus</i>	1	0	0	2	4	0	0	?	1	0	0	0	1	1	1	0	0	0	1	1	1	1	1	0
<i>V. discodactylus</i>	1	0	0	0	3	0	1	0	5	0	2	0	1	0	1	0	0	0	0	0	2	2	1	0
<i>P. gracilis</i>	4	1	3	0	0	1	0	3	4	1	3	0	1	0	0	1	2	2	0	0	4	3	1	1
<i>L. bufonius</i>	0	0	0	1	0	0	0	2	0	0	0	1	2	1	1	1	0	0	0	0	2	1	0	0
<i>L. fuscus</i>	0	0	0	1	0	0	0	0&2	0	0	0	0	2	1	2	0	0	0	0	0	2	1	0	0
<i>L. leptodaactyloides</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0
<i>L. melanotus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
<i>L. chaquensis</i>	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	3	0	1	0	0
<i>L. insularum</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0
<i>L. pentadactylus</i>	0	0	0	1	0	0	0	2	0	1	1	1	1	1	1	0	0	0	0	0	2	2	2	0
<i>L. diedrus</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	2	2	1	1	1
<i>L. riveroi</i>	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	2	3	3	0	0
<i>L. sivanimbubus</i>	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	4	0	1	1	1
<i>A. hylaedactyla</i>	2	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1
<i>Lith. lineatus</i>	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0
<i>V. discodactylus</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	2	1	1	1	0
<i>P. gracilis</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	3	1	1

(See text and Heyer, 1998, for character state descriptions).

APPENDIX 2

Molecular data matrix used for phylogenetic analysis. Regions in brackets correspond to ambiguous alignment and were not included in the analyses.

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BEGINS 12S DATA
Diedrus [AGCGTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTAACCCTTAAGATCAAC
Riveroi [-GGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCCCAGCCCTTAAGATCAAC
Silvani [-GGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAGACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAC
Bufoniu [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Fuscuss [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAGACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Chaquen [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Insular [AGCGTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Tyloide [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAATA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Melanon [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAC
Pentada [-GGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Vanzoli [AGCGTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAGACA] TAAAAGTTTGGTCTTGACCTTAAGATCAGC
Adenhya [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAT
Lithody [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAAC
Physala [-CGCTGAAGATGCTGAGATGGACCCATAAAAAGTCTTTAAACA] CAAAAGTTTGGTCTTGACCTTAAGATCAGT

Diedrus TCTTACTTAACTTACACATGCAAGTCTCAGCACCCCTGTGAAAACGCCCTTCAAATCCT-ACA-AGGGCAAGGAG
Riveroi TCTTACTTAACTTACACATGCAAGTCTCAGCGCCCGGTGAGAACGCCCTTCAAATCCA-CTA-AGGAACAAGGAG
Silvani TCTTACTTAACTTACACATGCAAGKCTCAGCACCCCTGTGAAAACGCCCTTCAAATCCC-CC--TGGAGTAAGGAG
Bufoniu TTTTACTTAACTTACACATGCAAGTCTCCGCACCCCTGTGAAAACGCCCTTAAAATTTCCCTTAGCGGACAAAGGAG
Fuscuss TTTTACTTAACTTACACATGCAAGTCTCCGCACCCCTGTGAGAACGCCCTCAAACCCCT-AAA-AGGACGAGGAG
Chaquen TTTTACTTAACTTACACATGCAAGTCTCAGCACCCCTGTGAGAACGCCCTTTAACTCCC-ATT-AGGAACAAGGAG
Insular TTTTACTTAACTTACACATGCAAGTCTCAGCATCCCTGTGAGAACGCCCTTTAACTCCCCCTA-AGGAGCAAGGAG
Tyloide TTTTACTTAACTTACACATGCAAGTCTCAGCACCCCTGTGAGAACGCCCTTTAACTCCC-GTT-AGGAACAAGGAG
Melanon TTTTACTTAACTTACACATGCAAGTCTCAGCATTTCTGTGAAAACGCCCTTTAACTCCT-TTA-CGGAACAAGGAG
Pentada TGTTACTTAACTTACACATGCAAGTCTCCGCACCTCTGTGAGAACACCCTTTAACCCCT-TTA-AGGGAAAAGGAG
Vanzoli TCTTACTTAACTTACACATGCAAGTCTCCGCCTTCTGTGAAAACGCCCTTAGACCCCT-CAA-AGGGAAAAGGAG
Adenhya TTTTACTTAACTTACACATGCAAGTATCCGCACCCCTGTGAAAACGCCCTTTAAATTCCT-TAT-AGGGATAAGGAG
Lithody TTTTCTTAACTTACACATGCAAGTATCCGCACCCCTGTGAAAACGCCCTTATATCCCC-GA--TAGGATAAGGAG
Physala TATTACTTAACTTACACATGCAAGTCTCCGCACCCCTGTGAAAACGCCCTTTAAATCCCC-TCT-CGGGATAAGGAG

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Diedrus CCGGTATCAGGCACACCAA -- AAGCCCAAAGACACCTAGCTATGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Riveroi CCGGTATCAGGCACAAAGTTTTAGCCCAAAGACACCTAGCCACAGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Silvani CTGGTATCAGGCGAAAACCT - TAGCCCAAAGACACCTAGCTATGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Bufoniu CTGGTATCAGGCACAAAACAT - TAGCCCAAAGACACCTAGCTTTGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Fuscuss CTGGTATCAGGCACAAAACAT - TAGCCCAAAGACACCTAGCCATGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Chaquen CTGGTATCAGGCACAAACCTT - TAGCCCAAAGACACCTAGCTACGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Insular CTGGTATCAGGCACAAAATCT - TAGCCCAAAGACACCTAGCCATGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Tyloide CTGGTATCAGGCACAAACCTT - TAGCCCAAAGACACCTAGCTAGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Melanon CTGGTATCAGGCACAAAATAT - TAGCCCAAAGACACCTAGCTAGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Pentada TTGGTATCAGGCTCAAAACAT - TAGCCCAAAGACACCTAGCTAGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Vanzoli CCGGTATCAGGCACATCTCT - TAGCCCAAAGACACCTAGCTATGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Adenhya CCGGTATCAGGCACATCAATATAGCCCAAAAACACCTAGCTATGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Lithody CTGGTATCAGGCACAAAAT - TAGCCCAAAGACACCTAGCTCAGCCACACCCACAAGGGAACTCAGCAGTGATTAAC
 Physala CTGGTATCAGGCCCCAAAATCT - GCCCAAAAACACCTAGCTATGCCACATCCACAAGGGAACTCAGCAGTGATTAAC

Diedrus ATTAACATGAGCGACAGCTTGATTCAGTTAAAAGAAAAGAGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA
 Riveroi ATGTGCATGAGCGCCAGCTCGACTCAATTAAGTAAAAAGGGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA
 Silvani ATTGAATATAAGCGACAGCTTGACTCAGTTAAAGTAAAAAGAGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA
 Bufoniu ATTGAATATAAGCGACAGCTTGACTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Fuscuss ATTGAATATAAGCGACAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Chaquen ATTGAATATAAGCGCCAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Insular ATTGAATATAAGCGCCAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA
 Tyloide ATTGAATATAAGCGCCAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Melanon ATTGGACATAAGCGACAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA
 Pentada ATTGAATATAAGCGGATAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Vanzoli ATTAACATAAGCGACAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA
 Adenhya ATTAATATCAGCGACAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Lithody ATTGAACATCAGCGACAGCTGGATTCAGTTAAAGTAAAAAGAGCCGGCTAATCTGGTGCCAGCCCGCGGGTTACA
 Physala ATTGAACATAAGCGACAGCTTGATTCAGTTAAAGTAAAAAGAGCCGGCAAATCTGGTGCCAGCCCGCGGGTTACA

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Diedrus CCACGTGGCTCAAAGTTGACCTTGCTCGGCCGTAAGCGTGATTTAAGAAATATGCCCA - TGGTGTCAAAAA - AGTTT
 Riveroi CCACGTGGCTCAAATTTGATCTCATCCGGCGTAAAGCGTGATTTAAGAGACAATCCCA - TGGTGTCAAAAA - AGTTT
 Silvani CCATGAGGCCCTAGTTGACCTTTCTCGGCCGTAAGCGTGATTTAAGAAA - ATATTTA - TGATGTCAAAAA - CTCAC
 Bufoniu CCACGTGGCTCAAATTTGATTTCTTCTCGGCCGTAAGCGTGATTTAAGGACATCCCTTT - TGGTGTCAAAAA - AGCAC
 Fuscuss CCACGTGGCTCAAATTTGATTTCTGATCGGCCGTAAGCGTGATTTAAGAGATTCCTCCCTTTGGTGTCAAAAA - GATAC
 Chaquen CCACGTGGCTCAAATTTGATTTTCTCGGCCGTAAGCGTGATTTAAGAGACCAATTCA - TGGTGTCAAAAA - AGCAC
 Insular CCACGTGGCTCAAATTTGATTTTCTCGGCCGTAAGCGTGATTTAAGGGATTAACCAA - TGGTGTCAAAAA - ATTAT
 Tyloide CCACGTGGCTCAAATTTGATTTTCTCGGCCGTAAGCGTGATTTAAGAGATCAATTC - TGGTGTCAAAAA - AGCAC
 Melanon CCACGTGGCTCAAATTTGATTTCTACTCGGCCGTAAGCGTGATTTAAGATA - CTACTCA - TGATGCCAAAA - AACAT
 Pentada CCACGTGGCTCAAATTTGACCTAACTCGGCCGTAAGCGTGATTTAAGGAA - ATACTTT - TGGTGTCAAAAA - TATAC
 Vanzoli CCATGTGGCTCAAAGTTGATTTTGTTCGGCGTAAAGCGTGATTTAAGCGT - TTAATTA - TGGTGTCAAAAA - AGTAC
 Adenhya CCACGTGGCTCAAATTTGACCAATTTTCTCGGCCGTAAGAGTGATTTAAGAGT - CCTATAATTTGGTGTCAAAAT - TTTAC
 Lithody CCACGTGGCTCAAAGTTGACCCCATCGGCCGTAAGCGTGATTTAAGAGACCAAAAT - TGGTGTCAAAAA - TTTAC
 Physala CCACGTGGTTCAAATTTGATTTCTTATCGGCCGTAAGCGTGATTTAAGCCATATACGAT - TGAAGTTGAACT - TAAAT

 Diedrus TAAGCTGTGACACGCTTGTCTTTAATAAGACCACAAAAACGAAAAGTTACACCAACCCGCACCTACTTTGAACCCACGACA
 Riveroi TAAGCTGTGACACGCTTGTGCCCCGAAAACCCCAAGACGAAAAGTTACACCCAGCCAAACCAACTTGAACCTCACGACA
 Silvani TAAGCTGTGACACGCTTGTGCCCCAGAAAGCCAGAAAACGAAAAGCTACATCAACC - AACCAACTTGAATTCACGACA
 Bufoniu TAAGCCGTGACACGCTTGTGCTTAAGAAAATCAAAAACGAAAAGTTACACCAACTCAACCAACTTGAACCTCACGACA
 Fuscuss TAAGCCGTGACACGCTTGTATTTCAAGAAGATCAGAAAACGAAAAGTTACACCAACTTAATCAACTTGAACCTCACGACA
 Chaquen TAAGCTGTGACACGCTTGTGCTCAGAAAGCCAGAAAACGAAAAGCTACACCAATATATCAACTTGAACCTCACGACA
 Insular TAAGCCGTGACACGCTTGTGATTTAGAAGCTCAAAAACGAAAAGCTACACCAATATATCAACTTGAACCTCACGACA
 Tyloide TAAGCTGTGACACGCTTGTGCTCAGAAAGCCAGAAAACGAAAAGCTACACCAATATATCAACTTGAACCTCACGACA
 Melanon TAAGCTGTGACACGCTTATGCTCTAGAAGCTCAAAAACGAAAAGTTGCTCAAT - AACCAACTTGAATTCACGACA
 Pentada TAAGCCGTGACACGCTTGTACATTAAGAAGCCAAAATCGAAAAGCTACACCAACTCAACCAACTTGAACCTCACGACA
 Vanzoli TAAGCCGTGACACGCTTGTACATAAGAAGCCCTAAAACGAAAAGTTACACCAACTCAATAAA - TGAACCCACGACA
 Adenhya TAAGCCGTAAACGCTTGCCTTTAGAAGCTCTAACACGAAAAGTTACCCCAATTTAATCAACTTGAACCTCACGACA
 Lithody TAAGCCGTGACACGCTTGTGCAAAAAGTACCTAAAACGAAAAGTTGTACCAACTTGAACCTCACGACA
 Physala TAAGCTGTGACACGCTTGTGTTTATCAGAAAACCAAAAAGTTACTCCAATTAACCTCTACTTGAACCTCACGACA

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Diedrus	GCTAGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-CAAATCGCCCGGG
Riveroi	GCCGGGAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-CAAATCGCCCGGG
Silvani	GCTTGGGAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-CITCCAATCGCCAGGG
Bufoniu	GCTAGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-TGATCGCCCTGGG
Fuscuss	GTTAGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAACCCGTAAACCTTTAACTTACACCTTTTATCGCCCGGG
Chaquen	GCTTGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-CAAATCGCCAGGG
Insular	GCTTGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-CCATCGCCAGGG
Tyloide	GCTTGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACNTTAACTTACACCT-NAATCGCCNCGG
Melanon	GCTTGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTAACTTACACCT-TTCTTATCGCCAGGG
Pentada	GCTAGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAGCCGTAAACCTTTTAACTTACACCT-ACATCGCCAGGG
Vanzoli	GCTAGGAAACAACCTGGGATTAGATACCCACACTATGCCCTAACCCGTAAACCTTTAACTTACACCT-CGATCGCCAGGG
Adenhya	GCTAAGAAACAACCTGGGATTAGATACCCACACTATGCCCTTGGCAATAAACCTTTAACTTACACCTCCACCTCCAAATCGCCCGGG
Lithody	GTCAAAGACACAACCTGGGATTAGATACCCACACTATGCCCTTGACCCGTAAACCTTTTAACTTACACCTTATCGCCAGGG
Physala	GTTAAGATACAACCTGGGATTAGATACCCACACTATGCCCTTAAACCCGTAAACCTTA-ATTTACACCT-TAAATCGCCCGGG
Diedrus	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTACAAATCG
Riveroi	AACTACAAGCCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Silvani	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Bufoniu	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Fuscuss	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Chaquen	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Insular	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Tyloide	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Melanon	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Pentada	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Vanzoli	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Adenhya	AACTATGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Lithody	AACTACGAGCTATGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG
Physala	AACTACGAGCAAAGCTTAAACCCCAAAGGACTTGACGGTACCCCAAATCCCACTAGAGGAGCCCTGTCTATAAATCG

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...continuation

Diedrus ATACTCCCCGCTTAAACCTCACCTCTTTTAGTCAITCAGTCTGTATACCTCCGTCGCCAGCTTACCCCTATGAGCGTCTC
 Riveroi ATAAACCCCGCTTAAACCTCACCTCTTTTGTAAATCAGCCCTGTATACCTCCGTCGTCAGCTTACCCGCTGAGCGCG
 Silvani ATAAACCCCGCTTAAACCTCACCACTTTTAGCCCTATCAGCCCTGTATACCTCCGTCGTCAGCTTACCACTGAGCGTCTC
 Bufoniu ATAAACCCCGCTTAAACCTCACCACTTTTGTCTTTTCAAGCTGTATACCTCCGTCGCCAGCTTACCCGCTGAGCGCT
 Fuscuss ATAAACCCCGCTTAAACCTCACCACTTTTGTCTATCAGCTGTATACCTCCGTCGCCAGCTTACCCGCTGAGCGTCTC
 Chaquen ATAAACCCCGCTTAAACCTCACCACTTTTGTCTATCAGCCCTGTATACCTCCGTCGTCAGCTTACCACTGAGCGCT
 Insular ATAAACCCCGCTTAAACCTCACCACTTTTGTCTGTAGCCCTGTATACCTCCGTCGTCAGCTTACCACTGAGCGCT
 Tyloide ATAAACCCCGCTTAAACCTCACCTCTTATGCCCCGTCAGCCCTGTATACCTCCGTCGTCAGCTTACCACTGAGCGCT
 Melanon ATAAACCCCGCTTAAACCTCACCACTTATGCCCCCTTCAAGCTGTATACCTCCGTCGTCAGCTTACCTCCGTCAGCGTCT
 Pentada ATAAACCCCGCTTAAACCTCACCACTTTTAGCAAAATCAGCTGTATACCTCCGTCGTCAGCTTACCTCCGTCAGCGCT
 Vanzoli ATAAACCCCGCTTAAACCTCACCTCTTGTGTCCATCAGCCCTGTATACCTCCGTCGTCAGCTTACCTCCGTCAGCGCT
 Adenhya ATAAACCCCGCTTAAACCTCACCACTTTCTAGCTAATCAGCCCTGTATACCTCCGTCGTCAGCTTACCTCCGTCAGCGGAA
 Lithody ATAAACCCCGCTTAAACCTCACCACTTTTGTAAAAATCAGCCCTGTATACCTCCGTCGTCAGCTTACCACTGTAACGCTC
 Physala ATAAACCCCGCTTAAACCTCACCAACTTTGTCTATTCAGCCCTGTATACCTCCGTCGTCAGCTTACCTCCGTCAGCGGAA

 Diedrus ACTAAGTGAGCCAAAATGCCCGCACGCCAAACACGTCAGGTCAAGGTGCAGCTAAATAAGAGGGGAAGAGATGGGCTAC
 Riveroi ACTCAGTGAGCTTAAATGCCCGTAAGCCAAACACGTCAGGTCAAGGTGCAGCTAAATAAGAGGGGAAGAGATGGGCTAC
 Silvani ACTAAGTGAGCTTAAATGCTATACATCAACACGTCAGGTCAAGGTGCAGCTCAA TGAAGTGGAAAGAGATGGGCTAC
 Bufoniu ATTAAGTGAGCTTAAATGACAAATACGCCAAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAAGATGGGCTAC
 Fuscuss CTTAAGTGAGCCCAAATGCCCATACGCCAAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Chaquen ATTAAGTGAGCTTAAATGCCCTACGCCAAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Insular ATTAAGTGAGCTTAAATGCCCTACGCCAAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Tyloide ACTAAGTGAGCCCAAATGTTTTATACATCAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Melanon ACCAAGTGAGCTTAAATGCCCTGTCCGCCAAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Pentada TTTAAGTGAGCCCAAATGCCAATACGCCAAATACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Vanzoli ATTAAGTGAGCTTAAATGCCCCCGCTCAACACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Adenhya ATATAGTGAGCTCAATGCCATTTTACCCTTACCTCAAGGTGCAGCTCA TGAAGTGGGAAAGAGATGGGCTAC
 Lithody TTATAGTGAGCTTAAACGCTTATTCACCAGTACGTCAGGTCAAGGTGCAGCTAA TGAAGTGGGAAAGAGATGGGCTAC
 Physala TATTAGTGAGCTTAAATGTCT-TTCAACCAATACGTCAGGTCAAGGTGCAGCACATGAGCTGGAAAGAGATGGGCTAC

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Diedrus
Riveroi
Silvani
Bufoniu
Fuscuss
Chaquen
Insular
Tyloide
Melanon
Pentada
Vanzoli
Adenhya
Lithody
Physala

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Diedrus
Riveroi
Silvani
Bufoniu
Fuscuss
Chaquen
Insular
Tyloide
Melanon
Pentada
Vanzoli
Adenhya
Lithody
Physala

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BEGINS 16S DATA

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Riveroi ATAAGAGGTCGGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Silvani ATAAGAGGTCAGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Bufoniu ATAAGAGGTCAGCCTGCCCA-GTGAC-TTT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Fuscuss ATGAGAGGTCAGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
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Insular ATAAGAGGTCAGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Tyloide ATAAAGGTCAGCCTGCCCA-GTGAC-TTT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Melanon ATAAGAGGTCAGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Pentada ATAAGAGGTCAGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
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Lithody ATAAGAGGTCAGCCTGCCCA-GTGAC-TCT--GTTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT
Physala ATAAGAGGTCAGCCTGCCCA-GTGAC-TCA--ATTCAAACGGCCGGGTATCCTAAACCGTGCGAAGGTAGCCGTAAT

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Riveroi CACTTGTTCTTAAATAAGGACCCGGTAGAATGGCAACGAAAGGTTATACTGTCTCCCTTTTCTAAATCAGTGAAA
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Insular CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAAAGGTTATACTGTCTCCCTTTTCTAAATCAGTGAAA
Tyloide CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAGGGTTTACTGTCTCCCTCCCTTAATCAGTGAAA
Melanon CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAAAGGTTATACTGTCTCCCTCCCTTAATCAGTGAAA
Pentada CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAAAGGTTATACTGTCTCCCTCCCTTAATCAGTGAAA
Vanzoli CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAAAGGTTATACTGTCTCCCTCCCTTAATCAGTGAAA
Adenhya CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAAAGGTTATACTGTCTCCCTTTCTAAATCAGTGAAA
Lithody CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAGGGTTGCACGTCTCCCTTTCTAAATCAGTGAAA
Physala CACTTGTTCTTAAATAAGGACTAGTAGTAAGGCAACGAGGGTTACACTGTCTCCCTTTTCTAAATCAGTGAAA

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Diedrus
 Riveroi
 Silvani
 Bufoniu
 Fuscuss
 Chaquen
 Insular
 Tyloide
 Melanon
 Pentada
 Vanzoli
 Adenhya
 Lithody
 Physala

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Diedrus
 Riveroi
 Silvani
 Bufoniu
 Fuscuss
 Chaquen
 Insular
 Tyloide
 Melanon
 Pentada
 Vanzoli
 Adenhya
 Lithody
 Physala

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 [-TAGCCCTACTCATTTACACA-----ACTCCAGATGAATA--CTTTAC-CCTGGCTCG--]ATAATTTATAGTT
 [-TTGT-TATAATGTTCCACC-----CTTCAGAGAAATAAATTTCTAC-TTTAACATA--]ATGCTCACCCAGTT

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Diedrus TTAGGTTGGGGTGACACGGAGCAAAAAACAACCTCCGCAGTGAATAGGGCCCTTTTTCCTTAAACCCAGGACTAC
 Riveroi TTTGGTTGGGGTGACCGCGGAG--AAAAACAACCTCCACAATGAATGGGACCCCCC--CCCTTAATTTACGGGCCAC
 Silvani TTAGGTTGGGGTGACCGCGGAGAAAAATAA--CCTCCACAATGAACAGGACTTA---TCTTAAATTTAGGATTA
 Bufoniu TTAGGTTGGGGTGACCGGAGTAAATTTAACCTCCGCAATGAACGGGGCTTT---CCCCTAAGATAAGAGCTAC
 Fuscuss TTAGGTTGGGGTGACCGGAGTAAAAACAACCTCCGCAGTGAAGGGGCTTTT---CCCCTAAGCAAGGGCTAC
 Chaquen TTAGGTTGGGGTGACCGGAGCAAAAAATAACCTCCGCAGTGAATGGAACCTTAT--TTCCTAAACCCAGGGCTAC
 Insular TTAGGTTGGGGTGACCGGAGATAAAAAATAACCTCCACAGTGAACGGGACTCAT--TCCCTAAACCAAGGGCTAC
 Tyloide TTAGGTTGGGGTGACCGGAGTAAAAATAGCCTCCACAGCGAA TGGGACTTC---TCCCTAAACTCAGGGCTAC
 Melanon TTAGGTTGGGGTGACCGGGTAAAAATAACCTCCACAGTGAATGGGG-TCTT---CCCCTAAACTCAGGGCCAC
 Pentada TTAGGTTGGGGTGACCGGAGTAAAAACAACCTCCGCAATGAACAGGGATCT--TCCCTTAAACCAAGGGCCAC
 Vanzoli TTAGGTTGGGGTGACCGGAGCAAAAAACAACCTCCACACTGGAAGGGACTT---TCCCTAAACCCAGGGCCAC
 Adenhya TTTGGTTGGGGTGACCGGAAATAAAAAACAACCTCCACAATGAA-AGAT-TCTCCTTCACTAAGTTAAGGACTAC
 Lithody TTTGGTTGGGGTGACCGGAGAAAAAGAAACCTCCGCAATGAAGACT--CTC--CTTCTTAGTTAGGACTAC
 Physala TTCGGTTGGGGTGACCGGAGATAAAAAACAACCTCCACGATAAAAAACTTAA--TCTCTTAAATCCAGAAATTA

Diedrus AACCTAAGATTCAACAAAAT-TGACACCCATT-GACCCAGTT--TCTGATCAATGAACCAAGTTACCCTAGGGATA
 Riveroi AGCCCTAAAAATCAACAAAAT-TGACATATATTTGACCCCAATCTTTTGRGCAACGAACCAAGTTACCCTAGGGATA
 Silvani AATCCCAAAAATCAATAAAT-TGACATCTATT-GACCCCAATATTTTGATCAATGAACCAAGTTACCCTAGGGATA
 Bufoniu GACTTAATAATCAACAAAAT-TGACACCAATT-GACCCCAATACACTTGATCAATGAACCAAGTTACCCTAGGGATA
 Fuscuss GACCTAAGAAATCAATAGAT-TGACACTAATT-GACCCCAATT-AATTGATCAATGAACCAAGTTACCCTAGGGATA
 Chaquen GACCTAAGAAATCAATAAAT-TGACACTGATT-GACCCCAATATTTTGATCAATGAACCAAGTTACCCTAGGGATA
 Insular AACCTAAGCATCAATAAAT-TGACACCTATT-GACCCCAATA-TTTTGATCAATGAACCAAGTTACCCTAGGGATA
 Tyloide GACCTAAGAAATCAATAAAT-TGACACCCATT-GACCCCAATT-TTTTGACCAATGAACCAAGTTACCCTAGGGATA
 Melanon AACCTAAAAATCAATAAAT-TGACACCCATT-GACCCCAATA-TTTTGATCAATGAACCAAGTTACCCTAGGGATA
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 Vanzoli AGCCCCAGAAATCAATAAAT-TGACACCTGTT-GACCCCAATA-TTTTGACCAATGAACCAAGTTACCCTAGGGATA
 Adenhya AACCTATACATCAATAAAT-TGACATA-ATT-GACCCCAACA-TATTGATCAATGAACCAAGTTACCCTAGGGATA
 Lithody TTTCTACGATCAATAAAT-TGACACATATT-TGACCAACACTTGATCAATGAACCAAGTTACCCTAGGGATA
 Physala GATTTAAGTACCAAAAAATT-TGATATACATT-GATCCCAATT-TATTGATCAACGAACCAAGTTACCCTAGGGATA

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Diedrus ACAGCGCAATCCA CTTCAAGAGCTCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGCATCCTAGT
 Riveroi ACAGGAAATCCA CTTTAAAGGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTACCCCAAGT
 Silvani ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTGTCCCAAGT
 Bufoniu ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Fuscuss ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Chaquen ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
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 Melanon ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Pentada ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Vanzoli ACAGCGCAATCCA CTTTAAAGAGCTCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Adenhya ACAGCGCAATCCA CTTTAAAGAGCTCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Li thody ACAGCGCAATCCA CTTCAAGAGCCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT
 Physala ACAGCGCAATCCA CTTCAAGAGCTCCTATCGACAAGTGGGTTTACGACCTCGATGTTGG-ATCAGGGTATCCTAGT

Diedrus GGTGTAGCCGCTA CTTAAAGGTTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
 Riveroi GGTGCAGCCGCTTACGGTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
 Silvani GGTGCAGCCGCTA CTTAAAGGTTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
 Bufoniu GGTGCAGCCGCTA CTTGATGGTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
 Fuscuss GGTGCAGCCGCTA CTTAATGGTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
 Chaquen GGTGCAGCCGCTA CTTAAAGGTTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
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 Adenhya GGTGCAGCCGCTA CTTAAGGTTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
 Li thody GGTGCAGCCGCTA CTTAAAGGTTTCGTTTGTTCAAACGATTAACCCCTACGTGATCTGAGTTCAGACCCGGAGTAATCC
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Diedrus
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 Physala

