

Eneopterinae crickets (Insecta, Orthoptera, Grylloidea) from Vanuatu

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Cardiodactylus,
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Vanuatu,
new species.

ABSTRACT

The present study deals with the Eneopterinae crickets from Vanuatu, in particular from Espiritu Santo Island. Seven new species are described: *Cardiodactylus aobaensis* n. sp., *C. epiensis* n. sp., *C. pentecotensis* n. sp., *C. tankara* n. sp., *Lebinthus santoensis* n. sp., *L. nattawa* n. sp., *L. malekulensis* n. sp., and two are redescribed (*C. cheesmani* Otte, 2007 and *C. enkraussi* Otte, 2007). Descriptions focus on male and female genitalia, and forewing venation, while data are presented to define fine-scaled habitat, behaviour, and song repertoires.

RÉSUMÉ

Grillons Eneopterinae (Insecta, Orthoptera, Grylloidea) du Vanuatu.

La présente étude porte sur les grillons Eneopterinae du Vanuatu, et d'Espiritu Santo en particulier. Sept espèces nouvelles sont décrites : *Cardiodactylus aobaensis* n. sp., *C. epiensis* n. sp., *C. pentecotensis* n. sp., *C. tankara* n. sp., *Lebinthus santoensis* n. sp., *L. nattawa* n. sp., *L. malekulensis* n. sp., et deux sont redécrites (*C. cheesmani* Otte, 2007 et *C. enkraussi* Otte, 2007). Les descriptions se concentrent sur les genitalia mâles et femelles et la nervation des ailes antérieures, et des informations sont également présentées concernant les habitats détaillés des espèces, leur comportement et leur répertoire acoustique.

MOTS CLÉS

Insecta,
Orthoptera,
Grylloidea,
Cardiodactylus,
Lebinthus,
habitat,
communication
acoustique,
Vanuatu,
espèces nouvelles.

INTRODUCTION

The cricket subfamily Eneopterinae Saussure, 1874 (Grylloidea) represents a very diversified clade in terms of acoustic communication. This diversity concerns the stridulatory apparatus (Robillard & Desutter-Grandcolas 2004a), the emitted signals (Desutter-Grandcolas 1997, 1998; Robillard 2004; Robillard & Desutter-Grandcolas 2004b, c; Robillard *et al.* 2007) and the reproductive behaviour (Toms 1984; Preston-Mafham 2000).

In Vanuatu, these crickets are abundant both in primary forests and secondary habitats (gardens, cultures, edges, costal areas). They are represented by two genera of the tribe Lebinthini Robillard, 2004: *Cardiodactylus* Saussure, 1878 and *Lebinthus* Stål, 1877 (Robillard & Desutter-Grandcolas 2004a, 2006, 2008). The Lebinthini are widely distributed throughout Melanesian archipelagos, in South-East Asia, Northern Australia and New Caledonia (Desutter-Grandcolas & Robillard 2006; Otte 2007a). They occupy an important part in the acoustic diversity of Eneopterinae, with originalities laying mainly in the spectral properties of their songs. Based on the analysis of the frequency spectra of the calling song in reference to phylogeny, previous studies showed that Lebinthini use high frequencies for calling (Robillard & Desutter-Grandcolas 2004b). Strikingly, whereas crickets usually call with dominant frequencies corresponding to the fundamental frequency, the high frequencies dominating Lebinthini's calling are corresponding to the second or third harmonic (Robillard *et al.* 2007).

To better understand the evolution of these unique acoustic features, basic data are needed for as many species as possible, which in turn necessitates taxonomic and biological studies. In this paper I analyse the crickets Eneopterinae from Vanuatu, which were known by only a few old specimens without information about biology, acoustics and habitats. The focus is given to Espiritu Santo Island, which was extensively sampled during the SANTO 2006 Expedition (see Desutter-Grandcolas 2009 and Hugel 2009, this volume). Four new species of *Cardiodactylus* and three of *Lebinthus* are described from the archipelago, and two species are redescribed, focusing on male and female genitalia and forewing

venation. Data are provided on fine-scaled habitat (Tables 1; 2), behaviour, and song repertoires. The biological information allows a precise description of the species' life habits, and the study of life habit evolution (Grandcolas *et al.* 2001).

MATERIAL AND METHODS

MATERIAL

Extensive fieldwork was made in many localities in Espiritu Santo with Laure Desutter-Grandcolas and Sylvain Hugel, within the "Forests, Mountains, Rivers" theme of SANTO 2006 Expedition. For a narrative of the expedition, see Bouchet *et al.* (2008). A review of the geography and natural history of Santo will be published by Bouchet *et al.* (in press). Specimens were collected by sight only, by night and day, in order to observe their precise habitat and type of activity. The collected specimens are deposited in the MNHN collections. Reared specimens (generations F1-F2) are also deposited in MNHN collections when associated to acoustic and/or behavioural data. Political districts and island within Vanuatu are mentioned for every specimen within lists of material, square brackets are used for additional information not mentioned on specimen labels.

MALE TEGMINAL VENATION

Male tegminal veins and cells (Fig. 1) are named after Desutter-Grandcolas (2003) for Ensifera and Robillard & Desutter-Grandcolas (2004a) for the subfamily Eneopterinae more specifically. FW dorsal field shows strong longitudinal veins and weaker transverse ones. The three/four most inner longitudinal veins are the distal parts of 1A-4A (abbreviations, see below); the others originate from CuA and are called CuA1 to CuAi, from the most basal to the most distal ones, and each pair of successive longitudinal veins delimit a cell alignment (A, B, C...).

MALE AND FEMALE GENITALIA

Male and female genitalia have been dissected in softened specimens by cutting the membranes between

TABLE 1. — Diurnal and nocturnal habitats of Eneopterinae species according to personal observations in Espiritu Santo Is. Abbreviations: **Cl**, calling song behaviour; **Ct**, courting behaviour; **F**, foraging behaviour; **juv.**, juvenile; **R**, resting behaviour. No data available for *Lebinthus nattawa* n. sp. at night (?), *Cardiodactylus cheesmani* Otte, 2007, *C. aobaensis* n. sp., *C. epiensis* n. sp., *C. pentecotensis* n. sp., *C. gagnei* Otte, 2007 and *L. malekulensis* n. sp.

Species	Day			Night		
	Leaf litter	Tree trunk	Plant	Leaf litter	Tree trunk	Plant
<i>Cardiodactylus novae-guineae</i> (Haan, 1842)			4 ♀♀, 4 ♂♂, 13 juv.	2 juv.		19 ♂♂ (1 F, 2 Ct, 5 Cl), 9 ♀♀ (2 Ct)
<i>C. enkraussi</i> Otte, 2007	1 ♀ (R), 1 ♂ (R), 6 juv.	2 ♀♀, 1 juv. (1.2 m)	10 ♀♀ (1 R), 2 ♀♀ (R, 0.4 m), 4 ♂♂, 1 ♂ (R, 0.4 m), 7 juv.		1 ♀	7 ♀♀, 15 ♂, 6 juv., 2 ♂♂ (Cl, 0.3 m), 1 ♀ (1 m), 1 juv. (F, 0.3 m), 2 ♂♂ (F, 0.5 m), 1 ♂ (Cl, 0.6 m), 1 ♀ (2 m), 1 ♂ (1 m), 1 ♂ (1.5 m)
<i>C. tankara</i> n. sp.		1 ♂ (Cl, 2 m)	1 ♂ (1 m), 1 ♂ (Cl, 1.5 m), 1 ♂ (Cl, 2.5 m), 2 juv.			
<i>Lebinthus santoensis</i> n. sp.	32 ♀♀, 31 ♂♂, 30 juv.		1 juv.	6 ♀♀, 12 ♂♂ (4 Cl), 2 juv.		1 ♂ (1.8 m), 1 ♂ (2 m), 2 ♂♂ (Cl, 1.5 m), 4 ♂, 2 ♀♀, 5 juv.
<i>L. nattawa</i> n. sp.	4 ♀♀, 2 ♂♂, 3 juv.			?	?	?

the paraprocts and the subgenital plate or between the ovipositor and the subgenital plate respectively; they have been observed after cleaning with cold KOH using a binocular magnifying glass Leica MZ16, at magnification up to 160, and then kept in glycerine in vials pinned under studied specimens. Male genitalia are named according to Desutter (1987), modified in Desutter-Grandcolas (2003) and Robillard & Desutter-Grandcolas (2004a). Dotted parts correspond to membranous areas. Abbreviations: see below.

ACOUSTIC DATA

The basic cricket song terminology follows Ragge & Reynolds (1998). One song unit is called a syllable and corresponds to one opening-closure cycle of the male forewings; a repeated group of syllables is called an echeme and corresponds to the calling unit of a species; a series of echemes constitutes a phrase. *Cardiodactylus enkraussi* Otte, 2007, *C. tankara* n. sp. and *L. santoensis* n. sp. were studied in the field and subsequently in the laboratory. The recordings were made with a

Condenser Microphone Capsule CM16, with a flat frequency response from 5 to 250 kHz (R. Specht pers. comm.), connected to a TASCAM HD-P2 digital recorder (96 kHz sampling frequency, 16 bit). Acoustic analyses were performed using the computer software Avisoft-SASLab Pro version 4.40 (Specht 2008) and Seewave version 1.4.6 (Sueur *et al.* 2007, 2008), a custom-made library of the “R” software platform (R Development Core Team 2004). Song features were measured using the automatic commands under Avisoft-SASLab Pro for five specimens per species. Mean values and standard deviation per individual and per species were calculated after adjustment for a common recording temperature of 25°C. All recording files have been deposited in the Sound Library of the Muséum national d’Histoire naturelle, Paris.

SCAN ELECTRON MICROSCOPY

Dry wings were directly imaged, without metalization, with a Philips XL-30 ESEM in environmental mode (1-2 Torr vacuum, acceleration of 20-25 MeV).

TABLE 2. — Mean minimal distance (**d**) between individuals measured as the distance between individual 1 (**ind1**) and the closest individual (individual 2, **ind2**), individual 2 being relative to individual 1; and height (**h**) of individual 1. Abbreviation: **juv.**, juvenile; **n**, number of specimens. Height was not calculated for *Lebinthus santoensis* n. sp. which lives on the ground.

Species	ind1/ind2 (n)	d (ind1/ind2) (cm)	h (ind1) (cm)
<i>C. novaeguineae</i> (Haan, 1842)	♂/♂ (1)	15	
	♂/♀ (4)	53 ± 53	124 ± 130
	♂/juv. (3)	93 ± 57	
	♀/♂ (2)	66 ± 91	105 ± 130
	juv./♂ (1)	25	
	juv./♀ (1)	40	86 ± 52
<i>C. enkraussi</i> Otte, 2007	♂/♂ (7)	50 ± 32	
	♂/♀ (4)	62 ± 51	55 ± 31
	♂/juv. (4)	59 ± 38	
	♀/♂ (4)	27 ± 18	
	♀/♀ (1)	50	73 ± 56
	♀/juv. (2)	90 ± 57	
<i>C. tankara</i> n. sp.	juv./♂ (3)	58 ± 36	30 ± 23
	juv./juv. (3)	43 ± 23	
<i>L. santoensis</i> n. sp.	♂/♂ (5)	c. 300	171 ± 57
	♂/♀ (2)	6 ± 4	–
	♂/juv. (10)	7 ± 2	–
	♀/juv. (2)	10 ± 6	–
	juv./♂ (3)	8 ± 2	–
	juv./juv. (34)	6 ± 3	–

ABBREVIATIONS

Descriptions

juv.	juvenile specimen;
Tarsomere III-1	basal segment of hind leg tarsomere;
FW	forewing.

Male genitalia

ec ap	ectophallic apodeme;
ec arc	ectophallic arc;
ec f	ectophallic fold;
en ap	endophallic apodeme;
en s	endophallic sclerite;
ps l	pseudepiphallallic lophi;
ps p	pseudepiphallallic paramere;
ps r	pseudepiphallallic dorsal ridges;
r	rami.

Tegminal venation

1A-4A	first to fourth anal veins;
CuA1, CuA2...	first, second... bifurcations of CuA;

CuA	anterior cubitus;
CuP	posterior cubitus;
MA, MP	anterior, posterior media veins;
R	radial vein;
c1-3	first to third cells of C alignment;
d1 cell (mirror)	first cell(s) of D alignment;
d2	second cell of D alignment;
ha	harp area.

Institutions

AMNH	American Museum of Natural History, New York;
ANIC	Australian Natural Insect Collections, Canberra;
BMNH	Natural History Museum, London (formerly British Museum of Natural History);
BNHM	Basel Natural History Museum, Basel;
BPBM	Bernice P. Bishop Museum, Department of Zoology, Honolulu;
MNHN	Muséum national d'Histoire naturelle, Paris;
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden;
SAMA	South Australia Museum, Adelaide, Australia.

Measurements (in mm, mean value in brackets)

PronL	pronotum length;
PronW	pronotum width at midlength;
FIIL	hind femur length;
FIIIW	hind femur maximal width;
TIIL	hind tibia length;
FWL	forewing length;
FWW	forewing width at midlength (at the first bifurcation of CuA1 in males);
OvipL	ovipositor length.

SYSTEMATICS

List of Eneopterinae species from Vanuatu:

Genus *Cardiodactylus* Saussure, 1878

Effordi group (Otte 2007a)

C. enkraussi Otte, 2007

C. pentecotensis n. sp.

Novaeguineae group (Otte 2007a)

C. aobaensis n. sp.

C. cheesmani Otte, 2007

C. epiensis n. sp.

C. gagnei Otte, 2007

C. noveaguineae (Haan, 1842)

C. tankara n. sp.

Genus *Lebinthus* Stål, 1877

L. santoensis n. sp.

L. nattawa n. sp.

L. malekulensis n. sp.

TABLE 3. — Measurements (in mm) of *Cardiodactylus enkraussi* Otte, 2007: minimum-maximum (mean). Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIILL	FIIIW	TIILL	OvipL
Males (n = 5)	2-2.3 (2.1)	3.3-4.1 (3.6)	13-15.4 (14)	3.3-3.6 (3.5)	13.7-14.9 (14.1)	3.2-3.4 (3.4)	11.6-12.9 (12.0)	—
Female (n = 5)	2.1-2.7 (2.3)	3.5-4.2 (3.9)	14.8-16.3 (15.8)	3.2-4.2 (3.8)	13.3-15.7 (14.5)	3.5-4 (3.8)	11.6-13.9 (12.7)	10.5-11.7 (11.2)

Genus *Cardiodactylus* Saussure, 1878

DIAGNOSIS. — Among Lebinthini genera, *Cardiodactylus* is characterised by its large size, long wings most often with whitish spots in both sexes, male FW venation (W-shaped harp veins, mirror incomplete generally elongated longitudinally), and male genitalia (pseudepiphallal dorso-lateral crests, posterior apex of pseudepiphallus more or less spoon-like).

REMARKS

Based on male genitalic structure, Otte (2007a) defined two species groups within *Cardiodactylus*, the *Efordi* group and the *Novaeguineae* group.

Efordi group (Otte 2007a)

Cardiodactylus enkraussi Otte, 2007

(Figs 1A, B; 2; 3C; 4A-C;
5A; 6A; 7A-C; 14; 17A-C)

Cardiodactylus enkraussi Otte, 2007a: 353; 2007b: 32. — Robillard *et al.* 2007: 1254.

TYPE MATERIAL. — Vanuatu. [Sanma Province], [Espiritu] Santo [Is.], Segond Channel, VIII.1950, Krauss, ♂ holotype (BPBM 16,789). — Paratype ♀: identified by Otte (2007a) without specification. Not examined.

TYPE LOCALITY. — Vanuatu, Espiritu Santo Is., Segond Channel.

MATERIAL EXAMINED. — Vanuatu (46 ♂♂, 38 ♀♀, 23 juv.). [Province Sanma], Espiritu Santo Is., Luganville, site du CTRAV, forêt côtière sur sable, 15°27'00"S, 167°12'26"E, 28.X.2006, nuit, 1 ♀ (TR-409), sur plante h = 1 m; 31.X.2006, nuit, 1 ♂ (TR-482), sur plante, photo S. Hugel, PIII: molec, T. Robillard (MNHN-ENSIF2312, 2313). — Nattawa, forêt pâturée, 15°19'29"S, 167°12'09"E, 29.X.2006, jour, 2 ♀♀ (TR-428-429), sur plante; 1 ♂ (TR-431), sous feuille de plante de sous-bois, T. Robillard (MNHN-ENSIF2314-2316). — Peavot,

rive N de la rivière principale, terrasse I, 14°59'37"S, 166°47'04"E, 38 m alt., forêt secondaire (ancien jardin), 20.X.2006, jour, 9AM-3PM, 1 ♀ (TR-247), litière et herbes basses, "repos" puis saute et vole si dérangée, 1 ♂ juv. (TR-238), 1 ♀ (TR-239), 1 ♀ juv., sur plante, 21.X.2006, nuit, 3 ♂♂ (TR-293-295), 1 ♀ (TR-289), sur plante, 1 ♂ (TR-331), sur plante de sous-bois h = 0,3 m, enregistrement en milieu naturel TR-take 331; 25.X.2006, nuit, 1 ♂ (TR-331), sur plante de sous-bois h = 0,3 m, enregistrement en milieu naturel TR-take 331, T. Robillard (MNHN-ENSIF2317-2326); 20.X.2006, jour, 4 juv. (n° 46, 48, 71, 72), litière; 21.X.2006, nuit, 2 ♂♂ (n° 60, 61), 1 ♀ (n° 63), 1 juv. (n° 64), sur plante, 1 ♀ (n° 62), sur plante, PIII molec, 1 ♂ juv. (n° 79), sur plante de sous-bois h = 0,3 m, sur feuille mangeant une fleur, tube 5-2006, L. Desutter-Grandcolas (MNHN-ENSIF2327-2336). — Peavot, Mont Nouresororo, 14°59'26"S, 166°45'14"E, 636 m alt., forêt de brume, 22.X.2006, nuit, 1 ♂ (TR-298), sur plante de sous-bois h = 0,5 m, en train de manger sur feuille, photo TR, 1 ♂ (TR-299), sur plante, enregistrement en semi-captivité (chant d'appel) TR-take 64-67, T. Robillard (MNHN-ENSIF2337, 2338); 22.X.2006, nuit, 1 ♀ juv. (n° 6), sur plante de sous-bois, L. Desutter-Grandcolas (MNHN-ENSIF2339). — Peavot, rive S de la rivière principale, terrasse I, 14°59'37"S, 166°47'04"E, 38 m alt., forêt secondaire (ancien jardin), 20.X.2006, jour, 9AM-3PM, 2 juv. (TR-230, 231), litière, 1 juv. (TR-228), sur plante, photo TR, 1 ♀ (TR-248), sur tronc, "repos" puis saute et vole quand dérangé; 20.X.2006, jour, 1 ♂ (TR-245), sur plante h = 0,4 m sous les feuilles, 1 ♂ (TR-246), litière, inactif; 21.X.2006, nuit, 2 juv. (TR-281, 282), sur plante; 24.X.2006, nuit, 1 ♀ (TR-310, alcool), PIII: molec, T. Robillard (MNHN-ENSIF2340-2348); 21.X.2006, jour, 1 ♀ juv. (n° 9), sous écorce détachée, arbre à contrefort, h = 1,20 m, photo, L. Desutter-Grandcolas (MNHN-ENSIF2349). — Peavot, rive S de la rivière principale, terrasse II, 14°59'37"S, 166°47'04"E, 38 m alt., forêt secondaire (ancien jardin), 23.X.2006, nuit, 1 ♀ (n° 16), sur arbre, L. Desutter-Grandcolas (MNHN-ENSIF2350). — Butmas, forêt du plateau de Tankara, 15°21'56"S, 166°59'E, 600 m alt., 16.X.2006, jour 10AM, espace dégagé près du camp, herbes hautes en bord de piste h = 1 m, 1 ♂ (TR-119), photo SH, 1 ♀ (TR-117), 1 ♀ (TR-118), photo SH;

TABLE 4. — Calling song parameters of *Cardiodactylus enkraussi* Otte, 2007. Abbreviations: **DE**, double echeme; **SE**, single echeme.

Specimens	T°C	Phrase		Single echeme						
		Number of SE	Number of DE	Dominant frequency (kHz)	Duration (ms)	Period (ms)	Syllable number	SE syllable		
								Duration (ms)	Period (ms)	Rate (/s)
TR-330	26.2	26	26	19.2 ± 0.5	167 ± 33	494 ± 76	8.8 ± 1.7	7.2 ± 1.5	19.6 ± 1.5	53 ± 5
TR-331	25.7	22	22	20.1 ± 0.4	185 ± 34	516 ± 137	10 ± 1.7	5.4 ± 0.9	19.7 ± 2.3	55 ± 2
Spec-EI3	22.6	25	23	20.9 ± 0.8	166 ± 21	834 ± 459	8.1 ± 1	8.1 ± 0.9	25 ± 3.4	49 ± 2
Spec-EI4	22.1	57	18	18.5 ± 1.1	173 ± 26	899 ± 332	8.4 ± 1.4	6.8 ± 2.4	22.4 ± 4.2	49 ± 4
Spec-EI7	22.4	—	16	18 ± 0.4	117 ± 21	649 ± 155	6.3 ± 0.8	7.4 ± 1.3	20.6 ± 2.4	54 ± 5

16.X.2006, nuit 6-10PM, 1 ♀ (TR-133), sur plante de sous-bois h = 2 m, pied de falaise, photo site LDG, PIII molec, 1 ♂ (TR-126), sur plante; 17.X.2006, nuit, 1 ♂ (TR-148), sur plante de sous-bois h = 1 m, bord de chemin, 1 ♂ (TR-147), herbes hautes en bord de piste/lisière, sur branche fine dans la végétation, T. Robillard (MNHN-ENSIF2351-2357). — Grotte de Fapon/sentier, 15°19'51,6"S, 166°57'53,6"E, forêt dans la doline, 14.X.2006, nuit, 1 ♂ (TR-76), sur plante de sous-bois h = 1,5 m en bord de piste près du camp, sous une fougère, enregistrement en semi-captivité (camp) takes 23, 25; 15.X.2006, jour, 1 ♂ (TR-80), adulte en élevage, pelouse/zone herbacée en bord de sentier, 1 ♀ (TR-84), sur feuille de plante de sous-bois, T. Robillard (MNHN-ENSIF2358-2360). — Matantas, Big Bay, Vatthé Conservation area, 15°20'S, 166°95'E, 25.X.2006, nuit, 2 ♀♀ (TR-328, 329), sur plante, 1 ♂ (TR-330), sur plante de sous-bois h = 0,6 m, sur feuille en arrière plan, enregistrement en milieu naturel TR-take 62; 27.X.2006, jour, 1 ♀ (TR-363), repos dans litière, photo TR-82-86, 1 ♀ juv. (TR-369), sur plante; X.2006, jour, 1 ♂ (TR-346, alccol), PIII: molec, T. Robillard (MNHN-ENSIF2361-2366). — Big Bay, Vatthé Conservation area, 15°20'S, 166°95'E, 26.X.2006, nuit, 3 ♂♂ (n° 46, 47, 48), 1 ♀ juv. (n° 49), sur plante de sous-bois; 27.X.2006, nuit, 3 ♂♂ (n° 52-54), sur plante de sous-bois, L. Desutter-Grandcolas (MNHN-ENSIF2367-2373). — Big Bay, Vatthé Conservation area, forêt secondaire près d'une grotte à chauve-souris: 26.X.2006, jour, 1 ♀ (TR-354), sur plante, photo habitat TR, 1 ♂ (TR-353), 1 juv. (TR-355), 2 ♀♀ (TR-348, 350), sur plante, 1 ♂ (TR-351), sur tige; 27.X.2006, nuit, 1 ♂ (TR-384) photo SH – 2 autres individus sur la même feuille: échant. bot. 4, 2 ♀♀ (TR-386), 2 ♂♂ (TR-390, 391), 1 ♀ juv. (TR-392), sur plante, T. Robillard (MNHN-ENSIF2374-2384). — Nattawa, forêt pâturée, 15°19'29"S, 167°12'09"E, 29.X.2006, jour, 2 ♀♀ juv. (TR-422, 433), sur plante, T. Robillard (MNHN-ENSIF2385, 2386). — Funafus, 15°32'46,4"S, 167°00'46"E, 30.X.2006, jour, 1 juv. (TR-460), 1 ♀ juv. (TR-461), 1 ♀ (TR-463), sur plante, 2 ♀♀ (TR-454, 455), sur plante h = 0,4 m, comportement de fuite: saute et vole si dérangée, T. Robillard (MNHN-ENSIF2387-

2391). — No precision, X.2006, 4 ♀♀, 2 ♂♂, T. Robillard (MNHN-ENSIF2392-2397). — Penaoru, Malaise, sol, 900 m A., 6-18.XI.2006, MG9 A1, 1 ♀ (MNHN-ENSIF2398), Malaise, sol, 900 m C., 6-18.XI.2006, MG9 C1, 1 ♀ C. Villemant (MNHN-ENSIF2399). — Penaoru, 600 m, XI.2006, 2 ♂♂ (ortho 14), Exped. SANTO 2006 (MNHN-ENSIF2400, 2401). — Reared in laboratory: F1, 2006-2007, 6 ♀♀, 9 ♂♂ (6 recorded, MNHN-ENSIF2402-2407), 9 juv.; F2, 2007-2008, 1 ♂ (recorded, MNHN-ENSIF2408), T. Robillard. — [Vanuatu Nouvelles-Hébrides. [Province Malampa], Malekula Is., 1 ♀, identified *C. canotus* by T. Robillard (Robillard & Desutter-Grandcolas 2004a, 2006), E. Aubert de la Rüe (MNHN-ENSIF1178).

DISTRIBUTION. — Vanuatu, Espiritu Santo Is. and Malekula Is. Otte (2007a) also mentions specimens from Eromango Is. but none could be examined in the present study.

DIAGNOSIS. — Size rather small, body slender, general colouration dark brown to grey brown, quite homogeneous with a characteristic two-part calling song with low intensity compared to that of *C. novaeguineae* and *C. tankara* n. sp. Species very similar to *C. pentecotensis* n. sp. (see below), but differing by male genitalia (enophallic sclerite).

REDESCRIPTION

In addition to the characters given in the original description: size small, body slender, general colouration dark brown to grey brown, quite homogeneous (Figs 2; 17B, C). Scapes and antennae generally homogeneously yellowish brown. Pronotum: dorsal disk trapezoidal, bisinuated posteriorly. Legs yellowish brown, femora more or less mottled with brown; tibiae more or less annulated. Fore tibiae bulbous at tympana level. Hind tibiae dorsal face with 7-11 inner (m = 9, n = 10) and 11-17 outer (m = 15, n = 10) spines above spurs, and 6-9 inner

TABLE 4. — Continuation.

Double echeme					Double echeme 1					Double echeme 2				
Dominant frequency (kHz)	Duration (ms)	Period (ms)	Syllable number	DE1/DE2 interval (ms)	Duration (ms)	Syllable number	DE1 syllable			Duration (ms)	Syllable number	DE2 syllable		
							Duration (ms)	Period (ms)	Rate (/s)			Duration (ms)	Period (ms)	Rate (/s)
20.2 ± 0.8	424 ± 23	910 ± 281	22.2 ± 1.6	171 ± 26	136 ± 23	8.1 ± 1	6.0 ± 1.4	18 ± 2.7	615 ± 4	120 ± 10	12.3 ± 1	6.9 ± 1.5	12 ± 8.3	100 ± 4
22.1 ± 0.1	425 ± 32	852 ± 87	24.1 ± 1.8	168 ± 17	144 ± 31	8.8 ± 1.4	5.1 ± 0.8	17.6 ± 3.1	62 ± 3	119 ± 9	12.6 ± 0.7	6.1 ± 1.1	11.9 ± 8.7	107 ± 3
18.8 ± 1.3	430 ± 38	889 ± 180	17.2 ± 1.7	183 ± 32	117 ± 21	5.8 ± 1.3	7.2 ± 1.2	19.8 ± 3.1	56 ± 5	125 ± 14	11 ± 1.3	9.7 ± 4.6	18.3 ± 2.8	816 ± 7
19.3 ± 0.4	473 ± 22	1037 ± 25	18.7 ± 2.1	178 ± 24	164 ± 17	8.3 ± 1.1	6.7 ± 1.5	20.9 ± 2.1	52 ± 1	115 ± 19	9.6 ± 2.3	8.7 ± 2.5	15.4 ± 9.8	81 ± 8
20.1 ± 0.2	433 ± 22	1044 ± 26	18.5 ± 1.2	197 ± 16	92 ± 16	6.1 ± 0.7	7.1 ± 1.3	17.1 ± 2.2	66 ± 4	125 ± 13	10.6 ± 1	9.8 ± 2.2	15.3 ± 10.3	835 ± 3

(m = 8, n = 10) and 8-11 outer (m = 9, n = 10) spines between spurs. Tarsomere III-1 with 3-7 spines on dorso-external edges (m = 4, n = 10). Hind wings longer than FWs, forming a dark brown tail four times as long as pronotum, increasing species gracile shape.

Male

FW (Fig. 1A, B). Dorsal field grey brown, translucent, quite homogeneous; veins whitish to grey brown; with faint dark spots, sometimes absent: above and along 1A, on FW inner edge anterior to 1A, in cell e1, in middle of harp near harp veins. Lateral field with sometimes a dark band on the dorsal edge, including veins MA, MP and R; ventral edge lighter. FW venation close to that of *C. novaeguineae*. 1A bisinuated (Figs 1A; 3C); stridulatory file with 166-179 teeth (m = 172, n = 5), located on both transverse (114-127 teeth, m = 119) and basal longitudinal (44-65 teeth, m = 52) parts of 1A (Fig. 3C). CuP missing. Harp narrow, 2 W-shaped harp veins. Mirror area variable, c1 long and narrow, c2 quite large; mirror (d1) prolonged by d2, forming together an ellipsoid surface, variably crossed by one or several accessory veins. Apical field lanceolate, with 4-5 longitudinal veins. Lateral field: latero-dorsal angle made by MP; R with 6-9 bifurcating veins.

Male genitalia (Fig. 4A-C): pseudepiphallus narrowed at midlength, with a large dorsal concavity and a narrow median process, slightly setose basally, concave dorsally, its apex spoon-like and more or less rounded. Pseudepiphallic parameres trilobate, a narrow divergent lobe fused with lateral membrane and two inner ventral lobes of variable shape. Membrane between base of para-

meres and ectophallic arc with a sclerite oriented posteriorly, forming wide membranous structures. Ectophallic arc complete and straight, anterior to parameres, with a median posterior expansion. Ectophallic apodemes variable in shape, not reaching rami apex. Apex of ectophallic fold between pseudepiphallic parameres, trilobate, the median lobe sponge-like, possibly glandular. Endophallic sclerite small, V-shaped, with a medio-posterior expansion. Endophallic apodeme made of a large medio-dorsal crest extended anteriorly. Membrane of endophallic cavity finely and transversally plicate.

Female

FWs grey brown to dark brown (Fig. 17C), veins slightly lighter than cells or of same colour, with lighter spots along CuA. FW venation (Fig. 5A): 9 or 10 strong longitudinal veins on dorsal field (3 anal veins). Ovipositor: shorter than hind femora; dorsal edge of apex slightly denticulate (Fig. 6A).

Female genitalia (Fig. 7A-C): copulatory papilla rounded with a basal sclerotized ring; apex narrowed and folded ventrally, against a rounded ventral bump.

Juvenile

Colouration variable from yellowish brown to dark brown, dorsum and femora more or less mottled with dark brown, tibiae with dark bands; lateral sides and sternites black, except a median yellow stripe. Head dorsum with same colouration as in adults; face dark brown to black with yellow patterns.

Measurements

See Table 3.

HABITAT AND LIFE HISTORY TRAITS

In Espiritu Santo, *C. enkraussi* lives in forested areas (Fig. 17A) together with *C. tankara* n. sp. (Butmas area) or *C. novaeguineae* (coastal areas), although in less conspicuous places.

Individuals are found deep in vegetation, on between large leaves, on stems, bushes or low trees, between 30 cm and 3 m in height. The species is active at night only, but some specimens are found in leaf litter by day, from where they escape by jumping and flying. At night, groups of specimens gather on plants in relatively dense populations (Tables 1; 2).

BEHAVIOUR

Calling song (Fig. 14; Table 4)

Males call from dusk to late at night, staying deep within vegetation, on leaves or branches. The calling song of *C. enkraussi* is less conspicuous than that of *C. novaeguineae* and *C. tankara* n. sp. The songs of five males recorded in the field (TR-330, TR-331, MNHN-ENSIF2363, 2325) and in the laboratory (spec-El-3 [MNHN-ENSIF2404], El-4 [2405], El-7) at 22–26.5°C are analysed here. At 25°C, the call consists of irregular song phrases (mean phrase duration \pm SD = 28.9 \pm 2.6 s). Each phrase generally begins with a series of 28 \pm 10, low amplitude, single echemes, followed by a series of 22 \pm 2 more intense double echemes subdivided into two sub-echemes by an interval of 174 \pm 23 ms, and/or by 1 to 3 intermediate syllables ($m = 2.13 \pm 0.45$) sometimes joining the two sub-echemes.

The initial single echemes (SE) have the following characteristics: SE rate = 103.2/min; SE duration = 169 \pm 27 ms; SE period = 581 \pm 232 ms; SE duty cycle = 29%. Each SE includes 8.9 \pm 1.3 syllables with the following characteristics: SE syllable rate = 56.5 \pm 3.2/s; SE syllable duration = 6.6 \pm 1.4 ms; SE syllable period = 20.5 \pm 9 ms; SE syllable duty cycle = 32%.

The double echemes (DE) have the following characteristics: DE rate = 66/min; DE duration = 429 \pm 27 ms; DE period = 909 \pm 120 ms; DE duty cycle = 47%; DE total number of syllables = 21.7 \pm 1.7. The first sub-echeme (DE1) of the double echeme is a low amplitude echeme equivalent to

the initial single echemes. Each first sub-echeme includes 7.9 \pm 1.1 syllables with the following characteristics: DE1 syllable rate = 60.5 \pm 3.5/s; DE1 syllable duration = 5.9 \pm 1.2 ms; DE1 syllable period = 18.2 \pm 2.6 ms; DE1 syllable duty cycle = 32%. The second sub-echeme (DE2) of the double echeme has much higher amplitude and includes 11.9 \pm 1.3 syllables with the following characteristics: DE2 syllable rate = 90.2 \pm 5.0/s; DE2 syllable duration = 7.2 \pm 2.4 ms; DE2 syllable period = 13.1 \pm 1.2 ms; DE2 syllable duty cycle = 55%.

The dominant frequency of *C. enkraussi* is the third harmonic of the song (single echeme: 19.5 \pm 0.6 kHz) (Robillard *et al.* 2007). Within the double echemes, the dominant frequency is slightly higher in syllables of DE2 (20.3 \pm 0.9 kHz) than in DE1 (19.6 \pm 0.7 Hz).

Courting song

The courting song is less intense than the calling song but similarly composed of single and double echemes unevenly arranged; series of one component sometimes repeated during several minutes without a clear phrase structure.

Aggressive song

Aggressive interactions between males were not observed despite many attempts in laboratory. This song could be absent from the repertoire of *C. enkraussi*.

Cardiodactylus pentecotensis n. sp.

(Figs 4D, E; 6C; 7D-F)

Cardiodactylus sp. – Robillard & Desutter-Grandcolas 2004a: 273; 2004b: 579; Robillard 2006: 674 (phylogeny and calling song study, identified as *C. canotus* Saussure, 1878 whose type was meanwhile re-examined).

TYPE MATERIAL. — [Vanuatu] Nouvelles-Hébrides. [Province Penama], île Pentecôte [Pentecost Is.], 1934, E. Aubert de la Rüe, ♂ holotype, identified as *C. canotus* by T. Robillard (Robillard & Desutter-Grandcolas 2004a) (MNHN-ENSIF1122). — Same locality, date and collector as holotype, ♀ allotype, identified as *C. canotus* by T. Robillard (Robillard & Desutter-Grandcolas 2004a) (MNHN-ENSIF1138). — [Vanuatu] Nouvelles-Hébrides. [Province Penama], île Pentecôte [Pentecost Is.], Mt.

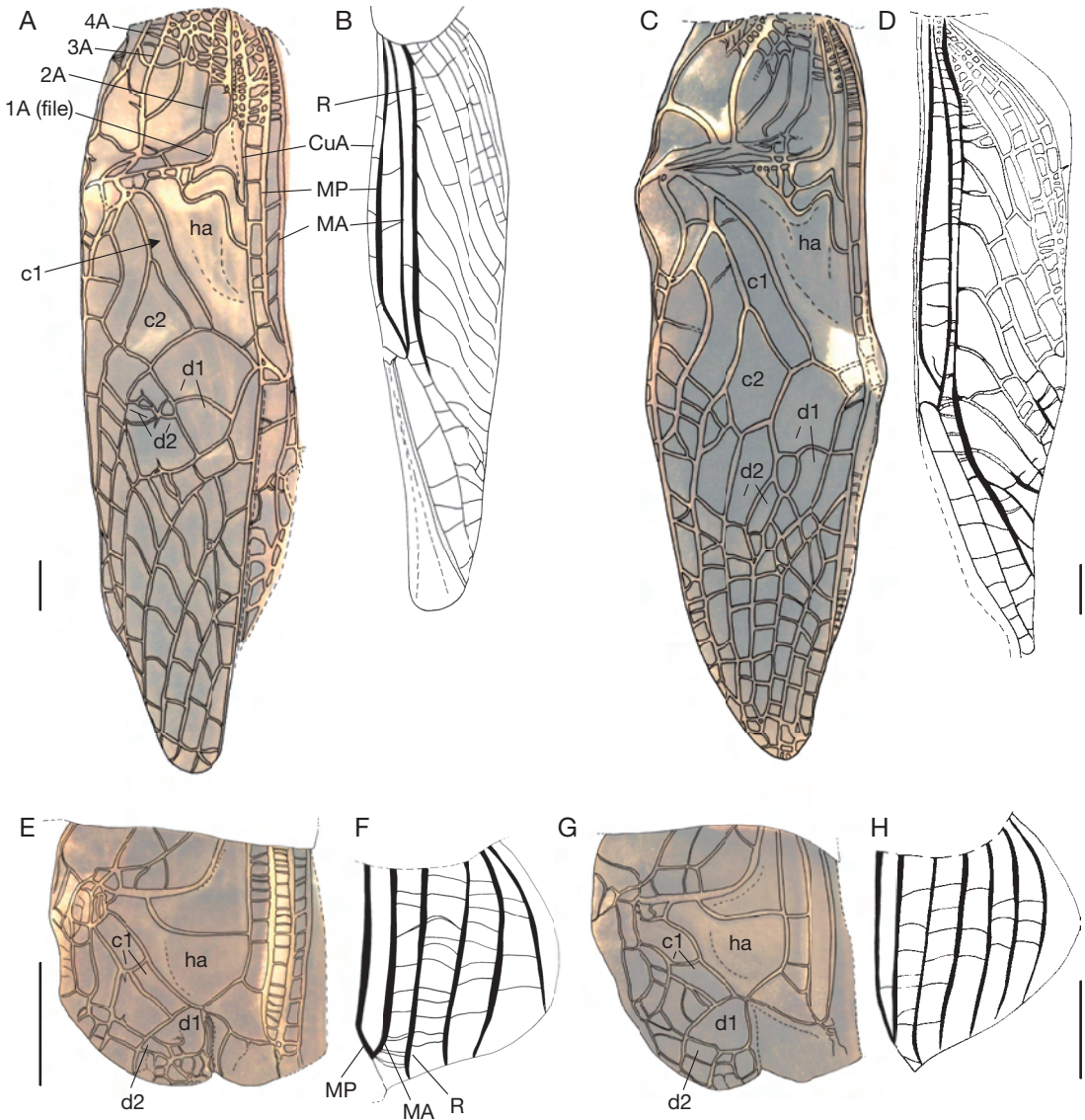


FIG. 1. — Male FW venation in dorsal and lateral views: **A, B**, *Cardiodactylus enkraussi* Otte, 2007; **C, D**, *C. tankara* n. sp.; **E, F**, *Lebinthus santoensis* n. sp.; **G, H**, *L. nattawa* n. sp. Abbreviations: see Material and methods. Scale bars: 1 mm.

Lerip, 1935-1936, E. Aubert de la Rüe, 1 ♀ paratype (MNHN-ENSIF1137).

TYPE LOCALITY. — Vanuatu, Pentecost Is.

ETYMOLOGY. — Species named after the type locality.

DISTRIBUTION. — Vanuatu, Pentecost Is.

DIAGNOSIS. — Species very similar to *C. enkraussi* in shape, size and colouration, homogeneous brown, but separate by male and female genitalia. The main difference between the two species is the wider shape and larger size of the endophallic sclerite in *C. pentecotensis* n. sp., the lateral arms of the sclerite being in continuity with the ectophallic fold sclerotization in *C. pentecotensis* n. sp. but not in *C. enkraussi*.

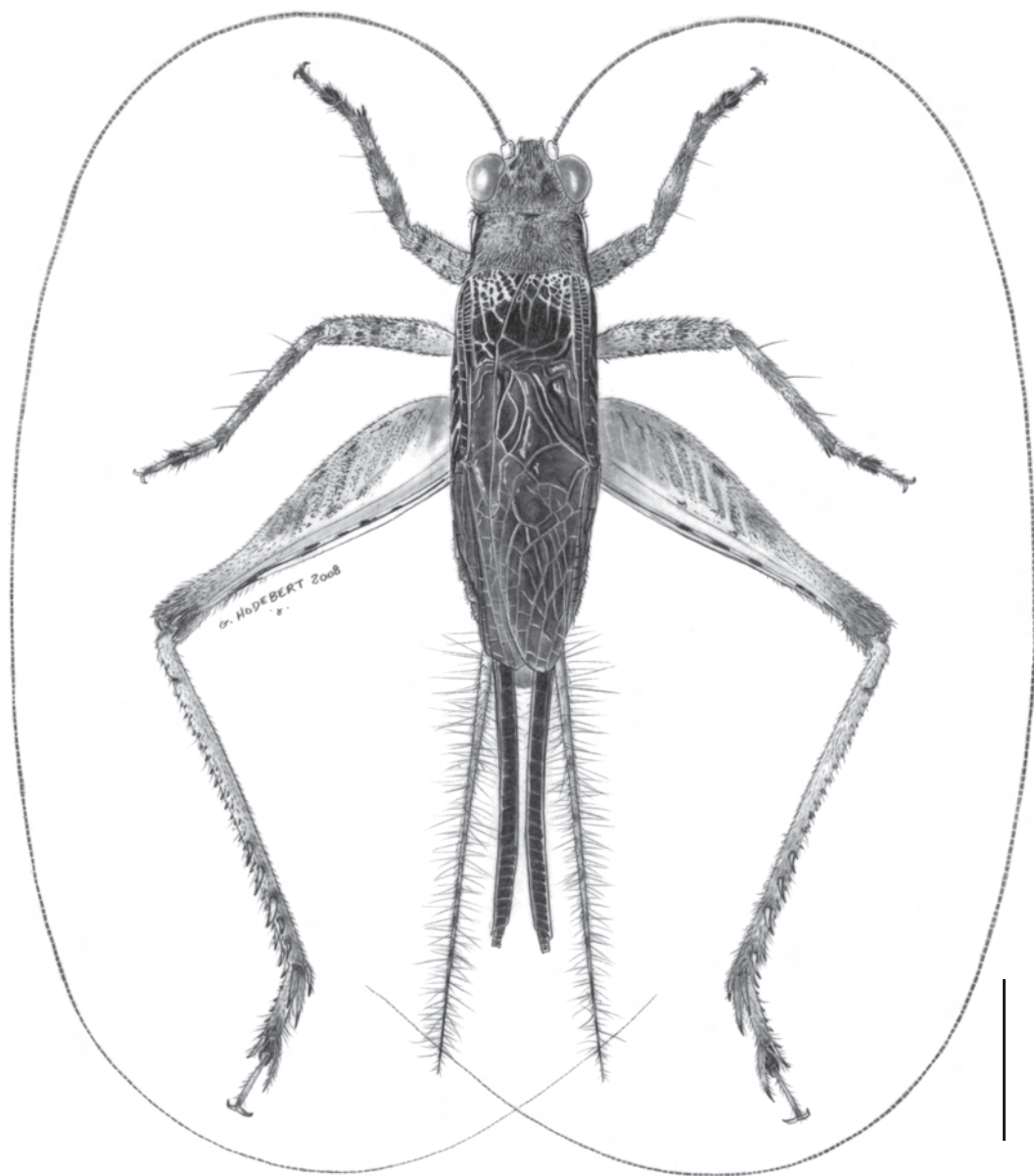


FIG. 2. — *Cardiodactylus enkraussi* Otte, 2007, male habitus. Scale bar: 5 mm.

DESCRIPTION

Species very similar to *C. enkraussi*. Hind tibiae dorsal face with 7-9 inner ($m = 8$, $n = 3$) and 12 or 13 outer ($m = 13$, $n = 3$) spines above spurs; 7 or 8 inner ($m = 7$, $n = 3$), 8-11 ($m = 9$, $n = 3$) outer spines between spurs. Tarsomeres III-1 with 4-6 spines on dorso-external edges ($m = 5$, $n = 3$).

Male

FW colouration: light brown, translucent, with the same pattern of faint dark areas as in *C. enkraussi*.

FW venation: Similar to *C. enkraussi*; stridulatory vein with 167 teeth (HT), located on both transverse (123 teeth) and basal longitudinal (42 teeth) parts of 1A. Apical field lanceolate with 4 bifurcations of

TABLE 5. — Measurements (in mm) of *Cardiodactylus pentecotensis* n. sp.: minimum-maximum (mean). Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIILL	FIILW	TIILL	OvipL
Male holotype	2.2	4.2	14	3.1	14.7	3.8	14.2	—
Female allotype	2.3	4.6	16.1	3.4	14.7	3.5	13.3	12.5
Females (n = 2)	2.3-2.5 (2.4)	4.3-4.6 (4.5)	16.1-17.2 (16.7)	3.4-3.7 (3.6)	14.7-15.2 (15)	3.5-4 (3.8)	13.3-13.9 (13.6)	12-12.5 (12.3)

CuA posterior to mirror. Lateral field: latero-dorsal angle made by MP; R with 8 bifurcating veins.

Male genitalia (Fig. 4D, E). Endophallic sclerite wide, larger than in *C. enkraussi*, its lateral arms in continuity with ectophallic fold sclerotization, unlike in *C. enkraussi*. Differs from *C. enkraussi* by many details concerning: shape of pseudepiphallus with narrowed posterior part, pseudepiphallic paramere structure, ectophallic fold sclerotization.

Female

FW venation: 9 or 10 strong longitudinal veins on dorsal field (including 3 anal veins). Ovipositor: Slightly longer than *C. enkraussi*, but still short; apex dorsal edge slightly denticulate (Fig. 6C).

Female genitalia (Fig. 7D-F): same general shape as *C. enkraussi*, but apex more protruding, and ventral bump narrower, with a median ventral sclerotized expansion.

Measurements

See Table 5.

HABITAT, LIFE HISTORY TRAITS AND BEHAVIOUR
Not documented.

Novaeguineae group (Otte 2007a)

Cardiodactylus novaeguineae (Haan, 1842)

Gryllus (Platydyctylus) novae-guineae Haan, 1842: 233.

Cardiodactylus novae-guineae – Saussure 1878: 659 (type comparison). — Kirby 1906: 88 (type species of *Cardiodactylus*). — Chopard 1915: 149; 1929: 49; 1931: 140; 1969: 312.

Cardiodactylus novaeguinea – Otte 1994: 65 (misspelling). — Robillard 2004: 29; 2006: 674 (morphological

phylogeny). — Robillard & Desutter-Grandcolas 2004a: 273; 2004b: 578 (calling song); 2006: 644 (molecular and morphological phylogeny). — Eades *et al.* 2008.

Cardiodactylus novaeguineae – Chopard 1968: 351. — Bhowmik 1981: 43. — Otte & Alexander 1983: 310. — Otte *et al.* 1987: 42. — Oshiro 1995: 44. — Yin & Liu 1995: 97. — Rentz 1996: 140 (Australian populations, biology, calling song). — Willemse 2001: 110 (biology). — Otte 2007a: 345. — Otte & Cowper 2007: 239. — Robillard *et al.* 2007 (calling song). — Robillard & Ichikawa in press (redescription and neotype definition).

TYPE MATERIAL. — **Indonesia**. [Papua Province], Biak Is., XI.1953, L.v.s. Hammen, ♂ neotype (RMNH). Paraneotypes (7 ♂♂, 14 ♀♀): **Indonesia**. [Papua Province], Biak [Is.], 20.II.1952, L. D. Brongersma, 1 ♂ (RMNH). — [Biak Is.], Base Biak, 17-24.III.1952, L. D. Brongersma & W. J. Roosdorp, 2 ♂♂, 1 ♀ (RMNH). — [Biak Is.], Schouten Islands, Base Biak, W of Sorido, 24.I.1955, L. D. Brongersma, 1 ♀ (RMNH). — Biak [Is.], X-XI.1953, Pers Kon Marine, 1 ♀ (RMNH).

Papua New Guinea. [Manus Province], Manus Is., Lorengau, 6.VI.1967, R. E. & R. M. Blackith, 1 ♀ (MNHN-ENSIF2044). — [Morobe Province], [Papua Is.], Lae, 29.V.1967, R. E. & R. M. Blackith, 2 ♂♂ (MNHN-ENSIF2045, 2046). — [Oro Province], [Papua Is.], Mt. Lamington, 1300-1500 ft., C. T. McNamara, 2 ♂♂, 4 ♀♀, identified *Cardiodactylus novae guineae* by L. Chopard (SAMA). — [Milne Bay Province], Misima Is., Louisiade Arch., Narian, 0-500 m (No 8), 1956, fifth Archbold Exped. to New Guinea, L.J. Brass, 1 ♀ (AMNH). — Misima Is., Louisiade Arch., Rev. R. J. Andrew, 1 ♀, identified *Cardiodactylus novae guineae* by L. Chopard (SAMA). — Rossel Is., Louisiade Arch., Abaleti, 0-500 m, fifth Archbold Exped. to New Guinea, L. J. Brass, 1 ♀ (AMNH). — [New Ireland Province], New Ireland [Is.], E. R. Waite, 2 ♀♀, identified as *Cardiodactylus novae guineae* by L. Chopard (SAMA).

TYPE LOCALITY. — Indonesia, Biak Is.

OTHER MATERIAL EXAMINED. — (For details and complete list of material see Robillard & Ichikawa in press) **Vanuatu**. Malampa Province, Malekula Is., 1 ♀. — Tafea

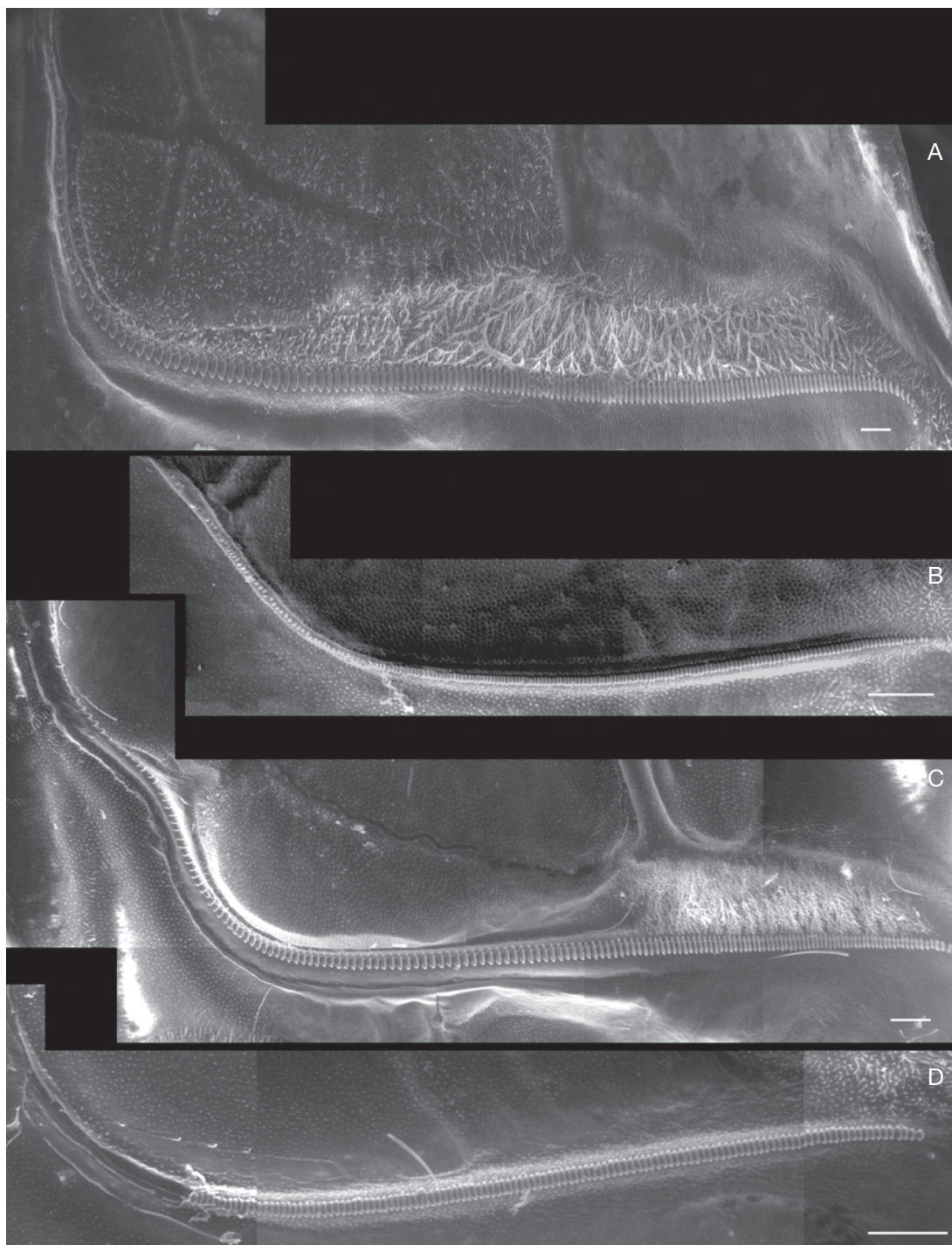


FIG. 3. — SEM view of stridulatory file: **A**, *Cardiodactylus tankara* n. sp.; **B**, *Lebinthus santoensis* n. sp.; **C**, *C. enkraussi* Otte, 2007; **D**, *L. nattawa* n. sp. Photos: S. Hugel. Scale bars: 100 μ m.

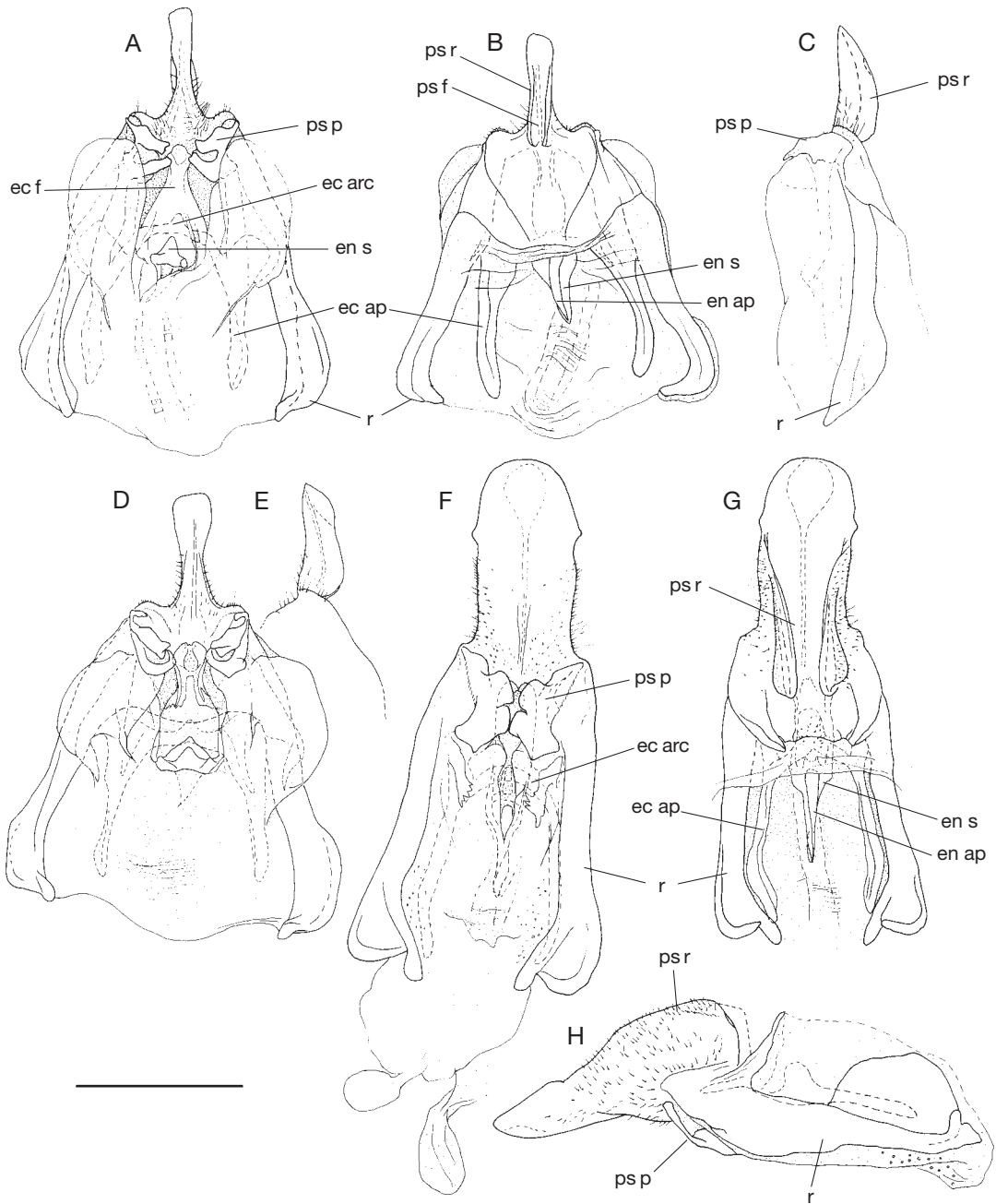


FIG. 4. — Male genitalia: **A-C**, *Cardiodactylus enkraussi* Otte, 2007, in ventral (**A**), dorsal (**B**) and lateral (**C**) views; **D, E**, *C. pentecotensis* n. sp., in ventral (**D**) and lateral (**E**) views; **F-H**, *C. tankara* n. sp., in ventral (**F**), dorsal (**G**) and lateral (**H**) views. Abbreviations: see Material and methods. Scale bar: 1 mm.

Province, Aneityum Is., 3 ♂♂, 4 ♀♀, 1 juv. — Tanna Is., 4 ♂♂, 4 ♀♀, 1 juv. — Erromango Is., 1 ♂. — Shefa Province, Efate Is., 3 ♀♀. — Epi Is., 1 ♀. — Penama Province, Pentecost Is., 1 ♂. — Aoba Is., 1 ♀. — Sanma Province, Espiritu Santo Is., 23 ♂♂, 18 ♀♀, 36 juv. — No precision, 1 ♂, 2 ♀♀. — Matantas, pointe de Quirros, 2 ♂♂, 6 juv. — Peavot, 12 ♂♂, 11 ♀♀, 14 juv. — Penaoru, 1 ♂, 1 ♀, 3 juv. — Big Bay, Vatthé Conservation Area, 2 ♂♂, 1 ♀ — Village de Kole, Loru Protected Area, 4 juv. — Nattawa, 4 juv. — Luganville, site du CTRAV, 2 ♂♂, 1 ♀, 2 juv. — Funafus, 3 ♂♂, 2 ♀♀, 3 juv.

DISTRIBUTION. — *Cardiodactylus novaeguineae* is widely distributed, occurring in coastal areas of most of the South Pacific Melanesian and Oceanian islands (Robillard & Ichikawa in press).

DIAGNOSIS. — Despite important variation in size and colouration related to its wide distribution, *C. novaeguineae* is generally a rather large species, with characteristic colouration pattern, a two-part calling song, and very distinctive male genitalia (Robillard & Ichikawa in press). See Robillard & Ichikawa (in press) for a complete redescription and a detailed list of material examined and distribution of the species.

HABITAT AND LIFE HISTORY TRAITS

The species lives in coastal regions in open forested areas, near borders and edges. Individuals are found in Espiritu Santo on or under large leaves, on low plants, bushes or low trees, between 30 cm and 3 m in height (Table 1). Juveniles commonly gather on the same plants and are sometimes found in the leaf litter, while adults are generally more spaced from one another (Tables 1; 2). Foraging occurs from afternoon to night and no difference was observed in positioning between day and night, either for adults or juveniles.

BEHAVIOUR

Calling song

Males call from dusk to late at night, but a few males were heard calling earlier during afternoon by cloudy days. The calling song consists of irregular phrases including single or two-part echemes (see Robillard & Ichikawa [in press] for measurements). For analysed songs, the dominant frequency is 15.8 ± 0.5 kHz at 25°C and corresponds to the third harmonic of the song (Robillard *et al.* 2007); the mean fundamental frequency is about three times lower (5.3 ± 0.2 kHz).

Courting song

This song is less intense than the calling song. It has similar long-syllable and short-syllable components as the calling song, but unevenly arranged, with series of one component sometimes repeated during several minutes.

Copulatory behaviour

Several matings were observed in the field in Espiritu Santo, on tree branches or large leaves at 1–3 m in height. During copulation, the female mounts the male while its FWs are raised at 90°, and pushes male's FWs forward with her head. Mounting lasts long compared to other species (pers. obs., c. 80 s, n=2). Multiple mating (2 or more) and male guarding behaviour have also been observed (pers. obs. 2008).

Cardiodactylus cheesmani Otte, 2007 (Figs 5D; 6E; 7G-I)

Cardiodactylus cheesmani Otte, 2007a: 350; 2007b: 31.

TYPE MATERIAL. — Vanuatu. [Tafea Province], Tanna Is., X.1930, L. E. Cheesman, ♂ holotype (BPBM 16,778). — Same locality, date and collector as holotype, ♀ paratype. Not examined.

MATERIAL EXAMINED. — [Vanuatu] Nouvelles-Hébrides. [Province Tafea], Tanna Is., 1924, E. Aubert de la Rüe, 1 ♀, identified *C. gaimardi* by L. Chopard (MNHN-ENSIF1179).

TYPE LOCALITY. — Vanuatu, Tanna Is.

DISTRIBUTION. — Vanuatu, Tanna Is.

DIAGNOSIS. — Species of average size, comparable to *C. tankara* n. sp. (see below). Colouration light brown, little contrasted. Dorsal disk of pronotum with incomplete lateral bands. Male FW with a clear light crescent including posterior part of mirror; male genitalia close to that of *C. tankara* n. sp., but differing by the shape of pseudepiphallic sclerite (dorsal crest not asymmetrical, lack of basal protuberance near median shrinkage).

REDESCRIPTION

In addition to the characters given by Otte (2007b): general colouration light brown, little contrasted. Scapes yellowish brown. Fastigium 1.5 times as long

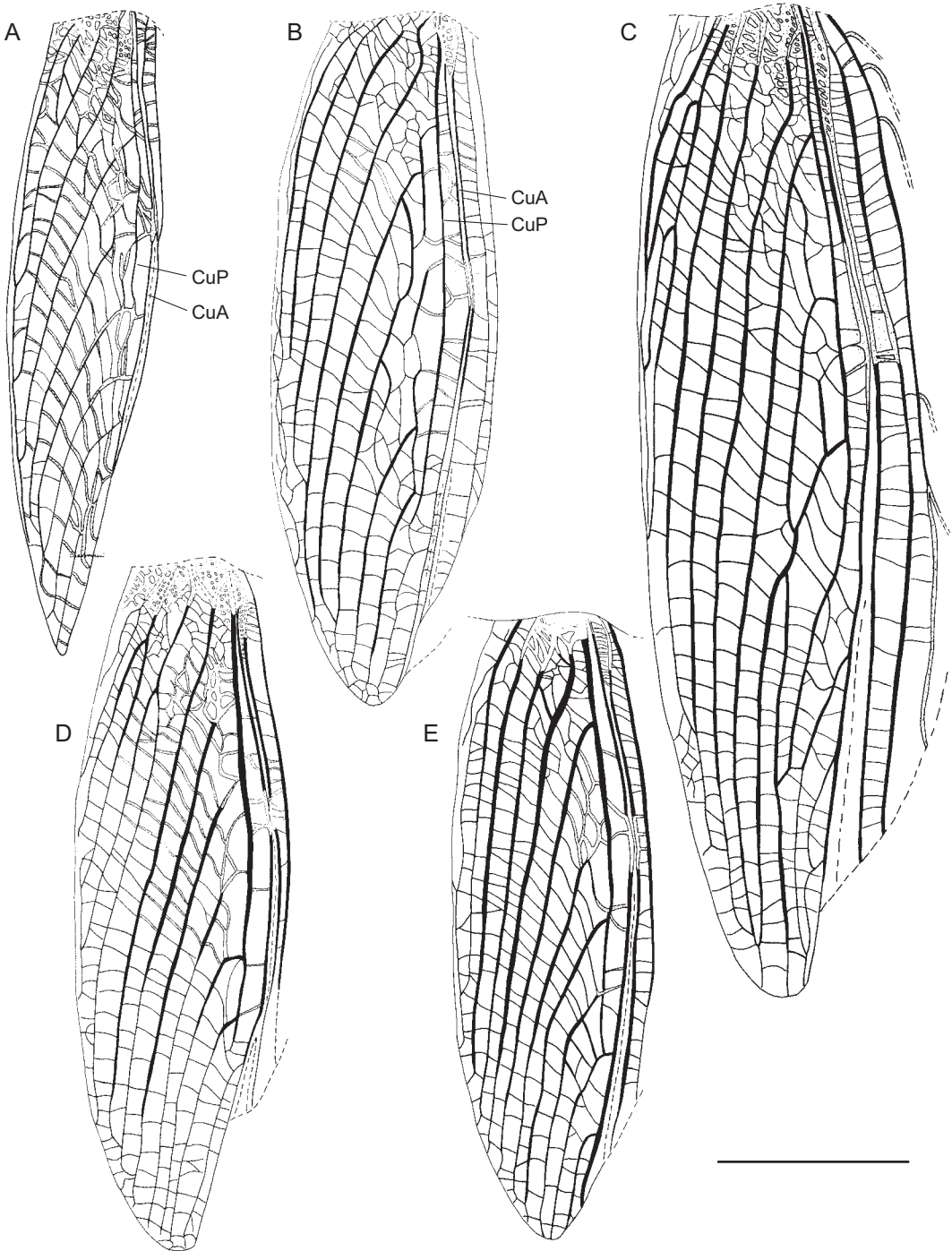


FIG. 5. — Female FW venation: **A**, *Cardiodactylus enkraussi* Otte, 2007; **B**, *C. tankara* n. sp.; **C**, *C. aobaensis* n. sp.; **D**, *C. cheesmani* Otte, 2007; **E**, *C. epiensis* n. sp. Dotted areas represent patterns of white or yellow areas. Abbreviations: see Material and methods. Scale bar: 5 mm.

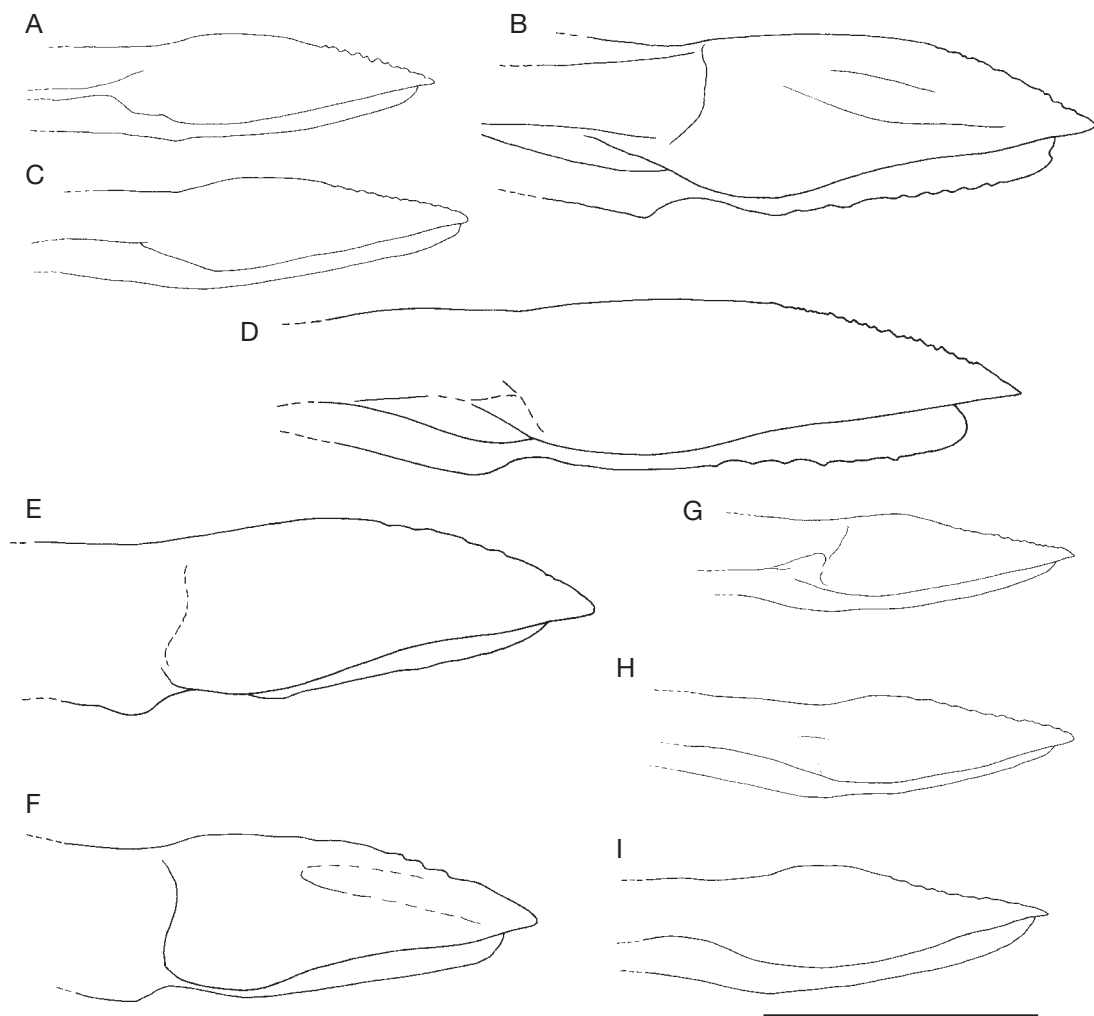


FIG. 6. — Apex of ovipositor in lateral view: **A**, *Cardiodactylus enkraussi* Otte, 2007; **B**, *C. tankara* n. sp.; **C**, *C. pentecotensis* n. sp.; **D**, *C. aobaensis* n. sp.; **E**, *C. cheesmani* Otte, 2007a; **F**, *C. epiensis* n. sp.; **G**, *Lebinthus santoensis* n. sp.; **H**, *L. nattawa* n. sp.; **I**, *L. malekulensis* n. sp. Scale bar: 1 mm.

as wide, median ocellus yellow. Pronotum: dorsal disk trapezoidal, slightly bisinuated posteriorly. Fore tibiae not widened at tympana level. Hind tibiae dorsal face with 6 inner and 14 outer spines above spurs, 4 inner and 10 outer spines between spurs ($n = 1$). Tarsomeres III-1 with 4 spines on dorso-external edges ($n = 1$). FWs slightly longer than abdomen; hind wings forming a short grey brown tail about 1.5 times as long as pronotum. Cerci homogeneously brown.

Female

FW colouration (Fig. 5D): dorsal field cells and longitudinal veins homogeneously brown, transverse veins whitish on FW anterior half; FW base with whitish sclerotization, including bases of 1-3A, CuP, CuA and MP; whitish area on anterior lateral angle, including MA/MP area, part of CuA and associated transverse veins. Area between CuA and CuP dark brown, except whitish transverse veins. Area between MP and R brown, R bifurcating veins whitish. FW venation: 10

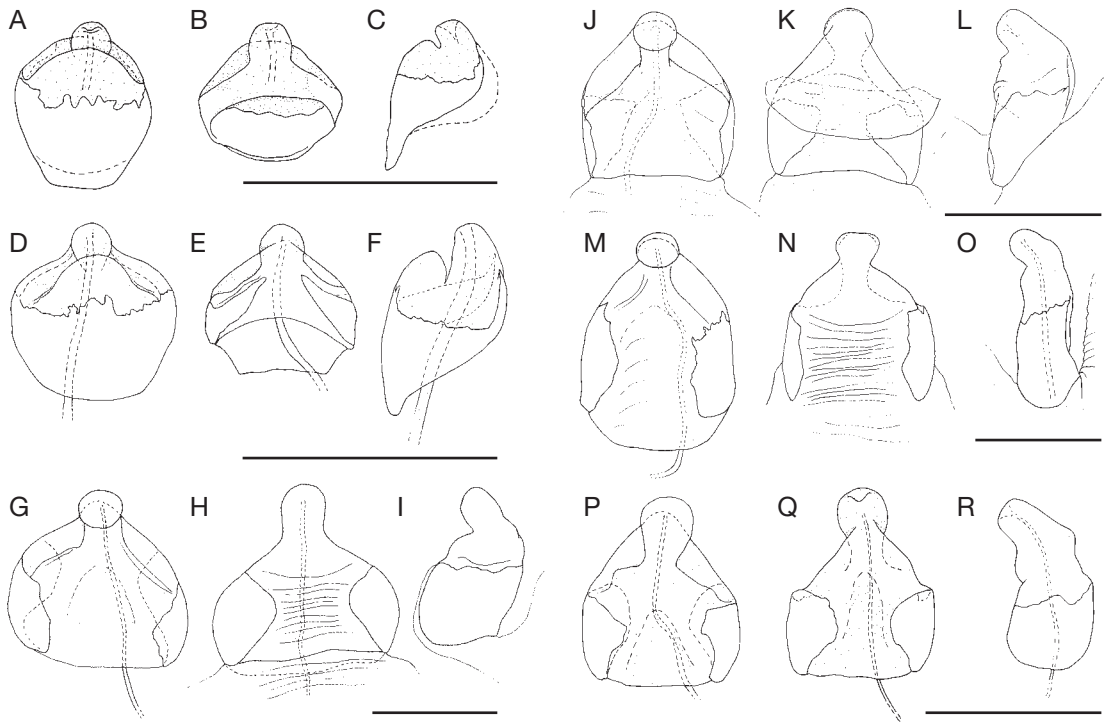


FIG. 7. — Female copulatory papilla in ventral, dorsal and lateral views: **A-C**, *Cardioactylus enkraussi* Otte, 2007; **D-F**, *C. pentecotensis* n. sp.; **G-I**, *C. cheesmani* Otte, 2007; **J-L**, *C. tankara* n. sp.; **M-O**, *C. aobaensis* n. sp.; **P-R**, *C. epiensis* n. sp. Scale bars: 1 mm.

TABLE 6. — Measurements (in mm) of *Cardioactylus cheesmani* Otte, 2007. Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIILL	FIILW	TIILL	OvipL
Female (n = 1)	3.5	5.7	19.2	4.7	18	5	16.6	15

strong longitudinal veins on dorsal field (including 1-3A). R with 7 bifurcating veins. Ovipositor: shorter than hind femora, as in *C. tankara* n. sp.; apex dorsal and ventral edges not clearly denticulate (Fig. 6E).

Female genitalia: copulatory papilla (Fig. 7G-I) similar to *C. tankara* n. sp., dorsal side concave, apex more prominent and its curvature less important; dorsal surface not plicate.

Measurements

See Table 6.

HABITAT, LIFE HISTORY TRAITS AND BEHAVIOUR
Not documented.

Cardioactylus tankara n. sp.

(Figs 1C, D; 3A; 4F-H; 5B; 6B; 7J-L; 8; 15; 17D, E)

Cardioactylus sp. — Robillard *et al.* 2007: 1254 (calling song analysis).

TYPE MATERIAL. — Holotype: Vanuatu. [Province Sanma], Espiritu Santo Is., Butmas, forêt du plateau de Tankara, 15°21'56"S, 166°59'E, 600 m alt., 13.X.2006, jour, 12AM, ♂ (TR-1), sur plante de sous-bois, sur tronç à h = 2 m, forte pente, enregistrement (chant d'appel) TR-take 16, photo + vidéo site SH, T. Robillard (MNHN-ENSIF2409).

Allotype: same locality and collector as holotype, 16.X.2006, nuit, 6-10PM, ♀ (TR-128), sur plante de

sous-bois, vidéo TR-V4 de ponte en semi-captivité, obs. copulation avec ♂ (TR-127) (MNHN-ENSIF2410). Paratypes (9 ♂♂; 2 ♀♀): same locality and collector as holotype, X.2006, adulte en élevage, souche F0, élevage Santo TR, 1 ♀ (MNHN-ENSIF2432); 13.X.2006, jour, 7-11AM, 1 ♂ (TR-57), sur plante de sous-bois, sur fougère à h = 1 m, enregistrement en semi-captivité (chant d'appel) TR-takes 24, 26-30; 13.X.2006, jour, 12AM, 1 ♂ (TR-2), sur plante de sous-bois, sur fougère, fauchage, h = 1,5 m, enregistrement TR-takes 17-19; 14.X.2006, jour, 12AM, 1 ♂ (TR-70), sur plante de sous-bois, fougère h = 2,5 m, photo SH, obs. chant d'appel; 16.X.2006, nuit, 6-10PM, 1 ♂ (TR-122), sur plante de sous-bois; 16.X.2006, nuit, 1 ♂ (TR-125), sur plante, vidéo TR-V1, 1 ♂ (TR-126), sur plante, 1 ♂ (TR-145), sur plante de sous-bois h = 2 m, 1 ♂ (TR-130), sur plante de sous-bois/fougère h = 1,5 m, terrain en pente et 2 ind. proches, enregistrement en milieu naturel (chant d'appel), TR-take 22, 1 ♂ (TR-128', alcool), sur plante, PIII: molec TR; 17.X.2006, nuit, 1 ♀ (TR-145'), sur plante, souche F0 élevage TR Santo, 1 ♂ (TR-146), herbes hautes en bord de piste, sur fougère h = 1,5 m, chant d'appel: vidéo SH (MNHN-ENSIF2411-2414, 2416-2422).

TYPE LOCALITY. — Vanuatu, Espiritu Santo Is., plateau of Tankara, near the village of Butmas.

OTHER MATERIAL EXAMINED. — **Vanuatu**. [Province Sanma], Espiritu Santo Is., Butmas, forêt du plateau de Tankara, 15°21'56"S, 166°59'E, 600 m alt., 16.X.2006, nuit, 6-10PM, 2 ♀♀ juv. (TR-123, 131), sur plante de sous-bois; 1 ♂ (TR-124), sur plante de sous-bois h = 1,8 m, vidéo TR-V2 5h30PM avant la tombée de la nuit; 17.X.2006, nuit, 1 juv. (TR-142), 1 juv., forêt de brume, sur plante de sous-bois h = 0,8 m feuille de liane, T. Robillard (MNHN-ENSIF2415, 2423-2425, 2566). — Butmas, Grotte de Fapon/sentier, 15°19'51,6"S, 166°57'53,6"E, forêt dans la doline, 15.X.2006, jour, 1 juv. (TR-78), sur plante; 15.X.2006, jour, 10-12AM, 1 juv. (TR-114), zone ouverte, sur plante de sous-bois h = 0,5 m, 1 ♀ juv. (TR-77), sur plante, PIII molec. TR, T. Robillard (MNHN-ENSIF2426-2428) — 13.X.2006, nuit, 1 ♂ juv. (n° 22), sur plante de sous-bois, L. Desutter-Grandcolas (MNHN-ENSIF2429). — Reared specimens: F1, 2006-2007, 4 ♂♂ (2 recorded, MNHN-ENSIF2430, 2431), 1 ♀; F2, 2007-2008, 1 ♂ (recorded, MNHN-ENSIF2433).

ETYMOLOGY. — Species named after the type locality, plateau of Tankara, near the village of Butmas, Espiritu Santo Is., Vanuatu.

DISTRIBUTION. — Vanuatu, Espiritu Santo Is., inland.

DIAGNOSIS. — Species close to *Cardiodactylus cheesmani* but differing by colouration darker. Size average, larger

than *C. enkraussi*, shape more stocky than *C. novaeguineae* (Figs 8; 17E). Male FW generally without a clear light crescent including posterior part of mirror; male genitalia close to that of *C. cheesmani*, but differing by the shape of the pseudepiphallallic sclerite (dorsal crest asymmetrical, basal protuberance near median shrinkage).

DESCRIPTION

Size average, stocky shape. General colouration dark brown, a few specimens lighter, with contrasted yellow or whitish patterns on dorsum and face. Scapes whitish with two dark brown spots, on inner sides and face; antennae homogeneously brown basally and including light areas. Head dorsum with 3 wide dark brown bands, bordered by a thin band behind eye and a yellow line more externally. Fastigium twice as long as wide, dark brown posteriorly, its apex yellow around dark median ocellus. Face with two more or less distinct dark brown curved patterns diverging from front head to below antennae. Mouth parts yellowish, separated from the face by a black line, highlighted by a horizontal yellow band. Palpi whitish, apex darker. Pronotum: dorsal disk trapezoidal, slightly bisinuated posteriorly; dark brown mottled with grey brown and sometimes with whitish, but generally little contrasted. Lateral lobes dark brown to grey brown near dorsal angle; ventral edge whitish. Legs yellowish brown, femora more or less mottled with brown; tibiae more or less banded. Fore tibiae not widened at tympana level. Hind tibiae dorsal face with 6-8 inner (m = 7, n = 8) and 12-15 outer (m = 14, n = 8) spines above spurs, and 5 or 6 inner (m = 6, n = 8) and 9 or 10 outer (m = 10, n = 8) spines between spurs. Tarsomeres III-1 with 2-6 spines on dorso-external edges (m = 3, n = 8). Hind wings longer than FWs, but proportionally shorter than in *C. enkraussi*, forming a dark brown tail 1.5 times as long as pronotum. Cerci dark brown, banded but little contrasted.

Male

FW colouration (Figs 1C, D; 17E): dorsal field generally dark brown, sometimes rust brown; not translucent; veins and cells of similar colour; with constant yellow and/or whitish patterns, including: FW base; 3A and part of 4A; 1A near file angle; harp veins; parts of chords; whitish sclerotized area at harp

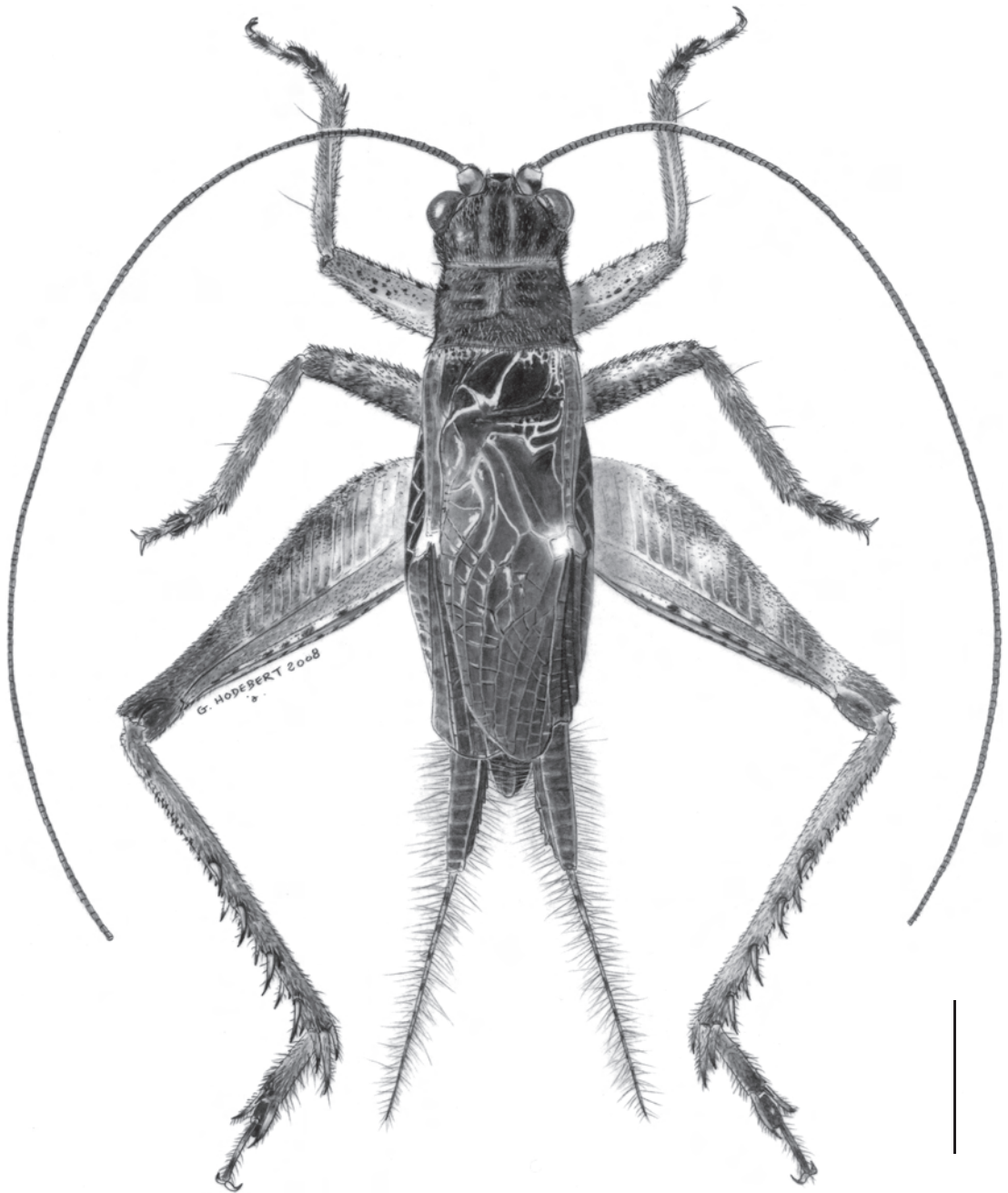


FIG. 8. — *Cardiodactylus tankara* n. sp., male habitus, paratype. Scale bar: 5 mm.

posterior angle. Harp with a dark triangle behind second harp vein, not distinct in darkest specimens. Transverse pale crescent behind mirror either absent

or slightly visible, unlike in *C. cheesmani* where it is very contrasted and includes part of the mirror (Otte 2007a: fig. 31). Lateral field dark brown dorsally,

TABLE 7. — Measurements (in mm) of *Cardiodactylus tankara* n. sp.: minimum-maximum (mean). Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIIL	FIIW	TIIL	OvipL
Male holotype	2.7	4.6	14.2	5.3	15.3	4.5	13.5	–
Female allotype	3.2	4.8	17.9	4.8	16.5	5.1	13.7	15
Males (n = 6)	2.5-2.9 (2.8)	4.5-4.9 (4.7)	13.5-15.7 (14.5)	4.7-5.6 (5.1)	14.4-16.2 (15.3)	3.9-4.5 (4.3)	12.2-13.7 (13.1)	–
Females (n = 3)	3-3.3 (3.2)	4.8-6 (5.4)	17.3-19.4 (18.2)	4.5-6 (5.1)	16.5-19.5 (17.8)	5.1-6.1 (5.5)	13.7-16.9 (15.1)	14.8-15.3 (15)

including MA, MP, R and bases of veins bifurcating from R; translucent ventrally with whitish veins. FW venation: 1A slightly bisinuated; stridulatory vein (Fig. 3A) with 134-166 teeth (m = 156, n = 5), located on both transverse (123-141 teeth, m=134) and basal longitudinal (11-32 teeth, m = 25) parts of 1A. CuP missing. Harp wider than in *C. enkraussi*, 2 W-shaped harp veins; posterior margin raised along diagonal vein. Mirror area variable, c1 long and narrow, c2 quite large; mirror (d1) longer than wide, not rounded, its shape prolonged by d2 and separated at second third by one or several accessory veins. Apical field short, triangular, CuA with 2 or 3 bifurcations posterior to mirror. Lateral field (Fig. 1D): latero-dorsal angle made by MP. R with 8 bifurcating veins.

Male genitalia (Fig. 4F-H): close to *C. cheesmani* and *C. guttulus* (Matsumura, 1913) (Robillard & Ichikawa in press). Pseudepiphallus very sclerotized and setose, slightly narrowed at midlength with a basal protuberance absent in *C. cheesmani*. Two parallel dorsal ridges, forming a gutter, their dorsal edges asymmetrically folded externally, the left one being shorter and widened in all examined males (n = 7; Fig. 4G). Pseudepiphallic sclerite extended laterally anterior to the ridges, but without a membranous sac as in *C. novaeguineae*. Apex of pseudepiphallus spoon-like and rounded, not separate from the rest of pseudepiphallus, its profile differing from *C. cheesmani*. Rami large, their base at level of pseudepiphallus narrowed part. Pseudepiphallic parameres trilobate, large and close together. Membrane at base of parameres sclerotized. Ectophallus almost hidden within the pseudepiphallus. Ectophallic arc complete, anterior to parameres. Ectophallic apodemes almost reaching rami apex. Apex of ectophallic fold almost hidden by pseudepiphallic parameres, trilobate, the

median lobe sponge-like, possibly glandular, shorter than lateral lobes. Endophallic sclerite small, without a medio-posterior expansion. Endophallic apodeme with both lateral lamellas and a short medio-dorsal crest. Membrane of endophallic cavity finely and transversally plicate.

Female

FW colouration: veins and cells dark brown, except: whitish FW base; large whitish spot at first third of length, including CuA and MP; and whitish transverse veins between CuP and CuA. Lateral field as in male. FW venation (Fig. 5B): 9 strong longitudinal veins on dorsal field (including 1-3A). Ovipositor: Shorter than hind femora; apex with both dorsal and ventral edges denticulate, more pronounced on ventral valve (Fig. 6B).

Female genitalia (Fig. 7J-L): copulatory papilla rounded with a basal sclerotized ring; apex narrowed and folded ventrally; ventral preapical convergent crests, concave posteriorly.

Juvenile

First instars observed in laboratory similar to that of *C. novaeguineae*, yellow with brown longitudinal bands. Later instars with more contrasted colouration, dark brown to black highly mottled with whitish and yellow. Head colouration as in adults, the head dorsum and face sometimes entirely black. Pronotum as in adults, sometimes more contrasted. Metanotum and tergites with median, paired black patterns; rest of abdomen dorsum brown with dark brown dots disposed in longitudinal lines.

Measurements

See Table 7.

TABLE 8. — Calling song parameters of *Cardiodactylus tankara* n. sp.

Specimens	T°C	Echeme			Syllable			
		Dominant frequency (kHz)	Duration (ms)	Period (ms)	Syllable number	Duration (ms)	Period (ms)	Rate (/s)
TR-1	22.8	13.4 ± 0.7	187 ± 26	5095 ± 2634	26.2 ± 4.8	1.2 ± 0.6	7.5 ± 4	139 ± 17
TR-2	22.7	13.9 ± 0.6	176 ± 7	5780 ± 4439	26.1 ± 1.7	1.1 ± 0.5	6.9 ± 3.9	147 ± 8
TR-57	24.4	14.2 ± 0.8	175 ± 2	2165 ± 345	31.7 ± 1.4		5.6 ± 3.1	181 ± 9
TR-130	21	12 ± 0.7	109 ± 2	9580 ± 5797	19.9 ± 6	1.1 ± 0.5	5.5 ± 3.3	180 ± 23
TR-145	26.5	14.2 ± 0.4	146 ± 2	1790 ± 383	25.9 ± 1.6	1.3 ± 0.5	5.8 ± 3.5	177 ± 11
TR-146	22.9	14.1 ± 0.7	135 ± 3	4129 ± 3367	23.7 ± 4.9	0.9 ± 0.4	5.9 ± 4.3	178 ± 19

HABITAT AND LIFE HISTORY TRAITS

Cardiodactylus tankara n. sp. lives in dense forested areas but is also found near borders and in open areas (Fig. 17D, E). Individuals are found on large leaves of trees, bushes of fern and creepers, or on tree trunks (including Pandanaceae) at about 2 m height. Singing males are distributed at relatively large distance from one another (Tables 1; 2). *Cardiodactylus tankara* n. sp. is sympatric with *C. enkraussi* at the plateau of Tankara. The population density is comparable to that of *C. novaeguineae*, and contrasts from the denser populations of *C. enkraussi*.

BEHAVIOUR

Mating behaviour not observed.

Calling song (Fig. 15; Table 8)

Males of *C. tankara* n. sp. are mostly acoustically active at night, but have been heard singing during daytime. The calling song is more conspicuous and noisy than that of sympatric *C. enkraussi*. Six males recorded in the field at 20-26°C (MNHN-ENSIF 2409, 2411, 2412, 2418, 2419, 2421) are analysed here. At 25°C, the calling song consists in an irregular succession of short echemes (mean echeme duration ± SD = 162 ± 7 ms; period = 2538 ± 1118 ms; duty cycle = 6.9 ± 0.7%; echeme rate = 26.3 echeme/min). The echeme is slightly accelerated from start to end (regular decrease of syllable period within echeme) and shows a crescent amplitude profile. Each echeme is made of 27.5 ± 2.1 syllables with the following characteristics: syllable rate = 170.8 ± 2.1/s; syllable duration = 1.2 ± 0.4 ms; syllable period = 6.2 ± 3.6 ms; syllable duty cycle =

19.5%; and each echeme is finished by a longer syllable, which is likely the contraction of 3 or 4 syllables (mean duration = 4.8 ± 1.9 ms).

The calling frequency of *C. tankara* n. sp. is relatively high (14.3 ± 0.4 kHz), and corresponds to the third harmonic of the song (Robillard *et al.* 2007); the mean fundamental frequency is 5.6 ± 0.2 kHz.

Courting song

This song was observed during forced interactions with females of *C. novaeguineae*; it is less intense than the calling song, but the echeme is similar to the calling song, except for its irregular period.

Aggressive song

This song was observed in laboratory during interactions between two singing males of *C. tankara* n. sp. After alternating their songs, one male sometimes charges the other one and sings more frequently in front of him. This aggressive song is quite similar to the calling song but of shorter duration and period.

Cardiodactylus aobaensis n. sp.

(Figs 5C; 6D; 7M-O)

TYPE MATERIAL. — [Vanuatu] Neue Hebriden. [Province Penama], recter Aoba [Is.], X.1911, b, (nach Zettelkarten) = Aoba (Neukaledonien), Dr. Sarrasin & Dr. Roux ?, Dr. F. Speiser [mentioned as *Cardiodactylus novaeguineae* in Chopard 1951], ♀ holotype (BMNH).

TYPE LOCALITY. — Vanuatu, Aoba Is.

ETYMOLOGY. — Species named after the type locality.

TABLE 9. — Measurements (in mm) of *Cardiodactylus aobaensis* n. sp. Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIIL	FIIW	TIIL	OvipL
Female holotype	4.5	7.2	25.4	5.5	22.8	6.0	22.2	22.7

DIAGNOSIS. — Largest *Cardiodactylus* species in Vanuatu. Stocky shape, morphologically close to *C. tankara* n. sp., *C. cheesmani* and *C. guttulus* (ovipositor size and apex, copulatory papilla). Dorsal disk of pronotum with a thin longitudinal median yellow line and lateral yellow bands interrupted at midlength by transverse dark brown bands.

DESCRIPTION

Large species for the genus, the largest one for Vanuatu, stocky shape. General colouration light brown, little contrasted. Scapes yellow with two dark brown spots, on inner and facial sides. Head dorsum almost entirely brown, with a median suture yellowish; yellow behind eye, with a transverse brown line posterior to eye. Fastigium 1.5 times as long as wide, median ocellus yellow. Face yellowish brown with two dark brown curved patterns diverging from front head to below antennae. Palpi yellowish brown, apex darker. Pronotum: dorsal disk trapezoidal, slightly bisinuated posteriorly; brown, with a thin longitudinal median yellow line, and lateral yellow bands interrupted at midlength by transverse dark brown bands. Lateral lobes of pronotum dark brown near dorsal angle; ventral edge progressively lighter. Legs light brown, fore and mid legs faintly spotted with dark brown, knees of mid legs dark brown. Fore tibiae not widened at tympana level. Hind tibiae dorsal face with 7 inner and 13 outer spines above spurs, with 7 inner and 8 outer spines between spurs. Tarsomeres III-1 with 4 spines on dorso-external edges. FWs much longer than abdomen; hind wings proportionally shorter than in *C. enkraussi*, making a dark brown tail 1.5 times as long as pronotum. Cerci brown, darker at apex.

Male

Unknown.

Female

FW colouration (Fig. 5C): dorsal field homogeneously brown (cells and veins) except: yellowish brown sclerotization on FW base, including bases

of CuP and 1-3A; first third of lateral angle whitish, including MP; part of CuA and MA and associated cells and transverse veins; area between CuP and CuA dark brown. Lateral field dark brown dorsally, including R, lighter ventrally, the veins bifurcating from R yellow. FW venation: 10 strong longitudinal veins on dorsal field (including 1-4A). R with 5 bifurcating veins. Ovipositor: quite long; apex dorsal and ventral edges slightly denticulate (Fig. 6D).

Female genitalia: copulatory papilla (Fig. 7M-O): Same general shape as *C. tankara* n. sp. but flatter; dorsal surface highly plicate transversally; ventral surface concave.

Measurements

See Table 9.

HABITAT, LIFE HISTORY TRAITS AND BEHAVIOUR
Not documented.

Cardiodactylus epiensis n. sp.

(Figs 5E; 6F; 7P-R)

TYPE MATERIAL. — [Vanuatu] Nouvelles-Hébrides. [Province Shefa], Epi Is., Baie de Nelson, 1935-1936, E. Aubert de la Rüe, ♀ holotype (MNHN-ENSIF1116).

TYPE LOCALITY. — Vanuatu, Epi Is., Baie de Nelson.

ETYMOLOGY. — Species named after the type locality.

DISTRIBUTION. — Vanuatu, Epi Is.

DIAGNOSIS. — Species of average size, close in size and colouration to *C. tankara* n. sp., *C. cheesmani* and *C. gagnei* Otte, 2007. Female differs from other species by patterns of whitish sclerotization on FW base, and shape of copulatory papilla, more elongate and apex larger than in *C. tankara* n. sp. and *C. cheesmani* (not observed in *C. gagnei*).

DESCRIPTION

Species of average size. General colouration brown, little contrasted. Fastigium black, 1.5 times as long

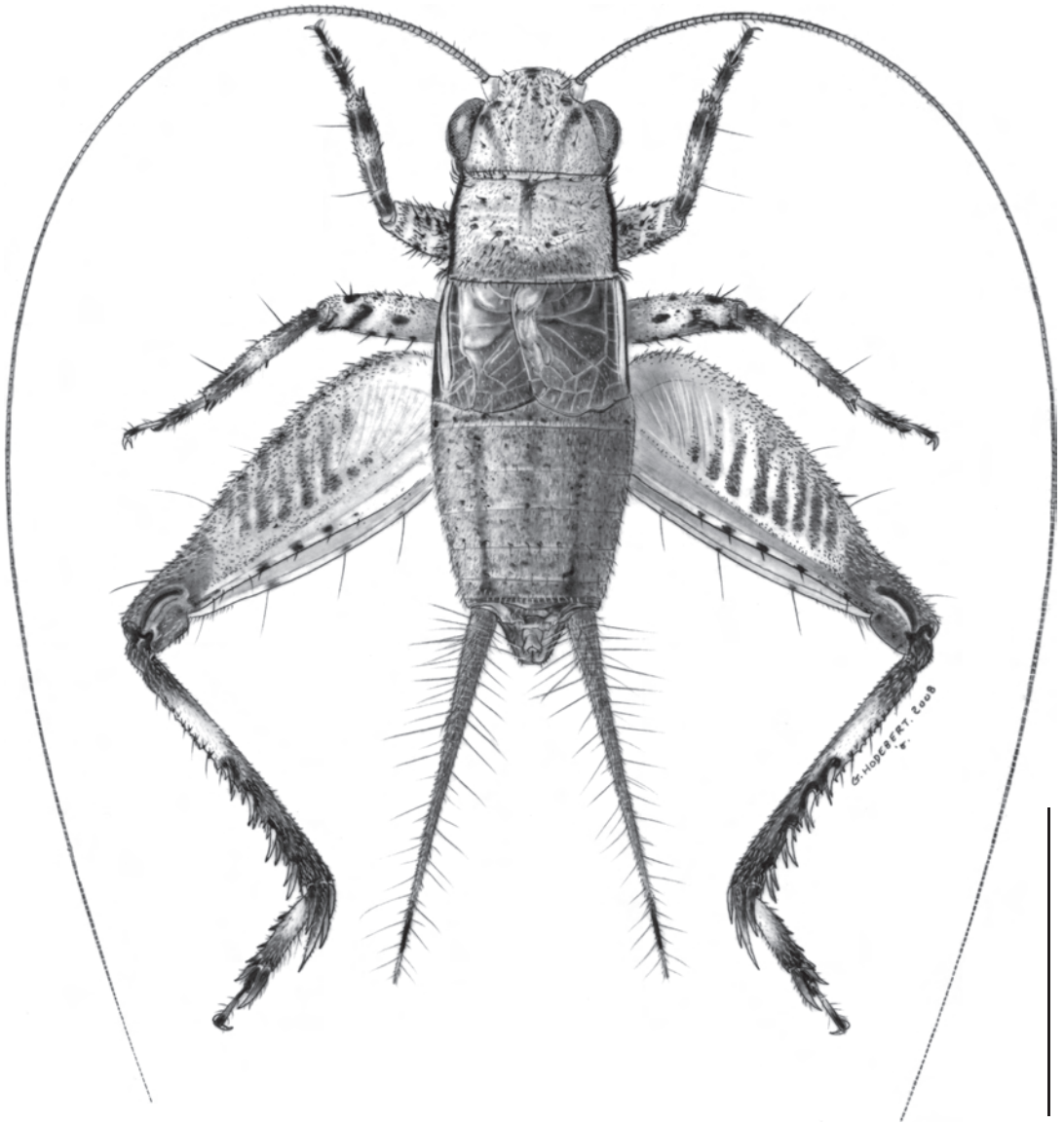


FIG. 9. — *Lebinthus santoensis* n. sp., male habitus, paratype. Scale bar: 5 mm.

as wide, median ocellus yellow. Head dorsum with 6 wide dark brown bands and 2 yellow bands behind eyes. Face with a yellow band above clypeus; 2 dark brown curved patterns diverging from front head to below antennae. Pronotum: dorsal disk trapezoidal, slightly bisinuated posteriorly; lateral lobes dark brown except ventral margin whitish.

Fore tibiae not widened at tympana level. Hind tibiae dorsal face with 6 inner and 12 outer spines above spurs, 6 inner and 10 outer spines between spurs ($n = 1$). Tarsomeres III-1 with 4 spines on dorso-external edges ($n = 1$). FWs as long as abdomen; hind wings making a short dark brown tail about 1.5 times as long as pronotum. Cerci

TABLE 10. — Measurements (in mm) of *Cardiodactylus epiensis* n. sp. Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIIL	FIIW	TIIL	OvipL
Female holotype	3.1	5.2	16.5	4.9	17.2	4.8	14.2	13.3

yellowish brown mottled with dark brown and banded apically.

Male

Unknown.

Female

FW colouration (Fig. 5E): dorsal field cells and longitudinal veins homogeneously brown; FW base with whitish sclerotization, including bases of veins 1-2A, CuP, CuA and MP; restricted whitish area on anterior lateral angle, including bases of CuA, MP and their associated transverse veins; part of CuA and MP whitish at third of length. Areas between CuA and CuP and between bases of CuA1 and CuA2 with whitish transverse veins. Area between MP and R brown, R bifurcating veins whitish. FW venation: 10 strong longitudinal veins on dorsal field (including 1-3A). R with 7 bifurcating veins. Ovipositor: quite short, as in *C. tankara* n. sp.; apex dorsal edge denticulate; ventral edge smooth (Fig. 6F).

Female genitalia: copulatory papilla (Fig. 7P-R): shape more elongate than *C. tankara* n. sp. and *C. cheesmani*; dorsal and ventral sides concave, dorsal surface not plicate; apex larger than in other species, slightly curved ventrally.

Measurements

See Table 10.

HABITAT, LIFE HISTORY TRAITS AND BEHAVIOUR
Not documented.

Cardiodactylus gagnei Otte, 2007

Cardiodactylus gagnei Otte, 2007a: 350; 2007b: 31.

TYPE MATERIAL. — **Vanuatu**. [Malampa Province], Ambrym [Is.], Ranon to Mt. Toyo, 0-500 m, 2.IX.1979, W. C. Gagné *et al.*, ♂ holotype (BPBM 16,777). Not examined.

TYPE LOCALITY. — Vanuatu, Ambrym Is.

DISTRIBUTION. — Vanuatu, Ambrym and Efate islands (Otte 2007a).

DIAGNOSIS. — Species of average size, close in size and colouration to *C. tankara* n. sp., *C. cheesmani* and *C. epiensis* n. sp. Male differs from *C. cheesmani* by male genitalia and from *C. tankara* n. sp. by FW colouration, with a large light crescent including posterior part of mirror, and by genitalia (pseudepiphallid dorsal crest symmetrical, no basal protuberance near median shrinkage of pseudepiphallus, shape of endophallic sclerite).

Genus *Lebinthus* Stål, 1877

DIAGNOSIS. — Among Lebinthini genera, *Lebinthus* is characterised by its rather small size, microptery in both sexes, male FW venation with mirror almost not differentiated from apical field, and male genitalia.

Lebinthus santoensis n. sp.

(Figs 1E, F; 3B; 6G; 9; 10A-C;
11A; 12A-C; 16; 18)

Lebinthus sp. — Robillard *et al.* 2007: 1254 (calling song analysis).

TYPE MATERIAL. — **Vanuatu**. [Province Sanma], Espiritu Santo Is., Peavot, végétation arbustive en arrière de la plage, 14°59'09"S, 166°47'39"E, 21.X.2006, jour (n° 16), L. Desutter-Grandcolas, ♂ holotype (MNHN-ENSIF2434). — Same locality, date and collector and as holotype, jour (n° 23), litière, ♀ allotype (MNHN-ENSIF2435).

Paratypes (39 ♂♂, 37 ♀♀): **Vanuatu**. [Province Sanma], Espiritu Santo Is., Matantas, pointe de Quirros, 15°09'54"S, 166°56'22"E, 20 m en haut de la plage, litière et herbes basses, 19.X.2006, jour, 6AM, 1 ♂ (TR-186), enregistrement en semi-captivité TR-take 49, 1 ♂ (TR-183), photo SH, 6 ♂♂ (TR-187-191), 2 ♂♂ (TR-194, 201, alcool), 6 ♀♀ (TR-183, 196-199, 202), T. Robillard (MNHN-ENSIF2436-2451). — Matantas, Big Bay, Vatthé Conservation area, 15°20'S, 166°95'E, végétation arbustive et basse en zone supralittorale,

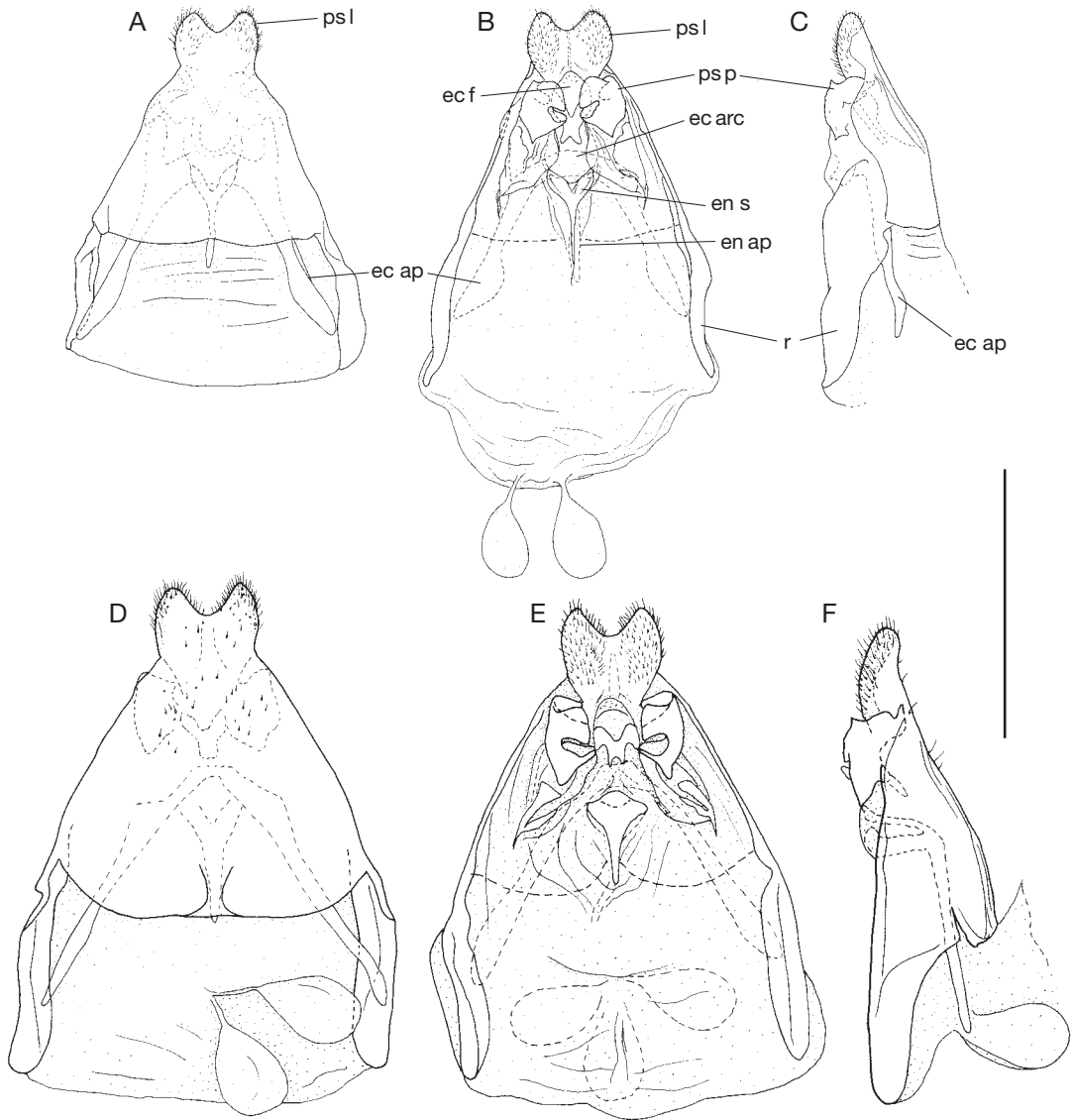


FIG. 10. — Male genitalia: **A-C**, *Lebinthus santoensis* n. sp., in dorsal (**A**), ventral (**B**) and lateral (**C**) views; **D-F**, *L. nattawa* n. sp., in dorsal (**D**), ventral (**E**) and lateral (**F**) views. Abbreviations: see Material and methods. Scale bar: 1 mm.

25.X.2006, jour, 1 ♂ (TR-344), litière de feuilles mortes; 27.X.2006, jour, 1 ♂ (TR-371), 4 ♀♀ (TR-374, 375, 378, 379), T. Robillard (MNHN-ENSIF2452-2457); 27.X.2006, jour, 3 ♂♂ (n° 16-18), 7 ♀♀ (n° 19-25), litière, L. Desutter-Grandcolas (MNHN-ENSIF2458-2467); 27.X.2006, jour, 1 ♂ (n° 15), litière, L. Desutter-Grandcolas (BMNH). — Matantas, Big Bay, Vathé Conservation area, 15°20'S, 166°95'E, haut de plage, 27.X.2006, jour, 1 ♂ (TR-382), photo TR site d'étude;

27.X.2006, nuit, 2 ♂♂, galets et zone médiolittorale émergée, litière, T. Robillard (MNHN-ENSIF2468-2470). — Peavot, rive S de la rivière principale, terrasse I, 14°59'37"S, 166°47'04"E, 38 m alt., forêt secondaire (ancien jardin), litière, 20.X.2006, jour 9AM-3PM, 3 ♂♂ (TR-237, 240, 243), 3 ♀♀ (TR-236, 242, 244); 21.X.2006, nuit, 1 ♀ (TR-280), 1 ♂ (TR-278), T. Robillard (MNHN-ENSIF2471-2475, 2477, 2478, 2492); 20.X.2006, jour, 1 ♀ (n° 54), photo SH, L. Desutter-

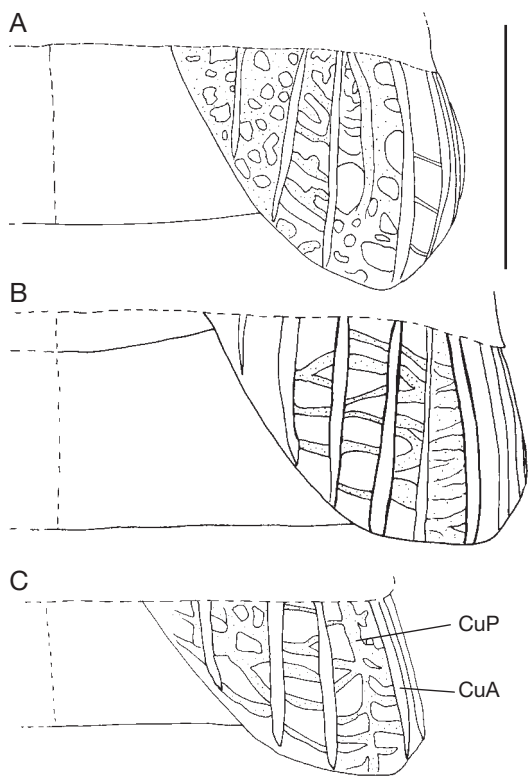


FIG. 11. — Female FW venation: **A**, *Lebinthus santoensis* n. sp.; **B**, *L. nattawa* n. sp.; **C**, *L. malekulensis* n. sp. Dotted areas represent patterns of white or yellow areas. Abbreviations: see Material and methods. Scale bar: 5 mm.

Grandcolas (MNHN-ENSIF2479). — Peavot, végétation arbustive en arrière de la plage, 14°59'09"S, 166°47'39"E, 21.X.2006, jour, 1 ♀ (TR-258), plage de galets et zone médiolittorale émergée, litière, 24.X.2006, jour, 2 ♀♀ (TR-312, 313), litière; 24.X.2006, nuit, 1 ♂ (TR-323), plage de galets et zone médiolittorale émergée, 200 m au sud du village, litière dans une feuille morte, enregistrement TR-takes 70-71, T. Robillard (MNHN-ENSIF2480-2483); 21.X.2006, jour, 1 ♀ (n° 19), litière, PIII: molec TR; 6 ♂♂ (n° 11-15, 17), 4 ♀♀ (n° 18, 20-22), litière; 24.X.2006, nuit, 1 ♂ (n° 14), L. Desutter-Grandcolas (MNHN-ENSIF2484-2490, 2493-2497). — Nattawa, forêt pâturée, 15°19'29"S, 167°12'09"E, 29.X.2006, jour, 1 ♀ (TR-421), litière en lisière, souche d'élevage TR-Santo, T. Robillard (MNHN-ENSIF2498); 29.X.2006, jour, 2 ♂♂ (n° 1, 2), 2 ♀♀ (n° 3, 4), litière et herbes basses en clairière, L. Desutter-Grandcolas (MNHN-ENSIF2499-2502). — Luganville, site du CTRAV, forêt côtière sur sable, 15°27'00"S, 167°12'26"E, 29.X.2006, nuit, 1 ♂ (TR-446), litière, feuilles mortes, enregistrement en

milieu naturel (chant d'appel) TR-takes 75-77, 2 ♀♀ (TR-447-448), 1 ♀ (TR-449), litière; 30.X.2006, nuit, 1 ♂ (TR-472), litière, enregistrement en milieu naturel (chant d'appel) TR-takes 79-81, 1 ♂ (TR-473), litière, vidéo SH, 2 ♂♂ (TR-475), 1 ♀ (TR-474), litière, PIII: molec TR; 31.X.2006, nuit, 1 ♂ (TR-481), litière, enregistrement en milieu naturel (chant d'appel) TR-take 88, T. Robillard (MNHN-ENSIF2503-2512).

TYPE LOCALITY. — Vanuatu, Espiritu Santo Is., Peavot, végétation arbustive en arrière de la plage, 14°59'09"S, 166°47'39"E.

ETYMOLOGY. — Species named after Espiritu Santo Is., Vanuatu.

OTHER MATERIAL EXAMINED. — (6 ♀♀, 7 ♂♂, 37 juv.) **Vanuatu**. [Province Sanma], Espiritu Santo Is., Matantas, pointe de Quirros, 15°09'54"S, 166°56'22"E, 20 m en haut de la plage, litière et herbes basses, 19.X.2006, jour 6AM, 1 ♀ juv. (TR-202), T. Robillard (MNHN-ENSIF2513). — Matantas, Big Bay, Varthé Conservation area, 15°20'S, 166°95'E, végétation arbustive et basse en zone supralittorale, 27.X.2006, jour, 1 ♀ juv. (TR-370), 4 juv. (TR-372, 373, 376, 377), litière, photo site TR, T. Robillard (MNHN-ENSIF2514-2518); 26.X.2006, jour, 1 juv. (n° 1), litière, L. Desutter-Grandcolas (MNHN-ENSIF2519). — Peavot, rive S de la rivière principale, terrasse I, 14°59'37"S, 166°47'04"E, 38 m alt., forêt secondaire (ancien jardin), 20.X.2006, jour 9AM-3PM, 2 juv. (TR-234, 235); 21.X.2006, nuit, 2 ♀♀ juv. (TR-277, 279), litière, T. Robillard (MNHN-ENSIF2476, 2520-2522); 20.X.2006, jour, 2 ♀♀ juv. (n° 43, 44), 8 juv. (n° 34, 35, 38-41, 45, 47), litière, 1 juv. (n° 63), pelouse/zone herbacée en clairière; 21.X.2006, jour, 3 juv. (n° 6-8), litière, L. Desutter-Grandcolas (MNHN-ENSIF2523-2536). — Peavot, végétation arbustive en arrière de la plage, 14°59'09"S, 166°47'39"E, 21.X.2006, jour, 3 juv. (TR-256-258), litière; 24.X.2006, jour, 1 ♀ juv. (TR-311); 24.X.2006, nuit, plage de galets et zone médiolittorale émergée, 200 m au sud du village, 1 juv. (TR-320), T. Robillard (MNHN-ENSIF2537-2541); 21.X.2006, jour, 4 juv. (n° 25-28), litière, 1 ♀ juv. (n° 24), litière; 24.X.2006, nuit, 1 ♀ juv. (n° 15), litière, L. Desutter-Grandcolas (MNHN-ENSIF2491, 2542-2546). — Penaoru, 600 m, XI.2006, 3 juv. (ortho 2) [alcool], molec. TR, Exped. SANTO 2006 (MNHN-ENSIF2547). — [Vanuatu] Nouvelles-Hébrides, [Province Penama], [Pentecost] Pentecôte Is., Baie Melsisi, 1935-1936, 1 ♀, E. Aubert de la Rüe (MNHN-ENSIF1170). — Reared specimens from Espiritu Santo Is.: F1, 2006-2007, 5 ♂♂ (4 recorded, MNHN-ENSIF2550-2553), 3 ♀♀, 1 juv. ♀ [alcool]; F2, 2007-2008, 2 ♂♂ (recorded, MNHN-ENSIF2554, 2555), 2 ♀♀, 1 juv., T. Robillard (MNHN).

DISTRIBUTION. — Vanuatu, Espiritu Santo Is. and Pentecost Is., coastal areas.

DIAGNOSIS. — Species of small size, close in shape, colouration, venation and genitalia to *Lebinthus lifouensis* Desutter-Grandcolas, 1997, from which it differs by details of colouration (dark apical ring on cerci), female copulatory papilla (basal sclerotized ring smaller), ovipositor (slightly more acute [Fig. 6G]), and by a calling song frequency of about 26.6 kHz (12.6 in *L. santoensis*: Robillard *et al.* 2007).

DESCRIPTION

Species of small size. Colouration (Figs 9; 18E, F) most often light brown dorsally and darker ventrally, with more or less contrasted colour patterns. Head dorsum light brown with 6 more or less visible longitudinal bands, 2 median ones, patchy at level of fastigium, next 2 lateral ones curved externally toward eyes midlength, 2 most external ones behind eyes. Some specimens with almost completely light brown or dark brown head dorsum with faint banded patterns. Eyes light brown dorsally, dark brown to black ventrally. Fastigium slightly wider than long, setose, whitish brown with a dark spot behind whitish median ocellus. Scapes whitish, antennae homogeneously brown. Face with 2 diverging black curved lines between antennae, with a median black triangle above clypeus; black areas bellow antennae; these elements more or less separated or fused according to specimen general melanisation. Mouth parts dark brown to black. Palpi whitish, banded with dark brown. Pronotum: Dorsal disk almost rectangular, straight posteriorly; light brown, whitish laterally, most often with dark spots arranged in uneven lines. Lateral lobes black except for whitish ventral margin, sometimes partly brown. Legs: fore and mid femora with large dark brown to black spots, fore and mid tibiae banded; fore tibia not widened at tympana level. Hind femur brown, with striated light patterns on external face, 3-5 black spots on each ventral edge, knees dark brown; distal half of hind tibiae and tarsomeres III-1 black. Hind tibiae dorsal faces with 5-9 inner (m = 6, n = 10) and 8-13 outer (m = 10, n = 10) spines above spurs, and 3-5 inner (m = 4, n = 10) and 2-5 outer (m = 5, n = 10) spines between spurs. Tarsomeres III-1 with 4 spines on dorso-external edges (n = 10). Hind wings absent, FWs short. Abdomen brown, with a black or dark brown band on each lateral side; each tergite with dark spots on

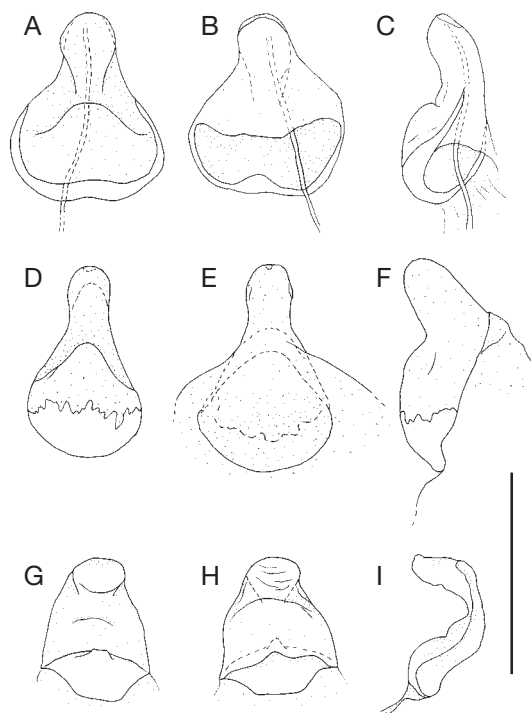


FIG. 12. — Female copulatory papilla in ventral, dorsal and lateral views: A-C, *Lebinthus santoensis* n. sp.; D-F, *L. nattawa* n. sp.; G-I, *L. malekulensis* n. sp. Scale bar: 0.5 mm.

posterior margin. Cerci homogeneously brown, dark brown at base ventrally, with a preapical black ring, unlike *L. lifouensis*.

Male

FW not reaching abdomen midlength (Fig. 9). FW colouration (Fig. 1E, F): cells brown, veins whitish, translucent; area between CuA and MP dark brown; intermedian area whitish; lateral field dark brown, its ventral margin lighter. FW venation: 1A angle wide (>130°); stridulatory file with 150-193 teeth (m = 172, n = 4), located on both transverse (121-135 teeth, m = 128) and basal longitudinal (29-66 teeth, m = 44) parts of 1A (Fig. 3B). CuP missing. Harp wide, with generally one harp vein parallel to transverse axis, but some specimens with 2 parallel harp veins. CuA curved internally at apex, the median fold triangular and short, located on dorsum. Cell c1 separated at midlength by an accessory vein, c2

TABLE 11. — Measurements (in mm) of *Lebinthus santoensis* n. sp.: minimum-maximum (mean). Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIII L	FIII W	TIII L	OvipL
Male holotype	1.9	2.8	2.2	1.7	7	2.5	5	–
Female allotype	2	3.2	0.7	0.8	7.8	2.7	5.8	6.6
Males (n = 6)	1.8-2.3	2.8-3.2	2.2-2.8	1.7-2.2	7-8.8	2.5-3.1	5-6.1	–
	(2)	(3)	(2.6)	(2.1)	(7.9)	(2.8)	(5.7)	
Females (n = 6)	1.8-2.3	2.9-3.5	0.7-1.1	0.7-1.1	7.3-8.9	2.6-3.4	5.5-6.5	6.2-7.1
	(2)	(3.2)	(0.9)	(0.9)	(8)	(2.9)	(5.9)	(6.7)

large. Mirror (d1) not rounded, barely widened compared to other cell alignments; d2 thin and rectangular. Apical field almost absent, including only 2 cells behind mirror (E alignment). Lateral field with 5 strong longitudinal veins including MA, R and 3 more ventral veins; latero-dorsal angle made by MP; R without strong bifurcating veins.

Male genitalia (Fig. 10A-C): very similar to *L. lifouensis*, but pseudepiphallic lophi more acute. Pseudepiphallic sclerite triangular, slightly convex dorsally; anterior apex straight or slightly indented; posterior apex with individualized lophi, setose. Pseudepiphallic parameres large, trilobate and close together. Ectophallic arc complete and wide, at midlength between pseudepiphallic parameres and anterior apex. Ectophallic fold short and wide, with a Y preapical sclerotization. Endophallic sclerite Y-shaped; endophallic apodeme made of a long and wide median crest, not disconnected from membrane.

Female

FWs short (Fig. 11A), exceeding posterior margin of first tergite, separated by a distance equal to length; dorsal field with 4 or 5 strong longitudinal veins, whitish or brown. Lateral field darker than dorsal field, with 3 or 4 strong dark brown longitudinal veins. Ovipositor short; apex lanceolate, denticulate on dorsal edge.

Female genitalia: copulatory papilla (Fig. 12A-C) with small basal sclerotized ring; apex narrowed and long, with a ventral bump.

Juvenile

Colouration generally more contrasted than adults, with a pair of dark brown patterns on first tergites (Fig. 18F).

Measurements

See Table 11.

HABITAT AND LIFE HISTORY TRAITS

Lebinthus santoensis n. sp. lives in leaf litter in open forested areas in coastal areas, near river banks or along beaches (Fig. 18A, B). It is found in dense populations in wet leaf litter, generally on or under large dead leaves (Tables 1, 2; Fig. 18C, D).

BEHAVIOUR

Mating behaviour has been observed in laboratory (TR, 2006-2008); multiple copulations have been recorded (2-6 copulations, n = 2); between each copulation (c. 45- 60 min) the male actively guards the passive female by singing almost constantly starting a few minutes after removal of previous spermatophore by the female.

Calling song (Fig. 16; Table 12)

Males start singing during the afternoon from within the leaf litter, but are fully active at night, mostly on top of leaf litter. Five males recorded in the field (MNHN-ENSIF2483, 2503, 2507) and in laboratory (MNHN-ENSIF2551, 2553) at 23-29°C are analysed here. At 25°C, the calling song consists of a continuous succession of two-part echemes separated by a short silence of 1.1 ± 0.4 s (mean echeme duration = 26.2 ± 9.7 s; period = 27.3 ± 10.1 s); each echeme starts by a slow trill, made of 42 ± 9.7 widely spaced syllables, followed by a fast trill (mean trill duration = 11.9 ± 0.6 s; period = 26.7 ± 3.0 s; fast trill/slow trill duty cycle = $45.3 \pm 17.7\%$; fast trill rate = 2.24/min) made of 463.9 ± 27.3 syllables. All syllables are amplitude modulated; syllables of slow trill have the following characteristics:

TABLE 12. — Calling song parameter of *Lebinthus santoensis* n. sp.

Specimens	T°C	Dominant frequency (kHz)	Echeme duration (s)	Echeme period (s)	Slow trill				
					Duration (s)	Syllable number	Slow trill syllables		
							Duration (ms)	Period (ms)	Rate (/s)
Spec-EI2	23.1	26.3 ± 2.7	13.8 ± 0.4	31.8 ± 6.9	18.2 ± 6.5	53.5 ± 17.2	9.7 ± 1	345 ± 40	2.9
TR-323	26.4	27.4 ± 0.8	9.5 ± 0.3	17.4 ± 0.5	8.1 ± 0.3	33.2 ± 5.1	12.2 ± 1.4	210 ± 64	4.8
TR-446	27.3	27.5 ± 1.3	8.2 ± 0.7	19.4	11.1	43 ± 5.7	9.1 ± 1.2	279 ± 60	3.6
TR-472	28.6	—	8.5	13.5	5	14	7.8 ± 1	380 ± 16	2.6
Spec-EI4	24.5	25.7 ± 1.5	14.1 ± 1.6	31.2 ± 12	17.2 ± 10.3	39.5 ± 10.6	13 ± 1.8	375 ± 71	2.7

Specimens	Fast trill					
	Duration (s)	Period (ms)	Syllable number	Fast trill syllable		
				Duration (ms)	Period (ms)	Rate (/s)
Spec-EI2	13.7 ± 0.4	32.8 ± 1.7	464 ± 23	10.4 ± 1.1	30 ± 11.4	34 ± 1
TR-323	9.3 ± 0.3	19.2 ± 1.7	393 ± 7	12.4 ± 2.9	23.7 ± 3.3	42 ± 1
TR-446	8.3	—	407 ± 14	7.0 ± 2.3	20.5 ± 9.5	49 ± 2
TR-472	8.5	—	451	6.2 ± 0.9	18.8 ± 1.6	53
Spec-EI4	14 ± 1.7	32.3 ± 8.3	540 ± 58	13.7 ± 1.7	25.9 ± 8.9	39 ± 1

syllable rate = 3.2 ± 0.9/s; syllable duration = 10.8 ± 1.3 ms; syllable period = 322.4 ± 92 ms; syllable duty cycle = 3.3%; whereas syllables of fast trill have the following characteristics: syllable rate = 39.9 ± 1.0/s; syllable duration = 10.9 ± 1.7 ms; syllable period = 25.8 ± 8.3 ms; syllable duty cycle = 42.2%.

The dominant frequency at 25°C is 26.6 ± 1.7 kHz and corresponds to the second harmonic of the song (Robillard *et al.* 2007); mean fundamental frequency is about twice lower (13.3 ± 0.8 kHz). The dominant frequency of *L. santoensis* n. sp. is the highest known so far for crickets (Robillard *et al.* 2007), and this feature constitutes the clearest criteria to distinguish this species from *L. lifouensis*, for which spectral pattern is similar, but with twice lower frequency values (dominant frequency = 12.6 kHz; fundamental frequency = 6.3 kHz) (Robillard *et al.* 2007).

Courting song

This song is less intense than the calling song but similar in temporal pattern.

Intercopulatory song

This song is similar to the calling song but less intense; the slow part of the song is more intense than the

echeme, and the syllables are more indented than in the calling song. This song is almost continuous and starts a few minutes after removal of previous spermatophore by the female.

Aggressive song

This song was not observed despite many observations of male interactions. It is probably absent from the repertoire of this species.

Lebinthus nattawa n. sp.

(Figs 1G, H; 3D; 6H; 10D-F; 11B; 12D-F; 13; 19)

TYPE MATERIAL. — **Vanuatu**. [Province Sanma], Espiritu Santo Is., Nattawa, forêt pâturée, 15°19'29"S, 167°12'09"E, 29.X.2006, jour, litière, adulte en captivité (TR-413), T. Robillard, ♂ holotype (MNHN-ENSIF2556). — Same locality, date and collector as holotype, jour, litière (TR-414), ♀ allotype (MNHN-ENSIF2557).

Paratypes (2 ♂♂; 5 ♀♀): same locality, date and collector as holotype, jour: 2 ♂♂ (TR-412, 418), 2 ♀♀ (TR-417, 419), litière (MNHN-ENSIF2558-2561); 1 ♀ (TR-420), litière sous feuilles mortes; 1 ♀ (TR-411), litière, photo SH; 1 ♀ (TR-415), litière, adulte en captivité, PIII: molec TR 2008 (MNHN-ENSIF2562-2564).

TYPE LOCALITY. — Vanuatu, Espiritu Santo Is., Nattawa.

ETYMOLOGY. — Species named after the type locality.

OTHER MATERIAL EXAMINED. — **Vanuatu.** Province Sanma, Espiritu Santo Is., Nattawa, forêt pâturée, 15°19'29"S, 167°12'09"E, 29.X.2006, jour (TR-416), litière, T. Robillard, 1 ♀ juv. (MNHN-ENSIF2565).

DISTRIBUTION. — Vanuatu, Espiritu Santo Is.

DIAGNOSIS. — Species of small size, close to *L. santoensis* n. sp. and *L. lifouensis* from which it differs by male genitalia and female copulatory papilla, wider and of more stocky shape (pronotum wider), and colouration dark brown dorsally and darker ventrally, with same dark apical ring on cerci.

DESCRIPTION

Species of small size, shape wider and more stocky than in *L. santoensis* n. sp. Colouration most often dark brown dorsally and darker ventrally (Figs 13; 19B, C). Head dorsum with 6 more or less visible dark brown longitudinal bands, sometimes with almost completely brown head dorsum, with faint band patterns still visible. Eyes light brown dorsally, dark brown to black ventrally, the dorsal margin with a dark brown area, thinner or absent in *L. santoensis* n. sp. Fastigium brown, wider than long and setose, apex whitish with a dark spot behind median ocellus. Scapes light brown, antennae homogeneously brown. Face almost entirely black, except a median yellow line on fastigium. Mouth parts dark brown to black. Palpi light brown, banded with black. Pronotum: Dorsal disk trapezoidal, wider posteriorly than in *L. santoensis* n. sp.; posterior margin straight; light brown with dark spots arranged in uneven lines; lateral lobes of pronotum almost entirely black, with a partial whitish band near ventral third, ventral margin whitish. Legs: colouration as in *L. santoensis* n. sp., but generally darker. Hind tibiae dorsal face with 4 or 5 inner ($m = 5$, $n = 8$) and 7 or 8 outer ($m = 7$, $n = 8$) spines above spurs, and 4 or 5 inner ($m = 5$, $n = 8$) and 5 outer ($m = 5$, $n = 8$) spines between spurs. Tarsomeres III-1 with 3-5 ($m = 4$, $n = 8$) spines on dorso-external edges. Hind wings absent, FWs short. Abdomen wide, brown with a black band on each lateral side; each tergite with dark spots on posterior margin. Cerci light brown,

entirely banded, including a preapical black ring, as in *L. santoensis* n. sp.

Male

FW not reaching abdomen midlength (Fig. 13). FW colouration (Fig. 1G, H): dorsal field homogeneously dark brown, except MP/MA area greyish; lateral field brown, MA/R area dark brown; veins slightly lighter than cells. FW venation similar to *L. santoensis* n. sp.: 1A angle wide ($>130^\circ$); stridulatory file with 149 teeth ($n = 1$), located on both transverse part (117 teeth) and angle (32 teeth) of 1A (Fig. 3D). CuP missing. Harp as wide as long, with one harp vein parallel to transverse axis. CuA curved internally at apex, the median fold triangular and short, located on dorsum. Cell c1 wider than in *L. santoensis* n. sp., separated at midlength by an accessory vein, c2 large. Mirror triangular, without accessory vein and larger than in *L. santoensis* n. sp.; d2 thin and rectangular. Apical field almost absent, including only 2 cells behind mirror (E alignment). Lateral field with 6 strong longitudinal veins including MA, R and 4 more ventral veins; latero-dorsal angle made by MP; R without strong bifurcations.

Male genitalia (Fig. 10D-F): very similar to *L. lifouensis*, but pseudepiphallic sclerite wider, rounded laterally, its anterior edge bisinuate, very indented medially; lophi setose, thinner than in *L. santoensis* n. sp. Pseudepiphallic parameres large, trilobate. Ectophallic arc complete and wide, immediately anterior to pseudepiphallic parameres. Ectophallic fold short and wide, with a Y preapical sclerotization. Endophallic sclerite Y-shaped, shorter than in *L. santoensis* n. sp., not reaching beyond anterior margin of pseudepiphallic sclerite; endophallic apodeme made of a thin median crest.

Female

FW dark brown, shorter than in *L. santoensis* n. sp., not reaching beyond posterior margin of first tergite, separated by a distance equal to length (Fig. 11B); dorsal field with 4 or 5 strong longitudinal veins. Lateral field with 3 or 4 strong longitudinal veins. Ovipositor short; apex lanceolate, denticulate on dorsal edge (Fig. 6H).

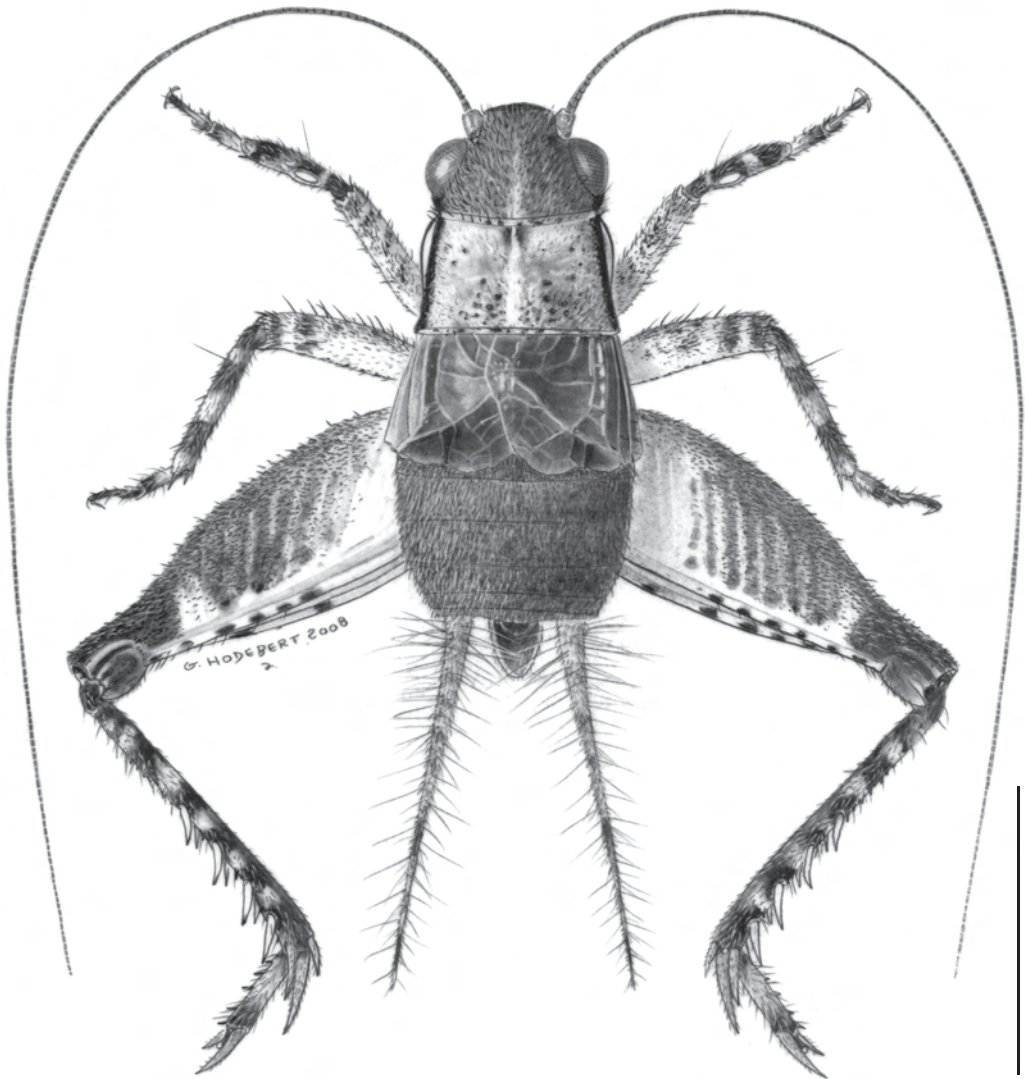


FIG. 13. — *Lebinthus nattawa* n. sp., male habitus, holotype. Scale bar: 5 mm.

Female genitalia: copulatory papilla (Fig. 12D-F) widened dorsally, more elongate than in *L. santoensis* n. sp., its basal sclerotized ring irregular; apex narrowed and long, curved ventrally, with a preapical ventral bump.

Juvenile

Subadults similar to adults in colouration.

Measurements

See Table 13.

HABITAT AND LIFE HISTORY TRAITS

Lebinthus nattawa n. sp. lives in leaf litter in forested areas (Fig. 19). Specimens are found in dense populations in wet leaf litter, generally on or under large dead leaves.

TABLE 13. — Measurements (in mm) of *Lebinthus nattawa* n. sp.: minimum-maximum (mean). Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIIL	FIIW	TIIL	OvipL
Male holotype	2.3	3.4	2.8	2.4	8.9	3	6.5	–
Female allotype	2.4	3.8	0.8	1.5	8.9	3.5	6.5	7
Males (n = 2)	2.2-2.3 (2.3)	2.8-3.4 (3.1)	2.1-2.8 (2.5)	2-2.4 (2.2)	8.9-9.1 (9)	3-3.2 (3.1)	6.4-6.5 (6.5)	–
Females (n = 5)	2.1-2.4 (2.2)	3.1-3.8 (3.5)	0.5-0.9 (0.7)	1-1.5 (1.2)	8.5-9 (8.8)	3-3.5 (3.3)	6.2-6.5 (6.4)	6-7 (6.6)

BEHAVIOUR

Not documented.

Lebinthus malekulensis n. sp.
(Figs 6I; 11C; 12G-I)

TYPE MATERIAL. — [Vanuatu] New Hebrides. [Province Malampa], Malekula Is., Ounua, II.1929 (176), L. E. Cheesman, ♀ holotype (B.M.1929-234).

TYPE LOCALITY. — Vanuatu, Malekula Is., Ounua.

ETYMOLOGY. — Species named after the type locality.

DISTRIBUTION. — Vanuatu, Malekula Is.

DIAGNOSIS. — Species of small size, dark brown general colouration, very similar to *L. santoensis* n. sp. and *L. lifouensis* in size, shape and colouration patterns. Dark ring on cerci apex present as in *L. santoensis* n. sp. The species clearly differs from *L. santoensis* n. sp. by female copulatory papilla only.

DESCRIPTION

Species of small size, dark brown general colouration. Dark ring on cerci apex present. Hind tibiae dorsal face with 5 inner and 7 outer spines above spurs, and 3 inner and 5 outer spines between spurs.

Male

Unknown.

Female

FWs short (Fig. 11C), reaching beyond posterior margin of first tergite, separated by a distance equal to length; dorsal field with 3 strong whitish and 2 fainter longitudinal veins. Lateral field darker than dorsal field, with 3 strong dark brown longitudinal

veins including MA and R. Ovipositor short but slightly longer than average *L. santoensis* n. sp.; apex lanceolate, slightly denticulate on dorsal edge (Fig. 6I).

Female genitalia: copulatory papilla flat (Fig. 12G, H), sclerotized on both basal and apical apex, deeply curved, the ventral side concave, with a ventral bump.

Measurements

See Table 14.

HABITAT, LIFE HISTORY TRAITS AND BEHAVIOUR
Not documented.

DISCUSSION

PATTERNS OF DISTRIBUTION, ECOLOGY
AND HABITATS

According to the detailed information obtained in Espiritu Santo, the crickets of the subfamily Eneopterinae are very abundant in Vanuatu, both in primary forests and secondary habitats (gardens, cultures, edges, costal areas). Two related genera belonging to the tribe Lebinthini are represented by several species (three *Cardiodactylus*, two *Lebinthus*) with the following pattern of distribution.

In every studied locality, a couple of *Cardiodactylus* sympatric species belonging to both species groups is present. The species *C. enkraussi* (*Efordi* group) is found everywhere on the island, together with a species of the *Novaeguineae* group: *C. novaeguineae* near coastal areas (Luganville, Peavot, Penaoru, Vathé, etc.), and *C. tankara* n. sp. in inland areas (Butmas). These two species are similar in terms of detailed

TABLE 14. — Measurements (in mm) of *Lebinthus malekulensis* n. sp. Abbreviations: see Material and methods.

	PronL	PronW	FWL	FWW	FIIL	FIIW	TIIL	OvipL
Female holotype	2.1	3.4	0.9	1.1	8.1	2.9	5.6	8

TABLE 15. — List of Eneopterinae species per island in Vanuatu.

	<i>Cardiodactylus</i>		<i>Lebinthus</i>
	<i>Novaeguineae</i> group	<i>Efordi</i> group	
Ambrym Is.	<i>C. gagnei</i>		
Aneityum Is.	<i>C. novaeguineae</i>		
Aoba Is.	<i>C. novaeguineae</i> , <i>C. aobaensis</i> n. sp.		
Efate Is.	<i>C. novaeguineae</i> , <i>C. gagnei</i>		
Epi Is.	<i>C. novaeguineae</i> , <i>C. epiensis</i>		
Erromango Is.	<i>C. novaeguineae</i>		
Espiritu Santo Is.	<i>C. novaeguineae</i> , <i>C. tankara</i> n. sp.	<i>C. enkraussi</i>	<i>L. santoensis</i> n. sp., <i>L. nattawa</i> n. sp.
Malekula Is.	<i>C. novaeguineae</i>	<i>C. enkraussi</i>	<i>L. malekulensis</i> n. sp.
Pentecost Is.	<i>C. novaeguineae</i>	<i>C. pentecostensis</i> n. sp.	<i>L. santoensis</i> n. sp.
Tanna Is.	<i>C. novaeguineae</i> , <i>C. cheesmani</i>		

habitats and ecology and seem mutually exclusive in term of distribution according to our sampling. On the reverse, the sympatric species show a clear ecological differentiation (Tables 1; 2): *C. enkraussi* (*Efordi* group) is present in relatively dense populations, deep within vegetation, and its song is little conspicuous, with limited intensity, while individuals of *C. novaeguineae* or *C. tankara* n. sp. (*Novaeguineae* group) are more spaced from one another and occupy more conspicuous and generally higher calling sites (large leaves of bushes, ferns or trees), and they also sing more loudly compared to *C. enkraussi*.

The situation is different in *Lebinthus*. *Lebinthus santoensis* n. sp., found in Espiritu Santo but also in Pentecost Is., is very similar to *L. lifouensis* (New Caledonia, Lifou Is.) and *L. malekulensis* n. sp. (Vanuatu, Malekula Is.). It is widespread in Espiritu Santo and has been found at every studied location, except in Butmas area, which is far from coastal areas and river banks.

According to homogeneous morphology, including male genitalia, FW venation, and calling song, the *Lebinthus* species from Vanuatu and the Loyalty Islands may belong to the same species group. Within this group, however, *L. nattawa* n. sp., endemic to Espiritu Santo, seems more different from *L. santoensis* n. sp. than the later is from *L. lifouensis*. The

two species are found in nearby areas in Nattawa, but *L. santoensis* n. sp. in open clearings and edge forested areas and *L. nattawa* n. sp. in forested areas. This suggests several successive colonization events, possibly related to behavioural and/or adaptive differentiation, which will be analyzed in upcoming molecular studies.

Further investigations in other islands of Vanuatu will be needed to draw clear conclusions about the pattern and history of colonisation of Eneopterinae in the archipelago. Despite the weak amount of data available so far, the information found on collection material and previous studies (Table 15) shows that the same general pattern may be found in several, if not most, other islands, with more or less complexity depending on the size of the islands. For instance, the islands Malekula and Pentecost show one species of each *Cardiodactylus* group and one *Lebinthus* species, while the islands Aoba, Efate, Epi and Tanna show a couple of *Cardiodactylus* species from the *Novaeguineae* group, which could be the equivalent of *C. novaeguineae* and *C. tankara* n. sp. in Espiritu Santo.

DIVERSITY OF ACOUSTIC TRAITS

The eneopterine species found in Espiritu Santo contribute to the knowledge and documentation of

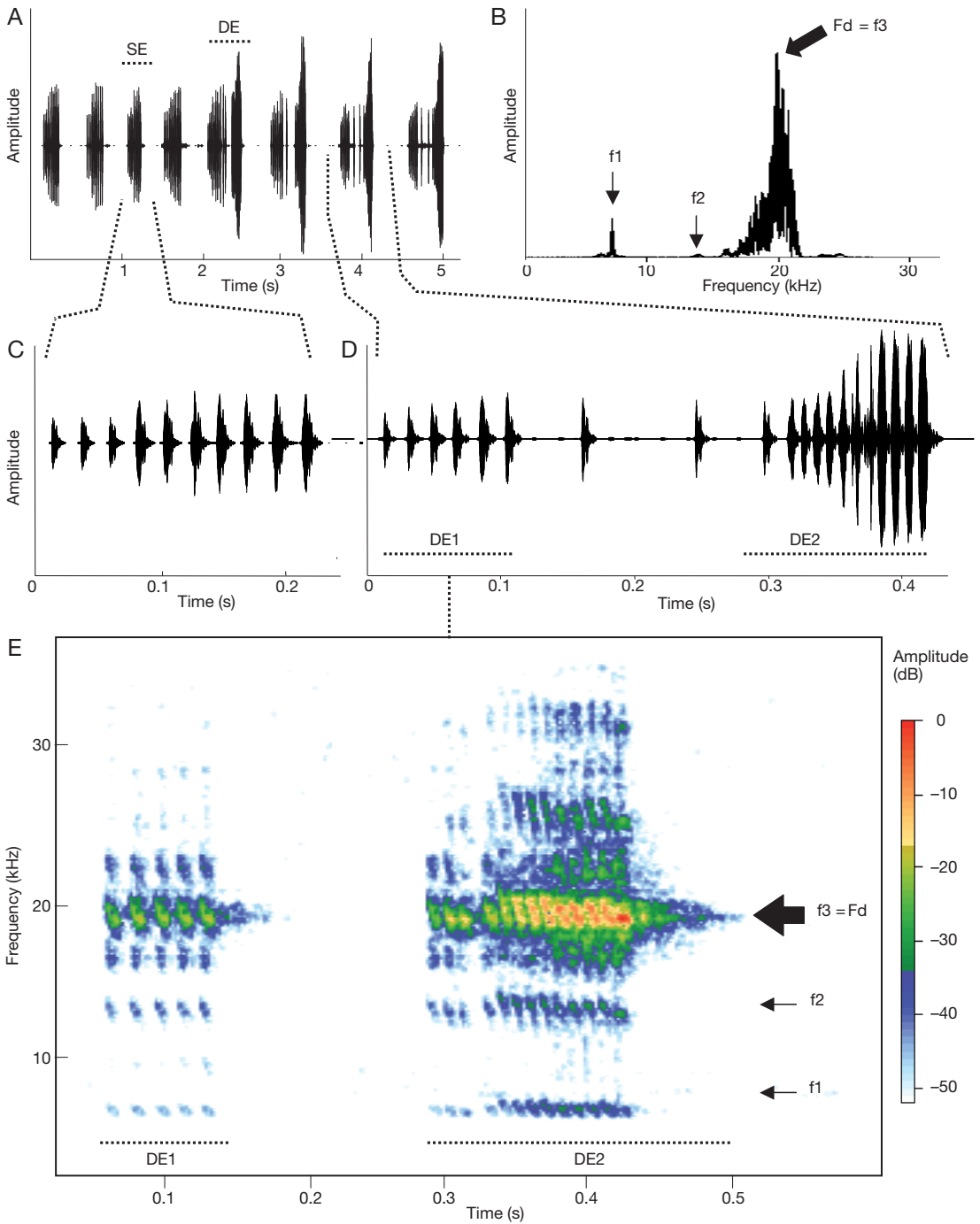


FIG. 14. — Calling song of *Cardiodactylus enkraussi* Otte, 2007: **A**, oscillogram showing four single echemes (**SE**) and four double echemes (**DE**); **B**, spectrogram (linear amplitude); **C**, oscillogram of a single echeme; **D**, oscillogram of a double echeme; **E**, songram of a double echeme. Abbreviations: f_1 - f_3 , first (fundamental) to third harmonic frequencies; F_d , dominant frequency.

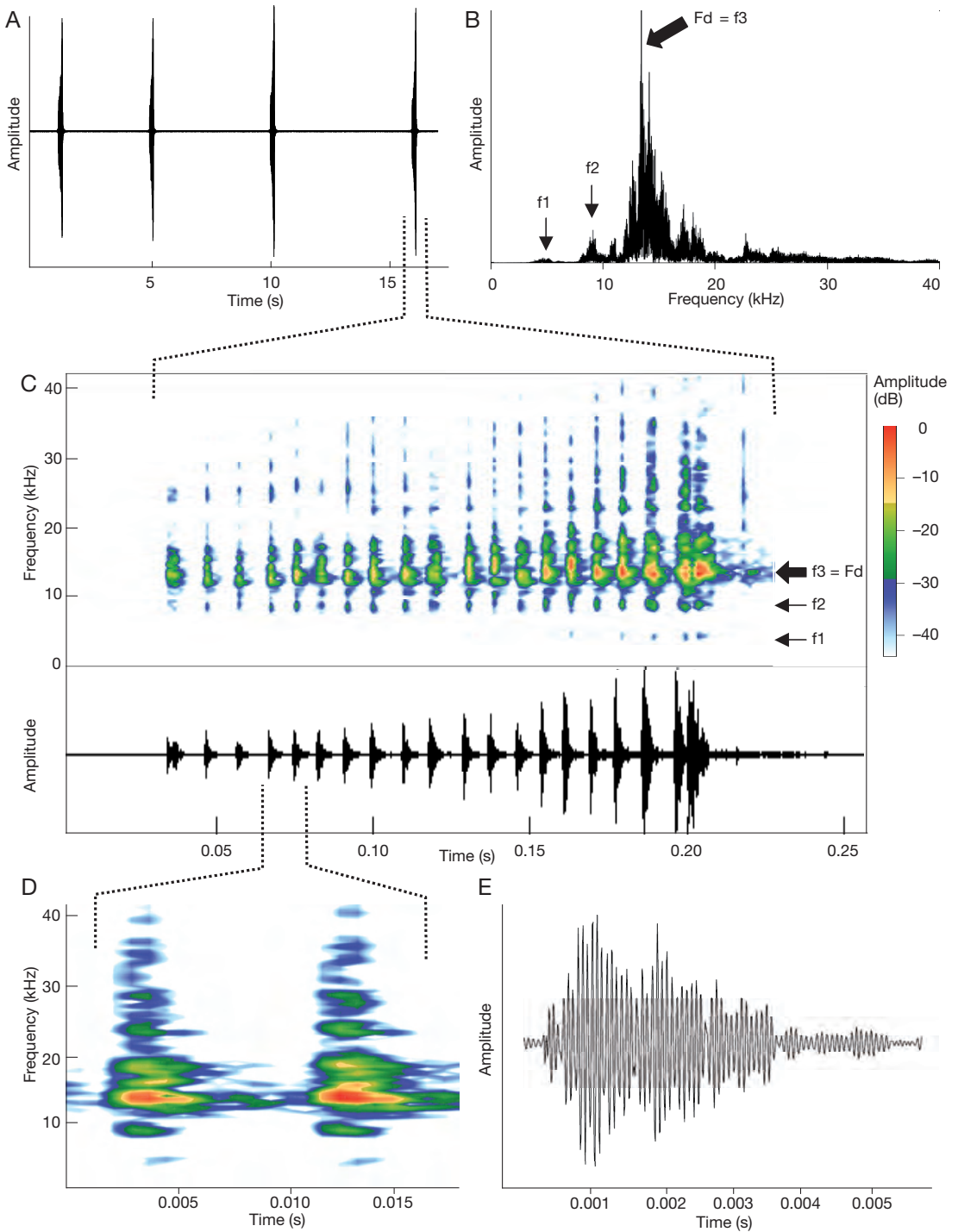


FIG. 15. — Calling song of *Cardiodactylus tankara* n. sp.: **A**, oscillogram showing 4 echemes; **B**, spectrogram (linear amplitude); **C**, sonogram of an echeme (top) coupled with oscillogram (bottom); **D**, detailed sonogram of a syllable; **E**, detail oscillogram of a syllable. Abbreviations: **f1-f3**, first (fundamental) to third harmonic frequencies; **Fd**, dominant frequency.

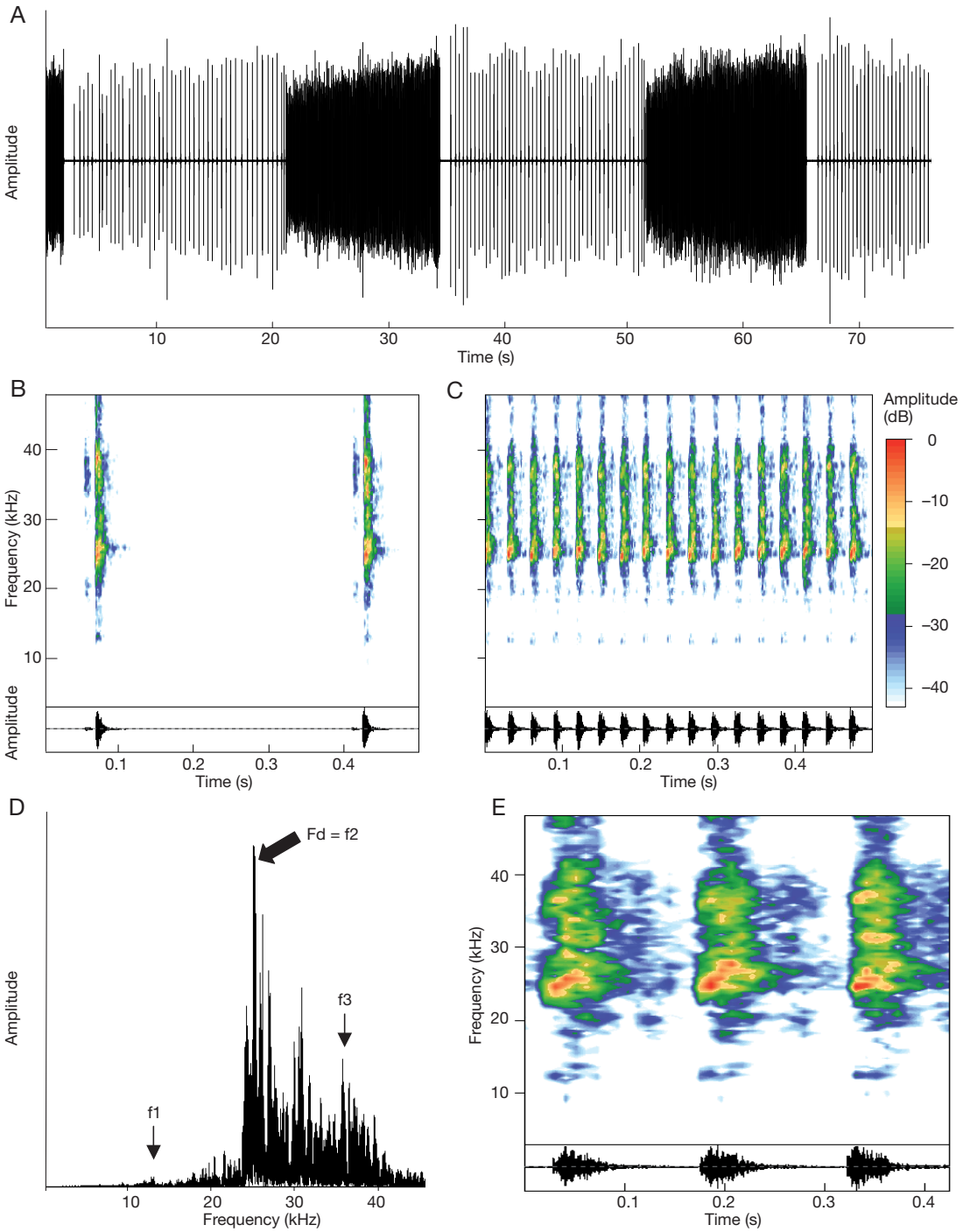


FIG. 16. — Calling song of *Lebinthus santoensis* n. sp.: **A**, oscillogram showing two successive echemes; **B**, detailed sonogram (top) and oscillogram (bottom) of two syllables within the slow part; **C**, **E**, detailed sonogram (top) and oscillogram (bottom) of 17 (**C**) and three (**E**) syllables within the fast part; **D**, spectrogram (linear amplitude). Abbreviations: **f1-f3**, first (fundamental) to third harmonic frequencies; **Fd**, dominant frequency.

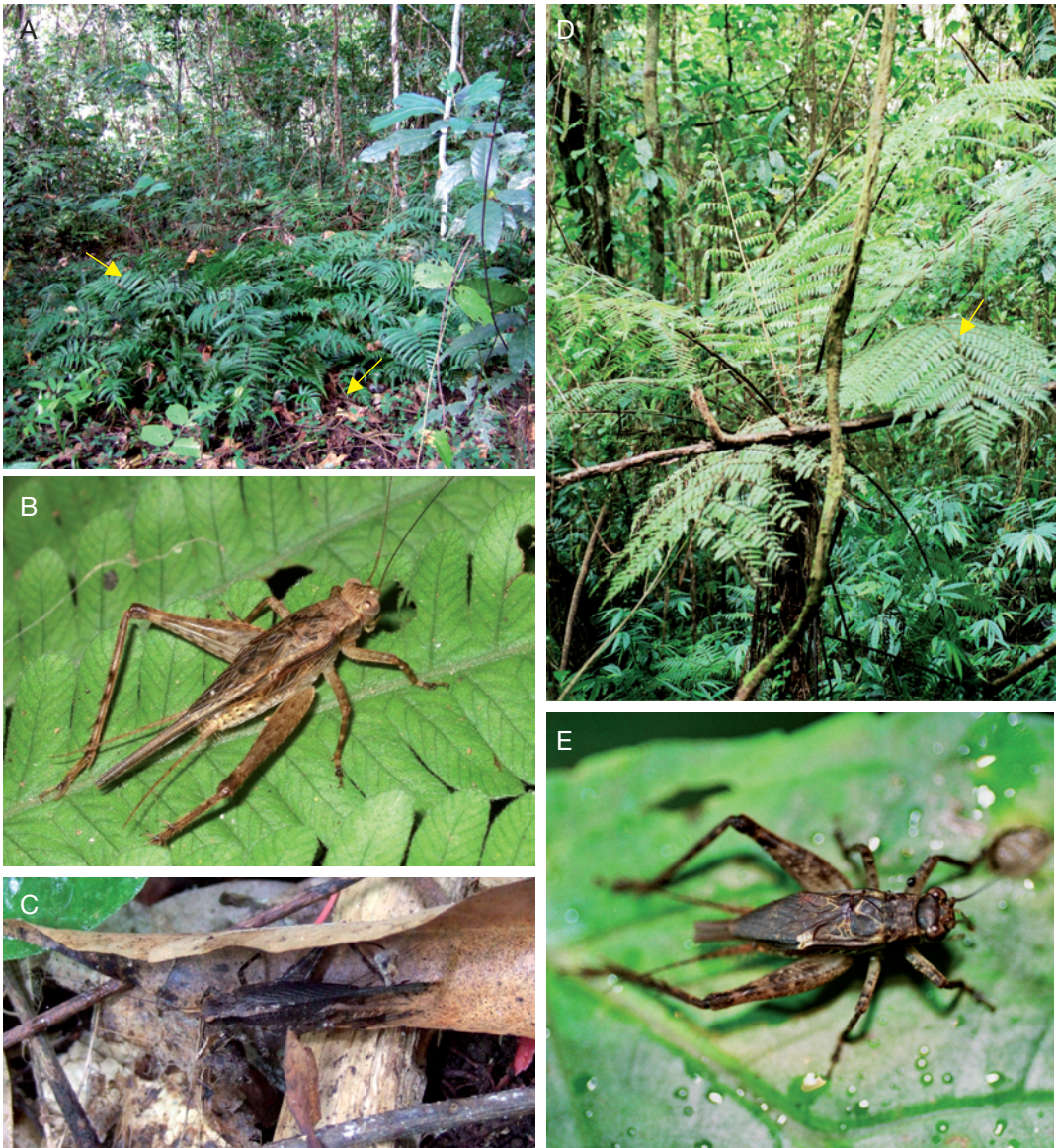


FIG. 17. — **A-C**, *Cardiodactylus enkraussi* Otte, 2007: **A**, habitat in Vathé conservation area, Espiritu Santo, Vanuatu, adults on (night) or under (day) plant leaves, or in leaf litter (day) (yellow arrows); **B**, male on plant leaf in Vathé (night), Espiritu Santo, Vanuatu; **C**, female hiding in leaf litter in Vathé (day), Espiritu Santo, Vanuatu; **D, E**, *C. tankara* n. sp.; **D**, habitat in Butmas, Espiritu Santo, Vanuatu, primary forest on Plateau de Tankara, adults on large plant leaves (yellow arrow); **E**, male on plant leaf by day in Butmas. Photos: T. Robillard (A, TR80; B, TR76; C, TR82) and S. Hugel (D, SH-14x06a; E, SH-14X06a).

the diversity of the subfamily in terms of acoustic signals and reproductive behaviours.

The new data confirm the main spectral properties of the Lebinthini tribe, i.e. the use of high dominant

frequencies (Robillard & Desutter-Grandcolas 2004b) and the use of harmonics as dominant frequency instead of the fundamental frequency (Robillard *et al.* 2007). All *Cardiodactylus* and *Lebinthus*



FIG. 18. — *Lebinthus santoensis* n. sp.: **A, C, E**, in Matantas, pointe de Quirros, Espiritu Santo, Vanuatu, by day; **A**, habitat; **C**, habitat close up; **E**, male; **B, D**, in Big Bay, Vatthé, Espiritu Santo, Vanuatu, by day, along beach; **B**, habitat; **D**, habitat close up with juveniles and adults in leaf litter; **F**, female juvenile, in Peavot, Espiritu Santo, Vanuatu, by day. Photos: S. Hugel (A, C, E, SH-19X06a; F, SH-20x06a) and T. Robillard (B, TR35; D, TR65).



FIG. 19. — *Lebinthus nattawa* n. sp.: **A**, habitat, **B**, female; **C**, male, in Nattawa, Espiritu Santo, Vanuatu, by day, pastured forest. Photos: T. Robillard (A, TR-114) and S. Hugel (B, C, SH-29x06a).

species presented here are conforming to the expectations in terms of frequency spectra, as their songs are consistent with species previously documented for both genera (Robillard *et al.* 2007).

However the new species *L. santoensis* n. sp. adds to the diversity of Eneopterinae, and of crickets in general, by having a dominant frequency of 26.5 kHz, thus reaching beyond the human audible frequency limit of about 20 kHz. Although ultrasonic frequencies are usual in tettigonids (e.g., Morris *et al.* 1989; Montealegre-Z & Morris 1999; Naskrecki 2000; Montealegre-Z *et al.* 2006), they had never been documented before in crickets, and *L. santoensis* n. sp. is consequently the first ultrasonic cricket. It clearly suggests that Eneopterinae crickets have evolved toward a new mode

of acoustic communication using the ultrasonic frequency range for calling.

To a lesser extent, the diversity of the subfamily is also increased in terms of temporal patterns. For instance, *Cardiodactylus* species documented here clearly show several distinctive song rhythms (two-part echemes vs. single echemes), which are likely to be only a sample of the diversity existing throughout the genus, as suggested by the songs of *C. novaeguineae* and *C. guttulus* (Robillard & Ichikawa in press).

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