

Resurrection of Genus *Kadua* for Hawaiian Hedyotideae (Rubiaceae), with Emphasis on Seed and Fruit Characters and Notes on South Pacific Species

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Communicating Editor: Paul S. Manos

ABSTRACT. We examined shapes and surface features of seeds of 19 species of Hawaiian Hedyotideae using scanning electron microscopy. The study concentrates on the Hedyotideae previously recognized in the genus *Hedyotis* and here recognized as the genus *Kadua*, lacking diplophragmous capsules, and having salverform, fleshy corollas with appendaged lobes. The seeds fell into four main morphological groups: (1) hat- or fan-shaped, laterally cuneate, compressed seeds (*Kadua* subg. *Kadua* and atypical species of *Gouldiopsis* and *Wiegmannia*); (2) ovoid or elliptic seeds with conspicuous bubble-shaped bodies included in the areoles (cells) (most of sect. *Wiegmannia*); (3) flat broadly winged seeds with a lateral hilum attached at wing margin (*Kadua* *centranthoides*, type species of sect. *Gouldiopsis*); (4) brick-like or blocky seeds with a centric ventral hilum (*Kadua* subg. *Gouldia*). The results of the seed study correlate with the taxonomic arrangement in the current Hawaiian flora. An appendix lists the *Kadua* names including necessary new combinations and their *Hedyotis* synonyms for the Hawaiian taxa and seven additional South Pacific taxa having the same corolla characters. The following new names are published: *Kadua* subg. *Gouldia* (A. Gray) W. L. Wagner & Lorence, *Kadua* sect. *Gouldia* (A. Gray) W. L. Wagner & Lorence, *Kadua* *fosbergii* (W. L. Wagner & D. R. Herbst) W. L. Wagner & Lorence, *Kadua* *axillaris* (Wawra) W. L. Wagner & Lorence, *Kadua* sect. *Phyllozygia* (W. L. Wagner & Herbst) W. L. Wagner & Lorence, *Kadua* *tryblium* (D. R. Herbst & W. L. Wagner) W. L. Wagner & Lorence, *Kadua* sect. *Oceanica* (Fosberg) W. L. Wagner & Lorence, *Kadua* sect. *Austrogouldia* (Fosberg) W. L. Wagner & Lorence, *Kadua* *lucei* (Lorence & J. Florence) W. L. Wagner & Lorence, *Kadua* *nukuhivensis* (J. Florence & Lorence) W. L. Wagner & Lorence, *Kadua* *tahuatensis* (Lorence & J. Florence) W. L. Wagner & Lorence, *Kadua* *grantii* (Fosberg) W. L. Wagner & Lorence, *Kadua* sect. *Protokadua* (Fosberg) W. L. Wagner & Lorence, *Kadua* *coriacea* (J. E. Smith) W. L. Wagner & Lorence, *Kadua* sect. *Gouldiopsis* (Fosberg) W. L. Wagner & Lorence, *Kadua* *foggiana* (Fosberg) W. L. Wagner & Lorence, *Kadua* sect. *Wiegmannia* (Meyen) W. L. Wagner & Lorence, *Kadua* *cordata* Cham & Schltld. subsp. *remyi* (Hillebr.) W. L. Wagner & Lorence, *Kadua* *cordata* Cham & Schltld. subsp. *waimaeae* (Wawra) W. L. Wagner & Lorence, *Kadua* *degeneri* (Fosberg) W. L. Wagner & Lorence, *Kadua* *degeneri* (Fosberg) W. L. Wagner & Lorence subsp. *coprosimifolia* (Fosberg) W. L. Wagner & Lorence, *Kadua* *elatior* (H. Mann) W. L. Wagner & Lorence, *Kadua* *flynnii* (W. L. Wagner & Lorence) W. L. Wagner & Lorence, and *Kadua* *st-johnii* (B. C. Stone & Lane) W. L. Wagner & Lorence.

The tribe Hedyotideae Cham. & Schltld. ex DC. includes herbaceous or shrubby rubiaceaceous genera having few to many seeds per capsule. The subtribe Hedyotidinae DC., as originally described (Candolle 1830), included (among other genera) *Hedyotis* with 28 species and *Oldenlandia* with 45 species. The genus *Hedyotis* has been a source of taxonomic problems for many years (Terrell 1996). Previous studies of the tribe Hedyotideae (Rubiaceae) have focused mainly on the North American representatives (Terrell et al. 1986, Terrell 1996 on *Houstonia*, inter alia). These studies have emphasized seed characters, which have been used in a limited way in many older classifications of the Rubiaceae, and chromosome numbers, which are unusually variable in the tribe compared to most of the family. A recent study (Terrell and Robinson 2003) of the Asian and Micronesian relatives of the type species of *Hedyotis*, *H. fruticosa* L., included all characters in establishing a base line for comparison of subgenus *Hedyotis*, or *Hedyotis* sensu stricto, with other species.

Recent molecular studies (Bremer 1996; Bremer and Manen 2000) showed that genera of the tribe Spermaceae are nested within the tribe Hedyotideae; however, when the two tribes are united, the older

name Spermaceae must be used following the rules of priority (Greuter et al. 2000). Terrell and Wunderlin (2002) found basic differences in the seed and fruit morphology of the two tribes, consequently we prefer to maintain the two tribes as distinct, with tribe Hedyotideae treated here in the more traditional sense.

Andersson et al. (2002), in a molecular study of the South American genus *Arcytophyllum* Willd. ex Schult., included four species of Hawaiian *Hedyotis* among many Hedyotideae-Spermaceae genera. They noted that the four species (*H. degeneri*, *H. hillebrandii*, *H. parvula*, and *H. schlechtendaliana*) formed a clade within the Spermaceae sens. lat. (including Hedyotideae), with *H. hillebrandii* sister to the three other species. Preliminary molecular data (Motley et al. 1998; Motley 2003) suggested that (1) Hawaiian *Hedyotis* resulted from a single colonization, (2) the Hawaiian species are divided into two clades, one with fleshy fruits and the other with dry fruits.

The present investigation of Hawaiian species of Hedyotideae continues use of scanning electron microscopy (SEM) in studying seed and fruit characters and provides additional data on inflorescence and corolla characters. The study shows that the seeds of the

TABLE 1. Collections of Hawaiian *Kadua* species examined in this study, with *Hedyotis* names in synonymy.

Kadua acuminata Cham. & Schltld. (*Hedyotis acuminata* (Cham. & Schltld.) Steudel). *Flynn & Bergau 1361* (PTBG), Hawaii, SEM B2; *Degener 11694* (US), Oahu, SEM B24; *Herbst 3073* (US), Oahu; *Fosberg 10783* (US), SEM R30.

K. affinis DC. (*H. terminalis* (Hook. & Arn.) W. L. Wagner & D. R. Herbst). *Chapin s.n.* (NTBG 910714), Kauai, SEM B4; *Degener 12732* (US), Oahu; *Perlman et al. 15353* (PTBG), Maui.

K. axillaris (Wawra) W. L. Wagner & Lorence (*H. hillebrandii* (Fosberg) W. L. Wagner & D. R. Herbst). *Wagner et al. 5870* (PTBG), Maui, SEM B13.

K. centranthoides Hook. & Arn. (*H. centranthoides* (Hook. & Arn.) Steudel). *Terrell & Terrell 5503* (US), Hawaii, SEM H36; *Kiehn* (NTBG-900593), Kauai, SEM B22; *Henrickson 4061A* (US); *Degener & Greenwell 21916* (US); *Perlman et al. 10499* (PTBG), Hawaii.

K. cookiana Cham. & Schltld. (*H. cookiana* (Cham. & Schltld.) Steudel). *Cult.* (NTBG 950509), Kauai, SEM B23.

K. cordata Cham. & Schltld. (*H. schlechtendaliana* Steudel). *Wood 1399* (PTBG), Kauai, SEM B19; *Wood 3643* (US), Kauai, SEM B44.

K. degeneri (Fosberg) W. L. Wagner & Lorence (*H. degener* Fosberg). *Wood 3432* (US), Oahu, SEM B25.

K. elatior (H. Mann) W. L. Wagner & Lorence (*H. elatior* (H. Mann) Fosberg). *Perlman 12003* (PTBG), Kauai, SEM B10; *Christenson 63* (US), Kauai, SEM B27.

K. fluviatilis C. N. Forbes (*H. fluviatilis* (C. N. Forbes) Fosberg). *Perlman 11293* (PTBG), Kauai, SEM B16.

K. flynnii (W. L. Wagner & Lorence) W. L. Wagner & Lorence (*H. flynnii* W. L. Wagner & Lorence). *Wood 1204* (PTBG), Kauai, SEM B5.

K. foggiana (Fosberg) W. L. Wagner & Lorence (*H. foggiana* Fosberg). *Lorence et al. 5324* (PTBG), Kauai, SEM B12; *Degener & Greenwell 21637* (US), Kauai, SEM B28.

K. formosa Hillebr. (*H. formosa* (Hillebr.) Fosberg). *Wood et al. 3943* (PTBG), Maui, SEM B9, B29.

K. fosbergii (W. L. Wagner & D. R. Herbst) W. L. Wagner & Lorence (*H. fosbergii* W. L. Wagner & D. R. Herbst). *Fosberg 12374* (US), Lanai, SEM B18.

K. knudsenii Hillebr. (*H. knudsenii* (Hillebr.) Fosberg). *Degener 12643* (US), Kauai, SEM H65, B26.

K. laxiflora H. Mann (*H. mannii* Fosberg). *Degener 11726* (US), Molokai, SEM H66.

K. littoralis Hillebr. (*H. littoralis* (Hillebr.) Fosberg). *Perlman 11202* (NTBG), Molokai, SEM B15; *Forbes 526* (US), Molokai.

K. parvula A. Gray (*H. parvula* (A. Gray) Fosberg). *Perlman 14665* (PTBG), Oahu, SEM B11; *Degener 12808* (US), Oahu.

K. st.-johnii (B. C. Stone & Lane) W. L. Wagner & Lorence (*H. st.-johnii* B. C. Stone & Lane). *Perlman & Wood 13331* (PTBG), Kauai, SEM B21.

K. tryblium (D. R. Herbst & W. L. Wagner) W. L. Wagner & Lorence (*H. tryblium* D. R. Herbst & W. L. Wagner). *Perlman 11675* (NTBG), Kauai, SEM B8.

Hawaiian species are distinct from Asian and Pacific species of *Hedyotis* subgenus *Hedyotis* and from North American species of Hedyotidae, and we resurrect the oldest genus name, *Kadua*, for these species.

MATERIALS AND METHODS

Seeds were supplied by D. H. Lorence from specimens in the herbarium of the National Tropical Botanical Garden (PTBG), and additional seeds were obtained by the first author from the US herbarium (Table 1). Seeds were examined by dissecting microscope and data were recorded on a computerized form. Mature well-formed seeds from capsules and dried formerly fleshy fruits were examined by scanning electron microscopy (SEM) by Terrell and Robinson at the Smithsonian Institution. These data supplemented earlier SEM work on the seeds of many collections of species of the tribe Hedyotideae (sensu Terrell and Wunderlin 2003) carried out at the Smithsonian Institution by Terrell and Robinson and by Terrell at the U. S. Department of Agriculture at Beltsville, Maryland prior to 1985. During this earlier work, two of the Hawaiian species, *Hedyotis acuminata* and *H. centranthoides*, had been examined. Table 1 lists the mature-seeded collections of the species examined and those treated by SEM, and includes *Kadua* and *Hedyotis* nomenclatural authors and collection data. Table 2 provides important seed data for selected groups of species, and Table 3 does the same for fruit and capsule characters. Table 4 compares data for selected inflorescence and corolla characters. Appendix 1 summarizes *Kadua* names and lists new combinations for Hawaiian species and seven South Pacific species.

The Hawaiian species are described here and in Table 2 according to the following seed characters: Length and width or diameter, thickness, compression type, compression extent, shape type, whether laterally cuneate, whether broadly winged, hilum wheth-

er centric or at margin, hilum type or size, testa surface, areoles (cells) shape, presence/absence of included bodies, areole walls thickness and whether they have projections. The compression type refers to whether the hilum is located on or near the center of the ventral face or along the margin of the seed; if centric (central) it is considered a dorsiventrally compressed seed; if marginal it is considered to be laterally compressed. With the exception of the sect. *Gouldia*, seeds of the Hawaiian species have lateral hila, and differ from seeds of other genera of Hedyotideae which are centric. In the hat- or fan-shaped seeds of the subg. *Kadua* the seeds are strongly compressed, thinner near the marginal hilum and thicker at the opposite end, a condition termed laterally cuneate.

Fruit characters (Table 3) are mainly length and width or diameter, shape, structure or texture, and endocarp sclerification. If endocarp sclerification is strong, the term woody may apply. The term disk apex (in text) refers to whether the apex of the capsule is truncate, raised, beaked, or depressed. Dehiscence is not included in Table 3, as all taxa except sect. *Gouldia* have capsules with initial loculicidal dehiscence, followed later in maturity by septical dehiscence. In sect. *Gouldia* the fruits are fleshy and indehiscent.

PACIFIC HEDYOTIDEAE WITH TAXONOMIC NOTES

The Hedyotideae of the Pacific that have been treated by Fosberg (1943) and Wagner et al. (1999) include three groups of species. The first of these groups treated by Wagner et al. (1999) among the Hawaiian species of *Hedyotis* include the pantropical weed *Oldenlandia corymbosa* L., the type species of *Oldenlandia* L., and *Oldenlandiopsis callitrichoides* (Griseb.) Terrell & W. H.

TABLE 2. Seed characters for seed groups.

	Seed group 1, subg. A <i>Kadua</i>	Seed group 1, subg. B <i>Kadua</i>	Seed group 2 <i>Wiegmannia</i>	Seed group 3 <i>Gouldiopsis</i> ; <i>K. centran.</i>	Seed group 4 <i>Gouldia</i> , <i>Phyllozgia</i>
Compression type	lateral	lateral	not apparent	lateral	dorsiventral
Shape type /outline	hat-or fan-shaped	hat-shaped/irreg.angulate	ellipsoid, ovoid	flat; suborbicular / oval	brick-like/blocky
Laterally cuneate?	yes	yes	no	no	no
Broad wing?	no	no	no	yes	no
Hilum location	marginal	marginal	surface	marginal	centric
Hilar area	punctiform	punctiform	punctiform	punctiform	0.3–0.7 diam.
Testa / Areole inclusions	embedded papillae	small, oval, smooth/wrinkled	large, bubble-like	none	none

Lewis (Terrell and Lewis 1990), the type of *Oldenlandiopsis* Terrell & W. H. Lewis. The latter was originally endemic to the West Indies, but occurs on O'ahu and Maui as a rare adventive species. *Oldenlandia* subg. *Oldenlandia* includes small herbs with small flowers and capsules; seeds trigonous, very small, usually 0.2–0.5 mm long and 50–100 or more per capsule; chromosome number $n = 9$. The genus *Oldenlandia* has a worldwide distribution of about 100 species and an African center of distribution and diversity (see taxonomic notes in Terrell and Robinson 2003).

The second group involves the *Hedyotis* species related to *H. fruticosa* L., the type species of *Hedyotis* (Terrell and Robinson 2003). This Asian and Micronesian group is *Hedyotis* sensu stricto, and can be summarized nomenclaturally as follows:

Hedyotis L., Gen. Pl. ed. 5, 44 (1754). Lectotype species: *Hedyotis fruticosa* L. *Hedyotis* subgenus *Hedyotis*. *Hedyotis* sect. *Diplophragma* Wight & Arn., Prodr. florae Peninsulae orientalis 1:405–418 (1834). Lectotype: *Hedyotis fruticosa* L.

The species of *Hedyotis* subgenus *Hedyotis* (Terrell and Robinson 2003) have seeds that are rather strongly dorsiventrally compressed, with an apical centric hilum on a conspicuous, elevated, ventral, hilar ridge. The capsules are termed diplophragmous, an old term referring to their splitting into two separate cocci each with a median slit opening into a locule. This primarily septical dehiscence is usually preceded by a partial apical loculicidal dehiscence.

The third group includes the Hawaiian and some other Polynesian species. It is these species that are the principle subject of study in this paper.

Hawaiian Taxa of Hedyotideae. The generic, subgeneric, and sectional names that are available for the native group of Hedyotideae in Hawaii are as follows, with the principal names arranged in chronological order.

Kadua Cham. & Schltdl., Linnaea 4: 157. 1829.—Type: *Kadua acuminata* Cham. & Schltdl. *Hedyotis* subg. *Kadua* (Cham. & Schltdl.) Fosberg, Bernice P. Bishop Mus. Bull. 174: 69. 1943.

Wiegmannia Meyen, Reise 2: 139. 1835.—Type: *Wiegmannia glauca* Meyen, non *Hedyotis glauca* W. W. Smith = *Hedyotis schlechtendaliana* Steud. = *Kadua cordata* Cham. & Schltdl. *Hedyotis* sect. *Wiegmannia* (Meyen) Fosberg, Bernice P. Bishop Mus. Bull. 174: 29. 1943.

Gouldia A. Gray, Proc. Amer. Acad. Arts 4: 310. 1860.—Lectotype: *Gouldia sandwicensis* A. Gray, nom. illeg. = *Hedyotis terminalis* (Hook. & Arn.) W. L. Wagner & Herbst. = *Kadua affinis* DC. *Hedyotis* sect. *Gouldia* (A. Gray) W. L. Wagner & Herbst in W. L. Wagner, Herbst and Sohmer, Occas. Pap. Bernice P. Bishop Mus. 29: 111. 1989.

TABLE 3. Fruit/capsule characters for selected taxa.

	Shape	Structure/texture
Subg. <i>Kadua</i> , subgroup A	turbinate/subglobose	str.quadrangular or winged
Subg. <i>Kadua</i> , subgroup B: four species	turbinate/subglobose	not quadrangular/grooved
Subg. <i>Kadua</i> , subgroup B: <i>K. formosa</i>	ellipsoid-cylindrical	not quadrangular
Sect. <i>Wiegmannia</i> : five species	turbinate/subglobose	not quadrangular
Sect. <i>Wiegmannia</i> : <i>K. littoralis</i>	obconical	not quadrangular
Sect. <i>Wiegmannia</i> : <i>K. st.-johnii</i>	sublenticular	not quadrangular
Sect. <i>Gouldiopsis</i> : <i>K. centranthoides</i>	subglob./turbinate/obovoid	strongly grooved
Sects. <i>Gouldia</i> , <i>Phyllozygia</i>	globose	fleshy

Hedyotis subg. *Polynesiotis* Fosberg, Bernice P. Bishop Mus. Bull. 174: 22. 1943.—Type: *Wiegmannia glauca* Meyen = *Kadua cordata* Cham. & Schltld. (by inclusion of *Wiegmannia* Meyen in synonymy). *Polynesiotis* has priority at subgeneric level, *Wiegmannia* has priority at generic and section levels.

Hedyotis sect. *Bikkiocarpa* Fosberg, Bernice P. Bishop Mus. Bull. 174: 25. 1943.—Type: *Kadua formosa* Hillebr.

Hedyotis sect. *Gouldiopsis* Fosberg, Bernice P. Bishop Mus. Bull. 174: 56. 1943.—Type: *Hedyotis centranthoides* (Hook. & Arn.) Steud.

Hedyotis sect. *Protokadua* Fosberg, Bernice P. Bishop Mus. Bull. 174: 23. 1943.—Type: *Hedyotis coriacea* J. E. Smith (by monotypy).

Hedyotis sect. *Phyllozygia* W. L. Wagner & Herbst in W. L. Wagner, Herbst, and Sohmer, Occas. Pap. Bernice P. Bishop Mus. 29: 112. 1989.—Type: *Hedyotis tryblium* Herbst & W. L. Wagner in W. L. Wagner, Herbst, and Sohmer (1989).

These elements were disposed in the following way by Fosberg (1943) in his study of the Polynesian *Hedyotis*. He held a broad view of the genus, but excluded *Gouldia* by placing it in a separate genus (Fosberg 1937). He commented (Fosberg 1943: 14) that subgenera are the main evolutionary lines in the genus *Hedyotis*, and stated that "Many botanists would regard these groups as genera." He subdivided *Hedyotis* into five subgenera: *Oldenlandia*, *Diplophragma*, *Kadua*, *Oceanica*, and *Polynesiotis*. In *Polynesiotis* he included five sections: *Wiegmannia*, *Protokadua*, *Gouldiopsis*, *Bikkiocarpa*, and *Austrogouldia*. Of these, *Austrogouldia* Fob., *Diplophragma* Wight & Arn. (= typical *Hedyotis*), and *Oceania* Fob. (based on *Coprosma oceania* W. R. B. Oliver) are not Hawaiian.

In dealing with the taxonomy of the Hawaiian species of *Hedyotis*, we were guided by Wagner et al.'s (1990, 1999) treatments in the manuals of the Hawaiian flora, which updated Fosberg's nomenclature and taxonomy, making several changes to the infrageneric taxa. They recognized subgenera *Oldenlandia* (see above), *Kadua*, and *Polynesiotis* Fosberg. Under *Polynesiotis* they included sections *Gouldia* (A. Gray) W. L. Wagner & Herbst, *Phyllozygia* W. L. Wagner & Herbst,

Wiegmannia (Meyen) Fosberg, *Protokadua* Fosberg, *Bikkiocarpa* Fosberg, and *Gouldiopsis* Fosberg.

The Hawaiian flora lists 20 species of *Hedyotis* (excluding *Oldenlandia* and *Oldenlandiopsis*). An additional species, *H. flynnii*, was described recently by Wagner and Lorence (1998). Two species, *Hedyotis coriacea* Sm. and *H. foliosa* (Hillebr.) Fosberg, are rare or extinct, respectively, and no seeds were available. Nineteen species, all endemic to the Hawaiian Islands, provided seeds for this study. Seventeen of the species are shrubs, subshrubs, or small trees up to 5 m, and two other species (*H. littoralis*, *H. st.-johnii*) are large succulent perennial herbs.

Following the recent more precise delimitation of typical *Hedyotis* (Terrell and Robinson 2003), a decision has been made by the authors that affects the generic treatment in the present study. The diplophragmous capsules with paired cocci in typical *Hedyotis* are lacking in the Hawaiian Hedyotideae and related South Pacific species, which have salverform, fleshy, long-tubed, and appendaged corollas. This definable grouping of Pacific Hedyotideae is recognized here under the oldest available and applicable generic name, *Kadua*. The names of the *Kadua* species are summarized in Appendix 1 (prepared by Wagner and Lorence).

Gouldia, which is also readily definable by its fleshy fruits, is only one element of the broader natural group as shown by molecular sequence studies (Motley et al. 1998), and the paraphyletic non-*Gouldia* remnant has no defining morphological characters, but could conceivably be subdivided into three or more separate groups, largely corresponding to the recognized sections. The broader concept is favored here with the assumption that accelerated evolutionary diversification has occurred in the group as it has in many other island taxa. This broader group of species forms an easily recognized group.

RESULTS

Seeds of the Hawaiian species of *Kadua* fall into four groups as outlined in Table 2. Results for the fruit morphology are given in Table 3. These seed and fruit results are described below in more detail and pertinent SEM micrographs are referenced. The *Kadua* names are

TABLE 4. Inflorescence and corolla characters for selected taxa.

	Subg. <i>Kadua</i> A (2 spp.)	Sect. <i>Wiegmannia</i> (9 spp.)	Sect. <i>Gouldiopsis</i> (3 spp.)	Sect. <i>Gouldia</i> (3 spp.)
Inflorescence position	axillary	terminal	terminal	terminal
Inflo. type (all cymose)	1 (-7) flowers	paniculate/thyrsoid	paniculate/thyrsoid	paniculate
Peduncles adnate to stem?	yes	no	no	no
Corolla buds: lobes	inflexed	inflexed	weakly inflexed	not inflexed
Corolla buds: limbs	not quadrangular	not quadrangular.	strongly quadrangular.	weakly quadrangular.
Corolla buds: apices	depressed	depressed	not depressed	not depressed

adopted in accord with our previous decision (see previous section) to recognize the species under the genus *Kadua*. *Hedyotis* synonyms are added if their epithets under *Kadua* are different. Nomenclature authorities are given in Table 1. Seed and fruit characters are described in the Materials and Methods.

Our results partly coincide with the subgenera and sections recognized by Fosberg (1943) and Wagner et al. (1999). For comparison of the seed results with Wagner et al.'s (1999) taxonomic arrangement of the *Hedyotis* species we list an outline of their arrangement, as follows, with mention of some correlated characters.

Hedyotis subg. *Kadua*: two species: *H. acuminata* and *H. fluviatilis*.

Hedyotis subg. *Polynesiotis*: seventeen species in the following sections: sect. *Wiegmannia* (*H. cookiana*, *H. degeneri*, *H. elatior*, *H. flynnii*, *H. littoralis*, *H. mannii*, *H. parvula*, *H. st.-johnii*, *H. schlechtendaliana*); sect. *Bikkocarpa* (*H. formosa*); sect. *Gouldiopsis* (*H. centranthoides*, *H. foggiana*, *H. knudsenii*); sect. *Gouldia* and *Phyllozygia* (*H. fosbergii*, *H. hillebrandii*, *H. terminalis*, *H. tryblium*).

Seed Group 1. Subgenus *Kadua sens. str.* The typical subgroup A includes two closely related species, *Kadua acuminata* and *K. fluviatilis*, of which the former (Fig. 1A–D) is the main representative species. The following description includes both species (Tables 2, 3): Seeds 0.5–1.3 × 0.4–0.8 mm, compression lateral, moderate or strong, hat-shaped or fan-shaped (Fig. 1A, B, E), or irregularly angulate, laterally cuneate with thinner area at apex (Fig. 1A, B, E), hilum marginal, punctiform on the thinner margin, testa with embedded papillae (Fig. 1C, D, F), areoles polygonal, walls thick, sometimes with small jagged projections. Capsules 6–13 × 5–13 mm, turbinate to subglobose, strongly quadrangulate or winged, woody, disk raised. *Kadua fluviatilis* seeds resemble *K. acuminata* seeds but are less compressed, less angulate (Fig. 1E–F).

The two species of this typical subgroup have the following three important non-seed characters: peduncles adnate or partly adnate to the stem, flowers 1–7 in axillary inflorescences, and capsules woody (Fosberg 1943, Wagner et al. 1999).

Seed group 1 subgroup B includes five additional species: *Kadua degeneri* and *K. elatior* from sect. *Wiegmannia*; *K. foggiana* and *K. knudsenii* from sect. *Gouldiopsis*; and *K. formosa* from sect. *Bikkocarpa* (Figs. 2, 3). The composite description of seeds of this group is as follows (Table 2): Seeds 0.4–1.0 × 0.3–0.8 mm, compression lateral, slight to strong, seeds hat- or fan-shaped (Fig. 2E, F) or irregularly angulate (Fig. 2A; Fig. 3A, C), laterally cuneate (Fig. 2C, F), hilum punctiform, marginal, testa usually smooth, areoles rounded or polygonal, enclosing small, oval (Fig. 2 B, D), sometimes wrinkled bodies (Fig. 3B, D), walls thin or in *K. knudsenii* rather thick. (Fig. 3 D). Capsules smaller

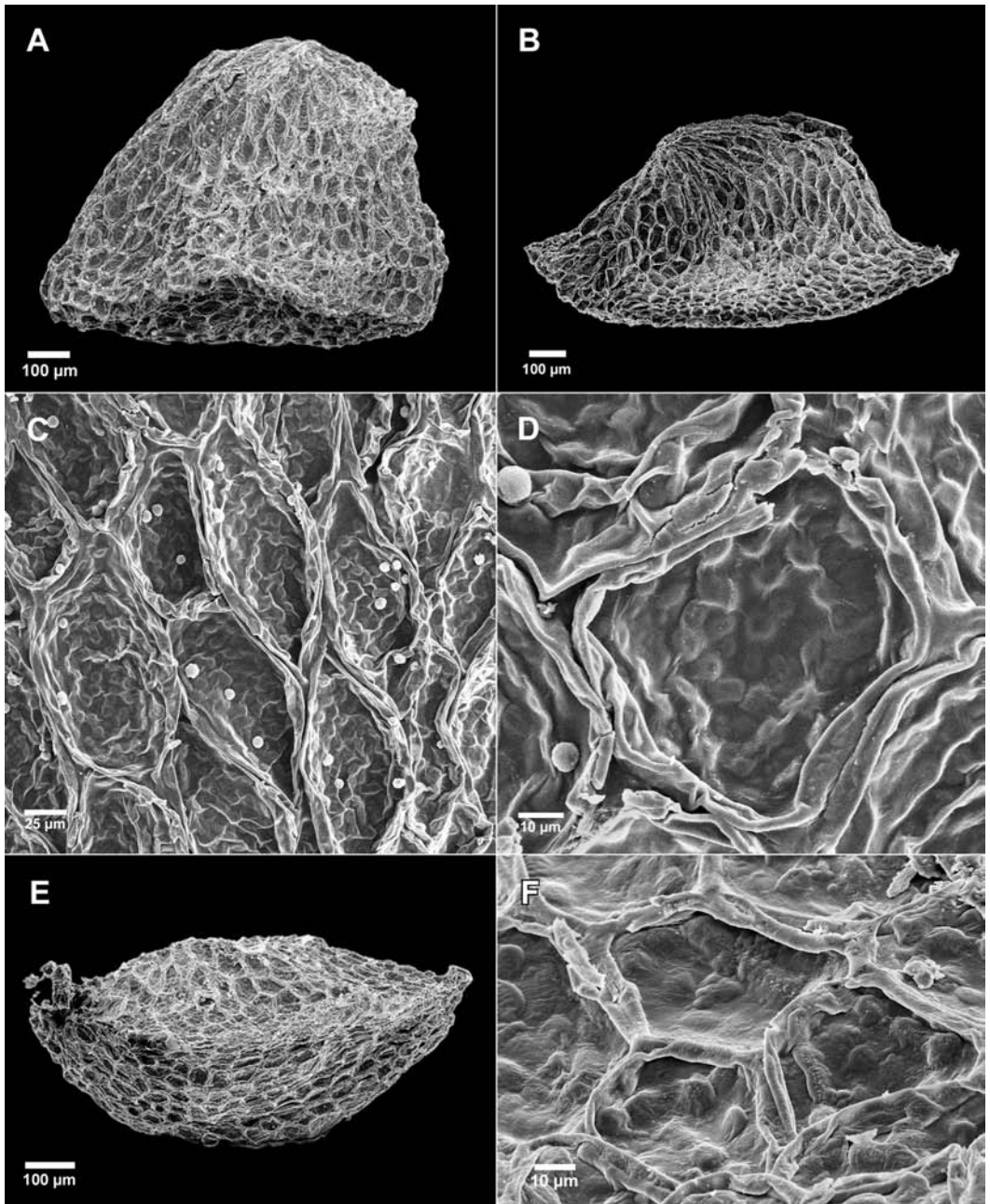


FIG. 1. Seeds of *Kadua* subg. *Kadua* sect. *Kadua* subgroup A, examined by SEM. A-D. *Kadua acuminata*. A. Side view with hilum at seed apex (sample B24). B. Side view (sample B2). C, D. Enlargement of areoles (sample B24). E, F. *K. fluviatilis* (sample B16). E. Side view. F. Enlargement of areoles. Collections data in Table 1.

than in subgroup A, except in *K. formosa*, which are ellipsoid (listed separately in Table 3).

The subgroup B species resemble the typical subgroup A in having seeds hat- or fan-shaped and laterally cuneate, but differs mainly in having small oval bodies in the areoles, with testa lacking embedded papillae and lacking any projections. This subgroup was earlier in this study considered to be intermediate,

however, it is included here in the first subgroup because the hat- or fan-shaped seeds are similar in shape to subgroup A although smaller. The oval bodies in the areoles are unlike the areolar bodies in Group 2 (see below). We conclude that the general seed shape in the two species in subgroup A and five species in subgroup B represent a form basic to the subgenus *Kadua*.

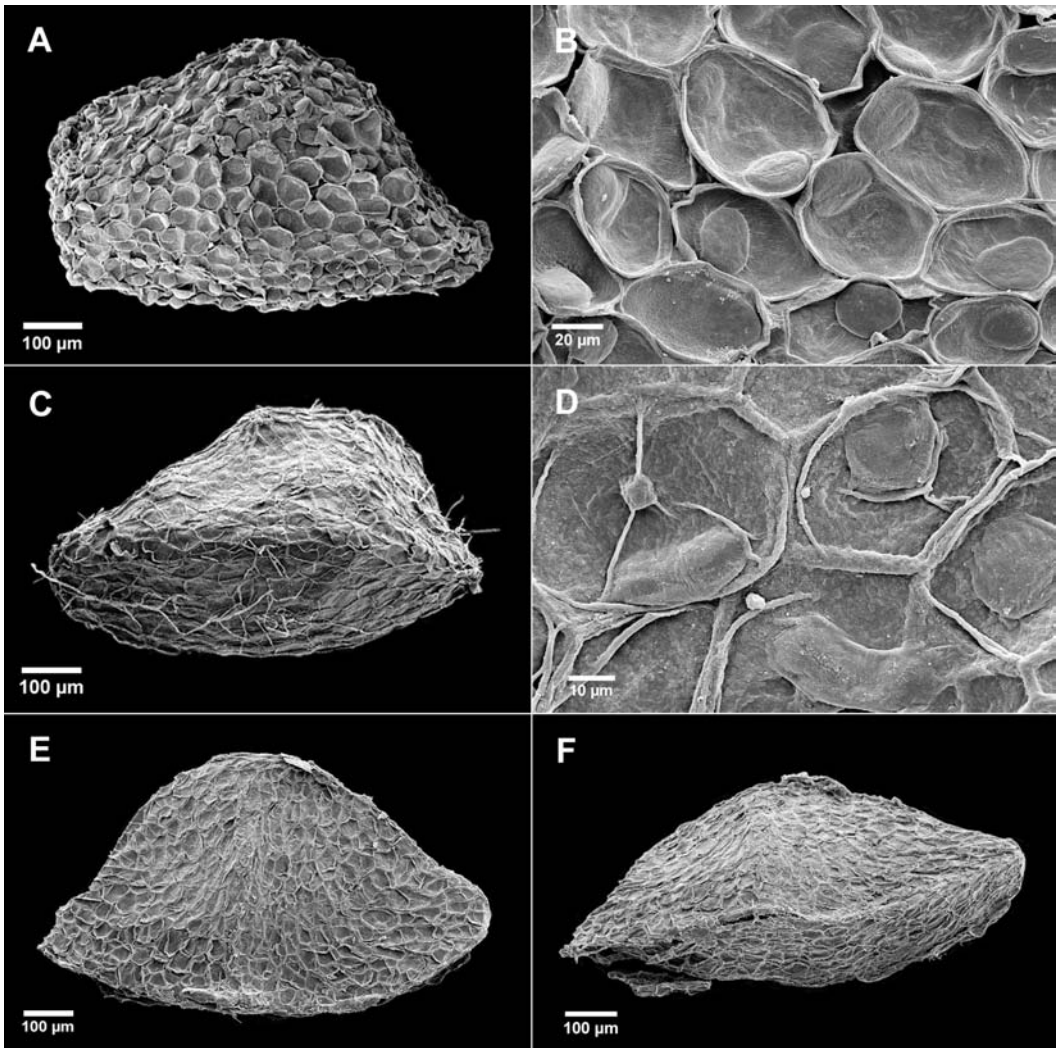


FIG. 2. Seeds of *Kadua* subg. *Kadua* subgroup B, examined by SEM. A, B. *Kadua degeneri* (sample B25). A. Side view with hilum at seed apex. B. Enlargement of areoles. C, D. *K. elatior* (sample B27). C. Side view, D. Enlargement of areoles. E, F. *K. foggiana* (sample B28), side views. Collections data in Table 1.

Seed Group 2. Section Wiegmannia. There are seven species in this group: *K. cookiana*, *K. cordata* (*H. schlechtendaliana*), *K. flynnii*, *K. laxiflora* (*H. mannii*), *K. littoralis*, *K. parvula*, *K. st.-johnii*.

The characteristics of these species are outlined as follows (Table 2): Seeds 0.2–0.8 × 0.2–0.5 mm, compression presumed lateral, but not apparent, slight or moderate, ellipsoid, ovoid, or obtusely angulate, hilum punctiform, inconspicuously attached on the rounded seed surface, areoles rounded or irregularly polygonal, each areole enclosing a bubble-like body, areole walls thin (Figs. 4, 5). Unique features are the ellipsoid or ovoid shape, hila inconspicuously attached on the rounded seed surface, and presence of one bubble-like body per areole (best seen in mature seeds of *K. cordata* in Fig. 4A,B and *K. flynnii* in Fig. 5A,B). The bubble-

like bodies, perhaps also describable as large papillae and to some extent visible at relatively low power, occur in all of the seven species (six species illustrated in Figs. 4, 5), and are a prominent surface feature not present in other *Kadua* groups.

The capsules (Table 3) of five of the species are as follows: 2–6 × 3–7 mm, turbinate to subglobose, thinly to strongly sclerified, disk raised, flat, or conical or beaked. *Kadua littoralis* has capsules somewhat different: 6–10 × 5–9 mm, obconical, slightly sclerified, and disk slightly raised. This capsule is more widely expanded at its apex than any other species in the genus. A seventh species, *K. st.-johnii*, needs future study. Its sublenticular capsules (Table 3) are very short and very wide (2.5–3 × 7–8 mm), and have a “squashed” appearance, certainly the oddest capsules of any of the

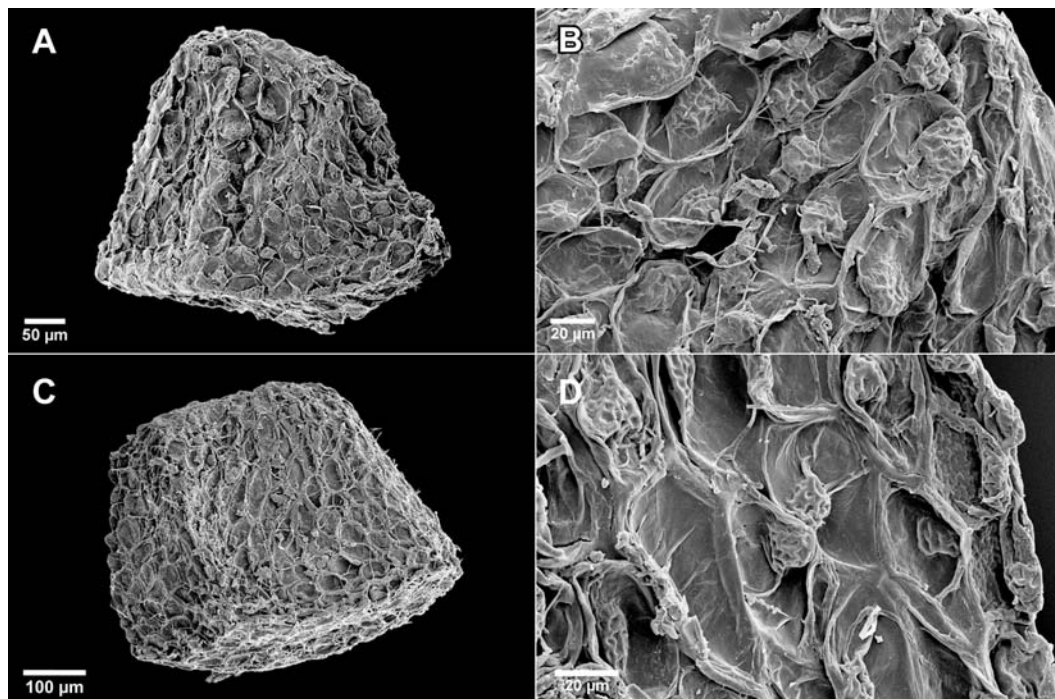


FIG. 3. Seeds of *Kadua* subg. *Kadua* subgroup B, examined by SEM. A, B. *Kadua formosa* (sample B29). A. Side view with hilum at seed apex. B. Enlargement of areoles. C, D. *K. knudsenii* (sample B26). C. Side view. D. Enlargement of areoles. Collections data in Table 1.

Kadua species. On the other hand, its seeds (Fig. 4E, F) appear generally similar to other group 2 species, although slightly smaller. *Kadua littoralis* (Fig. 4C, D), similar to *K. st.-johnii* only in being a perennial herb, is shown for comparison with the latter.

As noted previously, two additional species, *K. degeneri* and *K. elatior*, recognized by Wagner et al. (1999) as members of sect. *Wiegmannia*, are placed by us in seed group 1 subgroup B.

Seed Group 3. Section Gouldiopsis. This group includes three species, *Kadua centranthoides*, *K. foggiana*, and *K. knudsenii*. The last two of these differ distinctly in seed characters from the first species, and have been placed by us in seed group one. The composite section *Gouldiopsis* is discussed further in the Discussion.

The following seed description is based on eight studied collections of the type species of the section, *K. centranthoides* (Fig. 6). Seeds 0.7–1.2 × 0.5–1.1 mm, thin, compression lateral, strong, seeds flat, in outline orbicular, elliptical, or oval, central body (excluding wing) usually ca. 0.5–0.6 mm diam, more or less orbicular, wing 0.1–0.3 mm wide, wing margin entire or irregularly undulate, hilum marginal, punctiform on wing margin (Fig. 6A, B), testa surface appearing minutely roughened, areole walls thin, central body of seed with radially elongate areoles extending outward to the punctiform hilum, the remaining areoles irregularly angulate with sinuous walls (Fig. 6). Capsules

3–5 × 3.5–7 mm, subglobose to turbinate, obconic, or obovoid, slightly compressed, strongly grooved, somewhat sclerified, disk truncate or slightly raised (Table 3).

The seeds of the type species of the section, *Kadua centranthoides*, are unique (Fig. 6A–D). They are flat and thin, surrounded by a broad wing, and with a punctiform hilum attached at the wing margin. Although the vegetative parts of the plants do not seem to differ conspicuously from other species, the seeds are quite different from all other *Kadua* seeds. Functionally the *Kadua centranthoides* seed type would seem ill-adapted, with the developing wing severing the vascular trace furnishing nutrition to the seed. However, the wing is evidently late in developing or otherwise not a problem since the species is very successful and distributed on all the main islands except Ni‘ihau and Kaho‘olawe.

A chromosome number of $2n = ca.100$ was listed for *K. centranthoides* from Hawaii by Skottsberg (1955); Wagner et al. (1999) commented that this report needs to be confirmed.

Seed Group 4. Sections Gouldia, Phyllozygia. These plants occur on the main islands and include three similar species: *Kadua fosbergii*, *K. axillaris* (*H. hillebrandii*), and *K. affinis* (*H. terminalis*), the last one being the most common and widespread species. The plants have fleshy fruits and unique seeds (Fig. 7A–D). The section *Phyllozygia*, based on *Kadua tryblum*

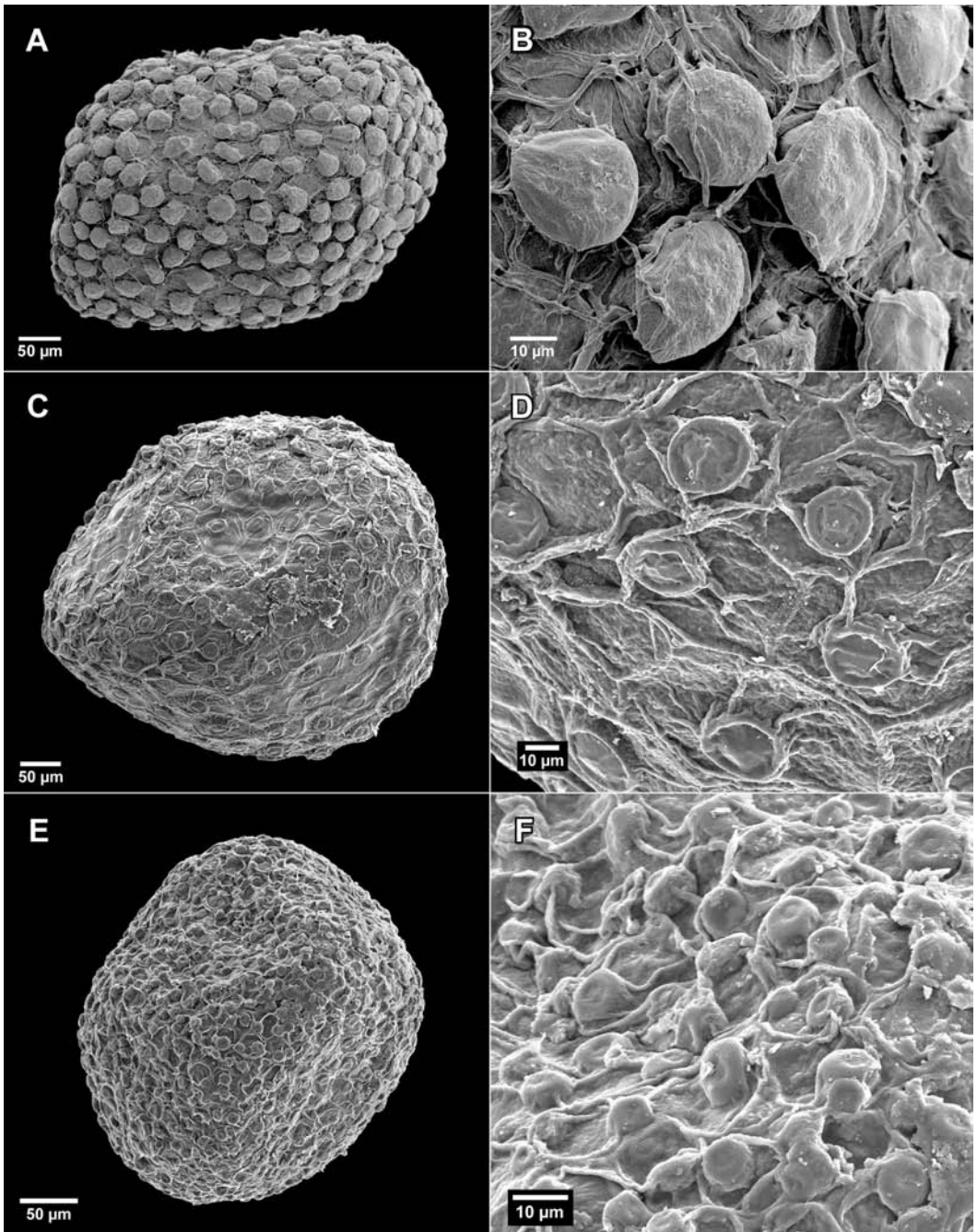


FIG. 4. Seeds of *Kadua* subg. *Kadua* sect. *Wiegmannia*, examined by SEM. A, B. *Kadua cordata* (sample B44). A. Whole seed. B. Enlargement of areoles. C, D. *K. littoralis* (sample B15). C. Whole seed. D. Enlargement of areoles. E, F. *K. st.-johnii* (sample B21). E. Whole seed. F. Enlargement of areoles. Collections data in Table 1.

and occurring only in Kauai, is similar to section *Gouldia* in its seeds (Fig. 7E, F) and fruits, but differs in four vegetative characters from the other species (Wagner et al. 1990, 1999). *Gouldia* was treated as a distinct genus by Fosberg (1937), however, Wagner et al. (1989,

1999) reduced it to a section of *Hedyotis* distinguished by several characters including the fleshy fruit.

Chromosome numbers ($2n$) reported by Skottsberg (1955) were as follows: *Gouldia axillaris* Wawra from Molokai, ca. 72; *Gouldia* cf. *ovata* (Wawra) Skottsberg (=

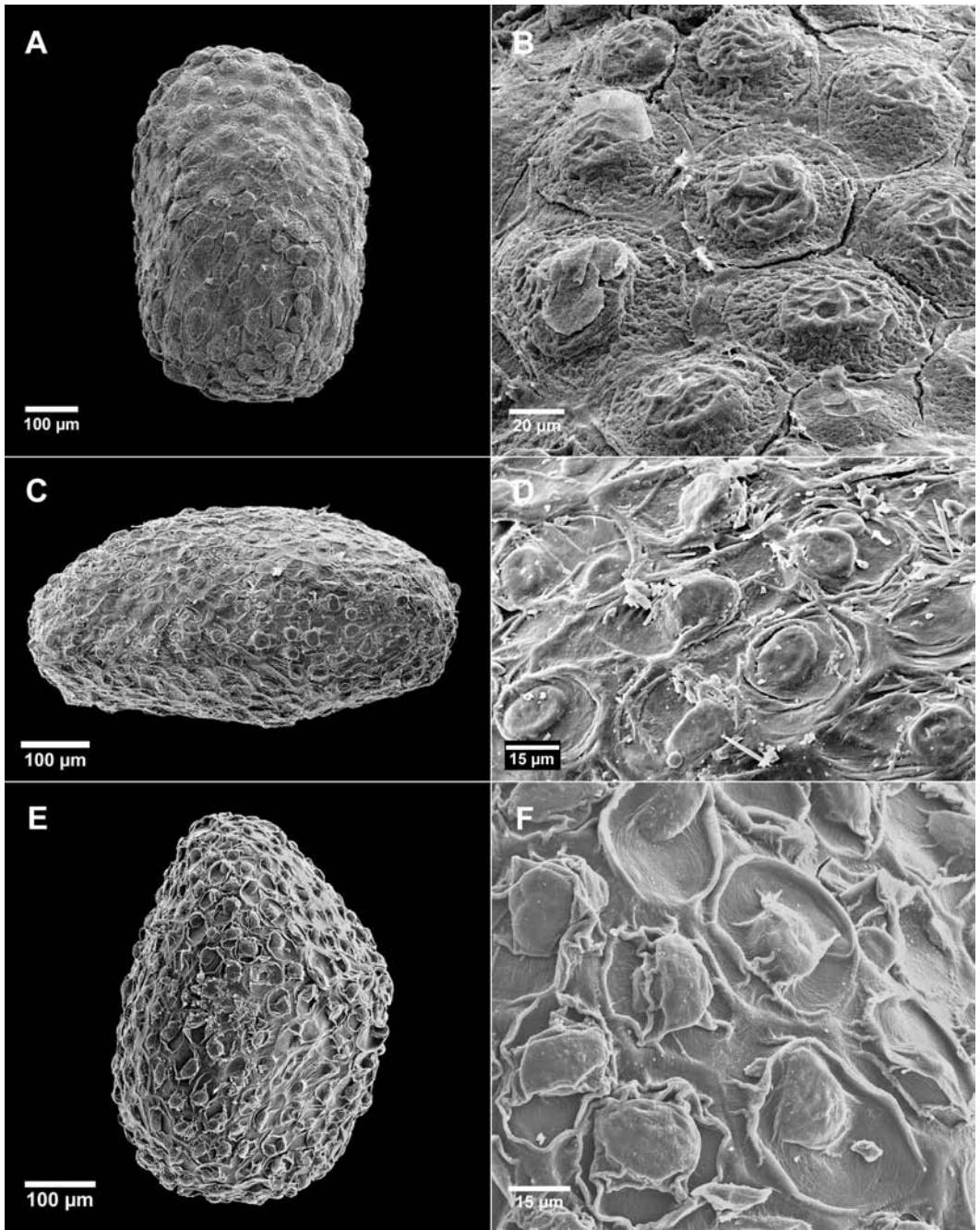


FIG. 5. Seeds of *Kadua* subg. *Kadua* sect. *Wiegmannia*, examined by SEM. A, B. *Kadua flynnii* (sample B5). A. Whole seed. B. Enlargement of areoles. C, D. *K. laxiflora* (sample H66). C. Whole seed. D. Enlargement of areoles. E, F. *K. parvula* (sample B11). E. Whole seed. F. Enlargement of areoles. Collections data in Table 1.

K. affinis) from Maui, ca. 102, 104; *Gouldia* spp. from Maui, Hawaii, and Lanai, ca. 93, 95–105. It is difficult to judge the significance of these numbers until more chromosomal data become available.

The seed data for both sections (Fig. 7) are combined here in one common description: Seeds 0.5–2.0 × 0.4–

1.7 × 0.3–0.8 mm, thicker than other Hawaiian Hedyotidineae seeds, compression dorsiventral, moderate or strong, irregularly brick-like, blocky, or angulate (Fig. 7A, C, E), irregularly polygonal, dorsal face convex to flat, ventral face slightly concave, hilum centric, with a circular or elliptical area ca 0.3–0.7 mm diam.,

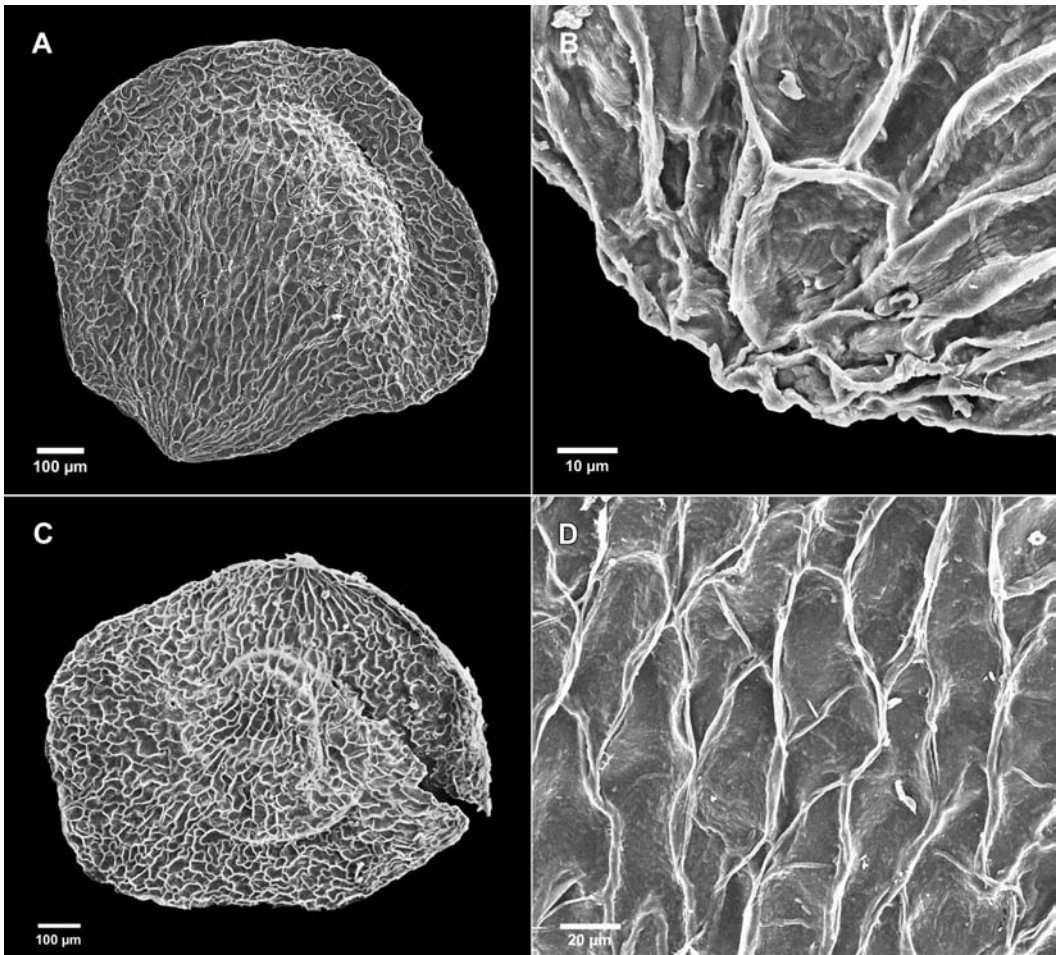


FIG. 6. Seeds of *Kadua centranthoides* (sect. *Gouldiopsis*), examined by SEM. A. Flat, broadly winged seed (Sample B22). B. Marginal winged hilar area (Sample B22). C. Flat, broadly winged fragile seed (sample H36). D. Enlargement of areoles (Sample B22). Collections data in Table 1.

testa appearing fibrous, often with marginal loosely attached cells (Fig. 7C), areoles small, round or polygonal, their walls thick, fibrous.

The fruits are 4–12 mm diam., globose, fleshy, indehiscent, bilobulate by a central septum, becoming dry with age. Fosberg (1937, pp. 25, 27, fig. 1), described them as dark blue or purplish black, crowned with a circular area having four tiny remote calyx teeth and containing 4–40 or more seeds having axile placentation near the midpoint of the septum, with an embryo straight or nearly so. Our observations of dried fruits broken manually showed an outermost blackish thick layer surrounding an inner brownish-yellow thinner hard layer. Seeds are tightly pressed together with the dorsal face outward against the hard inner layer and the opposite ventral face having a roundish hilar area faced peltately against the placentae. This compression causes great variation in seed shape.

The seeds and fruits of sections *Gouldia* and *Phylloz-*

ygia (see Discussion) differ strongly from those of the other taxa and, following Fosberg (1937), could suggest recognition as a genus.

DISCUSSION

Four main seed types occur in the Hawaiian species: (1) seeds moderately or strongly compressed, hat- or fan-shaped, laterally cuneate, with marginal hilum (subg. *Kadua*); (2) seeds ellipsoid or ovoid with inconspicuous hilar attachment on rounded surface and bubble-like areolar inclusions (sect. *Wiegmannia*), (3) seeds flat, broadly winged, with the hilum on the wing margin (*K. centranthoides*); (4) seeds brick-like, thickened, with central hilum (Sect. *Gouldia*). These seed types are unique to the Hawaiian species. They differ from those of *Oldenlandia* subgenus *Oldenlandia* by the fewer and larger seeds that are not 3-angled. Other hedyotoid genera indig-

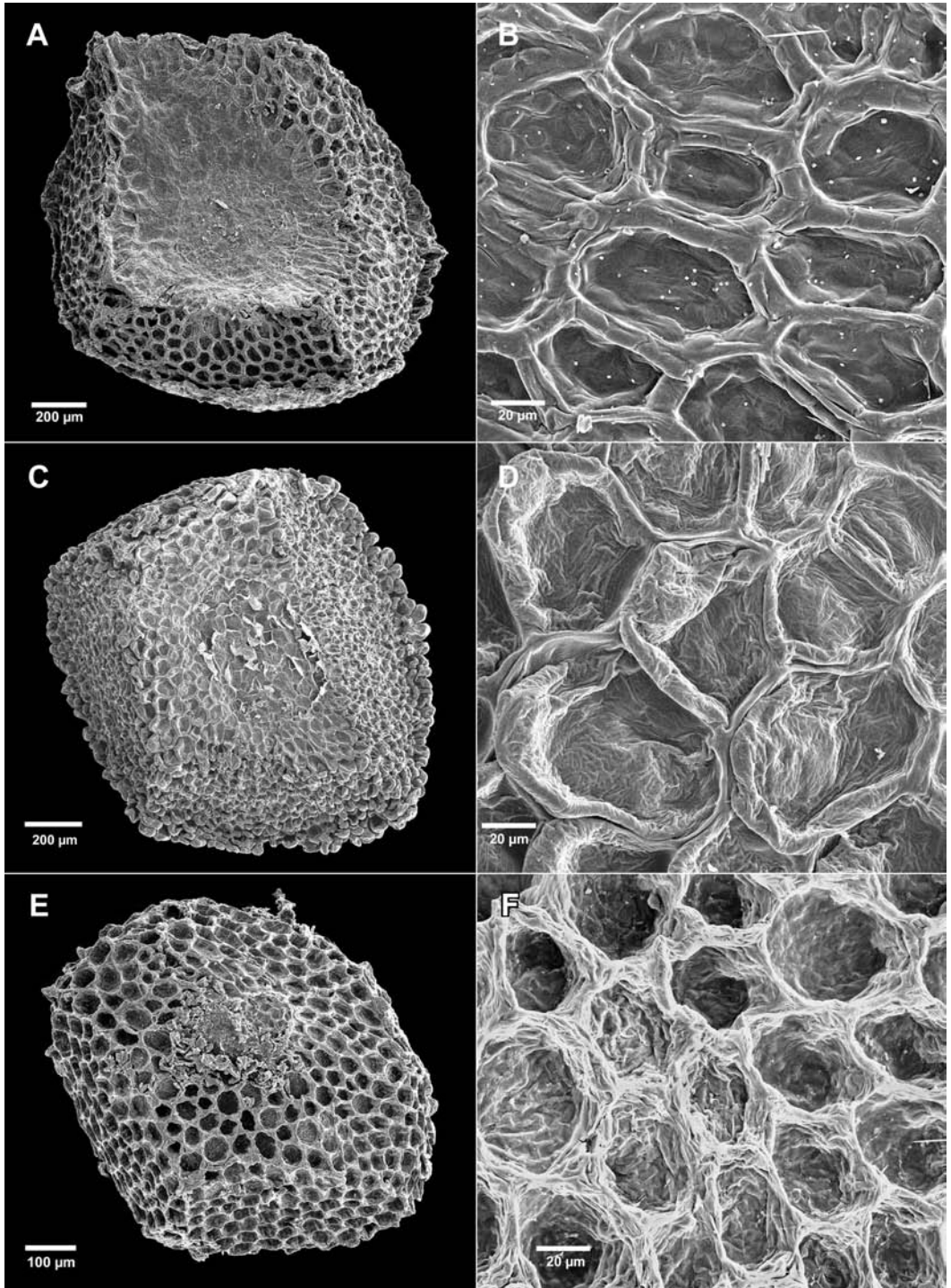


FIG. 7. Seeds of *Kadua* subg. *Gouldia*, examined by SEM. A, B. *Kadua affinis* (sample B4). A. Ventral face showing central hilar area. B. Enlargement of areoles. C, D. *K. fosbergii* (sample B18). C. Ventral face with central hilar area. D. Enlargement of areoles. E, F. *K. tryblium* (sample B8). E. Ventral face with small hilar area. F. Enlargement of areoles. Collections data in Table 1.

enous to other parts of the world, e.g., *Houstonia*, *Bouvardia*, *Arcytophyllum*, *Manettia*, *Neanotis*, *Stenaria*, and *Stenotis*, variously differ in part by having a centric hilum with or without a hilar ridge or a concave ventral face. Of these, the neotropical genera *Bouvardia* and *Manettia* differ particularly by the broad wings with a centric hilum, instead of the marginal hilum of *Kadua centranthoides*.

The Hawaiian species have four corolla characters in common. The corollas are fleshy, salverform, with

appendaged lobes, and with long, narrow corolla tubes usually 2–4 times longer than their lobes. With addition of the seed and fruit characters already discussed, strong support is seen for generic status for the native Hawaiian Hedyotideae. We resurrect the genus *Kadua*, the oldest genus name that refers to the Hawaiian species, to replace the name *Hedyotis*. Appendix 1 lists the *Kadua* names and their synonyms, and also includes seven South Pacific species that have the four corolla characters described above.

Key to Seed and Capsule Groups of Hawaiian Taxa

1. Seeds thick, brick-like or blocky; hilum centric with a small ventral circular area; fruits fleshy. Group 4. Sect. *Gouldia*
1. Seeds not brick-like; hilum punctiform, located on margin of seed or attached at a point on a rounded seed; fruits are capsules, not fleshy.
2. Seeds with a broad papery wing. Group 3. *Kadua centranthoides*
2. Seeds lacking a wing.
3. Seeds ellipsoid, ovoid, or obtusely angulate; not cuneate; hilum punctiform, attached on the rounded seed, areoles each with a bubble-like inclusion. Group 2. Sect. *Wiegmannia*
3. Seeds hat- or fan-shaped, or irregularly angulate, laterally cuneate and thinner at or near attachment of hilum, hilum punctiform, marginal.
4. Seeds with papillae embedded in testa, areole walls thick, sometimes with jagged projections; capsules 6–13 mm long, subglobose, woody. Subg. *Kadua* subgroup A
4. Seeds without papillae, areole walls usually thin; capsules 2.5–6 mm long, not woody, or in *K. formosa* 9–12 mm long, ellipsoid-cylindrical. Subg. *Kadua* subgroup B.

Rationalization of Seed Groups with Sections. Section *Gouldia* and Section *Phyllozygia*, which include *K. fosbergii*, *K. axillaris* (*H. hillebrandii*), *K. affinis* (*H. terminalis*), and *K. tryblium*, differ in Table 4 from subg. *Kadua* and sect. *Wiegmannia* in corolla bud characters: apices not depressed with lobes not inflexed, and limbs quadrangular. As described previously, the seeds and fruits differ strongly from all other taxa. Motley (2003) stated that there were two clades based on the dry versus fleshy fruits, and has further commented (pers. comm. January 2005) that he continues to consider these as separate clades based on his molecular sequence data. Although vegetatively similar to the rest of *Kadua* (Wagner et al. 1989, 1999) in seed structure, the traditional taxonomy based on corolla and fruit and molecular studies by Motley all agree that *Gouldia* is a distinctive subgroup, a subgroup here recognized as subgenus *Gouldia*.

Section *Gouldiopsis* traditionally includes *Kadua centranthoides*, *K. foggiana*, and *K. knudsenii*. Fosberg's (1943) key to sections stated that sect. *Gouldiopsis* has strongly quadrangular corolla bud limbs and capsules not much longer than wide. Of these, the capsule character seems unreliable, as other sections have capsules not much longer than wide. Fosberg stated that the three species differ from each other by characters of the thyrsoid inflorescence, leaf texture, and corolla lobe appendages. The most important of these characters are the corolla lobe appendages which occur in the Hawaiian and certain Pacific species. Wagner et al.

(1999) described *K. knudsenii* as having a long appendage and *K. centranthoides* with an inconspicuous appendage. Examination of recent collections reveals that *K. foggiana* has minute appendages. Fosberg (1943) commented that section *Gouldiopsis* seems to have given rise to the genus *Gouldia* through *K. knudsenii*, which "shows a strong resemblance to *G. terminalis* var. *elongata*" (*Kadua affinis*). This latter concept is rejected here as contrary to seed evidence and molecular evidence from Motley (pers. comm.). Our study of *K. foggiana* and *K. knudsenii* found them to have seeds generally similar to species in subg. *Kadua* subgroup B, a form considered here as plesiomorphic for the subgenus *Kadua*. They differ strongly in seed characters from *K. centranthoides* which is a highly derived form within the section needing further study.

An atypical element within section *Gouldiopsis* is the previously recognized section *Bikkiocharpa* for *Kadua formosa*, which is distinctive in its elongated capsules and in having corolla buds that are rounded, not strongly quadrangular. This species has the seed type described above in subg. *Kadua* subgroup B. Motley et al. (1998) suggested placement of *K. formosa* in sect. *Gouldiopsis* based on molecular evidence.

Of the four seed types in the Hawaiian Hedyotideae, one with a centric hilum is characteristic of the subgenus *Gouldia* (the *Gouldia* type). The three types with the hilum marginal are characteristic of the subgenus *Kadua*. Of the latter three, variants of the cuneate *Kadua* seed type are plesiomorphic for the subgenus *Kadua*.

The remaining two types occur in derived typical elements of the sections *Gouldiopsis* and *Wiegmannia*, the *Gouldiopsis* seed type in a single species, *K. centranchoides*, and the *Wiegmannia* seed type in sect. *Wiegmannia*.

In this way, seed structure correlates with the basic evolutionary pattern of the native Hawaiian Hedyotideae based on corollas and fruit characters and reinforced by the molecular study. The most basic phyletic division in the group is completely characterized by one seed type. The remaining two more derived seed types are represented in the Hawaiian Hedyotideae as end products even as transitional forms remain in existence. It is fortuitous for reference purposes that the *Gouldiopsis* seed type and the *Wiegmannia* seed type are found in the type species of their respective sections.

ACKNOWLEDGEMENTS. We thank Susann Braden for preparing the SEM micrographs and Marjorie Knowles for formatting and sizing the figures. We express our gratitude to two anonymous reviewers who made important suggestions. We thank Timothy Motley for providing helpful data from his molecular research. Ruth Schallert, botanical librarian, facilitated our hunts for hard-to-find Pacific literature.

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APPENDIX 1

List of *Kadua* names. This appendix provides a nomenclator for the genus *Kadua*, which was treated as a distinct genus until Fosberg's revision of the group (1943) where he included it within a broadly delimited *Hedyotis*, except for the fleshy-fruited species, which he treated in another segregate, *Gouldia*. Species of this group have been differentiated from the other species included within *Hedyotis* by their salverform, fleshy corollas with appendaged lobes, and either tardy and often incomplete septicial dehiscence of the capsules or having indehiscent drupaceous capsules. Motley's molecular sequence studies (Motley et al. 1998; Motley 2003) have shown this group to be monophyletic and distinct from *Hedyotis*. All of the necessary new combinations are made here by Wagner and Lorence for *Kadua* including species of sects. *Austrogouldia* and *Oceanica* not studied in this paper. Species already with valid names in *Kadua* are also listed for completeness and convenience. Brief distributional comments are given for the species of each section.

KADUA Cham. & Schldtl., *Linnaea* 4: 157. Apr 1829. *Hedyotis* subg. *Kadua* (Cham. & Schldtl.) Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 69. 1943.—LECTOTYPE: *Kadua acuminata* Cham. & Schldtl.; designated by K. M. Schumann in Engler & Prantl, *Nat. Pflanzenfam.* 4(4): 24. Jul 1891.

The genus *Kadua* currently comprises 28 species all indigenous to Pacific islands with the majority (21) species in a diverse clade in the Hawaiian Islands, three species endemic to the Marquesas Islands, two species endemic to the Society Islands, one endemic to Rapa, and one fairly widespread Polynesian species, *K. roman-zoffiensis*, from Tuamotu Archipelago, Austral Islands, Cook Islands, Ellice Islands, Gambier Islands, Line Islands, Pitcairn Islands, Society Islands, and Tokelau.

Kadua subg. **Gouldia** (A. Gray) W. L. Wagner & Lorence, comb. nov. *Gouldia* A. Gray, *Proc. Amer. Acad. Arts* 4: 310. Sep 1859. *Hedyotis* sect. *Gouldia* (A. Gray) W.L. Wagner & Herbst in W.L. Wagner, Herbst & Sohmer, *Bishop Mus. Occas. Pap.* 29:

111. 1989.—LECTOTYPE: *Gouldia sandwicensis* A. Gray, nom. illeg. (= *Kadua affinis* DC.); designated by W. L. Wagner & Herbst in Wagner, Herbst & Sohmer, Bishop Mus. Occas. Pap. 29: 111. 1989

A Hawaiian subgenus of two sections and four species.

Kadua sect. **Gouldia** (A. Gray) W. L. Wagner & Lorence, comb. nov. *Gouldia* A. Gray, Proc. Amer. Acad. Arts 4: 310. Sep 1859.

1. **KADUA AFFINIS** DC., Prodr. 4: 431. 1830.

Petesia? *terminalis* Hook. & Arn., Bot. Beechey Voy. 85. 1832. *Hedyotis terminalis* (Hook. & Arn.) W. L. Wagner & D. R. Herbst, in Wagner, Herbst & Sohmer, Bishop Mus. Occas. Pap. 29: 112. 1989.

2. **Kadua fosbergii** (W. L. Wagner & D. R. Herbst) W. L. Wagner & Lorence, comb. nov. *Hedyotis fosbergii* W. L. Wagner & D. R. Herbst, in Wagner, Herbst & Sohmer, Bishop Mus. Occas. Pap. 29: 111. 1989. *Gouldia st.-johnii* Fosberg, Bernice P. Bishop Mus. Bull. 147: 62. 1937.

3. **Kadua axillaris** (Wawra) W. L. Wagner & Lorence, comb. nov. *Gouldia axillaris* Wawra, Flora 57: 297. 1874.

Gouldia hillebrandii Fosberg, Bernice P. Bishop Mus. Bull. 147: 59. 1937. *Hedyotis hillebrandii* (Fosberg) W. L. Wagner & D. R. Herbst, in Wagner, Herbst & Sohmer, Bishop Mus. Occas. Pap. 29: 112. 1989.

Kadua sect. **Phyllozygia** (W. L. Wagner & Herbst) W. L. Wagner & Lorence, comb. nov. *Hedyotis* sect. *Phyllozygia* W. L. Wagner & Herbst, Bishop Mus. Occas. Pap. 29: 113. 1989.—TYPE: *Hedyotis tryblium* D. R. Herbst & W. L. Wagner (= *Kadua tryblium* (D. R. Herbst & W. L. Wagner) W. L. Wagner & Lorence).

A Hawaiian section of a single species closely related to sect. *Gouldia*.

4. **Kadua tryblium** (D. R. Herbst & W. L. Wagner) W. L. Wagner & Lorence, comb. nov. *Hedyotis tryblium* D. R. Herbst & W. L. Wagner, in Wagner, Herbst & Sohmer, Bishop Mus. Occas. Pap. 29: 113. 1989.

KADUA subg. **KADUA**

Kadua subg. *Kadua* is subdivided into the remaining six sections of the genus.

Kadua sect. **Oceanica** (Fosberg) W. L. Wagner & Lorence, comb. et stat. nov. *Hedyotis* subg. *Oceanica* Fosberg, Bernice P. Bishop Mus. Bull. 174: 67. 1943.—TYPE: *Hedyotis romanzoffiensis* (Cham. & Schldtl.) Fosberg (= *Kadua romanzoffiensis* Cham. & Schldtl.).

A unispecific section widespread on many of the low islands of southeastern Polynesia.

5. **KADUA ROMANZOFFIENSIS** Cham. & Schldtl., Linnaea 4:162. 1829. *Hedyotis romanzoffiensis* (Cham. & Schldtl.) Fosberg, Occas. Pap. Bernice P. Bishop Mus. 13 (19): 248. 1937.

Kadua sect. **Austrogouldia** (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis* sect. *Austrogouldia* Fosberg, Bernice P. Bishop Mus. Bull. 174: 28. 1943.—TYPE: *Hedyotis raiateensis* (J. W. Moore) Fosberg (= *Kadua raiateensis* J. W. Moore).

A section of six species of which one species is endemic to Rapa, two endemic in the Society Islands, and three endemic in the Marquesas Islands.

6. **Kadua lucei** (Lorence & J. Florence) W. L. Wagner & Lorence, comb. nov. *Hedyotis lucei* Lorence & J. Florence, Adansonia 22: 225. 2000.

7. **Kadua nukuhivensis** (J. Florence & Lorence) W. L. Wagner & Lorence, comb. nov. *Hedyotis nukuhivensis* J. Florence & Lorence, Adansonia 22: 224. 2000.

8. **Kadua tahuatensis** (Lorence & J. Florence) W. L. Wagner & Lorence, comb. nov. *Hedyotis tahuatensis* Lorence & J. Florence, Adansonia 22: 227. 2000.

9. **KADUA RAPENSIS** F. Br., Bernice P. Bishop Mus. Bull. 130: 283. 1935. *Hedyotis rapensis* (F. Br.) Fosberg, Occas. Pap. Bernice P. Bishop Mus. 13 (19): 250. 1937.

10. **KADUA RAIATEENSIS** J. W. Moore, Bernice P. Bishop Mus. Bull. 102: 43. 1933. *Hedyotis raiateensis* (J. W. Moore) Fosberg, Bernice P. Bishop Mus. Bull. 174: 28. 1943.

11. **Kadua grantii** (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis grantii* Fosberg, Bernice P. Bishop Mus. Bull. 174: 29. 1943.

Kadua sect. **Protokadua** (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis* sect. *Protokadua* Fosberg, Bernice P. Bishop Mus. Bull. 174: 23. 1943.—TYPE: *Hedyotis coriacea* J.E. Smith (= *Kadua coriacea* (J. E. Smith) W. L. Wagner & Lorence).

A unispecific Hawaiian section.

12. **Kadua coriacea** (J. E. Smith) W. L. Wagner & Lorence, comb. nov. *Hedyotis coriacea* J. E. Smith, in Rees, Cycl. 1734. 1811.

Kadua sect. **Gouldiopsis** (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis* sect. *Gouldiopsis* Fosberg, Bernice P. Bishop Mus. Bull. 174: 56. 1943.—TYPE: *Hedyotis centranthoides* (Hook. & Arn.) Steud. (= *Kadua centranthoides* Hook. & Arn.). *Hedyotis* sect. *Bikkiocharpa* Fosberg, Bernice P. Bishop Mus. Bull. 174: 25. 1943, syn. nov.—TYPE: *Hedyotis formosa* (Hillebr.) Fosberg (based on *Kadua formosa* Hillebr.).

A Hawaiian section here treated as consisting of four species. The single species formerly treated in *Hedyotis* sect. *Bikkiocharpa* was shown by molecular evidence to be nested within sect. *Gouldiopsis* by Motley et al. (1998), and differs morphologically only in its elongate capsules. The group has been shown to be monophyletic (Motley et al. 1998, pers. comm.) by molecular sequence data and by the buds apex not depressed as in other members of the genus, but has both intermediate and derived seed characteristics.

13. **KADUA CENTRANTHOIDES** Hook. & Arn., Bot. Beechey Voy. 85. 1832. *Hedyotis centranthoides* (Hook. & Arn.) Steud., Nomencl. bot., ed. 2, 1: 727. 1840.

14. **Kadua foggiana** (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis foggiana* Fosberg, Bernice P. Bishop Mus. Bull. 174: 65. 1943.

15. **KADUA KNUDSENI** Hillebr., Fl. Hawaiian Isl. 162. 1888. *Hedyotis knudsenii* (Hillebr.) Fosberg, Bernice P. Bishop Mus. Bull. 174: 57. 1943.

16. **KADUA FORMOSA** Hillebr., Fl. Hawaiian Isl. 165. 1888. *Hedyotis formosa* (Hillebr.) Fosberg, Bernice P. Bishop Mus. Bull. 174: 26. 1943.

Kadua sect. **Kadua**

A Hawaiian section of two very closely related and variable species.

17. **KADUA ACUMINATA** Cham. & Schldtl., Linnaea 4: 163. 1829. *Hedyotis acuminata* (Cham. & Schldtl.) Steud., Nomencl. bot., ed. 2, 1: 726. 1840.

18. **KADUA FLUVIATILIS** C. N. Forbes, Occas. Pap. Bernice P. Bishop Mus. 5(1): 6. 1912. *Hedyotis fluviatilis* (C. N. Forbes) Fosberg, Bernice P. Bishop Mus. Bull. 174: 90. 1943.

Kadua sect. **Wiegmannia** (Meyen) W. L. Wagner & Lorence, comb. et stat. nov. *Wiegmannia* Meyen, Reise 2: 139. 18–23 Aug 1834 ('1835'). *Hedyotis* sect. *Wiegmannia* (Meyen) Fosberg, Bernice P. Bishop Mus. Bull. 174: 29. 1943.—TYPE: *Wiegmannia glauca* Meyen (= *Kadua cordata* Cham & Schldtl.)

A complex section of 10 closely related Hawaiian species.

19. *KADUA COOKIANA* Cham. & Schltldl., *Linnaea* 4: 158. 1829. *Hedyotis cookiana* (Cham. & Schltldl.) Steud., *Nomencl. bot.*, ed. 2, 1: 727. 1840.
20. *KADUA CORDATA* Cham & Schltldl., *Linnaea* 4: 160. 1829.
- 20a. *KADUA CORDATA* Cham & Schltldl. subsp. *CORDATA*
Hedyotis schlechtendahliana Steud., *Nomencl. bot.*, ed. 2, 1: 728. 1840.
- 20b. *Kadua cordata* Cham & Schltldl. subsp. *remyi* (Hillebr.) W. L. Wagner & Lorence, comb. nov. *Kadua remyi* Hillebr., *Fl. Hawaiian Isl.* 162. 1888. *Hedyotis schlechtendahliana* Steud. subsp. *remyi* (Hillebr.) Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 40. 1943.
- 20c. *Kadua cordata* Cham & Schltldl. subsp. *waimeae* (Wawra) W. L. Wagner & Lorence, comb. nov. *Kadua waimeae* Wawra, *Flora* 57: 264. 1874. *Hedyotis schlechtendahliana* Steud. subsp. *waimeae* (Wawra) W. L. Wagner & Lorence, *Novon* 8: 316. 1998.
21. *Kadua degeneri* (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis degeneri* Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 55. 1943.
- 21a. *KADUA DEGENERI* (Fosberg) W. L. Wagner & Lorence subsp. *DEGENERI*
- 21b. *Kadua degeneri* (Fosberg) W. L. Wagner & Lorence subsp. *coprosmifolia* (Fosberg) W. L. Wagner & Lorence, comb. nov. *Hedyotis degeneri* Fosberg var. *coprosmifolia* Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 56. 1943.
22. *Kadua elatior* (H. Mann) W. L. Wagner & Lorence, comb. nov. *Kadua cookiana* Cham. & Schltldl. var. *elatior* H. Mann, *Proc. Amer. Acad. Arts* 7: 172. 1867. *Hedyotis elatior* (H. Mann) Fosberg, *Brittonia* 8: 167. 1956.
23. *Kadua flynnii* (W. L. Wagner & Lorence) W. L. Wagner & Lorence, comb. nov. *Hedyotis flynnii* W. L. Wagner & Lorence, *Novon*: 8: 311. 1998.
24. *KADUA FOLIOSA* Hillebr., *Fl. Hawaiian Isl.* 164. 1888. *Hedyotis foliosa* (Hillebr.) Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 44. 1943.
25. *KADUA LAXIFLORA* H. Mann, *Proc. Amer. Acad. Arts* 7: 171. 1867.
Hedyotis mannii Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 49. 1943.
26. *KADUA LITTORALIS* Hillebr., *Fl. Hawaiian Isl.* 166. 1888. *Hedyotis littoralis* (Hillebr.) Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 53. 1943.
27. *KADUA PARVULA* A. Gray, *Proc. Amer. Acad. Arts* 4: 317. [Sept]1859. *Hedyotis parvula* (A. Gray) Fosberg, *Bernice P. Bishop Mus. Bull.* 174: 54. 1943.
28. *Kadua st-johnii* (B. C. Stone & Lane) W. L. Wagner & Lorence, comb. nov. *Hedyotis st-johnii* B. C. Stone & Lane, *Pacific Science* 12: 141. 1958.