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Cecropia telenitida Cuatrec. (Urticaceae: Cecropieae): Phytochemical diversity, Chemophenetic implications and new records from Central America

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Abstract

The Neotropical genus *Cecropia* is the largest genus of Cecropieae in the Urticaceae family with 61 described species. For many years, the taxonomic study of *Cecropia* has been based on morphological and anatomical data. However, recent studies have shown that chemical entities present in *Cecropia* can be used to establish differences between species providing important additional support on its taxonomic classification. The goal of the present study was to contribute to the phytotaxonomic knowledge of this genus to better inform taxonomic decisions. In addition, this is the first time that chemical constituents have been described in the leaves of *Cecropia telenitida* Cuatrec., a species that until now had not been reported in Central America. We characterized and quantified the polyphenolic composition of the methanol leaf extract of *C. telenitida* using UPLC-DAD-MS and HPLC-DAD, respectively. Phytochemical analysis showed that this extract was rich in chlorogenic acid and flavone *C*-glycosides, with isoorientin and isoorientin 2″-*O*-xyloside as the main compounds. Our data showed a lower chemical diversity and metabolite concentrations than other related species. Morphological, distributional and taxonomic notes, images of the plant and phytochemical comparisons between *C. telenitida* and selected congeners from Panama are also provided.

Keywords

Biodiversity, Chemophenetics, Chemoecology, Taxonomy, Phenolic compounds, Chucantí.

41 **1. Introduction**
42
43 Urticaceae is one of the largest Angiosperm families. It comprises more than 2000 species
44 distributed worldwide in 54 genera, mainly in tropical regions (Wu et al., 2013). The Cecropieae
45 tribe (previously Cecropiaceae family) (Conn and Hadiah, 2009) includes three Neotropical
46 genera (*Cecropia*, *Coussapoa* and *Pourouma*) and two Afrotropic genera (*Musanga* and
47 *Myrianthus*). Recent molecular data indicated that both Cecropieae and its five representative
48 genera are monophyletic (Treiber et al., 2016; Gutiérrez-Valencia et al., 2017). The largest genus
49 in Cecropieae is the Neotropical genus *Cecropia*, with 61 described species (Berg and Franco-
50 Rosselli, 2005). *Cecropia* species have a relevant ecological significance due to their rapid
51 growth rate, which make them primary colonizers of deforested tropical areas (Monro, 2009) and
52 act as invasive species in non-native regions (Conn et al., 2012). Species of this genus are
53 naturally distributed across the tropical and subtropical rainforests from Mexico to Central and
54 South America below 2600 m above sea level (Franco-Rosselli and Berg, 1997). Currently, the
55 flora of Panama includes 11 out of the 12 species of *Cecropia* registered for Central America
56 (Berg, 2015).
57 Most *Cecropia* spp. are myrmecophytes, by their mutualistic relationship with a colony
58 of symbiotic ants (especially the genus *Azteca*). The myrmecophytism in this genus can vary
59 between species (also within species), and it is influenced by their geographical locations and
60 elevational gradients (Longino, 1989; Berg and Franco-Rosselli, 2005; Gutiérrez-Valencia et al.,
61 2017). *Cecropia* species provide specialized structures for housing and feeding these symbiotic
62 ants in exchange for protection against natural enemies as herbivores and encroaching vines
63 (Davidson and McKey, 1993; Davidson, 2005; Oliveira et al., 2015; Marting et al., 2018).
64 *Cecropia* trees can supply two types of food rewards in the form of trichomes: Müllerian bodies
65 and pearl glands (Berg and Franco-Rosselli, 2005). The Müllerian bodies usually occur in
66 patches of dense indumentum (called trichilia) at base of the petiole and is characterized by
67 being rich in lipids and contain proteins and glycogen (Rickson, 1971; Rickson, 1973; Rickson,
68 1976). The pearl bodies are found on the lower surface of leaf blades and contain glycogen
69 plastids, lipids and amino acids (Rickson, 1976; Davidson, 2005).
70 Because species of the genus *Cecropia* are used as traditional medicine and are
71 commercially available as food supplements, studies have been conducted on this genus in order
72 to determine their phytochemical composition (Rivera-Mondragón et al., 2017). A rich phenolic
73 profile from their leaf extract has been characterized, in which chlorogenic acid and glycosylated
74 flavonoids, such as flavone *C*-glycosides and flavonol *O*-glycosides have been found as the main
75 constituents. Apigenin, luteolin and diosmetin derivatives have been described to be the most
76 widely reported flavones in *Cecropia* leaves, whereas quercetin *O*-glycosides were
77 representative of the flavonols present in this genus (da Silva Mathias and Rodrigues de Oliveira,
78 2018; Ortmann et al., 2017; Rivera-Mondragón et al., 2019a, Costa et al., 2011). A literature
79 survey revealed that very little is known about the phytochemical composition of *C. telenitida*
80 Cuatrec. Previous research on the roots of this species collected in Colombia, established the

81 presence of abundant pentacyclic triterpenes (yarumic acid, isoyarumic acid, serjanic acid,
82 spergulagenic acid A, 20-hydroxy-ursolic acid and goreishic acid I) (Montoya Peláez et al.,
83 2013; Mosquera et al., 2018).

84 Plant chemophenetic studies are define as the characterization and description of an array
85 of natural chemical products of a taxon. The goal of plant chemophenetics is not to replace or
86 supplant phylogenetic studies based on DNA sequence analysis, but its information could be
87 used to support clades by means of a chemo-phenetic characterization (Zidorn, 2019). In this
88 context, chemophenetics (formerly referred to as chemosystematics or chemotaxonomy) can be
89 useful tools for solving challenges that may affect the establishment of natural classifications of
90 plants in general (Fairbrothers et al., 1975; Waterman and Gray, 1987; Reynolds, 2007). Taking
91 into account that current taxonomic studies on *Cecropia* rely only on morphological and
92 anatomical data (Berg, 1978; Berg and Franco-Rosselli, 2005), this work contributes to the
93 phytotaxonomic knowledge of this genus. As such, there is increasing evidence that the
94 phytochemical profile of *Cecropia* could be useful to establish differences between species
95 providing important information for a better taxonomic understanding of this genus (Rivera-
96 Mondragón et al., 2019a). Furthermore, this study provides the first chemical composition of
97 leaves of *C. telenitida*, whose presence in the Central American region was unknown up until
98 now. Additional photographs of the plant, geographical and taxonomic notes have been also
99 provided in this study.

100 Although a comprehensive discussion of the chemophenetic significance of
101 phytochemicals in *Cecropia* species lies beyond the scope of this study, this paper attempts to
102 compare the chemical composition of *C. telenitida* with other congeners from Panama. This
103 study was based on previous research on four *Cecropia* species (*C. obtusifolia* Bertol., *C. peltata*
104 L., *C. insignis* Liebm. and *C. hispidissima* Cuatrec.) reported by our research group (Rivera-
105 Mondragón et al., 2019b), accompanied by the newly phytochemical description of single
106 collections of *C. telenitida* and *C. angustifolia* Trécul.

107

108 2. Materials and Methods

109

110 2.1. Plant material and identification

111

112 Botanical specimens together with material for phytochemical analysis (leaf blades) were
113 collected at different locations on different dates from 2015 to 2018, throughout the Republic of
114 Panama. Collection permits were issued by the "Ministerio de Ambiente" (SC/P-4-19, SC/P-4-16
115 and SC/P-4-15). Vouchers were deposited at the University of Panama Herbarium (PMA) (Table
116 S1). In order to identify botanical specimens, literature from Berg and Franco-Rosselli (2005)
117 and Berg (2015) were consulted. Plant identifications were confirmed by comparing collected
118 voucher specimens with those identified earlier and housed at the University of Panama
119 Herbarium (PMA). In addition, type specimens of each species were examined by consulting the
120 JSTOR Global Plants database (Gallagher, 2010). Since *C. obtusifolia* had two distinctive

121 morphotypes, these were analyzed independently (see Table S1). Data on species distribution
122 were obtained from Berg and Franco-Rosselli (2005) and TROPICOS (2019).
123
124 **2.2. Reagents**
125
126 Methanol (HPLC grade) and acetonitrile (HPLC grade) were acquired from Fisher Chemical UK
127 Ltd. Formic acid (FA) (98+%, analytical grade) was obtained from Acros Organics (Belgium).
128 Ultrapure water with a resistivity of 18.2 × MΩ × cm at 25 °C (Milli-Q, Waters) was used as
129 extraction solvent and for mobile phase preparation.
130 External standards like chlorogenic acid (99.0%) and rutin (96.9%) were obtained from
131 Sigma-Aldrich (St. Louis, MO), while isovitexin, orientin and isoorientin (all with purity ≥ 99%)
132 were from Extrasynthese (Genay, France). Vitexin (99.7%) was purchased from Adipogen
133 (Liestal, Switzerland). Characterized extracts from *C. obtusifolia*, named as flavonoid rich
134 fraction and flavonolignans, were used as reference material.
135
136 **2.3. General experimental procedures**
137
138 **2.3.1. Plant extraction**
139
140 Three samples of dried leaves of *C. telenitida* and *C. angustifolia* were independently extracted
141 according to Rivera-Mondragón et al. (2019b). An UPLC-DAD-MS system was used for the
142 characterization of the chemical composition of these two plant species. Analysis was done using
143 a TQD mass spectrometer (Waters, Milford, MA, USA) coupled with an ACQUITY LC system
144 equipped with MassLynx version 4.1 software. For analysis, 5 µL of samples were injected on an
145 ACQUITY UPLC BEH C18 column (100 mm x 2.10 mm, 1.7 µm, Waters, Milford, MA, USA).
146 The mobile phase solvents consisted of H_2O + 0.1% FA (A) and ACN + 0.1% FA (B), and the
147 gradient was set as follows (min/B%): 0.0/5.0, 3.0/5.0, 18.0/15, 20.0/15, 28.0/100, 30.0/100,
148 32.0/5, 37.0/5. The flow rate was 0.4 mL/min. During the first analysis, full scan data were
149 recorded in ESI (-) and ESI (+) mode from m/z 120 to 1500. The spray voltage was set at either
150 +3.5 kV and -3.5 kV; cone gas flow and desolvation gas flow at 50.0 L/h and 850.0 L/h,
151 respectively; and source temperature and desolvation temperature at 120 °C and 500 °C,
152 respectively. Data were also recorded using MS2 scan mode in the positive and negative
153 ionization modes (three analysis per mode), and a ramp collision energy from 30 till 40 V was
154 applied to obtain additional structural information. DAD spectra were recorded between 190 and
155 400 nm.
156
157 **2.3.2. HPLC-DAD for quantitative analysis of chlorogenic acid, flavonoids and**
158 **flavonolignans**
159

160 A validated HPLC-DAD analysis was carried out according to Rivera-Mondragón et al. (2019b).
161 Briefly, an Agilent 1200 series system with degasser, quaternary pump, automatic injection,
162 thermostatic column compartment and a DAD (Agilent Technologies, Santa Clara, CA, USA)
163 was used. For analysis, 20 µL sample extract was injected on an RP-18 Kinetex column (2.10 ×
164 100 mm, 2.6 µm, Phenomenex, Torrence, CA, USA). Aqueous formic acid (0.1%, v/v) and
165 acetonitrile with 0.1% formic acid were used as mobile phases A and B, respectively. The
166 gradient program was set as follows: 10% B (0-5 min), 10-15% B (5-20 min), 15% B (20-30
167 min), 15-25% B (30-40 min), 25% B (40-45 min), 25-40% B (45-55 min), 40% B (55-60 min),
168 40-100% B (60-65 min), 100% B (65-70 min), 100-10% B (70-75 min), 10% B (75-85 min). A
169 flow rate of 0.7 mL/min was used. The column temperature was maintained at 26 °C. The DAD
170 signal was recorded between 190 and 500 nm. TF and CA were monitored at 340 nm, while FL
171 was detected at 390 nm.
172
173 **2.4. Data analysis**
174
175 Results were expressed as mean ± standard deviation (SD). Raw data files acquired from the
176 UPLC-DAD-MS analysis were processed with MassLynx (version 4.1, Waters, Milford, MA,
177 USA). Data processing, calculations and graphic plotting were performed using GraphPad Prism
178 for Windows (version 6.01, La Jolla, CA, USA). Multivariate data analysis was performed using
179 JMP Pro 14 (SAS Institute Inc., Cary, NC, USA). Hierarchical clustering algorithm (HCA) using
180 Euclidian distance measurements and Ward´s method without a second data standardization was
181 carried out. The number of clusters in HCA was chosen arbitrarily. Chemical diversity was
182 calculated using the specific richness index (S), the Margalef index (Dmg) and the Shannon
183 entropy (H). These last indices are widely used in ecological studies to provide a measure of
184 diversity (Krebs, 1999). In this study, the specific compound richness consisted in making an
185 inventory of the total number of chemical compounds identified in each studied species. The
186 Margalef index was calculated for each *Cecropia* species as $Dmg = (S-1)/\log(N)$, where N was
187 the total abundance of chemical compounds and S the number of chemical compounds. Shannon
188 entropy was calculated as $H = -\sum pi \log(pi)$, where pi is the proportion i.e. abundance of the
189 compound of an individual chromatogram. The calculations of diversity indices were performed
190 with PAST v.3.0 software (Hammer et al., 2001).
191
192 **3. Results**
193
194 **3.1. First report of *Cecropia telenitida* Cuatrec. in Central America**
195
196 ***Cecropia telenitida* Cuatrec.**, Revista Acad. Colomb. Ci. Exact. 6: 295 (Cuatrecasas, 1945).
197 **Type:** Colombia, Departamento Norte de Santander: Hoya de Samaria (municipio de Toledo),
198 2000–2100 m, 30 Oct 1941, *J. Cuatrecasas, R.E. Schultes & E. Smith 12781* [holotype: COL
199 (image seen!); isotype: F]. Fig. 1.

200
201 **3.1.1. Geographical distribution**
202
203 The specimens collected in this study represent the first records of *C. telenitida* in the Central
204 American region. This species has been now reported for Panama (western Darién), the Andean
205 region of Venezuela to southern Colombia, in the central and eastern cordilleras, and from
206 southern Ecuador to northern Peru (Fig. S1).
207
208 **3.1.2. Habitat and ecology**
209
210 *Cecropia telenitida* grows mainly in Andean cloud forests at 1200–2600 m. In Central America,
211 this species was found only in eastern Panama, specifically in cloud forests of Chucantí Nature
212 Reserve (Darién Province), between 1300–1450 m in *Premontane rain forest* and *Tropical wet*
213 *forest* life zones (Holdridge et al., 1971), in association with other montane tree genera like
214 *Oreomunnea* and *Quercus*. According to the ecoregion classification system, this location is part
215 of the *Eastern Panamanian montane forests* ecoregion, which is characterized by precipitation
216 that ranges between 3000–4000 mm annually and elevations between 500–1800 m (WWF 2018).
217 *C. telenitida*, like other species of montane habitats, lack myrmecophytism (Gutiérrez-Valencia
218 et al., 2017).
219
220 **3.1.3. Material examined (new records)**
221
222 Panama, Darién: Serranía de Majé, Reserva Privada Chucantí, Sendero Los Helicópteros, in
223 close proximity to the top of Cerro Chucantí, 8°47'45"N, 78°27'47"W, 1325 m, 4 April 2018 (♀
224 flowers and fruits), *O. Ortiz et al. 3144* (PMA, MO, FT, SCZ); Reserva Privada Chucantí,
225 camino hacia la cima del Cerro Chucantí, 8°47'31" N, 78°26'51" W, 699 m, 21 September 2018
226 (fruits), *O. Ortiz et al. 2962* (PMA); Serranía de Majé, Reserva Privada Chucantí, cima del Cerro
227 Chucantí, cerca de la lámina, 8°48′7.93″ N, 78°27′9.36″ W, 1300 m, 13 April 2019 (♀ and ♂
228 flowers), *O. Ortiz 3536* (MO, PMA, UCH).
229
230 **3.2. Identification and quantification of chemical constituents of *C. telenitida***
231
232 Qualitative characterization of phenolic compounds in the methanol extract of *C. telenitida* was
233 carried out by UPLC-DAD-MS in negative and positive ionization modes. Multiple approaches,
234 including authentic compounds, UV absorption spectra and ESI-MS data analysis were used for
235 structural identification. Information regarding the phenolic constituents, such as retention time
236 (min), UV absorption bands (nm), molecular formula, observed *m/z* values and concentration
237 (µg/g dried weight) are summarized in Table 1. Among these compounds, four (**1**, **3**, **4** and **7**)
238 constituents were unambiguously identified by comparison with reference standards and seven
239 (**2**, **5**, **6**, **8**–**11**) were determined in comparison to previous characterized samples from *C.*

240 *obtusifolia* (Rivera-Mondragón et al., 2019a). The UPLC-DAD profile and chemical structures
241 (Fig. 2) showed 11 main peaks corresponding to chlorogenic acid (**1**) and ten flavone glycosides
242 (**2**–**11**). Luteolin, apigenin and diosmetin in the form of mono *C*-glycosides and di-*C*,*O*-
243 glycosides were found to be the main flavones observed in *C. telenitida*. As shown in Table 1,
244 chlorogenic acid (325.9 ± 2.1 µg/g) and luteolin *C*-glycosides, such as isoorientin (1265.4 ± 17.7
245 µg/g) and isoorientin 2″-*O*-xyloside (613.1 ± 4.7 µg/g) were found to be the major compounds in
246 *C. telenitida*. In contrast to our earlier findings, malonyl *C*-glycosides, *O*-glycosides and
247 flavonolignans were not present in this plant.
248
249 **3.3. Phytochemical diversity in *C. telenitida* and comparison between selected congeners**
250 **from Panama**
251
252 Ten chemical categories were considered in order to achieve a better understanding of
253 differences and similarities between *C. telenitida* and related species (See supplementary Fig.
254 S3). Our results showed that out of the six species studied, *C. telenitida* has the lowest content of
255 chlorogenic acid (325.9 µg/g) and of total flavonoids (2682.0 µg/g). Similar to *C. hispidissima*,
256 flavonolignans were not detected in this species. In addition, the amount of luteolin and apigenin
257 *C*-glycosides (1915.8 and 634.4 µg/g, respectively) from the leaves of *C. telenitida* were below
258 the average content of the leaves of *C. obtusifolia*, *C. peltata*, *C. insignis* and *C. angustifolia*, but
259 higher to those reported for *C. hispidissima*. On the other hand, the concentration of diosmetin *C*-
260 glycosides in the leaves of *C. telenitida* (131.9 µg/g) was relatively higher than the content in the
261 leaves of *C. obtusifolia, C. peltata, C. angustifolia* and *C. hispidissima*, and similar to the
262 average reported for *C. insignis* (137.3 µg/g).
263 According to multivariate analysis, three main clusters were observed (Fig. 3). *Cecropia*
264 *telenitida* was located in Cluster 1 together with *C. obtusifolia* (CO-M1), *C. insignis* and *C.*
265 *angustifolia*, while *C. peltata* and *C. obtusifolia* (CO-M2) where located in Cluster 2. As
266 reported before, *C. hispidissima* was observed as belonging to Cluster 3 as the most distant
267 species (Rivera-Mondragón et al. 2019a). Inspection of Cluster 1 revealed that *C. telenitida* is
268 more related to *C. insignis* in term of its chemical profile: relatively low concentration or absence
269 of mono *C*-glycosides (such as **7** and **12**), *O*-malonyl glycosides (**20**–**25**) and quercetin *O*-
270 glycosides (**26**–**28** and **31**–**32**), and concentrations in a similar range of isoorientin (**6**),
271 isoorientin 2″-*O*-xyloside (**3**) and apigenin *C*-hexoside-*O*-pentoside (**13**).
272 The average number of chemical constituents detected ranged from 15 in *C. obtusifolia*
273 (CO-M1) to eight in *C. telenitida*. The highest richness of chemical compounds was observed in
274 *C. obtusifolia* (CO-M1), *C. angustifolia* and *C. insignis*; however, *C. telenitida* had the lowest
275 number of constituents (Fig. S4). These results coincide with those obtained using the Margalef
276 index (Fig. S4). According to the Shannon entropy index, the species with the greatest diversity
277 of compounds turned out to be *C. obtusifolia* (CO-M1). Almost all the studied species showed
278 relatively higher diversity values than *C. telenitida* (Fig. S4).
279

4. Discussion

4.1. Morphological comparison between *C. telenitida* and its relatives

Cecropia telenitida is characterized mainly by having leaf blades with arachnoid indumentum on the lower surfaces (in two distinct layers) and more or less dense arachnoid indumentum above, 7–10 blade segments and 7–16 lateral veins in the free part of the mid-segment of the blade, absent or present trichilia and large stipules (20–55 cm long). For more descriptive details of this species, see Berg and Franco-Rosselli (2005). According to Berg and Franco-Rosselli (2005), *C. telenitida* is part of the "*Cecropia telenitida*-group" that comprises many representatives with the upper leaf surface covered with more or less dense arachnoid indumentum. In this group of species, trichilia can be always absent, occur only in more or less reduced states (mostly without Müllerian bodies), or occur in states of being absent through being more or less reduced to occurring in two patches to well-developed and fused (Berg and Franco-Rosselli, 2005). Due to the presence of arachnoid indumentum on the upper blade surfaces, *C. telenitida* can be confused with *C. telealba* Cuatrec. However, the latter differs from *C. telenitida* in a number of important morphologic aspects: consistent well-developed trichilia and lower leaf blades covered with arachnoid indumentum in the areoles or extending to the smaller veins or also to the main veins (not distinctly in two layers as in *C. telenitida*) (Berg and Franco-Rosselli, 2005).

The individuals of the Central American population of *C. telenitida* registered in this study usually lack a developed trichilia, but sometimes they can present villous petioles (in all parts), with long white hairs, arachnoid indumentum and brown pluricellular trichomes at the base (which may suggest the occurrence of trichilia) (see Fig. 4), but never present Müllerian bodies. In Central America, *C. telenitida* is the only species to have blades with dense arachnoid indumentum above, as well as, arachnoid indumentum in two distinct layers on the lower surfaces (Supplemental Data S1). Because this species may lack well-developed trichilia (Fig. 1), it can be confused with *C. pittieri* B.L. Rob. from Cocos Island (Costa Rica). Nonetheless, the latter species differs from *C. telenitida* in having shorter stipules (8–17 cm vs. 20–55 cm in *C. telenitida*) and leaf blades without arachnoid indumentum above, with lamina incisions down to 2/10–3/10 from the margin (vs. 4/10–9/10 in *C. telenitida*).

4.2. Phytochemical constituents in *C. telenitida*

This is the first collecting evidence of this species in Central America, and first phytochemical characterization and quantitative analysis of leaf extracts for this species. Our results indicated that the content of polyphenols in *C. telenitida* was relatively lower than those reported for other *Cecropia* species from Panama. In a preliminary study (Rivera-Mondragón et al., 2019a), chlorogenic acid and *C*-glycosyl flavones were identified as the main constituents in leaves of *Cecropia* species from Panama. Despite their reduced phytochemical profile, low relative metabolite concentration and complete absence of *O*-glycosides and flavonolignans in the

320 methanol leaf extract of *C. telenitida*, our results indicated other similarities between this species
321 and other relatives such as *C. obtusifolia*, *C. peltata*, *C. insignis* and *C. angustifolia* in terms of
322 chlorogenic acid and *C*-glycosyl flavones profiles. These results are similar to those reported for
323 *C. obtusifolia*, *C. peltata*, *C. insignis*, *C. pachystachya* Trécul and *C. hololeuca* Miq. (da Silva
324 Mathias and Rodrigues de Oliveira, 2018; Ortmann et al., 2017; Rivera-Mondragón et al.,
325 2019a).
326
327 **4.3. Implication of the chemodiversity in chemoecological and chemophenetic aspects**
328
329 According to these chemodiverse results, the richness in chemical constituents of *C.*
330 *telenitida* was low and due to the predominant abundance of some chemical compounds (such as
331 luteolin and diosmetin *C*-glycosides), heterogeneity was also found to be low. Consequently, all
332 diversity indexes showed that when comparing the chemical profile of the leaf of *C. obtusifolia*
333 (CO-M1), this was clearly more diverse than the other *Cecropia* species (Fig. S4). In general, the
334 hypothesis about chemical diversity in plants has been associated mainly with the diversity of
335 defensive compounds and as well as the degree of specialization of herbivores (Richards et al.,
336 2015; Salazar et al., 2016). Latteman et al. (2014), found significant differences in the levels of
337 chemical defenses (tannins or phenolic compounds) between young and mature leaves of *C.*
338 *sciadophylla* Mart. (suggesting the possible importance of chemical defenses on herbivory, as
339 compensation by the absence biotic defenses). By contrast, no significant differences in the
340 levels of chemical defenses between young and mature leaves of *C. tacuna* C.C. Berg & P.
341 Franco (non-myrmecophytic Andean species) and *C. membranacea* (myrmecophytic lowland
342 species) were found. Taking into account that most *Cecropia* species (ca. 80%) have a
343 mutualistic relationship with ants that can protect the plant from predators (Davidson, 2005;
344 Marting et al., 2018), perhaps one hypothesis would be that the evolution of mutualism had some
345 impact on the chemical diversity among *Cecropia* species. Another explanation would be that the
346 low chemical diversity found in *C. telenitida* may be related mainly to the lack of production of
347 the Müllerian bodies and/or pearl bodies (pearl glands) and not so much to the presence or
348 absence of mutualistic strategies with ants (myrmecophytism). For example, *C. angustifolia*
349 (with higher chemical diversity than *C. telenitida*), is a species that lacks myrmecophytism but
350 produces Müllerian bodies. Perhaps the high chemical diversity in *Cecropia* is related to the
351 production of Müllerian bodies and/or pearl bodies, but to confirm this, additional chemical
352 studies must be done, particularly fractions from these structures, and from other *Cecropia*
353 species.
354 The results obtained through the multivariate analysis indicated that *C. telenitida* is more
355 related to *C. insignis* than the other *Cecropia* species. These results agree in part with those
356 obtained in the molecular phylogenetic inference made by Gutiérrez-Valencia et al. (2017),
357 where *C. telenitida* is located in a differentiated clade together with a few myrmecophytes like *C.*
358 *insignis* and several non-myrmecophytes Andean *Cecropia* species (Clade II). It is well known
359 that evolutionary factors related to the colonization of montane habitats could be implicated in

360 the absence of myrmecophytism in *Cecropia* (Janzen, 1973; Gutiérrez-Valencia et al., 2017).
361 One of the characteristics of this group of non-myrmecophytes Andean species is that they may
362 lack trichilia and Müllerian bodies (Gutiérrez-Valencia et al., 2017). It is important to mention
363 that the absence of myrmecophytism in *Cecropia* is not always linked to the absence of these
364 characteristics, since there are non-myrmecophytism montane species such as *C. angustifolia* and
365 *C. tacuna* that usually present trichilia and Müllerian bodies (Janzen, 1973; Latteman et al.,
366 2014).
367 According to the cluster analysis, *C. obtusifolia* morphotype 1 (CO-M1) and morphotype
368 2 (CO-M2) were located at different clusters. These results suggest the existence of inaccurate
369 taxonomic classification in this species. According to Berg and Franco-Rosselli (2005), *C.*
370 *obtusifolia* it is a highly variable species, mainly in the number of segments of the leaf blade, as
371 well as in the number of lateral veins in the free part of the mid-segment and in the arachnoid
372 indumentum on the lower leaf surfaces. The differences in the arachnoid indumentum has led to
373 the distinction of the "obtusifolia-type" which is characterized by comprising material with
374 arachnoid indumentum and the "burriada-type" with comprising individuals without arachnoid
375 indumentum (Berg and Franco-Rosselli, 2005). The individuals studied here as *C. obtusifolia*
376 (CO-M1) share characteristics with the "obtusifolia-type" and *C. obtusifolia* (CO-M2) lack
377 arachnoid indumentum as the "burriada-type". Other distinguishing characteristics observed in
378 the field is that the "obtusifolia-type" presented thin discolor blades (whitish beneath) and
379 reddish to yellowish veins on lower surfaces, while those of "burriada-type" have sub-coriaceous
380 concolor blades (greenish on both surfaces) and prominent purple to red-purple veins on lower
381 surfaces. The morphological data and the phytochemical evidence presented in this study could
382 provide substantial differences between these two morphotypes described as *C. obtusifolia* by
383 Berg and Franco-Rosselli (2005). Perhaps these two groups deserve a different taxonomic
384 recognition, but to obtain a more accurate conclusion, it is necessary to analyze individuals from
385 other populations throughout their range of geographical distribution.
386
387 **5. Conclusions**
388
389 Based on the morphological characteristics, *C. telenitida* is distinguished from all its Central
390 American relatives in having blades with dense arachnoid indumentum above and arachnoid
391 indumentum in two distinct layers on the lower surfaces. Although the current study is based on
392 a small number of specimens, the phytochemical findings suggest that *C. telenitida* is
393 distinguished from the other congeners analyzed in this work, by lacking flavone *O*-malonyl-*C*-
394 glycosides, flavonol *O*-glycosides and flavonolignans, as well as, by its lower chemical diversity
395 and metabolite concentrations. Due to practical constraints, this paper cannot provide extensive
396 chemophenetic implications. Therefore, the developing of a systematic sampling plan should be
397 further considered in order to obtain better insights and conclusions on the chemophenetic
398 significance for the genus *Cecropia*. Future phytochemical research including multiple plant
399 specimens (e.g. additional *C. telenitida* and *C. angustifolia*), multiple time points (e.g. dry and

400 rainy season), plant age (young and mature leaves), different locations and consideration of their
401 lineage as dioecious trees should be investigated.
402
403 **6. Acknowledgements**
404
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415
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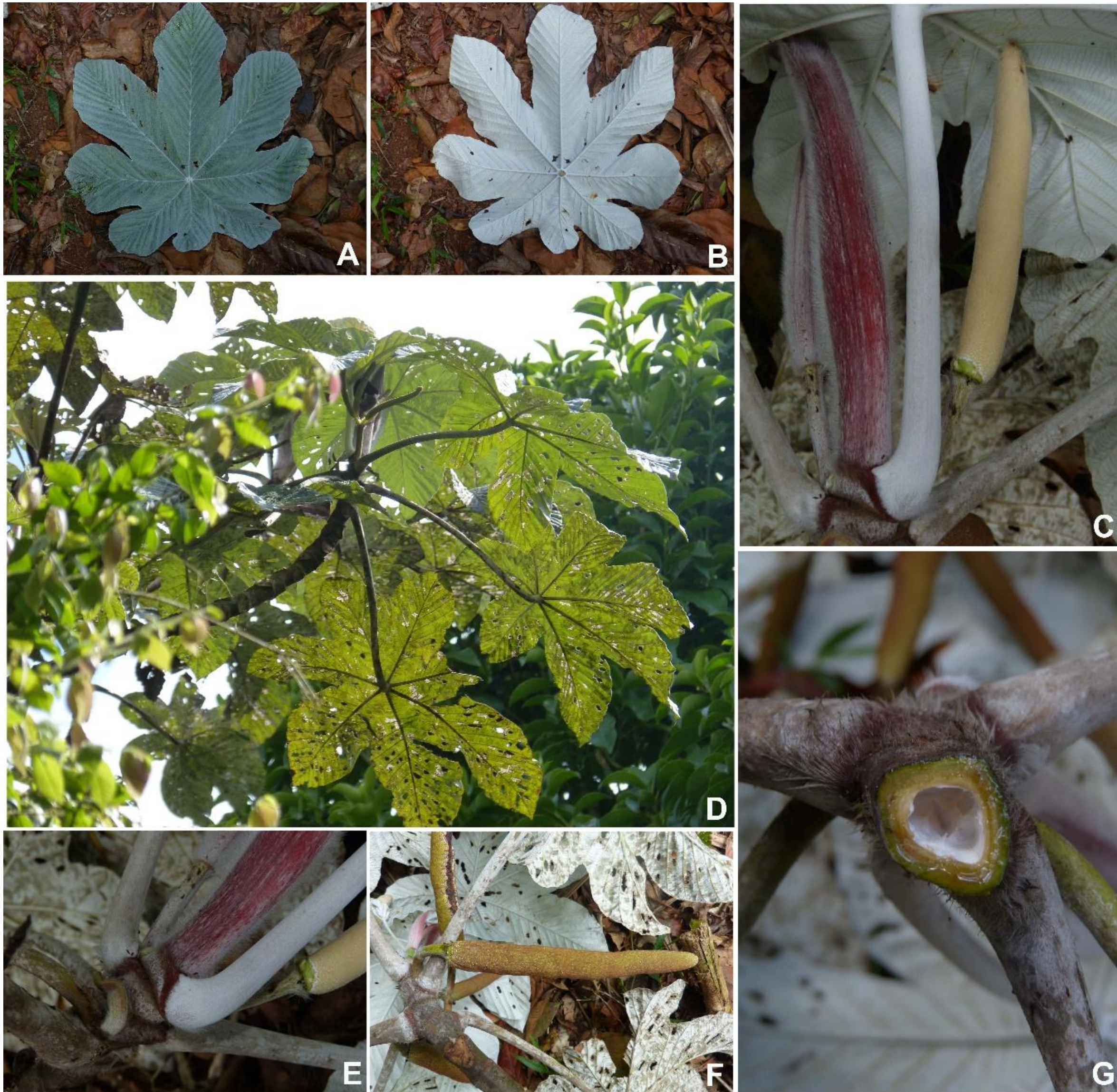
535
536 **Figure captions**
537
538 **Fig. 1**. *Cecropia telenitida* Cuatrec. (voucher specimen: *O. Ortiz et al. 3144*). (A) Leaf blade
539 (upper surface). (B) Leaf blade (lower surface). (C) Stipule and pistillate spike. (D) Branches
540 with the staminate inflorescence. (E) Petiole without trichilia. (F) Infructescence. (G) Internode
541 pith. Photo credit: Orlando O. Ortiz.
542
543 **Fig. 2.** UPLC-UV (340 nm) chromatogram with the structures of fully identified compounds of
544 the methanol extract of *C. telenitida*.
545
546 **Fig. 3**. Multivariate analysis of the phytochemical composition of *Cecropia* species. (A)
547 Hierarchical cluster analysis (HCA) for authentic plant species of *Cecropia* shown as a heatmap.
548 Colors represent the concentration (µg/g) in the samples from minimum (green) to maximum
549 (red). Numbers are referred to compounds name at supplementary Table S2. (B) Constellation
550 plot. (C) Principal component analysis with K-means clustering.
551
552 **Fig. 4**. Trichilia types in some species of *Cecropia* from Panama. (A) *C. angustifolia*. (B) *C.*
553 *heterochroma*. (C) *C. hispidissima*. (D) *C. insignis*. (E) *C. membranacea*. (F) *C. obtusifolia*
554 (Morphotype 1). (G) *C. obtusifolia* (Morphotype 2). (H) *C. peltata*. (I) *C. telenitida*. Photo credit:
555 Orlando O. Ortiz.
556

557



558

559 **Figure 1**. *Cecropia telenitida* Cuatrec. (voucher specimen: *O. Ortiz et al. 3144*). A. Leaf blade
560 (upper surface). B. Leaf blade (lower surface). C. Stipule and pistillate spike. D. Branches with
561 the pistillate inflorescence. E. Petiole without trichilia. F. Infructescence. G. Internode pith.
562 Photos: Orlando O. Ortiz.

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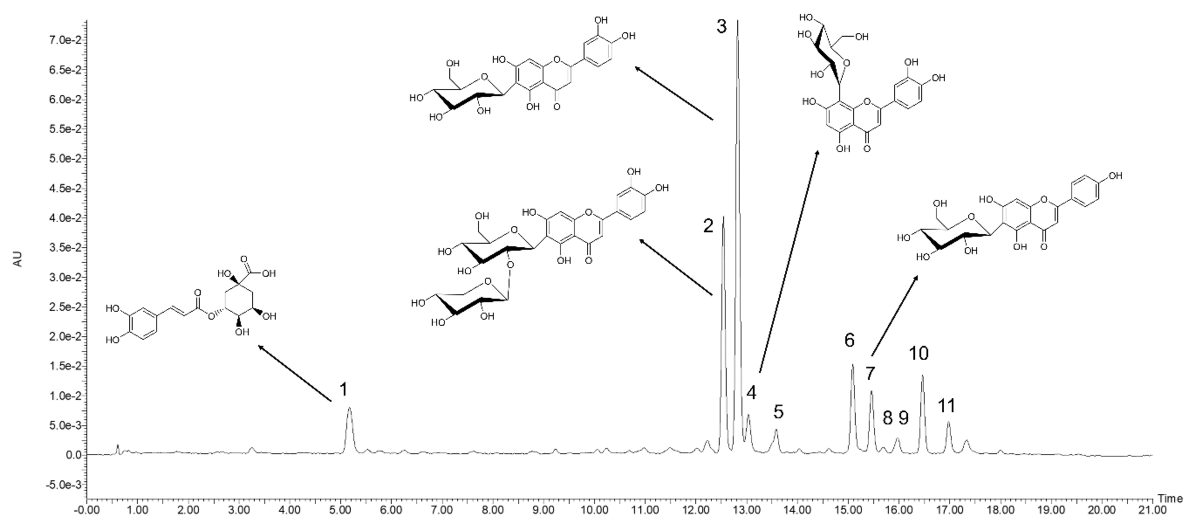

569

570 **Figure 2.** UPLC-UV (340 nm) chromatogram with the structures of fully identified compounds of

571 the methanol extract of *C. tenelitida*.

572

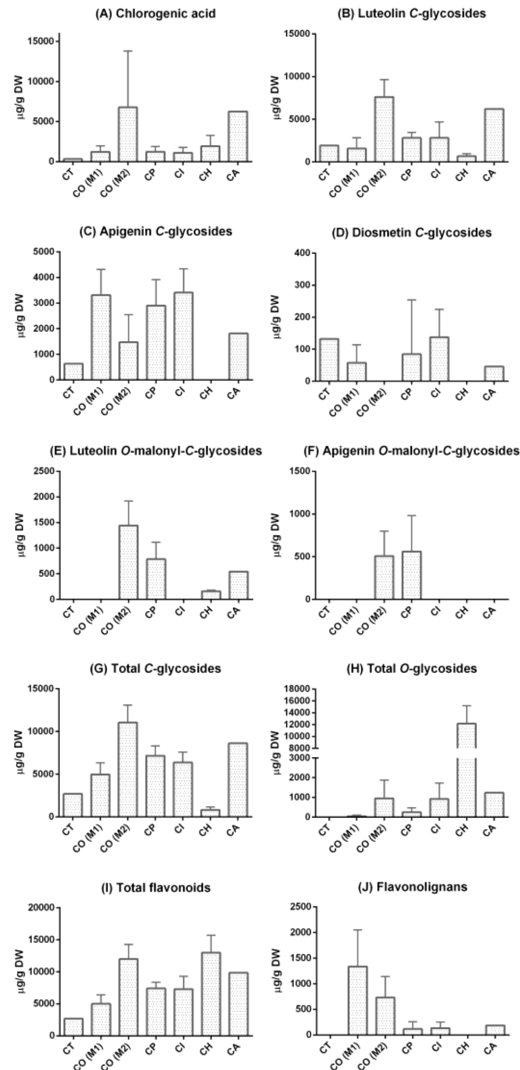

Figure 3. Phytochemical composition of *Cecropia* leaf samples. CT, CO, CP, CI, CH and CA correspond to *C. telenitida*, *C. obtusifolia* (Morphotype 1: M1; Morphotype 2: M2), *C. peltata*, *C. insignis*, *C. hispidissima* and *C. angustifolia*, respectively. Vertical bars represent the average of each species. Error bars represent the standard deviation of the data set. Note lack of variation in *C. telenitida* and *C. angustifilia*, where a single specimen was sampled and used for the analysis.

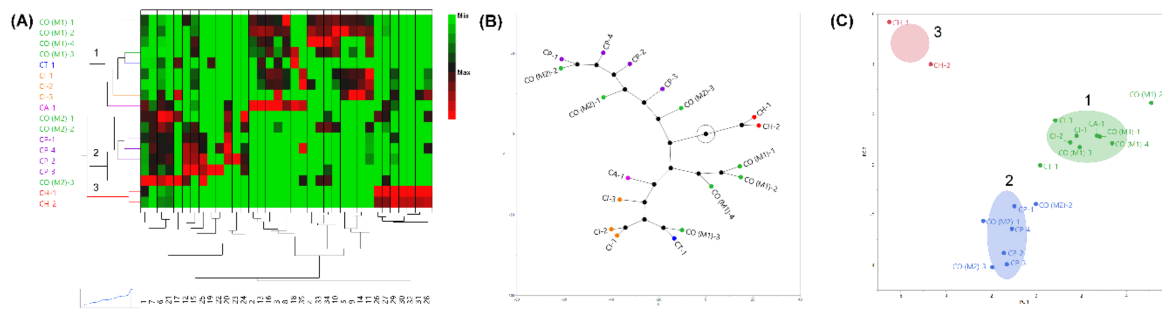

Figure 4. Multivariate analysis of the phytochemical composition of *Cecropia* species. (A) Hierarchical cluster analysis (HCA) for authentic plant species of *Cecropia* shown as a heatmap. Colors represent the concentration (µg/g) in the samples from minimum (green) to maximum (red). Numbers are referred to compounds name at supplementary Table S2. (B) Constellation plot. (C) Principal component analysis with K-means clustering.

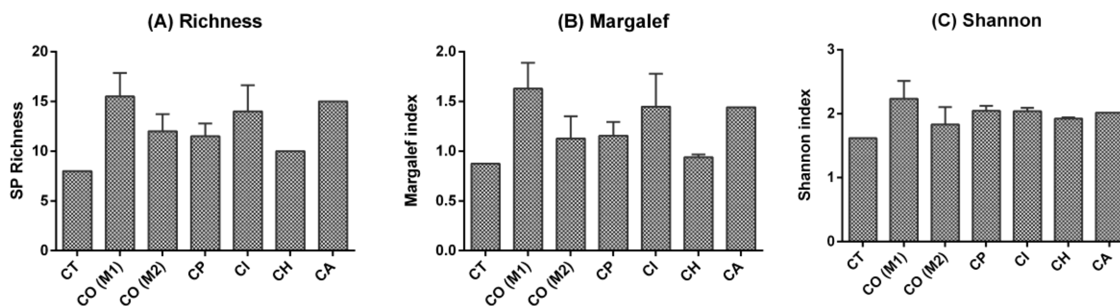

Figure 5. Chemical diversity of *Cecropia* species. Chemical diversity was estimated in *Cecropia* for (A) richness, (B) Shannon, and (C) Margalef indices. CT, CO, CP, CI, CH and CA correspond to *C. telenitida*, *C. obtusifolia* (Morphotype 1: M1; Morphotype 2: M2), *C. peltata*, *C. insignis*, *C. hispidissima* and *C. angustifolia*, respectively. Vertical bars represent the average of each species. Error bars represent the standard deviation of the data set.

600

601 **Figure 6**. Trichilia types in some species of *Cecropia* from Panama. A. *C. angustifolia*. B. *C.*
602 *heterochroma*. C. *C. hispidissima*. D. *C. insignis*. E. *C. membranacea*. F. *C. obtusifolia*
603 (Morphotype 1). G. *C. obtusifolia* (Morphotype 2). H. *C. peltata*. I. *C. telenitida*. Photographs:
604 Orlando O. Ortiz.

605

606 **Table 1.** List of phenolic compounds identified and quantified in the UPLC-DAD-MS and HPLC-
607 DAD profiles, respectively, of the methanol extract of *Cecropia telenitida.*

No.	Compound	Retention time (min)	λ_{max} (nm)	Molecular Formula	ESI negative full MS: $[M-H]^-$ *m/z*	ESI positive full MS: $[M-H]^+$ *m/z*	Concentration (µg/g DW)
	Phenolic acids						
1	Chlorogenic acid[a]	5.18	220, 324	$C_{16}H_{18}O_9$	353.0	355.0	325.9 ± 2.1
	Flavonoids (Flavones)						
	Luteolin glycosides						
2	Isoorientin-2''-*O*-xyloside[b]	12.55	270, 348	$C_{26}H_{28}O_{15}$	579.1	581.1	613.1 ± 4.7
3	Isoorientin[a]	12.83	270, 348	$C_{21}H_{20}O_{11}$	447.1	449.1	1265 ±18
4	Orientin[a]	13.04	270, 348	$C_{21}H_{20}O_{11}$	447.1	449.1	37.3 ± 0.6
5	Luteolin *C*-hexoside-*O*-pentoside[b]	13.56	275, 335	$C_{26}H_{28}O_{15}$	579.1	581.1	< LOD
	Apigenin glycosydes						
6	Apigenin *C*-hexoside-*O*-pentoside[b]	15.10	271, 338	$C_{26}H_{28}O_{14}$	563.1	565.0	241.3 ± 4.0
7	Isovitexin[a]	15.47	269, 335	$C_{21}H_{20}O_{10}$	431.0	433.0	393.1 ± 9.5
8	Isovitexin 2''-*O*-rhamnoside[b]	15.98	273, 338	$C_{27}H_{30}O_{14}$	577.2	579.1	< LOD
9	Apigenin *C*-hexoside-*O*-pentoside[b]	15.98	273, 338	$C_{26}H_{28}O_{14}$	563.1	565.0	< LOD
	Diosmetin glycosides						
10	Diosmetin *C*-hexoside-*O*-pentoside[b]	16.47	271, 345	$C_{27}H_{30}O_{15}$	593.0	595.0	49.3 ± 0.6
11	Diosmetin-*C*-hexoside[b]	16.99	271, 345	$C_{22}H_{22}O_{11}$	461.1	463.1	82.6 ± 1.5

608

609 [a]Identification by comparison with analytical standards. [b] Identification by comparison with characterized extracts
610 from *C. obtusifolia* (previouslty described by Rivera-Mondragón et al., 2019a. Contents of analytes are reported as
611 mean ± standard deviation (n = 3). Content below the limit of quantification: <LOQ. Dried weight: DW