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Diversification in the Comoros: Review of the *Laccophilus alluaudi* Species Group with the Description of Four New Species (Coleoptera: Dytiscidae) †

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‡ Contribution to the study of Dytiscidae 93.

Abstract: The *Laccophilus alluaudi* species group is an interesting case of an endemic species radiation of Madagascar and the Comoros. To date, a single species, *Laccophilus tigrinus* Guignot, 1959 (Anjouan), is known from the Comoro Islands, with eight other species known from Madagascar. Here we review the *Laccophilus alluaudi* species group from the Comoro Islands based on partly new material. We recognize five species, out of which four are here described as new: *L. mohelicus* n. sp. (Mohéli), *L. denticulatus* n. sp. (Grande Comore), *L. michaelbalkei* n. sp. (Mayotte) and *L. mayottei* n. sp. (Mayotte). Based on morphology of male genitalia, we hypothesize that the five species form a monophyletic group and originated from a single colonization event from Madagascar. If confirmed, this would constitute one of the few examples of intra-archipelago diversification in the Comoros. The knowledge of species limits in relation to their distribution in the Comoros archipelago is also urgently needed in the face of rapid habitat degradation.

Keywords: island biogeography; new species; taxonomy; biodiversity; colonization; endemism; species radiation; diving beetles; freshwater

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1. Introduction

Volcanic oceanic island archipelagos, such as the Galapagos, Hawaii and the Canaries, have long fascinated biologists [1–5]. In contrast to continental islands, oceanic islands have never had land contact with other larger landmasses, they are formed without life to start with, and many have existed for millions of years, forming natural laboratories of evolution [6]. For terrestrial and freshwater organisms, a large expanse of sea constitutes a dispersal barrier. This barrier is a semipermeable filter that has reduced, but over time allowed, arrivals at frequencies dependent on extrinsic factors, such as distance to mainland, ocean currents, trade winds and island size, and intrinsic factors such as dispersal capacity, body size, salinity tolerance and the ability to withstand restricted access to food and water for long periods [2,7]. Except for organism groups of very high dispersal capacity, this filter reduces the geneflow between the source population and a newly formed population after successful colonization, so that over time endemic island species evolve. On especially large and/or more heterogenous islands, or island archipelagos, further in situ or intra-archipelago speciation may occur [8].

The Comoros is one such archipelago of true oceanic islands of volcanic origin that, despite sea-level variation during their lifespan, have never been in land contact with the

continent of Africa or with Madagascar [9,10]. The archipelago is situated approximately midway between mainland east Africa and northern Madagascar in the northern part of the Mozambique Channel in the western Indian Ocean. Approximately 300 km of open sea separates the Comoros from either larger landmass. The archipelago consists of the four larger islands: Grande Comore (Ngazidja), Mohéli (Mwali), Anjouan (Ndzuani) and Mayotte (Maore) (Figure 1). Estimated ages of the four islands varies greatly depending on whether the age is inferred from the oldest dated exposed lava rocks, or from the estimated on-start and duration of magmatic activity. This is particularly true for the highest island, Grande Comore, which is dominated by the very active volcano Mount Karthala. The oldest-dated exposed rock is a mere 0.13 Ma, whereas Michon (2016) estimates 9 Ma of magmatic activity [10]. The underestimation of Grande Comore's age from exposed rocks has already been suggested based on dated endemic lineages ([11,12] and references therein). With either estimate, Mayotte, the easternmost island closest to Madagascar, is the oldest island, possibly emerging from the ocean soon after magmatic activity started 20 Ma ago, which considerably expands previous age estimates of the Comoros archipelago as a whole [10]. Uncertainty apart, the Comoros is clearly old enough to attract researchers interested in island colonization and species diversification processes [13–22].

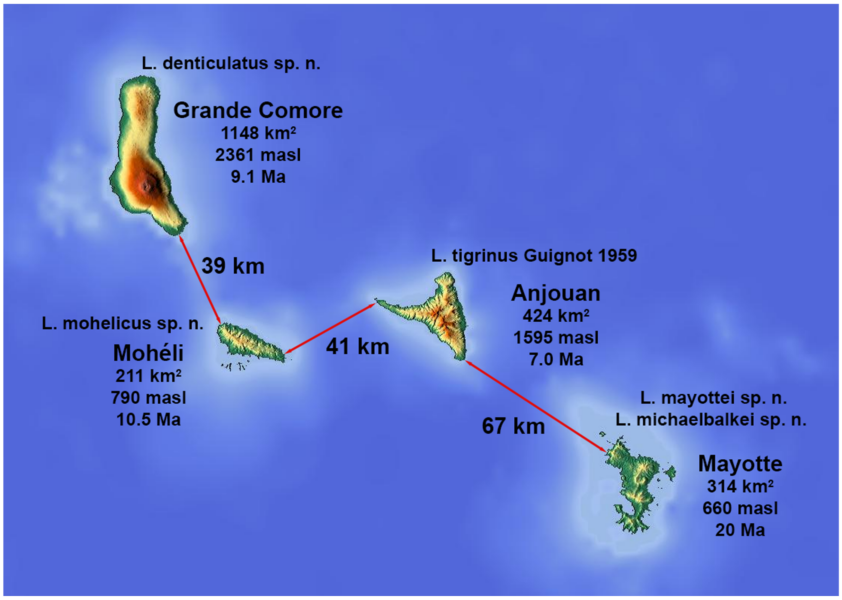

Figure 1. Topographic map of the Comoros archipelago, with indication of *Laccophilus alluaudi* group species occupancy based on our results. Terrestrial surface area in square kilometers and highest point in meters from [9], distance between islands in kilometers (calculated from Google Earth) and estimated beginning of magmatic activity in million years before present following [10] are given for each of the four main islands. Background map from https://maps-for-free.com, (accessed on 4 November 2021) released under Creative Commons CC0.

The Comoros have a maritime tropical climate with a warm rainy season from October to April [23]. From May to September southerly winds dominate, bringing cooler and drier air. Variable topography creates local differences in rainfall and air temperatures. Higher central areas of the islands are generally cooler and wetter than the coastal areas. Vegetation in the Comoro Islands resembles that of Madagascar [9]. Evergreen forest from sea level to approximately 1800 m is the original type of vegetation of the islands. Above the forest area, on Mount Karthala a high-mountain vegetation consists of mountain bushland and thicket [24]. Remaining natural forests constitute a small proportion of what once existed, and are today restricted to higher elevations [23,25]. The islands are partially surrounded by mangrove swamps. The soil of the islands consists of laterite, which is rich in minerals but poor in humus, being subject to erosion when sheltering forests are removed [23].

Maximum altitudes for the islands are the 2631 m peak of Mount Karthala on Grande Comore, a maximum of 1595 m on Anjouan, and below 800 m for the lower islands of Mayotte and Mohéli (Figure 1).

Based on endemism levels and loss of natural vegetation, the Comoros are part of the western Indian Ocean islands biodiversity hotspot [26]. This biodiversity hotspot is dominated by the much larger island of Madagascar, which seems to have been the most important source for many animal and plant groups on the Comoros [14,22,27–29]. Compared to Madagascar, the plant and animal diversity of the Comoros are certainly much lower. This is to be expected based purely on area-richness relationships, in addition to the Comoros' younger age. However, the Comoros are still relatively rich in endemic species. For plants, although poorly documented, as much as 33% are endemic [23], and for vertebrates approximately 20% [24]. The ongoing process of speciation is also demonstrated through many single-island endemic subspecies among the non-endemic birds [24]. While there is substantial species-level endemism, there are fewer examples of in situ diversification in the Comoros [8,13]. In contrast to the Galapagos, Mascarenes and Canaries, where intra-archipelago speciation has thrived, endemism in the Comoros is largely made up of immigrants and anagenesis from the parental stock, at least for vertebrates [8,13]. For invertebrates, diversity patterns, endemism levels and origination processes are still poorly explored in the Comoros.

Laccophilus is the second most diverse genus of diving beetles (Dytiscidae), with a worldwide distribution [30]. Members inhabit both running and standing water bodies and are found over a large altitudinal and habitat range. The *Laccophilus alluaudi* species group was established by Biström et al. while revising the African fauna of the genus [31]. Six species were recognized, five in Madagascar and one in the Comoros. Recently, Manuel and Ramahandrison added three more species to the group [32], and several additional species, all from Madagascar, are known but have yet to be described (Bergsten unpublished). It has become clear that the lineage is one of just a handful of larger (>10 spp.) in situ diversifications of diving beetles in Madagascar [32,33]. One species from the Comoros, *L. tigrinus*, was described by Guignot [34], and this is the only non-Madagascar species of the group. Guignot based his description on material from both Mohéli and Anjouan. While clearly belonging to the *Laccophilus alluaudi* species group, further investigation of this group in the Comoros has not yet attracted any attention from taxonomists. For instance, the multi-island species hypothesis of *Laccophilus tigrinus* has not been questioned, and material from Grande Comore and Mayotte has been lacking. Access to recently collected material from all four Comoro Islands prompted us to revise the group to shed light on both diversity patterns and diversification processes of Comoran fauna.

Here we show that, for one lineage of aquatic insects that has diversified in Madagascar and colonized the Comoros with a single known species [31,32], it actually constitutes a flock of island-endemic species in the Comoros. While not yet tested in a phylogenetic context, morphological evidence points towards a single colonization and intra-archipelago speciation.

2. Material and Methods

2.1. Preparation Technique and Measurements

The study material consisted of both dry-pinned specimens and specimens preserved in ethanol. Dry specimens were softened in hot water for some minutes prior to dissection. The apical part of the abdomen was then detached under a preparation microscope, and the genitalia extracted from surrounding tissue in warm water. Sometimes hardened tissue needed to be treated in a heater-device for about 10 min in 10% KOH solution. After this procedure, the genitalia were cleaned in water and ethanol and glued by the base on a card for photographing. Genitalia from specimens in ethanol were extracted directly without the need of softening in warm water, and both body and genitalia were glue-mounted on a card.

Measurements of body (length and width) were made using a Wild M 11 microscope (Wild Heerbrugg, Heerbrugg, Switzerland). The detailed technique is described in [31].

2.2. Photography

Photographs of specimens and genitalia were captured with a Canon EOS R digital SLR camera (Canon Inc, Tokyo, Japan) mounted on a motorized rail, Stackshot (Cognisys Inc., Traverse City, MI, USA). A long working distance metallurgic objective from Mitutoyo (Mitutoyo Corporation, Kanagawa, Japan) (5× for habitus; 10× for genitalia) was fitted to the camera using a Balpro bellows and customized adaptors (Novoflex, Memmingen, Germany). The stack-photography system was maneuvered with Zerene Stacker (Zerene Systems, Zerene Systems LLC, Richland, WA, USA) in combination with Canon EOS Utility (Canon Inc., Tokyo, Japan). Captured stacks of photos were merged using the Pmax algorithm in Zerene Stacker. Merged photos were prepared for plates in Adobe Photoshop (Adobe Inc., San Jose, CA, USA) and Adobe Illustrator (Adobe Inc., San Jose, CA, USA).

2.3. Depositories

Studied materials were deposited in the following institutions, which are referred to in the text by their abbreviations:

IRSNB—Institut Royal des Sciences Naturelles de Belqique, Brussels, Belgium
MRAC—Musée Royal de l'Afrique centrale, Tervuren, Belgium
MNHN—Muséum National d'Historie Naturelle, Paris, France
MZH—Finnish Museum of Natural History, Helsinki, Finland
NHRS—Swedish Museum of Natural History, Stockholm, Sweden
ZSM—Zoologische Staatsammlung, München, Germany.

3. Results

Based on morphological examination of material from each of the four main islands of the Comoros archipelago, it became clear that each island has at least one endemic species; we found no evidence of any species in common. In addition, examined material from Mayotte showed that multiple species can exist sympatrically. Below we give first a determination key, followed by the species descriptions. The known fauna of this group on the Comoros increases from one to five species as a result.

3.1. Key to Species of L. alluaudi Species Group in the Comoros

1. Pronotum anteriorly and head posteriorly darker; ferruginous to dark brown (Figure 2A–D) (rarely dark area indistinct in old, dry specimens) 2

   Pronotum and head unicolored testaceous to pale ferruginous (Figure 2E,F) 4

2. Smaller species (body length 3.36–3.76 mm); dark area on head and pronotum ferruginous; gradual delimitation of markings (rarely dark markings almost absent) (Figure 2D) (Mohéli) . . . . . *L. mohelicus*

   Larger species (body length 3.98–4.12 mm); dark area on head and pronotum darker and more distinctly delimited (Figure 2A–C) (Grande Comore, Anjouan) 3

3. Penis narrower and more strongly curved in ventral view (Figure 3C); apically with an asymmetric apical knob (right side in ventral view pre-apically straight to weakly concave) and subbasally with a distinct denticle (Figure 4B) (Grande Comore) . . . *L. denticulatus*

   Penis broader and less curved (Figure 3A,B); apically without an apical offset knob (right side pre-apically convex but apex with protrusion on left side); subbasal "shelf" not as sharply denticulated (Figure 4A in suboptimal condition, but similar to Figure 4C) (Anjouan) . . . . . *L. tigrinus*

4. Humeral region of elytra with an extensive pale area which lacks dark spots (Figure 2F); penis quite robust and sinuate (Figures 3F and 4E); (Mayotte) . . . . . *L. michaelbalkei*

   Humeral region with two vague, dark spots (Figure 2E); penis moderate-sized, non-sinuate but slightly curved (Figures 3E and 4D); (Mayotte) . . . . . *L. mayottei*

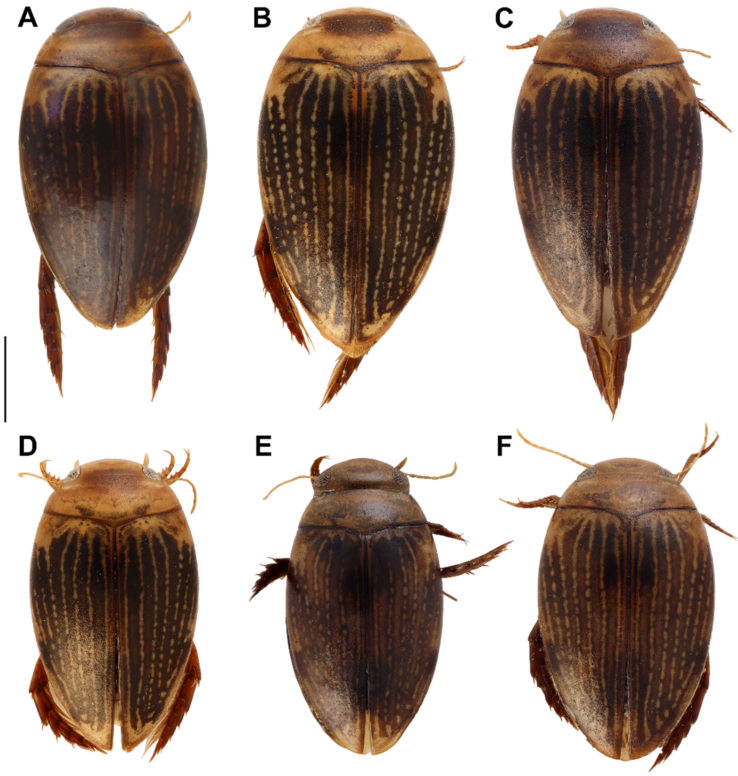

Figure 2. Habitus images of *Laccophilus alluaudi* species group members from Comoro Islands: (**A**) *L. tigrinus* (male, PT 13265); (**B**) *L. tigrinus* (female); (**C**) *L. denticulatus* (male); (**D**) *L. mohelicus* (male); (**E**) *L. mayottei* (male); (**F**) *L. michaelbalkei* (male). Scale bar 1 mm. Note that (**A**) (Photo: MNHN/Christophe Rivier) is photographed under different circumstances (equipment, angle and resolution).

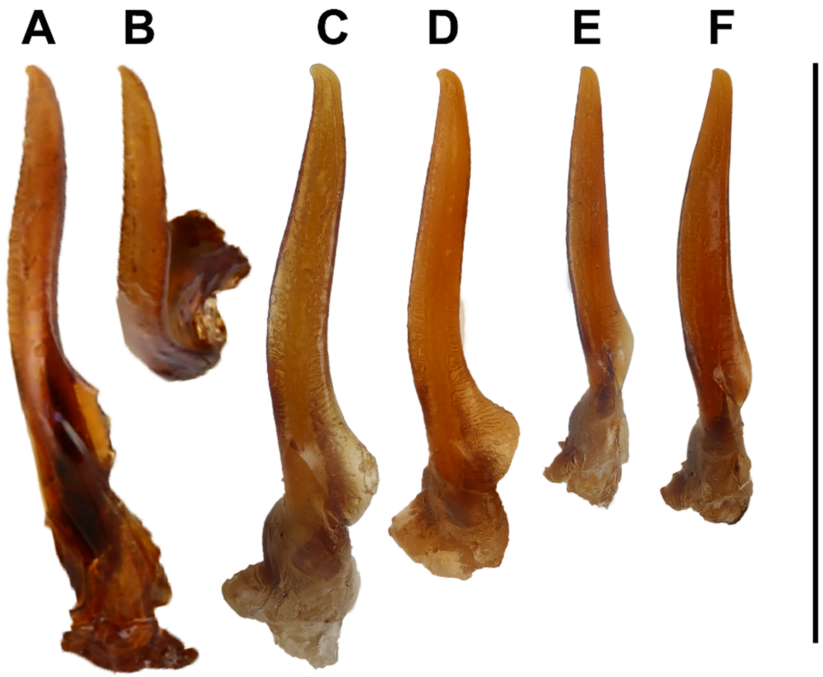

Figure 3. Penis in ventral view of *Laccophilus alluaudi* species group members from Comoro Islands: (**A**) *L. tigrinus* (PT 13265); (**B**) *L. tigrinus* (HT 13263); (**C**) *L. denticulatus*; (**D**) *L. mohelicus*; (**E**) *L. mayottei*; (**F**) *L. michaelbalkei*. Scale bar 1 mm. Note that (**A**,**B**) (Photos: MNHN/Christophe Rivier) are photographed under different circumstances (equipment, angle and resolution).

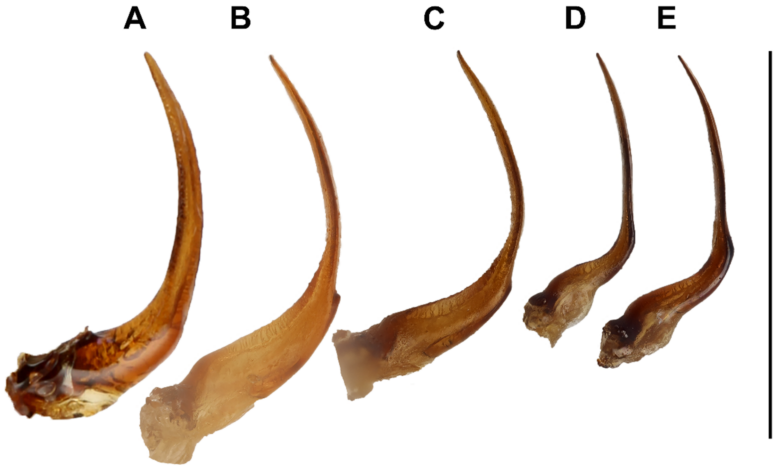

Figure 4. Penis in lateral view of *Laccophilus alluaudi* species group members from Comoro Islands: (**A**) *L. tigrinus* (HT 13263); (**B**) *L. denticulatus*; (**C**) *L. mohelicus*; (**D**) *L. mayottei*; (**E**) *L. michaelbalkei*. Scale bar 1 mm. Note that (**A**) (Photo: MNHN/Christophe Rivier) is photographed under different circumstances (equipment, angle and resolution) and is partly covered with residual glue hiding a subbasal shelf similar to in (**C**).

3.2. Taxonomic Treatment

The *Laccophilus alluaudi* species group is characterized by a pale body with elytra exhibiting longitudinal, dark-colored markings. Moreover, members of the species group are moderately sized (approximate length of 3–5 mm), and no stridulation apparatus is exhibited on metacoxal plates ventrally of the body. Male genitalia are asymmetrically shaped, with penis sinuate or curved from the basal part towards apex

Laccophilus tigrinus Guignot, 1959

Guignot, 1959: 76 (original description) [34]; Guignot 1961: 931 (faunistics) [35]; Wewalka 1980: 726 (faunistics) [36]; Nilsson 2001: 251 (catalogue) [37]; Biström et al. 2015: 43 (monograph) [31]; Nilsson & Hajek 2021; 231 (catalogue) [38].

Material studied:

Holotype, male: "Type/Anjouan Foret de M'Remani X-1953 (Millot)/F. Guignot det., 1955 L. tigrinus sp.n. Type [male symbol]/HOLOTYPE/HOLOTYPE Laccophilus tigrinus Guignot/MNHN, Paris EC13263 [QR code]/Data in NHRS JLKB 000030002" (MNHN).

Paratypes: "PARATYPE/F. Guignot det., 19 L. tigrinus sp.n. Paratype [male symbol]/PARATYPE Laccophilus tigrinus Guignot 1959/MNHN, Paris EC13265 [QR code]/Data in NHRS JLKB 000030003" [likely with same collecting data as holotype but not on labels] (1 ex. MNHN). "Paratype/PARATYPE Laccophilus tigrinus Guignot 1959/MNHN, Paris EC13245 [QR code]" (1 ex. MNHN).

Additional material studied: "Anjouan Comoros 12.27483 S, 44.47502 E, 18.3.2010, 798 m asl, Drinking water basin near Ouzini, SOH 0069/Laccophilus tigrinus Guignot, 1959 Det. J. Bergsten 2021" (1 ex. NHRS; 1 ex. MZH; 1ex. ZSM).

Total material studied: 6 specimens (MNHN; MZH; NHRS; ZSM).

Diagnosis: *L. tigrinus* is separated from other species in the group by the combination of a dark area frontally on pronotum and posteriorly on the head, a relatively larger body size (length 3.92-4.08 mm) and the lack of a distinct sharp denticle subbasally on penis.

Description:

Body (Figure 2A,B), length, male 3.92–4.08 mm, width 2.24–2.36 mm; female, length 3.98–4.12 mm, width 2.32–2.40 mm.

Head: Frontal outline of head broadly straight to almost straight; laterally foremargin somewhat curved towards eyes. Testaceous to pale ferrugineous. Posteriorly at pronotum with quite broad, dark ferrugineous area. Rather shiny although with fine reticulation which extensively is irregular. Shape of meshes variable, in part transverse. Extensively

impunctate, but at eyes with fine, scattered punctures. Area of punctures extends little towards mid-head. Antenna testaceous to pale ferrugineous, slender. Apical segment slightly longer than adjacent ones; apically pointed.

Pronotum: Testaceous to pale ferrugineous. Anteriorly, posterior to head with broad, brown to dark ferrugineous spot. Delimitation of dark spot sometimes slightly vague. Lateral outline of pronotum evenly curved; non-margined. Rather shiny although distinctly microsculptured. In part with double reticulation but size-classes of meshes indistinct and difficult to discern. Reticulation variable; meshes densest and smallest at margins, on disc slightly larger and irregularly shaped. Frontally and laterally with some irregularly distributed, somewhat indistinct punctures (hidden in dense microsculpture).

Elytra: Testaceous with distinct black to dark ferrugineous, longitudinal markings. Four inner markings reach almost to base of elytra. Three lateral markings end before elytral base and leave a moderately sized pale humeral area. Longitudinal markings in two female specimens broader and in part confluent. Extreme, lateral dark marking in part medially reduced (sometimes broken). Pale humeral area provided with 2–3 dark, vague spots. Slightly matte due to distinct microsculpture. Reticulation dense, meshes moderately sized, almost uniform in shape. Double reticulation reduced; indistinct and rudimentary. A fine and somewhat sparse and irregular row of discal punctures may be discerned in frontal half of elytra. Laterally with fine and sparse punctures which posteriorly form a distinct row which ends clearly before elytral apex. Scattered, very fine punctures discernible in posterior part of elytra.

Ventral aspect: Prosternum testaceous to pale ferrugineous. Metacoxal plates laterally dark, almost black. Towards middle, plates become slightly paler; dark ferrugineous. Metathorax dark ferrugineous; anteriorly pale ferrugineous. Metacoxal process and abdomen testaceous to pale ferrugineous. Sternites laterally sometimes with a vague dark spot. Metathorax and metacoxal plates almost impunctate; with fine, sparse punctures. Plates provided with a few transverse impressions which laterally are strongly bent to short, slightly curved impressions. Abdomen rather shiny, almost impunctate, provided with somewhat curved, sparse striae. Metacoxal plates and abdomen rather shiny; reticulation indistinct, plates with shagrination. Metacoxal lines with a blunt lateral extension. Ventrite in apical half almost keeled, with fine, irregular punctures.

Legs: Testaceous to pale ferrugineous. Pro- and mesotarsus somewhat enlarged, provided with adhesive discs.

Male genitalia: Penis almost evenly broad in medial part; less curved (Figure 3A,B); apically without an offset apical knob (right side pre-apically convex) but with small left-turned apical protrusion (Figure 3A,B); subbasal "shelf" not sharply denticulated (Figures 3A,B and 4A). Earlier dissection and mounting of male genitalia in imaged holotype may have effect on their present configuration except for apex, which is definitely different to shape of apex in *L. denticulatus*. Based on studied paratype material, *L. tigrinus* has subbasal shelf in lateral view, blunt and gently rising as in *L. mohelicus* (Figure 4C; also see illustration in [36]), but not sharply denticulate as in *L. denticulatus* (Figure 4B).

Female: Pro- and mesotarsi slender, lack adhesive discs.

Distribution: Anjouan (Figure 1).

Discussion. *L. tigrinus* was described by Guignot based on material from both Anjouan and Mohéli [34]. A type statement in the introduction qualifies as a holotype designation and the holotype (MNHN EC13263) is from Anjouan. The paratype material from Mohéli (MNHN EC13266) belongs to *L. mohelicus*.

Laccophilus denticulatus n. sp.

urn:lsid:zoobank.org:act:D1499466-D6B4-44DD-8D0C-8B6D8FC66B42.

Material studied:

Holotype, male; "Grande Comore Nioumbadjou R. Joqué 9.8. 1981/Holotype Laccophilus denticulatus n. sp. Bergsten & Biström, 2022" (1 ex. MRAC).

Paratypes: Same data as holotype but with paratype labels "Paratype Laccophilus denticulatus n. sp. Bergsten & Biström, 2022" (1 ex. MRAC; 1 ex. MZH).

Total material studied: 3 specimens (MRAC; MZH).

Etymology: Species name refers to the small basal denticle or tooth (latin noun: denticulus) subbasally on the penis.

Diagnosis: Similar in shape and size to *L. tigrinus* and shares an infuscated area posteriorly on head and anteriorly on pronotum. Separated from *L. tigrinus* based on the distinctly offset (pre-apical sinuation also on right side) asymmetric apical knob and the subbasal sharp denticle of penis. *L. mohelicus* described below has a somewhat similar asymmetric apical knob but not clearly preapically sinuate on right side. Its body size is smaller and it has a more vaguely delimited, less darkened area on head and pronotum.

Description (only differences to description of *L. tigrinus* observed).

Body (Figure 2C), length, male 3.92–4.08 mm, width 2.28–2.36 mm; female, length 3.96 mm, width 2.32mm.

Male genitalia: Penis in ventral aspect sinuate and with left turned and offset asymmetric apical knob (Figure 3C). Subbasally, on left side opposite of anterior portion of subbasal expansion with a distinct denticle (Figure 4B).

Distribution: Grande Comore (Figure 1).

Laccophilus mohelicus n. sp.

urn:lsid:zoobank.org:act:EFF85AA5-800C-4DC7-9FC6-781095558A1E.

Material studied:

Holotype, male: "Moheli Foret de Fomboni 600 m 2eme torrent 6.54/Institut scientifique Madagascar/Type/R. Mouchamps det. Laccophilus mohelicus n.sp. TYPE/Laccophilus tigrinus Guignot O. Biström det./Holotype Laccophilus mohelicus n. sp. Bergsten & Biström, 2022" (IRSNB).

Paratypes: Same data as holotype but labelled as allotype and "Paratype Laccophilus mohelicus n. sp. Bergsten & Biström, 2022" (1 ex. IRSNB); "Moheli Comoros, 1.III.2010 Lat -12.29384 Lon 43.65220, 251 m asl, Chalet St. Antoine, slope, puddle along creek through forest SOH 0031/Paratype Laccophilus mohelicus n. sp. Bergsten & Biström, 2022" (1 ex. dry, 2 exs. in ethanol NHRS; 1 ex. dry in MZH); "Moheli Comoros, 28.II. 2010, 12.30269S, 43.63731E, 23 m asl Miringoni SOH 0026/Paratype Laccophilus mohelicus n. sp. Bergsten & Biström, 2022" (1 ex. dry, 3 exs. in ethanol NHRS, ZSM).

Other material studied: "Paratype/Moheli Foret de Fomboni 600m 2eme torrent 6.54 (J.M.)/PARATYPE Laccophilus tigrinus Guignot, 1959/MNHN, Paris EC13266 [QR code]/[male symbol] (1 ex. MNHN);

Total material studied: 11 specimens (IRSNB, MNHN, MZH, NHRS, ZSM).

Etymology: We use the name "mohelicus" that was suggested, but not published by R. Mouchamps. The name refers to the Comoro island of Mohéli where the species occurs.

Diagnosis: Most similar to *L. tigrinus* and *L. denticulatus* but slightly smaller (maximum length 3.76 mm). Dark frontal marking of pronotum vague and not clearly delimited. In old specimen dark marking indistinct, leached and almost absent. Penis very similar to *L. tigrinus* (body size and colour patterns best diagnostic differences) and also resembles that of *L. denticulatus*, but smaller, ventral denticle blunt and apical knob less clearly offset.

Description:

Body (Figure 2D), male, length 3.36–3.68 mm, width 1.92–2.12 mm; female, length 3.52–3.76 mm, width 2.04–2.16 mm.

Head: Frontal outline straight, laterally towards eyes slightly curved. Testaceous, posteriorly at pronotum slightly darker; with vague, pale brown area. Darker area narrower and with more vague delimitation in comparison with *L. tigrinus*; sometimes dark area almost absent. Rather shiny, although finely to very finely microsculptured. Reticulation variable, in part double. Posteriorly head with fine and dense, almost isodiametric meshes. On disc fine reticulation almost absent and replaced by larger, somewhat irregular shaped meshes. Frontally larger and fine meshes appear mixed but size-classes in part difficult

to separate. At eyes with some irregular punctures, which medially extend for a short distance towards mid-head. Antenna testaceous, slender, apical segment slightly longer than preceding segments; apically pointed.

Pronotum: Testaceous to pale ferrugineous. Frontally in middle often with a vague pale brownish to ferrugineous spot (delimitation of spot gradual and diffuse). Lateral outline of pronotum evenly curved; non-margined. Rather shiny, although microsculptured. Reticulation in part double, but size-classes in part difficult to discern. Fine meshes anteriorly and posteriorly distinct; discally fine meshes indistinct and replaced by somewhat irregular-shaped, large meshes. Frontally and laterally with fine, but clearly discernible, irregular punctures.

Elytra: Testaceous with distinct, black to dark ferrugineous, longitudinal markings. Markings sometimes appear "hollow"; slightly paler in middle but outline of separate marking always distinct. Four inner markings reach almost elytral base, the most lateral marking being anteriorly somewhat expanded. Three lateral markings at base shorter, leaving a quite extensive humeral area pale-colored. Vague darker spot may sometimes be discerned in the pale area. Markings also in part confluent, the most lateral being, in part, reduced. Slightly matte due to distinct, dense microsculpture. Double reticulation reduced, indistinct and rudimentary. Fine, sparse but indistinct and irregular discal row of punctures may be discerned. Posteriorly with fine, scattered punctures. Laterally, in posterior part of elytron with fine, clearly discernible row of punctures, which fade away before reaching elytral apex.

Ventral aspect: Prosternum testaceous to pale ferrugineous. Metacoxal plates laterally almost black; towards middle plates become gradually paler; at metathorax and metacoxal process ferrugineous to pale ferrugineous. Abdomen pale ferrugineous to testaceous. Metathorax anteriorly with a few punctures, otherwise impunctate as metacoxal plates. Metathorax shiny without microsculpture or non-shagreened. Metacoxal plates slightly matte due to fine microsculpture, almost shagreened. Metacoxal plates almost impunctate, provided with few indistinct transverse depressions which laterally turn to a few distinct impressions. Metacoxal lines with blunt lateral extension. Abdomen rather shiny and almost impunctate; apical ventrite apically with some fine punctures and shagreened. Abdominal segments with sparse, curved striae.

Legs: Testaceous to pale ferrugineous. Hindlegs somewhat darker, ferrugineous. Pro- and mesotarsus somewhat enlarged and provided with adhesive discs.

Male genitalia: Penis in ventral view slightly sinuate and provided with apical knob, less distinctly offset compared with *L. denticulatus* (Figure 3D). In lateral view with modest smooth denticle or subbasal "shelf" which is blunt but clearly discernible (Figure 4C).

Female: Pro- and mesotarsus slender, no adhesive discs.

Distribution: Mohéli (Figure 1).

Laccophilus mayottei n. sp.

urn:lsid:zoobank.org:act:EF080A54-025D-4BBF-BE67-090FA086E72D.

Material studied:

Holotype, male; "Mayotte Hajangoua REF04 23 VIII.2013 Nathalie Mary/Holotype Laccophilus mayottei n. sp. Bergsten & Biström, 2022" (1 ex. MZH).

Paratypes: same data as holotype except "Paratype Laccophilus mayottei n. sp. Bergsten & Biström, 2022"(2exs. females MZH, NHRS); "Mayotte Djalimou REF09 22.VIII.2013 Nathalie Mary/Paratype Laccophilus mayottei n. sp. Bergsten & Biström, 2022" (1 ex. male MZH); "Mayotte Bouyouni Amont 30.VII. 2012 Nathalie Mary/Paratype Laccophilus mayottei n. sp. Bergsten & Biström, 2022" (2 exs. females MZH, ZSM).

Total material studied: 6 specimens (MZH, NHRS, ZSM).

Etymology: The name refers to the Comoro island Mayotte where the species occurs.

Diagnosis: *L. mayottei* has a unicolorous testaceous head and pronotum and in this respect resembles *L. michaelbalkei*. From the latter, *L. mayottei* can be distinguished based on a narrower and less sinuate penis in ventral view, and a relatively shorter and less strongly

developed basal region in lateral view. *Laccophilus mayottei* is also smaller in body size and has two diffuse darker spots in the pale humeral region of elytra.

Description:

Body (Figure 2E), (male), length 3.40–3.48 mm, width 1.92–2.00 mm; female, length 3.40–3.56 mm, width 1.92–2.04 mm. Body dorsally slightly globular; in species from Madagascar body over elytra somewhat flattened. Body a little smaller than in its sister species *L. michaelbalkei*.

Elytra: Testeceous, with dark longitudinal markings. Four inner markings as in sister species. Three lateral longitudinal markings end quite abruptly and a quite extensive pale area formed in humeral region. Pale humeral area anteriorly with two diffuse darker spots, which in part are united (spots absent in sister species). Three lateral longitudinal markings strongly modified and in part reduced, in part united with each other.

Ventral aspect: Bicolored. Metacoxal plates laterally blackish to dark ferrugineous; become gradually paler towards mid-body; metathorax dark ferrugineous to ferrugineous and metacoxal processes ferrugineous. Abdomen unicolored, distinctly paler, ferrugineous to pale ferrugineous. Lateral impression on metacoxal plates absent; replaced by a few backwards pointing striae. Metacoxal lines simple, lacks minor lateral extension, which is present in species from Madagascar.

Legs: Female pro- and mesotarsi slender, no adhesive discs.

Male genitalia: In lateral view similar to *L. michaelbalkei* but basal part prior to angle relatively shorter and not as strongly developed (Figure 4D). In ventral aspect not clearly sinuate but slightly curved with extreme apex almost straight with left side curved (Figure 3E). Basally moderately enlarged, provided with distinct basal extension (Figure 3E).

Distribution: Mayotte (Figure 1).

Laccophilus michaelbalkei n. sp.

urn:lsid:zoobank.org:act:0D973235-2430-4F83-8BD9-E467BA0CE820.

Material studied:

Holotype, male: "Mayotte Anatana REF08 22.VIII.2013 Nathalie Mary/Holotype Laccophilus michaelbalkei n. sp. Bergsten & Biström, 2022" (1 ex. MZH).

Total material studied:1 specimen (MZH).

Etymology: Named after the distinguished specialist of tropical Dytiscidae, Dr. Michael Balke in Munich, Germany.

Diagnosis: Head and pronotum of *L. michaelbalkei* is unicolored pale ferrugineous to testaceous when *L. tigrinus* and *L. denticulatus* has a dark marking frontally on pronotum. *L. mohelicus* also has a dark marking but it is vague and not distinctly delimited. In old dry specimens the dark marking seems to have been leached and it can therefore be almost absent. From *L. mayottei*, *L. michaelbalkei* is separated by larger body, by quite extensive pale area in humeral region of elytra; *L. mayottei* is smaller, with two vague darker spots in pale humeral area. Penis of *L. michaelbalkei* is in ventral aspect more robust and sinuate while in *L. mayottei* penis-size moderate and penis non sinuate but slightly curved. In lateral aspect the basal portion is relatively longer and more strongly developed prior to and at angle.

Description:

Body (Figure 2F), (male), length 3.60 mm, width 2.16 mm. Body dorsally slightly globular.

Head: Testaceous to pale ferrugineous. Rather shiny although finely microsculptured. Reticulation with two kind of meshes. Large meshes, when discernible contain 2–4 small meshes. Size-categories of meshes sometimes difficult to distinguish. At eyes with fine, irregular punctures, which extend short distance towards middle of head. Antenna testaceous, simple, slender, with quite long segments out of which the apical one is most extensive. No distinct modifications exhibited.

Pronotum: Unicolored, testaceous to pale ferrugineous. Lateral outline of pronotum non-margined, curvature moderate and even. Rather shiny, although finely microsculptured. With three kinds of microsculpture; at margins meshes of reticulation almost isodiametric, dense, fine and one-sized. Discally with double reticulation; two kinds of

meshes, smaller and larger meshes, which sometimes are difficult to distinguish, being almost of equal size. Larger meshes, when discernible, may contain 2–4 small meshes. Almost impunctate; laterally and at foremargin with quite dense and irregular punctures.

Elytra: Testaceous, with dark, longitudinal markings. Four inner markings reach almost to anterior margin of elytra. Outside them three lateral markings end frontally distinctly before reaching anterior margin of elytra, forming quite distinct, pale humeral area. The seventh (most lateral) marking of elytra is strongly reduced and only fragments of it are discernible. Rather shiny although finely microsculptured; elytra almost totally covered with fine, dense reticulation of one kind. Anteriorly at base and at suture with double reticulation. Large meshes, when discernible, may contain 2–4 small meshes. A fine and sparse discal row of punctures is discernible on elytron; posteriorly row of punctures mixed with scattered punctures. Elytra laterally with scattered, fine punctures not forming distinct rows.

Ventral aspect: Prosternum testaceous to pale ferrugineous. Metathorax and metacoxal process ferrugineous. Metacoxal plates blackish to dark ferrugineous. Abdomen ferrugineous to pale ferrugineous; little paler apically than at base. Metacoxal plates, metathorax and metacoxal process almost impunctate; sparse, very fine scattered punctures may be discerned. Quite shiny, microsculpture strongly reduced to fine shagrination. Metacoxal plates laterally with few, slightly irregular and shallow striae. Abdomen ferrugineous to pale ferrugineous. Sternites striated being densest at basal sternite and sparsest on apical sternite (3–4 reduced striae at each side). Almost impunctate; apical sternite apically with few fine punctures. Microsculpture reduced to fine shagrination. Metacoxal lines with reduced, blunt, lateral extension.

Legs: Pale ferrugineous to ferrugineous. Protarsus slender, mesotarsus slightly enlarged. Both provided with adhesive discs.

Male genitalia: Penis in lateral view with a quite steep angle in basal half (not evenly curved) (Figure 4E). In ventral aspect penis slightly sinuate, basally quite broad with quite distinct lateral extension (Figure 3F). Penis narrows evenly to quite slender apex, which is slightly turned leftwards (Figure 3F).

Female unknown.

Distribution: Mayotte (Figure 1).

4. Discussion

We found that the *Laccophilus alluaudi* species group, previously only known as one species from Anjouan and Mohéli [34], in fact has colonized all four major islands of the Comoros and likely constitutes an intra-archipelago species radiation. In addition, no species are common for any two islands, and on Mayotte sympatric sister-species occur. This contrasts with the broader patterns found for the Comoros, with very few cases of intra-archipelago cladogenetic events among, for instance, reptiles [8] or birds [13]. The *Laccophilus alluaudi* group has its largest diversity on the island of Madagascar [32], where currently eight species are described but several additional species are known (Bergsten unpublished). Since the species group is not known from the African mainland [31], it is almost certain the Comoros were colonized from Madagascar. This is a common pattern for many faunal and floral elements on the Comoros; for instance, Malagasy vangid birds, Mantellid frogs, bats, chameleons, *Phelsuma* day geckos and plants of the coffee family (Rubiaceae) all seem to have colonized the Comoros from Madagascar [14,22,27–29]. A review of reptile colonization patterns of islands in the western Indian Ocean point towards the direction of ocean currents being overwhelmingly important in the region supporting drift from northern Madagascar towards the Comoros [19]. This likely explains why much fewer colonization events of the Comoros from east Africa have taken place [27]. Reviews are lacking for insect colonization patterns of the Comoros, making it difficult to assess if this is a general pattern also for insects. Since insects may variously arrive both via drifting/rafting and through active or passive flight in the air, we can presume the direction of currents is less of a single, outstanding, explanatory variable. Flight capacity

and flight activity varies enormously among different insect groups, and the fact that an intra-archipelago diversification likely has taken place among the *Laccophilus alluaudi* species group suggests tens of kilometers of open sea constitutes a significant dispersal barrier (Figure 1).

All five species in the Comoros share the subbasal expansion on the right side of the penis, which is not present in any of the currently described species from Madagascar. This is therefore likely a synapomorphy carrying evidence of a single colonization event followed by diversification in the Comoros rather than multiple events. Furthermore, three circumfactual conditions point towards Mayotte being the island that was first colonized. Firstly, Mayotte is geographically closest to Madagascar, making it the most probable to be colonized based on island biogeography theory [2]. Second, it is the oldest of the four volcanic islands and hence has been available for colonization for the longest amount of time [10]. Finally, we conclude that among our studied material, Mayotte alone has two sympatric species, also in congruence with the species group having been present on the island the longest, allowing the most time for speciation. An alternative explanation for the two species on Mayotte would be secondary re-colonization from the other islands; however, based on morphology there is no doubt that among known species, the two on Mayotte are sister species, which implies intra-island cladogenesis. Since the subbasal expansion of the penis points towards a single colonization event from Madagascar, the other islands would have been colonized from Mayotte, if Mayotte was first. However, the two species in Mayotte are quite different from the three species on Mohéli, Anjouan and Grande Comore, which are more similar to one another (Figures 2–4). Until the diversity in Madagascar is further explored, and a comprehensive sampling of the group from both islands can be set in a phylogenetic context, some uncertainty will remain as to whether one or perhaps two colonization events most likely occurred.

As in many tropical countries, land use has decimated forests and degraded both terrestrial and freshwater ecosystems on the Comoro Islands. The rate of deforestation for the Union of Comoros is among the highest in the world [25,39]. Lowland forests up to 400 m asl are almost completely gone from the four islands [23]. The last remaining large forest block is on Grande Comore on the Karthala volcano [23,25]. The level of poverty and malnourishment, as well as dependency on forest resources, are extremely high. In concert with rapid population growth, the acute need of land for agriculture has led to an alarming rate of habitat loss [23,39]. Estimates from about a decade ago reported remaining closed forest cover made up somewhere between 4–9% of the Comoros [25,29], a number that has certainly decreased further since. Mayotte also has lost 50% of its native forests in the last 30 years, threatening its diversity (including many endemic species). The most recent surge in deforestation since 2010 has caused several calls of alarm, which in May 2021 led to the protection of 2800 hectares of forests on six of the island's massifs in "Réserve naturelle nationale des forêts de Mayotte" ([40]; Décret no 2021-545). Based on experiences from Madagascar, most of the *Laccophilus alluaudi* group of species are highly dependent on water systems in natural forests and are seldom found in, e.g., agricultural landscapes with eutrophied waters. However, a few species of the group do also occur in western Madagascar in more open landscape. It is likely that colonization of the Comoros stemmed from ancestors living in western Madagascar, which may be more adaptable to open arid landscapes. Such a pattern would mirror two examples of Mantellid frogs of Mayotte. Ecologically unusual species living in arid western Madagascar are the closest relatives, despite the fact that the diverse family Mantellidae is dominated by humid forest dwellers [22]. The protection of a large part of the remaining forests in Mayotte is, however, very positive for the long-term survival of the two endemic *Laccophilus alluaudi* group representatives and for many other freshwater organisms on the island.

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