New fossil discoveries reveal the diversity of past terrestrial ecosystems in New Caledonia

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Abstract

New Caledonia was, until recently, considered an old continental island harbouring a rich biota with outstanding Gondwanan relicts. However, deep marine sedimentation and tectonic evidence suggest complete submergence of the island during the latest Cretaceous to Paleocene. Molecular phylogenies provide evidence for some deeply-diverging clades that may predate the Eocene and abundant post-Oligocene colonisation events. Extinction and colonization biases, as well as survival of some groups in refugia on neighbouring paleo-islands may have obscured biogeographic trends over long time scales. Fossil data are therefore crucial for understanding the history of the New Caledonian biota, but occurrences are sparse and have received only limited attention. Here we describe five exceptional fossil assemblages that provide important new insights into New Caledonia's terrestrial paleobiota from three key time intervals: prior to the submersion of the island, following re-emergence, and prior to Pleistocene climatic shifts. They reveal important changes in floristic composition over time, even between the early and late Miocene.

Main Text

Integrating biological and geological knowledge is crucial for understanding biotic evolution[1] and recent reviews[2-6] have emphasized the need for more paleontological data to enable more powerful tests of evolutionary and biogeographic hypotheses. Despite New Caledonia's importance as a global biodiversity hotspot, such an integrative synthesis has not yet been fully developed for this Pacific archipelago, mainly because of a lack of detailed paleontological studies. New Caledonia has long fascinated biologists because of its isolated flora and fauna, but a deep understanding of the evolution and assembly of this biota has remained controversial because biological and geological data appeared to be in conflict regarding its age. The New Caledonian biota contains representatives of some deep-branching lineages, including the earliest-diverging flowering plant, *Amborella*. However, recent geophysical, tectonic, and sedimentological studies[7-8] suggest that the extant island is not nearly as old as many of these lineages, and that the ancestors of its modern biota must have migrated more recently from other regions[2,4-6]. These studies suggest a complex history, with the complete submergence of what is currently New Caledonia during the Late Cretaceous and Early Paleogene, possible sporadic re-emergence(s) during pre- and syn-obduction tectonic events between ~50 MY (millions of years) and ~34 MY[9], and finally, full emergence following obduction at some time between 34 MY and 25 MY[8,10]. Following this period of uplift, an ultramafic regolith developed over peridotites throughout the island, and owing to its specific geochemical features, dramatically controlled terrestrial colonization. Although evidence for erosion of an older regolith was described from early Miocene sediments[10-11], the ancient character of regolith development has generally been overlooked.

The geology of New Caledonia has been considered unfavourable for fossilisation. Sediments from the Permian to the Quaternary are present on the main island, but many are metamorphosed and large areas are covered by ultramafic peridotites resulting from obduction. Terrestrial fossil assemblages are therefore rare and very few have been documented. Among animals, some Holocene vertebrates and land snails are known[12-14]. Plants are better represented, but mainly by pollen and wood from scattered Permian to Miocene deposits[15-21]. Macrofloral remains are likewise rare, with a few Late Cretaceous angiosperms and leaves of the gymnosperm *Podozamites* mentioned in old literature[21], together with a probable leaf of Ginkgoales and leaves of *Taeniopteris* from the Triassic[18]. A variety of leaves, stems, and unidentified roots have also been reported form Miocene ferricretes derived from weathered peridotites[22], but more precise identifications were not possible. Subfossil copal resins have also been found, but without identifiable inclusions (RG pers. obs.). This record is too sparse to provide a clear understanding of the evolution and assembly of terrestrial paleobiotas before and after New Caledonia's submersion and subsequent re-emergence[23].

To address the lack of a detailed fossil terrestrial record, our research focused on potentially fossiliferous terrestrial sedimentary outcrops, particularly those likely to preserve plants and insects. New fossil assemblages were discovered across New Caledonia from the Upper Cretaceous 'Formation à charbon' of Moindou (northern part of South Province), the Upper Cretaceous of Haut-Robinson (Mont-Dore municipality), the lower Miocene of Nepoui (southwest coast of North Province), and the upper Miocene (?) of the Fluvio-Lacustrine Formation (Madeleine falls and 'Pont des Japonais' outcrops, South Province) (Fig. 1 and Supplementary Figs. 1,4,7,9). These discoveries dramatically expand the known diversity of plants and insects from the Cretaceous through the Neogene, provide important insights into past ecosystems on New Caledonia, and show that the island does indeed possess a rich and widespread paleontological record that helps to illuminate key moments in its geological, evolutionary, and ecological history. These floras and faunas serve as a crucial first step towards a more integrated understanding of the complicated biological history of the New Caledonian biota.

Results

The geologic context of the newly discovered fossil-bearing outcrops found across New Caledonia (Fig. 1, and Supplementary Figs. 1,4,6,8), their basic features, and their preserved biota are discussed below. As a matter of reference, the New Caledonia archipelago comprises a main island (Grande Terre), its offshore extensions (Isle of Pines and Belep Islands), and a girdle of smaller and much younger islands (Loyaly Islands) that extends parallel to the main island. The Grande Terre is the emerged northernmost part of the 'microcontinent' Zealandia[24].

Late Cretaceous of Haute-Nessadiou (H-Ness) and Haut-Robinson (H-Rob)

The Upper Cretaceous sedimentary cover of Grande Terre consists of a passive margin megasequence, with coarse detrital terrestrial to marine peri-continental sediments at its base and fine-grained marine transgressive deposits towards the top. We located several fossiliferous outcrops within this sequence in the Haute-Nessadiou area between village of La Foa, Boghen pass, and the village of Moindou. This area contains a NW-SE striking strip of Upper Cretaceous mudstones and thin sandstones, 4 km wide and 16 km long ('Formation à charbon', Supplementary Fig. 1) that reflect distal fluvial deposition. Marine bivalves and gastropods indicate deposition in estuarine marine environments while coal seams and other mudstone units contain *in situ* root horizons, indicating terrestrial deposition and development of soils. Marine invertebrate biostratigraphy (Supplementary Information) suggests a Turonian to late Santonian age (~90-85 MY). Plant fossils occur in millimeter-thick argillite beds in several places and are dominated by conifers, including cones of Araucariaceae and taxodiaceous Cupressaceae (Fig. 2a). Conifer foliage includes small needle-leaved taxa as well as broader leaved forms with a single midvein. One poorly preserved fern specimen and a possible cycad sporophyll with attached seeds were also recovered. At least five taxa of flowering plants (angiosperms) have been found in these deposits, including forms with both entire and toothed margins from moderately sized to large leaves (Fig. 2b-d). Precise systematic placement of these plant fossils is difficult because the cuticles and fine venation are not preserved, and because of the fragmentary nature of the material and thermal alteration of the sediments. No fossil insects were recovered from these sediments, but a number of the angiosperm leaves show marginal feeding traces, galling, and mining made by insects (Fig. 2c,e,f, Supplementary Fig. 3g). Typically, arthropod remains are rare in soft mudstone and non-consolidate sandstone sediments[25].

The Haut-Robinson plant outcrop is contained within the same general sequence as that at Haute-Nessadiou. Here the base of the Upper Cretaceous succession is interbedded with volcanic agglomerates, flows and sills 10 to 50 m thick (Supplementary Fig. 1) derived from the trachyte and rhyolite flows that directly overlie the Jurassic basement[26]. Fluvial sandstones and siltstones in this outcrop contain abundant small woody stems and other fragmentary evidence of vegetation. Leaf fossils are rare and are confined to a few horizons. The material includes at least three taxa of ferns tentatively assigned to *Microphyllopteri*s, *Cladophlebis*, and *Sphenopteris* (Supplementary Fig. 3). Similar fossil foliage is generally placed in Gleicheniaceae, Osmundaceae, and Dicksoniaceae, respectively. Small needle-leaved conifers, including the foliage from *Elatocladus* and *Pagiophyllum*, are also present. A possible cone scale (*Araucarites*) also suggests the presence of araucariaceous conifers. Angiosperm leaves are small and rare, but at least two taxa are present. The first has craspedodromous-like venation with the main secondaries terminating in a major tooth at the leaf margin. Similar types of leaves occur in the fossil assemblage from the Cretaceous Winton Formation of Australia[27]. The second taxon has larger leaves and more steeply/shallowly angled venation. The flora of the Haut-Robinson outcrop is distinct from that of the Haute-Nessadiou Formation, probably due to the more proximal mode of deposition. No fossil insects have been found at the Haut-Robinson plant outcrop, but the fossil leaves show numerous mines and galls.

Miocene of Nepoui Group (Nepoui) and of the Fluvio-Lacustrine Formation

In the absence of unconformably overlying younger sediments, obduction in New Caledonia is not precisely dated; however, there is a consensus that the post-obduction period started in the early Oligocene[7-8]. The oldest known aerial exposures of weathered ultramafic rocks (ferricretes) have been dated by paleomagnetism from the Late Oligocene[28]. The earliest terrestrial deposits containing fossils (dating to the early Miocene) are therefore very important for understanding the post-obduction recolonisation process and elucidating the origin of the key extant lineages. Miocene deposits of the Nepoui Formation, as well as possible Miocene deposits of the Fluvio-Lacustrine Formation, both contain diverse and well-preserved plant remains, although with only a few insects or other terrestrial animals (see below). Further field collections are needed to fill this gap.

Nepoui Group

The Nepoui Group is centered around the Pindai Peninsula on the west coast of Grande Terre. It comprises two formations[29]: the lowermost part of the lower formation is a ca. 100 m thick sequence of reefal and lagoonal limestones, reflecting the earliest post-obduction sedimentation (Supplementary Fig. 4). This is overlain unconformably by coarse conglomerates, ca. 100 m thick that grade upwards into a finer-grained 'intermediate unit' with both marine and terrestrial sediments. The intermediate unit is approximately 15 m thick and is made up of alternating bioclastic and lithoclastic sands, conglomerate lenses, and calcareous mudstone. Numerous imprints and molds of fossil leaves, as well as a few insects, occur in these beds. Silicified and ferruginous fossil wood fragments and silicified infructescences very similar in morphology to extant *Gymnostoma* (Casuarinaceae; see below) are also common in the conglomerate[30] (Supplementary Figs. 5j-k). These beds grade upward into the upper Nepoui Formation, which consists of about 25 m of bioclastic limestones that are rich in coral, algae, and echinoid fragments (Supplementary Information). The ages of both the lower and upper limestones are early Miocene, based on planktonic and benthic foraminifera. Specifically, the Upper Nepoui Formation has been dated to the Aquitanian-Burdigalian (21.4-17 MY), constraining the age of the plant fossils that occur immediately below it. We discovered a fossiliferous plant layer, approximately 10 cm thick within the intermediate unit (Figs 2g, h, Supplementary Fig. 5), that consisted of dense mats of leaves, suggesting an allochthonous accumulation. Preliminary analysis reveals a diverse floral assemblage consisting of more than 40 distinct leaf morphotypes, including around 40 dicot angiosperm leaf morphotypes, one scale-leaved conifer, and a fern, from a very small total collected exposure (ca. two square meters of rock) (Supplementary Information). The variety of forms in a limited exposure, as well as the representation of most morphotypes by only a single specimen, suggests that the Early Miocene source vegetation in this part of New Caledonia was highly diverse (Supplementary Information). The fossil leaves are difficult to assign to extant angiosperm genera or families because of their relatively poor preservation, but two types of woody infructescences recovered are consistent with assignment to *Gymnostoma* (Casuarinaceae). The larger type, with large prominent bracteoles and large subtending bracts, is broadly similar to infructescences assigned to extant *Gymnostoma* from the Eocene of Australia and Argentina[31]. The smaller type is more poorly preserved, but is also consistent with *Gymnostoma* in its prominent bracteoles that are more widely separated than *Casuarina* or *Allocasuarina*. Traces of insect activity occur frequently on the angiosperm leaves (margin feedings, galls; Figs. 2g,h). Compared to plants living in the extant dry, sclerophyll forest of the Pindai Peninsula today, the leaves of Miocene angiosperms were generally larger, suggesting greater precipitation (Supplementary Information). Together with the presence of *Gymnostoma*, which is abundant on New

Caledonia but not in the relatively dry Pindai Peninsula, paleobotanical data are congruent with previous suggestions of higher rainfall in New Caledonia during the early Miocene[32].

The Fluvio-Lacustrine Formation (Fig. 1) (Supplementary Information)

This formation comprises the sedimentary infill of depressions mainly located in the Massif du Sud in southern Grande Terre, which includes the Yaté Basin, Plaine des Lacs, Rivière des Pirogues, and Creek Pernod[33]. This unit, 70 to 80 m thick, formed from the erosion of weathering profiles that developed over peridotites or gabbro cumulates[34-35]. It also displays evidence of hydromorph (palustrine) pedogenesis with horizons of ferric crust and includes plant roots encrusted with iron oxides, as well as localized layers that are rich in well-preserved fossil plant remains (Figs 3-4). Over most of its area, it is capped by ferruginous cuirasses (Plateau de Gertrude, La Madeleine waterfall, etc.) that probably formed in association with an ancient water table. Fossiliferous layers are distributed throughout the whole series, including in some cuirasses (La Madeleine waterfall). The general pattern of the fossiliferous sites is broadly similar to fossiliferous travertine formations, and a few cases of iron travertine deposits are known in Spain[36-37] and in Greece, also on ultramafic formations with ferrihydrite encrusted leaves[38].

The precise age of these deposits is difficult to determine. Attempts at paleomagnetic dating of internal duricrusts and lateritic ferricrete on top of the sequence yielded contradictory results ranging from latest Oligocene (25 MY) to Miocene (15 MY). Folcher *et al.*[39] proposed several age hypotheses for the Fluvio-Lacustrine Formation, spanning the latest Oligocene to Holocene (ca. 120,000 years ago). They favour a possible early to middle Miocene age by correlation with tectonic events recorded in Nepoui sediments (coarse conglomerate and erosion sequence positions). We were unsuccessful in our attempt to use electron spin resonance (ESR) to date quartz grains at the two major fossil localities (La Madeleine and the Pont des Japonais), where quartz grains are exceedingly rare.

At the ‘La Madeleine locality’ (Mad), casts of leaves and wood fragments are at the surface of a ferruginous cuirass along the river La Madeleine close to its falls in the Plaine des Lacs. More productive, however, is a small (~10 m long) but rich fossil-bearing layer of ferricrust that occurs in a small hill near the Madeleine waterfall in the Plaine des Lacs (Supplementary Fig. 7). This matrix preserves plant remains in three dimensions and with cellular detail, including leaves, flowers, seeds, and wood (Supplementary Fig. 8). Poorly preserved casts of leaves and wood fragments were also found at the surface of a ferruginous cuirass along the river La Madeleine close to its falls. The fossils from the small hill are preserved as dense mats of plant material that accumulated in great quantity in small sinks, without particular orientation, suggesting deposition in the absence of current. They consist mainly of eudicot leaves (Figs. 3-4) with additional remains of flower petals, inflorescence bracts, and seeds, as well as remains of ferns and gymnosperm branches with attached leaves. Although original organic material is not present in these fossils, some show exceptional preservation of epidermal and anatomical details, including stomata, which should help to improve future identification. Preliminary results indicate the presence of at least 30 plant morphotypes, including likely representatives of the angiosperm families Ericaceae (ex Epacridaceae), Malvaceae-Sterculioideae, Thymelaeaceae, and Myrtaceae. Some fossil representatives are nearly identical to the leaves of extant taxa of Thymelaeaceae (*Solmsia*) and Ericaceae (*Styphelia*). Leaf physiognomy and the taxonomic composition of the fossil flora at the La Madeleine site are strongly consistent with present-day vegetation in the area, suggesting that similar plant communities may extend as far back at the late Miocene[40]. The La Madeleine site also preserves a three-dimension cast of a pair of beetle elytra, which were found in association with a dense leaf mat (Figs. 4a-c). These remains are attributed to an extinct species of scarabaeid beetle, likely related to an extant New Caledonian species found in the rainforest of the same area (Rivière Bleue) (Supplementary Information).

The ‘Pont des Japonais’ (PJap) outcrop includes several fossiliferous layers, along several hundred meters of exposure on a road to the Pont des Japonais. As at ‘Mad’, fossils are preserved in three dimensions in iron oxide and include leaves, seeds, and wood fragments (Figs. 3-4). The density of fossils is lower than at ‘Mad’ and leaves are not typically found as dense mats, but the ‘PJap’ assemblages nonetheless contain a high diversity of leaf morphotypes. The composition of the flora is also different, and includes likely gymnosperms, Calophyllaceae, Ericaceae (ex Epacridaceae), Lauraceae, Malvaceae-Sterculioideae, and Rhamnaceae. The leaf morphology and likely taxonomic affinities of the ’PJap’ fossils, especially the abundant leaf fossils that resemble those of extant New Caledonian Lauraceae, are consistent with a rainforest community similar to that of the current vegetation in the ‘Rivière Bleue’ reserve in the southern Grande Terre[41]. In general, the ’PJap’ fossil leaves are also larger than those ’Mad’, further consistent with a rainforest community rather than a maquis community. The ‘PJap’ assemblages also contain some evidence of insects; feeding marks are present on few leaves (margin and galls), one layer contains numerous wasp nests (Figs. 4d-f), and another ca. 4 m thick layer contains numerous bee nests built with consolidated mud and very small fragments of iron oxide. These nests, comprising clusters of cells that open to flat surfaces, can be attributed to the ichnogenus *Rosellichnus* Genise and Bown, 1996[42]. The contemporaneity of such ichnofossils with the rocks that contain them is difficult to establish[43], but the absence of any organic remains in them suggests they are fossils. A single fossil orthopteroid forewing has been recovered from the ’PJap’ deposits with an unusual plesiomorphic character (a simple anterior branch of the cubitus posterior CuPa). This feature, which is absent in the extant taxa (Fig. 4g), suggests a very basal position in orthopteroid phylogeny, close to some Permian taxa, and is consistent with the occurrence of early diverging plant and insect lineages throughout the extant biota of New Caledonia.

Comparison of the fossil assemblages

We carried out a correspondence analysis or COA (Supplementary Information) on a dataset that considers the ‘presence vs. absence of the plant families’ encountered in our preliminary analyses of the paleoflora. This analysis suggests, not surprisingly, that Cretaceous fossil floras tend to be different from extant ones. The three Neogene deposits show facies that correspond to different paleoenvironmental and sedimentary conditions, and share more similarities with the modern flora than the Cretaceous ones. The Cretaceous Haut Robinson outcrop (H-Rob) is unique in preserving several families of ferns, not yet found in other New Caledonian deposits, possibly indicating wetter conditions. The Cretaceous Haute-

Nessadiou (H-Ness) assemblage is characterized by the presence of Cycadales and Cupressaceae. The contrast between the Cretaceous 'H-Ness' and the Miocene Madeleine ('Mad') deposits could correspond to an ecological gradient (along axis 2) between a relatively humid environment ('H-Rob') and a drier one of a forest/maquis like that represented in the Madeleine deposit in the southern part of Grande Terre, with Nepoui being in an intermediate position. This inference is clearly more valid for the Miocene assemblages only than for a comparison that would include the Cretaceous floras.

The new discoveries show that the Late Cretaceous floras from New Caledonia are generally similar to those from contemporaneous eastern Gondwanan communities but contribute important new data, because such floras are rare. In Australia, the Winton Formation from central Queensland, which spans the Latest Albian or Cenomanian to early Turonian, is one of the few well-known macrofloras in the region[27,44]. Other Late Cretaceous floras include that from the Waare Formation in the Otway Basin in Central Australia[45]. New Zealand Late Cretaceous is better represented with floras of Albian to Cenomanian (Clarence Series)[46], Cenomanian to Turonian (Tupuangi Formation)[47-48], Campanian (Taratu Formation)[49] and Latest Cretaceous (Pakawau Group)[50]. Comparison of the New Caledonia assemblages to these floras confirms the widespread occurrence of taxodiaceous Cupressaceae, which dominate in distal deltaic settings (such as the Pitt Island sequences of the Tupuangi Formation), suggesting their importance in coastal environments. These particular Cupressaceae are absent on New Caledonia today, even though other groups of conifers (Araucariaceae, Podocarpaceae, different Cupressaceae, viz. *Callitris* and *Libocedrus*) are diverse. This prominence of conifers during the mid- to Late Cretaceous is consistent across the Gondwanan margin to the Antarctic Peninsula, where they occur in distal facies in the late Albian Alexander Island flora.

The rise of flowering plants during the mid-Cretaceous is not well documented in eastern Gondwanan macrofloras, but angiosperms are important in Late Cretaceous floras, including those of New Caledonia. The first Australian angiosperms appeared toward the end of the Early Cretaceous[51] and are widespread in Late Cretaceous assemblages. Late Cretaceous angiosperms from New Caledonia are similar to those of the Winton Formation of Queensland in general leaf physiognomy and especially in the predominance of small-toothed morphotypes. This contrasts with approximately coeval floras from New Zealand such as from the Clarence Series, which contains larger and entire-margined leaves, although it is unclear if this difference reflects contemporaneous spatial heterogeneity in climate and community composition or floras of slightly different ages. The presence of angiosperms in these communities is also associated with pronounced evidence of insect herbivory in the form of leaf damage, although no insect body fossils have been recovered from New Caledonia.

Although we have no fossil evidence from the Oligocene obduction interval, when fossil floras appear again in New Caledonia in the early Miocene, they are fundamentally different from those of the Late Cretaceous and are much more similar to those of modern New Caledonian vegetation. The early Miocene Nepoui flora is especially important as the first known post-obduction terrestrial paleobiota. Our results suggest this deposit preserves a highly diverse angiosperm community growing in a more humid climate than is found on the western coast of Grande Terre today, which is consistent with reconstructed paleoclimates[32]. The rich and diverse flora, together with the numerous traces of interactions with arthropods, are indicative of a complex paleobiota, suggesting extensive re-colonisation of the island potentially only ca. four million years following its final re-emergence. This Miocene fossil material also directly establishes the presence of some present-day groups in New Caledonia (e.g., *Gymnostoma*). The younger outcrops of the Fluvio-Lacustrine Formation document a rich, diverse, and complex tropical paleobiota. The diversity of leaf morphologies in the Fluvio-Lacustrine Formation, from those typical of wet forests at the Pont des Japonais to those at La Madeleine that are nearly identical to modern species living in ultramafic 'maquis' communities, demonstrate the existence of a diverse set of communities in southern Grande Terre during the Neogene, at least well before the arrival of humans. Such a mosaic landscape is still present today, in part maintained by wildfires before the last 50,000 yr[52-53] or, more recently, by fires of human origin.

Based on new fossil evidence, it is clear that the modern vegetation of New Caledonia differs fundamentally in composition from its Late Cretaceous plant communities, as well as those from eastern Gondwana more generally, and not only in a general shift away from conifer dominated lowland settings to diverse angiosperm forests. The New Caledonian flora then appears to have undergone similar kinds of changes as the broader biogeographic region in which it is situated, at least in terms of a basic taxonomic turnover towards angiosperm-dominated communities over long geological periods[54]. Present fossil evidence does not rule out the possibility that some of the characteristic deep-branched lineages endemic to New Caledonia (e.g., *Amborella*) are relicts of earlier ecosystems (viz. those of Zealandia) that potentially survived obduction on neighbouring now-drowned islands, as suggested by geological studies[55-56] and biogeographic analyses based on fossil and present-day taxa[2-3,57-59]. Nevertheless, assembly of the modern New Caledonian biota in the Oligocene to early Miocene is most consistent with the ages inferred by molecular dating for many extant clades[6] and the idea that much of the current biota was assembled via dispersal from elsewhere. Our fossil evidence demonstrates that highly diverse angiosperm communities, very similar to those found on New Caledonia today, were established on the island by the early Miocene. It also shows that these communities evolved during the Miocene. These fossil assemblages provide an important new minimum age for the assembly of the modern New Caledonian flora. On the basis of the current material and further study of these sites, as well as investigation of potential new sites, it will be possible to develop a detailed inventory of the New Caledonian Miocene flora and entomofauna, which will aid the molecular dating of modern clades and provide insight into the taxa that disappeared during regional aridification over the last 20 MY[60].

Methods

Materials. All material collected is the property of the Government of New Caledonia, Service Géologique de la Nouvelle-Calédonie (SGNC), and is temporarily deposited in the MNHN Paris, the Geological Sciences Department at Stanford University, and the Royal Botanic Gardens Victoria, Australia.

Imaging. The observations were made under a binocular microscope and photographs were taken with a digital SLR (NIKON D800 with a 60 mm F2,8 Nikkor lens) camera with a controlled oblique light. SEM microscope images have been performed with BSE mode and EDS X-ray analysis (service des collections, MNHN and Yale University).

Declarations

No nomenclatural act.

Data availability. All relevant data are available from the authors.

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Author Contributions

R.G., J.M., A.L., D.J.C., P.P.L., H.J., J.F., P.M., D.C., P.G., N.F., E.L., and A.N. collected the material. All of them plus P.V., W.F. and T.C. contributed equally to the study and manuscript preparation. R.G., J.M., P.C., J.-J.B. made photos. R.G., P.G., and A.N. designed the program. R.G. and A.N. are equal corresponding authors. P.G. and A.N. are equal last authors.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/naturecommunications

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Figures

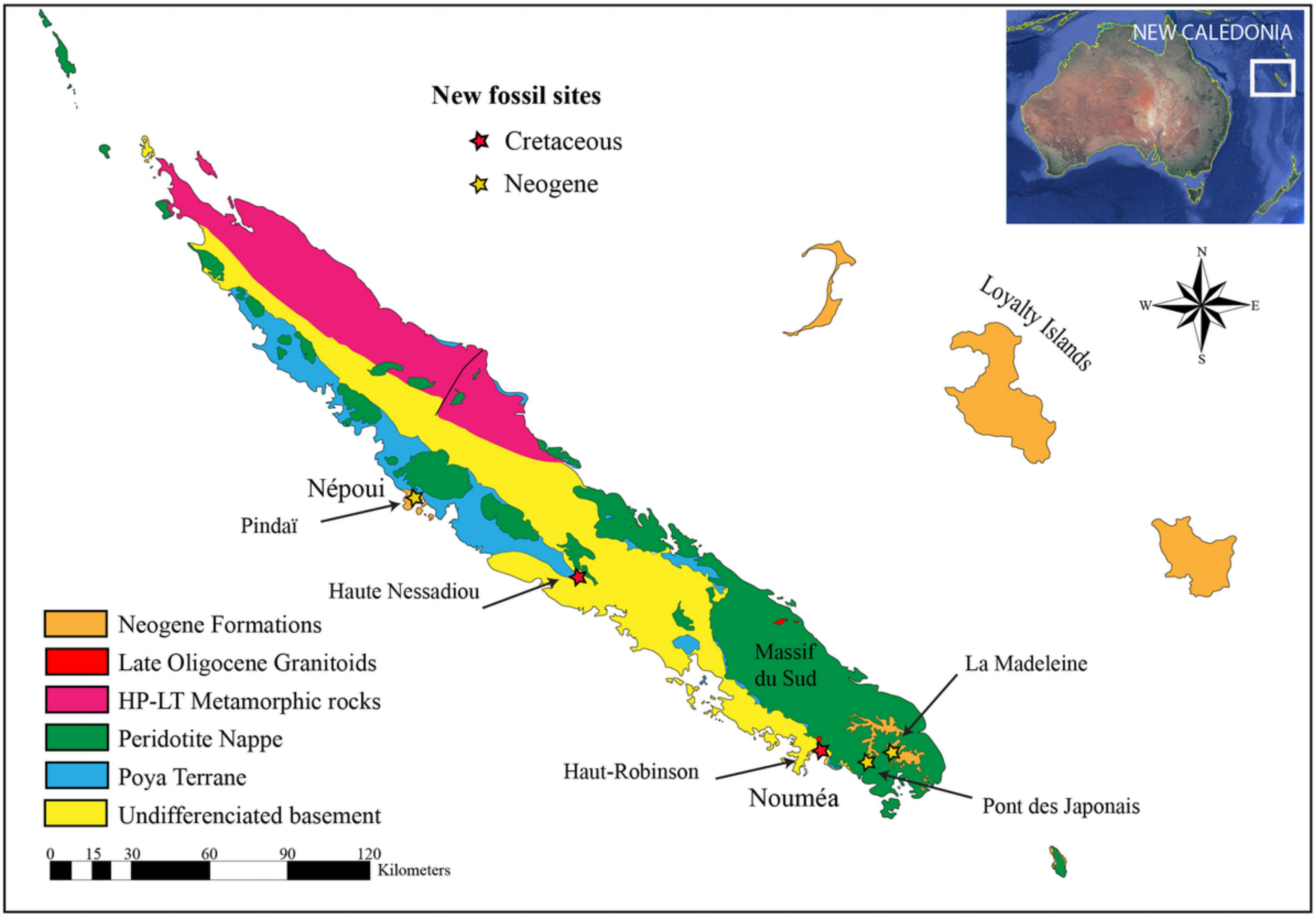

Figure 1

Simplified geological map of New Caledonia with locations of new fossil outcrops

Figure 2

Fossil plants and insect activities. (a) fruit; (b-d) leaves; (c) insect activities on a leaf (Late Cretaceous of Haute Nessadiou); (e, f) insect activities on leaves (Late Cretaceous, Haut-Robinson); (g, h) insect activities on leaves (Nepoui, early Miocene); Copyright R. Garrouste. Scale bars = 1 cm.

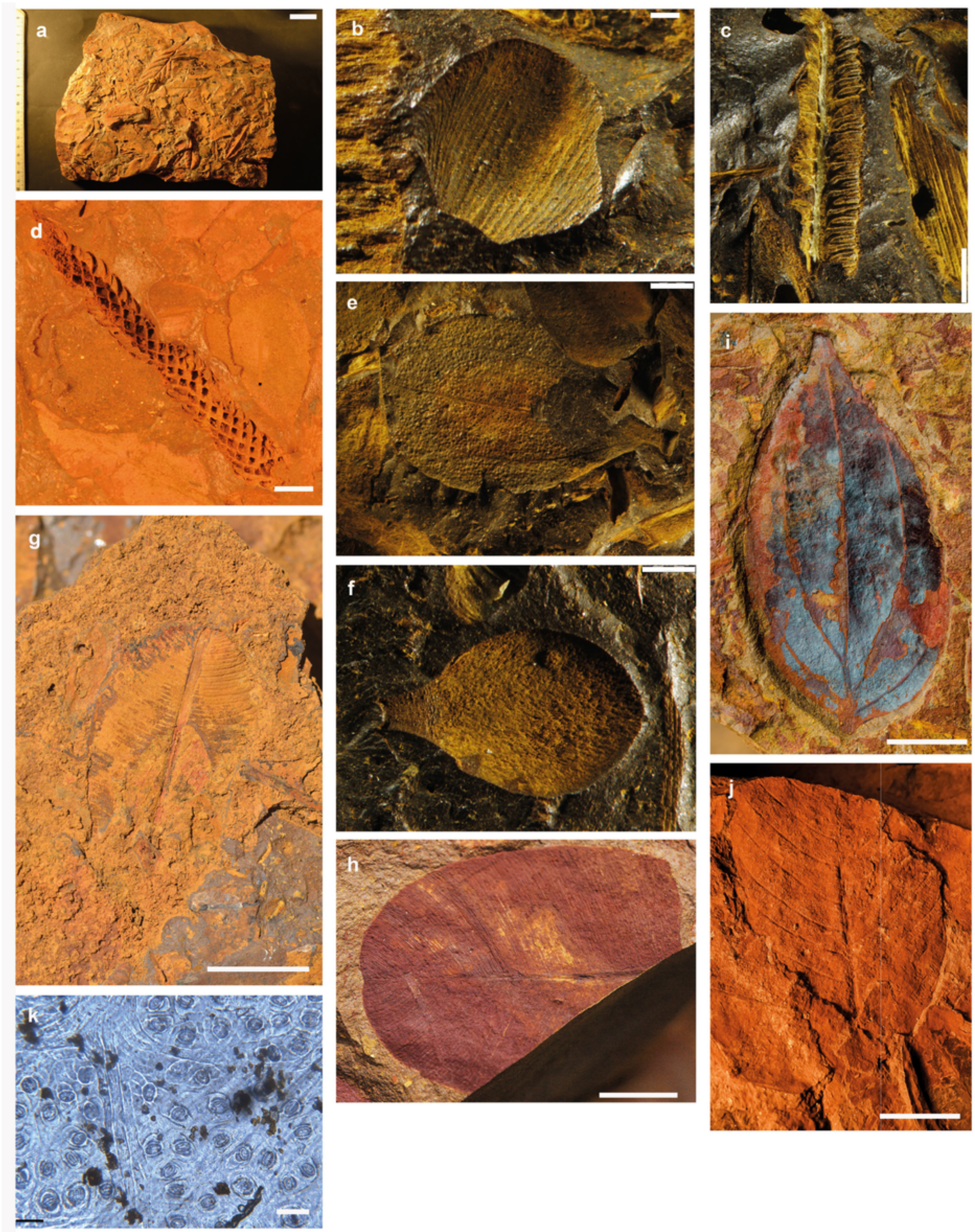

Figure 3

Late Miocene plants. (a-f) La Madeleine outcrop. (g-j) Pont des Japonais outcrop; (a) Mad_1 from Madeleine showing the very dense fossils assemblage; (b) inflorescence bract of Styphelia sp. (Ericaceae ex-Epacridaceae), Mad_1_A_Fe142; (c) fern pinnule, Mad_1_Fe49; (d) axis with 48 leaves of probable Dacrydium sp. (Podocarpaceae), Mad_17_A_Axe1; (e) leaf of Melaleuca sp. (Myrtaceae), Mad_1_A_Fe171; (f) probable petal of dicotyledon, Mad_1_A_Peta115; (g) leaf of Solmsia sp.

(Thymelaeaceae), Mad_22_A_Fe1; (h) leaves of Calophyllum cf. caledonicum (Calophyllaceae), Pjap_21_A; (i) leaf very similar to that of an extant species of Cryptocarya (Lauraceae), Pjap_46_A_Fe1; (j) leaf of Alphitonia cf. caledonica (Rhamnaceae), Pjap_55_A_Fe2; (k) imprint of Mad_6_Fe1 showing epidermis and stomata. Copyright J. Munzinger (a, h, i); Copyright J. Munzinger (a, h, i); Copyright Thibault Chaillon (b-f); Copyright R. Garrouste (g); Copyright Wyndy Foy (j,k). Scale bars b & f = 1 mm; e & c = 2 mm; d = 5 mm; k = 50μm.

Figure 4

Late Miocene ferricrust with plant and insect remains. (a-c) ‘La Madeleine’ outcrop. (d-g) ‘Pont des Japonais’ outcrop. (a) slab with non-oriented plants. NC. MAD 01 A; (b) detail of a pair of elytra of a beetle (Coleoptera: Scarabaeoidea). NC. MAD 01 A; (c) details of counterpart (NC. MAD 01 B); (d) ‘Rivière des Pirogues’ sedimentary basin landscape and outcrop, ‘Pont des Japonais’ area with ichnofossils (cf. Rosellichnus sp.), Fluvio-Lacustrine Formation (Miocene to present); (e) details of clustered ichnofossil cf. Rosellichnus sp., on subsurface of the latericrust; (f) ichnofossil cf. Rosellichnus sp. attributed to eusocial Hymenoptera NC-PJ-O2; (g) fossil insect wing print, NC-PJ-01. Copyright R. Garrouste. Scale bars a-d,f-g = 1 cm; e = 4 cm.

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