

***Rhyncogonus* and *Laparocerus* (Coleoptera, Curculionidae, Entiminae), a parallel case of success in island evolution. Report of a study trip to Moorea, Tahiti and Rurutu.**

ANTONIO MACHADO

c/ Chopin 1, 38208 La Laguna, Tenerife, Spain
Email: antonio.machado@telefonica.net

MACHADO, A. (2007). *Rhyncogonus* and *Laparocerus* (Coleoptera, Curculionidae, Entiminae), a parallel case of success in island evolution. Report of a study trip to Moorea, Tahiti and Rurutu. *VIERAEA* 35: 61-76.

ABSTRACT: This is a report of a study trip to the islands of Moorea, Tahiti and Rurutu to compare the Polynesian weevil genus *Rhyncogonus* with the Macaronesian genus *Laparocerus*, in the Atlantic. Both genera have radiated in these archipelagos, and the species are flightless and mostly single-island endemics. The general geological and environmental conditions in both archipelagos are briefly discussed and snapshots of both groups of weevils are provided. Common features are highlighted (wingless, endemicity, etc.) as well as some differences observed (nocturnal versus diurnal activity, feeding amplitude, abundance, size, morphological diversity, etc.). Despite the richer ecological diversity of Macaronesia and the lack of competition in Polynesia, *Rhyncogonus* and *Laparocerus* can be considered as ecologically homologous. Both genera have succeeded in colonising their archipelagos, followed by intensive radiation. The concentration of endemics per island is higher in Polynesia congruent with its greater isolation. The highest species density in the Canaries is found in La Gomera, with 0.8 sp/km², while in Rurutu it is 0.12 sp/km². The record species density is achieved in *Rhyncogonus* on Rapa-Iti with 0.27 sp/km², this figure is further surpassed by the cryptorhynchine genus *Miocalles* with 1.67 sp/km² on that same island. A high number of closely related but well-differentiated species on a small isolated island could be explained as the product of repeated colonising events from a single source lineage (therefore, the monophyly), punctuated in time (punctuated allopatric speciation). Key-words: Macaronesia, Canary Islands, Rurutu, Tahiti, Moorea, Curculionidae, *Rhyncogonus*, *Laparocerus*, Speciation, Radiation, Endemism.

RESUMEN: El autor visitó las islas de Moorea, Tahiti y Rurutu para comparar el género polinésico de gorgojos *Rhyncogonus* con el género macaronésico *Laparocerus*, en el Atlántico. Ambos géneros han radiado en estos archipiélagos, y las especies son ápteras y en su mayoría endémicas de una sola isla. Se comentan las características geológicas y ambientales de ambos archipiélagos y se presenta una sinopsis de los dos géneros, destacándose los rasgos comunes (apterismo, endemidad, etc.) así como algunas diferencias observadas (hábitos nocturnos versus diurnos, amplitud alimenticia, abundancia, tamaño, diversidad morfológica, etc.). A pesar de la mayor diversidad ecológica de la Macaronesia y de la ausencia de competencia en la Polinesia, los *Rhyncogonus* y *Laparocerus* se pueden considerar como ecológicamente homólogos. Ambos géneros han tenido éxito en colonizar los archipiélagos, seguidos de una intensa radiación. La concentración de endemismos por isla es mayor en la Polinesia en coherencia con su mayor carácter oceánico. El valor más alto en Canarias se alcanza en La Gomera, con 0,8 sp/km², mientras que en Rurutu es de 0,12 sp/km². El record en *Rhyncogonus* se da en Rapa-Iti, con 0,27 sp/km², pero es superado en dicha isla por el género *Miocalles* con 1,67 sp/km². Un número alto de especies estrechamente emparentadas, pero bien diferenciadas, presentes en islas pequeñas y aisladas, puede explicarse como el producto de colonizaciones repetidas a partir de una misma y única fuente (de ahí la monofilia), pautadas en el tiempo (especiación alopatrídica pautada).

Palabras clave: Macaronesia, Islas Canarias, Rurutu, Tahiti, Moorea, Curculionidae, *Rhyncogonus*, *Laparocerus*, especiación, radiación, endemismos.

INTRODUCTION

In Curculio (volume 50, March 2005) the featured researcher was Elin Claridge, a doctoral student of the University of California, Berkeley. I read about her research project on broad-nosed weevils in the genus *Rhyncogonus* Sharp, 1885 which occur on the Pacific Islands. Her interest was focused on the systematics and phylogeny of an island diversified group. To study evolution on oceanic islands is commonplace for many entomologists. In my case, I started a similar research project in 1999, on *Laparocerus* Schönherr, 1834 from Macaronesia (Azores, Madeira, Selvagens, and Canary Islands), in the Atlantic.

Obviously, I was very excited to learn of a analogous project being developed on islands in the antipodes and based on similar biological matter: broad-nosed weevils. Claridge (op.cit.) enumerated several striking reasons for her interest in *Rhyncogonus*: (1) it has successfully colonized some of the remotest oceanic islands in the world, despite being an atypical island colonist -species tend to be large, always flightless and generally slow moving, with soil-dwelling larvae, (2) species within the genus are almost exclusively single-island endemics, and are often restricted to a single valley or mountain top, (3) many islands have multiple endemic species. These circumstances can basically be applied *mutatis mutandi* to *Laparocerus*.

The opportunity of contrasting one's own experiences and ideas with another equivalent case is a very strong incentive for any scientist. Claridge has not yet published her results, nor have I finished mine. Thus, the only possibility was to discuss opinions directly with her and to see *Laparocerus'* partner-group *in natura*: an opportunity to compare! Are *Rhyncogonus* ecologically homologous to *Laparocerus*? How do they occupy the habitats? Are they nocturnal and abundant? Do they feed on specific plants or are they polyphagous? Are they monophyletic within each island? Has she found much variability in the mitochondrial genes sequences?... The array of intriguing questions was unbearable and it did not take long until I succumbed to temptation. Having financial support for my studies from the Fundación Biodiversidad (Madrid), I established contact with Elin Claridge, based in Moorea, and organised a short visit to French Polynesia in December 2005, a suitable collecting period. Needless to say, I thank the internet for existing.

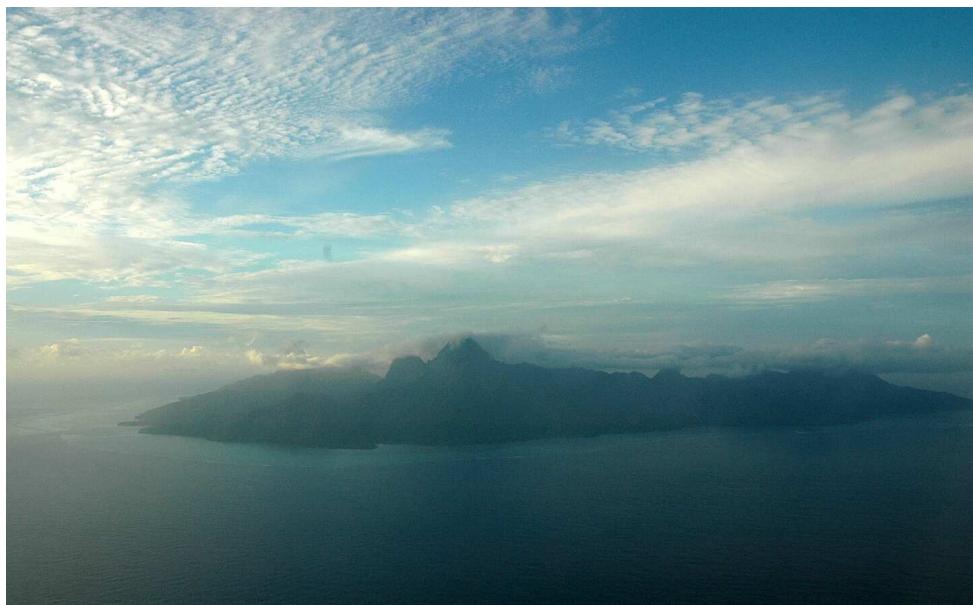


Figure 2. Island of Moorea (Polynesia). The highest point is Mount Tohiea (1,207 m).

The trip

The 30th of November 2005, after a 20,300 km flight departing from my home in the Canaries, I landed on Moorea with a delay of two days after being blocked in Paris to solve unexpected passport requirements for the US stop-over at Los Angeles.

As my departure was planned for the 12th of December, I decided to visit just two of the bigger islands: Tahiti (1,042 km², altitude 2,241 m) and Moorea (200 km², altitude 1,207 m), and the 600 km distant Rurutu (32.3 km²), which is quite small and not so elevated (altitude 422 m), but interesting as it is very isolated and has 4 species of *Rhyncogonus* (Gillespie et al. 2002). I spent my first three days in Moorea, using the facilities of the Richard B. Gump South Pacific Research Station of the University of California, which is the base-camp for Elin Claridge and a very convenient place to

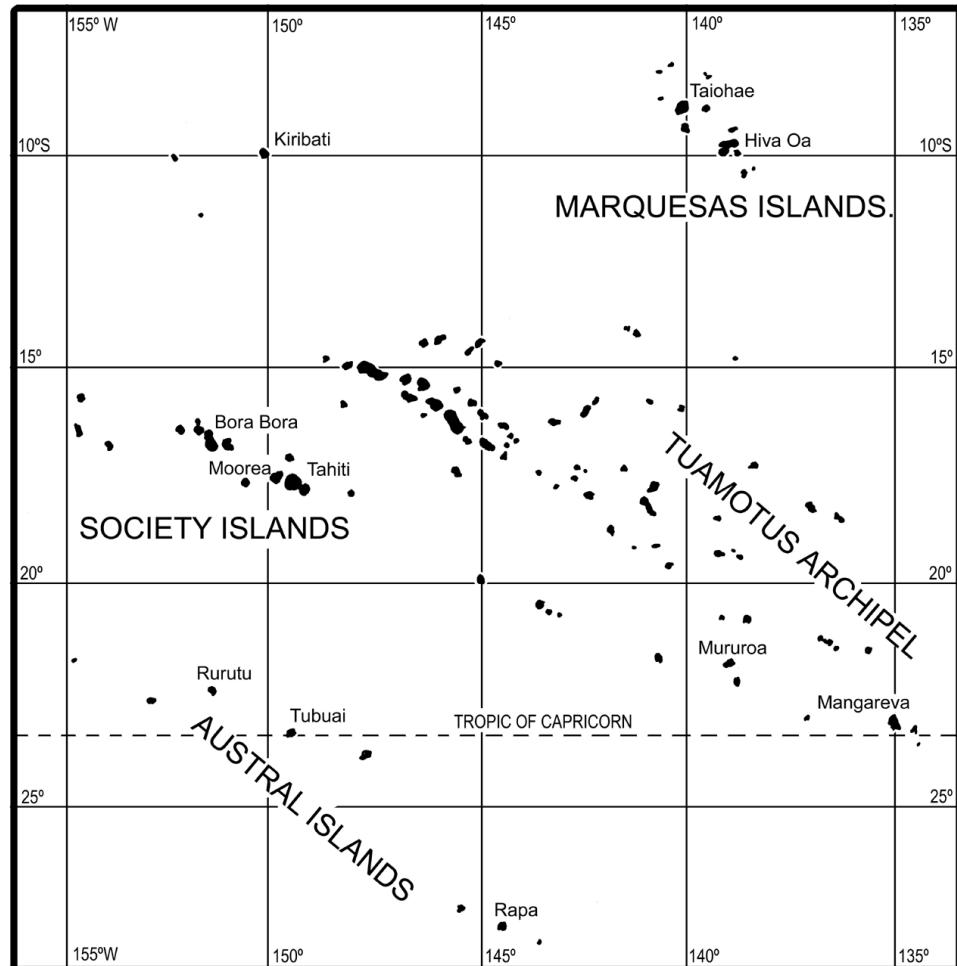


Figure 1. Map of Polynesia

stay and work. Three more days were dedicated to the island complex Tahiti/Tahiti-iti (two tangent volcanic islands), and for the last four days I enjoyed the hospitality of Elin's partner Viriamu Teuruarii, staying at Pension Teautamatea in Rurutu, a dreamy place far away from the world and well-traveled tourist routes. Here, I would like to express my deep gratitude to both of them.

MACARONESIA VERSUS FRENCH POLYNESIA

The differences between both groups of islands are considerable. Macaronesia –in geographical terms– comprises five volcanic archipelagos in the Northern hemisphere, distributed in the East Atlantic from parallel 40°N to parallel 15°N: Azores, Madeira,

Salvages, the Canaries, and the Cape Verde. In all, there are 41 islands with a total surface of ca. 14,600 km². Only the Cape Verdes are located within the tropical belt, below the Tropic of Cancer (no *Laparocerus* present). The geological age spans from 1 to 26 myrs, and the shortest distance to continental land is found at Fuerteventura (Canaries), 110 km from Africa; the most distant is Flores (Azores) 1,600 km from Europe and 4,000 km from North America (Báez & Sánchez-Pinto, 1983). Except for the 12 small islets, all the other islands are inhabited (> 2,600,000 people in total). Tenerife, in the Canaries, is the largest island with 2,034 km² surface and 3,716 m altitude.

French Polynesia includes 118 oceanic islands –volcanic high islands and atolls– scattered between the Equator and the Tropic of Capricorn (latitudes 7°S – 27°S) in the middle of the Pacific. With a total terrestrial surface of 3,660 km², only six islands are larger than 100 km² and 76 are inhabited. They are grouped in four archipelagos: The Society Islands (with Bora-Bora, Tahiti and Moorea), the Marquesas to the North, the Australs southwards, and the large chain of 77 atolls known as the Tuamotus eastwards. Tahiti, the largest island, is situated at 5,000 km distance from Australia and 6,500 km from Chile. Age varies from very young seamounts to the oldest steps of the hot-spot island chain, atolls which can be considerably more than 20 my old in the Tuamotus. The present population of French Polynesia is ca. 240,000 inhabitants (Rogers et al. 2003).

The environmental diversity in Polynesia is low when compared with Macaronesia. Vegetation in the atolls is very uniform (with no *Rhyncogonuss* present), and in the higher islands it grades from (1) sand-belt plants and trees, (2) a lowland tropical forest which has been completely destroyed and supplanted by gardens, cultivations and introduced species, and (3) a mountain subtropical forest, with a slightly dryer version and a very humid typical cloud forest¹. Rainfall is normally high, less from West (4,000 mm in Tahiti) to East (2,500 mm in Rurutu), with the rainy season running basically from October to February. There is no big temperature contrast between wet and dry seasons (Tahiti, coastal average 27°C).

In the Canaries –to choose the most eco-diverse archipelago from Macaronesia– one can find raw lava and ash fields (volcanism is still active), sand dunes, desert vegetation (< 100 mm, irregular rainfall), sub-desert shrub vegetation with cactus-like plants, thermophilous Mediterranean forest (mostly destroyed), laurel forest (an evergreen cloud-

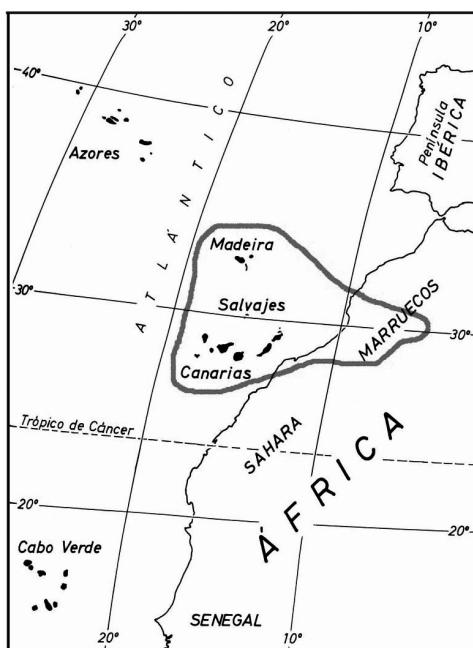


Figure 3. Map of Macaronesia showing the distribution of *Laparocerus*

¹ For a more detailed account of vegetation, see Mueller-Dombois & Fosberg (1998).



Figure 4. Mountains of Anaga in Tenerife (Canary Islands), 11 myrs old area and regional hotspot of biodiversity. It is the home of 15 species of *Laparocerus*.



Figure 5. Tahiti. *Left:* inaccessible mountain slopes in the interior. *Right:* the author collecting during the day on a ridge of Mount Marau, Tahiti, c.1,400 m (Photo Claridge).

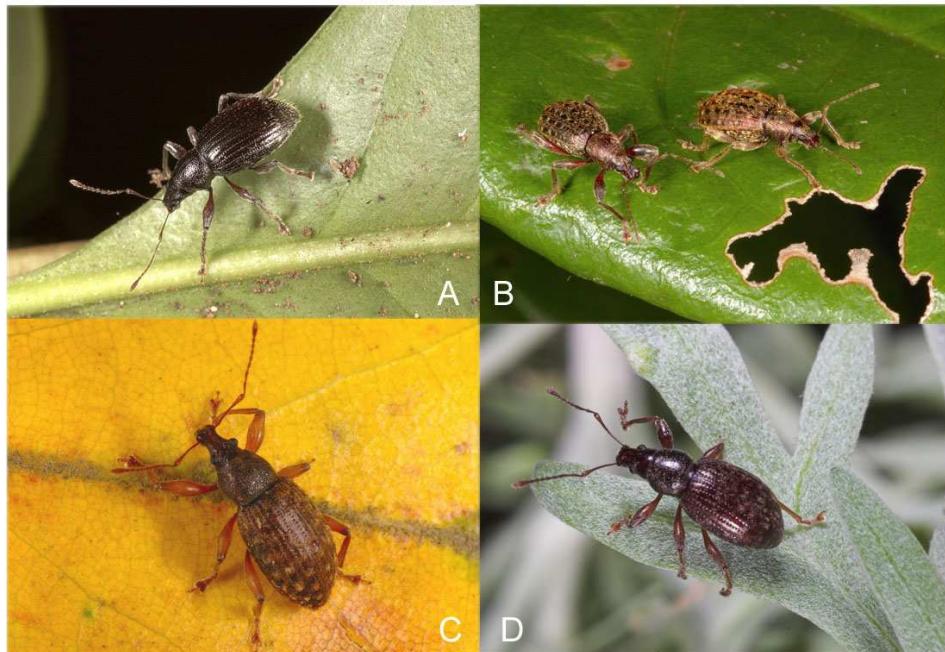


Figure 6. **A:** *Laparocerus grossepunctatus*, from Tenerife. **B:** *Laparocerus lamellipes*, from Madeira. **C:** *Laparocerus clavatus*, from Madeira, and **D:** *Laparocerus humeralis*, from La Gomera.

forest), pine forests, and a high-mountain scrub vegetation adapted to coldness and snowfall. Obviously, the Cape Verde have a more arid climate, while in the Azores the high latitude and oceanic rainfall influence is notorious (average rainfall 2,700 mm in São Miguel), the lofty elevations being dominated by *Sphagnum* mats. The seasons are much more marked, according to common temperate Mediterranean climate patterns.

In spite of being in the tropical realm, French Polynesia stands out for the disharmony of its flora (many plant families are absent), a circumstance that is directly linked to colonisation and the enormous distance to source continental areas. The depauperacy of the fauna is equivalent, lacking native representatives of several groups (bats, amphibians, reptiles, many insect families, etc.). In contrast, Macaronesia shows a much less oceanic character, particularly the Canaries, whose biota could hardly be termed as “truly-oceanic”. Conversely, in relative terms the level of endemism is higher in Polynesia. For instance, from a total of 65 breeding bird species, 10 are endemic to the Societies, 3 to the Australs and 13 more recorded as extinct (Fontaine et al. 1999), while in Macaronesia, from a total of some 100 breeding bird species, only 15 count as endemic (v. Clarke, 2006).

Another important difference between Macaronesia and French Polynesia is the amount of knowledge. The Macaronesian archipelagos are reasonably well prospected regarding their fauna and flora. Detailed geological and vegetation maps, comprehensive lists of all biota, etc. have been produced long ago and are regularly updated and improved. By comparison French Polynesia is very poorly studied. The one and only partial vegetation map can be found in the *Atlas de la Polynésie*

française, published by ORSTOM (1993) and it is at a large scale, though the Delegation de la Recherche is currently in the process of producing new and more comprehensive maps. Several groups, mainly invertebrates (i.e. parasitic Hymenoptera, Diptera Brachycera, micro-lepidoptera), are practically unknown (Paulian, 1998). Most of the work that has been carried out on the entomofauna has been part of the ongoing Pacific Biological Survey (PBS), which includes French Polynesia, and is mainly financed by the Bishop Museum of Hawaii (v. Englund, 2004). A current project, directed by Rosemary Gillespie at the University of California, Berkeley, coordinated by Elin Claridge at the Gump Station and financed by the National Science Foundation, USA, is an inventory of terrestrial arthropods in French Polynesia.

Perhaps, the inaccessibility of the interiors of some of the larger high islands – particularly the mountain tops – may partially explain the limited knowledge amassed. The population and agriculture in Moorea or Tahiti, for instance, is concentrated in the coastal and valley lowlands, as the mounting slopes above 100-200 m are void of human occupation, primarily because they are so precipitous and unsuitable for development. The roads and other infrastructures are very scarce or totally absent in the interior of the high islands. Consequently, the natural vegetation in the lowlands has been completely transformed and supplanted by cultivation or garden species, while the interior remains practically untouched, which is nothing comparable to the situation in the heavily-populated Macaronesian islands.

One would expect the inaccessible areas of the island interiors to be completely or quite natural, but this is not the case, thus contrasting with homologous inaccessible regions in Macaronesia. In the latter islands exotic species tend to be linked to human-made and altered environments; and invasive aliens –where present– are few and not so aggressively intruding into the natural environments. Surely linked to the strongly disharmonic biota of Polynesia, I observed a heavier impact of invasive aliens in the islands visited. In remote places one can easily find *Micconia calvescens* (the worst!), *Tecomia stans*, Malayan apple trees, guava trees, Gabon tulip trees, shampoo ginger, and the like, having been spread by birds or free-ranging domestic animals. Most of the insects that I casually collected in the forest were exotics! All the land birds in Rurutu are introduced, while the native birds have presumably disappeared. In other words, the “invisibility” of the Polynesian ecosystems seems to be much greater than in Macaronesia, and invasive species become more aggressive.

A snapshot of *Rhyncogonus*

“Weevils in the genus *Rhyncogonus* occur exclusively on oceanic islands in the Pacific, with a distribution that extends north-westwards from Pitcairn Island to Hawaii and Wake Island. All but one of the 127 described species in the genus are restricted to single island, though multiple species often occur on any one island” (Claridge & Roderick, 2001). In Hawaii there are 47 known species (Samuelson, 2003), and in French Polynesia 60, and to that add 16 new species discovered by Claridge (Marquesas 22, Society 16+13, Austral 22+3).

She is working in her molecular studies with both mitochondrial (COI, 12S, and 16S) and nuclear markers (EF). The group is monophyletic, but the individual archipelago faunas are not, and two or three different lineages may be coexisting on an island or

within a habitat. For instance, different lineages that share ancestry with the Cook Island and Hawaii are present in Tahiti. Tahiti is the largest island in French Polynesia (1,042 km², age 12.5 myrs) and has the largest number of species (14 spp.) with a density of 0.01 species per km². Undoubtedly a thorough survey of mountain tops in Tahiti (probably helicopter assisted) would increase these figures, but island-size and number of species does not always correlate positively, as generally thought. Rurutu, with only 32,3 km² has 4 species of *Rhyncogonus* (density 0.12 sp/km²), and Rapa-Iti, with 40 km² and 5 myrs age (Jarrad & Clague, 1977) bears the outstanding number of 11 species. This density of 0.27 sp/km² is a record in *Rhyncogonus*, but this figure is greatly exceeded by another weevil genus, *Miocalles* Pascoe, 1883 (Cryptorhynchinae), with 67 endemic species in Rapa! (Paulay, 1985). This is a density –if true– difficult to conceive (1.67 sp./km²). In Macaronesia, in *Laparocerus*, the highest species density is achieved on the island of La Gomera, with 0.08 sp./km².

A snapshot of *Laparocerus*

Laparocerus is the most diverse genus in Macaronesia. It is restricted to Madeira, Selvagens and the Canary Islands, with one species (probably a back-colonization) in northwest Morocco, facing the Canaries. They are not present in the Cape Verde islands and *Laparocerus* known from the Azores have been revealed to be an independent genus: *Drouetius* Méquignon, 1942. Conversely, the species of *Lichenophagus* Wollaston, 1854 described from Madeira and the Canaries fall within the monophyletic Madeiran and Canarian clades of *Laparocerus*, respectively. The systematic revision of the type material of previously described species concluded with 105 valid taxa, but additional 22 new species are pending publication, and another set, perhaps even larger, is in the pipeline. I cannot yet give exact figures of the final number of species, as the study is still ongoing.

Table I. Collecting results

- Rhyncogonus* sp. Moorea: Moputa 350 m, 2-12-2005, 3 exx.
- Rhyncogonus opacipennis*. Moorea: Moputa 350 m, 2-12-2005, 6 exx.
- Rhyncogonus nigroaeneus*. Tahiti: Plateau de Taravao, 500 m, 4-12-2005, 14 exx.
- Rhyncogonus tuberosus*. Tahiti: Mount Marau, 1400 m, 5-12-2005, 2 exx.
- Rhyncogonus testudineus*. Tahiti: Mount Marau, 1400 m, 5-12-2005, 11 exx.
- Rhyncogonus ventralis*. Tahiti: Mount Marau, 1400 m, 5-12-2005, 12 exx.
- Rhyncogonus corvinus*. Tahiti: Mount Marau, 1200 m, 5-12-2005, 6 exx.
- Rhyncogonus tenebrosus*. Rurutu: Plateau de Tetuanui, 220 m, 8-12-2005, 3 exx.
- Rhyncogonus excavatus*. Rurutu: Plateau de Tetuanui, 220 m, 8-12-2005, 25 exx.
- Rhyncogonus tenebrosus*. Rurutu: Mount Erai, 250 m, 10-12-2005, 5 exx.
- Rhyncogonus debilis*. Rurutu: Mount Erai, 250 m, 10-12-2005, 15 exx.

The first is a new species discovered by E. Claridge, the rest were described by Van Dyke (1937) based on material collected in 1934 by the Mangarevan Expedition of Bernice P. Bishop Museum.

Most *Laparocerus* species and subspecies are single-island endemics, but a few are present in two or three nearby islands. *Rassen-* and *Arten-Kreise* (superspecies) are common in this genus. Most phenological groups have been genetically delimited and, at



Figure 7. **A:** *Rhyncogonus corvinus* (Tahiti), feeding. **B:** *Rhyncogonus debilis* (Rurutu). **C:** *Rhyncogonus tenebrosus* (Rurutu), copulating. **D:** *Rhyncogonus opacipennis* (Moorea). **E:** *Rhyncogonus* sp. (Moorea). **F:** *Rhyncogonus nigroaeneus* (Tahiti). **G:** *Rhyncogonus excavatus* (Rurutu). **H:** *Rhyncogonus ventralis* (Tahiti).

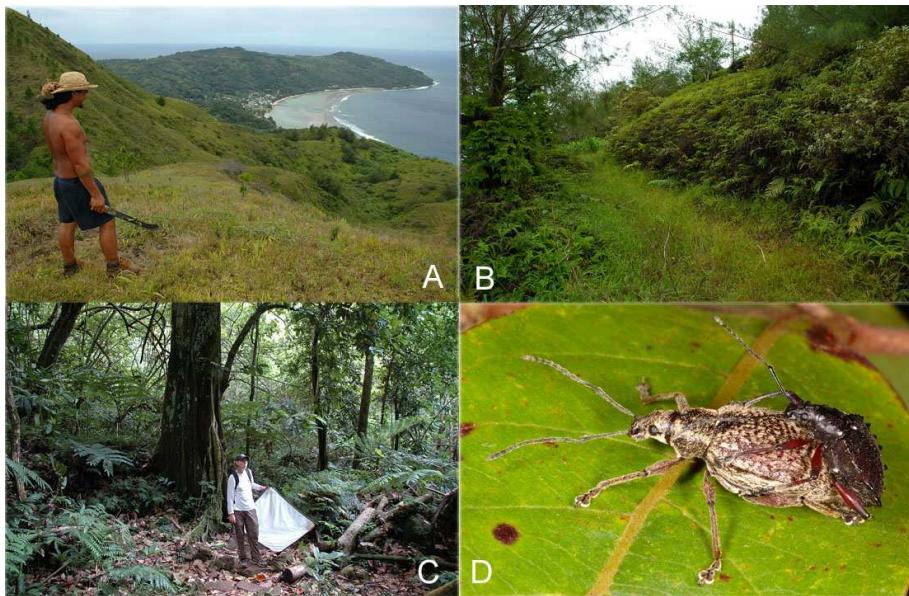


Figure 8. **A:** Island of Rurutu, view to the south end. **B:** Rurutu, habitat of *Rhyncogonus debilis*, at Mount Erai. **C:** Mountain forest at Belvedere (Moorea), with Elin Claridge. **D:** *Rhyncogonus tuberosus* from Tahiti, copulating. Notice the sex difference.

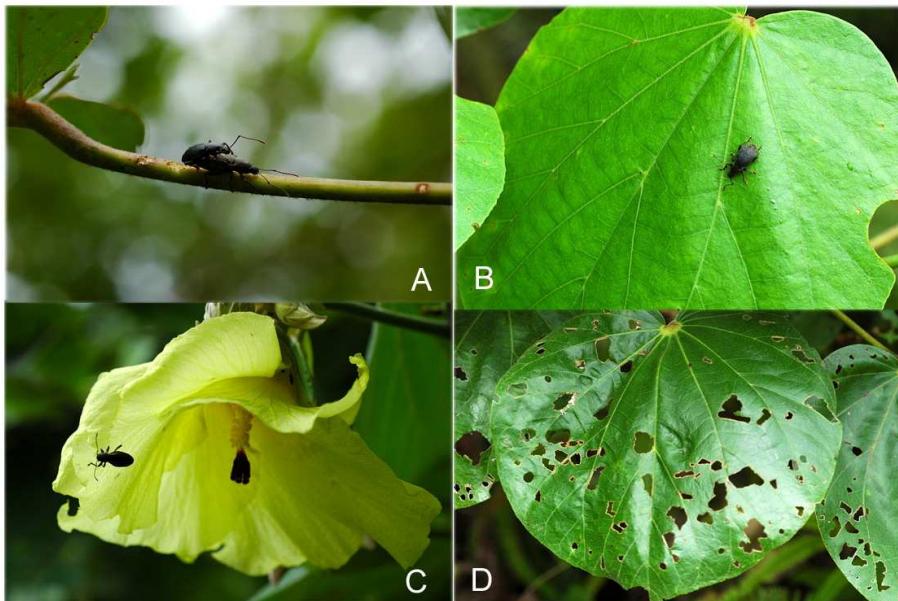


Figure 9. *Rhyncogonus excavatus* active at daylight on *Hibiscus tiliaceus*. **A:** copulating, **B:** resting on a leave, and **C:** feeding on the flowers.— **D:** Feeding marks on the leaves made by another insect, not by *Rhyncogonus*.

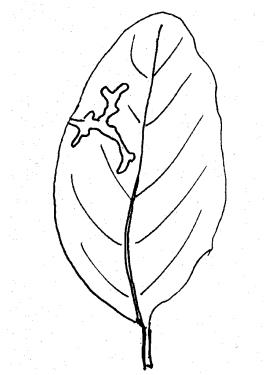
present, I am struggling with the high systematics (how these groups are related). The molecular studies are being developed in collaboration with Mariano Hernández and his team, from the University of La Laguna, and are based on two mitochondrial markers (COII and RNA16S), partially complemented with the nuclear elongation factor. Variability in COII is very high as expected for an old group, and phenetic differentiation is not always accompanied by greater genetic distances. It will be fantastic to compare results with those of Claridge, once concluded.

IMPRESSIONS (NOT CONCLUSIONS)

During my short stay in French Polynesia I did collect only ten *Rhyncogonus* species (Table I), and this was thanks to Elin Claridge's guidance. With such scarce material and a few observations, one cannot derive much science, hence what follows are by no means to be considered conclusions. I noticed that Claridge is more genetic-oriented in her approach, and I am more naturalistic. Perhaps some of the impressions here expressed may help stimulate further research.

- In Polynesia, *Rhyncogonus* is replacing (vicariance?) the Melanesian genus *Elytrurus* Boisdouval, 1835, which usually has widely-distributed species, highly variable, and rarely single-island endemic. In Macaronesia, *Laparocerus* is playing the ecological role of *Otiorhynchus* Schönherr, 1826 (a non-related genus) in Europe and North-Africa. The few *Otiorhynchus* species in Macaronesia are introduced and rarely in natural habitats, at least in Madeira and the Canaries. *Rhyncogonus* and *Laparocerus* are not directly related, but they have been fully successful in colonizing oceanic islands, and can be considered ecologically homologous in their respective archipelagos.
- *Rhyncogonus* species seem to be all climbing leaf-eaters, while *Laparocerus* show a greater ecological spectrum. The majority are leaf-eaters, but there are a few ground-detritivores (leaf-litter), blind cavernicole species (feeding on roots), and, at least, three eu-edaphic species (to be described). This circumstance is coherent with the richer ecological diversity offered by Macaronesia. In Porto Santo (Madeira), there is even a beach species, *L. mendax*, dwelling in sand and feeding on *Tamarix*.

- *Rhyncogonus* species are on average larger (8-30 mm) than *Laparocerus* species (3-20 mm), which is a normal tropical trend. The standard body shape is less modified in *Rhyncogonus* than in *Laparocerus*, where the morphological adaptations to different ways of life are evident, particularly in subgenus *Lichenophagus* or in blind species. Curiously, the presence of emergent nodules on the elytra of *R. tuberosus* and *R. nodosus* have their counterpart in *Laparocerus mateui*. The usefulness of such structures is still a mystery to me.



- There is not much published information on the biology or phenology of *Rhyncogonus* in French Polynesia. Elin Claridge commented that she has found adults active almost all year around. In *Laparocerus*, there are clear phenological patterns, varying with altitude and, to some extent, with latitude. In low-land arid habitats, for instance, *Laparocerus* have a short 2-3 months winter-centred activity period; in the laurel forest one can find species active all year around, and in the upper mountains, activity shifts towards summer like in Madeira's forests (v. Machado & Aguiar, 2006). In general, *Laparocerus* are only active during the night, and that is not the case with *Rhyncogonus*. I collected adults by day as well as by night (in Hawaii they are basically nocturnal, *fide* Samuelson, 2003). It seems they do not fear predation. In Rurutu I was astonished by the behaviour of *R. excavatus* which does not drop quickly from the leaves when touched (it walks away), as is the normal case with weevils; and is surely the case of the *Rhyncogonus* species collected on Tahiti and Moorea. Surprisingly, when mounting my specimens, I observed bite predation-marks (an introduced rodent?) on the pronotum of one *R. excavatus*, and another on the tip of the abdomen of a *R. corvinus* specimen.
- *Laparocerus* species are, in general, oligophagous with clear preference for some plant genera, families or group of tree species. They rarely feed on introduced species. Of course, there are exceptions, and I have found a few *Laparocerus* occasionally accepting grapevines, apple trees, or chestnuts. There are also some apparently monophagous species, but, as said, this is not the rule. Therefore, I was surprised to find *Rhyncogonus* as happy on aliens as on native plants, even in natural habitats. They seem to be clearly more polyphagous, a good colonising strategy, but contradicting the putative adaptive radiation as well as their absence in the lowland-areas, at least of Tahiti and Moorea (not in Rurutu), where the native vegetation has been practically replaced by exotics (Saquet, 1996).
- More striking for me was the low abundance of the *Rhyncogonus* species, in comparison with *Laparocerus*, of which a few hours night collecting could easily give several hundred specimens, if so desired. Elin Claridge confirms that this is the case, isolated individuals or just groups in patchy distribution, with no apparent explanation why they are not in-between, if the vegetation does not change. In the Canaries or Madeira it is very easy to detect the presence of *Laparocerus* by their feeding marks on the leaves (v. Machado 2003). In the laurel forest, for instance, it is hard to find a single untouched tree. In Polynesia, the leaves of plants and trees are generally not damaged or scarcely damaged by herbivores, something remarkable taking in account the huge biomass available. Is it all processed by fungi on the ground? A conspicuous exception is the abundant tree *Hibiscus tiliaceus*. The broad leaves are riddled with small irregular holes (Fig 8 D). Van Dyke (1937 p. 117) includes a photograph of a *Piper* leaf with the same pattern attributing the damage to *Rhyncogonus excavatus*. As *Laparocerus* –and other Entiminae I know– always start feeding leaves at the border and never in the interior, I carried out a little experiment. I cut out several squares of *Hibiscus* and placed them in a jar with ten specimens of *R. excavatus* for two days. All feeding marks started at the border and none from the interior. I do not know the agent causing the riddled pattern on *Hibiscus*

and *Piper* leaves, as at the time of my visit it was not present. Attached is a sketch from my field book of the typical socks-like digitiform marks, in this case, of *Rhyncogonus aeneotinctus* on *Cinchonia pubescens* leaves. It could well have been made by a *Laparocerus*.

- Another possible explanation for the low abundance of *Rhyncogonus* could be a lower fertility. *Laparocerus* species lay many eggs (30-60) and are small. I opened the abdomen of three females of *R. excavatus* and found none, five and seven large eggs. This is a small sample that concludes nothing, but a question that merits study. I also noticed that the last two ventrites in the females' abdomens are soft and not sclerotised, like in *Laparocerus*. This may be related to a different egg-laying practice. Entiminae are known to have free ground dwelling larvae that feed on roots. *Laparocerus* lay their eggs directly in the ground. In Hawaii, *R. extraneus* and *R. blackburni* place clusters of 2-12 eggs on the plants; upon hatching in 8-15 days the larvae drop to the ground (Swezey in Samuelson, 2003), but Elin Claridge (pers. comm.) has found females from Marquesan species with muddy tidemarks on their abdomens, consistent with laying into the soil.
- I also found several acari (Trombidiformes) in the space between the elytra and the soft integuments of the abdomen. In *Laparocerus* this type of parasitic acari is always exposed, attached to the external integuments.

Some thoughts on island evolution

To complete this report, I want to share some thoughts on island evolution. Both *Rhyncogonus* and *Laparocerus* have been referred to as paradigmatic cases of explosive radiation on oceanic islands. It is clear to me that an original lineage colonising simultaneously (star-shape phylogeny!) or step-wise the several island of an archipelago, can produce a set of monophyletic vicariant species (geographical speciation). The striking question is the presence of many closely-related species in some single islands, and often, living together. This has been interpreted as (1) an adaptive radiation event by the splitting of the original lineage into different niches, (2) allopatric (geographic) speciation in ecologically isolated regions within the island, and (3) populations differentiated during isolation by temporary barriers (usually lava flows) that fall in secondary sympatry when the barrier disappears (*kipukas*, for instance, see Zimmerman, 2001). In comparison with French Polynesia, we have older island in the Atlantic with a more complex geological history that could have favoured allopatric intra-island speciation (case 2 and 3) as well as differentiated habitats driving adaptive radiation (case 1). However, the intra-island speciation in *Rhyncogonus* –i.e. 4 species in Rurutu, 11 in Rapa– is markedly higher when related to the size and ecological diversity of these islands. This fact could have been favoured by less competition (no other important leaf-eater groups), but is contradicted by the fewer ecological niches available. If there are not so many habitats to adapt to, how can these species swarms build, particularly on rather small islands? The case of *Miocalles* in Rapa (67 endemic species!) is unparalleled, and perhaps as their larvae are endophytic, one could expect strict plant-species counter-adaptations, in the sense of Ricklefs & Cox (1978). But the figures are still too high, and this hypothesis is surely not valid for *Rhyncogonus*, which are by far more generalists.

One plausible explanation is the following. If we have a small isolated island and it receives a few colonising individuals (founder effect), genetic drift could be a factor that favours a speedy differentiation. If the same source lineage colonises a second time, after a sufficiently long interval (favoured by distance) the newcomers may not interbreed with the already differentiated local population, and even force more differentiation as usually happens with secondary sympatry (competition?), or just simply produce redundancy. Genetic drift will still be acting. If a third colonising event happens, the speciation process could be repeated and so on, up to a theoretical saturation (?). The final result is a set of closely related but well-differentiated species that could be (and have been) interpreted as one single radiation case, but that in reality they are the product of repeated colonising events from a single source lineage (therefore, the monophyly), punctuated in time. One would expect such a process –that could be termed punctuated allopatric speciation– to happen the smaller the island is (to some extent), and the longer the distance from the one source area. Rapa and Rurutu fit the profile.

ACKNOWLEDGEMENTS

I wish to express my appreciation once more to Elin Claridge (U.C. Berkeley) for her invaluable assistance during my stay in Polynesia, for fruitful discussions on *Rhyncogonus*, and for revising this report. My thanks also to Marnie Knuth for checking the text in English, and to the Fundación Biodiversidad (Madrid) for financing this study trip.

REFERENCES

- BÁEZ, M. & SÁNCHEZ-PINTO, M. (1983). *Islas de fuego y agua. Canarias, Azores, Madeira, Salvajes, Cabo Verde. Macaronesia*. Edirca S.L., Santa Cruz de Tenerife. 182 pp
- CLARKE, T. (2006). Birds of the Atlantic islands. Christopher Helm, London, 368 pp.
- CLARIDGE, E. & RODERICK, G.K. 2001. *Rhyncogonus* weevils of the Pacific islands. *Online:* http://esa.confex.com/esa/2001/techprogram/paper_2340.htm
- ENGLUND, R.A. (2004). Report for the 2003 Pacific Biological Survey, Bishop Museum Austral Islands, French Polynesia Expedition to Tubuai and Rurutu. Bishop Museum, Honolulu 29 pp. [Contribution No. 2004-001 to the Pacific Biological Survey]
- FONTAINE, P. ET AL. (1999). *Manu. Les oiseaux de Polynésie*. Manu Société d'Ornithologie de Polynésie française, Papeete. 63 pp.
- GILLESPIE, R.G., RODERICK, G.K., CLARIDGE, E. & GARB, J. (2002). Spiders, beetles, landhoppers & flies: Expedition to Austral islands. University of California.
- JARRARD, R. V. & CLAGUE, D.A. (1977). Implications of Pacific islands and seamount ages for the order of volcanic chains. *Review of Geophysics and Space Physics* 15: 57-66.
- MACHADO, A. (2003). Sobre el método de colectar *Laparocerus* Schönherr, 1834 y el reconocimiento de sus marcas en las hojas (Coleoptera, Curculionidae). *Vieraea*, 31: 407-420.

- MACHADO, A. & AGUIAR, A. (2005). Phenology of *Laparocerus* species in Tenerife, Canary Islands (Coleoptera, Curculionidae). *Boletim do Museu Municipal do Funchal*, 56 (314: 5-21).
- MUELLER-DOMBOIS, D. & FOSBERG, F.R. (1998). *Vegetation of the tropical Pacific islands*. Springer Verlag, New York, 733 pp.
- PAULAY, G. (1985). Adaptive radiation on an isolated oceanic island: the Cryptorhynchinae (Curculionidae) of Rapa revisited. *Biological Journal of the Linnean Society* 26: 95-187.
- PAULIAN, R. (1998). *Les insectes de Tahiti*. Société Nouvelle des Éditions Boubée, Paris. 331 pp.
- ROGERS, H., CARILLET, J-B. & WHEELER, T. (2003). *Tahiti & French Polynesia*. Lonely Planet Publications, Melbourne, 288 p. 6th edition.
- RICKLEFS, R.E. & COX, G.W. (1972). Taxon cycles in the West Indian avifauna. *The American Naturalist*, 106: 195-219.
- SAQUET, J-L. (1996). *Flore de Tahiti*. Polymages, Papeete, 128 pp.
- SAMUELSON, G.A., (2003). *Review of Rhyncogonus of the Hawaiian Islands (Coleoptera: Curculionidae)*. Bishop Museum Press, Honolulu. 107 pp.
- VAN DYKE, E.C., (1937). *Rhyncogonus of the Mangarevan Expedition. Occasional papers of Bernice P. Bishop Museum, Honolulu*, 13 (11): 89-129.
- ZIMMERMAN, E.C. (1948). *Insects of Hawaii. I. Introduction*. University of Hawaii Press, Honolulu. 205 pp [reissued 2001].