

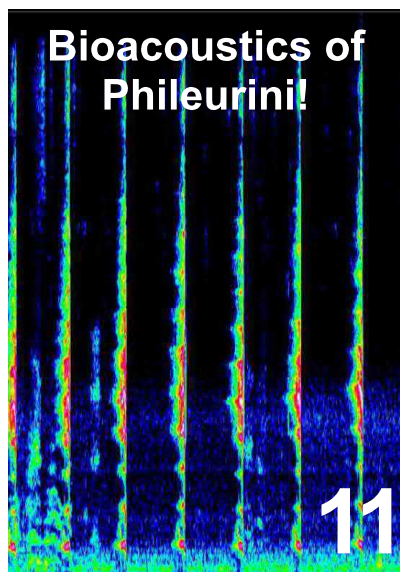


SCARABAEUS



THE IRREGULAR NEWSLETTER FOR ALL THINGS SCARAB

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Editorial: A message to our readers

Dear reader and fellow scarab enthusiast,

Over a year has gone by since the publication of our last issue of *Scarabaeus*. We wish to take the chance to apologize to you, our reader, for our delay publishing this new issue. Personal and work commitments, as well as a paucity of articles have continuously conspired to delay its publication over a year. We will try to do better next time but we also need your help. Please send us any news and trivia related to Scarabaeoidea so we can add them to future issues. The continued success of this newsletter relies on you more than anybody else, because it is your experiences and those of your colleagues that provide the substance on which it relies.

Gordon's aphodiines (Scarabaeidae: Aphodiinae: Aphodiini)

by

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In the winter of 2020, Dr. Robert Gordon (Fig.1), Professor Emeritus, Smithsonian Institution, and long-time researcher of Aphodiine scarabs, coccinellids, and dytiscids, decided that his personal comparative collection would be incorporated into the Guy Hanley Insect Research Collection (GHIRC) in Minot, North Dakota. Gordon Retired to the area of his family farmstead near Willow City, North Dakota, and Hanley has since built a friendship with him through many days in the field and in co-authoring several large revisionary works. Publications of Gordon and Hanley have described several hundred new South American coccinellid species, and a revision of the scarabaeiod genus *Glaresis* in the Americas. Field excursions led to the second specimen of *Glaresis* ever to be collected in North Dakota.



Fig. 1 Dr. Robert Gordon in the field.

The GHIRC now consists of approximately 20,000 specimens in diverse coleopteran families. Thanks to Gordon's addition, the collection now houses a comprehensive representation of North American aphodiines. The GHIRC also houses a significant bycatch of weevils and carabids collected by scarab specialist Mr. Ron McPeak. This material was collected during barrier pitfall trapping for *Stenothorax* (a winter active genus) in California, Idaho, Oregon, Utah, and Washington.

The COVID pandemic during 2020 allowed ample time to re-curate the entire Gordon collection, which consists of 2929 aphodiine specimens representing 239 of the approximately 250 species included in the 2007 revision of North American Aphodiini (Gordon & Skelley, 2007). 65 species are represented by paratypes. The collection is currently being digitized, and is about 1/3 complete. Many of the specimens given to Robert long ago were collected by such notables as Henry Howden and Oscar Cartwright, both of which were instrumental in their areas of scarab research. It is also very interesting to see label data of many "unknown" collectors, most likely amateur enthusiasts who provided specimens to Robert that now represent several rarely collected species. Dr. Gordon still occasionally takes part in field days and attends to story telling at local watering holes when his retirement activities around his farmstead allow. Although he no longer undertakes large revisionary work, his knowledge and enthusiasm for beetles continues to be of great value to those of us following in his footsteps.

Leaf litter deposits in spiny palms: a hideout for “rare” scarabs?

by

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As I described in my article in the first edition of *Scarabaeus* (Hielkema 2020), some years ago I made a cheap but strong beating sheet. Unfortunately, I've had little luck with beating for scarabs in the regular way; my score so far is a single *Rutelina lineola*, which may well be the most common diurnal ruteline in Suriname. Through luck, however, I discovered a novel and productive way of collecting scarabs with a beating sheet.

In 2010, veteran scarab collectors Paul Skelley and Bill Warner paid a visit to both Suriname and Conrad Gillett, who was at the time working at the National Zoological Collection of Suriname. I was invited to join them on one of their trips: a day-long journey in the savannah belt, about 40 km south of Paramaribo, the Surinamese capital. On an earlier trip they had placed some baited pitfalls and arboreal fruit traps, which now contained several scarabs (I can remember seeing the ubiquitous *Hoplopyga liturata* (Cetoniinae)). For me, the most interesting moment was when Paul draped a large white sheet on the ground against a trunkless spiny palm, and then proceeded to force out a quantity of decomposing leaves with a stick. The leaves had fallen on the palm fronds from the surrounding trees and had accumulated in the center of the palm between the many spiny fronds, where they started to decompose. After thus pulling out a pile of rotting leaves, he then picked up the sheet with all the debris, and in a more open spot we proceeded to search through the rotten mass of leaves, branches and spines. Although on this occasion we found no scarabs, Paul assured me that he had used this method in the same location to collect *Batesiana tuberculata*, an aphodiine with a unique warty appearance (Fig. 1). I tried Paul's method a couple of times on other occasions but never found any goodies and began to assume (falsely!) that his previous catch was more luck than skill.

A year later, I was on a month-long collecting trip deep in Suriname's rainforest, rather close to the

border with Guyana, in a remote resort called Arapahu. Like in many other primary forests in Suriname, there were spiny palms present. These palms were either much older than those on which Paul demonstrated his technique, or they belonged



Fig. 1. A specimen of *Batesiana tuberculata* (H. W. Bates, 1887) from the organic debris between the leaves of a spiny palm in Suriname.

to a different species; they had trunks of up to about 3 meters tall. I had not tried Paul's method here yet. After the daily chores of checking all my traps, one day I decided to work with my beating sheet again. As usual, this earned me hundreds of small ants and no scarabs. On a whim, I decided to put my beating sheet against a palm trunk at about 1.5 m height, and used my machete to pull a quantity of debris from between the fronds just above it. Who knew, maybe *B. tuberculata* could be found here? Still standing, I flipped over some of the rotten leaves on the beating sheet when I noticed a broad, somewhat flattened, shiny black beetle of about 7mm. First thought: “some clown beetle (Histeridae).” Second thought, less than a second later: “holy shit, a *Bdelyrus* (Scarabaeinae)!” (Fig. 2). Now, you should know that, at the time, my father and I were already working on our checklist of Scarabaeoidea of the Guianas (Hielkema and Hielkema 2019) and we knew of only one previous record of a *Bdelyrus* species in Suriname. That record was regarding the holotype and 6 paratypes of *Bdelyrus geijskesi* Huijbregts, 1984, all collected in 1949 in the rosettes of *Vriesea splendens* (Bromeliaceae) at 500m altitude on the ferrite cap of the Nassau Mountains in eastern Suriname. This species was, after the initial discovery, never collected again (or at least never reported), despite the revision of the genus by Cook (1998). *Bdelyrus* species have a



Fig. 2. A specimen of *Bdelyrus geijskesi* Huijbregts, 1984 from the organic debris between the leaves of a spiny palm in Suriname.

rather distinct appearance when seen dorsolaterally, and I remembered the shape from seeing the type series of *B. geijskesi* in the Naturalis Biodiversity Center in Leiden, the Netherlands. While standing there in the forest, I immediately realized that my discovery meant that I found either a new species for Suriname, or the first specimen of *B. geijskesi* in over 60 years. Further searching in neighboring palms yielded over a dozen more specimens. Since then, Fernando Vaz-de-Mello, who identified a number of Scarabaeinae for us, has confirmed these specimens as indeed belonging to *B. geijskesi*. This means that this species is not exclusively living in bromeliads, something Huijbregts (1984) already suspected.

Invigorated by the find of *B. geijskesi* at Arapahu, I proceeded to collect in the same manner in other locations. This resulted not only in more specimens of *B. geijskesi*, but also in *Batesiana tuberculata*, my original target. Next to these species I have so far found two species of *Astaenomoechus* (Hybosoridae: Ceratocanthinae) in palm debris, as well as some large scarab larvae which I assume belonged to Dynastinae and Cetoniinae. Unfortunately, I have not been able to rear the latter to their adult stage.

By now, I have found *B. geijskesi* in two more locations, both times in the decomposing biomass in the center of spiny palm species (*Bactris* sp. and/or *Astrocaryum* sp.). These places are Pingpe, near the village of Dyumu on the upper part of the Suriname River, in a forest comparable with that of Arapahu, and a forest on very poor white sands near Zanderij, where Suriname's international airport is situated. In both these locations I also

found *B. tuberculata*, in some instances even in the same palm specimens. In three other areas, I found *B. tuberculata* but no *B. geijskesi*. The range of forest types in which these two species are now found in Suriname suggests that both species are in fact widespread in Suriname and can probably also be found in neighboring Guyana and French Guiana, and possibly in northern Brazil as well. The unusual substrate they seem to prefer may well prove to be the only reason they are rarely collected. All known specimens of *B. geijskesi* were collected February–May while *B. tuberculata* specimens were collected January–August. This may mean that *B. geijskesi* is a seasonal species. During a trip at the end of July, I was not able to find *B. geijskesi* in its type location and type substrate at the Nassau Mountains. I suspect this species may be found again in its type location and in locations where I did not find it before, provided it is searched for in the right season.

The method I now use to find these and other species inhabiting the decomposing biomass in spiny palms is as follows. I assemble my beating sheet (see Hielkema 2020) and also take with me my machete (22" blade), my large but purposely



Fig. 3. The beating sheet is pressed against the palm trunk just below the mass of decomposing debris. A machete is then used to pull the rotting leaves from between the palm fronds. Snakes, centipedes, ants and more may come out to discuss the used collecting technique.



Fig. 4. After vigorously shaking the mass on the sheet, the larger leaves and branches are flicked off with a large knife.

very blunt fishing knife, a headlight and some collecting jars. Because of the palm spines and multitudes of non-coleopterous critters in the forest, I always wear sturdy boots, long trousers and, since a couple of years, cloth leg guards. When I see a promising palm, I use my machete to remove all rotten, hanging palm fronds that otherwise might fall on me while collecting the debris. This also creates more working space. Fronds that would require chopping are left in place, as I assume that the vibrations of the chopping might cause specimens to hide deeper or drop themselves. It would also needlessly damage these very slow-growing palms. I then forcefully push the beating sheet against the palm trunk just below the mass of rotting leaves, and use my machete to pull out as much rotten leaves as possible (Fig. 3). Of course, you have to look all the time at what comes out, since it's not unthinkable that you disturb some venomous snake or (as happened several times with me) a nest of very angry trap-jaw ants (*Odontomachus* sp.). When the beating sheet is full with leaves and other debris, I proceed to rapidly push the center of the sheet down several times with my blunt knife. By thus vertically shaking the debris on the sheet, the largest leaves and branches get on top, enabling me to flick them off (Fig. 4). I then take the sheet to a somewhat open spot on the forest floor to see if I got any interesting beetles. I usually put the sheet on the ground and kneel beside it to go through the leaves. As the shade and sporadic sun spots usually make it very difficult to clearly see small, dark specimens, I turn my headlight on, after which I use my knife, NOT my hands, to go through the debris (Fig. 5). I have already found a good number of scorpions, centipedes, large ants, spiders, whip scorpions

etc., and I would like to steer clear of their stings, bites and other defenses. Because the length of the crossbeams of my beating sheet forces the middle of the arcing cross to about 20 cm above the empty sheet (and to well over 30 cm when it's heavy with dead leaves), the leaf mass does not get against the hand with which I am holding it. Also, because the PVC crossbeams are rather smooth, I have not yet had trouble with beasties walking over them towards my hands. If there are still too many large leaves on the sheet, I may hold it up again, using my knife to shake loose anything that tries to hold on to a leaf by shaking the center of the sheet. Although I assume most people would rather use an aspirator / pooter to suck up the goodies, I use my knife to throw off large leaves and checked debris and to maneuver the specimens to an open spot on the sheet where I can pick them up.

I've not yet found scarabs in leaf masses that were dried out, and I don't search through very wet masses (like shortly after a rain shower) because of the weight of the wet debris. With wet debris, the chance of overlooking interesting specimens would also increase because of pieces of compost sticking to them. Interestingly, I have also never seen eggs, larvae or pupae of small scarabs, although I once found 3 teneral *B. tuberculata* in a single leaf mass. Whether they spend their early stages out of reach between the palm's leaf axils, elsewhere, or if I somehow overlooked them is unclear to me.

Once I've finished searching, I always check the whole sheet for palm spines that may have lodged



Fig. 5. After the larger objects have been removed, the sheet is put on the ground to carefully inspect the finer debris for scarabs. Note the headlight needed to spot small dark specimens in the dim forest understory.

themselves in it. These spines are very sharp and are known to easily cause nasty infections as they are covered in a biofilm of algae, fungi, bacteria, protozoa etcetera. I also check the four corner pockets of the beating sheet before taking it apart; a scorpion or something else might be hiding there.

I would love to hear the experiences of other people using this method, and also if beating sheets can be used in other unconventional ways. And please be sure to let me know if you ever plan to visit Suriname!

Acknowledgments

I'd like to thank Yvonne van Dam (Naturalis Biodiversity Center, Leiden, Netherlands) and Meindert Hielkema (Naturalis Biodiversity Center, Leiden, Netherlands) for providing me with the photos of *Bdelyrus geijskesi* and *Batesiana tuberculata*, and Jason Maté (Department of Entomology, The Natural History Museum, London, U.K.) for further processing those photos.

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On the Origin of *Goliathus atlas* Nickerl, 1887 (Scarabaeidae: Cetoniinae: Goliathini)

by

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An entomological enigma has persisted for more than a century. What is *Goliathus atlas* Nickerl, 1887? Is it a good species, a natural hybrid between *G. regius* and *G. cacicus*, or simply a morphological aberration of *G. regius*? There are three major morphological features that collectively define *G. atlas*: 1. A light yellow pronotum and scutellum. 2. A partial suture stripe. 3. Interrupted lateral bands. An additional feature can be observed. The white on the elytra of *G. regius* is minimally reflective of light while that of *G. cacicus* is highly iridescent. The white on the elytra of *G. atlas* is moderately reflective of light. All of the above features are intermediate traits between *G. regius* and *G. cacicus*. The true identity of *G. atlas* may be unveiled by either of two approaches: One is to perform a genetic analysis on specimens of *G. atlas*; and the other is to cross *G. regius* with a *G. cacicus* in captivity and see what happens. Although the first option is straightforward, it is extremely difficult if not impossible as *G. atlas* has not been sighted for approximately 50 years, probably due to massive deforestation across West Africa. The second option is much more involved, but still feasible to carry out.

In 2014, the decision was made to collect live *G. regius* and *G. cacicus* in West Africa, maintain them in captivity, and finally attempt to cross their virgin offspring to see if *G. atlas* can be produced experimentally. In 2015, an expedition was assembled and live *G. regius* was obtained in Ghana. Our team subsequently visited Ghana in 2016 and 2017, but no *G. cacicus* were found. During subsequent years (2018 and 2019), local



Fig. 1. Male *Goliathus atlas* used for the crossing experiments.



Fig. 2. Male *Goliathus regius*.

team members were continuously funded to make numerous expeditions extending to Ivory Coast and Liberia. All the formerly known ranges of *G. cacticus* were explored. Sadly, all of the expeditions were met with massive deforestation attributed to cacao plantation, oil palm plantation, rubber tree plantation, and timber production. Ivory Coast and Ghana are the number one and number two cacao producers in the world, respectively. It is heartbreaking to learn that a non-essential food such as chocolate can have such a catastrophic effect on nature. By 2019, *G. cacticus* had not been sighted for nearly 10 years. After searching for 5 years without any trace of *G. cacticus*, our team decided to steer away from the historical known distribution and explore primary forests far away from the coast where *G. cacticus* was once abundant according to old literature and anecdotal accounts from Europeans who collected extensively in Ivory Coast in the latter half of the 20th Century. Finally, in November 2019, *G. cacticus* was discovered in a new location.

Historically, *G. cacticus* mainly occupied coastal forests while *G. regius* mainly dwelled in inland forests. However, there are records of *G. cacticus* found more than 150 kilometers inland, and in 2019, our team discovered a population of *G. regius* right on the coast. In Ghana, *G. regius* feeds on the free-flowing sap of the Oba Tree (local name, scientific name unconfirmed, not *Vernonia* sp. or *Acacia* sp.). In Ivory Coast, *G. cacticus* had been observed to congregate on *Vernonia conferta* and *Acacia mangium* (introduced from Australia in the 1970s as a plantation tree). The newly discovered population of *G. cacticus* is approximately 80 kilometers from the coast. Incidentally, *G. regius* is also found here. Surprisingly, both *G. regius* and *G. cacticus* from this locality congregate exclusively on a species of tree that is different from the ones mentioned above, despite *V. conferta* and *A. mangium* both being present in this region. Although the identity of the beetles' mutual tree has not been confirmed, it may be a species belonging to *Vernonia*. However, it is neither *V. guineensis* nor *V. senegalensis*. Given *G. regius* and *G. cacticus* coexist in this region and even share the same species of tree, one could not help but wonder "Could there be *G. atlas*?" About 2 weeks after the rediscovery of *G. cacticus*, a wild specimen of *G. atlas* was collected among *G. regius* and *G. cacticus* for the first time in

approximately 50 years! This strongly supports the hypothesis that *G. atlas* is a natural hybrid of *G. regius* and *G. cacticus*. Our team also managed to record a video of this living specimen of *G. atlas*, which has never been done before. Shortly after filming, this *G. atlas* flew away! It was a small *G. atlas*, perhaps around 6 cm. But that little body held the genetic information that would put the mystery to rest once and for all. With no DNA to analyze, and with breeding stock in hand, the initial plan was to attempt to cross wild males of *G. cacticus* to virgin females of *G. regius* in captivity.

In December of 2019, the authors had available quite a few virgin females of *G. regius* from captive breeding. In total, 3 wild males of *G. cacticus* mated with 6 virgin females of *G. regius*. The males were placed directly on the dorsum of the females. The males very quickly recognized the scent of the females with their antennae as they would with females of their own species and proceeded to mate with no hesitation; the females also accepted the males readily. The copulations occurred as if the beetles were of the same species with no anomalies observed. Each mating lasted anywhere from 20 minutes to over 6 hours. Most of the pairs exhibited consecutive mating sessions. Several hundred eggs were produced, yet not a single one was viable! In this regard the example of the hinny came to mind. When a male donkey mates with a female horse, the offspring, mules, are easy to produce. However, when a male horse mates with a female donkey, the offspring, the hinny, is very difficult to obtain. Does this phenomenon also apply to *G. atlas*? Perhaps *G. atlas* is only possible when a male *G. regius* mates with a female *G. cacticus*. Given that *G. regius*, *G. cacticus* and *G. atlas* were found together on the same species of tree in this locality, the possibility that *G. atlas* was a hybrid between the other two species was the most likely possibility, though we would have to wait for one or two years before we could have virgin females of *G. cacticus* available for the crossings.

Luckily, in January of 2020, another specimen of *G. atlas* was found and successfully collected. The 88 mm *G. atlas* specimen was sent to Dr. Jen Pan Huang (Academia Sinica, Taiwan) who carried out the genomic and mitochondrial DNA analyses. Since mitochondrial DNA comes solely from the maternal side, and the combination of *G. cacticus* male crossing *G. regius* female failed to produce viable eggs, the prediction was that the mitochondrial DNA of this specimen of *G. atlas* must have

come from *G. cacticus*, assuming *G. atlas* is a hybrid. However the results of Dr. Huang's analysis were surprising. The mitochondrial DNA belonged to *G. regius*. This was unexpected, because all of the eggs from our hybrid experiment (*G. cacticus* male crossing *G. regius* female) were not viable. Furthermore, the genomic DNA revealed that the majority of the genes belonged to *G. regius*, which suggests that the atlas specimen was not the product of recent hybridisation but rather that it had occurred several generations prior. This meant that this *G. atlas* specimen was not an F1 hybrid and that *G. atlas* is fertile or at least capable of backcrossing with *G. regius*. This may explain why it is not uncommon to see specimens of *G. regius* with certain traits of *G. atlas*, such as a yellow pronotum and scutellum, a partial suture line, or thinning of lateral bands.

There are four species within *Goliathus* that can attain massive sizes: *regius*, *goliatus*, *orientalis*, and *cacticus*. All of them can hybridize with each other. This has been proven experimentally through captive breeding over the past 2 decades. F1 hybrids between *goliatus* and *orientalis*, as well as F1 hybrids between *regius* and *goliatus*, were produced in the early 2000s by a Japanese breeder and a German breeder, respectively. The German breeder attempted to propagate the F1 hybrids, but none of the eggs hatched. The first author produced F1 hybrids between *regius* and *orientalis* in 2019, some of which very much resemble *G. atlas* morphologically. The F1 hybrids were fertile and went on to produce F2 hybrids, which display an array of morphological characters: some resemble either *regius* or *orientalis* while others take on intermediate forms. Recently, the first author was able to cross a wild male of *G. cacticus* to a virgin female of *G. goliatus* to obtain 5 hybrid larvae. However, these larvae developed poorly and only one made a cocoon which died during the pre-pupa stage. Interestingly, the hatching rate for the F1 hybrid eggs between *G. regius* and *G. orientalis*, as well as the hatching rate for the subsequent F2 hybrid eggs, were nearly 100%. However, the hatching rate for the F1 hybrid eggs between *G. cacticus* and *G. goliatus* was only about 10%. This may be attributed to the increased genetic distance between *G. cacticus* and *G. goliatus*.

In early 2021, we attempted making *G. atlas* again by crossing several *G. cacticus* males to 4 virgin



Fig. 3. Mating of *G. cacicus* male and virgin *G. goliatus* female.

G. regius females. Dr. Huang's genetic analysis showed this can be done. This time around, about 400 eggs were obtained. Again, the hatching rate was extremely low. Only 40 eggs hatched. They came from two females. The poor hatching rate may explain the rarity of *G. atlas* despite *G. regius* and *G. cacicus* congregating on the same species of tree and mating with each other readily in captivity as if they were the same species. The genetic distance between *G. regius* and *G. cacicus* may be large, thus causing the observed low hybrid hatching rate. In August of 2021, the first *G. cacicus* and *G. regius* hybrid made a cocoon and in December of 2021, it successfully eclosed. The entomological mystery since 1887 was finally solved. The hybrid, a male specimen, corresponded perfectly with the holotype of Nickerl's Beetle. This result, together with Dr Huang's molecular data, confirmed beyond doubt that *G. atlas* is indeed the hybrid of *G. cacicus* and *G. regius*.

In this new locality, *G. cacicus* is observed from June through December. After December, the trees on which *G. cacicus* and *G. regius* congregate shed their leaves and the beetles do not come anymore. It is unclear if the adult beetles have died or they are congregating on other species of trees. According to collection data that our team has compiled from various experienced collectors who have found *G. cacicus* in the past, *G. cacicus* congregates on at least five species of trees (*Acacia mangium*, *Ficus* sp., *Vernonia conferta*, and two or three more species whose scientific names are unconfirmed). This is contrary to

literature from colonial times that *G. cacicus* only congregated on one species of tree. Furthermore, specimens of *G. cacicus* collected in December appeared very fresh (sharp claws, no missing parts, highly energetic, minimal scratches, etc.); they do not look like they are in the terminal stage of life. As a result, it is highly speculated that *G. cacicus* from January to June congregates on other species of trees.

Lastly, we want to convey our enormous relief to know that *G. cacicus*—and astonishingly *G. atlas*—are still flying in the remaining patches of the vanishing West African Upper Guinean Forests. Every effort will be exhausted to establish *G. cacicus* in captivity. It is only a matter of time before the last paradise is engulfed by human encroachment.



Fig. 4. Female *Goliathus atlas* produced by the hybridisation of a male *cacicus* and a female *regius*.

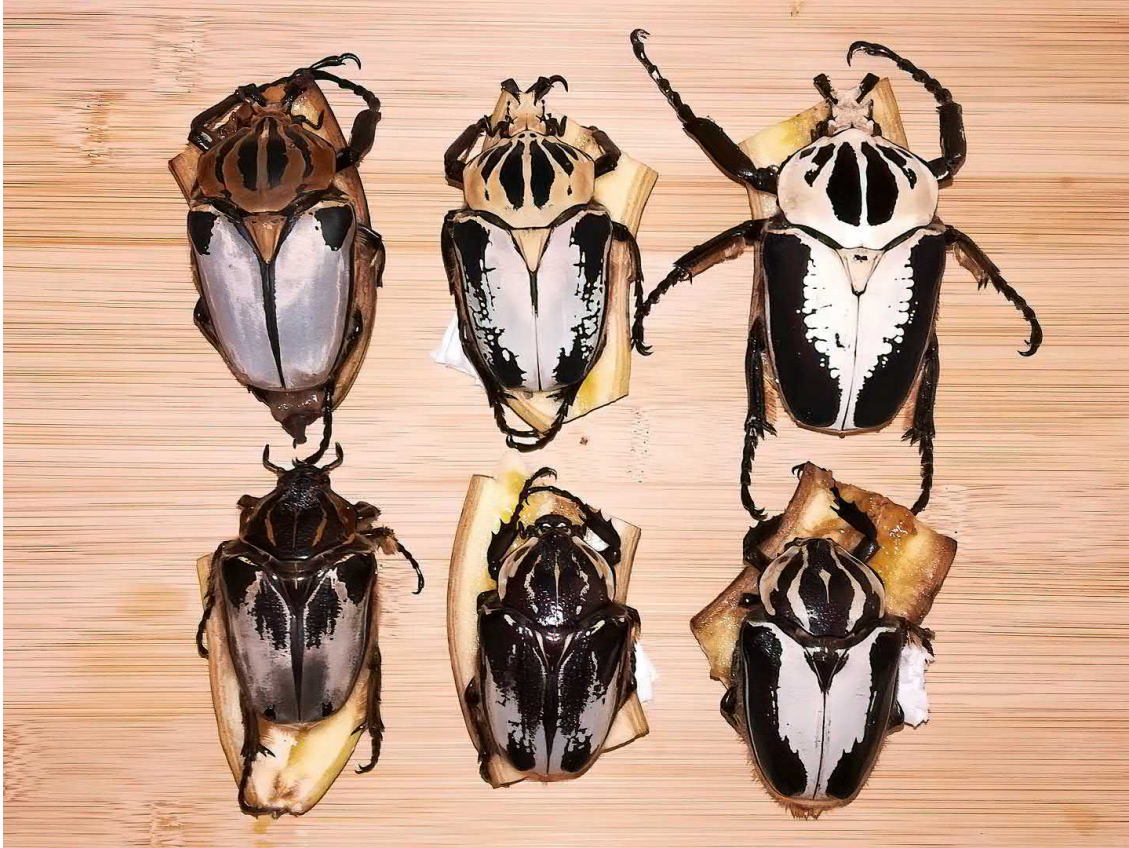


Fig. 5. Comparison of the hybrid F1 generation *G. atlas* (middle column, male above and female below) with the parental stock of *Goliathus cacicus* (left) and *Goliathus regius* (right).

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Notes on bioacoustics in the Phileurini: Passalidae are not the only social scarabaeoids!

by
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Neita et al. (2006) made the first observation of sounds produced by *Phileurus didymus* larvae: they mentioned that the larvae stridulated. However, no further data regarding the sound were presented. The first bioacoustic studies of the tribe were conducted on larvae of *Phileurus didymus* (Barria et al. 2020) and *Phileurus voirinae* (erroneously identified as *P. valgus*) (Barria et al. 2021). Both species were found with the adult female (mother) inside decaying tree trunks and the larvae of both species were docile, although this was not mentioned in Barria et al. (2020), but only in Barria et al. (2021). They presented the oscillograms and spectrograms of the sounds produced by the larvae; in the bioacoustic study of *P. didymus* only forced air was recorded. Neita et al. (2021), however, reported stridulation, so it is very likely that the larvae of *P. didymus* emit both kinds of sound, something that happens in *P. voirinae* too (Barria et al. 2021). Barria et al. (2020, 2021) mention that the forced air can be produced by

compression and release of air in the larva's intestine but more studies are needed to confirm the origin of the forced air. In *P. voirinae*, the recorded sound was a compound sound in which the larvae simultaneously produce both maxillo-mandibular stridulation and forced air sounds.

Both studies (Barria et al. 2020, 2021) were conducted only with larvae subjected to different "perturbation" experiments. They suggested that sound would have anti-predatory as well as social functions.

During the first quarter of 2021 I collected *Hemiphileurus variolosus* larvae in a decaying fallen log. These larvae were alone and exhibited aggressive behavior. Later, at the end of 2021 while on a walk, I found first and second instar larvae of *Homophileurus* sp. inside an abandoned termite nest on the ground. The larvae were accompanied by an adult female (presumed mother since the larvae were at an early stage and it was the only adult accompanying the larvae) and during all their stages they presented docile behavior. They did not survive long though, so it was not possible to obtain the adult stage. Fortunately, I was able to observe and record the compound sound emitted by the larvae (Fig. 1a, b). The recorded sound is similar to that recorded in *P. voirinae* by Barria et al. (2021). In the oscillogram, the stridulation and basal pulse (those bass pulses that are in the spectrogram basal region) are not differentiated (Fig. 1a). The spectrogram shows stridulation pulses followed by a basal pulse (Fig. 1b).

Cannibalistic behaviour has been observed on several occasions in different species of Phileurini

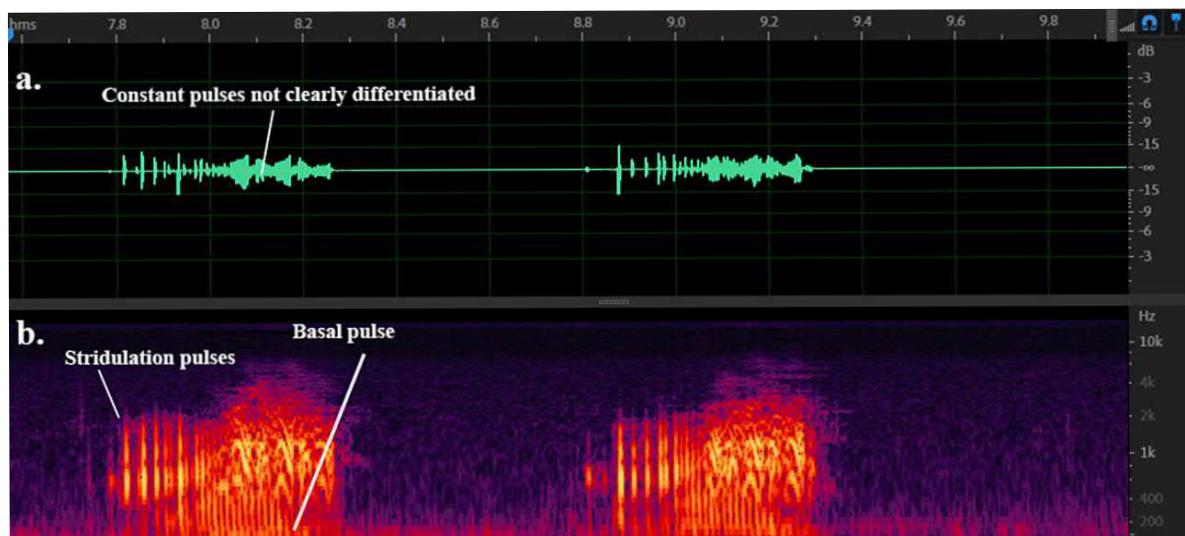


Fig. 1a-b. *Homophileurus* sp. larvae sound. a) Oscillogram. b) Spectrogram.

(Ratcliffe and Morón 1997; McCleve 2007). Considering the literatures and my limited observations, it appears that social behaviour is not expressed in all Phileurini species, and that these social species are the exception rather than the rule. Furthermore, the production of sound in Phileurini appears to be social in nature. Although I have observed that, even without the mothers present, larvae do not express cannibalistic behavior, the fact that in all species where vocalizing larvae have been reported these larvae are accompanied by an adult female and have a docile behavior is what makes me suspect that the sound production in Phileurini has a social function.

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Asymmetric segmental anomalies: review on teratology and examples in a variety of groups *Dynastes tityus* (Coleoptera: Scarabaeidae: Dynastinae), *Gromphadorhina oblongonota* (Blattodea: Blaberidae: Oxyhaloinae), *Lucihormetica subcincta* (Blattodea: Blaberidae: Blaberinae), *Heteropteryx dilatata* (Phasmatodea: Heteropterygidae), and *Porcellio expansus* (Isopoda: Porcellionidae).

by

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This report provides documentation including photographs and a diagram of unique teratological specimens for four different insect species and one crustacean. These are included in a review of abdominal sternite conjoined segment records, as well as equivalent thoracic and tergal oddities recorded in previous literature for arthropods (including arachnids and millipedes). A variety of other teratological specimens are discussed in context and a comparison to gynandromorphy is considered. Prevalence in populations is reviewed and discussed.

Asymmetric (conjoined) arthropod segment deformity:

Amongst the range of developmental deformities I have encountered, segmental ones are the most commonly seen, both in my experience of breeding a range of arthropod orders as well as by other breeders I have communicated with. In large immature and adult specimens, it is unlikely this

kind of deformity would go unnoticed by invertebrate breeders or specimen collectors, especially on the dorsal surface (tergites). However, it can be easily missed on small creatures such as fruit flies or species where wings or the color and shape of the body segments obscure the segmentation. Because of their rarity, I have photographically documented almost every case I have encountered, with the possible exception of a case in the cockroach species *Nauphoeta cinerea* (Blaberidae). Many of these cases of segmental anomalies were reported in two books specific to diplopodans (McMonigle 2012) and blattodeans (McMonigle 2016). In 2020 I observed my first segment deformity on an isopod *Porcellio expansus* (Fig. 1) and the first example of this anomaly on the hissing cockroach species *Gromphadorhina oblongonota* (Fig. 2, 3). Dryer (2020) provided data and images of the first case of segmental deformity I know of in a phasmid, which encouraged me to go down the rabbit hole that is this article, where I present a summary and estimated prevalence of developmental segment deformities from the observational data that I have collected over the years as well as those reported by others. For individual specimens, photographic documentation is included or cited.

The most common segmental deformity is where



Fig. 1. Specimen of *Porcellio expansus* demonstrating a segmental deformity.



Fig. 2. The first cockroach (*Gromphadorhina oblongonota*) I raised with a conjoined abdominal segment.

two segments fuse or split on one side only, resulting in asymmetric development of the abdomen or thorax. Often the asymmetry is balanced by a second fusion or split on a different segment (often spaced by a normal one) on the opposite side, appearing as if the segments cross back and forth. The segments on the opposite surface (dorsal or ventral) rarely, if ever, mirror the conjoined segments.

Although these misshapen segments seem like they should be a sticking point in ecdysis, I have not observed conjoined segments becoming stuck during a molt. Conjoined segments look similar in insects, arachnids, and crustaceans, but in millipeds there is a double deformity because it translates to the diplosegment as though it were a



Fig. 3. A view of the ventrum of the same cockroach (*Gromphadorhina oblongonota*) showing no abnormal development in the corresponding sternites.



Fig. 4. Specimen of *Atopochetus dollfusi* (formerly *Tonkibolus dollfusi*) demonstrating a conjoined segment.

single segment (Fig. 4). Conjoined segments are often located on the dorsal surface (tergite) without any sign of ventral surface (sternite) mirroring, though in the single phasmid I have documented, it occurs on the bottom (sternites) and is not mirrored on the top (tergites). In the isopod shown here, it is on the pereion rather than the abdomen (a similar thoracic segment deformity is documented for *Eurycotis decipiens*, a cockroach (McMonigle (2016))).

Body segment deformities are somewhat common (one out of hundreds or a few thousand specimens) in many arthropods, but in some they may only be a one in a million occurrence. Hence, segmental anomalies have been recorded in insects (beetle family Scarabaeidae and cockroach family Blaberidae, Epilamprinae and Oxyhaloinae subfamilies), millipedes (order Spirobolida), crustaceans (order Isopoda, family Porcellionidae) and arachnids (order Pseudoscorpiones). For the latter group there are several reports on segmental anomalies on wild populations. Curcic et al. (1991) documented 36 cases out of 4,825 specimens of pseudoscorpion collected in Yugoslavia, whilst Pedder (1965) recorded similar deformities across six different British pseudoscorpion species. My first recollection of learning about segment deformity documentation was in Weygoldt's book on pseudoscorpions (Weygoldt 1969), specifically in chapter 8 on teratology. The chapter contains two paragraphs with accompanying diagrams for each, where the author discusses the different segment deformities found in a large survey, as well as illustrates an extreme teratological example

where a pseudoscorpion had the right foreleg fused to the pedipalp.

Looking back, I barely remember that Weygoldt quoted Pedder's (1965) conclusion that deformities arose during the process of molting because they were rarely observed on second instar specimens and "never" on first. His comment was based on a survey of specimens collected from the wild rather than an attempt to follow development of any anomalous individuals, probably due to practical limits as it is almost impossible to see segment deformities on young pseudoscorpions with the naked eye. Even under high magnification, the segments in protonymphs and deutonymphs are poorly sclerotized, and difficult to discern from the pleural and intersegmental membranes on the abdomen. Initially I also assumed that these segmental defects occurred during molting as suggested by Pedder and Weygoldt before observing multiple specimens of different species of arthropods with this anomaly develop through consecutive stages without an increase or decrease of the deformity. It therefore appears that this type of segment deformity in arthropods must occur during segmentation in the embryo and is therefore congenital.

Examples old and new

Arachnids:

Most true spiders do not have a visibly segmented abdomen, hence segment deformities cannot be seen externally. The exception are the segmented spiders (Mesothelae, Liphistiidae) but they are rarely seen or kept (I only have half a dozen). On the other hand, a rare congenital deformity has been documented for some large tarantulas, namely gynandromorphy (Bergström 2006).

In addition I have reared a few thousand amblypygids (primarily *Damon*, *Heterophrynus* and *Phrynus*) and have not yet observed a conjoined segment.

In the case of pseudoscorpions, I have seen one deformed specimen of *Microchernes dentatus* (2007) out of approximately 400 reared over six years, sufficiently common to be seen in such small sample. Therefore I think that segment deformities are more commonly reported for pseudoscorpions not just because of the attention they have received but also due to a higher incidence than in other taxa, possibly due to their morphology. In many species the sternites and tergites are longitudinally split along the medial line, so segmental deformities would have a limited impact on their development.

Crustaceans:

In a colony of *Porcellio expansus* that produced around 1,000 specimens between 2017 and 2020 I only observed one case of segmental deformity. The deformity begins on the first and third pereonite starting just behind the head. This is my first observation despite having reared upwards of 50,000 *Porcellio* since 1997. One or two may have gone unnoticed on smaller, monochromic, *Porcellio* species over the decades, though it is unlikely.

Millipedes:

Segmental deformity observed on one wild-collected *Atopochetus dollfusi* (= *Tonkinbolus dollfusi*) specimen and one captive-bred *Chicobolus spinigerus* from the early 2000s. I have reared tens of thousands of other spirobolids and spirostreptids and have not observed other captive-reared offspring with this deformity.

Insects:

Beetles: *Dynastes tityus* larvae, 2 out of 176, from a small group of related animals (surveyed February 2021, eggs laid between November 2019 and July 2020). One displayed the standard crossing abdominal tergites seen in previous generations in similar frequency (maybe one out of every 100–200) (Fig. 5). The second is the only specimen I have seen with a reduction in the left side of the front thoracic segment (Fig. 6). From



Fig. 6. Larva (L3) of *Dynastes tityus* with a reduction on the thoracic segment.

starting the culture in 1995 till 2020, I have seen a dozen or more specimens from the same bloodline with crossing segment deformities but previously did not attempt to document prevalence, survival or ultimately what the adult looked like. The deformity is not noticeable in adult specimens, so I did not make an effort to cull it out of larval specimens. However, affected specimens tend to be mid-sized and commonly only the largest specimens are kept for breeding so it may be eliminated secondarily. Since the deformity is covered by the elytra on adult specimens it may be relatively harmless. This could be a case, like pseudoscorpions, where the deformity causes no problems and likewise concentrates in beetle larvae. Still, I do not recall seeing it once on tens of thousands of other scarab and related larvae over the decades. I have seen oddities including tiny heads (microcephaly) and double abdomens in cetoniid larvae, but they died days after hatching.

Adult gynandromorphs are known for *Mecynorhina polyphemus* (Ditzel and Larsen 2003) and *Allomyrina dichotoma* (Mizunuma and Tetsuo 1999). Most horn deformities, even the fantastic example of *Chalcosoma atlas* in Mizunuma and Tetsuo (1999) are probably a result of trauma rather than homeotic genes.



Fig. 5. Larva (L3) of *Dynastes tityus* with a typical abdominal crossover on the tergites.

Cockroaches:

Conjoined segments do not seem to cause developmental problems for most roaches but are quite rare compared to pseudoscorpions. Sternite crossing observed in the following species: one specimen of *Opisthopteria orientalis* (2008) out of approximately 1,000 specimens reared over a decade; one *Gromphadorhina grandidieri* (2008) out of a few thousand specimens reared from 1997–2020; and one specimen of *Gromphadorhina oblongonota* (Fig. 2, 3, 7) in 2020 out of less than 1,000 over a decade. On the other hand I have only observed one lobster roach (*Nauphoeta cinerea*) with conjoined abdominal tergites (2015), in over 25 years and tens of thousands of individuals bred as food for other stock. The nymphs of this species



Fig. 7. Specimen of *Gromphadorhina oblongata* with dorsal abdominal deformity.

have a uniformly colored abdomen and I do not often look at them closely (I offered this particular specimen to a tarantula) so other cases may have occurred without me noticing them. A female *Lucihormetica subcincta* from stock circa 2000 was found with crossing, conjoined deformity in 2021 (Fig. 8). A very unusual specimen of *Eurycotis decipiens* found in 2014 displayed the deformity on the thorax, with crossing tergites of the meso and metathorax (McMonigle 2016). On the other hand



Fig. 9. *Gyna centurio* gynandromorph (Photo by Alan Jeon).



Fig. 8. Female *Lucihormetica subcincta* with dorsal conjoined deformity (2021).

cockroach segment deformities do seem to be more common than gynandromorphs. There have been a few *Gromphadorhina portentosa* bilateral gynandromorphs reported over the last 45 years, but they probably occur at a rate of one out of 10,000–20,000 specimens. There is a report from 1967 of a *Blattella germanica* gynandromorph (Ross and Cochran 1967) and here I can report one observation in *Gyna centurio* (Fig. 9) from 2018.

Phasmids:

I have reared countless thousands of phasmids since the mid-1990s and do not recall ever seeing this deformity. Although it might be difficult to see on the long, skinny bodies of our native *Megaphas-*



Fig. 10. Female *Heteropteryx dilatata* female with crossed over abdominal segments.

ma, *Manomera*, *Diapheromera* and *Parabacillus*, conjoined segments would probably cause obvious, twisted bodies. Dryer (2020) reports the first observation (after 25 years of culturing) of conjoined segments for *Heteropteryx dilatata* (Fig. 10). He noticed the specimen had an oddly whorled abdomen at 2nd or 3rd instar but did not notice the cause until a few molts prior to adulthood (pers. comm. 2020). It successfully molted to maturity as depicted here (Fig. 11). The wings and rear legs are slightly deformed but functional. The whirled abdominal shape (Fig. 12),



Fig. 11. Same specimen after successful final moult to adulthood.

imperfect abdominal margins on the lower left side of the conjoined segments, and slightly mangled adult specimen suggest the crossing segments may not be the only developmental problems. The female molted to maturity (2-19-2021) and died shortly after (3-10-2021) without producing any eggs.

Several oddities including antennae replaced with legs (antennapedia gene complex also seen in *Drosophila* and Orthoptera) and an egg found in 1924 that hatched successfully into a conjoined monstrosity of the laboratory stick insect *Carausius morosus* have been documented (Cappe de Ballion 1927). There is also a specimen of *C. morosus* from 1968 with fused right middle and hind legs that died after hatching (Pijnacker 1968). Sometimes eggs are malformed, but rarely a female produces only malformed eggs. I have not been able to locate literature reporting asymmetric segment deformities in phasmids, though by themselves they may not rise to the level of a special report. More recently Dryer (2020) collated and reviewed reports on phasmid gynandromorphy (Fig. 13).

Insect teratology in general:

In many cases it can be difficult to tell if unusual deformities are the result of genetic defects (homeosis) or developmental problems resulting from a trauma in early development (heteromorphosis). Discovering which developmental oddities are caused by genes versus damage is part of the goal of research into teratology. Cockayne (1930) documented wing



Fig. 12. Same specimen photographed from the side demonstrating the ensuing abdominal whorl due to the segmental abnormality.



Fig. 13. Subadult gynandromorph of *H. dilatata*.

deformities in hundreds of specimens of various butterfly species with unusual deviations but also unusual eye development in carabid ground beetles and unusual mutations in laboratory fruit flies. In addition to many reports in journals, entire books have been dedicated to beetle teratology (Asmuss 1835) and insects across various orders (Cappe de Ballion 1927). Research into unusual development in insects has a long history and is responsible for much of our understanding of the genes that regulate development of anatomical structures. The fruit fly *Drosophila melanogaster* has long been a model of genetic study including the way homeotic genes structure development. Researchers have isolated a gene that causes legs to grow where the antennae should be and another where the antennae are replaced by wings. In one of the most visible, the mesothorax is enlarged and the halteres become a second pair of fully grown wings. These mutations in the homeotic genes were discovered in the 1920s (Cockayne 1930) and are still maintained in laboratories today.

The most documented and fantastic cases of insect teratology are the gynandromorphs (Asmuss 1835; Cappe de Ballion 1927; Ross and Cochran 1967; Brock 1999; Ditzel and Larsen 2003; Bergström 2006; McMonigle 2016; Dryer 2020; etc.), especially the bilateral forms. Gynandromorphy is inheritable in the sense that it is more common (or more commonly survivable) for some species than others, but it is not directly inheritable since examples are nearly always, if not always, infertile (Dryer 2020). Conjoined segment deformities might be directly inheritable, but they

are basic, structural monstrosities as uncommon as gynandromorphs and conjoined twins for most arthropods other than pseudoscorpions.

Asymmetric segment deformities seem like they should be a bit more common than gynandromorphs because they can probably produce offspring, but it is a similar failure to develop correctly in the earliest developmental stages when anatomical structures begin to line up.

Conclusion

Teratology, the study of abnormalities of physiological development, is a wide-ranging area of study of organisms. Arthropods with conjoined body segments are an interesting area that deserves further study due to the scarcity of data. Specifically, though I have never purposefully concentrated on segment abnormalities, I believe them to be an inheritable trait caused by a mutated or missing homeotic gene. Since abnormalities are more common for certain species or types of animals (i.e., pseudoscorpions) it seems likely to be the case that these abnormalities indicate a genetic predisposition and not just environmental influence. Alternatively, they could be indirectly inheritable like the likelihood for gynandromorphy, an inherited propensity for segments to form improperly in early development under the influence of multiple genes and small or large changes in environmental variables. In the past (with the exception of *Dynastes tityus*) I have purposefully removed malformed specimens from the breeding pool because I believed it would prevent further "defective" specimens from emerging, even though I do not know for certain if such specimens could reproduce or if the defect was inheritable. Multigenerational breeding, if possible, would prove or disprove heritability of this trait. In addition, thorough documentation of the prevalence of segmental teratology could improve our understanding of this unusual developmental malformation and aid in the understanding of other defects which, though more common, are less often seen due to their lethality during hatching, feeding or growing.

I think the prevalence estimates presented here would bear out in larger studies of the same species (with exception of *D. tityus*) but I am curious if there are any documented cases published for centipedes, segmented spiders, or others. Asymmetric segment deformities may be more common but commonly overlooked.

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Mammalian islanders and dung beetles: a clarification

by

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In a recent paper (Cupello et al., 2020), some colleagues and I tackled the issue as to why dung beetles (Scarabaeinae), though widespread on continents, are absent from most oceanic islands. The exceptions, as then known to us, were the well-known, rich scarabaeine fauna of the oceanic Antilles (Matthews 1966; Peck 2016) and the five-species community on Mauritius, a small volcanic island in the Indian Ocean Mascarene archipelago, circa 900 km east of the coast of Madagascar (Vinson 1946, 1947, 1951, 1958; Martínez and Pereira 1959; Motala and Krell 2007; Davis 2009). These five Mauritius species all belong to two genera endemic to the island, four in *Nesosisyphus* Vinson, 1946 (Sisyphini) and one in *Nesovinsonia* Martínez and Pereira, 1959 (incertae sedis in Scarabaeinae). Since the publication of our work, more scarabaeines have been reported from the other two main Mascarene islands: Rossini et al. (2021) described *Epactoides giganteus*, a new species putatively from Réunion, and reported the finding of 12 scarabaeine subfossils on Rodrigues. Apart from the Antilles and the Mascarenes, no dung beetles are known to occur on oceanic islands except for those introduced by humans (e.g., in Hawaii; Nishida 2002).

One of the factors pointed out by us to explain the virtual lack of scarabaeines from oceanic islands was the supposed absence on such islands of any native land mammals that could provide dung beetles with excrement and, therefore, food. On page 64, we stated that neither Mauritius, the Galapagos, nor Hawaii have ever had any autochthonous land mammals. This is incorrect. Each of those island/archipelagos has its living native terrestrial mammalian species (Wilson and Reeder 2005; Weksler et al. 2006; Gardner 2008; Goodman et al. 2008; Probst and Sanchez 2015; Pinzari et al. 2020) (Fig. 1). The Mascarenes, including Mauritius, have the greater Mascarene



Fig. 1. Land mammals from oceanic islands. A–B) Two of the three bat species inhabiting the Mascarenes: (A) The greater Mascarene flying fox (*Pteropus niger*) and (B) the Mauritian tomb bat (*Taphozous mauritanus*). C) The sole representative on the Hawaiian islands, the Hawaiian hoary bat (*Lasiurus semotus*). D–F) A selection of the Galapagos fauna: (D) The red bat (*Lasiurus blossevillii*), (E) the hoary bat (*Lasiurus cinereus*), and (F) the Galapagos rice rat (*Aegialomys galapagoensis*). All images from Wikipedia. See references.

flying fox (Chiroptera: Pteropodidae: *Pteropus niger* (Kerr, 1792)), the Mauritian little mastiff bat (Molossididae: *Mormopterus acetabulosus* (Hermann, 1804)), and the Mauritian tomb bat (Emballonuridae: *Taphozous mauritanus* Geoffroy Saint-Hilaire, 1818). The Hawaiian islands have a single species, the Hawaiian hoary bat, *Lasiurus semotus* (Allen, 1890) (Chiroptera: Vespertilionidae). And the Galapagos harbors the Galapagos rice rat (Rodentia: Cricetidae: *Aegialomys galapagoensis* (Waterhouse, 1839)), the Fernandina rice rat (*Nesoryzomys fernandinae* Hutterer and Hirsch, 1979), the indefatigable Galapagos mouse (*N. indefessus* (Thomas, 1899)), the Santiago Galapagos mouse (*N. swarthi* Orr, 1938), the red bat (Chiroptera: Vespertilionidae:

Lasiurus blossevillii (Lesson and Garnot, 1826)), and the hoary bat (*Lasiurus cinereus* (Beauvois, 1796)). Other, now extinct species – most, if not all, vanished after human arrival – have also been recorded from each of these islands (Ziegler et al. 2016, and references above)¹.

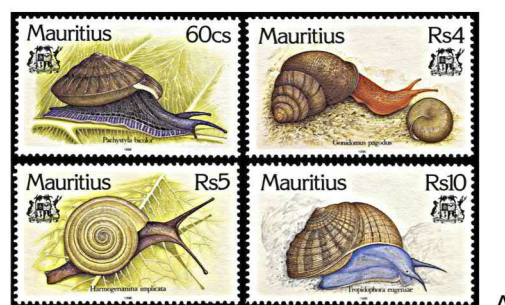
But in spite of these previously overlooked facts, our point still stands: coprophagous scarabaeines usually rely on the dung of medium- to large-sized herbivorous or omnivorous mammals. Only a minimal fraction of them feeds primarily on the excrement of either small-sized rodents or insectivorous bats, and the few that do are greatly localized in both geography and ecology (Halffter and Matthews 1966; Zunino and Halffter 2007). Except for the Mascarene flying fox (Nyhagen et al. 2005), all the other mammals present in the Macaranes, Hawaii, and the Galapagos fall in either of these two categories of small rodents or insectivorous bats (cf. Fenton et al. 1980; Whitaker and Tomich 1983; and the aforementioned references). Therefore, unless the potential colonizer were one of those extremely specialized dung beetles, the existence of these particular mammal species in Hawaii and the Galapagos does not invalidate our point that it was the lack of a suitable mammalian fauna – not any mammalian fauna – that has possibly prevented dung beetle castaways from establishing new populations in these archipelagos.

On the other hand, the colonization of the Mascarenes by at least two independent scarabaeine lineages now makes much more sense in light of the presence of flying foxes in them. These megabats, like most others, are not insectivorous, but frugivorous (Nyhagen et al. 2005), and perhaps, instead of the excrement of birds, giant tortoises, and snails as previously hypothesized (Vinson 1947, 1951; Halffter and Matthews 1966; Cambefort 1991; Cupello et al. 2020; Lopes et al. 2023; Fig. 2), which are equally unusual food sources for most Scarabaeinae, flying fox dung was what fed the newly arrived colonizers. If this is correct, then the Mascarene case would be an exception that proves the rule in the proper meaning of the expression (cf. Gould 1980): in spite of their limited flying capability, dung beetles were able to colonize the Mascarenes precisely because, unlike many other oceanic islands, they have a mammalian fauna suitable for the beetles' survival needs. In this scenario, flying fox dung may have

provided a stepping stone – or a life buoy – that allowed the colonizing dung beetles to settle themselves and establish a founding population on the islands. With time, they gradually broadened their feeding habits to include the dung (and carcasses) of the other, more diverse organisms present on the islands, such as birds, tortoises, and snails. In the process, they may have even lost their ancestral capacity of (or at least preference for) feeding on flying fox dung. Indeed, present-day Mauritius dung beetles have been recorded feeding on the excrement of native and introduced snails, a few introduced vertebrates, including chickens and the crab-eating macaque (*Macaca fascicularis* Raffles, 1821), and that of humans, but they have yet to be observed consuming flying fox dung (Vinson 1946, 1947, 1951; Halffter and Matthews 1966; Motala and Krell 2007; Lopes et al. 2023).

If my hypothesis is correct, feeding on the dung of continental herbivorous/ omnivorous/ frugivorous mammals was a pre-adaptation to feeding on insular frugivorous flying fox dung. If the only Chiroptera living on the Mascarenes were insectivorous ones, the colonizing scarabaeines would not have found a similar food source to that which they were already adapted in their ancestral continental home and their chances of surviving and founding a new population would be small. But the existence of flying foxes in the archipelago provided the right conditions for dung beetles first to establish and, then, with time, the opportunity to broaden and adapt their feeding habits to coprophagy on the abundant sauropsid and snail dung and/or necrophagy on their carcasses. Other oceanic islands, lacking both medium-sized mammals and flying foxes, could not provide this first, transitional step for the colonizations by dung beetles, and so they remained uninhabited by them until humans eventually established populations of both mammals and dung beetles over the last few centuries².

A possible way of testing my hypothesis is to offer in a controlled environment the different sorts of dung available on the islands to individuals of the closest continental relatives of the Mascarene dung beetles. My hypothesis predicts that they will prefer flying fox dung over that of reptiles, birds, and snails. If this is confirmed, then we can expect that the same was likely true for the ancestors of the Mascarene scarabaeines and that, upon their arrival in the archipelago, they did rely on megabat excrement as I imagine, only later expanding to the other available food sources.



A



B



C



D

Fig. 2. The original food providers? Some of the animals on whose excrements or carcasses the colonizing dung beetles have been hypothesized to have relied upon their arrival on Mauritius. (A) The island's several native snails, some of which have since become extinct. Here illustrated by a collection of postage stamps issued in 1996 by the Mauritian postal service. (B) The dodo (*Raphus cucullatus*), a now-extinct member of the Mauritian indigenous bird fauna. Vinson (1951) stated that whereas the dodos lived in the lowlands, the native dung beetles are found exclusively in the mountains; for this reason, he dismissed the idea of an association between the two groups. But what if the alleged dung beetle endemism to the mountains, even if correct, is secondary, a recent anthropogenic phenomenon due to the deforestation of the lowlands? Bird species proposed as candidate food providers by Vinson were the broad-billed parrot (*Lophopsittacus mauritianus*), the Mauritius scops owl (*Otus sauzieri*) and the Réunion harrier (*Circus maillardi*), all of which are now extinct, if not globally, at least on the island. The dodo illustration is a 1626 chalk drawing by the Dutch Golden Age painter Jan Savery (1589–1654), one of the most iconic depictions of the species, presently preserved in the E.B. Crocker Art Museum, Sacramento, California. Reproduced from Wikipedia. (C) The saddle-backed (*Cylindraspis inepta*) and (D) domed (*C. triserrata*) Mauritius giant tortoises, both of which became extinct, like the dodo and the island's other giant birds, following the arrival of humans in the 16th century. Paintings by Julian P. Hume, reproduced by his courtesy. Réunion and Rodrigues, too, had their own giant tortoises.

But there are three ways in which the experiment may falsify my hypothesis. First, it may show that these continental dung beetles (and, by extension, the ancestors to the modern insular community) are not able to survive or reproduce relying exclusively on either sauropsid or flying fox dung, or that they are not even attracted to them. This would rule out not only my hypothesis of ancestral reliance on flying fox dung, but also the idea that the colonizers established themselves exploiting sauropsid and snail excrements. But how could they have colonized the Mascarenes, then? Necrophagy might be the answer, but this, too, would need further testing using a similar protocol. Perhaps the “life buoy”, the first step in the adaptation to an island life was not feeding on flying fox dung as I propose, after all, but on carcasses, enabling a later adaptation and expansion to the indigenous reptile, bird, and snail dung. The second way that the experiment may fail to support my hypothesis is exactly the opposite: continental dung beetles being attracted indiscriminately to all sorts of dung. While this would confirm that the colonizing ancestors did have the capacity of feeding on flying fox dung as I propose, their generalist nature would hardly indicate an exclusive reliance on this kind of dung. The third and final way the experiment may falsify my hypothesis is if flying fox dung proves not to be suitable, but sauropsid’s does. Should this be the case, the hypothesis sustaining that the colonizing ancestors relied on sauropsid dung since their arrival in the archipelago, including that of the giant tortoises (Cupello et al., 2020; Lopes et al. 2023), will be greatly supported. It may be that the plasticity of at least some dung beetles of occasionally feeding on reptile dung even where mammals exist (see Lopes et al. 2023) was also present in the early colonizers and this pre-adapted them for an insular life without mammals. If confirmed, this would rule out the “hard” idea that the presence of a “suitable” mammalian fauna is necessary for scarabaeine colonization, leaving only a “softer” hypothesis that such fauna facilitates colonization.

And how did these dung beetles get to the Mascarenes? That this happened through overwater jump dispersal does not seem to be contentious (Scholtz 2009; Cupello et al. 2020; Rossini et al. 2021, 2022), and the way that they did so was likely by rafting (Cupello et al. 2020). Our knowledge about the exact history of each of

the three dispersal episodes is, nevertheless, still quite uneven. Very little is known about the phylogenetic relationships of *Nesosisyphus*. Due to its rarity in collections, the genus has not been included in the main phylogenetic studies of the Sisyphini so far performed (Barbero et al. 1991; Daniel et al. 2020). According to Vinson (1951), however, its closest living relatives live in India and Sri Lanka, which would suggest that the concestor³ of the genus came to Mauritius from the northeast, crossing ~4,000 km of open Indian Ocean (Fig. 3A). The alternative possibility that this crossing was made through island hopping across the islands of the Chagos-Laccadive Ridge or the Mascarene Plateau seems unlikely. Even though many of these islands may now be sunken and have consequently lost their land biota, no dung beetles exist on any of those that are still above water and could have served as “intermediate stops” for such an island-hopping ancestor, including the Seychelles, the Maldives, and the Chagos archipelago. It would be necessary to believe that these ancestral populations became extinct on each of these intermediate islands and only remained as living organisms or subfossils in the Mascarenes, a scenario unsupported by available evidence. So, if Vinson’s phylogenetic ideas are correct (and this is a big “if”), my hypothesis is indeed of a single rafting episode from continental India or Sri Lanka towards the Mascarenes. But note that Scholtz (2009), without explaining why, asserted in passing that the concestor of *Nesosisyphus* dispersed “probably from Africa”, which would require a shorter, but still impressive ~3,000-km voyage on a raft (Fig. 3A). For an African origin to be correct, nevertheless, Vinson’s hypothesis of a close relationship with Indian species must probably be mistaken.

As for *Epactoides giganteus*, available evidence indicates that, if it indeed ever existed in the Mascarenes (see Rossini et al. 2021 for the possibility that the only known specimen may be mislabeled), it came from from the west (Fig. 3B). Departing from the eastern African coast, the concestor of the whole genus *Epactoides* Olsoufieff, 1947 crossed the Mozambique Channel and reached Madagascar around 32 to 29 million years ago (Rossini et al. 2022). There, like so many other lineages that dispersed from Africa to Madagascar, from plants to lemurs to chameleons to frogs to other dung beetles (cf., e.g., Yoder and

Nowak 2006), *Epactoides* experienced considerable radiation, giving rise to at least 37 modern species (Schoolmeesters 2023). Then, at some moment over the last 3.4 million years, departing from Madagascar, one of its members – either *E. giganteus* proper or an ancestor – dispersed eastward overwater yet again, this time reaching Réunion, more than 700 km from the Malagasy coast (Rossini et al. 2022).

Finally, the exact origin of *Nesovinsonia vinsoni* is much less clear. Paulian (1976) hypothesized that, within a taxon that he called “longitarse Canthonina”, *Nesovinsonia* would be close to the eastern African endemic *Grebennikovius basilewskyi* (Balthasar, 1960) and a group of species that are now placed in *Epactoides*. Since *G. basilewskyi* and *Epactoides* are sister taxa, both placed in the tribe Epactoidini (Rossini et al. 2022), if Paulian is correct about their close affinity with *Nesovinsonia*, the latter genus should belong to this tribe as well and may even prove to be nested within *Epactoides*. Should the latter be true, then the endemism of *Nesovinsonia* on Mauritius likely represents a second overwater dispersal from the *Epactoides* cradle, Madagascar, towards the Mascarenes (Fig 3C, hypothesis 1). But if *Nesovinsonia*, while close to the clade *Grebennikovius+Epactoides*, is shown not to be nested within it, then perhaps it either somehow dispersed directly from Africa to Mauritius (Africa was the cradle of the Epactoidini; Rossini et al. 2022; Fig. 3C, hypothesis 2) or perhaps its ancestor, like that of *Epactoides*, rafted first from Africa to Madagascar, and then from Madagascar to Mauritius, subsequently becoming extinct on Madagascar (Fig. 3C, hypothesis 3). In the latter case, *Nesovinsonia* may be a relict genus, a paleoendemic, if it originated and radiated while still on Madagascar and only remained to modern times in the form of the Mauritius *N. vinsoni*. A further possibility is that the phylogenetic affinities of *Nesovinsonia* are not, after all, with *Grebennikovius+Epactoides*, but with the third genus in Epactoidini, *Ochicanthon* Vaz-de-Mello, 2003, from the Oriental Region (cf. Krikken and Huijbregts 2007), or even somewhere else among the Scarabaeinae. In such case, from where exactly the genus may have come is mysterious to me, and I would not rule out a possible origin from the Sunda Islands, especially if an *Ochicanthon* relationship is revealed (Fig 3C, hypothesis 4).

And, then, we have the Rodrigues subfossils. At

least based on the paucity of information available in the literature (Rossini et al. 2021), their identity is completely mysterious. Is it possible that they represent a fourth dispersal event towards the Mascarenes? If so, from where? Or are they the result of intra-archipelago dispersal, representing relatives of *Nesovinsonia*, *Nesosisyphus* or *Epactoides giganteus*? Only empirical investigations on the subfossils themselves may tell.

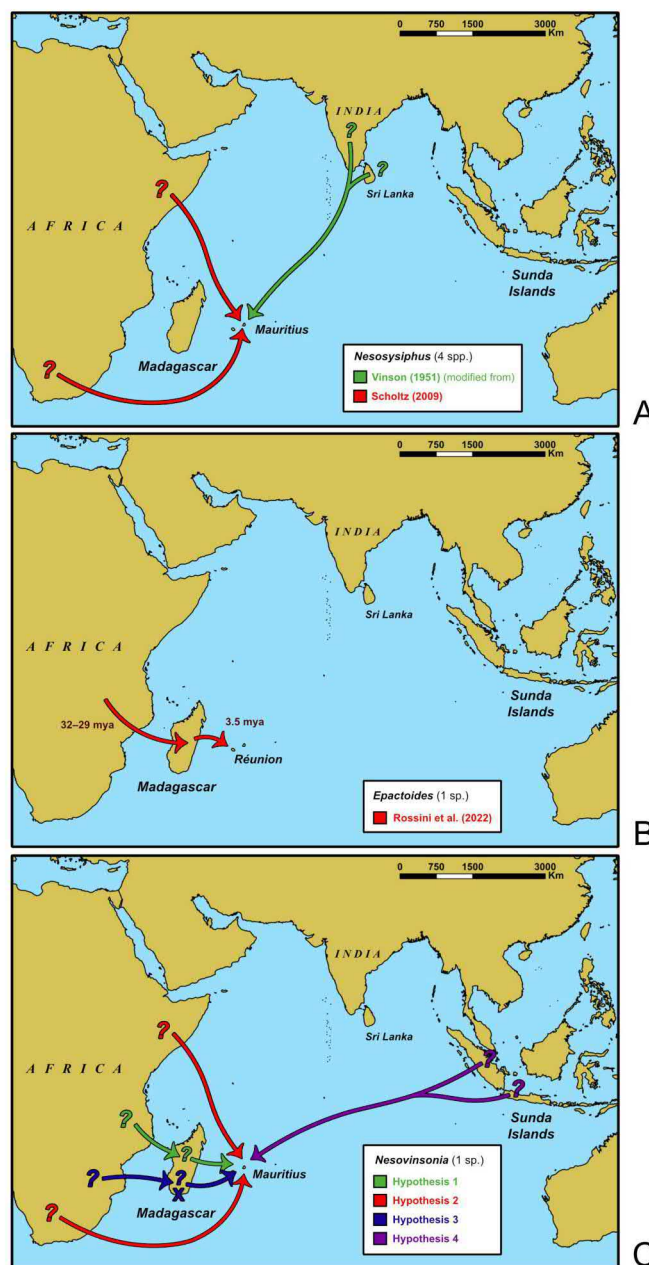


Fig. 3. Where did the Mascarene dung beetles come from? The (possible) dispersal paths of *Nesosisyphus* (A), *Epactoides* (B), and *Nesovinsonia* (C) toward the archipelago. See text for more details.

Glossary

Connective dispersal	Dispersal with the preservation of population connectivity, resulting from the collapse (i.e., disappearance) of a dispersal barrier (cf.). In the absence of this barrier, the metapopulation advances into the area which was previously unoccupied by it in a continuous fashion, without disrupting population (i.e., reproductive) connectivity and breaking up into geographic isolates (cf.). This dispersal may or may not result in the expansion of the range of the metapopulation (see "dispersal"). Connective dispersal stands in opposition to disruptive dispersal (cf.): while, as said, connective dispersal is dispersal by a single metapopulation continuously advancing its range without breaking up and, thus, maintaining population connectivity, disruptive dispersal is the foundation of a new, isolated metapopulation by movement over or through a geographic barrier, disrupting population connectivity.
Dispersal	The process through which an organism, (meta)population, subspecies, species, or any other taxon comes to occupy a geographic area where it was not previously present. The dispersal to this new area may increase its range (range expansion) or result in the relocation of the range (e.g., the size of the range may continue the same, but it can move north- or southward due to climatic oscillations). Dispersal can happen while population connectivity is maintained (connective dispersal) or by creating new, isolated populations (jump or disruptive dispersal).
Dispersal barrier	Any environmental restrictions, whether biotic or abiotic, preventing successful dispersal. If this dispersal barrier prevents an organism or taxon from reaching an area which otherwise would be successfully occupied, this dispersal barrier is also a geographic barrier (cf.).
Disruptive dispersal (or jump dispersal)	Dispersal with a break in population connectivity. This happens when an organism or group of organisms establishes a new population after crossing a geographic barrier (cf.) that proved not to be completely impermeable, but also not permeable enough to maintain, after dispersal, connectivity between the newly founded population and the ancestral population. Disruptive dispersal leads to disjunction in the range of the species and the formation of geographic isolates (cf.); a disjunction originating from disruptive dispersal is here called halmapatric disjunction (cf.). If this leads to speciation, then we have a case of halmapatric speciation, a kind of allopatric speciation.
Geodispersal	Events of expansion of the range of a metapopulation as a consequence of the collapse of a geographic barrier (cf.). For example, the formation of the Isthmus of Panama led to the closure of the Central American Seaway and hence to the collapse of the geographic barrier that once isolated the faunas of North and South America; as a result, geodispersal in both directions became possible, leading to the formation of mixed biotas. Geodispersal is a sub-kind of connective dispersal. If, in its advance, the metapopulation meets a conspecific geographic isolate, they will interbreed and a zone of secondary contact will be formed. Source: Lieberman & Eldredge (1996), as "geo-dispersal".
Geographic barrier	Any environmental feature preventing the movement of organisms between two or more geographic areas that would otherwise be successfully occupied. Geographic barriers can be abiotic features such as rivers, oceans, and other bodies of water, mountain ranges, deserts, and alike, or biotic elements, such as the presence of a highly lethal predator or parasite or the absence of a host species or otherwise an organism on which the would-be-disperser depends for living. Geographic barriers may be species-specific (a feature may be a barrier to a snail but not to a bird, and vice-versa), as well as specific to ontogenetic stages or even sexes; e.g., a river may be a barrier to an apterous female beetle, but not to the flying male, or open water may be a barrier to benthonic invertebrates as adults, but not to their gametes or planktonic larvae.
Geographic isolate	Conspecific populations isolated from one another – i.e., prevented from exchanging genes – by a geographic barrier (cf.). They can be formed either through an episode of disruptive dispersal (i.e., the crossing of an already established barrier) or through vicariance (the formation of a new barrier across a previously continuous metapopulation). Geographic isolates formed by the former process are in halmapatric disjunction (cf.), whereas those formed by the latter are in vicariant disjunction (cf.). Source: I am not sure who coined the expression "geographic isolate", but I took it from Mayr (1963), though his definition is slightly distinct.
Halmapatric disjunction	Geographic disjunction originating from an episode of disruptive dispersal (cf.); i.e., from the dispersal through an already established geographic barrier. It stands in opposition to vicariant disjunction (cf.). Source: My neologism. The word derives from the Ancient Greek noun ἄλμα (háлма), meaning "jump", "leap", "spring", plus the termination "patric", from the Ancient Greek πατρία (pátrā), meaning "native land", "fatherland". The latter has been commonly used in the formation of terms associated with speciation, population structure, and biogeography ever since Mayr (1942) revived Poulton's (1903: xc, 1908: 62) then-forgotten term "sympatric" and coined its antonym, "allopatric".
Island hopping	The same as stepping-stone dispersal (cf.).
Jump dispersal	The same as disruptive dispersal (cf.).
Long-distance dispersal	Disruptive dispersal over a wide geographic barrier, usually – but not necessarily – employed to refer to transoceanic dispersal, a particular kind of overwater dispersal (cf.).
Overwater dispersal	Dispersal over a body of water. It usually refers to disruptive dispersal (cf.); i.e., when the body of water represents a geographic barrier making successful dispersal over it unlikely.
Stepping-stone dispersal (or island hopping)	Disruptive dispersal from island to island across an island chain. Each dispersal episode is short, since the islands are not far from one another, but, in combination, these sequential episodes of short disruptive dispersal may lead to a wide expansion in the range of a species.
Vicariance (or vicariant event)	The formation of a geographic barrier across the range of a previously continuous metapopulation, so disrupting reproductive connectivity and creating geographic isolates.
Vicariant disjunction	Geographic disjunction originating from a vicariant event (cf.); i.e., from the formation of a geographic barrier within the previously continuous range of a species. Vicariant disjunction stands in opposition to halmapatric disjunction (cf.).

Table 1. My definition for biogeographic terms whose meaning may be unclear to readers or disputed in the literature. When known, I give the original source of the terms.

Endnotes

¹ Notice that we were not the only scarab workers to have made the mistake of saying that Mauritius was devoid of native land mammals. This error also appears in Halffter and Matthews (1966: 19; but on page 81 it is correctly said that there are bats on the island) and Cambefort (1991: 60).

² Though I am addressing true oceanic islands here, my discussion may prove useful to the study of dung beetle communities in other kinds of islands as well. New Caledonia and New Zealand, in particular, two other islands inhabited by scarabaeines, are not true oceanic islands – rather, they are microcontinents (i.e., continental fragments) once part of Gondwana –, but they equally lack native land mammals other than bats and their dung beetle fauna may also have had a jump-dispersalist origin (Davis 2009; but see Gunter et al. 2016, 2019 for two distinct, at least partly vicariant hypotheses). Therefore, from the perspective of someone interested in the biogeography of dung beetles, if their scarabaeine fauna indeed had a jump-dispersalist origin, they can be approached as virtual oceanic islands, their geological origin notwithstanding. Flying foxes, however, are also present in New Caledonia, and perhaps the process we propose here for the Mascarenes may have occurred there as well. New Zealand, in contrast, is inhabited only by Microchiroptera; unless the founding dung beetles consumed these microbats' droppings, they must have relied since the beginning on food other than mammalian excrement. The New Zealand scarabaeines may, thus, be a true exception to the “rule” that the colonization of isolated islands by dung beetles is prevented by their lack of a suitable mammalian fauna.

One must also keep in mind, however, that the presence of a suitable mammalian fauna or the lack thereof is not the only factor determining the successful colonization of an oceanic island by dung beetles. Cupello et al. (2020) listed a number of other elements that play a role, including the size of the island. New Zealand and New Caledonia are among the largest of the microcontinents; their coastlines are fairly extensive and the probability of a castaway reaching them by mere chance is considerable, and this has indeed happened at least once on each. The Seychelles archipelago, on the other hand, comprises much smaller islands, both granitic (i.e., microcontinental) and tiny coralline ones; it is thus not surprising that, even though harboring two species of flying foxes (Hutson 2004; Wilson and Reeder 2005) and, hence, a potentially suitable mammalian fauna, they are not known to have ever been colonized by scarabaeines. The same goes for the equally tiny, oceanic (and suitable-mammal devoid) Galapagos and Hawaiian islands. But what about the Mascarenes and the Lesser Antilles? Are they not as small as them and, yet, have been colonized multiple times? Yes, but here, in addition to the presence of a potentially suitable mammalian fauna in the Mascarenes, another factor comes into play: the distance from the nearest mainland. Of these six small-island archipelagos – the Galapagos, Hawaii, the Mascarenes, the Lesser Antilles, and the granitic and coralline Seychelles –, two of the three closest to their nearest mainland, the Mascarenes and the Lesser Antilles, are precisely the ones that have been spontaneously colonized by scarabaeines, the exception being Aldabra, in the coralline Seychelles. This proximity to the mainland may have been particularly important to the Lesser Antilles, for they lack any native land mammals other than microbats (though including some frugivorous ones), a few now extinct rodents and, solely on the southernmost island, Grenada, a mouse opossum, a Plio-Pleistocene megalonychid sloth, and possibly an armadillo (MacPhee et al.

2000; Gardner 2008; Wilson and Reeder 2005; Turvey et al. 2010; Dávalos and Turvey 2012; Giovas et al. 2012; Defler 2019). It may be, therefore, that the Lesser Antilles are, like New Zealand, another true exception to the “rule” that a suitable mammalian fauna is needed for the establishment of new dung beetle populations; proximity to South America has subjected the islands to repeated episodes of dispersal and colonization, increasing the probability that, eventually, scarabaeines that were able to survive without mammals would arrive, survive, and establish a new population, and they did. Small as they are and having such an impoverished mammalian fauna, were the Lesser Antilles placed more distant from their biological source, they would probably have never come to host such a rich scarabaeine community.

In essence, the dynamics of over-water dispersal and island colonization by dung beetles must be approached as a multifactorial, probabilistic phenomenon, not a deterministic, all-or-nothing one. Even though small, the Mascarenes harbor potentially suitable mammals, so they have been colonized at least twice, possibly from both a relatively close biological source (Madagascar) and other, much more distant places (either the African continent, India, or even the Sunda islands; see the text). New Caledonia, too, has a potentially suitable mammal and is much larger than the Mascarenes, but is more distant from its nearest landmass (Australia) and has been colonized only once (Monaghan et al. 2007; Davis 2009; Gunter et al. 2019). New Zealand, in turn, lacks suitable mammals, but is quite large, thus it has also been colonized at least once (Monaghan et al. 2007; Davis 2009; Gunter et al. 2019). The Lesser Antilles are small and lack suitable mammals, but are very close to one another and to South America, so they have witnessed several independent colonizations (Matthews 1966; Davis 2009). The granitic Seychelles harbor flying foxes, but are small and relatively isolated and have never been colonized (Gerlach 2009). The coralline Seychelles also harbor flying foxes and are even smaller, and though closer to Africa, they, too, have failed to be colonized (Gerlach 2009). Finally, the Galapagos and Hawaii are small, isolated, and lack a suitable mammalian fauna; as a consequence, they offer the most unlikely odds of being colonized and, indeed, they have never been (Peck 2006; Nishida 2002). Further factors that must be taken into account by such analyses are the age of the island (oceanic ones are much younger), fluctuations in eustatic sea level (might be relevant not only for continental islands, but also for oceanic ones placed closer to continents and to one another such as the Lesser Antilles), tectonic movements (which may bring an island closer to or farther from biological sources), the direction of the wind and ocean currents, the incidence of volcanism and other natural hazards such as hurricanes that may increase extinction rates (and so lead to secondary absences), and, finally, sheer chance (Cupello et al. 2020).

³ The same as “the last common ancestor” or “the most recent common ancestor” of two or more taxa; i.e., the species or subspecies whose splitting represents the last common cladogenesis in the phylogenetic history of two or more taxa. This term was coined from the contraction of “common ancestor” by Nicky Warren, and first appeared in a publication in Dawkins (2004). I prefer it over its synonyms because it encapsulates into a single word the same concept that the others require three or four. The cumbersomeness of the multi-word expressions is such that authors usually boil them down to the abbreviations “LCA” or “MRCA” in technical texts.

However, in my opinion, these abbreviations are both artificial as far as speech is concerned (unlike DNA, COI, or CFC, I have never heard anyone pronouncing the abbreviation letter by letter instead of saying all the words in full), and make phylogenetic texts seem “cold” and more difficult to understand to the uninitiated. It is not a coincidence that the elegant term “concestor” was coined precisely for a text aimed at a general audience. But why not adopting it for technical works as well? I encourage colleagues to use it in their works and, at least until the term enters common parlance, to cite its original source (viz., Warren in Dawkins 2004).

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Fig. 1A: https://de.wikipedia.org/wiki/Maskarenen-Flughund#/media/Datei:Pteropus_niger_cropped.jpg;
author: Luis Correia (title: "Maskarenen-Flughund (*Pteropus niger*) im Flug").

Fig. 1B: https://en.wikipedia.org/wiki/Mauritian_tomb_bat#/media/File:Pair_of_Mauritian_Tomb_Bats.jpg;
author: Frank Vassen ("A pair of Mauritian Tomb Bats in Ankarafantsika, Madagascar").

Fig. 1C: https://en.wikipedia.org/wiki/Hawaiian_hoary_bat#/media/File:Hawaiian_hoary_bat_Lasiurus_cinereus_semotus.jpg;
author: Frank Bonaccorso ("Hawaiian hoary bat (*Lasiurus cinereus semotus*), USA").

Fig. 1D: https://pt.wikipedia.org/wiki/Lasiurus_blossevillii#/media/Ficheiro:Lasiurus_blossevillii.jpg;
author: United States National Park Service ("The desert red bat, (*Lasiurus blossevillii*) also known as the Western Red Bat, is one of many species of bats. This species has been found in North America, southern Canada, Central America and to the northern part of South America.").

Fig. 1E: [https://en.wikipedia.org/wiki/Hoary_bat#/media/File:Hoary_bat_Lasiurus_cinereus_\(cropped\).jpg](https://en.wikipedia.org/wiki/Hoary_bat#/media/File:Hoary_bat_Lasiurus_cinereus_(cropped).jpg);
author: Paul Cryan ("A hoary bat (*Lasiurus cinereus*) roosting on the branch of a tree.").

Fig. 1F: https://en.wikipedia.org/wiki/Aegialomys_galapagoensis#/media/File:Galapagos_Rice-Rat.jpg;
author: unknown ("Galapagos Rice-Rat (*Aegialomys galapagoensis galapagoensis*) Depiction from 'The Zoology of the Voyage of H.M.S. Beagle' by Richard Owen from the years 1838 to 1843").

Fig. 2B: https://en.wikipedia.org/wiki/Dodo#/media/File:Roelandt_Savery_-_Dodo_Birds'_Chalk_black_and_amber_on_cream_paper.jpg;
author: Roelant Savery ("Sketch of three dodos, known as "the Crocker Art Gallery sketch".").

Erratum to Cupello et al. (2020)

Typos or erroneous modifications were implemented in the manuscript previously or during copy editing and only noticed after publication. The most consequential for understanding the text are here rectified.

Pag. 29, first paragraph: Where it reads "[...] since Harold's 19th century specimen of *Colonychus* shows this darker ventral colouration [...]", should be read as "[...] since Harold's 19th-century '*Colonychus*' specimen shows this darker ventral colouration". What is meant is that the MNHN specimen labeled as "*Colonychus*" by Harold, which is discussed in a few separate passages in the article, has a darker ventral coloration, not that it belongs to a taxon named "*Colonychus*", of course.

Pag. 38, ecology section: In the sentence, "The data obtained by the latter authors also show that *S. streblopus* can be [...]", the specific name was mistakenly replaced by a repetition of the generic name. It should be read, as it correctly appears in the rest of the section, as "*S. opatroides*".

Pag. 54, table 1: The reference for the number of species of *Genieridium* Vaz-de-Mello, 2008 is "Vaz-de-Mello 2008", not "Vaz-de-Mello 2000" as mistyped.

Pag. 55, first paragraph: "[...] and, then, farther east [...]" should be read as "[...] and, then, farther west".

Pag. 56, table 3: *Pseudepilissus* encompasses 14 species (Viera et al. 2019), not 2 as stated.

Pag. 67, third paragraph: The word in bold in the sentence "Contrary to the allegations of many vicariance biogeographers that **allude** to dispersal events is a leap of faith and therefore "unscientific", [...]" should be read as "alluding". We are referring to the act of alluding to dispersal events by those who do this, not to a possible act of alluding to dispersal events by vicariance biogeographers (which would make no sense either in reality or in our argumentation).