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Dioecy in the Endemic Genus *Dendrocacalia* (Compositae) on the Bonin (Ogasawara) Islands

Makoto Kato and Hidetoshi Nagamasu

Biological Laboratory, Yoshida College, Kyoto University, Kyoto, 606-01 Japan

Dendrocacalia crepidifolia **Nakai (Compositae, Senecioneae), the only species of this arboreal genus endemic to Haha Island in the Bonin Islands, was found to be dioecious. Male flowers differ from female ones in having a stunted style (style in female exserted from corolla and deeply bifurcating) and anthers filled with fertile pollen (anthers in the female lacking pollen). The size of the corolla and number of florets per head were similar between male and female flowers. The crown area of this arboreal species was also similar in male and female plants. The sex ratio was 0.55 male, not significantly different from 0.5. Both sexes produced nectar of similar sugar concentration (ca. 50%). The flowers are pollinated by feral honeybees (*Apis mellifera*), but they are thought to have been pollinated by small, less-hairy, endemic solitary bees before honeybees were introduced and subsequently became the dominant bee species on the island. The evolution of dioecy of *Dendrocacalia* on the island is thought to stem from the deleterious effects of inbreeding that are inherent in plants with geitonogamy. The increased geitonogamy on the island has resulted from increased woodiness (i.e., increased number of flowers per plant) and the original dependence on endemic bee pollinators, which are now endangered.**

Key words: Bonin Islands — Compositae — *Dendrocacalia* — Dioecy — Feral honeybee

Adaptive radiation of flowering plants is common on oceanic islands. For example, adaptive radiation is prominent in Hawaii (Carlquist 1974, Helenurm and Ganders 1985). Similar adaptive radiation, although on a much smaller scale, occurred in the Bonin (Ogasawara) Islands, 1,000 km south of the mainland of Japan. Characteristic speciation in *Pittosporum* (4 species, Pittosporaceae), *Symplocos* (3 spp., Symplocaceae), *Callicarpa* (3 spp., Verbenaceae) and *Crepidiastrum* (3 spp., Compositae) are good examples (Ono 1985, Nagamasu 1987, Kawakubo 1990, Ito and Ono 1990, Soejima *et al.* 1994). The flora of the Bonin Islands is composed of 260 flowering plant species, containing 112 endemic species and two endemic genera (Ono 1985). One of the endemic genera is *Boninia* (Rutaceae) which is closely related to *Melicope* (including *Pelea*, a genus endemic to Hawaii). The other endemic genus in the Bonin Islands is *Dendrocacalia* (Compositae, Senecioneae) which is thought to be a member of the subtribe Tussilagininae (Bremer 1994). *Dendrocacalia* is an example of a genus that evolved woodiness in the islands as have *Hedyotis* (Rubiaceae), *Lobelia* (Campanulaceae) and *Crepidiastrum* (Compositae).

We found that *Dendrocacalia*, previously known as a hermaphrodite, was actually dioecious. Relatively large proportions of dioecious species in oceanic islands are reported in Hawaii (Carlquist 1974), New Zealand (Godley 1975, Webb and Kelly 1993) and the Bonin Islands (Kawakubo 1990). The high prevalence of dioecy on oceanic islands was attributed to correlations between dioecy and the dispersal of seed by birds (Bawa 1980). *Dendrocacalia* is an exception to this trend because its seeds are wind-dispersed and its putative relatives are not dioecious. There are several genera in which species on islands are dioecious but their relatives on the nearest continent are hermaphrodite (Carlquist 1974, Kawakubo 1990). Thus, we confront the repeatedly discussed problem of why dioecy has evolved in oceanic islands.

A correlation between dioecy and pollination by small, generalist insects was pointed out by Bawa and Opler (1975). Are there any characteristics particular to the pollinator faunas of oceanic islands? Both Hawaii and the Bonin Islands had bizarre bee faunas characterized by small body size, high endemism and non-sociality (Perkins 1901, Kato 1992), although native pollinator faunas in these islands are now endangered by competition with naturalized honeybees (Messing 1991, Kato 1992) and predation by social wasps and ants (Cuddihy and Stone 1990). To consider the selection pressure favoring dioecy in oceanic islands, we investigated the distribution of males and females and the pollination biology of *Dendrocacalia* in the Bonin Islands. Unfortunately, the flowers were monopolized by naturalized honeybees everywhere the plant is distributed. We can only speculate about the original pollination system by observing native bee visits to other native flowers in adjacent small islands where honeybees have not yet invaded.

This paper describes dioecism in *Dendrocacalia*, reports the distribution and ecological traits of male and female plants, and examines the floral and pollination biology of this dioecious species. Finally, the evolution of dioecy in oceanic islands is discussed in the context of reducing geitonogamy caused by the woodiness and a dependence on small, endemic, solitary bees for pollination.

Materials and Methods

Dendrocacalia crepidifolia Nakai is an arboreal species about 3-5 m tall, and is only distributed across mountain ridges at altitudes of more than 300 m above sea-level on Haha Island (26°43′N, 142°8′E), Ogasawara-mura, Tokyo Prefecture, Japan (Fig. 1). It flowers in November and sets fruit in December to January.

Sexual characteristics of the flowers, and insect visits to the flowers, were observed from November 16 to 20, 1993 at Mt. Chibusa (462 m in altitude), Mt. Sakaigatake (444 m) and Mt. Sekimon (405 m). As preliminary observation revealed that this species was dioecious, the distribution of male and female plants was surveyed along a trail at the eastern slope of Mt. Sakaigatake. Over a distance of 200 m along the trail, 77 flowering plants were found, tagged and mapped. Floral sexual characters of these plants were investigated. Crown areas were estimated by measuring the length and width of the crown of each plant. One inflorescence was sampled from each of 19 of the 77 marked plants, and seed set of these was examined on December 23, 1993. Here, seed set was determined by the proportion of flowers that set a seed within a subset of inflorescences. Preliminary study showed that the filled seeds can germinate soon after sowing on a wet medium.

Insect visits to flowers of a male and a female plant per 10 minutes were observed from 9 : 00 to 11 : 00 am on November 18 at Mt. Sakaigatake. Flower visitors, mostly honeybees, were collected on male and female flowers from 9 : 00 to 10 : 00 am on November 19. Honey crop in the stomachs of the collected specimens was extracted by pressing their thoraces and abdomens, and the volume and sugar concentration of the honey crop were measured with microcapillary tubes and pocket refractometers, respectively. Nectar concentrations from honey stomachs of honeybees are known to be only slightly (0-1.8%) more dilute than the syrup (Park 1933). Pollen loads on corbiculae of the collected honeybees were surveyed by scanning electron microscopy (SEM), Hitachi S-2050, and pollen compositions were examined. Pollen attachment on the body of flower visitors was also surveyed by SEM.

For observation of floral morphology, the florets were fixed with 70% ethanol, and critical-point dried for SEM. Pollen stainability as an estimate of fertility was examined by light microscopy (LM), after staining the fixed anthers of both male and female florets with 0.5% cotton blue in lacto-phenol. Acetolysis of pollen grains was made following the standard method (Erdtman 1960), mounted in silicon oil for LM, and critical-point dried for SEM.

Results

Dendrocacalia crepidifolia was found to be dioecious. In the female floret, the style is thicker, exserted from the corolla and deeply bifurcated above (Figs. 2B, D); stamens lack a distinct anther-tube and are reduced (Fig. 2D), and anthers are lean, lacking pollen grains (Fig. 2F). In the male floret, the style is thinner and not completely exserted from the distinct anther-tube (Figs. 2A, C); the anthers are filled with fertile pollen grains (Figs. 2E, H). Pollen grains were tricolporate monads with echinate sexine (Fig. 2H).

The following characteristics were common to both male and female florets: heads are discoid in a dense

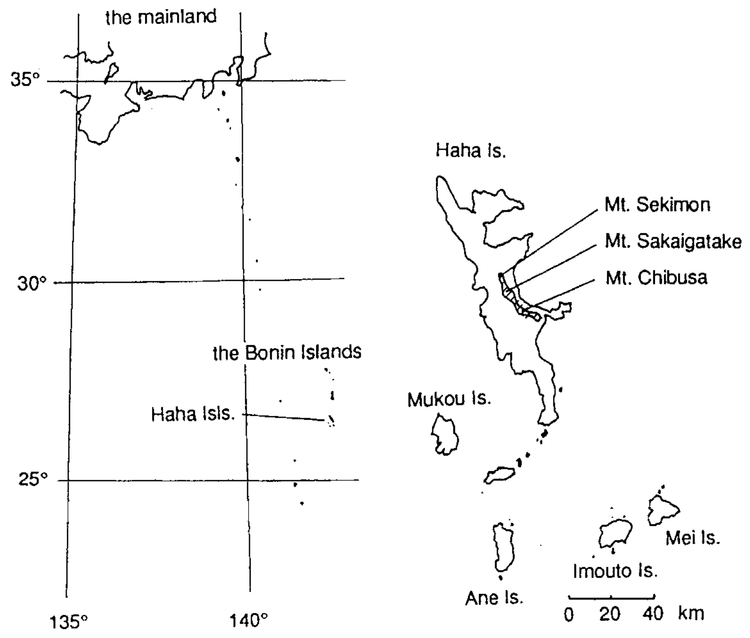

Fig. 1. A map of Bonin Islands. Shaded area refers to the range of *Dendrocacalia crepidfolia*.

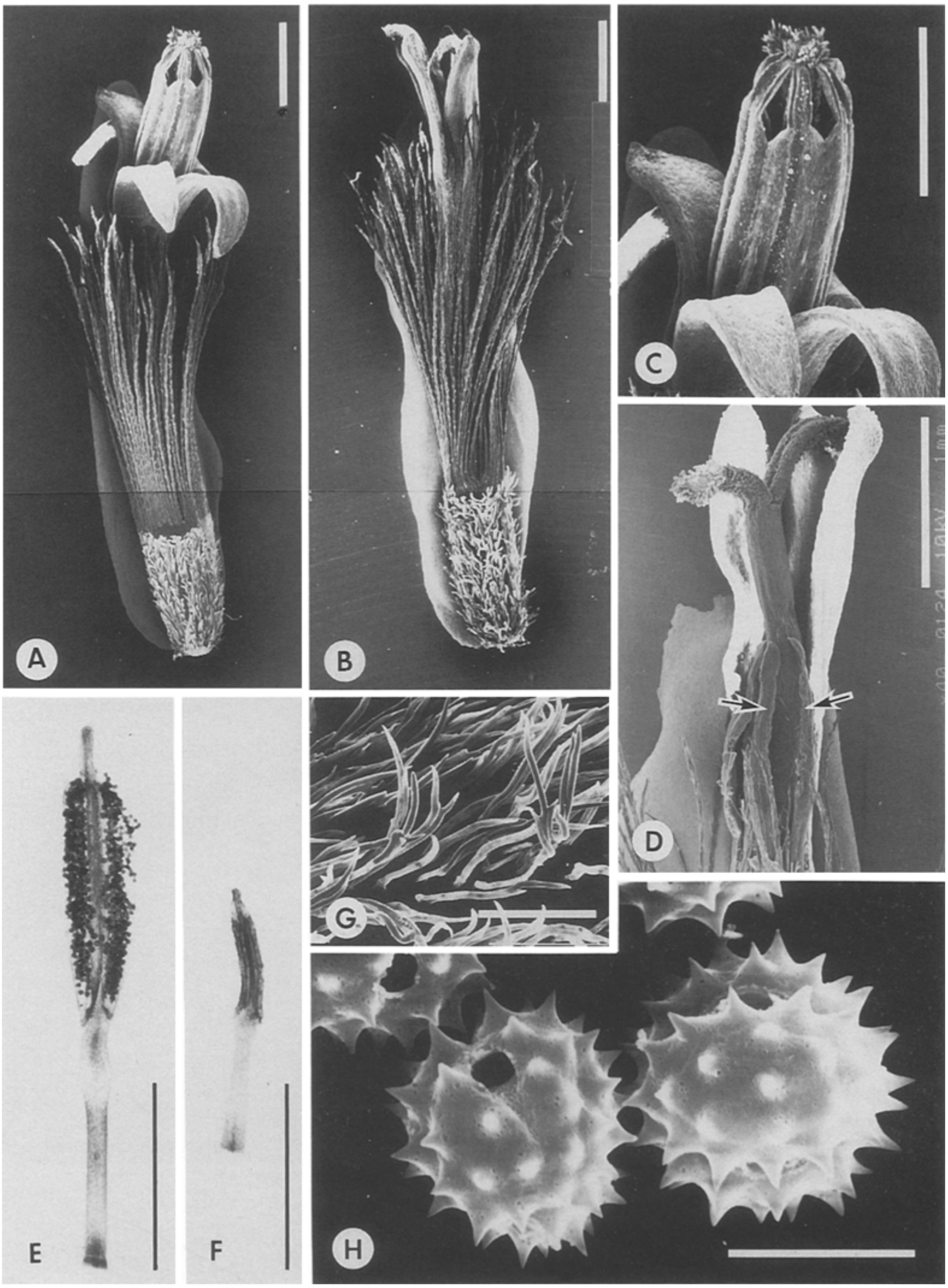

Fig. 2. Floral morphology of *Dendrocacalia crepidifolia*. A-B: Male and female florets. Bar=1 mm. C: Anther-tube in male floret. Bar=1 mm. D: Reduced stamens (arrows) and much recurved bifurcate style in female floret, corolla partly removed. Bar=1 mm. E: Stamen of male floret, anther sac is filled with fertile pollen grains. Bar=1 mm. F: Stamen of female floret, anther sac lacking pollen grains. Bar=1 mm. G: Appressed hairs on ovary of female flower, apex 2-3-divided. Bar=200 μm. H: Pollen grains. Bar=20 μm.

terminal corymbose panicle; bracts are arranged in 1 series, 5 in number, 5-6 mm long; each head is composed of 5 florets; corolla is pink, 4.5-6dmm long; pappus hairs are numerous, white, scabrous, 3-4 mm long; ovary is covered by white appressed hairs 2-3-divided at the apex (Fig. 2G), and is ca. 1.5 mm high, 0.6-1 mm in diameter with a single ca. 1 mm long ovule.

Among 77 plants found along a trail of 200 m at Mt. Sakaigatake, 35 (45%) were female and 42 (55%) were male. The sex ratio was not significantly different from 1 :

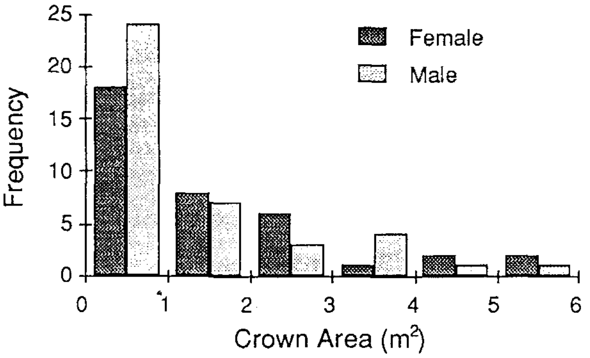

Fig. 3. Frequency distribution of crown area (m^2) of male and female plants of *Dendrocacalia crepidifolia*.

1 ($c2=0.64$, $p>0.05$). Frequency distribution of crown area was compared between male and female plants (Fig. 3). Mean crown area was 1.31 m^2 in male and 1.62 m^2 in female plants (the difference was not significant between sexes; Mann-Whitney U test, $U=615$, $p>0.05$).

The most dominant flower visitors during November 16 to 20 at Mt. Chibusa, Mt. Sakaigatake and Mt. Sekimon were honeybees, *Apis mellifera* (Figs. 4A-B). Flower visits by nitidulid beetles (*Heptoncurina motschulskii* Peitter) and tephritid flies (*Dioxyna sororcula* Wiedemann) were also observed though only rarely. Flower visits by endemic bees were not observed. Morning insect visits to male and female plants were observed from 0900 to 1,110 hr on November 18. The mean numbers of honeybee visits to a male and a female plants of similar crown area per ten minutes were 10.4±2.8 (± standard deviation) and 21.0±7.5, respectively (significantly different, $df=12$, $t=6.27$, $p<0.001$).

Of 25 honeybees collected on male flowers from 0900 to 1,000 hr on November 19, four (16%) had pollen loads on their corbiculae, whereas none of the 32 honeybees collected on female flowers had pollen loads. All the pollen loads of the four pollen-collecting honeybees were composed of pollen of *D. crepidifolia* (Fig. 4C). The mean volumes of nectar crop extracted from the stomach of honeybees collected on male and female flowers were 4.2±4.7 μl and 5.2±6.7 μl, respectively (not significantly different, $df=5$, $t=0.58$, $p>0.05$). The mean sugar con-

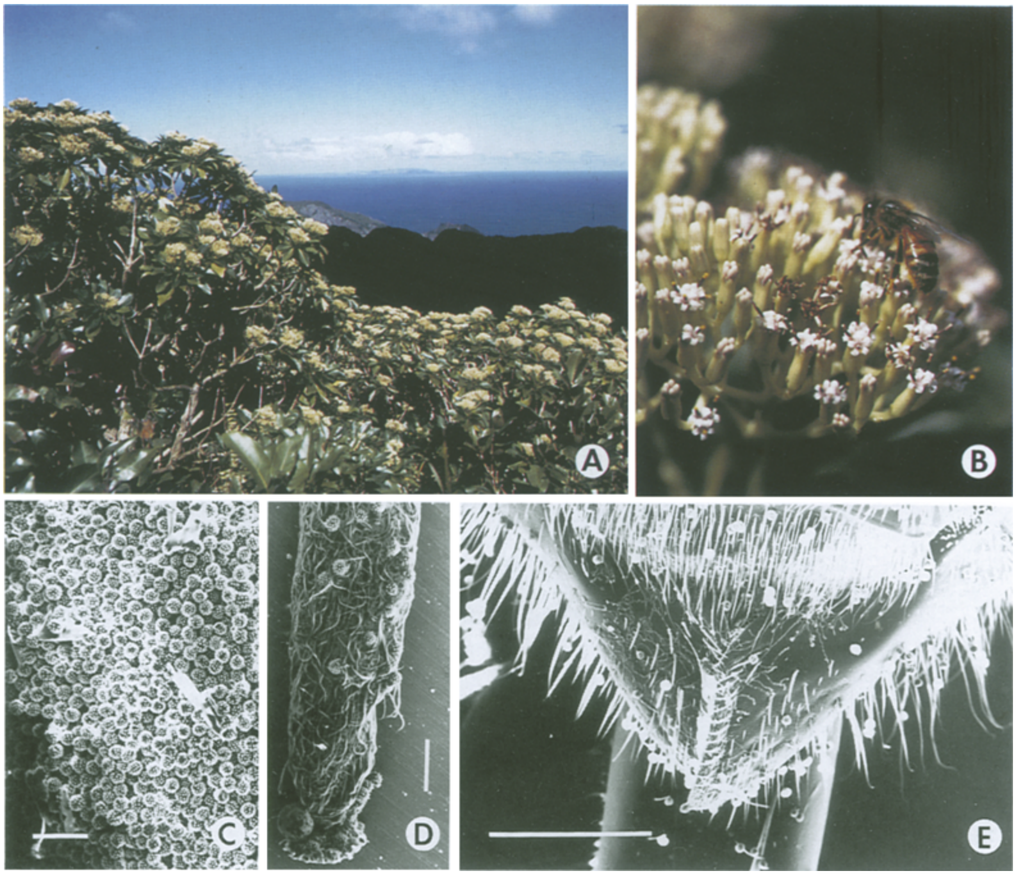

Fig. 4. Flowers of *Dendrocacalia crepidifolia* and honeybees visiting the flowers at Mt. Sakaigatake. A: Flowering arborescent plants. B: Female flowers visited by a nectar-seeking honeybees. C: Pollen loads on a corbicula of a honeybee collected on male flowers. Bar=100 μm. D: Glossa of honeybees collected on male flowers. Bar=100 μm. E: Mouth part of honeybees collected on male flowers. Bar=500 μm.

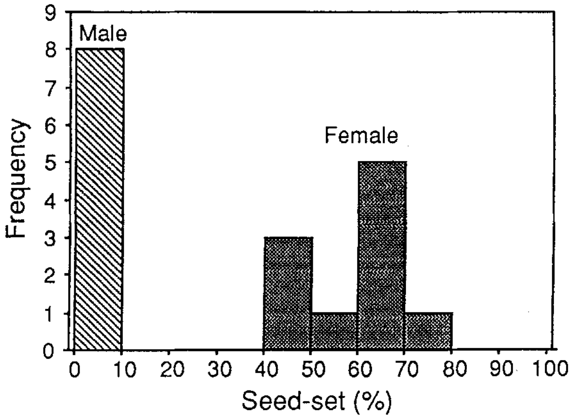

Fig. 5. Frequency distribution of seed set (%) of male and female plants of *Dendrocacalia crepidifolia*.

centrations of the nectar crop of honeybees collected on male and female flowers were 50.3±5.3% (N=5) and 50.7±4.1% (N=4), respectively. Much pollen was attached to almost all parts of the body of the honey-seeking and pollen-collecting honeybees collected from male flowers (Figs. 4D-E). Much less pollen was attached to the body of the honey-seeking honeybees collected on female flowers.

Both female and male florets produced achenes but most ovules of male florets were lean and sterile. However, a very low seed set of male flowers was detected. The mean seed set of female and male flowers was 59.3±12.6% (N=15) and 0.42±0.8% (N=10), respectively (Fig. 5). The seed set of female flowers was significantly larger than that of male ones (Scheffe F-test, F=173, $p<0.05$). The low seed set of male flowers indicates gender dimorphism in *Dendrocacalia* is not complete.

Dendrocacalia crepidifolia (Nakai) Nakai ex Tuyama

Dendrocacalia crepidifolia (Nakai) Nakai [Rigakkai, 26(5): 8 (1928), nom. nud.] ex Tuyama, Bot. Mag. Tokyo 50: 129 (1936).≡*Cacalia crepidifolia* Nakai, Bot. Mag. Tokyo 29: 12 (1915). —Type: *R. Yatabe & T. Uchiyama* (TI), Dec. 1879, in silvis Bonin.

Evergreen shrubs to 4 m high, dioecious. *Bark* gray-brown, longitudinally fissured. *Twigs* green to gray-brown, terete, glabrous, the leaf scars conspicuous. *Leaves* simple, exstipulate, alternate; blades thinly coriaceous, glabrous, rhomboid, obovate, or oblanceolate, apex obtuse with apiculate tip, base attenuate, margin slightly recurved, entire or coarsely crenate-dentate, (3-) 5-16 cm long, 2.5-6(-7) cm wide; midrib plane to slightly prominent above, prominent beneath; nerves 5-7 pairs, prominent beneath; petiole 1-3.5(-5) cm long, thickened at base. *Inflorescence*: heads in a terminal, dense corymbose-panicle; scaly leaves on peduncle linear to lanceolate, margin white pubescent, 1-3 mm long. *Involucre* cylindrical, 5-6 mm long, 2-2.5 mm in diameter; bracts 5 in 1 series, imbricate, oblong to narrowly oblong, 5-6 mm long, 1-2 mm wide, apex obtuse and ciliate, margin entire glabrous; receptacle plane, naked, areolate.

Male florets 5 per head. *Ovary* cylindrical, ca. 1.5 mm high, 0.6-1.0 mm in diameter, appressed hairy, the hairs 2-3-divided at apex. *Pappus* of many fine bristles in 1 series, white, scabrous, 3-4 mm long. *Corolla* pink, glabrous, 5-5.5 mm long; corolla tube 3-4 mm long; corolla lobes 5, subequal, 1.6-1.8 mm long, 1-nerved, apex obtuse to acute and papillate. *Stamens* 5, alternate with corolla lobes, attached to the middle of corolla; filaments ca. 2 mm long, glabrous, flattened, slightly widened in upper part; anthers connate forming an anther-tube, with 0.3 -0.4 mm long appendage on top of connective, anther sac ca. 1.5 mm long, base shortly auriculate. *Pollen grains* tricolporate monads, subspheroidal; amb circular; polar axis 22-25-28 μm long; equatorial axis 25-27-28 μm long; sexine echinate, echini 4-5 μm high, ca. 5 μm wide at base; colpi acute at ends; pori circular 4-5 μm in diameter. *Style* 5-6 mm long, terete, glabrous except papillate upper part, slightly gradually thickened toward base, ca. 0.3 mm in diameter at base; upper part divided into 2 stigmatic branches, the branch ca. 1 mm long, densely papillate and with a tuft of elongate cells on margin of truncate top, not completely exerted from anther-tube. *Ovule* 1, ca. 1 mm long.

Female florets 5 per head. *Ovary* cylindrical, ca. 1.5 mm high, 0.6-1 mm in diameter, appressed hairy, the hairs 2-3-divided at apex. *Pappus* of many fine bristles in 1 series, white, scabrous, 3-4 mm long. *Corolla* pink, glabrous, 4.5-5.5 mm long; corolla tube 3-3.5 mm long; corolla lobes 5, subequal, 1.4-2 mm long, 1-nerved, apex obtuse to acute, papillate. *Stamens* 5, alternate with corolla lobes, attached to the middle of corolla; filaments flattened, glabrous, 0.8-1.0 mm long, slightly widened just below anther sacs; anthers not forming distinct anther-tube, with ca. 0.2 mm long appendage on the top of connective; anther sac lacking pollen grains, ca. 0.5 mm long, base shortly auriculate. *Style* exserted from corolla, 5-6 mm long, terete, glabrous except papillate upper part, gradually thickened toward base, ca. 0.5 mm in diameter at base; upper part divided into 2 stigmatic branches, the branches much recurved and bifurcate, ca. 1 mm long, densely papillate, truncate on top. *Ovule* 1, ca. 1 mm long.

Achenes cylindrical, usually slightly compressed, narrowed at base, truncate at apex, 2-2.5 mm long, 0.6-1 mm in diameter, light brown, appressed white hairy, the hairs 2-3-divided at apex; pappus 3-4 mm long. *Seeds* 1, black, ca. 2 mm long. Both male and female florets grow achenes, and the size and shape are similar to each other. But the ovules of male florets are not developed and the achenes are mostly sterile.

Japanese name: Wadan-no-ki

Chromosome number. 2n=60 (Ono 1975)

Distribution. Bonin: Hahajima group (Haha Is., Mukou Is., Ane Is. and Mei Is.), Muko Is. (extinct ?), endemic.

Discussion

This is the first report of dioecy of *Dendrocacalia*. Male and female flowers are very similar and produce nectar of similar sugar concentration to attract pollinators. Male and female flowers mostly lack the functions of the opposite sex and very few male flowers develop fertile achenes. Dioecy in Senecioneae in Japan has been known only in *Petasites japonicus* (Siebold and Zucc.) Maxim., which flowers in early spring and is pollinated by syrphid flies. *Dendrocacalia* is the second dioecious species in Senecioneae in Japan, but differs from *Petasites* in many respects: woody habit, leaves with pinnate nerves, the small number of florets and bracts per head, and uniformity of florets in each individual. Although molecular phylogenetic analyses are not yet complete, there is no strong evidence that the genus *Dendrocacalia* is closely related to *Petasites* in the subtribe Tussilagininae. Thus, dioecy of *Dendrocacalia* is thought to have evolved in the Bonin Islands.

Relatively large proportions of dioecious species on oceanic islands have been reported in Hawaii (27.7%, Carlquist 1974), New Zealand (12-13%, Godley 1975) and the Bonin Islands (9%, Kawakubo 1990). The high prevalence of dioecy in oceanic islands was attributed to correlations between dioecy and the dispersal of seed by birds (Baker 1959, Bawa 1980). *Dendrocacalia* is the exception to this trend as if it is wind-dispersed and its putative relatives are not dioecious. There are several genera which are dioecious in islands although their relatives in their continental place of origin are hermaphrodite. Some examples are *Callicarpa* in the Bonin Islands (Kawakubo 1990), *Labordia* (Loganiaceae), *Bobea, Canthium, Hedyotis, Straussia* (Rubiaceae), *Santalum* (Santalaceae) and *Wikstroemia* (Thymelaeaceae) in Hawaii (Carlquist 1974). We believe that some selection pressure for dioecy exists in oceanic islands.

Two hypotheses have been proposed to explain selective pressures favoring dioecy. That is, dioecy may be selectively advantageous because it (1) increases outcrossing and reduces inbreeding depression (Charlesworth and Charlesworth 1978) and (2) optimizes resource allocation (Bawa 1980). No evidence supporting the latter hypothesis is found in *Dendrocacalia*. A viewpoint stressing the former effect focuses on the costs of geitonogamy (Thomson and Brunet 1990, de Jong *et al.* 1993). It has been shown in other species that geitonogamy decreases reproductive success in flowering plants. The loss of fitness due to geitonogamy results from reduced male fitness and interference with seed set in self-incompatible species (Galen *et al.* 1990, Waser and Price 1991) and from inbreeding depression in self-compatible species (Hessing 1988). Geitonogamy increases with increasing plant size (de Jong *et al.* 1992) and with decreasing pollen carry-over by less moving pollinators (Thomson and Brunet 1990).

In oceanic islands, there are two factors that result in increased geitonogamy. The first is increased woodiness of herbaceous plants accompanied by an increase in number of flowers per plant (Thomson and Brunet 1990). Oceanic plants are apt to become arboreal due to adaptation to aseasonal oceanic climates and release from competition with trees (Carlquist 1974). The second factor suggesting geitonogamy is the hypothesized dependence on native, small, solitary bees for pollination. A correlation between dioecy and pollination by small, generalist insects was proposed by Bawa and Opler (1975) and reassessed by Bawa (1994). Pollinators tending to increase geitonogamy, however, are not always restricted to small unspecialized flower visitors, which are often found to be pollinators of tropical dioecious angiosperms (Renner and Feil 1993).

The most characteristic feature of the native pollinator faunas of oceanic islands is a lack of eusocial bees, which are frequently excellent pollinators. Bumblebee queens are unable to fly very far, and their under-ground nests can not drift to the islands. Since the queens of honeybees and stingless bees can not start a nest without their workers, a single queen could not colonize oceanic islands by herself. The maximum distance for bee swarms to move at once is rather short. It is also difficult for their nests in wood cavities to arrive at oceanic islands by drifting because of their lack of diapause. Accordingly, the most important pollinators in oceanic islands are small soritary bees which nest in narrow borings in wood (Perkins 1901). These bees are thought to have colonized by the drifting of their nests in wood. Hawaii has 64 native bee species which belong to a single genus, *Hylaeus* (Colletidae, Table 1) (Perkins 1901, Howarth and Mull 1992). These small endemic bees are thought to have been the most important pollinators of native plants in Hawaii (Cuddihy and Stone 1990).

In the Bonin Islands, there are nine native bee species, four of which are *Hylaeus* species (Table 1) (Hirashima 1989, Kato 1992). The bees of the genus *Hylaeus* have small, less hairy bodies and look like sphecid wasps. The reduced hairiness is related to the fact that they carry pollen not on body hair but in the stomach (Michener 1974). There are two reasons why we consider that these

Table 1. Numbers of native bee species in the mainland of Japan, the Bonin and Hawaii Islands. Number in parenthesis denotes number of naturalized bee species. After Perkins (1901), Hirashima (1989) and Kato (1992)

Bee Families	Mainland of Japan	Bonin Islands	Hawaii Islands
Colletidae	26	4[a]	64[a]
Halictidae	98	0	0
Andrenidae	86	0	0
Melittidae	5	0	0
Megachilidae	54	3 (1)	0 (3)
Anthophoridae	112	2 (1)	0 (1)
Apidae	16 (1)[b]	0 (1)[b]	0 (1)[b]

[a] *Hylaeus* species. [b] *Apis mellifera*.

bees may promote geitonogamy. Firstly, the small body sizes of pollinators is thought to result in a restriction of pollen transfer distances because smaller bees collect a smaller quantity of nectar and/or pollen and cover less foraging area. In a Neotropical rainforest, small bees did not move between flowering conspecific trees whereas larger anthophorid bees did (Frankie *et al.* 1976). Secondly, pollen on a less hairy body will be detached earlier than pollen on pelage. In Australia, hairy halictid bees consistently carried pollen of *Acacia* more often than did less hairy wasps (Knox *et al.* 1985, Bernhardt 1987). Since bee faunas on oceanic islands are characterized by absence of hairy halictid and andrenid bees both of which nest in the soil, the less-hairiness of bees on oceanic islands may be an important factor promoting geitonogamy. To test this hypothesis, we will need to make direct observations on pollen transfer and within-plant movement patterns of these native bees.

In the Bonin Islands, nine native bees are endemic and are important pollinators of native plants (Kato 1992). Four species of *Hylaeus* and a species of *Ceratina* are small, less hairy bees less than 6.0 mm in body length. *Ceratina* bees are less hairy probably because they transport pollen not only on their hind legs but also in the gut (Strickler 1979). *Dendrocacalia* must be pollinated by these native bees before feral honeybees reached dominance as at present. In the Bonin Islands, honeybees were introduced for bee-keeping in 1880 (Funakoshi 1990) and have become naturalized even in natural forests in the islands probably because of absence of vespine wasp predators which hunt honeybees. The dioecious tree, *Callicarpa subpubescens* Hook. and Arn. is pollinated by *Hylaeus* spp. in Ane Island, where the honeybee has not yet invaded, whereas on Haha Island it is only visited by honeybees (Kato, personal observation). The increased geitonogamy due to visits by these small-sized, less-hairy, native solitary bees would be an important selection pressure in the evolution of dioecy in these oceanic islands. The recent expansion of feral honeybees and extinction of native bees may have changed pollen flow among native plants as in Hawaii (Messing 1991), and as a consequence the breeding systems of endemic plants may be changing.

There are three genera in which species in the mainland are herbaceous but those in the Bonin Islands are woody, i.e., *Heyotis* (Rubiaceae), *Lobelia* (Lobeliaceae) and *Crepidiastrum* (Compositae). These insular woody species, whose hight and crown size are much smaller than *Dendrocacalia*, are not dioecious. The fact that plant size rather than woodiness itself is related to dioecy suggests that geitonogamy might have played an important role in evolution of dioecy.

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