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## *Benna alternifolia* (Melastomataceae: Sonerileae), a new herbaceous genus and species from Guinea, West Africa

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**Abstract:** *Benna* is a new monospecific genus in the *Melastomataceae*, from the Benna Plateau in Forécariah Prefecture in Guinea, West Africa. Molecular sequence data show the genus *Benna* is nested within the tribe *Sonerileae* but clearly unrelated to the other African *Sonerileae* genera. The genus is weakly supported as sister to the South American *Sonerileae* genus *Phainantha*. Similarities and differences with African and American *Sonerileae* genera are listed. The new species *Benna alternifolia* is a perennial evergreen herb, half-spherical in shape, up to 1.2 m in diameter. A plant may have up to 60 alternate leaves, with petioles up to 45 cm long and blades up to 31 × 28 cm. The flowers are actinomorphic, with 4 sepals and 4 pink petals, 8 dimorphic stamens, and an inferior 4-locular ovary. The fruit is a capsule. The seeds are obovoid or nearly so, with a smooth testa. *Benna alternifolia* occurs in deep shade in canyons, on vertical or overhanging sandstone rocks out of reach of falling rain drops, and only where water is seeping all year round, including during the 6-month dry season. About 680 plants were found. *Benna alternifolia* is assessed to the IUCN category Near Threatened.

**Keywords:** Africa, alternate leaves, *Benna*, Guinea, *Melastomataceae*, Near Threatened, new genus, *Sonerileae*

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### Introduction

The Benna Plateau, or Benna Gadyah in the Susu language, is a sandstone plateau up to 1190 m high in the Forécariah and Kindia Prefectures in Guinea, West Africa. The plateau rises high above the villages of Dalonia and Gombokori, which are at 120 m altitude. The name Benna does not appear on any maps, and the exact location is therefore not well known except to villagers living on and around the plateau. The plateau was visited by several plant collectors in the 20<sup>th</sup> century, as demonstrated from specimens in GBIF (2021) and Kew's herbarium specimen database. The French naturalist Henri Jacques-Félix collected there several times in 1937 and returned in 1956. A number of plant taxa were described from collections made on the Benna Plateau; five of these were named after the plateau: *Bafodeya benna* (Scott Elliot) Prance ex F. White, *Ctenium bennae* Xanthos, *Heterosamarra bennae* (Jacq.-Fél.) Paiva, *Impatiens bennae* Jacq.-Fél., and *Mesanthemum bennae* Jacq.-Fél.

The BR, L and P herbaria do not hold any specimens collected in the past 60 years on the Benna Plateau (GBIF 2021), and staff of the National Herbarium of Guinea are not aware of any recent collecting expeditions, which suggests that the area may not have been visited by plant collectors in the past 60 years. When the first two authors prepared an expedition to the area, in February 2019, a rocky area with vertical cliffs and canyons was observed on Google Earth (2019). In these canyons, a plant species with large leaves, belonging to the *Melastomataceae*, was found occurring in shade on vertical rock. These plants did not resemble any species and genus known to the collectors, who have collected many plants in West and Central Africa. It was therefore immediately understood that the plants might represent an undescribed genus and species. Plants with leaves and flower buds were collected. On the next expedition, in October–November 2019, two collections with leaves, old fruits and seeds were collected in two canyons 4.3 km apart.

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We studied the three *Melastomataceae* specimens from the Benna Plateau by morphological and molecular analyses. Our studies confirmed that the species is new and cannot be placed in any existing genus of *Melastomataceae*. We present a phylogenetic tree showing the position of the new genus compared to related genera, and determine in which tribe the new genus should be placed. The morphology of the new genus is compared with that of related genera. We provide a description of the new species, an illustration, photographs and a distribution map.

## Material and methods

Expeditions to the Benna Plateau were planned using Google Earth (2019) imagery. Herbarium collections were immediately dried overnight on a portable gas dryer. Photographs of plants were taken with an Olympus Tough TG5. Research permits were obtained in advance of the expeditions, and export permits for the herbarium and seed collections were obtained before their export (see Acknowledgements). The three herbarium collections were morphologically compared with herbarium collections of *Melastomataceae* genera found at K and images of specimens on GBIF (2021). All herbarium specimens cited have been studied by the authors. Flower buds from one of the three collections were dissected and observed with a light microscope. Plant terminology follows Beentje (2016). The distribution map was prepared with Geocat (2021). An IUCN Red List assessment was made according to the methodology in IUCN (2012, 2019).

*Phylogenetic inference* — A total of 245 accessions representing all currently accepted *Melastomataceae* tribes were sampled for the phylogenetic placement of the theorized new species and genus. All African (including Madagascar) endemic genera (including type species) currently placed in the *Sonerileae* were sampled: *Amphiblemma* Naudin 12 of all 15 species were sampled, *Calvoa* Hook. f. 8/19, *Cinnobotrys* Gilg 4/8, *Dicellandra* Hook. f. 2/3, *Gravesia* Naudin 25/116 and *Preussiella* Gilg 1/2. Seventeen *Medinilla* Gaudich. species, from mainland Africa (1), Madagascar (4) and Asia (12), were also sampled. *Feliciadamia* Bullock could not be sampled; the genus was placed in *Feliciadamiaceae* by Jacques-Félix (1994). A total of 46 species of Asian *Sonerileae* and a single species of each of three American *Sonerileae* genera, *Boyania* Wurdack, *Phainantha* Gleason and *Tryssophyton* Wurdack, were also sampled. As outgroup, 105 species representing the remaining currently accepted *Melastomataceae* tribes were included.

Total genomic DNAs were extracted, amplified and sequenced as described in Veranso-Libalah & al. (2017, 2018, 2020). We amplified and sequenced two nuclear loci (the nuclear ribosomal internal transcribed spacer (nrITS) and the nuclear ribosomal external transcribed spacer (nrETS)) and three plastid loci (*accD-psaI*, *psbK-*

*psbL* and *ndhF*), which have been widely used in phylogenetic studies across the *Melastomataceae* (Michelangeli & al. 2004, 2008, 2011, 2013; Kriebel & al. 2015; Reginato & Michelangeli 2016; Rocha & al. 2016; Veranso-Libalah & al. 2017, 2018, 2020; Guimarães & al. 2019; Kartonegoro & al. 2021). Additional sequences were obtained from GenBank.

Using SEQUENCHER v.4.1.4 (Gene Codes Corporation, Ann Arbor, MI, U.S.A.), contigs of forward and reverse sequences were assembled and manually edited. Sequences were aligned using MAFFT v.7 (Katoh & Standley 2013) and then manually adjusted in MESQUITE v.3.10 (Maddison & Maddison 2016). The best-fit substitution model for each aligned locus was determined using the Akaike information criterion (AIC) in JMODELTEST 2.1.4 (Darriba & al. 2012). The GTR+ G model was suggested as the most appropriate nucleotide substitution models for nuclear and plastid datasets.

Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed using the CIPRES Science Gateway v.3.3 (<https://www.phylo.org/>, Miller & al. 2010). Phylogenetic analyses were initially conducted on the plastid (*ndhF*, *psbK-psbL* and *accD-psaI*) and nuclear (nrETS and nrITS) datasets using the ML and BI methods. Gene trees from the plastid and nuclear datasets revealed no well-supported topological conflicts. As such, all further analyses were performed using the concatenated 5-loci data set (*ndhF*, *psbK-psbL*, *accD-psaI*, nrETS and nrITS). Maximum likelihood analyses were performed using RAxML v.8 (Stamatakis 2014) with a GTRGAMMA model of sequence evolution. The ML analyses were conducted using default parameters in RAxML (Stamatakis 2014) with 1000 bootstrap replicates (Felsenstein 1985).

The BI analyses were performed using BEAST v.2.5.0 (Bouckaert & al. 2019). Four independent Markov chain Monte Carlo (MCMC) analyses were run, each of 30 million generations sampling every 3000 generations. All xml files were prepared using BEAUTI and ran on the CIPRES Science Gateway v.3.3 (<https://www.phylo.org/>, Miller & al. 2010). We used TRACER v.1.6 (Rambaut & Drummond 2013) to assess convergence and effective sampling size (ESS) of all parameters from the output log files. As burn-in, 25% of samples were removed prior to combining the independent runs using LOGCOMBINER v.2.5. (Bouckaert & al. 2019). A maximum clade credibility tree was constructed using TREEANNOTATOR v.2.5. (Bouckaert & al. 2019) and node support was expressed as posterior probability (PP).

## Results

*Phylogenetic placement* — Molecular sequence data obtained from two of the three collections, Burgt & al. 2274 and 2323, suggests they are nested within the tribe *Sonerileae* (Fig. 1). The two collections are unrelated to



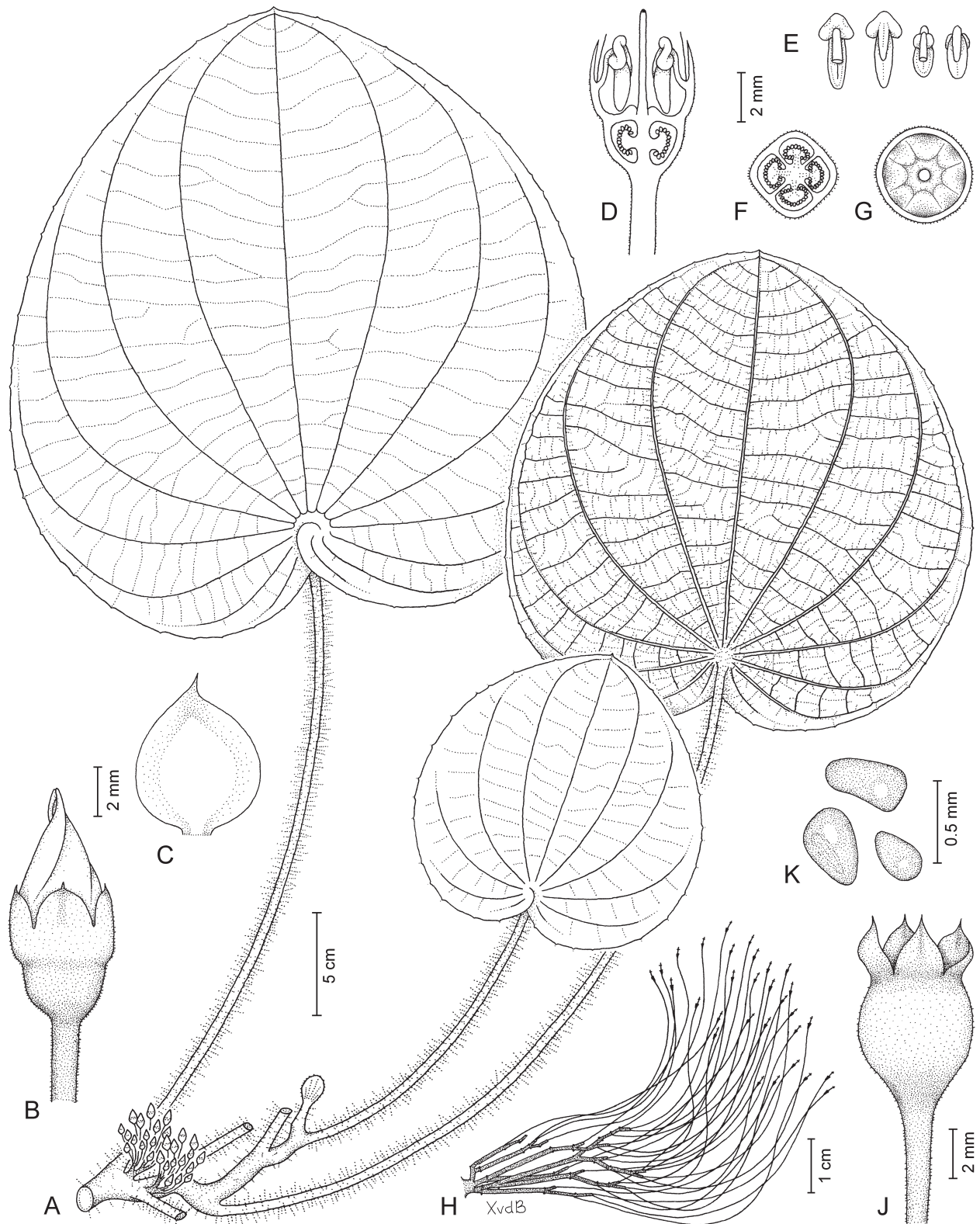


Fig. 2. *Benna alternifolia* – A: branch showing alternate leaf arrangement, with two inflorescences and seven leaves: five mature leaves of which three removed, a young leaf, and a very young leaf; B: flower bud; C: petal inner surface; D: flower bud in longitudinal section with petals partly removed; E: large stamen back and front, small stamen back and front; F: ovary of flower bud in transverse section; G: ovary of flower bud seen from above; H: old infructescence with fruits partly decomposed; J: fruit; K: seeds. – Origin: A from Burgt & al. 2274 (type gathering) and Burgt & al. 2323; B–G from Burgt & al. 2274; H–K from Burgt & Haba 2333. – Drawing by Xander van der Burgt.





Fig. 3. *Benna alternifolia* – A: the largest population was found in a deep canyon, of which the upper part is visible at the centre of the photograph, on a 1040 m-high hill on the Benna Plateau; B: plants in their habitat, on vertical rock in deep shade, under overhanging rocks, out of reach of falling rain drops, but within reach of permanently seeping water; C: group of four plants; D: single plant. – Origin: A, C from *Burgt & al.* 2274 (type gathering); B from *Burgt & al.* 2323; D from *Burgt & Haba* 2333. – All photographs by Xander van der Burgt.

the other African (including Madagascan) *Sonerileae* genera (Fig. 1), all of which were sampled in the present study. They are weakly supported (BS 57%) as sister to the South American genus *Phainantha*. Of the six currently accepted American *Sonerileae* genera, only three genera were sampled in the present study.

**Morphology** — The three collections from the Benna Plateau, *Burgt & al.* 2274, 2323 and *Burgt & Haba* 2333, clearly belong in *Melastomataceae*, shown by the leaf blade with 11–15 veins all starting from the top of the petiole (Fig. 2, 3, 4), as well as by the characters of the flower buds and fruits, which match the family description given by Utteridge & Bramley (2015). On morphological grounds, the three collections are placed in the *Sonerileae*; all other *Melastomataceae* tribes can be ruled out. For example, the three collections are not in the *Melastomateae* (the most diverse tribe in Africa) because the seeds are not cochleate. Most *Sonerileae* are herbaceous plants of shady habitats, with capsular, apically dehiscent fruits (Renner 1993), as are the plants from which the three collections were made (Fig. 2, 3). Morphologically, the three collec-

tions are different from all African (including Madagascan) *Melastomataceae* species, including all species in the seven currently accepted African *Sonerileae* genera. A morphological comparison between the three collections and these seven genera is presented in Table 1. The three collections also do not match any of the currently accepted American and Asian *Melastomataceae* genera. Leaves such as those of the three collections occur in a number of species outside of Africa, for example in *Ochtheophilus repentinus* Wurdack (*Merianieae*), *Quipuanthus epipetricus* Michelang. & C. Ulloa (*Cyphostyleae*) and *Tigridiopalma magnifica* C. Chen (*Sonerileae*), but the structure of the inflorescences and flowers of these species is very different.

A morphological comparison between all six American *Sonerileae* genera and the three collections from the Benna Plateau is presented in Table 2. African *Sonerileae* usually have 4- or 5-merous flowers with a 4- or 5-locular ovary (Table 1), but American species are typically anisomerous, having a 4-, 5- or 6-merous flowers with a 3-, 4- or 5-locular ovary with exceptions in *Tateanthus* Gleason and *Phainantha* (Table 2). We conclude from both morphological and molecular analysis that the three





Fig. 4. *Benna alternifolia* – A: leaf upper surface; B: leaf lower surface; C: inflorescence with flower buds; D: roots. – Origin: A, D from Burgt & Haba 2333; B, C from Burgt & al. 2274 (type gathering). – All photographs by Xander van der Burgt.

collections from the Benna Plateau, Burgt & al. 2274, 2323 and Burgt & Haba 2333, represent a new, monotypic genus. The genus is named *Benna* Burgt & Ver.-Lib. and the species is named *Benna alternifolia* Burgt & Ver.-Lib. in the taxonomy section of the present manuscript.

## Discussion

*Melastomataceae* are a pantropical family, with c. 160 genera, c. 5000 species and tropical centres of diversity in South America and SE Asia (Utteridge & Bramley 2015). Guinea has c. 63 *Melastomataceae* species in 27 genera, counted from specimens in GBIF (2021) and Kew's herbarium specimen database. Four genera are endemic or near-endemic to Guinea, as well as monospecific. The three endemic species are *Benna alternifolia*, *Cailliella praerupticola* Jacq.-Fél. and *Feliciadamia stenocarpa* (Jacq.-Fél.) Bullock (Lisowski 2009), while the near-endemic *Anaheterotis pobeguinii* (Hutch. & Dalziel) Ver.-Lib. & G. Kadereit (Veranso-Libalah & al. 2017) occurs also in Sierra Leone.

*Sonerileae* are a very diverse tribe that occurs in SE Asia (c. 800 species in 31 genera), Madagascar (184/2),

Africa (excluding Madagascar, 55/7) and America (12/6) (Michelangeli & al. 2020). It is remarkable that the closest relatives of the genus *Benna* occur in tropical America, because the *Sonerileae* diversity is much lower than in tropical Africa and Asia. There are other examples of African plants having South American affinities. Guinea, one of the African countries situated closest to the American continent, has several remarkable examples. In Guinea occur two near-endemic American families with a single species that is native outside America: *Bromeliaceae*, represented in Africa by the Guinea endemic species *Pitcairnia feliciana* (A. Chev.) Harms & Mildbr., and *Rapateaceae*, represented in Africa by the West African endemic species *Maschalocephalus dinklagei* Gilg & K. Schum. occurring from Guinea to Ivory Coast. These two species originated by long-distance seed dispersal from the American continent (Givnish & al. 2004; Renner 2004), as was hypothesized by Hepper (1965), Thorne (1973) and Brenan (1978). Another example of a Guinean plant species with South American affinities is *Calophyllum africanum* Cheek & Q. Luke (*Clusiaceae*). This species was described as endemic to Mali (Cheek & Luke 2016) but has been collected in 2019 on the Benna Plateau and several other places in Guinea by the first

two authors of the present study. The hypothesis is here proposed that the presence of *B. alternifolia* in Guinea is the result of a long-distance seed dispersal event from the American continent. This dispersal route is also similar for the tribe *Melastomateae* (Veranso-Libalah & al. 2018).

*Melastomataceae* species generally have an opposite leaf arrangement. Anisophylly occurs commonly, especially in *Sonerileae*, for example in *Amphiblemma* (Jacques-Félix 1974a) and *Cincinnobotrys* (Jacques-Félix 1976). The existing three collections of *Benna alternifolia* show no signs of anisophylly at all, and therefore the hypothesis is proposed here that the leaves are alternate. Future studies of living plants and of additional, new collections might confirm this hypothesis or determine that the leaf arrangement of *Benna* is an extreme example of anisophylly.

An alternate leaf arrangement, such as in *Benna alternifolia* (Fig 2A), is uncommon among *Melastomataceae*. A search for *Melastomataceae* species on IPNI (2021) and POWO (2021) with the species name *alternifolia*, *alternifolium* or *alternilamina*, resulted in five accepted species, from four different genera and tribes: *Bertolonia alternifolia* Baumgratz, Amorim & A. B. Jardim (*Bertoloniaeae*), *Blakea alternifolia* Gleason (*Blakeeae*), *Heteroblema alternifolium* (Blume) Cámara-Leret, Ridd.-Num. & Veldkamp (*Sonerileae*), *Miconia alternifolia* (Griseb.) Alain and *Miconia alternilamina* Michelang. (*Miconieae*). The tendency toward an alternate leaf arrangement seems to have originated independently among these lineages; as such, the alternate leaf arrangement of *Benna alternifolia* does not indicate in which tribe the species may be placed. There are more species with a tendency toward an alternate leaf arrangement among the c. 5000 *Melastomataceae* species. *Medinilla mirabile* (Gilg) Jacq.-Fél. may have alternate leaves on the lower part of the stem, while the leaves are verticillate on the upper stem (Hutchinson & Dalziel 1954, Jacques-Félix 1983). The species of *Cincinnobotrys* are small herbs with short stems and internodes. The degradation of one of the two leaves of a pair (Jacques-Félix 1976) gives the appearance of an alternate leaf arrangement. Species in the genus *Phainantha*, the hypothesized sister-group of *Benna*, may have opposite leaves, but the leaves more frequently appear alternate through abortion of one of the leaves of a pair (Ulloa Ulloa & Neill 2006). In *Phainantha*, all leaves on one side of the stem are replaced by climbing roots (Renner 1993: 527).

The alternate branching of the inflorescence in *Benna alternifolia* is not common among African *Melastomataceae*; however, in *Amphiblemma molle* Hook. f., the inflorescence is a uniparous cyme bearing alternate, subsessile flowers (Jacques-Félix 1974a). Among the African *Melastomataceae*, scorpioid cymes are very common as well as restricted to *Sonerileae*; but the inflorescence of *B. alternifolia* is not scorpioid. *Sonerileae* more rarely have paniculate cymes (Renner 1993: 532), as in *B. alternifolia*.

## Taxonomy

***Benna* Burtg & Ver.-Lib., gen. nov.**

Type: *Benna alternifolia* Burtg & Ver.-Lib.

**Diagnosis** — The genus *Benna* differs from all other African *Melastomataceae* genera by the following combination of characters: Herbs. Leaves alternate, venation acrodromous, margin dentate. Inflorescence cymose, paniculate, axillary, branching alternate. Flowers actinomorphic, epigynous, 4-merous, 8 dimorphic stamens. Fruit a capsule, apically dehiscent, containing many seeds. Seeds obovoid or nearly so, glossy, testa smooth. The genus *Benna* is placed in the tribe *Sonerileae*. A morphological comparison between *Benna* and the seven currently accepted African *Sonerileae* genera is presented in Table 1. A morphological comparison between *Benna* and the six currently accepted American *Sonerileae* genera is presented in Table 2.

***Benna alternifolia* Burtg & Ver.-Lib., sp. nov.** – Fig. 2, 3, 4.

Holotype: Guinea, Forécariah Prefecture, slopes of Benna Plateau, 3 km W of Gombokori village, 09°44'06"N, 12°49'00"W, 770 m, flower buds, 11 Feb 2019, *Burtg, Haba, Konomou & Xanthos* 2274 (HNG; isotypes: K001381567, MO, P, WAG).

**Description** — Herbs, perennial, evergreen, half-spherical in shape, up to 1.2 m in diam., with up to 60 leaves per plant. *Roots* woody; thin roots up to 0.5 m × 4 mm, radiating on rock surface and attaching plant to rock; thick roots up to 10 m × 2 cm, entering rock fissures in search of permanent water seepage, bark deeply fissured, up to 5 mm thick. *Stems* somewhat woody, branched from base, pendent, circular in cross-section, up to 28 cm × 6–12 mm, reddish green, densely to sparsely hairy with red hairs up to 4 mm long, puberulent with red glandular hairs up to 0.1 mm long; internodes up to 3 cm long, leaf petiole pointing in same direction as internode just below it. *Leaves* alternate; petiole succulent, 15–45 cm × up to 6 mm, reddish green to bright red, densely hairy to glabrescent with red hairs up to 7 mm long, puberulent with red glandular hairs up to 0.1 mm long; leaf blade round to ovate, 12–31 × 10–28 cm, shrinking a little during drying, lower surface dull glaucous light green, upper surface glossy green, both surfaces puberulent with red glandular hairs up to 0.1 mm long, veins below with red hairs up to 5 mm long; leaf base deeply cordate, left or right half of leaf base often overlapping other half; leaf margin dentate, teeth with a single red hair up to 4 mm long, distance between teeth 4–24 mm; leaf apex rounded, mucronate; leaf venation acrodromous, 11–15 veins all starting from top of petiole, central vein straight, other veins curved, otherwise similar in appearance to primary vein, secondary and tertiary venation scalariform, venation on lower surface prominent, light red, on upper



Table 1. Morphological comparisons of the new genus *Benna* with all seven *Sonerileae* genera occurring in Africa (including Madagascar): *Amphiblemma* (Jacques-Félix 1974a), *Caboa* (Figueiredo 2001), *Cinnibotrys* (Jacques-Félix 1976), *Dicellandra* (Jacques-Félix 1974b), *Gravesia* (Naudin 1851), *Medinilla* (Gaudichaud-Beaupré 1829–1830) and *Preussiella* (Jacques-Félix 1977). The dash (–) indicates unknown data.

| Characters/character states | <i>Benna</i>             | <i>Amphiblemma</i>                         | <i>Caboa</i>  | <i>Cinnibotrys</i>             | <i>Dicellandra</i>                    | <i>Gravesia</i><br>(excluding Madagascar) | <i>Medinilla</i><br>(African)           | <i>Preussiella</i>            |
|-----------------------------|--------------------------|--|---|--------------------------------|---------------------------------------|---|---|-------------------------------|
| Habit                       | herbs, epiphytes on rock | herbs, shrubs                              | herbs, shrubs, epiphytes                            | herbs                          | shrubs, epiphytes                     | shrubs, perennial herbs                   | shrubs, epiphytes                       | shrubs generally epiphytic    |
| Leaf arrangement            | alternate                | opposite, anisophyllous frequent           | opposite  | appearing anisophyllous        | opposite                              | opposite                                  | opposite, verticillate                  | opposite, decussate           |
| Leaf shape                  | round to ovate, cordate  | ovate, lanceolate, cordate                 | elliptic, ovate, lanceolate, oblanceolate, rhomboid | broadly ovate to orbicular     | broadly ovate-lanceolate, elliptic    | lanceolate, elliptic-oblong               | oblong-lanceolate, elliptic             | ovate-lanceolate              |
| Inflorescence               | cymose, paniculate       | cymose, thyse                              | scorpioid, cymose                                   | cymose or few-flowered         | thyse                                 | cymose, thyse                             | cymose                                  | uniparous, cymose, thyse      |
| Hypanthium                  | cupuliform               | campanulate, tubular                       | campanulate, obconic, tubular                       | campanulate                    | turbinate                             | obconic                                   | cupulate-pateiliform, globose-ellipsoid | obconic                       |
| Petal number                | 4                        | 5  | 5   | 4 or 5                         | 5                                     | 5   | 4                                       | 5                             |
| Stamen number               | 8                        | 10   | 10  | 8–10                           | 10                                    | 10  | 8                                       | 10                            |
| Stamen type                 | dimorphic                | dimorphic                                  | isomorphic or slightly unequal                      | isomorphic or slightly unequal | dimorphic                             | isomorphic                                | isomorphic                              | isomorphic                    |
| Stamen appendage            | 3-lobed                  | simple, 2-lobed, absent                    | squamiform  | emarginate                     | 2-lobed                               | 1-lobed                                   | 2-lobed, subulate                       | spatulate, clavate            |
| Ovary                       | inferior                 | inferior                                   | inferior  | inferior                       | inferior                              | inferior                                  | inferior                                | inferior                      |
| Locules number              | 4                        | 5  | 3–5   | 4 or 5                         | 5                                     | 5   | 4                                       | 5                             |
| Capsule shape               | urceolate                | globose, campanulate-urceolate, ± 5-angled | campanulate, cylindrical, sometimes ribbed          | campanulate                    | turbinate, ellipsoid                  | 5-angled                                  | globose, bacciform/urceolate            | 5-angled                      |
| Capsule apex                | –                        | crateriform formed by crown of scales      | with accrescent exerted scales                      | apically depressed             | crateriform formed by crown of scales | surrounded by 5 firm accrescent scales    | convex                                  | absent                        |
| Capsule dehiscence          | apical                   | valvate                                    | loculicidal and/or septicidal                       | apical                         | irregular                             | –   | apical                                  | loculicidal and/or septicidal |
| Seed                        | obovoid or nearly so     | oblong, ovoid-ellipsoid                    | oblong or obovoid                                   | obovoid-cuneate                | obconic                               | –   | oblong-cuneate/cuneate                  | linear funicle                |

Table 2. Morphological comparisons of the new genus *Benna* with all six *Sonerileae* genera occurring in tropical America: *Boyania* (Maguire & Wurdack 1964), *Nebelinanthera* Wurdack (Maguire & Wurdack 1964), *Opisthocentra* Hook. f. (Bentham & Hooker 1867), *Phainantha* (Ulloa & Neill 2006), *Tateanthus* (Gleason 1931) and *Tryssophyton* (Maguire & Wurdack 1964; Wurdack & Michelangeli 2019). The dash (–) indicates unknown data.

| Characters/character states | <i>Benna</i>             | <i>Boyania</i>                                 | <i>Nebelinanthera</i> | <i>Opisthocentra</i>   | <i>Phainantha</i>                           | <i>Tateanthus</i>               | <i>Tryssophyton</i>                           |
|-----------------------------|--------------------------|--|-----------------------|------------------------|---|---------------------------------|---|
| Habit                       | herbs, epiphytes on rock | stoloniferous or climbing herbs                | shrubs                | shrubs                 | trailing herbs, woody or epiphytic climbers | shrubs                          | rhizomatous herbs                             |
| Leaf arrangement            | alternate                | opposite                                       | opposite              | opposite               | opposite or alternate in appearance         | opposite                        | verticillate; opposite pairs of subequal size |
| Leaf shape                  | round to ovate, cordate  | broadly ovate or suborbicular                  | ovate                 | ovate                  | ovate-elliptic                              | elliptic or broadly ovate       | ovate to lanceolate                           |
| Inflorescence               | cymose, paniculate       | apically dichasia with subscorpioid branchlets | paniculate            | cymose or pauciflorous | cymose-paniculate or umbellate              | cymose                          | 1–4 flowers                                   |
| Hypanthium                  | cupuliform               | campanulate                                    | –                     | campanulate            | terete with a calyptra                      | conic-obovoid, broadly 5-winged | campanulate, obscurely costate                |
| Petal number                | 4                        | 5  | 6                     | 4                      | 4   | 5                               | 4   |
| Stamen number               | 8                        | 10   | 12                    | 8                      | 8   | 10                              | 8   |
| Stamen type                 | dimorphic                | isomorphic                                     | dimorphic             | isomorphic             | dimorphic                                   | isomorphic                      | slightly anisomorphic                         |
| Anther dehiscence           | –                        | apical-ventral pore                            | apical pore           | –                      | small apical pore                           | single ventral terminal pore    | terminal pore                                 |
| Connective appendage        | ventral                  | dorsal/ventral                                 | dorsal                | dorsal/ventral         | dorsal/ventral                              | –                               | ventral                                       |
| Ventral appendage           | 3-lobed                  | squamiform                                     | –                     | –                      | cordiform                                   | –                               | thickened annulus c. ventrally 2-lobed        |
| Ovary                       | inferior                 | superior                                       | superior              | inferior               | superior                                    | inferior                        | superior                                      |
| Locules number              | 4                        | 4 or 5   | –                     | 3                      | 4   | 5                               | 3 or 4  |
| Capsule shape               | urceolate                | 4- or 5-angled                                 | –                     | –                      | 4-angled with ribs                          | globose with wings              | 6–8-angled                                    |
| Capsule apex                | –                        | 4- or 5-lobed                                  | –                     | summit roundly 5-lobed | –   | summit roundly 5-lobed          | crowned by persistent calyx                   |
| Capsule dehiscence          | apical                   | septicidal                                     | –                     | –                      | loculicidal                                 | loculicidal                     | septicidal and loculicidal                    |
| Seed                        | obovoid or nearly so     | ovoid  | –                     | pyramidal              | –   | narrowly fusiform               | ovoid (bertolonoid type)                      |

surface flattened, light red. *Inflorescence* cymose, paniculate, axillary, up to 4 cm long when in bud, with up to c. 70 flower buds, branching alternate; peduncle up to 1 × 3 mm, internodes 0.5–15 mm long; bracts and bracteole persistent, lanceolate, c. 1 mm long; peduncle and rachides red, puberulent with red glandular hairs up to 0.1 mm long. *Flowers*: flower buds 4-merous, epigynous; pedicel up to 24 mm long, red, puberulent with red glandular hairs up to 0.1 mm long; hypanthium cupuliform, c. 4 × 4 mm, light reddish green, puberulent with red glandular hairs up to 0.1 mm long, part of hypanthium free from ovary c. 2 mm long; calyx lobes 4, free, triangular, c. 1.5 × 2.5 mm, light green with pink apex, puberulent with red glandular hairs up to 0.2 mm long, margin ciliate, apex mucronate, mucro c. 0.3 mm long; petals 4, free, convolute, overlapping counter-clockwise when viewed from above, alternate to sepals, round to ovate, in bud c. 6 × 5 mm, light pink, both surfaces and margin glabrous, acuminate with acumen c. 1 mm long, claw c. 0.5 × 1 mm; stamens 8, fertile, actinomorphic, dimorphic, glabrous; 4 antisepalous stamens: filaments c. 2 mm long, connective with a 3-lobed appendage, c. 2 × 2 mm, anther c. 3 × 1 mm, with 2 loculi; 4 antipetalous stamens: filaments c. 1 mm long, connective with a 3-lobed appendage, c. 1 × 1 mm, anther c. 2 × 1 mm, with 2 loculi; ovary inferior, in bud c. 2 mm long, 4-locular, loculi opposite sepals, each locule with c. 100 ovules; style straight, in bud c. 4 mm long, glabrous, stigma punctiform. *Infructescence* up to 9 cm long, with up to 70 fruits, peduncle up to 1 × 4 mm, internodes 0.5–18 mm long, lower internodes up to 2 mm long, middle internodes up to 18 mm long, upper internodes up to 5 mm long; bracts and bracteole caducous; peduncle and rachides red, puberulent with red glandular hairs up to 0.1 mm long. *Fruit* a capsule, urceolate, 4–5 × 3–4 mm, glabrescent, calyx persistent, fruit apically dehiscent, crown lobes not seen; fruit pedicel 20–60 mm long. *Seeds* up to 400 per fruit, obovoid or nearly so, 0.4–0.5 × 0.3–0.4 mm, glossy, testa smooth, yellow to light brown.

*Phenology* — *Benna alternifolia* flowers in February–March and fruits a few months later. Old, decaying fruits containing ripe seeds may remain on the plants until November, because the plants are little disturbed by wind and rain in their sheltered habitat.

*Distribution* — *Benna alternifolia* is endemic to Guinea (Fig. 5) and occurs in Forécariyah Prefecture near border with Kindia Prefecture, in canyons of the Benna Plateau near villages Dalonia and Gombokori.



Fig. 5. Distribution of *Benna alternifolia*, blue dots. Map data © Google 2021.

*Habitat and ecology* — *Benna alternifolia* occurs on vertical sandstone rock, in deep shade in canyons 10–100 m deep (Fig. 3), and on vertical sandstone rock in deep shade of trees, at 300–800 m altitude. Plants occur only under overhanging rocks (Fig 3B), out of reach of falling rain drops, and only on vertical rock where water is seeping all year round, within reach of the several-meter-long roots. In this habitat, the perennial, evergreen, herbaceous plants, which do not have a rootstock, can continue to grow during the six-month dry season.

*Benna alternifolia* is often found together with *Cinchinobotrys felicitis* (A. Chev.) Jacq.-Fél. (*Melastomataceae*), *Impatiens bennae* (*Balsaminaceae*) and *Mesanthemum bennae* (*Eriocaulaceae*). On the same vertical rocks, but higher up and in sunny, seasonally dry habitat, two plant species endemic to Guinea occur abundantly: *Cailliella praerupticola* (*Melastomataceae*) and *Pitcairnia feliciana* (*Bromeliaceae*), the only member of the family that is native outside America.

*Conservation status* — *Benna alternifolia* is currently known only in the Benna Plateau in Forécariyah Prefecture. The collectors searched for the species elsewhere in the region, without success. The habitat of the species was found to occur widespread in an expanse of sandstone plateaus occupying much of Coyah, Dubreka, Forécariyah and Kindia Prefectures in Guinea (Fig. 5), but the species was not found. The Benna Plateau is currently unprotected and was not proposed as a TIPA (Tropical Important Plant Area) by Couch & al. (2019), because the exact location of the Benna Plateau was unknown to



the authors at the time of that publication. The Benna Plateau is rich in rare plant species and is proposed here to become a TIPA.

The extent of occurrence of *Benna alternifolia* was 3.4 km<sup>2</sup> and the area of occupancy was 12 km<sup>2</sup>, both calculated with Geocat (2021). The extent of occurrence is changed to 12 km<sup>2</sup>, because it should not be smaller than the area of occupancy (IUCN 2019). The number of locations is two. These values may become larger if the species is found in other canyons. The species currently does not seem exposed to any threats. The habitat where the species occurs is free of fire. There are no known mineral deposits in the vicinity. Plants were only found in remote canyons where they will not be threatened by rock quarrying. In absence of any threats to the species, IUCN (2012) categories A, B and C are not eligible. About 680 mature individuals of *B. alternifolia* were found. There exist probably more than 1000 mature individuals, because some canyons in and near the Benna Plateau are yet to be explored. The species may be close to qualifying for the IUCN (2012) Red List category Vulnerable under criterion D1, which has a threshold of 1000 mature individuals, and *B. alternifolia* is therefore assessed here in the IUCN category Near Threatened.

*Seed conservation* — Seeds were collected from 12 plants of *Burgt & Haba 2333* and are stored in the seed bank of the National Herbarium of Guinea in Conakry (c. 250 seeds) and at Kew's Millennium Seed Bank (also c. 250 seeds).

*Etymology* — The genus is named for the Benna Plateau or Benna Gadyah in the Susu language. The Benna Plateau holds the only known locations for the species. The specific epithet refers to the alternate leaf arrangement.

*Vernacular name* — In the Susu language, the name of *Benna alternifolia* is Labalaba Khamè or Labalaba Hamey, which means “male soft leaf”. The name Labalaba is given to *Piper umbellatum* L. (Burkill 1997, vol 4: p. 441), a herb with leaves similar in size and appearance. On the Benna Plateau, *Piper umbellatum* is named Labalaba Guinë, which means “female soft leaf”.

*Additional specimens examined* — GUINEA: Forécariyah Prefecture, canyon at base of Benna Plateau, 3.5 km N of Dalonia village, 09°41'53"N, 12°50'03"W, 330 m, fruits, 26 Oct 2019, *Burgt, Haba & Holt 2323* (B, HNG, K, MO, P, WAG); slopes of Benna Plateau, 3.5 km W of Gombokori village, 09°44'07"N, 12°49'26"W, 810 m, fruits, 1 Nov 2019, *Burgt & Haba 2333* (HNG, K).

## Author contributions

SM hosted the research and arranged the research and plant export permits. XvdB planned the plant collecting expedi-

tions. XvdB and PMH led the plant collecting expeditions. XvdB performed the morphological analysis and wrote the description. MCVL performed the molecular analysis and verified the morphological analysis. All authors commented on the manuscript and approved the final version.

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### Supplemental content online

See <https://doi.org/10.3372/wi.52.52102>

Appendix 1. GenBank accession numbers for sequences used in the phylogenetic placement of the genus *Benna*.

Sequence alignments of nrITS, nrETS, *accD-psaI*, *psbK-psbL* and *ndhF* in Nexus format, used for the phylogenetic placement of the genus *Benna*.

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