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# New intertidal crickets from Comoros and Mascarene islands (Orthoptera: Trigonidiidae: Nemobiinae: Burcini)

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## Abstract

*Nemobiinae* crickets of the tribe *Burcini* Gorochov, 1986 are described for the first time from the shores of South Western Indian Ocean islands. The new genus *Makalapobius* n. gen. is proposed to include *M. aigrettensis* n. gen. n. sp. from Mauritius and *M. masihu* n. gen. n. sp. from Grande Comore, and the new genus *Gabusibius* n. gen. to include *G. ndzilu* n. gen. n. sp. from Anjouan, *G. mosi* n. gen. n. sp., from Mohéli, and *G. dzindzanu* n. gen. n. sp. from Mayotte. The species *Speonemobius littoreus* Vannini & Chelazzi, 1978 from Somalia coast is tentatively placed in the genus *Gabusibius* n. gen. as *G. ? litoreus* (Vannini & Chelazzi, 1978) n. gen. n. comb. The songs of *G. mosi* n. gen. n. sp. and *M. aigrettensis* n. gen. n. sp. are described. The threats to SWIO *Burcini* and endemism of Orthoptera from SWIO coastal areas are discussed.

**Key words:** Endemism; intertidal species; taxonomy, distribution, new species, Orthoptera, Nemobiinae

## Résumé

Des grillons *Nemobiinae* de la tribu des *Burcini* Gorochov, 1986 sont décrits pour la première fois des côtes des îles du sud-ouest de l'Océan Indien. Le nouveau genre *Makalapobius* n. gen. est proposé pour inclure *M. aigrettensis* n. gen. n. sp. de l'île Maurice et *M. masihu* n. gen. n. sp. de Grande Comore, et le nouveau genre *Gabusibius* n. gen. pour inclure *G. ndzilu* n. gen. n. sp. d'Anjouan, *G. mosi* n. gen. n. sp., de Mohéli, et *G. dzindzanu* n. gen. n. sp. de Mayotte. L'espèce *Speonemobius littoreus* Vannini & Chelazzi, 1978 de la côte somalienne est provisoirement placée dans le genre *Gabusibius* n. gen. en tant que *G. ? litoreus* (Vannini & Chelazzi, 1978) n. gen. n. comb. Les chants de *G. mosi* n. gen. n. sp. et *M. aigrettensis* n. gen. n. sp. sont décrits. Les menaces s'exerçant sur les *Burcini* des îles du sud-ouest de l'Océan Indien, et l'endémisme des orthoptères des milieux côtiers de ces îles sont discutés.

## Introduction

Together with *Marinemobiini* Gorochov, 1985, *Burcini* Gorochov, 1986 *Nemobiinae* live mostly on or near the shore, often in the intertidal habitats. Both tribes occur on Oriental, Australian, eastern Palearctic and Pacific regions (Cigliano *et al.* 2021; Gorochov, 1986; Gorochov *et al.* 2018; Otte & Alexander, 1983). One single species has been described from the Eastern coast of continental Africa (*Speonemobius litoreus* Vannini and Chelazzi, 1978) as belonging to *Speonemobius* Chopard, 1924, a genus that was later proposed to be moved to *Burcini*

(Gorochov *et al.* 2018). Except for this latter species, no Burcini was known from Africa nor from South Western Indian Ocean (SWIO) islands. During the surveys of Orthoptera on Mascarene islands (SH) and on Comoros (LDG and SH), we discovered new species of Burcini which are described in the present article.

## Material and methods

Specimens examined. The new taxa are described based on specimens collected over the last decade by SH on Mauritius and by SH and LDG on Comoros. Specimens were collected at night or dusk by sight using a headlamp and a net. Specimens from caves were collected by day using similar techniques.

Abbreviations and symbols for taxonomic results. Male genitalia: Genitalic structures follow Desutter (1987) and Desutter-Grandcolas (2003): **en. s.**, endophallic sclerite; **gl.**, paired glands of ejaculatory duct; **IEE**, epi-ectophallic invagination; **ps.**, pseudepiphallic sclerite; **r.**, ramus. General morphology: Movable and articulated outgrowths are called **spurs** whereas immovable outgrowths are called **spines** (e.g. Otte & Alexander, 1983; Jin & Kevan, 1992; Rentz, 1985).

Abbreviations: I, II, III, anterior, median, posterior (leg, tibia femur, tarsomere); ai1, 2, 3, tibial inner apical spur 1, 2 or 3; ao1, 2, 3, tibial outer apical spur; ai/o, inner/outer TIII apical spur; DD, LL, dorsal disc, lateral lobe of pronotum; sai1, 2, 3, tibial inner subapical spur 1, 2 or 3; sao1, 2, 3, tibial outer subapical spur; SGP, subgenital plate.

Measurements (in mm): BL, body length; PrnL, pronotum length (dorsal view); PrnW, pronotum width (dorsal view); FWL, fore wing length; FIL, FIIL, FIILL, length of femora I, II, III, respectively; FIIIw, maximal width of FIII; OvpL, length of ovipositor.

Song recordings and analysis. Recordings have been performed with an Audiotecnica AT822 stereo microphone, on a HDR HC1E Sony camcorder (sampling rate: 48 kHz) on the nightshot mode (to follow the insect behavior) or using a Field memory recorder Fostex FR-2LE (sampling rate: 48 kHz, stereo) with a Sennheiser K6/ME62 microphone (frequency range: 20 - 20 kHz  $\pm$  2.5 dB). Song analysis has been performed with Clampfit 10.2 software. Song recordings are deposited in both S.H. and MNHN acoustic databases. Acoustic terminology is from Stumpner *et al.* (2013). All recordings were performed *in natura* at ambient temperature. The first harmonic (fundamental) is the only carrier frequency given in the text; the recording device used in the field usually does not allow defining whether it corresponds to the dominant frequency.

Geographic names. In the present article, Comoros is used as a geographic name matter apart from any political consideration.

Repository. BMNH, The Natural History Museum, London (formerly British Museum of Natural History); MNHN, Muséum national d'Histoire naturelle, Paris; coll. SH: collection Sylvain Hugel, Strasbourg, France.

Databases and inventory numbers. The codes following specimen data correspond to the specimen numbers from SH or LDG field pad. Specimens deposited in the MNHN collections

have a unique inventory number, MNHN-EO-ENSIFXXXX, and can be found in the collection data base of the MNHN at the following address, <https://science.mnhn.fr/institution/mnhn/collection/eo/search>

## Results

List of studied taxa:

Tribe *Burcini* Gorochov, 1986

Genus *Makalapobius* n. gen.

*M. aigrettensis* n. gen. n. sp. [Mauritius – Ile Maurice]

*M. masihu* n. gen. n. sp. [Ngazidja – Grande Comore]

Genus *Gabusibius* n. gen.

*G. ndzilu* n. gen. n. sp. [Ndzuani – Anjouan]

*G. mosi* n. gen. n. sp. [Mwali – Mohéli]

*G. dzindzanu* n. gen. n. sp. [Maore – Mayotte]

*G. ? litoreus* (Vannini & Chelazzi, 1978) n. gen. n. comb. [Somalia]

## Etymology

The two new genera described in the present work are named after local traditional musical instruments which are both threatened with extinction. Makalapo is a long curved stick planted into the ground which is connected by a string to a sound box buried in the ground; it was traditionally used to play Sega in Mauritius. Gabusi is a short-necked lute similar to Qanbūs; it was widespread on Comoros. The name aigrettensis is derived from the type locality Ile aux Aigrettes, an islet managed by Mauritian Wildlife Foundation. New Comorian species belonging to *Gabusibius* n. gen. and *Makalapobius* n. gen. are named after words in Comorian: masihu means night, ndzilu means black, mosi means grey and dzindzanu means yellow.

## Makalapobius n. gen.

(Figs. 1-24; 71-72; 77)

**Type species.** *Malakapobius aigrettensis* n. gen., n. sp., here designated.

**Species included.** *Malakapobius* n. gen. includes *Malakapobius aigrettensis* n. gen., n. sp. and *Malakapobius masihu* n. gen. n. sp..

**Distribution.** South Western Indian Ocean: Mascarene islands, Mauritius; Comoros, Ngazidja (Grande Comore).

**Diagnosis.** *Makalapobius* n. gen. is superficially similar to *Burcus* Gorochov, 1986, to *Paraburcus* Gorochov, 2018, and to *Gabusibius* n. gen. It is characterized by the following characters. TIII with 2 sai (Fig. 5; unlike *Neoburcus* Gorochov, 2018 which has 3 sai). Male winged (Fig. 1; unlike *Taiwanemobius* Yang & Chang, 1996); with distinct stridulum (Fig. 7; unlike *Paranemobius* Saussure, 1877); wings oval, truncated (Fig. 1; unlike *Burcus* Gorochov, 1986 with relatively long FW); without mirror (Fig. 7; unlike *Speonemobius* Chopard, 1924 with full mirror); with relatively long diagonal vein (Fig. 7; unlike *Paraburcus* with short diagonal

vein). Male SGP trilobated (Figs. 6, 15); median lobe small, membranous, not longer than lateral lobes (unlike *Burcus* with only one single median lobe). Male genitalia (Figs. 19-24: pseudepiphallus lightly curved upwards distally (curved downwards in *Paraburcus*, strongly upcurved from the middle in *Burcus*); apex narrow in side view (unlike *Gabusibius* n. gen. with very wide apex in side view); apex with rounded distal lophi relatively contiguous; without apical lateral extensions forming large apical concavity visible dorsally (unlike most *Burcus* species). Epi-ectophallic invagination not extending more anteriorly than rami insertion (unlike *Burcus* and *Gabusibius* n. gen. with long epi-ectophallic invagination exceeding rami insertion); rami very wide in side view (unlike all other genera except *Gabusibius* n. gen.).

**Description.** Including characters shared by other Burcini.

Burcini of average size. General coloration typical for Burcini, from light grey to light yellowish, with numerous black patterns. Head, pronotum and femora with long black bristles (Figs. 1-3).

**Head.** Not wider than pronotum (Figs. 1, 12). Antennae dark, unbanded. Eyes moderately protruding, not flattened on head dorsum (Figs. 1-3, 12-13). Ocelli small; lateral ocelli rounded, well distinct; median ocellus less distinct, localized dorsally to fastigium tip; distance between lateral ocelli larger than distance between one lateral ocellus and median ocellus. Fastigium between antennae not wider than scapes (Figs. 3, 13); scapes wider than high (front view); palpi short, article length:  $5 > 3 > 4$ ; article 5 apex strongly widened.

**Thorax.** Pronotum (Figs. 1-2, 12) wider than long, 0.65-0.70 times as long as wide; DD sides subparallel, DD slightly narrower anteriorly, slightly enlarged before mid-length; DD anterior margin inconspicuously concave; DD posterior margin weakly rounded; DD longitudinal median furrow weakly imprinted; DD anterior transverse furrow distinct on the sides; LL shallow, higher anteriorly, less high posteriorly.

**Legs.** Legs of average size for Burcini, not elongated. TI with long narrowly oval outer tympanum; without inner tympanum. TI and TII with 2 ventral apical spurs, the inner the longest. FIII not particularly widened nor narrow (Figs. 4, 14): ca. 3.0-3.3 times as long as wide. TIII apical spurs typical of burcini (Figs. 4-5): 3 ao, 2 ai; relative length of apical spurs:  $ao_2 > ao_3 > ao_1$ ,  $ai_2 > ai_1$ . TIII with 3 outer and 2 inner subapical spurs; relative length of subapical spurs:  $sao_1 = sao_2 > sao_3$ ,  $sai_1 > sai_2$ . Hind tarsi long, particularly hind basitarsi. Hind basitarsi without dorsal serration (as usual in Nemobiini, see Desutter-Grandcolas *et al.* submit.); with 3 apical spurs: 2 dorsal apical spurs, the inner very small, 1 inner ventral apical spur longer than the dorsal outer one.

**Wings.** FW (Figs. 71, 72) present in males, absent in females. HW absent in both sexes.

**Coloration.** Head (Figs. 1-3, 12-13): Face with black patterns below the eyes converging to clypeus; semicircular area below antennae black; face black patterns surrounding a light yellow triangle pointing upwards; mandibles light yellow; scapes light yellow, antennae darker than scapes, not banded; palpi light yellow; genae light yellow; tip of fastigium black dorsally; semicircular area dorsal to antennae with dark pattern; occiput dark yellow. Thorax (Figs. 1-2, 12): Pronotum color variable, DD light yellow with black lateral spots near anterior margin or very dark with two light lateral spots near anterior margin; LL black, anterior ventral margin light yellow. Abdomen dark with or without light yellow spots. Legs (Figs. 4-5, 14): yellow or light yellow with darker bandings; FIII lateral side with dark basis, with 3 transverse dark bandings; TIII dark.

**Male. Wings.** FW (Fig. 1, 7, 12, 16) oval in shape, truncated apically. Stridulatory apparatus well developed, with relatively long diagonal vein; with well distinct chords, relatively long for

Burcini; without a mirror: FW distal part with reticulation (Fig. 7). **Subgenital plate.** Apex trilobated (Fig. 6), median lobe small, membranous, not longer than lateral lobes. **Genitalia** (Figs. 19-24). Pseudepiphallos narrow in dorsal view and side view, elongated, lightly curved upwards (sideview); apex with rounded distal lophi; without apical lateral extensions; without large apical concavity visible dorsally. Apodemes absent. Epi-ectophallic invagination not extending more anteriorly than rami insertion. Rami very wide (side view).

**Female.** No trace of wings (Figs. 18, 72). Subgenital plate (Fig. 8) trapezoidal. Ovipositor weakly up curved; weakly enlarged apically (Fig. 17). **Genitalia.** Copulatory papilla not examined.

**Calling song.** When known, male call is made of verses of increasing amplitude lasting more than 1 second (Fig. 9-11).

***Makalapobius aigrettensis* n. gen. n. sp.**

(Figs. 1-11; 19-21; 71-72; 77; Tab. 1)

*Makalapobius aigrettensis* n. gen. n. sp., here described.

**Distribution:** South Western Indian Ocean, Mascarene Islands, Mauritius.

**Holotype. Male.** Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 059), MNHN (MNHN-EO-ENSIF12130).

**Allotype. Female.** Same as Holotype; S. Hugel leg. (2011MauRodSH 064), MNHN (MNHN-EO-ENSIF12131).

**Paratypes, 7 males, 6 females.** 1♂ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (BIOTAS 2009 271), Coll. SH. 1♀ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (BIOTAS 2009 224), Coll. SH. 1♂ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 058), MNHN (MNHN-EO-ENSIF12132). 1 ♂ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 060), Coll. SH. 1 ♂ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 061), Coll. SH. 1 ♀ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 062), MNHN (MNHN-EO-ENSIF12133). 1 ♀ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 063), Coll. SH. 1 ♀ Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (2011MauRodSH 065), Coll. SH. 1 ♂ Ile Maurice, La Prairie, plage sous coraux, -20.4885, 57.3616, 0.5m; 28.IV.2011; S. Hugel leg. (2011MauRodSH 025), Coll. SH. (DNA sequences in Chintauan-Marquier et al. 2016 under the name *Tethella* sp\_MAU, sample LDG150). 1 ♂ Ile Maurice, La Prairie, plage sous coraux, -20.4885, 57.3616, 0.5m; 28.IV.2011; S. Hugel leg. (2011MauRodSH 026), Coll. SH. 1 ♀ Ile Maurice, La Prairie, plage sous coraux, -20.4885, 57.3616, 0.5m; 28.IV.2011; S. Hugel leg. (2011MauRodSH 028), Coll. SH. 1 ♀ Ile Maurice, La Prairie, plage sous coraux, -20.4885, 57.3616, 0.5m; 28.IV.2011; S. Hugel leg. (2011MauRodSH 027), Coll. SH. 1 ♂ Ile Maurice, Ile aux Aigrettes, grotte, -20.4187, 57.7304, 0.3m; 4.III.2008; S. Hugel leg. (BIOTAS2008 424), Recorded, Coll. SH.

**Other specimens** (non type material). 3 Juveniles. 1 juvenile, Ile Maurice, Ile aux Aigrettes, plage, -20.4190, 57.7302, 0.3m; 10.V.2009; S. Hugel leg. (BIOTAS 2009 272), Coll. SH. 1 juvenile, Ile Maurice, Ile aux Aigrettes, grotte, -20.4187, 57.7304, 0.3m; 4.III.2008; S. Hugel leg.

(BIOTAS 2009 230), Coll. SH. 1 juvenile, Ile Maurice, Ile aux Aigrettes, grotte, -20.4187, 57.7304, 0.3m; 4.III.2008; S. Hugel leg. (BIOTAS 2009 231), Coll. SH.

### Diagnosis.

This species is characterized by its color: light with black patterns (very dark in *M. masihu* n. gen. n. sp.); its relatively small size (BL < 9.5 mm vs. > 9.5 in *M. masihu* n. gen. n. sp.); its male genitalia: pseudepiphallus relatively short in dorsal view and wide in side view for the genus; apical lophi rounded in side view (unlike *M. masihu* n. gen. n. sp. with longer and very narrow pseudepiphallus, and lophi regularly narrowed toward apex in side view).

### Description. In addition to generic characters.

**Color.** Head (Figs. 1-3): Face with black patterns below the eyes converging to clypeus; semicircular area below antennae black; face black patterns surrounding a light yellow triangle pointing upwards; palpi light yellow; genae light yellow; tip of fastigium black dorsally; semicircular area dorsal to antennae with dark pattern; occiput dark yellow. Thorax (Figs. 1-2): Pronotum DD light yellow with black lateral spots near anterior margin; with two small posterior black spots near midline; LL black, anterior ventral margin light yellow. Abdomen dark with light yellow spots. Legs (Figs. 4-5): light with dark bandings; FIII lateral side with dark basis, with 3 transverse dark bandings; TIII darker than light parts of FIII.

**Male. Wings.** The two anterior-most chords delineating a long D-shaped cell. Stridulatory file with 51 teeth (paratype 2011MauRodSH 026). **Subgenital plate.** Apex trilobated: median lobe small, membranous; lateral lobes larger, rounded (Fig. 6). **Genitalia** (Figs. 19-21). Pseudepiphallus in dorsal view: narrow, distal half sub parallel; in side view: elongated, lightly curved upwards, with moderate enlargement near the apex at the upward bent, making it look like a hockey stick; apex with rounded contiguous distal lobes. Rami: very wide (side view), ventral margin linear; dorsal margin with two dorsal bumps. **Female.** SGP (Fig. 8) hind margin shallowly concave. Ovipositor (Fig. 8) with a subapical gap between dorsal and ventral valves.

**Song.** The call of this species has been recorded by day hours in Ile aux Aigrettes, in a small cave connected to the sea (30°C; Figs. 9-11). The male was isolated with no other specimen nearby. The first harmonic of the call peaks at 6.1 kHz. The call consists in long syllables of increasing amplitude. Syllable duration:  $4.2 \pm 0.2$  s (3.9-4.4 s); gap between syllables:  $58 \pm 122$  s (46-70 s).

**Biology.** The main habitat of this species is on Ile aux Aigrettes, and islet formed from coral-limestone localized 1 km East of Mauritius and declared nature reserve since 1965. This islet is managed by the Mauritian Wildlife Foundation (MWF). Most of the islet shore corresponds to small cliffs, often very concave, with numerous cracks and holes. At 10 m from the shore, the small cave is connected to the sea and smaller caves or faults connected to the sea seem to occur elsewhere on the islet. At low tide, a few small sand beaches or limestone rocky beaches emerge. *Makalapobius aigrettensis* n. gen. n. sp. occurs on all these sea-connected habitats, hiding on cracks and holes of the cliffs at high tide, and going out at night, particularly at low tide. By day hours, the discreet call of *Makalapobius aigrettensis* n. gen. n. sp. can be heard from the islet cliffs when approaching the shore from the sea. We also found this species

on large pebble beach in the South of Mauritius (in La Prairie), and observed it on the shore of Bambou Virieux, but at very low density.

The population of this remarkable species appears to have been directly impacted by the ecological disaster caused in August 2020 by the sinking of the tanker Wakashio. Despite searching, the species could not be found until February 2021 when a few specimens were observed again by Sooraj Dwarika (MWF).

**TABLE 1.** Measurements of *Makalapobius aigrettensis* n. gen. n. sp. (in mm).

	BL	PrnL	PrnW	FWL	FIL	FIIL	FIIL	FIILW	OvpL
♂ Holotype	7.75	1.50	2.15	2.50	2.75	2.80	5.15	2.40	
♀ Allotype	8.35	1.70	2.55	-	2.65	2.90	6.00	1.80	5.00
♂♂									
Average	7.89	1.53	2.22	2.31	2.73	2.68	5.24	1.88	-
Min	7.60	1.50	2.10	2.15	2.50	2.60	5.10	1.55	-
Max	8.50	1.60	2.40	2.50	2.85	2.80	5.40	2.40	-
♀♀									
Average	8.77	1.70	2.50	-	2.82	3.03	5.97	1.78	4.82
Min	8.35	1.60	2.40	-	2.65	2.90	5.80	1.70	4.70
Max	9.30	1.80	2.55	-	2.90	3.20	6.10	1.85	5.00

### ***Makalapobius masihu* n. gen. n. sp.**

(Figs. 12-18; 22-24; 77; Tab. 2)

*Makalapobius masihu* n. gen. n. sp., here described.

**Holotype. Male.** Comores, Grande Comores, Moroni, Itsandra, plage de galets, de sable et de corail, S11°41'04" E043°15'40"; 21.VIII.2010; S. Hugel & L. Desutter-Grandcolas leg. (LDG295), MNHN (MNHN-EO-ENSIF12147).

**Allotype. Female.** Comores, Grande Comores, Moroni, Itsandra, plage de galets, de sable et de corail, S11°41'04" E043°15'40"; 21.VIII.2010; S. Hugel & L. Desutter-Grandcolas leg. (LDG296), MNHN (MNHN-EO-ENSIF12148).

Other specimens (non type material). 1 juvenile, same as the holotype, S. Hugel & L. Desutter-Grandcolas leg. (LDG 297), MNHN.

**Distribution.** South Western Indian Ocean, Comoros, Ngazidja (Grande Comore).

### **Diagnosis.**

This species is characterized by its color: very dark, particularly abdomen (light with dark patterns in *M. aigrettensis* n. gen. n. sp.); its relatively large size (BL > 9.5 mm vs. < 9.5 in *M. aigrettensis* n. gen. n. sp.); its male genitalia: pseudepiphallus relatively long in dorsal view and narrow in side view for the genus; apical lophi regularly narrowed toward apex in side view (unlike *M. aigrettensis* n. gen. n. sp. with shorter and less very narrow pseudepiphallus, and lophi rounded in side view).



**Description.** In addition to generic characters

**Color.** Head (Figs 12-13): Face with black patterns below the eyes converging to clypeus; semicircular area below antennae black; face black patterns surrounding a light yellow triangle pointing upwards; palpi light yellow; genae light yellow; tip of fastigium black dorsally; semicircular area dorsal to antennae with dark pattern; occiput dark yellow. Thorax (Figs 12-18): Pronotum DD very dark with two light lateral spots near anterior margin in male holotype (Fig. 12); DD light yellow with black lateral spots near anterior margin and with two small posterior black spots near midline in female allotype (Fig. 18); LL black, anterior ventral margin light yellow. Abdomen dark in male holotype, with few light spots in female allotype. Legs (Figs. 12, 14): yellow with dark bandings; FIII lateral side with dark basis, with 3 transverse dark bandings; TIII darker than light part of FIII.

**Male. Wings. FW short and truncated straight.** The two anterior-most chords delineating a short D-shaped cell (Fig. 16 arrow). **Subgenital plate.** Distorted in the only male available. Apex trilobated: median lobe less sclerotized but as high as the lateral lobes; lateral lobes more rounded (Fig. 15). **Genitalia** (Figs. 22-24). Pseudepiphallus in dorsal view: very narrow with parallel margins; in side view: very elongated, very lightly curved upwards, with clear enlargement near the apex at the upward bent; apex with rounded contiguous distal lobes. Rami: short and very wide (side view), ventral margin linear; dorsal margin with two very short dorsal bumps. **Female.** SGP hind margin shallowly concave, with a narrow median emargination. Ovipositor (Fig. 17) with a subapical gap between dorsal and ventral valves.

**Table 2.** Measurements of *Makalapobius masihu* n. gen. n. sp. (in mm).

	BL	PrnL	PrnW	FWL	FIL	FIIIL	FIIIL	FIIIW	OvpL
♂ Holotype	9.60	1.60	2.15	2.00	2.60	2.80	5.70	1.70	-
♀ Allotype	9.80	1.75	2.35	-	2.30	2.45	5.50	1.85	5.00

## **Genus *Gabusibius* n. gen.**

(Figs. 25-70; 73-77)

**Type species.** *Gabusibius mosi* n. gen., n. sp, here designated.

**Species included.** *G. ndzilu* n. gen. n. sp.; *G. mosi* n. gen. n. sp.; *G. dzindzanu* n. gen. n. sp.. *Speonemobius litoreus* Vannini & Chelazzi 1978 is tentatively placed in the genus *Gabusibius* n. gen. n. comb..

**Distribution.** South Western Indian Ocean, Comoros, possibly Somalia.

**Diagnosis.** *Gabusibius* n. gen. is superficially similar to *Burcus* Gorochov, 1986, to *Paraburcus* Gorochov, 2018, and to *Malakapobius* n. gen. It is characterized by the following characters. TIII with 2 sai (Figs. 25, 29; unlike *Neoburcus* Gorochov, 2018 which has 3 sai). Male winged (Figs. 25, 33, 49, 57; unlike *Taiwanemobius* Yang & Chang, 1996); with distinct stridulum (Figs. 31, 40, 55, 60; unlike *Paranemobius* Saussure, 1877); wings oval, truncated (Fig. 25, 33, 49, 58; unlike *Burcus* with relatively long FW); without mirror (Figs. 31, 40, 55, 60; unlike

*Speonemobius* Chopard, 1924 with full mirror); with relatively long diagonal vein (unlike *Paraburcus* with short diagonal vein). Male SGP with only one apical lobe (Figs. 30, 39, 54; unlike *Malakapobius* n. gen. with trilobated SGP, Figs. 6, 15), median lobe small, membranous. Male genitalia (Figs. 62-70: pseudepiphallus dorsal margin not curved or weakly curved upwards (unlike *Paraburcus* with epiphallus curved downwards, and unlike *Malakapobius* n. gen, *Burcus*, *Neoburcus*, with pseudepiphallus curved upwards); distal part of pseudepiphallus broad in side view (unlike *Malakapobius* n. gen. with very narrow apex in side view); apex without rounded contiguous distal lobes (unlike *Malakapobius* n. gen.); without apical lateral extensions forming large apical concavity visible dorsally (unlike *Burcus*). Epi-ectophallic invagination extending more anteriorly than rami insertion (unlike *Malakapobius* n. gen. with short epi-ectophallic invagination not exceeding rami insertion); rami very wide in side view (unlike all other genera except *Malakapobius* n. gen.).

**Description.** Including characters shared by other Burcini.

Burcini of average size. General coloration typical for Burcini, from dark grey to light yellowish, with numerous black patterns. Head, pronotum and femora with long black bristles (Figs. 25, 33, 49, 58).

**Head** (Figs. 25, 33, 49, 58). Not wider than pronotum. Eyes moderately protruding, not flattened on head dorsum (Fig 1-3). Ocelli small; lateral ocelli rounded, well distinct; median ocellus less distinct, localized dorsally to fatigium tip; distance between lateral ocelli similar to distance between one lateral ocellus and median ocellus. Fastigium between antennae not wider than scapes; scapes wider than high (front view); palpi short, article length: 5>3>4; article 5 apex strongly widened.

**Thorax** (Figs. 25-26, 33-34, 49-50, 57-58). Pronotum wider than long, 0.61-0.72 times as long as wide; DD sides subparallel, DD slightly narrower anteriorly, slightly enlarged before mid-length; DD anterior margin straight or weakly rounded; DD posterior margin weakly rounded; DD longitudinal median furrow imprinted anteriorly; DD anterior transverse furrow distinct on the sides; LL shallow, higher anteriorly, less high posteriorly.

**Legs** (Figs. 25, 29, 36, 38, 52, 53). Legs of average size for Burcini, not elongated. TI with long oval outer tympanum; without inner tympanum. TI and TII with 2 ventral apical spurs of same length. FIII not particularly widened nor narrow: ca. 2.8-3.9 times as long as wide. TIII apical spurs typical of burcini: 3 ao, 2 ai; relative length of apical spurs:  $ao_2 > ao_3 > ao_1$ ,  $ai_2 > ai_1$ . TIII with 3 outer and 2 inner subapical spurs; relative length of subapical spurs:  $sao_1 > sao_2 > sao_3$ ,  $sai_1 > sai_2$ . Hind tarsi long, particularly hind basitarsi. Hind basitarsi without dorsal serration (as usual in Nemobiini, see Desutter-Grandcolas et al. submit.); with 3 apical spurs: 2 dorsal apical spurs, the inner very small; 1 inner ventral apical spur longer than the dorsal outer one.

**Wings.** FW (Figs. 73-76) present in males, absent in females. HW absent in both sexes.

**Coloration. Head** (Figs. 25-27; 33-35; 49-51; 57-59). Antennae dark, unbanded. Face with more or less extended black patterns below the eyes converging to clypeus; semicircular area below antennae with black pattern more or less extended; face black patterns surrounding a light yellow area, more or less extended and pointing upwards; mandibles of variable color; scapus usually light yellow, antennae dark, not banded; palpi light yellow; genae light; tip of fastigium black dorsally; area dorsal to antennae with dark patch of variable extent; occiput of variable color, from light yellow to dark. **Thorax** (Figs. 25-26, 33-34, 49-50, 57-58). Pronotum DD from light yellow to grey, with black or dark lateral spots near anterior margin; with two small posterior black spots near midline; LL dark or black, anterior ventral margin sometimes lighter. Abdomen dark with light yellow spots. **Legs** (Figs. 28-29; 36-38; 52-53; 57).

Light yellow with dark bandings; FIII lateral field with dark basis, with 3 transverse dark bandings, the distal one on the knee; TIII dark.

**Male. Wings.** FW (Figs. 31, 40, 55, 60) oval in shape, truncated apically. Stridulatory apparatus well developed, with relatively long diagonal vein; with well distinct chords, not particularly long for Burcini; without mirror: FW distal part with reticulation. **Subgenital plate.** Apex with only a median membranous lobe (Figs. 30, 39, 54). **Genitalia** (Figs. 62-70). Pseudepiphallus wide in dorsal view and side view, elongated, not particularly curved upwards (side view); apex without rounded contiguous distal lobes; without apical lateral extensions; without large apical concavity visible dorsally. Apodemes absent. Epi-ectophallic invagination extending more anteriorly than rami insertion. Rami very wide (side view), truncated anteriorly.

**Female.** No trace of wings (Figs. 74, 76). Subgenital plate (Figs. 32, 41, 56, 61) trapezoidal. Ovipositor weakly up curved; weakly enlarged apically (Figs. 32, 41, 56, 61). **Genitalia.** Copulatory papilla not examined.

**Calling song.** Only known from the type species *G. mosi* n. gen. n. sp and from *G. ? litoreus* (Vannini & Chelazzi) n. gen. n. comb. Male call is made of short verses of relatively constant amplitude and lasting less than 0.2 seconds (Figs. 42-48).

**Remark on coloration.** The only species observed on volcanic shingle beaches (*Gabusibius ndzilu* n. gen. n. sp.) is very dark as is its habitat, whereas species living on coral shores are lighter. It is not clear whether color corresponds to an inherited trait and a stable character allowing to distinguish species, or whether color is flexible and directly depending on the environment where juveniles have grown. Nevertheless, *Gabusibius mosi* n. gen. n. sp. known from various localities and numerous specimens displays conspicuous variation in the extent of the black patterns indicating that color is quite a variable character.

### ***Gabusibius ndzilu* n. gen. n. sp.**

(Figs. 25-32; 62-64; 77; Tab. 3)

*Gabusibius ndzilu* n. gen. n. sp., here described.

**Holotype. Male.** Comores, Anjouan, Dar Salam, plage de galets, -12.2533, 44.3841, 0.5m; 27.XI.2011; S. Hugel leg. (2010 COM SH 117), MNHN (MNHN-EO-ENSIF12134).

**Allotype. Female.** Same as Holotype; S. Hugel leg. (2010 COM SH 118), MNHN (MNHN-EO-ENSIF12135).

**Paratypes, 2♀.** 1♀, same as holotype; S. Hugel leg. (2010 COM SH 120), Coll. SH.; 1♀, same as holotype, S. Hugel leg. (2010 COM SH 119), Coll. SH.

**Distribution.** South Western Indian Ocean, Comoros, Ndzuan (Anjouan)

### **Diagnosis.**

This species differs from all other species of *Gabusibius* n. gen. by its dark coloration (Figs. 25-27), and male genitalia with spatulate pseudepiphallus (Figs. 62-64).

### **Description.**

In addition to generic characters. **Color.** Species dark. Body background color dark grey with black patterns; light triangle on the face hardly visible, narrow between antennae. Legs background color light yellow, patterns very distinct and black. **Male.** Stridulatory file not

examined. SGP (Fig. 30) larger than long (flattened). Genitalia (Figs. 62-64). Pseudepiphallus narrower in the middle, distal half spatulate with rounded ventral enlargement (dorsal view); dorsal margin slightly elevated distally (side view). Epi-ectophallic invagination exceeding moderately rami insertion and reaching anterior projection of endophallic sclerite (dorsal view). Rami very wide (side view), truncated anteriorly. **Female.** SGP hind margin shallowly concave (Fig. 32). OVP apex without distinct space between dorsal and ventral valves (Fig. 32).

**Biology/Habitat.** *Gabusibius ndzilu* n. gen. n. sp. lives on shingle beaches with large (> 10 cm) volcanic round stones from the sea level to 1 m in elevation.

**TABLE 3.** Measurements of *Gabusibius ndzilu* n. gen. n. sp. (in mm).

	BL	PrnL	PrnW	FWL	FIL	FIIL	FIILL	FIILW	OvpL
♂ Holotype	7.70	1.65	2.40	2.10	2.60	2.90	5.70	1.30	-
♀ Allotype	9.40	2.00	2.65		2.85	2.80	6.10	1.80	5.00
♀♀									
Average	8.70	1.90	2.45		2.78	2.80	6.20	1.73	4.83
Min	8.00	1.80	2.25		2.70	2.80	6.10	1.65	4.65
Max	9.40	2.00	2.65		2.85	2.80	6.30	1.80	5.00

### ***Gabusibius mosi* n. gen. n. sp.**

(Figs. 33-48; 65-67; 73-74; 77; Tab. 4)

*Gabusibius mosi* n. gen. n. sp., here described.

**Holotype. Male.** Comores, Mohéli, Chissioua Ouénéfou, plage de galets, -12.3924, 43.7072, 0.5m; 2.V.2010; S. Hugel leg. (Moheli.1 2010 098), MNHN (MNHN-EO-ENSIF12136).

**Allotype. Female.** Comores, Mohéli, Ouallah II, Miremani, plage, -12.3468, 43.6674, 0.5m; 24.VIII.2010; S. Hugel & L. Desutter-Grandcolas leg. (2011 COM SH 187), MNHN (MNHN-EO-ENSIF12137).

**Paratypes, 5♂, 12♀.** 1♂ same as holotype; S. Hugel leg. (Moheli.1 2010 097), Coll. SH. 1♀ same as holotype; S. Hugel leg. (Moheli.1 2010 099), Coll. SH.; 1♀ S. Hugel leg. (Moheli.1 2010 100), Coll. SH.; 1♀ S. Hugel leg. (Moheli.1 2010 101), Coll. SH.; 1♀ S. Hugel leg. (Moheli.1 2010 102), Coll. SH.; 1♀ S. Hugel leg. (Moheli.1 2010 103), Coll. SH.; 1♀ S. Hugel leg. (Moheli.1 2010 104), Coll. SH. 1♂ Comores, Mohéli, Ouallah II, Miremani, plage, -12.3468, 43.6674, 0.5m; 24.VIII.2010; S. Hugel & L. Desutter-Grandcolas leg. (2010 COM SH 186), Coll. SH; 1♀ same as allotype; S. Hugel & L. Desutter-Grandcolas leg. (2010 COM SH 188), Coll. SH; 1♂, same as allotype, S. Hugel & L. Desutter-Grandcolas leg. (LDG 338), in Chintauan-Marquier et al. 2016 molecular sampling LDG 028 as *Tethella* sp\_Com, MNHN (MNHN-EO-ENSIF3313); 2♂, same as allotype, S. Hugel & L. Desutter-Grandcolas leg. (LDG 339, LDG340), MNHN (MNHN-EO-ENSIF12138,12139); 5♀ same as allotype; S. Hugel & L. Desutter-Grandcolas leg., (LDG342-346), MNHN (MNHN-EO-ENSIF12140, 12141, 12142, 12143, 12144).

Other specimens (non type material). 3 specimens. 3 juveniles, same as the allotype, S. Hugel & L. Desutter-Grandcolas leg. (LDG 341, LDG347, LDG 348), MNHN.

**Distribution.** South Western Indian Ocean, Comoros, Mwali (Mohéli)

**Diagnosis.**

This species differs from *Gabusibius ndzilu* n. gen. n. sp. by its lighter color and from *Gabusibius ? littoreus* n. gen. n. comb. by the darker patterns. It differs from all Comorian species of *Gabusibius* n. gen. by male genitalia (Figs. 65-67): Pseudepiphallus with parallel sides converging in the last distal fifth; apex broadly rounded, not forming two lobes (dorsal view); apex not elevated distally (side view). Epi-ectophallic invagination exceeding anterior projection of endophallic sclerite; not spoon-shaped (unlike *Gabusibius dzindzanu* n. gen. n. sp.).

**Description.**

In addition to generic characters. **Color.** Species with light background and black patterns (Figs. 33-38). In holotype, body background color light yellow with black patterns; light triangle on the face distinct, with broad basis, narrow between antennae. Legs background color light yellow, patterns very distinct and black. Extent of black patterns variable on paratypes. **Male.** Stridulatory file with 56 teeth (holotype). SGP (Fig. 39) broader than long (flattened). Genitalia (Figs. 65-67). Pseudepiphallus with parallel sides converging in the last distal fifth; apex broadly rounded, not forming two lobes (dorsal view); apex not elevated distally (side view). Epi-ectophallic invagination exceeding anterior projection of endophallic sclerite; anterior part moderately concave, not spoon-shaped. Rami very wide (side view), truncated anteriorly. **Female.** SGP hind margin shallowly concave (Fig. 41). OVP apex without distinct space between dorsal and ventral valves (Fig. 41).

**Song.** The song has been recorded at 10 am, 25°C in an open cave in the shore (Figs. 42-48). Two types of songs have been recorded simultaneously and specimens switched from one to the other song type. Calling specimens were not directly observed, it is, therefore, not possible to associate the song type with a peculiar behavior (courtship, call, etc.). The first harmonic of both songs peaks at 5.5-6.6 kHz. One type of song is made of verses organized in syllables made of pulses at high rate (Fig. 44, 5 verses): verses duration: 680±869 ms (222-5177 ms), gap between verses: 633±113 ms (369-812 ms), number of syllables per verse: 4.6±5.3 (2-33), syllable rate during verses: 162.1±17.9 ms (136.3-212.6 ms), pulses during syllables: 3.3±0.5 (3-4), pulse rate during syllables: 15.6±4.6 ms (9.1-24.9 ms). The other type of song is made of verses not organized in syllables and made of pulses at low rate (Fig. 44, between 17.4 ms and 17.6 ms): verses duration: 116±40 ms (66-164 ms), gap between verses: 905±431 ms (273-1949 ms), pulses during syllables: 6.5±0.9 (5-8), pulse rate during syllables: 16.5±3.0 ms (10.0-19.0 ms).

**Biology.** This species occurs on rocky beaches (mixed limestone and volcanic pebbles of small diameter). It can be observed by night hours, particularly at low tide. In Miremani, it can be observed by day hours in a shallow cave on the shore.

**Table 4.** Measurements of *Gabusibius mosi* n. gen. n. sp. (in mm).

	BL	PrnL	PrnW	FWL	FIL	FIIL	FIIL	FIILW	OvpL
♂ Holotype	8.60	1.75	2.20	-	2.50	2.80	5.70	1.65	-
♀ Allotype	9.60	1.75	2.50	-	2.60	2.75	5.50	1.70	4.60

♂♂									
Average	8.70	1.58	2.28	2.28	2.53	2.60	5.47	1.47	-
Min	8.40	1.50	2.20	2.25	2.50	2.40	5.30	1.35	-
Max	9.10	1.75	2.45	2.30	2.60	2.80	5.70	1.65	-
♀♀									
Average	8.80	1.77	2.53	-	2.65	2.72	5.73	1.67	4.58
Min	7.60	1.70	2.30	-	2.60	2.60	5.50	1.50	4.50
Max	9.60	1.85	2.80	-	2.70	2.80	6.10	1.80	4.65

### ***Gabusibius dzindzanu* n. gen. n. sp.**

(Figs. 49-56; 68-70; 75-77; Tab. 5)

*Gabusibius dzindzanu* n. gen. n. sp., here described.

**Holotype. Male.** Mayotte, Bandrele, Saziley Be, plage, -12.9746, 45.2016, 0.5m; 7.V.2010; S. Hugel leg. (Mayotte.1 2010 136), MNHN (MNHN-EO-ENSIF12145).

**Allotype. Female.** Same as Holotype; S. Hugel leg. (Mayotte.1 2010 138), MNHN (MNHN-EO-ENSIF12146).

**Paratypes, 5♂, 2♀.** 1♂ same as holotype; S. Hugel leg. (Mayotte.1 2010 135), Coll. SH.; 1♂ S. Hugel leg. (Mayotte.1 2010 131), Coll. SH.; 1♂ S. Hugel leg. (Mayotte.1 2010 132), Coll. SH.; 1♂ S. Hugel leg. (Mayotte.1 2010 133), Coll. SH.; 1♂ S. Hugel leg. (Mayotte.1 2010 134), Coll. SH. 1♀ same as holotype; S. Hugel leg. (Mayotte.1 2010 137), Coll. SH.; 1♀ S. Hugel leg. (Mayotte.1 2010 139), Coll. SH.

**Other specimens** (non type material). 1 juvenile same as holotype; S. Hugel leg. (Mayotte.1 2010 130), Coll. SH.

**Distribution.** South Western Indian Ocean, Comoros, Maore (Mayotte)

### **Diagnosis.**

This species differs from *Gabusibius ndzilu* n. gen. n. sp. by its lighter color and from *Gabusibius ? littoreus* n. gen. n. comb. by the darker patterns. It differs from all Comorian species of *Gabusibius* n. gen. by male genitalia (Figs. 68-70). Pseudepiphallus with parallel sides in the anterior half, converging in the last distal half; apex with a shallow notch separating two lobes (dorsal view); apex not elevated distally (side view). Epi-ectophallic invagination exceeding anterior projection of endophallic sclerite distinctly spoon-shaped (unlike *Gabusibius ndzilu* n. gen. n. sp.).

### **Description.**

In addition to generic characters. **Color.** Species with light background and black patterns (Figs. 49-53). Body background color light yellow with black patterns; light triangle on the face distinct, with broad basis, narrow between antennae. Legs background color light yellow, patterns very distinct and black. **Male.** Stridulatory file with 52 teeth (paratype Mayotte.1 2010 135). SGP (Fig. 54) broader than long (flattened). Genitalia (Figs. 68-70). Pseudepiphallus with parallel sides converging in the last distal fifth; apex broadly rounded, not forming two lobes (dorsal view); apex not elevated distally (side view). Epi-ectophallic invagination exceeding anterior projection of endophallic sclerite; anterior part moderately concave, not spoon-shaped. Rami squared, very wide (side view), truncated anteriorly. **Female.** SGP hind

margin with V-shaped emargination (Fig. 56). OVP apex without narrow space between dorsal and ventral valves (Fig. 56).

**Biology.** This species occurs on rocky beaches (mixed limestone and volcanic pebbles of small diameter). It can be observed by night hours, particularly at low tide.

**Table 5.** Measurements of *Gabusibius dzindzanu* n. gen. n. sp. (in mm).

	BL	PrnL	PrnW	FWL	FIL	FIIL	FIIL	FIILW	OvpL
♂ Holotype	8.00	1.70	2.30	2.30	2.80	2.60	5.90	1.80	-
♀ Allotype	7.30	1.50	2.40		2.70	2.60	5.70	1.70	4.20
♂♂									
Average	7.89	1.64	2.18	1.98	2.70	2.68	5.59	1.81	-
Min	7.60	1.60	2.10	1.80	2.65	2.55	5.40	1.75	-
Max	8.25	1.70	2.30	2.30	2.80	2.80	5.90	1.90	-
♀♀									
Average	7.45	1.63	2.40	-	2.70	2.65	5.55	2.05	4.40
Min	7.30	1.50	2.40	-	2.70	2.60	5.40	1.70	4.20
Max	7.60	1.75	2.40	-	2.70	2.70	5.70	2.40	4.50

***Gabusibius ? litoreus* (Vannini & Chelazzi, 1978) n. gen. n. comb.**

(Figs. 57-61; Tab. 6)

*Speonemobius litoreus* Vannini & Chelazzi, 1978. *Monitore Zoologico Italiano*. (N.S.) Supplemto 11(1):2

**Distribution.** Africa, Northeast Tropical Africa, Somalia, Sar Uanle cliff (type locality)

**Material examined:** Male and female paratypes from Museo Zoologico of the University of Florence.

**Description complement.**

Measurements, missing from original description are given (Table 5).

Female SGP distal margin with a deep V-shaped emargination (Fig. 61).

**Remark.** The habitat of this species has been comprehensively described by Vannini & Chelazzi (1978). This habitat is strikingly similar to the type locality of *Malakapobius aigrettensis* n. gen., n. sp. This remarkable publication also provides the first record of the song from a Burcini which is similar to the song of *Gabusibius ndzilu* n. gen. n. sp. (Figs. 28-34).

**Table 6.** Measurements of *Gabusibius ? litoreus* (Vannini & Chelazzi, 1978) n. gen. n. comb. (in mm).

	BL	PrnL	PrnW	FWL	FIL	FIIL	FIIL	FIILW	OvpL
♂ Paratypes (n=2)	8.55	1.83	2.53	2.10	2.73	2.85	5.90	1.55	-
♀ Paratypes (n=2)	8.00	1.80	2.25	-	2.70	2.80	6.30	1.65	4.65

**Remarks on *Speonemobius* Chopard, 1924**

Eight species are currently considered as belonging to *Speonemobius* Chopard, 1924. This genus appears very heterogeneous, displaying very diverse male forewings (with or without distinct mirror) and male genitalia (elongated and narrow pseudepiphallus as in Burcini, or nemobiini like). Therefore, this genus needs to be reviewed since it most likely includes species belonging to different tribes, and genitalia of *Speonemobius* type species should be examined to define whether this genus should be kept in Burcini.

Importantly, *Speonemobius* type species *Speonemobius decoloratus* Chopard, 1924 has a distinct mirror. This is not the case for *Speonemobius alaesignatus* Ingrisch, 1987 which has genitalia and forewings corresponding to *Paraburcus* Gorochov, 2018 (Cigliano et al., 2021). It is worth noting that this species occurs on beaches as other Burcini. We, therefore, propose to temporarily transfer *Speonemobius alaesignatus* Ingrisch, 1987 to *Paraburcus* Gorochov, 2018 as *Paraburcus alaesignatus* (Ingrisch, 1987) n. comb., but this will need confirmation by direct examination of male genitalia.

*Speonemobius littoreus* has been described from coralline cliffs boarding the sea in Somalia. This species displays the external morphology typical of Burcini. All non-genitalic characters correspond to either *Gabusibius* n. gen., *Malakapobius* n. gen., *Burcus* or *Paraburcus*. Unfortunately, male genitalia of type and paratype specimens have been destroyed during failed attempts to dissect them (communication by Marco Vannini), but an intact male specimen may still exist in BMNH (not examined). Male FW of *S. littoreus* paratypes appears closer to *Gabusibius* n. gen., with shorter chords and larger anterior field (Fig. 60). For this reasons, we tentatively propose to place it under this genus as *Gabusibius* ? *litoreus* (Vannini & Chelazzi) n. gen. n. comb.

## Discussion

### Number of subapical spurs as a criterion

The tribe Burcini was originally proposed by Gorochov (1986) to include Nemobiinae crickets with long, narrow and apically bifurcated pseudepiphallus and with 3 outer apical and 3 outer subapical spurs and 2 inner apical and 2 inner subapical spurs. It is worth mentioning that taken alone, the number of subapical spurs may not be a reliable character: some species currently considered as belonging to *Speonemobius* do not display the characteristically long and narrow pseudepiphallus such as *S. decolyi* Chopard, 1969 (our observation) whether others like *S. alaesignatus* Ingrisch, 1987 do display it.

### Distribution of Burcini and endemism in coastal Orthoptera in SWIO islands

Two genera of Burcini are now recorded on SWIO islands, all species here described being single island endemics (Fig. 77). The genus *Gabusibius* n. gen. occurs on all Comoros with the remarkable exception of Grande Comore whereas the genus *Makalapobius* n. gen. occurs on both Grande Comore and Mauritius. This distribution with species from Grande Comore and Mauritius morphologically closer to other species from Comoros may appear surprising since



on SWIO islands, several genera of Orthoptera are endemic at the level of archipelagoes (see for example Hugel, 2012a; Hugel *et al.*, 2021). It is nevertheless not a unique case since similar situation occurs for birds (*Foudia* and *Zosterops*) as well as for plants (*Begonia*) (see discussion in Warren *et al.* 2013). Various scenarios may account for that peculiar distribution, including multiple dispersal events and even extinctions. The occurrence of *Gabusibius* n. gen. on Comoros islands of older volcanic origin (Mayotte, Mohéli, Anjouan) and not on Grande Comore may speculatively suggest that ancestors of *Gabusibius* n. gen. reached Comoros before the emergence of Grande Comore (volcanic origin estimates: 0.5 MYA). Alternatively, an extinction event might have occurred on Grande Comore, the surface of which is made of quite recent lavas (oldest exposed lavas 0.13 MYA) and harbors an active volcano (see discussion and references for dating in Warren *et al.* 2013). The lack of Burcini on Grande Comore would speculatively have left a vacant niche for subsequent colonization by ancestors of *Malakapobius masihu* n. gen. n. sp.. Such highly speculative scenarios will be examined by molecular approaches.

All species described in the present manuscript are single-island endemics. This is remarkable for lowland Orthoptera on SWIO islands since most species occurring on coastal SWIO habitats are widespread and not endemic (Hugel, *in press*). This is for example the case for the crickets *Myrmecophilus americanus* Saussure, 1877 and *Myrmecophilus quadrispina* Perkins, 1899, (Hugel and Blard, 2005; Hsu *et al.* 2020) *Trigonidium cicindeloides* Rambur, 1839, *Natula longipennis* (Serville, 1839) (Hugel, 2012b) and *Gryllodes sigillatus* (Walker, 1869) (Hugel, *in press*) as well as for the Caelifera *Aiolopus thalassinus rodericensis* (Butler, 1876) (Parnaudeau *et al.* 2013; Hugel, 2014) and *Xya minor* (Chopard, 1920) (Hugel, 2021) among others. Only very few coastal Orthoptera species are single-island-endemics, such as species belonging to the genus *Microlandrevia* Chopard, 1958 on Comoros and Mayotte (SH-LDG, unpublished observations), Mogoplistidae species on Comoros (SH-LDG, unpublished observations) and Mascarene islands (Warren *et al.* 2016), and the Grasshopper *Odontomelus ancestrus* Hugel, 2014 on Round Island, an islet North to Mauritius (Hugel, 2014). It has been suggested that this low level of endemism of Orthoptera in SWIO coastal habitats may be a consequence of habitat destruction at low altitude rather than a naturally occurring phenomenon (Hugel, *in press*).

Importantly, since intertidal habitats are not frequently examined by entomologists, and particularly by Orthopterists, the occurrence of more species of Burcini on SWIO islands is expected, and would deserve targeted surveys.

## Threats to Burcini

**Narrow habitat.** The habitat of Burcini in South Western Indian Ocean islands, and probably elsewhere, corresponds exclusively to intertidal areas, on the shore or on caves connected to the sea; in New Caledonia these have also been observed along rivers near the sea (LDG, unpublished observations). Although populations of these species can reach very high densities, their very habitat is small, mostly linear, corresponding to a very narrow stripe on the shore. Therefore, tools used to assess threat to these species according to their Extent of Occurrence (EOO) or Area of Occupancy (AOO) (IUCN, 2013) appear poorly adapted.

**Siltation.** Some of SWIO islands shores tend to silt up with mud as a consequence of deforestation and / or intensive farming practices. Burcini in SWIO seem absent from muddied

areas and may therefore be indirectly threatened by deforestation (mostly in Comoros) and intensive farming (mostly Mauritius).

**Sea level rise.** Sea-level rise associated with global warming is a direct threat to these species. Since beaches-backs to be submerged in the next decades are usually artificialized, a shift to equivalent habitats at higher elevation may not be possible. Nevertheless, in a few cases, riverbanks with pebbles might allow a shift to higher elevation.

**Modification of beaches for tourism.** In SWIO, *Burcini* do not occur on beaches where all but sand is removed. Removal of pebbles, driftwood and algae from sand beaches makes them unsuitable for *Burcini*. This tendency to force the shore to fit “postcard” expectations of tourists is mostly an issue in Mauritius where regulations may be needed.

**Pollution.** The population of *Makalapobius aigrettensis* n. gen. n. sp. appears to have been directly impacted by the ecological disaster caused in August 2020 by the oil slick following the sinking of the tanker Wakashio. Due to their narrow habitat in the intertidal area, sea water pollution should be considered as a major threat to *Burcini*.

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## Legends

**FIGURES 1–8.** *Makalapobius aigrettensis* n. gen. n. sp. 1, Male paratype in dorsal view (specimen 2011MauRod026). 2, same in side view. 3, same, face. 4, same, left hind leg in outer view. 5, same in inner view. 6, same, SGP, flattened. 7, same, right FW, flattened. 8, female paratype (specimen 2011MauRod027): Ovp in left side view (top) and in ventral view (bottom). Scales: 1-2: 10 mm; 3-8: 1 mm.

**FIGURES 9–11.** *Makalapobius aigrettensis* n. gen. n. sp. stridulation in natura (specimen BIOTAS2008 424, afternoon, 30°C; in a cave). 11, power spectrum of 10.

**FIGURES 12–18.** *Makalapobius masihu* n. gen. n. sp. 12, Male holotype in dorsal view. 13, same, face. 14, same, left FIII in outer view. 15, same, SGP, not flattened. 16, same, FW. 17-18, female allotype. 17, Ovp in right side view. 18, body in right side view. Scales: 12: 5 mm; 13–18: 1 mm.

**FIGURES 19–24.** *Makalapobius* n. gen. male genitalia. 19-21, *Makalapobius aigrettensis* n. gen. n. sp.; *Makalapobius masihu* n. gen. n. sp. Left panels: dorsal views; middle panel: ventral views; right panels: left side views. Scale: 1 mm.

**FIGURES 25–32.** *Gabusibius ndzilu* n. gen. n. sp. 25, Male holotype in dorsal view. 26, same in side view. 27, same, face. 28-29, same, left hind leg in  $\frac{3}{4}$  and in outer views. 30, same, SGP, flattened. 31, same, right FW. 32, female allotype: Ovp in left side view (top) and in ventral view (bottom). Scales: 25-26: 10 mm; 27-32: 1 mm.

**FIGURES 33–41.** *Gabusibius mosi* n. gen. n. sp. 33, Male holotype in dorsal view. 34, same in left side view. 35, same, face. 36, hind tibia inner view. 37-38, same, left hind leg in  $\frac{3}{4}$  and in outer views. 39, same, SGP, flattened. 40, same, right FW; flattened. 41, female allotype: Ovp in left side view (top) and in ventral view (bottom). Scales: 33-34: 5 mm; 35-41: 1 mm.

**FIGURES 42–48.** *Gabusibius mosi* n. gen. n. sp., stridulation in Mohéli, Miremani, 10h a.m.; 25°C. 42, full sequence with several specimens singing. 43-48; details of the sequence. 45, power spectrum of 44. 48, power spectrum of 47.

**FIGURES 49–56.** *Gabusibius dzindzanu* n. gen. n. sp. 49-50, Male holotype in dorsal view (49) and left side view (50). 51, same, face. 52, hind leg outer view. 53, hind leg inner view. 54, same, SGP, flattened. 55, same, right FW; flattened. 56, female allotype: Ovp in left side view (top) and in ventral view (bottom). Scales: 49-50: 10 mm; 51-56: 1 mm.

**FIGURES 57–61.** *G. ? litoreus* (Vannini & Chelazzi, 1978) n. gen. n. comb. paratypes. 57-58, male in right side view (57) and dorsal view (58). 59, same, face. 60, right FW, flattened. 61, Ovp in left side view (top) and ventral view (bottom).

**FIGURES 62–70.** Male genitalia of *Gabusibius* n. gen. 62-64, *Gabusibius ndzilu* n. gen. n. sp. 65-67, *Gabusibius mosi* n. gen. n. sp.; 68-70, *Gabusibius dzindzanu* n. gen. n. sp. Left panels: dorsal views; middle panel: ventral views; right panels: left side views. Scale: 1 mm.

**FIGURES 71–76.** *Makalapobius* n. gen. (71-72) and *Gabusibius* n. gen. (73-76) in natura. 71-72, *Makalapobius aigrettensis* n. gen. n. sp. 73-74, *Gabusibius mosi* n. gen. n. sp. 75-76, *Gabusibius dzindzanu* n. gen. n. sp. Left panels are males, right panels are females.

**FIGURE 77.** Distribution of *Makalapobius* n. gen. and *Gabusibius* n. gen. in South Western Indian Ocean.

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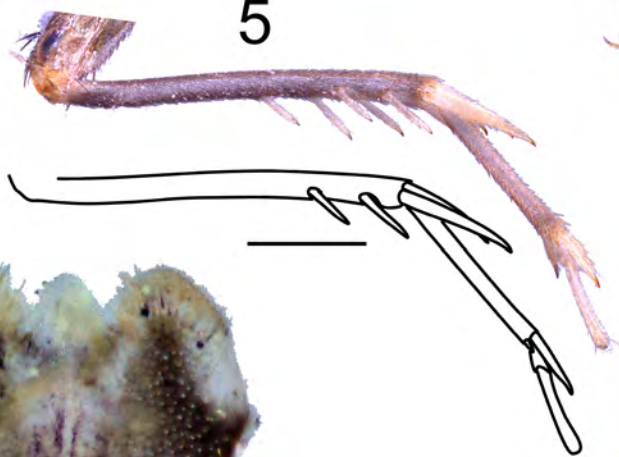
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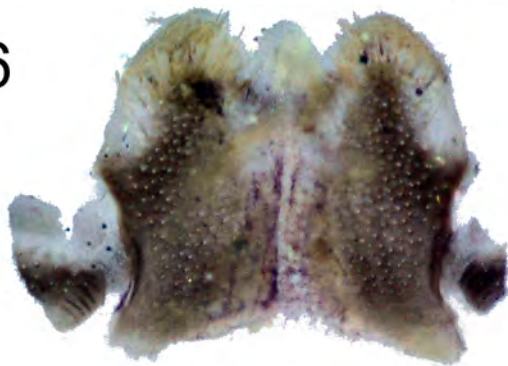
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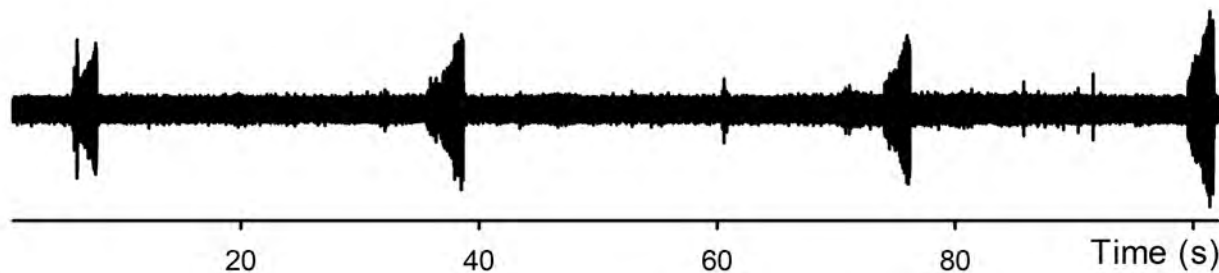


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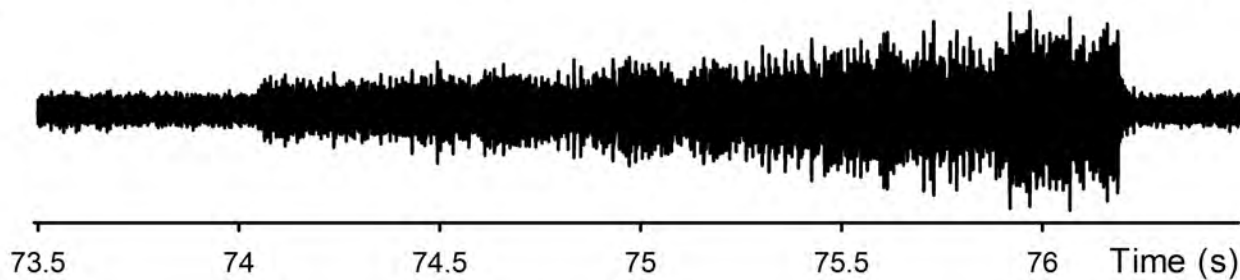




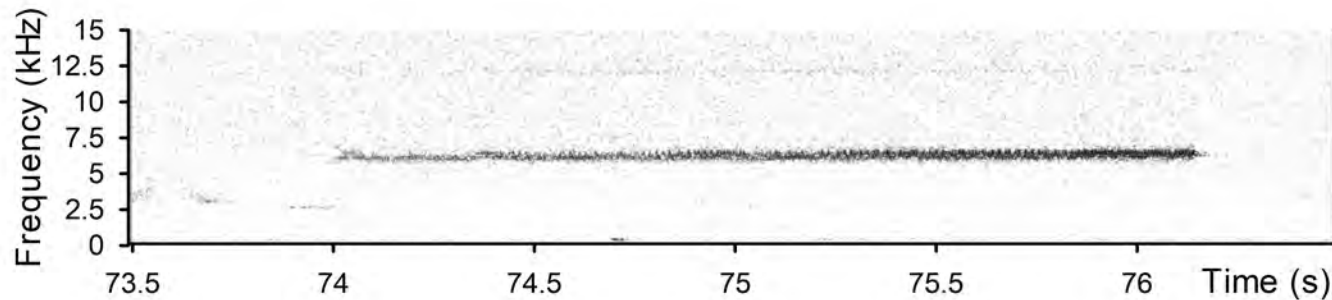
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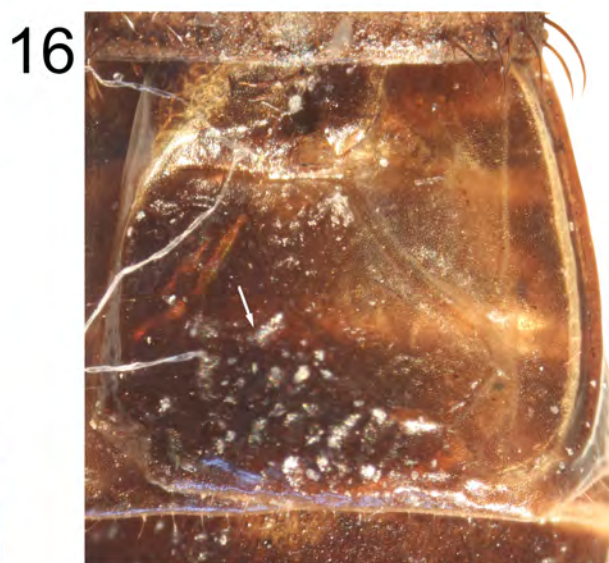


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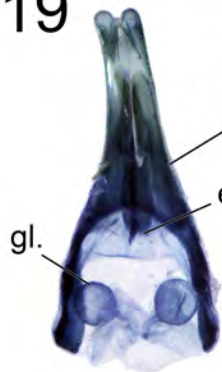
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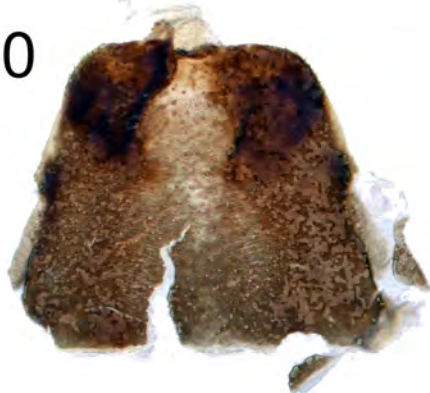
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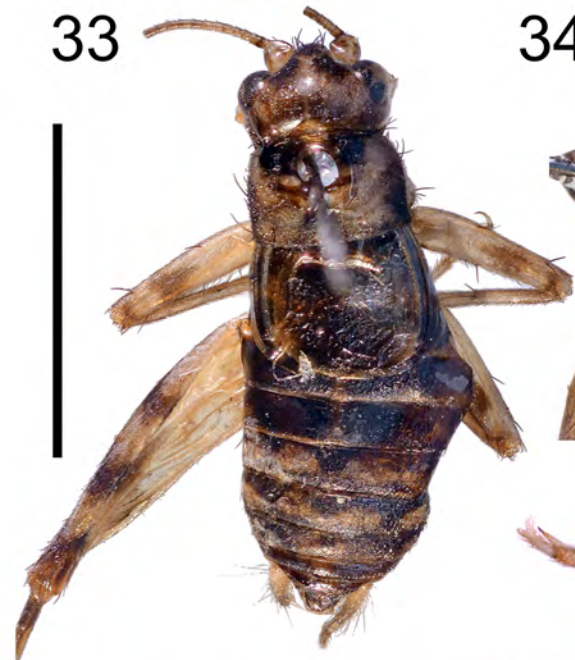


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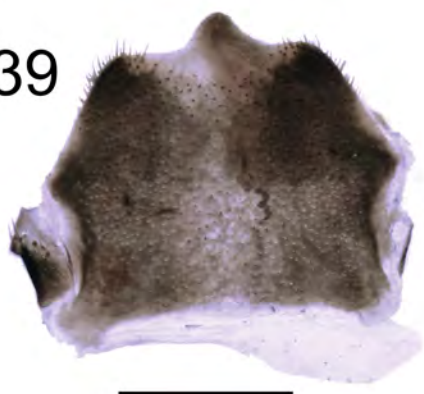
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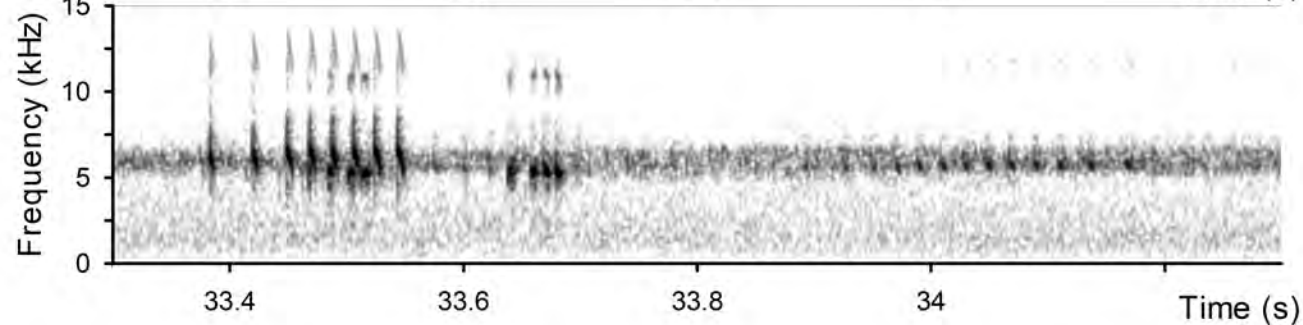
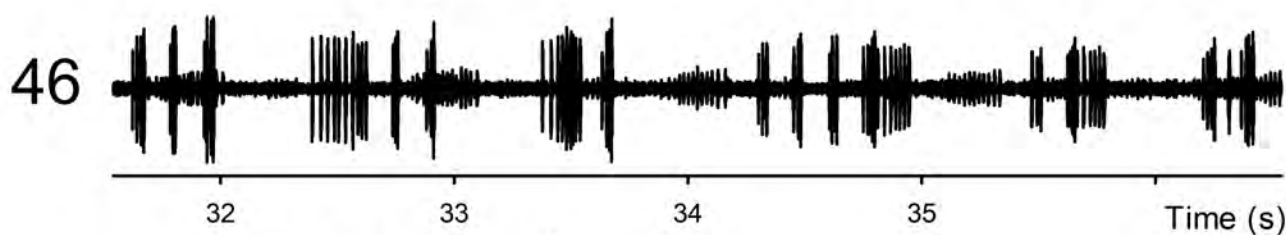
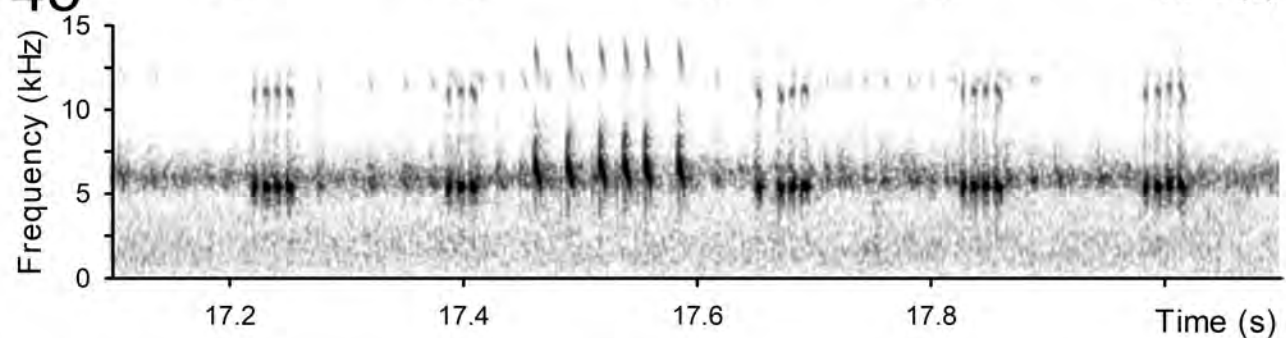
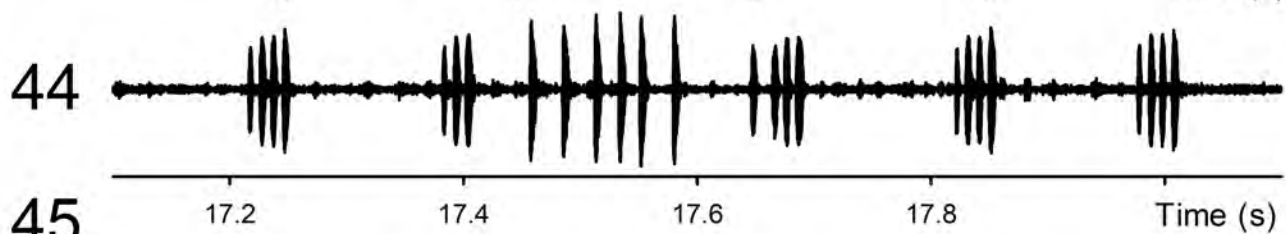
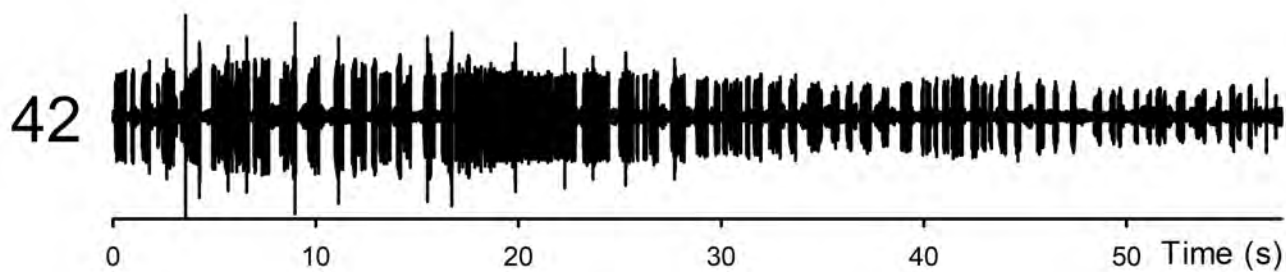


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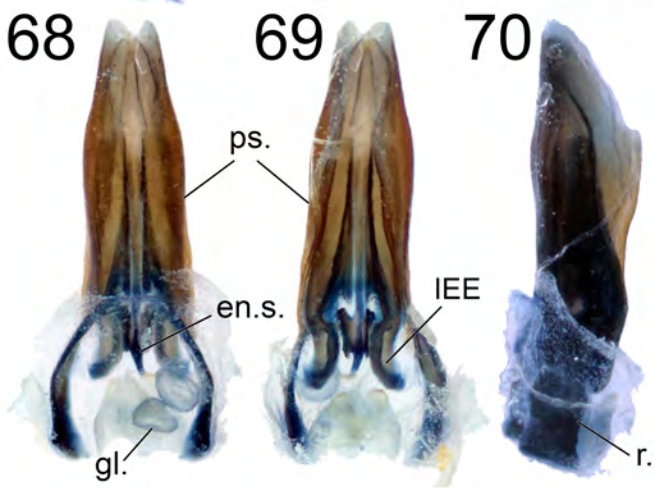
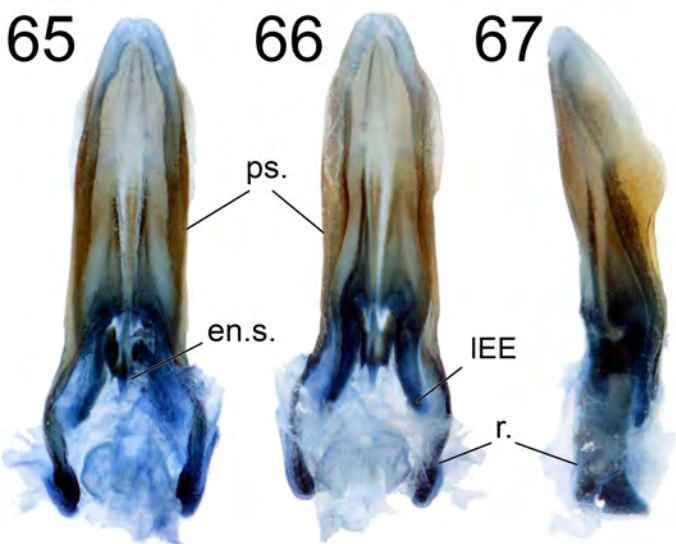
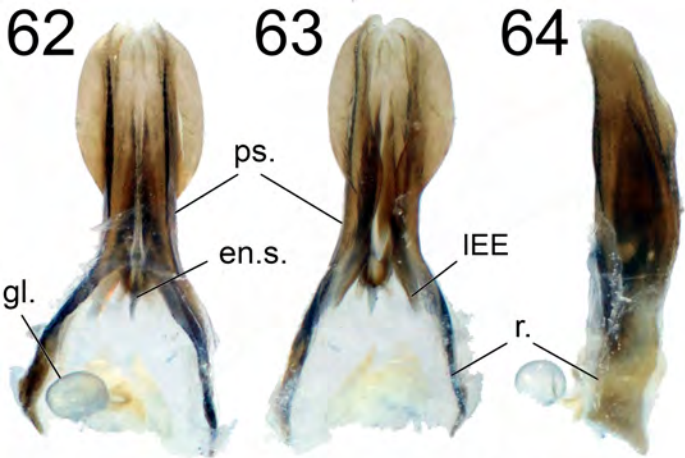


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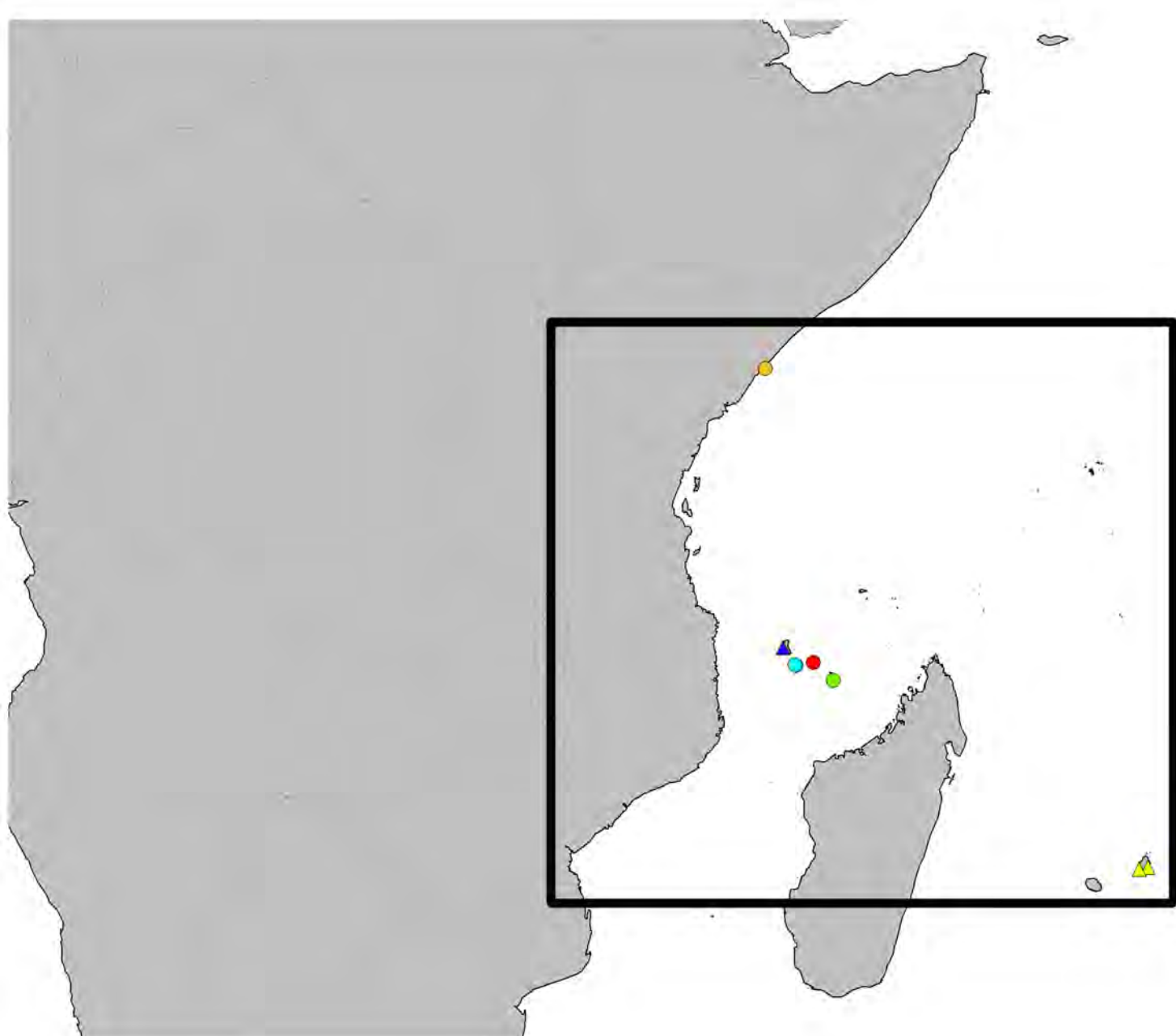
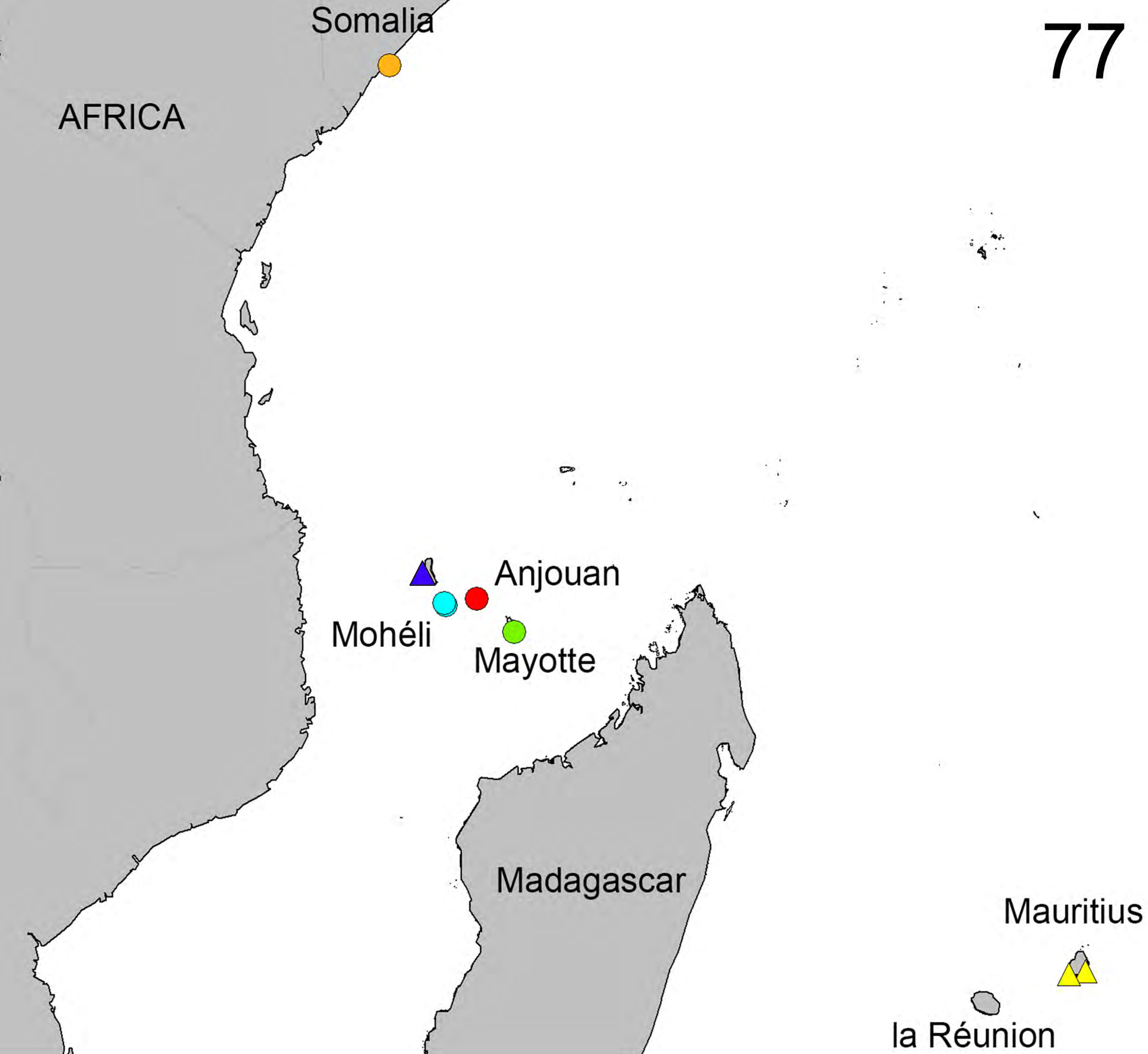




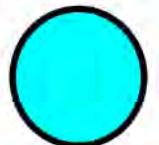


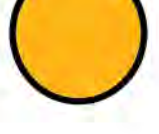










-  *Makalapobius aigrettensis* n. gen. n. sp.
-  *Makalapobius masihu* n.gen. n. sp.
-  *Gabusibius mosi* n. gen. n. sp.
-  *Gabusibius ndzilu* n. gen. n. sp.
-  *Gabusibius dzindzanu* n. gen. n. sp.
-  *Gabusibius ? litoreus*  
(Vannini & Chelazzi, 1978) n. gen. n. comb.