

A molecular phylogeny of the pantropical papilionoid legume *Aeschynomene* supports reinstating the ecologically and morphologically coherent genus *Ctenodon*

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ABSTRACT

The pantropical and morphologically diverse genus *Aeschynomene* (Leguminosae, Papilionoideae) comprises ca. 180 species, but its monophyly has never been comprehensively addressed in a molecular phylogenetic context of the dalbergioid clade. Here we have assembled the most complete DNA sequence data (nuclear ribosomal ITS/5.8S and the plastid genes *trnL* intron and protein-coding *matK*), representatively sampled both in *Aeschynomene* and the closely related *Dalbergia* and *Machaerium*, as well all currently accepted genera from the dalbergioids. The Bayesian and maximum likelihood phylogenetic analyses unequivocally confirm the non-monophyly of *Aeschynomene*. The pantropically distributed *Aeschynomene* sect. *Aeschynomene*, often inhabiting riparian and wetland habitats, is paraphyletic with respect to the mostly African genera *Bryaspis*, *Cyclocarpa*, *Geissaspis*, *Humularia*, *Kotschya*, and *Smithia*, as well as the South American monotypic genus *Soemmeringia*. The strongly supported and morphologically coherent clade comprising the American species traditionally classified within *Aeschynomene* sect. *Ochopodium*, with a greater ecological predilection for neotropical fire-prone savannas and the seasonally dry tropical forests and woodlands, is here elevated to generic rank. As such, this lineage is re-established as the previously monotypic genus *Ctenodon*. A complete description of *Ctenodon* and 78 new combinations for the American species and associated infraspecific taxa are provided, as well as 24 lectotypifications.

1 | INTRODUCTION

Molecular systematics have largely enhanced our understanding of evolutionary relationships in the Leguminosae in the last decades, providing the basis for new phylogenetic realignments (e.g. Wojciechowski et al. 2004; Bruneau et al. 2008; Cardoso et al. 2012a, 2012b; Gagnon et al. 2013, 2016; Koenen et al. 2020), placing phylogenetically enigmatic genera (e.g. Cardoso et al. 2015, 2017; Queiroz et al. 2017), and reorganizing subfamily and tribal classifications (e.g. Queiroz et al. 2015; LPWG 2017; De-la-Estrella et al. 2018). While there are several monotypic or species-poor genera still lacking any molecular data for assessing their phylogenetic placement, comprehensively addressing the monophyly of morphologically-heterogenous and species-rich genera is another important step to advance the legume systematics (Cardoso et al. 2013; LPWG 2013). This is particularly the case of *Aeschynomene* L. (Papilionoideae), a pantropically distributed genus of about 180 species (Klitgaard & Lavin 2005), of which at least 80 occur predominantly in the fire-prone savannas and seasonally dry tropical forests and woodlands, but also in Oak forests, pine-oak forests as well in pine woodlands.

The American species of *Aeschynomene* were the focus of a taxonomic revision by Rudd (1955), and since many new species have been described thus far (Rudd 1975, 1989; Lewis 1985, 1992, 1993; Queiroz & Cardoso 2008; Delgado-Salinas & Sotuyo 2012; Silva & Antunes 2014; Antunes & Silva 2017, 2019; Cardoso et al. 2019). Some have added striking new morphological features that were previously unknown in the genus. For example, *Aeschynomene* was often described as having pinnately-compound leaves, but aphyllous and unifoliolate species have been discovered (Lewis 1992; Cardoso et al. 2019). In addition to the heterogeneity in terms of leaf morphology, there is a clear morphological separation in the traditional concept of *Aeschynomene* that is reflected in its infrageneric classification (Vogel 1838; Rudd 1955; Fernandes 1996). Accordingly, the species with peltate or medifixed stipules, loment fruits with articles separated by septa, and a bilabiate calyx were classified in *Aeschynomene* sect. *Aeschynomene*, whilst *Aeschynomene* sect. *Ochopodium* comprised the species with basifixed stipules, loment articles separated by an isthmus, and campanulate calyx.

Many species-rich legume genera as traditionally circumscribed have already been thoroughly investigated in molecular phylogenies, such as the mimosoids *Inga* Mill. (Nicholls et al. 2015) and *Mimosa* L. (Simon et al. 2011), the caesalpinoid *Caesalpinia* Plum. ex L. sensu lato (Gagnon et al. 2013, 2016) and *Chamaecrista* Moench (Conceição et al. 2009; Rando et al. 2016), the cercidoid *Bauhinia* Plum. ex L. s.l. (Sinou et al. 2009), and the papilionoids *Astragalus* L. (Wojciechowski et al. 1999; Wojciechowski 2005), *Dalbergia* L.f. (Vatanparast et al. 2013), *Indigofera* L. (Schrire et al. 2009), *Lupinus* L. (Drummond et al. 2012), *Swartzia* (Torke & Schaal 2008), and *Vigna* Savi s.l. (Delgado-Salinas et al. 2011). However, the systematics of *Aeschynomene* has been evaluated at most by only a handful DNA sequences (Lavin et al. 2001; Ribeiro et al. 2007; Cardoso et al. 2013, 2019; LPWG 2017). Nevertheless, all molecular phylogenetic analyses have indicated that the traditionally circumscribed *Aeschynomene* could represent an intermingled collection of distinct

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evolutionary lineages. Lavin et al. (2001) were the first to recognize the non-monophyly of *Aeschynomene* using three molecular (ITS, *matK-trnK*, and *trnL*) and a morphological data set, which supported *A. sect. Ochopodium* apart from *Aeschynomene sensu stricto*. Later, Ribeiro et al. (2007) showed the most consistent evidence that *A. sect. Ochopodium* could be more closely related to *Dalbergia* and *Machaerium* Pers. than to *A. sect. Aeschynomene*. Despite their relatively good sampling within the latter genera, *Aeschynomene* was represented by just nine species in a combined analysis of nuclear ribosomal ITS/5.8S and plastid *trnL* intron DNA sequence data. Although focused on understanding the evolution of nodulation in *Aeschynomene*, the studies of Chaintreuil et al. (2013) and Brottier et al. (2018) also provided additional evidence of the non-monophyly of *Aeschynomene*, after including an improved taxon sampling of 31 and 42 species of the genus, respectively.

Here we assemble the most comprehensive molecular dataset to address the monophyly of *Aeschynomene* s.l. in a phylogenetic analysis, not just with denser taxon sampling but also combining variation from ITS/5.8S, *trnL* intron and the protein-coding gene *matK*. We also explore whether the contrasting ecology and evolutionary history of *A. sect. Aeschynomene* and *A. sect. Ochopodium* associated to distinct biomes can be expressed in terms of differences between climatic niche variation among extant species in the different clades.

2 | MATERIALS AND METHODS

Taxon sampling and DNA sequence data—The monophyly of *Aeschynomene* s.l. was evaluated using broad taxon sampling of nuclear ribosomal ITS/5.8S and the plastid genes *trnL* intron and protein-coding *matK*. These genes have often been successfully used in phylogenetic studies at several taxonomic levels in legumes (e.g. Bruneau et al. 2008; Cardoso et al. 2012a, 2013, 2015, 2017; Queiroz et al. 2015, 2017; LPWG 2017; De-la-Estrella et al. 2018), particularly in the dalbergioids (Lavin et al. 2001; Ribeiro et al. 2007; Cardoso et al. 2012b; Fortuna-Peres et al. 2018).

We assembled a *matK* dataset for an individual analysis including all currently accepted genera of the dalbergioid legume clade (Lavin et al. 2001; Cardoso et al. 2013), but maximizing sampling as much as possible across the taxonomic diversity within *Aeschynomene* (53 spp. sampled), *Dalbergia* (36 spp. sampled), and *Machaerium* (51 spp. sampled). The early branching amorphoid genera were used as outgroups, so that the total sampling of the individual *matK* dataset included 198 species. We also built an individual ITS/5.8S dataset and a concatenated dataset (ITS/5.8S, *matK*, and *trnL* intron) focusing on just the *Dalbergia* clade, and using the two genera of the *Pterocarpus* clade as outgroups. A total of 54 species of *Aeschynomene*, 17 of *Dalbergia*, and 15 of *Machaerium* were sampled for the ITS/5.8S dataset, while the concatenated dataset included 67 species of *Aeschynomene*, 41 of *Dalbergia*, and 54 of *Machaerium*. These non-overlapping numbers in taxon coverage for the concatenated dataset reflects the fact that we wanted to maximize taxon sampling even if some terminals had incomplete data. Combined phylogenetic analyses of empirical data and computational simulations have largely demonstrated that missing data do not negatively affect the

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results (Wiens 2003). Rather, analyses including taxa with less than 50% of data can even help breaking up long branches and improving phylogenetic accuracy (Wiens 2005; Wiens & Tiu 2012).

Most sequences used here were already published in our previous molecular systematic studies (Lavin et al. 2001; Cardoso et al. 2012b, 2019; LPWG 2017), but our sampling was also largely increased by recent evolutionary-focused studies in *Aeschynomene* nodulation (Chaintreuil et al. 2013; Brottier et al. 2018), all of which are taxonomically curated, vouchered, and have sequences available in GenBank (www.ncbi.nlm.nih.gov). GenBank accession numbers follow the terminal taxon labels in the presented phylogenetic trees. For the 15 newly generated sequences of ITS/5.8S, DNA isolation, polymerase chain reaction (PCR), amplifications, and sequencing were performed as described in our previous study (e.g. Lavin et al. 2001). All these new DNA sequences and associated voucher information are deposited in GenBank, and they are readily identified in the ITS phylogenetic tree by the accessions beginning with “MT”.

All DNA datasets were aligned manually with AliView version 1.17.1 (Larsson 2014). Accurate homologies among the nucleotide sites of the protein-coding *matK* gene were assessed by inserting gaps corresponding to complete codons in amino acid translated sequences (Wojciechowski et al. 2004). The individual DNA alignments were combined using a newly developed R package (D.Cardoso, unpubl. data) with functions that automatically build the concatenated dataset with missing data (sensu Wiens 2003).

Estimation of phylogenetic relationships—We used maximum likelihood and Bayesian inference as the phylogenetic reconstruction approaches to estimate evolutionary relationships based on the individual ITS/5.8S and *matK* datasets of and the concatenated dataset of ITS/5.8S, *matK*, and *trnL* intron sequences. The maximum likelihood tree was inferred with RAxML v8.2.812 (Stamatakis 2014), using the evolutionary model GTRGAMMA, where the invariant sites and gamma distribution were estimated during the run. Branch supports (BS) (Felsenstein 1985) were estimated by letting RAxML halt bootstrapping automatically (Stamatakis et al. 2008). The Bayesian analyses were run in MrBayes version 3.2.6 (Ronquist et al. 2012), using a best-fit nucleotide substitution model (GTR + I + G) selected via the Akaike information criterion (AIC) in jmodeltest2 (Darriba et al. 2012). In two separate runs of a Metropolis-coupled Markov Chain Monte Carlo (MCMC) permutation of parameters, eight simultaneous chains run for 15 million generations, sampling one tree at each 10,000th generation. A Bayesian majority-rule consensus tree at 50% was produced after a burn-in of 25%, where the group frequencies represent posterior probabilities (PP) (Huelsenbeck et al. 2002). We used FigTree version 1.4.0 for visualization of the Bayesian tree (Rambaut 2012) and Adobe Illustrator for final editing. All phylogenetic analyses were run in the CIPRES Science Gateway v. 3.3 on-line portal (www.phylo.org) (Miller et al. 2010).

Climate data—Because of conspicuous visual habitat differences between *Aeschynomene* sect. *Ochopodium*, centered in the savanna and seasonally dry tropical forests and woodlands (Rudd 1955; Queiroz & Cardoso 2008; Silva & Antunes 2014; Cardoso et al. 2019), and *Aeschynomene* sect. *Aeschynomene*, most abundant and diverse in low elevation riparian and wetland settings (Rudd 1955; Antunes & Silva 2017, 2019), we analyzed climate data associated with collection information

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accessed from Global Biodiversity Information Facility (GBIF, www.gbif.org). We used the R package 'rgbif' (Chamberlain et al. 2020) to retrieve the ~36,000 herbarium records for all American species of *A. sect. Ochopodium* and all species of *A. sect. Aeschynomene* and the phylogenetically related mostly African genera sampled in our combined molecular phylogeny. Data cleaning involved first standardizing the collector name (tagged in GBIF as "recordedBy") and associated number ("recordNumber"). We used a newly developed package of R functions (D.Cardoso, unpubl. data) which automatically clean the "recordedBy" column in the database by keeping just a uniformly formatted name of the principal collector. By doing so, we could exclude the duplicate specimens among the different herbaria more confidently. We then excluded records without any geographical coordinates or collector names, as well as any georeferenced records collected before 1930, so as to exclude the mostly erroneously georeferenced records of old, historical collections. Then we excluded duplicates by identifying those records with the same principal collector and associated number. After that we used the R package 'CoordinateCleaner' for further cleaning the database with respect to coordinates at sea, as country and province centroids, country capitals, urban areas, as well as around biodiversity institutions, which often comes from cultivated individuals (Zizka et al. 2019).

Because we also excluded all rampant, widespread species (e.g. *A. americana*, *A. rudis*, *A. hystrix*, etc.) with an estimated range size greater than 800,000 Km², as calculated with the R package 'letsR' (Vilela & Villalobos 2015), our database for the analysis of climatic niche variation ended up with just ~3,500 records from among 48 species of *A. sect. Aeschynomene* and related genera, and 51 American species of *A. sect. Ochopodium*. The reasoning here is that the signature of a constraining ecology would be left only on those relatively confined, small-range-sized species, since the more widespread, mostly weedy herbs usually break ecological constraints and have a too large climatic niche breadth, erasing any signature of a putatively phylogenetically inherited ecology. Using the R package 'raster' (Hijmans et al. 2020), we extracted WorldClim data (Fick & Hijmans 2017) and 250 m spatial resolution elevation data (<http://srtm.csi.cgiar.org/srtmdata/>) from the final set of geolocated *Aeschynomene* collections as well as for the mostly African related genera. Climate variables with greatest variance, identified using a standard biplot of the principal components analysis (PCA), were then analyzed for any significant differences between the *Aeschynomene* sections and related genera.

Taxonomic treatment—This work is based on standard revisionary studies, including a comprehensive literature review and analysis of specimens deposited in herbaria (acronyms according to Thiers 2020 [continuously updated]). The taxonomy adopted here at species and infraspecific level follows mostly Rudd's (1955, 1959, 1967, 1972, 1975, 1989) revisionary studies on *Aeschynomene* s.l., but with subsequent updates (Lewis 1985, 1992, 1993; Fernandes 1996; Queiroz & Cardoso 2008; Queiroz 2009; Delgado-Salinas & Sotuyo 2012; Silva & Antunes 2014; Vanni 2016; Antunes & Silva 2019; Cardoso et al. 2019). Additional information, including detailed data and images for the specimens and names examined, has been consulted in the following databases: Flora do Brasil 2020, GBIF, IPNI, JSTOR Global Plants (<https://plants.jstor.org>), The Plant

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List, and Tropicos®. Locations of known but unseen duplicates of specimens are included. Barcode numbers are cited consistently whenever available. Homotypic synonyms are indicated by the symbol “≡”, whereas heterotypic synonyms are indicated by “=”.

3 | RESULTS AND DISCUSSION

The Bayesian and maximum likelihood phylogenetic single region analyses of *matK* and ITS/5.8S datasets strongly resolve several key nodes among *Aeschynomene* s.l. and related genera (Figs. 1-2). These individual analyses essentially provide independent tests for the non-monophyly of *Aeschynomene* s.l. which collectively falls in two main clades. Such results are also largely congruent with the more strongly resolved combined analysis (Fig. 3).

The phylogenetic analysis of *matK* and combined data strongly support the *Aeschynomene* sect. *Aeschynomene* as paraphyletic with respect to the mostly African genera *Bryaspis* P.A.Duvign., *Cyclocarpa* Afzel. ex Urb., *Geissaspis* Wight & Arn., *Humularia* P.A.Duvign., *Kotschyia* Endl., and *Smithia* Aiton, as well as the South American monotypic genus *Soemmeringia* Mart. (Figs. 1, 3). Interestingly, species in this clade, particularly those in *A.* sect. *Aeschynomene*, are often hydrophytes growing in swamps, temporary or permanent ponds, and along streams and riverbanks (Rudd 1955; Antunes & Silva 2017; Chaintreuil et al. 2013), an ecological predilection that perhaps explains why stem nodulation ability have evolved several times in this clade (Chaintreuil et al. 2013; Brottier et al. 2018). Whether the whole clade will be circumscribed into an expanded concept of *Aeschynomene* s.str. amalgamated with the remaining genera should be the focus of a more resolved phylogeny and detailed comparative morphological studies. We believe that further nomenclatural changes here would be precipitated because of the poor taxon sampling across the morphologically and geographically diverse related genera from Africa and Asia. Also, our individual ITS Bayesian analysis recovered *A.* sect. *Aeschynomene* as a weakly supported sister clade of one comprising the abovementioned mostly African genera. Some phylogenetic studies of legumes involving next-generation phylogenomic approaches (Nicholls et al. 2015; Ojeda et al. 2019; Duan et al. 2020; Koenen et al. 2020; Zhang et al. 2020) suggest improved resolution could be attained by applying them to *A.* sect. *Aeschynomene*.

All our analyses are also congruent in strongly resolving the sister relationship between *Aeschynomene* sect. *Ochopodium* and *Machaerium*, and then this clade as sister to *Dalbergia* (Figs. 1-3). These relationships have been shown in previous studies with lower taxon sampling focused primarily on the broader dalbergioid legumes (Lavin et al. 2001; Cardoso et al. 2012, 2013) or just on *Aeschynomene* s.l. and related genera (Ribeiro et al. 2007; Chaintreuil et al. 2013; Vatanparast et al. 2013; Brottier et al. 2018). Interestingly, species of *A.* sect. *Ochopodium* are morphologically similar to *Machaerium* and *Dalbergia* by sharing the 5-lobed, campanulate calyx and often having pubescent outer surface of the standard petal.

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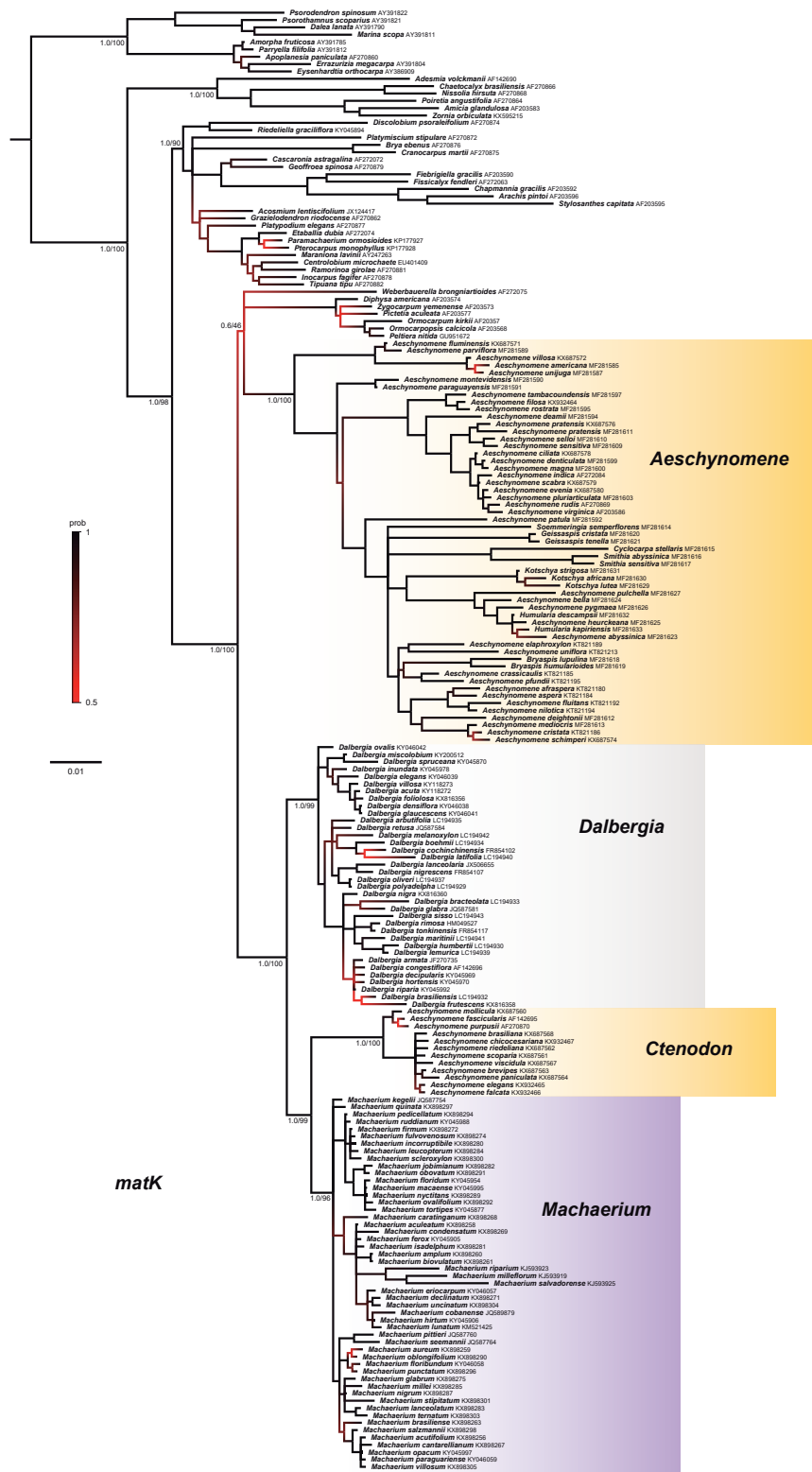


Figure 1. A *matK* Bayesian majority-rule consensus phylogram comprehensively-sampled across all lineages of the dalbergioid legumes (199 terminals by 1617 aligned sites). *Aeschynomene* (sensu Rudd 1955) appears as non-monophyletic, where *Aeschynomene* sect. *Ochopodium*, herein as the reinstated genus *Ctenodon*, is more closely related to *Machaerium*. Posterior probabilities from 0.5 to 1.0 are shown as color gradient from red to black on the branches. Numbers on some key nodes are posterior probabilities and maximum likelihood bootstrap values. GenBank accession numbers follow the terminal taxon labels.

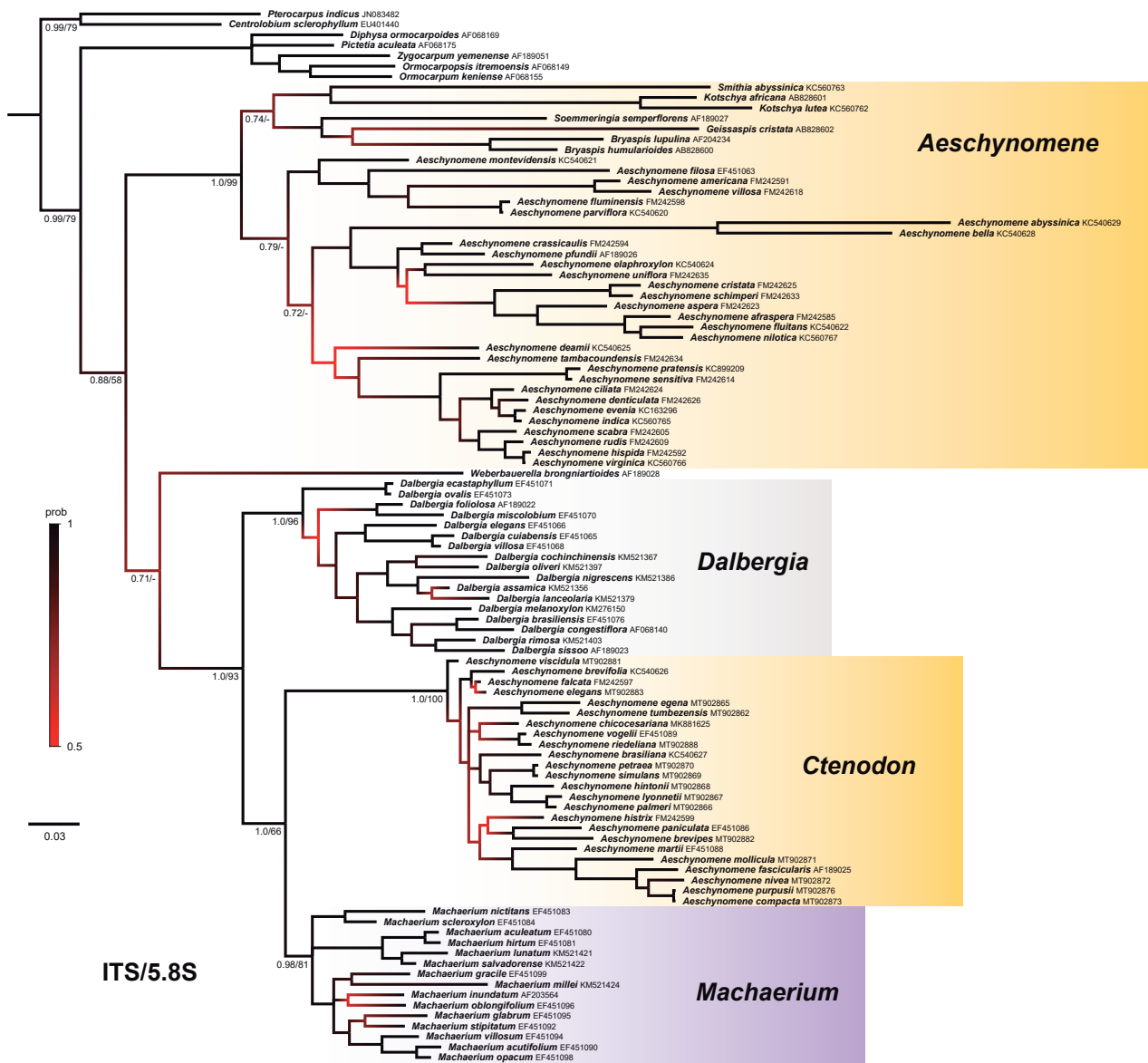


Figure 2. An ITS/5.8S Bayesian majority-rule consensus phylogram (101 terminals by 743 aligned sites) showing the non-monophyly of *Aeschynomene* (sensu Rudd 1955), where *A. sect. Ochopodium*, herein as the reinstated genus *Ctenodon*, is strongly supported as more closely related to *Machaerium*. Posterior probabilities from 0.5 to 1.0 are shown as color gradient from red to black on the branches. Numbers on some key nodes are posterior probabilities and maximum likelihood bootstrap values. GenBank accession numbers follow the terminal taxon labels.

Despite being phylogenetically closely related, *A. sect. Ochopodium* differs from *Machaerium* by the mostly multi-seeded loment fruits and mostly herbaceous or shrubby habit (vs. mostly trees or woody vines and fruits often a single-seeded samara with basal seed chamber and a terminal wing, or a wingless nuroid legume in *Machaerium*). Despite the limited taxon sampling, patterns of chromosomal and flower development variation as well as seedling morphology add further support on the distinctiveness of *A. sect. Ochopodium* from the remaining *Aeschynomene* species (Sampaio et al. 2013; Tapia-Pastrana et al. 2020; Rodrigues et al. 2019). Species of *A. sect. Ochopodium* have

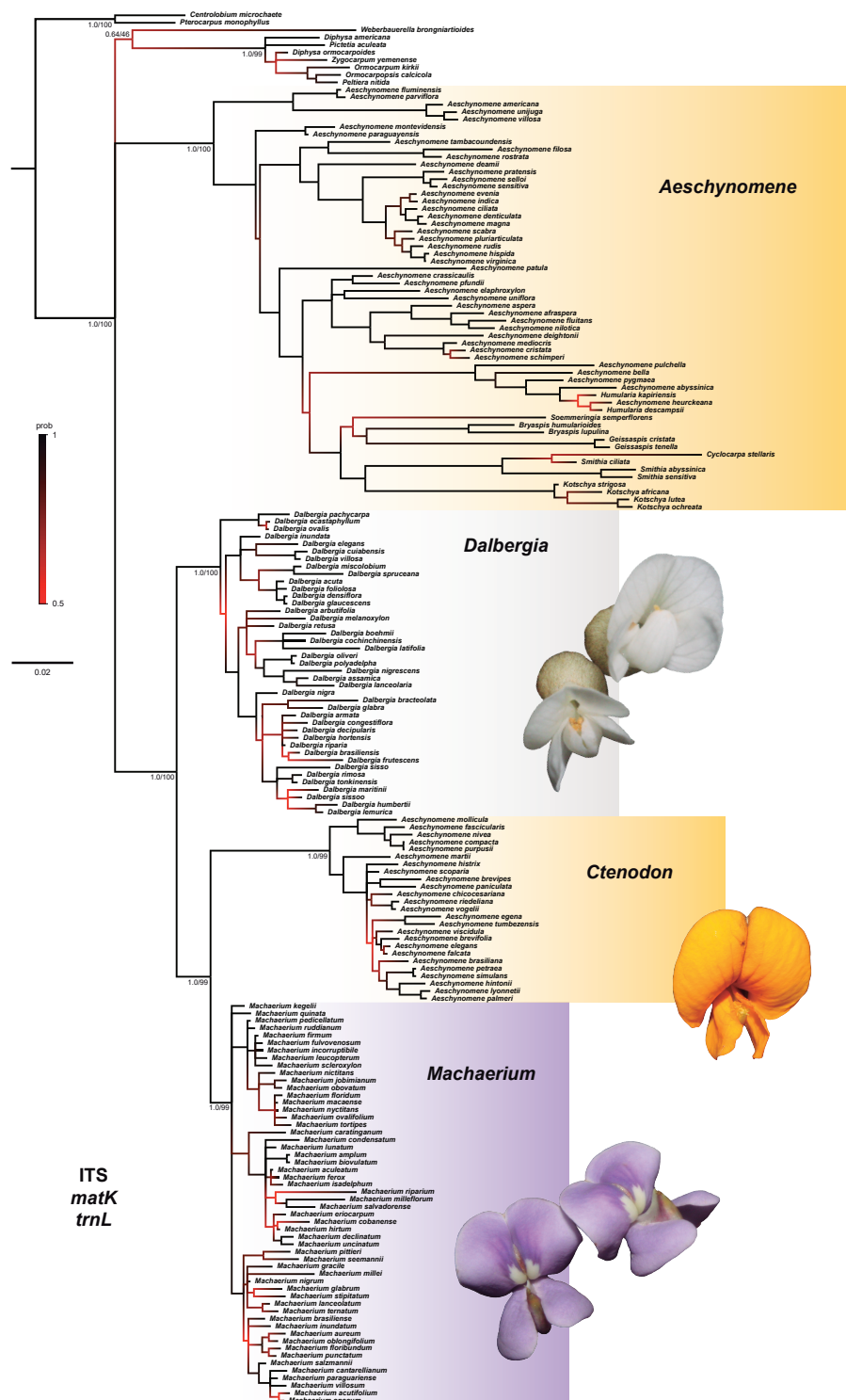


Figure 3. A Bayesian majority-rule consensus phylogram of combined ITS/5.8S, *matK*, and *trnL* intron sequence data (187 terminals by 2976 aligned sites), densely-sampled within *Aeschynomene* and the closely related species rich genera *Dalbergia* and *Machaerium*. The non-monophyly of *Aeschynomene* (sensu Rudd 1955) is evinced, where *A.* sect. *Ochopodium*, herein as the reinstated genus *Ctenodon*, is strongly supported as more closely related to *Machaerium*. Posterior probabilities from 0.5 to 1.0 are shown as color gradient from red to black on the branches. Numbers on specific key nodes are posterior probabilities and maximum likelihood bootstrap values. The photographs by Domingos Cardoso illustrate the general floral architecture of the reinstated genus *Ctenodon* and its closely related *Dalbergia* and *Machaerium*.

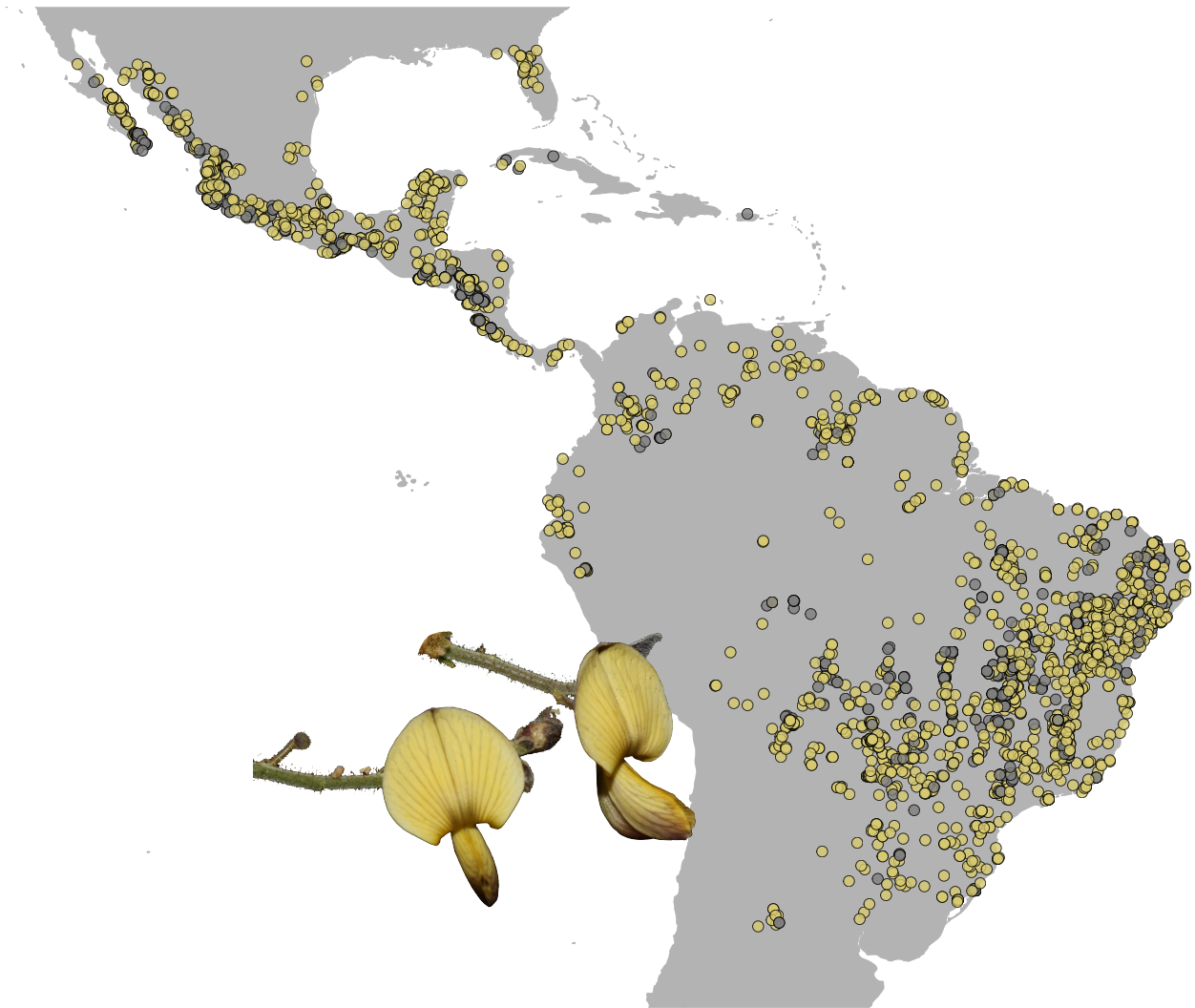


Figure 4. Geographical distribution of the reinstated genus *Ctenodon* in the American continent. Yellow points are records for species that were sampled in our molecular phylogenies, whereas the gray points are from any species that no accession were sampled in our phylogenies. The photograph by Domingos Cardoso shows the floral morphology of *Ctenodon sabulicolus*, an endemic species of the Caatinga seasonally dry woodlands along the São Francisco River sand dunes of Northeastern Brazil.

always been taxonomically differentiated from *A.* sect. *Aeschynomene* by possessing non-peltate, basifixed stipules, campanulate calyx with five subequal lobes, and loments with articles distinctly joined by an isthmus (Vogel 1838; Rudd 1955; Fernandes 1996). Also, they are terrestrial subshrubs or shrubs, sometimes treelets or a small tree reaching 8 m tall, that are more ecologically confined in fire-prone savannas and the seasonally dry tropical forests and woodlands, but also in oak forests, pine-oak forests as well in pine woodlands.

Although elevation and most climate variables differed significantly between *A.* sect. *Ochopodium* and *Aeschynomene* s.str. lineage, the actual differences were slight (Fig. 5). For example, the average elevation for the *Aeschynomene* s.str. lineage was 669 m and that of the *A.* sect. *Ochopodium* lineage 601 m, a difference of only 68 meters, which was significant given that the

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95% CI of differences between the two clades ranged 30-107 m. The one notable climate difference was annual precipitation (Fig. 5), which averaged 1543 mm for *Aeschynomene* s.str. lineage and 1059 mm for *A. sect. Ochopodium* lineage. The 95% CI of differences between the two clades for annual precipitation ranged 442-527 mm. Notably, these differences span the 1200-1300 mm threshold that distinguishes the lowland tropical seasonally dry biomes from wetter biomes (e.g. Oliveira-Filho et al. 2013; Ringelberg et al. 2020). This finding reflects the observation that *A. sect. Ochopodium* lineage is centered in seasonally dry neotropical forests and woodlands as well as savanna, whereas *Aeschynomene* s.str. lineage is centered in wetter lowland tropical and subtropical biomes. Inspection of the species distribution maps in Rudd (1955) reveals that species of *A. sect. Ochopodium* have more limited or narrower geographical distributions than species of *A. sect. Aeschynomene*. This pattern reflects the finding that dry lowland tropical biomes, such as seasonally dry tropical forests and woodlands, are more dispersal limited than wet lowland tropical biomes, at least with respect to woody plants (e.g. Pennington et al. 2009; Pennington & Lavin 2016).

Here we argue that this ecologically, morphologically, and phylogenetically coherent clade of *A. sect. Ochopodium* species should to be recognized at generic rank. Therefore we decided to reinstate the name *Ctenodon* Baill. to include all species of *A. sect. Ochopodium* (sensu Vogel 1838; Rudd 1955). *Ctenodon* was originally described as a monotypic genus by Baillon (1870) based on the Brazilian endemic, savanna-inhabiting species *Ctenodon weddellianus* Baill. [= *Ctenodon oroboides* (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima], which was later transferred to *Aeschynomene* by Rudd (1955). Although we have not sampled the type species of *Ctenodon* in our phylogenetic analyses, it is most likely related to the *A. sect. Ochopodium* lineage, because it bears the same morphological features traditionally used to define the section, and that are consistently found in all species of this clade (Rudd 1955). *Ctenodon oroboides* is somewhat distinctive by just the ovate-falcate leaflets. All other characters used once to classify it at genus level (e.g. pubescent fruits) are found variously in *A. sect. Ochopodium* (Rudd 1955).

The infrageneric name *Ochopodium* published earlier by Vogel (1838) cannot be raised to generic rank. *Ctenodon* is the legitimate generic name according to the Code Art. 11.2 (Turland et al. 2018) because there is no priority for a name outside the rank at which it was published. The generic names *Balisaea* Taub. and *Secula* Small, originally published for species later transferred to *A. sect. Ochopodium* (Rudd 1955, 1972), are here treated as synonyms of *Ctenodon*. All other generic names (*Herminiera* Guill. & Perr., 1832; *Macromiscus* Turcz., 1846; *Rueppelia* A.Rich., 1847; *Aedemone* Kotschy, 1858) ever associated under synonymy of *Aeschynomene* s.l. (Rudd 1955) and older than *Ctenodon* were based on type species that are shown here phylogenetically nested within the *Aeschynomene* s.str. lineage (Fig. 3). Noteworthy is the Old World species *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub. that is strongly resolved within *Aeschynomene* s.str. lineage (Fig. 3), but has been suggested by Taubert (1894), when synonymizing the genus *Herminiera*, as morphologically close to *A. sect. Ochopodium*.

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Ctenodon as herein newly circumscribed comprises 66 species in America but the genus could include as many as ca. 120 species. However, this will depend on a detailed taxonomic revision with the pantropical and African species, as well as the complex of infraspecific variation in American species. Because the taxonomic diversity of the African species of *A.* sect. *Ochopodium* is underrepresented in our molecular phylogenies, the nomenclatural proposals include only the American species. In the Americas, *Ctenodon* is particularly diverse in Mexico and Brazil, but there are also a few endemic species in the Andes (Fig. 4; Rudd 1955; Delgado-Salinas & Sotuyo 2012; Flora do Brasil 2020 under construction 2020). Species of the genus are poorly known with respect to floral and pollination biology, but the recent study by Carleial et al. (2015) described a striking mechanism of reflexed flowers in *Ctenodon mucronulatus* (= *Aeschynomene amorphoides*) that is rare in papilionoid legumes, but previously observed only in some species of the phylogenetically related genus *Machaerium*. The unique architecture of the papilionate flowers in *C. mucronulatus* involves the wing petals and keel highly curved against the standard petal that lies in obliquely horizontal position. The entire flower then serves as landing platform for pollinators and, more unusually, the distinctly-colored keel tip functions as color marking (maculae), which is otherwise a predominant feature of the standard petal in papilionoid legumes (Carleial et al. 2015).

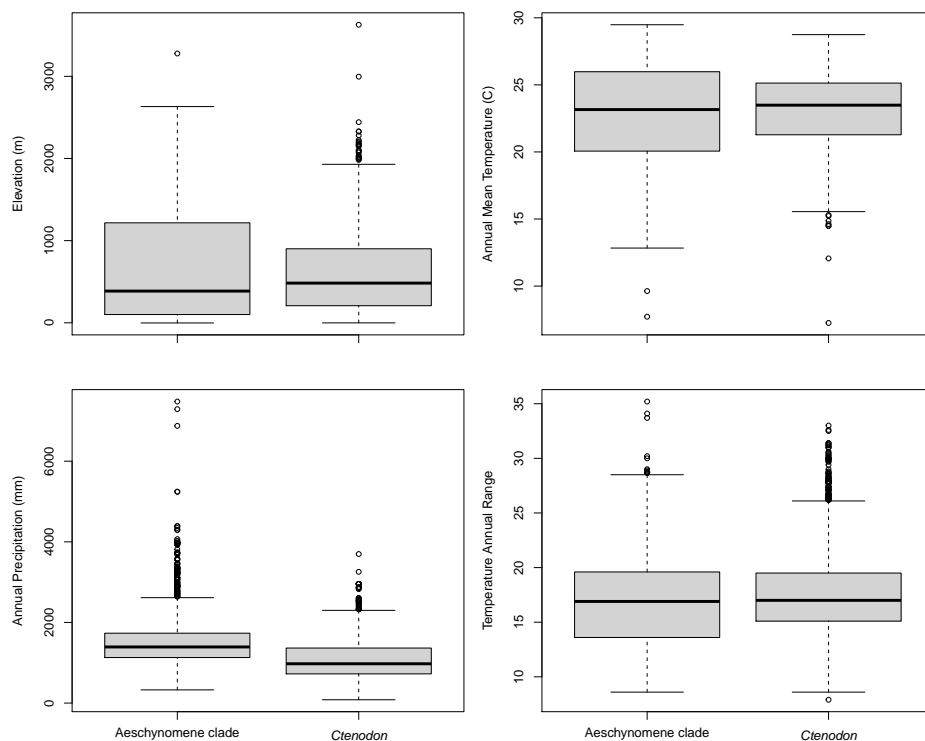


Figure 5. Elevation and climate differences between species of the *Aeschynomene* clade (*Aeschynomene* sensu stricto and the mostly African phylogenetically related genera) and the clade comprising *Ctenodon* species. For elevation, means for the two clades, respectively, are 669 versus 601 m (95% CI for the differences in these means range 30–107 m). For annual mean temperature, means for the two clades, respectively, are 22.8 versus 23.2 C (95% CI for the differences in these means range -0.5–0.11 C). For annual mean precipitation, means for the two clades, respectively, are 1543 versus 1059 mm (95% CI for the differences in these means range 442–527 mm). For annual mean temperature range (a measure of seasonality), means for the two clades, respectively, are 17.2 versus 17.8 C (95% CI for the differences in these means range -0.88–0.30 mm).

4 | TAXONOMY

Ctenodon Baill., *Adansonia* 9: 236. 1870. Type: *Ctenodon weddellianus* Baill., as "*weddellianum*" [= *Ctenodon oroboides* (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima].

= *Balisaea* Taub., *Bot. Jahrb. Syst.* 21: 436. 1895. Type: *Balisaea genistoides* Taub. [= *Ctenodon genistoides* (Taub.) D.B.O.S.Cardoso, Filardi & H.C.Lima].

= *Secula* Small, *Fl. Miami [Small]* 90: 200. 1913. Type: *Secula viscidula* (Michx.) Small [= *Ctenodon viscidulus* (Michx.) D.B.O.S.Cardoso & A.Delgado].

= *Aeschynomene* sect. *Ochopodium* Vogel, *Linnaea* 12: 86. 1838 ≡ *Aeschynomene* subgen. *Ochopodium* (Vogel) J.Léonard, *Bull. Jard. Bot. État. Brux.* 24: 84. 1954. Lectotype (designated by Rudd 1955): *Aeschynomene falcata* (Poir.) DC. [= *Ctenodon falcatus* (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima].

Herbs, pyrophytic or fire-sensitive subshrubs, shrubs, treelets or a small tree reaching up to 8 m tall; erect or prostrate; the stems covered by glandular hairs or simple pubescence, or the plants sometimes glabrous. Stipules striate, subcordate or triangular to lanceolate, non-peltate, basifixed. Leaves pinnately compound, 5–80-foliolate or more unifoliolate, or scale-like and then giving plant an aphyllous appearance; petiole often including a swollen pulvinus at the base; leaflets membranaceous to coriaceous, symmetrical or oblique, oblong to orbiculate, elliptic to ovate or obovate, or more rarely needle-like, glabrous to densely pubescent, with or without marginal glandular hairs. Inflorescence axillary or sometimes terminal, 2–3-flowered racemes to densely-flowered compound racemes or panicle-like inflorescences; pedicel bracteolate. Flowers bilaterally symmetrical, papilionate; calyx campanulate, lobes 5; petals bright to light yellow, red, pale pink or red purplish, clawed, the standard often pubescent externally, distinctly clawed; wing and keel glabrous; stamens 10, the filaments half the length fused into a sheath, monadelphous, sometimes diadelphous, glabrous, the anthers uniform, dorsifixed; gynoecium with the ovary stipitate, laterally compressed. Fruit a (1–)2–18-articulate loment, distinctly stipitate, the articles distinctly joined by an isthmus, glabrous or pubescent; seeds reniform, light brown to black, smooth.

Ctenodon acapulcensis (Rose) A.Delgado, *comb. nov.*

Basionym: *Aeschynomene acapulcensis* Rose, *Contr. U.S. Natl. Herb.* 5: 191. 1899. Type: MEXICO, Guerrero, Acapulco, Oct 1894–Mar 1895, *E. Palmer* 126 (holotype: US00001870; isotypes: BM000931568, V0058790F, V0058791F, V0058792F, V0058804F, GH00058419, GH00058420, K000297149, MICH1107075, MO-126284, NY00004974, PH00000045, UC80616, US00930889, US00930890).

= *Aeschynomene picachensis* Brandegees, *Univ. Calif. Publ. Bot.* 6: 181. 1915. Type: MEXICO, Oaxaca, Cerro de Pichaco, Jul 1914, *C.A. Purpus* 7162 (holotype: UC175043; isotypes: BM000931569, V0058799F, GH00058437, MO-128347, NY00004987, US00001919).

Distribution—Mexico.

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Ctenodon afranianus D.B.O.S.Cardoso, Filardi & H.C.Lima, **nom. nov.**

Basionym: *Aeschynomene venulosa* Afr.Fern., O Táxon *Aeschynomene* no Brasil: 111. 1996, *nom. illeg., hom. post.* (non Verdc. 1970). Type: BRAZIL, Alagoas, Maceió, Faz. Pau-Brasil, Jul 1977, A. Fernandes & Matos s.n. (holotype: EAC0003363).

Distribution—Brazil.

Ctenodon benthamii (Rudd) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene mollicula* var. *benthamii* Rudd, Contr. U.S. Natl. Herb. 32: 131. 1955
≡ *Aeschynomene platycarpa* Benth., Fl. Bras. 15(1): 63. 1859, *nom. illeg., hom. post.* (non Michx. 1803). Type: BRAZIL, Minas Gerais, "in saxosis umbrosis prope fluv. Jiquitinhonha [Jequitinhonha]", Dec 1824, L. Riedel 591 (lectotype designated by Rudd 1955: K000222449; isolectotype: LE00002482).

≡ *Aeschynomene benthamii* (Rudd) Afr.Fern., O Táxon *Aeschynomene* no Brasil: 113. 1996, *nom. inval.*

Distribution—Brazil.

Ctenodon bradei (Rudd) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene bradei* Rudd, J. Wash. Acad. Sci. 49: 51. 1959. Type: BRAZIL, Rio de Janeiro, Santa Maria Madalena, Pedra Dubois, Feb 1935, J. Santos Lima & A.C. Brade 14220 (holotype: RB00540115, RB00168508; isotype: US00001864).

Distribution—Brazil.

Ctenodon brasilianus (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Hedysarum brasilianum* Poir., Encycl. [J. Lamarck & al.] 6(2): 448. 1805. Type: BRAZIL, Rio de Janeiro, circa Rio de Janeiro, Jul 1767, P. Commerson s.n. (holotype: P-JU [Catal. No. 15624] – P00678649; isotypes: V0059317F, P01167838, P02913671, P02913680 [F neg. 36628]).

≡ *Aeschynomene brasiliana* (Poir.) DC., Prodr. [A. P. de Candolle] 2: 322. 1825.

= *Cassia biflora* Mill., Gard. Dict., ed. 8. n. 14. 1768, *nom. illeg., hom. post.* (non L. 1753) ≡ *Cassia houstoniana* Collad., Hist. Nat. Méd. Casses 132. 1816 ≡ *Aeschynomene biflora* Fawc. & Rendle, Fl. Jamaica 4: 27. 1920. Type: JAMAICA, 1730, W. Houstoun s.n. (holotype: BM000931561).

= *Aeschynomene paucijuga* DC., Prodr. [A. P. de Candolle] 2: 321. 1825. Type: FRENCH GUIANA, Cayenne, 1819, G.S. Perrottet s.n. (holotype: G-DC [F neg. 6959]; possible isotype: P02913696).

= *Aeschynomene paucijuga* var. *subscabra* DC., Prodr. [A. P. de Candolle] 2: 321. 1825. Type: "In America merid.", Anonymous s.n. (holotype: G-DC n.v.).

= *Hedysarum hirtum* Vell., Fl. Flumin.: 319. 1829; idem in Fl. Flumin. Icon. 7: t. 151. 1831, *nom. illeg., hom. post.* (non L. 1753). Type: BRAZIL, "Habitat campis paulo supra relatis", Oct. Lectotype (designated here): [icon] original plate on parchment of "Florae Fluminensis" (digital object: mss1198656_155) in the Manuscript Section of Fundação Biblioteca Nacional, Rio de Janeiro

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(Coleção Flora Fluminense; fonte: Conceição Vellozo, 1790, *Florae Fluminensis Icones fundamentales*. t. VII. p. [prancha] 151; I-17,04,001 – Manuscritos).

= *Aeschynomene trisperma* Klotzsch, *Reis. Br.-Guiana* [Ri. Schomburgk] 3: 1103. 1849. Type: GUYANA, "auf trockner Savanne in der Umgebung des *Rué-imeru*", Sep-Oct, *Ri. Schomburgk s.n.* (unlocated).

= *Aeschynomene guaricana* Pittier, *Bol. Tecn. Minist. Agric.* 5: 41. 1944. Type: VENEZUELA, Aragua, entre San Juan de los Morros y Uberito, Dec 1923, *H. Pittier 11324* (holotype: VEN3782).

Distribution—Widespread in tropical America.

Ctenodon brevipes (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene brevipes* Benth., *Fl. Bras. (Martius)* 15(1): 66. 1859. Type: BRAZIL, Piauí, rocky places near Oeiras, May 1839, *G. Gardner 2097* (lectotype designated here: K000092347; isolectotypes: BM000931738, GH n.v., L0018459). Other syntype: BRAZIL, Piauí, *in campis agrestibus*, May 1819, *C.F.P. von Martius s.n.* (M0233719 [F neg. 6269]).

= *Aeschynomene brevipes* var. *uliginosa* Benth., *Fl. Bras. (Martius)* 15(1): 66. 1859. Type: BRAZIL, Maranhão, Jun 1841, *G. Gardner 5997* (holotype: K000222439; isotypes: BM000931740, K000222438).

Distribution—Brazil.

Ctenodon carvalhoi (G.P.Lewis) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene carvalhoi* G.P.Lewis, *Kew Bull.* 40(3): 599. 1985. Type: BRAZIL, Bahia, Palmeiras, Morro do Pai Inácio, Km 224 da Rodovia BR 242, alt. 1000 m, Dec 1981, *G.P. Lewis et al.* 962 (holotype: CEPEC00030212; isotypes: HUEFS [99842], K000092398, M0233720, NY00004997, RB00540116, SPF00040115, US00091042).

Distribution—Brazil.

Ctenodon carichanicus (Rudd) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene brasiliiana* var. *carichanica* Rudd, *J. Wash. Acad. Sci.* 49: 48. 1959. Type: VENEZUELA, Bolívar, north end of Cerro Gavilan (Cerro Carichana), 100-300 m, Dec 1955, *J.J. Wurdack & J.V. Monachino 40885* (holotype: US00001886; isotypes: F0058807F, NY00004995, VEN40998).

≡ *Aeschynomene carichanica* (Rudd) G.B.Rodr. & G.Agostini, *Acta Bot. Venez.* 16(1): 123. 1991.

Distribution—Venezuela.

Ctenodon chicocesarianus (D.B.O.S.Cardoso & G.Ramos) D.B.O.S.Cardoso, **comb. nov.**

Basionym: *Aeschynomene chicocesariana* D.B.O.S.Cardoso & G.Ramos, *Syst. Bot.* 44(4): 811. 2019. Type: BRAZIL, Bahia, Ibicoara, Gerais do Machombongo, 13°13'58"S, 41°17'16"W, 1182 m, Jan 2015, *D. Cardoso et al.* 3640 (holotype: HUEFS0239018; isotypes: ALCB, CEPEC, K, MO, NY, RB).

Distribution—Brazil.

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Ctenodon compactus (Rose) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene compacta* Rose, Contr. U.S. Natl. Herb. 5(4): 191. 1899. Type: MEXICO, Oaxaca, Tomellin Canyon, Oct 1894, C.G. Pringle 5645 (lectotype designated by Rudd 1955: US00001904; isolectotypes: GH00058427, MEXU01169220, UC80604, UVMVT024909). Other syntypes: MEXICO, Oaxaca, from Juchitan to Chivela, Jun 1895, E.W. Nelson 2630 (US01108278). MEXICO, [Oaxaca], Cuesta de Ejulta, Naialtepec [Manialtepec], Jun 1895, L.C. Smith 452 (GH n.v., US02044797).

= *Aeschynomene oaxacana* Brandegees, Univ. Calif. Publ. Bot. 6: 181. 1915. Type: MEXICO, Oaxaca, Cerro de Picacho, Jul 1914, C.A. Purpus 7179 (holotype: UC175011; isotypes: BM000931570, V0058798F, GH00058433, MO-126286, NY00004984, US00001916).

Distribution—Costa Rica, Guatemala, and Mexico.

Ctenodon egenus (J.F.Macbr.) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene mollicula* var. *egena* J.F.Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 13: 443. 1943. Type: PERU, Cajamarca, Prov. Jaen, mountains between the rivers Tabaconas and Marañón, 1000-1200 m, Apr 1912, A. Weberbauer 6176 (holotype: F0043450F; isotypes: F0043443F, GH00058461, NY00005007, US00001888).

≡ *Aeschynomene egena* (J.F.Macbr.) Rudd, Contr. U.S. Natl. Herb. 32: 122. 1955.

Distribution—Peru.

Ctenodon elegans (Schltdl. & Cham.) D.B.O.S.Cardoso & A.Delgado, **comb. nov.**

Basionym: *Aeschynomene elegans* Schltdl. & Cham., Linnaea 5(4): 583. 1830. Type: MEXICO, Veracruz, Hacienda de la Laguna, Sep 1828, C.J.W. Schiede & F. Deppe s.n. [231] (lectotype designated here: HAL0098429; isolectotype: G [F neg. 27926]). Other syntype: MEXICO, Veracruz, "in collibus apricis prope Jalapam", Aug 1828, C.J.W. Schiede & F. Deppe s.n. [231] (HAL0098428). Possible original material: Hacienda de la Laguna, Aug 1829, C.J.W. Schiede & F. Deppe s.n. (BM000931567).

≡ *Aeschynomene falcata* (Poir.) DC. var. *elegans* (Schltdl. & Cham.) Kuntze, Revis. Gen. Pl. 1: 158. 1891.

Distribution—Widespread in tropical America.

Ctenodon elegans var. *elegans*

= *Aeschynomene tecta* Vogel, Linnaea 12: 87. 1838 ≡ *Aeschynomene falcata* var. *plurijuga* Benth., Fl. Bras. (Martius) 15(1): 68. 1859, p.p. Type: BRAZIL, "inter Campos-Victoria", F. Sellow s.n. (holotype: B†; probable isotype: K000222428).

= *Aeschynomene falcata* (Poir.) DC. var. *elegans* (Schltdl. & Cham.) Kuntze f. *glabrior* Kuntze, Revis. Gen. Pl. 1: 158. 1891. Type: VENEZUELA, Caracas, 1874, C.E.O. Kuntze s.n. (holotype: NY00005001).

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= *Aeschynomene arenicola* Brandegee, Univ. Calif. Publ. Bot. 10: 408. 1924. Type: MEXICO, Chiapas, on sandy soil in pine forests near Hacienda Monserrate, Sep 1923, C.A. Purpus 9148 (holotype: UC220377; isotypes: GH n.v., MO-126288, NY00004977, US00001867).

Ctenodon elegans* var. *robustior (Rudd) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene elegans* var. *robustior* Rudd, J. Wash. Acad. Sci. 49: 50. 1959. Type: BRAZIL, Goiás, "Brejon prope Santa Cruz", Jun 1820, J.E. Pohl s.n. [2560] (holotype: K000222429; isotypes: M0233731, W0067211).

Ctenodon falcatus (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Hedysarum falcatum* Poir., Encycl. [J. Lamarck & al.] 6(2): 448. 1805. Type: BRAZIL, Rio de Janeiro, "le long de la rivière de Rio-Janeiro", P. Commerson s.n. (holotype: P-JU [Catal. No. 15623] – P00678648; isotypes: F0059318F, P02297636, P02297637 [F neg. 36629], P00296593, P02913700).

≡ *Aeschynomene falcata* (Poir.) DC., Prodr. [A. P. de Candolle] 2: 322. 1825.

Distribution—Argentina, Bolivia, Brazil, Chile, Colombia, and Paraguay.

Ctenodon falcatus* var. *falcatus

= *Hedysarum diffusum* Vell., Fl. Flumin.: 320. 1829; idem in Fl. Flumin. Icon. 7: t. 153. 1831, *nom. illeg., hom. post.* (non Willd. 1802). Type: BRAZIL, "Habitat campis maritimis. Offendi ad urbis collem, quo inædificatum est Divi Antonii Cænobium", Nov. Lectotype (designated here): [icon] original plate on parchment of "*Florae Fluminensis*" (digital object: mss1198656_157) in the Manuscript Section of Fundação Biblioteca Nacional, Rio de Janeiro (Coleção Flora Fluminense; fonte: Conceição Vellozo, 1790, *Florae Fluminensis Icones fundamentales*. t. VII. p. [prancha] 153; I-17,04,001 – Manuscritos).

= *Aeschynomene falcata* var. *paucijuga* Benth., Fl. Bras. (Martius) 15(1): 67, tab. 14. 1859, includes type of species.

= *Aeschynomene apoloana* Rusby, Bull. New York Bot. Gard. 6: 511. 1910. Type: BOLIVIA, Apolo, grassy prairie, Mar 1902, R.S. Williams 25 (holotype: NY00004994; isotypes: BM000931553, K000222453, US00001868).

Ctenodon falcatus* var. *hassleri (Rudd) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene falcata* var. *hassleri* Rudd, J. Wash. Acad. Sci. 49: 52. 1959. Type: PARAGUAY, near Concepción, Sep 1901, E. Hassler 7461 (holotype: K000222433; isotypes: BM000538162, G n.v., NY00005000, P02297638, P02913580, S13-12015).

Ctenodon falcatus* var. *minor (N.F.Mattos) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene falcata* var. *minor* N.F.Mattos, Loefgrenia 53: 2. 1971. Type: BRAZIL, Mato Grosso do Sul, 3 léguas ao sul de Campo Grande, Fazenda Ibirussu, Jan 1933, J. Otero 173 (holotype: SP000945).

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Ctenodon fascicularis (Schltdl. & Cham.) A.Delgado, *comb. nov.*

Basionym: *Aeschynomene fascicularis* Schltdl. & Cham., *Linnaea* 5: 584. 1830. Type: MEXICO, Veracruz, "inter la Laguna Verde et Actopan", Mar 1829, C.J.W. Schiede & F. Deppe s.n. (holotype: B[†]; lectotype designated here: HAL0098430).

- = *Adesmia mimosoides* G.Don, *Gen. Hist.* 2: 282. 1832. Type: MEXICO, ex Herb. Lambert (not found).
- = *Aeschynomene fruticosa* Sessé & Moc., *Pl. Nov. Hisp.*: 122. 1890. Type: MEXICO, Michoacán, Apatzingam [Apatzingán], Sep, M. de Sessé & J. M. Mociño s.n. (Possible original material: [1940] F, MA601244, MA601245; [1941] F, MA601242; [1942] F, MA601243).
- = *Aeschynomene oligantha* Micheli, *Mém. Soc. Phys. Genève* 34: 256. 1903, *nom. illeg., hom. post.* (non Welw. ex Baker 1871). Type: MEXICO, Guerrero, La Mata San Dios, 200 m, Oct 1898, É. Langlassé 431 (holotype: G; isotypes: GH00058434, K000297148, MEXU00051016, P02914003, P02914004, US00001915).

Distribution—Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, and Venezuela.

Ctenodon foliolosus (Rudd) D.B.O.S.Cardoso, Filardi & H.C.Lima, *comb. nov.*

Basionym: *Aeschynomene foliolosa* Rudd, *Contr. U.S. Natl. Herb.* 32: 91. 1955. Type: COLOMBIA, Guaviare [Vaupés], San José del Guaviare, 270 m, Nov 1939, J. Cuatrecasas 7697 (holotype: US00001897; isotypes: COL000001730, V0058810F).

Distribution—Bolivia, Brazil, and Colombia.

Ctenodon genistoides (Taub.) D.B.O.S.Cardoso, Filardi & H.C.Lima, *comb. nov.*

Basionym: *Balisaea genistoides* Taub., *Bot. Jahrb. Syst.* 21: 437. 1896. Type: BRAZIL, Goiás, "in campis montium Serra de Balisa dictorum", Sep 1892, E.H.G. Ule 2837 [14] (holotype: B[†]; isotypes: HBG506552, P03383092, P03383093, P03383094, R000065277).

≡ *Aeschynomene genistoides* (Taub.) Rudd, *Phytologia* 23: 321. 1972.

Distribution—Brazil.

Ctenodon genistoides* var. *genistoides

- = *Aeschynomene irwinii* Rudd, *Phytologia* 15: 117, fig. 1. 1967. Type: BRAZIL, Goiás, Chapada dos Veadeiros, ca. 13 km N.W. of Veadeiros, 1200 m, Oct 1965, H.S. Irwin et al. 9367 (holotype: US00001908; isotype: NY00005002).

Ctenodon genistoides* var. *latifoliolus (G.P.Lewis) D.B.O.S.Cardoso, Filardi & H.C.Lima, *comb. nov.*

Basionym: *Aeschynomene genistoides* var. *latifoliola* G.P.Lewis, *Kew Bull.* 49(1): 95. 1994. Type: BRAZIL, Goiás, Alto Paraíso, Córrego Veredas, Nov 1991, G. Hatschbach et al. 55944 (holotype: MBM146604; isotypes: C10011415, CEPEC [62941], G00364569, HBG520675, INPA [201071], K000222450).

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Ctenodon gracilis (Vogel) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene gracilis* Vogel, *Linnaea* 12: 89. 1838. Type: BRAZIL, loco haud indicato, "inter Campos-Victoria", s.d., *F. Sellow s.n.* (lectotype designated here: K000189448; probable isoelectotype: K000189535).

= *Aeschynomene portoricensis* Urb., *Symb. Antill. (Urban)* 1(2): 325. 1899. Type: PUERTO RICO, Arecibo, Laguna Tortuguero, near Manatí, Apr 1887, *P.E.E. Sintenis* 6657 (lectotype designated here: US00001921; isoelectotypes: BM000931560, V0058805F, GH, HBG520670, K000222411, L0018471, M0233746, MO-022345, NY00004992, P02912509). Other syntype: PUERTO RICO, Maricao, Aguadilla, Sierra de Naguabo ad Rio Blanco, Nov 1886, *P.E.E. Sintenis* 4889 (US).

Distribution—Brazil, Colombia, and Puerto Rico.

Ctenodon graminoides (G.P.Lewis) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene graminoides* G.P.Lewis, *Kew Bull.* 47(1): 143. 1992. Type: BRAZIL, Goiás, Santo Antônio do Descoberto, divisa do Distrito Federal, Jan 1976, *E.P. Heringer* 15338 (holotype: IBGE; isotypes: RB00306230, RFA [17839], UB, UEC051896).

Distribution—Brazil.

Ctenodon hintonii (Sandwith) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene hintonii* Sandwith, *Hooker's Icon. Pl.* 35(2): tab. 3448. 1943. Type: MEXICO, Guerrero, Coyuca, Placeres [Placeres de Oro], Mar 1934, *G.B. Hinton et al.* 6104 (lectotype designated here: K000118279; isoelectotypes: K000118280, MICH1107078, NY00004983, RSA0002726, UC1098467, US00001895).

Distribution—Mexico.

Ctenodon histrix (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene histrix* Poir., *Encyc. [J. Lamarck & al.], Suppl.* 4: 77. 1816. Type: FRENCH GUIANA, "île de Cayenne", s.d., *J. Martin s.n.* (lectotype designated here: P02912637; isoelectotype: P02912675 ex Herb. Poiret in Herb. Moquin-Tandon).

≡ *Secula histrix* (Poir.) Small, *Man. S.E. Fl.*: 728. 1933.

Distribution—Widespread in tropical America.

Ctenodon histrix* var. *histrix

= *Aeschynomene cassioides* Desv. ex Ham., *Prodr. Pl. Ind. Occid.*: 51. 1825. Type: FRENCH GUIANA, Cayenne, ex Herb. Desvaux (holotype: P02912656).

= *Aeschynomene echinus* Vogel, *Linnaea* 12: 92. 1838. Type: BRAZIL, loco haud indicato, s.d., *F. Sellow s.n.* (holotype: B[†]).

= *Aeschynomene conferta* Benth., *Ann. Nat. Hist.* 3: 433. 1839. Type: GUYANA, 1837, *R.H. Schomburgk* 187 (lectotype designated here: K000222418; isoelectotypes: BM000931556,

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BR0000005119516, F0058808F, GH00058449, L1970334, MICH1107076, P02913646, P02913648, TCD0004354, US00001903).

= *Aeschynomene mucronulata* Benth., J. Bot. (Hooker) 2: 56. 1840 ≡ *Aeschynomene histrix* var. *mucronulata* Benth., Fl. Bras. (Martius) 15(1): 69. 1859. Type: GUYANA, dry savannahs, 1839, *R.H. Schomburgk* 822 (lectotype designated here: K000222419; isolectotypes: BM000931555, G [F neg. 27929]).

= *Aeschynomene pineticola* Standl. & L.O.Williams, Ceiba 1: 79. 1950. Type: HONDURAS: Morazán, rocky pine forest, along road from El Zamorano toward San Antonio de Oriente, 825-950 m, Sep-Nov 1948, *P.C. Standley* 12657 (holotype: F; isotype: EAP15549).

Ctenodon histrix* var. *apanus (Rudd) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene histrix* var. *apana* Rudd, J. Wash. Acad. Sci. 49: 50. 1959. Type: PARAGUAY, Centurión, "Zwischen Rio Apa und Rio Aquidaban, Dec 1908, *K. Fiebrig* 4387 (holotype: US00001894; isotypes: BM000538153, E00296480, E00296481, GH, K000222425).

Ctenodon histrix* var. *densiflorus (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene densiflora* Benth. J. Bot. (Hooker) 2: 56. 1840. Type: GUYANA, *R.H. Schomburgk* 846 (lectotype designated here: K000222423; isolectotypes: BM000931554, F0360740F, G00364570, L0018467, P02912697, P02913643, P02913644, TCD0004351, US00001901).

≡ *Aeschynomene histrix* var. *densiflora* (Benth.) Rudd, Contr. U.S. Natl. Herb. 32: 84. 1955.

Ctenodon histrix* var. *incanus (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene histrix* var. *incana* Benth., Fl. Bras. (Martius) 15(1): 69. 1859. Type: URUGUAY, Montevideo, *F. Sellow s.n.* (holotype: B⁺; lectotype designated here: K000222421; isolectotypes: V0058811F, K000222420, L1970338, M0233737, P02912696 [Herbier Impérial du Brésil no. 1486], W0067216).

≡ *Aeschynomene incana* Vogel, Linnaea 12: 90. 1838, *nom. illeg., hom. post.* (non G.Mey. 1818).

= *Aeschynomene puberula* DC., Prodr. [A. P. de Candolle] 2: 321. 1825. Type: "America meridionale", s.d., *Anonymous s.n.* (holotype: G-DC [F neg. 6960]).

Ctenodon histrix* var. *multijugus (Chodat & Hassl.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene brasiliiana* f. *multijuga* Chodat & Hassl., Bull. Herb. Boissier (ser. 2) 4: 882. 1904. Type: PARAGUAY, Departamento Canindeyú, "in campo pr. flumen Carimbatay", Dec 1898-1899, *E. Hassler* 5814 (lectotype designated by Vanni 2016: NY00004996; isolectotypes: BM000538155, G00381609, G00381610, G00381611, G00381612, GH00058453, K000222426, MO-022336, P02913685, P02913994, S13-12024).

≡ *Aeschynomene histrix* var. *multijuga* (Chodat & Hassl.) Rudd, J. Wash. Acad. Sci. 49: 49. 1959.

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Ctenodon interruptus (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene interrupta* Benth., J. Bot. (Hooker) 2(9): 56. 1840. Type: GUYANA, Rio Branco, 1840, *R.H. Schomburgk 803* (lectotype designated here: K000222445; isotypes: B[†] [F neg 2147], BM000931551, F, G, GH00058454, IAN [230], K000222446, L1970772, MO-1282367, P02913986, TCD0004350, US00001893).

Distribution—Brazil and Guyana.

Ctenodon lacabuendianus (Brandão) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene laca-buendiana* Brandão, Daphne 1(3): 5. 1991. Type: BRAZIL, Minas Gerais, Mocambinho, km 18 após o trevo de Janaúba-Mocambinho, *J.P. Laca-Buendia 1500* (holotype: RB; isotype: PAMG).

Distribution—Brazil.

Ctenodon langlassei (Micheli ex Rudd) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene langlassei* Micheli ex Rudd, Contr. U.S. Natl. Herb. 32: 117. 1955. Type: MEXICO, Guerrero, Sierra Madre, 1200 m, Feb 1899, *E. Langlassé 847* (holotype: US00001892; isotypes: G, GH00058429, K000297140, MPU022831, P02913969, P02913982).

Distribution—Mexico.

Ctenodon leptostachyus (Benth.) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene leptostachya* Benth., Fl. Bras. (Martius) 15(1): 65 (1859). Type: BRAZIL, Goiás, *in paludosis, prope Salinas*, 1844, *H.A. Weddell 2113* (holotype: K000222437 [Photo: P02913991]; isotype: P02914026).

Distribution—Brazil.

Ctenodon lewisianus (Afr.Fern.) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene lewisiana* Afr.Fern., O Táxon *Aeschynomene* no Brasil: 78. 1996. Type: BRAZIL, Bahia, Lençóis, Rio Mucugezinho, próximo a BR-242, próximo ao Morro do Pai Inácio, ca. 1000 m, Dec 1984, *G.P. Lewis et al. s.n.* (holotype: EAC0016790).

Distribution—Brazil.

Ctenodon lorentzianus (Bacigalupo & Vanni) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene lorentziana* Bacigalupo & Vanni, Hickenia 2(6): 33, f. 1. 1984. Type: ARGENTINA, Entre Rios, Depto. Federación, Cantera de Chaviyú, Nov 1976, *N.L. Troncoso et al. 1363* (holotype: SI001487; isotype: CTES0000458).

Distribution—Argentina.

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Ctenodon lyonnetii (Rudd) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene lyonnetii* Rudd, Acta Bot. Mex. 8: 31. 1989. Type: MEXICO, Guerrero, Iguala, Sep 1937, *E. Lyonnet 1717* (holotype: MEXU00278344; isotypes: CAS0000118, MEXU00278345, US00288959).

Distribution—Mexico.

Ctenodon marginatus (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene marginata* Benth., Fl. Bras. (Martius) 15(1): 66. 1859. Type: BRAZIL, Piauí, in sandy woods near Oeiras, Apr 1839, *G. Gardner 2098* (lectotype designated here: K000092312; isolectotypes: B[†] [F neg. 2149], BM000931741, F0058812F, GH00058458, GH00058459, L0018474, NY00005005, NY00005006, P02913972, P02913975, S-R-9501, W0067220). Other syntype: BRAZIL, Ceará, sandy hills Aracaty, Jul 1838, *G. Gardner 1543* (K000092313).

Distribution—Bolivia and Brazil.

Ctenodon marginatus var. *marginatus*

Ctenodon marginatus var. *grandiflorus* (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene marginata* var. *grandiflora* Benth., Fl. Bras. (Martius) 15(1): 67. 1859. Type: BRAZIL, Piauí, dry rocky hills near the city of Oeiras, May 1839, *G. Gardner 2099* (lectotype designated here: K000092315; isolectotypes: BM000931739, GH00058456, GH00058457, L0018475, NY00005004, NY00005022, P02913971, P02913973, P02913976, S-R-9500, W0067221, W18890044776).

Ctenodon martii (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene martii* Benth., Fl. Bras. (Martius) 15(1): 62, t. 13. 1859. Type: BRAZIL, Bahia, "in sylvis Catingas ad fluv. Salitre prope Joazeiro", Apr 1819, *C.F.P. von Martius* Observ. no. 2322 (lectotype designated here: M0233740). Other syntype: BRAZIL, Minas Gerais, "in campis et sepibus Serro Frio", Jul 1818, *C.F.P. von Martius s.n.* (M0233741). Other original material: BRAZIL, Bahia et Minas Gerais, s.d., *C.F.P. von Martius s.n.* (M0233742); idem, s.d., *C.F.P. von Martius s.n.* (M0233739).

= *Aeschynomene arbuscula* Rizzini, Leandra 4-5: 15, t. 13. 1974, *nom. illeg., hom. post.* (non Baker f. 1932) ≡ *Aeschynomene rizzinii* Schoenberg & Ferreira, Bol. Mus. Bot. Munic. 32: 1. 1977. Type: BRAZIL, Bahia, Campo Formoso, Fazenda Lagoa do Porco, Apr 1973, *D.P. Lima 13109* (holotype: RB00540113; isotypes: HUCPE [219], HUEFS [93748], IPA [75500], PEUFR [14597]).

Distribution—Brazil.

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Ctenodon matosii (Afr.Fern.) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene matosii* Afr.Fern., O Táxon *Aeschynomene* no Brasil: 97. 1996. Type: BRAZIL, Piauí, Sete Cidades, Piracuruca, Jul 1991, A. Fernandes & Matos s.n. (holotype: EAC0017998 – 2 sheets).

Distribution—Brazil.

Ctenodon molliculus (Kunth) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene mollicula* Kunth, Nov. Gen. Sp. [quarto ed.] 6: 532. 1823. Type: PERU, "inter Paramo de Yamoca et villam Colasey... (Provincia Jaen de Bracamoros)", Aug, A.J.A. Bonpland & F.W.H.A. von Humboldt s.n. [3586] (holotype: P00679170; isotypes: B-W 13729-01 0 [F neg. 2241], F0058813F, P02913965).

Distribution—Brazil, Colombia, Ecuador, and Peru.

Ctenodon molliculus* var. *molliculus

= *Aeschynomene pauciflora* Vogel, Linnaea 12: 93. 1838. Type: BRAZIL, Minas Gerais, Santo Antonio do Monte, Nov 1818, F. Sellow s.n. (holotype: B[†]).

Ctenodon molliculus* var. *breviflorus (Rudd) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene mollicula* var. *breviflora* Rudd, Contr. U.S. Natl. Herb. 32: 130. 1955. Type: COLOMBIA, Norte de Santander, between Chinácota and La Esmeralda, Mar 1927, E.P. Killip & A.C. Smith 20921 (holotype: US00001889; isotypes: GH00058460, NY00005021).

Ctenodon monteiroi (Afr.Fern. & P.Bezerra) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene monteiroi* Afr.Fern. & P.Bezerra, Bradea 2(50): 332. 1979. Type: BRAZIL, Ceará, Independência, encosta da Serra, Apr 1978, A. Fernandes & Matos s.n. (holotype: EAC0003772 – 2 sheets).

= *Aeschynomene monteiroi* var. *psilantha* G.P.Lewis, Kew Bull. 40(3): 603. 1985. Type: BRAZIL, Piauí, São Raimundo Nonato, Fundação Ruralista (Sede), 320 m, Jan 1982, G.P. Lewis & H.P.N. Pearson 1135 (holotype: CEPEC00029563; isotypes: K000092359, RB00540117).

Distribution—Brazil.

Ctenodon mucronulatus (Benth. ex Hemsl.) A.Delgado, **comb. nov.**

Basionym: *Drepanocarpus mucronulatus* Benth. ex Hemsl., Diagn. Pl. Nov. Mexic. 1: 8. 1878.

Type: MEXICO, Jalisco, Bolaños, Guadalajara [Guadalajara], s.d., T. Coulter s.n. (holotype: K000297144; isotype: TCD).

= *Brya amorphoides* S.Watson, Proc. Amer. Acad. Arts 22: 406. 1887 ≡ *Aeschynomene amorphoides* (S.Watson) Rose ex B.L.Rob., Proc. Amer. Acad. Arts 29: 315. 1894. Type: MEXICO, Jalisco, Tequila, in deep barranca, Aug-Sep 1886, E. Palmer 414 (holotype: GH00058424; isotypes: K000297147, NY00006284, US00001874, US00930891).

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- = *Hedysarum arborescens* Sessé & Moc., Fl. Mexic., ed. 2. 170. 1894. Type: MEXICO, Jalisco, "in *Prædio S. Tomæ, prope Hostotipaquillum*" [Santo Tomás near Hostotipaquillo], Jul, *M. de Sessé & J.M. Mociño* 2009 (lectotype designated by Nelson Sutherland 1997: MA601239; isolectotype: F). Other original material: *M. de Sessé & J.M. Mociño* 1938 (F, MA601240); *M. de Sessé & J.M. Mociño* 1948ter (F, MA601241); [icon] Torner Collection of Sessé and Mociño Biological Illustration No. 1890: drawing by Echeverría, 1790-1791, "Hedissarum arborescence" (Hunt Institute for Botanical Documentation: Art Accession Number: 6331.1890).
- = *Aeschynomene bracteolaris* L.Riley, Bull. Misc. Inform. Kew 1923(3): 115. 1923. Type: MEXICO, Sinaloa, San Ignacio, El Coacoyal, May 1921, *J. González Ortega* 586 (holotype: K000297145; isotype: K000297146).
- = *Aeschynomene guadalajarana* M.E.Jones, Contr. W. Bot. 18: 46. 1933. Type: MEXICO, Jalisco, La Barranca, Guadalajara, Nov 1930, *M.E. Jones* 27212 (Syntype: RSA0002730); idem, La Barranca, Nayarit, Feb 1927, *M.E. Jones* 23052 (Syntype: F, RSA0023934).

Distribution—Mexico.

Ctenodon nanus (Glaz. ex Rudd) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene nana* Glaz. ex Rudd, Phytologia 15: 118. 1967. Type: BRAZIL, Goiás, entre As Brancas et Hector près du Rio Roncador, Dec 1894, *A.F.M. Glaziou* 20921 (holotype fide Rudd 1967: P; lectotype designated here: P02914072; isolectotypes: BR0000005189861, C10011416, F n.v., G [F neg. 27930], IAN [23706], K000222442, MG, NY00005011, P02914067, P02914071, RB00158237, S-R-9502).

Distribution—Brazil.

Ctenodon nicaraguensis (Oerst.) A.Delgado, **comb. nov.**

Basionym: *Brya nicaraguensis* Oerst., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1853: 13. 1853. Type: NICARAGUA, "paa Vulkanen El Viejo ... og i Provindsen Segovia", Nov 1847, *A.S. Ørsted* 4701 (holotype: C10011419; isotypes: F0058966F, K000297138, S13-12057).

≡ *Aeschynomene nicaraguensis* (Oerst.) Standl., Trop. Woods 34: 41. 1933.

- = *Aeschynomene calderoniana* Standl., J. Washington Acad. Sci. 14: 93. 1924. Type: EL SALVADOR, Santa Ana, vicinity of Santa Ana, Jan 1930, *P.C. Standley* 20367 (holotype: US00001905; isotypes: GH00058426, NY00004979).

Distribution—El Salvador, Guatemala, Honduras, Mexico, and Nicaragua.

Ctenodon niveus (Brandege) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene nivea* Brandege, Proc. Calif. Acad. Sci., ser. 2, 2: 150. 1889. Type: MEXICO, Baja California Sur, La Purísima, Feb 1889, *T.S. Brandege* s.n. (holotype: UC80594; isotypes: GH00058431, NY n.v., PH00021835, US00001909).

Distribution—Mexico.

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Ctenodon oroboides (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene oroboides* Benth., Fl. Bras. (Martius) 15(1): 64. 1859. Type: BRAZIL, Mato Grosso do Sul, *in campis siccis secus Rio Pardo*, Sep 1826, L. Riedel 502 (lectotype designated here: K000222436; isolectotypes: B[†] [F neg. 2151], F0058815F, LE, P02914077). Other syntypes: BRAZIL, loco haud indicato, s.d., J. Schücht s.n. [45] (K000222434, W0027269). BRAZIL, Goiás, “Sertao d’Amaroleité” [Sertão de Amaro Leite], Sep 1844, H.A. Weddell 2771 (K000920313, P02914076).

= *Ctenodon weddellianus* Baill., Adansonia 9: 237. 1870, as “*Weddellianum*”. Type: BRAZIL, Goiás, “Sertao d’Amaroleité” [Sertão de Amaro Leite], Sep 1844, H.A. Weddell 2771 (lectotype designated here: P02914076; isolectotype: K000920313). Other syntype: BRAZIL, Mato Grosso, s.d., *Herbier Impérial du Brésil* no. 214 (P02914079, P02914080).

Distribution—Bolivia and Brazil.

Ctenodon palmeri (Rose) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene palmeri* Rose, Contr. U.S. Natl. Herb. 5: 192. 1899. Type: MEXICO, Guerrero, near Acapulco, 1894-1895, E. Palmer 106a (holotype: US00001913; isotypes: GH n.v., K000297141).

Distribution—Mexico.

Ctenodon paniculatus (Willd. ex Vogel) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene paniculata* Willd. ex Vogel, Linnaea 12(1): 95. 1838. Type: BRAZIL, loco haud indicato, s.d., F.W. Sieber s.n. [J. C. von Hoffmannsegg] (lectotype designated here: B-W 13740-00 0, B-W 13740-01 0 [F neg. 2242]); possible isolectotype: P02914020). Other syntypes: BRAZIL, Bahia, F. Sellow s.n. (B[†] [F0058816F – F fragm.]). BRAZIL, Bahia, Cruz de Casma, Jul 1835, B. Luschnath 223 (B[†], LE, W18890119766). BRAZIL, loco haud indicato, A.I. Gomes s.n. (B[†]).

= *Aeschynomene hedysaroides* M.Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(2): 181. 1843. Type: MEXICO, Oaxaca, “Cordillera”, savannes de Zacatepeque, Sep 1840, H.G. Galeotti 3184 (holotype: BR0000005119554; isotypes: G [F neg. 27928], P02912794).

= *Aeschynomene laevis* M.Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(2): 181. 1843, *nom. illeg., hom. post.* (non Noronha 1790). Type: MEXICO, Veracruz, les savanes de Zacuapan, Oct 1840, H.G. Galeotti 3261 (holotype: BR0000005119882; isotype: P02913984).

= *Aeschynomene gracilis* Miq., Linnaea 18: 566. 1844, *nom. illeg., hom. post.* (non Vogel 1838). Type: SURINAME, in savana arenosa ad plant. Berlyn, Sep 1844, H.C. Focke 966 (holotype: U0003457; isotypes: BR0000013054298, GH00058452).

Distribution—Widespread in tropical America.

Ctenodon paucifolius (Vogel) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene paucifolia* Vogel, Linnaea 12(1): 94. 1838. Type: BRAZIL, Minas Gerais, Santo Antonio do Monte, Nov 1818, F. Sellow s.n. (holotype: B[†]; probable isotype:

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K000222440). Possible original material: BRAZIL, Minas Gerais, Serra do Galheiro, Oct 1818, *F. Sellow 1004* (B⁺ [F neg. 2152]).

Distribution—Brazil.

Ctenodon paucifoliolatus (Micheli) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene paucifoliolata* Micheli, Mém. Soc. Phys. Genève 34: 256, t. 9. 1903. Type: MEXICO, Guerrero, El Calabazal, 200 m, Oct 1898, *E. Langlassé 474* (holotype: G; isotypes: GH00058435, K000297143, MEXU00051044, MPU022827, P02912304, P02912305, US00001912).

Distribution—Mexico.

Ctenodon petraeus (B.L.Rob.) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene petraea* B.L.Rob., Proc. Amer. Acad. Arts 27: 166. 1893. Type: MEXICO, Jalisco, rocky hills near Guadalajara, May 1891, *C.G. Pringle 5147* (holotype: GH00058436; isotypes: K000297136, MEXU01169216, US00001911, UVMVT024910).

Distribution—Mexico.

Ctenodon petraeus var. *petraeus*

Ctenodon petraeus var. *grandiflorus* (Rudd) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene petraea* var. *grandiflora* Rudd, Contr. U.S. Natl. Herb. 32: 122. 1955. Type: MEXICO, Durango, near Chacala, Feb 1899, *E.A. Goldman 329* (holotype: US00001910; isotype: NY00004986).

= *Aeschynomene glomerata* M.E.Jones, Contr. W. Bot. 15: 139. 1929. Type: MEXICO, Nayarit, Acaponeta, at El Tigre mine, Mar 1927, *M.E. Jones [23057] 23025* (holotype: RSA0002731; isotypes: F0058797F, GH n.v., NY00004982).

Ctenodon petraeus var. *madrensis* (Micheli) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene petraea* var. *madrensis* (Micheli) Rudd, Contr. U.S. Natl. Herb. 32: 121. 1955 ≡ *Aeschynomene madrensis* Micheli, Mém. Soc. Phys. Genève 34: 255, t. 8. 1903. Type: MEXICO, Guerrero, "Sierra Madre, versant oriental", [vicinity of Río Coyuquilla], 1500 m, Feb 1899, *E. Langlassé 865* (holotype: G; isotypes: GH00058430, K000297134, P02913980, P02913981, US00001891).

= *Aeschynomene pringlei* Rose, Contr. U.S. Natl. Herb. 8: 312. 1905. Type: MEXICO, Morelos, limestone hills near Jojutla, Aug-Oct 1902, *C.G. Pringle 8709* (lectotype designated here: US00001923; isolectotypes: ARIZ-BOT-0004085, BM000931565, C10011422, CAS0000119, CM0945, DAO000424204, E00394280, ENCB003331, V0058801F, GH00058439, GOET004619, HBG520669, K000297135, L0018468, L0018469, L0018470, LL00371217, M0233747, MEXU01169217, MEXU01169218, MICH1107080, MIN1000048, MO-128346, MSC0129843,

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NY00004978, P02912480, P02912502, P02912503, P02912504, PH00000047, RSA0002727, S-G-8844, UC80589, US01107508, UVMVT024911, UVMVT053376).

Ctenodon pinetorus (Brandege) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene pinetorum* Brandege, Univ. Calif. Publ. Bot. 10: 408. 1924. Type: MEXICO, Chiapas, in pine forests near Hacienda Monserrate, Sep 1923, C.A. Purpus 9064 (holotype: UC220371; isotypes: F0058800F, GH00058438, MO-128349, NY00004988, US00001920).

= *Aeschynomene chiapensis* Brandege, Univ. Calif. Publ. Bot. 10: 407. 1924. Type: MEXICO, Chiapas, near Hacienda Monserrate, Sep 1923, C.A. Purpus 9147 (holotype: UC220376; isotypes: F0058794F, GH00058425, MEXU00053652, MO-128348, NY00004980, US01108256).

Distribution—Mexico.

Ctenodon pleuronervius (DC.) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene pleuronervia* DC., Prodr. [A. P. de Candolle] 2: 321. 1825. *Smithia domingensis* Balb. ex DC., Prodr. [A. P. de Candolle] 2: 321. 1825, nomen. Type: DOMINICAN REPUBLIC, Santo Domingo, s.d., C.L.G. Bertero s.n. (holotype: G-DC [F neg. 33436]; isotypes: MO-022343, MO-022344, P02912467).

= *Aeschynomene aurea* Leonard, J. Washington Acad. Sci. 17: 67. 1927. Type: HAITI, Artibonite, vicinity of Ennery, Puilboreau road, 800 m, Jan 1926, E.C. Leonard 8818 (holotype: US00001866; isotype: GH00058444).

Distribution—Haiti and Dominican Republic.

Ctenodon podocarpus (Vogel) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene podocarpa* Vogel, Linnaea 12(1): 89. 1838 ≡ *Aeschynomene falcata* var. *plurijuga* Benth., Fl. Bras. (Martius) 15(1): 68. 1859, p.p. Type: BRAZIL, "Brasil. merid.", loco haud indicato, s.d., F. Sellow s.n. (holotype: B†).

Distribution—Brazil.

Ctenodon priscoanus (Afr.Fern.) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene priscoana* Afr.Fern., O Táxon *Aeschynomene* no Brasil: 86. 1996. Type: BRAZIL, Piauí, Ribeiro Gonçalves, Estação Ecológica de Uruçuí-Una, Apr 1981, A. Fernandes s.n. (holotype: EAC0010005).

Distribution—Brazil.

Ctenodon purpusii (Brandege) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene purpusii* Brandege, Zoë 5(11): 247. 1908. Type: MEXICO, Veracruz, Zacuapán, 1906, C.A. Purpus 1904 (holotype: UC83413; isotypes: F0058802F, GH00058440, MO-128350, NY00004989, P02912496, UC84877, US00001924, US00001925).

Distribution—Mexico.

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Ctenodon racemosus (Vogel) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene racemosa* Vogel, *Linnaea* 12(1): 92. 1838. Type: BRAZIL, Minas Gerais, Santo Antonio do Monte, Nov 1818, *F. Sellow s.n.* (holotype: B[†]).

Distribution—Bolivia and Brazil.

Ctenodon riedelianus (Taub.) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene riedeliana* Taub., *Flora* 72: 424. 1889. Type: BRAZIL, Minas Gerais, in glareosis pr. Diamantina, Dec 1824, *L. Riedel* 1223 (holotype: LE n.v.; isotypes: B[†] [F neg. 2154], K000222448, P02913159).

Distribution—Brazil.

Ctenodon rosei (C.V.Morton) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene rosei* C.V.Morton, *Contr. U.S. Natl. Herb.* 29: 84. 1944 ≡ *Aeschynomene fruticosa* Rose, *Contr. U.S. Natl. Herb.* 5(4): 192. 1899, *nom. illeg., hom. post.* (non Sessé & Moc. 1889). Type: MEXICO, Sinaloa, on stony hills near Topolobampo, Sep 1897, *E. Palmer* 204 (holotype: US00001896; isotypes: ARIZ-BOT-0004084, CAS0000117, FI010920, MICH1107081, P02297639, RSA0002732, S-G-8843, UC770356).

Distribution—Mexico.

Ctenodon sabulicolus (L.P.Queiroz & D.B.O.S.Cardoso) D.B.O.S.Cardoso, **comb. nov.**

Basionym: *Aeschynomene sabulicola* L.P.Queiroz & D.B.O.S.Cardoso, *Bot. J. Linn. Soc.* 157(4): 750. 2008. Type: BRAZIL, Bahia, Casa Nova, Fazenda Santarém, 9°31'47"S, 41°21'34"W, Oct 2004, *L.P. Queiroz et al.* 9640 (holotype: HUEFS0089017; isotypes: K, MBM336389, MO-2196354, NY00990979, SPF00181181).

Distribution—Brazil.

Ctenodon scoparius (Kunth) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene scoparia* Kunth, *Nov. Gen. Sp.* [quarto ed.] 6: 531. 1823. Type: PERU, Piura, "prope Guancabambam Peruvionorum" [Huancabamba], Aug, *A.J.A. Bonpland & F.W.H.A. von Humboldt s.n.* [3543] (holotype: P00679169; isotypes: B-W 13741-01 0) [F neg. 2243], F n.v., P02912477).

Distribution—Ecuador, Peru, and Suriname.

Ctenodon simplicifolius (G.P.Lewis) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene simplicifolia* G.P.Lewis, *Kew Bull.* 47(1): 141. 1992. Type: BRAZIL, Goiás, Chapada dos Veadeiros, about 22 km of Alto Paraíso, 1200 m, Aug 1971, *D.R. Gifford & S.G. da Fonseca* G241 (holotype: E00296478; isotype: UB [43048]).

Distribution—Brazil.

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Ctenodon simulans (Rose) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene simulans* Rose, Contr. U.S. Natl. Herb. 5: 192. 1899. Type: MEXICO, Sinaloa, between Rosario and Colomas, Jul 1897, *J.N. Rose 1616* (lectotype designated by Rudd 1955: US00001929; isolectotypes: GH00058441, K000297137). Other syntype: MEXICO, Tepic, Nayarit, Acaponeta, Jun 1897, *J.N. Rose 1487* (US01108255).

Distribution—Mexico.

Ctenodon soniae (G.P.Lewis) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene soniae* G.P.Lewis, Kew Bull. 49(1): 93. 1994. Type: BRAZIL, Bahia, 27 km S of Livramento do Brumado on road to Brumado near two hamlets of Fazendinha and Itapicuru, Apr 1991, *G.P. Lewis & S.M.M. de Andrade 2006* (holotype: CEPEC00050387; isotypes: BR0000005119943, E00296477, G00364571, HBG520662, HBG520663, HUEFS [99848, 99849], K000092403, K000092404, M0233754, MBM221652, MEXU00607347, MO-022339, NY00022635, SIO01488, SPF00092629, SFV, TEX00371218, US00432869).

Distribution—Brazil.

Ctenodon sousae (Rudd ex A.Delgado & Sotuyo) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene sousae* Rudd ex A.Delgado & Sotuyo, Revista Mex. Biodivers. 83(2): 330. 2012. Type: MEXICO, Oaxaca, Tehuantepec District, municipio Santo Domingo Tehuantepec, a 15 km sobre la desviación Buenos Aires a San Miguel Tenango, 16°18'48.2"N, 95°30'10.7"W, 700 m, Oct 2010, *A. Delgado-Salinas & S. Sotuyo 2732* (holotype: MEXU; isotypes: GH, K, MO, NY, TEX, US).

Distribution—Mexico.

Ctenodon standleyi (Ant.Molina) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene standleyi* Ant.Molina, Ceiba 3(2): 92. 1952. Type: HONDURAS, Department of Morazán, drainage of the Rio Yeguaré, 900 m, Nov. 1948, *A. Molina Rosito 1708a* (holotype: US00001930; isotype: F n.v.).

Distribution—Honduras, Nicaragua, Costa Rica, and Mexico.

Ctenodon tenuis (Griseb.) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene tenuis* Griseb., Cat. Pl. Cub. [Grisebach]: 72. 1866. Type: CUBA, Vueldabajo, Jul [1860-1864], *C. Wright 2306* (isotypes: BM000931559, GH00058447, K000222412, MO-022347, NY00004993, P02913163, S13-12035, S-R-9506, US00001931, YU001421).

Distribution—Cuba.

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Ctenodon tumbezensis (J.F.Macbr.) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene tumbezensis* J.F.Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 101. 1930. Type: PERU, Tumbes, Mountains east of Hacienda Chicama, 400-500 m, Feb 1927, A. Weberbauer 7669 (holotype: F0043417F; isotypes: GH00058465, NY00005015, US00001955).

Distribution—Ecuador and Peru.

Ctenodon veadeiranus (M.J.Silva, & L.L.C.Antunes) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene veadeirana* M.J.Silva, & L.L.C.Antunes, Phytotaxa 184(1): 32. 2014. Type: BRAZIL, Goiás, Teresina de Goiás, 13°54'39.5"S, 47°22'48"W, 1278 m, Jul 2014, M.J. Silva et al. 6127 (holotype: UFG; isotypes: CEN00100963, RB01340731, SP003689, UB0040052).

Distribution—Brazil.

Ctenodon venezolanus (Rudd) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene brasiliiana* var. *venezolana* Rudd, Contr. U.S. Natl. Herb. 32: 80. 1955. Type: VENEZUELA, Miranda, La Cortada, road to Guatire, near Petare, Nov 1923, H. Pittier 11233a (holotype: VEN3775; isotype: US00001906).

≡ *Aeschynomene venezolana* (Rudd) G.B.Rodr. & G.Agostini, Acta Bot. Venez. 16(1): 123. 1991.

Distribution—Venezuela.

Ctenodon vigil (Brandege) A.Delgado, **comb. nov.**

Basionym: *Aeschynomene vigil* Brandege, Proc. Calif. Acad. Sci. ser. 2, 3: 128. 1891. Type: MEXICO, Baja California Sur, San José del Cabo, Oct 1891, T.S. Brandege 142 (holotype: UC80586; isotypes: GH00058443, PH00000049).

Distribution—Mexico.

Ctenodon viscidulus (Michx.) D.B.O.S.Cardoso & A.Delgado, **comb. nov.**

Basionym: *Aeschynomene viscidula* Michx., Fl. Bor.-Amer. (Michaux) 2: 74. 1803. Type: UNITED STATES OF AMERICA, "in arenosis insulæ Cumberland et Floridæ", A. Michaux s.n. (holotype: P-MICH ?). Possible original material: "Amériq.[ue] Sept.[entrionale]", s.d., A. Michaux s.n. (P02913175).

≡ *Aeschynomene prostrata* Poir., Encyc. [J. Lamarck & al.] Suppl. 4: 76. 1816.

≡ *Secula viscidula* (Michx.) Small, Fl. Miami: 90. 1913.

= *Aeschynomene eriocarpa* Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 9. 1943. Type: GUATEMALA, Zacapa, rocky hills in vicinity of Santa Rosalia, Oct 1939, J.A. Steyerl. 29313 (holotype: F0058796F).

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= *Aeschynomene gilbertoi* Brandão, Daphne 1(2): 5. 1991. Type: BRAZIL, Minas Gerais, Mocambinho, Nov 1989, *J.F. Macedo* 567 (holotype: RB; isotype: PAMG).

Distribution—USA, Mexico, Central America, Bolivia, Brazil, and Venezuela.

Ctenodon vogelii (Rudd) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene vogelii* Rudd, J. Wash. Acad. Sci. 49: 48. 1959. Type: BRAZIL, Minas Gerais, Serra do Itambé, Oct 1818, *F. Sellow s.n. (1382)* (lectotype designated by Rudd 1959: K000222432; isolectotypes: BM000931742, V0058817F, NY00005009).

≡ *Aeschynomene falcata* (Poir.) DC. var. *multijuga* Benth., Fl. Bras. 15(1): 68. 1859.

Distribution—Brazil.

Ctenodon warmingii (Micheli) D.B.O.S.Cardoso, Filardi & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene warmingii* Micheli, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn: 68. 1875. Type: BRAZIL, Minas Gerais, Lagoa Santa, Dec 1865, *J.E.B. Warming* [3015/2] (lectotype designated here: C10011424; isolectotypes: B [F neg. 2155], C10011423, F, P02913199).

Distribution—Brazil.

Ctenodon weberbaueri (Ulbr.) D.B.O.S.Cardoso & H.C.Lima, **comb. nov.**

Basionym: *Aeschynomene weberbaueri* Ulbr., Bot. Jahrb. Syst. 37(5): 554. 1906. Type: PERU, Amazonas, Chachapoyas, "*supra Balsas, in declivibus vallis Marañon fluminis loco stepposo 2000-2100 m s. m.*", Jun 1904, *A. Weberbauer* 4274 (holotype: B[†] [F neg. 2156]; isotypes: V0043416F, USM n.v.).

Distribution—Ecuador and Peru.

5 | ACKNOWLEDGEMENTS

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