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Molecular taxonomy of the *Anadenobolus excisus* (Diplopoda : Spirobolida : Rhinocricidae) species-group on the Caribbean island of Jamaica

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Abstract. This paper documents the mtDNA genealogy and molecular taxonomy of the *Anadenobolus excisus* millipede species-group on the island of Jamaica. This endemic species-group originally comprised two nominal species, *A. excisus* (Karsch) and *A. holomelanus* Pocock. However, the latter species was considered by Hoffman likely to be a subspecies of the former, owing to their overall morphological and gonopodal similarity (the secondary sexual features most commonly used to delineate millipede species). We summarise molecular and morphological data that paints a rather different picture of the diversity in this group. Based on the *16S* rRNA gene of the mitochondrion and a comparative analysis of millipede size (reported here and elsewhere), we find that this species-group comprises at least three sibling species, one of which, *A. dissimulans*, sp. nov., is newly described. The study documents the first myriapod species diagnosed on the basis of molecular data.

Introduction

The Diplopoda (millipedes) are the third-most diverse class of terrestrial arthropods with over 10000 described species (Hoffman 1979, 1990). However, it remains among one of the largest understudied groups of animals to date. Comparatively little is known about this group's systematics, ecology, behaviour, and evolution. This in part may be due to their simple, uniform morphology, and consequently the paucity of features that can be used to delineate species, genera, and in some cases higher taxa at the family level and above. Distributed throughout the world, this myriapod group is found in almost every type of habitat and is likely to play an important ecological role in many, particularly tropical, ecosystems.

The Caribbean island of Jamaica is home to over 62 nominal millipede species (Hoffman 1999; Bond and Sierwald 2002*a*) distributed among 12 families belonging to six orders where they are the dominant macro-arthropod organisms. Of these, 51 species and four genera are endemic to Jamaica. Because Jamaica has probably never shared a land connection with Central America, or at the very least a land connection that postdates its last inundation during the late Eocene through early Miocene, these endemics are likely the descendants of colonising Central American taxa that have found their way to Jamaica over the last 10 million years (Buskirk 1985). Without question this is an already remarkable and noteworthy amount of taxonomic diversity, and an unusually high level of endemnicity for such a small land area (10380 square kilometres). However, the study that we summarise below suggests that when we take a closer look at Jamaican millipede diversity, we may find it to be much higher than the current number of described species would suggest.

Over a third of Jamaica's 62 millipede species can be attributed to members of the Spirobolida family Rhinocricidae. This is a large (over 500 species, P. E. Marek, J. E. Bond and P. Sierwald, unpublished data) family that has a mostly pantropical distribution (absent in Africa) with its greatest area of diversity in the New World tropics. Twenty-seven nominal species of Rhinocricidae occur on the island of Jamaica (Hoffman 1999; Bond and Sierwald 2002*a*), eight of which are placed in the genus *Anadenobolus* Silvestri, 1897, a large neotropical group with over 60 species (Hoffman 1999). Although re-evaluated by Mauriès (1980), the exact composition of the genus remains dubious and many species have been recently 'reassigned' to *Anadenobolus* by Hoffman (1999). However, with the exception of a number of anthropochoric species (Hoffman 1999) the alpha-level taxonomy appears to be relatively sound for this genus. The focus of this study is members of what we term the *Anadenobolus excisus* 'species-group' (Bond and Sierwald 2002*b*).

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Anadenobolus excisus (Karsch, 1881) is the largest nominal millipede species on the island of Jamaica, where it is both endemic and nearly ubiquitous, found associated with limestone formations (Fig. 1). Although there are other *Anadenobolus* species on Jamaica, other islands in the Greater and Lesser Antilles, and in Central America, *A. excisus* is clearly a distinct 'species' on the basis of a unique male genital morphology (Figs 2, 3). Figure 3 summarises the diagnostic anterior and posterior gonopod structure for members of the *Anadenobolus excisus* species-complex. A second species, *Anadenobolus holomelanus* (Pocock 1894), has been described from the central, Mandeville, area of Jamaica, but is considered tentatively by Hoffman (1999) to be a subspecies of *A. excisus* (discussed in more detail below). This species varies considerably in size across the island, but otherwise appears to be morphologically conservative, particularly with regard to male genitalic structure (Fig. 2). Figure 2 illustrates the lack of discrete anterior gonopod form and shape differences across this species' distribution and illustrates the variability in the structure. Based on gonopod shape (Fig. 3), the character traditionally used to delineate millipede species (Enghoff 1979; Hoffman 1990), we would quickly reach the conclusion that *A. excisus* is a single widespread species. However, based on molecular mtDNA *16S* rRNA gene data reported by us in another paper (Bond and Sierwald 2002*b*) we conclude that *A. excisus* represents a more complex pattern of underlying millipede diversification. These mitochondrial gene trees suggest the presence of three very divergent *A. excisus* lineages. This phylogeographic pattern (summarised in Fig. 4) has led us to conclude that the widespread populations of *A. excisus* examined as part of our study comprise at least three species rather than the one. An analysis of millipede size (summarised in Fig. 5), which demonstrates that clades II and III undergo some type of character displacement in sympatry, indicates that these distinct 'molecular' species maintain 'lineage cohesion' (Bond and Sierwald 2002*b*) where they co-occur. These results suggest that current morphological estimates of millipede species diversity on the island of Jamaica may be two to three times higher than previously thought. That is, there may actually be 54–81 Jamaican rhinocricid millipede species rather than 27. As in other arthropod groups with limited dispersal capabilities, for example trapdoor spiders (see Bond *et al.* 2001), species constructs based on genital morphology alone may grossly underestimate 'true' evolutionary diversity. The implications of this particular conclusion across all Diplopoda make Hoffman's estimate (Hoffman 1990) of the existence of at least 80000 species of millipedes quite likely.

The primary focus of this paper is, at least in a nomenclatural sense, very straightforward: the diagnosis and description of three Jamaican *Anadenobolus* species that compose the *A. excisus* species-group, one of these new to science. The *16S* rRNA gene of the millipede mitochondrion is used to determine which populations form distinct groups, or population aggregations. Using character tracing methods we determine which nucleotide site changes can be used to discriminate between species; that is, what are the unique combinations of nucleotide substitutions that define species within this complex. The species concept that we implement is explicitly the phylogenetic species concept (Nixon and Wheeler 1990): 'the smallest aggregation of populations diagnosable by a unique combination of character states' (as defined by Wheeler and Platnick 2000). The use of a unique *combination* of character states rather than non-homoplasious autapomorphies alone is preferred for a

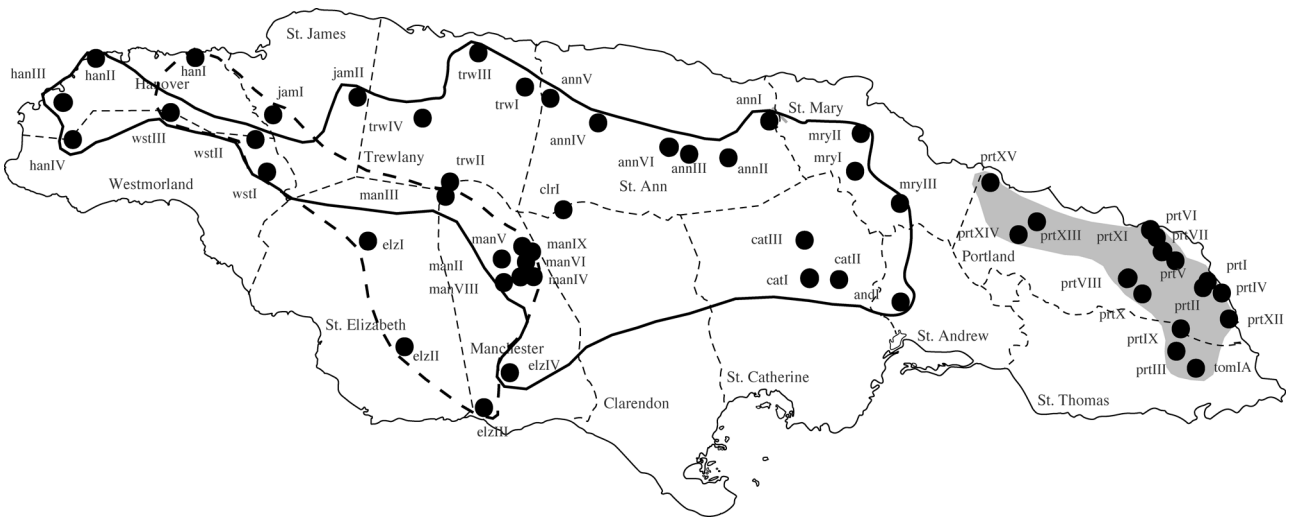

Fig. 1. Generalised summary of *Anadenobolus excisus* species-group distribution and collecting localities from Bond and Sierwald (2002*b*). Alpha-numeric locality designations correspond to those defined by Bond and Sierwald (2002*b*: appendix 1). Grey shaded area indicates Clade I distribution (*A. excisus*), dashed lines indicate Clade II (*A. dissimulans*) membership, and the solid line denotes distribution of Clade III (*A. holomelanus*).

number of pragmatic reasons. Foremost, as with any species diagnosis, we may never examine all possible sister and outgroup taxa and can therefore never be confident that any one diagnostic character is unique to a single taxon. Unique combinations of character states potentially ensure that as additional taxa are discovered and sequenced our diagnoses

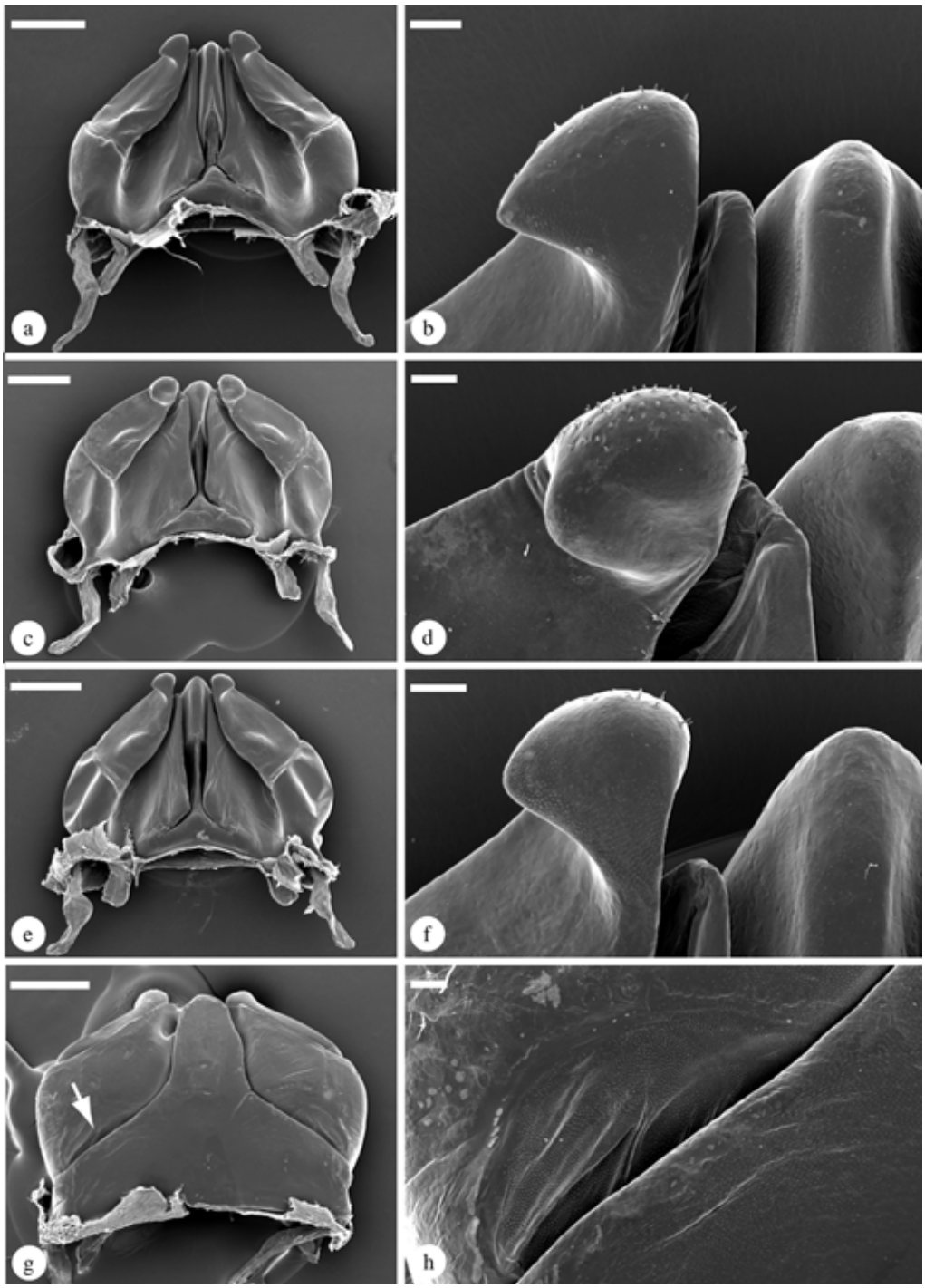

Fig. 2. Scanning electron micrographs of anterior male gonopod, coleopod. Left side of figure (*a*, *c*, *e*) shows full habitus of gonopod (scale bar = 1 mm), right side of figure (*b–f*) is an enlargement of the gonopod tip (right side) that shows small distal spines (scale bars = 100 m). *a, b*, *Anadenobolus excisus* from prtIII, posterior aspect; *c, d*, *A. dissimulans* from wstII, posterior aspect; *e, f*, *A. holomelanus* from mryI, posterior aspect; *g*, *A. holomelanus*, *anterior* aspect, small arrow points to lightly sclerotised pocket (Pk in Fig. 3); *h*, enlargement of sclerotised pocket from adjacent figure.

will remain useful. Admittedly, whether the species that we describe here are to be considered 'true' evolutionary lineages, hinges in part on what is philosophically an ontological problem. However, for the purposes of this paper this is, in a formal nomenclatural sense, not an issue. What is at issue is our ability to differentiate *empirically* (Goldstein *et al.* 2000) between what we consider to be nominal *Anadenobolus* species.

Materials and methods

Sampling and specimen vouchering

Over 400 specimens of putative *Anadenobolus excisus* were examined during the course of this study. Of these, we sampled the mitochondrial *16S* rRNA gene for 242 individuals (GenBank Accession nos. AF501371–AF501514) from 54 localities across the island of Jamaica (Bond and Sierwald 2002*b*, appendix 1). Each specimen used in this study was given a unique voucher number (FMMC number) and deposited in The Field Museum of Natural History's Insect Division collection. For specimens from which DNA sequence data were collected, a label denoting *16S* rRNA haplotype designation, corresponding to those listed in Bond and Sierwald (2002*b*, appendix 1), has been added to each vial.

Molecular diagnosis of putative Anadenobolus *species*

Nucleotide substitutions that are diagnostic for each species were determined using the character trace function in the computer program MacClade (Maddison and Maddison 2000). Because we are only interested in three nodes that are found in all recovered trees (see Results), tree choice was unimportant. Therefore one of the most parsimonious trees was chosen at random from the set of all equally parsimonious trees reported in Bond and Sierwald (2002*b*, fig. 2). All nucleotide substitutions were plotted onto this tree using the 'Trace All Changes' function with the 'Unambiguous Changes Only' option selected. Only those character-state changes that were non-homoplasious above the node of interest are used to diagnose species. However, substitutions that appear in other regions of the phylogeny are considered (we differentiate between the two below).

Each species diagnosis lists the character state (nucleotide) followed parenthetically by the nucleotide position number. The position number refers to the nucleotide position in the fully aligned data set used in this study. A reference alignment of all three species is available in electronic form on request from the first author and for download at http://core.ecu.edu/biol/bondja and is also available as Accessory Material from the journal's website. We adopt this approach because the region of *16S* sequenced is highly variable and is not easily aligned to commonly cited model arthropod genomes (e.g. *Drosophila yakuba*, Clary and Wolstenholme 1985).

Morphological terminology and methods

Ocelli, antennal cones and setal counts are taken from the left side unless otherwise stated. Setal counts are listed from the tarsus to the prefemur. All measurements are given in millimetres. Millipede size is estimated by width taken at three points (segment number given parenthetically after measurement for exemplar and type specimens), using digital calipers accurate to 0.01 mm. We use width in lieu of actual length because of the tendency for preserved specimens to differentially contract in ethanol. Width variation (see the Size variation section of each description) was estimated (n = 231, only those adult specimens for which we had genetic data) at three positions: directly behind the collum (1st segment), at approximately segment 20 (counting back from the anterior) and at approximately segment 10 (counting forward from the posterior end of the animal). We only measured specimens that were gravid females, or females with fully formed copulatory devices, and mature males, those with fully developed gonopods. These three widths were then averaged across each specimen. Counts of ring segments include all segments before the epiproct and starting at the collum.

We use Keeton's (1960) terminology when describing male genitalic structures (summarised in Fig. 3). Specimens were prepared for scanning electron microscopy by cleaning them with the aid of an ultrasonic cleaner, critical point drying and then coating them with gold. Muscle tissue was digested away from genitalia using trypsin.

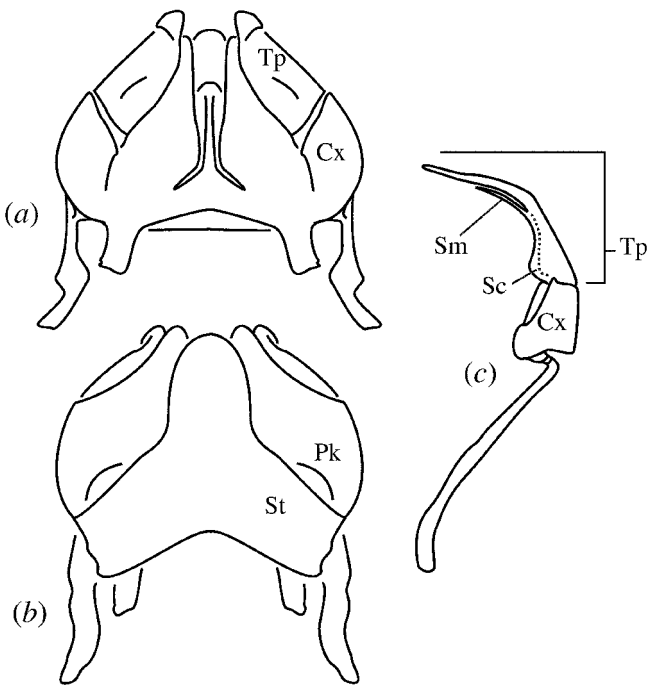

Fig. 3. Model of *A. excisus*-group male genitalia, anterior and posterior gonopod. *a*, Coleopod posterior view; *b*, coleopod anterior view; *c*, left phallopod posterior view. Tp, Telopodite; Cx, coxa; Sm, solenomerite; Pk, lightly sclerotised pocket; Sc, seminal canal; St, sternum.

Results

Molecular diagnosis of putative Anadenobolus *species*

Based on character optimisations in MacClade, each clade can be differentiated on the basis of a uniquely derived combination of nucleotide site substitutions. Figure 5 summarises the positions and character states that can be used in this diagnosis. Twenty, 33 and 13 uniquely derived nucleotide substitutions differentiate Clades I, II and III individuals respectively.

Millipede size: width and ring segment counts

The analysis of millipede size based on width is presented in detail in Bond and Sierwald (2002*b*), but we have summarised the results of this analysis again here in Fig. 6. The analysis, based on ring segment numbers, shows a similar type of pattern as the one demonstrated for millipede width. Figure 6 summarises the ring segment number distribution

for each species (Clades I–III). Clade II individuals tend to have fewer ring segments. Furthermore, Clade III has the greatest range of segment number (e.g. 43–56 for males examined). The disparity in ring segment number across Clade III individuals is also likely correlated with presence, or absence, in the zone of overlap. The number of segments for the three clades significantly differ for males (Kruskal–Wallis test, $\chi^2 = 18.72$, $P < 0.001$) and females ($\chi^2 = 34.00$, $P < 0.001$); however, these values do not differ in a discrete manner (i.e. the values for each clade overlap).

Discussion

Based on the results of the parsimony analysis using mtDNA (Bond and Sierwald 2002*b*) and the morphological data presented here, we conclude that the populations constituting the three major *Anadenobolus* clades (Fig. 4) deserve species

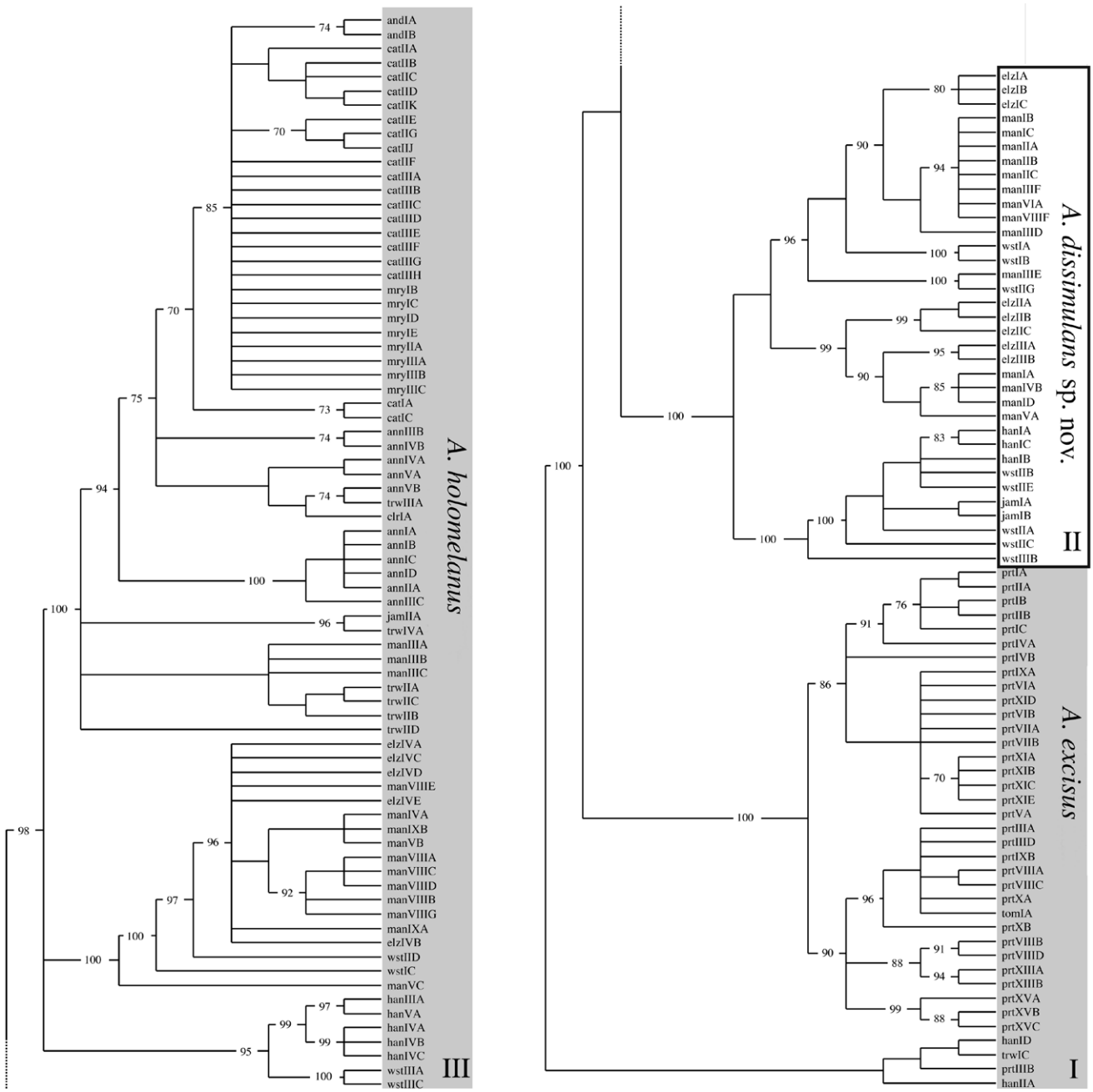

Fig. 4. Summary of results of the phylogenetic analysis of the *A. excisus* mtDNA haplotypes from Bond and Sierwald (2002*b*). Haplotype designation refers to localities depicted in Fig. 1. This tree is a strict consensus of 10045 trees showing relationships of 144 mtDNA haplotypes based on an analysis using parsimony. Grey boxes placed directly on nodes denote bootstrap values greater than 70%. Large Roman numerals (I–III) correspond to clade numbers used in text.

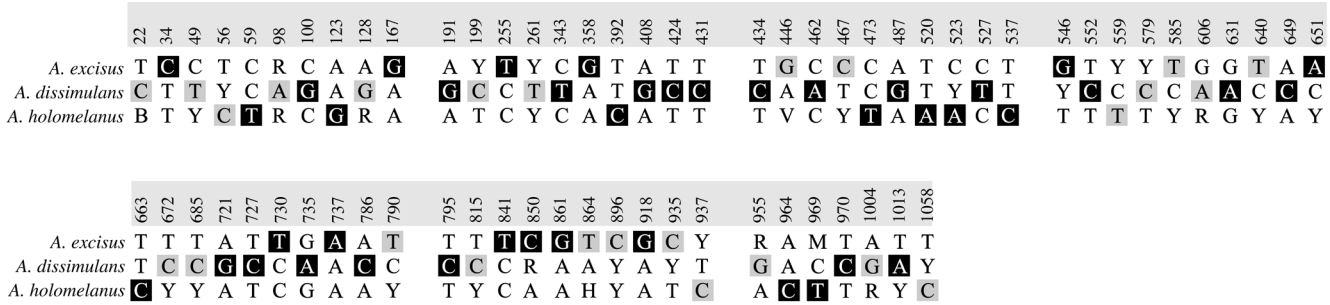

Fig. 5. Summary of diagnostic nucleotide changes for each species. Numbers indicate nucleotide position, solid black boxes denote those changes that are unique, grey boxes indicate that the nucleotide at that position is shared by another clade but is non-homoplasious for the species in question.

status; that is, they represent real cohesive genetic lineages. Twenty (8 unique), 33 (20 unique) and 14 (10 unique) nucleotide substitutions comprise the character state combinations that are used to diagnose *A. excisus*, *A. dissimulans*, sp. nov. and *A. holomelanus* respectively (Fig. 5). Based on these mtDNA data, we are both biologically (in terms of putative lack of mtDNA gene flow and lineage cohesion in sympatry) and in a strict nomenclatural (in terms of diagnosability) sense justified in our proposition of the following (below) taxonomic scheme for the *Anadenobolus* species-group. In addition to the description of a new species, we minimise the number of formal names in this group by retaining *A. holomelanus* as a valid taxon. This is in contradiction to Hoffman's (1999) suggestion that it only be retained as a subspecies of *A. excisus*, a conclusion that would not be warranted given our phylogenetic results. Additional discussion of the validity of the individual species in this group and biological justifications are given in the Discussion sections that are included in each species description.

In terms of evidence, synonymy that involves any combination of the three species described in this paper will require a heavy burden of proof. That is, future workers will need to demonstrate that the mtDNA markers we have used in fact do not define these lineages or, using another genetic marker, demonstrate that present day interspecific gene flow is occurring that we were unable to detect. These genetic data are particularly compelling in biological terms since they do indicate an apparent lack of gene flow when lineages coexist (Clades II (*A. dissimulans*, sp. nov.) and III (*A. holomelanus*)). We base this conclusion on the apparent size differences between *A. dissimulans*, sp. nov. and *A. holomelanus* in sympatry. If gene flow was occurring, we would then expect large and small morphs to be randomly distributed with respect to clade membership, a null hypothesis rejected by us previously (Bond and

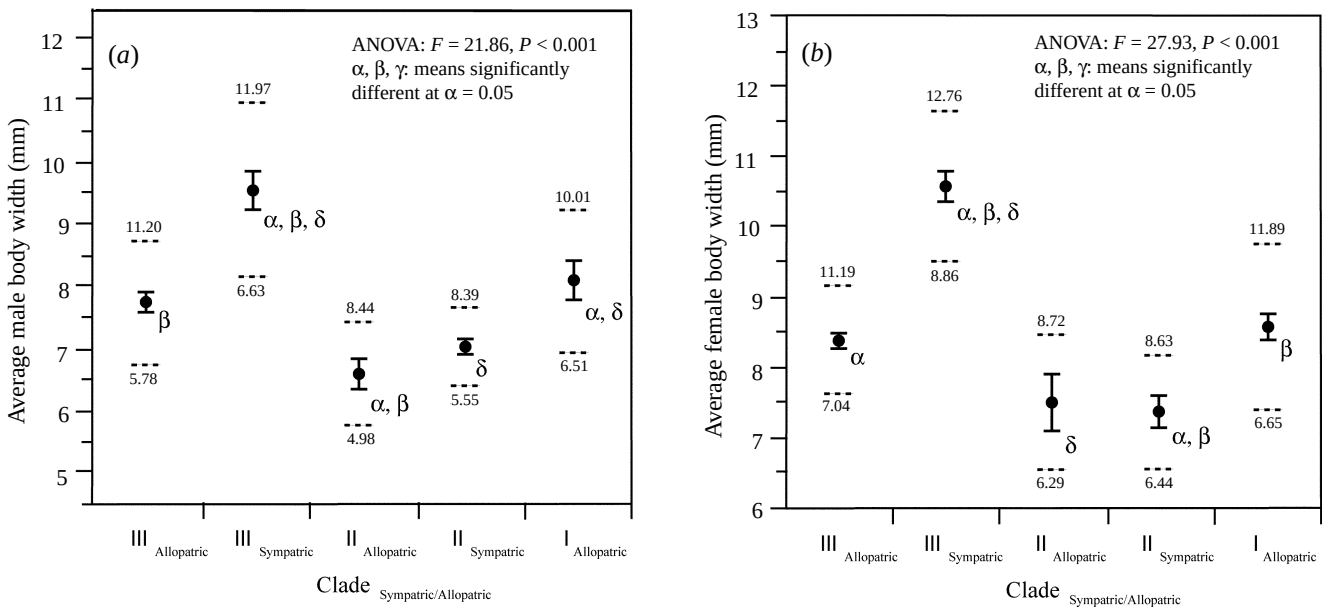

Fig. 6. Summary of descriptive statistics and statistical analysis of *A. excisus*-group body size. Solid dots indicate mean value, solid horizontal lines the standard error, dashed lines the standard deviation, numbers at dashed lines are the ranges. *a*, Male body size; *b*, female body size.

Sierwald 2002*b*), using a number of statistical and comparative approaches.

Since Clade I (*A. excisus*) is allopatric with respect to the others, hybridisation is remotely possible (future establishment of a secondary contact zone). We submit that this time-extended perspective (*sensu* Graybeal 1995) is not useful because it does not reflect the biological reality that exists at present. *Anadenobolus excisus* does not come into contact with, and, as a direct consequence, does not share genes with, either of the other two nominal species in this genus. We do not suggest, or even speculate, that *A. excisus* would, or would not, mate with the other species in a laboratory setting, we simply maintain that such speculation, in this case is without merit or taxonomic significance.

This paper documents the first millipede species diagnosed using DNA sequence data and may represent the beginning of a shift in our fundamental approach to millipede taxonomy. Our formal designation (Taxonomy section below) of these three 'molecular' lineages as nominal taxa (i.e. species) presents a rather interesting and novel situation for millipede taxonomy. These three species lack morphological features that can be used globally to differentiate them and thus do not meet the criteria traditionally used to diagnose millipede species. Because many millipedes have very similar life histories, very simple morphology and may therefore be prone to convergent or parallel evolution, it is not surprising that morphological approaches to delineating millipede species could fall short of circumscribing 'real' evolutionary lineages. One important implication is that in some (probably most) millipede groups, male genitalia may not define real 'biological' species. Similar gonopod morphology may only be useful in the delineation of more inclusive groups (e.g. species-groups like the one discussed in this paper). Although it may seem counterintuitive to the traditional taxonomist for purely pragmatic reasons (e.g. the accessibility of molecular techniques to everyone), as demonstrated here and elsewhere (e.g. Collin 2000; Bond *et al.* 2001; Westheide and Hass-Cordes 2001), molecular approaches to describing and subsequently identifying species may in the future prove to be the most simple, effective and reliable method for accurately assessing biological diversity.

Taxonomy

Family **RHINOCRICIDAE** Brölemann

Anadenobolus Silvestri

Anadenobolus Silvestri, 1897: 651.

Type species: *Spirobolus politus*, von Porat, 1888: 243, by original designation. Mauriès 1980: 1088; Hoffman 1999: 75.

Orthocricus Velez, 1963: 209.

Type species: *Julus arboreus* DeSaussure, 1859*a*: 331; by original designation. DeSaussure 1859*b*: 365. Synonymised by Hoffman 1999: 75.

Anadenobolus excisus (Karsch)

(Figs 2, 7, 8)

Spirobolus (*Rhinocricus*) *excisus* Karsch, 1881: 73 *Rhinocricus excisus* Pocock, 1894: 491.

Anadenobolus excisus Hoffman, 1999: 79.

Material examined

Holotype. *Spirobolus* (*Rhinocricus*) *excisus*, female, from Jamaica in Zoologisches Museum der Humboldt Universität, Berlin.

Exemplar material. Male exemplar and female exemplar, Jamaica, St Thomas Parish, John Crow Mtns near the town of Hayfield (locality prtIII, Fig. 1), elevation 1660, 18°58′40.1″N, 77°22′49.5″W, coll. J. Bond and M. Merwe, 5.ii. 2000, [deposited in the Field Museum of Natural History (FMNH; FMMC# 3522 and 3253)]. Additional male exemplar specimens from same locality deposited in FMNH (FMMC# 3257) and the Institute of Jamaica, Kingston, Jamaica (FMMC# 3259).

Non-type specimens examined. **Jamaica: Portland:** 7♀, 3♂, John Crow Mtns, near town of Rose Garden (Long Bay), elevation 450′; 3♀, 2♂, John Crow Mtns, small road turnout by town of Sherwood Forest, elevation 370′; 2♀, 1♂, near Reach Falls, elevation 180′; 2♀, 22 km south of Long Bay along main highway, elevation 170′; 4♀, 1♂, 1 km south-east of Williams Field, elevation 140′; 2♀, 1♂, 2.4 km west of Nonsuch, elevation 700′; 7♀, John Crow Mtns, near the town of Windsor, west side of the Rio Grande R.; 3♀, 3♂, John Crow Mtns near town of Comfort Castle, elevation 500′; 6♀, 1♂, main highway south of Port Antonio, ~4 km from town of Long Bay, elevation 10′; 2♀, 1♂, 3.7 road km south-west of intersection south of Shirley Castle and Bloomfield, elevation 480′; 2♀, Chelsea on west side of intersection near bridge between Swift R. and Bloomfield, elevation 480 m; 3♀, 2♂, Vinery, near cable and wireless station, 1.2 road km from intersection in Vinery, elevation 440 m. **St. Thomas:** 7♀, 2♂, John Crow Mtns, near town of Hayfield, elevation 1660′; 2♀, 2♂, near town of Bath, elevation 450′; 2♀, 4♂, John Crow Mtns, near the town of Melbane, elevation 500′; 3♀, 3♂, St Mary's Parish, ~2 km east of Windsor Castle, elevation 1290′.

Diagnosis

This species can be distinguished from its two sister species on the basis of the following combination of mtDNA *16S* rRNA gene nucleotide substitutions: C (34), G (167), T (255), G (358), G (446), C (467), G (546), T (585), T (640), A (651), T (730), A (737), T (790), T (841), C (850), G (861), T (864), C (896), G (918), C (935). (The alternative character states at each of the above positions for the remaining two species are listed in Fig. 7.) *Anadenobolus excisus* individuals tend to be consistently larger on average than *A. dissimulans*, sp. nov. individuals, but their sizes do overlap. The range of this species, throughout the John Crow Mtns, does not overlap with its two sister species.

Description of male exemplar

Head, antennae and collum uniform dark to light olive green when collected in the field, very dark reddish brown when preserved (colour change is usually the result of staining by released defensive secretions). Prozonite slightly darker in colour than metazonite. Ring segments divided by faint suture both longitudinally and laterally.

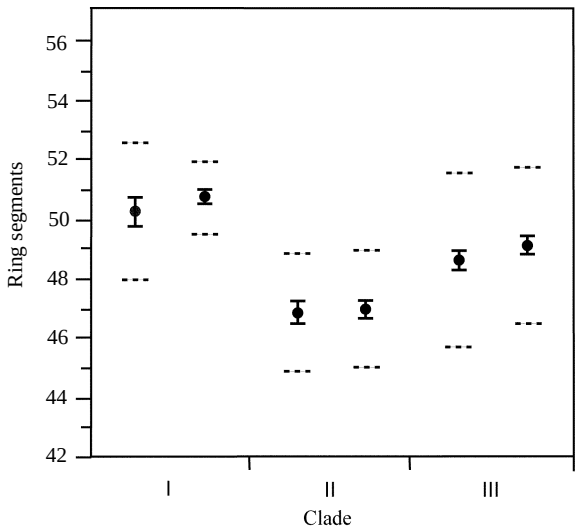

Fig. 7. Summary of *A. excisus* species-group ring segment numbers. For each clade male value appears closest to the y-axis on the left. Solid dots indicate mean value, solid horizontal lines the standard error, dashed lines the standard deviation.

Antennae with four sensory cones, 13–11 labral setae, clypeal groove very deep almost entire, 29 ocelli. Width 7.97 (1)–8.17 (20)–8.23 (45), 50 ring segments. Leg I setal formula: 8 – 4 – 2 – 2 – 2; Leg II: 7 – 3 – 0 – 2 – 2. Tarsi have rudimentary ventral pads that are slightly lighter in colouration. Scobinae formed as small distinct pits on the 8th– *c.* 17th segment. Epiproct short and blunt, does not extend beyond anal valves. Hypoproct short, triangular with blunt broadly rounded terminal end.

Coleopod (anterior gonopod) and phallopod (posterior gonopod) as illustrated in Figs 2*a*,*b*, 8. Sternum of coleopod broad and rounded distally (Fig. 8*b*,*e*). General shape of coxae (Cx) and telopodite (Tp) as in other rhinocricids (Fig. 8*a*,*d*). Anterior, proximal aspect of Cx with lightly sclerotised inner marginal pockets (Pk). Inner posterior margin of coleopod lightly sclerotised and divided longitudinally ~3/4 of its length. Distal-most aspect of coleopod Tp with patch of short setae (Fig. 2*b*). Phallopod telopod (Tp, Fig. 8*c*,*e*) a slender bifurcate structure. Solenomerite (Sm) extends at least half the distance to terminal-most aspect of telopod. Seminal canal (Sc) visible extending from coxae (Cx) up to solenomerite. Seventh segmental ring posterioventrally modified as postgenital bar to accommodate gonopods.

MtDNA haplotype designation and GenBank Accession # of male exemplar: prtIIIA, AF501500.

Variation

Colouration relatively uniform. Male gonopod structure with typical amount of shape variation, but no apparent discrete shape differences across its distribution. Size variable (summarised in Fig. 6, $n = 12$) ranging from small (6.51) to relatively large specimens (10.01). Some variation in number of ring segments (45–54) with mean value of 50 ($n = 20$).

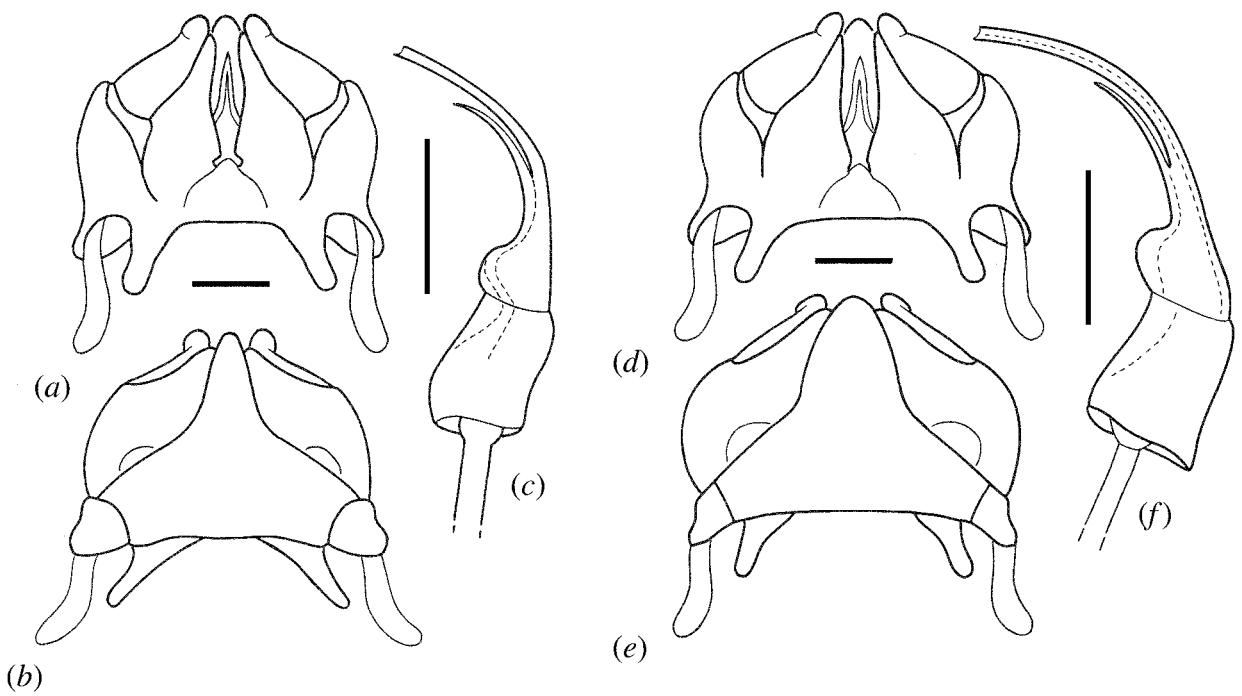

Fig. 8. *Anadenobolus excisus* Karsch. *a–c*, Gonopod of male exemplar specimen; *d–f*, gonopod of specimen from Portland Parish, near town of Long Bay (Rose Garden). Scale bars = 1 mm.

Description of female exemplar

Colouration as described for males. Antennae with four sensory cones, 13–13 labral setae, clypeal groove distinct, 27 ocelli. Width 8.07 (1)–9.27 (20)–9.08 (45), 49 ring segments. Leg I setal formula: 6 – 3 – 3 – 3 – 2; Leg II: 6 – 3 – 2 –3 – 2. Scobinae formed as small, distinct pits on the 16th–22nd segment. Epiproct and hypoproct same length and conformation as in males, short.

Cyphopods similar to those described for *Eurhinocricus rosenbergi* Bond and Sierwald, 2002*a*: Fig. 3. These are very simple, sclerotised structures comprising two caudal plates lacking setae, which open ventrally via lightly sclerotised operculum (not illustrated).

MtDNA haplotype designation and GenBank Accession # of female exemplar: prtIIIA, AF501500.

Variation

Female colouration also uniform across this species' distribution. Size variable ($n = 41$) ranging from small (6.65) to relatively large specimens (11.89). Some variation in the number of ring segments (48–53) with a mean value of 51 ($n = 37$).

Distribution and natural history

This species is restricted to the eastern-most end of Jamaica, distributed throughout the John Crow Mtns (Fig. 1) in the parishes of St Thomas and Portland. It is found almost exclusively in the thin layer of leaves on and around limestone. This represents a marginal departure in habitat from the other two *Anadenobolus* species described in this paper since they occur in an 'interstitial'-like manner among the limestone rubble.

Remarks

Karsch's 1881 description of this species lists the type locality (implied) only as Jamaica. Because there are several species within this group, distributed across most of Jamaica, the lack of a more specific type locality presents some problems for this group's taxonomy since it is impossible to know to which of the three *A. excisus*-group species the Karsch's holotype represents. Furthermore, the description of the holotype potentially fits specimens from all three clades (Fig. 4). For reasons discussed below we are confident that *A. holomelanus* is a Clade III specimen. However, based on size, the *A. excisus* type could likewise be attributed to a Clade III population in allopatry. We have chosen to arbitrarily attribute the name *A. excisus* to those specimens in Clade I. Albeit arbitrary, this decision minimises the number of new names introduced into the literature (e.g. an alternative would be considering *A. holomelanus* a subjective synonym of *A. excisus* and consequently describing two new species). By retaining *A. holomelanus* for Clade III and *A. excisus* for Clade I we describe one new species.

To clarify future studies of this species-group we describe male and female 'exemplar' specimens (functionally analogous to holotypes) that represent our concept of *A. excisus*. However, we may, in the future, formally petition to have the existing holotype set aside with the subsequent designation of the male exemplar, described above, as a neotype.

Anadenobolus dissimulans, sp. nov.

(Figs 2, 7, 9)

Material examined

Type material. Male holotype and female paratype, Jamaica, St Elizabeth's Parish, 4.7 km north of Newton, by Maggotty Hydroelectric Dam (locality elz1, Fig. 1), elevation 430′, 18°9′16.3″N, 77°45′25.3″W, coll. J. Bond and M. Merwe, 16.ii. 2000, [deposited in the FMNH (FMMC# 3389 and 3392) collection]. Male and female paratype from the type locality deposited in the Institute of Jamaica in Kingston, Jamaica.

Additional material examined. All material in FMNH. **Jamaica: Hanover:** 4♀, 3♂, small side road along coast at the town of Flint R., elevation 20–30′; 1♂, 5.2 km west of Lucea along highway A1, elevation 20′. **Manchester:** 3♀, 2♂, 4.5 km east of town of Mark Post, elevation 1318′; 2♀, 4♂; ~2.5 km east/south-east of Mile Gully, elevation 1720′; 3♂, 5.2 km north of Oxford, elevation 1210′; 2♀, 2♂, north-east of Allison, 1.8 road km from intersection in Allison, elevation 800′; 3♂, Martins Hill, 0.3 road km north/north-east of intersection elevation 530′; 2♀, 3♂, 2.7 km west of Plauden Hill, elevation 650′; 2♀, 3♂, Christiana, elevation 1350′; 1♀, 1♂, Mile Gully Mtn, 3.8 km south of intersection with paved road, elevation 820′. **St. Elizabeth:** 3♂, 4.7 km north of Newton, by Maggotty Hydroelectric Dam, elevation 430′; 1♀, 2♂, ~3.0 km from Malvern, elevation 1540′; **St. James:** 4♀, 2♂, 1.9 km south of Chester Castle, elevation 800′. **Westmorland:** 2♀, 2♂, ~5 km east of Rat Trap on secondary road between B6 and B7, elevation 1080′; 2♀, 3♂, ~5 km south of Haddo, elevation 720′; 1♀, 1♂, Town of Penny Cooke, elevation 750′.

Diagnosis

This species can be distinguished from its two sister-species on the basis of the following unique combination of mtDNA *16S* rRNA gene nucleotide substitutions: C (22), T (49), A (98), G (100), G (128), G (191), C (199), T (261), T (343), G (408), C (424), C (431), C (434), A (462), G (487), T (527), C (552), C (579), A (606), A (631), C (649), C (672), C (685), G (721), C (727), A (735), C (786), C (795), C (815), G (955), C (970), G (1004), A (1013). (The alternative character states at each of the above positions for the remaining two species are listed in Fig. 7.) Where sympatric with *A. holomelanus*, female *A. dissimulans* are much smaller and statistically have fewer segments (see results section above). Known size ranges in sympatry of *A. dissimulans* are 6.44–8.63, whereas sizes of *A. holomelanus* are 8.86–12.76 (Fig. 6). These species can also be discriminated in sympatry on the basis of colour. *Anadenobolus dissimulans* individuals are much lighter in colour, usually a dull olive-green, whereas individuals of

A. *holomelanus* are a shiny black. Scobinae of *A*. *dissimulans* are consistently 2–3× larger than those of *A*. *excisus*, however, because the scobinae of *A*. *holomelanus* are polymorphic (small and large) this character may not be very useful in differentiating these species.

Description of male holotype (FMMC# 3389)

Head, antennae and collum uniform dark olive green when collected in the field, very dark reddish brown when preserved (colour change is usually the result of staining by released defensive secretions). Prozonite slightly darker in colour than metazonite. Ring segments divided by faint suture both longitudinally and laterally.

Antennae with four sensory cones, 14–14 labral setae, clypeal groove very deep almost entire, 28 ocelli. Width 7.79 (1)–8.73 (20)–8.50 (45), 47 ring segments. Leg I setal formula: 7 – 2 – 3 – 2 – 2; Leg II: 8 – 2 – 2 – 1 – 2. Tarsi have prominent ventral pads that are light in colour and divided longitudinally. Scobinae formed as large distinct pits on the 8th– *c.* 17th segment. Epiproct short and blunt, does not extend beyond anal valves. Hypoproct short, triangular with blunt broadly rounded terminal end.

Coleopod and phallopod as illustrated in Figs 2 and 9. Sternum of coleopod broad and rounded distally (Fig. 9*b*,*e*,*h*). General shape of Cx and Tp as in *A*. *excisus* (Fig. 9*a*,*d*,*g*). Anterior, proximal aspect of Cx with lightly

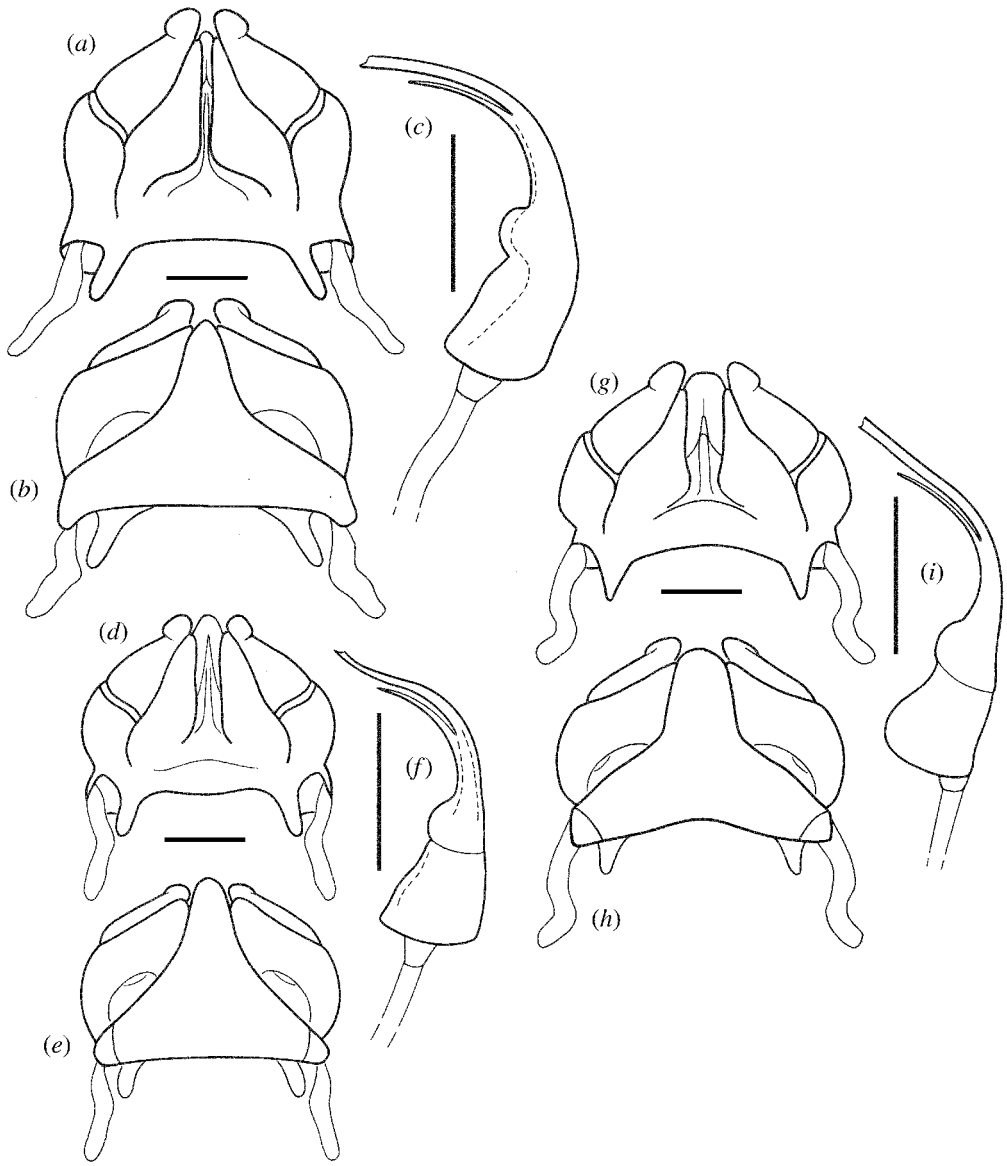

Fig. 9. *Anadenobolus dissimulans*, sp. nov. *a–c*, Gonopod of male holotype; *d–e*, gonopod of specimen from Manchester Parish, 5.2 km north of Oxford; *f–h*, gonopod of specimen from Hanover Parish, town of Flint. Scale bars = 1 mm.

sclerotised inner marginal Pk. Inner posterior margin of coleopod lightly sclerotised and divided longitudinally ~3/4 of its length (Fig. 9*a*,*d*,*g*). Distal-most aspect of coleopod Tp with patch of short setae (Fig. 2*d*). Phallopod Tp (Fig. 9*c*,*f*,*i*) is a slender bifurcate structure. Solenomerite extends at least half the distance to the terminal-most aspect of the telopod. Sc is visible extending from the Cx up to the solenomerite. Seventh segmental ring posterioventrally modified as a postgenital bar to accommodate gonopods.

MtDNA haplotype designation and GenBank Accession # of male exemplar: elz1B, AF501448.

Variation

Colouration relatively uniform. Male gonopod structure with typical amount of shape variation, but no apparent discrete shape differences across its distribution. Size variable (summarised in Fig. 6*a*), specimens relatively small (5.55–8.39, n = 18). Some variation in the number of ring segments (Fig. 7, 43–52) with a mean value of 47 (n = 31).

Description of female paratype (FMMC# 3392)

Colouration as described for males. Antennae with four sensory cones, 13–14 labral setae, clypeal groove distinct, 33 ocelli. Width 7.68 (1)–8.92 (20)–9.12 (45), 45 ring segments. Leg I setal formula: 7 – 4 – 2 – 3 – 1; Leg II: 9 – 3 – 3 –3 – 2. Tarsi lack prominent pads. Scobinae formed as distinct pits on the 7th–20th segment, smaller than in males. Epiproct and hypoproct same length and conformation as in males, short.

Cyphopods similar to those described for *Eurhinocricus rosenbergi* Bond and Sierwald, 2002*a*: Fig. 3. These are very simple, sclerotised structures comprising two caudal plates lacking setae, which open ventrally via lightly sclerotised operculum (not illustrated).

MtDNA haplotype designation and GenBank Accession # of female exemplar: elz1A, AF501447.

Variation

Female colouration also uniform across this species' distribution. Size variable (Fig. 6), relatively small (6.29–8.72, n = 36). Some variation in the number of ring segments (45–50; Fig. 7) with a mean value of 47 (n = 22).

Distribution and natural history

The first author has collected this species throughout the following parishes: St James, Hanover, Westmorland, Manchester and St Elizabeth (Fig. 1). This species occurs only in areas with lots of limestone, where it is found in an 'interstitial'-like manner amongst the limestone rubble. Most of its range overlaps with that of *A. holomelanus*.

Remarks

See Remarks under *A. holomelanus*.

Etymology

The specific epithet refers to the cryptic nature of this species.

Anadenobolus holomelanus (Pocock)

(Figs 2, 7, 10)

Rhinocricus holomelanus Pocock 1881: 492. (Female holotype from Jamaica most likely in The Natural History Museum (BMNH), not examined, probably lost.)

Anadenobolus holomelanus, Hoffman 1999: 79.

Material examined

Designation of neotype. Male neotype (FMMC# 3421) and female neoparatype (FMMC# 3422), Jamaica, Manchester Parish, Christiana, 18°08′34.3″N, 77°29′37.2″W (locality manV, Fig. 1), elevation 2660′, coll. J. Bond and M. Merwe, 18.ii. 2000, (FMNH).

Paratypes. Jamaica, Trewlany Parish, Troy, 18°14′47.9″N, 77°36′53.7″W, elevation 1410′, coll. J. Bond and M. Merwe, 16.ii. 2000, (Institute of Jamaica in Kingston, Jamaica).

Additional material examined. All material in FMNH. **Jamaica: Clarendon:** 1♀, 2♂, town of Burbage, elevation 1750′. **Hanover:** 1♀, small side road between green Island and Santoy, elevation 40′. **Manchester:** 3♀, 2♂, Christiana, elevation 1350′; 3♀, 8♂; 0.5 km south of Newport, elevation 2510′; 12♀, 8♂, 0.3 km north/north-east of intersection at Martins Hill, elevation 530 m; 3♀, 3♂, north-east of Allison, 1.8 road km from intersection in Allison, elevation 800′; 3♀, 3♂, 5.2 km north of Oxford, elevation 1210′. **St. Andrew:** 2♀, 1♂, 4.1 km east of Rock Hill, elevation 1440′. **St. Ann:** 2♀, 4♂, ~1 km from the south end of Fern Gully, small turnout near the base of large coral formation, elevation 910′; 4♀, 1♂; near town of Phoenix Park, elevation 1220′; 2♀, 2♂, Alderton, elevation 1460′; 3♀, ~4.1 km from town of Cedar Valley, elevation 2230′; 1♀, 2♂,~5.6 km north of Alexandria, elevation 1900′; 1♀, 2♂, 1.2 road km south of main intersection in Stewart Town. **St. Catherine:** 3♀, 3♂, 3.1 km east of Jackson, elevation 1550′; 7♀, 4♂; town of Bay Walk, elevation 230′; 11♀, between Works and Riverdale, elevation 150′. **St. James:** 2♀, 2♂, ~.07 road km S of Spring Vale, elevation 160′. **St. Mary:** 3♀, 3♂, ~2 km east of the town of Windsor Castle, elevation 1290′; 7♀, 3♂, Leinster, 1.8 road km south/south-west of intersection near bridge north of Tranquility, elevation 290 m. **Trewlany:** just south of Jackson Town; 4♀, 4♂; Cockpit Country, Windsor, Troy Trail, about 100 m south of Devils Hole, elevation 300 m; 1♀; Troy, elevation 1410′. **Westmorland:** 1♀, 2♂, ~5 km south of Haddo, elevation 720′; 3♀, 1♂, ~5 km north of Delue Bridge; 2♀, Town of Penny Cooke, elevation 750′.

Diagnosis

This species can be distinguished from its two sister species on the basis of the following unique combination of mtDNA *16S* rRNA gene nucleotide substitutions: C (56), T (59), G (123), C (392), T (473), A (520), A (523), C (537), T (559), C (663), C (937), C (964), T (969), C (1058). (The alternative character states at each of the above positions for the remaining two species are listed in Fig. 7.) Additional morphological features that may be helpful in distinguishing *A. holomelanus* from *A. dissimulans* are given in the Diagnosis of *A. dissimulans*. *Anadenobolus holomelanus*, where sympatric with *A. dissimulans*, behaves much differently than *A. dissimulans* (or *A. excisus*). When disturbed, *Anadenobolus holomelanus* thrashes about and sprays defensive secretions to distances in excess of a metre, whereas the other two species are more likely to curl up into a tight ball and ooze their defensive secretions.

Description of male neotype (FMMC# 3421)

Head, antennae and collum uniform dark olive green when collected in the field from the more eastern parishes (e.g. St Ann, St. Catherine, St Mary). In the more western parishes (e.g. Manchester), where this species co-occurs with *A. dissimulans*, specimens are often very shiny black (in the field; the colouration more subdued for specimens in alcohol) with lighter metazonite appearing almost white in contrast. Prozonite in all specimens slightly darker in colour than metazonite. Ring segments divided by faint suture both longitudinally and laterally.

Left antennae of neotype with five sensory cones, right with four, ~11–11 labral setae, clypeal groove very deep, 35 ocelli. Width 10.02 (1)–11.48 (20)–10.97 (45), 54 ring segments. Leg I setal formula: 6– 3 – 2 – 5 – 2; Leg II: 6 – 3 – 2 – 4 – 2. Tarsi have prominent ventral pads that are slightly lighter in colour and divided longitudinally. Scobinae formed as small distinct pits on the 8th– *c.* 18th segment. Epiproct short and blunt, does not extend beyond anal valves. Hypoproct short, triangular with blunt broadly rounded terminal end.

Coleopod and telopodite as illustrated in Figs 2 and 10. Sternum of coleopod broad and rounded distally (Fig. 10*b*,*e*,*i*,*k*). General shape of Cx and Tp as in *A. excisus* and *A. holomelanus* (Fig. 3). Anterior, proximal aspect of Cx with lightly sclerotised inner marginal Pk. Inner posterior margin of coleopod lightly sclerotised and divided longitudinally ~3/4 of its length. Distal-most aspect of coleopod Tp with patch of short setae (Fig. 2*f*). Phallopod Tp (Fig. 10*c*,*f*,*h*,*l*) slender bifurcate structure. Solenomerite extends at least half distance to terminal-most aspect of telopod. Sc visible extending from Cx up to solenomerite.

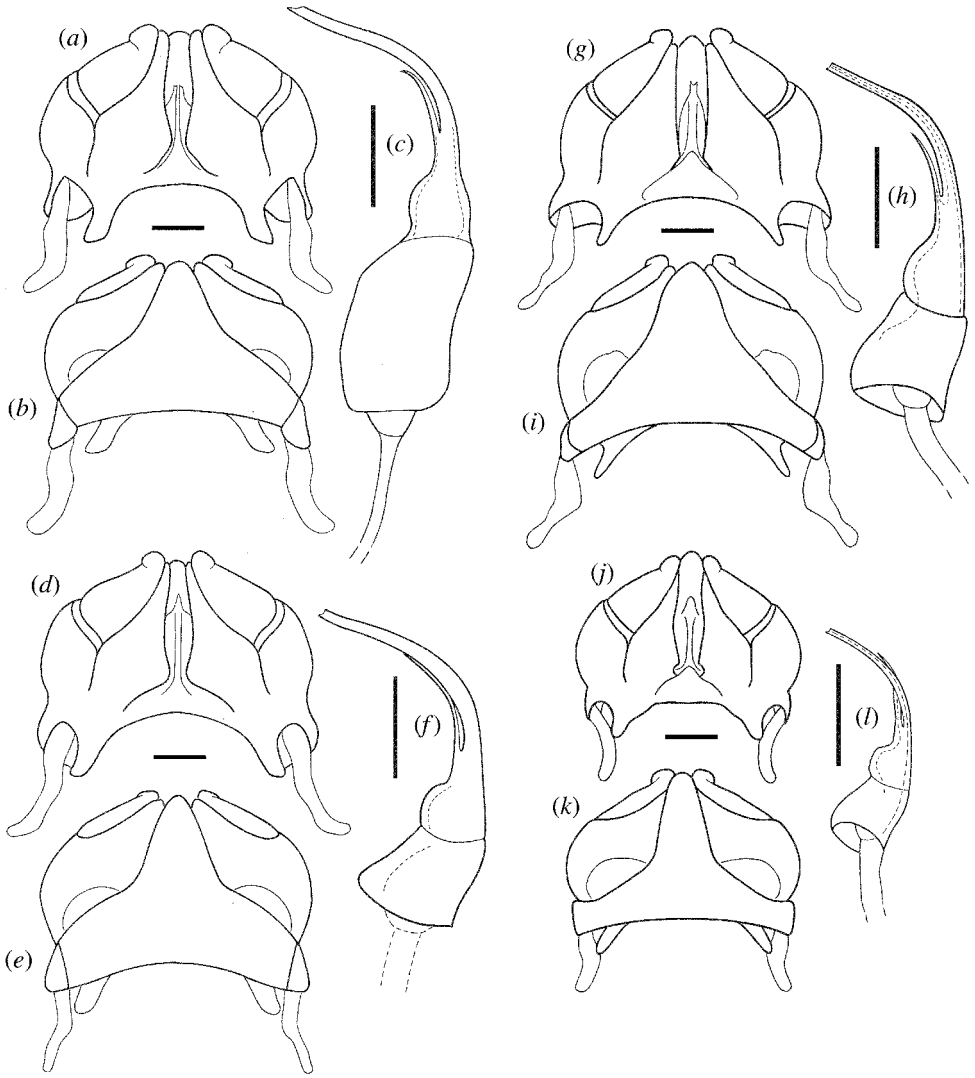

Fig. 10. *Anadenobolus holomelanus* Pocock. *a–c*, Gonopod of male neotype; *d–e*, gonopod of specimen from Manchester Parish, 0.5 km south of Newport; *f–h*, gonopod of specimen from Trewlany Parish, Troy; *i–k*, gonopod of specimen from Clarendon Parish, Burbage. Scale bars = 1 mm.

Seventh segmental ring posterioventrally modified as postgenital bar to accommodate gonopods.

MtDNA haplotype designation and GenBank Accession # of male neotype: manVC, AF501439.

Variation

Variation in colouration as described above, variation dependent upon region from which specimen is taken. Scobinae size variable in this species, in some specimens formed only as small pits, whereas in others they are much larger. Male gonopod structure with typical amount of shape, however, no apparent discrete shape differences across its distribution. Size highly variable (summarised in Fig. 6*a*), specimens range from relatively small to very large (5.7–11.20, $n = 57$) and tend to be largest where sympatric with *A. dissimulans*. Considerable variation in the number of ring segments (Fig. 7) appears to be concomitant with overall size variation (43–56) with a mean value of 49 ($n = 66$).

Description of female paratype (FMMC# 3342)

Colouration as described for males. Antennae with four sensory cones, 11–10 labral setae, clypeal groove distinct, 33 ocelli. Width 9.50 (1)–10.24 (20)–10.29 (45), 51 ring segments. Leg I setal formula: 7 – 3 – 5 – 4 – 2; Leg II: 6 – 3 – 2 –4 – 2. Tarsi lack prominent pads. Scobinae formed as distinct pits on the 8th–17th segment, equal in size to that of male neotype. Epiproct and hypoproct same length and conformation as in males, short.

Cyphopods similar to those described for *Eurhinocricus rosenbergi* Bond and Sierwald, 2002*a*: fig. 3. These are very simple, sclerotised structures comprising two caudal plates lacking setae, which open ventrally via lightly sclerotised operculum (not illustrated).

MtDNA haplotype designation and GenBank Accession # of female exemplar: manVB, AF501429.

Variation

Female colouration and scobinae size variation similar to that described for males. Size highly variable (7.04–12.76, $n = 67$), pattern of size variation as in males. Number of ring segments likewise variable (43–56) with a mean value of 49.

Distribution and natural history

The first author has collected this species throughout the following parishes: St Catherine, St. Ann, Trewlany, Manchester, Westmorland, St James and Hanover. This species occurs only in areas with lots of limestone where it is found in an 'interstitial'-like manner among the limestone rubble. Much of its range overlaps with that of *A. dissimulans*. As mentioned in the Remarks, this species behaves differently when disturbed. Unlike the other two species, *A. holomelanus* is quite active and is able to spray its defensive chemicals quite a distance.

Remarks

The original holotype of *A. holomelanus* was presumed by Hoffman (1999) to be deposited in The Natural History Museum collection in London, but the specimen could not be located (J. Beccaloni personal communication). Although unlikely to be deposited elsewhere, we made additional, unproductive inquiries, to the Museum National d'Histoire Naturelle, Paris; Zoologisk Museum, Universitet København; and Zoologisches Museum, Hamburg. The absence of this type specimen in the BMNH is consistent with what Hoffman (1999) has observed for many of the Biologi Centrali–Americana and later species that never were returned after Pocock's departure from the BMNH in 1903. To ensure the future nomenclatural stability of the *Anadenobolus excisus* species complex we find it necessary to designate a neotype for *A. holomelanus*. Due to the cryptic nature and widespread distribution of all three species in this group it is important that each species be represented by a type specimen collected from a specific type locality.

Pocock's (1894) description contains two clues that suggest that the Clade III specimens and the single specimen that we designate as the *A. holomelanus* neotype are captured by his concept of *A. holomelanus*. First, his general description states that the colour is 'black and shining' and the length is up to 105 mm. These colouration and size are features are consistent with Clade III individuals (Fig. 4) that are sympatric with *A. dissimulans* (Clade II). Secondly, Pocock does not give a specific type locality but he does mention specimens collected from Mandeville and Moneague. Although Clade II individuals have been collected from Mandeville and surrounding areas (see above), only Clade I and III individuals have been collected in the parishes east of Manchester. The choice of locality for the neotype specimen reflects our attempt to choose a specimen from an area close to those mentioned by Pocock (1894) in his description.

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