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COVER IMAGES

FRONT COVER: Figure 1 *in* Daniel, p. 342. Views of Príncipe island: southeastern portion looking south toward islet of Bone do Joquei (top) and southwestern portion looking northeastward (bottom).
Photos by expedition members M. Nadel (top) and R. Wenk (bottom).

COVER DESIGN

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A Revision of New World *Lyroda* Say, 1837 (Hymenoptera: Crabronidae)

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The North and South American *Lyroda* are revised and redescribed; the types of South American species are examined for the first time since their descriptions more than 150 years ago. A key for species identification is provided, including several previously unnoticed characters. Taxonomically important characters are illustrated, and a distribution map is provided for each species. The following new synonymies are established: *Morphota harpactoides* F. Smith, 1856 and *Morphota tridens* Taschenberg, 1870 = *Lyroda fasciata* (F. Smith, 1856); *Lyroda antillana* Genaro and Portuondo, 2001 = *Lyroda subita* Say, 1837. Neotypes are designated for *Lyroda subita* Say, 1837 and *Lyroda triloba* Say, 1837.

Lyroda Say, 1837, a genus of the Miscophini, includes 25 currently recognized species, but we reduce this number to 22. Originally described from the United States, the genus was subsequently found in South America, southeastern Asia (where most of the known species occur), Africa, and Australia. In the New World, two species were described from the United States by Say in 1837, three from Brazil by F. Smith in 1856, one from the same country by Taschenberg in 1870, and one from the Caribbean islands by Genaro and Portuondo in 2001. The South American species, in particular, have never been critically revised and remain unidentifiable, and are only mentioned in species lists by Kohl, 1885, Dalla Torre, 1897, Iwata, 1933, Bohart and Menke, 1976, and Amarante, 2002, in spite of the 150 or more years since their descriptions. This deplorable situation is corrected in the present paper.

Most members of *Lyroda* are easily recognized by its unique pronotal collar, whose lateral corner is separated by an impression from the median, obtuse projection (that narrows posteriorly), resulting in a trituberculate appearance (Fig. 1). These structures, however, are only inconspicuously expressed, barely perceptible, in some undescribed Australian species. Most species have three submarginal cells, but the Australian *L. errans* (R. Turner) and a few undescribed Australian species have two.

FIGURE 1. *Lyroda subita*: pronotum in dorsal view.

MORPHOLOGICAL TERMINOLOGY. The terminology used here follows Bohart and Menke (1976).

Origin of Material. The specimens examined or otherwise mentioned in the text are deposited in the institutions listed below. The institutions are referred to in the text by their respective capitalized abbreviations that precede their full names in the list below (the name of the person responsible for sending specimens is given in parentheses):

AMNH: American Museum of Natural History, New York, New York, USA (Christine LeBeau).

BISH: Bishop National Museum, Honolulu, Hawaii, USA (James H. Boone).

BMNH: The Natural History Museum, formerly British Museum (Natural History), London, United Kingdom (Gavin R. Broad).

CAS: California Academy of Sciences, San Francisco, California, USA.

CNC: Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada (John T. Huber).

DZUP: Departamento de Zoologia, Universidade Federal de Paraná, Curitiba, Paraná, Brazil (Gabriel A.R. Melo, Brunno Rosa).

FSCA: Florida Department of Agriculture and Consumer Services, Gainesville, Florida, USA, formerly Florida State Department of Agriculture or Florida State Collection of Arthropods (Elijah J. Talamas).

HYMB: Coleção de Hymenoptera do Museu da Biodiversidade, Faculdade de Ciencias Biológicas e Ambientais, Universidade Federal da Grande Dourados, Dourados, Mato Grosso do Sul, Brazil (Bhrenno M. Trad).

IML: Instituto de Entomología, Fundación Miguel Lillo, Tucumán, Argentina (Emilia Constanza Pérez).

MLUH: Zoologische Sammlung der Martin-Luther-Universität, Halle an der Saale, Germany (Karla Schneider).

MNHNC: Museo Nacional de Historia Natural de Cuba, Habana, Cuba.

UCD: Bohart Museum of Entomology, University of California, Davis, California, USA (Steve L. Heydon, Lynn S. Kimsey).

USNM: United States National Museum, Smithsonian Institution, Washington, D.C., USA (Seán Brady).

Neotype Designations. The type material of both North American *Lyroda* described by Thomas Say (1837) was subsequently lost, together with the majority of his collection (Fox, 1902). No specimen of either species is present among the 71 surviving Say's type specimens at the Museum of Comparative Zoology, Cambridge, Massachusetts (Mawdsley, 1993). In order to assure nomenclatural stability, we therefore designate a neotype for each of the species.

Say's original descriptions do not contain many specifics to species recognition, but his reference to the wing color is significant. According to him, the wings are "purple-fuliginous, almost opaque" in *L. triloba*, and "at tip dusky" in *L. subita*. This difference has been used in the existing keys for the two species (Fox, 1894; H. Smith, 1908; Williams, 1914; Rohwer *in* Viereck, 1925).

Lyroda subita was described from an unspecified locality in Indiana, and *L. triloba* just from North America, without a state or locality, but certainly from the eastern USA, as the species range does not extend into Canada and does so only insignificantly beyond the 100th meridian (in South Dakota). Not having seen any specimen of *L. subita* from Indiana, we designate as a neotype of this species a female from Michigan (a state adjacent to Indiana): Cheboygan County, no specific locality, 19 July 1952, D.G. Shappirio collector (USNM). For *L. triloba*, we designate as a neotype a female from Arkansas: Hampstead County: no specific locality, 14 August 1954, no collector (CAS).

Key to New World Lyroda

1. Gaster red basally (Fig. 6); tergum I with only a pair of basomedian carinae; forewing membrane in many specimens with dark, subapical, transverse fascia (Fig. 6), inconspicuous in male. South America 2

— Gaster all black; tergum I in vast majority of specimens with several smaller ridges in addition to pair of main basomedian carinae; forewing membrane without transverse fascia. North America and Caribbean islands 3

2. Propodeal dorsum with 10–15 longitudinal ridges in at least two thirds of its length (Fig. 2); mesopleural setae not concealing integument . . . . *concinna* (F. Smith)

– Propodeal dorsum with well-defined median ridge and with smaller, irregular, variously shaped ridges on each side of it (Fig. 8), median carina and smaller ridges lacking in some specimens; mesopleural setae concealing sculpture, at least from certain angles and on selected parts of mesopleuron. [Female: scutellum in most specimens microsculptured (except basally) and with few sparse, minute punctures (Fig. 7), appearing unsculptured under lower magnifications, all punctate in some specimens, with all intermediates] . . . . *fasciata* (F. Smith)

3. Propodeal side at most with evanescent ridges, with at least short, rudimentary spiracular groove (Fig. 12). Female: clypeus with three well-defined teeth on each side of lobe (Fig. 10); wing membrane all or largely translucent, except darkened in Floridian populations; clypeal setae silvery; vestiture of clypeus and propodeum silvery; gastral terga I-III with silvery pubescence on apical depressions. Male: clypeal free margin with obtuse median projection (Fig. 11). . . . . *subita* Say

— Propodeal side with well-defined ridges, without spiracular groove (Fig. 19). Female: clypeus with three pairs of inconspicuous (almost invisible) teeth on each side of lobe (Fig. 17); wing membrane dark; clypeal setae dark; vestiture of propodeum and gastral terga black. Male: clypeal free margin rounded mesally (Fig. 18) . . . . *triloba* Say

SPECIES DESCRIPTIONS

Lyroda concinna (F. Smith)

Morphota concinna F. Smith, 1856:294, ♀. Holotype by monotypy: Brazil: Pará: Tapajós River (BMNH), examined. – **As *Lyroda concinna***: Kohl, 1885:267 (new combination, in checklist of world *Lyroda*); Dalla Torre, 1897:696 (in catalog of world Hymenoptera); Iwata, 1933:7 (in list of world *Lyroda*); R. Bohart and Menke, 1976:299 (in checklist of world Sphecidae); Nascimento and Overal, 1980:7 (Brazil, Peru, determination uncertain); Amarante, 2002:41 (in catalog of Neotropical Crabronidae); Rasmussen and Asenjo, 2009:11 (in checklist of Crabronidae of Peru, determination uncertain).

RECOGNITION. Like *Lyroda fasciata*, the gaster is red basally in *L. concinna*. It differs from that species in having 10–15 roughly parallel longitudinal ridges on the propodeal dorsum (Fig. 2) and the mesopleural vestiture not concealing the integument.

DESCRIPTION. Propodeal dorsum with 10–15 roughly parallel longitudinal ridges, mainly extending to the dorsum's apex (Fig. 2), but reaching only about two thirds of dorsum's length in male from Tefé (CAS); propodeal side unridged, without spiracular groove. Tergum I with only a pair of basomedian carinae. Mesopleural vestiture not concealing integument.

Body black, but gaster red basally; legs black or tibiae partly dark red. Forewing membrane in some specimens with slightly darkened, subapical, transverse fascia.

♀: Free margin of clypeal lobe with three teeth on each side of lobe. Length 7.6 mm.

♂: Free margin of clypeal lamella slightly arcuate to slightly weaving. Length 5.6–7.6 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 3). Northern South America.

FIGURE 2. *Lyroda concinna:* propodeal dorsum of male.

FIGURE 3: Collecting localities of *Lyroda concinna.*

RECORDS. **BRAZIL**: **Amazonas**: Tefé (1 ♂, CAS). **Pará**: Belém: APEG [= Área de Pesquisa Ecológica do Guamá] Forest (1 ♂, CNC; 1 ♂, FSCA), Tapajós River (1 ♀, BMNH, holotype of *Morphota concinna*), no specific locality (1 ♂, CAS).

GUYANA: **Mahaica-Berbice**: Blairmont (1 ♂, BISH).

Lyroda fasciata (F. Smith)

Morphota fasciata F. Smith, 1856:294, ♀. Holotype by monotypy: ♀, Brazil: Pará: Santarém (BMNH), examined. – **As *Lyroda fasciata***: Kohl, 1885:267 (new combination, in checklist of world *Lyroda*); Dalla Torre, 1897:696 (in catalog of world Hymenoptera); Iwata, 1933:7 (in list of world *Lyroda*); R. Bohart and Menke, 1976:299 (in checklist of world Sphecidae); Nascimento and Overal, 1980:7 (Brazil); Amarante, 2002:41 (in catalog of Neotropical Crabronidae).

Morphota harpactoides F. Smith, 1856:294, ♀ (as *Harpactoides*, incorrect original capitalization). Holotype by monotypy: ♀, Brazil: no specific locality (BMNH), examined. **New synonym**. – **As *Lyroda harpactoides***: Kohl, 1885a:267 (new combination, in checklist of world *Lyroda*); Dalla Torre, 1897:696 (in catalog of world Hymenoptera); Iwata, 1933a:7 (in list of world *Lyroda*); R. Bohart and Menke, 1976:299 (in checklist of world Sphecidae); Amarante, 2002:41 (in catalog of Neotropical Crabronidae).

Morphota tridens Taschenberg, 1870:8, ♀. Holotype by monotypy: ♀, Brazil: Minas Gerais: Lagoa Santa (Halle), examined. **New synonym**. – **As *Lyroda tridens***: Kohl, 1885:267 (new combination, in checklist of world Lyroda); Dalla Torre, 1897:696 (in catalog of world Hymenoptera); Iwata, 1933:7 (in list of world *Lyroda*); R. Bohart and Menke, 1976:299 (in checklist of world Sphecidae); Nascimento and Overal, 1980:7 (Brazil); Amarante, 2002:41 (in catalog of Neotropical Crabronidae).

RECOGNITION. Like *Lyroda concinna*, this species has the gaster red basally, and the wing membrane in most specimens with slightly darkened, subapical, transverse fascia (Fig. 6), fascia inconspicuous in male. Unlike that species, the propodeal dorsum has at most one longitudinal carina and smaller, variously shaped ridges that are absent is some specimens (Fig.7); also the mesopleural pilosity conceal the integument (at least from certain angles and at least on some mesopleuron parts). Many females are unique within the genus in having the scutellum punctate only basally, mostly microsculptured and with a few sparse, minute punctures (Fig. 8), appearing unsculptured under lower magnifications; there are all intermediates to all punctate scutellum.

JUSTIFICATION OF NEW SYNONYMY. In spite of some minor differences, the holotypes of *Lyroda fasciata* and of *Lyroda harpactoides* are certainly conspecific. Both species were described in the same paper. Acting as first revisers (Article 24.2.2 of the Code), we select *L. fasciata* as the valid name, and *L. harpactoides* as its junior synonym.

The holotype of *Morphota tridens* is just an average specimen of *Lyroda fasciata*, not differing from other specimens of this species by any particular feature. Consequently, we also synonymize these two names.

TYPE LOCALITY OF *MORPHOTA TRIDENS*. This species was described from Lagoa Santa in Brazil. There are two places of this name in Brazil: one in Goiás, the other in Minas Gerais. The one in Goiás, however, was established only on 1 January 2001, whereas the one in Minas Gerais did exist already in 1863–1866, when paleontological excavations were conducted there. The holotype of *Morphota tridens*, described in 1870, must have been collected there during that time.

DESCRIPTION. Propodeal dorsum with median ridge and smaller, irregular, variously shaped ridges on each side of it (Fig. 8), median carina and smaller ridges lacking in some specimens; propodeal side unridged, without spiracular groove. Tergum I with only a pair of basomedian carinae.

Body black except two or three first gastral terga red (Fig. 6); legs black or male tibiae partly or all red. Forewing membrane in many specimens with slightly darkened, subapical, transverse fascia (Fig. 6) that is inconspicuous in male.

♀: Free margin of clypeal lobe varying: mostly with three teeth on each side of the lobe (Fig. 4), but with two teeth in some specimens (on one or both sides), without teeth on right side in one specimen from Potrillos del Guneda National Park, Bolivia. Length 7.1–9.2 mm.

♂: Free margin of clypeal lamella varying from slightly convex to shallowly concave (Fig. 5). Length 6.0–8.3 mm.

VARIATION. In most females, the scutellum is microsculptured (Fig. 7), with a few sparse, minute punctures, appearing unsculptured under lower magnification. In the females from the three following localities, however, the scutellum is all or nearly all punctate: Bolivia: Potrillos del Guneda National Park (one of three specimens); Brazil: Lagoa Santa (holotype of *Morphota tridens*); Paraguay: Caaguazú (one of four specimens). Some other specimens are intermediate.

GEOGRAPHIC DISTRIBUTION (Fig. 9). South America except southern Argentina and Chile.

RECORDS. **ARGENTINA**: **Entre Ríos**: Liebig (13 ♀, 27 ♂, AMNH). **Salta**: Pocitos (3 ♂, AMNH).

BOLIVIA: **Santa Cruz**: Potrillos del Guneda National Park at 17°40′S 63°27′W (2 ♀, 7 ♂, UCD), Ciudad Santa Cruz (1 ♀, AMNH), no specific locality (1 ♀, CAS). **Santiago**: Santiago (1 ♀, AMNH).

BRAZIL: **Espírito Santo**: Santa Teresa (1 ♂, DZUP). **Goiás**: Jatai (1 ♀, CNC). **Mato Grosso**: Cáceres (1 ♀, 1 ♂, DZUP). **Mato Grosso do Sul**: Serra da Bodoquena National Park (2 ♂, HYMB), 7 mi. N Nioaque (1 ♂, HYMB). **Minas Gerais**: Pedra Azul National Park (1 ♀, CNC), Lagoa Santa (1 ♀, holotype of *Morphota tridens,* MLUH). **Pará**: Belém (1 ♀, BISH; 1 ♀, CNC), no specific locality (1 ♀, CAS). **Paraíba**: Mamanguape (1 ♀, HYMB). **Paraná**: Piraquara (1 ♀, DZUP), Vila Velha State Park (1 ♀, DZUP). **Piauí**: Corrente (1 ♂, CAS). **Rondônia**: Vilhena (1 ♀, 1 ♂, DZUP).

GUYANA: **Cuyuni-Mazaruni**: Kartabo (1 ♀, CAS). **Mahaica-Berbice**: Blairmont (1 ♀, FSCA).

PARAGUAY: Asunción (2 ♀, USNM), Caaguazú (4 ♀, 1 ♂ AMNH), Cororo: San Pedro Department: Río Ypane (1 ♀, AMNH).

PERU: **Madre de Dios**: Río Tambopata National Park at 12°50'S 69°20'W (2 ♀, CAS).

SURINAM: Zanderij (1 ♂, CAS).

URUGUAY: Río Negro 15 km S Paysandú (1 ♀, AMNH).

FIGURE 4. *Lyroda fasciata*: female clypeus and mandibles.

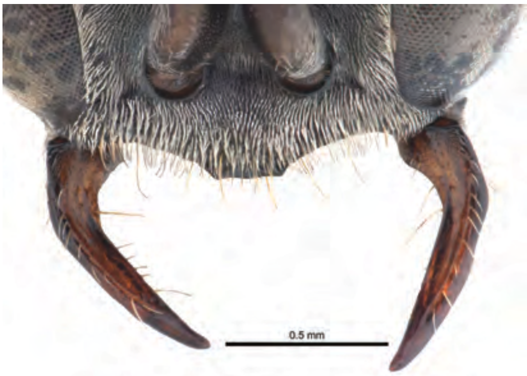

FIGURE 5. *Lyroda fasciata*: male clypeus and mandibles.

FIGURE 6. *Lyroda fasciata*: female body in lateral view.

FIGURE 7. *Lyroda fasciata*: scutellum of an average female.

FIGURE 8. *Lyroda fasciata*: propodeal dorsum of female.

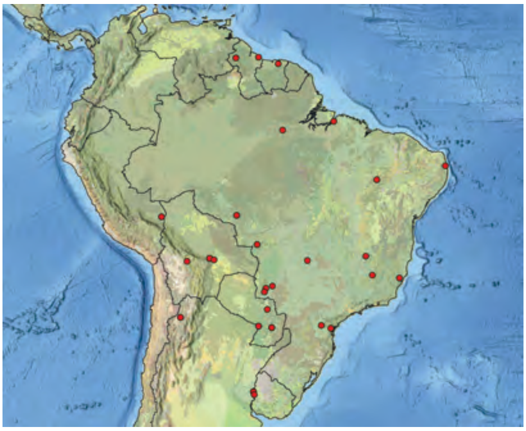

FIGURE 9. Collecting localities of *Lyroda fasciata*.

Lyroda subita Say

Lyroda subita Say, 1837:372, ♀. Holotype or syntypes: USA: Indiana: no specific locality (lost). Neotype: ♀, Michigan: Cheboygan County, no specific locality (USNM), **present designation**. – Le Conte, 1859:755 (original description copied); Patton, 1880:387 (in checklist of North American Larrinae); Provancher, 1882:49 and 1883:632 (original description translated into French); Kohl, 1885:267 (in checklist of world *Lyroda*); Cresson, 1887:277 (in catalog of North American Hymenoptera); W. Fox, 1892c:138 (does not belong to *Didineis*); Patton, 1892:90 (may belong to *Didineis*, prey carrying), 1893:202 (*Nemobius* prey is killed and not paralyzed); W. Fox, 1894:533 (in revision of North American Larrinae); Dalla Torre, 1897:696 (in catalog of world Hymenoptera); G. Peckham and E. Peckham, 1898:169 (nesting habits); Ashmead, 1899:250 (in checklist of North American Crabronidae); J. Smith, 1900:518 (in list of insects of New Jersey); Harrington, 1902:222 (Canada: Ontario: Ottawa); Adlerz, 1904:137 (known prey: gryllids); G. Peckham and E. Peckham, 1905:253 (nesting habits); Snow, 1906:134 (Arizona); H. Smith, 1908:374 (in revision of Nebraskan Sphecidae); J. Smith, 1910:684 (in new list of insects of New Jersey); F. Williams, 1914:174 (in revision of Larrinae of Kansas), 207 (nesting habits); Rohwer, 1916:683 (in catalog of Hymenoptera of Connecticut); Gahan and Rohwer, 1918:30 (Provancher's specimens not located); Mickel, 1918:408 (in catalog of Nebraskan Sphecidae); Rohwer *in* Viereck, 1925:683 (in key to Sphecidae of Connecticut; East Hartford, New Haven); J.Ch. Bradley, 1928:1010 (in catalog of New York Crabronidae); Hendrickson, 1930:159 (Iowa); Iwata, 1933:7 (in list of world *Lyroda*); Krombein, 1936:98 (New York: Buffalo; floral records); Brimley, 1938:443 (North Carolina: Fayetteville, Raleigh); Krombein, 1950:267 (North Carolina: Dare County), 1951a:143 (Virginia: Dunn Loring; visiting tuliptree honeydew); Krombein *in* Muesebeck, Krombein, and Townes 1951:941 (in catalog of North American Hymenoptera); Krombein, 1952:93 (USA: Virginia: Westmoreland State Park); K. Cooper, 1953:33 (Massachusetts: Island of Penikese); Krombein, 1953:328 (North Carolina); Gittins, 1960:135 (Idaho); Kurczewski and Kurczewski, 1963:146 (Pennsylvania: Presque Isle State Park); Evans, 1964:281 (description of larva), 282 (nesting habits); Krombein, 1963:273 (Maryland: Plummers Island near Washington, D.C.); G. Bohart, Nye, and Hawthorn, 1970:48 (Utah: Logan, onion pollinator); Kurczewski and Kurczewski, 1971:132 (prey: *Nemobius carolinus* Scudder, a gryllid); Evans, 1975:265 (unsuccessful colonizer of a new habitat); R. Bohart and Menke, 1976:299 (in checklist of world Sphecidae); L. Davis, 1978:217 (North Carolina: Kill Devil Hills, data from Krombein, 1953); Krombein, 1979:1633 (in catalog of North American Hymenoptera); Finnamore, 1982:109 (in Sphecid Fauna of southern Quebec); Kurczewski and Peckham, 1982:149–155 (nesting habits); Kurczewski and Spofford, 1985:113 (unusual prey: Tridactylidae); Radović, 1985:65 (sting apparatus analyzed); Piek and Spanjer, 1986:185 (in list of Sphecidae with known prey); Steiner, 1986:104 (references to publications on nesting habits); Spofford, Kurczewski, and Downes, 1989:256, 259 (reference to publications on nest parasites *Metopia argyrocephala* (Meigen) and *Senotainia trilineata* (Wulp), miltogrammine flies), 257, 260 (nest parasites: *Metopia luggeri* Townsend, *Phrosinella aurifacies* Downes, *Senotainia rubriventris* Macquart, *Senotainia vigilans* Allen, miltogrammine flies, and undetermined miltogrammine species); Kurczewski and Acciavatti, 1990:60 (New York: Cayuga County); Spofford and Kurczewski, 1990:746, 747, 748, 749, 751 (nest parasites: *Metopia luggeri* (Townsend), *Phrosinella aurifacies*, *Senotainia rubriventris* Macquart, *Senotainia trilineata* (Van der Wulp), *Senotainia vigilans* Allen, and unknown species of Miltogrammini, Sarcophagidae); Kurczewski, 1991:203 (burrow construction from ground surface); Spofford and Kurczewski, 1992:997 (species of miltogrammine parasites listed), 1002 (countercleptoparasitic habits: freeze-stop and face-off, diversionary flight), 1005 (post-larvipositional countercleptoparasitic habits: abandon prey); Ahlstrom, 1995:109 (in checklist of insects of North Carolina); Kurczewski, 1998:250 (pine barrens in upstate New York); Sugar *et al.*, 1998:15 (Canada: southern Ontario); Buck, 2004:25 (Canada: in checklist of Crabronidae of Ontario); Giles and Ascher, 2006:231 (New York: Black Rock Forest Preserve). – **As *Tachytes subitus***: F. Smith, 1856:307 (new combination, in catalog of Hymenoptera in British Museum). – **As *Lyrops subita***: Cresson, 1862:238 (new combination, in catalog of North American Hymenoptera). – **As *Larrada subita***: Cresson, 1873:213 (new combination, Texas).

Lyroda sp.: Alayo Dalmau, 1973:176 and 1976:21, corrected to *Lyroda antillana* by Genaro and Portuondo, 2001:45.

Lyroda antillana Genaro and Portuondo, 2001:45, ♀. Holotype: ♀, Cuba: Guantánamo: El Imbano, Cuchillas de Baracoa (MNHN Habana). Paratypes: Dominican Republic (FSCA), one paratype examined. **New synonym.** – Portuondo and Fernández, 2004:135 (Cuba: Sierra Maestra and Nipe-Sagua-Baracoa mountains); Amarante, 2005a:5 (in addendum to his 2002 catalog of Neotropical Crabronidae and Sphecidae); Genaro, 2006:54 (in checklist of Cuban Sphecidae and Crabronidae; also: Hispaniola); Perez-Gelabert, 2008:240 (in list of arthropods of island of Hispaniola).

Recognition. *Lyroda subita* resembles *L. triloba* in having a black gaster. Unlike that species, the propodeal side is at most inconspicuously ridged and has at least a short, rudimentary spiracular grove (Fig. 12), rather than with well-defined ridges and no spiracular grove. The female has three well defined teeth on each side of the clypeal lamella (Fig. 10), its wing membrane is mostly translucent except darkened in Floridian populations, the clypeal setae are silvery, and also silvery is the pubescence on the propodeum and the apical depressions of terga I-III (rather than the clypeal teeth inconspicuous, wing membrane dark, clypeal setae dark, and the pubescence of the propodeum and the gaster dark). In the male, the clypeal free margin has an obtuse, median projection (Fig. 11) rather than being rounded mesally.

Justification of New Synonymy. Genaro and Portuondo, 2001 differentiated *Lyroda antillana* from *L. subita* by a single character: a more intensely sculptured propodeal dorsum in the former species. We have examined a female paratype of *L. antillana* from the Dominican Republic as well as two males from that country, and were unable to detect any other difference. The presence of a spiracular groove on the propodeum is as in *L. subita*. We have also noticed that the sculpture of the propodeal dorsum varies significantly: it is inconspicuous in many specimens from the continental North America (Fig. 13), but almost as conspicuous in some specimens from Florida (Fig. 14) as in the Dominican paratype examined (Fig. 15). Based on these observations we conclude that *Lyroda antillana* in no more than a Caribbean population of *L. subita*, and we synonymize these two names.

Description. Propodeal side at most with evanescent ridges, with spiracular groove that varies from short, inconspicuous to long, well defined. Clypeal setae silvery. Tergum I in vast majority of specimens with several smaller ridges in addition to pair of main basomedian carinae. Body black. Wings membrane mostly translucent except darkened in Floridian populations.

♀: Anterior margin of clypeus with three teeth on each side, truncate medially (Fig. 10). Gastral terga I-III with silvery pubescence on apical depressions. Length 10.0–13.0 mm.

♂: Free margin of clypeal lamella with obtuse prominence mesally (Fig. 11). Length 6.1–10.0 mm.

Geographic Distribution (Fig. 16). North America from southern Canada south to Jalisco State in Mexico, also Cuba and the Dominican Republic.

Records. **CANADA**: **Alberta**: Writing-on-Stone Provincial Park (4 ♀, CAS). **Manitoba**: Aweme (1 ♀, CNC), Brandon (1 ♂, CNC), Carberry (2 ♀, CNC), 5 mi. W Carberry (2 ♀, CNC), 13 mi. N Glenboro: Bald Head Hills (1 ♀, CNC). **New Brunswick**: Kouchibouguac National Park (1 ♀, CNC), St. John (1 ♂, CNC). **Nova Scotia**: Kings Co. (1 ♀, CNC). **Ontario**: Belleville (1 ♀, 2 ♂ CNC), Brighton (1 ♀, 1 ♂, CNC), Dunrobin (1 ♀, CNC), Chatham (1 ♀, CNC), Jordan (1 ♀, CNC), Kearney (1 ♀, CAS), 15 mi. SE Kenora (1 ♂, CAS), Ottawa (2 ♀, 7 ♂, CNC), Point Pelee (3 ♀, CNC), Sant David (1 ♀, CNC), Spencerville (2 ♀, CNC), Strathroy (7 ♀, 1 ♂, CNC), Toronto (1 ♂, CNC), Vineland (1 ♀, CNC). **Quebec**: Aylmer (1 ♂, CNC), Harrington (1 ♂, CNC), Hemmingford (1 ♂, CNC), Hull (1 ♀, CNC). **Saskatchewan**: Fort Qu′Appelle (1 ♀, CNC).

CUBA (Genaro and Portuondo, 2001): **Guantánamo**: El Imbano: Cuchillas de Baracoa. **Santiago de Cuba**: Santa María de Loreto. **Holguín**: La Melba: Moa.

DOMINICAN REPUBLIC: **Hato Mayor**: Farm Mango Limpio 25 km NNW Hato Mayor

FIGURE 10. *Lyroda subita*: female clypeus and mandibles.

FIGURE 11. *Lyroda subita*: male clypeus and mandibles.

FIGURE 12. *Lyroda subita*: female propodeal side (arrow shows spiracular groove).

FIGURE 13. *Lyroda subita*: propodeal dorsum of female with average sculpture.

FIGURE 14. *Lyroda subita*: propodeal dorsum of female from Florida.

FIGURE 15. *Lyroda subita*: propodeal dorsum of a paratype female of *Lyroda antillana*.

FIGURE 16: Collecting localities of *Lyroda subita*.

(1 ♂, CAS). **Pedernales**: 21 km N Cabo Rojo (1 ♀, FSCA, paratype of *L. antillana*).

MEXICO: **Chihuahua**: 50 road km S Creel which is 27°46'S 107°39'W (1 ♀, CAS). **Jalisco**: Teocaltiche (2 ♀, CAS).

USA: **Arizona:** Cochise Co.: 28 mi. N Douglas (1 ♀, UCD). **Arkansas**: Benton Co.: 2 mi. N Siloam Springs (1 ♂, USNM). **California**: Davis (12 ♀, 6 ♂, UCD), Fresno Co.: Firebaugh (1 ♀, USNM), Merced Co.: Dos Palos (1 ♀, AMNH), Hayward (1 ♂, FSCA), Riverside Co.: 18 mi. W Blythe, Hopkins Well (1 ♀, 6 ♂, CAS), Mendota (1 ♀, USNM), Orange Co.: Santa Ana (1 ♀, 1 ♂, USNM), Shasta Co.: 10 mi. N Redding (1 ♀, 1 ♂, FSCA), Shasta Co.: 2 mi. W Shingletown (21 ♀, 2 ♂, FSCA), Kern Co.: 3 mi. SW Taft (1 ♀, UCD), Vacaville (1 ♂, UCD), Woodland (4 ♀, 1 ♂, UCD). **Colorado**: Boulder (2 ♀, USNM), Crook (1 ♀, AMNH), Larimer Co.: Fort Collins (2 ♀, CAS), Springs Co.: Fountain Valley (1 ♀, AMNH), Glenwood (1 ♀, AMNH), Yuma Co.: 4 mi. NE Idalia (2 ♀, AMNH), Shafter Co.: Kern (1 ♀, FSCA), White Rock (1 ♀, AMNH), no specific locality (3 ♀, USNM). **Connecticut**: East Haven (1 ♀, UCD), Hartford (1 ♀, UCD), North Canaan (1 ♀, AMNH), Saybrook (1 ♂, AMNH), Samford (1 ♀, USNM). **Delaware**: Dewey Beach (1 ♀, USNM). **District of Columbia**: Washington (5 ♀, 1 ♂, USNM). **Florida**: Austin Carey (2 ♂, FSCA), Jackson Co.: Florida Caverns (1 ♀, CNC), Gainesville (6 ♀, 9 ♂, FSCA), Interlachen (1 ♀, FSCA), Alachua Co.: 4 mi. N La Crosse (1 ♀, FSCA), Lake Placid (2 ♀, CAS), Quincy (14 ♀, 1 ♂, FSCA), Santa Rosa (1 ♀, FSCA), Tall Timbers (1 ♂, FSCA), Gulf Co.: Wewahitchka (1 ♂, FSCA), no specific locality (1 ♂, FSCA). **Georgia**: Clarke Co.: Athens (3 ♀, FSCA), Liberty Co.: St. Catherine Island (3 ♀, AMNH), Tarversville (1 ♀, FSCA, 1 ♂, FSCA), Clarke Co.: Whitehall Forest (1 ♂, FSCA). **Idaho**: Buhl (1 ♂, BISH), Notus (1 ♀, 1 ♂, UCD), Canyon Co.: Parma (1 ♀, UCD), Pingree (1 ♀, CNC). **Illinois**: Bellville (1 ♀, BISH), Chicago (1 ♀, USNM), Fort Sheridan (1 ♀, USNM), Scott Co.: Bluffs (3 ♀, UCD), Mason Co.: Farmer City (1 ♀, 2 ♂, CAS), Waukegan (1 ♀, AMNH), West Frankfort (1 ♀, UCD), no specific locality (1 ♀, AMNH). **Indiana**: Lafayette (1 ♀, USNM). **Iowa**: Ames (1 ♀, USNM), Ankeny (1 ♀, UCD), Bellevue (5 ♀, UCD), Sioux City (4 ♀, USNM), Clinton Co.: Clinton (1 ♀, 1 ♂, UCD), Coralville (1 ♀, CAS), Iowa City (1 ♀, UCD), Sioux (7 ♀, 1 ♂, CAS), Polk Co. (1 ♂, FSCA). **Kansas**: Baldwin (1 ♀, CAS, 3 ♀, USNM, 2 ♂, USNM), Dickson Co. (1 ♀, USNM), Douglas (1 ♀, CAS, 1 ♀, UCD, 1 ♂, USNM), Plainville (1 ♀, CNC), Rooks (1 ♀, CAS). **Louisiana**: Opelousas (3 ♂, USNM), Tallulah (1 ♀, AMNH), no specific locality (1 ♀, 2 ♂, USNM). **Maryland**: 4 mi. SW Ashton (2 ♀, USNM), Calvert Co. (2 ♀, USNM), Camp Springs (1 ♀, USNM), Beltsville (1 ♀, USNM), Burtonsville (2 ♀, CAS), Montgomery Co.: Colesville (1 ♀, UCD), Frederick Co. (1 ♀, USNM), Patuxent River: Rout 4 (1 ♀, USNM), Cecil Co.: Pleasant Hill (1 ♀, USNM), Plummers Island (1 ♂, CAS, 2 ♀, UCD, 1 ♀, 1 ♂, USNM), Montgomery Co.: Silver Spring (1 ♀, FSCA), no specific locality (1 ♂, UCD). **Massachusetts**: Billerica (2 ♀, CNC), Boston (2 ♀, UCD, 1 ♂, USNM), Forest Hills (8 ♀, CAS, 5 ♀, UCD, 1 ♀, USNM), Woods Hill (1 ♀, UCD). **Michigan**: Antrim Co. (1 ♀, AMNH), Cheboygan Co. (1 ♀, USNM), Detroit (1 ♂, UCD), Gratiot Co. (1 ♂, AMNH), Manistee Co. (1 ♂, IML), Mason Co. (1 ♂, AMNH), Menominee Co. (1 ♀, IML), Camp Miniwanka (1 ♀, FSCA), Montcalm Co. (1 ♂, AMNH). **Minnesota**: 6 mi. N Chillicothe (1 ♀, UCD), Nicollet Co.: Courtland (1 ♀, CNC), Itasca State Park (1 ♀, AMNH). **Mississippi**: Yalobusha Co.: Water Valley (1 ♀, UCD, 1 ♀, FSCA). **Missouri**: Henry Co.: Clinton (1 ♀, UCD), Columbia (4 ♀, USNM), Marion Co.: Hannibal (4 ♀, UCD). **Montana**: Columbia Falls (8 ♀, UCD, 1 ♀, USNM), no specific locality (4 ♀, 2 ♂, UCD). **Nebraska**: Hooker Co.: 1.5 mi. N Mullen (1 ♂, USNM), 8 mi. N Ogallala (6 ♀, 1 ♂, AMNH), Valley (1 ♀, CAS). **New Hampshire**: Durham (2 ♂, USNM), Belknap Co.: Gilford-Alton (1 ♀, USNM), Nelson (1 ♀, USNM). **New Jersey**: Burlington Co.: Atsion (2 ♀, UCD), Browns Mills (1 ♀, 1 ♂, AMNH), Kearny (1 ♀, AMNH), Metuchen (3 ♀, 1 ♂, FSCA), 3 mi. E Medford Lakes (2 ♀, UCD), Mountain View (1 ♂, AMNH), Bergen Co.: Norwood (1 ♀, AMNH), Palmyra (1 ♀, AMNH, 1 ♀, USNM), Princeton (1 ♀, USNM), Riverton (1 ♂, USNM), South Orange (1 ♀, AMNH), Teaneck (1 ♂, CAS), no specific locality (1 ♀, UCD, 1 ♂, AMNH). **New Mexico**: McKinley Co.: 19 mi. N Gallup (2 ♀, AMNH). **New York**: Auburn (1 ♀, UCD, 1 ♀, USNM), Bear Mountain State Park (1 ♀, USNM), Bronx Co.: Bartow-Pell Mansion (1 ♀, AMNH), Batavia (1 ♀, 1 ♂, BISH), Bushnellsville (1 ♀, AMNH), Buffalo (1 ♀, CAS), Chaffee (1 ♀, UCD), Ulster Co.: Cherrytown (14 ♀, AMNH), Colden (1 ♀, CAS), Ellenville (1 ♂, FSCA), Orange Co.: Cornwall, Black Rock Forest (5 ♀, 2 ♂, AMNH), Croton Falls (1 ♀, UCD), Suffolk Co.: Gardiners Island (3 ♀, AMNH), Great Kills (1 ♀, AMNH), Huntington (1 ♀, UCD), Tompkins Co.: Ithaca: Kite Hill (1 ♀, CAS, 1 ♀, 2 ♂, CNC, 4 ♀, AMNH), Westchester Co.: Lewisboro (4 ♀, AMNH), Long Island: Huntington (8 ♀, 4 ♂, AMNH), Long Island: South Haven (1 ♀, AMNH), New Rochelle (1 ♀, AMNH), New York City: Brooklyn (1 ♀, 1 ♂, AMNH), New York City: Central Park (1 ♀, AMNH), New York City: Flatbush (4 ♀, AMNH), New York City: Floyd Bennett Field (1 ♀, AMNH), New York City: Van Cortland Park (1 ♀, AMNH), New York City: no specific locality (1 ♂, AMNH), North Fairhaven (1 ♀, USNM), Oswego (1 ♂, USNM), Tompkins Co.: Ringwood (1 ♀, CAS), Orange Co.: 5 mi. NW Tuxedo (3 ♂, AMNH), Bronx Co.: Van Cortland Park (1 ♀, 2 ♂, AMNH), Grand Island: Warrendale (1 ♀, USNM), no specific locality (1 ♀, USNM). **North Carolina**: Cumberland Co.: Fort Bragg (3 ♀, CAS), Kill Devil Hills (1 ♀, CAS, 2 ♀, USNM), Swain (1 ♀, CNC), Wilmington Co.: Tidewater (1 ♂, FSCA), Tuckasegee (1 ♀, CNC). **North Dakota**: Bottineau (1 ♀, USNM), Cannon Ball (2 ♀, AMNH), Fargo (1 ♀, AMNH), Slope Co.: Logging Camp Ranch (2 ♀, AMNH), Moffit (1 ♀, AMNH), Walcott (1 ♀, AMNH). **Ohio**: Garfield Co. (1 ♀, FSCA), Stark Co.: Massillon (1 ♀, UCD). **Oklahoma**: Garfield Co. (2 ♀, USNM), Fairmont (1 ♂, FSCA), Norman (1 ♀, CNC), 2 mi. E Lake Texoma (6 ♀, UCD). **Oregon**: Harney Co.: Borax Lake (1 ♀, USNM). **Pennsylvania**: 5 mi. NW Davidsburg (1 ♀, USNM), Jeanette (1 ♂, UCD), Northampton Co.: Portland (1 ♂, USNM), Presque Isle (1 ♀, UCD, 1 ♀, AMNH, 1 ♀, USNM), Westmoreland Co. (1 ♀, USNM). **Rhode Island**: Newport (1 ♀, CNC), Washington Co.: Westerly (1 ♀, AMNH). **Texas**: Travis Co.: Austin BFL [= Brackenridge Field Laboratory] (1 ♀, CAS), Fedor (1 ♀, USNM), Kleberg Co.: 20 mi. SE Kingsville (1 ♀, CAS), Salmon (1 ♀, FSCA), Shenandoah (1 ♀, AMNH), Victoria (1 ♂, USNM), no specific locality (1 ♀, USNM). **Utah**: Cornish (1 ♀, CNC), Delta (2 ♀, UCD 1 ♂, CAS), Flowell (1 ♂, CAS), Newton (1 ♀, UCD), Pahvant Range (1 ♀, UCD), Provo (1 ♂, AMNH), Box Elder Co.: 10 mi. SW Tremonton (1 ♂, AMNH). **Vermont**: Fairfax Co.: near, Annandale (1 ♀, CAS, 1 ♀, USNM), Rutland Co.: Pico (1 ♂, FSCA). **Virginia**: Alexandria at 38°49′10.9″N 77°06′59.9″W (10 ♀, CAS), Arlington (1 ♀, USNM), Dunn Loring (1 ♂, USNM), Williamsburg (1 ♀, UCD), Isle of Wight Co.: 6 km S Zuni (1 ♀, USNM). **West Virginia**: Park Hardy Co.: Lost River (1 ♀, CNC). **Wisconsin**: Cranmoor (1 ♀, USNM), Waukesha Co.: Pine Lake (4 ♀, CAS), Clark Co.: Worden Township (6 ♀, 25 ♂, AMNH). **Illegible**: (2 ♀, USNM).

Lyroda triloba Say

Lyroda triloba Say, 1837:372, sex not indicated. Holotype or syntypes: North America: no specific locality (lost). Neotype: ♀, Arkansas: Hampstead County: no specific locality (CAS), **present designation**. – Le Conte, 1859:755 (original description copied); Patton, 1880:387 (in checklist of North American Larrinae); Provancher, 1882:49 and 1883:631 (original description translated into French); Kohl, 1885:267 (in checklist of world *Lyroda*); Cresson, 1887:277 (in catalog of North American Hymenoptera); Ashmead, 1890:33 (in checklist of Hymenoptera of Colorado); W. Fox, 1894:534 (in revision of North American Larrinae); Dalla Torre, 1897:696 (in catalog of world Hymenoptera); Ashmead, 1899:250 (in checklist of North American Crabronidae); Bridwell, 1899:209 (Kansas: no specific locality); J. Smith, 1900:518 (in list of insects of New Jersey); H. Smith, 1908:374 (in revision of Nebraskan Sphecidae); J. Smith, 1910:684 (in new list of insects of New Jersey: Camden County); F. Williams, 1914:174 (in revision of Larrinae of Kansas); Rohwer, 1916:683 (in catalog of Hymenoptera of Connecticut); Mickel, 1918:408 (in catalog of Nebraskan Sphecidae); Rohwer *in* Viereck, 1925:683 (in key to Sphecidae of Connecticut; Branford); Iwata, 1933:7 (in list of world *Lyroda*); Krombein *in* Muesebeck, Krombein and Townes, 1951:941 (in catalog of North American Hymenoptera); R. Bohart and Menke, 1976:299 (in checklist of world Sphecidae); Krombein, 1979:1633 (in catalog of North American Hymenoptera). – **As *Tachytes trilobus***: F. Smith, 1856:307 (new combination, in catalog of Hymenoptera in British Museum). – **As *Lyrops triloba***: Cresson, 1862:238 (new combination, in catalog of North American Hymenoptera). – **As *Larrada triloba***: Cresson, 1873:213 (new combination, Texas).

Lyrops caliptera Say, 1837:373. Nomen nudum or lapsus for *Lyroda triloba*. – Patton, 1880:387 (in checklist of North American Larrinae); Kohl, 1885:267 (in checklist of world *Lyroda*).

RECOGNITION. *Lyroda triloba* differs from its New World congeners in having the propodeal side with well-defined ridges (Fig. 19), the wing membrane dark, particularly in the female, and the large size (length of female 15.2–16.2 mm). In the other species, the propodeal side is either not ridged (most specimens) or (some *L. subita*) has inconspicuous ridges, the wings are light colored (except dark in Floridian populations of *L. subita*) and the female length does not exceed 13 mm. Unlike *L. subita*, the male of *L. triloba* has no median projection on the clypeal free margin (Fig. 18).

DESCRIPTION. Propodeal side with well-defined ridges (Fig. 19), without spiracular groove. Tergum I in vast majority of specimens with several smaller ridges in addition to pair of main basomedian carinae. Body deep black. Wing membrane uniformly dark, particularly in female.

♀: Free margin of clypeus with three pairs of inconspicuous (almost invisible) teeth on each side of lamella (Fig. 17). Clypeal setae dark. Pubescence of gastral terga all black. Length 15.2–16.2 mm.

♂: Clypeal free margin inconspicuously, roundly arcuate mesally (Fig. 18). Clypeal setae silvery. Length 9.6–13.8 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 20). Eastern North America, extending west beyond the 100th meridian only in South Dakota.

RECORDS. USA: **Arkansas**: Conway (1 ♀, CAS, 1 ♀, USNM), Hempstead (1 ♀, CAS, 2 ♀, USNM). **Georgia**: Hiawassee (1 ♀, CNC), Putnam Co. (5 ♀, USNM). **Kansas**: no specific locality (1 ♂, CAS). **Louisiana**: Tallulah (1 ♂, CAS). **Maryland**: Beltsville (2 ♀, USNM), Hudson (3 ♀, FSCA). **North Carolina**: Stafford (1 ♂, CAS), Washington Co. (1 ♀, FSCA). **South Dakota**: Butte Co. (1 ♂, USNM). **Texas**: McKinney (1 ♀, USNM), no specific locality (1 ♀, USNM). **Virginia**: Chance (1 ♀, USNM), Norfolk (1 ♀, USNM).

FIGURE 17. *Lyroda triloba*: female clypeus and mandibles

FIGURE 18. *Lyroda triloba*: male clypeus and mandible.

FIGURE 19. *Lyroda triloba*: propodeal side of female.

FIGURE 20. Collecting localities of *Lyroda triloba*.

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Mortality of a Baltimore Oriole (*Icterus galbula*) from Entanglement in Fishing Line in Ohio, with a Compilation of Oriole and Other Avian Entanglement Records Involving Fishing Lines

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An adult Baltimore Oriole (*Icterus galbula*) was found entangled in fishing line and hanging from a tree branch along a reservoir in Ohio, and the occurrence was documented with photographs. There have been several other entanglement records involving Baltimore Oriole and Bullock's Oriole (*Icterus bullockii*) in New Jersey, Oklahoma, Oregon, and an unspecified state, and there are numerous records for other bird species. Literature, databases, and the Internet were searched for other reported cases of injury and mortality to birds from recreational fishing line. Several compilations of bird entanglement records have appeared in recent decades; however, these concerned marine environments and most entanglements involved commercial fishing gear, whereas the present paper focuses on recreational fishing gear mostly in freshwater and inland environments. Undoubtedly there remain additional records in published and unpublished sources that were not discovered, but complete citations for all references are provided in order to assist others in compiling a more complete database of entanglement records.

KEYWORDS: monofilament fishing line, mortality, *Icterus galbula*, *Icterus bullockii*, Icteridae

"The causes of bird mortality are of interest to every student of ornithology." (Lincoln, 1931, p. 538)

There are a variety of natural causes of mortality for birds, including diseases, parasites, predators, starvation, severe weather, collisions with trees, and entanglement in natural materials (Lincoln, 1931; Bent, 1958; Jennings, 1961; Macdonald, 1963; Stewart, 1967; Batten, 1978; Sadler, 1993; Hager et al., 2009; Newton and Little, 2009); however, there are also an additional array of anthropogenic causes of bird mortality that includes marine fisheries (gillnets and other fishing gear), collisions with buildings, windows, vehicles, watercraft, wind turbines, TV towers, and power lines, entanglement in plastic debris, ingestion of plastic debris, oiling, hunting, predation by domestic cats, and poisoning (Lincoln, 1931; Bent, 1958; Coulson, 1961; Jennings, 1961; Macdonald, 1963; Glue, 1971; Mead, 1974; Batten, 1978; Norman, 1987; Schreiber and Mock, 1988; Manville, 2005; Newton and Little, 2009; Petersen et al., 2009; Ellis et al., 2013; Loss et al., 2013, 2014, 2015; Žydelis et al., 2013; Cannell et al., 2016; Kahle et al., 2016; Ryan, 1987, 2018).

Many reports of entanglements have concerned marine mammals and birds becoming entangled in active or derelict commercial fishing nets and lines, recreational fishing gear, and other plastic pollution (Laist, 1997; Žydelis et al., 2013; Kuhn et al., 2015; Ryan, 2018). Blettler and

Wantzen (2019) compared entanglements reported for marine and freshwater environments and concluded that much more attention was needed for entanglements of organisms in freshwater habitats. The present paper focuses more specifically on entanglement in recreational fishing line, with more emphasis on inland and freshwater environments. Entanglement can involve a piece of fishing line alone or might include a hook and other tackle attached to the line and can involve active (e.g., Burtch, 1920; Anthony, 1921; Anonymous, 1962) or lost/discarded fishing gear. Monofilament fishing line and associated fishing tackle such as hooks, lures, corks, and lead weights are often discarded or lost by recreational fisherman (Bell et al., 1985; Forbes, 1986; Cryer et al., 1987; O'Hara et al., 1988; Radomski et al., 2006; Carleton et al., 2019; author, pers. obs.), causing injury from penetration of hooks, entanglement in fishing line, a combination of hook penetration and subsequent tethering or entangling, and/or lead ingestion and poisoning (Zimmerman, 1976; Birkhead, 1982; McMullen, 1984; Scheuhammer and Norris, 1996; Franson et al., 2003; Scheuhammer et al., 2003; Sidor et al., 2003; Kelly and Kelly, 2004; Yorio et al., 2014).

On 1 June 2013, the author observed an adult Baltimore Oriole dangling from monofilament fishing line wrapped on a small branch of a slippery elm (*Ulmus rubra*) along the edge of a channel at the southeastern portion of Grand Lake St. Marys, Saint Marys Twp., Auglaize County, Ohio (Figs. 1A, B). The bird was photographed in place, then the branch was removed from the tree using a pole saw. Additional photographs were taken of the bird on the ground (Fig. 1C). The monofilament fishing line, cork, and lead head jig were collected and disposed in the trash. The dead adult oriole was left on the bank of the channel to decompose.

The oriole had fishing line wrapped around its neck, presumably resulting in asphyxiation (Figs. 1A, B, C). The bird might have been trying to gather the fishing line to use as nesting material (see below). The bird was not hooked on the small lead head jig, which was located within one meter of where the bird was hanging (Fig. 1B). This type of small foam cork and lead head jig with soft plastic body is a common rig used for catching crappies (*Pomoxis* spp.) and sunfishes (*Lepomis* spp.) at Grand Lake St. Marys. It's possible that the color of the fluorescent orange foam cork attracted the oriole. The height of the tree branch above the water would have prevented the angler from retrieving the lost lure and fishing line in this case. Baltimore Orioles are annual breeders in the area where the dead oriole was found, often being observed and heard from mid-Spring through mid-Summer (author, pers. obs.).

Many different bird species have been known to use artificial or unusual items (often man-made) as parts of nests or as the entire nest (Dixon, 1902; Verlis et al., 2014). Oriole biology and nests have been studied in detail (Sharp, 1903; Bent, 1958; Schaefer, 1976, 1980; Wedgwood et al., 1989), and Baltimore Orioles are known to use artificial materials to construct nests (Barthelemy, 1969; Wedgwood et al., 1989). Hunn (1926) reported the strangulation and death of a male Baltimore Oriole in a nest due to a "cord" that was woven into the nest. Hunn's record is among the earliest reports of bird entanglement and death, but it lacks specifics as to whether the "cord" was natural or artificial material. There are several other reports of entanglements in fishing line that resulted in either injuries or deaths of Baltimore Orioles and Bullock's Oriole in New Jersey, Oklahoma, Oregon, and an unspecified state (Groves, 1986; Stokes and Stokes, 1986; Mather, 1987; Heaton, 1993). Several examples of bird nests that contained fishing line were seen on websites, including one that was composed entirely of fishing line and associated tackle (Southwestern Bald Eagle Management Committee, undated), and there are other reports of fishing line being used as nest material by other species of birds (Dow, 1978; Inkley, 1984; Milwright, 1998; Smiddy and O'Halloran, 1998; Parker and Blomme, 2007). Use of fishing line and other unspecified string as nest material has resulted in entanglement, and in some cases mortalities, of chicks and adult birds (Slack, 1992; Smiddy and O'Halloran, 1998; Friesen, 2002; Parker and Blomme,

FIGURE 1. A and B) An adult Baltimore Oriole (*Icterus galbula*) entangled in monofilament fishing line and hanging from a branch of a slippery elm (*Ulmus rubra*) along a channel off Grand Lake St. Marys reservoir, Auglaize Co., Ohio, 1 June 2013. C) The same oriole on the ground after being removed from the tree. Photos by W.J. Poly.

2007). Some interactions of birds with fishing line do not result in death but still cause injuries, and some birds can be rehabilitated (Kelly and Kelly, 2004; Montesdeoca et al., 2017). Collisions with a tall TV tower was another substantial source of mortality of Baltimore Orioles and many other species of birds (Norman, 1987).

A wide variety of bird species representing raptors, piscivores, insectivores, and herbivores have become entangled in lost or discarded fishing line, often resulting in severe injury or death of the birds (Houston, 1966; Dunstan, 1969; Nero, 1972; Johnson and Sloan, 1975; Kovacs, 1975; Schreiber, 1975; Morgan and Glue, 1977; Anonymous, 1978; Batten, 1978; Denker, 1978; Mead, 1979; Mead et al., 1979; Knight et al., 1980; Lastavel, 1981; Birkhead, 1982; Inkley, 1984; Bartel, 1984; Kraak, 1986; Schreiber and Mock, 1988; Spearpoint et al., 1988; Parrish and Maurer, 1991;

Cooper et al., 1992; Harrigan, 1992; Clapp, 1993; Sadler, 1993; Taylor, 1996, 1997, 1999, 2004; Smiddy and O'Halloran, 1998; Stone and Okoniewski, 2001; Brown and Brown, 2002; Franson et al., 2003; Kelly and Kelly, 2004; Eaton and Hernandez, 2005; Parker and Blomme, 2007; Müller et al., 2007; Berón and Favero, 2009; Moore et al., 2009; Newton and Little, 2009; Abraham et al., 2010; Yorio et al., 2014; Perry and Wheeler, 2015; Fitzgerald, 2017; Heath et al., 2017; Montesdeoca et al., 2017; Jones et al., 2018; Pon et al., 2018; Blettler and Wantzen, 2019; Carleton et al., 2019; Five Rivers MetroParks, 2019; Zaluski et al., 2019; and compilations of entanglements by Laist, 1997; Kühn et al., 2015; Ryan, 2018).

Other cases of entanglement and mortality of birds have involved the strong, cotton, thread-like string of hip chains, which are used to measure distance (Loegering, 1997; Brown and Miller, 1997; Woolley, 1998). Birds also can become entangled in a variety of natural materials, such as plants and spider webs (Needham, 1909; Woods, 1934; Tucker, 1955; Burnett, 1970; Bramlett and Pitts, 1989; Woodson, 1998; Hager et al., 2009).

This compilation of bird entanglements in recreational fishing line is not considered to be complete. Earlier compilations were focused on entanglements in and ingestion of plastics in marine environments primarily (Laist, 1997; Kühn et al., 2015; Ryan, 2018), whereas this paper focuses on entanglements in recreational fishing line in freshwater and inland environments where there has been less attention (Blettler and Wantzen, 2019). There are likely numerous other cases of birds being hooked or entangled in fishing line that are in published accounts in the journals, bulletins, and newsletters of ornithological societies (e.g., Clapp, 1993 and references therein) and in records of Federal and State natural resource agencies (e.g., U.S. Fish and Wildlife Service Bird Banding Laboratory), animal rescue and rehabilitation centers, bird banding databases (e.g., British Trust for Ornithology [BTO]), beach patrol records, or veterinary clinics or are unreported observations by the public (see Moore et al., 2009; Abraham et al., 2010). Also, there must be many cases where birds have died or become prey items and were not observed by humans. Addition of fishing line receptacles and signs (Fig. 2) at recreational fishing sites decreases the amount of fishing line and tackle in the environment and should reduce the chances of wildlife encountering and becoming entangled in discarded line (Carleton et al., 2019; Southwestern Bald Eagle Management Committee, undated).

FIGURE 2. An example of a sign and receptacle posted near recreational fishing sites to encourage proper disposal of fishing line, thereby reducing both litter and entanglements of wildlife (Courtesy of Five Rivers MetroParks; used with permission).

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Notes on the Vascular Flora of the Island of Príncipe (São Tomé and Príncipe) in the Gulf of Guinea

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Based on recent plant collections from the island of Príncipe: first reports of presumably native occurrences are documented for two species of Acanthaceae (*Brillantaisia owariensis* and *Phaulopsis micrantha*) and for the whisk fern, *Psilotum nudum* (Psilotaceae); *Justicia secunda* (Acanthaceae) is reported as naturalized; new occurrences of two species of Acanthaceae previously known only from single occurrences on the island (*Dicliptera verticillata* and *Stenandriopsis thomensis*) are discussed; and new distributional (*Sciaphila ledermannii*, Triuridaceae), morphological (*Brillantaisia lamium*, Acanthaceae), and photographic (*Habenaria letouzeyana*, Orchidaceae) insights are offered for other species. Updated information is provided for the numbers of native lycophytes, ferns, and flowering plant species and infraspecific taxa for the country and island-only occurrences for each of Príncipe and São Tomé. Numbers of endemic taxa for the country and each island are also provided.

KEYWORDS: Range extensions, significant collections, floristic summaries, endemism, Acanthaceae, Orchidaceae, Psilotaceae, Triuridaceae

The four major islands in Africa's Gulf of Guinea are all volcanic in origin, but vary in age, size, elevation, distance from the continent, floristic composition, and nationality. The islands of Bioko (largest, highest, and closest to the continent) and Annabón (smallest, lowest, and farthest from the continent) both pertain to Equatorial Guinea. The two islands between Bioko and Annabón comprise the nation of São Tomé and Príncipe, the name of which derives from that of each island. This archipelago is somewhat unusual among tropical island systems by possessing both continental (Bioko) and oceanic islands (Annabón, Príncipe, São Tomé). The latter three, which lie beyond the continental shelf, have neither been connected to the African mainland nor any other island, but arose independently from the ocean floor. Naturally occurring organisms on oceanic islands are the result of either dispersal from offshore or *in situ* evolution of earlier arrivals. Recent lists of the vascular flora for each island in the Gulf of Guinea are available: Annabón (Velayos et al. 2013a), Bioko (Velayos et al. 2013b), and São Tomé and Príncipe (Figueiredo et al. 2011).

With an area of ca. 140 km^2, Príncipe (Fig. 1) is the second smallest island in the archipelago, and is also the oldest geologically (ca. 31 mybp). In his work on the plants of the oceanic islands in the Gulf of Guinea, Exell (1944) noted that Príncipe had been less thoroughly explored than the larger (ca. 6 times larger) and more accessible island of São Tomé. The most recent estimates of the numbers of presumably indigenous and endemic flowering plant species for the nation (i.e., both islands; Figueiredo et al. 2011:42) were: "1,104 species (301 introduced) plus 15 additional

FIGURE 1. Views of Príncipe island: southeastern portion looking south toward islet of Bone do Joquei (top) and southwestern portion looking northeastward (bottom). Photos by expedition members M. Nadel (top) and R. Wenk (bottom).

infraspecific taxa…119 taxa (107 species and 12 infraspecific taxa) are known to be endemic to the two islands.” Based on information provided for each taxon in Figueiredo et al. (2011), I counted the numbers of native species + infraspecific taxa that occurred on both islands, only on Príncipe, and only on São Tomé; I also totaled the numbers of species endemic to both islands (i.e., the country), Príncipe only, and São Tomé only. From their listing, I excluded 305 species + infraspecific taxa that were noted as “introduced” (whether naturalized or not) and 36 taxa that were noted to be based on questionable or doubtful occurrences (e.g., literature citations without vouchers) of both introduced and potentially native taxa. Table 1 shows the counts obtained augmented by the changes in occurrence data from taxa noted below. My counts for the country reveal 812 natives (797 species and 15 infraspecific taxa [i.e., subspecies and varieties in excess of one per species]) with 119 (107 species + 12 infraspecific taxa; 15%) of them endemic to it. São Tomé is ca. 6 times larger and has elevations ca. 2.1 times higher than those of Príncipe; it also contains more than twice as many native flowering plant species with more than four times as many (and more than twice the percentage) of them endemic to the island.

Although Príncipe is far less rich in plant species than São Tomé, it contains numerous endemics and species that otherwise are not known to occur on the larger island. The unispecific genus *Principina* Uittien (Cyperaceae) was originally recognized as endemic to Príncipe (Uittien

1935; Exell 1944), the type having been collected from the summit of Pico Papagaio. Following Koyama (1961), Figueiredo et al. (2011) treated the sole species, *P. grandis* Uittien, as *Hypolytrum grande* (Uittien) T. Koyama, and indicated its occurrence on both São Tomé and Príncipe. Mesterházy and Browning (2014) referred the report by Figueiredo et al. (2011) of the species on São Tomé to *H. africanum* Nees ex Steud., a species not otherwise reported from the country (and not included in the counts of Table 1). However, they rationalized generic recognition of *Principina* and reported the discovery of an occurrence of *P. grandis* on São Tomé (Mesterházy and Browning 2014).

TABLE 1. Numbers of presumably native occurrences (species + infraspecific taxa) of flowering plants in São Tomé and Príncipe by country and by island. See text for additional explanation.

	ST & P	ST	P
Total natives	812	727	356
Occurrences	268 [1]	458	86
Endemics (% per region)	17 [2] (2%)	83 (11%)	19 (5%)

[1] common to both islands
[2] common to both islands; total for the country = 119 (15%)

The following range extensions to and notes on poorly known species of Príncipe have been generated via collections and photographs during four expeditions sponsored by the California Academy of Sciences to both islands of São Tomé and Príncipe in the company of local guides and both scientists and students representing numerous disciplines. In terms of bryophytes and vascular plants these expeditions have resulted in more discoveries of range extensions (i.e., new island occurrences) on Príncipe than on São Tomé (e.g., Daniel 2010; Pócs et al. 2015). Because Príncipe is less visited and lacks considerable infrastructure, areas on that small but topographically rugged island (Fig. 1) remain incompletely explored. Below, vascular plant occurrences of Acanthaceae and Psilotaceae new to Príncipe are documented; occurrence data for poorly known taxa of Acanthaceae and Triuridaceae are updated; morphological variation in *Brillantaisia lamium* is documented; and photographs of an attractive terrestrial orchid that is endemic to the island are apparently provided for the first time.

ACANTHACEAE

***Brillantaisia owariensis* P. Beauv.**

Príncipe: N end of island, from cacao plantation along road 1.6 (air) km S of Bom Bom Island (01°40.897′N, 007°24.115′E, 65 m) to mouth of Água Grande at S end of Praia Bom Bom (01°41.390′N, 007°23.932′E, sea level), plantation grounds and moist lowland evergreen forest, 18 IV 2013 (sterile), *T. Daniel & J. Shevock 11992* (CAS).

A small population of ca. 12 plants occurring at ca. 40 m elevation in a weedy portion of a cacao plantation is readily identifiable (even sterile) by its robust stems and large, dentate leaves that bear a prominent wing along the entire length of the petiole (Fig. 2). This species occurs throughout tropical Africa, is often cultivated, and sometimes becomes naturalized (Daniel and Figueiredo 2009). It is newly reported from Príncipe, having previously been documented from at least two apparently disturbed sites on São Tomé. Elsewhere among islands in the Gulf of Guinea, *B. owariensis* also occurs on Bioko (e.g., Aedo et al. 1999; Velayos et al. 2013b). Although it was treated as native to São Tomé and Príncipe (e.g., Daniel and Figueiredo 2009; Figueiredo et al.

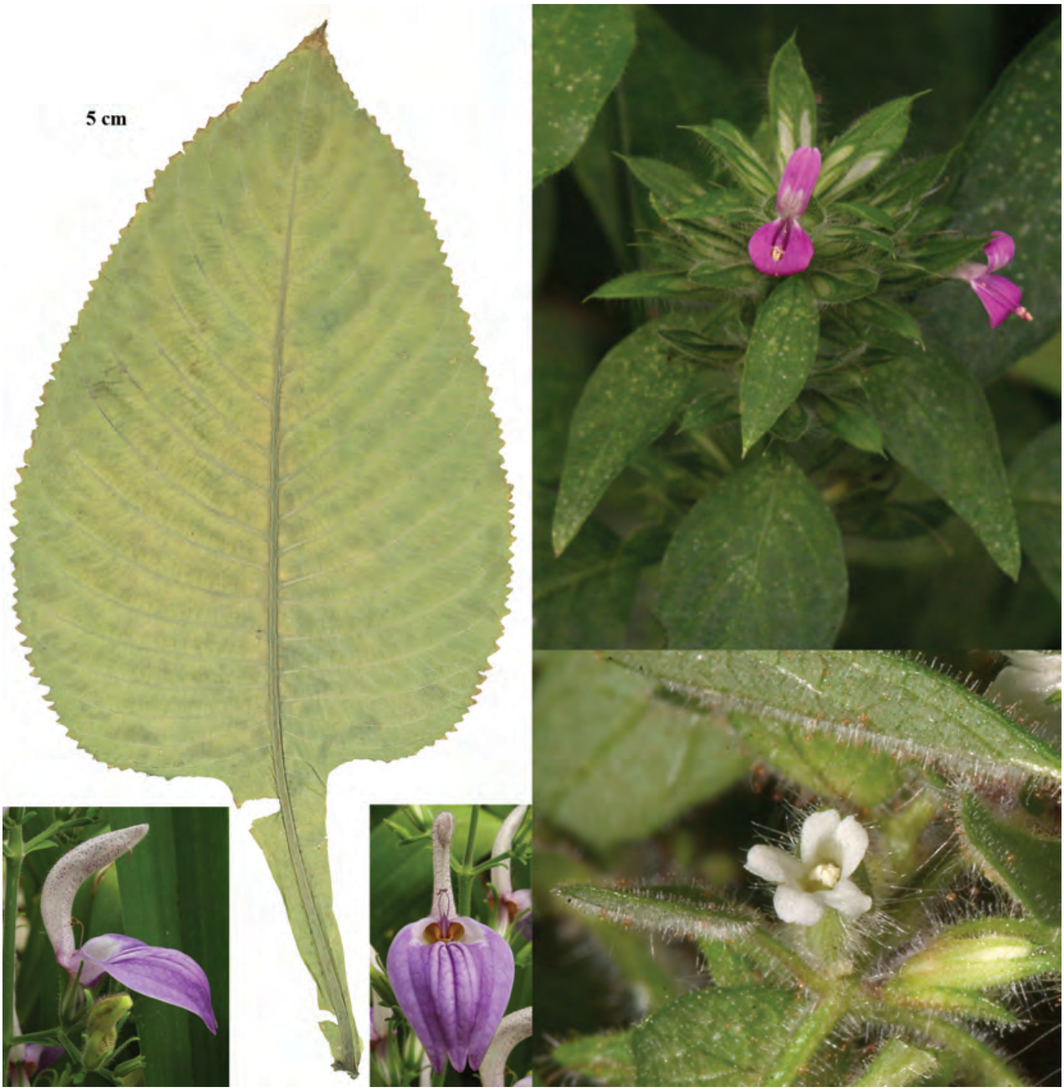

FIGURE 2. Miscellaneous Acanthaceae. *Brillantaisia owariensis* (left; *Daniel s.n.*, from plants cultivated at San Francisco Conservatory of Flowers), leaf and living flowers. *Dicliptera verticillata* (top right), inflorescence with flower (corolla resupinate 180°; cultivated at San Francisco Conservatory of Flowers from seed of *Daniel 11122* collected on São Tomé). *Phaulopsis micrantha* (bottom right), axillary flower (*Daniel 11145*, from São Tomé, field photo by W. Eckerman). Photos by the author except as noted.

2011), it is more likely that the species was intentionally introduced to the islands and has become naturalized there. Plants have been reported to be used as ornamentals, medicinal remedies, and for human consumption in parts of continental Africa (e.g., Okeke et al. 2009; Akuru and Amadi 2018; Kewscience 2020). Therefore, the species is excluded from the counts of native flowering plants in Table 1.

Brillantaisia lamium **(Nees) Benth.**

Príncipe: Road/trail from Terreiro Velho to Infante D. Henrique, vicinity of Roça Ribeira to Órgãos Basálticos/Os Dois Irmãos (01°35.002′N, 007°25.539′E, 115 m) to Rio Chibala (01°34.442′N, 007°25.218′E, 80 m), second growth forest and disturbed areas, 20 IV 2013 (flr, frt), *T. Daniel et al. 12023* (CAS)-purple corollas; same locale, 20 IV 2013 (flr, frt), *T. Daniel et al. 12024* (CAS)-white corollas.

In a taxonomic revision of *Brillantaisia* P. Beauv., Sidwell (1998:74) noted that plants with entirely white corollas were occasionally found among the otherwise usually blue-purple to violet-flowered species, including *B. lamium* and *B. vogeliana*, both of which occur in São Tomé and Príncipe. Daniel and Figueiredo (2009:646 and fig. 3G, H) noted the occurrence of both purplish- and white-flowered plants of *B. vogeliana* on São Tomé, which species only occurs on that island in the country. *Brillantaisia lamium* occurs on both islands, but the occurrence of both color forms for this species was noted only for São Tomé (Daniel and Figueiredo 2009). Both color forms of *B. lamium* are documented above on Príncipe, as well. Additional collections of *B. lamium* with both purple to blue-purple and white corollas have been made elsewhere on the island. Plants with corollas having a somewhat intermediate coloration, mostly white but with a faint lavender tinge, also occur in Príncipe (e.g., *Daniel et al. 11695* at CAS, from ca. 2 km south of Bela Vista along the Rio Papagaio).

Dicliptera verticillata **(Forssk.) C. Chr.**

Príncipe: N end of island, from cacao plantation along road 1.6 (air) km S of Bom Bom Island (01°40.897′N, 007°24.115′E, 65 m) to mouth of Água Grande at S end of Praia Bom Bom (01°41.390′N, 007°23.932′E, sea level), plantation grounds and moist lowland evergreen forest, 18 IV 2013 (sterile), *T. Daniel & J. Shevock 11993* (CAS).

Sterile plants were locally frequent at an elevation of about 40 meters on a disturbed site. The species (Fig. 2) is readily recognizable by its 6-angled stems with a ± dense cluster of elongate (up to 3.5 mm), flexuose, and eglandular trichomes at the vegetative nodes. Although collected numerous times from several sites on São Tomé, this appears to be only the second collection of the species on Príncipe (Daniel and Figueiredo 2009). The species was previously collected on that island at Sundi (i.e., *T. Monod 12073* at COI), ca. 2.5 to 3 km to the southwest of the collection noted above. Elsewhere in the Gulf of Guinea, *D. verticillata* also occurs on both Bioko and Annobón (Velayos et al. 2013a, b).

Daniel and Figueiredo (2009:652 and fig. 2E) illustrated and noted that corollas of most collections of *D. verticillata* collected on São Tomé were rotated 90° so that they appeared to be oriented on their sides. Plants grown from seed of *Daniel 11122* from that island eventually exhibited corollas resupinate both 90° and 180° (Fig. 2). The orientation of corollas of plants on Príncipe remains unknown.

Justicia secunda **Vahl**

Príncipe: 0.8 km N of airport terminal along road to Bom Bom Island, 01°40.302′N, 007°24.739′E, 180 m, disturbed roadside near houses, 1 V 2013 (flr), *T. Daniel & A. Stanbridge 12115* (CAS); along Água Grande, ca. 0.3 km S of entrance to Bom Bom Resort, 01°41.340′N, 007°24.126′E, ca. 5 m, disturbed moist evergreen forest, 24 IV 2013 (flr), *T. Daniel & J. Shevock 12034* (CAS). **São Tomé**: trail from Jardim Botânico de Bom Sucesso (00°16.866′N, 006°38.868′E; 1115 m) to Lagoa Amélia (00°15.972′N, 006°35.589′E; 1480 m), moist to wet montane forest and cultivated fields, 14 IV 2008 (flr), *T. Daniel 11142* (CAS).

This species (Fig. 3), a native of tropical America, was noted by Daniel and Figueiredo (2009) to be cultivated in São Tomé and Príncipe based on plants seen on both islands in 2008. Indeed, the specimen from São Tomé cited above was cultivated as a hedge near the botanical garden, and *Daniel & Stanbridge 12115* from Príncipe was both cultivated in a hedge (seen in 2008), but also appeared to be naturalizing nearby (collected in 2013). *Daniel & Shevock 12034* from another site on Príncipe (2.2 km distant from *Daniel & Stanbridge 12115*) consisted of a stand of ca. 100 naturalized and locally frequent plants that confirmed the species escape from cultivation, at least on that island. Infusions and decoctions (including an herbal tea) made from leaves or entire plants of *J. secunda* have putative medicinal attributes, and are used in both Africa and South America (e.g., Kitadi et al. 2019). Because this species was not treated by Daniel and Figueiredo (2009), a brief description of it (based on the collections cited above) and a revised key to the native and naturalized species of *Justicia* in the country are provided below.

Perennial herb to shrub to 3.5 m tall; leaves petiolate, blades ovate, 75–140 mm long, 22–53 mm wide, 2.6–3.6 × longer than wide, rounded to acute at base, acuminate at apex, surfaces pubescent with eglandular trichomes restricted to major veins. Inflorescence of axillary and/or terminal panicles of subracemose branches bearing alternate and unilateral (axillary branches) or opposite (terminal portion of main axis) 1-flowered and sessile dichasia. Bracts subtending dichasia subulate to lanceolate, 1–5 mm long (fertile bract usually longer than sterile bract when dichasia unilateral). Paired bracteoles subtending flowers subulate to lanceolate, 1.5-3 mm long. Flowers short-pedicellate, pedicels 0.8–1.5 mm long. Calyx 5-lobed, 6–10 mm long, lobes homomorphic, lance-linear to linear, 5–9 mm long, abaxially pubescent with glandular and eglandular trichomes. Corolla dark red, 35–38 mm long, externally pubescent with eglandular and stipitate glandular trichomes, tube 9–20 mm long, lips 16–27 mm long. Stamens inserted near base of corolla tube, 27–30 mm long, thecae of a pair conspicuously unequal in size, parallel to subperpendicular to one another, glabrous, lacking basal appendages. Capsule (based on extralimital specimens from tropical America) 9–11 mm long, externally pubescent with erect eglandular trichomes and sessile to subsessile glandular trichomes; seeds 2.5–3 × 2.7–3 mm, surface smooth, lacking trichomes.

1a. Annuals; leaf blades 1.4–2.6 × longer than wide; calyx 2.3–3 mm long, lobes heteromorphic (posterior lobe ½ or less as long as others); corolla 2.6–3 mm long . . . . *J. tenella* (Nees) T. Anders.
1b. Perennials; leaf blades 2.6–4.2 × longer than wide; calyx 3–10 mm long, lobes homomorphic or nearly so; corolla 7.5–38 mm long 2
2a. Young stems and leaves glabrous; calyx 3–5.5 mm long; corolla 7.5–9 mm long; stamens 5 mm long, distal theca dorsally pubescent, proximal theca with a basal appendage 0.8 mm long . . . . *J. thomensis* Lindau
2b. Young stems and leaves (on major veins) pubescent; calyx 6–10 mm long; corolla 35–38 mm long; stamens 27–30 mm long, both thecae of a pair glabrous and lacking basal appendages . . . . *J. secunda* Vahl

***Phaulopsis micrantha* (Benth.) C.B. Clarke**

Príncipe: N end of island, from cacao plantation along road 1.6 (air) km S of Bom Bom Island (01°40.897′N, 007°24.115′E, 65 m) to mouth of Água Grande at S end of Praia Bom Bom (01°41.390′N, 007°23.932′E, sea level), plantation grounds and moist lowland evergreen forest, 18 IV 2013 (flr), *T. Daniel & J. Shevock 11988* (CAS).

Although known from several collections on São Tomé (Fig. 2; Daniel and Figueiredo 2009), the one cited above is the first report of the species on Príncipe where it is presumed to be native.

FIGURE 3 Miscellaneous vascular plants. *Psilotum nudum* (top), fertile plants on base of coconut palm (*Daniel & Shevock 12035*). *Sciaphila ledermannii* (bottom left), fertile plant (*Daniel et al. 12085*, photo by M. Nadel). *Sciaphila ledermannii* (bottom center), fertile plant (*Daniel et al. 12084*, photo by M. Nadel). *Justicia secunda* (bottom right), inflorescence with flowers (photo and copyright: C. Feuillet, CC BY-NC, used with permission), taken in French Guiana.

It was collected at the same disturbed site as several other Acanthaceae that can become weedy: *Brillantaisia lamium* (*Daniel & Shevock 11990*), *B. owariensis* (*Daniel & Shevock 11992*), *Dicliptera verticillata* (*Daniel & Shevock 11993*), *Elytraria marginata* Vahl (*Daniel & Shevock 11989*), and *Nelsonia canescens* (Lam.) Spreng. (*Daniel & Shevock 11991*). Elsewhere among the islands of the Gulf of Guinea, *P. micrantha* also occurs on Annobón (Manktelow 1996; Velayos et al. 2013a). Two other species of the genus, *P. angolana* S. Moore and *P. ciliata* (Willd.) Hepper have been recorded on Bioko (Manktelow 1996).

Stenandriopsis thomensis (Milne-Redh.) Heine

Príncipe: Obo Natl. Park-Príncipe, trail from ruins of Francisco Mantero (Maria Correia) to Pico Mesa, from 1.5 km (air) SE of ruins (01°35.317′N, 007°21.483′E, 350 m, lowland to montane rain forest) to summit of Pico Mesa (01°34.930′N, 007°21.201′E, 500 m, dwarf cloud forest), 19 IV 2013 (old inflorescences), *T. Daniel et al. 11995* (CAS).

Several sterile plants and others bearing inflorescences lacking corollas were locally frequent under the forest canopy about two-thirds of the way up the prominent mesa in southwestern Príncipe. Although *Stenandriopsis thomensis* has been collected numerous times from several sites on São Tomé, this collection appears to represent only the second collection of the species on Príncipe (Daniel and Figueiredo 2009). It was previously collected on that island at Pico Papagaio (01°36′45″N, 007°23′30″E; i.e., *F. de Oliveira 547* at BRLU and STPH), some 5 km to the northeast. The species also occurs in Cameroon and Nigeria on mainland Africa (Vollesen 1992; Daniel and Figueiredo 2009), but it has not been reported from either Bioko or Annobón in the Gulf of Guinea. Although two other species of the genus occur on Bioko, this is the only species of *Stenandriopsis* in São Tomé and Príncipe.

ORCHIDACEAE

Habenaria letouzeyana (Szlach. & Olsz.) P.J. Cribb & Stévart

This relatively large (to about 7 dm tall) terrestrial orchid is endemic to Príncipe. When it was described by Szlachetko and Olszewski (1998) as *Podandriella letouzeyana*, it was known from a single collection (*Rose 412* at P, the holotype), and the habitat of the species was unknown. When they transferred the species to *Habenaria* Willd., Stévart and Cribb (2004) cited several collections, which included habitat information. A population of ca. 50 plants of the species was observed on three occasions over several years (2008, 2010, 2013) near the northern base of Pico Papagaio on relatively flat to slightly sloping and somewhat disturbed ground in tropical evergreen moist to wet forest at an elevation of ca. 300 meters. The species was in flower during March and April. Owing to its rarity and listing by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2019), no collections were made. Black-and-white drawings of various parts of the plant accompanied the protologue, and a colored illustration of the species (as *Habenaria procera* (Sw.) Lindl. var. *procera*) appeared in Stévart and Oliveira (2000:52, figs. 19, 20). However, apparently no photographs of living plants of *H. letouzeyana* have been published or made available online. Several views of this beautiful orchid are herewith provided (Fig. 4).

PSILOTACEAE

Psilotum nudum (L.) P. Beauv.

Príncipe: between Água Grande and Praia Bom Bom, ca. 10 m above and behind (SE of) high

FIGURE 4. *Habenaria letouzeyana*. Habit (top left). Portion of inflorescence with flowers (top right). Flower, front-view (bottom left). Flower, lateral view (bottom right, photo by W. Eckerman). Photos by the author in 2013 except as noted. All photos from northern base of Pico Papagaio except photo at bottom left from trail below Morro de Leste.

tide line, 01°41′24.3″N, 007°23′59.4″E, ca. 3 m, strand vegetation with *Cocos nucifera*, 24 IV 2013 (fertile), *T. Daniel & J. Shevock 12035* (CAS).

More than 100 plants of this distinctive pteridophyte were frequent on and around the bases of numerous coconut palms in the beach sands at the northern end of Príncipe (Fig. 3). The family and species are newly reported as naturally occurring plants on that island. *Psilotum nudum* was noted previously to occur in one locality (Praia Melão) on São Tomé (Figueiredo 2002; Klopper and Figueiredo 2013). Elsewhere among the islands in the Gulf of Guinea, *P. nudum* occurs on Bioko and Annobón (e.g., Velayos et al. 2008, 2013a).

In their updated checklist of ferns and lycophytes in the country, Klopper and Figueiredo (2013) cite 157 species (no species is represented by more than a single infraspecific taxon), with 145 on São Tomé and 77 on Príncipe. Three species of ferns were treated as naturalized, two occurring on both islands and one only on São Tomé. Among the 15 species of lycophytes in the country, 12 occur on São Tomé and eight occur on Príncipe; five species occur on both islands, seven are known only from São Tomé, and three are known only on Príncipe; one species is endemic to both islands, and one species is endemic to São Tomé. With the addition of *Psilotum nudum* on Príncipe, Table 2 provides a summary of the numbers of native and endemic species of ferns and lycophytes for the country and for each of its islands.

TABLE 2. Numbers of native species of ferns and lycophytes in São Tomé and Príncipe by country and by island. See text for additional explanation.

	ST & P	**ST**	**P**
Total natives	154	142	76
Occurrences	62 [1]	78	14
Endemics (% per region)	2 [2] (1%)	7 (5%)	3 (4%)

[1] common to both islands
[2] common to both islands; total for the country = 12 (8%)

TRIURIDACEAE

***Sciaphila ledermannii* Engl.**

Príncipe: Ribeira Banzu to summit ridge of Pico Príncipe, 01°35′25.7″N, 007°23′01″E, 524 m, moist to wet evergreen forest, 28 IV 2013 (flr, frt), *T. Daniel et al. 12084* (CAS); trail between ruins of S. Carlos do Fundão and Ribeira Banzu, 01°35′52.8″N, 007°23′18.1″E, 199 m, moist to wet evergreen forest, 28 IV 2013 (flr, frt), *T. Daniel et al. 12085*; along trail from near (SW of) Terreiro Velho to Morro de Leste, 01°35.843′N, 007°24.650′E, 400–500 m, moist lowland evergreen forest, 17 XI 2016 (flr, frt), *T. Daniel et al. 12241* (CAS).

This species (Fig. 3) was reported by Daniel (2010) as the first occurrence of Triuridaceae among the islands in the Gulf of Guinea and the first holosaprophyte (mycoheterotroph) in São Tomé and Príncipe. Subsequently, Figueiredo et al. (2011: 49) noted the occurrence on Príncipe of an unidentified species of *Gymnosiphon* Blume (Burmaniaceae), as a “colorless saprophyte.” The three collections for the bright red *Sciaphila* noted above add two additional watersheds (i.e., that drained by the Ribeira Banzu to the west and the Água da Ponte Grande to the east) to the two noted by Daniel (2010; i.e., regions drained by the Rio Papagaio to the northeast and the Ribeira São Tomé to the southwest, respectively) on Príncipe. More than 15 individuals were seen on a slope under a tree at the site of *Daniel et al. 12084*; more than 30 individuals were seen in open ground along a trail at the site of *Daniel et al. 12085*; and plants were infrequent in leaf litter in a flat, forested region at the site of *Daniel et al. 12241*. It is perhaps noteworthy that all of the collections noted above occur at higher elevations (up to 524 m) than those previously reported for collections on the island (i.e., up to 150 m; Daniel 2010). *Sciaphila ledermannii*, which otherwise only occurs in Cameroon and Nigeria on the African mainland (Cheek and Ndam 1996), is likely more common on Príncipe than the low number of collections suggests. The species remains unknown on all of the other islands in the Gulf of Guinea.

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Massif Speciation Events in New Caledonian Lizards: Diversification in the Genus *Marmorosphax* (Scincidae) Tracks Isolation on the Island's Ultramafic Surfaces

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An extensive molecular phylogeny of the endemic New Caledonian scincid lizard *Marmorosphax* based on the mitochondrial ND2 gene retrieves four major lineages. The basal divergences within the phylogeny progressively split off lineages concordant with the boundaries of the island's major ultramafic regions, and are believed to be the product of vicariant events. Three of these lineages are restricted to ultramafic surfaces and are allopatric in distribution: one, comprising a single species, *M. montana*, occurs in high elevation habitat in the ranges of the southern ultramafic region; another, comprising the taxa *M. kaala*, *M. boulinda*, and *M. taom*, occupies ultramafic massifs in the central-west and northwest region; and the third, represented by the undescribed species *M.* cf. *tricolor*, is present in the central-east region ultramafic ranges. The fourth major lineage is represented by the widespread species *M. tricolor* which, by default of earlier vicariant events, evolved within the northeastern/central-east metamorphic region, and its presence now on ultramafic surfaces is attributed to subsequent range expansion. Past periods of aridity and accompanying widespread loss of forest habitat at low to mid elevation are the likely historical processes initiating regional isolation of *Marmorosphax* populations on ultramafic surfaces, with the persistence of higher elevation forest and/or moister habitat providing refugia within which isolated populations in the ultramafic regions further diversified. While some of the newly sampled populations in this study potentially represent genetically distinct undescribed taxa, the samples to allow the complementary morphological comparisons required are insufficient. The *Marmorosphax* species restricted to particular ultramafic massifs are threatened primarily by activities of an expanding nickel mining industry, as are numerous other restricted range lizard species on these surfaces, and the described taxa have been assessed under International Union for the Conservation of Nature (IUCN) criteria as Endangered (*M. boulinda*, *M. montana*, and *M. taom*) to Critically Endangered (*M. kaala*).

KEYWORDS: New Caledonia, Scincidae, *Marmorosphax*, phylogeography, ultramafic.

INTRODUCTION

The scincid lizard fauna of New Caledonia is exceptionally rich and diverse with 63 recognized named species in 18 genera that are strictly endemic (or nearly so) to the territory. Molecular studies based on mitochondrial and nuclear DNA sequence data (Smith et al. 2007; Chapple et al. 2009) have identified the endemic skink genera of New Caledonia as part of a monophyletic 'Tasmantis' group that also includes the endemic New Zealand and Lord Howe Island taxa.

One of the most significant attributes of the New Caledonian lizard fauna to emerge in recent years is the presence of extensive narrow-range endemism throughout the main island, or Grande Terre. The exceptional diversity now documented likely reflects the historical interplay of geology, climate, and vegetation that has yielded numerous cladogenic events which have subdivided ancestral populations and promoted speciation within lineages. Underlying this exceptional diversity is the extent to which historical processes on the islands ultramafic surfaces have played in driving speciation in the endemic lizard fauna. The ultramafic surfaces in New Caledonia cover about 5,500 km^2 or about one third of its total land area (Jaffré et al. 1987), and are a dominant part of the landscape. They are derived from an overthrusting of oceanic lithosphere over continental lithosphere during the late Eocene to form the New Caledonian Peridotite Nappe. The timing at which emergent land was present in the region and the dating of the New Caledonian fauna and flora has been the focus of much debate (see Nattier et al. and Giribet and Baker 2019). The most recent assessment determined that emergent land has existed in the area occupied by the Grande Terre since 25Ma (Maurizot and Campbell 2020). Postobduction tectonic events and erosion have disrupted the Peridotite Nappe into units (massifs) of different sizes (Maurizot et al. 2020) seen today. Ongoing studies in the past two decades have identified both broad-scale and highly localized endemism on the islands ultramafic massifs, in particular those in the central-west/northwest regions (Bauer et al. 2006; Sadlier et al. 2004, 2009, 2014; Sadlier, Bauer et al. 2014a, 2014c), and on the ranges of the Chaîne Centrale in the southern region (Bauer et al. 2006, 2008; Sadlier et al. 2006, 2013, 2014 2018; Sadlier, Bauer et al. 2014b, 2014c). The presence of a number of endemic species on ultramafic surfaces in both areas has identified each region as a distinctive phylogeographic zone for lizards (Sadlier 2010) (see Fig. 1). For skinks the southern ultramafic ranges have an extensive suite of taxa restricted to the region which includes four endemic genera with nine constituent species and seven endemic species from within more widespread genera (in total ~40% of the scincid lizard fauna of southern New Caledonia). A similarly extensive suite of ten skink species is restricted to the central-west/northwest region ultramafic ranges, but no skink genera are endemic to the ultramafic surfaces of this region. By comparison, the extent of narrow-range endemism within the skink fauna on the island's metamorphic surfaces is modest, with only a few species restricted to small areas, one on the summit area of Mt. Aoupinié in the central-east region (*Nannoscincus greeri*) and one in the ranges of the Roche des Ouiaème in the northeast (*Nannoscincus exos*). Rather, the tendency is towards broader scale regional endemism as typified by the various species of *Caledoniscincus* (Sadlier et al. 1999) and most *Nannoscincus* (Sadlier et al. 2002). Similarly, high levels of microendemism characterize other elements of the island's fauna (Caesar et al. 2017), but none of these studies have sampled the ultramafic surfaces as extensively or documented the extent of microendemism seen in the New Caledonian lizard fauna on these surfaces.

While it is clear the endemic New Caledonian skink radiation is highly diverse with well-defined genera (Sadlier 2010; Sadlier et al. 2015), there are no clear and well supported relationships basally between groups of genera, other than for the diminutive *Nannoscincus* as the sister to a larger group containing most other New Caledonian taxa (see molecular phylogenies of Smith et

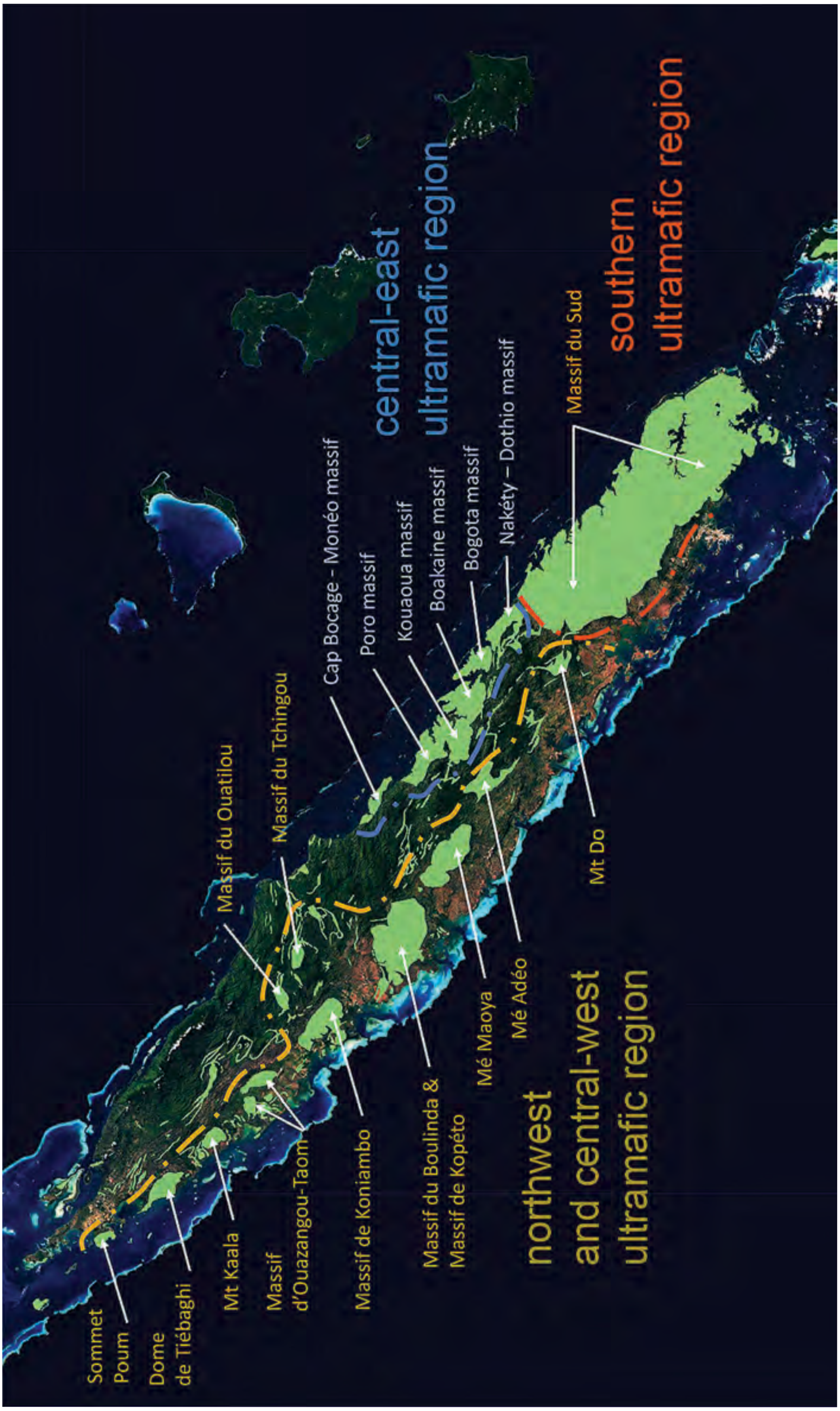

FIGURE 1. Distribution of ultramafic surfaces in New Caledonia: yellow = northwest and central-west ultramafic region; blue = centra-east ultramafic region; orange = southern ultramafic region.

al. 2007 and Chappell et al. 2009). As such, no broad phylogeographic trends are apparent in the distribution of the supra-generic groups identified by molecular data, and the clearest (and sometimes repeated) phylogeographic patterns come from the distribution of taxa within genera.

The genus *Marmorosphax* is one of the more speciose New Caledonian skink genera, with five described species and one or more undescribed putatively distinctive taxa. An earlier genetic study using DNA sequence data (Sadlier et al. 2009) identified three distinct evolutionary lineages within the genus, the southern ultramafic region species *M. montana*, a group of several narrow range species from the central-west/northwest ultramafic ranges comprising *M. kaala*, *M. taom*, and *M. boulinda*, and lastly, the widespread *M. tricolor*. Subsequent field studies have yielded additional genetically distinct massif-specific populations of *Marmorosphax* in the northwest ultramafic ranges, and a lineage restricted to the ultramafic surfaces of the central-east related to, but genetically distinct from, *M. tricolor*. These field studies have also greatly extended the range of genetic samples available for *M. tricolor*.

The species of *Marmorosphax* have a relatively specialized biology. Individuals of *M. tricolor* are active within the confines of their sheltering sites by day, but are secretive and rarely seen in the open, usually only appearing to venture beyond their sheltering sites in the late afternoon and evening, a behavioral trait that likely extends to other members of the genus. *Marmorosphax tricolor* has been recorded mainly from humid forest habitat on both metamorphic and ultramafic surfaces (Bauer and Sadlier 2000), but also extends into maquis habitats where the species niche requirements (a humid and cool microclimate) are met by the presence of a surface rock matrix that provides sheltering sites with the required niche attributes. On metamorphic surfaces the concordance between the distribution of *M. tricolor* to that of primary forest habitats is particularly strong, and it has not been recorded from other habitat types on this surface. Although less well known, the remaining species, all of which occur only on ultramafic surfaces, appear to have similar biological traits to *M. tricolor* and have been recorded mainly from mid to high elevation forest habitat but also occur in dense maquis habitat with a suitable surface rock matrix (*M. taom*, *M. montana* and *M.* cf. *tricolor*). Overall, the habits and habitat preferences of *Marmorosphax* spp. indicate they are 'moisture' dependent, that is they require a humid and cool environment, and their distribution across the landscape is tempered primarily by these factors.

Diversification within the genus is most pronounced on the massifs across the central-west/northwest ultramafic region. These massifs are mostly situated along or near the west coast in the rain-shadow of the eastern and interior ranges which form the extensive and continuous Chaîne Centrale, and typically experience much lower and marked seasonality in rainfall than eastern ranges. However, they are also subject to the 'Massenerhebung' effect which lowers the average altitude of formation of cloud masses, increasing atmospheric humidity until saturation and giving rise to significant "occult" or hidden precipitation at elevations between 600 and 1,500 m. (Fig. 2). This increased moisture in the form of fog and water droplets (Nasi et al. 2002) in turn supports peak and ridge-top forest formations. A number of lizard species are restricted to individual peaks and massifs of these central-west/northwest ultramafic ranges. Among the diplodactylid geckos five species of *Dierogekko* are each known only from a single massif (Bauer et al. 2006), as are several species of *Bavayia* in the *B. montana* complex and genus *Oedodera* (Bauer et al. unpublished research). A number of skinks are also known only from a single massif, most from forest habitat at or near the summit (*Nannoscincus koniambo* - Massif de Koniambo, *Nannoscincus manautei* - Massif de Kopéto, *Phaeoscincus taomensis* - Mt. Taom). Forest habitat on these massifs is now typically present as a mosaic of patches (Fig. 3a), usually on the summit area or in gullies on the slopes, with extensive areas of low open to dense maquis between. A feature of the summit areas is the presence of an exposed cuirasse rock cap that variably occurs on the tops of the

FIGURE 2. Persistent high elevation cloud formation on northwest Massif Katépahié (adjacent to the Massif de Koniambo) during the dry season.

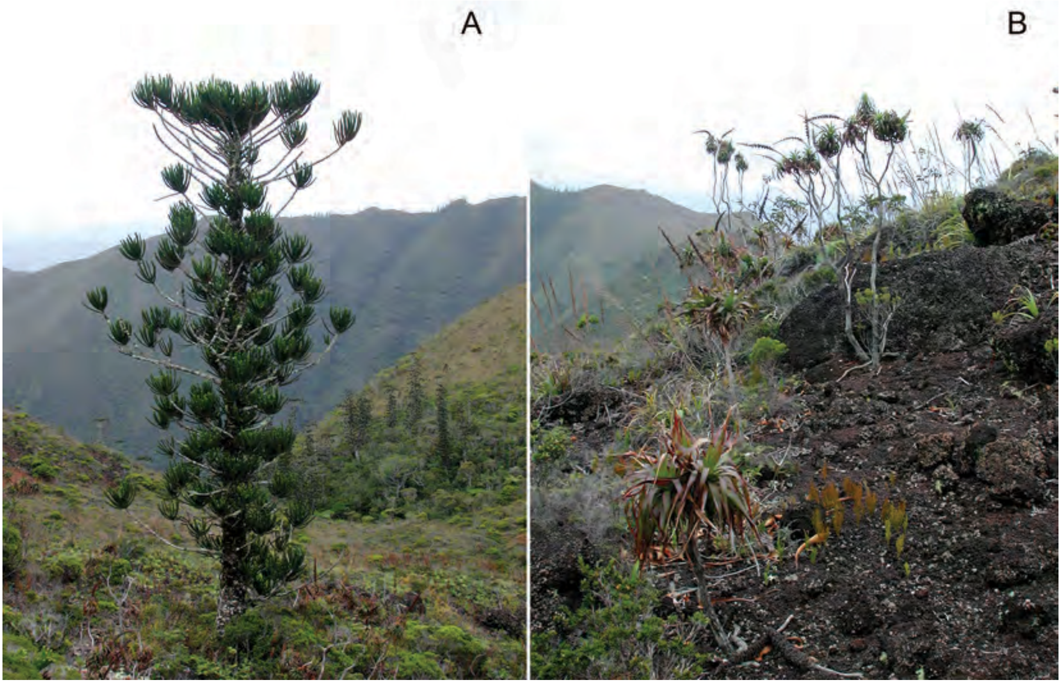

FIGURE 3. High elevation forest habitat on the Massif d'Ouazangou-Taom (A) and exposed cuirasse rock cap variably distributed across the summit area and ridges of massifs in the central-west and northwest ultramafic region (B).

massifs and associated ridges (Fig. 3b). This rock matrix provides important microhabitat for skinks in the form of both shelter and a cool and humid sub-surface environment in areas of both forest and dense maquis habitats. The southern ultramafic ranges also have a number of species restricted to higher elevation habitat, primarily forest. Of these several are localized in distribution (several narrow-range taxa in the genus *Sigaloseps* Sadlier, Bauer et al. 2014b, and *Phaeoscincus ouinensis* Sadlier, Bauer et al. 2014c), and *M. montana* shows substantial genetic sub-structuring of populations across peaks in the region.

The extent of micro-endemism seen on the islands ultramafic surfaces has most likely been driven by contraction and fragmentation of forest habitat in response to historically adverse climatic conditions, whereby preferred habitat is reduced to the upper altitudinal areas of massifs and ranges. Under such conditions populations of species that fail to adapt become isolated on the summit areas, a scenario consistent with the concept of niche conservatism as outlined by Wiens (2004). In this context, many of the narrow-range endemics on ultramafic surfaces represent the evolutionary end products of extreme cases of historical forest fragmentation and contraction, and their continued existence on these massifs and peaks not only identifies these areas as historical refugia, but also as potential refugia for taxa now more widely distributed under future climate warming.

The ultramafic surfaces of New Caledonia are rich in iron and magnesium and several heavy metals, most notably nickel, and as such, many are, or will be, under considerable pressure from mining activities (Pascal et al. 2008). Of all the landscapes in New Caledonia the ultramafic surfaces are of the highest conservation significance for lizards given their exceptionally high levels of regional and localized endemism. Almost half of the described endemic skinks (n = 28, ~45%) and geckos (n = 17, ~45%) are restricted to ultramafic surfaces, and the number of geckos restricted to central-west/northwest ultramafic ranges is expected to nearly double from 6 to 11 with the formal description of known new species. Further, the summit areas of a number of ultramafic peaks have either not, or only poorly, been investigated for lizards. As such, the current state of knowledge of species restricted to higher elevation habitats on ultramafic surfaces is likely to represent a substantial underestimation, as evidenced by the recent description of the two species of *Phaeoscincus*, each known from a single specimen, one (*P. toamensis*) from the summit of the massif of Mt. Taom in the northwest ultramafic region, and one (*P. ouinensis*) from the summit area of Mt. Ouin in the southern ultramafic region (Sadlier et al. 2014c).

Over half of the 25 (~55%) described lizard species restricted to ultramafic surfaces have been identified as Endangered or Critically Endangered on IUCN criteria, including three of five described species of *Marmorosphax*, with mining identified as the primary threat for 19 of these. The presence of such extensive narrow range endemism in areas actively or potentially under threat from intensive development clearly identifies the ultramafic ranges of New Caledonia as true 'hotspots' for conservation in the strictest sense of the term (Mittermeier et al. 1999). This situation is further exacerbated by many of these narrow range species being restricted to the summit areas of massifs, the area where remnant tracts of forest and/or exposed cuirasse rock cap habitat occurs, and where mining activity is often likely to be most intensive and destructive. Ironically, having survived millennia in an environment shaped by its geological heritage, the high elevation forests on New Caledonia's ultramafic surfaces and many of the lizard (and other) species peculiar to them, may be at the brink of extinction in the face of escalating development of the mineral resources they sit on (Fig. 4a and 4b).

The information presented here represents the result of extensive field work over a period of 20 years on the Grande Terre, and builds on the results of previous genetic work on *Marmorsphax* (Sadlier et al. 2009). Our primary purpose is to present the extent of diversity in the genus uncovered in this study which identifies further narrow range lineage endemism in the central-west/northwest ultramafic ranges and southern ultramafic ranges, reinforcing the identity of these regions each as phylogeographic zones for fauna, and providing some insight into the processes likely driving speciation on ultramafic surfaces across the whole of New Caledonia. We have refrained from attempting to formally describe some of the novel lineages identified in this study until samples to adequately assess the extent of morphological and/or genetic variation between these lineages are available. In this context further field research is required to fully appreciate and document the extent of diversity on the islands' ultramafic surfaces.

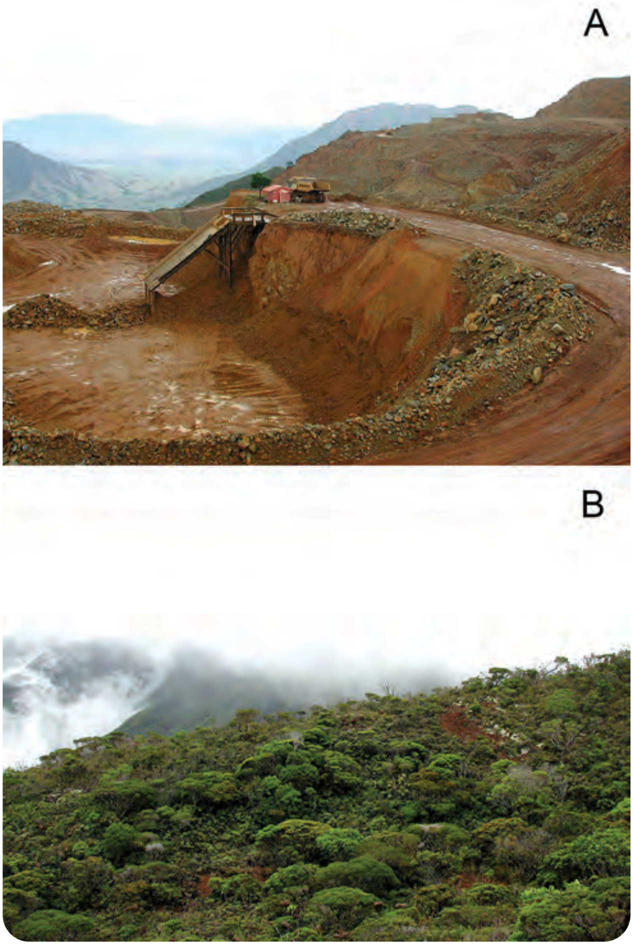

FIGURE 4. Mining on the Massif d'Ouazangou-Taom around 800 m. (A), only 200 m. in elevation below the summit area (B) which is home to the type population of *M. taom*, and only known location for the skinks *Phaeoscincus taomensis* and *Nannoscincus* cf. *manautei*, and the undescribed gecko *Bavayia* cf. *montana*.

MATERIAL AND METHODS

Acronyms: AMS - Australian Museum, Sydney; CAS - California Academy of Sciences; and MNHN - Muséum National d'Histoire Naturelle, Paris.

Genetic studies: The species phylogeny for *Marmorosphax* represents 162 individuals from 46 collecting sites distributed across the majority of large, extant humid forest blocks in New Caledonia.

We obtained sequence data from a 514 bp fragment of the mitochondrial NADH dehydrogenase subunit 2 gene (ND2) for all described species of *Marmorosphax* (Appendix 1). Outgroups were selected on the basis of a broader phylogenetic analysis of New Caledonian skinks by Smith et al. (2007) and sequences for these were obtained from GenBank (Appendix 1).

Total Genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). The target gene ND2 was amplified using a double-stranded Polymerase Chain Reaction (PCR). Included in the reaction were 2.5 μl genomic DNA, 2.5 μl (concentration 10μM) light strand primer (METF6 L4437a 5'-AAGCTTTCGGGCCCATACC-3', Macey et al. 1997), 2.5 μl (concentration 10μM) heavy strand primer (TRPR3 H5540 5'-TTTAGGGCTTTGAAGGC-3', Macey et al. 1997), 2.5 μl dinucleotide pairs (1.5 μM), 2.5 μl 5x buffer (1.5 μM), MgCl 10x buffer (1.5 μM), 0.18 μl Taq polymerase (5u/μl), and 9.82 μl H_2O. All reactions were executed on an Eppendorf Mastercycler gradient thermocycler under the following conditions: initial denaturation at 95ºC for 2 min, followed by a second denaturation at 95ºC for 35 s, annealing at 50–54ºC for 35 s, followed by a cycle extension at 72ºC for 35 s, for 31 cycles. PCR products were visualized on 1.0% agarose gel electrophoresis.

PCR products were purified using AMPure magnetic bead solution (Agentcourt Bioscience, Beverly, MA, USA) to remove any impurities in the PCR products. Purified PCR products were then sequenced using DYEnamic^{TM} ET Dye Terminator kit (GE Healthcare, Piscataway, NJ, USA). Products were purified using a Cleanseq magnetic bead solution (Agentcourt Bioscience, Beverly, MA, USA). Purified sequence reactions were analyzed using an ABI 3730XL automated sequencer. Sequences were analyzed from both the 3’ and the 5’ ends independently. Both the contiguous and the complimentary strands were uploaded and edited in Genious^{TM} version 5.4 (Drummond et al. 2011), ambiguous bases were corrected. After editing the sequences, they were initially aligned manually. Mesquite v3.61 (Maddison and Maddison 2015) was used to check for premature stop codons and to ensure that the alignment was in the correct amino acid reading frame.

We conducted both Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. We partitioned the data by codon partitions (three partitions in total) and estimated the best-fit models of molecular evolution for each partition in IQ-TREE (Nguyen et al. 2015) for the ML analysis using the Bayesian Information Criterion (BIC; Schwarz, 1978) implemented in ModelFinder (Kalyaanamoorthy et al. 2017). The ML analysis was performed using IQ-TREE v1.6.7 (Nguyen et al. 2015) with 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation (UFBoot) algorithm (Minh et al. 2013; Hoang et al. 2017). For the BI we used BEAST v2.6 (Bouckaert et al. 2014) and bModelTest (Bouckaert and Drummond 2017) to numerically integrate over uncertainty in models of substitution, while generating the phylogeny using a Markov chain Monte Carlo (MCMC). The MCMC chain was ran for 50 million generations while sampling every 5000 generation from the chain. To visualize if the effective sample sizes (ESS) were greater than 200 we used Tracer v1.7 (Rambaut et al. 2018) and if samples were, we assumed stationarity. Following conformation that all ESS values reached stationarity we constructed a maximum clade credibility (MCC) tree using TreeAnnotator v2.6 (Bouckaert et al. 2014) with a 25% burnin and using mean node heights. We considered nodes strongly supported if ML UFboot were ≥ 95 and BPP were ≥ 0.95 (Huelsenbeck et al. 2001; Erixon et al. 2003; Huelsenbeck and Rannala 2004; Wilcox et al. 2002; Nguyen et al. 2015). Average pairwise sequence divergences (*p*-distances) for the major clades of *Marmorosphax* were calculated for between group distances and within groups using MEGA v7 (Kumar and Tamura, 2016) under the following conditions: substitutions included; transitions and transversions; uniform rates among sites and gaps were treated as missing data.

RESULTS

Phylogenetic relationships: The final sequence alignment of ND2 comprised 514 bp with 275 parsimony-informative sites based on ingroup and outgroup samples. The ML analysis selected K2P+G4, TN+F+G4, and TIM2+F+G4 for the models of molecular evolution for the 1st, 2nd, and 3rd codon positions respectively. Models selected from the bModelTest were 121134 (cumulative support = 19.5%), 123143 (cumulative support = 27.8%), and 121341 (cumulative support = 59.0%), for the 1st, 2nd, and 3rd codon positions respectively. The ML and the BI analyses produced highly concordant trees with only a few branches not recovered by both analyses.

The monophyly of *Marmorosphax* has been strongly supported in previous molecular studies (Smith et al. 2007; Sadlier et al. 2009). The mitochondrial ND2 gene dataset presented here

(Fig. 5) includes extended sampling from across a broader range of locations is consistent with that result. It also gives a pattern of early divergence within the genus resulting in four well-supported groups (UFboot ≥ 99 and BPP = 1.0), with a substantial (9.8–10.8%) level of genetic divergence between these major Groups (Table 1).

The phylogenetic hypothesis generated in this study differ from the earlier study by Sadlier et al. (2009), which recovered *M. montana* (Group 2, this study) as the first branching lineage of *Marmorosphax*, whereas the present study places the strongly supported (UFboot = 100 and BPP = 1.0) clade comprising *M. kaala*, *M. taom*, and *M. boulinda* as the first branching lineage (Group

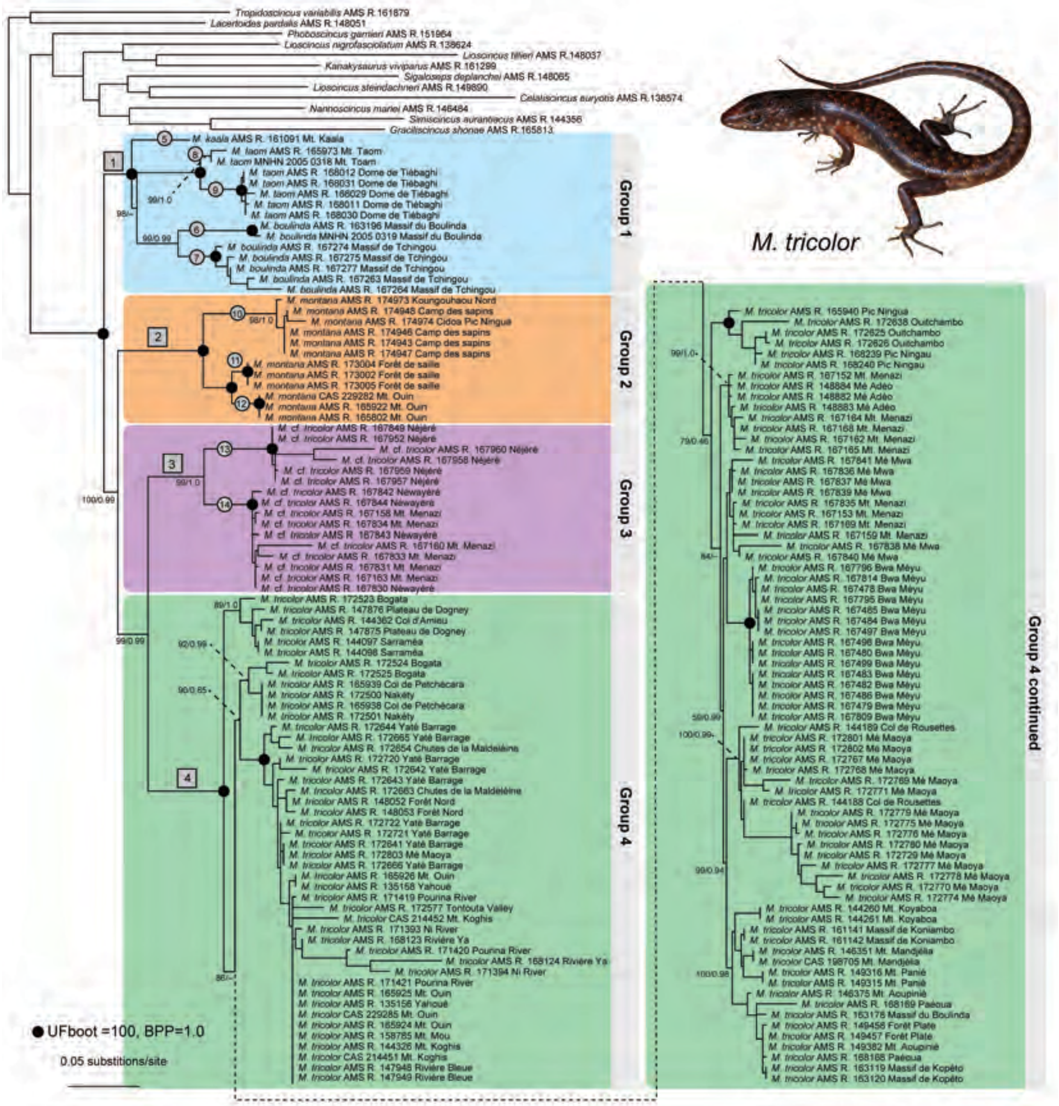

FIGURE 5. Phylogenetic relationships amongst the species and populations of *Marmorosphax*. Likelihood topology with UFboot and BPP Bayesian posterior probabilities shown respectively. UFboot equal to 100 and BPP equal to 1.0 are represented at nodes with black circles. The numbers in squares represent the four major groups of *Marmorosphax* and numbers present in circles represent groups for pairwise comparisons. – indicate nodes not recovered by both phylogenetic analyses.

TABLE 1: Pairwise matrix of mean genetic distances between major groups (Groups 1–4, Fig. 5) within *Marmorosphax* (uncorrected p-distances) for the mtDNA ND2 gene. Values in bold represent within population mean uncorrected p-distances.

	1	**2**	**3**	**4**
1 – central-west/northwest ultramafic region endemics	**6.60%**			
2 – southern ultramafic region endemics (*M. montana*)	10.10%	**3.10%**		
3 – central-east ultramafic endemics (*M.* cf. *tricolor*)	10.80%	10.10%	**4.20%**	
4 – *M. tricolor*	9.80%	10.40%	10.10%	**3.50%**

TABLE 2: Pairwise matrix of mean genetic distances between nodes within the central-west/northwest ultramafic region endemic *Marmorosphax* (Group 1 clades 5–9; Fig. 5) (uncorrected p-distances) for the mtDNA ND2 gene. Values in bold represent within-population mean uncorrected p-distances.

	5	**6**	**7**	**8**	**9**
5 – *M. kaala* Mt. Kaala	n/a				
6 – *M. boulinda* Massif du Boulinda	7.30%	**0.50%**			
7 – *M. boulinda* Massif du Tchingou	7.70%	7.20%	**1.60%**		
8 – *M. taom* Mt. Taom	6.50%	8.60%	9.00%	**1.20%**	
9 – *M. taom* Dôme de Tiébaghi	8.00%	9.80%	10.00%	3.30%	**0.20%**

TABLE 3: Pairwise matrix of mean genetic distances between nodes within *Marmorosphax montana* populations (Group 2 clades 10–12; Fig. 5) for the mtDNA ND2 gene. Values in bold represent within population mean uncorrected p-distances.

	10	**11**	**12**
10 – *M. montana* Camp des Sapins	**0.70%**		
11 – *M. montana* Forêt de Saille	7.80%	**0.00%**	
12 – *M. montana* Mt. Ouin	6.90%	2.90%	**0.00%**

1, this study) as the sister species to all other species of *Marmorospax*. The present study also differs in the inclusion of additional populations in Group 1 and Group 2 clades, and of populations comprising a previously unknown lineage, Group 3 *M.* cf. *tricolor*. The extent of within-group genetic differentiation derived from this much-expanded sampling is discussed below in the context of the lineages recovered.

Group 1 *M. boulinda/taom/kaala*: the earlier study by Sadlier et al. (2009) retrieved a relatively high level of genetic differentiation between taxa on the Kaala, Ouazangou-Taom and Boulinda massifs, which was pivotal in assigning species status to the three taxa described given sample sizes from each massif were small (n = 2, 5, and 2 respectively). A similarly high level of genetic differentiation is retrieved here between populations from these massifs (Table 2).

The expanded sampling for the central-west and northwest ultramafic regions now includes populations from the Massif du Tchingou and from Dome de Tiébaghi. The level of differentiation between the type population of *M. boulinda* from the Massif du Boulinda and the population from the Massif du Tchingou (uncorrected p mean 7.2% [Table 2]) is similar to that seen in pairwise comparisons between topotypic *M. boulinda*, *M. taom* and *M. kaala*. However, the type population of *M. boulinda* from Massif du Boulinda is known only from two individuals (an adult male and adult female) and the population from the Massif du Tchingou from eight specimens. Morphological comparisons have proved of limited utility in assessing the status of these two geographically disjunct populations given the small sample size of the type population on the Massif du Boulinda (n = 2), particularly with regard to color and pattern.

The population from Dome de Tiébaghi is here retrieved as the sister to the type population of *M. taom* from the Massif d'Ouazangou-Taom. The level of differentiation between the two populations is markedly lower (uncorrected p mean 3.3%) than that seen in pairwise comparisons of populations on other massifs in the region, and there are no corresponding morphological markers to differentiate these two populations. Rather, adult females from both populations share a unique dark chevron-shaped marking on the throat, a morphological trait that supports the close relationship of these populations as a single species, and which also serves to diagnose the species from all other *Marmorosphax*.

Group 2 *M. montana*: two populations from the southern ultramafic region not represented in the earlier study by Sadlier et al. (2009) are here included, one from Forêt de Saille and one from Camp des Sapins, both from the north of the region and extending the species distribution the full length of the Massif du Sud. The level of differentiation between the populations (Table 3) from Forêt de Saille and Mt. Ouin is low (uncorrected p mean 2.9%), but significantly greater between these and the population from Camp des Sapins (uncorrected p mean 7.8% and 6.9% respectively).

Group 3 *M.* cf. *tricolor*: the Group 3 *M.* cf. *tricolor* lineage from the central-east region ultramafic region was retrieved as the well supported (UFboot = 99 and BPP = 1.0), but moderately divergent (uncorrected p mean 7.8%) sister to Group 4 *M. tricolor*. It comprises two well supported sub-lineages in the north of the central-east ultramafic ranges, one a single population from Néjére near Poro, and one represented by populations scattered across Mt. Menazi – the two sub-lineages are disjunct in distribution and separated by the valley of the Koua River. The identity of the Menazi sub-lineage is confounded by discordance between the genetic assignment of some individuals and the pattern of throat color in females, the morphological trait that otherwise diagnoses it from *M. tricolor* (males of either the Group 3 *M.* cf. *tricolor* lineage and Group 4 *M. tricolor* are morphologically indistinguishable from each other).

Group 4 *M. tricolor*: the numerous populations referable to Group 4 *M. tricolor* lineage form a well-supported lineage (UFboot 100 and BPP 1.0). The internal genetic structure from a broad range of samples across the Grande Terre shows some regional sub-structuring but with overall relatively low levels of divergence, even towards the base of the species phylogeny. Further, the internal genetic structure within this lineage is characterized by low support for most basal splits in the phylogeny and a generally low level of inter-population genetic divergence, although some of the broader groups received a moderate level of support and showed a level of genetic differentiation (uncorrected p intrapopulational mean 3.5%) approaching that seen between disjunct populations of the Group 2 *M. montana* lineage.

In summary the genetic data supports monophyly and distinctiveness of lineages representing the five currently recognised species in the genus, and several previously unrecognized and highly differentiated lineages which at this point are problematic to define and require further investigation.

DISCSSION

The distribution of species Groups 1–3 and populations within are mostly consistent with geological boundaries of the island's ultramafic regions.The concordance between the distribution of the major genetic lineages and that of the islands ultramafic surfaces suggest vicariant events in the history of the genus driven by factors that progressively isolated regional metapopulations (physically and/or biologically) in the major ultramafic blocks. Initially by isolation of populations in the western ultramafic region that gave rise to the Group 1 lineage species (*M. kaala*, *M. boulinda*, and *M. taom*), followed by isolation of populations in the southern ultramafic region the Group 2 lineage (*M. montana*), followed by isolation of populations in the central-east region ultramafic surfaces from populations in the adjacent metamorphic surfaces of the central-east and northeast regions giving rise to the Group 3 (*M.* cf. *tricolor*) and Group 4 lineage (*M. tricolor*) species respectively. The extent of intra-lineage differentiation seen within these major lineages on ultramafic surfaces indicate ensuing lineage splitting arising from more localized isolation of populations after primary divergence events.

Historical changes in climate have been proposed as a significant factor in the distribution of vegetation on New Caledonia, particularly with respect to size, shape and area of humid forest (Pintaud et al. 2001), and its extent as historical refugia under periods of glacial aridity (Pintaud et al. 2001; Poncet et al. 2013; Pouteau et al. 2015). Historical aridity and accompanying widespread loss of forest habitat at low to mid elevation may have been causal in initiating regional and intra-regional isolation of *Marmorosphax* populations on ultramafic surfaces. Under such conditions species-specific niche conservatism (Wiens, 2004) likely played a fundamental role, whereby populations once continuously distributed at lower elevations fail to adapt to new and adverse environmental conditions and are forced to stay within (and follow) the limits of their preferred niche, and move to higher elevations. By failing to adapt to new environmental conditions and maintaining ecological traits that prevent dispersal across a new ecological barrier at lower elevations, gene flow is prevented between populations, leading to differentiation over time in the face of extended periods of separation maintained by the persistence of unsuitable conditions. While this may have been a likely scenario to account for the persistent isolation of genetically distinct lineages within the Group 1, 2 and Group 3 lineages, it would appear not to apply to the Group 4 lineage species, *M. tricolor*. Earlier vicariant events within the genus suggest it was originally limited in distribution to metamorphic surfaces of central-east and northeast. The northeast of the Grande Terre has been identified as one of four areas that received sufficient moisture during periods of Pleistocene aridity to maintain lowland rainforest refugia for palms (Pintaud et a. 2001). Such refugia would likewise have sustained elements of the moisture-dependant fauna. Thus, populations of the Group 4 lineage species, *M. tricolor*, may not have been subject to the same environmental pressures historically as other lineages, and may have maintained traits that allowed expansion into the Grande Terre across a broad altitudinal range under more favorable conditions. In the case of *Marmorosphax* niche conservatism would appear to be accompanied by morphological conservatism between and within lineages. Although the genus as a whole is characterized by a number of morphological apomorphies, the individual species of *Marmorosphax* are all very similar in overall body form, coloration, and behavior. Here we discuss the geographic attributes of the major lineage-based groups identified in the molecular phylogeny for *Marmorosphax*, the possible processes leading to their differentiation, and the potential role of the interplay between historical climate change and species niche conservatism in the extent of intra-lineage diversification observed.

Massif specific differentiation - the Group 1 lineage taxa of the central-west and northwest region ultramafic ranges. — The terms northwest ultramafic region and central-west region are used here as arbitrary divisions of the ultramafic surfaces primarily located on the western side of Grande Terre (see Fig. 1). These surfaces extend as a chain of near coastal massifs and ranges from Sommet Poum in the north to Mé Maoya near Bourail in the south but also include several adjacent interior massifs including the Massif du Tchingou and the Massif du Ouatilou. In the

FIGURE 6. The Mt. Kaala Massif in the distance from the summit of the Massif d'Ouazangou-Taom, separated by the low-lying Iouanga River valley.

northwest of the region to the north of the Pouembout Valley these massifs, Massif de Koniambo, Massif d'Ouazangou-Taom, Mt. Kaala and the Dôme de Tiébaghi, exist as isolated entities, separated from each other by low-lying (often broad) river valleys (Fig. 6). By contrast, the massifs in the central-west south of the Pouembout valley, Massif de Kopéto (including Paéoua), Massif du Boulinda, show some degree of connectivity via intervening mid-high elevation ranges, with the exception of the most southern, Mé Maoya, which is isolated from massifs to the north by the Poya River valley. The Massif du Tchingou is an isolated massif which lies inland of the Pouembout valley, and is treated here as part of the central-west region massifs.

The well-supported branching pattern within the Group 1 lineage suggests initial isolation of the sub-lineage on Mt. Kaala (*M. kaala*), but with only moderate support, followed closely by isolation and divergence of the other massif-specific sub-lineages. The extent of intra-regional massif-specific lineage splitting following primary divergence suggests an ongoing history of fragmentation and isolation of populations at a very localized scale within the ultramafic surfaces of central-west and northwest Grande Terre, equating to a scenario of multiple intra-regional vicariant events. Mount Kaala (*M. kaala*), the Massif du Boulinda (*M. boulinda s.s.*), the Massif du Tchingou (*M. boulinda*), Massif d'Ouazangou-Taom (*M. taom*), and Dôme de Tiébaghi) (*M. taom*) all have genetically divergent massif-specific populations. The level of genetic differentiation between these massif-specific lineages is typically high (between 6.5% and 10.0% - Table 2), indicating a history of long-standing inter-massif divergence. The exception is between the populations of *M. taom* from Massif d'Ouazangou-Taom and Dôme de Tiébaghi, in which the extent of differentiation is markedly lower (uncorrected p mean 3.3%), suggesting a more recent loss of connectivity between these two massifs or a recent expansion event from one massif to the other. The latter of these scenarios appears unlikely given the two widely separated and a lack of evidence for between-massif migration historically in the lineage.

Several isolated massifs in central-west and northwest ultramafic regions appear to lack Group 1 lineage taxa. Sommet Poum (maximum elevation 413 m) and Massif de Koniambo (maximum elevation ~950 m) in the northwest region have been well investigated, but there are no confirmed records of *Marmorosphax* from Sommet Poum, and only the Group 4 *M. tricolor* lineage has been recorded from the Massif de Koniambo. Similarly, the Massif de Kopéto (maximum elevation ~1050 m) in the central-west region has been well investigated, but only the Group 4 *M. tricolor* lineage has been recorded. Both the Koniambo and Kopéto-Paéoua massifs have areas of high elevation forest and maquis habitat at or above 900 m in elevation. Current habitat availability provides no explanation as to why Group 1 lineage taxa are absent from these massifs. Further, both massifs each have a suite of massif-specific endemic skinks and geckos, a number of which are restricted to high elevation habitat. The absence of any *Marmorosphax* on Sommet Poum, the most northern of the ultramafic massifs on the Grande Terre, is not entirely unexpected given its location in the dry far north of the island. This massif only rises to a plateau of 400 m in elevation and is separated from the nearest population of *Marmorosphax* to the south on Dôme de Tiébaghi (*M. taom*) by a straight-line distance of 25 km, and the nearest population to the east, on Mt. Mandjelia (*M. tricolor*), by 32 km.

Overall, the extent of intra-regional massif specific divergence and differentiation within the Group 1 lineage is interpreted as reflecting a history of progressive fragmentation and isolation of populations within the central-west and northwest regions early in its history, a pattern which in turn likely reflects an accompanying history of long-term and progressive isolation of forest habitat on the massifs via contraction to higher elevation in response to aridity, with post-isolation barriers to dispersal persisting.

High elevation endemism - the Group 2 lineage species *M. montana* of the Massif du Sud. — The ultramafic surfaces of southern Grande Terre extend as a near continuous block of ranges south of the Thio Valley (see Fig. 1), dropping to a plateau of ~250 m on the Plaine des Lacs in the far south. The region has been identified as an area rich in endemic lizard species and representing a distinct bioregion for lizards (Sadlier 2010; Sadlier et al. 2019), but also as having extensive intra-regional microendemism. Its northern boundary for the most-part is defined by the Thio Valley, which extends from the east coast nearly two-thirds of the way across the island to the Col de Nassirah (~450 m) at its upper reaches in the west to Thio in the east, with an extension of 'related' surfaces north along the coast to near Cap Bocage. To date the Group 2 lineage *M. montana* has only been recorded from higher elevation sites on the southern ultramafic ranges, at Mt. Ouin in the south (900–1100 m), Bwa Bwi (~1100 m) in the central area, and Forêt de Saille (750–800 m), Camp des Sapins (600–800 m) and Kongouhaou Nord (900–1000 m) near the northern boundary of the region. The vegetation cover of high elevation ranges in much of the region is now predominately maquis shrubland, often open and degraded, but with areas of forest of varying size towards the top of the ranges (Fig. 7), although these become progressively smaller and more isolated in the central and northern parts of the region. The species has been recorded mostly from high elevation forest habitat, but also occurs in adjacent maquis shrubland.

The extent of genetic differentiation between the three populations available for analysis is anomalous in the context of their proximity to each other. The population from Forêt de Saille and Mt. Ouin are 40 km distant but form a well-supported sub-lineage with a relatively low level of differentiation (uncorrected p mean 2.9%), whereas the population from Camp des Sapins (including adjacent Kongouhaou Nord) is highly differentiated from both the Mt. Ouin (uncorrected p mean 6.9%) and Forêt de Saille (uncorrected p mean 7.8%) populations, despite only being ~15 km straight line distance the latter.

An additional population of *M. montana* from Bwa Bwi, which also sits on this ridge at around 1200 m has recently been reported, but there is no genetic data available for this population. This ridge also includes the Massif du Humboldt, but neither *M. montana* or *M. tricolor* have been

FIGURE 7. High elevation ranges of southern Grande Terre (from Pic Ningua), predominately maquis shrubland but with isolated forest at the top of the ranges.

recorded from high elevation forest habitat on the massif (Sadlier and Jourdan, 2011), despite the presence of extensive 'moss forest' (forêt mousse) along the ridges between 1000–1400 m in elevation, although *M. tricolor* has been recorded from nearby sites at lower elevation (low elevation forest of the Ni Valley and low-mid elevation forest on the western drainage of Mt. Vulcain).

The landscape over much of the southern ultramafic region appears to have been extensively modified since the arrival of humans, and it is difficult to envisage to what extent natural forest habitat might have existed historically (pre-human), particularly on its northern ranges. In this context, the extent of genetic differentiation observed between populations suggests greater continuity of habitat (forest at high elevation) historically along the ranges than currently seen, with past connectivity between populations on Forêt de Saille and Mt. Ouin, possibly via high elevation habitat between these sites along a near continuous ridge that runs down the Massif du Sud, despite much of the intervening area now being dominated by maquis shrubland. Conversely, the extent of differentiation of the Camp des Sapins/Kongouhaou population suggests early and persistent isolation of those ranges.

The Group 3 *M.* cf. *tricolor* lineage in the central-east ultramafic ranges. — Differentiation of the Group 3 *M.* cf. *tricolor* lineage on ultramafic surfaces of the central-east ultramafic ranges follows the pattern of cladogenesis consistent with vicariance and isolation of populations seen in early in the history of the genus. By default, the distribution of populations giving rise to its sister species, the Group 4 *M. tricolor* lineage, would have originally been limited to the adjacent central-east and northeast metamorphic surfaces.

The Group 3 *M.* cf. *tricolor* lineage comprises two populations on ultramafic massifs in the central-east ultramafic ranges, one at Néjére on the Poro massif and one scattered over Mt. Menazi on the Kouaoua massif, each a well-supported sub-lineage (nodes 13 and 14 Fig. 5) and with a high level of interpopulation differentiation (uncorrected p mean 7.8%). These two populations are disjunct, being separated by the Koua River valley. On Mt. Menazi individuals genetically assignable to the Group 3 *M.* cf. *tricolor* lineage are locally sympatric with individuals genetically assignable to the Group 4 *M. tricolor* lineage. Throat color and pattern of juveniles, subadults and adult females is the sole morphological character that can otherwise diagnose the two taxa. The pattern of juveniles and subadults is carried over to adult females, whereas in adult males it becomes muted and adult males of the Group 3 *M.* cf. *tricolor* lineage and Group 4 *M. tricolor* lineage are not readily distinguished. All juveniles/subadults and adult females assigned to the Group 3 *M.* cf. *tricolor* genetic lineage had a muted marbled throat pattern. By comparison, juveniles/subadults and adult females assigned to the Group 4 *M. tricolor* lineage from elsewhere throughout the species range typically have a boldly marbled black and cream throat pattern.

Across Mt. Menazi the distribution of morphotypes and genotypes was complex. All juveniles/subadults and adult females on Mt. Menazi assigned to the Group 3 *M.* cf. *tricolor* genetic lineage had a muted marbled throat pattern. However, at one high elevation site where the two lineages occur in local sympatry, the *M. tricolor* genetic lineage contained adult females with a muted marbled throat pattern and juveniles/subadult individuals with the boldly marbled black and cream throat pattern. Further complicating this situation, seven adult females and two juveniles (and all males) from Bwa Méyu, 20 km to the southeast of Mt. Menazi and on the adjacent Boakaine massif, had the muted marbled throat pattern typical of the Group 3 *M.* cf. *tricolor* genetic lineage but were all uniformly assigned to the Group 4 *M. tricolor* genetic lineage. Aside from these discrepancies the Group 3 *M.* cf. *tricolor* genetic lineage is ringed by populations assigned to Group 4 *M. tricolor* on both ultramafic (Nakéty, Mé Adéo and Mé Maoya) and metamorphic (Plateau Dogny, Col d'Amieu and Col des Rousettes) substrates (Fig. 8), morphologically typical of that species.

The extent of genetic introgression between *M. tricolor* and *M.* cf. *tricolor* appears to be unidirectional, into the *M.* cf *tricolor* lineage, and in some instances, such as at Bwa Méyu to the south, might have completely swamped that population. The pattern of genetic introgression between the Group 3 *M.* cf. *tricolor* genetic lineage and sympatric Group 4 *M. tricolor* genetic

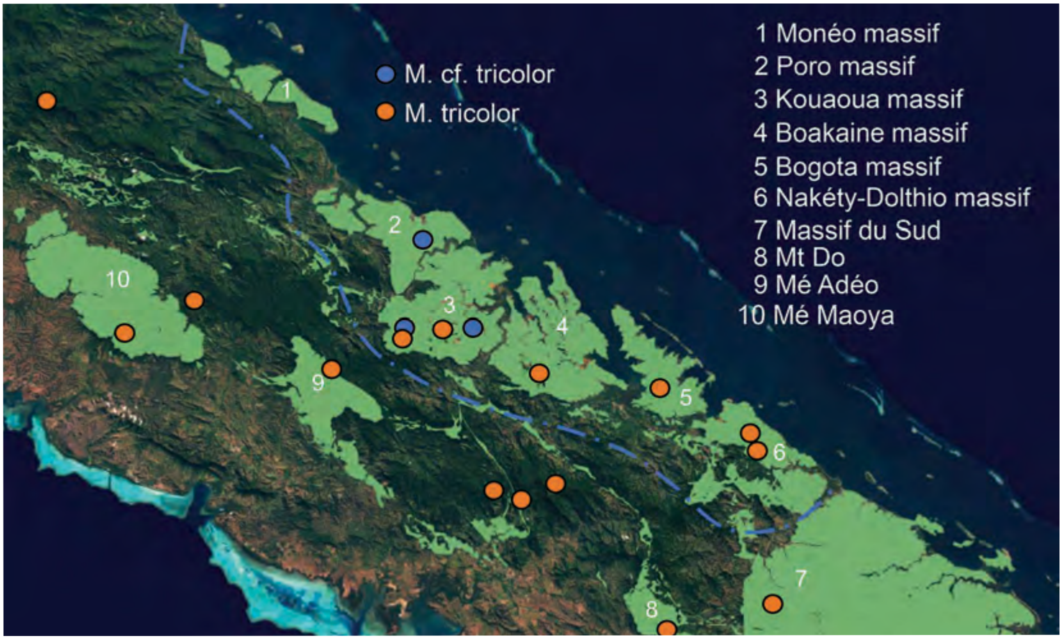

FIGURE 8. Distribution of ultramafic surfaces in the central-east region of Grande Terre showing location of populations in the Group 3 *M.* cf. *tricolor* lineage and regionally sympatric Group 4 *M. tricolor* lineage.

lineage on Mt. Menazi suggests secondary contact between the two lineages, probably via dispersal of *M. tricolor* from adjacent metamorphic surfaces to the east. In this regard the 'purity' of the population from Poro may be a legacy of isolation, being geographically disjunct from Mt. Menazi and from other Group 4 *M. tricolor* lineage populations in the region.

Distribution of the Group 4 *M. tricolor* lineage across Grande Terre - the case for range expansion onto the ultramafic surfaces. — Populations assigned to Group 4 *M. tricolor* lineage extend broadly across the main island, Grande Terre, but are absent from the Îles Belep and Île des Pins, extensions of mainland to the north and south respectively now separated by straits of ocean, and is found widely on both ultramafic and metamorphic surfaces. On ultramafic surfaces it has been recorded primarily from forest habitat, but also occurs in nearby maquis habitat in association with a surface rock matrix (see below). On metamorphic surfaces it is restricted to humid forest habitat and has not been recorded from secondarily (disturbed) habitat, or savannah woodland (naiouli).

Several intraspecific groups are retrieved in the phylogeny for the Group 4 *M. tricolor* genetic lineage, one a group including a cluster of populations on the central metamorphic ranges (Sarraméa, Plateau Dogny, Col d'Amieu) and central-east Bogota ultramafic massif (Bogota), one groups of populations on both metamorphic and ultramafic surfaces of the central and northern regions, and one a complimentary group of populations on the ultramafic and metamorphic surfaces to the south – but with no support for relationships between these groups. Within each of these 'northern' and 'southern' groups some sub-structuring concordant with broad geographic subregions was evident, and sometimes well supported, but with comparatively low levels of differentiation between these regionally discrete groups of populations. This pattern suggests the species distribution could, in part, be the product of a recent and rapid expansions in range, in some cases followed by post-expansion contraction, resulting in isolation and differentiation of regional groups of populations. In this context the genetic relationship of *M. tricolor* populations may provide insights into the distribution and natural disjunctions of forest across the landscape, which is now largely obscured by anthropogenic fragmentation and loss of forest habitat.

The relationships between populations of *M. tricolor* on the western ultramafic massifs and those on adjacent metamorphic surfaces also provide some support for a recent expansion of the species onto these ultramafic surfaces. *Marmorosphax tricolor* has been recorded from four massifs, (N-S) Koniambo, Kopéto-Paéoua, Boulinda, and Mé Maoya, in the central-east and northwest regions. The present-day distribution of the species suggests environmental conditions at lower elevation on these western ultramafic massifs are sub-optimal. On the more mesic east coast is known to occur at low-mid elevation (northeast ranges 300–500 m, Sadlier 1986; central-east coast ranges ~50 m, Bauer and DeVaney 1987; southeast ranges, Sadlier and Delafenetre 2009), but on the Koniambo and Kopéto-Paéoua massifs it has only been recorded from mid-high elevation habitat at or >600 m. Populations on these western ultramafic massifs are more closely related to populations on the adjacent metamorphic ranges than they are to other populations ultramafic ssurfaces. Those on the Kopéto-Paéoua and Boulinda ultramafic massifs cluster with populations from Mt. Aoupinié and Forêt Plate on metamorphic ranges to the east, the population on the Koniambo ultramafic massif with those from the Panié Range and Mt. Koyaboa on non-ultrabasic ranges to the northeast, and the population from the Mé Maoya ultramafic massif to the population from Col des Rousettes on metamorphic ranges to the southeast. This pattern of multiple, independent events of historical connectivity between the western ultramafic massifs and metamorphic ranges to the east suggests the species presence on these ultramafic massifs is the resultof expansion from the adjacent metamorphic ranges, likely via intervening mid-high elevation ranges (Fig. 9).

Marmorosphax tricolor has not been recorded from several massifs (Massif d'Ouazangou-Taom, Dôme de Tiébaghi, Sommet Poum) in the northwest ultramafic region, despite repeated survey work, indicating persistent region-wide isolation of these massifs from the metamorphic ranges to the east (Panié Range). Much of this intervening area is the white ranges of the Montagnes Blanches Nappe (Maurizot et al. 2020) which largely lacks suitable habitat (forest) today, and by inference historically. However, the recent discovery of a population of *M. tricolor* (no genetic data is yet available) on the Mt. Kaala massif indicates the distribution of this and other species of *Marmorosphax* in the region is more complex than anticipated.

Within the 'southern' group of *M. tricolor* there was strong support for a broad sub-group of populations within the southern ultramafic region of the Massif du Sud, but with little internal genetic differentiation or regional structure between these populations. The low level of genetic differentiation and lack of internal structure between populations in sub-group which extends from the Ni river to the southern tip of the island, suggests the species distribution in the southern ultramafic region to be the product of a recent expansion in range.

As such, aspects of the phylogeography of *M. tricolor* suggest its distribution on ultramafic surfaces of the central-west and northwest ultramafic regions, central-east region, and even southern ultramafic region, may stem from a number of independent historically recent expansion events into these regions.

SUMMARY

The scheme of relationships retrieved in the molecular phylogeny for *Marmorosphax* identified basal breaks in the ancestral species distribution concordant with the boundaries of the island's major ultramafic regions. The regional and intra-regional lineage diversification in the genus represents a pattern of historical fragmentation and contraction of populations, one which likely reflects a change in the distribution of preferred habitat. Given what is known of the biology of the species of *Marmorosphax*, loss of low elevation forest on ultramafic surfaces would appear to be a probable candidate in initiating isolation of ancestral populations that gave rise specific and intraspecific lineages. A scenario of historical fragmentation and contraction of preferred forest habitat in the face of changed climatic conditions, combined with the species reliant on that core habitat, is consistent with the dynamics of niche conservatism as outlined by Wiens (2004). While loss or marginalization of low elevation forest habitat on the ultramafic massifs in the face of adverse climatic conditions may have provided the mechanism to initiate speciation within *Marmorosphax*, it is likely the persistence of high elevation forest habitat on the ultramafic ranges, often limited to the summit areas, that provided the historical refugia for these lineages to differentiate in isolation over time.

The level of intraspecific genetic differentiation within *M. boulinda, M. montana* and *M.* cf. *tricolor* in some pairwise comparisons of populations was substantial and of a similar extent to that seen been recognized species within the genus. While these differences may be indicative of the existence of potentially undescribed taxa in these lineages, they either require further genetic analyses, and/or the samples available are insufficient for the complementary morphological comparisons required for their formal recognition, and further targeted field collections are required.

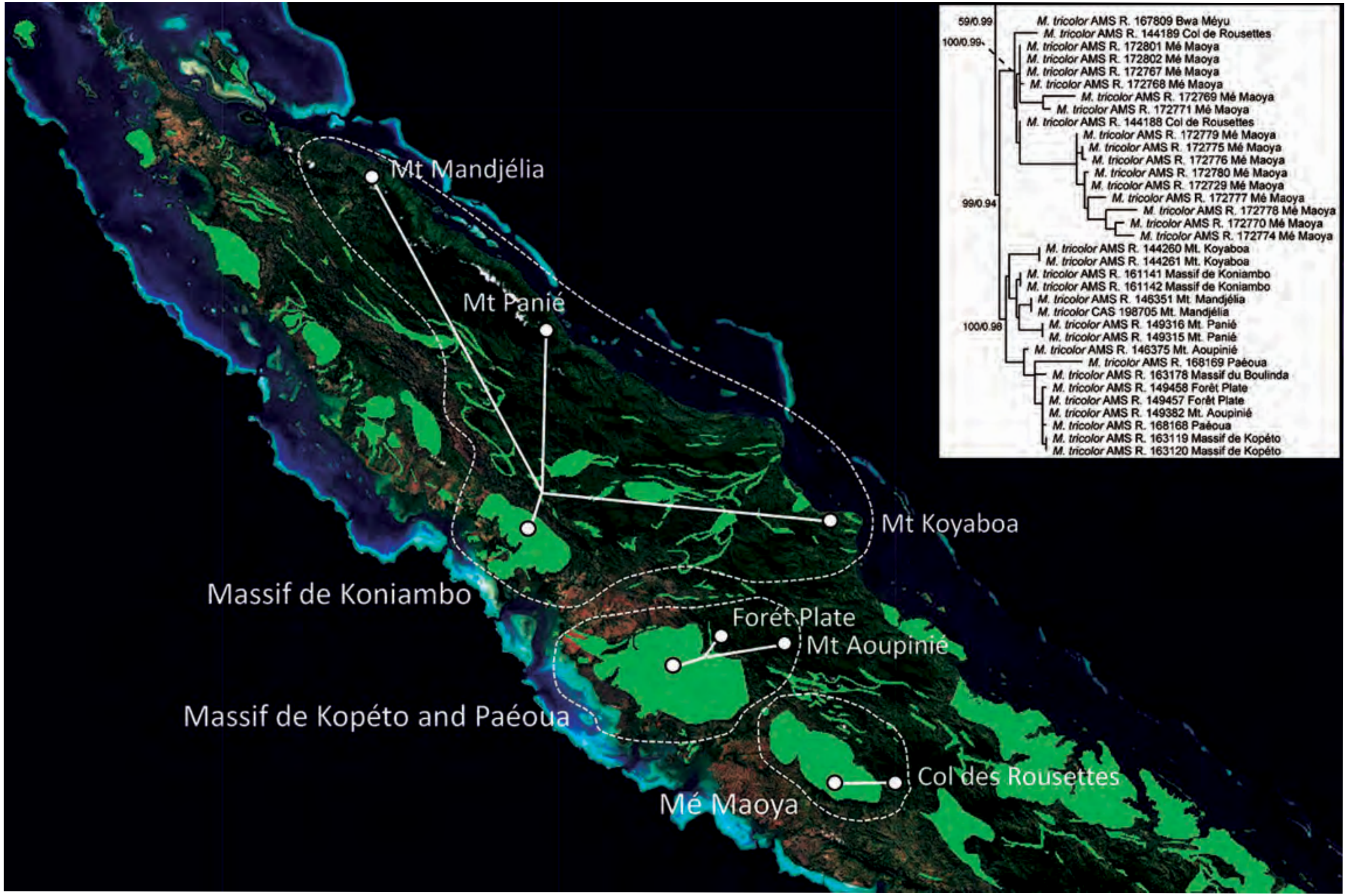

Figure 9. Approximate boundaries (dashed line) for related populations of *M. tricolor* in northern and central Grande Terre showing the affinities (solid line) of populations on the ultramafic massifs of the northwest and centralwest to populations on the metamorphic ranges to the east, rather than to each other. The relationships of these populations as retrieved in the ND2 phylogeny are shown in the inset.

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Appendix

Specimens used in the genetic study (for museum acronyms see Materials and Methods).

Genus	Species	Reg. No.	Location	Genbank ND2
Outgroup				
Celatiscincus	*euryotis*	AMS R.138574	Île des Pins	DQ675204
Graciliscincus	*shonae*	AMS R.165813	Mt. Ouin	DQ675207
Kanakysaurus	*viviparus*	AMS R.161299	Île Pott, Iles Belep	DQ675209
Lacertoides	*pardalis*	AMS R.148051	Kwa Néie	DQ675211
Epibator	*nigrofasciolatus*	AMS R.138624	Île des Pins	
Lioscincus	*steindachneri*	AMS R.149890	Mé Adéo	DQ675218
Phasmasaurus	*tillieri*	AMS R.148037	Mt. Vulcain	DQ675220
Nannoscincus	*mariei*	AMS R.146484	Mt. Mou	DQ675232
Phoboscincus	*garnieri*	AMS R.151964	Mt. Dore	DQ675237
Sigaloseps	*deplanchei*	AMS R.148065	Plaine des Lacs	DQ675238
Simiscincus	*aurantiacus*	AMS R.144356	Mt. Koghis	DQ675250
Tropidoscincus	*variabilis*	AMS R.161879	Kwa Né Mwa	DQ675242
Ingroup				
Marmorosphax	*kaala*	AMS R.161091	Mt. Kaala	KF176382
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