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The false click beetles (Coleoptera: Elateroidea: Eucnemidae) of the Dominican Republic. Part I: A look into the past

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Printed copies (ISSN 0749-6737) annually deposited in libraries

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Electronic copies (Online ISSN 1942-1354) in PDF format

Archived digitally by Portico
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The false click beetles (Coleoptera: Elateroidea: Eucnemidae) of the Dominican Republic. Part I: A look into the past

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Abstract. Thirteen new fossil eucnemid taxa (Coleoptera: Elateroidea) are described from amber deposits excavated from the vicinity of Santiago, Dominican Republic. Two **new genera**, *Mioxylobius* and *Paleoquirsfeldia* are described. The following 13 **new species** are described from Dominican amber: *Mioxylobius bicolor*, *Balistica serrulata*, *Paleoquirsfeldia epicrana*, *Dyscharachthis dominicana*, *Idiotarsus poinari*, *Euryptychus antilliensis*, *Euryptychus hispaniolus*, *Plesiofornax caribica*, *Fornax dominicensis*, *Fornax serropalpoides*, *Dromaeolus argenteus*, *Nematodes miocenensis* and *Nematodes thoracicus*. Each new species are both diagnosed and illustrated. *Calyptocerus* Guérin-Méneville and *Lissantauga* Poinar are shown to be congeneic, resulting in a **new combination**: *Calyptocerus epicranis* (Poinar, 2013). Summaries of fossil eucnemid discoveries, highlighting differing hypothesis of prehistoric Caribbean island formations/speciation, accounts of ancient Dominican Republic environmental conditions and Dominican Republic amber are provided.

Key words. West Indies, Hispaniola, new genera, new species, paleoentomology, paleogeography, paleogeology, paleoclimatology, paleoceanography, biogeography.

ZooBank registration. urn:lsid:zoobank.org:pub:48A76A23-E48B-46B5-8A35-A27DD6134B6D

Introduction

This is the first of two papers to cover the false click beetle fauna of the Dominican Republic on the island of Hispaniola in the Caribbean region. In this first paper, the false click beetle fauna of the past captured in high quality amber are highlighted as we begin to understand the composition of its diversity as it relates to the fauna in the present time on the island and in the region as a whole. The forthcoming second part will be covering the extant eucnemid fauna present in the Dominican Republic. Hypothesis of eucnemid biogeography for the Dominican Republic will be presented in part two of the paper factoring all taxa past and present.

Poinar and Poinar (1999) wrote, "The elegance of these fossils adds to their general enjoyment and fascination. Portrayed will be ancient life forms from a realm that no longer exists in the Greater Antilles, nor anywhere else in the world today! Such extinct forms can answer questions about paleobiodiversity, evolution and biogeography. They can also enlighten us about the past climates, insect-plant interactions, and parasitic relationships". Truly authenticated amber or impression fossils from any parts of the globe offer us a snap shot of the prehistoric microcosmos now frozen in time that existed long ago.

Since the first fossil eucnemid was described in 1914, a total of 76 species have been described and named from various literatures; much of it in the last 60 years. There are a number of taxa doubtfully placed in the family which requires further evaluations in the future. The current study will be adding 13 new, extinct species, including two new genera which at one time inhabited a small island in the Caribbean that now exists today as part of the larger Hispaniola, bringing the number of fossil Eucnemidae to 89 species.

Fossil eucnemid discoveries

Wickham (1914, 1916) were the first to describe the compression fossils of five extinct species of Eucnemidae found in the Miocene Florissant fossil bed near Denver, Colorado. Four of the five species still remain in Eucnemidae; which include *Microrhagus fossilis* (Wickham), *Microrhagus miocenicus* Wickham, *Microrhagus volcanicus* Wickham and *Fornax relictus* Wickham. Muona (1993) found one species, *Eucnemis antiquatus* Wickham, had

been misplaced in the family and may be a member of Ptinidae. He also transferred Wickham's *fossilis* from *Deltometopus* Bonvouloir to *Microrhagus* Dejean.

Britton (1960) described one species, *Potergites senectus* based on 15 specimens found in the Eocene London clay formation of Bognor Regis. He placed the species nearest to *Epipleurus* Fleutiaux within Eucnemidae. Muona (1993) affirmed Britton's theory of *Potergites*' placement nearest to *Epipleurus* based on the presence of tarsal grooves on the abdomen and its wide form. Muona noted deep striations on the elytra are a peculiar feature in Eucnemidae. He further added the possibility of *Potergites* may be an aberrant throscid as all the heads in these specimens are missing. Muona (2021) described a second *Potergites* species from Baltic amber and ascertains the group is a true eucnemid. He transferred the group to the tribe Dendrocharini Muona.

Iablokoff-Khnzorian (1962) described one species, *Throscogenius takhtajani* in Eocene Baltic amber as a throscid and erected a subfamily Throscogeniinae for the extinct species. Cobos (1963) argued that Throscogeniinae belong in Eucnemidae and transferred *Throscogenius* there. Muona (1993) later synonymized Throscogeniinae in the subfamily Macraulacinae Fleutiaux. The position and status of *Throscogenius* in Macraulacinae remains unsettled. *Throscogenius* is similar to *Deltometopus* Bonvouloir and possibly placed nearest to *Deltometopus* and *Thambus* Bonvouloir within the tribe Macraulacini Fleutiaux.

Muona (1993) identified a number of Eucnemidae in Eocene Baltic amber. Only 13 eucnemids received specific names. Twenty-one remaining eucnemids were identified either at the generic or tribal level, uncertain of their generic placement for some. He described two new extinct genera, *Erdaia* (type species: *Erdaia hageni*) and *Sieglindea* (type species: *Sieglindea siegmundi*). He briefly reconstructed Baltic environment that existed in the Eocene Epoch, which consisted of a subtropical environment with both coniferous and non-coniferous trees present; similar to the Caribbean coastline of North America.

Alexeev (2008) described the first Cretaceous eucnemid impression fossil, *Cretopoena gratshevi* from the lower Cretaceous of Mongolia. Presence of longitudinal grooves on the vertex and frons for this species is similar to some extant Eucnemidae, particularly some members of the Eucneminae and Macraulacinae. Additionally, presence of antennal grooves on genae, below the compound eyes also place the species in Eucnemidae. The fossil exhibits poor traces of the ventral areas, making its position within Eucnemidae uncertain. From examining the images in the paper, it is hard to make out the presence of excretory punctures along the elytral apices, a feature present in many Eucnemidae. At best, the species should be placed in Eucnemidae *incerte sedis*, until its generic status and specific position within the family or superfamily Elateroidea is fully resolved.

Poinar (2013) described the first eucnemid species in Dominican amber, *Lissantauga epicrana* without placing the group within the family. This species is diagnosed by its silver coloration, glabrous body, the position of the eyes relative to the antennal insertion and anterior elytral margins angled differently from eucnemid genera. Muona (2021) discussed the species and believed the group *Lissantauga* could be a junior synonym of the group *Adelothyreus* Bonvouloir. *Adelothyreus* is defined by the presence of a divided lateral pronotal ridge, pectinate antennae, caudally wide notosternal antennal grooves, and narrowing form. After reading descriptions and viewing associated images, this species is similar to *Isorhipis* Boisduval and Lacordaire and *Calyptocerus* Guérin-Méneville. Poinar (2013) described its antennae as strongly pectinate (flabellate in images as observed in figures 8 and 11). Absence of hypomeral antennal grooves (as seen in the images), simple lateral pronotal ridge, parallel-sided metacoxal plates, hypomera narrowing craniad, apical ventrite with median beak caudally and flabellate antennae places the species in the tribe Calyptocerini Muona. Parallel-sided metacoxal plates, narrowing hypomera, expanded elytral epipleura covering much of the episterna, strongly flabellate antennae, flattened antennal rami and a produced last abdominal ventrite (present in many extant species) are diagnostic for *Calyptocerus*, in which *Lissantauga* becomes a junior synonym of that genus. The species is therefore transferred to this genus resulting as *Calyptocerus epicranis* (Poinar) **new combination**.

Huali et al. (2016) described the first larval compression fossil for a Cretaceous eucnemid from the Yixian formation of China. That larva was named *Palaeoxenus sinensis* Huali et al. 2016. This discovery has led to the exposure of the extant *Palaeoxenus dohrnii* (Horn) from southern California, USA as a living fossil. Several features were outlined to distinguish the extinct species from that of the extant living fossil residing in several mountain ranges in southern California.

Oberprieler et al. (2016) described a number of elateroid taxa from the Upper Jurassic Talbragar Fish Bed of Australia for several families. Within Eucnemidae specifically, *Beattieellus jurassicus* Oberprieler et al. was

the only described species. Several other listed taxa were uncertain as to its assignment within Eucnemidae. In examining images of the described species in their publication, one feature, the specialized grooves and/or punctures at the elytral apices are absent in *B. jurassicus*. These specialized grooves/punctures were first discovered by Otto and Gruber (2016) and later determined to be a very important external synapomorphic character state for Eucnemidae (see Muona and Teräväinen (2020), Muona (2020) and Muona et al. (2020) for details), especially for identifying fossil Eucnemidae. It is best at least to treat the placement of *B. jurassicus* as either *incerte sedis* in Eucnemidae or transfer the species to Elateridae. Further evaluations are necessary to ascertain the placement of the species within Elateroidea.

Otto (2019) described two new elateroid taxa for Eucnemidae and Elateridae from Burmese amber. The very first eucnemid described from Burmese amber belonged to a new genus, *Cenomana* (type species: *Cenomana clavata*). It was originally described as a member of the tribe Jenibuntorini Muona; however, Muona (2020) transferred the group to the tribe Dirhagini Reitter after he described a second species within the group.

Li et al. (2020) described the second known eucnemid from Burmese amber a little more than a year after Otto's (2019) first described eucnemid. They described the eucnemid in their new group as *Muonabuntor* (type species: *Muonabuntor grandinotalis*). In their publication, they noted differences between *Jenibuntor* Muona and *Euryptychus* LeConte and how they differ from their group. According to Muona (*pers. com.*), the illustrated specimens authors identified as *Jenibuntor* were misidentified and belong to an undescribed species of *Euryptychus* from Australia. Muona (2020) provided illustrative means to diagnose *Jenibuntor* apart from *Muonabuntor* and *Euryptychus*.

Muona et al. (2020) outlined the external synapomorphic character states to identify species of elateroid beetles to their families. They re-checked 28 fossil taxa described in Elateridae from China. Although eight of these taxa couldn't be firmly identified at the family level, they transferred seven species from Elateridae to Eucnemidae and one other species to Throscidae based on observed external synapomorphic character states in the fossils.

Muona (2020) added eight new genera and 20 new species from Cretaceous Burmese amber. He noted that this study is the first installment of the work conducted on the fauna from Burmese amber and future work is in progress to elucidate the prehistoric eucnemid fauna from the region. Several groups were tentatively placed within Eucnemidae and noted further world-wide revisions using fossil and extant species together are necessary to clarify their positions within Eucnemidae.

Li et al. (2021) described the first representation for a member of the subfamily Anischiinae from a compression fossil excavated from the Yixian formation (Jehol Biota). The site is located within the Liaoning Province in China. Age of the fossil dates back 125 million years ago in the Hauterivian to Aptian age of the Cretaceous period. Discovery of the fossilized member of the subfamily, helps to firmly confirm the placement of the subfamily in relation to other groups within the family, which is now placed between the subfamilies Schizophilinae Muona and Palaeoxeninae Muona.

Muona (2021) added two new genera and 22 new species from Baltic amber deposits. Evolutionary implications between ancient eucnemid faunas of Myanmar and of the Baltic regions are discussed in the paper. Thirty-six species are now known from the Baltic amber deposits. Many more unknown Baltic amber specimens are currently in the GERP collection awaiting formal studies.

Muona (2022) has added several more new fossil Eucnemidae from the Americas including one from the Dominican Republic deposit, North Carolina U.S.A. deposit, and Colombia deposit. One new genus was described from North Carolina, U.S.A. *Thambus woodruffi* Muona was the second eucnemid species described from the Dominican Republic amber.

Zippel et al. (2022) described an ancient eucnemid larva captured and preserved in Cretaceous Burmese amber. Although they did not formally name it, they provided comparisons between the fossil eucnemid larva and known modern eucnemid larvae as well as noting its role in carbon cycling through breaking down rotten wood. The larva is superficially similar to the extant eastern North American eucnemid, *Schizophilus subrufus* (Randall). The fossil eucnemid larva is believed to be an early instar, approximately third instar based on its measurement. The presence of elongate setae, urogomphi and general form of the larva would suggest the larva may belong to one of the species in the subfamily Schizophilinae. *Apoclion* Cheng, Kirejtshuk & Ren and

Paradesmatus Cheng, Kirejtshuk & Ren are two known Asian extinct members of Schizophilinae present in the region thriving as early as the middle Jurassic to as late as the lower Cretaceous Epochs.

Alekseev and Bukejs (2022) described the second extinct Eocene member of *Isorhipis*. Their species, *Isorhipis muonai* differs from another extinct Eocene eucnemid, *Isorhipis balticus* Muona by the shape of the scutellar shield and overall length of the metatarsomere I. They have compared their new species against known extant species present in the western Palearctic region.

Differing prehistoric Caribbean island formations and biogeographical/colonization hypotheses

The Caribbean, including the Greater Antilles and the Lesser Antilles have a complex geological and biological history. According to Graham (2003), Proto-Greater Antilles were formed as submerged volcanic islands in the early Cretaceous Epoch, between the North American and South American land masses. The island arc, as a part of the Caribbean tectonic plate broke away from its original position and advanced northeastward throughout the Paleocene and Eocene Epochs until it collided with the Bahamas Platform. These islands emerged above the oceanic surface sometime in the Eocene Epoch. Throughout the early and middle Eocene, they began to coalesce as eastern Cuba, northern Hispaniola and Puerto Rico were added to western Cuba. During early and middle Miocene Epoch, western and northern Hispaniola, along with Puerto Rico broke away from eastern Cuba, as the northern edge of the plate continues to compress against the Bahamas Platform. Southern Hispaniola was added to northern Hispaniola later in the era. Puerto Rico broke away from Hispaniola during the Oligocene Epoch. Jamaica's geologic history was quite different, which the island remained submerged until late Miocene Epoch. Ricklefs and Bermingham (2008) wrote that Jamaica represents a fragment of the Central American continental crust, later dragged into the Caribbean basin by plate movement. Northern areas of the Lesser Antilles, including the Virgin Islands became emergent from the middle to late Eocene. Southern areas of the Lesser Antilles became emergent in the Oligocene Epoch. These islands were formed as a result of the subduction of the North American and South American plates under the Caribbean plate at the Atlantic seafloor.

Iturralde-Vinent and MacPhee (1999) offered an alternative hypothesis of paleogeography and Caribbean paleobiogeography of how these lands were formed as it relates to the development of faunas in the region. Their model was based largely on paleogeological and paleoceanographical evidences (*i.e.* rock formations, fossilized oceanic micro-organisms and paleo-oceanic currents) as well as species/area relationships from which the northern Greater Antilles Ridge was connected to northwestern South American microcontinent by means of a landspan they termed GAARlandia (Greater Antilles + Aves Ridge). They believed a narrow landspan or bridge was formed during the Eocene-Oligocene transitional period, in which the subaerial Aves Ridge (now submerged) at low oceanic levels, allowed megafaunas to disperse across it from the South American microcontinent towards the terminus (present day Cuba and Hispaniola).

Mechanisms for speciation on these islands have been greatly debated. Some (*i.e.* Rosen, 1975, 1978, 1985) have postulated continent-island dispersal allowed megafaunas such as reptiles and mammals to disperse to these islands and through endemism by vicariance, independently evolved as new species while the West Indies drifted away from these land masses. Iturralde-Vinent and MacPhee dismissed Rosen's explanation. Their hypothesis is a combination of two different elements, that being strict dispersal and strict continent-island vicariance. Continental landspan would have a greater diversity. A landspan, especially at the terminus, as in the case of GAARlandia would see a lack of continental diversity. Transfer from one faunal area through a newly developed landspan would be controlled by a number of factors (*i.e.* filters) that would affect the likelihood for some species' descendants would reach the terminus. Dispersion to islands at the terminus is likely at a time of low oceanic levels during that era. Connection from South America through the Aves Ridge was severed after oceanic levels rose, and allowed plants and animals to independently evolve on those islands. Iturralde-Vinent and MacPhee (1999) also reviewed experimental results from Brucks (1971) and Molinari et al. (1979) involving use of flotsam devices like buoys and drift bottles to map surface currents in the Caribbean Sea. They concluded oceanic currents are highly unpredictable following recovery of these devices at many locations west of the Greater Antilles along the Central American coastline after being released in the sea just north of South America, especially after the closure of the Panamanian Isthmus 4 million years ago. They further concluded, it is unlikely for faunas to disperse by means of rafting to the Greater Antilles from any of the continents.

Ali (2012) dismissed Iturralde-Vinent and MacPhees' GAARlandia model, based on a number of points. Ali argued Iturralde-Vinent and MacPhee never demonstrated a spike in the vertebrate's arrival during the transitional period, nor an exchange in biota between the Greater Antilles and South America, similar to the Great American Exchange between the North American and South American continents. He expressed concerns over the lack of ocean floor drilling data could have demonstrated the Aves Ridge were subaerial during that period. He believed the Aves Ridge was never subaerial nor played a role in the formation of the landspan, in which the ridge is currently situated west-southwest of the Lesser Antilles island chain. Lastly, Ali argued Iturralde-Vinent and MacPhee failed to consider computer-based paleoceanographic simulations to build their case on surface currents of the Caribbean Sea during the Eocene-Oligocene transitional period. Ali further emphasized, based on various models, oceanic currents flowed from northern South America towards the Greater Antilles during that period. Ali and Hedges (2021) continued to challenge the GAARlandia land-bridge hypothesis through examining updated colonization record of land vertebrates and new geological data. They examined the hypothesis using updated compilation of land-vertebrate colonization through 35 clades (23 reptiles, 6 amphibians, and 6 mammals) along with new data from a recently published study of the Aves Ridges and Grenada Basin. They concluded these Caribbean islands were colonized by means of over-water dispersal from nearby continents, for vertebrates, plants, and invertebrates. Additionally, they call upon the re-evaluation of many biogeographical scenarios proposed for the Greater Antillean biota after challenging the validity of the GAARlandia hypothesis.

Roncal et al (2020) looked at four different, primary hypotheses of island colonization including vicariance, GAARlandia, long distance dispersal and in-situ speciation (speciation occurring within or between islands) using plants from the Caribbean to revise the discussion of regional paleogeography. They used Time-For-Speciation Effect hypothesis to look at the colonization time for groups of plants in the region through phylogenetic analysis using mathematical equations to calculate estimated time of colonization taking place for each group. Their results showed plant colonization took place repeatedly over the last 60 million years from continental America, especially from Central and South America. Most colonization (over 80%) took place after the purported GARRlandia event as proposed by Iturralde-Vinent and MacPhee (1999), thereby refuting that hypothesis along with the Cretaceous vicariance model from Rosen (1975). Through their models, they concluded over water dispersal (especially for seed plants) from overall stronger sources coming from Central and South America allowed these plants to colonize and evolve on these islands, most taking place more recently than the Oligocene Epoch.

Webster (2020) developed Ancient Earth Globe (dinosaurpictures.org), an online, virtual, interactive globe depicting the arrangements of the continents and oceans through geologic time in history. Map data was based on the PALEOMAP project. In utilizing the feature, it may allow a possible hypothesis on the faunal transfers between continents through history. Fossil records indicate Eucnemidae have been present since early to middle Jurassic Epoch. At that time, about 170 million years ago, the South American/African continents (Gondwanaland) were very close to the North American continent. Potential flow of Eucnemidae from Gondwanaland may have taken place through Mexico (via land transfer) and/or southern United States (via over water dispersal). The North American continent began to separate from South America/Africa during the late Jurassic Epoch (~150 million years ago). Proto-Greater Antilles began to form between the North American and South American continents in early Cretaceous Epoch (120–105 million years ago). A land-bridge (Beringia) is present which connects western North America to Asia during that period. About 90 million years ago, during the Cretaceous Epoch, a shallow sea separates western North America (Laramidia) from eastern North America (Appalachia). Proto-Greater Antilles continues to drift between the two continents. At 66 million years ago, the land-bridge connecting Asia with western North America began to break up, while South America continue to drift further from North America. The shallow sea recedes, allowing western North America to reconnect with eastern North America and Proto-Greater Antilles is subaerial and positioned in the Atlantic Ocean near the present day Yucatan Peninsula. It is quite possible eucnemid fauna began on Proto-Greater Antilles through continent-island vicariance with the source coming from the southern North American continent (present day Mexico near the Yucatan Peninsula). Proto-Greater Antilles may be too far from South America to receive any eucnemid fauna during that time in history. In the Tertiary Epoch (~50 million years ago), Proto-Greater Antilles continue to drift while Central America began to form as series of islands that could eventually reconnect North America to South America. Proto-Greater Antilles is still in close proximity with the North American continent during the middle Tertiary Epoch (35 million years ago). During the Neocene Epoch (20 million years ago), the Greater Antilles is

positioned near the Bahamas in the Atlantic Ocean and Central America is formed. No depiction of GAARlandia have been observed through the interactive online globe.

Prehistoric plant communities of Hispaniola

Primitive plants like spore producing algae, moss, lichens and ferns help establish a complex of plant communities on these islands. Poinar and Poinar (1999) provided intimate details, reconstructed the primeval forest that existed on Hispaniola millions of years ago. Detailed reconstruction of the plant community was based on inclusions observed in pieces of amber excavated from the mountains of the Dominican Republic. The forests of Hispaniola (Dominican Republic) were a tropical wet forest with several strata of vegetation. The ancient forest consisted primarily of broad-leaved, evergreen, leguminous trees with acacias (Fabaeceae), palms (Palmaceae), and many other groups. The upper canopy consisted of algarrobo (*Hymenaea protera* Poinar; Fabaceae), nazareno (*Peltogyne* sp.; Fabaceae), cativo (*Prioria* sp.; Fabaceae), and sebo (*Virola* sp.; Myristiaceae), with the emergent tree, caoba (*Swietenia* sp.; Fabaceae) towering as high as 135 feet tall in the canopy. The subcanopy consists of sigua (*Nectandra* sp.; Lauraceae) with *Mimosa* sp. (Fabaceae), *Acacia* sp., and *Trichilia* sp. (Meliaceae). The shrub layer consists of other *Acacia* sp. and palms. Epiphytes, ferns, fungi, lianas (*Peritassa* sp.; Hippocrateaceae), lichens, liverworts, mosses, pega-pega (*Pharus* sp.; Gramineae), and vines were also present in the ancient forest. Although many species no longer inhabit Hispaniola, many of its descendants are present in Central and South America, including a single algarrobo species distributed on the West African continent.

Dominican Republic amber

The tree responsible for resin production came from the algarrobo. These trees were one of the primary components of the upper canopy level of the extinct forest system; which produced copious amounts of resin that entrapped arthropods, as well as plant artifacts including pollen, leaves and inflorescences. Vertebrates like entire reptiles and amphibians as well as artifacts like mammalian hairs and avian feathers were also entombed in fresh tree resin.

Fresh resins containing biological inclusions often fall onto the forest floor from these trees. Iturralde-Vinent and MacPhee (1996) examined amber excavated from the Yanigua strata formation, from which they concluded these deposits were imbedded in lignite and sandy clay, particularly in the eastern area, consisting of organically enriched sedimentary rock. The strata is composed of laminated sand, sandy clay and some intercalated lignite layers. They found sparse plant debris throughout the strata, along with absence of alluvial sediments and isolated beds of gravel and calcarenite. In addition to sparse plant debris and absence of alluvial sediments, presence of invertebrate and vertebrate fossils were observed in the strata, which they indicated, deposition occurred in the near-shore area, possibly a coastal lagoon flanked by nearby low, densely forested hills. Iturralde-Vinent and MacPhee observed the La Toca formation is of the same strata and age as the eastern deposits, later disrupted by movements along major fault lines. Strata differ by its sandstone composition with occasional conglomerates accumulated in a deltaic to deep-water environments. Presence of a thin layer of lignite and carbonized wood fragments were observed in the strata. They postulated these deposits were slope-washed into the river channel cutting the Cordillera Central then later transported with sand and silt into the deltaic and deep-water environments of the basin.

Iturralde-Vinent and MacPhee postulated, based on fossilized evidence of micro- and megafaunas found in the surrounding areas of the strata, the age of these amber deposits were of late Early to early Middle Miocene Epoch (15–20 million years ago). Their observations conflict with other estimates on the age that ranged from as early as the Cretaceous period to the most recent. Debate on the age estimates of Dominican amber deposits is still on-going which will rely on further analysis to calculate the age of these excavated pieces.

Materials and Methods

Many of the fourteen (13 polished, 1 rough) Dominican Republic amber pieces containing eucnemid inclusions were donated from Albert Allen to the collection of the Global Eucnemid Research Project over the last decade. Each piece was authenticated by black light, acetone tests and specific gravity using salt water developed by Poinar

(1982). All amber pieces were observed to fluoresce when illuminated with ultraviolet light. Small amounts of acetone were placed on a Q-Tip® and applied to the pieces. None of the amber specimens were tacky when the treated area was touched. Specific gravity test consists of dissolving 2.5 level tablespoons of salt in one cup of water, achieving a specific gravity of 1.1. All polished pieces floated in the salt water solution (a large, rough piece was not tested).

All images were taken with a JVC KY-F75U digital camera attached to a Leica® Z16 APO dissecting microscope with apochromatic zoom objective and motor focus drive, using a Synchroscopy Auto-Montage® Pro System and software version 5.01.0005. Holotype and paratype amber specimens are deposited in the collection of the Global Eucnemid Research Project (GERP) maintained at University of Wisconsin-Madison Department of Entomology, Madison, Wisconsin.

Systematics

Subfamily Melasinae Fleming, 1821

Tribe Xylobiini Reitter, 1911

Genus *Mioxylobius* Otto, new genus

Type species. *Mioxylobius bicolor* Otto, **new species**, designated here.

Description. Body approximately four times longer than wide, dorsally convex and ventrally sclerotized. **Head:** Hypognathous with elongate setae. Frons convex, without median ridge or groove. Antennae with 11 antennomeres; scape 4.0 times longer than pedicel; pedicel elongate, longer than flagellomere I; flagellomere I shorter than flagellomere II; flagellomeres II–VIII sub-equal in length, slightly longer than wide and rounded in cross sectional view; flagellomere IX asymmetrical, slightly longer than VIII. Compound eyes large, round. **Pronotum:** Subparallel-sided, convex and setose. Slightly longer than wide, with small hind angles. Lateral pronotal ridge entire. Notosternal suture as long as the hypomeral base. Hypomeron simple, without antennal grooves. **Elytron:** Elongate, convex, setose. Disc with very weak indications of striae. Interstices flattened. **Legs:** Pro-legs shortest, hind legs longest. Metatarsi, including claws as long as tibia. Metatarsomere I shorter than 2–5 combined. Metatarsomeres I–III simple. Metatarsomere IV excavate-emarginate, wider than III. Metatarsomere V elongate with simple claws. **Venter:** Setae inconspicuous. Elytral epipleurae not grooved. Metacoxal plates parallel-sided. Tarsal grooves absent on mesothoracic and metathoracic sterna. Abdomen with five visible ventrites, medially convex. Last visible ventrite caudally evenly rounded.

Etymology. The generic name is the combination of the stem, *Mio-* which is derived from the Greek word meíōn meaning "less" taken from the word Miocene, a Tertiary Epoch and the root, *Xylobius* Latreille, a eucnemid genus literally translated meaning "wood + I live".
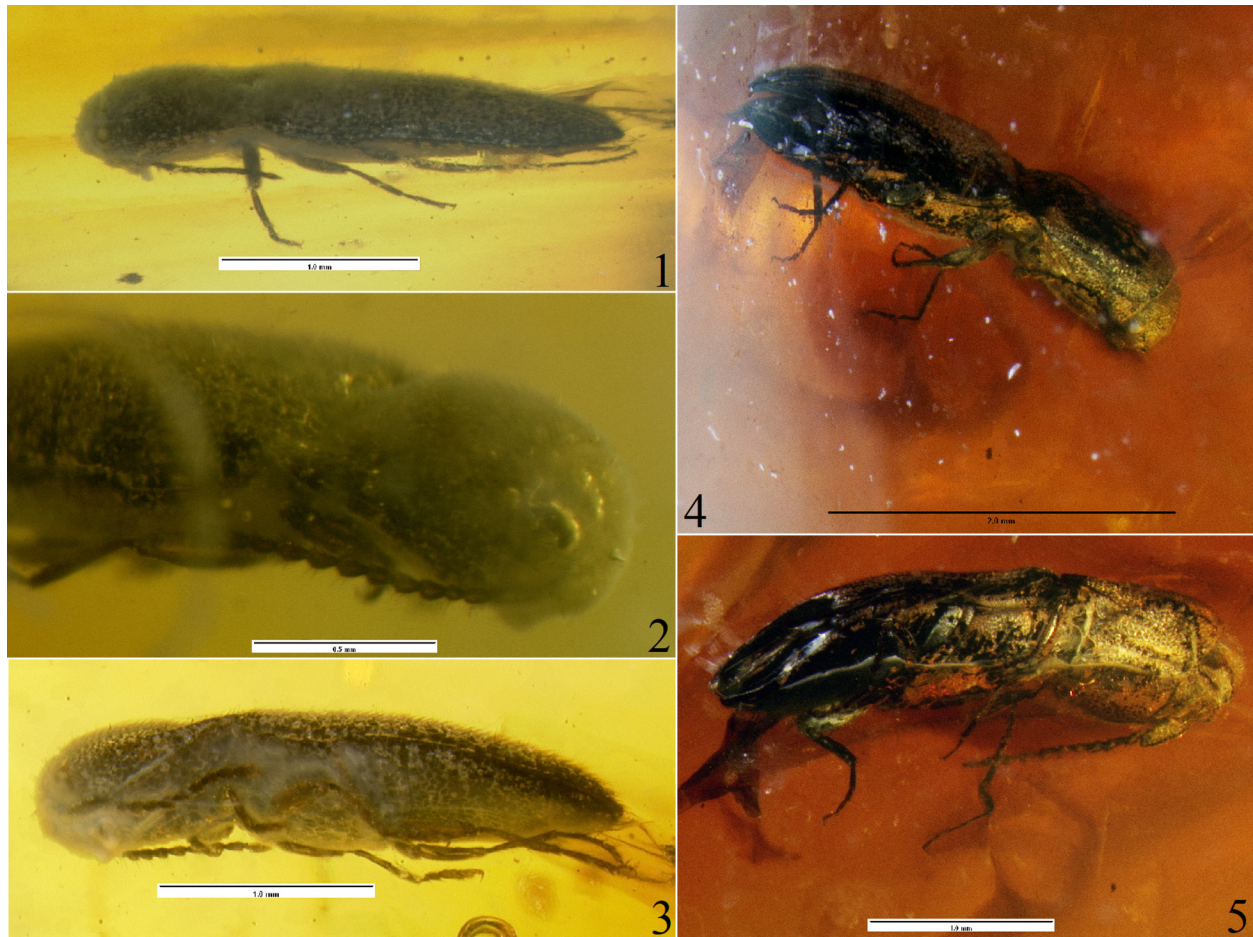
Mioxylobius bicolor Otto, new species
Fig. 1–3

Holotype. Embedded in ovoid Dominican Republic amber piece, 20 mm × 12 mm × 5 mm. Amber piece is clear yellow with small air bubbles and micro fractures.

Description. Length, 3.0 mm. Width, 1.0 mm. Elongate and tapering towards the elytral apex; head, elytra and venter dark black; pronotum, antennae and legs dark brown; head, pronotum and elytra with long black recumbent setae (Fig. 1). **Head:** Subspherical; surfaces deeply punctate, shiny; remaining areas of head obscured by microscopic froth; dark black. **Antennae** (Fig. 2)**:** Loosely serrate, extending to pronotal hind angles; dark brown. **Pronotum:** Shiny; surfaces deeply and widely punctate; dark brown. **Elytra:** Shiny with deep, widely spaced punctures; dark black. **Venter** (Fig. 3)**:** Shiny; deeply punctate; dark black.

Etymology. Specific epithet is derived from its dark brown and black colorations.

Figures 1–5. Dominican amber Eucnemidae. **1)** *Mioxylobius bicolor* Otto **sp. nov.**, dorsolateral view (distorted). **2)** *Mioxylobius bicolor* Otto **sp. nov.**, antenna. **3)** *Mioxylobius bicolor* Otto **sp. nov.**, ventrolateral view. **4)** *Balistica serrulata* Otto **sp. nov.**, lateral view. **5)** *Balistica serrulata* Otto **sp. nov.**, ventrolateral view. (Scale: 2 = 0.5 mm; 1, 3, 5 = 1.0; 4 = 2.0 mm).

Remarks. The extinct group belongs in the tribe Xylobiini based on its smaller size, simple hypomeron, cylindrical form and smaller flagellomere I. Lack of lateral ridges on the antennomeres, along with loosely serrate flagellomeres, places the group between *Bioxylus* Fleutiaux and *Xylophilus* Mannerheim. *Mioxylobius* **new genus** is distinguished by its much shorter flagellomere I compared with the pedicel or flagellomere II. Pedicel and flagellomere I are each short and sub-equal in both *Bioxylus* and *Proxylobius* Fleutiaux. Flagellomere I is slightly longer than the pedicel and flagellomeres II–V are tubular in *Xylophilus*. The presence of excavate-emarginate metatarsomere IV would suggest it belongs to Macraulacini, but the tarsal structure is also present in extant species of *Bioxylus*.

Tribe Dirhagini Reitter, 1911

Genus *Balistica* Motschulsky, 1861

Diversity and distribution. *Balistica* is a small group consisting of eight extant species largely distributed in the Far East region of the Palearctic, Indo-Malayan and Oceanic regions. Muona (1993) described one extinct species in Baltic amber.

Diagnosis. Apical margin of frontoclypeal region feebly trilobed and more than twice as wide as the distance

between antennal sockets; notosternal antennal grooves present; male prothoracic tarsomere I simple, without apical sex combs; metacoxal plates medially 3.0–6.0 times wider than laterally; last visible ventrite either rounded or truncated; hypomeral pits near prothoracic coxae deep, well-defined on all sides; tarsal claws simple; lateral surfaces of mesothoracic and metathoracic tibiae with setae only.

Balistica serrulata Otto, new species
Fig. 4–5

Holotype. Embedded in near pentangular Dominican Republic amber piece, 26 mm × 16 mm × 13 mm. Amber piece is clear dark yellow/orange with micro fractures and several additional undescribed insects (2 ant species and 1 beetle species).

Diagnosis. Longer than wide pronotum, basally wide notosternal antennal grooves along with simple, serrate antennae will distinguish the species from all other *Balistica* species.

Description. Length, 3.0 mm. Width, 1.0 mm. Habitus subcylindrical, elongate (caudal end destroyed); uniformly black; antennae and legs black; setae inconspicuous on head, pronotum and elytra (Fig. 4). **Head:** Closely punctate, subspherical with convex frons; surfaces shiny; apical margin of frontoclypeal region trilobed, about 2.5 times wider than base; mandibles stout, bidentate, densely punctate. **Antennae:** Serrate, reaching to mesocoxae; flagellomere I nearly as long as II and III combined; flagellomeres II–VIII triangular, longer than wide; flagellomere IX longer than VIII. **Pronotum:** Closely, deeply punctate; surface shiny; longer than wide, with short hind angles; parallel-sided; anterior portion of pronotum slightly arcuate; disc simple; sides with two ridges; anterior lateral hypomeral ridge short, caudally bent, less than one-fourth the length of pronotum; posterior lateral hypomeral ridge extend up to half the length of pronotum; hypomeron with shallow, basally wide notosternal antennal grooves; hypomeral pits well defined. **Scutellum:** Slightly punctate, oblong, triangular and distally rounded. **Elytra:** Striae absent; very closely, deeply punctate. **Legs:** First tarsomere as long as the combined lengths of the remaining four on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–III simple; metatarsomere IV truncate and excavate; metatarsomere V elongate with simple claws. **Venter** (Fig. 5)**:** Deeply punctate; setae inconspicuous; metepisternum caudally widened; metacoxal plates medially 2.5 times as wide as laterally.

Etymology. Specific epithet is derived from its simply serrate antennal segments.

Genus *Paleoquirsfeldia* Otto, new genus

Type species. *Paleoquirsfeldia epicrana* Otto, **new species**, designated here.

Description. Body approximately four times longer than wide, dorsally convex and ventrally sclerotized. **Head:** Hypognathous with elongate setae. Frons convex, without median ridge or groove. Antennae setose, with 11 antennomeres; scape 4.0 times longer than pedicel; pedicel longer than flagellomere I; flagellomere I shorter than II; flagellomeres II–VIII slightly longer than wide and rounded in apical view; flagellomere IX asymmetrical, slightly longer than VIII. Compound eyes small, round. Genae with antennal groove between mandibular base and compound eye. Apical margin of frontoclypeal region rectangular, truncate, less than 2.5 times wider apically than the distance between antennal sockets. Mandibles stout. Maxillary and labial palpi concealed behind mandibles. **Pronotum:** Subparallel, convex and setose. Lateral sides slightly arcuate. Slightly longer than wide, with very small hind angles. Lateral pronotal ridge entire, slightly sinuate near apical 1/2. Prothoracic sternal peg basally broad, short. Notosternal suture shorter than the hypomeral base. Hypomeron with wide, shallow notosternal antennal grooves. Deep genal pit present near anterior end of notosternal antennal groove. **Elytron:** Elongate, convex, setose. Disc with no indications of striae. **Legs:** Pro-legs shortest, hind legs longest. Metatarsi, including claws longer than tibia. Metatarsomere I appear to be shorter than 2–5 combined. Metatarsomeres I–III simple. Metatarsomere IV excavate-emarginate, wider than III. Metatarsomere V elongate with simple claws. **Venter:** Punctate with long, recumbent setae present. Elytral epipleura not grooved. Metaepisternum parallel-sided. Metacoxal plates parallel-sided. Tarsal grooves absent on mesothoracic and metathoracic sterna. Abdomen with five medially convex, visible ventrites. Last visible ventrite caudally produced.

Etymology. The generic name is the combination of the stem, *Paleo-* which is derived from the Greek word Palaios meaning "old" and the root, *Quirsfeldia* Cobos, an extant eucnemid genus currently found in South America.

Paleoquirsfeldia epicrana **Otto, new species**
Fig. 6–7

Holotype. Embedded in small slightly ovoid Dominican Republic amber piece, 12 mm × 11 mm × 6 mm. Amber piece is clear yellow with small air bubbles, micro fractures and two additional undescribed insects (1 thrips and 1 microscopic wasp).

Description. Length, 3.0 mm. Width, 1.0 mm. Elongate and tapering towards the elytral apex; dark black; antennae and legs dark black; head, pronotum and elytra with long black recumbent setae. **Head** (Fig. 6)**:** Subspherical; surfaces punctate, dullish; frontoclypeal region with pair of vertical inter-ocular ridges connected medially by a horizontal ridge; dark black. **Antennae:** Loosely serrate, extending to pronotal hind angles; dark black. **Pronotum:** Shiny, with punctate surfaces; dark black. **Elytra:** Shiny, with punctate surfaces; dark black. **Venter** (Fig. 7)**:** Shiny, slightly punctate; dark black.

Etymology. Specific epithet is derived from its rectangular epistome.

Remarks. The group is clearly a member of the tribe Dirhagini, based on a number of observations. These observations include produced last abdominal ventrite, hypomeron with very shallow, wide notosternal antennal grooves, along with its elongate form. The new group is placed nearest to *Quirsfeldia*. *Paleoquirsfeldia* **new genus** is distinguished from all extant groups, including *Quirsfeldia* by its shorter flagellomere I compared with the pedicel, instead of having longer flagellomere I.

Subfamily Eucneminae Eschscholtz, 1829

Tribe Dyscharachthini Muona, 1993

Genus *Dyscharachthis* Blackburn, 1900

Diversity and distribution. *Dyscharachthis* is a small group consisting of seven extant species distributed largely on the Australian continent. A single species has been described in South America. One species is present in the Far East Palearctic and Indo-Malayan regions. A number of undescribed species are present in both Australia and South America. Two extinct species have been described in Baltic amber.

Diagnosis. Apical margin of frontoclypeal region evenly rounded and more or less than twice as wide as the distance between antennal sockets; basally closed lateral antennal grooves present; antennae serrate and keeled on lateral sides; male prothoracic tarsomere I simple, without apical sex combs; metacoxal plates either medially 1.2–2.5 or 3.0–6.0 times wider than laterally; last visible ventrite either rounded or emarginate; tarsal claws simple; lateral surfaces of mesothoracic and metathoracic tibiae with setae only; male aedeagus dorsoventrally compressed, without secondary lateral lobes; median lobe simple, usually pointed apically, rarely rounded, entire; lateral lobes with apically secondary constriction, entire; aedeagal flagellum simple.
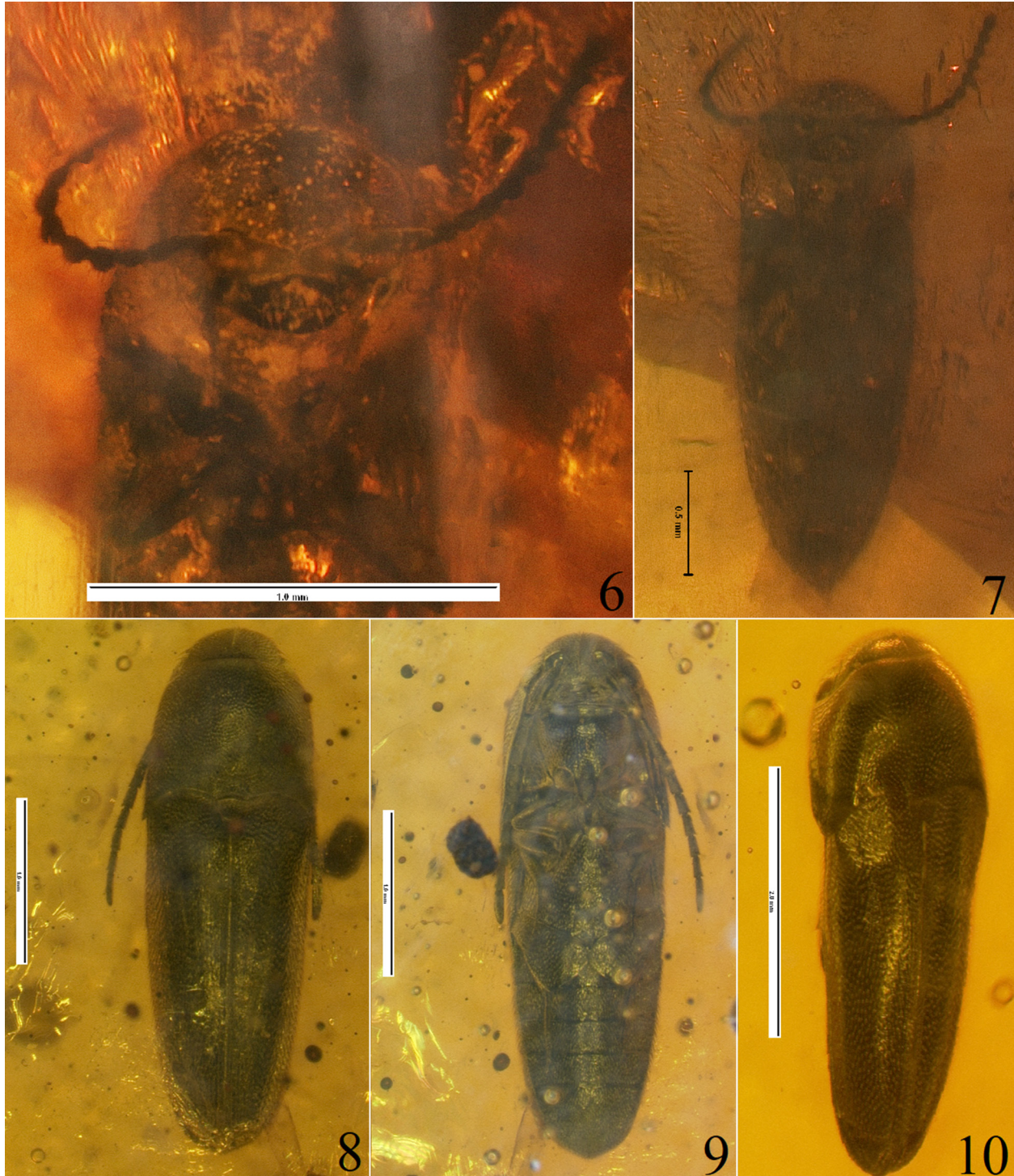
Dyscharachthis dominicana **Otto, new species**
Fig. 8–9

Holotype. Embedded in near triangular Dominican Republic amber piece, 19 mm × 10 mm × 5 mm. Amber piece is clear yellow with air bubbles and other debris.

Diagnosis. Structures and overall length of antennae proportional to its body length will distinguish the species from all known species.

Description. Length, 3.0 mm. Width, 1.0 mm. Habitus subcylindrical, moderately elongate and tapering towards the elytral apex; uniformly blackish; head, pronotum and elytra clothed with short recumbent setae (Fig. 8). **Head:** Closely punctate, subspherical with convex frons; median carina present on frontoclypeal region and frons; surfaces shiny; apical margin of frontoclypeal region fairly evenly rounded, about 2.0 times wider than base; mandibles stout, bidentate and densely punctate. **Antennae:** Weakly serrate, reaching about half the length of the body; lateral ridge present on scape, pedicel and flagellomeres I–VI; flagellomere I longer than II;

Figures 6–10. Dominican amber Eucnemidae. **6)** *Palaeoquirsfeldia epicrana* Otto **sp. nov.**, head. **7)** *Palaeo-quirsfeldia epicrana* Otto **sp. nov.**, ventral view. **8)** *Dyscharachthis dominicana* Otto **sp. nov.**, dorsal view. **9)** *Dyscharachthis dominicana* Otto **sp. nov.**, ventral view. **10)** *Idiotarsus poinari* Otto **sp. nov.**, dorsolateral view. (Scale: 6–9 = 1.0 mm; 10 = 2.0 mm).

flagellomere II as long as III; flagellomere III shorter than IV; flagellomeres IV–VIII longer than wide; flagellomere IX longer than VIII. **Pronotum:** Closely punctate; surface shiny; longer than wide; base wider, with short hind angles; sides slightly arcuate; disc simple; base with short, median impressed line above scutellum; hypomeron with basally closed lateral antennal grooves. **Scutellum:** Punctate, oblong, triangular and distally rounded. **Elytra:** Striae absent; disc closely punctate. **Legs:** First tarsomere as long as 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–IV simple; metatarsomere V elongate with simple claws. **Venter** (Fig. 9)**:** Punctate, with recumbent setae; grooves for reception of tarsi on metathoracic and abdominal sterna I–IV absent; metaepisternum parallel-sided; metacoxal plates medially nearly 4.0 times wider than laterally.

Etymology. Specific epithet is derived from the locality in which the fossilized resin with the specimen was unearthed.

Tribe Eucnemini Eschscholtz, 1829

## Genus *Idiotarsus* Bonvouloir, 1871

Diversity and distribution. *Idiotarsus* is a small group consisting of at least 13 extant species, all of which are distributed in the New World, majority of which are found in Central and South America. One species is present in the Nearctic region. A number of misplaced and undescribed species are known for the group from both Central and South America.

Diagnosis. Apical margin of frontoclypeal region evenly rounded and less than twice as wide as the distance between antennal sockets; hairy excretory pit present at basolateral corner of hypomera; basally closed lateral antennal grooves present; antennae serrate; male prothoracic tarsomere I simple, without apical sex combs; metacoxal plates medially 3.0–6.0 times wider than laterally; last visible ventrite produced; tarsal claws simple; lateral surfaces of mesothoracic and metathoracic tibiae either with setae and irregularly placed spines or setae and transverse rows of spines; male aedeagus dorsoventrally compressed, without secondary lateral lobes; median lobe simple, with separate apical median sclerite that is either entire or bifurcate; lateral lobes simple, entire, aedeagal flagellum simple.

Idiotarsus poinari Otto, new species
Fig. 10–11

Holotype. Embedded in a somewhat diamond-shaped Dominican Republic amber piece, 28 mm × 10 mm × 10 mm. Amber piece is clear dark yellow/orange with numerous small air bubbles, micro fractures and some debris.
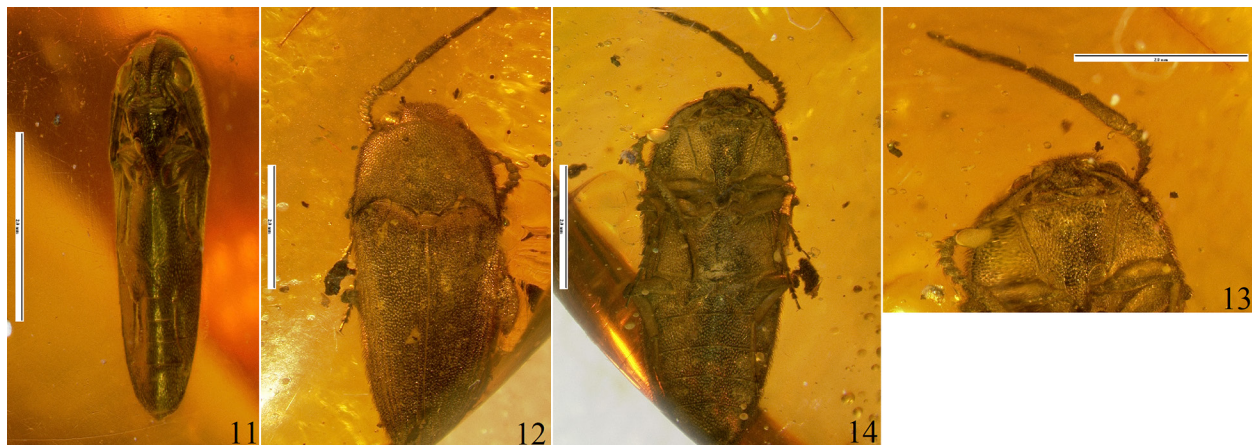
Figures 11–14. Dominican amber Eucnemidae. **11)** *Idiotarsus poinari* Otto **sp. nov.**, ventral view (distorted). **12)** *Euryptychus antilliensis* Otto **sp. nov.**, dorsal view. **13)** *Euryptychus antilliensis* Otto **sp. nov.**, antenna and pronotum. **14)** *Euryptychus antilliensis* Otto **sp. nov.**, ventral view. (Scale: 11–14 = 2.0 mm).

Diagnosis. Smaller size (3.5 mm), along with very short recumbent setae will distinguish the species from any known *Idiotarsus* species in Central and North America.

Description. Length, 3.5 mm. Width, 1.0 mm. Habitus subcylindrical, elongate and slightly attenuate towards the elytral apex; uniformly blackish; head, pronotum and elytra clothed with sparse, very short recumbent setae (Fig. 10). **Head:** Surfaces shiny with widely spaced, shallow punctures; subspherical with convex frons; median carina present on frontoclypeal region and frons; apical margin of frontoclypeal region evenly rounded, less than 2.0 times wider than base; mandibles stout, bidentate and densely punctate. **Pronotum:** Widely and shallowly punctate; surfaces shiny; longer than wide; base wider, with moderate hind angles; sides slightly arcuate, almost parallel-sided; disc simple; hypomeron with basally closed lateral antennal grooves. **Scutellum:** Very shallowly punctate, quadrate and distally rounded. **Elytra:** Striae absent; disc with widely spaced, shallow punctures. **Legs:** First tarsomere longer than 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–II simple; metatarsomeres III–IV ventrally lobed; metatarsomere V short with simple claws. **Venter** (Fig. 11)**:** Sparsely punctate, with short recumbent setae; metathoracic sternum and abdominal sterna I–IV with grooves for reception of tarsi; metaepisternum caudally widened; metacoxal plates medially 4.0 times wider than laterally.

Etymology. The species is dedicated in honor of Dr. George Poinar, Paleobiologist from Oregon State University for his work on amber, the reconstruction of the ancient forests of Dominican Republic and answering my many questions about amber.

Subfamily Macraulacinae Fleutiaux, 1922

Tribe Euryptychini Mamaev, 1976

Genus *Euryptychus* LeConte, 1852

Diversity and distribution. *Euryptychus* is a relatively small group distributed on five major continents, absent in the African and Antarctic continents. Three species are present in the Nearctic region. Two species are present in the Neotropical region. Three species are also present in Southeast Asia. Four species are present in the Palearctic region. Seven species are present in Australia, with several additional undescribed species. Many extinct species have been described in Baltic amber (Muona 1993, 2021). Four extinct species have been described from Burmese amber by Muona (2020), indicating the group have been around at least the Cretaceous Epoch.

Diagnosis. Apical margin of frontoclypeal region rounded and more than twice as wide as the distance between antennal sockets; antennae capitate with apical three flagellomeres expanded forming an elongate club; male prothoracic tarsomere I simple, with basal sex combs; metacoxal plates medially 3.0–6.0 times wider than laterally; last visible ventrite rounded; tarsal claws simple; male aedeagus dorsoventrally compressed, without secondary lateral lobes; median lobe simple, notched apically; lateral lobes simple, entire; aedeagal flagellum simple.

Euryptychus antilliensis Otto, new species
Fig. 12–14

Holotype. Embedded in an egg-shaped Dominican Republic amber piece, 20 mm × 12 mm × 5 mm. Amber piece is clear dark yellow/orange with numerous small air bubbles, micro fractures, debris and one additional large undescribed insect (fly).

Diagnosis. Smaller size (5.0 mm) and robust form will separate the new eucnemid species from any known species of *Euryptychus*. Short, simple mesothoracic and metathoracic tarsomere IV will also distinguish the species from any species of *Phlegon* Laporte. Strongly angulated metacoxal plate is a strange, unique feature only known from this species compared with any known encountered species in the group.

Description. Length, 5.0 mm. Width, 2.5 mm. Habitus moderately elongate, widest at humeral region and tapering towards the elytral apex; uniformly dark brownish; antennae and legs dark brownish; head, pronotum and elytra clothed with long brown recumbent setae (Fig. 12). **Head:** Closely, deeply punctate, subspherical with

convex frons; median ridge present on frons; surfaces shiny; apical margin of frontoclypeal region truncate, about 2.0–2.5 times wider than base; mandibles slender, somewhat punctate. **Antennae** (Fig. 13)**:** Capitate, ⅔–¾ as long as body. Scape elongate, about 4.0 times longer than pedicel, lateral ridge present; flagellomere I nearly as long as II and III combined; II–VI transverse; flagellomeres VII–IX each elongate and longer than pedicel–flagellomere VI combined; flagellomere IX longer than either VII or VIII. **Pronotum:** Closely, deeply punctate; surface shiny; wider than long, with moderately sized hind angles; basally wider, gradually narrowing towards cranium; lateral sides with one ridge; disc simple, with small median groove above scutellum; hypomeron simple, without antennal grooves. **Scutellum:** Slightly rugose, short, trapezoidally-shaped. **Elytra:** Faintly indicated striae present; interstices slightly elevated, very closely punctate. **Legs:** First tarsomere slightly shorter than 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; lateral surfaces of mesothoracic and metathoracic tibiae with single spines; metatarsomeres I–IV simple; metatarsomeres IV very short; metatarsomere V elongate with simple claws. **Venter** (Fig. 14)**:** Punctate; metaepisternum parallel-sided; metacoxal plates medially angulated, 5.0 times wider than laterally.

Etymology. Specific epithet is derived from the term Greater Antilles, a group of islands in the Caribbean Ocean that includes Hispaniola.

Euryptychus hispaniolus Otto, new species
Fig. 15–16

Holotype. Embedded in ovoid Dominican Republic amber piece, 23 mm × 10 mm × 4 mm. Amber piece is clear yellow with micro fractures and some debris.

Diagnosis. Expanded metacoxal plates distinguish this species from the Nearctic *Euryptychus arizonicus* (Van Dyke). Overall shape of the pronotum will separate the species from the Neotropical *Euryptychus viduus* (Horn); that being basally parallel-sided in *E. hispaniolus* **new species** and strongly arcuate in *E. viduus*.

Description. Length, 6.0 mm. Width, 2.5 mm. Habitus subcylindrical, moderately elongate and tapering towards the elytral apex; uniformly dull blackish; head, pronotum and elytra clothed with short, recumbent setae (Fig. 15). **Head:** Very closely and deeply punctate; subspherical with convex frons; surfaces dull; apical margin of frontoclypeal region evenly rounded, about 2.00 times wider than base; mandibles stout, bidentate, densely punctate. **Antennae:** Capitate, 1/2 as long as body; scape elongate, about 4.0 times longer than pedicel, lateral ridge absent; flagellomere I about as long as II and III combined; flagellomeres II–V quadrate; flagellomeres VII–IX each elongate and as long as flagellomeres I–III combined; flagellomere IX as long as VIII. **Pronotum:** Closely and deeply punctate; surfaces dull; longer than wide, with moderate hind angles; basal half parallel-sided; anterior portion of pronotum slightly convex; disc with median impressed line extending from base up three-fourths the length of pronotum; hypomeron simple, without antennal grooves. **Scutellum:** Punctate, oblong, triangular and distally rounded. **Elytra:** Faintly indicated striae present; interstices slightly elevated, very closely and deeply punctate. **Legs:** First tarsomere as long as 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; lateral surfaces of mesothoracic and metathoracic tibiae with setae and transverse rows of spine combs; metatarsomeres I–IV simple; metatarsomere V elongate with simple claws. **Venter** (Fig. 16)**:** Closely and deeply punctate, with short, recumbent setae; metaepisternum parallel-sided; metacoxal plates medially 6.0 times wider than laterally.

Etymology. Specific epithet is derived from the name of the island in which the extinct species once thrived.

Tribe Macraulacini Fleutiaux, 1922

Genus *Plesiofornax* Coquerel, 1866

Diversity and distribution. *Plesiofornax* is a moderately large group distributed in the Neotropical, Africa/Madagascar and Southeast Asian/Australian regions with 48 species. Of those, four species are present in Southeast Asian/Australian region. Twenty-three species are present in the Neotropical region. The remaining 21 species are largely present on Madagascar, Reunion Islands and Seychelles, along with two species on the African continent.
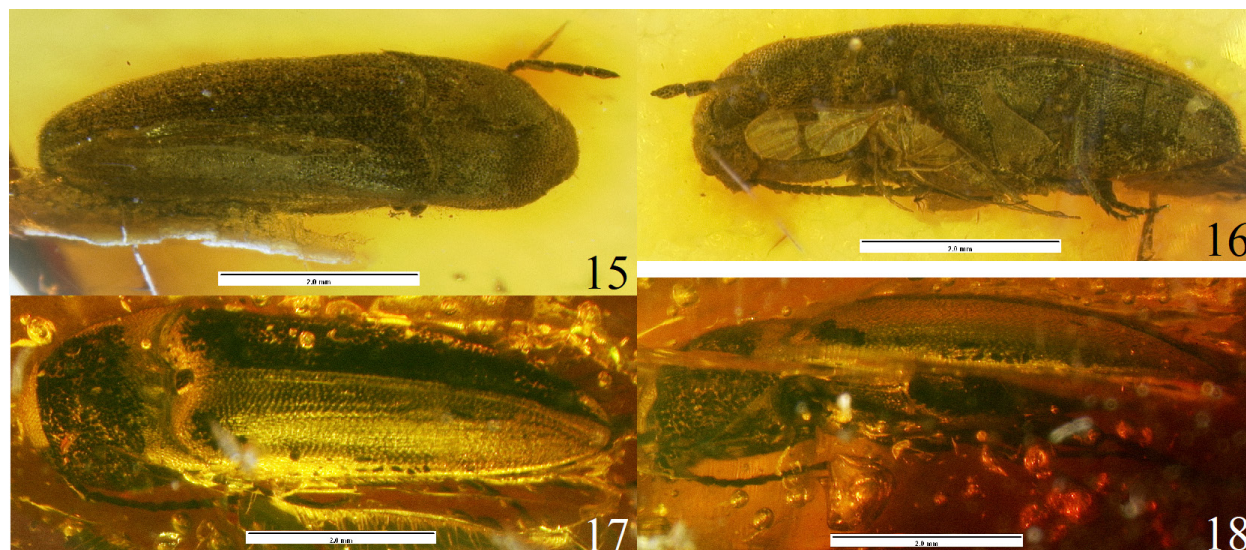
Figures 15–18. Dominican amber Eucnemidae. **15)** *Euryptychus hispaniolus* Otto **sp. nov.**, dorsal view. **16)** *Euryptychus hispaniolus* Otto **sp. nov.**, ventrolateral view. **17)** *Plesiofornax caribbeanus* Otto **sp. nov.**, dorsolateral view. **18)** *Plesiofornax caribbeanus* Otto **sp. nov.**, ventrolateral view. (Scale: 15–18 = 2.0 mm).

Diagnosis. Apical margin of frontoclypeal region evenly rounded and more than twice as wide as the distance between antennal sockets; medially undefined basally open lateral antennal grooves present; male prothoracic tarsomere I simple, with basal sex combs; metacoxal plates medially 3.0–6.0 times wider than laterally; last visible ventrite either strongly rounded or emarginate; tarsal claws simple; lateral surfaces of mesothoracic and metathoracic tibiae with setae and transverse rows of spine combs; male aedeagus dorsoventrally compressed, with laterally attached secondary lateral lobes; median lob simple, with moderately and narrowly bifurcate apices; lateral lobes simple, entire, aedeagal flagellum simple.

Plesiofornax caribica Otto, new species
Fig. 17–18

Holotype. Embedded in a large, rough Dominican Republic amber piece, 50 mm × 38 mm × 39 mm. Amber piece is clear dark yellow/orange with numerous small air bubbles and micro fractures.

Diagnosis. Dark black coloration and body form will distinguish this species from any extant Caribbean *Plesiofornax* species.

Description. Length, 6.0 mm. Width, 2.0 mm. Habitus moderately elongate and tapering towards the elytral apex; uniformly dark black; antennae and legs dark black; head, pronotum and elytra clothed with short, recumbent setae (Fig. 17). **Head:** Closely punctate, subspherical with convex frons. **Antennae:** Weakly serrate to filiform, reaching about half the length of the body. Flagellomere I elongate, slightly shorter than the combined lengths of II–III; flagellomere II shorter than III, as long as the pedicel; flagellomeres III–VII sub-equal, slightly longer than wide; flagellomere IX longer than VIII. **Pronotum:** Closely punctate; surface dull; slightly longer than wide, with large hind angles; lateral sides slightly convex; disc simple; lateral side with one ridge; hypomeron with medially vaguely defined, shallow, basally open lateral antennal grooves. **Scutellum:** Slightly punctate, oblong, and quadrate. **Elytra:** Faintly indicated striae present; interstices flattened, surfaces closely punctate. **Legs:** First tarsomere about as long as 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–III simple; metatarsomeres V excavated and emarginated; metatarsomere V short with basally toothed claws. **Venter** (Fig. 18)**:** Closely punctate; metaepisternum parallel-sided; metacoxal plates medially 7.0 times wider than laterally.

Etymology. Specific epithet is derived from the region, Caribbean, in which the species once flourished.

Genus *Fornax* Laporte, 1835

Diversity and distribution. *Fornax* is one of the largest group, consisting more than 300 species distributed world-wide in all regions, except Antarctica.

Diagnosis. Apical margin of frontoclypeal region evenly rounded and more than twice as wide as the distance between antennal sockets; well-developed basally open lateral antennal grooves present; male prothoracic tarsomere I simple, with basal sex combs; metacoxal plates medially more than 6.0 times wider than laterally; elytral epipleura basally grooved or evenly punctate; last visible ventrite either strongly produced, rounded or truncated; tarsal claws basally toothed; lateral surfaces of mesothoracic and metathoracic tibiae with setae and transverse rows of spine combs; male aedeagus dorsoventrally compressed, without secondary lateral lobes; median lob simple, with moderately and narrowly bifurcate apices; lateral lobes simple, entire, aedeagal flagellum simple.

Fornax dominicensis Otto, new species
Fig. 19

Holotype. Embedded in a square-shaped Dominican Republic amber piece, 13 mm × 8 mm × 4 mm. Amber piece is clear dark yellow/orange with numerous small air bubbles, micro fractures and one additional undescribed insect (fly).

Diagnosis. Smaller size along with brown antennae and legs will distinguish this eucnemid species from any extant known Caribbean *Fornax* species.

Description. Length, 5.0 mm. Width, 1.25 mm. Habitus subcylindrical, moderately elongate and tapering towards the elytral apex; uniformly black; antennae and legs medium to dark brown; head, pronotum and elytra clothed with short, recumbent setae (Fig. 19). **Head:** Closely punctate, subspherical with convex frons; surfaces shiny; apical margin of frontoclypeal region fairly evenly rounded, about 2.0 times wider than base; mandibles stout, bidentate, densely punctate. **Antennae:** Filiform, reaching about half the length of the body; flagellomere I longer than II; flagellomere II shorter than III; flagellomere III shorter than IV; flagellomeres II–VIII each sub-equal, longer than wide; flagellomere IX longer than VIII. **Pronotum:** Closely punctate; surface shiny; longer than wide, with moderate hind angles; sides gradually narrowing craniad, arcuate; disc simple; hypomeron with basally open lateral antennal grooves. **Scutellum:** Slightly rugose, triangular and distally rounded. **Elytra:** Striae absent; disc densely punctate to rugose. **Legs** (mesothoracic only)**:** Mesotarsomere I as long as 2–5 combined; tibiae rounded in cross section; mesotarsomeres I–III simple; mesotarsomere IV excavate-emarginate; mesotarsomere V short with simple claws. **Venter:** Punctate, with recumbent setae; metaepisternum parallel-sided; metacoxal plates medially 7.5 times wider than laterally.

Etymology. Specific epithet is derived from the location in which the fossil eucnemid was found.

Fornax serropalpoides Otto, new species
Fig. 20–21

Holotype. Embedded in ovoid Dominican Republic amber piece, 22 mm × 17 mm × 5 mm. Amber piece is clear dark yellow/orange with micro fractures, a few debris and one additional undescribed arachnid (spider).

Diagnosis. Very narrow, elongate form and smaller size (4.0 mm) will distinguish this species from any known Caribbean *Fornax* species.

Description. Length, 4.0 mm. Width, 1.25 mm. Habitus subcylindrical, moderately elongate and tapering towards the elytral apex; uniformly black; head, pronotum and elytra clothed with short, recumbent setae (Fig. 20). **Head:** Closely punctate, subspherical with convex frons; surfaces shiny; apical margin of frontoclypeal region fairly evenly rounded, about 2.0 times wider than base; mandibles stout, bidentate, densely punctate. **Antennae:** Filiform, reaching about half the length of the body; flagellomere I longer than II; flagellomere II shorter than III; flagellomere III shorter than IV; flagellomeres IV–VIII each longer than wide, sub-equal; flagellomere IX longer than VIII. **Pronotum:** Closely punctate; surface shiny; longer than wide, with moderate hind angles; sides gradually narrowing craniad; disc simple; hypomeron with basally open lateral antennal grooves. **Scutellum:** Punctate, oblong, triangular and distally rounded. **Elytra:** Faintly indicated striae present; interstices slightly elevated, very

Figures 19–23. Dominican amber Eucnemidae. **19)** *Fornax dominicensis* Otto **sp. nov.**, lateral view. **20)** *Fornax serropalpoides* Otto **sp. nov.**, dorsal view. **21)** *Fornax serropalpoides* Otto **sp. nov.**, ventrolateral view. **22)** *Dromaeolus argenteus* Otto **sp. nov.**, dorsolateral view. **23)** *Dromaeolus argenteus* Otto **sp. nov.**, ventrolateral view. (Scale: 19–23 = 2.0 mm).

closely punctate. **Legs:** First tarsomere as long as the combined lengths of the remaining four on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–III simple: metatarsomere IV excavate-emarginate; metatarsomere V short with simple claws. **Venter** (Fig. 21)**:** Punctate with short, recumbent setae; metaepisternum parallel-sided; metacoxal plates indistinct, obscured by exposed metathoracic wing.

Etymology. Specific epithet is derived from the unusual ventral appearance of the head and pronotum, which bears a close resemblance to a melandryid genus *Serropalpus* Hellenius.

Genus *Dromaeolus* Kiesenwetter, 1858

Diversity and distribution. *Dromaeolus* is one of the largest group, consisting of more than 200 species distributed in all regions of the world, except the Antarctica. Muona (1993) listed one un-named species of the group discovered in Baltic amber. A large number of undescribed species have been detected in several regions.

Diagnosis. Apical margin of frontoclypeal region feebly trilobed and more than twice as wide as the distance between antennal sockets; well-developed basally open or basally closed lateral antennal grooves present; male

prothoracic tarsomere I simple with basal sex combs; metacoxal plates medially 1.2–2.5 times wider than laterally; last visible ventrite either rounded or truncated; tarsal claws simple; lateral surfaces of mesothoracic and metathoracic tibiae either with setae and transverse rows of spine combs or setae and irregularly placed spines; male aedeagus dorsoventrally compressed, with laterally attached secondary lateral lobes; median lobe simple, with moderately and narrowly bifurcate apices; lateral lobes simple, entire; aedeagal flagellum simple.

Dromaeolus argenteus Otto, new species
Fig. 22–23

Holotype. Embedded in ovoid Dominican Republic amber piece, 15 mm × 9 mm × 4 mm. Amber piece is clear yellow with several air bubbles and micro fractures.

Diagnosis. Metallic silver luster on the surface, along with form and lateral pronotal ridge will distinguish this species from all other Caribbean *Dromaeolus*.

Description. Length, 4.0 mm. Width, 1.0 mm. Habitus subcylindrical, slightly wide, moderately elongate and tapering towards the elytral apex; metallic silver luster on all surfaces; head, pronotum and elytra clothed with inconspicuous, sparse, recumbent setae (Fig. 22). **Head:** Closely, deeply punctate to rugose, subspherical with convex frons; surfaces shiny; apical margin of frontoclypeal region very weakly trilobed, about 2.5 times wider than base; mandibles stout, bidentate, densely punctate. **Antennae:** Serrate, reaching about one-third the length of the body, up to hind angles of pronotum; flagellomere I longer than II; flagellomere II as long as the pedicel, shorter than III; flagellomeres III–VII each slightly longer than wide, sub-equal; flagellomere IX longer than VIII. **Pronotum:** Closely, deeply punctate to rugose; surface shiny; slightly longer than wide, with short hind angles; basal half parallel-sided; anterior half slightly arcuate; disc simple; base with short, median impressed line above scutellum; hypomeron with basally closed lateral antennal grooves. **Scutellum:** Shallowly punctate, oblong, triangular and distally rounded. **Elytra:** Shallow striae present; interstices slightly elevated, very closely punctate to transversely rugose. **Legs:** First tarsomere as long as 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–III simple; metatarsomere IV excavate-emarginated; metatarsomere V elongate with simple claws. **Venter** (Fig. 23)**:** Punctate, with sparse, recumbent yellow setae; metepisternum parallel-sided; metacoxal plates medially 3.5 times wider than laterally.

Etymology. Specific epithet is derived from the French term Argent which means "silver" for its metallic silver luster present on the exoskeletal surface as a result of its entombment in amber.

<div align="center">

Tribe Nematodini Leiler, 1976

Genus *Nematodes* Berthold, 1827

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Diversity and distribution. *Nematodes* is a moderately large group consisting of 36 extant species. Twenty-two species are distributed in the Neotropical region. Five species are present in the Nearctic region. One species is present on the African continent. Two species are distributed in Australia. Four species are present in Southeast Asia. Two species are present in the Palearctic region. A small number of new species are present in the group.

Diagnosis. Apical margin of frontoclypeal region feebly trilobed and more than twice as wide as the distance between antennal sockets; antennal grooves usually absent; male prothoracic tarsomere I simple with basal curved sex combs; metacoxal plates medially 3.0–6.0 times wider than laterally; last visible ventrite strongly produced; tarsal claws simple; lateral surfaces of mesothoracic and metathoracic tibiae with setae and transverse rows of spine combs; male aedeagus dorsoventrally compressed, with laterally attached secondary lateral lobes; median lobe simple, with moderately and narrowly bifurcate apices; lateral lobes simple, entire; aedeagal flagellum simple.

Nematodes miocenensis Otto, new species
Fig. 24–25

Holotype. Embedded in an oblonged, ovoid Dominican Republic amber piece, 33 mm × 10 mm × 10 mm. Amber piece is clear yellow with a few air bubbles, debris, micro fractures and one additional undescribed arachnid (spider).

Figures 24–27. Dominican amber Eucnemidae. **24)** *Nematodes miocenensis* Otto **sp. nov.**, dorsal view. **25)** *Nematodes miocenensis* Otto **sp. nov.**, ventral view. **26)** *Nematodes thoracicus* Otto **sp. nov.**, dorsolateral view. **27)** *Nematodes thoracicus* Otto **sp. nov.**, ventral view. (Scale: 24–27 = 2.0 mm).

Paratype. Embedded in a large, ovoid Dominican Republic amber piece, 42 mm × 26 mm × 15 mm. Amber piece is clear dark yellow/orange with small air bubbles, debris, micro fractures and six additional undescribed insects (1 ant, 1 wasp, 2 flies and 2 beetles of which includes 1 curculionid and 1 very unusual staphylinid).

Diagnosis. Large, robust form of the species and black coloration will distinguish this species from any *Nematodes* species distributed in the Greater Antilles.

Description. Length, 6.5 mm. Width, 2.0 mm. Habitus moderately elongate and tapering towards the elytral apex, robust, large; dark black; antennae and legs dark brown to black; pronotum and elytra clothed with very short, black recumbent setae (Fig. 24). **Head:** Closely punctate, subspherical with convex frons; surface matte; apical margin of frontoclypeal region very weakly trilobed, about 2.0–2.5 times wider than base; mandibles stout, bidentate, closely punctate. **Antenna:** Weakly serrate. Flagellomere I longer than II; flagellomere II shorter than III; flagellomere III shorter than IV; flagellomeres IV–VII each sub-equal in length, slightly enlarged; right flagellomeres VIII–IX are missing; left antenna is missing, except for the scape. **Pronotum:** Closely punctate; surface matte; wider than long with moderately sized, narrowed hind angles; basal three-fourths parallel-sided; anterior portion of pronotum slightly convex; base with median impressed line above scutellum; hypomeron simple, without antennal grooves. **Scutellum:** Closely punctate, sub-triangular and distally rounded. **Elytra:** Closely punctate, striae absent. **Legs:** First tarsomere about as long as 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–III simple; metatarsomeres IV excavated and emarginated; metatarsomere V elongate with simple claws. **Venter** (Fig. 25)**:** Closely punctate, with recumbent very short black setae; metaepisternum parallel-sided; metacoxal plates medially 3.5 times wider than laterally.

Variation. The paratype, although in its destroyed condition in a piece of amber is much larger and too different compared to the holotype, 14.0 mm long, 4.0 mm wide.

Etymology. Specific epithet is derived from the geologic time in which the two specimens were entombed in amber.

Nematodes thoracicus Otto, new species
Fig. 26–27

Holotype. Embedded in ovoid Dominican Republic amber piece, 22 mm × 15 mm × 5 mm. Amber piece is clear yellow with small air bubbles and a few pieces of debris.

Diagnosis. Smaller size (3.25 mm) along with carinulate dorsolateral aspects of pronotum will distinguish the new species from all known *Nematodes* species.

Description. Length, 3.25 mm. Width, 1.0 mm. Habitus very elongate, narrow and tapering towards the elytral apex; luster uniformly metallic silver; antennae and legs metallic silver; head, pronotum and elytra clothed with very short, brown recumbent setae (Fig. 26). **Head:** Closely punctate, subspherical with convex frons; surfaces shiny; apical margin of frontoclypeal region very weakly trilobed, about twice as wide as the base; mandibles stout, bidentate, densely punctate. **Antennae:** Weakly serrate, reaching about 1/3 the length of the body. Flagellomere I slightly longer than II; flagellomere III longer than II; flagellomeres IV–IX sub-equal, each longer than III. **Pronotum:** Closely punctate; surface shiny; longer than wide, with moderate, narrowed hind angles; basal three-fourths parallel-sided, sinuous; anterior portion of pronotum slightly arcuate; disc with oblong median impression; dorsolateral aspects carinulate; lateral sides with one ridge; hypomeron with extremely narrowed, well developed, basally open lateral grooves. **Scutellum:** Closely punctate, oblong, triangular and distally rounded. **Elytra:** Closely punctate; striae absent. **Legs:** First tarsomere shorter than 2–5 combined on mesothoracic and metathoracic tarsi; tibiae rounded in cross section; metatarsomeres I–III simple; metatarsomeres IV excavated and emarginated; metatarsomere V somewhat elongate with simple claws. **Venter** (Fig. 27)**:** Closely punctate, with recumbent short brown setae; metaepisternum parallel-sided; metacoxal plates medially 3.5 times as wide as laterally.

Etymology. Specific epithet is derived from the characteristics of the pronotum that set the species apart from any remaining species.

Discussion

Five now-absent genera, *Calyptocerus*, *Balistica*, *Dyscharachthis*, *Idiotarsus* and *Euryptychus* were once present on Hispaniola prior to the Pleistocene glacial periods. *Calyptocerus* is a small tropical group with five extant species. Two of these species are distributed in Southeast Asia, while the remaining three are found in both Brazil and French Guiana on the South American continent. *Balistica* are now largely distributed in the Old World regions. *Dyscharachthis* are present in southern Central America and much of South America with one extant species and a number of undescribed species. Many other species are distributed in the Old World tropics, as far north as Japan, with many undescribed species present in Australia and Oceanic regions. *Idiotarsus* are widespread from SE United States into Central and South America with more than a dozen extant species, many of which remain undescribed. Five extant species of *Euryptychus* are present in the New World, two of which are distributed in eastern North America. A third species, *Euryptychus arizonicus* (Van Dyke) is confined to the mountainous region of Arizona and New Mexico. Two species, *Euryptychus viduus* (Horn) and *Euryptychus monrosi* Cobos are present in Central and South America respectively. *Euryptychus arizonicus* and *E. viduus* are very similar and requires further research on both their status. None of these genera have been recovered on any of the islands in the region since the last glacial advancement, through any known surveys in the region. Future discoveries through examinations of additional pieces of Dominican Republic amber from different collections may uncover other extant genera, i.e. *Microrhagus*, *Adelothyreus*, *Entomophthalmus*, *Neomathion* and other groups entrapped in amber will ultimately provide a clearer understanding of the prehistoric eucnemid fauna that once persisted on these islands before the Ice Age.

It is too early to postulate any biogeographical theories given a small number of eucnemid species present on these islands and mechanisms for speciation taking place in the region. Part two of this series of papers will factor all taxa past and present studied to formulate a hypothesis on eucnemid colonization of the Greater Antilles and Hispaniola specifically. Some of the islands have been intensely sampled (as in the case of Guadeloupe), while others (*i.e.* Hispaniola) have not been sampled much at all. The Antilles is one of the Conservation International hotspot of biological diversity, with little understanding of speciation process in the region. The current study offers us a small snapshot of the prehistoric eucnemid fauna that existed at least 15 million years ago on Hispaniola, with many more bound to be discovered later. Examining specimens from any surveys conducted on these islands will ascertain overall biodiversity of the family on each of these islands, factoring extinct species entombed in amber excavated from the Dominican Republic will lead to a better understanding of Antillean eucnemid biogeography and phylogeny of the family in the region. These surveys may also offer a chance to test these speciation hypotheses and potentially recover some of the genera that once inhabited the primeval Antillean forests prior to the Pleistocene Glacial periods.

Acknowledgments

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