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Research article

Bopopia, a new monotypic genus of Gesneriaceae (Gesnerioideae, Coronanthereae) from New Caledonia

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Abstract. A new genus of Gesneriaceae, *Bopopia* Munzinger & J.R.Morel gen. nov., is described from New Caledonia. The genus is based on *B. parviflora* Munzinger & J.R.Morel gen. et sp. nov., a new species collected during an expedition on Mt Katalupaik, in the North Province of New Caledonia's main island. Originally considered as a species of *Coronanthera*, our phylogenetic analysis – including 19 species within Coronanthereae and two individuals of *B. parviflora* gen. et sp. nov., and using three molecular markers (nuclear rDNA ITS, and chloroplast regions *trnL-trnF* and *trnE-trnT*) – showed that the new species is not close to *Coronanthera* in subtribe Coronantherinae, but belongs to subtribe Negriinae where it is sister to *Depanthus*. From that genus *Bopopia* gen. nov. differs in floral symmetry (zygomorphic vs actinomorphic) and the number of stamens (4 vs 5). From the other genera of Negriinae the new genus differs in the white corolla and its indeterminate thyrses with 3 to 5 levels of branching. The morphological circumscription of the subtribe Negriinae is amended to include *Bopopia* gen. nov. Two keys are provided, one to the subtribes in the tribe Coronanthereae, and one to the genera in subtribe Negriinae. Following the IUCN Red List categories and criteria, the conservation status of *B. parviflora* gen. et sp. nov. is provisionally assessed as Endangered (EN).

Keywords. Gesneriaceae, Gesnerioideae-Coronanthereae-Negriinae, La Planète Revisitée, New Caledonia, Grande Terre, Mt Katalupaik, molecular phylogeny, taxonomy.

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Introduction

New Caledonia is a biodiversity hotspot with an estimated autochthonous flora of 3409 species of flowering plants, of which nearly 75% are endemic (Morat *et al.* 2012; Munzinger *et al.* 2020). Nevertheless, this biodiversity is still poorly known: on average, one new species is described each

month from the New Caledonian archipelago (Gâteblé *et al.* 2018). To complete the knowledge of this biodiversity, the research program ‘La Planète Revisitée’ (<http://www.laplaneterevisitee.org/fr>) organized several expeditions between 2016 and 2018 in various unexplored and difficult-to-access areas of New Caledonia. In 2017, the southern face of the isolated Mount Katalupaik, a ‘no data area’ of the archipelago (see map in Birnbaum *et al.* 2015), was inventoried from 300–900 m altitude. During this expedition, 340 species were collected, 13 being supposedly new to science, nine could be assigned to specimens already present in herbaria, while four were collected for the first time (Munzinger *et al.* 2018).

One of these potentially new species was a relatively abundant shrub in this locality and is represented by the specimens Bruy *et al.* 1139 and Munzinger *et al.* 7980. The plants were flowering at the time of the collection in October. Several characters suggested placement in the family Gesneriaceae Rich. & Juss. ex DC., including shrubby habit, opposite simple petiolate leaves without stipules, pair-flowered cymes, pentamerous zygomorphic flowers, gamosepalous calyx, gamopetalous corolla, four stamens with connate anthers, presence of hypogynous disk, syncarpous unilocular gynoecium of two carpels, one style, and two stigmas. The new species was initially considered to belong to the genus *Coronanthera* Vieill. ex C.B. Clarke (Gesnerioideae-Coronanthereae-Coronantherinae; Woo *et al.* 2011; Weber *et al.* 2013), because of its shrubby habit, slightly serrate leaves with similar shape and dimensions (blade and petiole), small zygomorphic corolla with four connate stamens, and annular nectary adnate to the ovary.

In order to test the identity of the New Caledonian specimens, and the generic and subtribal position of the species, a molecular phylogenetic study was performed. The combination of molecular and morphological data, consistent with the geographical distribution, confirms that this is a new species and genus. This methodology has been shown to be particularly efficient in the circumscription of genera and species, including the discovery of a considerable number of new genera in the Gesneriaceae (e.g., Araújo *et al.* 2010; Clark *et al.* 2010; Wei *et al.* 2010; Middleton & Möller 2012).

Material and methods

Sampling

Specimens of this new species were collected in the North Province of New Caledonia, on Mt Katalupaik, in October 2017 by David Bruy, Jérôme Munzinger and Marc Pignal. The plants were cut with clippers poles and pressed in the field, then dried at the base camp, notes and photos were taken in the field, and the flowers were preserved in alcohol. Vouchers were deposited at MPU, NOU and P (Appendix 1); acronyms of herbaria follow Index Herbariorum (Thiers continuously updated).

Molecular phylogenetic analysis

Leaves from the two collections of the new species were dried and preserved in silica gel. DNA was extracted using the mixed alkyltrimethylammonium bromide (MATAB) protocol as described in Scarcelli *et al.* (2006). DNA quality and quantity were then checked by optical density with the Nanodrop™ 8000 (Thermo Fisher Scientific, Waltham, Massachusetts, United States) and by agarose gel electrophoresis.

The selection of gene regions and analysis methods follows Woo *et al.* (2011) in order to get results that are directly comparable to their study.

PCR reactions were done in a total volume of 25 µl as follows: 12.5 µl of QIAGEN Multiplex PCR Master Mix (Qiagen, Germany), 5 µl of Qiagen Q-solution, 0.1 µl of each primer (forward and reverse) at 10 mM, 2.5 µl DNA template (of ca 15–20 ng/µl), and water qs 25 µl. The rDNA ITS region (ITS1, 5.8S gene and ITS2) was amplified using ITS5 and ITS28CC primers (White *et al.* 1990; Wagstaff & Garnock-Jones 1998). The intergenic spacer *trnL-trnF* was amplified with the *trnL-c/trnF* and the *trnL-c/*

trnL-d primers (Taberlet *et al.* 1991). The intergenic spacer *trnE-trnT* was amplified with the *trnE/trnT* primers (Doyle *et al.* 1992). PCR were done on an Applied Biosystems® Veriti® 96-Well thermal cycler (Applied Biosystems, Foster City, USA) with an activation step of 95°C for 15 min, followed by 38 cycles of 94°C denaturation for 30 s, 50°C for 30 s for annealing, 72°C for 2 min of extension, and a final extension phase at 72°C for 10 min.

Sanger sequencing (Sanger *et al.* 1977) was performed by GENEWIZ® (Leipzig, Germany) with Dye Terminator Big Dye ver. 3.1 (Life Technologies/ThermoFisher). DNA sequencing reactions were purified using in-house beads (magnetic bead-based) before being charged on an ABI 3730 XL DNA analyzer (Life Technologies/ThermoFisher). Base calling was done using KBAAnalysis (KB basecaller ver. 1.4.1). Reverse and forward reads were assembled using CodonCode Aligner ver. 8.0.2 (<https://www.codoncode.com>).

In order to determine the taxonomic coverage to be included in our phylogenetic analysis, we evaluated the taxonomic proximity of our DNA sequences using blastn suite (NCBI) and relying on the query coverage and the percentage of identity. For ITS, the closest taxa to the new species were *Lenbrassia australiana* var. *glabrescens* B.Morley (query coverage: 81%; percent identity: 95.4%), *Lenbrassia australiana* var. *australiana* (C.T.White) G.W.Gillett (81%; 95.1%) and *Depanthus glaber* S.Moore (81%; 95.1%). The *trnL-trnF* sequence was closest to *Lenbrassia australiana* var. *australiana* (99%; 99.8%), *Sarmienta scandens* Pers. (99%; 98.7%) and *Negria rhabdothamnoides* F.Muell. (91%; 100%). The *trnE-trnT* was closest to *Lenbrassia australiana* var. *australiana* (98%; 98%), *Negria rhabdothamnoides* (98%; 97.9%) and *Depanthus glaber* (98%; 97.8%).

All these taxa are included in the tribe Coronanthereae Fritsch. Thus, the sequence matrix of Woo *et al.* (2011), covering the Southeast Pacific Gesneriaceae, was reduced to 35 samples corresponding to an exhaustive sampling of Coronanthereae genera. Sequences produced subsequently to Woo's work were also included in the matrix, from *Coronanthera* (Serrano-Serrano *et al.* 2017) and from *Negria* F.Muell (Perret *et al.* 2013). All GenBank sequence accessions and their corresponding vouchers can be found in Appendix 1.

Two members of the tribe Beslerieae Bartl. were selected as outgroups based on phylogenetic relationships shown in Woo *et al.* (2011): *Gasteranthus atratus* Wiehler from Ecuador and *Cremosperma castroanum* C.V.Morton from Peru. The 39 sequences were first aligned using MAFFT under default parameters (Kato *et al.* 2017) and corrected manually to minimize substitutions and indels by event-based criteria in order to constitute homology hypotheses (Morrison 2006). Then, we used GBLOCKS 0.91b (Castresana 2000) on each ITS, *trnL-trnF* and *trnE-trnT* alignments. GBLOCKS deletes segments of contiguous non-conserved positions, gap positions and non-conserved flanking positions. It has consequently proven very useful in increasing phylogenetic accuracy (e.g., Roalson & Roberts 2016). For ITS alignment, we used the default stringent parameters, disallowing smaller final blocks, gap positions and non-conserved flanking positions. Less stringent parameters were used (allowing gap position within the final blocks and less strict flanking positions) for *trnL-trnF* and *trnE-trnT*. The characteristics of the different DNA sequences are given in Table 1.

We analyzed the cpDNA and ITS independently (not shown) in order to assess whether or not the data could be concatenated. We used the model GTR + I + Γ for maximum likelihood (ML) analysis and the following models for Bayesian inference (BI) analysis: SYM + Γ for ITS, GTR + I for *trnL-trnF* and GTR + I + Γ for *trnE-trnT*. The partition-homogeneity test (Farris *et al.* 1994) as implemented in PAUP* ver. 4.0a (Swofford 2002) was performed with 10 000 bootstrap replicates and did not find significant differences between any partitions ($p = 0.8487$). Therefore, a combined analysis of the DNA regions could be performed.

Table 1. Nucleotide sequence characteristics of the gene regions analysed.

	No. sequences	Length range (bp)	Aligned length (bp)	Fraction retained by GBlocks (%)	Final length of alignment (bp)
ITS	39	613–639	675	82%	554
<i>trnL-trnF</i> spacer	32	836–885	863	96%	835
<i>trnE-trnT</i> spacer	27	725–773	769	96%	739

The research of the optimal substitution model was performed with PartitionFinder2 (Lanfear *et al.* 2016) using the Akaike Information Criterion (AIC; Posada & Buckley 2004). ML analysis was run on the partitioned data set in RaxML ver. 8 (Stamatakis 2014) with 100 bootstrap replicates. BI analysis was run in MrBayes ver. 3.2.7 (Ronquist *et al.* 2012). All the parameters values were unlinked across partitions and estimated during the Markov chain Monte Carlo (MCMC) runs. Two independent analyses, starting from different random trees, were run, each with four Markov chains (one cold chain and three incrementally heated chains). Independent analyses were conducted with 5 000 000 generations each, with a sampling frequency of 1 tree every 1000 generations. Convergence between the two independent runs was checked using Tracer ver. 1.7.1 (Suchard *et al.* 2018). We discarded the first 25% of the trees as burn-in, and the retained ones were summarized in a majority rules consensus tree (Fig. 1).

Specimens examined and morphology

After confirmation that the collected species was indeed a member of Gesneriaceae, we examined all collections within this family from Oceania and Asia present in MPU, NOU and P, as well as all specimens without family identification from the same areas in these herbaria. In addition, we used virtual collections: Global Plant initiative (<https://plants.jstor.org/>), e-ReColNat infrastructure (<https://www.recolnat.org/fr/>), and Z herbarium (<https://www.herbarien.uzh.ch/en/belegsuche.html>).

Morphological descriptions were prepared using standard terminology (Harris & Harris 2001). Vegetative parts were measured directly on herbarium specimens. Details of androecium and gynoecium were measured in flowers preserved in alcohol (part of the collection Munzinger *et al.* 7980). The measurements are given as follows: (minimum) first quartile–third quartile (maximum) (following Munzinger *et al.* 2016). For the remaining measurements with fewer observations, we chose to only give the minimum and maximum values observed. The drawings of the new species are based on photographs taken in the field and of specimen parts preserved in alcohol. We applied the IUCN Red List categories and criteria (IUCN 2019) to propose a conservation assessment of the species.

Abbreviations used in figures 2, 4 and 6

- AF_n = axillary flower of the axis n
- An = axis of the nth level
- AS_n = axis of the nth level with accessory origin
- FAn = front axis of the axis n, terminating by a front flower (Fn)
- Fn = front flower of the axis n (Weber 1982)
- ISU = inflorescence sub-unit
- PFC = pair-flowered cyme
- T_n = terminal flower of the axis n
- α_n, β_n = bracts on the axis n, axillary of the two axis n+1
- γ = bracteole on the axis n, axillary of the front axis (or front flower) n, = γ-bracteole sensu Haston & De Craene (2007)
- ISU = axis developing into an inflorescence sub-unit

Results

Molecular phylogenetic analysis

Fig. 1 shows the 50% majority-rule consensus tree obtained with the Bayesian analysis. The maximum likelihood tree has the same topology, aside from two nodes which were not supported (<60% bootstrap value).

Subtribe Negriinae is strongly supported with a posterior probability (PP) value of 1 and a bootstrap value (BS) of 100. The separation between subtribes Coronantherinae Fritsch and Mitrariinae Hanst. is supported with a PP value of 0.9 and a BS value of 66. Monophyly for all genera represented by two or more species is strongly supported (PP = 1; BS = 100).

The new species is supported as a member of subtribe Negriinae (PP = 1; BS = 100) and as sister to the genus *Depanthus* S.Moore (PP = 0.8; BS = 81).

Herbarium study

We found that this taxon had never been collected before.

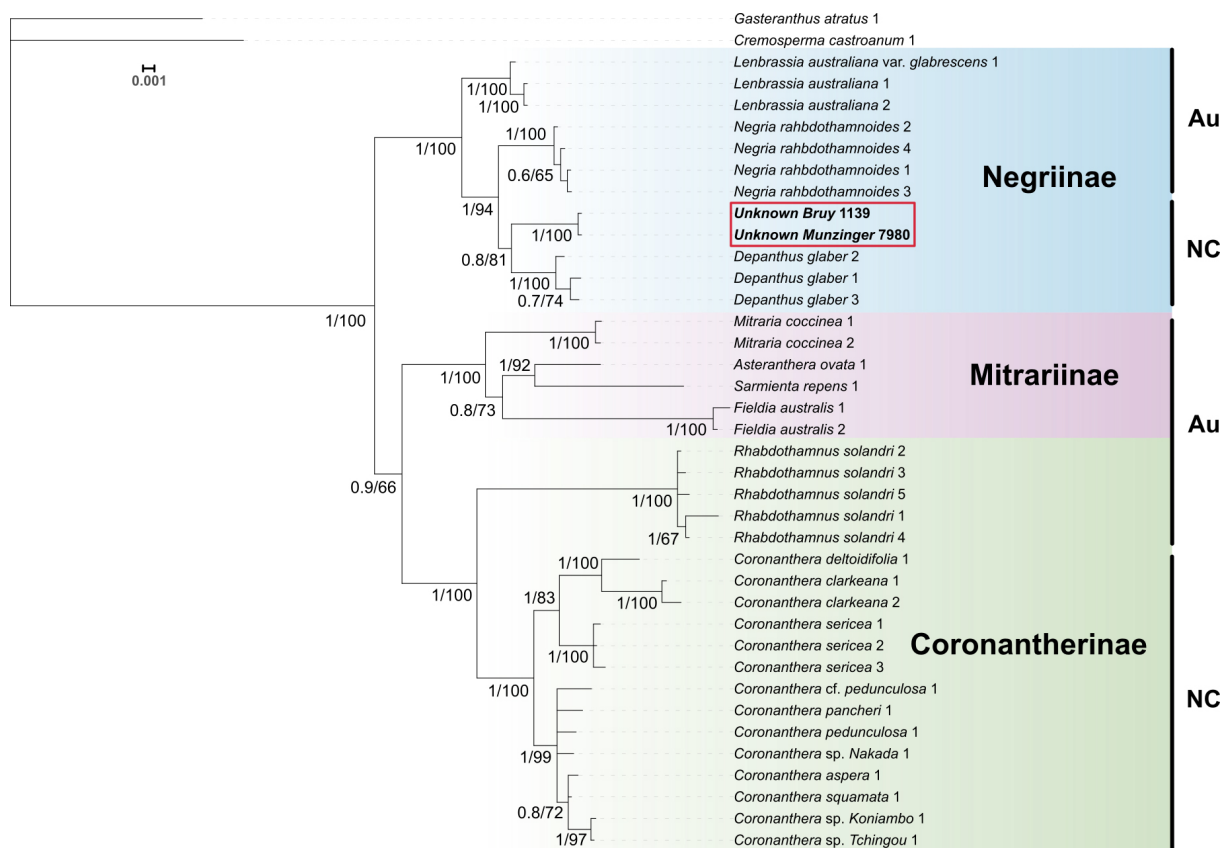


Fig. 1. 50% Bayesian majority-rule consensus cladogram based on combined markers. Numbers indicating clade support: left of slash = Bayesian posterior probability value; right of slash = maximum likelihood bootstrap value. Au = Australia; NC = New Caledonia.

Key to the subtribes in the tribe Coronanthereae

1. Epiphytic creepers and subshrubs to 1 m tall; leaves small, 0.5–4 cm long; inflorescence axillary, solitary; stamens 2–4; fruit an indehiscent berry subtribe **Mitrariinae** Hanst.
 - Tree to shrubs >2 m tall; leaves small to large, 2–25 cm long; inflorescence an axillary cyme or indeterminate thyse (Fig. 2), or flower solitary; stamens 4–5; fruit a dry capsule or an indehiscent berry (unknown in *Bopopia* gen. nov.) 2
2. Trees and shrubs, 2–15 m tall; leaves toothed or weakly toothed, small to large, 2–25 cm long; inflorescence an axillary cyme, peduncle short, generally 3–8-flowered, or flower solitary (*Rhabdothamnus* A.Cunn.); flowers zygomorphic; stamens 4, staminode 1, anthers coherent, in coronal formation; fruit an ovoid dry capsule, four-valved, valves apically coherent, dehiscing by basal slits, septicidally then loculicidally subtribe **Coronantherinae** Fritsch
 - Trees, 6–13 m tall; leaves entire or toothed, large, 5–20 cm long; inflorescence an axillary cyme, peduncle short to long, 1–3-flowered or an indeterminate thyse with 3–5 levels of branching (*Bopopia* gen. nov.); flowers zygomorphic or actinomorphic; stamens 4–5, anthers free or coherent; fruits beaked, fleshy, and indehiscent, or dry, woody, two-valved, apically septicidally dehiscent, or four-valved, dehiscing septicidally plus loculicidally (unknown in *Bopopia* gen. nov.) subtribe **Negriinae** V.L. Woo, J.F. Smith & Garn.-Jones

Key to the genera in the subtribe Negriinae

1. Inflorescence an indeterminate thyse with 3–5 levels of branching (Fig. 2) (New Caledonia) *Bopopia* Munzinger & J.R. Morel gen. nov.
 - Inflorescence a cyme 1–3-flowered, or solitary flower (Australia or New Caledonia) 2
2. Fruit a berry (NE Australia) *Lenbrassia* G.W. Gillett
 - Fruit a capsule 3
3. Corolla actinomorphic, stamens 5, capsule dehiscing septicidally by 2 valves (New Caledonia) *Depanthus* S. Moore
 - Corolla zygomorphic, stamens 4, capsule dehiscing septicidally plus loculicidally by 4 valves (Australia: Lord Howe Island) *Negria* F. Muell.

Taxonomic treatment

Class Magnoliopsida Brongn.
 Order Lamiales Bromhead
 Family Gesneriaceae Rich. & Juss. ex DC.
 Subfamily Gesnerioideae Burnett
 Tribe Coronanthereae Fritsch

Subtribe **Negriinae** V.L. Woo, J.F. Smith & Garn.-Jones

Emended diagnosis

To include *Bopopia* gen. nov., the diagnosis of the subtribe Negriinae is modified as follows:
 Trees, 6–13 m tall; leaves glabrous or pubescent, entire or toothed, lanceolate to ovate, elliptic to obovate, 5–20 cm long × 2.5–11 cm wide; inflorescence an axillary cyme, peduncle short (0.5–1.5 cm) to long (3–14 cm), 1–3-flowered or an indeterminate thyse with 3–5 levels of branching; flowers zygomorphic or actinomorphic, white, yellow or orange in color; stamens 4–5, anthers free or coherent; fruits (unknown in *Bopopia* gen. nov.) beaked, fleshy, and indehiscent, or dry, woody, two-valved, apically septicidally dehiscent, or four-valved, dehiscing septicidally plus loculicidally. Seeds (unknown

in *Bopopia* gen. nov.) subglobose to elliptic, striated, 0.7–0.9 mm long, numerous; pollen spheroidal to mildly prolate in shape, 12–22 µm in diameter.

Genera included

Depanthus, *Bopopia* gen. nov., *Lenbrassia*, *Negria*.

Genus *Bopopia* Munzinger & J.R.Morel gen. nov.

[urn:lsid:ipni.org:names:77215492-1](https://nomenclature.ipni.org/urn:lsid:ipni.org:names:77215492-1)

Type species

Bopopia parviflora Munzinger & J.R.Morel gen. et sp. nov., by present designation.

Diagnosis

Bopopia gen. nov. differs from other genera of Coronanthereae in its inflorescence: an axillary indeterminate thyrses with ultimate axes being pair-flowered cymes and inferior axes being indeterminate thyrses with three to five levels of branching (vs 3-flowered cymes or solitary flowers); it differs from *Depanthus* in floral symmetry (zygomorphy vs actinomorphy), stamen number (4 vs 5); from *Negria* in inserted (vs exserted) stamens, and connate (vs free) anthers; from *Lenbrassia* in bilobed (vs spatulate) stigma.

Etymology

The genus is named after the land and people of Bopope (Pwöpöp), in the vicinity of Mt Katalupaik.

Bopopia parviflora Munzinger & J.R.Morel gen. et sp. nov.

[urn:lsid:ipni.org:names:77215493-1](https://nomenclature.ipni.org/urn:lsid:ipni.org:names:77215493-1)

Figs 2–7

Diagnosis

Bopopia parviflora gen. et sp. nov. is similar to *Coronanthera clarkeana* Schltr., *C. deltoidifolia* Vieill. ex C.B.Clarke, *C. pinguior* C.B.Clarke and *Depanthus glaber* in its glabrous adaxial leaf surface but differs in its unique inflorescence structure within the tribe and also vegetatively in leaf measurements, blade, apex and base shape, margin (entire vs serrate), and abaxial indumentum, as well as petiole length and indumentum (Table 2).

Etymology

The specific epithet refers to the small flowers as compared to other Gesneriaceae known from New Caledonia.

Type

NEW CALEDONIA • North Province, Bopope, southern slope of Mount “Katalupaik” [Katalupaik]; 20°50'27" S, 165°0'38" E; alt. 500 m; 29 Oct. 2017; fl.; *J. Munzinger, D. Bruy & M. Pignal 7980*; holotype: P[P01073391]; isotypes: G, MO, MPU[MPU312888][MPU312889], NOU[NOU090953], P[P00865080], W.

Paratype

NEW CALEDONIA • North Province, Bopope, southern slope of Mount “Katalupaik” [Katalupaik]; 20°50'28" S, 165°0'38" E; alt. 500 m; 29 Oct. 2017; fl.; *D. Bruy, J. Munzinger, & M. Pignal 1139*; K, MO, MPU[MPU311450][MPU312887], NOU[NOU090952], P[P01073272].

Table 2. Vegetative characters differentiating *Bopopia* Munzinger & J.R.Morel gen. nov. from *Coronanthera clarkeana* Schltr., *C. deltoideifolia* Vieill. ex C.B.Clarke, *C. pinguior* C.B.Clarke and *Depanthus glaber* S.Moore. Characters of species of *Coronanthera* and *Depanthus* adapted from Woo (2007).

	<i>Bopopia parviflora</i> sp. nov.	<i>Depanthus glaber</i>	<i>Coronanthera clarkeana</i>	<i>Coronanthera deltoideifolia</i>	<i>Coronanthera pinguior</i>
Habitus	shrub to 5 m tall	tree to 9 m tall	tree to 4 m tall	shrub to 3 m tall	shrub to 3 m tall
Length (mm)	(91-)100-156(-198)	(110-)120-200	(43-)50-70(-75)	(38-)40-60(-75)	(70-)80-100(-120)
Width (mm)	(40-)45-65(-82)	(44-)60-108(-114)	(15-)20-30	(15-)20-25(-29)	(24-)30-60(-70)
Shape	elliptic to obovate	ovate, obovate to rotund	elliptical to ovate	deltoid to elliptic	elliptic to obovate
Margin	slightly serrate	entire	entire to subentire	entire	entire
Apex	acute to obtuse	acuminate to obtuse	acute to obtuse	acuminate	acuminate to acute
Base	cuneate	acute to obtuse	acute to cuneate	cuneate	acute
Abaxial indumentum	tomentulose	glabrous or hairy	glabrous, occasional hairs	glabrous, occasional hairs	glabrous
Length (mm)	(25-)30-46(-62)	(12-)20-40(-52)	(6-)7-10(-11)	(4-)8-10(-12)	14-20
Indumentum	tomentulose	glabrous or hairy	glabrous	glabrous	glabrous
Petiole					

Description

Shrub up to 5 m tall, rarely branched. Twigs all orthotropous (Fig. 3A) green to red (Fig. 3B), angular and tomentulose, simple pluricellular trichomes appressed toward the apex, terminal vegetative bud densely tomentulose. Leaves opposite and decussate; clustered at the top of branches (Fig. 3A); blade (9.1–)10–15.6(–19.8) × (4–)4.5–6.5(–8.2) cm, elliptic to obovate, dark green above (Fig. 3C, E), pale green below (in vivo; Fig. 3G), glabrous adaxially, tomentulose abaxially, base cuneate, apex acute to obtuse, margin slightly serrate, lateral veins (3–)4(–5) per side. Petiole yellow (in vivo; Fig. 3B, G), (25–)30–46(–62) mm long, (1–)1.6–2.2(–2.7) mm wide, tomentulose. Inflorescence axillary, indeterminate thyrses, with ultimate axes being pair-flowered cymes (Fig. 4), and inferior axes being indeterminate thyrses; three to five levels of branching (Figs 2, 3B), axes tomentulose, (12–)15–32(–38) flowers per inflorescence, with peduncle/first axis (17–)32–61(–72) mm long, (0.5–)0.8–1.2(–1.3) mm wide, tomentulose. Second axis 10–23(–32) mm long, 0.3–0.7(–1) mm wide, bracteoles linear, (2.5–)3–4.2(–4.5) mm long; third axis 3–11(–14) mm long, (0.2–)0.3–0.5(–0.6) mm wide, bracteoles linear, (1.5–)1.9–2.6(–2.8) mm long, pedicels 1.5–6.5 mm long. Calyx with 5 equal lobes, sepals broadly triangular, (1.2–)1.4–1.8(–2) mm long, 0.4–0.5 mm wide at base, slightly connate at the base and attenuate at apex (Figs 3F, 5B–C), tomentulose outside and glabrous inside (Fig. 5C), the lobes not exceeding 25% of the total length of the calyx (Fig. 3F, 5B–C). Corolla zygomorphic, uniformly white, shortly ventricose, tube curved, (2.2–)2.6–3.6(–4.1) mm long, limb of five unequal oval to orbicular lobes, rounded, strongly curled outwards, the median lobe ca 1.5 × 1.3 mm, the two lateral lobes ca 1.0 × 1.0 mm, the two dorsal lobes ca 0.5 × 0.6 mm; outer surface of corolla tomentulose, inner surface of corolla glabrous (Fig. 5D). Androecium, four stamens, inserted, alternating with corolla lobes, subequal (Fig. 5D); filaments broad, 0.1 mm in diameter, flattened near the base, glabrous, adnate to the base of the corolla tube for 1–2 mm (Fig. 5D); four anthers connate, flat, irregularly cordiform (Fig. 5D–E),

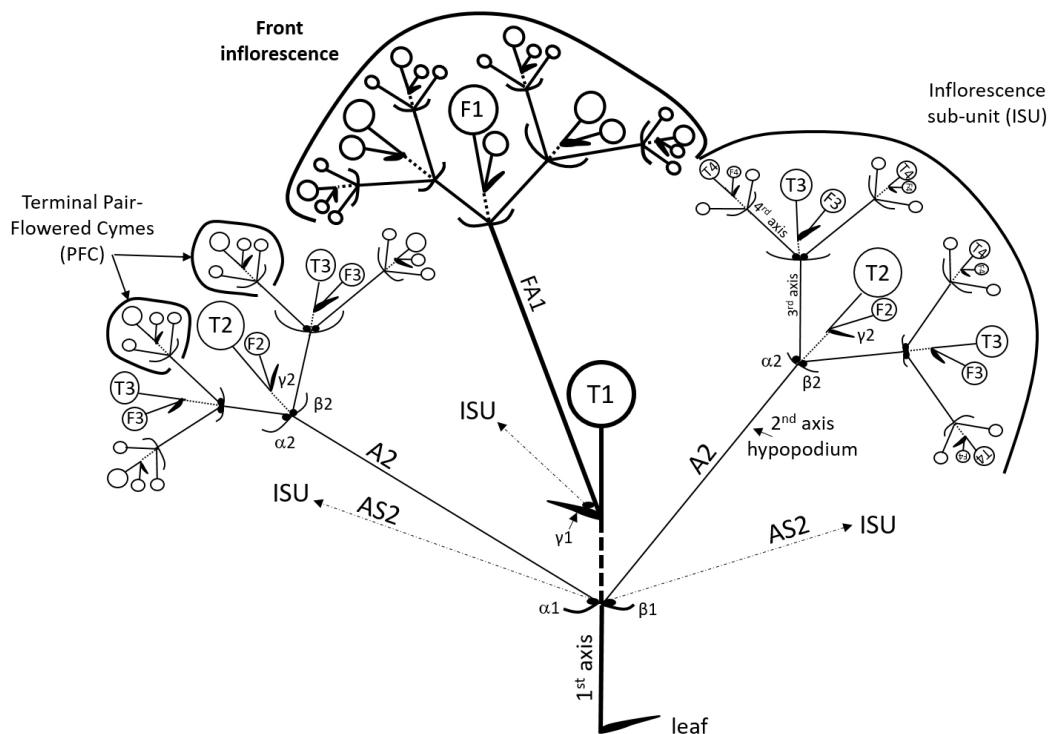


Fig. 2. Schema of the inflorescence of *Bopopia parviflora* Munzinger & J.R.Morel gen. et sp. nov., an indeterminate thyrses. Only four axes are represented on this schema (while up to 5 were seen on herbarium specimens).

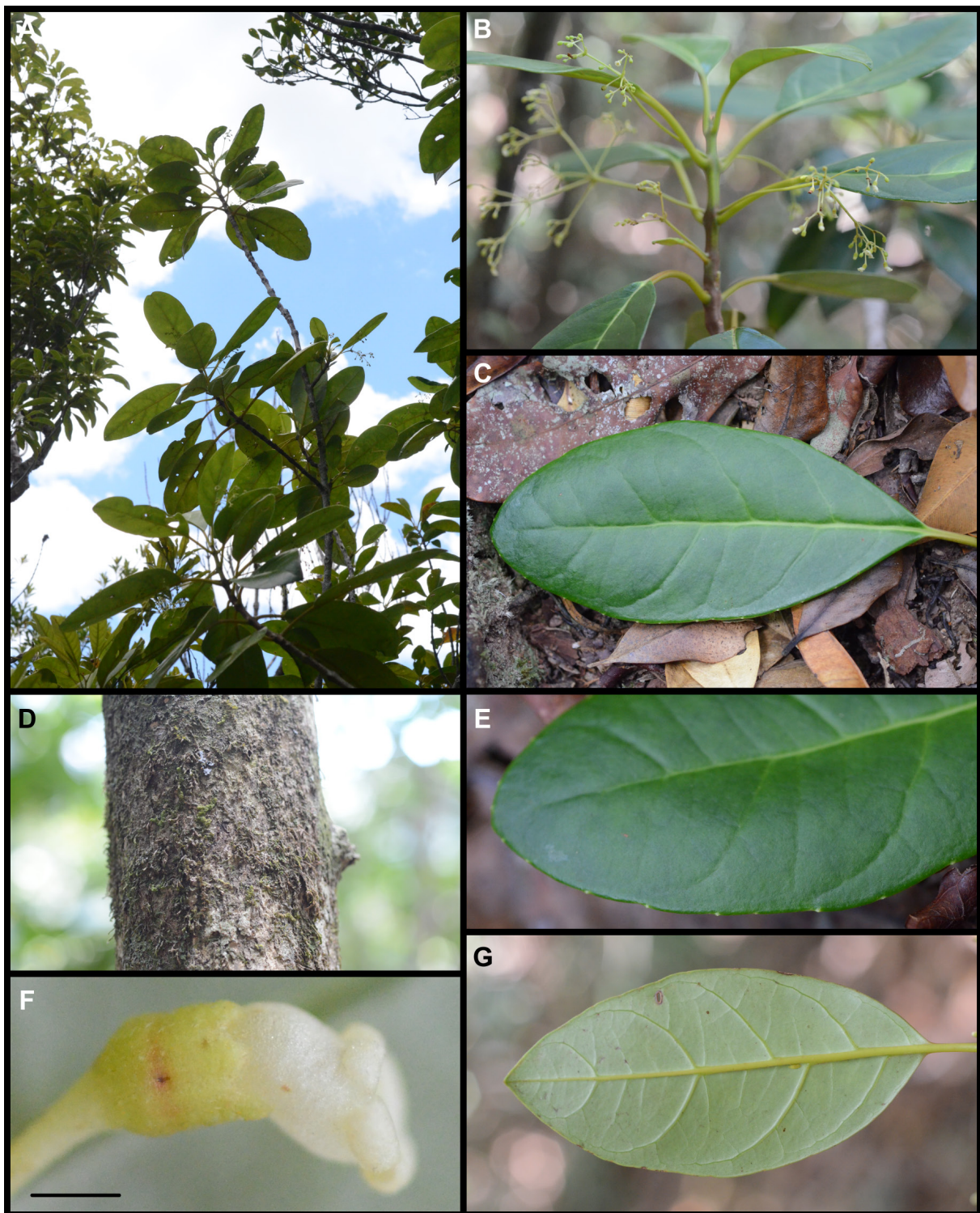


Fig. 3. *Bopopia parviflora* Munzinger & J.R.Morel gen. et sp. nov. **A.** Habit. **B.** Upper part of stem and axillary inflorescences **C.** Adaxial side of leaf. **D.** Trunk. **E.** Magnified leaf showing leaf teeth (or hydathodes?). **F.** Flower in lateral view. **G.** Abaxial side of leaf. Scale bar: F = 1 mm. Photographs taken by Jérôme Munzinger.

pollen spheroidal, 11–14 μm . Nectary ring-shaped, ca 0.25 mm thick, continuous or with shallow lobes at the rim, pinkish (preserved in alcohol), adnate at the base of the ovary (Fig. 5C). Gynoecium ovoid, ca 1 \times 1 mm, pubescent, bicarpellate, bilocular, style short, ca 0.15 mm long, ca 0.4 mm wide, stigma bilobed (Fig. 5C); ovules numerous (ca 50), ellipsoid, 100–130 μm long. Fruit unknown.

Distribution

The new species is presently only known from the North Province of New Caledonia's main island Grande Terre, on the south flank of Mt Katalupaik, around 500 m a.s.l. (Fig. 7), about 17 km as the crow flies south of Hienghène.

Habitat and ecology

The plants occur in dense humid forests from low to medium elevations on volcano-sedimentary substrates (Jaffré *et al.* 2012). Collecting points projected on the geological map (Gouvernement de la Nouvelle-Calédonie 2019) fall in a wide area of black siltites surrounded by basalts, dolerites, undifferentiated gabbros or fine tuffs. They are quite far from serpentine veins (ultramafic) in that area; thus the species is considered to grow on non-ultramafic substrates. Individuals of *B. parviflora* gen. et sp. nov. were observed to be relatively abundant in the valley that was explored (~100 m wide). Additional surveys are needed in the surrounding valleys.

Phenology

Plants collected in flower in October 2017. The length of the flowering time and the period of fructification are currently unknown.

Conservation status

Bopopia parviflora gen. et sp. nov. is only known from one population corresponding to a single location sensu IUCN (2019), and was estimated to contain <250 individuals. This population is not in a protected area. The forest on the southern flank of Mt Katalupaik is highly fragmented by fire (Fig. 7), and fire appears to be a recurrent threat. The conservation status of the species is therefore preliminarily assessed as Endangered [EN: D]. This assessment has been submitted to the New Caledonian Plant Red List Authority for review and validation.

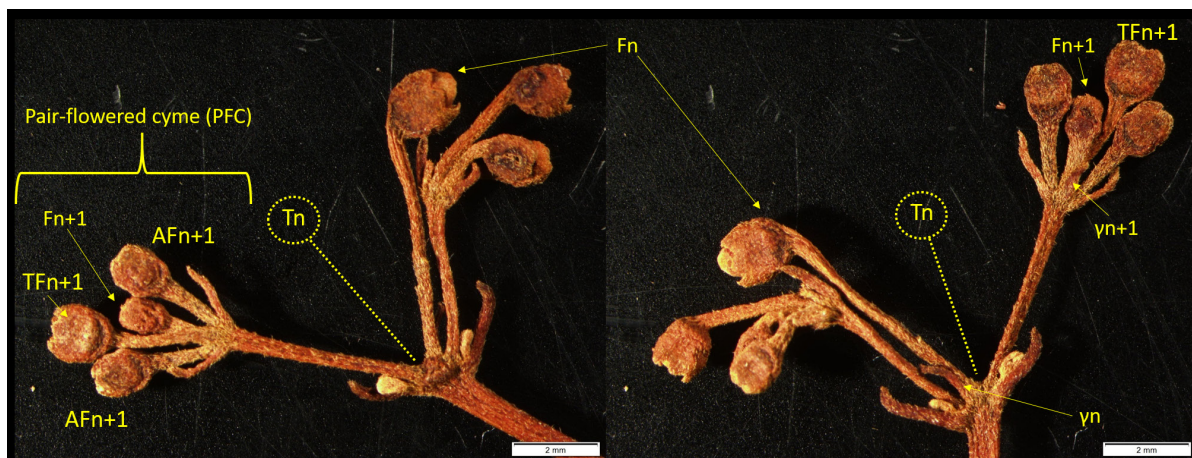


Fig. 4. Recto and verso photographs of an ultimate inflorescence axis of *Bopopia parviflora* Munzinger & J.R.Morel gen. et sp. nov., showing the pair-flowered cyme.

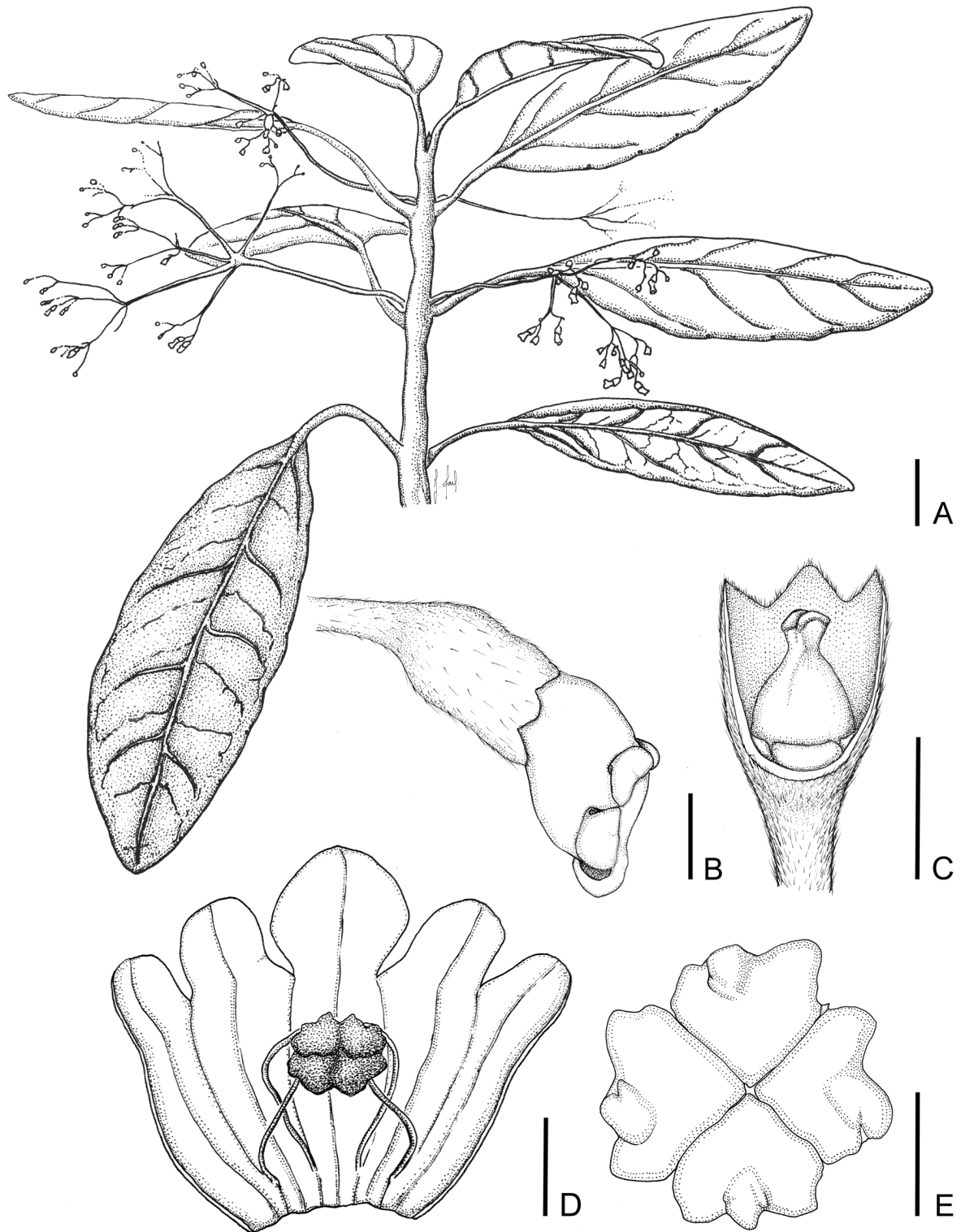


Fig. 5. *Bopopia parviflora* Munzinger & J.R.Morel gen. et sp. nov. **A.** Part of plant showing opposite leaves and axillary inflorescences. **B.** Flower in lateral view. **C.** Calyx cut open to show the gynoecium. **D.** Longitudinal section of corolla, showing stamens (lobes unrolled). **E.** Top view of connate anthers. Scale bars: A = 20 mm; B–D = 1 mm; E = 0.4 mm. Drawn from photographs taken by Jérôme Munzinger and parts of the specimen *Munzinger et al.* 7980 preserved in alcohol.

Discussion

Gesneriaceae are a family in the order Lamiales and comprise ca 150 genera and over 3400 species worldwide (Perret *et al.* 2013; Woo *et al.* 2011; Weber *et al.* 2013). In New Caledonia, this family is represented by the genera *Cyrtandra* J.R.Forst. & G.Forst (Didymocarpoideae-Trichosporeae), *Coronanthera*, and *Depanthus* (Gesnerioideae-Coronanthereae). *Cyrtandra* comprises more than 650 species (Atkins *et al.* 2013), although only a single species is found in New Caledonia, *Cyrtandra mareensis* Däniker, which is endemic to Maré Island (Morat *et al.* 2001; Cronk *et al.* 2005). *Coronanthera* and *Depanthus* are part of the tribe Coronanthereae that comprises nine genera in total (Woo 2007; Woo *et al.* 2011; Weber *et al.* 2013). *Depanthus* is a genus endemic to New Caledonia, with two described species, *D. glaber* and *D. pubescens* Guillaumin, although Woo (2007) considers these species to be synonymous in his PhD thesis (not validly published). All known species of *Coronanthera* are found in the archipelago of New Caledonia except *Coronanthera grandis* G.W.Gillett, an endemic of the Solomon Islands (Bougainville and Ysabel islands; Gillett 1967). Woo *et al.* (2011) published a phylogenetic study of Coronanthereae based on nuclear (ITS) and chloroplast (*trnL-trnF* and *trnE-trnT*) sequences. This study confirmed the monophyly of the tribe that can be subdivided into three subtribes: Coronantherinae Fritsch, Mitrariinae Hanst., and Negriinae V.L.Woo, J.F.Smith & Garn.-Jones. Furthermore, it showed that *Coronanthera* and *Depanthus* fall into different subtribes, Coronantherinae and Negriinae, respectively. Ancestral-area reconstruction and molecular dating of the subtribes supported multiple migrations from New Caledonia based on long-distance dispersal events in the Miocene (Woo *et al.* 2011): two migrations of Negriinae to Queensland (*Lenbrassia*) and Lord Howe Island (*Negria*), one migration of Coronantherinae to New Zealand (*Rabdothamnus*), and a potential (untested) migration to Solomon islands (*Coronanthera*).

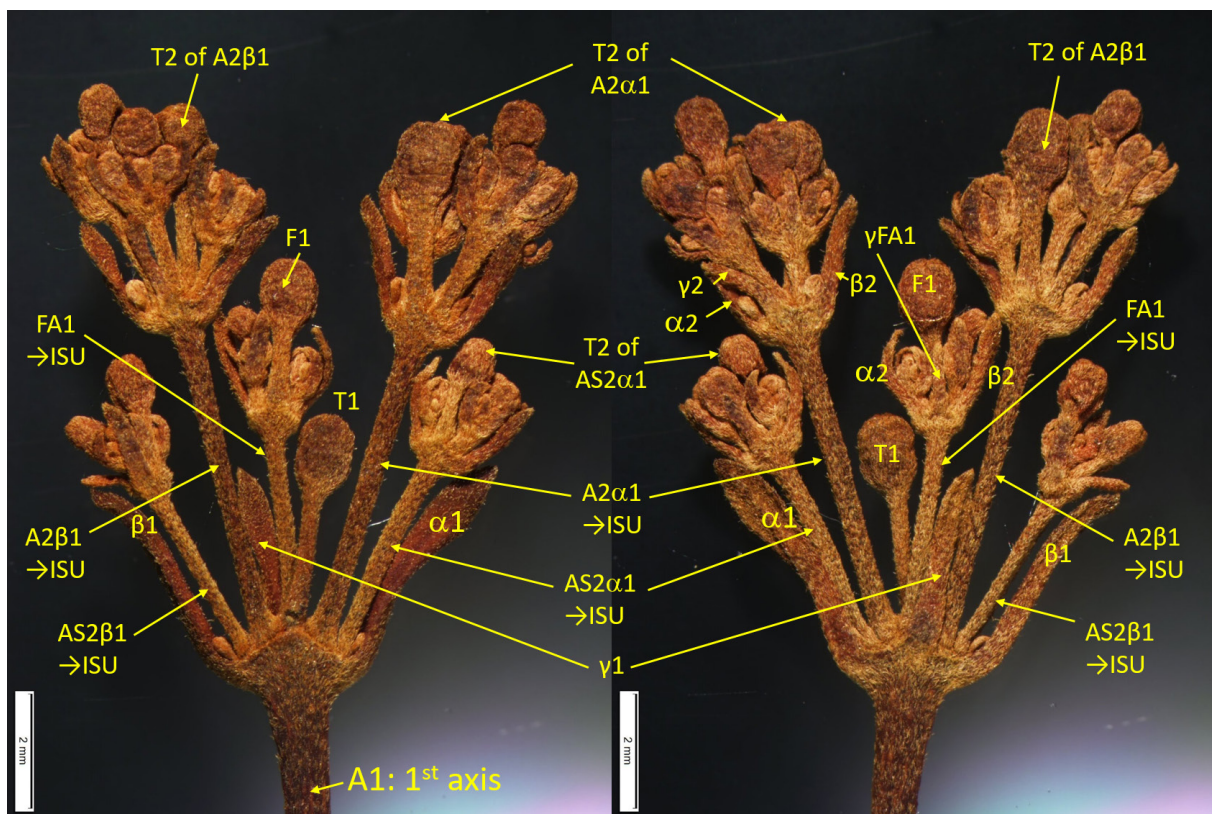


Fig. 6. Recto and verso photographs of a very young inflorescence of *Bopopia parviflora* Munzinger & J.R.Morel gen. et sp. nov.

Herbaria are a major frontier for species discovery (Bebber *et al.* 2010), and indeed Woo (2007) listed nine new species of *Coronanthera*, based on herbaria collections, in need of formal description. Several of these were collected a long time ago and are still waiting for the attention of a taxonomic specialist. An examination of all New Caledonian Gesneriaceae in major herbaria showed that the species described here as *Bopopia parviflora* gen. et sp. nov. was never collected before. Thus field expeditions, such as ‘La Planète Revisitée’, are still very important to complete the inventory of New Caledonia’s flora.

The molecular data place the new species into tribe Coronanthereae, but surprisingly, not in *Coronanthera* and subtribe Coronantherinae, but in subtribe Negriinae, here being the sister taxon to the genus *Depanthus* (Fig. 1). It is important to note that the placement of the new species as sister to *Depanthus* is only weakly (PP = 0.8) to moderately (BS = 81) supported. Consequently, additional taxon sampling and/or inclusion of additional loci (particularly nuclear) is warranted. Morphologically, the cyme structure is in general agreement with Gesneriaceae, with ultimate axes ending by pair-flowered cymes (PFC) (Weber 1982, 1995) as illustrated in Fig. 4. But, in Gesneriaceae, the front flower generally

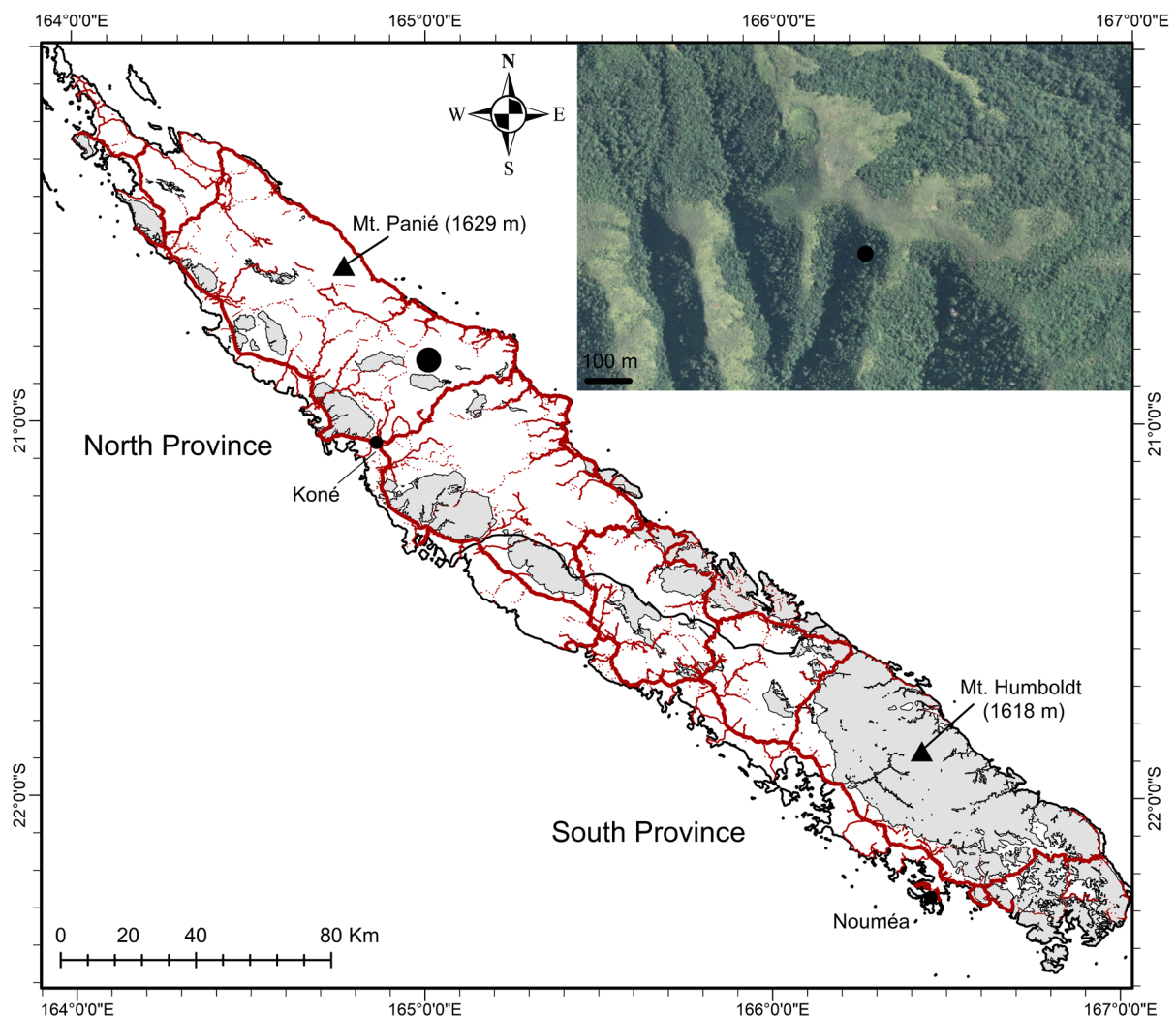


Fig. 7. Map of New Caledonia’s main island, Grande Terre, with main roads in thick red lines and secondary side roads in thin red lines. Black dot = collecting locality of *Bopopia parviflora* gen. et sp. nov. Inset, an enlarged image of the vegetation of the area shows forest fragmentation by fire (from Gouvernement de la Nouvelle-Calédonie 2019).

has no subtending bracteole, this latest being vestigial (Weber 2004; Haston & De Craene 2007) except in *Microchirita hamosa* (R.Br.) Yin Z. Wang and *Sinningia bulbosa* (Ker Gawl.) Wiehler (Weber 1973, 2013). In *Bopopia* gen. nov. all front flowers are subtended by a distinct bract (γ -bracteole) (Figs 4, 6). Its inflorescence is also strongly distinguished by the fact that one (or two) inflorescence(s) are born from the axil of the γ -bracteole of the first axis (Figs 2, 6), and not a solitary flower as classically described in the Gesneriaceae and more broadly the Lamiales (Weber 2013), with the exception of *Penstemon serrulatus* Menzies ex Sm. (Scrophulariaceae) which, however, develops only a single-branched cyme (Weber 1973). In *Bopopia parviflora* gen. et sp. nov., two axes develop from the axils of bracts α and β of the first axis (Figs 2, 6) into what we call the inflorescence sub-unit (ISU) (Fig. 2). One of these axes has an accessory origin. The material available already shows that, in addition to its molecular position in Negriinae, its inflorescence is unique, at least within the subtribe, and confirms that *Bopopia* gen. nov. deserves a special taxonomic rank. Further studies are needed, ideally with material at more advanced developmental stages, to define the variability and the complexity of this surprising inflorescence and to consider whether other taxonomic ranks need to be amended, including potentially the delimitation of the Gesneriaceae.

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Appendix 1 (continued on the next page). Voucher specimens for molecular phylogenetic analysis with GenBank accession numbers indicated. --- = sequence not available for this study; ! = voucher or its scan seen.

Species	Voucher	Herbarium	ITS	<i>trnL-F</i>	<i>trnE-T</i>	References
<i>Asteranthera ovata</i> 1	RBGE 19980608	E	EF445669	EF445726	EF445777	Woo <i>et al.</i> 2011
<i>Bopopia parviflora</i> gen. et sp. nov. 1	Bruy 1139!	K, MO, MPU, NOU, P	MW628180	MW650110	MW650108	This study
<i>Bopopia parviflora</i> gen. et sp. nov. 2	Munzinger 7980!	G, MPU, NOU, P, W	MW628181	MW650111	MW650109	This study
<i>Coronanthera aspera</i> 1	Munzinger 1032!	NOU, P	EF445670	EF445727	---	Woo <i>et al.</i> 2011
<i>Coronanthera clarkeana</i> 1	Woo 05-015!	WELTU	EF445672	EF445728	EF445778	Woo <i>et al.</i> 2011
<i>Coronanthera clarkeana</i> 2	McPherson & Werff 17771!	MO, NOU, P	EF445671	---	---	Woo <i>et al.</i> 2011
<i>Coronanthera deltoidiifolia</i> 1	Woo 05-001!	WELTU	EF445673	EF445729	EF445779	Woo <i>et al.</i> 2011
<i>Coronanthera pedunculosa</i> 1	MacKee 3746!	E, L[L.2821937]	EF445675	---	---	Woo <i>et al.</i> 2011
<i>Coronanthera pancheri</i> 1	Woo 02-029!	WELTU	EF445674	EF445730	EF445780	Woo <i>et al.</i> 2011
<i>Coronanthera sericea</i> 1	MacKee 46088!	E	EF445677	EF445732	EF445782	Woo <i>et al.</i> 2011
<i>Coronanthera sericea</i> 2	Woo 02-008!	WELTU	EF445676	EF445731	EF445781	Woo <i>et al.</i> 2011
<i>Coronanthera sericea</i> 3	Woo 02-026!	WELTU	EF445678	---	---	Woo <i>et al.</i> 2011
<i>Coronanthera squamata</i> 1	Munzinger 1204!	NOU, P[P00239726]	EF445679	EF445733	EF445783	Woo <i>et al.</i> 2011
<i>Coronanthera cf. pedunculosa</i> 1	Callmander 830!	G, NOU	KU991235	KY858606	---	Serrano-Serrano <i>et al.</i> 2017
<i>Coronanthera sp. Koniambo</i> 1	CHR 442982	CHR	EF445680	---	---	Woo <i>et al.</i> 2011
<i>Coronanthera sp. Nakada</i> 1	Munzinger 784!	MO, NOU, P[P00217278]	EF445681	EF445734	EF445784	Woo <i>et al.</i> 2011
<i>Coronanthera sp. Tchingou</i> 1	Munzinger 527!	MO, NOU, P[P00217279]	EF445682	EF445735	EF445785	Woo <i>et al.</i> 2011
<i>Cremosperma castroanum</i> 1	R.O. Hall 03-32	WELTU	EF445708	EF445759	EF445800	Woo <i>et al.</i> 2011
<i>Depanthus glaber</i> 1	Woo 05-010	WELTU	EF445685	EF445737	---	Woo <i>et al.</i> 2011
<i>Depanthus glaber</i> 2	Woo 03-010	WELTU	EF445683	EF445736	EF445786	Woo <i>et al.</i> 2011
<i>Depanthus glaber</i> 3	Woo 05-008	WELTU	EF445684	---	---	Woo <i>et al.</i> 2011
<i>Fieldia australis</i> 1	Woo 03-027	WELTU	EF445686	EF445738	EF445787	Woo <i>et al.</i> 2011

Appendix 1 (continued). Voucher specimens for molecular phylogenetic analysis with GenBank accession numbers indicated. --- = sequence not available for this study; ! = voucher or its scan seen.

Species	Voucher	Herbarium	ITS	<i>trnL-F</i>	<i>trnE-T</i>	References
<i>Fieldia australis</i> 2	CHR 470158	CHR, NSW	EF445687	EF445739	EF445788	Woo <i>et al.</i> 2011
<i>Gasteranthus atratus</i> 1	USBRG 06-013	US	EF445712	EF445763	EF445804	Woo <i>et al.</i> 2011
<i>Lenbrassia australiana</i> 1	Telford & Rudd 11314	E	EF445688	EF445740	EF445789	Woo <i>et al.</i> 2011
<i>Lenbrassia australiana</i> 2	Telford & Rudd 11299	E	EF445689	EF445741	EF445790	Woo <i>et al.</i> 2011
<i>Lenbrassia australiana</i> var. <i>glabrescens</i> 1	AD 99846103	AD	EF445690	EF445742	---	Woo <i>et al.</i> 2011
<i>Mitrararia coccinea</i> 1	RBGE 19792696	E	EF445691	EF445743	EF445791	Woo <i>et al.</i> 2011
<i>Mitrararia coccinea</i> 2	Woo 03-028	WELTU	EF445692	---	---	Woo <i>et al.</i> 2011
<i>Negria rahbdothamnoides</i> 1	Stewart s. n.	US	EF445693	EF445744	EF445792	Woo <i>et al.</i> 2011
<i>Negria rahbdothamnoides</i> 2	Brown 2003/33 b	NSW	EF445694	EF445745	EF445793	Woo <i>et al.</i> 2011
<i>Negria rahbdothamnoides</i> 3	Brown 2003/33 d	NSW	EF445695	EF445746	---	Woo <i>et al.</i> 2011
<i>Negria rahbdothamnoides</i> 4	Savolainen 19043	K	KY858372	GQ383564	---	Perret <i>et al.</i> 2013
<i>Rhabdothamnus solandri</i> 1	Woo 03-012	WELTU	EF445697	EF445748	EF445795	Woo <i>et al.</i> 2011
<i>Rhabdothamnus solandri</i> 2	Woo 03-101	WELTU	EF445698	EF445749	EF445796	Woo <i>et al.</i> 2011
<i>Rhabdothamnus solandri</i> 3	AK 133215	AK	EF445699	EF445750	EF445797	Woo <i>et al.</i> 2011
<i>Rhabdothamnus solandri</i> 4	Woo 03-131	WELTU	EF445700	EF445751	EF445798	Woo <i>et al.</i> 2011
<i>Rhabdothamnus solandri</i> 5	Woo 03-322	WELTU	EF445696	EF445747	EF445794	Woo <i>et al.</i> 2011
<i>Sarmienta repens</i> 1	Gardner & Knees 4033	E/K	EF445701	EF445752	EF445799	Woo <i>et al.</i> 2011