The occurrence of sympatric speciation (i.e., the divergence within the same place of distinct groups of organisms that could be recognized as taxonomic species) is a much-debated subject in evolutionary biology (Fitzpatrick et al. 2008). Evidence supporting this is scarce (Coyne and Corr 2004), and in many cases an allopatric phase of differentiation, occurring at a very small scale (e.g., “microallopatry”), cannot be ruled out. Most examples of putative sympatric speciation are from islands, where the isolation of populations can be easily evaluated. For birds, the few possible cases are reviewed in Coyne and Price (2000) and in Grant and Grant (2010). The three best examples of sympatric speciation are all from relatively small oceanic islands (less than 10,000 km²): buntings (Nesospiza spp., Thraupidae) in the Tristan da Cunha group (Ryan et al. 2007), finches (Geospiza spp., Thraupidae) in the Galápagos Islands (Grant and Grant 2010), and storm-petrels (Oceanodroma spp., Hydrobatidae) in eastern Atlantic islands (Friesen et al. 2007). The latter case refers to a special scenario of allochrony (i.e., the occurrence on the same island of two distinct breeding periods, specific to each divergent population).

Birds are usually considered highly mobile, and this could explain the rarity of sympatric speciation in this group. However, bird
populations can be isolated by a barrier at a very small scale on the same island or archipelago: for instance, the Mascarene Grey White-eye (Zosterops borbonicus, Zosteropidae) shows population differentiation caused by altitude or natural barriers like lava fields on Réunion Island in the Indian Ocean (Mila et al. 2010), and in the Fiji archipelago in the Pacific Ocean the Orange Fruit Dove group (Chrysoena spp.) is composed of species endemic to islands separated by sea distances less than 100 km (Gibbs et al. 2001). These examples suggest that microallopatric speciation does occur for insular birds, despite their initial dispersal capacity that permitted the colonization of remote oceanic islands.

Among insular birds, the fruit doves (Ptilinopus spp. and their close allies Drepanoptila, Alectroenas, and Chrysoena; Columbidae) represent one of the groups having species that occur sympatrically on the same island. With more than 50 species, fruit doves are distributed on both sides of the Wallace Line (Gibbs et al. 2001). They are particularly diverse on the large continental island of New Guinea, which was found to be the ancestral area for several nodes within the phylogeny, as shown in the biogeographic analysis of the group (Cibois et al. 2014). All fruit doves are arboREAL and frugivorous, and many species play an important role in seed dispersal of insular ecosystems (Steadman 1997b, Steadman and Freifeld 1999, Shanahan et al. 2001a,b). On oceanic islands, all cases of sympatric fruit doves correspond to the coexistence of two species, except in Fiji where three species (Crimson-crowned Fruit Dove, Ptilinopus porphyraceus; Many-colored Fruit Dove, P. pereisii; and Orange Fruit Dove, Chrysoena victor) coexist on the same small island (Lauca, 12 km²) (Watling 1989 and pers. comm.). In each case, the sympatric species have colonized the island independently and at different times (Cibois et al. 2014). This result supports the hypothesis that for fruit doves, like for most birds, speciation occurs in allopatry.

We found, however, an exception to this pattern in the Marquesas Islands (eastern Polynesia), where the two fruit doves that occurred sympatrically on several islands in historical times are also sister species on the phylogenetic tree: the Red-moustached Fruit Dove, Ptilinopus mercierii, and the White-capped Fruit Dove, Ptilinopus dupetitbouarsii. Their divergence was estimated at ca. 2 Ma (Cibois et al. 2014). This result supports the hypothesis of Diamond (1977) of one rare case of “intra-archipelago speciation,” as opposed to the double colonization scenario proposed by most authors (Mayr 1940, 1942, Ripley and Birckhead 1942, Cain 1954, Goodwin 1967, Holyoak and Thibault 1978). But how did this speciation occur on one of the most remote archipelagos in Oceania? In this article we first review the life history and then analyze the morphology of the two species. Then we present geological information on the volcanic formation of the Marquesas archipelago and discuss the most likely scenarios for the emergence of the two sympatric fruit doves.

**MATERIALS AND METHODS**

We compiled data on the biology of the Marquesas fruit doves from the available literature and from examination of specimens stored in the following museums: MNHN, Muséum National d’Histoire Naturelle (Paris); AMNH, American Museum of Natural History (New York); NHM, Natural History Museum (Tring); NML, National Museum Liverpool; and USNM, National Museum of Natural History, Smithsonian Institution (Washington). The first detailed account of the Marquesas avifauna comes from the Whitney South Sea Expedition, led by the AMNH in 1921–1922, and the unpublished journals of this expedition were a major source of information on the fruit doves’ biology (Beck n.d., Quayle n.d.). We conducted a morphometric analysis on measurements of 15 White-capped Fruit Doves and eight Red-moustached Fruit Doves collected on Hiva Oa (all adult males, specimens held at AMNH and NML). Measurements consisted of wing length, bill length from skull, bill length from nostril, bill width (at nostril), bill height (at nostril), tarsus length, and tail length. Measurements were first examined though a one-way analysis of variance (ANOVA) (K = 2, N = 23) using R (R Core team 2013). Then we used principal
components analysis (PCA) on standardized variables to summarize patterns of variation in the morphometric data in producing independent composite variables (PC axes). The PCA analysis was conducted using the package ggbiplot in R (Vu 2011). The fruit doves’ molecular phylogeny and analysis of plumage evolution were conducted by Cibois et al. (2014). The genes used for the molecular phylogeny were three mitochondrial genes (ND2, ND3, COI) and two nuclear genes (FGB exons 5 to 6 and intron 5, and RAG1); however only mitochondrial genes were sequenced for the extinct Red-moustached Fruit Dove. Finally, we summarized the information available from the literature on the volcanic formation of the Marquesas archipelago.

RESULTS

Distribution of Marquesas Fruit Doves

The Red-moustached Fruit Dove (hereafter RMFD) is now extinct. It was a polytypic species with nominate mercierii (Des Murs & Prévost, 1849) on Nuku Hiva, known by a single specimen collected in 1848 and held at MNHN (Voisin et al. 2004), and subspecies tristrami (Salvadori, 1892) on Hiva Oa, with 12 specimens found in collections: one at NML (the type), seven at AMNH, one at USNM, and three at NHM. Subfossil records from Ua Huka, identified as cf. P. mercierii, suggest the possibility of a more widespread distribution within the archipelago in the past (Figure 1) (Steadman 1989). The RMFD was never seen again on Nuku Hiva after its discovery. On Hiva Oa, it was rare at the beginning of the twentieth century (Ripley and Birkhead 1942) and disappeared before the 1970s (Holyoaik and Thibault 1984). The White-capped Fruit Dove (hereafter WCFD) is a polytypic species with nominate dupetithouarsii (Neboux, 1842) in the northern Marquesas (Nuku Hiva, Ua Huka, Ua Pou), and subspecies viridior (Murphy, 1924) in the southern islands of the archipelago (Hiva Oa, Tahuata, Mohotani, Fatu Iva). Today the WCFD is common on the main islands of the archipelago (Figure 1) and absent on islands where resources of fleshy fruits are absent, due to a degraded vegetation cover (Eiao) or a naturally depauperate flora (Hatut’a’a, Fatu Huku, Hatu Iti).

Life History

Although data are scarce for the RMFD, evidence suggests that both species were frugivorous like all fruit doves (Gibbs et al. 2001). Several expeditions observed the two species foraging in the same tree, suggesting they occupied the same habitats (Schmeltz and Krause 1881, Beck n.d., Quayle n.d.). On Nuku Hiva, the only known specimen of RMFD was collected in a tree near the shore (Voisin et al. 2004) where the WCFD was common, as it still is today. On Hiva Oa in 1922, the Whitney South Sea Expedition recorded the RMFD mostly inland, whereas the WCFD was abundant all over the island. Beck (n.d.) and Quayle (n.d.) also mentioned that both species perched in the same trees, feeding together on fruits.

Plumage Variation

Both species present a similar pattern of green on the upperparts and yellow or orange on the belly. They differ mostly by the crown and malar patches, red in the RMFD, white in the WCFD (Figure 1). The plumage of the
nominate *mercierii* differs slightly from that of subspecies *tristrami* (see Gibbs et al. 2001), but the unique specimen of the nominate taxon is old and its coloration could have been altered. Differences of coloration are well marked in the WCFD subspecies: the nominate *dupetithouarsii* presents a pronounced orange patch of the belly contrasting with the gray breast, whereas in subspecies *viridior* the orange belly-patch is less extensive and the breast is green (Gibbs et al. 2001, Murphy 1924).

**Morphological Analysis**

All measurements of the RMFD are significantly smaller than those of the WCFD (ANOVA: $F$ between 31.9 and 4.9; degrees of freedom $K-1 = 1$, $N-K = 21$; $P < .05$); for instance on average RMFD’s wing length is $138.9 \pm 3.9$ mm, whereas WCFD’s is $148.3 \pm 3.8$ mm. The first axis of the PCA explained most of the variation (51.5%), with the main contribution of wing length, bill length from nostrils, and bill width. Bill height and bill length from skull are the main characters that accounted for the variation of the second axis (19.4% of total variation). The results of the PCA (Figure 2) show that the RMFD specimens are distinct from the WCFD in Hiva Oa, suggesting that the two sympatric taxa did not present the same morphology.

**Figure 2.** PCA of the Marquesas fruit doves. Black circles represent the RMFD, white circles the WCFD. Arrows indicate the direction of the variables: WING, wing length; BILL1, bill length from skull; BILL2, bill length from nostril; BILL.W, bill width (at nostril); BILL.D, bill height (at nostril); TARSUS, tarsus length; and TAIL, tail length.
Molecular Phylogeny

Both RMFD and WCFD belong to a monophyletic group that colonized most Pacific archipelagos, often referred to as the “purpuratus” group (Cain 1954, Cibois et al. 2014). They are the first lineage to branch off this clade and are sister taxa in all analyses with good support (i.e., posterior probabilities > .95 and bootstrap values > 70%; only the mercierii clade is not well supported in the Bayesian analysis, a result probably due to the shorter sequences of some individuals) (Figure 3). The sampling was based on several RMFD from Hiva Oa (toe pads from specimens held at AMNH and from the type specimen held at NML). Unfortunately it was not possible to study the nominate subspecies from Nuku Hiva because we could not retrieve DNA from the only known specimen.

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Figure 3. Phylogeny of the “purpuratus” group, modified from Cibois et al. (2014). Asterisks indicate nodes supported by posterior probabilities (PPs) ≥ .95 and bootstrap (BT) values ≥ 70%. When support differs between methods, PPs are indicated first and BT second with support below significance labeled by a dash (see Cibois et al. [2014] for details).
The two subspecies of WCFD were sequenced based on fresh material from several islands (Fatu Iva, Nuku Hiva, Tahuata, Ua Huka, and Ua Pou). No reciprocal monophyly was found between the two WCFD subspecies. Although the sampling was limited to a few individuals per island, the absence of a geographical structure in the genetic data suggested either ongoing gene flow between islands or incomplete lineage sorting between the two subspecies. The fruit dove phylogenetic tree was calibrated using a relaxed clock and fossil data. The Marquesas fruit dove clade represents the first of the two colonizations of eastern Polynesia, estimated at ca. 5 Ma. The second colonization of eastern Polynesia involved the Cook, Society, Tuamotu, Austral archipelagos, and Henderson Island and took place more recently at ca. 2 Ma. The genetic distance between the two Marquesas taxa was 1.4% (mitochondrial sequence data, uncorrected distance), and the estimate of time of divergence of the two species was 1.8 Ma (95% CI 0.8–2.8 Ma).

Plumage Evolution

The analysis of plumage coloration showed that the red crown (including all variations from orange to purple) is the plesiomorphic state for this character for all fruit doves of the “purpuratus” group (Cibois et al. 2014). Three taxa evolved from this red coloration, which is based on carotenoid pigments (Mahler et al. 2003), to other colors probably based on structural coloration (Gill and McGraw 2006): blue in Blue-capped Fruit Dove, *P. monacha* (Moluccas); gray in Silver-capped Fruit Dove, *P. richardsii* (Melanesia); and white in WCFD in the Marquesas. Experiments have shown that in a feather of the American Goldfinch, *Carduelis tristis*, the yellow color was actually produced by a combination of carotenoid pigments with an underlying white structural coloration (Shawkey and Hill 2005). Thus the white color of the WCFD’s crown and malar patches probably results from the disappearance of the carotenoid pigments that are still present in the RMFD. This major change in plumage coloration could constitute a signal for species selection, by character reinforcement in sympatric species after speciation in allopatry (Liou and Price 1994, Sætre et al. 1997).

Fruit doves exhibit in general little intraspecific plumage variation, but geographical phenotypic variation occurs in some species: one of the most extreme cases is found within the Rose-crowned Fruit Dove, *P. regina*, where a clinal variation of the crown color is observed between populations from Australia (pinkish red) to Indonesia (pale gray with light lilac tint) (Baptista et al. 1997). Morphs are usually defined as the presence within a species of individuals of the same sex and age with distinct plumages that are genetically determined (Buckley 1987). Because the main difference between RMFD and WCFD lies in a change of their crown and malar patch color, one can ask whether two distinct morphs formed within the same species. This seems unlikely, however, because of the size difference between the taxa, as well as the deep divergence found in the molecular phylogenetic tree.

Marquesas Islands Geology

The Marquesas archipelago (141°–138° W long., 7°–11° S lat.) is composed of 11 islands and seamounts spread over 470 km along a northwest–southeast axis (Figure 1). Like most islands of Polynesia they are of volcanic origin, formed by a “hot spot” where magma extruded from the earth’s mantle through the crust, building huge shield volcanoes. Over time, the weight of a new island, associated with motion from the hot spot, caused a relatively rapid decrease in island elevation and area (Moore et al. 1989, Moore et al. 1994). This phenomenon was particularly spectacular in the Marquesas (Moore et al. 1989, Brousse et al. 1990, Desonie and Duncan 1993, Moore et al. 1994, Guille et al. 2002). Estimates of whole-rock 40K–40Ar isotope ages are given for every island in Table 1 (Guille et al. 2002, Legendre et al. 2005, 2006). Older islands are located in the northwest (from Eiao to Ua Pou) and younger ones in the southeast (from Hiva Oa to Fatu Iva). The volume of the main islands was consider-
ably larger before the collapse of their caldera: the bulk of underwater debris was estimated from half of the original shield volcano (Nuku Hiva, Ua Huka, and Fatu Iva) to even three-fourths for Eiao (Filmer et al. 1994, Wolfe et al. 1994). Although no modeling was conducted on the Marquesas to estimate the original elevation of the islands, the collapse of a large part of the original volcanoes likely led to a major decrease of the islands’ elevation.

Nuku Hiva, where the two fruit doves occurred in the same habitats, is the largest of the northern old islands and very likely played an important role in the beginning of the fruit doves’ colonization of the Marquesas. Its morphology is typical for the archipelago, with a succession of caldera walls encased toward the south (Brousse et al. 1978, Le Dez et al. 1996). The two main volcanoes (the external volcano Tekao and the internal Taiohae) were active during the 4.8–3.1 Ma period, with a major collapse of Tekao that formed the Toovii plateau around 4 Ma (Le Dez et al. 1996). On Ua Huka and Ua Pou, the areal volcanic activity was particularly long (ca. 2 myr), interspersed by a period of volcanic quiescence (Guille et al. 2002, Legendre et al. 2005, 2006). This long period of activity could have delayed the establishment of habitats favorable to fruit doves.

The volcanic activities for the southern islands are mostly contemporaneous during the 3–1.6 Ma period, although Fatu Iva is likely the youngest formation of this group (Guille et al. 2002). The largest southern island, Hiva Oa, was formed by a series of volcanoes along a west–east line, characterized by the collapse of the calderas that formed the cliffs surrounding the summits of the island today (Le Dez et al. 1996). The time of this collapse is unknown. The total radiometric data obtained for this group suggest that the areal volcanic activity lasted for 1.3 myr.

### Discussion

The two species of fruit doves lived together on at least three islands of the archipelago: Nuku Hiva, Ua Huka, and Hiva Oa. Life history data, although scarce for the extinct RMFD, indicate that both species shared the same resources and did not live in separate habitats. Although sympatric speciation, linked with different ecological adaptations, cannot be completely ruled out, we consider that hypothesis highly unlikely based on the absence of obvious ecological differences between the two species. Then, two main scenarios can be proposed to explain the speciation in the Marquesas: (1) microallopatry (within-island speciation) and (2) intra-archipelago speciation.

The microallopatry hypothesis takes into account the large volume of the main islands, especially in the old northern group, that existed between their emergence and the collapse of the volcanoes’ calderas. According to the molecular phylogeny, the fruit doves colonized the archipelago not long after its formation at ca. 5 Ma. At that time, the largest island was Nuku Hiva, where the two fruit doves were still found in historic times (Figure 4, Period 1). Eiao and Hatuta’a are older, but they were most probably smaller, and the presence of fruit doves has never been documented there in historic times. The maximum altitude of Nuku Hiva at the time of its emergence is unknown (1,227 m today), but its volume was likely twice that of today (estimated at up to 13,000 km³ [Wolfe et al. 1994]). Its surface was probably covered by large patches.

### Table 1

<table>
<thead>
<tr>
<th>Island</th>
<th>Age of Volcanic Activities (Ma)</th>
<th>Area (km²)</th>
<th>Elevation (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern group</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eiao</td>
<td>5.5–4.9</td>
<td>40</td>
<td>578</td>
</tr>
<tr>
<td>Hatuta’a</td>
<td>4.9–4.7</td>
<td>4</td>
<td>428</td>
</tr>
<tr>
<td>Nuku Hiva</td>
<td>4.6–3.1, 4.7–3.0</td>
<td>380</td>
<td>1,227</td>
</tr>
<tr>
<td>Ua Huka</td>
<td>3.1–2.4, 1.1–0.7</td>
<td>77</td>
<td>884</td>
</tr>
<tr>
<td>Ua Pou</td>
<td>4.0, 2.9–2.3</td>
<td>105</td>
<td>1,252</td>
</tr>
<tr>
<td>Southern group</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hiva Oa</td>
<td>3.9–1.8, 2.9–1.6, 1.9–1.8</td>
<td>320</td>
<td>1,276</td>
</tr>
<tr>
<td>Tahuata</td>
<td>2.9–1.8, 2.0</td>
<td>70</td>
<td>1,050</td>
</tr>
<tr>
<td>Mohotani</td>
<td>2.3–2.1</td>
<td>15</td>
<td>520</td>
</tr>
<tr>
<td>Fatu Iva</td>
<td>2.5–1.9, 1.2</td>
<td>84</td>
<td>960</td>
</tr>
</tbody>
</table>
of different native habitat types: coastal (littoral) forests, dry (xeric) and semidry (mesic) forests in the lowlands, wet (rain) forests in the valleys and uplands, and cloud forests in the mountains. Such diversity could shelter different populations of fruit doves that became isolated by a partitioning of their distributions, in microallopatry (Figure 4, Period 2). This situation could have lasted until the major collapse of the caldera, ca. 4 Ma: this period of 1 myr is probably sufficient for speciation in insular birds (see for instance Fleischer et al. [1998] for Hawaiian creepers). Then the collapse of the caldera led to the re-

![Figure 4. The microallopatry scenario. For each period, only the emergent islands are mapped, first with an enlarged size that corresponds to the island before the collapse of its main volcano.](image)
duction of half of the island size and put the two populations in contact (Figure 4, Period 3). The conjunction of isolation and character displacement at secondary contact could then have led to the different phenotypes of the two taxa, which subsequently colonized the rest of the archipelago (Figure 4, Period 4). This scenario implies that, at least in Nuku Hiva, island resources were sufficient, since a short time after its emergence, to sustain several species of frugivorous birds. Although the paleoflora of the Marquesas remains to be studied (Melinda Allen, pers. comm.), its subfossil record supports this hypothesis with six frugivorous (or partially frugivorous) species that coexisted on several islands in prehistoric times: the two *Ptilinopus* spp. and the Marquesan Imperial Pigeon (*Ducula galeata*, Columbidae), plus two extinct *Vini* spp. and the Ultramarine Lorikeet (*Vini ultramarina*, Psittacidae) (Steadman 2006). Today the large *Ducula galeata* and the WCFD often share the same fruit resources, but the largest fruits can only be eaten by the Imperial Pigeon, suggesting a possible niche distinction linked to fruit size (McConkey et al. 2004; J.-Y.M., pers. obs.). The body size difference between the Marquesan Imperial Pigeon and the WCFD is, however, much greater than the difference between the WCFD and the RMFD, which probably ate fruits of similar diameter.

The second possible scenario involves an intra-archipelago speciation and takes into account the sequential emergence of the islands. As in the microallopatry hypothesis, the colonization of fruit doves took place in the northern part of the Marquesas, probably the largest island, Nuku Hiva (Figure 5, Period 1). From there, this ancestral fruit dove colonized all islands of the archipelago, reaching the southern group after its emergence (Figure 5, Period 2). Then the two fruit dove populations became isolated, separated by more than 100 km: during that time of isolation their genomes accumulated mutations by drift and local adaptation and subsequently formed two distinct taxa (Figure 5, Period 3). Finally, a change in climate or wind regime, or a general increase in the populations’ number could have allowed the two taxa to resume interisland dispersal, leading to sympatric distributions on at least three islands of the archipelago (Figure 5, Period 4).

The microallopatry scenario implies that the speciation process has been limited to a single island, similar to what happened to the white-eyes on Réunion Island (Mila et al. 2010). Although this scenario provides a simpler explanation for the presence of both fruit doves in the archipelago (a global dispersal after the establishment of the two taxa), the general mobility of fruit doves argues against the isolation of two populations on the same island. Today, the availability of pigeons’ and doves’ food resources is irregular on Polynesian islands, with the seasonal fruit production of native or endemic species (e.g., the banyan fig-tree *Ficus prolixa var. prolixa*). The birds’ movements within islands are well known, flying over mountain passes regularly in the search for fruiting trees (Holyoak and Thibault 1984; J.-C.T. and J.-Y.M., pers. obs.). The only known exception takes place on small Henderson Island (37 km²), where the Scarlet-capped Fruit Dove (*P. insularis*) may be territorial (Graves 1992). It is difficult, however, to evaluate what we know of the fruit doves’ ecology in the context of the initial island conditions, when islands were larger and higher, with pristine native habitats. Those were extensively altered during the last millennium, first by the Polynesians, then by Westerners (Bailleul 2001, Allen et al. 2011). Regardless of the ecology of the birds, the divergence time of the two taxa, estimated at ca. 2 Ma based on molecular characters, favors the intra-archipelago scenario because it corresponds well with the emergence time of the southern islands group. Part of this scenario (Period 2) evokes the monarchs’ (*Pomarea* spp., Monarchidae) colonization of the Marquesas: the phylogeny of the species was consistent with the sequential appearance of the islands, from the northern and oldest group to the southern and youngest islands (Cibois et al. 2004). But the last part of the intra-archipelago scenario (Period 4) also implies a back colonization from younger islands to older ones, a pattern found in the Hawaiian flora and fauna (Cowie and Holland 2008, Havran et al. 2009) but undocumented in the
Marquesas Islands. In the microallopatry scenario, the isolation of the two taxa supposedly ended with the reduction of size of the island caused by the collapse of the main caldera, estimated at ca. 4 Ma: this event predates the divergence time of the two taxa, thus making this scenario less likely.

CONCLUSIONS

Our review of the Marquesas fruit doves’ life history, morphology, and phylogeny, coupled with geological data on the islands, is in favor of the intra-archipelago scenario for the divergence of the two taxa. It is worth noting,
however, that this conclusion depends partly on the time of divergence obtained in a previous phylogenetic analysis (Cibois et al. 2014). The past occurrence of other Ptilinopus species in the Marquesas can also mislead our analysis: the two Marquesas fruit doves may not be sister species, or one of them could have hybridized with an extinct species and kept the mtDNA haplotype of the other species by introgression (see Rheindt and Edwards [2011] for a review of genetic introgression in birds). However we found the existence of other extinct fruit doves unlikely because the subfossil record of the archipelago has been well studied, with new extinct taxa found in all the major land-bird groups. Based on this record and on the results of the molecular phylogeny, we consider a sister-species relationship between the RMFD and the WCFD to be the most parsimonious hypothesis.

Regardless of the pattern of colonization, on the same island or on separate islands distant by more than 100 km, the occurrence of sympatric sister species is still unique among fruit doves in Oceania: in Fiji, the three Chrysoena species that belong to the same radiation do not occur on the same islands. In the Marquesas, the other cases of congeneric sympatric species involve crakes (Zapornia spp., Rallidae) and lorikeets (Vini spp., Psittacidae); most of them are extinct today. The morphological examination of the subfossil data suggests that these taxa originated from multiple independent colonizations (Steadman 2006). Unfortunately, the only genetic study including subfossils failed to obtain DNA data from material extracted from Marquesas archeological excavations (Kirchman 2012, on Rallidae). Further phylogenetic studies should be conducted on other subfossil material to test the colonization patterns of these birds.

Both Marquesas fruit doves conjointly inhabited several islands for a long time, until the extinction of the RMFD less than a century ago. The reasons for its extinction are unclear, but human activities probably played a major role. Habitat degradation (deforestation, fires, introduction of predatory animals, grazing ungulates, and invasive plants) and the hunt for red feathers, a color prized by Polynesians (Stokes 1925), may have jointly driven the RMFD’s extinction (Steadman 1997a). Conversely, the WCFD is still common today throughout its range and even benefited from introduced fruiting trees as new food resources (Holyoak and Thibault 1984). This suggests that the RMFD was a more vulnerable species, either associated during parts of its life cycle with a type of native habitat becoming rare, or sensitive to introductions and disturbances. Because its extinction precludes the ecological study of the coexistence of the two related species, the sympatric Marquesas fruit doves will remain an enigma for this remote oceanic archipelago, where islands are relatively small compared with the Hawaiian Islands or the Galápagos.

**Acknowledgments**

We are grateful to the following people and institutions: Joel Cracraft, Mary Lecroy, and Paul Sweet (American Museum of Natural History), Donna Dittmann and Frederick Sheldon (Louisiana State University), Sharon Birks (University of Washington, Burke Museum), Jon Fjeldså (Zoological Museum of Copenhagen), Clemency Fisher and Tony Parker (National Museums Liverpool), Robert Prys-Jones and Mark Adams (Natural History Museum, Tring), and Erica Spotswood (University of California, Berkeley). For their help and support during fieldwork in French Polynesia, J.-C.T. and A.C. thank Philippe Raust and Thomas Ghestemme (Société d’Ornithologie de Polynésie), Claude Serra (Direction de l’Environnement, French Polynesia), and the Institut de Recherche pour le Développement (IRD Tahiti). We are also grateful to Dick Watling (Environment Consultants Fiji) and Melinda Allen (University of Auckland) for providing additional information, and to Richard Camp and an anonymous reviewer for their helpful comments on the manuscript.

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