Deciphering the *Heteropterys pannosa* species complex (Malpighiaceae)

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We describe three new species of Malpighiaceae that are endemic to central Brazil and related to the *Heteropterys pannosa* complex, a group of xylopodiferous, unbranched subshrubs with fruit in mericarps that have a strongly reduced or no dorsal wing. *Heteropterys tocantinensis* is more common in eastern Tocantins State and on the border with Bahia State, and there are a few records from Mato Grosso State. *Heteropterys veadeirensis* is restricted to northern Goiás State and *H. walteri* has a wider distribution, occurring in some municipalities in northern Goiás and southern Tocantins. Additionally, we also provide detailed redescriptions of *H. pannosa* and *H. rosmarinifolia*, the two previously known species in this complex. All species are considered Endangered (EN) based on IUCN criteria, especially due to the low area of occupancy. Illustrations, distribution maps, and information about phenology and habitat are also provided for all taxa.

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17   ABSTRACT

19   We describe three new species of Malpighiaceae that are endemic to central Brazil and in the

20   *Heteropterys pannosa* complex, a group of xylopodiferous, unbranched subshrubs with fruit in

21   mericarps that have a strongly reduced or no dorsal wing. *Heteropterys tocantinensis* is more

22   common in eastern Tocantins State and on the border with Bahia State, and there are a few

23   records from Mato Grosso State. *Heteropterys veadeirensis* is restricted to northern Goiás State

24   and *H. walteri* has a wider distribution, occurring in some municipalities in northern Goiás and

25   southern Tocantins. Additionally, we also provide detailed redescriptions of *H. pannosa* and *H.*

26   *rosmarinifolia*, the two previously known species in this complex. All species are considered

27   Endangered (EN) based on IUCN criteria, especially due to the low area of occupancy.

28   Illustrations, distribution maps, and information about phenology and habitat are also provided

29   for all taxa.

31   Subjects

32   Biodiversity, Plant Science, Taxonomy

34   Keywords

35   Brazilian savannas, Endemism, Malpighiales, Parabanisteria, Taxonomy

37   INTRODUCTION

39   *Heteropterys* Kunth is a highly diverse genus of Malpighiaceae due to its remarkable vegetative

40   and reproductive morphological variability. It comprises approximately 158 species of

41   subshrubs, shrubs, small trees and robust lianas that are distributed from Mexico to South

42   America, including the West Indies (Anderson 2001a; Anderson 2013; Amorim & Marinho

43   2020). Only *Heteropterys leona* (Cav.) Exell has a disjunct intercontinental distribution. It occurs

44   from Belize to northern Brazil and on the west coast of Africa (Anderson 2001a). *Heteropterys*

45   has a single synapomorphy: the fruit is a schizocarp where each mericarp or nut has a dominant

46   dorsal wing with a thick inferior margin and lateral wings that are absent or rarely strongly

47   reduced (Amorim 2003; Pessoa & Amorim 2016). The genus was recovered as monophyletic

48   and well-placed in the tetrapteroid lineage, which basically comprises plants with a mericarp

49   with dominant lateral wings and a reduced or no dorsal wing (Davis & Anderson 2010).

50

51   Despite the extensive work conducted to solve the problematic taxonomy of *Heteropterys*, in the

52   last ten years novelties in this genus have been continuously reported from different habitats.

53   These novelties can often be placed in informal groups-supported by lineages in a recent

54   *Heteropterys* phylogeny (Davis & Amorim, pers. comm. 2021), which sometimes correspond to

55   infrageneric categories, such as those proposed by Niedenzu (1903; 1928). Notable examples are

56   new taxa of *Heteropterys* recently revealed in the Aptychia (Amorim & Marinho 2020),

57   Metallophyllis (Amorim et al. 2017), Parabanisteria (Almeida & Pellegrini 2021)*,* Rhodopetalis

58   (Pessoa & Amorim 2016), Stenophyllarion (Sebastiani & Mamede 2010) and Xanthopetalis

59   groups (Anderson 2014; Pessoa et al. 2019). Likewise, the resolution of Malpighiaceae species

60   complexes in different genera have been continuously investigated with the objective of

61   clarifying the vegetative and reproductive variability among close species. For example, the

62   resolution of the *Amorimia rigida* complex (Almeida et al. 2016) where three new species were

63 proposed, the *Galphimia langlassei* complex (Anderson 2003) where two new species were

64 proposed, and the *Mascagnia cordifolia* complex (Anderson 2005) and *Mascagnia sepium*

65 complex (Anderson 2001b) where three and seven new species were proposed, respectively.

66 Notable changes in *Heteropterys* include the resolution of the *Heteropterys anomala* complex

67 (Amorim 2003), where four new species were proposed, and *Heteropterys oblongifolia* complex

68 (Anderson 1981), where one new species was proposed, but it is argued that other taxonomic

69 novelties might arise when more collections are available for the latter complex.

70

71 The Parabanisteria group is the most diversified lineage of *Heteropterys*. It comprises at least 44

72 species and occurs in several habitats, such as upland forests, white-sand vegetation and

73 floodplains forests in the Amazon basin. It is also occasionally found in *tabuleiro* and

74 *mussununga* forests (i.e., two kinds of white-sand forest in northeastern Brazil) and few species

75 occur in inselberg vegetation in the Atlantic Forest domain. However, most species of the

76 Parabanisteria group occur in central Brazil and grow in clay or sand in highland savannas,

77 gallery forests, dry forests and on rock outcrops in the Cerrado domain. Species of this group are

78 recognized by their inflorescence rachis, peduncle, pedicels and sepals covered by a ferrugineous

79 indumentum, eglandular bracteoles at the apex of the peduncle, sepals concealing the petals in

80 bud and revolute at anthesis, and petals spreading and all vivid yellow (Anderson 1981;

81 Anderson 2001a). The mericarp is strongly variable in form and size but generally has a large

82 dorsal wing and lacks lateral wings or crests.

83

84 Many species in the Parabanisteria group have morphological characteristics adapted to open

85 vegetation in the Cerrado domain, such as an arborescent or shrubby habit with woody stems,

86 coriaceous leaves and inflorescences that often develop after the deciduous leaves fall. Among

87 them, *Heteropterys pannosa* Griseb. stands out. It is a subshrub with a xylopodiferous

88 underground stem system, erect and elongate pseudoraceme inflorescences and mericarps

89 without a dorsal wing or with this structure strongly reduced to an apical crest (Figs.1a, k and

90 2a–b). *Heteropterys pannosa* was described from a collection made by Johann Emanuel Pohl in

91 Goiás State (Grisebach 1858). Since then, this name has been applied to many collections from

92 different localities in central Brazil (Fig. 3a). Our study clarified the geographical and

93 morphological patterns along the distribution of the *H. pannosa* species complex and that this

94 complex comprises more than just the two species currently recognized: *H. pannosa* and the

95 recently described *H. rosmarinifolia* R.F.Almeida & M.Pell. Thus, in this work we describe three

96 new species of *Heteropterys* and provide detailed redescriptions of *H. pannosa* and *H.*

97 *rosmarinifolia*. We also include an identification key, distribution maps, illustrations, and the

98 estimated conservation status for all the species in the *H. pannosa* complex.

99

100 MATERIAL & METHODS

101

102 We analyzed 82 specimens of the *Heteropterys pannosa* complex from the ALCB, CEPEC,

103 CEN, HUEFS, MICH, RB, UB, UESC, UFG, SP and SPF herbaria (acronyms following Thiers

104 2021 - continuously updated). We also used web-based resources, such as the Reflora Virtual

105 Herbarium (Available at http://reflora.jbrj.gov.br and accessed in November 2021) and

106 SpeciesLink (Available at http://splink.cria.org.br/ and accessed in November 2021), to check

107 additional specimens (as digital images), including types. Descriptions of the characters are

108 based on dried material. The geographic distributions maps were created using the website

109 SimpleMappr (Shorthouse 2010). The conservation status of each species was assessed using

110 IUCN (2017) guidelines and criteria; the area of occupancy and extent of occurrence were

111 calculated using GeoCAT (Bachman et al. 2011).

112

113 The electronic version of this article in Portable Document Format (PDF) will represent a

114 published work according to the International Code of Nomenclature for algae, fungi, and plants

115 (ICN), and hence the new names contained in the electronic version are effectively published

116 under that Code from the electronic edition alone. In addition, new names contained in this work

117 which have been issued with identifiers by IPNI will eventually be made available to the Global

118 Names Index. The IPNI LSIDs can be resolved and the associated information viewed through

119 any standard web browser by appending the LSID contained in this publication to the prefix

120 "http://ipni.org/". The online version of this work is archived and available from the following

121 digital repositories: PeerJ, PubMed Central SCIE, and CLOCKSS".

122

123 RESULTS

124

125   KEY TO THE SPECIES OF THE *Heteropterys pannosa* COMPLEX

126

127   1. Young stems, petiole and lamina glabrous...*H. veadeirensis*

128   1.' Young stems, petiole and lamina covered by indumentum with simple and basifixed or Y-V-

129   T-shaped trichomes…………………………………………………………..….…………2

130   2. Young petiole, midrib of lamina, inflorescence rachis, peduncle and pedicel covered by hispid

131   indumentum……………………….........................…………………..………*H. walteri*

132   2.' Young petiole, midrib of lamina, inflorescence rachis, peduncle and pedicel covered by

133   sericeous or tomentose indumentum……………………………………………..…3

134   3. Lamina of larger leaves linear or narrowly oblong-oblanceolate, strongly conduplicate and

135   arranged on stem with short internodes (< 2 rarely 2.5 cm long)……..……....*H. rosmarinifolia*

136   3.' Lamina of larger leaves elliptical, lanceolate, oblong, obovate to ovate, not conduplicate and

137   arranged on stem with large internodes (≥ 2 cm long)…………………….…………….....4

138   4. Peduncle shorter than pedicel at anthesis, anthers irregularly pilose, styles dorsally apiculate at

139   apex…..*H. tocantinensis*

140   4.' Peduncle generally equaling pedicels or longer at anthesis, anthers glabrous, styles dorsally

141   obtuse or truncate at apex…………..…………….…………...……………………..*H. pannosa*

142

143   ***Heteropterys pannosa* Griseb. in Mart. Fl. Bras. 12(1): 70. 1858.**

144

145   (Figs. 1 and 2a–b)

146   ***Type***

147   [Brazil], Goyaz: Serra S. Felis bei Rio Custodio, *J.E. Pohl* 1940 [d 1 5 3 0] (Holotype: BR

148   barcode BR000000986917!, Isotypes: K barcode K000427071!, W-0069487!, W-0069488!).

149

150   ***Description***

151   Subshrub, 0.2–0.8 m tall, stems erect, cylindrical, 1–2(–3) mm diam., sericeous to glabrate with

152   age, lenticels not seen, unbranched or nearly so, all arising from a xylopodium. Leaves opposite

153   or occasionally 3-whorled on the same stem, internodes 2–4(–6.8) cm long; petiole (1.5–)3–5

154   mm long, densely sericeous to glabrate with age, eglandular; stipules not seen; lamina of larger

155   leaves 5.7–9(–11.7) cm long, (0.7–)1.1–3 cm wide, subcoriaceous to coriaceous, not

156   conduplicate, elliptical, lanceolate or oblong to slightly obovate, the base cuneate, rarely obtuse

157   or attenuate, the apex obtuse or sometimes (on the same stem) gradually tapered and becoming

158   acute or acuminate, the margins entire or rarely slightly revolute, densely sericeous or

159   tomentose-ferrugineous to irregularly glabrate with age on basal leaves and densely and

160   persistently sericeous or tomentose-ferrugineous on leaves closer to the inflorescence, glands

161   absent or inconspicuous, hidden by indumentum, the lateral veins and reticulum prominent,

162   especially on the abaxial surface. Inflorescence a pseudoraceme, axillary or terminal, erect, 3–

163   6.6 cm long, densely sericeous-ferrugineous, sometimes glabrate with age, with irregular

164   internodes between every 1 or 2 flowers, mostly comprising (4-)10-16 flowers distributed

165   throughout the rachis; bracts 3–4 mm long, 1–1.5 mm wide, lanceolate, densely sericeous,

166   margins entire, eglandular, persistent; peduncle 4–7(–10) mm long, 0.5–1 mm wide, densely

167   sericeous-ferrugineous; bracteoles apical, 1.5–2 mm long, 0.8–1.3 mm wide, ovate-lanceolate,

168   persistent, eglandular; pedicel 4–6(–10) mm long, 0.5–1 mm wide, uniformly slender, densely

169   sericeous-ferrugineous. Sepals 4.5–5.5 mm long, 1.5–2.5 mm wide, ovate, acute at apex, revolute

170   at anthesis, not appressed against filaments at anthesis, abaxially sericeous-ferrugineous,

171   adaxially glabrous, the anterior sepal eglandular, the 4 lateral sepals biglandular, the glands 1–2

172   mm diam., green. Petals not exposed in the enlarging bud, vivid yellow, glabrous,

173   membranaceous, not keeled, irregularly erose and eglandular at the margin, the posterior-lateral

174   and anterior-lateral petals similar to each other, spreading, the claw 1.5–3 mm long, the limb 3–5

175   mm long, 2.5–5 mm wide; posterior petal spreading, the claw 1–2 mm long, the limb 3.4–5 mm

176   long, 2.4–4.5 mm wide. Stamens with filaments strongly heteromorphic, glabrous, 2.6–4.4 mm

177   long, 0.9–1 mm wide at base, all straight and slender, basally connate; anthers 1.1–1.3 mm long,

178   glabrous, slightly reflexed at anthesis, all alike; the connective uniformly brown. Ovary 1–1.4

179   mm tall, densely sericeous-ferrugineous; styles slightly unequal, 3–3.7 mm long, larger than the

180   largest stamens, the anterior style straight and the 2 posterior styles slightly divergent at base,

181   glabrous, dorsally obtuse or truncate at apex; stigmas lateral, all 3 facing the center of the flower.

182   Mericarp with ellipsoidal nut, 7–11 mm long, 5–7 mm wide, with parallel longitudinal veins on

183   each side, sericeous to glabrate with age; lateral wings or crests absent; dorsal wing absent or

184   strongly reduced and not arising at style, ca. 1 mm wide; ventral areole 3–4 mm tall, ca. 2.5 mm

185   wide, ovate.

186

187 ***Distribution, phenology and conservation status***

188 *Heteropterys pannosa* occurs in Goiás State and for the first time is recorded for Minas Gerais

189 State (Fig. 3b). It grows in sandy soils (i.e., quartzite and plinthite formation) in grassy meadows

190 with subshrubs and small shrubs, and on rocky outcrops on the highest and driest slopes,

191 between 400 and 1700 m a.s.l. *Heteropterys pannosa* is often found in vegetation associated with

192 *Manihot* spp. (Euphorbiaceae). This species has been collected with buds and/or flowers in

193 March, April, June and from August to December. Fruits have been collected from November to

194 April. Although it has a wide extant of occurrence, *H. pannosa* is Endangered (EN) due to an

195 area of occupancy less than 40 km² [B2aii].

196

197 ***Additional Specimens Examined***

198 Brazil. Goiás: Mun. Alto Horizonte, região da Sururuca, Fazenda Cajás, 14º11'49''S,

199 49º16'42''W, ca. 404 m, 22 August 2016 (bud, fl), *J.E.Q. Faria* 6470 (HDJF, UB); Mun. Alto

200 Paraíso de Goiás, Chapada dos Veadeiros, ca. 25 km by road N of Alto Paraíso, 13º53'59.1''S,

201 47º23'48.9''W, ca. 1.700 m, 8 March 1973 (ste), *W.R. Anderson et al.* 6673 (MICH, NY, UB);

202 ca. 40 km by road of Alto Paraíso, 13º53'59.1''S, 47º23'48.9''W, ca. 1.500 m, 10 March 1973

203 (fr), *W.R. Anderson et al.* 6769 (MICH, NY, UB); Mun. Cavalcante, RPPN Serra do Tombador,

204 13º40'01''S, 47º48'04''W, without date (fl), *C.B.R. Munhoz et al.* 7971 (UB); RPPN Serra do

205 Tombador, 13º38'04''S, 47º49'06''W, ca. 857 m, 29 October 2011 (fl), *A.R.O. Ribeiro et al.* 278

206 (UB); Mun. Cristalina, 10 km by road N of Cristalina, 13º53'59.1''S, 47º23'48.9''W, ca. 1080

207 m, 3 April 1973 (fl, fr), *W.R. Anderson et al.* 8049 (MICH, NY, UB); ca. 5 km em direção a

208 Brasília, margem da Rodovia BR-040, 16º45'S, 47º40'W, 29 July 2007 (bud), *M.A. Silva* 6155

209 (IBGE, UB); ca. 5 km em direção a Brasília, lado esquerdo da BR-040, 7 January 2008 (fr), *M.A.*

210 *Silva* 6314 (CEPEC, IBGE); ca. 5 km of Cristalina, 17ºS, 48ºW, ca. 1.175 m, 2 November 1965

211 (fr), *H.S. Irwin et al.* 9794 (NY, RB, UB); Serra dos Cristais, ca. 3 km S of Cristalina, 17ºS,

212 48ºW, ca. 1.200 m, 3 March 1966 (fl), *H.S. Irwin et al.* 13381 (NY, UB); Serra dos Cristais, 5

213 km by road E of Cristalina, ca. 1.200 m, 5 April 1973 (ste), *W.R. Anderson* 8168, 8169, 8170,

214 8171 (MICH, UB); Serra dos Cristais, 6 km de Cristalina em direção a Unaí, GO-309, 10

215 September 1998 (bud, fl), *V.C. Souza et al.* 21412 (CEN, CEPEC, ESA, RB, SP); Serra dos

216 Cristais, 6 km de Cristalina em direção a Unaí, GO-309, 10 September 1998 (old fl), *V. C. Souza*

217 *et al.* 21378 (CEPEC, ESA, RB); Serra dos Cristais, 5 km S of Cristalina, 17ºS, 48ºW, ca. 1.175

218 m, 1 November 1965 (bud, fl), *H.S. Irwin et al.* 9735 (NY, UB); RPPN Linda Serra dos

219 Topázios, 16º45'S, 47º40'W, 29 October 1995 (bud, fl), *C. Proença & G. L. Moretto* 1315

220 (CEPEC, UB); Linda Serra dos Topázios, 16º45'S, 47º40 W, 26 October 1996 (ste), *C. Proença*

221 *& R.S. Oliveira* 1564 (UB); 16º45'S, 47º40 W, ca. 461 m, 9 km by road S of Catalão, 4 April

222 1973 (old fl), *W.R. Anderson* 8092 (MICH, UB); Serra dos Cristais, RPPN Linda Serra dos

223 Cristais, trilha que leva ao Poço da Diretoria, 16º45'S, 47º40'W, 23 March 1996 (fr), *G. L.*

224 *Moretto* 53 (UB); estrada de terra a NE de Cristalina, ca. 1.6 km da cidade, 16º44'49''S,

225 47º37'28''W, ca. 1.170 m, 16 December 2014 (fl), *J.B.A. Bringel et al.* 1137 (CEN); Mun.

226 Teresina de Goiás, descida para Cavalcante, 17 October 1990 (bud, fl), *G.M. Hatschbach & J.*

227 *M. Silva* 54683 (CEPEC, MBM, NY); GO-309, ca. 5 km do Mun. Teresina de Goiás, ca. 40 km

228 N Alto Paraíso de Goiás, a NE de Cristalina, 16º42'37''S, 47º35'23''W, 15 December 2014 (fr),

229 *J.B.A. Bringel et al.* 1127 (CEN, CEPEC); 13º53'59.1''S, 47º23'48.9''W, ca. 1.500 m, 16 March

230 1973 (bud, fl, fr), *W.R. Anderson et al.* 7156 (MICH, NY, UB), Fazenda Hotel Ecológico Alpes

231 Goianos, GO-118, km 202, 13º53'59.1''S, 47º23'48.9''W, 31 July 2000 (fr), *V.C. Souza et al.*

232 24795 (CEPEC, ESA, RB). Minas Gerais. Mun. Monte Azul, Serra da Formosa em frente ao

233 Pico da Formosa, 15º13'48''S, 42º48'14''W, 27 October 20 (bud, fl), *L.P. de Queiroz et al.*

234 15036 (CEPEC, HUEFS); Mun. Paracatu, ramal entrando a NE da BR-040, 16º47'58''S,

235 47º34'00''W, 30 October 20 (bud, fl), *L.P. de Queiroz et al.* 15056 (HUEFS, RB).

236

237 ***Remarks***

238   The type collection of *Heteropterys pannosa*, made by Johann Emanuel Pohl (1782–1834)

239 in Goiás State, does not have a date and is annotated with the enigmatic location of "Serra S. Felis

240 bei Rio Custódio." Based on the travel diary of Pohl that narrates the details of his journey in Brazil

241 (Pohl 1976), we assume that the type was collected on 8 July 1819, the only time Pohl was in this

242 locality. In this diary, Pohl also notes that the Custódio River is near the Traíras and Maranhão

243 rivers (Pohl 1976). An antique map of Goiás State (ArPDF 2020) shows "Chapada de São Félix"

244 (i.e., annotated by Pohl as "Serra de S. Felis"). This plateau is near the Maranhão River, which is

245 actually the Tocantins River. The point on the map for Goiás State (ArPDF 2020) is at 13° latitude.

246 We carefully looked at this region using Google Maps® and found the Custódio River, which is

247 part of the Tocantins River hydrographic basin. Thus, this region is probably the *H. pannosa* type

248 collection locality and is delimited by the municipalities of Minaçu in Goiás State and Paranã in
249 Tocantins State.

250

251   The vegetative morphology of *Heteropterys pannosa* is extremally variable (Fig. 1a–b,
252 d). In the type (*Pohl* 1940) and several other collections (e.g., *Souza* 24795, Fig. 1b), the shape of
253 the leaf lamina is elliptic. In other collections, the lamina is lanceolate (e.g., *Queiroz* 15056, Fig.
254 1d) or oblong-obovate (e.g., *Hatschbach* 54683, Fig. 1a, d). Further, many collections have
255 different lamina shapes on the same stem (i.e., especially *Anderson* 6673) and a large variation in
256 the indumentum density caused by the gradual loss of trichomes. For these reasons, the absence
257 of diagnostic differences in reproductive characteristics and the fact that many individuals occur
258 in sympatry in some areas (Anderson, pers. comm. 2003), we decided to define *H. pannosa*
259 within a broad concept. This position should be re-evaluated when extensive fieldwork can be
260 conducted throughout the area of occurrence and there are more and better specimens available
261 for study. The vegetative and reproductive characters of *H. pannosa* are illustrated for the first
262 time.

263

264   ***Heteropterys rosmarinifolia* R.F.Almeida & M.Pell. PhytoKeys 175: 47. 2021.**

265

266 (Figs. 2c–d and 4)

267 *Type*

268 Brazil. Goiás: Mun. Cavalcante, Reserva Natural Serra do Tombador, road GO-241, estrada de
269 terra para o Engenho II, a direita da estrada, 13°42'S, 47°48'W, 25 July 2014 (fl), *R. Sartin et al.*
270 576 (Holotype: UFRN barcode UFRN00024927!; Isotype: RB barcode RB01408371!).

271

272 *Description*

273 Subshrub, 0.2–0.8(–1.2) m tall, stems erect, cylindrical, 1.5–2 mm diam., densely sericeous to
274 glabrate with age, developing scattered lenticels, unbranched or nearly so, all arising from a
275 xylopodium. Leaves opposite or usually 3-4-whorled on the same stem, internodes 0.3–2(–2.5)
276 cm; petiole 1–3 mm long, sericeous to glabrate, eglandular; stipules ca. 0.5 mm long, persistent,
277 generally hidden by indumentum; lamina of larger leaves 1.3–11.4 cm long, 0.1–1.3 cm wide,
278 subcoriaceous to coriaceous, strongly conduplicate, linear or narrowly oblong-oblanceolate, the

279 base acute, the apex acuminate or rarely acute, the margins entire to slightly revolute, abaxial

280 surface very sparsely sericeous to glabrate with age or densely and persistently sericeous on

281 leaves near the inflorescence, sometimes with 2 large glands at base and usually a row of smaller

282 impressed and inconspicuous glands near or somewhat inside the margin, glands rarely absent,

283 adaxial surface glabrate, the lateral veins and reticulum prominent on both surfaces.

284 Inflorescence a pseudoraceme, axillary or terminal, erect, (1–)3.5–10.5 cm long, densely

285 sericeous-ferrugineous, with irregular internodes between each pair of flowers, mostly

286 comprising (4-)10-16 flowers distributed throughout the rachis; bracts 2–4 mm long, 0.7–1 mm

287 wide, linear-lanceolate, margins entire, eglandular or with 1-2 glands at base, the glands ca. 0.2

288 mm diam., persistent; peduncle 6–10 mm long, sericeous-ferrugineous; bracteoles apical, 1–2.8

289 mm long, 0.5–1 mm wide, lanceolate, persistent, eglandular or with 1-2 glands at base, the

290 glands ca. 0.2 mm diam.; pedicel 5–9(–11.5) mm long, 0.5–1.1 mm wide, uniformly slender,

291 sericeous-ferrugineous. Sepals 4–5.5 mm long, 1.5–2.3 mm wide, narrowly ovate, acute at apex,

292 revolute at anthesis, not appressed against filaments at anthesis, abaxially sericeous-ferrugineous,

293 adaxially green and glabrous, all eglandular or all biglandular or the anterior sepal eglandular

294 and the 4 lateral sepals biglandular, the glands 1–2 mm diam., green. Petals not exposed in the

295 enlarging bud, vivid yellow, glabrous, membranaceous, not keeled, irregularly erose and

296 eglandular at the margin, the posterior-lateral and anterior-lateral petals similar to each other,

297 spreading, the claw 1–3.7 mm long, the limb 3.5–6 mm long, 2.5–5.5 mm wide; posterior petal

298 spreading, the claw 1–2.5 mm long, the limb 3.4–5.3 mm long, 2.4–4 mm wide. Stamens with

299 filaments slightly heteromorphic, glabrous, 2.5–4.5 mm long, 0.9–1 mm wide, all straight and

300 slender, basally connate; anthers 1–1.2 mm long, glabrous, irregularly reflexed at anthesis, all

301 alike; the connective uniformly yellow. Ovary 1.1–1.5 mm tall, sericeous-ferrugineous; styles

302 slightly unequal, 3–3.5 mm long, larger than the largest stamens, the anterior style erect and

303 straight, the 2 posterior styles slightly divergent, glabrous, obtuse at apex; stigmas lateral, all 3

304 facing the center of the flower. Fruit unknown.

305

306 ***Distribution, phenology and conservation status***

307 The recently described *Heteropterys rosmarinifolia* was originally known from two specimens

308 collected in the Serra do Tombador Natural Reserve (Almeida & Pellegrini 2021) and was

309 therefore assessed as data deficient (DD) by the authors. We increased the distribution area of the

310   species to another protected area, Chapada dos Veadeiros National Park, which is also in

311   northern Goiás State (Fig. 3c). An extent of occurrence less than 3,000 km^2 and an area of

312   occupancy less than 16 km^2 means *H. rosmarinifolia* is Endangered (EN) based on IUCN (2017)

313   criteria, even though it occurs in two protected areas [B1 + B2a]. *Heteropterys rosmarinifolia*

314   grows in sandy savannas, between 1100 and 1300 m a.s.l. This species has been collected with

315   buds and/or flowers from July to September.

316

317   ***Additional Specimens Examined***

318   Brazil. Goiás: Mun. Alto Paraíso de Goiás, Parque Nacional da Chapada dos Veadeiros, Fazenda

319   São Bento, Córrego Almócegas, 14°09'58"S, 47°35'31"W, 10 August 2007 (bud, fl), *C. Proença*

320   *& S.A. Harris* 3384 (SP, UB); Fazenda São Bento, entre as Cachoeiras Almécegas I e São Bento,

321   14°10'22"S, 47°35'27"W, ca. 1.110 m, 30 June 2018 (bud), *P.Q. Rosa et al.* 2257 (HEPH, UB);

322   Rodovia Alto Paraíso de Goiás a Brasília, GO 118, 4 km do trevo sul de Alto Paraíso de Goiás,

323   14°10'37"S, 47°30'55"W, ca. 1.280 m, 04 September 2013 (bud, fl), *J.R. Pirani et. al.* 6421

324   (CEPEC, SPF); Mun. Cavalcante, caminho para a Cachoeira da Ave-Maria, ponto onde se vê a

325   cachoeira, 13º44'26"S, 46°52'46"W, 22 September 2015 (fl), *L. Rocha et al.* 668 (Paratypes:

326   CEPEC, HUEFS);

327

328   ***Remarks***

329   *Heteropterys rosmarinifolia* is redescribed here due to the analysis of a larger number of

330   collections. As noted by Almeida & Pellegrini (2021), this species is related to the Parabanisteria

331   group and very close to *H. pannosa*, although collections with fruits have not been found.

332   *Heteropterys rosmarinifolia* can be distinguished from the other species of the *H. pannosa*

333   complex by the linear or narrowly oblong-oblanceolate and strongly conduplicate laminae

334   arranged on short internodes. The vegetative and reproductive characters of this species are

335   illustrated for the first time. Some herbarium collections of *H. rosmarinifolia* were misidentified

336   as *Byrsonima linearifolia* A.Juss., a species with linear and strongly conduplicate leaves, also

337   present in the state of Goiás.

338

339   ***Heteropterys tocantinensis* Amorim & Francener *sp. nov.***

340

341 (Figs. 2e–f and 5)

342 *Type*

343 Brazil. Tocantins: Mun. Mateiros, Região do Jalapão, estrada Mumbuca a Boa Esperança,

344 próximo ao posto Naturantins, 10º23'38''S, 46º36'46''W, 8 December 2005 (bud, fl), *G.H. Rua*

345 *et al.* 681 (Holotype: CEN!; Isotype: CEPEC!).

346

347 *Diagnosis*

348 *Heteropterys tocantinensis* differs from the remaining *H. pannosa* species in the complex due to

349 its peduncle that is shorter than the pedicel at anthesis (vs. peduncle generally equaling the

350 pedicel or rarely longer), anthers irregularly pilose (vs. glabrous), styles dorsally apiculate (vs.

351 hooked, obtuse or truncate) and dorsal wing of mericarp present and 5–6 mm wide (vs. absent or

352 rarely reduced to an apical crest and 1–3 mm wide).

353

354 *Description*

355 Subshrub, ca. 1 m tall, stems erect, cylindrical, 2–4 mm diam., densely sericeous to glabrate with

356 age, developing small, scattered lenticels, all arising from a xylopodium. Leaves opposite,

357 arranged in internodes 3–4.6 cm long; petiole 2–3 mm long, sericeous to glabrate with age,

358 eglandular; stipules not seen; lamina of larger leaves (4.8–)6–9(–11.2) cm long, 2.8–6 cm wide,

359 coriaceous, oblong to slightly obovate, the base obtuse to cordate, the apex obtuse or slightly

360 cuspidate, the margins entire, adaxially sparsely sericeous, abaxially densely sericeous to early

361 glabrate, the midrib, primary, and secondary veins on both surfaces sericeous, sometimes with 2

362 glands abaxially at base near the midrib and usually with 6-8 smaller impressed glands in an

363 inframarginal row on each side of the lamina, the glands ca. 0.5 mm diam., the lateral veins and

364 reticulum strongly prominent on both surfaces. Inflorescence a pseudoraceme, mostly elongate,

365 axillary or terminal, erect, 5–11 cm long, sericeous to tomentose, with measurable and irregular

366 internodes between groups of 2-3 flowers, mostly comprising 6-21 flowers distributed

367 throughout the rachis; bracts persistent, 2–3 mm long, ca. 0.7 mm wide, abaxially tomentose,

368 ovate, margins entire, eglandular; peduncle 2–4 mm long, ca. 1 mm wide, tomentose; bracteoles

369 apical, 1.5–2 mm long, ca. 0.8 mm wide, abaxially tomentose, ovate, persistent, eglandular;

370 pedicel 6–8 mm long, ca. 1 mm wide, uniformly slender, tomentose. Sepals 3–3.3 mm long, 1.5–

371 1.7 mm wide, narrowly ovate, acute at apex, strongly revolute at anthesis, not appressed against

372   filaments at anthesis, abaxially tomentose, adaxially glabrous, the anterior sepal eglandular, the 4

373   lateral sepals biglandular, the glands 0.7–1.2 mm diam. Petals not exposed in the enlarging bud,

374   vivid yellow, glabrous, membranaceous, not keeled, erose and eglandular at the margin, the

375   posterior-lateral and anterior-lateral petals similar to each other, spreading, the claw 3–3.5 mm

376   long, the limb 7–7.5 mm long, 6–6.5 mm wide; posterior petal suberect, the claw 3–4 mm long,

377   the limb 5.5–6 mm long, 4–5 mm wide. Stamens with filaments slightly heteromorphic,

378   glabrous, 3–4.2 mm long, 0.3–0.5 mm wide, all straight and slender, basally connate; anthers

379   0.7–1 mm long, irregularly pilose, slightly reflexed at anthesis, all alike; the connective

380   proximally dark brown, distally pale yellow. Ovary 2–2.5 mm tall, densely sericeous-

381   ferrugineous; styles slightly unequal, 3.5–4.5 mm long, larger than the largest stamens, all

382   straight, somewhat divergent, glabrous, dorsally apiculate at apex; stigmas lateral, all 3 facing

383   the center of the flower. Mericarp with rounded nut, 6–8 mm long, ca. 6 mm wide, with

384   inconspicuous longitudinal veins, densely sericeous, the trichomes persistent; lateral wings or

385   crests absent; dorsal wing reduced and arising slightly at style, 5–6 mm wide, widest near distal

386   side of nut; ventral areole ca. 3 mm tall, ca. 2.8 mm wide, rounded.

387

Distribution, phenology and conservation status

389   *Heteropterys tocantinensis* occurs in the state of Tocantins, on the border of the states of Bahia

390   and Maranhão. A few records from the state of Mato Grosso were also found, on the border of

391   the state of Goiás (Fig. 3d). In these locations it grows from 400 to 700 m a.s.l. *Heteropterys*

392   *tocantinensis* is associated with clay soil, which is similar to *H. walteri* and differs from *H.*

393   *pannosa*, *H. rosmarinifolia*, and *H. veadeirensis* that are associated with sandy soils. The species

394   has been collected with buds and/or flowers in March and from September to January and with

395   fruits from September to November. Although *H. tocantinensis* has a broad extant of occurrence,

396   for now it should be considered Endangered (EN) [B2ii] because of its area of occupancy less

397   than 40 km^2. Additional expeditions in areas with clay soil in bordering states might reveal new

398   populations of *H. tocantinensis*.

399

Paratypes

401   Brazil. Bahia: Formosa do Rio Preto, ESEC Serra Geral do Tocantins, ca. 15 km NE da Vila dos

402   Prazeres, 10º42'58"S, 45º58'22"W, ca. 692 m, 3 October 2018 (fl), *M.F. Simon et al.* 3430

403 (CEN, RB); Estrada Formosa do Rio Preto para Mateiros, Fazenda Bom Jesus, 63 km de

404 Formosa do Rio Preto, 10º37'18"S, 45º26'55"W, ca. 700 m, 2 March 2015 (bud, fl), *Amorim et*

405 *al.* 9196 (CEPEC, RB); Mato Grosso: Mun. Barra do Garça, Parque Estadual da Serra Azul,

406 15º50'33"S, 52º16'49"W, 18 November 2008 (old fr), *E.S. Medeiros et al.* 517 (CEPEC, RB);

407 Mun. Torixoréu, 15º59'S, 52º22'W, 24 October 1977 (fr), *J.S. Costa* 67 (RB); Tocantins: Mun.

408 Dianópolis, 11º37'02"S, 46º24'53"W, ca. 628 m, 28 September 2003 (bud, fl), *T.B. Cavalcante*

409 *et al.* 3250 (CEN); Ponto 404, 11º33'35"S, 46º28'48"W, ca. 670 m, 24 September 2003 (bud),

410 *A.O. Scariot et al.* 672 (CEN); 11º36'48"S, 46º26'31"W, 27 September 2003 (fr), *A.O. Scariot et*

411 *al.* 902 (CEN, CEPEC); Mun. Mateiros, Estação Ecológica Serra Geral do Tocantins, próximo a

412 terra do Posseiro Manelão, 10º46'14"S, 46º43'10"W, ca. 461 m, 31 January 2015 (fl), *G.M.*

413 *Antar et al.* 748 (SPF); Região do Jalapão, estrada Mumbuca a Boa Esperança, próximo ao posto

414 Naturantins, 10º23'38"S, 46º36'46"W, 8 December 2005 (old fl), *G.H. Rua et al.* 680 (CEN);

415 Jalapão, próximo ao Rio Pedro de Amolar, 9 September 1995 (old fl), *M. Alves* 1062 (CEPEC,

416 HPN); Mun. Pindorama do Tocantins, ca. 37,4 km da BR-010, 11°20'49.56"S, 47°36'7.9"W, 5

417 October 2007 (fl), *J. Paula-Souza et al.* 8932 (CTES, SI, SPF).

418

419 ***Etymology***

420 The specific epithet refers to its occurrence near the Tocantins River basin in central Brazil.

421

422 ***Remarks***

423 For some vegetative characters, such as shape, consistency and size of the lamina, *Heteropterys*

424 *tocantinensis* resembles *H. pannosa* and *H. walteri.* However, the new species can be

425 differentiated by the stems and leaves covered by a sericeous indumentum that is early

426 caducuous (vs. stems and leaves glabrous in *H. veadeirensis* and densely and persistently hispid

427 in *H. walteri*). Also, in *H. tocantinensis* the peduncle is strongly reduced, the anthers are pilose

428 and the mericarp has a small dorsal wing, characteristics not observed in other species of this

429 complex. Most records of *H. tocantinensis* are from Tocantins State but this species is not

430 sympatric with *H. walteri,* which also occurs in Tocantins (see Fig. 3d, f). In herbarium

431 collections, *H. tocantinensis* was often misidentified as *H. byrsonimifolia* A. Juss., a very

432 common species that generally grows in highland savannas and on rock outcrops but has an

433 arborescent habit and paniculate inflorescence.

434

435 ***Heteropterys veadeirensis* Amorim & Francener *sp. nov.***

436

437 (Fig. 6)

438 ***Type***

439 Brazil. Goiás: Mun. Alto Paraíso de Goiás, estrada Alto Paraíso a Colinas, ca. 35 km de Alto

440 Paraíso, próximo a São Jorge, 14º10'S, 47º49'W, 2 August 2000 (bud, fl, fr), *R.C. Forzza et al.*

441 1671 (Holotype: SPF!; Isotypes: CEPEC!, RB!, UESC!).

442

443 ***Diagnosis***

444 *Heteropterys veadeirensis* differs from the remaining species in the *H. pannosa* complex due to

445 its glabrous stems, petiole and lamina (vs. densely hispid or sericeous to sparsely sericeous), very

446 sparsely sericeous to glabrate peduncle and pedicel (vs. densely hispid, sericeous or tomentose)

447 and styles dorsally short-hooked at the apex (vs. obtuse, truncate or slightly apiculate, except in

448 *H. walteri*).

449

450 ***Description***

451 Subshrub, 0.2–0.4 m tall, stems erect, cylindrical, ca. 1.5 mm diam., glabrous, lenticels not seen,

452 unbranched or nearly so, all arising from a xylopodium. Leaves opposite; petiole 1–2.5 mm long,

453 glabrous, eglandular; stipules minute protuberances, ca. 0.3 mm long, apparently absent from old

454 leaves; lamina of larger leaves (2.4–)5.5–9.7 cm long, (2.5–)4.3–5.9 cm wide, subcoriaceous to

455 coriaceous, oblong to ovate, rarely elliptic, the base rounded or cordate, the apex obtuse, rounded

456 or rarely acute, the margins entire, slightly revolute, glabrous, sometimes with 1-2 impressed

457 glands abaxially near the base and smaller glands irregularly scattered throughout lamina, the

458 lateral veins and reticulum prominent on both surfaces. Inflorescence a pseudoraceme, axillary or

459 terminal, erect, (5.2–)8.2–12.6(–17) cm long, glabrous or very sparsely sericeous on the distal

460 part of the rachis, with irregular internodes between each pair of flowers, mostly comprising 6-12

461 flowers distributed throughout the rachis; bracts 3–3.5 mm long, 0.5–0.7 mm wide, linear-

462 lanceolate, abaxially sericeous, margins entire, eglandular; peduncle (3–)6–9 mm long, very

463 sparsely sericeous to glabrate; bracteoles apical, 1–1.5 mm long, 0.5–0.7 mm wide, ovate to

464 lanceolate, abaxially sericeous, persistent, minutely glandular at margin; pedicel 5–6 mm long,

465   0.4–0.6 mm wide, uniformly slender, very sparsely sericeous to glabrate. Sepals 2.7–3 mm long,

466   1.5–2.5 mm wide, minutely oblong, acute at apex, revolute at anthesis, not appressed against

467   filaments at anthesis, abaxially sparsely sericeous-ferrugineous, adaxially glabrous, the anterior

468   sepal eglandular, the 4 lateral sepals biglandular, the glands 1–2 mm diam. Petals not exposed in

469   the enlarging bud, vivid yellow, glabrous, membranaceous, not keeled, erose and eglandular at

470   the margin, the posterior-lateral and anterior-lateral petals similar to each other, spreading, the

471   claw 3–5 mm long, the limb 5.7–7 mm long, 2.8–5 mm wide; posterior petal spreading, the claw

472   4–6 mm long, the limb 5–5.5 mm long, 4.5–5.5 mm wide. Stamens glabrous; filaments slightly

473   heteromorphic, 3–3.5 mm long, 0.3–0.5 mm wide, all straight and slender, basally connate;

474   anthers 0.7–1 mm long, slightly reflexed at anthesis, all alike; the connective proximally dark

475   brown, distally yellow. Ovary 1.5–2 mm tall, minutely sericeous; styles slightly equal, 2.5–3 mm

476   long, equaling or slightly exceeding the anthers, all erect and straight, glabrous, dorsally short-

477   hooked at apex; stigmas lateral, all 3 facing the anterior sepal. Mericarp with ellipsoidal or

478   rounded nut, 6–9 mm long, 5–6 mm wide, with several parallel longitudinal veins on each side,

479   sericeous to glabrate; lateral wings or crests absent; dorsal wing absent or strongly reduced to an

480   apical crest, a crest arising slightly at the style, ca. 1 mm wide; ventral areole 3–4 mm tall, ca. 2

481   mm wide, ovate.

482

483   ***Distribution, phenology and conservation status***

484   *Heteropterys veadeirensis* is restricted to northern Goiás State (Fig. 3e) and grows on rock

485   outcrops between 1000 and 1200 m a.s.l. This species has been collected with buds and/or

486   flowers from July to November and with fruits from August to October. Almost all records have

487   been made in a protected area called Chapada dos Veadeiros National Park; the only exception is

488   a collection made about 300 km to the south, in the municipality of Cristalina. Although these

489   specimens are protected and there is a considerable distance between the two localities, the

490   species is assessed as Endangered (EN) according to IUCN (2017) criteria. The extent of

491   occurrence is less than 4,000 km^2 and area of occupancy less than 28 km^2. We still do not know

492   if the specimens from Alto Paraíso de Goiás belong to only one population, but it is likely that

493   there are less than five populations [B1 + B2a]."

494

495   ***Paratypes***

496   Brazil. Goiás: Mun. Alto Paraíso de Goiás, 14º04'14"S, 47º54'54"W, 25 September 1995 (fr),

497   *M.L. Fonseca & F.C.A. Oliveira 547* (RB, SPF); Chapada dos Veadeiros, Estrada entre Alto

498   Paraíso e São Jorge, 14º08'08"S, 47º43'21"W, 15 October 2010 (bud, fl), *A. Francener et al.*

499   *1009* (CEPEC, UB, UFG, UFMT,); Estrada para o Vale da Lua, 14º10'25"S, 47º47'05"W, 15

500   October 2010 (bud, fl, fr), *A. Francener et al. 1021* (CEPEC, CGMS, UFG); próximo a sede do

501   Parque Nacional da Chapada dos Veadeiros,   14º09'32"S, 47º47'41"W, 16 October 2010 (bud,

502   fl), *A. Francener et al.* 1025 (CEPEC, UFG); Parque Nacional da Chapada dos Veadeiros,

503   14°10'29.3"S, 47°49'25.7" W, 3 October 2007 (fr), *J. Paula-Souza et al.* 8817 (SPF); 3 October

504   2007 (fl), *J. Paula-Souza et al.* 8818 (SPF); Rodovia GO-239 em direção a São Jorge, 32,5 km

505   do entroncamento com a GO-118, 14°09'47.2" S, 47°46'48.7" W, 4 October 2007 (fl), *J. Paula-*

506   *Souza et al.* 8872 (SPF); 4 October 2007 (fr), *J. Paula-Souza et al.* 8882 (SPF); Vale da Lua,

507   trilha para o Rio São Miguel, 14°11'19.95"S, 47°47'27.2"W, 21 October 1996 (fr), *R. Marquete*

508   *et al.* 2737 (RB); Mun. Cristalina, Lages, ca. 12 km ao sul de Cristalina, 16º52'20"S,

509   47º37'02"W, ca. 966 m, 30 July 2011 (fl), *J.E.Q. Faria et al.* 1499 (CEN, HUEG, UB); Mun.

510   São João da Aliança, Parque Nacional da Chapada dos Veadeiros, 29 November 1988 (old fl),

511   *T.B. Cavalcanti et al.* 26 (SPF).

512

513   ***Etymology***

514   The specific epithet refers to the region of Chapada dos Veadeiros, a wide formation of

515   mountains where this species is found. This region probably has the highest diversity of

516   Malpighiaceae on earth, including several endemic species in the group.

517

518   ***Remarks***

519   *Heteropterys veadeirensis* is distinguished from all other species in the *H. pannosa* complex by

520   its glabrous vegetative morphology. All the other species have simple and basifixed or Y-V-T-

521   shaped trichomes on the stems and leaves. The shape and size of *H. veadeirensis* leaves resemble

522   the old leaves of *H. tocantinensis* but most collections of this species have a distinctive

523   indumentum. *Heteropterys veadeirensis* is also distinguished by its lamina base that sometimes

524   has 1-2 impressed glands abaxially and smaller glands irregularly scattered throughout the

525   lamina. An isolated population know only from one specimen (*Faria* 1499) from an area in the

526   southern part of the Brazilian Federal District differs from all other specimens by having an

527   elliptical lamina shape (Fig. 6b). More representative collections from this area are needed to

528   confirm this difference.

529

530   ***Heteropterys walteri* Amorim & Francener *sp. nov.***

531

532   (Fig. 7)

533   ***Type***

534   Brazil. Goiás: Município Niquelândia, Estrada Niquelândia a Uruaçu, ca. 50 km Uruaçu,

535   14º19'42''S, 48º06'29''W, 15 July 2000 (bud, fl, fr), *V.C. Souza et al.* 23900 (Holotype: ESA!;

536   Isotypes: CEN!, CEPEC!, RB!, SP!, UESC!).

537

538   ***Diagnosis***

539   *Heteropterys walteri* differs from the remaining species in the *H. pannosa* complex due to its

540   stems, petiole, leaf midrib, inflorescence rachis, peduncle and pedicel densely and persistently

541   hispid (vs. densely or sparsely sericeous to glabrous) and abaxial and adaxial lamina surfaces

542   densely tomentose (vs. abaxial and adaxial lamina surfaces densely or sparsely sericeous to

543   glabrous).

544

545   ***Description***

546   Subshrub, 0.3–0.5 m tall, stems erect, cylindrical, ca. 4 mm diam., densely hispid to glabrate

547   with age, lenticels not seen, unbranched or nearly so, all arising from a xylopodium. Leaves

548   opposite or rarely 3-whorled on the same stem; petiole 3–5 mm long, densely hispid, eglandular;

549   stipules minute, ca. 0.5 mm long, hidden by indumentum; lamina of larger leaves (6.7–)8–11.8(–

550   14) cm long, 3.2–7.2 cm wide, coriaceous, oblong or slightly obovate, rarely elliptical, the base

551   cuneate or rarely obtuse, the apex rounded and often mucronate, the margins entire, abaxially

552   and adaxially densely tomentose, glabrescent with age, the midrib and primary veins on both

553   surfaces densely hispid, sometimes with 2 large glands abaxially at base and usually with 7-13

554   smaller impressed glands in an inframarginal row on each side of the lamina or rarely glands

555   absent, the glands ca. 0.5 mm diam., the lateral veins and reticulum prominent on abaxial

556   surface. Inflorescence a pseudoraceme, mostly elongate, axillary or terminal, erect, 8–16(–19.5)

557   cm long, densely hispid, with measurable and irregular internodes between each groups of 2-3

558 flowers, mostly comprising 14-21 flowers distributed throughout the rachis; bracts persistent, 2–
559 3 mm long, ca. 1 mm wide, abaxially densely hispid to tomentose, linear-lanceolate, margins
560 entire, eglandular or with 1-2 glands near the base, the glands ca. 0.5 mm diam., generally hidden
561 by indumentum; peduncle 5–8 mm long, ca. 1 mm wide, densely hispid; bracteoles apical, 1.7–2
562 mm long, ca. 0.5 mm wide, abaxially densely hispid to tomentose, linear-lanceolate, persistent,
563 eglandular or with 1-2 glands near the base, the glands ca. 0.3 mm diam., hidden by
564 indumentum; pedicel 5.5–7 mm long, ca. 1 mm wide, uniformly slender, densely hispid. Sepals
565 3.5–4 mm long, 1.5–2 mm wide, narrowly ovate, acute at apex, revolute at anthesis, not
566 appressed against filaments at anthesis, abaxially densely tomentose, adaxially glabrous, the
567 anterior sepal eglandular, the 4 lateral sepals biglandular, the glands 1–1.5 mm diam. Petals not
568 exposed in the enlarging bud, vivid yellow, glabrous, membranaceous, not keeled, erose and
569 eglandular at the margin, the posterior-lateral and anterior-lateral petals similar to each other,
570 spreading, the claw 3–4 mm long, the limb 3.5–4.5 mm long, 3.5–4.5 mm wide; posterior petal
571 spreading, the claw 3.5–4 mm long, the limb 5–5.3 mm long, 4–4.4 mm wide. Stamens with
572 filaments heteromorphic, glabrous, 2.5–3 mm long, 0.3–0.5 mm wide, all straight and slender,
573 basally connate; anthers 0.8–1 mm long, glabrous, slightly reflexed at anthesis, all alike; the
574 connective proximally dark brown, distally yellow. Ovary 1.3–1.5 mm tall, densely sericeous-
575 ferrugineous; styles slightly unequal, 1.7–2 mm long, equaling or slightly exceeding the anthers,
576 the anterior style erect and straight, the 2 posterior styles divergent, glabrous, dorsally short-
577 hooked at apex; stigmas lateral, all 3 facing the center of the flower. Mericarp with rounded nut,
578 9–12 mm long, 7–10 mm wide, with several parallel longitudinal veins on each side, densely
579 sericeous-ferrugineous, the trichomes persistent; lateral wings or crests absent; dorsal wing
580 absent or strongly reduced to an apical crest, a crest arising slightly at the style, 1–3 mm wide,
581 widest near distal side of nut; ventral areole 3–5 mm tall, 3–5 mm wide, ovate.
582

583 ***Distribution and conservation status***
584 *Heteropterys walteri* occurs on the border of the states of Goiás and Tocantins (Fig. 3f) and is
585 generally associated with clay soil between 280 and 940 m a.s.l. This species has been collected
586 with buds and/or flowers in March and from July to December and with fruits in March and from
587 July to November. Most specimens were collected along highways and roads, although many
588 collections were recently made in the Serra do Tombador Natural Reserve Protection Area in

589 Goiás State. Based on an area of occupancy less than 96 km², *H. walteri* can be considered

590 Endangered (EN). The list of paratypes is long but most of these collections were made outside

591 protected areas and close to urban areas and roads, which interfere with the habitat quality

592 [B2bii, iii].

593

594 ***Paratypes***

595 Brazil. Goiás: Mun. Campinaçu, Estrada Niquelândia a Campinaçu, 14º03'S, 48º30'W, ca. 420

596 m, 6 October 1995 (bud, fl), *T. B. Cavalcante et al.* 1812 (CEN); Região da Fazenda Praia

597 Grande, ca. 6 km após o córrego Praia Grande, 13º59'S, 48º23'W, ca. 430 m, 6 October 1995

598 (bud, fl), *B.M.T. Walter et al.* 2680 (CEN); Mun. Cavalcante, Estrada Balsa Porto dos Paulistas,

599 Rio Tocantins, Buracão e Curral de Pedra, a ca. 5.8 km do rio, 13º27'43''S, 48º07'16''W, ca.

600 410 m, 9 November 2000 (old fl), *G. Pereira-Silva et al.* 4379 (CEN, CEPEC); Estrada Canteiro

601 da Obra do Rio São Félix, km 12, 13º22'32''S, 48º03'49''W, ca. 430 m, 19 September 2001 (fr),

602 *G. Pereira-Silva et al.* 5389 (CEN, CEPEC); Estrada de acesso ao Rio Traíras, ca. 9 km da

603 cidade, 12º20'07''S, 48º08'33''W, ca. 350 m, 27 November 2007 (fr), *G. Pereira-Silva* 12375

604 (CEN); Estrada entre Cavalcante e Minaçú, 77 km de Cavalcante, 13º38'06''S, 47º48'07''W, ca.

605 860 m, 24 July 2014 (bud, fl), *M.F. Simon & L.M. Borges* 2473 (CEN); RPPN Serra do

606 Tombador, ca. 12 km no sentido a Cavalcante, 13º38'02''S, 47º44'46''W, ca. 908 m, 11

607 November 2014 (fr), *M. Mendoza et al.* 4385a (CEN); Reserva Natural da Serra do Tombador,

608 Campina, 13º42'S, 47º47'W, 21 August 2017 (bud, fl), *H.L. Zirondi* 39 (CEN, HRCB); Reserva

609 Natural da Serra do Tombador, Estrada GO 241, Cavalcante a Minaçu, 3,5 km após a sede da

610 reserva, 13º40'49''S, 47º49'12''W, 5 March 2017 (fr), *C.O. Andrino et al.* 406 (CEN); Mun.

611 Colinas do Sul, Estrada pelo dique 2 na direção do Rio Tocantins, próximo a Serra da

612 Mesa/Colinas, 13º53'S, 48º19'W, ca. 410 m, 20 October 1996 (fr), *B.M.T. Walter et al.* 3487

613 (CEN); Mun. Minaçu, Serra da Mesa, a 7 km do canteiro de obras, 13º34'S, 48º10'W, ca. 840 m,

614 11 October 1991 (old fl), *T.B. Cavalcante et al.* 1027 (CEN); Mun. Niquelândia, Embarcadouro

615 da CODEMIM, após o portão principal, 14º08'54"S, 48º19'34''W, 14 December 1998 (old fl),

616 *A.A. Santos et al.* 371 (CEN, CEPEC); Estrada Niquelância a Indaianópolis, ca. 10 km sw

617 Indaianópolis, 14º14'29.9''S, 48º32'36.1''W, 11 September 1998 (old fl), *V.C. Souza et al.*

618 21528 (ESA); Estrada Niquelândia a Colinas, 14°21'S, 48°06'W, 17 September 1998 (bud, fl),

619 *E.L. Jacques et al.* 796 (CEN, SP); Estrada Niquelândia a Uruaçu, ca. 25 km de Uruaçu,

620 14º19'42''S, 48º06'29''W, 12 September 1998 (bud, fl), *V.C. Souza et al.* 21569 (CEPEC, ESA,

621 RB); Estrada de chão vicinal à Rodovia GO-132, 14º19'44''S, 48º06'33''W, ca. 557 m, 27

622 November 2014 (fr), *J.A. Oliveira et al.* 513 (CEN, CEPEC, RB); Mun. São João da Aliança,

623 Serra Geral do Paranã, ca. 3 km de São João, 14°33'59"S, 47°22'38"W, ca. 850 m, 16 March

624 1971 (bud, fl), *H.S. Irwin et al.* 31940 (NYBG, UB). Tocantins, Mun. Paranã, Canteiro de Obras

625 do UHE São Salvador, 12º48'18''S, 48º13'59''W, ca. 260 m, 19 October 2006 (bud, fl, fr), *G.*

626 *Pereira-Silva et al.* 10898 (CEN); Estrada de acesso ao vilarejo Rozario, ca. 3 km após a entrada

627 principal da obra, 12º47'42''S, 48º11'58''W, 24 March 2007 (old fl); *G. Pereira-Silva et al.*

628 11462 (CEN); 12º49'33''S, 48º13'14''W, 27 September 2007 (bud, fl); *G. Pereira-Silva et al.*

629 12111 (CEN, CEPEC) .

630

631 ***Etymology***

632 The epithet honors Dr. Bruno Machado Teles Walter, a researcher at the Embrapa Recursos

633 Genéticos e Biotecnologia (CENARGEN) and Curator at the CEN herbarium. Besides collecting

634 some of the paratypes, he has conducted several important studies about community structure in

635 the Cerrado domain.

636

637 ***Remarks***

638 *Heteropterys walteri* is notable for its stems, petiole, leaf midrib, inflorescence rachis, peduncle

639 and pedicel covered by a densely hispid indumentum, which is mostly formed by simple and

640 basifixed trichomes. In some collections, especially those with old flowers and fruits, the lamina

641 indumentum on both surfaces is glabrescent, which often makes it difficult to distinguish this

642 species from some relatives. Within this difficult species complex, *H. walteri* is also

643 distinguished by its long inflorescence rachis (reaching up to 19.5 cm) with more than 20 flowers

644 in some specimens. This species resembles *H. tocantinensis* in leaf shape (for more detail, see

645 comments above). In herbarium collections, *H. walteri* is often misidentified as *H. duarteana* A.

646 Juss., a species that is also present in the Cerrado domain but has a shrubby habit with no

647 xylopodium, large paniculate inflorescence and mericarps with a well-developed dorsal wing.

648

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744

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751

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761

762 Competing Interests

763 The authors declare there are no competing interests.

764

765 Author Contributions

766 André M. Amorim conceived and designed the experiments, performed the experiments,

767 analyzed the data, designed figures 1 and 3–6, and wrote and reviewed drafts of the manuscript.

768 Lucas C. Marinho prepared figures 2 and 3, adjusted figures 1 and 3–6, wrote the distribution

769 and conservation status for all species and reviewed drafts of the manuscript.

770 Augusto F. Gonzaga analyzed the data and wrote and reviewed drafts of the manuscript.

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Figure Legends

Figure 1 *Heteropterys pannosa*. (A) Habit with a xylopodium. (B) Fruiting branch from different individual. (C) Detail of stem and leaf base. (D) Leaves in abaxial view showing the variation in lamina shape. (E) Detail of leaf margin showing the indumentum. (F) Floral bud in lateral view. (G) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (H) Androecium in adaxial view. (I) Gynoecium showing anterior style at center. (J) Detail of stigma. (K) Nut in lateral view. (A, C, E–J from Hatschbach 54683, B from Souza 24795, D from Hatschbach 5468 (left) and Queiroz 15056 (right), K from Moretto 53).

Figure 2 *Heteropterys pannosa*. (A) Habit with detail of a nut. (B) Detail of the inflorescence. *Heteropterys rosmarinifolia*. (C) Habit. (D) Detail of an inflorescence. *Heteropterys tocantinensis* (E) Habit. (F) Detail of an inflorescence. (Photos A–B by HG Silva, C–D by C Proença, E–F by GM Antar).

Figure 3 Geographic distribution of *Heteropterys pannosa* and related species. (A) General distribution of *H. pannosa* complex by Brazilian state based on all specimens. (B) Distribution of *H. pannosa* (red triangle shows the probable type locality of this species). (C) Distribution of *H. rosmarinifolia*. (D) Distribution of *H. tocantinensis*. (E) Distribution of *H. veadeirensis*. (F) Distribution of *H. walteri*. Maps produced using the SimpleMappr website (Shorthouse 2010).

Figure 4 *Heteropterys rosmarinifolia*. (A) Habit with a xylopodium. (B) Detail of stem and leaf base. (C) Detail of stem, showing the indumentum. (D) Leaf in abaxial view and detail of a transversal section. (E) Detail of leaf in abaxial view. (F) Detail of leaf in adaxial view. (G) Floral bud in lateral view. (H) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (I) Androecium in adaxial view. (J) Gynoecium showing anterior style at center. (K) Detail of stigma. (A–K from Pirani 6421).

Figure 5 *Heteropterys tocantinensis*. (A) Habit with a xylopodium. (B) Flowering branch from different individual. (C) Detail of stem and leaf base. (D) Leaf in abaxial view. (E) Details of leaf margin showing the glands, abaxial view. (F) Floral bud in lateral view. (G) Petals:

803   posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (H)

804   Androecium in adaxial view. (I) Gynoecium showing anterior style at center. (J) Detail of

805   stigma. (K) Nut in lateral view. (A, C–J from Rua 681, B from Amorim 9196, K from Rua 680).

806

807   Figure 6 *Heteropterys veadeirensis*. (A) Habit with a xylopodium, showing enlargement of stem

808   and leaf base. (B) Flowering branch from different individual. (C) Detail of stem. (D) Leaf in

809   abaxial view. (E) Details of leaf margin in abaxial view. (F) Details of leaf margin in adaxial

810   view. (G) Floral bud in lateral view. (H) Petals: posterior – p and posterior-lateral – pl in

811   adaxial view; anterior-lateral – al in abaxial view. (I) Androecium in adaxial view. (J)

812   Gynoecium showing anterior style at center. (K) Detail of stigma. (L) Nut in lateral view. (A,

813   C–L from Forzza 1671, B from Faria 1499).

814

815   Figure 7 *Heteropterys walteri*. (A) Habit with a xylopodium. (B) Detail of stem and leaf base.

816   (C) Detail of stem showing the indumentum. (D) Leaf in abaxial view. (E) Details of young leaf

817   margin showing the glands, abaxial view. (F) Details of old leaf margin in adaxial view. (G)

818   Floral bud in lateral view. (H) Petals: posterior – p and posterior-lateral – pl in adaxial view;

819   anterior-lateral – al in abaxial view. (I) Androecium in adaxial view. (J) Gynoecium showing

820   anterior style at center. (K) Detail of stigma. (L) Nut in lateral view. (A–K from Souza 23900, L

821   from G. Pereira-Silva 5389).

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Figure 1

Heteropterys pannosa.

Figure 1 *Heteropterys pannosa*. (A) Habit with a xylopodium. (B) Fruiting branch from different individual. (C) Detail of stem and leaf base. (D) Leaves in abaxial view showing the variation in lamina shape. (E) Detail of leaf margin showing the indumentum. (F) Floral bud in lateral view. (G) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (H) Androecium in adaxial view. (I) Gynoecium showing anterior style at center. (J) Detail of stigma. (K) Nut in lateral view. (A, C, E–J from Hatschbach 54683, B from Souza 24795, D from Hatschbach 5468 (left) and Queiroz 15056 (right), K from Moretto 53).
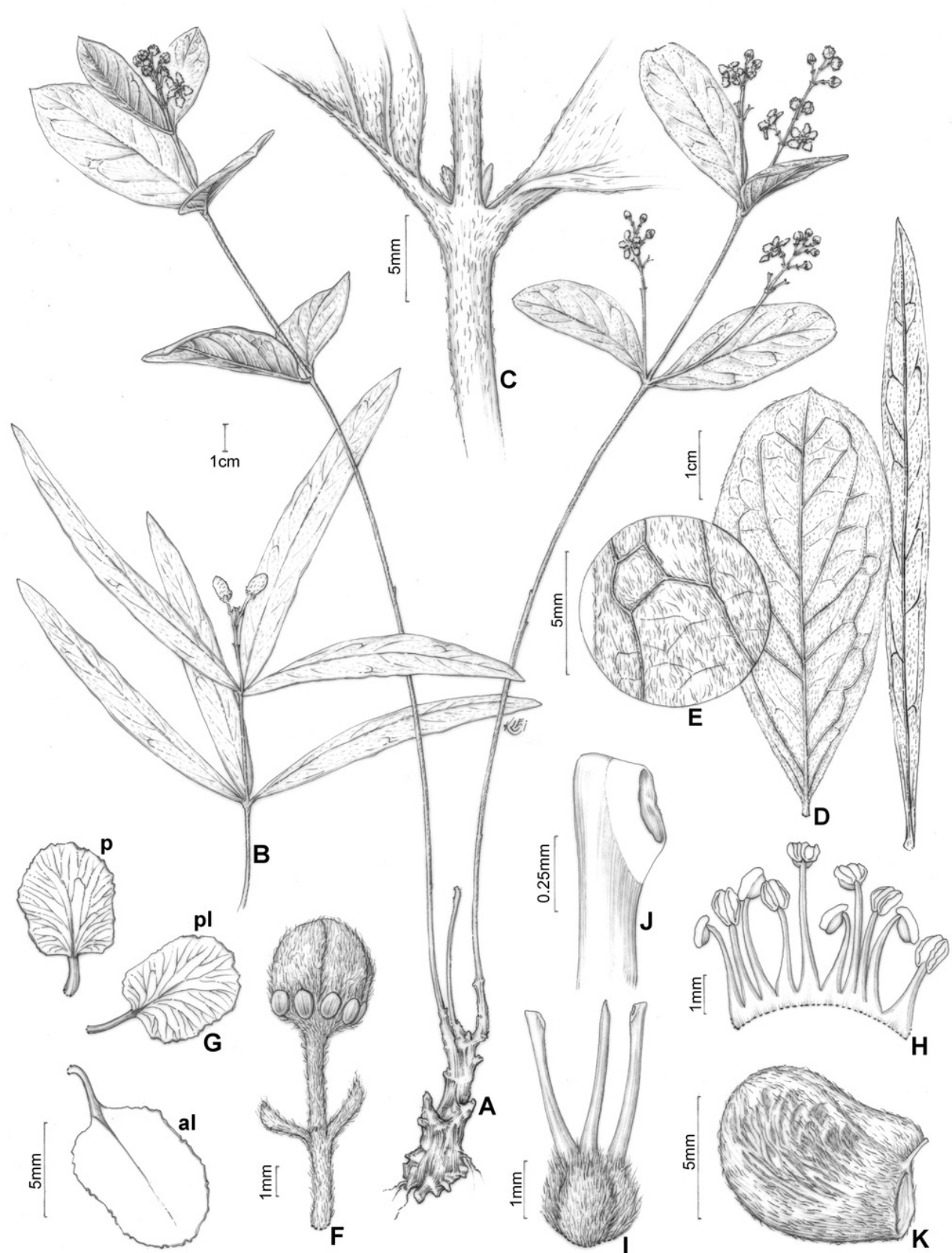
Figure 2

Heteropterys pannosa complex.

Figure 2 *Heteropterys pannosa*. (A) Habit with detail of a nut. (B) Detail of the inflorescence. *Heteropterys rosmarinifolia*. (C) Habit. (D) Detail of an inflorescence. *Heteropterys tocantinensis* (E) Habit. (F) Detail of an inflorescence. (Photos A–B by HG Silva, C–D by C Proença, E–F by GM Antar).

Figure 3

Geographic distribution of *Heteropterys pannosa* and related species.

Figure 3 Geographic distribution of *Heteropterys pannosa* and related species. (A) General distribution of the *H. pannosa*complex by Brazilian states based in all specimens. (B) Distribution of the *H. pannosa* (red triangle shows the probable type locality of this species). (C) Distribution of the *H. rosmarinifolia*. (D) Distribution of the *H. tocantinensis*. (E) Distribution of the *H. veadeirensis*. (F) Distribution of the *H. walteri*. Maps produced using the SimpleMappr website (Shorthouse 2010).
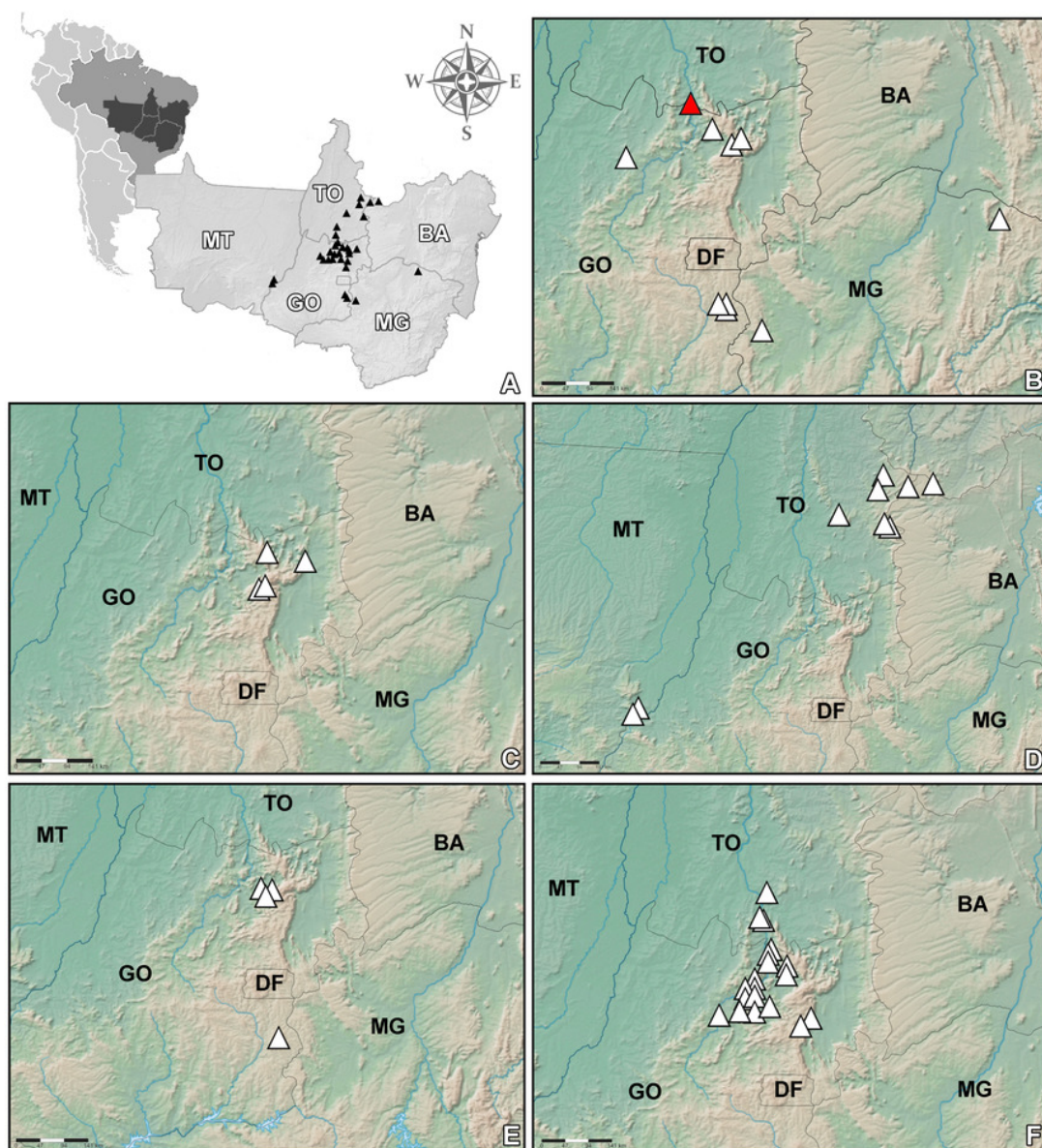
Figure 4

Heteropterys rosmarinifolia.

Figure 4 *Heteropterys rosmarinifolia*. (A) Habit with a xylopodium. (B) Detail of stem and leaf base. (C) Detail of stem, showing the indumentum. (D) Leaf in abaxial view and detail of a transversal section. (E) Detail of leaf in abaxial view. (F) Detail of leaf in adaxial view. (G) Floral bud in lateral view. (H) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (I) Androecium in adaxial view. (J) Gynoecium showing anterior style at center. (K) Detail of stigma. (A–K from Pirani 6421).
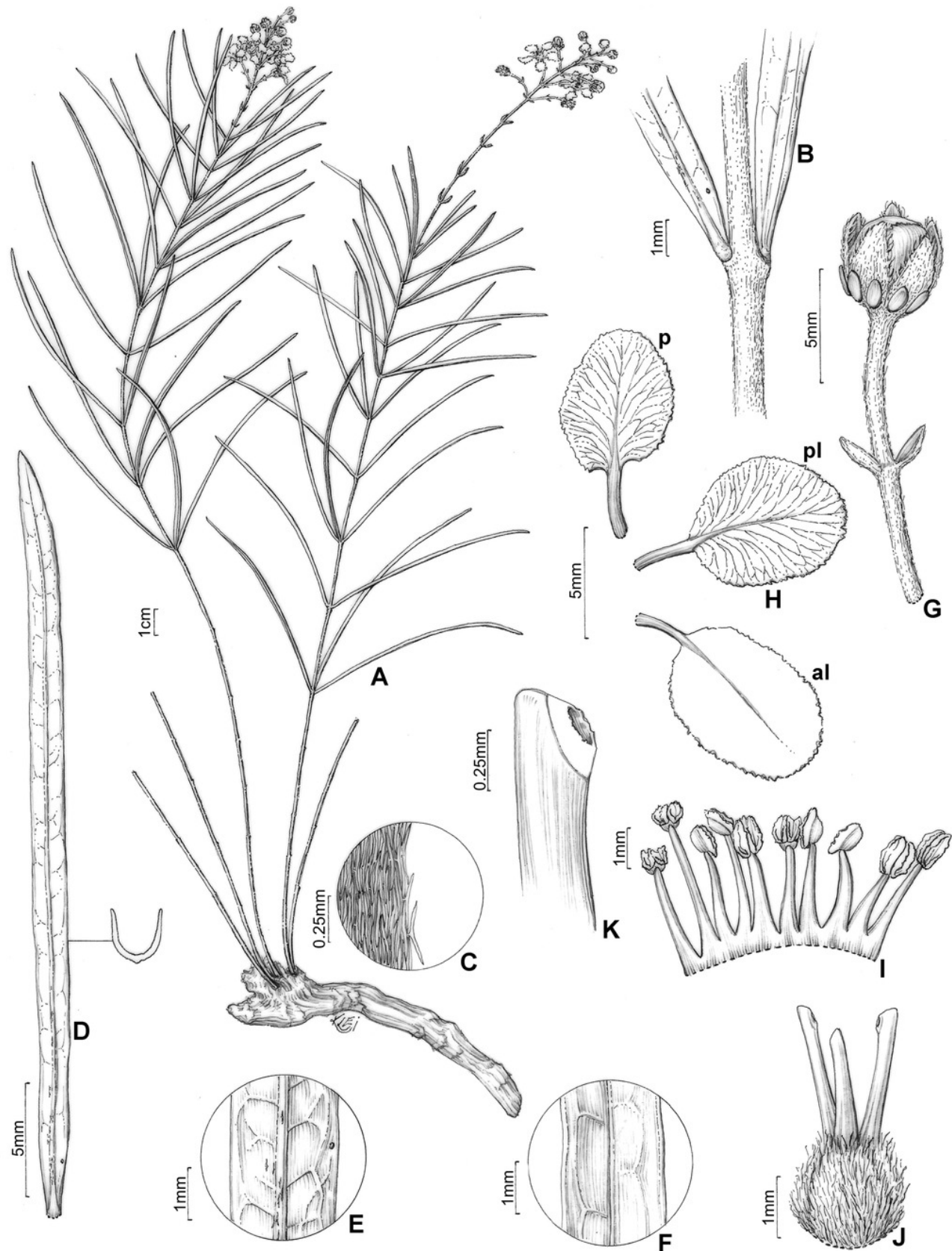
Figure 5

Heteropterys tocantinensis.

Figure 5 *Heteropterys tocantinensis*. (A) Habit with a xylopodium. (B) Flowering branch from different individual. (C) Detail of stem and leaf base. (D) Leaf in abaxial view. (E) Details of leaf margin showing the glands, abaxial view. (F) Floral bud in lateral view. (G) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (H) Androecium in adaxial view. (I) Gynoecium showing anterior style at center. (J) Detail of stigma. (K) Nut in lateral view. (A, C–J from Rua 681, B from Amorim 9196, K from Rua 680).
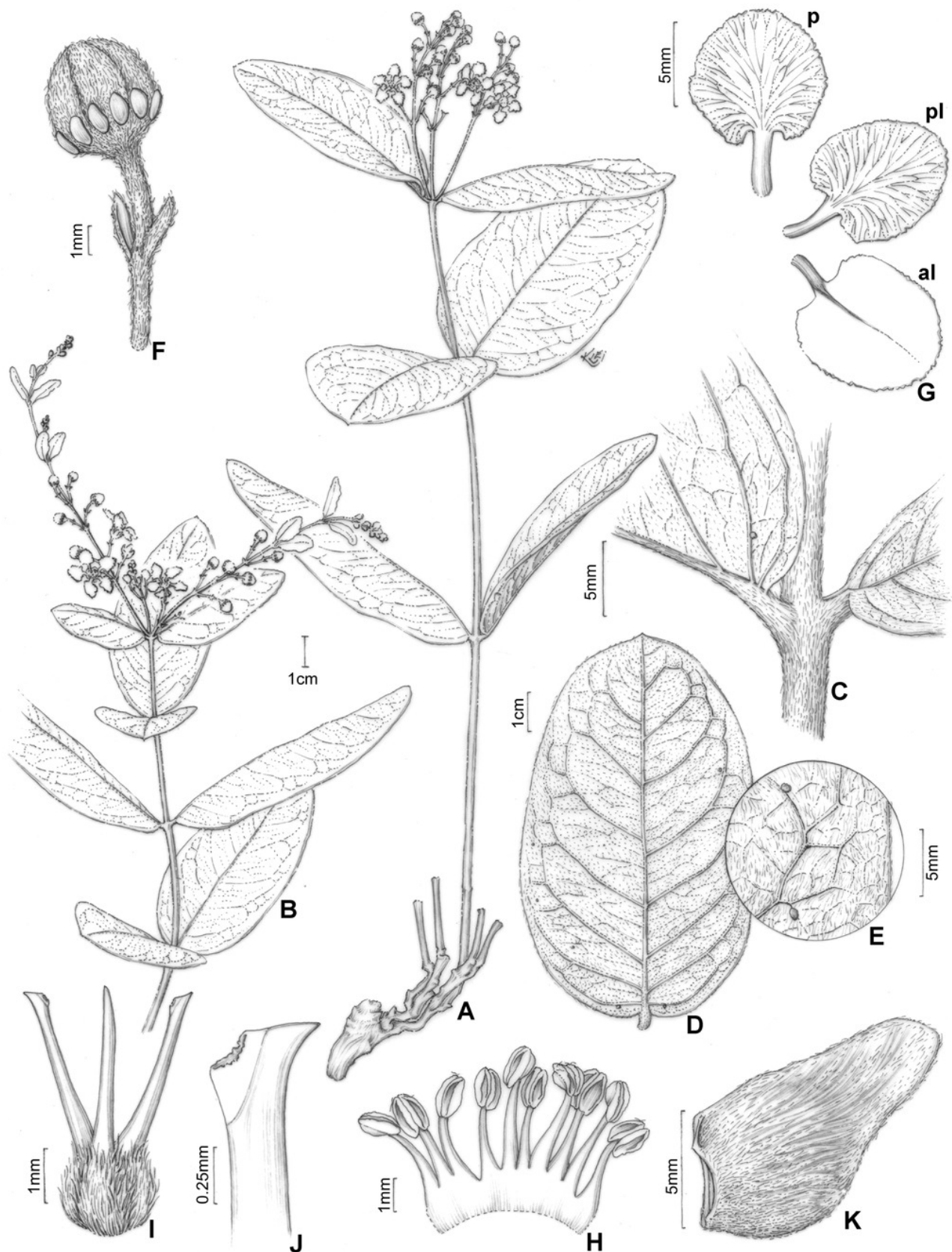
Figure 6

Heteropterys veadeirensis.

Figure 6 *Heteropterys veadeirensis*. (A) Habit with a xylopodium, showing enlargement of stem and leaf base. (B) Flowering branch from different individual. (C) Detail of stem. (D) Leaf in abaxial view. (E) Details of leaf margin in abaxial view. (F) Details of leaf margin in adaxial view. (G) Floral bud in lateral view. (H) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (I) Androecium in adaxial view. (J) Gynoecium showing anterior style at center. (K) Detail of stigma. (L) Nut in lateral view. (A, C–L from Forzza 1671, B from Faria 1499).

Figure 7

Heteropterys walteri.

Figure 7 *Heteropterys walteri*. (A) Habit with a xylopodium. (B) Detail of stem and leaf base. (C) Detail of stem showing the indumentum. (D) Leaf in abaxial view. (E) Details of young leaf margin showing the glands, abaxial view. (F) Details of old leaf margin in adaxial view. (G) Floral bud in lateral view. (H) Petals: posterior – p and posterior-lateral – pl in adaxial view; anterior-lateral – al in abaxial view. (I) Androecium in adaxial view. (J) Gynoecium showing anterior style at center. (K) Detail of stigma. (L) Nut in lateral view. (A–K from Souza 23900, L from G. Pereira-Silva5389).