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SPECIAL PAPER

Evolutionary and biogeographical history of the land snail family Urocoptidae (Gastropoda: Pulmonata) across the Caribbean region

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ABSTRACT

Aim Land snails, because of their low vagility, are ideal organisms for probing biogeographical hypotheses. This study is the first to examine the evolutionary and biogeographical history of a group of land snails from the Caribbean region using molecular phylogenetics. It focuses on the family Urocoptidae that displays extraordinary diversity, particularly in the Greater Antilles.

Location Caribbean region.

Methods We reconstructed the phylogeny of Urocoptidae based on multilocus (partial 28S, H3 and COI sequences) analyses (MrBayes, BEAST, GARLI) of 65 species, representing 44 recognized genera. Biogeographical analyses of a subset of the time-calibrated BEAST trees were made both with (DEC and DEC+J analysis in BioGeoBEARS) and without (S-DIVA in RASP) palaeogeographical assumptions. In the DEC and DEC+J analyses we examined the effect of different settings for dispersal between directly connected areas relative to that between areas without direct land connection.

Results Urocoptidae has been present on the Greater Antilles Arc from at least Middle Eocene onwards. Morphologically diverse and previously unrecognized clades evolved on most Caribbean (palaeo)islands. Jamaica was colonized at least twice. Dispersal multiplier matrices with moderately constrained dispersal between areas without direct land connections describe the phylogeographical history of the family with higher DEC and DEC+J lnL scores than uniform matrices.

Main conclusions Urocoptids constitute an old element of the Greater Antillean biota, predating a proposed GAARlandia landspan connection to South America. The biogeographical history and evolution of Urocoptidae were shaped primarily by the geographical distribution of Caribbean landmasses, in combination with occasional oversea dispersal. Oversea dispersal allowed colonization of palaeogeographically isolated areas, such as Jamaica and present-day western Cuba, where presumably the absence of ecological competitors led to independent radiations into similar shell types.

Keywords
Antilles, colonization, dispersal, endemic clades, morphological radiation, Urocoptidae, West Indies

INTRODUCTION

The West Indies are one of the world's most important biodiversity hotspots (Smith *et al.*, 2005) and a 'laboratory of biogeography and evolution' (Ricklefs & Bermingham, 2008) offering important biogeographical insights (see Carstensen *et al.*, 2012). The evolution of a diverse and largely unique West Indian biota is attributed to the area's long and complex geological history and to the position of the Antilles as separate islands near the two ancient continental landmasses of North and South America. The Greater Antilles Arc (consisting of Cuba, northern Hispaniola and Puerto Rico)

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formed when a proto-Antillean volcanic island arc, situated at the edge of the north-east moving Caribbean plate, collided with the North American continental plate during the early Cenozoic (Pindell, 1994; Iturralde-Vinent & MacPhee, 1999; Pindell & Kennan, 2009). Since then, horizontal and vertical tectonic movements and changes in sea level have led to changes in the areas exposed and their interconnections (Iturralde-Vinent & MacPhee, 1999). Jamaica is not part of the Greater Antilles Arc and has remained an island since its emergence in the Miocene (Pindell, 1994; Robinson, 1994; Pindell & Kennan, 2009; but see Iturralde-Vinent & MacPhee, 1999). The Lesser Antilles emerged comparatively recently, as the subaerial part of two volcanic arcs (Bouysse *et al.*, 1990).

The origin of the Antillean biota has been explained by three scenarios, assuming different time-scales and source areas: (1) vicariance, assuming a connection between the proto-Antillean island arc and the southern tip of the North American continent in the Late Cretaceous and Early Cenozoic (Rosen, 1976, 1985), (2) overwater dispersal throughout the Cenozoic from the surrounding landmasses (Hedges, 1996), (3) a combination of overland dispersal and subsequent vicariance, assuming a late Eocene/early Oligocene Greater Antilles + Aves Ridge landspan (GAARlandia) to South America (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). In recent years, the debate has revolved around the contribution of a GAARlandia landspan versus oversea dispersal in seeding the West Indian biota (see Ali, 2012).

With their generally low vagility, land snails are ideal for tests of vicariance (Hausdorf & Hennig, 2006), for studies on passive dispersal (Cowie & Holland, 2006), and for models of island biogeography (Cameron *et al.*, 2013). The limited dispersal propensity of land snails can leave an imprint on distributional patterns of species and genera, even in the absence of obvious barriers (e.g. see Uit de Weerd *et al.*, 2004). The only modes of oversea dispersal available to snails are passive dispersal by rafting (Dall, 1896) or by air, either by hurricanes or by hitchhiking on other organisms (Rees, 1965; Vagvolgyi, 1975; Parent & Crespi, 2006). The significance of land snails for studies of West Indian biogeography has long been recognized (Simpson, 1895; Scharff, 1912: 265–273; Schuchert, 1935: 89–93). Even so, no comprehensive molecular phylogenetic analyses have previously been published on any group of land snails from the Caribbean region.

The family Urocoptidae, a family of generally medium-sized, high-spired pulmonate land snails, has an extremely appropriate distribution to test hypotheses about Caribbean biogeography and the evolution of Caribbean biodiversity (Pilsbry, 1904: xx–xxiv; Paul, 1989). The family occurs on the Greater Antilles, the Lesser Antilles, some of the Bahama Islands, the Cayman Islands, and along the continental Caribbean coast, and the Gulf coast of North America. It contributes considerably to the land snail diversity of the Greater Antilles. Five subfamilies are recognized: Urocoptinae, Microceraminae, Tetrentodontinae, Brachypodellinae and Apominae (Uit de Weerd, 2008; Thompson, 2012). Together these contain 65 genera (Schileyko, 1999; Uit de Weerd, 2008) and at least 714 species (Richardson, 1991). Most of the genera are confined to the Greater Antilles. The distribution of three genera extends to mainland coastal regions: *Cochlodinella* (populations of an otherwise Cuban species in Florida), and *Brachypodella* (Caribbean coastal regions of South and North America), and *Microceramus* (Costa Rica to Texas, Florida, Leeward Antilles off South America).

Previous studies on the superfamily Urocoptoidea provide a relevant phylogenetic and biogeographical framework for more in-depth studies of urocoptids. Within Urocoptoidea, Urocoptidae constitutes a monophyletic group (Uit de Weerd, 2008) defined by an anatomically distinguishable (plaited) jaw. The basal lineages and earliest fossils of the Urocoptoidea are found in south-west North America (see Uit de Weerd, 2008; and references therein). An Antillean distribution of subgroups of Urocoptoidea has been explained by either the tectonic eastward movement of the proto-Antillean island arc during the Late Cretaceous and early Cenozoic (Uit de Weerd, 2008) or overland dispersal via South America to the GAARlandia landspan during the Late Eocene/Early Oligocene (Harasewych, 2012). Either hypothesis could potentially apply to the distribution of Urocoptidae. The possibility that some of the mainland species – in particular the North and South American species of the possibly non-monophyletic genus *Brachypodella* (see Paul, 1989) – represent basal offshoots within the family cannot be excluded *a priori*. Alternatively, urocoptids may have arrived on the Greater Antilles by oversea dispersal within a wider temporal window (see Hedges, 2006). The explanatory power of these three alternative hypotheses can be compared if the approximate age and the origin of the urocoptid clade are known.

Relationships and biogeographical patterns within Urocoptidae are expected to reflect the geological history of the Caribbean area (see Paul, 1989). The phylogeny of Urocoptidae, however, is still unclear. Most studies have been limited to single islands. Thus, Tetrentodontinae and Apominae were originally defined as island-endemic subfamilies in studies focusing on Cuba (Jaume & de la Torre, 1976) and Jamaica (Paul, 1983), respectively, without reference to urocoptids from other areas. Hypotheses about urocoptid interrelationships across wider geographical spans have been based on one or a few conflicting morphological characters, i.e. conchological characters (Pilsbry, 1903, 1904; Paul, 1989) and characters of the feeding apparatus of 43 species (Pilsbry, 1903, 1904). As these characters interact with the external environment, they may be susceptible to parallel or convergent evolution.

As an independent data set, DNA sequences have the potential to resolve the interrelationships within Urocoptidae. This study aims to address the following questions: firstly, what is the age and geographical origin of Urocoptidae as a

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clade?, and secondly, to what extent do patterns of phylogenetic relationships within Urocoptidae reflect Caribbean geological history?

MATERIALS AND METHODS

Samples and laboratory procedures

Taxon sampling was based on diversity at the genus level, geographical distribution, and accessibility through fieldwork or existing collections. As nearly all urocoptid genera are highly endemic, in most cases a single species per genus was sampled. We sampled an ingroup of 65 urocoptid species representing 44 described genera (see Table S1.1 in Appendix S1 in Supporting Information) from all five previously recognized subfamilies. The sampling sites cover all Greater Antillean islands, as well as the Cayman Islands, many of the Lesser Antilles, and mainland South and North America. We expanded the taxonomic sampling to the species level when the morphology-based generic delineation was uncertain (*Autocoptis* versus *Urocoptis* + *Bactrocoptis*, *Brachypodella*). For *Cochlodinella* and *Brachypodella* we added samples from Florida and continental Caribbean regions, respectively, to take into account the reach of their distribution beyond the Antilles. Three undescribed species were sampled, all from Hispaniola. One of these was identified as *Brachypodella* sp., the other two ('*species A*', '*species B*') could not be assigned to any described genus. As outgroups we selected *Eucalodium*, *Archegocoptis*, and *Cerion*. These taxa represent the groups most closely related to Urocoptidae (Uit de Weerd, 2008). When confirmation of the phylogenetic position inferred for a particular sample was needed (*Autocoptis evelynae* sample), we added another sample assigned to the same species.

For DNA-extraction a Qiagen extraction kit was used, as described by Uit de Weerd (2008). As phylogenetic markers we selected partial 28S, partial COI, and partial histone H3. The 28S primers and PCR conditions were as described in Uit de Weerd (2008), but omitting the primers 28S1489F and 28S2210R that amplify the highly conserved and therefore at this level largely uninformative 3′ region. For nine specimens 28S sequences had already been determined by Uit de Weerd (2008). For two of these, *Autocoptis (Autocoptis) menkeana* and *Cerion striatellum crassilabris*, we used an existing H3 sequence (Uit de Weerd & Gittenberger, 2013). For the H3 primers and PCR reaction we followed Uit de Weerd & Gittenberger (2013). For COI various primer combinations were used in the PCR and the sequencing reaction (see Tables S1.2 & S1.3 in Appendix S1). PCR product was cleaned using Qiagen columns, preceded by gel purification if multiple bands were present. Following Big Dye single extension reactions with each of the initial PCR primers, sequences were obtained on a CEQTM 8000 sequencer (Beckman Coulter) or through Macrogen (Korea, Amsterdam).

Phylogenetic analyses

Sequences were assembled and checked using the programs Pregap 4 and Gap 4 (Staden Package; Staden *et al.*, 2000), respectively, and were subsequently aligned in CLC Free Workbench 4.0.1 (CLC bio A/S). Ambiguously aligned regions in the 28S alignment were excluded from further analyses.

Prior to phylogenetic analyses the amount of transitional saturation in the 28S, H3 and COI data sets was checked in DAMBE 5.3.0 (Xia, 2013) by comparing the pairwise number of transitional and number of transversional differences versus the simultaneously estimated ML TN93 distances. In addition, we ascertained that there were no significant between-taxon differences in base frequencies within any data set (Chi-square test). We employed PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) (with options branchlengths = linked; models = mrbayes/=beast; model_selection = BIC; search = all) to find the best-fit partitioning scheme for the three markers used, together with substitution and rate heterogeneity models for those partitions. We considered the possibility of conflicting phylogenetic signal between partitions by performing all phylogenetic analyses for each partition individually and comparing the results using Treegraph 2 (Stöver & Müller, 2010).

Phylogenetic relationships were first reconstructed without any assumptions about node ages, using both a maximum likelihood (ML) bootstrap analysis (GARLI 2.01) and a Bayesian approach (MrBayes 3.2.4) with the partitions and models selected by PartitionFinder 1.1.1. The ML bootstrap analysis consisted of 1000 replicates. For each replicate default settings were used, except for modifications in order to speed up the analysis (genthreshfortopoterm = 10000 searchreps = 1 treerejectionthreshold = 25.0, but numberofprecreductions = 20) and to reduce the size of the output files (log every = 100000, save every = 100000). In the MrBayes analyses the stationary nucleotide frequencies, the rate matrix parameters, and, where relevant, the gamma shape parameter and proportion of invariable sites were unlinked across partitions. Default prior distribution parameter settings were used. The analysis consisted of two parallel runs with six chains each. These were run for 60,000,000 generations, discarding the first 10,000,000 generations as a burn-in. Parameters and trees both were sampled every 1000th generation, resulting in 100,000 states and trees.

To place the phylogenetic relationships within the temporal framework of Caribbean geological history we subsequently performed an analysis in BEAST 1.8.1, assuming an uncorrelated relaxed clock with a lognormal distribution. The root of the tree was calibrated to be of the Maastrichtian (66.0–72.1 Ma) age, using a lognormal prior distribution with a minimum age of 66.0 and a median value of 68.63 Ma and an upper 95% quantile coinciding with the start of the Maastrichtian 72.1 Ma (parameter settings mean = "3" stdev = "0.51" offset = "66.0" meanInRealSpace = "true").

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This was based on the earliest fossil evidence of our combined ingroup and outgroup, namely a late Maastrichtian fossil assigned to the Cerionidae lineage (Roth & Hartman, 1998), and the earliest evidence for the split between our combined ingroup plus outgroup and its holospirid sister lineage (see Uit de Weerd, 2008; Thompson, 2012) based on an early Maastrichtian fossil of *Holospira* (del Carmen Perrilliat *et al.*, 2000). Such a relatively well-corroborated deep fossil calibration can provide an alternative to ingroup calibration (Sauquet *et al.*, 2012; Mello & Schrago, 2014), given the absence of fossils that can be unambiguously assigned to extant taxa within Urocoptidae itself. A different starting tree compatible with the age priors was used for each BEAST run. All settings for the Markov chain Monte Carlo (MCMC) were as in MrBayes. For both the MrBayes and the BEAST analysis we checked if the two parallel runs had converged within the burn-in of 10,000,000 generations by comparing the harmonic mean of the post-burnin samples for both runs, and by comparing the tree topology within these runs using AWTY (Nylander *et al.*, 2008). The effective sample size of the combined post-burnin runs was calculated using Tracer 1.6 (Rambaut *et al.*, 2014). Maximum clade probability trees with mean node heights for the set of 100,000 post-burnin trees from the MrBayes and from the BEAST analysis were obtained using TreeAnnotator 1.8.0.

Biogeographical analyses

All biogeographical analyses were based on trees from the BEAST analyses, with outgroup taxa removed. We first explored the effect of different dispersal multiplier matrices and different models on maximum likelihood ancestral range reconstructions. These analyses were performed on the maximum probability tree with mean node heights using BioGeoBEARS (Matzke, 2014). This program implements both a DEC (Dispersal-Extinction-Cladogenesis) model and a DEC+J model. The DEC model may be inappropriate when terminal taxa are restricted to single areas (Ree & Smith, 2008). For this reason the DEC+J model adds founder event speciation to the DEC model (Matzke, 2014).

We assigned the terminal taxa, based on collection site, to 11 different areas representing currently or previously more or less discrete landmasses in the Caribbean (see Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006). These are: (1) western Cuba, (2) central Cuba, (3) eastern Cuba, (4) southern Hispaniola (following Maurrasse *et al.*, 1980), (5) northern Hispaniola, (6) Puerto Rico + Virgin Islands (following Larue, 1994), (7) Lesser Antillean island arcs + Barbados, (8) Cayman Islands, (9) Jamaica, (10) continental South America (south of the Panama isthmus) including the faunistically associated (see Dávalos, 2004; Hedges, 2006; Crews & Gillespie, 2010) Aruba-Tobago Belt (Iturralde-Vinent & MacPhee, 1999), (11) continental North America (north of the Panama isthmus). The middle of the Havana-Matanzas channel at 82°00′ W longitude was considered the boundary between western and central Cuba, the Guacanayabo-Nipe Fault was used to separate central Cuba from eastern Cuba (in both cases following Iturralde-Vinent & MacPhee, 1999; MacPhee *et al.*, 2003). These two barriers are thought to have left their imprint in the geographical patterning of relationships of several Cuban groups (Glor *et al.*, 2004; Rodríguez *et al.*, 2010). The maximum range size was set to 3. This is, to our knowledge, the maximum number of areas covered by any extant urocoptid species, namely *Microceramus gossei* (see Pilsbry, 1904; Rosenberg & Muratov, 2006; Franke & Fernández, 2012).

We distinguished seven time slices (see Table S2.4 in Appendix S2) based on differences in the subaerial presence of areas (coded in a stratified areas-allowed matrix) and land connectivity between them (coded as a stratified dispersal multiplier matrix). In the stratified dispersal multiplier matrix, we distinguished between dispersal between directly connected adjacent land areas and land areas separated by sea or other land areas. In land snails, active dispersal and gradual range expansion can only occur between areas directly connected by land, whereas dispersal across longer stretches of land or across sea barriers must always be passive.

We first selected an optimal dispersal multiplier matrix based on its likelihood score on the maximum clade credibility tree from the BEAST analyses. Under a DEC and DEC+J model we examined a set of 16 stratified dispersal multiplier matrices in which dispersal probabilities between directly connected areas versus dispersal between areas not directly connected varied (1.0, 0.5, 0.1, 0.01) independently relative to continued existence in the same area, i.e. the diagonal in the dispersal multiplier matrices (set to 1). In these BioGeoBEARS analyses shortcuts that speed up the ML search were avoided (run_object$speedup=FALSE). Using the dispersal multiplier matrix yielding the highest lnL score on the maximum clade credibility tree we optimized the ancestral areas on a subset of 100 trees from the BEAST analysis (sampling every 1,000,000th generation, for computational reasons) in BioGeoBEARS using both a DEC and DEC+J model. This approach yields the probabilities (marginal distributions) of alternative ancestral ranges of the most recent common ancestor of the Urocoptidae while taking into account not only biogeographical uncertainty for that particular node but also phylogenetic and clade age uncertainties in other parts of the tree. Apart from using the standard shortcut (run_object$speedup=TRUE) for computational reasons, all settings were identical to those in the previous analyses. Any trees that had a root age younger than the oldest imposed time period (40–56 Ma) were re-analysed separately with this last time period removed from the time periods matrix, the stratified areas-allowed matrix and the stratified dispersal multiplier matrix. The probabilities of alternative ancestral ranges for the most recent common ancestor (mrca) of the Urocoptidae were calculated by averaging the probability of each range for this node across the 100 trees. To compare the DEC and DEC+J lnL score under the selected dispersal mul-

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tiplier matrix with the lnL scores under equal dispersal rates between all areas (no effect of direct land connections), the analysis was repeated for each of the 100 trees using uniform dispersal rates of 1, 0.5, 0.1 or 0.01.

To test the robustness of the biogeographical reconstructions under a fundamentally different model (see Matzke, 2014), we performed parsimony-based S-DIVA analysis in RASP 3.2 (Yu *et al.*, 2010, 2014). This was done on a subsample of 10,000 trees from the BEAST analysis with the options 'allow extinction' and 'allow reconstruction' in effect. The only further input for this analysis consisted of the areas of the terminal taxa.

RESULTS

Sequence data

The region of 28S spanned by the primers 28S2 and 28S2119R ranged in length from 1602 bases (*Brachypodella morini*) to 1646 (*Anoma levis*) for the complete sequences. Indels were confined to 20 regions. Five of these contained a single base indel, two a three-base indel. In addition, *Brachypodella morini* and *Brachypodella speluncae* shared a 41-base deletion. The remaining 12 regions could not be aligned unambiguously, and were therefore excluded from the analyses. All H3 sequences were 267 bases long. The length of COI sequences varied due to different successful 3′ reverse primers (see Tables S1.2 & S1.3 in Appendix S1). Most COI sequences were 1256 bases in length. For sequences extending further in the 3′ direction only the part overlapping with the regular 1256 bases was considered in further analyses. We found strong indications of transitional saturation of COI in DAMBE, caused by the third codon position (see Fig. S3.7 in Appendix S3). This position was subsequently excluded from all further analyses.

Phylogenetic analyses

PartitionFinder 1.1.1 identified the following partitions and substitution and heterogeneity models: (1) 28S, with a GTR+I+G model; (2) histone H3, with a SYM+I+G model; (3) COI (codon position 1 and 2), with a GTR+I+G model. Separate phylogenetic analyses of these partitions generally highly support (≥ 0.95 Bayesian posterior probability, ≥ 75% ML bootstrap) identical clades (see Figs. S3.8–S3.29 in Appendix S3). The only discordance between partitions is their occasional support (≥ 0.95 BPP) for conflicting placements of *Amphicosmia salleana*, *Apoma chemnitzianum*, *Brachypodella dubia*, *Macroceramus microdon* and *Tomelasmus irroratus* in the Bayesian analyses (see Figs. S3.21–S3.29 and Table S3.6 in Appendix S3). The GARLI ML bootstrap analyses of the separate partitions did not yield any conflicting ≥ 75% bootstrap supported clades. Overall, most of the highly supported clades are relatively young, as the markers by themselves fail to resolve many of the more basal branches within Urocoptidae with high support values. Based on these observations all further analyses were based on the concatenated data set.

The two runs of each Bayesian analysis (MrBayes and BEAST) converged within the burnin of 10,000,000 generations, as shown by their similar lnL values (harmonic mean of −14276.21 and −14276.58 in MrBayes; harmonic mean of −14328.44 and −14315.40 in BEAST) and clade support values for the post-burnin part of each run. Clade support values for the parallel runs differed by 0.0007 (0.07%) on average between the parallel MrBayes runs and by 0.0021 (0.21%) on average between the parallel BEAST runs. The effective sample size across the postburnin samples exceeded 200 for all parameters in the MrBayes (≥ 38208) and in the BEAST (≥ 931) analyses, as recommended (Drummond *et al.*, 2007). The mean standard deviation of the uncorrelated lognormal relaxed clock employed in the BEAST analysis was 0.36 (95% HPD 0.25–0.48), indicating relatively clocklike evolution (Drummond *et al.*, 2007).

All analyses (MrBayes, BEAST, GARLI) retrieved several identical highly supported (BPP ≥ 0.95, ML bootstrap ≥ 75%) ingroup clades (Fig. 1), some of which are discussed below. The BEAST analysis dates the most recent common ancestor of Urocoptidae at a mean 48.1 (95% HPD 37.1–58.6) Ma (Table 1, Fig. 1). As a basal division within Urocoptidae all analyses identify a clade (clade A) containing most genera with medium-sized cylindrical, conic or fusiform shells traditionally assigned to the subfamily Urocoptinae, and a clade (clade B) containing mostly genera with relatively small and slender shells, most of which are assigned to the Brachypodellinae. However, this basal phylogenetic bipartition does not completely coincide with the taxonomic distinction between these two subfamilies. Notably, *Autocoptis (Urocoptola) evelynae*, a species with a narrow cylindric shell 'not closely related to any other species' according to Clench (1935), is nested within clade B separated from the supposedly consubgeneric *Autocoptis (Urocoptola)* species in clade A. This surprising placement is strongly and consistently supported for both *Autocoptis (Urocoptola) evelynae* samples by all three markers independently (see Figs. S3.21–S3.29 in Appendix S3). The Microceraminae and nearly all genera assigned to Tetrentodontinae are part of clade A. Apominae and Brachypodellinae are contained in clade B.

Most genera cluster according to geographical region rather than subfamily. Clade A contains several subclades with high support from the concatenated data set and containing at least three genera or subgenera all confined to one Greater Antillean island or a region thereof: (1) a western Cuban clade, (2) a central Cuban clade, (3) an eastern Cuban clade, (4) a Hispaniolan clade and (5) a Jamaican clade. With the exception of the western Cuban clade, all clades are also supported (≥75% ML bootstrap and/or ≥ 0.95 BPP) by at least two markers separately (see Table S3.7 in Appendix S3). Only the central Cuban clade contains a genus also known from a mainland area, namely *Cochlodinella*, found in central Cuba and in southern Florida (both areas sampled). The mean ages assigned to these clades (Fig. 1,

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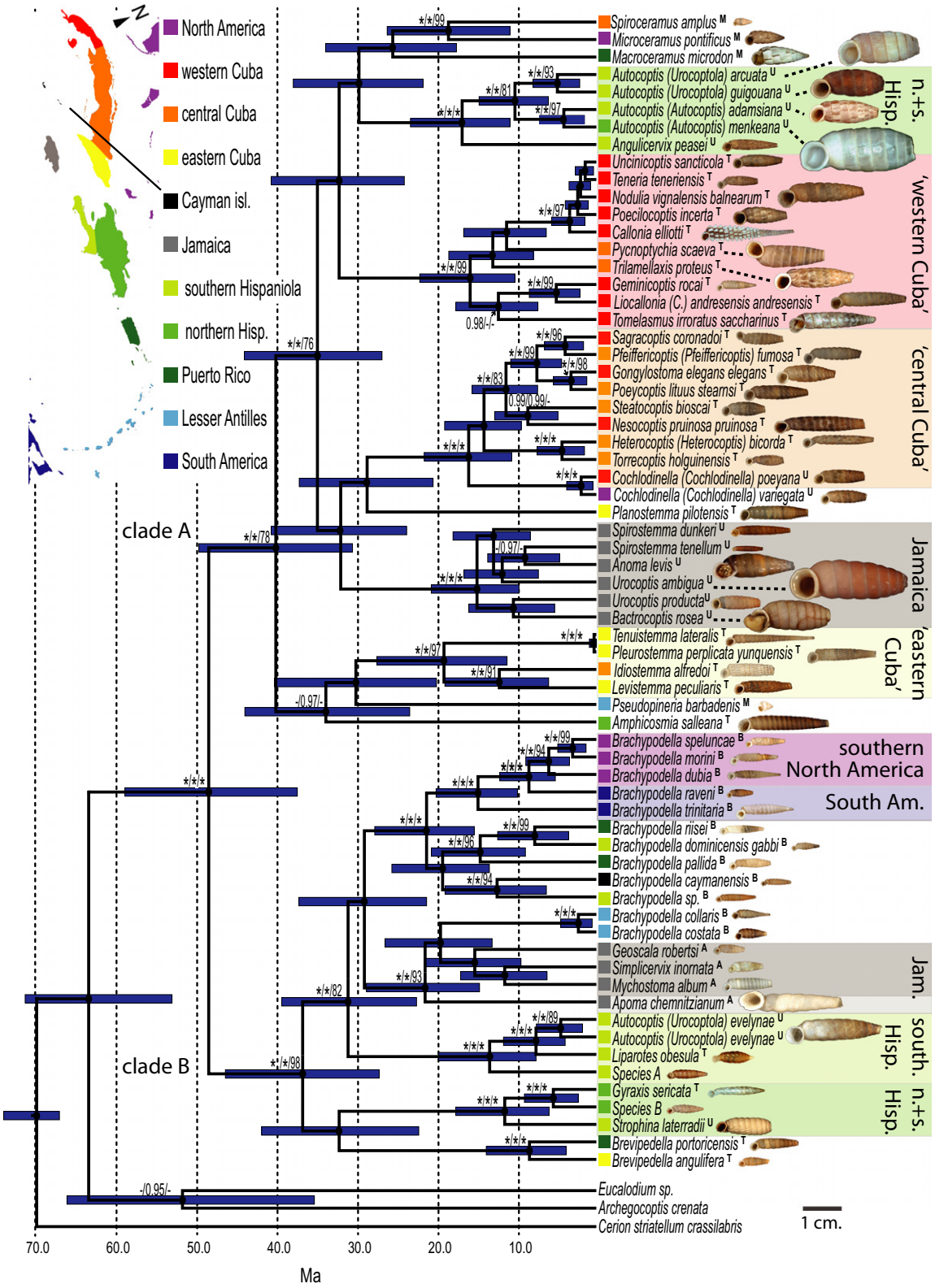


Figure 1 Maximum clade credibility tree with mean node heights from the BEAST analysis. Blue bars indicate 95% confidence intervals for node ages. The scale bar below denotes the time in million years ago (Ma). Letters in superscript behind species names refer to the subfamilial assignment according to Schileyko (1999): A = Apominae, B = Brachypodellinae, M = Microceraminae, T = Tetrentodontinae, U = Urocoptinae. Numbers above branches are MrBayes posterior probabilities (≥ 0.95), BEAST posterior probabilities (≥ 0.95) and GARLI maximum likelihood bootstrap values (≥ 75), respectively. Complete support from an analysis, i.e. Bayesian posterior probabilities of 1.0 or bootstrap values of 100, is indicated with an asterisk. The 1 centimetre scale bar refers to shell size.

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Table 1 Mean age and 95% highest posterior density (HPD) interval of selected clades according to the BEAST analysis. As clade age and time to the most recent common ancestor of Apominae taxa examined coincide in < 99% of the trees, clade ages are shown here separately between parentheses.

Basal clade	Area	Clade composition	tmrca mean	tmrca 95% HPD lower	tmrca 95% HPD upper	tstem mrca mean	tstem mrca 95% HPD lower	tstem mrca 95% HPD upper
N/A	Circum-Caribbean	Urocoptidae	48.1	37.1	58.6	66.1	53.7	75.0
A	Western Cuba	*Uncinicoptis*, *Teneria*, *Nodulia*, *Poecilocoptis*, *Callonia*, *Geminicoptis*, *Liocallonia*, *Tomelasmus*, *Pycnoptychia*, *Trilamellaxis*	15.7	10.1	21.9	31.3	22.5	40.2
A	Central Cuba	*Cochlodinella*, *Heterocoptis*, *Torrecoptis*, *Gongylostoma*, *Poeycoptis*, *Pfeiffericoptis*, *Sagracoptis*, *Steatocoptis*, *Nesocoptis*	15.9	10.5	21.4	29.9	20.8	39.6
A	Eastern Cuba	*Levistemma*, *Idiostemma*, *Tenuistemma*, *Pleurostemma*	18.9	11.1	27.3	30.6	20.3	41.3
A	Northern + southern Hispaniola	*Autocoptis (Autocoptis) adamsiana*, *Autocoptis (Autocoptis) menkeana*, *Autocoptis (Urocoptola) arcuata*. *Autocoptis (Urocoptola) guigouana*, *Angulicervix peasei*	16.7	10.7	23.1	30.0	21.5	38.6
A	Jamaica	*Anoma*, *Spirostemma*, *Bactrocoptis*, *Urocoptis*	14.8	9.6	20.5	30.8	21.7	39.9
B	South America + southern North America	*Brachypodella trinitaria*, *B. raveni*, *B. dubia*, *B. morini*, *B. speluncae*	14.7	9.8	19.9	20.5	14.6	26.9
B	Southern North America	*Brachypodella dubia*, *B. morini*, *B. speluncae*	5.9	3.3	8.8	8.4	5.0	12.0
B	Southern Hispaniola (Massif de la Hotte)	*Liparotes obesula*, *Autocoptis (Urocoptola) evelynae*, *species* A	13.3	7.5	19.6	30.3	22.0	39.0
B	N+S Hispaniola	*Strophina*, *Gyraxis*, *species* B	11.4	5.9	17.5	32.6	22.9	42.8
B	Jamaica (+ Barbados and Guadeloupe)	mrca Apominae* (*Apoma*, *Mychostoma*, *Simplicervix*, *Geoscala*)	21.0 (21.3)	14.0 (14.5)	28.3 (28.6)	28.0	17.6	37.1
B	Jamaica (+ Barbados and Guadeloupe)	mrca *Mychostoma*, *Simplicervix*, *Geoscala*	15.5 (15.1)	9.0 (9.4)	22.5 (21.2)	20.3	12.6	29.2

*The most recent common ancestor also has *Brachypodella collaris* from Guadeloupe and/or *Brachypodella costata* from Barbados as descendent species in at least some of the BEAST trees.

Table 1) are relatively similar, ranging from 14.8 Ma (95% HPD 9.6–20.5) for the Jamaican clade to 18.9 (95% HPD 11.1–27.3) Ma for the eastern Cuban clade. The extraordinarily high sequence similarity of the morphologically disparate samples of *Tenuistemma lateralis* and *Pleurostemma perplicata yunquensis* in the latter clade (see Fig. 1) will be dealt with in a subsequent paper that will zoom in to the intraspecific and population level (Uit de Weerd, in prep.). Clade B contains two highly supported subclades endemic to Hispaniola, both independently supported (≥75% ML bootstrap and/or ≥ 0.95 BPP) by all three markers (see Table S3.7 in Appendix S3). One of these, consisting of the genus *Liparotes* together with *Autocoptis* (*Urocoptola*) *evelynae* and unassigned *species A*, is confined to the Massif de la Hotte on the western side of the Tiburon Peninsula in southern Hispaniola. The other consists of the genus *Strophina*, from Beata Island near southern Hispaniola, as a sister group to *Gyraxis* and unassigned *species B* from the province Hato Mayor, north-western Dominican Republic. Both subclades are of similar age (mean age 13.3 and 11.4 Ma respectively).

The monophyly of the Jamaican endemic subfamily Apominae in clade B is neither confirmed nor refuted by any well-supported nodes. The four genera assigned to it (*Apoma*, *Mychostoma*, *Simplicervix* and *Geoscala*) group with *Brachypodella collaris* from Guadeloupe and *Brachypodella costata* from Barbados in a strongly supported but relatively poorly resolved clade (age 21.3 Ma, 95% HPD 14.5–28.6),

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rendering the genus *Brachypodella* non-monophyletic. *Geoscala*, *Mychostoma* and *Simplicervix* form a clade (age 15.1 Ma, 95% HPD 9.4–21.2) –albeit not highly supported– to the exclusion of *Apoma*, as was suggested by Paul (1983) on morphological grounds. In most, but not all, trees *Apoma* splits off before the lineage leading to *Brachypodella collaris* and *Brachypodella costata*. The remaining *Brachypodella* species in clade B constitute a highly supported separate clade, with all (southern) North American species as a clade (mean age mrca 5.9 Ma, 95% HPD 3.3–8.8) nested successively among the South American (mean age mrca 14.7 Ma, 95% HPD 9.8–19.9) and among the West Indian species.

Biogeographical analyses

All ML scores in the ancestral area reconstruction on the maximum clade credibility tree with mean node heights were significantly higher under a DEC+J model than under a DEC model (see Table S2.5 in Appendix S2) irrespective of the dispersal multiplier matrices used. For both the DEC and the DEC+J model the highest likelihood score on the maximum clade credibility tree (lnL = −185.4 and −166.2 respectively) was obtained with a dispersal probability of 0.5 between directly and 0.1 between not directly connected areas. This dispersal multiplier matrix was subsequently used to infer the ancestral range of Urocoptidae in the DEC and DEC+J analyses of the subset of 100 trees in BioGeoBEARS. In both analyses it yielded significantly higher lnL scores (Wilcoxon signed-rank test: $P < 0.001$; mean -188.08 ± 9.99 for DEC, mean -169.37 ± 12.56 for DEC+J) than any of the matrices assuming equal dispersal rates of 1, 0.5, 0.1 or 0.01 between all areas. Under the optimal matrix, across the 100 trees the mean estimate for founder event speciation was high under the DEC+J model ($j = 0.309 \pm 0.050$), compared to that of anagenetic range expansion ($d = 0.009 \pm 0.002$; 0.033 ± 0.002 for DEC) and contraction ($e = 0.008 \pm 0.002$; 0.022 ± 0.002 for DEC).

In the DEC+J analyses, the Jamaican clade consisting of *Anoma*, *Spirostemma, Bactrocoptis* and *Urocoptis* has a non-Jamaican mrca as most probable reconstruction in 36 of the 100 trees sampled. Such a non-Jamaican mrca was invoked in trees in which the age of the clade exceeded or approached the earliest inclusion of Jamaica (16 Ma, see Table S2.4 in Appendix S2) in the time slices. These conditions led, respectively, to zero probabilities for a Jamaican distribution by anagenetic range expansion and contraction events prior to the mrca, or to low probabilities for these events compared to a combination of jump dispersal, anagenetic range expansion and contraction events in the daughter lineages of the mrca under the DEC+J model. The latter did not happen under the DEC model, which gave a non-Jamaican area as the most probable distribution for the mrca in 30 of the trees.

For all analyses (DEC, DEC+J, S-DIVA) of a subset of BEAST trees, the probability that the most recent common ancestor of Urocoptidae was present in the Greater Antilles Arc region exceeded 0.95 (Table 2).

Table 2 Probabilities of the ancestral range of the Urocoptidae covering a particular area, calculated as the average fraction of reconstructions across a subset of BEAST trees (100 for DEC and DEC+J; 10.000 for DIVA) including that area.

Ancestral area	P (DEC)	P (DEC+J)	P (DIVA)
Including western Cuba	0.16	0.20	0.099
Including central Cuba	0.56	0.34	0.404
Including eastern Cuba	0.54	0.56	0.468
Including southern Hispaniola	0.00*	0.00*	0.894
Including northern Hispaniola	0.52	0.61	0.448
Including Puerto Rico	0.57	0.48	0.127
Including the Lesser Antilles	0.00*	0.00*	0.448
Including the Cayman Islands	0.00*	0.00*	0.000
Including Jamaica	0.00*	0.00*	0.033
Including South America	0.19	0.16	0.000
Including North America	0.13	0.09	0.078
Including (part of) the Greater Antilles Arc (Cuba, northern Hispaniola, Puerto Rico)	1.00	1.00	0.973

*Area coded as absent in the basalmost timeslice.

DISCUSSION

Age and origin of Urocoptidae

The BEAST, DEC, DEC+J and S-DIVA analyses together support the presence of the mrca of the extant Urocoptidae on the Greater Antilles Arc in the Palaeogene (48.1 Ma, 95% HPD 37.1–58.6 Ma). The lineage leading to the extant Urocoptidae probably colonized the Greater Antilles Arc shortly after the Arc's formation in the early Eocene and just prior to the divergence into the basal urocoptid lineages. The inferred age and ancestral distribution of the mrca of Urocoptidae coincide with the first emergence of parts of the Greater Antilles Arc, between approximately 55–49 Ma onward (Graham, 2003; Crews & Gillespie, 2010). An earlier late Cretaceous vicariant origin of the Urocoptidae by means of a Proto-Antillean island arc connection with North America (see Uit de Weerd, 2008) cannot be excluded on the basis of our data, given the old stem age of the lineage leading to the mrca of Urocoptidae. Our data rule out a role of a GAARlandia landspan, as this supposed landspan existed 35–33 Ma, well after the mrca of Urocoptidae.

While Graham (2003) sets the 'early and sustained emergence of most of the proto-Antilles' at the middle Eocene (49 Ma), Iturralde-Vinent & MacPhee (1999) argue that of these areas 'none seems to have survived as emergent land into the subsequent interval (latest Eocene to Middle Miocene)'. The inferred survival of two lineages of Urocoptidae in the area from approximately 48.1 Ma onwards fits well with the scenario proposed by Graham (2003). We cannot, however, exclude the more dynamic scenario proposed by Iturralde-Vinent & MacPhee (1999). Lineages may have survived by 'seeding' from one island to another, a situation similar to that inferred for some lineages of squamate reptiles on the geologically younger Lesser Antilles (Thorpe *et al.*, 2005, 2008).

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To our knowledge this is the first indication of a pre-Oligocene terrestrial biota on the Greater Antilles. Admittedly Cuba and Hispaniola contain some very old lineages. These are the eulipotyphlan insectivore *Solenodon* (Roca *et al.*, 2004) with two species from Hispaniola and Cuba respectively, the monotypic lizard genus *Cricosaura* from south-eastern Cuba (Noonan *et al.*, 2013), the Cuban cycad genus *Microcycas* (Francisco-Ortega *et al.*, 2007), and the Caribbean frog genus *Eleutherodactylus* (Heinicke *et al.*, 2007). However, although the divergence of these lineages from their mainland sister group dates back to the late Cretaceous or early Cenozoic, there is no evidence for pre-Oligocene *in situ* Greater Antillean divergences within these lineages. Therefore, later oversea dispersal to the Greater Antilles Arc from the mainland, and subsequent extinction outside the Greater Antillean area in these cases cannot be excluded. One other clade of land snails, the clausiliid subfamily Neniinae endemic to Hispaniola and Puerto Rico, may have been present in the contemporary Greater Caribbean island arc nearly as long as the Urocoptidae (Uit de Weerd & Gittenberger, 2013).

Congruence with the fossil record of Urocoptidae

Two fossils have been assigned to Urocoptidae: (1) *Urocoptis antiquus* from the Pliocene Gurabo formation in northern Hispaniola (Pilsbry & Olsson, 1954); (2) *Cylindrella floridana* of the Late Oligocene to Early Miocene (King & Wright, 1979) Ballast Point beds in Florida (Dall, 1890). *Urocoptis antiquus* has 'the external appearance of the genus *Autocoptis* Pils., special to Hispaniola' according to Pilsbry & Olsson (1954). Their delimitation of the genus *Autocoptis* coincides with the current subgenus *Autocoptis* (*Autocoptis*) (Thompson, 2012). A position within this subgenus is congruent with the BEAST tree. The Gurabo formation spans from approximately 3.9 to 5.33 Ma (McNeill *et al.*, 2008), which is within the 95% HPD age interval of the split between the northern and southern Hispaniolan *Autocoptis* (*Autocoptis*) lineages (Fig. 1). *Cylindrella floridana* is more difficult to align with extant taxa. The hypothesis that this species is an ancestor of *Cochlodinella variegata* in Florida (Dall, 1890), can be ruled out. Our results and the otherwise Cuban distribution of *Cochlodinella variegata* and the genus *Cochlodinella* (Pilsbry, 1903), suggest the presence of *Cochlodinella variegata* in Florida is very recent.

Role of land connections

The changing configuration of landmasses has played an important role in the biogeographical history of Urocoptidae. According to the DEC and DEC+J analyses of the subset of 100 BEAST trees, the present-day distribution of taxa is explained with significantly higher likelihood by assuming increased dispersal probabilities between areas when directly connected than by assuming no effect of such direct land connections. We identify two major periods of divergence, both corresponding with palaeogeographical changes. First, in the latest Eocene-early Oligocene, between approximately 36–28 Ma, clade A and clade B diversify into the lineages leading to the endemic clades and other taxa. This roughly coincides with a period of uplift around the Eocene-Oligocene transition (35–33 Ma) probably exposing most of the Greater Antilles Arc as potential habitat, followed by marine incursions in the Oligocene between 33–25 Ma (Iturralde-Vinent & MacPhee, 1999). Second, around 16 Ma, clades geographically more or less coinciding with specific (palaeo)islands present (see Iturralde-Vinent & MacPhee, 1999; MacPhee *et al.*, 2003) started to diversify (Fig. 1). The northern plus southern Hispaniolan distribution of two clades may be due to dispersal of lineages between the eastern part of the southern Hispaniolan and the northern Hispaniolan palaeoisland in the Pliocene, when both areas were first linked or in close proximity (Maurrasse *et al.*, 1980). Similarly, there is some geographical overlap between neighbouring main Urocoptidae clades in Cuba, as would be expected after sea barriers (Havana-Matanzas channel and the Guacanayabo-Nipe Fault Zone) disappeared and the areas between the palaeoislands emerged in the late Miocene (Graham, 2003; Iturralde-Vinent, 2006).

We do not find any traces of a vicariant origin of clades in the strict sense (see Crisp *et al.*, 2010), i.e. any marine barrier formed coinciding with the spatial and temporal separation between any two sister lineages. Possibly, some partitioning of lineages across different areas within the Greater Antilles Arc occurred prior to and independent of its break-up into smaller islands, as has been observed in clades of land snails from continuous landmasses (e.g. see Uit de Weerd *et al.*, 2004; Köhler & Criscione, 2015). Also, the palaeogeographical reconstructions of the region may lack the required spatial and temporal resolution to detect vicariance. Knowledge about the geological history of the Caribbean region is not easily translated into a detailed palaeogeographical reconstruction, as pointed out by Iturralde-Vinent & MacPhee (1999).

Role of oversea dispersal

Besides direct land connectivity, oversea dispersal also contributed to urocoptid distributional patterns. The support for the DEC+J model over the DEC model suggests a role of founder event speciation, which is generally associated with the presence of sea barriers (see Matzke, 2014). The contribution of founder event speciation may be slightly overestimated in some parts of the trees, however. For instance, it was occasionally assumed within the entirely Jamaican *Anoma* + *Spirostemma* + *Bactrocoptis* + *Urocoptis* clade.

The clearest example of oversea dispersal within the Greater Antilles comes from the presence of Urocoptidae on Jamaica. They demonstrate that repeated and relatively prompt oversea colonization is possible even in the continued absence of land connections to other areas. Our analyses indicate that two or three early dispersal events account for

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the island's entire endemic urocoptid fauna: (1) the ancestor to the clade consisting of *Anoma, Spirostemma, Bactrocoptis* and *Urocoptis*; (2) the ancestor to *Geoscala*, *Mychostoma*, *Simplicervix*; (3) the *Apoma* lineage. The 95% HPD of the age of *Anoma* + *Spirostemma* + *Bactrocoptis* + *Urocoptis* (14.8 Ma, 95% HPD 9.6–20.5 Ma) and of the less supported *Geoscala* + *Mychostoma* + *Simplicervix* clade (15.1 Ma, 95% HPD 9.4–21.2 Ma) is congruent with geological evidence that 'most of the island has been subaerially exposed since the end of the Middle Miocene' (Donovan & Paul, 2013). If colonization of Jamaica by the mrca of *Geoscala*, *Mychostoma*, *Simplicervix* and *Apoma* is assumed, followed by dispersal of the ancestor of *Brachypodella collaris* and *Brachypodella costata* to the Lesser Antilles, this would push the date of colonization of Jamaica deeper back in time (21.0 Ma, 95% HPD 14.0–28.3 Ma). Western Cuba was probably also colonized as an island, but dispersal via a short-lived land connection with central Cuba around the Oligocene-Miocene boundary (see MacPhee *et al.*, 2003) cannot be excluded. The age of the *Liparotes* + *Autocoptis (Urocoptola) evelynae* + *species A* clade from the Massif de la Hotte area in southern Hispaniola suggest colonization of the southern Hispaniolan palaeoisland shortly after its emergence (see Maurrasse *et al.*, 1980).

Three urocoptid genera colonized the North or South American mainland from the Antilles: (1) *Microceramus*; (2) *Cochlodinella*; (3) '*Brachypodella*' (excluding *Brachypodella costata* + *Brachypodella collaris)*. Of these '*Brachypodella*' uniquely colonized South America and subsequently southern North America. The branching sequence within the South and North American *Brachypodella* clade suggests colonization of mainland South America near the point of contact with the Lesser Antillean island arc (Trinidad), followed by subsequent westward and northward spread along the Caribbean coast. The colonization must have occurred between 14.7 Ma (95% HPD 9.8–19.9 Ma) (age of the clade) and 20.5 Ma (95% HPD 14.6–26.9 Ma) (age of its stem lineage). This is not early enough to support the idea of a GAARlandia land bridge. However, it is consistent with the first emergence of a complete string of islands between the Greater Antilles and South-America during the Oligocene to early Miocene (Speed *et al.*, 1993; Ricklefs & Bermingham, 2008).

Passive dispersal across the Caribbean Basin may occur by rafting, following sea currents, or through air by hurricanes or birds (see Hedges, 2006). Distributional patterns in the related and geographically partly overlapping genus *Cerion* have generally been attributed to hurricanes (see Harasewych & Strauss, 2006; and references therein), but *Cerion* snails may also survive exposure to sea water under rafting conditions (Bartsch, 1912; Mayr & Rosen, 1956). Prevailing westwards sea surface currents and hurricane tracks could have facilitated colonization of Jamaica, southern Hispaniola and western Cuba by Urocoptidae (see Hedges, 2006; see Reynolds *et al.*, 2013). Unlike *Cerion*, the most widespread Urocoptidae genera '*Brachypodella*' and *Microceramus* are characterized by relatively small shells, often smaller than 10 mm (Fig. 1). Two other urocoptid genera, both sampled in our study, have shells of similar or even smaller size. These are *Pseudopineria,* with a peculiarly disjunct distribution (see Paul, 1989), and *Spiroceramus,* in Cuba and some of the Bahama Islands (Clench, 1967). Snails within this range of shell sizes (< 10 mm) are thought to be relatively easily transported by air, either through birds or wind (Vagvolgyi, 1975). It is unclear whether this also applies to the founders of the Jamaican clades, because of the wide range of shell sizes and the poor phylogenetic resolution within these clades (see Fig. 1).

Local radiations

Our analyses identify independent radiations of Urocoptidae on Jamaica, western Cuba, central Cuba, eastern Cuba and Hispaniola. The unique urocoptid fauna of all of these areas, except central Cuba, was recognized by Pilsbry (1904: xix–xx). He noted that most of these regions had four forms in common 'to fill the various stations or sets of conditions available': (1) 'rather large terrestrial species, with many functional radular teeth' (e.g. *Pycnoptychia* in western Cuba, *Urocoptis* on Jamaica); (2) 'partially arboreal forms, with incomplete or very shortly free peristome' (e.g. *Tomelasmus* in western Cuba; *Anoma* on Jamaica) (3) 'Elongate, slender, rock-living forms' (e.g. *Callonia* in western Cuba; *Mychostoma* and *Apoma* on Jamaica) (4) 'slender, small, long-necked species, with the inner four teeth of the radula enlarged' (e.g. *Tetrentodon* in western Cuba; *Geoscala* on Jamaica). According to Pilsbry (1904: xxii), this regional diversity 'may well have been due to independent local adaptive radiations'.

Our analyses show that the forms distinguished by Pilsbry arose locally even more often than anticipated (cf. Pilsbry, 1904; p. xx). For instance, what was long held to be a single genus *Urocoptis* distributed in Jamaica and Hispaniola, turns out to be composed of three independent lineages: one Jamaican group and two Hispaniolan lineages that were both recently (Thompson, 2012) accommodated in the now evidently polyphyletic genus *Autocoptis*. The existence of a clade of Jamaican *Urocoptis* with the endemic Jamaican genera *Anoma*, *Spirostemma* and *Bactrocoptis* has to our knowledge never been recognized. Molecular phylogenetic studies similarly identified apparently old, although undated endemic Jamaican clades in other groups (Hedges, 1996; Schubart *et al.*, 1998; Jackman *et al.*, 1999; Crews & Gillespie, 2010). Unlike our study none of these comprised several recognized genera.

Urocoptid diversity within islands is probably at least partly due to adaptive radiations. The observations made by Pilsbry on different genera, combined with our results satisfy two of the criteria, namely 'multiplication of species and common descent' and 'extraordinary burst of diversification', for identifying adaptive radiations as formulated by Glor (2010). The remaining criterion of 'adaptation' is far more difficult to test, due to a lack of detailed and systematic field observations on Urocoptidae. While there can be little doubt

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that ecological factors such as food sources and habitat play a key role in divergences in radula structure and in shell form (Goodfriend, 1986; Heller, 1987), in this case the actual selective processes remain unknown. That different genera of Urocoptidae occur sympatrically in localities on Cuba (pers. obs. Uit de Weerd), Jamaica (see Rosenberg & Muratov, 2006), Puerto Rico and Hispaniola (pers. obs. Robinson) suggests that some form of food or habitat partitioning has occurred at the generic level (cf. Chiba, 2002, 2004). Intrageneric diversity in urocoptid island clades is mostly allopatric (e.g. de la Torre & Bartsch, 1976, 2008; Rosenberg & Muratov, 2006). Both habitat diversity and island area may have contributed to the within island diversity of Urocoptidae, as in other groups of land snails (Parent, 2012).

The evolution of morphologically similar genera on different islands is most striking for Jamaica and western Cuba (Pilsbry, 1904). These areas were islands throughout, respectively, all and most of their subaerial history (MacPhee *et al.*, 2003; Iturralde-Vinent, 2006), and contain the most spectacular radiations into different shell forms within Urocoptidae (Fig. 1). Replicated adaptive radiations on different Antillean islands have also been reported in tree frogs (Moen & Wiens, 2009) and anoles (Mahler *et al.*, 2010). Those radiations were attributed to similar ecological opportunity upon colonizing islands not occupied by competitors and by subsequent within-clade resource competition (but see Burbrink *et al.*, 2012; Yoder *et al.*, 2010). Similarly, ecological opportunity for Galápagos land snails was found to be greatest on younger islands (Parent & Crespi, 2009). Subsequent ecological diversification of early colonizing lineages may have prevented the establishment of later urocoptid lineages in Jamaica (excepting the widespread species *Microceramus gossei*) and most of western Cuba by competitive exclusion.

CONCLUSIONS AND IMPLICATIONS

The Urocoptidae constitute an old element of the Greater Antillean biota with a common ancestor that was present in the Greater Antillean Island Arc region from at least the Middle Eocene onwards, prior to a presumed GAARlandia land bridge. Presence of the family on the South and North American mainland is secondary. Changing land connections between areas and occasional oversea dispersal have shaped the distribution of Urocoptidae in the Caribbean region. On various Greater Antillean islands or palaeoislands similar morphotypes of Urocoptidae evolved in independent evolutionary radiations, most spectacularly so on Jamaica and in western Cuba, probably facilitated by the relative isolation of these areas.

Some species that are part of the endemic radiations in western Cuba and Jamaica are threatened or possibly extinct due to habitat destruction (Rosenberg & Muratov, 2006; Oliva-Olivera & Real, 2009). Other areas of endemicity identified in this study, particularly the Massif de la Hotte in south-westernmost Hispaniola, have never been fully surveyed, as illustrated by the undescribed species. Our study demonstrates that Urocoptidae represent a unique and old element of the biota of the Greater Antilles and should be valued as such.

The results of this study necessitate a taxonomic revision of the family and of the genus *Brachypodella*. These will be presented in a separate publication.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Samples and COI primers.
Appendix S2 BioGeoBEARS DEC and DEC+J analyses.
Appendix S3 Results for the individual markers (28S, H3, COI).

DATA ACCESSIBILITY

The 28S rRNA, Histone H3 and Cytochrome oxidase I sequences determined and used in this study are available for download at Genbank (http://www.ncbi.nlm.nih.gov/genbank/) under accession numbers KT602611-KT602806.

Sequence alignments and trees (maximum clade credibility trees for the MrBayes and BEAST analyses, GARLI bootstrap consensus tree) are available for download at TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S18209).

BIOSKETCHES

Dennis R. Uit de Weerd is currently assistant professor at the Open Universiteit Netherlands and research associate at Naturalis Biodiversity Center. He studies the evolution and biogeographical history of diverse and endemic groups of land snails using molecular phylogenetic approaches, and has an interest in island biogeography.

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Gary Rosenberg is curator of molluscs at the Academy of Natural Sciences of Philadelphia and a professor at Drexel University. He studies patterns of diversity in the Mollusca using biodiversity informatic and phylogenetic approaches, with particular interest in the origins of the Jamaican terrestrial malacofauna.

Author contributions: D.U.W. lead data collection and data analysis. D.G.R. provided essential samples and advised on taxonomy. D.U.W. wrote the first draft of the manuscript, which all authors contributed to revising. G.R. obtained funding for a post-doctoral fellowship for D.U.W., but the research extended beyond the term of the fellowship.

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