Molecular phylogeny of Pacific Island Colymbetinae: radiation of New Caledonian and Fijian species (Coleoptera, Dytiscidae)

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We present a molecular phylogeny and taxonomic review of the Pacific island colymbetine diving beetles, focusing on the Fijian and New Caledonian faunas. Four new species are described: *Rhantus monteithi* and *R. poellerbauerae* from New Caledonia, and *R. kini* and *R. bula* from Fiji. We also describe the 3rd instar larvae of *R. monteithi* and *R. poellerbauerae* spp. nov., assigned to adults using mtDNA sequence data and discuss larval characters in the light of phylogeny. The phylogenetic hypotheses derived from both parsimony and Bayesian inference based on 3508 aligned nucleotides from a combination of mitochondrial (*cox1*, *cob* and *rrnL-tRNALeu-Nad1*) and nuclear genes (18S rRNA and H3) reveal a clade comprising *R. novaecaledoniae*, *R. alutaceus*, *R. pseudopacificus*, *R. monteithi* sp. nov. and *R. poellerbauerae* sp. nov., which agrees with the *R. pacificus* group *sensu* Balke (1993). *Carabdytes upin* was included within this clade, possibly indicating paraphyly of the genus *Rhantus*. *Rhantus annectens*, *R. bacchusi*, *R. supranubicus*, *R. suturalis*, *R. simulans*, and the Palearctic *R. exsoletus*, *R. latitans* and *R. bistriatus* formed a clade corresponding to the *R. suturalis* group *sensu* Balke (2001). *Rhantus vitiensis*, previously assigned to the *R. pacificus* group, was included in the *R. suturalis* clade. We find some support for a scenario where the Pacific was colonized out of the Northern hemisphere only during the past *c.* 12 million years, rejecting a Gondwanan origin of the morphologically isolated endemics. The new species are all characterized by mtDNA haplotype clusters, the degree of divergence between sister species pairs ranging from 1.3 to 7%, while *R. novaecaledoniae* individuals from all over New Caledonia apparently form one morphospecies, with moderate genetic diversity (up to 2.3% mtDNA divergence between populations). The sisters *R. pollerbauerae* sp. nov. + *R. monteithi* sp. nov. occur sympatrically on Mont Panié but appear ecologically segregated, while the sisters *R. vitiensis* + *R. bula* sp. nov. were encountered syntopically on Viti Levu. Comparing genetic and morphological data of Fijian *Rhantus* and *Copelatus* diving beetles, we here show that even in island radiations it is not *per se* possible to know if mitochondrial DNA barcoding would perform well (*Rhantus*: YES, *Copelatus*: NO). At the same time we show that fixed cutoff values, as sometimes used to discriminate between barcodes, thus species, might be meaningless. We underpin the importance of morphology for sustainable exploration of global diversity.

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Introduction

The insect fauna of the Pacific islands (here defined as including New Guinea, Australia and New Zealand, i.e. roughly east of 110°E and west of the American coastline, but not including Japan) is of mainly Oriental or Laurasian origin (Gressitt 1974). Ever since Wallace and Darwin, the larger Pacific islands or archipelagos, such as New Guinea, New Caledonia, Hawaii and Galapagos, have inspired biogeographers and evolutionary biologists (e.g. van Oosterzee 1997). While the Pacific fauna becomes more and more filtered with increasing distance to the mainland, there are still spectacular examples of radiations on remote, even very small, islands. For example, Rapa Island, French Polynesia, is no larger than 40 km^2 yet is home to more than 60 species of the weevil genus *Miocalles* (Paulay 1985).

In this paper we focus on Dytiscidae, or diving beetles, of the subfamily Colymbetinae, which are widely distributed throughout the Pacific. Colymbetinae contains 10 genera (*c.* 130 species) world-wide (Nilsson 2001). Of these, two occur on Pacific islands: the monotypic New Guinea endemic genus *Carabdytes* Balke, Hendrich & Wewalka, 1992 and the cosmopolitan genus *Rhantus* Dejean, 1833 (97 spp.) (Balke 2001). These beetles are rather conspicuous owing to their size (*c.* 8–16 mm) and lively coloration. They occur in various kinds of freshwater habitats such as pools, streams and stream-related habitats (streampools, rockpools, etc.). Prior to this paper, *c.* 28 species of Colymbetinae were found to be mostly endemic to the Pacific Islands (see Appendix).

The Australo-Pacific members of genus *Rhantus* have recently been subdivided into the *R. suturalis*, *R. pacificus* and 'American' species-groups (Balke 1993, 1998, 2001; Peck & Balke 1993). Species of both the *R. suturalis* and the *R. pacificus* groups have been reported for New Caledonia and Fiji: *Rhantus suturalis* (W.S. MacLeay), *R. alutaceus* Fauvel and *R. novaecaledoniae* J. Balfour-Browne in New Caledonia; *R. annectens* Sharp and *R. vitiensis* J. Balfour-Browne in Fiji (Balke 1993). These records, however, are based on very few specimens and localities.

Despite intense previous collecting efforts and unbroken interest in the Pacific Island biota (notably the surveys initiated by J.L. Gressitt in the 1950s (Miller 1996), and the Fiji Arthropod Survey launched in 2005 (hbs.bishopmuseum.org/fiji/)), phylogenetic studies of Pacific island insects remain scarce, and hardly any molecular phylogenetic or phylogeographic work has been published to date. Exceptions include work by Foley *et al.* (1998) and Beebe & Cooper (2002) on Australoasian mosquitoes; Arensburger *et al.* (2004) on New Zealand cicadas; Murienne *et al.* (2005) on New Caledonian cockroaches; Filardi & Moyle (2005) on Pacific Monarchs, and Monaghan *et al.* (2006) on a large radiation of Fijian diving beetles in the genus *Copelatus*.

It is generally held that Pacific islands featuring some elevation and permanent aquatic ecosystems also house endemic species of Colymbetinae (Ramsdale & Balke 2006). This prompted our study of Colymbetinae in New Caledonia and Fiji, which are known to harbour a fairly diverse water beetle community (Balfour-Browne 1945). The objectives of this paper are: (1) to review the *Rhantus* fauna of New Caledonia and Fiji and to describe four new species (including the larvae of two of these) assisted by DNA sequence data; (2) to provide a molecular phylogeny of these beetles in an attempt to understand their evolutionary patterns. We also highlight two remarkable cases of syntopic occurrence of sister species.

Materials and methods

Abbreviations

Specimen depositories are as follows:

BMNH	Natural History Museum, London, UK
CHB	Coll. Hendrich, Berlin, Germany
CWW	Coll. Wewalka, Wien, Austria
IRSN	Institut Royale des Sciences Naturelles de Belgique, Brussels
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMW	Naturhistorisches Museum, Wien, Austria
QLDB	Queensland Museum, Brisbane, Australia

Collecting sites

In the French overseas area under special status, known as New Caledonia, we collected from localities all around the main island, or Grande Terre, which is in the text simply referred to as New Caledonia (Fig. 1A). In Fiji we managed to visit the main islands, Viti Levu, Vanua Levu, Kadavu and Taveuni; on each island we attempted to sample from as many localities as possible. Localities from which we took *Rhantus* are, as for New Caledonia, labelled according to the locality number (e.g. FI 08, NC 16) and a complete list is available upon request from M. Balke (Fig. 1B).

DNA sequencing

Genomic DNA was non-destructively extracted from individual beetles using the DNeasy tissue kit (Qiagen, Hilden, Germany). Three mtDNA and two nDNA gene regions were chosen to combine information from different gene loci. These genes for which extensive datasets already exist proved to be useful in previous studies of the Dytiscidae (e.g. Balke *et al.* 2004).

Using standard PCR protocols and double-stranded sequencing with PCR primers, we sequenced the 3′ ends of the *rrnL*, the entire tRNALeu and part of the 5′ of *Nad1* (primers 16Sar, ND1A: Simon *et al.* 1994), the 3′ end of cytochrome c oxidase 1 (UURL) and the 5′ end of cytochrome *c* oxidase 2 genes (partition *cox1-cox2*; *cox1* primers Pat, Jerry: Simon *et al.* 1994; *cox2* primers forward: George 5′-ATA CCT CGA CGT TAT TCA GA-3′ reverse: CO2F 5′-GCT CCA CAA ATT TCT GAG CA-3′), and a central fragment of cytochrome oxidase *b* (*cob*; primers CB3, CB4) (Barraclough *et al.* 1999). Nuclear gene fragments sequenced were the 5′ end of 18S rRNA (primers 18S 5′, 18S b5.0: Shull *et al.* 2001) and a fragment of histone 3 (H3; H3 AF- H3 AR: Colgan *et al.* 1998). Sequences were edited using the Sequencher 4.2 software package (GeneCodes Corp.) and were submitted to GenBank (accession numbers AM296116–AM396356).

DNA sequence analysis

Species from the Palearctic region were used as outgroups; trees were rooted using *Dytiscus dimidiatus* Bergsträsser, 1778,

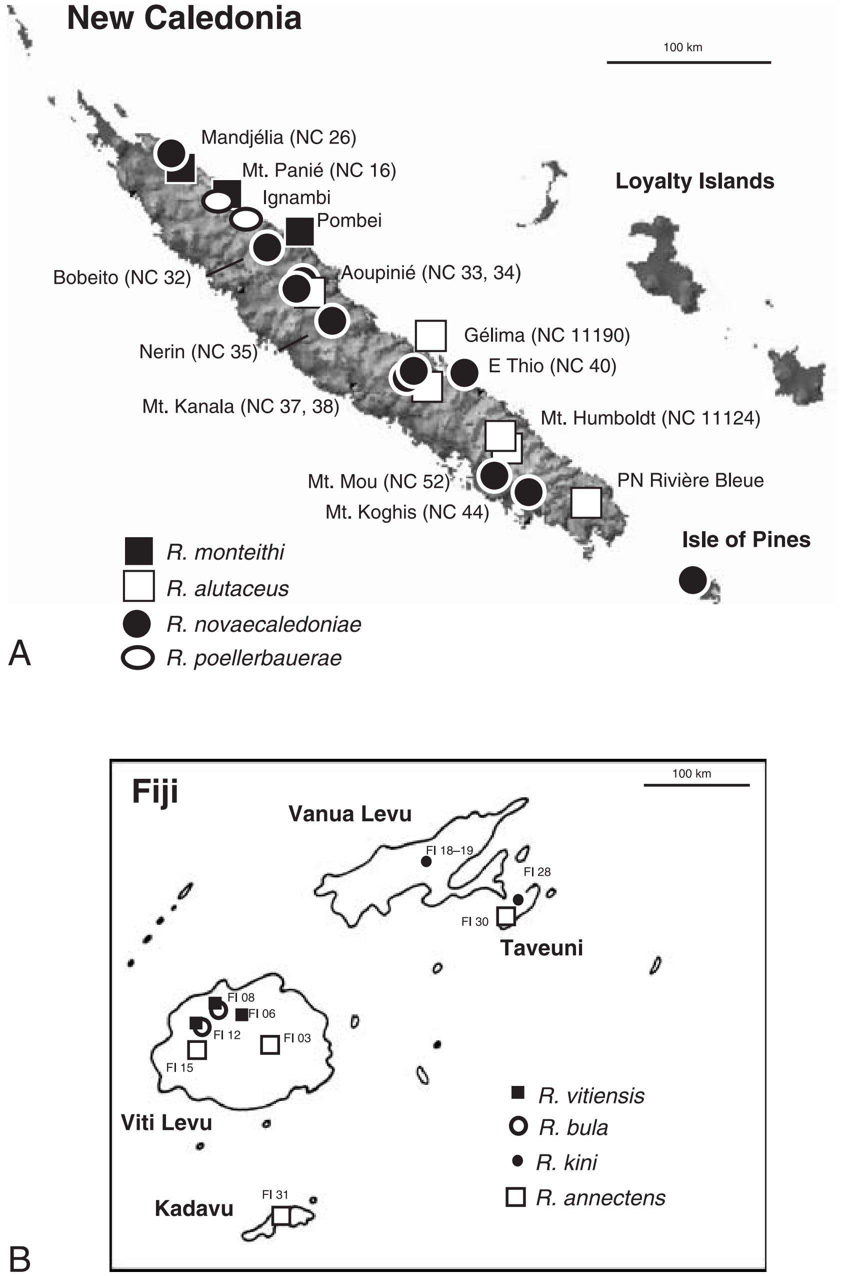

Fig. 1 A, B. Maps of —A. New Caledonia and —B. Fiji, indicating collecting localities.

a member of the subfamily Dytiscinae clearly outside the group of interest.

Alignment was conducted by eye, as the *rrnL* and 18S sequences were only slightly length-variable (see Results). Our main data matrix of 3508 aligned characters from 37 Colymbetinae and the outgroup individual was analysed running equally weighted parsimony searches with PAUP* version 4.0b10 (Swofford 2002) using TBR heuristic searches, 1000 random addition sequences, and gaps coded as a fifth character state (Giribet & Wheeler 1999).

Confidence in the topology found was estimated by calculating two widely-used measures of support: (1) bootstrapping, with 1000 pseudoreplicates and 100 random additions per pseudoreplicate (Felsenstein 1985); (2) branch support (Bremer 1988), established by searching on constrained trees generated with TreeRot (Sorenson 1996).

Bayesian analyses was conducted with MrBayes 3.04 (Huelsenbeck & Ronquist 2001), using GTR + I + G (the optimal model as estimated with Modeltest; Posada & Crandall 1998). We used the default priors starting with random trees and ran the three heated and one cold Markov chains for 5000 000 generations, sampled at intervals of 1000 generations. To determine the point at which the Markov chains reached stationarity, the log-likelihood scores were plotted against generation time and visually determined when the log-likelihood values reached a stable equilibrium. Trees (once burn-in samples were discarded, the first 100 000 generations) were combined in a single majority consensus topology and the percentage of the nodes were taken as *a posteriori* probabilities (Huelsenbeck & Ronquist 2001). We conducted two analyses: the first on the combined dataset, the second unlinking our user-defined partitions (= sequenced fragments), allowing for independent parameter evaluation during the analysis.

A likelihood ratio test (Felsenstein 1981) was used to test for compliance with a molecular clock. As the clock-behaviour of the data was significantly rejected, we used the penalized likelihood (PL) method of Sanderson (2002) to obtain an ultrametric tree, as implemented in the software program r8s (http://ginger.ucdavis.edu/r8s/), using the topology and branch lengths obtained in MrBayes (excluding outgroups). As there is no known fossil record of any of the included species, the analyses were run without temporal constraints, with an arbitrary age of the root of 100 time units. The smoothing parameter was determined by a process of cross-validation in a preliminary analysis using the truncated Newton (TN) method, and a second analysis was run with the smoothing parameter set to the optimal value obtained previously (Sanderson 2002).

Approximate calibration of absolute time was based on the standard insect molecular clock estimate of roughly 2% divergence per million years (Myr) for mtDNA (Brower 1994), corresponding to a base rate (per branch) of 0.01 substitutions/site/Myr. This calibration for a combination of mitochondrial genes has been used before in related lineages of beetles (Leys *et al.* 2003; Ribera *et al.* 2003; Ribera & Vogler 2004; Monaghan *et al.* 2006), and similar rates have been independently derived from dated vicariant events in other groups of Coleoptera (see Gómez-Zurita *et al.* 2000).

After analysis of the main matrix and detection of longer branches within what were first considered samples of the same species from Viti Levu, Taveuni Island and Vanua Levu, we sequenced the 3′ of *cox1* of nine additional specimens of *R. vitiensis sensu lato* from Viti Levu, the largest island of the Fiji archipelago to possibly detect additional clusters. A separate analysis including all Fijian specimens and two outgroups (*R. suturalis* and *R. simulans*) was conducted using *cox1* sequences only. This dataset includes 22 taxa and 752 characters; 20 of the specimens were from Fiji, of which four belong to *R. annectens* (see Fig. 5).

Larval analysis

The methods, terminology, and format of larval descriptions follow those of recent studies on larval morphology of the Colymbetinae (Alarie *et al.* 1998; Alarie & Larson 1998; Alarie & Balke 1999; Shaverdo 2003; Alarie & Wang 2004; Michat 2005; Alarie & Hughes 2006). Larval specimens of each species were disarticulated and mounted on standard glass slides with Hoyer's medium. Examination at magnifications of 80–800× was done using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. Voucher specimens are deposited in the research larval collection of Y.Alarie (Laurentian University, Department of Biology, Sudbury, Ontario, Canada). To ensure correct interpretation of some terms in the morphometric analysis, notes of explanation are provided (abbreviations, if used in the text, are given in parantheses):

Head length (HL): total head length including the frontoclypeus measured medially along the epicranial stem.
Head width (HW): maximum width measured posterior to the stemmata.
Length of frontoclypeus (FCL): from the apex of the nasal to the back of the ecdysial suture.
Occipital foramen width (OcW): maximum width measured along the dorsal margin of the occipital foramen.
Length of antenna (AL): derived by adding the length of each individual antennomere; comparison among antennomeres was made using the capital letter A with a number corresponding to the segment considered (e.g. A1 for antennomere 1); A3′ is used as an abbreviation for the lateral elongation of antennomere 3.
Length of maxillary palpus: derived by adding the length of each individual palpomere (e.g. MX1 for palpomere 1).
Length of maxillary galea (GalL): maximal length measured from the apex of the galea to the margin of the maxillary stipes (i.e. including the palpifer).
Length of maxillary stipes (StpL): maximal length of stipes measured along the outer margin.
Length of mandible (MndL): maximal length measured from the apex to the mandibular condyla.
Width of mandible (MndW): maximal width measured across the proximal portion of the mandible.
Length of labial palpus: derived by adding the length of each individual palpomere (e.g. LB1 for palpomere 1).
Length of legs: derived by adding the length of each individual segment including the longest claw; the length of each segment was taken at the longest point except for the trochanter which includes only the proximal portion (the length of the distal portion being included in the femoral length).

Dorsal length of last abdominal segment (LLAS): includes the whole sclerite measured dorsally along the mid-line from the anterior margin to the posterior margin; siphon refers to the dorsal prolongation of the eighth (= last) abdominal segment; the length of the siphon was determined by measuring the difference between the dorsal and ventral lengths of the segment.

Length of urogomphus (UROL): measured along the lateral margin.

Chaetotaxic analysis

Primary (observed in instar I) and secondary (added throughout the ontogenetic development) setae and pores were distinguished on the cephalic capsule, head appendages, legs, last abdominal segment, and urogomphi. The setae and pores are coded according to the systems proposed by Alarie (1995) for the legs, the last abdominal segment, and urogomphi, and by Alarie (1998) for the cephalic capsule and head appendages. Instar I larvae of the Colymbetinae may be characterized by the presence of a variable number of additional setae on some leg articles; these were included in the count of secondary setae. [Additional setae are primary setae which are not part of the ground-plan system of the Colymbetinae. In Colymbetinae, instar I may have a variable number of additional setae on some leg articles. In order to be able to discriminate additional from secondary setae, which are added through the ontogenetic development of the larva, one needs to have access to first instars. This was not possible in the context of our paper as we did not have first instar. On the other hand, the primary groundplan setae are consistent throughout the family (in opposition to variable for the additional setae); accordingly, they can be excluded from the count of secondary setae even in absence of first instar, as we know exactly how many are found on each leg article.]

Setae are coded by two capital letters corresponding to the first two letters of the name of the structure on which the seta is located (AN, antenna; CO, coxa; FE, femur; MX, maxilla; LA, labium; TA, tarsus; TI, tibia; TR, trochanter) and a number. Pores are coded in a similar manner except that the number is replaced by a lower case letter. The position of the sensilla is described by adding the following abbreviations: A, anterior; AV, anteroventral; D, dorsal; Di, distal; Pr, proximal; PV, posteroventral.

Results

Molecular phylogenetics and divergence

Length of 18S sequences ranged from 596 bp (*R. pseudopacificus*, *R. alutaceus*) to 605 bp (*Dytiscus*); that of *rrnL-Nad1* ranged from 770 bp (*Dytiscus*) to 774 (e.g. *R. novaecaledoniae*). There was a 16 bp insertion (GTTTAGTTTTCATTTC) in the *rrnL* sequence of all four *R. pseudopacificus* individuals sequenced (only one individual was used for the present analysis). The normalized Partitioned Bremer Support (PBS) (Table 2) reveals strong positive overall support from 18S (0.781), followed by *rrnL* (0.336), H3 (0.324), *cob* (0.198) and *cox1-cox2* (0.073).

The combined parsimony analysis of all 3508 aligned, equally weighted characters resulted in 52 trees (2630 steps, CI = 0.462 (without uninformative characters = 0.408), RI = 0.72). There were 688 parsimony informative charactesr and 216 parsimony uninformative variable characters. The phylogram of the first of these trees is shown in Fig. 2.

Bayesian analysis of unlinked partitions (Fig. 3) identified the same overall clades, but suggested subordination of *Colymbetes* within *Rhantus* as currently delineated. However, the backbone of the tree is not significantly supported (posterior probabilities less than 95%) and would, if collapsed, be principally compatible with the parsimony topology. Bayesian analysis of partitions not unlinked revealed the same overall topology, but did not retrieve a single clade for *Rhantus s.l.* (shown as node with 64% posterior probability in Fig. 3). Overall, magnitude of support was very similar in both analyses.

Rhantus novaecaledoniae, *R. alutaceus*, *R. pseudopacificus*, *R. monteithi*, and *R. poellerbauerae* formed a clade. The first three were previously placed in the '*Rhantus pacificus*' group of Balke (1993). Here, *Carabdytes upin* was also assigned to this clade in the combined parsimony analyses as well as the analysis of Protein Coding Genes (PCGs) only. It was, however, placed at the base of Colymbetini in the combined analysis excluding gapped characters (Fig. 4A,B).

Rhantus annectens, previously assigned to the *R. suturalis* group, grouped with *R. bacchusi*, *R. supranubicus*, *R. suturalis* and *R. simulans*, as predicted by Balke (1993, 2001); the Palearctic *R. exsoletus*, *R. latitans* and *R. bistriatus* which were also assigned to the *R. suturalis* group (Balke 2001). However, this clade also comprised *R. vitiensis*, previously assigned to the *R. pacificus* group. The latter grouping was also supported using only nDNA data (not shown).

Our study reveals comparably deep splits (marked with dots on the nodes in Figs 2 and 3) between the *R. vitiensis*-like specimens from Fiji (node 1) and the *R. novaecaledoniae*-like individuals from New Caledonia (node 3). Within the New Caledonian clade, *cox1* divergence was 2.8–3.2% at node 4 compared to 4.2–6.2% at node 3. In the Fijian clade, *cox1* divergence was 7.0–8.1% at node 1.

A separate analysis of 20 Fijian specimens (752 bp *cox1*, rooted in *R. simulans* and *R. suturalis*) revealed four trees of 236 steps (CI = 0.75, RI = 0.8806). The phylogram resulting from these trees is shown in Fig. 5 (first tree chosen). In addition to the break found between specimens from the smaller islands of Taveuni + Vanua Levu and Viti Levu (i.e. node 1, Fig. 2), an additional, shallower break was found between specimens from Viti Levu (i.e. node 2, Fig. 2), with a divergence of 1.4–1.9%. The haplotype clusters here interpreted as species were the same in all trees found, and were also present in the strict consensus tree; differences involved the grouping of individuals within the clusters.

The divergences depicted above were confirmed *a posteriori* by a morphological analysis, which led to the description of four new species: *R. monteithi* and *R. poellerbauerae* from New

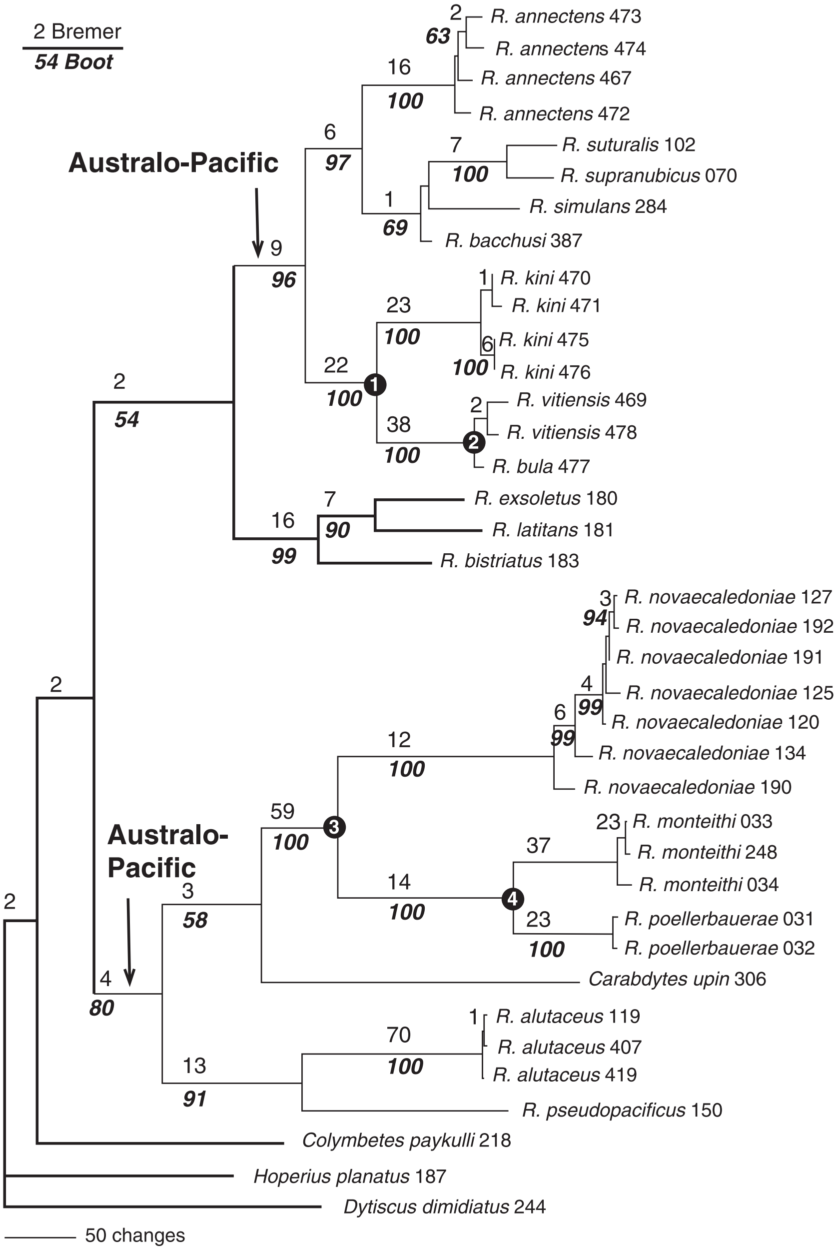

Fig. 2 The first of the 52 most parsimonious trees found running PAUP* (2630 steps, CI = 0.462, RI = 0.72) and using the complete dataset. Thin branches lead to Australo-Pacific species. Nodes labelled 1–4 are explained in the text; they mark clusters which include the new species named here. Nodes without support values indicated are collapsed in the strict consensus.

Caledonia; *R. kini* and *R. bula* from Fiji. Moreover, New Caledonian larval specimens 093 (Table 1, not included in final analysis) and 248 (Fig. 2) were unambiguously assigned to *R. poellerbauerae* and *R. monteithi*, respectively, based on *cox1* sequence data. Both are described in this paper.

In the r8s analysis, the optimal value of the smoothing parameter was 1.58. The average rate of the ultrametric tree is 0.1258 substitutions per site, which means that the age of the root, using a calibration of 2% per Myr for both branches, is 0.1258 × 100, which is 12.6 Myr (Fig. 6).

Discussion

The New Caledonian and Fijian Colymbetinae fauna now comprises nine species. Following our molecular phylogeny, these species are clearly subdivided into two clades: the *R. pacificus* species-group (*R. novaecaledoniae*, *R. monteithi*, *R. poellerbauerae*, *R. alutaceus*) and the *R. suturalis* species-group (*R. annectens*, *R. suturalis*, *R. bula*, *R. kini*, *R. vitiensis*). The inclusion of *R. vitiensis* (previously in the *R. pacificus* group), *R. bula* and *R. kini* in the *R. suturalis* group suggests reduction of trumpet-shaped 'suction' hairs on the parameres as well as double elytral reticulation

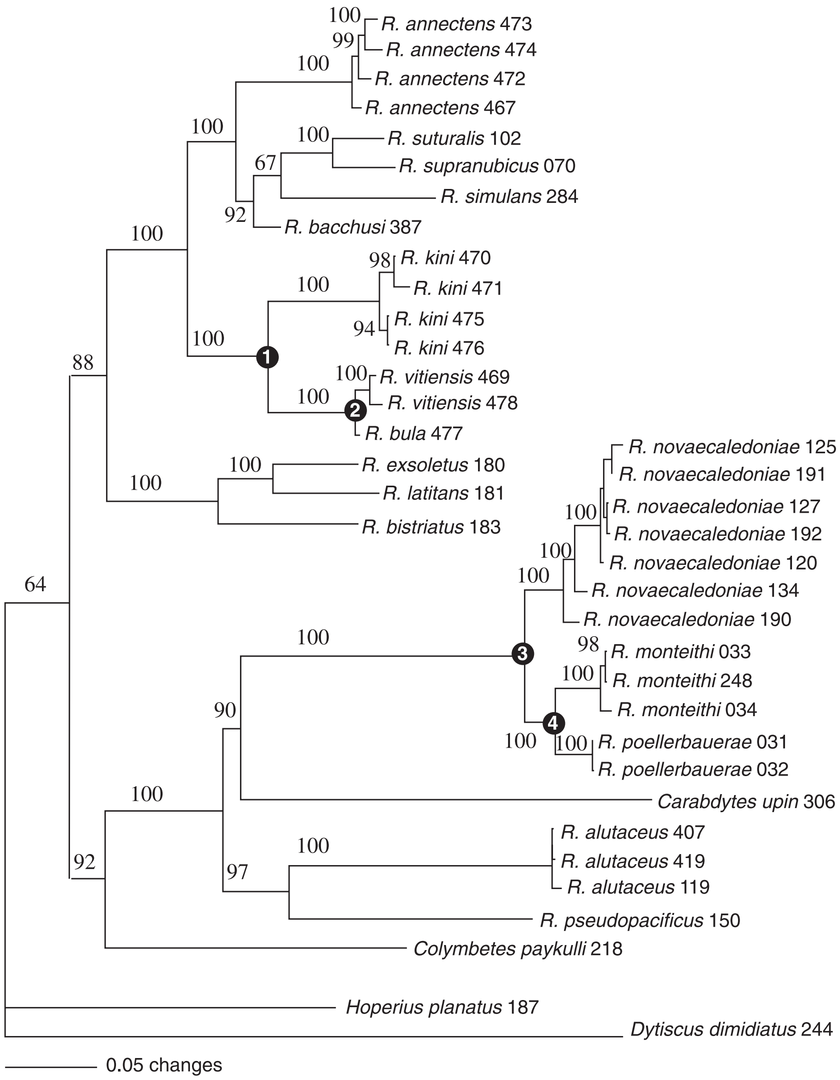

Fig. 3 Phylogenetic relationships inferred using MrBayes and the complete dataset, partitions unlinked, 50% majority rule consensus tree once burn-in samples were discarded. Values above branches are posterior probabilities. Nodes labelled 1–4 are explained in the text; they mark clusters which include the new species named here.

in these Fijian species (see Balke 1993, 2001). Both groups, as currently defined, overlap in range in the South Pacific (in Hawaii, only the *R. pacificus* group is found, while west of the Solomon Islands and east of Fiji only the *R. suturalis* group is present).

Palearctic species of the *R. suturalis* group (e.g. *R. bistriatus*) were placed as sister to the clade comprising *R. suturalis*, as suggested in the definition of the *R. suturalis* group (e.g. Balke 2001). However, support for this clade was either low (parsimony all data, parsimony no gapped characters) or not significant (Bayesian analysis). Analysing Protein Coding Genes only (Fig. 4A), the clade was not retrieved.

A Laurasian origin was postulated for New Guinean or Australo-Pacific *Rhantus* of the *R. suturalis* group; the suggestion that these beetles entered the region only during the later Miocene (Balke 2001) is supported, if weakly, by our present findings (Fig. 6). According to this scenario, cool- or seasonal-climate adapted species dispersed via the mountain ranges of south-east Asia into the New Guinean highlands, Australia and the South Pacific. In temperate or more seasonal regions, members of the *R. suturalis* group occur in the lowlands again. This stepping-stone dispersal must have occurred *c.* 15–5 Myr ago (Mya), or even more recently, as very little land, and few mountains, existed in the region before that time (Hall 1998). This hypothesis is fully supported here, with, e.g. the New Guinean species radiation around *R. bacchusi* coinciding with uplift of the central mountain ranges since 10–5 Mya (Hall 1998) (Fig. 6).

According to our study, the extremely widely distributed *R. suturalis* is a recent species, having originated only in the past 2.5 Myr (Fig. 6).

The somewhat carabid-shaped, rheobiont *Carabdytes upin* grouped within *Rhantus* in most analyses, with a group of species previously characterized as the *R. pacificus* group. We suggest that an analysis of a wider range of Colymbetini,

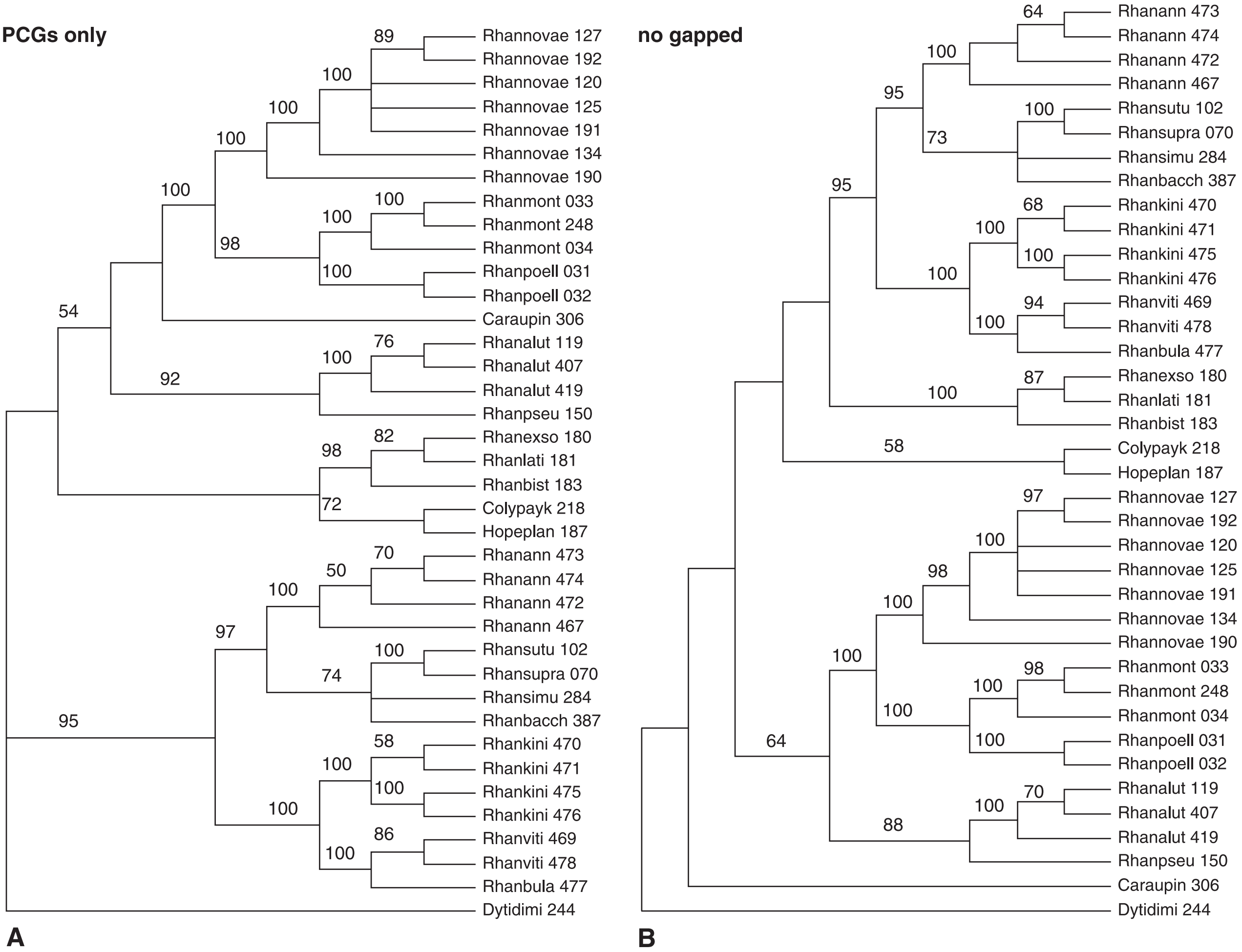

Fig. 4 A, B. Parsimony analyses. —A. Protein Coding Genes only (1 of 26 trees, CI = 0.4334, RI = 0.7046). —B. Gapped characters excluded from analysis (1 of 16 trees, CI = 0.4582, RI = 0.7202). Bootstrap values given above branches.

especially *Rhantus* species, should be conducted to decide whether *Rhantus* as currently defined is in fact paraphyletic as suggested by Nilsson & Hilsenhoff (1991), or whether *Carabdytes* merely represents a morphologically highly derived species of *Rhantus*. In the latter case, *Carabdytes* would have to be synonymized, while in the former it would be an available genus name for the *R. pacificus* group and perhaps other species currently in *Rhantus*.

A most intriguing finding of the present study was the syntopic occurrence of sister species in both New Caledonia and Fiji.

The Fijian species *R. vitiensis* and *R. bula* appear to have a broader range of distribution all over Viti Levu highlands, where they were encountered syntopically in tiny waterholes in otherwise dry stream beds (Fig. 17B). The New Caledonian species *R. monteithi* and *R. poellerbauerae* appear to be mostly restricted to Mt. Panié, where they occur in the same stream. It is noteworthy that both these species were segregated ecologically. Whereas *R. monteithi* was abundant in streampools, *R. poellerbauerae* adults and two larvae were collected predominantly from underneath rocks in a dry first-order stream bed only a few meters above the streampools. The first-order stream feeds the streampools when it rains; only then will small puddles form in the dry depressions from which we collected hidden *R. poellerbauerae*.

New Caledonian and Fijian *Rhantus* exhibit different levels of differentiation, both morphologically and genetically. *Rhantus vitiensis* and *R. bula* are morphologically very similar and only differ slightly by the form of the median lobe of the aedeagus; the *cox1* divergence amounts to merely 1.4–1.9%. These two species differ from the allopatrically distributed *R. kini* by a much narrower median lobe and 7.0–8.1% *cox1* divergence. The New Caledonian sisters *R. monteithi* and *R. poellerbauerae* strongly differ in habitus (Fig. 7B,C) and

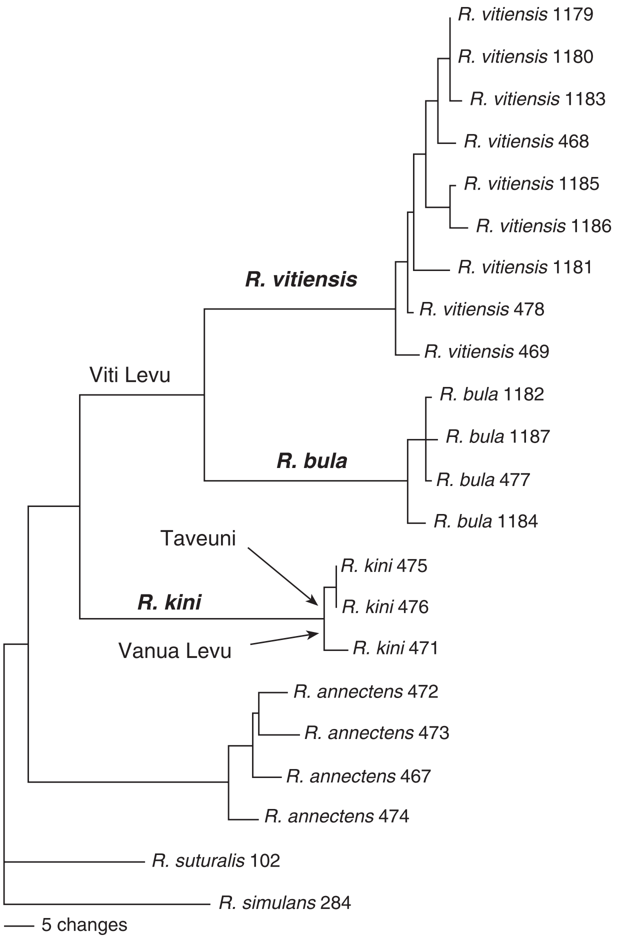

Fig. 5 The first of four parsimonious trees (236 steps, CI = 0.75, RI = 0.8806) found rnunning PAUP*; the extended Fijian dataset usese *cox1* sequence data only.

2.8–3.2% *cox1* divergence; they differ from their sister *R. novaecaledoniae* in the shape of the median lobe and/or size, habitus and coloration as well as 4.2–6.2% *cox1* divergence. Meanwhile, *R. novaecaledoniae* populations from north, south and central New Caledonia appear to form one genetically moderately diverse morphospecies; total *cox1* variation within *R. novaecaledoniae* was 0–2.9%.

This geographical structure might indicate ongoing separation. Future analysis employing much denser sampling would help us to understand the mechanisms generating insular diversity as encountered in the present study.

In this paper, we have shown that mtDNA sequence data might help to characterize new species, even cryptic ones; genetically very similar clusters were congruent with comparably similar morphospecies as diagnosed by sexual characters of the male. We have also shown that *cox1* genetic divergence (up to 2.9%) within the more widely spread morphospecies *R. novaecaledoniae* might be larger than that between two morphologically very distinct species such as *R. monteithi* and *R. poellerbauerae* (2.8–3.2%). Meaningful species delineation is thus only achieved combining genetic and morphological evidence. Based on DNA sequence data, it is here possible to assign unknown larvae to adults.

Monaghan *et al.* (2006) analysed the Fijian radiation of *Copelatus* diving beetles, which often co-occur with *Rhantus* species there. There are *c.* 25 species of *Copelatus* in Fiji. However, mtDNA clusters and morphospecies grouping were mostly incongruent, which might be due to recent gene flow. Molecular clock estimation for the age of Fijian *Copelatus* ranged from 9 to 5 Myr, which is approximately the estimate for the Fijian radiation of *Rhantus* in the *R. vitiensis* complex.

Recently, mtDNA barcoding was introduced as a powerful tool to identify species, different semaphoronts of species, and to detect cryptic species (Hebert *et al.* 2003). Here we show that even in an Oceanic island setting such as Fiji it is not *per se* possible to predict whether or not this approach works, and we argue that morphology plays an important role if we are to characterize global diversity in a meaningful manner.

New Caledonia and Fiji have sometimes been suggested as harbouring Gondwanan relics (e.g. Lowry 1998; see also Murienne *et al.* 2005). Though Colymbetinae are represented by a number of morphologically rather odd species, in part resembling other Southern forms, we found no evidence supporting an old phylogenetic age of these beetles.

Larval morphology

The larval morphology of most *Rhantus* species is still poorly known. World-wide the larvae of 17 species have been described and/or figured, in most cases very superficially (Meinert 1901; Williams 1936; Bertrand 1928; Galewski 1963; Watts 1963; James 1969; Barman 1972; Nilsson 1987; Costa *et al.* 1988; Klausnitzer 1991; Alarie & Wang 2004). Except for *R. fennicus* Huldén (Nilsson 1987) and *R. formosanus* Kamiya (Alarie & Wang 2004) none of these descriptions used chaetotaxy as a diagnostic feature, which hampers attempts at comparing those larvae in the context of the system proposed for several species of the subfamily Colymbetinae (Alarie 1995, 1998; Alarie & Balke 1999; Alarie & Larson 1998; Alarie, Spangler & Perkins 1998; Shaverdo 2003).

Quite surprisingly, larvae of both *R. monteithi* and *R. poellerbauerae* differ strongly from any other known species of *Rhantus*. Like other *Rhantus* larvae, they are characterized by: (1) a relatively large head, slightly broader than long; (2) the pore-like condition of the sensory appendage on antennomere 3 (A3′); (3) the mandibles relatively long in proportion to their width (about 3× longer than wide); (4) a broad maxillary stipes, without short spine-like structures along the inner margin; (5) a single segmented galea shorter than

Table 1 Species studied along with our voucher numbers and collecting localities (LA = third larva extracted; voucher – DNA and dry mounted beetle are in the BMNH collection).

Species	Voucher	Locality	Altitude	Collector	Date
Rhantus novaecaledoniae	MB 120	New Caledonia: Aoupinié, W slopes (NC 34)	700 m	Balke & Wewalka	14.xi.2001
Rhantus novaecaledoniae	MB 125	New Caledonia: Nérin, water reservoir, Me Maoya slopes (NC 35)	600 m	Balke & Wewalka	14.xi.2001
Rhantus novaecaledoniae	MB 127	New Caledonia: Mt. Canala — Foa road, W of pass (NC37)	700 m	Balke & Wewalka	15.xi.2001
Rhantus novaecaledoniae	MB 134	New Caledonia: Mt. Koghis, trek to cascade (NC 44)	500 m	Balke & Wewalka	18.xi.2001
Rhantus novaecaledoniae	MB 190	New Caledonia: Mandjelia, below summit (NC 26)	560 m	Balke & Wewalka	11.xi.2001
Rhantus novaecaledoniae	MB 191	New Caledonia: Bobeito, old mining road, 25 km W Pombei (NC 32)	300 m	Balke & Wewalka	13.xi.2001
Rhantus novaecaledoniae	MB 192	New Caledonia: Mt. Canala — Foa road, E of pass (NC 38)	620 m	Balke & Wewalka	16.xi.2001
Rhantus novaecaledoniae	MB 345	New Caledonia: Nérin, water reservoir, Me Maoya slopes (NC 35)	600 m	Balke & Wewalka	14.xi.2001
Rhantus novaecaledoniae	MB 346	New Caledonia: Nérin, water reservoir, Me Maoya slopes (NC 35)	600 m	Balke & Wewalka	14.xi.2001
Rhantus novaecaledoniae	MB 347	New Caledonia: Nérin, water reservoir, Me Maoya slopes (NC 35)	600 m	Balke & Wewalka	14.xi.2001
Rhantus novaecaledoniae	MB 348	New Caledonia: Nérin, water reservoir, Me Maoya slopes (NC 35)	600 m	Balke & Wewalka	14.xi.2001
Rhantus novaecaledoniae	MB 349	New Caledonia: Mandjélia, below summit (NC 26)	560 m	Balke & Wewalka	11.xi.2001
Rhantus novaecaledoniae	MB 350	New Caledonia: Mt. Koghis, track to cascade (NC 44)	500 m	Balke & Wewalka	18.xi.2001
Rhantus novaecaledoniae	MB 351	New Caledonia: Mt. Koghis, track to cascade (NC 44)	500 m	Balke & Wewalka	18.xi.2001
Rhantus novaecaledoniae	MB 352	New Caledonia: Mt. Koghis, track to cascade (NC 44)	500 m	Balke & Wewalka	18.xi.2001
Rhantus novaecaledoniae	MB 376	New Caledonia: Aoupinié, W slopes (NC 34)	700 m	Balke & Wewalka	14.xi.2001
Rhantus poellerbauerae	MB 031	New Caledonia: Mont Panié, below summit (NC 17)	1550 m	Balke & Wewalka	9.xi.2001
Rhantus poellerbauerae	MB 032	New Caledonia: Mont Panié, below summit (NC 17)	1550 m	Balke & Wewalka	9.xi.2001
Rhantus annectens	MB 467	Fiji: Viti Levu, Lautoka, road Abaca to coast (FI013)	200 m	Balke, Wewalka & Mailautoka	12.xi.2003
Rhantus vitiensis	MB 468	Fiji: Viti Levu, Lautoka, Abaca, waterfall (FI012)	500–700 m	Balke, Wewalka & Mailautoka	11.xi.2003
Rhantus vitiensis	MB 469	Fiji: Viti Levu, Lautoka, Abaca, waterfall (FI012)	500–700 m	Balke, Wewalka & Mailautoka	11.xi.2003
Rhantus kini	MB 470	Fiji: Vanua Levu, Mount Delaikoro (FI018)	800 m	Balke, Wewalka & Mailautoka	14.xi.2003
Rhantus kini	MB 471	Fiji: Vanua Levu, Mount Delaikoro (FI018)	800 m	Balke, Wewalka & Mailautoka	14.xi.2003
Rhantus annectens	MB 472	Fiji: Taveuni Island: 9.5 km S Somosomo (FI030)	50 m	Balke, Wewalka & Mailautoka	21.xi.2003
Rhantus annectens	MB 473	Fiji: Viti Levu, E Raraimatuku Plateau, Serea — Naitauvoli (FI003)	150 m	Balke, Wewalka & Mailautoka	7.xi.2003
Rhantus annectens	MB 474	Fiji: Viti Levu: Nausori Highlands, Nausori (FI015)	650 m	Balke, Wewalka & Mailautoka	12.xi.2003
Rhantus kini	MB 475	Fiji: Taveuni Island, Des Voeux Peak (FI028)	1100 m	Balke, Wewalka & Mailautoka	20.xi.2003
Rhantus kini	MB 476	Fiji: Taveuni Island, Des Voeux Peak (FI028)	1100 m	Balke, Wewalka & Mailautoka	20.xi.2003
Rhantus bula	MB 477	Fiji: Viti Levu, Nadarivatu, just N of pass towards coast (FI008)	650 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus vitiensis	MB 478	Fiji: Viti Levu, Nadarivatu, just N of pass towards coast (FI008)	650 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus vitiensis	MB 1179	Fiji: Viti Levu, Navai, Mt. Victoria (FI006)	800–900 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus vitiensis	MB 1180	Fiji: Viti Levu, Navai, Mt. Victoria (FI006)	800–900 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus vitiensis	MB 1181	Fiji: Viti Levu, Navai, Mt. Victoria (FI006)	800–900 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus bula	MB 1182	Fiji: Viti Levu, Nadarivatu, just N of pass towards coast (FI008)	650 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus vitiensis	MB 1183	Fiji: Viti Levu, Nadarivatu, just N of pass towards coast (FI008)	650 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus bula	MB 1184	Fiji: Viti Levu, Nadarivatu, just N of pass towards coast (FI008)	650 m	Balke, Wewalka & Mailautoka	8.xi.2003
Rhantus vitiensis	MB 1185	Fiji: Viti Levu, Lautoka, Abaca, waterfall (FI012)	500–700 m	Balke, Wewalka & Mailautoka	11.xi.2003
Rhantus vitiensis	MB 1186	Fiji: Viti Levu, Lautoka, Abaca, waterfall (FI012)	500–700 m	Balke, Wewalka & Mailautoka	11.xi.2003
Rhantus bula	MB 1187	Fiji: Viti Levu, Lautoka, Abaca, waterfall (FI012)	500–700 m	Balke, Wewalka & Mailautoka	11.xi.2003
Rhantus alutaceus	MB 119	New Caledonia: Aoupinié, 25 km SW Ponérihouen (NC 34)	700 m	Balke & Wewalka	14.xi.2001
Rhantus alutaceus	MB 407	New Caledonia: Gélima (NC 11190)	730 m	Burwell & Monteith	15.xi.2002
Rhantus alutaceus	MB 419	New Caledonia: Mt. Humboldt, refuge creek (NC 11124)	1350 m	Burwell	5–6.xi.2002
Rhantus pseudopacificus	MB 150	USA: Hawaii, Big Island		Englund	14.ii.2002
Carabdytes upin	MB 306	PNG: Simbu Province: Kegsugl (PNG21)	2500–2600 m	Balke	24.ix.2002
Hoperius planatus	MB 187	USA		Steiner	
Colymbetes paykulli	MB 218	Germany: Brandenburg		Hendrich	viii.2002
Rhantus bistriatus	MB 183	Russia: 12/5 : 2, Astrakhan oblast, Nishniy Baskuntyak		Nilsson	
Rhantus latitans	MB 181	Austria: Vorarlberg, Bodensee		Ribera	
Rhantus exsoletus	MB 180	Germany: Lüneburger Heide		Ribera & Cieslak	vii.2002
Rhantus bacchusi	MB 387	PNG: EHL Province: Aiyura	1600 m	Sagata	ii.2003
Rhantus simulans	MB 284	Australia:WA: GinGin Brook		Hendrich	
Rhantus supranubicus	MB 070	West Papua: Lake Habbema	3600 m	Phyllodrom Expedition	2000
Rhantus suturalis	MB 102	Australia: SA: Watts Gully nr Adelaide		Balke & Watts	28.x.2001
Root					
Dytiscus dimidiatus	MB 244	Germany: Brandenburg		Hendrich	viii.2002

Table 2 Tree statistics and branch support.

Partition	Chars.	Inform	Steps	Trees	CI	RI	Summed PBS	Min steps	PBS/min steps
*rrnL**	794	109	354	> 1000	0.641	0.812	121.6	362	0.336
*cox1-cox2**	1449	384	1509	> 1000	0.447	0.681	110.9	1522	0.073
cob	355	121	523	9	0.380	0.720	106.2	537	0.198
H3	322	49	146	> 1000	0.562	0.855	50.2	155	0.324
18S*	608	25	42	33	0.786	0.944	45.2	54	0.781
Combined	3508	688	2630	52	0.462	0.720	434.1	2630	0.165
Comb., no gaps	3466	666	2547	16	0.459	0.720	—	—	—
PCGs only	2106	554	2202	26	0.434	0.705	—	—	—

**rrnL* — 24 trees/removing eight individuals with completely missing sequences; *cox1-cox2* — 17 trees/4 removed; H3–82 trees/1 removed; 18S — 319 trees/1 removed. PCGs — protein coding genes.

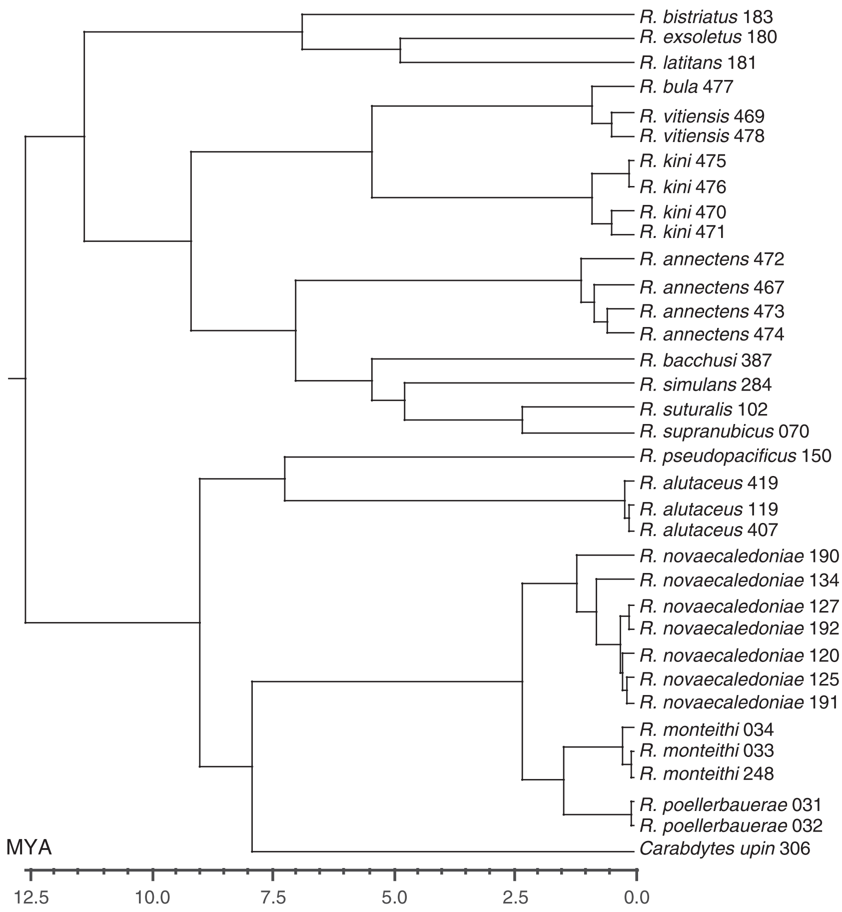

Fig. 6 Bayesian branch lengths fitted to a clock using Penalized Likelihood as implemented in r8s, and utilizing the insect mtDNA molecular clock of roughly 2% divergence/Myr suggested by Brower (1994). MYA = million years ago.

the maxillary stipes; (6) maxillary palpomere 3 and labial palpomere 2 shorter than maxillary palpomere 2 and labial palpomere 1, respectively; (7) the presence of natatory setae on the dorsal margin of the femur, tibia and tarsus; (8) the eighth abdominal segment elongated, with a reduced dorsal elongation (= siphon); (9) a single segmented urogomphus.

Larvae of the two New Caledonian species described in this paper differ from any other known larva of *Rhantus* by: (1) the absence of marginal spinulae along the ventral margin of the meso- and metatibiae and meso- and metatarsi; (2) the absence of tarsal spinulae ventro-proximally, and (3) the reduced number (*R. monteithi*; Fig. 10F) or absence of secondary setae (*R. poellerbauerae*; Fig. 10G) on the urogomphus. The latter character state is noteworthy knowing that the presence of secondary setae on urogomphi is characteristic for most species of Colymbetini (Nilsson & Hilsenhoff 1991; Alarie & Hughes 2006), including all known larvae of *Rhantus*.

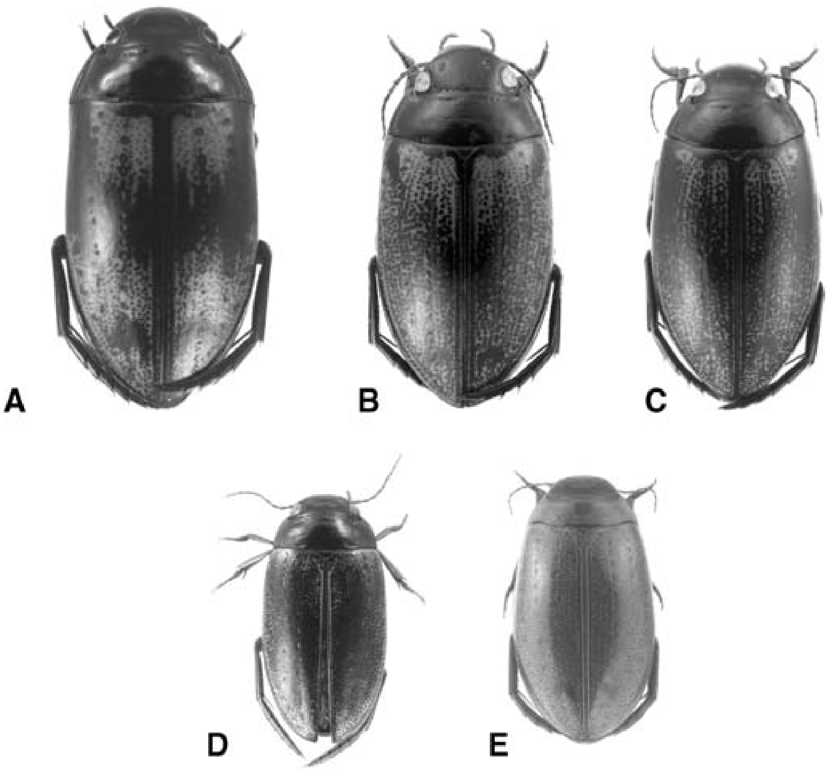

Fig. 7 A–E. Habitus and coloration: —A. *R. monteithi*. —B. *R. poellerbauerae*. —C. *R. novaecaledoniae*. —D. *R. vitiensis*. —E. *R. annectens*.

Recent studies on the larval morphology of the Colymbetini (Michat 2005; Alarie & Hughes 2006) have postulated a monophyletic origin of the Colymbetini based on: (1) the rather distad position of the primary pore ANg on antennomere IV; (2) the elongate shape of the primary seta TI7 on the tibia, and (3) the presence of basoventral spinulae on the pretarsal claws. Whereas larvae of both *R. poellerbauerae* and *R. monteithi* also have the primary pore ANg articulated more distally, both lack basoventral tarsal spinulae; this is postulated to represent a reversal from the derived condition. We were unable to determine whether the primary seta TI7 is elongate in these species owing to absence of first instars.

Taxonomy

Genus* Rhantus *Dejean, 1833

***Rhantus novaecaledoniae* J. Balfour-Browne, 1944a** (Figs 1, 7C and 8)

Colymbetes marmoratus Perroud & Montrousier, 1864: 77, 78 (nec Hope, 1832).

Rhantus marmoratus Perroud: Sharp 1882: 763; Fauvel 1883: 342, 343, 1903: 249; Heller 1916: 239; Zimmermann 1920: 202.

Rantus (sic!) *marmoratus* Perroud: Balfour-Browne 1939: 370.

Rantus (sic!) *novae-caledoniae* J. Balfour-Browne, 1944a: 354 (replacement for *C. marmoratus*).

Rhantus novaecaledoniae J. Balfour-Browne: Balke 1993: 44; Nilsson 2001: 51.

Type locality. New Caledonia, South Province, Kanala.

Type material. Lectotype ♂ from 'Kanala' (= New Caledonia) (designated by Balke 1993) in IRSN.

Material examined (see also Balke 1993). 2 ♂♂: New Caledonia, North Prov., 10 km SE Ouégoa, road to Mandjélia, 560 m, 11.xi.2001, Balke & Wewalka (NC 26) (NMW); 2 ♀♀: New Caledonia: North Prov., Aoupinié, 15–25 km SW Ponérihouen, 500–700 m, 14.xi.2001, Balke & Wewalka (NC 33) (CWW); 1 ind. New Caledonia: North Prov., Aoupinié, top camp, loc. 8715, 21°11′S 165°19′E 2–3.xi.2001, Burwell & Monteith (QLDB); 2 inds: New Caledonia: North Prov., Mandjélia, 600–750 m, 11–13.v.1984, Monteith & Cook (QLDB); 12 ♂♂, 5 ♀♀: New Caledonia: North Prov., Me Maoya Area, 4 km S Nérin, 600 m, 14.xi.2001, Balke & Wewalka (NC 35) (NMW, CWW); 6 ♂♂, 1 ♀: New Caledonia: South Prov., Mt. Kanala, 15–20 km S Kanala, 600 m, 15.xi.2001, leg. Balke & Wewalka (NC 37) (NMW, CWW);

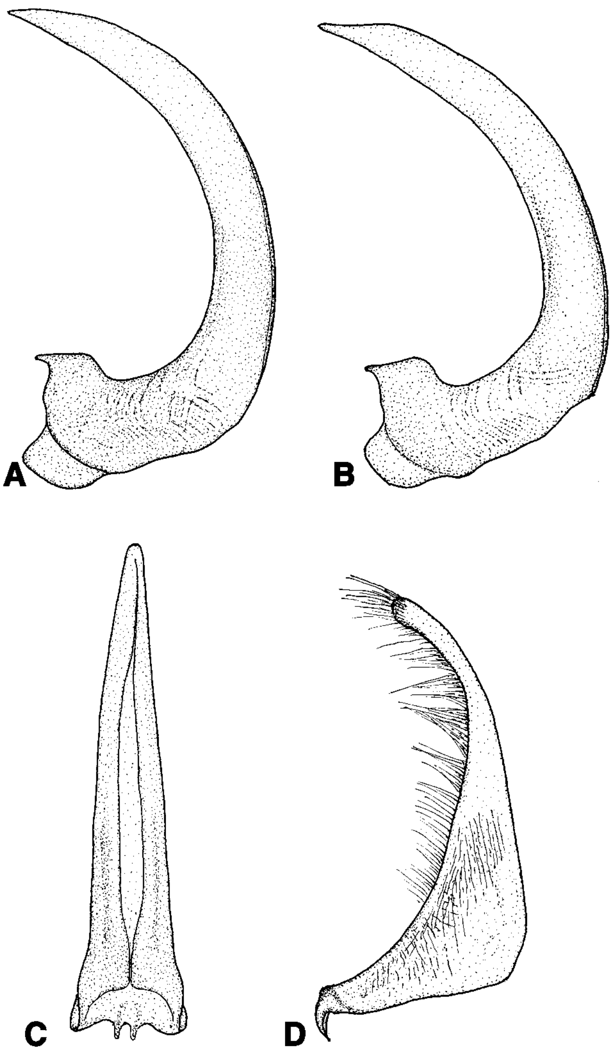

Fig. 8 A–D. *Rhantus novaecaledoniae*. Median lobe of aedeagus in —A. lateral view (Mt. Koghis), —B. lateral view (Mt. Mandjélia), —C. ventral view. —D. Paramere, external view.

3 ♂♂, 1 ♀: New Caledonia: South Prov., Mt. Kanala, 22 km S Kanala, road to La Foa, 620 m, 15.xi.2001, Balke & Wewalka (NC 38) (NMW); 1 ♂: New Caledonia: South Prov., 16 km W Thio, 350 m, 16–17.xi.2001, Balke & Wewalka (NC 40) (CWW); 8 ♂♂, 10 ♀♀: New Caledonia: South Prov., Mt. Koghis, 500 m, 19.xi.2001, Balke & Wewalka (NC 44) (NMW, CWW); 1 ♂, 2 ♀♀: New Caledonia: South Prov., Mt. Mou, near Sanatorium, 400 m, 23.xi.2001, Balke & Wewalka (NC 52) (NMW). For sequenced specimens see Table 1 (BMNH).

Habitus. Body regularly oval, moderately convex; pronotum at posterior angles as broad as elytra at shoulders, lateral margin almost straight in middle; elytra regularly oval, broadest almost in the middle (Fig. 7C).

Measurements. (n = 20) TL = 11.8–13.5 mm (mean 12.8 mm); TL-h = 10.6–12.3 mm (mean 11.8 mm); TW = 6.0–6.9 mm (mean 6.5 mm).

Colour. Head black, often with a vague reddish frontal mark. Pronotum black, sometimes vaguely reddish laterally and along the anterior margin. Elytra reddish with many black speckles as in Fig. 7C. Ventral surface black.

Surface sculpture. Head double punctation distinctly impressed, meshes well-defined posteriorly; Pronotum double punctation distinctly impressed, similar to that on head, and well-impressed, hardly defined meshes only present along lateral margins. Elytra with a very dense fine microreticulation which is missing only in a small area along the suture anteriorly and fine punctation of almost uniform size; in areas with microreticulation punctures are hardly visible.

Structures. Pronotum with lateral rim moderately broad (0.15 mm), missing on anterior seventh.

Male. Pro- and mesotarsomeres I–III distinctly dilated, with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: 2× *c.* 14 (I), *c.* 14 (II), *c.* 10 (III), and on mesotarsi: 2× *c.* 12 (I), *c.* 12 (II), *c.* 8 (III). Protarsal claws simple, gently curved and of equal length, distinctly shorter than tarsomere 5. Penis and parameres (Fig. 8A–D). The tip of the northern specimens from Mt. Mandjélia (Fig. 1) is a bit more flattened in lateral view (Fig. 8B) compared to the southern specimens from Mt. Koghis (Fig. 8A). However, we found intermediate forms.

Larva. Unknown.

Diagnosis. R. novaecaledoniae is very similar to *R. poellerbauerae* in size, shape of body and coloration, but can be separated by its fine, relatively dense elytral punctation (punctures almost of equal size) and male genitalia.

Habitat. Pools in intermittent streams as well as small waterholes in rocks at the edge of such streams at altitudes of 350–700 m. In some cases, beetles were retrieved from rock holes only a few centimetres in diameter, filled with black, foul water.

Distribution. Widespread in New Caledonia (Fig. 1). Balke (1993) documented an old report from the Ile des Pins, where the species was not encountered during the 2001 expedition (Balke & Wewalka).

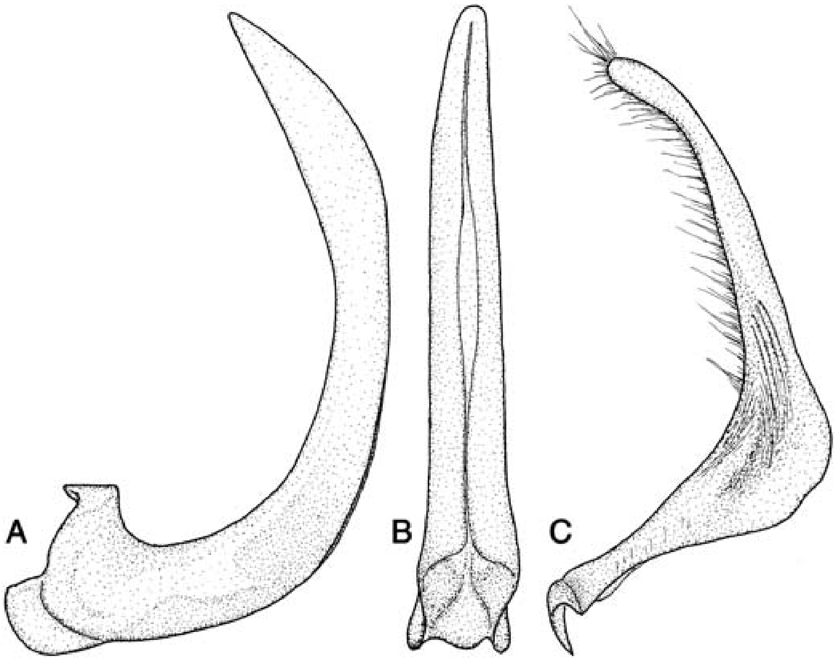

Fig. 9 A–C. *Rhantus monteithi*. Median lobe of aedeagus in —A. lateral and —B. ventral view. —C. Paramere, external view.

Rhantus monteithi **sp. nov.** (Figs 1, 7A, 9 and 10A,C,D,F)
Rhantus novaecaledoniae J. Balfour-Browne: Balke 1993: 45 (partim).

Type locality. New Caledonia, North Province, Mt. Panié.

Material examined. Holotype ♂. New Caledonia: North Prov. Mt. Panié, 1350 m, 8–9.xi.2001, Balke & Wewalka (NC 16) (MNHN). Paratypes: 21 ♂♂, 16 ♀♀ and 1 3rd larva, with same data (NMW, CWW); 1 ♂: New Caledonia: North Prov., Paompaii, 16.9.1914, P.D. Montague (BMNH); 1 ex. New Caledonia: North Prov., Mt. Panié, 950–1300 m, 14–16.v.1984, Monteith & Cook (QLDB); 1 ex. New Caledonia: North Prov., Mt. Panié, loc. 9938, 20°34′S 164°46′E, 1300 m, 16–18.xi.2000, Bouchard, Burwell & Monteith (QLDB). For sequenced specimens see Table 1 (BMNH). Additional specimen (identity uncertain). 1 ♂: New Caledonia: Prov. Nord, Mandjélia, 600–750 m, 11–13.v.1984, Monteith & Cook (QLDB).

Habitus. Body oblong-oval, distinctly convex; pronotum slightly broader at posterior angles than elytra at shoulders, lateral margin moderately curved; elytra almost parallel sided in anterior part, sides slightly concave anteriorly, broadest distinctly behind the middle (Fig. 7A).

Measurements. ($n = 10$) TL 14.5–15.9 mm (mean 14.8 mm); TL-h 13.1–14.1 mm (mean 13.2 mm); TW 7.1–7.9 mm (mean 7.5 mm).

Colour. Head black, sometimes with a very vague reddish frontal mark. Pronotum black, sometimes very vaguely reddish laterally. Elytra black with three broad reddish bands one subbasal neither reaching the suture nor the lateral margin, one postmedian reaching the lateral margin and one apical band which is connected with the postmedian one laterally; the posterior bands are interrupted by many black speckles, the anterior one only by very few (Fig. 7A). Ventral surface black.

Surface sculpture. Head with scarcely impressed double punctation and hardly defined meshes present only along eyes and posteriorly. Pronotum with fine double punctation similar to that on head and well impressed, hardly defined, wrinkle-like meshes only present along lateral margins. Elytra with a very dense fine microreticulation which is missing along the suture anteriorly and fine double punctation similar to that on head; in areas with microreticulation only the larger punctures are visible.

Structures. Pronotum with lateral rim very broad (0.29 mm), missing only on anterior corner.

Male. Pro- and mesotarsomeres I–III distinctly dilated with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: *c.* 2 × 14 (I) — *c.* 12 (II) — *c.* 10 (III), and on mesotarsi: *c.* 2 × 12 (I), *c.* 10 (II), *c.* 8 (III). Protarsal claws simple, gently curved and of equal length, distinctly shorter than tarsomere 5. Penis and parameres (Fig. 9A–C).

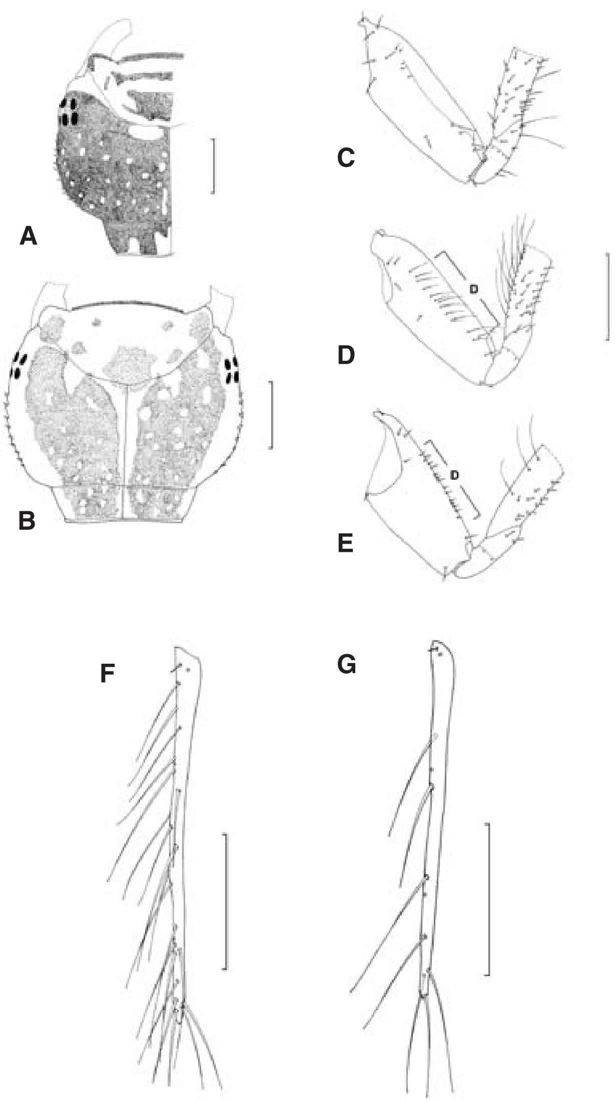

Fig. 10 A–G. Larval characters (3rd instar). Head capsule, dorsal aspect of —A. *R. monteithi*, —B. *R. poellerbauerae*. (C, D) Proximal portion of metathoracic legs of *R. monteithi*: —C. anterior and —D. posterior surfaces. —E. *R. poellerbauerae*, posterior surface. Dorsal surface of urogomphus of —F. *R. monteithi* and —G. *R. poellerbauerae*.

Larva. Instar III (*n* = 1). *Colour* (alcohol-preserved specimens). Dorsal surface of cephalic capsule predominantly dark brown; parietale with several minute yellow maculae posteriorly; frontoclypeus yellowish, with a dark brown reticulate pattern mesally; head appendages yellow, proximal articles lightly infuscate; thoracic terga predominantly dark brown, yellow along lateral margin; meso- and metatergum with a yellowish macula mesally; legs predominantly dark yellow, coxa dark brown dorsally; abdominal terga dark brown; urogomphus dark yellow.

Head. (Fig. 10A) HL = 3.75 mm; HW = 4.28 mm; FCL = 1.38 mm. Cephalic capsule subquadrate, broader than long (HL/HW = 0.88), strongly constricted posteriorly at level of occipital suture, HW/OcW = 2.11; coronal suture short, 0.63× HL; occipital suture well-developed; frontoclypeus strongly convex mesally, 0.37× HL, extending medially at about level of lateral lobes [= adnasalia]; apical margin of frontoclypeus with several club-shaped setae variable in size; ocularium present, stemmata visible ventrally and subdivided into two vertical series; tentorial pits visible ventrally on each side of middle at about midlength. *Antenna*. AL = 2.43 mm, shorter than HW; (AL/HW = 0.53–0.56); A1 = A2 > A3 = A4, A2/A3 = 1.17; lateral elongation of antennomere 3 pore-like; antennomere 3 with a ventroapical spinula. *Mandible*. Falciform, MndL/MndW = 3.10; MndL/HL = 0.62; mandibular channel present, pubescence developed along inner margins. *Maxilla*. Stipes subrectangular, short and thick; cardo and galea present, lacinia lacking; StpL = 0.71 mm, Stpl/length of maxillary palpus = 0.37; GalL = 0.28–0.20 mm, 0.36× length of maxillary palpomere 1; palpus length = 1.95 mm, palpifer developed like a palpomere, AL/length of maxillary palpus = 1.24; palpomere 1 > 2 > 3, length of palpomere 3/length of palpomere 2 = 0.76. *Labium*. Prementum subrectangular, broader than long, slightly sinuated mesally; labial palpus length = 1.41 mm; length of maxillary palpus/length of labial palpus = 1.39; palpomere 2 is 0.67× length of palpomere 1. *Chaetotaxy*. Head capsule with several secondary setae, lateral margin of parietal with 11 short spines; head appendages lacking secondary setae except mandible with several tiny secondary setae (pore-like at lower magnifications).

Thorax. Pronotum trapezoidal dorsally, ovate laterally, widest at about mid-length; length of pronotum about twice that of mesonotum; metanotum subequal to mesonotum in length, both as broad as pronotum; pronotum with a posterotransverse carina; meso- and metanota both with antero- and posterotransverse carina; maximum body width at level of prothorax; thoracic venter membranous; spiracular openings present anterolaterally on mesothorax.

Legs. (Fig. 10C,D) Metathoracic legs longest, about 1.30× length of prothoracic legs, and 2.30× HW; femur > coxa > tibia = tarsus > trochanter; tarsus with two claws, posterior claw slightly shorter than anterior claw on pro- and mesothoracic legs, slightly longer on metathoracic leg; anterior metathoracic claw 0.21× length of metatarsus; spinulae on ventral margin of protibia and protarsus strongly developed; tarsal claws lacking spinulae ventroproximally. *Chaetotaxy*. Position and number of secondary setae as shown in Table 3.

Abdomen. Eight-segmented; LLAS = 2.65 mm; dorsally sclerotized; segments 1–6 membranous ventrally, segments 7 and

Table 3 Number of secondary setae* on the legs of the third instar of *Rhantus poellerbauerae* (RPO), *Rhantus monteithi* (RMO) and *Carabdytes upin* Balke *et al.* (CUP). A = anterior, AD = anterodorsal, AV = anteroventral, CO = coxa, D = dorsal, Di = distal, FE = femur, NS = natatory setae, PD = posterodorsal, Pr = proximal, PV = posteroventral, TA = tarsus, TI = tibia, TR = trochanter, V = ventral, *n* = number of specimens studied, na = not available, range = number of secondary setae on segment.

Segment	Sensillar series	RPO ($n = 2$)	RMO ($n = 2$)†	CUP ($n = 2$)	Segment	Sensillar series	RPO ($n = 2$)	RMO ($n = 2$)†	CUP ($n = 2$)
ProCO	D(NS)	27	23–25	24–28	MesoTI	NS (PD)	31–34	30	7–8
	A	15–16	18	10–20		AD	16–17	23–24	13–19
	V	0	1	5–12		AV	12–14	14–18	5–7
	Total	42–43	42–43	39–60		PD	0–1	5–7	3–5
ProTR	Pr	5	6–7	4–7		PV	6–12	9–13	5–7
	Di	1–3	4	5–7		Total	67–76	85–88	35–45
	Total	6–8	10–11	11–13	MesoTA	NS (PD)	29–30	28–29	7–11
ProFE	NS (PD)	31	20–21	3–4		AD	16–18	19–20	na
	AD	28	34–36	16–23		AV	13–14	12–15	na
	AV	24–27	32–36	16–20		PD	1–2	2	na
	PD	1	10	2–6		PV	9–12	12–15	na
	PV	14–15	24–26	21–27		Total	69–75	74–80	na
	Total	99–101	123–126	62–72	MetaCO	D(NS)	17–20	15–19	30–33
ProTI	NS (PD)	29–30	23–25	5–7		A	24	20–21	21–24
	AD	12–14	19–22	10–13		V	0	0–1	14–19
	AV	7–11	9–11	7–10		Total	41–44	36–40	60–71
	PD	1	1–5	0–2	MetaTR	Pr	7–9	9–10	11–12
	PV	8	11–12	0		Di	1	3–4	5–9
	Total	59–62	64–74	30–35		Total	8–10	12–14	16–21
ProTA	NS (PD)	19–20	15–17	5–8	MetaFE	NS (PD)	18–23	9–10	1–3
	AD	8	10–14	na		AD	23–30	40–43	21–24
	AV	11	11–14	na		AV	12–20	23–26	23–27
	PD	0	4–5	na		PD	0	4–10	4–7
	PV	9	9–11	na		PV	16	26–28	25–29
	Total	47–48	52–58	na		Total	74–84	107–112	78–84
MesoCO	D(NS)	30	25–26	27–31	MetaTI	NS (PD)	33–39	37–38	11–14
	A	21	22	16–22		AD	16–19	25–31	19–21
	V	0	0–1	10–15		AV	12–14	15–17	7–9
	Total	51	48	58–61		PD	0–1	0–5	4–5
MesoTR	Pr	7	10	5–8		PV	9–12	13–16	5–7
	Di	1–2	3	5–7		Total	75–80	98–99	5–51
	Total	8–9	13	10–15	etaTA	NS (PD)	33–38	37–39	12–16
MesoFE	NS (PD)	24–27	20–21	2–3		AD	14–17	20–21	na
	AD	20–27	32–43	18–22		AV	10–11	14	na
	AV	14–19	26–30	17–21		PD	0	0–1	na
	PD	0–1	1–10	1–5		PV	7–10	13	na
	PV	15–19	33–34	21–24		Total	64–76	85–87	na
	Total	73–93	123–127	64–71					

*Including additional setae, cf. Material and Methods; †Both legs included from 1 larva.

8 completely sclerotized; terga 1–7 with antero- and posterodorsal transverse carina, tergum 8 with an anterodorsal transverse carina only; segments 1–7 with a pair of spiracular openings; segment 8 subcylindrical, LLAS/HW = 0.62, abruptly narrowing posterior to insertion of urogomphi; siphon 0.22× LLAS, shortly sinuated mesally. *Chaetotaxy.* Secondary setae predominantly short and spine-like.

Urogomphus. (Fig. 10F) One-segmented, lacking a subbasal suture; total length of urogomphus = 2.83 mm, 1.10× LLAS, and 0.66 × HW. *Chaetotaxy.* Urogomphus with 11 hair-like secondary setae.

Diagnosis. Adults. Rhantus monteithi has a similar coloration to *R. novaecaledoniae* and *R. poellerbauerae* but can be separated both from these species and other species of *Rhantus* by its body shape, with pronotum slightly broader at posterior angles than elytra at shoulders and elytra almost parallel-sided in anterior part, broadest distinctly behind the middle. *Larvae. Rhantus monteithi* can be distinguished from

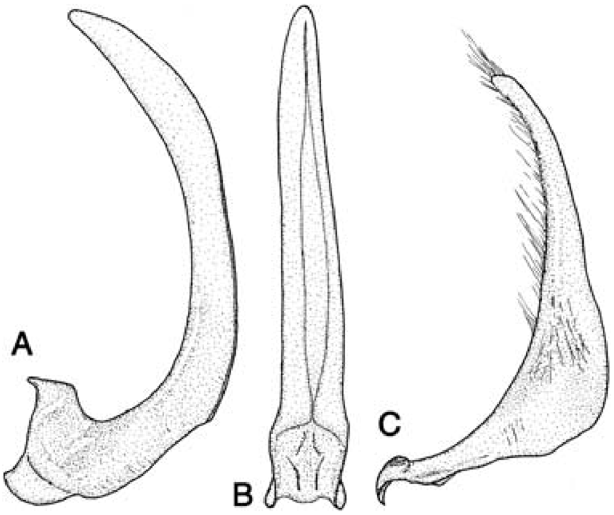

Fig. 11 A–C. *Rhantus poellerbauerae*. Median lobe of aedeagus in —A. and —B. ventral view. —C. Paramere, external view.

R. pollerbauerae by the following combination of characters: larger size, presence of secondary setae on urogomphus (Fig. 10F), larger number of secondary setae on legs and reduced number of natatory setae on metafemur (< 10 compared to > 18) (Table 3). *Rhantus monteithi* is also characterized by the presence of hair-like secondary setae along the dorsal margin of coxae (Fig. 10D), a feature reported for the first time for *R. formosanus* Kamiya (Alarie & Wang 2004).

Etymology. Named after Dr Geoff Monteith of the Queensland Museum in Brisbane, Australia, for his help and endless enthusiasm.

Habitat. Rockpools of clear streams of high mountains (1350 m).

Distribution. North Province of New Caledonia: Mont Panié; Paompaii (BMNH); ? Mandjélia (QLDB) (Fig. 1).

Note. One specimen from Mandjélia, a mountain north of Panié, is much smaller than all the other individulas studied: TL 12.0 mm vs. TL 14.5–15.9 mm. DNA sequence data from that population would help to establish its taxonomic status.

***Rhantus poellerbauerae* sp. nov.** (Figs 1, 7B, 10B,E,G and 11)
Rhantus novaecaledoniae J. Balfour-Browne: Balke 1993: 45 (partim).

Type locality. New Caledonia, North Province, Mt. Panié.

Material examined. Holotype ♂: New Caledonia: North Prov. Mt. Panié, 1350 m, 8–9. xi.2001, Balke & Wewalka (NC 16) (MNHN). Paratypes: 31 ♂♂, 36 ♀♀, 2 3rd larvae, with same data as holotype (NMW, CWW); 5 ♂♂, 2 ♀♀: New Caledonia, North Prov., Mt. Panié, 1200 m, 9.xi.2001, Balke & Wewalka (NC 15) (CWW); 3 ♂♂ 3 ♀♀: New Caledonia, North Prov., Mt. Panié, 1400 m, 9.xi.2001, Balke & Wewalka (NC 19) (NMW); 1 ♀: New Caledonia, North Prov., Mt. Panié, 1100 m, 9.xi.2001, Balke & Wewalka (NC 18a) (NMW); 1 ind., New Caledonia: North Prov., Ignambi, 1300 m, 2.ix.1914, Montague (BMNH); 5 inds: New Caledonia: North Prov., Mt. Panié, summit, loc. 8772, 20 34′S 164°46′E 1660 m, 9.xi.2001, Burwell (QLDB); 8 inds: New Caledonia: North Prov., Mt. Panié, loc. 9938, 20°34′S 164°46′E, 1300 m, 16–18.xi.2000, Bouchard, Burwell & Monteith (QLDB); 2 inds: New Caledonia: North Prov., Mt. Panié, 1300–1600 m, 15.v.1984 Monteith & Cook (QLDB). For sequenced specimens see Table 1 (BMNH).

Habitus. Body regularly oval, moderately convex; pronotum at posterior angles as broad as elytra at shoulders, lateral margin moderately curved; elytra regularly oval, broadest almost in the middle (Fig. 7B).

Measurements. (*n* = 20) TL 11.9–14.1 mm (mean 13.4 mm); TL-h 11.0–12.6 mm (mean 12.2 mm); TW 6.1–6.9 mm (mean 6.7 mm).

Colour. Head black, sometimes with a very vague reddish frontal mark. Pronotum black, sometimes very vaguely reddish laterally. Elytra reddish with many black speckles which are concentrated in the middle near suture, at the anterior part of suture, near shoulders and near apex; in the subbasal area black speckles are almost missing forming reddish triangle bands neither reaching the suture nor the lateral margin and the base (Fig. 7B). Ventral surface black.

Surface sculpture. Head with distinctly impressed double punctation and hardly defined meshes present only along eyes and posteriorly. Pronotum with distinctly double punctation similar to that on head and well-impressed hardly defined wrinkle-like meshes only present along lateral margins. Elytra with a very dense fine microreticulation which is missing only in a small area along the suture anteriorly and fine double punctation similar to that on head; in areas with microreticulation only the larger punctures are visible.

Structures. Pronotum with lateral rim moderately broad (0.15 mm), absent on anterior eighth.

Male. Pro- and mesotarsomeres I–III distinctly dilated with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: *c.* 2 × 14 (I) — *c.* 14 (II) — *c.* 10 (III), and on mesotarsi:

c. 2 × 12 (I) — *c.* 12 (II) — *c.* 8 (III). Protarsal claws simple, gently curved and of equal length, distinctly shorter than tarsomere 5. Penis and parameres (Fig. 11A–C).

Larva. Instar III ($n = 2$). *Colour* (alcohol-preserved specimens). Dorsal surface of head capsule yellowish to pale brown; frontoclypeus with a light brown macula posteriorly; parietal brownish, with several yellowish maculae posteriorly; head appendages yellow; thoracic terga dark brown mesally with several yellowish maculae, yellowish along lateral margins; legs yellow to pale brown; abdominal terga I–VI predominantly dark brown; abdominal terga VII and VIII dark yellow; urogomphus dark yellow.

Head. (Fig. 10B) HL = 3.10–3.35 mm (mean = 3.23 mm); HW = 3.48–3.55 mm (mean = 3.51 mm); FCL = 1.10–1.15 mm (mean = 1.13 mm). Cephalic capsule rounded to subquadrate, as broad as long (HL/HW = 0.89–0.94), strongly constricted posteriorly at level of occipital suture, HW/OcW = 2.17–2.25; coronal suture short, 0.65–0.66× HL; occipital suture well-developed; frontoclypeus strongly convex mesally, 0.34–0.36× HL, extending medially at about level of lateral lobes [= adnasalia]; apical margin of frontoclypeus with several club-shaped setae [lamellae clypeales of Bertrand (1972)] variable in size; ocularium present, stemmata visible ventrally and subdivided into two vertical series; tentorial pits visible ventrally on each side of middle at about midlength. Antenna. AL = 1.94–1.98 mm (mean = 1.96 mm); shorter than HW; (AL/HW = 0.56); A1 > A2 > A3 > A4, A2/A3 = 1.17–1.20; lateral elongation of antennomere 3 pore-like; antennomere 3 with a ventroapical spinula. *Mandible*. Falciform, MndL/MndW = 3.41–3.43; MndL/HL = 0.54–0.59; mandibular channel present, pubescence developed along inner margins; *Maxilla*. Stipes subrectangular, short and thick; cardo and galea present, lacinia lacking; StpL = 0.55 mm, Stpl/length of maxillary palpus = 0.37; GalL = 0.24–0.26 mm (mean = 0.25 mm), 0.40–0.43× length of maxillary palpomere 1; palpus length = 1.47–1.50 mm (mean = 1.48 mm); AL/length of maxillary palpus = 1.30–1.35; palpomere 1 > 2 > 3, length of palpomere 3/length of palpomere 2 = 0.83–0.84. *Labium*. Prementum subrectangular, broader than long, slightly sinuated mesally; palpus length = 1.15–1.16 mm (mean = 1.15 mm); length of maxillary palpus/length of labial palpus = 1.26–1.30; palpomere 2 0.63 as long as palpomere 1. *Chaetotaxy*. Head capsule with several secondary setae, lateral margin of parietal with nine short spines; head appendages lacking secondary setae except mandible with several tiny secondary setae (pore-like at lower magnifications).

Thorax. Pronotum trapezoidal dorsally, ovate laterally, widest at about mid-length; length of pronotum about twice that of mesonotum; metanotum subequal to mesonotum in length, both as broad as pronotum; pronotum with a posterotransverse carina; meso- and metanota both with antero- and posterotransverse carina; maximum body width at level of prothorax; thoracic venter membranous; spiracular openings present anterolaterally on mesothorax.

Legs. (Fig. 10E) Metathoracic legs longest, about 1.36× length of prothoracic legs, and 2.28× HW; femur > coxa > tibia = tarsus > trochanter; tarsus with two claws, posterior claw slightly shorter than anterior claw on pro- and mesothoracic legs, slightly longer on metathoracic leg; anterior metathoracic claw 0.23–0.29× length of metatarsus; spinulae on ventral margin of protibia and protarsus strongly developed; tarsal claws lacking spinulae ventroproximally. *Chaetotaxy*. Position and number of secondary setae as shown in Table 3.

Abdomen. Eight-segmented; LLAS = 2.28–2.30 mm (mean = 2.29 mm); dorsally sclerotized; segments 1–6 membranous ventrally, segments 7 and 8 completely sclerotized; terga 1–7 with antero- and posterodorsal transverse carina, tergum 8 with an anterodorsal transverse carina only; segments 1–7 with a pair of spiracular openings; segment 8 subcylindrical, LLAS/HW = 0.64–0.66, abruptly narrowing posterior to insertion of urogomphi; siphon 0.17–0.19× LLAS, shortly sinuated mesally. *Chaetotaxy*. Secondary setae predominantly short and spine-like.

Urogomphus. (Fig. 10G). One-segmented, lacking a subbasal suture; total length of urogomphus = 2.35–2.40 mm (mean = 2.29 mm), 1.03–1.06× LLAS, and 0.66–0.69× t HW. *Chaetotaxy*. Urogomphus lacking secondary setae.

Diagnosis. Adults. *R. poellerbauerae* is very similar to *R. novaecaledoniae* in size, shape of body and coloration, but can be separated by its double punctation on elytra as well as the shape of male genitalia. Larvae of *R. poellerbauerae* are dintinguished from all other known larvae of the genus *Rhantus* by the absence of secondary setae on the urogomphus. See under *R. monteithi*.

Etymology. This species is dedicated to Dr Christine Pöllerbauer, Noumea, New Caledonia.

Habitat. Most specimens of *R. poellerbauerae*, adults and larvae, were collected from underneath rocks at the bottom of dried-out streampools of a first-order stream, where the beetles gathered in clusters. These places were still moist, but water seemed only to collect during extended periods of rainfall. The locality was situated directly above the streampools from which we collected *R. monteithi*; the dried-out first-order stream feeds into these pools. Only one specimen of *R. poellerbauerae* was collected from the pools.

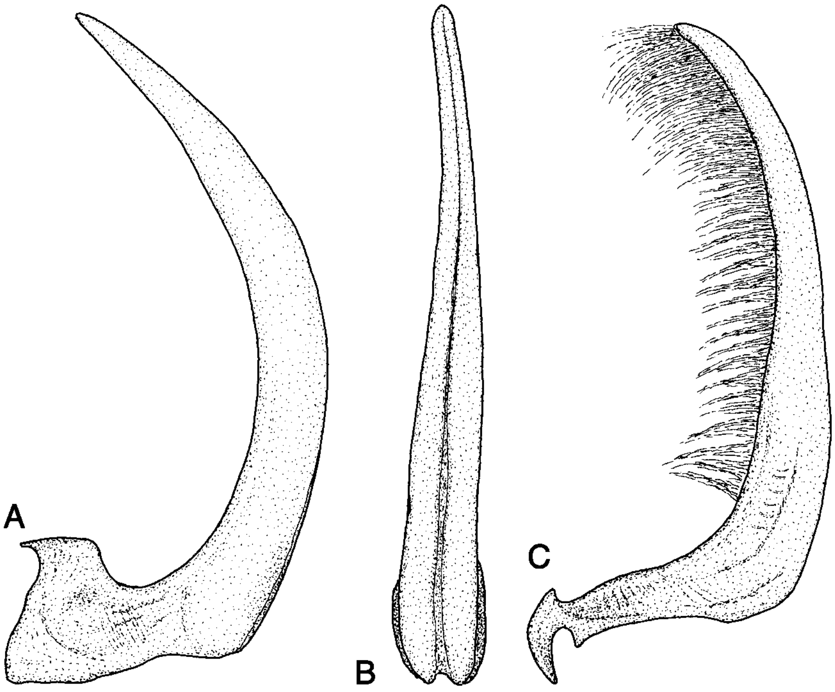

Fig. 12 A–C. *Rhantus alutaceus*. Median lobe of aedeagus in —A. lateral and —B. ventral view. —C. Paramere, external view.

Distribution. North Province of New Caledonia (Fig. 1).

***Rhantus alutaceus* Fauvel, 1883** (Figs 1 and 12)
Rhantus alutaceus Fauvel, 1883: 343; Heller 1916: 239; Zimmermann 1920: 197; Balke 1993: 43; Nilsson 2001: 48.

Type locality. New Caledonia.

Material examined. Holotype ♂ from 'N.elle Calédonie' (see Balke 1993) in IRSN.

Other specimens. 4 ♂♂, 7 ♀♀: New Caledonia: North Prov., Aoupinié, 15–25 km SW Ponérihouen, 500–700 m, 14.xi.2001, Balke & Wewalka (NC 33) (CWW); 4 ♂♂, 2 ♀♀: New Caledonia: North Prov., Aoupinié, 15–25 km SW Ponérihouen, 700 m, 14.xi.2001, Balke & Wewalka (NC 34) (NMW); 1 ind. New Caledonia: North Prov., Aoupinié, sawmill, loc. 8929, 21°10′S 165°19′E 550 m, 23.xi.2001–1.ii.2002, G. Monteith (QLDB); 3 ♂♂: New Caledonia: South Prov., Mt. Kanala, 15–20 km S Kanala, 600 m, 15.xi.2001, Balke & Wewalka (NC 37) (NMW); 4 ♀♀: New Caledonia: South Prov., Mt. Kanala, 22 km S Kanala, road to La Foa, 620 m, 15.xi.2001, Balke & Wewalka (NC 38) (NMW); 1 ex. New Caledonia: South Prov., Rivière Bleue, 19.iii.1994, Schöller (CHB). For sequenced specimens see Table 1 (BMNH).

Habitus. Body regularly oval, moderately convex; pronotum at posterior angles as broad as elytra at shoulders, lateral margin almost straight in middle; elytra regularly oval, broadest almost in the middle.

Measurements. ($n = 10$) TL 14.0–15.1 mm (mean 14.5 mm); TL-h 12.6–13.7 mm (mean 13.4 mm); TW 7.3–7.8 mm (mean 7.5 mm).

Colour. Head black, often with a vague reddish frontal mark and reddish also at the clypeal margin. Pronotum black, vaguely reddish laterally and at the anterior margin and sometimes at the posterior margin. Elytra black, in the posterior third reddish between black speckles. Ventral surface black.

Surface sculpture. Head with distinctly impressed double punctation; sometimes with very dense and fine microreticulation posteriorly and hardly defined wrinkle-like meshes present posteriorly and along the eyes. Pronotum with distinct punctation and well impressed, hardly defined, wrinkle-like meshes. Elytra with a very dense fine microreticulation, with distinct punctation of almost uniform size and defined meshes which are wrinkle-like on the anterior half.

Structures. Pronotum with lateral rim relatively fine (0.1 mm), missing on anterior sixth.

Male. Pro- and mesotarsomeres I–III distinctly dilated with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: *c.* 8 + 9

(I), *c.* 9 (II), *c.* 6 (III), and on mesotarsi: *c.* 9 + 10 (I), *c.* 10 (II), *c.* 8 (III). Protarsal claws simple, gently curved and of equal length, almost as long as tarsomere 5. Penis and parameres (Fig. 12A–C).

Larva. Unknown.

Diagnosis. Adults of *R. alutaceus* are similar to those of *R. novaecaledoniae* and *R. poellerbauerae*. *Rhantus alutaceus* can readily be separated from these species by: (1) its slightly larger size, (2) the predominantly black elytra, (3) the much stronger punctation and wrinkle-like meshes of the elytra, and (4) the typical shape of the median lobe (Fig. 12A–C).

Habitat. Pools in intermittent streams of medium altitude (350–700 m) as well as small waterholes in rocks at the edge of such streams.

Distribution. South and North Provinces of New Caledonia (Fig. 1).

***Rhantus suturalis* (W.S. MacLeay, 1825)**
Colymbetes suturalis W.S. MacLeay, 1825:31.

Type locality. Indonesia, Java.

Material examined. 1 ♀: New Caledonia, South Prov., Dumbea, 50 m, near road to Mt. Koghis, 3.xi.2001, leg. Balke & Wewalka (NC 1) (CWW); 1 ♀: New Caledonia: North Prov., 10 km E Pouembout, 50 m, 6.xi.2001, Balke & Wewalka (NC 7) (CWW); 1 ♂, 1 ♀: New Caledonia: North Prov., 9 km SSE Ouégoa, road to Mandjélia, 100 m, 12.xi.2001, Balke & Wewalka (NC 27) (CWW); 3 ♂♂: New Caledonia: South Prov., Mt. Mou, near Sanatorium, 400 m, 23.xi.2001, Balke & Wewalka (NC 52) (NMW, CWW). For sequenced specimen see Table 1 (BMNH).

Measurements. (New Caledonian beetles, *n* = 6) TL 11.4–12.2 mm (mean 11.6 mm); TL-h 10.4–11.3 mm (mean 10.6 mm); TW 5.9–6.5 mm (mean 6.2 mm).

This species has already been described in detail by, amongst others, Watts (1978) and Balke (1993). Synonymies, type localities, type specimen data and references are provided by Balke (1993). It is very similar to *R. annectens* (Fig. 7E) and in fact males should be examined for reliable identification. While the male fore and middleclaws are subequal in length in *R. annectens*, the inner claw is distinctly shorter in *R. suturalis*, the inner foreclaw also more strongly curved (Balke 1993).

Habitat. New Caledonia. Backflows of slowly flowing streams and streampools at lower altitudes (50–400 m).

Distribution. Palearctic, Oriental and Australian regions (in the latter in Australia, New Guinea, New Caledonia, New Zealand).

Fijian species
***Rhantus vitiensis* J. Balfour-Browne, 1944b** (Figs 1, 7D and 13)
Rhantus vitiensis J. Balfour-Browne, 1944b: 99; Balke 1993: 47; Nilsson 2001: 53.

Type locality. Fiji, Viti Levu, Nadarivatu.

Material examined. Lectotype ♂ from Nadarivatu (designated by Balke 1993) in BMNH. Other specimens. 3 ♂♂: Fiji: Viti Levu, Navai, Mt. Victoria, 800–900 m, 8.xi.2003, Wewalka, Balke & Mailautoka (FI 06) (BMNH); 2 ♂♂: Fiji: Viti Levu, Nadarivatu, N of pass, 650 m, 8.xi.2003, Wewalka, Balke & Mailautoka (FI 08) (CWW, BMNH); 7 ♂♂: Fiji: Viti Levu, Lautoka, Abaca, near waterfall, 500–700 m, 11.xi.2003, Wewalka, Balke & Mailautoka (FI 12) (BMNH, CWW, NMW). Based on morphology, females can not be assigned to either *R. vitiensis* or *R. bula*. For sequenced specimens see Table 1 (BMNH).

Habitus. Body oblong-oval, moderately convex; pronotum at posterior angles as broad as elytra at shoulders, lateral margin regularly rounded; elytra regularly oval, broadest almost in the middle (Fig. 7D).

Measurements. (*n* = 5) TL 10.7–11.5 mm (mean 11.0 mm); TL-h 9.7–10.1 mm (mean 10.0 mm); TW 5.4–5.7 mm (mean 5.6 mm).

Colour. Head black, with a reddish transverse frontal mark often divided into two. Pronotum black, vaguely reddish at the lateral margin. Elytra reddish with many black, often confluent, speckles, they are concentrated near apex, forming a black spot; narrow lines along suture and at lateral margin are free of speckles. Ventral surface black (Fig. 7D).

Surface sculpture. Head with finely impressed double punctation; with hardly defined meshes present on the posterior third and along eyes. Pronotum with finely impressed double punctation and well impressed polygonal meshes. Elytra with a very dense and distinct microreticulation which is missing on the anterior half near suture; with distinct punctation of almost uniform size, in areas with microreticulation punctures are hardly visible; with hardly defined meshes visible only in the area without microreticulation.

Structures. Pronotum with lateral rim relatively fine (0.1 mm) and entire; prosternal process.

Male. Pro- and mesotarsomeres I–III distinctly dilated with rows of elongate suction discs ventrally. Number of discs

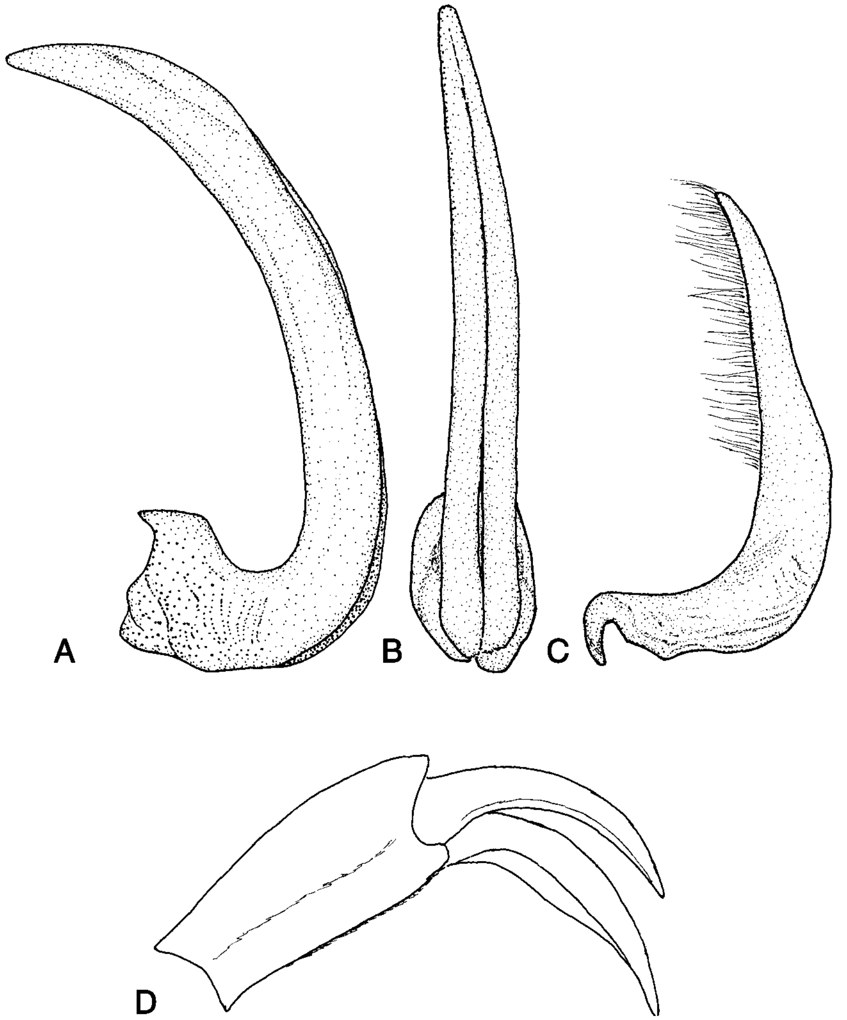

Fig. 13 A–D. *Rhantus vitiensis*. Median lobe of aedeagus in —A. lateral and —B. ventral view. —C. Paramere, external view. —D. Male foreclaw.

per row and the corresponding segment, respectively, on protarsi: 10–12 + 11–13 (I), 10–12 (II), 9–10 (III), and on mesotarsi: 10–12 + 11–14 (I), 12–13 (II), 10–11(III). Protarsal claws simple, gently curved and of equal length, almost as long as tarsomere 5; inner claw broadened (Fig. 13D). Penis and parameres (Fig. 13A–C).

Female specimens of *R. vitiensis* cannot be differentiated from specimens of *R. bula* based on morphology. Females examined, see below. When desired, females could be assigned to males based on DNA sequence data (see Fig. 5).

Diagnosis. Very similar to both *R. bula* and *R. kini*; see the respective species for diagnosis.

Habitat. Pools of streams at higher altitudes (500–900 m).

Distribution. Fiji (Viti Levu) (Fig. 1).

***Rhantus bula* sp. nov.** (Figs 1 and 14)

Type locality. Fiji, Viti Levu, Nadarivatu.

Material examined. Holotype ♂: Fiji: Viti Levu, Nadarivatu, N of pass, 650 m, 8.xi.2003, Wewalka, Balke & Mailautoka (FI 08) (NMW); Paratypes: 7 ♂♂: with same data as holotype (BMNH, CWW, NMW); 4 ♂♂: Fiji: Viti Levu, Lautoka, Abaca, waterfall, 500–700 m, 11.xi.2003, Wewalka, Balke & Mailautoka (FI 12) (BMNH, CWW, NMW). For sequenced specimens see Table 1 (BMNH).

Description. Only characters different from *R. vitiensis* are mentioned.

Measurements. (*n* = 7) TL 10.7–11.0 mm (mean 10.9 mm); TL-h 9.6–10.1 mm (mean 9.7 mm); TW 5.2–5.5 mm (mean 5.2 mm).

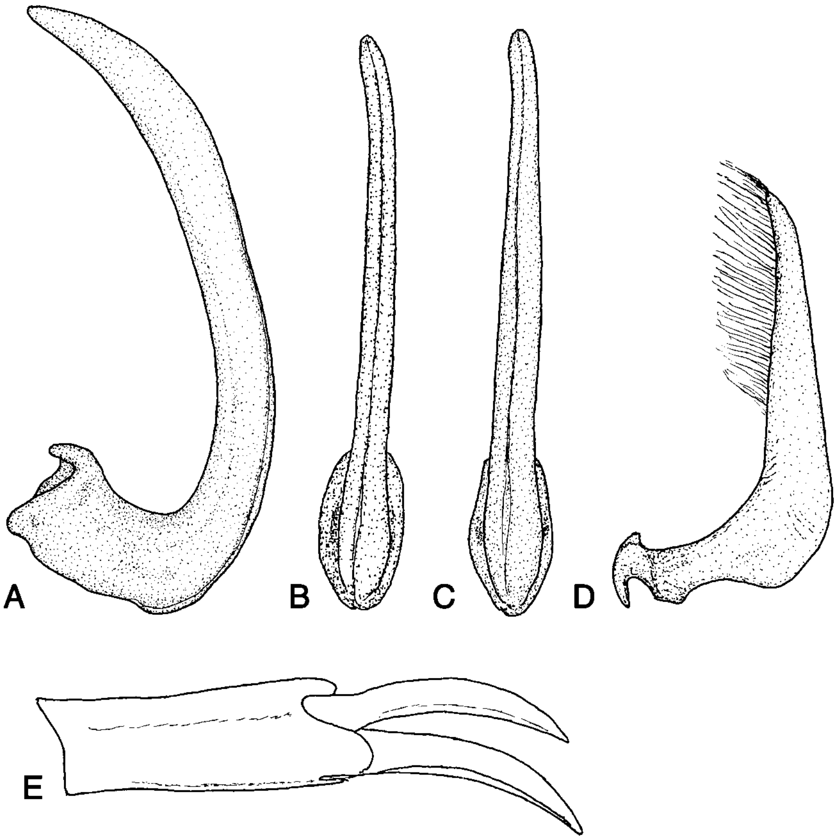

Fig. 14 A–E. *Rhantus bula*. Median lobe of aedeagus in —A. lateral and —B. ventral view (Abaca), —C. ventral view (Nadarivatu). —D. Paramere, external view. —E. Male foreclaw.

Male. Pro- and mesotarsomeres I–III distinctly dilated with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: 7–9 + 9–10 (I), 8–10 (II), 7–8 (III), and on mesotarsi: 7–10 + 8–10 (I), 8–10 (II), 7–8 (III). Protarsal claws simple, gently curved and of equal length, almost as long as tarsomere 5; inner claw not broadened (Fig. 14E). Penis and parameres (Fig. 14A–D). Penis, in ventral view, slightly narrower in a specimen from Abaca (FI12: Fig. 14B) than Nadarivatu (FI08: Fig. 14C).

Female. See under *R. vitiensis*.

Diagnosis. Males can be differentiated from *R. vitiensis* by the narrower median lobe of aedeagus, not broadened inner claw of protarsus, elongate suction discs on pro- and mesotarsomeres I–III less numerous, and the slightly more slender body.

Etymology. Bula is the most widely used Fijian welcome address, a friendly ‘hello!’.

Habitat. Pools of streams at higher altitudes (500–700 m).

Distribution. Fiji (Viti Levu) (Fig. 1).

Females of either *R. vitiensis* or *R. bula*: 4 ♀♀: Fiji: Viti Levu, Nadarivatu, N of pass, 650 m, 8.xi.2003, Wewalka, Balke & Mailautoka (FI 08) (CWW, NMW); 9 ♀♀: Fiji: Viti Levu, Lautoka, Abaca, waterfall, 500–700 m, 11.xi.2003, Wewalka, Balke & Mailautoka (FI 12) (CWW, NMW).

***Rhantus kini* sp. nov.** (Figs 1 and 15)

Type locality. Fiji, Vanua Levu, Mt. Delaikoro.

Material examined. Holotype ♂: Fiji: Vanua Levu, Mt. Delaikoro, below peak, 800 m, 14.xi.2003, Wewalka, Balke & Mailautoka (FI 18) (NMW); Paratypes: 6 ♂♂, 13 ♀♀: with same data as holotype (CWW, NMW); 1 ♂, 6 ♀♀: Fiji: Vanua Levu, Mt. Delaikoro, 600 m, 14.xi.2003, Wewalka, Balke & Mailautoka (FI 19) (CWW, NMH); 4 ♂♂, 5 ♀♀: Fiji: Taveuni, Des Voeux Peak, 1100 m, 20.xi.2003, Wewalka, Balke & Mailautoka (FI 28) (CWW, NMH). For sequenced specimens see Table 1.

Description. Only characters different from *R. vitiensis* are mentioned.

Habitus. Body oblong-oval, moderately convex; pronotum at posterior angles as broad as elytra at shoulders, lateral margin

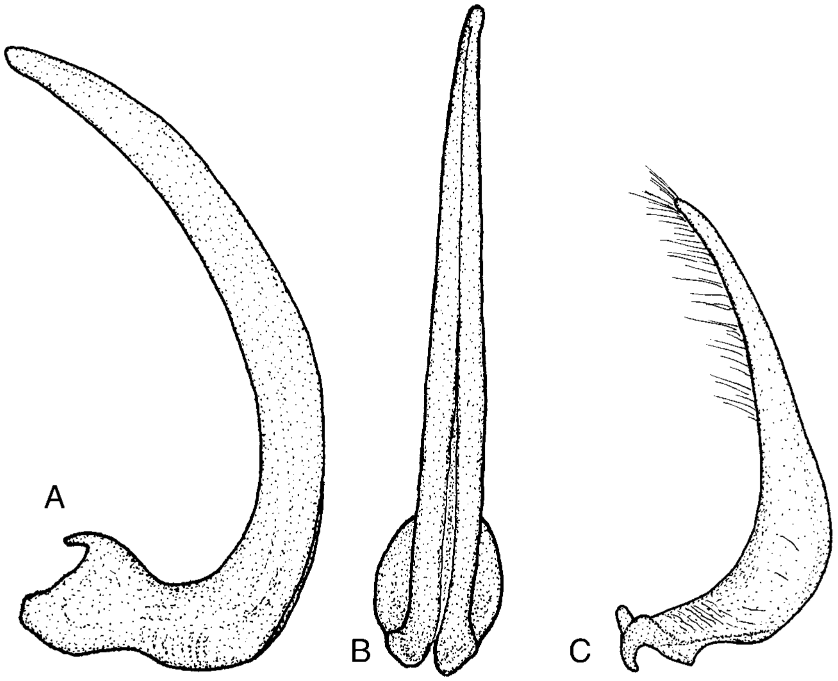

Fig. 15 A–C. *Rhantus kini*. Median lobe of aedeagus in —A. lateral and —B. ventral view. —C. Paramere, external view.

regularly rounded; elytra regularly oval, broadest almost in the middle.

Measurements. (*n* = 27) TL 9.8–11.0 mm (mean 10.4 mm); TL-h 8.9–9.9 mm (mean 9.4 mm); TW 4.8–5.5 mm (mean 5.1 mm).

Male. Pro- and mesotarsomeres I–III distinctly dilated with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: *c.* 8 + 10 (I), *c.* 10 (II), *c.* 8 (III), and on mesotarsi: *c.* 10 + 10 (I), *c.* 10 (II), *c.* 8–10 (III). Protarsal claws simple, gently curved and of equal length, almost as long as tarsomere 5. Penis and parameres (Fig. 15A–C).

Diagnosis. Males can be differentiated from *R. vitiensis* and *R. bula* by the much narrower median lobe of aedeagus, and from *R. vitiensis* by the not broadened inner claw of protarsus. Females of *R. kini* can readily be separated from *R. bula* and *R. vitiensis* based on geographical distribution.

Etymology. For Mr Kinikoto Mailautoka, our travel companion, guide and source of wisdom during the fieldwork in Fiji.

Habitat. Streampools, also rather small ones of first-order streams, or in tiny spring 'pools', at higher altitudes (600–1100 m).

Distribution. Vanua Levu and Taveuni (Fig. 1).

Rhantus annectens **Sharp, 1882** (Figs 1, 7E and 16)
Rhantus annectens Sharp, 1882: 608; Zimmermann 1920: 197; Balke 1993: 56; Nilsson 2001: 48.

Type locality. Samoa Islands (Navigator Islands).

Material examined. Lectotypus ♂ from '? Navigators islands' (= Samoa) designated by Balke (1993), in BMNH. Other specimens 2 ♂♂, 1 ♀: Fiji: Viti Levu, E Raraimatuku Plateau, betw. Serea-Naitauvoli, 150 m, 7.xi.2003, Wewalka, Balke & Mailautoka (FI 03) (CWW); 2 ♂♂: Fiji: Viti Levu, Nausori Highlands, Nausori, 650 m, 12.xi.2003, Wewalka, Balke & Mailautoka (FI 15) (CWW); 3 ♂♂, 3 ♀♀: Fiji: Taveuni, 9.5 km, SW Somosomo, roadside, 50 m, 21.xi.2003, Wewalka, Balke & Mailautoka (FI 30) (CWW); 3 ♂♂, 1 ♀: Fiji: Kadavu, nr Vunisea, 100 m, 24.xi.2003, Wewalka, Balke & Mailautoka (FI 31) (CWW). For sequenced specimens see Table 1 (BMNH).

Habitus. Body regularly oval, moderately convex; pronotum at posterior angles as broad as elytra at shoulders, lateral margin regularly rounded; elytra regularly oval, broadest behind the middle (Fig. 7E).

Measurements. (*n* = 15) TL 10.9–12.9 mm (mean 12.2 mm); TL-h 10.1–11.8 mm (mean 10.9 mm); TW 5.9–6.6 mm (mean 6.4 mm).

Colour. Head testaceous, black alongside the eyes and posterior margin and with black lobes reaching from the eyes

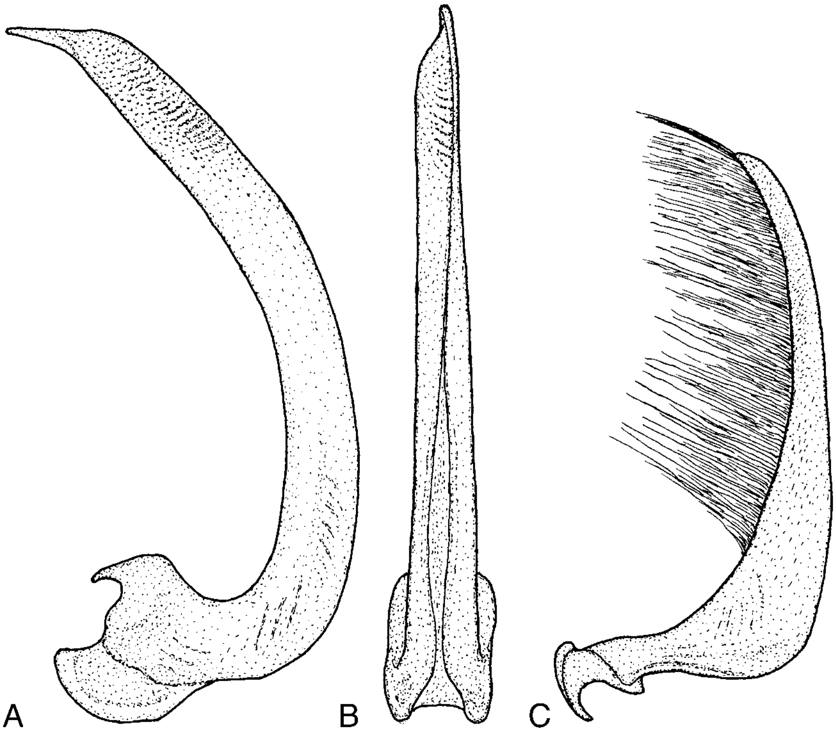

Fig. 16 A–C. *Rhantus annectens*. Median lobe of aedeagus in —A. lateral and —B. ventral view. —C. Paramere, external view.

almost to the centre; this forms a transverse testaceous mark on the frons. Pronotum testaceous with a almost round black spot in the centre. Elytra testaceous, with many black, often confluent, speckles; they are concentrated near the apex, forming a black spot; narrow lines along suture and at lateral margin are free of speckles (Fig. 7E). Ventral surface black.

Surface sculpture. Head with distinctly impressed double punctation and additional clearly defined and distinctly impressed meshes present on the posterior two thirds. Pronotum with well impressed double punctation and distinctly impressed polygonal meshes. Elytra with a very dense microreticulation which is less distinct on the anterior half near suture; regular polygonal meshes more impressed on the anterior half and with distinct punctation of almost uniform size situated mostly in grooves of meshes.

Structures. Pronotum with lateral rim relatively fine (0.07 mm), missing on anterior tenth.

Male. Pro- and mesotarsomeres I–III distinctly dilated, with rows of elongate suction discs ventrally. Number of discs per row and the corresponding segment, respectively, on protarsi: 6–7 + 7–8 (I), 6–8 (II), 5 (III), and on mesotarsi: 6–7 + 6 (I), 5 (II), 5 (III). Protarsal claws simple, gently curved and of almost equal length, distinctly shorter than tarsomere 5. Penis and parameres (Fig. 16A–C).

Diagnosis. *Rhantus annectens* is similar to *R. suturalis* in coloration and sculpture, but can be separated by the male genitalia and the simply curved male fore and middle claws of *R. annectens*.

Habitat. Streampools, 50–650 m.

Distribution. Fiji (Viti Levu, Taveuni, Kadavu) (Fig. 1) and perhaps Samoa Islands (Navigator Islands).

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Fig. 17 A, B. Habitat of —A. *Rhantus annectens* on Kadavu; —B. *R. vitiensis* and *R. bula* at Nadarivatu (small waterhole and thick mats of leaves caught in between rock in otherwise dry first-order stream bed, within white line).

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Appendix

Checklist of Pacific island (incl. New Guinea) *Rhantus* (References see Nilsson 2001)

R. pacificus group _sensu_ Balke (1993)

R. alutaceus Fauvel, 1883	New Caledonia
R. guadalcanalensis Balke, 1998	Solomon Islands
R. monteithi sp. nov.	New Caledonia
R. novaecaledoniae J. Balfour-Browne, 1944a	New Caledonia
R. poellerbauerae sp. nov.	New Caledonia
R. schauinslandi Ordish, 1989	New Zealand
R. pacificus complex	
R. oceanicus Balke, 1993	Hawaiian Islands
R. pacificus (Boisduval, 1835)	Hawaiian Islands
R. pseudopacificus Balke, 1993	Hawaiian Islands

***R. suturalis* group *sensu* Balke (1993, 2001, this paper)**

R. annectens Sharp, 1882	Fiji (? Samoa,? Tonga)
R. anggi Balke, 2001	West Papua
R. bacchusi Balke, 2001	Papua New Guinea
R. bula sp. nov.	Fiji
R. cheesmanae Balke, 1993	Vanuatu
R. debilis Sharp, 1882	French Polynesia
R. englundi Ramsdale & Balke, 2006	French Polynesia
R. hiekei Balke, 1993	Samoa (? Papua New Guinea)
R. intermedius Balke, 1993	French Polynesia
R. kini sp. nov.	Fiji
R. liopteroides Zimmermann, 1927	Samoa
R. papuanus J. Balfour-Browne, 1939	Papua New Guinea
R. riedeli Balke, 2001	West Papua
R. schereri Balke, 1990	French Polynesia
R. supranubicus Balke (2001)	West Papua
R. vitiensis J. Balfour-Browne, 1944b	Fiji

'*R. suturalis* complex'

R. dani Balke, 2001	West Papua
R. ekari Balke & Hendrich, 1992	West Papua
R. kakapupu Balke, 2001	West Papua
R. suturalis (W.S. MacLeay, 1825)	Palearctic, Oriental, Australian, in the region: Australia, New Zealand, New Guinea, New Caledonia
R. simulans Régimbart, 1908	SW Australia

'American Species' (Balke 1993)

R. gutticollis (Say, 1830)	Hawaiian Islands (Oahu), Nearctic, S to Panama

***R. signatus* group**

R. galapagoensis Balke & Peck, 1993 (in Peck & Balke)	Galapagos Islands
R. plantaris Sharp, 1882	New Zealand