

THE TAXONOMY AND BIOGEOGRAPHY OF THE THICK-BILLED FLOWERPECKER COMPLEX IN BORNEO

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ABSTRACT.—The Western Foundation of Vertebrate Zoology expedition to Sabah, East Malaysia (North Borneo) collected specimens and field data on Brown-backed Flowerpeckers (*Dicaeum everetti*) and Thick-billed Flowerpeckers (*D. agile*) in 1982 and 1983. *Dicaeum agile* had not been known from Borneo previously, and its presence there changes the biogeographic assumptions Salomonsen (1960) used to classify the "thick-billed" flowerpeckers. Salomonsen's *D. everetti* was found to be a valid species, but his splitting of the Philippine Striped Flowerpecker (*D. aeruginosum*) from *D. agile* was not justified. *Dicaeum agile* of Borneo is here placed in the race *remotum* with the Malayan form of the species. The Bornean and Malayan races of *D. everetti* are grouped in the subspecies *everetti*. Received 2 October 1984, accepted 12 February 1985.

THE thick-billed flowerpecker complex of India, Southeast Asia, and the Philippines is listed by Salomonsen (1967) as comprising three species, the Thick-billed Flowerpecker (*Dicaeum agile*), the Brown-backed Flowerpecker (*D. everetti*), and the Striped Flowerpecker (*D. aeruginosum*). Of these species, only *D. agile* of India and Sri Lanka is common and well documented (Ali and Ripley 1974). In other parts of Southeast Asia, the three species rarely have been recorded, and their statuses are uncertain. This is especially true in Sundaland, the areas of land such as Malaya, Borneo, and much of the Indonesian archipelago associated with the Sunda shelf. *Dicaeum everetti* in Malaya is known from only four specimens. *Dicaeum agile* in Java is known from only two specimens. *Dicaeum everetti* in the Natuna Islands and *D. agile* in Sumatra are known from only one specimen each.

In 1982 and 1983, the Western Foundation of Vertebrate Zoology expedition to Sabah, East Malaysia collected both *D. agile* and *D. everetti*. The *D. agile* specimens were thought to be the first from Borneo (Smythies 1981). However, museum study subsequent to the expedition has shown that specimens of *D. agile* have existed from Borneo, in small numbers, since 1898. The

D. everetti specimens were thought to be the first from Borneo in 27 years (Pfeffer 1961). In fact, no specimens of *D. everetti* have been collected from Borneo since 1901, even though several museums have specimens labeled as such. The two species have been confused for 85 years, largely because the scarcity and dispersion of specimens have led to oversights in the taxonomic literature.

The Western Foundation field data and the new and old specimen material permit a critical evaluation of Salomonsen's (1960) classification of the thick-billed flowerpecker complex. His controversial separation of *D. everetti* from *D. agile* (*sensu* Mayr and Amadon 1947) is strongly supported, but questions are raised about some of his racial taxonomy and about the scheme proposed to explain the radiation and speciation of the thick-billed flowerpeckers in the Sunda and Philippine islands.

TAXONOMIC HISTORY

Salomonsen (1967) divided the thick-billed flowerpecker complex into three species based on his 1960 review: *D. agile*, encompassing the races *agile*, *zeylonicum*, *modestum*, *remotum*, *atjehense*, *finschi*, *tinctum*, and *obsoletum*; *D. everetti*, comprising *everetti*, *bungurensis*, and *sordidum*; and *D. aeruginosum*, composed of *affine*, *aeruginosum*, and *striatissimum*. He considered *D. everetti* and *D. aeruginosum* to constitute a super-species. The only sympatric forms in the

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TABLE 1. Ranges and characteristics of the subspecies of the thick-billed flowerpecker complex.

Subspecies	Locality	Dorsum ^a	Underparts	Tail	Wing ^b (mm)	Bill shape
<i>agile</i>	India, Pakistan	Olive-gray	Faint streaks	Bright spots	55-65 ^c	Thick
<i>zeylonicum</i>	Sri Lanka	Dark olive-gray	Moderate streaks	Bright spots	55-57 ^c	Thick
<i>modestum</i>	Assam-Indochina	Olive-green	Moderate streaks	Bright spots	57-61 (13)	Thin
<i>remotum</i>	Malay Peninsula, Borneo	Olive	Moderate streaks	Faint spots	57-63 (24)	Thin
<i>atjehense</i>	Sumatra	Olive	Moderate streaks	Faint spots	—	Thin ^d
<i>finschi</i>	Java	Olive	Moderate streaks	No spots	62 (1)	Thin
<i>tinctum</i>	Sumba, Lesser Sundas	Olive	Faint streaks	Faint spots	54-59 (9)	Thick
<i>obsoletum</i>	Timor	Grayish olive	No streaks	Faint spots	53-62 (11)	Thick
<i>everetti</i>	Borneo	Olive-brown	No streaks	No spots	54-60 (14)	Thin
<i>bungurensis</i>	Great Natuna Island	Olive-brown	No streaks	No spots	63 ^e	Thin
<i>sordidum</i>	Malaya, Riau Archipelago	Olive-brown	No streaks	No spots	59-61 (3)	Thin
<i>affine</i>	Palawan	Grayish olive	Heavy streaks	Bright spots	61-66 (7)	Thick
<i>aeruginosum</i>	Mindoro, Negros, Cebu, Mindanao	Olive-green	Heavy streaks	Faint spots	62-68 (8)	Thick
<i>striatissimum</i>	Luzon, Sibuyan	Brownish olive	Heavy streaks	Faint spots	64-65 (2)	Thick

^a Color terminology follows Smithe (1975).

^b Sample sizes are given in parentheses, except in instances where measurements are taken from independent sources.

^c Measurements from Ali and Ripley 1974.

^d Measurements from Chasen 1939b.

^e Measurements from Chasen 1934.

complex known to Salomonsen were *D. a. remotum* and *D. e. sordidum* of Malaya. The distinguishing features of the three species are as follows: *D. agile* has a comparatively pale olive or gray dorsum, streaked underparts, and (except for *finschi*) white spotting at the tail tip; *D. everetti* has a browner dorsum, no underpart streaking, and no tail spotting; and *D. aeruginosum* has the same characteristics as *D. agile* but generally is larger and darker (Salomonsen 1960). The ranges and characteristics of these races are summarized in Table 1.

Until Salomonsen's review of *Dicaeum*, the member races of the thick-billed flowerpecker complex had been classified in a variety of ways. For example, Sharpe (1885) included the 5 then-known forms as full species of the genus *Prionochilus*. Oberholser (1923) split the group into 3 genera and 5 species. Mayr and Amadon (1947) transferred the group from *Prionochilus* to *Dicaeum* and lumped all the races into a single species, *D. agile*. To understand the relationships of the Bornean members of the complex, the treatments given the Malayan forms, *sordidum* and *remotum*, must be emphasized because these Malayan birds are virtually identi-

cal to the Bornean forms of the species *D. everetti* and *D. agile*, respectively.

Chasen (1935, 1939a) grouped the Sundaland forms, *sordidum*, *everetti*, and *bungurensis*, with the Indian race, *agile*, in the species "*Piprisoma*" *agile* (*Piprisoma* being a subjective synonym of *Dicaeum*, with type species *agile*), and he united *remotum* and *modestum* in *P. modestum*. Although it attempted to recognize the distinctiveness of the *sordidum-everetti-bungurensis* group, this arrangement was counterintuitive. It ignored the dissimilarity between the Indian and Sundaland birds, and it created a disjunct distribution in which the continental Southeast Asian *P. modestum* separated the Indian from the Sunda forms. Had Chasen united *agile*, *remotum*, and *modestum* in one species and *sordidum*, *bungurensis*, and *everetti* in another, his classification of these taxa would have made more morphological and geographical sense. As they were, Chasen's groupings did more harm than good because they were believed to be the product of over-splitting and, consequently, were later ignored or attacked in reviews. As further complications, the few existing specimens of *sordidum* and *bungurensis*, deposited in

TABLE 2. Specimen records of *Dicaeum agile* collected in Borneo.^a

Number	Date	Locality	Habitat	Altitude (m)	Museum ^b
3	Dec 1898	Upper Mahakam R. (Kalimantan)	—	—	RHNL, USNM
4	Dec 1947–Jan 1948	Kelabit Plateau, Sarawak	2° forest, fruit trees	1,000	AMNH, SM
1	28 Sept 1952	Long Tinkalat, Tinjar R., Sarawak	2° forest	300	SM
7	Sept 1956	Long Peso, Kajan R., eastern Borneo	2° forest, village fruit trees	150–200	MHNP
4	July 1982	Sabah Softwoods, Brumas, Sabah	<i>Albizia</i> groves	250	WFVZ

^a Three poorly prepared specimens (2 in the PMNH and 1 in the SM) collected 9 October 1952 on Mt. Matang, Sarawak have been omitted from this list because their identities are uncertain. They could be either *D. agile* or *D. everetti*.

^b RHNL = Rijksmuseum van Natuurlijk Historie, Leiden; USNM = U.S. National Museum; AMNH = American Museum of Natural History; SM = Sarawak Museum; MHNP = Museum d'Histoire Naturelle de Paris; WFVZ = Western Foundation of Vertebrate Zoology; PMNH = Peabody Museum of Natural History, Yale University.

the Raffles Museum in Singapore, were inaccessible during World War II when the major review work was undertaken, and Chasen, the only active ornithologist familiar with the Malayan birds, was killed.

Deignan (1945), apparently in response to Chasen's taxonomic arrangement, condemned the splitting of "*Piprisoma*" on the Asiatic mainland and lumped all mainland forms in *P. agile modestum*, including by implication *sordidum*. Then followed a series of important works citing Deignan (1945) and discounting the distinct *sordidum-everetti-bungurensis* group. Mayr and Amadon (1947) merged all the Asian (including Philippine) races into *D. agile*, ignored *sordidum*, and called all Malayan forms *modestum*, as did Delacour (1946, 1947).

Salomonsen (1960: 5) departed from the trend to lump the thick-billed flowerpeckers for two reasons. First, he realized that the two forms occurring together on the Malay Peninsula, *sordidum* and *remotum*, were distinct. Second, Salomonsen found that the form he examined from Borneo was "very similar" to *sordidum* in Malaya. He believed that *sordidum* derived from the Bornean *everetti* and, therefore, that they should be joined as *D. everetti*, originally described by Sharpe (1877). Salomonsen retained *remotum* in *D. agile*. This arrangement left the Philippine races, which have white tail spotting, streaked underparts, and olive backs, geographically removed from their most similar

morphological counterparts in the Indonesian archipelago and on the Asian mainland. No simple pattern of *D. agile* radiation could account for this anomaly. Salomonsen decided that the Philippine forms were derived from *D. everetti* on Borneo, but he placed them in a separate species (*D. aeruginosum*) because of their distinctiveness from *D. everetti*. To reflect the logic of his radiation scheme, however, Salomonsen chose to unite *D. everetti* and *D. aeruginosum* as a superspecies.

Deignan (1960) investigated the validity of separating *D. everetti* from *D. agile* by examining the sole Bornean specimen of the thick-billed flowerpecker complex in the U.S. National Museum. Deignan pointed out that this specimen had white tail spots, a fact in direct contradiction with Salomonsen's assertion that *everetti* of Borneo had no tail spots. Salomonsen examined only four Bornean specimens—too few to discover that *D. agile* also occurs on Borneo; Deignan, by chance, had come across one of the *D. agile* specimens that Salomonsen missed.

Apart from Deignan's initial criticisms, Salomonsen's proposals generally were accepted (duPont 1971, King et al. 1975, Medway and Wells 1976, Smythies 1981).

MATERIALS AND METHODS

Primary data for this paper come from the specimen material and field notes collected by members

TABLE 3. Specimen records of *Dicaeum everetti* collected in Borneo.

Number	Date	Locality	Museum ^a	Remarks
1	1875?	Bintulu, Sarawak	BMNH	Type (Sharpe) 1877
1	1877?	Labuan, North Borneo (Sabah)	BMNH	Plate in Sharpe 1879
7	1891-1898	Kuching, Sarawak	SM, USC	—
2	24 Dec 1893	Kenepai, central Borneo (Kalimantan?)	RHNL	—
2	Nov-Dec 1897	Tutong R., Brunei	AMNH	—
1	1901?	Lawas, northwestern Borneo (Brunei)	BMNH	—
1	3 Mar 1983	Binsulok, Sabah	WFVZ	Adult male in <i>kerangas</i>

^a BMNH = British Museum of Natural History; SM = Sarawak Museum; USC = University of Singapore Collection; RHNL = Rijksmuseum van Natuurlijke Historie, Leiden; AMNH = American Museum of Natural History; WFVZ = Western Foundation of Vertebrate Zoology.

and associates of the Sabah expedition and from previously collected specimens (see Tables 2, 3). One *D. everetti* and 4 *D. agile* skins were collected during March 1981 to September 1983. These were measured and compared with 15 other *D. agile* and 13 other *D. everetti* specimens from Borneo. The Western Foundation specimens also were compared with skins of all the other forms in the thick-billed flowerpecker complex except *bungurensis* and *atjehensis*, which are known only from 1 specimen each, stored in the British and Bogor museums, respectively (see Table 1).

DESCRIPTIONS AND MEASUREMENTS

Dicaeum agile.—The Bornean *D. agile* has its head and back uniformly olive, with a slightly yellower rump. The wing coverts and flight feathers are strongly edged with yellowish olive-green. The breast is pale buffy gray moderately streaked with grayish brown. The tail is marked with faint but distinct white spots on the tips of the inner vanes of the outer three or four rectrices. Its maxilla is black or dark gray, mandible dark gray with a paler base, iris light brown with an orange tinge, and legs and feet black. The sexes of this species are alike. Measurements [size \pm SD (range), $n = 16$]: wing 60 ± 1 mm (57-63), culmen 7.7 ± 0.5 mm (7.2-8.5), gape 10.0 ± 0.5 mm (9.6-10.8), tarsus 12.4 ± 0.5 mm (11.9-13.6), tail 30 ± 1 mm (28-32).

Dicaeum everetti.—The single specimen of *D. everetti*, an adult male, is olive-brown on the head and back and darker brown on the tail. The edges of the primaries are slightly tinged with olive. Underneath, it is light grayish-brown on its chest and flanks and somewhat paler on the throat, center of chest, and belly. There are no obvious streaks on the breast and no white spots in the tail. Its maxilla is dark gray, mandible gray, iris dull yellow, and legs

and feet dark gray. Measurements: wing 57 mm, culmen from feathers 7.6 mm, gape 11.4 mm, tarsus 12.6 mm, tail 29 mm. This description also applies to the other Bornean specimens of this species. The sexes are alike. Measurements ($n = 14$): wing 57.5 ± 2.0 mm (54-60), culmen 7.7 ± 0.4 mm (6.8-8.4), gape 10.5 ± 0.6 mm (9.5-11.1), tarsus 12.7 ± 0.6 mm (12.4-13.5), tail 28 ± 1 mm (25-30).

FIELD OBSERVATIONS

Few, if any, reliable published accounts can be found of *D. agile* and *D. everetti* in Borneo because of their apparent rarity and because of the danger of confusing the two species.

Dicaeum agile.—*Dicaeum agile* were observed in June and July 1982 during a survey in groves of the exotic pulp-wood tree, *Albizia falcataria*, at Sabah Softwoods near Tawau, Sabah (4°32'N, 117°34'E). The birds always foraged in the canopy of the older trees (25-30 m) in mixed flocks with sunbirds and other small insectivores. These flocks usually contained from 3 to 10 flowerpeckers, but occasionally large flocks numbered from 15 to 30 flowerpeckers. *Dicaeum agile* fed mainly on the tiny caterpillars (e.g. *Eurema blanda*) that infested the plantation, and this abundant food source may have been responsible for attracting such large numbers. Tom Harrison of the Sarawak Museum (specimen label data) collected a bird out of a flock of 30 individuals in a tall fruit tree and another from the top of a village coconut palm in the Kelabit Plateau of Sarawak. Charles Francis of the Sabah Forest Department (pers. comm.) observed three birds at 40 m in primary forest at Lumerau near Lahad Datu in October 1982 (5°12'N, 118°52'E). The birds were foraging in

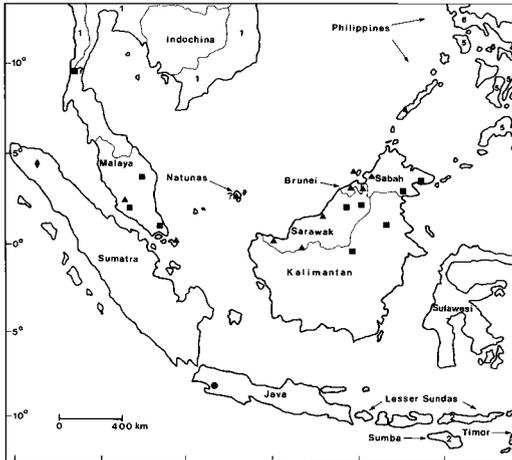


Fig. 1. The distribution of the thick-billed flowerpecker complex in Sundaland and outlying areas. Symbols indicate specific sites of all the known records for the corresponding races; square = *Dicaeum agile remotum*, diamond = *D. a. atjehense*, circle = *D. a. finschi*, triangle = *D. everetti* (including the Malayan *sordidum* and the Natunan *bungurensis*). Numbers indicate general racial distribution for those forms that have been more commonly collected or recorded; 1 = *D. a. modestum*, 2 = *D. a. tinctum*, 3 = *D. a. obsoletum*, 4 = *D. a. aeruginosum affine*, 5 = *D. a. aeruginosum*, 6 = *D. a. striatissimum*. Question marks indicate taxonomic uncertainty.

the tree tops along a river edge, and Francis noted the diagnostic tail wagging (see below), breast streaking, and white tail spotting. Pfeffer (1961) reported *D. agile* as common in fruit gardens of the village of Long Peso on the Kajan River, eastern Kalimantan in early September 1956, but he was not able to find them in similar situations elsewhere. Pearson (1975) recorded this species as uncommon and occurring in the upper strata and canopy of primary forest in Kutai Reserve, eastern Kalimantan. However, he collected no specimens and provided no description.

Although it is an obscure, dull brown bird, *D. agile* in Borneo has the unmistakable habit of wagging and fanning its tail from side to side. This tail-wagging behavior (perhaps related to the white tail spotting) makes this species the easiest of the nondescript flowerpeckers to identify at long distances.

Dicaeum everetti.—We saw *D. everetti* only once in 3 years, at Binsulok, Sabah (5°31'N, 115°40'E). A bird was found foraging on 3 March 1983 in

a viny bush in moderately disturbed coastal *kerangas*, a habitat of podzolized soil dominated by shrubs and stunted trees. It did not sing, but chipped constantly as it foraged. Its testes were enlarged (5 × 3 mm).

D. M. Batchelor (Smythies 1981, pers. comm.) reported seeing *D. everetti* on several occasions in Mawao, Klias, Bongawan, and Lumahat in the southwestern coastal region of Sabah in the early 1960's. He watched a pair at Lumahat in February 1962 adding to a nest some 5–6 m up a tree. "The nest appeared to be a felty pouch, whitish in appearance, which suggested that it was built of lalang seed heads or perhaps kapok down; it was suspended from the end of one of the outer branches and was quite inaccessible" (pers. comm.). Unfortunately, because of the possibility of his confusing species, it is not certain whether Batchelor saw *D. everetti* or *D. agile*. However, the plate in Smythies (1960), which was the guide used by Batchelor, is an excellent likeness of *D. everetti*, and the area where he saw the birds is adjacent to the Western Foundation's collecting site and presents similar habitat.

RESULTS AND DISCUSSION

The discovery of *D. agile* on Borneo supports Salomonsen's (1960) separation of *D. everetti* from *D. agile*. These are morphologically distinct species, sympatric in Malaya and Borneo. An assessment of the Bornean *D. agile*'s affinities and a reevaluation of the subspecific status of the Bornean *D. everetti*, however, suggest that modification of Salomonsen's racial taxonomy is required. In addition, the presence of *D. agile* on Borneo changes the assumptions used by Salomonsen in his speculations on the speciation of *D. aeruginosum*. A simpler explanation of the relationship of this species to the Sunda birds is now possible.

Dicaeum agile of Borneo is indistinguishable from *D. a. remotum* (Robinson and Kloss), 1915, of Malaya and here is assigned to that subspecies. The Bornean bird also is similar to *atjehense* and *modestum*, which are geographically juxtaposed to the Malayan *remotum* (see Fig. 1). In fact, Chasen's (1939b) description of *atjehense* and Deignan's (1945, 1960) discussions of *modestum* indicate that these races and *remotum* probably could be lumped into *modestum*. I have not examined *atjehense* and cannot venture a

sound opinion on its taxonomy. However, I find *remotum* to have a somewhat browner back and whiter underparts than *modestum* and choose, therefore, to follow Salomonsen (1960) in keeping these two races separate. More specimens of Malayan and Sumatran birds are needed before these problems can be resolved with confidence. The other Sunda races of *D. agile* are easily distinguished from *modestum*, *remotum*, and *atjehense* (see Table 1).

The affinity between *modestum* and the Bornean *remotum* also is evidenced by the tail wagging and fanning behavior shared by these races (King et al. 1975). This behavior, which is unusual for flowerpeckers, probably plays a role in species recognition and may relate to the white tail spotting. For this reason, it would be a useful taxonomic tool in determining whether a race such as *finschi*, which lacks white tail spots, merits specific status. Unfortunately, the only field records available are those of *remotum* and *modestum*.

Salomonsen (1960) apparently recognized the established *D. everetti* races—*sordidum*, *bungurensis*, and *everetti*—mainly because of their geographic separation. He stated (1960: 14) that the specimen of *bungurensis* "differs from the other two subspecies of *D. everetti* only in being slightly larger" and that *sordidum* "is extraordinarily like the Bornean *everetti*." Indeed, there are no substantial differences between *sordidum* and *everetti* in bill shape, plumage, or soft-part colors, and the apparent average size differences are not verifiably significant because of the small number of specimens (only four are known). I consider *sordidum* Robinson and Kloss, 1918, a synonym of nominate *everetti* Sharpe, 1877. However, because there is only one specimen of *bungurensis*, which I have not examined, it is difficult to assess its racial validity. Its larger size (wing 63 mm, Chasen 1934) is not far out of the range for the other supposed races, and it is intermediate between the two in geographic position. On the other hand, living on a small island, it may have diverged more quickly than "*sordidum*" and *everetti*.

The current distribution of *D. agile* and *D. everetti* on Malaya and Borneo is consistent with what is known about Sunda paleogeography. The Bornean avifauna is most similar to that of Malaya in terms of shared species (Banks 1937), and this similarity is attributable largely to the continental and drainage conditions prevailing

when Sundaland was emergent in the Miocene and early Pleistocene, and again in the late Pleistocene. In particular, the northwestern Bornean distribution of *D. everetti*, a species that seems to be restricted to poor soil habitats such as *kerangas*, fits neatly with what is known of the phytogeography of the region. Ashton (1972) noted a strong affinity between the eastern Malayan, Riau, and northwestern Bornean podzolic soil floras. These floras were once part of a continuum that developed in the middle and late Pliocene following the Miocene uplift of the present central Bornean mountains, when the bulk of Sundaland was above sea level. All records of *D. everetti* fit the distribution-habitat pattern of the podzolic soil floras (see Fig. 1). In addition, some other Sunda endemic birds, such as the Hook-billed Bulbul (*Setornis criniger*) and Gray-breasted Babbler (*Malacopteron albogulare*), approximate this pattern.

Dicaeum aeruginosum, which has all the defining characters of *D. agile*, should be joined with *D. agile* as originally proposed by Delacour and Mayr (1946) and Mayr and Amadon (1947). The existence of *D. agile* on Borneo fills a gap in the distribution of the thick-billed flowerpeckers and provides the biogeographic link between *D. aeruginosum* in the Philippines and *D. agile* in the Indonesian archipelago and on the Asian mainland.

How the present distribution of the thick-billed flowerpecker complex developed is still not clear. Salomonsen (1960) proposed that the group radiated from *D. agile* stock that originated on the Asiatic mainland and dispersed through the Malay Peninsula and Sunda Islands, eventually reaching the Philippines. But to view the present-day distribution of these species as the result of an island-hopping invasion is probably too simple an approach. Most species of *Dicaeum* and *Prionochilus* occur in the Philippines and Sundas, thereby implying that the roots of the Dicaeidae lie in these islands (Mayr and Amadon 1947). It is most likely that the *D. agile-everetti* progenitor originated in Sundaland or the Philippines and that the radiation of the group was driven by geographic changes in the Tertiary followed by eustatic sea-level changes in the Quaternary, creating conditions for reiterative isolation and colonization. The mainland forms are probably outliers, and the rarity of many of the island forms may

be the result of the disappearance or spottiness of Quaternary habitats.

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