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On the Monophyly and Relationships of Several Genera of Hylini (Anura: Hylidae: Hylinae), with Comments on Recent Taxonomic Changes in Hylids

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Abstract. We present a molecular phylogenetic analysis of the hylid tribe Hylini, with the goals of testing the monophyly of the genera *Duellmanohyla, Isthmohyla,* and *Ptychohyla* and providing a discussion on the monophyly of *Bromeliohyla, Charadrahyla, Ecnomiohyla, Exerodonta, Megastomatohyla,* and *Sarcohyla.* Our results indicate the paraphyly of *Ptychohyla,* with *Bromeliohyla* and *Duellmanohyla* nested within it, and, as in previous analyses, the paraphyly of *Duellmanohyla* (due to *Ptychohyla legleri* and *P. salvadorensis* being nested within it). To resolve this situation, we restrict the contents of *Ptychohyla,* redelimit those of *Duellmanohyla* and *Bromeliohyla,* and erect two new genera, one to include the former *Ptychohyla panchoi* and *P. spinipollex,* and the other for the former *Ptychohyla acrochorda, P. sanctaecrucis, P. zoque,* and tentatively, *P. erythromma. Exerodonta* as currently defined is not monophyletic, inasmuch as *Exerodonta juanitae* is nested within *Charadrahyla.* Consequently, we transfer this species and, tentatively, *E. pinorum* to *Charadrahyla.* Also, we discuss some possible taxonomic problems within *Exerodonta.* Our results indicate that *Isthmohyla* is polyphyletic, the bromeliad-dwelling *Isthmohyla melacaena* being the sister taxon of our only exemplar of *Bromeliohyla, B. bromeliacia.* For this reason, we transfer *I. melacaena* to *Bromeliohyla,* rendering *Isthmohyla* monophyletic. The former *Isthmohyla pictipes* Group is shown to be paraphyletic due to having the non-monophyletic *I. pseudopuma* Group within it. Accordingly, we recognize a redelimited *I. pseudopuma* Group (contents: *I. infucata* and *I. pseudopuma*), an *I. zeteki* Group (contents: *I. picadoi* and *I. zeteki*), and a newly defined *I. tica* Group (contents: *I. angustilineata, I. calypsa, I. debilis, I. graceae, I. lancasteri, I. pictipes, I. tica, I. rivularis,* and, tentatively, *I. insolita* and *I. xanthosticta*). The three groups of *Isthmohyla* are supported by molecular evidence with jackknife support values > 90%, and two of them by putative morphological synapomorphies. We discuss the recognition of *Dryophytes, Hyliola, Rheohyla,* and *Sarcohyla* and whether it is useful to recognize *Anotheca, Diaglena,* and *Triprion* as three distinct, monotypic genera. Finally, we discuss a recent taxonomic proposal involving changes in rank and from ranked to unranked names in hylids that overall we consider to have been poorly justified and only superficially discussed.

Keywords. Amphibia; Phylogeny; Systematics.

INTRODUCTION

In their study of phylogenetic relationships of hylid frogs, Faivovich et al. (2005) recovered four major clades within the subfamily Hylinae Rafinesque, 1815. One of these includes most Mesoamerican and Holarctic hylids and was recognized as the tribe Hylini, which includes 187 species in 21 genera (Frost, 2018). Since the analysis of

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Faivovich et al. (2005), a number of analyses and reanalyses including all their sequences and a variable number of new sequences have corroborated both their major results and the deficiencies they identified while also exposing a number of new problems (Wiens et al., 2006; Smith et al., 2007a; Wiens et al., 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016). With the notable exception of relationships within *Hyla* Laurenti, 1768 (Stöck et al., 2008; Hua et al., 2009; Li et al., 2014) and more recently *Sarcohyla* Duellman et al., 2016 (Caviedes-Solis and Nieto-Montes de Oca, 2018), most of these problems were noted casually or went undiscussed.

Some of the most relevant known problems involving relationships of hylinine genera include the individual monophyly of *Duellmanohyla* Campbell and Smith, 1992, *Isthmohyla* Faivovich et al., 2005, *Ptychohyla* Taylor, 1944, the newly erected *Sarcohyla,* and to a lesser extent *Triprion* Cope, 1866. Several analyses (Wiens et al., 2005; Smith et al., 2007a; Duellman et al., 2016) recovered *Duellmanohyla* as being paraphyletic with respect to *P. salvadorensis* (Mertens, 1952). Furthermore, the reanalysis of Duellman et al. (2016) obtained *Ptychohyla* paraphyletic with respect to *Bromeliohyla* Faivovich et al., 2005 and *Duellmanohyla,* and *P. salvadorensis* as the sister taxon of *D. uranochroa* (Cope, 1875). The taxon sampling of these analyses included only three of the eight species of *Duellmanohyla* (*D. soralia* [Wilson and McCranie, 1985], *D. rufioculis* [Taylor, 1952], and *D. uranochroa*) and only added *P. salvadorensis* to the sampling of six described species of *Ptychohyla* originally included by Faivovich et al. (2005), out of the 14 currently recognized (Frost, 2018).

Faivovich et al. (2005) erected *Isthmohyla* to include most species of the former *Hyla pictipes* and *H. pseudopuma* Groups as defined by Duellman (2001), with the exception of *H. hazelae,* Taylor 1940a and *H. thorectes* Adler, 1965, which were transferred to the genus *Plectrohyla* Brocchi, 1877. *Isthmohyla* currently is comprised of 15 species, 14 of them included in two groups, the *I. pictipes* and the *I. pseudopuma* Groups (Faivovich et al., 2005; Frost, 2018). Faivovich et al. (2005) recognized these two groups tentatively, following Duellman (2001), because the very reduced taxon sampling available to them precluded a reasonable test of the monophyly of each group. Subsequently, McCranie and Castañeda (2006) described a new species from Honduras, *I. melacaena,* which has not been assigned to any group, although it shares some similarities with *I. zeteki* (Gaige, 1929) from the *I. pictipes* Group (McCranie and Castañeda, 2006).

Duellman et al. (2016), in a reanalysis of GenBank hylid sequences, corroborated most results of all previous phylogenetic analyses (Faivovich et al., 2005; Wiens et al., 2006: supp. data, 2010; Smith et al., 2007a; Pyron and Wiens, 2011; Pyron, 2014: suppl. data). They provided superficial discussions on some specific clades, and they proposed a number of taxonomic changes at the family and subfamily level, recognition of new subfamilies, and resurrection of generic names, or erection of new genera.

The goals of this paper are to perform a more rigorous test of the monophyly of *Duellmanohyla, Isthmohyla,* and *Ptychohyla* through a phylogenetic analysis of Hylini. Most recent advancements of our knowledge of hylinine relationships have gone undiscussed, and on the basis of our results we discuss the monophyly of *Bromeliohyla, Charadrahyla* Faivovich et al., 2005, *Ecnomiohyla* Faivovich et al., 2005, *Exerodonta* Brocchi, 1879 *Megastomatohyla* Faivovich et al., 2005, and *Sarcohyla,* including several comments on the systematics of Hylini. Furthermore, we discuss the recent proposals of Duellman et al. (2016) regarding Hylini and changes involving rank at the tribe and subfamily level and from ranked to unranked taxa.

MATERIALS AND METHODS

Taxon sampling

Our analyses included all relevant sequences of Hylini available in GenBank produced by Faivovich et al. (2005), Wiens et al. (2005, 2010), Smith et al. (2005, 2007a, 2007b), Batista et al. (2014), Caviedes-Solis and Nieto-Montes de Oca (2018) and complemented with sequences from Moriarty and Cannatella (2004), Li et al. (2014), and Köhler et al. (2016). New sequences were also produced for this project, mostly for species of *Isthmohyla,* but also *Duellmanohyla salvavida, Ptychohyla legleri* (Taylor, 1958), *P. panchoi* Duellman and Campbell, 1982, *P. sanctaecrucis* Campbell and Smith, 1992, and *Megastomatohyla pellita* (Duellman, 1968). Furthermore, sequences were produced for additional specimens of *D. rufioculis, P. euthysanota* (Kellogg, 1928), *P. hypomykter* McCranie and Wilson, 1993, *P. macrotympanum* (Tanner, 1957), and *P. spinipollex* (Schmidt, 1936), and to complement those already available for some specimens that had been included in previous analyses (Faivovich et al., 2005, 2010). Collection codes used throughout the paper are those of Sabaj (2016). See Appendix S1 for collection and locality data of vouchers for which sequences were produced for this study.

Our study of voucher specimens suggested that the specimen (MVZ 207211) identified as *Isthmohyla tica* (Starrett, 1966) in the analyses of Smith et al. (2005, 2007b) is an unnamed species that we refer to as *Isthmohyla* sp. As outgroups, we included some exemplars of all the other hyline tribes, and the subfamily Phyllomedusinae. The dataset included a total of 205 terminals, of which 13 are outgroups. The trees were rooted with *Phrynomedusa dryade* Baêta et al., 2016, an exemplar species of the earliest diverging clade of Phyllomedusinae (Faivovich et al., 2010).

Character sampling

Our analyses included the four mitochondrial genes (12–16S RNA, cytochrome *b,* and NADH ubiquinone oxidoreductase 1) and intervening tRNAs and 13 nuclear gene fragments from 12 genes (28S, beta-crystallin, c-myc gene exon 2, c-myc gene exon 3, proopiomelanocortin A, prostaglandin E2 receptor EP4 subtype, protein tyrosine phosphatase non-receptor type 12, recombination activating-1, rhodopsin exon 1, seven in absentia homolog 1, sodium/calcium exchanger 1, tensin 3, and tyrosinase) used in Faivovich et al. (2005), Smith et al. (2007a, 2007b), and Wiens et al. (2005, 2010).

DNA isolation and sequencing

Whole cellular DNA was extracted from ethanol-preserved tissues with the DNeasy (QIAGEN, Valencia, CA) isolation kit. Amplification was carried out in a 25 μL reaction using Fermentas TAQ and reagents. For all the amplifications, the PCR program included an initial denaturing step of 2 min at 94°C, followed by 35 (mitochondrial gene fragments) or 45 (nuclear gene fragments) cycles of amplification (94°C for 30 s; 48–64°C for 30 s; 72°C for 60 s), with a final extension step at 72°C for 6–10 min. Polymerase chain reaction (PCR) amplification products were cleaned using Exo I/SAP (Fermentas), and sequenced by Macrogen, Inc. (Seoul, South Korea); all samples were sequenced in both directions to check for potential errors. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher 5.2 (Gene Codes Corporation, 2014). Complete sequences were edited with BioEdit (Hall, 1999). See Appendix S2 for GenBank numbers of all sequences included in this study.

Phylogenetic analysis

The rationale for using parsimony as an optimality criterion was advanced by Farris (1983) and discussed, among others, by Goloboff (2003) and Goloboff and Pol (2005). The phylogenetic analyses included treatment of DNA sequences both as dynamic homologies and as static homology hypotheses. The consideration of optimizing sequences simultaneously with tree searches has been discussed and justified by Sankoff et al. (1973), Sankoff and Rousseau (1975), Felsenstein (1988), Wheeler (1996, 2002, 2012), De Laet (2005), Kluge and Grant (2006), Grant and Kluge (2009), and Varón and Wheeler (2012, 2013). Static alignments (multiple alignments) independent of tree searches are the most common procedure in molecular phylogenetics, regardless of the omnipresent and ignored problem of the lack of an optimality criterion to choose among competing alignments. For the reasons discussed by all those authors, we favor direct optimization, although we realize that many disagree, and so, with the objective of collegiality, we additionally performed a multiple sequence alignment (see below) and analyzed it using both parsimony and Bayesian inference.

The phylogenetic analysis using direct optimization was performed with POY v5.1.1 (Wheeler et al., 2015), using simple parsimony of equal weights for all transformations (substitutions and unit insertion/deletion events). Sequences of 12S, 16S, tRNAVal, and tRNALeu were preliminarily delimited in sections of putative homology (Wheeler et al., 2006) and equal-length sequences of protein-coding genes were assumed as aligned to accelerate the searches (available as File S3).

Searches were performed using the command "search." This command implements a driven search building Wagner trees using random addition sequences (RAS), Tree Bisection and Reconnection (TBR) branch swapping followed by Ratchet (Nixon, 1999), and Tree Fussing (Goloboff, 1999). The command stores the shortest trees of each independent run and does final tree fusing using the pooled trees as a source of topological diversity. The resulting topologies were submitted to a final round of TBR using iterative pass optimization (Wheeler, 2003).

Phylogenetic analyses using POY were executed in parallel using the Museu de Zoologia da Universidade de São Paulo's high-performance computing cluster Ace, which consists of 12 quad-socket AMD Opteron 6376 16-core 2.3-GHz CPU, 16 MB cache, 6.4 GT/s compute nodes (= 768 cores total), eight with 128 GB RAM DDR3 1,600 MHz (16 × 8 GB), two with 256 GB (16 × 16 GB), and two with 512 GB (32 × 16 GB), and QDR 4X InfiniBand (32 GB/s) networking.

We also performed a multiple alignment (preliminary assessment of site homology) of the sequences employing MAFFT version 7 (Katoh and Standley, 2013). For the regions of 12S, tRNAVal, and 16S, and the fragment including the complete upstream section of 16S, the intervening tRNALeu, NADH dehydrogenase subunit 1 (ND1), and tRNAIle we employed the alignments generated with Q-INS-i strategy (secondary structure of RNA is considered), whereas the alignments for the remaining genes were generated with G-INS-i (global homology considered). This multiple alignment was employed for the static parsimony and Bayesian analyses (available in different formats as Files S1 and S2). For the phylogenetic analysis using parsimony we employed TNT Willi Hennig Society Edition (Goloboff et al., 2008). Searches were done using the new technology search under search level 50, which included sectorial searches, tree drift and tree fusing (Goloboff, 1999), and requesting the driven search to hit the best length 500 times. Parsimony jackknife absolute frequencies (Farris et al., 1996) were estimated using new technology requesting 10 hits with driven searches under search level 15, for a total of 1,000 replicates. Alignment files were merged and exported in different formats using SequenceMatrix (Vaidya et al., 2011). Trees were edited with FigTree (Rambaut, 2014).

For the Bayesian analysis, best fitting models for each partition and combinations of partitions were selected using the corrected Akaike Information Criterion with PartitionFinder v2.1.1 (Lanfear et al., 2016), using the greedy algorithm (Lanfear et al., 2012) on PhyML (Guindon et al., 2010). First, second, and third codon positions were treated as separate partitions for each protein-coding gene. Bayesian analyses were performed in MrBayes 3.2 (Ronquist et al., 2012). Analyses consisted of four runs, each composed of two replicate Monte-Carlo Markov Chains. Each run used four chains and default settings for priors (Dirichlet for substitution rates and state frequencies, uniform for the gamma shape parameter and proportion of invariable sites, all topologies equally likely a priori, and branch lengths unconstrained: exponential). Two analyses running 60 million generations were performed (with a burn-in fraction of 0.20). Stabilization of resulting parameters was evaluated using Tracer (Rambaut et al., 2014). Uncorrected p-distances were calculated in PAUP* (Swofford, 2002).

RESULTS

The phylogenetic analysis using POY resulted in 12 trees of 36,198 steps. One of these trees is shown in Figures 1, 2, and 3 indicating the nodes that collapse in the strict consensus tree. The conflict among the optimal trees is restricted to internal relationships in *Pseudacris* (Fig. 1). The analysis using the MAFFT alignment in TNT considering gaps as fifth state resulted in 216 most parsimonious trees of 36,938 steps (see Appendix S3), a 2% increase in the number of evolutionary transformations required for the static-alignment trees over the direct optimization trees. The incongruence between these optimal trees and those from the POY analysis involves a number of clades with < 60% jackknife support that are collapsed in the strict consensus of the former. These include internal relationships of *Sarcohyla* and the relationships among the clades including (1) *Charadrahyla* Faivovich et al., 2005 (including *Exerodonta juanitae* [Snyder, 1972], see below) and *Megastomatohyla* Faivovich et al., 2005; (2) *Bromeliohyla, Duellmanohyla, Ecnomiohyla, Ptychohyla,* and *Rheohyla* Duellman et al., 2016; and (3) *Anotheca* Smith, 1939, *Diaglena* Cope, 1887, *Hyla, Isthmohyla, Smilisca* Cope, 1865, *Tlalocohyla* Faivovich et al., 2005, and *Triprion*. The results of the Bayesian analysis using the MAFFT alignment differ minimally from those of the POY analysis, involving only the position or resolution of some clades with < 60% jackknife support (see Appendix S4).

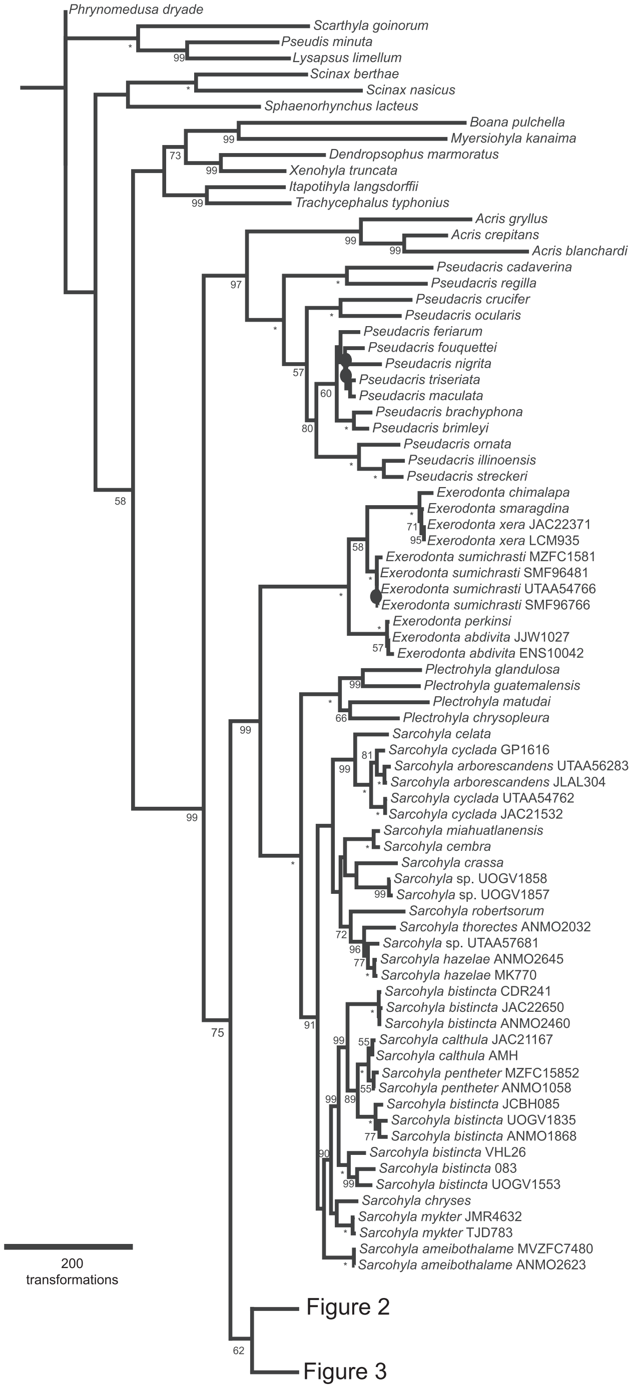

Figure 1. Phylogenetic relationships of Hylini and the ougroups as recovered in one of the 12 most parsimonious trees obtained with direct optimization (length 36,198 steps) under equal weights for all transformations. Part 1 of the tree. See Figures 2 and 3 for the other parts. Black circles indicate nodes that collapse in the strict consensus. Values around nodes are parsimony jackknife values estimated for the static alignment analyzed with parsimony in TNT with gaps as fifth state. An asterisk (*) indicates nodes with 100% jackknife support. Nodes lacking values have < 50% jackknife support.

DISCUSSION

The optimal topologies recovered for Hylini in our analyses (Figs. 1, 2, 3, Appendices S3, S4) are mostly congruent with those of Faivovich et al. (2005) and the subsequent analyses adding new sequences to their dataset (Wiens et al., 2006, 2010; Smith et al., 2007a, 2007b; Pyron and Wiens, 2011; Pyron, 2014: suppl. data; Duellman et al., 2016). The points of incongruence among the different analyses are further discussed through the remainder of this paper.

Exerodonta: polyphyly and taxonomic confusion

Faivovich et al. (2005) resurrected *Exerodonta* for a clade including the available exemplars of the former *Hyla sumichrasti* Group (*H. chimalapa* Mendelson and Campbell, 1994 and *H. xera* Mendelson and Campbell, 1994) and two exemplars of the former, polyphyletic *H. arborescandens* Group sensu Duellman (2001), the former *H. melanomma* Taylor, 1940a, and *H. perkinsi* Campbell and Brodie, 1992. On the basis of these results, Faivovich et al. (2005) also included the other species of the former *H. sumichrasti* Group that were not available (*H. sumichrasti* Brocchi, 1879 and *H. smaragdina* Taylor, 1940b) and the species associated with *H. melanomma* in the former *H. pinorum* Group by Duellman (1970), Snyder (1972), and Campbell and Duellman (2000), subsequently included in the former *H. arborescandens* Group (Duellman, 2001; the former *H. abdivita* Campbell and Duellman, 2000, *H. bivocata* Duellman and Hoyt, 1961, *H. catracha* Porras and Wilson 1987, *H. juanitae,* and *H. pinorum* Taylor, 1937). Smith et al. (2007a) corroborated the inclusion of the former *H. abdivita, H. smaragdina,* and *H. sumichrasti* in *Exerodonta.*

Our results regarding *Exerodonta* require discussion from three perspectives. These are (1) the non-monophyly of this genus as defined by Faivovich et al. (2005), as *E. juanitae* is recovered as only distantly related; (2) an evident problem with voucher identification; and (3) the poor support for the monophyly of the *E. sumichrasti* Group and possible taxonomic problems of some of its species. Our results indicate that *E. juanitae* is nested within *Charadrahyla* (Fig. 2). Considering that this species was included in *Exerodonta* on the basis of previous, tentative associations, its recovery within *Charadrahyla* does not create serious conflicts in character distributions in *Exerodonta.* To preserve the monophyly of *Exerodonta,* the former *Hyla juanitae* needs to be removed from this genus. This required move presumably applies as well to the former *H. pinorum,* for which sequences are not available, as these two species were considered to be closely related by Snyder (1972) and differ mostly in color pattern; among other character states, these two species share the absence of a tympanum. See discussion below under *Charadrahyla* and *Megastomatohyla*.

A study of the voucher specimen of the sequences of *Exerodonta melanomma* (UTA A-54766) produced by Faivovich et al. (2005) indicated that it is actually *E. sumichrasti.* The voucher specimen of the sequences of *E. melanomma* (ENS 10042) produced by Wiens et al. (2005) is currently housed at the Herpetological collection of the Instituto de Biología, Universidad Nacional de Mexico (Eric Smith, pers. comm.) and could not be examined; however, a color slide of this specimen indicates that it is actually *E. abdivita* (JAC pers. obs.). Before this report, several analyses (Wiens et al., 2006, 2010; Smith et al., 2007a; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016) included the sequences of both vouchers

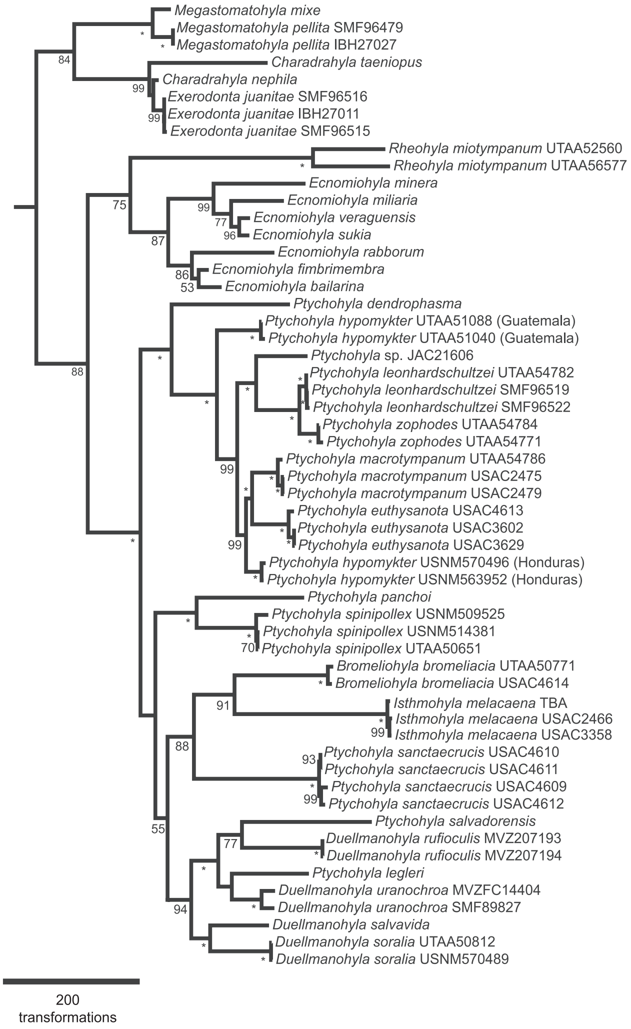

Figure 2. Phylogenetic relationships of Hylini as recovered in one of the 12 most parsimonious trees obtained with direct optimization (length 36,198 steps) under equal weights for all transformations. Part 2 of the tree. See Figs. 1 and 3 for the other parts. Values around nodes are parsimony jackknife values estimated for the static alignment analyzed with parsimony in TNT with gaps as fifth state. An asterisk (*) indicates nodes with 100% jackknife support. Nodes lacking values have < 50% jackknife support.

missidentified as *E. melanomma* as a single chimaeric terminal—despite the fact that its 12S sequences differ in 6.18%.

Within *Exerodonta* (Fig. 1) there is a basal divergence between a clade composed of *E. perkinsi* and *E. abdivita,* and its sister taxon, the poorly supported (58% jackknife support) *E. sumichrasti* Group. This group includes the nominal species and a well supported clade (100% jackknife support) with *E. chimalapa, E. smaragdina,* and *E. xera.*

The 16S fragment of our topotype of *Exerodonta chimalapa* differs in 0.52% from that of the topotype of *E. xera.* These species were differentiated on the basis of a number of characters by Mendelson and Campbell (1994), including size (although adult snout–vent length [SVL] ranges overlap; see Mendelson and Campbell, 1994: table 1), leg length, snout shape, finger size and shape, finger webbing, development of tarsal fold, presence or absence of palmar and ulnar tubercles, and some differences in color pattern. The 12S sequences available for *E. smaragdina* differ from those of *E. xera* and *E. chimalapa* in 0.34% and 0.45% respectively. The relatively low p-distances in 12S and 16S suggest that the limits and extent of morphological variation in these three species needs to be reevaluated.

The sequence divergence among our two samples of *Exerodonta abdivita,* (one of which is a topotype, JJW1027) and *E. perkinsi* from near the type locality, is very low, to the point that the monophyly of the two *E. abdivita* is poorly supported (Fig. 1). Among the comparable mitochondrial sequences, the 12S is identical among both species, and ND1 differs only in 0.19–0.56%. These species were differentiated on the basis of color pattern, and the occurrence of a rostral keel and contact of maxilla and quadratojugal in the latter (both absent in *E. abdivita;* Campbell and Duellman, 2000). This situation requires additional research.

Tadpoles of *Exerodonta* are known for *E. catracha* (McCranie et al., 1993a; but see below), *E. melanomma* (Duellman, 1970), and some species in the *E. sumichrasti* Group (*E. sumichrasti, E. smaragdina, E. xera;* Duellman, 1970; Canseco-Márquez et al., 2003). Known tadpoles of the *E. sumichrasti* Group share a depressed body, enlarged oral disc, and labial tooth row formulae (LTRF) of 3/6 or 3/7. The tadpoles in Gosner (1960) stage 25 that Duellman (1970) associated with *E. melanomma,* have a smaller oral disc (described as half as wide as maximum body width) and LTRF of 2/5. This association was based on a metamorphosing froglet found in a stream where the tadpoles occurred (Duellman, 1970). If this identification was correct, then the addition of one anterior and one or two posterior labial rows and the enlarged oral disc are putative synapomorphies of the *E. sumichrasti* Group, as are the large nasals in the adults and possibly the depressed body of the larva (this would depend on appropriate definitions of alternative character states of body shape). It is curious that the monophyly of a putative clade (the *E. sumichrasti* Group) sharing all mentioned character states is so poorly supported by molecular data as obtained in our results. Besides the need to include *E. melanomma* in a phylogenetic analysis (see below), we suggest that the identity of the larvae assigned to this species by Duellman (1970) requires corroboration, as they are remarkably similar to those of *Hyla pinorum* (Duellman, 1970), referred to *Charadrahyla* below.

Excluding the former *Exerodonta pinorum,* the species of *Exerodonta* not included in phylogenetic analyses are *E. bivocata, E. melanomma,* and *E. catracha.* As explained above, the sequences included as *E. melanomma* by Faivovich et al. (2005) and Wiens et al. (2005) do not belong to that species. We tentatively maintain the former *Hyla melanomma,* and the closely related *H. bivocata* (Duellman, 1966a, 1970; H. Smith and Brandon, 1968) in *Exerodonta* on the basis of the similarities with *E. abdivita* pointed out by Campbell and Duellman (2000), and Duellman (2001).

Porras and Wilson (1987) considered *Hyla catracha* to be closely related to *H. melanomma* on the basis of a similar SVL, dorsum and thigh color pattern, finger and toes webbing, and osteological characters; for that reason, it was subsequently included in *Exerodonta.* However, the tadpole of *E. catracha* described by McCranie et al. (1993a) differs from other larvae of *Exerodonta* in having a 2/3 labial tooth row formula, a well-defined row of submarginal papillae on the anterior and posterior labia, and bluntly rounded tip of the tail. These character states are similar to those found in several species of *Plectrohyla* and *Sarcohyla* (see Duellman, 2001). Resolving the phylogenetic position of at least *E. catracha* and *E. melanomma* is critical for the corroboration of the monophyly of *Exerodonta.*

Charadrahyla* and *Megastomatohyla

Charadrahyla and *Megastomatohyla* are sister taxa in our and in most recent analyses (Fig. 2), unlike the position obtained by Faivovich et al. (2005) where they were successive sister taxa of the clade including *Tlalocohyla, Isthmohyla, Hyla, Triprion, Anotheca,* and *Smilisca.* The sampling for both genera remains incomplete, as only two of the four species of *Megastomatohyla* (missing *M. mixomaculata* [Taylor, 1950] and *M. nubicola* [Duellman, 1964a]) and two of the seven species of *Charadrahyla* (missing *C. altipotens* [Duellman, 1968], *C. chaneque* [Duellman, 1961a], *C. esperancensis* Canseco-Márquez et al., 2017a, *C. tecuani* Campbell et al., 2009, and *C. trux* [Adler and Dennis, 1972]) are available. Remarkably our analyses recover *Exerodonta juanitae* nested in *Charadrahyla,* as the sister taxon of *C. nephila,* but with 58% jackknife support. Considering this low support and the fact that only partial 16S sequences produced by Köhler et al. (2016) are available, the addition of more DNA sequences of this species, and the missing species of *Charadrahyla,* would allow a better understanding if *E. juanitae* is actually nested in *Charadrahyla* or is its sister taxon. In the meantime, we transfer this species and the former *E. pinorum* (considered to be closely related to *E. juanitae* by Snyder, 1972) to *Charadrahyla.* These species should now be recognized as *Charadrahyla juanitae* (Snyder, 1972) **comb. nov.** and *Charadrahyla pinorum* (Taylor, 1940b) **comb. nov.** (see Figure S1 for the phylogenetic hypothesis with updated taxonomy).

Charadrahyla juanitae and *C. pinorum* share, among other characters, the absence of a tympanum (Snyder, 1972; Duellman, 2001) and much smaller SVL (combined SVL, males 27.6–35.5 mm, females 34.9–39.8 mm; Snyder, 1972; Duellman, 2001) than the other six species of *Charadrahyla* (combined SVL of all species, males 44.3–81.0 mm, females 59.6–80.7 mm; Mendelson and Campbell, 1999; Duellman, 2001; Campbell et al., 2009; Canseco-Márquez et al., 2017a). These two character states are shared with the four species of *Megastomatohyla* (combined SVL of all species, males 25.2–36.7 mm, females 31.6–37.3 mm; Duellman, 1970), the sister taxon of *Charadrahyla.* Unlike *Megastomatohyla, C. juanitae* and *C. pinorum* have a nuptial pad with dark papillary epidermal projections (PEPs) (Duellman, 1970; Snyder, 1972; Jhon Jairo Ospina-Sarria, pers. comm.).

Our analyses of molecular data support the monophyly of *Megastomatohyla,* for which there is also phenotypic evidence, such as the enlarged larval oral disc and 7–10 anterior and 10–11 posterior labial tooth rows (Duellman, 1970; Faivovich et al., 2005; Köhler et al., 2015). The absence of a tympanum in this genus (Duellman, 1970) might be a synapomorphy of a more inclusive clade, considering its absence also in *Charadrahyla juanitae* and *C. pinorum,* as discussed above. The clade *Charadrahyla* + *Megastomatohyla* is weakly supported as the sister taxon of *Ecnomiohyla* + the paraphyletic *Ptychohyla* (including *Bromeliohyla* and *Duellmanohyla*).

The paraphyly of *Ptychohyla* and *Duellmanohyla*

The monophyly of the clade including *Bromeliohyla, Duellmanohyla,* and *Ptychohyla* has 100% jackknife support. *Bromeliohyla* and *Duellmanohyla* are nested in *Ptychohyla.* Within this clade, a major clade with 100% jackknife support includes most species of *Ptychohyla* available from previous analyses (*P. dendrophasma* [Campbell et al., 2000], *P. hypomykter, P. euthysanota, P. leonhardschultzei* [Ahl, 1934], and *Ptychohyla* sp.) and *P. macrotympanum.* This clade is the sister taxon of a poorly supported clade (< 50% jackknife support) that includes the sister taxa *P. panchoi* + *P. spinipollex,* a clade including *P. sanctaecrucis,* and *Bromeliohyla bromeliacia* (Schmidt, 1933) + *Isthmohyla melacaena,* and the paraphyletic *Duellmanohyla* (including two species of *Ptychohyla* nested in it).

Duellmanohyla is not monophyletic due to the placement of *Ptychohyla legleri* and *P. salvadorensis* within it (Fig. 2). Wiens et al. (2005) found *P. salvadorensis* to be nested within *Duellmanohyla* as the sister taxon of *D. rufioculis;* they referred to the non-monophyly of *Duellmanohyla,* but provided no further comments. Subsequently, and without justification, Wiens et al. (2006: suppl. data) did not include *P. salvadorensis* in their analysis. Smith

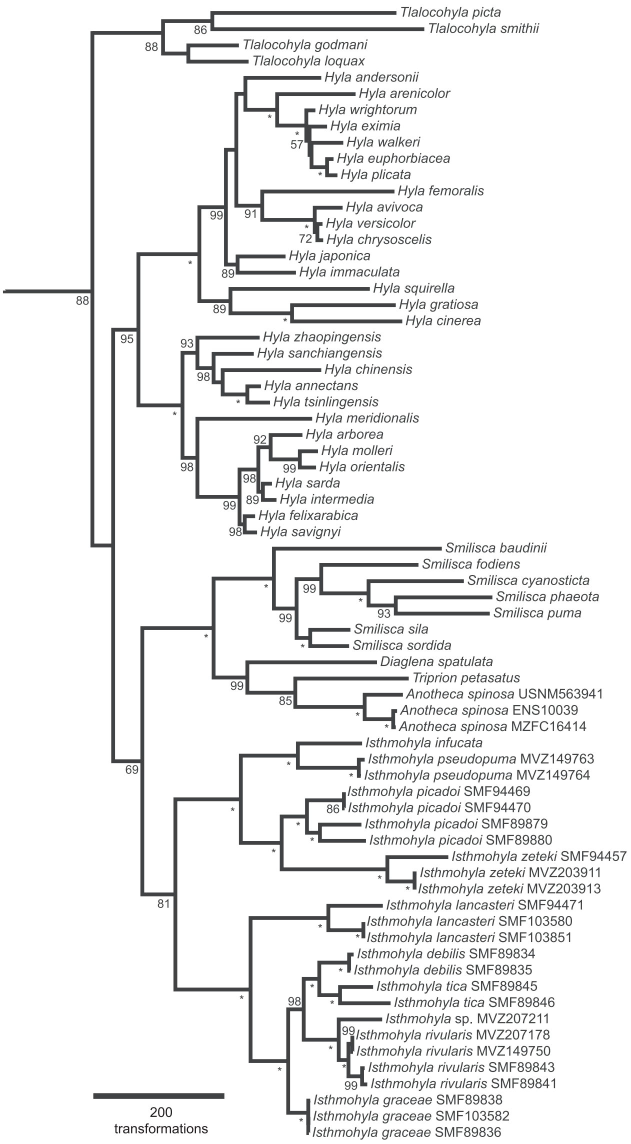

Figure 3. Phylogenetic relationships of Hylini as recovered in one of the 12 most parsimonious trees obtained with direct optimization (length 36,198 steps) under equal weights for all transformations. Part 3 of the tree. See Figs. 1 and 2 for the other parts. Values around nodes are parsimony jackknife values estimated for the static alignment analyzed with parsimony in TNT with gaps as fifth state. An asterisk (*) indicates nodes with 100% jackknife support. Nodes lacking values have < 50% jackknife support.

et al. (2007a) slightly increased the taxon sampling of Hylini with respect to Faivovich et al. (2005) and Wiens et al. (2005), adding new nuclear sequences for *P. salvadorensis*. In their results, *P. salvadorensis* is nested within *Duellmanohyla,* being the sister taxon of *D. rufioculis* + *D. uranochroa,* and the inclusive clade being the sister of *D. soralia*. The authors mentioned the paraphyly of *Duellmanohyla* with respect to *P. salvadorensis,* but without further comment. Subsequently, in a new reanalysis of hylid sequences from GenBank, Wiens et al. (2010) stated that they excluded *P. salvadorensis* because of very limited sampling of genes available, and particularly the absence of 12S data. Furthermore, they stated that *P. salvadorensis* should probably be assigned to *Duellmanohyla,* citing Smith et al. (2007a). The large reanalyses of GenBank sequences by Pyron and Wiens (2011) and Pyron (2014) excluded *P. salvadorensis*.

In the reanalysis by Duellman et al. (2016), *Ptychohyla* was found to be paraphyletic with respect to *Bromeliohyla* and *Duellmanohyla,* and *P. salvadorensis* to be the sister taxon of *D. uranochroa*. These authors emphasized differences in larval morphology and reproductive biology among the three genera and added (p. 19):

> Low nodal support values in the clade containing *Bromeliohyla, Duellmanohyla,* and *Ptychohyla salvadorensis,* indicate that the existing molecular data are unable to resolve their relationships. Although the deep nesting of *P. salvadorensis* in this clade suggests that *Ptychohyla* is paraphyletic, more molecular data are needed to corroborate this. Therefore, we retain this species in the genus *Ptychohyla*.

In the present analyses we added new partial 12S + 16S, cytochrome *b,* ND1, Rhodopsin and Rag-1 sequences of *Ptychohyla salvadorensis,* as well 12S + 16S and ND1 for *P. legleri*. We also added new partial 12S + 16S sequences of *Duellmanohyla salvavida* and *D. uranochroa*. Our results, like all previous analyses, indicate that *P. salvadorensis* is nested within *Duellmanohyla* (Fig. 2), as also is *P. legleri.* The former is recovered as the sister taxon of *D. rufioculis* with 77% jackknife support, while the latter is recovered alternatively as the sister taxon of *D. uranochroa* or *P. salvadorensis* + *D. rufioculis*.

Although *Ptychohyla legleri* had previously been considered to be related to *Duellmanohyla rufioculis* and *D. uranochroa* (the former *Hyla uranochroa* Group) on the basis of possessing a red iris (Duellman, 1966a; Starrett, 1966), Duellman (1970) placed it with the former *Hyla salvadorensis* (in the *H. salvadorensis* Group) on the basis of unspecified similarities in cranial osteology and similar oral discs and labial tooth-row formulae in larvae. Subsequent phylogenetic analyses employing, by today's standards, small datasets of phenotypic evidence and different taxon sampling (Campbell and Smith, 1992; Duellman, 2001) found no support for the close relationship of these two species, and our data do not support it either.

Duellmanohyla was erected by Campbell and Smith (1992) to contain the former *Ptychohyla schmidtorum* Group and the former *Hyla uranochroa* Group, as recognized by Duellman (1970) and expanded by Wilson and McCranie (1985) and McCranie and Wilson (1986). Campbell and Smith (1992) inferred four phenotypic synapomorphies, all from tadpole morphology, derived from a phylogenetic analysis rooted with the former *Hyla miotympanum* Cope, 1863. These synapomorphies are a greatly enlarged, subterminal or ventral pendant oral disc; long, pointed serrations on the jaw-sheath; upper jaw-sheath lacking lateral processes; and greatly shortened labial tooth-rows.[1] Duellman (2001), in an analysis constraining the monophyly of *Duellmanohyla* (for using as only outgroup the former *Hyla miotympanum*) inferred as synapomorphies the same synapomorphies as Campbell and Smith (1992) with the addition of a white labial stripe expanded below the orbit, and a bright red iris color. Note that pointed serrations of variable length in the jaw-sheaths occur as well in *Bromeliohyla* (Duellman, 1970).

Unlike the tadpoles of *Duellmanohyla,* those of *Ptychohyla legleri* and *P. salvadorensis* have been described as having a smaller ventral oral disc with 2–3 anterior and 5 posterior regular length labial tooth rows (Duellman, 1970). The position of *P. legleri* and *P. salvadorensis* nested within *Duellmanohyla* has the notable consequence that the optimization of the origin of the morphological character states associated with the umbelliform oral disc is ambiguous, being equally parsimonious for it to have originated once in the common ancestor of *Duellmanohyla* with two subsequent losses in *P. legleri* and *P. salvadorensis* or three times in *D. rufioculis, D. uranochroa,* and the common ancestor of *D. salvavida* and *D. soralia* (Fig. 4).

One possibility that should be considered is whether the larvae associated with *Ptychohyla legleri* and *P. salvadorensis* were correctly identified. Duellman (1970) reported a developmental series of tadpoles of *P. legleri,* but only two Gosner (1960) stages (25 and 38) of *P. salvadorensis*. McCranie and Wilson (2002) described tadpoles of *P. salvadorensis* in stage 37 that are congruent with the description provided by Duellman (1970).

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[1] Wilson and McCranie (1985), Duellman (2001), and McCranie and Wilson (2002) referred to these oral discs as funnel-shaped. In the anuran literature, enlarged oral discs with reduced jaw-sheaths, labial tooth rows reduced or absent, large submarginal papillae that project radially from the mouth, and marginal papillae complete but reduced in size, have been called umbelliform when they are in an upturned (McDiarmid and Altig, 1999), terminal position (Grosjean et al., 2011), or ventral position (Grant and Myers, 2013). This description applies perfectly to the described oral discs of all species included in *Duellmanohyla* by Campbell and Smith (1992), and for this reason we apply this term for their oral discs.

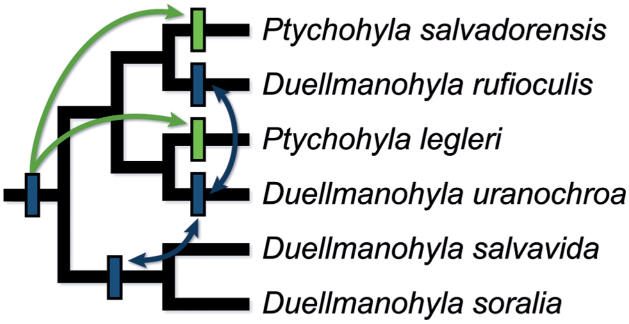

Figure 4. A condensed topology of our results (Fig. 2) involving the paraphyletic *Duellmanohyla,* showing the alternative optimizations of the set of four co-occuring character states associated with an umbelliform oral disc in larvae (greatly enlarged, subterminal or ventral pendant oral discs; long and pointed serrations on the jaw-sheath; upper jaw-sheath lacking lateral processes; and greatly shortened labial toothrows). Blue boxes depict origins of this combination of character states, and green boxes, reversions. See text for more discussion.

Although Proy (1993) did not provide a full description of the tadpoles of *P. legleri,* he did not refer to differences from Duellman's (1970) description, and his figure 2 depicts a tadpole that does not have the umbelliform oral disc that occurs in the tadpoles associated with *Duellmanohyla.* Our sequence of the 16S + ND1 fragment of *P. salvadorensis* is 100% identical to the corresponding fragment produced by Smith et al. (2007a), so there is no doubt about possible contaminations. Larvae of these two species require careful study to clarify the optimization of the umbelliform oral disc in *Duellmanohyla* and the possibility that such an uncommon character state has evolved multiple times in such a small clade of frogs. Additionally, the position of the four unavailable species of *Duellmanohyla* (see below) will likely affect this inference. Note that a bronze or copper colored iris, as occurs in *P. salvadorensis* (Duellman, 2001; McCranie and Wilson, 2002), has also been described in three species of *Duellmanohyla* (*D. chamulae* [Duellman, 1961b], *D. ignicolor* [Duellman, 1961b], *D. schmidtorum* [Stuart, 1954]; Duellman, 2001).

Our sample of *Duellmanohyla* lacks *D. lythrodes* (Savage, 1968), *D. chamulae, D. ignicolor,* and *D. schmidtorum.* Duellman (1970) considered the first species a synonym of *D. rufioculis,* but it was resurrected by Myers and Duellman (1982); the other three species were considered a monophyletic group within *Duellmanohyla* by Campbell and Smith (1992) and Duellman (2001). These authors inferred a number of synapomorphies, including the absence of nuptial excrescences, the presence of hypertrophied ventrolateral glands, vestigial webbing between fingers, and a bronze iris. Of these, the polarity of the hypertrophied ventrolateral glands would need to be reevaluated if topologies of analyses including those species are congruent with our hypothesis, as these glands also occur in several species of *Ptychohyla* and could end up being plesiomorphic for *Duellmanohyla.*

Another problem affecting the monophyly of *Ptychohyla* involves the unstable position of the clade including *P. panchoi* + *P. spinipollex.* In previous analyses, the position of *P. spinipollex* changed from being the sister taxon of the remaining species of *Ptychohyla* (Faivovich et al., 2005; Smith et al., 2007a; Wiens et al., 2010; Pyron, 2014: supp. data) to being the sister taxon of *Bromeliohyla* + *Duellmanohyla* (Pyron and Wiens, 2011; Duellman et al., 2016). In our analyses, *P. spinipollex* and *P. panchoi* are recovered as sister taxa with 100% jackknife support. This clade is supported with < 50% jackknife support as the sister taxon of the clade including (*P. sanctaecrucis* + *Bromeliohyla*) + *Duellmanohyla* as redefined here (Fig. 2).

Ptychohyla panchoi was originally thought by Duellman and Campbell (1982) to have intermediate character states between those of the then *P. euthysanota* Group (then including the two subspecies of *P. euthysanota, P. hypomykter* [under the name *P. spinipollex;* see McCranie and Wilson, 1993], and *P. leonhardschultzei*) and the former *P. schmidtorum* Group (then including *P. ignicolor* and the two subspecies of *P. schmidtorum,* now considered three distinct species of *Duellmanohyla;* Campbell and Smith, 1992). They suggested that *P. panchoi* was the sister taxon of the then *P. schmidtorum* Group on the basis of having a red iris and what they described as a multi-note call (no audiospectrogram shown). Wilson and McCranie (1989) considered *P. spinipollex* (as *Ptychohyla merazi* Wilson and McCranie, 1989, a junior synonym; McCranie and Wilson, 1993) to be most closely related to *P. panchoi* on the basis of the shared presence of a well-defined ventrolateral white line, a multi-note call, and discs larger than those of other species of *Ptychohyla.* They further added that the ventrolateral glandular structure in *P. panchoi* and *P. spinipollex* was unique in having small, isolated glands scattered on ventral and ventrolateral surfaces instead of being a continuous layer, as in the other species of the *P. euthysanota* Group.

The analysis of Campbell and Smith (1992), however, recovered *Ptychohyla panchoi* as related to most species of the *P. euthysanota* Group on the basis of the presence of enlarged spines on the nuptial pad in males, and ventrolateral glands also in males (homoplastic with the species of the former *P. schmidtorum* Group, which in the same paper are transferred to *Duellmanohyla*). Campbell and Smith (1992) further added that the glands in *P. panchoi* are continuous, and not isolated and scattered, as observed by Wilson and McCranie (1989), and they coded them in their data matrix as hypertrophied. In the analysis of *Ptychohyla* by Duellman (2001), *P. panchoi* is recovered in a position similar to that obtained by Campbell and Smith (1992). Duellman (2001) considered the ventrolateral glands in *P. panchoi* to be hypertrophied and those in *P. spinipollex* as a cluster of mucous glands.

There are still three species of *Ptychohyla* for which sequences are not available: *P. acrochorda* Campbell and

Duellman, 2000, *P. erythromma* (Taylor, 1937), and *P. zoque* Canseco-Márquez et al., 2017b. The phylogenetic analysis presented by Duellman (2001) using 13 morphological characters assumed the monophyly of *Ptychohyla,* so the transformation polarities in that study should be considered carefully relative to the more complex scenario raised in our molecular phylogenetic analyses. *Ptychohyla acrochorda* has been confused with the poorly known *P. erythromma,* with which it shares a reticulated palpebral membrane, but from which it differs by having a red iris, a more acute snout in dorsal view, smaller finger and toe discs, and slightly different hand and foot webbing formulae (Campbell and Duellman, 2000). Adult males of *P. erythromma* are unknown (Campbell and Duellman, 2000; Duellman, 2001). Duellman (2001) tentatively considered *P. erythromma* to be the sister taxon of *P. acrochorda* on the basis of external characters of the subadult female and the tadpoles, without providing further details. The only putative synapomorphy shared by *P. acrochorda* and *P. erythromma* that we can infer from the available information is the presence of a reticulated palpebral membrane.

Canseco-Márquez et al. (2017b) noticed a number of character states shared by *Ptychohyla acrochorda, P. zoque,* and *P. sanctaecrucis*. These include the green dorsal coloration (called lime green by Campbell and Duellman, 2000) with dark blotches, an increase in sexual size dimorphism with respect to other *Ptychohyla* (and also *Bromeliohyla* and *Duellmanohyla;* unknown in *P. erythromma*), and the advertisement call with similar dominant frequency (2266 and 2519 Hz in *P. acrochorda* and *P. zoque,* respectively; unknown in *P. erythromma* and *P. sanctaecrucis*), which they considered the lowest pitched calls in *Ptychohyla*. The green coloration with dark blotches could be considered a putative synapomorphy of a clade including these three species; however, a discussion would be required regarding how this coloration is defined and how it differs from the green coloration found in several species of *Duellmanohyla,* a clade that is only one node away.

The consideration of similarity of advertisement call with similar dominant frequency, however, should be taken carefully, as the dominant frequency may not say much about how similar calls actually are or how they should be interpreted. Further, although Canseco-Márquez et al. (2017b) were aware of the published results pointing to the paraphyly of *Ptychohyla* with respect to *Duellmanohyla* and *Bromeliohyla,* they restricted their comparisons to most available calls of *Ptychohyla*. Available information on advertisement calls of *P. legleri, P. salvadorensis, D. rufioculis,* and *D. uranochroa* indicate that these have a similar or lower dominant frequency (1274 Hz, 2345 Hz, 2320 Hz, and 1969 Hz respectively; Duellman, 1970).

Ptychohyla acrochorda further shares with *P. sanctaecrucis* a large abdominal, disc-shaped, presumably serous gland. This gland has been reported as absent in *P. zoque*. In our analyses (Fig. 2), *P. sanctaecrucis* is the sister taxon of *Bromeliohyla bromeliacia* and *Isthmohyla melacaena,* with 88% jackknife support. Our study of male *B. bromeliacia* and *I. melacaena* (USNM 523171 and 523178, and 562865–8, respectively) and photographs of male *B. dendroscarta* (KU 23889, 23890) show that they also have a noticeable abdominal disc-shaped glandular structure. The histology of this gland requires study.

There are three options to preserve the monophyly of *Ptychohyla:* (1) restrict the contents of *Ptychohyla,* transfer *P. legleri* and *P. salvadorensis* to *Duellmanohyla,* include *Isthmohyla melacaena* in *Bromeliohyla,* erect a new genus to accommodate *P. panchoi* + *P. spinipollex,* and erect a new genus for *P. sanctaecrucis* and tentatively associated species; (2) restrict *Ptychohyla,* transfer *P. legleri* and *P. salvadorensis* to *Duellmanohyla,* include *Isthmohyla melacaena, P. sanctaecrucis,* and tentatively associated species in *Bromeliohyla,* and erect a new genus to accommodate *P. panchoi* + *P. spinipollex;* (3) transfer all of the species of *Bromeliohyla* and *Duellmanohyla* as well as *Isthmohyla melacaena* into *Ptychohyla* which would then contain 25 species.

Each option has its limitations. Options 1 and 2 would remedy the paraphyly of *Ptychohyla* only as long as the four unanalyzed species of *Duellmanohyla* remain in that clade once they are included in phylogenetic analyses. This looks viable, considering that the tadpoles of these three species also have umbelliform oral discs (Duellman, 1970). Even though the optimization of this character state is ambiguous in the context of our topology, it is more parsimonious to expect that the missing species will be associated with one of the clades where the umbelliform disc occurs than to represent an additional independent origin.

Option 1 is further dependent on whether the hypothesized association of the three missing species *Ptychohyla acrochorda, P. erythromma,* and *P. zoque* with *P. sanctaecrucis* is corroborated when they became available. The monophyly of this putative clade is supported by the occurrence of a strong sexual dimorphism in SVL in *P. acrochorda, P. sanctaecrucis,* and *P. zoque* (see discussion above). Male and adult female *P. erythromma* are unknown, but it might be related to *P. acrochorda,* given that they share a reticulated palpebral membrane. See discussion above regarding the occurrence of green coloration in these three species.

Option 2 will provide a stable taxonomy as long as *Ptychohyla acrochorda, P. erythromma,* and *P. zoque* are more closely related to *Bromeliohyla* than to any other clade, regardless of whether these species and *P. sanctaecrucis* are monophyletic or not. While this option is more conservative than Option 1 in terms of required generic names, the evidence associating those three species with a potentially redefined *Bromeliohyla* is already mostly linked to *P. sanctaecrucis* (the sexual size dimorphism, and the evidence linking *P. erythromma* to *P. acrochorda*) and only secondarily with the clade as a whole (the sexually dimorphic abdominal gland is shared by *P. acrochorda, P. sanctaecrucis, B. bromeliacia,* and *Isthmohyla melacaena,* unknown in *P. erythromma,* and absent in *P. zoque*).

Option 3 would provide more taxonomic stability to potential topologic changes generated by the five named species that are missing from our analysis than would Options 1 and 2. This choice would be made, however, at the price of erasing all the accumulated phylogenetic knowledge for this group of frogs. We therefore favor Option 1 and formally present the new taxonomic rearrangement, including the description of the two new genera, at the end of Discussion (see Fig. S1 for the phylogenetic hypothesis with updated taxonomy).

Tlalocohyla

Tlalocohyla is nested in a clade including *Anotheca, Diaglena, Hyla, Isthmohyla, Smilisca,* and *Triprion,* as obtained by Faivovich et al. (2005), Smith et al. (2007a), Wiens et al. (2010), and Pyron and Wiens (2011). Its relationships within this clade, however, are unresolved. Whereas the monophyly of *Tl. godmani* (Günther, 1901) and *Tl. loquax* (Gaige and Stuart, 1934) is supported with 88% jackknife support, the monophyly of *Tl. picta* (Günther, 1901) and *Tl. smithii* (Boulenger, 1902) has < 50% jackknife support. The levels of sequence variation among the four species of *Tlalocohyla* are remarkable (see branch lengths in Fig. 3).

The paraphyly of *Triprion:* Maximally uninformative taxonomy

Faivovich et al. (2005) included *Triprion petasatus* (Cope, 1865) as the exemplar species of *Triprion* Cope, 1866, stating that they did not consider its monophyly controversial on the basis of three unique character states indicated by Trueb (1970) and considered synapomorphies by Duellman (2001): maxilla greatly expanded laterally, prenasal bone present (with known instances of homoplasy in *Aparasphenodon* Miranda-Ribeiro, 1920, Lophyohylini Miranda-Ribeiro, 1926), and presence of parasphenoid odontoids. Contrary to this evidence, the inclusion of sequences of *T. spatulatus* (Günther, 1882) by Smith et al. (2007a), supported its position as the sister taxon of *T. petasatus* + *Anotheca spinosa* (Steindachner, 1864), indicating the paraphyly of *Triprion*. Smith et al. (2007b) resurrected *Diaglena* to remedy this problem, pointing out the necessity to recognize the distinctiveness of *Anotheca*. Although this taxonomic decision allowed the status quo to be maintained, it also resulted in a clade of three species placed in three monotypic genera and effectively erasing all hierarchic information content in the taxonomy of this reduced clade. For this reason, we prefer to include *Anotheca* and *Diaglena* in the synonymy of *Triprion,* resulting in the combinations *Triprion spatulatus* Günther, 1882 **stat. nov.** and *Triprion spinosus* (Steindachner, 1864) **comb. nov.** (see Fig. S1 for the phylogenetic hypothesis with updated taxonomy).

Faivovich et al. (2005) produced sequences of *Triprion spinosus* from a specimen from the central highlands of Oaxaca (Ixtlán de Juárez: Santiago Comaltepec: Vista Hermosa). Smith et al. (2007b) added sequences from a specimen from Oaxaca (between Santa Maria Guienagati and Santiago Lachiguiri). The overlapping sequences of both specimens are nearly identical. In this study (Fig. 3), we also included sequences from a specimen from northeastern Honduras (Gracias a Dios: San San Hil). Although *T. spinosus* has been considered a species with a wide distribution, from southeastern Mexico to western Panama (Duellman, 1970), the 16S fragment of our specimen from Honduras differs from those of Oaxaca in 2.9%. Better understanding of the sequence variation among these samples and those from the easternmost part of the distribution of *T. spinosus* is required, but a taxonomic revision of the different populations assigned to this species seems to be necessary.

The monophyly of *Ecnomiohyla* and the erection of *Rheohyla*

Faivovich et al. (2005) erected *Ecnomiohyla* for a clade composed of the exemplars of the former *Hyla tuberculosa* Group and for the then *H. miotympanum*. This decision resulted from their results supporting the monophyly of the sole exemplar of the former *Hyla tuberculosa* Group (*H. miliaria* [Cope, 1886]; actually, they included two exemplars, but the other, the former *H. dendrophasma,* ultimately was found to be related to *Ptychohyla* and transferred to that genus by Faivovich et al., 2005) and former *H. miotympanum*. Faivovich et al. (2005) tentatively included in *Ecnomiohyla* all other species previously associated with the *H. tuberculosa* Group, warning that in the future it might be found not monophyletic. The former *H. tuberculosa* was historically associated with *H. miliaria* (Firschein and Smith, 1956; Duellman, 1960, 1961c, 1970) and for that reason was included in *Ecnomiohyla* by Faivovich et al. (2005), who expressed doubts regarding the monophyly of this genus as they defined it. More recently Ron et al. (2016) showed that species to be a member of the lophyohyline *Tepuihyla* and transferred it to that genus.

The former *Hyla miotympanum* has been considered a primitive, generalized stream-breeding tree frog on the basis of its larval morphology, including a relatively small oral disc, the presence of an anterior gap in the marginal papillae, and its 2/3 labial tooth row formula (Duellman and Campbell, 1992). For this reason, it was employed as outgroup in several phylogenetic analyses (Duellman and Campbell, 1992; Campbell and Smith, 1992; Duellman, 2001).

Subsequent to Faivovich et al. (2005), the analyses by Smith et al. (2007a), Wiens et al. (2010), and Pyron and Wiens (2011) did not recover the monophyly of *Ecnomiohyla* as delimited by Faivovich et al (2005). Instead, they obtained *E. miotympanum* as the poorly supported sister taxon of *Ptychohyla* as redefined above, and *E. miliaria* as the sister taxon of the newly added *E. minera* (Wilson et al., 1985) (which apparently was a misidentified *E. miliaria,* as their sequences are identical; see Appendix S2). Batista et al. (2014), using a reduced dataset of a fragment 16S for an analysis of several species of *Ecnomiohyla,* noticed that they still obtained *E. miotympanum* in a clade with the other available species of *Ecnomiohyla.*

Savage and Kubicki (2010) stated that 8 of the 10 species then known of *Ecnomiohyla* are characterized by having scalloped dermal fringes on the outer margin of the forearm and foot, large terminal digital discs, and enlarged prepollices in males; however, because *E. miotympanum* lacks these character states, they considered its assignment to *Ecnomiohyla* to be problematic. Duellman et al. (2016) stated that "…these authors [Faivovich et al., 2005] noted the morphological differences between the species, a factor emphasized by Mendelson et al. (2008), who eliminated *E. miotympanum* from their discussion of species of *Ecnomiohyla,*" and proceeded to erect the monotypic genus *Rheohyla* for the former *E. miotympanum.* However, Faivovich et al. (2005:69) stated that they were not aware of any morphological synapomorphy for *Ecnomiohyla,* and Mendelson et al. (2008) simply excluded the species from their diagnosis, without questioning the monophyly of *Ecnomiohyla.* Duellman et al. (2016) did not propose autapomorphies for their new genus or synapomorphies for their redelimited *Ecnomiohyla.*

Considering the exclusion of the former *Hyla tuberculosa* by Ron et al. (2016), our results (Fig. 2) corroborate the monophyly of *Ecnomiohyla* as delimited by Faivovich et al. (2005) with 75% jackknife support. The recognition of *Rheohyla* is not the result of a problem stemming from the definition provided by Faivovich et al. (2005) or phylogenetic results. This action, however, could be seen as taxonomically convenient considering that the exclusion of *R. miotympanum* from *Ecnomiohyla* renders this genus with several putative phenotypic synapomorphies (scalloped dermal fringes on the outer margin of the forearm and foot; large discs on fingers and toes; possibly an increase in SVL with respect to other related clades, known tadpoles with subterminal oral discs; when known, oviposition in tree holes). It should be noted, however, that this action supports the recognition of *Rheohyla* only on the basis of lacking the phenotypic synapomorphies of the restricted *Ecnomiohyla,* not on the basis of any autapomorphy.

Our two samples identified as *Rheohyla miotympanum* originated from Cuetzalan, Puebla (reported as JAC 22438, now UTA A-56577; sequences produced by Faivovich et al., 2005) and the Sierra de Los Tuxtlas, Veracruz (UTA A-52560; sequences produced by Wiens et al., 2005, Smith et al., 2007a, and supplemented here). Our comparison of the 16S sequences indicate a 4.08% uncorrected p-distance (note that these were not combined as a single chimaeric terminal as done by Smith et al., 2007a; Wiens et al., 2010; Pyron and Wiens, 2011; and Duellman et al., 2016), consistent with the differences in iris coloration and advertisement call between populations from the Sierra Madre Oriental and Sierra de Los Tuxtlas noticed by Duellman (1970, 2001) and suggestive of the existence of at least two different species. A taxonomic revision of the available material of *R. miotympanum* is warranted.

Subsequent to the erection of *Ecnomiohyla,* four new species of this genus have been named, *E. bailarina* Batista et al., 2014, *E. rabborum* Mendelson et al., 2008, *E. sukia* Savage and Kubicki, 2010, and *E. veraguensis* Batista et al., 2014. Savage and Kubicki (2010) divided the species of *Ecnomiohyla* into three groups on the basis of the occurrence of a humeral projection and dark, spine-shaped PEPs on the prepollex and Finger II of males. Group 1 included *E. minera, E. rabborum,* and *E. salvaje* (Wilson et al., 1985); Group 2 included *E. echinata* (Duellman, 1961b) and *E. fimbrimembra* (Taylor, 1948); and Group 3 included *E. miliaria, E. phantasmagoria* (Dunn, 1943), *E. sukia* Savage and Kubicki, 2010, and *E. valancifer* (Firschein and Smith, 1956). *Ecnomiohyla thysanota* (Duellman, 1966b) remained unassigned to any group, as it is known only from a female holotype. We understand the groups of Savage and Kubicki (2010) to be similarity groupings inasmuch as the authors provided no discussion of character polarity or evidence of monophyly and recognized that their groups conflicted with the taxonomic distribution of other characters, such as the occurrence of skin coossification with the skull and shape of the prepollex.

Batista et al. (2014) named two new species, *Ecnomiohyla bailarina* and *E. veraguensis,* and provided the first phylogenetic analysis of *Ecnomiohyla* based on a fragment of 16S. Their analysis included the two new species and exemplars of *E. fimbrimembra, E. miliaria, E. miotympanum, E. rabborum,* and *E. sukia.* Their results supported the monophyly of *Ecnomiohyla* and were congruent with the similarity groupings of Savage and Kubicki (2010). Batista et al. (2014) recognized three species groups in *Ecnomiohyla,* the *E. fimbrimembra, E. miliaria,* and *E. miotympanum* Groups, including some of the missing species on the basis of sharing some character states; *E. tuberculosa* (Boulenger, 1882) and *E. thysanota* were not assigned to species groups. In the analysis of Batista et al. (2014)

the *E. fimbrimembra* Group included the nominal species, *E. bailarina,* and *E. rabborum;* further they included *E. echinata, E. minera,* and *E. salvaje*. They characterized this group by the occurrence of a conspicuous cluster of dark, spine-shaped PEPs on Finger II and prepollex and presence or absence of a humeral projection. The *E. miliaria* Group was represented in their analysis by the nominal species, *E. sukia,* and *E. veraguensis,* and they further included *E. phantasmagoria* and *E. valancifer.* This group was characterized by males lacking humeral projections (although Mendelson et al. [2015] subsequently noted its occurrence in *E. valancifer*) and dark, spine-shaped PEPs on prepollex; if these spines are present on Finger II, they are fewer than 10, usually pale brown, and widely spaced.

Our results (Fig. 2) corroborate the monophyly of the *Ecnomiohyla miliaria* Group as defined by Batista et al. (2014). However, they also indicated the non-monophyly of the *E. fimbrimembra* Group, as *E. minera* is supported as the sister taxon of the available exemplars of the *E. miliaria* Group (*E. miliaria, E. sukia,* and *E. veraguensis*) with 99% jackknife support. Batista et al. (2014) did not discuss the polarity of the character states that they employed to characterize the *E. miliaria* and *E. fimbrimembra* Groups or to associate the species that were missing from their analysis. *Ecnomiohyla minera* has a humeral projection and a conspicuous cluster of dark, spine-shaped PEPs on Finger II and prepollex (Wilson et al., 1985). Considering the structure of the nuptial pads of *Rheohyla miotympanum* and closely related groups such as *Charadrahyla, Hyla, Isthmohyla, Ptychohyla, Smilisca, Tlalocohyla,* and *Triprion* (where all PEPs are concentrated in a cohesive nuptial pad; Duellman, 1970; Köhler, 2011), assuming a similar histological structure, the scattered spine-shaped PEPs in the *E. miliaria* Group could be considered a putative synapomorphy of the *E. miliaria* Group, while the PEPs in a cohesive nuptial pad are possibly plesiomorphic. In the context of our results the humeral spines are more parsimoniously interpreted as homoplastic in *E. minera* and *E. rabborum*. The species currently included in the *E. miliaria* Group share the presence of a projecting prepollical spine (see Savage and Kubicki, 2010: fig. 1; Batista et al., 2014: fig. 8F; Duellman, 1970: fig. 166E), a putative synapomorphy of this clade (Mendelson et al., 2008). The state that occurs in *E. minera* appears to be different (see Mendelson et al., 2015); a study of the osteology of the prepollex and associated structures in species of *Ecnomiohyla* will help identify the different character states involved.

The inclusion in a phylogenetic analysis of the remaining five species of *Ecnomiohyla* (*E. echinata, E. phantasmagoria, E. salvaje, E. thysanota,* and *E. valancifer*) will allow a much better understanding of character evolution in this group of frogs. In the meantime, considering our results, it seems appropriate to include *E. minera* in the *E. miliaria* Group and to retain *E. phantasmagoria* there as well on the basis of the occurrence of a projecting prepollical spine (Dunn, 1943). We retain the *E. fimbrimembra* Group, but only for the species that have been included in phylogenetic analyses (*E. bailarina, E. fimbrimembra,* and *E. rabborum*); *E. echinata, E. salvaje,* and *E. valancifer* should better be considered unassigned to species groups, like *E. thysanota,* until they can be included in a phylogenetic analysis or putative synapomorphies are identified to associate them with any of the recognized groups.

***Sarcohyla:* brand new genus, same old problems**

The possibility that *Plectrohyla,* as defined then, was nested in the former *Hyla bistincta* Group was raised several times (Duellman and Campbell, 1992; Toal, 1994; Wilson et al., 1994a; Toal and Mendelson, 1995; Ustach et al., 2000; Canseco-Márquez et al., 2002). On the basis of their own results, Faivovich et al. (2005) included all species of the former *H. bistincta* Group and some species of the former *H. miotympanum* and *H. pictipes* Groups in a redefined *P. bistincta* Group. All species included in *Plectrohyla* until that time were recognized as the *P. guatemalensis* Group.

Faivovich et al. (2005) specified that their test of the monophyly of the *Plectrohyla bistincta* Group was poor and recognition of the group was tentative. Overall, they stressed the low number of exemplars of each group of *Plectrohyla* available to them (5 of the 21 species of the *P. bistincta* Group as they redefined it, and 4 of the 18 species of the *P. guatemalensis* Group). Furthermore, they mentioned that the absence of species of the *P. bistincta* Group with intermediate combinations of characters (they were referring in particular to *P. calvicollina* [Toal, 1994], *P. charadricola* [Duellman, 1964b], *P. chryses* [Adler, 1965], *P. labedactyla* [Mendelson and Toal, 1996], and *P. sabrina* [Caldwell, 1974]) was a particular weak point of their test.

In subsequent years, sequences of a few genes of three additional species of the *Plectrohyla bistincta* Group became available: *P. pentheter* (Adler, 1965), *P. ameibothalame* (Canseco-Márquez et al., 2002), and *P. siopela* (Duellman, 1968) (Smith et al., 2007a; Lemmon et al., 2007a). Therefore, 7 of the 21 species of the *P. bistincta* Group were available for Duellman et al. (2016). Although their results were fully congruent with those of Faivovich et al. (2005), Duellman et al. (2016:19) stated that "Contrary to their concern, additional species […] showed a complete separation of *Plectrohyla* from the '*Hyla bistincta* Group' recognized herein as the genus *Sarcohyla*." This complete separation described by Duellman et al. (2016) involved the monophyly of the seven exemplars of the *P. bistincta* Group with 68% bootstrap support and the monophyly of the *P. guatemalensis* Group with 80% bootstrap support. The monophyly of the overall clade of *Plectrohyla* (sensu lato) has 100% bootstrap support.

Duellman et al. (2016:18) defined *Sarcohyla* as "Moderate to large frogs having thick, glandular skin and enlarged prepollex without a projecting spine [...], and the alary process of the premaxilla not bifurcate posteriorly". The reference to the size of the frogs applies equally to *Plectrohyla* (as defined by Duellman et al., 2016; see data on SVL in Duellman, 2001). The alary process of the premaxilla posteriorly bifurcate is a synapomorphy of *Plectrohyla,* so the posteriorly non-bifurcate alary process is a plesiomorphy with no evidential value for the monophyly of *Sarcohyla*. The thick glandular skin was considered and questioned as a taxonomic character in this group by Toal and Mendelson (1995) and Kaplan et al. (2016), and Duellman (2001) and Canseco-Márquez et al. (2002) mentioned thin skin in some species that Duellman et al. (2016) included in *Sarcohyla* (viz., *P. ameibothalame, P. calvicollina, P. charadricola, P. chryses, P. labedactyla,* and *P. sabrina*). On the basis of all these facts, it seems reasonable to state that at the time of the erection of *Sarcohyla* nothing had advanced in terms of our knowledge regarding the monophyly of the former *Plectrohyla bistincta* Group, with the same doubts valid in 2005 being valid then.

More recently, Caviedes-Solis and Nieto-Montes de Oca (2018) tested the monophyly of *Sarcohyla* using fragments of six genes and intervening tRNAs (12S, 16S, ND1, rhodopsin, RAG-1, POMC). Their taxon sampling included 17 of the 24 named species, plus the four species of *Plectrohyla* (sensu stricto) available in GenBank, and a number of other outgroups. Their results supported the monophyly of *Sarcohyla* with 95% bootstrap support, although internal relationships among its major clades were poorly supported.

Our analyses included sequences of exemplars of all major clades resulting from the study of Caviedes-Solis and Nieto-Montes de Oca (2018). Our results corroborate the monophyly of *Sarcohyla* with 91% jackknife support and recover the same major clades with their relationships poorly supported (< 50% jackknife support; Fig. 1). The question that remains is how well-corroborated the monophyly of *Sarcohyla* actually is considering that the seven species that are still missing include several of the species that Duellman (2001) considered to be thin skinned (*S. calvicollina, S. charadricola, S. labedactyla,* and *S. sabrina*) and hypothesized to be a basal grade to the other species of the then *P. bistincta* Group. Furthermore only four of the 19 recognized species of *Plectrohyla* have been included in phylogenetic analyses (*P. chrysopleura* Wilson et al., 1994a, *P. glandulosa* [Boulenger, 1883], *P. guatemalensis* Brocchi, 1877, and *P. matudai* Hartweg, 1941). On the basis of the doubts regarding the monophyly of the former *P. bistincta* Group, and the fact that there are no putative synapomorphies that could associate the species of *Sarcohyla* that are still missing with those whose monophyly has been corroborated, its monophyly should be considered strictly tentative.

Dryophytes **Fitzinger, 1843: Not a Herculean argumentative effort**

Hercules lost Hylas, his companion, and cried out his name, a call repeated in religious ceremonies for Hylas, which inspired Laurenti (1768) to coin *Hyla* (see Myers and Stothers, 2006). The huge, non-monophyletic *Hyla,* as defined during the 19th and 20th centuries, was redelimited by Faivovich et al. (2005) and restricted to the Holarctic *H. arborea, H. cinerea, H. eximia,* and *H. versicolor* Groups and *H. femoralis* Daudin, 1800. The limits of this redefined *Hyla* originated in the idea of generating a monophyletic taxonomy that respected as many of the generic names in use at that time as feasible. The monophyly of *Hyla* sensu Faivovich et al. (2005) was subsequently corroborated in several analyses (Wiens et al., 2006: supp. data, 2010; Smith et al., 2005, 2007a,b; Pyron and Wiens, 2011; Pyron, 2014: supp. data; Duellman et al., 2016), and its internal relationships studied in further detail by Stock et al. (2008), Hua et al. (2009), Bryson et al. (2010, 2014), and Li et al. (2014). Hua et al. (2009) redefined the *H. eximia* Group as defined by Faivovich et al. (2005), recognizing an *H. japonica* Group for a clade including three Asiatic species, *H. immaculata* Boettger, 1888, *H. japonica* Günther, 1859, and *H. suweonensis* Kuramoto, 1980. Although the recognition of this species group is equally congruent with its continuing inclusion in the *H. eximia* Group, Hua et al. (2009) based their recognition of the *H. japonica* Group solely on its geographic distribution, as taxonomically its species are very difficult to differentiate from species in the *H. eximia* Group (Hua et al., 2009). Subsequently, Li et al. (2014), on the basis of a phylogenetic analysis, further divided the *H. arborea* Group, recognizing the *H. chinensis* Group for all its eastern Asiatic species: *H. annectans* (Jerdon, 1870), *H. chinensis* Günther, 1858a, *H. sanchiangensis* Pope, 1929, *H. simplex* Boettger, 1901, *H. tsinlingensis* Liu and Hu *in* Hu et al., 1966, and *H. zhaopingensis* Tang and Zhang, 1984. Li et al. (2014) are explicit in that their only criterion is the geographic distribution and the deep molecular divergence.

Duellman et al. (2016) obtained results mostly congruent with all published analyses of *Hyla* since Faivovich et al. (2005). However, despite the monophyly of *Hyla* sensu Faivovich et al. (2005) in their results, and only stating that "These genera are separated geographically" (p. 23), Duellman et al. (2016) restricted *Hyla* to the former *H. arborea* and *H. chinensis* Groups and resurrected *Dryophytes* for its sister taxon, including the North American *H. femoralis, H. cinerea, H. eximia,* and *H. versicolor* Groups and the Asiatic *H. japonica* Group. Although we consider the resurrection of *Dryophytes* of dubious taxonomic value, it cannot be denied that in the case of *Hyla* this generic division follows—implicitly, perhaps even unknowingly as no paper is cited—the recent trend of recognizing additional species groups not strictly required by the phylogenetic evidence (i.e., not required to eliminate non-monophyly); the difference is that this time it implies a formal taxonomic group. Given the optional nature of the recognition of *Dryophytes,* and the almost casual nature of its resurrection without any substantial discussion as to its goal or taxonomic utility, we suggest its recognition provides no deeper understanding of *Hyla* (sensu lato), particularly when the historical groups of real interest below *Hyla* (sensu lato) are the species group. We do not cry out for *Hyla,* however. Ultimately, its adoption or oblivion will depend on the perception of the large community of users of Holarctic hylid taxonomy.

***Pseudacris* Fitzinger, 1843 (and *Hyliola* Mocquard, 1899)**

Duellman et al. (2016) obtained a similar or congruent topology for *Pseudacris* to those obtained in multiple recent analyses (Moriarty and Cannatella, 2004; Faivovich et al., 2005; Smith et al., 2005; Lemmon et al., 2007a, 2007b; Wiens et al., 2005, 2006: sup. data; 2010; Pyron and Wiens, 2011; Pyron, 2014: supp. data; Barrow et al., 2014). Stating that "Previous phylogenetic analyses of *Pseudacris* (e.g., Hedges, 1986; Cocroft, 1994) consistently showed *P. cadaverina* [Cope, 1866] and *P. regilla* [Baird and Girard, 1852] to be sister species and separated from other *Pseudacris*"[2] (p. 11), Duellman et al. (2016) resurrected *Hyliola* Mocquard, 1899 for the clade including *P. cadaverina, P. hypochondriaca* (Hallowell, 1854), *P. regilla,* and *P. sierra* (Jameson et al., 1966). The authors added that "The generic separation also recognizes the geographic separation of *Hyliola* and *Pseudacris*" (Duellman et al., 2016:11). All results published in the last 12 years obtained the *P. cadaverina + P. regilla* clade as the sister taxon of the remaining species of *Pseudacris.* As such, the resurrection of *Hyliola* is both congruent with our phylogenetic knowledge, and optional on the same grounds. Given the optional nature of the recognition of *Hyliola* and the lack of any substantial discussion as to its taxonomic utility, we see no reason to follow it. Its adoption will depend on the perception of the large community of users of Holarctic hylid taxonomy.

The polyphyly of *Isthmohyla*

The monophyly of *Isthmohyla* has not been tested exhaustively in the past, as only two of the fifteen species (one of each recognized species group) were included by Faivovich et al. (2005), subsequently raised to four by Wiens et al. (2005, 2006) and five by Smith et al. (2007a), including sequences only partially overlapping with those produced by Faivovich et al. (2005). The support values for the monophyly of *Isthmohyla,* particularly with the enhanced sampling of Wiens et al. (2005, 2006) and Smith et al. (2007a), have been quite variable (see also Wiens et al., 2010; Pyron and Wiens, 2011), whether due to taxon sampling density (both ingroup and outgroup), alignment method, or optimality criterion, is unknown. The results obtained here (Figs. 2, 3) recover *Isthmohyla* as polyphyletic, with *I. melacaena* found as the sister taxon of *Bromeliohyla bromeliacia* (Fig. 2) with 87% jackknife support.

The bromeliad-dwelling *Isthmohyla melacaena* was described as *Hyla melacaena* by McCranie and Castañeda (2006), who, citing a personal communication from Faivovich, noted a number of similarities with the similarly bromeliad-dwelling *I. picadoi* (Dunn, 1937) and *I. zeteki* (Gaige, 1929). These similarities include a small, depressed body and enlarged nuptial pad that, however, differs in the latter two species by being pale and lacking a cluster of dark, spine-shaped PEPs.

The genus *Bromeliohyla* was created by Faivovich et al. (2005) to accommodate the two species included in the former *Hyla bromeliacia* Group, the nominal species and *B. dendroscarta* (Taylor, 1940b). Although only sequences of *B. bromeliacia* were available to Faivovich et al. (2005) and all subsequent analyses, the monophyly of *Bromeliohyla* has been considered on the basis of some apparent synapomorphies, including oviposition in bromeliads (homoplastic with *Isthmohyla picadoi* and *I. zeteki,* as well as other hylids like the *Scinax perpusillus* Group and some members of Lophyohylini) and tadpoles having a depressed body and elongate tail. Our results suggest that *Hyla melacaena* McCranie and Castañeda, 2006, actually should be removed from *Isthmohyla* and, as discussed earlier, included in *Bromeliohyla* (see section at the end of Discussion).

The exclusion of the former *Hyla melacaena* renders *Isthmohyla* monophyletic with 81% jackknife support (Fig. 3), this test including the densest taxon sample of the genus to date. As in previous analyses (e.g., Faivovich et al., 2005; Wiens et al., 2005, 2006, 2010), *Isthmohyla* is the sister taxon, although with weak support, of a Mexican–Central American clade (*Smilisca + Triprion*).

Faivovich et al. (2005) stressed that their recognition of the *Isthmohyla pictipes* Group as defined by Duellman (2001) and redefined by them (i.e., excluding *Hyla thorectes,* currently nested within *Sarcohyla*) was tentative, because they had only one species available for genetic analysis. Faivovich et al. (2005) also stressed that there are no morphological synapomorphies known to support its monophyly. This group is composed of all

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[2] The selection of phylogenetic results exemplified by Duellman et al. (2016) is curious inasmuch as the Distance Wagner procedure on allozyme data by Hedges (1986) obtained *P. cadaverina + P. regilla* nested in *Pseudacris* (not as the earliest diverging clade), and the analysis by Cocroft (1994) using morphology did not support the monophyly of *Pseudacris*, with the position of *P. cadaverina + P. regilla* being unresolved in relation to the other *Pseudacris* and the other holarctic hylids.

Table 1. Uncorrected p-distances between the 16S fragment among specimens of several species of *Isthmohyla,* expressed as percentage.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
I. debilis SMF89834	-												
I. debilis SMF89835	0.52	-											
I. graceae SMF103582	3.64	3.46	-										
I. graceae SMF89836	3.81	3.29	0.17	-									
I. graceae SMF89838	3.64	3.46	0.00	0.17	-								
I. lancasteri SMF103580	9.60	9.78	8.56	8.74	8.56	-							
I. lancasteri SMF103851	9.60	9.78	8.56	8.74	8.56	0.00	-						
I. lancasteri SMF94471	9.27	9.45	7.87	8.04	7.87	4.37	4.37	-					
I. rivularis SMF89841	4.16	3.81	3.81	3.81	3.81	8.92	8.92	8.76	-				
I. rivularis SMF89843	4.16	3.81	3.81	3.81	3.81	8.92	8.92	8.76	0.00	-			
I. rivularis MVZ149750	4.51	3.99	3.46	3.28	3.46	8.92	8.92	9.11	1.91	1.91	-		
I. tica SMF89845	3.47	3.29	2.60	2.77	2.60	8.91	8.91	8.93	3.81	3.81	3.82	-	
I. tica SMF89846	3.47	3.30	3.12	3.30	3.12	8.57	8.57	8.06	3.30	3.30	3.82	1.91	-
I. sp. MVZ207211	5.20	5.03	3.63	3.80	3.63	9.79	9.79	9.29	3.30	3.30	3.29	3.82	4.00

members of the former *H. lancasteri, H. pictipes, H. rivularis,* and *H. zeteki* Groups as defined by Duellman (1970), with the sole addition of the former *H. calypsa* Lips, 1996 and *H. insolita* McCranie and Wilson, 1993, described subsequently and originally associated with the former *H. lancasteri* Group.

Our analyses included 9 of the 14 species of *Isthmohyla* as redefined here. Of these, five were already included in previous studies (*I. pseudopuma* [Günther, 1901] from the *I. pseudopuma* Group, and *I. lancasteri* [Barbour, 1928], *I. rivularis* [Taylor, 1952], *I. tica,* and *I. zeteki* from the *I. pictipes* Group), and four were included for the first time (*I. graceae* [Myers and Duellman, 1982] and *I. infucata* [Duellman, 1968], from the *I. pseudopuma* Group, *I. debilis* [Taylor, 1952] and *I. picadoi,* from the *I. pictipes* Group). For most species included in previous analyses, we produced sequences for more specimens for this project. The species that remain missing from the analysis are *I. angustilineata* (Taylor, 1952), *I. calypsa, I. pictipes* (Cope, 1875), *I. insolita,* and *I. xanthosticta* (Duellman, 1968) (this last species is known only from its holotype).

The results obtained here recover *Isthmohyla* composed of two major clades (each with 100% jackknife support) that result from the paraphyly of the *I. pictipes* Group, as currently defined, with the polyphyletic *I. pseudopuma* Group nested within it (Fig. 3). The *I. pseudopuma* Group (*I. pseudopuma, I. angustilineata, I. graceae,* and *I. infucata*) has been defined on the basis of cranial and larval similarities (Duellman, 1970) of uncertain polarity, and no synapomorphy has been recognized (Faivovich et al., 2005). Faivovich et al. (2005) retained the group tentatively because they had available only *I. pseudopuma* for their analysis and, therefore, the monophyly of the group could not be tested. In this study, only one species of the group is missing, *I. angustilineata.* Whereas *I. infucata* + *I. pseudopuma* is monophyletic and the sister clade of *I. picadoi* + *I. zeteki, I. graceae* is only distantly related, being nested within the clade of stream breeding species of *Isthmohyla* as the sister taxon of the common ancestor of all species with tadpoles with modifications associated with life in high gradient streams (e.g., enlarged oral disc; see below; Fig. 3).

Our analysis included two samples of *Isthmohyla lancasteri* from the same locality in Panama (SMF 103580 and 103851) and another from Costa Rica (SMF 94471). While the monophyly of the Panamanian and Costa Rican samples has a jackknife support of 100%, we note that the uncorrected p-distance in the 16S fragment among them is 4.3% (Table 1). The Panamanian specimens were collected on the Atlantic slopes of Cerro Pando, approximately 1,300 m elevation. The Costa Rican specimen was collected on the Atlantic versant at approximately 600 m elevation. Trueb (1968) and Lips (1996) discussed differences between upland and lowland populations. The Costa Rican lowland specimen has bright yellow on the posterior surfaces of the thighs, barred with black bands. Additionally, the groin and inner surfaces of the shanks and tarsi are bright yellow. In contrast, the posterior surfaces of the thigh in the Cerro Pando specimens are unpigmented with scattered black blotches, a character shared with *I. calypsa*. However, *I. lancasteri* from Cerro Pando differs from *I. calypsa* by the dorsal skin having low scattered, rounded protuberances and adult males lacking dark nuptial pads. The dorsal skin of the Costa Rican specimen is smooth. A more thorough study is needed to resolve the taxonomy of these populations.

Table 2. Uncorrected p-distances between the 16S fragment among specimens of *Isthmohyla picadoi* and *I. zeteki,* expressed as percentage.

	1	**2**	**3**	**4**	**5**	**6**
I. picadoi SMF89879	-					
I. picadoi SMF89880	4.91	-				
I. picadoi SMF94469	5.91	6.11	-			
I. picadoi SMF94470	5.85	6.23	0.00	-		
I. zeteki SMF94457	7.49	9.24	8.01	7.99	-	
I. zeteki MVZ203911	8.01	8.69	9.40	9.42	3.81	-
I. zeteki MVZ203913	8.10	8.61	9.31	9.42	3.86	0.00

The monophyly of *Isthmohyla picadoi* + *I. zeteki* (the former *H. zeteki* Group of Duellman, 1970) is well supported by molecular evidence (Fig. 3) and congruent with available phenotypic evidence (see below). Our analyses included four specimens of *I. picadoi* and three of *I. zeteki*. In both species, large uncorrected p-distances in the 16S fragment (Table 2) indicate that deeper taxonomic analyses are needed. Two specimens of *I. picadoi* from near the type locality at Volcán Barva in the Cordillera Central, Costa Rica (SMF 94469, SMF 94470) show a p-distance of 6.2–6.3% from a specimen (SMF 89880) collected in Las Nubes in the Cordillera de Talamanca of western Panama. The Las Nubes specimen, however, has a p-distance of 4.6% from a specimen (SMF 89879) of *I. picadoi* from Cerro Saguí in the Serranía de Tabasará, Panama. These three mountain chains (i.e., Cordillera Central, Cordillera de Talamanca, and Serranía de Tabasará) are separated from each other by depressions that might currently act as climatic barriers for obligate upland species such as *I. picadoi*. Hertz and Lotzkat (2012) reported that the coloration of the specimen from the Serranía de Tabasará differs from specimens from other localities. Because this is the only specimen so far collected in the Serranía de Tabasará, this will be the subject of future studies.

The 16S p-distance between two specimens of *Isthmohyla zeteki* (MVZ 203911, MVZ 203913) from the northern rim of the Cordillera de Talamanca, Costa Rica and a specimen (SMF 94457) from the Serranía de Tabasará, Panamá is 3.9% (Table 2). We are not aware of characters to distinguish these lineages morphologically.

There are different ways to remedy the paraphyly of the *Isthmohyla pictipes* Group and the polyphyly of the *I. pseudopuma* Group. These range from abandoning the groupings within *Isthmohyla* to redelimiting its species groups or even partitioning *Isthmohyla* into different genera. We believe that the first option would constitute an erasure of our knowledge on genealogical history of the group, particularly after our results have greatly increased such knowledge. The erection of new genera is only optional, as the monophyly of *Isthmohyla* is supported with 81% jackknife support, so with the explicit intention of avoiding taxonomic changes beyond necessity imposed by non-monophyly, we preserve the usage of *Isthmohyla* as defined by Faivovich et al. (2005). For this reason, a redefinition of the species groups of *Isthmohyla* seems the most reasonable approach.

The *Isthmohyla pseudopuma* Group

We restrict our definition of this group to include *Isthmohyla pseudopuma* and *I. infucata*. The monophyly of this group is supported by molecular data (100% jackknife support). A putative morphological synapomorphy of its two species is the presence of a single, subgular, bilobed vocal sac (Duellman, 1970: fig. 118; 2001:992). Whereas Duellman (1970, 2001) included *I. angustilineata* in the *I. pseudopuma* Group, we tentatively consider it to be related to *I. graceae,* the species to which it was considered most similar by Duellman (2001).

The *Isthmohyla zeteki* Group

Considering the well-supported monophyly of the two members of the former *Hyla zeteki* Group and its sister taxon relationship with the *Isthmohyla pseudopuma* Group as defined above, its recognition constitutes an appropriate first step to remedy the non-monophyly of the *I. pictipes* Group as defined by Faivovich et al. (2005). Besides being well supported by molecular evidence, *I. picadoi* and *I. zeteki* share a number of synapomorphies in adult and larval morphology and reproductive biology. These include the enlarged, light colored nuptial pad in adult males (see Köhler, 2011: figs. 507f, g), massive temporal musculature, reduction in labial tooth rows in the larvae, absence of submarginal papillae in the angular region, terminal position of the larval oral disc, reduced caudal fin, and oviposition above the water in bromeliads (Dunn, 1937; Duellman, 1970, 2001; Robinson, 1977). Further, both species share the basic characteristics of the male advertisement call (Hertz et al., 2012), although vocalization-related characters require more study. Dunn (1937) noted the occurrence of one (*I. zeteki*) or two (*I. picadoi*) odontoids in the lower jaw of these species. While the osteological correlates of these odontoids require further study, their occurrence is another putative synapomorphy of this clade; these structures were not mentioned in a review on anuran odontoids (Fabrezi and Emerson, 2003).

In the context of our analysis, the plesiomorphic labial tooth row formula for *Isthmohyla* is 2/3. The available information on larval morphology and ontogeny of *I. picadoi* + *I. zeteki* is quite restricted and although there are evident reductions in at least one anterior and two posterior labial tooth rows, at this point it is not possible to hypothesize which of the individual rows (e.g., P2 and P3?) do not occur. We do not think that this uncertainty diminishes the value of these transformations as synapomorphies.

Larval oophagy has been reported in *Isthmohyla zeteki,* which lays eggs on leaves above the water and breeds in bromeliads (Duellman, 1970, 2001), and *I. pseudopuma,* which lays eggs in water, adhered to submerged vegetation. Although it has not been observed in *I. picadoi,* a species with similar reproductive habits to *I. zeteki,* tadpole morphology (Robinson, 1977) suggests that its tadpole is oophagous as well, and we tentatively consider it as such, as also suggested by Savage (2002) and Leenders (2016). *Isthmohyla pseudopuma* is an explosive breeder at ephemeral ponds (Duellman, 1970). Crump (1983) reported tadpoles of *I. pseudopuma* at Gosner (1960) stages 35–38 consuming conspecific eggs under natural conditions in the five breeding sites she studied. Considering that larvae of *I. pseudopuma* lack all character states related to specialized oophagy, Crump (1983) concluded that *I. pseudopuma* tadpoles are only opportunistically oophagous (she used the term cannibalistic). The strictly oophagous larval diet would be a putative synapomorphy of the *I. zeteki* Group if corroborated in *I. picadoi,* as opposed to facultative oophagy.

Lannoo et al. (1987) defined a morphological type of arboreal tadpole that has a small body, labial tooth rows absent or reduced, highly reduced gill filters and gill filaments, and little or no pigment. Among the tadpoles that fit into this group are those of *Isthmohyla picadoi* and *I. zeteki.* Although the reduction or modification of the larval oral disc is associated with the diet, the report of oophagy in the typical pond larvae of *I. pseudopuma* indicates that an oophagous diet might be historically independent of the highly modified larval morphology commonly associated with oophagy and bromeliad habits. Although information on larval morphology and diet of *I. infucata* is still lacking, the fact that the *I. zeteki* Group is the sister of *I. infucata* + *I. pseudopuma* (the *I. pseudopuma* Group) might indicate that larval oophagy in *Isthmohyla* evolved earlier than bromeliad breeding and the origin of the several unique larval character states associated with oophagous habits noted by Lannoo et al. (1987). This interpretation is contingent on both the occurrence of facultative larval oophagy in *I. infucata* and its phylogenetic relationships.

The *Isthmohyla tica* Group

We propose to apply this name to the clade that includes *Isthmohyla debilis, I. graceae, I. lancasteri, I. tica,* and *I. rivularis,* and as hypothesized below, *I. angustilineata, I. calypsa, I. insolita, I. pictipes,* and *I. xanthosticta.* Although most of these species were included in the *I. pictipes* Group as redefined by Faivovich et al. (2005), here demonstrated to be paraphyletic, it differs greatly in content from the three previous usages of this informal name: the *Hyla pictipes* Group of Duellman (1970) was monotypic, the *H. pictipes* Group of Duellman (2001) included the members of the former *H. hazelae, H. lancasteri, H. pictipes, H. rivularis,* and *H. zeteki* Groups, and the *I. pictipes* Group of Faivovich et al. (2005) followed Duellman (2001) but transferred the members of the former *H. hazelae* Group to *Plectrohyla* as redefined by those authors (now in *Sarcohyla*). The use of *I. tica* (Starrett, 1966) instead of *I. lancasteri* (Barbour, 1928) is based on the fact that if *I. calypsa, I. insolita,* and *I. lancasteri* turn out to be monophyletic, restricting the name to that clade would require a new change in the name of the species group.

Although the monophyly of the *Isthmohyla tica* Group as here conceived has 100% jackknife support with molecular evidence, the position of *I. graceae* renders ambiguous the optimization of two potential phenotypic synapomorphies of the group. One of these is the presence of submarginal papillae along the anterior and posterior labia of tadpoles. Submarginal papillae are plesiomorphically absent along anterior and posterior labia, as they do not occur in the larvae of the *I. pseudopuma* and *I. zeteki* Groups, the sister taxon of *Isthmohyla, Hyla,* and *Tlalocohyla* (see Duellman, 1970, 2001; Robinson, 1977; Lips, 1996). The other would be the presence of a complete row of marginal papillae in tadpoles of most species, which is homoplastic with *I. zeteki* (Starrett, 1960; Duellman, 1970). Both transformations are ambiguous in that the larvae of *I. graceae* have an anterior gap in the marginal papillae and lack submarginal papillae along anterior and posterior labia (Myers and Duellman, 1982; Duellman, 2001). Therefore, it is equally parsimonious to hypothesize a single origin of both character states in the hypothetical ancestor of the *I. tica* Group with a subsequent reversal of both in *I. graceae,* or independent origins in *I. lancasteri* and in the hypothetical ancestor of *I. debilis, I. rivularis* and *I. tica* (and presumably *I. pictipes* and *I. xanthosticta,* see below).

Unlike the species of the now restricted *Isthmohyla pseudopuma* Group that use highland ponds for reproduction, Myers and Duellman (1982) report that *I. graceae* reproduces in low-gradient streams, which they consider to be minimally different from ponds. Myers and Duellman (1982) and Duellman (2001) stated that *I. graceae* is most similar to *I. angustilineata* on the basis of a color pattern with a pale dorsolateral stripe. Duellman (2001) also refers to similarities in adult and tadpole morphology, but without further details. On the basis of this association, we tentatively include *I. angustilineata* in the *I. tica* Group. It shares with *I. graceae* tadpoles the presence of an anterior gap in the marginal papillae and the lack of submarginal papillae along anterior and posterior labia (Duellman, 1970).

Isthmohyla lancasteri is the sister taxon of a clade, with 100% jackknife support, that includes *I. graceae, I. debilis, I. rivularis, I. tica* and an unnamed species (Fig. 3). A character state shared by *I. debilis, I. pictipes, I. rivularis,* and *I. tica* is the lack or extreme reduction of the quadratojugal (Duellman, 1970, 2001), which is present and in contact with the maxilla in *I. lancasteri, I. graceae,* the *I. pseudopuma* and *I. zeteki* Groups, *Hyla, Smilisca, Tlalocohyla,* and *Triprion* (as redefined here: Duellman and Trueb, 1966; Trueb, 1968, 1970; Duellman, 1970, 2001; Myers and Duellman, 1982). Larvae of *I. debilis, I. pictipes, I. rivularis,* and *I. tica* share the presence of an enlarged oral disc (Duellman, 2001). The last three species further share a broad band of conical submarginal papillae on the posterior labium, about three rows of submarginal papillae in the anterior labium, and an "M"-shaped anterior jaw sheath (Duellman, 2001). The absence of these character states in the tadpole of *I. debilis* described by Duellman (1970) implies their ambiguous optimization in this clade. We suggest that the identification of those tadpoles requires corroboration. The occurrence of all these character states in *I. pictipes* (Duellman, 1970), a species for which we lack tissue samples, allows us to associate it with this clade. *Isthmohyla xanthosticta* is known only from a female holotype (Duellman, 1968, 2001), but it is tentatively included in this group on the basis of its association with *I. pictipes* by Duellman (2001). The inclusion of the former *Hyla insolita* in *Isthmohyla* follows the association of this species with the former *H. lancasteri* Group by McCranie et al. (1993b), Wilson et al. (1994b), Lips (1996), and Duellman (2001). This association was based on a number of shared characters with the nominal species and *H. calypsa,* including the presence of granular dorsal skin (Duellman, 2001) and the presence of dark ventral pigmentation (Wilson et al., 1994b). *Isthmohyla calypsa* and *I. insolita* further share the occurrence of unpigmented eggs, terrestrial oviposition on vegetation overhanging water bodies, and egg attendance by the adult (Wilson et al., 1994b; Lips, 1996; Castañeda and McCranie, 2011). Wilson et al. (1994b) considered the possibility that the former *H. thorectes* (currently in *Sarcohyla*), a Mexican species having dark ventral pigmentation and terrestrial oviposition on vegetation overhanging water bodies (Duellman, 1970), might also be related to the former *H. lancasteri* Group. The results of Faivovich et al. (2005) suggested that the former *H. hazelae* Group as defined by Duellman (1970) and including the former *H. thorectes* and the nominal species, were actually members of the *P. bistincta* Group, as corroborated by Caviedes-Solis and Nieto-Montes de Oca (2018) and our results (Fig. 1). We are not aware of evidence clearly supporting a relationship of the former *H. insolita* with *Isthmohyla* over an alternative association with *P. hazelae* and *P. thorectes.* In the meantime, on the basis of the suggestions advanced by McCranie et al. (1993b), Wilson et al. (1994b), Lips (1996), and Duellman (2001), on a strictly tentative basis and pending its corroboration in a phylogenetic analysis, we retain the association with *Isthmohyla.*

Even if the inclusion of *Hyla insolita* in *Isthmohyla* were corroborated, the resurrection of a group with the contents of the former *H. lancasteri* Group would be premature. Granular skin, as described in *I. calypsa, I. insolita,* and *I. lancasteri,* is also present in *I. tica* (Duellman, 1970, 2001; McCranie et al., 1993b), which is only one node away from *I. lancasteri* in our results. The oviposition mode of *I. calypsa* and *I. insolita* is certainly unique within *Isthmohyla,* but ova are known for few species of *Isthmohyla.* In *I. calypsa, I. insolita,* and *I. rivularis,* the eggs are unpigmented (Starrett, 1966; Wilson et al., 1994b: fig. 2; Lips, 1996). Pigmented eggs occur in *I. lancasteri* (Lips, 1996), *I. pseudopuma* (Duellman, 1970: plate 8), and *I. zeteki* (Taylor, 1958), and in most taxa related to *Isthmohyla,* including *Hyla, Smilisca, Tlalocohyla,* and *Triprion* (Pope, 1931; Wright, 1931; Pyburn, 1966; Jungfer, 1996; Altig and McDiarmid, 2015). In the absence of other data, it might be equally parsimonious to postulate a sister group relation of *I. calypsa* + *I. insolita* with the other members of the *I. tica* Group on the basis of the occurrence of unpigmented eggs.

Recent taxonomic changes involving ranks in Hylidae

Duellman et al. (2016) proposed a number of taxonomic changes. These include the treatment of the family Hylidae as the unranked higher-taxon Arboranae and elevation of the hylid subfamilies Hylinae, Pelodryadinae Günther, 1858b, and Phyllomedusinae Günther, 1858b to family rank; the recognition of four new subfamilies (Acridinae Mivart, 1869, Pelobiinae Fitzinger, 1843 [subsequently replaced by Litoriinae Dubois and Fretey, 2016], Pseudinae Fitzinger, 1843, and Scinaxinae Duellman et al., 2016); the redefinition of a subfamily (Pelodryadinae); the elevation of the four tribes of Hylinae recognized by Faivovich et al. (2005) to subfamily rank (Cophomantinae, Dendropsophinae, Hylinae, and Lophyohylinae); and the resurrection of five genera (*Dryophytes, Dryopsophus* Fitzinger, 1843 [a junior synonym of *Ranoidea* Tschudi, 1838; see Dubois and Fretey, 2016], *Hyliola, Ololygon* Fitzinger, 1843, and *Pithecopus* Cope, 1866) and erection of five new genera (*Julianus, Sarcohyla, Rheohyla, Callimedusa,* and *Colomascirtus,* Duellman et al., 2016).

Two taxonomic changes made by Duellman et al. (2016), the non-recognition of Dendropsophini Fitzinger, 1843 due to non-monophyly and the resurrection of *Ranoidea* to avoid the paraphyly of *Litoria* Tschudi, 1838 (if *Nyctimystes* Stejneger, 1916 is recognized), were required to preserve the monophyly of the existing taxonomy, which by itself has been repeateadly corroborated since 2005. Although valid taxonomically, and in some cases possibly perceived as beneficial (e.g., *Rheohyla*), most changes correspond to a number of criteria that are poorly discussed by the authors and resulted in definitions without any regard for synapomorphies, whether proposed in the study or even by earlier authors (the term synapomorphy does not appear in the 110 pages of the document; the term "derived" in the sense of a derived character, appears only once).

The taxonomic changes implemented by Duellman et al. (2016) can be understood at two levels: those involving the recognition of additional genera, either resurrected or newly erected, and those involving modifications in rank or from ranked to unranked taxa. Regarding the former, we discussed earlier in this paper our majority position regarding Hylini (their Hylinae) generic changes. Taxonomic changes introduced by Duellman et al. (2016)

involving genera of the other hyline tribes and Phyllomedusinae will be dealt with in upcoming articles.[3]

The adoption of the unranked name Arboranae for Hylidae (sensu lato) is based on a parallel established by Duellman et al. (2016:8) with their own research on Brachycephaloidea:

> This name also is complementary to the higher taxon Terraranae (emended from Terrarana), which includes terrestrial breeding "land frogs." Also see the discussion in Heinicke et al. (2009) regarding the formation of higher taxa names, which are unregulated by the Code. Hedges et al. (2008) discussed why they chose an unranked taxon for landfrogs, and their reasoning applies here to the treefrogs, a similar-sized group (~ 1,000 species). The numbers of taxa in both groups are growing at a high rate, which will necessitate further taxonomic subdivision. Erection of a superfamily in both cases would constrain that growth, making an unranked taxon more appropriate.

The basis for equating the phylogenetic knowledge of hylids to that of brachycephaloids is highly questionable, as phylogenetic relationships in hylids have been quite stable since the study of Faivovich et al. (2005). Furthermore, the growth in number of species at a scale that could be minimally comparable to that of brachycephaloids has been restricted to few genera (*Boana* Gray, 1825, *Dendropsophus* Fitzinger 1843, *Litoria, Nyctimystes, Ranoidea,* and *Scinax* Wagler, 1830; see Frost, 2018) without any impact on the taxonomic structure outside those genera. This nullifies the argument of a hypothetical necessity of further taxonomic subdivisions (presumably at the suprageneric level) that might be restricted by the recognition of Hylidae in the sense of Faivovich et al. (2005).

We find that difficulty in the manageability of a very large group like Hylidae, also invoked by Duellman et al. (2016:5) as justification for their taxonomic changes, is questionable insofar as it means different things to different students of the group and end users of its taxonomy. For instance, it is unclear in which cases the lack of a supposed manageability has been a liability in the recent study of hylid diversity. From our perspective, the whole idea of desiring manageability is an atavism from a time when phylogenetic hypotheses did not exist for most or all taxonomic groups, and so relatively small, well-defined units were useful to produce short taxonomic diagnoses. The existence of densely sampled phylogenetic hypotheses, as available for hylids, coupled with phenotypic synapomorphies, known and to be discovered through current and future studies, should be useful in reducing diagnoses should that be desirable. Similarly, the hylid subfamilies Hylinae, Phyllomedusinae, and Pelodryadinae experienced no significant changes since the establishment of the current usage (Duellman, 1970, 1977); it is unclear what actual advantage to their study is brought about by modifying their rank. As such it is better to continue recognizing these clades as subfamilies.

Considering the arguments outlined above, the former tribes of Hylinae recognized by Faivovich et al. (2005), elevated to subfamily rank by Duellman et al. (2016), are better considered as tribes again. That is a relatively trivial problem; what actually requires discussion, and which was not provided by Duellman et al. (2016), is which tribes should be recognized. Duellman et al. (2016) partitioned Hylini as defined by Faivovich et al. (2005) into two subfamilies, Acridinae and Hylinae, the former including the genera *Acris, Pseudacris,* and the resurrected *Hyliola,* and the latter including all remaining genera (*Exerodonta, Plectrohyla, Ptychohyla, Bromeliohyla, Duellmanohyla, Isthmohyla, Smilisca, Tlalocohyla, Megastomatohyla, Charadrahyla, Hyla, Anotheca, Triprion, Diaglena, Ecnomiohyla,* the newly erected *Sarcohyla,* and the resurrected *Dryophytes*). The benefits derived from partitioning their Hylinae are not discussed anywhere in the text. Dubois et al. (2017) noted that Acridina Mivart, 1869 is a junior homonym of Acridina Macleay, 1821 (Orthoptera) and proposed to recognize two tribes inside this subfamily, Acridini (for *Acris*) and Hyliolini[4] (for *Hyliola* and *Pseudacris*). Given the burden of recognizing two tribes in a clade whose recognition as a subfamily we find highly questionable—and that not even Duellman et al. (2016) bothered to discuss—we prefer to simply retain the tribe Hylini as defined by Faivovich et al. (2005).

Faivovich et al. (2005) recognized the tribe Dendropsophini to include the genera *Dendropsophus* Fitzinger, 1843, *Lysapsus* Cope, 1862, *Pseudis* Wagler, 1830, *Scarthyla* Duellman and de Sá, 1988, *Scinax,*

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[3] Regarding generic changes introduced by Duellman et al. (2016) in Cophomantini Hoffman, 1878, Rojas-Runjaic et al. (2018) recentely showed that the recognition of their new genus *Colomascirtus* (erected despite the cautionary remarks on the taxonomy of *Hyloscirtus* Peters, 1882 by Rivera-Correa et al., 2016:38) for the former *Hyloscirtus armatus* and *H. larinopygion* Groups makes *Hyloscirtus* as redefined by Duellman et al. (2016) paraphyletic, leading them to consider *Colomascirtus* to be a junior synonym of *Hyloscirtus*. Faivovich and De la Riva (2006) had explicitly questioned the monophyly of the *Hyloscirtus bogotensis* Group as defined by Duellman (1972) and Faivovich et al. (2005), for which Duellman et al. (2016) restricted the genus *Hyloscirtus*. Those authors showed that the only putative phenotypic synapomorphy of this group, the mental gland, occurred as well in the *H. armatus* Group. Subsequently, evidence accumulated that the mental gland is plesiomorphic for Cophomantini (Faivovich et al., 2013; Brunetti et al., 2015).

[4] Among the diagnostic characters employed by Dubois et al. (2017) for the tribes for Acridini and Hyliolini, it is remarkable that they refer to presence or absence of the *m. intermandibularis*, respectively. Most likely they meant to refer to the apical supplementary elements of this muscle (Tyler, 1971), as the *m. intermandibularis* is invariably present in anurans.

Sphaenorhynchus Tschudi, 1838, and *Xenohyla* Izecksohn, 1998. Dendropsophini was the relatively less supported of the tribes they recognized. Subsequent analyses rejected (Wiens et al., 2006: supp. data; Pyron and Wiens, 2011) or corroborated (Wiens et al., 2010) their monophyly, always with relatively low support for both its monophyly or alternative topologies. In the reanalysis of Duellman et al. (2016) the authors obtained Dendropsophini as non-monophyletic. In their results, a clade including *Scarthyla, Lysapsus,* and *Pseudis* is the sister taxon of *Dendropsophus* + *Xenohyla,* whereas an unsupported clade (49% bootstrap with RAxML) with *Scinax* + *Sphaenorhynchus* is only distantly related. On the basis of these results, Duellman et al. (2016) restricted Dendropsophini (as Dendropsophinae) to *Dendropsophus* + *Xenohyla,* resurrected Pseudinae for *Scarthyla, Lysapsus,* and *Pseudis,* and erected Scinaxinae for *Scinax* + *Sphaenorhynchus.* Besides the possible incongruency in preferring two subfamilies (Dendropsophinae and Pseudinae) that are monophyletic with 79% bootstrap support but recognizing a single subfamily for a clade with 49% bootstrap support (Scinaxinae), there is a stability problem that cannot be overlooked: relationships among these clades have been unstable since the first recognition of Dendropsophini. If the redefinition of that tribe were required on the grounds of some desire of stability besides recognizing Pseudini and a restricted Dendropsophini (sensu Duellman et al., 2016), the logical step would be to restrict Scinaxini **stat. nov.** to *Scinax* (we follow Lourenço et al., 2016, in considering *Julianus* and *Ololygon* as synonyms of *Scinax* for the time being) and erect a new family-group name for *Sphaenorhynchus.* As such, unless future analyses bring some stability to the relationships among these four clades, the arrangement would not be affected by the topological instability within Dendropsophini (sensu Faivovich et al., 2005) seen in the last 12 years. For this reason, we recognize Sphaenorhynchini **trib. nov.,** to include the genus *Sphaenorhynchus* (see section at the end of Discussion for diagnosis and comments). As for Cophomantini and Lophyohylini, Duellman et al. (2016) introduced no change or relevant comment other than the subfamily rank; we continue recognizing them as tribes.

Taxonomic changes in Hylini

Ptychohyla Taylor, 1944

Type species. *Ptychohyla adipoventris* Taylor, 1944 (= *Hyla leonhardschultzei* Ahl, 1934) by original designation.

Sister taxon. The poorly supported clade including *Bromeliohyla, Duellmanohyla,* and the two new genera described below.

Diagnosis. *Ptychohyla* as redefined here is supported only by molecular data with 100% jackknife support. The combination of occurrence of dark spine- or cone-shaped (see Comments below) PEPs in the nuptial pads in low number (44–203, McCranie and Castañeda, 2006), hypertrophied ventrolateral glands in adult males, and larvae with 4/6 labial tooth row formulae, differentiate *Ptychohyla* from other genera of Hylini. We are not aware of any phenotypic synapomorphy supporting this genus.

Characterization. Frogs of this genus have an SVL of 28.5–39.1 mm (adult males) and 30.5–46.1 mm (adult females; Duellman, 2001); the only known specimen of *P. dendrophasma,* a female has an SVL of 84 mm (see comments below for this species). When known, males have nuptial pads with dark colored spine-shaped or cone-shaped PEPs in low numbers (44–203; McCranie and Castañeda, 2006). Males of all species have been described to have hypertrophied ventrolateral glands (Campbell and Smith, 1992; Duellman, 2001). The tarsal fold is thick and rounded. Larvae have a large oral disc surrounded by a double row of marginal papillae, and a 4/6 labial tooth row formula (Duellman, 2001). Campbell and Smith (1992) described the advertisement call of all species of this genus as redefined here as having a single note.

Content. Six species. *Ptychohyla dendrophasma* (Campbell et al., 2000); *Ptychohyla euthysanota* (Kellogg, 1928); *Ptychohyla hypomykter* McCranie and Wilson, 1993; *Ptychohyla leonhardschultzei* (Ahl, 1934); *Ptychohyla macrotympanum* (Tanner, 1957); *Ptychohyla zophodes* Campbell and Duellman, 2000.

Comments. The phenotypic synapomorphies identified for *Ptychohyla* by Campbell and Smith (1992), and expanded by Duellman (2001) do not optimize as synapomorphies of *Ptychohyla* as redefined here, but of the larger, well-supported clade including *Bromeliohyla, Duellmanohyla, Ptychohyla,* and the new genera described here. Although Campbell and Smith (1992) considered that a higher number of labial tooth rows was a synapomorphy of *Ptychohyla,* in the context of our topology—and actually those of other recent analyses as well—the presence of at least a third anterior labial tooth row (most have between 4 and 6 rows) is a putative morphological synapomorphy of a more inclusive clade (with instances of homoplasy in *Megastomatohyla, Exerodonta,* and some species of *Duellmanohyla,* with a polymorphism of 2–3 anterior tooth rows in the former *Bromeliohyla, D. legleri,* and *D. salvadorensis;* Duellman, 1970, 2001).

Hypertrophied ventrolateral glands, present in males in reproductive condition, have been among the most prominent characters in the taxonomy of *Ptychohyla.* These have been considered as either hypertrophied or as an almost continuous layer of small rounded glands, considered as probably mucoid by Campbell and Smith (1992) and described as clusters of mucous glands by Duellman (2001). However, knowledge on its structure is limited to the study of Thomas et al. (1993) that included one male of *Duellmanohyla schmidtorum,* and showed its glands to be of serous nature. These glands occur showing apparently different levels of development (Campbell and Smith, 1992) in *Ptychohyla, Bromeliohyla,* and *Duellmanohyla* as redefined here, and in the new genera described below. A thorough histological study on the structure and variation of these glands is required. Sexually dimorphic skin glands occur in males of several anuran clades. When these are studied in detail, both histologically and in terms of its taxonomic distribution, the glands show complex patterns of independent origins and reversions (e.g., Vences et al., 2007; Brunetti et al., 2015).

The dark PEPs of the nuptial pads of species of *Ptychohyla* have been described as spine-shaped ("spines" or "enlarged spines"; Campbell and Smith, 1992). As Luna et al. (in press) discuss, the spine-shaped PEPs differ from other PEPs (called "small papillae" by those authors) in histological structure and, in most cases, size. In a few cases, however, size overlaps between small, spine-shaped PEPs and the large, cone-shaped PEPs. When this occurs, the two morphologies can only be distinguished through histological study. Our study of some photographs of nuptial pads of *P. euthysanota, P. leonhardschultzei, P. macrotymanum,* and *P. zophodes* indicates the need for a histological study in these species to clarify the morphology of their PEPs.

McCranie and Wilson (1993) clarified the taxonomic confusion surrounding *Ptychohyla hypomykter* and *P. spinipollex,* showing that the latter is restricted to the Cordillera Nombre de Dios, on the Atlantic versant of north-central Honduras. Conversely, *P. hypomykter* has a more extensive distribution in mountainous regions in Guatemala, El Salvador, Honduras, and Nicaragua (Duellman, 2001; McCranie and Wilson, 2002). Our samples of *P. hypomykter,* from Guatemala (Izabal and Baja Verapáz) and Honduras (Santa Bárbara and Ocotepeque) are recovered in different, well-supported positions (Fig. 2). Whereas the Honduran specimens are the sister taxon of *P. euthysanota* + *P. macrotympanum,* the specimens from Guatemala are the sister taxon of a clade including most species of *Ptychohyla* as redefined here with the exception of *P. dendrophasma.* The taxonomy of *P. hypomykter* should be reassessed, as more than one species is included under that name, corroborating to some degree suggestions by Duellman (1970) and McCranie and Wilson (1993).

The only known specimen of *Ptychohyla dendrophasma* is an adult female (SVL 84 mm). The association of this species, originally related with other species now included in *Ecnomiohyla* (Campbell et al., 2000), with *Ptychohyla* was based exclusively on molecular data. Faivovich et al. (2005) discussed how unexpected was this result, and noticed that as previous notions of relationships in *Ptychohyla* were based on adult male morphology and larvae, the discovery of males of *P. dendrophasma* could shed light on these results. Alternatively, there is always the possibility that the association of the former *Hyla dendrophasma* with *Ptychohyla* was based on mislabeled tissues of a still undescribed species of *Ptychohyla.*

Duellmanohyla Campbell and Smith, 1992

Type species. *Hyla uranochroa* Cope, 1875, by original designation.

Sister taxon. *Bromeliohyla* + *Quilticohyla* **gen. nov.**

Diagnosis. As redefined here, *Duellmanohyla* is supported by molecular data with 90% jackknife support. These frogs can be differentiated from other hylines by having tadpoles with a ventral umbeliform oral disc and a reduced labial tooth row formula (2/2, 2/3 or 3/3) or, if the disc is not umbelliform, by the combination of an oral disc with a labial tooth row formulae of 2/5 or 3/5 and a red or bronze-reddish iris (Duellman, 1970).

Characterization. Frogs of this genus have an SVL of 25.1–37.0 mm (adult males) and 33.5–41.8 mm (adult females; Duellman, 2001; Furbush et al., 2017). Males lack a nuptial pad, or, if present, it has multiple, dark colored PEPs. Sexually dimorphic mental glands present in males of *D. chamulae* and *D. ignicolor,* and hypertrophied ventrolateral glands present in males of these two species and in *D. schmidtorum* (Duellman, 1970; Campbell and Smith, 1992). Ventrolateral glands described as "clusters of mucous glands" in *D. legleri* and *D. salvadorensis* (Duellman, 2001); apparently absent in the other species. The iris has been described as different tones of red in most species (Campbell and Smith, 1992; Savage, 2002), with the exception of *D. chamulae, D. ignicolor, D. salvadorensis,* and *D. schmidtorum,* where iris color has been described as bronze, copper, or copper-reddish-colored (Duellman, 1970; Campbell and Smith, 1992; McCranie and Wilson, 2002). A white labial blotch occurs in most species with the exception of the former *P. salvadorensis* and *P. legleri.* These two species further differ from other *Duellmanohyla* in that their tadpoles have oral discs with 2/5 or 3/5 labial tooth row formulae, instead of having large ventral umbeliform oral discs, with a reduced labial tooth row formula, and greatly shortened labial tooth-rows as in most other species. Campbell and Smith (1992) described the advertisement call in most species of this genus as a multinote call; the only exception is *D. legleri,* where it was described as having single note (Duellman, 1970).

Content. Ten species. *Duellmanohyla chamulae* (Duellman, 1961b); *Duellmanohyla ignicolor* (Duellman, 1961c); *Duellmanohyla legleri* (Taylor, 1958) **comb. nov.;**

Duellmanohyla lythrodes (Savage, 1968); *Duellmanohyla rufioculis* (Taylor, 1952); *Duellmanohyla salvadorensis* (Mertens, 1952) **comb. nov.;** *Duellmanohyla salvavida* (McCranie and Wilson, 1986); *Duellmanohyla schmidtorum* (Stuart, 1954); *Duellmanohyla soralia* (Wilson and McCranie, 1985); *Duellmanohyla uranochroa* (Cope, 1875).

Comments. Besides the synapomorphies associated with the ventral umbelliform oral disc in the larvae, that optimize ambiguously in our phylogenetic hypothesis (Fig. 4), Campbell and Smith (1992) and Duellman (2001) suggested that the long and pointed serrations on the jawsheaths were a synapomorphy of *Duellmanohyla.* These are known to occur as well in the larva of *Bromeliohyla bromeliacia* and *B. dendroscarta* (Duellman, 1970), since larvae of *B. melacaena* remain unknown, this character state could well be a synapomorphy of a more inclusive clade or optimize ambiguously. Duellman (2001) further added as synapomorphies of *Duellmanohyla* a bright red iris color and a white labial stripe expanded below the orbit. The polarity of these two transformations is actually dependent on the position of the missing species *D. chamulae, D. ignicolor,* and *D. schmidtorum,* as they lack both character states (see Duellman, 2001).

Other than in *Duellmanohyla,* an umbelliform oral disc is known to occur, in different positions (ventral, subterminal, terminal, and dorsal) and showing remarkable differences in morphology (Grosjean et al., 2011), in the genera *Leptodactylodon* Andersson, 1903 (Arthroleptidae, Astylosterninae; Amiet, 1970; Mapouyat et al., 2014), *Silverstoneia* Grant et al., 2006 (Dendrobatidae; Grant and Myers, 2013), *Phasmahyla* Cruz, 1991 (Hylidae, Phyllomedusinae; Lutz and Lutz, 1939; Cruz, 1991), in the subgenus *Chonomantis* of *Mantidactylus* Boulenger, 1895 (Mantellidae; Blommers-Schlösser, 1979; Grosjean et al., 2011), in *Megophrys* Kuhl and Van Hasselt, 1822 (Megophryidae; M. Smith, 1926; Delorme et al., 2006), and in some species of *Microhyla* Tschudi, 1838 (Microhylidae; M. Smith, 1916; Poyarkov et al., 2014). Knowledge on phylogenetic relationships and taxonomic distribution of the umbelliform oral disc in these groups is relatively good (e.g., *Leptodactylodon:* Portik and Blackburn, 2016; *Megophrys:* Mahony et al., 2017; *Mantidactylus:* Vieites et al., 2009; *Phasmahyla:* Faivovich et al., 2010; *Silverstoneia:* Grant et al., 2017), being poorly known in *Microhyla*. *Duellmanohyla* is the only case so far known where there are transformations from a plesiomorphic umbelliform to a regular oral disc.

Bromeliohyla **Faivovich et al., 2005**

Type species. *Hyla bromeliacia* Schmidt, 1933, by original designation.

Sister taxon. *Quilticohyla* **gen. nov.**

Diagnosis. This genus is supported by molecular evidence with 87% jackknife support. Putative phenotypic synapomorphies of this clade include, when known, oviposition in bromeliads, and larvae with an anterior gap in marginal papillae, a flattened body, and an elongate tail with low caudal fins (known in *Bromeliohyla bromeliacia* and *B. dendroscarta;* Duellman, 1970).

Characterization. Frogs of this genus have an SVL of 21.8–31.6 mm (adult males) and 24.2–35.7 mm (adult females). There is a large disc-shaped gland in the abdominal region in males. Nuptial pads are composed of multiple, dark colored PEPs (*Bromeliohyla bromeliacia* and *B. dendroscarta*) or forming a cluster of 7–10 spine-shaped PEPs (*B. melacaena*). Quadratojugal described by Duellman (1970) as absent (*B. bromeliacia;* Duellman 1970: fig. 220, however, illustrates its occurrence) or present (*B. dendroscarta*). Oviposition in bromeliads, where larvae complete their development. When known, eggs with animal pole pigmented (*B. bromeliacia,* Duellman, 1970). Known larvae with oral discs with an anterior gap in the marginal papillae, and a 2/5 labial tooth row formula (Duellman, 1970). Advertisement calls have only been described for *B. bromeliacia,* which shows a multinote call (Duellman, 1970).

Content. Three species. *Bromeliohyla bromeliacia* (Schmidt, 1933); *Bromeliohyla dendroscarta* (Taylor, 1940b); *Bromeliohyla melacaena* (McCranie and Castañeda, 2006) **comb. nov.**

Comments. Although there is direct evidence that *Bromeliohyla bromeliacia* and *B. dendroscarta* use bromeliads for reproduction (Schmidt, 1933; Taylor, 1940b; Stuart, 1943; Duellman, 1970) the evidence for the use of bromeliads for reproduction in *B. melacaena* is still indirect (McCranie and Castaneda, 2006). The tadpole of *B. melacaena* remains undescribed.

Quilticohyla **gen. nov.**

Type species. *Ptychohyla sanctaecrucis* Campbell and Smith, 1992.

Sister taxon. *Bromeliohyla.*

Diagnosis. This genus is supported by molecular evidence. A synapomorphy of this genus is the occurrence of a strong sexual dimorphism in size (see Comments below). Frogs of this genus are diagnosed by the combination of a green dorsal coloration with dark blotches, iris pinkish or bronze, nuptial pads present, with or without multiple dark colored PEPs, and known tadpoles with ventral oral disc not forming an umbelliform structure.

Characterization. Frogs of this genus have an SVL of 28.5–36.4 mm (adult males) and 41.2–57.8 mm (adult females). A large disc-shaped gland in the abdominal region in males–called "chest gland"–has been reported to occur in *Q. acrochorda* and *Q. sanctaecrucis* (Campbell and Duellman, 2000), and to be absent in *Q. zoque* (Canseco-Márquez et al., 2017b); males unknown in *Q. erythromma*. Ventrolateral glands, described as clusters of mucous glands by Duellman (2001), have been reported in *Q. acrochorda* and *Q. sanctaecrucis;* Canseco-Márquez et al. (2017b) made no reference to presence or absence of these glands in *Q. zoque*. When known, eggs with animal pole pigmented (*Q. sanctaecrucis,* Campbell and Smith, 1992). Known larvae have a large, ventral oral disc surrounded by a double row of marginal papillae, and 4/6 (*Q. acrochorda, Q. erythromma*) or 5/7 (*Q. sanctaecrucis*) labial-tooth row formulae (Campbell and Smith, 1992; Campbell and Duellman, 2000; Duellman, 2001). Advertisement calls of species in this genus have been described as single note calls (*Q. acrochorda;* Duellman, 1970; Campbell and Duellman, 2000) or as multinote calls (*Q. sanctaecrucis;* Campbell and Smith, 1992). The call of *Q. zoque* includes two different notes (Canseco-Márquez et al., 2017b).

Etymology. *Quiltic* meaning green in Nahuátl language + connecting *o* + *Hyla*. In reference to the green coloration of these frogs. The gender is feminine.

Content. Four species. *Quilticohyla acrochorda* (Campbell and Duellman, 2000) **comb. nov.;** *Quilticohyla erythromma* (Taylor, 1937) **comb. nov.;** *Quilticohyla sanctaecrucis* (Campbell and Smith, 1992) **comb. nov.;** *Quilticohyla zoque* (Canseco-Márquez et al., 2017b) **comb. nov.**

Comments. The association of the former *Ptychohyla erythromma,* only known from an adult female, juveniles and tadpoles, is tentative, based on the occurrence of reticulated palpebral membrane, as it occurs as well in *Q. acrochorda* (see discussion for further comments). In *Quilticohyla,* females are notably larger than males, much more so than in *Bromeliohyla, Duellmanohyla, Ptychohyla,* and the new genus described below. Sexual dimorphism per se is not a character, but rather the consequence of males and females being independent semaphoronts. For this reason, a study of the evolution of sexual size dimorphism in these genera would allow to better define if the sexual size dimorphism observed in *Quilticohyla* is the result of an increase in female SVL or a decrease in male SVL with respect to closely related clades.

Canseco-Márquez et al. (2017b) noticed that nuptial pads in *Quilticohyla zoque* are present but described them as "small nonspinous", as opposed to what they described as the "dark nuptial excrescences composed of spines" in *Q. acrochorda* and *Q. sanctaecrucis*. Our observations on pads of the latter two species indicate that they are composed of dark PEPs that are present in high numbers and are smaller than those occurring in *Atlantihyla* **gen. nov.** and *Ptychohyla*.

Available information on the ova of a number of hylinine genera is limited. Although Duellman (1963), Caldwell (1973) and Lang (1995) provided valuable data on mature oocyte and egg diameter, and/or ovarian complement size and clutch size for several species, they provided no information regarding pigmentation of the animal pole. A pigmented animal pole is known in *Bromeliohyla bromeliacia* (Duellman, 1970), *Duellmanohyla legleri* (Proy, 1993), and *Quilticohyla sanctaecrucis* (Campbell and Smith, 1992); it is unpigmented in the former *Ptychohyla panchoi* and *P. spinipollex* (Duellman and Campbell, 1982; McCranie and Wilson, 2002), *D. salvavida* (McCranie and Wilson, 2002), and *D. uranochroa* (Starrett, 1960). Among other closely related Hylini, eggs have a pigmented animal pole in *Rheohyla miotympanum* (Duellman, 1970), and an unpigmented animal pole in the few species of *Plectrohyla* where egg clutches are known (Duellman and Campbell, 1992), in *Sarcohyla thorectes,* the only species of *Sarcohyla* with illustrated egg clutches (Delia et al., 2013: fig. 1K), and in *Exerodonta sumichrasti,* the only species of *Exerodonta* where egg coloration has been described (Starrett, 1960). This sparse knowledge on taxonomic distribution is too poor to infer the plesiomorphic state of pigmentation of the animal pole in the clade including *Bromeliohyla, Duellmanohyla, Ptychohyla, Quilticohyla,* and the new genus described below. However, in the context of our topology it is more parsimonious to infer that the pigmented animal pole in *Bromeliohyla* + *Quilticohyla* is a putative synapomorphy of this clade.

***Atlantihyla* gen. nov.**

Type species. *Hyla spinipollex* Schmidt, 1936.

Sister taxon. The poorly supported clade including *Bromeliohyla, Duellmanohyla,* and *Quilticohyla*.

Diagnosis. This genus is supported by molecular evidence with 100% jackknife support. The combination of a nuptial pad with dark colored spine-shaped PEPs in relatively low numbers (35–55; McCranie and Castañeda, 2006), the presence of a well-defined ventrolateral white stripe, and a vertical rostral keel differentiate this genus from other hyline genera. The only putative phenotypic synapomorphy so far known is the presence of a well-defined ventrolateral white stripe, homoplastic with *Ptychohyla euthysanota*.

Characterization. Frogs of this genus have an SVL of 31.2–39.1 mm (males) and 37.3–46.1 mm (females). Hypertrophied ventrolateral glands in adult males occur in *Atlantihyla panchoi,* whereas they have been described as clusters of mucous glands in *A. spinipollex* (Campbell and Smith, 1992; Duellman, 2001). A vertical rostral keel is present. Eggs with animal pole unpigmented (Duellman and Campbell, 1982; McCranie and Wilson, 2002). Larvae have large oral discs surrounded by a double row of marginal papillae; labial tooth-row formula 4/7 or 6/9. Duellman and Campbell (1982) and Wilson and McCranie (1989) described the advertisement call in the two species of this genus as a multinote call.

Etymology. From *Atlantis + Hyla,* in reference to the Atlantic versants in Guatemala and Honduras, where the species of this genus occur. The gender is feminine.

Content. Two species. *Atlantihyla panchoi* (Duellman and Campbell, 1982) **comb. nov.;** *Atlantihyla spinipollex* (Schmidt, 1936) **comb. nov.**

A new tribe of Hylinae

Sphaenorhynchini new tribe

Diagnosis. As this tribe includes only the genus *Sphaenorhynchus,* the putative morphological synapomorphies that diagnose this tribe are redundant with those diagnosing that genus as reported by Faivovich et al. (2005). The character that optimize as synapomorphies are: posterior ramus of pterygoid absent; zygomatic ramus of squamosal absent or reduced to a small knob; *pars facialis* of maxilla and alary process of premaxilla reduced; postorbital process of maxilla reduced, not in contact with quadratojugal; palatine reduced to a sliver or absent; *pars externa plectri* entering tympanic ring posteriorly (rather than dorsally); *pars externa plectri* round; hyale curved medially; coracoids and clavicle elongated; prepollex ossified, bladelike (Duellman and Wiens, 1992); differentiation of the *m. intermandibularis* into a small apical supplementary element; extreme development of the *m. interhyoideus* (Tyler, 1971; Faivovich et al., 2005); nostrils with fleshy flanges in tadpoles, and anteriorly directed (Faivovich et al., 2005; Araujo-Vieira et al., 2015); and presence of a white parietal peritoneum in adults (Faivovich et al., 2005).

Characterization. Small to medium treefrogs (SVL 15.1–35.0 mm) with a greenish dorsal background, translucent skin, green bones, and white parietal peritoneum; adults generally inhabit ponds in open areas and forest edges; males vocalize while perched on floating vegetation or partially submerged in the water and, more rarely, on bushes and trees; large vocal sacs, notably distended while males are calling.

Content. One genus. *Sphaenorhynchus,* which includes 15 species (Frost 2018; Araujo-Vieira et al., in press).

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ONLINE SUPPORTING INFORMATION

The following supporting information is available for this article online:

Appendix S1. Specimen data of vouchers of sequences produced for this study.

Appendix S2. GenBank accession numbers.

Appendix S3. Strict consensus of the most parsimonious trees from the parsimony analysis of the MAFFT alignment considering gaps as a fifth state.

Appendix S4. Models and partitions employed for the Bayesian analysis and 50% Majority Rule consensus tree from the Bayesian analysis.

File S1. Dataset from the MAFFT alignment employed for static parsimony and Bayesian analyses. NONA/TNT format.

File S2. Dataset from the MAFFT alignment employed for static parsimony and Bayesian analyses. Nexus format.

File S3. Compressed folder containing all sequence files for the POY analysis.

Figure S1. Phylogenetic relationships of Hylini. Same as shown in Figures 1–3 but with updated taxonomy. Black circles indicate nodes that collapse in the strict consensus. Values around nodes are parsimony jackknife values estimated for the static alignment analyzed with parsimony in TNT with gaps as fifth state. An asterisk (*) indicates nodes with 100% jackknife support. Nodes lacking values have < 50% jackknife support.