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REGULAR PAPER

Two new species of *Phialiphora* (Spermacoceae, Rubiaceae) exemplify drought adaptations in western Madagascar

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Background – *Phialiphora* (Spermacoceae, Rubiaceae) is a herbaceous genus restricted to unconsolidated white sands in open spaces in dry forests in northwestern Madagascar. The genus is characterized by the semi-succulent nature of its leaves and stems, its basal leaf rosette, its head-like inflorescences subtended by large leaf-like involucrate bracts and its isostylous flowers. Hitherto, only two species were described.
Methods – Classical methods of herbarium taxonomy are followed.
Key results – Two new *Phialiphora* species, *P. glabrata* De Block and *P. valida* De Block, are described, which brings the number of species in the genus to four. The two new species differ from the two previously described species by their glabrous branches, bracts, ovaries, calyces and fruits. They are easily distinguished from each other by the shape and size of the calyx lobes. A detailed description, illustration, distribution map and preliminary conservation assessment is given for the new species, which are assessed as critically endangered. We also present a key for the genus and discuss in detail the typical branching system, the capsules and the dispersal mechanism of *Phialiphora*. The description of these two new species exemplifies the uniqueness of the dry vegetations on unconsolidated white sands in western Madagascar, which are characterized by a high level of endemicity.

Keywords – Capsules; dispersal; dry forest; endemic; herbaceous; IUCN assessment; Madagascar; Spermacoceae; succulence; unconsolidated white sands.

INTRODUCTION

The Rubiaceae are the second largest family of flowering plants in Madagascar, with c. 98% of the Malagasy species endemic to the island (Davis & Bridson 2003). While the family mainly comprises woody species, a few lineages include herbaceous taxa. The Spermacoceae are the largest predominantly herbaceous tribe within the family. This tribe has a pantropical distribution, c. 62 genera and more than 1200 species (Groeninckx et al. 2009a). The Spermacoceae are variable in most characters but a majority of the representatives is herbaceous and has fimbriate stipules and tetramerous flowers (Groeninckx et al. 2009a).

During the last twenty years, extensive field collecting took place in Madagascar. This allowed phylogenetic studies focused on the African and Malagasy Spermacoceae to be carried out (Kårehed et al. 2008; Groeninckx et al. 2009a, 2009b, 2010a, 2010b, 2010c; Janssens et al. 2016). As a result, the generic limits of the Spermacoceae genera were tested and adapted and this, together with thorough morphological-anatomical and taxonomic studies, lead to the description of three new endemic Spermacoceae genera and

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16 new species. The importance of field collecting cannot be stressed enough, especially when executed by taxonomists or parataxonomists with knowledge of the flora. The two new species described here are the result of a single collecting trip in a floristically little-known and under-collected region. The dry forests and shrublands in western Madagascar host far less species than the eastern humid forests. Nevertheless, they are home to important biodiversity and characterized by a high level of endemicity (Waeber et al. 2015). We need further field, taxonomic and floristic studies to fully understand the diversity of these vegetation types.

In Madagascar, the Spermacoceae are represented by nineteen genera, some of which are not native. This is the case for the neotropical genera *Mitracarpus* Zucc. and *Richardia* L., and for *Dentella* L., which occurs in Australia, Southeast Asia and the southwestern Pacific (Razafimandimbison & Manjato 2019; Catalogue of the Plants of Madagascar 2020). Each of these three genera has a single naturalised species in Madagascar. Six genera are endemic to Madagascar: *Amphistemon* Groeninckx, *Astiella* Jovet, *Gomphocalyx* Baker, *Lathraeocarpa* Bremek., *Phialiphora* Groeninckx and *Thamnoldenlandia* Groeninckx (Baker 1887; Jovet 1941; Bremekamp 1957; Dessein et al. 2005; Groeninckx et al. 2009b, 2010a, 2010b, 2017). Five genera have an African distribution, sometimes including parts of the Arabian Peninsula or the Western Indian Ocean Islands: *Agathisanthemum* Klotzsch, *Cordylostigma* Groeninckx & Dessein, *Mitrasacmopsis* Jovet, *Pentodon* Hochst. and *Phylohydrax* Puff (Puff 1986; Dessein et al. 2005; Groeninckx et al. 2010c). Three genera have a pantropical distribution: *Oldenlandia* L., *Spermacoce* L. and *Edrastima* Raf. Both *Oldenlandia* and *Spermacoce* have, besides endemic and native species, also naturalised foreign species in Madagascar (e.g., the Asian *Spermacoce pusilla* Wall.), while *Edrastima* is represented by a single species with an African-wide distribution (formerly known as *Oldenlandia goreensis* (DC.) Summerh.). The genus *Hexasepalum* Bartl. ex DC. is distributed in Africa and America and American species are also present in Madagascar (e.g., *Hexasepalum teres* (Walter) J.H.Kirkbr., formerly known as *Diodia teres* Walter). A last Malagasy representative of the Spermacoceae is *Hedyotis trichoglossa* Baker. The genus *Hedyotis* L. is in fact an Asian genus and the exact taxonomic position of this Malagasy species remains unknown.

Of these eighteen Malagasy Spermacoceae genera, only two are woody: the only species of *Thamnoldenlandia*, *T. ambovombensis* Groeninckx, is a densely branched shrub up to 1.5 m tall, whereas the two *Lathraeocarpa* species are subshrubs up to c. 25 cm tall with well-developed woody taproots (Groeninckx et al. 2009b, 2010a). The other Malagasy Spermacoceae genera only have herbaceous representatives, but it should be noted that a woody base is common in perennial species. Only three genera have more than one or two Malagasy representatives: this is the case for *Astiella* (12 species), *Oldenlandia* (< 20 species) and *Spermacoce* (< 20 species). Ten genera have only a single species in Madagascar. Five others, amongst which *Phialiphora*, have two Malagasy representatives. Most Spermacoceae species occur in dry vegetation types in west, south and north Madagascar, although some species are also found in the eastern humid forests, e.g., *Astiella homolleae* Groeninckx and *Hedyotis trichoglossa*, which occur in east Madagascar (Groeninckx 2009; Groeninckx et al. 2017).

Studies by Groeninckx et al. (2009b, 2010a, 2010b, 2017) and Dessein et al. (2005) helped clarify the taxonomic framework of the Spermacoceae in Madagascar. However, the tribe is still in need of study, which is exemplified by the fact that exact species numbers in e.g., *Oldenlandia* and *Spermacoce* are not known. The study of herbaceous species is rendered difficult by the great variability in habit, depending on the ecological circumstances in which they grow. Also, while many species are narrow endemics, others are widespread or even invasive weeds with their characters variable to a great extent. While collecting in Madagascar is being undertaken on a relatively large scale by institutions such as Royal Botanic Gardens, Kew and Missouri Botanical Garden, the focus is mostly on woody species. Collecting activities concentrating on herbaceous species are bound to bring novelties to light.

Phialiphora is currently known from two species endemic to the Mahajanga Province in NW Madagascar. The genus is characterized by its semi-succulent leaves and stems, a basal leaf rosette, head-like inflorescences subtended by large leaf-like bracts, isostylous flowers with anthers and stigma exserted at anthesis and heart-shaped placentas distally attached to the septum (Groeninckx et al. 2010b). *Phialiphora* was included in three molecular studies. In Groeninckx et al. (2010b), the genus (represented by a single species) was a member of a Malagasy clade, and resolved as sister to *Astiella*; this clade in turn was sister to another Malagasy clade formed by *Amphistemon* and *Thamnoldenlandia*. The same relationships were retrieved in Neupane et al. (2015) and also in Janssens et al. (2016), comprising two and five species of *Phialiphora* and *Astiella,* respectively. For the Malagasy clade to which *Phialiphora* belongs, an ancestral distribution range situated in tropical America, an origin in the Oligocene and a radiation in the Miocene were postulated (Janssens et al. 2016).

In this study, we describe two new species of the genus *Phialiphora*, bringing the species number up to four. We give detailed descriptions, illustrations, distribution maps and preliminary conservation assessments of the novelties as well as an identification key to the species of the genus.

MATERIAL AND METHODS

Descriptions were mostly based on dried and alcohol-preserved samples collected during recent fieldwork in Madagascar. Terminology followed Robbrecht (1988) but leaf shape was described according to the terminology of simple symmetrical plane shapes (Anonymous 1962). Methods followed normal practice of herbarium taxonomy (De Vogel 1987). For vegetative characters, colours and sizes were given for dried plant parts; for flower and fruit characters, colours were given for living material except when specified differently. Sizes of flowers and fruits covered the range of dried and alcohol-preserved material. Specimens were cited alphabetically by collector. Localities were cited as given by the collectors on the specimen labels. The distribution maps were drawn using QGIS Desktop v.3.4.11 (QGIS Develop-

ment Team 2020). Preliminary conservation status was assessed by applying the IUCN Red List Category criteria (IUCN 2019) using GeoCAT (Geospatial Conservation Assessment tool; Bachman et al. 2011).

Photographs of fruits were made using a digital microscope Keyence vhx-5000 (Keyence Co., Itasca, IL, U.S.A.). For SEM, the material was washed twice in ethanol 70% for 5 minutes, transferred to a 1:1 mixture of dimethoxymethane (DMM)/ethanol 70% for 5 minutes and then to 100% DMM for 20 minutes. Subsequently, the material was critical point dried using liquid CO_2 with a Balzers CPD 030 critical point dryer (BAL-TEC, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs using carbon adhesive tape Leit-C and coated with gold with a SPI-Module™ sputter coater (SPI Supplies, West-Chester, PA, U.S.A.). SEM micrographs were obtained with a JEOL JSM6360 scanning electron microscope (JEOL Ltd., Tokyo, Japan).

RESULTS AND DISCUSSION

Two species new to science

Hitherto, *Phialiphora* was known from two species, *P. bevazahensis* and *P. capitulata*. The genus is characterized by the following characters: herbaceous, rosulate habit; semi-succulent leaves, stems and bracts; basal leaf rosette; head-like inflorescences subtended by large leaf-like involucrate bracts, from the axils of which branches may originate which also terminate in head-like inflorescences (involucrate capitula); isostylous flowers with anthers and stigma exserted at anthesis; heart-shaped placentas attached to the upper half of the septum and bearing numerous ovules; capsular fruits, dehiscing loculicidally and septicidally. The genus is restricted to unconsolidated white sands in northwestern Madagascar (Groeninckx et al. 2010b).

The two new species described here show all the above-mentioned characters and are found on unconsolidated white sands. There is, therefore, no doubt that they belong to the genus *Phialiphora*. They differ from *P. bevazahensis* and *P. capitulata* by their glabrous branches, bracts, ovaries, calyces and fruits. In addition, the four species can be distinguished by characters such as shape and size of the involucrate bracts, shape and size of the calyx lobes, length of the corolla tube, size of the anthers and filaments, length of the exserted part of the stigma at anthesis, etc. Table 1 gives an overview of the distinguishing characters of the four species.

Habitat of *Phialiphora*

The four species of *Phialiphora* are restricted to unconsolidated white sands in western Madagascar. The climax vegetation on these sands is dry deciduous forest, characterized by a high local endemism at species and genus level and this for both plants and animals (Waeber et al. 2015; Crowley 2020). According to Moat & Smith (2007), the dry deciduous western forests differ in composition depending on the geological substrate, e.g.,, unconsolidated sands, sandstone, limestone, basement rock. While some overlap is possible, many species are restricted to a single geological substrate (Du Puy & Moat 1998) and forests on different substrates may differ considerably in floristic composition (Du Puy & Moat 1996). So, while the eastern rainforests are much richer in number of species, the dry deciduous western forests nevertheless host important biodiversity, often consisting of endemic species with narrow distributions (Waeber et al. 2015). Within these dry western forests, unconsolidated white sands constitute a specialized habitat that demands special adaptations of the plant species occurring there because of the nutrient-poor soils that have no moisture-holding capacity. This extreme lack in nutrients makes regeneration almost impossible once the vegetation has been denuded (Jacobs 1988). Several Rubiaceae taxa are endemic to this forest on unconsolidated white sands, such as *Coffea ambongensis* J.-F.Leroy ex A.P.Davis & Rakotonas., *Homollea longiflora* Arènes, *Hyperacanthus grevei* Rakotonas. & A.P.Davis, and *Schizenterospermum majungense* Homolle ex Arènes (Rakotonasolo & Davis 2002; Davis & Rakotonasolo 2008; De Block 2018).

Dry deciduous western forests are less conserved in Protected Areas than eastern rainforests: 29% vs. 46% of the remaining c. 52 000 km^2 forest cover for each forest type (Waeber et al. 2015). Furthermore, the western dry forests are under severe threat by large-scale mining, oil exploration and agro-industrial projects (Waeber et al. 2015) in addition to the threats of subsistence farming, burning and grazing. More study is necessary to understand the species richness and level of endemism in the dry forests on white unconsolidated sands in western Madagascar.

The genus *Phialiphora* is well-adapted to the dry habitat on unconsolidated white sands in which it occurs. Adaptations are found in the growth form and branching pattern, the texture of the leaves, the compact inflorescences, the early investment in the formation of seeds and the dispersal mechanism.

Morphology of *Phialiphora*

Habit – In its most simple form a *Phialiphora* plant consists of a pair of opposite vegetative leaves, a branch and a terminal capitate inflorescence subtended by a pair of leaf-like involucrate bracts that are arranged decussately relative to the vegetative leaves (figs 4A, 7D). In larger plants, several branches arise from a basal rosette (figs 4B, C, 7B). In even more robust plants, one or a few pairs of leaves occur above the basal rosette, subtending the lowermost ramifications (fig. 4D). In *P. glabrata* and *P. valida*, these leaves differ from the ones in the basal rosette in that they are ± linear and 10–30 × 1.5–3 mm (vs. narrowly obovate, narrowly ovate or narrowly elliptic, 10–75 × 2.5–18 mm). They have the same pubescence as the leaves in the basal rosette and interpetiolar stipules are present (figs 1C, 2B). As such, the non-basal leaves in *P. glabrata* and *P. valida* differ from the involucrate bracts, which are glabrous and do not have stipules; instead, the stipular and foliar parts of the bracts are fused into one structure (*P. glabrata*: fig. 1D) or fused with a central lobe (*P. glabrata*: fig. 1E; *P. valida*: fig. 2C).

Leaf rosette – Most Rubiaceae are woody. Within the herbaceous lineages of the family, rosulate herbs are rare and scattered. Basal rosettes are often seen as an adaptation to growth on rocks and cliffs, as e.g., in the Chinese *Wendlandia acaulis* (H.S.Lo) P.W.Xie & D.X.Zhang (tribe Augusteae; Xie et

Table 1 – **Distinguishing characters for the four *Phialiphora* species.**
The characters of *P. bevazahensis* and *P. capitulata* were adapted from Groeninckx et al. (2010b).

	P. bevazahensis	***P. capitulata***	***P. glabrata***	***P. valida***
Plant height	2–15 cm	5–15 cm	5–22 cm	20–40 cm
Stems	densely pilose	sparsely to densely pilose at least at the base, higher up often glabrous	glabrous	glabrous
Leaf blades	1.5–5.3(–8.3) × 0.4–1.1(–2.2) cm, pubescent above and glabrous below	0.5–2.9 × 0.1–0.8 cm, pubescent on both leaf surfaces	1–7 × 0.25–1.8 cm, pubescent above and glabrous below	3–7.5 × 0.4–1 cm, pubescent above and glabrous below
Involucrate bracts: pubescence	upper surface densely pubescent, lower surface densely or sparsely pubescent	upper surface densely pubescent, lower surface densely or sparsely pubescent	glabrous on both surfaces	glabrous on both surfaces
Involucrate bracts: foliar parts	0.5–4 × 0.2–2.1 cm	0.8–2 × 0.4–0.6 cm	0.7–3 × 0.2–0.5 cm	1.3–2.2 × 0.2–0.5 cm
Involucrate bracts: stipular parts	often absent, if present, then forming an ovate sheath 1–4 mm long	forming a narrowly triangular sheath 3–10 mm long	completely fused with the bases of the foliar parts, or, rarely, forming an ovate sheath up to 1.5 mm long	forming a narrowly ovate to narrowly triangular sheath 2–3 mm long
Higher order bracts/ bracteoles	broadly ovate, c. 3.5 × 2 mm	Unknown	broadly ovate, c. 0.5 × 1 mm	narrowly triangular to linear, 7–8 × 1–1.5 mm
Calyx	pubescent outside, glabrous inside	pubescent or rarely glabrescent outside, glabrous inside	glabrous outside and inside	glabrous outside and inside
Calyx lobes	broadly ovate, 0.8–2.5 × 1–2.5 mm	narrowly ovate, 1.2–2 × 0.3–0.5 mm	ovate, leaf-like or broadly triangular, 0.6–1 × 1–1.5 mm	narrowly triangular; 2–4 × 0.5–1 mm
Corolla tube	3.5–5.5 mm long	c. 5 mm long	c. 3.5 mm long	c. 5 mm long
Corolla lobes	(2.8–)4–4.5 × 2.2–3 mm	c. 2 × c. 1 mm	2.5–3 mm × c. 1.5 mm	5–7 × 2–3 mm
Anthers	1.3–1.4 mm long	0.5–0.7 mm long	c. 0.8 mm long	c. 2 mm long
Filaments	2.2–2.8 mm long	c. 1.5 mm long	c. 2 mm long	c. 1.5 mm long
Ovary	1–1.5 mm long, densely pubescent	c. 0.8 mm long, upper half densely pubescent	c. 1 mm long, glabrous	c. 1.5 mm long, glabrous
Style and stigma exserted from the corolla tube	for 3–4 mm	for c. 2 mm	for 2–3 mm	for c. 5 mm
Capsules (persistent calyx included)	2–5.5 × 2.8–3.5 mm, densely pubescent	1.5–3 × 1.4–3 mm, only upper half densely pubescent	3–4 × 2–2.3 mm, glabrous	6–7.5 × c. 2 mm, glabrous
Air chambers at the top of each locule	absent	present	absent	absent

al. 2014) or the West African *Kindia gangan* Cheek (tribe Pavetteae; Cheek et al. 2018). However, this is not the case for the Malagasy *Phialiphora* species, which all occur on unconsolidated white sands. Other examples of species forming basal leaf rosettes are found in the tribes Ophiorrhizeae (e.g., *Spiradiclis loana* R.J.Wang; Ruijiang 2002), Knoxieae (e.g., *Knoxia rosettifolia* Geddes; Puff 2007) and Spermacoceae (e.g., *Houstonia caerulea* L.; Holm 1907). Most of these rosette-forming species are Asian with the exception of the North American *Houstonia* and the African *Kindia*. *Phialiphora* is the only Rubiaceae genus in which all species form a basal leaf rosette. The rosette is formed as a result of very short internodes at the base of the plant.

Succulence – Succulence is uncommon in the Rubiaceae but occurs sporadically in several tribes in all tropical regions. In Madagascar, the montane subshrub *Nematostylis anthophylla* (A.Rich. ex DC.) Baill. (tribe Alberteae; Puff et al. 1984) has semi-succulent stems and leaves and the beach-dwelling *Phylohydrax madagascariensis* (Willd.) Puff (tribe Spermacoceae; Puff 1986) is ± succulent in the entire vegetative region. *Dentella repens*, newly discovered in northwestern Madagascar, also has semi-succulent leaves (S. Razafimandimbison, Stockholm, Sweden, pers. comm.). Other examples of succulence in the Rubiaceae are found in epiphytic woody genera such as the American *Hillia* Jacq. and *Cosmibuena* Ruiz & Pav. (tribe Hillieae; semi-succulent

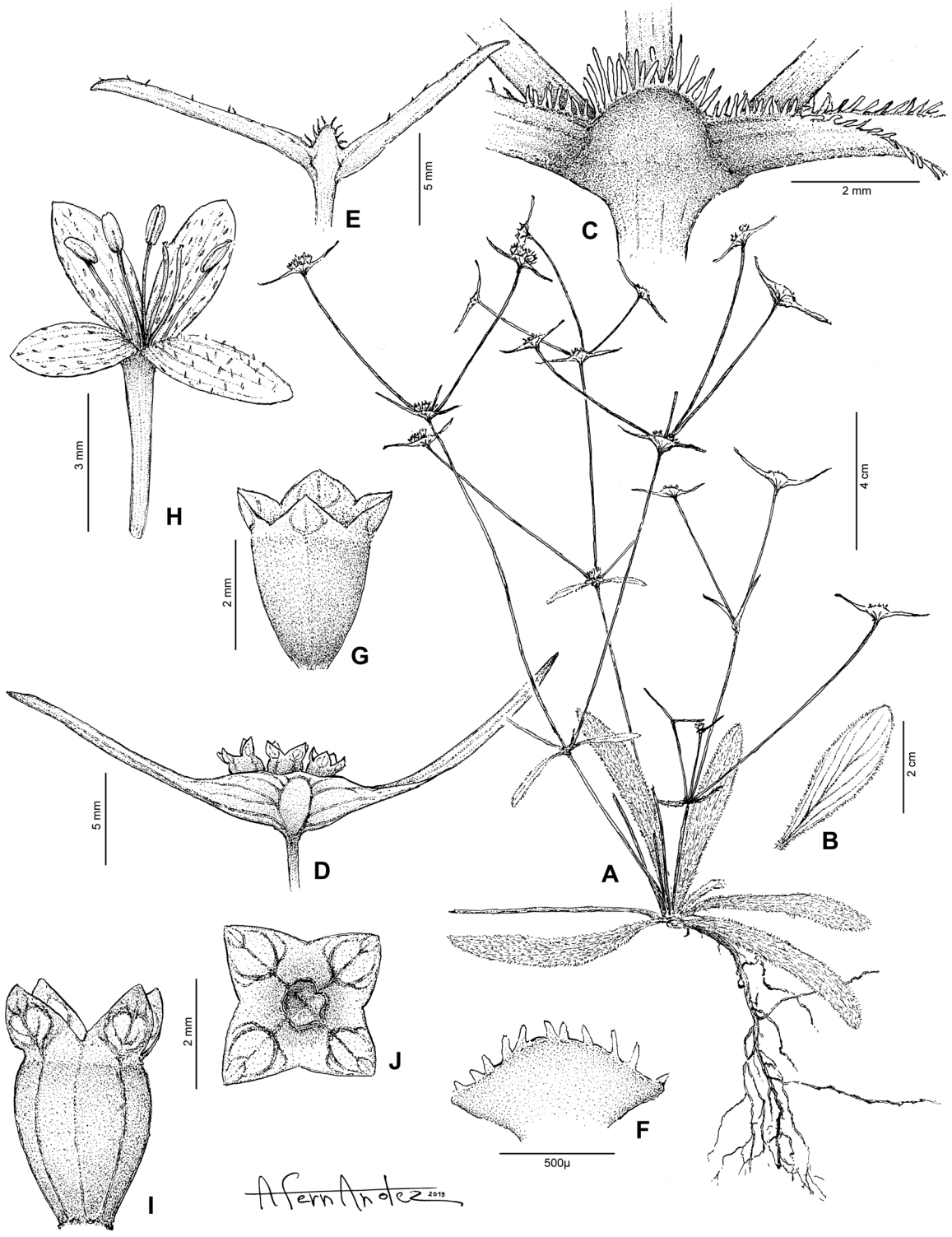

Figure 1 – *Phialiphora glabrata*. **A**. Habit. **B**. Leaf, showing secondary nerves ± parallel to the midrib. **C**. Node and stipule, showing the bases of two non-basal leaves and three branches. **D**. Inflorescence showing involucrate bracts, typical form. **E**. Inflorescence showing involucrate bracts, atypical form. **F**. Higher order bract. **G**. Ovary and calyx. **H**. Corolla, stamens, style and stigma. **I**. Fruit, lateral view. **J**. Fruit, top view showing the central apical opening through which seeds are dispersed. A–D, I, J from *De Block, Groeninckx & Rakotonasolo 2344*; E from *Morat 2654*; F–H from *De Block, Groeninckx & Rakotonasolo 2342*. Drawn by A. Fernandez.

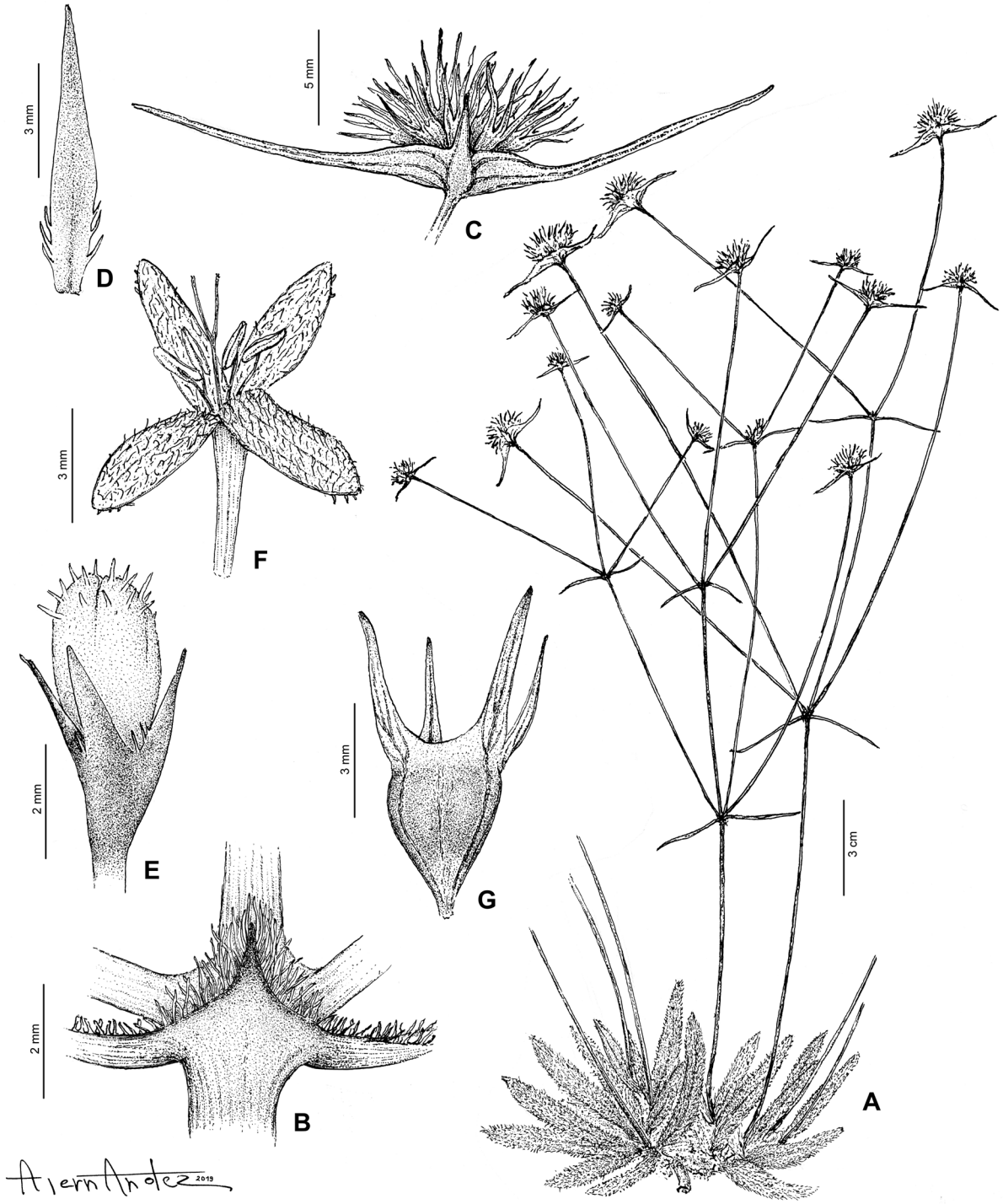

Figure 2 – *Phialiphora valida*. **A**. Habit. **B**. Node and stipule, showing the bases of two non-basal leaves and three branches. **C**. Inflorescence showing the involucrate bracts. **D**. Higher order bract. **E**. Ovary, calyx, flower bud. **F**. Corolla, stamens, style and stigma. **G**. Fruit, lateral view. A–G from *De Block, Groeninckx & Rakotonasolo 2349*. Drawn by A. Fernandez.

leaves and succulent leaves and stems, respectively; Taylor 1992, 1994) or myrmecophytic woody epiphytes such as the Pacific *Squamellaria* Becc. (tribe Psychotrieae; semi-succulent leaves; Chomiki & Renner 2016). Succulence also occurs in herbaceous genera such as the Asian *Ophiorrhiza* L. (tribe Ophiorrhizeae; stems succulent; Tao & Taylor 2011). In *Phialiphora*, the leaves and involucrate bracts are semi-succulent.

Leaf pubescence – With the exception of *P. capitulata*, *Phialiphora* species have leaves with a pubescent upper surface and a glabrous lower surface. This is different from most Rubiaceae, which usually are more densely pubescent on the lower surfaces of their leaves. This is because leaves in the Rubiaceae are mostly hypostomatic. In *Phialiphora*, we observed stomata on both leaf surfaces. The absence of hairs on the lower leaf surface could be explained by the fact that the basal leaves occur very close to or on the ground. Dense pubescence on the basal leaf surface would hardly be advantageous in these circumstances.

Inflorescences – The inflorescences in *Phialiphora* are terminal, capitate and are subtended by a pair of leaf-like involucrate bracts, i.e., capitula (figs 5A, D, 7C). The foliar parts of the bracts are relatively wide at the base (encompassing the whole inflorescence) and become narrower away from the inflorescence. *Phialiphora glabrata* and *P. valida* differ from the other two species of the genus by the much narrower bracts (foliar parts 2–5 vs. 4–20 mm wide) and by the fact that both surfaces of the bracts are glabrous. The stipular parts are completely fused with the foliar parts in *P. glabrata* (fig. 1D) but form a distinct lobe in the other three species (e.g., figs 2C, 7C). The stipular parts are sometimes absent in *P. bevazahensis*.

Branching in *Phialiphora* is essentially cymose and dichasial. One to several branches arise from either the basal rosette (figs 4A–C, 7B, D), from the axils of a stipulate pair of leaves above the basal rosette (fig. 4D) or from the axils of the involucrate bracts of the capitula (figs 4C, D, 5A, D, 7B, E). At the end of all these branches, involucrate capitula are formed (fig. 4A–D). This pattern can be repeated up to three times (fig. 7A, E) and can be interpreted in two ways. First, a whole branched structure can be considered as a single inflorescence and each capitulum subtended by involucrate bracts as a partial inflorescence. In that case, the basal branch is the peduncle of this inflorescence.

However, several aspects of the branching in *Phialiphora* seem to differ from the general structure of inflorescences in Rubiaceae: 1) The branches arising from the axils of the involucrate bracts are not shorter than the branches arising from the basal rosette. 2) Rubiaceae inflorescences are usually trichotomously branched. In *Phialiphora*, though, branches do not occur in threes. 3.) In case of several branches arising from the axil of each of the involucrate bracts, the development of the branches is not synchronous, resulting in older and younger branches (fig. 5D). This is unlike the usual development of a Rubiaceae inflorescence, where all axes develop more or less at the same time. Therefore, a second

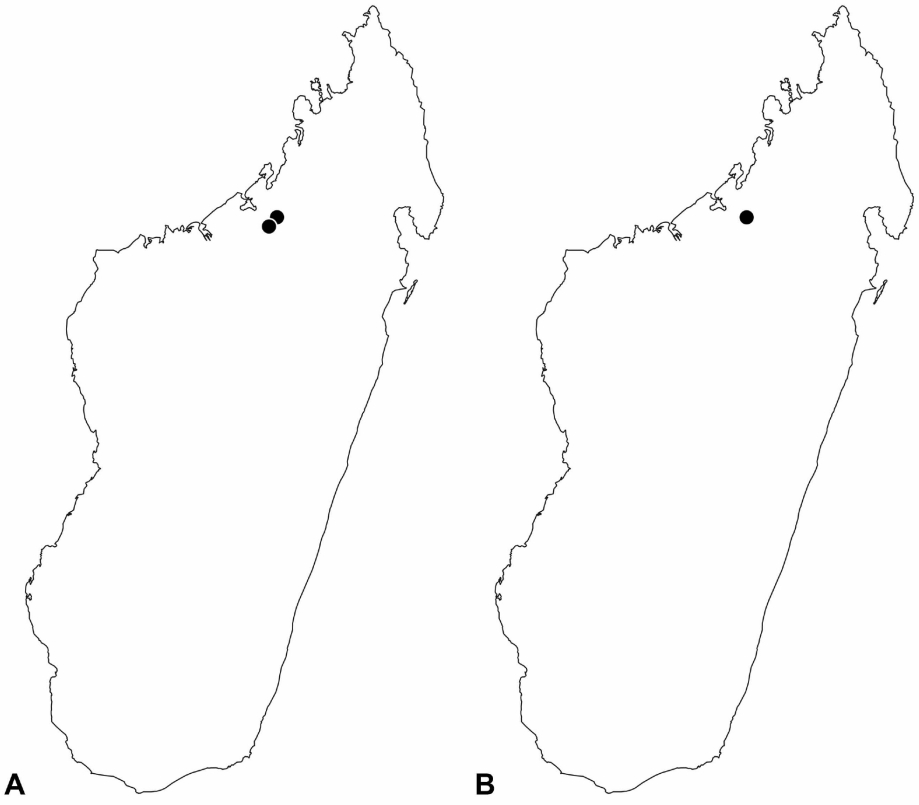

Figure 3 – Distribution maps. **A**. *Phialiphora glabrata*. **B**. *P. valida*. Maps created using using QGIS Desktop v.3.4.11 (QGIS Development Team 2020).

interpretation of the branching pattern is that the branches arising from the involucrate inflorescences can be considered as vegetative branches, each of which develops a sessile, terminal, capitate, involucrate inflorescence.

In *Phialiphora*, the development of the capitula is asynchronous both within single capitula (fig. 7D–G) and within plants. During most of the life of the plants, capitula possess flowers and fruits at different developmental stages, from fruits with mature seeds to very young buds (verified for *P. glabrata* and *P. valida*; plant material collected from January to April). Furthermore, within a plant, new capitula keep developing throughout its life span (fig. 5D). This asynchronous development within and between capitula can be explained as an adaptation to drought. The plants quickly produce seeds, either from few-flowered capitula from which later on new branches with capitula arise (fig. 5D), again producing seeds as soon as possible, or from a few flowers in many-flowered capitula in which later more flowers will bloom.

Capsules – The diaspores in *Phialiphora* are the minute seeds (fig. 5L, M), as is typical for Rubiaceae species with many-seeded dry fruits (Robbrecht 1988). The capsules in *Phialiphora* open loculicidally and septicidally. At first, an ovate opening is present at the apex of the fruit in the region of the nectary disc (perpendicular to the septum; fig. 6C, G, J, M). Ripe seeds are released through this opening upon movement of the capsules by wind. Also, seed dispersal through ombrohydrochory (dispersal by dew or rain) occurs, with rain drops washing out exposed seeds in the opened capsules. This dispersal mechanism was observed by the authors in *P. bevazahensis* (fig. 7G) and it likely also occurs in the other *Phialiphora* species. It is a common dispersal mechanism in arid habitats in low herbaceous plants with many small seeds (Van der Pijl 1969; van Rheede van Oudtshoorn & van Rooyen 1998). In some species from arid habitats, hygrochasy occurs, i.e., the opening of fruits in a humid atmosphere resulting from changing water content in either cell lumina (cohesion mechanism) or in cell walls

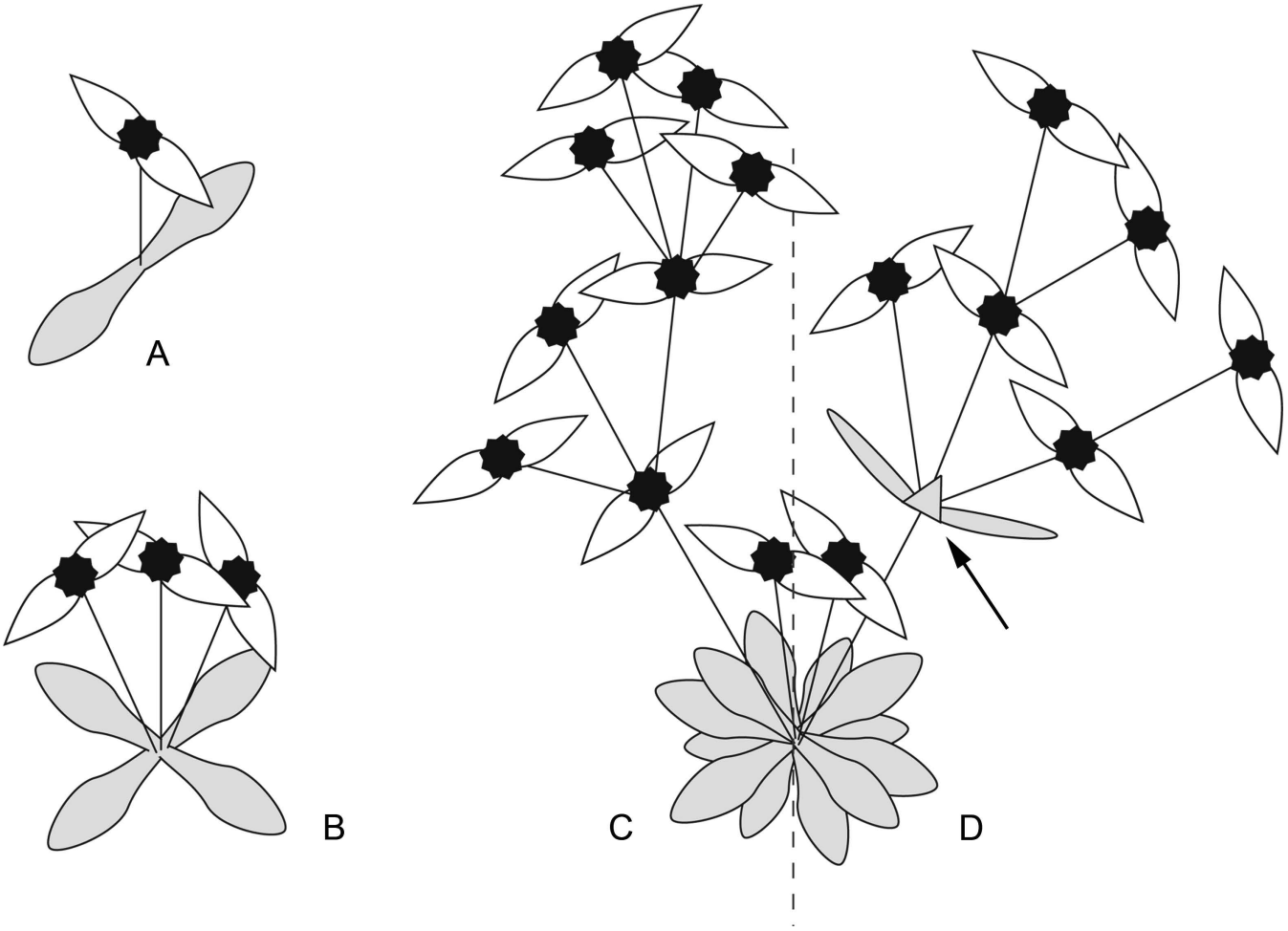

Figure 4 – Schematic representation of the branching patterns in *Phialiphora*. **A**. Plant in its simplest form, consisting of a pair of basal leaves, a branch and an involucrate capitulum. Note that the involucrate bracts are oriented perpendicular to the basal leaves. **B**. Plant consisting of a basal leaf rosette from which several branches arise, each bearing an involucrate capitulum. **C**. Plant consisting of a basal rosette from which several branches arise. From the axils of the involucrate bracts of a capitulum, one or more branches may arise, each ending in an involucrate capitulum. This pattern can be repeated up to three times. **D**. Plant consisting of a basal rosette from which several branches arise. Branching pattern similar to that in C except for the node with a pair of stipulate non-basal leaves (arrowed) subtending several branches terminating in involucrate capitula, from which again branches bearing capitula may arise.

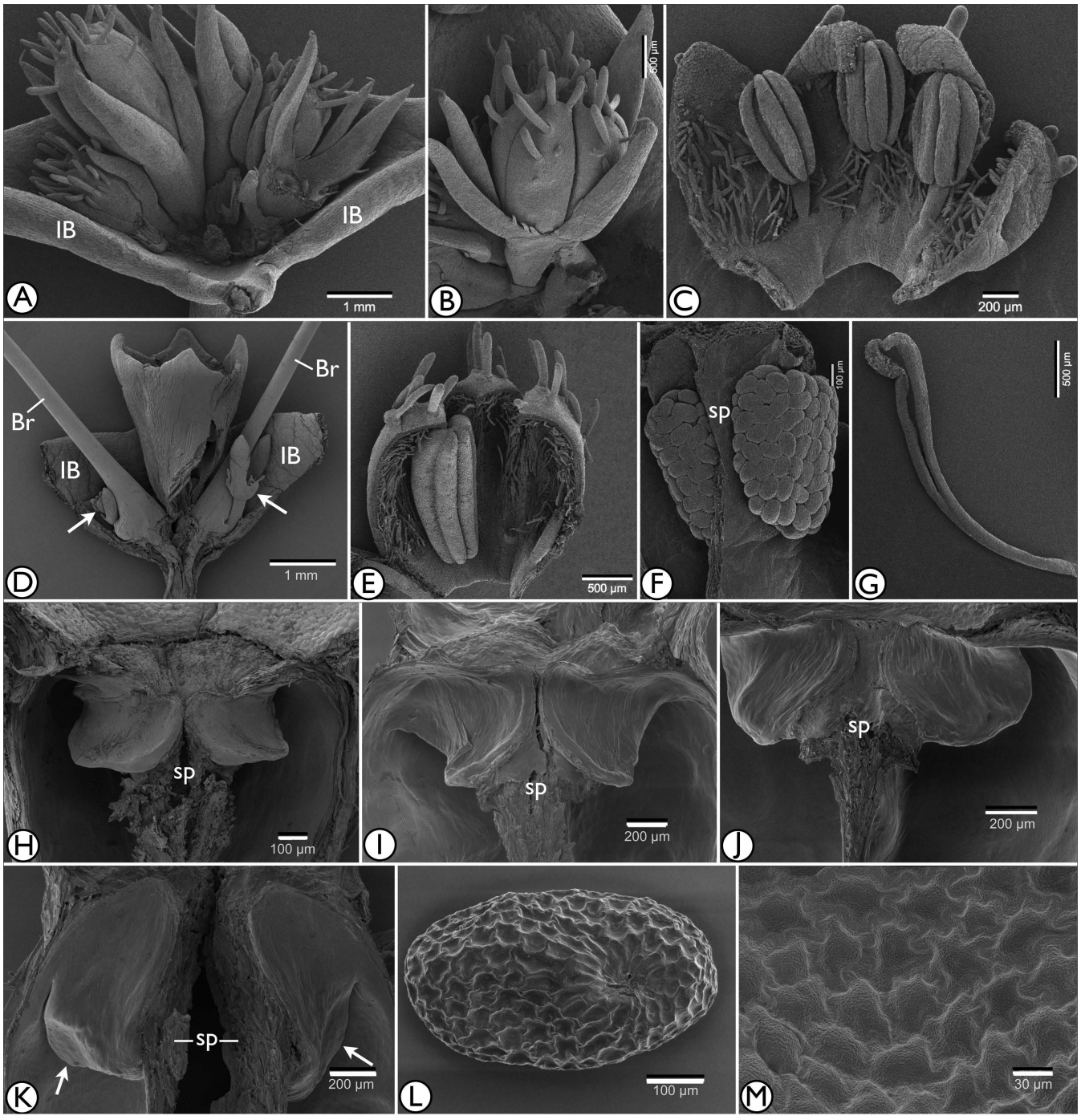

Figure 5 – Flowers and fruits in *Phialiphora* (SEM). **A**–**C**, **J**. *P. valida*. **D**–**G**, **I**, **L**, **M**. *P. glabrata*. **H**. *P. bevazahensis*. **K**. *P. capitulata*. **A**. Flower buds inside involucrate bracts. **B**. Flower bud; note the robust hairs on the abaxial surface of the tips of the corolla lobes. **C**. Flower bud longitudinally opened; note the different trichome types on the abaxial and adaxial surface of the corolla lobes. **D**. Single-flowered capitulum. From the axils of each involucrate bract a branch ending in a capitulum arises. Next to these branches, a second set of juvenile branches develop (arrowed). At the tip of these juvenile branches, the involucrate bracts are visible with leaf-like foliar parts and ovate stipular parts bearing colleters on the margins. **E**. Flower bud longitudinally opened; note the different trichome types on the abaxial and adaxial surface of the corolla lobes. **F**. Large placentas attached to the septum and bearing numerous ovules. **G**. Stigma at anthesis. **H**–**K**. Endocarp extensions in the region of the apical opening of the capsule; note the air chambers in *P. capitulata* (K, arrowed). **L**. Adaxial view of seed, showing the hilum. **M**. Seed-coat. Abbreviations: Br, branch ending in a capitulum; IB, involucrate bract; sp, septum. A–C, J from *De Block, Groeninckx & Rakotonasolo 2349*; D–G, I, L, M from *De Block, Groeninckx & Rakotonasolo 2344*; H from *De Block, Groeninckx & Rakotonasolo 2360*; K from *Decary 8084*.

Key to the species of *Phialiphora*

1. Branches densely or, more rarely, sparsely covered with long erect hairs at least at the base; involucrate bracts moderately to densely covered with erect hairs on both surfaces or hairs centred around the base below; ovaries, calyces and fruits at least with some hairs 2
1'. Branches completely glabrous; involucrate bracts glabrous on both surfaces (margins of stipular parts sometimes sparsely ciliate); ovaries, calyces and fruits completely glabrous 3

2. Leaves from the basal rosette pubescent on both surfaces; involucrate bracts with foliar parts 8–20 mm and stipular parts 3–10 mm long; calyx lobes narrowly ovate, 1.2–2 x c. 0.5 mm; corolla tube 5–8 mm long; only upper ½ of ovary densely covered with long erect hairs; endocarp extensions near apical opening of capsule enclosing air-chambers ..... ***P. capitulata***
2'. Leaves from the basal rosette pubescent above, glabrous below; involucrate bracts with foliar parts 5–40 mm and stipular parts 1–4 mm long; calyx lobes broadly ovate, 0.8–2.5 x 1–2.5 mm; corolla tube 3.5–5.5 mm long; ovary densely, moderately or sparsely covered with long erect hairs over most of the surface; endocarp extensions near apical opening of capsule less developed, not enclosing air-chambers ..... ***P. bevazahensis***

3. Involucrate bracts with stipular parts completely fused with the broad bases of the foliar parts or rarely distinct as an ovate sheath up to 1.5 mm long; calyx lobes ovate, leaf-like or broadly triangular, 0.6–1 mm long; corolla tube c. 3.5 mm long; corolla lobes 2.5–3 mm long, inner surface sparsely covered with long thin erect hairs; anthers c. 0.8 mm long ..... ***P. glabrata***
3'. Involucrate bracts with stipular parts distinct as a narrowly ovate to narrowly triangular sheath, 2–3 mm long; calyx lobes narrowly triangular, 2–4 mm long; corolla tube c. 5 mm long; corolla lobes 5–7 mm long, inner surface densely covered with long thin erect hairs; anthers c. 2 mm long ..... ***P. valida***

(imbibition mechanism) (Van der Pijl 1969; van Rheede van Oudtshoorn & van Rooyen 1998). We have no information, however, on whether the apical opening of the capsules in *Phialiphora* occurs in times of rainfall or more generally upon maturation of the fruit. Dispersal of seeds by rain wash has been observed for other Spermacoceae, notably *Oldenlandia* and *Spermacoce*, by Ridley (1930), although he defined rain wash as the washing along of already fallen seeds (there is no mention of rain drops washing seeds out of capsules). It is highly probable that also this type of rain wash occurs in *Phialiphora*, since the plants are often found in patches. The seeds of *Phialiphora* do not become mucilaginous when moistened, as is the case in certain other species of Spermacoceae from dry habitats (Bremekamp 1952).

The loculicidal opening of the fruits continues laterally over the whole length (along vascular bundles) and the fruit splits in half (fig. 6B, E, I, L), further releasing seeds. In *P. capitulata*, each half fruit splits again (septicidal splitting), resulting in quarter fruits (fig. 6F). This septicidal splitting was only observed in *Decary 8084*, a specimen collected in June when the plants are at the end of their life cycle. For the other three *Phialiphora* species, no such mature specimens are available (collections made in January–April) and no septicidal splitting was observed on the herbarium specimens. However, when dissected, the fruits open readily along their entire length both loculicidally and septicidally. We therefore believe that they also split into quarters at a very mature stage. The quarter fruits may function as secondary diaspores for remnant seeds, the persistent calyx lobe aiding wind and water dispersal.

The two new species have the same capsule type as *P. bevazahensis* (fig. 6A–C). They lack the apical air-chambers, formed by extensions of the endocarp, which are present in each quarter capsule of *P. capitulata* (Groeninckx et al. 2009b) (figs 5K, 6D–G). Extensions of the endocarp are also present in the three species lacking air-chambers (figs 5H–J, 6B, I, L) but they are less developed than in *P. capitulata*. The air-chambers probably enhance the dispersal of the quarter capsules of *P. capitulata* by wind or water.

TAXONOMIC TREATMENT

Phialiphora glabrata De Block, **sp. nov.**

Figs 1, 5D–G, I, L, M, 6H–J, 7A, B

Diagnosis – Differing from *Phialiphora bevazahensis* by the glabrous stems, bracts, ovaries, calices and fruits, the generally narrower bracts (2–5 mm wide vs. 4–20 mm wide in *P. bevazahensis*), the shorter corolla lobes (2.5–3 vs. 3–5 mm long) and the smaller capsules (c. 3 × 2–2.3 mm vs. 4.5–6 × 2–3.5 mm with persistent calyx included).

Type – Madagascar: Mahajanga Province, Sofia Region, Bongolava, 15°36′47.2″S, 47°35′19.2″E, 228 m, 18 Mar. 2010, *De Block, Groeninckx & Rakotonasolo 2344* (holotype: BR[BR0000005519347, https://www.botanicalcollections.be/specimen/BR0000005519347]; isotypes: K, MO, TAN).

Description – Annual, semi-succulent, rosulate herb, 5–22 cm tall, often with multiple stems arising from the basal leaf rosette and with a thin taproot; at the end of the life cycle plants sometimes completely coloured reddish (fig. 7A, B); branching cymose and dichasial; stems drying brown to reddish brown, glabrous, smooth, terete in cross-section. Leaves arranged in a basal rosette; blades narrowly obovate, narrowly ovate or narrowly elliptic, 1–7 × 0.25–1.8 cm, semi-succulent, drying green to brown and not discolorous, densely covered with long erect hairs on the upper surface (hairs 0.9–1.3 mm long), glabrous on the lower surface; margins densely ciliate (hairs often shorter and somewhat curved); base broadly attenuate, amplexicaul; tip obtuse or rarely acute; midrib hardly raised below; secondary nerves 3–4 on each side of the midrib, running mostly parallel to the midrib; secondary and higher order nerves often indistinct on either surface. In larger plants, lowermost ramifications subtended by a stipulate leaf pair with blades ± linear, 1.5–2.5 × 0.15–0.3 cm and pubescence identical to that of basal leaves; stipules wider than high, broadly triangular to broadly ovate, c. 1.5–2 mm long, glabrous outside but margin sparsely to densely ciliate (hairs up to 1.3 mm long). Inflorescences either consisting of a single capitulum or composed of several capitula; capitula very compact, with few to up to 20 flowers (rarely single-flowered), subtended by a semi-succulent pair of involucrate bracts, from the axils of which branches may originate which also terminate in capitula; involucrate bracts glabrous on both surfaces, consisting of leaf-like foliar parts and smaller stipular parts, foliar parts narrowly ovate or narrowly triangular, 0.7–3 × 0.2–0.5 cm, stipular parts sometimes sparsely ciliate, ovate to broadly ovate, 1.5–4 mm long, completely fused with the broad bases of the foliar parts (fig. 1D) or rarely forming a distinct ovate sheath up to 1.5 mm long (fig. 1E), nervation prominent abaxially on the stipular parts and the base of the foliar parts (when dry); higher order bracts wider than high, broadly ovate, c. 0.5 × 1 mm, ciliate, tip rounded. Flowers sessile, isostylous, with both anthers and style and stigma exserted at anthesis and reaching ± the same height. Calyx glabrous outside but often with 1 or few colleters in the sinuses of the calyx lobes, glabrous and without colleters inside; tube c. 0.1–0.2 mm long when flowering (up to 0.5 mm long in fruiting stage); lobes often somewhat unequal, with nerves prominent on both surfaces when dry, bases not overlapping, tips acute to obtuse, in flowering stage lobes ovate or leaf-like, often longer than wide, 0.6–1 × 0.7–0.8 mm, in fruiting stage lobes broadly triangular, usually wider than high, 0.6–1 × 1–1.5 mm. Corolla white with bluish hue, pink around the throat; tube narrowly cylindrical, c. 3.5 mm long, glabrous on both surfaces; lobes 2.5–3 mm × c. 1.5 mm, sparsely covered with ± short, robust, erect hairs on the tips outside, sparsely covered with long, thin, erect hairs over the whole surface inside, tips acute to obtuse. Anthers c. 0.8 mm long, bluish; filaments c. 2 mm long. Ovary c. 1 mm long, glabrous, placenta attached to upper half of septum, ovules numerous. Style and stigma white, exserted from the corolla tube for 2–3 mm at anthesis; style glabrous; stigma bilobed, lobes linear, straight, c. 2.5 mm long. Capsules without apical air-chambers, 3–4 × 2–2.3 mm (persistent calyx included), glabrous, opening loculicidally and septicidally, initially only at the apex (loculicidally), later along the entire length of the fruit (loculicidally and septicidally); seeds c. 0.5 × 0.2–0.3 mm, pale brown.

Etymology – *Phialiphora glabrata* is named for the glabrous stems, bracts, ovaries, calyces and fruits.

Habitat – Lowland dry deciduous forest on sand, often in open sunny places with little or no plant growth except for low herbs; alt. 150–250 m.

Distribution – *Phialiphora glabrata* is only known from the Bongolava Key Biodiversity Area, Port Bergé district, Sofia region, in northwestern Madagascar (fig. 3A).

Phenology – Flowering and fruiting in March and April.

Preliminary IUCN assessment – Critically Endangered: CR B1ab(iii) + 2ab(iii). The extent of occurrence (EOO) of *Phialiphora glabrata*, estimated to be 2.6 km^2, and the area of occupancy (AOO), estimated at 8 km^2, fall within the limits of the Critically Endangered category under criterion B1 and B2, respectively. It should, however, be noted that *Phialiphora glabrata* is only known from five specimens and one recent observation (https://www.inaturalist.org/observations/5525768). Geographical coordinates are available for five of the six specimens/observations and represent four unique occurrences. It is likely that a thorough inventory of the dry deciduous forests in northwestern Madagascar could lead to further discoveries of this species, especially since collecting efforts in Madagascar are biased towards woody species. Currently, *Phialiphora glabrata* is known from a single location, Bongolava Key Biodiversity Area, which falls within the limits of the Critically Endangered category under subcriterion 'a' of criterion B2. In 2003, following the Durban Declaration, the Bongolava Forest Corridor was established as a new Protected Area (Gardner et al. 2018). It was managed by the NGO Conservation International (CI) until 2012, when CI withdrew from the region. Currently, Bongolava Forest Corridor is considered a Key Biodiversity Area and is managed by the local organisation FBM (Fikambanana Bongolava Maitso) with very little funding. The main threat to *Phialiphora glabrata* is habitat loss as a result of deforestation for subsistence farming. The local people in the region practice slash and burn agriculture, recently for new crops such as maize, with large parts of the forest being burned to clear land every year (Mahaboubi et al. 2015, Gereti 2017). Habitat degradation with a, probably, lesser impact on *P. glabrata* occurs as a result of illegal logging for timber, charcoal production and the collection of firewood and forest products (Grounded 2019). A decline in the extent and quality of the habitat of *Phialiphora glabrata* is estimated. Based on this information, *Phialiphora glabrata* is assessed as Critically Endangered.

Additional material examined – **Madagascar**: Mahajanga Province. Sofia Region. Bongolava, 15°36′42.8″S, 47°35′32.7″E, 185 m, 18 Mar. 2010, *De Block, Groeninckx & Rakotonasolo 2339* (BR[BR0000005519811, https://www.botanicalcollections.be/specimen/BR0000005519811], TAN) & *2340* (BR[BR0000005519712, https://www.botanicalcollections.be/specimen/BR0000005519712], TAN); Bongolava, 15°36′49.2″S, 47°35′21″E, 215 m, 18 Mar. 2010, *De Block, Groeninckx & Rakotonasolo 2342* [BR (BR0000005519644, https://www.botanicalcollections.be/

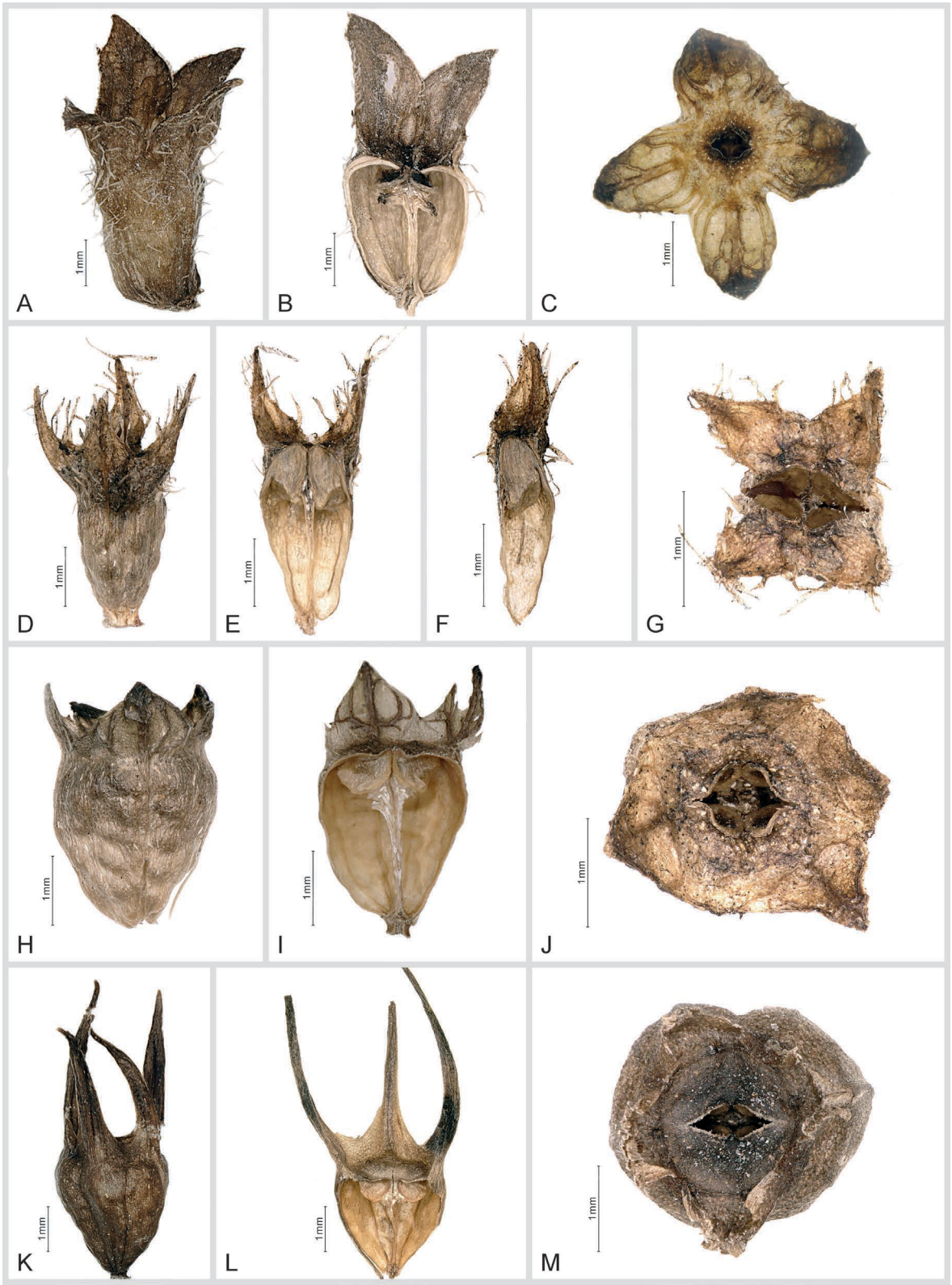

Figure 6 – Capsules in *Phialiphora*. **A**–**C**. *P. bevazahensis*; **D**–**G**. *P. capitulate*. **H**–**J**. *P. glabrata*. **K**–**M**. *P. valida*. **A**, **D**, **H**, **K**. Lateral view. **B**, **E**, **I**, **L**. Half capsule, showing endocarp outgrowths at the apex. Note that the outgrowths in *P. capitulata* are more extensive and enclose an air-chamber. **C**, **G**, **J**, **M**. View from above showing the apical opening of the capsules. **F**. Quarter capsule. A, B from *De Block, Groeninckx & Rakotonasolo 2360*; C from *Groeninckx Rakotonasolo & De Block 254*; D–G from *Decary 8084*; H, I from *De Block, Groeninckx & Rakotonasolo 2342*; J from *De Block, Groeninckx & Rakotonasolo 2344*; K–M from *De Block, Groeninckx & Rakotonasolo 2349*.

specimen/BR0000005519644), TAN]; Bongolava, N de Majunga, Apr. 1967, *Morat 2654* (P, TAN).

Additional observation record – Sofia region, Port Bergé district, Andranomena commune, Bongolava Key Biodiversity Area, Rakotonasolo, 19 Mar. 2017 (see photograph at: https://www.inaturalist.org/observations/5525768).

Phialiphora valida De Block, **sp. nov.**

Figs 2, 5A–C, J, 6K–M, 7C

Diagnosis – Similar to *Phialiphora glabrata* by the glabrous stems, bracts, ovaries, calyces and fruits; differing from this species by the greater height (20–40 cm tall vs. 5–22 cm tall in *P. glabrata*) and more robust habit, the longer calyx lobes especially in fruiting stage (narrowly triangular, 2–4 × 0.5–1 mm vs. broadly triangular to ovate, 0.6–1 × 0.7–1.5 mm), the longer corolla tube (c. 5 mm vs. c. 3.5 mm long), corolla lobes (c. 5–7 mm vs. 2.5–3 mm long) and anthers (c. 2 mm vs. c. 0.8 mm long) and the densely pubescent inner surface of the corolla lobes (vs. sparsely pubescent in *P. glabrata*).

Type – Madagascar: Mahajanga Province, Sofia Region, Bongolava, 15°36′53.7″S, 47°35′13″E, 242 m, 18 Mar. 2010, *De Block, Groeninckx & Rakotonasolo 2349* (holotype: BR[BR0000005519354, https://www.botanicalcollections.be/specimen/BR0000005519354]; isotypes: K, MO, P, TAN).

Description – Annual, semi-succulent, rosulate herb, 20–40 cm tall, with multiple stems arising from the basal leaf rosette and with a taproot of more than 10 cm long; branching cymose and dichasial; stems drying brown or pale brown, glabrous, smooth, terete in cross-section. Leaves arranged in a basal rosette; blades narrowly obovate, narrowly ovate, narrowly elliptic or narrowly oblong, 3–7.5 × 0.4–1 cm, semi-succulent, drying brownish and not discolorous, densely covered with long erect or spreading hairs on the upper surface (hairs 0.9–1.3 mm long), glabrous on the lower surface; margins densely ciliate (hairs often shorter and somewhat curved); base broadly attenuate, amplexicaul; tip acute to obtuse; midrib raised below when fresh (less so in dried condition); secondary nerves 3–4 on each side of the midrib,

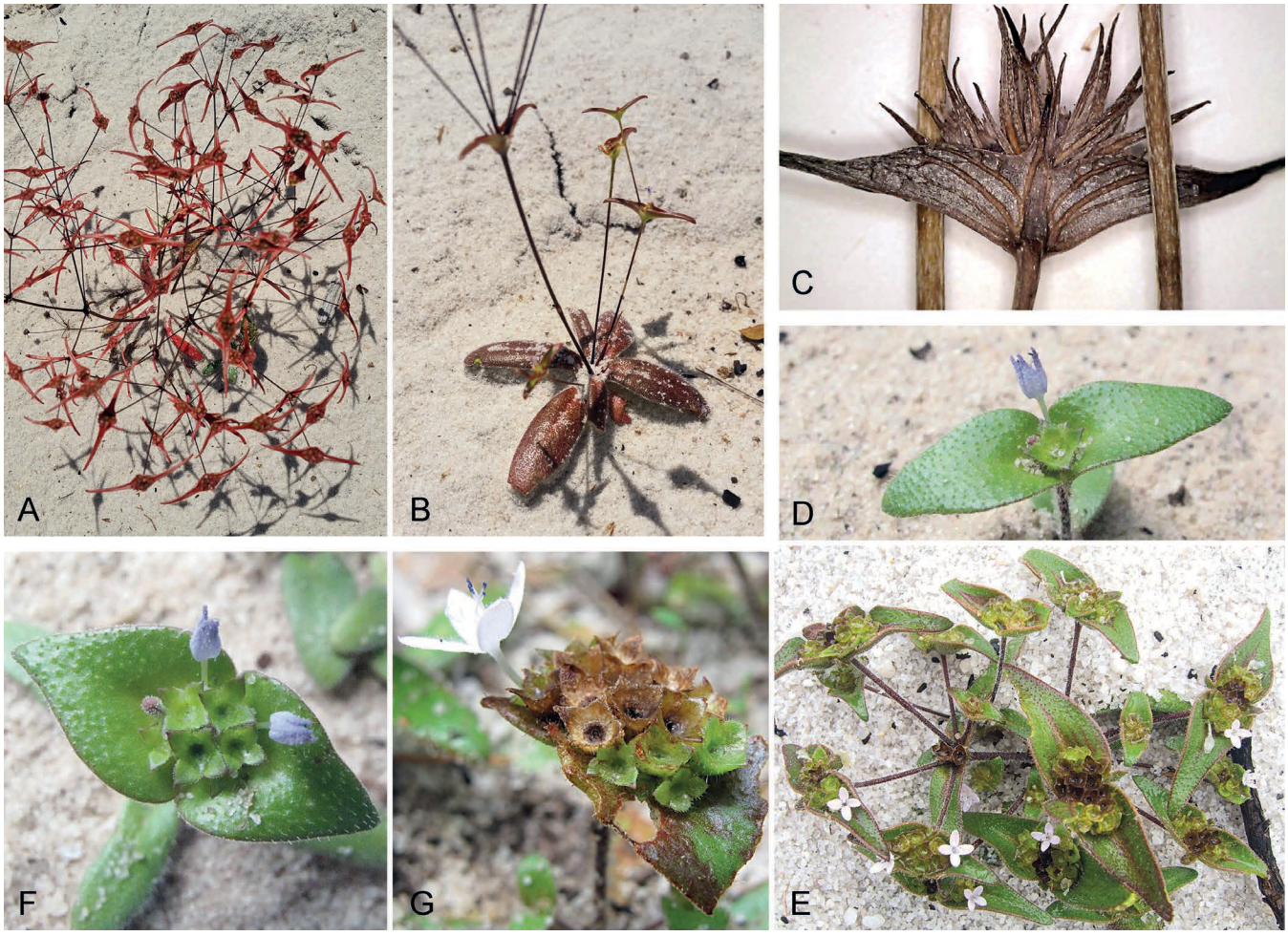

Figure 7 – *Phialiphora* species. **A**–**B**. Habit of *P. glabrata.* **C**. Involucrate capitulum (herbarium material) of *P. valida*, note the long, narrowly triangular calyx lobes. **D**–**G**. *P. bevazahensis.* **D**. Plant in its simplest form, consisting of a pair of basal leaves, a branch and an involucrate capitulum. **E**. Habit of a well-developed plant. **F**. Involucrate capitulum at flowering stage. **G**. Involucrate capitulum at fruiting stage, note the blue anthers and the mature, open (brown) capsules. Photographs: F. Rakotonasolo (A, B); P. De Block (C–E); I. Groeninckx (F, G).

running mostly parallel to the midrib; secondary and higher order nerves often indistinct on either surface. Lowermost ramifications subtended by stipulate leaf pair with blades ± linear, 1–3 × 0.2–0.3 cm and pubescence identical to that of basal leaves; stipules wider than high, triangular with acute tip or more rarely broadly ovate with rounded tip, c. 1.5–2 mm long, glabrous outside but sometimes with a few hairs on the margin near the tip or the base. Inflorescences either consisting of a single capitulum or composed of several capitula; capitula very compact, with few to up to 20 flowers (rarely single-flowered), subtended by a semi-succulent pair of involucrate bracts, from the axils of which branches may originate which also terminate in capitula; involucrate bracts glabrous on both surfaces, consisting of leaf-like foliar parts and smaller stipular parts, foliar parts narrowly ovate or narrowly triangular, 1.3–2.2 × 0.2–0.5 cm, stipular parts forming distinct, narrowly ovate to narrowly triangular, 2–3 mm long and sometimes ciliate sheaths, nervation prominent abaxially and adaxially on the stipular parts and on the base of the foliar parts (when dry); higher order bracts mostly absent, if present then narrowly triangular to linear, 7–8 × 1–1.5 mm, glabrous on both surfaces but with a few long hairs on the margins at the base, tip acute. Flowers sessile, isostylous, with both anthers and style and stigma exserted at anthesis and reaching ± the same height. Calyx glabrous outside but often with one or few colleters in the sinuses of the calyx lobes, glabrous and without colleters inside; tube c. 0.1–0.2 mm long when flowering (up to 0.3 mm long in fruiting stage); lobes often somewhat unequal, narrowly triangular, with midrib and 1 pair of basal secondary nerves prominent on both surfaces when dry, bases not overlapping, tips acute, rarely tipped by a single trichome, in flowering stage lobes 2–2.5 × c. 0.5 mm, in fruiting stage lobes 3–4 mm × 0.5–1 mm. Corolla white; tube narrowly cylindrical, c. 5 mm long, glabrous on both surfaces; lobes 5–7 × 2–3 mm, sparsely covered with ± short, robust, erect hairs on the tips outside, densely covered with long thin erect hairs over the whole surface inside, tips acute. Anthers c. 2 mm long; filaments c. 1.5 mm long. Ovary c. 1.5 mm long, glabrous, placenta attached to upper half of septum, ovules numerous. Style and stigma white, exserted from the corolla tube for c. 5 mm at anthesis; style glabrous; stigma bilobed, lobes slender, straight, 2.5–3 mm long. Capsules without apical air-chambers, 2–3 × c. 2 mm (6–7.5 × c. 2 mm with persistent calyx included), glabrous, opening loculicidally and septicidally, initially only at the apex (loculicidally), later over the complete length of the fruit (loculicidally and septicidally); mature seeds unknown.

Etymology – *Phialiphora valida* is named for its height and robustness.

Habitat – Lowland dry deciduous forest on sand, in open sunny places with little or no plant growth except for low herbs; alt. c. 250 m.

Distribution – *Phialiphora valida* is only known from the Bongolava Key Biodiversity Area, Port Bergé District, Sofia Region, in northwestern Madagascar (fig. 3B).

Phenology – Flowering and fruiting in March.

Preliminary IUCN assessment – Critically Endangered: CR B2ab(iii). The extent of occurrence (EOO) of *Phialiphora valida* cannot be calculated because only one specimen has been collected. Its area of occupancy (AOO) is 4 km^2, which falls within the limits of the Critically Endangered category under criterion B2. Clearly, this species is severely undercollected. However, it likely occurs in a single location, the Bongolava Key Biodiversity Area, which falls within the limits of the Critically Endangered category under subcriterion 'a' of criterion B2. Similar to *P. glabrata*, the main threat to *P. valida* is habitat loss as a result of deforestation for subsistence farming. For a discussion on the location and the threats, see *P. glabrata*, but based on the habitat degradation *P. valida* is assessed as Critically Endangered.

Critical remarks – The species is only known from the type collection.

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