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Anisophylly in South American Acanthaceae

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Abstract: Attention is drawn to the nature and occurrence of anisophylly in South American species of Acanthaceae. Consultation of existing scientific literature and herbarium records has enabled the compilation of an extensive list of Acanthaceae species known to exhibit the phenomenon within the region, where it is most common in *Justicia* L., *Lepidagathis* Willd., *Sanchezia* Ruiz & Pav., and *Pseuderanthemum* Radlk. Some insights are drawn into the occurrence, systematic patterns, and potential ecological implications of anisophylly in this family, but the character is shown to be of limited use in species diagnosis. Six new species of *Justicia* from Peru, Ecuador and Colombia that exhibit this unusual morphological characteristic are described, *J. impar* J.R.I.Wood & P.Gallego, *J. imparifolia* J.R.I.Wood & P.Gallego, *J. maynasana* J.R.I.Wood & P.Gallego, *J. microcalyx* J.R.I.Wood & P.Gallego, *J. obliqua* J.R.I.Wood & P.Gallego and *J. yariguiorum* P.Gallego & J.R.I.Wood. The paper is illustrated with maps and line drawings. Notes on related species, distribution and conservation are provided.

Key words: Asymmetric leaves, Colombia, Ecuador, New species, Peru, Taxonomy.

Introduction

Acanthaceae Juss. comprise a species-rich angiosperm family with *c*. 4900 species and 191 genera currently recognized (Manzitto-Tripp *et al*., 2022). The family consists of herbs and subshrubs (trees are rare) which are characterized by the presence of simple and opposite leaves, often with cystoliths, and bisexual flowers with corolla sympetalous and often 2-lipped (Simpson, 2019). Current classifications of Acanthaceae (Manzitto-Tripp *et al*., 2022; Scotland & Vollesen, 2000) recognize four subfamilies: Nelsonioideae, Avicennioideae, Thunbergioideae, and Acanthoideae, the last of which exhibits the highest taxonomic diversity and possesses the distinctive fruit in which the seeds are borne on small outgrowths that serve as ejaculators. Species are concentrated in the tropical and subtropical regions of the world, with a smaller number of taxa present in temperate latitudes. South America is considered one of the most important centres of diversity of the family due to the great heterogeneity of habitats, ecosystems and biotic interactions that have favoured speciation (Tripp & Tsai, 2017) resulting in at least 54 genera and *c*. 1250 species being reported (Ulloa Ulloa *et al*., 2017). This diversity encompasses a remarkable morphological variability expressed mainly in terms of habit, floral forms, pollen types and vegetative attributes, some of which remain poorly understood, including anisophylly discussed in this paper.

Variation in leaf size and shape may arise by a number of different mechanisms. Heterophylly is a type of phenotypic plasticity whereby the leaves of some plant species can undergo considerable form alteration in response to environmental conditions (Li *et al*., 2019). This phenomenon is well-known in many plants, notably aquatic species which develop floating leaves which differ considerably from the usually narrower leaves that develop below the water's surface (Arber, 1919). In contrast, anisophylly refers to a condition in which the two leaves in an opposite pair differ in size and/or form from each other and is far more rarely noted or commented on. Yet it is a relatively common feature noted in various families including Gesneriaceae, Melastomataceae, Urticaceae (Dengler, 1999; Esquivel Muelbert *et al*., 2010) and Solanaceae as well as in Acanthaceae discussed in this paper. According to Goebel (1928)

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anisophylly can occur in two forms: habitual anisophylly, which is consistently persistent in the adult shoot system and is associated with creeping or climbing habits, and lateral anisophylly where the condition is restricted to plagiotropic lateral branches and is linked with taxa with orthotropic, isophyllous main axes. In some taxa, the expression of habitual anisophylly could be facultative and varies in response to changes in environmental factors (Morley, 1973, 1974). Additionally, lateral anisophylly could be reversible, as removing the main orthotropic shoot results in a reorientation of plagiotropic shoots and loss of anisophylly (Dengler, 1999). Therefore, the taxonomic significance of both types of anisophylly as a diagnostic character is unclear. Esquivel Muelbert *et al*. (2010) suggest that anisophylly may be related to efficiency in light capture by reducing the amount of self-shading but this is speculative and seems improbable. Apart from this, as far as we are aware, no one has suggested an evolutionary value in anisophylly and there is no obvious explanation for its occurrence.

As far as we are aware, the first mention of anisophylly in Acanthaceae is the description of *Ruellia anisophylla* Wall. ex Hook. (Hooker, 1826: t. 191) based on a manuscript name by Nathaniel Wallich. The accompanying illustration shows a strongly anisophyllous plant with one leaf much reduced in size and with a distinctive zigzag stem, which is often associated with anisophylly. Hooker comments: "The appearance of the plant is most singular for one of its natural family; one of each alternate pair of leaves being so small as to be scarcely perceptible." The implication being that this was the first time anisophylly had been observed in Acanthaceae.

The history of the taxonomic treatment of *Ruellia anisophylla* has wider significance. In *Plantae Asiaticae Rariores*, Nees von Esenbeck (1832: 88) accepted the species, transferring it to the genus *Goldfussia* as *G. anisophylla* (Wall. ex Hook.) Nees. In the same work, he went on to describe a *Goldfussia isophylla* Nees, which resembled *G. anisophylla* differing only in a few additional minor characters apart from the equal leaves. Clarke (1884) in the *Flora of British India* treated both species in *Strobilanthes* and with more material available commented on *S. anisophyllus* (sic) "except in the unequal slightly broader leaves, this wholly agrees with *S. isophyllus* (sic); and as *S. isophyllus* cannot be found wild, it may prove a reversionary (under cultivation) form of *S. anisophyllus*." A hundred and ten years later, Wood (1994: 229) formally treated *Strobilanthes isophylla* (Nees) T.Anderson as a mere forma *isophylla* (Nees) J.R.I.Wood of *Strobilanthes anisophylla* (Wall. ex Hook.) T.Anderson. In support of his decision, Wood (1994) quoted Parker's text in *A forest flora of the Punjab with Hazara and Delhi* (1918: 389): "*Strobilanthes isophylla* is a form with the leaves in equal pairs. Intermediates (with *S. anisophylla*) are common and the relative size of the leaves in each pair is by no means constant on the same plant." No one has challenged Wood's decision. This history suggests that anisophylly should be treated cautiously, if not sceptically, as a character to delimit species in the absence of additional distinguishing characters.

Many Acanthaceae specialists have ignored or paid only passing attention to anisophylly and interest has not even been much raised by the paper by Brummitt (1989) which is rarely cited. There have been occasional exceptions, notably Manktelow (1996) whose monograph of *Phaulopsis* Willd., an essentially paleotropical genus, discussed anisoclady (unequal branching) and anisophylly in some detail and considered they "constitute a generic character" for the genus (*l. c*. 24). As noted earlier, Nees was aware of anisophylly and occasionally referred to it, as in his description of *Leptostachya heterophylla* Nees (=*Justicia parahyba* P.L.R. Moraes) from Brazil (Nees von Esenbeck, 1847a: 150). Other Acanthaceae specialists, such as Clarke, Lindau and Leonard, rarely mentioned it and largely ignored it as a taxonomic character. In contrast, Bremekamp (1944) laid emphasis on the character (*l.c.*: 21–22) in his generic descriptions in his monograph of the Strobilanthinae (*l.c.*: 55–64) but Bremekamps's genera are not generally accepted today, serving again as a warning about its use as a diagnostic character in the absence of other characters.

During our studies of Acanthaceae in the Andes of South America, we became increasing aware of the presence of anisophylly in a number of species, including several of which had never been described and are apparently new.

Materials and Methods

Specimens of Acanthaceae from South America were examined to find evidence of anisophylly in the herbaria we were able to visit, principally BM, COL, HUA, JAUM, K, and USM. Similarly,

we searched online virtual herbaria, particularly JSTOR (https://www.jstor.org), Tropicos (https://tropicos.org), Reflora (https://www.reflora.jbrj.gov.br) and those associated with COL, K, NY, RB and US. Our observations were combined with a study of Acanthaceae literature where anisophylly might be mentioned (Leonard, 1951–1958; Brummitt, 1989; Wasshausen & Wood, 2004; Kameyama, 2008; Wasshausen, 2013; McDade, 2020). Particular attention was focused on species and genera where anisophylly was reported or observed. It was striking how few publications mentioned anisophylly except in passing, with Manktelow (1995), Kameyama (2008) and McDade (2020) the principal exceptions apart from Brummitt (1989).

Species descriptions were prepared based on herbarium collections from F, HUA, JAUM, K, MO, OXF and US. All cited specimens were seen unless indicated otherwise. Specimens were examined using a stereo microscope and measurements were based on dried material, moistened using Libsorb where necessary. Terminology follows Stearn (1973), Ellis *et al.* (2009) and Harris and Harris (1994). In order to determinate the anisophyllous degree of expression we use the term "strongly anisophyllous" for those species in which the smaller leaf is less than half the size of the larger leaf in each pair and "weakly anisophyllous" when it is more than half of its size. We think it is impractical to grade anisophylly from one to ten as proposed by Esquivel Muelbert *et al*. (2010), particularly as there is often intraspecific variation.

Distribution maps were generated using geographical data from herbarium specimens and online databases from Tropicos (https://www.tropicos.org/), and the Smithsonian Institution (https://collections.nmnh.si.edu/) and mapped using QGIS v.3.28.2 (QGIS Development Team, 2023). Preliminary conservation assessments were evaluated according to IUCN criteria (IUCN, 2022) and were assigned using the R package "ConR" (Dauby, 2019; R Core Team, 2019).

Results and Discussion

In extreme cases anisophylly is easy to see but in most cases, it is not obvious unless the researcher is looking for it. This explains, at least in part, why it is so rarely mentioned in the literature even by Acanthaceae specialists. It is also the case that occasional examples of slightly unequal leaves occur apparently serendipitously in otherwise isophyllous species. We think this is why *Stenostephanus crenulatus* Britton ex Rusby (as *Hansteinia crenulata* Britton), *Thyrsacanthus secundus* (Leonard) A.L.A.Côrtes & Rapini (as *Anisacanthus secundus* Leonard), and *Aphelandra glabra* Willd. (as *A. pulcherrima* (Jacq.) Kunth) were cited as examples of anisophyllous species by Brummitt (1989). Examination of specimens suggests that anisophylly is neither characteristic of these species nor of the genera to which they belong, but random occurrences of this sort make it difficult to compile a comprehensive list of anisophyllous species.

There is also much variation in the degree of anisophylly exhibited, an issue Bremekamp (1944: 21–22) alluded to with the phrase "paulum anisophyllae" noting that "in some instances... the smaller leaves measure but a few millimetres in length, and as they are moreover early deciduous, they are easily overlooked (whereas) in other species the difference is on the contrary but slight and between these two extremes all intergrades occur." This ambiguity is also apparent in McDade (2020), where several genera and species are treated as "isophyllous or weakly anisophyllous". Anisophylly varies from almost imperceptible in some species to where it is very marked with the smaller leaf almost completely suppressed, the leaves appearing to be arranged alternately. Some species are so weakly anisophyllous that anisophylly can only be perceived in the leaf pair below a terminal inflorescence. In species with marked anisophylly, it may affect not only the patterns of leaf development, but also shoot symmetry, phyllotaxis, and bud development (Dengler, 2011). Manktelow (1996) suggests that in *Phaulopsis* it is most marked in species with long-petiolate ovate leaves but is less characteristic of species with narrower subsessile leaves. Our observations and the illustrations accompanying this paper give little support to the generalisation of this observation. Anisophylly is quite often associated with a zigzag stem as in the case of *Strobilanthes anisophylla* discussed above and in some of the new species described below. It is also commonly associated with leaf asymmetry (also noted by Manktelow, 1996, who referred to it as 'obliquity'), where the leaf base is oblique as in the case of nearly all the new species described below (Figs. 1–8).

Sometimes anisophylly occurs strongly in some examples of a particular species but is absent from other specimens of the same species. One example

is *Pseuderanthum congestum* S.Moore, a relatively widespread species of eastern Bolivia and central Brazil. Strongly anisophyllous examples can be found, such as *Wood et al.* 16585 (K, LPB) while, in contrast, isophyllous specimens such as *Wood* 12522 (K, LPB) also occur. Most specimens lie between these two extremes. The same appears to be true of *Justicia metallica* Lindau (Kiel in McDade, 2020: 112) from Central America, and also of *Lepidagathis floribunda* (Pohl) Kameyama from the Cerrado biome of Bolivia and Brazil. *Odontonema rubrum* (Vahl) Kuntze, discussed below is yet another example where isophyllous and strongly anisophyllous specimens are known (Fig. 8). It is thus obvious that anisophylly should be treated with extreme caution as a diagnostic character in species delimitation in the absence of other distinguishing characters.

We have tried to look for patterns in the occurrence of anisophylly. There is some evidence that it is more common in species from humid forest as we have found few examples of its occurrence in species characteristic of dry forest including those found in the Caatinga, Chaco or Cerrado biomes. In contrast it seems more common in the humid forests of eastern Peru from where many of the anisophyllous species of *Justicia* L., *Sanchezia* Ruiz & Pav. and *Suessenguthia* Merxm. come. We cannot confirm or refute the suggestion that it is more common in climbing or creeping plants (Goebel, 1928).

Anisophylly is also characteristic of certain genera and clades although rarely of all species in any particular case. *Justicia* is the genus that stands out most prominently (Table 1). Many of the consistently most strongly anisophyllous species of *Justicia* (*J. aymardii* Wassh., *J. impar* J.R.I.Wood & P.Gallego, *J. imparifolia* J.R.I.Wood & P.Gallego, *J. luschnathii* Lindau, *J. maynasana* J.R.I.Wood & P.Gallego, *J. microcalyx* J.R.I.Wood & P.Gallego, *J. tarapotensis* Lindau and *J. yaruguiorum* P.Gallego & J.R.I.Wood) are only known from five or less collections so it is not possible to be certain that they are always anisophyllous.

Anisoclady has also been reported in *Justicia* but it has been rarely observed or discussed. There seems to be no good correlation with anisophylly, at least this is true for *Justicia comata* (L.) Lam., discussed by Sell (1969), thus raising doubts about Manktelow's observation that anisoclady and anisophylly are usually connected (Manktelow, 1996: 24).

Anisophyllous species are also prominent in the genus *Lepidagathis* Willd. amongst species previously placed in *Lophostachys* Pohl. This genus was the subject of a paper by Kameyama (2008), which is one of very few to highlight anisophylly in Acanthaceae. She comments that the leaves "in most of the species are evidently anisophyllous" (*l. c.* 566) and unusually makes use of anisophylly as a key character (*l. c.* 580) to distinguish two species pairs.

"10. Subtly anisophyllous, larger leaf of each pair *c.* 1.5 times longer than smaller leaf. Eastern Brazil.... 11

10. Prominently anisophyllous, larger leaf of each pair *c.* 3 to 5 times longer than smaller leaf. Peru, Bolivia, Argentina, Paraguay, and Brazil ..... 12"

Kameyama's use of "subtly anisophyllous" mirrors Bremekamp's phrase "paulum anisophyllae" noted earlier. Based on her publication and our herbarium observations, the following species are usually distinctly anisophyllous, all except the first are essentially Brazilian: *Lepidagathis alvarezia* (Nees) Kameyama ex Wassh. & J.R.I.Wood, *L. callistachys* Kameyama, *L. floribunda* (Pohl) Kameyama, *L. meridionalis* Kameyama, *L. montana* (Nees) Kameyama, *L. nemoralis* (Mart. ex Nees) Kameyama, and *L. paraensis* Kameyama. However, this list needs some qualification. *Lepidagathis paraensis* is only known from three collections but is consistently strongly anisophyllous with a zigzag stem, whereas *L. alvarezia* and *L. floribunda* are sometimes strongly anisophyllous but are not consistently so. The remaining species appear to be consistently anisophyllous but only weakly so.

We note that anisophylly occurs in three out of six genera of American Trichantherinae Benth. & Hook.f. in the classification of Manzitto-Tripp *et al.* (2022), although it is not present in all species of these genera and is never strongly marked in any individual species.

1. *Sanchezia* Ruiz & Pav. is a South American genus centred on Peru with all species characteristic of moist forest at low altitudes, often in the Andean foothills. The revision of the genus by Leonard and Smith (1964) makes no mention of anisophylly, but Brummitt (1989) noted several anisophyllous species. Examination of herbarium specimens suggests it is common in the genus and all the following species exhibit some degree of anisophylly: *S. ecuadorensis* Leonard, *S. klugii* Leonard & L.B.Sm., *S. longiflora* (Hook.) Hook.

Table 1. Anisophyllous South American species of *Justicia* showing their distribution, degree of anisophylly and related characteristics.

Species	Distribution	Degree of anisophylly	Additional observations
Justicia archeri Leonard	Colombia	Weakly anisophyllous	Stems not zigzag
Justicia aymardii Wassh.	Venezuela	Strongly anisophyllous	Stems obscurely zigzag, leaves oblique
Justicia carajensis F.A. Silva, A. Gil & Kameyama	Brazil	Weakly anisophyllous	
Justicia cuneifolia Nees & Mart.	Brazil	Weakly anisophyllous	Leaves somewhat oblique
Justicia floribunda (K.Koch) Wassh.	Brazil	Weakly to strongly anisophyllous	Stems sometimes zigzag. Leaves oblique
Justicia glaziovii Lindau	Bolivia, Brazil, Venezuela	Weakly anisophyllous	Stems not zigzag
Justicia impar J.R.I.Wood & P.Gallego	Peru	Strongly anisophyllous	Leaves slightly oblique
Justicia imparifolia J.R.I.Wood & P.Gallego	Peru	Strongly anisophyllous	Leaves very asymmetric, base oblique
Justicia luschnathii Lindau	Brazil	Strongly anisophyllous	Stems often zigzag, leaves oblique
Justicia magdalenensis J.R.I.Wood	Colombia	Strongly anisophyllous	Stems zigzag
Justicia manserichensis Wassh	Peru	Strongly anisophyllous	Leaves appear alternate as smaller leaf always (?) absent
Justicia maynasana J.R.I.Wood & P.Gallego	Peru	Strongly anisophyllous	Stems zigzag
Justicia microcalyx J.R.I.Wood & P.Gallego	Ecuador, Peru	Strongly anisophyllous	Stems weakly zigzag, leaves asymmetric with oblique base
Justicia obliqua J.R.I.Wood & P.Gallego	Peru	Strongly anisophyllous	Stems strongly zigzag, leaves asymmetric with oblique base
Justicia parahyba P.L.R. Moraes	Brazil	Strongly anisophyllous	Stems zigzag, leaf base oblique
Justicia prevostiae Wassh.	French Guiana	Weakly anisophyllous	Stems not zigzag, leaf base strongly oblique
Justicia riopalenquensis Wassh.	Ecuador	At most weakly anisophyllous	Stems not zigzag
Justicia tarapotensis Lindau	Peru	Strongly anisophyllous	Stems not zigzag, leaf base oblique
Justicia trianae (Leonard) J.R.I.Wood	Colombia	Weakly anisophyllous	Leaves slightly dimorphic, base weakly oblique
Justicia yaruguiorum P.Gallego & J.R.I.Wood	Colombia	Strongly anisophyllous	Stems sometimes zigzag. Leaves slightly oblique
Justicia yurimaguensis Lindau	Peru, Bolivia	Weakly anisophyllous	Stems not zigzag,

f. ex Planch., *S. parvibracteata* Sprague & Hutch., *S. punicea* Leonard & L.B.Sm., *S. putumayensis* Leonard, *S. rhodochroa* Leonard & L.B.Sm., *S. rosea* Leonard, *S. scandens* (Lindau) Leonard & L.B.Sm., *S. spucei* Lindau, *S. stenomacra* Leonard & L.B.Sm. and *S. williamsii* Leonard

2. *Suessenguthia* Merxm. is closely related to *Sanchezia* with a small number of species in the southwest Amazonian region. It was revised by Schmidt-Lebuhn (2003) but without mention of anisophylly despite the earlier reference to its occurrence by Brummitt (1989). The following species all exhibit weak anisophylly: *S. barthleniana* Schmidt-Leb., *S. multisetosa* (Rusby) Wassh. & J.R.I.Wood, *S. trochilophila* Merxm. and *S. vargasii* Wassh.

3. *Tricanthera* Kunth is a tree genus from northwest South America with a single species, *T. gigantea* (Humb. & Bonpl.) Nees, which is clearly anisophyllous. Although another tree species, *Bravaisia integerrima* (Spreng.) Standl. was listed as an anisophyllous species (Brummitt, 1989), we can see no evidence for this in the specimens we examined, and it was also treated as isophyllous by Daniel (1988) and McDade (2020).

Anisophylly is also present in five out of 11 New World genera of Graptophyllinae T.Anderson.

1. *Herpetacanthus* Moric. is a small genus with most species from Brazil. Most species are rarely collected but almost all appear to be weakly anisophyllous including the following:

   H. longiflorus Moric., *H. magnobracteolatus* Indriunas & Kameyana, *H. melancholicus* Nees and *H. rotundatus* (Lindau) Bremek.

2. *Odontonema* Nees ex Endl. is represented by several species in South America, one of which, *O. rubrum* (Vahl) Kuntze, is sometimes strongly anisophyllous. It is discussed in more detail below.

3. The genus *Oplonia* Raf. is poorly represented in South America but *O. jujuyensis* Wassh. & C. Ezcurra from Argentina and Bolivia appears to be weakly anisophyllous.

4. *Psilanthine* Nees is represented by a single rarely collected, weakly anisophyllous Ecuadorian endemic, *P. eggersii* Lindau.

5. *Pseuderanthemum* Radlk. consists of a number of species noted for their anisophylly, including: *P. chilianthum* Leonard, *P. congestum* (S.Moore) Wassh., *P. diachylum* Leonard and *P. heterophyllum* (Nees) Radlk. All four species are strongly anisophyllous although *P. congestum* is not consistently so. All are somewhat asymmetric in their leaf shape and *P. chilianthium* also has a weakly zigzag stem. It seems likely that other species of *Pseuderanthemum* will be shown to be anisophyllous.

Anisophylly has also been reported in *Hypoestes phyllostachya* Baker (Sell, 1968), which is naturalised sporadically in South America, and in *Phaulopsis talbotii* S.Moore (Manktelow, 1996). The latter may be an introduction to the Americas in the early modern period (*l. c*. 163) as the genus is otherwise unknown in the neotropics.

There are occasional mentions of anisophylly in other species (Brummitt, 1989), which we cannot confirm.

In conclusion, our observations show that in some species anisophylly is constant, marked and diagnostic, while in others anisophylly is expressed in a gradient from weak to strong, consequently with unclear taxonomic significance. We have exclusively focussed on documenting the phenomenon in South American species of Acanthaceae, but do not discuss its evolution and cannot suggest satisfactory explanatory factors despite discussion of diverse correlated factors (Givnish, 1984; Dengler, 1999). Clearly, further experimental studies are necessary, particularly those employing a phylogenetic approach.

Species descriptions and notes

The following species descriptions and notes document various species novelties and unpublished examples of anisophylly in Andean Acanthaceae, principally from *Justicia*, where most examples of marked anisophylly have been observed (Table 1).

JUSTICIA L.

Justicia yariguiorum P.Gallego & J.R.I.Wood, **sp. nov.** **Fig. 1**

Amongst Colombian species of *Justicia*, the strong anisophylly of *J. yariguiorum* merits comparison with *Justicia magdalenensis* J.R.I.Wood, but *J. yariguiorum* is probably unrelated and distinguished *inter alia* by the pubescent inflorescence of only 2–5 flowers

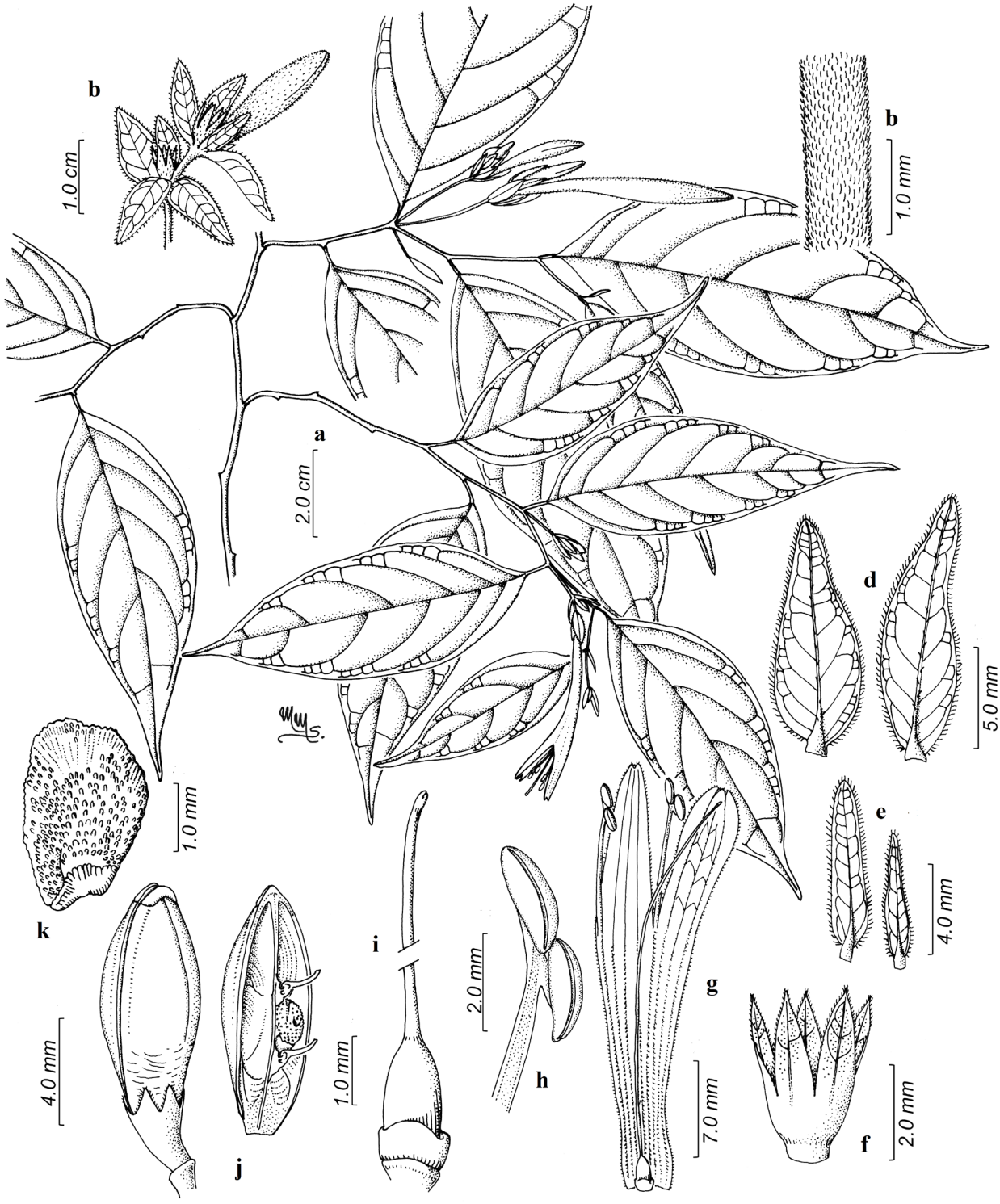

Fig. 1. *Justicia yariguiorum* P.Gallego & J.R.I.Wood: **a**. Habit; **b**. Portion of inflorescence; **c**. Detail of stem, showing indumentum; **d**. Bracts; **e**. Bracteoles; **f**. Calyx; **g**. Corolla; **h**. Anthers; **i**. Ovary style; **j**. Capsule exterior and interior of valve; **k**. Seed (from *Tobón & Torralba* 2233; drawn by Marcela Morales).

(which lack spreading hairs), calyx 2–3 mm long (not 11–14 mm) and capsule glabrous (not pubescent). The new species will key out in Leonard (1951–1958) as *J. leptochlamys* Leonard in terms of leaf shape and indumentum, bract size and glabrous capsule, but the bracts are ovate, rather than oblong-elliptic, the bracteoles lanceolate to narrowly ovate (not linear) and the corolla orange-red (not white). It also shows some affinity *to J. erythrantha* Leonard in flower colour, leaf shape, bract size and obtuse glabrous capsule, but is herbaceous (not shrubby) the spikes few-flowered, lax (not many-flowered and dense), the bracts are ovate, obtuse (not lanceolate, acuminate) and the bracteoles narrowly ovate, obtuse (not linear-lanceolate, acuminate).

Type: COLOMBIA, **Santander**, Mun. Girón, Vereda Parroquia, Caño Piedras, Via Lisboa-San Vicente de Chucurí, S 7°03'40.1", W 73°21'10.1", 320 m, March 2017, *Juan Pablo Tobón* & *Luis Torralba* 2233 (holo JAUM [JAUM091799!]).

Anisophyllous herbs or subshrubs to 80 cm. Stems terete, pale brown, adpressed pubescent, ±glabrescent, upwards subquadrangular, weakly zigzag, dark green, lenticels 0.3–0.5 mm diam. circular, prominent. Leaves very unequal, petiolate; larger leaves 5–11.5 × 2–4 cm, ovate-elliptic, acuminate to an obtuse apex, base slightly oblique, cuneate, margins entire, lateral veins 4–6 pairs, both surfaces glabrous except for the pubescent veins and margins; smaller leaves 0.6–1.1 × 0.2 cm, narrowly oblong-elliptic, acute, slightly falcate, caducous. Petioles 0.4–0.7(–1) cm long, sulcate, thinly hirsute in channel and on margins. Inflorescence of few-flowered pedunculate cymes arising in the uppermost leaf axils, flowers 1–5, subsessile; peduncles 1.5–2.5 cm, slender bifariously pubescent. Bracts 6–11.5 × 3–5.5 mm, ovate, obtuse, entire, pubescent and ciliolate. Bracteoles 5.0–7 × 1–2.5 mm, narrowly ovate, obtuse, entire, pubescent and ciliolate. Calyx 3–4.5 mm long, 5-lobed; lobes 2.2–2.8 × 0.7–1.2 mm, lanceolate, acute, ciliolate. Corolla orange-red, 2.8–5 cm long, exterior pubescent, inner surface scabridulous; 2-lipped, tube 15–20(–30) mm long, slightly widened upwards to 6 mm, lips subequal, 10–15(–20) mm long, upper lip notched with small triangular lobes *c*. 0.5 mm long, lower lip very shallowly 3-lobed, the lobes ovate, rounded, *c*. 2 mm long. Stamens 2, 2.2–4.7 cm long, glabrous, except for pilose base; thecae 2–2.5 × 1 mm, oblong-elliptic, superposed. Ovary ovoid *c*. 1.75 mm long, glabrous; style 2.5–4.5 cm long, glabrous, stigma 0.15–0.2 mm wide; nectary disk oblate, glabrous. Capsules 9–10 × 4.0 mm, clavate, glabrous, dark brown, apex obtuse. Seeds suborbicular, *c*. 2.5 × 2 mm, light brown.

Flowering & fruiting: Not accurately known but collected in flower in March and April and in fruit in October.

Habitat: On rocky soils, sometimes riparian, in the transition zone between tropical moist forests of the Magdalena River basin and tropical dry forest with influence of the xerophytic vegetation of the Chicamocha canyon. It has been recorded between 320 and 500 m.

Distribution: Endemic to a small area of the Río Sogomoso valley in Santander in northeastern Colombia (Fig. 2).

Etymology: This species is named after the Yarigui people who in pre-colonial times occupied the territory where this species grows. They long resisted conquest but repeated incursions into their territory resulted in their extinction over a century ago.

Specimens examined: COLOMBIA, **Santander**, Finca Cruces, debajo de la vía nueva, N 07°05'31", W 73°22'25", 500 m, 22.04.2014, *Heriberto David* & *José Miguel Torres* 4906 (HUA); Mun Girón, Vereda Parroquia, Caño Piedras, vía a San Vicente de Chucurí, N 07°03'35", W 73°19'59", 334 m, 10.10.2016, *Diego A. Zapata C. et al.* 1858 (JUAM); *Ibid*., N 07°03'33", W 73°19'49", 465 m, 10.10.2016, *Diego A. Zapata C. et al.* 1865 (JUAM).

Conservation status: *Justicia yariguiorum* is only know from a single population in the dry forests of northeastern Colombia. This ecosystem has experienced a loss of at least 90% of its original cover in the country, and about 30% of the remaining fragments comprise mostly early and intermediate successional stages, with barely 4% of the original cover represented by mature forest (García *et al.,* 2014; González-M *et al*., 2018). According to González-M *et al.* (2018) tropical dry forests in Colombia are highly fragmented and are threatened by high impact disturbances such as cattle ranching, human infrastructure, agriculture and fires. In view of this scenario and considering that this species occurs in small, fragmented forest patches, outside of protected areas, with an Area of Occupancy (AOO) of only 12 km², we propose that it should be considered as Endangered (EN) B2ab(iii).

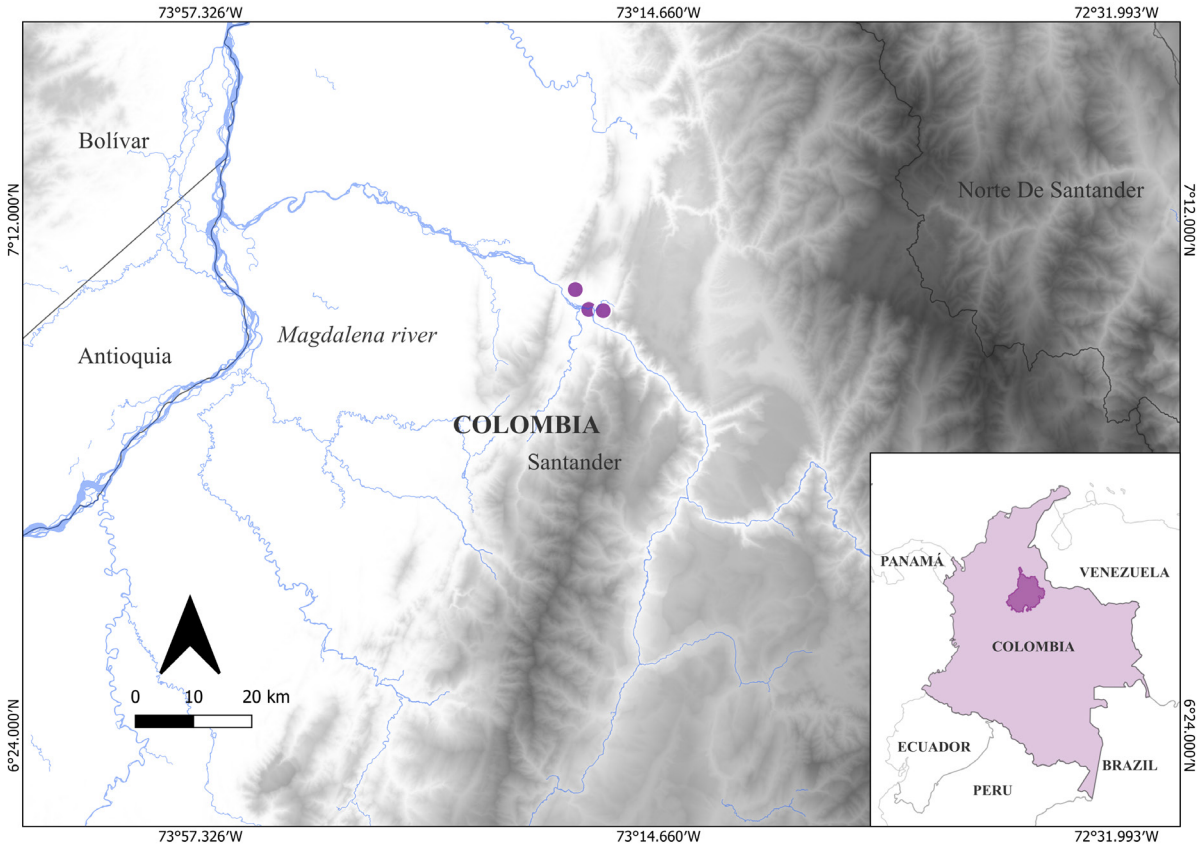

Fig. 2. Distribution of *Justicia yariguiorum* P.Gallego & J.R.I.Wood with inset of its location in Colombia. Map prepared using QGIS v.3.28.2 (QGIS Development Team, 2023).

Justicia microcalyx J.R.I.Wood & P.Gallego, **sp. nov.** **Fig. 3**

A strongly anisophyllous species that resembles *Justicia obliqua* in the 4-lobed calyx which is only 3–4 mm long (not *c*. 9 mm), and differs also *inter alia* in the near glabrous leaves (not pilose) and smaller corolla 8–9 mm long (not 23–27 mm). The small calyx might suggest *J. impar* J.R.I.Wood & P. Gallego but in that species the calyx is 5-lobed and the corolla glabrous and 10–12 mm long whereas in *J. microcalyx* it is only 8–9 mm long and pubescent.

Type: ECUADOR, "In jugo centrali Andium, Equator," 1800 m, 1876, *E. André* 4312 bis (holo K [K000994467!], sheet with rootstock, capsules and pencil drawing of anthers; iso K [K000994468!, K000994469!].

Anisophyllous perennial herbs reaching *c*. 5 cm high. Stems becoming woody, shortly bifariously scurfy, often appearing glabrous, often branched above, straight or somewhat zigzag. Leaves unequal, very shortly petiolate, narrowly oblong-elliptic, the larger 2.5–4 × 0.8–1 cm, the smaller 0.6–1.6 × 0.3–0.8 cm, narrowed to an obtuse apex and an oblique cuneate base, glabrous apart from a few hairs on the abaxial midrib, cystoliths prominent. Inflorescence of short, narrow, terminal spikes 1–2 cm long and *c*. 0.5 cm wide, the flowers mostly in opposite pairs *c*. 3 mm apart; rachis thinly pilose. Bracts 2 × 0.5 mm, linear, thinly pilose, cystoliths prominent. Bracteoles *c*. 2 × 0.25 mm, linear, thinly pilose. Calyx 4-lobed; lobes 3–4 × 0.5–1 mm, linear-lanceolate, thinly ciliate. Corolla 8–9 mm long, pink, pubescent on exterior, two lipped, tube 4–5 mm long, lips *c*. 3 mm long, upper lip entire, deltoid, lower lip shallowly 3-lobed, lobes *c*. 1 mm wide and long, broadly ovate. Filaments *c*. 2 mm long, pubescent below, glabrous above, anthers bithecous; thecae 1 × 0.5 mm, weakly superposed, puberulent. Style thinly pilose, ovary narrowly conical, *c*. 1.25 mm high, obscurely appressed puberulent. Capsule oblong, 7–9 × 1.5 mm, pubescent, 4-seeded. Seeds 0.75 mm diam., strongly rugose.

Flowering & fruiting: Unknown.

Habitat: "Primary forest".

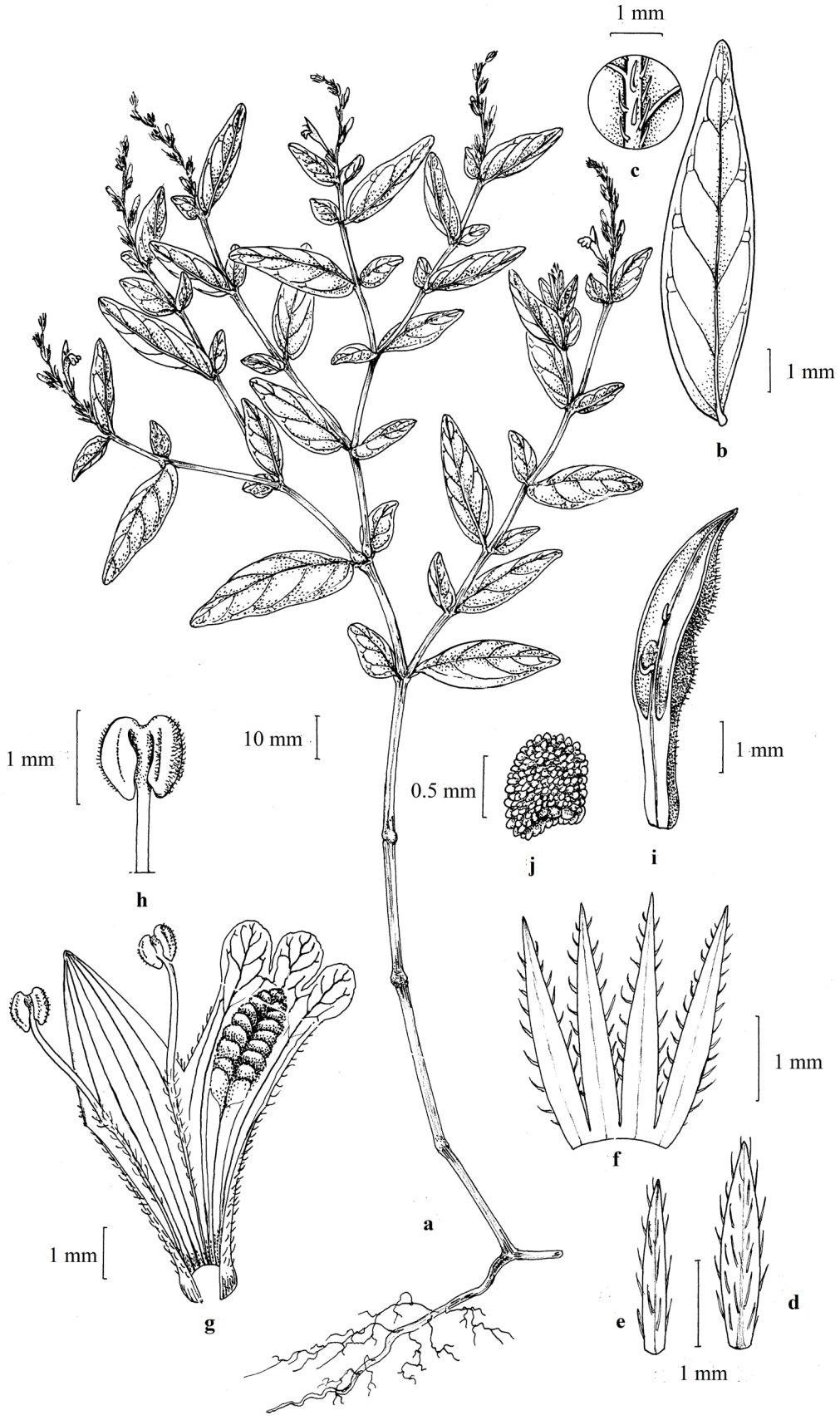

Fig. 3. *Justicia microcalyx* J.R.I.Wood & P.Gallego: **a**. Habit; **b**. Leaf; **c**. Detail of abaxial surface of leaf; **d**. Bract; **e**. Bracteole; **f**. Calyx; **g**. Corolla opened out to show androecium; **h**. Anthers; **j**. Valve of capsule; **k**. Seed (from *Andre* 4312; drawn by Margaret Tebbs).

Distribution: Northern Peru and Ecuador but not accurately known. The map (Fig. 4) shows the only record we are able to localise from Peru near the border with Ecuador.

Etymology: The name *microcalyx* refers to the very small calyx of this species.

Specimens examined: PERU, **Cajamarca**, San Ignacio, Dist. Namballe. Bosque el Pacashal, margen derecho del Río Canchis, S 5°01', W 79°01', 650–800 m, 10.07.1997, *E.Rodríguez* & *O. Pesantes* 1662 (F, MO, US, USM).

Conservation status: This species is only known from two collections, one unlocalised from about 150 years ago. There is no information on its habitat or frequency. It is small and inconspicuous and could easily be overlooked so it is hoped that it is more frequent than the scant records suggest. Therefore, it is provisionally assessed as Data Deficient (DD).

Notes: Unfortunately, *Rodríguez* & *Pesantes* 1662 lacks corollas and capsules so is not suitable for selection as type.

Justicia obliqua J.R.I.Wood & P.Gallego, **sp. nov.** Fig. 5

Strongly anisophyllous subshrub with woody stems, subsessile, strongly oblique leaves superficially somewhat similar to *Justicia imparifolia* described below but the leaves hirsute (not nearly glabrous), bracts < 8 mm long (not 11–18 mm) and calyx 4-lobed, densely pilose (not 5-lobed, thinly pubescent).

Type: PERU, **Ucayali**, Coronel Portillo, Padre Abad, La Divisoria, cerca Río Chino, 1400–1600 m, 11.06.1976, *J. Schunke V.* 9215 (holo MO [MO2736883!]; iso F!, US [US2901548!], USM [USM88453!]).

Perennial anisophyllous herbs or subshrubs 0.5–1 m high. Stems at first rooting at the nodes, forming low ground cover, then ascending or erect to 1 m, usually conspicuously zigzag, pilose with multicellular hairs on younger stems, scurfy-pubescent on older growth. Leaves very unequal, subsessile to shortly petiolate, softly pilose with multicellular hairs; larger leaves 1.6–3.5 × 0.6–1.5 cm, asymmetrically oblong-lanceolate to narrowly oblong-elliptic, apex obtuse, base cuneate, oblique; smaller leaves obliquely suborbicular, 0.3–0.9 cm in diam. Petioles 0–2 mm, pilose. Inflorescence of shortly pedunculate, terminal spikes 1–2 cm long (sometimes also from the uppermost leaf axils); peduncles 0.5 cm, pilose. Bracts and bracteoles similar, 7–7.5(–8) × 0.5–0.75 mm, linear-filiform, pilose. Calyx 4-lobed; lobes linear-lanceolate, *c*. 9 × 0.5 mm, pilose, pale green with a distinct midrib. Corolla magenta with pale tube, glandular-pubescent, 2.3–2.7 cm, long, 2-lipped, tube 12–18 mm long, gradually widened from *c.* 2 mm at base to 4.5 mm at mouth, upper lip 6–7 mm long, erect, entire, slightly hooded, lower lip recurved, 8–11 mm long, 3-lobed, lobes broadly oblong, *c*. 3 × 2 mm. Stamens included in upper lip, filaments *c*. 8 mm long, white, anthers bithecous; thecae 1.25 × 0.75 mm, ellipsoid, basally acute, white, obscurely asperous, weakly superposed. Ovary narrowly ovoid, comose; style thinly pubescent below, glabrous upwards, stigma white. Capsule and seeds not seen.

Flowering & *fruiting*: Found in flower from February to September.

Habitat: 'Bosque alto tropical en sombra' – in shade in primary tropical forest, on humid soil, on margins and clearings in dense cloud forest, 700–1800 m.

Distribution: Endemic to Peru. Moist hill forest around La Divisoria, where the departments of Huánuco and Ucayali meet (Fig. 4).

Etymology: The name *obliqua* refers to the distinct oblique, unequal leaf base characteristic of this species.

Specimens examined: PERU, **Huánuco**, Coronel Portillo, Divisoria, Tingo María–Pucallpa, 1600–1800 m, 28.02.1947, *R. Ferreyra* 1676 (US, USM); Cordillera Azul east of Tingo María, east of Koenig's, 22.06.1959, *M.E. Mathias* & *D. Taylor 3465* (F, MO); Coronel Portillo, Padre Abad, La Divisoria, carretera a Pucallpa, 1400–1600 m, 26.04.1980, *J. Schunke V.* 11408 (MO, US, USM); La Divisoria, Tingo María–Aguaytia, Cordillera Azul, 1500–1600 m, 03.06.1983, *A. Gentry et al.* 41439 (MO, US, USM); Leoncio Prado, Dist. Pucayacu, sector Nueva Esperanza, P.N. Cordillera Azul, S 8°29'29", W 76°05'42.7", 1362 m, 21.06.2017, *L. Valenzuela et al.* 32048 (USM). **Ucayali**, Divisoria, 700 m, 02.08.1942, *V. Cárdenas* USM no. 13843 (US, USM); La Divisoria, Plantación Margarita, 14.08.1946, *R. Ferreyra* 988 (US); Leoncio Prado, 80 km NE of Tingo María towards Aguaytia, near Divisoria, 1600 m, 13.09.1946, *F. Woytkowski* 34522 (F, MO); Ibid., 900 m, 18.01.1976, *A. Gentry et al.* 16034 (MO); Leoncio Prado, Divisoria, 1610 m, 31.05.1978, *L.E. Skog et al.* 5118 (US); W of the limit with Ucayali, S 9°05', W 75°46', 10.08.1980, *A. Gentry et al.* 29600 (F, MO, USM).

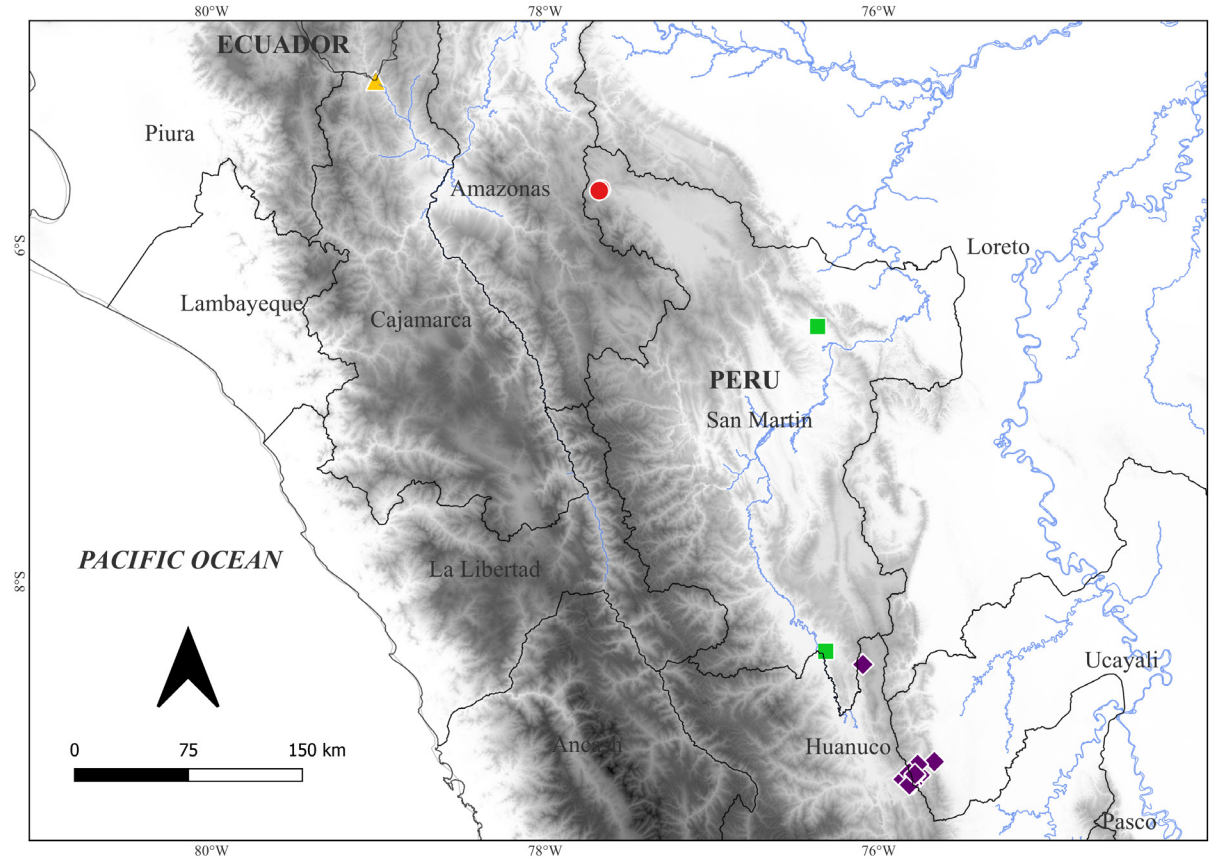

Fig. 4. Distribution of selected anisophyllous species of *Justicia* L. in Peru: *J. impar* J.R.I.Wood & P.Gallego (green squares); *J. imparifolia* J.R.I.Wood & P.Gallego (red circles); *J. microcalyx* J.R.I.Wood & P.Gallego (pale brown triangle); *J. obliqua* J.R.I.Wood & P.Gallego (violet diamonds). Map prepared using QGIS v.3.28.2 (QGIS Development Team, 2023).

Conservation status: *Justicia obliqua* has an Area of Occupancy (AOO) of 36 km² and an Extent of Occurrence (EOO) spanning 1000 km², based on 12 collections, geographically separated in three different sub-populations. Most records come from foothill and mountain ecosystems along the Federico Basadre Highway, between the Huánuco and Ucayali departments. According to Bax *et al.* (2016), this paved road, constructed in the 1940s, has served as the primary catalyst for deforestation in the Ucayali region. Its existence has led to a landscape deeply fragmented by various human activities, including shifting cultivation, commercial agriculture, timber extraction, and cattle ranching, among other alterations to land use (Ichikawa *et al.*, 2014). However, one population has been found within the limits of the Cordillera Azul National Park and it is plausible that distribution of this species covers a wide area extending into regions integrated within the national system of protected areas. In consequence, we propose that it should be considered as Endangrered[EN] according to criteria B1a+B2ab(i,ii,iv).

Justicia imparifolia J.R.I.Wood & P.Gallego, **sp. nov.** **Fig. 6**

Justicia imparifolia is a strongly anisophyllous species somewhat resembling *Justicia obliqua* but differing in the nearly glabrous (not pilose) leaves, relatively large bracts 11–18 mm (not 7–8 mm) in length and longer 5-lobed calyx *c.* 12 mm in length (not 4-lobed, *c.* 9 mm long).

Type: PERU, **San Martin**, along road from Rioja to Pedro Ruiz, S 5°40'26", W 77°40'35", 1170 m, 05.03.2001, *H. Van der Werff et al.* 16764 (holo MO [MO6991485!]; iso USM [USM178458!]).

Perennial anisophyllous herbs to 40 cm tall. Stems at first decumbent and rooting at nodes, glabrous to very shortly bifariously stiffly pubescent. Leaves shortly petiolate, very unequal, glabrous except for a few crisped hairs on veins beneath, margins crenulate; larger leaves 2–4.2 × 1–2.1 cm, asymmetric, very narrowly oblong-elliptic, narrowed to an oblique cuneate base and obtuse weakly falcate

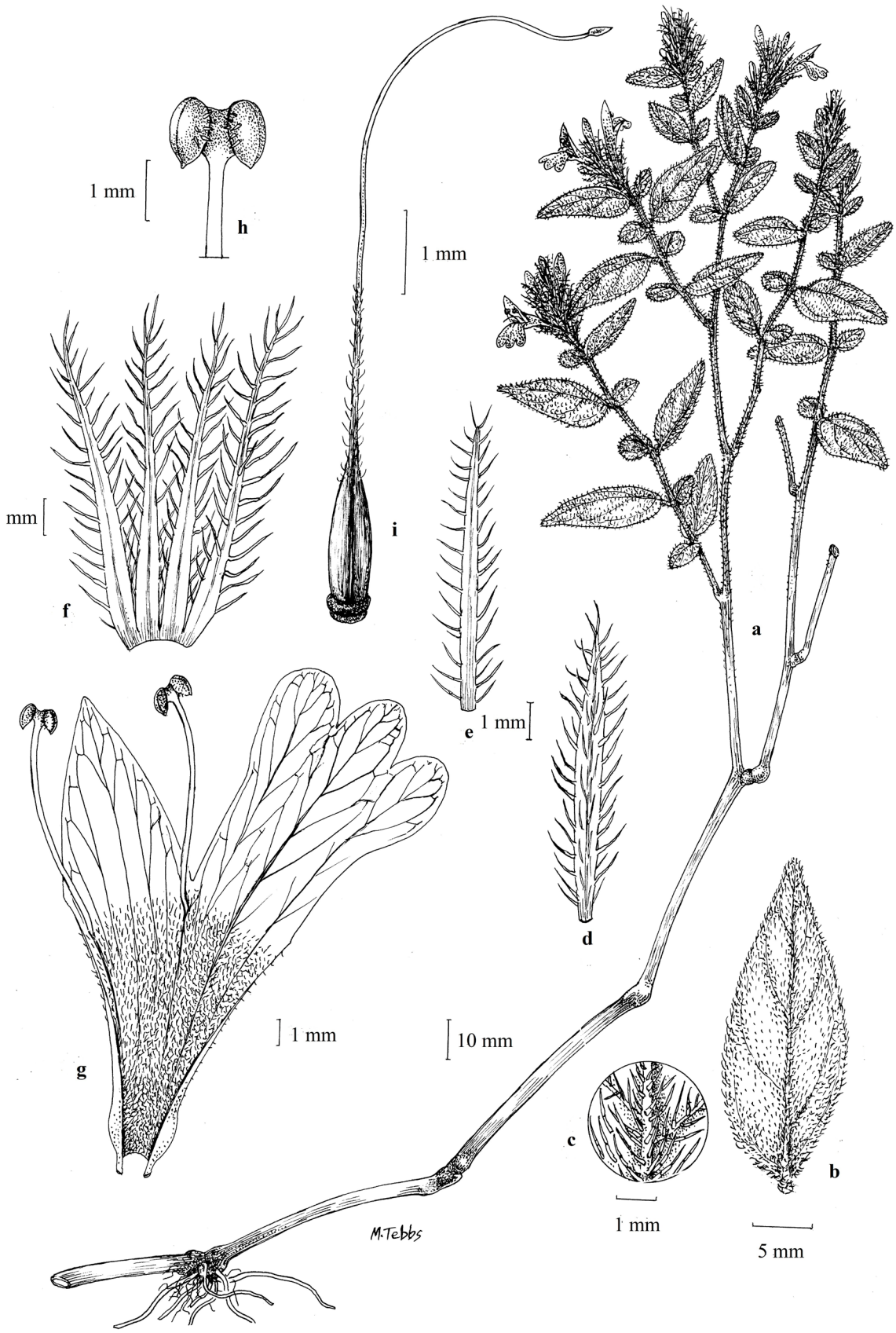

Fig. 5. *Justicia obliqua* J.R.I.Wood & P.Gallego: **a**. Habit; **b**. Leaf; **c**. Detail of abaxial surface of leaf; **d**. Bract; **e**. Bracteole; **f**. Calyx; **g**. Corolla opened out to show androecium; **h**. Anthers; **j**. Ovary (from Schunke 9215; drawn by Margaret Tebbs).

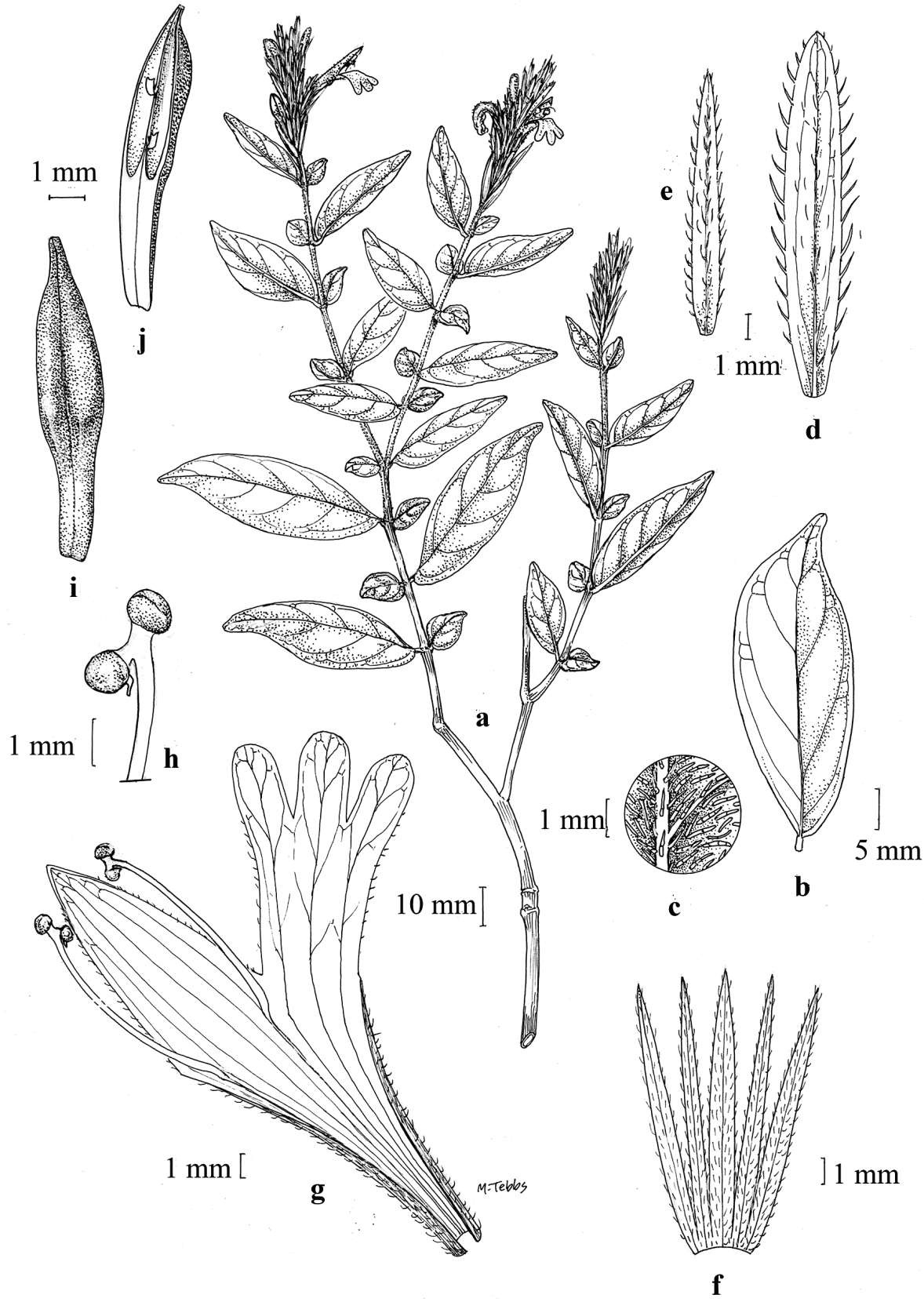

Fig. 6. *Justicia imparifolia* J.R.I.Wood & P.Gallego: **a**. Habit; **b**. Leaf; **c**. Detail of abaxial surface of leaf; **d**. Bract; **e**. Bracteole; **f**. Calyx; **g**. Corolla opened out to show androecium; **h**. Anthers; **i**. Capsule; **j**. Open valve of capsule (a–c from *Van der Werff* 16764; d–j from *Van der Werff* 16611. Drawn by Margaret Tebbs).

apex; smaller leaves subsessile, obliquely ovate to suborbicular, 0.5–1 cm in diam. Petioles 1–2 mm, crisped pubescent. Inflorescence of subsessile, terminal spikes. Bracts foliose, 11–18 × 2–3 mm, narrowly oblong-elliptic, subacute, subglabrous to thinly pilose. Bracteoles *c*. 11 × 1.5 mm, oblong. Calyx 5-lobed, lobes slightly unequal, outer two *c*. 12 × 1.75, sparsely pubescent, inner three *c*. 11 × 1 mm, nearly glabrous. Corolla 2.6 cm long, blue, pubescent on exterior, 2-lipped, tube 12–13 mm long, slightly widened from 1.5 mm at base to 2.5 mm, upper lip 10–12 mm long, lower lip *c*. 9 mm long, deflexed, 3-lobed, lobes *c*. 2 × 1 mm, oblong, rounded. Stamens included in upper lip, filaments 11–12 mm long, white, glabrous; anthers bithecous; thecae ellipsoid, *c*. 0.75 × 0.5 mm, superposed, lower theca with a very small basal appendage. Ovary narrowly ovoid, 5 mm long, glabrous; style 10–11 mm long, glabrous. Capsule *c*. 9 × 2 mm, glabrous, clavate, 4-seeded. Seeds not seen.

Flowering & fruiting: Found in flower and fruit in March and April.

Habitat: Low forest in a limestone area with a thick humus layer at 1170–1972 m.

Distribution: Endemic to Peru in the zone between Rioja and Pedro Ruíz in San Martin and a nearby area of Amazonas from where all four collections come (Fig. 4).

Etymology: The name *imparifolia* refers to the very unequal leaves which are a characteristic of this species.

Specimens examined: PERU, **Amazonas**, Prov. Utcubamba, Bagua Grande, entre Vista Hermosay Santa Clara, S 5°53'58", W 78°25'46", 1972 m, *A. Orejuela et al.* 2716 (E n.v., USM). **San Martin**, Rioja, along road Rioja–Pedro Ruiz, S 5°40'27", W 77°40'35", 1170 m, 23.03.1998, *H. Van der Werff et al.* 15525 (F, MO, US); Aguas Verdes, S 5°40', W 77°40', 02.04.2001, *H. Van der Werff et al.* 16611 (MO, USM).

Conservation status: All four collections come from the same area, three possibly from the same population. There is no information about the size of the populations nor the conservation state of the forest where it grows. Any conservation assessment other than Data Deficient (DD) would be premature.

The *Justicia candelariae* (Oerst.) Leonard complex

The following two species are part of a complex of neotropical species of which *Justicia candelariae* (including *J. chlorostachya* Leonard) is the best known. This includes *Justicia angustibracteata* Leonard and *J. pittieri* Lindau from Central America, *J. neurochlamys* Leonard from Colombia, *J. riopalenquensis* Wassh. from Ecuador, *J. loretensis* Lindau from Peru and *J. longiacuminata* Rusby from Bolivia. All of these species share the oblong(-lanceolate), green, pilose or ciliate bracts of *J. tarapotensis* and *J. impar* but are immediately distinguished *inter alia* by their isophylly or at most weak anisophylly. All tend to have a reduced fifth calyx lobe and some, *J. chlorostachya* (Leonard, 1951–1958) for example, are usually reported to have a 4-lobed calyx. *J. yurimaguensis* Lindau and *J. ruiziana* (Nees) Lindau would also appear to belong to this complex although their bracts are ovate/suborbicular; they both exhibit a tendency towards anisophylly.

The following two species are strongly anisophyllous:

Justicia tarapotensis Lindau, Bull. Herb. Boiss., ser 2, 4: 410. 1904. *Type*: PERU, Tarapoto, 1855–1856, *R. Spruce* 4938 (holo B†; iso K [K000202090!], K [K000202089!], BM [BM000617760!], OXF [OXF00194057!]). **Fig. 7**

Ascending herbs to 80 cm tall. Stems at first rooting at nodes, then ascending, much branched, branches whitish-pubescent, slightly zigzag. Leaves unequal, petiolate; larger leaves 4.5–7.5 × 1.5–3 cm, oblong, acuminate, base rounded, oblique, veins 5 pairs; smaller leaves 0.8–2 × 0.4–1.5, ovate, obtuse, base truncate, oblique, both surfaces subglabrous or puberulous, densely so on veins, abaxially paler, the cystoliths prominent. Petioles to 1 cm, white-pubescent. Inflorescence of shortly pedunculate, mostly terminal spikes; peduncles 1–3 cm long. Bracts *c*. 10 × 5 mm, narrowly elliptic, obtuse to rounded, thinly pubescent with conspicuous shortly ciliate margin, rigid, slightly shiny and prominently veined abaxially. Bracteoles 4–5 × 0.5–1 mm, linear-oblong, pubescent. Calyx unequally 5-lobed, lobes 2.5–3 × *c*. 0.5 mm, linear-lanceolate, pubescent, one much smaller and narrower. Corolla *c*. 10 mm long, 2-lipped, pink, puberulent, tube 6 × 2 mm, white, cylindrical; upper lip *c*. 3 × 2 mm, notched, lower lip 3–4 × *c*. 3 mm, shallowly 3-lobed, lobes 2–3 ×

c. 2 mm. Stamens enclosed in upper lip, filaments *c*. 4 mm long, glabrous, anthers bithecous; thecae *c*. 0.5 × 0.25 mm, pubescent superposed. Style 11 mm long, glabrous; ovary narrowly ovoid, 2 mm long, glabrous. Capsule *c*. 7 × 2 mm, narrowly clavate, glabrous, 4-seeded. Seeds c. 1 mm diam.

Flowering & *fruiting*: Found in flower and fruit at end of May.

Habitat: By streams ("rivulis") in rain forest.

Distribution: A rarely collected species endemic to low altitudes in Peru. (Fig. 8).

Specimens examined: PERU, **Cusco**, La Convención, Cordillera Vilcabamba, opposite Hac. Luisiana, Río Mapituriani, a tributary of the Apurimac, 680 m, 30.05.1975, *D. Wasshausen* & *F. Encarnacion* 490 (K, MO, US), S 12°48', W 73°36'. **San Martin,** Tarapoto, 1855-56, *R. Spruce* 4938 (BM, K, OXF).

Notes: We only accept *Justicia tarapotensis* provisionally as it seems to be almost indistinguishable morphologically from *J. candelariae* (Oerst.) Leonard apart from by its anisophylly. We retain it partly because it is very disjunct from other populations of *J. candelariae*, which is widespread from southern Mexico through Central America to Colombia reaching northern Ecuador (Fig. 8) and partly because of its calyx. *Justicia candelariae* is usually reported to have a 4-lobed calyx, whereas *J. tarapotensis* has a 5-lobed calyx, the fifth lobe much reduced and easily

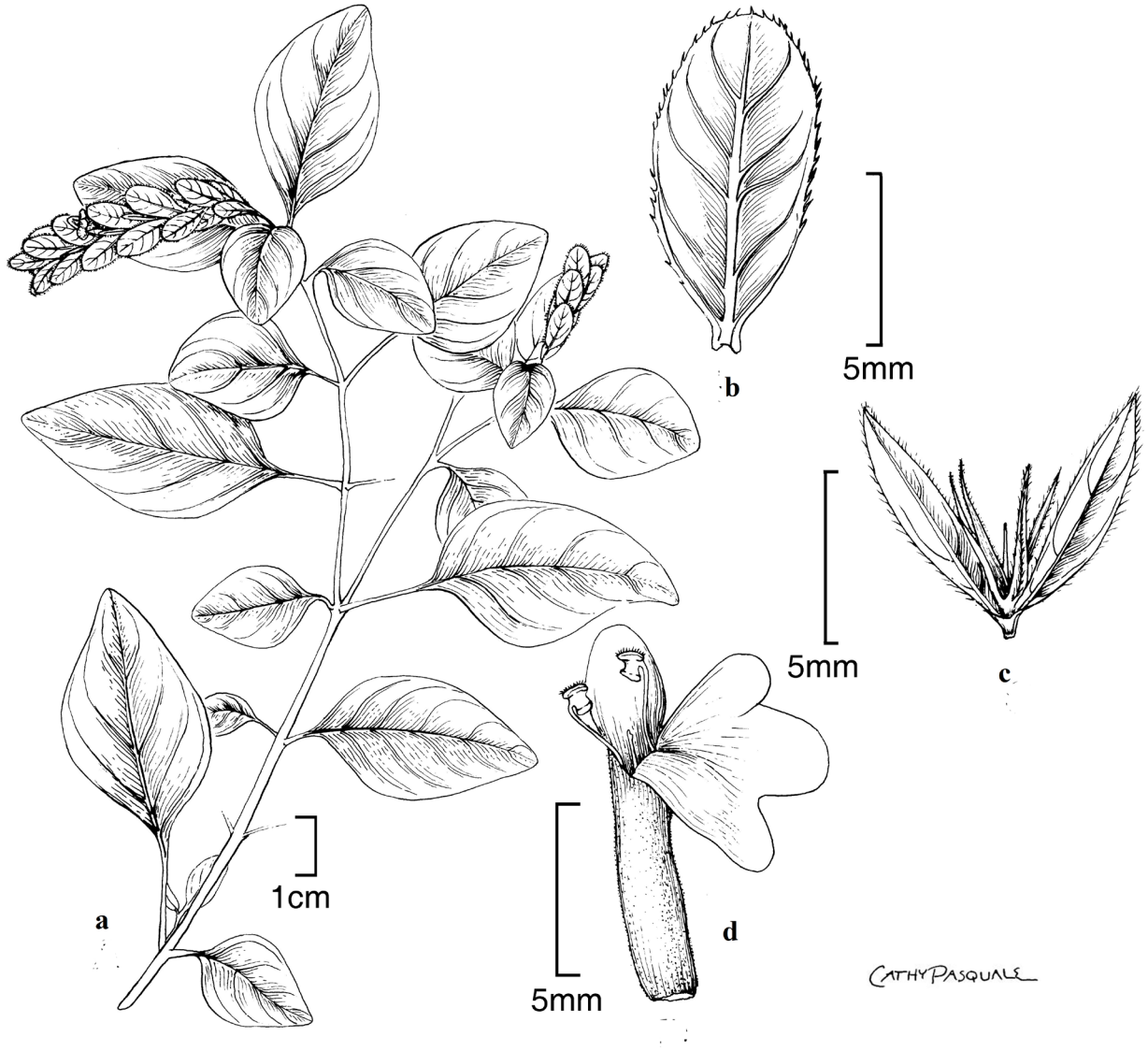

Fig. 7. *Justicia tarapotensis* Lindau: **a**. Habit; **b**. Bract; **c**. Bracteoles and calyx; **d**. Corolla (from *Wasshausen & Encarnación* 490; drawn by Cathy Pasquale).

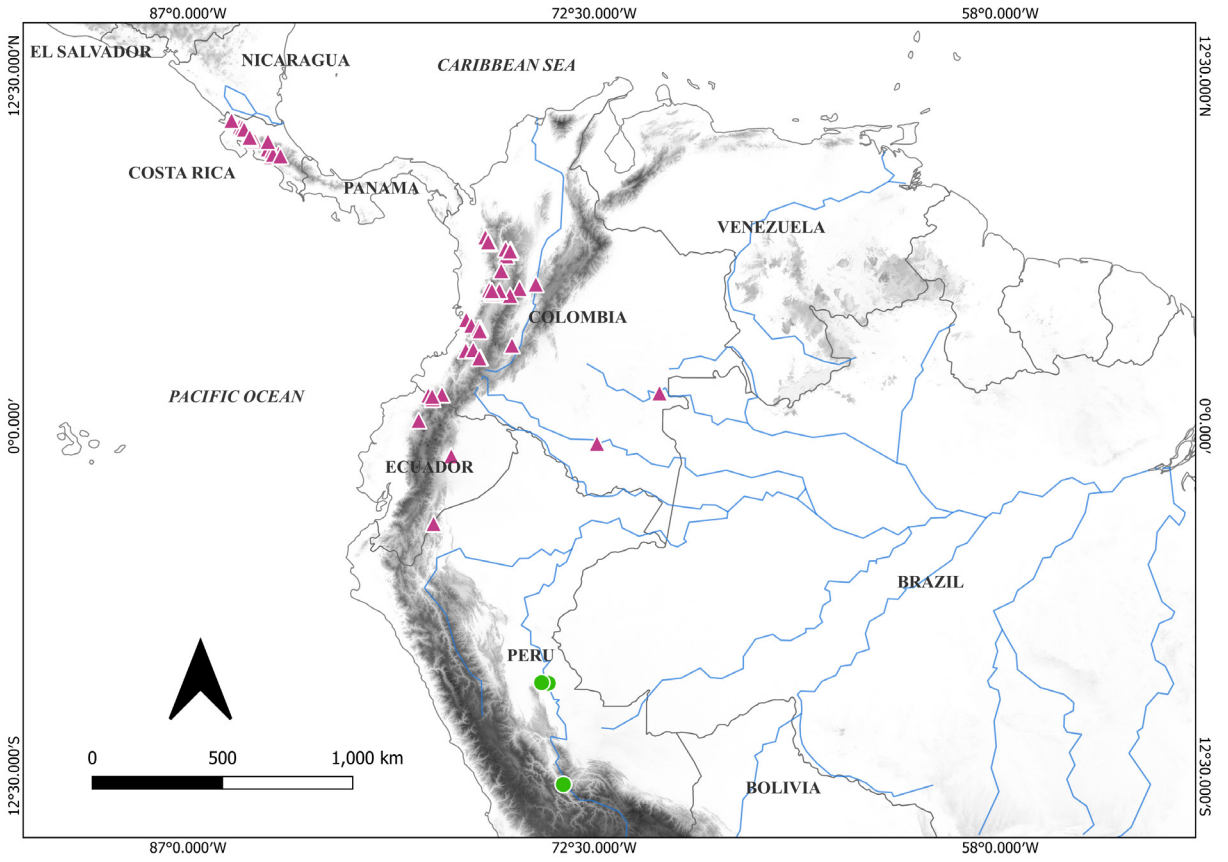

Fig. 8. Distribution of *Justicia tarapotensis* Lindau (green circles) and *J. candelariae* (Oerst.) Leonard (purple triangles) from Nicaragua southwards. Map prepared using QGIS v.3.28.2 (QGIS Development Team, 2023).

missed. Lindau (1904) described *J. tarapotensis* as having a 4-lobed calyx but in fact a small fifth lobe seems always to be present. Future molecular studies are needed to help clarify its status.

Wasshausen & *Encarnación* 490 has subglabrous leaves while those of the type are puberulous.

Justicia impar J.R.I.Wood & P.Gallego, **sp. nov.** Fig. 9

A very strongly anisophyllous plant close to *Justicia tarapotensis* but differing in the oblong-elliptic, acute, pilose, membranaceous bracts (not oblong, obtuse, glabrous to minutely ciliolate, rigid in texture) and subsessile (not distinctly pedunculate) spikes and pubescent (not glabrous) capsule. It somewhat resembles *Justicia riopalenquensis* in the shape of the bracts and calyx but is strongly anisophyllous, the leaves tapering to a cuneate base (not weakly anisophyllous and rounded at base), peduncles short, 0–1 cm (not 1.5–4.5 cm long), bracts 5–7 mm long (not 3–4 mm), the spikes relatively short and stout, 10–20 × 10–15 (not 25–40 × 6–9 mm).

Type: PERU, **San Martin**, Mariscal Cáceres, 2 km del caserío de Nuevo Progreso, carretera a Río Uchiza, S 8°27'04", W 76°19'33", 500 m, 23.06.1969. *J. Schunke V.* 3215 (holo F!; iso K!, US!, USM!).

Perennial herbs. Stems decumbent and rooting, weakly zigzag, crisped-pubescent; flowering branches ascending reaching 40 cm in length, sparingly branched. Leaves very unequal; larger leaves 3–4 × 0.8–2 cm, oblong-elliptic, base cuneate, somewhat oblique, apex shortly acuminate, obtuse, paler beneath glabrous except puberulent veins; smaller leaves 1–1.5 × 0.7–1 cm, broadly ovate, obtuse, base oblique, truncate. Petioles 2–6 mm long, puberulent. Spikes terminal, usually solitary, 1–2 cm long; flowers imbricate; peduncles 0–10 mm long. Bracts 6–9 × 2–3 mm, narrowly rhomboid to oblong-elliptic, acute, membranaceous, thinly pilose. Bracteoles *c*. 4 × 1.5 mm, narrowly oblong, pilose. Calyx 5-lobed to near base, lobes 2–2.5 × *c*. 0.25 mm, slightly unequal in length with one shorter than the other four, ciliate. Corolla 10–12 mm long, violet, glabrous; 2-lipped, tube *c*. 6 mm long, upper lip *c*. 5 mm long, ovate, obtuse, entire; lower lip *c*. 6 mm

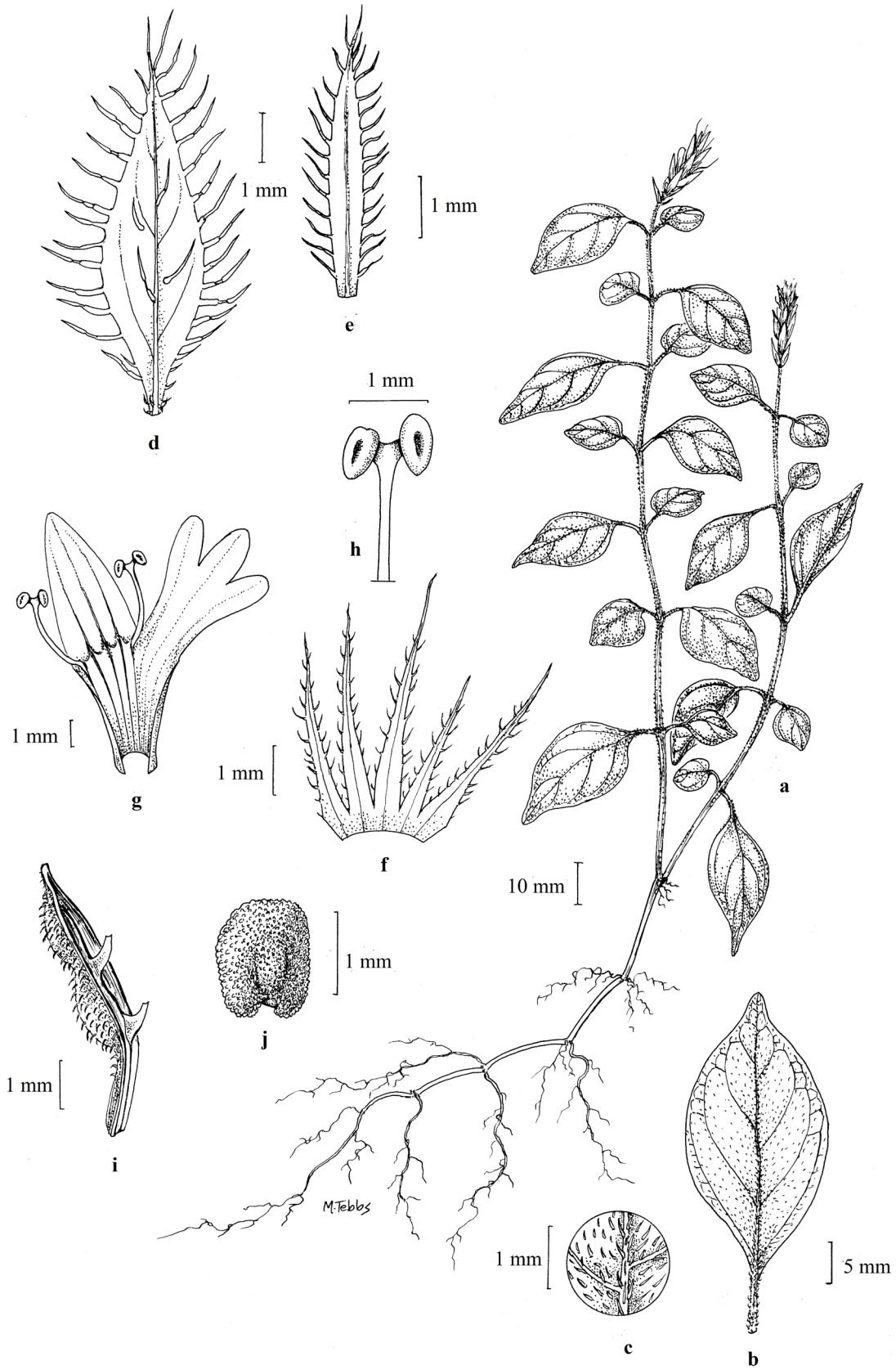

Fig. 9. *Justicia impar* J.R.I.Wood & P.Gallego: **a**. Habit; **b**. Leaf; **c**. Detail of abaxial surface of leaf; **d**. Bract; **e**. Bracteole; **f**. Calyx; **g**. Corolla opened out to show androecium; **h**. Anthers; **j**. Valve of capsule; **k**. Seed (a–g from *Rimachi* 4760; j-k from *Schunke* 3215; drawn by Margaret Tebbs).

long, 3-lobed, lobes *c*. 1.5 × 1 mm, ovate, rounded. Filaments glabrous, *c*. 3 mm long, anthers included; thecae ellipsoid, *c*. 0.75 × 0.5 mm, glabrous, lacking basal appendages. Style 10 mm long, glabrous; ovary puberulent, rostrate. Capsule 5–6 × *c*. 2 mm, 4-seeded, pubescent. Seeds suborbicular, *c*. 1.5 × 1.5 mm. rugose.

Flowering & fruiting: Found in flower in December, June and July, and in fruit in December and June.

Habitat: "Bosque alto." Wet tropical forest, on rocks.

Distribution: Endemic to Peru. Only recently collected in San Martin (Fig. 4).

Etymology: The epithet *impar* (unequal) refers to the very unequal leaves characteristic of this species.

Specimens examined: PERU, **Huánaco**, Cassapi, *Mathews* 1598 (K). **San Martin**, Tarapoto, km 12–14 Carretera de Tarapoto a Yurimaguas, S 6°29', W 76°22', 2250 ft, 03.12.1979, *M. Rimachi* 4760 (US); Ibid. 09.07.1970, *S. McDaniel* 13814 (US).

Conservation status: This species is only known from four collections, two of them from the same place, one without exact geographical information and the most recent made about 45 years ago. We have no idea of the size of the original populations nor of what threats they face. The somewhat disjunct distribution suggests it may be very scattered in distribution so unlikely to be vulnerable to a single catastrophic event. Although it is more likely to have been overlooked than to have become extinct, it is clearly rare. Data Deficient (DD).

Notes: *Mathews* 1598 was identified as *Leptostachya heterophylla* var. *acutior* Nees in Nees von Esenbeck (1847b: 377). It is not a type, as it was not cited in the earlier publication by Nees von Esenbeck (1847a: 150), where the variety was first described.

The *Justicia trichotoma* (Kuntze) Leonard complex

This consists of three strongly anisophyllous species: *Justicia trichotoma, J. magdalenensis* and *J. maynasana*, which are described below. These three species are similar in facies and might even be considered as

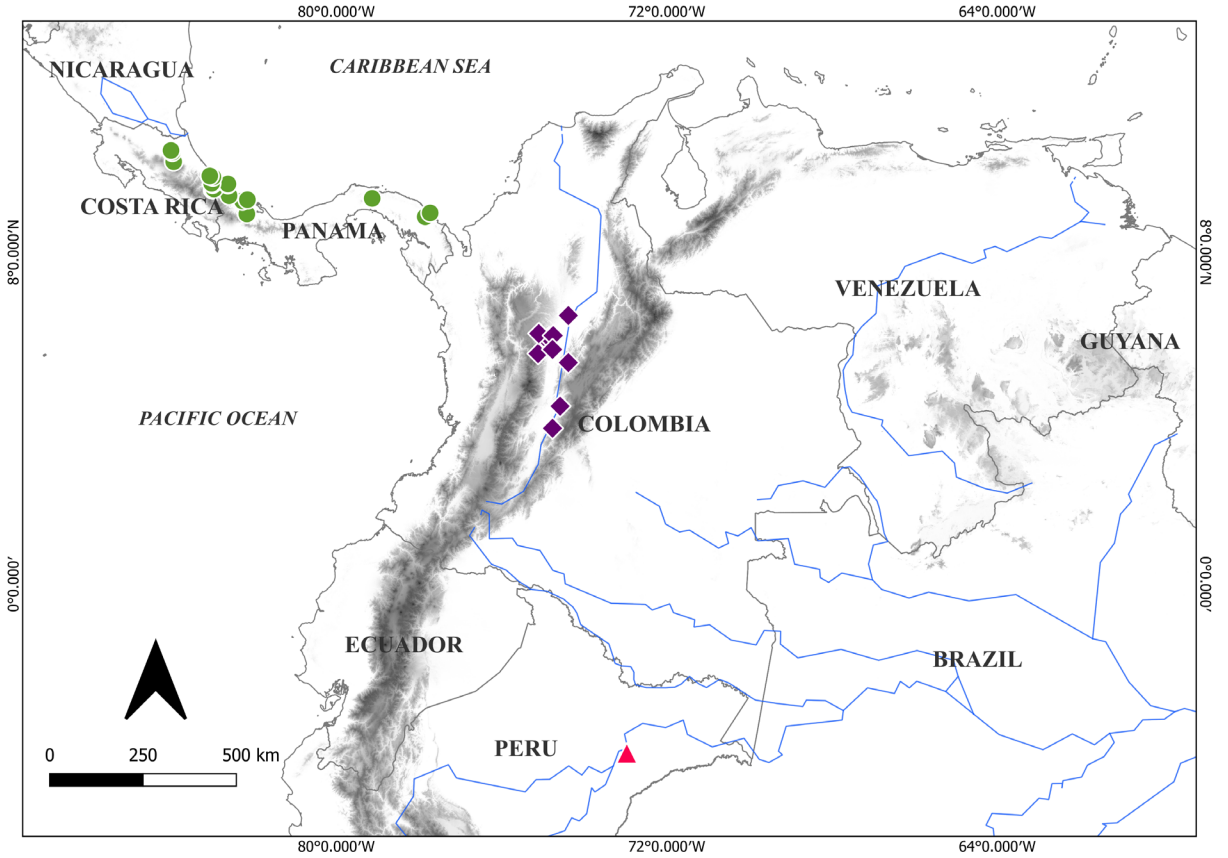

Fig. 10. Distribution of three related anisophyllous species of *Justicia* L.: *J. trichotoma* (Kuntze) Leonard (green circles) in Costa Rica and Panama; *J. magdalenensis* J.R.I.Wood (violet diamonds) in Colombia; *J. maynasana* J.R.I.Wood & P.Gallego (red triangle) in Peru. Map prepared using QGIS v.3.28.2 (QGIS Development Team, 2023).

subspecies of a single species, but their distribution is very disjunct (Fig. 10), and without extensive molecular studies it seems wisest to maintain them as separate species. They can be separated by the following key:

1. Inflorescence of simple axillary spikes (Amazonian Peru)..... *J. maynasana*
1. Inflorescence of trichotomously branched (apparently never simple) spikes..... 2
2. Calyx lobes 5.5–8 mm long (Costa Rica and Panama)..... *J. trichotoma*
2. Calyx lobes 11–13 mm long (Magdalena valley, Colombia)..... *J. magdalenensis*

Justicia trichotoma appears to be quite common in Costa Rica (McDade, 2020) and Panama (*fide* Tropicos), whereas *J. magdalenensis* is restricted to the Medio Magdalena region of Colombia (Fig. 10). The following is a new species:

Justicia maynasana J.R.I.Wood & P.Gallego, **sp. nov.** **Fig. 11**

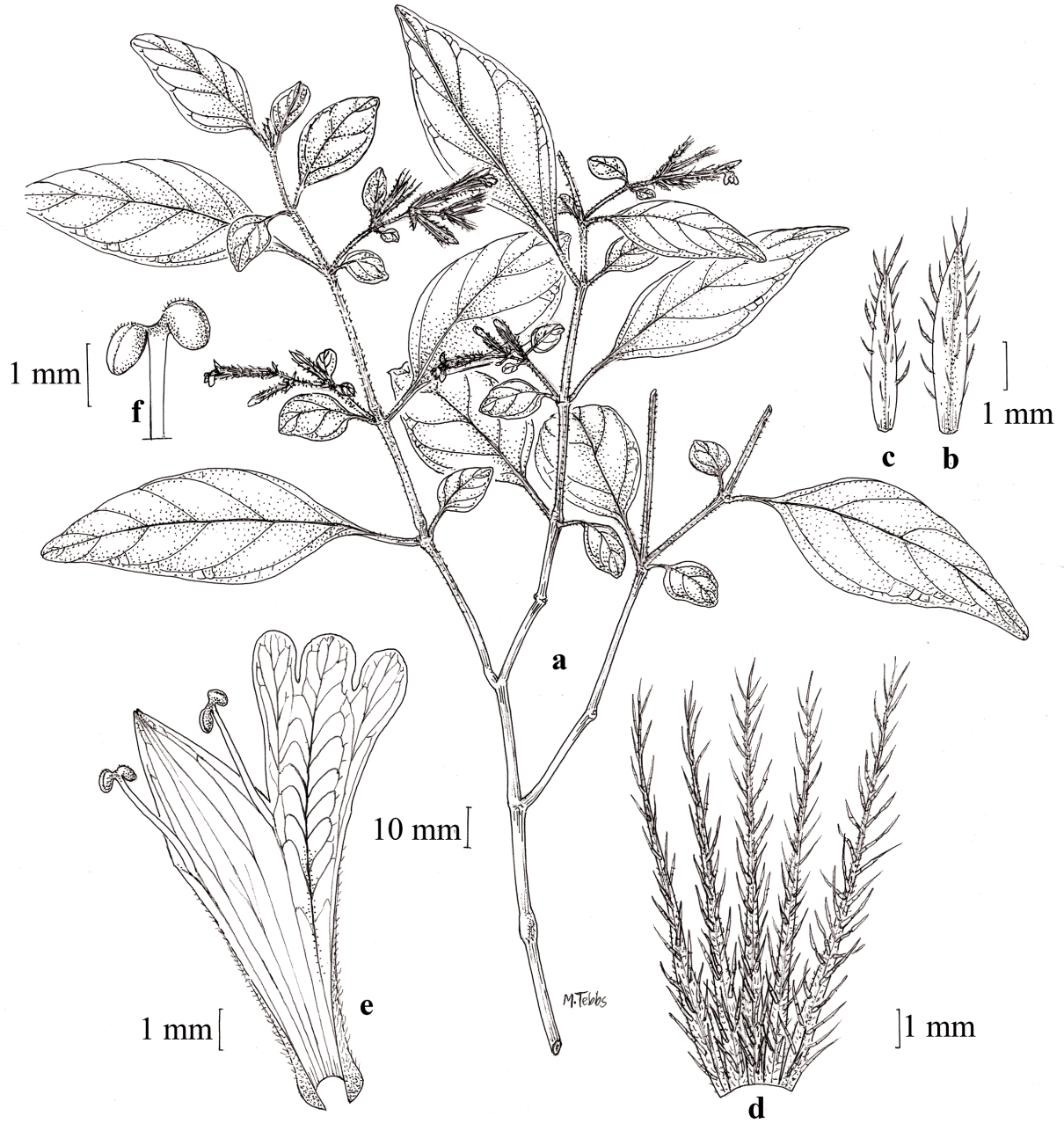

Fig. 11. *Justicia maynasana* J.R.I.Wood & P.Gallego: **a**. Habit; **b**. Bract; **c**. Bracteole; **d**. Calyx; **e**. Corolla opened out to show androecium; **f**. Anthers (drawn by Margaret Tebbs from *Gentry et al.* 29258).

This species is clearly closely related to both *Justicia magdalenensis* and *J. trichotoma*, but the inflorescence is spicate, not cymosely branched as in the other two species, a characteristic implied by the epithet *trichotoma* for the latter. Apart from the form of the inflorescence, the new species fits *J. magdalenensis* perfectly but both the new species and *J. magdalenensis* have relatively long calyx lobes at 11–13 mm in length (not 5.5–8 mm as in *J. trichotoma*). In contrast the corolla of *J. trichotoma* is 16–20 mm in length, thus exceeding that of both *J. magdalenensis* and *J. maynasana*.

Type: PERU, **Loreto**, Maynas, Caseria Alianza, Río Tamshiyacu, trail towards Río Manití, 140 m, S 4°05', W 72°58', 01.08.1980, *Al Gentry, R. Vasquez, N. Jaramillo, E. Andrade* & *P. Stern* 29258 (holo MO [MO2887413!], iso US [MO2979020!], USM [fragment!]).

Anisophyllous subshrubs reaching at least 40 cm in height. Stems at first decumbent and rooting at the nodes, eventually erect to *c*. 30 cm tall, ±quadrangular, pubescent with crisped hairs, sometimes slightly zigzag. Leaves petiolate, unequal in each pair; larger leaves 4–8 × 1.6–3.7 cm, ovate to broadly oblong-elliptic, shortly acuminate to an obtuse apex, cuneate to attenuate at base, margin undulate; smaller leaves 0.6–1 × 0.6–0.8 cm, ovate to suborbicular, acute, glabrous, abaxially paler. Petioles subglabrous, 0.5–2 cm. Inflorescence of lax, axillary spikes 3–5 cm long; peduncles 7–11 mm long, puberulent; rachis puberulent. Bracts at base of spike resembling small leaves; floral bracts *c*. 4 × 0.5 mm, linear, apiculate, thinly pilose with multicellular hairs. Bracteoles similar but only 2–3 mm. Calyx subequally 5-lobed to base, lobes 11–13 × 0.25 mm, filiform, pilose with multicellular hairs. Corolla lavender, 14–15 mm long, 2-lipped; tube subcylindrical 8–9 × *c*. 1 mm, pubescent, lips *c*. 4 mm long, upper lip ovate, obtuse, entire; lower lip 3-lobed, lateral lobes *c*. 1 × 1.5 mm, central one *c*. 1 × 2 mm, broadly ovate, rounded. Filaments 3–4 mm long. glabrous, anthers bithecous; thecae ellipsoid, *c*. 0.5 mm long, puberulent. Style pale pink, *c*. 14 mm long, glabrous; ovary ovoid, *c.* 1 mm long, glabrous. Capsule and seeds not seen.

Flowering & fruiting: Found in flower and fruit in August.

Habitat: Non-inundated forest on lateritic soil at 140 m.

Distribution: Endemic to Amazonian Peru, where it grows in Maynas province of Loreto region.

Etymology: This species is named after the province Maynas, the part of Loreto where it was found.

Specimens examined: Only known from the type (Fig. 10).

Conservation status: This species is only known from a single collection made in relatively poorly known Amazonian Forest. We have no information about the state of conservation of the forest in this area nor of the size of the population of the new species. It may be very rare or locally common and overlooked. Data Deficient (DD).

Odontonema Nees

Odontonema rubrum (Vahl) Kuntze, Revis. Gen. Pl. 2: 494. 1891. *Justicia rubra* Vahl, Eclog. Amer. 2: 1. 1798. *Type*: COLOMBIA, **Magdalena**, Santa Marta, *Rohr* s.n. (holo C [C10005060!]).

Odontonema bracteolatum var. *parviflorum* Leonard, Contr. U.S. Natl. Herb. 31(3):399. 1958. *Type*: COLOMBIA, *H.H. Smith* 1389, *p.p.* (holo US [US00136951!]). **Figs. 12 & 14**

Notes: The type of *Odontonema rubrum* (Vahl) Kuntze is a specimen collected by Rohr at Santa Marta in Colombia and named *Justicia rubra* by Vahl (1798). All specimens from Colombia identified by Leonard (1951–1958) as *Odontonema bracteolatum* should be treated as *O. rubrum*. Leonard also described a variety *parviflorum* of *O. bracteolatum* which likewise should be included in *O. rubrum*. The presence of *O. bracteolatum* in Colombia awaits confirmation.

Odontonema rubrum is relatively common in Panama, northern Colombia and adjacent parts of Venezuela. It is known from Choco, Antioquia, Atlántico, Bolivar, Magdalena, Cesar and Norte de Santander with an anomalous but apparently correct record (*Betancur* & *Churchill* 2257) from further south in Caquetá (Fig. 13). There is considerable variation in leaf size as noted by Leonard (1951–1958) but there is also variation in the relative size of the leaves in each pair, something that Leonard did not note. Both the type of *O. bracteolatum* var. *parviflorum* (*H.H. Smith* 1389, p.p.) and another specimen cited by Leonard under that name (*Dugand* & *Jaramillo* 4153) are moderately anisophyllous as are a few other specimens, such as *Al Gentry* 78443 (US) from Bolivar. None, however, is so remarkably anisophyllous as two specimens from

Fig. 12. The flower of *Odontonema rubrum* (Vahl) Kuntze. (Photo by Yeison Londoño-Echeverri)

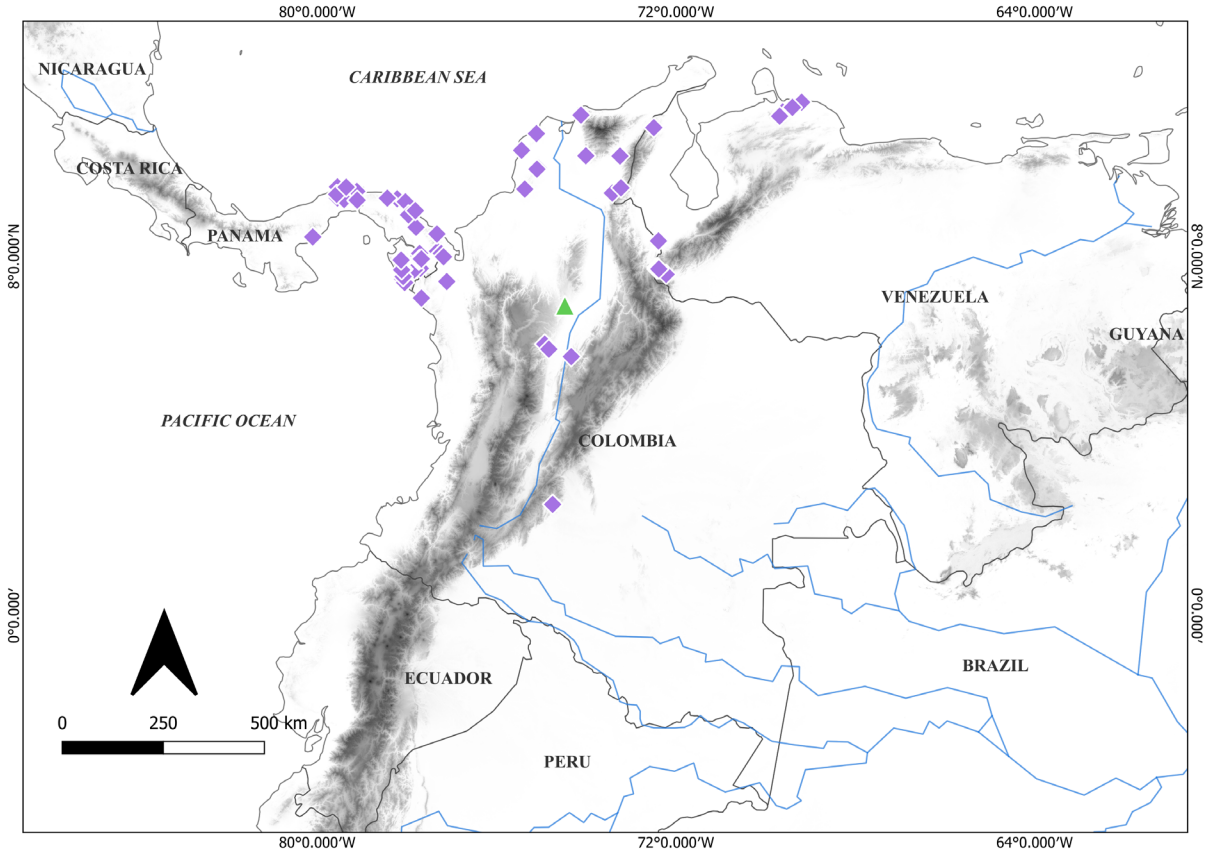

Fig. 13. Distribution of *Odontonema rubrum* (Vahl) Kuntze in Panama, Colombia and Venezuela. Note the strongly anisophyllous example (*Londoño & Trujillo* 221) with a green triangle. Map prepared using QGIS v.3.28.2 (QGIS Development Team, 2023).

Antioquia, Yeison Londoño & Ana M. Trujillo 221 (HUA) and 239 (HUA), both from Mun. Remedios, Vereda Río Negrito at 350 m. This plant is illustrated in Figs. 12 and 13.

The existence of this strongly anisophyllous form of *Odontonema rubrum* underlines the point we made earlier in this paper that anisophylly in the absence of other characters is not a character that can be used to delimit a species. *Odontonema rubrum* is a species that exhibits the complete range of variation in its leaves from isophylly to strong anisophylly.

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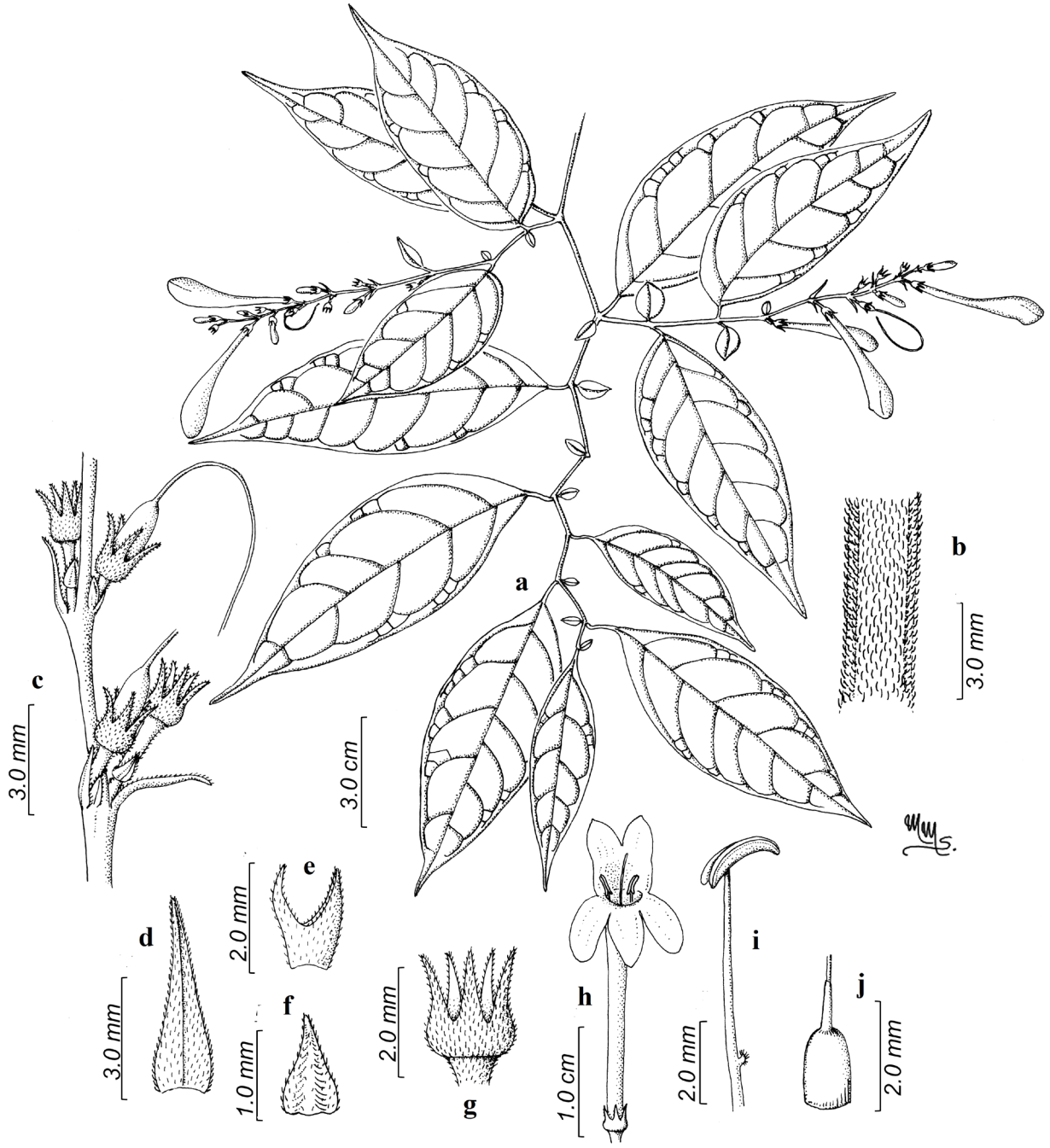

Fig. 14. *Odontonema rubrum* (Vahl) Kuntze: **a**. Habit; **b**. Detail of stem, showing indumentum; **c**. Part of inflorescence; **d**. Bract; **e**. Bracteoles; **f**. Bracteole; **g**. Calyx; **h**. Corolla; **i**. Stamens with anthers; **j**. Ovary (drawn by Marcela Morales from Londoño & Trujillo 221).

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