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Oparanthus (Asteraceae, Subtribe Coreopsidinae) Revisited

ROBYNN K. SHANNON AND WARREN L. WAGNER¹

ABSTRACT

A revised circumscription of the French Polynesian genus *Oparanthus* (Asteraceae, Heliantheae, Coreopsidinae) is presented, with illustrations and complete descriptions of all species. In this classification four species are included, two from the Marquesas Islands and two from the island of Rapa. Recognition of *Oparanthus* as a genus, rather than including it in *Bidens*, is merited on the basis of a suite of floral characters not found together in any species of *Bidens sensu stricto* (pistillate ray florets, functionally staminate disk florets, and disk florets always with four corolla lobes) as well as two vegetative characters that are uncommon in *Bidens* (simple leaves and shrubby or arborescent habit). Two new combinations are made, transferring *Bidens hivoana* O. Deg. & Sherff and *Bidens teikiteetini* Florence & Stuessy to *Oparanthus*, and a new section is described. The two sections are distinguished mainly on the basis of different corolla colors, striking differences in leaf thickness, and differences in the involucre and ray achenes; these characters correlate exactly with geographic distribution, *O. sect. Albiflori* being endemic to the Marquesas Islands and *O. sect. Oparanthus* being endemic to Rapa. Previous taxonomic, systematic, and anatomical research on these species is reviewed, and possible relationships within the subtribe are discussed.

“I THINK THIS IS *OPARANTHUS*”

—annotation by F. R. Fosberg
on a sheet of *O. hivoanus*

INTRODUCTION

There has been considerable confusion surrounding the French Polynesian endemic genus *Oparanthus* Sherff, (Asteraceae, tribe Heliantheae, subtribe Coreopsidinae), much of it centered on the relationship of *Oparanthus* to *Bidens* L. For example, the two Marquesan species included in *Oparanthus* in the present treatment were originally described as species of *Bidens* (*B. hivoana* O. Deg. & Sherff and *B. teikiteetini* Florence & Stuessy), and a year after *B. hivoana* was described, the type of that species was cited in the description of *Chrysogonum album* F. Br. (a species later transferred to the new genus *Oparanthus* by Sherff)!

In this revision, the genus *Oparanthus* includes four species, two (and a putative interspecific hybrid) endemic to the island of Rapa in the Austral (Tubuai) Islands and two endemic to the Marquesas Islands. These four species are possibly closely related to *Bidens* (Ryding & Bremer, 1992), but clearly exhibit several distinctive features not found in *Bidens sensu stricto* and should be referred to a separate genus.

In this paper, one of a series presenting preliminary research for a flora of the Marquesas Islands, we provide a thorough taxonomic revision of *Oparanthus*,

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including nomenclature and descriptions of all taxa. The revised taxonomy and descriptions are based on an examination of all available herbarium collections and considerably more field data than were available when the group was previously revised (Sherff, 1937a; Stuessy, 1977a). Preceding the taxonomic treatment is a section reviewing previous taxonomic work on the group and one addressing relationships between *Oparanthus* and other genera of the Coreopsidinae, particularly *Fitchia* Hook. f. (also Polynesian), *Petrobium* R. Br. (endemic to the South Atlantic island of St. Helena), and the nearly cosmopolitan *Bidens* (the former two considered with *Oparanthus* to form a monophyletic subgroup in the cladistic sense by Ryding and Bremer, 1992). The section on relationships includes a review of Carlquist's (1957) anatomical work on *Oparanthus*.

TAXONOMIC HISTORY

The four species referred to *Oparanthus* in the present treatment do not share a common taxonomic history. The first to be described was *Bidens hivoana*, from the Marquesas Islands, by Sherff in 1934. In 1935, Brown described *Chrysogonum* section *Quadrimeria*, in which he included *C. rapense* and *C. coriaceum*, both from Rapa, and *C. album* from the Marquesas Islands, distinguished within the genus by "(1) their woody stems, (2) the 4-merous disc-florets. . . ." Sherff (1937a) later elevated Brown's section *Quadrimeria* to generic status as *Oparanthus* (without any comment on his reasons for doing so), and in the same publication described *O. intermedius* from Rapa. *Oparanthus* was revised by Stuessy (1977a) as a genus of two species endemic to Rapa (with *O. intermedius* treated as a hybrid), which he later submerged into *Bidens* (Stuessy, 1988), based mostly on their similarity to *B. hivoana* of the Marquesas Islands. Other than this placement in *Bidens* by Stuessy, treatments of Coreopsidinae have recognized *Oparanthus* as distinct (Carlquist, 1957; Robinson, 1981; Mabberley, 1987; Ryding & Bremer, 1992; Karis & Ryding, 1994). Following Stuessy's (1988) classification, Florence and Stuessy (1988) described *B. teikiteetini* from the Marquesas Islands.

Stuessy's classification (1988) submerging *Oparanthus* into *Bidens* is based largely, though not solely, on the similarity between the Rapan species of *Oparanthus* and *Bidens hivoana*. In discussion of his Table I he stated that "all the other character states [besides entire leaves in *Oparanthus*] regarded initially as unique . . . are also found in at least one other species of *Bidens*," that species, at least in the case of floral sexuality (a character which Stuessy recognized as being significant "for revealing relationships"), being *B. hivoana* (Stuessy, 1988). Stuessy's recognition that *O. coriaceus* and *O. rapensis* were closely related to *B. hivoana*, ("*Bidens hivoana* provides a strong link between the two genera") led him to submerge *Oparanthus* into *Bidens*. The same recognition of a close relationship between the three species led us to acknowledge another possibility: that *B. hivoana* had been incorrectly placed in *Bidens* by Sherff (1934), based on a single specimen, before *Oparanthus* or even *Chrysogonum* sect. *Quadrimeria* had been described. In fact, when Brown described *C. album* he included in it the type specimen of *B. hivoana*!

The difficulty in understanding the relationship of *Bidens hivoana* to *Oparan-*

thus is greater because of confusion over the type specimen of *B. hivoana* (Adams & Mumford 469). Brown (1935) cited Mumford & Adams 469 (BISH, undoubtedly the same collection, even though the collectors names are reversed) as a paratype of his new species *Chrysogonum album*. It is clear that Brown was aware of the publication of *B. hivoana*, although it was published just a year earlier, because in the same publication in which he cited Mumford & Adams 469 as a paratype of *C. album*, he synonymized *B. hivoana* with *Campylotheca henryi* (Sherff) F. Br., again citing Mumford & Adams 469. Sherff transferred *Chrysogonum album*, almost without comment, to *Oparanthus* when he described the genus, apparently not realizing that Brown's name was illegitimate. Stuessy (1977a) claimed that the confusion of Brown, and particularly of Sherff, over this collection "suggests a strong connection between the two genera" (*Bidens* and *Oparanthus*). It seems that confusion over the type of *B. hivoana* suggests not a strong connection between the two genera, but rather that Sherff and Brown simply erred. Brown (1935) synonymized *B. hivoana* based on Sherff's description alone, which did not include key characters of *Oparanthus*; he never saw the holotype and apparently did not connect it with the BISH sheet of the same collection that he cited under *Chrysogonum album*, especially since the collectors' names were in the reverse order on the BISH sheet. Sherff must not have realized that Brown had cited the type of *B. hivoana* as a paratype of *Chrysogonum album*. It is clear, however, that he thought *Oparanthus* should be retained as a distinct genus, as he published a monograph on *Bidens* the same year he published *Oparanthus*.

It is unclear which characters of *Oparanthus* (and *Petrobium*) Stuessy (1977a, b) considered important and meaningful for determining relationships, and which he considered merely as adaptations to island habitats. In his review of the Heliantheae (1977b) he grouped *Oparanthus* and *Petrobium* informally within the subtribe Coreopsidinae, presenting the following as "changes that can occur in island habitats: entire leaves; 4-merous disk florets; a tendency toward weakly connate anthers; and the acquisition of a shrubby habit." It is not clear why Stuessy associated 4-merous disk florets, a character he cited earlier (Stuessy, 1977a) as significant for revealing relationships, with adaptation to island habitats; among the possible adaptive advantages to be gained by the change from a 5-merous to a 4-merous condition given by Gardner (1977) there is no mention of island habitats. The acquisition of a shrubby habit is more convincing. Carlquist (1965, 1974) has discussed in detail the phenomenon of insular woodiness, citing numerous examples including *Oparanthus*. While it is true that some *Bidens* have acquired a woody habit (most notably *B. hendersonensis* Sherff from Henderson Island and Oeno Island in the Pitcairn group, and *B. menziesii* (A. Gray) Sherff from the Hawaiian Islands, arborescent shrubs up to 4 m high with basal stem diameter reaching about 3 cm), we know of no *Bidens* that displays the degree of arborescence found in *Oparanthus* and *Petrobium*; *Oparanthus teikiteetini* is known to reach a height of 12 m and a diameter of 35 cm (Florence & Stuessy, 1988), and *O. rapensis* has been known to be used for firewood (Stokes & Brown 76, BISH) and posts for house construction (Stokes & Brown 60, BISH), while *Petrobium* has been reported to reach heights of nearly 7 m (Carlquist, 1965).

Stuessy (1988: 196) seems to have been less than convinced of his own classification. He stated that "the morphological differences separating *Oparanthus* and *Petrobium* are greater than those uniting them," yet submerged both into *Bidens*.

We agree with Ryding and Bremer (1992) and Karis and Ryding (1994), contrary to Carlquist (1995), that further expansion of the large, probably paraphyletic, genus *Bidens* will only obscure the phylogeny of the Coreopsidinae, and that the most appropriate approach is to retain smaller, clearly monophyletic groups such as *Oparanthus* and *Petrobium* as separate genera.

The four species here referred to *Oparanthus* all have the following suite of characters that distinguishes them from *Bidens* (*Oparanthus* characters listed first): ray florets pistillate vs. sterile; disk florets functionally staminate vs. hermaphroditic or pistillate; disk florets with four corolla lobes exclusively vs. five, rarely three or four; leaves simple vs. compound, lobed, or occasionally simple; and shrubs or trees vs. herbs or rarely shrubs. *Bidens* is a large genus, and exceptions to all of the characters listed above have been reported (e.g., Sherff, 1937b; Karis & Ryding, 1994; Mesfin Tadesse & D. Crawford, unpubl.); however, we are not aware of any species of *Bidens* that have all of the characters listed above for *Oparanthus*. Additionally, Mesfin Tadesse and D. Crawford (unpubl.) have brought to our attention that the lamina to tube ratio in ray florets is 0.4–0.9 in *Oparanthus* vs. 2.0–10.0 in *Bidens*; the lobe to tube ratio in disk florets is 0.5–1.2 in *Oparanthus* vs. 0.01–0.10 in *Bidens*; *Oparanthus* has graded monomorphic involucre bracts whereas *Bidens* has dimorphic involucre bracts; and style branches in *Oparanthus* are underdeveloped or not well developed whereas they are well developed with distinct stigmatic surfaces in *Bidens*.

Among the characters separating *Oparanthus* from *Bidens*, sex of florets and exclusively 4-lobed disk florets seem to be the most important. We know of no species of *Bidens* that is monoecious (F. Ganders, pers. comm.), although a few are gynodioecious (Mesfin Tadesse and D. Crawford, pers. comm.). The issue of 4-lobed disk corollas is a bit more problematic. F. Ganders (pers. comm.) has not found 4-lobed disk corollas in Hawaiian species of *Bidens*, except for obvious deformities or developmental abnormalities. Stuessy (1988) reported 3–5 corolla lobes for *B. hawaiiensis* and 4–5 for *B. hendersonensis* from specimens at F; we found only 5-lobed disk florets upon careful examination of specimens of these taxa at US. Sherff (1937b) reported that several North American species of *Bidens* have 4-lobed disk corollas, with which Mesfin Tadesse and D. Crawford (unpubl.) concur. The latter researchers, however, point out that 4-lobed disk corollas is not a consistent feature in any species of *Bidens*. In contrast, we have not seen any specimen of *Oparanthus* that had disk corollas with other than four lobes. Brown's (1935) original sectional name *Quadrimeria* reflects the significance of 4-merous disk florets, and Stuessy (1988) recognized that 4-merous corollas are "of significance for revealing relationships." Gardner (1977) showed that the 4-merous condition, widespread in the Asteraceae, is useful in both descriptive taxonomy and in determining phylogenetic relationships. According to Mesfin Tadesse and D. Crawford (unpubl.), the 4-merous condition, where present in *Bidens*, seems

to follow a reduction series apparently controlled by a single gene locus or a few loci, accentuated by changes in microenvironmental features.

RELATIONSHIPS

The phylogenetic analyses of the Coreopsideae by Ryding and Bremer (1992) suggest division of the tribe into three possibly monophyletic groups, which were treated as subtribes by Ryding and Bremer, but as merely informal generic groups by Karis and Ryding (1994). The one including *Oparanthus* is in their view a well-supported clade that also includes *Fitchia*, *Petrobium*, *Moonia* Arn., and *Hidalgoa* La Llave & Lex. In Ryding and Bremer's preferred hypothesis, *Bidens* is the sister taxon to this clade. Based on this cladistic assessment, the placement of both *Oparanthus* and *Petrobium* into *Bidens* (as by Stuessy, 1988) would require including the other three genera of this clade as well. Expanding *Bidens* by submerging the five genera listed above seems ill-advised, even when one only considers the differences between *Bidens*, *Oparanthus*, and *Petrobium*. The characters separating *Oparanthus* from *Bidens* are given in the previous section; *Petrobium* segregates from *Bidens* on the basis of its being entirely discoid and having consistently 4-merous florets and a dioecious breeding system.

Ryding and Bremer's (1992) conclusions concerning relationships within the Coreopsideae should be viewed with some caution because their data are insufficient to support them. There is a fundamental problem with the Ryding and Bremer assessment, the more serious aspect of which is the large amount of missing data. This is a problem throughout the data matrix. Largely as a result of missing data for the other taxa, the more anatomically studied *Oparanthus*, *Fitchia* (both from Polynesia), *Petrobium* (South Atlantic), *Moonia* (southern Asia), and *Hidalgoa* (neotropics) fall together in a single clade. For example, the two unique synapomorphies (achenes with 8 or more wall bundles and achenes with secretory canals) and one homoplasious synapomorphy (ovules with one trace) that unite the members of this clade do so because these taxa are the only ones in which the characters have been assessed (19 of 26 taxa unknown). The characters that unite *Petrobium*, *Fitchia*, and *Oparanthus* are likewise unknown for nearly half of the taxa in the data matrix. Overall, many of the characters used by Ryding & Bremer are known from only a few taxa, or the character is variable in several of the taxa studied. Therefore, we must conclude that the relationships of this clade are imperfectly known at best, and can be elucidated only after detailed examination of other genera, especially for anatomical characters.

Oparanthus and *Fitchia* are most likely sister taxa, as they share a number of unique traits within the subtribe as discussed by Carlquist (1957). Other investigators (Robinson, 1981; Ryding & Bremer, 1992) have accepted these two genera along with *Petrobium* as forming a monophyletic group based on the shared simple leaves, shrubby to arborescent habit, and three floral anatomical characters from Carlquist's 1957 study (disk florets with partial or complete median bundles, two secretory canals beside corolla veins, and style branches with the entire surface stigmatic). Carlquist (1957), in his detailed studies of the genus *Fitchia*, compared it to several other genera including *Oparanthus*, and noted several char-

acters that suggest a close relationship between *Oparanthus*, *Fitchia*, and *Petrobium*. In fact, he called the anatomical resemblances among the three genera "quite striking." For example, fusion of vascular bundles at the corolla lobe tips does not occur in either *Oparanthus* or *Fitchia*, in contrast to the great majority of Asteraceae known in this respect. *Oparanthus* is one of only a few genera showing appreciable similarity to the elaborate venation and secretory canal pattern observed by Carlquist in the flowers of *Fitchia* (*Petrobium* being another). At least in *O. rapensis*, the pattern of secretory canals in both the ray and disk corollas (described in detail by Carlquist, 1957) is remarkably similar to that in both *Fitchia* and *Petrobium*. This feature is unknown elsewhere in the tribe, except in *Bidens cosmoides* (A. Gray) Sherff of the Hawaiian Islands (Carlquist, 1957), in which it is apparently independently derived. Other similarities that Carlquist (1957) found between *Oparanthus* and *Fitchia* (and *Petrobium* as well) are the relatively thick corolla, which is nowhere fewer than four cells thick (in contrast to other genera Carlquist examined), and the anatomy of the achene and awn trichomes, which differ markedly from those characteristic of the Asteraceae as a whole. Carlquist also showed that the vascular bundles of the achenes are similar, especially the presence of a pair of prominent marginal bundles, in *Oparanthus* and *Fitchia*. The similarity also extends to the presence of secretory canals in the achene awns of *O. rapensis*, *Fitchia*, and *Petrobium*. Carlquist (1957) pointed out that the involucre bracts of the smaller-flowered species of *Fitchia* are similar to those of both *Petrobium* and *Oparanthus*.

Despite the apparently close relationship between *Fitchia* and *Oparanthus*, *Fitchia* is highly specialized in a number of features relating primarily to a shift to bird pollination. These features include large heads, hermaphroditic florets, morphologically ligulate corollas, and a number of anatomical features detailed by Carlquist (1957). These characters are so distinctive that proper placement of *Fitchia* within the Asteraceae was problematic prior to Carlquist's monograph, and though now included in the subtribe Coreopsidinae (Karis & Ryding, 1994), it had been placed in its own subtribe by earlier researchers (Carlquist, 1957; Stuessy, 1977b), reflecting the difficulty in aligning it with other taxa.

Carlquist (1957) also recorded observations on the ray florets of *Oparanthus*, even though these are not directly comparable to florets of the morphologically ligulate *Fitchia*. Ray florets of *Oparanthus hivoanus* tend to have more bundles in both the corolla and the style than those of *O. rapensis*. The presence of four or five bundles in the style of *O. hivoanus* ray florets compared to only two in the style of the disk florets may reflect the sterile nature of the latter.

Among vegetative features of *Oparanthus*, Carlquist (1957) described leaf anatomy in the most detail, and commented on the differences between the Rapan species and *O. hivoanus*. The differentiation of the leaf margin, particularly the notably large marginal vein and the presence of secretory canals which are not related to specific poles of a vein, he claimed to be characteristic of the genus, but noted that the differentiation was most prominent in the highly derived *O. coriaceus*. Since *O. teikiteetini* was not described when Carlquist did his anatomical work, it is not known whether it shares the leaf margin features of the other species. Morphologically, there appears to be a progression from the strongly

differentiated margin of *O. coriaceus* through *O. rapensis* and *O. hivoanus* to the seemingly undifferentiated margin of *O. teikiteetini*. The large, simple, decussate, petiolate leaves in *Oparanthus* and *Fitchia* are very similar to each other in gross morphology and anatomy.

Carlquist (1957) examined several other genera of Heliantheae in conjunction with his more detailed studies of *Fitchia*, *Oparanthus*, and *Petrobium*. The data summarized above suggest a close relationship between *Oparanthus* and *Fitchia*, but more data are needed before any satisfactory conclusion can be reached about how closely they are related to *Petrobium*, or how closely related *Bidens* is to any of these three genera. Many more species representing a fuller diversity of taxa in the Coreopsidinae need to be examined in order to make a viable phylogenetic assessment based on these anatomical characters. Cytology of *Oparanthus* and *Petrobium* would almost certainly add to our understanding of the relationships between these three genera, as chromosome numbers are known for *Fitchia* and are anomalous within the subtribe (Stuessy, 1977b).

The present revision includes the Marquesan species originally described as *Bidens hivoana* and *B. teikiteetini*, and the Rapan species *Oparanthus rapensis* and *O. coriaceus*, all within the genus *Oparanthus*. Plants originally referred to *O. intermedius* are treated as interspecific hybrids between the two Rapan species, as first suggested by Stuessy (1977a). We have divided *Oparanthus* into two sections, based on geography and morphology, including both vegetative and floral features.

Although division into sections may at first appear unnecessary in such a small genus, it is warranted by the extent of morphological variation between the Rapan and the Marquesan species. This variation is not surprising given the geological history of the Austral-Cook and Marquesan archipelagoes. Though Rapa, at ca. 4.1–4.8 My (Diraison, 1991), is not much older than Nuku Hiva, at 3.1–4.8 My (Brousse et al., 1990), the former is one of the youngest of the Austral Islands, whereas the latter is one of the oldest of the Marquesas Islands. The oldest of the Austral-Cook island chain, Mangaia, is more than 17–19.4 My (Turner & Jarrard, 1982), making it possible for an endemic species on Rapa to be the product of a much older lineage within the archipelago than an endemic species in the Marquesas Islands, where the oldest islands (Eiao and Hatutu) are 5–6 My old (Brousse et al., 1990). The establishment of *Oparanthus* in the Marquesas Islands is therefore almost certainly more recent than on Rapa. Not only is Rapa older than Hiva Oa and Nuku Hiva, but, according to Paulay's (1985) analysis of the weevil genus *Miocalles* on Rapa, *Oparanthus* has been on Rapa longer than most other flowering plant genera. Paulay claims that host plants that have been on Rapa the longest have the highest diversity of host-specific weevils, and only one other genus, *Coprosmia*, has as many species of host-specific weevils as *Oparanthus*. Research on both plants and animals in the Hawaiian Islands (Wagner & Funk, 1995) has shown that early-evolved species of older lineages often show more specializations than those of younger lineages, and this certainly appears to be the case in *Oparanthus*. For example, entire leaf margins and thick, coriaceous leaves, which can be seen as tendencies in the Marquesan species, are much more extreme in the Rapan species. Carlquist investigated the differences in leaves

between the two sections at the anatomical level and found that *O. coriaceus* and *O. rapensis* have a greater development of the bundle sheath extension, the secretory canals, where present, being within these structures; they have thicker mesophyll, at least one layer of which is differentiated as a hypodermis; and they lack the abundant development of diffuse sclerids seen in *O. hivoanus*. An interesting collection of an entire juvenile plant of *O. rapensis* (Paulay 78, US) has leaves with a striking similarity to leaves of *O. hivoanus*, perhaps an example of ontogeny recapitulating phylogeny.

Paulay (1985) suggests a scenario in which *Bidens*, or a *Bidens*-like ancestor, colonized Rapa (or perhaps an older island of the Austral-Cook archipelago), and diverged evolutionarily to become *Oparanthus*, which later migrated to the Marquesas Islands. Although various *Bidens* species are found throughout the Pacific, many of them endemic, there are presently none on Rapa, except for the cosmopolitan and recently-introduced *B. pilosa* L. (Paulay, 1985). None of the Pacific island species of *Bidens* appear to be closely related to *Oparanthus*. Nor does this hypothesis account for the presumed close relationship of *Oparanthus* to *Petrobium* or *Fitchia*. Carlquist (1957) suggested a common origin for all three genera. If that is the case, the establishment of the group in southeastern Polynesia was probably early in the differentiation of the tribe Heliantheae, and the common ancestor to *Oparanthus*, *Petrobium*, and *Fitchia* must have had a much wider distribution in Africa and/or Asia. More recently, Carlquist (1974: 417, 450) has stated that the South Atlantic *Petrobium* and the Polynesian lineage which gave rise to both *Oparanthus* and *Fitchia* were presumably independently derived from a *Bidens*-like ancestor, a hypothesis with which we agree.

Within *Oparanthus*, the same type of divergence appears to have occurred in each of the two sections: *O. teikiteetini* (*O. sect. Albiflori*) and *O. rapensis* (*O. sect. Oparanthus*) are both trees of wet forests, whereas *O. hivoanus* (*O. sect. Albiflori*) and *O. coriaceus* (*O. sect. Oparanthus*) are both shrubs of more exposed habitats in or approaching the cloud zone. Within each section, the relative thickness of the leaves of each species corresponds to this ecological pattern, with the species having thinner, less coriaceous leaves occurring in wet forest. It is not clear what habitat the ancestor of *Oparanthus* occurred in, but perhaps it was a shrub or small tree of the wet forest. If so, divergence would have occurred as some individuals became more adapted to windy ridge habitats and others even better adapted to the less exposed wet forests. There also seems to be a trend toward simpler capitulescences in each section.

In *Oparanthus sect. Albiflori*, speciation seems to have occurred with an ecological shift coupled with interisland colonization. The Rapan species, however, coexist on a small island but have differentiated from each other ecologically. It is conceivable that one or both of the Rapan species originally evolved on another (older) island of the Austral group followed by colonization to Rapa, and were maintained on Rapa by ecological separation, with only infrequent hybrids being formed. The evolution of *O. sect. Oparanthus* has involved changes in the capitulescence. Capitulescences of *O. rapensis* have numerous smaller capitula, whereas those of *O. coriaceus* have fewer, larger, capitula more densely arranged. In *O. coriaceus* there are usually three capitula in a tight cluster that appears like

one larger, irregular, compound capitulum, or sometimes this is apparently reduced to only one large capitulum.

TAXONOMIC TREATMENT

Oparanthus Sherff, Occas. Pap. Bernice P. Bishop Mus. **12**(19): 9. 1937. *Chryso gonum* L. sect. *Quadrimeria* F. Br., Bernice P. Bishop Mus. Bull. **130**: 341. 1935. LECTOTYPE: *O. rapensis* (F. Br.) Sherff, designated by Stuessy, Fieldiana Bot. **38**: 65. 1977.

Functionally monoecious shrubs or small trees up to 12 m, wood fibrous, at least in young stems. Leaves simple, decussate, thin and relatively brittle when dry to extremely thick and tough, petiolate; petioles narrowly conduplicate, the basal end flared, the bases sheathing. Capitulescences erect, terminal, cymose, the branches lignified, compressed, ridged and angled, persisting after achenes are shed, the lowermost disintegrating and the capitulescence becoming pendent, capitula in groups of 3 or, less often, in groups of 2 or solitary. Involucre campanulate to abruptly campanulate, the bracts in 1 irregular series or in 2–3 series, coriaceous. Receptacle convex; receptacular bracts coriaceous, apex acute or obtuse, upper margin and apex entire or weakly erose, those of ray florets oblong or occasionally slightly enlarged apically, those of disk florets linear, abruptly angled at 60° near apex and enlarged and cupped above this point, partially surrounding the floret. Ray florets pistillate, the lamina 3-, rarely 2- or 4-lobed or toothed, white or yellow; stigma bifid and recurved, entire surface receptive. Disk florets functionally male (ovule does not form, only a vestigial vascular trace forms), 4-merous; corolla white or yellow; anthers linear, black, coherent, apex triangular, base weakly sagittate; stigma linear or slightly clavate, bifid but branches not developing and not separating or separating only slightly, stigmatic hairs poorly differentiated and stigmatoid tissue lacking (at least in *O. rapensis*). Ray achenes lignified, obcompressed, elliptic to narrowly elliptic, with two prominent marginal vascular bundles, narrowly winged on one or both margins, the wings extending above the achene apex as a stout short or elongate awn, median achene veins sometimes extending above achene apex as linear awns. Disk achenes sterile, linear, with 1–2 readily deciduous linear awns.

A genus of four species in southeastern French Polynesia with two species in the Marquesas Islands (*Oparanthus* sect. *Albiflori*) and two on Rapa in the Austral Islands (*O.* sect. *Oparanthus*). All species occur in mesic to wet forests; two occur in windy sites in or approaching the cloud zone.

In the following descriptions, measurements are given for the corollas of the disk florets that represent the entire length of the corolla from the base of the tube to the base of the lobes. Because the term “tube” generally refers to that part of the corolla below the insertion point of the stamens, and the term “throat” generally refers to the part between the insertion point of the stamens and the base of the lobes, the length measurements given are for the combined tube and throat.

KEY TO SECTIONS AND SPECIES OF *OPARANTHUS*

- Leaves thin to only slightly thickened, relatively brittle at least when dry; involuclral bracts in 2–3 well-defined series; florets white; achene awns and wing margins glabrous; plants of the Marquesas Islands *O.* section *Albiflora*
- Plants glabrous; low shrubs 0.5–2 m tall, rarely trees to 5 m; leaf margin dentate, at least along apical $\frac{2}{3}$; capitula 7–12 mm in diameter, 9–13 mm high; peduncles 5–35 mm long; ray florets 8–9; disk florets ca. 20 1. *O. hivoanus*
- Plants hirsute, especially on inflorescences and young shoots and leaves; trees up to 12 m tall; leaf margin entire (rarely dentate on young shoots); capitula 14–20 mm in diameter, 16–25 mm high; peduncles 25–73 mm long; ray florets 20–30; disk florets 50–60 2. *O. teikiteetunii*
- Leaves moderately to extremely thickened, tough; involuclral bracts in one irregular series; florets yellow; achene awns and usually also wing margins erose and ciliate; plants of Rapa *O.* section *Oparanthus*
- Trees or shrubs to 8 m tall; leaves slightly to moderately thickened and tough, secondary veins 7–10 mm apart, tertiary veins reticulate, margins often at least obscurely toothed; capitula 3–6 mm in diameter, 5–6 mm high, (9–) 12–45 in large, many-branched capitulescences 3. *O. rapensis*
- Shrubs 1–3 m tall; leaves extremely thickened and tough, secondary veins 2–5 mm apart, tertiary veins conspicuously nearly parallel, margins entire; capitula 5–12 mm in diameter, 9–15 mm high, 1–3 tightly clustered in compound capitulescences 4. *O. coriaceus*

Oparanthus section *Albiflora* R. K. Shannon & W. L. Wagner, sect. nov. TYPE: *O. hivoanus* (O. Deg. & Sherff) R. K. Shannon & W. L. Wagner.

Ab *O.* sect. *Oparantho* foliis tenuibus vel leviter incrassatis et corollis albis differt.

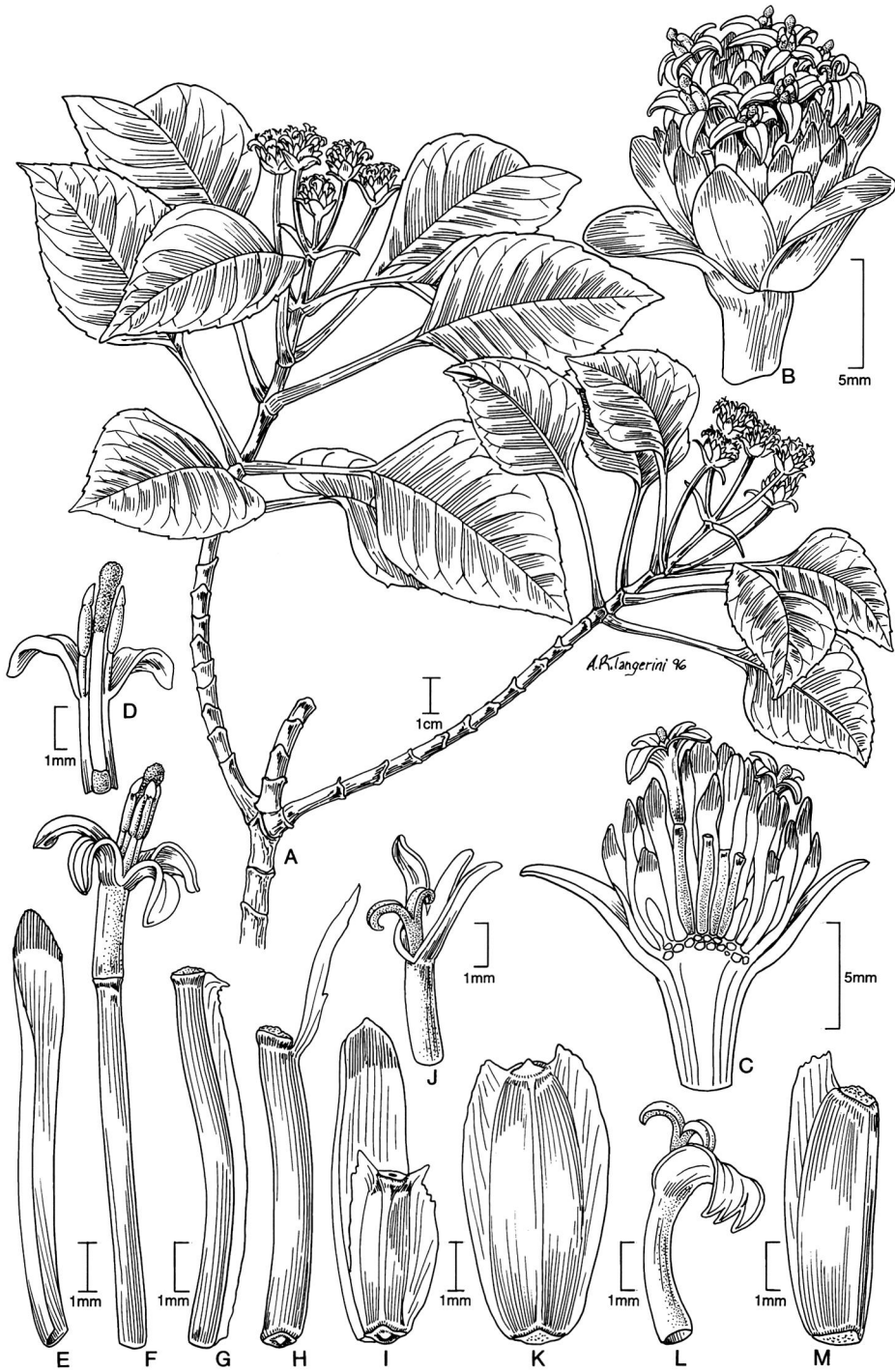
Plants hirsute or glabrous. Leaves relatively thin to slightly thickened and subcoriaceous, blade ovate to elliptic or obovate, marginal veins obscure or inconspicuous. Involuclral bracts in 2–3 well defined series. Receptacular bracts of ray florets 7–8 mm long, those of the disk florets 9–12.5 mm long. Ray florets 8–30, disk florets 20 or 50–60, the corollas white. Achene wings and awns glabrous.

Oparanthus sect. *Albiflora* is described here to accommodate the two Marquesan species, which are especially distinctive in leaf texture, corolla color, involuclral bracts, and ray achenes. Carlquist (1957) drew attention to the differences in leaf anatomy between the Rapan species and *O. hivoanus*. By describing the section we call attention to these characters, but especially to the geographical pattern that appears to correspond to a single colonization of the Marquesas Islands by a common ancestor of these two species.

- 1. ***Oparanthus hivoanus*** (O. Deg. & Sherff) R. K. Shannon & W. L. Wagner, comb. nov. *Bidens hivoana* O. Deg. & Sherff, in Sherff, Bot. Gaz. (Crawfordsville) 96: 143. 1934. TYPE: MARQUESAS ISLANDS. HIVA OA: Tenatinaei, on crest north of summit of Mt. Temetiu, in typical forest of cloud zone, 3620 ft, 24 July 1929, A. Adamson & E. Mumford 469 (HOLOTYPE: NY! [photo F!]; ISOTYPES: BISH-92780!, P!). FIGURE 1.

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FIGURE 1. *Oparanthus hivoanus*. A, habit; B, capitulum; C, longitudinal cutaway view of capitulum; D, longitudinal cutaway view of disk floret; E, receptacular bract of disk floret; F, disk floret; G and H, disk achenes; I, ray achene with receptacular bract; J and L, ray florets (ovaries removed); K and M, ray achenes, showing variation. (A from Schäfer 5190A, BISH and us, and Perlman 10217, us; B–M from Perlman 10181, BISH)



Chrysogonum album F. Br., Bernice P. Bishop Mus. Bull. **130**: 342. 1935. Nom. illeg. [ICBN Articles 7.5 and 52.1, 1994]. *Oparanthus albus* Sherff, Occas. Pap. Bernice P. Bishop Mus. **12**(19): 12. 1937. Nom. illeg. [ICBN Article 52.1, 1994]. TYPE: MARQUESAS ISLANDS. Hiva Oa: Feani, 850 m, 15 December 1921, *F. Brown & E. Brown 1088* (HOLOTYPE: BISH-91417!). Brown included the type of *Bidens hivoana* (*Mumford & Adamson 469*) in his description of *C. album*, and he erroneously synonymized the name *Bidens hivoana* under *Campylotheca henryi*.

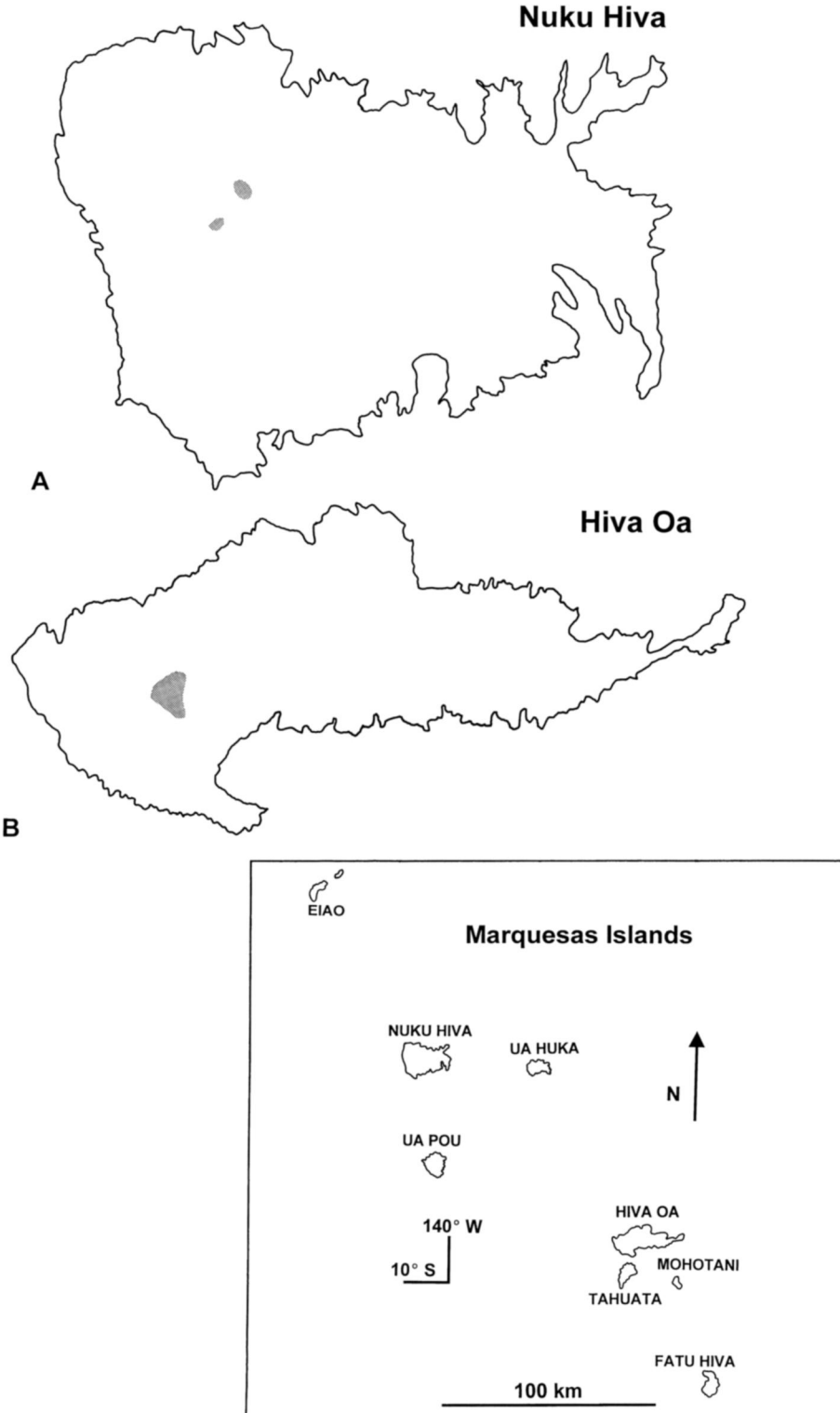
Glabrous shrub 0.5–2 m tall or, in protected sites, a small tree to 5 m tall and trunk to 20 cm in diameter, bark brown, wood cream colored; young stems with very short internodes. Leaves subcoriaceous, the blade ovate to broadly ovate, 2.3–8 cm long, 1.3–4.5 cm wide, on young shoots up to 13 cm long and 11 cm wide, secondary veins 3–9 mm apart, and up to 13 mm apart on young shoots, tertiary venation reticulate, margins dentate, sometimes along apical $\frac{2}{3}$ only, to entire, on young shoots coarsely serrate, apex acute, base obtuse to occasionally truncate or oblique; petioles 1.5–5 cm long, those on young shoots up to 10 cm long, the flared part 0.2–0.8 cm long. Capitula generally in clusters of 3, 7–12 mm in diameter, 9–13 mm high; peduncles 5–35 mm long. Involucre campanulate; involucre bracts 7–8, in 2 series, 6.5–8 mm long, the external ones wider and thicker. Receptacular bracts of ray florets 7.5–8 mm long, those of disk florets 9–11 mm long. Ray florets 8–9 in 1–3 series, corolla tube and throat 3–4 mm long, lamina 3–3.3 mm long, shallowly lobed or toothed. Disk florets 20, corolla tube and throat 2.5 mm long, the lobes 3 mm long. Ray achenes narrowly elliptic, at least 7 mm long, winged on one or both margins, the wings up to 1 mm wide, the wing margin smooth to weakly erose apically, extending slightly beyond the achene apex. Disk achenes ca. 4.5 mm long, sometimes with one wing, this sometimes extending slightly beyond the apex of the ovary.

DISTRIBUTION: Endemic to the Marquesas Islands, restricted to the western part of the island of Hiva Oa, from Mt. Temetiu to Mt. Feani and toward Hanamenu (FIGURE 2B). Scattered to relatively common in the cloud zone, in scrubby forest of *Freycinetia*, *Metrosideros*, *Weinmannia*, *Cheirodendron*, *Reynoldsia*, *Cyathea*, *Scaevola*, and *Crossostylis*, and understory rich in ferns, mosses, and epiphytes, from 850 to 1200 m, usually on windswept slopes of summit areas, less commonly in high elevation valleys. Known to flower from January through September.

Oparanthus hivoanus is typically a low shrub with stiff branches. It is the only species of the genus occurring primarily in the cloud zone, which corresponds to its summit ridge habitat. R. Oliver (pers. comm.) observed a few plants in one site in a protected area of a high elevation valley that were trees rather than shrubs, with heights up to 5 m. Because the overall terrain of the region where *O. hivoanus* grows is rugged and inaccessible in parts, it is not known how common the larger form is; however, the old trail from Atuona to Hanamenu is one of the most frequently collected areas in the archipelago making this species one of the

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FIGURE 2. Distributions of *Oparanthus teikiteetini* and *O. hivoanus*. A, map of Nuku Hiva, showing distribution of *O. teikiteetini*; B, map of Hiva Oa, showing distribution of *O. hivoanus*; inset, map of the Marquesas Islands.



most often collected in the genus. Pollination has not been observed in this species, but judging from morphology and the insect groups known from the Marquesas Islands, it is presumably moth pollinated. Carlquist (1957) found that awns were rarely present on the disk achenes, and when present they were not vascularized.

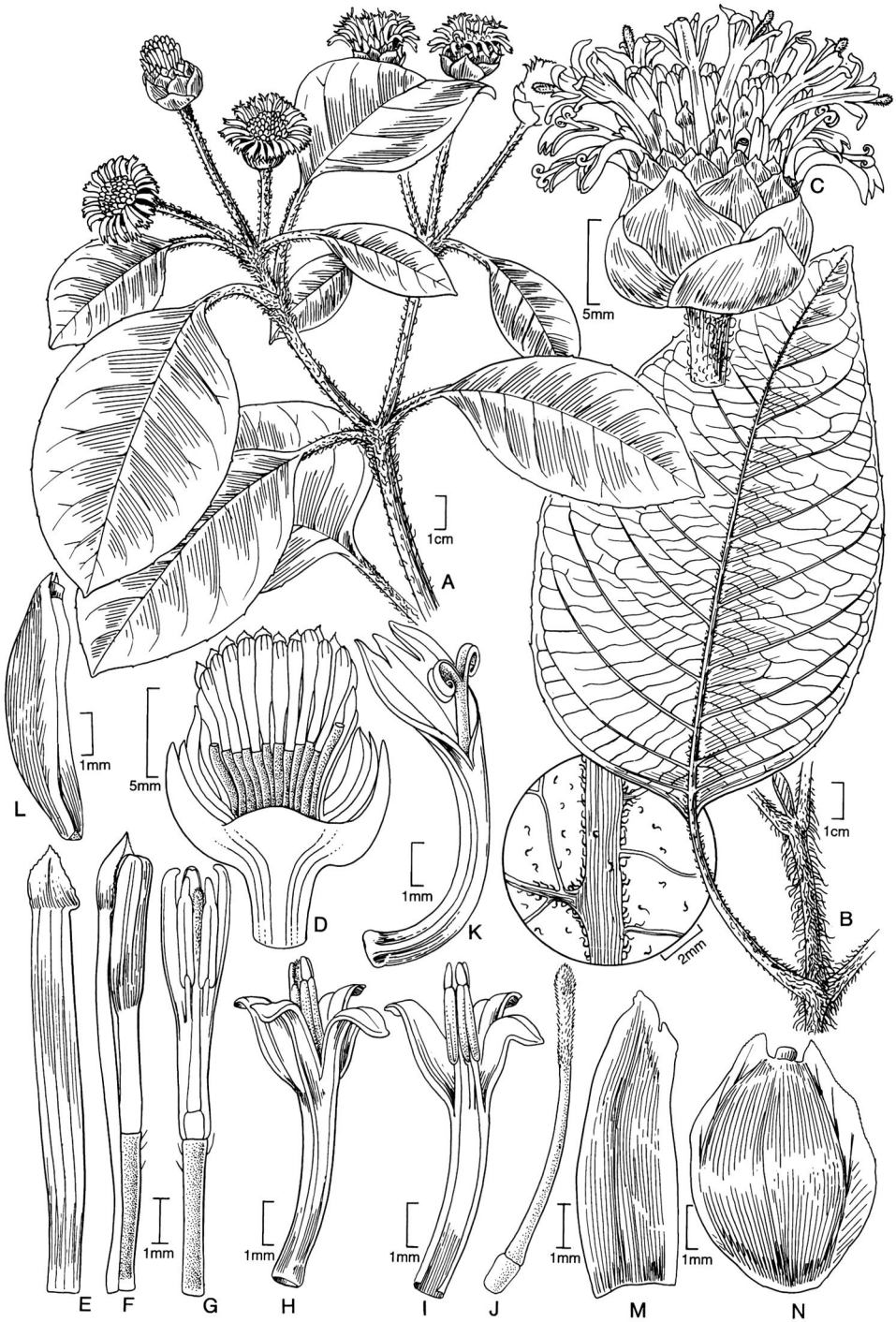
SPECIMENS EXAMINED. MARQUESAS ISLANDS. HIVA OA: Feani, *LeBronnec 805* (BISH [2], K, NY); road to Hanamenu, high plateau, *M. Henry s.n.* (P); [no locality], high plateau, *M. Henry 13* (P); where trail toward Hanamenu turns into dry ridge, on summit crest, *Perlman 10217* (BISH, PTBG, US); trail from Atuona to Hanamenu through Feani, ridge beside Hanamenu, *Schäfer 5190A* (BISH, K, US), *Schäfer 5190B* (US), *Schäfer 5190C* (US); Atuona-Feani Trail, upper part of trail, just below crest of ridge, *Sachet & Decker 1137* (BISH, US); Mt. Feani, trail from Atuona to Hanamenu, *Oliver & Schäfer 3103* (BISH, PTBG, US), *Oliver & Schäfer 3117* (BISH, US), *Oliver & Schäfer 3235* (BISH, US), *Oliver & Schäfer 3236* (BISH, L, PTBG, US [2]); trail to Feani and Hanamenu, *Perlman et al. 10180* (BISH, PTBG); trail to Feani and Hanamenu, along plateau rim and ridge trail, *Perlman 10181* (BISH, PTBG); old Atuona-Hanamenu trail, on high ridge leading to Mt. Feani, *Lorence et al. 6233* (PTBG); N side of Mt. Temetiu, *Mumford & Adamson 153* (BISH).

2. *Oparanthus teikiteetini* (Florence & Stuessy) R. K. Shannon & W. L. Wagner, comb. nov. *Bidens teikiteetini* Florence & Stuessy, Bull. Mus. Natl. Hist. Nat., B, Adansonia 10: 121. 1988. TYPE: ILES MARQUISES [MARQUESAS ISLANDS]. NUKU HIVA: Route Toovii-Terre Déserte, 6 km après le col, 1050 m, 5 June 1984, *J. Florence 6911* (HOLOTYPE: P; ISOTYPES: BISH, K, NY!, OS, P!, PAP, US!). FIGURE 3.

Tree to 12 m tall and trunk to 35 cm in diameter, bark gray, brown on younger stems, wood cream colored; young stems circular in cross section, densely hirsute, the hairs multicellular, crinkled, spreading to antrorsely appressed, reddish brown to black (reddish in dried specimens). Leaves relatively thin, the blade elliptic to ovate or occasionally obovate, 5–24 cm long, 2.5–15 cm wide, hirtellous when young, the abaxial surface densely so, becoming sparsely hirtellous, mainly along midrib, or glabrate, secondary veins (6–)7–12(–18) mm apart, tertiary venation reticulate, margins entire, at least sometimes dentate-apiculate on young actively growing shoots, apex acute to obtuse, rarely mucronate, base obtuse, occasionally truncate or oblique; petioles 1.5–13 cm long, hirtellous, pubescence densest on adaxial surface, the flared part (0.6–)1–2 cm long. Capitula solitary or in clusters of 3, rarely in clusters of 2, 14–20 mm in diameter, 16–25 mm high, peduncles 25–73 mm long, hirsute, glabrate. Involucre abruptly campanulate; involucre bracts 12, in 3 series, 7–12 mm long, becoming lignified in fruit, free or connate at the base, glabrous, the external ones thick and broadly triangular, the internal ones usually shorter and wider, sometimes elliptic. Receptacular bracts of the ray florets 7–8 mm long, those of the disk florets 10–12.5 mm long. Ray florets 20–30, in 2–4 series, corolla tube and throat 7 mm long, lamina 2–4 mm long, shallowly or rarely deeply 3(4)-lobed. Disk florets 50–60, corolla tube and throat

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FIGURE 3. *Oparanthus teikiteetini*. A, habit; B, leaf, abaxial side, with inset showing detail of hairs; C, capitulum; D, longitudinal cutaway view of capitulum; E, receptacular bract of disk floret; F, immature disk floret with receptacular bract; G, longitudinal cutaway view of immature disk floret; H, disk floret (ovary removed); I, longitudinal cutaway view of disk floret (ovary removed); J, detail of style of disk floret; K, ray floret (ovary removed); L and M, receptacular bracts of ray florets; N, ray achene. (A from *Perlman et al. 10094*, PTBG, and *Lorence et al. 6078*, BISH; C from *Lorence et al. 6078*, US; B, D–N from *Wagner et al. 6089*, US)



6–8 mm long, the lobes 3.5 mm long. Ray achenes elliptic, 6–8 mm long, distinctly winged, the wings 1–2 mm wide, extending beyond the achene apex as an awn, also with 1–2 linear deciduous awns arising from median achene veins. Disk achenes 8–9 mm long, with 2 awns.

DISTRIBUTION: Endemic to the Marquesas Islands, restricted to the Toovii region, W of Mt. Tekao on the island of Nuku Hiva (FIGURE 2A). Occurring in mesic to wet forest, ravines and steep slopes, with dominant plants such as *Cyathea*, *Freyinetia*, *Crossostylis*, *Psychotria*, *Metrosideros*, and *Fagraea*, and understory of *Macropiper*, *Pipturus*, *Cyrtandra*, and numerous epiphytic and terrestrial ferns, from 990 to 1050 m. Known to flower from June through August and in December.

Oparanthus teikiteetini is distinctive within the genus for its large size, attaining heights of up to 12 m, and for its large, often solitary capitula. The corollas are also the largest in the genus. No observation of pollination has been made so it is not known whether this size increase of the capitula and the individual florets corresponds to a pollinator shift. *Oparanthus teikiteetini* is also unique in the genus in having long, dark reddish brown to nearly black hairs, especially on young stems and leaves. This species has only been collected from a small area on the north side of the Toovii Plateau region, but many other portions of this region have not been adequately collected and much of the region has been severely degraded by pine plantations.

SPECIMENS EXAMINED: MARQUESAS ISLANDS. NUKU HIVA: Toovii, SER property, north trail, shoulder W of Mt. Tekao, *Florence et al.* 9439 (US); Toovii–Terre Déserte road, 6 km beyond col, *Florence* 4360 (BISH, P, US); Terre Deserte, ridge W of Mt. Akaupe, *Florence* 8544 (BISH, P); Toovii region, NW of l'Economie Rurale complex, along new road to airport over flanking mountains, *Lorance et al.* 6078 (BISH, PTBG, US), *Perlman et al.* 10094 (BISH, PTBG [2], US), *Wagner et al.* 6089 (PTBG, US).

Oparanthus section *Oparanthus*

Plants glabrous. Leaves thick to very thick and coriaceous, partially folded along midrib and sometimes splitting along midrib or secondary veins (especially when pressed), shape variable, marginal vein thickened and prominent. Involucral bracts in 1 irregular series. Receptacular bracts of ray florets 3–5 mm long, those of the disk florets 3–6 mm long. Ray florets 5–12, disk florets 8–25, the corollas yellow. Achene awns and usually also wing margins erose and ciliate.

G. Paulay (unpubl.) observed moths visiting the flowers of *O. coriaceus*, and Clarke (1971) reported that *O. rapensis* is a food plant for larvae of the moth *Eurhodope ardescens* Meyrick (Pyrilidae). The Rapan species of *Oparanthus* are also known to host at least four species of the weevil genus *Miocalles* (Paulay, 1985).

- 3. *Oparanthus rapensis*** (F. Br.) Sherff, Occas. Pap. Bernice P. Bishop Mus. **12**(19): 11. 1937. *Chrysogonum rapense* F. Br., Bernice P. Bishop Mus. Bull. **130**: 343. 1935. *Bidens rapensis* (F. Br.) Stuessy, Brittonia **40**: 198. 1988. TYPE: AUSTRAL ISLANDS. RAPA: Maitua, on talus with other trees and ferns, 600 ft [180 m], 10 Oct. 1921, A. M. Stokes 337 (HOLOTYPE: BISH-92759!). FIGURES 4 and 5.

Glabrous tree or shrub to 8 m tall and trunk to 20 cm in diameter, bark smooth

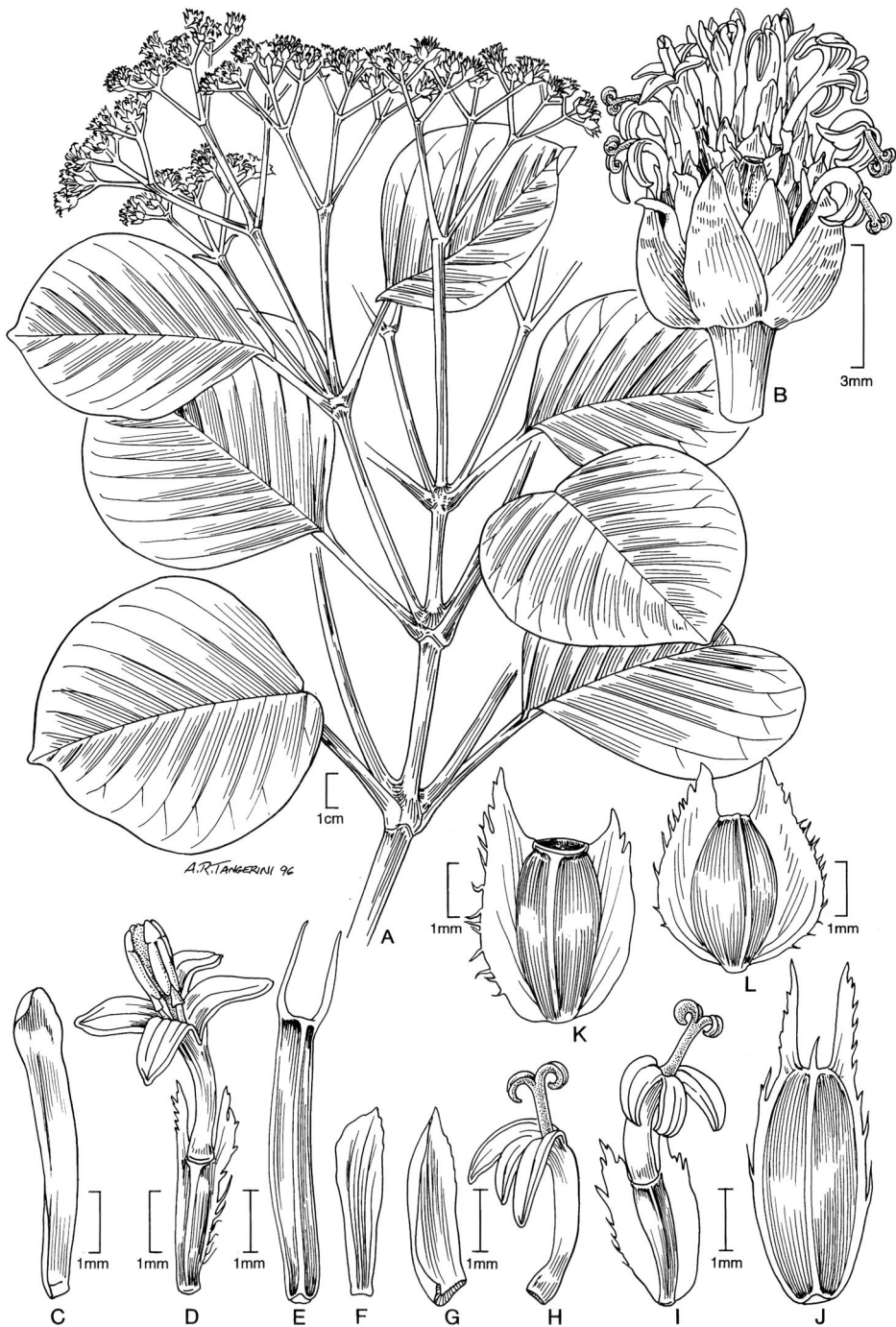


FIGURE 4. *Oparanthus rapensis*. A, habit; B, capitulum; C, receptacular bract of disk floret; D, disk floret, showing erose, ciliated margins and awns of ovary; E, disk achene showing glabrous margins and awns; F and G, receptacular bracts of ray florets; H, ray floret (ovary removed); I, ray floret; J-L, ray achenes, showing variation. (All from Chapin 907, A)



FIGURE 5. Photograph of *Oparanthus rapensis* (foreground), showing the arborescent habit, thick, coriaceous, partially folded leaves, and old, persistent, pendent capitulescences. The plant in the upper left quadrant and background is *Metrosideros collina*. (Photo by P. Bruner)

grayish brown, upper branches somewhat flattened, wood soft, cream colored. Leaves coriaceous, the blade very broadly ovate or suborbicular, sometimes elliptic to very broadly elliptic, rarely very broadly obovate, 3.5–14 cm long, 3.5–16 cm wide, occasionally splitting along midrib from apex, venation conspicuous, secondary veins 7–10 mm apart and tertiary veins conspicuously reticulate, margins slightly thickened, entire or slightly dentate, especially on young shoots, apex mucronulate to obtuse, acute, or retuse, base obtuse to oblique, truncate, or weakly cordate; petioles 2–10 cm long, the flared part 0.5–1 cm long. Capitula (9–)12–45 in large, many-branched capitulescences, each branch terminating in a cluster of 3 capitula, the capitula 3–6 mm in diameter, 5–6 mm high, the central one of each cluster sessile or pedunculate, peduncles, where present, 1–3(–6) mm long, those of the lateral capitula 5–15(–20) mm long. Involucre campanulate; involucre bracts 6–10, in 1 irregular series, 3–5 mm long. Receptacular bracts of ray florets 3–5 mm long, those of the disk florets 3–4 mm long. Ray florets 10–12, in 1–2 series, corolla tube and throat 2 mm long, lamina 1.8 mm long, deeply 3-lobed. Disk florets 8–20, corolla tube and throat 1.8–2 mm long, the lobes 1.4–

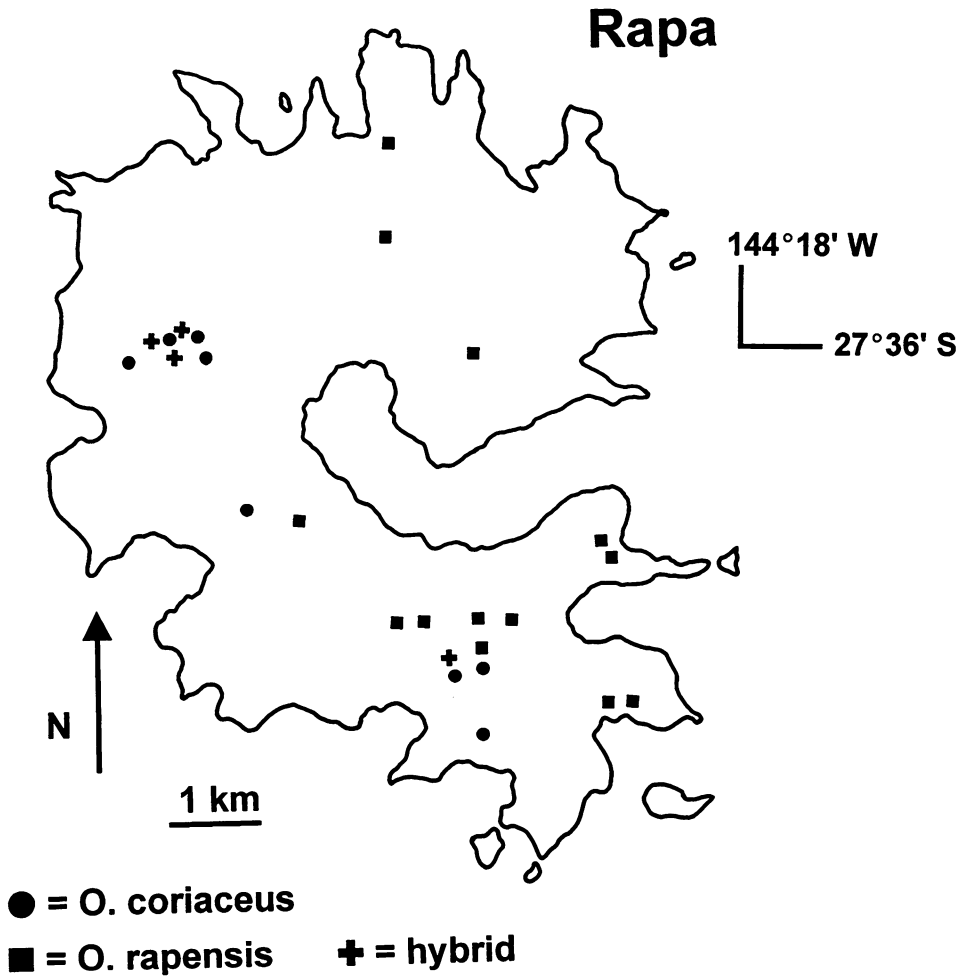


FIGURE 6. Map of Rapa, showing distributions of *Oparanthus rapensis*, *Oparanthus coriaceus*, and their putative hybrid.

1.6 mm long. Ray achenes narrowly elliptic to elliptic, 3.8–4.5 mm long, winged on both margins, the wings 0.2–0.6 mm wide, the wing margin ciliate, becoming erose apically, extending beyond the achene apex as an erose and ciliate awn. Disk achenes ca. 5 mm long, with 1–2 linear awns to 1.5 mm long.

DISTRIBUTION: Endemic to the island of Rapa, Austral Islands (FIGURE 6). Occurring in mesic to wet forest with *Freycinetia*, *Eurya*, and *Metrosideros* dominant, and understory rich in ferns, on slopes, sometimes on cliffs, from 50 to 350 m. Flowering material collected in January, February, July, and October through December; apparently flowering primarily from October through February.

Vernacular names “*laupata*” (Stokes 337; Stokes & Brown 76, 389) and “*anei*” (Stokes & Brown 60).

SPECIMENS EXAMINED: AUSTRAL (TUBUAI) ISLANDS. RAPA: ridge between Ororangi and Mangaoa, *N. Hallé* 7668 (P); SE of Tupuaki Bay, *N. Hallé* 7363 (P); ridge between Mt. Vairu and Mt. Ruatara, *Florence* 6260 (P); Pake, mountain side, *Stokes & Brown* 389 (BISH [2]); Morogouta, *N. Hallé* 7511 (P), *Stokes & Brown* 60 (BISH), *Stokes & Brown* 76 (BISH); [no locality], 1921–1922, *Stokes & Brown* s.n. (BISH); dry cliffs above Maitua, 10 July 1934, *Zimmerman* s.n. (BISH); Maungaai, E of Mangaoa Peak, *St. John & Maireau* 15372 (BISH [2], GH, K); Peatuakaviri, W of Mt. Tautautu, *St. John & Maireau* 15401 (A, BISH, GH, US); valley $\frac{2}{3}$ mile E of Ahurei, *St. John & Fosberg* 15264 (BISH [2], GH, P, US); SE slope of Mt. Ororangi, *Fosberg* 11413 (A, BISH, GH, P); Mt. Tepiahu, *Fosberg* 11501 (BISH); [no locality], *Chapin* 907 (A, GH, NY); between Ngapiri and Maitua nako, *Paulay* 24 (A); W side of fort Pukutaketake, *Paulay* 51 (A, US); just S of Ororangi, *Paulay* 67 (A); N side of Anatakuri nako valley, midway, *Paulay* 78 (US); Anatakuri Bay, *Clarke & Clarke* R40 (US).

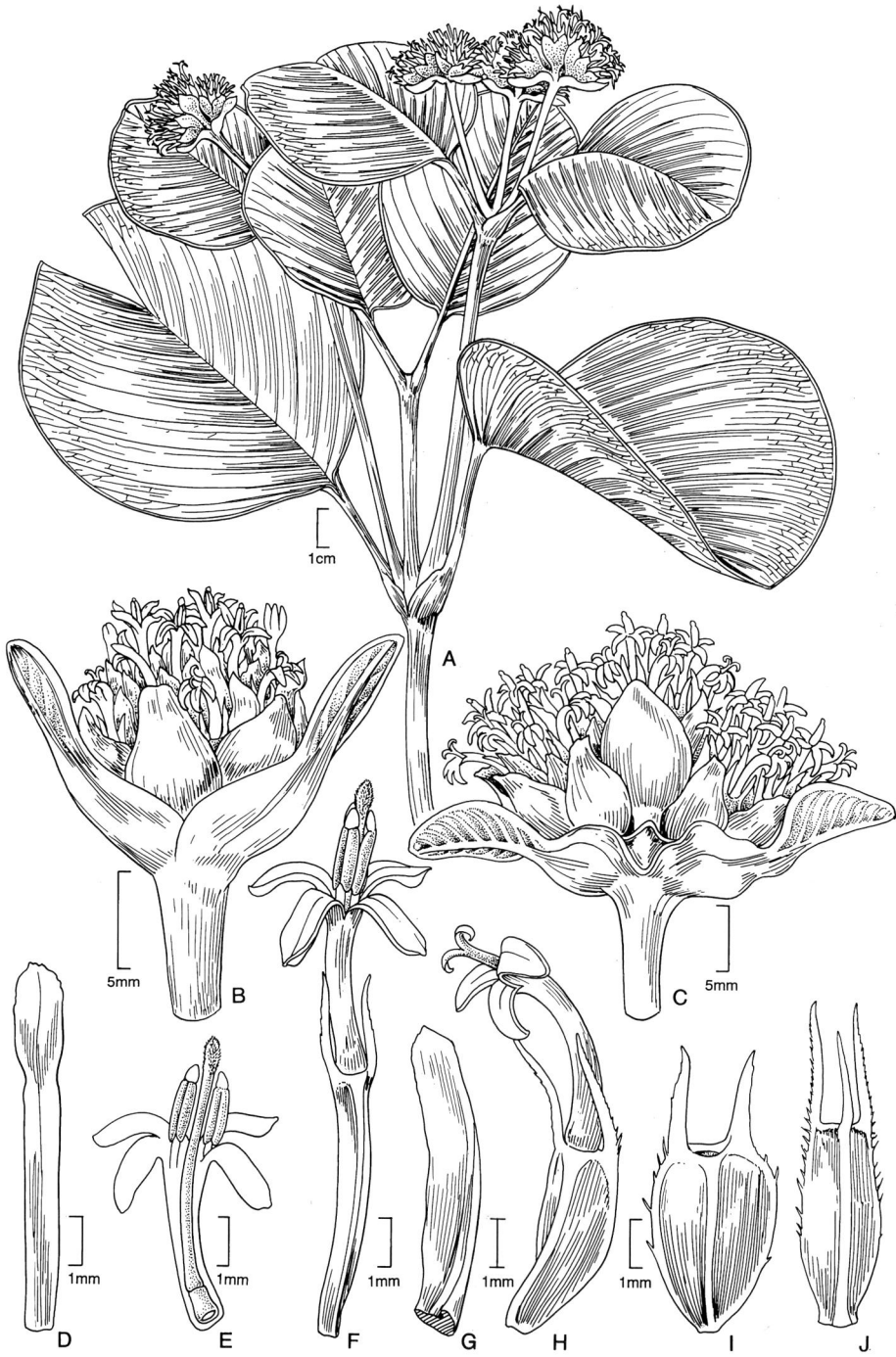
4. *Oparanthus coriaceus* (F. Br.) Sherff, Occas. Pap. Bernice P. Bishop Mus. 12(19): 11. 1937. *Chrysogonum coriaceum* F. Br., Bernice P. Bishop Mus. Bull. 130: 344. 1935. *Bidens tubuaiensis* Stuessy, nom. nov. TYPE: AUSTRAL ISLANDS. RAPA: 1922, *E. H. Quayle* X (HOLOTYPE: BISH-445035!). FIGURE 7.

Glabrous shrub 1–3 m tall and trunk to 2 cm in diameter, bark smooth brown, upper branches somewhat flattened, wood soft, cream colored. Leaves extremely thick and coriaceous, the blade elliptic, very broadly obovate, or suborbicular, 4.5–12 cm long, 3–12 cm wide, frequently splitting along midrib from apex or along one or more of the secondary veins, secondary veins 2–5 mm apart and tertiary veins conspicuously nearly parallel to the secondary veins, marginal vein prominent, margins greatly thickened, entire, occasionally weakly undulate, apex obtuse, acute, or retuse, base obtuse; petioles, 2–4.5 cm long, basal end conspicuously flared, the flared part 1–2 cm long. Capitula in clusters of 3, occasionally only 1–2, tightly clustered, forming a dense compound capitulum 5–12 mm in diameter, 9–15 mm high, sessile or pedunculate; peduncles up to 3 mm long. Involucre campanulate; involucre bracts 6–8, in 1 irregular series, 4.5–8 mm long. Receptacular bracts of ray florets 4.5–7 mm long, those of the disk florets 6–9 mm long. Ray florets 6–13, in 1–2 series, corolla tube and throat 3.7–4 mm long, lamina 1.2 mm long, deeply 3-lobed. Disk florets 12–16, corolla tube and throat 3.8–4 mm long, the lobes 2–2.2 mm long. Ray achenes narrowly elliptic to elliptic, 4–6 mm long, winged on both margins, the wings 0.1–0.3 mm wide, the wing margin smooth or ciliate, wings extending beyond the achene apex as a ciliate awn 2–2.5 mm long, sometimes also with an additional linear median awn 2–2.2 mm long arising from the keeled adaxial face. Disk achenes 6–7 mm long, with 1–2 linear awns 1.5–3 mm long.

DISTRIBUTION: Endemic to the island of Rapa, Austral Islands (FIGURE 6). Occurring at upper elevations in wet forest and in cloud zone in dense vegetation dominated by *Metrosideros*, *Eurya*, *Corokia*, and other shrubs, and understory rich in ferns and mosses, on slopes, sometimes on cliffs, from 280 to 600 m.

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FIGURE 7. *Oparanthus coriaceus*. A, habit; B, capitulum; C, three tightly clustered capitula giving the appearance of a single capitulum; D, receptacular bract of disk floret; E, longitudinal cutaway view of disk floret (ovary removed); F, disk floret; G, receptacular bract of ray floret; H, ray floret; I and J, ray achenes, showing variation. (A from *Hallé* 7640, 7634, P; B from *Hallé* 7640, P; C, H, and I from *Paulay* 88, A; D–G, J from *Clarke & Clarke* R35, US)



Flowering material collected in April, July, and November; apparently flowering throughout much of the year.

SPECIMENS EXAMINED: AUSTRAL (TUBUAI) ISLANDS. RAPA: Kaimaru, S ridge of Mt. Perahu, *St. John & Maireau 15517* (BISH, GH, K, P); SE Namuere, *N. Hallé 7634* (P), *Florence 6488* (BISH, P, US), near the ridge, *N. Hallé 7640* (P); [no locality], *N. Hallé 7653bis* (P); Maungaoa ridge, *Clarke & Clarke R35* (US); Piringa, *Paulay 23* (A); ridge between Pumarua and Tangahiri, *Paulay 88* (A, US); ridge between Morogouta and Pukutaketake W, *Paulay 40* (US); E ridge of Namuere, *Paulay 123* (A); Mitiperu, *Fosberg 11574* (A [pro parte], BISH).

***Oparanthus coriaceus* (F. Br.) Sherff × *O. rapensis* (F. Br.) Sherff.** *Oparanthus intermedius* Sherff, Occas. Pap. Bernice P. Bishop Mus. **12**(19): 10. 1937.
TYPE: AUSTRAL ISLANDS. RAPA: Taratika, E side of Mt. Perahu, thicket on steep ridge, 500 m, 21 July 1934, *H. St. John, J. Maireau, & F. R. Fosberg 15640* (HOLOTYPE: BISH-92760!; ISOTYPES: F!, GH!, P!, US!).

Almost certainly an interspecific hybrid between *O. coriaceus* (female?) and *O. rapensis* (male?), as suggested by Stuessy (1977a). Known from only four collections, all of which were made in the same localities as collections of *O. coriaceus*, it exhibits leaf and capitulescence characters intermediate between the two parental species (Stuessy, 1977a). Details of leaf anatomy also support the notion that this entity represents a hybrid (Carlquist, 1957). Since all four collections of the putative hybrid were made at the same localities as collections of *O. coriaceus*, only one of them even near localities for *O. rapensis*, we are hypothesizing that *O. coriaceus* is the maternal parent. The parental species both occur in wet forest habitats throughout the island (G. Paulay, pers. comm.), and overlap slightly in their elevational ranges, making hybridization on this small island quite plausible. Since the elevational ranges for the two species are more separate than overlapping, hybridization is not likely to be widespread.

SPECIMENS EXAMINED: AUSTRAL (TUBUAI) ISLANDS. RAPA: Mitiperu, *Fosberg 11574* (A [pro parte], K); SE Namuere, *N. Hallé 7653* (P); E ridge of Namuere, *Paulay 118* (US).

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