A MONOGRAPH OF *OPERCULINA* (CONVOLVULACEAE)[1]

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ABSTRACT

A comprehensive systematic monograph is presented for the genus *Operculina* Silva Manso (Convolvulaceae). Formerly included in tribe Merremieae D. F. Austin, now incertae sedis, recent systematic studies have clarified the phylogenetic relationships for *Operculina* and unequivocally demonstrated that it is monophyletic as currently circumscribed and that the unique operculate capsule is a synapomorphy for the genus. Other morphological characters useful for recognizing the genus are: large sepals forming a "pear-shaped" calyx that is broad at the base and tapers upward; calyx that is accrescent and persistent, often cupping the mature fruit; strongly spirally coiled anthers after dehiscence; and axial parts of the plant body (stems, petioles, peduncles, pedicels) that are often prominently winged. The current monograph accepts 13 species, including one variety and one purported hybrid; these taxa are distributed throughout the tropics globally. The hybrid is proposed to accommodate the extraordinary phenotypic variability and intermediacy among South Pacific populations of *Operculina*. The monograph provides detailed descriptions for all taxa, as well as an identification key, distribution maps, and summaries of ecology, phenology, vernacular names, and uses, with comments on synonymy, typification, variability, biology, and conservation, where appropriate. All names published or combined in *Operculina* (about 60 epithets) are accounted for as accepted names, synonyms, misapplied names, or uncertain names, or are excluded from the genus. New reductions to synonymy are proposed as follows: *O. brownii* Ooststr. becomes a synonym of *O. codonantha* (Benth.) Hallier f.; *O. tansaensis* Santapau & V. Patel becomes a synonym of *O. ventricosa* (Bertero) Peter. Lectotypes, neotypes, and epitypes are designated where necessary to stabilize names in current use. An index to numbered collections examined is provided to aid in specimen identification and herbarium curation.

Key words: Convolvulaceae, generic delimitation, hybrid, nomenclature, *Operculina*, plant systematics, typification.

Historically the generic delimitation for Convolvulaceae has been problematic for centuries: while species are often readily recognized and delineated, meaningful generic concepts have proven elusive. What we characterize as "agglomerative taxonomy" (Simões & Staples, 2017)—the grouping together of superficially similar species into "genera"—has been a common practice throughout the history of studies for Convolvulaceae. Over the course of time, the agglomeration of superficially similar species leads to genus concepts that are highly polymorphic (not to mention non-monophyletic), and when enough exceptions to the generic character states accumulate, the "genus" becomes undiagnosable.

However, in recent years the application of more rigorous cladistic methods and molecular phylogenetics has begun to change our understanding of generic

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delimitation, and progress has been made in untangling the end products of agglomerative taxonomy, defining instead monophyletic lineages, to which the nomenclature then has to be reconciled. For example, systematic study of *Porana* Burm. f. and tribe Poraneae Hallier f. (Staples, 2006) showed that on morphological grounds *Porana*, as historically conceived, was highly polyphyletic. There was ample morphological evidence to support recognition of four segregate genera: *Dinetus* Buch.-Ham. ex Sweet, *Duperreya* Gaudich., *Poranopsis* Roberty, and *Tridynamia* Gagnep., plus a much narrowed *Porana* s. str. (Staples, 2006). Molecular phylogenetic analysis (Stefanović et al., 2002) largely corroborated the new generic delimitation and went even further, showing that these segregate genera were not all members of the same tribe: *Porana* s. str. was removed to tribe Dichondreae (Choisy) Choisy, while *Dinetus*, *Poranopsis*, and *Tridynamia* were assigned to a new tribe, Cardiochlamyeae Stefanović & D. F. Austin (Stefanović et al., 2003). The available phylogenetic evidence indicated these two tribes are not closely related at all, an unexpected outcome at that time, but a harbinger of things to come.

An analogous situation existed with *Merremia* Dennst. ex Endl. and tribe Merremieae D. F. Austin (Simões et al., 2015; Simões & Staples, 2017). *Merremia*, as historically conceived, comprised slightly more than 100 species worldwide (Staples, 2010), and the included species encompassed such great morphological diversity that the genus had become undiagnosable. There was no single character that united all 100+ species of *Merremia*, there being some exceptions at species level to any generic character chosen to define and delimit the genus concept. A comprehensive morphological and molecular phylogenetic analysis of the tribe (Simões et al., 2015) showed that multiple monophyletic lineages were present within the "genus" *Merremia* s.l. and these were subsequently recognized as monophyletic, clearly diagnosable genera: *Camonea* Raf., *Decalobanthus* Ooststr., *Distimake* Raf., and a much narrowed *Merremia* s. str. (Simões & Staples, 2017). The monophyly of tribe Merremieae could not be proven (Stefanović et al., 2002; Simões et al., 2015), and for that reason the tribe has been dissolved and the constituent genera considered to be incertae sedis (Simões & Staples, 2017).

We anticipate that similar patterns and outcomes will be found for additional genera in Convolvulaceae that have been shaped by agglomerative taxonomy, such as *Bonamia* Thouars, which was already shown to be polyphyletic based on molecular phylogenetic analysis with limited taxon sampling (Stefanović et al., 2002).

Molecular phylogenetic evidence (Simões et al., 2015) showed incontrovertibly that *Operculina* Silva Manso was a strongly supported monophyletic genus, a welcome point of stability in the face of so many other taxonomic upsets and recircumscriptions. And somewhat surprising also because of the ambiguous status *Operculina* has had throughout its taxonomic history. We present here a systematic revision for *Operculina*, the first of several indicated by Simões and Staples (2017), which synthesizes the available molecular, morphological, and palynological data for the first time on a global basis for all known species.

Taxonomic History

The development over time of *Operculina* as a genus concept mirrors the evolution of taxonomic concepts and practices in taxonomy of Convolvulaceae as a whole.

Two species now considered to belong in *Operculina* were first named by Linnaeus (1753): *Convolvulus turpethum* L. and *C. macrocarpus* L. For the next 80-plus years these species, and others described after, were retained in the Linnaean genera *Convolvulus* L. or *Ipomoea* L. Silva Manso (1836: 49), in a treatise about medicinal plants from Brazil, first proposed a new genus for *C. turpethum* because that species has a fruit type that he characterized as "a transition from capsule to drupe." He first called the unique fruit structure an "operculum," but later in the same work (Silva Manso, 1836: 49) revised this term to "sarcocarpus." The generic name *Operculina* references the dehiscent cap, the *operculum*, that detaches from this unusual fruit type. Silva Manso made a new combination for the Linnaean species, *C. turpethum*, as *O. turpethum* (L.) Silva Manso, and also diagnosed a second species, *O. convolvulus* Silva Manso, now considered a synonym of *O. macrocarpa* (L.) Urb.

Other generic names soon followed. Bojer (1837) published *Spiranthera*, a mixed concept that included species now referred to three genera: *Decalobanthus* (*D. peltatus* (L.) A. R. Simões & Staples), *Distimake* (*D. aegyptius* (L.) A. R. Simões & Staples), and *Operculina* (*O. turpethum*). However, "*Spiranthera* Bojer" is invalid (nomen nudum) and would be illegitimate because there is an older *Spiranthera* A. St.-Hil. (1823, Rutaceae). A year after Bojer, Rafinesque (1838) published in his *Flora Telluriana* two generic names that are (at least possibly) referable to *Operculina*. Although Rafinesque's work shows the date of 1836 on the title page, the pages in Part IV containing the Convolvulaceae were actually printed in mid-1838 (Barnhart, 1907; Stafleu & Cowan, 1983), so Rafinesque's generic names post-date *Operculina*. *Turpethum* Raf. (Rafinesque, 1838: 71) created new combinations for two previously named species, both of which are now synonyms of *O. turpethum*; the genus name *Turpethum* is accordingly a nomenclatural synonym for *Operculina*. The second genus, *Nemanthera* Raf. (Rafinesque, 1838: 80), was founded solely on *Convolvulus bufalinus* Lour., an ambiguous species concept that has never been resolved because no original material (specimen nor illustration) has been found, and the protologue is sufficiently vague that the name can neither be clearly applied nor reduced to synonymy. Thus, various authors have taken up the epithet *bufalina* in multiple genera, or set it aside as ambiguous in favor of later-published names that could be applied more precisely. Merrill (1935: 327) pointed out that *N. bufalina* (Lour.) Raf. must be a synonym for some species of *Ipomoea* or *Merremia* but did not typify the basionym and so left the entire situation unresolved. We rectify this situation by proposing rejection for *C. bufalinus* Lour. (Staples et al., 2017) and, informally at least, reduce *Nemanthera* to synonymy under *Operculina*. Finally, a few years later, Reichenbach (1841) published the genus name *Piptostegia* Rchb., which was soon reduced under *Operculina* (Meisner, 1869) and disappeared from general usage.

The question of priority for *Operculina* versus other generic names aside, there was no general agreement in botanical literature, for about 60 years after Silva Manso proposed it, that the genus was distinct from *Ipomoea* or *Convolvulus*. Among those works rejecting *Operculina* in favor of dispersing the species to other genera were Wight (1837), Steudel (1841), Choisy (1845), Miquel (1857), Grisebach (1864), Bentham and Hooker (1873), and Clarke (1883), among others.

However, with passage of time, some authors did accept *Operculina* as a distinct genus: Meisner (1869), Peter (1891), Schlepegrell (1892), Hallier (1893), and Svedelius (1906) among them. Peter (1891) is the only author to have recognized sections within *Operculina*. He recognized three sections, *Pteropodae* Peter, *Apterae* Peter, and *Digitatae* Peter, based chiefly on two features: leaves entire versus palmately lobed and presence versus absence of wings on the axis of the inflorescence.

Hallier (1893) made the first comprehensive study of the Convolvulaceae on a global basis, incorporating thorough examination of the anatomy and pollen in addition to macromorphology. He concluded that *Operculina* should be recognized as a distinct genus, firstly based on the circumscissile, operculate capsule being a unique character in the family. Hallier placed *Operculina* in close proximity to *Merremia*, both having non-spinulose pollen grains, and more distant from *Ipomoea*, with spinulose pollen. However, these three genera are similar in having a single style, two biglobose stigmas, and large, showy flowers, similarities which contributed to the ambiguity in generic placement over the following century and more.

In his generic diagnosis for *Operculina*, Hallier (1893: 582) pointed out that, in addition to the unique fruit type, other distinguishing characteristics often present are the winged stem, petioles, and peduncles; the ventricose "pear-shaped" calyx that is greatly enlarged in fruit; and the spirally contorted anthers. In his concept of *Operculina*, the genus included 15 species distributed throughout the tropics. Ironically, we recognize very close to the same number of species that Hallier did, but the current species composition diverges widely. About half the species Hallier included in his generic concept have later been shown to belong in other genera. In fact, missing stages in the life cycle (no mature fruits available for study) combined with the misinterpretation of fruit structure (when pressed on herbarium sheets the fruits are crushed and frequently difficult to interpret correctly) led Hallier to combine in *Operculina* some species that would today be referred to *Decalobanthus*, *Distimake*, and *Merremia*; these species lack the operculate capsule that defines *Operculina*. Despite some mistakes in his interpretation of the characters at species rank, Hallier's generic concept for *Operculina* was well-reasoned and is essentially congruent with our own contemporary understanding. Later, Hallier (1911: 21–22) realized that some of the species he had placed in *Operculina* actually belonged in *Merremia* (and vice versa), and he corrected several of his mistakes (as well as those made by House, 1906), making reductions or new combinations as necessary and citing specimens to document his changed understanding of the generic placements for each species.

In the decades following Hallier's synthesis of generic relationships and tribal classification for Convolvulaceae, some authors followed his system of generic concepts and adopted *Operculina*, including, among others, House (1906), Ooststroom (1939, 1953), O'Donell (1950), Meeuse (1957), Macbride (1959), Heine (1963), and Verdcourt (1963). However, other authors rejected *Operculina* and continued to disperse the constituent species among the genera *Ipomoea*, *Merremia*, or *Convolvulus*: Kuntze (1898), Baker and Wright (1904), Baker and Rendle (1905), and Gagnepain and Courchet (1915) among them.

Through the mid-20th century the situation regarding generic concepts in Convolvulaceae remained unstable and ambiguous, with lack of universal acceptance for *Operculina*. The boundaries between *Operculina*, *Merremia*, and *Ipomoea* remained unclear and porous: over time the same species had frequently been classified in all three genera, and the accepted names in current use were confused by cases of over-description. This led Staples, supervised by Austin, to investigate generic delimitation between these three genera for a master's thesis project (Staples, 1979), exploring non-traditional characters such as cotyledons and stigma micromorphology to determine whether they were taxonomically informative. Those findings and observations are summarized and included in this revision. We also clarified some generic delimitation issues (Austin & Staples, 1980; Staples & Austin, 1981; Austin & Staples, 1983), and since that time we have accepted *Operculina* as a genus distinct from *Merremia* in our own floristic and systematic publications, including Austin and Ghazanfar (1979), Austin (1980, 1982a, 1982c, 1998a, 2001), Austin and Cavalcante (1982), Fang and Staples (1995), Staples and Yang (1998), Staples (2010, 2018), Simões et al. (2011), Austin et al. (2012), and Staples and Syahida-Emiza (2015), among others.

The end result of this complex evolution of taxonomic concepts is that information about the genuine *Operculina* species is widely dispersed today in regional taxonomic treatments, such information is found under multiple names, and no comparative study of the bona fide species across the full distribution range has ever been attempted. A contemporary and comprehensive systematic revision that seeks to rectify these problems and synthesize available information is timely.

PHYLOGENETIC RELATIONSHIPS

Operculina was included (along with *Merremia*, *Convolvulus*, and *Jacquemontia* Choisy, among others) in tribe Convolvuleae (Choisy) Choisy by Hallier (1893), and subsequent publications accepted this arrangement until the later 20th century. Austin (1982a) first named and characterized tribe Merremieae and assigned several genera to it. Early molecular phylogenetic studies (Stefanović et al., 2002) suggested that Merremieae is not a monophyletic group and indicated that the genus *Merremia* is polyphyletic. More comprehensive species-level sampling from all genera in tribe Merremieae (Simões et al., 2015) resolved several monophyletic lineages within the historically circumscribed *Merremia* s.l. In consequence, the vague and confusing concept of *Merremia* s.l. was broken up and several distinct monophyletic genera recognized (Simões et al., 2015; Simões & Staples, 2017). These findings enabled a clearer and more precise delimitation of all genera formerly included within Merremieae and underscored that *Operculina* is a well-supported genus: this same molecular phylogenetic analysis showed *Operculina* is monophyletic with 100% support (Simões et al., 2015).

The first molecular phylogenetic study to include *Operculina* (Stefanović et al., 2002) sampled two species—*O. pteripes* (G. Don) O'Donell and *O. turpethum*—plus an unidentified sample, referred to as *Operculina* sp.; these three samples were resolved in a monophyletic group with strong support, sister to a clade that included *Hewittia* Wight & Arn. and *Xenostegia* D. F. Austin & Staples. This suggested the monophyly of *Operculina*, but with such limited sampling (three out of an estimated 15 species), and one of the samples not identified to species rank, the monophyly could not be established with confidence. We decided to examine the voucher specimens cited by Stefanović et al. (2002) for those *Operculina* samples to make an independent verification of the taxonomic identifications. We located the voucher for *O. pteripes*, *B. Hammel 18628* (MO), and found it was correctly determined by D. F. Austin in 1992. We failed to locate the voucher for *O. turpethum*, *Wang 867* (MO), during a visit to MO; however, a duplicate of *Wang 867* in GH is here confirmed as *O. turpethum*. And the voucher cited for the unidentified *Operculina*, *G. Romero 1701* (GH), actually proved to be the species known until recently as *Merremia maypurensis* Hallier f., which seemed, at first, to call into question the inclusion of this sample in the *Operculina* clade with such strong support.

In a later and more species-rich molecular phylogenetic study, Simões et al. (2015) significantly increased the taxon sampling of *Operculina* (10 out of the 14 named species) and included a sample of *Merremia maypurensis* from a different source (voucher: *Gröger & Llamozas 1145* at M). The results unequivocally demonstrated that *Operculina* is monophyletic and that *M. maypurensis* is correctly nested in this clade. As in Stefanović et al. (2002), the genus *Operculina* was resolved as sister to the clade that included *Hewittia* and *Xenostegia*, as well as *Hyalocystis* Hallier f. and a number of African species of *Merremia* (Simões et al., 2015) (Fig. 1).

Following these results, a revised classification of *Merremia* and allied genera was proposed (Simões & Staples, 2017) that maintained *Operculina*, enumerated the accepted species, summarized the global distribution, and provided a key to distinguish *Operculina* from the other genera formerly assigned to tribe Merremieae.

METHODS

This monographic study began in the 1970s when Austin and Staples prepared a draft account of *Operculina* for the Neotropics, which was never published. Preliminary papers derived from Staples's M.Sc. dissertation explored the West Indian taxa (Staples & Austin, 1981; Austin & Staples, 1983). The Neotropical study was later expanded by Staples for the Asian (Fang & Staples, 1995; Staples, 2010, 2018; Staples & Syahida-Emiza, 2015) and Pacific species (Staples, 2007). Simões worked on the systematics and evolution of tribe Merremieae, which included *Operculina*, for her Ph.D. thesis (2009–2013). Her molecular phylogeny analyzed DNA samples for 10 species (out of 14 taxa in the genus), which provided conclusive evidence that *Operculina* is a monophyletic group and is one of the best supported genera that had been included in the tribe Merremieae (Simões et al., 2015). Simões and Staples further augmented and finalized the revision after Austin's death in 2015, synthesizing all

Figure 1. Phylogenetic tree for former tribe Merremieae. Modified from Simões et al. (2015), based on combined phylogenetic analyses of chloroplast and nuclear markers. Some of the larger clades and genera are condensed as triangles for ease of interpretation. The clade where *Operculina* Silva Manso is resolved is represented in full with no taxa excluded nor any of the subclades condensed. In the *Operculina* clade the Bayesian posterior probabilities (PP) are indicated above the corresponding node; PP values below 85 are not presented.

data—morphological, palynological, ecological, molecular—gathered over nearly 40 years. More than 1300 herbarium collections were examined from herbaria worldwide including: A, AAH, AAU, ALCB, ANDA, ARIZ, ASU, B, B-W, BCU, BISH, BK, BKF, BM, BO, BR, C, CANB, CEN, CGMS, CHR, CICY, COL, DS, E, ECON, F, FAU, FOF, G, G-DC, G-PREL, GH, GOET, GUAM, H, HAST, HBG, HITBC, HN, HNL, HNMN, HNU, HUEFS, IAN, INB, INPA, IPA, K, KEP, KKU, KUN, L, LINN, LINN-HS, LPB, M, MA, MBK, MO, NA, NY, P, P-Bonpland, P-JU, P-LA, PAP, PE, PEUFR, PSU, PTBG, RAF, QBG, S, SAN, SAR, SING, SINU, SP, TAI, TCD, TEPB, TEX, TO, U, UB, UC, UPS, US, USF, USZ, W. It is unfortunate that two of the most important regional herbaria for the South Pacific, BSIP and SUVA, have been closed for many years and their collections were not accessible. All specimens studied have been entered in a BRAHMS database, and in the late stages of writing the revision this database comprised 635 *Operculina* collections from the Americas; 663 from Asia/Pacific; and 42 from Africa, Madagascar, and the Indian Ocean islands, for a total of 1340 collections.

The BRAHMS database was used to generate the distribution maps through the QGIS (QGIS, 2020) interface; to compile the geographic distribution summary, ecology, elevation, phenology, vernacular names, and ethnobotanical uses; and to generate the exsiccatae lists for each species, as well as the comprehensive index to specimens examined. Additional information on type specimen images and related literature was retrieved from JSTOR Global Plants (<http://plants.jstor.org/>) and TROPICOS® (<http://www.tropicos.org/>).

Field study of living plants was performed by Staples in Brazil, China, Indonesia, Laos, Malaysia, Taiwan, Thailand, and the United States. Cultivated plants for study were grown in the living collections of Florida Atlantic University, U.S.A.; Singapore Botanic Gardens, Singapore; and the Collection Nationale des Convolvulacées, Chatenay-Malabry, France.

For practical purposes of taxon delimitation (de Queiroz, 2007) in writing descriptions and the key we recognize taxa based on shared morphological similarity between individuals (or specimens) and discriminate morphological gaps that separate taxa. This concept works very well for most of the *Operculina* specimens available, allowing for some variability in phenotypes within the same species. However, two extraordinary circumstances where the morphological information presents ambiguous results are mentioned following the summary of Morphology.

Finally, a note about limitations on our morphological observations is warranted: it has not been possible to examine internal floral structures (androecium and gynoecium) for every species because this requires destructive sampling to open the corolla and expose these organs. Understandably, curators do not always permit researchers to do this. Consequently, some gaps remain in the summary of Morphology as well as in the descriptions because we did not have adequate material available, or permission, to dissect flowers on herbarium sheets. It is worth pointing out that the impression gained at this time, based on dried herbarium material with imperfectly preserved internal floral parts, is that future targeted investigations of stigmas and androecium characters using fresh or spirit-preserved flowers will likely lead to recognition of new, taxonomically informative characters derived from the micromorphology of the stigma surfaces and the presence, nature, distribution, and abundance of the staminal filament trichomes. Our preliminary observations, based on limited taxon sampling and by no means comprehensive, suggest that stigma characters are informative for generic delimitation (Staples, 1979), whereas the filament trichomes are highly species-specific.

Morphology

This brief morphological summary is based primarily on dried pressed herbarium specimens augmented by observations for living plants of six species: *Operculina hamiltonii* (G. Don) D. F. Austin & Staples, *O. macrocarpa*, *O. petaloidea* (Choisy) Ooststr., *O. pinnatifida* (Kunth) O'Donell, *O. riedeliana* (Oliv.) Ooststr., and *O. turpethum*. *Operculina* follows the fundamental ground plan common to many genera of Convolvulaceae: herbaceous or woody twiners with alternate leaves, no tendrils, and inflorescences composed of cymose units bearing flowers with radially symmetrical sympetalous corollas.

HABIT

All species are stem twiners where support is available on which to climb (Fig. 2A–C); when support is absent, the plants grow as prostrate creepers. The stems twine sinistrally, and there are no tendrils or other climbing aids present. Most species are perennial. *Operculina aequisepala* (Domin) R. W. Johnson was reported by Johnson (1980) to be an annual; *O. pinnatifida* is described by collectors as having perennial roots and annual stems; and several species have no data recorded about plant habit or duration.

INDUMENTUM

The indumentum in *Operculina* comprises three distinct types of trichomes: simple hairs, sessile glands, and various types of elongate glandular hairs (Svedelius, 1906). Most trichomes on the vegetative plant body are simple and unicellular, varying in density across the

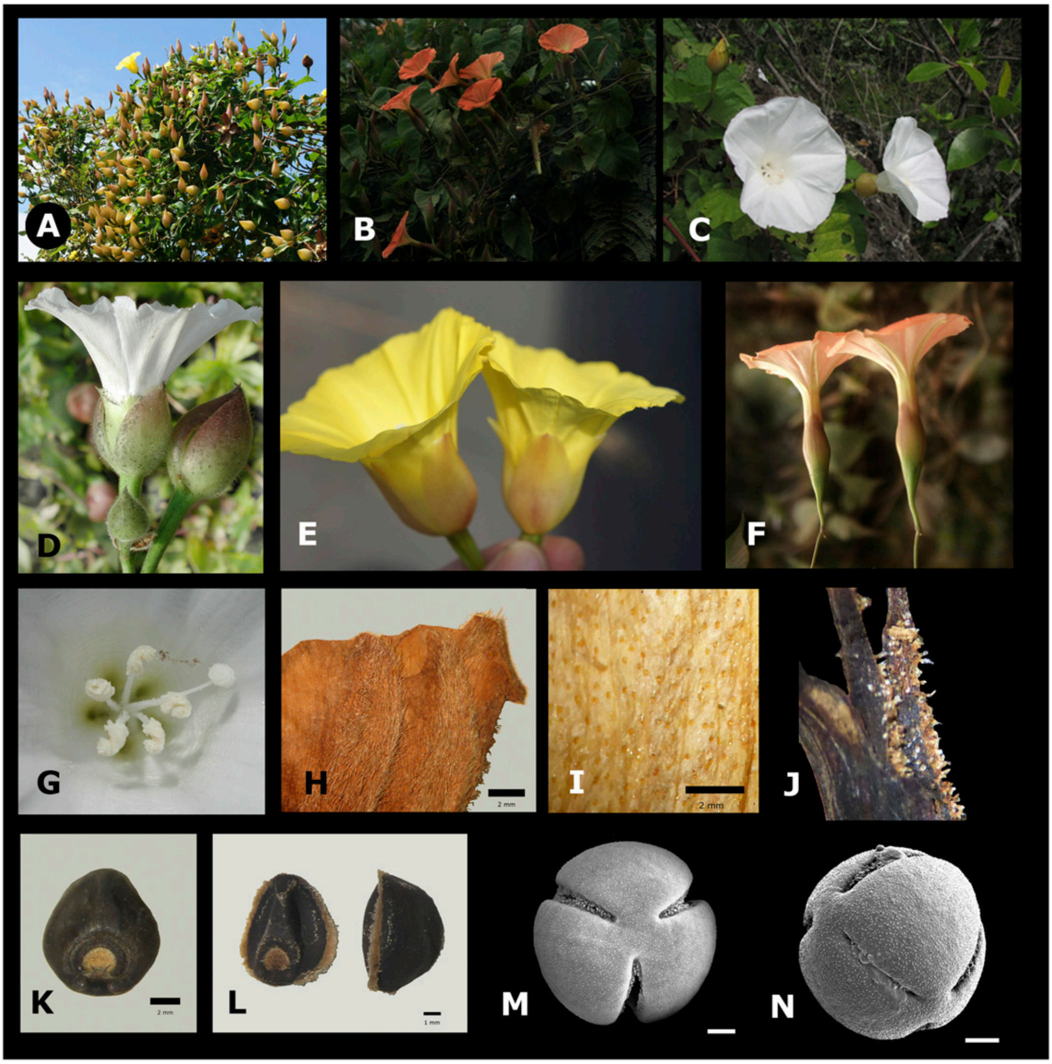

Figure 2. Habit, floral morphology, and pollen in *Operculina* Silva Manso. A–C. Climbing habit. —A. *Operculina hamiltonii* (G. Don) D. F. Austin & Staples (photo: Wesley P. F. S. Cordeiro; voucher: *Lourenço et al. 123* [PEUFR]). —B. *Operculina pteripes* (G. Don) O'Donell (photo: André Moreira; voucher: *Zanatta & Faria 2005* [UB]). —C. *Operculina codonantha* (Benth.) Hallier f. (photo: Jean-François Butaud; voucher: *Butaud 1573* [PAP]). D–F. Corolla morphology, color, and presentation. —D. Broadly funnel-shaped white corolla of *O. turpethum* (L.) Silva Manso, showing inflated, pinkish calyx and uppermost bracteole; note vague blackish dots visible in both, a characteristic for this species (photo: Maxim Nuraliev; no voucher). —E. Campanulate yellow corolla of *O. hamiltonii* showing sepals appressed to corolla tube (photo: Wesley P. F. S. Cordeiro; voucher: *Lourenço et al. 123* [PEUFR]). —F. Subsalverform orange corolla of *O. pteripes* (photo: André Moreira; voucher: *Zanatta & Faria 2005* [UB]). —G. Included stamens and pistil showing spirally dehiscent anthers and biglobose stigmas, *O. turpethum* (photo: Maxim Nuraliev; no voucher). H–J. Micromorphological floral characters. —H. Dense indumentum on the outside of the corolla along the midpetaline bands, *O. riedeliana* (Oliv.) Ooststr. (photo: G. Staples; voucher: *Foale 23* [A]). —I. Detail of glandular dots on the outer surface of the corolla, *O. turpethum* (photo: G. Staples; voucher: *Staples & Ueachirakan 210* [A]). —J. Glandular hairs at the base of the filaments in *O. riedeliana* (photo: G. Staples; voucher: *Takeuchi 14325* [A]). K, L. Seeds of *Operculina* with different indumentum patterns. —K. Glabrous seed of *O. ventricosa* (photo: G. Staples; voucher: *Britton & Shafer 1660* [NY]). —L. Seeds of *O. riedeliana* with golden-brown trichomes around the seed edges (photo: G. Staples; voucher: *Aban G. & Diwol S. SAN 95400* [A]). M, N. Pollen grains in *Operculina*. —M. Trizonocolpate grain, polar view, *O. pteripes* (photo: reproduced from Simões et al. [2019: fig. 2D]; voucher: *Williams & Alston 341* [BM]). —N. Hexapantocolpate grain, *O. petaloidea* (photo: reproduced from Simões et al. [2019: fig. 1L]; voucher: *Haines 4916* [K]). Simões et al. (2019) pollen images reproduced with permission of Taylor & Francis, <https://www.tandfonline.com/doi/abs/10.1080/00173134.2018.1511750>.

structures they cover. Trichomes present on the flowers (calyx, corolla), the outer fruit wall, and the seeds (*O. petaloidea*, *O. riedeliana*) are likewise simple and unicellular. In most species of *Operculina* the midpetaline bands on the exterior of the corolla are more or less shaggy with long hirsute hairs (Fig. 2H), a useful field character. However, a few species lack hirsute hairs and, in their place, the entire outer surface of the corolla (not just the midpetaline bands) is dotted with tiny sessile glands that dry golden in color (Fig. 2I). In two species both simple hairs and golden gland dots are present. Table 1 summarizes the presence and type of corolla hairs and glandular indumentum.

Table 1. Trichome distribution on corollas of *Operculina* Silva Manso species.

Species name	Golden glands	Simple hairs
O. aequisepala	present	absent
O. polynesica	present	not evident
O. turpethum	present	absent
O. ventricosa	present	absent
O. macrocarpa	present	present
O. riedeliana	present	abundant
O. codonantha	not evident	abundant
O. hamiltonii	absent	present
O. petaloidea	not evident	abundant
O. pinnatifida	absent	abundant
O pteripes	not evident	abundant
O sericantha	–[1]	abundant
O. maypurensis	sparsely present	sparsely sericeous on tips

[1] There were no flowering specimens available of *Operculina sericantha*; digital images examined online do not have sufficient resolution to see microscopic gland dots, but the simple hairs are clearly visible on the corolla.

A third trichome type is found inside the flower on the lower filaments, at and below the point where the filaments are inserted on the corolla tube. These trichomes are highly variable in shape, size, and precise location but all appear to be fundamentally glandular, multicellular trichomes. In all species we could study, the adnate portion of the filament is broad and only the margins have glandular indumentum (typically, multicellular glandular trichomes, sometimes with an enlarged apical cell); the center of the adnate portion is glabrous (Fig. 2J). At the insertion point, different trichome types (such as sessile, multicellular glands or simple, unicellular hairs) may be present; above the insertion point the filaments become free, filamentous, and are consistently glabrous.

Svedelius (1906) described and illustrated both stalked and sessile glandular trichomes on the adaxial surfaces of the three inner sepals; these occur singly or in complexes. During fruit development in two species he observed (*Operculina turpethum*, *O. codonantha* (Benth.) Hallier f. under the name *Ipomoea alata* R. Br.) these *Drüsenhaaren* (glandular hairs) function like hydathodes and secrete a watery fluid into the space between the calyx and the immature fruit. Svedelius pointed out that the glandular hairs in *O. turpethum* are not true hydathodes, which secrete only water, because the fluid trapped between the accrescent calyx and the developing fruit is slimy, and this indicates that other substances are being secreted by the glandular hairs as well. We did not observe these glandular hairs on the sepals in herbarium material, and it is possible they disappear during pressing and drying.

Finally, Svedelius (1906: 248, fig. 18) pointed out that *Operculina turpethum* also has glandular hairs on the abaxial leaf surfaces: these are rare, sunken in the leaf surface (not protruding), and have the same structure as the sepal glandular hairs. They can be observed on herbarium specimens under adequate magnification (a binocular microscope is sufficient).

ROOTS

The roots of some species have been reported to be enlarged. Silva Manso (1836) described tuberous, oblong-turbinate roots for *Operculina macrocarpa* (under the name *Convolvulus turpethum*) in his treatise on medicinal plants of Brazil. Ooststroom (1939) stated that *O. turpethum* has slender, fleshy, much-branched roots. *Operculina pinnatifida* is reported to have "deep-seated, perennial roots" (ex label *Runyon 2398*), from which annual stems arise. And collectors report that *O. hamiltonii* has tuberous roots (*D. Fairchild 2858*, *R. L. Froes 1764*). However, Johnson (1980) reported that *O. aequisepala* has a taproot. For most other species the root system is unknown. Probably there is a range of morphological root types represented in the belowground parts. Enlarged storage roots are typical for geophyte perennial plants (Raunkiaer, 1934) growing under a seasonal dry climate regime (Landrein, 2001); vegetative shoots die down to the ground during the dry season and the roots serve as the resting stage until the rainy season begins and active growth resumes.

PLANT AXIS

One of the useful field characters for recognizing the genus *Operculina* is the presence of lengthwise membranous wings, ridges, or prominent angles on the axial organs: stems, petioles, peduncles, or pedicels. More than half the species have one or more parts of the plant axis prominently winged. The exceptions are *O. polynesica* Staples, *O. riedeliana*, *O. sericantha* (Miq.) Ooststr., and *O. ventricosa* (Bertero) Peter, which appear to lack alate development on any portion of the plant axis. Stems may be herbaceous or semi-woody (that is, woody near the stem base and herbaceous toward the shoot tips) and solid or fistulose, at least when dry.

LEAVES

Leaves in all species are bifacial with a petiole and distinct blade. Petioles may be short and stout or elongated and slender. The shape in cross-section varies from cylindrical, terete and smooth to adaxially sulcate (giving a reniform cross-section); some species have wings running lengthwise along the sides of the petiole (*Operculina codonantha*, *O. hamiltonii*, *O. petaloidea*, *O. turpethum*). Leaf blades in most species are simple and entire, cordiform or ovate-orbicular (often triangular in *O. codonantha*; variably shaped in *O. petaloidea*, *O. turpethum*); in one species the blades are deeply, palmately 5- to 7-lobed or -parted (*O. macrocarpa*), and in another the blades are irregularly pinnately dissected with five to nine angles or lobes (*O. pinnatifida*). The blades are herbaceous to slightly fleshy, membranous or coriaceous; the basal lobes are separated by a broad, shallow sinus or a deep U-shaped sinus; exceptionally, the leaf base in *O. turpethum* may have a truncate, emarginate, or rounded shape. The blades vary from completely glabrous to sparsely appressed pilose adaxially and sericeous abaxially; trichomes are typically denser along the veins.

Leaf venation is typically pinnate with the main secondary veins looping within the blade margin to join the next higher vein in a brochidodromus pattern. Tertiary veins are scalariform and the finer order veins are reticulate. The midvein and secondary veins are usually raised and slightly prominent on the abaxial leaf surface; either flat or slightly sunken on the adaxial surface. In a few cases the blade texture and tertiary and finer venation patterns can be taxonomically informative, but these characters are never definitive for making a species identification.

INFLORESCENCES

Inflorescences are fundamentally cymose with usually two or three flowers in most species, sometimes reduced to solitary flowers, or the cymes aggregated into panicles (*Operculina pteripes*, *O. turpethum*, *O. ventricosa*) with up to 12 flowers. Peduncles vary from shorter than the subtending petiole and stout, to slender and much longer than the subtending petiole; peduncles may be terete and smooth to variously striate, angled or prominently alate. Populations of *O. ventricosa* from Guam and the northern Mariana Islands frequently have modified (aberrant?) inflorescences in which the secondary and tertiary branches are reduced or suppressed, producing a crowded, dense, bracteose inflorescence with a different appearance from those of conspecific populations from other parts of the Pacific and the West Indies.

Bracts may be inconspicuous and scalelike or larger and foliaceous, and vary from early deciduous to persistent into fruiting stages (*Operculina turpethum*, *O. ventricosa*). When persistent, the bracts are often convex and boat-shaped, contrasting in color with the calyx or corolla: pinkish, tawny, green, or reddish brown. Second and third order bracts, when present, are similar in shape and texture to the lower bracts, but diminish in size toward the apex of the inflorescence.

Pedicels may be slender or distinctly clavate, terete to prominently alate with wavy, undulate-crisped wings (*Operculina macrocarpa*). The pedicels may enlarge and thicken when the fruit develops, so that the pedicels are more massive than the subtending peduncle that supports them.

FLOWERS

Typically, *Operculina* flowers are medium to large (small in *O. maypurensis* (Hallier f.) A. R. Simões & Staples), diurnal, odorless, always radially symmetrical, and presented in an erect to ascending posture. One species, *O. polynesica*, may have nocturnal flowers: fully open flowers have been collected in late afternoon, near sundown, and also in the early morning hours (J. F. Butaud, pers. comm. 2018). The timing suggests the flowers are nocturnal; field observations of floral anthesis are needed to confirm this conjecture.

CALYX

As in most Convolvulaceae, there are five sepals arranged in a quincuncial pattern (Fig. 8-1′) so that two outer sepals have both margins exposed, the third (middle) sepal has one margin exposed and one covered, and the two inner sepals have both margins covered. Several species have what has been described (House, 1906) as a "pear-shaped" (pyriform or ampliate) calyx: broader and inflated at the base, tapering upward so that the sepal apices are appressed against the corolla tube. The sepals are free, with no basal fusion.

During fruit development, the calyx enlarges and, initially, tightly enfolds the young fruit; as maturation proceeds, the drying calyx reflexes and pulls away so that the capsule is exposed. The mature fruiting calyx may form a bowl-shaped enclosure with the fruit freestanding in the center or the sepals may reflex away and downward, against the pedicel, leaving the fruit fully exposed at the apex of the pedicel. This three-dimensional arrangement is ruined when the mature fruits are pressed for drying so herbarium vouchers can be difficult or impossible to interpret correctly. In fact, the difficulty in correctly interpreting the structure and arrangement of the mature fruit from pressed herbarium specimens was one factor responsible for the historical taxonomic confusion about whether a species belonged in *Merremia*, *Operculina*, or *Ipomoea*.

Svedelius (1906) provided a detailed anatomical description for the postfloral development of the accrescent calyx for two species of *Operculina* (*O. turpethum*, *O. codonantha* under the name *Ipomoea alata*), which he termed a *wasserkelch* (water calyx). This name refers to a clear fluid like water held within the accrescent calyxes of several Convolvulaceae during fruit development. It is possible in the field to turn an immature *O. turpethum* fruit upside down and pour out (or squeeze out) from the accrescent calyx a watery liquid. Heine (1960: 399) mentions that in African populations of *O. macrocarpa* young fruits also contain water, which oozes out when the fruit is plucked. By the time the fruit is fully mature the watery fluid disappears and the ripe capsule is quite dry. The function of the fluid is unknown: Svedelius (1906) explored the anatomical basis for its presence but he did not speculate on the functional reason for its development.

In the dry state, the calyx of several species (*Operculina codonantha*, *O. hamiltonii*, *O. pteripes*, *O. sericantha*) develops a distinctly reddish-brown hue; this can be a useful character for recognizing these species in the herbarium. In nearly all species the sepal margins erode and break off irregularly when the sepals are mature and become brittle; thus, in herbarium material the shape of the sepal apex and margins may be difficult to assess.

COROLLA

As with most Convolvulaceae, the five petals are fused into a sympetalous, radially symmetrical corolla with a constricted tubular base, widening above into a flaring throat, and ending in an erect to spreading limb. Nearly all species have a campanulate to broadly funnelform corolla, the limb entire to slightly 5-lobed and spreading (Fig. 2D, E); one species (*Operculina pteripes*) has a salverform corolla with a reflexed limb, spreading at a right angle from the throat (Fig. 2F). Corolla size ranges from small (ca. 2–3 cm long in *O. maypurensis*) to as much as 7–8 cm long and 8–9 cm across the corolla limb (*O. polynesica*). Corolla color is typically pure white or white with a yellow tube base inside (Fig. 2C, D), or pale yellow, and one species has a bright butter-yellow corolla (*O. hamiltonii*) (Fig. 2E), while one species (*O. pteripes*) has a distinctive pinkish to salmon-orange corolla with yellow inside the tube (Figs. 2F, 16). Midpetaline bands, as defined by Staples and Brummitt (2007: 109), in preference to the older term *interplicae*, are a prominent feature of the corolla exterior. Eight *Operculina* species have hairy midpetaline bands (Fig. 2H) on the outside of the corolla (Table 1). Tiny, glistening golden glands (Fig. 2I) are visible on the outside of the corolla in six species (Table 1). Two species (*O. macrocarpa*, *O. riedeliana*) have both simple hairs and gland dots on the corolla exterior.

ANDROECIUM

The androecium is typically included within the corolla tube (exserted in *Operculina pteripes*) and the stamens may be equal or markedly unequal in length. Typically, the pistil overtops the anthers, or it may reach the same height as the anthers (*O. codonantha*, *O. hamiltonii*). As in most of the family, the lower portions of the filaments are adnate to the corolla tube and flattened against it for some portion of their length and free, filamentous, and terete above the insertion point. Measurements of stamen length reported here include the lower adnate portion of the filament + the distal, free portion of the filament + the anther length. The insertion point itself might have thickenings or ridged buttresses that act as support elements for the free portion of the filaments bearing the anthers. Also present around and below the insertion point on each filament are glandular trichomes of various types: these can be simple and unicellular, simple and septate (Fig. 2J), or multicellular and capitate; they range from mere protrusions on the filament to several millimeters in length.

The anthers themselves are among the longest in the family: bilocular, basally or subbasally attached on the filament apex, and dehisce lengthwise while simultaneously undergoing spiral coiling so that the fully dehisced anther forms one to four complete 360° revolutions around the central axis (Fig. 2G). These tightly coiled, spirally dehiscent anthers are an excellent field character for recognizing *Operculina*. Although present in other genera formerly included in Merremieae (viz. *Daustinia* Buril & A. R. Simões, *Decalobanthus*, *Distimake*, *Remirema* Kerr) and in *Merremia pterygocaulos* (Choisy) Hallier f. (see below), this coiled anther dehiscence feature is not known to occur in speciose genera such as *Ipomoea* and *Convolvulus*, which have lengthwise dehiscing anthers.

POLLEN

Pollen morphology information is summarized from a comprehensive work on pollen of *Operculina* that was recently published (Simões et al., 2019). Pollen grains in *Operculina* vary from oblate to subprolate in shape, the size is up to 120 μm in both polar and equatorial diameters; the apertural pattern is typically 3-zonocolpate (three colpi distributed around the equator of the grain) (Fig. 2M). Several species (*O. aequisepala*, *O. hamiltonii*, *O. maypurensis*, *O. petaloidea*) present heteromorphic pollen with both 3-zonocolpate and 6-pantocolpate grains (Fig. 2N) occurring within the same anther (Simões et al., 2019). These pollen-heteromorphic species do not define a clade (Simões et al., 2015), meaning that this feature evolved independently in the different species;

therefore, the presence of pollen heteromorphism has no taxonomic significance at the present level of knowledge. A sculptured apertural membrane is often present. The exine is tectate, punctate, and microechinate-microgranulate and varies between 3.1 and 6.2 μm in thickness; it comprises a layer of collumellae, each ramified from the base, middle, or apical portion (Simões et al., 2019). No pollen data were available for *O. ventricosa* and *O. riedeliana*. Although the latter species was listed by Ferguson et al. (1977: 772), we have established this is a misidentification: the voucher specimen cited there (*MacKee 4594*) is reidentified here as *O. codonantha*.

GYNOECIUM

The pistil is inserted in a superior position on the floral receptacle and comprises a bicarpellate ovary and a single terminally attached style ending in two stigmas. The base of the ovary is often surrounded by a nectary disc, usually annular, sometimes 5-lobed, and in living material the nectary is frequently contrastingly colored (orange, green, yellow) with the whitish ovary wall. The ovary is bilocular, varies in shape with the species, and each locule contains two basally attached ovules. The style is included (exserted in *Operculina pteripes*), filiform, usually glabrous (whitish tomentose below the middle in some specimens of *O. ventricosa*), and terminates in two short branches, each ending in a capitate stigma; the paired stigmas overtop the stamens.

Anatomical study of stigmas of one species, *Operculina pinnatifida*, revealed details of the micromorphology and vasculature. In *O. pinnatifida* the two stigmas are crowded so closely together that each stigma takes a hemispherical shape (Fig. 3A). Each stigma is highly architectural with a complex three-dimensional structure: the surface of each hemisphere is developed in irregularly shaped, elongated arms (Fig. 3B) that radiate outward from the central fusion point with the style branches. These arms almost double the size of the stigma; they are crowded close together and the outer/upper surface of each arm is densely covered in bulbous papillae, with the papilla apex swollen and larger in diameter than the base (Fig. 3B, C). Two vascular bundles pass through the style and diffuse outward, one into each stigmatic hemisphere.

FRUIT

Operculina typically possesses a circumscissily dehiscent capsule (for exceptions, see below), a fruit type known generally as a *pyxidium* and reported to occur in 17 vascular plant families (Ho & Costea, 2018). Yet the fruit of *Operculina* differs from a typical pyxidium, exemplified by the fruits of Lecythidaceae or *Portulaca* L. (Portulacaceae). Within Convolvulaceae, only the distantly related parasitic genus *Cuscuta* L. also has species possessing a circumscissile capsule. However, the circumscissily dehiscent capsules in *Cuscuta* are distinct from those found in *Operculina*: in *Cuscuta* the fruits dehisce “in a clean circle around the capsule, towards the base” (Felger et al., 2015). This constitutes a different structure as well as a different method of dehiscence than described here for fruits of *Operculina*. The *Operculina* fruit, as defined here, is an *operculate capsule*: the ovary develops after fertilization into a depressed globose, often 4-lobed (quatrefoil) fruit with two visible hemispheres demarcated by a line passing more or less around the equator. The texture and color of the fruit wall are different above and below the line. Distal to the demarcation line a fleshy or leathery lid (Fig. 4A, D)—the exocarp or *operculum*—separates during maturation and detaches after drying (Fig. 4C, G). Beneath the operculum is a thin, brittle, translucent layer (endocarp), which usually shatters irregularly after the fruit is fully mature and dry (valvate dehiscent in *O. petaloidea*). Below (proximal to) the demarcation line the fruit wall (pericarp) remains intact, in a single continuous layer (Fig. 4). Thus, the dehiscence of an *Operculina* fruit occurs in two discrete stages: the detachment of the operculum during fruit ripening (Fig. 4B, C, G) and the dehiscence of the brittle endocarp an indefinite time later to release the seeds (Fig. 4F, I, J, L, M). When fully mature, the operculate capsule is erect and the thin, brittle endocarp is exposed, pointing upward (Fig. 4E–H). These mature fruits are reported to persist for several months on dead stems (*O. codonantha*, *O. hamiltonii*).

One species, *Operculina petaloidea*, has a fruit structure that is intermediate between a valvate capsule and an operculate capsule: the fruit has an operculum that covers half or more of the fruit surface; it detaches first and beneath that the endocarp has two or four visible valves, which split open at a later time (Fig. 4F) or may shatter irregularly (pressed fruits on herbarium sheets are not easily interpretable regarding the dehiscence mechanism).

The intact fruit of *Operculina maypurensis* has not been observed yet; the flattened fruits present on the only known fruiting specimen, preserved on a herbarium sheet, are too ambiguous to interpret.

SEEDS

Typically there are four seeds produced per fruit, or fewer if some ovules do not develop. When four seeds are present, the shape of each is ovoid-trigonous and carinate: with two flattened faces and an outer, curved face. The seeds fit together with the flattened faces adjacent and aligned along the central axis of the fruit; the curved seed faces are positioned against the outer fruit

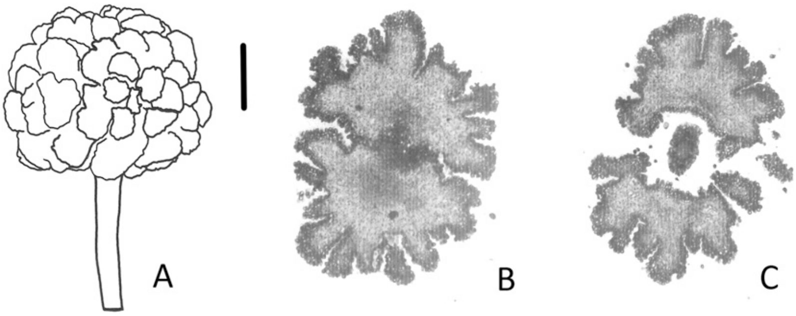

Figure 3. Stigma morphology of *Operculina pinnatifida* (Kunth) O'Donell. —A. Whole stigma, drawn by camera lucida. —B. Photomicrograph of cross-section through mid-level of stigmas, showing two halves closely appressed in center and radial development of irregular, elongated arms covered in bulbous papillae. —C. Cross-section through lower level of same stigma, style visible in center with two vascular strands. Voucher: *Staples s.n.* (FAU). Scale bar = 1 mm.

wall. The seeds are broader at the base and taper slightly toward the apex or may be rounded. The hilum is basal, prominent, reniform to semicircular, C-shaped, or D-shaped. The seed coat is shiny or dull, blackish or dark brown, usually glabrous (Fig. 2K) but sometimes (*O. petaloidea*, *O. riedeliana* [Fig. 2L]) pilose along the angles. When some ovules abort, the mature seeds may be ellipsoid or almost globose, lacking the flattened surfaces.

COTYLEDONS

Cotyledons have been observed for three species: *Operculina macrocarpa*, *O. pinnatifida* (Staples, 1979), and *O. turpethum* (Sampathkumar, 1982). In all three species, the cotyledons are similar: epigeal, paired, with distinct petioles; the blades are broadly depressed elliptic to depressed ovate, basally cordate, apically deeply emarginate or bilobed; venation shows one pair of strong veins departing from the petiole apex, sometimes a second pair of weaker veins is present and medial to the first (outer) pair, in this case the venation appears flabellate, with all four veins spreading from the petiole apex.

TWO MORPHOLOGICAL OUTLIERS

Having established the morphological basis for defining *Operculina*, we now point out two situations in which interpretation of the gross morphology is ambiguous for taxonomic understanding. The first case impacts generic delimitation while the second confounds species delimitation. These cases raise interesting questions for evolutionary studies and character state evolution as well as suggesting the possibility of interspecific hybridization in *Operculina*.

Merremia pterygocaulos—A possible case of parallel evolution

In examining specimens from Africa for this revision we noted a remarkable similarity between *Merremia pterygocaulos* and the species of *Operculina* and wondered if this species was correctly placed in terms of its generic assignment. The vegetative and floral morphology of *M. pterygocaulos* conforms closely with that defined above for the genus *Operculina* (sensu Simões & Staples, 2017): plants have prominently alate axial parts; shaggy-hairy midpetaline bands on the white or pale yellowish corollas; and strongly spirally dehiscent anthers. However, the fruit structure and dehiscence mode of *M. pterygocaulos* are typical 4-valved capsules, quite unlike the truly operculate capsules with a tardily shattering endocarp.

The available molecular data (Simões et al., 2015) placed *Merremia pterygocaulos* in a different clade from *Operculina* (Fig. 1). Even though the deeper nodes in the tree, which define the relationship of *M. pterygocaulos* with the remaining species of *Merremia* s.l., are weakly supported (Fig. 1), the genus *Operculina* was resolved as monophyletic with strong support. If the observed morphological similarities between *M. pterygocaulos* and *Operculina* are based on a close evolutionary relationship, we would expect *M. pterygocaulos* to be included in the *Operculina* clade. In fact, the correct placement of *M. pterygocaulos* is still uncertain and more molecular phylogenetic studies will be necessary to determine its generic placement. Furthermore, a few other African species (not yet sampled for molecular analysis) remain "parked" in *Merremia* (Simões & Staples, 2017); some of these species may be allied with *M. pterygocaulos*.

It may be that the observed morphological similarities between *Merremia pterygocaulos* and *Operculina* are a case of parallel evolution sensu Austin (1998b): possibly *M. pterygocaulos* acquired a similar morphology independently from the *Operculina* clade, as an adaptation to environmental conditions. However, it is equally likely, at the present level of knowledge about evolutionary trends and character states in Convolvulaceae, that the similarity is due to shared common descent. Molecular phylogenetic results by Simões et al.

(2015) suggest an early ancestral connection between *Operculina* and the clade containing *M. pterygocaulos.* In this scenario, *M. pterygocaulos* retained some synapomorphic characters of the common ancestor shared with the *Operculina* clade, while the other taxa in the same clade (e.g., *Hewittia*, *Hyalocystis*, and *Xenostegia*) accumulated genetic changes and diverged morphologically. Improved molecular phylogenetic hypotheses and more detailed taxonomic studies are necessary to resolve relationships within this African clade to determine the correct generic delimitation.

It would be easy to consider *Merremia pterygocaulos* as a member of *Operculina*: the remarkable similarity in the vegetative organs and floral morphology is so striking. Nevertheless, the critical diagnostic characters of the fruit type and method of dehiscence are lacking. Significantly from 1893, when Hallier first assigned this species to *Merremia* (Hallier, 1893), up until the present time, *M. pterygocaulos* has never been considered to belong in *Operculina* by botanists studying the African flora (Baker & Wright, 1904; Baker & Rendle, 1905; Heine, 1963; Verdcourt, 1963; Gonçalves, 1987; Lejoly & Lisowski, 1992; Meeuse & Welman, 2000; Sebsebe Demissew, 2006, among others). We follow their example and retain *M. pterygocaulos* separate from *Operculina* and highlight this species for further investigation. The remarkable similarity between this species and *Operculina* could make an interesting case study for character evolution.

Polymorphism, intergradation, and taxon delimitation—Evidence for hybridization?

The second situation concerns the extraordinary variability and polymorphism among South Pacific specimens of *Operculina*. Staples (2007) pointed out the intermediate nature of multiple collections from the South Pacific that could not readily be assigned to one species, but instead seemed to combine characters from two or more species. While few new Pacific specimens have been examined in the decade since then, the available Pacific specimens were compared with material from other geographic regions and this comparison has provided better context for understanding the intermediates.

For example, the populations of *Operculina ventricosa* from Guam and the Mariana Islands have a distinctive facies: crowded, bracteose inflorescences due to shortened inflorescence branches and persistent, large bracts. When only Pacific plants are considered, these Guam/Mariana populations seem entirely distinctive from all other Pacific *Operculina*. However, when West Indian material of *O. ventricosa* was compared with these North Pacific specimens, it became clear that the Guam/Mariana plants are actually rather aberrant: the crowded inflorescences with dense clusters of bracts are not typical for the species as a whole. In fact, some Pacific specimens of *Operculina* that Staples considered intermediate in 2007 agree quite closely with West Indian plants of *O. ventricosa*, and these have been renamed accordingly in this revision. Thus, *O. ventricosa* as currently understood is a more widespread and variable plant found throughout the entire Pacific.

The second dilemma is how to correctly apply the name *Operculina turpethum* to Pacific plants, the name having been used almost indiscriminately for virtually all *Operculina* growing on the Pacific islands. Some of the misapplications of the name have been corrected already (Staples, 2007). Now, further comparison of mainland Asian and Philippine populations called *O. turpethum* with those from across the Pacific Basin demonstrated that there is a consistent facies to *O. turpethum* from the western Pacific Rim. And there are specimens from widely scattered Pacific island locales that match this morphology: from Fiji, French Polynesia, the Cook Islands, and single isolated collections from Hawaii, the Solomons, and New Guinea (both Indonesian and Papua). However, there are also plants from the high islands of Micronesia, New Guinea, the Solomons, Vanuatu, New Caledonia, and Samoa—all called *O. turpethum*—that look different from the typical Asian plants. After much comparison and exploration of many possible diagnostic characters, we failed to correlate any morphological characters to distinguish a new species or even a variety: there is simply too much intergradation and variation visible in all characters we examined. The intermediacy bridges *O. turpethum*, *O. ventricosa*, and *O. polynesica*.

Our solution is to propose these Pacific island populations as a hybrid, a hypothesis to be tested. Hybridization has been shown to be quite widespread in higher plants: at least 25% of plant species are involved in hybridization and introgression (Mallet, 2005, 2007). “Hybrids combine different genotypes and generate phenotypic traits that are often intermediate between their parents, and that in turn are often used as evidence for hybridization in morphological analyses” (Landrein et al., 2017: 257). By giving these intermediate plants a name and a status, we put them “on the radar” for field collectors, and hopefully new collections, digital photographs, and molecular samples will be forthcoming in the near future. Unfortunately, no *Operculina* samples from the Pacific islands were included in molecular phylogenetic analyses to date; application of suitable molecular tools to these baffling Pacific populations would be highly instructive in testing our proposal that hybridization is responsible for this extraordinary level of intermediacy in their morphology. In future, a more intensive study of additional material for South Pacific populations of *Operculina* might clarify the evolution,

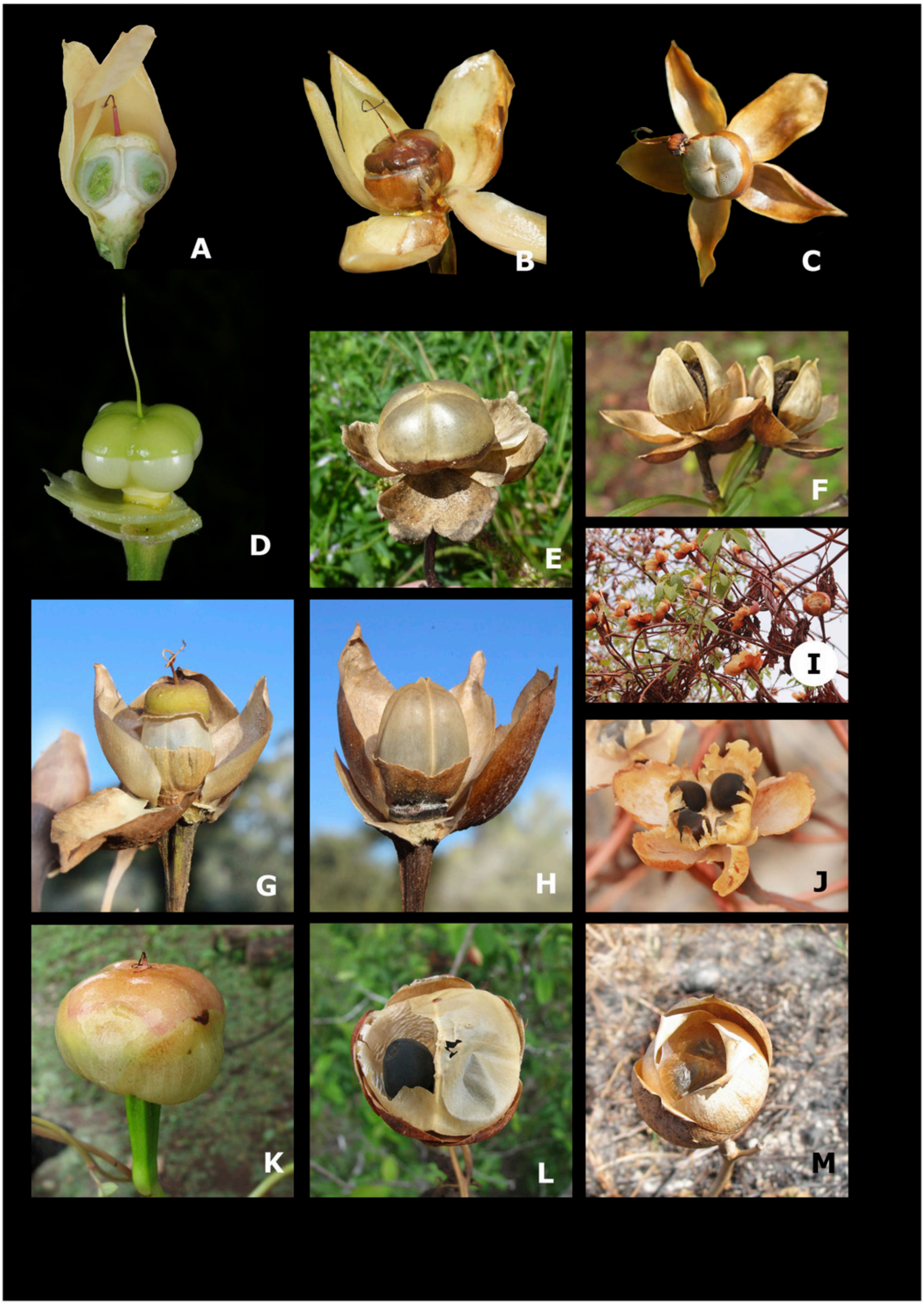

Figure 4. Fruits and fruiting calyxes in *Operculina* Silva Manso. A–C. Fruit developmental stages in *O. hamiltonii* (G. Don) D. F. Austin & Staples (photos: Wesley P. F. S. Cordeiro; voucher: *Lourenço et al. 123* [PEUFR]). —A. Immature fruit in longitudinal section, showing operculum and style base in situ, sepals appressed against fruit, and green cotyledons inside seeds. —B. Almost mature fruit with the operculum still in situ, beginning to detach around line of abscission, the sepals manually pulled away to show fruit more clearly. —C. Mature fruit with calyx reflexed at 90° to pedicel, operculum dehisced, barely attached, revealing whitish endocarp underneath; the seeds are contained within the endocarp. —D. *Operculina turpethum* (L.) Silva Manso, immature fruit with calyx removed showing nectary disc at base of fruit, intact operculum and persistent style; note pronounced

biogeography, distribution, and dispersal for members of this genus.

DISTRIBUTION AND HUMAN DISPERSAL

Operculina is now distributed globally throughout the tropics (Fig. 5). Naturally occurring species are present in Asia, Australia, Oceania, and the American tropics. There is no evidence that *Operculina* occurred on the African continent prior to human activity yet two species occur there now. Oceanic dispersal also seems to have been a factor in the distribution for the genus, with several *Operculina* species widely distributed across the Pacific islands and one (*O. codonantha*) extending from Australia to the northwest coast of South America. The contemporary distribution of three species appears to have been influenced by human dispersal to continents or countries where they did not naturally occur. We briefly comment on the three species that have evidently been dispersed by human activity.

Operculina turpethum

Operculina turpethum (Fig. 27) is probably native in the Indian subcontinent and, from there, it was carried westward across the Indian Ocean to Madagascar and the Indian Ocean islands as far as the east coast of Africa, following ancient Arab trading routes. *Operculina turpethum* was also carried eastward, from India to Southeast Asia and thence to China, again corresponding closely with well-known trade routes followed—for centuries before the advent of Europeans—by merchants from China who met their Arab counterparts at trading entrepôts in modern-day Malaysia, Indonesia, and Singapore (Mabberley, 1998; Keay, 2010). The current distribution of *O. turpethum* in Southeast Asia/Malesia reflects the principal seagoing trade routes across this vast region. Ooststroom's (1953: 456) comment that the distribution for *O. turpethum* in Malesia is "restricted to regions with a medium or strong east monsoon" is perspicacious. Likewise, Pacific island populations of bona fide *O. turpethum* are almost certainly the result of human dispersal; the plants in Fiji, for example, could very well have been introduced there in course of the Indian diaspora. Similarly, *O. turpethum* reached the West Indian islands, where it was probably introduced by European merchant sailors who encountered it in either Asia or Africa (Ooststroom, 1953: 456; Staples & Austin, 1981). The motive for moving this plant over such enormous distances was its importance as a medicinal drug, which made the dried roots a valuable item in international commerce (Austin, 1982b).

Operculina macrocarpa

A second species likely dispersed by humans is *Operculina macrocarpa*, which appears almost confined to Brazil in the Neotropics but also has populations established in west tropical Africa (Heine, 1960) (Fig. 12). This peculiar amphi-Atlantic distribution suggests that *O. macrocarpa* could have been carried from Brazil across the Atlantic to Africa, possibly by Portuguese or others engaged in the slave trade or missionary efforts (Heine, 1960). Although not so well known in international commerce, the dried roots of *O. macrocarpa* were used medicinally as a substitute for those of *O. turpethum*, and this provides a suitable motive for its transport across the Atlantic. Heine (1960) proposed another theory, based on observations from Ghana, regarding motives for transcontinental transport for this species: Roman Catholic missionaries coming from Portuguese settlements in Brazil deliberately introduced *O. macrocarpa* to Africa because the hard seeds would be useful for making beads (i.e., rosaries).

Operculina ventricosa

This species now has widely disjunct populations around the world (Fig. 30): humans must have been responsible for this peculiar distribution in such remote places, although determining the original distribution for the species would require extensive phylogeographic research. Literature reports about the provenance for *Operculina ventricosa* are contradictory. Fosberg and

←
color difference between operculum and lower fruit wall (photo: Preecha Karaket; voucher: *Staples et al. 1332* [BKF]). —E. *Operculina macrocarpa* (L.) Urb., mature fruit with operculum detached, the endocarp intact, translucent, the accrescent calyx reflexed about 90°, the sepal margins scarious and eroded (photo: G. Staples; voucher: *Staples et al. 1656* [PEUFR]). —F. *Operculina petaloidea* (Choisy) Ooststr., mature fruit with operculum detached, the endocarp showing valvate dehiscence, and accrescent calyx reflexed about 90° (photo: Mathieu Leti; voucher: *S. K. Cheng et al. CL-1075* [P]). G, H. Fruit development in *O. pteripes* (G. Don) O'Donell (photos: Fernanda Satori Petrongari; voucher: *Petrongari & Fernandes 133* [SP]). —G. Almost mature fruit with the operculum detached but still in place, endocarp visible beneath; the sepals have been manually pulled back to show fruit details. —H. Fully mature fruit with the operculum detached, the accrescent calyx cupping the fruit (one sepal removed to show fruit details). I, J. Mature fruits of *O. macrocarpa* (photos: Lucas Richter; no voucher). —I. Plant habit with mature, dehiscing fruits. —J. Fully mature fruit with shattered endocarp and reflexed calyx exposing the glabrous seeds. K, L. Fruit development in *O. codonantha* (Benth.) Hallier f. (photos: Jean-François Butaud). —K. Immature fruit with operculum intact, accrescent calyx appressed against fruit (voucher: *Butaud 1573* [PAP]). —L. Mature fruit with operculum detached and endocarp shattered to reveal seeds, the accrescent calyx tightly enclosing the fruit (voucher: *Butaud & Jacq 1582* [PAP]). —M. *Operculina polynesica* Staples, mature fruit with operculum detached, translucent hyaline endocarp intact, the accrescent calyx tightly cupping the fruit (photo: Jean-François Butaud; voucher: *Butaud 1506* [PAP]).

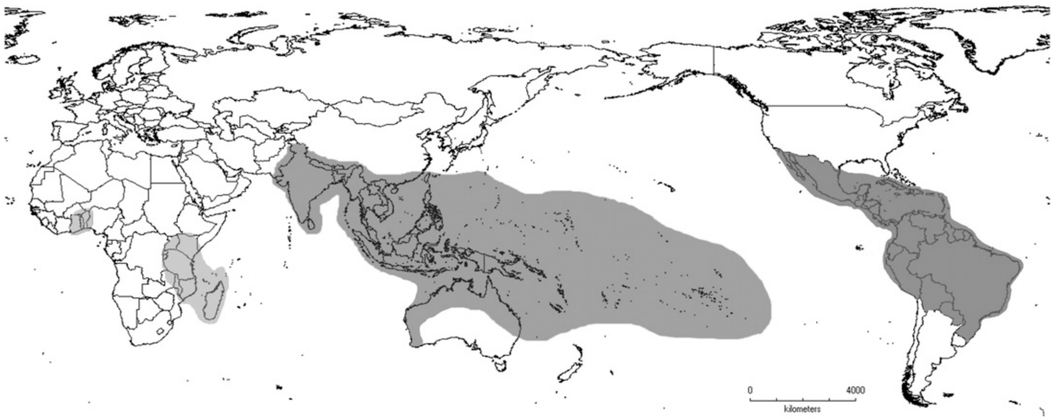

Figure 5. World distribution for *Operculina* Silva Manso. Dark shading indicates the natural distribution for *Operculina* species; the lighter shading indicates the introduced, naturalized populations for *O. macrocarpa* (West Africa) and *O. turpethum* (East Africa, Madagascar, the Indian Ocean islands).

Sachet (1977: 30) stated that *O. ventricosa* is native to tropical America but has been present for a long time in Micronesia. They postulated that aircraft during World War II might have dispersed the plants from Saipan or Tinian to Guam, where it spread rapidly. However, the vouchers from American populations, principally the West Indian specimens, nearly all state that the plants were cultivated. Indeed, the type specimen for *Convolvulus ventricosus* Bertero came from a plant cultivated on Guadeloupe, where it was said to be introduced from St. Barts (Colla, 1824: 37). Given what this revision demonstrates about the diversity of *Operculina* in the tropical Pacific, we now speculate that *O. ventricosa* might have originated in the Pacific islands and been dispersed from there by humans to the Caribbean and other parts of the world.

Ecology and Habitats

Like many Convolvulaceae, *Operculina* species are heliophytes that grow in full sunlight. All species are climbers, if there is support on which the stems can twine, or prostrate creepers on the ground if there is no support. Some species are found in forest margins, clearings, or the canopy of primary forests; others are tolerant of (or thrive due to) human disturbance. *Operculina turpethum* is often found in secondary regrowth and along roadsides, in vacant agricultural land, or waste places. A few species appear to be evergreen perennials; most are deciduous perennials; one is an annual. Drought seems to be a major factor in the life cycle: species with enlarged storage organs underground (i.e., geophytes sensu Raunkiaer, 1934) may survive drought by going dormant. The stems and leaves die back and the underground parts persist in a resting state until rainfall stimulates new growth. Other species are annuals that survive drought periods as seeds. Collectors in the Marquesas Islands noted that *O. codonantha* was present as dead vines in thickets and on top of trees, the dry fruits persisting for several months during the dry season.

Pollination Syndromes and Fruit/Seed Dispersal

Typically, *Operculina* flowers are medium to large (small in *O. maypurensis*), diurnal, odorless, with included stamens and pistil, and presented in an erect to ascending posture; these *Operculina* species have flower morphology and floral presentation consistent with a bee pollination syndrome. Anthesis begins at mid-morning: in Thailand, *O. petaloidea* flowers open from about 9:00 a.m.; in Brazil, flowers of *O. hamiltonii* were observed open by 9:30 a.m. and not before. This contrasts with typical “morning glories” (genus *Ipomoea*) that undergo anthesis before dawn and aligns with floral behavior for *Merremia* s.l., known as “noon flowers” because their flowers open so much later in the day.

However, two species have markedly different floral morphology and behavior: *Operculina pteripes* has a salverform red-orange corolla, exserted stamens and stigma, and a horizontal to ascending presentation (Fig. 2B, F). These characteristics are typical for a hummingbird-pollinated species, and hummingbirds have been observed to visit the flowers (Felger et al., 2012: 522). In contrast, *O. polynesica* has a pure white, funnelform corolla with included stamens and stigma. Open flowers have been collected as early as 7:00 a.m. and as late in the afternoon as 5:30 p.m. (J.-F. Butaud, pers. comm. 2018). This hints at a nocturnal anthesis: opening near sundown and remaining open until the morning hours the following day. The pure white corolla and funnelform shape are indicative of a moth-pollination syndrome. Field observations are needed to confirm this conjecture.

The tardily dehiscent fruit with accrescent calyx arrangement is one exemplar of a *wasserkelch* (water calyx) as described for diverse taxa of Convolvulaceae (Svedelius, 1906). The functional role of this peculiar development of fruit and calyx is unknown; we have been unable to identify a role for the *wasserkelch* in dispersal. Our field observations indicate that the mature fruit, some time after the operculum dehisces, breaks open while still attached to the plant and the seeds are the dispersal units. The erect, upward-pointing fruit with its thin brittle endocarp is positioned so that a falling raindrop will shatter the endocarp, thereby releasing the seeds contained within. Anyone who has experienced being struck by raindrops in a tropical rainstorm will appreciate that there is considerable force behind falling water. Following their release from the fruit the seeds are evidently dispersed by flotation in water, either rainwash across the ground for short distances, or floating in freshwater streams and rivers, or in seawater, over longer distances. Ridley (1930) states that the ability of Convolvulaceae seeds to float is variable and depends on whether the embryo entirely fills the interior of the testa or whether there is a cavity (an air space) within: some seeds float, others do not. Paraphrasing Guppy, Ridley (1930: 304) goes on to say that seeds of *Operculina turpethum* "vary in floating powers from a few weeks to months and it may have been conveyed from island to island by sea." We traced these observations to Guppy (1906) in which he provided more details about the purely mechanical basis for flotation of *Operculina* seeds. Guppy (1906: 110) documented that embryos may shrink dramatically during the maturation and drying phase of seed development, and it is this shrinkage that creates an air space inside the seed testa.

We can conclude from these historical literature reports that seed flotation is a likely means for dispersal in *Operculina*, possibly for all species. Given the frequent and widespread distribution of several *Operculina* species on oceanic islands, the seeds must be able to withstand lengthy exposure to saltwater and still remain viable in order for long-distance oceanic dispersal to be effective. It is also necessary to mention a caveat concerning the identification of Pacific plants as "*Operculina turpethum*," given what we now know about widespread misapplication of that name to multiple species in the Pacific Basin, as documented elsewhere. It is quite possible that more than one Pacific *Operculina* species has been mixed up under the name *O. turpethum* used in the historical literature.

ECONOMIC USES

Operculina turpethum was historically a widely used medicinal plant and has long been a drug in Unani and Ayurvedic medicine in Asia (Austin, 1982b; Ahmad et al., 2017). Ahmad et al. (2017) report that the species is used in both medicinal systems as an expectorant, brain tonic, and laxative and has also been indicated for the treatment of arthritis, ascites, gout, hemiplegia, and facial palsy. The pharmacological properties of the plant, still being studied, include anti-inflammatory, analgesic, antioxidant, anti-diabetic, anti-ulcer, anti-diarrheal, antispasmodic, bronchodilator, anti-cancer, antimicrobial, and hepatoprotective actions (Ahmad et al., 2017). This extraordinary range of applications and properties is highly supportive of the hypothesis that *O. turpethum* has been widely dispersed by humans as a drug plant for many centuries.

Operculina macrocarpa is not as rich in pharmaceutical properties and medicinal uses, but it is well known in popular medicine in Brazil. It is called *batata-de-purga* or *jalapa*, and is cultivated on a commercial scale for its laxative, purgative, and skin healing properties; it is also used in the treatment of leukorrhea (Matos [1982] and Martins et al. [2000] in Michelin, 2008). Finally, extracts of *O. hamiltonii* have been reported to have anti-parasitic activity (Sobral et al. [2011] in Moreira et al., 2016).

An excellent review of the secondary metabolites in *Operculina* responsible for these medicinal properties is provided in Eich (2008).

TAXONOMIC TREATMENT

We now present a full systematic revision of *Operculina* that provides detailed morphological descriptions for 13 currently recognized species and one variety, plus one purported hybrid, and fully reconciles the nomenclature—about 60 names published or combined in *Operculina* are accounted for—with full synonymies and a list of Excluded Species. A key for identification is provided as well as summaries for the geographic distribution of each taxon and notes compiled from specimen labels and the published literature pertinent to the ecology, phenology, ethnobotanical uses, and vernacular names. Selected species are illustrated. An index to numbered collections examined is provided to aid in identifying and curating herbarium material (Appendix 1).

ORGANIZATION OF THE TAXONOMIC PART

Distribution is based on specimens we have examined and is derived from specimen label data entered in a BRAHMS database. The distribution maps are created directly from the specimen database, using QGIS software (QGIS, 2020). Only georeferenced collections are mapped; some older collections have legibility issues with handwriting, or the old place names used on the labels could not be rationalized with modern place names. Several online gazetteers were used to obtain the latitude/longitude coordinates, the principal source being the U.S. Board on Geographical Names (<http://geonames.usgs.gov/>)—USBGN—and its servers dedicated to place names within the United States and its dependencies, and a separate site for place names outside the political boundaries of the United States. When coordinates could not be located with the USBGN, we utilized Wikipedia, Google Maps, Falling Rain, Fuzzy Gazetteer, and several similar sites where obscure or very old place names can sometimes be found.

Ecology is compiled and summarized from specimen label information, supplemented, where available, by the authors' direct observations of living plants in the field.

Phenology is presented in tabular form, showing the number of flowering and fruiting collections seen per month. For this purpose, one collection includes all duplicates of the same collection number; multiple sheets are not counted individually. When organized in this way, it is relatively easy to visualize seasonality in reproductive behavior.

Vernacular names are listed alphabetically by country and with the source cited in parentheses. The source is either a voucher specimen where the name was recorded on the label or a publication in which the vernacular name was cited.

Typification of names without a holotype or prior lectotype choice is made here, with the goal to stabilize names in current use to the greatest extent possible. Where no original material could be found, some neotypes are proposed. In a few cases, we declined to choose a lecto- or neotype, because we have not been able to study the material known or reported to exist.

Uses are compiled primarily from statements on specimen labels, the voucher specimen cited in parentheses, supplemented with information published in the literature, followed by citation for the source.

Specimens examined indicate that we have cited all the collections we studied; this has been done for the rarer species that have rather few collections, usually less than 50, in herbaria. *Selected specimens examined* indicates that we cite only a portion of the specimens we studied, usually one collection per major administrative division (state, province, district) in a country, or one collection per island in the case of the oceanic species.

Selected species are illustrated by reproducing botanical illustrations that have been chosen because they demonstrate the characters that are taxonomically informative at the genus and species levels. Photographic plates illustrate specific diagnostic characters that are taxonomically useful (Figs. 2, 4).

A comprehensive index of numbered collections examined (Appendix 1) is provided at the end of the taxonomic treatment; the index omits all collections that are without collection number and is alphabetically arranged according to the surname of the primary collector and cross-referenced to the taxon numbers used in the body of the text.

Operculina Silva Manso, Enum. Subst. Braz.: 16, 49. 1836. TYPE: *Operculina turpethum* (L.) Silva Manso.

Turpethum Raf., Fl. Tellur. 4: 71. 1838 [title page 1836]. TYPE: *Turpethum indicum* Raf. (lectotype, designated by Manitz [1974: 639]).

Nemanthera Raf., Fl. Tellur. 4: 80. 1838 [title page 1836]. TYPE: *Nemanthera bufalina* (Lour.) Raf. [see Excluded Species].

Piptostegia Hoffmanns. & Rchb. in Hoffmanns., Preis-Verzeich Pfl., ed. 10: 11, 81. 1841. TYPE: *Piptostegia gomezii* Hoffmanns., nom. illeg. [= *Operculina macrocarpa*].

Ipomoea L. sect. *Operculina* (Silva Manso) Griseb., Fl. Brit. W. I.: 467. 1861.

Herbaceous twiners or lianas. Stems twining or prostrate; axial parts (stems, petioles, peduncles, pedicels) often winged, angled, or ribbed. Indumentum of 3 distinct types: simple unicellular trichomes; sessile glandular trichomes; elongate glandular trichomes. Leaves simple, entire, pinnately 5- to 9-lobed or palmately parted into 5 or 7 entire lobes; petioles stout or slender, terete or sulcate adaxially, base often swollen. Inflorescences cymose, or reduced to a solitary flower, or the cymes aggregated into panicles with up to 12 flowers; peduncles shorter than subtending petiole and stout, or elongate, slender, longer than subtending petiole; bracts small, deciduous, or foliose and persistent. Flowers usually medium to large (small in *Operculina maypurensis*), diurnal (possibly nocturnal in *O. polynesica*), odorless. Calyx ventricose (pear-shaped), broader at base, tapering upward and appressed to corolla, persistent and accrescent in fruit, cupping the mature fruit or the sepals may reflex away and downward, against the pedicel, leaving the fruit fully exposed at the apex of the pedicel, sepals becoming stiffly chartaceous to coriaceous, margins often eroding. Corolla campanulate or broadly funnelform (salverform in *O. pteripes*), midpetaline bands on the exterior of the corolla pilose, sericeous, or ± shaggy with long hirsute hairs, sometimes only sparsely so (glabrous in *O. aequisepala*, *O. polynesica*, *O. turpethum*, *O. ventricosa*), sometimes dotted with tiny golden glands, limb erect or spreading, entire or ruffled, rarely lobed. Stamens included (exserted in *O. pteripes*), filaments basally flattened, broadly adnate to corolla tube for 1/4 to 1/2 their length, free and filamentous above insertion point, glabrous except for trichomes on and around insertion point, anthers spirally coiled at dehiscence. Pollen 3-zonocolpate to sometimes 6-pantocolpate, micro-echinate to micro-granulate. Pistil included (exserted in *O. pteripes*);

nectary disc annular, surrounding ovary base; ovary superior, 2-locular, each locule 2-ovulate, glabrous or hirsute; style terminal, filamentous, glabrous or basally hirsute or rarely whitish tomentose almost to middle (*O. ventricosa*); stigmas 2, terminal, deeply lobed, lobes elongate, densely covered in filiform or bulbous papillae. Fruiting calyx accrescent, persistent, cupping fruit or reflexed against pedicel. Fruit an operculate capsule: apical fruit wall (operculum, exocarp) fleshy at first, drying leathery and dehiscing circumscissily; endocarp underneath brittle, thin, translucent, tardily and irregularly shattering; lower fruit wall indehiscent. Seeds 4 or fewer, ovoid-trigonous and carinate or subglobose, dull, blackish or brown, completely glabrous or with trichomes along the angles only (*O. petaloidea*, *O. riedeliana*); hilum basal, sunken, C- or D-shaped, glabrous or densely covered in short trichomes. Cotyledons 2, broadly ovate, entire, petiolate; laminas basally rounded or emarginate, apically emarginate or bilobed, the lobe apices broadly and smoothly rounded.

Distribution. A pantropical genus (Fig. 5) comprising 13 species, including one variety, and one purported hybrid, with six of the species native in the Neotropics (and two more naturalized there), five in Oceania, four in Asia/Malesia, and three in Australia. *Operculina* is not native in Africa or Madagascar; two species are naturalized there.

Discussion. *Operculina* has three diagnostic characters that set it apart from other genera with a single style and biglobose stigmas: the development of wings on portions of the plant axis; the spirally twisted anther dehiscence; and the unique operculate fruit structure and circumscissile dehiscence mechanism. These morphological features are taxonomically useful for recognizing species of *Operculina*. Although we prefer to avoid single-character genera and have tried to identify other characters to delimit *Operculina*, at the present level of understanding the unique fruit structure and dehiscence mechanism are the only morphological features that absolutely define *Operculina*; other morphological characters are indicative, but not definitive, for genus discrimination. The alate axial parts, hirsute midpetaline bands, and spirally twisted anthers are good field characters for recognizing some species of *Operculina*, but not every species has all three characters.

Vernacular names. The USDA PLANTS Database proposes the English common name "lid-pod" for all taxa of *Operculina* that occur in the United States and its territories (USDA, NRCS, 2016). Additional vernacular names are listed under each taxon.

The species are arranged in alphabetical order by species epithet, except for the hybrid, which follows the two purported parent species. Synonyms are grouped into homotypic blocks ordered in chronological sequence, basionym first.

KEY TO SPECIES OF *OPERCULINA*

1. Leaves deeply pinnately or palmately lobed or parted 2

1′. Leaves entire or shallowly 3-lobed basally (rarely irregularly 5- or 7-toothed in *O. pinnatifida*) 3

2. Leaves palmately lobed or parted; corollas 4–7.5 cm long; capsule 2.5–3.8 cm diam. . . . . *O. macrocarpa* (L.) Urb.

2′. Leaves irregularly pinnately lobed or divided; corollas 3.5–5 cm long; capsules 1.5–2 cm diam. . . . . *O. pinnatifida* (Kunth) O'Donell

3. Corolla yellow, orange, or reddish 4

3′. Corolla white, with or without yellow inside at tube base 7

4. Corolla salverform, pink, red-orange to red-salmon; stamens and pistil exserted; peduncles winged near middle . . . . *O. pteripes* (G. Don) O'Donell

4′. Corolla campanulate or broadly funnelform, yellow; stamens and pistil included; peduncles terete or slightly angled . . . 5

5. Corolla bright butter-yellow; calyx drying reddish brown . . . . *O. hamiltonii* (G. Don) D. F. Austin & Staples

5′. Corolla pale yellow or creamy; calyx drying tan to black-brown, with straw-colored margins 6

6. Sepals elliptic; leaf blades narrowly ovate to oblong, linear, or elliptic, drying reddish and often glaucous, base rounded to truncate or slightly emarginate . . . . *O. petaloidea* (Choisy) Ooststr.

6′. Sepals broadly elliptic to orbicular; leaf blades broadly ovate to orbicular, drying brown or black-brown, base cordate . . . . *O. riedeliana* (Oliv.) Ooststr.

7. Corolla midpetaline bands (interplicae) shaggy-hairy with simple hairs (reduced to tiny apical tufts in *O. maypurensis*); tiny golden gland dots absent or not evident 8

7′. Corolla midpetaline bands without shaggy indumentum of simple hairs; corolla exterior ± covered in tiny golden gland dots 12

8. Corollas 2.2–2.8 cm long; leaf blades narrowly lanceolate or linear-oblong, 4.3–7 × 0.5–0.9 cm . . . . *O. maypurensis* (Hallier f.) A. R. Simões & Staples

8′. Corollas 3.5 cm and larger; leaf blades usually broader (if lanceolate or linear-oblong then at least 8 × 3 cm) 9

9. Leaves irregularly 5- to 9-lobed; corollas 3.5–5 cm long . . . . *O. pinnatifida* (Kunth) O'Donell

9′. Leaves entire; corollas (4–)4.5–7 cm long 10

10. Leaves triangular to hastate to narrowly ovate-cordate; petioles winged near base . . . . . *O. codonantha* (Benth.) Hallier f.

10′. Leaves broadly cordate to ovate-orbicular (rarely narrowly oblong to linear-lanceolate); petioles terete to longitudinally striate 11

11. Sepals 13–17 mm long, broadly elliptic-orbicular; capsules 1.5–3 cm diam.; seeds pubescent along angles . . . . *O. riedeliana* (Oliv.) Ooststr.
11′. Sepals 17–30 mm long, elliptic to broadly ovate; capsules 3.5–4 cm diam.; seeds glabrous . . . *O. sericantha* (Miq.) Ooststr.
12. Stems usually spirally longitudinally alate, sometimes only angulate or narrowly alate 13
12′. Stems terete or longitudinally striate or angulate—not obviously alate 14
13. Sepals abaxially glabrous or nearly so (rarely sparsely sericeous toward base); corolla 2–3 cm long; capsule 0.6–0.9 cm diam.; annual plant with tap root . . . . *O. aequisepala* (Domin) R. W. Johnson
13′. Sepals abaxially pubescent with dimorphic hairs: densely velvety with shorter appressed hairs and scattered, longer pilose-erect hairs; corolla 3–4 cm long; capsule 1.5–1.8 cm diam.; perennial plant with fleshy, branched roots . . . . *O. turpethum* (L.) Silva Manso
14. Inflorescence bracts 1.1–1.3 cm long, caducous; stems and leaves pubescent; sepals 1.8–2.3 cm long at flowering, apically emarginate or praemorse . . . . *O. polynesica* Staples
14′. Inflorescence bracts 2.4–7 cm long, present at flowering, deciduous in fruit; stems and leaves glabrous or sparsely pubescent; sepals 2.5–4.4 cm long, apically rounded to obtuse . . . . *O. ventricosa* (Bertero) Peter

NOTE

Specimens of taxon 14, the purported hybrid between *Operculina turpethum* × *O. ventricosa*, key out at couplets 13–14; it proved impossible to separate this polymorphic assemblage from the parental species due to the intergrading character states observed.

1. **Operculina aequisepala** (Domin) R. W. Johnson, J. Adelaide Bot. Garden 2(4): 355. 1980. *Ipomoea aequisepala* Domin, Biblioth. Bot. 22(89^5): 535. [Beiträge zur Flora und Pflanzengeographie Australiens 2: 1089.] 1928. TYPE: Australia. Queensland: "inter opp. Hughenden et Cloncurry, 1909–10," *Domin 7959* (lectotype, designated here, PR PR-530569 image!, excluding the detached tendril in center of sheet [see Comments]).

Annual creeper or twiner, said to be odoriferous (*Jensen s.n.*); all parts nearly glabrous; sap copious, milky. Stems robust, 1–5 m, greenish drying brownish, angulate-alate, glabrescent or sparsely pilose. Root a tap root. Leaf blades entire, broadly ovate to reniform or suborbicular, (2–)7–20 × (2–)7–25 cm, membranous, adaxially darker, ± glabrous (few hairs along veins), abaxially paler, sparsely minutely appressed pilose on veins, base cordate, basal sinus broad, apex obtuse or scarcely acute, mucronate; secondary veins 5 to 7 either side of midvein, prominent underneath, tertiary veins thin, transverse; petioles 7–8(–9) cm, narrowly alate distally, glabrescent or sparsely appressed pilose. Inflorescences axillary, cymose, 1- to 3-flowered; peduncles ca. 1–5 cm, slightly pilose, distally angled-alate; bracts and bracteoles elongate-elliptic to narrowly obovate, 0.7–2 cm, shortly mucronate to caudate-apiculate, subscarious, tardily deciduous, glabrate or abaxially thinly pilose especially on veins, margins ciliolate; pedicels slightly clavate, ca. 0.5–2.5 cm, angulate, glabrous. Flowers diurnal. Sepals ± equal, broadly ovate, 1.2–1.7(–2) cm, the outer 2 slightly wider, quite glabrous or abaxially sparsely sericeous toward the base, apex obtuse to rounded, at first mucronulate, persistent and accrescent in fruit. Corolla campanulate-funnelform, entirely white or with yellow inside the constricted tube base, about twice as long as the calyx, 2–3 cm, glabrous inside and out, outside covered in tiny sessile golden glands. Stamens inserted on the lower fifth of the corolla; anthers linear-oblong, ca. 2.5 mm, spirally twisted. Pollen 3-zonocolpate to 6-pantocolpate. Pistils included; disc unknown; ovary bilocular; style filiform, ca. 13 mm; stigmas globose, almost fused into one. Fruiting calyx enclosing fruit; sepals broadly rounded or emarginate, greenish tinged reddish on exposed parts, drying light brown to straw-colored, glabrate, margins and apex scarious-erose. Capsule depressed globose, often 4-lobed, straw-colored; operculum ca. 6–9 mm diam., deciduous; endocarp pale tan, hyaline, shattering. Seeds 4 (or less), blackish, glabrous.

Distribution. *Operculina aequisepala* is endemic to Australia where it occurs in the Northern Territory, Queensland, Western Australia, and was collected once in New South Wales. It is also cultivated in the Capital Territory at a research station (Fig. 6).

Ecology. *Operculina aequisepala* is a prostrate creeper or low twiner usually reported in grasslands. The habitats noted by collectors include: a flat alluvial plain of heavy podsol with *Astrebla* F. Muell. ex Benth. species; on red crackling clay plain (crabholed) with *Eragrostis xerophila* Domin and *Acacia victoriae* Benth.; sandy island beach; riverbank in *Eucalyptus camaldulensis* Dehnh. low woodland on well-drained, alluvial sands; in sparse steppe vegetation on craggy dissected limestone; in riverine woodland; rolling downs with grassland (*Iseilema* Andersson, *Cynodon* Trin., *Panicum* L., etc.) and scattered low shrubs (*Terminalia* L.?) on gray-brown clay soil; irrigation project, under tall *Sorghum* Moench on gray clay soil; open roadside in farming area; treeless blacksoil plain; on black soil cracking clay, in Mitchell grass flat; in gilgais in gray, heavy-textured soil with *Iseilema* grassland; substrates reported typically mention clays but also include black soil, gray soil, sandy, lateritic, and limestone. The elevation is rarely recorded; one report states 600 m.

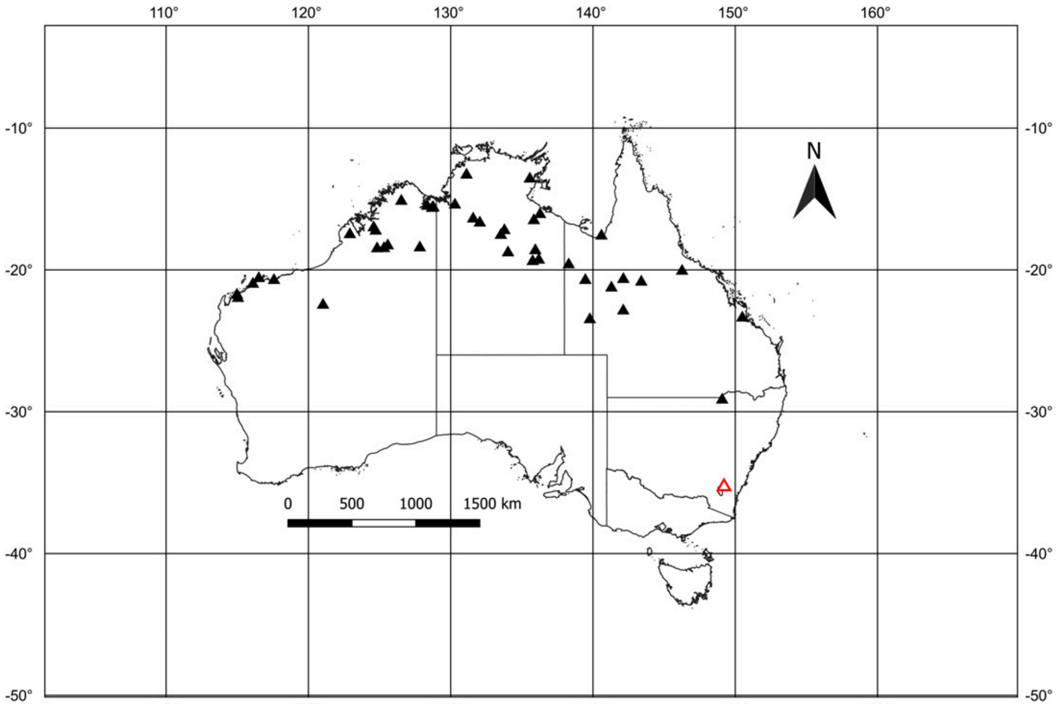

Figure 6. Distribution map for *Operculina aequisepala* (Domin) R. W. Johnson. Solid triangles are natural populations; open triangle is a cultivated specimen.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections		1	4	4	3	1	1	1	1	1		
Fruiting collections			6	4	3	1	1			1		

Vernacular names. None recorded.

Typification. There are two syntypes collected by Domin in the Prague (PR) herbarium; we have chosen as lectotype the one numbered 7959, which has the most complete material and also has Domin's handwritten analysis and sketch of the floral parts. However, this sheet has one extraneous element: the detached tendril and single stem node in the center of the sheet are evidently Vitaceae and must be excluded as type material for this convolvulaceous name.

How to correctly cite Domin's work is problematic: the volume and pagination are confusing and the several parts published in the journal *Bibliotheca Botanica* were then collected and bound as a single work, *Beiträge zur Flora und Pflanzengeographie Australiens*. The citation provided here follows the recommended format for citing the work (Stafleu & Cowan, 1976: 668, entry 1496), which gives first the journal volume (heft, part) and pagination. We also provide in brackets the collected work title, volume, and pagination. This should help to alleviate confusion in how to correctly associate the volumes, parts, heft, and dual series of pagination.

Uses. *Operculina aequisepala* was once reported to be "greedily eaten by sheep and cattle" (*Hanning s.n.*) so is perhaps a good forage plant for livestock.

Comments. When making the combination in *Operculina*, Johnson (1980) claimed the protologue is in error in the following points: plants are not perennial from an enlarged tuberous root, but surely an annual with a taproot; also he suggested the operculum is small: just 6–9 mm in diameter. Morphologically *O. aequisepala* is quite similar to *O. turpethum*, and for a long time all Australian specimens were included under that species. Johnson (1980) separated *O. aequisepala* based on more or less glabrous sepals (vs. pubescent in *O. turpethum*) and smaller flowers ($<$ 3 cm length); he also pointed out the nearly disjunct distributions of the two species, with *O. aequisepala* widespread in semi-arid inland sites across northern and western Australia, and *O. turpethum* being found in coastal habitats of eastern and far northern Australia. However, now that more collections are available, the distributions for these two species in Australia seem to overlap (AVH, 2016).

Specimens examined [54 collections total]. AUSTRALIA. **New South Wales:** Moree Plains, 45 km N of Moree, 29°10′S, 149°05′E, 20 Mar. 2007, *M. Jensen s.n.* (NSW). **Northern Territory:** Adelaide River township, 13°18′S, 131°07′E, Feb. 1979, *S. E. Pickering s.n.* (K, L, MEL); Alexandria, 19°18′S, 136°12′E, 25 Mar. 1981, *T. S. Henshall 3458* (BRI, NT, PAUH, SP); Alroy Downs, 19°24′S, 135°46′E, 8 Mar. 1959, *G. Chippendale 5381* (CANB, K, L); Auvergne Station, 15°25′S, 130°18′E, 14 July 1977, *J. Must 1622* (CANB); Banka Banka homestead, 18°47′S, 134°02′E, 23 Mar. 1955, *R. E. Winkworth 1018* (CANB); Beetaloo, 17°13′S, 133°47′E, 10 Mar. 1959, *G. Chippendale 5444* (K, L); Borroloola, 16°05′S, 136°17′E, 13 May 1983, *K. L. Wilson 5345* (NSW); Brunette Downs H.S., Bishop's Bore, 18°38′S, 135°57′E, 10 Oct. 1958, *G. Chippendale 5013* (L); Elliott, 17°33′S, 133°32′E, 27 Mar. 1963, *R. Swinbourne 736* (CANB, NSW); 15 mi. SE of Elliott, 17°33′S, 133°32′E, 12 Mar. 1969, *N. Byrnes NB1428* (DNA, K); Kynum, June 1903, *J. H. Hanning s.n.* (NSW); McArthur River Station, 16°31′S, 135°51′E, 4 Apr. 1979, *M. O. Rankin 1891* (CANB); Ranken, 13°35′S, 135°34′E, 20 June 1960, *G. Chippendale 7242* (K, L); Top Springs, 16°41′S, 132°03′E, 20 Apr. 1983, *K. L. Wilson 4729* (NSW); Top Springs, 16°24′S, 131°35′E, 21 Apr. 1983, *K. L. Wilson 4747* (NSW). **Queensland:** Burke distr., 19°38′S, 138°18′E, 27 May 1948, *R. A. Perry 967* (CANB); Charters Towers, 20°05′S, 146°16′E, 3 May 1965, *D. A. Carrigan s.n.* (CANB); Flinders River, 17°36′S, 140°36′E, anno 1882, *E. Palmer s.n.* (MEL); Georgina River sources, 23°30′S, 139°47′E, anno 1887, *A. H. Glisson s.n.* (MEL); inter Hughenden et Cloncurry, 20°39′36″S, 142°08′24″E, 1909–10, *Domin 7958* (syntype PR); 78 km W of Hughenden, 20°51′S, 143°24′E, 17 Apr. 1975, *A. E. Orchard 4717* (K, L); McKinlay Township, 7 mi. N of McKinlay, 21°16′S, 141°18′E, 19 Mar. 1954, *M. Lazarides 4425* (CANB, K, NSW); Mt. Isa, 20°44′S, 139°28′E, 600 m, 1 Aug. 1971, *M. M. J. van Balgooy 1432* (L); 20 mi. E of Mt. Isa, 20°44′S, 139°28′E, Oct. 1963, *J. Mathews s.n.* (NSW); Mueller's Range, 22°53′S, 142°08′E, s.d., *C. M. Birch s.n.* (MEL); Rockhampton, 23°23′S, 150°30′E, s.d., *unknown s.n.* (MEL). **Western Australia:** Ashburton River vic., 21°46′07″S, 114°58′47″E, s.d., *E. Clement s.n.* (K); Carawine Pool, 22°28′40″S, 121°01′50″E, 5 July 1984, *K. Newbey 10315* (K); Cherrabin, 18°29′S, 125°19′E, 18 Apr. 1972, *T. E. H. Aplin 4734* (CANB, K, PERTH); Dampier Archipelago, Enderby Island, 20°36′S, 116°31′E, 28 Mar. 1984, *B. R. Maslin 5559* (K); Dampiers Land, 17°30′S, 122°55′E, anno 1883, *Gazelle Expedition 20* (MEL); Dumas Lookout, 15°37′S, 128°45′E, 23 Apr. 1983, *K. L. Wilson 4811* (K, NSW); Fortescue River, 21°00′S, 116°06′E, June 1878, *unknown s.n.* (MEL); Gogo, 18°17′24″S, 125°34′48″E, 10 Apr. 1951, *C. A. Gardner 10006* (CANB, K); Kalumburu Mission, 15°09′S, 126°32′E, 31 Aug. 1954, *Lazarides 4835* (CANB); Kalumburu Mission, 31 Aug. 1954, *N. H. Speck 4835* (CANB); Kimberley Research Station, 15°39′S, 128°42′E, 10 Aug. 1967, *Kimberley Research Station staff s.n.* (CANB); Kununurra, 15°36′S, 128°47′E, 12 Apr. 1970, *R. Pullen 10170* (CANB); Mindaroo Station, 22°00′S, 115°03′E, 14 Apr. 1978, *A. A. Mitchell 538* (CANB); Noonkanbah, 18°30′S, 124°50′E, 10 Jan. 1911, *E. Mjoberg 42* (S); Ord River, 15°30′S, 128°21′E, May 1966, *P. Wright s.n.* (NSW); Palm Spring, Duncan Hwy., 29 km SE of Halls Gap, 18°26′S, 127°50′E, 19 May 1988, *H. Streimann 8291* (A); Sherlock River, 20°44′S, 117°35′E, 28 July 1878, *unknown s.n.* (MEL); Van Emmerick Range, 17°01′10″S, 124°35′30″E, 4 May 1988, *M. J. S. Sands 4700* (K); Wombarella Creek, 17°15′15″S, 124°43′50″E, 13 Apr. 1988, *M. J. S. Sands 4371* (K).

Cultivated. AUSTRALIA. **Capital Territory:** Canberra, cultivated at CSIRO Black Mountain labs, 35°17′S, 149°13′E, 20 Sep. 1967, *M. Evans 2626* (AAH, K, L).

FRANCE. **Hauts-de-Seine:** Arboretum de la Vallée-aux-Loupes, living collections of the Collection Nationale des Convolvulacées, 26 Aug. 2009, *A. R. Simões 14* (BM).

UNITED KINGDOM. **England:** Surrey, Royal Botanic Gardens, Kew, June 1864, *Kew Gardens s.n.* (K).

Additional specimens of *Operculina aequisepala* can be found online via the Australian Virtual Herbarium site (AVH, 2016). We have not, however, verified the identifications for these online records because most of them lack digital images of the specimens.

2. **Operculina codonantha** (Benth.) Hallier f., Bot. Jahrb. Syst. 16: 550. 1893. *Ipomoea codonantha* Benth., Pl. Hartweg.: 120. 1843. TYPE: Ecuador. Guayas: Guayaquil, *Hartweg 675* (lectotype, designated here, K [barcode] K000613069!; isolectotypes, BM not seen, K [bc] K000613068!, LD [bc] LD1409878!). Figures 7, 8.

Operculina brownii Ooststr., Blumea 3: 366. 1939, syn. nov., replacement name for *Ipomoea alata* R. Br., Prodr.: 484. 1810, non *O. alata* Urb., 1902. *Convolvulus alatus* (R. Br.) Spreng., Syst. Veg. 1: 596. 1824. TYPE: Australia. Northern Territory: islands near Cape Wilberforce, 22–23 Feb. 1803, *R. Brown s.n.* [under *Iter Australiensis 2742*] (syntype, BM [bc] BM000832566 image!).

Perennial vine or liana, all parts glabrous or nearly so; sap unknown. Stems twining to 5 m, ca. 3 mm diam., fistulose, cylindrical, longitudinally striate-angular or narrowly winged; innovations with few (caducous) trichomes. Leaf blades triangular or hastate to narrowly ovate-cordate, 6.2–13 × 4.8–9.5 cm, basal sinus broad and shallow, lobes rounded or angulate-hastate, margins entire, slightly undulate, apex obtuse, acute, or attenuate, glabrous or sometimes with a patch of pilose trichomes abaxially near the lamina base; secondary veins 7 or 8 either side of midrib; petiole 1–4 cm, slightly winged near the base. Inflorescences axillary, flowers usually solitary; peduncles stout, longer than the subtending petioles, (2–)5.5–17.8 cm, 3- or 4-angled, alate basally or along the entire length; bracts caducous, not seen; pedicels clavate, angular-striate but not alate, 1.5–3 cm, 0.5 cm wide apically, thickened and 5-angled in fruit, glabrous. Flowers diurnal, showy, odorless. Sepals subequal, broadly elliptic-obovate to orbicular, (1.4–)2.2–2.7 × (1.2–)1.6–2 cm, basally truncate, margins entire, occasionally drying undulate, apex broadly rounded or inner ones emarginate, glabrous. Corollas broadly campanulate to broadly funnelform, white, 4.5–6.5 × 4–5.5 cm, limb 5-toothed; midpetaline bands sparsely to densely appressed villous with a mixture of longer wavy-undulate trichomes and shorter wavy ones, golden gland dots not seen. Stamens ± equal, included,

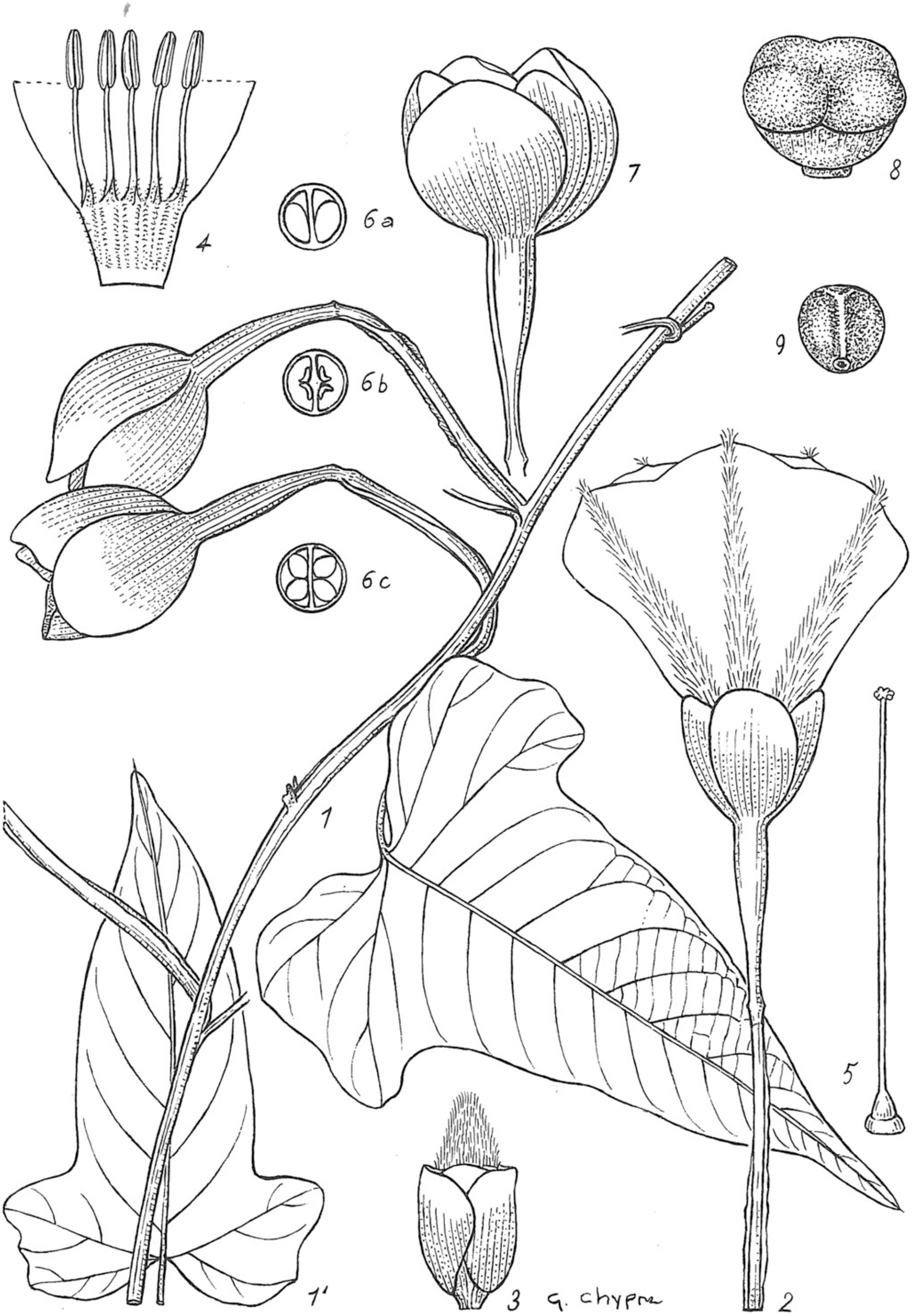

Figure 7. An illustration for *Operculina codonantha* (Benth.) Hallier f. Original caption, translated: 1. flowering branch; 1′. leaf blade; 2. flower in side view; 3. flower bud; 4. lower corolla opened, showing undehisced anthers; 5. pistil; 6a–c. ovary in sectional views; 7. fruiting calyx; 8. capsule; 9. seed. Vouchers for illustration: *Balansa 3350*, *MacKee 39103*, both in P. Reproduced from *Flore de la Nouvelle-Calédonie* (Heine, 1984: 33, plate 9, drawn by G. Chypre) under the name *O. brownii*. © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris. Reproduced with permission.

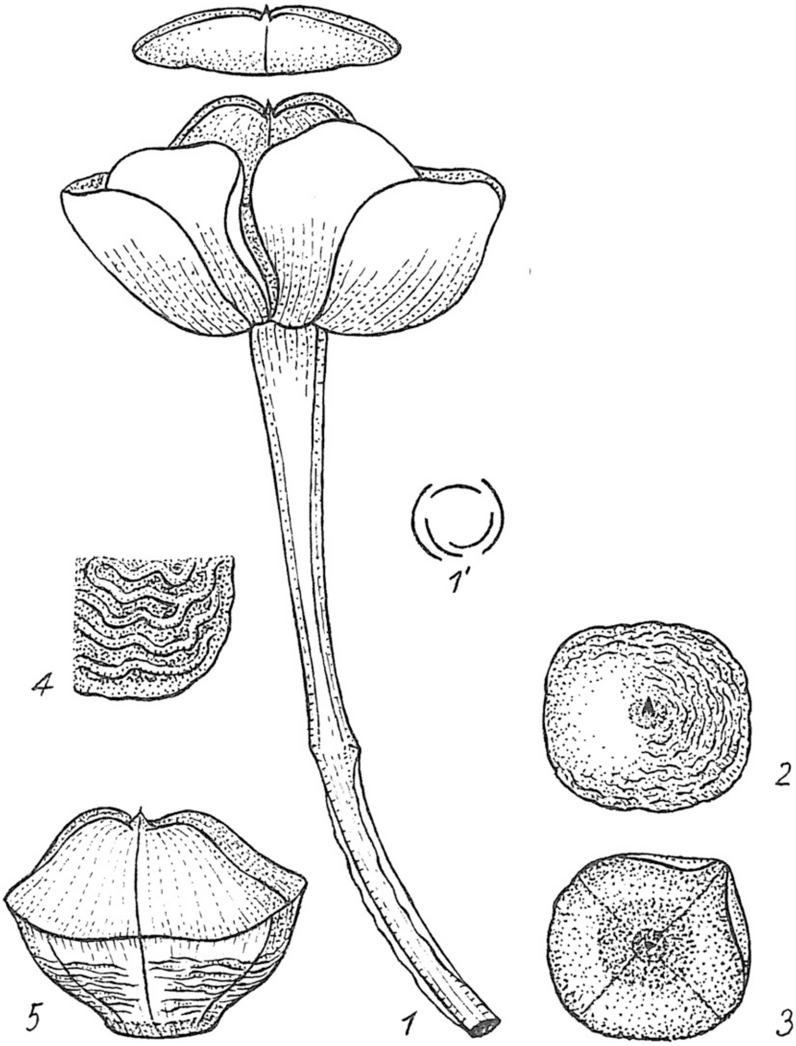

Figure 8. An illustration for *Operculina codonantha* (Benth.) Hallier f. Original caption, translated: 1. fruiting calyx enclosing the capsule, the detached operculum above; 1′. schema of quincuncial sepal arrangement in fruiting calyx; 2. operculum, abaxial (outer) surface; 3. operculum, adaxial (inner) surface; 4. detail of operculum, abaxial surface; 5. capsule, the calyx and operculum removed. Voucher for illustration: *MacKee 39103* in P. Reproduced from *Flore de la Nouvelle-Calédonie* (Heine, 1984: 35, plate 10, in part, drawn by G. Chypre) under the name *O. brownii*. © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris. Reproduced with permission.

white; filaments 3.2–3.5 cm, broadly adnate to the corolla tube for 1/3 to 1/2 their length, margins capitate-glandular where adnate, middle glabrous, free portions filamentous, basally bearded, glabrous above; anthers spirally twisted at maturity, 4–7 mm, base shallowly sagittate. Pollen 3-zonocolpate. Pistil included, glabrous; disc prominent, annular; ovary globose to conical, slightly 4-lobed, 2 mm tall; style filiform, 3.3–3.5 cm; stigma biglobose, superficially tetraglobose, lobed and papillose. Fruiting calyx ± enclosing capsule, woody, drying reddish brown; sepals accrescent, up to 3 cm; margins often erose. Capsule depressed globose, 4-lobed, 3–4 cm diam., 2-celled, each cell 1- or 2-seeded; operculum drying leathery, 1.7–2.2 cm diam., blackish brown, coarsely wrinkled; endocarp yellowish, hyaline, breaking irregularly. Seeds 4 or less, ovoid-carinate, ca. 15 mm, dull black, glabrous.

Distribution. *Operculina codonantha* occurs in Australia (Northern Territory, Queensland, Western Australia) and the southwestern Pacific islands (Tonga, Fiji, New Caledonia), Java (cultivated), then disjunct to eastern French Polynesia in the Marquesas (Eiao, Hiva Oa, Nuku Hiva, Tahuata). In the Neotropics, it is known from Panama, Ecuador, Peru, and Bolivia (Fig. 9).

Ecology. The Pacific populations are reported by collectors as growing along hillsides and on ridge crests in dry scrub forest and secondary regrowth, associated with *Cordia lutea* Lam., *Waltheria indica* L., *Premna* L., *Dodonaea* Mill., and *Thespesia* Sol. ex Corrêa. In the Neotropics, the vines grow in forests, among weeds and ruderales; and *zona de bosque muy seco tropical* [very dry tropical forest zone] (*L. A. de Escobar 1179*). Elevation ranges from 50 to 400 m. The vines often die during the dry season, but the enlarged calyces and fruits persist and are visible entangled in, and on top of, thickets and trees.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections		1	6	3	4	1	2		1			
Fruiting collections	2	1		3	3	3	2		3		1	

The phenology combines data for the Pacific and South America specimens seen.

Vernacular names. Marquesas Islands: *pania oke* (Sachet, 1975: 32, citing *Dupetit-Thouars 20*). Panama: *batatilla* (*Woodworth & Vestal 684*).

Comments. We are unable to find any consistent morphological characters to separate *Operculina brownii* in the South Pacific from *O. codonantha* in the Neotropics and are here merging them under the latter name. Although Ooststroom (1939: 361, 366) stated the corolla of *O. brownii* was completely glabrous, this is not the case generally; possibly the specimen he cited (*Jaheri 490* from Thursday Island [BO]) has a glabrous corolla, but we have seen many Australian and Pacific specimens with the shaggy midpetaline bands typical for Neotropical *O. codonantha*. Plants from throughout the wide distribution of this species are remarkably similar in appearance, sharing a triangular leaf blade, glabrous calyx, shaggy-hirsute midpetaline bands, and distinctive reddish-brown sepal color in dry material.

This species has been long confused with, and often misidentified as, *Operculina turpethum* in the Pacific islands (Sachet, 1975; Smith, 1991). Ooststroom proposed a replacement name for this species because the oldest epithet he was aware of for it (*Ipomoea alata* R. Br.) is preoccupied in *Operculina* by *O. alata* Urb.

Selected specimens examined [101 collections]. AUSTRALIA. **Northern Territory:** Port Darwin, 12°25′S, 130°48′E, Oct. 1869, *R. Schomburgk 231* (K); Cannon Hill, 12°23′S, 132°57′E, 50 m, 24 July 1971, *M. M. J. van Balgooy et al. 1331* (L); Pobassoo Island, 11°54′42″S, 136°26′52″E, Feb. 1803, *R. Brown Iter Australiensis 2742* (BM). **Queensland:** Cook Distr., Seisia, 10°50′42″S, 142°22′30″E, 13 Mar. 1999, *B. M. Waterhouse BMW-5123* (BRI); Thursday Island, June 1897, *F. M. Bailey 87* (BRI); Yam Island, Torres Strait, 28 Mar. 2003, *B. M. Waterhouse BMW-6598* (BRI); Cape York Peninsula, s. loc., 29 June 1885, *W. Bäuerlen 33* (MEL). **Western Australia:** Augustus Island, Bonaparte archipelago, 14 May 1972, *P. G. Wilson 10772* (PERTH); Cape Voltaire, W side of Krait Bay, 17 Mar. 1994, *A. A. Mitchell 3418* (BRI); Koolan Island, 16°07′S, 123°46′E, 2 June 1985, *P. A. Fryxell et al. 4607* (L); Port Warrender, N Kimberley, 8 June 1974, *J. S. Beard 7005* (PERTH). FIJI. **Lomaiviti group:** Ngau island, Sawaieke vic., 17°59′S, 179°16′E, 30–200 m, anno 1953, *A. C. Smith 7952* (BISH, GH, K, L, N, NY, P, S, U, US). **Vanua Levu group:** Vanua Levu island, Bua, 16°50′S, 178°45′E, 20 Sep. 1933, *Mrs. H. B. R. Parham 365* (K). **S. loc.:** 1838–1842, *U.S. South Pacific Exploring Expedition s.n.* (GH). FRENCH POLYNESIA. **Marquesas Islands:** Eiao, 8°00′S, 140°42′W, 400 m, 20 Sep. 1922, *W. B. Jones 1517* (BISH); Eiao, Opituha Gulch, 8°00′S, 140°42′W, 270 m, 7 July 1998, *J. Florence et al. 9343* (BISH, P, PAP, PTBG, US); same locality, 274 m, 7 July 1988, *S. Perlman et al. 10048* (BISH); Hiva Oa, Tahauku, 9°48′S, 139°01′W, 250 m, 16 Nov. 1974, *M.-H. Sachet 1867* (BISH, PAP); Taaoa, 9°45′S, 139°00′W, 250 m, 15 Jan. 1975, *M.-H. Sachet 2111* (BISH, PAP); Nuku Hiva, aéroport vic., 8°49′S, 140°13′W, 300 m, 14 Mar. 1986, *J. Florence 7543* (BISH, P, PAP); Nuku Hiva, Henua a Taha, 8°52′S, 140°12′W, 400 m, 15 May 2007, *J. F. Butaud 1573* (PAP); same locality, 28 May 2007, *J. F. Butaud 1575* (PAP); same locality, 344 m, 6 June 2007, *J. F. Butaud & F. Jacq 1582* (PAP); Nuku Hiva, s. loc., 8°49′S, 140°13′W, anno 1919, *M. Henry 57* (P), anno 1855, *L. Jardin s.n.* (P); Tahuata, Hanatetena, 9°57′S, 139°05′W, 25 May 1994, *J. P. Luce 115* (P); Tahuata, Taipioho valley, 9°57′S, 139°05′W, 25 May 1994, *J. P. Luce 114* (P); Ua Huka, Col Hinitaihava to Hane, 8°54′S, 139°33′W, 194 m, 22 Apr. 2013, *J. F. Butaud 3177* (PAP). **S. loc.:** s.d., *Dupetit-Thouars 114B* (P). NEW CALEDONIA. Balade, 20°19′S, 164°30′E, 10 m, 19 May 1981, *H. S. MacKee 39103* (K, L, P); Diahot, 21°51′S, 165°54′E, s.d., *B. Balansa 3350* (A, BISH, K, L, P); Poum, 20°14′S, 164°01′E, 10 m, 20 May 1956, *H. S. MacKee 4594* (E, K, L, P), same loc., 29 June 1982, *H. S. MacKee 40555* (K, P); Poum, Malabou, 14 May 1983, 5 m, *H. S. MacKee 41488* (P). TONGA. **Vavau group:** Vavau, 18°40′S, 174°00′W, June 1891, *C. S. Crosby 126* (K).

BOLIVIA. **Pando:** Manuripi, entornos de Conquista, 160 m, 30 Jan. 1983, *Fernández Casas & Susanna 8552* (MO). ECUADOR. **Bolívar:** s. loc., 1°35′S, 79°05′W, s.d., *C. Jativa et al. 17* (NY). **El Oro:** Arenillas, 15 Mar. 1955, *E. Asplund 15763* (S); San Antonio, 22 Mar. 1967, *C. Pineda 65* (S). **Esmeraldas:** Hacienda Guayas, ± 20 km S of Esmeraldas, 14 Apr. 1967, *Sparre 15511* (S). **Guayas:** Chongon, 1 Apr. 1962, *Gilmartin 652* (NY); Guayaquil, Cerro Azul, 29 Apr. 1959, *G. Harling 4858* (MO, S); Guayaquil, 0–50 m, June 1923, *A. S. Hitchcock 20155* (GH); Guayas, Aug. 1836, *Gaudichaud 91* (P). **Los Ríos:** Jauneche Forest, Km. 70 along the Quenedo-Palenque rd., 1°16′S, 79°42′W, 70 m, 26 Mar. 1980, *C. H. Dodson & A. Gentry 9914* (FAU, MO). **Manabí:** El Recreo, May 1897, *H. F. A. von Eggers 15770* (M, P). PANAMA. **Canal Zone:** Barro Colorado Island, in new garden, second point E of the laboratories, 17 Jan. 1932, *Wetmore & Abbe 246* (A, F, GH). **Colón:** Chagres, 9°09′N, 80°06′W, 8 Jan. 1850, *A. Fendler 245* (MO); Frijoles, 24 Feb. 1932, *Woodworth & Vestal 684* (GH). PERU. **Lambayeque:** Cienego, Tonnenbaum-mischvold, 6°42′37″S, 79°56′03″W, 17 May 1957, *Ellenberg 1416* (U). **San Martín:** Juanjuí Mpio., Km. 9 Juanjuí to Jacanche, 13 Sep. 1990, *J. Diaz 4327* (FAU).

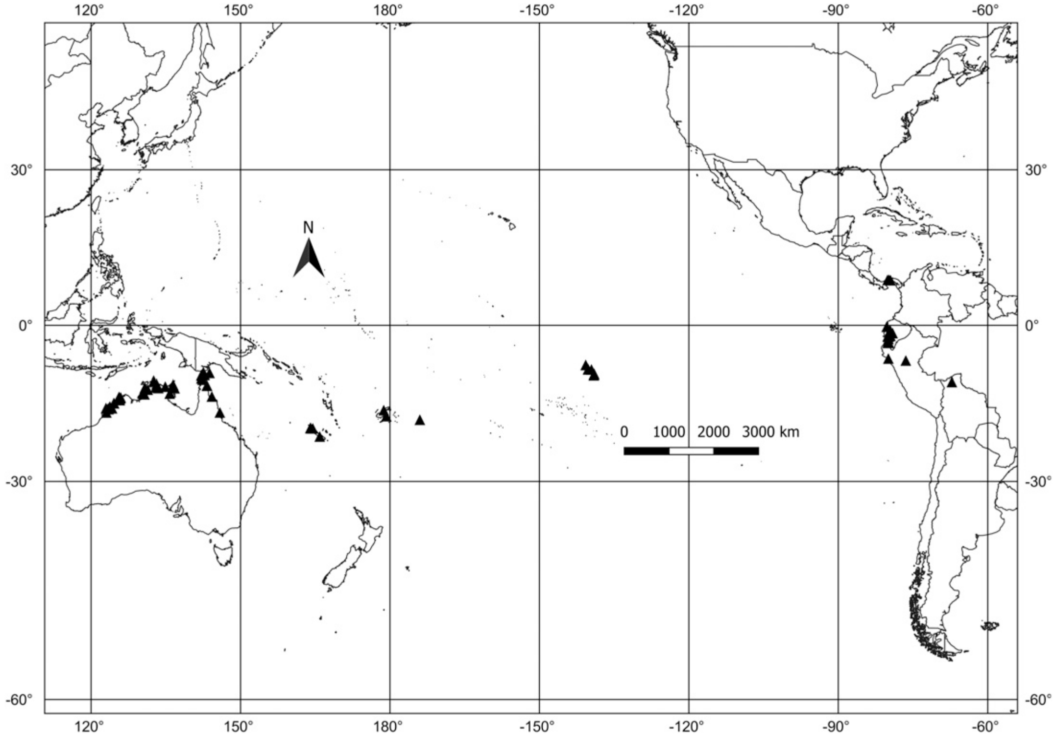

Figure 9. Distribution map for *Operculina codonantha* (Benth.) Hallier f.

Cultivated. FRANCE. **Hautes-de-Seine:** Arboretum de la Vallée-aux-Loupes, living collections of the Collection Nationale des Convolvulacées, 26 Aug. 2009, *A. R. Simões 8* (BM).

INDONESIA. **Java:** Jawa Barat, Bogor Botanic Garden, 6°35′51″S, 106°47′54″E, 11 Sep. 1907, *P. van Harreveld 5077* (L).

Many more specimens identified as *Operculina brownii* can be found online via the Australian Virtual Herbarium site (AVH, 2016). We have not, however, verified the identifications for all these digital records because rather few have specimen images associated with the records. At least some of them are misidentifications for *O. aequisepala* or *O. turpethum*, based on duplicate specimens we have studied from herbaria outside Australia.

3. Operculina hamiltonii (G. Don) D. F. Austin & Staples, J. Arnold Arbor. 64: 487. 1983. *Ipomoea hamiltonii* G. Don, Gen. Hist. 4: 268. 1838. *Convolvulus alatus* Ham., Prodr. Fl. Ind. Occ.: 24. 1825, nom. illeg., non *C. alatus* (R. Br.) Spreng., 1824. *Operculina alata* Urb., Symb. Antill. 3: 343. 1902. TYPE: Tobago. "in sepibus propre oppidum Scarborough," Oct.–Nov., *Hamilton s.n.* (holotype, not found). Tobago. Scarborough, 28 Nov. 1913, *W. E. Broadway 4801* (neotype, designated here, GH [bc] 00395309!; isoneotypes, BM [bc] BM001253072 image!, MO [bc] MO876098 image!, P [bc] P03878703 image!, U [bc] U.1232014 image!).

Ipomoea alulata Miq., Linnaea 18: 599. 1845. TYPE: Surinam. s. loc., s.d., *H. C. Focke 778* (lectotype, designated here, U [bc] U0001434!).

Ipomoea altissima Mart. ex Choisy in DC., Prodr. 9: 359. 1845, nom. illeg. *Operculina altissima* (Mart. ex Choisy) Meisn. in Mart., Fl. Bras. 7: 213. 1869. TYPE: Brazil. Amazonas: prov. Rio Negro, *Martius Iter. Brasil. '33'* (lectotype, designated here, M [bc] M0184761!).

Ipomoea pterodes Choisy in DC., Prodr. 9: 361. 1845. *Operculina pterodes* (Choisy) Meisn. in Mart., Fl. Bras. 7: 213. 1869. TYPE: French Guiana. anno 1802, *Gabriel 740* (holotype, G [bc] G00448102!).

Ipomoea ampliata Choisy in DC., Prodr. 9: 361. 1845. *Operculina ampliata* (Choisy) House, Bull. Torrey Bot. Club 33: 503. 1906. TYPE: Mexico. Campeche, "ins. oceani Pacifici," anno 1730, *W. Houstoun s.n.* (holotype, BM [bc] BM000953207!).

Operculina pterodes f. *pubescens* Pilg., Bot. Jahrb. Syst. 30: 186. 1901. *Operculina alata* var. *pubescens* (Pilg.) O'Donell, Lilloa 30: 61. 1960. TYPE: Brazil. Mato Grosso: Bandeira bei Cuiabá, Mar. 1899, *H. Meyer 325* (holotype, B†).

Perennial woody vines or lianas; roots tuberous; sap clear or white. Stems reddish, winged, the older woody portions spirally longitudinally striate, to at least 5 mm diam., glabrous to sparsely pubescent. Leaves simple; blades narrowly to broadly cordate, occasionally hastate, 4.5–9 × 3–7.5 cm, base cordate, the sinus deep or occasionally so shallow as to give the leaf base a rounded appearance, margins entire or broadly 3- or 5-lobate, the lobes separated by shallow sinuses, apex acute or attenuate, lateral lobes rounded or obtuse, subglabrous to hirtellous with simple trichomes, densest along the veins on the abaxial surface; petiole alate or striate, subglabrous, 0.8–3.5 cm. Inflorescences axillary, flowers solitary, rarely in few-flowered cymes; peduncles striate to angulate, sometimes winged distally, glabrous, greatly exceeding the subtending petiole, 3.3–8 cm; bracts 2, lanceolate to ovate, 7–16 × 3–6.5 mm, base rounded, blade membranous, apex acute to attenuate, fugacious, when present drying reddish brown, glabrous or subglabrous, margins with few trichomes; pedicels clavate, winged or angulate, glabrous, 1.5–2.5 cm, thickening in fruit, becoming strongly 5-angled. Flowers erect, diurnal, odorless. Calyx with sepals equal, broadly ovate to suborbicular, 2.3–3 × 1.6–2.1 cm, basally obtuse to acute, margins thin and membranous, entire, apices rounded, obtuse or acute, mucronate, glabrous, reddish brown in dry state, enlarging and becoming woody in fruit. Corolla campanulate, bright yellow, 3.5–5.2 × 3.3–5.1 cm, limb 5-toothed, midpetaline bands hirsute throughout or toward tips, minute glands not seen. Stamens included, subequal, 2.2–2.5 cm; basally adnate to corolla for about 1/2 their length, margins lined with glandular hairs up to insertion point, medially glabrous, free, filamentous and glabrous above insertion point; anthers spirally dehiscent, 8–10 mm, yellow, bases sagittate. Pollen 3-zonocolpate or 6-pantocolpate. Pistil included; style filiform, to 20 mm; ovary conical, 1.5–2 mm high, drying black, glabrous; stigma biglobose, the lobes pendent. Fruiting calyx accrescent, chartaceous to semi-woody, drying red-brown, reflexing in fruit; sepals 2.8–3.5 cm. Capsule depressed globose, 4-lobed, 1.5–2 cm diam., septate, 2-celled, each cell 1- or 2-seeded; operculum reddish brown, 1.2–1.4 cm diam., minutely apiculate; endocarp whitish, translucent. Seeds 4 or fewer, globose-carinate, 4–8 mm, dull brownish, glabrous; hilum broadly hippocrepiform (horseshoe-shaped), black, glabrous.

Two varieties are known; they are separable by the following key:

1. Leaves broadly ovate, hastate, or cordate . . . . *O. hamiltonii* var. *hamiltonii*
1′. Leaves narrowly lanceolate-hastate, often distinctly mucronate . . . . *O. hamiltonii* var. *mucronata*

3a. **Operculina hamiltonii** var. **hamiltonii.**

Distribution. Variety *hamiltonii* occurs in Mexico (possibly in error, see Comments), Central America (Costa Rica, Panama), the West Indies (Cuba, Dominican Republic, Haiti, Lesser Antilles, Trinidad and Tobago), and South America (Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Venezuela) (Fig. 10).

Ecology. *Operculina hamiltonii* var. *hamiltonii* is an opportunistic taxon that thrives on human disturbance, springing up in openings and margins in forest and secondary regrowth, in *bosque primario seco tropical* [primary dry tropical forest] (*G. Tipaz et al. 904*), along roadsides. It is reported in *tabuleiro* woodland, among closely spaced low trees and tall shrubs; as weedy in agricultural fields and field edges, abandoned fazendas and in *campo aprico*; on dry clay or sandy soil; and was also collected near a stream. Elevation ranges from 100 to 200 m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	2	1	3	1	3	2	2	1	4	4	3	6
Fruiting collections	1		1	2	2	2	2	1	1	1	1	1

Evidently, flowering occurs at any time of the year, with a peak from September through December, when the day length is decreasing. The showy, bowl-shaped, bright yellow flowers appear to fit the bee pollination syndrome. Collectors report the flowers are open only by 9:30 a.m. (*D. F. Austin et al. 6948*, *J. A. A. M. Lourenço et al. 123*).

Vernacular names. Brazil: batata-de-purga (*Franco 67*), batata-rana (*Huber 808*), batatão (*Austin et al. 6948*), batatão-da-mata (*Austin et al. 6968*), flor da pau (*Urbano 12333*), jalapa-amarela (*Froés 11851*), jalapa-da-terra (*Froés 1764*), purga do cipo (*Hoehne Comm. Rondon 3062*), unha de gato (*Silva 15*); batata-amarela, batatarana (Austin & Cavalcante, 1982: 123). Cuba: bejuco mechuacan (*Leon 791*). Panama: batatilla (*Wetmore & Vestal 684*). Trinidad and Tobago: wild morning glory (*Fairchild 2858*).

Typification. According to *Taxonomic Literature II* (Stafleu & Cowan, 1979), the collections of William Hamilton are deposited in the Paris herbarium. We failed to find any specimen in Paris, or any other herbarium, that could be original material for *Convolvulus alatus* Ham. We are therefore choosing a neotype for this name and the later names based on it: the specimen *Broadway 4801* from the type locality and collected in the same month, with duplicates in several herbaria, is an excellent choice, and we have designated it here to stand in place of the missing original material.

Uses. This plant is used as a laxative and a purgative against worms (Sobral et al., 2011). Information recorded by collectors about its uses mentions: *raiz ralada fabrica-*

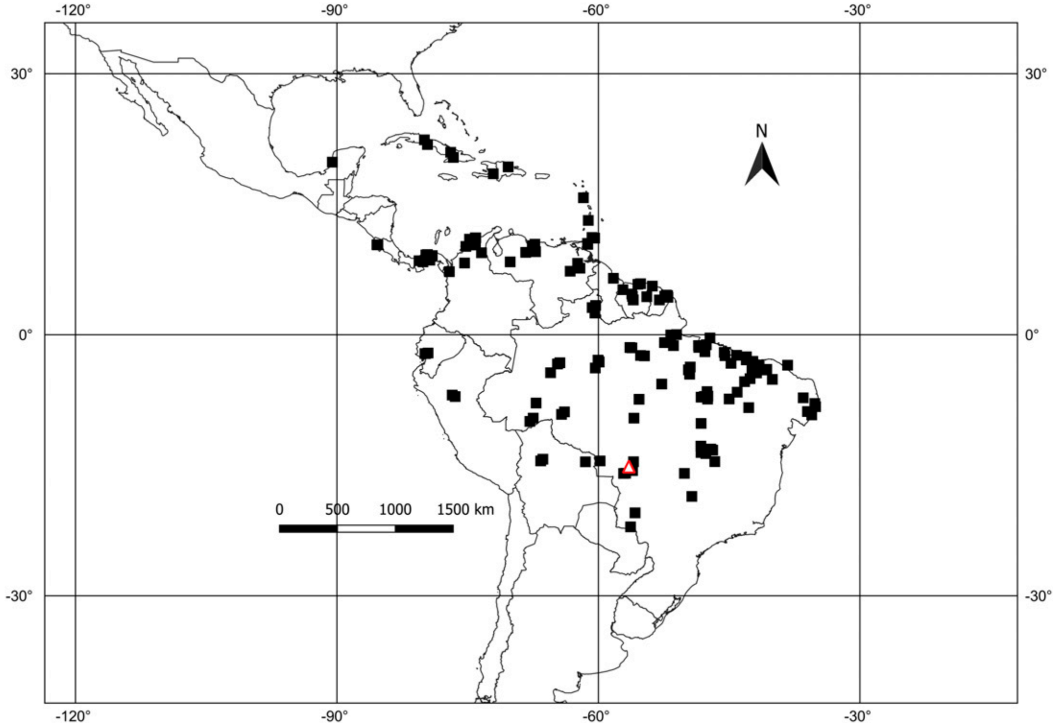

Figure 10. Distribution map for *Operculina hamiltonii* (G. Don) D. F. Austin & Staples var. *hamiltonii* (squares) and variety *mucronata* D. F. Austin & Staples (triangle).

se purgantes para curar ameba e outras doenças [the grated root is used to make purgatives to cure amoeba and other diseases] (*Rosa & Santos 1829*); *purgativa e depurativa* [purgative and purifying] (*Chagas 909*); and *raiz drastica, venenosa em altas dose* [root drastic (e.g., purgative), poisonous in high doses] (*Luis 1024*).

Comments. The single report of *Operculina hamiltonii* from Mexico is a poorly localized specimen collected by William Houstoun in 1730 from “Campeche”; it is the type gathering for *Ipomoea ampliata*. Houstoun did collect in the Yucatán region of Mexico as well as Cuba, Jamaica, and parts of Spanish America, and was shipwrecked near modern Veracruz in 1730, so perhaps he did collect the specimen in Mexico. But it is suspicious that so conspicuous a plant as *O. hamiltonii* has never been collected again in Mexico since 1730: we did not locate a single specimen from Mexico nor was *O. hamiltonii* included in the *Flora de Veracruz* Convolvulaceae account (McDonald, 1993), the *Etnoflora Yucatanense* account (McDonald, 1997), or mentioned in the recent comprehensive checklist of Mexican flora (Villaseñor, 2016). We strongly suspect the species does not occur in Mexico.

Austin (1975: 187) misapplied the name *Operculina triquetra* in the *Flora of Panama* Convolvulaceae account to what is actually *O. hamiltonii*. Genuine *O. triquetra* (Vahl) Hallier f. is a taxonomic synonym of *O. turpethum*.

Selected specimens examined [192 collections total]. BOLIVIA. **Beni:** Gral. Ballivian, Estación biológica del Beni, 14°18′00″S, 66°22′12″W, 200 m, 14 May 1995, *J. Balderrama 551* (LPB, SP). **Santa Cruz:** Velasco, 14°36′13″S, 61°29′28″W, 200 m, 19 Mar. 1997, *L. Sánchez A. et al. 450* (MO, SP, USZ). BRAZIL. **Acre:** Rio Branco, 3 Oct. 1980, *S. R. Lowrie et al. 362* (INPA, NY). **Amapá:** Macapa, 3 Oct. 1979, *D. F. Austin et al. 6968* (FAU, NY). **Amazonas:** Manaus, 28 Sep. 1971, *P. J. M. Maas et al. 471* (COL, INP, MO, U, USF). **Ceará:** Pacujá, 3°59′S, 40°41′W, 17 May 2007, *J. R. Lemos 16* (HUEFS). **Goiás:** Monte Alegre de Goias, 600 m, 13 Mar. 1973, *W. R. Anderson 7008* (FAU, NY, UB). **Maranhão:** Maracassumé, 12 July 1932, *R. L. Froés 1764* (F, GH, K, MO, NY, P, S, U); “in maritimis,” s. loc., *Martius Obs. 2465* p.p. (syntype M). **Mato Grosso:** Conquista d’Oeste, 14°30′05″S, 59°48′09″W, 266 m, 18 May 2013, *J. E. Q. Faria et al. 3565* (SP, UB). **Mato Grosso do Sul:** Aquidauana, 20°28′S, 55°48′W, Mar. 1999, *F. Uchôa s.n.* (UB). **Minas Gerais:** Ituiutaba, 20 Apr. 1946, *Macedo 317* (MO, S). **Pará:** Belém, capoeira baixa do I.A.N., 1°27′S, 48°29′W, 17 Sep. 1945, *R. L. Froés 195* (GH); Itaituba Mun., Km. 974–980 along BR-163, 7°25′S, 55°20′W, 5 Dec. 1983, *M. N. Silva 295–3417* (INPA, NY); Salinópolis, 23 Sep. 1979, *D. F. Austin et al. 6948* (GH). **Paraíba:** Granguro, 7°15′S, 36°30′W, Aug. 1935, *P. von Luetzelburg 26711* (M). **Pernambuco:** Pau d’Alho, 7°53′56″S, 35°10′26″W, 27 July 1992, *A. M. Miranda et al. 525* (HUEFS, PEUFR). **Piauí:** Altos, FLONA Palmares, 5°02′48″S, 42°35′58″W, 160 m, 13 June 2016, *J. A. A. M. Lourenço et al. 141* (PEUFR); "inter Brejo et Ilha Praedia," *Martius Obs. 2465* p.p. (syntype M). **Rondonia:** Jaciparaná, 25 June 1968, *G. T. Prance et al. 5181* (INPA, K, L, MO). **Roraima:** Rio Branco, Feb. 1909, *E. Ule 8287* (B, K, L, U, UC). **Tocantins:** Palmas, 22 Mar. 2000, *E. A. Soares et al. 612* (UB). **S. loc.:** Rio Negro, in sylvis ad Japurafé, *Martius '33'* (syntype M); Rio Negro, *Martius s.n. '880'* (syntype M), *Martius s.n. '882'* (syntype M). COLOMBIA. **Atlántico:** Baranoa, 14 Jan. 1941, *Dugand et al. 2820* (COL). **Bolívar:** Arjona, 30–50 m, 15 Nov. 1926, *E. P. Killip et al. 14511* (COL, F, GH, MO, NY, P, S). **Cesar:** Poponte, 5 Oct. 1924, *C. Allen 767* (MO). **Chocó:** Mpio. de Riosucio, 25 Nov. 1976, *Leon 543* (MO). **Cordoba:** Planeta Rica, 4 Nov. 1976, *P. López 4003* (COL). **Magdalena:** Fundacion, 29 Nov. 1943, *Haught 3909* (COL); Santa Marta, 100 m, Nov., *H. H. Smith 1584* (F, GH, L, MO, P, S, U). COSTA RICA. **Guanacaste:** Hacienda Palo Verde, 10°19′48″N, 85°18′00″W, 23 Nov. 1973, *K. H. Keeler 193* (FAU, MO, UC); Bagaces, Puerto Chamorro, Valle de Tempisque, 10°20′24″N, 85°24′36″W, 24 Nov. 1995, *U. Chavarría 1334* (MO). CUBA. **Granma:** Bayamo, 20°22′54″N, 76°38′34″W, Nov., *C. Wright 3083* p.p. (GH, NY, P). **Las Tunas:** Victoria de las Tunas, 20°58′N, 76°57′W, 27 Oct. 1922, *E. L. Ekman 15586* (F, GH, NY, S, US). **Villa Clara:** Santa Clara Mpio., Santa Clara, 22°24′N, 79°58′W, 18 Apr. 1933, *Rutten-Pekelharing 352* (U); Lomas de Banao, Aug.–Oct. 1920, *Fr. Leon 791* (NY). DOMINICA. **St. Joseph:** Grande Savanne, 15°44′44″N, 61°43′14″W, 23 Nov. 1964, *D. H. Nicolson 2042* (US). DOMINICAN REPUBLIC. **Santiago:** Nigua, 20 m, 8 Nov. 1973, *Liogier 20602* (F, NY, US). ECUADOR. **Guayas:** Guayaquil Cantón, 100 m, 6 May 1992, *G. Tipaz et al. 904* (FAU, MO, QCNE). FRENCH GUIANA. Acarouany, 5°35′32″N, 53°48′44″W, anno 1858, *Sagot 374* (BR, P, U); Cayenne, May 1986, *D. Y. Alexandre 488* (CAY). **Kaw:** Kaw, 140 m, 13 Sep. 1987, *A. Weitzman et al. 312* (FAU, MO, U, US). GUYANA. **East Berbice-Corentyne:** Orealla, Nov. 1879, *E. F. Im Thurn s.n.* (P). **Essequibo Islands–West Demerara:** Hubu, Oct. 1905, *Bartlett 8579* (NY). HAITI. **Centre:** Mirebalais, 150 m, 2 Dec. 1928, *E. L. Ekman 10878* (F, GH, NY, US). MEXICO. **Campeche**: Campeche, 19°50′17″N, 90°31′40″W, anno 1730, *W. Houstoun s.n.* (BM). PANAMA. **Canal Zone:** Fort Clayton vic., out rd. C-15, near TTC Albrook Tower, 5 Jan. 1966, *K. E. Blum 2048* (MO). **Coclé:** Chorillo, 9 Nov. 1975, *Fernandez 13* (MO). **Panamá:** Chepo, 23 Feb. 1969, *Tyson 5351* (MSU). **Veraguas:** Río Concepción, 5 m, 4 Dec. 1967, *W. H. Lewis et al. 2870* (MO). PARAGUAY. **Amambay:** Bella Vista, Dec. 1901–02, *E. Hassler 8268* (C, G, GH, MO, NY, P, S, UC). PERU. **San Martín:** Juanjuí, 400–800 m, 1 May 1936, *G. Klug 4335* (F, GH, MO, NY, U, UC). ST. VINCENT AND THE GRENADINES. **St. Patrick:** Barrouallie, 400 m, s.d., *H. H. Smith et al. 1159* (GH, NY). SURINAME. **Paramaribo:** Paramaribo vic., 5°52′N, 55°10′W, Apr. 1843, *H. C. Focke 778* (lectotype U). **Saramacca:** Groningen, forest of the station, 5°48′N, 55°28′W, 10 May 1916, *J. A. Samuels 397* (GH). **Sipaliwini:** Voltz Berg, 22 Sep. 1957, *J. P. Schultz 7791* (BBS, FAU, U). **S. loc.:** anno 1846, *Hostmann et al. 802 a* (P), *Hostmann & Kappler 802* (MO, U). TRINIDAD AND TOBAGO. **Tobago:** Barolet, 20 Oct. 1889, *H. F. A. von Eggers 5471* (F, GH, L, P); Scarboro, 11°10′52″N, 60°44′00″W, 11 Jan. 1953, *F. W. Hunnewell 19984* (GH). **Trinidad:** Saint George Co., Tacarigua, 29 Aug. 1953, *G. F. Mees s.n.* (L); s. loc., 10°30′N, 61°15′W, 15 Feb. 1932, *D. Fairchild 2858* (L). VENEZUELA. **Aragua:** Maracay vic., Dec. 1931, *C. Vogl 805* (U). **Barinas:** 30 km N of Barinas, 2 Aug. 1974, *D. F. Austin & S. K. Austin 6032* (FAU). **Bolívar:** Ciudad Guayana, 1 Mar. 1972, *G. S. Bunting et al. 4620* (NY). **Cojedes:** Macanilla, Nov. 1976, *Delascio et al. 4661* (FAU). **Guárico:** San Juan de los Morros, 3 Jan. 1939, *Alston 6031* (NY, USF). S. loc. "in vice-regno Peruviano et Chilensi lectae," anno 1799, *Ruiz & Pavon 1799* (F).

Cultivated. FRANCE. **Hautes-de-Seine:** Arboretum de la Vallée-aux-Loupes, living collections of the Collection Nationale des Convolvulacées, 27 Sep. 2010, *A. R. Simões 59* (BM).

PANAMA. **S. loc.:** Dec. 1859, *Hayes 583* (NY).

3b. **Operculina hamiltonii** var. **mucronata** D. F. Austin & Staples, J. Arnold Arbor. 64: 488. 1983. TYPE: Brazil. Mato Grosso: Serra das Araras, in campo áprico, 14 Feb. 1894, *C. A. M. Lindman A2997* (holotype, S! S07-4342; isotype, S! S07-4358).

Herbs, glabrous; sap unknown. Stems prostrate or perhaps twining at the tips, glabrous, cylindrical, striate to subalate, to 2 mm diam. Leaf blades lanceolate-hastate, 7.4–8.7 × 0.7–1.4 cm, basally cordate to auriculate, margins entire, slightly revolute, apically attenuate, mucronate, mucro to 1 mm when present, texture chartaceous; nerves impressed adaxially and prominent abaxially; petiole stout, 5–12 mm, striate, sulcate adaxially. Flowers solitary, axillary; peduncles slender, greatly exceeding subtending petioles, 5–7 cm, striate basally or throughout, distally alate; bracts 2, attenuate-deltoid, 5–9 mm, 2 mm wide at base, membranous, basally truncate, apically attenuate, probably caducous; pedicels clavate, 9–15 mm, 3–4 mm wide at apex, striate to 5-angled. Calyx pyriform, sepals ± equal, obovate, 16–18 × 7–8 mm, reddish brown when dried, membranous, basally truncate, margins entire, apically acute, mucronate. Corolla campanulate, yellow, 3.6–3.8 × 3.8–4.3 cm, sericeous on the tips of the interplicae, otherwise glabrous. Stamens unequal, included; anthers spirally dehiscent, 3–4 mm. Pistil not seen. Fruits and seeds unknown.

Distribution. *Operculina hamiltonii* var. *mucronata* is endemic to Brazil (Fig. 10).

Phenology. Flowering occurs in February.

Comments. We failed to locate any additional specimens for variety *mucronata* despite searching several Brazilian herbaria during personal visits and searching the Brazilian virtual herbaria online (*species*Link, 2018). Superficially, *Operculina hamiltonii* var. *mucronata* is similar to *O. maypurensis* in terms of the diminutive habit, narrowly lanceolate leaves, and small flowers. However, the yellow corolla, the ampliate calyx that is reddish brown when dried, and the sepal shape and proportionality are distinctive, and the two taxa are separable on these technical characters. For now this remains an enigmatic taxon that collectors are urged to seek out and document.

Specimens examined. *Operculina hamiltonii* var. *mucronata* is known only from the type gathering.

4. Operculina macrocarpa (L.) Urb., Symb. Antill. 3: 343. 1902. *Convolvulus macrocarpos* L., Syst. Nat. ed. 10, 2: 923. 1759. *Merremia macrocarpa* (L.) Roberty, Candollea 14: 37. 1952. TYPE: [icon] "*Convolvulus foliis palmato-pedatis, pedunculis unifloris*" in Plumier, Pl. Amer. ed. Burmann, pl. 91. fig. l. 1756. (lectotype, designated by Staples & Jarvis [2006: 1021]).

Convolvulus frutescens Mill., Gard. Dict. ed. 8: page unnumbered, *Convolvulus* #13. 1768. TYPE: [icon] "*Convolvulus foliis palmato-pedatis, pedunculis unifloris*" in Plumier, Pl. Amer. ed. Burmann, pl. 91. fig. l. 1756 (lectotype, designated here). Figure 11.

Convolvulus operculatus Gomes, Observ. Bot.-Med. Nonnullis Bras. Pl. 1: 23, pl. 3. 1803; reprinted in Mem. Math. Phis. Acad. Real Sci. Lisboa 3: 27. 1812, isonym. *Ipomoea operculata* (Gomes) Mart. in Spix & Mart., Reise Bras. 2: 547. 1828. *Piptostegia gomesii* Mart., Syst. Mat. Med. Bras.: 78. 1843, nom. superfl. (cited as synonyms *Convolvulus operculatus* Gomes, *Ipomoea operculata* (Gomes) Mart.). *Operculina convolvulus* Silva Manso, Enum. Subst. Brazil.: 49. 1836, nom. superfl. TYPE: [icon] Gomes' plate 3 (1803) (lectotype, designated here).

Merremia alata Rendle, Fl. Trop. Afr. 4(2): 102. 1905. TYPE: Togo. Near Lome, *O. Warnecke 273* (lectotype, designated by Heine [1960: 398], BM [bc] BM000930496 image!; isolectotypes, BR [bc] BR0000008885661 image!, K [bc] K000097366!, P [bc] P00442744 image!).

Suffruticose herbs; sap cloudy-watery. Stems glabrous, twining, reddish, terete to 4-angled to narrowly 4-winged. Leaf blades palmately (3- to)5- to 7-lobed or -parted, 3.8–10(–16) × 4–11 cm, glabrous, chartaceous, secondary veins 4 to 7 either side of midvein in each lobe, middle lobe largest, 1.2–5 cm wide, all lobes oblong to elliptic, attenuate basally and apically; petiole 2.5–7.5 cm, angled or narrowly winged lengthwise, glabrous. Inflorescences axillary, flowers 1 to several in cymose clusters; peduncles 5–13 cm, terete below, membranous-winged above, glabrous or minutely puberulous basally; bracts elliptic-oblong, 0.9–1.3(–3) cm, acuminate, caducous; bracteoles similar, smaller; pedicels clavate, 2.5–4 cm, glabrous, undulate-winged, wing 1–2 mm wide. Flowers diurnal, erect, odorless. Sepals broadly ovate, 2–3.5 × 1.4–2 cm, papery, straw-colored, glabrescent, basally strongly convex and rounded, margins scarious, apically obtuse to rounded or emarginate. Corollas campanulate, white, 4–7.5 cm, midpetaline bands abaxially pilose, outer surface of corolla dotted with tiny golden glands. Stamens subequal, included, white; filaments 11–12 mm, glandular pubescent at insertion; anthers 6–7 mm, spirally dehiscent. Pollen 3-zonocolpate. Pistil included, slightly overtopping the stamens, white; style filamentous, glabrous; stigmas biglobose. Fruiting calyx accrescent, becoming brown and coriaceous, at first enclosing fruit, at maturity reflexed at right angle to pedicel; sepal margins scarious, eroding. Capsule depressed globose, 3- or 4-lobed, 2.5–3.8 cm diam., glabrous, 2-locular; operculum brown, drying wrinkled; endocarp papery, thin, white. Seeds 1 to 4, broadly ovoid to ovoid-trigonous, 1–1.3 cm, black, glabrous except minutely pubescent near hilum, apically obtuse.

Distribution. *Operculina macrocarpa* is present in the West Indies (Guadeloupe, Martinique), South America (Brazil, Paraguay), and in tropical West Africa (Côte d'Ivoire, Ghana, Togo), where it was likely introduced long ago and is now naturalized (Fig. 12).

Literature reports of *Operculina macrocarpa* from Cuba (Leon & Alain, 1957 [reprinted 1974]: 230) are incorrect; evidently the report is based, at least in part, on a misidentified specimen of *O. hamiltonii* (*Ekman 15586*), which Urban labeled as *O. macrocarpa* before it was distributed. We found no bona fide Cuban specimens of *O. macrocarpa* in our revisionary study, and H. Manitz (pers. comm. 2018) confirms that the species does not occur on the island.

Ecology. This species is found often twining through grasses and over shrubs; along roadsides in *cerrado* and *campo rupestre*; in regrowth forest; in *floresta estacional (mata de cipó) zona de transiçao, em solo areno argiloso-pedrogoso* [seasonal forest (*mata de cipó*) transition zone, in clayey-stony sandy soil] (*G. E. L. Macedo et al. 751*); in hyper-xeric caatinga; and on stony ground. Elevation ranges from near sea level to 700(to 1215) m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections		1	3	3	6	1		1	1	1	1	1
Fruiting collections		1	1	2	1	2		1	1	2	1	

Evidently, flowering and fruiting occur throughout the year. The broadly campanulate, white corollas are suited for bee pollination.

Vernacular names. Brazil: batata-de-purga (*Sousa 216* and in Gomes [1812]), jalap (*Miranda & Estevas 150*), jalapinha (*Glaziou 7881*), purga-da-batata (*Santos 163*), roda-de-batata (*Gomes 81*), sipipira (*Lucena 1487*); amarelo leite, batata de purga da branca, cipó purga (Austin & Cavalcante, 1982: 124). Ghana: abia, ebia (Heine, 1960: 398–399). Paraguay: batata de purga (*Hassler 7373*).

Typification. Having failed to locate any authentic Philip Miller specimen, we designate here a published Plumier drawing as the lectotype for *Convolvulus frutescens*. (Fig. 11). As it happens, this is the same element chosen as lectotype for *C. macrocarpus* (Staples & Jarvis, 2006). Philip Miller (1768) cited only one

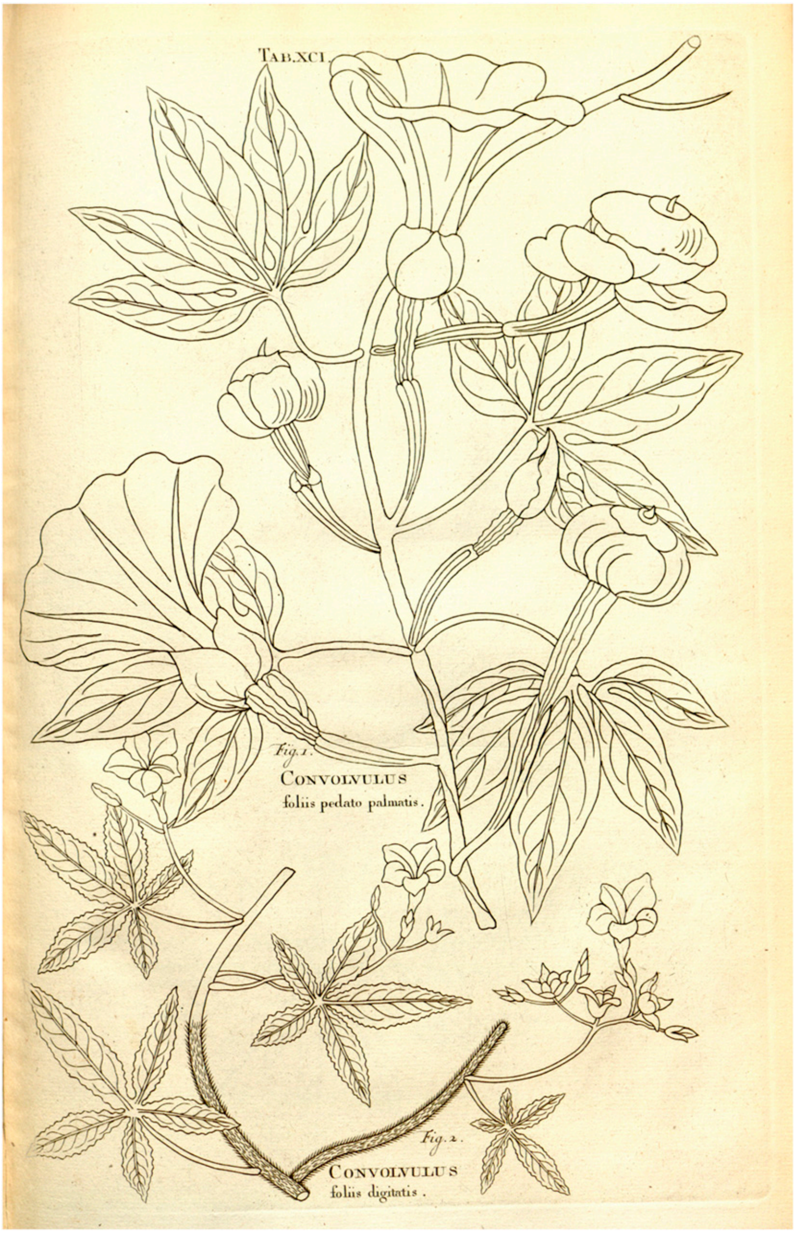

Figure 11. Illustration chosen as lectotype for *Convolvulus frutescens* Mill. Reproduced from *Plantarum Americanarum* (Plumier, 1756: plate 91); lectotype is fig. 1 only.

element when he named his *C. frutescens*: "*Convolvulus pentaphyllos* [sphalm.], *flore & fructu purpureis maximis*. Plum. Cat." which can be linked via the name citations in the text, to the plate published later (as plate 91, fig. 1) in the *Plantarum Americanarum* (Plumier, 1755–1760). In fact, Miller cited the polynomial incorrectly, writing "*pentaphyllos*" instead of "*polyphyllos*," but the other details correspond exactly between Plumier's *Catalogus* (Plumier, 1703) and the plates published later under Jan Burman's editorship. This type choice stabilizes the nomenclature and preserves the name in current use.

We have chosen the plate (Fig. 13) accompanying Gomes's earliest publication as the lectotype for his *Convolvulus operculatus*; this entire work was reprinted in 1812 in Mem. Math. Phis. Acad. Real Sci. Lisboa 3: 27, as pointed out by *Taxonomic Literature II* (Stafleu & Cowan, 1976). Although the *Index Kewensis* cites the

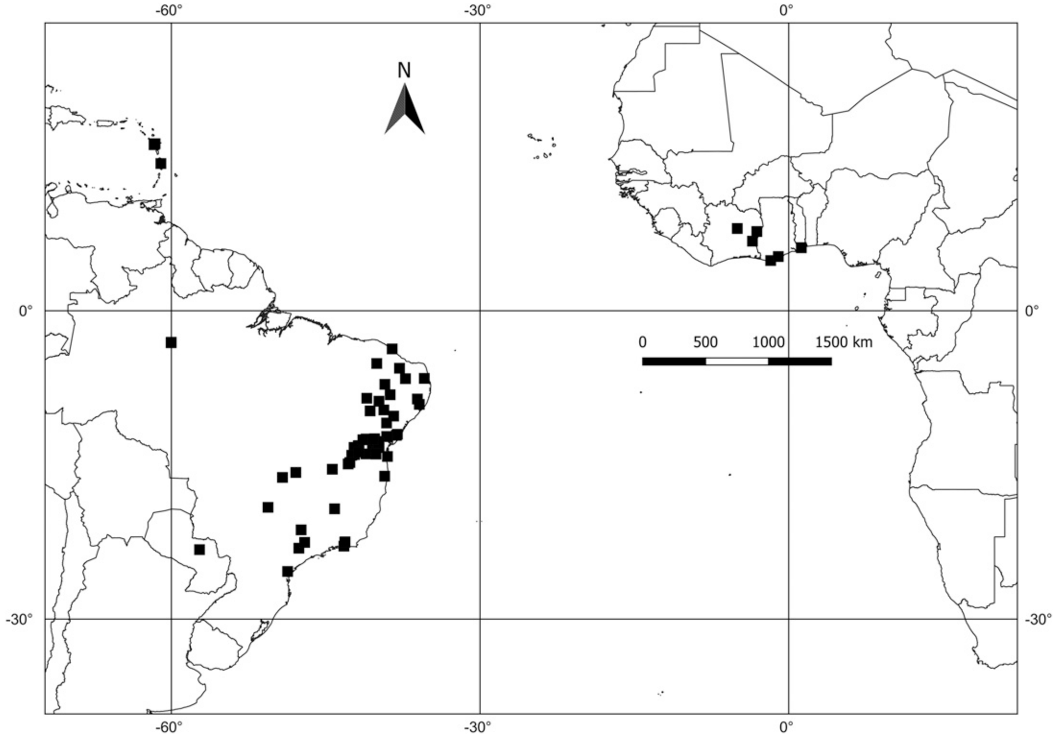

Figure 12. Distribution map for *Operculina macrocarpa* (L.) Urb.

1812 publication, this is a later place of publication; the name *C. operculatus* dates from Gomes's 1803 publication. No types were found for *Operculina convolvulus*; this is a superfluous name based on *C. operculatus*.

Selected specimens examined [72 collections examined]. BRAZIL. **Amazonas:** Manaus, 3 Aug. 1955, *Chagas 1548* (MG). **Bahia:** Itacaré, 100 m, 30 Mar. 1974, *R. M. Harley et al. 17512* (K, M, MO, NY, U); Caetité, estrada para Brumado, 14°03′36″S, 42°28′12″W, *M. T. Buril 237* (HUEFS); Itaberaba Mun., BR-242 roadside, 19 May 2015, *G. Staples et al. 1656* (PEUFR). **Ceará:** Sitio B. Inácio de Azevedo, Sep. 1937, *J. Eugenio 1033* (GH); Serra Araripe, 18 Apr. 1910, *Lofgren 607* (S). **Goiás:** Ouro Verde de Goiás, 16°13′S, 49°12′W, 938–1140 m, 4 May 2006, *C. S. P. Silva et al. 160* (UB). **Minas Gerais:** Rio Pandeiros, 520 m, 18 Apr. 1973, *W. R. Anderson et al. 9106* (FAU, NY, UB); Sete Lagoas, May 1882, *A. F. M. Glaziou 14131* (C, K, P). **Paraíba:** Areia, 16 Sep. 1947, *de Melo 66* (IAN). **Pernambuco:** Afrânio, 8°30′54″S, 41°00′18″W, 23 Apr. 1971, *E. P. Heringer et al. 301* (PEUFR, UB); Santa Maria da Boa Vista, 8°48′14″S, 39°49′17″W, 4 May 1984, *T. Ramos et al. 17* (PEUFR). **Rio Grande do Norte:** Lagoa do Junco, 6°36′24″S, 37°15′01″W, 216 m, 23 May 2006, *R. T. Queiroz 931* (PEUFR). **Rio de Janeiro:** Rio de Janeiro, Feb. 1836, *Ackermann s.n.* (BR); Ilha do Governador, 18 Mar. 1875, *A. F. M. Glaziou 7881* (C, K, P). **São Paulo:** Catumbi, 9 Mar. 1826, *Burchell 4033* (BR); Sta. Elisa, 4 May 1944, *Theisen 7457* (IAN, UC). GUADELOUPE. **S. loc.:** 16°08′58″N, 61°40′41″W, *D. C. s.n.* (P); *Grisebach s.n.* (MO). MARTINIQUE. Trois-Îlets, 15 m, 2 Sep. 1937, *H. Stehlé 2116* (US). PARAGUAY. **Concepción:** prope Concepción, in sepibus, Sep. 1901/02, *Hassler 7373* (G).

CÔTE D'IVOIRE. **S. loc.:** 8° N, 5° W, *J. Mertens et al. 84* (BR). GHANA. **Gold Coast:** Adumassu, 6°46′15″N, 3°31′37″W, 25 Oct. 1898, *W. H. Johnson 155* (K); Zanzan, Krobo Plains, 7°42′35″N, 3°06′06″W, 19 Dec. 1899, *W. H. Johnson 514* [sphalm '*517*'] (K). **Western:** Takoradi, 4°53′04″N, 1°45′19″W, 3 Oct. 1925, *F. N. Howes 979* (K). **S. loc.:** Mankessim vic., 5°16′18″N, 1°00′55″W, 5 Nov. 1963, *K. Obeng-Darko 5188* (K). TOGO. **Golfe pref.:** Lomé, 6°07′56″N, 1°13′22″E, Nov. 1913, *Mildbraed 7502* (K).

There are additional specimens cited in the Brazilian virtual herbaria (e.g., *species*Link, 2018), but we have not verified them all since rather few have images associated with the specimen records.

5. Operculina maypurensis (Hallier f.) A. R. Simões & Staples, Bot. J. Linn. Soc. 183: 580. 2017. *Merremia maypurensis* Hallier f., Jahrb. Hamburg. Wiss. Anst. 16 (Beih. 3): 36. 1899 [title page 1898]. TYPE: Venezuela [or Colombia, see Comments]. Amazonas: near Maypures on the Orinoco, June 1864, *Spruce 3593* (holotype, W not seen; isotypes, K [bc] K000612891!, K000612892!).

Herbaceous twiners, almost totally glabrous; sap white, abundant. Stems 0.5–2 m, to 1 mm diam., slightly striate. Leaf blades narrowly lanceolate or linear-oblong, 43–70 × 5–9 mm, basally or subpeltately attached, chartaceous, basally rounded or emarginate to subcordate, margins entire, apex long-tapering to attenuate, mucronulate; secondary veins indistinct, reticulate; petioles slender, 6–11 mm. Flowers solitary, axillary; peduncles slender, 23–42 mm, terete, greatly exceeding subtending petioles; bracts caducous; pedicels clavate, thicker than the peduncles, 7–11 mm, 2 mm wide at apex. Sepals unequal, elliptic-ovate, outer 5.5–7 × 2–3 mm, inner 7–9 × 3–4 mm, apically obtuse, mucronate. Corollas funnelform, white (or yellow?) with tube base yellow inside, 22–28 × 12–23 mm, midpetaline bands glabrous outside except sericeous hair-tufts at tips, golden gland dots sparse. Stamens unequal, included, in total 14–17 mm, white; filaments basally dilated and adnate to corolla tube for about 1/2 their length, margins of adnate portion pubescent, distally free, filamentous and glabrous; anthers 2–3 mm, spirally dehiscing. Pollen 3-zonocolpate or 6-pantocolpate. Pistil included, 15–18 mm, glabrous; ovary ovoid-ellipsoid, ca. 1.5 mm tall; style filiform, 14–16 mm, white; stigma biglobose. Fruiting calyx slightly enlarged and persistent. Capsule subglobose, 10–12 mm diam., straw-colored to pale brown; operculum not seen. Seeds 1 or 2, subglobose, 6–7 mm diam., brown-black, glabrous, with fugacious hyaline outer layer at first.

Distribution. *Operculina maypurensis* is found in Venezuela and Colombia (Fig. 14). Its presence in Colombia was documented as recently as 1998 (Austin, 1998a: 417), based on a single collection.

Ecology. *Operculina maypurensis* is confined to the granite inselbergs and sandstone *lajas* of Venezuela and Colombia and their associated vegetation: shrubby secondary regrowth; rocky savannas with *Trachypogon* Nees on hillsides; grassy savannas with mixed herbs; shrub islands on *lajas*. Collectors note the plants were found in disturbed sites and along roads in the area surrounding Puerto Ayacucho. Elevation ranges from 75 to 150 m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections					3	7	2		1	2	1	
Fruiting collections										1	1	

The limited specimen data available hint at a bimodal flowering period, with a primary flowering event in May to July, peaking in June, and a second flowering period later in the year.

Vernacular names. None recorded.

Typification. It has been pointed out to us (G. Romero, pers. comm. 2016) that the type locality could be in Colombia rather than Venezuela, as Hallier (1899: 36) implied: "Guiana venezol., prope Maypures, ad flumen Orenoco." Because the river with the Maypures rapids now forms the border between the two countries, and we have no idea on which side of the river Spruce collected the type gathering, we have presented the information as Hallier wrote it in the protologue. It is now documented that *Operculina maypurensis* is present in both countries, but is rare and apparently confined to a specific habitat.

Hallier (1899: 36) created an invalid name when he listed *Ipomoea maypurensis* Spruce as a synonym under the name he accepted for this species, *Merremia maypurensis*.

Comments. The fruits of *Operculina maypurensis* are rarely collected and had been presumed to be valvate capsules. After molecular analysis showed *Merremia maypurensis* is nested in the *Operculina* clade, we requested José Grande Allende to examine fruiting collections in the VEN herbarium. A single fruiting specimen (*L. W. Williams 16025*) was found in VEN and he kindly confirmed that the fruit was not a valvate capsule and that no operculum was present, but the precise nature of the fruit had been obscured by pressing. We suppose the fruit of *O. maypurensis* will be found to be an operculate capsule but this requires study of living plants, photographs taken in the field, or examination of whole fruits that have not been flattened in a plant press.

Stefanović et al. (2002) extracted DNA from the specimen *Romero 1701* (GH), which was originally identified as *Aniseia cernua* Moric. Stefanović et al. (2002, 2003) pointed out that this sample grouped with the *Operculina* clade and not with *Aniseia*, which was removed from tribe Merremieae and formally recognized as a distinct tribe, Aniseieae Stefanović & D. F. Austin (Stefanović et al., 2003). The GH specimen was returned after the study with only a pencilled query "Operculina ?!" and refiled as *A. cernua*. Independently, we had examined images of the duplicate for *Romero 1701* in VEN, provided by José Grande Allende, and identified this collection as *Merremia maypurensis*, which is now confirmed to belong in *Operculina* on both morphological and molecular evidence (Simões et al., 2015; Simões & Staples, 2017).

Specimens examined [16 collections]. COLOMBIA. **Guainía:** Casuarito, 5°40′N, 67°37′W, 90 m, 22 June 1984, *G. Davidse et al. 26406* (NY). VENEZUELA. **Amazonas:** Atures Dpto., El Burro vic., 5°09′N, 67°48′W, 2 Oct. 1993, *A. Gröger & S. Llamozas 1145* (M, MO, VEN); Atures Dpto., Parque Sucre, 5°43′N, 67°37′W, 75 m, 8 Sep. 1985, *J. A. Steyermark et al. 131595* (MO, VEN); Puente Samariapo, 21 June 2007, *Y. Espinosa et al. 492* (VEN); Atures Dpto., Puerto Ayacucho, 5°38′08″N, 67°36′02″W, 100 m, 28 June 1975, *A. Gentry et al. 14431* (MO, VEN); same locality, 90 m, 23 June 1984, *G. Davidse et al. 26451* (NY); 100 m, 28 June 1975, *A. Gentry et al. 14476* (MO, QCA, VEN); 25 May 1977, *O. Huber 810* (MO); 100 m, 18 May 1940, *Ll. Williams 12980* (US, VEN); N of Puerto Ayacucho, 5°36′56″N, 67°36′00″W, 100 m, 17 Nov. 1977, *G. Morillo 6654* (VEN); 3.5 km N of Puerto Ayacucho, ca.

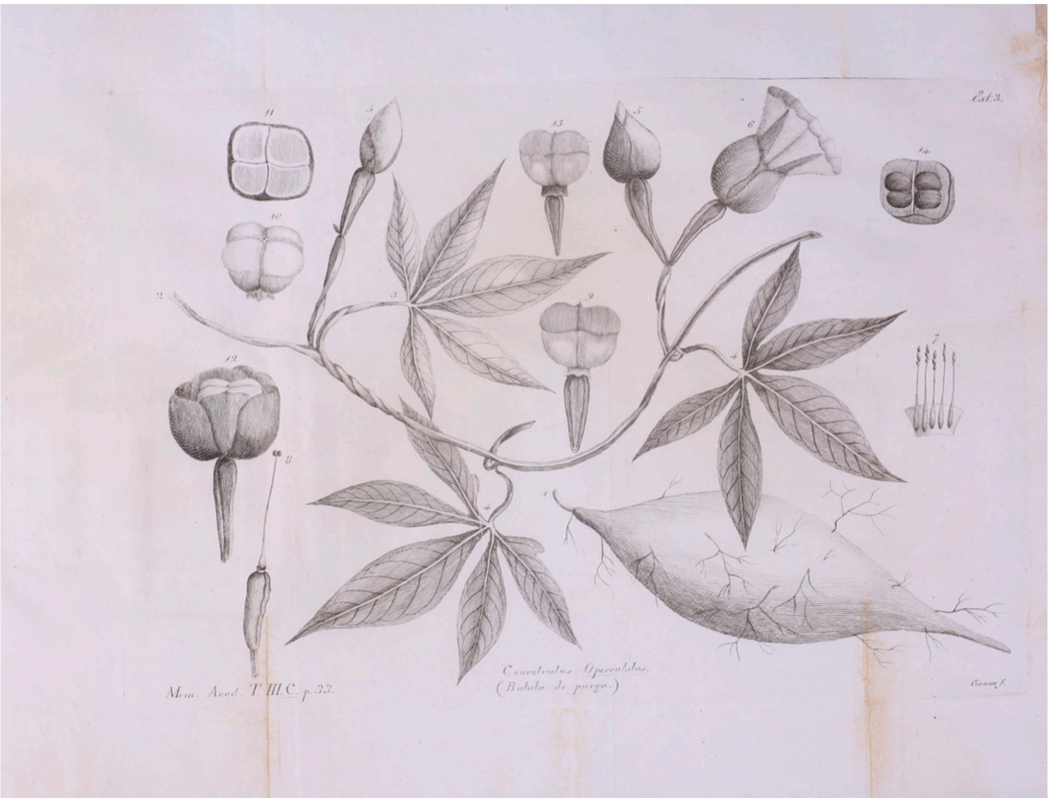

Figure 13. An illustration for *Operculina macrocarpa* (L.) Urb. Original caption, translated: 1. enlarged root; 2. flowering and fruiting stem; 3. adaxial leaf surface; 4. abaxial leaf surface; 5. flower bud, unopened; 6. flower; 7. lower corolla tube, opened to show stamens; 8. pistil, attached to pedicel; 9. immature fruit, operculum attached; 10. immature fruit, operculum removed; 11. operculum; 12. mature fruit enclosed by accrescent, persistent calyx; 13. mature fruit after operculum detached; 14. fruit in transverse section, showing four seeds. Reproduced from *Observationes Botanico-medicae de nonnullis Brasiliae plantis* (Gomes, 1812: plate 3), under the name *Convolvulus operculatus*.

80 m, 14 Oct. 1988, *G. A. Romero 1701* (GH, NY, VEN); S of Puerto Ayacucho, 26 July 2003, *S. Novawa et al. 240* (VEN); Atures Dpto., Puerto Venado vic., 5°15′N, 67°48′W, 27 May 1992, *A. Gröger 443* (M, VEN); Cataniapo, June 1940, *Ll. Williams 13453* (US, VEN); Samariapo, 150 m, 4 July 1942, *Ll. Williams 16025* (F, US, VEN). **S. loc.:** Maypures rapids, 5°13′14″N, 67°50′11″W, June 1854, *R. Spruce 3593* (K, W).

6. Operculina petaloidea (Choisy) Ooststr., Blumea 3: 369. 1939. *Ipomoea petaloidea* Choisy, Mém. Soc. Phys. Genève 6: 451 [Conv. Orient. 69]. 1834. *Merremia crispatula* Prain, Bengal Pl. 2: 730. 1903, nom. superfl. *Merremia petaloidea* (Choisy) Burkill, Bull. Misc. Inform. Kew 1935: 318. 1935. TYPE: [Myanmar. Bago Division,] Prome, Jan. 1827, *Wallich s.n.* (lectotype, designated here, G [bc] G00227273!). Figure 15.

Ipomoea xanthantha Kurz, Forest Fl. Burma 2: 219. 1877. TYPE: [Myanmar. Bago Division,] Pegu Yomah, E and W slopes, 28 Mar. 1871, *Kurz 2336* (syntypes, CAL not seen, K [bc] K000830925!).

Ipomoea petaloidea var. *pauciflora* C. B. Clarke, Fl. Brit. India 4: 212. 1883. *Operculina petaloidea* var. *pauciflora* (C. B. Clarke) Parmar, J. Econ. Taxon. Bot. 18: 251. 1994, syn. nov. TYPE: India. [Uttarakhand,] Kumaon, Kuntagong, May 1845, *T. Thomson '1156'* (lectotype, designated here, K [bc] K000830922!; isolectotypes, K [bc] K000830923!, K000830924!).

Herbaceous twiner, glabrous or nodes yellowish puberulent; sap thinly milky. Stems terete, striate-angulate, or narrowly alate below nodes. Leaves entire, ovate, broadly elliptic, or oblong-linear, 5.8–11.3 × 2.7–5.8 cm, pubescent when young, later glabrate, drying reddish and often glaucous, base rounded to truncate or slightly emarginate, apex obtuse or acute, mucronulate; secondary veins 7 to 9 per side; petiole 1.5–2.6 cm, ridged to narrowly winged. Inflorescence axillary or terminal on lateral branches, cymose, 1- to 9-flowered; peduncles terete, 0.9–2 cm; bracts linear-lanceolate, 7–20 mm, deciduous; pedicels clavate, striate-angulate, 1–1.8 cm. Flowers erect, diurnal,

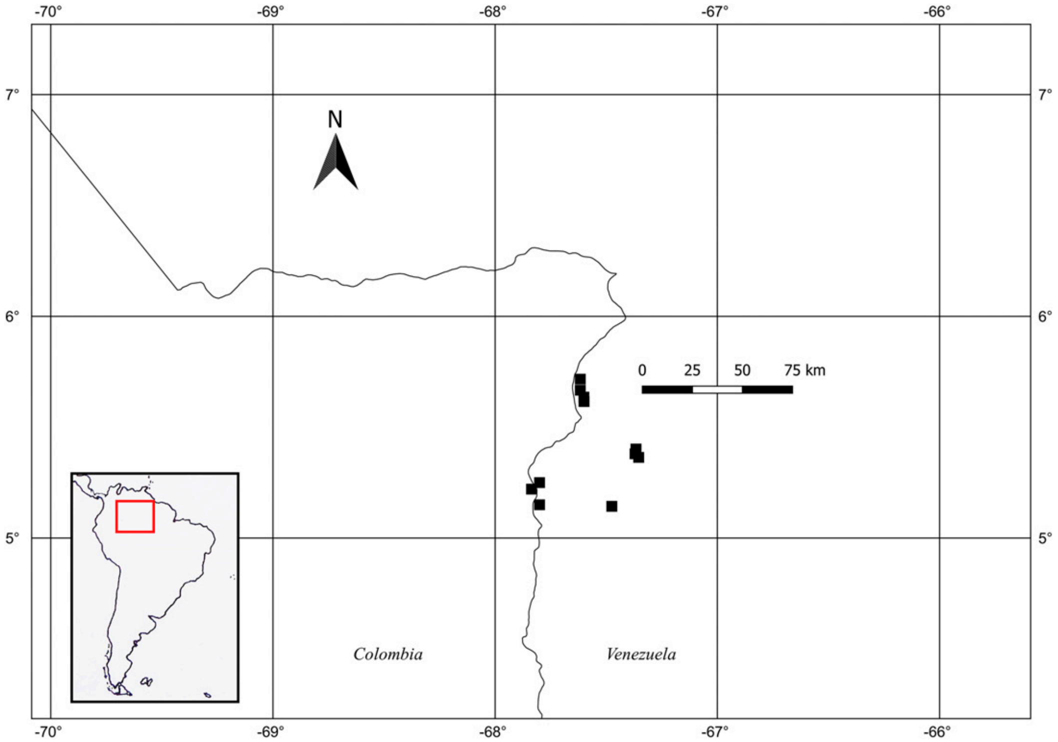

Figure 14. Distribution map for *Operculina maypurensis* (Hallier f.) A. R. Simões & Staples.

odorless. Sepals subequal, elliptic, convex, 2 outer 1.3–1.5 cm, narrower, 3 inner 1.5 cm, broader, apex mucronulate. Corolla flaring funnelform, pale yellowish, 3.5–4 cm, midpetaline bands tomentose-sericeous outside, tiny gland dots not evident. Stamens subequal, included, 1.4–1.8 cm; filaments glandular below insertion; anthers spirally dehiscent. Pollen 3-zonocolpate or 6-pantocolpate. Pistil included, 1.7–1.9 cm, glabrous; disc annular, 1 mm tall, blackish; ovary conical-ovoid, 2–2.5 mm tall, brownish, glabrous. Fruiting calyx accrescent, initially cupping fruit, later reflexing to about right angles with it, drying tan to black-brown, margins straw yellow and erose. Capsule ovoid, ca. 1.5 cm diam., tan; operculum blackish brown, extending below middle of capsule, often apiculate by indurated style base; endocarp cartilaginous, yellowish, with 2 or 4 valves, or shattering irregularly. Seeds 4, ovoid, 5–6 mm, black, margins hairy with stiff, erect, whitish trichomes.

Distribution. *Operculina petaloidea* is widespread across India, Myanmar, and Thailand, reaching east to Cambodia and Vietnam; it is seemingly absent from Bangladesh and Laos but likely to be found in both countries when collecting density improves (Fig. 16).

Ecology. *Operculina petaloidea* is a locally common plant—in some localities in Thailand (Uttaradit Province, *Staples et al. 1388*) lining roadsides for several kilometers—where it grows in sunny areas in evergreen forest, along stream banks, in pastures and fallow agricultural land, as well as disturbed areas. Elevation ranges from 180 to 1200 m. Plants often trail along the ground or may twine high into trees and shrubs. Flowering plants have been observed with large black ants clustered on the inflorescences (*Staples et al. 1388*).

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	4		3	5	1	1					1	
Fruiting collections			1	1								

Flowering occurs from lateral branches in full sunlight; portions of the same stem growing in deep shade do not develop flowers. The corolla color is typically pale yellow but varies to almost pure white. Anthesis has been observed with flowers just opening at 9:20 a.m. (*Staples et al. 1372*) and flowers closing after sunset (ca. 6:15 p.m.) (*Staples et al. 1388*).

Vernacular names. Cambodia: voir sandek (*Eanghourt 38*). India: bana etka (Santali language, *Watt 9242*). Myanmar: kya hin gyi (*Khin Myo Htwe 28159*).

Thailand: ban bai (บานบ่าย) (Smitinand, 2001), kreua kou kom (Laotian, *Kerr 1036*), kur-ji-jo-kew (*Khantchai 772*), khrue-chicho-khaeng (เครือจี้จ้อแข็ง) (Staples, 2010).

Typification. Choisy (1834) cited three collections (syntypes) when he named *Ipomoea petaloidea*, and these are a mixture of two species. We have chosen as lectotype the specimen in Geneva that has Choisy's handwritten annotation on the label, and the specimen represents the species known as *Operculina petaloidea*. One of the other syntypes, *Leschenault s.n.* from Timor, is actually *O. riedeliana*. By choosing the lectotype as we have, this stabilizes the nomenclature in current use.

When naming his *Ipomoea xanthantha*, Kurz cited the localities Martaban, Prome, and Pegu Yomah, which suggests multiple syntypes. However, we found only one sheet in Kew that could be original material for this name and believe there are more specimens in CAL that should be examined before choosing a lectotype.

We found three sheets in Kew that are original material (syntypes) for *Ipomoea petaloidea* var. *pauciflora*. Clarke (1883) cited what seem to be two collections (syntypes): "Ipomæa, n. 44, *Herb. Ind. Or. H.f. & T.*" and *Thomson s.n.* However, the three sheets now in Kew demonstrate that these are actually a collection made by T. Thomson under his number 1156 that was distributed under the printed "*Ind. Or. H.f. & T.*" labels as "Ipomæa, n. 44." Ooststroom had already annotated one of the Kew sheets in 1947 as the "type" for Clarke's variety, and we agree that this specimen is a sound choice as lectotype and so designate it here.

The name "*Convolvulus crispatulus*" is a nomen nudum; Wallich (1829) included it in his "Catalogue" as entry 1403 without any description. Likewise *Merremia crispatula* Prain (1903) is a superfluous name because Prain cited *Ipomoea petaloidea* sensu C. B. Clarke in synonymy.

Comments. Several authors, beginning with Clarke (1883), have tried to distinguish infraspecific taxa based on leaf width. As shown by Songkhla and Khunwasi (1993: figs. 34, 35), the leaves vary considerably in shape and these can all be found on the same plant. In our field study of living plants, we observed mature specimens of *Operculina petaloidea* in Thailand that exhibited broad, leathery cauline leaves on older, mature stems, while the leaves on younger lateral shoots may be the same shape, only smaller, or they may be much narrower and linear-oblong in shape. When grown in cultivation at the Singapore Botanic Gardens, juvenile plants of *O. petaloidea* developed linear to oblong leaves for the first two years. We have seen herbarium specimens from India, Myanmar, and Cambodia with linear-oblong leaves that have been segregated at varietal rank, but we do not think this polymorphic variation worthy of taxonomic recognition.

The fruit of *Operculina petaloidea* is transitional between the valvate capsule of other genera and the operculate capsule typical of *Operculina*. In some fruits at least, there is both a prominent operculum (extending from the apex to below the middle of the fruit) and two or four valves underneath, which dehisce after the operculum falls off.

Selected specimens examined [65 collections total]. CAMBODIA. **Pursat:** Veal Veng distr., 12°14′32″N, 103°08′04″E, 240 m, 21 June 2000, *K. Eanghourt 38* (K). **Stung Tréng:** s. loc., 13°27′58″N, 106°03′23″E, 86 m, 2 Apr. 2009, *S. K. Cheng et al. CL-1075* (P, SING). INDIA. **Andhra Pradesh:** Godavari, Godavari river, 16°38′N, 82°18′E, s.d., *R. H. Beddome 5601* (BM), *5602* (BM). **Gujarat:** Baroda, Kanjeta, 22°35′N, 74°07′E, 21 Apr. 1962, *S. J. Bedi 1965* (K). **Jharkhand:** Chandwa, 23°41′N, 84°44′E, June 1905, *H. H. Haines 808* (K). **Madhya Pradesh:** Shankargarh, 25°11′N, 81°37′E, 20 Apr. 1921, *W. Dudgeon et al. s.n.* (MO). **Maharashtra:** Chandrapur distr., Chandrapur, 19°57′N, 79°18′E, 25 Jan. 1891, *J. F. Duthie 10474* (K). **Orissa:** Angul, 20°51′N, 85°06′E, 13 Mar. 1917, *H. H. Haines 4916* (K). **Uttar Pradesh:** Oudh, 26°48′N, 82°12′E, 13 May 1900, *J. F. Duthie et al. 23746* (E). **Uttarakhand:** Kumaon, 29°50′N, 79°30′E, May 1845, *T. Thomson 1156* (type K). **West Bengal:** Cooch Behar, 26°18′N, 89°32′E, s.d., *S. Kurz s.n.* (K). MYANMAR. **Bago Division:** Pegu, 21°59′N, 95°32′E, s.d., *S. Kurz 1095* (K); Prome, 18°50′N, 95°14′E, s.d., *Wallich Cat. 1403/1* (G-DC). **Mandalay Division:** Kyaukpadaung Township, Mt. Popa Park, 20°55′38″N, 95°13′01″E, 26 Feb. 2003, *Khin Myo Htwe 028159* (BISH, MBK). **Shan State:** "Csoteik" [= Gokteik], 22°21′N, 96°55′E, May 1933, *F. G. Dickason 5983* (A); Minle, Jan. 1903, *Shaik Mokim 1201* (G); Shan Hills, s. loc., 21°30′N, 98°00′S, 914 m, Feb. 1888, *C. B. Collett 6* (K). THAILAND. **Northern:** Chiang Mai, Doi Suthep, 18°50′N, 98°55′E, 426 m, 3 Mar. 1910, *A. F. G. Kerr 1036* (K, TCD); Chiang Rai, Muang Pan, 18°45′N, 99°30′E, 21 Mar. 1921, *A. F. G. Kerr 5118* (A, BK, E, K, TCD); Lampang, Toen, 17°43′N, 99°14′E, 22 Mar. 1994, *Herbarium Trip 874* (BCU); Mae Hong Son, Huay Pon On reservoir, 290 m, 11 Jan. 2010, *G. Staples et al. 1372* (A, BM, L, P, QBG, SING); Tak, Tha Song Yang, 17°14′11″N, 98°35′06″E, 240 m, 21 Mar. 2005, *R. Pooma et al. 5006* (AAU, BKF, E, K, L, P); Uttaradit, Ta Pla distr., 17°54′52″N, 100°38′03″E, 200 m, 15 Jan. 2010, *G. Staples et al. 1388* (A, BM, KEP, P, QBG, SING). **Southwestern:** Kanchanaburi, Km. 80 along Hwy. 323, 16 Nov. 1985, *G. Staples et al. 289* (A, AAU, B, BKF, L, P). VIETNAM. **Son La:** Song Ma distr., Muong Hung, 20°56′N, 103°53′E, 20 Oct. 1977, *T. D. Ha 233* (HN).

7. Operculina pinnatifida (Kunth) O'Donell, Lilloa 23: 432. 1950. *Convolvulus pinnatifidus* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 3: 108. 1819. *Ipomoea pinnatifida* (Kunth) G. Don, Gen. Hist. 4: 280. 1838. *Merremia pinnatifida* (Kunth) Hallier f., Bot. Jahrb. Syst. 16: 552. 1893. TYPE: Cuba. Habana, *Bonpland s.n.* (holotype, P-Bonpl. [bc] P00670766!) [see Typification comments]. Figure 17.

Ipomoea ornithopoda B. L. Rob., Proc. Amer. Acad. Arts 27: 183. 1893. *Operculina ornithopoda* (B. L. Rob.) House, Bot. Gaz. 49: 414. 1909. TYPE: Mexico. San Luis Potosí:

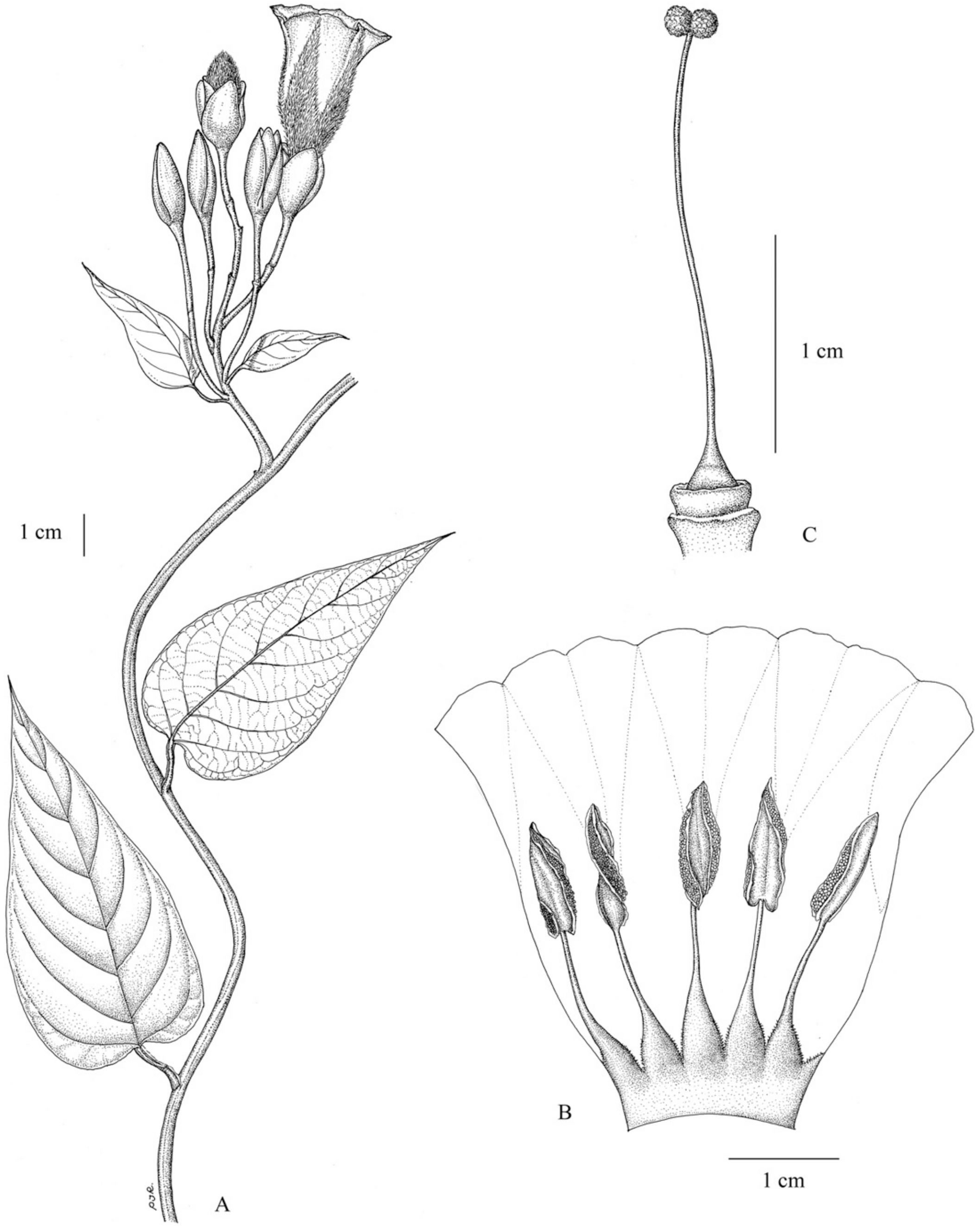

Figure 15. An illustration for *Operculina petaloidea* (Choisy) Ooststr. —A. Habit of flowering stem showing broad leaf form. —B. Corolla, opened to shown stamens. —C. Pistil. Reproduced with permission from *Flora of Thailand* (Staples, 2010: 450, fig. 36), drawn by Pajaree Inthachub.

Canoas, July 1890, *C. G. Pringle 3553* (holotype, GH [bc] 00054523!; isotype, F!).

Operculina pectinata House, Muhlenbergia 5: 69. 1909. TYPE: Mexico. Oaxaca: about Lagunas, *E. W. Nelson 2646* (holotype, US [bc] US01094783!; isotypes, GH [bc] 00054682!, NY [bc] NY336587!, US [bc] US00111354!).

Operculina angustiloba House, Bull. Torrey Bot. Club 33: 501. 1906. TYPE: Mexico. San Luis Potosí: San Dieguito, *E. Palmer 112* (holotype, US [bc] US00111352!; isotype, GH [bc] 00054681!).

Operculina roseana House, Bull. Torrey Bot. Club 33: 500. 1906. TYPE: Mexico. Sonora: Agiabampo, *E. Palmer 781*

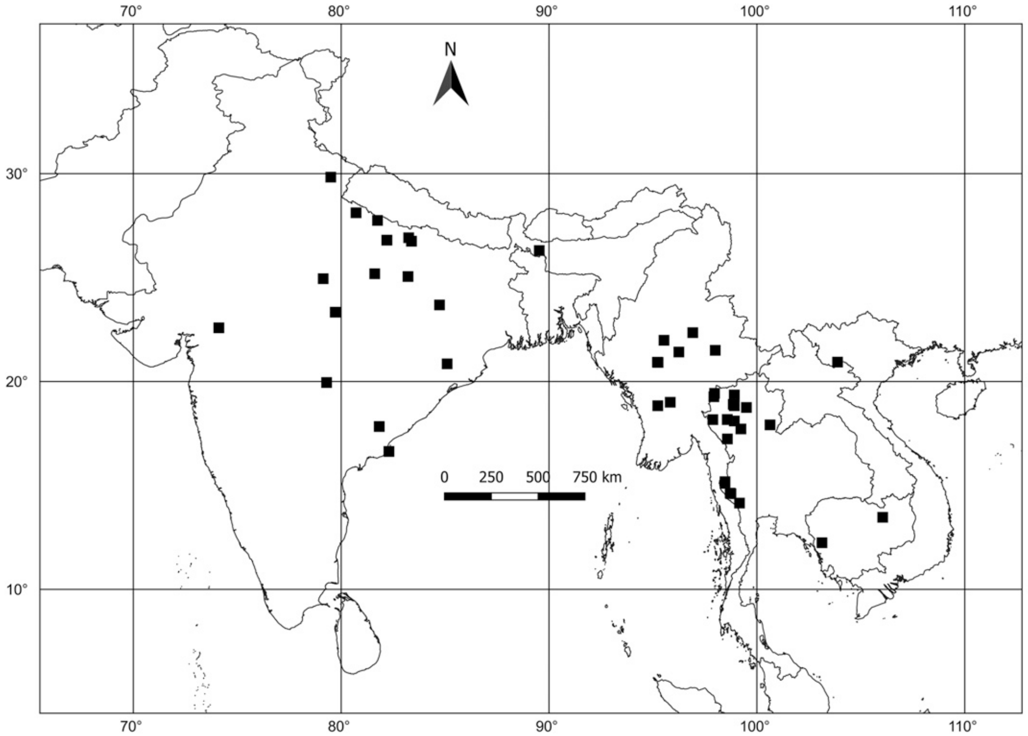

Figure 16. Distribution map for *Operculina petaloidea* (Choisy) Ooststr.

(holotype, US [bc] US00111355!; isotypes, GH [bc] 00054683!, K [bc] K001081721!, NY [bc] NY00336588!, U [bc] U0001435!).

Ipomoea megacarpa Brandegee, Zoe 5: 218. 1905. *Operculina ornithopoda* var. *megacarpa* (Brandegee) B. L. Rob., Proc. Amer. Acad. Arts 51: 530. 1916. TYPE: Mexico. [Sinaloa:] growing about Culiacan, *Brandegee s.n.* (holotype, UC [bc] UC105130!, UC105129!; isotypes, GH [bc] 00054518!, US [bc] US00008200!).

Herbaceous twiners; roots enlarged, perennial; sap unknown. Stems 1–3 m, cylindrical or angular when dried, glabrous. Leaf blades ovate in outline, 2–12 × 2–11 cm, base cordate to subtruncate, margins pinnately lobed or pinnately dissected, lobes often 5 to 9, linear, oblong, ovate or less commonly obovate or irregularly lobed, middle segment linear, ovate-lanceolate to ovate, mostly long acuminate, lobe bases often constricted, both sides sparsely hairy along veins; petioles 1–6.5 cm, sparsely pubescent near base. Inflorescences axillary, flowers 2 or 3 in monochasial cymes or solitary; peduncles 3–12 cm, glabrous, sometimes winged in upper portion; bracts lanceolate to linear, 7–10 mm; pedicels 12–20 mm, enlarged toward apex, sometimes angular and slightly alate, clavate in fruit. Flower diurnal, ascending to erect, odorless. Sepals subequal, 15–16 mm, convex, all glabrous; 2 outer obovate, 10–13 mm wide, apex rounded, obtuse, or truncate, mucronate; 3 inner obovate, 9–13 mm wide, margins scarious, paler. Corollas campanulate, white, 3.5–5 × 4–5 cm, midpetaline bands hirsute with long trichomes, tiny gland dots not evident. Stamens included, equal or unequal (2 short, 2 medium, 1 long); filaments 15–19 mm, basally adnate for 1/2 their length, bearded along margins of adnate portion, filamentous, free and glabrous above insertion point; anthers 7–9 mm, white, spirally dehiscent, bases subsagittate. Pollen 3-zonocolpate. Pistil included, equaling stamens, glabrous; disc annular; ovary ovoid, 2 mm, 2-locular; style filamentous; stigma biglobose. Fruiting calyx cupping fruit; sepals pale brown, papery, sometimes with blackish blotches. Capsules subglobose to depressed globose, 1.5–2 cm diam., pale brown; operculum 1–1.5 cm diam., dark brown; endocarp hyaline, translucent. Seeds 4 or fewer, subglobose, weakly carinate, 5–7 mm, dull black, glabrous; hilum C-shaped, black, glabrous.

Distribution. *Operculina pinnatifida* is widespread in Mexico (with populations concentrated in eastern and southern areas) and extending south into Guatemala, the northern distribution limit just reaching southern Texas, around Brownsville; it is absent from Belize. The species does not occur in Cuba (O'Donell, 1950: 433) (Fig. 18).

Ecology. A twiner often found in grasslands and thickets, it grows among the grass-herbaceous layer, or climbs into shrubs and low trees. Habitats and environments reported on collection labels include: chaparral; dry roadside in shrub forest; grassy slope with scattered trees and shrubs; Sinaloan thornscrub; and *vegetacion herbacea con arboles o arbustos de poca altura, en sitios expuestos sobre suelos calcareo* [herbaceous vegetation with low-growing trees or shrubs, in exposed sites on limestone soils] (*F. May et al. 1240*). Substrates reported are rich alluvial soil, clay, and limestone. Vegetation associates mentioned include *Acacia* Mill. (frequently), *Annona* L., *Bursera* Jacq. ex L., *Daphnopsis* Mart., *Erythrina flabelliformis* Kearney, *Gliricidia* Kunth, and *Ziziphus amole* (Sessé & Moc.) M. C. Johnst. Elevation ranges from sea level to 300(to 830) m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections						3	6	1	3	3	1	
Fruiting collections						2	1		1	2		

According to label data, the flowers open by 10 a.m. and close by 4 p.m. (*Runyon 3155*).

Vernacular names. Guatemala: quiebra cajete (*Steyermark 51336*). Mexico: manto (*Hinton et al. 7748*, *8157*), pato de gallo (*Edwards 477*); gallinita, pata-de-gallo (Carranza, 2008: 97; Felger et al., 2012: 521); chiquinces, xa-kontikin, chukinsis, kump ak-koontikin (McDonald, 1997: 69). U.S.A.: correveula de las doces (*Runyon 3155*); tansy-leaf lid-pod (USDA, NRCS, 2016).

Typification. Although the type of *Convolvulus pinnatifidus* is labeled as originating in Cuba, no subsequent collections have ever been made there. O'Donell (1950: 433) thoroughly investigated the situation, including visits to three herbaria in Havana during a trip in 1948, and concluded that there was very likely a label mix-up: a specimen from Mexico was mislabeled as originating in La Habana. Based on an inquiry to Prof. Dr. Walter Lack, he informed us (Lack, pers. comm. 2008) that the specimens collected by Humboldt and Bonpland conserved in the Herbier Bonpland at Paris are to be considered the holotypes for names published by Humboldt, Bonpland and Kunth; see Lack (2003) for details.

Convolvulus triflorus Sessé & Moc. was reduced to synonymy under *Operculina pinnatifida* by McDonald (1993: 85, 1997: 69); see Insufficiently Known Species for further details regarding the typification and nomenclature for this name.

Comments. The status of *Operculina pinnatifida* in the United States flora needs to be verified: Brownsville, Cameron County, Texas, was the only known locality in the United States for this species. This population was last collected in 1940, and we have seen no recent vouchers that confirm *O. pinnatifida* still survives there; these northernmost outlier populations require investigation to ascertain whether the species is extant there and what their current status is. Development and land clearing in this area during the second half of the 20th century could have exterminated these Texas populations.

Selected specimens examined [96 collections]. GUATEMALA. **Huehuetenango:** Santa Ana Huista, 26 Aug. 1942, *J. A. Steyermark 51336* (F, NY). **Petén:** La Libertad, 4 Apr. 1933, *C. L. Lundell 2477* (F, GH); s. loc., 30 May 1933, *C. L. Lundell 3504* (F, L, S). MEXICO. **Chiapas:** Ocozocoautla, 830 m, 18 Apr. 1972, *D. E. Breedlove 24623* (DS, MO, NY); Venustiano Carranza Mpio., Rancho Carmen, 2600 m, 3 May 1966, *R. M. Laughlin 877* (DS, F). **Guerrero:** Coyuca, Cutzamala de Pinzón, 18°28′04″N, 100°34′51″W, 9 May 1935, *G. B. Hinton et al. 7748* (GH); Galeana, Atoyac, 22 Nov. 1937, *G. B. Hinton et al. 10952* (F, GH, MO, NA, NY); Iguala, Aug. 1905, *Rose 9317* (NY); Rincon de Villa, 700 m, 5 Aug. 1962, *E. Matuda 37310* (GH). **México State:** Temascaltepec, 19 Sep. 1933, *G. B. Hinton 4772* (GH). **Michoacán de Ocampo:** Tacupa, Huetamo, 18 Jan. 1934, *G. B. Hinton et al. 5503* (F, GH, MO); Tizupan distr., Coalcomán, 18°47′N, 103°09′W, 20 June 1939, *G. B. Hinton et al. 13819* (GH). **Morelos:** Cuernavaca, 1 Sep. 1972, *D. F. Austin et al. 5037* (FAU); Yautepec, 18°53′N, 99°04′W, 17 June 1901, *C. G. Pringle 9645* (GH). **Nuevo León:** Montemorelos, 17 July 1971, *J. D. Dwyer et al. 22* (MO). **Oaxaca:** Almoloya, 17 June 1910, *Orcutt 5237* (MO); Laguna, 850 m, 5 June 1895, *E. W. Nelson 2646* (type GH, NY, US); s. loc., July 1937, *Williams 9786* (F). **Quintana Roo:** Chichancanab, 38 m, s.d., *G. F. Gaumer 1372* (F, GH, MO, U); same locality, *G. F. Gaumer 1865* (B, C, F, GH, L, MO). **San Luis Potosí:** Canoas, 21°59′N, 100°22′W, 15 July 1890, *C. G. Pringle 3553* (type F, GH); Ciudad Valles vic., 21°59′47″N, 99°00′39″W, 27 Apr. 1972, *E. Matuda et al. 38436* (GH); Rascón, June 1905, *E. Palmer 668* (F, GH, NY, US); San Dieguito, June 1904, *E. Palmer 112* (type GH, US); Tamazunchale, 10 July 1937, *M. T. Edwards 477* (F, GH, MO, UC); Tancanhuitz, s.d., *E. W. Nelson 4369* (US). **Sinaloa:** Culiacan, 6 Sep. 1904, *T. S. Brandegee s.n.* (GH, UC, US); Labradas, W of railroad track, 23°47′N, 106°22′W, 27 Sep. 1925, *R. S. Ferris & Y. Mexia 5243* (GH); Villa Union, 75 m, 4 Sep. 1967, *R. L. Oliver et al. 828* (MO). **Sonora:** Jeberojaquia, 10 m, 20 Oct. 1994, *S. L. Friedman et al. 435-94* (ARIZ, ASU, FAU); Huatabampo, Agiabampo, 27°12′N, 109°31′W, anno 1890, *E. Palmer 781* (GH, K, NY, U, US). **Tabasco:** Tenosique Mpio., Estapilla, 27 June 1939, *E. Matuda 3508* (F, GH, MO, NA, NY). **Tamaulipas:** Hacienda Buena Vista, 16 June 1919, *Wooton s.n.* (US); Gomez Farias vic., 22°53′01″N, 99°01′34″W, 13–21 Apr. 1907, *E. Palmer 329* (GH); El Limón, edge of canal, 22°49′30″N, 99°00′18″W, 30 Aug. 1948, *K. L. Kenoyer & Crum 3636* (GH); Tampico, 15 m, June 1910, *E. Palmer 569* (F, MO, NY, US); Victoria, *E. Palmer 389* (F, GH, MO, NY, US); Xicotencatl roadside, 20°33′50″N, 98°12′31″W, 29 Aug. 1948, *K. L. Kenoyer & Crum 3470* (GH). **Veracruz:** Acazónica, July 1919, *C. A. Purpus 8404* (GH, MO, NY); Baños el Carrizal, 19°19′16″N, 96°37′45″W, Aug. 1912, *C. A. Purpus*

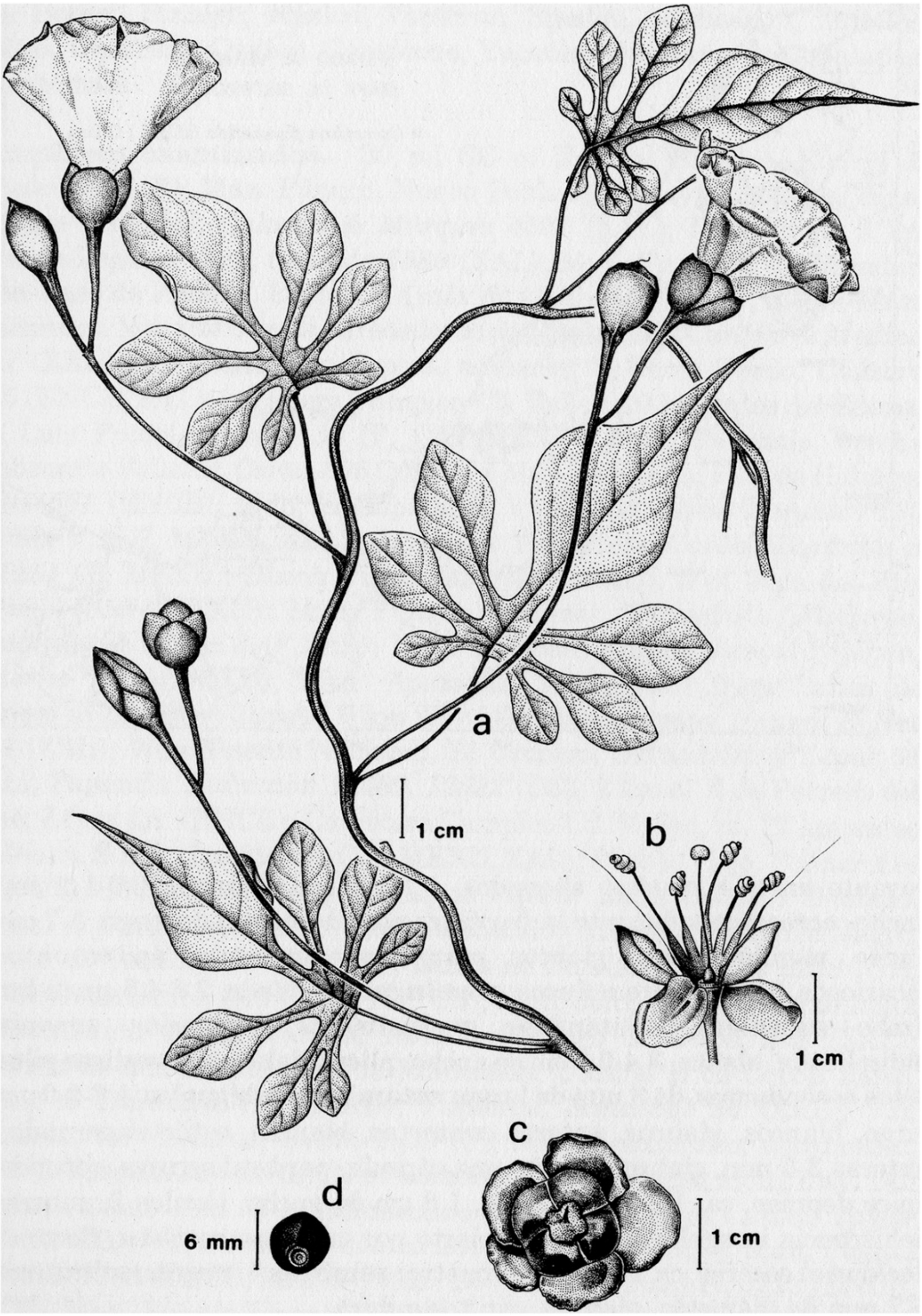

Figure 17. An illustration for *Operculina pinnatifida* (Kunth) O'Donell. Original caption, translated: a. flowering branch; b. floral dissection showing four sepals, five spirally dehiscent anthers, and the pistil; c. mature fruit with operculum in place; d. seed. Reproduced with permission of the *Flora de Veracruz* editorial committee, from McDonald (1993: 87, fig. 9), drawn by E. Saavedra.

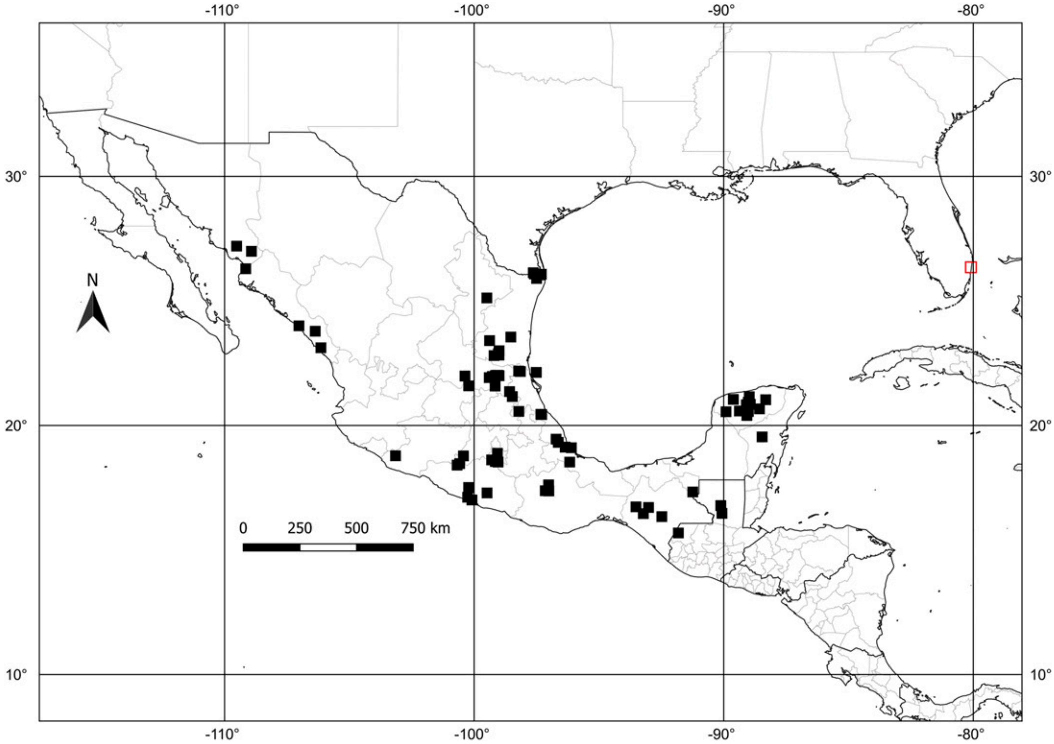

Figure 18. Distribution map for *Operculina pinnatifida* (Kunth) O'Donell. Black squares are collections made in the wild; open square is a cultivated plant.

6238 (GH); Boca del Río Mpio., S of Boca del Río, 17 July 1977, *J. D. Dwyer 14555* (BM, MEXU, MO); Panuco Mpio., 10 km before Ebano, 22°10′01″N, 98°08′48″W, 13 Aug. 1970, *F. Chiang 33* (GH); Pueblo Viejo, 15 m, 23–31 May 1910, *E. Palmer 414* (GH, MO, NY, US); Rio Atoyac, 24 Mar. 1970, *R. W. Long et al. 3159* (F, FAU, USF). **Yucatán:** Mérida, 26 Aug. 1972, *D. F. Austin et al. 5018* (FAU); Izamal, 20°56′N, 89°01′W, 15–20 m, anno 1895, *G. F. Gaumer 596* (BR, C, F, GH, MO, NY, U, UC); SE of Kancabdzonot, May 1919, *G. F. Gaumer et al. 23877* (GH); Opichén Mpio., Calcehtok, 20°33′00″N, 89°54′27″W, 30–100 m, 30 July 1998, *F. May et al. 1240* (CICY); Suitun, 20°51′N, 88°56′W, June 1916, *G. F. Gaumer et al. 23362* (ECON, F, GH); Chichen Itza, in forest Valladolid, 29 June 1932, *Steere 1653* (F). **S. loc.:** *Karwinsky 602* (H); *Linden 300* (BR). U.S.A. **Texas:** Cameron Co., Barreda Station, Brownsville, only occurs betw. Olmito & San Benito, 15 Oct. 1936, *Runyon 2398* (TEX); Barreda, 4 July 1939, *Runyon 3155* (TEX); Russelltown, 14 Sep. 1940, *Runyon 2008* (F); San Benito, *Ferris et al. 3212* (MO); Cameron Co., s. loc., 4 July 1939, *Runyon 5149* (M).

Carranza (2008: 99–100) and McDonald (1993: 89–90) cited additional Mexican specimens of *O. pinnatifida*. However, we have not verified the identifications for these records.

Cultivated. U.S.A. **Florida:** Palm Beach Co., Boca Raton, cultivated in garden at 135 Pine Circle for M.S. thesis, 1978, *G. Staples s.n.* (FAU).

8. Operculina polynesica Staples, Pacific Sci. 61: 588. 2007. TYPE: Pitcairn Islands. Henderson Island, *J. Florence, Chepstov-Lusty & Waldren 10909* (holotype, K [bc] K000649672!; isotypes, BISH [bc] BISH1001150!, BM not seen, CHR not seen, E not seen, L [bc] L0281977!, P [bc] P04472951!, PAP [bc] PAP001830!, PTBG [bc] PTBG1000000011!, TCD!, US not seen). Figure 19.

Prostrate trailer or twiner; sap white, abundant. Stems herbaceous, to 5 m, 5–14 mm diam., terete or striate-ridged when dry, finely puberulous to glabrate, fistulose. Leaves entire, broadly cordiform, suborbicular to broadly ovate, 9.3–21 × 8.6–20 cm, herbaceous to slightly fleshy, base cordate, deeply U-shaped, apex tapering acuminate to cuspidate, mucronulate, adaxially appressed sericeous to glabrous, abaxially villous to subglabrous, trichomes denser along veins; petiole (2–)5.5–9.5(–13.5) cm, adaxially sulcate. Inflorescences axillary, cymose, 1- to 3-flowered; peduncles stout, terete, not winged, 5–12.4(–18) cm; branches (0.6–)1.7–2 cm; bracts paired, elliptic to oblong, 1.1–1.3 cm, incurved around pedicel, caducous; pedicels 2–4.3 cm, angulate, in fruit thickened and clavate (then thicker than peduncle). Flowers showy, diurnal, odorless. Sepals equal or inner slightly shorter, convex, clasping corolla tube base, broadly elliptic to subcircular, subequal, 1.8–2.3 cm; outer 3 rounded, emarginate to praemorse apically, abaxially glabrous or finely puberulous medially; inner 2 obtuse, mucronulate, glabrous. Corolla flaring funnelform, white, 5–6.5(–8) cm × 3.5–4.5(–9) cm, glabrous outside, covered in tiny golden gland dots. Stamens subequal, 18–20 mm, included; filaments basally dilated and adnate to corolla tube for 1/6 to 1/4 their length, margins of adnate portion pubescent, filamentous, free, glabrous above insertion; anthers spirally dehiscent, 4–6 mm, white. Pollen 3-zonocolpate. Pistil included, 3–3.3 cm; disc annular, wider than ovary, blackish; ovary ovoid, ca. 3 mm, glabrous; style filiform, stigma biglobose. Fruiting calyx accrescent, enclosing the fruit, sepals adaxially stramineous, shiny, finely pitted, abaxially tan to pale brownish, (sub)glabrous. Capsule subglobose, ca. 3 × 2.5 cm, glabrous, circumscissile above the middle; operculum not seen; endocarp thinly papery, translucent. Seeds 4 or less, carinate, 10–12 × ca. 10 mm, black, glabrous, surface finely roughened, matte; hilum basal, reniform to semicircular, ca. 4 × 5 mm, yellowish in center.

Distribution. *Operculina polynesica* is widely distributed across Polynesia: from Niue and the Cook Islands in the western Pacific via the Tuamotus to the Pitcairn Islands (Henderson) in the eastern Pacific (Fig. 20).

Ecology. Apparently, *Operculina polynesica* is a species that thrives on low coral atolls, from small uninhabited *motus* (islets) to the littoral strand on ocean beaches and sheltered inland valleys on larger/higher islands. Label data reports: a thicket in a shallow gully, surrounded by ferns; in abandoned cultivated land and *cocoteraie* (coconut plantations); in areas that are frequently burned; along roads and trails in forested areas; along the roadside at the margin of a *Hibiscus tiliaceus* L.–dominated forest area; and frequently reported to grow on various alkaline substrates: coralline sands, gravel, or coral blocks and *makatea* limestone.

Collectors report that *Operculina polynesica* is found growing in association with trees such as *Allophylus* L., *Casuarina* L., *Celtis* L., *Cocos* L., *Cyclophyllum* Hook. f., *Hibiscus tiliaceus*, *Meryta* J. R. Forst. & G. Forst., *Pandanus* Parkinson, *Pisonia* L., and *Tournefortia* L., with a shrub layer that includes *Capparis* L., *Guettarda* L., *Jossinia* Comm. ex DC., *Morinda* L., *Pipturus* Wedd., *Scaevola* L., *Sesbania* Adans., *Timonius* DC., and a ground layer of creepers and herbaceous plants that includes *Boerhavia* L., *Canavalia sericea* A. Gray, *Cassytha* Osbeck, *Heliotropium* L., *Ipomoea pes-caprae* (L.) R. Br., *I. macrantha* Roem. & Schult., *Pemphis* J. R. Forst. & G. Forst., *Psilotum* Sw., and *Triumfetta* L. Elevation ranges from sea level to 60 m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections					1	4	5	2		2	1	
Fruiting collections	1				1	2	3	1		3	1	

Comments. Label data from Cook Islands specimens (*Sykes 3740/CI* and *3878/CI*) indicate that the fresh corollas are as much as 7–8 cm long and 8–9 cm across the limb. The largest corollas seen in dried material are 6.5 cm long. It is hoped that further collecting in the Tuamotus will provide fertile specimens that can be identified with certainty. Several intermediate collections are here referred to a purported hybrid between *Operculina turpethum* and *O. ventricosa* (q.v.). The following collections are confidently placed as bona fide *O. polynesica*.

Specimens examined [25 collections]. COOK ISLANDS. **Atiu Island:** Atiu airport, 19°59′30″S, 158°07′10″W, 30 July 1991, *W. R. Sykes 3878/CI* (BISH, CHR); Teenui distr., Taunganui, 20°07′S, 157°24′W, 23 July 1991, *W. R. Sykes 3740/CI* (BISH, CHR). **Mangaia:** Ivirua, 21°55′04″S, 157°53′55″W, 17 July 1986, *A. Whistler 5845* (B). FRENCH POLYNESIA. **Austral Islands:** Rimatara, débarcadère Teanini, 22°38′S, 152°51′W, 4 m, 1 Nov. 2004, *J. F. Butaud 706* (PAP). **Tuamotu Islands:** Anaa, Tukuhora, 17°21′S, 145°30′W, 5 m, 17 June 2005, *J. F. Butaud 1152* (PAP); Anaa, Tukuhora, 17°21′S, 145°30′W, 5 m, 25 Aug. 2008, *J. F. Butaud & J. Kape 1912* (PAP); Kaukura, Motu Maoa Sud-Ouest, 16°45′S, 146°42′W, 3 m, 16 Jan. 2010, *J. F. Butaud 2496* (PAP); Makatea, Moumu, 15°50′S, 148°15′W, 4 m, 2 July 2009, *J. F. Butaud & F. Jacq 2320* (PAP); Mataiva, Vaitetuna, 14°53′S, 148°40′W, 13 Nov. 2004, *J. F. Butaud & E. Lagouy 775* (PAP); Mataiva, Fenua Manu, 14°53′S, 148°40′W, 4 m, 16 Jan. 2009, *J. F. Butaud & F. Jacq 2109* (PAP); Niau, Tupana village, 16°08′S, 146°20′W, 2 m, 14 Oct. 2006, *J. F. Butaud 1506* (BISH, PAP); Nukutavake, Tevai, 19°17′S, 138°50′W, 6 m, 10 Mar. 2009, *J. F. Butaud 2152* (PAP); Rangiroa, Motu Taereere, 15°12′S, 147°50′W, 4 m, 27 June 2009, *J. F. Butaud & F. Jacq 2300* (BISH, PAP); Tikehau, Tuherahera village, 15°06′S, 148°15′W, 1 m, 26 Oct. 1984, *J. Florence 7034* (BISH, K, P, PAP); Toau, Motu Matariua, 15°48′S, 146°09′W, 1 m, 3 Apr. 1990, *J. Florence 10237* (P, PAP). Two sterile collections that, based on vegetative characters, appear to belong here include: Niau, Tupana village, 16°09′S, 146°19′W, 1 m, 1 Apr. 1990, *J. Florence 10180* (BISH, K, P, PAP, US); Rangiroa, Motu Otepipi, 15°19′S, 147°29′W, 1 m, 19 Jan. 1990, *J. Florence 10008* (BISH, K, P, PAP, US). NIUE. **Tautu:** Tauku, near Liku, 19°02′S, 169°47′W, 27 Oct. 1965, *W. R. Sykes 169783* (BISH). PITCAIRN ISLANDS. **Henderson Island:** SW Point, 24°23′S, 128°20′W, 35 m, 15 May 1991, *J. Florence et al. 10909* (type BISH, BM, CHR, E, K, L, P, PAP, PTBG, TCD, US); same locality, 22 June 1991, *J. Florence et al. 10989* (BISH, K, L, P, PAP, TCD, US).

9. Operculina pteripes (G. Don) O'Donell, Lilloa 23: 435. 1950. *Calonyction pteripes* G. Don, Gen. Hist.

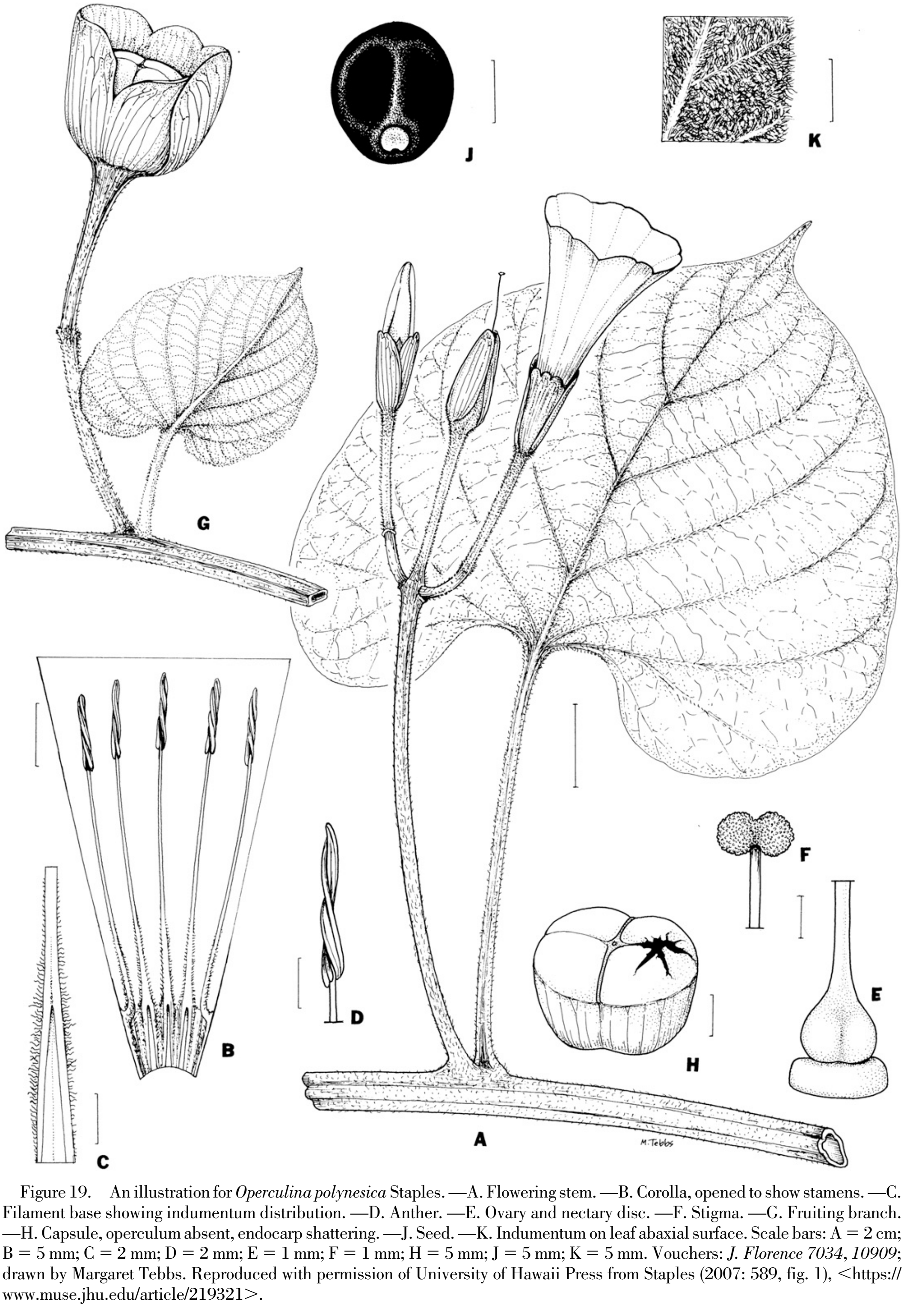

Figure 19. An illustration for *Operculina polynesica* Staples. —A. Flowering stem. —B. Corolla, opened to show stamens. —C. Filament base showing indumentum distribution. —D. Anther. —E. Ovary and nectary disc. —F. Stigma. —G. Fruiting branch. —H. Capsule, operculum absent, endocarp shattering. —J. Seed. —K. Indumentum on leaf abaxial surface. Scale bars: A = 2 cm; B = 5 mm; C = 2 mm; D = 2 mm; E = 1 mm; F = 1 mm; H = 5 mm; J = 5 mm; K = 5 mm. Vouchers: *J. Florence 7034*, *10909*; drawn by Margaret Tebbs. Reproduced with permission of University of Hawaii Press from Staples (2007: 589, fig. 1), <https://www.muse.jhu.edu/article/219321>.

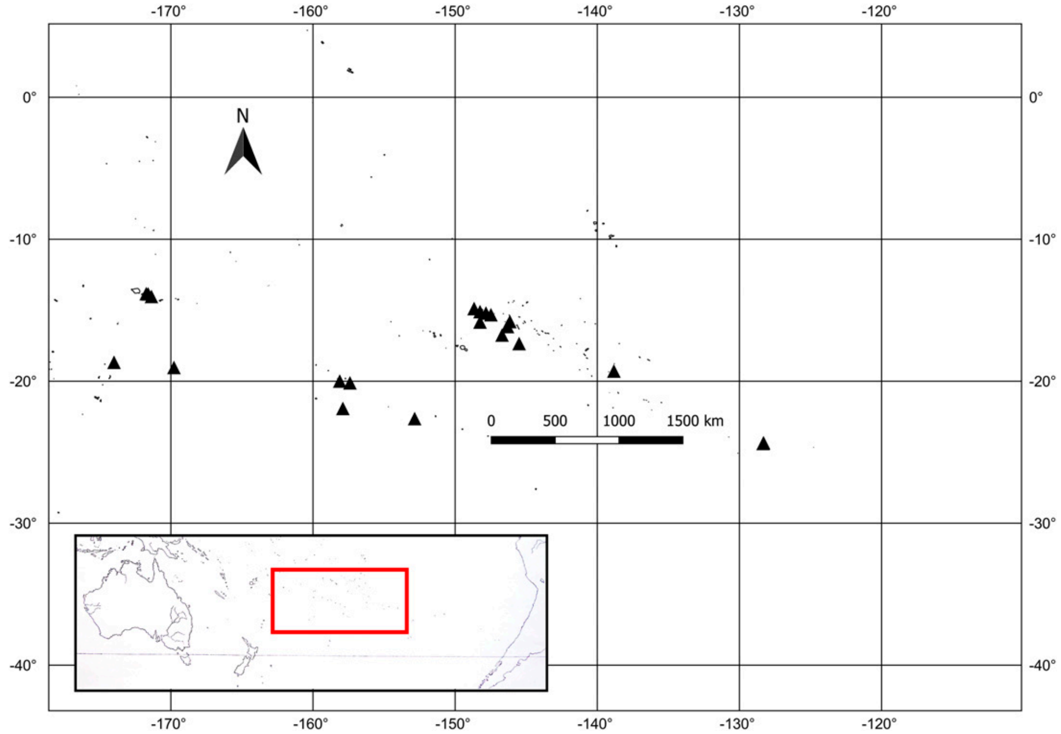

Figure 20. Distribution map for *Operculina polynesica* Staples.

4: 264. 1838. TYPE: Ecuador. "Huayaquil," herb. *Ruiz & Pavón "8/21"* (lectotype, designated here, MA [bc] MA818859 image!; isolectotypes, F [bc] F0042363F!, MA [bc] MA818860 image!). Figure 21.

Ipomoea alatipes Hook., Bot. Mag. 88: pl. 5330. 1862. *Operculina alatipes* (Hook.) House, Bull. Torrey Bot. Club 33: 499. 1906. TYPE: Venezuela. "prope coloniam Tovar" betw. Biscaina & La Victoria, 2300 ft., 8 Sep. 1856, *A. Fendler 2084* (lectotype, designated here, GH [bc] 00054583!).

Ipomoea alata Rose, Contr. U.S. Nat. Herb. 1: 108. 1891, nom. illeg., non R. Br., 1810. Replacement name: *Operculina rubicunda* House, Bull. Torrey Bot. Club 33: 498. 1906. TYPE: Mexico. Sonora: Alamos, 16–30 Sep. 1890, *E. Palmer 706* (holotype, US [bc] US00111358!; isotypes, F!, GH! [bc] 00054480!, K [bc] K000613073!, US [bc] US00930939!, US00930940!).

Ipomoea rhodocalyx A. Gray, Proc. Amer. Acad. Arts 22: 439. 1887. *Operculina rhodocalyx* (A. Gray) House, Bull. Torrey Bot. Club 33: 498. 1906. TYPE: Mexico. Jalisco: at base of hills, Tequila, *E. Palmer 421* (holotype, GH [bc] 00054534!; isotypes, K!, MO!, US!).

Operculina lancifolia House, Muhlenbergia 5: 68. 1909. TYPE: Mexico. Chiapas: valley of Jiquipilas, 16–18 Aug. 1895, *E. W. Nelson 2923* (holotype, US [bc] 00008198!).

Herbaceous twiners; sap milky, abundant. Root slightly enlarged. Stems 2–8 m, cylindrical, striate to angular, glabrous, bases somewhat woody in some plants. Leaves entire, ovate to ovate-lanceolate, 3–13 × 2–8 cm, basally cordate to subtruncate, basal lobes usually rounded and sinus shallow, apically acute to acuminate, mucronate, glabrous or base sometimes abaxially pubescent; petioles 1–8 cm, glabrous or pubescent toward apex. Inflorescences axillary, flowers 2 to 12 in cymose clusters, less often solitary; peduncles 2–15 cm, 3-winged in middle (rarely unwinged), wings 0.6–3.5 mm wide, attenuate toward both ends; bracts caducous, bracteoles lanceolate, 9–10 × 3–3.5 mm, acute, caducous; pedicels 1.5–3.5 cm, thicker toward apex. Flower diurnal, ascending-erect, odorless. Sepals subequal, glabrous, outer 2 ovate to ovate-elliptic, 2.2–2.6 × 1.5–1.9 cm, basally truncate, apically obtuse or subacute, inner 3 ovate, 2.3–2.5 × 1.5–1.8 cm, basally rounded, apically subobtuse to obtuse. Corolla subsalverform, pink, red-orange to red-salmon, 4–7 cm, tube 0.5–1 cm diam., limb 3–5.8 cm diam., tube and interplicae densely tomentose, tiny gland dots not evident. Stamens subequal, exserted, 4–5 cm; anthers spirally dehiscent, 7–8 mm. Pollen 3-zonocolpate. Pistil exserted, equaling stamens; ovary ovoid, glabrous; stigma biglobose. Fruiting calyx accrescent, at first surrounding fruit, later reflexing from it. Capsule ellipsoid, 1.5–2 cm diam., brown; operculum olivaceous drying brown, capped by indurated style base; endocarp translucent. Seeds 1 to 4, oblong-ovoid, 8–9 mm, black, glabrous.

Distribution. *Operculina pteripes* is widespread from northern Mexico, where it follows the Pacific slope of the *sierra madre occidentale*, throughout Central America (Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama) and then sporadically in South America (Bolivia, Brazil, Colombia, Ecuador, Venezuela) (Fig. 22). The species is absent from Belize and the islands of the Caribbean; while it is listed for Peru (Macbride, 1959: 479; Brako & Zarucchi, 1993: 374) we have seen no bona fide specimens from there.

Ecology. Collectors report a wide array of habitats in their label data: in Mexico there are several reports of tropical deciduous forest, tropical Sonoran forest, and oak-pine forest. Other habitats and environments reported include: chaparral; *bosque Amazonico*; *mata de galeria antropizada em cerrado* [disturbed gallery forest in cerrado] (*T. B. Cavalcanti et al. 1934*); along roadside in canyon; in open pasture on rocky slopes and deciduous forest on basaltic mesas; roadside thickets; rocky riverbank; *zona muy intervenida con papayas escapadas, lado del camino en zona perturba* [heavily trafficked zone with escaped papayas, at side of road in disturbed area] (*M. Mendoza & C. Rivadeneira 2409*); *matorrales húmedas-pedregosos, bosques pantanosos* [stony-wet thickets in swamp forests] (*P. J. Shank & A. Molina R. 4579*); low hills in savanna, brushy secondary growth; in xeric secondary vegetation; upper tropical dry forest associated with pine-oak; *bosque seco tropical* [tropical dry forest] (*W. Robleto 1651*); *en vegetacion secundaria, xerica sobre afloramiento rocoso* [in xeric secondary vegetation, on rocky outcrop] (*A. Fernandez & E. Sanoja 4979866*). Substrates reported include sandy; volcanic area on basaltic substrate; and *suelo basaltico en procese de meteorizacion* [basaltic soil in process of weathering] (*A. Grijalva 3111*). Vegetational associates include: *Anadenanthera macrocarpa* (Benth.) Brenan, *Attalea phalerata* Mart. ex Spreng., *Bursera*, *Byrsonima* Rich. ex Kunth–*Curatella* Loefl. savanna, *Ceiba* Mill., *Heliocarpus* L., *Pinus oocarpa* Schiede ex Schltdl., *Quercus pennivenia* Trel., and *Xanthoxilum* (sic). As recorded on labels, elevation ranges from 50 to 850(to1250) m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	1		1	2	1		2	4	15	14	7	6
Fruiting collections	1							1	1	1		

Evidently, this is the only species of *Operculina* that is adapted for hummingbird pollination. The salverform corolla shape, genitalia exserted from the corolla and flesh-colored to salmon-orange or red corolla color all conform to a syndrome for bird-pollinated flowers in the Neotropics, and hummingbirds have been reported to visit the blooms (Felger et al., 2012: 522).

Vernacular names. Brazil: derruba-velho (*Petrongari & Fernandes 133*). Costa Rica: methuacan (*Ørsted 12600*). El Salvador: mechoacán (*Calderón 2058*). Guatemala: chorreque (*Standley 75841*). Honduras: camotillo (*Standley 27007*). Mexico: campanilla chocolate (Felger et al., 2012). Panama: michoican (*Hayes 543*).

Typification. George Don indicated he saw material in the Ruiz & Pavón herbarium (now MA), and we have chosen a specimen in Madrid collected by Ruiz and Pavón that fits the protologue closely. Meisner created a superfluous name when he named *Operculina pteropus* because he cited two older names in synonymy. It is possible Meisner was actually trying to make a new combination in *Operculina*, based on *Calonyction pteripes* G. Don, but he misspelled the epithet *pteripes* as "*pteropus*" and cited a Pavon specimen in LE; if this specimen is a duplicate of the same Pavon collection on which George Don based his *C. pteripes*, then Meisner's name is illegitimate as well as superfluous. It seems likely that *C. pterodes*, published by Choisy, is simply an orthographic variant, in error, for *C. pteripes* G. Don.

Hooker (1862) based his *Ipomoea alatipes* on a cultivated plant grown in the glasshouse at Kew and also cited three collections from Panama and Venezuela (syntypes). We found no voucher specimen in Kew for the cultivated plant, and one of the syntypes in Kew, *Fendler 2084*, is missing. However, *Fendler 2084* is present in the Gray Herbarium, and it is a very complete specimen; we have chosen it as the lectotype for Hooker's name. One wonders whether Hooker gave one of the syntypes to his friend Asa Gray; we found no other duplicates anywhere for *Fendler 2084*.

Seemann (1854: 171) misapplied the name *Ipomoea pterodes* to what is actually *Operculina pinnatifida*, a different taxonomic concept than *I. pterodes* Choisy (a synonym of *O. hamiltonii*).

Selected specimens examined [157 collections]. BOLIVIA. **Beni:** Cachuela Esperanza, Rio Beni, July 1922, *G. Meyer 231* (NY). **Concepción:** Palestina vic., 15°35′06″S, 62°09′13″W, 481 m, 4 May 2007, *M. Mendoza et al. 2409* (LPB, MO, USZ). **Pando:** Madre de Dios, cerca barraca Sena, 220 m, 3 Sep. 1985, *M. Moraes 454* (FAU, LPB, MO). BRAZIL. **Goiás:** Ipameri Mun., vic. ponte São Bento, 17°42′52″S, 48°29′54″W, 950 m, 11 Apr. 1996, *T. B. Cavalcanti et al. 1934* (CEN, TEPB). **Mato Grosso:** Vila Bela da Santíssima Trindade, 14°35′54″S, 59°44′24″W, 233 m, 15 May 2013, *M. R. V. Zanatta & J. E. Q. Faria 2005* (SP, UB). COLOMBIA. **Bolívar:** Torrecilla, near Turbaco, 150–300 m, Nov. 1926, *E. P. Killip & A. C. Smith 14638* (F, GH, MO, NY, S). **Cesar:** Poponte, 14 Oct. 1924, *C. Allen 770* (MO). **Magdalena:** Santa Marta, Nov. 1898–1901, *H. Smith 1565* (COL, F, GH, L, MO, P, S, U). COSTA RICA. **Alajuela:** Carrillos de Poás, 26 Oct.

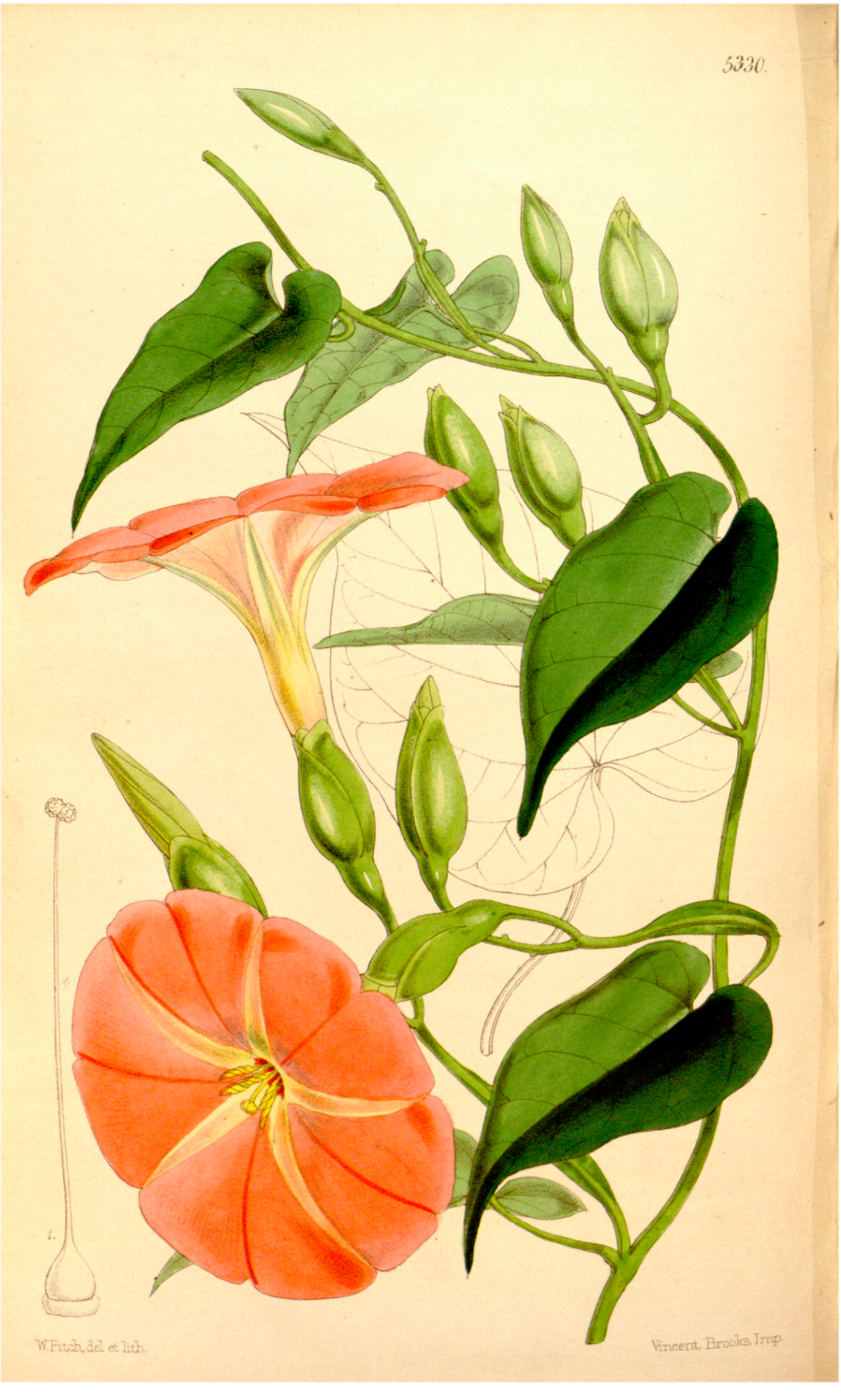

Figure 21. An illustration for *Operculina pteripes* (G. Don) O'Donell. Habit of flowering stem, note the winged peduncles and salverform corolla. Original caption: 1. pistil, arising from nectary disc. Reproduced from *Curtis's Botanical Magazine* (Hooker, 1862: plate 5330), under the name *Ipomoea alatipes* Hook.

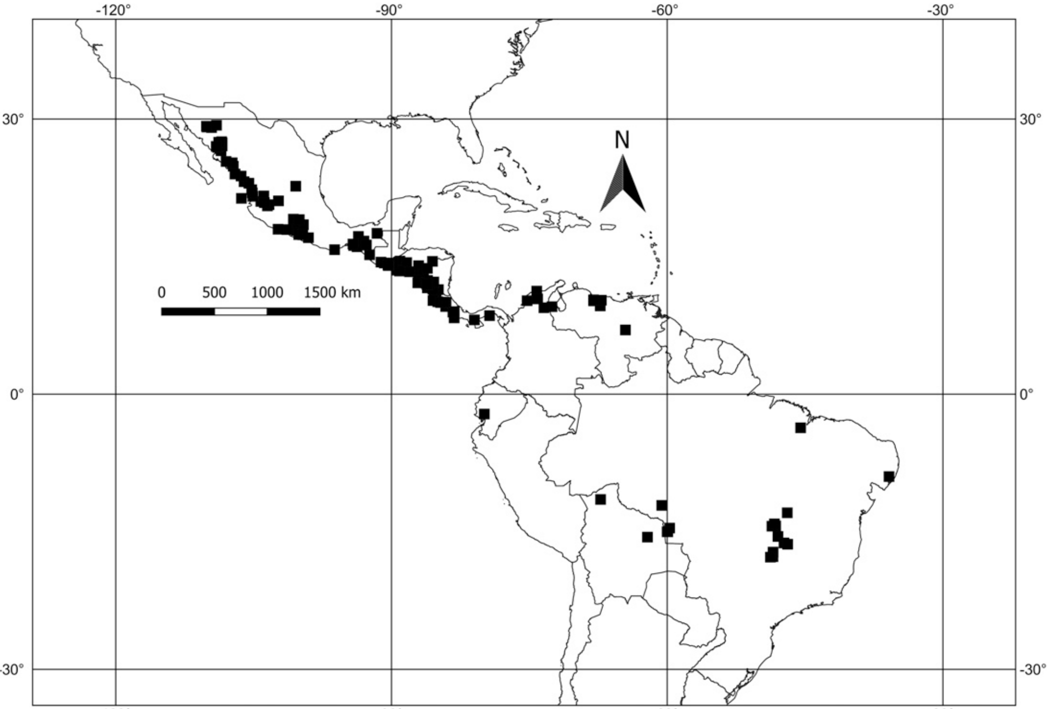

Figure 22. Distribution map for *Operculina pteripes* (G. Don) O'Donell.

1931, *A. M. Brenes 14347* (F, GH, NY). **Guanacaste:** Matapalo to Salinas, 15 Dec. 1990, *P. Dobbler 3830* (M). **Heredia:** Heredia, anno 1933, *A. M. Brenes s.n.* (NY). **Puntarenas:** Puerto Nuevo, 8°58′10″N, 83°18′35″W, 70 m, 19 Dec. 1992, *D. F. Austin 7832* (FAU, INB, MO, US). **San José:** Piedades de Santa Ana, 3 Nov. 1963, *M. Jimenez 1292* (F). **S. loc.:** Esparsa, 1845–1848, *A. Ørsted 12600* (C), Tacares, 13 Nov. 1932, *M. Valerio 301* (F). ECUADOR. **Guayas:** Guayaquil, anno 1800, *Ruiz et al. s.n.* (type F, MA). EL SALVADOR. **Ahuachapán:** Cerro de Apaneca, 15 Oct. 1957, *Gonzalez 1655* (USF). **Morazán:** Montecristo, 3 Dec. 1941, *Tucker 459* (F, UC); San Salvador, anno 1924, *S. Calderón 2058* (GH). GUATEMALA. **Chiquimula:** Chiquimula, 21 Oct. 1939, *J. A. Steyermark 30135* (F, NY). **Escuintla:** betw. Escuintla & Puerto San José, 150 m, 15 Nov. 1967, *A. Molina R. 21169* (F, GH, NY). **Jutiapa:** region of El Tamblón, NE of Jutiapa, 31 Oct. 1940, *P. C. Standley 75841* (F). **Santa Rosa:** Casillas, 1300 m, Nov. 1892, *Heyde & Lux 4351* (GH). **Sololá:** s. loc., July 1891, *Shannon 408* (US). HONDURAS. **Choluteca:** vic. of Pespire, 18–25 Oct. 1950, *P. C. Standley 27007* (F). **Copán:** Quebrada Seca, 500 m, 19 Nov. 1969, *A. Molina R. et al. 24644* (F, MO, NY); **Francisco Morazán:** Oyuca, Nov. 1943, *Rodrigues 1592* (F). **Lempira:** Gracias, anno 1852, *Hjalmarson s.n.* (S); **Olancho:** Valle Catacamas, 19 Nov. 1963, *R. Molina 13294* (F, NY). MEXICO. **Chiapas:** hacienda Monserrate, Sep. 1923, *C. A. Purpus 9186* (F, GH, MO, NY, UC). **Chihuahua:** Rio Mayo, Guasaremos, 23 Aug. 1936, *H. S. Gentry 2433* (GH, MO). **Guerrero:** Taxco el Viejo vic., 18°29′00″N, 99°35′03″W, 18 Sep. 1937, *R. Q. Abbott 435* (GH); Temisco, 320 m, 30 Oct. 1937, *Y. Mexía 8715* (B, F, GH, MO, NY, U, UC). **Jalisco:** Guadalajara, open fields near Río Grande de Santiago, 26 Aug. 1941, *W. & M. Leavenworth 1873* (F); Tequila, Aug. 1886, *E. Palmer 421* (type GH, K, MO, US). **México:** Temascaltepec, 26 Sep. 1933, *G. B. Hinton 4817* (F, GH, K, MO, NA). **Michoacán:** Zitácuaro Mpio., Tuzantla-Tiquicheo, 650 m, 1 Oct. 1938, *G. B. Hinton et al. 13296* (F, GH, K, MO, NA). **Nayarit:** Ixtlán del Río, 23 Sep. 1926, *Y. Mexía 732* (C, NA, UC); Tres Marias Islands, Maria Madre, 180 m, 23 Oct. 1925, *R. S. Ferris 5657* (MO). **Oaxaca:** San Pedro Tapanatepec, 30 Aug. 1971, *Cruden 1918* (FAU, UC). **Sinaloa:** Choise, El Potrerillos, s.d., *Ortega 873* (F); Culiacan, 1 Oct. 1904, *T. S. Brandegee s.n.* (GH, UC). **Sonora:** 3 mi. NE of Mátape, 29°07′N, 109°58′W, 799 m, 8 Sep. 1941, *Wiggins & Rollins 398* (ARIZ, GH, MO, NY, UC); Yécora, La Concepción, 29°19′25″N, 109°02′20″W, 650 m, 18 July 1997, *W. Trauba s.n.* (ARIZ, FAU); **S. loc.:** Guatulco, Oct. 1842, *Liebmann 12513* (C). NICARAGUA. **Chinandega:** Chinandega, 45 m, 13 Jan. 1903, *C. F. Baker 36* (GH, MO, NY, UC). **Chontales:** bosques de San Miguelito, drenaje del Lago Granada, 30 m, 13 Nov. 1951, *P. J. Shank & A. Molina R. 4579* (F, GH). **Granada:** La Perra, 100 m, 17 Nov. 1983, *A. Grijalva et al. 3243* (FAU, MO). **Managua:** Managua, field near University Centroamericana, 150 m, 30 Sep. 1976, *D. Neill 916* (MO). **Masaya:** Volcan Masaya, 13 Oct. 1983, *A. Grijalva 3111* (FAU, MO). **Matagalpa:** Santa Maria de Ostuma, 1200–1500 m, s.d., *Heller 1* (F). **Nueva Segovia:** El Jicaro, Cerro El Coyolito, 13°43′N, 86°06′W, 600–700 m, 27 Dec. 1984, *P. P. Moreno 25269* (FAU, MO). **Rivas:** La Esperanza, 200–400 m, 14 Dec. 1984, *W. Robleto 1651* (HNMN, MO). PANAMA. **Canal Zone:** Thatcher Ferry Bridge, 10–25 m, 5 Dec. 1971, *A. H. Gentry 2858* (F, MO, NY). **Veraguas:** Santiago, ca. 50 m, Nov. 1938, *P. H. Allen 1011* (GH, L, MO); s. loc., Dec. 1861, *S. Hayes 543* (types BM, K); s. loc., s.d., *Seemann 176* (type K). VENEZUELA. **Aragua:** prope coloniam Tovar, 2300 m, 8 Sep. 1856, *A. Fendler 2084* (type GH). **Bolívar:** Sucre, Jabillal, 70 m, Mar.

1989, *A. Fernandez et al. 4979866* (MO). **Carabobo:** Bárbula, 500 m, 12 Dec. 1938, *L. Williams et al. 341* (NY, P, S, U, USF). **Guárico:** Ortiz, Oct. 1963, *Aristeguieta 5193* (COL, F, MO, U). **Zulia:** carretera Machiques-Colón, 20 Nov. 1968, *Aristeguieta 6787* (NY).

10. Operculina riedeliana (Oliv.) Ooststr., Blumea 3: 366. 1939. *Ipomoea riedeliana* Oliv., Hooker's Icon. Pl. 15: 19, pl. 1424. 1883. *Merremia riedeliana* (Oliv.) Hallier f., Bot. Jahrb. Syst. 16: 552. 1893. TYPE: Indonesia. Buru, *Riedel s.n.* (lectotype, designated here, K [bc] K000830917!). Figure 23.

Ipomoea petaloidea Choisy var. *andamanica* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 110. 1894. *Merremia crispatula* Prain var. *andamanica* (Prain) Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(2): 307. 1896. TYPE: [India. Andaman & Nicobar Islands:] South Andaman, Chauldari, 27 Feb. 1893, *King's Collector P63* (syntypes, CAL not seen, K [bc] K000830920!, P [bc] P03544710!); South Andaman, Port Mouat, 11 Mar. 1893, *King's Collector P62* (syntypes, CAL not seen, K [bc] K000830921!); Andamans, s. loc., *Kurz s.n.* (syntype, CAL not seen).

Liana, all parts glabrous; sap milky white. Stems to 10 m, up to 1 cm diam., cylindrical, terete, basally woody, smooth or minutely warty, glaucous when young. Leaves entire, broadly ovate to orbicular, rarely oblong, narrowly oblong or linear-lanceolate, 8–18 × 3–6(–15) cm, often drying brown to black-brown, base cordate, subcordate to truncate, apex abruptly acuminate, mucronulate; secondary veins 6 to 8 per side; petiole slender, 2–10 cm, terete, drying blackish brown. Inflorescences usually several-flowered; peduncles stout, 2–11 cm, base terete, apically flattish; bracts oblong, 10–15 mm, scarious, caducous; pedicels clavate, stout (always thicker than subtending inflorescence branch), 1–2(–3) cm, thickened in fruit, apically constricted below calyx. Flowers diurnal, odorless. Sepals subequal, convex, broadly elliptic to orbicular, 1.3–1.7 cm, drying tan or straw-colored, apex broadly rounded or emarginate, minutely mucronulate; outer 2 leathery; inner 3 with broad, scarious margins. Corolla broadly funnelform, pale yellow to cream-white, 4–5(–6.3) cm, midpetaline bands outside densely sericeous-pilose (especially noticeable in buds), outside of whole corolla dotted with tiny golden glands. Stamens included, subequal; filaments 1.5–1.7 cm, basally adnate to corolla for about 1/2 their length, margins lined with glandular hairs up to insertion point, medially glabrous, free, filamentous and glabrous distally; anthers ca. 3 mm, spirally twisted. Pistil included; ovary conical, glabrous; style filiform, ca. 1.8 cm; stigmas globular, papillose. Fruiting calyx accrescent, cup-shaped and enclosing fruit; sepals ca. 2 cm. Capsule 1.5–3 cm diam.; operculum 1.7–2 cm diam., thickly leathery, dark brown, apiculate by indurated style base; endocarp stramineous, translucent. Seeds 1 to 4, ovoid, carinate, 5–7 mm, dull black, edges pilose-papillose with erect, pale yellow hairs, otherwise glabrous; hilum prominent, tan.

Distribution. *Operculina riedeliana* is found in Australia (Queensland), Brunei, China (see Comments), India (Andaman Islands only), Indonesia, Malaysia (Peninsular, Sabah), Papua New Guinea, Philippines, Solomon Islands, and Thailand (Fig. 24). Apparently, this is a widespread species that is nowhere common.

Ecology. *Operculina riedeliana* is reported on dry hillsides and in grasslands; lowland mixed forest, hill jungle; edges of disturbed areas in evergreen forest; primary forest; riverbank; in bamboos overhanging a stream; disturbed ground in full sun; along old road line, in secondary regrowth; and overtaking an old Para rubber plantation. Substrates include volcanic basaltic clay; sandy-clay; and granitic. Elevation ranges from near sea level to 300(to 500) m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	1	6	2	2	1	1	3			1		
Fruiting collections			3	2						1		

The whitish or pale cream, campanulate corollas suggest a bee-pollination syndrome.

Vernacular names. Australia: what seems to be a recently coined name in northeastern Queensland is "Cook's glory" (Cairns to Cape Tribulation, 2016) evidently referring either to the Cook District or Cookstown, where the species grows, and the common name morning glory. Malaysia: kangkong bukit (*Alvins 1181*). Papua New Guinea: bohurèh, bohudèh (Orakaiva, *Hoogland 3499*); kukumtainan (Wanigela, *Hoogland 4311*). Philippines: bulakán dágat (Tagalog, Ooststroom, 1939: 368, citing Merrill). Thailand: Ching-cho-ta-lab (จิงจ้อตลับ) (*Khunwasi 44*).

Typification. We are designating a lectotype here for *Ipomoea riedeliana* based on the only known specimen found to date. Although previously we considered this to be the holotype, the current *International Code of Nomenclature* (Turland et al., 2018) does not allow this interpretation: Oliver (1883) did not indicate a holotype in the protologue and the published plate is considered equally a syntype. In accordance with Art. 9.12 we are designating the specimen as the lectotype in preference to the published illustration.

"*Convolvulus platypeltis* Zipp. ex Span." (Spanoghe, 1841) is invalid because it was published in synonymy. Furthermore, "*Merremia platypeltis* Prain" is invalid because Prain (1906: 307) did not accept it when he published this name: he treated the taxon as a variety of *M. crispatula* and said that if it proved to be specifically

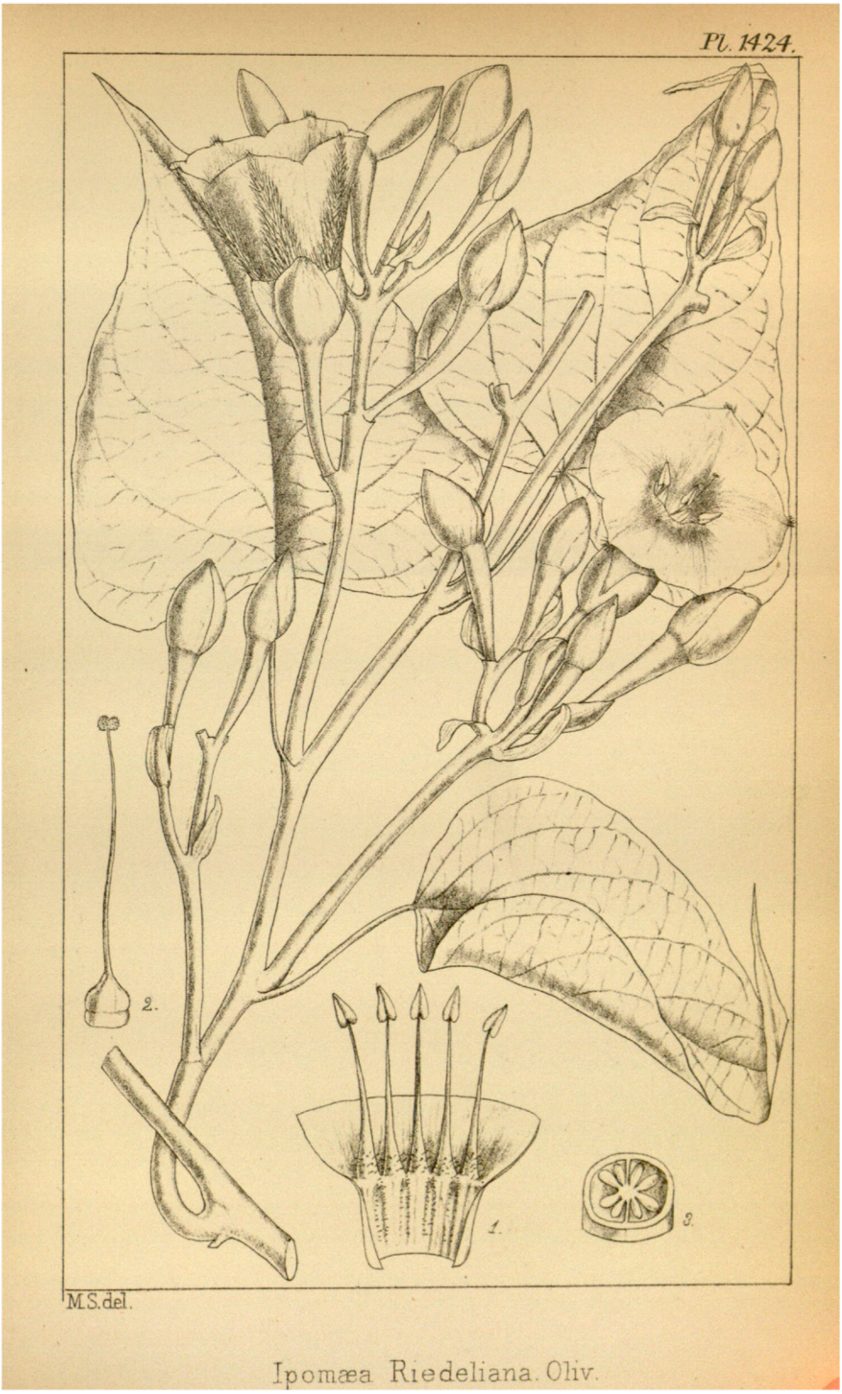

Figure 23. An illustration for *Operculina riedeliana* (Oliv.) Ooststr. Original caption: 1. base of corolla, laid open, with the stamens; 2. pistil and disk; 3. transverse section of ovary; 4. the ovules are basal and ascending. (I am not sure that four occur in *each* cell. I have, however, found five in one, an aberration unusual in *Ipomoea*.) Reproduced from *Hooker's Icones Plantarum* (Oliver, 1883: plate 1424), under the name *Ipomoea riedeliana*. Two anomalies must be pointed out in this illustration: first, Oliver was unsure about the ovules as shown in the drawing, as he stated in his caption. Second, the anthers are drawn without a spiral twist; Oliver did not mention the stamens or anther dehiscence in his brief diagnosis. A likely explanation is that the artist who prepared the plate drew the stamens from a mature, unopened flower bud, rehydrated for dissection; at this stage of floral development the undehisced anthers have not yet begun to spirally coil.

distinct, it would be called *M. platypeltis*. For the disposition of *C. bufalinus*, which has sometimes been equated with *Operculina riedeliana*, see the Excluded Species. One of the syntypes for *Ipomoea petaloidea* is actually a specimen of *O. riedeliana* (Ooststroom, 1939); Leschenault collected it during his voyage of 1800–1804 (Van Steenis-Kruseman, 1950), which twice stopped at Dutch Timor, now part of Indonesia. To stabilize the nomenclature for both of these species we chose a different syntype as the lectotype for *I. petaloidea*.

Comments. *Operculina riedeliana* is often found misidentified in herbaria as *Merremia* or *Ipomoea*; the operculate capsule distinguishes it. The diagnostic characters to recognize the species include: the shaggy midpetaline bands; the distinctive club-shaped peduncles, always thicker than the inflorescence branch that supports it; and the glabrous, circular sepals. Pale yellowish corollas and operculate capsules are also indicative. In the field, living plants often have a glaucous bloom on the younger stems and twigs; this easily rubs off but is a good field character when present.

A single specimen has been seen from Yunnan Province in western China, quite a long disjunction from the usual distribution of *Operculina riedeliana*. The specimen label does not state if the plant was cultivated or not. The presence of *O. riedeliana* in China requires confirmation; we suspect a label mix-up could have occurred for the specimen cited below or the plant was cultivated.

Two historic specimens from “Timor” but lacking a locality were referred by Ooststroom (1939: 368) to the Indonesian part of Timor. We have seen no specimen to document the occurrence of *Operculina riedeliana* in East Timor nor did Simões et al. (2011: 66) cite any, but there is every likelihood the species is present there.

Like *Operculina petaloidea*, the leaf shape for *O. riedeliana* is quite variable. A plant cultivated in Singapore (*Staples 1469*) showed lanceolate to oblong leaves initially and with increasing maturity produced broader, ovate leaves higher up on the same stems. It may be that narrower leaves are a juvenile condition and broader leaves represent a mature stage of growth. Some herbarium specimens show this same pattern of dimorphic leaves on a single sheet, but more often the leaves on a single gathering are all similar in shape. In the wild plants might revert back to juvenile leaf forms when subjected to environmental stress or to herbivory.

Uses. Minor medicinal uses are mentioned in Peninsular Malaysia, where the leaves are poulticed and used to relieve “jungle fever” (teste Ooststroom, 1939: 368, citing *Alvins 1161*). *Operculina riedeliana* is being promoted as a native ornamental for planting in northeastern coastal Queensland, Australia (Cairns to Cape Tribulation, 2016).

Selected specimens examined. [61 collections]. AUSTRALIA. **Queensland**: Cook Distr., Thursday Island, s. loc., May 1901, *Jaheri s.n.* (BO). BRUNEI. **Belait distr.:** Seria, 4°37′N, 114°19′E, 7 Mar. 1965, *J. P. Van Niel 3759* (L). CHINA. **Yunnan:** Simao Prefecture, Simao Kang, 22°32′N, 100°36′E, 800 m, 24 Mar. 2000, *H. Wang 4514* (HITBC). INDIA. **Andaman & Nicobar Islands:** South Andaman, Port Mouat, 11°37′N, 92°37′E, 11 Mar. 1893, *King’s collector s.n. / P62* (K). **West Bengal:** Howrah distr., Howrah, 22°59′N, 88°31′E, Apr. 1837, *C. Gaudichaud et al. 128* (G, P). INDONESIA. **Kalimantan:** Kalimantan Timur, Sangatta, 0°50′N, 117°40′E, 20 m, 14 Apr. 1995, *P. J. A. Kessler et al. PK-1187* (A, BO, K, L, P, SAN, WAN). **Maluku:** Buru, 3°24′39″S, 126°39′34″E, s.d., *Riedel s.n.* (type K). **Nusa Tenggara Timur:** Flores, Reo vic., 8°18′35″S, 120°29′21″E, 19 May 1965, *A. J. G. H. Kostermans et al. 942* (K); Timor, s. loc., *Leschenault s.n.* (P, syntype for *I. petaloidea* Choisy), *Zippelius 45/6* (L). **Papua Barat**: Vogelkop, Ransiki (S of Manokwari), 1°30′30″S, 134°10′15″E, 3 Aug. 1948, *A. J. G. H. Kostermans 2629* (A). **Sulawesi:** Palopo, 2°59′33″S, 120°11′49″E, 24 July 1957, *G. Kjellberg 1957* (S); Sulawesi Tenggara, Unaaha, 3°51′14″S, 122°02′31″E, 100 m, 12 Oct. 1978, *S. Prawiroatmodjo et al. 1085* (BO, K). MALAYSIA. **Johor:** Pulau Aur, Bukit Makam, 20 Aug. 1996, *Boo et al. 409* (SINU). **Kedah:** Sungai Kuak, 6°21′N, 100°44′E, 17 Feb. 1988, *R. Kiew RK-2630* (KEP); Langkawi Island, Kampung Sungei Itau, 6°25′75″N, 99°49′26″E, 20 m, 4 Mar. 2010, *Imin K. & Staples FRI-70121* (BM, KEP, L, SING). **Kelantan:** Gua Musang, 4°53′N, 101°58′E, 23 Feb. 1972, *H. S. Loh FRI-19254* (A, K, KEP, L, SING). **Negeri Sembilan:** Bukit Dusun Paya, 11 Mar. 1885, *V. M. Alvins 1181* (SING). **Pahang:** Rompin Distr., Lesong, 2°45′N, 103°05′E, 19 Feb. 1980, *J. F. Maxwell 80-64* (AAU, L); Pulau Tioman betw. Juara & Tekek, 2°48′N, 104°11′E, 30 Apr. 1995, *A. Zainudin et al. 5492* (K, L). **Sabah:** Labuk/Sugut distr., Kapuakan, 6°10′N, 116°54′E, 18 Apr. 1983, *Aban Gibot et al. SAN-95400* (A, SAN). PAPUA NEW GUINEA. **Madang:** Josephstaal FMA, along Guam River, 4°33′19″S, 144°37′23″E, 80 m, 22 Aug. 1999, *W. Takeuchi et al. 14325* (A). **Milne Bay:** Peria Creek, Kwagira River, 9°34′50″S, 149°26′27″E, 50 m, 2 Sep. 1953, *L. J. Brass 24292* (A). **Morobe:** Kassam Pass, 6°15′S, 146°15′E, 304 m, 18 June 1965, *A. N. Gillison NGF-22244* (A, K). **Northern**: Divinikoari village, Aug. 1953, *R. D. Hoogland 3499* (L). **Western**: Murray subdistr., Lake Daviumbu, Middle Fly River, 7°35′S, 141°17′E, Sep. 1936, *L. J. Brass 7719* (A). PHILIPPINES. **Cebu Island:** s. loc., 10°20′N, 123°45′E, Mar. 1912, *M. Ramos BS-11103* (L, SING). **Guimaras Island:** Buenavista, vic. of Barrio Salvacion, 4 Mar. 1950, *M. D. Sulit PNH-11792* (A, L). **Luzon Island:** Benguet Province, Baguio, 16°25′N, 120°36′E, 29 Feb. 1980, *W. Schwabe s.n.* (B); Cagayan Province, Peñablanca, 17°37′N, 121°47′E, anno 1929, *M. Ramos BS-76826* (SING); Ilocos Norte Province, Bangui, 14°12′N, 120°38′E, anno 1917, *M. Ramos BS-27596* (K, P); Isabela Province, San Mariano, 16°59′N, 122°00′E, Mar. 1926, *M. Ramos et al. BS-47133* (NY); Manila, Novaliches, 14°43′04″N, 121°02′12″E, 19 Mar. 1891, *A. Loher 4140* (K); Rizal Province, Antipolo, 14°31′38″N, 121°07′06″E, Jan. 1914, *M. Ramos BS-2078* (G, L, MO, NY, P, SING); Union Province, Bauang, 16°31′51″N, 120°19′59″E, Feb. 1904, *A. D. E. Elmer 5622* (K, L, NY). **Mindoro Island:** Mindoro Oriental, Puerto Galera, 13°30′00″N, 120°57′15″E, 12 May 1952, *J. V. Santos 5342* (L). **Palawan Island:** Culion Island, 11°53′N, 120°01′E, 25 Apr. 1931, *A. W. Herre 1038* (NY). **Pangasinan Island:** Mangatarem, Manluluwang, 15°47′N, 120°18′E, Feb. 1974, *D. Madulid et al. PNH-120904* (AAU). SOLOMON ISLANDS. **Kolombangara:** Maregisi, 8°00′S, 157°05′E, s.d., *P. Bacon H-1145/81* (K); Manigisi, 5 July 1982, *P. E.*

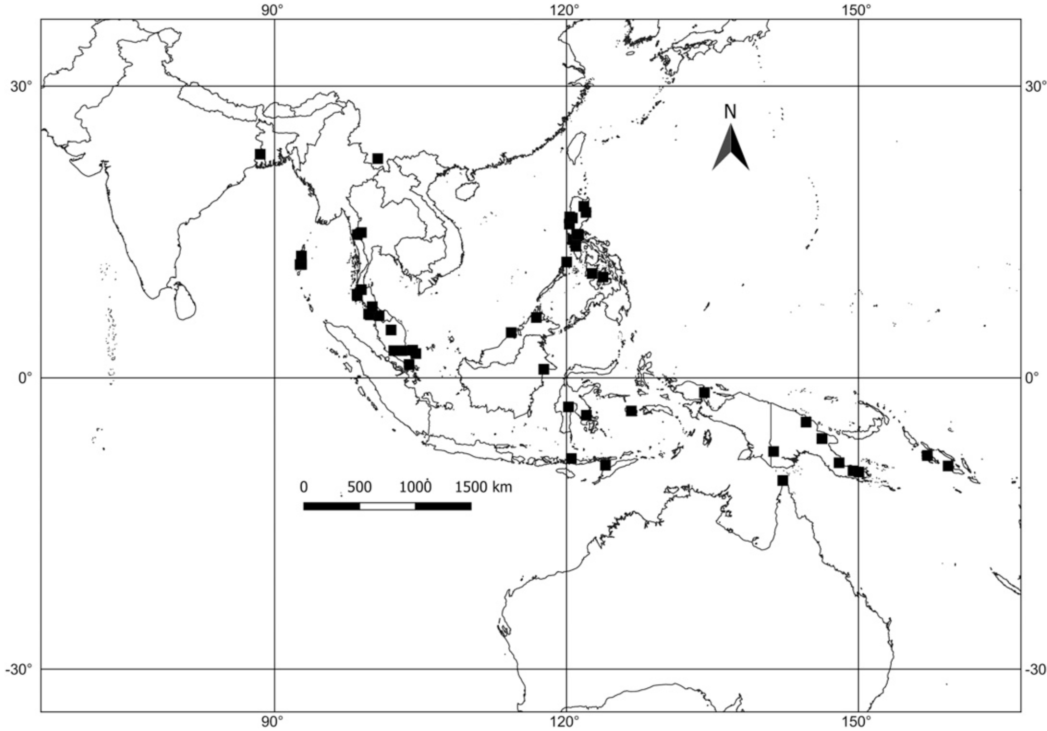

Figure 24. Distribution map for *Operculina riedeliana* (Oliv.) Ooststr.

Neil SI-442 (K, P). **Russell Islands**: Mbanika Island, Yanisa, Lingatu, 9°04′36″S, 159°13′15″E, July 1962, *M. A. Foale 23* (A). THAILAND. **Peninsular:** Phangnga, 8°25′N, 98°30′E, Dec. 1989, *C. Khunwasi 44* (BCU); Phattalung, Tha Chang waterfall access rd., 7°16′50″N, 100°02′06″E, 52 m, 26 Oct. 2012, *G. Staples et al. 1492* (BKF); Satun, Talo Wao, 6°32′N, 99°40′E, 40 m, 18 Feb. 1979, *G. Congdon et al. 262* (A, AAU, PSU); Surat Thani, Ratchaprapha Dam, 8°34′12″N, 98°28′17″E, 120 m, 21 Feb. 2001, *K. Chayamarit et al. 2598* (BKF). **Southwestern:** Kanchanaburi, Khao Laem Dam, 14°55′N, 98°55′E, 140 m, 11 Jan. 1985, *H. Koyama et al. T-49027* (L).

Cultivated. SINGAPORE. Singapore Botanic Gardens, Plant Resources Centre, accession 20080996, 23 Dec. 2010, *G. Staples 1469* (SING).

11. Operculina sericantha (Miq.) Ooststr. in Pulle, Fl. Surinam 4: 87. 1932. *Ipomoea sericantha* Miq., Stirp. Surinam. Select.: 131. 1851. TYPE: Surinam. "flumen Marrowyne superius," Aug. 1844, *Kappler 1864* (lectotype, designated here, U [bc] U0001436!; isolectotypes, P [bc] P03878750!, S [bc] S12-908!).

Operculina surinamensis Meisn. in Mart., Fl. Bras. 7: 214. 1869. TYPE: Surinam. "ad Paramaribo et Caxanama, in Garten," *Wullschlägel 854* (lectotype, designated here, BR [bc] BR0000006991838!; isolectotype, BR [bc] BR0000006992163!).

Lianas or vigorous herbaceous climbers; all vegetative parts glabrous; sap unknown. Stems to several meters long, to 6 mm diam., smooth or striate, never alate, fistulose. Leaves entire, usually broadly cordate, occasionally ovate-lanceolate, 7.5–16 × 2–11.5 cm, coriaceous, basally cordate, margins entire, undulate, apically attenuate or caudate; secondary veins slightly impressed on adaxial surface and prominent abaxially; petiole slender, 3.5–7.5 cm, longitudinally striate, basally swollen. Inflorescences dichasial or flowers solitary; peduncles stout, usually exceeding the subtending petioles, 5.5–15.5 cm, to 3–4 mm diam., cylindrical, smooth, never alate; bracts and bracteoles lanceolate to elliptic, 7–15 × 2–6 mm, reddish brown, membranous, fugacious, basally truncate, apically rounded to acute; pedicels slender, clavate, 1.7–4 cm, striate to faintly 5-angled, thickening in fruit. Flowers diurnal, erect-ascending. Sepals ± equal or outer 2 slightly longer, elliptic to broadly ovate, 1.7–3 × 0.8–2 cm, membranous, basally rounded or truncate, margins slightly scarious, apically obtuse or rounded, mucronate. Corollas broadly campanulate, white, 5.5–7 cm, limb entire or slightly 5-lobed, 4–5.5 cm wide, midpetaline bands sericeous. Stamens subequal, included, white; anthers spirally dehiscing, 6–8 mm. Pollen 3-zonocolpate. Pistil included, glabrous; disc annular; ovary conical, 2 mm; style filiform; stigma 2-globose. Fruiting calyx accrescent, chartaceous, surrounding the fruit. Capsules depressed globose, 3–3.5 cm, 3.5–4 cm diam., often 2-locular, each locule 1- or 2-seeded. Seeds 1 to 4, subglobose, 1–1.3 cm diam., dark brown to black, glabrous; hilum prominent.

Distribution. *Operculina sericantha* is found in northern South America: Venezuela, Guyana, French Guiana, Suriname, Brazil (Amapá) (Fig. 25).

Ecology. Little information has been recorded by collectors; one noted the plants were found along a riverbank. Elevation is 50 m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections		1	1				1	2				
Fruiting collections		1	1							2	1	

Vernacular names. None recorded.

Comments. *Operculina sericantha* is an enigmatic species, still poorly documented despite increased collecting activity in recent decades in areas where it occurs. In general aspect, *O. sericantha* resembles *O. codonantha* and it may prove (when both species are sampled for molecular analysis) that the plants from northern South America are no more than a robust form of that Pacific and western South American species.

Specimens examined [13 collections]. BRAZIL. **Amapá:** entre Santana e Mazagão, beira do Rio Preto, 1 Nov. 1979, *D. F. Austin et al. 7299* (FAU, GH, MG, NY); Cachoeira Manauá, 15 Sep. 1960, *H. S. Irwin et al. 48266* (IAN, NY); Cachoeira Camarau on Rio Oiapoque, ca. 3 km S of mouth of Rio Camopi, 2 Oct. 1960, *L. Y. Th. Westra 48553* (L). FRENCH GUIANA. Cayenne, s.d., *Martin s.n.* (P). GUYANA. **Upper Takutu-Upper Essequibo:** Surama village, 4°10′N, 59°05′W, 70 m, 20 Feb. 1990, *P. Acevedo-Rodríguez et al. 3334* (FAU, MO, P, US). SURINAME. **Marowyne:** Marowyne river, Aug. 1844, *Kappler 1864* (type P, S, U); Albina, July 1904, *Versteeg 545* (U). **Para:** Jodensavanne, Mar. 1961, *Schulz 8693* (U). **Paramaribo:** Paramaribo vic., 5°50′N, 55°10′W, *Wullschlägel 854* (type BR). **Sipaliwini:** vic. of Blanche Marie Waterfall on the Nickerie River, 4°45′30″N, 56°52′50″W, 50 m, 31 Mar. 1997, *R. J. Evans et al. 2695* (MO); Wonotobo, 6 Aug. 1935, *Rombouts 100* (U). **S. loc.:** Coppename River, Aug. 1901, *Went 117* (U). VENEZUELA. **Delta Amacuro:** Dpto. Antonio Diaz, Caño Guayo, 50 m, 21 Oct. 1977, *J. A. Steyermark et al. 115156* (FAU, MO).

12. Operculina turpethum (L.) Silva Manso, Enum. Subst. Brasil.: 16. 1836. *Convolvulus turpethum* L., Sp. Pl. 1: 155. 1753. *Ipomoea turpethum* (L.) R. Br., Prodr.: 485. 1810. *Spiranthera turpethum* (L.) Bojer, Hortus Maurit.: 226. 1837. *Merremia turpethum* (L.) Rendle, Fl. Trop. Afr. 4(2): 102. 1905. *Turpethum australe* Raf., Fl. Tellur. 4: 71. 1838, nom. superfl. *Piptostegia pisonis* Mart., Syst. Mat. Med. Bras.: 78. 1843, nom. superfl. TYPE: Ceylon. herb. *Hermann* 2: 68, #74 (lectotype, designated by Verdcourt [1963: 61], BM!; isolectotype, U not seen). Figure 26.

Convolvulus anceps L., Syst. Nat. ed. 12, 2: 156; Mant. Pl.: 43. 15–31 Oct. 1767. *Ipomoea anceps* (L.) Roem. & Schult., Syst. Veg. 4: 231. 1819. *Ipomoea turpethum* var. *anceps* (L.) Miq., Fl. Ned. Ind. 2: 607. 1857. TYPE: Indonesia. Java (West): Tjikao, near waterfall, July, *Blume 1219* (neotype, designated by Staples & Jarvis [2006: 1020], L! L-901, 163-376; isoneotype, L! L-901, 184-318).

Convolvulus triqueter Vahl, Symb. Bot. 3: 30. 1793. *Ipomoea triquetra* (Vahl) Roem. & Schult., Syst. Veg. 4: 231. 1819. *Operculina triquetra* (Vahl) Hallier f., Bot. Jahrb. Syst. 18: 120. 1893 (*Operculina triquetra* (Vahl) J. F. Macbr., Publ. Field Mus. Natl. Hist., Bot. Ser. 13(5/1): 480. 1959, isonym). *Merremia triquetra* (Vahl) Roberty, Candollea 14: 36. 1952. TYPE: U.S. Virgin Islands. St. Croix, *West s.n.* in herb. Vahl (holotype, C [bc] C10009737!).

Convolvulus maximus Blanco, Fl. Filip.: 91. 1837, nom. illeg. TYPE: not located.

Turpethum indicum Raf., Fl. Tellur. 4: 71. 1838. TYPE: [icon] Bot. Reg. 4: plate 279. 1818 (lectotype, designated here).

Argyreia alulata Miq., Fl. Ned. Ind. 2: 587. 1857. TYPE: [Indonesia.] Java: Soerakarta, *Horsfield 1185 'Conv. 11'* (lectotype, designated here, K [bc] K000830918!; isolectotypes, K [bc] K000830919!, L [bc] L0171359!, U [bc] U0001437!).

Argyreia alata Montrouz., Mém. Acad. Roy. Sci. Lyon, Sect. Sci. 10: 236. 1860. TYPE: New Caledonia. île Art, *Montrouzier s.n.* (holotype, LY not found).

Ipomoea diplocalyx Baker, Bull. Misc. Inform. Kew 1894: 71. 1894. TYPE: Mozambique. Zambezi delta betw. Manbucha & Keult, *L. Scott s.n.* (holotype, K [bc] K000097363!).

Operculina turpethum var. *heterophylla* Hallier f., Verslag Staat's Lands Plantentuin Buitenzorg 1895: 127. 1896. TYPE: Indonesia. Java: cultivated in Hort. Bot. Bogor (formerly Buitenzorg), *Hallier XV.H.24* (holotype, BO not found).

Ipomoea turpethum var. *humilior* Haines, Bot. Bihar Orissa 4: 600. 1922. TYPE: India. [Jharkhand:] Santal Parganas, Dec. 1916, *Haines 4668* (syntype, K!); Bhagalpur, *Thomson s.n.* (syntype not found).

Perennial herbaceous twiner; all vegetative parts velutinous at first, later glabrescent; sap copious, white. Roots fleshy, slender, much-branched. Stems cylindrical, 1–4 m, 4–6 mm diam., reddish, pilose-tomentose at first, later glabrescent, spirally longitudinally alate; wings 3 to 5, hyaline, 0.5–2 mm wide; shoot tips silvery canescent. Leaves variable: cordate-circular, ovate, broadly ovate, ovate-lanceolate, or lanceolate, 4–14 × 3.5–14 cm, base truncate, broadly obtuse, shallowly subcordate (rarely some cauline blades with deep, U-shaped sinus), margins entire or undulate, apex obtuse to acute, or acuminate, mucronulate, adaxially appressed pilose to glabrous, abaxially pubescent and

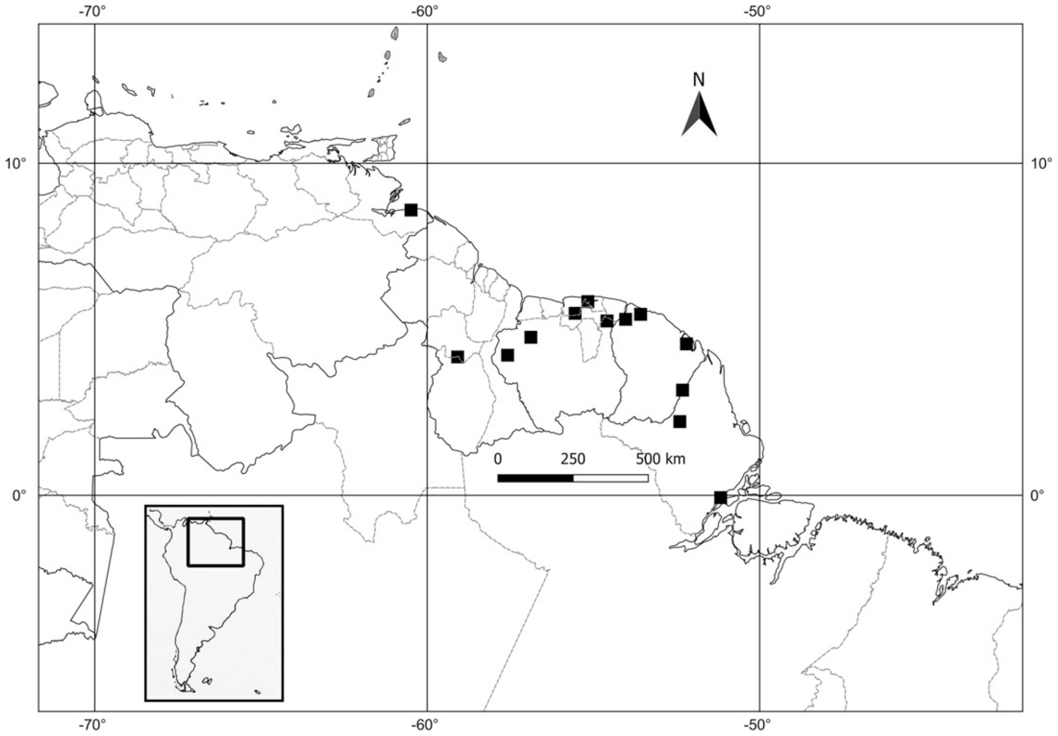

Figure 25. Distribution map for *Operculina sericantha* (Miq.) Ooststr.

sparsely dotted with glands; secondary veins 8 to 11 either side of midvein, impressed adaxially and prominent abaxially; petiole slender, 2–10 cm, narrowly 2-winged, striate distally; adaxially sulcate. Inflorescences axillary, cymose or flowers solitary; peduncles stout, longer than the subtending petiole, 2–11.5 cm, terete, smooth or faintly striate; bracts 2, convex, broadly ovate, oblong to ovate-oblong, 1–2.5 × 0.5–1.1 cm, green to pinkish rose, often faintly blackish dotted, pubescent, persistent at flowering, usually deciduous in fruit, basally truncate, apically acute and mucronulate to apiculate; bracteoles 2, like bracts only smaller; pedicels stout, 1.4–2.2 cm, striate to angulate, thickened apically, lengthening to 4 cm in fruit. Flowers diurnal, erect-ascending, odorless. Sepals unequal, ovate to broadly ovate, 2 outer 1.5–2.4 × 0.9–1.8 cm, often faintly blackish dotted, abaxially pubescent with dimorphic hairs: densely velvety with shorter, appressed hairs and scattered, longer pilose-erect hairs, basally rounded to truncate, apices obtuse to acute, mucronulate; 3 inner sepals shorter, subglabrous. Corolla campanulate to broadly funnelform, 3–4 cm, limb 5-lobed, 3–3.6 cm diam., white, sometimes with yellow inside tube, outside completely glabrous, minutely yellowish gland-dotted. Stamens included, equal, 15–18(–22) mm, white; filaments basally dilated and adnate to corolla tube for 1/3 to 1/2 their length, margins of adnate portion pubescent, distally free, filamentous and glabrous; anthers 4–5 mm, spirally twisted, bases shallowly sagittate. Pollen 3-zonocolpate. Pistil included, longer than stamens, white, glabrous; disc annular, orange; ovary globose; style filiform, 1.5–1.7 cm; stigma biglobose, papillose. Fruiting calyx accrescent, initially secretory on the adaxial faces of the 3 inner sepals, drying stiffly chartaceous, broadly cup-shaped, to 6 cm diam.; sepals 3–3.5 cm. Capsules depressed globose, 3- or 4-lobed (quatrefoil), 1.2 cm high, 1.5–1.8 cm diam., glabrous; operculum leathery, wrinkled, brownish; lower pericarp tan to straw-colored; endocarp translucent. Seeds 2 to 4, subglobose or ovoid-trigonous, 5–7 mm, blackish, glabrous; hilum prominent, glabrous.

Distribution. A species whose natural distribution, before humans altered it, was most likely Paleotropical; the contemporary distribution is pantropical (Fig. 27). It has certainly been introduced in the West Indian Islands and eastern tropical Africa. In Asia *Operculina turpethum* is known to be present in: Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Laos, Malaysia (Peninsular, Sabah), Myanmar, Nepal, Philippines, Singapore, Sri Lanka, Thailand, and Vietnam. In the Pacific it is known from coastal and far northern and eastern Australia, Papua New Guinea, and many of the Pacific Islands—Cook Islands, Fiji, French Polynesia, Hawaii, Micronesia, Okinawa, Samoa, Solomon Islands, Tonga, and Vanuatu. It is naturalized in tropical eastern Africa (Kenya, Mozambique, Tanzania, Zambia, Zimbabwe), Madagascar, and the Indian Ocean islands (Comoros, Mauritius, Reunion, Rodrigues, Seychelles) where it was likely introduced pre-European advent. And there may be a naturalized population in the U.S. Virgin Islands: the current status of these Caribbean plants requires confirmation. The most recent collection seen dates from 1906 and contemporary publications (Acevedo-Rodríguez, 2005) include *O. turpethum* on the basis of historical records; no recent collections having been seen (Acevedo-Rodríguez, pers. comm. 2018).

Ecology. *Operculina turpethum* is a species that thrives in disturbed habitats near human habitation such as abandoned agricultural fields, pastures, on roadsides, vacant lots, hedge rows, and is capable of spreading from there into more natural vegetation: open forest, grassy plains, brushy secondary regrowth replacing rainforest, disturbed primary forest, and deciduous forest. It has been recorded as a cultivated plant in house compounds and as a weed in banana plantations, rice paddies, as well as abandoned garden plots. *Operculina turpethum* prefers well-watered places and is often found growing along roadsides in swales and drainage ditches where moisture collects, and has also been collected along stream banks. Plants are tolerant of diverse substrates including lateritic soil, rocky soil near the seashore, limestone, sandy soil in a riverbed, moist sandy clay, loam, serpentine rocky slopes, coarse sand, and gravel overlying granite bedrock. Vegetation associates mentioned by collectors typically include introduced, alien plants associated with disturbed habitats, among them: *Achyranthes aspera* L., planted *Albizia falcataria* (L.) Fosberg forest, *Cocos*, *Derris* Lour., *Dioscorea bulbifera* L., *Eucalyptus polycarpa* F. Muell. open forest with *Heteropogon* Pers. and *Themeda* Forssk. understory, *Hibiscus tiliaceus*, *Mangifera* L., *Passiflora maliformis* L., *Premna*, *Psidium* L. grove, *Tridax* L., and *Zizyphus* L. [*Ziziphus* Mill.]. Elevation ranges from near sea level to 350(to 600) m.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	9	10	8	5	5	6	12	17	4	11	17	13
Fruiting collections	4	5	8	2	1	3	7	6	4	4	5	4

All specimen data have been combined for this phenological summary; if the collections examined were broken down by geographical provenance, a seasonal pattern might be evident. When combined, the species appears to flower and fruit year-round. The broadly campanulate, pure white corolla, oriented more or less vertically, fits the profile for a bee pollination syndrome. Anthesis has been reported to begin in late morning (*Maxwell 93-1443*). Fruit production is prolific and possibly the flowers are autogamous.

Vernacular names. Bhutan: Indian jalap, turpeth root (English) (Mill, 1999: 855). China: 盒果藤 he guo teng (Fang & Staples, 1995: 320); additional names (in Chinese) are listed by Fang and Huang (1979: 80). Fiji: puketeraufasa’ (*St. John 19721*), wandamdam (*Degener 15404*); wa ika, wa kai, wa mbutho, wa ndamundamu, wa sala, wa uvi, wa vulavula (Smith, 1991: 45). India: Watt (1890: 493) provided a comprehensive list of vernacular names in several languages spoken in the subcontinent. Japan (including Okinawa): fūsen asagao (Walker, 1976: 873; Yamazaki, 1993: 198). Laos: keuah diem (*Maxwell 98-64*), khua chi cho (*Vidal 2665*). Madagascar: Deroin (2001: 130) listed several Malagasy vernacular names. Malesia (Indonesia, Malaysia, Philippines): Ooststroom (1939: 365) provided a comprehensive list of vernacular names in several languages spoken in the region. Mascarene Islands: turbith (Bosser & Heine, 2000: 14). Myanmar: kya-hin (*Po Khant 1865*), nyan-lein (*MG Gale-2 12253*). Pakistan: nisot (Austin & Ghazanfar, 1979: 59). Sri Lanka: trastawalu (Sinhalese) (Austin, 1980: 357). Tahiti: pone (*D. Hummel s.n.*). Thailand: chingcho liam (จิงจ้อเหลี่ยม) (*Na Songkhla 607*), no-wai-pai (*Prayoon 10*), chingcho daeng (จิงจ้อแดง) (Staples, 2010). U.S. Virgin Islands: St. Thomas lid-pod (USDA, NRCS, 2016). Vietnam: aban töi’ röman (jörai dialect, *J. Dournes s.n.*), biêm biêm dai là (annamite dialect, *Chevalier 50*), giay muõ’ng (*Eberhardt 4415*).

Typification. A few type specimens could not be examined for this study. Ooststroom (1939: 364) cited the type for *Operculina turpethum* var. *heterophylla* in the Buitenzorg (now Bogor) herbarium; G.S. could not locate this sheet during a visit there in 2008. The curator at BO confirmed that this type could not be located (A. Retnowati, pers. comm. Feb. 2017). We follow Ooststroom (1939) in reducing this varietal name to synonymy under *O. turpethum*.

Likewise the Montrouzier collection, said to be at LY, disappeared between 1955 and 1970 (F. Danet, pers. comm. June 2017) and is not now to be found in either LY or LYJB, thus we were unable to study the type material for *Argyreia alata*. We follow Heine (1984) in reducing this name to synonymy under *O. turpethum*.

Choisy (1834: 450) created two invalid names when he mentioned “*Convolvulus gaudichaudii* Choisy” and “*C. riedlei* Choisy” in synonymy under his account for *Ipomoea turpethum*. Likewise, *Piptostegia pisonis* and

Figure 26. An illustration for *Operculina turpethum* (L.) Silva Manso. Original caption: 1. stamens and base of the corolla; 2. capsule with its green scale [= operculum]; 3. capsule from which the scale has fallen. Reproduced from *Botanical Miscellany* (Wight, 1833: plate 38), under the name *Convolvulus turpethum*.

Turpethum australe are superfluous names because both authors cited *I. turpethum* in synonymy.

Uses. The enlarged fleshy roots have been cut and dried for use as a purgative drug since antiquity (Austin, 1982b). For centuries *turpeth* was an item of commerce between ports in western India and the Arabian Peninsula and the eastern coast of Africa. Watt (1890: 493–496 and references therein) provided a comprehensive overview of the plant, the drug, and its historical uses in India. Today the drug has all but disappeared from medicinal use outside India and communities of the Indian diaspora. In Fiji circa 1941, where *Operculina turpethum* was stated to be an "uncommon garden and roadside weed," Degener reported that "after childbirth, squash leaf in water and drink as tonic. No good as 'string'" (*Degener 15404*).

Comments. Operculina turpethum, like several other widespread weedy Convolvulaceae, is morphologically variable in leaf shape, size, and degree of development of wings on the axial parts, yet it has a remarkably uniform aspect that is recognizable everywhere it occurs in the world (Fig. 26): the reddish, winged stems, softly hairy leaves, white, campanulate corollas that are glabrous outside on the midpetaline bands, and papery fruits clasped by the accrescent calyx are distinctive. Only in the southwestern Pacific have extremes of variation been noted, as well as intermediates with other *Operculina* species (Staples, 2007).

Selected specimens examined [323 collections]. AUSTRALIA. **Northern Territory:** Alber River, s.d., *Oldfield s.n.* (K). **Queensland:** Thursday Island, 10°34′52″S, 142°13′07″E, 28 May 1948, *L. J. Brass 18934* (K); Endeavor River, 15°28′S, 145°15′E, July 1819, *A. Cunningham 366* (K); North Kennedy distr., Long Island, 20°21′53″S, 148°51′31″E, 23 July 1935, *C. T. White 12158* (A); Port Curtis distr., South Percy Island, 21°45′S, 150°20′E, 5 m, 25 Oct. 1989, *G. N. Batianoff et al. 11432* (K). **S. loc.:** *R. Brown Iter Australiensis 2745* (K). BANGLADESH. **Khulna distr.:** Khulna, 22°26′N, 90°13′E, 6 Feb. 1963, *M. S. Khan 523* (K). **S. loc.:** Khoolua, 5 May 1883, *C. B. Clarke 33474B* (K); Noabolly, 22° N, 89° E, 16 Dec. 1850, *Genl. Walker 32* (K). BHUTAN. **S. loc.:** s.d., *Griffith Herbar. Cat. 5861* (K). CAMBODIA. **Kratie:** riverbank rte. to Sambor, 12°36′76″N, 106°01′33″E, 42 m, 4 Apr. 2009, *S. K. Cheng et al. CL-1094* (P). **Siem Riep:** Angkor, 13°25′N, 103°52′E, 12 Dec. 1911, *H. Lecomte et al. 1765* (P). **S. loc.:** Pailin to Battambang, 12°50′54″N, 102°51′50″E, 41, 23 Dec. 2007, *K. C. Cheng et al. CL-885* (P). CHINA. **Guangdong:** Guangzhou, 23°07′N, 113°15′E, 28 Oct. 1929, *W. Y. Chun 7864* (SING); Ting Wu Shan, 23°10′N, 112°32′E, 5 Nov. 1928, *C. O. Levine 1488* (F). **Hainan:** Yaichow, 19°00′N, 109°30′E, Feb. 1933, *F. C. How et al. 70089* (B, F, K, NY); Ch'ang-Kiang distr., Ka Chik Shan vic., 19°00′N, 109°30′E, 31 Dec. 1933, *S. K. Lau 3031* (BISH, S). **Hong Kong:** Lantao Island, 22°15′41″N, 113°56′27″E, 1 Oct. 1940, *Y. W. Taam 1839* (F, NY); Po-on distr., Tai-Mo Shan, 22°25′N, 114°08′E, 1097 m, 26 Apr. 1932, *T. M. Tsui 283* (F, K, NY). **Yunnan:** Cheli Xian, Mang Ting Village, 21°59′28″N, 100°44′03″E, 21 Feb. 1953, *B. Y. Qiu et al. 70* (KUN); Gengma DaiVa Auton. Xian, He Xi, 24°08′37″N, 102°38′55″E, 1 Mar. 1960, *Y. H. Li 2197* (HITBC, KUN). TAIWAN. **Kaohsiung Hsien:** Kaohsiung, 2°38′N, 120°16′E, s.d., *A. Henry s.n.* (MO, NY). **Pingtung Hsien:** Hengchun town, 21°58′40″N, 120°47′19″E, 5 m, 1 Oct. 1996, *G. Staples et al. 1087* (BISH). **Tainan Hsien:** Ma-tou,

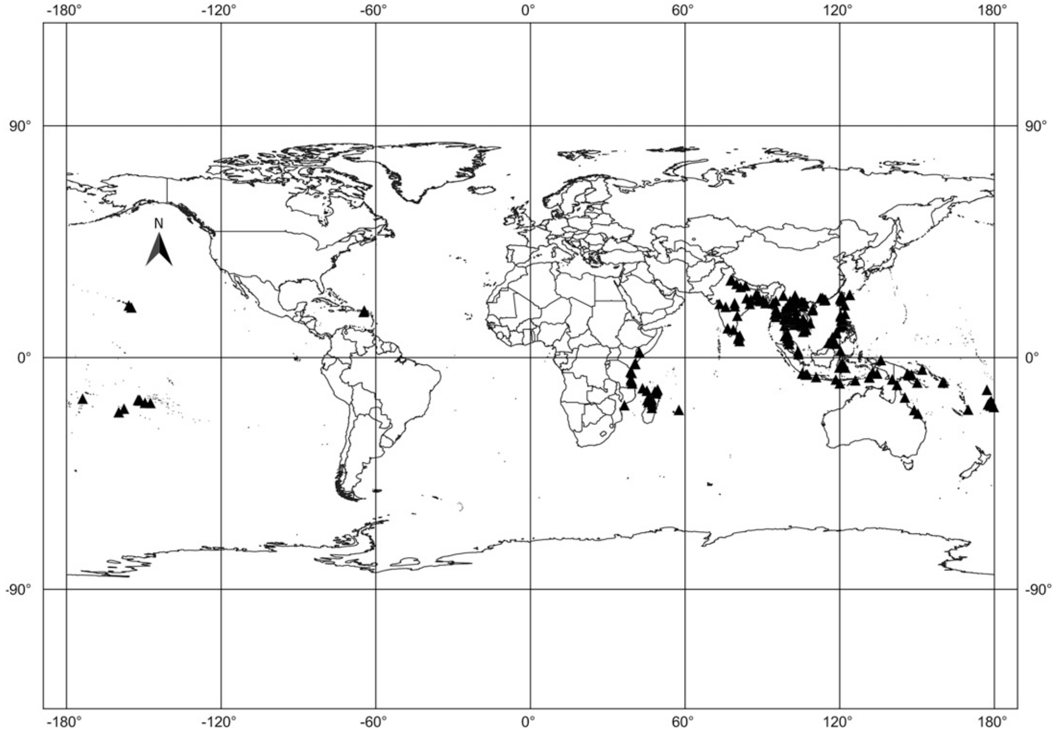

Figure 27. Distribution map for *Operculina turpethum* (L.) Silva Manso.

23°11′09″N, 120°14′47″E, 4 Dec. 1985, *M.-.T. Kao 10177* (L). **S. loc.:** Bankinsing mtns., 22°45′N, 120°20′E, s.d., *A. Henry 1624* (K, MO); Takaw Plain, Dec., *G. M. H. Playfair 333* (K). COOK ISLANDS. **Mitiaro Island:** near Atai plantation, seen in only this one place, 19°49′S, 157°43′W, 28 July 1986, *A. Whistler 5909* (BISH, US). **Rarotonga Island:** Tupapa, Ara Metua roadside, 21°12′39″S, 159°44′36″W, 14 July 1991, *W. R. Sykes 3562/CI* (BISH, CHR). FIJI. **Lau group:** Mothe Island, 18°40′S, 178°30′W, 16 Aug. 1924, *E. H. Bryan 483* (BISH). **Moala group:** Matuku Island, 19°10′S, 179°46′E, 3 July 1924, *E. H. Bryan 241* (BISH). **Rotuma group:** Solkope island, 12°30′S, 177°05′E, 122 m, 24 Aug. 1938, *H. St. John 19721* (BISH). **Vanua Levu group:** Vanua Levu, Bua, 16°50′S, 178°45′E, 16 Aug. 1933, *Mrs. H. B. R. Parham 346* (K). **Viti Levu group:** Ovalau Island, 17°40′S, 178°48′E, Oct. 1860, *Seemann 327* (K); Viti Levu island, Ra, Rewasa vic., 17°24′S, 178°11′E, 50–200 m, 3 June 1941, *O. Degener 15404* (BISH, F, K, MO, NY, P, S, US); Viti Levu island, Sigatoka, 18°11′S, 177°31′E, 27 July 1955, *H. S. MacKee 2858* (E). FRENCH POLYNESIA. **Society Islands:** Bora Bora, Crête Sud de Anau, 16°30′S, 151°44′W, 100 m, 4 July 2004, *J. F. Butaud & E. Lagouy 494* (PAP); Maupiti, Patao, 16°27′S, 152°15′W, 27 Aug. 1985, *J. Morris 34a* (BISH); Tahaa, Paripari, 16°36′S, 151°31′W, 155 m, 22 Sep. 1983, *J. Florence 5354* (BISH, P); Tahiti, Papeete, 17°32′S, 149°34′W, 1 m, 4 Nov. 1982, *J. Florence 4024* (BISH, NY, P, US). INDIA. **Andhra Pradesh:** Kistna distr., Kondavidu, 16°15′N, 80°15′E, Feb. 1890, *J. S. Gamble 21765* (K). **Assam:** s. loc., s.d., *Colonel Jenkins 239* (K). **Chhattisgarh:** Sanna, 23°04′N, 83°49′E, Jan. 1881, *J. S. Gamble 9186* (K). **Gujarat:** Unai, 20°51′N, 73°21′E, 30 Oct. 1953, *M. Santapau 16966* (MO). **Himachal Pradesh:** Sermore distr., 30°01′N, 77°40′E, 14 Dec. 1885, *J. R. Drummond 20796* (K). **Jharkhand:** Santhal Pargana distr., Santal Parganas, 24°30′N, 87°30′E, Dec. 1916, *H. H. Haines 4668* (K); Singhbhum distr., Longabera Valley, 22°30′N, 85°30′E, 22 Dec. 1902, *H. H. Haines 530* (K). **Maharashtra:** Nagpur, 21°10′N, 79°12′E, 19 Mar. 1962, *K. U. Nafday 24* (K); Chandrapur distr., Chandrapur, 19°57′N, 79°18′E, 30 Dec. 1889, *J. F. Duthie 9601* (K). **Orissa:** Tikarpara, Angul, 20°51′N, 85°06′E, Mar. 1917, *H. H. Haines 4915* (K). **Tamil Nadu:** Nilgiri hills, 11°25′N, 76°30′E, s.d., *G. Thomson s.n.* (TCD); Tiruchi distr., Tiruchi, 10°48′18″N, 78°41′08″E, 65 m, 12 Feb. 1977, *K. M. Matthew 6654* (K). **Uttar Pradesh:** Ambai, 30°19′N, 78°03′E, 457 m, Nov. 1892, *J. S. Gamble 22998* (K); Mala, 28°36′N, 79°56′E, 14 Oct. 1970, *C. L. Malhotra 42768* (K). **West Bengal:** Murshidabad, 24°11′N, 88°16′E, 15 Dec. 1957, *S. K. Mukherjee 4516* (BKF); Howrah, Botanic Garden, 22°33′38″N, 88°17′13″E, s.d., *Wallich 113* (S). INDONESIA. **Java:** Jawa Barat, Tjikao, 6°30′10″S, 107°23′32″E, July, *L. Blume 1219* (L); Jawa Barat, Bogor, 6°35′51″S, 106°47′54″E, 19 May 1965, *A. J. G. H. Kostermans et al. 968* (K); Jawa Tengah, Surakarta, s.d., *T. Horsfield s.n.* (K, L, U). **Maluku:** Tanimbar, Aruibab, 7°43′S, 131°32′E, 200 m, 15 Nov. 1985, *Purwaningsih et al. 86* (K). **Nusa Tenggara Barat:** Sumbawa, Dompoe, 8°32′S, 118°28′E, s.d., *H. Zollinger 1439* (S). **Nusa Tenggara Timur:** Timor, 8°50′S, 126°00′E, s.d., *unknown s.n.* (G-DC, K, S). **Sulawesi:** Rapang, 3°50′32″S, 119°49′04″E, 20 m, 12 June 1937, *Eyma 319* (K); Kawata, 2°31′30″S, 121°07′31″E, 50 m, Oct. 1929, *G. Kjellberg 3143* (S); Wawotobi distr., 3°52′35″S, 122°06′32″E, 100 m, 15 Mar. 1929, *G. Kjellberg 855* (S). **Papua:** Biak Numfor Regency, Kampong Landbouw, 30 m, 23 Nov. 1959, *Versteegh et al. BW-8338* (K); Merauke Regency, Merauke, 8°28′S, 140°20′E, 24 Apr. 1967, *Soegeng*

Reksodihardjo 194 (K). JAPAN. **Okinawa Prefecture:** Ryukyu Islands, Taketomi-cho, Nobaru, 24°21′16″N, 123°56′15″E, 3 Nov. 2002, *K. Yasuda 1016* (A); Iriomote Island, E end of Funaura Bridge, 24°23′35″N, 123°49′25″E, 20 Apr. 1998, *K. Yonekura 98320* (A). LAOS. **Champassak:** Paksé, 15°07′N, 105°47′E, 23 Nov. 1938, *E. Poilane 28530* (P); Khong distr., Khong Island, 14°09′N, 105°49′E, 75 m, 30 Jan. 1998, *J. F. Maxwell 98-64* (FOF, L). **Louang Prabang:** Ban Long O, 19°48′58″N, 102°12′18″E, 2 Mar. 1969, *R. Pottier 30C* (P). **Vientiane:** Nong Thevada, 18°02′56″N, 103°04′10″E, 5 Feb. 1954, *J. E. Vidal 2665* (P). MALAYSIA. **Johore:** Mersing, 2°26′N, 103°50′E, 22 July 1949, *J. Sinclair SF38578* (SING). **Kedah:** Langkawi Island, Tanjung Rhu, 6°27′49″N, 99°49′30″E, 6 m, 4 Mar. 2010, *Imin K. & G. Staples FRI-70123* (KEP). **Penang:** Seberang Perai, Mudo river bund, 5°23′N, 100°23′E, 23 Jan. 1918, *I. H. Burkill 3041* (SING). **Sabah:** Banggi Karakit Island, 6°54′46″N, 117°04′53″E, 8 Oct. 1991, *Berhaman Ahmad SAN-133154* (KEP, L, SAN, SAR); Kinabatangan distr., Sukau, 5°32′N, 118°17′E, Aug. 2001, *Postar et al. SAN-144704* (KEP, L, SAN); Kota Belud distr., Kampung Rajunah, 6°16′78″N, 116°26′95″E, 57 m, 12 Mar. 2011, *J. B. Sugau et al. SAN-152888* (BM, KEP, SAN, SING); Kuala Penyu, Pulau Tiga, 5°43′N, 115°39′E, 10 m, 11 Mar. 1988, *A. A. S. Amin SAN-114994* (SAN). MYANMAR. **Ayeyarwady Division:** Bassein, 16°47′N, 94°44′E, 30 m, 9 Apr. 1951, *Po Khant et al. 1865* (RAF). **Bago Division:** Prome, 18°50′00″N, 95°14′E, 23 Jan. 1895, *J. H. Lace 2734* (K); Tharrawaddy distr., Thin-daw-yo Res., 17°42′N, 95°47′E, 11 Jan. 1971, *MG Gale-2 12253* (L). **Chin State:** Saw village to Kan Gyi, 21°10′N, 91°10′E, 350–600 m, 1 Mar. 2004, *N. Kuroiwa et al. 030383* (MBK); Kanpetlet to Saw, 21°12′00″N, 94°01′50″E, 7 Feb. 2011, *Ling Shein Man 87032* (MBK); Natma Taung Natl. Park, Saw to Mindat, 21°06′34″N, 94°11′23″E, 390 m, 1 Mar. 2013, *S. Sangvirotjanapat et al. 91175* (MBK). **Magway Division:** Agigatin village, 8 Feb. 2011, *Ling Shein Man 87036* (MBK); Saw Township, Saw to Long Shei village, 21°03′35″N, 94°08′23″E, 461 m, 23 Feb. 2014, *P. Srisanga et al. 97176* (MBK, US). **Mandalay Division:** Sedaw, Jan. 1908, *A. E. Meebold 8142* (K). **Sagaing Division:** E of Monywa, Kanpharlay village, 22°05′58″N, 95°10′30″E, 72 m, 6 Dec. 2004, *S. Kobayashi et al. 31527* (BISH). **Tenasserim Division:** Mergui distr., 12°26′N, 98°36′E, s.d., *Griffith Herbar. Cat. 5861* (K). **Yangon Division:** Mingaladon, 16°55′26″N, 96°06′01″E, 15, 27 Feb. 1949, *Po Khant 1137* (RAF); Insein distr., Sawbwagyigon, 16°54′N, 96°08′E, 30 m, 23 Mar. 1950, *Po Khant 719* (RAF). NEPAL. **Central:** Parsar, near Amrai, Dang, 27°54′55″N, 83°25′25″E, 27 Oct. 1952, *O. Polunin et al. 5926* (A); s. loc., s.d., *P. R. Huter 509* (K). PAPUA NEW GUINEA. **Milne Bay:** Cape Vogel, 9°42′S, 150°03′E, 5 m, 4 Apr. 1953, *L. J. Brass 21813* (A, K). **Morobe:** Finschhafen, 6°36′S, 147°51′E, s.d., *O. Warburg s.n.* (B); Kaiapit ["Kajabit"] Mission vic., 6°15′57″S, 146°16′03″E, 23 Nov. 1939, *M. S. Clemens 10830bis* (A). PHILIPPINES. **Balabac Island:** s. loc., 7°57′N, 117°10′E, Apr. 1906, *L. Mangubat BS-436* (NY). **Batan:** Batanes, Ivana, 20°22′14″N, 121°54′52″E, 24 Mar. 1991, *E. B. Barbon et al. PPI-1616* (KEP, L). **Luzon:** Cavite Province, Ternate, 14°42′N, 120°38′E, 27 Mar. 1995, *Reynoso et al. PPI-17125* (L); Ilocos Norte Province, Bangui, 14°12′N, 120°38′E, Mar. 1917, *M. Ramos BS-27412* (MO); Isabela Province, San Mariano, Barrio Disulap, Dimalasud Forest, 16°58′58″N, 122°00′51″E, 20 May 1961, *H. G. Gutierrez PNH-78299* (A); Laguna Province, Los Baños, 14°10′00″N, 121°14′34″E, 30 m, 24 Feb. 1965, *B. F. Hernaez 1115* (MO); Manila, Lorreta vic., 14°35′N, 121°00′E, May 1907, *A. L. Day 577* (MO); Rizal Province, Bosoboso, 14°37′37″N, 121°14′32″E, Dec. 1904, *Ahern's collector FB-1999* (F, K, NY, SING); Union Province, Bauang, 16°31′51″N, 120°19′59″E, Feb. 1904, *A. D. E. Elmer 5571* (K, NY). **Oriental Mindoro:** Mindoro Island, Mansalay, 12°31′13″N, 121°26′21″E, Dec. 1952, *M. D. Sulit PNH-17013* (K). **Palawan:** Puerto Princesa, 9°44′N, 118°44′E, 22 Mar. 1957, *Y. Kondo et al. PNH-36567* (BISH); Culion island, 11°53′N, 120°01′E, 18 Dec. 1902, *E. D. Merrill 538* (K); s. loc., 9°30′N, 118°30′E, Jan. 1906, *J. Bermejos BS-298* (NY). **Pangasinan:** San Carlos distr., San Carlos, 15°55′N, 120°20′E, 22 Dec. 1914, *P. Sanchez 8376* (MICH). SINGAPORE. Tanah Merah, on reclaimed land ca. 1 km E of Tanah Merah Country Club, 1988, *H. T. W. Tan 1988-14* (SINU). SOLOMON ISLANDS. **Guadalcanal:** Kukum, near Honiara, only 1 plant seen, roadside, 9°26′S, 159°59′E, 13 Dec. 1954, *H. S. MacKee 1652* (K, L); Tenam [Tanamo] River near sea, 9°42′S, 160°11′E, 14 Oct. 1945, *J. C. Riley 60* (US). SRI LANKA. **Central Province:** Matale distr., Sigiriya, *D. F. Austin et al. 6155A* (US). **North Eastern Province:** Trincomalee, 8°34′N, 81°14′E, 12 m, 14 Dec. 1943, *T. B. Worthington 1353* (K). **Uva Province:** Moneragala distr., Tanamalwila, *D. F. Austin et al. 6116* (FAU, PDA, US). **S. loc.:** s.d., *J. G. Koenig s.n.* (L); *D. van Royen s.n.* (L). THAILAND. **Central:** Ang Thong, 14°35′N, 100°27′E, 7 Mar. 1971, *J. F. Maxwell 71-121* (BK); Krung Thep Maha Nakhon, Bangkok, 13°45′N, 100°30′E, 9 Jan. 1920, *A. F. G. Kerr 3916* (K); Nakhon Pathom, Mahidol University, 13°47′N, 100°18′E, 25 Jan. 1999, *J. F. Maxwell 99-51* (L); Phra Nakhon Si Ayutthaya, Ayutthaya, 14°20′N, 100°32′E, 25 Feb. 1976, *W. Schwabe s.n.* (B); Saraburi, Phu Kae Botanical Garden, 14°40′46″N, 100°52′43″E, 67 m, 3 Nov. 2009, *G. Staples et al. 1332* (A, BKF, BM, SING). **Northeastern:** Maha Sarakham, Kosum Phisai, 16°13′N, 103°01′E, s.d., *B.G.O. staff 8385* (QBG). **Northern:** Chiang Mai, Mae Rim, 18°54′44″N, 98°56′23″E, 300 m, 27 Apr. 2002, *P. Srisanga 2503* (QBG, SING); Chiang Rai, Chiang Kham, 19°30′N, 100°17′E, 25 Dec. 1967, *Prayad 1151* (BK); Lampang, Lakawn Lampang, 18°17′54″N, 99°30′27″E, 250 m, 15 Jan. 1914, *A. F. G. Kerr 3088* (K, TCD); Phrae, Huae Mae Chem, 18°07′N, 100°09′E, 200 m, 7 Jan. 1972, *C. F. van Beusekom et al. 4708* (BISH, BKF, K, MO); Sukhothai, 17°00′N, 99°51′E, 20 Dec. 1984, *O. Ryding 804* (UPS); Tak, Ban Palata, 15°50′22″N, 98°51′10″E, 435 m, 8 Nov. 2012, *G. Staples et al. 1535* (KKU, QBG, SING). **Peninsular:** Krabi, Ao Luk, 8°23′N, 98°43′E, 25 Oct. 1985, *G. Staples et al. 199* (BKF); Phattalung, Ban Bak Klong, 7°44′18″N, 100°03′48″E, 14 m, 23 Oct. 2012, *G. Staples et al. 1486* (BKF, PSU, SING); Satun, Ban Khuan, 6°42′N, 100°04′E, s.d., *P. Sirirugsa 13* (PSU); Songkhla, Haad Yai, 7°01′N, 100°28′E, 27 Oct. 1985, *G. Staples et al. 210* (BKF); Surat Thani, Don Sak, Hat Nang Kam, rd. along seaside, 9°18′96″N, 99°44′52″E, 19 Dec. 2006, *R. Pooma et al. 6451* (A); Trang, 7°33′N, 99°36′E, 24 Oct. 1985, *G. Staples et al. 183* (BKF). **Southeastern:** Chanthaburi, Ban Salut, 12°44′45″N, 102°14′17″E, 8 m, 16 Feb. 2009, *M. Norsaengsri 4929* (QBG); Rayong, Km. 56.3, Hwy. 3138, 5 Nov. 1985, *G. Staples et al. 243* (BKF). **Southwestern:** Kanchanaburi, 14°01′N, 99°32′E, 10 Mar. 1960, *Prayoon 10* (BKF, L); Ratchaburi, Tha Pha Ban Pong, 13°34′N, 99°44′E, 23 Feb. 1965, *Sakol 377* (BK). TONGA. **Vavau:** Niuatoputapu, 15°57′S, 173°45′W, 100–200 m, 17 July 1978, *G. P. Buelow 1105* (US). U.S.A. **Hawaii:** Hawai'i Island, Kapoho, 19°30′22″N, 154°50′55″W, 24 Apr. 1959, *L. W. Bryan s.n.* (BISH); Kamuela, 20°14′31″N, 155°50′02″W, 6 Mar. 1954, *H. F. Clay s.n.* (BISH). VANUATU. **New Hebrides group:** Anatom Island, 20°12′S, 169°49′E, May 1859, *MacGillivray 56* (K, P). VIETNAM. **Bac Giang:** Kep, 21°24′N, 106°16′E, Dec. 1931, *P. A. Pételot 2337* (HNU). **Cân Tho:** Cân Tho, 10°02′N, 105°47′E, 25 Jan. 1914, *A. Chevalier 30325* (P). **Dac**

Lac: Hau Bôn, 13°24′N, 108°27′E, s.d., *J. Dournes s.n.* (P). **Ha Nôi:** Gia Lam distr., 21°02′N, 105°51′E, Nov. 1935, *P. A. Pételot 2534* (HNU). **Hô Chi Minh Ville:** Saigon Botanic Garden, 10°46′10″N, 106°40′55″E, anno 1871, *L. Pierre 5* (K, P). **Phú Tho:** Phu-to à Phu-Doan, 21°37′21″N, 105°11′05″E, 26 Oct. 1911, *H. Lecomte et al. 654* (P). **Vinh Long:** Cái Son, 10°06′07″N, 105°55′22″E, 5 Mar. 1919, *A. Chevalier 50* (P).

U.S. VIRGIN ISLANDS. **St. Croix:** s. loc., 17°44′23″N, 64°44′20″W, s.d., *West s.n.* (C). **St. John:** America Hill, 15 Mar. 1906, *Raunkiaer s.n.* (C). **St. Thomas:** Sugar Estate, Jan. 1887, *H. F. A. von Eggers 152* (C, US); sur les mornes de la partie du sud, Feb. 1821, *A. Plée s.n.* (P).

COMOROS. **Anjouan:** Ndzouani, 11°54′05″S, 43°28′38″E, *Lavanchie s.n.* (P). **Mayotte:** Mayotte Island, 12°50′S, 45°10′E, Dec. 1906, *C. d'Alleizette s.n.* (L). KENYA. **Lamu distr.:** Lake Mukunguya, 2°24′35″S, 40°40′52″E, 5 Nov. 1957, *Greenway et al. 9447* (K). **Tana River:** Belazoni, 2°31′S, 40°22′E, 6 m, 26 Mar. 1934, *H. C. Sampson 59* (K). MADAGASCAR. **Antsiranana:** DIANA, Nosy Be, 13°07′S, 48°16′E, June 1847, *Boivin 2097* (P). **Mahajanga:** Ambato-Boeni, 16°28′18″S, 46°42′56″E, Aug. 1952, *F. Bosser 3468* (P); Boeny, Ampijoroa, 16°19′S, 46°47′E, 85–150 m, 11 Aug. 1987, *G. E. Schatz et al. 1440* (K, MO, P). **Toliara:** Miandrivazo, 19°31′S, 47°04′E, anno 1897, *Hure s.n.* (P). MAURITIUS. **S. loc.:** 20°18′S, 57°35′E, anno 1849, *Boivin 1247bis* (TCD). MOZAMBIQUE. **Zambézia:** Chinde, Vicente vic., 18°28′37″S, 36°26′33″E, 29 Sep. 1887, *W. L. Scott s.n.* (K). SOMALIA. Mansur, 2°11′54″N, 42°13′41″E, *Guidotti 202* (MOD). TANZANIA. **Lindi:** Lake Lutamba, 10°03′S, 39°28′E, Sep. 1934, *H. J. Schlieben 5380* (K); Kilwa, Mavugi vic., 9°03′14″S, 39°18′59″E, 100 m, 7 July 2003, *C. J. Kayombo & Yohana 4261* (BISH, MO, P). **Pwani:** Rufiji, 8°18′57″S, 38°57′39″E, 250 m, 2 Sep. 1998, *O. A. Kibure 276* (MO). **Tanga:** Pangani distr., 5°30′S, 38°50′E, 100 m, 23 Aug. 1955, *R. E. S. Tanner 2085* (MO, NY). **Zanzibar:** Mudera swamp, 16 Nov. 1930, *J. H. Vaughan 1679* (K).

Cultivated. FRANCE. **Hautes-de-Seine:** Arboretum de la Vallée-aux-Loupes, living collections of the Collection Nationale des Convolvulacées, 26 Aug. 2009, *Simões 18* (BM).

13. Operculina ventricosa (Bertero) Peter in Engl. & Prantl, Nat. Pflanzenfam. 4(3a): 32. 1891. *Convolvulus ventricosus* Bertero in Colla, Hortus Ripul.: 37. 1824. *Ipomoea ventricosa* (Bertero) G. Don, Gen. Hist. 4: 274. 1838. *Operculina turpethum* var. *ventricosa* (Bertero) Staples & D. F. Austin, Brittonia 33: 595. 1981. TYPE: Guadalupe. "ubi in hortis cultus ex Ins. S. Bartholomei," anno 1819, *Bertero s.n.* (lectotype, designated here, large leaf only, excluding small leaf and two flowers, TO! TO-5082). EPITYPE: Guadeloupe. Basse Terre, "introduit et cultivée dans les jardins," Nov. 1892, *Duss 3081* (epitype, designated here, NY [bc] 01434626!]. Figures 28, 29.

Ipomoea demerariana Choisy in DC., Prodr. 9: 361. 1845. TYPE: Guyana. Demerara, cultivated in Blake's garden, *Parker s.n.* (lectotype, designated here, K [bc] K001097082!; isolectotype, K [bc] K001097083!).

Ipomoea saundersiana Baker, Fl. Cap. 4(2): 60. 1904, syn. nov. TYPE: South Africa. Cultivated in Natal Botanic Garden, *J. M. Wood 1635* (holotype, K [bc] K000097362!; isotype, NH [bc] NH0007294-0 image!).

Operculina tansaensis Santapau & V. Patel, Trans. Bose Res. Inst. Calcutta 22: 33. 1958, syn. nov. TYPE: India. Maharashtra: shores of Tansa Lake, 60 mi. N of Bombay, 18 Dec. 1955, *V. Patel 1619* (holotype, BLAT not seen; isotypes, all BLAT, numbered *1613*, *1614*, *1615*, *1618* not seen, *1620* image!).

Lianas; all parts glabrous or some parts variously pubescent; sap unknown. Stems terete or striate, not winged, 3–10 m, 6–8 mm diam., fistulose, basally becoming woody, herbaceous above, silvery-canescent toward tips. Leaves orbicular or cordiform, 9.5–22 × (3–)8–18.5 cm, basally deeply cordate with U-shaped sinus, apically acute to acuminate, pubescence denser along veins; venation impressed adaxially and prominent abaxially; petiole slender, (1.5–) 3.5–18 cm, 4 mm diam., base slightly swollen, longitudinally striate-angulate, often sulcate adaxially. Inflorescences axillary 3- to 5(to 7)-flowered cymes, or occasionally flowers solitary; peduncles stout, cylindrical, terete, longer than subtending petioles, (5–) 9.5–27(–40 in fruit) cm, 3–5 mm diam., smooth or slightly striate; bracts suborbicular to broadly ovate, 2.4–7 × 0.6–5.3 cm, thinly papery, present at flowering, usually deciduous at fruiting, basally truncate, apex caudate-apiculate, both sides puberulous; secondary bracts and bracteoles similarly shaped but smaller, 15–25 × 3–9 mm; pedicels clavate, 1.5–4.5(–5) cm, smooth, striate or 5-angulate, silvery canescent when immature, thickening and becoming glabrescent in fruit. Flowers diurnal, ascending to erect, odorless. Sepals subequal or outer slightly larger, elliptic-ovate, 2.5–4.4 × 1–3.5 cm, abaxially pilose, base rounded, apex rounded to obtuse, mucronate-apiculate. Corolla campanulate to broadly funnelform, white, 6–7.5(–9.5) cm, 5–8.5 cm diam., midpetaline bands glabrous, outside minutely golden gland-dotted. Stamens subequal, 2.3–2.5 cm, included; filaments broadly adnate to tube for about 1/3 their length, margins of adnate portion capitate-glandular, middle glabrous, insertion thickened, protruding into center of corolla, distally free, filamentous, glabrous; anthers spirally coiled, 4–7 mm, whitish; base minutely sagittate. Pollen not seen. Pistil included, 4.7–5 cm, longer than stamens; disc annular, black, glabrous; ovary broadly ovoid, 3–4 mm tall, glabrous and black (rarely densely whitish tomentose); style filamentous, glabrous (rarely whitish tomentose almost to middle); stigma biglobose. Fruiting calyx accrescent, cupping the fruit, leathery to stiffly chartaceous, brownish; sepal apices often recurved, erose, breaking off. Capsules depressed-globose, 4-lobed, 2–3.5 cm diam., tan to pale brown, 2-chambered, each cell 1- or 2-seeded; lower exocarp glabrous or hirsute; endocarp hyaline. Seeds 2 to 4, subovoid, trigonous, 8–10 mm, dull black, glabrous; hilum prominent, whitish in center.

Distribution. The original provenance for *Operculina ventricosa* is unknown: this has been obscured by human dispersal over 500-plus years, and today discrete populations are known from several widely disjunct places in the world. The specimen label data are difficult to interpret because it presents a mosaic of known cultivated specimens and other specimens that do not indicate if the plants were cultivated or growing in the wild.

We can provide this summary of known populations (Fig. 30)—tropical Pacific: Guam and the northern Mariana Islands in Micronesia, New Caledonia, and Vanuatu, with one isolated collection from Indonesian New Guinea (where possibly introduced and cultivated);—Asia: India, evidently naturalized in Maharashtra, cultivated in the Calcutta Botanic Garden in 1837, and known to be cultivated and possibly naturalized in Kerala; cultivated in the Saigon Botanic Garden in Ho Chi Minh Ville, Vietnam;—the Americas: Bonaire, Dominican Republic, Haiti, Jamaica, Martinique, Puerto Rico, Saba, Saint Eustatius, Saint Martin, U.S. Virgin Islands; and cultivated at Demerara, Guyana, and Coppename, Suriname;—Africa: once cultivated in the Natal Botanic Garden, South Africa. Although *Operculina* was included for South Africa by Meeuse (1957) based on this cultivated record from Natal, the genus was later excluded from the South African convolvulaceous flora (Meeuse & Welman, 2000). We found no information that *O. ventricosa* has naturalized in South Africa as it has in many other places where it was introduced as an ornamental flowering climber.

The botanical literature is contradictory about the place of origin for *Operculina ventricosa*, and there is no way to establish it now with any degree of confidence. Fosberg and Sachet (1977) stated that the Micronesian populations were introduced from the Americas. Likewise, in New Caledonia the population there was considered introduced from the Americas (Heine, 1984). Floras for the West Indies either do not indicate where the species is native (Grisebach, 1864; Boldingh, 1909; Liogier, 1994; Liogier & Martorell, 2000; Fournet, 2002) or state that *O. ventricosa* is native to the Lesser Antilles (House, 1906; Urban, 1910; Britton & Wilson, 1925; Powell, 1979). In contrast to all these indications, the plants in Puerto Rico and the Virgin Islands were stated to be introduced to the Antilles from the Old World (Acevedo-Rodríguez, 2005).

Ecology. In the Americas, collectors recorded very little ecological information, merely noting that the vines trail in the dry littoral zone across calcareous sands at sea level.

In the Pacific islands, collectors were more forthcoming with information on their field labels indicating that plants were found in forest edges, disturbed sites, wooded slopes and cliffs, abandoned agricultural fields, on an old cauldera wall, among swordgrass and low shrubs, in open grassy areas; on thick red soil with coral debris, loose volcanic soil, volcanic ash soil and lava rocks, tuff cliffs, on limestones, and serpentine soils. Elevations ranging from 3 to 185 m were recorded.

Several collectors reported that the vines will cover the ground and low shrubs, festoon coconut trees in plantations, climb all over trees and cover them up, and otherwise create "vegetable blankets" carpeting the vegetation underneath. Other species of Convolvulaceae in the Pacific that form such vegetable blankets (for example, *Decalobanthus peltatus*) have been labeled as invasive species for this capability. Given the rampant growth and broad ecological amplitude reported for *Operculina ventricosa*, possibly this species should be monitored for adverse impacts.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	5	5	4	1	1		3		2	1	3	2
Fruiting collections		1	1	1	1	1				1		1

The table combines phenological observations from plants worldwide: on this global basis the plants appear to flower and fruit year-round. If the collections were broken down based on geographical origin, a seasonal pattern in reproductive activity might become apparent.

Vernacular names. Guadeloupe: belle de nuit (*Stehlé 114*), liane blanche (*Duss 3081*), liane d'argent (Powell, 1979: 246). Guyana: cephalic vine (*Parker s.n.*). Martinique: liane bord de mer (Powell, 1979: 246), liane serpent (*Duss 427*). Northern Mariana Islands: Saipan—alalag (*Stone 5163*); burning bean, wood rose (*Courage 30*); Tinian—alalag taki (*Gaudichaud 15*). Dutch Caribbean: hoofdpijnblad (Boldingh, 1909); Bonaire—gehweeht, verwilderd (*Arnoldo 361*). U.S. Virgin Islands: St. Thomas lid-pod (USDA, NRCS, 2016).

Typification. The original material for *Convolvulus ventricosus* in TO is a mixture of two taxa mounted on the same sheet: a single large leaf is evidently *Operculina ventricosa* but there are also two small pieces recognizable as *Aniseia martinicensis* (Jacq.) Choisy mounted with it. We have therefore chosen the single large leaf as the lectotype for this name, excluding the *Aniseia* elements, and designated a more complete specimen as an epitype to clarify the species concept. Leaves alone are seldom adequate for making a species determination in Convolvulaceae, so we have indicated as epitype a flowering specimen of *O. ventricosa* with leaves, flowers, buds, and bracts attached to the inflorescence axis so that the taxonomic concept we are following is clear.

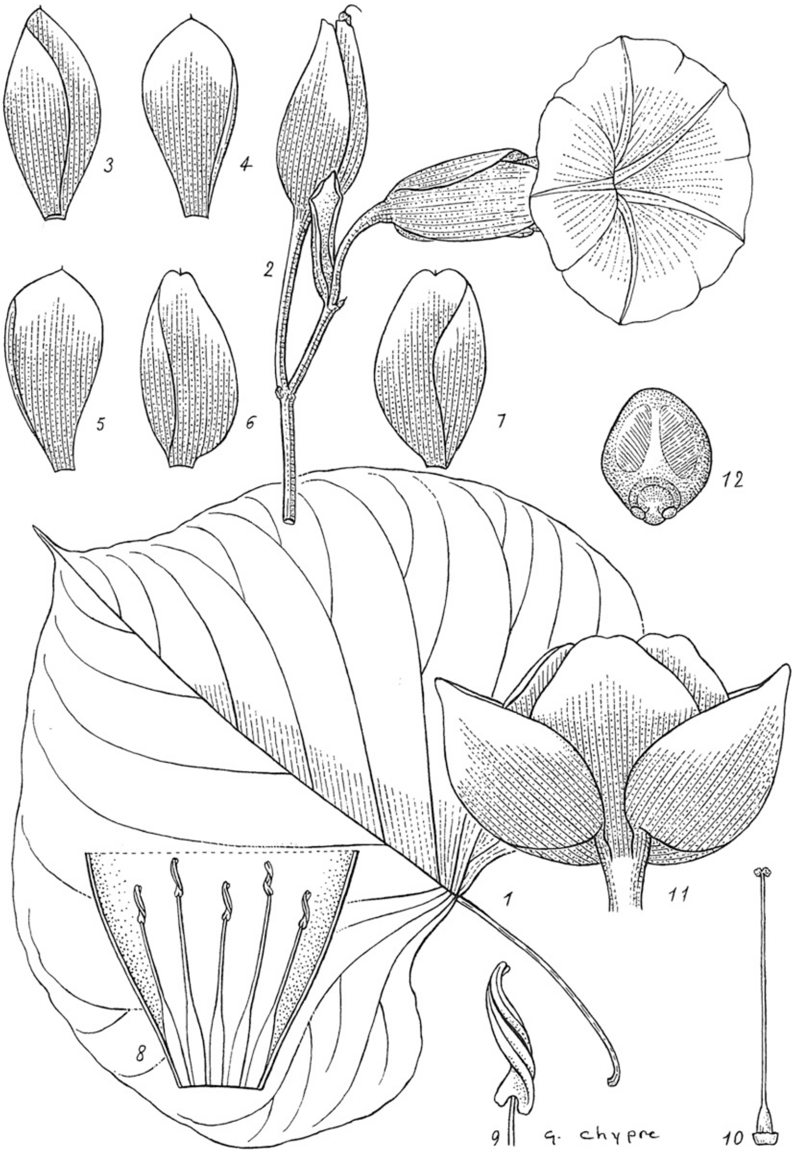

Figure 28. An illustration for *Operculina ventricosa* (Bertero) Peter. Original caption, translated: 1. leaf; 2. inflorescence; 3–7. sepals; 8. lower corolla opened to show stamens; 9. spirally dehiscent anther; 10. pistil; 11. fruiting calyx; 12. seed. Vouchers for illustration: *Schmid 2198*, *Balansa 3352*, *544*, all in P. Reproduced from *Flore de la Nouvelle-Calédonie* (Heine, 1984: 25, plate 5, drawn by G. Chypre). © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris. Reproduced with permission.

We have chosen as lectotype for *Ipomoea demerariana* the sheet in Kew that was previously labeled as the "holotype" for this name: [barcode] K001097082. Since Choisy did not choose a holotype the two sheets now in Kew must be considered syntypes under the current *Code* (Turland et al., 2018) and the lectotype as chosen stabilizes the taxonomic concept for the name.

The taxonomic and nomenclatural confusion surrounding the name "*Convolvulus grandiflorus*" as misinterpreted and misapplied by House (1909) has been clarified by Powell et al. (1978). According to their explication of the problem, *Operculina grandiflora* sensu House (House, 1909: 69) is a misapplication for *O. ventricosa*, but the type for *C. grandiflorus* Jacq. is actually *Ipomoea violacea* L.

Uses. *Operculina ventricosa* is grown as an ornamental flowering climber, particularly in the West Indian islands, where Fr. Duss has recorded *cultivée dans les jardins pour le formation des tonnelles* [cultivated in

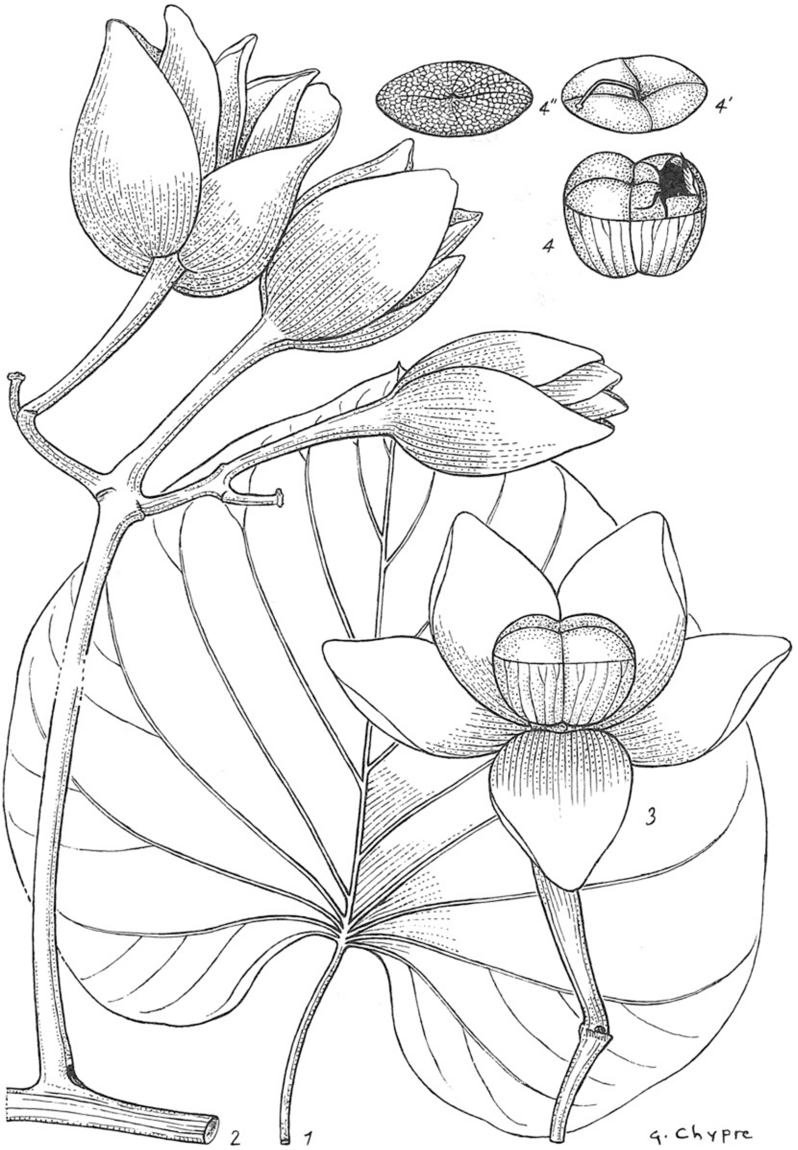

Figure 29. An illustration for *Operculina ventricosa* (Bertero) Peter. Original caption, translated: 1. full-sized cauline leaf; 2. inflorescence; 3. fruiting calyx and capsule; 4. capsule, endocarp shattered; 4′. operculum, abaxial (upper) side; 4″. operculum, adaxial (inner) side. Vouchers for illustration: *Balansa 3352*, *544*, both in P. Reproduced from *Flore de la Nouvelle-Calédonie* (Heine, 1984: 27, plate 6, drawn by G. Chypre). © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris. Reproduced with permission.

gardens for the formation of arbors] (*Duss 427*). Possibly the profusion of large white flowers is responsible for the movement of this species around the world by humans.

There is an intriguing comment recorded on the label for *Parker s.n.* (K) that "no vermin are found near it" in reference to a plant cultivated in a garden in Demerara, Guyana. Given the extraordinary wealth of secondary compounds known from Convolvulaceae in general and *Operculina* in particular, an investigation of the chemical compounds contained in *O. ventricosa* might prove worthwhile.

Comments. *Operculina ventricosa* has evidently been moved around the world at an early date by humans and it was then later described as a new species from South Africa and India. We reduce *O. tansaensis* to synonymy here based on study of the protologue and a digital image of one of the isotypes (*Patel 1620*), kindly shared by

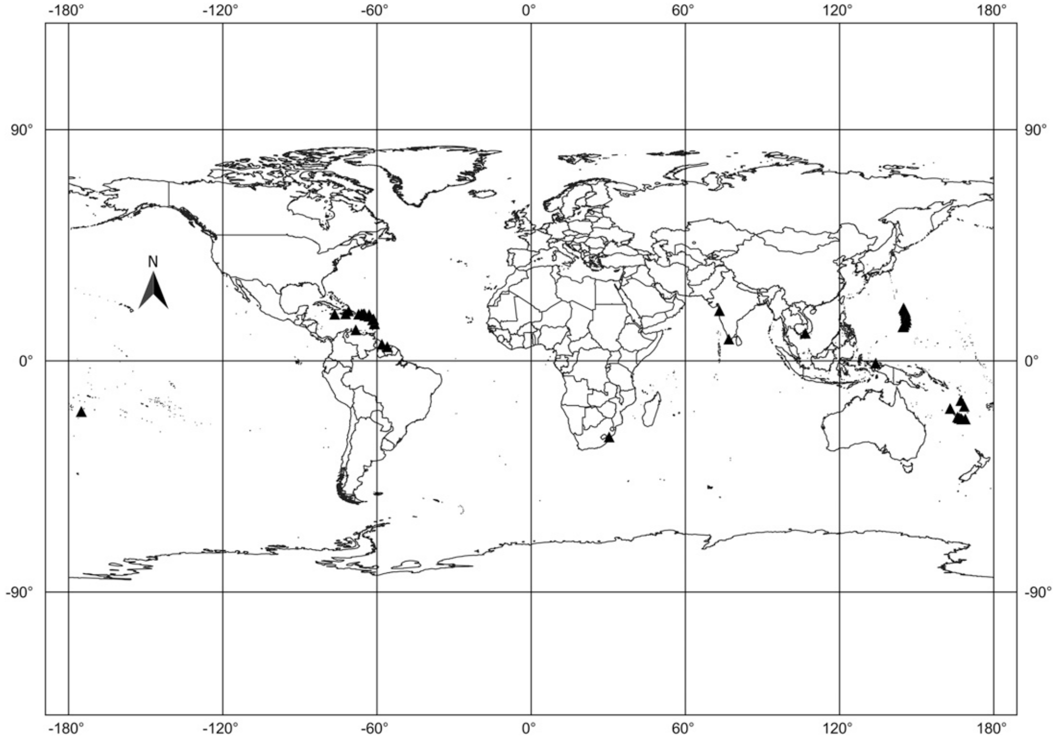

Figure 30. Distribution map for *Operculina ventricosa* (Bertero) Peter.

BLAT. We note that *O. ventricosa* has also been collected in Kerala State and the label clearly indicated the plants there were cultivated and possibly naturalizing. *Ipomoea saundersiana* was previously reduced to synonymy under *O. turpethum* by Meeuse (1957: 708) who commented that *Operculina* had never been found outside cultivation in South Africa; we here reduce the name to synonymy under *O. ventricosa* for the first time.

In the Southwest Pacific a remarkable case of convergence has occurred between *Operculina ventricosa* and the Solomon Islands endemic, *Decalobanthus bracteatus* (P. S. Bacon) A. R. Simões & Staples. Both are lianas or expansive herbaceous climbers with enlarged, persistent bracts in the inflorescence, and a large corolla (5 cm and larger in both species). They can be confused in the herbarium based on their general appearance; however, *D. bracteatus* always has yellow corollas whereas *O. ventricosa* has a white corolla. *Decalobanthus bracteatus* differs in the stems covered in lenticels; stems of *O. ventricosa* are terete and smooth or finely longitudinally ridged. Other small differences appear when detailed measurements of internal floral parts are taken.

Selected specimens examined [78 collections]. DOMINICAN REPUBLIC. **Puerto Plata:** La Boca, most probably escaped, 10 Mar. 1930, *E. L. Ekman 14358* (K, NY, S, US). DUTCH CARIBBEAN. **Bonaire:** Lima, 17 Jan. 1947, *Fr. Arnoldo 361* (U). **Saba:** windward side, 18 July 1906, *I. Boldingh 1243* (U). **Saint Eustatius:** s. loc., 17°29′06″N, 62°58′24″W, anno 1905, *Groll-Meyer 6999* (U). **Saint Martin/Sint Maarten:** St. Martin, cultivated, 9 Dec. 1964, *Fr. Arnoldo 3168* (U, USF). GUADELOUPE. **Basse-Terre:** Basse-Terre, "introduit et cultivé dans les jardins," 10 Mar. 1893, *Duss 487* (P); Nov. 1892, *Duss 3081* (type NY). **Grande-Terre:** Moule, 16°19′59″N, 61°20′50″W, *H. Stehlé 1489* (US); s. loc., anno 1819, *Bertero s.n.* (type TO). GUYANA. **Demerara-Mahaica:** Demerara River, in Blake's garden, Mar. 1824, *C. S. Parker s.n.* (type K). HAITI. **West:** Port au Prince, cultivated in gardens, 11 Nov. 1927, *E. L. Ekman 9275* (S). JAMAICA. **Portland:** Port Antonio, *C. F. Millspaugh 980* (F, U). MARTINIQUE. s. loc., anno 1881, *Duss 427* (F, K, MO, NY, US); anno 1879, *Duss 427* (NY). PUERTO RICO. **Fajardo:** Playa de Fajardo, cultivated, Mar. 1913, *N. L. Britton et al. 1660* (NY, US). **San Juan:** Martín Peña, cultivated, 9 Mar. 1920, *E. E. Barker 27* (NY); Rio Piedras, cultivated, 2 Jan. 1916, *J. A. Stevenson 3624* (NY). SURINAME. **Coronie:** Coppename, im garten, s.d., *Wullschlägel 1038* (BR). U.S. VIRGIN ISLANDS. **St. Croix:** Tipperary Estate, planted around house, 24 Feb. 1974, *F. R. Fosberg 55369* (US). **St. Thomas:** s. loc., 18°20′N, 64°55′W, anno 1932, *Dna. Gerva Lamb s.n.* (C).

GUAM. Agfayan Bay, Merizo, 13°15′48″N, 144°40′11″E, 24 Nov. 1963, *B. C. Stone 4911* (K); Barrigada, 13°28′06″N, 144°47′56″E, 15 July 1977, *R. Tsutsui 6* (BISH, L, US); Chalau Pago, 13°27′N, 144°47′E, 14 Dec. 1987, *L. Raulerson 16382* (K); Malojlol, 13°18′17″N, 144°45′32″E, 50 m, 15 Jan. 1966, *M. Evans 1474* (US); Ritidian Point, 13°39′02″N, 144°51′37″E, 29 Aug. 1954, *R. Moran 4523* (BISH); s. loc., 13°27′N, 144°47′E, 185 m, 7 Jan. 1954, *F. R. Fosberg 35384* (BISH, K, L, P). INDIA. **Kerala:** Thiruvananthapuram distr., Poojappura, way side in urban area, 8°30′N, 76°55′E, 5 Apr. 1995, *S. D. Biju 42121* (K). **Maharashtra:** Tansa Lake, 19°34′04″N, 73°15′49″E, 18 Dec. 1955, *V. M. Patel 1620* (type BLAT, image). **West Bengal:** Calcutta Botanic Garden, Apr. 1837, *Gaudichaud 128* (or *734*) (G). INDONESIA. **West Papua:** Manokwari, Reremy, 0°51′40″S, 134°03′45″E, 15 Oct. 1960, *V. W. Moll BW-9783* (L). NEW CALEDONIA. Diahot, 21°51′S, 165°54′E, Apr. 1871, *B. Balansa 3352* (A, L, P); île des Pins, Gadjy, 18 July 1965, *H. S. MacKee 13116* (P); île Walpole, calcareous plateau ca. 80 m elev., 10 Nov. 1972, *H. Hmakone & G. Sam* [under MacKee number] *25862* (sterile) (P). COMMONWEALTH OF THE NORTHERN MARIANA ISLANDS. **Agrihan:** Agrihan, 18°56′03″N, 145°40′02″E, 17 Feb. 1950, *F. R. Fosberg 31617* (US). **Alamagan:** Asongsong Village, 17°36′02″N, 145°50′00″E, 3–15 m, Feb. 1950, *F. R. Fosberg 31722* (BISH). **Asuncion:** Asuncion, 19°40′N, 145°24′E, 129 m, 29 Feb. 1984, *D. R. Herbst 7434* (BISH). **Farallon de Medinilla:** Farallon de Medinilla, 16°01′N, 146°04′E, 4 Mar. 1984, *D. R. Herbst et al. 7525* (BISH). **Maug islands:** East island, 20°01′N, 145°14′E, 24 Feb. 1984, *D. R. Herbst 7345* (BISH); West island, 20°01′N, 145°13′E, 25 Feb. 1984, *D. R. Herbst 7377* (BISH). **Pagan:** Pagan, 18°05′N, 145°45′E, 45 m, 1 Aug. 1954, *L. D. Bonham 2* (BISH); airstrip vic., 18°05′N, 145°45′E, 12 Apr. 1979, *M. V. C. Falanruw MVCF-3257* (US). **Rota:** As Malote, 14°09′13″N, 145°12′11″E, 27 Feb. 1950, *F. R. Fosberg 31876* (US); Poniya Point, 14°09′13″N, 145°12′11″E, 350–500 m, 26 May 1966, *M. Evans 2191* (K); Songsong, 14°09′13″N, 145°12′11″E, 10–30 m, 31 May 1973, *M.-H. Sachet 1766* (BISH, L). **Saipan:** Army Hill, 15°10′51″N, 145°45′21″E, Feb. 1958, *E. G. Courage 30* (US); Garapan vic., 15°10′51″N, 145°45′21″E, 28 June 1946, *F. R. Fosberg 25215* (BISH); Magicienne Bay, 15°10′51″N, 145°45′21″E, 75 m, 1 Feb. 1950, *F. R. Fosberg 31273* (BISH, L, US). **Sarigan:** Sarigan, 16°42′18″N, 145°46′48″E, 10–100 m, 21 June 1966, *M. Evans 2337* (BISH). **Tinian:** Marpo Valley, 15°00′N, 145°38′E, June 1946, *F. R. Fosberg 24812* (BISH, L, US); s. loc., anno 1830, *Gaudichaud 15* (G-DC). TONGA. **Haapai group:** Tofua, 19°45′S, 175°05′W, 60 m, 13 June 1982, *G. Buelow 2585* (BISH); Kao, 19°40′S, 175°02′W, 6 Aug. 1982, *G. Buelow 3093* (BISH). VANUATU. **Efate [Île Vaté] island:** Forari, 17°40′S, 168°31′E, 3 June 1965, *M. Schmid 241* (P). **Espiritu Santo island:** Saraotou, 15°26′S, 167°12′E, May 1977, *P. Morat 5588* (P). VIETNAM. **Hô Chi Minh Ville:** cultivated in Saigon Botanic Garden, 10°47′17″N, 106°42′17″E, Nov. 1867, *L. Pierre s.n.* (P).

SOUTH AFRICA. **KwaZulu-Natal:** cultivated in Natal Botanic Gardens, 29°36′28″S, 30°20′47″E, Oct. 1882, *J. M. Wood 1635* (type K, NH).

14. **Operculina turpethum** (L.) Silva Manso × **O. ventricosa** (Bertero) Peter. Figures 31, 32.

Intermediate between the two purported parent species in morphology and size. Stems, petioles, and peduncles usually angled or striate but not alate. Leaves often broadly ovate to orbicular, the base cordate with a U-shaped sinus. Corolla midpetaline bands glabrous, outside minutely golden gland-dotted. Ovary glabrous or with caducous hairs around base. Fruit sparsely to densely hirsute on lower pericarp, below line where operculum detaches, or glabrous.

Distribution. This hybrid occurs in the South Pacific (Fig. 33) including the island of New Guinea (Indonesian and Papua), the high volcanic islands of the Federated States of Micronesia (Chuuk, Kosrae, Pohnpei, Yap), Palau, New Caledonia, Samoa (American and Western), the Solomon Islands, and Vanuatu.

Ecology. Apparently it is a plant of mesic to wet forest margins, riverbanks, abandoned gardens, and secondary regrowth; on red volcanic soils, rocky hillsides, or sandy soil over limestone. Elevation ranges from 2 to 400 m. In contrast to *Operculina polynesica*, which is always found on coral atolls or on limestone, the hybrid seems to thrive on more fertile soils with adequate moisture.

Phenology.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Flowering collections	2	1	1			3	3	3	2		1	1
Fruiting collections	2		4			2	2	3	2		1	

Vernacular names. Federated States of Micronesia: Chuuk [Truk] State— afaamac (*C. C. Y. Wong 253*); Yap State: Falalap islet—havarnash (*Fosberg 47242*). Palau: besbus (*Fosberg 47471*). Samoa: fue vao? (*Uchiyama et al. 241*). Solomon Islands: Rennell Island—sopi (*Watanabe et al. SIMB–739*).

Uses. In Palau "The leaves are wrapped around sea anemone and tridacna, cooked and eaten" (*Fosberg 47471*).

Comments. Some Pacific island populations of *Operculina* show remarkable phenotypic diversity, and we have not been able to confidently name all the Pacific specimens examined for this revision; some specimens are intermediate in their characters between two or more of the species we recognize here; these variants fall within the species-complex centered on *O. turpethum* and including also *O. polynesica* and *O. ventricosa*. Other specimens show an extraordinary variability in character states that is not displayed in *Operculina* plants from outside the Pacific region. Clearly, something unusual is going on with *Operculina* in the South Pacific, and we point out some unresolved questions here that indicate the need for future study by those able to visit island populations and study living plants.

A decade ago Staples wrote about Pacific *Operculina* and pointed out several cases of intermediates among specimens examined for that study (Staples, 2007). The investigation was hindered at that time because the rich collections from the South Pacific housed in the BSIP and SUVA herbaria were not available for study; both herbaria had been closed indefinitely and our inquiries about specimen loans were not answered. In the 10 years since then, it has not proven possible to investigate further the morphological variability among Pacific *Operculina*: there have been few additional specimens available to us for study and the older material that is available has not allowed a definitive taxonomic resolution. In the botanical literature, and in herbaria, much of the variability has been included under the name *O. turpethum* (Fosberg & Sachet, 1977: 29; Heine, 1984: 30; Smith, 1991: 45) and Pacific plants and specimens so-called require further, careful scrutiny. Geographically, the islands where the greatest levels of phenotypic diversity or intermediacy have been noted include: the Micronesian states of Kosrae and Pohnpei; Palau; the Samoan Islands, both Western and American; and New Caledonia, where the plants called *O. turpethum* by Heine (1984) have a different appearance from those in mainland Asia.

Unfortunately, there are no molecular data for the Pacific plants/populations, which have not so far been sampled in molecular phylogenetic studies (Stefanović et al., 2002; Simões et al., 2015). Likewise, the Pacific plants/populations have not been included in palynological analyses (Ferguson et al., 1977; Simões et al., 2019). These techniques might shed light on the variability and intermediates present among Pacific *Operculina*. For now, we are attributing the intermediacy and variability to hybridization between species as Staples (2007) conjectured. Further field study, morphological observations based on herbarium specimens, and possibly a population genetics study would help ascertain the boundaries between species and pinpoint any localities where hybridization has most likely occurred. We enumerate below the observed intermediates to guide such future study.

Selected specimens examined [52 collections—several sterile collections included are indicated with (sterile) following the collector name]. AMERICAN SAMOA. **Ofu:** Toaga, at Muaʻava, 22 June 1925, *D. W. Garber 1099* (BISH). **Tau:** Faleulu Valley, Muaos plantation S of Fale, 1/2 mi. from shore, 27 Jan. 1938, *W. Harris 135* (BISH, P, US); Siufaga, 13°57′S, 171°24′W, 7 Oct. 1939, *T. G. Yuncker 9289A* (BISH). **Tutuila:** Tafuna, 14 Aug. 1959, *A. W. Wisner 113* (BISH); disturbed area by roadside at Fagatele Bay, 21 July 1975, *W. A. Whistler W-2842* (BISH, K, US). FEDERATED STATES OF MICRONESIA. **Chuuk State:** Truk, 7°25′N, 151°47′E, 2 Nov. 1947, *C. C. Y. Wong 253* (BISH, US). **Kosrae State:** Mwot [= Mot], 26 Jan. 1936, *M. Takamatsu 445* (BISH). **Pohnpei State:** Pohnpei, Toletik, 6°54′25″N, 158°13′57″E, 7 Feb. 1936, *M. Takamatsu 991b* (BISH, K). **Yap State:** Namoluk atoll, Falalap islet in village, 7°14′35″N, 144°26′05″E, 1–2 m, 13 Aug. 1965, *F. R. Fosberg 47242* (sterile) (NY, US). INDONESIA. **Papua:** Hollandia distr., Lake Sentani, 2°37′S, 140°34′E, 20 m, 25 July 1954, *P. van Royen 4504* (A, K, P, SING). NEW CALEDONIA. Cap Lafon, 21°02′S, 167°06′E, 90 m, 30 Aug. 1973, *H. S. MacKee 27216* (K, P); Basse Tiwaka, 20°54′S, 165°13′E, 19 Aug. 1976, *H. S. MacKee 31724* (K, P); Haute Tschamba, 50 m, 1 June 1970, *H. S. MacKee 22012* (CANB, G, P, SING); vallée de la Tchamba, 21°02′S, 165°23′E, 15 Jan. 1963, *H. S. MacKee 9998* (K, P); Yaouhe, 22°16′S, 166°27′E, 21 Sep. 1902, *R. Schlechter 14729* (E, K, P). **Loyalty Islands:** île Lifou, July 1869, *Balansa 1670* (P). PALAU. **Angaur:** Angaur island, 10 Mar. 1950, *F. R. Fosberg 31977* (BISH, K, NY, US); same loc., 18 Dec. 2002, *B. M. Waterhouse BMW-6578* (BISH, BRI, GUAM); central part, 26 July 1946, *F. R. Fosberg 25878* (sterile) (BISH). **Koror:** Ngarakabesang [= Arakabesan] island, 23 Mar. 1950, *F. R. Fosberg 32277* (BISH, NY, US). **Oreor:** Aulupse'el island [= Auluptagel], Ngerebe'ed Beach on E end, sand flat betw. beach & taro marsh, 23 Aug. 1965, *F. R. Fosberg 47471* (sterile) (BISH); Malakal island, 11 Mar. 1974, *D. O. Otobed s.n.* (BISH). **Peleliu:** Peleliu island, W of Bloodynose Ridge, 10 Mar. 1950, *F. R. Fosberg 32004* (BISH, NY); SC part of island, 9–10 Mar. 1950, *F. R. Fosberg 32005* (BISH); secondary vegetation on SW side, 27 July 1946, *F. R. Fosberg 25982* (sterile) (BISH); s. loc., 26 Jan. 1978, *L. Stemmermann 3391* (BISH). PAPUA NEW GUINEA. **Central:** Cape Suckling, behind fore dune, 9°01′28″S, 146°37′42″E, 9 Aug. 1979, *G. Leach UPNG-3614* (A, K); Rigo subdistr., Kwikila, 9°48′15″S, 147°40′31″E, 91 m, 16 Aug. 1967, *A. Kairo & H. Streimann NGF-30797* (A, BISH, K, SING). **Madang:** Kar Kar island, 4°40′S, 146°00′E, 3 m, 11 June 1969, *J. Vandenberg & E. Mann NGF-42210* (A, K, L). **Morobe:** Markam Valley, Nadzab, 6°33′S, 146°42′E, 18 June 1954, *A. Floyd 5766* (A, K, LAE). **Western:** Gaima, 8°19′S, 142°59′E, Nov. 1936, *L. J. Brass 8317* (K). PHILIPPINES. **Luzon:** Manila Airport, 14°31′N, 121°00′E, Jan. 1954, *M. L. Steiner 383* (BISH). SAMOA. **Aleipata Islands:** Fanuatapu, 13°59′S, 171°20′W, 75 m, 6 July 1980, *W. A. Whistler W-4410* (B). **Savaiʻi:** above Patamea, crater rim of Mt. Tagotago, 15 Sep. 1968, *M. L. Bristol 2331* (BISH, GH, K, L, SING, US); back of Safune, coconut plantation, 13 Aug. 1931, *E. Christophersen & E. P. Hume 2427* (BISH); Salaʻilua, plantation, 8 Oct. 1931, *E. Christophersen 2845* (sterile) (BISH); Vaipouli, 13°27′57″S, 172°22′08″W, July 1894, *Reinecke 62a* (K). **Upolu:** Apia, 13°50′S, 171°44′W, June 1927, *S. Gemhell s.n.* (S); Sauniatu, 13°55′S, 171°34′W, 3 Aug. 1972, *W. A. Whistler W-264* (BISH); Utumapu, 16 Sep. 1973, *W. A. Whistler W-665* (BISH); along roadside down to Fagaloa Bay, 3 Aug. 1972, *W. A. Whistler W-253* (BISH); in front of Faleolo airport, on roadside, 3 Sep. 1999, *Uchiyama, Matuzaki & Watanabe 241* (BISH); Nuutele, 14°02′S, 171°22′W, 19 July 1980, *W. A. Whistler W-4487* (B). SOLOMON ISLANDS. **Makira-Ulawa prov.:** San Cristobal island, Hagataro Ridge Top, 10°28′04″S, 161°55′28″E, 6 Sep. 2011, *T. Watanabe et al. SIMB-1712* (MBK). **Rennell & Bellona prov.:** Rennell island, S of Tinggoa Airport, 11°13′12″S, 160°03′28″E, 7 m, 12 July 2009, *T. Watanabe et al. SIMB-739* (MBK); Rennell island, s. loc., 11°40′S, 160°10′E, 20 June 1938, *Templeton Crocker Exped. s.n.* (BISH); 18 Aug. 1962, *H. Dissing 2761* (L). VANUATU. **Espiritu Santo island:** Malao, 15°10′S, 166°51′E, 12 Sep. 1971, *H. S. MacKee RSNH-24263* (K, P). **Vanua Lava:** rainforest, 13°50′S, 167°28′E, sea level, 9 July 1928, *S. F. Kajewski 450* (A, BISH, K, P).

Insufficiently Known Species

Convolvulus triflorus Sessé & Moc., Fl. Mexic.: 37. 1893, nom. illeg. TYPE: Mexico. “in Ahualulci montibus,” *Sessé & Mociño* (syntype, MA not found).

McDonald (1993: 85; 1997: 69) reduced this illegitimate name to synonymy under *Operculina pinnatifida*, citing as an isotype the specimen *Sessé & Mociño 1603*

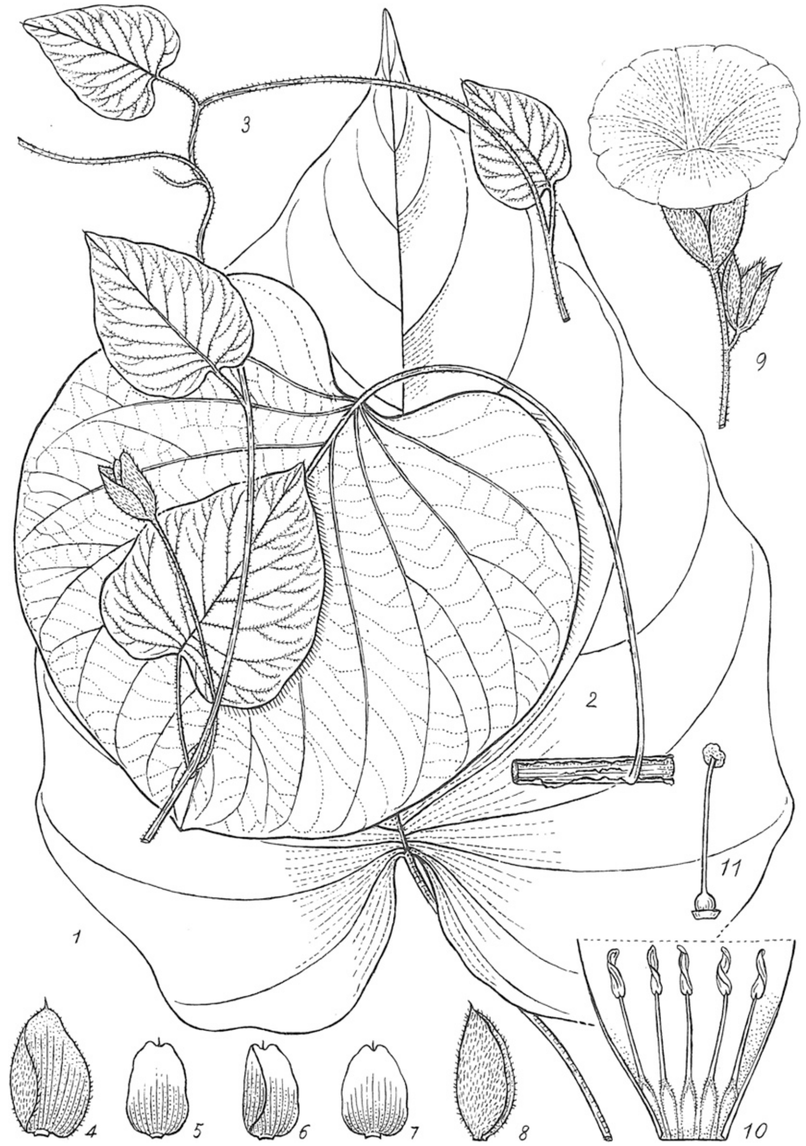

Figure 31. An illustration for *Operculina turpethum* (L.) Silva Manso × *O. ventricosa* (Bertero) Peter. Original caption, translated: 1. full-sized cauline leaf; 2. leaf from middle of stem; 3. flowering branch; 4–8. sepals; 9. flower; 10. lower corolla opened to show stamens; 11. pistil. Vouchers for illustration: *MacKee 27216, 22012, 31724*, all in P. Reproduced from *Flore de la Nouvelle-Calédonie* (Heine, 1984: 29, plate 7) under the name *O. turpethum*. © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris. Reproduced with permission.

in the MA herbarium. We failed to locate this specimen in online searches of the JSTOR Global Plants digital archive and in the MA virtual herbarium. However, two specimen images were returned when the name "Convolvulus triflorus" was searched in JSTOR Global Plants: one (barcode MA814685) is either an *Ipomoea* species or *Merremia quinquefolia* with palmately compound leaves that was collected in Peru by *Ruiz, Pavon & Dombey*; this cannot possibly be original material for *C. triflorus* Sessé & Moc., despite that name being written on the label. The other specimen (barcode MA603898) was collected in Mexico by *Sessé & Mociño* and is *O. pinnatifida*. This specimen disagrees strongly with the protologue, which describes a plant with cordate-ovate, entire leaves and purple flowers longer than the leaves. On this basis we do not think the specimen bearing MA603898 is suitable as a lectotype choice for *C. triflorus* Sessé & Moc. We suspect there

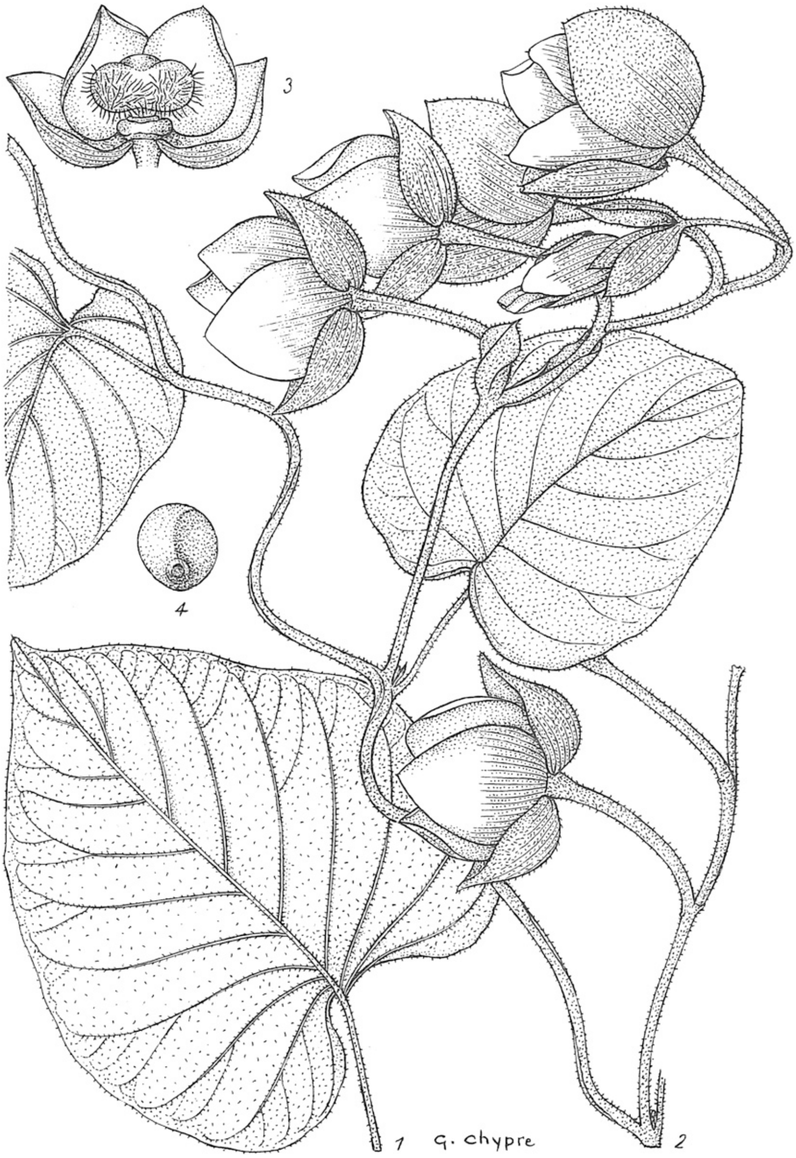

Figure 32. An illustration for *Operculina turpethum* (L.) Silva Manso × *O. ventricosa* (Bertero) Peter. Original caption, translated: 1. leaf showing blade shape and secondary venation; 2. fruiting branch; 3. fruiting calyx, one sepal removed, note hirsute lower fruit wall; 4. seed. Vouchers for illustration: *MacKee 22012*, *Balansa 1670*, both in P. Reproduced from *Flore de la Nouvelle-Calédonie* (Heine, 1984: 31, plate 8, drawn by G. Chypre) under the name *O. turpethum*. © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris. Reproduced with permission.

must be additional specimens in MA that are not yet digitized and possibly one of these will better fit the protologue. For now, we are treating *C. triflorus* Sessé & Moc. as a confused name of uncertain application, and not as a synonym of *O. pinnatifida*, until further research can resolve its nomenclatural status.

Convolvulus ventricosus Silva Manso, Enum. Subst. Braz.: 20. 1836, as "*ventricorus*" corr. to *ventricosus* in errata, nom. illeg., non Bertero, 1824. Replacement name: *Ipomoea silvana* Choisy in DC., Prodr. 9: 374. 1845. *Ipomoea ventricosa* Stellfeld, Tribuna Farm. 13: 86. 1945, nom. illeg. TYPE: Brazil. "na beira do Rio Paraná," *Silva Manso s.n.* (not traced).

Silva Manso's description is too vague to recognize what species this could be, and we have not located any original material for the name in herbaria nor digital

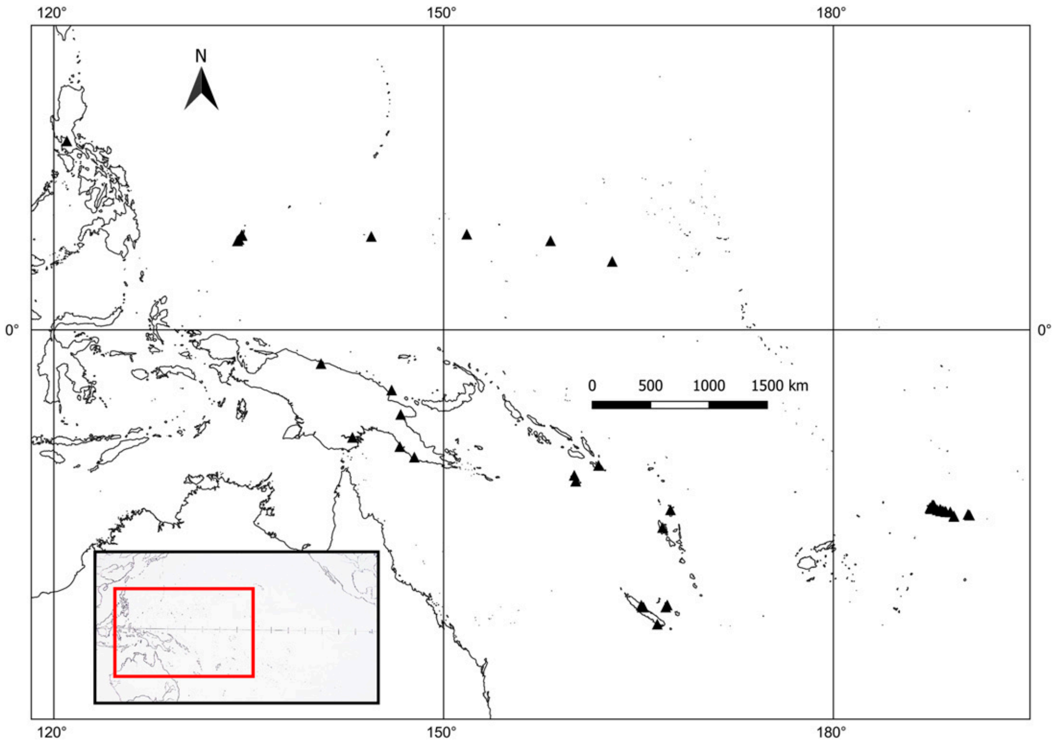

Figure 33. Distribution map for *Operculina turpethum* (L.) Silva Manso × *O. ventricosa* (Bertero) Peter.

images in online virtual herbaria (JSTOR Global Plants; *species*Link, 2018). Steudel (1841) did not mention the Silva Manso name in his *Nomenclator botanicus*; Choisy (1845) recognized that *Convolvulus ventricosus* was preoccupied and provided a replacement name for it. Meisner (1869: 274) accepted *Ipomoea silvana* in his *Flora brasiliensis* account but made plain "Plantam non vidimus." Stellfeld (1945) attempted to transfer the epithet *ventricosus* into *Ipomoea*, creating another illegitimate name in the process. After that point, later authors have ignored *C. ventricosus* Silva Manso and equated the homotypic names that followed it with *Operculina*, but this was purely speculative: Austin and Huamán (1996) equated both *I. silvana* and *I. ventricosa* Stellfeld with *O. turpethum* var. *ventricosa*; Flora do Brasil (2020) reduced *I. silvana* to synonymy under *O. turpethum*. Unless some original material is discovered for *C. ventricosus* Silva Manso, this name will likely remain ambiguous and unresolved.

Operculina leptoptera Urb., Symb. Antill. 3: 342. 1902. TYPE: Martinique. Hauteurs des Trois Islets, *Père Duss 426* (holotype, B†; isotypes, not found in A, B, F, GH, LE, MO, NY, P, US).

This species is an enigma. Powell (1979: 245) condensed Urban's detailed description and pointed out that nothing matching this description had ever been collected again on Martinique; she nonetheless accepted the species as did Powell and Staples (1989). The type specimen in the Berlin herbarium was likely destroyed, and there is no image of it preserved in the Field Museum images for Berlin type specimens (Field Museum Berlin Negatives, 2019). We have not located any duplicates in other herbaria—although specimens collected by Duss were often deposited in several institutions, that does not seem to be the case with his number 426.

To be sure, Urban's protologue mentions several characters that suggest a placement in *Operculina*: "ramis ca. 1 mm late membranaceo-alatis … antherae … demum contortae; pollinis granula laevia, plicis 3 munita." However, these details aside, the rest of his description and diagnosis are entirely compatible with one of the *Ipomoea* species from the West Indies having violet flowers, such as *I. philomega* (Vell.) House or *I. setifera* Poir. Austin, before his death, and Staples, had doubts about the generic placement for this species, and so it remains here with other insufficiently known taxa. More than a century has elapsed since Duss collected the type gathering on Martinique; the odds this species survives there seem slim.

Excluded Species

Operculina aegyptia (L.) House, Bull. Torrey Bot. Club 33: 502. 1906. ≡ **Distimake aegyptius** (L.) A. R. Simões & Staples

Operculina aurea (Kellogg) House, Muhlenbergia 5: 68. 1909. ≡ **Distimake aureus** (Kellogg) A. R. Simões & Staples

Operculina bufalina (Lour.) Hallier f., Meded. Rijks-Herb. 1: 26. 1911 [title page 1910], nom. inval. ≡ *Convolvulus bufalinus* Lour., Fl. Cochinch.: 109. 1790. ≡ *Ipomoea bufalina* (Lour.) Choisy, Mém. Soc. Phys. Genève 6: 452 [Conv. Orient. 70]. 1834. ≡ *Nemanthera bufalina* (Lour.) Raf., Fl. Tellur. 4: 80. 1838. ≡ *Merremia bufalina* (Lour.) Merr. & Rolfe, Philipp. J. Sci., C 3: 122. 1908.

The basionym of this block of names, *Convolvulus bufalinus* Lour., has been proposed for rejection on the grounds that no original material has been located from which a lectotype could be chosen and furthermore that the epithet has been confusingly applied in multiple genera. See Staples et al. (2017) for details.

Operculina coptica (L.) House, Bull. Torrey Bot. Club 33: 500. 1906. ≡ **Ipomoea coptica** (L.) Roth ex Roem. & Schult.

Operculina discoidesperma (Donn. Sm.) House, Muhlenbergia 5: 68. 1909. ≡ **Merremia discoidesperma** (Donn. Sm.) O'Donell

Operculina dissecta (Jacq.) House, Bull. Torrey Bot. Club 33: 500. 1906. ≡ **Distimake dissectus** (Jacq.) A. R. Simões & Staples

Operculina flammea (Nees) Meisn. in Mart., Fl. Bras. 7: 212. 1869. = **Distimake igneus** (Schrad.) A. R. Simões & Staples

Operculina grandiflora sensu House, Muhlenbergia 5: 69. 1909. = **Ipomoea violacea** L., p.p., and **Operculina ventricosa** (Bertero) Peter, p.p.—see Powell et al. (1978: 199–202) for details.

Operculina hirsuta Standl., J. Wash. Acad. Sci. 14: 242. 1924. = **Ipomoea clavata** (G. Don) Ooststr. ex J. F. Macbr.

Operculina kentrocaulos (C. B. Clarke) Hallier f., Bot. Jahrb. Syst. 16: 550. 1893. ≡ **Distimake kentrocaulos** (C. B. Clarke) A. R. Simões & Staples

Operculina palmeri (S. Watson) House, Bull. Torrey Bot. Club 33: 502. 1906. ≡ **Distimake palmeri** (S. Watson) A. R. Simões & Staples

Operculina passifloroides (Benth. ex Meisn.) Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 474. 1932. = **Maripa violacea** (Aubl.) Ooststr. ex Lanj. & Uittien

Operculina pavonii Hallier f., Bot. Jahrb. Syst. 16: 550. 1893. ≡ **Merremia pavonii** (Hallier f.) D. F. Austin & Staples

Operculina peltata (L.) Hallier f., Bot. Jahrb. Syst. 16: 549. 1893. ≡ **Decalobanthus peltatus** (L.) A. R. Simões & Staples

Operculina platyphylla (Fernald) House, Bull. Torrey Bot. Club 33: 502. 1906. ≡ **Merremia platyphylla** (Fernald) O'Donell

Operculina populifolia Hallier f. ex Urb., Symb. Antill. 7: 342. 1912. = **Merremia discoidesperma** (Donn. Sm.) O'Donell

O'Donell (1941: 495) pointed out when making the combination in *Merremia* that *Operculina populifolia* is a mixed concept: *Wright 3083* (syntype) is a mixture of two species mounted together. The other syntype, *Christ 2176*, has not been found and was likely destroyed at Berlin, where Urban worked while writing his *Symbolae Antillanae*; there is no image for *Christ 2176* in the Field Museum Berlin Negatives (2019). Gunn (1977: 250) discussed the problem of two species mounted together on the syntypes he studied in GH and MO, but without proposing a lectotype to resolve the ambiguity. Since the reduction to synonymy has already been made by O'Donell it remains now to choose a lectotype so that the nomenclature is stabilized.

We here designate as lectotype for *Operculina populifolia* the duplicate of *Wright 3083* (MO! [barcode] MO-150302): it has been cut up and remounted so that all the material now on the sheet is *Merremia discoidesperma*; furthermore, the MO sheet bears the handwritten annotation of Hallier himself (1909) as *O. populifolia* as well as of O'Donell (Aug. 1949) as *M. discoidesperma*. Other duplicates of *Wright 3083* that we have found (GH!, NY!) are mixtures of two species on the same sheet, which could lead to confusion in interpreting the concept: we exclude them as unsuitable choices and they are not to be considered isolectotypes for that reason. The second species mounted on these sheets is *O. hamiltonii*.

Operculina tuberosa (L.) Meisn. in Mart., Fl. Bras. 7: 212. 1869. ≡ **Distimake tuberosus** (L.) A. R. Simões & Staples

Operculina violacea (Aubl.) Barb. Rodr., Vellosia, ed. 2, 1: 60, pl. 16. 1891. ≡ **Maripa violacea** (Aubl.) Ooststr. ex Lanj. & Uittien.

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Appendix 1. Index of numbered collections examined.

This index includes a list of taxa and all numbered collections examined for the monograph, whether cited in the text or not; unnumbered collections, "s.n.," are not included. Only the first collector name is mentioned; these are arranged in alphabetical order by surname, initials, then sequentially by collector number (roman font). Types have been indicated in parentheses ("type") where applicable, followed by taxon number used in the treatment.

1. *Operculina aequisepala* (Domin) R. W. Johnson
2. *Operculina codonantha* (Benth.) Hallier f.
3. *Operculina hamiltonii* (G. Don) D. F. Austin & Staples
3b. *Operculina hamiltonii* var. *mucronata* D. F. Austin & Staples
4. *Operculina macrocarpa* (L.) Urb.
5. *Operculina maypurensis* (Hallier f.) A. R. Simões & Staples
6. *Operculina petaloidea* (Choisy) Ooststr.
7. *Operculina pinnatifida* (Kunth) O'Donell
8. *Operculina polynesica* Staples
9. *Operculina pteripes* (G. Don) O'Donell
10. *Operculina riedeliana* (Oliv.) Ooststr.
11. *Operculina sericantha* (Miq.) Ooststr.
12. *Operculina turpethum* (L.) Silva Manso
13. *Operculina ventricosa* (Bertero) Peter
14. *Operculina turpethum* (L.) Silva Manso × *O. ventricosa* (Bertero) Peter

Aban Gibot SAN-95400 (10); Abbott, R. Q. 435 (9); Acevedo-Rodríguez, P. 3334 (11); Ahern's collector FB1999 (12); Alexandre, D. Y. 488 (3); Allen, C. 767 (3), 770 (9); Allen, P. H. 1011 (9); Almeida, J. C. de INPA909 (3); Alston 6031 (3); Alvins, V. M. 1181 (10); Amaral-Santos, A. 1230 (9); Amin, A. A. S. SAN-114994 (12); Anderson, E. F. 4165 (12); Anderson, W. R. 7008 (3), 9106 (4); Aona, L. Y. S. 3885 (4); Aplin, T. E. H. 4734 (1); Aristeguieta 5193, 6787 (9); Arnoldo, Fr. 361, 3168 (13); Asplund, E. 5192, 15763 (2); Austin, D. F. 4237 (3); 5018, 5037 (7); 6032 (3); 6155A (12); 6948, 6968 (3); 7299 (11); 7832 (9).

B. G. O. staff 8385 (12); Bacon, P. H-1145/81 (10); Bailey, F. M. 87 (2); Baker, C. F. 36 (9); Balansa, B. 544 (13), 810 (12), 1670 (14), 3352 (13), 3549 (12); Balansa, N. 3350 (2); Balderrama, J. 551 (3); Balgooy, M. M. J. van 1331 (2), 1432 (1); Balick, M. J. 1524 (9); Barbon, E. B. PPI-1616 (12); Barker, E. E. 27 (13); Barkley 2636, 17-M-131 (7); Barnes 229 (9); Bartlett 8579 (3), 10837 (7); Batianoff, G. N. 11432 (12); Bäuerlen, W. 33 (2); Beard, J. S. 7005 (2); Beddome, R. H. 5601, 5602 (6); Bedi, S. J. 1965 (6); Benzon, E. E. 144-3803 (13); Berhaman Ahmad SAN-133154 (12); Bermejos, J. BS-298 (12); Beusekom, C. F. van 4708 (12); Bierens du Haan 125, 126 (4); Biju, S. D. 42121 (13); Blum, K. E. 2048, 2068 (3); Blume, L. 1219 (type 12); Boivin, L. H. 1247bis, 2097, 3240 (12); Boldingh, I. 1243 (13); Bon, H. F. 1718, 1841, 5265 (12); Bonham, L. D. 2 (13); Boo 409 (10); Bosser, F. 3468 (12); Branch, L. C. 153 (3); Brass, L. J. 7719 (10); 8317 (14); 18934, 21813 (12); 24292 (10); Breedlove, D. E. 13504, 19842, 20403, 20713 (9); 24623 (7); 28344 (9); Brenes, A. M. herbarium 14317, 14347, 14641, 17206 (9); Bristol, M. L. 2331 (14); Britton, N. L. 1660 (13); Broadway, W. E. 4801 (3); Brock, J. 532 (2): Brown, R. Iter Austr. 2742 (2), It. Austr. 2745 (12); Bryan Jr., E. H. 241, 483 (12); Buelow, G. P. 1105 (12); 2585, 3093 (8); Bult, M. van de 845 (6); Bunchuai, K. 61 (12); Bunting, G. S. 4620 (3); Burchell 4033 (4); Buril, M. T. 237 (4); Burkill, I. H. 3041 (12); Butaud, J. F. 494 (12); 706, 775, 1152, 1506 (8); 1573, 1575, 1582 (2); 1912, 2109, 2152, 2300, 2320, 2496 (8); 2782 (12); 3177 (2); Byrnes, N. NB1428 (1).

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