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A NEW SPECIES OF THE PAPILIONOID LEGUME GENUS *AESCHYNOMENE* FROM THE *CANGA* OF SERRA DOS CARAJÁS, PARÁ, BRAZIL

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We describe a new species of the papilionoid legume genus *Aeschynomene* (Leguminosae, Papilionoideae) that is tightly ecologically associated with Amazonian *campos rupestres* on iron-rich *canga* soils of the Serra dos Carajás mountain range, Pará, Brazil. The new species is morphologically similar to *Aeschynomene rudis*, but it differs by the smaller leaflets, larger flower, glabrous ovary, and a longer and sigmoid fruit stipe. We present a complete description, taxonomic comments, illustrations, and a distribution map for the new species. Additionally, we provide its phylogenetic position and an identification key to all *Aeschynomene* and *Ctenodon* species occurring on the *canga* of the Serra dos Carajás.

Keywords. Amazonia, Fabaceae, Leguminosae, rock fields, taxonomy
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Introduction

The papilionoid legume genus *Aeschynomene* L. comprises c.180 species and has a global distribution (Klitgaard & Lavin, 2005). However, molecular phylogenies over the past two decades (Lavin *et al.*, 2001; Ribeiro *et al.*, 2007; Chaintreuil *et al.*, 2013; Brottier *et al.*, 2018) demonstrated that *Aeschynomene* was not monophyletic, and it was recently divided into two distinct genera, *Aeschynomene* s. str. and the resurrected *Ctenodon* Baill.

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(Cardoso *et al.*, 2020). The genus *Ctenodon*, which was traditionally recognised as a section of *Aeschynomene* (*Aeschynomene* sect. *Ochopodium*; Rudd, 1955), was shown to be phylogenetically closer to the genera *Dalbergia* L.f. and *Machaerium* Pers. (Cardoso *et al.*, 2020). *Ctenodon* is morphologically recognised by the combination of basifixed stipules, loment articles separated by an isthmus, and campanulate calyx, in contrast to the peltate or modified stipules, lomentaceous fruits with articles separated by septa, and the bilabiate calyx of *Aeschynomene* s. str. (Rudd, 1955; Cardoso *et al.*, 2020).

Despite the clear delimitation between the two genera, supported by molecular, morphological and ecological features, *Aeschynomene* s. str. remained paraphyletic with *Bryaspis* P.A.Duvign., *Cyclocarpa* Afzel. ex Urb., *Geissaspis* Wight & Arn., *Humularia* P.A.Duvign., *Kotschya* Endl., *Smithia* Aiton and *Soemmeringia* Mart. nested in it (**Figure 1**; Cardoso *et al.*, 2020). These genera share a predominantly hydrophytic habit, generally growing in swamps, temporary or permanent ponds, and along streams and riverbanks (Rudd, 1955; Antunes & Silva, 2017; Chaintreuil *et al.*, 2013; Cardoso *et al.*, 2020). However further studies are needed to clarify the true number of *Aeschynomene* species, their distribution, and ecological predilections (Cardoso *et al.*, 2020). Currently, Brazil is home to an estimated 20 species of *Aeschynomene* s. str., four of which are endemic. It is distributed across all major biomes (Amazon, Atlantic Forest, Caatinga, Cerrado, Pampas, and Pantanal) and ranges from herbs and subshrubs to shrubs and trees up to 5 m tall (Mattos *et al.*, 2025).

In the Serra dos Carajás mountain range (200–700 m elevation) in northeastern Brazilian Amazonia, the landscape is dominated by forest interspersed with savanna-like patches growing on iron-rich substrates known as *canga* or ironstone formations (Porto & Silva, 1989; Giulietti *et al.*, 2019). This open, fire-adapted vegetation, often referred to as *campos rupestres*, occurs on old, climatically buffered, infertile landscapes (OCBILs) (Giulietti *et al.*, 2019; Silveira *et al.*, 2020). The unique iron deposits of *canga* give rise to numerous endemic species specially adapted to these ecologically singular, iron-rich soil environments. This is exemplified by the many recently described new species for the region in different angiosperm families (e.g. Gonçalves & Arruda, 2014; Araujo & Chautems, 2015; Salas *et al.*, 2015; Pereira *et al.*, 2016; Nunes *et al.*, 2017; Costa-Lima & Loiola, 2018; Monteiro, 2018; Moura *et al.*, 2018). This region is known as one of the world's largest mineral provinces with extensive lateritic cover; it is the source of copper-gold, iron, manganese, nickel and nickel sulphide deposits (Freitas, 1986; Santos, 1986; Viana *et al.*, 2016). As Brazil is one of the largest exporters and users of mined iron, the flora associated with iron deposits is severely threatened and its conservation is challenging (Giulietti *et al.*, 2019).

A small part of the iron deposits of Serra dos Carajás is today protected under the area of the National Forest of Carajás (FLONA Carajás) and Parque Nacional dos Campos Ferruginosos (PARNA Campos Ferruginosos), which together cover the main plateaus of the Serra dos Carajás: Serras Norte and Sul, Serra do Tarzan and Serra da Bocaina (Viana

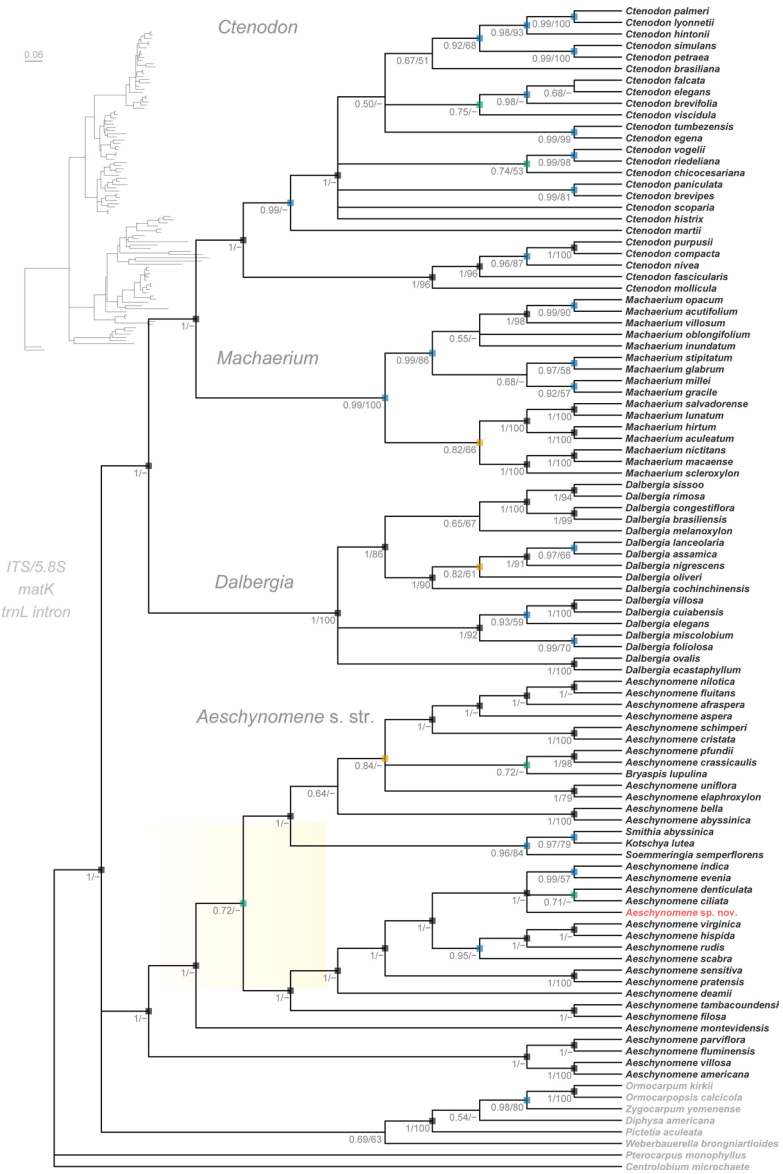

Figure 1. Majority-rule consensus tree of *Aeschynomene* s.l., *Ctenodon* and related genera, derived from the combined Bayesian analysis of the nuclear (ITS/5.8S) and plastid (*matK* and *trnL intron*) DNA sequence data, showing the phylogenetic placement of the *Aeschynomene* sp nov. (highlighted in red) in the *Aeschynomene* s. str. clade (highlighted in yellow). Branch lengths are shown in the associated phylogram. Bayesian posterior probabilities (PPs) and maximum-likelihood bootstrap support (BS) values are reported below branches. Black nodes are supported by PP = 1, blue nodes by PP = 0.9–0.99, orange nodes by PP = 0.8–0.89, and cyan nodes by PP = 0.7–0.79. PP values < 0.5 and BS values < 50% are represented by a dash (–).

et al., 2016; Mota *et al.*, 2018). Both protected areas are located in southwestern Pará state, in the municipalities Canaã de Carajás and Parauapebas, a region characterised by its rugged terrain, the isolated ferruginous rocky plateau, and the mineral resource richness (Viana *et al.*, 2016). To fully conserve the ferruginous areas of Serra do Tarzan and Serra da Bocaina from mining activities, the PARNA Campos Ferruginosos was created in 2017 (Zappi, 2017; Mota *et al.*, 2018; ICMBio, 2023, 2024; Unidades de Conservação no Brasil, 2025). The PARNA Campos Ferruginosos expanded the protection area as far as Serra da Bocaina in the municipality of Canaã dos Carajás and included the Serra do Tarzan, an area which previously belonged to the FLONA Carajás in the municipality of Parauapebas (ICMBio, 2003, 2023, 2024).

The climate of the FLONA Carajás (5°52'S to 6°33'S and 49°53'W to 50°45'W) and PARNA Campos Ferruginosos (6°9'22"S to 6°23'40"S and 50°22'34"W to 49°47'58"W) (**Figure 2A**) is classified as Aw based on the Köppen system (1948); Aw means a humid tropical climate, with a dry season from June to September and a rainy season from November to April, and an average annual rainfall of 1900–2400 mm (Ab'Saber, 1986; ICMBio, 2003, 2023, 2024; Unidades de Conservação no Brasil, 2025). The average temperature varies from 23°C to 26°C (ICMBio, 2003, 2023). These protected areas belong to the Dissected Plateau of Southern Pará, where strata of pre-Cambrian rocks rich in iron are prominent (ICMBio, 2003, 2023, 2024). According to the classification of Veloso (Brasil, 1974), the region has two distinct phytophysiognomies: a predominant dense rain-forest vegetation and a shrubby sclerophyll ecosystem, i.e. the *canga* vegetation, with an extension of approximately 9,031.55 ha. The relief is characterised by a series of discontinuous mountain ranges with a maximum altitude of 897 m (ICMBio, 2023, 2024).

The FLONA Carajás has an area of 411,948.87 ha and encompasses the Serra Norte (subdivided into nuclei N1–N8), located in the municipality of Parauapebas, and the Serra Sul (subdivided into nuclei S11-A–S11-D), in the municipality of Canaã dos Carajás. The PARNA Campos Ferruginosos covers 79,029 ha, of which 60,317 ha overlap with the FLONA Carajás. It encompasses the Serra do Tarzan, in the municipality of Canaã dos Carajás, and Serra da Bocaina, located in Parauapebas, where their combined plateau is dominated by *canga* vegetation (ICMBio, 2023, 2024).

During taxonomic studies of Leguminosae from FLONA Carajás, 74 taxa were recognised (Mattos *et al.*, 2018), including four species with bilabiate calyces that could clearly be ascribed to *Aeschynomene* s. str. However, one of these species remained without a reliable, complete identification. After additional phylogenetic and morphological analyses, it has been confirmed that this represents an undescribed species. Thus, a full morphological description of this new *Aeschynomene* species, including illustrations and a distribution map, is provided. Additionally, its phylogenetic position is shown, and a comparative identification key for all species of *Aeschynomene* and *Ctenodon* occurring in the Serra dos Carajás is presented.

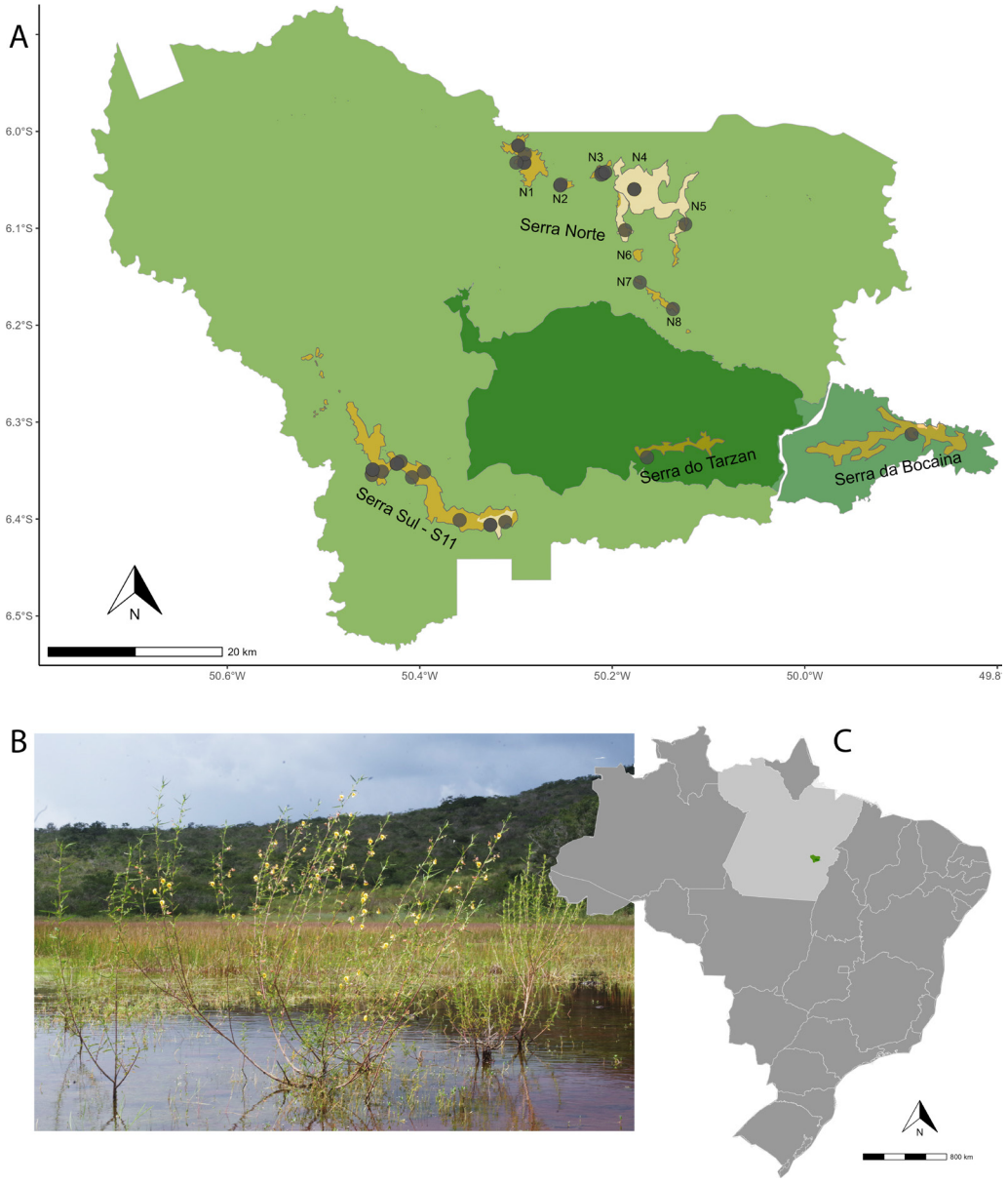

Figure 2. A, Map showing the distribution of *Aeschynomene* sp.nov. (grey circles) in Serra dos Carajás; FLONA Carajás is shown in an intermediate green, and PARNA Campos Ferruginosos in dark green. Areas of *canga* vegetation are shown in yellow-orange, with a lighter shade indicating areas degraded by mining activities. Nuclei of *canga* vegetation are labelled: Serra Norte, N1–N8; Serra Sul, S11; Serra da Bocaina; and Serra do Tarzan. **B**, Flooded area in *canga* vegetation, where the new species was found. **C**, Map of Brazil, with Pará state in light grey and the FLONA Carajás and PARNA Campos Ferruginosos in green. Photograph: Pedro Lage Viana.

Material and methods

Collections in the *canga* were made during 2008 and 2015 and covered different seasonal periods. The collecting method in the field followed Filgueiras *et al.* (1994), and collection was carried out in partnership with the Vale S.A. mining company. Silica gel samples were collected for molecular studies; root nodules were also collected, when present. All collected specimens were georeferenced. The voucher material was deposited in the RB herbarium, with duplicates sent to the BHCB, HCJS and MG herbaria (herbarium codes follow Index Herbariorum, updated continuously). The collections made were compared with 1328 herbarium specimen records of Leguminosae from the FLONA Carajás and PARNA Campos Ferruginosos (see Mattos *et al.*, 2018, to access the complete list) available in herbaria with the most representative collections from the Serra dos Carajás (BHCB, HCJS, IAN, MG and RB).

Vegetative and reproductive organs were measured using a millimetre-graduated calliper, and both maximum and minimum values were recorded. Measurements were taken at the widest part of the structures, and for flowers and fruits from the base of the calyx or the point of insertion on the pedicel to the apex of the organ. The calyx tube was measured from its base to the base of the calyx teeth. The measurements were taken with the aid of a stereomicroscope (Zeiss Stemi SV-6; Zeiss, Oberkochen, Germany) at different magnifications. For the terminology used to describe morphological characters, Harris & Harris (1994), Radford *et al.* (1974) and Hickey & King (2000) were followed. Fruit and inflorescence terminology follows Barroso *et al.* (1999) and Queiroz (2009), respectively. The terminology used to recognise open vegetation formations follows Secco & Mesquita (1983).

The occurrence points of the new species were mapped using the polygon data designed by Dr Pedro Lage Viana (Instituto Nacional da Mata Atlântica – INMA) and ICMBio (https://www.gov.br/icmbio) and the R packages *ggplot2* (Wickham *et al.*, 2025) and *raster* (Hijmans *et al.*, 2025). *Canga* areas degraded due to mining activity were identified using images from Google Earth (accessed 31 December 2020) and Mota *et al.* (2018). However, more data are needed to enhance the accuracy of the areas already degraded in Serra dos Carajás.

The provisional extinction risk assessment followed the protocols of the Centro Nacional de Conservação de Plantas (CNCFlora) of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (JBRJ), which is the IUCN SSC Brazil Plant Red List Authority (IUCN SSC BP-RLA). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were estimated using the automated system of CNCFlora, which is integrated with the Flora e Funga do Brasil database (v.393.412), in accordance with the standards of the GeoCAT geospatial tool (Bachman *et al.*, 2011) and adopting the standard 2 km^2 grid cell size for AOO, as recommended by the IUCN. A formal conservation assessment will be published by the CNCFlora.

To place the new *Aeschynomene* species in the Dalbergioid phylogeny, we generated new nuclear ribosomal ITS/5.8S and plastid *trnL intron* DNA sequences (GenBank Nucleotide Database accessions PZ058464 and PZ053428, respectively). The analysis included comprehensive sampling across Dalbergioid lineages (Cardoso *et al.*, 2020), most of which were generated as part of previously published molecular phylogenies of papilionoid legumes (e.g. Cardoso *et al.*, 2012, 2015) that are publicly available in GenBank (http://www.ncbi.nlm.nih.gov/genbank/).

DNA isolation and amplification were carried out following the methods used in previous molecular phylogenetic studies (Cardoso *et al.*, 2012). Sequencing reactions were performed in both directions using the BigDye Terminator kit v.3.1 (Applied Biosystems/Life Technologies Corporation, Carlsbad, California, USA). The sequencing products were analysed on an Applied Biosystems ABI 3500 sequencer, following the manufacturer's protocol, at the sequencing facility of Universidade Federal do Amazonas (UFAM). The forward and reverse sequences were assembled with Sequencher 4.7 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Consensus sequences were aligned with muscle algorithm in SeaView v.4 (Gouy *et al.*, 2010). To avoid inconsistencies derived from automated multiple alignment, the sequences were then manually edited with SeaView v.4 (Gouy *et al.*, 2010). Gaps were inserted by comparing amino acid translation in sequences of the protein-coding *matK* gene (Wojciechowski *et al.*, 2004).

To identify any case of incongruence between partitions, the individual topologies were analysed. A best-fit nucleotide substitution model was selected via the Akaike information criterion in *jmodeltest2* (Darriba *et al.*, 2012). The chosen models were SYM+I+gamma for ITS/5.8S and GTR+G for *matK* and *trnL intron*. To estimate the phylogenetic position of the new species, we performed maximum likelihood and Bayesian inference via the CIPRES Science Gateway v.3.3 online portal (https://www.phylo.org) (Miller *et al.*, 2010). Maximum-likelihood reconstruction was done in RAxML v.8 (Stamatakis, 2014), with the nucleotide substitution model GTR+GAMMA, using the gamma distribution and invariant sites estimated during running. Support values of the nodes were estimated with 1000 bootstrap replicates, for which values ≥ 0.95 were considered strong (Stamatakis *et al.*, 2008). Bayesian inference was run in the MrBayes v.3.2.1 (Ronquist *et al.*, 2012) in two separate runs of a Metropolis-coupled Markov Chain Monte Carlo permutation of parameters.

Eight simultaneous chains were initiated with a random tree for 10 million generations through the phylogenetic tree space, sampling one tree at each 10,000 generation. Non-correlated samples at the stationary phase were summarised in a Bayesian majority-rule consensus tree at 50% after a burn-in of 25%, which was determined according to the average standard deviation of split frequency values. Visualisation and partial editing of the Bayesian tree were done in FigTree v.1.4.4 (Rambaut, 2018). To plot the phylogenetic tree figures, we used the R packages *phytools* (Revell, 2025), *ggtree* (Yu *et al.*, 2025a), *treeio* (Yu *et al.*, 2025b) and *catGgenes* (https://github.com/DBOSlab/catGenes).

Results

Phylogenetic analyses corroborated the previous molecular studies on *Aeschynomene* s.l., in which the species were divided into two genera, *Aeschynomene* s. str. and *Ctenodon* (Cardoso *et al.*, 2020). The *Aeschynomene* s.l. phylogeny still needs improved resolution in the context of the paraphyletic *Aeschynomene* s. str. with respect to the genera *Bryaspis*, *Kotschya*, *Smithia* and *Soemmeringia*, and its interspecific phylogenetic relationships. Regardless, the placement of the new species is strongly supported in the Bayesian analysis (PP = 1) as part of the *Aeschynomene* s. str. and grouped with the species *A. ciliata* Vogel, *A. denticulata* Rudd, *A. evenia* C.Wright and *A. indica* Burm.f. (**Figure 1**). The new species, although phylogenetically placed with these species, is morphologically most similar to *A. rudis*, *A. sensitiva*, *A. montevidensis* and *A. scabra*, which it is diagnosed against. The placement of the new species within *Aeschynomene* is ecologically supported by its hydrophytic preference and its morphological concurrence, specifically its bilabiate calyx and lomentaceous fruits with articles separated by septa.

Taxonomic treatment

Species description

Aeschynomene delmoana C.M.J.Mattos, S.M.deFaria & H.C.Lima, **sp. nov.**

The new species is morphologically most similar to *Aeschynomene rudis* Benth., *A. sensitiva* Sw., *A. montevidensis* Vogel and *A. scabra* G.Don that share leaflets with central midvein and bilabiate calyx with carinal lip denticulate. However, *Aeschynomene delmoana* differs from *A. rudis* by leaflets 1–8 × 1–2 mm (vs 8–10 × 2–3 mm), a glabrous ovary (vs sericeous), a stipe sigmoid, 1–2.3 cm long (vs straight or slightly curved, 0.3–0.6 cm long), and a loment with 2–7 articles (vs 7–12 articles). The new species also differs from *Aeschynomene sensitiva* in having a habit not exceeding 1 m tall (vs 4 m tall), branches glabrous to subglabrous or rarely villous-pubescent (vs hispid), and flowers 1–2.2 cm long (vs 0.4–0.9 cm long); and from *A. montevidensis*, which does not occur in Pará, by its fruit stipe sigmoid (vs straight or slightly curved). The long-sigmoid stipe and pendulous fruit of *Aeschynomene delmoana* resemble those of *A. scabra*, but *A. delmoana* differs by its glabrous to subglabrous stems or rarely villous-pubescent (vs hispidulous), leaflets 1–8 × 1–2 mm (vs leaflets 3–7 × 1 mm), flowers 1–2.2 cm long (vs 0.8–1 cm long), and a loment 2- to 7-articulate (vs 10- to 14-articulate). – Type: Brazil, Pará, Canaã dos Carajás, Floresta Nacional dos Carajás, Serra Sul, S11-A, estrada de acesso ao Corpo A, alagado na beira da estrada, 6°20'34"S, 50°25'26"W, 754 m, 30 iv 2015, *C.M.J. Mattos* et al. 079 (holotype RB [barcode 00972369 (No. 626529)]; isotypes BHCB, HCJS, MG). **Figures 3, 4.**

Subshrub or erect shrub to 1 m tall; stem straight, striate, brown to green *in sicco*, brownish-purple or brown-green *in vivo*, usually branching near the base, cylindrical, glabrous to

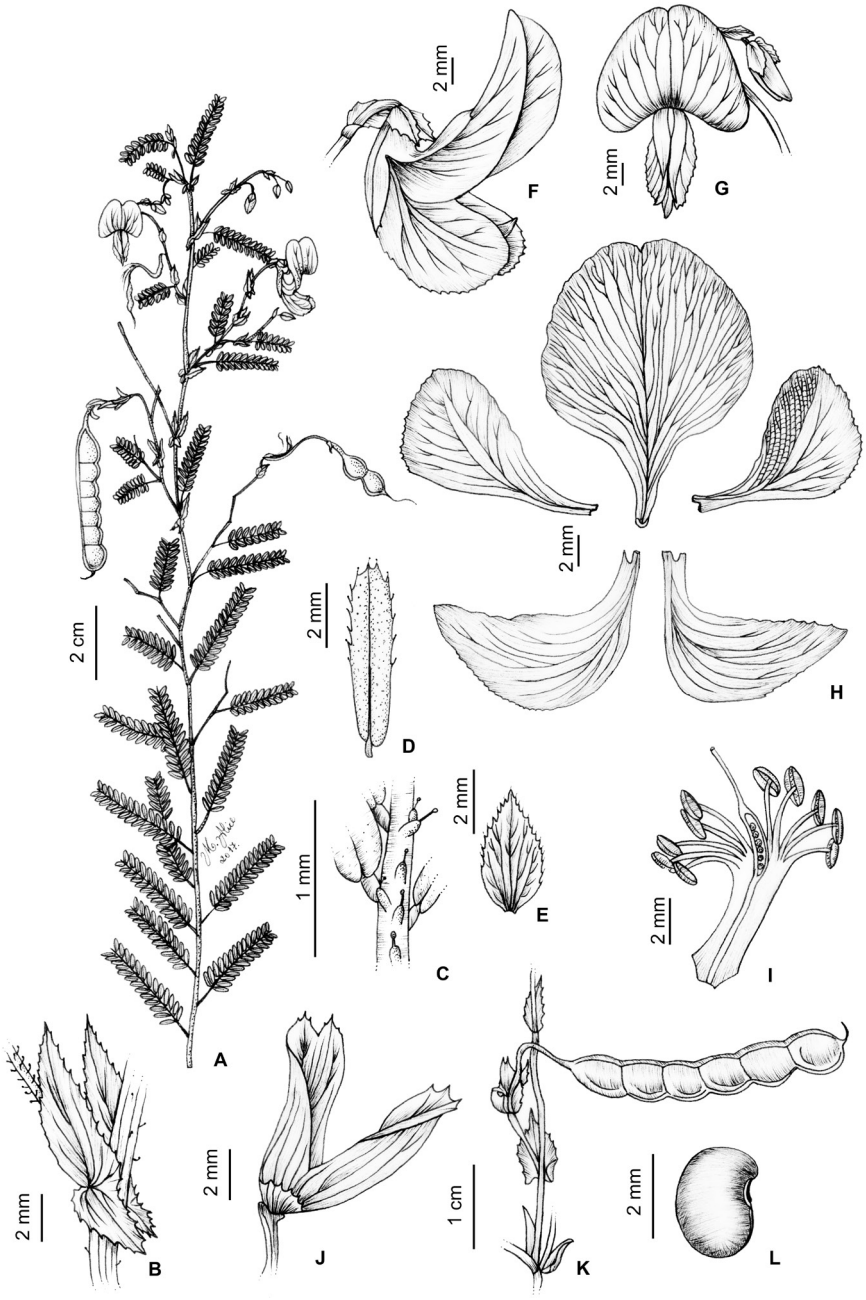

Figure 3. *Aeschynomene delmoana* C.M.J.Mattos, S.M.deFaria & H.C.Lima, sp. nov. A, Habit; B, stipules; C, glandular trichomes; D, leaflet; E, bract; F, flower, lateral view; G, flower, frontal view; H, corolla, petal detail (standard, wings and keel petals); I, androecium and gynoecium; J, calyx detail; K, loment; L, seed. Drawn by Maria Alice de Rezende from *C.M.J. Mattos* et al. 079.

Figure 4. Morphology and habitat of *Aeschynomene delmoana* C.M.J.Mattos, S.M.deFaria & H.C.Lima, sp. nov. A, *Aeschynomene delmoana* in flooded habitat in *canga* of Serra dos Carajás; B, flower detail, showing the papilionate corolla; C, mature, spherical root nodules (black arrows) developed for symbiotic nitrogen fixation; D, detail of the lomentaceous fruit, showing the articles separated by septa. Photographs: A, Pedro Lage Viana; B and D, Cilene M. J. Mattos (from *C.M.J. Mattos* et al. 079); and C, Lourival Tyski.

subglabrous or rarely villous-pubescent with glandular trichomes. *Stipules* persistent, peltate, 4–19 mm long, glabrous, margin ciliate, often with glandular trichomes; upper appendage 1–15 × 1–5 mm, lanceolate-asymmetrical, lower appendage 1–5 × 1–3 mm, elliptic-lanceolate, asymmetrical. *Leaf* pinnate, 0.9–6.5 cm long; petiole 0.1–0.7 cm long, glabrous or with glandular trichomes; rachis 0.8–6 cm long. *Leaflets* 9–36 pairs per leaf, opposite to subopposite, 1–8 × 1–2 mm, those at the leaf apex slightly smaller, blade oblong, sometimes slightly oblanceolate, chartaceous, both surfaces glabrous, green to purple-green *in vivo*; brown-green *in sicco*, base oblique, apex rounded, occasionally mucronate, rarely emarginate, margin entire to sparsely ciliate, adaxial surface with inconspicuous venation; abaxial surface with 1 prominent central principal vein, rarely subcentric. *Inflorescence* an axillary raceme, 3- to 7-flowered; bracts 3–6 × 1–3 mm, persistent, inserted at the rachis, lanceolate to ovate, base acute, acuminate or rounded, apex acute, margin ciliate with glandular trichomes, with 4 or 5 veins arising from the same point, persistent; bracteoles 3–5 × 1–2 mm, persistent, inserted at the base of the calyx, lanceolate, base obtuse, apex acute, margin ciliate, with 4 or 5 veins. *Flowers* 1–2.2 cm long; pedicel 3–6 mm long, glabrescent with sparse glandular trichomes; calyx 6–11 mm long, bilabiate, vexilar lip entire or minutely emarginate, carinal lip 3-minutely tridenticulate; standard petal 10–17 × 8–16 mm, orbicular-ovate to broad-ovate, the blade 9–15 mm long, base rounded, apex emarginate, margin ciliolate, claw 2–3 mm long, glabrous; wings 9–15 × 5–9 mm, obovate-subfalcate, the blade 6–11 mm long, margin crenulate, ciliate, claw 2–5 mm long, glabrous; keel 10–15 × 4–6 mm, falcate, blade 11–13 mm long, margin crenulate to ciliate, claw 2–4 mm, glabrous; androecium diadelphous, stamens 5 + 5, glabrous, anthers dorsifixed, dehiscence longitudinal, oblong; ovary 4–6 × 1 mm, oblong-linear subfalcate, glabrous, 6 or 7 ovules; style 2–5 mm long, filiform, straight, glabrous; stigma truncate. *Fruit* a loment 2.7–4 cm long, upper margin straight or slightly sinuous, lower margin crenate, surface verrucose or smooth, fertile articles 2–7 per loment, 4–6 × 4–6 mm, subquadrate, glabrous, brown to brownish-green *in sicco*; stipe 1–2.3 cm long, sigmoid. *Seed* 2–4 × 2–3 mm, subreniform, brown, reddish-brown or dark brown.

Distribution. This species is probably endemic to the ferruginous rock outcrop vegetation of the Serra dos Carajás (Figure 2).

Habitat and ecology. Found in the *canga* vegetation of the Serra Norte, Sul, Tarzan and Bocaina, where it is abundant during the rainy season, in flooded areas of the *canga*, swamps and near rivers and lakes, and often growing with its roots submerged (**Figures 2B, 4**). Specimens were collected with flowers in February and from April to November, and with fruits in February and from April to August.

Etymology. The epithet *delmoana* is a tribute to Delmo Fonseca da Silva, an important plant collector and parataxonomist renowned for his extensive work on the *canga* vegetation, especially for having collected many specimens of Leguminosae in the Serra dos Carajás.

Proposed IUCN conservation category. The available data prevent us from assessing the species under any criteria other than Criterion B. We calculated an EOO of 970 km^2 and an AOO of 64 km^2. The species has been recorded on a regular basis, from 1972 to 2016, within protected areas. However, we observed that all occurrence records are in areas where there is mining activity, more specifically two mining concessions to Vale S.A., for iron and copper ore exploitation. These concessions are ongoing, with the most recent activities in May 2025 (Agência Nacional de Mineração – ANM, 2025). We also observed the conversion of habitat to pasture area or a mosaic of land uses where *Aeschynomene delmoana* occurs (MapBiomas, 2023). Considering that the mining activity is the main threat to *Aeschynomene delmoana*, we assessed two locations under threat. We recorded a decline in (i) extent of occurrence; (ii) area of occupancy; (iii) area, extent and quality of habitat; (iv) number of locations or subpopulations; and (v) number of mature individuals. All these conditions are due to actual or potential threat activities. Thus, the species meets the thresholds for being assessed as Endangered (EN), under criteria B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v).

Notes. *Aeschynomene delmoana* is placed in the genus *Aeschynomene*, mainly based on the results of our molecular analysis. This close evolutionary relationship is also further corroborated by the species' ecological preference for water habitats and by its bilabiate calyx, and lomentaceous fruits with articles separated by septa (**Figures 3**, **4**). Some individuals of *Aeschynomene delmoana* found in the Serra Sul have vegetative parts and fruit with a reddish colour and more evident orange insect guides on the petals than individuals collected in the Serra Norte. We observed a higher frequency of individuals collected in the Serra Sul with sparse-glandular-hispid trichomes and slightly larger flowers and longer fruit stipes. Despite these differences, we consider them insufficient to separate into two distinct taxa, as the variation in their indumentum and size of the reproductive structures is probably influenced by the environment in which they grow.

All *Aeschynomene* and *Ctenodon* species, including *A. delmoana*, are efficient nitrogen-fixing plants that develop determinate round-shaped nodules (**Figure 4C**) (Chandler, 1978; de Faria *et al.*, 1989; Boogerd & van Rossum, 1997). The central tissue of these nodules consists mainly of infected cells with a homogeneous cytoplasmic content, whereas interstitial (uninfected) cells are sparse and rarely observed due to the active mitotic activity of the infected cells.

Additional specimens examined. Brazil. **Pará**: Canaã dos Carajás, [Parauapebas], FLONA Carajás, *canga* da Serra Sul, 6°20'33"S, 50°25'25"W, 750 m, 26 vi 2009, *R.D. Ribeiro* et al. 1198 (INPA, RB); ibid., Serra Sul, S11-A [Corpo A], 6°20'56"S, 50°26'56"W, 750 m, 26 vi 2009, *R.D. Ribeiro* et al. 1210 (INPA, RB); ibid., *canga* Serra Sul, 6°24'11"S, 50°18'40"W, 750 m, 26 xi 2009, *R.D. Ribeiro* et al. 1414 (MG, RB); [Marabá], FLONA Carajás, Serra Norte, 10 viii 1983, *C.A. Joly & W.H. Stubblebine* 14814 (RB, UEC); ibid., Serra Norte, N1, 31 v 1986, *M.P.M. Lima & G.M. Barroso* 053 (MG, RB); Parauapebas, [Marabá], Serra dos Carajás, acampamento 1, 700 m, 19 viii 1972, *N.T. Silva & B.S. Ribeiro* 3557 (IAN); [Parauapebas], Serra dos Carajás, Serra Norte, 4 vii 1987, *S.M. Silva* 1349 (MBM); [Marabá], Serra dos Carajás, lago do N1, 17

iv 1986, *L.M.M. Carreira* 1073 (MG); ibid., N1, arredores do lago, 4 ix 1987, *N.A. Rosa & J.F. Silva* 5035 (MG); FLONA Carajás, Serra Sul, 6°21'16"S, 50°26'59"W, 21 iv 2015, *L.M.M. Carreira* et al. 3458 (MG); ibid., *canga* da Serra Sul, 6°21'5"S, 50°23'44"W, 750 m, 27 vi 2009, *R.D. Ribeiro* et al. 1231 (RB); ibid., S11-A, lagoa Três Irmãs, 6°20'57"S, 50°26'57"W, 732 m, 30 iv 2015, *C.M.J. Mattos* et al. 082 (RB); ibid., Corpo S11-A, bacia de drenagem da lagoa Três Irmãs, 6°21'04"S, 50°26'22"W, 2 iv 2016, *L.M.M. Carreira* et al. 3511 (MG); ibid., *canga* N4 W Sul, Serra Norte, 6°06'7"S, 50°11'12"W, 26 iii 2009, *S.M. de Faria* et al. 2592 (RB); ibid., Serra Norte, N7, vegetação em área alagada, 6°09'21"S, 50°10'17"W, 650 m, 25 vi 2009, *R.D. Ribeiro* et al. 1188 (RB); ibid., *canga* N1, 6°00'53"S, 50°17'52"W, 650 m, 24 xi 2009, *R.D. Ribeiro* et al. 1362 (RB); FLONA Carajás, *canga* N2, 6°03'17"S, 50°15'13"W, 710 m, 23 ii 2010, *R.D. Ribeiro* et al. 1424 (MG, RB); Mina N5 W Sul, próximo à lagoa, 6°05'45"S, 50°07'27"W, 700 m, 8 vii 2011, *H.C. Lima & D.F. Silva* 7174 (BHCB, HCJS, MG, RB); FLONA Carajás, Serra Norte, *canga* N3, 6°02'41"S, 50°12'42"W, 712 m, 24 vii 2012, *H.C. Lima & D.F. Silva* 7505 (HCJS, IAN, INPA, MG, RB); FLONA Carajás, Serra Norte, *canga* N3, 6°02'37"S, 50°12'34"W, 662 m, 2 v 2015; *C.M.J. Mattos* et al. 103 (RB); FLONA Carajás, Serra Norte, *canga* N3, 6°02'37"S, 50°12'34"W, 662 m, 2 v 2015, *C.M.J. Mattos* et al. 104 (RB); Serra dos Carajás, Serra Norte, N2, 6°03'21"S, 50°15'15"W, 756 m, 28 iv 2015, *A. Gil* et al. 461 (MG); Serra dos Carajás, *canga* do N3, 6 vi 1989, *N.A. Rosa & J.P. Silva* 494 (BHCB, HCJS, MG, RB); *canga* de N8, 6°11'00"S, 50°08'12"W, 14 v 2010, *L. Tyski* 668 (HCJS, RB); S11-B, 6°20'26"S, 50°25'12"W, 820 m, 4 viii 2010, *M.O. Pivari* et al. 1636 (BHCB, IAN, MG); S11-D, 6°24'4"S, 50°21'31"W, 820 m, 18 v 2010, *M.O. Pivari* et al. 1523 (BHCB, IAN, MG); S11-B, 6°21'25"S, 50°24'29"W, 700 m, 19 v 2010, *L.V. Costa* et al. 887 (BHCB); Serra do Tarzan, 6°20'11"S, 50°09'50"W, 750 m, 24 v 2010, *M.O. Pivari* et al. 1569 (BHCB); S11-D, Serra Sul, 22 vi 2013, *R.S. Santos & A.E.S. Rocha* 07 (MG); S11-D, Serra Sul, 22 vi 2013, *R.S. Santos & A.E.S. Rocha* 20 (MG).

Key to the species of Aeschynomene *and* Ctenodon *in the Serra dos Carajás*

1a. Stipule without a basal appendage; calyx campanulate _____ *C. histrix* var. *densiflorus*

1b. Stipule with a basal appendage; calyx bilabiate _____ 2

2a. Stipule with upper segment lanceolate-falcate; leaflets asymmetrical, subfalcate, and palmate-nerved _____ *A. americana* var. *glandulosa*

2b. Stipule with upper segment lanceolate or lanceolate-ovate, leaflets symmetrical, oblong to oblanceolate and pinnate-nerved _____ 3

3a. Leaflets sparsely pubescent on the abaxial surface; loment with 1 or 2 articles *A. filosa*

3b. Leaflets glabrous on the abaxial surface; loment with 3–7 articles _____ 4

4a. Stems glabrous, rarely sparsely glandular-hispid; flowers 1–2.2 cm long; fruit stipe sigmoid, 1–2.3 cm long _____ **A. delmoana**

4b. Stems densely glandular-hispid; flowers 0.4–0.7 cm long; fruit stipe straight or slightly curved, 0.4–0.7 cm long _____ *A. sensitiva* var. *hispidula*

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