A taxonomic revision of the Malagasy endemic genus Nematostylis (Rubiaceae), with description of two new species

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A taxonomic revision of the Malagasy endemic genus Nematostylis (Rubiaceae), with description of two new species

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Abstract

KAINULAINEN, K. (2023). A taxonomic revision of the Malagasy endemic genus Nematostylis (Rubiaceae), with description of two new species. *Candollea* 78: 177–188. In English, English and french abstracts. DOI: http://dx.doi.org/10.15553/c2023v782a9

Nematostylis Hook. f. (*Rubiaceae*) is a genus of semi-succulent shrubs endemic to Madagascar, mostly found growing on rocky outcrops in the Northern, Central, and Southern Highlands. This paper provides a revision of the genus in which three species are recognized: *N. anthophylla* (A. Rich. ex DC.) Baill. and the newly described *N. citriflora* Kainul. and *N. incarnata* Kainul. An identification key of the genus is presented, as well as a distribution map, field pictures, line drawings, and species risk of extinction assessments. A neotype is designated for *N. anthophylla* and a lectotype for *N. loranthoides* Hook. f.

Résumé

KAINULAINEN, K. (2023). Révision taxonomique du genre Nematostylis (Rubiaceae) endémique de Madagascar, avec la description de deux nouvelles espèces. *Candollea* 78: 177–188. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2023v782a9

Nematostylis Hook. f. (*Rubiaceae*) est un genre d'arbustes semi-succulents endémiques de Madagascar, que l'on trouve principalement sur les pitons rocheux des Hautes Terres du nord, du centre et du sud. Cet article présente une révision du genre dans lequel trois espèces sont reconnues: *N. anthophylla* (A. Rich. ex DC.) Baill. et les espèces nouvellement décrites *N. citriflora* Kainul. et *N. incarnata* Kainul. Une clé d'identification du genre est proposée, ainsi qu'une carte de répartition, des photos de terrain, des dessins au trait et des évaluations du risque d'extinction des espèces. Un néotype est désigné pour *Nematostylis anthophylla* ainsi qu'un lectotype pour *N. loranthoides* Hook. f.

Keywords

RUBIACEAE – *Alberteae* – *Nematostylis* – Madagascar – Inselbergs – New species – Taxonomy

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Introduction

The genus *Nematostylis* Hook. f. is part of the tribe *Alberteae* in the flowering plant family *Rubiaceae*. It is endemic to Madagascar where it is distributed in the Northern Highlands, the Central Highlands, and in the hills of southeastern regions Androy and Anosy. *Nematostylis* is a genus of semi-succulent shrubs with dichotomous branching. The inflorescences are very conspicuous particularly because one calyx lobe of each flower forms an expanded and showy "calycophyll" that is pink to bright red. The calycophyll persists on the dry indehiscent fruit, and functions as a wing promoting dispersal by wind (Puff et al., 1984; Madagascar Catalogue, 2023). *Nematostylis* is readily recognized from the other genera of the tribe (i.e. *Alberta* E. Mey., endemic to eastern South Africa, and *Razafimandimbisonia* Kainul. & B. Bremer, endemic to Madagascar) by their erect, flat-topped inflorescences of compound scorpioid cymes; narrowly cylindrical flowers with (bicoloured) yellow to red corollas and pink to red calyx lobes; and semi-succulent branches and leaves with indistinct venation (Puff et al., 1984; Kainulainen et al., 2009). The fruits are indehiscent and one-winged unlike the fruits of *Razafimandimbisonia* which are usually schizocarpic with five calycophylls (only one leaf-like calycophyll in *R. sambiranensis* (Homolle ex Cavaco) Kainul. & B. Bremer). Another distinguishing characteristic is the presence of root nodules (Schatz, 2001), whose likely function is storage of water and nutrients and possibly represent a synapomorphy for the genus *Nematostylis*. In a morphological study of the tribe, Puff et al. (1984), who only recognized one species in the genus, described the leaves of *N. anthophylla* (A. Rich. ex DC.) Baill. as being somewhat succulent, soft, short-lived, and amphistomatic (with stomata on both leaf surfaces), with an unilacunar petiole (having only a single vascular bundle). These are likely apomorphic traits that represent xerophytic specialization. Mott et al. (1982), hypothesized that amphistomatic leaves are an adaptation by plants in high-light habitats to maximize carbon-uptake at times when water is available. *Nematostylis* is ecologically specialized and mostly found growing on exposed rocky outcrops and inselbergs.

As noted by Kainulainen et al. (2009), a taxonomic revision of *Nematostylis* is warranted. The populations from the Northern and Southern Highlands are morphologically distinct from the typical *N. anthophylla* in the Central Highlands. In particular, the size and shape of the leaves differ between the species as well as the size and colour of the flowers. In this study, I recognize a total of three species in Madagascar, with *N. citriflora* Kainul. and *N. incarnata* Kainul. being newly described. Cavaco (1968; p. 383), previously recognized the latter two species as forms of "*Alberta loranthoides*", but the names were not validly published since Latin descriptions or diagnoses were not included (Turland et al., 2018: ICN Art. 39.1).

Nematostylis is most closely related to *Razafimandimbisonia* (Kainulainen et al., 2009). In the biogeographic study by Kainulainen et al. (2017), divergence time estimates from plastid DNA indicated that the two genera diverged around 21.6 Ma (with a 95% highest posterior density interval of 13.7–29.1 Ma), and that this corresponds to the minimum age for the dispersal of this lineage from Africa to Madagascar.

Taxonomic treatment

Nematostylis Hook. f., Gen. Pl. 2: 110. 1873.

Typus: *Nematostylis anthophylla* (A. Rich. ex DC.) Baill.

Shrubs up to 3 m tall; dichotomously branching, with semi-succulent twigs; young stems puberulent, soon glabrous. *Leaves* decussate, petiolate or subsessile, semi-succulent and brittle to coriaceous, ovate, rhomboid, broadly elliptic to lanceolate or oblanceolate, amphistomatic, with indistinct secondary and tertiary venation; petioles adaxially canaliculate, unilacunar; domatia absent; stipules interpetiolar, triangular, persistent, with colleters. *Inflorescences* terminal, umbel-like cymes of branched, reddish, scorpioid cymules, puberulent, each flower subtended by a pale green bract. *Flowers* numerous, subsessile, ± erect, 5-merous, bisexual, ± zygomorphic; hypanthium narrowly urceolate; calyx lobes free, triangular to obovate, ± erect, unequal (one being enlarged, elliptic, spreading), orange pink to bright red, persistent; colleters present between lobes; corolla narrowly cylindrical, tube straight to ± curved, glabrous (puberulent) externally, pale yellow to reddish, abruptly widening below the lobes, usually ± curved, pubescent in the lower to middle part of the tube; lobes suborbicular, contorted in bud, overlapping to the left; stamens subsessile, attached in the widened upper part of the corolla tube; anthers linear, included, glabrous, with one apical and two basal appendages; ovary bilocular with one pendulous ovule per locule, disk yellow; style linear, exserted, slightly swollen below the stigma, smooth, glabrous, stigma shortly bifid, lobes rounded 0.5–1 mm long. *Fruits* dry indehiscent, ellipsoidal, longitudinally ridged, sparsely puberulent, crowned by persistent, now translucent calyx lobes. *Seeds* minute, narrowly ellipsoidal.

Distribution, habitat and ecology. – *Nematostylis* is endemic to Madagascar and distributed in the Northern, Central, and Southern Highlands (Fig. 1). *Nematostylis* appears ecologically specialized to rocky habitats. The species are often collected on rocky outcrops in open grasslands or in shrubland, with inselbergs being a typical habitat. Rabarimanarivo et al. (2019) studied the flora of the inselbergs in Madagascar's central plateau and found *Nematostylis* in most sites that they visited. Although often found growing on rocks, they are not obligate lithophytes.

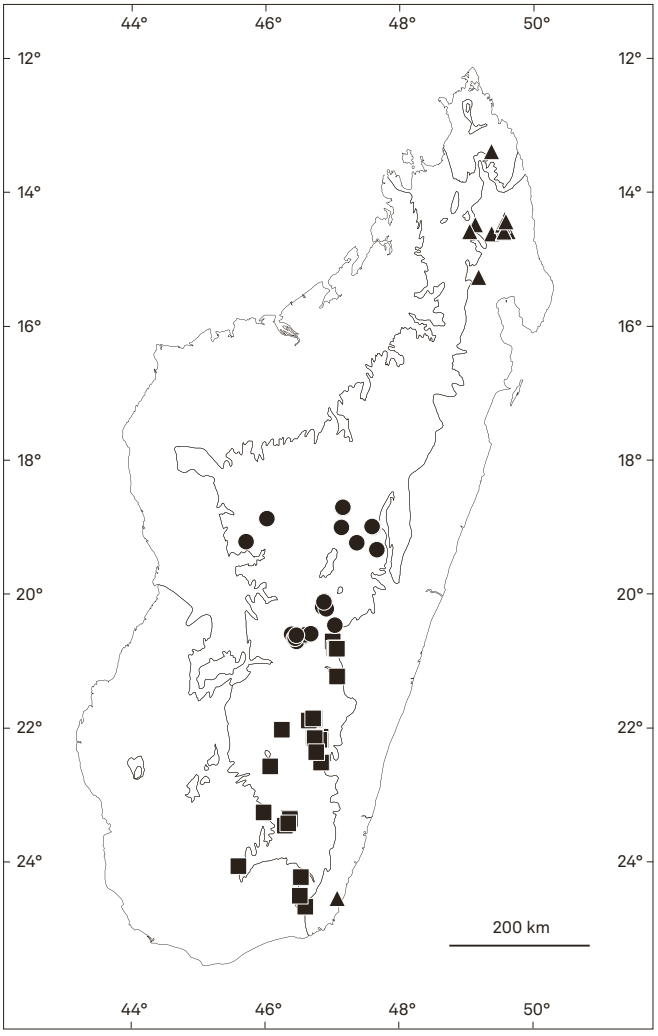

Fig. 1. Distribution map of *Nematostylis anthophylla* (A. Rich. ex DC.) Baill. (circles), *N. citriflora* Kainul. (squares), and *N. incarnata* Kainul. (triangles) in Madagascar mapped on the bioclimatic zones of Madagascar (after Cornet, 1974; see Schatz, 2000).

Nematostylis anthophylla and *N. citriflora* are deciduous, and I have only seen a few specimens collected between July to October (none from August to September) during the dry season when the plants usually lose their leaves. However, in *N. incarnata* the leaves may persist for more than one growing season (although they are commonly confined to shoots of the current growing season). Specimens with both flowers and fruits are common in all species, indicating that the flowering period can be long. The flowers are protandrous and show secondary pollen presentation. As the style extends and the flower opens, pollen is deposited on a slightly swollen portion of the style just below the stigma. Pollen usually does not remain when the style is fully extended and the stigmatic lobes open. The narrowly cylindrical flowers are pollinated by butterflies (Puff et al., 1984; see Fig. 1I in Kainulainen et al., 2009), and the fruits are dispersed by wind, with the persistent calycophyll acting as a wing.

Key to the species of Nematostylis

1. Upper and lower leaf blade surfaces distinctly different (upper surface darker, glossier); leaves semi-deciduous or persistent (confined to shoots of the most recent growing season or not); corolla tube 6–14 mm; style exerted to c. 7 mm ..... ***N. incarnata***

1a. Upper and lower leaf blade surfaces of similar colouration and texture; leaves deciduous (confined to shoots of the most recent growing season); corolla tube 10–27 mm; style exserted to c. 20 mm 2

2. Leaves broadly elliptic to ovate or rhomboid (lanceolate), 2.5–10 × 1–6 cm; calyx/calycophyll red, rarely pink; corolla tube 10–21 mm, ± bicoloured, bright yellow in the upper dilated part and red or reddish in the middle and lower portion ..... ***N. anthophylla***

2a. Leaves oblanceolate (lanceolate), 1.5–5.5(–6) × 0.4–2(–2.7) cm; calyx/calycophyll orange pink to pink (pale red); corolla tube 18–27 mm, usually pale greenish yellow and orange pink towards base ..... ***N. citriflora***

Taxonomy

1. ***Nematostylis anthophylla*** (A. Rich. ex DC.) Baill. (Fig. 2A, 2F, 3).

   ≡ *Pavetta anthophylla* A. Rich. ex DC., Prodr. 4: 492. 1830.

   Neotypus (designated here): **Madagascar. Reg. Analamanga [Prov. Antananarivo]:** Distr. Antananarivo Avaradrano, Ambohimanga Rova, "in monte Ambouimanga", s.d., *Anon. s.n.* (P [P03938508] image!).

   = *Nematostylis loranthoides* Hook. f., Gen. Pl. 2: 110. 1873. ≡ *Alberta loranthoides* (Hook. f.) Cavaco in Adansonia, sér. 2, 5: 517. 1965. **Lectotypus** (first-step designated by Puff et al., 1984: 349; second-step designated here): **Madagascar:** sine loco, s.d., *Parker s.n.* (K [K000034310] image!).

Shrubs to 2 m tall; young stems with bark smooth, dark grey to pale brown. *Leaves* deciduous; petioles 1–10 mm long; leaf blades broadly elliptic to ovate or rhomboid (lanceolate), 2.5–10 × 1–6 cm, rounded, cuneate, or attenuate at base, acute at apex, abaxial and adaxial surfaces green when fresh (often with reddish leaf margins), drying (blackish or greyish) olive green, smooth and matte, glabrous, semi-succulent, midrib prominent, pale green to reddish when fresh, greenish brown when dry; stipules broadly triangular to shortly acuminate, 2–4.5 × 2–4.5 mm. *Inflorescences* to c. 12 cm tall, flower-subtending bracts lanceolate, 4–25 × 1–5 mm. *Flowers* with hypanthium 2.5–6 × 1–2 mm, puberulent; calyces bright red (rarely pink); enlarged calyx lobe elliptic 4.5–20 × 2–7 mm, the smaller lobes 2–5 × 0.5–1.5 mm; corolla tube 10–21 mm

long, 0.8–2 mm in diam., widened in its upper part (2–5 mm in diam.), externally red in the lower part to yellow in the upper part, internally yellow; corolla lobes externally yellow, internally yellow, 1.5–2.5 × 1.5–3.5 mm, recurved at anthesis; stamens attached c. 3 mm below corolla sinus; anthers 2–3 × 0.4–0.6 mm; style 25–40 mm long, exserted to c. 20 mm; stigma c. 0.5 mm long. *Fruits* 3–7 × 1.5–3.5 mm.

Vernacular names. – "Voun-zaza-vavi" (*Anon. s.n.*, P03938508; meaning fruit/flower for girl).

Distribution, habitat and ecology. – *Nematostylis anthophylla* is known from 1,200 to 2,000 m in elevation in Analamanga, Amoron'i Mania, Bongolava, Itasy, and Vakinankaratra regions. The species is confined to the ecoregion "Madagascar subhumid forest" (Fig. 1). It grows in open vegetation on rocky outcrops and in rocky soils (on calcite, granite, metamorphic rocks, or quartzite).

Phenology. – Flowering material has been collected in October and from December to April, and fruiting material from January to July.

Conservation status. – *Nematostylis anthophylla* is known from more than ten localities in central Madagascar, and its distribution includes three protected areas, i.e., Angavokely, Ibity, and Itremo. However, this species is ecologically specialized to rocky outcrops and inselbergs and the populations are severely fragmented. The area of occupancy is estimated to be less than 2,000 km², and as noted by Rabarimanarivo et al. (2019) habitat quality of most inselbergs in Madagascar is decreasing in recent times. *Nematostylis anthophylla* can therefore be assigned a preliminary conservation status of "Near Threatened" [NT] according to the IUCN Red list Categories and Criteria (IUCN, 2012).

Notes. – Following Kirkbride & Wiersema (2022), the name *Pavetta anthophylla* was coined by Richard (1830, December) but first published by Candolle (1830, September), who copied Richard's description. Since no original material was cited in the protologue, the typification of this name should be resolved by the designation of a neotype from material seen by Richard. The specimen P03938508 in the Paris herbarium, which lacks collector name and number, is likely the material used by Richard considering that it originates from his herbarium and is identified as "*Pavetta anthophylla* A. Rich" in Richard's hand. Locality information is given on the specimen as "in monte Amboui-manga", which probably refers to Ambohimanga, a hill c. 24 km NE of Antananarivo (I have not seen any recent gathering from this locality).

Nor did Hooker (1873) provided a type when he published his description (descriptio generico-specifica, see ICN Art. 38.5) of *Nematostylis loranthoides*. In the absence of cited specimens (no illustration is cited either), it is very difficult to trace the material that was used by Hooker to prepare the description. Puff et al. (1984: 349) cited *Parker s.n.* (K) as the type. Two specimens are kept at K: one belonging to Herbarium Hookerianum that matches the information provided in the protologue [K000034310]; and a duplicate, K000034309, not belonging to Hooker's herbarium and received in 1880. Although the specimen K000034310 is not identified or annotated by Hooker, it is designated as the second-step lectotype of the name *N. loranthoides.*

Nematostylis anthophylla is variable in leaf shape. On a single plant the leaf shape can vary from ovate, elliptic to lanceolate and even be similar to that of *N. citriflora* (*Andriantiana et al. 708*). However, in general the leaves are not widest near the tip as in *N. citriflora*. The two species are perhaps sympatric (introgressing?) in the area around Ambositra.

Additional material examined. – Madagascar. **Reg. Analamanga [Prov. Antananarivo]:** Distr. Andramasina, Ambohimiadana, Iaramalaza Inselberg, 19°16'19"S 47°48'18"E, 1552 m, 18.II.2011, fr., *Ramananjanahary et al. 335* (MO); Distr. Ankazobe, Ikopa valley, 15.III.1930, fr., *Decary 7578* (P); Fihaonana, Lohavohitra, 18°38'26"S 47°17'04"E, 1539 m, 11.III.2011, fl., *Rabarimanarivo et al. 374* (P); ibid. loco, 18°37'38"S 47°17'18"E, 9.III.2010, fl., *Rajaonary 34* (P); Distr. Manjakandriana, Manjakandriana, Angavokely, 18°55'34"S 47°45'04"E, 1610 m, 26.III.2004, fl. & fr., *Almeda et al. 8768* (CAS, TAN); ibid. loco, II.1959, fl., *Bosser 12767* (P, TAN); ibid. loco, 1550 m, 13.II.2000, fl., *Bremer et al. 4079* (UPS); ibid. loco, II.1960, fl., *Keraudren 1* (P); ibid. loco, 1700–1800 m, 14.I.1960, fl., *Leandri 2569* (P); ibid. loco, 1700–1800 m, 25.II.1960, fl., *Leandri 3152* (P); ibid. loco, 14.I.1960, fl., *Peltier & Peltier 1726* (P, TAN); ibid. loco, X.1914, fl., *Perrier de la Bâthie 12929* (P); ibid. loco, 1600 m, 28.II.1988, fl., *Pettersson & Nilsson 208* (UPS); ibid. loco, 18°56'S 47°45'E, 1600 m, 13.II.1992, fl., *Pettersson & Nilsson 518* (UPS); ibid. loco, 22.IV.1957, fr., *Poisson s.n.* (TAN); ibid. loco, 18°55'22"S 47°44'23"E, 1641 m, 7.III.2011, fl., *Rabarimanarivo et al. 333* (P); ibid. loco, 18°55'12"S 47°43'56"E, 1559 m, 7.III.2011, fl. & fr., *Ramahefaharivelo et al. 338* (MO, P); ibid. loco, 1.I.1949, fl. & fr., *Service Forestier 103* (P). **Reg. Bongolava [Prov. Antananarivo]:** Distr. Tsiroanomandidy, Belobaka, Analandraisoa forest, [19°09'S 45°49'E], IV.1963, fl. & fr., *Bosser 17632* (P, TAN); Ambohiby forest, [18°48'S 46°08'E], 1600 m, IV.1933, fl. & fr., *Leandri 753* (P, TAN). **Reg. Itasy [Prov. Antananarivo]:** Distr. Arivonimamo, Antongona, [18°56'S 47°16'E], 1200 m, 14.III.1960, fl. & fr., *Cours 5717* (P). **Reg. Vakinankaratra [Prov. Antananarivo]:** Iarinandriana, [19°10'S 47°30'E], XII.1959, fl., *Bosser 13651* (TAN); Distr. Antsirabe II, Ibity, 20°05'24"S 47°00'23"E, 1840–1890 m, 15.III.2004, fl., *Almeda et al. 8702* (CAS, TAN); ibid. loco, 20°03'26"S 47°00'40"E, 1650 m, 2.II.2003, fl. & fr., *Andriamihajarivo et al. 79* (MO, P, TAN); ibid. loco, 5.III.1985, fr., *Barnett 485* (MO, P, TAN); ibid. loco, 1700 m, 28.III.1972, fl. & fr., *Cremers 2038* (P, TAN); ibid. loco, 6.III.1985, fl., *Dorr et al. 3851* (MO, P, TAN); ibid. loco, 20°05'S 47°01'E, 1500 m, 14.VII.1989, fr., *Du Puy & Du Puy MB240* (TAN); ibid. loco, 20°07'S 47°01'E, 21.I.2006, fl., *Eriksson et al. T977* (S); ibid. loco, 13.V.1901, fr., *Grandidier s.n.* (P); ibid. loco, 2000 m, I.1973, fr., *Guillaumet s.n.* (TAN); ibid. loco, 20°08'40"S 46°58'53"E, 1426 m, 21.VI.2005, fr., *Hongwa 337* (P); ibid. loco, 20°10'14"S 47°02'10"E, 1634 m, 23.II.2003, fl., *Koopman & Andriamihajarivo 162* (MO); ibid. loco, 20°03'59"S 47°00'01"E, 1657 m, 16.III.2011, fl. & fr., *Randrianaivo et al 1803* (G, P). **Reg. Amoron'i Mania [Prov. Fianarantsoa]:** Distr. Ambositra, Tsarasaotra, Ambohitrinimasina inselberg, 20°25'12"S 47°09'59"E, 1482 m, 12.III.2010, fl., *Andriantiana et al. 708* (MO, P); Distr. Ambatofinandrahana, 1600–1800 m, 17.II.1933, fl. & fr., *Decary 13033* (P); ibid. loco, 4.II.1942, fl. &

Fig. 2. A–C: Flowers in side-view; **D, E**: Corolla interior; **F–H:** Fruits in side-view.
A, F: *Nemastylis anthophylla* (A. Rich. ex DC.) Baill., **B, E, G:** *Nemastylis citriflora* Kainul.; **C, D, H:** *Nemastylis incarnata* Kainul.
[**A:** *Lantz 160*; **B, E, G:** *Krüger & Razafimandimbison 75*; **C, H:** *Bremer et al. 5294*; **D:** *Bremer et al. 5310*; **F:** *Pettersson & Nilsson 208*]

Fig. 3. *Nematostylis anthophylla* (A. Rich. ex DC.) Baill. **A.** Flower buds; **B, C.** Habitat and habit; **D, E.** Flowering branches; **F.** Young fruits.
[**B:** *Labat et al. 3058*; **D:** *Eriksson et al. T977*]
[Photos: **A:** F. Randriatsara, Andranofeno, 14.I.2016; **B:** J-N. Labat; **C, F:** F. Rakotonasolo, Itremo, Ambatofinandrahana, 14.II.2010; **D:** K. Kainulainen; **E:** Len deBeer, Angavokely, 25.II.2012]

fr., *Decary 17368* (MO, P); Antsirakambiaty, 20°34'36"S 46°33'39"E, 1535 m, 25.IV.2012, fr., *Andrianaivoravelona et al. ANB 574* (BR, K, MO, TAN); ibid. loco, 20°33'30"S 46°30'30"E, 1600 m, 17.II.2011, fl., *Rakotonasolo RNF 1750* (CAS); Itremo, 20°35'4"S 46°42'2"E, 1710 m, 27.III.1999, fl. & fr., *Labat 3058* (BR, K, MO, P, TAN); ibid. loco, 20°40'S 46°35'E, 1600 m, 23.III.1971, fl., *Mabberley 760* (K, MO, TAN); ibid. loco, X.1963, fl., *Morat 118* (P); ibid. loco, 20°34'00"S 46°42'40"E, 1250 m, 11.III.1992, fl. & fr., *Phillipson et al. 3839* (TAN); ibid. loco, 20°33'S 46°48'E, 12.VI.1994, fr., *Ranaivojaona et al. 8* (MO, P, TAN); ibid. loco, 20°37'S 46°33'E, 1630–1650 m, 7.IV.1998, fl. & fr., *Randrianaivo et al. 167* (BR, G, MO, P, TAN); ibid. loco, 20°37'05"S 46°33'50"E, 1670 m, 13.III.1992, fl. & fr., *Clement et al. 2031* (MO, P, TAN); ibid. loco, 20°34'21"S 46°34'54"E, 1580–1700 m, 10.III.2000, fl., *Schatz et al. 3966* (MO, P). **Sine loco:** s.d., fl., *Baron 751* (K, P); "Central Madagascar", s.d., fl. & fr., *Parker s.n.* (K); cultivated in the Botanical Garden, Uppsala [accession 1996-3124]; *Nilsson s.n.* [probably collected in Angavokely], 2004, fl., *Lantz 160* (UPS).

2. ***Nematostylis citriflora*** Kainul., **sp. nov.** (Fig. 2B, 2E, 2G, 4).

Holotype: Madagascar. Reg. Matsiatra-Ambony [Prov. Fianarantsoa]: Distr. Ambalavao, Réserve d'Anja, 21°5010"S 46°50'58"E, 1171 m, 22.III.2006, fl., *Labat et al. 3653* (P [P00533697]!; iso-: K, MO, TAN).

– *Alberta loranthoides* f. *linearifolia* Cavaco in Adansonia, sér. 2, 8: 383. 1968 [nom. inval.].

Nematostylis citriflora Kainul. differs from N. anthophylla (A. Rich. ex DC.) Baill. in its smaller leaves (1.5–6 × 0.4–2.7 cm vs. 2.5–10 × 1–6 cm) that are oblanceolate to lanceolate (vs. broadly elliptic to ovate or rhomboid [lanceolate]); orange pink calyx (vs. usually bright red); and its longer corolla (tube 18–27 mm vs. 10–21 mm), that is usually pale yellow, often orange pink towards the base (vs. ± bicoloured corolla tube that is bright yellow in the upper dilated part and red to reddish in middle and lower part).

Shrubs to 2 m tall; young stems with bark smooth, dark grey to pale brown. *Leaves* deciduous; petioles 1–10 mm long; leaf blades oblanceolate to lanceolate, 1.5–5.5(–6) × 0.4–2(–2.7) cm, attenuate to cuneate at base, acute at apex, abaxial and adaxial surfaces green when fresh (often with reddish leaf margins), drying (blackish or greyish) olive green, usually ± wrinkled, matte or ± glossy, glabrous (pubescent), semi-succulent, midrib prominent, pale green to reddish when fresh, drying greenish brown; stipules triangular, 1.5–3 × 2–4 mm. *Inflorescences* to c. 8 cm tall, flower-subtending bracts lanceolate, 3–8 × 1.5–3.5 mm. *Flowers* with hypanthium 3–4.5 × 1–3 mm, puberulent; calyces pale red, pink to orange pink; enlarged calyx lobe 7.5–20 × 2–5.5 mm, the smaller lobes 1.5–4 × 0.5–1.0 mm; corolla tube 18–27 mm long, 1–2 mm in diam., widened in its upper part (2–3 mm in diam.), externally pale (greenish) yellow but often pink towards the base, internally pale yellow; corolla lobes externally and internally pale yellow, 1.5–2.5 × 1.5–3 mm, recurved at anthesis; stamens attached c. 2.5 mm below corolla sinus; anthers c. 2.5 × 0.5 mm; style 35–45 mm long, exserted to c. 20 mm; stigma 0.5–1 mm long. *Fruits* 5–8 × 2–4 mm.

Etymology. – The specific epithet *citriflora* refers to the yellow corolla of this species.

Vernacular name. – "Maroatody" (*Cours 5770*; *Rakotovao et al. 803*).

Distribution, habitat and ecology. – *Nematostylis citriflora* is known from 750 to 2,400 m in elevation in Amoron'i Mania, Androy, Anosy, Ihorombe, and Matsiatra-Ambony regions. Like *Nematostylis anthophylla*, *N. citriflora* is mainly confined to the ecoregion "Madagascar subhumid forest", but its distribution is in the southern part (Fig. 1). It grows in open vegetation on rocky outcrops and in rocky soils (on granite and gneiss).

Phenology. – Flowering material has been collected from November to June, and fruiting material from March to June and in September.

Conservation status. – *Nematostylis citriflora* has a wide distribution in Central and South Madagascar and is known from several protected areas including Andohahela, Andringitra, Anja, Ivohibe, and Kalambatrita. It can therefore be assigned a preliminary conservation status of "Least Concern" [LC] according to the IUCN Red list Categories and Criteria (IUCN, 2012).

Notes. – Like the other species of *Nematostylis* the leaves of *N. citriflora* are usually ± glabrous, but there are a few collections from Kalambatrita that have pubescent leaves (*Andrianjafy et al. 589*; *Humbert 11791*). *Nematostylis citriflora* is similar to and presumably closely related to *N. anthophylla*. They mainly differ in leaf size and shape and flower colour. The leaf shape of the latter species is variable but is usually ovate or rhomboid to elliptic, whereas in *N. citriflora* the leaves are oblanceolate. In dried herbarium specimens the leaves of *N. citriflora* usually appear wrinkled (vs. ± smooth in *N. anthophylla*), indicating that the living leaves may be more succulent than in *N. anthophylla*. A specimen that appears intermediate is *Phillipson et al. 3918*, collected South of Ambalavao in Matsiatra-Ambony. It has smooth, elliptic, relatively larger leaves (up to 6 × 2.7 cm) similar to *N. anthophylla*, but the yellow, longer (22 mm) corolla tube of *N. citriflora*. It is here tentatively included in the latter, but it is possible that it represents introgression between the two species.

Whereas flowers of *Nematostylis anthophylla* usually have a ± bicoloured corolla (the corolla lobes and upper dilated portion of the tube is bright yellow, the middle and lower tube is red or reddish), in *N. citriflora* the corolla is usually

pale yellow, although often turning orange pink towards the very base. In general, the colour of the calyces/calycophylls also appears to differ somewhat, usually bright red (rarely pink) in *N. anthophylla* vs. orange pink, pink, or pale red in *N. citriflora* (Fig. 3, 4). The vernacular name "maroatody" means many eggs and it refers to the presence of root tubercules. Tubercules are preserved on the specimen *Frasier 195* [P05376628] and are orbicular and c. 1.5 cm in diam.

Additional material examined. – **Madagascar. Reg. Amoron'i Mania [Prov. Fianarantsoa]:** Distr. Ambatofinandrahana, III.1960, fl. & fr., *Keraudren 160* (P); Distr. Ambositra, 21.III.1960, fr., *Peltier & Peltier 2233* (BR, P); Ivato, [20°40'S 47°08'E], 6.II.1998, fl., *Allorge 2050* (P); Ambalamanakana, Andriatsitovia, 20°46'47"S 47°09'38"E, 28.I.2004, fl., *Rakotonasolo RNF 750* (BR, K); Ankazomivady, 20°46'18"S 47°10'48"E, 1560 m, 14.V.1993, fl., *Jongkind & Rapanarivo 902* (MO, P, TAN); ibid. loco, 20°46'42"S 47°11'52"E, 1770 m, 15.III.2016, fl., *Rabarimanarivo et al. 900* (MO, TAN). **Reg. Matsiatra-Ambony [Prov. Fianarantsoa]:** Distr. Ambalavao, Andringitra, 22°11'31"S 46°54'01"E, 2229 m, 17.IX.2006, fr., *Almeda et al. 9396* (CAS); ibid. loco, 22°06'57"S 46°56'55"E, 1710 m, 14.I.2006, fl., *Anderberg et al. 75* (MO, P, S); ibid. loco, IV.1964, fl. & fr., *Bosser 19517* (MO, P, TAN); ibid. loco, 2000 m, 9.V.1957, fr., *Cours 5770* (P); ibid. loco, 22°07'35"S 46°51'57"E, 2144 m, 25.III.2004, fl. & fr., *Davis & Rakotonasolo APD 3165* (BR, G, K, MO, P); ibid. loco, 22°10'14"S 46°57'03"E, 2120 m, 4.IV.2010, fl. & fr., *Krüger & Razafimandimbison 75* (S); ibid. loco, 14.I.2006, fl., *Larsson et al. L039* (UPS); ibid. loco, 2400 m, VI.1965, *Morat 1323* (P); ibid. loco, 22°07'S 46°50'E, 1640 m, 11.I.2006, fl., *Morawetz et al. 240* (BR, P); ibid. loco, 22°10'S 46°56'E, 1650 m, 8.IV.1997, fr., *Rakotovao et al. 803* (MO, P); ibid. loco, 22°09'43"S 46°55'48"E, 14.II.2007, fl., *Ranarivelo RTI 520* (P); ibid. loco, 4.IV.1951, fl., *Réserves Naturelles 3036* (P, TAN); ibid. loco, 30.III.1952, fr., *Réserves Naturelles 4005* (P, TAN); ibid. loco, 22°08'12"S 46°51'60"E, 2136 m, 14.I.2017, fl., *Thureborn et al. 37* (S); Anja reserve, 21°51'11"S 46°51'11"E, 1170 m, 17.III.2010, fl., *Frasier 195* (BR, MO, P); Besoa, 21°52'10"S 46°46'15"E, 950 m, 17.III.1992, fl., *Phillipson et al. 3918* (BR, MO, TAN, UPS); Iarintsena, Ambalalova inselberg, 21°50'13"S 46°50'11"E, 1124 m, 15.III.2010, fl., *Rakotoarivelo et al. 268* (MO, P); Vohitsaoka, 14.I.1955, fl., *Réserves Naturelles 7275* (P); ibid. loco, 16.XII.1950, fl., *Réserves Naturelles 2299* (P); Ankafina forest [21°12'S 47°12'E], II.1881, fl., *Hildebrandt 3921* (G [2 sheets], K, P). **Reg. Ihorombe [Prov. Fianarantsoa]:** Distr. Ihosy, Bemanda, [22°34'S 46°11'E], 750 m, II.1955, fl., *Cours 5134* (P, TAN); Zazafotsy, Bonnet du Pape inselberg, 22°00'32"S 46°21'44"E, 1133 m, 22.III.2010, fl., *Ramandimbisoa et al. 111* (P); ibid. loco, 22°00'33"S 46°21'39"E, 1173 m, 13.XII.2011, fl., *Ramandimbisoa et al. 205* (P); Ivohibe summit, [22°30'30"S 46°57'24"E], 1500–2000 m, 11.V.1924, fl. & fr., *Humbert 3338* (K, P); Ivohibe, 22°21'S 46°53'E, 1100 m, 29.V.2010, fl. & fr., *Ranarivelo et al. RHS 1362* (CAS). **Reg. Androy [Prov. Toliara]:** Ampandrandava, [24°05'S 45°42'E], 1000 m, VI.1943, fl. & fr., *Seyrig 732* (P). **Reg. Anosy [Prov. Toliara]:** Andohahela (RN XI), [24°42'S 46°43'E], 1700 m, I.1974, fl., *Morat 4412* (P); ibid. loco, II.1954, fl., *Paulian s.n.* (TAN); Distr. Amboasary Sud, Tranomaro, Andohahela, 18.III.1953, fl. & fr., *Réserves Naturelles 5051* (P, TAN); Distr. Betroka, [23°16'S 46°05'E], II.1963, fl., *Bosser 17369* (P, TAN); ibid. loco, VI.1963, fl., *Bosser 17842* (P); Kalambatritra [23°22'S 46°29'E], 1000 m, XI.1933, fl., *Humbert 11791* (BR, MO, P); Ivahona, Kalambatritra RS, 23°28'04"S 46°24'22"E, 1320 m, 8.XI.2004, fl., *Andrianjafy et al. 589* (MO, P, TAN); ibid. loco, 23°25'57"S 46°27'27"E, 1568 m, 29.V.2005, fl. & fr., *Andrianjafy et al. 1168* (MO, P); Fort-Dauphin, II.1955, fl. & fr., *Descoings 420* (TAN); Morahariva Mt., [24°32'S 46°38'E], 1000–1400 m, XII.1933, fl., *Humbert 13087* (BR, P); Amboahangy Mt., [24°15'S 46°39'E], 1000–1150 m, 25.XI.1928, buds, *Humbert 6817bis* (BR, P). **Sine loco:** "Betsileo land", s.d., fl., *Baron 168* (K, P).

3. ***Nematostylis incarnata*** Kainul., **sp. nov.** (Fig. 2C, 2D, 2H, 5).

Holotype: Madagascar. Reg. SAVA [Prov. Antsiranana]: Distr. Andapa, Manantenina, Marojejy National Park, trail between camp#3 and the summit of Marojejy NP, 14°25'S 49°43'E, 20.IV.2008, fl. & fr., *Bremer et al. 5294* (S09-42307!; iso-: TAN).

– *Alberta loranthoides* f. *latisepala* Cavaco in Adansonia, sér. 2, 8: 383. 1968 [nom. inval.].

Nematostylis incarnata Kainul. is similar to N. anthophylla (A. Rich. ex DC.) Baill. in its broadly elliptic leaves and its reddish flowers with yellowish corolla lobes, but it differs in its leaves with the abaxial and adaxial surface of distinct colour and texture (vs. being of similar colour and texture), the apex (retuse) obtuse to rounded (vs. acute), and in having shorter flowers (corolla tube 6–14 mm vs. 12–21 mm).

Shrubs up to 3 m tall; young stems with bark (yellowish) grey and smooth. *Leaves* semi-deciduous; petioles 0–6 mm long; leaf blades semi-succulent to coriaceous, broadly elliptic (ovate) to suborbicular, 2–6 × 1–3 cm, cuneate to rounded at base, obtuse (acute) to rounded or retuse at apex; adaxial surface dark green when fresh, drying blackish green or greenish brown, smooth and glossy, glabrous, semi-succulent, midrib prominent, pale green to reddish when fresh, ± the same colour as the leaf when dry; abaxial surface pale green when fresh, drying greenish-brown; stipules broadly triangular, 1–2 × 3–4 mm. *Inflorescences* 2.5–7 cm tall, flower-subtending bracts elliptic, 3–10 × 1–6 mm. *Flowers* with hypanthium 3–4 × 1–1.5 mm, sparsely puberulent; calyces bright red; enlarged calyx lobe narrowly elliptic to suborbicular, spreading, 4.5–15 × 1.5–7 mm, the smaller lobes 1–3.5 × 0.5–1.5 mm, triangular to obovate, ± erect; corolla tube 6–14 mm long, 0.8–2 mm in diam., widened in its upper part (1.5–3 mm in diam.) externally bright red (reddish yellow), internally yellow; corolla lobes externally reddish yellow, internally yellow, 1–1.5 × 1–1.6 mm, erect at anthesis(?); stamens attached c. 2 mm below corolla sinus; anthers c. 2.5 × 0.5 mm; style 10–17 mm long, exserted to c. 7 mm; stigma c. 0.5 mm long. *Fruits* 3–7 × 1.5–3 mm.

Etymology. – The specific epithet *incarnata* refers to the red inflorescences of this species.

Vernacular name. – "Takasimena" (*Randrianasolo 2*).

Distribution, habitat and ecology. – *Nematostylis incarnata* occurs from (400–)700 to 2,130 m in elevation in the SAVA and Sofia regions, and is primarily known from the Marojejy Massif, but it has recently also been collected from a low elevation (271 m) locality in the Anosy region. The high elevation

Fig. 4. *Nematostylis citriflora* Kainul. **A, B.** Habit and habitat; **C.** Leaves; **D–G.** Flowering branches; **H.** Young fruits.
[**F:** *Rabarimanarivo et al. 590*; **G:** *Rakotoarivelo et al. 268*]
[Photos: **A:** B. Gehrke, Andringitra, 6.XII.2004; **B, C, H:** F. Rahaingoson, Anja, 7.V.2019; **D:** M.T. Rajaonah, Ambalavao, 26.I.2016; **E:** K. Behrens, Andringitra, 8.I.2021; **F:** R. L. Andriamiarisoa; **G:** N. Rakotoarivelo]

of the Marojejy Massif corresponds to the ecoregion "Madagascar subhumid forest", but several specimens have been collected in "Madagascar lowland forests", and at least one specimen is known from "Madagascar dry deciduous forest" (in Daraina). Consequently, in terms of habitat it is perhaps the least ecologically specialized species in the genus. It grows in grassy meadows, low ericoid vegetation, but also shrubby thickets (see Fig. 5A), usually on rocky slopes, ridges, and cliffs.

Phenology. – Flowering material has been collected from November to April, and fruiting material from January to April.

Conservation status. – Most collections of *Nematostylis incarnata* are from Marojejy National Park, although it is also known from the protected Anjiabe forest. However, the estimated area of occupancy (AOO) is less than 2,000 km^2, it is known from fewer than 10 locations, and populations are severely fragmented. The quality of habitat can be projected to decline in at least some of the locations such as Tsitongambarika forest (1–2 % cleared per year for tavy; Olsen et al., 2011), therefore, this species can be assigned a preliminary conservation status of "Vulnerable" [VUB2ab(ii,iii)] according to IUCN Red list Categories and Criteria (IUCN, 2012).

Notes. – *Nematostylis incarnata* can be readily recognized from the other species in the genus by its broadly elliptic to suborbicular leaves with an obtuse to rounded (or retuse) apex and conspicuously revolute leaf margin. Unlike the other species the upper and lower surfaces of the leaf blades are remarkably different. Compared to the other species the leaves are usually (adaxially) glossy and darker green. Dried herbarium specimens are often distinctly glossy, some almost appearing varnished. *Nematostylis incarnata* is probably not truly deciduous, but better described as semi-deciduous. In several specimens the leaves are not confined to shoots of the most recent growing season, at least some leaves are retained on shoots from the previous growing season (e.g. *Humbert 22611*; see also Fig. 5B). The flowers are smaller and also differ in corolla lobes that are erect rather than spreading at anthesis, and in the exserted part of style usually being distinctly shorter than the included part (vs. of similar length in the other two species). It is common to observe flowers in which besides the calycophyll, also one or more of the other calyx lobes are expanded to some degree (but not equalling the size of the calycophyll).

The specimen *Razakamalala et al. 4141* from Tsitongambarika forest in Toalagnaro District in southeastern Madagascar is tentatively included here. It conforms to *N. incarnata* in its small flowers and elliptic-suborbicular leaves with obtuse-rounded apex, revolute leaf margins and distinctly different coloration of the abaxial and adaxial surfaces. The specimen label also describes the flowers as being red. This specimen was collected in 2008. I was not successful in relocating it at this locality in 2013. The widely disjunct distribution between this and the nearest known population in the Sofia region is remarkable. The specimen is also notable in that root tubercules are preserved [MO-3597198]. The root nodules are orbicular and c. 1.5 cm in diameter.

Additional material examined. – **Madagascar. Reg. SAVA [Prov. Antsiranana]:** Distr. Andapa, Andrakengy forest, 14°19'43"S 49°18'08"E, 1412 m, 9.XI.2006, fl., *Razakamalala et al. 2909* (BR, P); Doany, 29.III.1956, fl., *Réserves Naturelles 7883* (P, TAN); Betsomanga, [14°15'S 49°45'E], 700–800 m, XI.1950, fl., *Humbert & Capuron 24296* (P); ibid. loco, 1200–1350 m, XI.1950, fl., *Humbert & Capuron 24328* (P); Marojejy National Park, 20.IV.2008, fl., *Bremer et al. 5310* (S); ibid. loco (Ambatosoratra Mt.), [14°25'S 49°43'E], 400 m, 5.I.1949, fr., *Cours 3297* (BR, P, TAN); ibid. loco, [14°27'S 49°42'E], 26.III.1949, fl., *Cours 3443* (G, P, TAN); ibid. loco, 1700 m, XII.1948, fl., *Humbert 22611* (G, P); ibid. loco (Ambatosoratra Mt.), 1000–1100 m, I.1949, fl., *Humbert 22866* (BR, G, P); ibid. loco (Beondroka Mt.), [14°26'S 49°48'E], 1000–1450 m, III.1949, fl. & fr., *Humbert 23540* (BR, P); ibid. loco, 1850–2137 m, 2.IV.1949, fl. & fr., *Humbert 23711* (P); ibid. loco, 14°26'50"S 49°43'03"E, 1995 m, 18.II.2014, fl., *Koenen et al. 576* (G, P); ibid. loco, 14°26'S 49°44'E, 1950 m, 16.XI.1996, fl., *Messmer et al. NM 399* (G, K, MO, P); ibid. loco, 14°26'S 49°44'E, 1300–1600 m, 15.II.1989, fl. & fr., *Miller & Lowry 4116* (MO, P, TAN); ibid. loco, 1900–2133 m, 15.II.1989, fl., *Miller & Lowry 4159* (MO, TAN); ibid. loco, 2000–2137 m, XII.1972, fl., *Morat 4068* (P); ibid. loco, 2000–2137 m, XII.1972, fl., *Morat 4084* (P); ibid. loco, 2000–2137 m, XII.1972, fl., *Morat 4092* (TAN); ibid. loco, 1200 m, XI.1912, fl., *Perrier de la Bâthie 3746* (P); ibid. loco, 14°26'S 49°43'E, 1600–2137 m, 28.III.1990, fl., *Randrianasolo 135* (MO, P, TAN); ibid. loco, 14°28'S 49°33'E, 1295–1620 m, 5.XII.1989, *Randrianasolo 2* (MO); ibid. loco, 14°25'45"S 49°39'30"–49°42'15"E, 1672 m, 7.III.1994, fl., *Rasoavimbahoaka 101* (BR, G, P, TAN); ibid. loco, 14°20'S 49°43'E, 720–800 m, 19.X.1994, fl., *Rasoavimbahoaka 370* (MO, P); ibid. loco, 14°26'50"S 49°43'57"E, 2132 m, 23.III.1995, fr., *Rasoavimbahoaka 529* (G, P, TAN); ibid. loco, 1700–1800 m, 3.II.2006, fl., *Razafimandimbison & Ravelonarivo 616* (G, S); ibid. loco, 14°26'41"S 49°44'10"E, 1886 m, 16.II.2020, fl., *Razafimandimbison & Razafindrahaja* 2972 (BR, S); ibid. loco, 19.I.1958, fl., *Réserves Naturelles 9503* (P); ibid. loco, 11.II.1959, fl. & fr., *Réserves Naturelles 10094* (P); ibid. loco, 14°26'20"S 49°44'15"E, 2050 m, 22.XI.2003, *Schmidt et al. 4297A* (MO); Distr. Sambava, Mt. Anjenabe, [14°17'S 49°46'E], 800 m, XI.1950, fr., *Humbert & Capuron 24095* (P); ibid. loco, 1000–1130 m, XI.1950, fr., *Humbert & Capuron 24115* (P); Distr. Vohémar, Daraina, Antsahabe forest, 13°13'S 49°32'E, 949 m, 9.XII.2004, fl., *Nusbaumer & Ranirison LN 1321* (G, P). **Reg. Sofia [Prov. Antsiranana]:** Distr. Befandriana-Nord, Anjiabe forest, 15°07'40"S 49°21'09"E, 1418–1446 m, 9.II.2008, fl., *Ravelonarivo et al. 2691* (G, MO). **Reg. Anosy [Prov. Toliara]:** Distr. Taolagnaro, Tsitongambarika forest, 24°34'16"S 47°12'05"E, 271 m, 1.IV.2008, fl. & fr., *Razakamalala et al. 4141* (MO, P).

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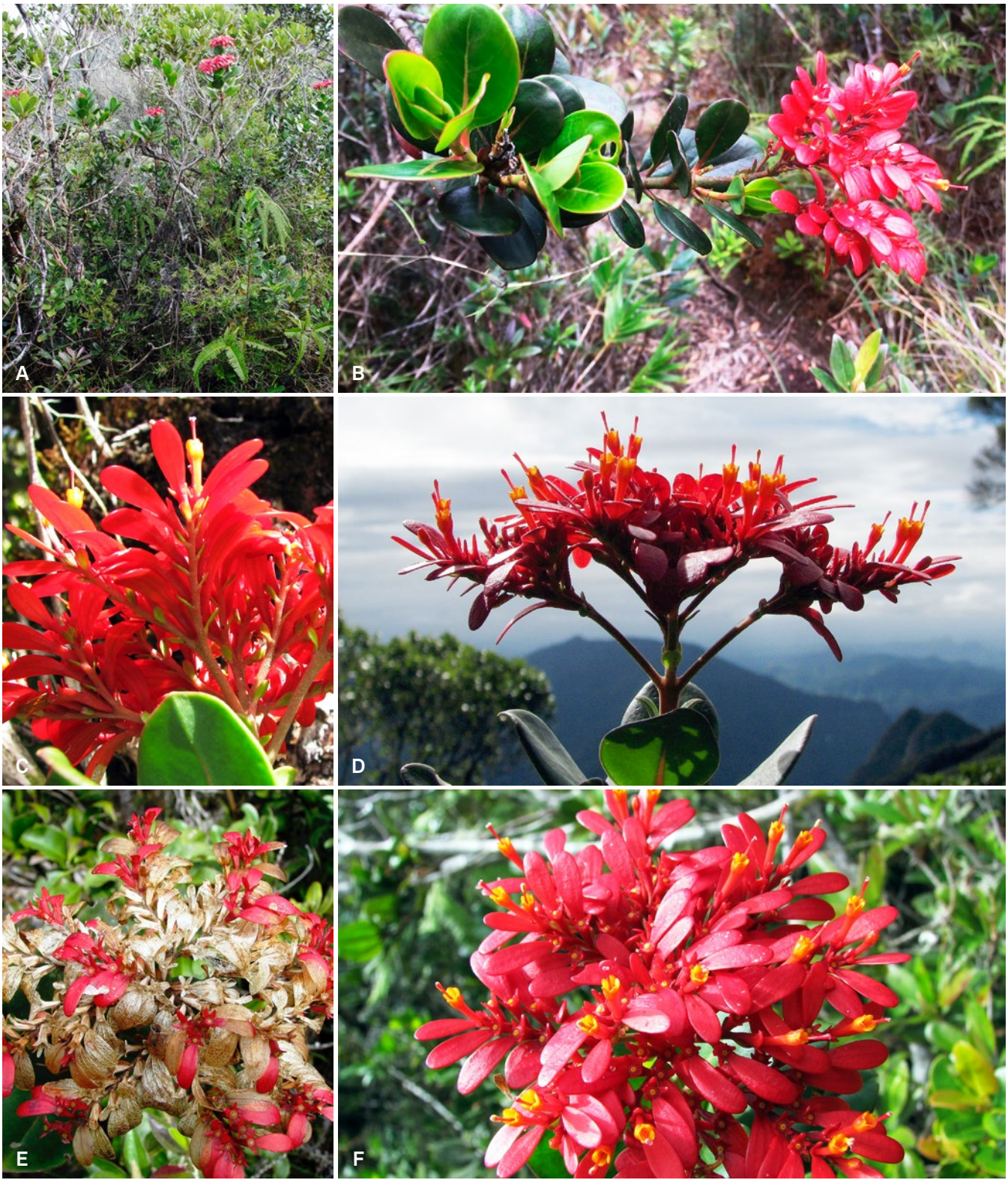

Fig. 5. *Nematostylis incarnata* Kainul. **A.** Treelet growing in thicket; **B.** Flowering branch (note the flush of new leaves with persistent older leaves); **C.** Bottom-view of an inflorescence, showing leafy bracts; **D.** Side-view of an inflorescence; **E.** Infructescence with acropetally maturing fruits (note the now translucent calycophylls); **F.** Top-view of an inflorescence (note the bright yellow disks of the flowers).
[**C–F:** *Bremer et al. 5294*] [Photos: **A, C–F:** K. Kainulainen, Marojejy National Park, 20.IV.2008; **B:** K. Behrens, Marojejy National Park, 21.X.2020]

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