

On the origin of the Chrysomelid fauna of New Caledonia

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Abstract. The Chrysomelid fauna of the archipelago of New Caledonia is disharmonious in comparison with the fauna of other Gondwanan landmasses. This is true also for many insect groups there. Some subfamilies, like Sagrinae, are missing, while they are present in Australia, and even in Madagascar. Lamprosomatinae, on the other hand, are present in New Caledonia, though they seem missing in Australia. As compared to New Zealand, New Caledonian fauna seems richer in the total number of subfamilies, but a little poorer in the total number of species. Many subfamilies are little represented, such as are Chrysomelinae with a unique genus, *Zira*, a mountain form, which seems to have South American connections. New Caledonia possesses a few real Gondwanan relics, but also, when dealing with Chrysomelidae, it has more modern forms, which have been populated passively (or introduced intentionally by man) through recent arrivals from Indonesia and neighbouring countries. Cassidinae are practically represented by one or two species and are very rare. Native Hispinae are almost restricted to monocots, mostly Palmae; many of them remain to be described. Eumolpinae, including the archaic Spilopyrini and the recent arrivals, are the most diversified subfamily in the archipelago.

Keywords. Gondwana, tectonics, dispersal, vicariance, Drake Passage, *Nothofagus*.

1. Introduction

This communication is preliminary to a catalogue of the Chrysomelidae of New Caledonia, currently under preparation by the senior author and C. Mille. We present here some of the data in the catalogue. It is evident that many new species remain to be described, mostly among the Eumolpinae, Galerucinae and Alticinae. New Hispinae may also be found on various monocots. In spite of continued efforts the catalogue will remain incomplete, and many synonyms will have to be cleared. Actually Ron Beenen in Holland, Matthias Schöller, in Berlin; Maurizio Biondi in Roma and Alan Samuelson in Honolulu are studying some genera or

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subfamilies. The catalogue will give a provisional idea of the chrysomelid fauna of the archipelago. Pioneers, such as Xavier Montrouzier, Benoit Perroud, Albert Fauvel, have studied the lowland chrysomelids of New Caledonia. They will be mentioned along with more recent entomologists, such as J. Linsley Gressitt, in the extensive bibliography of the catalogue, when printed. They are being cited at some places in this communication.

2. Material and methods

Four recent trips of the senior author to New Caledonia have allowed leaf beetle collecting in the plains and over the central mountains. Routine collecting is also done by local entomologists under the direction of Christian Mille, in IAC in Pocquereux, using light traps, Malaise traps and other interception traps.

A few native leaf beetles feed on low plants, like Criocerinae on orchids or some Galerucinae-Alticinae. Most of the Eumolpinae, as many other beetles in New Caledonia, are tree dwellers and may be collected by beating the branches of trees. They are relatively polyphagous, but Spilopyrini and many other species seem to feed mainly on Myrtaceae. *Zira nitens* (Chrysomelinae) is strictly restricted to trees of the family Myodocarpaceae, formerly Araliaceae.

3. Geology

The geology of New Caledonia is extremely complex. New Caledonia emerged on a ridge situated between the Australian continent and the eastern active island arc (Solomon, Vanuatu, Tonga, Kermadec) (Paris 1981). As traditionally seen, Gondwanaland was a supercontinent, by break up of which arose, at the end of Palaeozoic, South America, Africa, Australia, India, Madagascar, Antarctica, and part of New Zealand and New Caledonia. New Caledonia was accreted to the east Gondwana margin in the latest Jurassic times (Cluzel *et al.* 1994). Breaking up of Gondwana at the beginning of Mesozoic led to the present distribution of the emerged lands in the Southern hemisphere. According to Sanmartin (2002), India began to drift away from Australia-Antarctica 165 Myr ago and a bit earlier Madagascar and India broke away from Africa. The separation of Africa and South America began in the early Cretaceous (–121 Myr). During all the Mesozoic (–210 to –65 Myr) there were periods of submergence and periods of emergence, and during this time some land connections existed with Gondwanan lands of Australia, Antarctica, New Guinea, and New Zealand. The marine transgressions in New Caledonia were then stopped by the orogenesis of the Cretaceous (Anonymous 1992, Picard 1999; Paris 1981). During all the Cretaceous up to Middle Eocene basaltic flows were frequent. It is at the end of the Eocene (–37 Myr) that the peridotites (nickel ore) appeared. During the Oligocene, a regression appeared, then a partial (some say a total) submergence occurred. During Miocene there were instances of partial submergence. The discrete islands of Lord Howe and Norfolk (McLoughlin 2001) have some

insects in common with New Caledonia (*Dematochroma*, for instance). They are not elements of Gondwana s. str. Their colonization by chrysomelines was probably passive. Hooker (1853) and more recently Brundin (1965) believe that Antarctica during the Mesozoic formed a part of a temperate austral centre of evolution. According to Poole and Gottwald (2001), Antarctica provided a biotic gateway between East and West Gondwana.

The microcontinent of New Caledonia is a patchwork of continental terrains and ophiolites formed at different periods (Cluzel *et al.* 1994). Although the relationships between New Caledonia and the neighbouring lands or islands are not clear, during the Cretaceous the main island was a shaky part of Gondwana. It is evident that, as in New Zealand, a total submergence in the Oligocene is unthinkable (Waters and Craw 2006; Murienne *et al.* 2005). Some plants, such as *Nothofagus* and the insects Spilopyrini are witnesses of an old distribution. Both vicariance and dispersal played a role in the current distributional patterns of *Nothofagus* (Cook and Crisp 2004; Hill 1992; Heads 2006a and b; Swenson *et al.* 2001), and the last paper (Swenson *et al.*) evokes some form of an ancient land link between New Caledonia and New Zealand. It is definite that, after the break up of Gondwana, speciation occurred from primitive common stocks. Several recent papers (Richier de Forges *et al.* 1998; Sanmartin 2002; Sanmartin and Ronquist 2004) suggest a very old dispersal of the biota. Heads and Craw (2004) refer to the great differences among geologists as to how much land of NZ was in existence in the Oligocene. The same is true for New Caledonia where at least high peaks must have kept part of the land fauna and the flora during the marine transgressions. The Chatham Islands, separated from New Zealand since the late Cretaceous (Emberson 1995, 1998), have a beetle fauna closely related to New Zealand, but this does not hold true for leaf beetles, except for *Chaetocnema moriori* Samuelson, which is related to a Southern Island species. There are weevils (Curculionidae) in the subantarctic islands but no chrysomelids, except a doubtful case in the Falkland. New Guinea is made out of the northern part of the Australia craton (Heads 2006a), and it is not surprising to see there also some Spilopyrini, related to New Caledonian and Australian ones.

Until opening of the Drake Passage at Eocene-Oligocene (–30 to –28 Myr), Antarctica had a temperate climate and a deciduous forest (*Nothofagus*, Lauraceae, Winteraceae, Podocarpaceae, and Proteaceae). According to some authors it happened –41 Myr (Sanmartin 2002; Sanmartin and Ronquist 2004), and there was simultaneous opening of the Tasmanian Gateway upstream (Kerr 2006). That led to the Antarctic glaciation and the destruction of that extraordinary centre of Gondwanian diversity. Some authors (Clarke *et al.* 2005) place the occurrence of the Antarctic Circumpolar Current and the separation of Australia from Antarctica at –25 Myr. However, according to Isabel Sanmartin (*loc. cit.*), it is possible that forests of *Nothofagus* and others still existed along the Atlantic coast of Antarctica until early Pliocene (fossil evidence). According to Knapp *et al.* (2005), Gondwanian relationships with *Nothofagus* extend back into the Cretaceous era. Transoceanic

distribution of species seems almost inconceivable in view of that *Nothofagus* seeds are poorly suited for dispersal across oceans. However, dispersal and vicariance can be both considered in this context. As for *Agathis*, the interpretation remains complex. Gunneraceae have also mostly a Gondwanan distribution, and are present in Africa, Hawaii and Malaysia, even if missing in Australia (except Tasmania) and New Caledonia (Wanntorp *et al.* 2003, 2004). Probably passive distribution (Cook and Crisp 2004) through dispersal and extinction of certain forms are also involved in the development of such a biogeography, but the plant shows certainly an Antarctic pattern.

It is evident that the total submergence of New Zealand (McGlone 2005; Waters and Craw 2006; Murienne *et al.* 2005), at the Oligocene, advocated by certain geologists, is a hardly acceptable choice. There are colleagues (Pole 1994; Macphail 1997; Winkworth *et al.* 2002) who tend to believe that the entire forest-flora of New Zealand arrived by long-distance dispersal, and some authors are not far from saying the same for New Caledonia. How was a passive recolonisation at the Miocene possible for animals and plants through the seas, particularly in the case of Rhynchocephalia (*Sphenodon*), already extinct elsewhere in the Eocene? Fresh water fishes could be hardly reintroduced by birds, and moas could not fly back with their wing stumps. Also a total submergence in the Oligocene could not fit with the existence of several living fossils among the insects, as the Spilopyrini in New Caledonia. McLoughlin (2001) thinks that they continued to exist during the Oligocene, in places such as small islands, formed by peaks of mountains, projecting above the level of submergence, where land animal and plant survival was possible. Some living fossils, among the Chrysomelidae, have been found in New Caledonia over the mountains or at middle altitudes, *e.g.* *Zira nitens* and *Bohumiljania* spp. (Reid and Smith 2004; Jolivet *et al.* 2003, 2005). Both seem related to some South American genera. Some authors (Marshall and Coetzee 2000) are in favour of a Gondwanan origin for a continental mite genus, *Maudheimia*. They believe in an in situ post-Gondwanan speciation.

4. Biology and distribution

The abundance of species remains at a peak during the months of January-February, during the Austral summer and after the first rains. However, there are some beetles available almost throughout the year. Some species seem to present two generations annually, and it is highly probable that there are years of abundance for some species and also years of scarcity, specially over the mountains. Not all the central and northern mountains have been explored, and there must still be some more missing and unrecorded forms among the Gondwanan stock.

It is certain that New Caledonia and New Zealand have disharmonious fauna as compared to the fauna of neighbouring lands of the Gondwanan origin, due to the Oligocene partial submergence, which probably destroyed a great part of the Mesozoic stock. Rather curiously, the biology of the beetles is different in New Caledonia

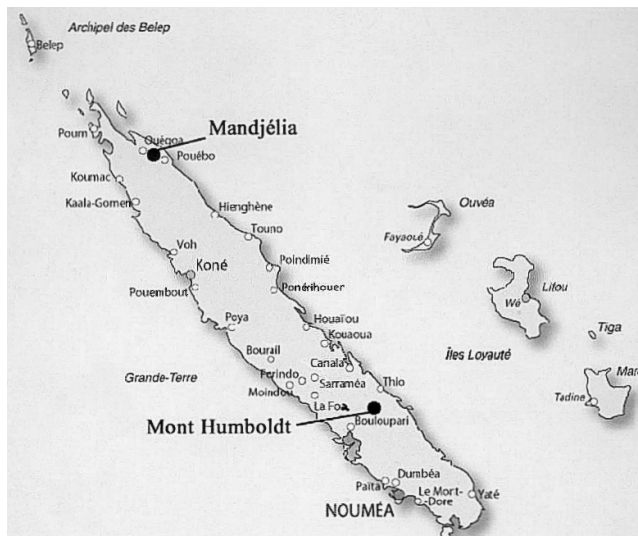


Figure 1. Map of New Caledonia (from Jolivet *et al.* 2005)

and New Zealand. Most of the Eumolpinae, the Lamprosomatinae (missing in Australia), and many Galerucinae and Alticinae, in New Caledonia, frequent the trees. In New Zealand, according to LeSage (pers. comm.), leaf beetles are found in unusual places, often at the foot of the plants or in the understory vegetation (Kuschel, 1990).

Criocerinae, which are missing in New Zealand, are found along the coast in New Caledonia, from Nouméa to Bourail and around Canala on the East coast. Also they have been captured over small mountains (Mt Do). They all feed on various orchids, such as *Erioxis rigida* (Reichenbach fil.). There are two or three species of *Stethopachys*, one described from Lifu. Their affinities are with their Australian counterparts, and the species are endemic to New Caledonia.

Recently, specimens of another subfamily, in common with Australia, the Zeugophorinae (Mauro Daccordi, pers. comm.) have been collected at low altitudes in New Caledonia (Col d'Amieu) and in Île des Pins (Schöller, pers. com.).

Cryptocephalinae are also interesting and endemic to the NC archipelago. *Scaphodius* seems endemic. *Ditropidus* has Australian affinities, and other genera have to be studied and reclassified.

Lamprosomatinae, dropping from leaves and epiphytes, belong at least to two species of *Oomorphus*, with Indo-Malaysian affinities. Curiously, Lamprosomatinae, which are missing in Australia and in New Zealand, have not yet been collected in Malaysia (Mohamedsaid, 2004).

Eumolpinae are numerous and varied (Jolivet *et al.* 2005, 2007a and b; Verma & Jolivet 2006), and many remain to be named and recorded. Primitive ones (Spilopyrini), with Patagonian affinities are represented by two species of the genus *Bohumiljanina*. One of them, *B. humboldti*, is exclusively found in higher altitudes on Mt. Humboldt (Fig. 1). Both feed on various Myrtaceae. One modern eumolpine (*Cazeresia montana* Jolivet *et al.* 2005) lives in mountainous areas and feeds on

Dracophyllum involucreatum (Epacridaceae). There are five or six additional advanced genera, including *Dematochroma* and *Taophila*, which are often found on local or imported fruit trees; they are all polyphagous in the adult stage. However, larvae are root feeders, but the larvae of Spilopyrini are partly borers in the first instar, and thereafter they become exposed feeders on the leaves; pupation occurs in the soil. Jolivet *et al.* (2007a and b) have been adding several new species to Eumolpinae. *Dematochroma* is also present in Lord Howe and Norfolk islands on the eastern side of Australia (Jolivet *et al.* 2006). A recent study, not including some of the New Caledonian genera (Gomez-Zurita *et al.* 2005), deals with a general classification of the Eumolpinae.

So far, only one native Chrysomelinae has been found, *Zira nitens* Reid and Smith. *Chalcolampra octodecimpunctata* (Fabricius) and *Chrysophtharta cloelia* Stål have been imported, the first one feeding on *Vitex* spp., the second on *Eucalyptus* spp.

Ron Beenen in The Netherlands studies New Caledonian Galerucinae, which are not much varied. *Aulacophora* and *Monolepta* dominate, the first live mostly on plants of Cucurbitaceae, and the second on various crops and vegetables.

Alticinae of NC have been studied by Alan Samuelson, who has cleared much confusion, since many eumolpines had been confused with alticines. Some other genera, such as *Arsipoda* are of Australian origin. Others, such as *Argopistes*, an oleacean feeder, are of uncertain affinities. Thirteen other genera are cosmopolitan, having come from the neighbouring landmasses, and, some, such as *Chaetocnema confinis*, being very small and light bodied, can be easily transported by wind for long distances. Their diet is varied, but some are relatively monophagous on Brassicaceae, Convolvulaceae, Solanaceae, Onagraceae, etc.

The Hispinae, present in New Caledonia, belong to oceanic groups (Gressitt, 1960), but some are endemic (*Caledonispa*). The fauna is rather rich, not related to Australian forms, but closer to those in the Solomons and New Guinea. The main host plants are Palmaceae, but are also found on Pandanaceae, Cyperaceae and Orchidaceae, all monocots.

There is only one (or perhaps two) Cassidinae (*Aspidimorpha*) in NC, the rest of the subfamily missing as are the Hispinae in New Zealand. The New Caledonian *Aspidimorpha* feed on Convolvulaceae like all other species of the genus.

There are ten chrysomelid subfamilies (Zeugophorinae, Criocerinae, Cryptocephalinae, Lamprosomatinae, Eumolpinae, Chrysomelinae, Galerucinae, Alticinae, Hispinae and Cassidinae) represented in New Caledonia, while there are only four in New Zealand (Cryptocephalinae, Eumolpinae, Chrysomelinae, Galerucinae). In both the archipelagos, NC and NZ, the archaic or advanced Sagrinae are missing, although they are well represented in Australia. There are five endemic genera of Chrysomelinae in New Zealand, while there is only one in New Caledonia. The New Zealander ones are small species, but *Zira* in New Caledonia is a large species. Eumolpinae (four genera in New Zealand) are much more numerous in New Caledonia, where they are divided into two groups, the Spilopyrini (Spilopyrinae for Reid), Gondwanan and primitive, and the rest, which are advanced

eumolpines, coming from the common eumolpine fauna in Australia, Western Pacific and Indonesia. *Dematochroma*, a genus which has its center of differentiation in New Caledonia, is also represented in Lord Howe and Norfolk islands (Jolivet et al 2006) and in Timor (*Dematochroma timorensis* Jacoby) (Jacoby 1894; Mohamedsaid submitted). That means that the genus must have a much wider distribution and must be present also at least in the Solomons and Vanuatu. In New Caledonia and New Zealand, little is known about the host plants of the species. It is easier to find them in New Caledonia where beetles are found on plants or on the trees. In New Zealand, the common localization of beetles at the foot of the plants, which situation renders it more difficult to identify the host. However, Kuschel (1990) has identified quite a lot of plants, and progress, in this direction could be made rapidly in New Caledonia. The total numbers of genera and species are well known in New Zealand, but discovery of many new forms is expected in New Caledonia. Four species are imported into New Caledonia, whereas there are many more migrant species in New Zealand.

Reid and Leschen (2004) estimate the total number of Chrysomelidae known in New Zealand to be 151, including, among the Chrysomelidae s. str., 15 exotics and 20 undescribed ones. We estimate the actual number of Chrysomelidae in New Caledonia to be around 120 species, including around 20 undescribed Eumolpinae and Galerucinae and four exotics. The New Zealand fauna is richer, despite the missing subfamilies, due to local differentiation of certain chrysomeline, galerucine and eumolpine genera. This is a very common phenomenon in isolated areas due to absence of much competition and predation. Classical examples of this are the great differentiation of the Paropsini in Australia, and of *Cratopus* in the Mascareignes, to quote a few examples. In New Zealand the Chrysomelinae are represented only by Phyllochari(t)ini, and, in New Caledonia, only one genus is present, *Zira* (Reid and Smith 2004), which probably belongs to Dicranosternini, with a possible neotropical connection.

In New Caledonia, new findings are expected, mostly among Eumolpinae, Galerucinae and Hispinae. The diversity of Eumolpinae is great and a few new genera remain to be described.

It is evident that, as in New Zealand, for plants and insects, dispersal is a continuing process (Reid and Leschen 2004). Some authors, like Pole (1994) consider the possibility of entirely long-distance dispersal for the flora. This view is in fashion now for plants and animals, as a consequence of suggestion of the so called Oligocene submergence of some archipelagos of the Western Pacific. That part of the flora and fauna was eliminated is a possibility, but some Gondwanan elements might have survived on emergent areas and probably radiated later on in the Miocene. Actually the native phanerogamic flora of New Caledonia is estimated to consist of 2973 species, including 2363 endemics (Jaffré 1993). Morat *et al.* (1986) question the positive influence of the ultrabasic substrates on the floristic richness and on the conservation of archaic ancestral components. On ultramafic rocks, as well as on metamorphic mountain groups, chrysomeline endemics are numerous

and, in contrast with several polyphagous eumolpine species, most of them seem to be restricted to a plant or to a family of plants. The abundance of leaf beetles seems to be seasonal (maximum in January-February), but there seem to be also years when the beetles are more abundant, that is probably linked to rainfall or other climatic influences. As shown in the paper by Richier de Forges *et al.* (1998), the Gondwanan influence appears unquestionable in New Caledonia as well as in New Zealand.

5. Discussion

The presence of some archaic forms in one land of Gondwanan origin and their absence from another may be due to two reasons: (1) they may have become extinct in one land, either due to being a losing contender in selection against later arriving more modern forms, or due to habitat loss, while they continue to survive in the other land, (2) they may have arrived by dispersal from a nearby Gondwanan land, after a period of submergence, but have not reached another land of similar origin.

Recently it has been suggested that New Zealand was fully submerged during the Oligocene (Campbell and Landis 2003; McGlone 2005). A similar suggestion has been made for New Caledonia too. Imagining complete 'drowning' of these landmasses attempts have been made to explain their biogeography through passive marine dispersal, and the Gondwana Hypothesis has been challenged (Waters and Craw 2006). Before accepting these views some very difficult questions have to be answered satisfactorily, (i) If vicariance biogeography is rejected, how is it that such Gondwanan forms as Metatheria, Ratitae birds, Pleurodire turtles, Dipnoi lung fishes, Spilopyrini, Sagraeae, the fern *Glossopteris* and many others mostly could not reach lands of Laurasian origin through marine passive dispersal? Of course ostriches could enter the Arabian part of Asia and opossums could reach some states of USA, but their dispersal has been through land bridges, and not across seas, (ii) Rhynchocephalia (which include *Sphenodon* of New Zealand) became extinct elsewhere after the Triassic. How could *Sphenodon* could arrive in NZ by passive marine dispersal after recovery of the landmass from the Oligocene submergence (Fig. 2)?

Waters and Craw (2006) say that the evidences in favour of complete submergence of NZ are not conclusive. It is very likely that during the Oligocene submergence of NZ and NC peaks of mountains remained above sea level, making survival possible for the Gondwanan land forms. Supporting this possibility is that in New Caledonia *Bohumiljania* (Eumolpinae, Spilopyrini) and the chrysomeline *Zira*, both resembling certain South American genera, occur on mountains and at middle altitudes. Noonan and Chippindale (2006) have studied molecular phylogeny of boid snakes (Boidae) and found that the evolutionary history of the group "is the result of several vicariant and dispersal events... associated with the fragmentation of the Gondwanan supercontinent". Boas survived in all Loyalty islands, which are supposed to be entirely volcanic.

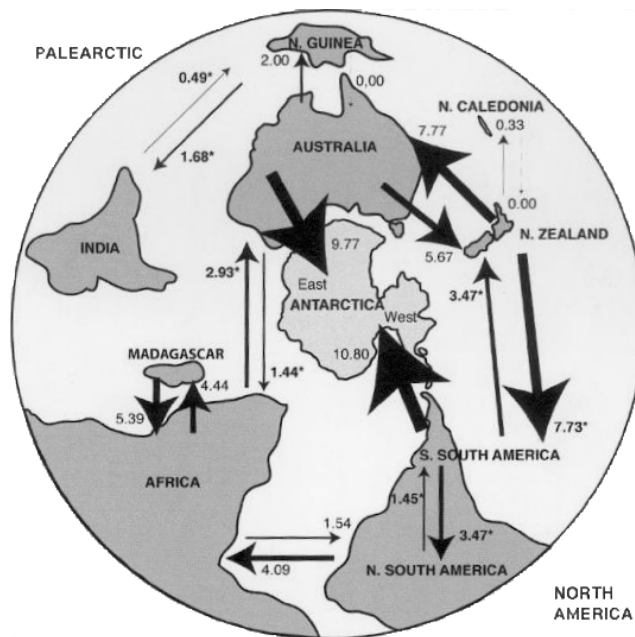


Figure 2. Polar view of the Southern hemisphere in the late Cretaceous – early Tertiary, showing dispersal of animals just before the partial submersion of New Caledonia and New Zealand during the Oligocene. It seems that New Zealand was also partially connected (small arrow) a certain time with New Caledonia. Plants show a similar plan of dispersion. (After Sanmartin and Ronquist 2004.)

Even if there are compelling geological evidences supporting the view of complete submergence of an island or an archipelago during the Oligocene, one should hesitate to use such revolutionary titles as ‘Goodbye Gondwana’, as the hypothesis concerns totality of landmasses of southern origin.

Acknowledgements

We are indebted to our friend Christian Mille, chief entomologist, in the Fruit Research Station of the IAC in Pocquereux and to his dynamic team. Without them we would never have been able to explore so efficiently the main island. Also we thank Dr. Isabel Sanmartin from the department of Systematic Zoology of Uppsala University, in Sweden, for her discussions about Gondwana, Dr. Michael Heads, from University of Fiji, also about Gondwana; Dr. Jerome Munzinger, from the MNHN, at IRD, Nouméa, who identified many host plants, Dr. Hervé Jourdan, entomologist at IRD, Nouméa, who allowed us to borrow material from his collection; Dr. G. Alan Samuelson, from Bishop Museum, in Honolulu, who helped us with the Alticinae.

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