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Taxonomy of the Hawaiian Genus Broussaisia (Saxifragaceae)

By F. RAYMOND FOSBERG

University of Pennsylvania

INTRODUCTION

Broussaisia is a common tree or shrub in the wetter portions of the forests of the Hawaiian islands. According to Hillebrand, the Hawaiian names for this plant were puahanui and kanawau.

This genus belongs in the Saxifragaceae-Hydrangeoidae-Hydrangeae of Engler's (5)¹ classification and is most closely related to the genus *Dichroa* (*Adamia*) of southern Asia, Malaysia, and New Guinea. This relationship was first pointed out by Gray (8, pp. 682-686) and is confirmed by a careful study of these and related genera. *Broussaisia* differs from *Dichroa febrifuga*, the best known species of *Dichroa*, in the strictly terminal panicles, strictly opposite or verticillate leaves, in the united style and stigma, in the more strongly intruded placentae with seeds only on the reflexed outer portion, not on the parts toward the axillary position, which in *Broussaisia* are weakly united, and in the much smaller embryo. Otherwise the seeds show a striking resemblance. Several New Guinea species of *Dichroa* may not agree with *D. febrifuga* in some of these respects.

HISTORY

Broussaisia was first described by Gaudichaud (6, pp. 479-480, pl. 69) and dedicated to F. J. V. Broussais, famous French physician, author of a treatise on physiology applied to pathology (2). Gaudichaud had only the staminate plant and consequently misinterpreted it as having hemaphrodite flowers with a superior ovary. His plate

¹ Numbers in parentheses refer to Literature Cited, p. 60.

also shows that he misunderstood the structure of the ovary, making it 5-celled with axile placentation. One species, *B. arguta*, was recognized.

Hooker and Arnott (10, p. 84) published a short description of *B. arguta*, again from a staminate plant only, adding nothing further to the understanding of the genus.

Gaudichaud, on his second voyage around the world in the *Bonite* had more opportunity to study his genus, this time finding that it was dioecious and working out the details of its structure with great care. A plate of a second species, *B. pellucida* (7, Atlas, pl. 9), shows the plant to be dioecious and presents detailed analyses of the flowers which are so carefully done that only a trifling inaccuracy in the position of the ovules had to be corrected by later workers. Unfortunately no text was published to accompany the plates of the phanerogams illustrated in this atlas, and Gaudichaud died soon after. Subsequent authors have considered that several figures in this plate belong to *B. arguta* rather than to *B. pellucida*, but there is no way of ascertaining Gaudichaud's intentions in the matter.

Gray (8, pp. 682-686, pl. 87) at about the same time published a full and careful discussion of the genus, agreeing in all but the details of the placentation with the second plate of Gaudichaud, and recognizing with some doubt both of Gaudichaud's species. He correctly suggested the genus *Adamia* (*Dichroa*) as the nearest relative of *Broussaisia*.

Baillon (1, p. 343) suggested that B. pellucida might well be only a form of B. arguta with somewhat different leaves.

Hillebrand (9), Rock (12), Skottsberg (13), and other recent writers on Hawaiian plants recognize two species in the genus but give various criteria for separating them.

Engler (5) places *Broussaisa* between *Dichroa* and *Decumaria*, but his figures show that he misunderstood the structure of the ovary, considering it to be truly 5-celled and the placentae axile. His observations are not borne out by examination of actual cross sections.

Hillebrand (9, p. 120) considered the genus polygamo-dioecious, but, to my knowledge, only one other has reported this condition; the plants seem to be unquestionably dioecious.

Hutchinson (11, p. 100) published a treatment of the genera of the Hydrangeaceae in which he dissociates the group altogether from the Saxifragaceae, considering them similar only as a result of parallel development. Broussaisia and Dichroa are even placed in a different subfamily from Hydrangea, along with Philadelphus and its relatives. These conclusions are based chiefly on the single character of woody habit. In his discussion of Broussaisia, Hutchinson says that the flowers are polygamo-dioecious, apparently copying Hillebrand's error.

TAXONOMY

In the field the similarities between *Broussaisia arguta* and *B. pellucida* seem far more striking than the differences. In herbaria the plants I examined, segregated into each of these supposed species, were quite heterogeneous, and identical plants occurred frequently in both covers. An examination of several treatments of the genus made by botanists who have had extensive field acquaintance with it reveals that, though all agree that there are two species, various authors differ as to the characters on which these species are based.

Hillebrand (9, p. 120) separates them simply on the basis of ternate or opposite leaves, flower color in the male flowers, and the stigma sessile or styled in the female. In his descriptions it is evident that there is a difference in flower and fruit size, and in the degree of adnation of the calyx to the ovary. Also he mentions that *B. arguta* is very rarely ternate.

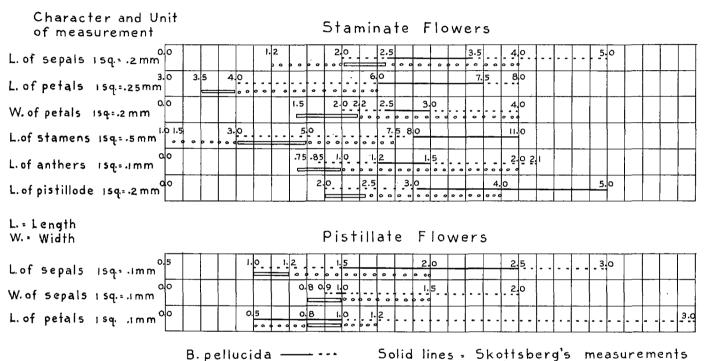
Rock uses these characters and adds that the female corymb is larger and the veins perfectly pellucid in *B. pellucida* while opaque in *B. arguta*. He also states that the leaves are "never ternate" in *B. arguta*, and that they are narrower in *B. pellucida*.

Skottsberg (13, pp. 235-237) rejects as inconstant Rock's key characters of ternate and opposite leaves and flower color. He apparently accepts as constant the pellucid or opaque veins in the leaves. He elaborates a series of flower characters based on measurements and presented in tabular form, supported by excellent drawings. For the ternate leaved plants with the floral characters of *B. arguta* he creates the name *B. arguta* f. ternata, which name he credits to Forbes, evidently on the basis of a pencilled annotation, "var. ternata", on the labels of several Forbes collections in Bishop Museum. No type is designated.

The specimens available can be segregated into two groups on the basis of almost any of the above-mentioned characters, but the groups do not correspond. As Skottsberg points out, ternate leaves occur in plants with both types of flowers. The same is true of opposite leaves. Furthermore, I have found both ternate and opposite leaves on four plants, three times on sucker shoots of opposite-leaved plants, and once both ternate and opposite-leaved flowering branchlets on a ternate branch of a ternate plant. Two of these were found on Molokai where both types are common, the other two on Oahu where all other plants observed in the vicinity had opposite leaves. The width of the leaves varies conspicuously in groups based upon any other characteristics. This distinction between pellucid and opaque veins must be rather subtle. I have never seen any *Broussaisia* plant whose veins I would not consider pellucid, though some are more pellucid than others.

Flower color varies rather strikingly, but the variation is not parallel to that of any other character. On this basis it would be impossible to separate the plants into two species, but they could be divided into several poorly defined groups. The plants in certain regions are characterized by certain flower colors: in Kaluanui Valley, Oahu, the flowers tend to be very dark bluish; on Mount Kaala, Oahu, they tend to be pink. Those that I have seen on Maui are pinkish. Anyone who would attach taxonomic importance to flower color of the anthocyanin type, other than mere presence or absence, should consider carefully a recent article by Chenery (3, pp. 304-320) who concludes, on the basis of much analytical data, that available aluminium ions in the soil are responsible for blue color rather than pink in *Hydrangea*. This conclusion may possibly be valid for related genera as well as for *Hydrangea*.

At first glance the floral characteristics tabulated by Skottsberg (13, p. 237) seem convincing. Two points, however, lessen one's assurance. The table is based on a very few collections. Taking all the collections available in Bishop Museum and my own collections, segregating them as nearly as possible into two species according to Skottsberg's treatment, measuring the parts and tabulating the figures as he did, then plotting the figures graphically, I obtained a very different result (table, p. 53). The graph shows an overlapping in every character; in many there is complete overlapping. Almost all of the differences brought out in Skottsberg's table are those which might be expected in a small-flowered form. A simple reduction in flower size would account for every difference between the two species except for the short style in the pistillate flower and, perhaps, the extreme reduction and possible partial sterilization of the anthers of



B. arguta ----

Dotted lines - Additional measurements

the staminate ones. Small-flowered forms are known in many other species of plants, and when they are not constant, are seldom given specific rank.

It is difficult to be certain about fruiting plants, but plants with flowers may be divided into two groups: one with a very short style in the pistillate flower and extremely reduced anthers in the staminate, the other with a well developed style and anthers well over 1 mm. long. These correspond roughly to what have been called *B. pellucida* and *B. arguta*. Certain plants with short stamens, petals, etc., fall into *B. arguta* because of the large anthers. The other characters which have been used to segregate the two do not correlate at all.

Each of these groups may be further divided into an oppositeand a ternate-leaved group. The leaf-width varies continuously in all these groups, so is valueless. The amount of pubescence also varies continuously with no correlation with the other characters used and helps very little. One specimen, however, from Kauai, which is entirely glabrous, has abundant anthocyanin pigment in all parts and the leaves are elliptical and markedly acuminate. This seems separable, though it is approached by several other specimens in one or more of these characters. These groups do not fit my concept of species. Rather I consider them forms which may be grouped into two varieties with two forms under one and three forms under the other.

The peculiar pistillate flower pictured by Skottsberg under B. arguta f. ternata with very long calyx lobes represents an extreme variation, perhaps even a monstrosity, attained or approached in all the groups of which we have a large number of collections.

The collections cited here which are marked (D) are in the herbarium of Otto Degener, those marked (G) in the Göteborg Botanical Garden, and all others are in the herbarium of Bernice P. Bishop Museum.

Broussaisia Gaud., Voy. Uranie Bot., p. 479, 1830.

Tree or shrub, usually more or less hirsute or hirsute-pilose on many parts (stem, petioles, under side of leaves, inflorescence branches), rarely glabrous, branchlets cylindrical, 1-2 cm. in diameter, leaf scars conspicuous, broadly triangular-heart-shaped, up to 1 cm. broad; leaves opposite or ternate, petiolate, petiole usually 1-4 cm. long, up to 8 cm., blade usually 10-15 cm. long, 4-6 cm. wide, sometimes larger, often reduced above, on sucker shoots often twice as large, oblanceolate to obovate-cuneate, oblong or elliptical, rarely somewhat ovate, base acute to cuneate or attenuate, apex acute or obtuse, usually slightly acuminate, rarely markedly so, veins pellucid, impressed above, very prominent beneath, margin crenate-serrate, with each tooth bearing a blunt, forward-

appressed lobe or mucro, the outer margin of each tooth closely revolute, texture coriaceous, glossy above; inflorescence a corymbiform thyrsoid panicle, several times branched, varying from dense and small to loose and large; flowers dioecious; staminate flowers subhypogynous, with well-developed pistillode, calyx adnate to base of pistillode, with 5 lanceolate lobes 1-5 mm. long, petals 5, free, ovate, valvate, 3.5-8.0 mm. long, 1.5-4.0 mm. wide, stamens 10, in one ring, both opposite and alternate with the petals, filaments subulate, 1-11 mm. long, varying greatly even in the same flower, some tend to have the opposite and the alternate filaments of different lengths, anthers oblong, basifixed, purple to brown, dehiscing by two longitudinal slits, pollen granular, purple, pistillode 2-5 mm. long, with a well-developed ovary bearing ovules, usually with a welldeveloped style, stigma and placentation similar to that of pistillate flowers but smaller; staminate inflorescence disintegrating and dropping after anthesis; pistillate flowers almost epigynous, only the small conical top portion of ovary free, calyx lobes lanceolate or ovate, 1-3 mm. long, 0.8-2.5 mm. wide, petals triangular, much reduced, 0.5-3.0 mm. long, stamens completely absent, ovary urn-shaped, fundamentally 1-celled, but falsely 4-5-celled due to ingrowth of the 4 or usually 5 parietal placentae until they touch and fit closely together, ovules many, restricted to the outer and reflexed portions of the placentae, style more or less developed, stigma with 4 or 5 lobes formed by the radial loops of a fleshy ridge that surrounds the top of the stigma in a scalloped manner; fruit a mealy-fleshy berry, ellipsoidal to spherical, 1 cm. or less long, red to maroon outside, white inside; seeds numerous, horizontally placed, minute, elliptical, minutely beaked at one end, 1 mm. or less long, testa thin, longitudinally reticulate, light brown, endosperm rather soft, embryo very small.

One species known, endemic to the Hawaiian islands.

The peculiar form of the stigma and the placentation of the ovary may be best understood by examination of figure 1. The placentation really combines the features illustrated by Gray and by Gaudichaud in their plates.

Good plates and figures of this genus have been published by Gaudichaud (6, pl. 69; 7, pl. 9), by Gray (8, pl. 87), by Rock (12, pl. 59, p. 150), by Skottsberg (13, p. 236), and by Degener (4, pl. 43, p. 167).

Key to forms

Style of pistillate flowers less than 1 mm. long, anthers of staminate flowers
1 mm. or less long.
Leaves ternate
Leaves opposite
Style and anthers well over 1 mm. long.
Plant glabrous with purplish red stems, petioles and veins; leaves
elliptic, acuminate

² To anyone who is dismayed by the number of quadrinomials proposed it may be pointed out that, though the binomial *Broussaisia arguta* is sufficient for most practical purposes, a more detailed classification is necessary for a thorough understanding of the genus.

Plant more or less hirsute, not as above.

Broussaisia arguta Gaud. var. arguta Fosberg, new name (fig. 1).

Antherae supra 1 mm. longae, stylus in florae pistillatae supra 1 mm. longus.

Anthers more than 1 mm. long, style (portion smaller in diameter than stigma) more than 1 mm. long.

This variety occurs on all of the six largest islands of the Hawaiian group. Three forms can be segregated within it.

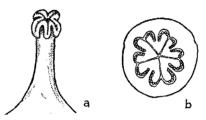


FIGURE 1.—Broussaisia arguta var. arguta: a, style and stigma; b, cross section of immature fruit.

Broussaisia arguta Gaud. var. arguta Fosberg f. arguta Fosberg, new name (fig. 1).

Broussaisia arguta Gaud., Vov. Uranie Bot., p. 479, 1830.

Planta hirsuta, folia opposita.

Plant with vegetative parts ordinarily more or less hirsute, not strongly reddish purple, leaves opposite, not strongly acuminate.

Hawaiian islands, no locality given, Mann and Brigham 755, 522 (lower specimen on sheet).³

Kauai: Waioli Valley, Forbes 112.K; Power Line Trail, Forbes 159.K; Waimea drainage basin, west side, Forbes 847.K; Waimea drainage basin, west side, Kalalau Trail, Forbes 1045.K; Kaholuamanoa [Kaholuamanu] above Waimea, Heller 2302; northwest end of Alakai Swamp, Na Pali-Kona Forest Reserve, St. John and others 10750a; Kalaheo, above Kahili bog, alt. 2,300 ft., St. John and Fosberg 13529; Kokee, Degener 9087 (D); Waineke Swamp, Degener 10925 (D); Hanapepe Falls, Degener 2298 (D).

Oahu, Waianae Mountains: east slope of Puu Kaua, alt. 950 m., Fosberg 13754; Puu Kaala, Degener 9078 (D); southeast slope of Puu Kaala, Degener and others 11577 (D); Puu Kaala, Waia-

³ To save space, dates of collections are not given where collectors' numbers are available.

naeuka, at various altitudes, St. John 9931, 9923, Hume 46, Krauss (Jan. 8, 1933), Tanaka (Nov. 30, 1929), Fosberg 13668, 13668a, 13661a (with one branch ternate, others opposite).

Oahu, Koolau Range: Kipapa Gulch, Waipio, alt. 650-850 m., Fosberg 9757, 9760, 9769, 9782, Nitta (Degener's) 9093 (D), A. M. Octavio (Nov. 10, 1929); south ridge of south Opaeula Gulch [on later maps Poamoho Trail, Helemanu Gulch], alt. 740 m., Fosberg 8739; Palolo-Waialaenui ridge, alt. 550 m., Fosberg 10724; Kaluanui Valley, alt. 650 m., Fosberg 13754; main divide, near head of Castle Trail, Kaipaupau, alt. 900 m., Fosberg and Hosaka 13950, 13957; head of Kawainui Gulch, main divide, alt. 840 m., Fosberg and Hosaka 13693 (ternate and opposite sucker shoots on same plant); Palolo, Shaw; Pupukea-Kahuku Trail, alt. 1,650 ft., Hasegawa (Mar. 6, 1932); Punaluu, alt. 2,050 ft., Hume 102; Punalou [Punaluu ?] Mountain, (Rock?, Aug. 18, 1908); Kalihi, Faurie 1023; Wilhelmina Rise, Degener and Park 9076 (D); near Honolulu, in small valley east of Wilhelmina Rise, Degener 1605 (D); east ridge of Manoa Valley, alt. 2,000 ft., Degener and others 3517 (D); Pupukea-Kahuku region, Degener and others 9077 (D); Pig-God Trail, Punaluu Valley, Degener 4351 (D); Mount Olympus, Nitta (Degener's) 9095 (D); Tantalus, Degener 9088 (D); Waimano Trail, near summit, Degener and others 10926 (D); ridge east of Kuliououiki, Forbes 2010.O; Lanihuli Trail, Forbes and Stokes (June 28, 1908); Waiolani ridge, Lanihuli Trail, Forbes (Sept. 17, 1908); Konahuanui-Olympus trail, Garber 494, 239; Konahuanui ridge. Forbes (July 28, 1908); Konahuanui, Yoshinaga (Dec. 26, 1929); ridge south of South Opaeula Gulch [Helemanu Gulch on later maps], Paalaa, Onouve (Sept. 24, 1933). The last five collections cited have unusually long calyx lobes.

Molokai: mountains above Puu Kolekole, Forbes 208.Mo; Wailau Valley, near U.S.G.S. gage station, Waikeakua Stream, alt. 250 m., Fosberg 13455; sloping plateau east of Mapulchu Valley, alt. 850 m., Fosberg 13362, 13360; top of cliff at head of Wailau Valley, alt. 900 m., Fosberg 13383, 13380, 13382, 13381, 13384 (approaching var. pellucida but young). The last two collections cited have both ternate-and opposite-leaved branches.

Lanai: mountains east end, Forbes 213.L; ridge left of Kaiholena, Forbes 323.L (in part, pistillate twig only); flat topped ridge northwest of Puu Aalii, alt. 900 m., Fosberg 12514.

Maui along Olinda pipeline, Degener and Wiebke 3520 (D). So far as available collections reveal, this form is absent from Hawaii.

Broussaisia arguta Gaud. var. arguta Fosberg f. glabra Fosberg, new form.

Planta glabra, partes herbaceae rubro-purpureae, folia elliptica valde acuminata opposita.

Plant entirely glabrous, vegetative parts (except upper surface of leaves) reddish purple, leaves opposite, elliptical, strongly acuminate.

Kauai: Lihue-Koloa Forest Reserve, base of mountains near north fork of Waialua River, alt. 1,250 ft., Catto 72 (type).

One other specimen, cited under f. arguta, Forbes 847.K from Kauai, approaches this form in being almost glabrous, but has leaf shapes well within the range of the ordinary form; no note was made on the label as to the presence or absence of anthocyanin in stems and leaves.

Broussaisia arguta Gaud. var. arguta Fosberg f. ternata Forbes ex Skottsberg, Acta Hort. Göteborg., vol. 2, p. 235, 1925.

Like f. arguta but with ternate leaves.

Kauai: Kaholuamanu behind Waimea, Forbes 412.K; northwest end of Alakai Swamp, Na Pali-Kona Forest Reserve, St. John and others 10750b.

Oahu: ridge north of Waimea Valley, Forbes 2046.0; Punaluu, alt. 2,000 ft., Hume 101 (a sterile twig resembling a sucker shoot, no note as to its occurrence).

Molokai: south of Pepeopae, *Degener 9079* (D); between Waikolu Valley and probably northern base of Puu Alii, *Degener and Wiebke 3519* (D); Kamoku, *Forbes 689.Mo*.

Lanai: mountains east end, Forbes 213.L (part of collection opposite-leaved, cited under f. arguta); Lanaihale, Munro 145.

Maui, west: on way to Mount Eke from last ditchman's house at stream, *Degener and Wiebke 2308* (D); Puu Kukui, between Nakalalua and summit, alt. 1,675 m., *Fosberg 10021*, 10025; Puu Kukui, *Neal* (Aug. 16, 1933); *Skottsberg 776* (G).

Maui, east: Makawao district, Haiku-uka trail, alt. 950 m., Fosberg 9882; above Makulau [Mokulau] Landing, Forbes 1763.M; north of Olinda along ditch trail, Degener and Wiebke 2309 (D); along Olinda pipeline, Degener and Wiebke 3518 (D), 3522 (D), Degener 9082 (D); Olinda, Kula pipeline, alt. 4,500 ft., St. John

10308; northeast slope of Haleakala, Koolau Gap, Ainaho, alt. 5,800 ft., G. E. Olson (Nov. 20, 1936); Ukulele, Forbes 950.M. The last collection, part of St. John 10308, and those by Neal and Skottsberg from Puu Kukui have unusually long calvx lobes.

Hawaii: Kohala mountains, upper Hamakua ditch trail, head of Alakahi fork of Waipio Valley, alt. 1,075 m., Fosberg 10212; Hilo, Lydgate; Awehi Stream, above Hilo, alt. 510 m., Fosberg 10477; near Glenwood, Degener 9083 (D); along pig-hunter's trail running northwest of 27 milepost, Kilauea, Degener and Iwasaki 9081 (D); 29 Miles, Kilauea, Degener 9085 (D); tree-fern forest, Kilauea, Degener 1603 (D); Kilauea (Oct. 7, 1902, no collector noted); W. T. Brigham (1899); Kilauea, rim of Napau Crater, alt. 800 m., Fosberg 10477; Kona, Kaalapuuwale, Forbes 285.H.

Skottsberg cites other collections of his own from Hawaii which I have not seen. Two collections cited above, *Fosberg 10104 and 10477* approach var. *pellucida*.

Broussaisia arguta Gaud. var. pellucida (Gaud.) Fosberg, new comb. Broussaisia pellucida Gaud., Voy. Bonite, Bot., pl. 9, 1846-49.

Differs from var. arguta in the strongly reduced anthers, 1 mm. or less long, and in the much shortened and thickened style, also less than 1 mm. long, with the stigma almost sessile on the conical upper portion of the ovary.

Two forms may be distinguished.

Broussaisia arguta Gaud. var. pellucida (Gaud.) Fosberg f. pellucida Fosberg, new name.

Folia ternata. Leaves ternate.

Hawaiian islands, without data, Rock 8855.

Kauai: Kaholuamano [Kaholuamanu] Rock 10068.

Molokai: sloping plateau east of Mapulehu Valley, alt. 800-850 m., Fosberg 13357, 13363, 13361, 13385; between Waikolu Valley and probably northern base of Puu Alii, Degener and Wiebke 3519 (D). The last three collections cited approach var. arguta f. ternata.

Maui, west: Puu Kukui, Neal (Aug. 16, 1933).

Maui, east: Kailua, above upper ditch trail, Lyon (Rock's?) 10069; Makawao district, Haiku-uka Trail, alt. 950 m., Fosberg 9863.

Hawaii: Kohala mountains, upper Hamakua ditch trail, head of Alakahi fork of Waipio Valley, alt. 1,075 m., Fosberg 10217; woods above Waimea, Rock 4323; Hilo, Nakahanaloa, Puu Uauaka, Skotts-

berg 488; Awehi Stream, above Hilo, alt. 485 m., Fosberg 10497; between Glenwood and 29 Miles, Degener 9084 (D), 9086 (D); Kilauea, alt. 1,200 m., Skottsberg 571; forest below Volcano House (Kilauea), Skottsberg 1916; Kilauea, Chain of Craters, between Makaopuhi and Napau Craters, alt. 840 m., Fosberg 10105; Hualalai, west slope Moonuiakea, Rock 3763, 3837.

Broussaisia arguta Gaud. var. pellucida (Gaud.) Fosberg f. oppositifolia Fosberg, new form.

Folia opposita. Leaves opposite.

Kauai: Kaholuamano [Kaholuamanu], Rock 5431.

Maui: along Olinda pipeline, Degener and Wiebke 3521 (D).

Lanai: Puu Aalii, alt. 900 m., Fosberg 12376 (type); Lanaihale, Munro 16; ridge left of Kaiholena, Forbes 323 (in part, staminate twig only). The last collection has the anthers a trifle too large, and may really belong with var. arguta. Certainly it is intermediate. Careful collecting may reveal this form on some of the other islands.

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