

# Multiple origins of the *Phaenonotum* beetles in the Greater Antilles (Coleoptera: Hydrophilidae): phylogeny, biogeography and systematics

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Received 20 February 2017; revised 21 July 2017; accepted for publication 25 August 2017

The systematics and the phylogenetic position of the Caribbean representatives of *Phaenonotum* Sharp (Coleoptera: Hydrophilidae) are investigated to understand the composition of the Caribbean fauna and its origin. Phylogenetic analysis based on mitochondrial and nuclear genes has revealed the Caribbean species to be situated in three deeply nested clades, inferring multiple colonization of Caribbean islands from the continent. Time-tree analysis and BioGeoBEARS analyses of ancestral ranges estimated the oldest clade, consisting of wingless single-island endemics of Cuba (*P. delgadoi*), Jamaica (*P. Ondreji* sp. nov.) and Hispaniola (*P. laterale* sp. nov.), to have diverged c. 46.6 Mya from the South American ancestor and subsequently colonizing the Caribbean most likely via the GAARlandia land bridge connecting South America with the Greater Antilles. The remaining three Caribbean species, including the Puerto Rican endemic, *P. borinquenum* sp. nov., are of more recent (Miocene to Pliocene) origin and colonized the Greater Antilles by over-water dispersal. All the Caribbean species are illustrated and diagnosed, and three new species are described. The genus *Phaenonotum*, excluding *P. caribense* Archangelsky, is confirmed as a monophylum. We demonstrate that species-level taxonomy of *Phaenonotum* is difficult to solve by morphology alone and ideally requires the combination of morphology and molecular markers.

ADDITIONAL KEYWORDS: ancestral range analysis – Caribbean biogeography – endemics – GAARlandia – molecular dating – new species – phylogeny – systematics – taxon cycle.

## INTRODUCTION

The Greater Antilles (i.e. islands of Cuba, Hispaniola, Jamaica and Puerto Rico in the Caribbean Region) are known for their high species diversity and endemism and are considered one of the world biodiversity hot-spots (Mittermeier *et al.*, 2005). The complex geological history of the region, characterized by emergence and sinking of particular islands and changes in their interconnections, has played a crucial role in generating

these diverse and endemic faunas. The Antilles first emerged as the Antillean volcanic arc system in the Cretaceous in the gap between North and South America and repeatedly emerged and submerged while moving eastward into the Proto-Caribbean Sea later during the Cenozoic. The uplift of the core Greater Antilles started during the Middle Eocene and reached its maximum at the Eocene–Oligocene boundary. The area of the islands was reduced during the higher sea-level period in the Late Oligocene to Middle Miocene, but the islands remained emerged, possibly with the exception of parts of today's Jamaica and Hispaniola, which are believed to have emerged permanently only

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during the Neogene (e.g. [Iturralde-Vinent & MacPhee, 1999](#); [Bartolini, Lang & Spell, 2003](#); [Iturralde-Vinent, 2006](#)).

The origin of the present day terrestrial and freshwater biota of the archipelago has been explained by three alternative scenarios. The first scenario assumes that ancestors of extant lineages colonized the Antillean volcanic arc system from southern North America (via land bridges or by short-distance over-water dispersal) during the Late Cretaceous and Early Paleogene and survived there as relicts to the present (e.g. [Rosen, 1975, 1985](#)). This scenario was originally proposed for solenodons and *Cricosaura* lizards (e.g. [Hedges, 2006](#)), but only the *Cricosaura* clade has been confirmed to be old enough ([Noonan \*et al.\*, 2013](#); [Sato \*et al.\*, 2016](#)). Under this scenario, the ancient Antillean fauna would have had to survive the collision of the large bolide with the Earth at the Yucatan Peninsula 65 Mya and its consequences that exterminated most of the Cretaceous terrestrial life forms in the Caribbean region ([Iturralde-Vinent, 1982](#); [Iturralde-Vinent & MacPhee, 1999](#); [Tada \*et al.\*, 2003](#)). The second scenario suggests long-distance over-water dispersal from the surrounding landmasses during the Cenozoic (e.g. [Hedges, Hass & Maxson, 1992](#); [Hedges, 2006](#)), which was recently documented, for example, for solenodons ([Sato \*et al.\*, 2016](#)) and urocoptid snails ([Uit de Weerd, Robinson & Rosenberg, 2016](#)). In contrast to over-water dispersal, [Iturralde-Vinent & MacPhee \(1999\)](#) introduced the GAARlandia theory (GAAR = Greater Antilles + Aves Ridge) assuming a land bridge connection of the Greater Antilles with northern South America resulting from a tectonic uplift and sea-level fall at the Eocene–Oligocene boundary. This third scenario assumes that numerous terrestrial and freshwater organisms colonized the archipelago during a relatively short period (*c.* 35–33 Mya), as was suggested, for example, for *Peltophryne* toads ([Alonso, Crawford & Bermingham, 2012](#)), poeciliid fishes ([Weaver \*et al.\*, 2016](#)) or heroine cichlid fishes ([Řičan \*et al.\*, 2013](#)). The GAARlandia hypothesis is still a subject of debate: [Hedges \(2006\)](#) and [Ali \(2012\)](#) point to the absence of geological evidence and lack of any clear signal in vertebrate phylogenetic analyses and hypothesize GAARlandia as no more than a chain of widely spaced islands situated between northern South America and the Greater Antilles.

The above scenarios have been tested by numerous phylogenetic studies, which make the Caribbean one of the model regions for understanding historical island biogeography. Paradoxically, the vast majority of these studies are focused on vertebrates (i.e. relatively species-poor clades with rather

young modern crown-groups; e.g. [Roelants \*et al.\*, 2007](#); [Claramount & Cracraft, 2015](#); [Foley, Springer & Teeling, 2016](#)) and plants (i.e. groups with resistant seeds facilitating long-distance dispersal; e.g. [Sanmartín & Ronquist, 2004](#)). Little is known about the origin and biogeography of Caribbean insects and other terrestrial or freshwater arthropods, that is species-rich old groups that may provide numerous independent examples of evolutionary histories corroborating or contradicting the above biogeographic scenarios. Dated molecular phylogenetic studies have been performed only for selected groups of Caribbean butterflies ([Wahlberg, 2006](#); [Wahlberg & Freitas, 2007](#); [Matos-Maraví \*et al.\*, 2014](#); [Lewis \*et al.\*, 2015](#)), wasps ([Ceccarelli & Zaldívar-Riverón, 2013](#); [Rodríguez, Pitts & von Dohlen, 2015](#)) and arachnids (e.g. [Crews & Gillespie, 2010](#); [Zhang & Maddison, 2013](#); [McHugh \*et al.\*, 2014](#); [Dziki \*et al.\*, 2015](#); [Esposito \*et al.\*, 2015](#); [Agnarsson \*et al.\*, 2016](#)). Only a single very recent study is available for Caribbean beetles (Coleoptera), which is the most speciose and most intensively studied insect group ([Zhang \*et al.\*, 2017](#)).

The beetle family Hydrophilidae comprises *c.* 3350 species inhabiting both aquatic and terrestrial habitats and is distributed worldwide ([Hansen, 1999](#); [Short & Fikáček, 2013](#); [Lawrence & Slipinski, 2014](#); [Seidel, Arriaga-Varela & Fikáček, 2016](#)). In the Caribbean, the family is represented by 16 genera, 11 of which contain at least one species endemic to the Greater Antilles ([Hansen, 1999](#); [Short, 2004](#); [Spangler & Short, 2008](#); [Deler-Hernández, Cala-Riquelme & Fikáček, 2013a](#); [Deler-Hernández, Fikáček & Cala-Riquelme, 2013b](#); [Deler-Hernández, Cala-Riquelme & Fikáček, 2014](#); [Arriaga-Varela \*et al.\*, 2017](#)). Among them, the genus *Phaenonotum* Sharp, 1882 contains 18 described and many undescribed species in the Neotropical and southern Nearctic Regions, and one East-African species ([Hansen, 1999](#)), all inhabiting semiaquatic or terrestrial habitats. A single widespread species, *Phaenonotum exstriatum* (Say, 1835), was originally recorded from the Caribbean, until the surprising discovery of *P. delgadoi* Deler-Hernández *et al.*, 2013 endemic to eastern Cuba ([Deler-Hernández \*et al.\*, 2013a](#)). Our subsequent fieldwork revealed additional candidates for endemic species in Jamaica, Hispaniola and Puerto Rico, indicating that *Phaenonotum* possibly underwent an island radiation in the Greater Antilles. In this paper, we analyse the systematics and evolutionary history of the Caribbean *Phaenonotum* in order to understand to what extent it corroborates the aforementioned scenarios explaining the origin of Caribbean faunas.

## MATERIAL AND METHODS

## DNA SEQUENCES

The molecular study is based on *Phaenonotum* specimens collected in all main islands of the Greater Antilles during our fieldwork in 2010–2016. Specimens were collected either manually from aquatic habitats, rotten plant debris and at the light traps, or by sifting of forest leaf litter and extracting the beetles from sifting samples using Berlese and/or Winkler funnels. All specimens were collected in 96% ethanol and stored at  $-20^{\circ}\text{C}$  in the lab. To understand the origin of the Caribbean fauna, we included *Phaenonotum* species from Costa Rica, Guatemala, Venezuela, Suriname, Guyana, Ecuador, Peru and the USA, that is all continental DNA-grade material available to us. To test the monophyly of *Phaenonotum*, we also included all available DNA-grade specimens of the genera *Phaenostoma* Orchymont, 1937 and *Lachnodacnum* Orchymont, 1937, which form a strongly supported clade with *Phaenonotum* (V. Sýkora *et al.*, unpubl. data). Outgroup taxa consist of selected genera representing the main clades of the tribe Coelostomatini (*Cyclotypus* Sharp, 1882, *Dactylosternum* Wollaston, 1854 and *Coelostoma* Brullé, 1835) and the sphaeridiine tribes Protosternini (*Sphaerocetum* Fikáček, 2010) and Sphaeridiini (*Sphaeridium* Fabricius, 1775). Most specimens used for this study were newly extracted and sequenced, but in a few cases, we adopted the sequences published by Short & Fikáček (2013).

DNA was extracted from complete specimens cut into two parts between prothorax and mesothorax, using the commercial DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany) following the manufacturer's instructions. Voucher specimens and DNA extractions are kept in the collection of the Department of Entomology of the National Museum, Prague (NMPC).

Our gene selection corresponds with those used in previous phylogenetic studies of the family Hydrophilidae (e.g. Short & Fikáček, 2013) and contains three mitochondrial genes (3' end cytochrome c oxidase I, cytochrome c oxidase II and 16S rRNA), and two nuclear genes (18S rRNA and 28S rRNA); sequences of 18S rRNA were amplified in two parts (3' end and 5' end) and subsequently combined; for primers and PCR conditions, see Supporting Information, Supplement S1. Ten microlitres of each PCR product were purified by adding 1.0  $\mu\text{L}$  Exonuclease 1 [Exo1 (20 U/ $\mu\text{L}$ )] (ThermoFisherScientific) and 2.0  $\mu\text{L}$  Thermosensitive Alkaline Phosphatase [FastAP (1 U/ $\mu\text{L}$ )] (ThermoFisherScientific) and incubating the mixture for 15 min at  $37^{\circ}\text{C}$  followed by a 15 min inactivation step at  $80^{\circ}\text{C}$ . Sanger sequencing was performed by BIOCEV (Vestec, Czech Republic). DNA sequences

were assembled and edited using Geneious 7.1.9 and submitted to GenBank under the accession numbers shown in Supporting Information, Supplement S1. In total, we obtained sequences for 36 terminal taxa (25 specimens of *Phaenonotum*, four of *Phaenostoma*, one of *Lachnodacnum* and six outgroup taxa).

## PHYLOGENETIC ANALYSES

Our molecular data set includes sequences of three ribosomal genes, which are non-trivial for alignment especially in case of distantly related taxa (e.g. Bocák *et al.*, 2014), and a rather large proportion of missing data for *cox2* and 16S genes, which we failed to amplify despite repeated effort. To test the impact of these problems, we compared the results of analyses of three different data sets:

- (1) 35 taxa data set: contains all *Phaenonotum* + *Phaenostoma* + *Lachnodacnum* specimens and all outgroups;
- (2) 30 taxa data set: contains all *Phaenonotum* + *Phaenostoma* + *Lachnodacnum* specimens, but is only rooted with closely related *Cyclotypus* (eliminates the problem with alignment of distantly related taxa);
- (3) 22 taxa data set: contains only *Phaenonotum* + *Phaenostoma* + *Lachnodacnum* with three and more genes, and is rooted by *Cyclotypus* (eliminates the problem with the alignment of non-related taxa and the effect of missing *cox2* and 16S data).

Specimens MF1736 and MF1741 from Venezuela were genetically very close (2.1% in *cox1*), corresponding to intraspecific variation in *cox1* found in *Phaenonotum exstriatum* (0.0–3.1%), and were hence considered as conspecific; they were combined for our analyses and included in all three data sets.

Sequences were aligned with MAFFT algorithm as implemented in Geneious 7.1.9 software, using the default settings (score matrix = 200PAM/ $k = 2$ , gap open penalty = 1.53, offset value = 0.123). The final alignment has the total length of 4827 bp, consisting of the following gene fragments: *cox1* (778 bp), *cox2* (694 bp), 16S (530 bp), 18S (1798 bp) and 28S (1027 bp). The data set was divided into nine partitions (by genes, plus *cox1* and *cox2* were both divided by codon positions). Each data set was analysed using Bayesian inference and maximum likelihood. Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012) using four chains of 25 000 000 generations and sampling the chain every 1000 generations. We sampled across the substitution model space in the Bayesian MCMC

analysis itself (Huelsenbeck, Larget & Alfaro, 2004; Ronquist *et al.*, 2012) instead of prior testing for an appropriate model for each of nine partitions. Results were examined in Tracer v.1.6 (Rambaut *et al.*, 2014) to check for the proper effective sample size, proper mixing of chains and reaching the stationary phase; 25% burn-in was used for the construction of the final consensus tree. Maximum likelihood analyses were performed using RAxML 8.0 (Stamatakis, 2014) with a GTR substitution model and 1000 bootstrap replicates. Resulting trees were visualized in FigTree 1.4.3 (Rambaut, 2012).

#### DIVERGENCE DATING

We performed a divergence dating analysis using the full data set of 35 taxa in BEAST 2.4.5 (Bouckaert *et al.*, 2014) with fixed tree topology as revealed by the Bayesian analysis of the 35 taxa data set; the internal topology of *P. exstriatum* was manipulated to be bifurcate in agreement with results of the maximum likelihood analyses of 35 and 30 taxa. We divided the data set into five partitions corresponding to each gene (*cox1*, *cox2*, 16S rRNA, 18S rRNA and 28S rRNA) and used PartitionFinder v1.1.1 (Lanfear *et al.*, 2012) to estimate the evolutionary model that best fit the data for each partition separately. The following substitution models were selected using Bayesian information criterion and used for particular genes in the divergence dating analysis: GTR + I + G for *cox1*, *cox2* and 28S; GTR + G for 16S; and TrNef + I + G for 18S.

Due to the absence of fossils belonging to the tribe Coelostomatini, we used the combination of a rate dating and node dating constraining the age of the most recent common ancestor (MRCA) of the Coelostomatini. Molecular clock models were linked into two partitions (mtDNA: *cox1*, *cox2*, 16S rRNA; nDNA: 18S rRNA, 28S rRNA) and substitution rates were set to 0.0133 (mtDNA) and 0.0017 (nDNA) substitutions per million years following Papadopoulou, Anastasiou & Vogler (2010). The age of the MRCA of the Coelostomatini was constrained to 152.5 Mya [95% highest posterior density (confidence interval): 134–170 Mya], following the results of the time tree analysis of the whole family Hydrophilidae performed by Bloom, Fikáček & Short (2014) based on a wide spectrum of fossil calibrations (for list of fossils used see supplementary material in Bloom *et al.*, 2014). We performed a Bayes Factor comparison to test alternative clock models (non-clock, strict clock, relaxed clock) using a stepping-stone method (Xie *et al.*, 2011) as implemented in MrBayes 3.2.6 (Ronquist *et al.*, 2012) (see Supporting Information, Supplement S1).

The birth–death model was used for the tree prior as this model is commonly used to model speciations and extinctions in inferring phylogenies using Bayesian methods; thus, at any point in time, every lineage can undergo speciation at rate  $\lambda$  or go extinct at rate  $\mu$  (Stadler, 2009). Due to the problems with convergence of parameters, we performed two separate runs each with MCMC chain length set to 500 million generations and sampling frequency of every 25 000 generations. We combined both runs using LogCombiner 2.4.0 and applied a 10% burn-in fraction after checking the convergence of parameters in TRACER 1.6 (Rambaut *et al.*, 2014). TreeAnnotator 2.4.1 was used to summarize the information of all trees in the sample onto the maximum clade credibility tree. The resulting tree was visualized in FigTree 1.4.3 (Rambaut, 2012).

#### HISTORICAL BIOGEOGRAPHY RECONSTRUCTION

For historical biogeography estimation, we used the time tree resulting from the divergence dating analysis as the input tree, from which we excluded all outgroups except *Cyclotypus*. Four specimens of *P. exstriatum* were included into the analysis, each representing a geographically distinct population. An alternative set of analyses with a single terminal for *P. exstriatum* was also performed.

The distribution ranges were divided into the following eight areas: A – North America incl. Mexico; B – Central America; C – northern South America (corresponding to Guiana Shield + northwestern Venezuela and northern Colombia, i.e. regions on the Caribbean coast and in direct contact with Central America); D – South America (remaining continent south of the former region); E – Cuba; F – Jamaica; G – Hispaniola; H – Puerto Rico. As no inter-island divergences are present in our phylogeny, we coded the Caribbean islands in their current shape, without considering their historical composition of multiple paleoislands. Islands of the Lesser Antilles were not considered as separate areas, as only the youngest and widespread *P. exstriatum* is known to occur in some of them; instead, the presence/absence of the Lesser Antilles was considered when setting dispersal multipliers for the time-stratified analysis (see below). The distribution of terminal taxa is based on examined specimens in all undescribed species; distribution of *P. exstriatum* and *P. laevicolle* complex on the continent follows Smetana (1978); Hansen (1999); Oliva, Fernández & Bachmann (2002) and González-Rodríguez, García-Hernández & Clarkson (2017).

We carried out the historical biogeography analyses in the R package BioGeoBEARS (Matzke, 2014) to estimate the timing of *Phaenonotum* colonization of the Greater Antilles archipelago. This package contains three models implemented in a maximum likelihood framework: DEC model (Ree & Smith, 2008), DIVALIKE model (likelihood version of the DIVA model: Ronquist, 1997) and BAYAREALIKE model (likelihood version of BayArea model: Landis *et al.*, 2013). Moreover, each model is available in its original version and with an additional parameter *j* representing the founder event, that is speciation following long-distance dispersal; six different models are hence available in total.

We conducted non-time-stratified and time-stratified analyses to estimate ancestral area distribution on given nodes, each with all six models. Unconstrained non-stratified analyses were done using default parameter values. For time-stratified analyses, time periods were defined as follows, to reflect different paleogeography of the area in each period (Iturralde-Vinent, 2006; O’Dea *et al.*, 2016): (1) 0–2.8 Mya: from present to the closing of Isthmus of Panama; (2) 2.8–9 Mya: the Greater Antilles emerged, the chain of islands (Lesser Antilles) present between the Greater Antilles and South America; (3) 9–32 Mya: the Greater Antilles significantly reduced in area and widely separated from South America by deep sea; (4) 32–38 Mya: the Greater Antilles connected to northern South America by GAARlandia land bridge; (5) 38–55 Mya: the Greater Antilles started to form and were well separated from surrounding continents; (6) 55–110 Mya: prior to the formation of the Greater Antilles. Dispersal probabilities were set to reflect the paleogeography as follows: 0.8 for adjacent continental areas; 0.5 for non-adjacent continental areas; 0.2 for adjacent islands (or island-continent) separated by less than 200 km from sea; 0.05 for connection by island chain (e.g. Lesser Antilles) or intermediate island (e.g. Hispaniola between Cuba and Puerto Rico); 0.001 for long-distance dispersal (areas separated by more than 200 km from sea); 0.000001 when dispersal was not possible (i.e. when the area was submerged; we followed the BioGeoBEARS manual in setting extremely low rather than zero probabilities in such cases). Areas not present during particular time slice (e.g. Cuba in the Late Cretaceous) were not allowed for the reconstruction using the Areas Allowed matrix. Models of both non-time-stratified and time-stratified analyses were compared using likelihood values and Akaike information criterion corrected for small sample sizes (AICc) (Matzke, 2013). All input files for the biogeography

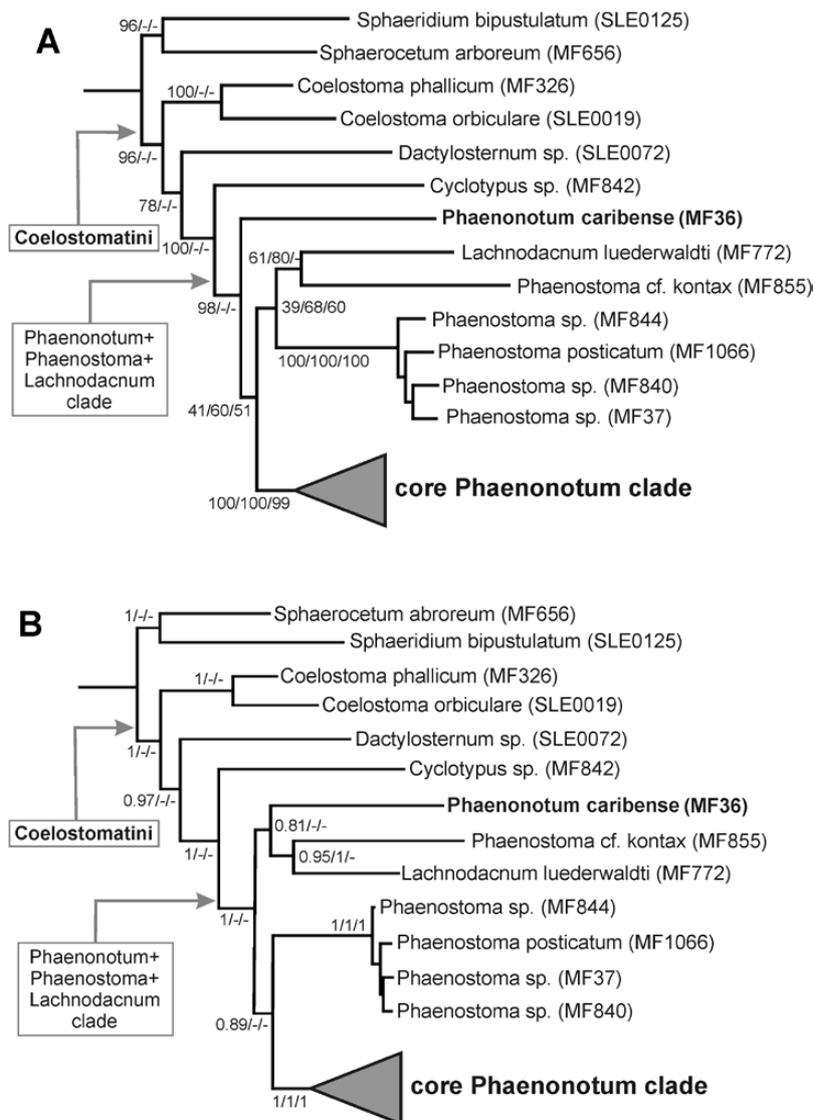
analyses are available in Supporting Information, Supplement S2.

MORPHOLOGY AND TAXONOMY

Examined specimens are deposited in the following collections:

BMNH	Natural History Museum, London, United Kingdom (M.V.L. Barclay);
CMN	Canadian Museum of Nature, Ottawa, Canada (R. Anderson);
DZRJ	Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Instituto de Biologia, Universidade Federal de Rio de Janeiro, Rio de Janeiro, Brazil (B. Clarkson);
MCZ	Museum of Comparative Zoology, Cambridge, USA (P. Perkins);
MNHNSD	Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic (C. Suriel);
NHMW	Naturhistorisches Museum, Wien, Austria (M. Jäch, A. Komarek);
NMPC	National Museum, Prague, Czech Republic (M. Fikáček);
SBNM	Santa Barbara Museum of Natural History, California, USA (M. L. Gimmel);
SBPC	Stewart Peck Personal Collection, Ottawa, Canada;
UPRM	University of Puerto Rico, Mayagüez, Puerto Rico (A. Segarra);
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (J. Frisch, B. Jäger).

Habitus photographs were taken using Canon EOS 550D digital camera with attached Canon MP-E65mm f/2.8 1–5× macro lens and subsequently adapted in Adobe Photoshop CS5 and CorelDRAW Home & Student X8. Photographs of genitalia were taken using Canon EOS 1100D digital camera attached to Olympus BX41 compound microscope and subsequently combined with Helicon Focus software. Scanning electron micrographs of the holotype of the new species were taken using a Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum in Prague. General morphological terminology follows Smetana (1978), Archangelsky (1989) and Hansen (1991). All Caribbean species were compared with type specimens of the Central and South American species deposited in the Natural History Museum, London (Sharp collection; see Deler-Hernández & Fikáček, 2016) and in the Institut



**Figure 1.** The phylogenetic position and polyphyly of *Phaenonotum* as revealed by our maximum likelihood (A) and Bayesian analyses (B). Branch support is indicated for analyses with 35, 30 and 22 terminal taxa, respectively.

Royal des Sciences Naturelles de Belgique, Brussels (Orchymont collection), and with unidentified material from Mexico, Costa Rica, Ecuador and Peru deposited in National Museum, Prague, in order to reveal whether or not they might be conspecific with continental species. Complete data of all examined specimens in DarwinCore-formatted Excel spreadsheet are available in Supporting Information, Supplement S3 and in the data set submitted to Zenodo.

#### DEPOSITORY OF PRIMARY DATA

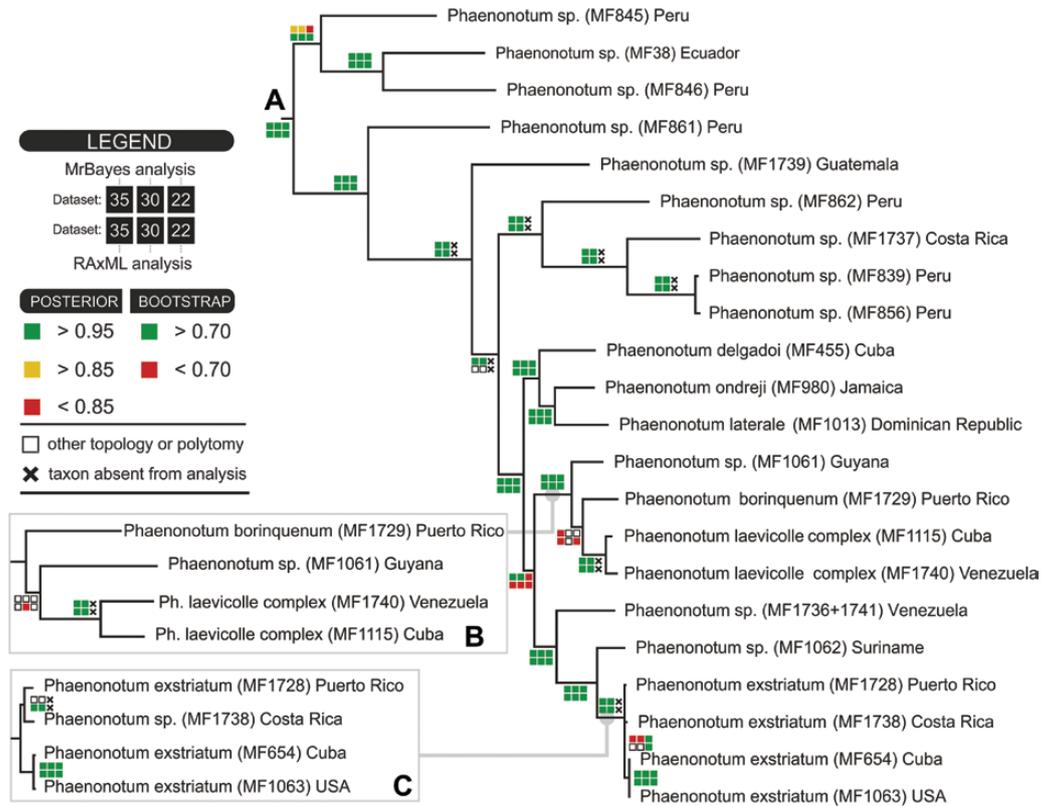
All primary data and results of all analyses were uploaded as a.zip file into the Zenodo depository (<https://zenodo.org/>) under doi: 10.5281/zenodo.850595.

Parts of the data were also uploaded to specialized archives as specified below.

## RESULTS

### PHYLOGENETIC ANALYSES

All analyses performed revealed a strongly supported clade consisting of Neotropical genera *Phaenostoma*, *Phaenonotum* and *Lachnodacnum*, but do not support the current status of the genera (Fig. 1). *Phaenonotum caribense* Archangelsky, 1989 is revealed as not related to the remaining *Phaenonotum* species and is revealed as a sister group to the rest of the Neotropical clade in most analyses (strongly supported by Bayesian



**Figure 2.** Summary of the internal topology of the core *Phaenonotum* clade revealed by Bayesian and maximum likelihood analyses of all three data sets (35 taxa, 30 taxa and 22 taxa, see Material and methods for details). A, topology resulting from Bayesian inference of 35 taxa data set, with the presence and support of particular clades in all analyses mapped by colour squares; B, alternative topology of the *borinquenum*–*laevicolle* clade obtained from maximum likelihood analysis of the 30 taxa data set; C, alternative internal topology of *P. exstriatum* clade obtained from maximum likelihood analyses of 35 and 30 taxa data sets.

analysis with 30 and 22 taxa, weakly supported by maximum likelihood analyses); in the Bayesian analysis with 35 taxa, it is revealed as sister to *Phaenostoma kontax* Gustafson & Short, 2010 and *Lachnodacnum*, with moderate support. When *P. caribense* is excluded, the genus *Phaenonotum* (= core *Phaenonotum* hereafter) is revealed as strongly supported monophylum in all analyses. The genus *Phaenostoma* is revealed as sister to the core *Phaenonotum* in most analyses (moderately supported by Bayesian analysis except that with 35 taxa, weakly supported by all maximum likelihood analyses), with *Lachnodacnum* always nested within *Phaenostoma*. In the Bayesian analysis with 35 taxa, *Phaenonotum caribense* + *Phaenostoma kontax* + *Lachnodacnum* clade is revealed as sister to the *Phaenostoma posticum* + core *Phaenonotum*.

Within the core *Phaenonotum* clade, all six analyses revealed the same five strongly to moderately supported clades and two undescribed species (MF1739 from Guatemala and MF861 from Peru) not closely

related to other species and forming deeply divergent separate clades (Fig. 2). The relationships between these seven principal clades are the same in all analyses performed, with the exception of MF1739, which is revealed as early branching in Bayesian analyses and more deeply nested in maximum likelihood analyses. All Caribbean species are part of the strongly supported deeply nested monophylum containing three of the principal clades: the clade of the endemic Cuban, Jamaican and Hispaniolan species; the clade containing Puerto Rican endemic *P. borinquenum* sp. nov., *P. laevicolle* complex and an undescribed species from Guyana (MF1061); and the clade consisting of *P. exstriatum* and undescribed species from Venezuela and Suriname. Within the Caribbean endemic clade, the internal topology is the same in all analyses, with the Cuban *P. delgadoi* diverging first, and the Jamaican *P. ondreji* sp. nov. and Hispaniolan *P. laterale* sp. nov. as sister taxa. The internal topology of the *P. borinquenum* + *laevicolle* clade varies the most among analyses, with either *P.*

*borinquenum* or the undescribed species from Guyana (MF1061) revealed as the earliest diverging taxon. The internal topology of *P. exstriatum* clade differs between Bayesian and maximum likelihood analyses, with Puerto Rican (MF1728) and Costa Rican (MF1738) revealed as sister taxa in maximum likelihood ones; the Cuban specimen (MF654) is always revealed as sister to the one from USA: Delaware (MF1063).

#### DIVERGENCE DATING

The relaxed clock model was identified as the best-fitting clock model based on the Bayes factor comparison (see Supporting Information, Supplement S1), and it was hence implemented in BEAST time tree analysis. The core *Phaenonotum* clade was estimated to originate during the middle Cretaceous (c. 102 Mya), with the diversification of modern clades starting in Late Cretaceous (c. 83 Mya). The clade composed of the endemic Cuban, Jamaican and Hispaniolan *Phaenonotum* diverged during the Eocene (c. 47 Mya), with *P. delgadoi* from Cuba diverging at about Eocene–Oligocene boundary (c. 36 Mya), and *P. ondreji* (Jamaica) from *P. laterale* (Hispaniola) during the Oligocene (c. 26.4 Mya). The Puerto Rican endemic *P. borinquenum* diverged in the early Miocene (c. 19 Mya). The divergence of the Cuban and Venezuelan specimens of *P. laevicolle* complex was dated to the Pliocene–Pleistocene (c. 4.7 Mya), and the modern populations of the widespread *P. exstriatum* diverged at about Pliocene–Pleistocene boundary (c. 2.4 Mya). Precise ages and 95% confidence intervals are listed in Table 1 for the principal *Phaenonotum* clades

**Table 1.** Divergence ages and their confidence intervals for major *Phaenonotum* clades including all Caribbean ones

	Age (Mya)	95% confidence interval (Mya)
<i>Phaenonotum</i> stem	101.7	81.7–121.9
<i>Phaenonotum</i> crown	82.5	65.4–100.2
Caribbean <i>Phaenonotum</i> stem	46.6	35.6–58.1
<i>P. delgadoi</i>	35.7	25.5–47.2
<i>P. ondreji</i> and <i>P. laterale</i>	26.4	17.2–36.5
<i>P. borinquenum</i>	19.2	12.1–27.1
<i>P. laevicolle</i> from Cuba	4.7	2.2–7.9
<i>P. exstriatum</i> crown	2.4	1.3–3.7

and illustrated in Supporting Information, Supplement S1 for all clades.

#### BIOGEOGRAPHY ANALYSES

Of the six models included in BioGeoBEARS, those implementing a founder event (i.e. peripatric speciation, *j* parameter in the analyses) fit the data better both in time-stratified and non-time-stratified analyses than those not allowing for jump dispersal (Table 2). Analyses allowing the founder event resulted in identical ancestral area estimates in all nodes and corners in non-time-stratified analyses under all three basic models (DEC + J, DIVALIKE + J and BAYAREALIKE + J) and in identical estimates in time-stratified analyses

**Table 2.** Comparison of the models used for non-time-stratified and time-stratified analyses of the data set with multiple populations of *P. exstriatum*

	LnL	npar	<i>d</i>	<i>e</i>	<i>j</i>	AIC	AICc
Non-time constrained							
DEC	-91.91	2	0.0013	< 0.0001	0	187.8	188.3
DEC + J	-70.21	3	0.0004	< 0.0001	0.046	146.4	147.3
DIVALIKE	-84.36	2	0.0016	< 0.0001	0	172.7	173.2
DIVALIKE + J*	-69.8	3	0.0005	< 0.0001	0.060	145.6	146.5
BAYAREALIKE	-125.4	2	0.0023	0.026	0	254.8	255.2
BAYAREALIKE + J	-70.56	3	0.0004	< 0.0001	0.049	147.1	148
Time constrained							
DEC	-104.9	2	0.016	0.0049	0	213.9	214.3
DEC + J	-98.94	3	0.011	0.0039	0.17	203.9	204.8
DIVALIKE	-100.2	2	0.017	0.0042	0	204.4	204.8
DIVALIKE + J*	-95.44	3	0.012	0.0034	0.099	196.9	197.8
BAYAREALIKE	-134.2	2	0.033	0.025	0	272.5	272.9
BAYAREALIKE + J	-101.8	3	0.0077	0.0066	0.24	209.5	210.5

AIC, Akaike information criterion; AICc, size-corrected AIC; LnL, log likelihood; n par, number of parameters in the analysis; *d*, *e*, *j*, parameters of the model (*d*, dispersal; *e*, extinction; *j*, founder event).

\*Best-performing model for each group of analyses.

with DEC + J and DIVALIKE + J models (time-stratified analysis with BAYAREALIKE + J model is nearly identical, only with slightly different scenario for *P. exstriatum* clade and *P. borinquenum*, see Supporting Information, Supplement S2 for details). Models not implementing the founder event resulted in very different ancestral area estimates for each model in non-time-stratified analyses, but in identical estimates under all three models in time-stratified ones. The number of continent-to-Caribbean and Caribbean-to-continent dispersal events (and source/sink regions on continents) for all three models in non-time-stratified and time-stratified analyses are shown in Table 3. Based on the AICc metrics, the best-performing models were DIVALIKE + J for both non-time-stratified and time-stratified analyses (Fig. 3).

Most analyses infer South America as the ancestral range of the MRCA of *Phaenonotum* (Fig. 3), with several independent colonizations of northern South America and Central America (through northern South America in time-constrained analyses). Most analyses (non-time-stratified allowing for founder event and all time-stratified except BAYAREALIKE + J model) infer that ancestor(s) of *P. delgadoi* + *P. laterale* + *P. ondreji* colonized the Caribbean from northern South America: non-time-stratified models and time-stratified models not allowing for founder event infer a single colonization followed by series of founder events (non-time-stratified analyses) or combination

of range expansions and vicariance events (time-stratified analyses); time-stratified analyses allowing for founder event infer two independent colonizations followed by vicariance event between Jamaica and Hispaniola. *Phaenonotum borinquenum* and Caribbean *P. laevicolle* were estimated to colonize the Caribbean independently by the non-time-stratified analysis. In contrast, time-stratified analysis favours earlier colonization of the Caribbean by the ancestor of these taxa and back-colonization from the Caribbean to the continent in *P. laevicolle*. *Phaenonotum exstriatum* was revealed to be of South American origin in non-time-constrained analyses allowing for founder event and all time-constrained analyses; the ancestral range of its MRCA was either Caribbean or Caribbean + Central America, depending on the model implemented. The results of all analyses are available in the Supporting Information, Supplement S2.

Alternative analyses with *P. exstriatum* as a single terminal resulted in estimates nearly identical to those treating the four populations of *P. exstriatum* separately, with DEC + J as the best-performing model for time-stratified and non-time-stratified analyses. Both analyses revealed northern South America as an ancestral range of the MRCA of *P. exstriatum* and its sister species (undescribed species from Suriname, voucher MF1062). Results of these analyses are available in Supporting Information, Supplement S2.

**Table 3.** Number of continent-to-Caribbean and Caribbean-to-continent colonization events (total number and number of colonizations from/to each continental area) inferred for the genus *Phaenonotum* in analyses including four populations of *P. exstriatum*

Model	Time constraints	Continent-to-Caribbean events					Caribbean-to-Continent events			
		Total	NA	CA	nSA	CA + SA	NA + CA + SA	Total	NA	CA
DEC	Non-strat.	3x		1x	2x	-	-	1x	1x	-
DIVALIKE	Non-strat.	4x		-	4x	-	-	0x	-	-
BAYAREALIKE	Non-strat.	5x		2x	-	3x	-	1x	1x	-
DEC + J	Non-strat.	4x		-	3x	-	1x	2x	1x	1x
DIVALIKE + J	Non-strat.	4x		-	3x	-	1x	2x	1x	1x
BAYAREALIKE + J	Non-strat.	4x		-	3x	-	1x	2x	1x	1x
DEC	Time-strat.	3x		-	3x	-	-	2x	1x	1x
DIVALIKE	Time-strat.	3x		-	3x	-	-	2x	1x	1x
BAYAREALIKE	Time-strat.	3x		-	3x	-	-	2x	1x	1x
DEC + J	Time-strat.	4x		-	4x	-	-	3x	1x	2x
DIVALIKE + J	Time-strat.	4x		-	4x	-	-	3x	1x	2x
BAYAREALIKE + J	Time-strat.	5x	1x	-	4x	-	-	1x	-	1x

Models best fitting the data are marked in grey. Abbreviations of source/sink areas: CA, Central America; NA, North America; nSA, northern South America. Time constraint, non-strat., non-time-stratified analysis; time-strat., time-stratified analysis.

SYSTEMATICS OF THE CARIBBEAN *PHAENONOTUM*KEY TO THE CARIBBEAN *PHAENONOTUM*

1. Eyes small, interocular distance 5.0–6.0× the width of one eye in dorsal view (Fig. 6A–C). Metaventrite very short, its total width 5.0–6.0× the length behind mesocoxae (Fig. 7A–C). Species without hind wings (apterous)..... 2
  - Eyes moderately large, interocular distance 3.5–4.0× the width of one eye in dorsal view (Fig. 6D–F). Metaventrite moderately long, its total width 3.0–4.0× the length behind mesocoxae (Fig. 7D–E). Species with fully developed hind wings (macropterous)..... 4
2. Metaventrite with pubescent cavities at sides of meso-metaventral process (Fig. 7A). Elytral suture strongly elevated posteriorly; elytral punctation very coarse (Fig. 5A). Pronotum with moderately coarse punctation, without microsculpture. Eastern Cuba (Fig. 4). ..... *P. delgadoi* Deler-Hernández et al., 2013.
  - Metaventrite without pubescent cavities at sides of meso-metaventral process (Fig. 7B–F). Elytral suture weakly elevated posteriorly; elytral punctation never extremely coarse. Pronotum either with distinct microsculpture or with extremely fine (nearly invisible) punctation..... 3
3. Body length 3.1–3.4 mm. Head and pronotum with mesh-like microsculpture and distinct punctation. Elytral punctation rather coarse, yellowish margins of elytra present in apical half only (Fig. 5B). Mesoventral process moderately wide, median portion of metaventrite with narrow highly elevated median keel (Fig. 7C). Aedeagus 0.6 mm long (Fig. 6H). Jamaica (Fig. 4). ..... *P. ondreji* sp. nov.
  - Body length 2.5–2.7 mm. Head and pronotum without microsculpture, pronotal punctation extremely fine, almost invisible. Elytral punctation fine, whole lateral margins of elytra with yellowish stripe (Fig. 5C). Mesoventral process very narrow, metaventrite with slightly elevated median portion, without median keel. Aedeagus 0.35 mm long (Fig. 6I). Hispaniola (Fig. 4). ..... *P. laterale* sp. nov.
4. Median lobe of the aedeagus wide; gonopore large, situated in apical third of the median lobe. Bases of lateral struts of the median lobe weakly expanded laterally (Fig. 6L). Widespread in the Greater Antilles (Fig. 4). ..... *P. laevicolle* complex
  - Median lobe of the aedeagus narrow; gonopore small, situated subapically. Bases of lateral struts of the median lobe largely expanded laterally (Fig. 6J, K). ..... 5
5. Body length 3.3–4.0 mm. Bases of parameres meeting in single point (Fig. 6K). Widespread in Greater and Lesser Antilles (Fig. 4). ..... *P. exstriatum* (Say, 1835)
  - Body length 3.2–3.3 mm. Bases of parameres widely joined together (Fig. 6J). Puerto Rico (Fig. 4). ..... *P. borinquenum* sp. nov.

***PHAENONOTUM BORINQUENUM* SP. NOV.**

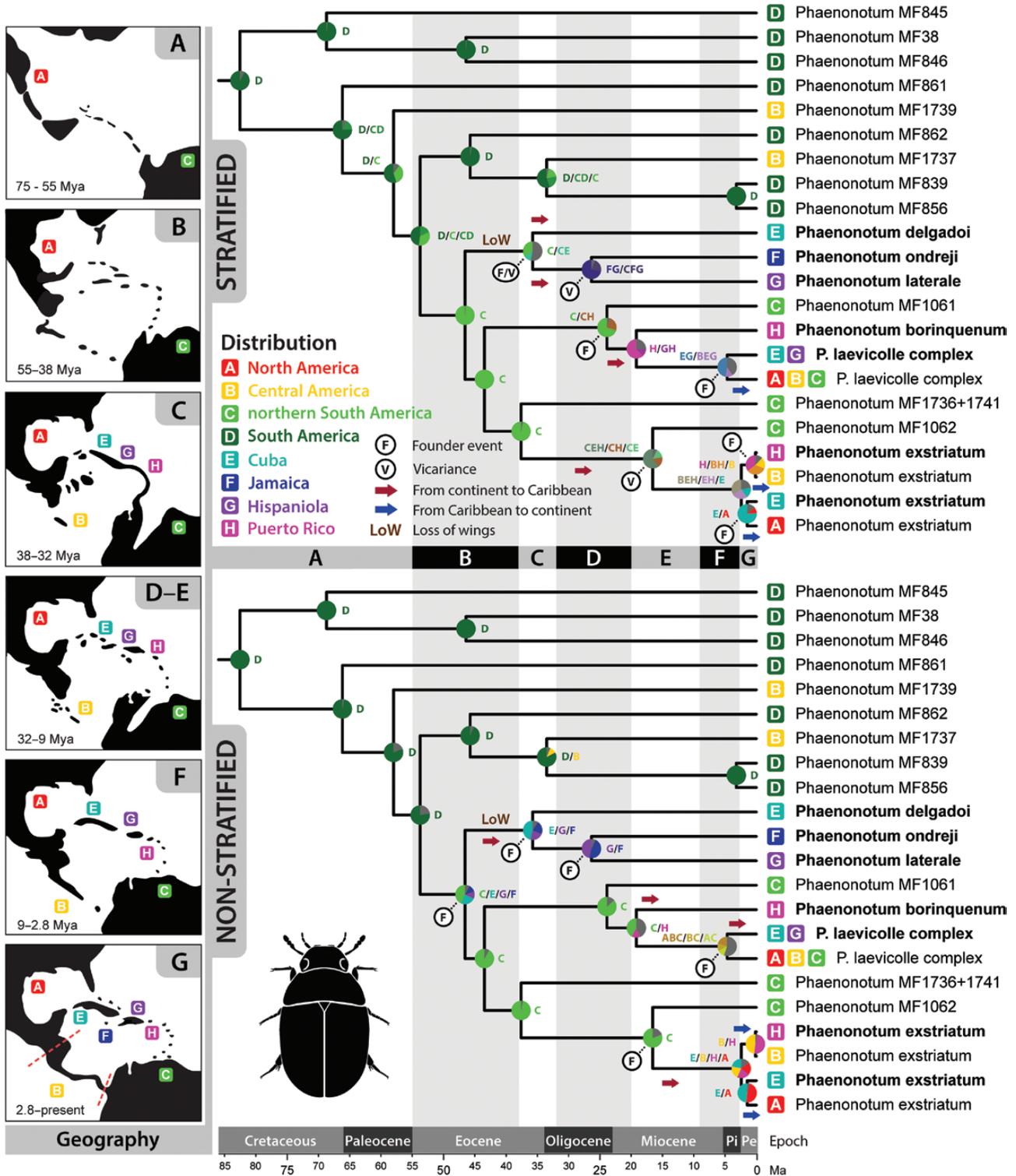
(Figs 4A, 5D, 6D, J, 7D)

*Type locality:* Puerto Rico, Naguabo, El Yunque National Forest, 18°16.1'N 65°48.1'W, 575 m.

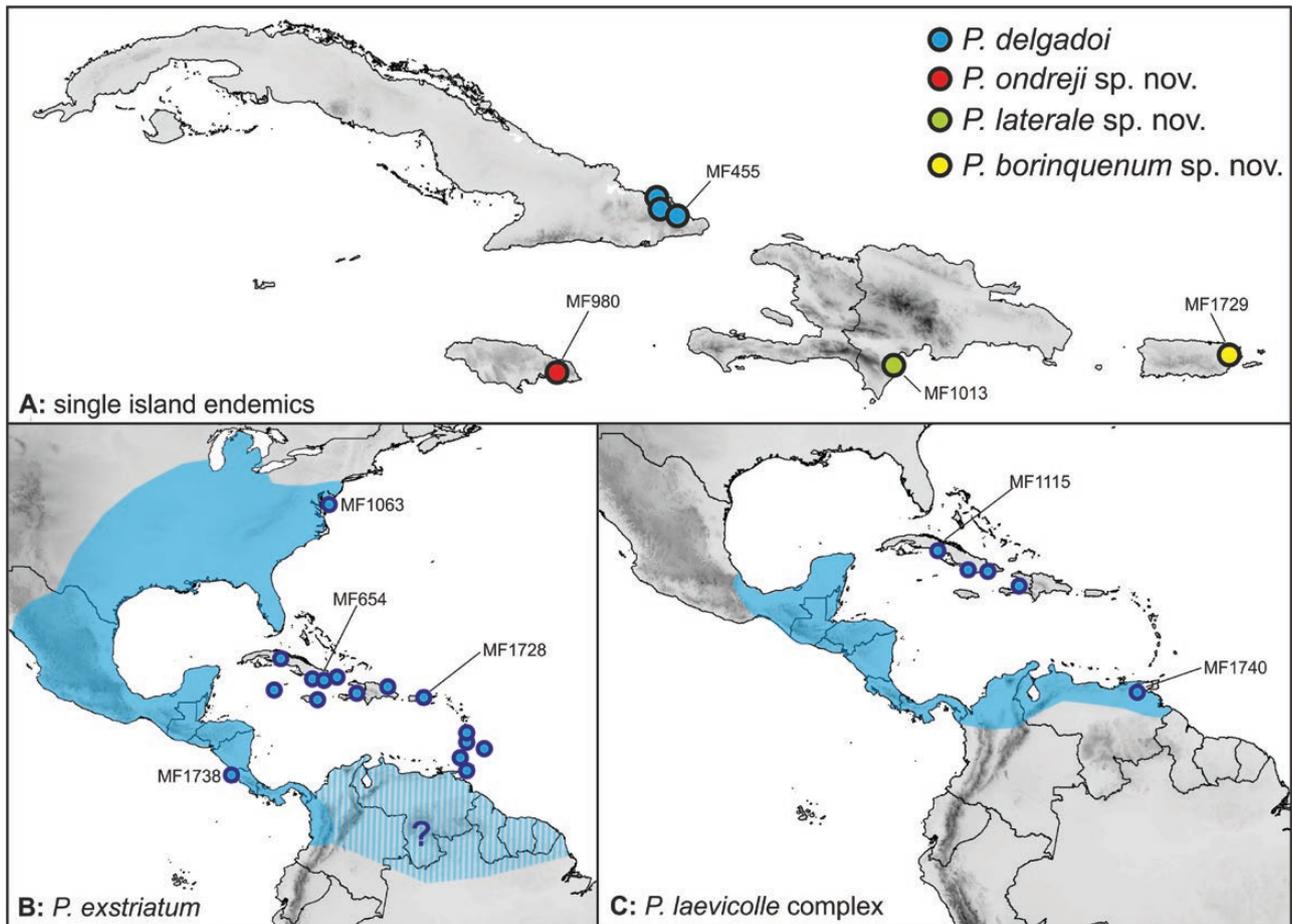
*Type material:* Holotype: male (NMPC): 'PUERTO RICO: Naguabo: El Yunque Nat. Forest, S part La Sabana recr area 5.25 km N of Río Blanco above rd. PR191, 18°16.1'N 65°48.1'W, elevation 575 m, 21.vi.2016, A. Deler-Hernández lgt., PR05/DNA isolation: MF1730, isolated by A. Deler-Hernández 2016, isolate deposited at Department of Entomology, National Museum in Prague (green printed)' (molecular voucher MF1730). Paratype: one female (NMPC; associated with the holotype by *cox1* sequence): Puerto Rico: Naguabo, El Yunque Nat. Forest, S part La Sabana recr area 5.6 km N of Río Blanco at rd. PR191, 18°16.1'N 65°47.6'W, 510 m a.s.l., 21.vi.–2.vii.2016, Deler-Hernández, Fikáček, Seidel lgt., PR03/DNA isolation:

MF1729, isolated by A. Deler-Hernández 2016, isolate deposited at Department of Entomology, National Museum in Prague (green printed)' (Molecular voucher MF1729).

*Description:* Habitus as in Figure 5D. Body size 3.2–3.3 mm (holotype: 3.3 mm). Body elongate oval, moderately convex, elytral suture not elevated. Dorsum black (dark brown in the teneral paratype), lateral margins of pronotum and elytra without distinct paler stripe; ventral surface dark brown to black; femora and tibiae black; antennae, maxillary palpi and tarsi yellowish. Head with sparse and moderately coarse punctation, without microsculpture (except posteriorly on frons); eyes moderately large, separated by 4.0× dorsal width of one eye (Fig. 6D). Pronotum with sparse punctures slightly finer than on head, interstices without microsculpture. Elytral punctation strongly impressed, coarser than on pronotum and head; elytral interstices



**Figure 3.** Results of the ancestral area estimation using time-stratified and non-time-stratified DIVALIKE + J model of BioGeoBEARS. Maps (A–G) show simplified continent and island positions in the respective time window used for the time-stratified analysis. Pie charts show two or three most probable ancestral areas for the respective node.



**Figure 4.** Current distribution of the genus *Phaenonotum* in the Caribbean. A, single island endemics; B, *P. exstriatum*; C, *P. laevicolle* complex. The localities of sequenced specimens are shown and marked by the code of the respective DNA extract.

without microsculpture. Wings present, fully developed. Mesoventral elevation as wide as metaventral process posteriorly, narrowing anteriorly, with distinct anterior hood; metaventrite without pubescent pits on sides of metaventral process; metaventrite *c.* 4.0× wider than its length posterior of mesocoxae; median moderately elevated part of metaventrite narrow throughout (Fig. 7D). Aedeagus 0.5 mm long (Fig. 6J). Median lobe rather widely triangular, *c.* 1.8× longer along midline than wide; apex not reaching apices of parameres; gonopore moderately large, subapical; lateral struts projecting laterad. Parameres distinctly sinuate on lateral margin, slightly expanded subapically; widely meeting each other basally. Phallobase longer than wide.

**Etymology:** The species name is a Latinized adjective derived from the Spanish version of the indigenous Taíno name of the islands of Puerto Rico.

**Diagnosis:** *Phaenonotum borinquenum* may be distinguished from other Caribbean species by the

combination of moderately large eyes, moderately long metaventrite, presence of wings and morphology of the aedeagus. It is extremely similar to *P. exstriatum* in its external morphology and genital morphology, and may be distinguished from it only by its smaller body size and widely meeting bases of parameres only. Despite the strong morphological similarity, it is not closely related to *P. exstriatum*.

**Distribution:** *Phaenonotum borinquenum* is only known from the eastern part of Puerto Rico (Fig. 4A).

*PHAENONOTUM DELGADOI* DELER-HERNÁNDEZ,  
CALA-RIQUELME & FIKÁČEK, 2013  
(FIGS 4A, 5A, 6A, G, 7A)

**Type material examined:** See Deler-Hernández *et al.* (2013), including one sequenced paratype from the type locality (molecular voucher MF455).

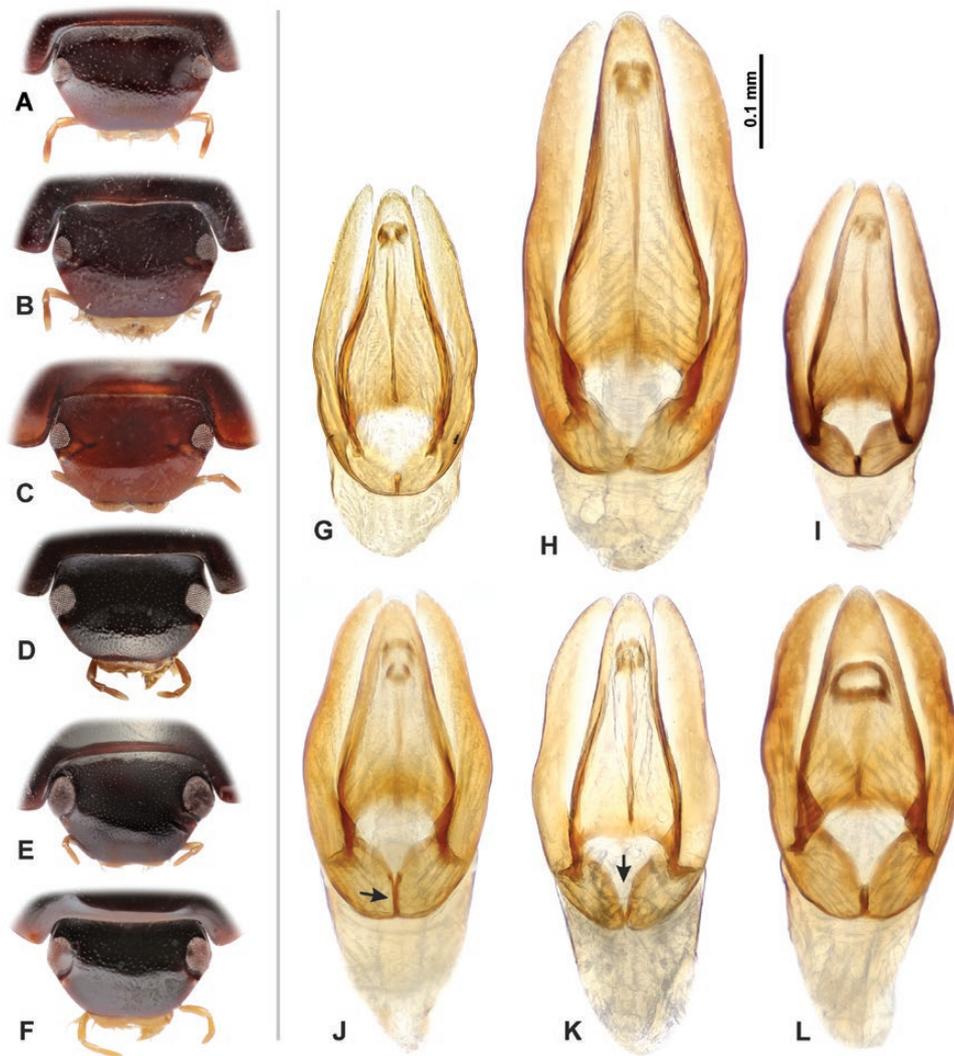


**Figure 5.** Habitus of the Caribbean *Phaenonotum* (dorsal and lateral views). A–D, species endemic for the Greater Antilles: A, *P. delgadoi* Deler-Hernández *et al.*, 2013 from eastern Cuba; B, *P. ondreji* *sp. nov.* from Jamaica; C, *P. laterale* *sp. nov.* from southern Hispaniola; D, *P. borinquenum* *sp. nov.* from Puerto Rico. E, F, non-endemic species: E, *P. exstriatum* (Say, 1835) from Cuba; F, *Phaenonotum* *sp.* from the *P. laevicolle* complex from Cuba.

**Additional material examined:** **Cuba:** Holguín Prov.: 5 spec. (NMPC): La Melba, Parque Nacional Alexander von Humboldt, 20.43352°N 74.82507°W, 336 m, rain-forest litter, 21.ix.2014, R. Anderson, F. Cala-Riquelme, A. Deler-Hernández lgt. (2014-002); 4 spec. (NMPC): 20.45396°N 74.82342°W, 510 m, pluviselva litter, 22.ix.2014, R. Anderson, F. Cala-Riquelme, A. Deler-Hernández lgt. (2014-011); 19 spec. (NMPC): road out La Melba, 20.51524°N 74.81844°W, 407 m, elfin forest litter, 24.ix.2014, R. Anderson, F. Cala-Riquelme, A. Deler-Hernández lgt. (2014-015); 8 spec. (NMPC): road out La Melba, road out of La Melba, 20.59086°N 74.83627°W, 130 m, scrub forest litter, 24.ix.2014, R. Anderson, F. Cala-Riquelme, A. Deler-Hernández lgt. (2014-016).

**Published records:** Cuba: Guantánamo Prov.: El Yunque de Baracoa (Deler-Hernández *et al.*, 2013a). Holguín Prov.: La Melba (Deler-Hernández *et al.*, 2013a).

**Redescription:** Habitus as in Figure 5A. Body length 2.2–2.5 mm (holotype: 2.3 mm). Body oval, strongly convex, elytral suture distinctly elevated posteriorly. Dorsum black, lateral margins of pronotum and elytra without distinct paler stripe; ventral surface brown to dark brown; femora and tibiae reddish; antennae, maxillary palpi and tarsi yellowish. Head with sparse fine punctation, without microsculpture (except posteriorly on frons); eyes small, separated by 5.2× dorsal width of one eye (Fig. 6A). Pronotum with very



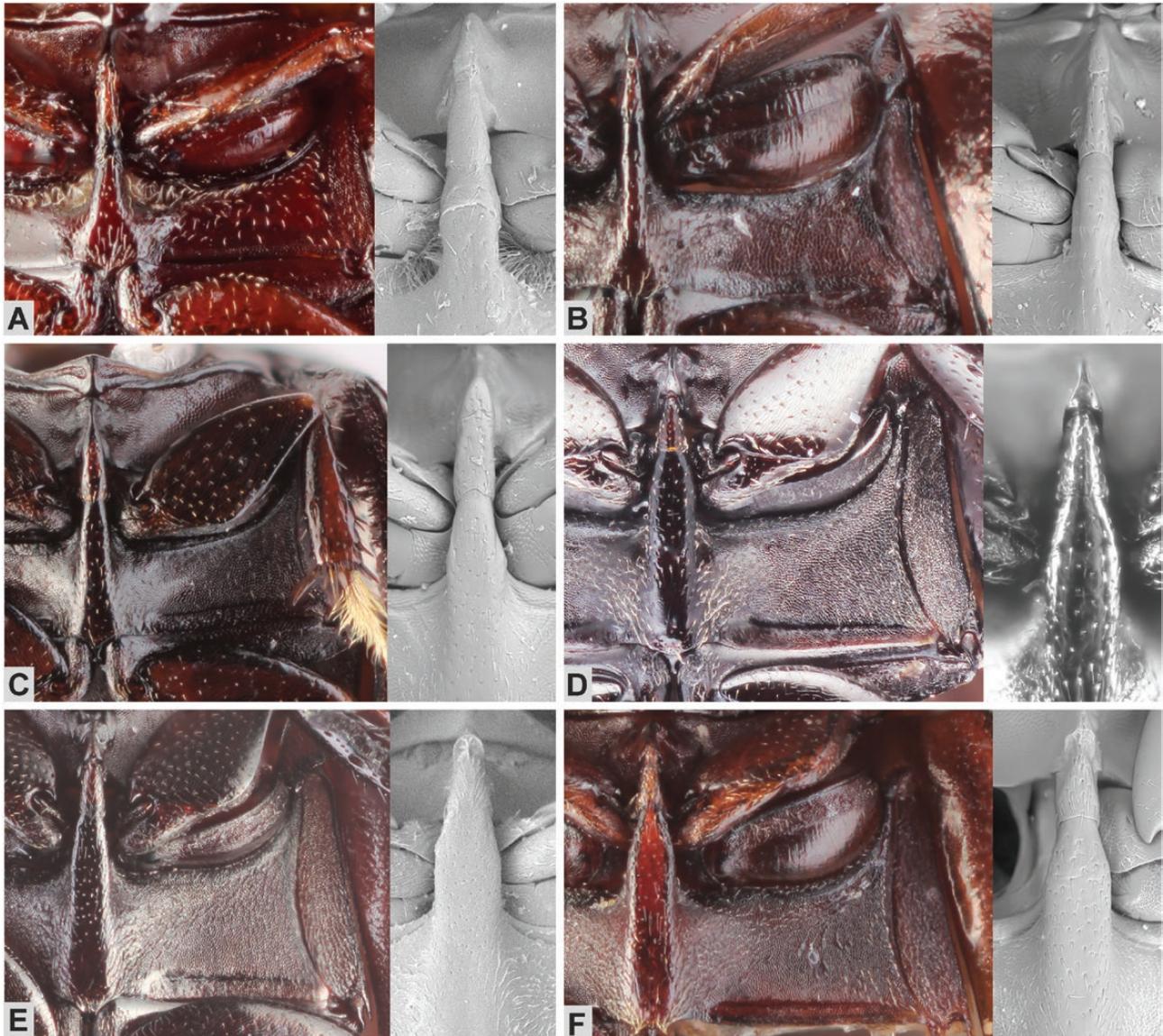
**Figure 6.** Head in frontal view (A–F) and aedeagus (G–L) of the Caribbean *Phaenonotum*. A, G, *P. delgadoi* Deler-Hernández *et al.*, 2013; B, H, *P. ondreji* *sp. nov.*; C, I, *P. laterale* *sp. nov.*; D, J, *P. borinquenum* *sp. nov.*; E, K, *P. exstriatum* (Say, 1835); F, L, *Phaenonotum* *sp.* from the *P. laevicolle* complex from Cuba. A–F, not to scale.

sparse minute punctures much smaller than on head, interstices without microsculpture. Elytral punctation very strongly impressed, much coarser than on pronotum and head; elytral interstices without microsculpture. Wings completely absent. Mesoventral elevation as wide as metaventral process throughout, not narrowing anteriorly, with distinct anterior hood; metaventricle with a deep pubescent pit on each side of metaventral process; metaventricle *c.* 5.8× wider than its length posterior of mesocoxae; median moderately elevated part of metaventricle narrow anteriorly, widening posteriorly (Fig. 7A). Aedeagus 0.4 mm long (Fig. 6G). Median lobe rather narrowly triangular, *c.* 1.9× longer along midline than wide; apex not reaching apices of parameres; gonopore small, subapical;

lateral struts simple, not expanded. Parameres indistinctly sinuate, nearly evenly arcuate on lateral margin, not expanded subapically, broadly meeting each other basally. Phallobase slightly wider than long.

*Diagnosis:* *Phaenonotum delgadoi* may be distinguished from all other *Phaenonotum* known to us by the combination of extremely coarse elytral punctation, elevated elytral suture and deep pubescent pits on each side of metaventral process. See Identification Key for additional characters.

*Distribution:* *Phaenonotum delgadoi* is only known from eastern Cuba, all known localities are situated in the Nipe-Sagua-Baracoa mountain system (Fig. 4A).



**Figure 7.** Meso-metaventral morphology of the Caribbean *Phaenonotum* (left: middle and right portions of complete meso-metaventrite, right: detail of mesoventral elevation and anterior metaventral process). A, *P. delgadoi* Deler-Hernández *et al.*, 2013; B, *P. laterale* *sp. nov.*; C, *P. ondreji* *sp. nov.*; D, *P. borinquenum* *sp. nov.*; E, *P. exstriatum* (Say, 1835); F, *Phaenonotum* *sp.* from the *P. laevicolle* complex from Cuba. Not to scale.

*PHAENONOTUM EXSTRIATUM* (SAY, 1835)

(FIGS 4B, 5E, 6E, K, 7E)

*Type material:* Neotype of *Hydrophilus exstriatus* Say, 1835 designated by Smetana (1978) from southeastern states of USA (deposited in Museum of Comparative Zoology, Harvard University, Boston, USA): not examined in our study. Types of *Phaenonotum dubium* Sharp, 1882 were examined by Deler-Hernández & Fikáček (2016) and confirmed as being conspecific to North American specimens treated as *P. exstriatum* (synonymy proposed by Smetana, 1978).

*Material examined:* **Barbados:** 1 spec. (SBPC): Jack-in-Box Gully, forest, 13°11'N 59°34.3'W, 230 m, UV light, 23.vi.2007, S & J. Peck lgt. (07-25). **Cuba:** Cienfuegos prov.: 1 spec. (NMPC): Soledad, 22.12682°N 80.33289°W, 71 m, MV light, 21.v.2013, A.B.T. Smith lgt. Guantánamo prov.: 2 spec. (NMPC): Baracoa, Jobo Dulce, 20°18'18.00"N 74°27'21.60"W, 94 m, 29.x.2010, R. Correa lgt; El Yunque, 3.2 km SW of campismo, 20°19'N 74°34'W, 150 m, 13.vi.2012, A. Deler-Hernández lgt. Holguín Prov.: 1 spec. (NMPC): Mayarí, Guatemala, Guarina Nuñez, 20°42'4.06"N 75°40'24.45"W, c. 27 m, 26.iii.2013, A. Deler-Hernández

lgt. Granma Prov.: 1 spec. (NMPC): Cauto Cristo, Rio Cauto, El Sitio, 20°16'22.80"N 76°29'2.40"W, 135 m, 1.v.2005, L. Chaves. Santiago de Cuba prov.: 9 spec. (NMPC): El Vivero, 1.3 km NEE of Dos Caminos, 20°10'49.36"N 75°46'41.43"W, c. 170 m, at light, 23.v.2013, Deler-Hernández & A. Smith lgt. (1 spec: molecular voucher MF654); 1 spec. (NMPC): Daiquirí, 1–4.vi.1985, S. Bílý lgt. **Dominica**: 8 spec. (BMNH): La Plaine, 97-67, 22.i.1889, G. A. Ramage lgt. **Dominican Republic**: 1 spec. (NMPC): Samaná, 6.4 km N of Samaná, road to El Valle, 19°15.78'N 69°20.23'W, 21 m, 5.ix.2014, Deler, Fikáček, Gimmel (DR36). **Grenada**: 1 spec. (SBPC): Grand Etang Forest Reserve, 12°04.952'N 61°42.162'W, 434 m, nursery edge forest, UV trap, 14.viii.2010, S. Peck lgt. (10–69); 25 spec. (BMNH): Grand Etang (Windward side), 1900 ft, H. H. Smith.; 1 spec. (SBPC): Par. St. Andrew, Mirabeau, Agric. Lab, UV trap, 23.ii.1990, R. E. Woodruff lgt.; 34 spec. (BMNH): Mount Gay Est. (Leeward side), H. H. Smith lgt.; 3 spec. (BMNH): Chantilly Est. (Windward side), H. H. Smith lgt.; 8 spec. (BMNH): Balthazar (Windward side), H. H. Smith lgt.; 1 spec. (BMNH): Vendome Est. (Leeward side), H. H. Smith lgt. **Cayman Islands**: 1 spec. (BMNH): Grand Cayman, by freshwater lake near George Town., UV light trap, 4.viii.1970, Joy Farradane lgt. **Haiti**: 1 spec. (BMNH): Port au Prince., 1.iii.1908, M. Cameron lgt. Jamaica: 1 spec. (BMNH): Kingston., 16.ii.1908, M. Cameron lgt.; 9 spec. (SBPC): Ewarton, St. Cath. Par., St. Clair Cave, 27.xii.1972, S & J. Peck. **Montserrat**: 1 spec. (BMNH): Salem 8.ix.1975, J. Cooter lgt. **Saint Lucia**: 1 spec. (SBPC): Mon Repos, 6.5 km W of Fox Grovelnn, 13°52.5'N 60°56.4'W, 300 m, submontane forest litter, 22.vii.2007, S & J. Peck lgt. (07-76). **Saint Vincent and the Grenadines**: 1 spec. (SBPC): Saint Vincent, Brighton Bay Village, 13°07.97'N 61°10.06'W, 1 m, streamside UV trap 8.vi.2007, S & J. Peck lgt. (07-10); 15 spec. (BMNH): Saint Vincent, without additional data, H. H. Smith lgt. **Puerto Rico**: 7 spec. (NMPC): Naguabo, El Yunque Nat. Forest, S part 3.45 km N of Río Blanco at rd. PR191, 18°14.8'N 65°47.7'W, 170 m, 24.vi.2016, Deler, Fikáček & Seidel lgt. (1 spec.: molecular voucher MF1728). **Trinidad & Tobago**: 2 spec. (BMNH): Trinidad, St. Augustine, 15.iv.1926, C. L. Withycombe lgt.; 1 spec. (BMNH): Trinidad, St. Margarita, 11.vi.1942. E. C. Humphries lgt. **USA**: Florida: 1 spec. (NMPC): Highlands Co., Venus, 4 miles W of Fish Eating Creek, 15.viii.1965, W. Suter lgt., det. A. Smetana; 1 spec. (NMPC): Alachua Co., Gainesville, black light, 19.vii.1978, F. N. Young lgt., det. A. Smetana; 1 spec. (NMPC): Kansas: Douglas Co., Bridenthal Ecological Reserve, 3.2 miles N of Baldwin City, 38.81043°N 95.18669°W, 270 m, ix.2009, Eldgedge & Fikáček lgt.; 1 spec. (NMPC): Douglas Co., Lawrence Baker Wetlands, 27.viii.2009, Gustafson, Eldgedge & Fikáček lgt.; 1 spec. (NMPC): Delaware: New Castle

Co., Frenchtown Woods Natural Area, 23.v.2004, at light, A. E. Z. Short lgt. (AS-04-065) (molecular voucher MF1063). **Costa Rica**: 1 spec. (NMPC): Guanacaste: 6.6 km from main road, roadside gravel stream running through culvert, 10°09'26.7"N 85°22'47.5"W, 50 m, 13.i.2004, Short & Lebbin lgt. (AS-04-037) (molecular voucher MF1738).

*Redescription*: Habitus as in [Figure 5E](#). Body length 3.3–4.0 mm. Body elongate oval, moderately convex, elytral suture not elevated posteriorly. Dorsum black, lateral margins of elytra with very narrow indistinct paler stripe, pronotum paler in posterolateral corners; ventral surface dark brown to black; femora and tibiae black; antennae, maxillary palpi and tarsi yellowish. Head with sparse moderately coarse punctation, without microsculpture (except posteriorly on frons); eyes moderately large, separated by 4.0× dorsal width of one eye ([Fig. 6E](#)). Pronotum with sparse fine punctures, slightly smaller than on head, interstices without microsculpture. Elytral punctation moderately impressed, coarser than on pronotum and head; elytral interstices without microsculpture. Wings present, well developed. Mesoventral elevation as wide as metaventral process posteriorly, slightly narrowing anteriorly, with distinct anterior hood; metaventrite without pubescent pits on sides of metaventral process; metaventrite c. 3.9× wider than its length posterior of mesocoxae; median moderately elevated part of metaventrite moderately wide throughout ([Fig. 7E](#)). Aedeagus 0.4 mm long ([Fig. 6K](#)). Median lobe narrowly triangular, c. 2.1× longer along midline than wide; apex reaching apices of parameres; gonopore small, subapical; lateral struts expanded laterally. Parameres distinctly sinuate on lateral margin, slightly expanded subapically. Phallobase longer than wide.

*Diagnosis*: *Phaenonotum exstriatum* may be distinguished from Caribbean species except *P. borinquenum* by the combination of moderately large eyes, moderately long metaventrite, presence of wings and morphology of the aedeagus. It may be distinguished from *P. borinquenum* by larger body size and bases of parameres meeting in single point only. Despite the strong morphological similarity, it is not closely related to *P. borinquenum* (see [Fig. 2](#)).

*Distribution*: *Phaenonotum exstriatum* is widespread in the eastern USA and in Central America ([Smetana, 1978](#); [Deler-Hernández & Fikáček, 2016](#)) as well as in Greater and Lesser Antilles ([Fig. 4B](#)). The only record from South America is from eastern Colombia ([González-Rodríguez, García-Hernández & Clarkson \(2017\)](#)), but the species is probably widespread in northern South America as it is common in southern islands of Lesser Antilles and it also occurs in Trinidad.

*PHAENONOTUM LAEVICOLLE* SHARP, 1882 COMPLEX

(FIGS 4C, 5F, 6F, L, 7F)

*Type material examined:* Types of *P. laevicolle* Sharp, 1882, see [Deler-Hernández & Fikáček \(2016\)](#).

*Material examined:* **Cuba:** Cienfuegos Prov.: 1 male (NMPC): Río Cabagan, Gruta Mengoa, 21.93123°N 80.08461°W, 651 m, 20.v.2014, A. Deler-Hernández lgt. (molecular voucher MF 1115); 3 spec. (ZMHB): Sierra del Escambrai, 5 km N Topes de Collantes, c. 600 m, sifting of leafs, 17.xii.2007, M. Schülke lgt. (CU7-4). Sancti Spiritus Prov.: 9 spec. (ZMHB): Sierra del Escambrai, Topes de Collantes, c. 700 m, Streu, Totholz, 17.xii.2007, M. Schülke lgt. (CU7-3). Granma Prov.: 7 spec. (ZMHB): Sierra Maestra, La Habanita, 35 km NE Pilón, 900–1000 m, sifted hay, 20.xii.2007, M. Schülke lgt. (CU7-8). Santiago de Cuba Prov.: 1 spec. (NMPC): El Vivero, 1.6 km E of Dos Caminos, 20°10.8'N 75°46.4'W, 150 m, 20–21.vi.2012, A. Deler-Hernández & Fikáček (MF18). **Haiti:** 3 spec. (BMNH): Port au Prince, 1.iii.1908, M. Cameron lgt. **Venezuela:** 1 male (NMPC): Monagas small pond between Morichal Largo & Temblador, 9°05'47.9"N 62°43'37.1"W, 29 m, 2.ii.2010, Short, García & Joly lgt. (VZ10-0202-03A) (molecular voucher MF1740).

*Redescription:* (refers to the Caribbean specimens examined): Habitus as in [Figure 5F](#). Body length 2.7–3.1 mm. Body elongate oval, moderately convex, elytral suture not elevated posteriorly. Dorsum black, lateral margins of elytra with paler stripe reaching subapically, pronotum paler in posterolateral corners; ventral brown to dark brown; femora dark brown to reddish, tibiae reddish; antennae, maxillary palpi and tarsi yellowish. Head with sparse fine punctation, without microsculpture (except posteriorly on frons); eyes moderately large, separated by 3.6× dorsal width of one eye ([Fig. 6F](#)). Pronotum with sparse fine punctures similar to that on head, interstices without microsculpture. Elytral punctation moderately impressed, coarser than on pronotum and head; elytral interstices without microsculpture. Wings present, well developed. Mesoventral elevation slightly narrower than metaventral process posteriorly, slightly narrowing anteriorly, with distinct anterior hood; metaventrite without pubescent pits on sides of metaventral process; metaventrite c. 3.5× wider than its length posterior of mesocoxae; median moderately elevated part of metaventrite moderately wide throughout ([Fig. 7F](#)). Aedeagus 0.5 mm long ([Fig. 6L](#)). Median lobe rather triangular, c. 1.7× longer along midline than wide; apex reaching apices of parameres; gonopore large, wide, situated in apical third of median lobe; lateral struts very shortly expanded laterally. Parameres distinctly sinuate on lateral margin, strongly expanded subapically,

broadly meeting each other basally. Phallobase longer than wide.

*Comments:* Both sequenced specimens (MF1115 from Cuba and MF1740 from Venezuela) form a strongly supported clade in the molecular analysis and are evidently closely related (pairwise distance of *cox1* sequences is 4.8%). Both specimens correspond with each other in external morphology and the characteristic shape of male genitalia, and only differ in body size: the Cuban specimen is smaller (2.8 mm), the Venezuelan specimen larger (3.4 mm). In this aspect, the sequenced Cuban specimen corresponds to all additional Greater Antillean specimens examined, which are also rather small (2.7–3.1 mm). Hence, it seems probable that Venezuelan specimen is not conspecific with the Greater Antillean ones, but additional material is necessary to evaluate the intraspecific genetic and morphological variability properly to decide whether the sequenced specimens represent one or two species.

The external morphology, body size and the morphology of genitalia of the Caribbean specimens correspond to the types of *P. laevicolle* Sharp, 1882 described from Guatemala and examined by [Deler-Hernández & Fikáček \(2016\)](#). However, due to the absence of DNA-grade specimens of *P. laevicolle* from Central America, we are unable to determine whether the Greater Antillean specimens are conspecific. For that reason, we consider all above specimens as members of the *Phaenonotum laevicolle* species complex whose taxonomy needs to be addressed once more material will be available.

*Distribution:* The Caribbean specimens of the *Phaenonotum laevicolle* complex are known from central and eastern Cuba and western Hispaniola (Haiti). Outside the Caribbean, the species complex clearly occurs in southernmost Northern and Central Americas (types of *P. laevicolle*) and in northern South America [as *P. globulosum* (Mulsant, 1844) from Colombia ([Hansen, 1999](#); not examined by us) and the Venezuelan specimen sequenced by us]. The records from Argentina (types of *P. spegazzinii* Bruch, 1915 not examined by us) seem doubtful ([Oliva et al., 2002](#)) and are not considered here. Based on these sources, we estimate the distribution of the species complex to be as shown in [Figure 4C](#).

*PHAENONOTUM LATERALE* SP. NOV.

(FIGS 4A, 5C, 6C, I, 7B)

*Type locality:* Dominican Republic, Barahona, Monumento Natural Miguel Domingo Fuerte 'Cachote' 18°5.91'N 71°11.35'W, 1188 m.

*Type material:* Holotype: male (NMPC): ‘Dominican Republic: Barahona, MN Domingo Fuerte “Cachote,” 18°5.91′N 71°11.35′W, 1188 m, 14.viii.2014, Deler, Fikáček, Gimmel DR03/montane broadleaf cloud forest with numerous *Cyathea*: sifting of thin layer of wet leaf litter and mosses’. Paratypes: Dominican Republic: 10 spec. (NMPC): same data as holotype (including molecular voucher MF1013); 25 spec. (CMN, NMPC, MNHNSD, NHMW): MN Domingo Fuerte ‘Cachote’, 18°5.21′N 71°11.46′W, 1205 m, sparse montane cloud forest with ferns and mosses here and there, sifting of thin layer of leaf litter, 14.viii.2014, M. Fikáček lgt. (DR03a); 49 spec. (BMNH, DZRJ, MCZ, MNHNSD, NMPC, SBMN): MN Domingo Fuerte ‘Cachote’, 18°4.48–5.37′N 71°11.03–11.54′W, 1188 m, 14.viii.2014, secondary montane broadleaf forest with sparse ferns and moss, sifting of leaf litter, Deler-Hernández, Fikáček & Gimmel lgt. (DR04).

*Description:* Habitus as in [Figure 5C](#). Body length 2.5–2.7 mm (holotype: 2.7 mm). Body oval, moderately convex, elytral suture slightly elevated posteriorly. Dorsum brown to dark brown, lateral margins of pronotum and lateral and sutural margins of elytra with distinct yellowish stripe; ventral surface brown to reddish brown; femora and tibiae reddish; antennae, maxillary palpi and tarsi yellowish. Head with sparse fine punctation, without microsculpture (except posteriorly on frons); eyes small, separated by 5.1× dorsal width of one eye ([Fig. 6C](#)). Pronotum with very sparse and very fine punctures much smaller than on head, interstices with not very distinct mesh-like microsculpture. Elytral punctation sparse and moderately impressed, similar to that on head, much coarser than on pronotum; elytral interstices without microsculpture. Wings completely absent. Mesoventral elevation extremely narrow, as wide as metaventral process throughout, not narrowing anteriorly, without distinct anterior hood; metaventrite without deep pubescent pits at sides of metaventral process; metaventrite *c.* 5.0× wider than its length posterior of mesocoxae; median weakly elevated part of metaventrite narrow throughout ([Fig. 7B](#)). Aedeagus 0.35 mm long ([Fig. 6I](#)). Median lobe rather narrowly triangular, *c.* 2.1× longer along midline than wide; apex reaching apices of parameres; gonopore small, subapical; lateral struts simple, not expanded. Parameres indistinctly sinuate on lateral margin, not expanded subapically, widely meeting each other basally. Phallobase as long as wide.

*Etymology:* The species name refers to the conspicuous yellow stripe along lateral margins of pronotum and elytra characteristic of this species.

*Diagnosis:* *Phaenonotum laterale* may be distinguished from other Caribbean species, based on its brown-yellow coloration, obsolete pronotal punctation

and extremely narrow meso-metaventral keel. See Identification Key for further diagnostic characters.

*Distribution:* *Phaenonotum laterale* sp. nov. is only known from a high altitude cloud forest region in the southwestern Dominican Republic, geologically situated on the southern paleoisland of Hispaniola ([Fig. 4A](#)).

#### ***PHAENONOTUM ONDREJI* SP. NOV.**

([FIGS 4A, 5B, 6B, H, 7C](#))

*Type locality:* Jamaica, Blue Mountains National Park, 18°5′14.13″N 76°43′37.55″W, 1279 m.

*Type material:* Holotype: male (NMPC): Jamaica: Blue Mountain, 18°5′14.13″N 76°43′37.55″W, 1279 m, 14.xi.2013, F. Cala-Riquelme leg. Paratypes: Jamaica: 19 spec. (CMN, MCZ, NMPC, NHMW) same data as holotype (including molecular voucher MF980); 2 spec. (BMNH): Newcastle, 19–22.viii.1908, M. Cameron lgt.

*Description:* Habitus as in [Figure 5B](#). Body length 3.2–3.4 mm (holotype: 3.1 mm). Body oval, highly convex, elytral suture slightly elevated posteriorly. Dorsum dark brown to black, posterolateral corners of pronotum and apical part of lateral margins of elytra distinctly yellowish; ventral surface brown to reddish brown; femora and tibiae yellowish to reddish; antennae, maxillary palpi and tarsi yellowish. Head with sparse moderately coarse punctation, with mesh-like microsculpture; eyes small, separated by 6.9× dorsal width of one eye ([Fig. 6B](#)). Pronotum with sparse and fine punctures, smaller than on head, interstices with distinct mesh-like microsculpture. Elytral punctation sparse, moderately impressed, coarser than on head and pronotum; elytral interstices without microsculpture. Wings completely absent. Mesoventral elevation very narrow, as wide as metaventral process throughout, not narrowing anteriorly, without distinct anterior hood; metaventrite without deep pubescent pits at sides of metaventral process; metaventrite *c.* 5.1× wider than its length posterior of mesocoxae; median highly elevated portion narrow throughout ([Fig. 7C](#)). Aedeagus 0.6 mm long ([Fig. 6H](#)). Median lobe very narrowly triangular, *c.* 2.3× longer along midline than wide; apex slightly overlapping apices of parameres; gonopore small, subapical; lateral struts weakly expanded. Parameres sinuate on lateral margin, weakly expanded subapically, narrowly meeting each other basally. Phallobase as long as wide.

*Etymology:* This species is named in honour of Ondřej Jelínek, a good friend of the senior author, in appreciation of his friendship.

*Diagnosis:* *Phaenonotum andreji* may be distinguished from other Caribbean species by the combination of small eyes, head and pronotum with distinct mesh-like

microsculpture, and narrow highly elevated meso-metaventral keel. See Identification Key for additional diagnostic characters.

*Distribution:* *Phaenonotum ondreji* sp. nov. is only known from the eastern part of the island (Blue Mountains range, Fig. 4A).

## DISCUSSION

### BIOGEOGRAPHY OF *PHAENONOTUM* AND ORIGIN OF CARIBBEAN SPECIES

Caribbean lineages of *Phaenonotum* diverged from their sister taxa during the middle Eocene to early Pleistocene (c. between 47 and 2.4 Mya), that is long after the bolide impact to the Caribbean region at the Cretaceous–Paleogene (K–Pg) boundary c. 65.5 Mya (Schulte *et al.*, 2010). This is incongruent with the vicariance hypothesis of Rosen (1975, 1985), which assumes that Caribbean lineages originated by the colonization of the proto-Antillean volcanic arc in the Late Cretaceous and survived the K–Pg boundary. The Cenozoic origin of *Phaenonotum* lineages however corresponds to other insect and spider groups studied so far, of which Caribbean clades were dated to originate between the Eocene and the Miocene (Wahlberg, 2006; Wahlberg & Freitas, 2007; Ceccarelli & Zaldívar-Riverón, 2013; Zhang & Maddison, 2013; Matos-Maraví *et al.*, 2014; McHugh *et al.*, 2014; Dziki *et al.*, 2015; Lewis *et al.*, 2015; Rodríguez *et al.*, 2015; Zhang *et al.*, 2017). The Caribbean *Phaenonotum* fauna originated from three to four independent colonization events from northern South America, the earliest of which correspond(s) in timing to the timespan of the GAARlandia land bridge connecting northern South America and the Greater Antilles through the emerged Aves Ridge at the Eocene–Oligocene boundary (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). Subsequent colonizations happened during the late Oligocene to early Miocene after the Antillean archipelago lost direct connection to the continent (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). Hence, the evolutionary history of *Phaenonotum* may be best explained by the combination of colonization via a land bridge in some lineages and the over-water dispersal events (i.e. founder events) in others.

The oldest colonization of *Phaenonotum* to the Caribbean gave rise to a small clade today containing three single-island endemics: *P. delgadoi* from eastern Cuba, *P. ondreji* from eastern Jamaica and *P. laterale* from southern Hispaniola. The divergence of this clade from modern continental clades slightly predated the timespan of the GAARlandia land bridge, which allows for two possible scenarios of colonizations: single colonization of the Greater Antilles via

GAARlandia and subsequent split into multiple species in the archipelago, or parallel colonizations of the Greater Antilles via GAARlandia by several species of the clade and subsequent speciation in the archipelago (our BioGeoBEARS analyses propose both scenarios as possible, depending on the model and time-stratification used and whether a founder event is allowed or not). Naturally, we cannot totally exclude the over-water dispersal in case it coincided by age or slightly predated the timespan of the land bridge (Poux *et al.*, 2006; de Queiroz, 2016). However, unlike all other *Phaenonotum* examined, all three species of this clade are wingless, indicating that their MRCA probably had no metathoracic wings either. The expected limited dispersal abilities of the members of the clade together with the time overlap of their arrival to the Greater Antilles with the timespan of the GAARlandia land bridge make the scenario of the over-land colonization of the Greater Antilles more probable than the over-water dispersal alternative.

The divergence of the Cuban *P. delgadoi* from the remaining two species of the clade was dated to the Eocene–Oligocene boundary (c. 36 Mya), coinciding with the maximum landspan of the GAARlandia and pre-dating the subdivision of the Greater Antilles into particular palaeoislands (separation of Puerto Rico from Hispaniola + Cuba by Mona Passage c. 30–20 Mya and separation of eastern Cuba from central Hispaniola by Windward Passage c. 17–14 Mya; Iturralde-Vinent & MacPhee, 1999; Matos-Maraví *et al.*, 2014). Both clades may have split while colonizing separate mountain ranges of the GAARlandia peninsula (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006) or before colonizing the peninsula. In contrast, the divergence of the Hispaniolan *P. laterale* and Jamaican *P. ondreji* was dated to the Late Oligocene (c. 26 Mya) when only the Blue Mountain range of Jamaica was emergent and widely isolated from other islands (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). This implies a long-distance over-water founder event, improbable for wingless mountain species. Interestingly, Jamaica–Hispaniola divergences of similar age are also found in some other animal groups (c. 22 Mya in *Osteopilus* tree frogs: Moen & Wiens, 2009; c. 20 Mya in *Exophthalmus* weevils: Zhang *et al.*, 2017; c. 15 Mya in *Calisto* butterflies: Matos-Maraví *et al.*, 2014). This may indicate either much closer geological connection between Hispaniola and Jamaica in the Late Oligocene to Early Miocene, or a constellation largely facilitating Hispaniola to Jamaica dispersal (e.g. by strong sea currents or hurricanes; Hedges, 2006).

Puerto Rico was a part of the GAARlandia land bridge, but no species of the above *Phaenonotum* clade has been recorded from the island, in contrast to the

predictions of the over-land GAARlandia scenario. Similarly, the endemic occurrence of the Hispaniolan *P. laterale* in the southern part of the island that emerged in the Late Miocene, largely postdating the origin of the species (26.4 Mya, Late Oligocene) also disagrees with the current model of historical geography of the Greater Antilles. This indicates that range shifts and extinctions probably played a significant role in the evolutionary history of *Phaenonotum* beetles in the Caribbean. On the other hand, the absence of the members of this *Phaenonotum* clade from the Lesser Antilles is congruent with the GAARlandia hypothesis: older Lesser Antilles islands are of c. Oligocene to Miocene origin, the younger ones arose during the Pliocene only and none of them were part of the GAARlandia land bridge, which was situated slightly more to the west in the place of the nowadays submerged Aves Ridge (Iturralde-Vinent & MacPhee, 1999; Thorpe et al., 2004; Iturralde-Vinent, 2006).

The remaining *Phaenonotum* clades probably colonized the Caribbean by two or three independent events during the Late Oligocene to Pliocene by over-water dispersal. One of these events (dated to Early Miocene, c. 19 Mya) gave rise to the Puerto Rican *P. borinquenum*, that is the only single-island endemic, which is not a member of the Caribbean endemic lineage discussed above. Both widespread continental-Caribbean species (*P. laevicolle* and *P. exstriatum*) were estimated to originate in the Caribbean and back-colonized the continent during the Pliocene and Pleistocene in the time-stratified BioGeoBEARS analyses. Our ancestral range estimates may be, however, strongly influenced by incomplete sampling of continental *Phaenonotum* species and limited knowledge on their distribution, and additional studies are hence necessary to corroborate our results. Nevertheless, our data suggest that the Caribbean Region may act not only as a sink of colonizations from the continent, but also a source of taxa colonizing North and Central America. This corresponds to the situation recently revealed for the *Exophthalmus* weevils and for *Heracleidos* butterflies, both of which colonized Central America from the Caribbean during the Miocene to Pleistocene (Lewis et al., 2015; Zhang et al., 2017); multiple examples are also known for vertebrates (Bellemain & Ricklefs, 2008; Ricklefs & Bermingham, 2008). Moreover, Central America was an archipelago similar to today's Greater Antilles during the Miocene to Pliocene, and Caribbean species hence probably colonized islands with unbalanced fauna rather than a continent with diverse well-established fauna characterized by strong interspecific competition (Bellemain & Ricklefs, 2008).

All four single-island endemic *Phaenonotum* species inhabit leaf litter in lowland (*P. delgadoi*) or montane cloud forests (*P. andreji*, *P. laterale* and *P. borinquenum*),

the primary forest habitats in the island interior. In contrast, the remaining two species are more widespread (*P. exstriatum* is recorded from all Greater Antillean islands including the Cayman Islands, and from most islands of the Lesser Antilles, while *P. laevicolle* is known from Cuba and Hispaniola; Fig. 4), and inhabit disturbed lowland habitats (*P. exstriatum* aquatic and semiaquatic habitats and decaying plant material, *P. laevicolle* decaying plant material including hay piles and leaf litter in farmland). When biology and distribution data are correlated to the age of the respective species, they are in a good agreement with the taxon cycle hypothesis proposed originally by Wilson (1959, 1961) for Melanesian ants and subsequently confirmed, for example, for Lesser Antillean birds (Ricklefs & Cox, 1972) (see Ricklefs & Bermingham, 2002 for review and multiple examples, and Economo & Sarnat, 2012 for detailed re-analysis of taxon cycle in Melanesian ant fauna). Following the predictions of the taxon cycle, the recently colonizing species (*P. laevicolle* and *P. exstriatum*) inhabit wider spectrum of lowland disturbed habitats and are good dispersers (range expansion phase), whereas the locally endemic species are remnants of ancient colonizations inhabiting exclusively inland primary habitats and having poor dispersal abilities (they switched from the expansion phase at the time of colonization into the range contraction phase; this may be followed by another range expansion phase or by extinction).

#### SPECIES-LEVEL SYSTEMATICS OF *PHAENONOTUM*

Despite the beetles being frequently collected, the systematics of *Phaenonotum* beetles has not been studied properly until now, and very little is known about the continental fauna of the genus. Sixteen species are known from the continental Neotropics and two from the Nearctic (with the widespread *P. exstriatum* inhabiting both regions). The real species diversity seems to be much higher, which is illustrated, for example, by the fact that of the c. 13 continental species included in our analysis, we were only able to identify two of them (*P. exstriatum* and *P. laevicolle*), whereas remaining ones probably represent undescribed species. The extreme morphological similarity of the species and limited number of characters useful for species-level identification are clearly the main obstacles for species-level studies and identification of *Phaenonotum*. Moreover, extreme similarity in external morphology and male genitalia does not necessarily indicate a close phylogenetic relationship between species. This is illustrated by *P. exstriatum* and *P. borinquenum* sp. nov., which are not closely related, yet are nearly identical in morphological characters. In contrast, the *P. laevicolle* complex seems closely related to *P. borinquenum* but can be very easily distinguished from it by

genital morphology (compare Fig. 6L, J). The combination of morphology and molecular data seems hence necessary for proper understanding of species limits even in distantly related species in *Phaenonotum*. The same is naturally true for closely related similar species. This is the reason why we refrain from describing the Cuban and Hispaniolan species of the *P. laevicolle* complex and do not decide whether the sequenced specimens from Cuba and Venezuela belonging to this species complex represent one or two species. Sequences of freshly collected specimens from the type locality of *P. laevicolle* or its surroundings and from multiple specimens across the range of the species complex would be necessary to analyse the species limits in this case.

#### NEOTROPICAL COELOSTOMATINI AND THE POSITION OF *PHAENONOTUM*

Despite limited taxon sampling, our analyses indicate that the Neotropical endemic genera of Coelostomatini (*Cyclotypus*, *Phaenonotum*, *Phaenostoma*, *Lachnodacnum*) form a monophyletic group. This result corresponds with topology revealed in the phylogenetic analysis containing a wider spectrum of coelostomatine genera but fewer Neotropical taxa (V. Sýkora, unpubl. data) and suggests that the early evolution of the Coelostomatini was strongly influenced by paleogeography: the origin of this clade was revealed as Early-Middle Cretaceous in our analysis when South America was largely isolated from other continents. The internal topology of the Neotropical clade disagrees with current generic concepts, which are based on the combination of a few easy-to-observe morphological characters (Hansen, 1991; Clarkson *et al.*, 2014): *Phaenonotum* is revealed polyphyletic when comprising the morphologically aberrant *P. caribense*, and the bromeliad inhabiting genus *Lachnodacnum* is nested within the polyphyletic *Phaenostoma*. The fact that the aberrant morphology corresponds to a separate phylogenetic position in one taxon (*Phaenonotum caribense*) but to biology rather than phylogenetic position in another (*Lachnodacnum*) clearly indicates that solving the systematics of the Neotropical clade of Coelostomatini (and in fact of the tribe as a whole) is a complex task. Additional studies combining morphological and molecular characters are necessary to understand the higher-level systematics of the group and to recognize ecology-based morphological characters from phylogeny-informative ones. Additional taxa also need to be included in the analyses – this especially concerns *Hydroglobus puncticollis* (Bruch, 1915) from Argentina, which probably belongs to the Neotropical clade.

The clade of the core *Phaenonotum* (i.e. *Phaenonotum* after excluding *P. caribense*) corresponds well with

the current morphology-based concept of the genus (Hansen, 1991), with African *P. africanum*, whose assignment to the genus is doubtful and needs to be tested, being the only exception. Based on our analyses, the core *Phaenonotum* are either sister group to *Phaenostoma* + *Lachnodacnum* (Fig. 1A) or to just the *Phaenostoma posticatum* clade (Fig. 1B). The latter topology seems to be better supported by morphology, as both *Phaenostoma posticatum* and the core *Phaenonotum* species share the unique shape of the metanepisternum (widened in posterior third, narrowing anteriorly, Fig. 7); all remaining coelostomatine species examined including *Phaenostoma kontax*, *Lachnodacnum*, *Phaenonotum caribense* and *Cyclotypus* have the metanepisternum with lateral margins parallel-sided (and hence the same width) throughout. However, the undescribed *Phaenonotum* species from Peru (MF845) bears the parallel-sided rather than anteriorly narrowing metanepisternum despite being strongly supported as a member of the core *Phaenonotum* clade in our analyses. Hence, the phylogenetic significance of this character needs to be further tested.

#### ACKNOWLEDGEMENTS

We are grateful to the authorities and personnel of the Cuban Ministry of Science, Technology and Environment (CICA-CITMA) and the Empresa Nacional para la Protección de la Flora y la Fauna (ENPFF) for providing access to protected areas under their control; to Carlos Suriel, Edda Martínez Caléz and Marilyn Colon Negron for their help with arranging the collecting permits in the Dominican Republic and Puerto Rico; to Robert Anderson (Canadian Museum of Nature, Ottawa), Matthew L. Gimmel (Santa Barbara Museum of Natural History) and people of the Cuba and Jamaica CarBio teams for their help during our fieldwork; to S. Peck (Carleton University) and curators of the institutional collections (see Material and methods) for the possibility to examine their collections; and to Andrew Short (University of Kansas, Lawrence, USA), Joseph Parker (Columbia University, New York) and Bruno Clarkson (Universidade Federal do Rio de Janeiro) for providing continental specimens used in our analyses. We specially acknowledge the comments and critique of Andrew Short and two anonymous reviewers on the earlier version of this draft, and Robert Angus (BMNH) for a careful correction of our English text. The study was supported by the grant SVV 260 434/2017 at the Department of Zoology, Charles University and the Rufford Foundation (15144-1) to A.D.H. and by the Ministry of Culture of the Czech Republic (DKRVO 2017/14, National Museum, 00023272) to M.F.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Supplement S1.** Molecular data and phylogenetic and divergence dating analyses.

**Supplement S2.** Input data and results of the BioGeoBEARS analyses.

**Supplement S3.** Complete data of all examined specimens.