

Article

Description of a Highly Modified Endemic Ground Beetle (Coleoptera, Carabidae) from the Oceanic Island of Malpelo, Colombia [†]

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urn:lsid:zoobank.org:act:DAB5E944-3D60-4CD0-B77D-AF09EB4DAF18;
urn:lsid:zoobank.org:act:2DC3945F-F194-404F-A575-668F014D2FE7.

Abstract: The oceanic island of Malpelo, 380 km west of the Colombian mainland, stands out from other islands of the Tropical Eastern Pacific by its harsh environment and depauperate flora and fauna, thus imposing strong selective pressure on the small number of invertebrates that inhabit it. The endemic taxon described here, *Dyscolus (Cacothrix) malpelensis*, n. subgen., n. sp. (Carabidae, Platynini), is a remarkable example of adaptation to this unique ecosystem. The modifications of its body shape, including a tight coaptation of elytra and pronotum, might be a response to strong environmental constraints, from predation by lizards and land crabs to the absence of deep soil that forces the beetle to seek shelter in caves and rock crevices.

Keywords: new species; new subgenus; Tropical Eastern Pacific; island speciation; harsh environment; morphological adaptation



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1. Introduction

The genus *Dyscolus* Dejean, 1831 is a highly speciose taxon of neotropical Platynini (Carabidae), distributed from Mexico to northern Chile, with 476 described species [1,2] and several hundreds of undescribed ones. Most members of *Dyscolus* live in tropical mountains, from the lower montane forest to the high altitude páramo, but some species are also found at low elevations in subtropical environments.

The presence of members of the tribe Platynini in remote oceanic islands, far off the coast of South America, has been known for a long time, thanks to the description of three endemic species from the Galápagos Islands, seventy years ago [3]. They were placed initially in the genus *Agonum*, then to *Platynus* by some authors [4], but key morphological traits, especially those of the female genitalia, appear to be characteristic of the *Dyscolus* supraspecific complex [5]. An undescribed “*Platynus*”—more probably a *Dyscolus*, according to the drawing published by Erwin [6]—has also been registered from Cocos Island, Costa Rica [7].

However, for decades, there has been no information on the presence of any ground beetle on the island of Malpelo, another emerged land mass in the Pacific Ocean off the American continent, about 380 km west of the Colombian mainland and 360 km south of Panama (Figure 1). The Malpelo Flora and Fauna Sanctuary was designated as a World Natural Heritage Site by UNESCO in 2006. It comprises 120 ha of insular land [8] and 857,150 ha of surrounding maritime zone [9]. The island is a rock formation, of volcanic origin, belonging to Colombia [8,10]. It is the only emerged portion of a submarine ridge

known as the Malpelo Ridge, which rises from about 4 km depth. This ridge is located in the Panama Basin and originated about 18 million years ago, in the Lower Miocene [11]. The eruptions that gave rise to this ridge are mostly basaltic of the tholeiitic type.

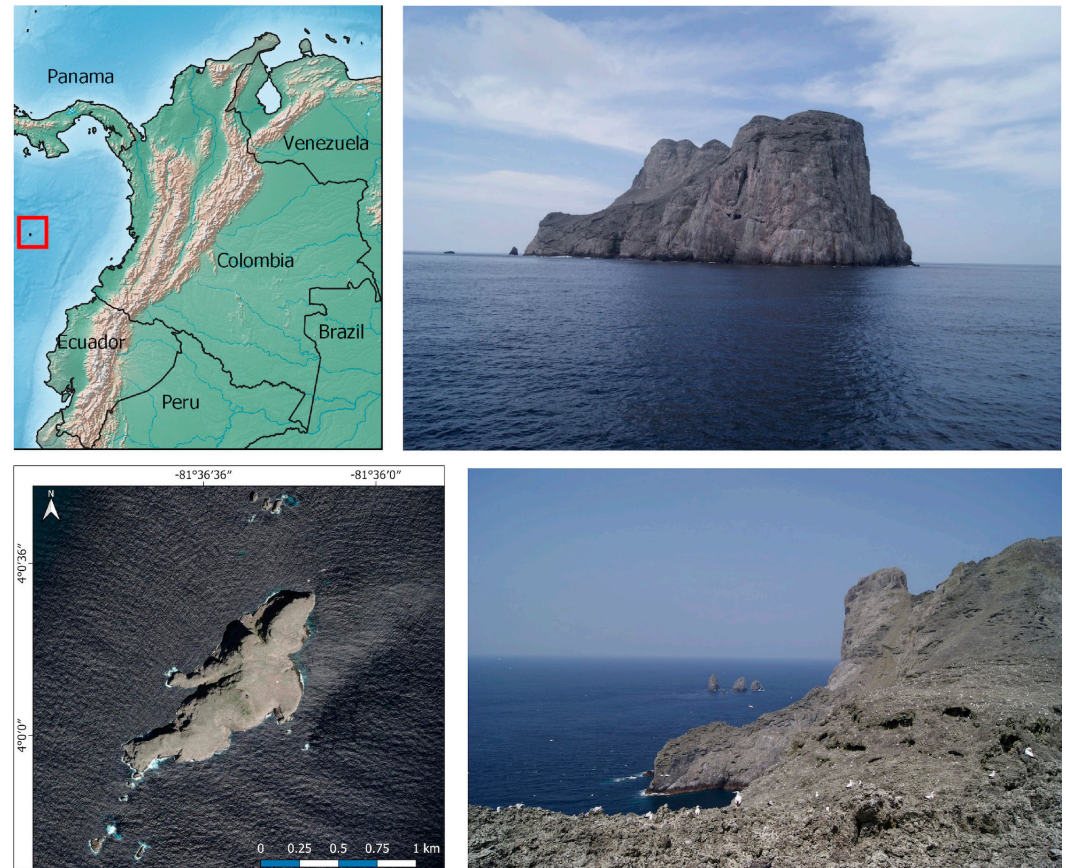


Figure 1. Situation map, vertical aerial photograph and views of Malpelo Island. The red square indicates the location of Malpelo.

Other oceanic islands of the Tropical Eastern Pacific (TEP), much bigger in size, profusely covered by vegetation, and exhibiting a high level of spatial and ecological heterogeneity, allowed many groups of terrestrial organisms to evolve with enough food sources. In contrast, Malpelo is small, almost devoid of superior vegetation, and ecologically homogeneous, which did not give way to similar processes, at least during the last few million years. A good example of this situation is the presence of endemic bird species on almost all the islands of the TEP, except Malpelo.

The first published record of the presence of a ground beetle species on Malpelo [12], based on specimens collected in 1998, briefly commented on its unusual morphology and the possibility that it could be a new and endemic species. Later, Calero et al. [13] studied the composition and trophic networks of macroinvertebrates of this island, reporting this species as part of the predatory guild. Upon first examination of the insect, it was immediately clear that this discovery was of special interest, not only for adding a new taxon to the island fauna but also, in the context of island speciation, because its impressive morphological evolution has no equivalent in the Galapagos and Cocos faunas.

The aim of this brief contribution is to describe the new taxon, provide information on its biology, and draw up preliminary hypotheses on its phyletic relationships and on the adaptive triggers of the modifications of its body shape.

2. Materials and Methods

2.1. Study Area

The topography of the island is irregular and there are no permanent water sources, despite an annual average rainfall around 2500 mm, a relative humidity above 70%, and mean annual temperatures around 28 °C [8]. The flanks of Malpelo are steep and the surfaces are irregular, with the presence of pebbles and boulders of different sizes (Figure 1). Small, scattered sectors of acid soils (pH: 2.7–5.1) are composed by a mixture of clay, organic material, and feces, mostly in sheltered areas and caves [8,10]. The scarce vegetation cover consists of a fern, some grasses, lichens, and microalgae. Lichens are the dominant component of the island's flora. The terrestrial fauna consists of seabirds, three endemic lizards, an endemic land crab, and 80+ other terrestrial macroinvertebrate species [13–15].

2.2. Material

This study is based on eleven specimens of the new taxon, collected between 2004–2013 on Malpelo island. Only the six ones collected in July 2013 are associated with detailed biological information. More material collected in the 1990s, not studied here, is likely kept at Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá [12]. The material examined in this study will be deposited at the following institutions:

IAvH: Instituto de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia.

MPUJ: Museo de Historia Natural de la Pontificia Universidad Javeriana, Bogotá, Colombia.

MUSENUV: Museo de Entomología de la Universidad del Valle, Cali, Colombia.

PMC: Pierre Moret Collection, University of Toulouse, France.

UNAB: Museo Entomológico de la Universidad Nacional Agronomía, Bogotá, Colombia.

2.3. Morphological Examination and Measurements

Specimens were examined, measured, and photographed using a Zeiss Stemi 508 trinocular stereo microscope coupled with a Zeiss AxioCam 105 microscope camera (at Toulouse university) and a Nikon SMZ 800-N stereo microscope coupled with a DSLR Camera Nikon-D5600 (at Universidad del Valle, Cali). Z-series of photographs were stacked using Helicon Focus Software version 4.2.9 (Helicon Soft Ltd., Kharkiv, Ukraine), then enhanced with Photoshop®. Images from scanning electron microscopy (SEM) were obtained using a Zeiss Evo 25 apparatus equipped with a lanthanum hexaboride (LaB₆) emission source. Images were acquired with a Cascade Current Detector (C2D) in low vacuum mode (pressure 30 Pa) at a working energy of 10 kV.

Measurements of body parts are encoded as follows: BL: overall body length from the apex of the mandible to apex of longer elytron; HL: length of head, measured along midline from anterior margin of clypeus to apex of neck, just before pronotum; HW: maximum width of head, including the eyes; AL: length of antennae measured as the sum of all the antennomeres; PL: length of pronotum from base to apex along midline; PW: maximum width across pronotum; EL: length of elytra, from base to apex of the longer elytron; EW: maximum width across both elytra; MLL: length of median lobe of males, measured from base to apex; SL: length of spermatheca; SGL: length of spermathecal gland.

3. Results and Discussion

3.1. Taxonomic Treatment

3.1.1. *Cacothrix* Moret & Arenas, subg. nov.

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Diagnosis: This subgenus is characterized by the combination of the following apomorphic characters, allowing separation from any other supraspecific division of the genus *Dyscolus*: body oval, tapered anteriorly, exhibiting a unique coaptation of acute humeri, concave base of elytra and convex base of pronotum (Figure 2); antennae and legs long and slender; absence of dorsal setae on elytra, pronotum, and head, except the posterior pair of supraocular setae; presence of specialized hyaline phanera at apex of the 4th tarsomere of

all tarsi (Figure 3); presence of a depressed area and a longitudinal smooth ridge on the ventro-apical surface of the aedeagal shaft (Figure 4). The single included species, described below, provides the basis for the subgeneric description.

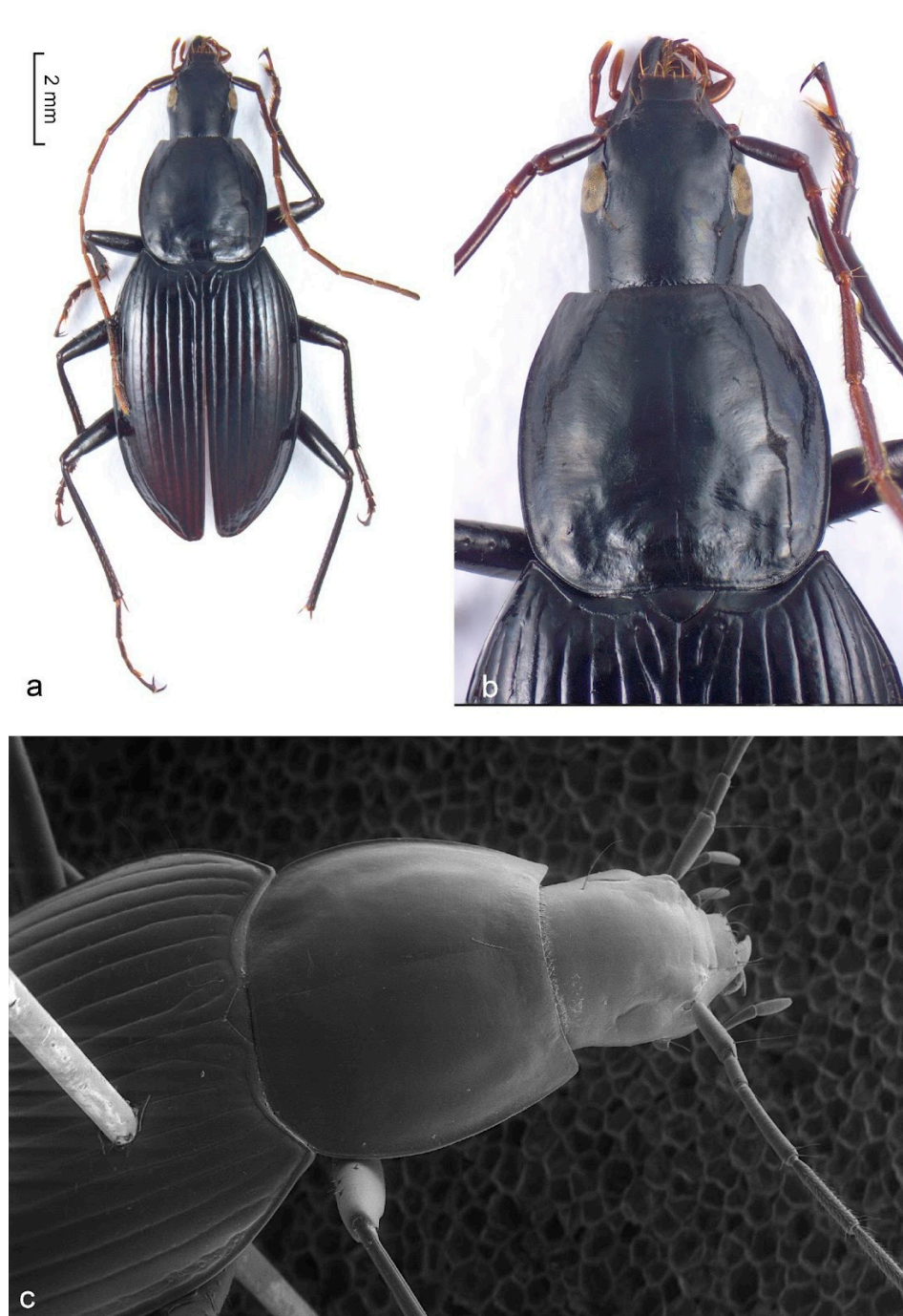


Figure 2. Habitus of *Dyscolus (Cacothrix) malpelensis*. (a) Male paratype, full picture; (b) detail of forebody; (c) SEM image of a female paratype.

Etymology: Noun formed on the Greek adjective *kakos*, meaning “bad” (*malo* in Spanish), and the Greek substantive *thrix*, meaning “hair” (*pelo* in Spanish), as a tentative Greek transposition of the Spanish name of the island. Actually, although *malpelo* may be understood as “bad hair”, the true etymology of the toponym is unknown. As *thrix* is feminine in Greek, the subgenus name is of feminine gender, according to Article 30.1.2 of the International Code of Zoological Nomenclature.

Geographic distribution: Endemic to Malpelo island.

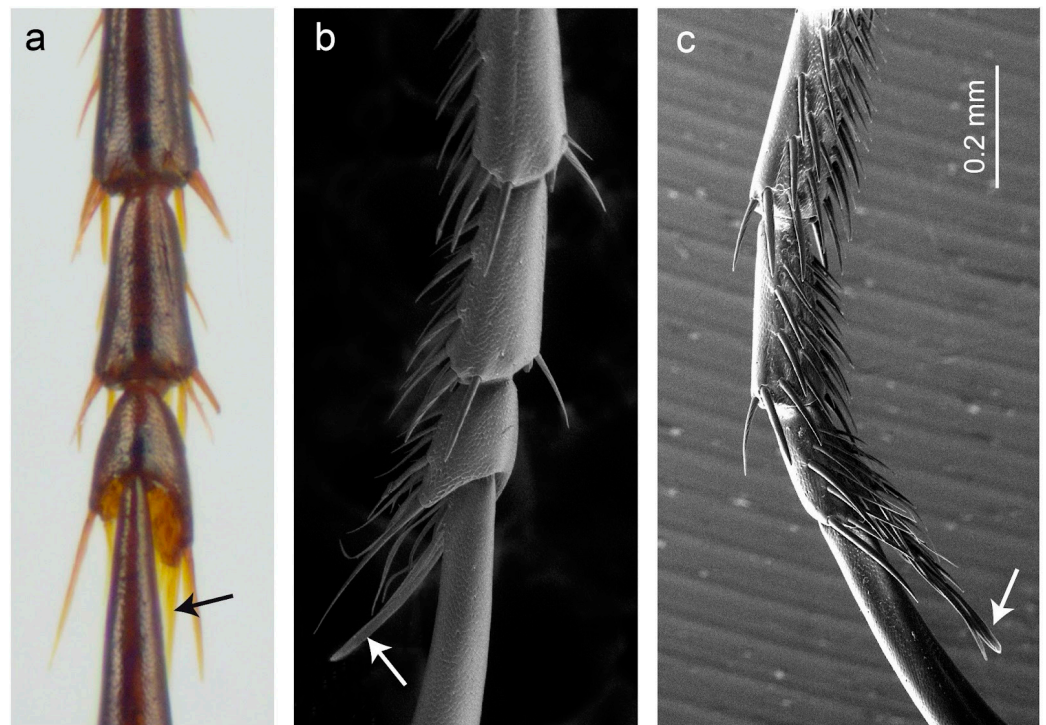


Figure 3. Metatarsus of *Dyscolus (Cacothrix) malpelensis*. (a) Right metatarsus, dorsal view; (b) the same, dorsolateral view by SEM; (c) left metatarsus, lateral view by SEM. The arrows point to the hyaline phanera of the fourth metatarsomere.



Figure 4. Aedeagus of *Dyscolus (Cacothrix) malpelensis*. (a) Median lobe in lateral view, parameres detached; (b) detail of the apex of the median lobe, dorsal view; (c) detail of the apex of the median lobe, ventral view.

3.1.2. *Dyscolus (Cacothrix) malpelensis* Arenas & Moret, sp. nov.

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Holotype: ♂, Colombia, Departamento Valle del Cauca, Buenaventura, Santuario de Flora y Fauna Malpelo, 4°00'5.98" N, 81°36'30.86" W, 0–330 msnm, en rocas, 24–25.VII.2013, M. López-Victoria leg. (MUSENUV).

Paratypes: 6 ♀, same data as the holotype (MUSENUV, MPUJ, IAvH, UNAB); 1 ♂, 1 ♀, Valle del Cauca, SFF Malpelo, bajo piedra, 14.VII.2004, leg. J. Zamudio (MUSENUV); 1 ♂, 1 ♀, Valle del Cauca, SFF Malpelo, 01.VI.2006, leg. D. Calero (MUSENUV, PMC).

Description: Overall body length: 9.6 to 12.6 mm. Body oval-shaped, tapered anteriorly, with very elongated appendages (Figure 2). Body tegument black and shiny, without metallic luster; microsculpture formed by a slightly impressed isodiametric mesh pattern on head and elytra, and a transverse, less distinct pattern on pronotum; ventral surface of body piceous; antennal segments 1 to 3, mandibles, and labrum reddish brown; antennal segments 4 to 11 and palpi light brown; legs with coxa, trochanter, and basal quarter of femora reddish brown; rest of the femora black, tibiae, and tarsi brown.

Head: HL 1.45 to 1.95 mm; HW 1.35 to 1.75 mm. Disc with a slightly impressed, polygonal, isodiametric microsculpture. Antennae very long; length 7 to 8.5 mm, AL/BL 0.61 to 0.76, longer in males than in females; antennomeres pubescent from the fourth. Eyes reduced, almost flat; temples very short, slightly more convex than the eyes, gradually fused with the neck. Only one pair of supraorbital setae, posterior to the eyes; dorsal surface of the head convex, without constriction between vertex and neck. Mandibles moderately robust, elongate, and slightly arcuate apically. Median tooth of the mentum simple, broadly margined, and subquadrate at apex; submentum with two pairs of setae.

Pronotum subovate (PL 2.45 to 3 mm; PW: 2.4 to 3.2 mm), as long as wide (PL/PW: 0.93 to 1.02), much wider than head (PW/HW: 1.67 to 1.85), maximum width at basal third. Sides evenly arcuate on their entire length; hind angles broadly rounded; anterior angles markedly protruding; lateral keel narrow and shallow, disappearing apically and reduced basally; basal margin straight, with full basal groove, basolateral depressions shallow. Pronotum surface faintly ridulate, microsculpture shallowly impressed on the pronotal disc, consisting of fine transverse meshes; median longitudinal groove thin and shallow. Lateral setae absent. Prosternal process rounded, not margined.

Hindwings vestigial, reduced to minute stumps. Elytra elongate (EL: 5.5 to 7 mm; EW: 3.5 to 4.6 mm; EL/EW: 1.45 to 1.53), broader than pronotum (PW/EW: 0.66 to 0.70); maximum width at middle; base abutting the posterior margin of pronotum, with acute humeri projected forwards and a concave basal margin mirroring the convexity of the pronotum. Striae deeply impressed from base to apex, without punctuation; parascutellar stria short, joined to stria 1 in most specimens, parascutellar pore present; striae 1 and 2 reaching the apex, stria 1 bearing one apical seta, stria 7 with preapical and apical setae; intervals 1–3 weakly convex, 4–8 flat; third interval without setae; preapical sinuation slightly marked. Microsculpture consisting of isodiametric to slightly oblong meshes, ca. 15 μ m wide. Setae of the umbilicate series varying in number, from 12 to 17, disposed as follows: an anterior group of 5 to 7 setae, 2 or 3 medially scattered setae, and a distal group of 5 to 9 setae. Metepisternum short, as long as wide basally. Posterior margin of the last visible abdominal ventrite evenly arcuate, bearing a pair of setae in males, two pairs in females.

Legs with fore coxae devoid of setae; middle coxae with one seta on outer margin and other near the middle; hind coxae with two setae near the outer margin; anterior and middle trochanters bearing one seta near the apex; hind trochanters short, about 1/5 the length of hind femora, bearing a hairlike seta near the middle. Dorsal and anterodorsal surface of the femora bearing a varying number of short, spiny setae: 9–13 on profemora, 11–16 on mesofemora, and 2–4 on metafemora; ventral surface with 1 (profemora), 3–5 (mesofemora), and 1 seta (metafemora). Tibiae bearing rows of setae throughout; anterior tibia with basal and distal spurs in cleaning organ subequal in size; middle and hind apical spurs subequal in size. Tarsi slightly depressed dorsally; dorsolateral sulci obsolete on protarsomeres 1–2, absent on protarsomere 3, well impressed on mesotarsomeres 1–3, and almost obsolete on metatarsomeres 1–3 (Figure 3). Protarsomere 4: apical lobes rounded, inner lobe 1.5 times longer than outer lobe; ventral surface medially with a dense vestiture of thin setae, laterally with two rows of longer setae; both lobes with two robust subapical setae and two long hyaline, spatuliform phanera. Mesotarsomere 4: apical lobes rounded, asymmetrical, and outer lobe 1.6 times longer than inner lobe; ventral surface medially with a dense vestiture of thin setae, laterally with two rows of more robust setae; two long subapical setae on the outer lobe, one subapical seta on the inner lobe; apex of both lobes

with two hyaline phanera. Metatarsomere 4 (Figure 3): apical lobes very asymmetrical, outer lobe elongate, 2.8 times longer than inner lobe; ventral surface glabrous basally, moderately setose distally, with a few ventrolateral more robust setae and a pair of long subapical setae; apex of outer lobe with two falcate hyaline phanera, narrower than on protarsi.

Male genitalia (Figure 4): median lobe curved (MLL: 2.3 mm; MLL/BL: 0.26); basal bulb not inflated; median shaft evenly curved; apex short, obtusely pointed; endophallus evenly covered with numerous small scales along the entire surface; presence of a depressed area and a longitudinal smooth ridge on the ventro-apical surface of the aedeagal shaft. Left paramere oval; basal outer lobe simple, not bifurcated apically; right paramere slender.

Female genitalia (Figure 5): laterotergite IX with 21 to 23 setae near apical margin, gonocoxite 1 with 4 or 5 setae in a row at apical margin, and gonocoxite 2 short and stout, with two lateral ensiform setae and one dorsal ensiform seta; bursa copulatrix quite large, divided into an almost cylindrical distal part and a much broader, wrinkled proximal part; median zone of the bursa covered all around by a band of spikelike microtrichia; spermatheca small, shorter than spermathecal duct (SL: 0.25 mm); spermathecal gland very large and sausage-like (SGL: 1.25 mm).

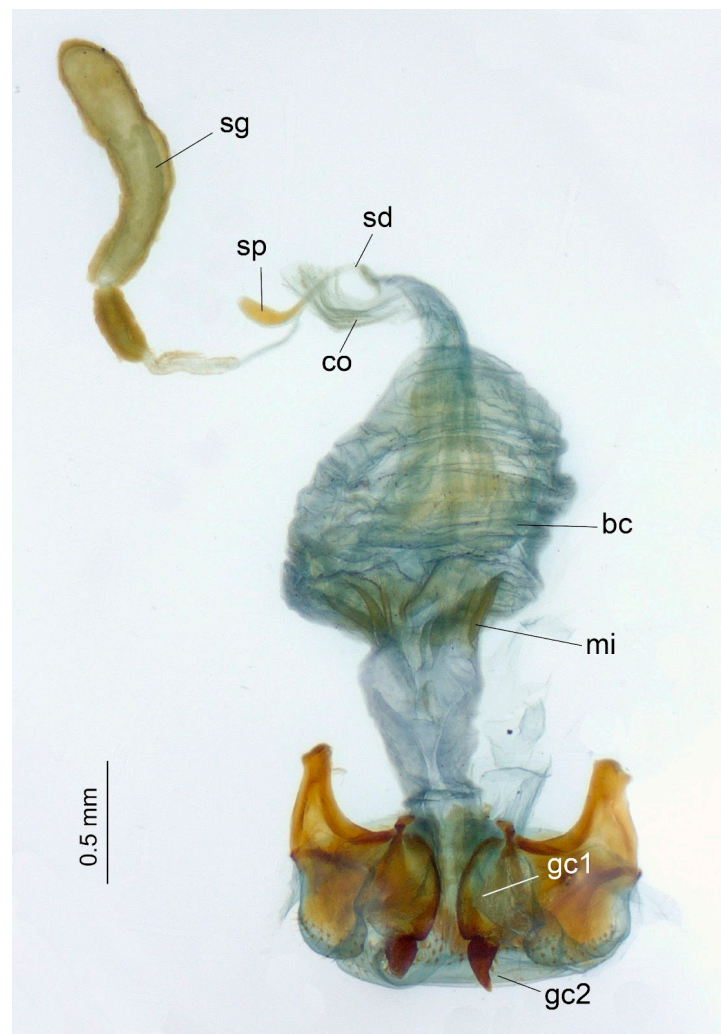


Figure 5. Female genitalia of *Dyscolus (Cacothrix) malpelensis*. bc: bursa copulatrix; co: common oviduct; gc1: gonocoxite 1; gc2: gonocoxite 2; mi: band of microtrichia; sd: spermathecal duct; sg: spermathecal gland; sp: spermatheca.

Sexual dimorphism: on average, females are larger than males (Table 1).

Table 1. Measurements of the new species.

	Female Specimens							Male Specimens			
	1	2	3	4	5	6	7	1	2	3	4
Body Length (BL)	12.6	12.5	11.6	11.3	11.2	10.1	10	11.1	10.6	10.1	9.6
Head Width (HW)	1.75	1.75	1.7	1.6	1.6	1.5	1.5	1.6	1.4	1.35	1.35
Head Length (HL)	1.85	1.8	1.6	1.5	1.95	1.5	1.7	1.65	1.5	1.5	1.45
Antennae Length (AL)	7.7	8.5	7.4	7.8	7.4	7.2	7.2	8.2	7.3	7.7	7.2
Pronotum Length (PL)	3	3	2.7	2.9	2.7	2.45	2.55	2.8	2.5	2.3	2.5
Pronotum Width (PW)	3.1	3.2	2.9	2.9	2.9	2.5	2.5	2.8	2.5	2.4	2.5
Elytra Length (EL)	6.9	7	6.6	6.3	6.5	5.5	5.5	6.1	5.8	5.5	5.6
Elytra Width (EW)	4.5	4.6	4.3	4.2	4.4	3.7	3.8	4.1	3.8	3.5	3.7
PL/PW	0.97	0.94	0.93	1.00	0.93	0.98	1.02	1.00	1.00	0.96	1.00
EL/EW	1.53	1.52	1.53	1.50	1.48	1.49	1.45	1.49	1.53	1.57	1.51
AL/BL	0.61	0.68	0.64	0.69	0.66	0.71	0.72	0.74	0.69	0.76	0.75
HL/HW	1.06	1.03	0.94	0.94	1.22	1.00	1.13	1.03	1.07	1.11	1.07
PW/HW	1.77	1.83	1.71	1.81	1.81	1.67	1.67	1.75	1.79	1.78	1.85
EW/PW	1.45	1.44	1.48	1.45	1.52	1.48	1.52	1.46	1.52	1.46	1.48

Etymology: Adjective based on the name of the island, followed by the suffix *-ensis* used in Latin to designate an inhabitant.

Habitat: Small caves and crevices of different sizes in basaltic rock formations with very scarce soil and vegetation.

Geographic distribution: Endemic to Malpelo island.

3.2. Relationships with Other *Platynina*

We will only make preliminary observations on the position of this taxon within *Platynina*, pending a molecular study. The phyletic position of *Cacothrix* is obscured by several autapomorphies probably resulting from behavioral adaptations to the unusual environmental conditions of the island (see below, Section 3.4): apterism; reduced eyes; long and slender appendages; no neck constriction; tapered shape of the forebody; and especially the coaptation of the base of pronotum and the base of elytra, to our knowledge a conformation unparalleled among *Platynina*.

However, three character states bring *Cacothrix* close to *Dyscolus* Dejean, 1831 and clearly separate it from *Platynus* Bonelli, 1810 (= *Limodromus* sensu Schmidt, 2000) and *Batenus* Motschulsky, 1865 (= *Platynus* sensu Schmidt, 2000): submentum with two pairs of setae; basal outer lobe of the aedeagal left paramere simple, not bifurcated (Figure 6a); and presence of a median band of spikelike microtrichia on the surface of the bursa copulatrix (Figure 5). The absence of the anteriorly directed process observed in *Platynus* and *Batenus* at the apex of the basal outer lobe of the left paramere (Figure 6d,e) is an important diagnostic character, rightly pointed out by Schmidt [16].

Two other derived character states, absent in the ground plan of *Dyscolus*, are less easily linked to a local process of adaptive evolution after arrival on the island. The first one is the absence of fixed dorsal setae on elytra, pronotum, and head. In the subtribe *Platynina*, the reduction in the standard number of trichoid sensilla is rarely observed together on the three segments. This character state has only been mentioned in a few New Guinean endemic genus-level taxa, such as *Fortagonum* Darlington [17]. The apomorphic loss of mechanoreceptors on the dorsal surface of the body is much probably homoplastic in these two distantly related lineages. It cannot be easily explained in terms of selective advantage, as it implies fewer sensory organs, hence less tactile sensitivity, while the visual capacity of *Cacothrix* is hindered by the reduction in the volume of the eyes.

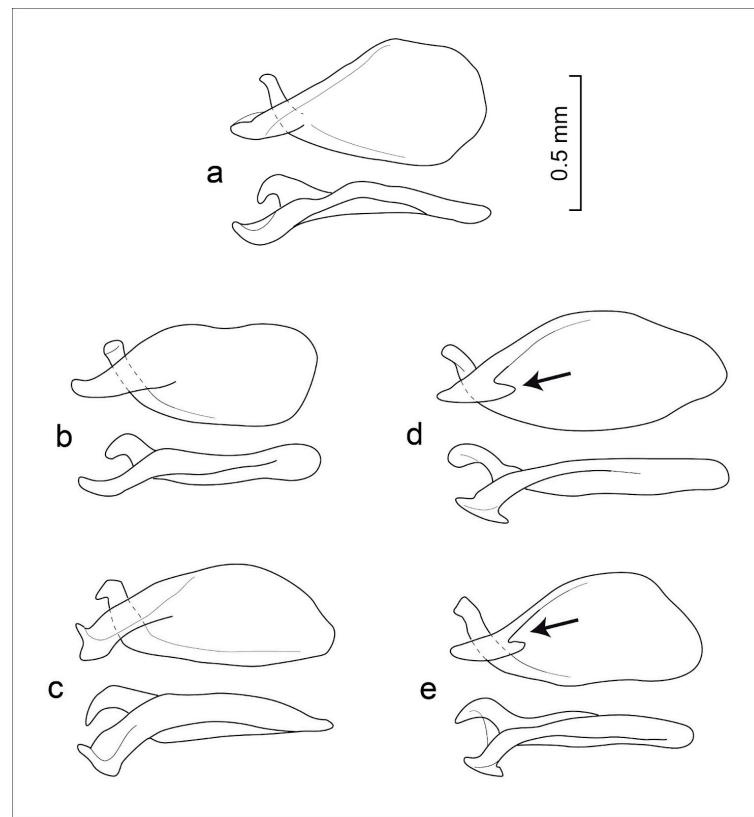


Figure 6. Left paramere of the aedeagus of various *Dyscolus* and *Platynus* species, drawn from the lateral side (top) and, after ca. 90° rotation, from the ventral side (bottom), according to Schmidt [16]. The arrow points to the anteriorly directed process of the outer basal lobe, present in *Platynus* and absent in *Dyscolus*. (a) *Dyscolus* (*Cacothrix*) *malpелensis*; (b) *Dyscolus brunneomarginatus* (Mannerheim, 1843); (c) *Dyscolus purpuratus* Reiche, 1843; (d) *Platynus assimilis* (Paykull, 1790); (e) *Platynus decentis* (Say, 1823). (b,d,e) redrawn from [16] (Figure 2).

The second derived character whose importance we wish to emphasize is the transformation of tarsal trichoid sensilla into translucent, flattened strips on the apical lobes of the fourth tarsomeres (Figure 3). These modified structures were named hyaline phanera by Deuve [18], the first to recognize their phyletic significance. They are documented in other platynine genera such as *Glyptolenoides* Perrault, 1991 on pro- and mesotarsi [18], *Onypterygia* Dejean, 1831 on protarsi [unpublished data], and *Blackburnia* Sharp, 1878 on metatarsi [19] (fig. 133), thus appearing to be homoplastic. Some mainland *Dyscolus* species exhibit more or less distinct hyaline phanera on the fourth protarsomere, but never on the metatarsi; at most, part of the distal setae of the fourth metatarsomere get translucent at apex, but they do not exhibit the characteristic flattened and widened profile observed in *Cacothrix*. It can be assumed that these phanera help the insect to adhere to smooth and wet surfaces—a frequent situation in the rocky and frequently wet environment of Malpelo. However, it should be noted that in the genus *Dyscolus*, many species adapted to a riparian habitat, capable of holding on soaked rocks, have undergone a different evolution of their metatarsal setation via the multiplication of setae rather than the structural transformation of some of them [2]. A complete inventory of tarsal morphologies, particularly in Mesoamerican lineages, will therefore be needed to properly assess the significance of this trait.

A comparative study should also be undertaken with the Platynini known from the Cocos and Galapagos Islands. The only species reported from Cocos Island looks very different, according to a drawing published without an accompanying description in [6] (fig. 56), with standard setation on head (2 pairs), pronotum (2 pairs), and elytra (3 dorsal setae) and with strong humeri possibly suggesting a full-winged condition. The three endemic

species known from the Galapagos archipelago [4] have at least one distinctive trait in common with *Cacothrix*: the presence of hyaline phanera on pro- and mesotarsi, though not on metatarsi [unpublished data]. However, the general body shape of the Galapagos *Dyscolus* species is much closer to the standard morphology of mainland members of the genus.

3.3. Habitat and Biology

D. malpelensis is found during the day hidden under rocks and in crevices. Its activity is nocturnal. The average density of the species is 0.36 individuals/m² (n = 22 sample plots of 50 × 50 cm, located from 20 to 270 m a.s.l.). Based on the areas inhabited by this beetle, the total population estimate is between 300,000 and 400,000 individuals. *D. malpelensis* shares the island ecosystem with at least 71 other terrestrial macroinvertebrate morphospecies, 32 of which belong to the same trophic guild (predators). Species available for potential feeding include land snails, some Julida (Myriapoda: Diplopoda), springtails, Isopods, and micro-Lepidoptera larvae [13,20].

The nocturnal behavior of *D. malpelensis* prevents potential predatory pressure that could be exerted during the day by the two larger lizards (*Dactyloa agassizi* Stejneger, 1900 and *Diploglossus millepunctatus* O'Shaughnessy, 1874) and the land crab *Johngarthia malpilensis* (Faxon, 1893), a voracious predator which is more active during dawn and dusk [21]. According to field observations, *D. malpelensis* defends itself from consumption attempts by *Diploglossus millepunctatus* by expelling a defensive secretion, easily detectable by smell, when touching or catching the beetle.

3.4. Morphological Adaptations to the Environment

The platynine species that arrived fortuitously on the island of Malpelo or on another, now disappeared island of the Malpelo ridge had to face extremely harsh environmental conditions, with hardly any vegetation or soil, and the omnipresence of predators. This situation, without an equivalent on the continent (or in the Galapagos and Cocos Islands), imposed a drastic selective pressure that might explain the evolution undergone by this insect. Four morphological characters likely are a consequence of an adaptation to this specific habitat: reduced and flattened eyes; very long antennae (on average as long as 70% of the overall body length); elongate and slender legs; oval, fusiform body without constriction between pronotum and elytra and with a small and cylindrical head.

Reduced eyes and very long antennae are typical adaptive traits of cave-dwelling species, having evolved independently in many carabid lineages, including the subtribe Platynina in caves of Hawaii [19] and South America [18]. However, the eye degeneration is only incipient in *D. malpelensis*, which lacks other typical characters of cavernicolous ground beetles, such as depigmentation, elongate and slender shape of pronotum, effaced humeri, and lengthening of sensory setae.

The general body form recalls certain *Calathus* species (tribe Sphodrini) adapted to hide in shallow fissures of the soil beneath the leaf litter in native forests of the Canary Islands [22]. The use of underground crevices as habitat, an evolutionary trend well known in ground beetles [23,24], may explain this convergence of body shape. Ground beetles which live in restricting habitats, such as fissures in the ground, tend to be shallower in depth, with a prothorax similar in width to the hind body. It has been suggested that this type of body form would minimize friction by causing less obstruction when moving through confined spaces [25]. In the case of *D. malpelensis*, the peculiar shape of the body eliminates all protuberances and protruding angles that could hinder the insect's progression in narrow crevices. This is particularly striking in the tight coaptation of pronotum and elytra, since the humeri, instead of receding as is usual in apterous species, have expanded forward, fitting exactly into the curve of the pronotum. The same connection exists between head and pronotum: when the head is retracted into the prothoracic cavity (not as in Figure 2), the anterior angles of the pronotum fit snugly against the sides of the head capsule, just before the eyes. These morphological modifications were especially

useful on a rocky and barren island where the usual shelters of carabid beetles, such as leaf litter, base of tussocks, or stones lying on humic soil, are entirely lacking.

On the other hand, long and slender legs and small metatrochanters are features that allow this taxon to be included in the category of fast runners [26], in line with its predatory lifestyle, based on nocturnal activity. This morphology considerably reduces the capacity of *D. malpelensis* in terms of axial wedge-pushing, which is widespread in many groups of carabid beetles, allowing them to move among dense vegetation or to burrow into the ground [27]. But in the absence of such environmental conditions on Malpelo, a weak wedge-pushing ability could not affect the species' survival prospects.

In summary, the morphology of *D. malpelensis* appears to be adapted to an extraordinarily harsh environment by combining features that allow it to be an active nocturnal predator (long and slender legs, long antennae) and to find shelter in narrow rock crevices (flattened and oval-shaped body without any protruding angle).

Another factor may have contributed to the development of a close coadaptation between the pronotum and the elytra as a response to predation by lizards and land crabs. This coadaptation eliminates a weak point in the middle of the body on which the lizards' jaws or the crabs' claws could preferentially attack, the constriction existing in most Platynini species between the pronotum and the elytra. With its continuously oval shape and smooth surface, *D. malpelensis* offers less grip and can slide out more easily.

Finally, the predation behavior of *D. malpelensis* could be a third factor explaining its peculiar body shape. Although the species has not yet been observed when feeding, a likely preferential prey is the endemic land snail *Malpelina labiata* Hausdorf, Kroll & López-Victoria, 2012, which shares the same habitat and also has nocturnal activity [28]. The oval aperture of the shell of this species is 2×1.5 mm. With a similarly oval section and a maximum width between 1.35–1.75 mm, the head of *D. malpelensis* fits into it, enabling the beetle to sink its mandibles more than 1 mm into the shell. Tapered head with slender mandibles is a morphological character state that has been frequently observed in carabid beetles feeding on land snails and interpreted as an adaptive trait based on feeding habits consisting in inserting the head into the shell [29]. Interestingly, during the dry season (January–April), the snails withdraw deeply into crevices and under rocks, where *D. malpelensis* could be able to track them thanks to its shallow and fusiform body shape.

4. Conclusions

D. malpelensis is the only member of the family Carabidae so far known to live in the depauperate and very harsh environment of the Malpelo oceanic island. As frequently observed in insect taxa that evolved in isolated islands and became flightless, it presents a combination of derived morphological characters that distinguish it from all its congeners living on the mainland, justifying the creation of a subgenus. Alongside the lengthening of legs and antennae and the reduction in the setation pattern on the upper surface of head, pronotum, and elytra, the most striking of these derived characters is the oval shape of the entire body, resulting from a peculiar coadaptation of the concave base of the elytra and the convex base of the pronotum. An unresolved question, in the absence of sufficient field observations, is to what extent this morphological evolution is adaptive and related to the species' lifestyle, diet, and interactions with predators. Comparison with similar modifications of the body shape in other ground beetle lineages allowed us to postulate some hypotheses, but a field observation program would be needed to test them and understand how this insect was able to thrive in such a rugged and challenging environment.

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