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Monograph

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A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), including a reappraisal of the taxonomic history of '*Canthon* sensu lato'

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Abstract. Although extensively studied by different authors over the past 150 years, the taxonomy of *Canthon* Hoffmannsegg, 1817 and allied genera (which are here informally referred to as '*Canthon* sensu lato') still remains problematic. With the aim of resolving some of the questions surrounding these taxa, the present work reviews the taxonomy of one of them, the genus *Sylvicanthon* Halffter & Martínez, 1977. As defined here, *Sylvicanthon* is distributed mainly throughout the vast areas of tropical rainforests in the Neotropical region and includes 15 species divided into two groups: the *enkerlini* group, with a single species, *S. enkerlini* (Martínez *et al.*, 1964) comb. nov., and the *candezei* group, with five subgroups: the *candezei* subgroup, with *S. candezei* (Harold, 1869), *S. genieri* sp. nov. and *S. foveiventris* (Schmidt, 1920); the *aequinoctialis* subgroup, with *S. aequinoctialis* (Harold, 1868) comb. nov. and *S. proseni* (Martínez, 1949) stat. et comb. nov.; the *bridarollii* subgroup, with *S. bridarollii* (Martínez, 1949), *S. seag* sp. nov., *S. edmondsi* sp. nov. and *S. attenboroughi* sp. nov.; the *furvus* subgroup, with *S. furvus* (Schmidt, 1920), *S. monnei* sp. nov., *S. mayri* sp. nov. and *S. obscurus* (Schmidt, 1920); and the *securus* subgroup, with a single species, *S. securus* (Schmidt, 1920) comb. nov. Three species originally included in *Sylvicanthon* are here (re)transferred to *Canthon*: *Canthon xanthopus* Blanchard, 1846 and *C. machadoi* (Martínez & Pereira, 1967) comb. nov., as well as *C. cobosi* (Pereira & Martínez, 1960) stat. et comb. nov., which had been previously in synonymy under *C. xanthopus*. Descriptions, redescriptions, illustrations and comparative tables on the external morphology (including the genital capsule) of the genus and its species are presented, as well as a detailed discussion on their biogeography, comparative morphology, hypotheses on their phylogenetic relationships, data on natural history and a detailed historical revision of the classification of '*Canthon* sensu lato'. Finally, we also discuss the so-called 'species problem' (i.e., the definition of the scientific term 'species') and its consequences to dung beetle taxonomy and favour the solution offered by the Biological Species Concept.

Keywords. Systematics, taxonomy, *Glaphyrocanthon*, new species, Biological Species Concept.

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Introduction

As discussed elsewhere (Vaz-de-Mello & Cupello in press; Edmonds & Zídek 2012), the systematics of the New World dung beetles has witnessed a very active period of new landmark publications and unexpected findings, with a great number of modern taxonomic revisions published over the past 25 years (see Vaz-de-Mello & Cupello in press: table 1). Nonetheless, some big challenges still face the scarabaedologists, including a complete revision of the megadiverse genera *Dichotomius* Hope, 1838, *Canthidium* Erichson, 1847, *Ateuchus* Weber, 1801, *Uroxys* Westwood, 1842, *Onthophagus* Latreille, 1802, *Deltochilum* Eschscholtz, 1822 and *Canthon* Hoffmannsegg, 1817. Some relatively small genera, however, despite their low number of species and the consequent supposed taxonomic simplicity, have also never had their taxonomy properly treated using modern standards, as, for instance, most of the groups in Deltochilini (sensu Tarasov & Génier 2015; Tarasov & Dimitrov 2016). In the present paper, we deal with the taxonomy of one of those small, poorly known deltochiline taxa, the genus *Sylvicanthon* Halffter & Martínez, 1977.

Sylvicanthon was described by Halffter & Martínez (1977) to include five South American species then placed in the genus *Glaphyrocanthon* Martínez, 1948: *S. candezei* (Harold, 1869) from the Amazon forest, *S. xanthopus* (Blanchard, 1846) from Bolivia, *S. furvus* (Schmidt, 1920) from Peru and Bolivia, *S. bridarollii* (Martínez, 1949) from Amazonia, and *S. machadoi* (Martínez & Pereira, 1967) known from a single locality in the Brazilian state of Pernambuco only. As the new genus was established in the four-part revision of the 'Canthonina' genus-category classification by Halffter & Martínez (1966, 1967, 1968, 1977), special attention was given only to the description of *Sylvicanthon* and its relationships with other groups of 'Canthonina', and almost nothing was said about its alpha taxonomy. As a consequence, the only descriptions available for its species were the original ones, which, in most cases, are rather brief and focus on poorly informative characters. In addition, as no identification keys were published, a correct determination of specimens of *Sylvicanthon* was virtually impossible. Not surprisingly, the results of the present revision show that a great proportion of the specimens deposited in most of the studied collections belong to new species or have been misidentified, especially in the contexts of *S. candezei* and *S. bridarollii*. In addition, some synonymies proposed by Halffter & Martínez (1977) have proven to be incorrect. The species distributions were also largely unknown. Usually, either the type locality was the only known provenance (e.g., *S. xanthopus*, *S. furvus*, *S. obscurus*, *S. securus* comb. nov. and *S. machadoi*), or, due to misidentifications, what is regarded as the geographical range of a single widely-distributed species was, actually, the distribution of a group of populations belonging to different species (as in the case of the distribution generally cited for *S. candezei* and *S. bridarollii*; see details below).

Apart from alpha taxonomy, we also found problems related to the limits of the genus and its species composition. It was discovered, for instance, that two of the originally included species – *S. xanthopus* and *S. machadoi* – belong, in fact, to another genus, while some species currently placed in *Canthon* actually have more affinities with those in *Sylvicanthon*. Also little discussed were the biogeography and the phylogenetic relationships of *Sylvicanthon* with other genera in Deltochilini.

Several doubts on the systematics of *Sylvicanthon* and its species remained, therefore, open. In the present work, based on an extensive revision of the historical bibliography, external morphology, male genitalia and distribution of the species in *Sylvicanthon* and related genera, we propose solutions to some of those problems. At the same time, however, we raise new questions about the phylogeny, biogeography and evolution of this interesting group to be addressed by future studies.

Material and methods

Collections studied

We examined 5487 specimens for this work representing all known species of *Sylvicanthon* as well as *Canthon cobosi* (Martínez & Pereira, 1960), *C. machadoi* (Martínez & Pereira, 1967) and *C. xanthopus* Blanchard, 1846. The specimens are housed at the following 31 collections (curators or contacts in parenthesis). Between the acceptance of the manuscript of this monograph and the production of its first proofs, the senior author (MC) was able to examine some additional specimens of *Sylvicanthon*, including some further paratypes of two of the new species, which are listed in Appendix 2.

AMBC = Ayr de Moura Bello private collection, Rio de Janeiro, Brazil (Ayr de Moura Bello)
BMNH = The Natural History Museum, London, United Kingdom (Max Barclay)
CEMT = Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil (Fernando Z. Vaz-de-Mello)
CEAH = Coleção Entomológica Adolph Hempel, Instituto Biológico, São Paulo, Brazil (Sergio Ide)
CJAN = Colección de Referencia Jorge Ari Noriega, Bogotá, Colombia (Jorge Ari Noriega)
CLEI = Laboratório de Ecologia de Insetos, Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Ricardo Ferreira Monteiro and Raissa Drufrayer)
CMNC = Canadian Museum of Nature, Ottawa, Canada (François Génier)
CNCI = Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (Serge Laplante and Patrice Bouchard)
FIOC = Coleção Entomológica do Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil (Márcio Felix)
FSCA = Florida State Collection of Arthropods, Gainesville, Florida, United States (Paul Skelley)
INPA = Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (Marcio L. de Oliveira)
ISNB = Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (Alain Drumont)
MACN = Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (Juan José Martínez)
MCNZ = Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (Luciano de Azevedo Moura)
MCZC = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States (Charles Farnum and Rachel Hawkins)
MNHN = Muséum national d'Histoire naturelle, Paris, France (Olivier Montreuil and Antoine Mantilleri)
MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Miguel A. Monné and Marcela L. Monné)
MUSM = Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (Luis Figueroa)
MZFS = Coleção Entomológica Prof. Johann Becker, Museu de Zoologia, Universidade Estadual de Feira de Santana, Feira de Santana, Brazil (Freddy Bravo)
MZSP = Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Sonia Casari and Carlos Campaner)
NHRS = Naturhistoriska Riksmuseet, Stockholm, Sweden (Johannes Bergsten)
NHMW = Naturhistorisches Museum Wien, Vienna, Austria (Harald Schillhammer)
NMPC = National Museum (Natural History), Prague, Czech Republic (Jiří Hájek)
OUMNH = Hope Entomological Collections, Oxford University Museum of Natural History, Oxford, United Kingdom (Darren Mann)

SEAN = Museo Entomológico de León, León, Nicaragua (Jean-Michel Maes)
SMTD = Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Dresden, Germany (Klaus-Dieter Klass and Olaf Jäger)
TAMU = Texas A&M University, College Station, Texas, United States (Edward G. Riley)
UFPA = Coleção Zoológica, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil (Fernando Augusto Barbosa Silva)
UFPE = Coleção Entomológica da Universidade Federal de Pernambuco, Recife, Brazil (Luciana Iannuzzi)
UNSM = University of Nebraska State Museum, Lincoln, Nebraska, United States (Brett Ratcliffe)
ZMHB = Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Joachim Willers and Johannes Frisch)

In the section ‘Material examined’, information for each specimen examined is listed alphabetically as follows: sex, collecting locality, collecting method, date of collection, collector (depository collection). In cases where the specimens were not examined microscopically, ‘undetermined sex’ is specified.

Type material

It was possible to study in person at least part of the type material of all the species-group names addressed in this work. To locate the whereabouts of some types, we consulted Horn & Kahle (1935, 1936, 1937) and Evenhuis (1997a, 1997b). The great majority of the type material described by the French entomologist Émile Blanchard (1819–1900) and by the German coleopterist Edgar von Harold (1830–1886) was deposited in the MNHN, the latter via the collection of René Oberthür (1852–1944); some of Harold’s type specimens studied for this work were also found at the ISNB and ZMHB.

The personal collection of the German scarabaedologist Adolf Schmidt (1856–1923), composed largely of Aphodiinae, but also including several type specimens of species of *Canthon* he described, was donated to the NHRS in 1924, one year after Schmidt’s death, where it is still housed. Additionally, Additionally, Schmidt (1920), in a paper where he described four dung beetle species today placed in *Sylvicanthon*, stated that he had studied material from four other German collections: the Senckenberg Deutsches Entomologisches Institut, today in Müncheberg, but at that time located in Dahlem, Berlin (Gaedike 1995); the Zoologisches Institut und Zoologisches Museum, Universität Hamburg, in Hamburg; the ZMHB, in Berlin; and the collection of the firm Bang-Hass of insect dealers from Blasewitz, Dresden (“*In letzter Zeit wurde mir freundlichst das zahlreiche Material des Museums in Dahlem und Hamburg, das der Firma Bang-Haas in Blasewitz und eine kleine Auslese aus dem Berliner Zool. Museum zur Verfügung gestellt* [...]”). Studying a vast amount of dung beetle type material in several European museums in 2013 and 2014, FZVM located syntypes of the four nominal species established by Schmidt (1920) at the ZMHB, SMTD (ex Bang-Hass collection) and NHRS. Specimens deposited at the Hamburg museum are certainly lost, since a great part of its collection was destroyed by World War II allied bombings in 1943 (Klapperich 1948; Weidner, 1976). Finally, the Müncheberg collection was visited by MC in June 2016, but no syntypes of Schmidt’s *Sylvicanthon* species were found there.

The type material of species described by the Argentinian Antonio Martínez (1922–1993) is divided between two collections: holotypes and allotypes are deposited at the MACN, while paratypes, along with the rest of his former personal collection, are at the CMNC (via collection Henry & Anne Howden). Those species described in co-authorship with the Brazilian Padre Francisco Pereira (1913–1991) also have paratypes deposited at the MZSP.

For names currently borne by a series of syntypes, we designate lectotypes in accordance with Article 74 of the International Code of Zoological Nomenclature (ICZN 1999; hereafter, cited as ‘the Code’) in order to stabilize the nomenclature and to avoid any future misunderstanding. It is also important to highlight that the Code's Recommendation 73F states that, when we have no data in the original description allowing us to know with certainty that the type series of a given name was composed of just a single specimen (and, subsequently, that specimen would automatically be the holotype of that name by monotypy), we should assume the type series was formed of two or more individuals, which, as a consequence, are the name's syntypes. That being so, even when we found just one specimen in the collections studied (e.g., for *Canthon xanthopus* and *Sylvicanthon securus*), we consider that specimen as part of a series of syntypes and, thus, eligible to be the lectotype of the name it bears.

Publication dates of historical works

Some 19th-century books cited in this work followed a very long and complicated process of publication, having been published in a series of independent fascicles (the so-called '*livraisons*'; see Evenhuis 1997a). Years later, these were often bound under a single cover with a publication date, which usually reflects the date of the last part published. Consequently, the year printed on the cover not always corresponds to the real issuing date of all parts of the book.

As publication dates are essential in zoological nomenclature, we checked that information in specialized literature in every situation where we had doubts about the year of appearance of a book cited in this work. Thus, publication dates of the cited parts of the series *Biologia Centrali-Americana* (Bates 1887, 1889) were based on Lyal (2011), those of Dejean's catalogues (1833–1836, 1836–1837) on Madge (1988), of the *Voyage dans L'Amérique Méridionale* (Blanchard 1846) on Sherborn & Woodward (1901) and Evenhuis (1997b), of *Recueil d'observations de zoologie et d'anatomie comparée* (Humboldt & Bonpland 1805–1810) on Sherborn (1899) and Evenhuis (1997a), and of *Histoire naturelle des insectes* (Brullé 1838) on Brockhaus & Avenarius (1839). Bouquest (2016), which appeared after the conclusion of the first draft of this work, was consulted in order to verify our previous datings.

Terminology

Throughout the descriptions of the external morphology, we employed the terminology established by Halffter & Martínez (1966, 1967, 1968, 1977), Edmonds (1972) and Canhedo (2006), with the updates organized by Beutel & Lawrence (2005) and Lawrence *et al*. (2010) based on more modern interpretations of the evolutionary development of the ventral sclerites of thorax and abdomen. For the microsculpture of the tegument surface, in particular, we followed Harris (1979) and Krell (1994) (see more details below in the section 'Comparative morphology of species of *Sylvicanthon*'). For the male genitalia, we adopted the terminology of Medina *et al*. (2013) (but see Zunino (2014) for some criticism).

Measurements

Using a ocular micrometer, specimens were measured as follows:
EW = greatest width of elytra
PgL = length of pygidium
PgW = greatest width of pygidium
PL = length of pronotum
PW = greatest width of pronotum
TL = total length

To each variable, we specify, in millimeters, the average and standard deviation (ME) and range with maximum (MX) and minimum (MN) values.

Geographical distribution and maps

The geographical distribution for each species is given in three different ways. The first is a general description of the species' distribution, citing relevant biomes where it occurs. The second is according to the division of the globe in ecoregions as proposed by Olson *et al*. (2001) (an interactive map with information about these ecoregions is available online by WWF 2006). Finally, the third way is based on the political division of each country. In this latter case, countries and first order subdivision (e.g., states, provinces or departments) are presented in a geographical order (i.e., in a sequence north-south and west-east), while lower divisions are given in alphabetical order. The only exception was French Guiana, an overseas department of the French Republic, but treated here as equivalent to the national category only for practical purposes. Information on the geographical distribution was mainly based on specimen labels. Information found in literature – which is often less reliable than specimen label data – was also included; in those cases, the locality is written in italics in the section 'Collecting sites' of each species.

Distribution maps presented in this work were made using the program ArcView GIS 10.2. Within this program, we used the shapefile of Löwenberg-Neto (2014) to confirm the presence of each species in the biogeographical provinces defined by Morrone (2014).

Notes

Notes in the text are explained in the Appendix at the end of the monograph.

Species concept and species taxon recognition

> "W*hen one is dealing with evolving biological populations – and that is what species of organisms are – one cannot expect the simplicity and unambiguousness that one encounters among parameters in the physical sciences*."
>
> Ernst Mayr (1988a)

Systematics[1], like any other science, works through hypotheses raising and testing. Consequently, it is of utmost importance that systematists try to make as clear as possible the epistemological framework in which their research was developed. It is only in that way that the confrontation of antagonistic hypotheses taken by different authors to explain the same phenomenon is possible. For a systematic revision dealing essentially with alpha taxonomy, the concept most sensitive to debates and disagreements is, without doubt, that of the species category. As Ernst Mayr (e.g., 1982, 2004a) and others have stated several times, this is probably the most discussed topic in the entire history of the philosophy of systematics. Despite that, there has never been a consensus about the meaning of the word 'species', although, as shown by de Queiroz (1998, 1999, 2005a, 2005b, 2007), most of the modern concepts share a common basis. When a given group of organisms has its taxonomy revised by different authors with distinct stances on the definition of the species category, it is almost certain that the number of delimited species in that group will differ in the final results of those works (Mayr 1963; Cracraft 1997, 2000; Agapow *et al.* 2004; Zachos 2014), which may lead to the problem (or conflict) known as taxonomic inflation (Isaac *et al.* 2004; Zachos 2014) and its counterpart, taxonomic inertia (after Zachos 2018). Therefore, following what Ratcliffe (2013) listed as one of the good practices in taxonomic work, in the following paragraphs we present a brief summary of our[2] current understanding of what is the best definition for the species category (i.e., what exactly we intend to refer to when using the word 'species'), and which are the criteria we use to recognize such entities. In other words, we will present our view on what de Queiroz (2007) defined as being species concept and species delimitation, respectively, – or Mayr's analogue terms species category and species taxon (Mayr 1963, 1988a, 2000, 2004a). It is important to stress that our somewhat long discussion on this topic is necessary because it will serve as a basis not only for the present study, but also for our future publications on alpha taxonomy.

Since the Darwinian revolution in the second half of the 19th century, following through August Weismann's (1834–1914) Neodarwinism and the Evolutionary Synthesis in the 1930s–1940s, Darwinian evolutionism, based on the five or six main theories developed by Charles Darwin[3], has become one of the unifying theoretical axis of the entire biology, connecting as distant fields as enzymology and astrobiology to marine biology, plant physiology and dung beetle taxonomy. As the famous phrase by Dobzhansky (1973) clearly summarized: “nothing in biology makes sense except in the light of evolution”. Thereby, the best concept for the species category will be the one that refers to sets of organisms that, after being recognized by the taxonomist, have their historical origin explained by complex evolutionary processes and, at the same time, help to answer questions raised by evolutionary biology. Of little use are those taxonomic works that delimit species having as their sole goal the pure recognition of discrete morphological units serving uniquely to the daily work of the collection curator, but which have nothing to say about the evolutionary history of the taxon it is studying. The species listed by a taxonomist will only have meaning beyond simple classification if delimited in the light of evolution.

With that conclusion in mind, throughout this work the term species is employed based largely on the definition of the Biological Species Concept as presented by Mayr (1942: 120): “a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (see also Mayr 1940, 1963, 1970, 1982, 1988a, 1988b, 2000, 2004a; and, more recently, Dubois 2011, where the biological species is called *mayron*). A given species may give rise to one or more daughter species through speciation processes (i.e., the rising of new discontinuities to gene flow), during which the ancestral species may or may not become extinct. It always depends on whether the speciation was dicopatric, on the one hand (when the ancestral species will cease to exist), or either peripatric or, much more rarely, sympatric by hybridization (when the ancestral species continues more or less intact and as cohesive as before[4]), on the other hand. We also agree with Hausdorf (2011) (a vision that had been championed earlier by Mayr 2004b) that the Evolutionary Species Concept (Simpson 1951, 1961; Wiley 1978, 1980, 1981; Wiley & Mayden 2000) is, to a large extent, a different dimension of the biological concept (i.e., the opposition between non-dimensional and dimensional species concepts as discussed by Mayr 1963). Evolutionary lineages can only remain integrated and independent (and, consequently, have their “own separate and unitary evolutionary role and tendencies”, as argued by Simpson 1951) if, through time, they were reproductively separated from other such lineages; otherwise, they would simply merge into a single lineage.

Indeed, Simpson (1951: 290) himself stated that his new concept was simply a “shift of emphasis” in relation to Mayr’s, whereas Wiley (1978, 1981) recognized reproductive isolation as one of the corollaries of his version of the Evolutionary Concept. The Unified Species Concept, as conceived by de Queiroz (2005b, 2007; see also de Queiroz 1998, 1999), on the other hand, although very close to the Biological Concept in stating that species are “Separately evolving metapopulation lineages”, clearly argues that populations reproductively isolated from one another by means only of extrinsic barriers should also have their condition as independent species recognized by the taxonomist (e.g., de Queiroz 2005a, 2005b). That is, intrinsic interbreeding barriers would not be a necessary condition for a given group of populations to be recognized as a distinct species from its most closely related group of populations. Should the Unified Concept be largely employed, we would enter into a phase of wide classificatory instability, with historically ephemeral species being formed and merged at a much more accelerated pace, and in a much more confusing way, than if we recognize solely species separated by intrinsic reproductive barriers. In this latter case, although we still recognize the possibility of reticulate evolution (see below), the species would be more historically lasting and stable. It is also worth emphasizing that another distinction between de Queiroz’s and Mayr’s concepts is that the former author seems to be agnostic in relation to the cohesive factors that maintain a species united (e.g., de Queiroz 1999: 68), while the latter expressly asserts that interbreeding is the fundamental cohesive factor that, in combination with reproductive isolation, maintains the integrity and individuality of the species taxa through time and space (properties that, in turn, confer them the ontological status of logical individuals; see Ghiselin 1974, 1997; Hull 1976; Mayr 1988b).

It is important to stress that the Biological Concept as conceptualized by Mayr in no way resembles the simplistic version that several authors (both its critics and its enthusiasts) in general cite, where species would be separated by insurmountable sterility barriers. In that misleading version of the concept, to determine whether two individuals belong to the same species, it would be sufficient to obtain a hybrid between them and evaluate its fertility or viability. If the offspring were infertile or inviable, then the progenitors would belong to different species; on the other hand, if the offspring were fertile or viable, then the progenitors would be conspecific. Nothing could be more different from Mayr's concept (or from the one employed in this work).

As established in its original definition (Mayr 1940, 1942), the Biological Concept is populational, not individual; it does not work in an essentialist or determinist way, but rather it is probabilistic. Species may indeed show sterility barriers, but they may equally present hybridizing individuals or even populations. This stands clear when Mayr discusses topics such as reticulate evolution and hybrid speciation, when two formally independent species enter into physical contact and merge their populations, forming a single evolutionary lineage (e.g., Mayr 1963, 1970, 1982; see also Dubois 2011; Lamichhaney *et al.* 2018), introgression, secondary contact and secondary intergradation (Mayr 1963, 1970), the breakdown of isolating mechanisms (Mayr 1963), and the so-called 'difficulties' in the application of the biological concept (Mayr 1940, 1957, 1963). In that way, the biological species should be understood as a group of populations showing a broad reproductive transit and gene flow, and that, as a whole, is separated from such other groups of reproductively independent populations. Or, in other words, "different species, he [Ernst Mayr] believed, are those populations possessing any factors intrinsic to their member individuals that will act to prevent interbreeding *between* the populations **of a degree** as free as that within each population" (Wilson & Brown 1953; their italics, our bold).

The misinterpretation that many authors give to the Biological Concept was already noted by Wilson & Brown (1953) in the decade following the Evolutionary Synthesis. As discussed by them, several authors were not capable of understanding the probabilistic nature of the Biological Concept and, consequently, they converted it into a deterministic method of species delimitation where the hybrid barrier would function as a straightforward yardstick separating individuals belonging to a same species from those that should be classified in distinct species[5]. The need felt by many taxonomists for a simple and universal concept for species recognition resembles largely the use of universal laws and principles in Newtonian physics. But evolutionary biology, unlike physics, deals with populations in gradual evolutionary change dictated by natural and sexual selection, mutation, migration, and genetic drift. Therefore, its objects of study are not fixed and discontinuous entities, but rather mutable lineages connected gradually and historically to other such lineages, which makes any form of essentialist philosophy or methodology extremely inadequate. As well argued by Mayr (1982, 2004b), it was Charles Darwin and his evolutionary theories that brought this completely unique character to biology.

Having discussed the meaning of the word 'species' (i.e., which species concept will be followed in this work), the second question to be answered is how to recognize biological species. Or, using the terminology of de Queiroz (2007), how to delimit them. In the present work, populations of *Sylvicanthon* were studied exclusively through individuals collected and stored dry in the 31 collections consulted. Thus, the two main sources of evidence for species recognition were the geographical provenance and, especially, the morphology of the specimens, in which this work actually followed most of the modern insect taxonomic revisions (although other methods might equally be employed, as discussed by de Queiroz 2005a, 2005b, 2007 and Mayr 1988a). Therefore, since it was not possible to observe directly how the populations of the studied species behave and interact in nature (and this would be almost impossible), all the taxonomic conclusions drawn here are based on the inference that, to some degree, distinct character conditions suggest distinct evolutionary histories (and, therefore, the existence of independent reproductive communities), whereas similar characters suggest a shared history (as stated by Mayr 1988a: "Species taxa […] are based on inference from the species concept"). Hence, at a same locality, the more similar the individuals, the greater the confidence they belong to the same population, while the more similar two populations are (and this includes similitudes in intrapopulation variation, such as the one seen, for instance, in the micropunctation of the pronotal tegument of *S. proseni* (Martínez, 1949)), the greater the confidence they are conspecific. There are instances where the level of morphological distinction is such (that is, the volume of evidence that gene flow is minimal or has completely ceased), that there is little doubt we are dealing with distinct species (for example, *S. foveiventris* (Schmidt, 1920) and *S. obscurus* (Schmidt, 1920), two species with an overlapping distribution). On the other hand, there are cases where the distinction is tenuous enough to give us confidence we are dealing with a case of intraspecific variation, being it either intrapopulational or geographical (for example, colouration in *S. obscurus*).

Certainly, this method (which was called simply the "morphological method" in the revision of the operational criteria for species delimitation of Sites & Marshall 2004) involves arbitrary aspects. Commonly, there is a grey area between what should be considered sufficient a distinction to categorize two populations as conspecific or as independent species (Mayr 1988a, 2004a; Zachos 2018); the cryptic species example well illustrates that this criterion of "degree of differences" has its flaws. But this is precisely the kind of situation we expect to find in a scenario where evolution exists, speciation is a gradual and populational process, and the species are historically and continuously interconnected throughout the tree of life (Wilson & Brown 1953; Mayr 1963, 1988a; Hey *et al.* 2003; Ridley 2004; de Queiroz 2005a, 2005b, 2007; Zachos 2014, 2018). In a world where species were temporally fixed and speciation came about in sudden leaps, one would expect that species would be discontinuous entities and situations of uncertainty about the boundaries between a pair of them would be rare and, when occurring, highly problematic. As this is not the reality of the world in which we live, the uncertainty on the categorization as full species of two incipient and very similar lineages (or reproductive units) should be perfectly acceptable, especially if we are dealing with allopatric populations. The species taxa proposed here, as in any other revision, should be understood as hypotheses to be tested in the light of new evidence and interpretations. Consequently, no revision should hope to be the last word to be said on the taxon which it is dealing with, a hope that the present work certainly does not nurture.

Results

Phylum Arthropoda von Siebold, 1848[6]
Subphylum Hexapoda Blainville, 1816[7]
Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758[8]
Suborder Polyphaga Emery, 1886
Superfamily Scarabaeoidea Latreille, 1802[9]
Family Scarabaeidae Latreille, 1802
Subfamily Scarabaeinae Latreille, 1802

Tribe **Deltochilini** Lacordaire, 1856

A taxonomic history of '*Canthon* sensu lato'

The taxonomic history of *Sylvicanthon* is intimately associated with that of *Canthon* and allied genera. Thereby, a full understanding of the context within which the genus was established by Halffter & Martínez (1977) is essential to any person interested in the taxonomy of *Sylvicanthon*, especially in the light of recent publications questioning the validity of the genus (Ratcliffe 2002; Solís & Kohlmann 2012). As the last revision of this history was published over 50 years ago (Halffter 1961; Halffter & Martínez 1968) and great taxonomic activity has occurred since then, we present here a brief discussion on the taxonomic history of *Canthon* and allied groups (hereafter referred as '*Canthon* sensu lato'[10]) with the dual goal of presenting a historical background to the description of *Sylvicanthon* by Halffter &

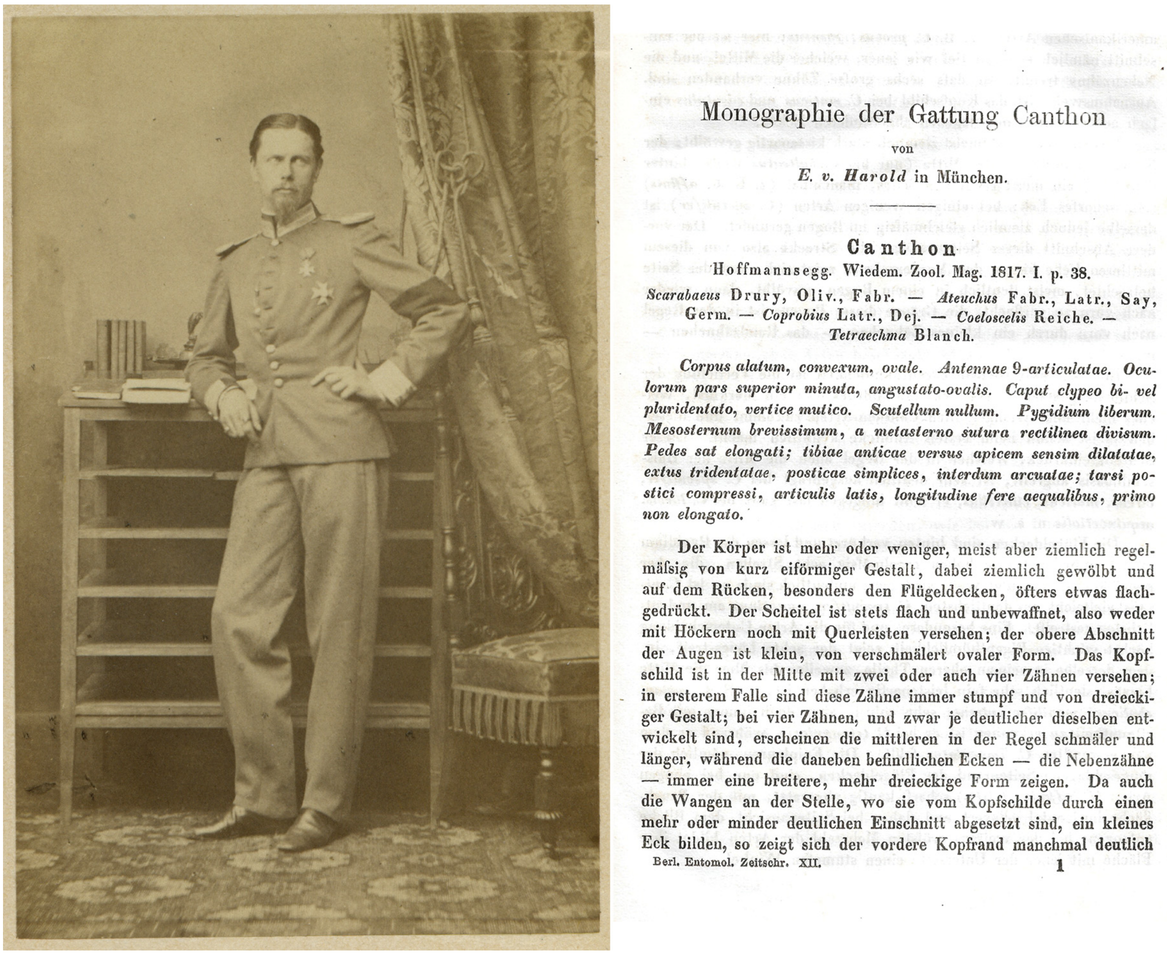
Martínez (1977), and providing some basic information that shall help future taxonomic works in Deltochilini.

In his 1817 revision of the insects described by the French entomologist Pierre André Latreille (1762–1833) (Fig. 1B) in the work of Humboldt & Bonpland (1805–1810), the German naturalist Johann Centurius von Hoffmannsegg (1766–1849) (Fig. 1A) proposed the genus *Canthon* for *Ateuchus septemmaculatus* Latreille, 1807 and 14 other species not cited by Latreille (1807). The type species of *Canthon*, *Scarabaeus pilularius* Linnaeus, 1758, would be designated only 120 years later by Paulian (1939: 22). Probably unaware of the description of Hoffmannsegg (1817), Latreille (1829) established the new genus *Coprobius* to accomodate several species that had already been transferred to *Canthon* by Hoffmannsegg. Even so, Latreille's new nominal genus was adopted by contemporary French entomologists such as Brullé (1838), Reiche (1841) and Dejean (1833–1836, 1836–1837). The German author Jacob Sturm (1843), in the second edition of the catalogue of his beetle collection, was the first to recognize the synonymy between *Canthon* and *Coprobius*, but, interestingly enough, he used the second name as valid and indicated the first edition of his own catalogue ('St. Cat.'; Sturm, 1826) as the original publication of *Canthon*. Nonetheless, by consulting Sturm (1826), we see that in that work the authorship of *Canthon* (there considered a valid name) was attributed to the German entomologist Johann Karl Wilhelm Illiger ('Illig.') and not considered a new genus. As far as we could find, Illiger never cited the name *Canthon* in his own works, neither before nor after Hoffmannsegg's description.

Fig. 1. Authors who initiated the studies on '*Canthon* sensu lato' in the first half of the 19th century. **A**. The German naturalist Johann Centurius Graf von Hoffmannsegg (1766–1849), author of the genus *Canthon* (image courtesy of Editha Schubert, from the archives of the Senckenberg Deutsches Entomologisches Institut). **B**. The French entomologist Pierre André Latreille (1762–1833), author of *Ateuchus septemmaculatus* Latreille, 1807, species treated in detail by Hoffmannsegg (1817) in his description of *Canthon*. Latreille was also the author of *Coprobius*, name considered valid for decades before being synonymized with *Canthon* by Harold (1868a) (image courtesy of the United States National Library of Medicine).

Finally, Castelnau (1840) also recognized the synonymy between *Canthon* and *Coprobius*, but, contrary to Sturm (1843), he was the first to consider *Canthon* as the valid name in this synonymy, a decision that, with the notorious exception of Burmeister (1874), has been followed until the present day. A second name that is currently considered a junior synonym of *Canthon*, '*Coeloscelis*', was proposed by Reiche (1841) to accommodate only '*C. coriaceus* Dej.'. Erichson (1847) synonymized *Canthon* and *Coeloscelis*, but Lacordaire (1856) returned using *Coeloscelis* as valid and transferred some further species to this genus. The definitive synonymy would only come with Harold (1868a), in the first great comprehensive revision of the genus *Canthon*.

One of the greatest specialists of Scarabaeinae in the 19th century, the German entomologist Edgar von Harold (1830–1886) (Fig. 2) was responsible for some landmark revisions of genera with a large number of species and a very complex taxonomy which are still fundamental to our understanding of the diversity of New World dung beetles. Among those works are Harold's revisons of *Canthidium* Erichson, 1847 (Harold 1867), *Ateuchus* Weber, 1801 (cited as *Choeridium* Lepeletier de Saint-Fargeau & Audinet-



Monographie der Gattung Canthon

von

E. v. Harold in München.

Canthon

Hoffmannsegg. Wiedem. Zool. Mag. 1817. I. p. 38.

Scarabaeus Drury, Oliv., Fabr. — *Ateuchus* Fabr., Latr., Say, Germ. — *Coprobius* Latr., Dej. — *Coeloscelis* Reiche. — *Tetraechma* Blanch.

Corpus alatum, convexum, ovale. Antennae 9-articulatae. Oculorum pars superior minuta, angustato-ovalis. Caput clypeo bi- vel pluridentato, vertice mutico. Scutellum nullum. Pygidium liberum. Mesosternum brevissimum, a metasterno sutura rectilinea divisum. Pedes sat elongati; tibiae anticae versus apicem sensim dilatatae, extus tridentatae, posticae simplices, interdum arcuatae; tarsi postici compressi, articulis latis, longitudine fere aequalibus, primo non elongato.

Der Körper ist mehr oder weniger, meist aber ziemlich regelmäſsig von kurz eiförmiger Gestalt, dabei ziemlich gewölbt und auf dem Rücken, besonders den Flügeldecken, öfters etwas flachgedrückt. Der Scheitel ist stets flach und unbewaffnet, also weder mit Höckern noch mit Querleisten versehen; der obere Abschnitt der Augen ist klein, von verschmälert ovaler Form. Das Kopfschild ist in der Mitte mit zwei oder auch vier Zähnen versehen; in ersterem Falle sind diese Zähne immer stumpf und von dreieckiger Gestalt; bei vier Zähnen, und zwar je deutlicher dieselben entwickelt sind, erscheinen die mittleren in der Regel schmäler und länger, während die daneben befindlichen Ecken — die Nebenzähne — immer eine breitere, mehr dreieckige Form zeigen. Da auch die Wangen an der Stelle, wo sie vom Kopfschilde durch einen mehr oder minder deutlichen Einschnitt abgesetzt sind, ein kleines Eck bilden, so zeigt sich der vordere Kopfrand manchmal deutlich

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Fig. 2. The German coleopterist Edgar von Harold (1830–1886), one of the first specialists in scarab beetles and author of the only 19th century revision of *Canthon* Hoffmannsegg, 1817, in which 97 species were recognized as valid, 46 as new. Harold described two species today positioned in *Sylvicanthon* Halffter & Martínez, 1977: *S. aequinoctialis* (Harold, 1868) comb. nov. and *S. candezei* (Harold, 1869) (portrait courtesy of Editha Schubert, from the archives of the Senckenberg Deutsches Entomologisches Institut; title page of Harold's revision of *Canthon* scanned from an original copy housed at the first author's personal library).

Serville, 1828; Harold 1868b) and *Canthon* (Harold 1868a). In this latter work, Harold recognized *Canthon* as the senior synonym of *Coprobius*, *Coeloscelis*, and *Tetraechma* Blanchard, 1846, and being composed of 97 species – 46 of them new – distributed throughout the American continent. Twenty-three other nominal species were listed as of unknown assignment, the majority of them described by French entomologists such as Blanchard, Lucas, Castelnau and Guérin-Méneville, and the American LeConte, and whose type material Harold (1868a) did not have access to. Harold (1868a) also redescribed *Canthon*, discussed in fine detail the morphological variation observed in the genus, compared it to other taxa considered as close relatives such as *Deltochilum*, *Anachalcos* Hope, 1837 and *Megathopa* Eschscholtz, 1822, and, perhaps his most important contribution, presented the first identification key to the species of *Canthon*. The following year, after examining some type material deposited in the MNHN, Harold (1869c) presented new information about some of the species considered as unknown to him in 1868.

During the second half of the 19th century and the early 20th century, the number of species in *Canthon* continued to grow. In the catalogue of Harold (1869b), 123 species were included in the genus, while that

Fig. 3. The two great revisers of *Canthon* Hoffmannsegg, 1817 in the first half of the 20th century. **A**. The German coleopterist Adolf Schmidt (1856–1923). After the publication of his two works on Scarabaeinae (Schmidt 1920, 1922), *Canthon* was composed of 143 valid species. Schmidt was the first author to recognize a group of species that, more than 50 years later, would constitute the core of the genus *Sylvicanthon* as proposed by Halffter & Martínez (1977). **B**. The Czech coleopterist Vladimír Balthasar (1897–1978), one of the first authors to recognize explicitly the great heterogeneity and artificiality of *Canthon* and to propose its division into several genera and subgenera. (Both images courtesy of Editha Schubert, from the archives of the Senckenberg Deutsches Entomologisches Institut.)

number rose to 144 in the catalogue of Gillet (1911). In the interwar period, Adolf Schmidt (1856–1923) (Fig. 3A), a German specialist in Aphodiinae, devoted himself to the elaboration of a second revision of *Canthon*, the only scarabaeine genus on which he has ever published (Vaz-de-Mello & Cupello in press). In his first work, Schmidt (1920) described 26 new species-group taxa in *Canthon.* Shortly after, Schmidt (1922) proposed 27 additional new species and presented an updated identification key to 143 species of *Canthon* (not including 20 names he did not know how to apply to species taxa).

With the description of 16 additional new species, the Czech entomologist Vladimír Balthasar (1897–1978) (Fig. 3B) updated Schmidt's key in 1939 expanding it to encompass 162 species; 23 other names were not included by being of unkown application to species taxa. As Balthasar (1939) himself recognized several times throughout his text and even in its title ("*Eine Vorstudie zur Monographie der Gattung Canthon*", or "*A Preliminary Sudy Towards a Monograph of the Genus* Canthon"), his modifications were only a first draft towards a future revision of *Canthon*, a genus that, in his opinion, was extremely heterogeneous and ill defined. In the future, Balthasar (1939) believed, with a deeper analysis of the relationships between its species, groups of species and their morphological diversity, *Canthon* would inevitably be divided into several other genera and subgenera (e.g., on page 236, where he wrote "Die ganze Gattung [*Canthon*] scheint sehr heterogen zu sein und ich bin mir dessen gut bewusst, dass beim näheren Studium sich als notwendig zeigen wird, mindestens einige Arten als selbständige Gattungen abzugliedern").

In fact, this process of dividing *Canthon* into small, peripheral genera had already been started in the 19th century. As examples, we can cite the description of *Tetraechma* Blanchard, 1846, *Pseudocanthon* Bates, 1887, *Agamopus* Bates, 1889 and, later on in the early 20th century, *Zonocopris* Arrow, 1932, *Plesiocanthon* Gillet, 1933 (currently a junior synonym of *Zonocopris*) and *Canthochilum* Chapin, 1934. Furthermore, new species that, in the past, would probably have been positioned in *Canthon*, were being described in new monotypic or oligodiverse genera such as *Sinapisoma* Boucomont, 1928, *Canthonella* Chapin, 1930, *Canthonidia* Paulian, 1939, *Canthotrypes* Paulian, 1939, *Paracanthon* Balthasar, 1938 and *Cryptocanthon* Balthasar, 1942. Even so, the situation continued to be one of extreme chaos. On the one hand, there were disagreements over the validity of some of those names (*Pseudocanthon* and *Tetraechma*, for instance, were considered junior synonyms of *Canthon* by most authors almost until the second half of the 20th century). On the other hand, the newly-proposed divisions helped little to reduce the great heterogeneity and artificiality of *Canthon*, since this genus continued to contain almost 200 species, while the other small genera were composed of at most three species.

The 1940s–1970s represented, however, a period of intense changes in that panorama thanks to the joint effort of three Latin American entomologists: the Brazilian priest Father Francisco Silvério Pereira (1913–1991) (Fig. 4A), the Argentinian Antonio Martínez (1922–1993) (Fig. 4B) and the Spanish-born Mexican Gonzalo Halffter (b. 1932) (Fig. 4C). In a series of taxonomic works (among them, we highlight: Pereira 1946, 1949, 1953; Martínez 1948a, 1948b, 1950, 1952, 1953; Martínez & Pereira 1956; Halffter, 1958, 1961; Pereira & Martínez 1956, 1959, 1960; Martínez *et al.* 1964; Vulcano & Pereira 1964, 1966; Martínez & Halffter 1972), culminating in the four-part major revision of the New World 'Canthonina' by Halffter & Martínez (1966, 1967, 1968, 1977), new species were described and the genus *Canthon* was divided into a large number of taxa (sometimes categorized as its subgenera, sometimes as full genera). Halffter & Martínez (1977), in the final part of their series of revisions, recognized 28 valid genera, with the genus *Canthon* itself divided into nine subgenera and its nominotypical subgenus into 22 groups or lineages ('*líneas*') of species.

Therefore, as discussed so far, the historical tendency in the taxonomy of '*Canthon* sensu lato', especially in the second half of the 20th century, has been the division of the former concept of the genus *Canthon* into several small, peripherical subgenera and genera, a classification that, in principle, attempts to

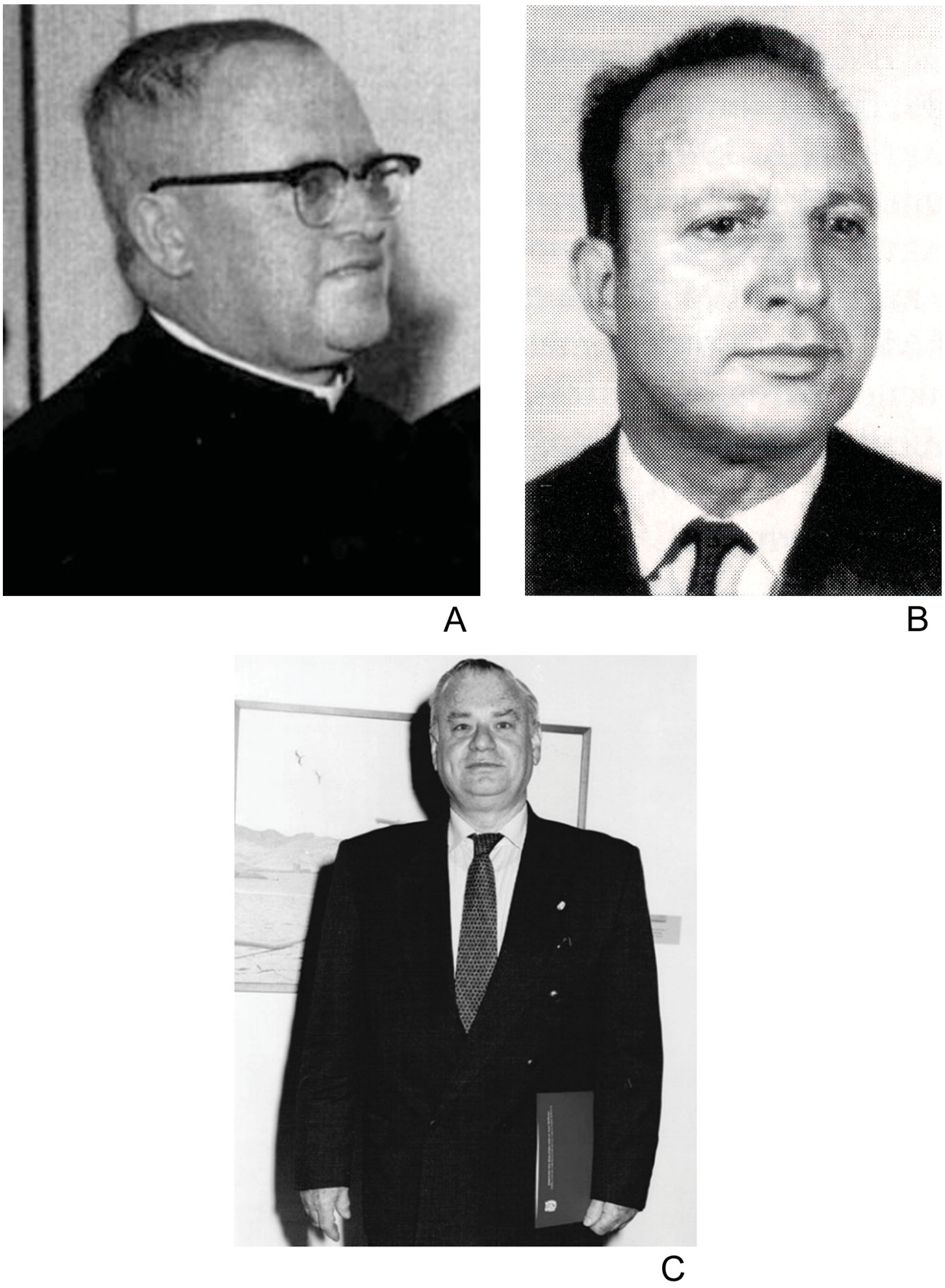

Fig. 4. The three scarab beetle specialists responsible for the intense period of taxonomic activity that '*Canthon* sensu lato' passed through during the 1940s–1970s. Throughout that period and through tens of papers, the former concept of the genus *Canthon* Hoffmannsegg, 1817 was divided into several genera and subgenera, including *Sylvicanthon* Halffter & Martínez, 1977, published in the last work of that series. **A**. The Brazilian cleric, Padre Francisco Silvério Pereira, CMF (1913–1991) (image courtesy of Everardo Grossi and Brett Ratcliffe). **B**. The Argentinian entomologist Antonio Martínez (1922–1993) (modified from Fritz 1994). **C**. The Mexican entomologist Gonzalo Halffter (b. 1932) (modified from Morrone 2015a).

reflect the phylogeny of the group. Nevertheless, as argued by Solís & Kohlmann (2002, 2012) and Medina *et al.* (2003), that goal, in reality, has not been fully met, something recognized even by both Martínez (1987), who considered *Canthon* an "omnibus genus", and Halffter (2003). As shown by Solís & Kohlmann (2002, 2012) and Medina *et al.* (2003), several of the characteristics used to define supraspecific taxa do not have an adequate phylogenetic signal as to indicate old relationships. These features (e.g., shape of meso- and metatarsi, eyes and clypeus) have apparently been subject to strong action from directional natural and sexual selection and, hence, are in constant change, passing through convergences, parallelisms and reversions throughout the evolutionary history of the group. Having been based on such plastic characteristics, the classification proposed by Halffter & Martínez (1977) is largely artificial[12].

In an exploratory cladistic analysis of '*Canthon* sensu lato' based on 39 species and 83 characters, Medina *et al.* (2003) found that *Canthon*, as defined by Halffter & Martínez (1977), is highly artificial, with several other genera such as *Sylvicanthon*, *Scybalocanthon* Martínez, 1948, *Anisocanthon* Martínez & Pereira, 1956 and *Melanocanthon* Halffter, 1958, nested within it. Based on those results, Solís & Kohlmann (2002, 2012) proposed the rejection, at least temporarily, of a large part of the generic and subgeneric names and that their species be referred to *Canthon*. This latter name would then represent only a miscellany of not-particularly-closely-related species waiting for a revision that could form natural groups (i.e., monophyletic sensu Hennig, 1966) based on more robust and stable suite of characters having stronger phylogenetic information.

Although we certainly agree with the diagnosis presented by Solís & Kohlmann (2002, 2012), we disagree on the temporary solution put forward by them. At the moment, the most urgent concern about '*Canthon* sensu lato' is, in our view, the alpha taxonomy, since it is crystal clear that we still have a very limited knowledge of its species diversity. Three revealing examples are the revision of the Mexican *Glaphyrocanthon* by Rivera-Cervantes & Halffter (1999), which described 10 new species and hence doubled the number of known representatives of this group in that country, the revision of *Hansreia* Halffter & Martínez, 1977 by Valois *et al*. (2015), which added five species to a genus considered monotypic for almost 40 years, and the present work, which triples the number of species in *Sylvicanthon* (including the description of six new species).

If we gather again under the same name '*Canthon*' the cohesive and easily identifiable groups of species (i.e., genera and subgnera) delimited during the second half of the 20th century (such as *Sylvicanthon*), we would have once more an overly inflated and heterogeneous genus. Naturally, this situation would inhibit the start of any taxonomic revision with the group, as it had already occurred during the 19th and the early 20th centuries and, in fact, still occurs with *Canthon s. str*. Moreover, contrary to what was written by Solís & Kohlmann (2002), the results obtained by Medina *et al.* (2003) do not tell us that the genera peripheral to *Canthon* (e.g., *Sylvicanthon*) are artificial (i.e., whether they are polyphyletic or paraphyletic). In fact, for the most part, this would be impossible to ascertain, since only a single species of each group was included in the analysis (Medina *et al.* (2003: 59) indeed recognized that: "[...] only a few species from the other genera were included in the analysis [...], so we cannot speculate as to whether genera such as *Anisocanthon*, *Melanocanthon*, or *Sylvicanthon* are natural species groups"). On the other hand, except for the genus *Canthon* as a whole and *Glaphyrocanthon* in particular, the other two groups of genus/subgenus rank that had more than one species included in the analysis, *Francmonrosia* Pereira & Martínez, 1959 and *Scybalocanthon*, appeared monophyletic.

The major problem, thus, seems to be the delimitation of *Canthon* (especially *Canthon s. str.* and *Glaphyrocanthon*) and not necessarily that of its closely related taxa. Therefore, the synonymy of *Sylvicanthon* and other genera and subgenera with *Canthon* as proposed by Solís & Kohlmann (2012) and Ratcliffe (2002) seems to be overly conservative and would only bring more uncertainty to our understanding of the diversity of "*Canthon* sensu lato". Future phylogenetic analyses based on both morphological and molecular data will lead us closer to a natural classification, but this will only be possible with a deep understanding of the species and morphological diversity of "*Canthon* sensu lato". For now, we should follow a bottom-up approach; i.e., from the delimitation of closely related species to the recognition of their slightly more distant phylogenetic affinities (something already suggested by Solís & Kohlmann, 2002: 3). Hence, the formation of easily identifiable sets of species with similar morphology is of great utility and practicality, even if these groups are not monophyletic. The next step, at last, will be of unravelling the deeper and older relationships between those species. When we finally have a sound understanding of their phylogeny, it will be time to propose a new classification reflecting it, one that will leave no room for non-monophyletic groups.

Accordingly, here we follow Halffter & Martínez (1977) and consider valid *Sylvicanthon* and all the other names categorized by them as genera and subgenera. Despite that, we do believe that the taxa considered by them as subgenera of *Canthon* will eventually turn out to be independent genera, since there is no synapomorphy nor clear diagnostic characteristic bringing them together, and there are evident affinities between some of the subgenera of *Canthon* with other genera of "*Canthon* sensu lato" (e.g., between *Sylvicanthon* and at least some groups of *Glaphyrocanthon* Martínez, 1948). See Table 1 for information on the genus-group names proposed throughout the taxonomic history of '*Canthon* sensu lato'.

Genus ***Sylvicanthon*** Halffter & Martínez, 1977

Sylvicanthon Halffter & Martínez, 1977: 36, 45, 61–63.

Sylvicanthon – Halffter & Edmonds 1982: 139. — Martínez 1987: 47. — Kohlmann & Halffter 1990: 8. — Hanski & Cambefort 1991: 472. — Medina & Lopera-Toro 2000: 301, 311. — Vaz-de-Mello 2000: 186, 195. — Escobar 2000a: 200, 210. — Medina *et al.* 2001: 133. — Solís & Kohlmann 2002: 2. — Halffter 2003: 31. — Medina *et al.* 2003: 25, 29–30, 36, 38–41, 45, 59, 62. — Durães *et al.* 2005: 724. — Scheffler 2005: 14. — Hamel-Leigue *et al.* 2006: 3. — Medina & Pulido 2009: 56. — Scholtz *et al.* 2009: 567. — Carvajal *et al.* 2011: 99, 117, 316. — Vaz-de-Mello *et al.* 2011a: 6, 11, 19, 26, 33, 41. — Krajcik 2012: 63 (as junior synonym of *Canthon*). — Solís & Kohlmann 2012: 3 (as junior synonym of *Canthon*). — Boilly & Vaz-de-Mello 2013: 107. — Medina *et al.* 2013: 468, 473. — Noriega *et al.* 2015: 101. — Feer 2015: 8. — Pacheco *et al.* 2016: 145. — Tarasov & Dimitrov 2016: 15. — Chamorro *et al*. 2018: 76, 98. — Espinoza & Noriega 2018: 147, fig. 2.
Silvicanthon [sic] – Noriega 2004: 39.

Type species

Canthon candezei Harold, 1869, by original designation (Halffter & Martínez 1977: 62).

Diagnosis

The following combination of characters is found uniquely in *Sylvicanthon*: small- to medium-sized species usually with dark colouration (black, dark blue, dark green or purple, but also light green and coppery) and, sometimes, with metallic sheen, and general body shape oval, flat and compact; clypeus with two small, contiguous at base or only slightly separated apical teeth, never with emargination between them (group *candezei*, 14 species, Fig. 6B–G), or clypeus with four large teeth, but also without emargination between them (group *enkerlini*, a single species, Fig. 14); external margin of genae with an evident denticle adjacent to the junction with clypeus; dorsal surface of eyes large (width about one fifth of that of interocular space); pronotum with lateral edges forming a strong medial angle and without prescutellar depression; anterior region of hypomera strongly excavated and delimited posteriorly by a complete hypomeral carina (Fig. 35); external margin of anterior region of hypomera with a very small tubercle or simple, without tubercle; mesoventrite horizontal and very short (Fig. 54); mesocoxae with

Table 1 (continued on next two pages). Genus-group names proposed for ‘*Canthon* sensu lato’. Validity status follows Halffter & Martínez (1977) and Vaz-de-Mello *et al*. (2011). Abbreviation ‘sg’ indicates names originally described in the genus category, but considered as subgenera of *Canthon* by Halffter & Martínez (1977).

Year	Genus	Authorship	Current status (number of valid species)	Type species
1817	*Canthon*	Hoffmannsegg	Valid (155 spp. in the genus, 48 spp. in the nominotypical subgenus and 22 in *incertae sedis*[3,15,16,17])	*Scarabaeus pilularius* Linnaeus, 1758, by subsequent designation of Paulian (1939)
1829	*Coprobius*	Latreille	Junior subject synonym of *Canthon* Synonymy firstly recognized by Sturm (1843)	*Scarabaeus volvens* Fabricius, 1792, by subsequent designation of Reiche (1841)
1841	*Coeloscelis*	Reiche	Junior subject synonym of *Canthon* Synonymy firstly recognized by Erichson (1847)	*Coeloscelis coriaceus* Reiche, 1841, **nomen dubium**, by original designation
1846	*Tetraechma*	Blanchard	Valid (2 spp.[2])	*Tetraechma sanguineomaculata* Blanchard, 1846, by original monotypy
1887	*Agamopus*	Bates	Valid (6 spp.[3])	*Agamopus lampros* Bates, 1887, by original monotypy
	Pseudocanthon	Bates	Valid (9 spp.[2,3])	*Canthon perplexus* LeConte, 1847, by original monotypy
1893	*Paedohyboma*	Kolbe	Junior subjective synonym of *Canthon* (Halffter & Martínez, 1977)	*Canthon aberrans* Harold, 1868, by original monotypy
1928	*Sinapisoma*	Boucomont	Valid (1 sp.[2,4])	*Sinapisoma minuta* Boucomont, 1928, by original monotypy
1930	*Canthonella*	Chapin	Valid (18 spp.[3,5,6])	*Canthonella parva* Chapin, 1930, by original designation
1932	*Zonocopris*	Arrow	Valid (2 spp.[3,7])	*Zonocopris bucki* Arrow, 1932, by original monotypy
1933	*Plesiocanthon*	Gillet	Junior subjective synonym of *Zonocopris* (Pereira, 1946)	*Canthon gibbicollis* Harold, 1868, by original monotypy
1934	*Canthochilum*	Chapin	Valid (23 spp.[3,8])	*Canthochilum oakleyi* Chapin, 1934, by original designation
1935	*Ipselissus*	d’Olsoufieff	Junior subjective synonym of *Canthochilum* (Halffter & Martínez, 1977). Senior objective synonym of *Ipsepilissus*	*Epilissus silphoides* Harold, 1867, by original monotypy
1938	*Paracanthon*	Balthasar	Valid (4 spp.[2,3])	*Paracanthon trichonotulus* Balthasar, 1938, by original monotypy
1939 [1]	*Canthonidia*	Paulian	Valid (2 spp. [2,3])	*Canthonidia hirsuta* Paulian, 1939, by original designation
	Canthotrypes	Paulian	Valid (1 sp. [3,4])	*Canthotrypes oberthuri* Paulian, 1939, by original designation
	Ipsepilissus	Paulian	Junior objetive synonym of *Ipselissus*	*Epilissus silphoides* Harold, 1867, by original designation

Table 1 (continued).

Year	Genus	Authorship	Current status (number of valid species)	Type species
	Paracanthon	Paulian	Junior subjetive synonym (Balthasar, 1942) and junior homonym of *Paracanthon* Balthasar	*Paracanthon hirsutus* Paulian, 1939, by original designation
1942	*Cryptocanthon*	Balthasar	Valid (38 spp. [3,9,10])	*Cryptocanthon paradoxos* Balthasar, 1942, by original designation
1947	*Opiocanthon*	Paulian	Junior subjective synonym of *Pseudocanthon* (Matthews, 1966)	*Canthon vitraci* Fleutiaux & Sallé, 1889, by original designation
1948	*Glaphyrocanthon*	Martínez	Valid [sg] (50 spp. [3])	*Glaphyrocanthon variabilis* Martínez, 1948, by original designation
	Scybalocanthon	Martínez	Valid (19 spp. [14])	*Canthon moniliatus* Bates, 1887, by original designation
1949	*Deltepilissus*	Pereira	Valid (2 spp. [2,3])	*Deltepilissus travassosi* Pereira, 1949, by original designation
1950	*Coprocanthon*	Martínez	Junior subjetive synonym of *Glaphyrocanthon* (Halffter & Martínez, 1977)	*Glaphyrocanthon rufocoeruleus* Martínez, 1948, by original designation
1952	*Xenocanthon*	Martínez	Valid (1 sp. [2,3])	*Xenocanthon vianai* Martínez, 1952, by original designation
1953	*Peltecanthon*	Pereira	Valid [sg] (3 spp. [2,3,16])	*Peltecanthon staigi* Pereira, 1953, by original designation
	Scybalophagus	Martínez	Valid (5 spp. [3,11])	*Scybalophagus patagonichus* Martínez, 1953, by original designation
1954	*Pseudepilissus*	Martínez	Valid [sg] (5 spp. [2,3])	*Canthon lunatus* Schmidt, 1922, by original designation
1956	*Anisocanthon*	Martínez & Pereira	Valid (4 spp. [2,3])	*Deltochilum pygmaeum* Gillet, 1911, by original designation
	Holocanthon	Martínez & Pereira	Valid (1 sp. [2,3])	*Holocanthon mateui* Martínez & Pereira, 1956, by original designation
	Nesocanthon	Pereira & Martínez	Valid [sg] (3 spp. [2,3])	*Canthon callosus* Harold, 1868, by original designation
	Goniocanthon	Pereira & Martínez	Valid [sg] (3 spp. [15])	*Scarabaeus smaragdulus* Fabricius, 1781, by original designation
	Geocanthon	Pereira & Martínez	Junior subjective synonym of *Glaphyrocanthon* (Halffter & Martínez, 1977)	*Canthon rubrescens* Blanchard, 1846, by original designation
1958	*Boreocanthon*	Halffter	Valid [sg] (15 spp. [2,3])	*Ateuchus ebenus* Say, 1823, by original designation
	Melanocanthon	Halffter	Valid (4 spp. [2,3])	*Canthon bisp.inatus* Robinson, 1941, by original designation

Table 1 (continued).

Year	Genus	Authorship	Current status (number of valid species)	Type species
1959	*Canthomoechus*	Pereira & Martínez	Junior subjective synonym of *Canthon* (Halffter & Martínez, 1977)	*Canthon quadratus* Blanchard, 1846, by original designation
	Trichocanthon	Pereira & Martínez	Valid sg (1 sp. [2,3])	*Canthon sordidus* Harold, 1868, by original designation
	Francmonrosia	Pereira & Martínez	Valid sg (6 spp. [2,3,16,17])	*Canthon rutilans* Castelnau, 1840, by original designation
1960	*Vulcanocanthon*	Pereira & Martínez	Valid (1 sp. [2,3])	*Canthon seminulum* Harold, 1867, by original designation
1964	*Pseudoepirinus*	Ferreira	Junior subjetive synonym of *Scybalophagus* (Scholtz & Howden, 1987)	*Epirinus zumpti* Frey, 1963, by original monotypy
1966	*Antillacanthon*	Vulcano & Pereira	Junior subjective synonym of *Canthochilum* (Matthews, 1969)	*Canthon histeroides* Harold, 1868, by original designation
	Chapincanthon	Vulcano & Pereira	Junior subjective synonym of *Canthochilum* (Matthews, 1969)	*Canthochilum hisp.idum* Chapin, 1935, by original designation
1977	*Hansreia*	Halffter & Martínez	Valid (6 spp. [12])	*Canthon affinis* Fabricius, 1801, by original designation
	Sylvicanthon	Halffter & Martínez	Valid (15 spp. [17])	*Canthon candezei* Harold, 1868, by original designation
2002	*Paracryptocanthon*	Howden & Cook	Valid (2 sp. [3, 13])	*Cryptocanthon borgmeieri* Vulcano *et al*, 1976, by original designation

[1] Paulian (1938) included the four genus names in his "Canthonides" identification key, but by not fixing a type species for them, he did not make them available (Article 13.3, ICZN [1999]); it was only the following year that Paulian (1939) complied with the provisions of the Code. [2] Halffter & Martínez (1977). [3] Schoolmeesters (2017). [4] Halffter & Martínez (1968). [5] Ratcliffe & Smith (1999). [6] Ivie & Philips (2008). [7] Vaz-de-Mello (2007a). [8] Philips & Ivie (2008). [9] Cook (2002). [10] Arias & Medina (2014). [11] Ocampo & Molano (2011). [12] Valois et al. (2015). [13] Pacheco & Vaz-de-Mello (2017). [14] Vaz-de-Mello & Silva (2017). [15] Nunes et al. (2018). [16] Vaz-de-Mello & Cupello (2018). [17] Results of the present work.

very broad external margin (Figs 21–22); tarsal claws with a very rudimentary basal angle (Fig. 10); protibiae with two or three teeth and with internal margin expanded or straight (Figs 33–42); second metatarsomere equal to or longer than basal tarsomere; metafemur margined anteriorly on its ventral face (posterior margin present or not) (Figs 46–53, 114–115); elytra without scutellar depression and with very narrow, usually ill-delimited striae of variable number; pygidium and propygidium separated by a very fine, medially angulate carina.

Etymology

Masculine, from the Latin word '*silva*', meaning forest (Brown 1956), and the Greek '*canthon*', an insect name (Harold 1869b; Pereira & Martínez 1959). Although this was not explicitly stated by them, it is likely that Halffter & Martínez (1977) chose this name inspired by the fact that species of *Sylvicanthon* are typical inhabitants of New World tropical rainforests.

Redescription

HEAD. Clypeus with two tiny apical, obtuse or slightly acute teeth without emargination between them (Fig. 6B–G; group *candezei*) or with four large, acute teeth also without emargination between them (Fig. 6A; group *enkerlini*); a single row of setae covering teeth's base (except in *S. securus*, which has an individual row of setae for each tooth); apical margin of clypeus clearly or only slightly bent upwards. Genae with strong or rudimentary tooth after junction with clypeus (Fig. 6). Clypeo-genal suture complete, fine and well impressed; fronto-clypeal suture indistinct in the middle and present only on the sides. Dorsal portion of eyes large – interocular distance four times the largest width of eyes – and without internal margin. Posterior edge of head with or without a margin between the eyes. Tegument of dorsal region of head varying from smooth or with evident micropunctation to strong three-dimensional alveolar microsculpture obliterating micropunctation. Maxilary and labial palps with three palpomeres.

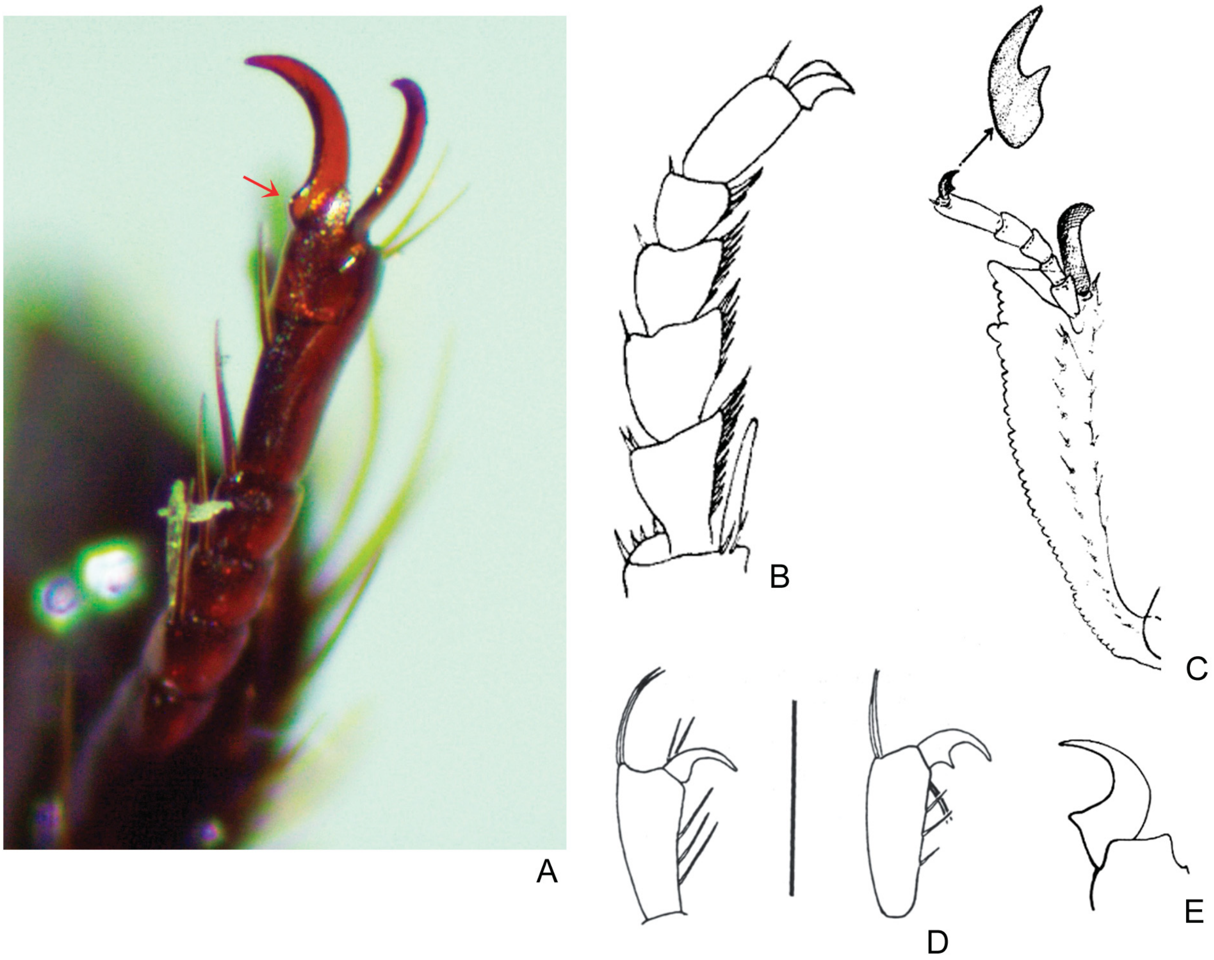

Fig. 5. Subdentate tarsal claws in different groups of dung beetles. The presence of this form of tarsal claw was seen as evidence for a close phylogenetic relationship between several groups of Scarabaeinae distributed over the continents of former Gondwana. **A**. Protarsal claws of *Sylvicanthon proseni* (Martínez, 1949) stat. et comb. nov. Red arrow indicates the basal agularity of the claw. **B**. *Pseudocanthon vitraci* (Fleutiaux & Sallé, 1889) (modified from Matthews 1966). **C**. *Canthonella parva* (Chapin, 1930) (modified from Halffter & Martínez 1967). **D**. *Lepanus penelopae* Matthews & Weir, 2002 (left) and *L. loftyensis* Matthews & Weir, 2002 (right) (modified from Matthews & Weir 2002). **E**. *Oficanthon mirabilis* Paulian, 1985 (modified from Paulian 1985).

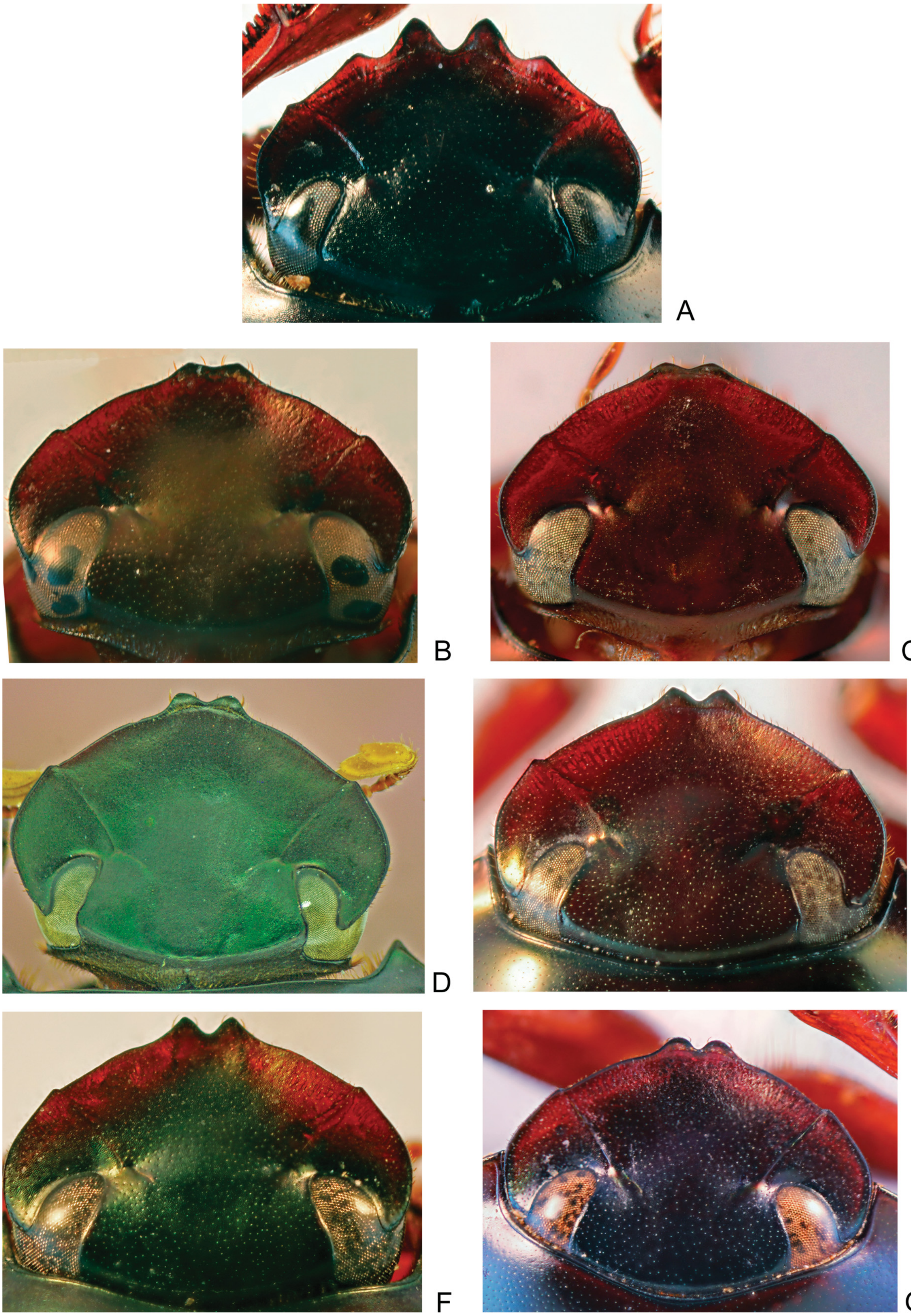

Fig. 6. Head, dorsal view. **A**. *Sylvicanthon enkerlini* (Martínez *et al.*, 1964) comb. nov. **B**. *S. candezei* (Harold, 1869). **C**. *S. genieri* sp. nov. **D**. *S. proseni* (Martínez, 1949) stat. et comb. nov. **E**. *S. seag* sp. nov. **F**. *S. securus* (Schmidt, 1920) comb. nov. **G**. *S. furvus* (Schmidt, 1920).

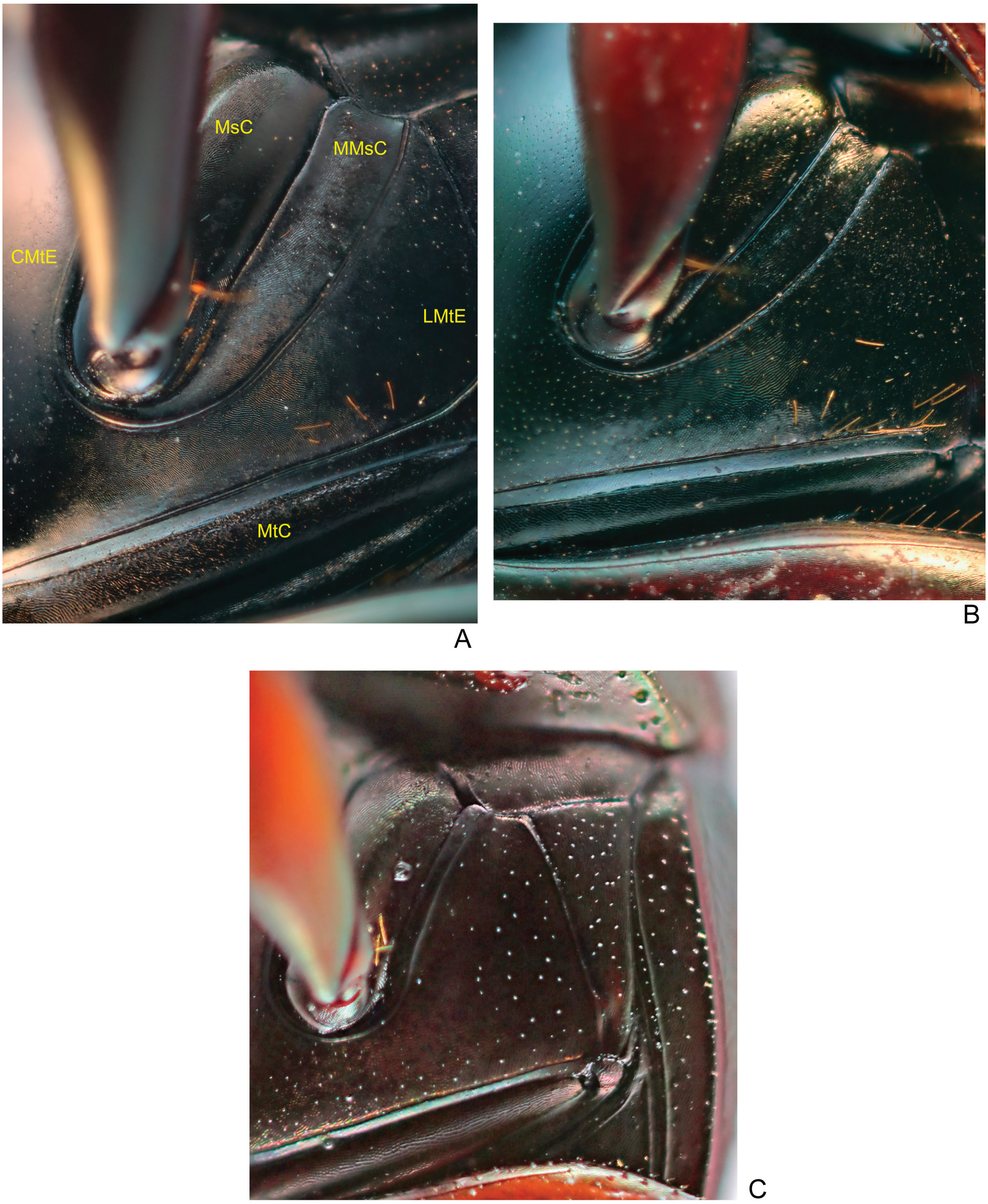

Fig. 7. Pterothorax, ventrolateral views. **A**. *Sylvicanthon aequinoctialis* (Harold, 1868) comb. nov. **B**. *S. obscurus* (Schmidt, 1920). **C**. *Canthon xanthopus* Blanchard, 1846. Abbreviations: MsC = mesocoxa; MMsC = external margin of mesocoxa; CMtE = centre of metaventrite; LMtE = lateral region of metaventrite; MtC = metacoxa.

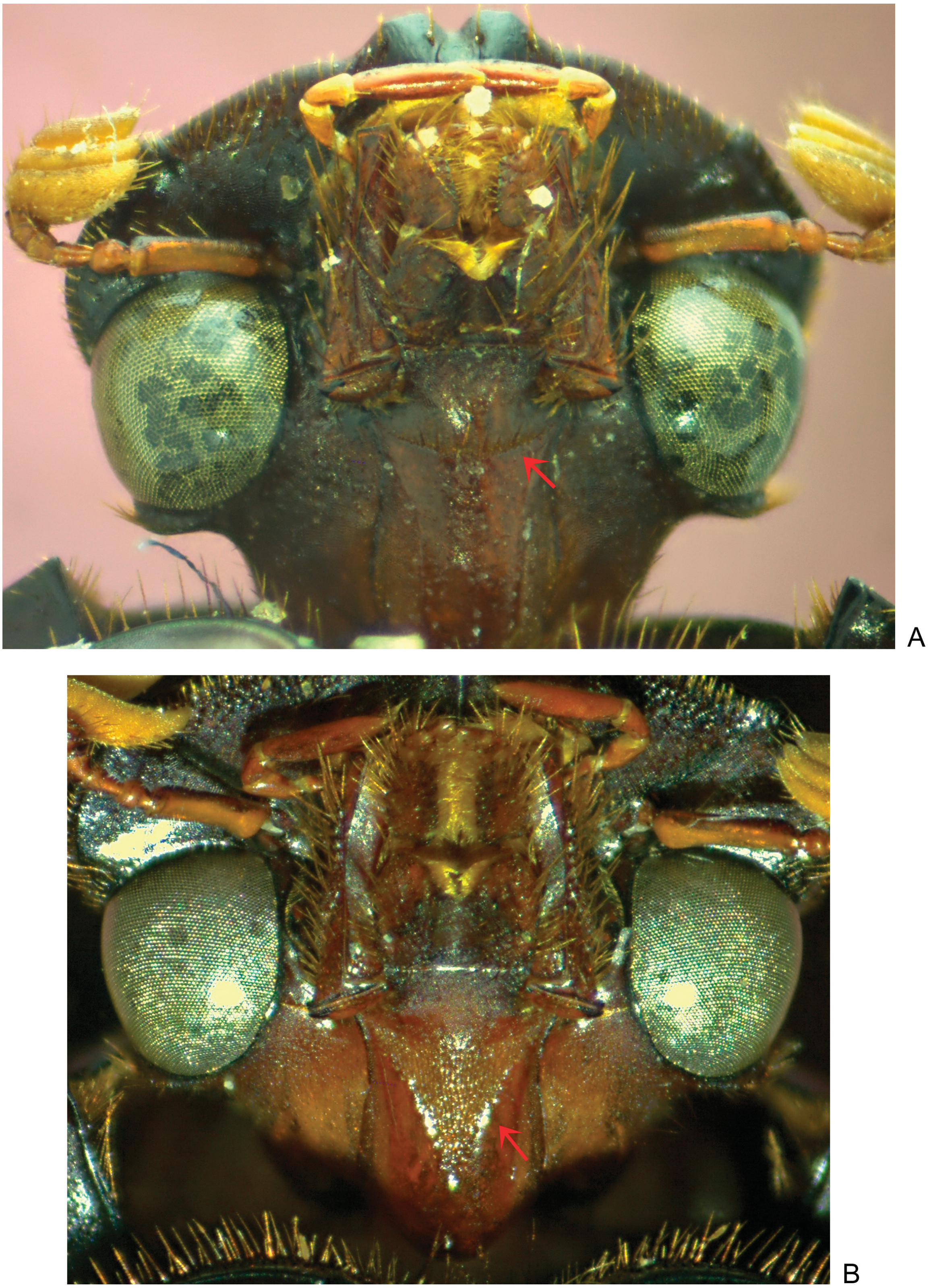

Fig. 8. Head, ventral view. **A**. *Sylvicanthon bridarollii* (Martínez, 1949). **B**. *S. proseni* (Martínez, 1949) stat. et comb. nov. See the differences in the shape of the suture between submentum and gula in these two species (red arrows), which is rounded in *S. bridarollii* and most of the other species of *Sylvicanthon*, while it has a 'Y'-shape in the two representants of the *aequinoctialis* subgroup.

Labium distinctly 'U'-emarginate on its anterior edge (Fig. 8). Suture between mentum and submentum rounded (Fig. 8b) or in a deep 'Y' shape (Fig. 8a).

Thorax. Pronotum margined only anteriorly and laterally, with lateral edges strongly angulated in the middle; posterior edge unmargined and, in most of the species, with a fine transverse line at the centre (usually, extending up to second elytral stria); tegument ranging from smooth, bright and with strong micropunctation to with strong three-dimensional alveolar microsculpture, diffuse shinning and obliterate micropunctation; lateral fossae and prescutellar depression absent. Hypomera divised into two parts by a complete transversal hypomeral carina; anterior part strongly excavated and delimited posteriorly by a low vertical wall; tegument with strong rivose microsculpture, glabrous at centre (Fig. 35A–B) or covered by long and dense erect yellow setae (Fig. 35C–D); external edge, in general, with a tiny tubercle or, sometimes, simple, without tubercle; posterior part with tegument strongly microsculptured; entirely glabrous (group *candezei*) or with a few long, individual setae aligned longitudinally close to external edge (Fig. 9D; group *enkerlini*). Mesepimeron, metepisternum and prosternum glabrous and with microsculptured tegument. Mesoventrite very short and horizontal (Fig. 14A); in the middle, with a triangular projection towards body's anterior region which has a very shallow fovea in its centre (in

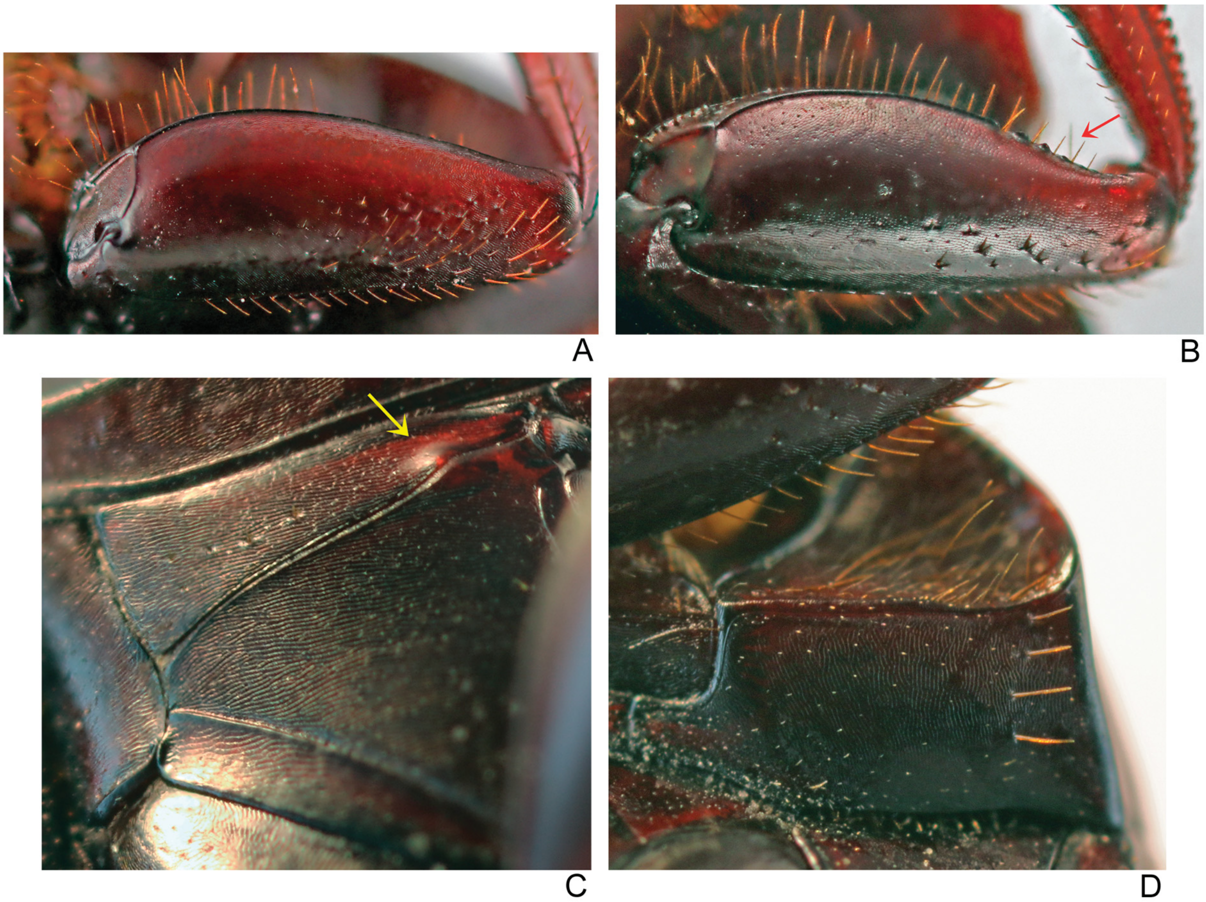

Fig. 9. A. *Sylvicanthon bridarollii* (Martínez, 1949), profemur. Note that, as occurs in the other species of the *candezei* group, there is no denticulation on the anterior edge, which is, by contrast, completely smooth. **B**. *S. enkerlini* (Martínez *et al.*, 1964) comb. nov., profemur. Arrow indicates the denticulation of anterior edge, a condition present in both sexes and unique in the genus. **C**. *S. enkerlini*, metepisternum. Arrow indicates the small tubercle at the suture between metepisternum and the lateral region of metaventrite. **D**. *S. enkerlini*, hypomeron. Notice the row of long setae present on the lateral of posterior region, a condition seen uniquely in this species in *Sylvicanthon*.

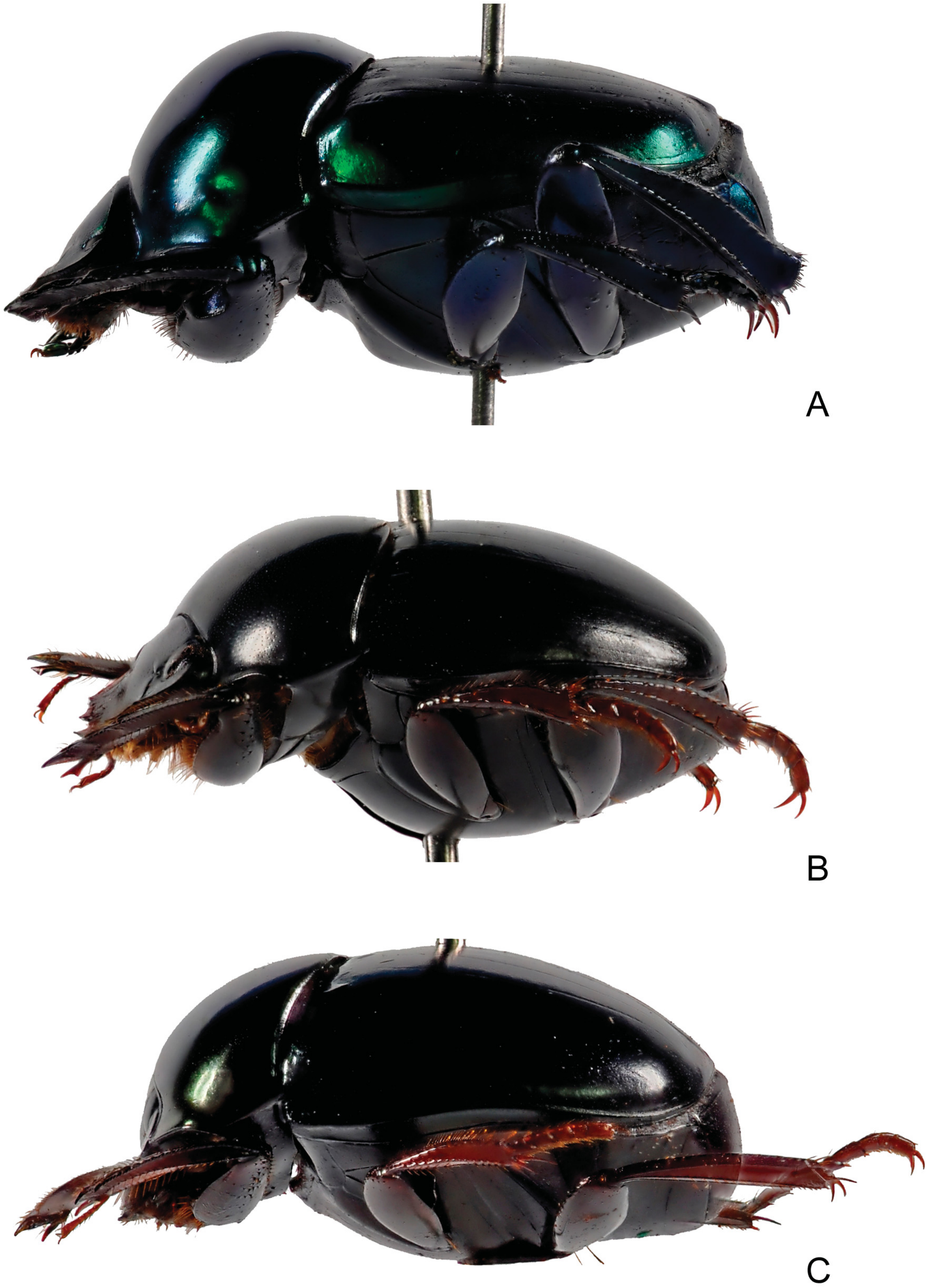

Fig. 10. Lateral view. **A**. *Canthon* (*Francmonrosia*) sp. **B**. *Sylvicanthon enkerlini* (Martínez *et al.*, 1964) comb. nov. **C**. *S. candezei* (Harold, 1869).

general, projection covered by prosternum in pinned specimens); tegument with micropunctation and with a transverse row of very short setae. Meso-metaventrite margin very fine and straight. Metaventrite very wide between mesocoxae and slightly convex; tegument with strong rivose microsculpture on the sides and on anterior region between mesocoxae; at centre, tegument ranging from microsculpture absent to well-marked micropunctation to strong three-dimensional alveolar microsculpture with discrete micropunctation.

LEGS. Tarsal claws of all legs slightly angulate at base (more clearly so in protarsi, Fig. 5A). Profemora with tegument always covered by microsculpture (rivose or alveolar); anterior margin, at apex of

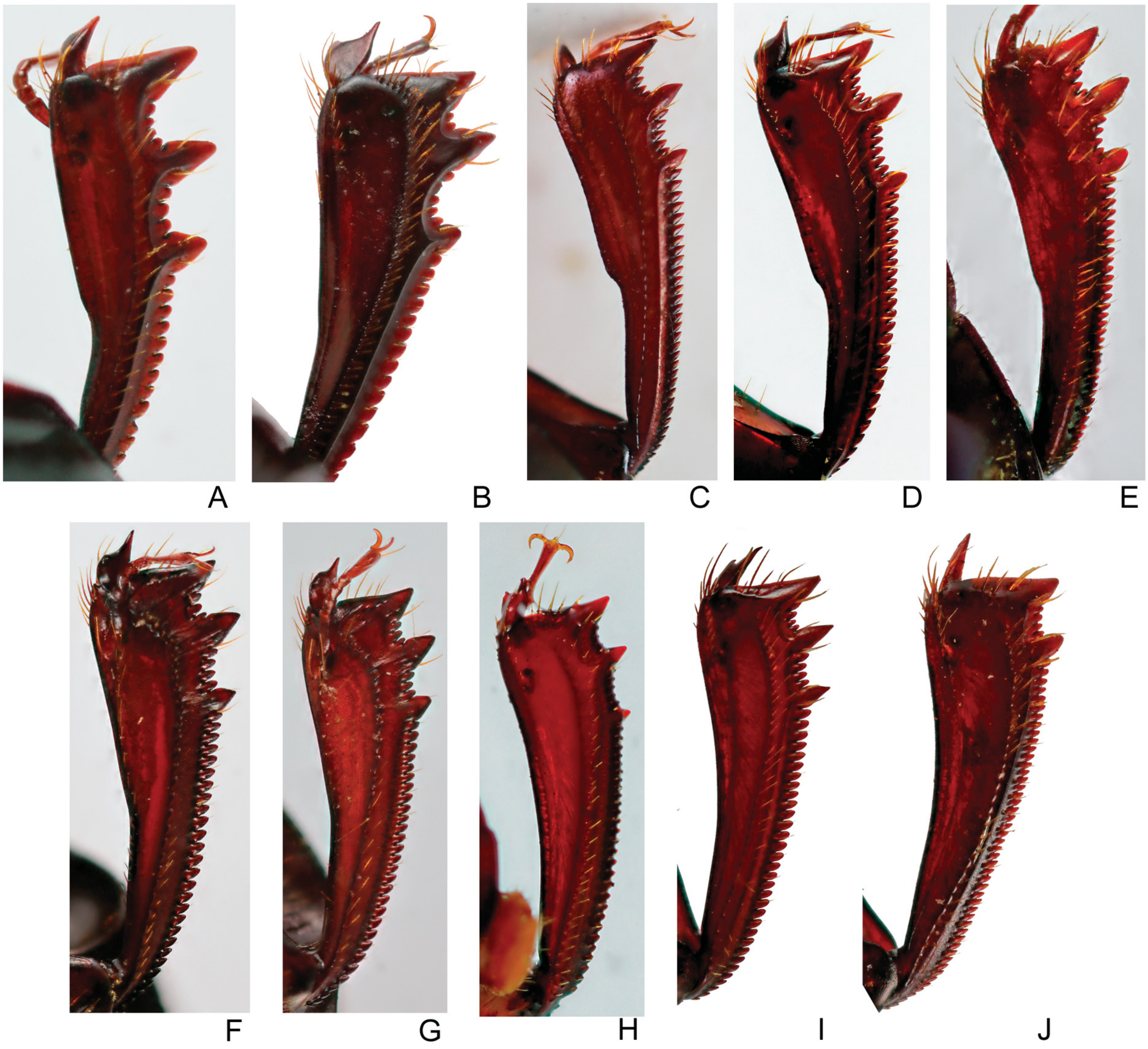

Fig. 11. Morphological diversity in the protibiae of *Sylvicanthon* Halffter & Martínez, 1977. **A**. *S. enkerlini* (Martínez *et al.*, 1964) comb. nov. **B**. *S. aequinoctialis* (Harold, 1869) comb. nov. **C**. *S. securus* (Schmidt, 1920) comb. nov. **D**. *S. obscurus* (Schmidt, 1920). **E**. *S. furvus* (Schmidt, 1920). **F**. *S. bridarollii* (Martínez, 1949) (southern populations). **G**. *S. bridarollii* (northern populations). **H**. *S. attenboroughi* sp. nov. **I**. *S. edmondsi* sp. nov. **J**. *S. candezei* (Harold, 1869). Note the variation related to the presence and degree of development of an expansion on the internal edge of protibiae and to the number, size and position of the external teeth.

profemora, smooth (Fig. 9A; group *candezei*) or with a row of denticules in both sexes (Fig. 9B; group *enkerlini*). Protibiae truncate at apex, narrow or wide, and with internal margin straight or strongly expanded at its apical half; with two or three teeth on external margin varying in size from large, wide, and well separated from one another to small, narrow, and restricted to apical third of protibiae; external edge of protibiae covered by smaller denticules, including area between larger teeth (Fig. 11). Dorsal face of protibiae with four longitudinal lines: the most external one very fine, entirely glabrous and, in general, indistinct at the apical expansion; the second most internal one covered by a row of short setae only at its apex; the third one covered by longer setae from its base to apex; the fourth line (the most external one) strongly carinate, entirely glabrous and interrupted at the basal lateral teeth. Ventral surface of protibiae with two longitudinal lines, one parallel to the internal edge and the other at the middle, both interrupted by setae; the latter line keeled at its basal half. Protarsi with five tarsomeres; basal and apical tarsomeres at least as long as tarsomeres II–IV combined. Mesocoxal cavities with wide external margin (Fig. 7A–B) and narrow internal margin. Meso- and metatrochanters with a fine tuft of long yellowish setae turned back at their posterior edges. Meso- and metafemora very flattened. Mesofemora margined

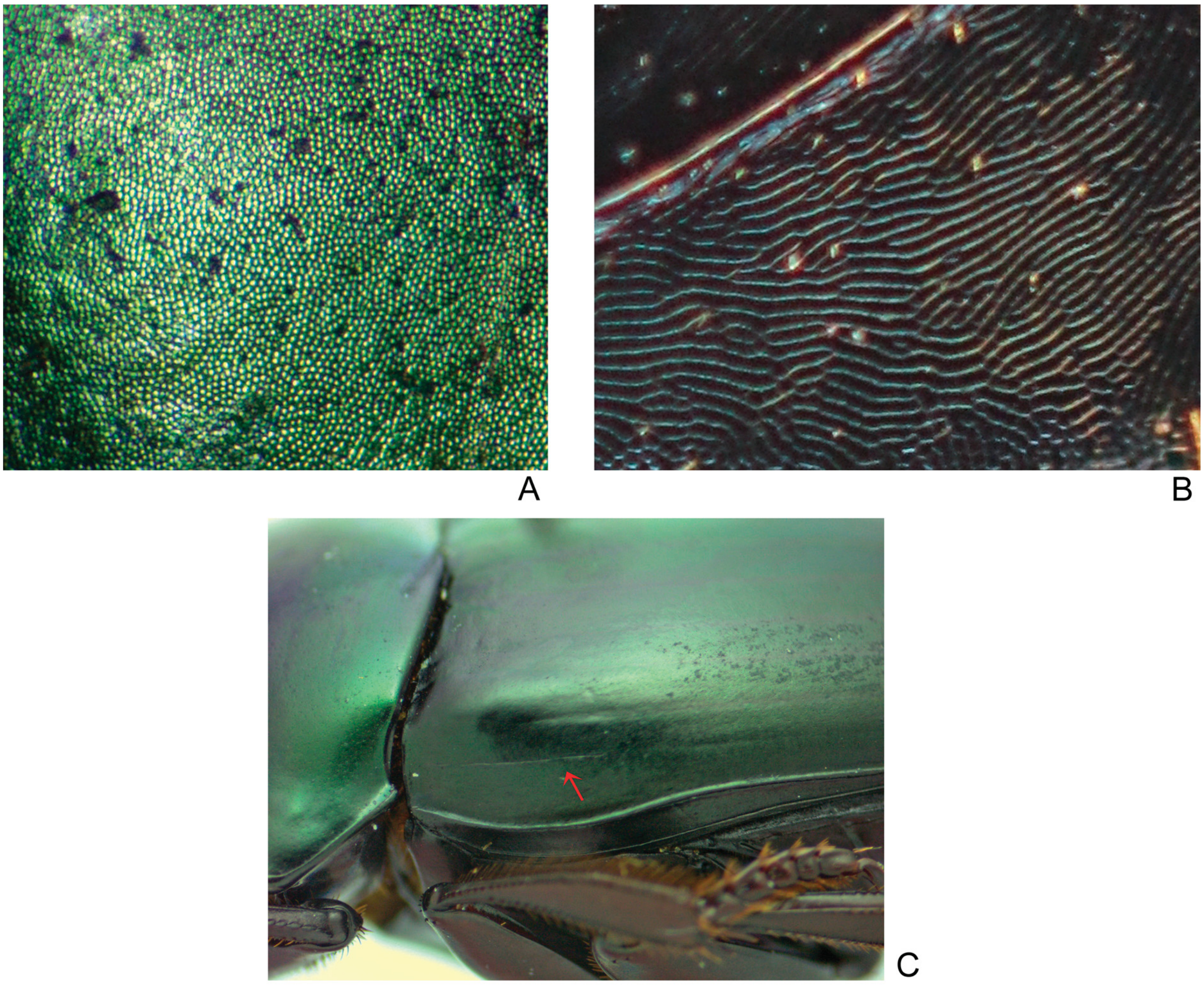

Fig. 12. Tegument variation in *Sylvicanthon* Halffter & Martínez, 1977. **A**. Tridimensional alveolar microsculpture of the elytra in *S. proseni* (Martínez, 1949) stat. et comb. nov.. **B**. Rivose microsculpture on the external side of metaventrite in *S. obscurus* (Schmidt, 1920). **C**. *S. proseni* stat. et comb. nov., humeral carina, feature present also in *S. aequinoctialis* (Harold, 1869) and in about two-fifths of the studied specimens of *S. obscurus* (Schmidt, 1920).

anteriorly at its basal two thirds; non-margined area with a row of very short setae; posterior margin absent. Metafemora with ventral face always margined anteriorly (Fig. 13), posterior margin present only in the *aequinoctialis* subgroup (Fig. 114–115); apical half of anterior edge covered by row of setae; micropunctation present throughout the tegument; at base, with or without coarse elongate punctation. Metatibiae curved, metatibial spur straight. Meso- and metatarsi flattened. Metatarsomeres II and V subequal in length and longer than the other tarsomeres; metatarsomere IV shorter than the others; meso- and metatarsi with a continuous row of setae throughout its internal edge.

ELYTRA. Scutellar depression absent. With nine to seven visible striae; from elytral suture, striae progressively more effaced; humeral carina present (Fig. 12C) or not. Tegument of interstriae ranging from smooth with evident micropunctation to with strong three-dimensional alveolar microsculpture

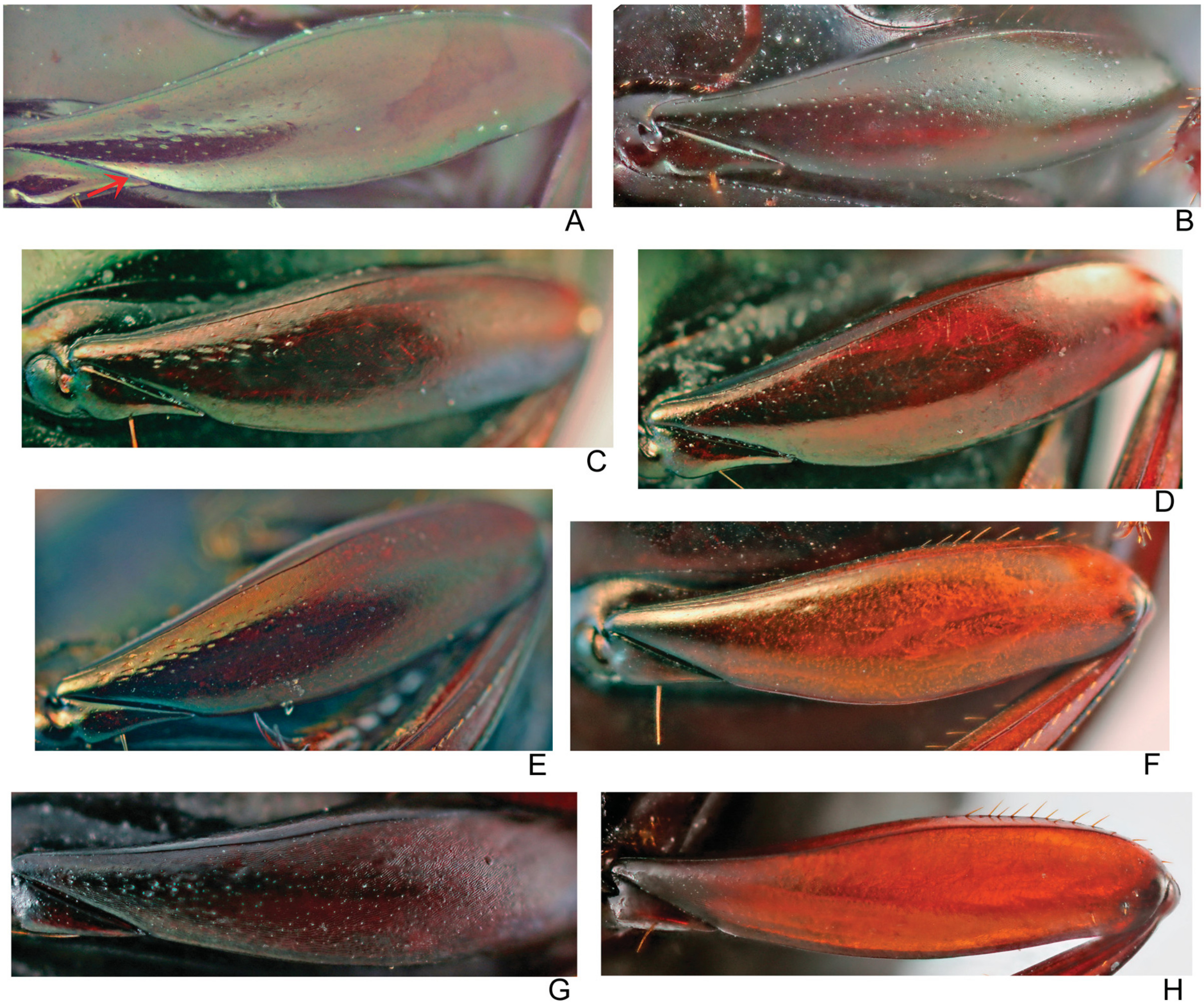

Fig. 13. Morphological variation in the metafemora of *Sylvicanthon* Halffter & Martínez, 1977. **A**. *S. foveiventris* (Schmidt, 1920). Note the presence of coarse elongate punctures at the base of the metafemur (arrow) and the tegument without microsculpture. **B**. *S. obscurus* (Schmidt, 1920). Observe the tegument entirely covered by coarse non-elongate punctures. **C**. *S. monnei* sp. nov. **D**. *S. mayri* sp. nov. **E**. *S. furvus* (Schmidt, 1920). **F**. *S. edmondsi* sp. nov. **G**. *S. bridarollii* (Martínez, 1949) (southern populations). **H**. *S. bridarollii* (Martínez, 1949) (northern populations). Note the differences in colouration and in the presence of coarse punctation at the base of metafemur in the two ends of the clinal variation observed in *S. bridarollii*.

obliterating micropunctation. Epipleural carina well marked; epipleura slightly sinuous, almost straight, in lateral view, and with tegument with strong rivose microsculpture.

Abdomen. Six visible abdominal segments (ventrites); tegument of ventrites I–V with strong rivose microsculpture; ventrite VI with very diffuse rivose microsculpture at middle and more clearly marked on the sides; micropunctation absent or very subtle. Pygidium curvilinear, subtriangular and at least slightly convex in both sexes; entirely margined, apical margin much wider than lateral margin in both sexes (usually wider in males); margin between pygidium and propygidium arched; tegument with alveolar microsculpture always present, but ranging from strong to diffuse.

Aedeagus. Parameres shorter or as long as phallobase and very variable in shape, with external faces symmetrical or asymmetrical; when asymmetrical, external face of right paramere flat and external face of left paramere concave. In lateral view, parameres with or without ventral keel or notch and with simple or bifurcate apices. Basal piece of phallobase always with depressed dorsal area.

Sexual dimorphism. **Males**: Protibial spur (Fig. 15) narrow or wide, apex with a profound notch or straight with two lateral spines of unequal length. Ventrite VI strongly narrowed at middle by emargination on its posterior edge (Fig. 14D); anterior margin covered by weak medial expansion of ventrite V, or ventrite V without medial expansion. Abdomen without lateral foveae. **Females**: Protibial spur spiniform (Fig. 15F) (except in *S. proseni*, whose spur is bifid, Fig. 15H). Ventrite VI very wide at middle, posterior edge straight, without emargination (Fig. 14B–C, E); anterior margin distinctly covered by medial expansion on the posterior margin of ventrite V, or ventrite V without medial expansion. Abdomen with or without three pairs of lateral foveae between ventrites I–II, II–III and III–IV (Fig. 74–77).

Taxonomic history of *Sylvicanthon*

The first species of what was to become *Sylvicanthon* was described by Harold (1868a) in his landmark revision of the genus *Canthon*, namely *C. aequinoctialis* Harold, 1868, from "*Columbien, Neu-Granada*". In the following year, Harold (1869a) described two other new species for the genus, including *Canthon candezei* Harold, 1869, from "*Tapajos*", Pará, Brazil, another species currently included in *Sylvicanthon*.

The next author to describe species of *Sylvicanthon* was Schmidt (1920), in his first paper on *Canthon*. There, he presented *Canthon furvus*, from "*Peru, Bolivien*"; *C. securus*, from "S*urinam*"; and *C. obscurus* and *C. foveiventris*, both from "*Espirito Santo*". After having described them, Schmidt (1920) asserted that they were close to *C. candezei* and that, besides colour, those five species were similar in their oval body shape and by the presence of protibiae with a truncate apex and small, apical lateral teeth, clypeus with only two tiny teeth, large eyes, hypomeron with a transverse carina (wrongly cited as "*Prosternum*", common misunderstanding among old works on Scarabaeinae, as firstly noted by Halffter 1958, 1961, but who, in turn, misinterpreted them as being the propleura) and metafemora with anterior margin. Finally, Schmidt (1920) proposed a key to differentiate those five species. It is worth noting that this group and its unique character combination was an early draft of what would eventually be proposed as the genus *Sylvicanthon*.

As explained above, in his second work on the genus, Schmidt (1922) updated Harold's key to the species of *Canthon* and, there, he grouped *C. aequinoctialis* with *C. candezei* and the four species he had described in 1920 under the following steps: 2. Metatibiae with a single spur; 3. Clypeus with teeth; 10. Dorsum, excepting scutellar impression, without elevations or depressions; 26. Large eyes, i.e., space between eyes only five times larger than the diameter of each eye; 27. Clypeus with two teeth; 30. Pygidium with an angulate margin; 31. Protibiae with truncate apex, prosternum [*sic*] with a complete transverse carina and with external margin with a nodule or a very weak tooth. In the following couplet, he grouped *C. obscurus* and *C. aequinoctialis* by the presence of a humeral carina, on the one side, and

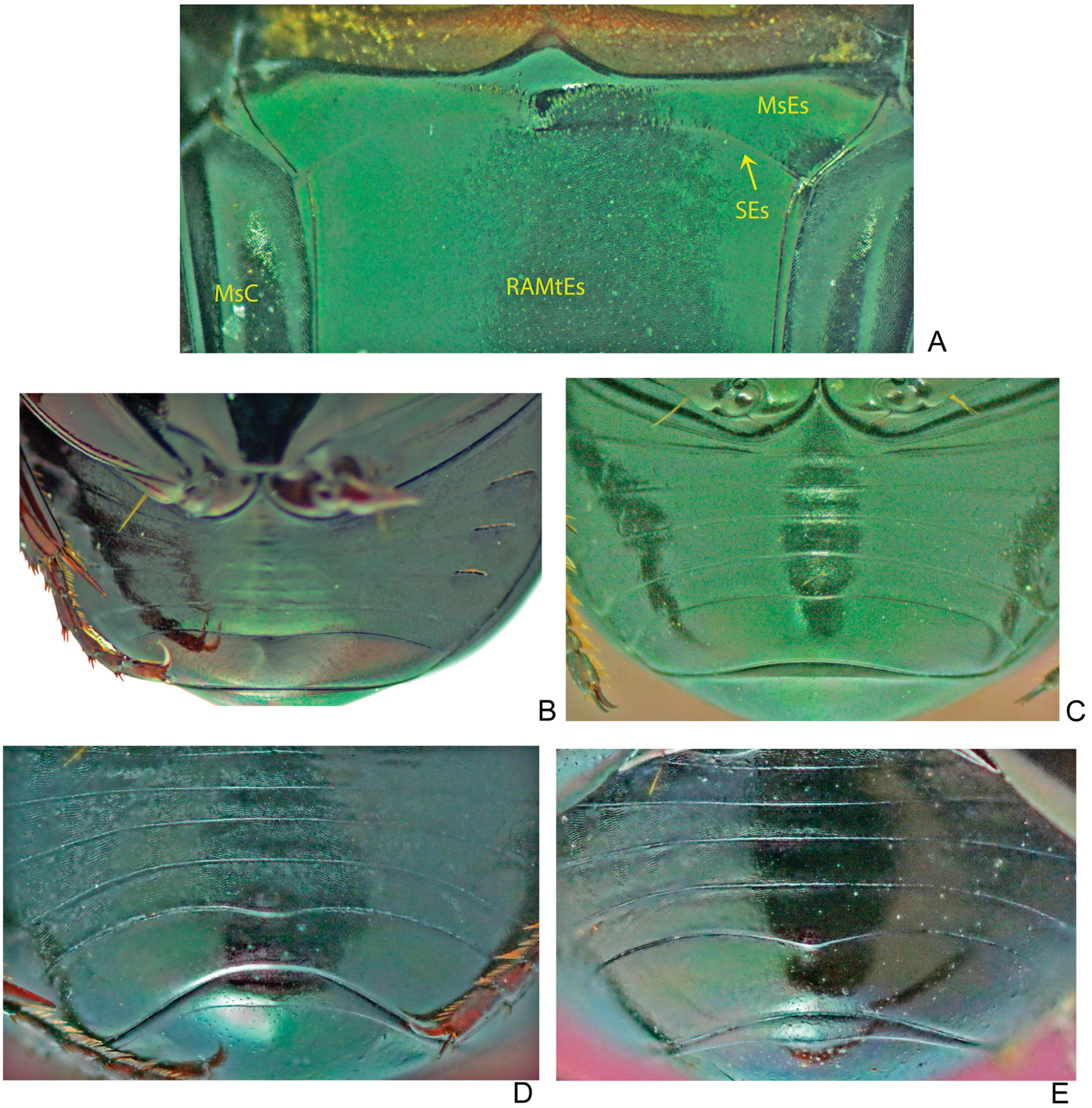

Fig. 14. A. Ventral view of the anterior region of the pterothorax of *S. proseni* (Martínez, 1949) stat. et comb. nov. Abbreviations: MsEs = mesoventrite; SEs = meso-metaventrite suture; MsC = mesocoxa; RAMtEs = anterior region of metaventrite. **B–E**. Sexual dimorphism in the abdominal ventrites of *Sylvicanthon* Halffter & Martínez, 1977. **B**. *S. foveiventris* (Schmidt, 1920), ♀. Note the three lateral foveae between ventrites I–II, II–III, and III–IV and the broad ventrite VI at the middle, without emargination on its posterior edge and without its anterior edge covered by a medial flange of ventrite V. **C**. *S. proseni* stat. et comb. nov., ♀, ventrite VI broad. **D**. *S. candezei* (Harold, 1869), ♂. Note how the ventrite VI is narrow at the middle due to the emargination on its porterior edge and to the medial flage of the posterior edge of the ventrite V. **E**. *S. candezei* (Harold, 1869), ♀. Despite its posterior edge not being emarginate, its anterior edge is covered by a well-developed medial flange of ventrite V, which gives a narrowed aspect to the centre of ventrite VI.

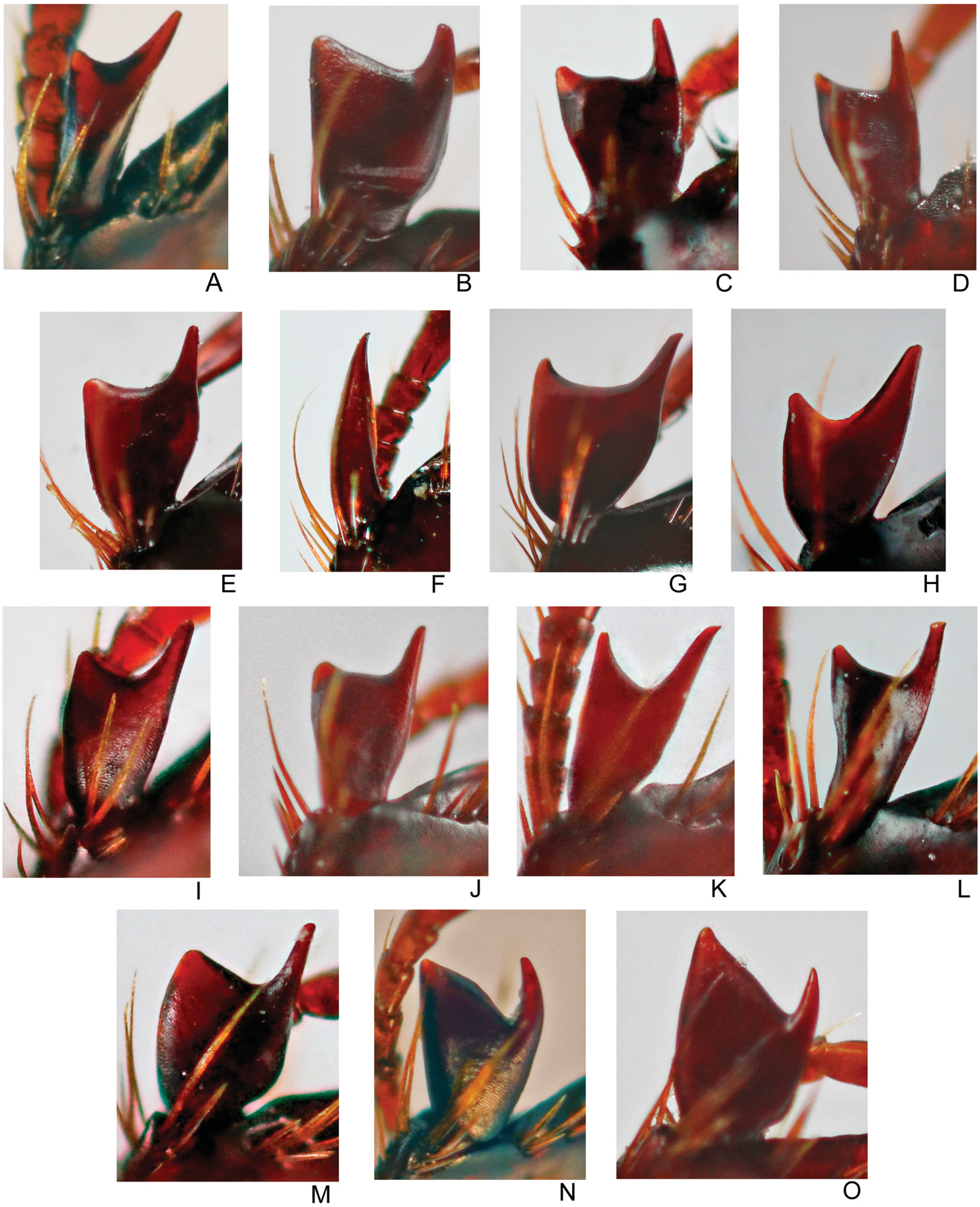

Fig. 15. Morphological variation and sexual dimorphism in the protibial spur of *Sylvicanthon*. **A**. *S. enkerlini* (Martínez *et al.*, 1964) comb. nov., ♂. **B**. *S. foveiventris* (Schmidt, 1920), ♂. **C**. *S. candezei* (Harold, 1869), ♂. **D**. *S. genieri* sp. nov., ♂. **E**. *S. aequinoctialis* (Harold, 1868), ♂. **F**. *S. aequinoctialis* comb. nov., ♀. **G**. *S. proseni* (Martínez, 1949) stat. et comb. nov., ♂. **H**. *S. proseni* stat. et comb. nov., ♀. **I**. *S. bridarollii* (Martínez, 1949), ♂. **J**. *S. seag* sp. nov., ♂. **K**. *S. edmondsi* sp. nov., ♂. **L**. *S. attenboroughi* sp. nov., ♂. **M**. *S. obscurus* (Schmidt, 1920), ♂. **N**. *S. furvus* (Schmidt, 1920), ♂. **O**. *S. securus* (Schmidt, 1920) comb. nov., ♂.

C. furvus, *C. securus*, *C. foveiventris* and *C. candezei* by its absence, on the other; next, the presence of a protibial internal expansion joins *C. furvus* with *C. securus*, while its absence groups *C. candezei* and *C. foveiventris*. The steps leading to the group of five species that was to form *Sylvicanthon*, as well as those differentiating them, remained almost unchanged in the updated version of Schmidt's key by Balthasar (1939).

Already during that 'Latin-American phase' of taxonomic activity on '*Canthon* sensu lato' exposed above, *Glaphyrocanthon*, a taxon described as an independent genus, but lowered to subgenus of *Canthon* by Halffter & Martínez (1977), shares much of its taxonomic history with *Sylvicanthon*. Martínez (1948a) described the genus to accommodate only two Venezuelan species, but the following year (Martínez 1949a), he added two new species from Bolivia: *G. bridarollii* Martínez, 1949, from the province of Chapare, department of Cochabamba, and *G. proseni* Martínez, 1949, from the province of Nor Yungas, department of La Paz. Regarding the first species, Martínez (1949a) stated it appeared to be closely related to *Canthon foveiventris*, a species that he believed should be transferred to *Glaphyrocanthon* ("*creo que deberá ser incluída en* Glaphyrocanthon"), while he asserted that *G. proseni* was close to *Canthon aequinoctialis*, another species that he supposed to be assignable to *Glaphyrocanthon*. Those transfers were formally proposed by Pereira & Martínez (1956), who, among several other transfers, positioned in *Glaphyrocanthon* the four species that Schmidt (1920, 1922) had grouped with *C. foveiventris* and *C. aequinoctialis* (i.e., *C. candezei*, *C. obscurus*, *C. furvus*, and *C. securus*) and presented an identification key to them. Soon after, Pereira & Martínez (1960) described *Glaphyrocanthon cobosi*, from the Cordillera province, Santa Cruz department, Bolivia, a species that was thought to be related to *G. obscurus*.

Martínez *et al.* (1964), in a review of *Glaphyrocanthon*, recognized four species assemblages in the genus: the *variabilis*, *juvencus* and *aequinoctialis* species groups, of the nominotypical subgenus, and the subgenus *Coprocanthon* Martínez, 1950. The *aequinoctialis* group corresponded to the assemblage composed of *C. candezei* and allied species proposed by Schmidt (1920, 1922), and differed from other *Glaphyrocanthon* in having the unique combination of large eyes and ventral surface of metafemora with a fine anterior margin. According to Martínez *et al.* (1964), that group was composed of *G. aequinoctialis*, *G. proseni*, *G. candezei*, *G. obscurus*, *G. foveiventris*, *G. securus*, *G. furvus*, *G. bridarollii*, *G. cobosi* and their new species *G. enkerlini*, from São Luis, Maranhão, Brazil. Three years later, Martínez & Pereira (1967) described a last species for the group, *G. machadoi*, an inhabitant of the 'brejos de altitude' (Caatinga moist-forest enclaves) of Serra Negra, Pernambuco, Brazil, and which was said to be closely related to *G. foveiventris* and *G. bridarollii*.

Halffter & Martínez (1977) then made major changes in the classification of '*Canthon* sensu lato'. In their work, *Glaphyrocanthon*, *Coprocanthon*, and *Geocanthon* Pereira & Martínez, 1956 were synonymized (the first name remaining valid) and the taxon was lowered to subgenus status under *Canthon*. The former *aequinoctialis* group, in particular, was totally dismembered and none of its species remained in *Glaphyrocanthon*: *G. enkerlini* was transferred to the *Canthon* subgenus *Francmonrosia* mainly because of its denticulate anterior edge of profemora (Fig. 9B) and protibiae with strong internal expansion (Fig. 11A), while *G. aequinoctialis* and *G. proseni* were synonymized and the species transferred to *Canthon* s. str. (both acts without any formal justification), where it remained isolated as the single member of the *aequinoctialis* lineage ("*línea aequinoctialis*").

Five species of the former *aequinoctialis* group, however, *G. candezei*, *G. furvus*, *G. bridarollii*, *G. machadoi* and *G. cobosi* (the latter considered by them a junior synonym of *Canthon xanthopus* Blanchard, 1846, name of unknown application by entomologists for more than a hundred years; see discussion below), remained grouped and were transferred to the new genus *Sylvicanthon*. This latter genus was said by Halffter & Martínez (1977) to be related to *Pseudocanthon* and *Vulcanocanthon* Pereira & Martínez, 1960, sharing with them the presumed absence of a fine margin on the posterior edge of their head. Those authors also presented a discussion on the differences between *Sylvicanthon* and *C. aequinoctialis* and the reason why, according to them, this species should not be part of that genus. Lastly, Halffter & Martínez (1977) also judged that the remaining three species of the former *aequinoctialis* group (*C. obscurus*, *C. foveiventris* and *C. securus*), judging from Schmidt's descriptions, would "very likely" be close to the species included by them in *Sylvicanthon*, but no formal transfer was proposed.

As the main goal of Halffter & Martínez (1997) was to reevaluate the supraspecific classification of '*Canthon* sensu lato', and not to make a detailed study of its alpha taxonomy, questions such as species redescriptions and distributions, as well as a new identification key, were not addressed by them. Therefore, as no other work has so far reevaluated the taxonomy of *Sylvicanthon*, our knowledge about its species was extremely fragmentary and sometimes simply incorrect.

As addressed several times throughout this work, the geographical distribution attributed to some species of *Sylvicanthon* was largely wrong (*S. candezei* is the best example), while the majority of the species were known only from their type locality (e.g., *S. securus*, *S. obscurus*, *S. furvus* and *S. enkerlini*). Besides, the species delimitation and identification were problematic, with as many as six different species identified in publications and collections under the same name (e.g., *S. bridarollii*, *S. edmondsi* sp. nov., *S. attenboroughi* sp. nov., *S. genieri* sp. nov., *S. seag* sp. nov. and *S. candezei*, all of them mingled under the name *S. bridarollii* or *S. candezei*) and with wrong synonymies (between the species now known as *Canthon xanthopus* and *C. cobosi*, and *S. aequinoctialis* and *S. proseni*). Finally, even the definition of *Sylvicanthon* had serious flaws as a consequence of character states believed to be universal in the genus not being found in some of its species (the most obvious being the absence of a fine margin on the posterior edge of the head), the inclusion of some species that clearly do not belong to the genus (*C. xanthopus*, *C. machadoi* and *C. cobosi*) and, at the same time, the exclusion of some species that are close to those belonging to *Sylvicanthon* (*S. aequinoctialis* comb. nov., *S. proseni* and *S. enkerlini*). The only modifications proposed to the taxonomy of *Sylvicanthon* since Halffter & Martínez (1977) were the "informal transfers" (or, as put by Sikes & Barclay 2017, "accidental" transfers; i.e., species cited in *Sylvicanthon* for the first time without the status of new combinations explicitly recognized) of *Canthon foveiventris* (by Vaz-de-Mello & Louzada 1997) and *C. obscurus* (by Vaz-de-Mello 2000), following the conjectures of Halffter & Martínez (1977) that those species belonged to *Sylvicanthon*.

Phylogenetic relationships of *Sylvicanthon*

Halffter & Martínez (1977) included *Sylvicanthon* among the Canthonina, considered by them as one of the six subtribes of Scarabaeini (see Halffter & Martínez (1966) for a deeper discussion about the positioning of Canthonina). In more modern classifications (e.g., Smith 2006; Scholtz *et al.* 2009; Bouchard *et al.* 2011; Tarasov & Génier 2015; Tarasov & Dimitrov 2016), this taxon is raised to the tribe category and renamed to its senior synonym Deltochilini (see Bouchard *et al.* 2011). Scarabaeini, in turn, is now composed of only a handful of African genera (see Forgie *et al.* 2005, 2006; Scholtz *et al.* 2009). Until very recently, Deltochilini comprised over 120 genera and 800 species that despite being distributed all over the world had their global distribution largely centred in the Gondwanian continents (Scholtz 2009; cited as Canthonini). Nevertheless, despite being widely considered as valid, successive phylogenetic analyses –being based either on morphological (e.g., Philips *et al.* 2004; Vaz-de-Mello 2007b; Tarasov & Génier 2015) or on molecular evidence (e.g., Ocampo & Hawks 2006; Monaghan *et al.* 2007; Sole & Scholtz 2010; Mlambo *et al.* 2013; Tarasov & Dimitrov 2016) – have shown that the tribe Deltochilini is not monophyletic, being instead composed of a large number of non-closely related lineages (Tarasov & Génier 2015; Tarasov & Dimitrov 2016; see also the extensive discussion about the phylogeny of Canthonini presented by Scholtz 2009). However, several of the New World taxa of Deltochilini, including the type genus *Deltochilum*, form together a recurring monophyletic group in most of those analyses.

In the studies of both Ocampo & Hawks (2006) and Monaghan *et al.* (2007), all the New World Deltochlini included in their analyses formed a single clade (species of the genera *Deltochilum*, *Scybalophagus* Martínez, 1953, *Malagoniella* Martínez, 1961, *Megathopa* Eschscholtz, 1822, *Eudinopus* Burmeister, 1840 and *Canthon*, in Ocampo & Hawks (2006), and of *Canthon*, *Scybalocanthon*, *Scybalophagus*, *Hansreia*, *Deltochilum*, *Eudinopus* and *Megathoposoma* Balthasar, 1939, in Monaghan *et al.* (2007)). Tarasov & Génier (2015), who included a much broader sample of genera, also recovered an exclusive New World Deltochilini clade, which had as members the genera *Anomiopus* Westwood, 1842, *Scatonomus*, *Scybalocanthon*, *Tetraechma*, *Hansreia*, *Canthon*, *Scybalophagus*, *Deltochilum*, *Malagoniella*, *Megathoposoma* and *Sylvicanthon*, and was referred to as Deltochilini sensu stricto by the authors. Other American genera of Deltochilini, however, appeared very distant from this clade, such as *Paracanthon*, *Zonocopris*, *Canthochilum* and *Cryptocanthon*. Previously, with a smaller number of genera, Vaz-de-Mello (2007b) had already obtained a very similar result to that of Tarasov & Génier (2015) concerning the American Deltochilini, with a clade composed of *Canthon*, *Sylvicanthon*, *Scatonomus* and *Anomiopus*, while genera like *Zonocopris*, *Canthonella*, *Paracryptocanthon* and *Cryptocanthon* appeared scattered among different branches of the tree. Finally, the molecular phylogeny of Tarasov & Dimitrov (2016) also recovered a monophyletic group composed exclusively of New Wold Deltochilini genera. Based both on the topology of the molecular (Tarasov & Dimitrov 2016) and morphological (Tarasov & Génier 2015) trees and on some diagnostic apormorphies found by Tarasov & Génier (2015), Tarasov & Dimitrov (2016) formally redefined Deltochilini to include only 22 American dung beetle genera, *Sylvicanthon* included among them; the other groups previously included in Deltochilini were regarded as *incertae sedis* in Scarabaeinae.

Despite the previously described similarities, the four analyses that included species of *Sylvicanthon* have found very distinct relationships for the genus among the Deltochilini. In the tree conceived by Medina *et al.* (2003), which had the goal of studying the phylogenetic relationships of what we are denominating as the '*Canthon* sensu lato', '*Sylvicanthon bridarollii*'[13] appeared forming a clade with *Canthon* (*Glaphyrocanthon*) *politus* Harold, 1868, species widely distributed in Central America and northern South America (Vulcano & Pereira 1964). That clade, in turn, appeared as a sister to the topology (*Anisocanthon villosus* (*C.* (*G.*) *luteicollis* (*C.* (*G.*) *femoralis* (*C.* (*G.*) *rubrescens* + *C.* (*G.*) *angustatus*)))), of which all the analysed *Glaphyrocanthon* and *Anisocanthon* were part. That group as a whole, called "node I" by Medina *et al.* (2003), was supported by three synapomorphies: anterior part of hypomeron (erroneously cited as "proepimeron") deeply excavated and glabrous, and posterior part of hypomeron (erroneously cited as "prosternon") glabrous in the area close to the border with pronotum. Interestingly enough, two of those three character states are variable among species of *Sylvicanthon*: the pilosity of the anterior part of hypomeron varies extensively in density from almost totally absent (e.g., *S. candezei* and *S. seag* sp. nov., Fig. 35A) to present with long and dense setae (e.g., *S. bridarollii*, Fig. 35C–D), while the posterior part of hypomeron is indeed glabrous in the *candezei* group, but has an ill-delimited row of setae parallel to the margin with the dorsal portion of pronotum in *S. enkerlini*, the single species of its group (Fig. 9D).

The other two phylogenetic analyses that included *Sylvicanthon* species – Vaz-de-Mello (2007b) and Tarasov & Génier (2015) – were not aimed at studying the particular relationships between the genera of '*Canthon* sensu lato' nor even that of the American Deltochilini, but, rather, they studied the phylogeny of the Ateuchini (Vaz-de-Mello 2007b) and the evolutionary history of the major lineages in Scarabaeinae (Tarasov & Génier 2015). As a natural consequence, their results are less informative as to the *Sylvicanthon* relationships than those of Medina *et al.* (2003).

As we have seen, much remains to be studied about the relationships between *Sylvicanthon* and the other groups of '*Canthon* sensu lato'. To reach a sound understanding of this issue, a greater number of species of *Sylvicanthon*, of different groups and subgroups, should be included in future phylogenetic analyses, as well as different representatives of Deltochilini, especially those taxa more similar in morphology to *Sylvicanthon*. Based on the comparative studies performed for this work (including several species still undescribed), the tentative hypothesis that we propose for testing by formal phylogenetic analyses is the following: among the Deltochilini sensu Tarasov & Dimitrov (2016), *Glaphyrocanthon* as considered today (i.e., sensu Halffter & Martínez 1977) should represent a large paraphylum composed of non-closely related lineages[14]. Within that paraphylum, a number of smaller genera with a uniform morphology – e.g., *Sylvicanthon* and *Pseudocanthon* – should be nested. These genera could form either a single clade within *Glaphyrocanthon*, or (which we believe is most likely) represent distinct lineages with independent origins within '*Glaphyrocanthon*'. If this latter hypothesis is retrieved in phylogenetic analyses, *Glaphyrocanthon* will need to be divided once again into different genera as it was in the past (*Coprocanthon* and *Geocanthon*, former genus/subgenus, were synonymized with *Glaphyrocanthon* by Halffter & Martínez 1977). Then, its limits will possibly be restricted to those of what Martínez *et al.* (1964) considered to be the *variabilis* species group of *Glaphyrocanthon*. In fact, this hypothesis has several similarities to the results of Medina *et al.* (2003), who obtained *Glaphyrocanthon* paraphyletic with one species of both *Sylvicanthon* and *Anisocanthon* nested within it; the major difference is that we do not include *Anisocanthon* among the possible members of this great 'clade *Glaphyrocanthon*'. It is also interesting to point out that in the phenogram presented by Kohlmann & Halffter (1990) for the American 'Canthonina', *Sylvicanthon* and *Glaphyrocanthon* appeared grouped by about 50% of similitude and isolated from the remainder '*Canthon* sensu lato', so revealing a close morphological connection between these two taxa.

A second hypothesis that has already been raised (FZVM, personal observations; Olivier Montreuil, personal communication to MC in June 2014) says that *Sylvicanthon* and some other '*Canthon* sensu lato' genera (especially *Pseudocanthon* and *Canthonella*) would be close to a group of genera of Gondwanian distribution formally placed in Deltochilini that are sometimes separated in a tribe by their own, Epilissini (e.g., d'Olsoufieff 1947; Lebis 1953; Montreuil 2008, 2010, 2011; Montreuil & Thery 2011, 2016; Montreuil & Viljanen 2011; Montreuil *et al.* 2014; Vaz-de-Mello *et al.* 2011b). Montreuil (2010) revalidated Epilissini from the synonymy with Canthonini (which, in turn, is today a junior synonym of Deltochilini) based on two main morphological features presented by those genera: protibiae truncate at apex and hypomeron strongly excavated anteriorly. These two characteristics, in fact, are seen in *Sylvicanthon* and in several other Neotropical deltochiline genera, including *Pseudocanthon* and some *Glaphyrocanthon*, hence indicating a possible close relationship between them and the Epilissini sensu Montreuil (2010). The overall shape of the meso- and metatarsi, which are strongly flattened ("foliaceous") and with tarsomeri slightly rectangular, is also very similar between *Sylvicanthon* and the Epilissini.

Although both hypotheses are not mutually exclusive – the 'clade *Glaphyrocanthon*' could be part of Epilissini, which would make Deltochilini sensu stricto as defined by Tarasov & Dimitrov (2016) polyphyletic – none of the phylogenetic analyses published so far supports a close relationship between either *Sylvicanthon* or *Glaphyrocanthon* with Epilissini nor that this tribe is monophyletic. In Tarasov & Génier (2015), for example, genera of Epilissini appeared scattered throughout the phylogeny. In that analysis, *Canthonella*, *Ochicanthon* Vaz-de-Mello, 1999 and *Epactoides* d'Olsoufieff, 1947 (all of them included in Epilissini) were clustered with *Tanzanolus* Scholtz & Howden, 1987 from Africa and which was not included among the Epilissini by Montreuil (2010), forming the sister clade of almost all the remainder Scarabaeinae. *Bohepilissus* Paulian, 1975 and *Tesserodoniella* Vaz-de-Mello & Halffter, 2006, in turn, the other two genera of Epilissini sensu Montreuil (2010) included in the analysis, were separated one from the other in distinct branches of the tree. In the molecular analysis of Monaghan *et al.* (2007) the scenario was no different: genera included in Epilissini such as *Arachnodes* Westwood, 1847, *Aleiantus* d'Olsoufieff, 1947 and *Paronthobium* Paulian, 1984 did not show any close relationship[15]. This panorama is repeated in every single phylogenetic analysis so far published.

Lastly, a third phylogenetic hypothesis also involving *Sylvicanthon* – which is inconsistent with the 'clade *Glaphyrocanthon*' hypothesis championed by us – is based mainly on the morphology of the tarsal claws. In the taxonomic discussion presented by Halffter & Martínez (1977) to distinguish *Sylvicanthon* among the Deltochilini, the authors stated that their new genus differed from *Pseudocanthon* by the form of their claws, which are simple in *Sylvicanthon*, while having a distinct basal angle in *Pseudocanthon*. However, we observed during our studies that this statement is not correct. All the species of *Sylvicanthon* have, in fact, a small angulosity at the base of their claws (more easily seen on protarsi, even though present in all legs) (Fig. 5A) which, despite the distinct contrast with the strong angulosity of *Pseudocanthon* (Fig. 5B), we interpret to be homologous to it and different only in size.

It is worth noting that a similar angulosity is present in an even larger size and moved towards the centre of the claw in other former deltochiline genera and, hence, in a more obvious way than in both *Pseudocanthon* and *Sylvicanthon*. Those genera are *Canthonella* (Fig. 5C) and *Ipselissus* d'Olsoufieff, 1935 from the New World; *Temnoplectron* Westwood, 1841 and *Sauvagesinella* Paulian, 1934 from Australasia; *Lepanus* Balthasar, 1966 (Fig. 5D) from the islands of Java, New Guinea and Australia; *Oficanthon* Paulian, 1985 (Fig. 5E) from New Guinea; and, to a lesser degree, *Nesovinsonia* Martínez & Pereira, 1959 from the island of Mauritius (Martínez & Pereira 1959; Halffter & Martínez 1967; Matthews 1974; Paulian 1985). Halffter & Martínez (1967) raised the hypothesis – which would be later favoured also by Matthews (1974) – that the presence of tarsal claws with a basal angle would be homologous among at least some of these taxa. Therefore, that feature would be evidence for the existence of an ancient lineage of a wide Gondwanian distribution represented nowadays by those relict genera.

Although not included in their discussion, *Sylvicanthon* and *Pseudocanthon* share all the main characteristics listed by Halffter & Martínez (1967) to support that hypothesis. Even though one could argue that the claw angulosity of *Sylvicanthon* is basal (rather than medial) and much shorter, it is possible to observe a clear, gradual transition between the extreme form seen, for example, in *Canthonella* (Fig. 5C), passing through the less-developed and closer-to-base forms of *Oficanthon* (Fig. 5E) and *Pseudocanthon* (Fig. 5B), and, finally, to *Sylvicanthon* (Fig. 5A), so indicating the possible homology between these structures. *Lepanus* alone shows this wide variation, as seen, for instance, in two Australian species described by Matthews & Weir (2002): *L. loftyensis*, with a long tooth displaced from the base of the claw, and *S. penelopae*, with a basal angulosity similar to that of *Sylvicanthon* (Fig. 5D). Interestingly enough, all these genera with toothed claws have the hypomeron strongly excavated anteriorly, one of the characteristics highlighted by Montreuil (2010) in his definition of the tribe Epilissini. Therefore, within the context of Montreuil's hypothesis, we could see the group proposed by Halffter & Martínez (1967) and Matthews (1974) as one of the internal branches of Epilissini and, in this way, several different lineages of this tribe would have been spread independently across Gondwana. Matthews (1974), for instance, supposed another Gondwanian lineage represented in the Americas by *Cryptocanthon* and *Canthochilum*, and by *Tesserodon* Hope, 1937 and *Ignambia* Heller, 1916 in Australasia, a hypothesis that was later expanded and discussed in further detail by Vaz-de-Mello & Halffter (2006).

Refinement of the phylogenetic placement of *Sylvicanthon* should be a task for future works. The three hypotheses discussed here – 'clade *Glaphyrocanthon*', tribe Epilissini, and the 'tarsal claw' hypothesis – are not entirely incompatible, but the scenario endorsed by us is that the first hypothesis is most likely correct and that the 'clade *Glaphyrocanthon*' is part of the Deltochilini sensu Tarasov & Dimitrov (2016). As the alpha taxonomy of *Glaphyrocanthon* is yet largely unknown and several species still await description, it is firstly necessary that this genus undergo a broad taxonomic revision before formal phylogenetic analyses are performed.

Limits of *Sylvicanthon* and morphological comparison with allied genera

As herein delimited, the genus *Sylvicanthon* is composed of a cohesive and easily identifiable group of species. The diagnosis offered above is very similar to the definition given by Schmidt (1920) to the group formed by *Canthon candezei* and his four new species (see 'Taxonomic history' above) and to that of the *aequinoctialis* group of *Glaphyrocanthon* sensu Martínez *et al*. (1964). Characteristics such as the presence of large eyes, metafemora with anterior margin, complete hypomeral carina, and excavated hypomeron had already been used by different authors for the delimitation of those groups, as well as by Halffter & Martínez (1977) in the original description of *Sylvicanthon*. These latter authors, however, considered the supposed absence of a fine margin on the posterior edge of the head as one of the features that would most readily diagnose *Sylvicanthon*. Nonetheless, we concluded instead that this character is neither suitable to mark the limits of *Sylvicanthon* nor to indicate its phylogenetic placement for two main reasons. Firstly, as recognized even by Halffter & Martínez (1977) themselves, head without posterior margin is a condition seen not only among the *Sylvicanthon*, but also in a number of other New World deltochiline genera, such as *Pseudocanthon*, *Vulcanocanthon* and some species of *Cryptocanthon* and *Anomiopus*. On the other hand, contrary to what was said by Halffter & Martínez (1977), the posterior margin is not absent in not all of the species originally included in *Sylvicanthon* by them. All the specimens of *Canthon machadoi* and *C. xanthopus* possess a complete posterior margin, whereas this characteristic is variable in *S. furvus* and *S. bridarollii*, from completely absent to marked only very finely and being interrupted. *Sylvicanthon candezei* is the only species originally included in *Sylvicanthon* by Halffter & Martínez (1977) of which we have not observed any specimen with at least a vague trace of a margin on the posterior edge of the head. This margin is absent or vestigial also in seven of the nine new species herein described or transferred to *Sylvicanthon* (*S. foveiventris*, *S. genieri* sp. nov., *S. seag* sp. nov., *S. edmondsi* sp. nov., *S. attenboroughi* sp. nov., *S. obscurus*, and *S. monnei* sp. nov.), while in two other species (*S. enkerlini* and *S. aequinoctialis*) this margin is always present and usually complete. In *S. proseni*, all the variation seen in the genus can be found: in a same population, specimens range from having a complete margin to those with a totally absent margin. Although there is a clear tendency for the posterior margin to be absent or atrophied in *Sylvicanthon*, this is a variable characteristic with very little taxonomic value or phylogenetic signal.

Genera with which *Sylvicanthon* can be sometimes confused are *Pseudocanthon*, *Glaphyrocanthon* and *Canthonella*, all of which share the excavated hypomeron, which is transversally divided by a complete hypomeral carina (incomplete in several species of *Glaphyrocanthon*). With *Pseudocanthon*, in particular, *Sylvicanthon* shares large eyes and the absence of prescutellar and scutellar impressions, but they can be easily distinguished from one another by the shape of the pronotum (with lateral edge forming a medial angle in *Sylvicanthon*, and lateral edges straight and subparallel in *Pseudocanthon*), shape of protibiae (with three large teeth and distinctly expanded at middle in *Pseudocanthon*, and with internal expansion or not and with two or three small apical teeth (*candezei* group) or three large teeth distributed through the apical half of protibiae (*enkerlini* group) in *Sylvicanthon*), and elytral pilosity (glabrous in *Sylvicanthon*, and covered by minute setae in *Pseudocanthon*), as well as the overall body shape, which is much shorter and flatter in *Sylvicanthon* than in *Pseudocanthon*. Number and shape of clypeal teeth also vary between the two taxa: in *Pseudocanthon*, there are always four acute teeth, the middle two larger than the lateral ones, and with base covered by a single row of short setae extending almost to genae. In *Sylvicanthon*, in turn, these characters vary widely between the two species groups. In the *candezei* group, there are two small teeth and the row of setae (which can be single or divided into two smaller fragments at the base of each tooth) hardly extends beyond the base of the teeth (Fig. 6B–G). In *S. enkerlini*, the single species of its group, an intermediate condition is seen: there are four large teeth similar to those of *Pseudocanthon*, but the row of setae is limited to the base of the teeth as in the other species of *Sylvicanthon* (Fig. 6A).

Canthonella, in turn, is readily differentiated from *Sylvicanthon* by tarsal claws with a strong basal tooth (while this tooth is very small in *Sylvicanthon*), shape of clypeal teeth and presence of a trochantofemoral pit on the front legs, while this latter feature is absent in *Sylvicanthon* (Vaz-de-Mello *et al.* 2011). *Glaphyrocanthon*, as already discussed, is probably paraphyletic and, hence, some of its species are more closely related to *Sylvicanthon* (and, consequently, share some apomorphies with this genus) than to other of their congeneric species. The set of species that today forms *Glaphyrocanthon* is similar to *Sylvicanthon*, among other characteristics cited throughout this work, by the shape of pronotum, whose lateral edges have a medial angulosity. Even so, *Glaphyrocanthon* can be easily differentiated from *Sylvicanthon* by having profemora lacking both the anterior and the posterior margins on its ventral surface (anterior margin always present in *Sylvicanthon*, posterior margin present or not), eyes with a very narrow dorsal portion (wide in *Sylvicanthon*) and protibiae obliquely truncate at apex (rectly truncate in *Sylvicanthon*, Fig. 11).

Species composition

As defined in the present work, *Sylvicanthon* has 15 species divided into two groups: the *enkerlini* group, with a single species, *S. enkerlini*, and the *candezei* group, with five subgroups: the *candezei* subgroup, with *S. candezei*, *S. foveiventris* and *S. genieri* sp. nov.; the *aequinoctialis* subgroup, with *S. aequinoctialis* and *S. proseni*; the *furvus* subgroup, with *S. obscurus*, *S. furvus*, *S. monnei* sp. nov. and *S. mayri* sp. nov.; the *bridarollii* subgroup, with *S. bridarollii*, *S. attenboroughi* sp. nov., *S. edmondsi* sp. nov. and *S. seag* sp. nov.; and the *securus* subgroup, with the sole *S. securus*. This new composition differs from that of Halffter & Martínez (1977) in three main aspects: 1) two species originally included in *Sylvicanthon* (the former *S. machadoi* and *S. xanthopus*, along with a former junior synonym of the latter, *Glaphyrocanthon cobosi*, here revalidated) are removed from *Sylvicanthon* and transferred to *Canthon*; 2) six species previously placed in *Canthon* are transferred to *Sylvicanthon*: *C. aequinoctialis*, positioned in *Canthon s. str.* by Halffter & Martínez (1977), and its former junior synonym, *Glaphyrocanthon proseni*, which is here revalidated; *Glaphyrocanthon enkerlini*, placed in *Canthon* (*Francmonrosia*) by Halffter & Martínez (1977); and *C. securus*, *C. foveiventris*, and *C. obscurus*, species mentioned as possible *Sylvicanthon* by Halffter & Martínez (1977), but never formally transferred (but see 'Taxonomic history' above for more details about previous informal transfers of the latter two species); and 3) six new species are herein delimitated, described, and named for the genus. Furthermore, the recognition of two groups and five subgroups of species in *Sylvicanthon* is also new. In the following paragraphs, we discuss the proposed changes.

Although the results of this work undoubtedly show that *Canthon xanthopus*, *Glaphyrocanthon cobosi* and *G. machadoi* (hereafter cited in their original combinations) do not belong to *Sylvicanthon*, the genus to which they should be transferred is not as clear. The transfer of *C. xanthopus* is the least problematic and made with the most confidence. Among the evidence indicanting that this species does not belong to *Sylvicanthon* are a) shape of clypeal teeth (large, acute and very apart from each other in *C. xanthopus* (Fig. 45), and small, usually obtuse and contiguous or very close in *Sylvicanthon*, Fig. 6B–G); b) size of eyes (small eyes of about one-eighth of the width of the interocular space in *C. xanthopus*, and large eyes of about one-fifth of the width of the interocular space in *Sylvicanthon*); c) shape of protibiae (with large teeth and apex occupied by the apical tooth in *C. xanthopus*, and small teeth and truncate apex in *Sylvicanthon*, Fig. 11); d) shape of hypomeron (only slightly depressed anteriorly and with hypomeral carina incomplete in *C. xanthopus*, and deeply excavated and with complete hypomeral carina in *Sylvicanthon*, Fig. 35); and e) external margin of mesocoxae (narrow in *C. xanthopus*, see Fig. 7C, but very wide in *Sylvicanthon*, see Fig. 7A–B), among several other characters. At the same time, this species conforms with the definition (certainly artificial) of *Canthon* given by Halffter & Martínez (1977). Therefore, we propose that *C. xanthopus* be returned to its original combination (see below for more details on the relationship of this species with other *Canthon*).

Finding a proper generic placement for *Glaphyrocanthon machadoi* and *G. cobosi* is a more complicated task given the peculiar combination of characters that these two closely related species possess. Among the main differences with *Sylvicanthon* are a) clypeal teeth very separated from one another (teeth contiguous or very close in *Sylvicanthon*); b) dorsal portion of eyes narrow and with a fine internal margin (large unmargined eyes in *Sylvicanthon*); and c) external margin of anterior part of hypomeron strongly sinuous and with a strong tooth (straight or only slightly sinuous and usually with a very tiny tubercle in place of the tooth in *Sylvicanthon*). On the other hand, these two species have their general morphology very similar to that of *Glaphyrocanthon*, especially concerning the shape of the head (clypeus and eyes) and the excavated hypomeron. Even so, the presence of an anterior margin on the metafemora of these two species differentiates them from *Glaphyrocanthon*, whose species (at least the described ones) have unmargined metafemora[16]. Using the keys of Halffter & Martínez (1977) and Vaz-de-Mello *et al.* (2011), these species would be identified as *Canthon*. Based on that, and knowing that *Canthon* is highly artificial and comprises a large number of *incertae sedis* species of '*Canthon* sensu lato' (i.e., it is a 'wastebasket' taxon), we propose the temporary transfer of *G. cobosi* and *G. machadoi* to this genus. We believe, however, that when future works will have dedicated themselves to revise both *Glaphyrocanthon* and *Canthon* and given a new definition to these genera, those two species should be repositioned in some genus other than *Canthon*; possibly, a new one (see discussion on the revalidation of *Canthon cobosi* from the synonymy with *C. xanthopus* in the section dedicated to the former species).

Six other species formely positioned in *Canthon* by Halffter & Martínez (1977) are here incorporated into *Sylvicanthon*. As previously mentioned, Halffter & Martínez (1977) synonymized *Canthon aequinoctialis* and *Glaphyrocanthon proseni*, stating that the species, which was considered by previous authors to be close to those that today form *Sylvicanthon* (e.g., Schmidt 1922; Balthasar 1939; Martínez *et al.* 1964), would be isolated in its own lineage among the *Canthon s. str*. and, hence, had no intimate relationship with *Sylvicanthon*. In the discussion of the latter genus, Halffter & Martínez (1977) stated that *Canthon aequinoctialis* indeed had several similarities with *Sylvicanthon*, but they were nevertheless different in the following characters present allegedly only in the former species: a) posterior edge of head margined between eyes; b) mentum with anterior edge emarginate in 'U'; c) suture between submentum and gula 'Y'-shaped; d) protibial teeth of medium size; e) meso- and metatarsomeri I of length subequal to that of meso- and metatarsomeri II; and f) mesocoxae with very narrow external margin.

Save the one concerning character (c), all the other arguments are refuted in the present work and, based on the description and diagnosis given above, *Canthon aequinoctialis* and *Glaphyrocanthon proseni* are transferred to *Sylvicanthon*. Characteristic (a) was discussed above and we saw that, contrary to what was written by Halffter & Martínez (1977), the presence or absence of a margin on the posterior edge of head is highly variable among the *Sylvicanthon* (and presumably also among other genera such as *Pseudocanthon*), both intra- and interspecifically, and, hence, it is not a good indicator of generic limits. Besides, several specimens of the now *Sylvicanthon proseni* lack this margin, although the majority of the specimens show at least some vague traces of it.

Regarding character (b), it was seen that the so-called 'U'-emarginate mentum in *S. aequinoctialis* and *S. proseni* is at most only slightly different from the shape seen in the other *Sylvicanthon* (Fig. 8), the same occurring to character (f) (Fig. 7B–C). As for characteristic (d), the protibial teeth in those two species are indeed different from the remaining *Sylvicanthon* of the *candezei* group (Fig. 11B), but it seems to be an intermediate condition between that seen in *S. enkerlini* (Fig. 11A) and other related groups such as *Glaphyrocanthon* and the other species of the *candezei* group. Therefore, we can see these differences as a transformation series from the more general condition observed in *Glaphyrocanthon* and *S. enkerlini*, where the protibial teeth are large and well separated from one another, passing through the state present in *S. aequinoctialis* and *S. proseni*, whose teeth are of medium size, to the pattern found among the remaining *Sylvicanthon*, which have small teeth limited to the apical region of the protibiae (members of the *candezei* subgroup took a further step in this sequence and lost the basal tooth, keeping only the two apical ones).

Finally, characteristic (c) is indeed unique to the *aequinoctialis* subgroup: while the suture between the submentum and gula has a 'Y' shape (shape highlighted by a row of long setae covering it, Fig. 8B) in the members of this subgroup, in all the other species of *Sylvicanthon* this suture is rounded and may or may not be covered by a row of setae (Fig. 8A). Nonetheless, as previously noted by Halffter & Martínez (1977), the shape of this suture is extremely variable in *Canthon* and, therefore, it should not be taken as evidence of phylogenetic affinity between its species and the *aequinoctialis* subgroup. In this way, the 'Y'-shaped suture is here interpreted as a synapomorphy of the *aequinoctialis* subgroup, a modification of the rounded shape found among the other *Sylvicanthon* and supposedly present in the ancestor of this genus.

In addition, *Canthon securus*, *C. foveiventris* and *C. obscurus* – all species that were considered to be closely related to today's *Sylvicanthon* by previous authors (e.g., Schmidt 1920, 1922; Balthasar 1939; Martínez *et al*. 1964; Halffter & Martínez 1977) – are here at last transferred to the latter genus. These three species show all the characteristics present in the description and diagnosis given above and are intimately related to the other members of the *candezei* group, with which they are commonly confused both in collections and in publications. Halffter & Martínez (1977) stated that, very likely, these three species would have to be transferred to *Sylvicanthon*, but they did not argue why they themselves did not make these transfers (probably because they had not seen the type specimens, though). Although those transfers had never been proposed in a formal manner until now (i.e., explicitly stating they were new combinations and giving the arguments for the new taxonomic acts), subsequent authors started citing two of them – *S. foveiventris* and *S. obscurus* – in combination with *Sylvicanthon* (e.g., Vaz-de-Mello & Louzada 1997; Vaz-de-Mello 2000; Hernández 2002; Durães *et al*. 2005; Falqueto *et al*. 2005; Almeida & Louzada 2009; Hernández & Vaz-de-Mello 2009; Hernández *et al*. 2011; Larsen 2012; Culot *et al*. 2013), including important online biodiversity databases such as the *Encyclopedia of Life* and the *Catalogue of Life*.

Finally, the last transfer to *Sylvicanthon* presented herein is that of *Glaphyrocanthon enkerlini*, considered part of the *aequinoctialis* species group of *Glaphyrocanthon* by Martínez *et al.* (1964) – and thus close to today's *Sylvicanthon* – but placed in *Canthon* (*Francmonrosia*) by Halffter & Martínez (1977). These latter authors justified their transfer of *G. enkerlini* to *Francmonrosia* with the following characteristics: a) profemora with denticulation on its anterior margin; b) protibiae with internal expansion and c) with truncate apex. The latter two characteristics are, in fact, also present in *Sylvicanthon* and, thus, can be equally used as an argument to place *G. enkerlini* in this latter genus (protibiae with internal expansion is also seen in *Glaphyrocanthon*). Profemora with denticulation on its anterior margin, however, are not seen in any other *Sylvicanthon* and are indeed a characteristic present in all *Francmonrosia* (as currently defined, at least), which could be seen to support Halffter & Martínez's hypothesis. However, the denticulation in *G. enkerlini* is very distinct from the one shown by the great majority of the *Francmonrosia*: in species of the latter subgenus, teeth tend to be large, few in number, and present only in males, while they are small and, together, give a serrate appearance to the profemora of both sexes in *G. enkerlini* (Fig. 9B). *Canthon* (*F.*) *carbonarius* Harold, 1868, however, is unique in its subgenus in being similar to *G. enkerlini* concerning this characteristic and, indeed, it was cited by Halffter & Martínez (1977) as the closest relative of *G. enkerlini*.

Despite the similarities between *G. enkerlini* and *C. carbonarius*, in particular, and the putative affinity of *G. enkerlini* with *Francmonrosia*, in general, several observations were made in the present work that, in our opinion, refute Halffter and Martínez's classification and simultaneously give support to the proposed placement of *G. enkerlini* in *Sylvicanthon*: 1) shape of metaventrite, which is swollen on its anteromedial region and has a strong transverse depression on its anterior region in *Francmonrosia*, while it is entirely flat and has an area of rivose microsculpture typical of *Sylvicanthon* on its anterior part in *G. enkerlini*; 2) size of dorsal portion of eyes, which is wide in *G. enkerlini* and *Sylvicanthon* (Fig. 6), while it is narrow in *Francmonrosia*; 3) external margin of mesocoxae, which is broad in *G. enkerlini* and *Sylvicanthon* (Fig. 7A–B), but narrow in *Francmonrosia* (Fig. 7C); 4) presence of scutellar depression in *Francmonrosia*, while it is absent both in *G. enkerlini* and in *Sylvicanthon*; 5) the relative width between pronotum and elytra, the former being wider than, or subequal to, the latter in *Francmonrosia*, while elytra are distinctly wider than pronotum in *Sylvicanthon* and *G. enkerlini*; and 6) shape of pronotum, which is swollen, strongly convex and, in lateral view, much higher than the elytra in *Francmonrosia* (Fig. 10A), while it is flat and at the same level as the elytra both in *Sylvicanthon* and in *G. enkerlini* (Fig. 10B–C). Other characteristics differing *G. enkerlini* from *Francmonrosia*, on the one hand, and approximating it to *Sylvicanthon*, on the other, are size and overall body shape (*Francmonrosia* includes species much larger and more robust than *Sylvicanthon*). The margin of the posterior edge of head, notwithstanding the problems discussed above, also gives some indications of a closer relationship between *G. enkerlini* and *Sylvicanthon* than of that species with *Francmonrosia*. In this latter subgenus, this margin is always complete and well marked, while in *G. enkerlini* it is fine and, sometimes, almost imperceptible, in the same way as seen in the majority of the *Sylvicanthon*. Due to all these arguments, *G. enkerlini* is herein transferred from *Canthon* (*Francmonrosia*) to *Sylvicanthon*.

However, there are clear differences between *S. enkerlini* and the other *Sylvicanthon*. The most obvious of them is the shape of clypeus, structure that in *S. enkerlini* possesses four large, acute teeth (Fig. 6A), while all the remaining species have only one pair of small, obtuse or slightly acute teeth (Fig. 6B–G). Furthermore, the shape of protibiae, as already discussed, is very different between *S. enkerlini* and the other *Sylvicanthon*; the condition seen in that species is very similar, however, to that found in many *Glaphyrocanthon* (see drawings in Rivera-Cervantes & Halffter (1999), for example). Presence of denticulation on the anterior margin of profemora (Fig. 9B) and pilosity on the posterior part of hypomeron (Fig. 9D) are also conditions seen in *Sylvicanthon* exclusively in *S. enkerlini*. Therefore, together with characteristics in habitat preferences (see details further in the text in the sections 'Biogeography' and 'Natural history'), the differences between *S. enkerlini* and the remaining *Sylvicanthon* are used here to divide the genus into two species groups: the *enkerlini* group, with the single *S. enkerlini*, and the *candezei* group, with all the other 14 species of the genus.

It is interesting to note that *S. enkerlini* has an 'intermediate' overall morphology between the *Sylvicanthon* of the *candezei* group and *Glaphyrocanthon*, presenting characteristics interpreted here as either apomorphies of *Sylvicantahon* (such as metafemora with anterior margin (Fig. 21B), eyes with wide dorsal portion (Fig. 6A), mesocoxae with wide external margin (Fig. 7A–B), hypomeron strongly excavated anteriorly strongly excavated (Fig. 9D), protibiae truncate at apex (Fig. 11A) and absence of scutellar and prescutellar depressions) or plesiomorphies shared with *Glaphyrocanthon* that are not present in other *Sylvicanthon* (e.g., the overall shape of protibiae (Fig. 11A), including large teeth and the expansion on their internal margin, and pilosity on the posterior part of hypomeron (Fig. 9D)). Besides, *S. enkerlini* shows some unique apomorphies within the genus, such as denticulate profemora (Fig. 9B). Therefore, this new vision of *Sylvicanthon* presented herein brings with it intrinsic hypotheses about the morphological evolution and evolutionary relationships within the genus that should be tested in future phylogenetic analyses.

The *candezei* group, in turn, has as unique, easily observable features protibial teeth of smaller size (Fig. 11B–J) and, especially, a clypeus with only two small apical teeth (Fig. 6B–G). The 14 species are divided into five cohesive subgroups of species. The *candezei* subgroup, with three species, is immediately separated from the remaining *Sylvicanthon* by the presence of only two protibial teeth (Fig. 11J), while all the other members of the genus have three (Fig. 11A–I). The *aequinoctialis* subgroup, with only two species, is distinct from the remaining species in the shape of its protibiae (wider and with more robust teeth than the other *Sylvicanthon* of the *candezei* group, Fig. 11B), presence of metafemora with posterior margin (Fig. 31), suture between submentum and gula 'Y'-shaped (Fig. 8B), and constant presence of humeral carina (Fig. 12C; in *S. obscurus*, this carina is only present in some specimens). The four members of the *furvus* subgroup are differentiated from the other *Sylvicanthon* in having, in combination, protibiae with a clear internal expansion (Fig. 11D–E), abdomen with three pairs of lateral foveae in females (Fig. 16A–C; see discussion in the next section) and parameres bifurcate at the apex (Fig. 19B–E), while the four members of the *bridarollii* subgroup possess protibiae with straight

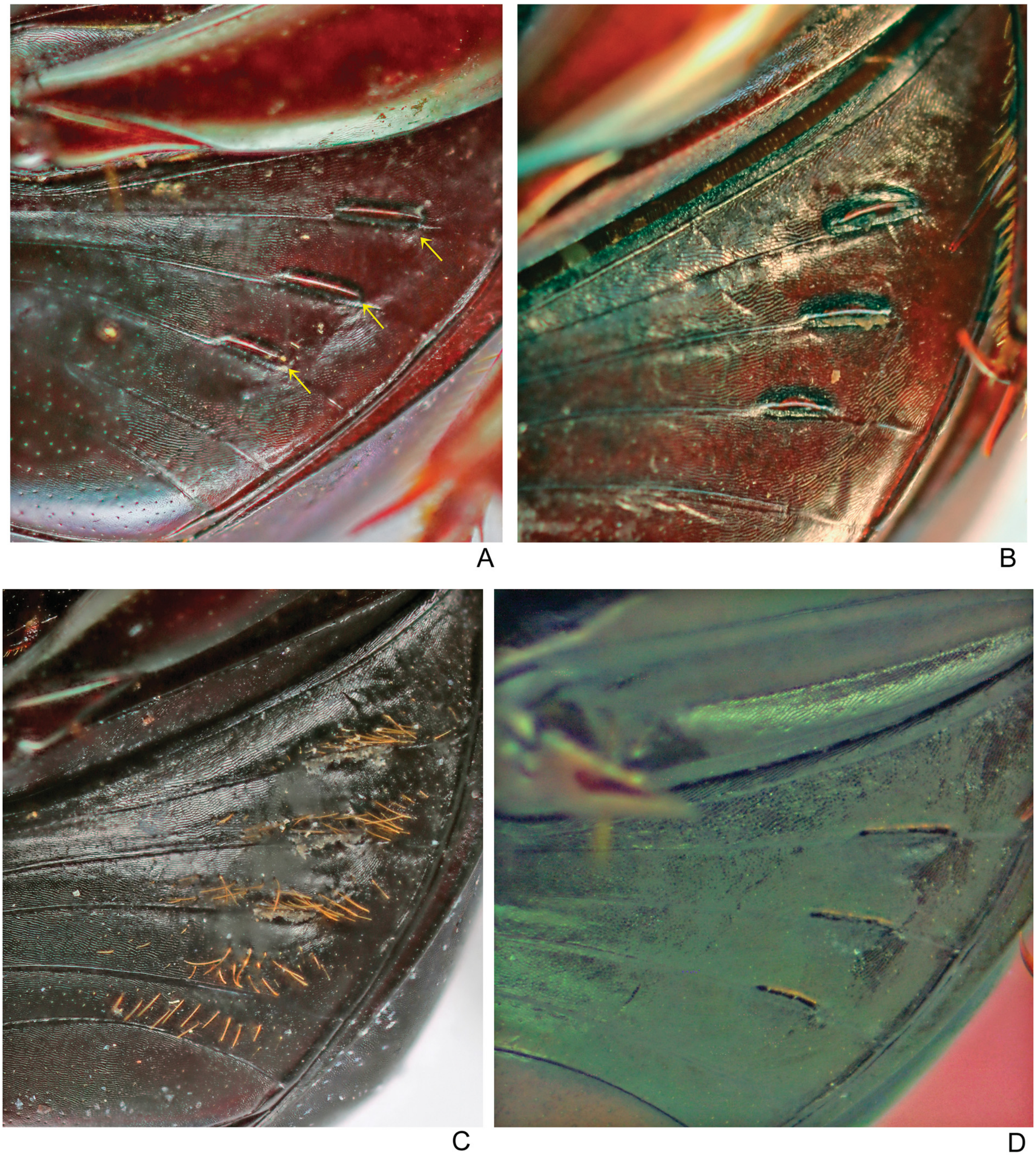

Fig. 16. Abdominal lateral foveae of females (arrows). **A**. *Sylvicanthon furvus* (Schmidt, 1920). **B**. *S. mayri* sp. nov. **C**. *S. obscurus* (Schmidt, 1920). **D**. *S. foveiventris* (Schmidt, 1920).

internal margin (Fig. 11H–I) (except *S. bridarollii*, Fig. 11F–G) and abdomen lacking lateral foveae in both sexes. The remaining subgroup only includes *S. securus*, a species that has ambiguous relationships with two of the other four subgroups. On the one hand, *S. securus* is close to the *furvus* subgroup in view of the strong internal expansion on its protibiae (the strongest protibial expansion in any species of the *candezei* group, Fig. 11C), but it is distinct from its species in having simple parameres (Fig. 19A) and because its females do not bear abdominal foveae, characters that, in turn, are typical of the species of the *bridarollii* subgroup.

Although this classification in subgroups has the aim of representing monophyletic groups, future formal phylogenetic analyses should test this scheme, present a clearer positioning for *S. securus*, and evaluate with more robust data the complex evolution of the characters used to delimit the subgroups (especially the evolution of the abdominal foveae, which, apparently, had multiple origins in different subgroups; see discussion below). Table 2 summarizes the characteristics used in this classification of the species of *Sylvicanthon*.

Comparative morphology of species of *Sylvicanthon*

The differences between the species of *Sylvicanthon*, especially among members of a same subgroup, are usually very subtle and lie in a combination of characters related to colour, microsculpture of the tegument and shape of parameres. In this section, we present a detailed comparison between the species of *Sylvicanthon* in relation to key structures both to the delimitation and to the identification of its species.

Dorsal colouration. Excluding *S. genieri* sp. nov., which has a coppery colouration throughout the body, the other species of *Sylvicanthon* possess darker shades such as green (*S. securus*, *S. candezei*, *S. mayri* sp. nov., *S. monnei* sp. nov. and some specimens of *S. seag* sp. nov.), dark blue (some specimens of *S. seag* sp. nov. and in *S. edmondsi* sp. nov.) or black with bluish or violet reflexes (*S. aequinoctialis*, *S. proseni* and *S. enkerlini*). The more common pattern, however, is the bicolour one, in which pronotum and head are purple and elytra are black, dark blue or dark green, as seen in *S. foveiventris*, *S. bridarollii*, *S. attenborough* sp. nov., *S. obscurus* and some specimens of *S. furvus* and *S. seag* sp. nov. In *S. obscurus* and *S. seag* sp. nov., the colouration pattern varies geographically: in *S. obscurus*, populations in Espírito Santo (Brazil) show a gradient where individuals may have head and pronotum green or yellow, at the one extreme, or purple, at the other, while elytra are always dark green or dark blue. In the Brazilian northeast, however, only specimens close to the 'purple-head-and-pronotum extreme' were observed (see more details in the discussion of this species). In *S. seag* sp. nov., the colouration also varies in a north-south axis: populations close to the banks of the Amazon river (e.g., Manaus and Belém) and those in the state of Maranhão show the bicolour pattern described above, while individuals from the Guianas, Venezuela and Trinidad possess a purple head, and green or blue pronotum and elytra (see detailed description in the discussion of this species).

Teneral specimens of all the species possess colouration distinct from the one described above. They are clearer and, most of the time, brownish with weak bluish and greenish reflexions. As this pattern is common to all the species, only the mature colouration is described and discussed throughout this work. Therefore, it is important to keep always in mind that occasional teneral specimens will not fit what is presented in each species' description.

Sculpture of the tegument. The pattern of the tegument sculpturing on head, pronotum, elytra, and metaventrite was one of the main sources of evidence for the species delimitation in *Sylvicanthon*. The terminology for the description of the microsculpture has been employed in a very inconsistent and imprecise way in the literature concerning '*Canthon* sensu lato'. Therefore, it is necessary to clarify the meaning of the terms used throughout this work.

Table 2. Summary of the morphological and distributional differences between species groups and subgroups in *Sylvicanthon*

	enkerlini **group (1 sp.)**	***candezei*** **subgroup (3 spp.)**	***aequinoctialis*** **subgroup (2 spp.)**	***bridarollii*** **subgroup (4 spp.)**	***furvus*** **subgroup (4 spp.)**	***securus*** **subgroup (1 sp.)**
Number of clypeal teeth	Four	Two	Two	Two	Two	Two
Transversal line on pronotal posterior edge	Present	Present	Absent in most specimens. Some vague traces present in *S. aequinoctialis*	Present (variable in *S. bridarollii*)	Present	Present
Shape of the suture between submentum and gula	Rounded	Rounded	‘Y’-shaped	Rounded	Rounded	Rounded
Number of protibial teeth	Three	Two	Three	Three	Three	Three
Shape of internal edge of protibiae	Strongly expanded	Straight	Straight	Straight (expanded in some *S. bridarollii*)	Expanded	Strongly expanded
Coarse punctation at base of metafemora	Absent	Present only in *S. foveiventris*	Absent	Present only in *S. bridarollii*	Present	Absent
Pilosity on the sides of metaventrite	Present	Present in some *S. foveiventris*	Present in some specimens	Absent	Present	Present
Lateral foveae of female abdomen	Absent	Present only in *S. foveiventris*	Absent	Absent	Present	Absent
Humeral carina	Absent	Absent	Present	Absent	Absent (variable in *S. obscurus*).	Absent
Distribution	Dry forest between Cerrado, Caatinga, the Atlantic Forest, and the Amazonia	Humid forests in southern Amazonia, on the slopes of the Andes, and in the Atlantic Forest	Humid forests in Central America, Chocó, on the slopes of the Andes, and the Amazon Basin	Humid forests in Trinidad, the Guianas, the Oricono and the Amazon Basins, and on the slopes of the Andes	Humid forests on the slopes of the Andes, western and southern Amazonia, and northern Atlantic Forest	Humid forests in the Guianas and northern Amazon Basin

When the surface of the tegument does not show any visible microsculpture, it is denominated smooth, even though micropunctation (i.e., small, individual non-sericeous perforations of the tegument) may be present. Microsculpture (i.e., the pattern of impressions or elevations on the surface of the body seen under microscopic lens; modified from the definition of 'sculpture' by Torre-Bueno 1989), in turn, can be present among *Sylvicanthon* in two general ways: the first one, when the tegument surface is covered by a net of tiny, well-delimited polygons[17] contiguous to one another, is denominated alveolar microsculpture (following Krell 1994 and Harris 1979) (Fig. 12A). The second one, where microsculpture does not show a well-defined regular pattern and is, instead, formed of a conjunct of tiny lines running in a non-parallel way, is denominated rivose microsculpture (following Harris 1979) (Fig. 12B). The alveolar pattern may have a three-dimensional appearance, being clearly present in the tegument's most external layer, or may have a flatter aspect, when it seems to be internal to the tegument, and more externally covered by a translucid, smooth layer (i.e., an external layer without microsculpture). In the second case, the alveolar microsculpture is always more difficult to observe and, in some occasions, only some vague traces can be seen, when they are called 'diffuse microsculpture'. Krell (1994) discussed in detail several aspects of the evolution, physiology and structure of the insect alveolar microsculpture and how this feature can serve to delimitate species.

All the species of *Sylvicanthon* have a very complex microsculpture pattern, which can show either only a little variation among conspecific individuals (e.g., in the four species of the *furvus* subgroup) or a remarkable intrapopulational (e.g., *S. proseni*) or geographical (e.g., *S. seag* sp. nov. and *S. candezei*) variation. The meaning of those different levels of intraspecific variation is, for now, unknown to us. Some areas of the tegument, however, have a similar sculpturing in all the individuals of *Sylvicanthon*: hypomeron (both the anterior and the posterior parts), mesepimera, metepisterna, prosternum, epipleura, and the external sides and antero-medial region of metaventrite are always covered by strong rivose microsculpture (Fig. 12B). It is actually on the tegument of the centre of the pronotum and elytra where lies the greater part of the variation.

The pronotum of *S. enkerlini*, *S. foveiventris*, *S. edmondsi* sp. nov., *S. securus* and the species of the *furvus* subgroup, as well as in the northern populations of *S. candezei*, is smooth and has evident micropunctation; in *S. aequinoctialis*, *S. bridarollii*, *S. seag* sp. nov., *S. attenboroughi* sp. nov. and in the southern populations of *S. candezei*, the alveolar microsculpture on the pronotum may be present, but it is always flat and micropunctation is evident; *S. genieri* sp. nov. is the only species where the pronotum always presents a strong alveolar microsculpture at the centre with the micropunctation obliterated by it, while *S. proseni* shows all the variation discussed above. In turn, elytra of *S. foveiventris*, *S. securus*, *S. monnei* sp. nov. and individuals from northern populations of *S. candezei* and *S. seag* sp. nov. are smooth and have dense micropunctation; those of *S. aequinoctialis* have a very subtle alveolar microsculpture, while those of *S. mayri* sp. nov. have a diffuse microsculpture, being the micropunctation evident in both species; and the elytra of the southern populations of *S. candezei* and *S. seag* sp. nov. and those of *S. genieri* sp. nov., *S. proseni*, *S. bridarollii*, *S. edmondsi* sp. nov., *S. attenboroughi* sp. nov. (majority of the specimens) and *S. furvus* show an evident alveolar microsculpture obliterating the micropunctation. Finally, a unique pattern is seen on the elytra of *S. obscurus* and *S. enkerlini*: the tegument of the centre of the elytra is smooth and has a dense micropunctation, while that of the sides and apex has a strong alveolar microsculpture obliterating micropunctation.

TRANSVERSE LINE ON THE POSTERIOR EDGE OF PRONOTUM. Schmidt (1920, 1922) assigned the presence of a fine transverse line at the centre of the posterior edge of the pronotum only to *S. furvus*, which is one of the features used by him to differentiate this species from *S. obscurus* in his key. In fact, this fine, sulcate line is absent in *S. obscurus*, as well as in *S. foveiventris*, but it is present in *S. candezei*, *S. securus* and *S. aequinoctialis*, species studied by Schmidt (1920, 1922), as well as in *S. enkerlini*, *S. genieri* sp. nov., *S. proseni*, *S. seag* sp. nov., *S. edmondsi* sp. nov., *S. attenboroughi* sp. nov., *S. monnei* sp. nov., *S. mayri* sp. nov. and the majority of the specimens of *S. bridarollii* (see discussion on the geographical variation on this character in *S. bridarollii* in this species' section). Therefore, in the same way as for other characteristics thought earlier to be exclusive to only one species in the genus (see below the discussion about the coarse punctation on metafemora and the three pairs of female abdominal foveae), the transverse line of pronotum is actually a feature widely present among the *Sylvicanthon*.

Coarse punctation at the base of metafemora. In four species of *Sylvicanthon*, *S. foveiventris* (Fig. 13A), *S. furvus* (Fig. 13E), *S. monnei* sp. nov. (Fig. 13C) and individuals from southern populations of *S. bridarollii* (Fig. 13G), the ventral surface at the base of metafemora has a group of elongate and narrow impressions that is here denominated coarse punctation of the base of metafemora. Schmidt (1920, 1922) was the first author to observe this characteristic, saying it was present in *S. foveiventris*. Martínez (1949a), in the original description of *S. bridarollii*, observed the same coarse marks in this species and, indeed, he said his new taxon was close to *S. foveiventris*. In the present work, besides having observed for the first time this feature in *S. furvus* and *S. obscurus*, and describing it for the new species *S. monnei* sp. nov., we also noticed a curious geographical variation in *S. bridarollii* (Fig. 36): individuals from populations from central Bolivia, in places such as Cochabamba and Santa Cruz, have a very evident coarse punctation, whereas farther north in Bolivia and in southern Peru, this punctation is sparser and ill marked. Northwards in Peru and in Ecuador and Colombia, this punctation becomes increasingly thinner (almost undistinguishable from the micropunctation of the rest of the tegument) and, in the northernmost populations, it is completely absent. This clinal variation is very interesting because it shows that the coarse punctation is likely to be homologous to the micropunctation of the remainder of the tegument (which is present in all the other *Sylvicanthon*). Since species in three different subgroups show this kind of punctation, it is possible that it has evolved at least three times in *Sylvicanthon*. A final species, *S. obscurus*, is noteworthy in presenting, apparently, an intermediate condition: in the entire surface of its metafemora, the punctation is thicker and more evident than the micropunctation seen in other species (e.g., *S. securus*, *S. edmondsi* sp. nov., etc; or in the apical region of *S. foveiventris*, *S. furvus*, *S. monnei* sp. nov. and *S. bridarollii*), but they are not as elongated and deep as in the species with coarse punctation (Fig. 13B).

In the same way as for the abdominal foveae (see below), it is reasonable to suppose that the coarse punctation of the mefemora has a role in the chemical communication (through pheromones) between individuals of a same species. In the four species that possess it, the density of this punctation can vary intrapopulationally, but, with the sole exception of a specimen of *S. foveiventris* collected in Itamonte (Minas Gerais, Brazil), which has only vague vestiges of it, all the remaining specimens studied clearly show the coarse marks at the base of their metafemora. Other members of '*Canthon* sensu lato' that have similar coarse punctuation are two of the species of *Canthon* (*Peltecanthon*) Pereira, 1953, namely *C. staigi* (Pereira, 1953) and *C. sulcatus* Castelnau, 1840 (see Halffter & Martínez 1967: figs 9–10).

Elytral striae. Halffter & Martínez (1977) and Tarasov & Génier (2015) stated that *Sylvicanthon* have nine elytral striae and, indeed, this is probably the ancestral condition in the genus. In all the species, counting the number of striae is usually a difficult task, since, save the three or four more internal ones, they are very effaced, fine and discontinuous. As an effect, the maximum number of observable striae vary among the species: in *S. proseni*, *S. obscurus* and the members of the *bridarollii* subgroup the maximum number is nine; in *S. candezei*, *S. genieri* sp. nov. and *S. aequinoctialis* it is eight; and in *S. foveiventris*, *S. securus*, *S. furvus*, *S. monnei* sp. nov. and *S. mayri* sp. nov., seven. Another important feature to stress related to the elytral striae is the presence of a fine carina on the humeral region of the eighth stria; because of its position, this carina is hereafter called the humeral carina (Fig. 12C). Three species of *Sylvicanthon* possess it: *S. aequinoctialis*, *S. proseni* and *S. obscurus*. In the latter species, only two-fifths of the individuals studied show the humeral carina; in the other specimens, the eighth stria is flat and very fine in the same way as the other internal striae (see more details in the discussion of this species). On the other hand, all the specimens of *S. aequinoctialis* and *S. proseni* evidently show this carina, although in the first species it tends to be longer than in the second. Other groups of Neotropical Deltochilini also show a humeral carina, including species of *Canthon* and *Scybalocanthon* (e.g., see the discussion on *Canthon xanthopus* below).

Sexual dimorphism. As commonly observed in Deltochilini, few secondary sexual characteristics are evident among the species of *Sylvicanthon*, a fact that turns the sexing of specimens into a difficult task. Being telecoprids, they have not developed the horns and other armaments that evolved among paracoprid dung beetles and which are used in combats between males inside tunnels and other closed spaces (see Emlen & Philips (2006) for a detailed discussion on the relation between horns and paracoprid behaviour). In this way, sexual dimorphism is limited in *Sylvicanthon* to more discreet features, such as the shape of the sixth ventrite (Fig. 14B–E) and that of the protibial spur (Fig. 15).

In all *Sylvicanthon*, the fit between the apex of the pygidium and the sixth ventrite is distinct between males and females: in males, ventrite six has an emargination on its posterior edge that allows the pygidium to extend itself further into the ventral side of the abdomen (Fig. 14D); in females, there is no evident emargination and the pygidium does not extend towards the ventral side of the abdomen (Fig. 14B–C, E). Thus, it is possible to differentiate both sexes observing that the sixth ventrite of males is narrowed at the middle, whereas it is wide in females. Some species, however, exhibit modifications on the posterior edge of ventrite five that makes the observation of this difference difficult. Mainly in females of *S. candezei*, *S. seag* sp. nov., *S. edmondsi* sp. nov., *S. attenboroughi* sp. nov.and both sexes of *S. securus*, ventrite five has a weak medial expansion on its posterior edge covering the anterior region of ventrite six and thus giving a narrowed appearance to the latter (Fig. 14E). In males of those species, ventrite five also presents this medial flange and, in general (except in *S. securus*), it can be as or even more developed than in females (Fig. 14D).

Another sexual dimorphism found among the species of *Sylvicanthon* lies in the shape of the protibial spur: in females, this spur is spiniform and simple, without any bifurcation or apical expansion (Fig. 15F); the only exceptions are the females of *S. proseni*, whose spur is apically bifurcate (Fig. 15H). In sharp contrast to this uniform female shape, males of *Sylvicanthon* show wide interspecific variation in the morphology of their protibial spurs, with a unique pattern found in each species (excepting the group formed by *S. furvus*, *S. monnei* sp. nov. and *S. mayri* sp. nov., which shows the same shape in all the three species). In *S. enkerlini*, the spur is long, narrow and bifurcate at the apex, with the external branch longer than the internal (Fig. 15A). In the *candezei* subgroup, the spur is broad and bifid, with the external branch always longer than the internal one: in *S. foveiventris*, the internal branch is very broad and only slightly shorter than the external one, which is spiniform (Fig. 15B); in *S. candezei*, the internal branch is only slightly indicated and the separation between it and the external branch is horizontal (Fig. 15C); in *S. genieri* sp. nov., an intermediate condition is seen (Fig. 15D). In the *aequinoctialis* subgroup, the spur is also broad and bifid: in *S. aequinoctialis*, the internal branch is only slightly indicated (Fig. 15E), while it is much more developed in *S. proseni* (Fig. 15G); the female spur of *S. proseni* differs from males in being more narrowed and having the separation between external and internal branches in a closer angle (in 'V', Fig. 15H), whereas in males it is much broader (in 'U'). In the *bridarollii* subgroup we see the highest level of interspecific variation: in *S. bridarollii* (Fig. 15I), the spur is narrowed and the internal branch is only slightly developed; in *S. seag* sp. nov., the spur is broad and the internal branch is also short (Fig. 15J) (in a single specimen from French Guiana, one of the spurs has a small tubercle in the space between the two branches); in *S. edmondsi* sp. nov., the two branches are very developed (the external one slightly longer) (Fig. 15K); and, lastly, in *S. attenboroughi* sp. nov., the spur has a narrow base, the apical region is broad and the internal branch is only slightly developed, clearly shorter than the external one (Fig. 15L). In the *furvus* subgroup, a shape is observed in *S. obscurus*, whose internal branch is broad and much shorter than the external one, from which it is separated by an open angle

(Fig. 15M), and the one observed in the other three species, where the external and the internal branches are subequal in length and separated by a very close angle (Fig. 15N). Finally, the spur of *S. securus* differs from all the other species in having the internal branch, which is very broad, longer than the external one, which is spiniform (Fig. 15O). Such sheer diversity in the shape of the male protibial spur must have been the fruit of an intense pressure from sexual selection, although the role played by the protibial spurs in the life of the *Sylvicanthon* is still unknown.

A third sexually dimorphic characteristic is restricted to only five species in the genus: *S. foveiventris* and members of the *furvus* subgroup. Females of these five species possess three pairs of foveae located on the sides of the abdomen at the sutures between ventrites I–II, II–III and III–IV (Fig. 16). It is interesting to note that the presence of these foveae among the species and sexes in *Sylvicanthon* was matter of a wide confusion in the literature.

Schmidt (1920) included this characteristic in the description of *S. foveiventris* (and, probably, it was thanks to this feature that the species was named as such), but he did not make any mention whether these foveae were present in both sexes or whether they were unique to just one of them. It is curious to note, actually, that this was the only one of the four species of *Sylvicanthon* described by Schmidt (1920) without the sexual dimorphism discussed by him. For *S. obscurus* and *S. furvus*, although he had described sexual dimorphism related to the protibial spur, Schmidt (1920) did not mention the presence of abdominal foveae. Two years later, Schmidt (1922) erred again by assigning the presence of abdominal foveae to both sexes of *S. foveiventris*, an opinion that was repeated by most of the subsequent authors (Pereira & Martínez 1956; Martínez *et al*. 1964). The exception was Balthasar (1939), who, in turn, was also wrong in suggesting that foveae might be a male characteristic in *S. foveiventris* ("nur beim ♂?", p. 189); once more, nothing was mentioned about the presence of this characteristic in both *S. furvus* and *S. obscurus*. As demonstrated in the present work, not only are the abdominal foveae present in other species than *S. foveiventris*, but in all these species they are restricted to females, being the easiest and the most reliable way to separate the sexes.

Little variation exists between the abdominal foveae of *S. foveiventris* (Fig. 13E, 16D), *S. furvus* (Fig. 16A) and *S. monnei* sp. nov. In *S. obscurus*, there is a row of long setae covering the anterior margin of each fovea, which, therefore, stand out from the remaining tegument of the abdomen (Fig. 16C). In the two females of *S. mayri* sp. nov. studied, in contrast, the abdominal foveae are clearly more narrowed and superficial than those seen in the other four species (Fig. 16B; see more details in the discussion of *S. mayri* sp. nov.).

In the same way as for the coarse punctation at the base of metafemora, it is here hypothesized that the abdominal foveae should also play a role in the intraspecific chemical communication, and, in this particular case, as they are secondary sexual characteristics, probably related to the sexual behaviour. The presence of tegumentary exocrine glands secreting semiochemicals is known for several groups of Scarabaeinae (e.g., Tribe 1975; Pluot-Sigwalt 1982; Houston 1986; Burger *et al.* 1990, 1995a, 1995b, 2002, 2008). Pluot-Sigwalt (1982), having studied several dung beetle genera, found an intricate distribution pattern of exocrine glands in the abdominal ventrites. In some cases, both males and females had these glands (although there was a remarkable sexual dimorphism in their numbers and dispositions), while in other cases they were restricted to just one sex. Interestingly enough, there was a clear distinction between telecoprid and paracoprid groups, with a much larger number of genera of the first group – to which *Sylvicanthon* belongs – presenting glands than of the second (Pluot-Sigwalt 1982).

The row of setae seen exclusively in the foveae of *S. obscurus* (Fig. 16C) may work as a kind of net to capture and concentrate close to the female's body the pheromones released into the air by the abdominal glands. Houston (1986), for instance, described two exocrine gland complexes associated to a tuft of setae present in the front legs of some species of *Onitis* Fabricius, 1789. Following his hypothesis, the pheromone secreted by one group of glands present only in males could work as a trail marker and, in this way, it could indicate to females the path to the dung mass or to the nest entrance. Therefore, the tuft of setae associated to exocrine glands would serve to deposit the pheromone to the substrate while the path is being marked. Although in *S. obscurus* these glands and associated setae are exclusive to females, not males, it is still possible that some similar behaviour occurs in this species. Studies on the reproductive habits of the *Sylvicanthon* species are necessary in order to know the actual function of the abdominal foveae in this group.

Aedeagus. As discussed above, males of *Sylvicanthon* do not differ from the majority of the other telecoprid dung beetles in not having horns or any other kinds of armaments. In these groups, it is in the shape of the parameres and pieces of the internal sac and their counterpart in the female sexual organ that the sexual selection should act in a more intense way (see for a discussion on the evolution and anatomy of the copulatory organs of a model species of dung beetle: Werner & Simmons 2008; House & Simmons 2003; Tarasov & Solodovnikov 2011). This fact is reflected in the large variety of forms of aedeagi seen in *Sylvicanthon*, where even closely related species with a very similar external morphology may have entirely distinct parameres. The morphology of the female genitalia was not studied for this work, but, as seen in other groups of Scarabaeinae that had it examined (e.g., Zunino 1971, 1972, 1975, 1976, 1978, 2012; Zunino & Halffter 1988; Marchisio & Zunino 2012), it probably varies in a similar degree as the aedeagus. As emphasized by Zunino (1987), Méndez & Córdoba-Aguilar (2004) and Ah-King *et al.* (2014), among several other authors, there is no reason to suppose that there is a higher morphological diversity among the male genitalia than among the female ones, since these structures evolve jointly in a complex interaction of evolutionary pressures derived from female choice and intra- and intersexual conflicts (see also Simmons 2014).

It is in the *candezei* and *bridarollii* subgroups where we can find the greatest diversity in paramere shapes. In the first subgroup, the parameres may be straight and simple (i.e., without any notch or keel in the ventral region; *S. foveiventris*, Fig. 17B), may have a strong ventral keel and a short notch on its posterior region (*S. genieri* sp. nov., Fig. 17D), or may bear a deep ventral notch without any keel (*S. candezei*, Fig. 17C). In the *bridarollii* subgroup, in turn, the parameres may be simple (*S. bridarollii*, Fig. 18A), with a short ventral keel (*S. edmondsi* sp. nov., Fig. 18C and *S. attenboroughi* sp. nov., Fig. 18D) or be highly modified with a ventral keel so deep that almost divide the parameres into two halves (*S. seag* sp. nov., Fig. 18B). With the exception of *S. foveiventris* and *S. bridarollii*, all the other species have sharply asymmetric parameres, with external faces differing from one another by being either concave or flat.

In the *furvus* subgroup, whose parameres are apically bifurcate and have no ventral keels or notches, the difference between the species is subtler in three of the four species. In *S. furvus* (Fig. 19C) and *S. mayri* sp. nov. (Figs 19E, 44A–B), the inferior branch of the bifurcation is distinctly projected and divergent from the superior branch, whereas in *S. monnei* sp. nov. (Figs 19D, 44C–D) the inferior branch is only slightly projected and is parallel to the superior branch. In those three species, both branches are connected by a fine membrane, but in the fourth member of their subgroup, *S. obscurus*, both branches are free and the superior branch projects itself much stronger than the inferior one, which has an acuminate apex (Fig. 19B). In the *aequinoctialis* subgroup, different from the other subgroups discussed before, there is no difference between the species (Fig. 17E–F); in both, the parameres are simple and have a broad depressed area at the apex which extends posteriorly farther in the left paramere than in the right. Finally, *S. securus* (Fig. 19A) and *S. enkerlini* (Fig. 17A) have elongate and simple parameres, without any ventral keel or notch.

Biogeography

Sylvicanthon are largely distributed in the Neotropical region as defined by Morrone (2014, 2015b), occurring from Honduras to the Amazon Basin, the Atlantic Forest in NE and SE Brazil, and in the transition zone between the latter two biomes and the Brazilian Cerrado and Caatinga (Figs 20, 22). Among the areas into which Morrone (2014) divided the Neotropical region, *Sylvicanthon* is present in two of the three subregions (Brazilian and Chacoan), in all of the six dominions and in 24 of the 53 provinces. Four species (*S. genieri* sp. nov., *S. bridarollii*, *S. edmondsi* sp. nov. and *S. furvus*) are also present in the province of Paramo, in the South American Transitional Zone between the Neotropical and the Andean regions.

The *candezei* species group and *S. enkerlini* are very distinct with respect to the environments in which they live (Fig. 20). Species of the first group are distributed in the four great areas of tropical rainforests in the Neotropical region – the Central American tropical forests, the Choco, the Amazon forest and the Atlantic Forest –, where temperature and humidity are high, there is a dense and continuous canopy and the sunlight incidence on the surface of the soil, in the leaf litter in the understory and in the lower tree layers is very low. Thanks to these factors, mammalian dung, upon which *Sylvicanthon* feed, remains fresh and available for consumption and nidification for a longer time in those habitats. In contrast, *S. enkerlini* occurs in the transitional zones between Amazonia, Cerrado, Caatinga and the Atlantic

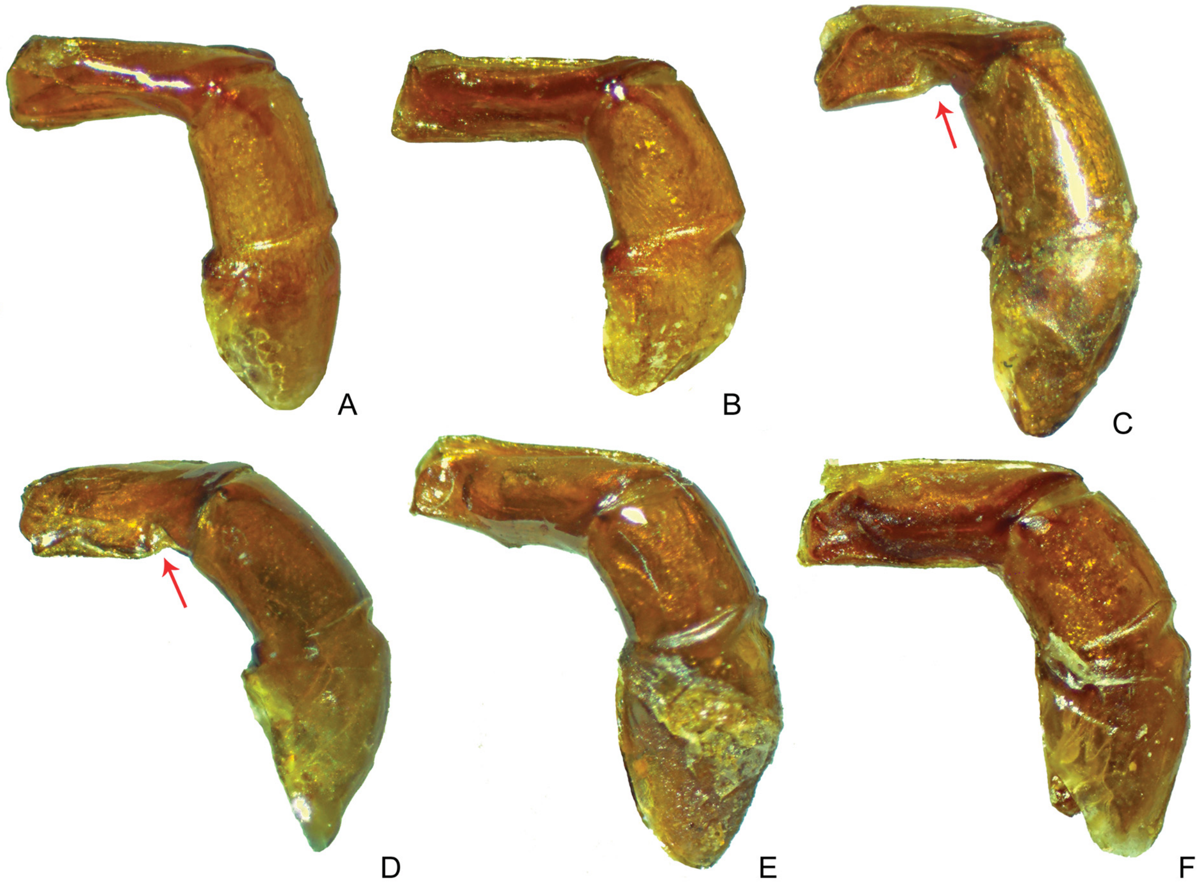

Fig. 17. Aedeagus morphological diversity in *Sylvicanthon*. **A**. *S. enkerlini* (Martínez *et al.*, 1964) comb. nov. **B**. *S. foveiventris* (Schmidt, 1920). **C**. *S. candezei* (Harold, 1869) (arrows points to the ventral notch). **D**. *S. genieri* sp. nov. (idem). **E**. *S. aequinoctialis* (Harold, 1868). **F**. *S. proseni* (Martínez, 1949) stat. et comb. nov.

Forest, in more open, shorter and drier semidecidual forests, such as the Mata dos Cocais, in Maranhão, the tableland forests (from the Portuguese '*matas de tabuleiro*') in the coast of Ceará, and dryer forested areas typical of Cerrado and Caatinga in the interior of the Brazilian states of Piauí, Bahia, and Minas Gerais (Figs 20, 22; see more details on the distribution of *S. enkerlini* in the 'Natural history' section for this species).

Martínez *et al.* (1964) raised the hypothesis that *Sylvicanthon* (cited as "*grupo aequinoctialis*" of *Glaphyrocanthon*) originated in Amazonia and, from there, it dispersed to the other areas where it is present today. The greatest species diversity in the genus is indeed located in the Western Amazonia, in cloud forest areas close to the slopes of the Andes in Bolivia, Peru, Ecuador and Colombia, where *S. genieri* sp. nov., *S. proseni*, *S. bridarollii*, *S. edmondsi* sp. nov., *S. attenboroughi* sp. nov., *S. furvus* and *S. mayri* sp. nov. occur. The distribution of three of these species – *S. proseni* (Fig. 30), *S. bridarollii*

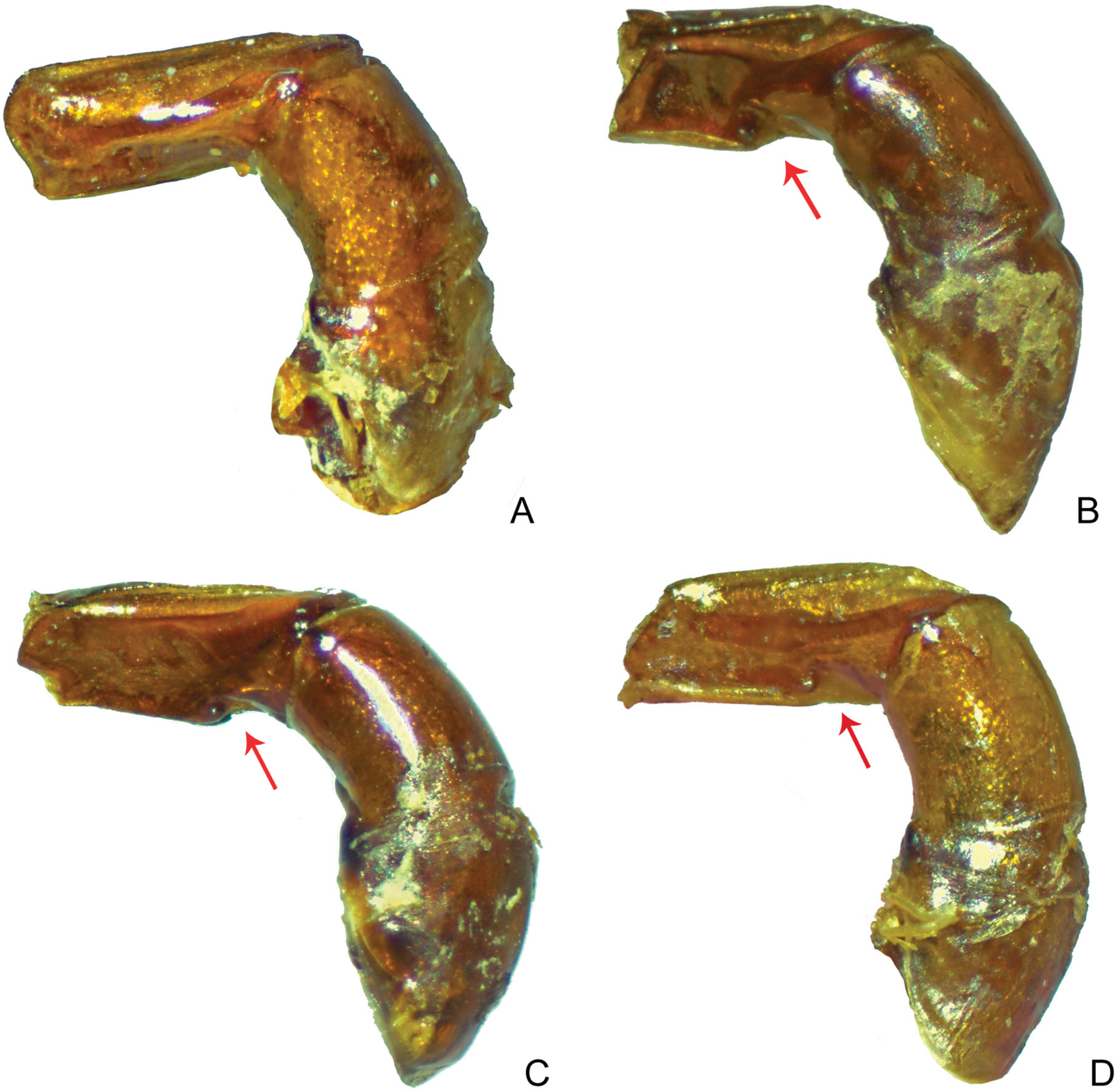

Fig. 18. Aedeagus morphological diversity in the *bridarollii* subgroup. **A**. *S. bridarollii* (Martínez, 1949). **B**. *S. seag* sp. nov. (arrow points to the ventral notch). **C**. *S. edmondsi* sp. nov. (idem). **D**. *S. attenboroughi* sp. nov. (idem).

and *S. attenboroughi* sp. nov. (Fig. 34) – extends eastwards into the Amazon Basin, but the latter two are absent on the left banks of the Amazon river. In the latter region, it occurs *S. securus* (Fig. 41) and *S. seag* sp. nov. (Fig. 34), whose distribution extends farther north into the Guianas and, in the case of the latter species, also towards Venezuela and the island of Trinidad, the only insular record for the genus. Two further species occur in the Amazon region: *S. monnei* sp. nov., which is distributed throughout the forests of northern Mato Grosso and southern Pará, a dryer Amazon area with a more pronounced seasonality where rainy and dry seasons are sharply demarcated (Fig. 41), and *S. candezei*, which exhibits a very peculiar bow-shaped distribution from the mouth of the Tapajós River through the dry forests of the transitional region bordering the Cerrado in southeastern Pará and goes southwards into southern Amazon and its transition zone with the Pantanal region (Fig. 24). Together, therefore, eleven of the fifteen species of *Sylvicanthon* are typical elements of the Amazon forest. Following the hypothesis of Martínez *et al.* (1964), which is championed here, at least three distinct dispersal waves departed from the Amazonian centre of origin: the ancestors of *S. foveiventris* (*candezei* subgroup) and *S. obscurus* (*furvus* subgroup) towards the Atlantic forest, and those of *S. aequinoctialis* into Central America (Fig. 20).

The dispersal of *Sylvicanthon aequinoctialis* into the forests of Central America probably occurred only after the uplift of the Isthmus of Panama. The chronology about when this landbridge connecting North and South Americas was formed enough to allow the passage of fauna is yet a matter of great debate. Some authors argue for an older formation, where the vast marine passage connecting the Caribbean Sea

Fig. 19. Aedeagus morphological diversity in *Sylvicanthon*. **A**. *S. securus* (Schmidt, 1920) comb. nov. **B**. *S. obscurus* (Schmidt, 1920). **C**. *S. furvus* (Schmidt, 1920). **D**. *S. monnei* sp. nov. **E**. *S. mayri* sp. nov.

and the Pacific Ocean, the so-called Central American Seaway, was closed in the Miocene, some 15 million years ago, and, thereafter, the right conditions allowing the biotic movement between the Americas were fully present (e.g., Montes *et al.* 2012a, 2012b, 2015; Jaramillo *et al.* 2017). Other authors, instead, argue that, between 15 million and about three or four million years ago, Central America and the northwest coast of South America were indeed close (about 200 km away from one another), but yet separated by a very deep sea, which prevented faunistic interchange until the final completion of the Isthmus of Panama

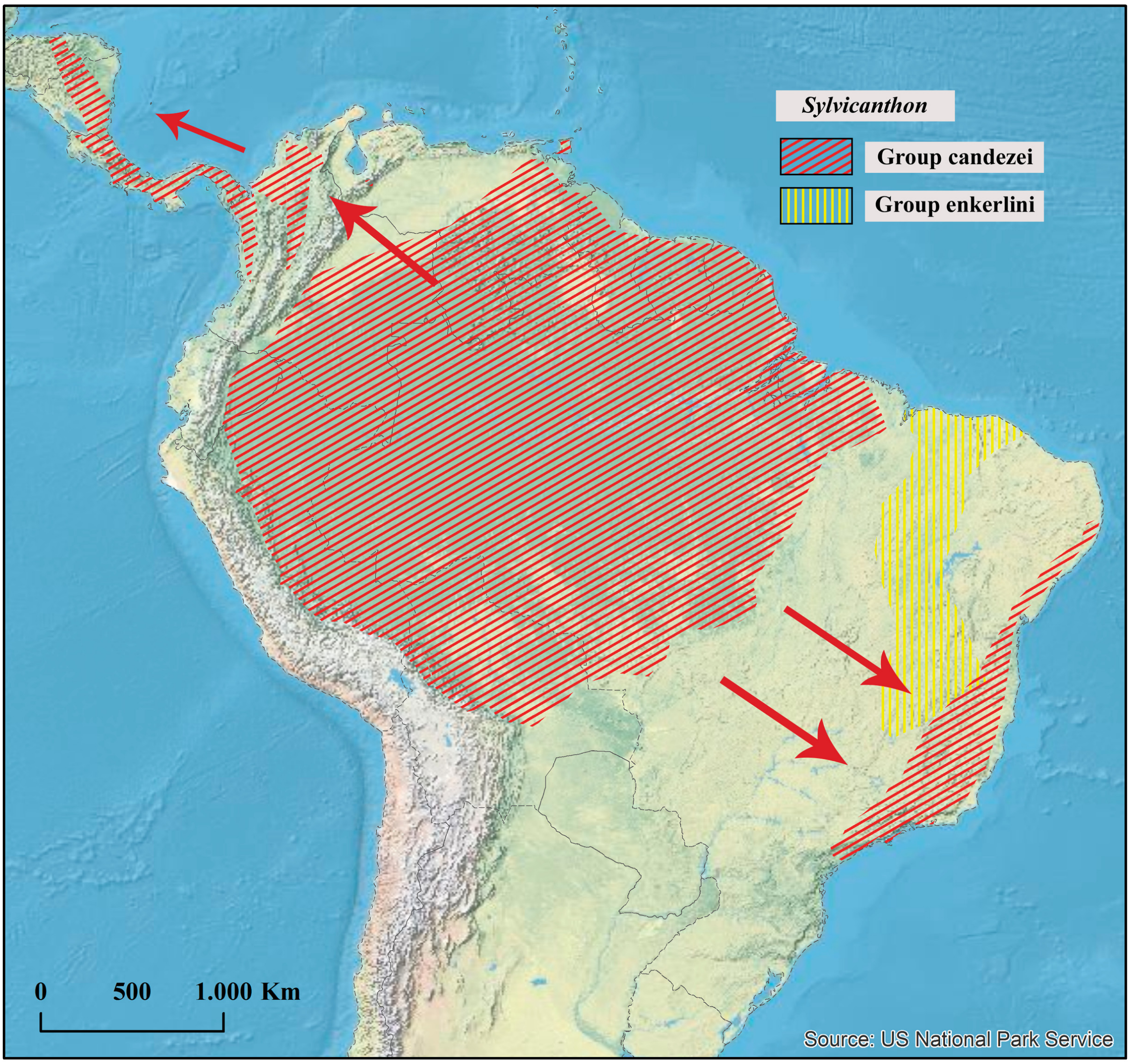

Fig. 20. Combined distribution of the species of *Sylvicanthon* in the Neotropical region. Note that the genus occupies the four great areas of tropical humid forest of the American continent: Central American forests, the Choco of the South American northwest, the Amazon Rainforest and the Atlantic Forest. Following the hypothesis of Martínez *et al.* (1964) that the Amazon Basin was the ancestral area of the *Sylvicanthon* of the *candezei* group, three lineages have independently dispersed from there (arrows): that of the ancestors of *S. aequinoctialis* (Harold, 1868), which, from the Choco, invaded Central America at the pace of the tropical forests' gradual northwards advance, occurred during the Plio-Pleistocene, and those of the ancestors of respectively *S. obscurus* (Schmidt, 1920) and *S. foveiventris* (Schmidt, 1920), which reached the Atlantic Forest through the corridors of humid forests that bridged that biome to the Amazon forest during the wettest periods of the Neogene (see a more detailed discussion in the text).

about 3 million years ago (e.g., Coates & Stallard 2013; O'Dea *et al.* 2016). This latter case would be an analogous situation to the current Wallace and Lydekker lines, on the limits, respectively, of the Sunda and Sahul continental shelves, in Indonesia, which mark the separation between the faunas of the Oriental and Australasian biogeographical regions (Coates & Stallard 2013).

Curiously enough, studies on the dung beetle dispersal from South to North America argue that this movement occurred in two independent waves, one during the Miocene and another during the Plio–Pleistocene (Kohlmann & Halffter 1988, 1990; Edmonds 1994; Price 2009; Halffter & Morrone 2017). Not coincidently, these two migratory waves correspond exactly to those two distinct phases in the geological history of the Isthmus of Panama as theorized by Coates & Stallard (2013) and O'Dea *et al.* (2016) (but see the replies by Jaramillo *et al.* 2017 and Molnar 2017). The first migratory wave would have advanced through a chain of several small islands in the then-existing strait between Central America and South America's northwest coast, while the second wave would have occurred during the gradual advance of the South American tropical forest into Central America after the uplift of the Isthmus of Panama was completed. Being a tropical forest dweller, *S. aequinoctialis* should have invaded Central America from the Choco forest in northern South America during this second migratory wave (Fig. 20), in the same way as done by *Glaphyrocanthon* and allied groups (Kohlmann & Halffter 1990).

Together, those migratory waves were part of the so-called Great American Biotic Interchange of the Neogene. Several groups of dung beetles of a clear South American origin, such as *Phanaeus* MacLeay, 1819, *Coprophanaeus* d'Olsoufieff, 1924, *Dichotomius* Hope, 1838, *Ontherus* Erichson, 1847, *Canthidium*, *Ateuchus*, *Uroxys*, *Deltochilum*, *Canthon* and *Scybalocanthon*, trod this very same path from the southern continent towards Central America and, in the most successful cases, to North America, places where some of these groups have undergone a remarkable adaptive radiation. The reverse path, that is, from North to South America, was traveled by a much smaller number of lineages, including *Onthophagus* Latreille, 1802 and *Copris* Geoffroy, 1762. It is interesting to note that this was exactly the opposite migration pattern of the mammals, whose primary direction was southwards and which were the focus of much of the studies on the Great American Interchange (e.g., Simpson 1980); in this context, it is especially important to remember that mammals are the main group of vertebrates which dung beetles depend on for food. Birds, on the other hand, migrated mainly from south to the north (Weir *et al.* 2009), in the same way as it seems to have occurred with some scarab groups (e.g., *Dynastes* Kirby, 1825; Huang 2016) and dung beetles (personal observations[18]). We agree that future studies on the participation of the dung beetles and other insect taxa in the Great American Interchange will shed light on the ecological factors driving the distinct patterns seen in different groups of organisms. But most importantly, the dung beetle northwards migration pattern shows that simplistic hypotheses championing a 'more competitive nature' of North American elements fail to explain the whole biotic movement, to say the least.

The other two species of the *candezei* group, occuring outside Amazonia, are *S. foveiventris* and *S. obscurus*, both inhabitants of the Atlantic Forest (Figs 24, 41). Although the South American Dry Diagonal formed by the Caatinga, Cerrado and Chaco separates the humid forests of Amazonia and the Atlantic Forest, both biomes have never been completely isolated from one another and, in fact, they have a long and complex history of interactions throughout the Cenozoic (Costa 2003; Batalha-Filho *et al.* 2013; Daniel & Vaz-de-Mello 2016; Ledo & Colli 2017; and references cited therein). Studies based mainly on the distribution and phylogeny of land vertebrates showed that there was a great mixture of fauna between those two areas, especially during intervals of more humid climate, when gallery forests and patches of humid forests penetrated more strongly into the interior of the dry regions of central South America and in this way served as bridges connecting the two biomes. Batalha-Filho *et al.* (2013), for example, found that there were two great bird interchange movements between Amazonia and the Atlantic Forest during the Neogene, the oldest having occurred between southwestern Amazonia and southern Atlantic Forest during the Miocene (24 to 5 million years ago) and the most recent one during the Plio–Pleistocene (the last 5 million years) between northeastern Amazonia and the northern portion of the Atlantic Forest. In this way, the phylogeny of South American animals shows several cases where sister species or sister groups occur separately, one in the Amazon, the other in the Atlantic Forest.

If *Sylvicanthon* and other Deltochilini took part in episodic migratory waves as those of the example discussed above, or if they had a history of a continuous communication between the Amazonia and the Atlantic Forest, is still a question for further research. What is clear, nonetheless, is that at least two lineages – the one which gave origin to *S. obscurus* and the other which originated *S. foveiventris* – arrived independently at the Atlantic Forest from the Amazon region. As argued by Costa (2003), the dispersal history of any animal group between these two biomes should have been extremely complex and deeply influenced by local events that varied over time, scale and mainly in the effect that they had in different groups of organisms, as shifts in river courses, climate changes or refuge formations. Therefore, hardly a single phenomenon or pattern will be found to explain the whole movement of fauna between the Atlantic Forest and the Amazon which *Sylvicanthon* species could fit in. In order to understand in deep detail the biogeography of *Sylvicanthon*, it is necessary that we first study empirically the phylogenetic relationships between its species.

It is also interesting to note here that each of the polytypic subgroups of *Sylvicanthon* show both a distribution and a phylogenetic pattern that could lead an evolutionary biologist to classify them as superspecies, that is "monophyletic group[s] of allopatric or nearly allopatric taxa that are known or believed to have evolved to the species level" (Amadon 1966, 1968; see also Mayr 1931, 1942, 1963, 1970; Mayr & Diamond 2001; Mayr *et al.* 1953; Haffer 1986; Mallet 2007). This observation may indicate that the species of at least some of the subgroups represent very recent events of allopatric speciation, since even in cases where the former geographic barrier seems to have already collapsed, the allospecies (i.e., each constituent species of a superspecies) remain largely allopatric or parapatric in relation to its sister or other closely-related species.

For instance, in the *bridarollii* subgroup, the distribution of *S. bridarollii* and *S. attenboroughi* sp. nov. are parapatric, with a clear overlap in southern Peru and northwestern Brazil, but neither penetrates completely into the range of the other, with *S. bridarollii* being the only species occurring both south to Bolivia and north to Colombia, while *S. attenboroughi* sp. nov. is the only one to occur farther east in Brazil (Fig. 34). *Sylvicanthon edmondsi* sp. nov., on the other hand, is found in sympatry with *S. bridarollii* throughout its distribution range, although no possible case of hybridization has been found, indicating thereby that a complete reproductive isolation must already have been developed, which in turn made sympatry possible without the merging of both species. The fourth member of this subgroup/superspecies, *S. seag* sp. nov., is the only one completely allopatric in relation to the other three species, being separated from them by the Amazon River.

The case of the *candezei* subgroup is probably distinct, since the three allospecies are distributed very apart from each other, one in the Atlantic Forest (*S. foveiventris*), the second in the southeastern Amazonia (*S. candezei*), and the third on the slopes of the Andes (*S. genieri* sp. nov.) (Fig. 24). This may indicate instead a relict distribution pattern of a subgroup that was once widely distributed in the Amazon Basin and, perhaps, even in the Atlantic Forest. The distribution of the species in the *furvus* subgroup (Fig 41), in turn, is so poorly known that it is difficult to make any generalization. Given the very suble morphological differences between its three Amazonian allospecies (*S. furvus*, *S. monnei* sp. nov. and *S. mayri* sp. nov.), however, we believe this subgroup, in the same way as discussed above for the *bridarollii* subgroup, should have experienced a series of recent speciation events. As for the *aequinoctialis* subgroup, the continuing uplift of the Colombian Andes, with the subsequent isolation of two independent demes on either side of the mountain range, should have been the vicariance event responsible for the division of the ancestral species that gave origin to *S. aequinoctialis* and *S. proseni* (Fig. 30).

Although the concept of superspecies has been mostly applied to vertebrate taxa (particularly birds), some authors such as Huang (2017), dealing with the genus *Dynastes*, and Mayr (1963: 501), referring to the *Mycotrupes* LeConte, 1866 studied by Olson *et al.* (1954), have already used it to refer to monophyletic groups of allopatric species in Scarabaeoidea. Although one could argue that the adoption of this term would only add more uncertainty to an already rather turbulent epistemological context (see the discussion on the species concept above), the first author of this monograph believes that its synthesis of both biogeographical (allopatry) and phylogenetic (monophyly) information is of great value for evolutionary studies, particularly for those dealing with allopatric speciation processes (i.e., the formation of geographic barriers to the gene flow, the development of reproductive isolation and the multiplication of species). Therefore, he encourages a more widespread application of the superspecies concept in biogeographical and taxonomic works dealing with scarab beetles. See Amadon (1966, 1968) for a more detailed defence of the value of the term superspecies.

Natural history

Literature and label information make it clear that *Sylvicanthon* species are primarily coprophagous, consuming human faeces and other primate, pig and cow dung, although there are also some records of specimens feeding on carcases. All the species are nocturnal, as can be inferred from their large eyes with smooth corneas (Caveney & McIntyre 1981; McIntyre & Caveney 1998) and from their usual dark colouration (Hernández 2002; Feer & Pincebourde 2005). It is curious to note that, in this genus context, some species can be classified as eurytopic, such as *S. proseni*, *S. aequinoctialis*, *S. bridarollii* and *S. seag* sp. nov., as they live in a wide altitudinal gradient, have a vast distribution and are very abundant (usually, they are among the most abundant species in the dung beetle communities of which they are part), while other species, thanks to their rarity or environmental specificity (or both factors), are clearly stenotopic, like *S. securus*, *S. foveiventris* and, especially, *S. furvus*, *S. monnei* sp. nov. and *S. mayri* sp. nov. *Sylvicanthon foveiventris*, for instance, although not rare, is found only in forest areas higher than 600 m, whereas *S. securus*, despite having a wide distribution in the north of the Amazon region, is a very rare species. In fact, this relationship between specialist and less-abundant species in contraposition to more generalist and more abundant ones is clear when we compare the relative abundance of *S. seag* sp. nov. and *S. securus* in places where those two species occur in sympatry: the relation can vary from three up to 65 *S. seag* sp. nov. for each *S. securus* in the same area, according to the data gathered for the present work (see more details in the discussion of *S. securus*). Nothing is known about the nesting behaviour of *Sylvicanthon*, although it is reasonable to assume they belong to Pattern IV as defined by Halffter & Edmonds (1982), where most of the American Deltochilini are classified to.

Identification key to the species of *Sylvicanthon* Halffter & Martínez, 1977

1. Clypeus with four teeth (Fig. 6A). Anterior margin of profemora with denticulation at its apical half (Fig. 9B). Protibiae with three large and widely separated teeth and with a strong expansion on its internal edge (Fig. 11A). Hypomera with posterior part with about 5 long setae forming a longitudinal row close to external edge (Fig. 9D). Ecotone between the Amazon rainforest, Cerrado, and the Atlantic Forest in Brazil (Maranhão, Piauí, Ceará, Bahia, and Minas Gerais) .... ***enkerlini* group**: *Sylvicanthon enkerlini* (Martínez *et al.*, 1964) comb. nov.
– Clypeus with only two small apical teeth (Fig. 6B–G). Anterior margin of profemora without denticulation (Fig. 9A). Protibiae with two or three small or medium-sized teeth; if teeth are large, internal edge always straight; if small, internal edge straight or expanded (Figs 11C–J). Hypomera with posterior part glabrous. Humid tropical forest in Central America, Amazonia and Atlantic Forest .... ***candezei*** group: 2

2. Protibiae with two small teeth and internal edge always straight (Fig. 11J) ... *candezei* subgroup: 3.
– Protibiae with three small or large teeth and internal edge straight or expanded (Fig. 11C–I) 5

3. Head and pronotum purplish and elytra green or dark blue (Fig. 23A). Pronotum and elytra with no microsculpture at centre. Metafemora with coarse elongate punctation at base (Fig. 13A). Females with three pairs of lateral foveae on abdomen between ventrites I–II, II–III, and III–IV (Fig. 14B, 16D). Parameres simple, without ventral keel or notch (Fig. 17B). Forests above 600 m in southeastern Brazil ....***Sylvicanthon foveiventris*** (Schmidt, 1920).
– Different colour pattern. Centre of pronotum and elytra with strong microsculpture (*S. genieri* sp. nov.) or with smooth or even absent microsculpture (*S. candezei*). Metafemora without coarse punctation at base. Abdomen of both sexes without lateral foveae. Parameres with ventral keel and/or notch (Fig. 17C–D). Amazonia 4

4. Dorsal colouration of the body dark green (Fig. 25A). Centre of pronotum, elytra, and pygidium without microsculpture (northern populations) or with flat alveolar microsculpture weakly marked (southern populations); in both cases, micropunctation abundant (denser on pronotum than on elytra). Posterior edge of ventrite V, in males, with a weak flange covering anterior edge of ventrite VI (Fig. 14D); in females, posterior edge of ventrite V with a strong medial expansion over ventrite VI (Fig. 14E). Parameres with strong ventral notch and without ventral keel (Fig. 17C). Humid tropical forests from the mouth of the Tapajós River down to the semideciduous forests of southern and southeastern Amazonia in Brazil (Pará and Mato Grosso) ....***Sylvicanthon candezei*** (Harold, 1869).
– Dorsal colouration bright coppery (occasionally, with greenish reflections on head and on the sides of elytra) (Fig. 27A). Centre of pronotum, elytra, and pygidium with strong alveolar microsculpture obliterating micropunctation. Posterior edge of ventrite V, in males, without medial flange (rarely, with a very weak trace of flange over anterior edge of ventrite VI); in females, posterior edge of ventrite V with weak medial flange over ventrite VI. Parameres with short ventral notch and strong ventral keel (Fig. 17D). Cloud forests of western Amazonia and slopes of the Andes in Ecuador and Peru ....***Sylvicanthon genieri*** sp. nov.

5. Suture between submentum and gula Y-shaped (Fig. 8B). Protibiae with internal edge straight and medium- or large-sized teeth at their apical half (Fig. 11B). Ventral face of metafemora with posterior margin (Fig. 31). Humeral carina always presente (Fig. 12C). Parameres with depressed apical area (Fig. 17E–F); without ventral keel or notch. Central America and Amazon Basin .... ***aequinoctialis*** subgroup: 6.
– Suture between submentum and gula rounded (Fig. 8A). Protibiae with internal edge straight or expanded and with small and narrow teeth at their apical third (Fig. 11C–I). Ventral face of metafemora without posterior margin (Fig. 13). Humeral carina usually absent (present only in some specimens of *S. obscurus*). Parameres without depressed apical area; with or without ventral keel and notch. Amazon Basin and Atlantic Forest 7

6. Dorsum, ventral surface of metafemora, and pygidium with bright and lustrous appearance. Centre of pronotum and elytra without microsculpture or with very subtle flat alveolar microsculpture. Ventral surface of metafemora and pygidium with very fine three-dimensional alveolar microsculpture (i.e., with tiny alveoli). Posterior edge of head with margin between eyes always complete. Posterior margin of metafemora extending from apex to at least the height of trochanter (usually going beyond it) (Fig. 31A). Protibial spur of females spiniform (Fig. 15G). From Honduras to northern Colombia .... ***Sylvicanthon aequinoctialis*** (Harold, 1868) comb. nov.
– Dorsum, ventral surface of metafemora, and pygidium with diffuse shine and with a more matte appearance. Centre of pronotum, ventral surface of metafemora and pygidium with very strong

three-dimensional alveolar microsculpture; micropunctation ranging from very dense to absent. Posterior edge of head with margin between eyes complete, incomplete, or absent. Posterior margin of metafemora not reaching trochanter (usually extending little beyond the apical half of metafemur) (Fig. 31B). Protibial spur of female bifid (Fig. 15H). Amazonia (Colombia, Ecuador, Brazil, Peru, and Bolivia) ....***Sylvicanthon proseni*** (Martínez, 1949) stat. et comb. nov.

7. Protibiae with internal margin straight (Fig. 11H–I) (moderately expanded in northern populations of *S. bridarollii* (Fig. 11G) and only slightly expanded in southern populations of this species (Fig. 11F); in these cases, pronotum with alveolar microsculpture). Lateral portions of metaventrite completely glabrous. Abdomen of both sexes without lateral fovea. Amazonia ....***bridarollii*** subgroup: 8

– Protibiae with internal edge clearly expanded (Fig. 11C–E). Pronotum without alveolar microsculpture. Sides of metaventrite with some few setae near metacoxae (Fig. 7B). Abdomen of females with (Fig. 16A–C) or without lateral foveae (absent only in *S. securus*) Amazonia and Atlantic Forest 11

8. Hypomeral cavity covered at centre by long yellowish erect setae (Fig. 25C–D). Protibiae with internal edge moderately (Fig. 11G; northern populations) or only slightly (Fig. 11F; southern populations) expanded. Metafemora with (Fig. 13G) or without (Fig. 13H) coarse elongate punctation at base. Metaventrite covered at centre by strong three-dimensional alveolar microsculpture. Pygidium with three-dimensional alveolar microsculpture strongly marked and with very subtle, almost imperceptible punctation. Parameres symmetrical (both with external face flat) and simple, without ventral keel or notch (Fig. 18A). Western Amazonia in Colombia, Ecuador, Brazil (Acre, Rondônia), Peru and Bolivia ....***Sylvicanthon bridarollii*** (Martínez, 1949).

– Hypomeral cavity glabrous at centre (Fig. 35A–B; rarely with one or two very short setae); setae, if present, restricted to anterior and posterior regions of the cavity. Protibiae with internal edge straight (Fig. 11H–I). Metafemora without coarse elongate punctation at base (except in rare especimens of *S. attenboroughi* sp. nov.) (Fig. 13F). Metaventrite with very fine alveolar microsculpture at centre and progressively more diffuse towards posterior region. Pygidium with or without alveolar microsculpture strongly marked and with micropunctation of variable density, but always evident. Parameres asymmetrical (external face of left paramere excavated and external face of right paramere flat) and with ventral keel (Fig. 18B–D). Amazonia 9

9. Anterior edge of ventrite VI of females distinctly covered by medial flange of posterior edge of ventrite V. Parameres with strong ventral notch and with ventral carina strongly projected; apical half of parameres squared (Fig. 18B). Northern Amazonia, in Trinidad, Venezuela, Guyana, Suriname, French Guiana and Brazil; except the region east of its mouth, always limited to the left banks of the Amazon River ....***Sylvicanthon seag*** sp. nov.

– Anterior edge of ventrite VI of females only subtly covered by weak medial expansion of posterior edge of ventrite V. Parameres with elongate appearance and shorter ventral keel (Fig. 18C–D). Western and southern Amazonia 10

10. Head dark purple, pronotum with strong greenish or bluish shine at centre and purplish on sides, elytra dark blue or purple, and meso- and metafemora orangish-brown or yellowish (Fig. 38A–B). Dorsal surface of head with very subtle, almost imperceptible micropunctation. Northwestern Amazonia, mainly in Sub-Andean areas in Colombia, Ecuador and Peru ....***Sylvicanthon edmondsi*** sp. nov.

– Head and pronotum entirely very dark purple (almost black), without central greenish or bluish central spot on pronotum; elytra dark green or dark blue; meso- and metafemora orangish-brown, reddish-brown or dark brown (Fig. 38C–D). Dorsal surface of head with micropunctation evident on posterior region of clypeus and mainly on frons. Southern Amazonia, on the right margin of the Amazon River, in Brazil and Peru ....***Sylvicanthon attenboroughi*** sp. nov.

11. Each clypeal tooth with base covered by a separate row of setae. Elytra with dense micropunctation and without trace of alveolar microsculpture. Internal edge of protibiae strongly expanded (Fig. 11C). Abdomen of both sexes without lateral foveae. Parameres simple, without apical bifurcation (Fig. 88). Northern Amazonia, in Suriname, French Guiana and Brazil ....***Sylvicanthon securus*** (Schmidt, 1920) comb. nov.

– Pair of clypeal teeth with base covered by a single row of setae. Elytral sculpture variable, alveolar microsculpture present or not. Internal margin of protibiae not as strongly expanded as in *S. securus* (Fig. 11D–E). Females with three pairs of foveae at the sides of the abdomen between ventrites I–II, II–III, and III–IV (Fig. 16A–C). Parameres bifurcate at apex (Fig. 19B–E). Southern and western Amazon and the Atlantic Forest ....***furvus*** subgroup: 12

12. Elytra with strong micropunctation and without microsculpture at centre and with strong three-dimensional alveolar microsculpture on sides and apex. Humeral carina present in about two-fifths of the specimens (Fig. 12C). Metafemora without coarse elongate punctation at base (Fig. 13B). Lateral foveae of abdomen of females covered by row of long setae (Fig. 16C). Parameres with branches of apical bifurcation free, with no membrane connecting them (Fig. 19B). Northern Atlantic Forest, from Alagoas to Espírito Santo (Brazil) ....***Sylvicanthon obscurus*** (Schmidt, 1920).

– Elytra with different sculpture pattern; either entirely microsculptured or entirely smooth. Humeral carina always absent. Metafemora with coarse elongate punctation (Fig. 13C, E) (except *S. mayri* sp. nov., Fig. 13D; see comments above). Lateral foveae of female abdomen glabrous (Fig. 16A–B). Parameres with branches of apical bifurcation connected by a fine membrane (Fig. 19C–E). Amazonia 13

13. Head with diffuse shine and strong alveolar microsculpture covering the entire tegument. Meso- and metafemora with ventral surface completely covered by rivose microsculpture, with no smooth areas and with strong three-dimensional alveolar microsculpture. Elytra with diffuse shine and entirely covered by strong three-dimensional alveolar microsculpture. Pygidium with diffuse alveolar microsculpture at centre and apex, and with strong rivose microsculpture at base. Eastern slopes of the Andes in Peru and Bolivia ....***Sylvicanthon furvus*** (Schmidt, 1920).

– Head shiny and with weak alveolar microsculpture, which, in some areas, is totally absent. Meso- and metafemora with ventral surface almost entirely smooth and with evident micropunctation, except on anterior apical area with rivose microsculpture. Elytra shiny, entirely smooth or with very diffuse microsculpture and ill-delimited alveoli. Pygidium completely smooth at centre and with rivose microsculpture occasionally present on sides of base. In general, in lower Amazon areas; with no records from the Peruvian and Bolivian Andes 14

14. Elytra smooth, with no trace of microsculpture throughout its surface. Metafemora with coarse elongate punctation at base (Fig. 13C). Abdominal foveae of females always well marked and deep (Fig. 16A). Parameres with inferior branch of apical bifurcation weakly projected or straight, without posterior excavation (Fig. 44C). Southern Brazilian Amazonia (Pará and Mato Grosso)..***Sylvicanthon monnei*** sp. nov.

– Elytra with diffuse microsculpture, which is difficult to see and has ill-defined alveoli. Metafemora with coarse punctation modified in fine, simple points at centre of base (Fig. 13D; but see discussion above). Abdominal foveae of females very shallow (especially between ventrites III–IV) (Fig. 16B). Parameres with inferior branch of apical bifurcation well projected and largely divergent from superior branch, with strong posterior excavation (Fig. 44A). Western Amazonia in Colombia, Brazil (Amazonas and Acre) and Peru ....***Sylvicanthon mayri*** sp. nov.

The enkerlini *group*

Sylvicanthon enkerlini (Martínez *et al.*, 1964) comb. nov.

Figs 6A, 9B–D, 10B, 11A, 15A, 17A, 20–22

Glaphyrocanthon (*Glaphyrocanthon*) *enkerlini* Martínez *et al.*, 1964: 5, 8, 13, 17–21, figs 1–2.

Canthon (*Francmonrosia*) *enkerlini* – Halffter & Martínez 1977: 86.
Canthon enkerlini – Krajcik 2012: 63.
Sylvicanthon sp. – Lima *et al.* 2013: 91–93.

Etymology

Eponym after the Mexican entomologist Dieter Enkerlin Schallenmüller (1926–1995) (Martínez *et al.* 1964).

Material examined

Holotype

BRAZIL: ♂, Maranhão, São Luís ("*BRASIL* / *Eº Maranhao* / *São Luiz* / *Coll. Martínez* / *Sep. 955*", "HOLOTYPUS", "*Glaphyrocanthon* / *enkerlini* / *♂* / *sp. nov.* / *M. H. y H.* / A. Martínez det 19*63*", "*FICHADO*", "MACN-En / 1050"), genital capsule removed and glued in a triangular label (MACN-En / 1050) (Fig. 21C).

Additinal material (47 ♂♂, 44 ♀♀)

BRAZIL: **Bahia**: 1 ♀, Barreiras, Oct. 1991, light trap, without collector (CEMT); 1 ♀, Barreiras, Nov. 1991, without collector (CEMT); 2 ♂♂, 1 ♀, Barreiras, Jan. 2003, P. Schmidt leg. (CEMT); 2 ♀♀, Pilão Arcado, Barra do Brejo, 10º06.677′ S, 42º53.678′ W, 416 m, 5 Dec. 2005, P.P. Lopes leg. (CEMT); 2 ♀♀, Pilão Arcado, Barra do Brejo, 10º06.677′ S, 42º53,678′ W, 416 m, 27 Mar. 2006, V. Mendes leg. (MZFS). – **Maranhão**: 2 ♂♂, 4 ♀♀, Mirador, Parque Estadual do Mirador, Povoado Pindaíba (Mel), 06º41′06″ S, 45º00′26″ W, 1–5 Jun. 2010, pitfall with human faeces, F. Limeira-de-Oliveira, M.M. Abreu and J.S. Pinto leg. (CEMT). – **Minas Gerais**: 1 ♀, Bandeira ("*R. Bandeira*"), Jan. 1932, José Blaser leg. (MZSP); 1 ♂, Jaíba, Mocambinho, 15º09′03.1″ S, 43º56′03.4″ W, 450 m, 28 Mar. 2012, pitfall with human faeces, A. Fialho leg. (CEMT); 1 ♀, Três Marias, 17 Mar. 1992, without collector (CEMT). – **Piauí**: 1 ♂ (dissected), 2 ♀♀, Canto do Buriti, 18–22 Nov. 1991, C.R.F. Brandão leg. (MZSP); 2 ♂♂, 1 ♀, Canto do Buriti, 42º48′05″ W, 08º11′12″ S, 254 m, 5 Apr . 2008, trap with dung, Gillett leg. (CEMT); 1 ♂, Corrente ("10 km N Corrente"), Fazenda Maracujá, 23–27 Nov. 1991, E.M. Cancello and M.T. Ponte leg. (MZSP); 1 ♂, Corrente ("10 km N Corrente"), Fazenda Maracujá, 23–27 Nov. 1991, S.T.P. Amarante and C.F. Martins leg. (MZSP); 1 ♂, Floriano, Fazenda Buriti Sol, 5–12 Oct. 1991, S.T.P. Amarante leg. (MZSP); 6 ♂♂, 3 ♀♀, Oeiras ("5 km E Oeiras"), Fazenda Talhada, 13–17 Nov. 1991, C.R.F. Brandão and P. Moutinho leg. (MZSP); 5 ♂♂, 1 ♀, Oeiras ("5 km E Oeiras"), Fazenda Talhada, 13–17 Nov. 1991, E.M. Cancello and M.T. Ponte leg. (MZSP); 1 ♀, Oeiras ("5 km E Oeiras"), Fazenda Talhada, 13–17 Nov. 1991, S.T.P. Amarente leg. (MZSP); 1 ♀, Piripiri, Parque Nacional de Sete Cidades, 04º05′51″ S, 41º42′30″ W, 170 m, 7–12 Feb. 2013, pitfall with human faeces, Vaz-de-Mello and Grossi leg. (CEMT); 1 ♂, 4 ♀♀, same collecting data as for preceding but 180 m (CEMT); 9 ♂♂ (1 dissected), 9 ♀♀, Piripiri, Parque Nacional de Sete Cidades, 04º05′54″ S, 41º42′31″ W, 170 m, 13 Feb. 2013, flight interception trap, Vaz-de-Mello and Grossi leg. (CEMT); 9 ♂♂, 4 ♀♀, Piripiri, Parque Nacional de Sete Cidades, 04º05′38″ S, 41º42′35″ W, 200 m, 13 Feb. 2013, pitfall with human faeces, Vaz-de-Mello and Grossi leg. (CEMT); 1 ♀, Piripiri, Parque Nacional de Sete Cidades, 04º06′38″ S, 41º44′48″ W, 180 m, 12 Feb. 2013, flight interception trap, Vaz-de-Mello and Grossi leg. (CEMT); 1 ♀, Piripiri, Parque Nacional de Sete Cidades, 04º05′03″ S, 41º42′34″ W, 190 m, 7–12 Feb. 2013, pitfall with human faeces, Vaz-de-Mello and Grossi leg. (CEMT); 1 ♂, Ribeiro Gonçalves, Estação Ecológica

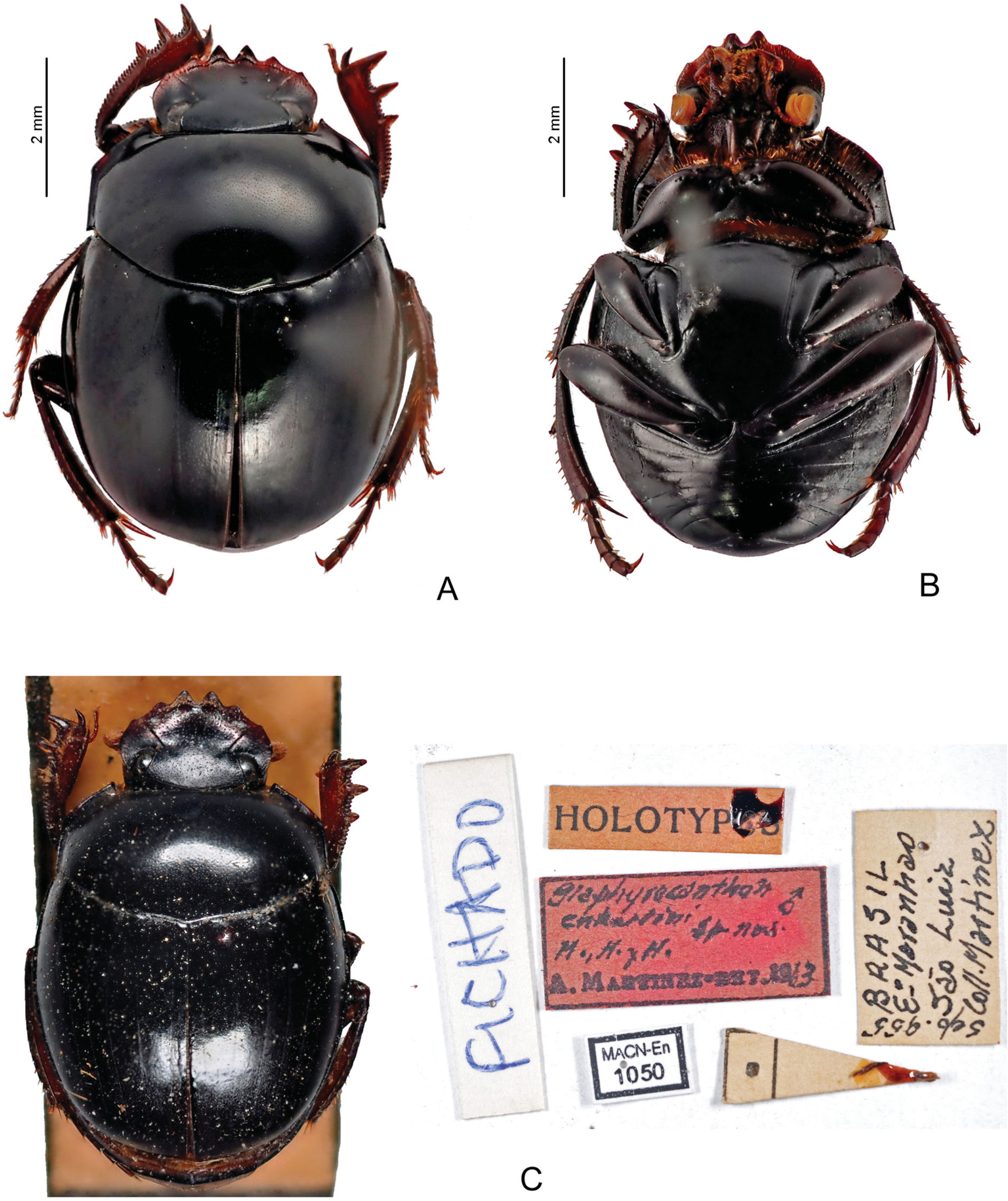

Fig. 21. *Sylvicanthon enkerlini* (Martínez *et al.*, 1964) comb. nov. **A**. Dorsal view. **B**. Ventral view. **C**. Holotype and its labels.

Uruçuí-Una, 08º52′ S, 44º57′ W, 19–29 Jan. 2001, G.G. Montingelli leg. (MZSP); 4 ♂♂, 1 ♀, São Raimundo Nonato, Parque Nacional da Serra da Capivara, Jan. 1999, C.A. Matrangolo leg. (CEMT); 2 ♀♀, São Raimundo Nonato, Parque Nacional da Serra da Capivara, Zabelê, 12 Apr. 2001, A.C.A. Moura leg. (CEMT); 2 ♂♂, Teresina, Jan. 1953, Oliveira leg. (CMNC).

Redescription

Colouration. Dorsum, metaventrite and pygidium entirely black, without metallic reflections; external edge of clypeus occasionally dark brown. Ventral face of legs ranging from black to dark brown; dorsal face of protibiae reddish-brown.

Head. Tegument with diffuse shine and strong alveolar microsculpture, which is usually more marked on frons and genae than on clypeus, which can present diffuse microsculpture; micropunctation always evident throughout dorsal surface, more impressed in areas with sparser microsculpture. Clypeus with four large, acute teeth well separated from one another (Fig. 6A; in worn specimens, teeth obtuse); external edge (including teeth) clearly folded up; with a single row of setae covering the base of the four teeth. Genae with strong tooth immediately behind clypeal-genal juncture. Posterior edge of head with a fine margin between eyes; occasionally, margin lacking only at the area adjacent to eyes.

Thorax. Pronotum with shiny and lustrous tegument; alveolar microsculpture usually restricted to sides, where it is very dense; centre with strong micropunctation and without microsculpture, or with very diffuse microsculpture. Posterior edge with fine transverse line at centre (usually extending up to the second elytral stria). Hypomeral cavity with tegument densely covered by long yellowish setae and with depressed area close to external margin, the latter with a weak tubercle; posterior part of hypomeron with long, individual setae (around five) aligned longitudinally close to its external edge (Fig. 9D). Metepisternum with posterior region, at the suture with metaventrite, with an evident tubercle (Fig. 9C). Metaventrite entirely glabrous; tegument with strong rivose microsculpture at lateral and anterior regions; at centre, alveolar microsculpture very fine and diffuse, slightly more delimited at posterior region; micropunctation very fine, but distinct at centre.

Legs. Profemora with tegument with strong alveolar microsculpture at anterior region, and alveolar microsculpture at posterior region; without micropunctation; anterior margin, at apex of profemur, interrupted by row of denticles (Fig. 9B). Protibiae wide and with internal margin strongly expanded at their apical half (Fig. 11A); in its apical half, external margin with three large, acute teeth widely separated from one another, the apical two of subequal length and longer than the basal. Mesofemora margined anteriorly only at their basal two-thirds; unmargined portion with a row of very short setae; tegument with strong alveolar microsculpture at anterior region and gradually with more diffuse microsculpture towards posterior and basal regions, where micropunctation is strong. Metafemora margined only anteriorly, posterior margin absent; tegument with strong rivose microsculpture at apical and anterior regions, with microsculpture gradually more diffuse towards posterior region and base; micropunctation present throughout the tegument, more marked in areas of diffuse microsculpture, especially at base, where it can be very dense. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others; the entire meso- and metatarsi with a single continuous row of setae throughout its internal margin.

Elytra. With nine very narrow visible striae; in general, first six to seven striae well marked, but never carinulate; from them, striae progressively more effaced and interrupted; humeral carina absent. Tegument of interstriae at centre of elytral disc lustrous and without microsculpture (or with very diffuse microsculpture); lateral and apical regions with strong alveolar microsculpture and diffuse shine; micropunctation present throughout tegument, but more distinguishable in areas without microsculpture.

Abdomen. Ventrite VI with diffuse rivose microsculpture at middle and more clearly marked on the sides; micropunctation absent or very subtle; both sexes without lateral foveae. Pygidium with tegument with diffuse shine and covered by strong alveolar or rivose microsculpture; in some specimens, microsculpture weaker or even absent at apex; micropunctation obliterated by microsculpture and usually indistinct.

Aedeagus. Parameres almost as long as phallobase and symmetrical, both faces flat. In lateral view, parameres simple, without any ventral keel or notch (Fig. 17A).

Sexual dimorphism. **Males**: Protibial spur narrow and bifid at apex, with spiniform projections, the external project longer than the internal one (Fig. 15A). Ventrite VI strongly narrowed at middle; anterior margin covered only slightly by weak medial expansion of posterior edge of ventrite V. Pygidium very long (length between 1.2 and 0.9 mm). **Females**: Protibial spur spiniform, simple, and distinctly bent towards external side. Ventrite VI very wide at middle; anterior margin covered by medial flange of posterior edge of ventrite V. Pygidium shorter (between 1.0 and 0.7 mm).

Measurements

Males (N = 14). **TL:** AV: 6.6 ± 0.64; MX: 8; MN: 5.8. **EW:** AV: 4.6 ± 0.38; MX: 5,5; MN: 4.1. **PL:** ME: 2.1 ± 0.2; MX: 2.5; MN: 1.8. **PW:** AV: 4.0 ± 0.35; MX: 4.8; MN: 3.5. **PgL:** AV: 1.0 ± 0.09; MX: 1.2; MN: 0.9. **PgW:** AV: 1.7 ± 0.23; MX: 2.2; MN: 1.3.

Females (N = 15). **TL:** AV: 6.4 ± 0.58; MX: 7.3; MN: 5.7. **EW:** AV: 4.5 ± 0.39; MX: 5.2; MN: 3.9. **PL:** AV: 2.0 ± 0.18; MX: 2.3; MN: 1.7. **PW:** AV: 3.8 ± 0.31; MX: 4.4; MN: 3.3. **PgL:** AV: 0.9 ± 0.08; MX: 1; MN: 0.7. **PgW:** AV: 1.7 ± 0.11; MX: 1.9; MN: 1.5.

Geographical distribution

Dry forests between Cerrado, Caatinga, Amazonia and the Atlantic Forest in the Brazilian north- and southeast.

Ecoregions

Maranhão Babaçu Forests, Cerrado, Caatinga, Bahia Interior Forests.

Collecting sites (Fig. 22)

BRAZIL. **Maranhão**: São Luís, Mirador (Parque Estadual do Mirador). **Piauí**: Canto do Buriti, Corrente, Floriano, Oeiras, Parnaíba, Piripiri (Parque Nacional de Sete Cidades), Ribeiro Gonçalves (Estação Ecológica de Uruçuí-Una), São Raimundo Nonato (Parque Nacional da Serra da Capivara), Teresina. **Ceará**: Caucaia. **Bahia**: Barreiras, Pilão Arcado. **Minas Gerais**: Bandeira, Jaíba, Três Marias.

Intraspecific variation and taxonomic discussion

If, on the one side, *S. enkerlini* comb. nov. seems to be the most isolated species in the genus and with no close relationships to any known Deltochilini, on the other side, the studied populations form a cohesive entity without any noticeable geographical variation. In the same way, little intrapopulational variation was observed. The exceptions are the specimens (two males and one female) collected in 2003 by P. Schmidt in Barreiras (Bahia): the alveolar microsculpture of the entire tegument is much stronger on them than on the other individuals, being evident even at the centre of the pronotum (where it is diffuse in the other specimens). The two females collected at the same place in 1991, on the other hand, have microsculpture typical of the rest of the distribution of *S. enkerlini*, as well as the four females collected between 2005 and 2006 in the municipality of Pilão Arcado, distant only about 300 km from Barreiras. The reason for that difference is unknown to us.

Natural history

Martínez *et al.* (1964) described *S. enkerlini* based solely on the male holotype collected in a humid forest surrounding a water reservoir in the outskirts of the city of São Luís, Maranhão, Brazil ("*el ejemplar holotipo y único* [...] *fue capturado en las afueras de la ciudad de Sao Luiz, dentro del bosque tropical y húmedo que rodea la reserva de agua potable de esa población*"). As they were aware of only this single geographical record, those authors considered *S. enkerlini* as being a typical Amazonian species. Nonetheless, over the past 25 years, several collections in transitional regions between the Cerrado, Caatinga and Amazonia, in the Brazilian states of Piauí, Bahia, Ceará and Minas Gerais, have revealed the presence of *S. enkerlini* in that vast area, whereas other collections in regions farther west in the Amazon forest, such as in the state of Pará, have not yielded the species. Therefore, it seems

Fig. 22. Distribution of *Sylvicanthon enkerlini* (Martínez *et al.*, 1964) comb. nov. Note that the species occupies transition zones between the Amazonia, Cerrado, Caatinga and Atlantic Forest biomes, regions much dryer and more open than the humid forests occupied by the species of the *candezei* group.

that *S. enkerlini* is actually an inhabitant of open and dry lowland forests typical of the transitional zone between those three biomes, including the Mata dos Cocais, in the transitional zone between the Amazon rainforest and the Caatinga, where the babaçu palm (*Attalea speciosa* Mart.) predominates. One specimen was collected in 1932 in the municipality of Bandeira, Minas Gerais, an area originally covered by the Atlantic rainforest (ecoregion of Bahia Interior Forests). However, due to the intense anthropogenic activity across this entire ecoregion converting the former humid forest into open areas for agriculture and pasture, it was given the right conditions for the immigration of a fauna typical of Cerrado into that region, *S. enkerlini* included.

Based on the specimen labels, it is possible to know that *S. enkerlini* occurs in altitudes between 170 and 416 m and is collected between October and June (no records for May) using pitfall traps baited with human faeces as well as flight interception traps and light traps. The only record of flight activity time is that of Martínez *et al.* (1964), who said the holotype was collected during the first hours of the evening.

The *candezei* group

The candezei subgroup

Sylvicanthon foveiventris (Schmidt, 1920)
Figs 13A, 14B, 15B, 16D, 17B, 20, 23–24

Canthon foveiventris Schmidt, 1920: 132–133.

Canthon foveiventris – Schmidt 1922: 64, 75. — Balthasar 1939: 188–189. — Martínez 1949a: 287. — Halffter & Martínez 1977: 63. — Krajcik 2012: 63.
Canthon foveiventre – Blackwelder 1944: 199.
Glaphyrocanthon (*Glaphyrocanthon*) *foveiventris* – Pereira & Martínez 1956: 126, 128. — Martínez *et al.* 1964: 5, 8, 10, 14. — Vulcano & Pereira 1964: 662. — Martínez & Pereira 1967: 53.
Sylvicanthon foveiventre – Vaz-de-Mello & Louzada 1997: 57. — Vaz-de-Mello 2000: 195. — Hernández 2002: 598. — Falqueto *et al*. 2005: 20. — Hernández & Vaz-de-Mello 2009: 610–611. — Hernández *et al.* 2011: 7–8, fig. 3.
Sylvicanthon foveiventris – Durães *et al.* 2005: 725. — Almeida & Louzada 2009: 37-39. — Culot *et al.* 2013: 85, 87.

Etymology

From the Latin words '*fovea*' and '*ventris*', a likely reference to the three pairs of foveae present on the sides of the abdomen of females of this species.

Material examined

Lectotype (here designated)
BRAZIL: ♂, Espírito Santo ("9652 / E92 +", "24 / *56*", "LECTOTYPE ♂ / *Canthon* / *foveiventris* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*13*", "*Glaphyrocanthon* / *foveiventris* / *(Schm.)* / P. Pereira det. *66*", "*foveiventr*.", "Esp. Santo") (NHRS) (Fig. 23Ca, b).

Paralectotypes
BRAZIL: 1 ♀, ("*foveiventris* / Schm.", "9653 / E92 +", "Espir. / Santo", "*foveiventr*", "*foveiventris* / *A. Schm*.", "PARALECTOTYPE / ♀ / *Canthon* / *foveiventris* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*13*") (NHRS) (Fig. 23Cc); 1 ♂ ("PARALECTOTYPE / ♂ / *Canthon* / *foveiventris* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *foveiventris* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *foveiventris* / *Schmidt*

/ des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *foveiventris* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♀, ("Typus", "Esp. Santo", "Coll. C. Felsche / Kauf 20, 1918", "*Canthon* / *foveiventris* / *A. Schmidt*", "PARALECTOTYPE / ♀ / *Canthon* / *foveiventris* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*") (SMTD) (Fig. 23Cd).

Fig. 23. *Sylvicanthon foveiventris* (Schmidt, 1920). **A**. Dorsal view. **B**. Ventral view. **C**. *S. foveiventris* type material: **a**. Lectotype. **b**. Lectotype's labels. **c**. Paralectotype 1's label. **d**. Paralectotype 6's labels.

Additional material (140 ♂♂, 144 ♀♀)
BRAZIL: 1 ♀, no further data, B. Schwarzer leg.,ex. coll. Balthasar (NMPC). – **Bahia**: 1 ♂, no other data ["homeótipo"] ("F. Ohaus S.") (MZSP); 1 ♀ (NMPC). – **Espírito Santo**: 1 ♂, 1 ♀, no other data (BMNH); 5 ♀♀ (NMPC); 1 ♂ (ZMHB); 1 ♂, Jean-Theodore Descourtilz ("Descourtils") leg. (BMNH); 1 ♂, 1 ♀, Conceição do Castelo, Feb. 1994, Vaz-de-Mello leg. (MCNZ); 4 ♂♂, 1 ♀, Conceição do Castelo, 20º22′ S, 41º15′ W, Feb. 1994, human faeces, Arnaud, Grossi and Vaz-de-Mello leg. (CEMT); 2 ♂♂, 3 ♀♀, same collecting data as preceding (CMNC); 1 ♂, 1 ♀, Domingos Martins, Jan. 2000, C.-L. Andrade leg. (NMPC); 3 ♂♂, 1 ♀, Domingos Martins, Parque Estadual da Serra Azul, 1500 m, Jan. 2000, Lopes-Andrade and Vaz-de-Mello leg. (CEMT); 1 ♀, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha Indaia-Açu, 19º58′13″ S, 40º32′06″ W, 779 m, 29 Jan. 2015, pitfall trap baited with human faeces, T. Vargas leg. (CEMT); 1 ♀, Vargem Alta, Jan. 2000, Louzada and Louzada leg. (CEMT); 1 ♀, Vargem Alta, 680 m, 15 Sep. 1995, J.N.C. Louzada leg. (CEMT); 1 ♀, Venda Nova do Imigrante, Lavrinhas, 20º12′29″ S, 41º07′23″ W, Jan. 2013, L.F. Vaz-de-Mello leg. (CEMT); 1 ♀, Venda Nova do Imigrante, Lavrinhas, 20º12′29″ S, 41º07′23″ W, 850 m, 10–14 Jan. 2011, human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 1 ♀, Venda Nova do Imigrante, Vila Santa Cruz, 20º20′02″ S, 41º08′18″ W, 800 m, 10–14 Jan. 2011, human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 1 ♀, Venda Nova do Imigrante, Lavrinhas, 20º18′40″ S, 41º08′16″ W, Dec. 2012, L.F. Vaz-de-Mello leg. (CEMT). – **Minas Gerais**: 2 ♀♀, Barão de Cocais, Vale Mineração, 19º57′17″ S, 43º33′51″ W, 860 m, 4 Nov. 2011, human faeces, R.N. Mota leg. (CEMT); 1 ♂, Conceição dos Ouros, Rio Sapucaí, 19 Feb. 2003, without collector (CEMT); 1 ♂, 1 ♀, Carrancas, Intituto de Permacultura Cerrado-Pantanal ("Inst. Perm. Cer. Pantanal"), 1217 m., -21.4556′ S, -44.6203′ W, 21 Oct. 2008, pitfall with human faeces, Clever Pinto col. (CEMT); 5 ♂♂, 4 ♀♀, Diamantina, Campus UFVJM, 17 Dec. 2005, S.L. Assis Junior leg. (CEMT); 1 ♂, Itamonte, 22º21′ S, 44º48′ W, 1737 m, 12 Oct. 2009, T. Vidaurre *et al.* leg. (CEMT); 1 ♂, Lavras, May 1997, J. Louzada leg. (CEMT); 1 ♀, Lavras, 21º19′02.54″ S, 44º59′25.29″ W, 20 Jan. 2008, M.R. Rocha and D.H.T. Takahashi leg. (CEMT); 1 ♀, Lavras, Serrinha da Bocaina, 27 Apr. 2012, pig dung, A. Díaz-Rojas leg. (CEMT); 2 ♀♀, Lima Duarte, Parque Estadual do Ibitipoca, Dec. 1997, Souza *et al.* leg. (CEMT); 2 ♂♂, Nova Lima, Parque Estadual da Serra do Rola-Moça, 2005, G. Schiffler leg. (CEMT); 1 ♀, Prados, 21º04′40″ S, 44º08′06.1″ W, 1090 m, 17 Feb. 2012, pitfall with human faeces, Letícia Vieira *et al.* leg. (CEMT); 2 ♂♂, Rio Acima, 20º00′20″ S, 43º41′37″ W, 993 m, 29 Nov. 2007, E. Bordoni leg. (CEMT); 2 ♀♀, Rio Acima, Vale Mineração, 20º03′27″ S, 43º40′23″ W, 1334 m, 10 Oct. 2010, human faeces, R.N. Mota leg. (CEMT); 2 ♂♂, 1 ♀, São Gonçalo do Rio Abaixo, Estação Ambiental Peti, 19º53′21″ S, 43º21′43″ W, 1 Dec. 2010, F. França leg. (CEMT); 1 ♀, São João Evangelista, 18º33′11″ S, 42º53′58″ W, 898 m, 2. Apr. 2011, human faeces, R.N. Mota leg. (CEMT); 2 ♂♂, 2 ♀♀, Viçosa, Mata do Paraíso, 20º48′18″ S, 42º51′20″ W, 750 m, 3 Feb. 2000, F. Génier leg., trap with dung (CMNC); 1 ♀, Viçosa, Mata do Paraíso, 20º48′18″ S, 42º51′20″ W, 750 m, 4 Feb. 2000, F. Génier leg., trap with dung (CMNC). – **Rio de Janeiro**: 1 ♂, no more data (ISNB); 1 ♂, 1 ♀, Itatiaia, Jan. 1961, Dirings leg. (MZSP); 1 ♂, Itatiaia, 700 m, Feb. 1959, W. Zikan leg. (CEMT); 2 ♀♀, same collection data as preceding (MNRJ); 1 ♀, Itatiaia, Mar. 1992, C. Godinho Junior leg. (CEMT); 1 ♀, Nova Friburgo, Jan. 1995, F.Z. Vaz-de-Mello leg. (CEMT); 4 ♂♂, 4 ♀♀, Nova Friburgo, 22º23′04″ S, 42º33′30″ W, 750 m, 21 Jan. 2000, trap with dung, F. Génier and S. Ide leg. (CMNC); 4 ♂♂, 3 ♀♀, Nova Friburgo, 22º23′04″ S, 42º33′30″ W, 750 m, 23 Jan. 2000, trap with dung, F. Génier and S. Ide leg. (CMNC); 1 ♀, Nova Friburgo, Macaé de Cima, Jan. 2006, B. Miller leg. (AMBC); 1 ♂, 1 ♀, Nova Friburgo, Macaé de Cima, 1500 m, Mar. 2000, Lopes-Andrade, Gumier and Vaz-de-Mello leg. (CEMT); 1 ♀, Nova Friburgo, Muri ("Mury"), 22º21′49″ S, 42º33′07″ W, 1150 m, 22 Jan. 2010, trap with dung, F. Génier and S. Ide leg. (CMNC); 2 ♀♀, Parque Nacional da Serra dos Órgãos (PARNASO), 850 m, Dec. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PARNASO, 950 m, Dec. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♀, PARNASO, 1030 m, Jan. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♀, PARNASO, 1080 m, Jan. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PARNASO, 1130 m, Jan. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg.

(CLEI); 1 ♂, PARNASO, 1150 m, Dec. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PARNASO, 1230 m, Jan. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PARNASO, 1230 m, 28–30 Jan. 2014, pitfall trap, Cristina Araújo and Raissa Andrade leg. (CEMT); 1 ♂, PARNASO, 1280 m, Jan. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 3 ♂♂, PARNASO, 1330 m, Jan. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♀, PARNASO, 1400 m, Dec. 2014, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, 1 ♀, Parque Nacional do Itatiaia (PNI), 700 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♂♂, 1 ♀, PNI, 750 m, 22–24 Oct. 2010, pitfall with human faeces, Wallace Beiroz and Mario Cupello leg. (MNRJ); 1 ♂, PNI, Casa do Pesquisador, 750 m [sic], 11–13 Nov. 2011, pitfall, Mario Cupello leg. (MNRJ); 1 ♂, PNI, 750 m, Jan. 2012, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PNI, 800 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♀, PNI, Casa do Pesquisador, 810 m, 22–25 Feb. 2013, pitfall with human faeces, Mario Cupello leg. (CEMT); 6 ♂♂, 1 ♀, same sollecting data as for preceding (MNRJ); 1 ♀, PNI, Casa do Pesquisador, 850 m, 03–06 Oct. 2013, A. Carelli and J.P. Botero leg. (MNRJ); 1 ♂, PNI, 900 m, dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♀♀, PNI, 900 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 16 ♂♂, 7 ♀♀, PNI, 1000 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♀, PNI, 1050 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 3 ♂♂, 6 ♀♀, PNI, 1050 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PNI, 1050 m, Aug. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PNI, 1100 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. CLEI); 1 ♂, PNI, 1200 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♂♂, 2 ♀♀, PNI, 1250 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♂♂, 1 ♀, PNI, 1250 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 5 ♂♂, 6 ♀♀, PNI, 1300 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, 1 ♀, PNI, 1350 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♂♂, PNI, 1400 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, 1 ♀, PNI, 1400 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, 1 ♀, PNI, 1450 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♂♂, PNI, 1450 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, 2 ♀♀, PNI, 1500 m, Dec. 2011, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♀, PNI, 1550 m, Aug. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, PNI, 1600 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 2 ♀♀, PNI, 1750 m, Jan. 2012, pitfall with human faeces, Cristina Araújo and Raissa Drufrayer leg. (CLEI); 1 ♂, Rio de Janeiro, Grajau, Nov. 1965, H.S. Lopes leg. (CEMT). – **São Paulo**: 1 ♀, Mogi das Cruzes, Parque das Neblinas, 23º47′28″ S, 46º11′48″ W, 810 m, Nov. 2015, pitfall trap baited with human faeces, R.V. Nunes leg. (CEMT); 2 ♀♀, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, Sede Itamambuca, 23º19′30″ S, 45º04′58″ W, 18 Jan. 2012, pitfall trap baited with human faeces, E. Bovy leg. (CEMT); 7 ♂♂, 12 ♀♀, Parque Estadual da Serra do Mar, Núcleo Virgínia, Sede Vargem Grande, 23º26′15″ S, 45º14′16″ W, 17 Jan. 2012, human faeces, E. Bovy leg. (CEMT); 18 ♂♂, 25 ♀♀, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, Sede Itamambuca, 23º19′27″ S, 45º05′08″ W, 18 Jan. 2012, human faeces, E. Bovy leg. (CEMT); 2 ♂♂, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, Sede Vargem Grande, 23º26′35″ S, 45º14′21″ W, 17 Jan. 2012, human faeces, Marion Boutefeu leg. (CEMT); 1 ♂, Salesópolis, Estação Biológica de Boracéia, Jan. 2006, M. Uehara leg. (CEMT); 1 ♂, Salesópolis, Estação Biológica de Boracéia, Feb. 2006, M. Uehara leg. (AMBC); 1 ♂, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, Mar. 2005, M. Uehara leg. (CEMT); 2 ♂♂, 1 ♀, São Miguel Arcanjo, Parque Estadual Carlos Botelho, 24º03′43″ S, 47º58′45″ W, 812 m, 29 Jan. 2012, human faeces, E. Bovy leg. (CEMT); 2 ♀♀, Serra do Japi, 23º14′ S, 46º56′ W, 1050 m, 1998, pitfall with dung, M.I.M. Hernández leg. (CEMT).

Redescription

Colouration. Dorsum lustrous and shiny. Head, pronotum, pygidium and ventrite VI dark purple. Elytra dark green or dark blue. Meso- and metafemora reddish-brown. Venter with purplish reflections.

Head. Tegument shiny and covered by dense micropunctation and very fine alveolar microsculpture; sometimes, microsculpture lacking at the posterior region of frons. Clypeus with two apical teeth obtuse and contiguous at base; with a single transverse row of very short setae covering the base of both teeth. Genae with a weak tooth immediately behind clypeal-genal juncture. Posterior edge of head unmargined between eyes (some few specimens with traces of a fine line between eyes).

Thorax. Pronotum with shiny tegument; alveolar microsculpture restrict to a very narrow strip above lateral margins; rest of tegument smooth, with dense micropunctation, almost as dense as on head. Posterior edge with a fine transverse line at middle (extending just beyond the second elytral stria) Hypomeral cavity with tegument with some long yellowish setae at centre; external margin with a minute tubercle. Metaventrite with some few setae close to metacoxae on the sides, and entirely glabrous at centre; anterior region with tegument with strong rivose microsculpture; centre and posterior region with dense micropunctation.

Legs. Protibiae very narrow and without expansion on its internal margin; at their apical seventh, with two tiny, acute teeth of unequal length. Mesofemora margined anteriorly only at its basal half or third; tegument with sparse, almost imperceptible micropunctation. Metafemora margined only anteriorly; with strong coarse elongate punctation at base and with sparse micropunctation at the rest of tegument (Fig. 13A). Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. With only eight visible striae: first four to five striae strongly marked, finely carinulate and widened at base; sixth to eighth striae very effaced and discontinuous; seventh stria absent at humerus; all striae lack their carinulae at the apex of elytra, being either marked only by microsculpture or completely indistinct; humeral carina absent. Tegument of interstriae shiny, without microsculpture and with shallow, but evident micropunctation.

Abdomen. Ventrite VI smooth at centre and with diffuse microsculpture on the sides (Fig. 14B). Pygidium slightly convex in both sexes and with shiny tegument, without microsculpture and with evident micropunctation.

Aedeagus. Parameres almost as long as phallobase and symmetrical, with both external faces flat. In lateral view, simple, without any ventral notch or keel and with truncate apex (Fig. 17B).

Sexual_dimorphism. **Males**: protibial spur wide and bifid, with external projection long, straight, and fine, and internal projection shorter, bent, and widened (Fig. 15B). Pygidium very long (length between 1.1 and 1.4 mm). Ventrite VI strongly narrowed at middle; ventrite V without medial expansion on its posterior edge. **Females**: protibial spur fine and spiniform. Abdomen with three pairs of transverse foveae located in the suture between ventrites I–II, II–III and III–IV, respectively; foveae not margined by row of long setae (Figs 14B, 16D). Pygidium shorter (between 0.9 and 1.1 mm). Ventrite VI wide at middle, only slightly narrowed by medial expansion on the posterior edge of ventrite V (Fig. 14B).

Measurements

Males (N = 16). **TL:** AV: 7 ± 0.53; MX: 7.9; MN: 6.2. **EW:** AV: 5.2 ± 0.29; MX: 5.8; MN: 4.7. **PL:** AV: 2.4 ± 0.13; MX: 2.6; MN: 2.2. **PW:** AV: 4.4 ± 0.21; MX: 4.8; MN: 4.1. **PgL:** AV: 1.2 ± 0.07; MX: 1.4; MN: 1.1. **PgW:** AV: 2.2 ± 0.12; MX: 2.4; MN: 2.

Females (N = 21). **TL:** AV: 6.3 ± 0.38; MX: 7.5; MN: 6.36. **EW:** ME: 5.3 ± 0.39; MX: 6; MN: 4.5. **PL:** AV: 2.4 ± 0.16; MX: 2.6; MN: 2.1. **PW:** AV: 4.5 ± 0.3; MX: 5; MN: 3.9. **PgL:** AV: 1 ± 0.09; MX: 1.1; MN: 0.9. **PgW:** ME: 2.3 ± 0.12; MX: 2.5; MN: 2.

Geographical distribution

Atlantic Forest above 600 m in the Brazilian southeast.

Ecoregions

Bahia Interior Forests, Bahia Coastal Forest, Alto Paraná Atlantic Forest, Serra do Mar Coastal Forests.

Collecting sites (Fig. 24)

BRAZIL. **Bahia** (?). **Minas Gerais**: Barão de Cocais, Belo Horizonte (Parque Estadual da Serra do Rola-Moça), Carrancas (Chapada das Perdizes), Conceição dos Ouros, Diamantina, Itamonte, Lavras, Lima Duarte (Parque Estadual do Ibitipoca), Nova Lima (Parque Estadual da Serra do Rola-Moça), Prados, Rio Acima, São João Evangelista, Viçosa. **Espírito Santo**: Conceição do Castelo, Domingos Martins (Parque Estadual da Pedra Azul), Santa Teresa (Estação Biológica Santa Lúcia), Vargem Alta, Venda Nova do Imigrante. **Rio de Janeiro**: Itatiaia (Parque Nacional do Itatiaia), Nova Friburgo, Parque Nacional da Serra dos Órgãos, Rio de Janeiro. **São Paulo**: Mogi das Cruzes (Parque das Neblinas), Parque Estadual da Serra do Mar (Núcleo Santa Virgínia), Salesópolis (Estação Biológica de Boracéia), São Luiz do Paraitinga, São Miguel Arcanjo (Parque Estadual Carlos Botelho), Serra do Japi.

Intraspecific variation and taxonomic discussion

Apart from the colouration of the teneral specimens, little intraspecific variation was observed in *S. foveiventris*. Although the majority of the specimens do not show any trace of a margin between the eyes, a few individuals have a very short, tenuous line at the centre of the posterior edge of the head. Another noticeable variation refers to the density of coarse punctation at the base of metafemora: at one extreme, this punctation is deep and dense, being easily observed (Fig. 13A). At the other extreme, there are a few short points – in the male from Itamonte (Minas Gerais), especially, these points are almost absent, only weakly marked on the left metafemur. Between those extremes, a complete gradual variation exists. Finally, variation is also seen in the elytral striae, with some specimens showing all the first five striae well marked and carelunate, while others have only the first four striae in that way, whereas the fifth stria is as effaced and discontinuous as the more external striae.

Being a member of the *candezei* subgroup, *S. foveiventris* is closely related to *S. candezei* and *S. genieri* sp. nov. It differs from both species by the dorsal colouration pattern (Fig. 23A), the presence of a coarse punctation at the base of the metafemora (Fig. 13A), the presence of three pairs of abdominal foveae in females (Figs 14B, 16D), the shape of the parameres (Fig. 17B), and the distribution (Fig. 24). From *S. candezei*, in particular, *S. foveiventris* is distinct also in the shape of the posterior edge of ventrite V (Fig. 14B) and from *S. genieri* sp. nov. in the microsculpture of the surface of the pronotum, elytra and pygidium. Table 3 summarizes the differences between these three species.

Since they are found in sympatry in at least some localities in Espírito Santo, specimens of *S. obscurus* have been misidentified as *S. foveiventris* in several collections. Nonetheless, it is possible to readily separate the two species by the number of protibial teeth (two in *S. foveinvetris*, Fig. 11J, and three

Table 3. Summary of the morphological and distributional differences between the three species of the *candezei* subgroup.

	***S. candezei* (Harold, 1868)**	***S. genieri* sp. nov.**	***S. foveiventris* (Schmidt, 1920)**
Dorsal colouration	Dark green	Shiny copper	Head and pronotum dark purple, elytra green or dark blue
Tegument at centre of pronotum	Alveolar microsculpture absent or weakly impressed; micropunctation dense	Alveolar microsculpture very strong obliterating micropunctation	Alveolar microsculpture absent and micropunctation very strong
Pilosity on the sides of metaventrite	Absent	Absent	Present in a few specimens
Coarse punctation at the base of metafemora	Absent	Absent	Present
Tegument of elytra and pygidium	Microsculpture absent and micropunctation strong	Alveolar microsculpture very strongly impressed obliterating micropunctation	Microsculpture absent and micropunctation dense
Lateral foveae of female abdomen	Absent	Absent	Present at suture between ventrites I–II, II–III, and III–IV
Shape of posterior edge of female ventrite V	With strong medial flange covering anterior edge of ventrite VI	With very subtle medial flange covering anterior edge of ventrite VI	With very subtle medial flange covering anterior edge of ventrite VI
Parameres (lateral view)	With a strong notch on its ventral region, which divides the parameres at middle; without ventral keel	With a short notch on its ventral region and with a strong ventral keel	Elongated and simple, without both ventral keel and notch
Distribution	Eastern and southern Brazilian Amazon (Pará and Mato Grosso)	Slopes of the Andes in Peru and Ecuador	Atlantic Forest in southeastern Brazil

in *S. obscurus*, Fig. 11D), shape of the internal margin of the protibiae (straight in *S. foveiventris* and strongly expanded in the apical half in *S. obscurus*), by the coarse punctation at the base of the metafemora (present in *S. foveiventris*, Fig. 13A, and absent in *S. obscures*, Fig. 13B), pilosity on the female abdominal foveae (glabrous in *S. foveiventris*, Figs 14B, 16D, and with a row of long setae on the anterior margin in *S. obscurus*, Fig. 16C), among other features. Besides, the distribution of both species does not entirely overlap: *S. obscurus* occurs throughout the Atlantic Forest from Alagoas to Espírito Santo (Fig. 41), while *S. foveiventris* is present in the mountain ranges of southeastern Brazil (Minas Gerais, Espírito Santo, Rio de Janeiro and São Paulo) (Fig. 24); sympatry was observed only in the municipalities of Santa Teresa and Venda Nova do Imigrante, in Espírito Santo state.

Comments

In a very vague way, without specifying either an exact locality or the source for the new record, Martínez *et al.* (1964) cited *S. foveiventris* as being present in Paraguay. Although we have studied the specimens deposited in the Martínez collection (now at the CMNC) and in the MACN, institution where Martínez worked, we could not find any specimens of *S. foveiventris* from that country or from Brazilian localities bordering Paraguay. Thus, we consider the Paraguayan record for *S. foveiventris* erroneous and possibly fruit of a misidentification of specimens of *Canthon cobosi* (e.g., Pereira & Martínez (1960) considered *C. cobosi* close to *S. foveiventris*). In reality, based on the material gathered for this work, *S. foveiventris* seems to be a species restricted to the mountain ranges of southeastern Brazil; the only other records outside that region are two specimens labelled "Bahia" deposited in the MZSP and NMCP, which we consider a doubtful record.

Natural history

In the same way as for the other species in the genus, *S. foveiventris* seems to be strictly coprophagous, having been attracted to human faeces (Vaz-de-Mello & Louzada 1997; Hernández 2002; Falqueto *et al.* 2005; Almeida & Louzada 2009; Hernández & Vaz-de-Mello 2009; Hernández *et al.* 2011; MC, personal observation; and information from specimen labels) and to a mixture of maned wolf (*Chrysocyon brachyurus* (Illiger, 1815)), capuchin monkey (*Sapajus apella* (Linnaeus, 1758)) and coati (*Nasua nasua* (Linnaeus, 1766)) dung (Duraes *et al.* 2005). Other baits offered apart from dung, such as cow spleen (Vaz-de-Mello & Louzada 1997; Falqueto *et al.* 2005; Almeida & Louzada 2009) and rotten bananas and fungi (Falqueto *et al.* 2005), did not attract individuals of *S. foveiventris*. The time of foraging activity is also the one expected for the genus, i.e., nocturnal. In Serra do Japi (São Paulo), Hernández (2002) collected eight specimens at night, four at sunset, and only one at sunrise, having found no specimens during the day.

Sylvicanthon foveiventris seems to be a seasonal species, with adults active mainly during the rainiest and hottest season of the year, which, in the Brazilian southeast, occurs during spring and summer. This is corroborated both by label data (one specimen recorded for September, five for October, 29 for December, 110 for January and 14 for February, and only two specimens in August, in the second half of the winter) and by the results obtained by Hernández & Vaz-de-Mello (2009) during a year of

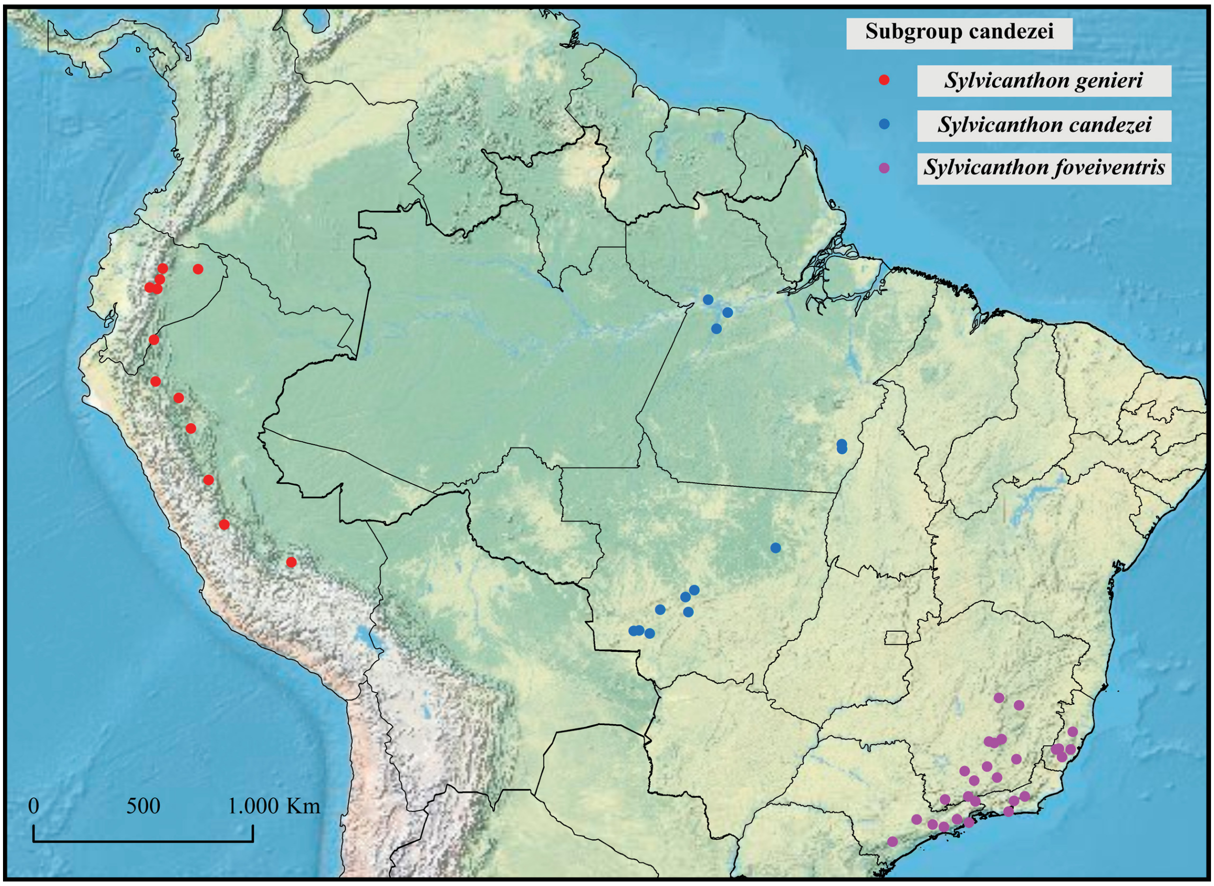

Fig. 24. Distribution of the three species of the *candezei* subgroup.

monthly collecting in Serra do Japi. The species was reported exclusively in altitudes between 680 and 1727 m (data compiled from Vaz-de-Mello & Louzada 1997; Duraes *et al.* 2005; Almeida & Louzada 2009; and specimen labels). Indeed, *S. foveiventris* is present in several mountain ranges in southeastern Brazil, such as Serra Capixaba, Serra da Mantiqueira, Serra dos Órgãos and Serra do Mar, areas covered predominantly by ombrophilous and dense or semidecidual Atlantic Forest.

The strategy of arboreal foraging, a notable behavioural characteristic of *S. foveiventris*, was reported for this species by Vaz-de-Mello & Louzada (1997). In forest fragments in Viçosa (Minas Gerais), those authors hoisted some traps baited with human faeces 10 m from the ground and 22 specimens of *S. foveiventris* were collected as a result. As discussed by Vaz-de-Mello & Louzada (1997) (and, before them, by Howden & Young 1981), arboreal mammal and bird dung can usually attach to leaves and branches high in the trees. Consequently, dung beetles that developed a special capacity of three-dimensional foraging (i.e., the ability of searching for food in several different strata in the forest, in contrast to searching only horizontally above the ground) had access to an alternative food source to the dung deposited in the forest floor, which is heavily disputed by a rich guild of coprophagous arthropods. For Vaz-de-Mello & Louzada (1997), perching on leaves, a behaviour displayed by many tropical dung beetles, was a preadaptation to the evolution of arboreal foraging – indeed, one of the specimens of *S. foveiventris* collected in the Parque Nacional do Itatiaia (Rio de Janeiro) was caught perching on a leaf on the understory (Juan Pablo Botero, 2014, personal communication to MC).

Sylvicanthon candezei (Harold, 1869)

Figs 6B, 10C, 11J, 14D–E, 15C, 17C, 20, 24, 25–26A–B

Canthon candezei Harold, 1869a: 96.

Canthon candezei – Harold 1869b: 990. — Gillet 1911: 28. — Schmidt 1920: 133; 1922: 64, 73. — Balthasar 1939: 188. — Blackwelder 1944: 198. — Halffter & Martínez 1977: 62–63. — Krajcik 2012: 63.

Glaphyrocanthon (*Glaphyrocanthon*) *candezei* – Pereira & Martínez 1956: 126, 129. — Martínez *et al.* 1964: 5, 8–9, 14, 20. — Vulcano & Pereira 1967: 561.

Glaphyrocanthon (*Glaphyrocanthon*) *candèzei* – Vulcano & Pereira 1964: 661.

Sylvicanthon candezei – Halffter & Martínez 1977: 63. — Feer 2000: 32 (error: refers to *S. seag* sp. nov.); 2008: 62 (error: refers to *S. seag* sp nov.). — Vaz-de-Mello 2000: 195. — Escobar 2000a: 210 (error: probably refers to *S. genieri* sp. nov. or *S. mayri* sp. nov.). — Medina *et al.* 2001: 137 (idem). — Feer & Pincebourde 2005: 30 (error: refers to *S. seag* sp nov.). — Scheffler 2005: 19. — Medina & Pulido 2009: 59 (error: probably refers to *S. genieri* sp. nov. or *S. mayri* sp. nov.). — Carvajal *et al.* 2011: 117, 316 (error: refers to *S. genieri* sp. nov.).

Etymology

Eponym after the Belgian entomologist Ernest Candèze (1827–1898). One of the specimens studied by Harold (1869a) belonged to the Candèze collection – nowadays largely housed at the ISNB (Horn & Kahle 1935) – and this may have been the reason for the homage.

Material examined

Lectotype (here designated, Fig. 26)

BRAZIL: ♂, Pará, the Tapajós River (some point at the 170 km above its mouth in the Amazon River or across the banks of the Cupari River (Fig. 26B); see more details below), type locality cited by Harold (1869): "*Tapajos*". Labels: ("*Candezei* / *Harold. Hefte V*.", "Muséum Paris / 1952 / Coll. R. Oberthur", "*Tapajos*", "Ex-Musæo / H. W. Bates / 1892", "LECTOTYPE ♂ / *Canthon* / *candezei* / *Harold* / des. F. Z. Vaz-de-Mello, 20*14*") (MNHN).

Paralectotypes (4 ♂♂, 4 ♀♀)
BRAZIL: 1 ♂, (“*Tapajós*”, “Ex-Musæo / H. W. Bates / 1892”, “Muséum Paris / 1952 / coll. R. Oberthür”, “PARALECTOTYPE / ♂ / *Canthon* / *candezei* / *Harold* / des. F. Z. Vaz-de-Mello, 20*14*”) (MNHN); 1 ♂, (“*Tapajos*”, “*Candezei* / *Harold*”, “Ex-Musæo / E. Harold”, “S*ylvicanthon* / *candezei* / *Harold* / *G. H. y A. M. det. 76*”, “PARALETOTYPE / *Canthon candezei* / Harold, 1869 ♂ / des. Cupello & Vaz-de-Mello, 2015”) (MNHN); 1 ♂ (dissected) (“*Tapajos*”, “*Candezei* / *Harold*”, “Ex-Musæo / E. Harold”, “S*ylvicanthon* / *candezei* / *Harold* / *G. H. y A. M. det. 76*”, “PARALECTOTYPE / ♀ / *Canthon* / *candezei* / *Harold* / des. F. Z. Vaz-de-Mello, 2015”) (MNHN); 1 ♀ (“*Tapajos*”, “Ex-Musæo / H. W. Bates / 1892”, “*candezei* / *Harold* / [ilegível] *Har.* [illegible]”, “Muséum Paris / 1952 / coll. R. Oberthür” “PARALECTOTYPE / ♀ / *Canthon* / *candezei* / *Harold* / des. F. Z. Vaz-de-Mello, 2014”) (MNHN) (Fig. 26); 1 ♀, (“*Tapajos*”, “Ex-Musæo / H. W. Bates / 1892”, “PARALECTOTYPE / ♀ / *Canthon* / *candezei* / *Harold* / des. F. Z. Vaz-de-Mello, 20*14*”) (MNHN); 1 ♀ (“*Tapajos*”, “Ex-Musæo / H.W. Bates / 1892”, “Muséum Paris / 1952 / coll. R. Oberthür” “PARALECTOTYPE / ♀ / *Canthon* / *candezei* / *Harold* / des. F.Z. Vaz-de-Mello, 2014”) (MNHN); 1 ♀, (“*Tapajos*” “*Candezei* / *Harold*”, “Type”, “Collection / E. CANDÈZE”, “PARALECTOTYPE / ♀ / *Canthon* / *candezei* / *Harold* / des. F.Z. Vaz-de-Mello, 2014”) (ISNB); 1 ♂ (“*Tapajos*”, “PARALECTOTYPE / ♂ / *Canthon* / *candezei* / *Harold* / des. F. Z. Vaz-de-Mello, 2014”) (CEMT, ex MNHN).

Additional material (103 ♂♂, 54 ♀♀)
BRAZIL: **Mato Grosso**: 1 ♀, Araputanga, Fazenda Araputanga, Bacia Jauru, 15º21′48″ S, 58º26′03″ W, Dec. 2002, M. Santos Filho leg. (CEMT); 1 ♂, Araputanga, Fazenda Bandeirantes, 15º22′18″ S, 58º26′23″ W, 297 m, 21–23 Jan. 2013, pitfall with human faeces, R. J. Silva leg. (CEMT); 1 ♂, Araputanga, Fazenda Bandeirantes, 15º22′14″ S, 58º26′02″ W, 338 m, 20–22 Jan. 2013, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 1 ♂, Curvelândia, Fazenda Calça Vermelha, Bacia Cabaçal, 15º33′02″ S, 58º00′57″ W, Feb. 2004, M. Santos-Filho leg. (CEMT); 1 ♀, Diamantino, Fazenda São João, 14º14′10″ S, 56º08′11″ W, 11 Jan. 2001, flight interception trap, Génier and Vaz-de-Mello leg. (CMNC); 1 ♂, Diamantino, Fazenda São João, 14º14′10″ S, 56º08′11″ W, 400 m, 13 Jan. 2001, flight interception trap, Génier and Vaz-de-Mello leg. (CMNC); 1 ♀, Diamantino, Fazenda São João, 14º23′49″ S, 56º09′30″ W, 480 m, 13 Jan. 2001, trap with faeces, Génier and Vaz-de-Mello leg. (CMNC); 1 ♂, 1 ♀, Indiavaí, Fazenda Nova Canaã, Bacia Jauru, 15º16′31″ S, 58º40′06″ W, Jul. 2004, M. Santos-Filho leg. (CEMT); 1 ♂, 1 ♀, Nobres, Jan. 2001, A. Bello leg. (AMBC); 1 ♀, Nova Mutum, 13º48′07″ S, 56º05′22″ W, 23 Jan. 2011, human faeces, M.F. Souza leg. (CEMT); 2 ♂♂, Nova Mutum, 13º48′07″ S, 56º05′22″ W, 25 Jan. 2011, human faeces, M.F. Souza leg. (CEMT); 8 ♂♂, 4 ♀♀, Nova Mutum, 13º48′07″ S, 56º05′22″ W, 18 Apr. 2011, human faeces, M.F. Souza leg. (CEMT); 1 ♂, Nova Mutum, 13º48′07″ S, 56º05′22″ W, 2 May 2011, human faeces, M.F. Souza leg. (CEMT); 1 ♀, Nova Mutum, Trivelato, 15 Dec. 1995, W.O. Silva-Filho leg. (CEMT); 1 ♂, 2 ♀♀, Querência, Fazenda São Luiz, 12º39.68′ S, 52º22.14′ W, 8 Jul. 2008, flight interception trap, R. Andrade leg. (CEMT); 2 ♀♀, Querência, Fazenda São Luiz, 12º39.81′ S, 52º22.74′ W, 17 Jul. 2008, pitfall, R. Andrade leg. (CEMT); 2 ♀♀, Querência, Fazenda São Luiz, 12º39.94′ S, 52º21.85′ W, 14– Jul. 2008, pitfall, R. Andrade leg. (CEMT); 1 ♂♂, 5 ♀♀, Querência, Fazenda São Luiz, 12º39.64′ S, 52º22.74′ W, 17 Jul. 2008, pitfall, R. Andrade leg. (CEMT); 2 ♂♂, Querência, Fazenda São Luiz, 12º40.48′S, 52º21.86′W, 13 Feb. 2009, pitfall, R. Andrade leg. (CEMT); 1 ♂, 3 ♀♀, Tangará da Serra, 16 Jul. 2008, pitfall with human faeces, R.J. Silva leg. (CEMT); 2 ♂♂, Tangará da Serra, Fazenda “Ap. Da Serra”, 14º19′15″ S, 57º43′51″ W, 640 m, 20–22 Apr. 2017, pitfall with human faeces, R.J. Silva leg. (CEMT); 8 ♂♂, 1 ♀, Tangará da Serra, Fazenda Bahia, 14º37′19″ S, 57º25′07″ W, 419 m, 12–14 Jan. 2011, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 1 ♂, 1 ♀, Tangará da Serra, Fazenda Bahia, 14º37′13″ S, 57º24′50″ W, 428 m, 26–28 Jan. 2012, pitfall with cow dung, R.J. Silva leg. (CEMT); 1 ♂, Tangará da Serra, Fazenda Curitiba, 14º21′47″ S, 57º28′17″ W, 345 m, 2–9 Apr. 2012, flight interception trap, R.J. Silva leg. (CEMT); 11 ♂♂ (1 dissected), 1 ♀, Tangará da Serra, Fazenda Filé do Boi, 14º38′07″ S, 57º24′41″ W, 439 m, 25–27 Jan. 2011, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 1 ♂, Tangará da

Serra, Fazenda Fontosa, 14º35′36″ S, 57º50′37″ W, 296 m, 6 Feb. 2012, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 2 ♂♂, Tangará da Serra, Fazenda Netolândia, 14º39′56″ S, 57º54′08″ W, 304 m, 20–22 Mar. 2012, pitfall trap baited with human faeces and pig dung, R.J. Silva leg. (CEMT); 5 ♂♂, 1 ♀, Tangará da Serra, Fazenda Netolândia, 14º39′54″ S, 57º55′08″ W, 329 m, 12–14 Mar. 2012, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 11 ♂♂, 8 ♀♀, Tangará da Serra, Fazenda Netolândia, 14º39′56″ S, 57º54′08″ W, 304 m, 20–22 Mar. 2012, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 6 ♂♂, 4 ♀♀, Tangará da Serra, Fazenda Netolândia, 14º41′05″ S, 57º54′08″ W, 263 m, 25–27 Mar. 2012, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 1 ♀, Tangará da Serra, Fazenda Paraíso, 14º41′46″ S, 57º24′40″ W, 503 m, 13–15 Jan. 2011, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 2 ♂♂ (1 dissected), 1 ♀, Tangará da Serra, Fazenda Paraíso, 14º41′45″ S, 57º24′38″ W, 520 m, 15–22 Jan. 2011, flight interception trap, R.J. Silva leg. (CEMT); 4 ♂♂, Tangará da Serra, Fazenda Rosa Branca, 14º33′59″ S, 57º52′33″ W, 312 m, 18–25 Feb. 2011, flight interception trap, R.J. Silva leg. (CEMT); 3 ♂♂, Tangará da Serra, Fazenda Rosa Branca, 14º33′57″ S, 57º52′34″ W, 321 m, 20–27 Feb. 2011, flight interception trap, R.J. Silva leg. (CEMT); 2 ♂♂, Tangará da Serra, Fazenda Rosa Branca, 14º34′00″ S, 57º52′24″ W, 468 m, 18–20 Feb. 2011, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 7 ♂♂, 4 ♀♀, Tangará da Serra, Fazenda Sudamata, 14º37′18″ S, 57º58′01″ W, 354 m, 10–17 Mar. 2012, flight interception trap, R.J. Silva leg. (CEMT); 3 ♂♂, 1 ♀, Tangará da Serra, Fazenda Sudamata, 14º37′18″ S, 57º58′01″ W, 354 m, 21–23 Feb. 2012, pitfall with human and swine dung, R.J. Silva leg. (CEMT); 1 ♂, Tangará da Serra, Sítio Mauá, 14º39′39″ S, 57º24′20″ W, 479 m, 19–26 Jan. 2011, R.J. Silva leg. (CEMT). – **Pará**: 1 ♀, Belterra, 54º32′36″ W, 02º36′50″ S, 15 Jul. 2016, human and pig dung, F. França leg. (CEMT); 1 ♂ ([dissected), Óbidos, 4 Mar. 1938, Zellibor-Hauff leg. (MNRJ); 1 ♂ (dissected), Óbidos, Nov. 1955, C.A.C. Seabra leg. (CMNC); 1 ♂, 1 ♀, Pau-d’Arco, Fazenda Marajoara, 07º50′ S, 50º16′ W, 13 Oct. 1998, P.Y. Scheffler leg. (CEMT); 1 ♂ (dissected), Redenção, Pinkaiti-Aik, 07º44′ S, 52º02′ W, Jun. 1999, P.Y. Scheffler leg. (CEMT); 1 ♂, Redenção, Pinkaiti-Aik, 07º46′ S, 51º58′ W, Oct. 1999, P.Y. Scheffler leg. (CEMT); 1 ♀, Redenção, Pinkaiti-Aik, 07º50′ S, 50º16′ W, Nov. 1999, P.Y. Scheffler leg. (CEMT); 3 ♀♀, Tapajós River [1852], H.W. Bates leg. (BMNH); 2 ♂♂, 2 ♀♀, Santarém, May 2010, V.H. Oliveira leg. (CEMT).

Ambiguous data: 1 ♂, “*Amazon*” (ISNB – Coll. J. Thomson).

Redescription

Colouration. Surface of the entire body with very dark shades. Head predominantly purple with greenish reflections, especially at centre. Pronotum with green shine at centre and purplish on the sides. Elytra usually dark green with purplish striae; in some specimens, elytra dark blue. Metaventrite very dark, with coppery or purple reflections. Meso- and metafemora dark brown or reddish-brown. Pygidium dark green.

Head. Tegument shiny, with strong alveolar microsculpture and covered by dense micropunctation, which is almost imperceptible or even absent only at the external edge of head (Fig. 6B). Clypeus with two apical teeth obtuse and contiguous at base; with a single transverse row of very short setae covering the base of both teeth. Genae with a weak tooth immediately behind clypeal-genal juncture. Posterior edge of head unmargined between eyes.

Thorax. Tegument of pronotum with diffuse shine, dark and with dense micropunctation at centre, denser and more marked than on head; towards the sides, micropunctation less dense and less marked, being completely absent or only very weakly impressed on the lateral margin; tegument with strong microsculpture throughout pronotal surface (southern populations) or with weak or almost absent microsculpture (northern populations). Posterior edge of head with a fine transverse line at centre (usually extending a little beyond the second elytral stria). Hypomeral cavity with tegument entirely glabrous or with only some few long or short yellowish setae at posterior region near to hypomeral carina, but always glabrous at centre; external margin simple, without any trace of tubercle. Metaventrite entirely glabrous; anterior region with tegument with distinct rivose microsculpture; centre and posterior region with dense alveolar microsculpture obliterating micropunctation.

Legs. Ventral surface of all femora and tibiae dark (Fig. 25B). Profemora with tegument with strong alveolar microsculpture at their anterior half and with strong rivose microsculpture at posterior half. Protibiae narrow and straight on internal margin; at their apical seventh, with two tiny, acute external teeth – the apical one slightly larger than the second (Fig. 11J). Mesofemora margined anteriorly only at their basal three-fourths; unmargined portion of anterior edge with a row of short setae; tegument with strong rivose microsculpture. Metafemora margined only anteriorly; apical third of anterior edge covered by a row of setae; tegument with strong rivose microsculpture obliterating micropunctation, which is almost imperceptible; without coarse elongate punctation at base. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. With only seven narrow visible striae: first four to five striae strongly impressed, very finely carinulate and widened at base; fifth, sixth and seventh striae progressively more effaced and interrupted; all striae lack carenule before reaching apex of elytra, where they are marked only by microsculpture or are completely indistinct; humeral carina absent. Tegument of interstriae either with alveolar microsculpture and very dense micropunctation (southern populations) or with very weak or even absent alveolar microsculpture (northern populations).

Abdomen. Ventrite VI smooth at centre and with weaker rivose microsculpture on the sides (Fig. 14D–E). Pairs of foveae absent in both sexes. Pygidium with tegument with strong alveolar microsculpture and dense micropunctation; average length equal in both sexes.

Aedeagus. Parameres short, less than half as long as phallobase, and slightly asymmetrical: external face of left paramere flat or concave and external face of right paramere convex (difference more easily seen

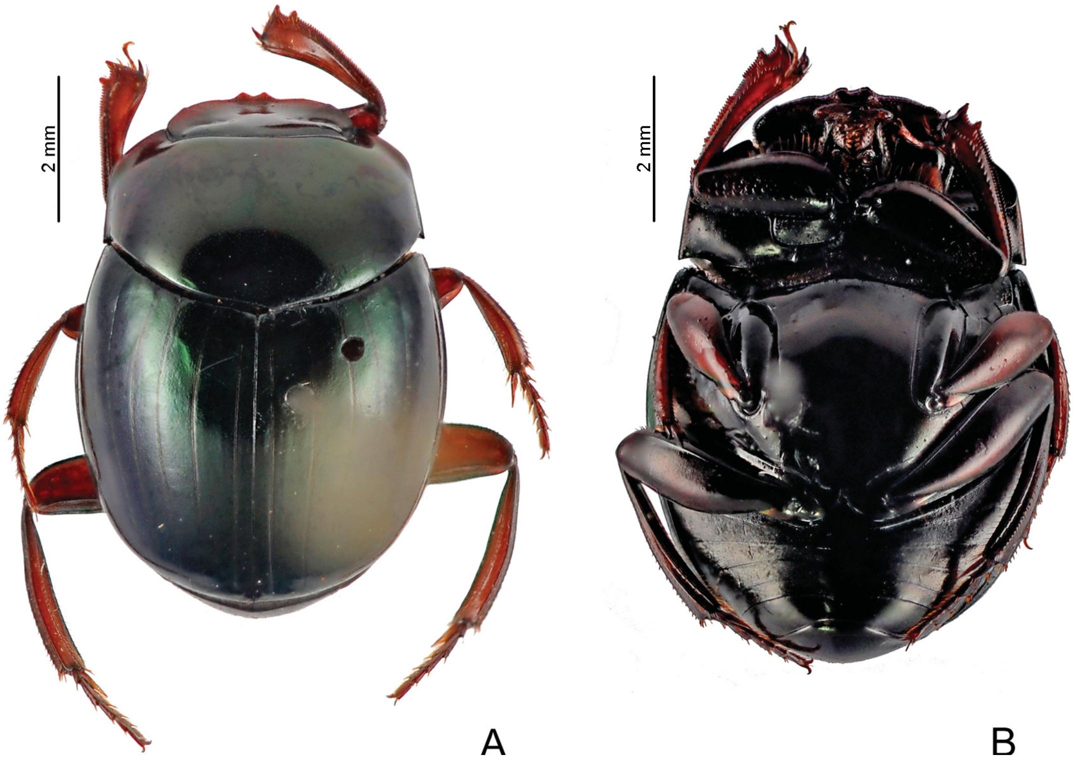

Fig. 25. *Sylvicanthon candezei* (Harold, 1869). **A**. Dorsal view. **B**.Ventral view.

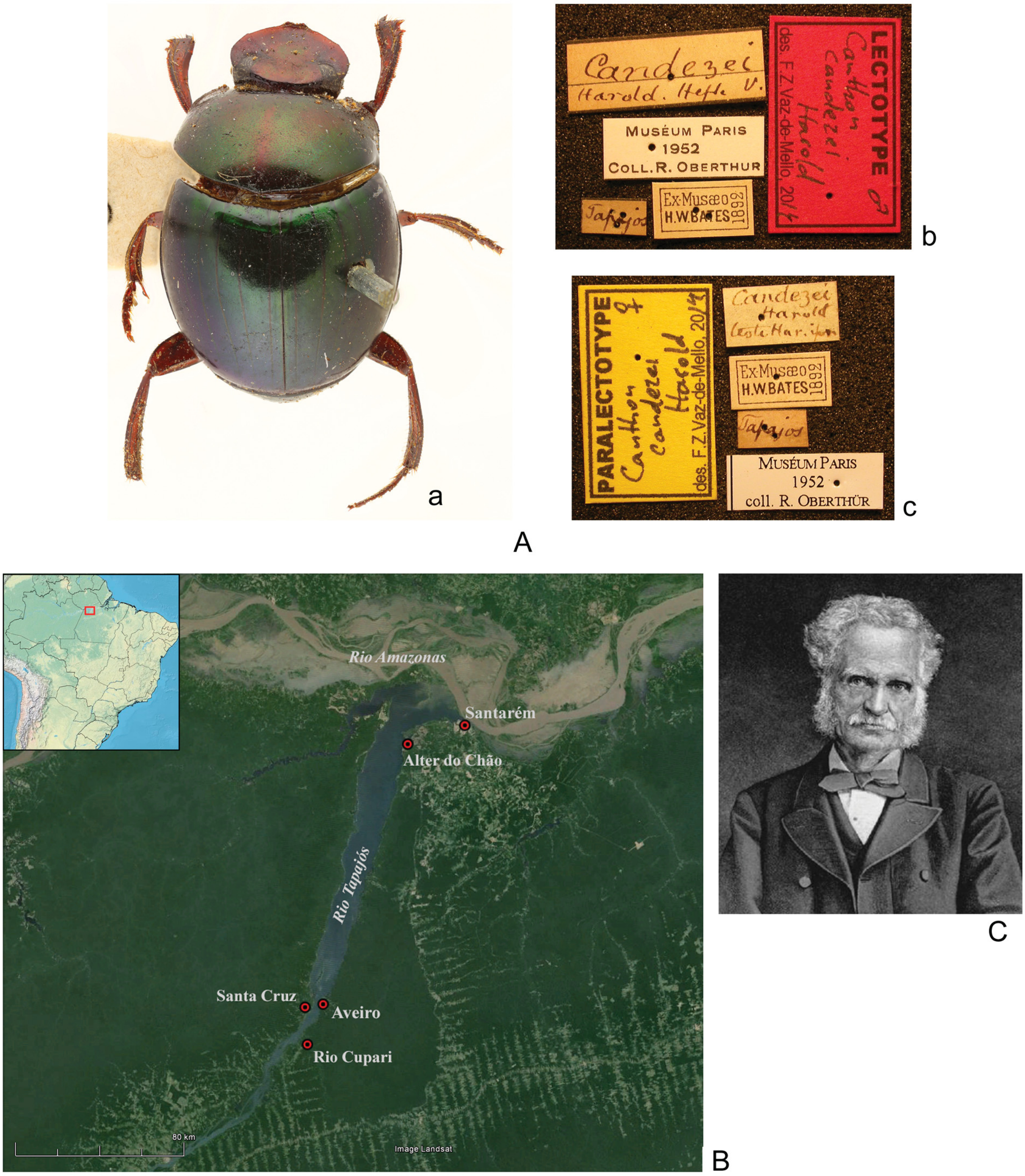

Fig. 26. *Sylvicanthon candezei* (Harold, 1869) type material. **A**. **a**. Lectotype. **b**. Labels of lectotype. **c**. Labels of paralectotype 3. **B**. The four localities where *S. candezei* type series may have been collected by Bates in the lower Tapajós region in 1852 (see discussion in the text). **C**. The English naturalist Henry Walter Bates (1825–1892), the collector of the *S. candezei* type series (modified from Bidau 2014).

in ventral view). In lateral view, parameres without ventral keel and with a profound notch at middle (Fig. 17C).

Sexual dimorphism. **Males**: Protibial spur wide and bifid, with external projection spiniform, straight, and not very long, and internal projection bent and wide (Fig. 15B). Ventrite VI strongly narrowed at middle by emargination of its posterior edge and covered anteriorly by medial projection of ventrite V (Fig. 14D). **Females**: Protibial spur spiniform, simple. Ventrite VI wide at middle and covered anteriorly by medial projection of ventrite V, which gives a narrowed appearance to it (but never as in male) (Fig. 14E).

Measurements

Males (N = 13). **TL:** AV: 6.7 ± 0.56; MX: 7.6; MN: 5.8. **EW:** AV: 4.8 ± 0.38; MX: 5.3; MN: 4.1. **PL:** AV: 2.0 ± 0.22; MX: 2.5; MN: 1.8. **PW:** AV: 4.1 ± 0.29; MX: 4.5; MN: 3.6. **PgL:** AV: 1.4 ± 0.19; MX: 1.9; MN: 1.1. **PgW:** AV: 2.0 ± 0.17; MX: 2.3; MN: 1.7.

Females (N = 14). **TL:** AV: 6.7 ± 0.48; MX: 7.4; MN: 6. **EW:** AV: 4.8 ± 0.25; MX: 5.3; MN: 4.4. **PL:** AV: 2.26 ± 0.16; MX: 2.5; MN: 1.9. **PW:** ME: 4.2 ± 0.2; MX: 4.6; MN: 3.9. **PgL:** ME: 1.4 ± 0.09; MX: 1.2; MN: 1.5. **PgW:** AV: 2.1 ± 0.11; MX: 2.3; MN: 1.9.

Geographical distribution

Humid tropical forests from the mouth of the Tapajós River down to the semideciduous forests of southern and southeastern Amazonia in Brazil.

Ecoregions

Uatuma-Trombetas Moist Forests, Madeira-Tapajós Moist Forests, Tapajós-Xingu Moist Forests, Mato Grosso Tropical Dry Forest, Chiquitiano Dry Forest.

Collecting sites (Fig. 24)

BRAZIL. **Pará**: Belterra, Óbidos, Pau-d'Arco, Redenção, Santarém. **Mato Grosso**: Araputanga, Curvelândia, Diamantino, Indiavaí, Nobres, Nova Mutum, Querência, Tangará da Serra.

Intraspecific variation and taxonomic discussion

Since the beginning of the 20th century, specimens of *Sylvicanthon* collected throughout the Amazon region have been misidentified as *S. candezei*, both in collections and in publications. Nevertheless, even individuals from places as distant from that biome as Rio de Janeiro also suffered from that mistake, as a specimen of *S. foveiventris* colleted in Itatiaia in 1959 and now deposited in the MNRJ has shown. Two other species that were largely confused with *S. candezei* are *S. seag* sp. nov. and *S. genieri* sp. nov. The great confusion in the recognition of the true identity of *S. candezei* naturally brought to publication a large amount of incorrect information on the geographical distribution of this species. Schmidt (1922), for example, cited "*Amazonas, Surinam, Cayenne, Ecuador*" as being the distribution of *S. candezei*, and that was followed by Martínez *et al.* (1964), who considered this species was distributed in most parts of the Amazonia, including Venezuela, Suriname, French Guiana, Brazil, and Ecuador.

In the present work, we observed that *S. candezei* has actually a much more restricted distribution than previously thought, being limited to eastern Amazonia, from the mouth of the Tapajós River, in Pará, south to the state of Mato Grosso (Fig. 24). Interestingly enough, in Mato Grosso and southern Pará, specimens of *S. candezei* were found only at sites in the outer limits of the Amazon forest, i.e., places close to the transition between that biome and the Cerrado and Pantanal; no specimens were collected farther inland in this part of the Amazon region despite extensive collections made in places such as Cotriguaçu, Alta Floresta, Carlinda, and Nova Bandeirante, in Mato Grosso, and Novo Progresso, in

Pará. This information tells us that *S. candezei* has possibly its southern distribution more closely related to the peripherical areas of the Amazon Rainforest, whereas northern populations are present farther inland in that biome.

Apart from this supposed difference in habitat preference, southern and northern populations of *S. candezei* also exhibit clear morphological distinctions. Specimens collected in Óbidos, Santarém, and in the region of the lower Tapajós River, in Pará, have pronotal and elytral tegument with a more smooth microsculpture, which is sometimes almost absent, so giving a brighter appearance to the entire body and a greater contrast to the elytral striae. Conversely, southern population in southern Pará (Pau d'Arco and Redenção) and in Mato Grosso have a strong microsculpture, with a very dark pronotum and elytra and very subtle elytral striae. Concerning colouration, such a variable feature among other *Sylvicanthon*, in *S. candezei* it is much more uniform, with the majority of the specimens of all populations being dark green with a weak metallic sheen.

Comments

The type series of *S. candezei* was collected by the much-celebrated English naturalist and explorer Henry Walter Bates (1825–1892) (Fig. 26C) during his long and famous collecting period in the Amazon Basin between 1848 and 1859. As the type locality of *S. candezei*, Harold (1869a) cited "*Tapajos*" and this information is indeed present on the labels of all the syntypes. Nevertheless, the Tapajós River is one of the largest tributaries of the Amazon, covering almost eight hundred kilometres from its formation in the convergence of the Teles Pires and Juruena Rivers to its mouth situated near the city of Santarém, in Pará. Therefore, where exactly in this vast area would have Bates collected the oldest known specimens of *S. candezei*?

In his journey's narrative, Bates (1863) dedicated a full chapter to his exploration of the Tapajós River. After spending almost six months in Santarém, a city on the banks of the Amazon, Bates decided to explore the lower region of the Tapajós. With that goal in mind, he rented a suitable vessel, hired a small crew and set off on the 8th of June 1852. For the next four months, he navigated approximately 170 km upstream in the Tapajós and made collections in four main localities: Alter do Chão and Aveiro, on the right banks of the Tapajós, and Santa Cruz, on the left banks, besides having gone up for a few days the much narrower Cupari River, a tributary on the right banks of the Tapajós (Fig. 26B). At the end of this trip, Bates returned to Santarém, from where he then left to go up the Amazon River towards Ega (nowadays known as Tefé). By reading his accounts, it is not possible to find any mention to dung beetle collections, although it is clear that Bates collected a large number of insects in that region. Therefore, although we do not have the exact locality where Bates caught the type series of *S. candezei*, we do know at least that it was in the lower Tapajós area, very likely either in Alter do Chão, Aveiros, Santa Cruz or at some point along the Cupari River, between June and October 1852.

Apart from the nine specimens listed in the type series above, three other females collected by Bates in the Tapajós were found in the BMNH collection. Two of them bear circular blue labels handwritten "*Tapayo*", on one side, and "*54 / 18*", on the other. According to Max Barclay (personal communication to MC, 2015), curator of Coleoptera at the BMNH, this code refers to a lot consisting of 237 beetles collected by Bates in "Amazon (Alta de Chia) 100 miles from Santaren on the Japayos". This lot was bought in 1854 by the BMNH at the J.C. Stevens Auction Rooms, London, an auction house specialized in natural history and antiquities and then property of J.C. Stevens, brother of Samuel Stevens, English naturalist who arranged Bates' travel to the Amazon region and from whom he received material there collected (Anonymous 1899; Carrington 1899). 'Alta de Chia' certainly refers to Alter do Chão, whereas 'Japayos' is a corruption of Tapajós. The third female in the BMNH, differently, has a circular blue label handwritten "*Braz / Tapajos*", on the one face, and "*53 / 27*", on the other, code referring to, according to Barclay, 232 beetles collected by Bates in "Brazil, Banks of the Rio Japayos" and also auctioned by Stevens in 1854.

As none of those three females bears any label with Edgar von Harold's handwriting, we do not consider them syntypes of *S. candezei*. Nonetheless, two of them have rectangular pinkish identification labels with other names: one was identified as "*castanipes Reiche*", *nomen in litteris* that we do not know whether it was cited in the literature before, while the other specimen is labelled "S*errimanus mihi*" (*mihi*, from the Latin, meaning "belonging to me"; Schenk & McMasters 1956). According to Harold (1868a, 1869b), "*serrimanus*" was a *nomen in litteris* used by the French entomologist Auguste Chevrolat (1799–1884) to refer to the species named by Harold as *C. chevrolati* Harold, 1868, nowadays a subspecies of *Canthon indigaceus* LeConte, 1886, from North and Central America. Therefore, in principle, Chevrolat should have been the author of that identification label; indeed, although the majority of his Scarabaeinae collection is currently housed in the SMTD (via C. Felsche collection), other Coleoptera groups of his collection, such as Cerambycidae, were deposited at the BMNH (Horn & Kahle 1935). Even so, as *C. indigaceus chevrolati* is completely distinct from *S. candezei* in both morphology and distribution, it would be curious that such an experienced entomologist as Chevrolat could have confused them. Alternative explanations are that Harold perhaps confused the actual application of the name "*serrimanus*" by Chevrolat and that this latter entomologist used that name to refer to the current *S. candezei*, or that, in reality, the label's author was not Chevrolat but, instead, a third unidentified entomologist who used the name '*serrimanus*' independently from Chevrolat to refer to *S. candezei*. Although these *nomina in litteris* are unavailable and, therefore, cannot affect the validity of the name *Canthon candezei*, tracing their histories is worthy because it allows us to better understand the dynamics of discovering and naming taxa in the 19th century, as well as communication between entomologists during the period.

Natural history

No information about the biology of *S. candezei* has been published until now. Label data state the species occurs in altitudes between 263 and 520 m and is attracted to pitfall traps baited with human faeces and cow and pig dung, and that it can also be collected using flight interception traps. Apparently, adults of *S. candezei* are active throughout the year, having been collected between January and May, and in July, October and December. Nonetheless, it is worth noting that it was during the first four months of the year that 115 out of the 157 examined specimens were caught (January: 35 specimens; February: 20; March: 47; April: 13), indicating that, although active throughout the year, *S. candezei* should be more abundant during the rainiest and hottest months than during the dry season in the middle of the year.

Sylvicanthon genieri sp. nov.

urn:lsid:zoobank.org:act:AB21F887-15E7-40CD-BBA8-673CDB21ED37

Figs 6C, 15D, 17D, 20, 24, 27

Sylvicanthon sp. 2: Celi *et al.* 2004: 46.

Sylvicanthon candezei – Carvajal *et al.* 2011: 117, 316 (error).

Etymology

The specific name, a noun in the genitive case, is an homage to the Canadian entomologist François Génier, one of the leading specialists in Scarabaeinae and author of some great works on this group, in recognition of his immense help and kindness in loaning more than one thousand specimens of *Sylvicanthon* (including 131 *S. genieri* sp. nov.) from the CMNC to us. As far as we know, Génier was the first entomologist to recognize this species as new, having identified since 1998 several specimens in the CMNC collection as "S*ylvicanthon* sp. nov".

Material examined

Holotype

ECUADOR: ♂, Tungurahua, 6 km east from Río Negro, 1500 m (“ECU: Tungurahua / 6 kmE RioNegro 1500m / 13–17.vii.76 S.Peck / for. car. tps. 40–50”), genital capsule removed and glued to a triangular label (CMNC).

Paratypes (112 ♂♂, 89 ♀♀)

ECUADOR: **Morona Santiago**: 1 ♂, Untsuants, site 4, 1100 m, 20 Jan. 2002, J. Celi and M. Ortega leg. (CMNC); 3 ♂♂, Untsuante, site 7, 900 m, 23 Jan. 2002, J. Celi and M. Ortega leg. (CMNC). – **Napo**: 11 ♂♂, 7 ♀♀, “Km 7.3 Sarayacu-Loreto Road”, 1200 m, 11 Jul. 1994, dung trap, F. Génier leg. (CMNC); 1 ♀, same collecting data as for preceding (MCNZ); 7 ♂♂, 3 ♀♀, “Km 7.3 Sarayacu-Loreto Road”, 1200 m, 14 Jul. 1994, dung trap, F. Génier leg. (CMNC); 3 ♂♂, 2 ♀♀, “Km 7.3 Sarayacu-Loreto Road”, 1200 m, 20 Jul. 1994, dung trap, F. Génier leg. (CMNC); 1 ♂, 1 ♀, “Km 11.1 Sarayacu-Loreto Road”, 1200 m, 20 Jul. 1994, dung trap, F. Génier leg. (CMNC); 1 ♀, same collecting data as for preceding (MCNZ); 2 ♂♂, 2 ♀♀, “Km 25.4 Sarayacu-Loreto Road”, 950 m, 12 Jul. 1994, dung trap, F. Génier leg. (CMNC); 3 ♂♂, 3 ♀♀, “Km 25.4 Sarayacu-Loreto Road”, 950 m, 14 Jul. 1994, dung trap, F. Génier leg. (CMNC). – **Orellana**: 1 ♀, Onkone Gare Camp, 00º39′10″ S, 76º26′00″ W, 220 m, 4–12 Oct. 1995, active collecting beneath the leaf litter, T.L. Erwin Ecuador Expedition 1995, G.E. Ball and D. Shpeley leg. (CMNC). – **Pastaza**: 3 ♀♀,4.3 km Rio Negro, 1200 m, 18 Jul. 1994, dung trap, F. Génier leg. (CMNC); 1 ♂, “09 km ESE Veracruz”, 22–24 Aug. 1975, dung trap, R. Webster leg. (CMNC); 1 ♂, 1 ♀, Pastaza, “22 km SE Puyo”, 900 m, 16 Jul. 1976, dung trap, S. Peck leg. (CMNC); 5 ♂♂, 2 ♀♀, Pastaza, Puyo, Llandia, “17 km N Puyo”, 19 Jul. 1994, dung trap, F. Génier leg. (CMNC); 2 ♂♂, Mera, 1 km E Mera, 1100 m, 13–17 Jul. 1976, dung trap, S. Peck leg. (CMNC); 1 ♂, Pastaza, Puyo, Llandia, “17 km N Puyo”, 20 Jul. 1994, dung trap, F. Génier leg. (CMNC). – **Tungurahua**: 1 ♂, 3 km W Río Negro, 1200 m, 18 Jul. 1994, dung trap, F. Génier leg. (CMNC); 1 ♂, 4.3 km E Río Negro, 1200 m, 18 Jul. 1994, dung trap, F. Génier leg. (CMNC); 1 ♂, 3 ♀♀, 4.3 km E Río Negro, 1200 m, 20 Jul. 1994, dung trap, F. Génier leg. (CMNC); 3 ♂♂, 6 km E Río Negro, 1500 m, 13–17 Jul. 1976, dung trap, S. Peck leg. (CMNC); 16 ♂♂ (1 dissected), 19 ♀♀, 8 km E Rio Negro, 10 km W Pastaza (= Shell), 1400 m, 13–17 Jul. 1976, dung trap, S. Peck leg. (CMNC); 9 ♂♂, 6 ♀♀, Baños, “El Topo”, 01º23′41″ N, 78º22′52″ W, 1590 m, 23 Jan. 2011, human faeces, G. Maldonado leg. (CEMT). – **Zamora Chinchipe**: leg. 2 ♂♂, Upper Río Comainas, Cordillera del Cóndor, 03º54′ S, 78º25′ W, 1150 m, Jul. 1994, human faeces, A. Forsyth (MUSM).

PERU: **Amazonas**: 5 ♂♂, 3 ♀♀, Comainas River, Jul. 1994, A. Forsyth leg. (MUSM); 4 ♂♂, 1 ♀, Comainas River, 21 Jul. 1994, A. Forsyth leg. (MUSM); 7 ♂♂, 12 ♀♀, Comainas River, 23 Jul. 1994, A. Forsyth leg. (MUSM). – **Cuzco**: 1 ♀, La Convención, Echarate, Campamento Segakiato, 11º45′38.6″ S, 73º14′57.7″ W, 908 m, 2 Mar. 2011, M. Alvarado and E. Rázuri leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Otsanampiato, 12º39′32.18″ S, 73º09′18″ W, 1681 m, 22–24 Jan. 2010, C. Carranza and C. Rossi leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Otsanampiato, 12º39′41.03″ S, 73º09′30.98″ W, 1723 m, 15–17 Sep. 2010, pitfall, M. Alvarado and J. Peralta leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º33′54.41″ S, 73º05′36.85″ W, 1747 m, 26–29 Jan. 2010, C. Carranza and C. Rossi leg. (MUSM); 1 ♀, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′13.56″ S, 73º05′12.13″ W, 1707 m, 18–21 Sep. 2010, M. Alvarado and J. Peralta leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′12.73″ S, 73º05′13.73″ W, 1709 m, 18–21 Sep. 2010, M. Alvarado and J. Peralta leg. (MUSM); 1 ♂ (dissected), 2 ♀♀, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′13.18″ S, 73º05′50.23″ W, 1422 m, 14 Oct. 2009, light, C. Carranza and C. Rossi (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′10.12″ S, 73º05′13.85″ W, 1587 m, 18–21 Sep. 2010, M. Alvarado and J. Peralta leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′21.70″ S, 73º05′16.91″ W, 1685 m, 26–29 Jan. 2010,

C. Carranza and C. Rossi leg. (MUSM); 1 ♂, 2 ♀♀, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′10.72″ S, 73º05′15.17″ W, 1693 m, 18–21 Sep. 2010, pitfall, M. Alvarado and J. Peralta leg. (MUSM). – **Huánuco**: 1 ♂, 3 ♀♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva ("Tingo María Universidad"), Jul. 1974 (CMNC); 10 ♂♂ (1 dissected), 5 ♀♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva ("Tingo María Universidad"), Dec. 1974 (CMNC). – **Junín**: 1 ♀, Chanchamayo, San Ramón, 10 May 2002, F.G. Horgan leg. (MUSM); 2 ♀♀, Chanchamayo, San Ramón, Oct. 2002, pitfall with human faeces, F.G. Horgan leg. (MUSM). – **San Martín**: 1 ♀, Rioja, Yuracyacu, 05º57′07″ S, 77º11′12″ W, 805 m, 6–7 Sep. 2008, C. Albujar leg. (MUSM); 1 ♂ (dissected), Mariscal Cáceres, Juanjuí, Mar. 2010 (CEMT).

Incorrect data: VENEZUELA: **Bolívar**: 1 ♂ (dissected), "150 km sur Caicara, R. Suapare", 3–10 Apr. 1977, Bordón leg. (CMNC).

Description

Colouration. Head, pronotum, elytra, metaventrite, and pygidium largely coppery; pygidium and, more rarely, centre of head occasionally with greenish reflections. Meso- and metafemora orangish.

Head. Tegument shiny, with strong alveolar microsculpture on frons, and more diffuse (yet clearly present) microsculpture on clypeus and genae; micropunctation fine and very subtle, sometimes almost imperceptible throughout most of the head, but often clearly seen on frons (Fig. 6C). Clypeus with two apical teeth obtuse and contiguous at base; with a single transverse row of setae covering the base of both teeth. Genae with a weak tooth immediately behind clypeal-genal juncture. Posterior edge of head unmargined between eyes.

Thorax. Pronotum with shiny tegument and dense micropunctation at centre, denser and with more marked punctures than head (in some specimens, however, punctation can be weaker); towards the sides, micropunctation progressivily less dense and well marked, being completely absent on the lateral margin; tegument with strong alveolar microsculpture throughout its surface. Posterior edge with a fine transverse line at centre (usually extending little beyond the second elytral stria). Hypomeral cavity with variable density of setae, from almost glabrous to with long yellowish setae covering the entire interior of the hypomeral cavity; external margin simple, without any trace of a tubercle. Metaventrite entirely glabrous; anterior region with tegument with distinct alveolar microsculpture; centre and posterior region with dense alveolar microsculpture obliterating weak micropunctation, or micropunctation completely absent.

Legs. Profemora with tegument with strong alveolar microsculpture on their anterior half and with strong rivose microsculpture on their posterior half. Protibiae narrow and straight on their internal edge; at their apical seventh, external edge with two small acute teeth – the apical one slightly longer than the second. Mesofemora margined anteriorly only at their basal half; unmargined portion of anterior edge with row of very short setae; tegument with strong alveolar micosculpture. Metafemora margined only anteriorly, posterior margin absent; apical third of anterior edge covered by row of setae; tegument with strong alveolar microsculpture obliterating micropunctation, which is almost imperceptible; base without coarse elongate punctation. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. With only eight visible striae: first four or five striae clearly marked, finely carinulate, and without basal widening; fifth to seventh striae progressivily more effaced and interrupted, the seventh occasionally vestigial; eighth stria vestigial, present only as a weak mark parallel to the apical half of epipleura; all striae lack their carinulae at the apex of elytra, where they are marked only by microsculpture or are completely indistinct; humeral carina absent. Tegument of interstriae with strong alveolar microsculpture obliterating micropunctation, which is almost imperceptible.

ABDOMEN. Ventrite VI smooth at centre and with weak rivose microsculpture on the sides. Lateral foveae absent in both sexes. Pygidium with tegument with strong alveolar microsculpture and effaced, frequently imperceptible micropunctation; of equivalent length in both sexes.

AEDEAGUS. Parameres about half as long as phallobase, and slightly asymmetrical: left paramere laterally flat or concave, right paramere convex (difference more easialy seen from ventral view). In lateral view, parameres with strong ventral keel and with short notch close to base (Fig. 17D).

SEXUAL DIMORPHISM. **Males**: Protibial spur broad and bifid, with external projection spiniform, straight, and long, and internal projection bent and widened (Fig. 15D). Ventrite VI strongly narrowed at middle; ventrite V usually without medial flange on its posterior edge or only slightly indicated over anterior edge of ventrite VI. **Females**: Protibial spur spiniform. Ventrite VI broad at middle and with anterior edge only slightly covered by weak flange of posterior edge of ventrite V.

Measurements

Males (N = 16). **TL:** AV: 7.0 ± 0.36; MX: 7.4; MN: 6.5. **EL:** AV: 4.9 ± 0.39; MX: 5.7; MN: 4.3. **PL:** AV: 2.1 ± 0.17; MX: 2.5; MN: 1.9. **PW:** AV: 4.1 ± 0.26; MX: 4.5; MN: 3.7. **PgL:** AV: 1.4 ± 0.09; MX: 1.5; MN: 1.3. **PgW:** AV: 2.1 ± 0.13; MX: 2.3; MN: 1.9.

Females (N = 21). **TL:** AV: 7.2 ± 0.50; MX: 8.2; MN: 6.6. **EW:** AV: 4.9 ± 0.23; MX: 5.3; MN: 4.6. **PL:** AV: 2.1 ± 0.14; MX: 2.3; MN: 1.9. **PW:** AV: 4.1 ± 0.19; MX: 4.5; MN: 3.9. **PgL:** AV: 1.4 ± 0.08; MX: 1.5; MN: 1.3. **PgW:** AV: 2.1 ± 0.11; MX: 2.3; MN: 1.9.

Geographical distribution

Cloud forests of western Amazonia and slopes of the Andes in Ecuador and Peru.

Ecoregions

Napo Moist Forests, Cordillera Oriental Montane Forest, Marañón Dry Forest, Ucayali Moist Forests, Peruvian Yungas.

Collecting sites (Fig. 24)

ECUADOR. **Orellana**: Onkone Gare Camp. **Napo**. **Tungurahua**: Baños de Agua Santa, Río Negro. **Pastaza**: Pastaza (Puyo: Llandia), Mera. **Morona Santiago**: Untsuante. **Zamora Chinchipe**: Cordillera del Cóndor.

PERU. **Amazonas**. **San Martín**: Rioja (Yuracyacu), Mariscal Cáceres (Juanjuí). **Huánuco**: Leoncio Prado (Rupa-Rupa: Tingo María). **Junín**: Chanchamayo (San Ramón). **Cuzco**: La Convención (Echarate).

Intraspecific variation and taxonomic discussion

It is interesting to note that many specimens of *S. genieri* sp. nov. studied for this work bear labels identifying them as *S. candezei*. It is not surprising that both species have been confused for such a long time, since they, together with *S. foveiventris*, share several characteristics not found in any other *Sylvicanthon*. The most obvious of them is the presence of only two protibial teeth (Fig. 11J), while all the other species have three, but we can list also protibiae without internal expansion (absent also in the *aequinoctialis* subgroup and in the majority of the species of the *bridarollii* group) and elytral striae very fine and progressively less marked from the elytral suture. Furthermore, among *Sylvicanthon*, it is only in *S. genieri* sp. nov. and *S. candezei* that the hypomeral tubercle is completely absent, fact that leads these two species to key out at the same couplet in all the identification keys published so far (Schmidt 1922; Balthasar 1939; Pereira & Martínez 1956; Martínez *et al.* 1964; Vulcano & Pereira 1967).

Even so, also based on identification labels, it is possible to see that with the increasing accumulation of material collected during the 1990s and 2000s, some entomologists were able to recognize the true identity of *S. genieri* sp. nov. as a distinct species. From 1998 on, François Génier identified some specimens of this species as '*Sylvicanthon* sp. nov.', whereas Trond Tarsen, in 2012, determined others as '*Sylvicanthon* sp. ≠ *candezei*'. In fact, even at first sight, *S. genieri* sp. nov. and *S. candezei* are easily differentiated by colouration: the former species has a bright coppery colouration (occasionally, with greenish reflexions on head) (Fig. 27A), while *S. candezei* is entirely dark green (Fig. 25A). The degree of punctation and microsculpture throughout the body also varies between the two species: in *S. candezei*, punctures at the centre of pronotum are strong and easily seen, little obliterated by microsculpture, while punctures are very weak in *S. genieri* sp. nov. and usually almost completely obliterated by the strong microsculpture at the centre of the pronotum. On the elytra and pygidium, the microsculpture is always very strong and punctures are weak or even absent in *S. genieri* sp. nov., whereas, although not as well marked as at the centre of pronotum, they are still completely visible in *S. candezei*.

A difference is also seen on the ventrites: in males of *S. candezei*, ventrite five shows a weak medial flange over the anterior margin of ventrite six (Fig. 14D), while in females this flange is much stronger, giving a false impression of a medial narrowing to ventrite six (characteristic usually associated to males in *Sylvicanthon*) (Fig. 14E). In *S. genieri* sp. nov., on the other hand, males usually lack any trace of a flange on ventrite five or, at most, it is very weak, almost imperceptible, while in females this flange is not very strong either, being similar to the one present in males of *S. candezei*, which does not obscure the true broad, typically female nature of ventrite six. Lastly, the clearest morphological difference

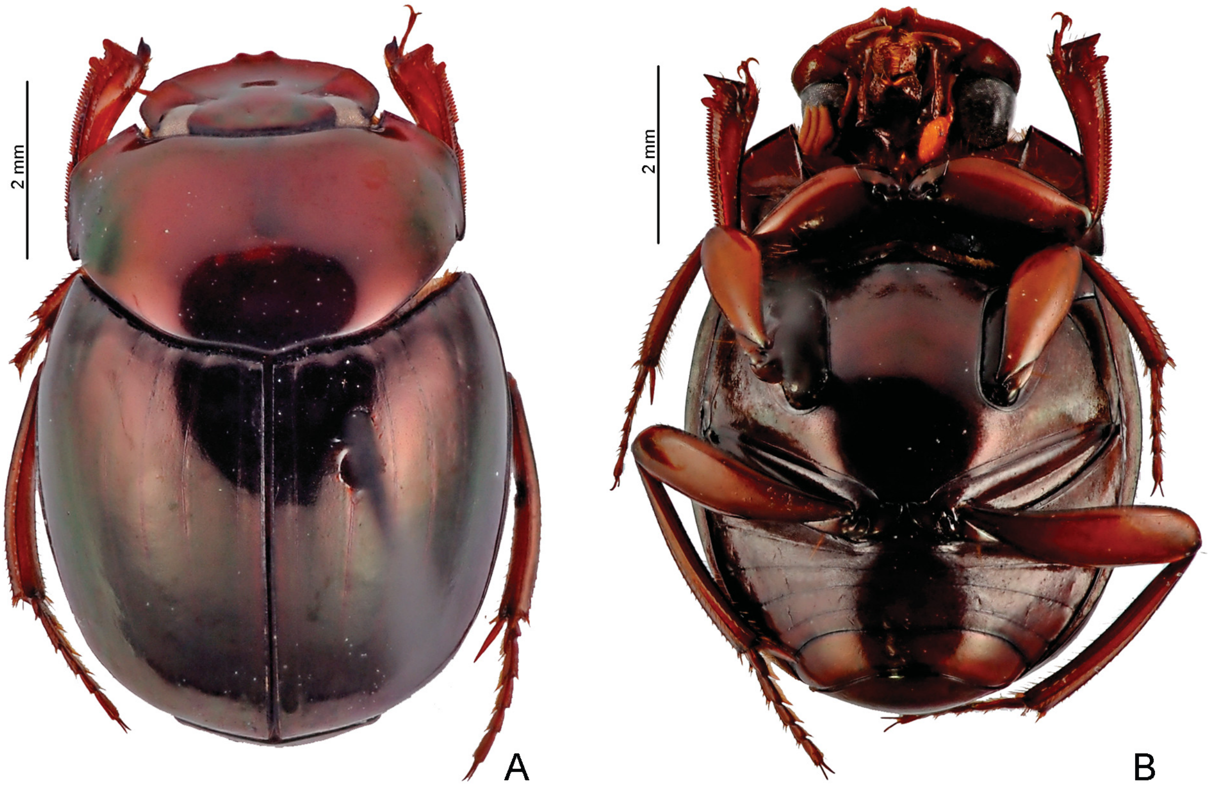

Fig. 27. *Sylvicanthon genieri* sp. nov. **A**. Dorsal view. **B**. Ventral view.

between these two species lies on the shape of the parameres: in *S. candezei*, they have a deep ventral notch, dividing the parameres into two regions (the anterior one subrectangular) (Fig. 17C), and lack a ventral keel, whereas *S. genieri* sp. nov. presents a much shorter notch (which does not divide the parameres into two distinct parts) and has a strong ventral keel (Fig. 17D).

From *S. foveiventris*, the third species of the *candezei* subgroup, *S. genieri* sp. nov. is distinct in presenting a strong alveolar microsculpture on the pronotum, elytra and pygidium, whilst the former species does not possess any sign of microsculpture, with tegument marked only by micropunctation. The absence of paired foveae on the female ventrites (present in three pairs in *S. foveiventris*, Figs 14B, 16D), the paramere shape (with a ventral keel and a notch in *S. genieri* sp. nov., Fig. 17D; and simple in *S. foveiventris*, Fig. 17B), and colouration also distinguish both species. On the other hand, *S. genieri* sp. nov. and *S. foveiventris* are similar by the presence of a weak (rather than strong) medial flange of ventrite five of females (although this structure is even less developed in *S. foveiventris*, Fig. 14B, than in *S. genieri* sp. nov.).

Limited morphological variation was observed in *S. genieri* sp. nov., none of it related to distribution. The few variable characteristics are related to the micropunctation of the pronotum and the elytra (which can be clearly present or almost entirely effaced and imperceptible; on the elytra, in particular, sometimes it is completely absent), the pilosity of the hypomeral cavity (which can be entirely glabrous or present several yellowish setae all over its surface), and the colouration (which can vary from a very dark coppery with little sheen to light reddish with greenish reflections on the head, with the majority of the specimens being in an intermediate position between these two extremes, with a bright coppery colouration without any trace of greenish reflexions). The colouration of the meso- and metafemur also varies, with one end of the variation spectrum being light yellow and the other dark brown. Teneral specimens are entirely yellow.

Comments

Judging from the cited locality, specimens identified as *S. candezei* by Carvajal *et al.* (2011) from Ecuador are probably *S. genieri* sp. nov.. In addition, having studied some specimens of the species that Celi *et al.* (2004) called "S*ylvicanthon* sp. 2", it was possible to see that this species is actually *S. genieri* sp. nov. (see discussion about this and other identifications by Celi *et al.* on the comments under *S. edmondsi* sp. nov.).

Natural history

Based on the label information, it is possible to say that *S. genieri* sp. nov. is mainly collected with pitfall traps baited with human faeces. A male was collected in La Convención (Cuzcu, Peru) with a light trap and a female was found beneath the leaf litter in Onkone Gare Camp (Orellana, Ecuador). Living on the Amazon slopes of the Andes, *S. genieri* sp. nov. is in the *candezei* group the species which occurs at the highest elevation, having been recorded mostly in altitudes ranging from 805 to 1685 m; just one specimen was caught at 200 m in the Onkone Gare Camp. This species was collected throughout the year (January, March, April, May, July, August, September and October), but July (125) and January (22) concentrated the record of the vast majority of the 202 specimens studied.

The aequinoctialis *subgroup*

Sylvicanthon aequinoctialis (Harold, 1868) comb. nov.
Figs 7A, 11B, 15E–F, 17E, 20, 28A–B, 29A–B, 30, 31A

Canthon aequinoctialis Harold, 1868a: 2, 5, 14, 79, 141.

"*Coprobius aequinoctialis*" – Dejean 1833: 136.
"*Coprobius aequinoctialis*" – Dejean 1836: 151. — Harold 1868a: 79 (as synonym of *C. aequinoctialis*). **Nomen nudum**.
Canthon aequinoctialis – Harold 1869b: 989; 1880: 16. — Bates 1887: 33. — Gillet 1911: 27. — Schmidt 1922: 64, 72. — Balthasar 1939: 187; 1941: 341 (error: refers to *S. proseni*); 1951: 326 (error: refers to *S. proseni*). — Martínez 1949a: 290. — Vulcano & Pereira 1967: 561. — Gill 1991: 225–226, 228. — Escobar 2000a: 206 (error: refers to *S. proseni*); 2000b: 114, 121 (mixed information with *S. proseni*). — Medina *et al.* 2001: 135 (mixed information with *S. proseni*); 2003: 27, 51, 57–58, figs 9, 164; 2012: 93, 115, 171, 192. — Ratcliffe 2002: 12. — Solís & Kohlmann 2002: 1, 4, 6–8, 53–54, 64, figs 1f, 31; 2012: 3, 21. — Halffter 2003: 43. — Celi *et al.* 2004: 42 (error: refers to *S. proseni*). — Noriega-Alvarado 2004: 40 (idem). — Kohlmann *et al.* 2007: 9, 28; 2010: 553. — Noriega *et al.* 2008: 78–79 (error: refers to *S. proseni*). — Carpio *et al.* 2009: 462, 464, 469 (*idem*). — Medina & Pulido 2009: 58 (error: refers to *S. proseni*). — Arango & Montes 2010: 262. — Figueroa & Alvarado 2011: 210–211, fig. 1c (error: refers to *S. proseni*). — Solís *et al.* 2011: 36, 38. — Krajcik 2012: 63. — Noriega 2012: 4 (error: refers to *S. proseni*). — Ratcliffe *et al.* 2015: 195 (error: refers to *S. proseni*).
Canthon aequinoctiale – Blackwelder 1944: 198; 1973: 2. — Gacharná 1951: 221. — Howden & Young 1981: 20, 27–28, 153, 167, figs 36–37. — Vaz-de-Mello & Louzada 1997: 56. — Vaz-de-Mello 1999: 449–450 (error: refers to *S. proseni*). — Young 2009: 322.
Canthon cf. *aequinoctialis* – Noriega *et al.* 2007b: 81. — Martínez *et al.* 2010: 24.
Canthon (*Canthon*) *aequinoctialis* – Halffter & Martínez 1977: 62, 90–91. — Noriega *et al.* 2007a: 54–55 (error: refers to *S. proseni*).
Canthon (*Canthon*) *aequinoctiale* – Vaz-de-Mello 2000 (error: refers to *S. proseni*).
Canthon (*Canthon*) *aequinotialis* [sic] – Noriega-Alvarado 2009. — Culot *et al*. 2011: Supporting information, table S1 (error: refers to *S. proseni*).
Canthon (*Glaphyrocanthon*) *aequinoctialis* – Howden 1966: 730.
Glaphyrocanthon (*Glaphyrocanthon*) *aequinoctialis* – Pereira & Martínez 1956: 126, 128. — Martínez *et al.* 1964: 3, 5, 8–10, 13. — Vulcano & Pereira 1967: 561.
Glaphyrocanthon (*Glaphyrocanthon*) *aequinotialis* [sic] – Vulcano & Pereira 1964: 661.

Etymology

From the Latin '*aequinoctialis*', meaning 'equinox' or 'equinoctial'. Probable reference to the type locality, region crossed by the Equator.

Material examined

Lectotype (here designated)
COLOMBIA: ♂, type locality cited by Harold (1868a) as "*Columbien, Neu-Granada*", ("*æquinoctialis / t. Har*", "*Nov. Grenade*", "Ex-Musæo / E. Harold", "HOLOTYPE", "*TIPO / Canthon / (Canthon) / aequinoctialis / Harold / G. H. y A. M. det. 76*") (MNHN) (Fig. 29A).

Paralectotype
COLOMBIA: ♀, ("26381", "*Nov Granad. Gom.*", "Type", "*aequinoctialis / Harold* / Nov. Granada*", "PARALECTOTYPE / Canthon *aequinoctialis* / Harold, 1868 / des. Cupello & Vaz-de-Mello, 2015") (ZMHB) (Fig. 29B).

Additional material (282 ♂♂, 210 ♀♀, 81 unsexed specimens)
COLOMBIA: 1 ♀, "*Lebas*" (collector or locality?) (ISNB, Gillet collection); 1 ♂, illegible locality, 1921 (MZSP); 1 ♂, "New Granada", R. Bunch leg. (BMNH, E.Y. Western coll.). – **Antioquia**: 2 ♂♂, San Luis, Sonsón, Reserva Natural Cañon del Río Claro, 1440 m, 2 Mar. 1994, Harold M. Parra leg. (CEMT); 2 ♂♂, San Luis, Sonsón, Reserva Natural Cañon del Río Claro, 1440 m, 3 Mar. 1994, H.M.

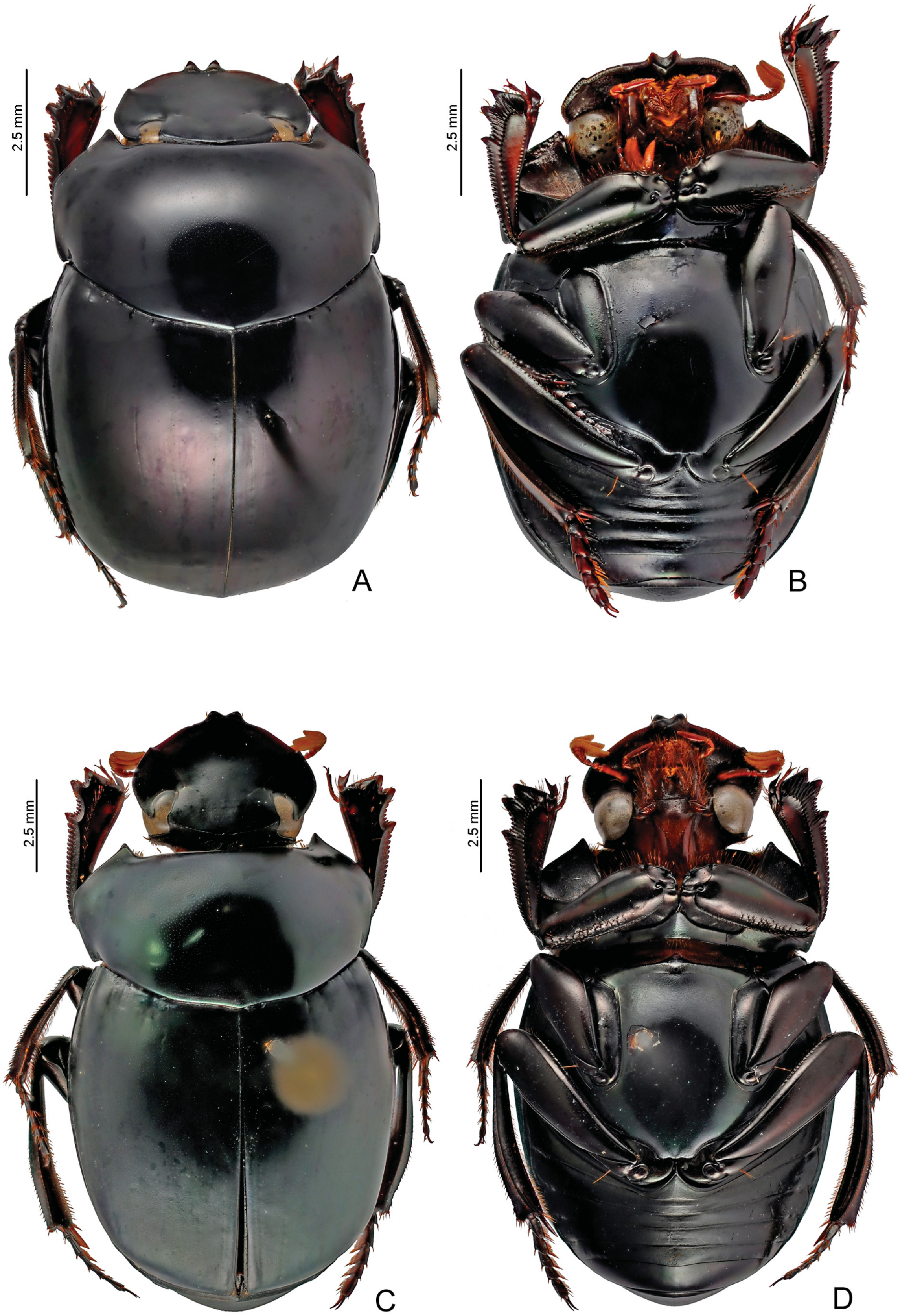

Fig. 28. **A–B**. *Sylvicanthon aequinoctialis* (Harold, 1868) comb. nov. **A**. Dorsal view. **B**. Ventral view. **C–D**. *S. proseni* (Martínez, 1949) stat. et comb. nov. **C**. Dorsal view. **D**. Ventral view.

Parra leg. (CEMT); 1 ♀, San Luis, Sonsón, Reserva Natural Cañon del Río Claro, 1440 m, 3 Mar. 1994, H.M. Parra leg. (MCNZ). – **Cesar**: 1 ♂, 1 ♀, Chimichagua, Finca Señor Reyes, 09º21′9.8″ N, 73º48′22.2″ W, 42 m, 7 Mar. 2010, pitfall with human faeces, P. Delgado leg. (CEMT). – **Chocó**: 2 ♂♂ (1 dissected), 1 ♀, Acandí, Capurganá, "caminho 'Al Cielo'", 10 m, 6 Jan. 1999, A. Vitolo leg. (CEMT); 2 ♂♂ (1 dissected), Acandí, Capurganá, "Jardin", 08º37′42″ S, 77º21′12″ W, 30 m, 16–18 Jan. 2008, pitfall with human faeces, Arias *et al.* leg. (CEMT); 1 ♂, 4 ♀♀, Lloró, 05º31′ N, 76º33′ W, 90 m, 20 Feb. 2003, Olaya and Mosquero leg. (TAMU); 1 ♀, Parque Nacional Natural Ensenada de Utría, 19 Jun. 1997, pitfall with human faeces, Llanos-Jurado leg. (CEMT); 2 ♂♂, 1 ♀, Quibdó, Tutunendó ("20 km NE Quibdó"), 60 m, 26 Nov. 2001, J.C. Neita leg. (TAMU); 3 ♂♂, Quibdó, Estación Ambiental Pandó, 05º42′43″ S, 76º37′59″ W, 43 m, 9–11 Jun. 2010, pitfall with human faeces, J. Arias leg. (CEMT); 4 ♂♂, 6 ♀♀, Quibdó, Pacurita, 05º41′ N, 76º40′ W, 53 m, 25 Nov. 2001, dung, J.C. Neita leg. (TAMU); 2 ♀♀, Quibdó, Pacurita, "Arriba de la quebrada Aguas Claras", 05º42′ N, 76º40′ W, 43 m, 9–11 Jun. 2010, pitfall with human faeces, J. Arias leg. (CEMT); 2 ♂♂, Unión Panamericana, 05º32′45″ N, 76º44′33″ W, 115 m, J.C. Neita leg. (TAMU); 3 ♂♂ (1 dissected), 1 ♀, Unión Panamericana, Salero, 05º32′ N, 76º44′ W, 120 m, 3–5 Jun. 2010, pitfall with human faeces, J. Arias leg. (CEMT). – **Distrito Capital**(?): 1 specimen, Bogotá (BMNH). – **Santander**: 3 ♂♂, 1 ♀, Serranía de las Quinchas, Reserva El Paujil, Jul. 2006, pitfall with *Alouatta seniculus* dung, Santos Zarate leg. (CEMT); 1 ♂, 1 ♀, Serranía de las Quinchas, Reserva El Paujil, Sep. 2006, pitfall with *Alouatta seniculus* dung, Santos Zarate leg. (CEMT). – **Tolima**: 1 ♂, 300 m, Nov. 1995, human faeces, F. Escobar leg. (CEMT). – **Valle Del Cauca**: 1 ♂, Estación Agro-Forestal Bajo Calima, 50 m, 2 Oct. 1995, A. Lopera leg. (CEMT); 1 ♂ (dissected), Dagua, Río Escalerete, 31 Mar.–4 Apr. 1991, L.C. Pardo Locarno leg. (CEMT).

COSTA RICA: **Guanacaste**: Volcán Rincón de la Vieja, Hacienda Guachipelín, 13 Aug. 1999, trap with human faeces, J. L. Moreno & T. Mestre leg. 1 ♂ (CEMT). – **Limón**: Río Reventazón, Humburgfarm, 15 Apr. 1923, without collector – 1 ♀ (MZSP); Río Reventazón, Humburgfarm, 27 Aug. 1925, F. Nevermann leg. 1 ♂ (MZSP). – **Puntarenas**: Osa, 10–15 Aug. 1966 [trap with rotten flesh], S. Peck leg. 1 ♂ (CNCI); 11 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º30.259′ N 83º35.958′ W, 18 m, 17–20 Jul. 2009, Mehrabi *et al.* leg. (OUMNH); 20 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º30.502′ N, 83º36.285′ W, 29 m, 29–31 Jul. 2009, Mehrabi *et al.* leg. (OUMNH); 52 ♂♂ (1 dissected), 46 ♀♀, Península de Osa, Sirena Biological Station, 08º30′ N, 83º36′ W, 30 m, Jul. 2009, swine dung, Mann leg. (CEMT); 7 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º29.891′ N 35º998′ W, 31 m, 11–14 Jul. 2009, Mehrabi *et al.* leg. (OUMNH); 9 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º29.46′ N 83º35.57′ W, 41 m, Jul. 2009, Mehrabi, Coals, Cowburn and Yu leg. (OUMNH); 2 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º30.897′ N 83º35.847′ W, 42 m, 31 Jul.–2 Aug. 2009, Mehrabi *et al.* leg. (OUMNH); 2 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º28.230′ N 83º35.275′ W, 47 m, 26–29 Jul. 2009, Mehrabi *et al.* leg. (OUMNH); 8 specimens, Península de Osa, Corcovado National Park, Sirena Biological Station, 08º29.287′ N 83º35.327′ W, 49 m, 19–22 Jul. 2009, Mehrabi *et al.* leg. (OUMNH); 1 specimen, Península de Osa, Osa Biodiversity Centre, 08º24′14″ N 83º20′09″ W, 115 m, Apr. 2010, Mann and Mehrabi leg. (OUMNH); 3 ♂♂, 1 ♀, Reserva Biológica Bosque Nuboso Monteverde ("Parque Nacional Monteverde"), 13 Aug. 1999, J.L. Moreno and T. Mestre leg. (CEMT).

HONDURAS: **Atlántida**: 1 ♂ (dissected), 2 ♀♀, 15 km W of La Ceiba, 15–19 Jun. 1996, flight interception trap, R. Lehman leg. (TAMU).

NICARAGUA: **Chontales**: 1 specimen, T. Belt leg. (BMNH, BCA). – **Jinotega**: 2 ♀♀, Reserva Natural Cerro Kilambé, 1000 m, Aug. 2001, M.A. Guatemala leg. (SEAN); 1 ♀, Santa Maura, 1215 m, Mar. 2002, L. Pivotti leg. (SEAN). – **Matagalpa**: 41 ♂♂, 17 ♀♀, Matiguas, 5–6 Dec. 2003, B. Hernández

Fig. 29. Type material of the *aequinoctialis* subgroup. **A–B**. *Sylvicanthon aequinoctialis* (Harold, 1868) comb. nov., type series. **A**. Lectotype and its labels. **B**. Paralectotype and its labels. **C–E**. *S. proseni* (Martínez, 1949) stat. et comb. nov., type series. **C**. Holotype and its labels. **D**. Paratype 1. **E**. Paratype 2.

leg. (SEAN); 3 ♂♂, 4 ♀♀, Matiguas, 8–9 Feb. 2004, B. Hernández leg. (SEAN); 5 ♂♂, 2 ♀♀, 13–14 Feb. 2004, B. Hernández leg. 5 (SEAN); 18 ♂♂, 21 ♀♀, Matiguas, 10–11 Mar. 2004, B. Hernández leg. (SEAN); 3 ♂♂, 1 ♀, Matiguas, 14–15 Mar. 2004, B. Hernández leg. (SEAN); 1 ♀, Matiguas, 21–22 Apr. 2004, B. Hernández leg. (SEAN); 11 ♂♂, 17 ♀♀, Matiguas, 23–24 Apr. 2004, B. Hernández leg. (SEAN); 27 ♂♂, 23 ♀♀, Matiguas, 26–27 Apr. 2004, B. Hernández leg. (SEAN); 9 ♂♂, 2 ♀♀, Matiguas, 3–4 Jun. 2004, B. Hernández leg. (SEAN); 9 ♂♂, 5 ♀♀, Matiguas, 19–20 Jun. 2004, B. Hernández leg. (SEAN); 7 ♂♂, Matiguas, 23–24 Jun. 2004, B. Hernández leg. (SEAN); 2 ♂♂, 4 ♀♀, Matiguas, 29–30 Jun. 2004, B. Hernández leg. (SEAN); 1 ♂, Matiguas, 2–3 Jul. 2004, B. Hernández leg. (SEAN); 2 ♂♂, Reserva Natural Biósfera de Bosawas, Macizo de Peñas Blancas, 29–30 Apr. 2017, B. Hernández leg (CEMT). – **Río San Juan**: 1 ♂, Reserva Biológica Indio Maíz, 10º58′24″ N, 84º04′52″ W, 14–15 Jun. 2002, P. Schmit and B. Hernández leg. (SEAN).

PANAMA: **Chiriquí**: 1 specimen, David, San José de David, Champion leg. (BMNH – BCA); 1 ♂, Gualaca, Hornito, Finca La Suiza, 9–15 May 1999, pitfall with human faeces, Wappes and Morris leg. (TAMU). – **Colón**: 1 ♀, Chagres, Fort San Lorenzo (“San Lorenzo Forest” sic), 09º17′ N, 79º58′ W, May 2004, flight interception trap, A. Tishechkin leg. (CEMT); 1 ♂, Colón, 2 km S of Sabanitas, 09º19′19″ N, 79º47′54″ W, 25–26 Jun. 1999, UV light, A. Gillogly leg. (TAMU). – **Panamá**: 3 ♀♀, Canal Zone, Fort Kobbe, 14 Jun. 1976, E.G. Riley leg. (TAMU); 9 ♂♂, 4 ♀♀, Canal Zone, Fort Kobbe, 4–21 Jun. 1985, pitfall with human faeces, E.G. Riley leg. (TAMU); 1 specimen, Canal Zone, Lago Gatún, Barro Colorado Island, K.W. Cooper leg. (MNHN); 1 ♂, Canal Zone, Lago Gatún, Barro Colorado Island, 22 Feb. 1955, R. Freund leg. (CNCI); 1 ♀, Canal Zone, Lago Gatún, Barro Colorado Island, 13 Feb. 1960, S. Breeland leg. (CNCI); 4 ♂♂, 3 ♀♀, Canal Zone, Lago Gatún, Barro Colorado Island, 18 Jul. 1963, L. J. Bottimer leg. (CNCI); 7 specimens, Canal Zone, Gatún Lake, Barro Colorado Island, Mar. 1975, O.P. Young leg. (BMNH); 1 ♂, Canal Zone, Gatún Lake, Barro Colorado Island, Jun. 1978 (CEMT); 2 ♂♂, 1 ♀, Canal Zone, Gatún Lake, Barro Colorado Island, 9 Jul. 1978, dung trap, A. Forsyth leg. (TAMU); 1 ♂, Canal Zone, Gatún Lake, Barro Colorado Island, 19 Jul. 1978, dung trap, A. Forsyth leg. (TAMU); 1 ♂, Canal Zone, Gatún Lake, Barro Colorado Island, 16 Aug. 1978, dung trap, A. Forsyth leg. (TAMU); 4 specimens, Canal Zone, Gatún Lake, Barro Colorado Island, 12–14 May 1981, B. Gill leg. (BMNH); 1 specimen, Canal Zone, Gatún Lake, Barro Colorado Island, 20–28 May 1981, B. Gill leg. (BMNH); 1 ♂, 1 ♀, Canal Zone, Río Changena, 21 Sep. 1961, C.E. Yunker leg. (CNCI); 1 ♂, Canal Zone, Skunk Hollow, 13 Jul. 1975, B.C. Ratcliffe leg. (ZMHB); 5 specimens, Canal Zone, Skunk Hollow, 6 mi. NW of Gatún Lake, 17–31 May 1980, B.C. Ratcliffe leg. (BMNH); 4 ♂♂, 1 ♀, same collecting data as for preceding (ZMHB); 2 ♂♂, Cerro Azul, 12–13 May 1996, Wappes, Huether and Morris leg. (TAMU); 2 ♀♀, Cerro Azul, 21–24 May 1996, Wappes, Huether and Morris leg. (TAMU); 1 ♀, El Llano-Carti Road, Km 7.5, 350 m, 4–6 Jun. 1995, flight interception trap, A.R. Gillogly leg. (TAMU); 1 ♂, 1 ♀, El Llano-Carti Road, Km 8–13, 21–24 May 1996, Wappes, Huether and Morris leg. (TAMU); 1 ♀, Nusagandi, Ina Igar (Trail), 18–21 May 1993, pitfall with human faeces, E.G. Riley leg. (CEMT); 19 ♂♂ (1 dissected), 9 ♀♀, same collecting data as for preceding (TAMU); 1 ♀, Parque nacional Soberanía, 23–27 May 1996, Wappes, Huether and Morris leg. (TAMU); 1 ♀, Pipeline Road, Km 01–12, 26–30 Jun. 1997, Wappes and Morris leg. (CEMT); 3 ♂♂, 3 ♀♀, same collecting data as for preceding (TAMU); 1 ♂, 1 ♀, Pipline Road, Km 6.1, “near Gambba”, 40 m, 7–21 Jun. 1995, J. Ashe and R. Brooks leg. (MCNZ).

No data: 1 ♂, 1 ♀ (ISNB, Gillet collection), 3 ♀♀ (ISNB, J. Thomson collection, pseudotypes).

Redescription

COLOURATION. Entire body surface bright and glossy, including the surface of pygidium. Head, pronotum, elytra, and pygidium usually purple, blue, or, occasionally, green. Metaventrite dark green or dark blue. Meso- and metafemora dark brown and, in general, with greenish reflections.

Head. Tegument entirely covered by alveolar microsculpture and without any trace of micropunctation or, occasionally, with very weak, almost imperceptible micropunctures among microsculpture. Clypeus with two apical teeth obtuse and contiguous at base; with a single transverse row of very short setae covering the base of both teeth. Genae with evident tooth immediately behind clypeal-genal juncture. Posterior edge of head with complete margin between eyes.

Thorax. Pronotum very shiny and with tegument at centre ranging from completely smooth, with no trace of microsculpture or micropunctation, to with very weak and effaced alveolar microsculpture and micropunctation; on the sides, always with fine alveolar microsculpture. Posterior edge, in general, without transverse line at centre; in some specimens, with traces of fine transverse line at centre. Hypomeral cavity with long setae on posterior region and as long or shorter setae at centre and on external edge; external edge with a turbercle which can be clearly present or almost imperceptible. Metaventrite entirely glabrous (or, occasionally, with few setae at lateral region close to metacoxae, Fig. 7A); with uniform alveolar microsculpture throughout ventral region of metaventrite (i.e., between metacoxae) and with very tenuous micropunctation, which, in general, is only visible under high magnification (higher than 35 ×).

Legs. Ventral surface of all femora bright and with silky appearance. Profemora with tegument completely covered by alveolar microsculpture. Protibiae broad and without internal expansion; at their apical half, external edge with three medium-sized, broad and acute or obstuse teeth – the two apical much larger than basal ones (Fig. 11B). Mesofemora margined anteriorly only at basal half; unmargined portion of anterior edge with row of very short setae; tegument with rivose microsculpture at external (anterior) half and with alveolar microsculpture at internal (posterior) half. Metafemora with both anterior and posterior margins (Fig. 31A); posterior margin extending from the apex of femur until, at most, little beyond the trochanter; tegument as on mesofemora, with no trace of micropunctation or coarse punctation at base. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. With only eight very subtly-marked, fine and superficial striae, all of which without carinulae; first seven striae equally marked (only seventh stria, occasionally, more effaced and discontinuous); eighth stria present only on humerus and subtly carinate (humeral carina). Tegument bright with alveolar microsculpture and micropunctation very subtle and effaced, only visible under magnification of at least 30 ×; microsculpture more evident only on the outer sides.

Abdomen. Ventrite V and, especially, ventrite VI smooth at centre and with weaker rivose microsculpture on the sides. Lateral foveae absent in both sexes. Pygidium with shiny tegument and very diffuse effaced rivose microsculpture; of equivalent length in both sexes.

Aedeagus. Parameres long, slightly shorter than phallobase, and clearly asymmetrical: left paramere laterally with apical depression more profound and wide than depression on left paramere (difference more easily seen in dorsal view). In lateral view, parameres with central angularity and without ventral keel or notch.

Sexual dimorphism. **Males**: Protibial spur wide and foliaceous, external edge projected into an acute long spine, while internal edge has no prolongation or has a very short spine; area between both spines straight or slightly excavated (Fig. 15E). Ventrite VI strongly narrowed at centre; ventrite V usually without medial flange or only slightly indicated over anterior edge of ventrite VI. **Females**: Protibial spur spiniform (Fig. 15F). Ventrite VI broad at centre and with anterior edge slightly covered by weak medial flange of ventrite V.

Measurements

Males (N = 20). **TL:** AV: 10.5 ± 0.93; MX: 12.3; MN: 9.0. **EW:** AV: 7.1 ± 0.66; MX: 7.8; MN: 5.7. **PL:** AV: 3.4 ± 0.3; MX: 3.9; MN: 2.7. **PW:** AV: 6.3 ± 0.83; MX: 7.4; MN: 5.3. **PgL:** AV: 1.9 ± 0.16; MX: 2.1; MN: 1.6. **PgW:** AV: 3.4 ± 0.29; MX: 3.7; MN: 2.8.

Females (N = 21). **CT:** AV: 10.4 ± 0.88; MX: 11.8; MN: 8.7. **EW:** AV: 7.0 ± 0.51; MX: 7.6; MN: 6. **PL:** AV: 3.4 ± 0.29; MX: 3.9; MN: 2.9. **PW:** AV: 6.3 ± 0.47; MX: 5.3; MN: 6.8. **PgL:** AV: 1.7 ± 0.14; MX: 2.0; MN: 1.5. **PgW:** AV: 3.3 ± 0.27; MX: 3.7; MN: 2.8.

Geographical distribution

Widespread throughout the tropical forests from Honduras to northern Colombia.

Ecoregions

Central American Atlantic Moist Forests, Central American Montane Forests, Isthmian-Atlantic Moist Forests, Talamancan Montane Forests, Costa Rican Seasonal Moist Forests, Isthmian-Pacific Moist Forests, Chocó-Darién Moist Forests, Guajira-Barranquilla Xeric Scrub, Magdalena-Urabá Moist Forests, Magdalena Valley Montane Forests, Magdalena Valley Dry Forests.

Collecting sites (Fig. 30)

HONDURAS. **Atlántida**: La Ceiba.

NICARAGUA. **Jinotega**: Reserva Natural Cerro Kilambé, Santa Maura. **Matagalpa**: Matiguas, Reserva Natural Biósfera de Bosawas (Macizo de Peñas Blancas). **Chontales**. **Río San Juan**: Reserva Biológica Indio Maíz.

COSTA RICA. **Guanacaste**: *Cerro El Hacha*, Volcán Rincón de la Vieja. ***Alajuela**: Playuelas, San Ramón de dos Ríos, Volcán Tenorio (Colonia Río Celeste)*. ***Heredia***: *Sarapiquí (Estación Biológica La Selva)*. **Puntarenas**: *Golfitos (Las Torres)*, Osa (*Albergue Ecoturístico Cerro de Oro*), Parque Nacional Corcovado (Estación Biológica Sirena), Reserva Biológica Bosque Nuboso Monteverde. ***San José***: *Santa Ana (Ciudad Colon), Turrúcares*. **Limón**: *Guácimo (Parque Nacional Tortuguero), Limón (Río Blanco), Pococí (Cedrales de la Rita, Cerro Cocorí, Refugio Nacional de Fauna Silvestre Barra del Colorado), Refugio de Vida Silvestre Gandoca-Manzanillo (Manzanillo), Talamanca (Bratsi: Amubri)*.

PANAMA. **Chiriquí**: *Barú (Progreso)*, David (San José de David), Gualaca (Hornito), **Colón**: Chagres (Fort San Lorenzo), Colón. **Panamá**: Panama Canal (Fort Kobbe; Lago Gatún: Isla Barro Colorado; Skunk Hollow), Cerro Azul, Nusagandi, Parque Nacional Soberanía.

COLOMBIA: ***Atlántico***: *Juan de Acosta (Reserva de Tierra Arena)*. **Cesar**: Chimichagua. **Santander**: Serranía de las Quinchas (Reserva El Paujil). **Antioquia**: San Luis (Sonsón). **Chocó**: Acandí (Capurganá), Lloró, Parque Nacional Natural Ensenada de Utría, Quibdó (Tutunendó, Estación Ambiental Pandó, Pacurita), Unión Panamericana (Salero). ***Caldas***: *Norcasia (Reserva Natural Río Manso)*. **Valle del Cauca**: Estación Agro-Forestal Bajo Calima, Dagua. ***Cundinamarca***. **Tolima**.

Intraspecific variation and taxonomic discussion

Despite its extensive geographical distribution and the large number of specimens studied for this work, limited morphological variation was observed in *S. aequinoctialis* apart from colouration and size[19]. The most noticeable variation is related to the sculpture at the centre of the pronotum, which can be almost completely smooth, without any trace of alveolar microsculpture or micropunctation, in some specimens, or have microsculpture and micropunctation present, but very fine and effaced, in others. It is interesting to note that in its sister species, *S. proseni*, the degree to which the pronotal micropunctation is marked varies intrapopulationally at a much stronger intensity. A detailed comparison between *S. aequinoctialis* and *S. proseni* is present in the taxonomic discussion of the latter species.

Comments

The earliest references found in the literature on the species we now know as *S. aequinoctialis* are the records by Dejean (1833, 1836) of the presence of "*Coprobius æquinoctialis*", from "Carthagena", in his beetle collection. As for other nominal species firstly established in the catalogues of Dejean, this name is unavailable as it was not published along with a description or indication and, therefore, it is out of the availability criteria adopted by the Code (Articles 11 and 12). Only thirty years later, Harold (1868a), in his revision of *Canthon*, at last described the species, now with the name *Canthon aequinoctialis*, from "Columbien, Neu-Granada".

There is no doubt that the two specimens here recognized as part of the type series of *S. aequinoctialis* were indeed described by Harold (1868a). The now-lectotype, besides having originated from Harold's personal collection (nowadays deposited at the MNHN), bears a label with the information "*æquinoctialis / t. Har*" in Harold's own handwriting (Fig. 29A). The paralectotype, in turn, housed at the ZMHB, has an old drawer label written "*aequinoctialis / Harold* / Nov. Granada*" (Fig. 29B). According to Joachim Willers (personal communication to MC, 2015), curator at ZMHB, the asterisk following the author's name indicates that the collection has at least one type specimen of that nominal species which, in this case, should be the female here recognized as paralectotype (and it is worth noting that Harold (1868a:

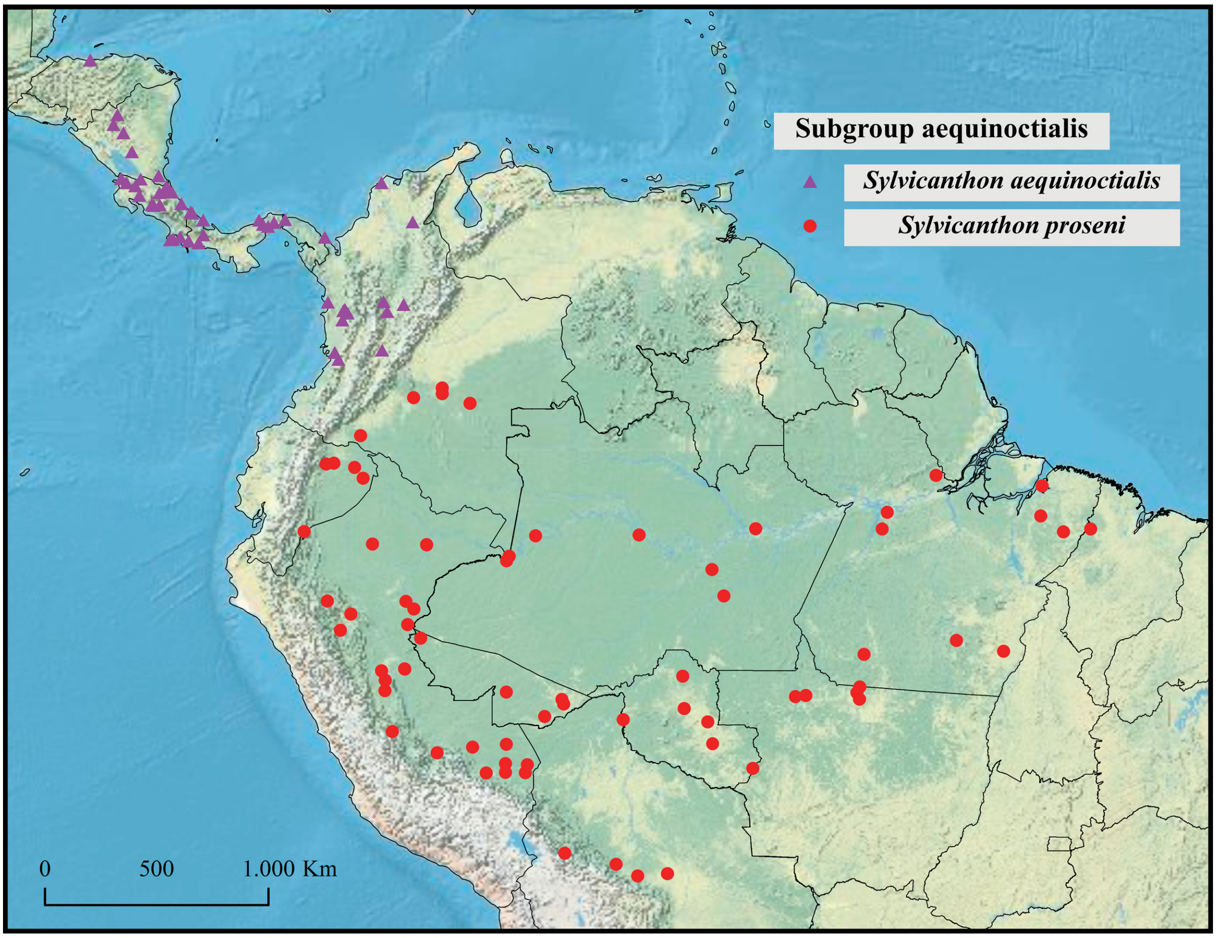

Fig. 30. Distribution of the two species of the *aequinoctialis* subgroup.

10) indeed made it clear he had examined specimens from the ZMHB for his revision of *Canthon*). The choice which of the two known syntypes should be designated as lectotype was not a simple one: while the female is in perfect condition, the male is significantly damaged around the pin, although no known diagnostic characters of the species have been lost. On the other hand, the male belongs to the Edgar von Harold collection, has a label handwritten by the nominal species' author and, the most important fact, it is of the same sex as all the other name-bearing types in *Sylvicanthon* (i.e., holotypes and lectotypes). Therefore, the male syntype was chosen instead of the female to be here designated as lectotype.

As *S. aequinoctialis* was for a long time confused with *S. proseni*, much of what is published under the former name actually refers to the latter species (see the discussion of *S. proseni* for more details). In particular, the geographical distribution cited in the literature for *S. aequinoctialis* suffered from this problem. In general, the species is cited as occurring in large parts of Central America and throughout the Amazon region, including Brazil, Peru and Bolivia. In reality, however, in South America, *S. aequinoctialis* is present only in the portion west of the Cordillera Oriental[20], in the Colombian Andes, specifically on the Caribbean coast (department of Atlántico), in the Chocó biogeographical region (maybe also present in Ecuador, although not recorded from there yet) and in the valleys between the Central and Oriental Cordilleras, in places such as Tolima and Caldas. In Central America, the species occurs at least from Panama northwards to Honduras (Fig. 30). Howden & Young (1981), Kohlmann & Solís (2002) and Halffter (2003), without citing their primary sources, said that *S. aequinoctialis* was also present in Belize, but this information is probably incorrect, since we could not find any specimens

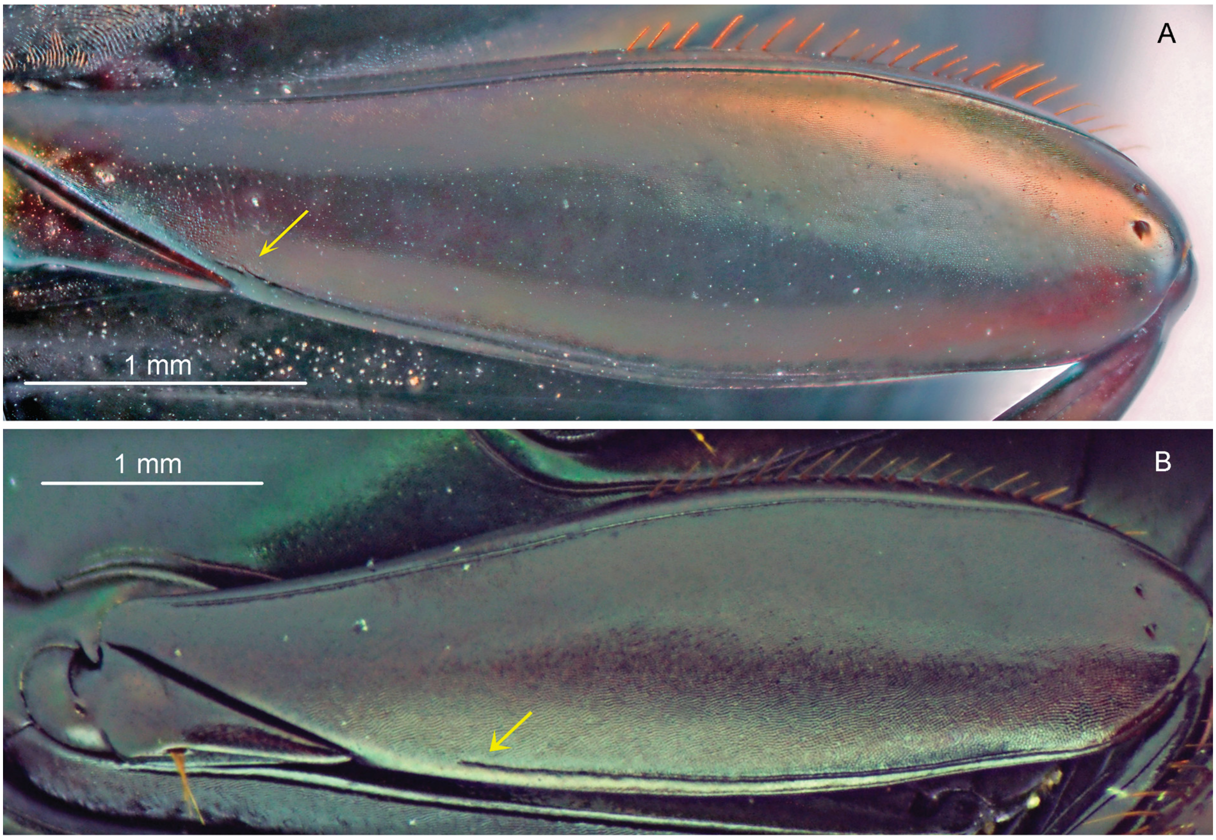

Fig. 31. Metafemora of the two species of the *aequinoctialis* subgroup. **A**. *Sylvicanthon aequinoctialis* (Harold, 1868) comb. nov. **B**. *S. proseni* (Martínez, 1949) stat. et comb. nov. Arrow indicates the basal end of the posterior margin of the ventral face of metafemora (note that it is longer in *S. aequinoctialis* comb. nov. than in *S. proseni* stat. et comb. nov. and may exceed the trochanter in the first species).

with this provenance in none of the studied collections (including the former private collection of Henry Howden, today housed at the CMNC; François Génier, personal communication to MC, 2015), nor researchers having recently collected in that country found the species living there (Latha Thomas, University of Belize, personal communication to MC, 2015). Halffter (2003) added that this species occurred in Guatemala and most probably also in southern Mexico, but these records were equally unsupported by more detailed information.

Natural history

In contrast to the other species of *Sylvicanthon*, of which only fragmentary biological information has been published, it is possible to find far more detailed data about *S. aequinoctialis* in the literature. Howden & Young (1981), for example, in their important monograph on the Panamanian dung beetles, described several aspects of the life of this species based on populations from the island of Barro Colorado, in the Gatun Lake of the Panama Canal. According to the authors, *S. aequinoctialis* breeds throughout the year and is one of the most abundant dung beetle species on the island, not showing any seasonal variation in its population density. During the rainy season (May to December), they feed on both dung and carrion, with the consumption of carcasses of animals such as the agouti [*Dasyprocta punctata* (Gray, 1842)], collared peccary [*Pecari tajacu* (Linnaeus, 1758]), and rat, as well as human faeces and coati [*Nasua nasua* (Linnaeus, 1758)], jaguarundi [*Puma yagouaroundi* (Geoffroy Saint-Hilaire, 1803)] and tapir [*Tapirus bairdii* (Gill, 1865)] dung, being reported. During the dry season (December to May), however, when carcasses are scarcer and consumed mainly by vertebrates or specialist necrophagous dung beetles (Young 1978, 1980), *S. aequinoctialis* is found only on dung. Regarding their circadian cycle, *S. aequinoctialis*, as the other species in the genus, is crepuscular and nocturnal, with an activity period between 5 and 9 pm (Howden & Young 1980). In Barro Colorado, *S. aequinoctialis* is the most abundant roller dung beetle, having been responsible for the consumption of at least one-fourth of the total volume of tapir dung utilized in experiments by Young (2009) on the island.

Farther north, we have information about some populations of *S. aequinoctialis* from Costa Rica given by Kohlmann & Solís (2002). Like in Panama, Costa Rican adults of *S. aequinoctialis* from both sides of the Continental Divide (i.e., both on the Caribbean and the Pacific coasts of Costa Rica) are active throughout the year and are among the most abundant nocturnal dung beetles of humid lowland forests. There, they live up to 800 m altitude on the Atlantic side of the Continental Divide, and up to 900 m on the Pacific side. Specimens were collected on human and equine dung, as well as using flight interception traps and through active collections on the ground or beneath fallen tree trunks.

Lastly, we have data for populations in Colombia. Medina *et al.* (2012) also highlighted *S. aequinoctialis* as one of the most common species in the Magdalena River Valley region at an altitude between 180 and 300 m, and stated that the species was collected with traps baited with human faeces and cow dung, mushrooms and, occasionally, with rotten fish. Additionally, Solís *et al.* (2011) stated that this species was present in the Atlántico department in altitudes between 160 and 500 m.

Several of the specimens examined also have bionomic information on their labels. There are records of specimens collected using traps baited with swine, human and howler monkey [*Alouatta seniculus* (Linnaeus, 1758)] dung, as well as rotten flesh, and also in flight interception traps and with ultraviolet light. Specimens were collected in all the months of the year, but there is an apparent higher concentration during the rainiest months (March: 49; April: 87; May: 52; June: 76; July: 63), when 327 out of the 573 studied specimens were caught. In relation to the altitudinal amplitude, there are representatives of *S. aequinoctialis* collected from at approximately the sea level up to areas as elevated as 1000 m in the Reserva Natural Cerro Kilambé (Jinotega, Nicaragua) and 1440 m in San Luis (Antioquia, Colombia). Therefore, after combining all the available data, what we see is that *S. aequinoctialis* is, throughout its distribution, an opportunistic species that explores several food sources and habitats and that is resistant to the seasonal changes, characteristics that make it one of the most abundant and dominant species among the roller Scarabaeinae of the New World tropical forests.

Sylvicanthon proseni (Martínez, 1949) revalidation and comb. nov.

Figs 5A, 6D, 8B, 12A, 12C, 14A, 14C, 15G–H, 17F, 20, 28C–D, 29C–E, 30, 31B

Glaphyrocanthon proseni Martínez, 1949a: 282, 287–291, fig. 2.

Glaphyrocanthon proseni – Halffter & Matthews 1966: 43, 293. — Halffter & Martínez 1977: 90–91 (as synonym of *C. aequinoctialis*). — Solís & Kohlmann 2002 (as synonym of *C. aequinoctialis*).
Glaphyrocanthon (*Glaphyrocanthon*) *proseni* – Martínez 1950: 170–171. — Pereira & Martínez 1956: 92, 126, 128. — Martínez *et al.* 1964: 3, 5, 8, 10–11, 13. — Vulcano & Pereira 1964: 663; 1967: 561.
Canthon (*Canthon*) *proseni* – Vaz-de-Mello *et al.* 2011b: 82, 86, 93. — Chamorro *et al*. 2018: 87, 92, fig. 10D, F.
Canthon proseni – Jacobs *et al.* 2008: 642. — Korasaki *et al.* 2012: 425, 427. — Silva *et al.* 2014: 348. — Nunes *et al.* 2014: 410–411. — Silva *et al*. 2017: 490.
Canthon aequinoctialis sensu – Balthasar 1941: 341; 1951: 326. — Escobar 2000a: 206; 2000b: 114, 121 (mixed information with *S. aequinoctialis* comb. nov.). — Medina *et al.* 2001: 135 (*idem*). — Celi *et al.* 2004: 42. — Noriega-Alvarado 2004: 40. — Noriega *et al.* 2008: 78–79. — Carpio *et al.* 2009: 462, 464, 469. — Medina & Pulido 2009: 58. — Figueroa & Alvarado 2011: 210–211, fig. 1c. — Noriega 2012: 4. — Ratcliffe *et al.* 2015: 195.
Canthon aequinoctiale sensu – Vaz-de-Mello 1999: 449–450.
Canthon (*Canthon*) *aequinoctiale* sensu – Vaz-de-Mello 2000.
Canthon (*Canthon*) *aequinoctialis* sensu – Noriega *et al.* 2007a: 54–55.
Canthon (*Canthon*) *aequinotialis* [sic] – Culot *et al*. 2011: Supporting information, table S1.

Etymology

Eponym after the Argentinian entomologist Alberto F. Prosen (1902–1972).

Material examined

Holotype

BOLIVIA: ♂, La Paz, Nor Yungas, confluence between the Choro and Coroico Rivers, 700 m (Martínez 1949), (“*BOLIVIA / Dep. La Paz / Prov. Nor Yungas / Ríos Coroico y Choro / 700 mts. alt. / Coll. Martínez / Ene.-949*”, “HOLOTYPUS”, “*Glaphyrocanthon / proseni ♂ / sp. nov.* / A. Martínez det. 19*49*”, “MACN-En / 1412”, “*FICHADO*”), genital capsule removed and glued on a square label (MACN) (Fig. 29C)

Paratypes

BOLIVIA: 1 ♂, (“BOLIVIA / Yungas de Palmar / 1000 M. – Zischka”, “H. & A. Howden / COLLECTION / ex. A. Martinez coll.”, “PARATIPO”, “*Glaphyrocanthon / proseni / sp. n. / ♂* / A. Martinez – det. 19*49*”) (CMNC) (labels examined by photograph, Fig. 29D); 1 ♂, (“Prov. del Sara / Cent. Bolivia / *450* m. 19~~09~~*26*” / J. Steinbach”, “H. & A. Howden / COLLECTION / ex. A. Martinez coll.”, “PARATIPO”, “*Glaphyrocanthon / proseni / sp. n. / ♂* / A. Martinez – det. 19*49*”) (CMNC) (labels examined by photograph, Fig. 29D).

Additional material (495 ♂♂, 328 ♀♀, 31 unsexed specimens)

BOLIVIA: **Cochabamba**: 3 ♂♂, 1 ♀, José Carrasco, Valle del Sacta, 17º04′18″ S, 64º46′00″ W, 250 m, 21–22 Dec. 2004, pitfall with human faeces, Mann, Hamel and Simmons leg. (OUMNH); 2 ♀♀, Chapare, Mar. 1994 (CEMT).

BRAZIL: 1 unsexed specimen, "Amazon", H.W. Bates leg. (BMNH); 1 ♂, Rio Purus, Ehrenreich leg. (ZMHB); 1 ♂, Rio Xingu, Ponte Nova, Feb. (no year) (CEMT). – **Acre**: 14 ♂♂, 20 ♀♀, Mâncio Lima, 07º28.584′ S, 72º54.110′ W, 5 Dec. 2012, H.M.B. Luiz and N.S.G.F. Adem leg. (CEMT); 40 ♂♂, 15 ♀♀, Manoel Urbano, Parque Estadual Chandless, 09º22′26″ S, 69º55′20″ W, 24 Jun. 2013, T.F. Brito leg. (CEMT); 41 ♂♂, 14 ♀♀, Manoel Urbano, Parque Estadual Chandless, 09º22′36″ S, 69º55′20″ W, 1 Jul. 2013, T.F. Brito leg (CEMT); 1 ♀, Rio Branco, Jul. 1996, M. Castro leg. (CEMT); 1 ♂, 1 ♀, Senador Guiomard, 10º04′ S, 67º37′ W, 14 Apr. 2017, human faeces, Bruna S. Bitencourt leg. (CEMT); 1 ♂, 1 ♀, Senador Guiomard ("Rio Branco"), Fazenda [Experimental] Catuaba, Feb. 1997, F.Z. Vaz-de-Mello leg. (CEMT); 1 ♀, Xapuri, Reserva Chico Mendes, 10º20.975′ S, 68º40.840′ W, 17 Oct. 2008, pitfall with human faeces, J. Silveira leg. (CEMT); 1 ♂,Xapuri, Reserva Chico Mendes, 10º18.930′ S, 68º40.756′ W, 18 Oct. 2008, pitfall with human faeces, J. Silveira leg. (CEMT). – **Amazonas**: 1 ♂, without specific locality, 4 Jun. 1939 (MZSP); 1 ♂, 1 ♀, Benjamin Constant, Mar.–Apr. 1942, Parko leg. (MNRJ); 1 ♂, same collecting data as for preceding (MZSP); 1 ♀, Benjamin Constant, Dec. 1979, A. Lise leg. (MCNZ); 1 ♂, Benjamin Constant, Rio Javari, Dec. 1960, Dirings leg. (MZSP); 1 ♂, 1 ♀, Beruri, BR-319, Km 350, 05º12′56,4″ S, 61º50′22,6″ W, 30 Jul.–2 Aug. 2007, H. Gasca leg. (CEMT); 1 ♂, Manaus, Jan. 1937 (MZSP); Manaus, II.1941, Parko leg. 1 ♀ (CEMT); 1 ♀, Manaus, Nov. 1941 (MZSP); 1 ♂, Manaus, Rio Negro, Dec. 1941, B. Pohl leg. (MNRJ); 1 ♂, 1 ♀, same collecting data as for preceding (MZSP); 1 ♂, Manicoré, Rio Madeira, Jun. (no year), J.F. Zikán leg. (FIOC); 1 ♂, São Paulo de Olivença ("Olivenza") (ZMHB); 1 ♀, São Paulo de Olivença, Nov. (no year), J.F. Zikán leg. (MZSP); 1 ♂, São Paulo de Olivença ("Olivenza"), O. Thieme leg. (ZMHB); 1 unsexed specimen, Tefé (Ega), H.W. Bates leg. (BMNH); 1 ♀, Tefé, 1921, J.F. Zikán leg (FIOC). – **Maranhão**: 1 ♀, Centro Novo do Maranhão, Igarapé Gurupi-Uma, Aldeia Araçu, 50 km E of Canindé, May 1963, Malkin leg. (MZSP). – **Mato Grosso**: 2 ♂♂, 1 ♀, Alta Floresta, 09º52′52″ S, 56º06′12″ W, Mar. 2008, pitfall with human faeces, E. Berenguer leg. (CEMT); 18 ♂♂, 18 ♀♀, Alta Floresta, 09º50′22″ S, 56º00′21″ W, pitfall with human faeces, Apr. 2008, E. Berenguer leg. (CEMT); 31 ♂♂, 29 ♀♀, Alta Floresta, 09º47′56″ S, 55º55′33″ W, May 2008, pitfall with human faeces, E. Berenguer leg. (CEMT); 11 ♂♂, 8 ♀♀, Alta Floresta, 09º53′40″ S, 56º16′35″ W, Jun. 2008, pitfall with human faeces, E. Berenguer leg. (CEMT); 5 ♂♂, 8 ♀♀, Alta Floresta, CEPLAC, 6 Feb. 2009, pitfall, V. Gonçalves leg. (CEMT); 3 ♂♂, 3 ♀♀, Alta Floresta, CEPLAC, 24 May 2009, V. Gonçalves leg. (CEMT); 1 ♀, Alta Floresta, CEPLAC, 4 Dec. 2009, pitfall, V. Gonçalves leg. (CEMT); 1 ♂, Alta Floresta, CEPLAC, 1 May 2010, human faeces, V. Gonçalves leg. (CEMT); 2 ♀♀, Alta Floresta, CEPLAC, 9 Jan. 2010, pitfall, V. Gonçalves leg. (CEMT); 1 ♀,Carlinda, 13 May 2008, C.R. Menezes leg. (CEMT); 1 ♂, Carlinda, 13 May 2008, J. Ortega leg. (CEMT); 1 ♂, Carlinda, 13 May 2008, C. Rosseto leg. (CEMT); 1 ♂, 1 ♀, Carlinda, 14 May 2008, M.E. Ortiz leg. (CEMT); 1 ♂, 14 May 2008, J.E. Silva leg. (CEMT); 1 ♂, Carlinda, 15 May 2008, M. Francisco leg. (CEMT); 1 ♂, Carlinda 16 May 2008, M.L. Santos leg. (CEMT); 1 ♀, Carlinda, 14 Oct. 2008, E. Macena leg. (CEMT); 1 ♀, Carlinda, 21 Oct. 2008, B.C. Kain leg. (CEMT); 2 ♂♂, Carlinda, 22 Oct. 2008, L. Sabino leg. (CEMT); 1 ♂, Carlinda, 23 Oct. 2008, E.P.P. Cruz leg. (CEMT); 1 ♂ (dissected), 1 ♀, Carlinda, 23 Oct. 2008, K. Segatto leg. (CEMT); 1 ♀, Carlinda, 10 Oct. 2009, E. Teles leg. (CEMT); 1 ♀, Cotriguaçu, May 2011, R.E. Vicente leg. (CEMT); 4 ♂♂, Cotriguaçu, Fazenda São Nicolau, 09º50′24″ S, 58º15′10″ W, 250 m, 6 Oct. 2009, human faeces, Vaz-de-Mello leg. (CEMT); 9 ♂♂, 1 ♀, Cotriguaçu, Fazenda São Nicolau, 09º50′24″ S, 58º15′10″ W, 250 m, 8 Oct. 2009, human faeces, Vaz-de-Mello leg. (CEMT); 3 ♂♂, Cotriguaçu, Fazenda São Nicolau, 09º50′24″ S, 58º15′10″ W, 250 m, 12 Oct. 2009, flight interception trap, Vaz-de-Mello leg. (CEMT); 1 ♂, Cotriguaçu, Fazenda São Nicolau, 10 Dec. 2009, black light, M.R. Barreto leg. (CEMT); 3 ♂♂, 3 ♀♀, Cotriguaçu, Fazenda São Nicolau, 09º50′53″ S, 58º14′36″ W, 11–13 Dec. 2009, human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 1 ♂, 1 ♀, Cotriguaçu, Fazenda São Nicolau, Castanheira, 09º49′18″ S, 58º17′18″ W, 12–14 Dec. 2009, pitfall with human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 1 ♂, 1 ♀, Cotriguaçu, Fazenda São Nicolau, Mata do Juruena, 09º52′05″ S, 58º13′35″ W, 202 m, 15 Dec. 2009, pitfall, F.Z. Vaz-de-Mello leg. (CEMT); 28 ♂♂, 4 ♀♀, Cotriguaçu, Fazenda São Nicolau, Matinha, 09º50′19″ S, 58º15′03″ W, 8 Oct. 2009, pitfall with human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 2 ♂♂, 3 ♀♀, Cotriguaçu, Fazenda São

Nicolau, Matinha, forest edge, 09º50′19″ S, 58º15′03″ W, 13 Dec. 2009, pitfall, Vaz-de-Mello leg. (CEMT); 2 ♂♂, 1 ♀, Cotriguaçu, Fazenda São Nicolau, Matinha, forest centre, 09º50′19″ S, 58º15′03″ W, 13 Dec. 2009, pitfall, Vaz-de-Mello leg. (CEMT); 5 ♂♂, 2 ♀♀, Cotriguaçu, Fazenda São Nicolau, Prainha, 09º51′36″ S, 58º12′53″ W, Oct. 2009, pitfall, F.Z. Vaz-de-Mello leg. (CEMT); 6 ♂♂, 6 ♀♀, Cotriguaçu, Fazenda São Nicolau, Prainha, 09º51′36″ S, 58º12′53″ W, 11–13 Dec. 2009, pitfall with human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 2 ♂♂, Cotriguaçu, banks of Juruena river, 09º52′47.67″ S, 58º14′07.09″ W, Oct. 2010, pitfall with human faeces, R.V. Nunes and M. Gigliotti leg. (CEMT); 1 ♂, 1 ♀, Nova Bandeirante, banks of Juruena river, 09º52′47″ S, 58º14′07″ W, Oct. 2010, pitfall with dung, R.V. Nunes and M. Gigliotti leg. (CEMT); 1 ♀, Novo Mundo, Parque Estadual do Cristalino, May 2013, manual collection, V.S. Corrêa leg. (CEMT). – **Pará**: 1 ♂, Almeirim, Monte Dourado, Jan. 1993 (CEMT); 1 ♂, Alter do Chão, RESEX Tapajós/Arapiuns, 22 Dec. 2008, flight interception trap (CEMT); 10 ♂♂, 6 ♀♀, Belém, IPEAN, Oct. 1984 [FIT], N. Degallier leg. (CEMT); 1 ♂, Belém, IPEAN, Nov. 1984, N. Degallier leg. (CEMT); 3 ♂♂, 1 ♀, Belterra, 15 Jul. 2016, pitfall with human and pig dung, F. França leg. (CEMT); 1 ♂, Estrada Belém-Brasília, Km 93, Oct. 1959, E. Lobato leg. (FIOC); 2 ♀♀, Novo Progresso, Fazenda Florentino, 07º08′51″ S, 55º23′38″ W, 230 m, Jan. 2011, pitfall with human faeces, Pelissari leg. (CEMT); 6 ♂♂, 3 ♀♀ (1 dissected), Novo Progresso, Fazenda Florentino, 06º53′18.18″ S, 55º30′26.25″ W, 2 Jan. 2011, pitfall with human faeces, T.D. Pelissari leg. (CEMT); 1 ♀, Novo Progresso, Fazenda Florentino, 07º08′00″ S, 55º26.6′00″ W, 230 m, 12 Mar. 2011, pitfall with cow dung, Pelissari leg. (CEMT); 3 ♂♂, 3 ♀♀, Paragominas, Jan.– Jul. 2011, Solar *et al.* leg. (CEMT); 1 ♂, Redenção, Pinkaiti-Aik, 07º46′ S, 51º58′ W, Jun. 1999, P.Y. Scheffler leg. (CEMT); 1 ♂, Redenção, Pinkaiti-Aik, 07º46′ S, 51º58′ W, Nov. 1999, P.Y. Scheffler leg. (CEMT); 1 ♂, 1 ♀, Santarém, Mar. 1923, Boy leg. (FIOC); 1 ♀, Santarém Jun. 1924, H.C. Boy leg. (MNRJ); 3 ♂♂, 2 ♀♀, Santarém, May 2010, V.H. Oliveira leg. (CEMT); 1 ♂, 1 ♀, Santarém, 03º00′01″ S, 54º52′38″ W, 300 m, 8 Jun. 2010, pitfall with dung, Victor H.F. Oliveira leg. (UFPA); 1 ♂, Santarém, Reserva Tapajós, 2º36.662′ S, 55º36.513′ W, 7 Jan. 2009, pitfall with human faeces, R. Andrade leg. (CEMT); 1 ♂, São Félix do Xingu, Pinkaití Reserve, 07º45′ S, 51º57′ W, 31 Oct. 1998, P.Y. Scheffler leg. (CEMT); 2 ♂♂, 2 ♀♀, Tailândia, “Empresa Agropalma”, 9–15 Jul. 2016, F. Silva leg. (CEMT); 3 unsexed specimens, Tapajós, H.W. Bates leg. (BMNH). – **Rondônia**: 1 ♂, Cacaulândia (“Caucalandia” sic), 10º32′ S, 62º48′ W, 160–350 m, 10–11 Oct. 1991, John R. Macdonald leg. (CEMT); 2 ♂♂, Cacaulândia, Fazenda Rancho Grande, Feb. 1997, Vaz-de-Mello leg. (CEMT); 4 ♂♂, Cacaulândia (“62 km So. Ariquemes”), Fazenda Rancho Grande, 18–29 Sep. 1996, D.G. Marques leg. (TAMU); 8 ♂♂, 7 ♀♀, Guajará-Mirim, 10º44′53.56″ S, 65º17′31.1″ W, 14–16 Feb. 2010, pitfall with human faeces, Fabricio Coletti leg. (CEMT); 2 ♂♂ (1 dissected), 3 ♀♀, Guajará-Mirim, 10º44′57.62″ S, 65º19′0.32″ W, 138 m, 24 Feb. 2010, cow spleen, F. Coletti leg. (CEMT); 1 ♂, Guajará-Mirim, Fazenda Agropecuária A.J.B., 10º37′59″ S, 64º59′58″ W, 180 m, 15 Jan. 2010, cow spleen, F. Coletti leg. (CEMT); 1 ♂, 2 ♀♀, Itapuã do Oeste, Floresta Nacional [“FloNa”] do Jamari, 09º11′25″ S, 63º06′49″ W, 20 Feb. 2013, *Mazama gouazoubira* dung, J.F. Cerveira leg. (CEMT); 3 ♂♂, Itapuã do Oeste, Floresta Nacional [“FloNa”] do Jamari, 09º05′20″ S, 63º09′47″ W, 24 Feb. 2013, *Mazama nana* dung, J.F. Cerveira leg. (CEMT); 1 ♂, Ji-Paraná (“V. Rondônia”, or Vila de Rondônia), 25 Jan.–9 Feb. 1961, Pereira and A. Machado leg. (MZSP); 1 ♂, “Marmelo”, Rio Abunã, Nov. 1962, W. Bokermann leg. (MZSP); 1 ♂, 1 ♀, Porto Velho, Abunã, 09º36′38″ S, 65º21′33″ W, 200 m, 19 Nov. 2010, pitfall with human faeces, J.C.F. Falcão leg. (CEMT); 2 ♂♂, Porto Velho, Abunã, 09º35′03″ S, 65º22′36″ W, 7 Apr. 2011, pitfall with human faeces, L.R. Silva and M.F. Souza leg. (CEMT); 1 ♂, 3 ♀♀, Porto Velho, Bom Jesus, Rio das Garças, 08º49′47″ S, 63º46′51″ W, 5 Apr. 2017, flight interception trap, D.C. Santos and K.K.G. Silva leg. (CEMT); 3 ♂♂, 3 ♀♀, Porto Velho, Caiçara, 09º26′59″ S, 64º48′42″ W, 27 Jun. 2010, flight interception trap, J.C.F. Falcão and L.R. Silva leg. (CEMT); 1 ♂, Porto Velho, Caiçara, 09º26′42″ S, 64º49′41″ W, 20 Mar. 2011, pitfall with human faeces, M.F. Souza and L.R. Silva leg. (CEMT); 2 ♂♂, 6 ♀♀, Porto Velho, Caiçara, 09º26′42″ S, 64º49′41″ W, 29 Mar. 2011, pitfall with human faeces, M.F. Souza and L.R. Silva leg. (CEMT); 1 ♂, 1 ♀, Porto Velho, Caiçara, 09º26′59″ S, 64º48′42″ W, 30 Mar. 2011, flight interception trap, L.R. Silva and M.F. Souza leg. (CEMT); 1 ♂, Porto Velho, Caiçara, 09º26′10″ S, 64º49′59″ W, 10 Jan. 2012, flight interception trap, M.F. Souza leg. (CEMT); 3 ♂♂, 3 ♀♀, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 4–6 Dec. 2011, pitfall with bananas, M.A.P.A. Silveira leg. (CEMT); 1 ♂, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 4–6 Dec. 2011, pitfall with human faeces, M.A.P.A. Silveira leg. (CEMT); 1 ♂, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 5–7 Dec. 2011, pitfall with bananas, M.A.P.A. Silveira leg. (CEMT); 9 ♂♂, 10 ♀♀, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 9–11 Dec. 2011, pitfall with chicken meat, M.A.P.A. Silveira leg. (CEMT); 1 ♂, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 8–12 Aug. 2012, pitfall with bananas, M.A.P.A. Silveira leg. (CEMT); 2 ♂♂, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 15 Aug. 2012, pitfall with human faeces, M.A.P.A. Silveira leg. (CEMT); 1 ♂, 1 ♀, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 19 Oct. 2012, pitfall with human faeces, M.A.P.A. Silveira leg. (CEMT); 1 ♂, 1 ♀, Porto Velho, Mutum-Paraná [“Mutum”], 09º38′36″ S, 65º26′54″ W, 14 May 2010, pitfall with human faeces, F. Albertoni and L.R. Silva leg. (CEMT); 2 ♂♂, 2 ♀♀, Porto Velho, Mutum-Paraná [“Mutum”], 09º35′ S, 65º03′ W, 250 m, 15–17 Sep. 2010, human faeces, J.C.F. Falcão and L.R. Silva leg. (CEMT); 3 ♂♂, 1 ♀, Porto Velho, near Mutum-Paraná, “Prainha”, 12 May 2010, cow dung, F.F. Albertoni and L.R. Silva leg. (CEMT); 1 ♀, Porto Velho, Nova Mutum-Paraná, 09º26′25″ S, 60º13′19″ W, 27–28 Feb. 2010, human faeces, L.R. Silva and R.L.R. Silva leg. (CEMT); 4 ♂♂, 2 ♀♀, Porto Velho, Nova Mutum-Paraná, 09º26′55″ S, 61º09′57″ W, 1–2 Mar. 2010, human faeces, L.R. Silva and R.L.R. Silva leg. (CEMT); 3 ♂♂, 4 ♀♀, Porto Velho, Nova Mutum-Paraná [“Mutum”], 09º35′46″ S, 65º02′27″ W, Jan. 2012, R.V. Nunes leg. (CEMT); 1 ♂, Porto Velho, Nova Mutum-Paraná [“Mutum”], 09º38′36″ S, 65º26′54″ W, 3 Apr. 2012, flight interception trap, M.S.G. Carvalho leg. (CEMT); 1 ♂, Porto Velho, Nova Mutum-Paraná [“Mutum”], 09º34′49″ S, 65º03′13″ W, 3 Apr. 2012, pitfall with human faeces, M.S.G. Carvalho leg. (CEMT); 7 ♂♂, 4 ♀♀, Porto Velho, Nova Mutum-Paraná [“Mutum”], 09º35′46″ S, 65º02′27″ W, 250 m, Nov. 2012, pitfall with human faeces, R.V. Nunes leg. (CEMT); 2 ♂♂, Rolim de Moura, 11º44′4.33″ S, 61º55′10.39″ W, 218 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro and N.S.G.F. Adem leg. (CEMT); 1 ♂, 1 ♀, Rolim de Moura, 11º44′05″ S, 61º55′11.62″ W, 219 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro and N.S.G.F. Adem leg. (CEMT); 3 ♂♂, 5 ♀♀, Rolim de Moura, 11º44′3.83″ S, 61º55′10.97″ W, 220 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro and N.S.G.F. Adem leg. (CEMT); 4 ♂♂, 2 ♀♀, Rolim de Moura, 11º44′3.83″ S, 61º5510.97″ W, 221 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro and N.S.G.F. Adem leg. (CEMT); 3 ♂♂, 4 ♀♀, Rolim de Moura, 11º44′3.91″ S, 61º55′12.11″ W, 222 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro and N.S.G.F. Adem leg. (CEMT); 3 ♂♂, 2 ♀♀, Rolim de Moura, 11º44′3.33″ S, 61º55′11.53″ W, 223 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro and N.S.G.F. Adem leg. (CEMT); 2 ♀♀, Vilhena, Nov. 1987, O. Roppa and P. Magno leg. (MNRJ).

COLOMBIA: **Amazonas**: 1 ♀, Leticia, Monilla Amena, 27 Jun. 1997, pitfall with human faeces during night time, I. Quintero leg. (CEMT). – **Guaviare**: 1 ♂, El Retorno, Elí farm., 02º21′46″ N, 72º38′29″ W, 15 Jul. 2007, *Lagothrix lagotricha* dung, Zárate leg. (CEMT); 1 ♂, San José del Guaviare, Finca La Esmeralda, 02º33′ N, 72º37′ W, 240 m, 6 Oct. 2003 (TAMU); 1 ♂, San José del Guaviare, Finca La Esmeralda, 02º33′ N, 72º37′ W, 240 m, 7 Oct. 2003 (TAMU); 1 ♂, San José del Guaviare, Finca La Esmeralda, 02º33′ N, 72º37′ W, 240 m, 12 Jul. 2007 (TAMU). – **Meta**: 1 ♂, 1 ♀, Parque Nacional Natural Tinigua, Centro de Investigaciones Ecológicas La Macarena, Rio Duda, 02º40′ N, 74º10′ W, 350 m, Jan. 1996, human faeces, I. Jiménez leg. (CEMT).

ECUADOR: **Orellana**: 1 ♂, 1 ♀, Estación Científica Yasuní, 215 m, 5–10 Sep. 1999, E.G. Riley leg. (CEMT); 19 ♂♂, 14 ♀♀, same collecting data as for preceding (TAMU); 5 ♂♂, 1 ♀♀, Parque Nacional Yasuní (“Scyasuni”), 200 m, 25–27 Oct. 1997, D. Padilla and I. Tapia leg. (CEMT); 1 ♀, same collecting data as for preceding (MCNZ); 2 unsexed specimens, Payamino Research Station, 0º29′36″ S, 77º17′29″ W, 300 m, Jul.–Aug. 2007, Gillett and Orellana leg. (OUMNH); 2 ♂♂, Puerto Francisco de Orellana (“Coca”), R. Haensch leg. (ZMBH); 5 ♂♂, 5 ♀♀, Rodrigo Borja, IAMOE, 4 Jun. 2000, pitfall with human faeces, A. Dávalos leg. (CEMT); 5 ♂♂, 3 ♀♀, 21 unsexed specimens, Tiputini Biodiversity Station, 0º38′ S 76º09′ W, 220 m, Sep. 2000, pitfall with human faeces, D. Inward leg. (BMNH); 1 ♂, 1 ♀, same collecting data as for preceding (MUSM); 2 ♂♂, 6 ♀♀, Yasuni Scientific Research Station, 9–17 Sep. 1999, D.G. Marqua leg. (TAMU).

PERU: 1 unsexed specimen, Río Tambopata, Jan.–Apr. 1995, B.J. Selman leg. (BMNH). – **Cuzco**: 2 ♀♀, La Convención, Echarate, Comunidad Nativa de Timpia, 12º06′41.38″ S, 72º49′59.34″ W, 429 m, 22 Oct. 2009, M. Alvarado and E. Rázuri leg. (MUSM); 1 ♀, La Convención, Echarate, Comunidad Nativa de Timpia, 12º06′47.61″ S, 72º49′32.67″ W, 536 m, 25–31 Jan. 2010, E. Razuri and C. Espinoza leg. (MUSM). – **Huánuco**: 1 ♀, Estación Biológica Panguana (Forschungsstation Panguana), Rio Pachitea, Rio Yuyapichis, 09º37′ S, 74º56′ W, 260 m, 28 Aug.–14 Sep. 1986, Listabarth leg. (NHMW); 1 ♂, Puerto Inca, Clayton, 09º11′55.37″ S, 74º55′12.1″ W, 243 m, 16–18 Jun. 2009, C. Carranza leg. (MUSM). – **Junín**: 1 ♀, Satipo, Oct.–Nov. 2002 (CEMT); 2 ♂♂, Satipo, 600 m, 23 May–3 Jun. 2004, A. Santibañez leg. (TAMU); 2 ♂♂, 2 ♀♀, Satipo, 1100 m, 4–15 Apr. 2003 (CEMT); 2 ♂♂, 1 ♀, Satipo, Fundo Santa Teresa, 2 Oct. 2007, M. Alvarado and L. Figueroa leg. (MUSM); 1 ♂, Satipo, Rio Tambo, Campamento Kampitiare, Comunidad Nativa Shevoja, 11º42′ S, 73º01′ W, 250 m, 10 Jan.–7 Feb. 2005, Williams Paredes leg. (MUSM). – **Loreto**: 1 ♀, Loreto, Urarinas, right bank of Urituyacu river, 140 m, 18 Nov. 2009, L. Sulca leg. (MUSM); 2 ♂♂, Loreto, Urarinas, Rio Copalyacu, 03º42′59″ S, 75º26′00″ W, 161 m, 7–8 Oct. 2009, L. Sulca leg. (MUSM); 1 ♂, Maynas, Iquitos, 4 Nov. 2005, L. Culot leg. (MUSM); 1 unsexed specimen, Maynas, Iquitos, 03º96′46″ S 73º15′49″ W, Dec. 1997, M.V.L. Barclay leg. (BMNH); 1 ♂, Maynas, Iquitos, Agua Blanca, 02º55′16.3″ S, 74º49′0.1″ W, 160–177 m, 'bait trap', Felipe Meza Velez leg. (MUSM); 1 ♂, Maynas, Miraflores, 03º47′4.8″ S, 73º41′43″ W, 69 m, 10 May 2012, C. Ampudia leg. (MUSM); 1 ♂, Maynas, Napo, Rio Curacay, Gaseoducto Barrett, 16–18 Mar. 2008, W. Paredes leg. (MUSM); 1 ♂, Requena, Masisea, Comunidad Nativa Santa Teresa, 06º00′55.07″ S, 74º04′59.95″ W, 87 m, 12 Aug. 2008, C. Carranza leg. (MUSM); 1 ♂, Requena, Sierra del Divisor ("a 5 km del Rio Capanagua"), 06º19′30″ S, 73º46′09″ W, 160 m, 20–21 Oct. 2008, A. García leg. (MUSM); 1 ♀, Requena, Sierra del Divisor ("cerca de Rio Punga"), 06º55′11.2″ S, 73º50′47″ W, 222 m, 22–24 Oct. 2008, C. Espinoza leg. (MUSM); 3 ♂♂, 2 ♀♀, Rio Ungumayo, 04º13′56″ S, 76º48′43″ W, 171 m, 29–30 Nov. 2009, L. Sulca leg. (MUSM); 1 ♂, 1 ♀, Ucayali, Sierra del Divisor ("cerca de Sarayacu"), 06º57′21.06″ S, 74º01′27.4″ W, 195 m, 10–11 Oct. 2008, C. Espinoza leg. (MUSM). – **Madre De Díos**: 10 ♂♂, 2 ♀♀,Parque Nacional del Manu, Estación Biológica Cocha Cashu, 11º55′ S, 77º18′ W, 380 m, 18 Aug.–5 Sep. 1986, D.C. Darling and A.B. Forsyth leg. (MUSM); 1 ♀, Parque Nacional del Manu, Estación Biológica Cocha Cashu, 11º55′ S, 77º18′ W, 380 m, 20–22 Aug. 1986, D.C. Darling leg. (MUSM); 1 ♂, Parque Nacional del Manu, Pakitza, 11º53′ S, 70º58′ W, 400 m, 16 Nov. 1990, J. Macdonald leg. (CEMT); 1 ♂, Manu, Centro de Investigación y Capacitación Río Los Amigos (CICRA), Yuguntoro trail, 12º33′ S, 70º05′ W, 283 m, 16 Nov. 2006, flight interception trap, A. Asenjo leg. (MUSM); 1 ♂, Manu, CICRA, 12º34′ S, 70º05′ W, 280 m, 10–14 Jul. 2010, C. Chaboo leg. (MUSM); 1 ♂, Manu, Reserva Comunal Amarakaeri, naciente Qda. Pinquiri, 12º55′43″ S, 70º51′41″ W, 421 m, 4 Jun. 2011, M. Vilchez leg. (MUSM); 1 ♀, Reserva Biológica CICRA ["Centro de Investigación y Capacitación Río Los Amigos"], 23 Jan. 2007, flight interception trap, Angelico Asenjo leg. (CEMT); 1 ♂, Rio Palma Real Grande, Limon, 12º32′20″ S, 68º51′41″ W, 400 m, 5–6 Apr. 1999, pitfall with human faeces, T. Larsen leg. (MUSM); 1 ♀, Rio Palma Real Grande, Limon, 12º32′20″ S, 68º51′40″ W, 220 m, pitfall with human faeces, T. Larsen leg. (MUSM); 2 ♂♂, 1 ♀, Tambopata, 12º27′49.27″ S, 69º07′30.69″ W, 233 m, 17–19 Apr. 2011, O. Huaches leg. (MUSM); 1 ♀,Tambopata, 300 m, 18–22 Apr. 1983, E. Perez leg. (MUSM); 1 ♂, Tambopata, Inambari, Primavera Baja, 12º54′ S, 70º05′ W, 234 m, 4–11 Nov. 2009, C. Castillo and E. Martinez leg. (MUSM); 1 ♂, 1 ♀, Tambopata, Puerto Maldonado, Madama, 12º31′20″ S, 69º03′44″ W, 19–20 Jul. 2009, 182 m, M. Alvarado leg. (MUSM); 1 ♂, 1 ♀, Tambopata, Puerto Maldonado, sector Triunfo, 12º33′42″ S, 69º11′47″ W, 198 m, 23 Jul. 2009, M. Alvarado leg. (MUSM); 1 ♂, 1 ♀, Tambopata, Puerto Madonado, Sudadero, 12º21′19″ S, 69º01′48″ W, 221 m, 21–22 Jul. 2009, M. Alvarado leg. (MUSM);

2 ♂♂, 1 ♀, Tambopata, Reserva Nacional Tambopata, Explorer's Inn, 12º50′30″ S, 69º17′31″ W, 161 m, 15–18 May 2009, L. Figueroa and M. Alvarado leg. (MUSM); 1 ♂, Tambopata, Rio Tambopata, Colpa de Guacamayos, 13º08.5′ S, 69º36.4′ W, 300 m, Oct. 1995, A. Forsyth leg. (MUSM). – **San Martín**: 1 ♂, Mariscal Cáceres, Juanjuí, 7 Jul. 2007, P. Melendes leg. (TAMU); 1 ♀, San Martín, El Porvenir, Bosque El Pelejo, 06º19′28.3″ S, 81º50′38.4″ W, 161 m, 17–19 May 2010, J. Robledo leg. (MUSM); 1 unsexed specimen, San Pedro de Cumbasa ("Cumbase") (MNHN). – **Ucayali**: 1 ♂, Coronel Portillo, 08º20′40.04″ S, 73º42′42.64″ W, 212 m, 10–12 Oct. 2012, P. Sanchez leg. (MUSM); 1 ♀, Coronel Portillo, Binocura, 08º53′16.9″ S, 74º00′0.21″ W, 140 m, 15–16 Jul. 208, M. Alvarado leg. (MUSM); 2 ♂♂, 2 ♀♀, Coronel Portillo, Puerto Alegre, 08º44′6.76″ S, 74º09′4.54″ W, 196 m, 21–22 May 2008, L. Figueroa leg. (MUSM); 1 ♀, Coronel Portillo, Puerto Purin, 08º45′16.7″ S, 74º10′16.8″ W, 125 m, 17–18 May 2008, L. Figueroa leg. (MUSM); 2 ♂♂, 4 ♀♀, Coronel Portillo, Puerto Purin, 08º44′59.2″ S, 74º08′19.52″ W, 122 m, 19 May 2008, L. Figueroa leg. (MUSM); 3 ♂♂, 1 ♀, Coronel Portillo, Rio Inamapuya, 08º44′33.7″ S, 74º06′15.9″ W, 135 m, 23–24 May 2008, L. Figueroa leg. (MUSM); 1 ♀, Coronel Portillo, Rio Tamaya, 08º52′32.3″ S, 74º06′52.1″ W, 155 m, 11–12 May 2008, L. Figueroa leg. (MUSM); 1 ♂, Coronel Portillo, Rio Tamaya, 08º52′39.2″ S, 74º07′7.1″ W, 155 m, 13–14 May 2008, L. Figueroa leg. (MUSM); 1 ♀, Coronel Portillo, Rio Tamaya, 08º51′41.9″ S, 74º04′20.6″ W, 150 m, 15–16 May 2008, L. Figueroa leg. (MUSM); 1 ♂, Padre Abad, Alexander von Humboldt, 08º48′46.2″ S, 75º04′15.7″ W, 245 m, 10–11 Jun. 2009, C. Carranza leg. (MUSM).

No data: 3 ♂♂ (CEMT – ex V.M. Diéguez M. coll.); 1 ♂ (ISNB).

Redescription

Colouration. Head, pronotum, elytra, pygidium, and underside – including ventral surface of femora – with diffuse shine. Head, pronotum, and pygidium with blue, purple, or greenish reflections; in some specimens, pronotum with strong olive green shine. Elytra dark and with silky aspect; usually dark blue or purple; in some specimens, totally black or with greenish reflections. Meso- and metafemora dark brown and usually with greenish reflections.

Head. Tegument with silky aspect and micropunctation almost absent, more evident only on frons (Fig. 6D). Clypeus with two small apical teeth obtuse and contiguous at base; with a single transverse row of short setae covering base of both teeth. Genae with acute tooth immediately behind clypeal-genal juncture. Posterior edge of head usually with a fine line between eyes which can be effaced on the sides, or even totally absent.

Thorax. Pronotum with tegument at centre ranging from bright with dense micropunctation and without microsculpture to with strong alveolar microsculpture obliterating micropunctation; lateral region always without micropunctation, with alveolar microsculpture present and tegument perceptibly more matte than at centre. Posterior edge without fine transverse line at centre. Hypomeral cavity with very short yellowish setae at centre. Metaventrite entirely glabrous (occasionally, with some setae on the sides close to metacoxae); micropunctation indistinct at centre and visible only on region adjacent to apices of metacoxae.

Legs. Ventral surface of all femora and tibiae with diffuse shine of silky aspect. Protibiae with three obstuse or slightly acute teeth at their apical third, the two apical teeth of similar size and larger than the basal one. Mesofemora margined anteriorly only at their basal half; unmargined portion of anterior edge with row of very short setae. Metafemora with both anterior and posterior magins; posterior margin incomplete, always present at apical half and ranging in length at basal half, but never reaching trochanter (Fig. 31B). Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. Nine fine elytral striae only weakly marked, almost imperceptible. Base of striae I–V carinulate and well marked. Tegument of interstriae with a silky shine and with dense three-dimensional alveolar microsculpture obliterating indistinct micropunctation. Fine humeral carina distinct and long, sometimes present throughout basal fourth of elytra (Fig. 12C).

Abdomen. Ventrites V–VI smooth, shiny and with micropunctation at centre. Lateral foveae absent in both sexes. Pygidium with diffuse shine, with well-marked alveolar microsculpture and without micropunctation.

Aedeagus. Parameres long, little shorter than phallobase and clearly asymmetrical: left paramere laterally with apical depression much deeper and wider than depression on right paramere (difference more easialy seen in dorsal view). In lateral view, parameres with central angulosity and without ventral keel and notch (Fig. 17F).

Sexual dimorphism. **Males**: Protibial spur broad and foliaceous, external edge extended into an acute long spine, while internal edge has no prolongation or has much shorter spine; area between both spines straight or slightly excavated (Fig. 15G). Pygidium very long (length between 1.9 and 2.9 mm) and convex; apical margin of pygidium much wider than lateral ones. Ventrite VI strongly narrowed at middle. **Females**: Protibial spur wide and with strong apical incision, with two long spines of uneven length, the internal spine shorter than the external one (Fig. 15H). Pygidium shorter (between 1.5 and 2.2. mm) and flat; apical margin only slightly wider than lateral ones. Ventrite VI as wide at middle as on sides.

Measurements

Males (N= 40). **TL:** AV: 12.1 ± 0.78; MX: 15; MN: 10.5. **EW:** AV: 8.2 ± 0.36; MX: 8.8; MN: 7.4. **PL:** AV: 4 ± 0.25; MX: 4.5; MN: 3.4. **PW:** AV: 7.5 ± 0.41; MX: 8.5; MN: 6.5. **PgL:** AV: 2.2 ± 0.18; MX: 2.9; MN: 1.9. **PgW:** AV: 3.8 ± 0.22; MX: 4.3; MN: 3.1.

Females (N = 20). **TL:** AV: 11.8 ± 1; MX: 14; MN: 9.8. **EW:** AV: 7.9 ± 0.6; MX: 8.7; MN: 6.1. **PL:** AV: 3.8 ± 0.31; MX: 4.2; MN: 2.9. **PW:** AV: 7.1 ± 0.54; MX: 7.9; MN: 5.7. **PgL:** AV: 1.9 ± 0.18; MX: 2.2; MN: 1.5. **PgW:** AV: 3.8 ± 0.28; MX: 4.2; MN: 3.

Geographical distribution

Widespread in the Amazon Basin.

Ecoregions

Negro-Branco Moist Forests, Caquetá Moist Forests, Napo Moist Forests, Cordilleira Oriental Montane Forest, Ucayali Moist Forests, Iquitos Varzea, Southwest Amazon Moist Forests, Purus Varzea, Bolivian Yungas, Purus-Madeira Moist Forests, Monte Alegre Varzea, Madeira-Tapajós Moist Forests, Mato Grosso Tropical Dry Forests, Tapajós-Xingu Moist Forests, Xingu-Tocantins-Araguaia Moist Forests, Tocantis-Pindaré Moist Forests.

Collecting sites (Fig. 30)

COLOMBIA. **Meta**: Parque Nacional Natural Tinigua (Centro de Investigaciones Ecológicas La Macarena). **Guaviare**: El Retorno, *Parque Nacional Natural Nukak*, San José del Guaviare. **Amazonas**: Leticia (Monilla Amena).

ECUADOR. ***Sucumbíos***: *"Chiruisla Station"*. **Orellana**: Parque Nacional Yasuní, Payamino Research Station, Puerto Francisco Orellana, Tiputini Biodiversity Station. ***Morona Santiago***: *Cordillera de Cutucú*.

PERU. **Loreto**: Loreto (Urarinas), Maynas (Iquitos, Miraflores, Napo), Requena (Masisea: Comunidad Nativa Santa Teresa; Sierra del Divisor), Ucayali (Sierra del Divisor). **San Martín**: Mariscal Cáceres (Juanjuí), San Martín (El Porvenir), San Pedro de Cumbasa. **Huánuco**: Estación Biológica Panguana, Puerto Inca (Clayton). **Ucayali**: Coronel Portillo (Puerto Alegre, Puerto Purin), Padre Abad (Alexander von Humboldt). **Junín**: Satipo. **Cuzco**: La Convención (Echarate). **Madre de Dios**: Manu (Centro de Investigación y Capacitación Río Los Amigos, Reserva Comunal Amarakaeri), Parque Nacional del Manu (Estación Biológica Cocha Cashu), Reserva Biológica "Centro de Investigación y Capacitación Río Los Amigos" (CICRA), Tambopata (Inambari: Primavera Baja; Puerto Maldonado; Reserva Nacional Tambopata).

BRAZIL. **Amazonas**: Benjamin Constant, Beruri, Manaus, Manicoré, São Paulo de Olivença, Tefé. **Acre**: Mâncio Lima, Manoel Urbano (Parque Estadual Chandless), Rio Branco, Senador Guiomard, Xapuri (Reserva Extrativista Chico Mendes). **Rondônia**: Cacaulândia, Guajará-Mirim, Itapuã do Oeste (Floresta Nacional do Jamari), Ji-Paraná, Rolim de Moura, Vilhena. **Pará**: Almeirim (Monte Dourado), Alter do Chão, Belém, Belterra, Novo Progresso, Paragominas, Redenção, Santarém, São Félix do Xingu, Tailândia. **Maranhão**: Centro Novo do Maranhão. **Mato Grosso**: Alta Floresta, Carlinda, Cotriguaçu, Nova Bandeirante, Novo Mundo (Parque Estadual do Cristalino).

BOLIVIA. **La Paz**: Nor Yungas. **Cochabamba**: José Carrasco (Valle del Sacta), Chapare. **Santa Cruz**: Sara.

Intraspecific variation and taxonomic discussion

Although formally described only in 1949, it is possible to trace back the beginning of the taxonomic history of *S. proseni* to the late 19th century, when Bates (1887) was the first author to realize that the South American populations of '*Canthon aequinoctialis*' differed from the Central American ones in having individuals of considerable different size: "Central-American differ from South-American exemples only in being smaller (11 millim.), the latter varying little from 14 millim" (Bates 1887: 33). Indeed, Henry Walter Bates himself collected some specimens of *S. proseni* in the Amazon region which were examined for this work. Nonetheless, over the following 60 years, no author noticed those differences or discovered others, treating under the same name *C. aequinoctialis* specimens coming from both Central America and the Amazon Basin, including the revisions of Schmidt (1922) and Balthasar (1939).

Eventually, already in the mid-20th century, Martínez (1949) described *Glaphyrocanthon proseni* stating his new species was close to *C. aequinoctialis*, but distinct from this latter species by the metafemora with a margin on both edges (while *C. aequinoctialis* would have only the anterior margin) and colouration. It is clear, however, that Martínez did not have on hand specimens of *S. aequinoctialis*, since both species have metafemora with posterior margin and, actually, this margin is even longer in *S. aequinoctialis* than in *S. proseni* (Fig. 31) (indeed, Martínez wrote "S*egún la descripción*" when referred to *C. aequinoctialis*).

Later, however, Pereira & Martínez (1956), in a key to the species then-positioned in *Glaphyrocanthon*, noted colouration differences between the species, *G. proseni* being blue-violet and opaque ("azul violeta e opaco") and *G. aequinoctialis* being black and bright ("preto e brilhante"). Martínez *et al.* (1964) refined those descriptions writing that *G. proseni* had indistinct elytral striae, and the elytra, pygidium and ventral surface of femora opaque, while *G. aequinoctialis* had fine, but perceptible elytra striae and the entire body bright; they were also the first authors to note that *S. aequinoctialis* was restricted to Central and northern South America. But despite these considerations, they also wrote that, the differences between the two taxa being restricted to the microsculpture and elytral striae only, *G. proseni* would possibly represent a southern subspecies of *G. aequinoctialis* instead of a full species.

Then, Vulcano & Pereira (1967), in a key to the dung beetle species of Amazonia, distinguished the two species, apart from their distribution, only by colouration and size (resuming, for the first time and, probably independently, the observation taken by Bates 1887). Lastly, Halffter & Martínez (1977), after having studied some type specimens of both names (Fig. 29), synonymized *C. aequinoctialis* and *G. proseni* without presenting, however, the reasons for that act, although it is reasonable to imagine they did so based on the arguments given by Martínez *et al.* (1964). In this way, except for some recent faunistic inventories that treated *C. proseni* as a valid species (e.g., Vaz-de-Mello *et al.* 2011b; Korasaki *et al.* 2012; Nunes *et al.* 2014; Chamorro *et al*. 2018), these two names have remained in synonymy ever since. Next, we present evidence that, in our view, supports the present revalidation of *S. proseni* and demonstrates its independence from *S. aequinoctialis*.

As noted by Bates (1887) (despite having considered them different populations of a same species), the average body size of *S. aequinoctialis* and *S. proseni* is truly distinct. The average body length of *S. proseni* is 12 mm, ranging from individuals measuring only 9.8 mm to those of 15 mm, while S. *aequinoctialis* has an average length of 10 mm, with the smallest specimens measure 8.7 mm to the largest ones 12.3 mm. It is interesting to note that the lowest value recorded for *S. proseni* is only slightly lower than the average of *S. aequinoctialis*, while the largest *S. aequinoctialis* examined is only a little longer than the average of the specimens of *S. proseni*. This pattern is repeated in all the other measurements taken for this work, including the elytral width (average of 8.1 mm for *S. proseni*, with a maximum of 8.8, a minimum of 5.7 and an average of 7.0 mm for *S. aequinoctialis*, with a maximum of 7.8 and a minimum of 5.7 mm) and the greatest width of the pronotum (an average of 7.3 mm, with a maximum of 8.2. and a minimum of 5.7 mm for *S. proseni*, and an average of 6.3, with a maximum of 7.4 and a minimum of 5.3 for *S. aequinoctialis*).

Also part of the group of characteristics already used in the past to distinguish both species are the differences in microsculpture and other aspects of the tegument, which form one of the strongest indications for the evolutionary independence of *S. aequinoctialis* and *S. proseni*. By seeing them with the naked eye, it is possible to realize that the pronotum, ventral surface of femora, pygidium and especially the elytra of *S. aequinoctialis* are very bright and have a smooth surface, while they reflect light in a more diffuse way and, consequently, have a more opaque, silky appearance in *S. proseni*. This is so thanks to the microsculpture present in the tegument of these two species. In *S. aequinoctialis*, the microsculpture is absent or very effaced at the centre of the pronotum and on the elytra, and, although clearly present, it is very fine (i.e., the microsculpture's 'alveoli' are very small) on the femora and pygidium. This condition makes the tegument of this species (or gives the appearance of being) much smoother than that of *S. proseni*, which has a strong alveolar microsculpture covering the entire pronotum, femora, elytra and pygidium (Fig. 12A).

The elytral striae are also much more marked and visible in *S. proseni* than in *S. aequinoctialis*, where they are almost imperceptible; this difference is more easily seen looking at the base of elytra, where the striae are finely marked and expanded in *S. proseni* and completely indistinct in *S. aequinoctialis*. Regarding the micropunctation, both species differ in the way the micropunctures are marked. In the majority of the specimens of *S. proseni* (but not all; see below), the pronotum, elytra and pygidium have a very visible micropunctation, which, in general, is not strongly obliterated by the microsculpture. In *S. aequinoctialis*, on the other hand, punctures may be completely absent or, more commonly, they are only weakly marked and are almost imperceptible, having the appearance of being shallower than those of *S. proseni*. Also in relation to the tegument, we see differences between *S. aequinoctialis* and *S. proseni* in the humeral carina (Fig. 12C) (which is longer and more strongly marked in the latter species), on the posterior margin of the metafemora (the margin extends from the apex of metafemur to beyond or immediately before the trochanter in *S. aequinoctialis* (Fig. 31A), while it never reaches the trochanter and, in general, is present only slightly beyond the middle of metafemur in *S. proseni*,

Fig. 31B) and on the posterior margin of the head (which is always present in *S. aequinoctialis*, and may be incomplete or even completely absent is some specimens of *S. proseni*).

Despite all the differences listed above, the strongest evidence for the isolation between these two species rests on the shape of the female protibial spur. In *S. aequinoctialis*, this spur is spiniform and has an acuminate apex (Fig. 15F), while females of *S. proseni* have a wider and profoundly bifid spur which has the external branch longer than the internal one (separation between both branches 'V'-shaped, Fig. 15H). In fact, the presence of this bifid spur distinguishes females of *S. proseni* from all the other females in the genus and is here reported for the first time.

Lastly, the disjunct geographical distribution of *S. aequinoctialis* and *S. proseni*, separated by the great barrier constituted by the Andes (Fig. 113), adds to the morphological evidence discussed above. *Sylvicanthon aequinoctialis* is present from Honduras in the north, south to the Choco region on the Pacific coast of South America, and in the great valley between the central and western mountain ranges in Colombia. In turn, *S. proseni* is distributed throughout most of the Amazon Basin, from Maranhão in the east to the Yungas on the eastern slopes of the Andes in Bolivia, Peru and Ecuador; in Colombia, the latter species was recorded only from the lower areas in the Amazon forest. Ecologically, both species do not seem to be very distinct from one another. Both inhabit a large variety of forest habitats with a very remarkable altitudinal range, living from low and coastal regions (e.g., *S. proseni* in Belém, on the banks of the Baía de Marajó, Brazil; *S. aequinoctialis* in La Ceiba on the Caribbean coast of Honduras) to the Andean regions above 1000 m (e.g., *S. proseni* in Satipo, Peru, at 1110 m a.s.l.; *S. aequinoctialis* in the Reserva Natural Cañon del Río Claro, Colombia, at 1440 m). In all those places, *S. aequinoctialis* and *S. proseni* are among the most abundant dung beetle species, and there they exploit a wide array of food sources (dung, carrion and rotten fruits). Therefore, despite the differences in morphology, both species seem to have little diverged in their life habits.

Being such an abundant and widely-distributed species, *Sylvicanthon proseni* would be expected to show a great degree of instraspecific variation, and this is indeed what occurs. The variation on the density of pronotal micropunctation is easily seen: even within a single given population it is possible to encounter specimens with a very densely-punctated tegument (and with a very bright pronotum) and others with a very fine, almost imperceptible micropunctation. The most common pattern, however, is the one with fine, but easily visible micropunctation. The size of the dorsal portion of the eyes also varies intraspecifically, the width ranging from approximately one-fifth to one-sixth of the interocular space. Lastly, a very important variation is seen on the posterior edge of the head: in the majority of the specimens a fine line runs across the entire interocular space. In some specimens, however, this line is effaced near the eyes and is marked only at the middle; progressively, this central line disappears, and in some individuals, it is completely absent.

Comments

Because this species was confused with *S. aequinoctialis* for such a long time, especially after the synonymy proposed by Halffter & Martínez (1977), most of what is known about *S. proseni* is published under the name *Canthon aequinoctialis*. Concerning specifically its geographical distribution, the records of Balthasar (1941, 1951) from "*Mishujacu, Iquitos*" (Peru), Vaz-de-Mello (1999) from Acre (Brazil), Celi *et al.* (2004) and Carpio *et al.* (2009) from Ecuador, Noriega-Alvarado (2004), Noriega *et al.* (2007a) and Noriega (2012) from Meta (Colombia), Noriega *et al.* (2008) from Amazonas (Colombia), and Figueroa & Alvarado (2011) from Tambopata (Peru) certainly refer to *S. proseni*, not to *S. aequinoctialis* as originally mentioned.

The village of San Pedro de Cumbasa, in the department of San Martín, Peru, was included in the distribution of *S. proseni* based on a specimen in MNHN labelled "*Cumbase*" without any further information. Takiya *et al.* (2003), in their study of the leafhopper genus *Hyogonia* China, 1927 (Hemiptera, Cicadellidae), also studied a specimen labelled "Cumbase" and, according to them, this word probably refers to San Pedro de Cumbasa. Similarly, the register from Novo Centro do Maranhão, the only known locality of this species in the Brazilian state of Maranhão, was obtained from a single specimen housed at the MZSP labelled "*Igarapé Gurupi-Uma, Aldeia Araçu, 50 km E. de Canindé*", information that probably refers to that locality according to Pinto & Lamas (2011).

Natural history

Sylvicanthon proseni is widely distributed in the Amazon Basin and seems to be a very common species in all the regions where it lives. In several dung beetle community inventories carried out in the Amazon region, *S. proseni* was one of the most abundant species (e.g., Noriega *et al.* 2007a: in Meta, Colombia, it corresponded to 4.66% of the collected specimens; Korasaki *et al.* 2012: Amazonas, Brazil, 5.6%; Vaz-de-Mello 1999: Acre, Brazil, 23%; Noriega *et al.* 2008: Amazonas, Colombia, 29.9%; Carpio *et al.* 2009: Sucumbíos, Ecuador, 55%). This species seems to be absent only in grasslands and agricultural fields, but, where some small patch of forest is left standing or there is secondary regeneration, *S. proseni* can be found (Vaz-de-Mello 1999; Noriega *et al.* 2007a; Korasaki *et al.* 2012), including river floodplain areas (Escobar 2000b; Nunes *et al.* 2014). These observations clearly show the species' flexibility and its considerable resistance against anthropic impact.

The individuals studied for this work were collected in all months and within an altitudinal range between 68 and 1100 m (nonetheless, the greater part of the specimens was collected between 100 and 500 m). Although we are aware of just a single time-activity record – which was taken from the label of a specimen from Leticia, Colombia, collected at night –, the information that specimens were collected with a light trap (Vaz-de-Mello *et al.* 2011) and our knowledge about the other species of *Sylvicanthon* (especially *S. aequinoctialis*) allows us to confidently believe that *S. proseni* is a nocturnal species.

Sylvicanthon proseni was mainly collected using human faeces as bait and it seems to be preferably coprophagous (Martínez *et al.* 1949; Vaz-de-Mello 1999; Noriega *et al.* 2007a, 2008; Figueroa & Alvarado 2011; Korasaki *et al.* 2012; Nunes *et al.* 2015; and information from specimen labels). Some individuals collected in Porto Velho (Rondônia, Brazil), however, were caught using pitfall traps baited with chicken meat and rotten bananas. Furthermore, *S. proseni* was also collected on dung of the woolly monkey [*Lagothrix lagotricha* (Humboldt, 1812)] (Noriega 2012) and cows (specimen labels information), with a flight interception trap (Vaz-de-Mello 1999) and a light trap (Vaz-de-Mello *et al.* 2011).

Pereira & Martínez (1956) and Martínez *et al.* (1964) reported a very interesting case of phoretic behaviour between *S. proseni* and tapirs [*Tapirus terrestris* (Linnaeus, 1758)]. Nevertheless, neither work stated the primary source for that information (authors' observation?) or any further detail (e.g., place of observation, number of individuals, or whether the tapir was alive or dead when the observation was made, which could rule out the possibility of simple necrophagy). Therefore, whether this information is reliable or not is yet to be resolved. Nevertheless, phoresy has indeed been observed in a great number of other dung beetles, including the relationship between two distinct lineages of *Onthophagus* and macropod marsupials (wallabies and rat-kangaroos) in Australia (Matthews 1972). In the Neotropical region, phoresy was observed between species of the dung beetle genera *Uroxys* and *Bradypodidium* Vaz-de-Mello, 2008 with three-toed sloths [*Bradypus* Linnaeus, 1758] (Ratcliffe 1980; Howden & Young 1981; Vaz-de-Mello 2008), and species of *Canthidium* with the coppery titi monkey, *Callicebus cupreus* (Spix, 1823) (Herrera *et al.* 2002). In Deltochilini, Pereira & Martínez (1956) reported phoretic behaviour of *Glaphyrocanthon subhyalinus* (Harold, 1867) (cited as "*Canthon hyalinus*") in the brown titi monkey, *Callicebus brunneus* (Wagner, 1842), while Jacobs *et al.* (2008)

described in detail the relationship between *Glaphyrocanthon* aff. *quadriguttatus* (Olivier, 1789) and both *Callicebus brunneus* and the saki monkey species *Pithecia irrorate* Gray, 1842.

As hypothesized by Herrera *et al.* (2002) and Jacobs *et al.* (2008), this phoretic strategy may be related to the behaviour known as the 'sit and wait' strategy, which is largely beneficial to the dung beetles that employ it because, being mounted on the dung-producing animal itself and positioned around its anus, those beetles can reach the dung as soon as it is released. In doing so, they can start the consumption of the dung before it dries out and before the arrival of competitors. In tropical forest with a low density of large mammals such as those in South America, competition between dung beetles can be intense and, consequently, arriving first at the food source brings a considerable advantage. If the alleged phoresy of *S. proseni* in tapirs is confirmed, it will be the phoretic relationship between the largest host and the largest dung beetle yet discovered. Ratcliffe (1980) and Jacob *et al.* (2008) give an excellent discussion on the phoretic relationship between Scarabaeinae and mammals.

The **bridarollii** *subgroup*

Sylvicanthon bridarollii (Martínez, 1949)

Figs 8A, 9A, 11F–G, 13G–H, 15I, 18A, 20, 32–34, 35C–D, 36

Glaphyrocanthon bridarollii Martínez, 1949a: 282–287, 290.

Glaphyrocanthon bridarollii – Halffter & Martínez 1977: 63.
Glaphyrocanthon (*Glaphyrocanthon*) *bridarollii* – Martínez 1950: 170–171. — Pereira & Martínez 1956: 126, 128. — Martínez *et al.* 1964: 5, 8, 10, 14. — Vulcano & Pereira 1964: 661; 1967: 561. — Martínez & Pereira 1967: 53.
Sylvicanthon bridarollii — Halffter & Martínez 1977: 63. — Amézquita *et al.* 1999: 119–120. — Medina & Lopera-Toro 2000: 312, fig. 9d, h. — Vaz-de-Mello 2000: 195. — Escobar 2000a: 210; 2000b: 121. — Medina *et al.* 2001: 137; 2003: 44, fig. 100; 2013: 464–466, 469, 471, figs 89, 117, 131, 240. — Carpio *et al.* 2004: 464, 469. — Celi *et al.* 2004: 46. — Larsen 2004: 261. — Horgan 2006: 364. — Medina & Pulido 2009: 59. — Carvajal *et al.* 2011: 117, 316. — Price & Feer 2012: 327 (error: referring to *S. seag* sp. nov.) . — Ratcliffe *et al.* 2015: 196. — Tarasov & Génier 2015: 21–24, 54, figs 4–7, 29g.
Silvicanthon bridarollii [sic] – Horgan 2005a: 609–610; 2005b: 131; 2009: 3532, 3537. — Chamorro *et al*. 2018: 98.
Sylvicanthon bridarolli [sic] – Figueroa & Alvarado 2011: 210–211, fig. 1b. — Chamorro *et al*. 2018: 86, fig. 9D. — Espinoza & Noriega 2018: 146, 149.
Sylvicanthon sp. – Kirk 1992: 54 (tentative).
Canthon bridarollii – Krajcik 2012: 63.

Etymology

Eponym refers to the Argentinian naturalist and Jesuit priest Albino J. Bridarolli (1903–1949) (Martínez 1949).

Material examined

Holotype

BOLIVIA: ♂, Cochabamba, Chapare, Coni River, 400 m ("*BOLIVIA* / *Dep. Cochabamba* / *Chapare - 400mts*. / *R. Zischka - leg.* / *Coll. Martínez*", "BOLIVIA / Chapare / 400 M / Zischka", "*HOLOTIPO* ♂", "*Glaphyrocanthon* / *bridarollii* / ♂ / *sp. n.* / A. Martínez det. 1*949*", "*FICHADO*", "MACN-En / 937"), genital capsule removed and glued to a triangular card point (MACN) (Fig. 33A).

Paratypes (3♂♂ and 4 ♀♀ examined)
Two paratypes, male and female, could not be located (they were possibly deposited at the Zischka collection, now housed at the Zoologische Staatssammlung München, Munich, Germany; see comments below).

BOLIVIA: 1 ♀ (allotype) (“CHAPARE / BOLIVIA / ZISCHKA col. / *Coll. Martínez / 24-V-48*”, “*ALOTIPO* ♀”, “*Glaphyrocanthon / bridarollii* / ♀ / *sp. n.* / A. Martínez det. *1949*”, “*FICHADO*”, “MACN-En / 938”) (MACN) (Fig. 33B); 1 ♂ (dissected) (“*BOLIVIA / Dep. Cochabamba / Chapare 400mts. / R. Zischka-leg. / Coll. Martínez*”, “Bolivia / Region subandina / Prov. Chapare – 400m / ex coll Zischka”, “*Glaphyrocanthon / bridarollii* ♂ / *sp. n.* / A. Martínez-det *1949*”, “PARATYPE”, “*PARATIPO* ♂”, “H. & A. Howden / Collection / ex. A. Martínez coll.”, “Canadian Museum of / Musée canadien de la / NATURE / CMNEN 00012714”) (CMNC); 1 ♂ (“*BOLIVIA / Dep. Cochabamba / Chapare 400mts. / R. Zischka-leg. / Coll. Martínez*”, “*Glaphyrocanthon / bridarollii* ♂ / *sp. n.* / A. Martínez-det *1949*”, “*PARATIPO* ♂”, “PARATYPE”, “H. & A. Howden / Collection / ex. A. Martínez coll.”, “Canadian Museum of / Musée canadien de la / NATURE / CMNEN 00019064”) (CMNC), 1 ♀ (“*BOLIVIA / Dep. Cochabamba / Chapare 400mts. / R. Zischka-leg. / Coll. Martínez*”, “*Glaphyrocanthon / bridarollii* ♀ / *sp. n.* / A. Martínez-det *1949*”, “PARATYPE”, “*PARATIPO* ♀”, “H. & A. Howden / collection / ex. A. Martínez coll.”, “Canadian Museum of / Musée canadien de la / NATURE / CMNEN 00019065”) (CMNC); 1 ♂ (dissected) (“♂”, “BOLÍVIA / tropica / Region CHAPARE / (400 Mtr.) / DIRINGS”, “*BOLIVIA / Dep. Cochabamba / Chapare 400mts. / R. Zischka-leg. / Coll. Martínez*”, “*Glaphyrocanthon / bridarollii* ♂ / *sp. n.* / A. Martínez-det 1*949*”, “*PARATIPO* ♂”) (MZSP); 1 ♀ (“♀”, “BOLIVIA / tropica / Region CHAPARÉ / (400 Mtr.) / DIRINGS”, “*BOLIVIA / Dep. Cochabamba / Chapare 400 mts. / R. Zischka-legit. / Coll. Martínez*”, “*PARATIPO* ♀”, “*Glaphyrocanthon / bridarollii* ♀ / *sp. n.* / A. Martínez-det. *1949*”) (MZSP); 1 ♀ (“♀”, “BOLIVIA / tropica / Region CHAPARÉ / (400 Mtr.) / DIRINGS”, “*BOLIVIA / Dep. Cochabamba / Chapare 400 mts. / R. Zischka-legit. / Coll. Martínez*”, “*PARATIPO* ♀”, “*Glaphyrocanthon / bridarollii* ♀ / *sp. n.* / A. Martínez-det. *1949*”) (MZSP).

Additional material (382 ♂♂, 256 ♀♀)
BOLIVIA: 1 ♀, eastern Bolivia (“Ost Bolivien”), Steinbach S.V. leg. (ZMHB, labelled as syntype of *Canthon obscurus* by the ZMHB staff, but, very likely, a pseudotype). – **Beni**: 3 ♂♂, 4 ♀♀, Mamoré, San Ramón, Estancia San Lorenzo, 13º25′36″ S, 64º26′06″ W, 140 m, 11 Oct. 2003, pitfall with human faeces, A.C. Hamel and K. Walker leg. (OUMNH); 2 ♂♂, 1 ♀, Mamoré, San Ramón, Estancia San Lorenzo, 13º25′36″ S, 64º26′06″ W, 140 m, 12 Oct. 2003, pitfall with human faeces, A.C. Hamel and K. Walker leg. (OUMNH); 2 ♂♂, 3 ♀♀, Mamoré, San Ramón, Estancia San Lorenzo, 13º25′36″ S, 64º26′06″ W, 140 m, 13 Oct. 2003, pitfall with human faeces, A.C. Hamel and K. Walker leg. (OUMNH). – **Cochabamba**: 2 ♂♂, 1 ♀, Cercado, 124 km E of Cochabamba, Río Espírito Santo, 17º03′45″ S, 65º38′38″ W, 700 m, 6–8 Feb. 1999, dung trap, F. Génier leg. (CMNC); 2 ♂♂, 1 ♀, Chapare, Villa Tunari, Oct. 1992, Arnagada(?) leg. (CMNC); 21 ♂♂ (1 dissected), 10 ♀♀, Estación Biológica Villa Carmen, Universidad San Simon, 67.5 km E of Villa Tunari, 17º06′19″ S, 64º46′57″ W, 300 m, 7–9 Feb. 1999, F. Génier leg. (CMNC); 14 ♂♂ (1 dissected), 7 ♀♀, Estación Biológica Villa Carmen, Universidad San Simon, 67.5 km E of Villa Tunari, 17º06′19″ S, 64º46′57″ W, 300 m, 9–13 Feb. 1999, F. Génier leg. (CMNC); 3 ♂♂, 4 ♀♀, José Carrasco, Chimoré, 250 m, Jan. 1972, A. Martínez leg. (CMNC); 3 ♀♀, “PD Altamachi”, 16º02′ S, 66º40′ W, 1150 m, 25 Sep. 2004, trap with human faeces, A.C. Hamel leg. (OUMNH); 1 ♀, “PD Altamachi”, 16º02′ S, 66º40′ W, 1150 m, 27 Sep. 2004, trap with human faeces, A.C. Hamel leg. (OUMNH). – **La Paz**: 1 ♂, 1 ♀, Larecaja, Guanay, San José, 17 Oct. 2001, G. Castillo leg. (CEMT); 1 ♀, Larecaja, Guanay, Uyapi, 15 Oct. 1995, G. Arriágada leg. (CEMT); 1 ♂, 2 ♀♀, Larecaja, Guanay, 10 Nov. 2004, A. U-Peña leg. (CEMT); 1 ♀, Nor Yungas, Coroico (MZSP); 1 ♀, Parque Nacional Madidi, 13º38′ S, 68º44′ W, 260 m, 26 Jul. 2004, trap with human faeces, C. Hamel leg. (OUMNH); 2 ♂♂ (1 dissected), 7 ♀♀, Parque Nacional Madidi, 13º38′ S, 68º44′ W, 260 m, 27 Jul. 2004, trap with human faeces, C. Hamel leg. (OUMNH). – **Santa Cruz**: 1 ♀, Andrés Ibáñez, El Espejo(?), Feb. 1961,

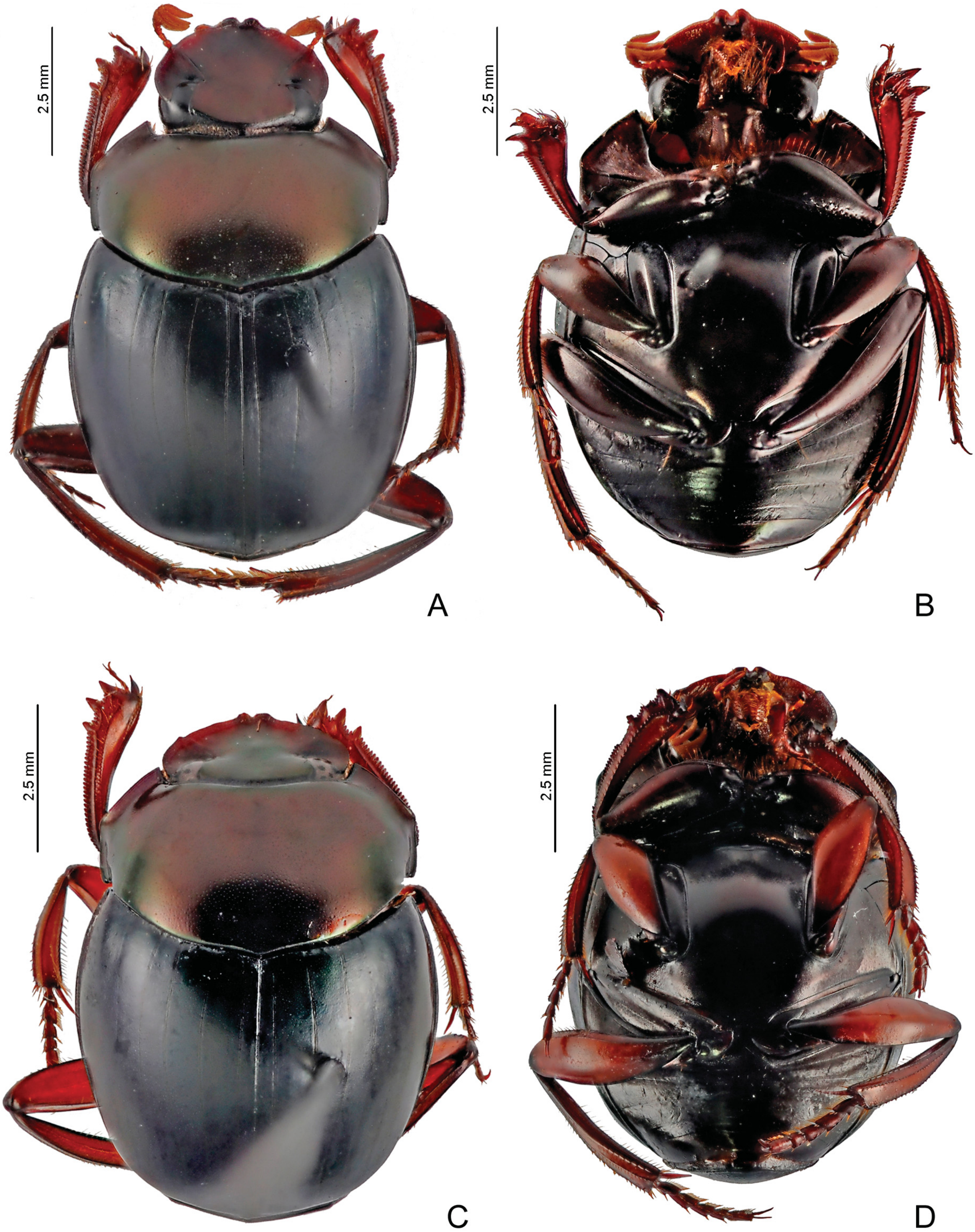

Fig. 32. *Sylvicanthon bridarollii* (Martínez, 1949). **A–B**. Individual from southern Bolivia. **A**. Dorsal view. **B**. Ventral view. **C–D**. Individual from Ecuador. **C**. Dorsal view. **D**. Ventral view.

Martínez leg. (CMNC); 2 ♀♀, Andrés Ibáñez, Santa Cruz de la Sierra, Jardín Botánico, 29 Sep. 2006, T. Vidaurre, M. Amaya and G. Mollos leg. (CEMT); 4 ♂♂, Andrés Ibáñez, Santa Cruz de la Sierra, Jardín Botánico, 17º47′02″ S, 63º03′47″ W, 400 m, W.D. Edmonds leg. (TAMU); 2 ♂♂, 2 ♀♀, Andrés Ibáñez, Santa Cruz de la Sierra, Jardín Botánico, 17º46′00″ S, 63º04′13″ W, 420 m, 5–6 Nov. 2006, pitfall with human faeces, Mann and Hamel leg. (OUMNH); 3 ♂♂ (1 dissected), 2 ♀♀, Andrés Ibáñez, Santa Cruz de la Sierra, Jardín Botánico, 17º46′00″ S, 63º04′13″ W, 420 m, 7–8 Nov. 2006, pitfall with human faeces, Mann and Hamel leg. (OUMNH); 3 ♂♂, Andrés Ibáñez, Santa Cruz de la Sierra, Jardín Botánico, 17º46′00″ S, 63º04′13″ W, 420 m, 8–9 Nov. 2006, pitfall with human faeces, Mann and Hamel leg. (OUMNH); 4 ♀♀, Andrés Ibañez, Santa Cruz de la Sierra, Jardín Botánico, “8.5 Km Carretera a Cotoca”, 17º45′51.3″ S, 63º39′30.8″ W, 10–12 Nov. 2006, Scarabnet leg. (CEMT); 1 ♀, Ichilo, Buena Vista (“4–6k SSE Buena Vista”), Hotel Fauna and Flora, 420–450 m, 2–12 Feb. 2000, pitfall with dung/carrion, J.E. Wappes leg. (TAMU); 1 ♀, Ichilo, Buena Vista (“3.7 km SSE Buena Vista”), Hotel Fauna and Flora, 17º29′ S, 63º33′ W, 29Apr.–6 May 2004, flight interception trap, A.R. Cline leg. (CMNC); 3 ♀♀, Obispo Santistevan, General Saavedra, “CIMCA”(?), 9 Sep. 1988, C.J. Pruetti leg. (CMNC); 1 ♀, San Pedro(?), 12 Sep. 1997, C. J. Pruetti leg. (CMNC).

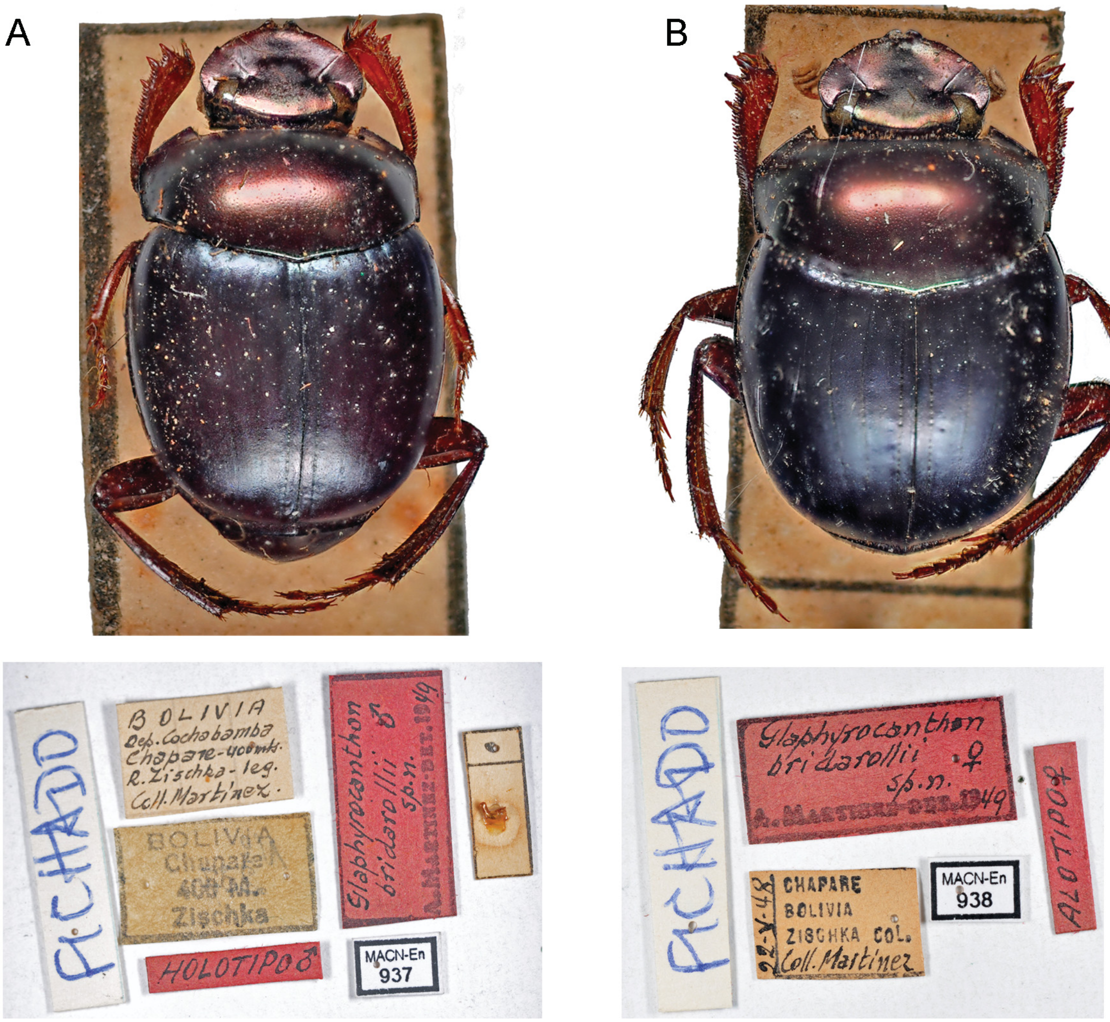

Fig. 33. *Sylvicanthon bridarollii* (Martínez, 1949) type material. **A**. Holotype and its labels. **B**. Allotype and its labels.

BRAZIL: **Acre**: 8 ♂♂, 4 ♀♀, Manoel Urbano, Parque Estadual Chandless, 09º22′26″ S, 63º55′20″ W, 24 Jun. 2013, T.F. Brito leg. (CEMT); 1 ♂, 1 ♀, Manoel Urbano, Parque Estadual Chandless, 09º22′26″ S, 63º55′20″ W, 1 Jul. 2013, T.F. Brito leg. (CEMT); 1 ♀, Rio Branco, Jul. 1996, M. Castro leg. (CEMT); 1 ♂, 1 ♀, Senador Guiomard, 67º37′ W, 10º04′ S, 14 Apr. 2017, pitfall W ith human faeces, Bruna S. Bittencourt leg. (CEMT); 1 ♂, 2 ♀♀, Tarauacá, Nov. 1956, W erner leg. (MZSP); 2 ♂♂, 2 ♀♀, Tarauacá, Dec. 1956, Dirings leg. (MZSP); 5 ♂♂, 3 ♀♀ (1 dissected), Xapuri, Reserva Chico Mendes, 500 m, 19 Oct. 2008, Rafael Andrade leg. (CEMT); 1 ♂, Xapuri, Reserva Chico Mendes, 10º17.607′ S, 68º41.638′ W, 500 m, 20 Oct. 2008, pitfall W ith human faeces, J. Silveira leg. (CEMT). – **Rondônia**: 1 ♂, 1 ♀, Cacoal, Loteamento Pichek, 11º26′26″ S, 61º25′22″ W, 228 m, 14 Jan. 2017, pitfall W ith human faeces, R. Silva leg. (CEMT); 13 ♂♂, 6 ♀♀, Colorado do Oeste, "Laticínio", 13º07′05.49″ S, 60º33′28.04″ W, 16–18 Dec. 2016, pitfall W ith human faeces, C.B.S. Souza leg. (CEMT); 6 ♂♂, 3 ♀♀, Colorado do Oeste, "Laticínio", 13º07′05.49″ S, 60º33′28.04″ W, 20–22 Feb. 2017, pitfall W ith human faeces, C.B.S. Souza leg. (CEMT); 2 ♂♂, Porto Velho, Abunã, 09º36′38″ S, 65º21′33″ W, 200 m, 19 Sep. 2010, pitfall W ith human faeces, J.C.F. Falcão leg. (CEMT); 1 ♂, 1 ♀, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 83 m, 10–12 Nov. 2013, pitfall W ith human faeces, M.A.P.A. Silveira leg. (CEMT); 2 ♀♀, Porto Velho, Nova Mutum-Paraná ["Mutum"], 09º35′46″ S, 65º02′27″ W, Jan. 2012, R.V. Nunes leg. (CEMT); 1 ♂, Porto Velho, Nova Mutum-Paraná ["Mutum"], 09º35′46″ S, 65º02′27″ W, 200 m, Sep. 2012, pitfall with human faeces, R.V. Nunes leg. (CEMT); 1 ♀, Rolim de Moura, 11º44′04.87″ S, 61º55′08.64″ W, 214 m, 27–29 Jul. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 1 ♂, 2 ♀♀, Rolim de Moura, 11º44′04.93″ S, 61º55′09.19″ W, 215 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 4 ♂♂, Rolim de Moura, 11º44′4.96″ S, 61º55′10.4″ W, 217 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 2 ♂♂, Rolim de Moura, 11º44′03.77″ S, 61º55′09.74″ W, 218 m, 27–29 Jul. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 1 ♂, 1 ♀, Rolim de Moura, 11º44′03.77″ S, 61º55′09.74″ W, 218 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 1 ♂, Rolim de Moura, 11º44′05″ S, 61º55′11.62″ W, 219 m, 27–29 Jul. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 2 ♂♂, 3 ♀♀, Rolim de Moura, 11º44′04.42″ S, 61º55′11.59″ W, 220 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 1 ♂, 1 ♀, Rolim de Moura, 11º44′05.02″ S, 61º55′12.19″ W, 220 m, 27–29 Jul. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 4 ♂♂, 1 ♀, Rolim de Moura, 11º44′05.04″ S, 61º55′12.78″ W, 221 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 5 ♂♂, 1 ♀, Rolim de Moura, 11º44′04.48″ S, 61º55′12.75″ W, 222 m, 8–10 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 6 ♂♂, 3 ♀♀, Rolim de Moura, 11º43′43.42″ S, 61º53′32.13″ W, 255 m, 7–9 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 3 ♂♂, 3 ♀♀, Rolim de Moura, 11º43′43.42″ S, 61º53′32.13″ W, 255 m, 27–29 Jul. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 2 ♀♀, Rolim de Moura, 11º44′25.01″ S, 61º55′24.14″ W, 272 m, 27–29 Jul. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 3 ♂♂, 3 ♀♀, São Francisco do Guaporé, Bacabalzinho, REBIO Guaporé, Campo do Murundu, 12º31′ S, 63º26′ W, 2 Oct. 2013, S.E. Silva leg. (CEMT).

COLOMBIA: **Caquetá**: 1 ♂ (dissected), Parque Nacional Natural Sierra de Chiribiquete, 300 m, pitfall with human faeces, Feb. 2000, J. Noriega leg. (CPJN).

ECUADOR: **Morona Santiago**: 3 ♂♂ (1 dissected), Untsuants, Sítio 1, 700 m, 8 Dec. 2001, J. Celi and J. Torres leg. (CMNC); 1 ♂, Untsuante, Sítio 3, 700 m, 19 Jan. 2002, pitfall with human faeces, J. Celi and M. Ortega leg. (CMNC); 4 ♂♂, Untsuante, Sítio 5, 600 m, 22 Jan. 2002, J. Celi and M. Ortega leg. (CMNC); 3 ♂♂ (1 dissected), 4 ♀♀, Untsuante, Sítio 6, 600 m, 22 Jan. 2002, pitfall with human faeces, J. Celi and M. Ortega leg. (CMNC). – **Napo**: 1 ♂, Jatun Sacha Biological Station, 21 km E of Puerto Napo, 400 m, 8 Jul. 1994, dung trap, F. Génier leg. (CMNC); 2 ♂♂, 1 ♀, Puerto Misahualli, Jungle Hotel, 8–20 Sep. 1997, D.G. Marqua leg. (TAMU); 3 ♂♂, 7 ♀♀, Tena, 400 m, 15–21 Feb. 1986, human faeces trap, François Génier leg. (CMNC); 11 ♂♂ (1 dissected), 8 ♀♀, Tena ("5 km W Tena"), 500 m, 6–9 Jul. 1976, dung trap, S. Peck leg. (CMNC); 3 ♂♂, 1 ♀, Tena ("20 km S Tena"), 600 m, 9–11 Jul. 1976, S.

Peck leg. (CMNC). – **Orellana**: 2 ♂♂ (1 dissected), 1 ♀, Tiputini Biodiversity Station, 0º38′ S, 76º09′ W, 220 m, Sep. 2000, carrion trap, D. Inward leg. (BMNH). – **Sucumbíos**: 1 ♂ (dissected), Shushufindi, Reserva Biológica Limoncocha (“Limoncocha”), 0º28′ S, 76º36′ W, 300 m, 31 Mar. 1974, H.P. Stockwell leg. (CMNC); 3 ♂♂, 2 ♀♀, Shushufindi, “Limoncocha”, 10–15 Mar. 1975, J.M. Campbell leg. (CMNC); 3 ♂♂, 5 ♀♀, Shushufindi, “Limoncocha”, 250 m, 18–24 Jun. 1976, dung trap, S. Peck leg. (CMNC).

PERU: 1 ♂, “Peru mont. / O. Thieme V.” (ZMHB, labelled as Syntype of *Canthon obscurus* by the ZMHB Staff, but, very likely, a pseudotype). – **Amazonas**: 1 ♀, Rodríguez de Mendoza, Quebrada Huancabamba, 06º35′30″ S, 77º33.2′ W, 2360 m (“2100m”), 14 Jun.–23 Jul. 2010, D. Chunga leg. (MUSM). – **Cuzco**: 1 ♀,La Convención, Echarate, Centro Poblado Tunquio, 12º15′44.30″ S, 72º52′37.08″ W, 960 m, 26 Sep.–1 Oct. 2010, C. Carranza and S. Cavero leg. (MUSM); 1 ♂, 1 ♀, La Convención, Echarate, Comunidad Tupac Amaru, 12º06′49.78″ S, 72º49′35.47″ W, 371 m, 22 Oct. 2009, M. Alvarado and E. Rázuri leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Tupac Amaru, 11º56′52.58″ S, 72º54′50.06″ W, 536 m, 17–19 Jan. 2010, C. Espinoza and E. Razuri leg. (MUSM); 1 ♂, La Convención, Echarate, Campamento Segakiato, 11º45′38.6″ S, 73º14′57.7″ W, 908 m, 2 Mar. 2011, M. Alvarado and E. Rázuri leg. (MUSM); 1 ♂, 1 ♀,La Convención, Echarate, Campamento Segakiato, 11º45′38.6″ S, 73º14′57.7″ W, 908 m, 1–4 May 2011, S. Cavero and C. Espinoza leg. (MUSM); 1 ♂, 1 ♀, La Convención, Echarate, Quebrada Pomoreni, 65º06′09.8″ S, 77º41′51.97″ W, 488 m, 21–24 Apr. 2010, L. Figueroa and D. Chunga leg. (MUSM). – **Huánuco**: 1 ♀, Estación Biológica Panguana (Forschungsstation Panguana), Rio Pachitea, Rio Yuyapichis, 09º37′ S, 74º56′ W, 260 m, 28 Aug.–14 Sep. 1986, Listabarth leg. (NHMW); 4 ♂♂ (1 dissected), 5 ♀♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva (“Tingo María Universidad”), Jul. 1974 (CMNC); 1 ♂, 2 ♀♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva Dec. 1974 (CMNC); 1 ♂, 2 ♀♀, Puerto Inca, Clayton, 09º11′53.37″ S, 74º55′12.1″ W, 243 m, 10–12 Apr. 2009, C. Carranza leg. (MUSM); 2 ♀♀, Puerto Inca, Clayton, 09º11′53.37″ S, 74º55′12.1″ W, 243 m, 16–18 Jun. 2009, C. Carranza leg. (MUSM); 1 ♂, 1 ♀, Puerto Inca, Tournavista, 08º56′11.75″ S, 74º43′23.3″ W, 178 m, 18–19 Jun. 2009, C. Carranza leg. (MUSM). – **Junín**: 2 ♂♂, Chanchamayo, San Ramón, pitfall, F.G. Horgan leg. (MUSM); 1 ♂,Chanchamayo, San Ramón, May 2002, human faeces pitfall, F.G. Horgan leg. (MUSM); 1 ♂, 1 ♀, Chanchamayo, San Ramón, 8 May 2002, human faeces pitfall, F.G. Horgan leg. (MUSM); 1 ♂, 5 ♀♀, Chanchamayo, San Ramón, 17 May 2002, human faeces pitfall, F.G. Horgan leg. (MUSM); 1 ♂ (dissected), 2 ♀♀, Chanchamayo, San Ramón, Oct. 2002, human faeces pitfall, F.G. Horgan leg. (MUSM); 1 ♂, Chanchamayo, San Ramón, Oct. 2002, human faeces pitfall, F.G. Horgan leg. (MUSM); 1 ♀, Chanchamayo, San Ramón, Catarata El Tirol (“El Tirol”), 820–1000 m, Jul. 2000, dung trap, C. Torpoco leg. (CMNC); 2 ♂♂, 2 ♀♀ (1 dissected), Satipo (CEMT); 1 ♂, 1 ♀, Satipo, 600 m, 23 May–3 Jun. 2004, A. Santibañez leg. (TAMU); 1 ♂, 1 ♀, Satipo, 11º14′22″ S, 74º39′37″ W, 1008 m, 28 Aug.–2 Sep. 2011, I. Medina and L. Figueroa leg. (MUSM). – **Loreto**: 1 ♂, Alto Amazonas, Teniente César López Rojas, 02º35′39.6″ S, 76º06′55″ W, 230–305 m, 18–26 Jul. 1993, flight interception trap, R. Leschen leg. (CMNC); 3 ♂♂,Reserva Nacional Pacaya Samiria, Rio Samiria, Cocha Shinguito, 26 Aug. 1991, T.L. Erwin Exp. Res. Pacaya-Samiria, G.E. Ball and D. Shpeley leg. (CMNC); 2 ♂♂, Reserva Nacional Pacaya Samiria, Rio Samiria, Cocha Shinguito, 26–29 Aug. 1991, T.L. Erwin Exp. Res. Pacaya-Samiria, G.E. Ball and D. Shpeley leg. (CMNC); 1 ♀, Zona Reservada Sierra del Divisor, 07º04′01″ S, 74º01′21″ W, 213 m, 16–19 Feb. 2009, C. Espinoza leg. (MUSM); 1 ♂, 1 ♀, Zona Reservada Sierra del Divisor, 2 km from Rio Hubuya, 196 m, 13–14 Oct. 2008, C. Carranza leg. (MUSM); 1 ♂, Reservada Sierra del Divisor, Quebrada Ubuya, 06º57′19″ S, 74º01′24″ W, 202 m, 2–3 Mar. 2009, C. Espinoza leg. (MUSM). – **Madre De Díos**: 2 ♂♂, Manu, Manu, Salvación (“near Salvación”), 13º50′37″ S, 71º19′57″ W, 650 m, Nov. 1999, human faeces pitfall, T. Larsen leg. (CMNC); 3 ♂♂ (1 dissected), 4 ♀♀, Manu, Parque Nacional del Manu (“Manu National Park”), 15–30 Aug. 1986, A. Forsyth leg. (CMNC); 10 ♂♂, 2 ♀♀, Manu, Parque Nacional del Manu, Estación Biológica Cocha Cashu, 11º55′ S, 77º18′ W, 380 m, 18 Aug.–5 Sep. 1986, D.C. Darling & A.B. Forsyth leg. (MUSM); 7 ♂♂ (1 dissected), 1 ♀, Manu, Parque Nacional del Manu, Estación Biológica Cocha

Cashu, 11º53′45″ S, 71º24′24″ W, 350 m, 17–19 Oct. 2000, flight interception trap, R. Brooks leg. (CMNC); 1 ♂, Manu, Reserva Comunal Amarakaeri, 12º56′32.48″ S, 70º48′23.30″ W, 333 m, 24–26 Oct. 2010, J. Costa and M. Vilchez leg. (MUSM); 1 ♀, Río Patuyacu, Oculto Camp, 12º39′00″ S, 68º55′33″ W, 400 m, 25–26 Mar. 1999, human faeces pitfall, T. Larsen leg. (MUSM); 1 ♀, Tambopata, 290 m, 21 Mar. 1987, pitfall, P. Lozada leg. (MUSM); 1 ♂, 2 ♀♀, Tambopata, Las Piedras, fundo vivero El Bosque, 12º27′49.27″ S, 69º07′30.69″ W, 17–19 Apr. 2011, O. Huaches leg. (MUSM); 1 ♀, Tambopata, Puerto Maldonado, Madama, 12º31′20″ S, 69º03′44″ W, 29 Mar. 2009, L. Figueroa leg. (MUSM); 3 ♂♂, 2 ♀♀, Tambopata, Puerto Maldonado, Madama, 12º31′20″ S, 69º03′44″ W, 19–20 Jul. 2009, 182 m, M. Alvarado leg. (MUSM); 5 ♂♂, 3 ♀♀, Tambopata, Puerto Maldonado (“15 km N.E. Puerto Maldonado”), Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 13 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 1 ♂, Tambopata, Puerto Maldonado (“15 km N.E. Puerto Maldonado”), 13 Jul. 1989, J. Ashe and R. Leschen leg. (MUSM); 2 ♂♂, Tambopata, Puerto Maldonado (“15 km N.E. Puerto Maldonado”), 200 m, 15 Jul. 1989, J. Ashe and R. Leschen leg. (MUSM); 1 ♂,Tambopata, Puerto Maldonado (“15 km N.E. Puerto Maldonado”), 200 m, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 13 Jun. 1989 (CMNC); 10 ♂♂, 4 ♀♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 15 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 1 ♂, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 16 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 12 ♂♂, 5 ♀♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 17 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 18 ♂♂, 8 ♀♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 20 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 1 ♂, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 22 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 26 ♂♂ (1 dissected), 13 ♀♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 24 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 7 ♂♂, 2 ♀♀,Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 26 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 7 ♂♂, 2 ♀♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 28 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 14 ♂♂ (1 dissected), 4 ♀♀,Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 30 Jun. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 2 ♂♂, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 4 Jul. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 3 ♂♂, 1 ♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 7 Jul. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 1 ♀, Tambopata, Puerto Maldonado, Reserva Cuzco Amazonica, 12º33′ S, 69º03′ W, 200 m, 16 Jul. 1989, flight interception trap, Ashe and Leschen leg. (CMNC); 1 ♂, Tambopata, Puerto Maldonado, Reserva Nacional Tambopata, 18–22 Apr. 1983, Enrique Perez leg. (MUSM); 1 ♂, 1 ♀, Tambopata, Puerto Maldonado, Reserva Nacional Tambopata (“Rio Tambopata Res. / 30 km (air) Sw. Pto. Malonato”), 12º50′ S, 69º20′ W, 3 Oct.–15 Nov. 1983, 290 m, N.E. Stork leg. (BMNH); 1 ♂, Tambopata, Puerto Maldonado, Sector Triunfo, 69º11′47″ W, 12º33′42″ W, 198 m, 25 Mar. 2009, L. Figueroa leg. (MUSM); 6 ♂♂, 1 ♀, Tambopata, Puerto Maldonado, Sector Triunfo, 69º11′47″ W, 12º33′42″ W, 198 m, 23 Jul. 2009, M. Alvarado leg. (MUSM); 3 ♂♂, 3 ♀♀, Tambopata, Reserva Nacional Tambopata, Explorer’s Inn, 12º50′30″ S, 69º17′31″ W, 161 m, 15–18 May 2009, L. Figueroa and M. Alvarado leg. (MUSM). – **Pasco**: 1 ♂, 2 ♀♀, Oxapampa, Parque Nacional Yanachaga-Chemillén, Puesto Huampal, 10º10′57″ S, 75º34′25.6″ W, 1001 m, 7–10 Nov. 2010, C. Carranza and J. Peralta leg. (MUSM). – **San Martín**: 1 ♂, Picota, Pilluana, Fundo Mishquiyacu, 06º04′20.1″ S, 76º58′33.8″ W, 990 m, 11–12 Dec. 2008, C. Albujar leg. (MUSM). – **Ucayali**: 3 ♂♂, 2 ♀♀, Coronel Portillo, Masisea, C.N. Betel(?) leg., 08º25′39.01″ S, 74º15′53.55″ W, 118 m, 8 Aug. 2008, C. Espinoza leg. (MUSM); 1 ♂, Coronel Portillo, Puerto Alegre, 08º44′06.76″ S, 74º09′4.54″ W, 196 m, 21–22 May 2008, L. Figueroa leg. (MUSM); 7 ♂♂, 7 ♀♀, Coronel Portillo, Puerto Purin, 08º44′59.2″ S, 74º08′19.52″ W, 122 m, 19 May 2008, L. Figueroa leg. (MUSM); 1 ♀, Coronel Portillo, Puerto Purin, 08º44′59.2″ S, 74º08′19.52″ W, 196 m, 21–22 May 2008, L. Figueroa leg. (MUSM); 1 ♂, Coronel Portillo, Puerto Purin, 08º44′59.2″ S, 74º08′19.52″ W, 122 m, 17 Jul. 2008, L. Figueroa leg. (MUSM); 1 ♂, Coronel Portillo, Río Inamapuya, 08º44′33.7″ S, 74º06′15.9″ W, 135 m, 11–12 Jul. 2008, M. Alvarado leg. (MUSM); 1 ♂, 1 ♀, Padre Abad, Irázola, Alexander von Humboldt, 08º49′04.72″ S, 75º04′14.88″ W, 233 m, 1–2 Apr. 2009, C. Carranza leg. (MUSM); 1 ♂, 1 ♀, Padre Abad, Irázola, Alexander von Humboldt, 08º49′04.72″ S, 75º04′14.88″ W, 233 m, 8–10 Jun. 2009, C. Carranza leg. (MUSM).

Ambiguous data: PERU?: 1 ♂, "*7-8.XI.87* / *CUPERJALI*" (MUSM).

Erroneous data: BRAZIL: **Pará**: 1 ♂ (dissected), Itaituba, Rio Tapajós, Mar. 1964, Dirings leg. (MZSP); 1 ♀, Redenção, Pinkaiti-Aik, 07º46′ S, 51º58′ W, Nov. 1999, P.Y. Scheffler leg. (CEMT).

Redescription

Colouration. Head and pronotum dark purple or coppery; occasionally, with weak greenish reflections. Elytra dark green or dark blue; when green, striae sometimes with dark blue colouration and slightly more contrasting with elytral tegument. Metaventrite black or coppery; usually with slight greenish reflections. Meso- and metafemora ranging in a north-south cline from dark brown (Bolivia) to reddish-brown (Peru and Brazil) and orangish or yellowish (northern Peru, Ecuador, and Colombia), but base always distinctly darker than at least apical two-thirds. Pygidium, sometimes, with shine predominantly greenish and with some coppery reflections, especially at base.

Head. Tegument with little shine, with strong alveolar microsculpture obliterating almost completely micropunctation which is almost imperceptible or even absent across the outer edge of head. Clypeus with two apical teeth obtuse and only slightly separated from one another; with a single transverse row of short setae covering base of both teeth. Genae with strong tooth just behind clypeal-genal juncture. Posterior edge of head without margin between eyes, or margin very fine and tenuous.

Thorax. Pronotum with tegument with diffuse shine and alveolar microsculpture very fine and strongly marked obliterating micropunctation, which is usually very weak at centre and completely absent on sides. Posterior edge may have an evident fine transverse line at centre (generally extending beyond second elytral stria), or transverse line very tenuous and short, or even absent. Hypomeral cavity with long yellowish setae at centre (Fig. 35C); external margin with weak tubercle. Metaventrite glabrous, including lateral region; tegument with strong rivose microsculpture on anterior region and adjacent to internal margin of mesocoxae and with strong alveolar microsculpture and fine micropunctation at centre and on posterior region.

Legs. Ventral surface of all femora and tibiae with diffuse shine. Profemora with tegument with strong rivose microsculpture and without micropunctation (Fig. 9A). Protibiae narrow and with expansion on internal edge, which can be evident (southern populations in Bolivia and Peru, Fig. 11F), or only slightly indicated (especially in Ecuador and Colombia, Fig. 11G); at their apical third, external edge with three small acute teeth on external edge, two apical ones of subequal size and longer than the basal. Mesofemora margined anteriorly only at their basal half; unmargined portion of anterior edge with row of very short setae; posterior margin absent; tegument with strong rivose microsculpture. Metafemora margined only anteriorly, posterior margin absent; apical half of anterior edge covered by row of setae; tegument entirely covered by strong rivose microsculpture and with coarse elongate punctation at base geographically variable: individuals from southern populations in Bolivia with coarse punctation evident (Fig. 13G) which becomes progressively finer and imperceptible northwards until being completely absent in populations in Ecuador and Colombia (Fig. 13H). Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

ELYTRA. With at most nine visible striae: in general, the first two to four striae well marked, finely carinulate, and without basal widening; remaining striae progressively more effaced and interrupted; eighth and ninth striae observable only in specimens with well-marked striae and, in those cases, always very subtle; all striae lack their carinulae before reaching the apex of elytra, where they are completely indistinct; humeral carina absent. Tegument of interstriae with diffuse shine, with strong alveolar microsculpture throughout its surface; micropunctation obliterated by microsculpture and almost imperceptible.

ABDOMEN. Ventrite VI with rivose microsculpture diffuse at centre and weak on the sides; both sexes without lateral foveae. Pygidium with tegument with diffuse shine and entirely covered by alveolar microsculpture; micropunctation, if present, completely obliterated by microsculpture and difficult to see.

AEDEAGUS. Parameres at least half as long as phallobase and symmetrical, both faces flat. In lateral view, parameres simple, with truncate apex and without ventral keel or notch (Fig. 18A).

SEXUAL DIMORPHISM. **Males**: Protibial spur narrow and widely bifid at apex, with spiniform projections, the external projection much longer than the internal one (Fig. 15I). Ventrite VI with posterior edge strongly narrowed at middle; anterior edge covered very slightly by weak medial expansion of ventrite V. **Females**: Protibial spur simple, spiniform. Ventrite VI much wider at middle; anterior edge subtly covered by weak medial expansion of posterior edge of ventrite V.

Measurements

Males (N =14). **TL:** AV: 8.1 ± 0.76; MX: 9.2; MN: 6.6. **EW:** AV: 5.7 ± 0.43; MX: 6.3; MN: 4.8. **PrL:** AV: 2.4 ± 0.27; MX: 3.0; MN: 1.9. **PrW:** ME: 4.8 ± 0.83; MX: 5.5; MN: 2.2. **PgL:** ME: 1.4 ± 0.10; MX: 1.5; MN: 1.2. **PgW:** AV: 2.3 ± 0.24; MX: 2.6; MN: 2.0.

Females (N = 12). **TL:** AV: 8.1 ± 0.54; MX: 8.9; MN: 7.5. **EW:** AV: 5.6 ± 0.48; MX: 6.4; MN: 4.9. **PrL:** ME: 2.4 ± 0.26; MX: 2.9; MN: 2.1. **PrW:** AV: 4.9 ± 0.43; MX: 5.6; MN: 4.3. **PgL:** ME: 1.2 ± 0.11; MX: 1.5; MN: 1.1. **PgW:** AV: 2.3 ± 0.25; MX: 3.0; MN: 2.1.

Geographical distribution

Western Amazonia in Colombia, Ecuador, Brazil, Peru, and Bolivia.

Ecoregions

Llanos, Caquetá Moist Forests, Napo Moist Forests, Cordillera Oriental Montane Forests, Iquitos Varzea, Ucayali Moist Forest, Peruvian Yungas, Southwest Amazon Moist Forests, Bolivian Yungas, Bolivian Montane Dry Forest, Chiquitano Dry Forests.

Collecting sites (Fig. 34)

COLOMBIA. ***Meta***: *Puerto Colombia*. **Caquetá**: Parque Nacional Natural Sierra de Chiribiquete. ***Guaviare***: *San José del Guaviare (Parque Nacional Natural Nukak)*.

ECUADOR. **Sucumbíos**: Shushufindi (Reserva Biológica Limoncocha). **Napo**: Reserva Biológica Jatun Sacha, Puerto Misahualli, Tena. **Orellana**: Tiputini Biodiversity Station. **Morona Santiago**: *Cordillera Cutucú*, Untsuants.

PERU. **Loreto**: Alto Amazonas (Teniente César López Rojas), Reserva Nacional Pacaya Samiria, Zona Reservada Sierra del Divisor. **Amazonas**: Rodríguez de Mendoza (Quebrada Huancabamba). **San Martín**: Picota (Pilluana: Fundo Mishquiyacu). **Ucayali**: Coronel Portillo (Puerto Alegre, Puerto Purin), Padre Abad (Irázola: Alexander von Humboldt). **Huánuco**: Estación Biológica de Panguana, Leoncio Prado (Rupa-Rupa: Tingo María), Puerto Inca. **Pasco**: Oxapampa (Parque Nacional Yanachaga-

Chemillén). **Junín**: Chanchamayo (San Ramón), Satipo. **Cuzco**: La Convención (Echarate, *Santuario Nacional Megantoni*). **Madre de Díos**: Manu (Manu: Salvación; Parque Nacional del Manu: Estación Biológica Cocha Cashu; Reserva Comunal Amarakaeri), Tambopata (Las Piedras; Puerto Maldonado: Madama, Reserva Cuzco Amazonica, Reserva Nacional Tambopata, Sector Triunfo).

BRAZIL. **Acre**: Manoel Urbano (Parque Estadual Chandless), Rio Branco, Senador Guiomard, Tarauacá, Xapuri (Reserva Extrativista Chico Mendes). **Rondônia**: Cacoal, Porto Velho, Rolim de Moura, São Francisco do Guaporé.

BOLIVIA. **Beni**: Mamoré (San Ramón). **La Paz**: Larecaja (Guanay), Nor Yungas (Coroico), Parque Nacional Madidi. **Cochabamba**: Cercado (Cochabamba), Chapare (Villa Tunari), Estación Biológica Villa Carmen, José Carrasco (Chimoré). **Santa Cruz**: Andrés Ibáñez (Santa Cruz de la Sierra), Ichilo (Buena Vista), Obispo Santistevan (General Saavedra).

Intraspecific variation and taxonomic discussion

Although the four species composing the *bridarollii* subgroup are very similar to one another, *S. bridarollii* is precisely the one that we can more readily differentiate from the others. The following characteristics are unique to *S. bridarollii* in its subgroup: pronotum and pygidium with alveolar microsculpture strongly marked and with a very weak micropunctation, which, in general, is indistinct; hypomeral cavity with long setae at centre (Fig. 35C–D); metaventrite with a strong alveolar microsculpture at centre; protibiae with internal margin expanded at their apical half (Fig. 11F–G; see below discussion about the geographical variation of this character); and parameres elongated, simple (i.e., without any ventral keel or notch) and symmetric, both with external faces equally flat (Fig. 18A). Furthermore, the metafemora with a dark brown colour and with well-impressed coarse punctures at base is a characteristic exclusive of the southern populations of *S. bridarollii* (Fig. 13G; see more details below).

As can be seen on the map of Fig. 34, *S. bridarollii* is distributed parallel to the Andes throughout western Amazonia, in altitudes between 100 and 2360 m. The only representative of the *bridarollii* subgroup with which it is never found in sympatry is *S. seag* sp. nov., a species exclusive to the northern Amazon region. Apart from the characteristics listed above, these two species are different by the head and pronotal micropunctation, shape of the male protibial spur (Fig. 15I–J), shape of ventrites V and VI of females, the tegument of pygidium and, especially, the totally distinct shape of the parameres (Fig. 18A–B) (see Table 4). Pronotum and elytra with a bright green or dark blue colouration typical of the northern populations of *S. seag* sp. nov. (Fig. 37B–C) are not seen in *S. bridarollii*; on the other hand, specimens of *S. seag* sp. nov. collected on the banks of the Amazon River and in Maranhão have a similar colouration to the one observed in *S. bridarollii* (Fig. 37A).

The other two species of the *bridarollii* subgroup, *S. edmondsi* sp. nov. and *S. attenboroughi* sp. nov., by contrast, can be found in sympatry with *S. bridarollii*, respectively, in Colombia, Ecuador and Peru, and in Brazil and Peru. From *S. edmondsi* sp. nov., *S. bridarollii* can be promptly differentiated by its dorsal colouration (Figs 32A, C, 38A) and the shape of its parameres (Fig. 18A, C), but the populations of both species also differ in the average of the total body length (Table 3). It is worth noting that Celi *et al.* (2004), having placed pitfall traps across an altitudinal gradient in Morona Santiago (Ecuador), collected twice as many specimens of *S. edmondsi* sp. nov. (116) as of *S. bridarollii* (57) (the former species was collected at altitudes between 600 and 1000 m and the latter between 500 and 900 m); at one point at 700 m altitude, they collected 114 *S. edmondsi* sp. nov. vs only 25 *S. bridarollii*. In order to test whether this result is indeed a real general pattern of relative abundance between these two species, it would be interesting if future ecological works evaluated other sympatric populations of *S. bridarollii* and *S. edmondsi* sp. nov. Finally, *S. attenboroughi* sp. nov. is the species most similar to *S. bridarollii*. Nevertheless, both species are distinguished by the unique characteristics of *S. bridarollii* listed above and also by the degree of excavation of the hypomeral cavity (Fig. 35B–C) and by the head micropunctation (Table 3).

Within *Sylvicanthon*, *S. bridarollii* is the species that shows the most remarkable form of morphological variation, which is intimately associated with the species' geographical distribution in a clear north-south cline (Fig. 36). Colouration and presence of coarse punctures on femora, shape of protibiae, and the presence of a fine transverse line on the posterior edge of the pronotum vary along this cline in the following way: individuals from southern populations in the Bolivian provinces of Santa Cruz and Cochabamba have meso- and metafemora black at the base and dark brown on the rest of their surface, metafemora with strong, coarse punctures of irregular shape at their base (Fig. 13G), protibiae with internal margin with an evident expansion at their apical half (Fig. 11F) and pronotum without any trace of a transverse line on its posterior edge. Towards the north of Bolivia, in places like Guanay and the Madidi National Park (province of La Paz) and southern Peru, in the Madre de Díos region, the colouration of meso- and metafemora becomes lighter, being dark brown or reddish-brown; the metafemur punctures are shallower and sparser (in southern Peru, they are almost imperceptible); and the posterior edge of the pronotum starts to show some indications of a medial transverse line; the protibiae, on the other hand, continue to be essentially similar to the shape seen farther south. In central Peru, in the regions of Cuzco, Junín, Pasco, Huánuco, Ucayali, Amazonas and San Martínez, and, in a lesser degree, in the states of Acre and Rondônia, Brazil, individuals have clearly bicolour meso- and metafemora, with a dark brown basal area and the rest of the surface reddish-brown; the punctures at the base of the

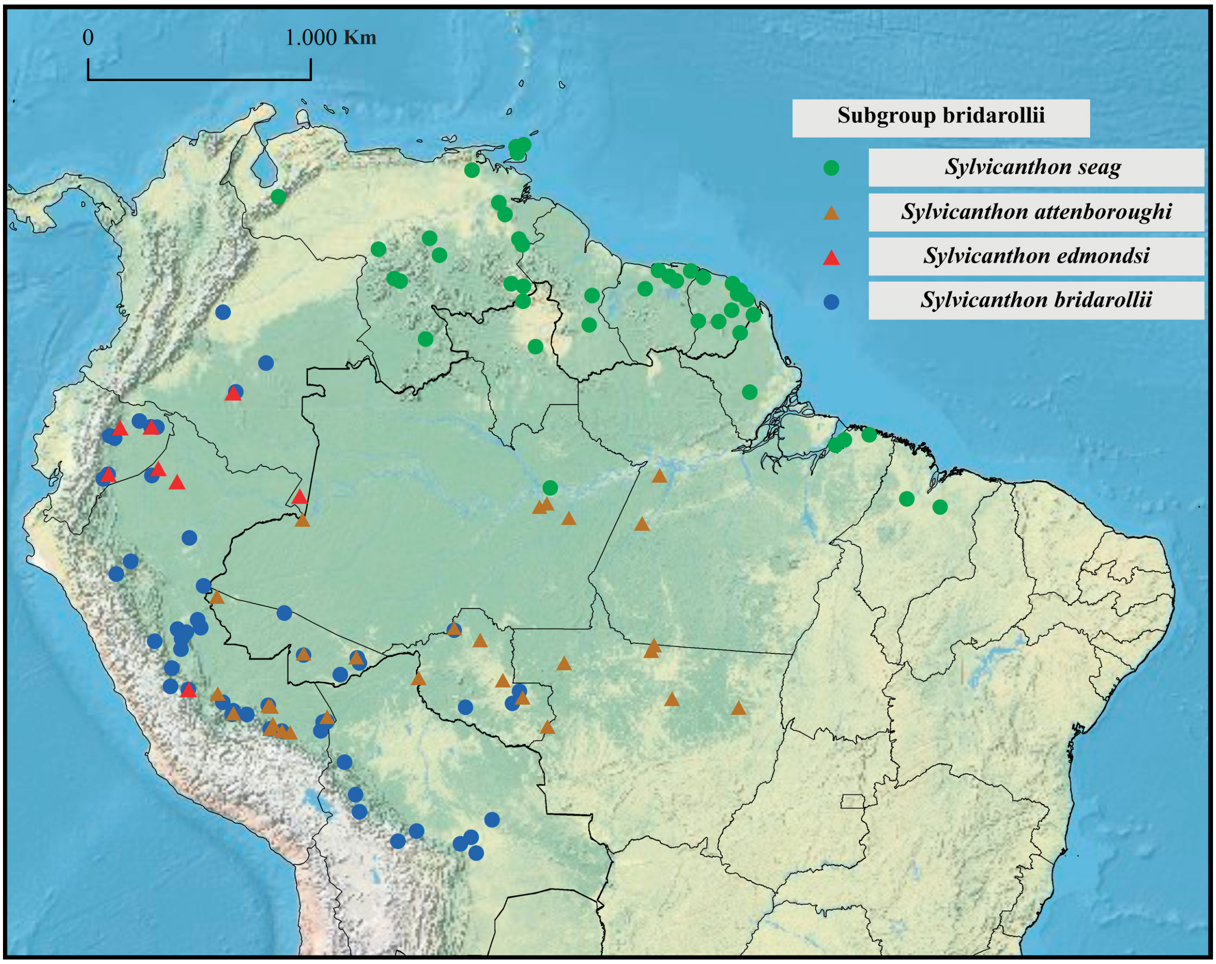

Fig. 34. Distribution of the four species of the *bridarollii* subgroup.

metafemora are very tenuous and almost imperceptible; in most of the specimens, the transverse line on the posterior edge of the pronotum is clearly seen; and the internal expansion of the protibiae becomes less pronounced. Then, from Zona Reservada Sierra del Divisor, in the Peruvian region of Loreto, north to Ecuador and Colombia, specimens have meso- and metafemora with a much lighter colouration pattern, the base being dark brown and the rest of the surface orange or yellowish (Fig. 13H); the punctures at the base of the metafemora are extremely tenuous and almost imperceptible (Loreto) or totally absent (Ecuador and Colombia); and all the examined specimens show a clear transverse line on the posterior edge of the pronotum. In those northern populations, the internal expansion of the protibiae is much more tenuous than those in the southern populations (Fig. 11G). If not directly compared with the protibiae of the species that really lack any expansion (i.e., the other members of the *bridarollii* subgroup and those of the *candezei* subgroup), one might be misled to think that those populations of *S. bridarollii* do not possess a protibial expansion either.

Although the previous description was presented by separating the distribution of *S. bridarollii* into four distinct parts, the clinal variation found is completely continuous in that north-south axis (Fig. 36), indicating that this cline is most likely the case of a primary intergradation rather than a secondary intergradation due to secondary contact of formerly allopatric demes, although this possibility should

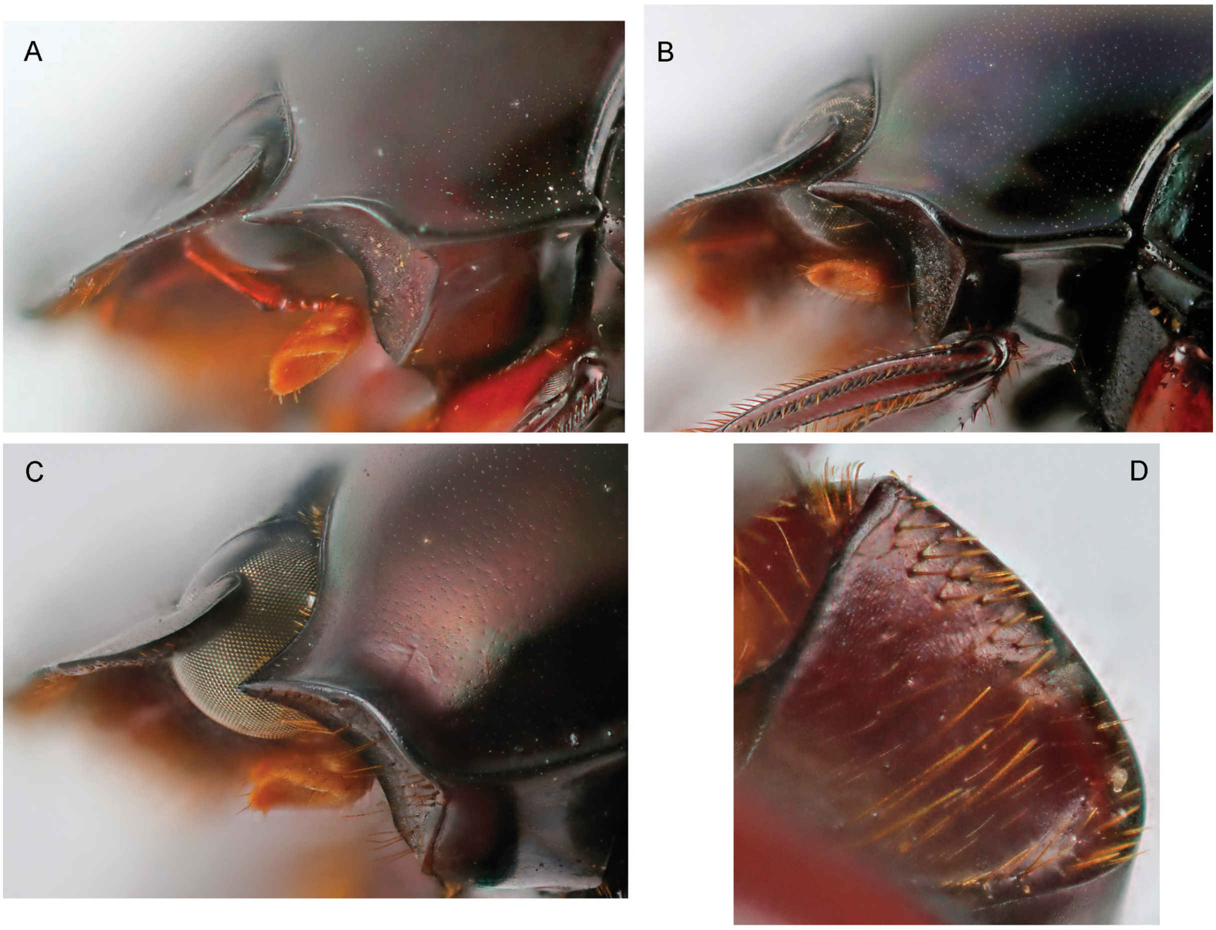

Fig. 35. Variation on the pilosity at the centre of the hypomeral cavity among members of the *bridarollii* subgroup. **A**. *Sylvicanthon seag* sp. nov. **B**. *S. attenboroughi* sp. nov. **C–D**. *S. bridarollii* (Martínez, 1949). Note the first two species have the hypomeral cavity entirely glabrous or with setae limited to its periphery (centre always glabrous), whereas *S. bridarollii* possesses long and dense setae throughout the tegument of the hypomeral cavity.

Table 4 (continued on next page). Summary of the morphological and distributional differences between the four species of the *bridarollii* subgroup.

	S. bridarollii **(Martínez, 1949)**	***S. seag*** **sp. nov.**	***S. edmondsi*** **sp. nov.**	***S. attenboroughi*** **sp. nov.**
Dorsal colouration	Head and pronotum purple or coppery. Elytra dark green or dark blue	Head and pronotum purple, and elytra greenish (southern populations), or head purple with greenish reflexions, and pronotum and elytra bright green or dark blue (northern populations)	Entire body with very dark tonalities; head dark purple, pronotum with greenish sheen at centre and purplish at sides, and elytra dark blue or purple	Entire body with dark tonalities; head and pronotum dark purple; elytra dark green or dark blue
Tegument of head	Strong microsculpture; micropunctation almost imperceptible	Strong microsculpture; micropunctation evident on clypeus posterior region and mainly on frons	Strong microsculpture; micropunctation almost imperceptible	Strong microsculpture; micropunctation evident on clypeus posterior region and mainly on frons
Tegument at centre of pronotum	With a diffuse, silky shine; microsculpture fine, but always present; micropunctation, in general, very weak	Shiny and reflective; microsculpture, in general, very diffuse and effaced or even absent; micropunctation very dense and well marked	Slightly shiny and reflective; microsculpture fine and sometimes effaced; micropunctation dense and well marked	Shiny and reflective; microsculpture, in general, very diffuse and effaced or even absent; micropunctation very dense and well marked
Hypomeral cavity	Moderately excavated; with long setae at centre	Very strongly excavated; centre glabrous or with sparse very short setae; long setae, if present, limited to posterior or anterior regions	Moderately excavated; centre glabrous or with sparse very short setae; long setae, if present, limited to posterior or anterior regions	Very strongly excavated; centre glabrous or with sparse very short setae; long setae, if present, limited to posterior or anterior regions
Tegument at centre of metaventrite	Microsculpture strong; micropunctation evident	Microsculpture very fine and progressively more diffuse towards posterior region; micropunctation not particularly evident	Microsculpture very fine and progressively more diffuse towards posterior region; micropunctation very shallow, but always evident	Microsculpture very fine and progressively more diffuse towards posterior region; micropunctation very shallow, but, in general, distinct
Shape of internal margin of protibiae	Varying from slightly (Colombia, Ecuador, Peru) to distinctly (Peru, Brazil, Bolivia) expanded	Entirely straight, without any trace of expansion	Entirely straight, without any trace of expansion	Entirely straight, without any trace of expansion (some few specimens seem to have a very slight expansion at apical half)
Shape of protibial spur of males	Narrow and bifid at apex, with external projection longer than the internal one	Wide at base and with two apical projections, the external one longer than the internal, which, in general, is only slightly indicated	Narrow and widely bifid at apex, with external projection much longer than the internal one	Narrow and widely bifid at apex, with external projection much longer than the internal one
Colouration of meso- and metafemora	Ranging gradually from yellow and orangish (northern populations) to dark brown (southern populations)	Reddish-brown or dark brown	Orangish-brown or yellowish	Orangish-brown, reddish-brown or dark brown

Table 4 (continued).

	S. bridarollii (Martínez, 1949)	*S. seag* sp. nov.	*S. edmondsi* sp. nov.	*S. attenboroughi* sp. nov.
Coarse punctation at base of metafemora	Ranging gradually from completely absent (northern populations) to with well-visible coarse punctures (southern populations)	Absent	Absent	Usually absent. In some few specimens, with slight traces at base
Anterior edge of female ventrite VI	Subtly covered by a weak flange of posterior edge on ventrite V	Distinctly covered by median flange of posterior edge on ventrite V	Subtly covered by a weak flange on posterior edge on ventrite V	Subtly covered by a weak flange on posterior edge on ventrite V
Tegument of pygidium	With strong microsculpture; micropunctation, if present, very subtle and almost imperceptible	Microsculpture ranging from distinctly marked (southern population), diffuse or totally absent (northern populations) at centre; on sides, always present; micropunctation always clearly marked	With strong microsculpture; micropunctation subtle, but always evidente	With strong microsculpture; micropunctation subtle, but always evident
Shape of parameres	Symmetrical, both external faces flat; in lateral view, without ventral keel or notch; elongated	Asymmetrical: external face of left paramere strongly excavated; in lateral view, with ventral keel strongly projected; apical half of parameres with squarish appearance	Asymmetrical: external face of left paramere excavated; in lateral view, with projected ventral keel; elongated	Asymmetrical: external face of left paramere excavated; in lateral view, with projected ventral keel; elongated
Body length (mm)	6.6–9.2 (AV: 8.1±0.65)	6.8–8.5 (AV: 7.7±0.44)	6.1–8.0 (AV: 7.1±0.53)	7.2–9.6 (AV: 8.4±0.54)
Distribution	Western Amazonia: Colombia, Ecuador, Peru, Brazil (Acre, Rondônia), and Bolivia	Northern Amazonia: Trinidad, Venezuela, Guianas, and Brazil (Amazonas, Roraima, Amapá, Pará, and Maranhão)	Northwestern Amazonia, mainly in Sub-Andean areas in Colombia, Ecuador, and Peru	Southern Amazonia, to the right banks of the Amazon River Brazil and Peru

not be ruled out based only on our morphological observations (see the discussion by Mayr 1963 on how complex the history of intergradation gradients can be). Therefore, a question is raised: what were the evolutionary forces that ultimately led to the emergence of this clinal pattern? To give a proper answer to this question, it will be necessary first to acquire further knowledge on the biological roles of the varying features and the environmental factors changing at an equivalent rate along the north-south axis. Other species of *Sylvicanthon* also show noticeable geographical variations, such as *S. seag* sp. nov. and *S. obscurus* (in relation to colouration) and *S. candezei* (the pattern of pronotal microsculpture), which may have some relation to those seen in *S. bridarollii*.

Comments

The male from MZSP allegedly collected in Itaituba, in the Brazilian state of Pará, is certainly mislabelled, since *S. bridarollii* does not occur so far east (Fig. 34). This specimen originates from the former collection of the German-Brazilian amateur entomologist Richard von Diringshofen (cited as “Dirings” on specimen labels), which was incorporated in the MZSP collection in 1987 (Costa 1999; Ferreira *et al.* 2016), and this is not the only specimen housed there with erroneous collecting data. Cupello & Vaz-de-Mello (2014), for instance, found in that same collection two individuals of *Coprophanaeus saphirinus* (Sturm, 1826), a species present only in the southern Atlantic Forest, labelled as coming from

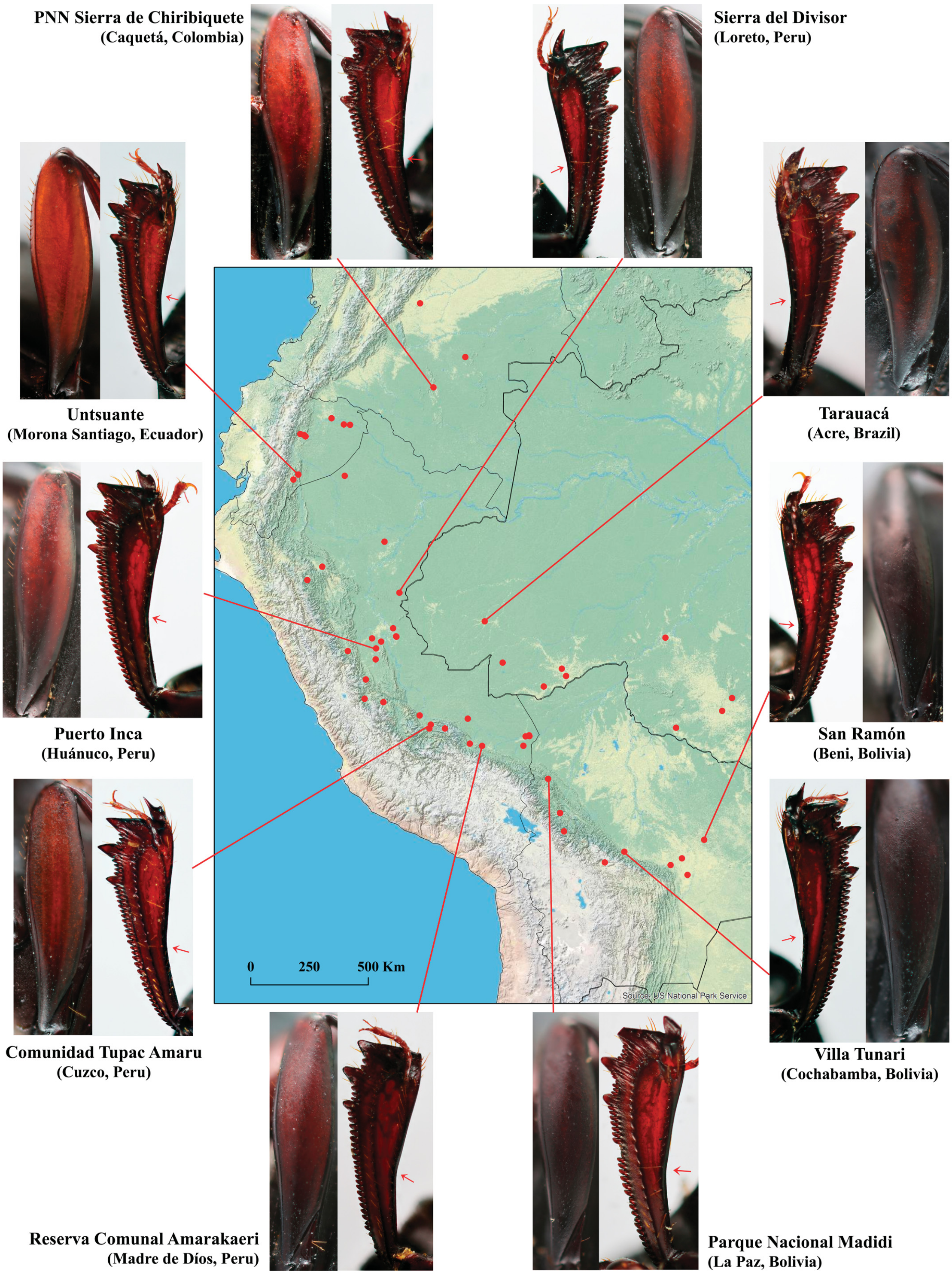

Fig. 36. Clinal morphological variation in *S. bridarollii* (Martínez, 1949). Note that, from south to north, the colouration of metafemora gradually fades from dark brown to reddish brown and orange with a light-brown base in populations of northern Peru, Ecuador, and Colombia, and that the internal margin of protibiae (indicated by the red arrows) becomes progressively much subtler. Other features varying along this north-south cline are the presence of coarse elongate punctures at the base of metafemora (present in southern populations and absent in the northern ones) and of a fine transverse line on the posterior edge of pronotum (absent in the southern populations). See the text for more details.

Pará; one of them, curiously enough, also from Itaituba. As a great part of the collection of Diringshofen was bought unprepared (Costa 1999; Ferreira *et al.* 2016), it is possible that, over time, specimens from different envelopes have been accidentally mixed up, so bringing us to this situation where mislabelling seems not to be such a rare problem.

The type series of *Glaphyrocanthon bridarollii* is composed of 10 specimens (Martínez 1949): the male holotype (Fig. 33A), the female allotype (Fig. 33B) and eight other paratypes, four males and four females. As expected, both the holotype and the allotype are deposited in the MACN, and, of the paratypes, two males and one female were found in the CMNC, while a male and two females were found in the MZSP, probably deposited there via Padre Francisco Pereira. Therefore, we did not find two of the paratypes, male and female. Martínez (1949) stated he deposited "two couples" of paratypes in the collection of Rodolfo Zischka (1895–1980), from Cochabamba, Bolivia, the type series' collector. Since 1979, Zischka's collection is housed at the Zoologische Staatssammlung München, Munich, Germany (ZSM 2014) and, thus, this museum is probably the place where the missing pair of paratypes (not 'two couples', as said by Martínez) is being conserved.

In their list of the dung beetles occurring in Colombia, Medina *et al.* (2001) and Medina & Pulido (2009) cited *S. bridarollii* for the departments of Casanare, Guainía, Guaviare, Meta and Vichada. For Meta (Amézquita *et al* 1999) and Guaviare (Escobar 2000b), it was possible to find more precise literature records and, therefore, those departments were included in the geographical distribution given above. On the other hand, for the other three departments, no accurate locality records were found; consequently, we preferred to include them neither in the geographical list above nor on the map.

Natural history

Following *S. aequinoctialis* and *S. proseni*, *S. bridarollii* has the greatest amount of bionomic information available in the literature and on specimen labels. After compiling all these data, it is possible to say that *S. bridarollii* does not differ from the genus pattern, having food habits preferentially coprophagous, although the species can occasionally be attracted to carrion, as shown by the specimens collected by D. Inward at the Tiputini Biodiversity Station (Orellana, Ecuador). On the other hand, Figueroa & Alvarado (2011), collecting at the Reserva Nacional Tambopata (Madre de Díos, Peru), although having used pitfall traps baited with both dung and carrion, caught *S. bridarollii* only with the first kind of bait. A large number of the specimens here studied were collected with flight interception traps.

Having collected during the dry season in Puerto Colombia (Meta, Colombia), Amézquita *et al.* (1999) found that *S. bridarollii* was the third most abundant species in that region, corresponding to more than 13% of the collected specimens, following only "*Onthophagus haematopus* Harold, 1975"[21], with 15%, and an unidentified species of *Uroxys*, with 28%. On the other hand, four other inventories – Figueroa & Alvarado (2011), at the Reserva Nacional Tambopata, in the Peruvian department of Madre de Díos; Larsen (2004), at the Zona Reservada Megantoni, in Cuzcu, Peru; Celi *et al.* (2004), in the Ecuadorian province of Morona Santiago; and Carpio *et al.* (2009), in Sucumbíos, also in Ecuador – did not find *S. bridarollii* among the most abundant species. In fact, in the third paper, another species of the same genus, *S. proseni* (cited as *Canthon aequinoctialis*), was the most abundant dung beetle in the region.

Regarding habitat preferences, it seems that *S. bridarollii* is restricted to dense rainforests, be it either primary or secondary. Larsen (2004) also collected specimens in a bamboo (*Guadua* Kunth and *Chusquea* Kunth) forest. Carpio *et al.* (2009), in a study on the effect of the opening of a new road at the centre of a pristine forest in Sucumbíos, saw that *S. bridarollii* was among the five dung beetle species that have their abundance progressively increased from the road towards the forest interior.

As for the altitudinal amplitude, specimens studied for this work were mostly collected between 140 and 1100 m, but one female was caught in Rodríguez de Mendoza (Amazonas, Peru) at about 2300 m a.s.l. The specimens examined also show that adults of *S. bridarollii* are active throughout the year, although a much higher number of individuals has been collected between May and October.

Sylvicanthon seag sp. nov.

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Figs 6E, 15J, 18B, 20, 34–35A, 37

Sylvicanthon candezei – Feer 2000: 32 (error); 2008: 62 (error). — Feer & Pincebourde 2005: 30.
Sylvicanthon bridarollii – Price & Feer 2012: 327 (error).
Sylvicanthon sp. – Larsen *et al.* 2009: 1294. — Vaz-de-Mello *et al.* 2011a: 67, figs 164–165 (tentative association). — Boilly & Vaz-de-Mello 2013: 105, fig. 130.
Sylvicanthon sp. 32 – Feer 2015: 3 (tentative association).

Etymology

A tribute to the Société entomologique Antilles-Guyane (SEAG), founded in 2007 by a group of amateur entomologists with the aim of facilitating the collection and promoting the study of the entomofauna of the French territories in the Americas. This society was responsible for the collection of 440 of the 1204 *S. seag* sp. nov. studied in this work, and it was thanks to this enormous volume of specimens that we could see in fine detail the morphological variation – especially the colour variation – shown by this species. The specific name is a noun in apposition.

Material examined

Holotype

FRENCH GUIANA: ♂, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, (“GUIANA FRANCESA: Saint- / Laurent-du-Maroni, / Bélvédère de Saül, / 3º37′22″N, 53º12′57″ W, / 326m, 15 Sep. 2011 / SEAG col.”, “HOLOTYPE ♂ / *Sylvicanthon seag* / sp. nov. Cupello & / Vaz-de-Mello des. 2016”) (MNHN).

Paratypes (574 ♂♂, 527 ♀♀, 103 unsexed specimens)

BRAZIL: **Amapá**: 1 ♂, Pedra Branca do Amaparí (“Cava Urucum-Amapari”), Serra do Navio, 00º53′06″ N, 51º52′53″ W, Sep. 2000, R. Ribon leg. (CEMT). – **Amazonas**: 1 ♀, 25 Feb. 1976, I.S. Goraveb leg. (INPA); 1 ♀, 16 Jun. 1976, I.S. Goraveb leg. (INPA); 1 ♂ (dissected), 1 ♀, Dec. 1977, R. Ducke leg. (CEMT); 3 ♂♂ (2 dissected), 2 ♀♀, Manaus, Apr. 1977, B. Ratcliffe leg. (CEMT); 1 ♂, Manaus, May 1977, B.C. Ratcliffe leg. (AMBC); 1 ♂, Manaus, Jun. 1977, Ratcliffe leg. (MCNZ); 1 ♂, Manaus, 1 Jul. 1977, B.C. Ratcliffe leg. (INPA); 5 unsexed Specimens, Manaus, 11–13 Oct. 1977, B.C. Ratcliffe leg. (UNSM); 1 ♂, 1 ♀, Manaus, 6 Dec. 1977, B.C. Ratcliffe leg. (CEMT); 13 ♂♂ (3 dissected), 12 ♀♀, Same collecting data as for preceding (INPA), 16 unsexed specimens, same collecting data as for preceding (UNSM); 12 ♂♂ (1 dissected), 11 ♀♀, Manaus, 20 Dec. 1977, B.C. Ratcliffe leg. (INPA); 20 unsexed specimens, same collecting data as for preceding (UNSM); 1 ♀, Manaus, 29 Dec. 1977, B.C. Ratcliffe leg. (INPA); 48 unsexed specimens, Manaus, 3 Jan. 1978, B.C. Ratcliffe leg. (UNSM); 13 unsexed specimens, Manaus, 13 Jan. 1978, B.C. Ratcliffe leg. (UNSM); 1 ♀, Manaus, 30 Jan. 1978, L.P. Albuquerque leg. (INPA); 1 ♀, Manaus, Campus do INPA, Estrada do Aleixo, Km 4, 6 Mar. 1976, L.F. Albuquerque leg. (INPA); 1 ♀, Manaus, INPA, 30 Jan. 1978, L.P. Albuquerque leg. (INPA); 1 ♀, Manaus, INPA, Sede Manaus, 18 May 1976, A.P.A. Luna Dias leg. (INPA). – **Maranhão**: 1 ♂ (dissected), Bom Jardim, Reserva Biológica Gurupi, 1–6 Nov. 2010, light trap, M.M. Abreu, J.A. Silva, G.A. Reis & E.A.S. Barbosa leg. (CEMT); 4 ♂♂, 2 ♀♀, Itapecuru-Mirim, 03º32′54″ S, 44º22′08″ W, 31 Aug. 2010, pitfall with human faeces, R. Matayelli and A. Campos leg. – **Pará**: 8 ♂♂

(3 dissected), 1 ♀, Belém, IPEAN, Oct. 1984, flight interception trap, N. Degallier leg. (CEMT); 3 ♀♀, Belém, IPEAN, Nov. 1984, N. Degalier leg. (CEMT); 1 ♂, Belém, IPEAN, May 1985, N. Degallier leg. (CEMT); 1 ♂, 1 ♀, Primavera, 01º01′27″ S, 47º06′34″ W, 13 Sep. 2013, human faeces pitfall, F. Silva leg. (CEMT); 37 ♂♂, 9 ♀♀,Primavera, 5–7 Sep. 2015, dung pitfall, FF. Silva leg. (UFPA); 1 ♂ (dissected), 1 ♀, Santo Antônio do Tauá, Jun. 1982, P. Jauffret leg. (MNHN). – **Roraima**: 2 ♂♂, 3 ♀♀, Cantá, Serra Negra, Sep. 1996, Ribeiro and Vaz-de-Mello leg. (CEMT); 8 ♂♂, 2 ♀♀, Pacaraima (“Vila Pacaraima”), 04º27′ N, 61º07′ W, 820 m, Sep. 1996, Ribeiro and Vaz-de-Mello leg. (CEMT).

FRENCH GUIANA: 24 ♂♂, 31 ♀♀, SEAG leg. (CEMT); 1 ♀, Cayenne (ISNB); 1 ♂, Cayenne (“*Cay*”) (MNHN, “Ex-Museo D. Sharp 1890”); 2 ♂♂ (1 dissected), Cayenne (“20 km SW”), 04º48′18″ N, 52º28′41″ W, 30 m, 29 May 9 Jun. 1997, flight interception trap, J. Ashe and R. Brooks leg. (CMNC); 1 ♀, Cayenne, Camopi, Rio Oyapock, Îlet Massikiri, 17 Nov. 1969, dung, G. Halffter leg. (CMNC); 1 ♀, Cayenne, Kourou, Forêt de Wayabo, Dec. 2013, M. Duranton leg. (CEMT); 2 ♂♂, 1 ♀, Cayenne, Kourou, Rte. Cayenne-Sinnamary, RN1, PK84, Jan. 2013, flight interception trap, SEAG leg. (CEMT); 3 ♂♂ (1 dissected), 2 ♀♀, Cayenne, Matoury, [Hôtel] La Chaumière, IV.1978, P. Arnaud leg. (CMNC); 1 ♂, Cayenne, Matoury, Mont Grand Matoury, dubious date (1995 or 14 Jun. 2011?), M. Trýzna leg. (CEMT); 4 ♂♂, Cayenne, Matoury, Mont Grand Matoury, Oct.–Dec. 2012, SEAG leg. (CEMT); 6 ♂♂, 1 ♀, Cayenne, Matoury, Réserve Naturelle Nationale du Mont Grand Matoury, 04º51′ N, 52º21′ W, 215 m, 2 Aug. 2012, SEAG leg. (CEMT); 12 ♂♂, 22 ♀♀, Cayenne, Montsinéry-Tonnegrande, Montagne des Chevaux, 04º44′56″ N, 52º26′28″ W, 75 m, 30 Oct. 2011, SEAG leg. (CEMT); 2 ♂♂, 2 ♀♀, Cayenne, Montsinéry-Tonnegrande, Montagne des Chevaux, 04º44′56″ N, 52º26′28″ W, 75 m, 27 Jan. 2013, SEAG leg. (CEMT); 2 ♂♂, 1 ♀, Cayenne, Régina, [Réserve Naturelle Nationale des] Nouragues, 04º05′ N, 52º40′ W, 155 m, Mar. 1997, F. Feer leg. (CEMT); 3 ♀♀, Cayenne, Régina, [Réserve Naturelle Nationale des] Nouragues, 04º05′ N, 52º40′ W, May 2003, F. Feer leg. (CEMT); 12 ♂♂, 16 ♀♀, Cayenne, Régina, [Réserve Naturelle Nationale des] Nouragues, 4 Apr. 2010, F. Feer leg. (CEMT); 14 ♂♂, 5 ♀♀, Cayenne, Régina, [Réserve Naturelle Nationale des] Nouragues, Inselberg, 04º05′ N, 52º41′ W, 411 m, 4 Apr. 2010, SEAG leg. (CEMT); 2 ♂♂ (1 dissected), 2 ♀♀, Cayenne, Régina, [Réserve Naturelle Nationale des] Nouragues, Saut-Pararé, 04º02′16″ N, 52º40′21″ W, 30 Nov. 2009, Stéphanie Brule leg. (BMNH); 5 ♂♂, 4 ♀♀, Cayenne, Paracou Field Station, 05º02′ N, 53º00′ W, 55 m, Oct. 2003, F. Feer leg. (CEMT); 4 ♂♂ (1 dissected), Cayenne, Roura (“18.4 km SSE”), 04º36′38″ N, 52º13′25″ W, 240 m, 22–24 May 1997, J. Ashe and R. Brooks leg. (CMNC); 3 ♂♂, 1 ♀, Cayenne, Roura (“18.4 km SSE”), 04º36′38″ N, 52º13′25″ W, 240 m, 25–29 May 1997, flight interception trap, J. Ashe and R. Brooks leg. (CMNC); 1 ♂, 1 ♀, Cayenne, Roura (“18.4 km SSE”), 04º36′38″ N, 52º13′25″ W, 240 m, 10 Jun. 1997, flight interception trap, J. Ashe and R. Brooks leg. (CMNC); 4 ♂♂, 2 ♀♀,Cayenne, Roura (“18.4 km SSE”), 04º36′38″ N, 52º13′25″ W, 240 m, 29 May–10 Jun. 1997, flight interception trap, J. Ashe and R. Brooks leg. (CMNC); 1 unsexed Specimen, Cayenne, Roura, Réserve Naturelle Régionale Trésor, 225 m, 4º36′38″ N, 52º16′45″ W, Dec. 2009, malaise trap (BMNH); 1 ♂, 2 ♀♀, Cayenne, Saint-Georges-de-l’Oyapock, 03º54′ N, 51º48′ W, 35 m, May 2014, F. Feer leg. (CEMT); 1 ♂, “Nouveau Chantier”, “octobre” (MNHN); 1 ♀, Régina (“S of Régina”), 30 Dec. 2006, Snižek leg. (NMPC); 1 ♀, Same collecting data as for preceding (OUMNH); 1 ♂ (dissected), Régina, Kaw (“Kaw rd”), PK-38, 23–27 Aug. 1995, J.E. Wappes leg. (CMNC); 1 ♂, Régina, Route de Kaw (“Caiman Camp env.”), 7 Dec. 2006, M. Snižek leg. (NMPC); 1 ♀, Régina, Route de Kaw (“Caiman Camp env.”), 20 Dec. 2006, Snižek” (OUMNH); 4 ♂♂, 4 ♀♀, Saint-Laurent-du-Maroni, Jul. 1975, P. Arnaud leg. (MNHN); 1 ♂, Saint-Laurent-du-Maroni, Mana, Acarouany, VI.1993, Marek and Seidl leg. (CEMT); 1 ♀, Saint-Laurent-du-Maroni, Maripasoula (“Maripa”), 27 Nov. 1969, dung, G. Halffter leg. (CEMT); 1 ♀,Saint-Laurent-du-Maroni, Maripasoula, Route de Belizon, PK 10, 29 Jan. 1990, O. Schmitt leg. (MNHN); 2 ♂♂,Saint-Laurent-du-Maroni, Maripasoula, Saül, Mar. 1977 (CNCI); 10 ♂♂, 6 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, 11 Jan. 2011 (CEMT); 16 ♂♂, 20 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, 27 May 2011 (CEMT); 1 ♂, 2 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, 9 Sep. 2011 (CEMT); 14 ♂♂, 25 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 11 Jan. 2011, SEAG leg. (CEMT); 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 28 Feb. 2011, SEAG leg. (CEMT); 3 ♂♂, 5 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 13 May 2011, flight interception trap, SEAG leg. (CEMT); 23 ♂♂, 22 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 15 Jun. 2011, SEAG leg. (CEMT); 33 ♂♂, 32 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 23 Jun. 2011, SEAG leg. (CEMT); 3 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 30 Jun. 2011, SEAG leg. (CEMT); 21 ♂♂, 13 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 28 Jul. 2011, SEAG leg. (CEMT); 15 ♂♂, 27 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 24 Aug. 2011, SEAG leg. (CEMT); 11 ♂♂, 14 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 9 Nov. 2011, SEAG leg. (CEMT); 10 ♂♂, 6 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 15 Sep. 2011, SEAG leg. (CEMT); 13 ♂♂, 21 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, Grand Boeuf Mort, 10 Oct. 2007, SEAG leg. (CEMT); 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Montagne Pelée, 20 May 2011, SEAG leg. (CEMT); 1 ♂, Saint-Laurent-du-Maroni, Maripasoula, Saül (“7 km N”), Les Eaux Claires, 03º39′46″ N, 53º13′19″ W, 220 m, 30 May–4 Jun. 1997, flight interception trap, J. Ashe and R. Brooks leg. (CMNC); 1 ♂, 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül (“7 km N”), Les Eaux Claires, 03º39′46″ N, 53º13′19″ W, 220 m, 31 May–3 Jun. 1997, human faeces trap, J. Ashe and R. Brooks leg. (CMNC); 2 ♂♂ (1 dissected), 2 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül (“7 km N”), Les Eaux Claires, 03º39′46″ N, 53º13′19″ W, 4–8 Jun. 1997, 220 m, malaise, J. Ashe and R. Brooks leg. (CMNC); 1 ♂ (dissected), Saint-Laurent-du-Maroni, Maripasoula, Saül, Mount Galbao, 03º37′18″ N, 53º16′42″ W, 5–7 Jun. 1997, J. Ashe and R. Brooks leg. (CMNC).

GUYANA: **Pataro-Siparuni**: 1 ♂, Iwokara Rain Forest, 04º39′ N, 58º41′ W, 70 m, 13 Apr. 2009, flight interception trap, S. Phelps leg. (OUMNH); 1 ♂, Iwokara Rain Forest, 04º39′ N, 58º41′ W, 70 m, 13 Apr.–31 May 2009, baited trap, S. Phelps leg. (OUMNH). – **Upper Takutu-Upper Essequibo**: 2 ♂♂, Upper Essequibo Conservation Concession, 03º30′37″ N, 58º13′98″ W, 100 m, 22–26 Sep. 2007, pitfall with human faeces, G.C. McGavin leg. (OUMNH).

SURINAME: 1 ♂, 1 ♀ (BMNH); 1 ♂ (dissected) Same collecting data as for preceding (CEMT, “Ex-Museo van Lansberge”), 2 ♂♂, Same collecting data as for preceding (MZSP), 1 ♂, Same collecting data as for preceding (NMPC, ex. coll. Balthasar). – **Brokopondo**: 2 ♂♂, 3 ♀♀,Brownsburg Nature Reserve, 04º56′55″ N, 56º10′53″ W, 450 m, 23 Jun. 1999, flight interception trap, Z. Falin leg. (CMNC); 2 ♂♂, 3 ♀♀, Brownsburg Nature Reserve, 04º56′55″ N, 56º10′53″ W, 450 m, 25 Jun. 1999, flight interception trap, Z. Falin leg. (CMNC). – **Commewijne**: 1 ♀, Akintosoela, 05º16′17″ N, 54º55′15″ W, 40 m, 29 Jun.–3 Jul. 1999, flight interception trap, Z. Falin leg. (CMNC); 1 ♂, Akintosoela, 05º16′17″ N, 54º55′15″ W, 40 m, 3 Jul. 1999, flight interception trap, Z. Falin leg. (CMNC). – **Marowijne**: 1 ♀, Christian Kondre, Oct. 1963, B. Malkin leg. (MZSP); 3 ♀♀, Palumeu, 03º20′56″ N, 55º26′18″ W, 9 Jul. 1999, flight interception trap, Z. Falin leg. (CMNC). – **Para**: 4 ♂♂, 2 ♀♀, Zanderij, 11 km SE of Zanderij Airport, 30 m, 20 Jun. 1999, flight interception trap, Z. Falin leg. (CMNC). – **Saramacca**: 1 ♀, W. Suraname Rd. (East-West Link?), 108 km WSW of Zanderij Airport, 30 m, 05º13′37″ N, 55º52′54″ W, 14 Jun. 1999, Z. Falin leg. (CMNC).

TRINIDAD AND TOBAGO: 3 ♂♂, 1 ♀, Trinidad, Arima, 16 km N of Arima, Andrews Trace, 620 m, 7–24 Jun. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 4 ♂♂, 2 ♀♀, Trinidad, Arima, 16 km N of Arima, Andrews Trace, 620 m, 24 Jun.–7 Jul. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂, 1 ♀, Trinidad, Arima, 19 km N of Arima, Lalaja Trace, 650 m, 8–24 Jun. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂, Trinidad, Arima, William Beebe Tropical

Research Station ("Simla (N. Y. Zool. Soc. Sta.)"), 11 Jun. 1977, pitfall trap With pig dung, R.E. Woodruff leg. (CMNC); 20 ♂♂, 4 ♀♀, Trinidad, Couva-Tabaquite-Talparo, Quesnell Farm, 13 km S of Arima, 2 km N of Talparo, 50 m, 12–22 Jun. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 4 ♂♂, 1 ♀, Trinidad, Couva-Tabaquite-Talparo, Quesnell Farm, 13 km S of Arima, 2 km N of Talparo, 50 m, 22 Jun.–8 Jul. 1993, flight interception trap, S. and J. Peck leg. (CMNC); leg. 1 ♀, Trinidad, Sangre Grande, Arena Forest Reserve, 10º33′18″ N, 61º13′13″ W, 20 Jul. 2012, G.H. Simpson (OUMNH); 2 ♀♀, Trinidad, Sangre Grande, Arena Forest Reserve, 10º30′18″ N, 61º13′13″ W, 22 Jul. 2012, G.H. Simpson leg. (OUMNH); 3 ♂♂, Trinidad, Sangre Grande, Arena Forest Reserve, 80 m, 13–22 Jun. 1993, S. and J. Peck leg. (CEMT); 12 ♂♂ (2 dissected), 8 ♀♀, Same collecting data as for preceding (CMNC); 2 ♂♂, 1 ♀, Trinidad, Sangre Grande, Arena Forest Reserve, 80 m, 22 Jun.–8 Jul. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂ (dissected), Trinidad, Sangre Grande, Arena Forest Reserve, 10º33′18″ N, 61º13′13″ W, 22 Jul. 2012, pitfall with human faeces, G.H. Simpson leg. (OUMNH); 1 ♂, 2 ♀♀, Trinidad, Tunapuna-Piarco, Mount Saint Benedict, 550 m, 5–21 Jun. 1998, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂, Trinidad, Tunapuna-Piarco, Mount Saint Benedict, 550 m, 21 Jun.–8 Jul. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂, Trinidad, William Beebe Tropical Research Station ("Simla, 5mi. N. / Arima"), 19 Aug. 1969, H. and A. Howden leg. (CMNC); 1 ♂, 2 ♀♀, Trinidad, William Beebe Tropical Research Station ("Simla Res. Sta."), 8 km N of Arima, 240 m, 6–10 Jun. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 3 ♂♂ (1 dissected), 1 ♀, Trinidad, William Beebe Tropical Research Station ("Simla Res. Sta."), 8 km N of Arima, 260 m, 6–14 Jun. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 3 ♂♂, 5 ♀♀, Trinidad, William Beebe Tropical Research Station ("Simla Res. Sta."), 8 km N of Arima, 260 m, 14–24 Jun. 1993, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂, 5 ♀♀, Trinidad, William Beebe Tropical Research Station ("Simla Res. Sta."), 8 km N of Arima, 260 m, 24 Jun.–8 Jul. 1993, flight interception trap, S. and J. Peck leg. (CEMT); 3 ♂♂, 3 ♀♀, Same collecting data as for preceding (CMNC), 1 ♂, 1 ♀, Same collecting data as for preceding (MCNZ); 1 ♂, 1 ♀, Trinidad, William Beebe Tropical Research Station ("Simla, N Arima"), 21 Jun.–6 Jul. 2007, E.G. Hancock leg. (OUMNH).

VENEZUELA: **Amazonas**: 3 ♂♂, 2 ♀♀, Alto Orinoco ("*T.F.A. Atabapo / Alto Orinoco*"), Platanal, Jun. 1979 (CMNC); 9 ♂♂ (1 dissected), 10 ♀♀, Alto Orinoco ("*T.F.A. Atabapo / Alto Orinoco*"), Trapichate, Jun. 1979 (CMNC); 1 ♂, 1 ♀, Puerto Ayacucho, Atures, Cerro Camani, Jul. 1979 (CMNC); 1 ♂ (dissected) and 1 ♀, San Juan de Manapiare, Alto Ventuari ("*1º Atures / Alto Ventuari / Camani (Aramare)*"), Jun. 1979 (CMNC). – **Bolívar**: 1 ♀, Gran Sabana, Km 40 Sta. Elena Icabaru Road, 4–6 Aug. 1986, 100 m, B. Gill leg. (CMNC); 1 ♀, Gran Sabana, San Francisco Yuruaní ("*J. F. Yuruani*"), Jan. 1988, illegible collector (CMNC); 1 ♂, 1 ♀, Isla Anacoco, 7 Aug. 2006(CEMT); 1 ♀, Las Trincheras ("35 km N Las Trincheras", "15 km N Corocito"), 17 Jun. 1987, UV light trap, S. and J. Peck leg. (CMNC); 4 ♂♂, Las Trincheras, Río Caura, 10–11 Aug. 1986, B. Gill leg. (CMNC); 1 ♂, 5 ♀♀, Mata de Corocito ("10 km N Corocito"), 18 Jun.–3 Aug. 1987, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♀, Padre Pedro Chien, 20 km EL Palmar, 18 Jun. 1996, dung, H. and A. Howden leg. (CMNC); 1 ♀, Río Chicanan, 40 km SW of El Dorado, 22–23 Jul. 1986, B. Gill leg. (CEMT), 27 ♂♂, 12 ♀♀, Same collecting data as for preceding (CMNC); 7 ♂♂, 9 ♀♀, Río Sipao, 110 km E of Caicara, 17 Jun.–4 Aug. 1987, flight interception trap, S and J. Peck leg (CMNC); 2 ♀♀, Sinfontes, 10 km S of El Dorado, 200 m, 17 Jul. –7 Aug. 1986, B. Gill leg. (CEMT); 35 ♂♂ (1 dissected), 49 ♀♀, Same collecting data as for preceding (CMNC); 2 ♂♂, 1 ♀, Sinfontes, 20 km S. of El Dorado, 220 m, 20–23 Jul. 1986, B. Gill leg. (CMNC); 2 ♂♂, Sinfontes, 22 km S. of El Dorado, 25 Jun.–12 Jul. 1987, flight interception trap, S. and J. Peck leg. (CMNC); 5 ♂♂, 3 ♀♀, Sinfontes, 33 km S of El Dorado, 220 m, 2–7 Aug. 1986, B. Gill leg. (CMNC); 1 ♂, Sinfontes, El Dorado, 7 Aug. 1966, Milan Křiž leg. (OUMNH); 2 ♂♂, Sucre, Salto Pará, 250 m, 20–22 Nov. 1978, A.H.Chacon leg. (CMNC). – **Delta Amacuro**: 1 ♂, 1 ♀, Casacoima, 11 km W of Piacoa, 14–31 Jul. 1987, flight interception trap, S. and J. Peck leg. (CMNC). – **Mérida**: 1 ♂, Libertador, Mérida, Monte Zerpa, Nov. 1987, D. Harraner(?) leg. (CMNC). – **Monagas**: 2 ♀♀, Maturín, 15 km N of Maturín, 19–31 Jul. 1987, flight interception trap, S. and J. Peck leg. (CMNC); 1 ♂ (dissected), Teresen (?), 800 m, 12 Jun. 1963, R. Hernandez leg. (CMNC).

Erroneous data: ECUADOR: **Napo**: 1 ♀, Lago Agrio, Feb. 1986, illegible collector (CMNC).

PERU: **Huánuco**: 1 ♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva (“Tingo María Universidad”), Jul. 1974 (CMNC).

No data: 1 ♀ (ISNB, “Collection E. Candeze”), 1 ♂ (MNHN).

Description

Colouration. With evident geographical variation on dorsum: in southern populations (specimens examined from Manaus, Belém and Bom Jardim), head and pronotum purple and elytra greenish with contrasting striae (usually of the same colour as, or darker than, pronotum) (Fig. 37A); individuals from northern populations with head purple with greenish reflections and pronotum and elytra bright green (Fig. 37C) or dark blue (Fig. 37B), with elytral striae contrasting; pronotum usually with purplish reflections, especially on the sides. Metaventrite dark, with purplish or coppery reflections (Fig. 37D); specimens from Trinidad and a few others from Venezuela with greenish reflections at centre of disc. Meso- and metafemora reddish-brown or dark brown, base distinctively darker than apical two-thirds. Pygidium ranging from predominantly coppery with greenish shine, to the south, to totally greenish or bluish, on northern populations.

Head. Tegument with little shine and strong alveolar microsculpture; micropunctation evident on posterior region of clypeus and especially on frons (Fig. 6E). Clypeus with two apical teeth obtuse and only slightly separated; with a single transverse row of setae covering base of both teeth. Genae with strong tooth immediately behind clypeal-genal juncture. Posterior edge of head completely unmargined.

Thorax. Pronotum with shiny, lustrous tegument, with microsculpture in general very diffuse and effaced or even totally absent at centre; on sides, with stronger alveolar microsculpture; micropunctation denser and more clearly marked at centre and progressively weaker towards the sides. Posterior edge with fine transverse line at centre (usually extending up to the second elytral stria). Hypomeral cavity entirely glabrous or, at most, with some very few short setae at centre; long setae, when present, restricted to posterior region (Fig. 35A); external margin with very short tubercle. Metaventrite entirely glabrous; tegument with evident rivose microsculpture on sides and anterior region, and weaker microsculpture adjacent to internal margin of mesocoxae; at centre, alveolar microsculpture very fine and progressively more diffuse and ill delimited towards posterior region; micropunctation very fine and not evident.

Legs. Ventral surface of all femora and tibiae bright. Profemora with tegument with strong rivose microsculpture and without micropunctation. Protibiae narrow and with internal edge straight and simple, without expansion; at their apical third, with three small acute teeth on external edge, the two most apical ones subequal in length and larger than basal tooth. Mesofemora margined anteriorly only at their basal half; unmargined portion of anterior edge with row of very short setae; posterior margin absent; tegument with effaced rivose microsculpture. Metafemora margined anteriorly, posterior margin absent; apical half of anterior edge covered by a row of setae; tegument covered by effaced rivose microsculpture and without any trace of coarse punctation at base. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. In most cases with nine well-visible striae: in general, the first six or seven striae well marked, very finely carinulate and slightly widened at base; seventh stria finer than the others, but always visible; eighth and ninth striae very fine; all striae lack carinulae at apex of elytra, where they are completely indistinct; humeral carina absent. Tegument of interstriae very shiny and lustrous; at centre, ranging from weak alveolar microsculpture (populations on the banks of the Amazon River) to diffuse microsculpture or even totally smooth; at apex and on sides, always with strong alveolar microsculpture; micropunctation clearly visible at 20 × magnification.

Abdomen. Ventrite VI with very diffuse rivose microsculpture, or microsculpture absent; in both cases, micropunctation very subtle; in both sexes without lateral foveae. Pygidium with tegument distinctly micropunctated and with variable microsculpture: at centre, alveolar microsculpture distinctly marked

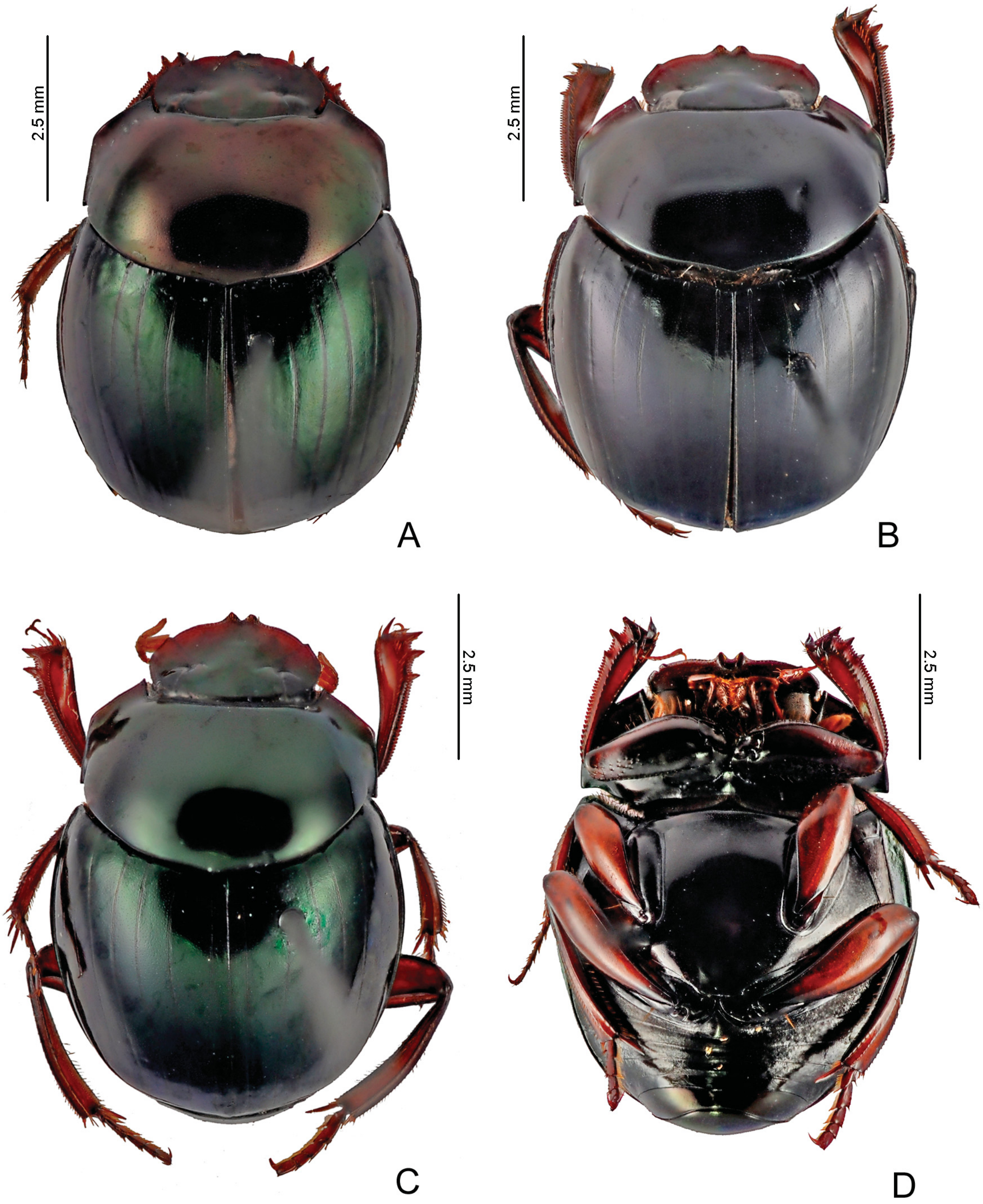

Fig. 37. *Sylvicanthon seag* sp. nov. **A**. Dorsal view of a bicolour specimen (present only on the banks of the Amazon River and in the Brazilian state of Maranhão). **B**. Dorsal view of a bluish specimen. **C**. Dorsal view of a greenish specimen. **D**. Ventral view of a greenish specimen.

(populations on the banks of the Amazon River), diffuse, or even totally absent; on the sides, alveolar microsculpture always present.

Aedeagus. Parameres half as long as phallobase and strongly asymmetrical: external face of right paramere flat and external face of left paramere concave, strongly excavated. In lateral view, parameres with ventral keel strongly projected, giving squarish appearance to apical half of parameres, and with pronounced notch posteriorly to ventral keel (Fig. 18B).

Sexual dimorphism. **Males**: Protibial spur wide at base and with two apical projections: external projection spiniform and longer than internal one, usually only slightly indicated (Fig. 15J). Ventrite VI with posterior edge strongly narrowed at centre; anterior edge slightly covered by medial flange of ventrite V. **Females**: Protibial spur spiniform, simple. Ventrite VI very wide at centre, posterior edge straight, without emargination; anterior edge distinctly covered by medial flange of posterior edge of ventrite V.

Measurements

Males (N = 15). **TL:** AV: 7.5 ± 0.46; MX: 8.5; MN: 6.8. **EW:** AV: 5.7 ± 0.31; MX: 6.1; MN: 5.2. **PrL:** AV: 2.3 ± 0.18; MX: 2.7; MN: 2.1. **PrW:** AV: 4.8 ± 0.28; MX: 5.3; MN: 4.4. **PgL:** AV: 1.4 ± 0.05; MX: 1.5; MN: 1.3. **PgW:** AV: 2.3 ± 0.13; MX: 2.5; MN: 2.1.

Females (N = 13). **TL:** AV: 7.9 ± 0.31; MX: 8.4; MN: 7.4. **EW:** ME: 6.01 ± 0.24; MX: 6.3; MN: 5.6. **PrL:** AV: 2.6 ± 0.12; MX: 2.9; MN: 2.5. **PrW:** AV: 5.0 ± 0.21; MX: 5.5; MN: 4.8. **PgL:** AV: 1.4 ± 0.08; MX: 1.5; MN: 1.3. **PgW:** AV: 2.5 ± 0.12; MX: 2.7; MN: 2.2.

Geographical distribution

Northern Amazonia in Trinidad, Venezuela, Guyana, Suriname, French Guiana and Brazil.

Ecoregions

Venezuelan Andes Montane Forests, Trinidad and Tobago Moist Forests, Guianan Highlands Moist Forests, Negro-Branco Moist Forests, Guianan Moist Forests, Paramaribo Swamp Forests, Guianan Savanna, Uatuma-Trombetas Moist Forests, Japurá-Solimões-Negro Moist Forests, Tocantins-Pindaré Moist Forests.

Collecting sites (Fig. 34)

TRINIDAD AND TOBAGO. Arima (William Beebe Tropical Research Station), Couva-Tabaquite-Talparo, Sangre Grande (Arena Forest Reserve), Tunapuna-Piarco (Mount Saint Benedict).

VENEZUELA. **Mérida**: Libertador (Mérida: Monte Zerpa). Monagas: Maturín. **Delta Amacuro**: Casacoima. **Bolívar**: Gran Sabana (San Francisco Yuruaní), Isla Anacoco, Las Trincheras, Mata de Corocito, Padre Pedro Chien, Sinfontes, Sucre (Salto Pará). **Amazonas**: Alto Orinoco, Puerto Ayacucho (Atures: Cerro Camani), San Juan de Manapiare.

GUYANA. **Potaro-Siparuni**: Iwokrama Forest. **Upper Takutu-Upper Essequibo**: Upper Essequibo Conservation Concession.

SURINAME. Saramacca. **Commewijne**: Akintosoela. **Marowijne**. **Para**: Zanderij. **Brokopondo**: Brownsburg Nature Reserve.

FRENCH GUIANA. Cayenne (Camopi; Kourou; Matoury: Réserve naturelle nationale du mont Grand Matoury; Montsinéry-Tonnegrande: Montagne des Chevaux; Régina: Kaw, Réserve naturelle nationale des Nouragues; Roura: Réserve naturelle régionale Trésor; Saint-Georges-de-l'Oyapock), Saint-Laurent-du-Maroni (Maripasoula: Saül; Mana: Acarouany).

BRAZIL. **Roraima**: Cantá (Serra Negra), Pacaraima. **Amazonas**: Manaus. **Amapá**: Pedra Branca do Amaparí. **Pará**: Belém, Primavera, Santo Antônio do Tauá. **Maranhão**: Bom Jardim (Reserva Biológica Gurupi), Itapecuru-Mirim.

Intraspecific variation and taxonomic discussion

Sylvicanthon seag sp. nov. is the only representative of the *bridarollii* subgroup that, as far as we know, is totally allopatric in relation to the other species of its group: it occurs from the Cordillera de Mérida, in western Venezuela, and the island of Trinidad, in the Caribbean Sea, to the Guianas and the northern region of the Brazilian Amazonia (Fig. 34). Throughout most of its extension, the distribution of *S. seag* sp. nov. is restricted to the left banks of the Amazon River, crossing to the other side only near to its mouth with the Atlantic Ocean, being present in localities such as Belém and Santo Antônio do Tauá in Pará, and at the Reserva Biológica Gurupi in Maranhão. *Sylvicanthon attenboroughi* sp. nov., the species most closely related to *S. seag* sp. nov., is limited to the right banks of the Amazon. Because the distribution of *S. attenboroughi* sp. nov. does not cross to the right banks of the Tapajós River, this species does not occur so far east to be found in sympatry with the populations of *S. seag* sp. nov. in Pará and Maranhão.

Throughout this vast area, *S. seag* sp. nov. shows a noteworthy geographical variation related to the sculpture of pygidium and colouration. Individuals from southern populations, including those on the banks of the Amazon River (e.g., Manaus and Belém), have a pygidium covered by a distinct alveolar microsculpture and dorsal colouration very similar to that seen in *S. attenboroughi* sp. nov.: head and pronotum purple and greenish elytra (Fig. 37A). To the north, the pygidial microsculpture becomes weaker and, in some specimens, the tegument seems to be completely smooth at the centre. Regarding the colouration, individuals from the Guianas and Venezuela possess a purple head with greenish reflections and pronotum and elytra shiny green or dark blue (the former colour more common than the latter) (Fig. 37B–C). A few specimens from French Guiana, however, have the pronotum mostly covered by a purple colouration, so appearing to be an intermediate phase between the colouration seen farther south and the more typical one seen in this part of the distribution of *S. seag* sp. nov. Likewise, the two specimens known from Santo Antônio do Tauá also have this intermediate phase between the northern and southern colouration patterns. In Trinidad, finally, the colouration pattern is typically northern, but it differs from the continental populations in having the dark blue as the most frequent colour instead of shiny bright green.

Despite the wide geographical variation discussed above, there is one fundamental characteristic for the identification of *S. seag* sp. nov. that does not seem to vary significantly, either intra- or interpopulationally: the shape of the parameres. In *S. seag* sp. nov., these structures are strongly asymmetric (the external face of the right paramere is flat, while the external face of the left paramere is strongly excavated) and, in lateral view, possess a ventral keel strongly projected, with a squarish appearance (Fig. 18B). No other species of *Sylvicanthon* has such an elaborate aedeagus. If, externally, individuals of *S. attenboroughi* sp. nov. are extremely similar to specimens from southern populations of *S. seag* sp. nov. and can be easily confused with them, the examination of the parameres leaves no doubt as to the correct identification of the specimens (Fig. 18D). Other differences between both species rest in the metaventral micropunctation, on the anterior margin of the female ventrite VI and on the pygidial tegument (see Table 4).

From the other two species of the *bridarollii* subgroup, *S. seag* sp. nov. is different simultaneously in having an evident micropunctation on the head, and by the hypomeral cavity strongly excavated

(Fig. 35A), the shape of the anterior margin of female ventrite VI, metaventral and pygidial tegument, the shape of parameres (Fig. 18B) and the distribution (Fig. 34). Specifically from *S. edmondsi* sp. nov., *S. seag* sp. nov. is different in dorsal colouration (Fig. 37A–C) and size, while it is distinguished from *S. bridarollii* by the tegument of pronotum, the absence of setae at the centre of the hypomeral cavity (Fig. 35A), the shape of the protibiae (Fig. 11H–I), and the absence of coarse punctation at the base of the metafemora (Table 4).

Comments

Two specimens from the collection of Antonio Martínez are certainly mislabelled: a female supposedly collected at Lago Agrio, in Napo, Ecuador, and another female labelled "Tingo María Universidad", in Huánuco, Peru. From this latter locality, we have examined specimens of *S. genieri* sp. nov. and *S. bridarollii*, species that indeed occur in Huánuco and, therefore, should be correctly labelled. As they came from the same collection, it is possible the female of *S. seag* sp. nov. now labelled "Tingo María Universidad" has been accidently mixed up with the material collected in that region and, consequently, received – erroneously – the same provenience label.

Natural history

Specimen labels show that *S. seag* sp. nov. can be collected with a wide variety of traps: pitfalls baited with human faeces and pig dung, flight interception traps, malaise and light traps, both white and ultraviolet light. This species is collected year-round, but, in the Guianas, Venezuela, and Trinidad, places from where we could examine more material, it is clearly more abundant between May and September. Lastly, labels tell us that *S. seag* sp. nov. occurs between 30 and 800 m (but near 2000 m for the sole specimen collected in Cordillera de Mérida).

Feer & Pincebourde (2005), studying the flight activity time of dung beetles from a locality in French Guiana, classified *S. seag* sp. nov. (cited as *S. candezei*) as a diurnal species, a fact that would differentiate it from the other members of *Sylvicanthon*. Nevertheless, by examining their data more carefully, we see that they collected only two specimens of *S. seag* sp. nov., one at 9:00 and other at 21:00. Therefore, their results are very far from being conclusive for this species. The truth is that the few data we have on the flight time of *S. seag* sp. nov. point to a nocturnal life: as said above, specimens are attracted to light traps, and a female collected in 1969 by Gonzalo Halffter at Îlet Massikiri, on the Oyapock River, also in French Guiana, was caught at night.

Sylvicanthon edmondsi sp. nov.

urn:lsid:zoobank.org:act:6C7F8A07-DAB4-4CB9-B0BA-D7CF986C19F5

Figs 11I, 13F, 15K, 18C, 20, 34, 38A–B

Sylvicanthon sp. 1 – Celi *et al.* 2004: 46.
Sylvicanthon cf. *bridarolli* [sic] – Noriega *et al.* 2008: 79 (tentative association).

Etymology

A tribute to the great American scarabaeidologist W.D. Edmonds, a student of the tribe Phanaeini and author of some of the major classics on the biology and morphology of Scarabaeinae. In recognition of his very kind support and continuous encouragement to MC since their very first contact. The holotype of *S. edmondsi* sp. nov. is deposited in the TAMU collection, the institution where the formerly private Edmonds collection is now housed (Streit 2012). The specific name is a noun in the genitive case.

Material examined

Holotype

ECUADOR: ♂, Orellana, Parque Nacional Yasuní, Estación Científica Yasuní, 215 m (“ECUADOR: Napo Prov. / Estación Cientifica Yasuní / IX-5-10-1999, 215 m / Coll. E. G. Riley”, “TAMU-ENTO / X0668859 / [código de barras]”) (TAMU).

Paratypes (42 ♂♂, 43 ♀♀)

COLOMBIA: **Amazonas**: 1 ♂, 1 ♀, Leticia, Parque Nacional Natural Amacayacu, Dec. 1998, J. Noriega leg. (CPJN). – **Caquetá**: 1 ♀, Parque Nacional Natural Sierra de Chiribiquete, 300 m, Feb. 2000, pitfall with human faeces, J. Noriega leg. (CPJN).

ECUADOR: **Morona Santiago**: 5 ♂♂ (1 dissected), 2 ♀♀, Untsuants, sítio 3, 700 m, 13 Jan. 2002, pitfall with human faeces, J. Celi and M. Ortega leg. (CMNC). – **Orellana**: 1 ♂, Parque Nacional Yasuní, Estación Científica Yasuní, 00º38′ S, 76º36′ W, 215 m, 27. Jul.–1 Aug. 1998, pitfall with human faeces, Ratcliffe, Jameson, Smith and Villatoro leg. (CMNC); 29 ♂♂ (2 dissected), 32 ♀♀, Parque Nacional Yasuní, Estación Científica Yasuní, 215 m, 5–10 Sep. 1999, E.G. Riley leg. (TAMU); 1 ♂, Parque Nacional Yasuní, Estación Científica Yasuní, 9–17 Sep. 1999, D.G. Marqua leg. (TAMU); 1 ♂, Parque Nacional Yasuní, via Maxus km “Onkone Gare”, 220 m, 14 Nov. 2001, canopy fogging, P. Araujo leg. (CEMT); 2 ♂♂, 1 ♀, Rodrigo Borja, IAMOE, 4 Jun. 2000, pitfall with human faeces, A. Dávalos leg. (CEMT); 1 ♂, Tiputini Biodiversity Station, 0º38′ S, 76º09′ W, 220 m, sep. 2000, carrion trap, D. Inward leg. (BMNH); 2 ♀♀, Tiputini Biodiversity Station, Río Tiputini, 0º40.5′ S, 76º24′ W, Jul. 1999, flight interception trap, A. Tishechkin leg. (CEMT).

PERU: **Junín**: 1 ♂, Satipo, Oct.–Nov. 2002 (CEMT). – **Loreto**: 3 ♀♀, Campamento San Jacinto, 02º18′44.85″ S, 75º51′46″ W, 175–215 m, 3–12 Jul. 1993, flight interception trap, R. Leschen leg. (CMNC); 1 ♀, Río Pucacuro, 203 m, 21 Nov. 2007, dung pitfall, Cesar Moreno leg. (CEMT).

Description

COLOURATION. Entire body with very dark tonalities. Head dark purple (in some specimens, frons with greenish reflections). Pronotum with strong greenish or bluish sheen at centre and purplish reflections on sides. Elytra usually dark blue or purple, occasionally with weak greenish reflections; striae with same colouration as the rest of tegument and not contrasting with it. Metaventrite black with very weak greenish or coppery shine. Meso- and metafemora orange-brown or yellowish, with base distinctly darker than at least apical two-thirds. Pygidium usually with predominant greenish shine and some coppery reflections, especially at base.

HEAD. Tegument little shiny, with strong alveolar microsculpture obliterating almost completely micropunctation, which is almost imperceptible or even absent throughout outer edge of head. Clypeus with two apical teeth obtuse and only slightly separated from one another; with single transverse row of setae covering base of both teeth. Genae with strong tooth immediately behind clypeal-genal juncture. Posterior edge of head completely unmargined.

THORAX. Pronotum with tegument slightly bright and lustrous, with very fine microsculpture (sometimes absent at centre), and dense, clearly marked central micropunctation. Posterior edge with fine transverse line at centre (usually extending only up to second elytral stria). Hypomeral cavity entirely glabrous or at most with very few short setae at centre; long setae, if present, restricted to anterior and posterior regions (Fig. 35B); external margin with weak tubercle. Metaventrite entirely glabrous; tegument with strong rivose microsculpture on anterior region and weaker microsculpture adjacent to internal margin of mesocoxae; at centre, alveolar microsculpture very fine and progressively more diffuse and undifferentiated towards posterior region; micropunctation very fine, but always evident.

Legs. Ventral surface of all femora and tibiae bright. Profemora with tegument with strong rivose microsculpture and without micropunctation. Protibiae narrow and with internal edge straight and simple, without expansion; at apical third, with three acute teeth, two apical ones of subequal length and larger than basal (Fig. 11I). Mesofemora margined anteriorly only at their basal half; unmargined portion of anterior edge with row of very short setae; posterior margin absent; tegument with effaced rivose microsculpture. Metafemora margined anteriorly, posterior margin absent; apical half of anterior edge covered by row of setae; tegument covered by diffuse rivose microsculpture and without any trace of coarse punctation at base (Fig. 13F). Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

Elytra. With at most nine very narrow visible striae: in general, first two to four striae well marked, very finely carinulate, and without basal widening; remaining striae progressively more effaced and interrupted; eighth and ninth only seen in specimens with very well-marked striae and, in these cases, always very subtle; all striae lack carinulae before reaching apex of elytra, where they are completely indistinct; humeral carina absent. Tegument of interstriae with diffuse shine and lustrous, with alveolar microsculpture throughout elytra surface; micropunctation, in general, clearly visible at 20x magnification.

Abdomen. Tegument of ventrites I–V with rivose microsculpture, in general, diffuse at centre; ventrite VI with rivose microsculpture very diffuse and micropunctation very subtle; both sexes without lateral foveae. Pygidium with shiny tegument and covered by alveolar microsculpture; micropunctation subtle, but always evident among microsculpture.

Aedeagus. Parameres at least half as long as phallobase and asymmetrical: external face of right paramere flat, external face of left paramere concave, strongly excavated. In lateral view, parameres with ventral keel (Fig. 18C).

Sexual dimorphism. **Males**: Protibial spur narrow and bifid at apex, with spiniform projections, the external projection much longer than the internal one (Fig. 15K). Ventrite VI with posterior edge strongly narrowed at centre; anterior edge covered only very slightly by weak medial flange of ventrite V. **Females**: Protibial spur simple, spiniform. Ventrite VI very broad at centre; anterior edge covered by weak medial flange of posterior edge of ventrite V.

Measurements

Males (N =10). **TL:** AV: 7.0 ± 0.70; MX: 8.0; MN: 6.1. **EW:** AV: 5.3 ± 0.42; MX: 5.7; MN: 4.3. **PrL:** AV: 2.3 ± 0.10; MX: 2.5; MN: 1.8. **PrW:** AV: 4.5 ± 0.36; MX: 4.9; MN: 3.7. **PgL:** AV: 1.4 ± 0.12; MX: 1.5; MN: 1.1. **PgW:** AV: 2.2 ± 0.17; MX: 2.3; MN: 1.8.

Females (N = 12). **TL:** AV: 7.2 ± 0.49; MX: 8.0; MN: 6.4. **EW:** AV: 5.2 ± 0.30; MX: 5.7; MN: 4.7. **PrL:** AV: 2.3 ± 0.19; MX: 2.6; MN: 2.0. **PrW:** AV: 4.5 ± 0.26; MX: 4.9; MN: 4.1. **PgL:** AV: 1.3 ± 0.10; MX: 1.4; MN: 1.1. **PgW:** AV: 2.2 ± 0.17; MX: 2.5; MN: 1.9.

Geographical distribution

Northwestern Amazonia, mainly in Sub-Andean areas in Colombia, Ecuador, and Peru.

Ecoregions

Napo Moist Forests, Cordillera Oriental Montane Forests, Peruvian Yungas.

Collecting sites (Fig. 34)

COLOMBIA. **Caquetá**: Parque Nacional Natural Sierra de Chiribiquete. **Amazonas**: Leticia (Parque Nacional Natural Amacayacu).

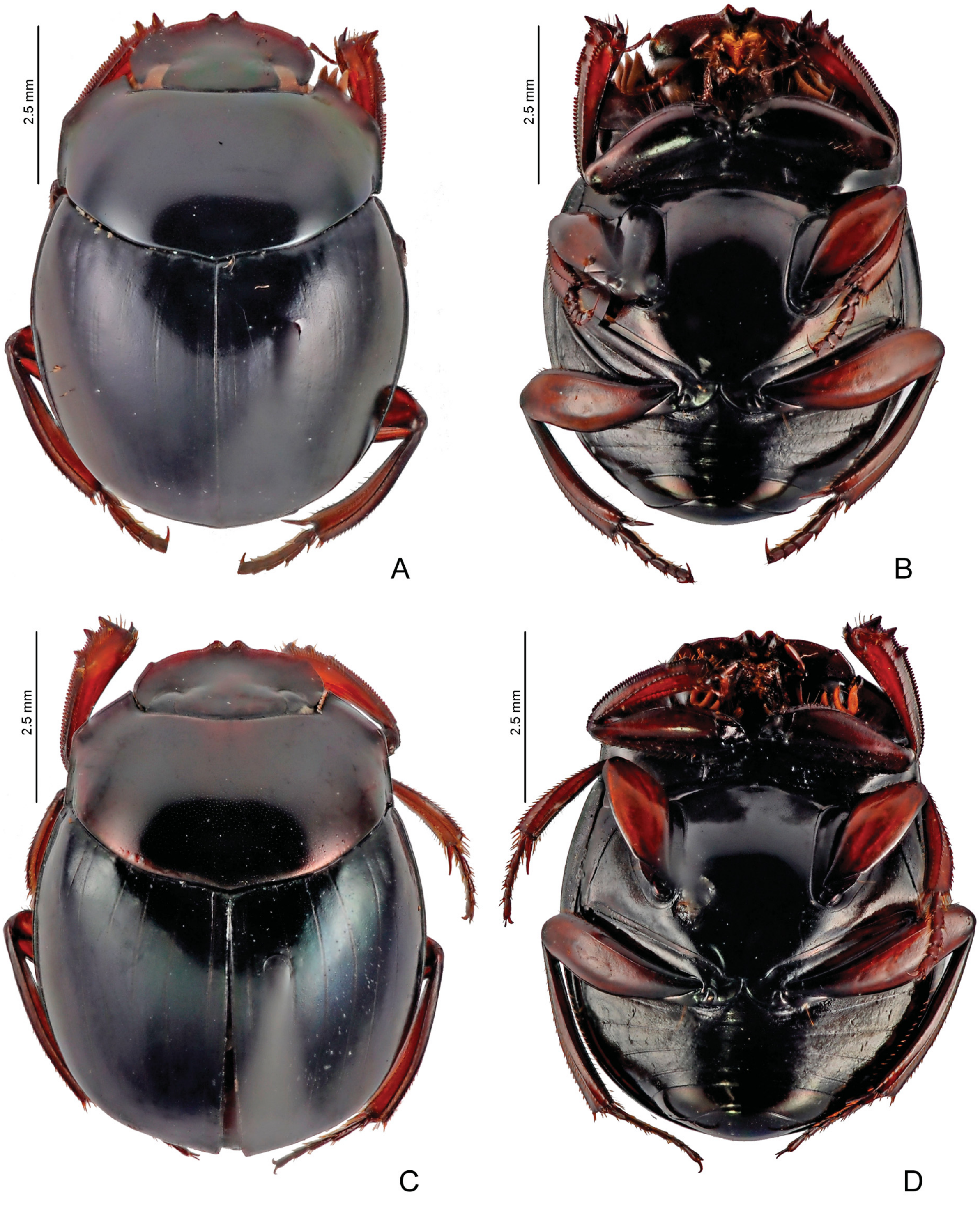

Fig. 38. A–B. *Sylvicanthon edmondsi* sp. nov. **A**. Dorsal view. **B**. Ventral view. **C–D**. *Sylvicanthon attenboroughi* sp. nov. **C**. Dorsal view. **D**. Ventral view.

ECUADOR. **Orellana**: Parque Nacional Yasuní, Tiputini Biodiversity Station. **Morona Santiago**: Untsuants.

PERU. **Loreto**: Campamento San Jacinto. **Junín**: Satipo.

Intraspecific variation and taxonomic discussion

Sylvicanthon edmondsi sp. nov. is an interesting case of a species easily recognizable at first glance by its darker colouration (Fig. 38A), its very subtle elytral striae, and its smaller size, but that does not have any exclusive morphological character, as the shape of the parameres or a specific micropunctation or microsculpture pattern, that could differentiate it from the other species in a more objective way. Along with *S. seag* sp. nov. and *S. attenboroughi* sp. nov., *S. edmondsi* sp. nov. is distinguished very easily from *S. bridarollii* by the shape of the parameres: in lateral view, a strong ventral keel is seen in *S. edmondsi* sp. nov. (Fig. 18C), while the parameres are simple in the latter species (Fig. 18A); besides, the parameres' external faces are asymmetrical in *S. edmondsi* sp. nov. (left paramere with external face excavated and right paramere flat), while they are symmetric (both faces flat) in *S. bridarollii*. Furthermore, *S. edmondsi* sp. nov. distinguishes itself from *S. bridarollii* by the tegument at the centre of the pronotum, which shows a fine, sometimes smoothed microsculpture, and a very dense, clearly marked micropunctation; by the absence of long setae at the centre of the hypomeral cavity (Fig. 35A–B); metaventrite with a very fine microsculpture at the centre; and the shape of the protibiae (Fig. 11I). From *S. attenboroughi* sp. nov. and *S. seag* sp. nov., *S. edmondsi* sp. nov. differs simultaneously by head with micropunctation almost imperceptible and hypomeral cavity not as strongly excavated as in the first two species; from *S. seag* sp. nov., in particular, *S. edmondsi* sp. nov. is different mostly because of the shape of the protibial spur (Fig. 15K), the shape of the anterior margin of the female ventrite VI, and the shape of the parameres (Fig. 18C). See Table 4 for a detailed comparison between *S. edmondsi* sp. nov. and the other species of the *bridarollii* subgroup.

The distribution of *S. edmondsi* sp. nov. is the most limited in the *bridarollii* subgroup: this species is present in the humid forests on the slopes of the Andes, in altitudes between 200 and 1110 m, from Colombia in the north to Peru in the south (Fig. 34). We have not seen any geographical variation among the studied populations.

Comments

It was possible to verify that the morphotype named "*Sylvicanthon* sp. 1" by Celi *et al.* (2004) is, in fact, *S. edmondsi* sp. nov. because we examined some of the specimens collected by them (which are now housed at the CMNC) and found the following results: six specimens of *S. edmondsi* sp. nov. from site ("*Sítio*") 3 (700 m); three specimens of *S. bridarollii* from site 1 (700 m), one from site 3 (700 m), four from site 5 (600 m) and seven from site 6 (600 m); and a male *S. genieri* sp. nov. from site 4 (1100 m) and three others from site 7 (900 m). Table 3 of Celi *et al.* (2004) shows that what they called *S. bridarollii* was collected between 500 and 900 m, "*Sylvicanthon* sp. 1", between 600 and 1110, and "*Sylvicanthon* sp. 2", between 600 and 1300 m. Putting all these data together, we conclude that the specimens of *S. bridarollii* were correctly identified by Celi *et al.* (2004), while morphotypes "*Sylvicanthon* sp. 1" and "*Sylvicanthon* sp. 2" refer, respectively, to *S. edmondsi* sp. nov. and *S. genieri* sp. nov.

Natural history

Label information tell us that adults of *S. edmondsi* sp. nov. are active at least between June and January (during that period, no records only from October and December). Specimens were collected mostly in pitfall traps baited with human faeces, but a male from the Tiputini Biodiversity Station (Morona Santiago, Ecuador) was attracted to carrion. Another male was collected at the Parque Nacional Yasuní (Orellana, Ecuador) by the canopy fogging method, but there are no data as to the height of the trees. As for the altitudinal amplitude, studied specimens were collected between 200 and 700 m; in Morona

Santiago, Celi *et al.* (2004) collected 116 specimens between 600 and 1110 (cited as "*Sylvicanthon* sp. 1"; see the discussion of *S. bridarollii* for details on the sympatry between that species and *S. edmondsi* sp. nov.).

Sylvicanthon attenboroughi sp. nov.

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Figs 11H, 15L, 18D, 20, 34, 35B, 38C–D

Sylvicanthon cf. sp. nov. – Larsen 2004: 261.
Sylvicanthon sp. 1 – Silva *et al.* 2014: 348.
Sylvicanthon sp. – Pacheco *et al.* 2016: 143, 147, fig. P.

Etymology

A tribute to the great British naturalist and broadcaster Sir David Attenborough. In recognition of his profoundly influential work on the public understanding of natural history and evolutionary biology, which, for more than six decades, has been inspiring young people of successive generations (including the first author) to pursue a career as a biologist and the general public to know and preserve the beautiful world in which we live. We paraphrase him: "I did so because I know of no pleasure deeper than that which comes from contemplating the natural world and trying to understand it" (Attenborough 2002). The specific name is a noun in the genitive case.

Material examined

Holotype

BRAZIL: ♂, Mato Grosso, Cláudia, Fazenda Iracema, 11º37′44″ S, 55º05′54″ W, ("BRASIL: Mato Grosso. Cláudia. / Faz. Iracema. 11º37′44″ S; 55º0 / 5′54″ W. Hum. dung. 20-II-2011. / M. F.Souza."), genital capsule extracted and glued to a triangular card (CEMT).

Paratypes (63 ♂♂, 67 ♀♀)

BRAZIL: **Acre**: ♀, Manoel Urbano, Parque Estadual Chandless, 09º22′26″ S, 69º55′20″ W, 24 Jun. 2013, T.F. Brito leg. (CEMT); 2 ♂♂ (1 dissected), Mâncio Lima, 07º28.584′ S, 72º54.110″ W, 5 Dec. 2012, H.M.B. Luiz & N.S.G.F. Adem leg. (CEMT); 1 ♀, Senador Guiomard ["Rio Branco"], Fazenda Experimental Catuaba ["Catuaba"], 9 Apr. 1996, A. Bonaldo leg. (MCNZ); 1 ♂, 4 ♀♀, Senador Guiomard ["Rio Branco"], Fazenda Experimental Catuaba, Feb. 1997, F.Z. Vaz-de-Mello leg. (CEMT). – **Amazonas**: 1 ♂, Benjamin Constant, Sep. 1962, Seabra leg. (CMNC); 1 ♂, Borba, BR-319, km 220, 04º22′55″ S, 60º57′19″ W, 29 Nov. 2015, pitfall with human faeces, D. Pires leg. (CEMT); ♀, Borba, BR-319, km 220, 04º24′06″ S, 60º55′22″ W, 30 Nov. 2015, pitfall with human faeces, D. Pires leg. (INPA); 1 ♂ (dissected), Careiro, BR-319, KM 34, 03º21′46″ S, 59º51′10″ W, 9 Dec. 2015, pitfall with human faeces, D. Pires leg. (INPA); 1 ♂ (dissected), Manaquiri, BR-319, km 100, 03º40′34″ S, 60º17′46″ W, 6 Dec. 2015, pitfall with human faeces, D. Pires leg. (INPA). – **Mato Grosso**: 8 ♀♀, Alta Floresta, 09º56′52″ S, 56º03′02″ W, May 2008, pitfall with human faeces, E. Berenguer leg. (CEMT); 3 ♂♂, 5 ♀♀, Alta Floresta, 09º53′40″ S, 56º16′35″ W, Jun. 2008, pitfall with human faeces, E. Berenguer leg. (CEMT); 1 ♀, Aripuanã, 10º03′10″ S, 59º29′42″ W, 320 m, 26 Jan. 2012, H.A.B. Faria leg. (CEMT); 1 ♀, Cláudia, Fazenda Iracema, 11º37′44″ S, 55º05′54″ W, 20 Feb. 2011, human faeces, M.F. Souza leg. (CEMT); 2 ♀♀, Novo Mundo, Parque Estadual do Cristalino, 09º27′53″ S, 55º49′30″ W, May 2013, pitfall, V. Magalhães leg. (CEMT); 1 ♀,Querência, Fazenda São Luiz, 12º39.85′ S, 52º22.18′ W, 50 m, Feb. 2009, flight interception trap, R. Andrade leg. (CEMT). – **Pará**: 1 ♂ (dissected), 1 ♀, Itaituba, Uruá, 65 km SW of Itaituba on BR230 ["BR320"], 12–15 Oct. 1977, B.C. Ratcliffe leg. (CMNC); 1 ♀, Santarém, Reserva Extrativista Tapajós-Arapiuns, 03º03′ S, 55º30′ W, 22 Dec. 2008, flight interceptation trap (CEMT); 1 ♂ (dissected), 1 ♀, Santarém, Reserva Extrativista

Tapajós-Arapiuns, 02º36′662″ S, 55º36′513″ W, 7 Jan. 2009, pitfall with human faeces, R. Andrade leg. (CEMT). – **Rondônia**: 1 ♂, Itapuã do Oeste, Floresta Nacional [“FloNa”] do Jamari, 09º05′21″ S, 63º09′48″ W, 20 Feb. 2013, *Mazama gouazoubira* dung, J.F. Cerveira leg. (CEMT); 1 ♂, 1 ♀, Itapuã do Oeste, Floresta Nacional [“FloNa”] do Jamari, 09º05′20″ S, 63º09′47″ W, 24 Feb. 2013, *Mazama Nana* dung, J.F. Cerveira leg. (CEMT); 2 ♂♂, 2 ♀♀, Itapuã do Oeste, Floresta Nacional [“FloNa”] do Jamari, 09º05′19″ S, 63º09′42″ W, 26 Feb. 2013, *Mazama Nana* dung, J.F. Cerveira leg. (CEMT); 21 ♂♂, 6 ♀♀, Guajará-Mirim, 10º44′53.56″ S, 65º17′31.1″ W, 14–16 Feb. 2010, pitfall with human faeces, Fabricio Coletti leg. (CEMT); 1 ♂, Guajará-Mirim, Fazenda Agropecuária A.J.B., 10º37′47.59″ S, 64º59′52.58″ W, 180 m, 15 Jan. 2010, human faeces, F. Coletti leg. (CEMT); 1 ♀, Guajará-Mirim, Fazenda Benezi, 10º44′53.56″ S, 65º17′31.10″ W, 170 m, 16 Feb. 2010, human faeces, F. Coletti leg. (CEMT); 1 ♂, Ji-Paraná (“V. Rondonia (378 km S de P. Velho)”), 25 Jan.–9 Feb. 1961, Pereira and Machado leg. (MZSP); 1 ♂, Pimenta Bueno, 11º43′04.43″ S, 61º28′21.45″ W, 249 m, 9–11 Dec. 2015, pitfall with human faeces, D.C. Castro leg. (CEMT); 1 ♂, Porto Velho, Bom Jesus, Rio das Garças, 08º49′48″ S, 63º46′45″ W, 20 Apr. 2017, flight interception trap, D.C. Santos and K.K.G. Silva leg. (CEMT); 1 ♂, Porto Velho, Bom Jesus, Rio das Garças, 08º49′48″ S, 63º46′45″ W, 27 Jul. 2017, flight interception trap, D.C. Santos and K.K.G. Silva leg. (CEMT); 1 ♂, Porto Velho, Bom Jesus, Rio das Garças, 08º49′47″ S, 63º46′51″ W, 29 Nov. 2017, flight interception trap, D.C. Santos and K.K.G. Silva leg. (CEMT); 1 ♂ (dissected), Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 15 Aug. 2012, pitfall with human faeces, M.A.P.A. Silveira leg. (CEMT); 1 ♂, 1 ♀, Porto Velho, ESEC Cuniã, 08º04′11.82″ S, 63º28′34.64″ W, 83 m, 10–12 Nov. 2013, pitfall with human faeces, M.A.P.A. Silveira leg. (CEMT); 1 ♂, 4 ♀♀, Porto Velho, Nova Mutum-Paraná, 09º26′24″ S, 60º13′19″ W, 27–28 Feb. 2010, human faeces, L.R. Silva and R.L.R. Silva leg. (CEMT); 1 ♂, Porto Velho, Nova Mutum-Paraná [“Mutum”], 09º35′46″ S, 65º02′27″ W, Jan. 2012, R.V. Nunes leg. (CEMT); 1 ♀, Porto Velho, Nova Mutum-Paraná [“Mutum”], 09º35′46″ S, 65º02′27″ W, 250 m, Sep. 2012, pitfall with human faeces, R.V. Nunes leg. (CEMT); 1 ♀, Vilhena, Nov. 1986, O. Roppa and P. Magno leg. (CEMT); 7 ♂♂ (1 dissected), 7 ♀♀, Same collection data as for preceding (MNRJ); 1 ♂, 2 ♀♀, Same collection data as for preceding (BMNH).

PERU: **Cuzco**: 1 ♀, La Convención, Echarate, Comunidad Kitaparay, 12º12′47.24″ S, 72º49′16.12″ W, 479 m, 13 Nov. 2009, C. Espinoza and E. Rázuri leg. (MUSM). – **Junín**: 1 ♂, Satipo, Mashira, Río Tambo, 11º25′20.25″ S, 73º27′16.14″ W, 672 m, 2 Feb. 2010, J. Grados leg. (MUSM). – **Madre De Díos**: 1 ♂, Manu, Huepetuhe (“Huaypetue”), 12º59′27.07″ S, 70º32′06.74″ W, 15–17 Nov. 2010, J. Costa and M. Vilchez leg. (MUSM); 2 ♂♂ (1 dissected), 1 ♀, Manu, Manu, Salvación (“near Salvación”), 13º50′37″ S, 71º19′57″ W, 650 m, Nov. 1999, pitfall with human faeces, T. Larsen leg. (CMNC); 1 ♂, Manu, Pakitza Biological Station, 28 Sep. 1987, B. Trocha leg. (MUSM); 2 ♀♀, Manu, Pantiacolla Lodge, 8 km NW of El Mirador Trail, Alto Madre de Dios River, 12º38′30″ S, 71º16′41″ W, 800 m, 23–26 Oct. 2000, flight interception trap, R. Brooks leg. (CMNC); 1 ♂ (dissected), 1 ♀, Manu, Parque Nacional del Manu (“Manu National Park”), 15–30 Aug. 1986, A. Forsyth leg. (CMNC); 1 ♀, Manu, Parque Nacional del Manu, Estación Biológica Cocha Cashu, 11º53′45″ S, 71º24′24″ W, 350 m, 17–19 Oct. 2000, flight interception trap, R. Brooks leg. (CMNC); 1 ♀, Manu, Reserva Comunal Amarakaeri, 12º59′51.87″ S, 70º50′26.05″ W, 864 m, 2–4 Nov. 2010, J. Costa and M. Vilchez leg. (MUSM); 2 ♀♀, Manu, Reserva Comunal Amarakaeri, 12º59′51.87″ S, 70º50′26.05″ W, 864 m, 10–14 Nov. 2010, J. Costa and M. Vilchez leg. (MUSM); 1 ♂ (dissected), Río Amiguillos, 12º22′25.4″ S, 70º22′13.2″ W, 260 m, May 2000, human faeces, T. Larsen leg. (MUSM); 1 ♂, 2 ♀♀, Tambopata, Puerto Madonado, Sudadero, 12º21′19″ S, 69º01′48″ W, 221 m, 26–27 Mar. 2009, L. Figueroa leg. (MUSM).

Description

Colouration. Entire body with very dark tonalities. Head and pronotum dark purple. Elytra dark green or dark blue; when green, striae dark blue and slightly contrasting with the rest of tegument. Metaventrite black. Meso- and metafemora orangish-brown, reddish-brown, or dark brown, with base distinctly darker than at least apical two-thirds. Pygidium usually coppery; occasionally, with greenish reflections.

HEAD. Tegument little shiny, with strong alveolar microsculpture; micropunctation evident on posterior region of clypeus and especially on frons. Clypeus with two apical teeth obtuse and only slightly separated; with single transverse row of short setae covering base of both teeth. Genae with strong tooth immediately behind clypeal-genal juncture. Posterior edge of head completely unmargined.

THORAX. Pronotum with slightly shiny and lustrous tegument, with very fine alveolar microsculpture (sometimes effaced at centre), and with dense, clearly marked micropunctation at centre, progressively weaker towards the sides. Posterior edge with fine transverse line at centre (usually extending only up to second elytral stria; sometimes effaced and almost indistinct). Hypomeral cavity entirely glabrous or at most with very few short setae at centre; long setae, if present, restricted to posterior region; external margin with weak tubercle. Metaventrite entirely glabrous; tegument with strong rivose microsculpture on anterior region and weaker adjacent to internal margin of mesocoxae; at centre, alveolar microsculpture very fine and progressively more diffuse and undifferentiated towards posterior region; micropunctation very fine, but usually distinct.

LEGS. Ventral surface of all femora and tibiae shiny. Profemora with tegument with strong rivose microsculpture and without micropunctation. Protibiae narrow and with internal edge straight and simple, without expansion; at apical third, with three small acute teeth on external edge, two most apical ones of subequal length and larger than basal (Fig. 11H). Mesofemora margined anteriorly only at basal half; unmargined portion of anterior edge with row of very short setae; posterior margin absent; tegument with effaced rivose microsculpture. Metafemora margined only anteriorly, posterior margin absent; apical half of anterior edge covered by row of setae; tegument covered by effaced rivose microsculpture and, in a few specimens, with traces of coarse elongate punctation at base. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

ELYTRA. With at most nine very narrow visible striae: in general, first five or six striae well marked, very finely carinulate and slightly widened at base; remaining striae progressively more effaced; eighth and ninth striae seen only in specimens with very well-marked striae and, in these cases, always very subtle; all striae lack carinulae before reaching apex of elytra, where completely indistinct; humeral carina absent. Tegument of interstriae with diffuse shine; at centre, with alveolar microsculpture ranging from clearly marked, in most specimens, to diffuse; at apex, always with strong alveolar microsculpture; micropunctation in general clearly visible at 20 × magnification.

ABDOMEN. Tegument of ventrites I–V with strong rivose microsculpture at centre; ventrite VI with very diffuse rivose microsculpture and very subtle micropunctation; both sexes without lateral foveae. Pygidium with bright tegument covered by alveolar microsculpture; micropunctation subtle, but always evident among microsculpture.

AEDEAGUS. Parameres at least half as long as phallobase and asymmetrical: external face of right paramere flat, external face of left paramere concave, strongly excavated. In lateral view, parameres with strong ventral keel (Fig. 18D).

SEXUAL DIMORPHISM. **Males**: Protibial spur narrow and bifid at apex, with spiniform projections, external projection longer than internal one (Fig. 15M). Ventrite VI with posterior margin strongly narrowed at centre; anterior edge covered very slightly by weak medial flange of ventrite V. **Females**: Protibial spur simple, spiniform. Ventrite VI very broad at centre; anterior edge slightly covered by medial flange of posterior edge of ventrite V.

Measurements

Males (N = 13). **TL:** AV: 8.5 ± 0.54; MX: 9.6; MN: 7.5. **EW:** AV: 6.1 ± 0.35; MX: 6.6; MN: 5.5. **PrL:** ME: 2.5 ± 0.14; MX: 2.9; MN: 2.3. **PrW:** AV: 5.1 ± 0.29; MX: 5.5; MN: 4.6. **PgL:** AV: 1.6 ± 0.11; MX: 1.7; MN: 1.3. **PgW:** AV: 2.6 ± 0.18; MX: 2.9; MN: 2.3.

Females (N = 13). **TL:** AV: 8.4 ± 0.55; MX: 9.4; MN: 7.2. **EW:** AV: 6.1 ± 0.29; MX: 6.8; MN: 4.9. **PrL:** AV: 2.5 ± 0.14; MX: 2.8; MN: 2.4. **PrW:** AV: 5.2 ± 0.32; MX: 5.8; MN: 4.6. **PgL:** AV: 1.7 ± 0.15; MX: 1.9; MN: 1.4. **PgW:** AV: 2.6 ± 0.20; MX: 2.9; MN: 2.3.

Geographical distribution

Southern Amazonia in Brazil and Peru.

Ecoregions

Southwest Amazon Moist Forests, Peruvian Yungas, Madeira-Tapajós Moist Forests, Mato Grosso Tropical Dry Forests.

Collecting sites (Fig. 34)

BRAZIL. **Acre**: Mâncio Lima, Manoel Urbano (Parque Estadual Chandless), Rio Branco. **Amazonas**: Benjamin Constant, Borba, Careiro, Manaquiri. **Pará**: Itaituba (Uruá), Santarém (Reserva Extrativista Tapajós-Arapiuns). **Rondônia**: Guajará-Mirim, Itapuã do Oeste (Floresta Nacional do Jamari), Ji-Paraná, Pimenta Bueno, Porto Velho, Vilhena. **Mato Grosso**: Alta Floresta, Aripuanã, Cláudia, Novo Mundo (Parque Estadual do Cristalino), Querência.

PERU. **Junín**: Satipo (Mashira). **Cuzco**: La Convención (Echarate). **Madre de Díos**: Manu (Huepetuhe; Manu: Salvación; Pakitza Biological Station; Pantiacolla Lodge; Parque Nacional del Manu; Reserva Comunal Amarakaeri), Tambopata (Puerto Madonado: Sudadero).

Intraspecific variation and taxonomic discussion

The distribution of *S. attenboroughi* sp. nov. is very interesting because, based on the data we have on hand, it seems to be clearly delimited by two major rivers in the Amazon Basin: the Amazon, which constrains dispersal towards forests farther north, and the Tapajós, the eastern limit of the distribution of *S. attenboroughi* sp. nov. in the centre of the Amazon Basin (i.e., excluding the populations in southern Amazonia in the state of Mato Grosso). Beyond those rivers (i.e., to the left banks of the Amazon and to the right banks of the Tapajós) inhabits *S. seag* sp. nov., a species very similar to *S. attenboroughi* sp. nov. and its possible sister species. Southern populations of *S. seag* sp. nov. (i.e., those closer to the range of *S. attenboroughi* sp. nov.) show colouration and pygidial tegument very similar to (if not totally indistinguishable of) those of *S. attenboroughi* sp. nov., but both species are easily separated from one another by the shape of the parameres, which are much simpler in *S. attenboroughi* sp. nov. (Fig. 18D) than the very complex shape seen in *S. seag* sp. nov. (Fig. 19A). Other differences that do not vary geographically between these two species are the shape of the male protibial spur and the shape of the anterior margin of female ventrite VI (Table 4; see also section on *S. seag* sp. nov. for a detailed discussion on the geographical variation seen in that species).

Sylvicanthon bridarollii is the only representative of the *bridarollii* subgroup to be found in sympatry with *S. attenboroughi* sp. nov. Both species are differentiated by the tegument of the head, pronotum, metaventrite and pygidium, the presence or absence of setae on the hypomeral cavity (Fig. 35), the shape of protibiae (Fig. 11F–H), the presence or absence of a coarse punctation at the base of the metafemora (Fig. 13F–H) and, finally, by the shape of the parameres (Fig. 18A, D) (Table 4). From *S. edmondsi* sp. nov., the fourth species of the *bridarollii* subgroup, *S. attenboroughi* sp. nov. is different in colouration (Fig. 38), size, head tegument and hypomeral cavity; the parameres, which are usually very distinctive among the species of *Sylvicanthon*, do not show any remarkable differences between *S. attenboroughi* sp. nov. and *S. edmondsi* sp. nov. (Fig. 18C–D) (Table 4).

Two intraspecifically-variable characters seen in *S. attenboroughi* sp. nov. call attention: the shape of the protibiae and the presence of coarse punctation at the base of the metafemora. In the great majority of the individuals of this species, the internal margin of the protibiae is straight (Fig. 11H) and the metafemora do not show any trace of coarse punctation at their base (Fig. 13F), in the same way as in *S. seag* sp. nov. and *S. edmondsi* sp. nov. However, some very few specimens from Rondônia (Brazil) have the internal margin of the protibiae with a weak indication of expansion (similar to specimens of *S. bridarollii* from Ecuador and Colombia) and weak traces of a coarse punctation at the base of the metafemora (in the same way as in the populations of *S. bridarollii* from northern Peru). Future phylogenetic analyses will unveil whether those features are homologous to the states seen in *S. bridarollii* or whether they are homoplastics; if they are homologous, it will be interesting to know whether they constitute a synapomorphy between these two species or a symplesiomorphy in the subgroup that was completely lost independently in the majority of the *S. attenboroughi* sp. nov., the northern populations of *S. bridarollii* and by *S. edmondsi* sp. nov. and *S. seag* sp. nov..

Natural history

Very little information on the biology of *S. attenboroughi* sp. nov. is available on specimen labels. Adult activity seems to be restricted to the spring and summer months, with records from all months between September and March. Specimens were collected using pitfall traps baited with human faeces and flight interception traps. In relation to the altitudinal amplitude, *S. attenboroughi* sp. nov. seems to occur between 170 and 864 m a.s.l.

The securus *subgroup*

Sylvicanthon securus (Schmidt, 1920) comb. nov.
Figs 6F, 11C, 15O, 19A, 20, 39, 40A, 41

Canthon securus Schmidt, 1920: 131, 133.

Canthon securus – Schmidt 1922: 64, 80. — Balthasar 1939: 188. — Halffter & Martínez 1977: 63. — Krajcik 2012: 64.
Canthon securum – Blackwelder 1944: 201.
Glaphyrocanthon (*Glaphyrocanthon*) *securus* – Pereira & Martínez 1956: 126, 128. — Martínez *et al.* 1964: 5–6, 9, 14, 20. — Vulcano & Pereira 1964: 664.
Sylvicanthon cf. *securus* – Larsen 2012: “92”, 99.

Etymology

Possibly from the Latin ‘*securis*’, meaning ‘axe’ or ‘hatchet’, in reference to the shape of protibiae, which have a strong internal expansion. The Latin word ‘*securus*’, ‘free of doubts’, does not seem to be the origin of this name, unless Schmidt (1920) has referred to the fact that this species is extremely different from the others and, therefore, he had no doubts about its validity.

Material examined

Lectotype (here designated)
SURINAME: ♂, (“Surinam”, “S*ecurus*”, “S*ecurus* / *A. Schm.*”, “*Glaphyrocanthon* / *securus* / *(Schm.)* / P. Pereira det. *60*”, “3205 / E92 +”, “S*ecurus* / Schmidt”, “34 / 56”, “NHRS-JLKB / 000021093” “LECTOTYPE ♂ / *Canthon* / *securus* / *A. Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*”) (NHRS) (Fig. 11H).

Additional material (22 ♂♂, 27 ♀♀, 1 unsexed specimen)
BRAZIL: 1 ♂, no further data (BMNH). – **Amazonas**: 2 ♀♀, Manaus, ZN 03, Km 41, 1996–1997 [*Alouatta seniculus* (?) dung], Ellen Andressen leg. (CEMT); 1 ♂, same collecting data as for preceding (INPA). – **Pará**: 1 ♂, Almeirim, Monte Dourado, 01º01’ S, 52º44’ W, 150 m, Jul. 2004, dung pitfall, T.A. Gardner leg. (CEMT).

FRENCH GUIANA: 4 ♂♂, 1 ♀, SEAG leg. (CEMT); 1 ♂, Cayenne, Kourou, Rte. Cayenne-Sinnamary, RN1, PK84, Jan. 2013, flight interception trap, SEAG leg. (CEMT); 1 ♀, Cayenne, Montsinéry-Tonnegrande, Montagne des Chevaux, 04º44’56″ N, 52º26’28″ W, 75 m, 30 Oct. 2011, SEAG leg. (CEMT); 1 ♀, Cayenne, Montsinéry-Tonnegrande, Montagne des Chevaux, 04º44’56″ N, 52º26’28″ W, 75 m, 27 Jan. 2013, SEAG leg. (CEMT); 1 ♂, Cayenne, Montsinéry-Tonnegrande, Montagne des Chevaux, 04º44’56″ N, 52º26’28″ W, 75 m, 21 Dec. 2013, SEAG leg. (CEMT); 2 ♂♂, Cayenne, Régina, [Réserve naturelle nationale des] Nouragues, Nov. 1996, F. Feer leg. (CEMT); 1 unsexed specimen, Cayenne, Régina, [Réserve naturelle nationale des] Nouragues, Oct. 2001, Kelly leg. (BMNH); 2 ♂♂, 3 ♀♀, Cayenne, Régina, [Réserve naturelle nationale des] Nouragues, Inselberg, 04º05′ N, 52º41′ W, 411 m, 4 Apr. 2010, SEAG leg. (CEMT); 1 ♀, Cayenne, Régina, [Réserve naturelle nationale des] Nouragues, Inselberg, 04º05′ N, 52º41′ W, 411 m, 13 Oct. 2012, SEAG leg. (CEMT); 1 ♂, Cayenne, Régina, [Réserve naturelle nationale des] Nouragues, Inselberg, 04º05′ N, 52º41′ W, 411 m, 14 Jun. 2013, SEAG leg. (CEMT); 1 ♂ (dissected), Cayenne, Régina, [Réserve naturelle nationale des] Nouragues, Inselberg, 04º05′ N, 52º41′ W, 411 m, 19 Sep. 2013, SEAG leg. (CEMT); 2 ♀♀, Cayenne, Roura, Montagne de Kaw, Nov. 1996, F. Feer leg. (CEMT); 1 ♀, Cayenne, Roura, Montagne de Kaw, 3 Feb. 2007, F. Feer leg. (CEMT); 1 ♀, Cayenne, Roura, Montagne de Kaw, 17 Feb. 2009, F. Feer leg. (CEMT); 1 ♀, Cayenne, Roura, Montagne de Kaw, 18 Feb. 2009, F. Feer leg. (CEMT); 2 ♀♀, Saint-Laurent- du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 11 Jan. 2011, SEAG leg. (CEMT); 1 ♂, 2 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 27 May 2011, SEAG leg. (CEMT); 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 15 Jun. 2011, SEAG leg. (CEMT); 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 23 Jun. 2011, SEAG leg. (CEMT); 1 ♂, 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 28 Jul. 2011, SEAG leg. (CEMT); 3 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 03º37′22″ N, 53º12′57″ W, 326 m, 9 Sep. 2011, SEAG leg. (CEMT); 1 ♂, 1 ♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, 15 Sep. 2011, SEAG leg. (CEMT); 2 ♂♂, 2 ♀♀, Saint-Laurent-du-Maroni, Maripasoula, Saül, Bélvédère de Saül, Grand Boeuf Mort, 10 Oct. 2007, SEAG leg. (CEMT).

No data: 1 ♂ (ISNB – “Coll. J. Thomson”); 1 ♂ (MNHN).

Description

Colouration. Head bicolour, with wide purplish or coppery area covering in general outer edge (apex of clypeus and genae) and posterior region (frons, posterior portion of clypeus, and, occasionally, part of genae) bright green. Pronotum entirely green, never with purplish or coppery spot. Elytra green, with striae contrasting or not. Metaventrite with greenish shine at centre and purplish or coppery at rest of tegument. Meso- and metafemora yellowish or orangish; profemur slightly darker than others. Pygidium bright green.

Head. Tegument with strong alveolar microsculpture throughout dorsal surface; micropunctation strongly marked on frons and progressively more effaced towards outer edge of head (Fig. 6F). Clypeus triangular, with very acute pair of apical teeth; each tooth individually margined at base. Genae with clear denticle immediately behind clypeal-genal juncture (denticle sometimes reduced by wear). Posterior edge of head usually with margin at centre (margin absent adjacent to eyes); in some specimens, margin very fine and almost imperceptible, or even absent.

Thorax. Pronotum with shiny tegument and dense, well-marked micropunctation at centre; towards sides, micropunctation progressively less dense and well marked, and sometimes absent; tegument among micropunctation smooth, without microsculpture; alveolar microsculpture restricted to very narrow strip of tegument on anterior edge of pronotum and anterolateral angles. Posterior edge with very fine transverse line at centre (usually extending little beyond the second elytral stria). Hypomeral cavity covered by long yellowish setae; external margin simple, without any trace of tubercle (occasionally, with only very weak callosity marking location of tubercle). Metaventrite glabrous at centre and with a group of very few yellowish setae on sides near external extremity of metacoxae; anterior region of metaventrite with tegument with strong rivose microsculpture; centre and posterior region with strong and dense micropunctation among smooth tegument, without any trace of microsculpture.

Legs. Profemora with tegument with diffuse rivose microsculpture, but hardly visible. Protibiae very narrow at basal half and with strong angulose expansion at apical half of internal edge, making apical half twice as wide as basal half; at apical fourth), with three small acute teeth on external edge – the most basal tooth distinctly smaller than others (Fig. 11C). Mesofemora margined anteriorly only at basal half; unmargined portion of anterior edge with row of very short setae; posterior margin absent; tegument smooth and lustrous, except for narrow strip on anterior edge with effaced rivose microsculpture. Metafemora margined only anteriorly, posterior margin absent; apical third of anterior edge covered by row of setae; tegument almost entirely smooth and lustrous, with weak traces of rivose microsculpture only at some regions; without coarse elongate punctation at base. Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

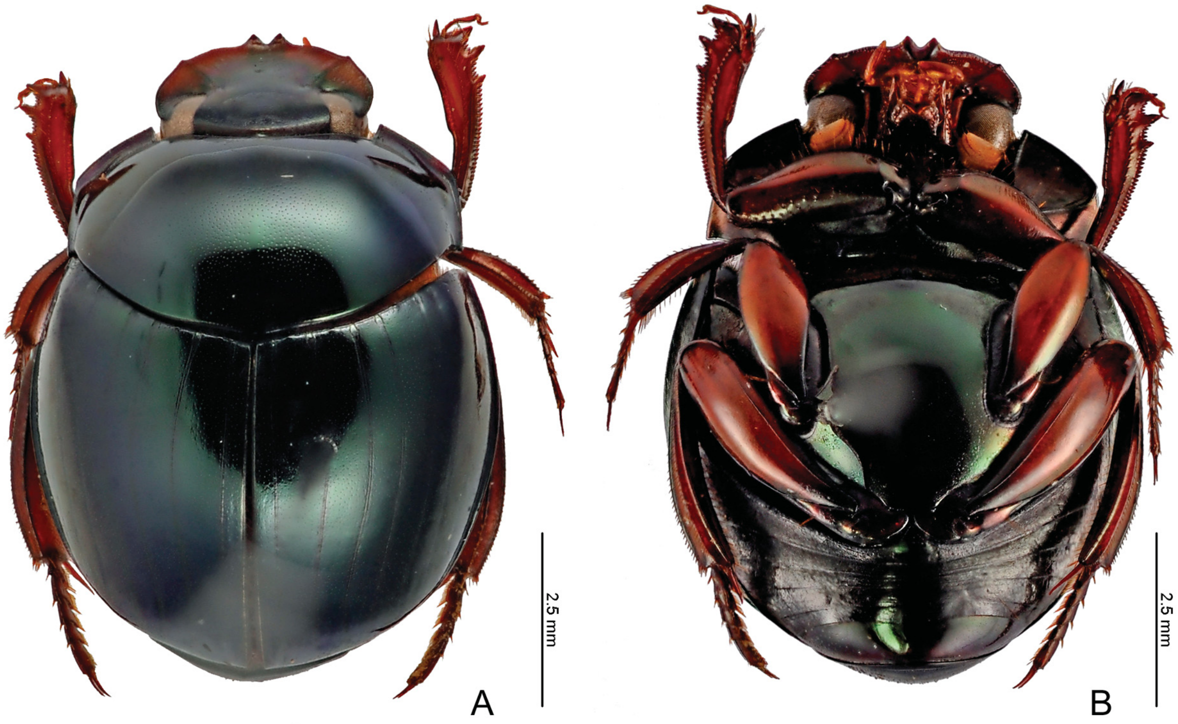

Fig. 39. *Sylvicanthon securus* (Schmidt, 1920) comb. nov. **A**. Dorsal view. **B**. Ventral view.

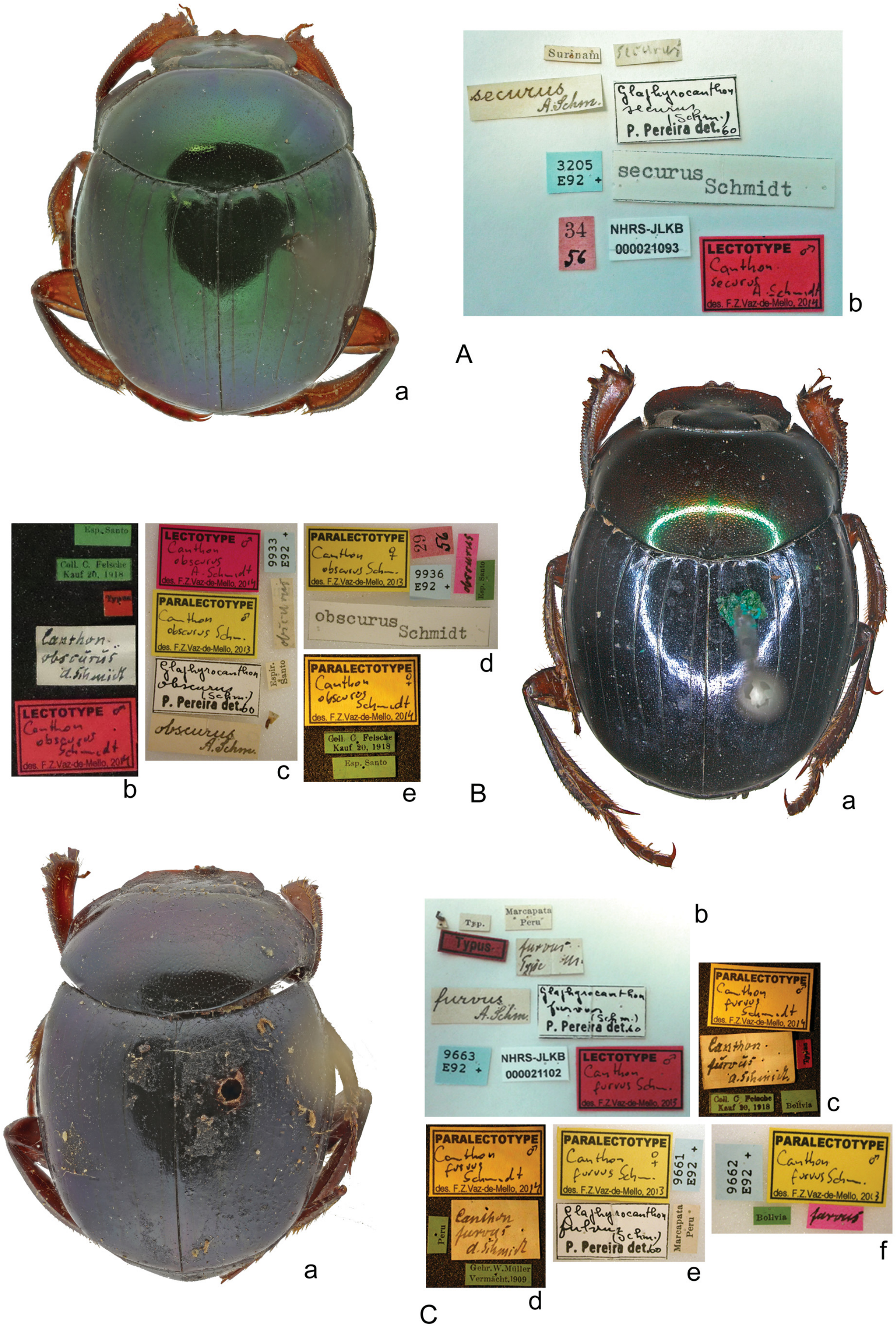

Fig. 40. Type material of three species of *Sylvicanthon* described by Schmidt (1920). **A**. *S. secures* (Schmidt, 1920) comb. nov. **a**. Lectotype. **b**. Lectotype's labels. **B**. *S. obscurus* (Schmidt, 1920). **a**. Lectotype. **b**. Lectotype's labels. **c**. Paralectotype 1. **d**. Paralectotype 3. **e**. Paralectotype 9. **C**. *S. furvus* (Schmidt, 1920). **a**. Lectotype. **b**. Lectotype's labels. **c**. Paralectotype 4. **d**. Paralectotype 6. **e**. Paralectotype 3. **f**. Paralectotype 1.

Elytra. With seven very narrow visible striae: first five striae well marked, finely carinulate, and distinctly widened at base; sixth and seventh striae progressively more effaced and interrupted; seventh stria occasionally vestigial or even completely absent; all striae lack carinulae before reaching apex of elytra. Interstriae with dense, well-marked micropunctation at centre among smooth tegument; without any trace of microsculpture.

Abdomen. Tegument of ventrites I–V with strong rivose microsculpture; ventrite VI bright, without microsculpture, and with sparse micropunctation at centre, and with very weak rivose microsculpture on sides. Both sexes without lateral foveae. Pygidium with dense, well-marked micropunctation among tegument mostly smooth, with rivose microsculpture restricted to narrow strip adjacent to basal margin.

Aedeagus. Parameres simple, very long (only slightly shorter than phallobase), without ventral keel or notch, and with no noticeable asymmetry: both parameres with flat external face (Fig. 19A).

Sexual dimorphism. **Males**: Protibial spur broad and bifid, with internal projection broad and much longer than external projection, which is short and spiniform (Fig. 15O). Ventrite VI strongly narrowed at centre by emargination on posterior edge; ventrite V with weak medial flange on posterior edge covering anterior edge of ventrite VI. **Females**: Protibial spur spiniform. Ventrite VI very broad at centre, without emargination on posterior edge; ventrite V as in males.

Measurements

Males (N = 11). **TL:** AV: 6.1 ± 0.14; MX: 6.9; MN: 6.5. **EW:** AV: 5.2 ± 0.28; MX: 5.9; MN: 4.8. **PrL:** AV: 2.3 ± 0.10; MX: 2.4; MN: 2.1. **PrW:** AV: 4.5 ± 0.22; MX: 4.9; MN: 4.1. **PgL:** AV: 1.0 ± 0.07; MX: 1.2; MN: 0.9. **PgW:** AV: 2.1 ± 0.10; MX: 2.3; MN: 2.

Females (N = 11). **TL:** AV: 6.8 ± 0.21; MX: 7.0; MN: 6.3. **EW:** AV: 5.0 ± 0.10; MX: 5.2; MN: 4.9. **PrL:** AV: 2.1 ± 0.07; MX: 2.3; MN: 2.1. **PrW:** AV: 4.2 ± 0.10; MX: 4.4; MN: 4.1. **PgL:** AV: 1.0 ± 0.08; MX: 1.1; MN: 0.9. **PgW:** AV: 2.1 ± 0.11; MX: 2.3; MN: 1.9.

Geographical distribution

Northern Amazonia in Suriname, French Guiana and Brazil.

Ecoregions

Guianan Moist Forests, Marajó Varzea, Uatuma-Trombetas Moist Forests, Japurá-Solimões-Negro Moist Forests

Collecting sites (Fig. 41)

SURINAME. **Sipaliwini**: *Coeroeni*.

FRENCH GUIANA. Cayenne (Kourou; Montsinéry-Tonnegrande: Montagne des Chevaux Régina: Réserve naturelle nationale des Nouragues; Roura: Montagne de Kaw), Saint-Laurent-du-Maroni (Maripasoula: Saül).

BRAZIL. **Amazonas**: Manaus. **Pará**: Almeirim (Monte Dourado).

Intraspecific variation and taxonomic discussion

It is interesting to note that *S. securus* is one of the rarest and, at the same time, one of the most easily recognizable species of *Sylvicanthon*, being the most isolated species in the genus in terms of morphology. Despite that, most of the studied specimens of *S. securus* were either unidentified in collections or mingled among specimens of *S. seag* sp. nov. In fact, throughout its distribution range –

i.e., in the Guiana Shield and the Amazon region north of the Amazon River – *S. securus* is sympatric with *S. seag* sp. nov., a species that in turn extends its distribution far beyond this area both northwestwards, reaching Venezuela and Trinidad, and eastwards, reaching the Amazon fragments of the Brazilian state of Maranhão (Fig. 41). Besides, at first glance, *S. securus* and *S. seag* sp. nov. may be confused by colouration which, in the Guianas, is almost always shiny green in both species (Figs 37C, 39A) and by the number of protibial teeth, three (Fig. 11C). Nonetheless, at a closer look, the differences between *S. securus* and *S. seag* sp. nov. become evident.

The easiest way to differentiate both species is by examining the protibiae: *S. seag* sp. nov. has their internal margin straight and simple (Fig. 11H–I), while *S. securus* has them strongly expanded, with the apical half of the protibiae almost twice as wide as the basal half (Fig. 11C). In fact, the expanded internal margin of the protibiae is a very common feature in *Sylvicanthon*, being present in all the four species of the *furvus* subgroup (*S. obscures* (Fig. 11D), *S. mayri* sp. nov., *S. monnei* sp. nov., and *S. furvus* (Fig. 11E)), in *S. bridarollii* (Fig. 11F–G; the other species of the *bridarollii* subgroup have a simple internal margin), and *S. enkerlini* (Fig. 11A), but it is much more pronounced in *S. securus* than in any other species of the genus (something already noted by Schmidt (1922) and Balthasar (1939)). Other groups of Deltochilini also show this feature, e.g., several species of *Glaphyrocanthon* and *Francmonrosia*.

Fig. 41. Distribution of *Sylvicanthon securus* (Schmidt, 1920) comb. nov. and the four species of the *furvus* subgroup.

The overall texture of the tegument is distinct between *S. seag* sp. nov. and *S. securus*: in the former species, the pronotum, metaventrite, elytra and pygidium are covered by a strong alveolar microsculpture which obliterates the micropunctation (which, consequently, is very weak). In *S. securus*, on the other hand, there is no trace of microsculpture on the pronotum, at the centre of metaventrite, on the elytra or at the centre of the pygidium (in these latter two cases, sometimes there is a very diffuse indication of microsculpture), and the micropunctation is strong and clearly visible. *Sylvicanthon securus* also differentiates from *S. seag* sp. nov. by the presence of a fine margin at the centre of the posterior edge of the head in the majority of the specimens, while all the examined individuals of the latter species have the posterior edge of the head without any trace of margination. Nonetheless, this characteristic is largely variable in *S. securus*: the fine margin may be clearly present and almost reaches the eyes, or it may be gradually shorter or even almost absent.

Other morphological structures distinguishing *S. securus* from *S. seag* sp. nov. are the shape of the edge of the clypeus, which is completely rounded in *S. seag* sp. nov. (Fig. 6E) and is slightly sinuous adjacently to the apical teeth in *S. securus* (Fig. 6F); the basal margin of the clypeal teeth, which is divided into two non-continuous parts (i.e., each tooth has its own basal margin) in *S. securus*, and is one-piece (i.e., a single margin covers the base of both teeth) in *S. seag* sp. nov.; and the shape of the male protibial spur, which has the internal branch much longer than the external one in *S. securus* (Fig. 15N), whereas the opposite condition is seen in *S. seag* sp. nov. (Fig. 15J). Clear differences also exist in the shape of the parameres: in *S. securu* comb. nov., they are simple, fine and laterally flat, without any ventral keel or notch (Fig. 19A). In turn, in *S. seag* sp. nov. the parameres are strongly asymmetrical (the external face of the right paramere flat and the external face of the left paramere excavated) and, in lateral view, there is a ventral keel strongly projected, giving a squarish appearance to the apical half of the parameres and it also has a notch posteriorly to that keel (Fig. 18B).

Differences are seen in the colouration of fully mature specimens (i.e., excluding teneral individuals): in the Guianas, *S. seag* sp. nov. has an overall dorsal colouration shiny green similar to that seen in *S. securus*, but it differs from this latter species in having the head and, occasionally, the pronotum covered by a purplish spot (Fig. 37C), while in *S. securus* the pronotum is always as green as the elytra, and head possesses a narrow purplish spot limited to the the apex of the clypeus (Fig. 39A). Ventrally, the differences are seen on the colouration of the metaventrite – which, although sometimes mostly copper-coloured, always shows some greenish reflections at the centre in *S. securus* (Fig. 39B), while it is always coppery without any greenish reflection in *S. seag* sp. nov. (Fig. 37D) – and of the profemora – which are light brown in *S. securus*, and much darker brown in *S. seag* sp. nov. Farther south, in Brazil, individuals of *S. seag* sp. nov. have a very distinct colouration, with bluish elytra and a purplish pronotum (Fig. 37A), in which they do not resemble in anything the bright green colouration of *S. securus*.

Comments

Schmidt (1920) did not cite the number of specimens he examined for the description of *S. securus*, but from his text, it is possible to conclude that he had only males at his disposal, since he described the male shape of the protibial spur, but did not cite how this structure was in females. The only specimen from the type series of *S. securus* found by us was a male deposited in the NHRS which is here designated as lectotype.

One of the specimens found at the BMNH bears a circular blue label handwritten "*54* / *60*", without any further indication. According to Max Barclay (personal communication to MC, 2015), this code refers to a large acquisition of several Brazilian dung beetle species made by the museum from the French entomologist Henri Jekel (1816–1891). This specimen also has another rectangular white label handwritten "*N…* / *serricornis* / *n…*", probably an apocryphal *nomen in litteris* that we are unware of having been applied to any other specimen or cited in any publication.

Natural history

Sylvicanthon securus is a rare species, inhabiting lowland forests in the northern Amazon region (with records from 75 up to 411 m of altitude), where it is sympatric with *S. seag* sp. nov. Most of the specimens of *S. securus* studied for this work originated from French Guiana and, of the two species of *Sylvicanthon* that occur there, *S. securus* was collected in an evident lower abundance: a total of 43 specimens of *S. securus* were caught in French Guiana, in comparison to 601 *S. seag* sp. nov., a number almost 15 times higher. Taking the series of specimens studied for this work into account, it was possible to see that, in individual collecting episodes, the ratio between the abundance of *S. seag* sp. nov. and *S. securus* varied from 3:1 up to 65:1. From Suriname, in turn, only the lectotype of *S. securus* is known, while 25 specimens of *S. seag* sp. nov. were caught in that country.

With such a discrepancy in the relative abundance between these two species, it is really remarkable that *S. securus* was described still in the early 20th century, while *S. seag* sp. nov. had to wait until now to have its condition as a distinct species recognized. However, an obvious question arises from these observations: what is the ecological factor, or conjunct of factors, responsible for the remarkable difference in abundance between *S. seag* sp. nov. and *S. securus*? Nonetheless, it would be fair to question whether this apparent rarity of *S. securus* is not a simple artefact generated by some unknown idiosyncratic life habit of the latter species; for example, some other food preference than primate dung (i.e., human faeces used to bait pitfalls). Be that as it may, only with more research on the biology of both *S. securus* and *S. seag* sp. nov. it will be possible to give a proper answer to these questions.

Judging from the specimen labels, we know that *S. securus* was collected in pitfall traps baited with human faeces and flight interception traps. Besides, the two females from Manaus (Amazonas, Brazil) were attracted to howler monkey dung; although their labels indicate that the primate was an *Alouatta seniculus* (Linnaeus, 1766), the correct identity of this species should be *A. macconnelli* Elliot, 1910, or, less probable, *A. nigerrima* Lönnberg, 1941, the only two species of the *A. seniculus* complex present in that area (Gregorin 2006). Regarding the species' annual phenology, adults of *S. securus* were collected throughout the year, including the months of January, February, May, June, July, September, and October.

The **furvus** *subgroup*

Sylvicanthon obscurus (Schmidt, 1920)

Figs 7B, 11D, 12B, 13B, 15M, 16C, 19B, 20, 40B, 41–42

Canthon obscurus Schmidt, 1920: 131–133.

Canthon obscurus – Schmidt 1922: 64, 78. — Balthasar 1939: 187–188. — Halffter & Martínez 1977: 63. — Krajcik 2012: 64.
Canthon obscurum – Blackwelder 1944: 200.
Glaphyrocanthon (*Glaphyrocanthon*) *obscurus* – Pereira & Martínez 1956: 126, 128. — Pereira & Martínez 1960: 45. — Martínez *et al.* 1964: 5, 8, 13. — Vulcano & Pereira 1964: 663.
Sylvicanthon obscurum: Vaz-de-Mello 2000: 195.
Sylvicanthon sp. – Costa *et al.* 2009: 90; 2013: 330–331. — Silva *et al.* 2010: 362. — Iannuzzi *et al.* 2016: 201.

Etymology

From the Latin word '*obscurus*', meaning 'dark'. Probable reference to the dark green or dark blue elytra.

Material examined

Lectotype (here designated)
BRAZIL: ♂, Espírito Santo, ("Esp. Santo", "Coll. C. Felsche / Kauf 20, 1918", "Typus", "*Canthon* / *obscurus* / *A. Schmidt*", "LECTOTYPE ♂ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*") (SMTD) (Fig. 40Ba–b).

Paralectotypes (7 ♂♂, 4 ♀♀)
BRAZIL: 1 ♂, ("LECTOTYPE ♂ / *Canthon / obscurus* / *A. Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "PARALECTOTYPE / ♂ / *Canthon* / *obscurus Schm.* / des. F. Z. Vaz-de-Mello, 20*13*", "*Glaphyrocanthon* / *obscurus* / *(Schm.)* / P. Pereira det. *60*", "*obscurus* / *A. Schm.*", "9933 / E92 +", "*obscurus*", "Espir. / Santo") (NHRS) (Fig. 40Bc); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *obscurus Schmidt* / des. F. Z. Vaz-de-Mello, 20*13*", "*obscurus*", "Espir. / Santo", "9935 / E92 +") (NHRS); 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *obscurus Schmidt* / des. F. Z. Vaz-de-Mello, 20*13*", "29 / *56*", "9936 / E92 +", "*obscurus*", "Esp. Santo", "obscurus / Schmidt") (NHRS) (Fig. 40Bd); 1 ♀, ("*Glaphyrocanthon* / *obscurus* / *(Schm.)* / P. Pereira et. *60*", "Espir. Santo", "9934 E92 +", "PARALECTOTYPE / ♀ / *Canthon* / *obscurus Schmidt* / des. F. Z. Vaz-de-Mello, 20*13*") (NHRS); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Coll. C. Feslche / Kauf 20, 1918") (SMTD); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo"), (SMTD); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♂ ("PARALECTOTYPE / ♂ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD) (Fig. 40Be) ; 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *obscurus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Esp. Santo") (SMTD); 1 ♂, ("S. *Amerika* / *W. Meier* / *Hamburg*", "*Ypilissus spec?*", "*Canthon* / *obscurus* / *A. Schmidt*", "SYNTYPUS / Canthon / obscurus Schmidt, 1920 / labelled by MNHUB 2014") (ZMHB).

Additional material (141 ♂♂, 126 ♀♀)
BRAZIL: 1 ♂, no further data (NMPC, ex coll. Balthasar, B. Schwarzer and Lansberge). – **Alagoas**: 1 ♂, 2 ♀♀, Ibateguara, edge of Coimbra fragment, 6 Oct. 2011, B. Filgueiras leg. (UFPE). – **Bahia**: 1 ♂, Encruzilhada, Nov. 1980, A. Martínez and M. Alvarenga leg. (CMNC); 1 ♀, Santa Teresinha, Serra da Jiboia, 12º51,31′ S, 39º28,575′ W, 2 Feb. 2009, P.P. Lopes and L.R. M. Oliveira leg. (MZFS). – **Espírito Santo**: 1 ♀, no further data (BMNH); 1 ♂, no further data (MNHN, van de Poll collection); 1 ♂, no further data (ZMHB); 5 ♂♂, 3 ♀♀, Marechal Floriano, Jan. 2003, pitfall, L. Dias leg. (CEMT); 1 ♂, Santa Teresa, Estação Biológica Augusto Ruschi, Trilha da Preguiça, 19º54′39″ S, 40º32′30″ W, 760 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 3 ♂♂, Santa Teresa, Estação Biológica Augusto Ruschi, Trilha da Preguiça, 19º54′37″ S, 40º32′31″ W, 761 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♂, Santa Teresa, Estação Biológica de Santa Lúcia, 19º58′25″ S, 40º31′45″ W, 648 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♂, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha Bonita, 19º58′26″ S, 40º31′46″ W, 659 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♀, Santa Teresa, Estação Biológica de Santa Teresa, Trilha Bonita,19º58′30″ S, 40º31′50″ W, 684 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♂, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha do Rio, 19º58′22″ S, 40º31′45″ W, 649 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♂, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha Indaia-Açu, 19º57′56″ S, 40º32′24″ W, 626 m, 28 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♀, Santa Teresa, Estação Biológica de Santa Teresa, 19º57′57″ S, 40º32′23″ W, 631 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♂, Santa Teresa, Estação Biológica de Santa Teresa, Trilha Indaia-Açu, 19º57′57″ S, 40º32′21″ W, 661 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 3 ♂♂, 1 ♀, Santa

Teresa, Estação Biológica de Santa Teresa, Trilha Indaia-Açu, 19º58′18″ S, 40º32′09″ W, 742 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 5 ♂♂, 1 ♀, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha Indaia-Açu, 19º58′13″ S, 40º32′06″ W, 779 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 3 ♂♂, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha Tapinoã, 19º58′07″ S, 40º31′55″ W, 679 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 7 ♂♂, 2 ♀♀, Santa Teresa, Estação Biológica de Santa Lúcia, Trilha Tapinoã, 19º58′10″ S, 40º31′48″ W, 692 m, 29 Jan. 2015, pitfall with human faeces, T. Vargas leg. (CEMT); 1 ♂, 1 ♀, Venda Nova do Imigrante, Dec. 2000, F.Z. Vaz-de-Mello (“V-de-M”) leg. (AMBC); 1 ♂, same collecting data as for preceding (CEMT); 41 ♂♂, 42 ♀♀, Venda Nova do Imigrante, Lavrinhas, 20º12′29″ S, 41º07′23″ W, 850 m, 10–14 Jan. 2011, human faeces, F.Z. Vaz-de-Mello leg. (CEMT); 31 ♂♂, 39 ♀♀, Venda Nova do Imigrante, Lavrinhas, 20º18′40″ S, 41º08′16″ W, Dec. 2012, L.F. Vaz-de-Mello leg. (CEMT); 22 ♂♂, 20 ♀♀, Venda Nova do Imigrante, Lavrinhas, 20º12′29″ S, 41º07′23″ W, I.2013, L.F. Vaz-de-Mello leg. (CEMT). – **Minas Gerais**: 4 ♂♂, 7 ♀♀, Berizal, Barreiros, Serra do Anastácio, 1375 m, 18–19 Dec. 2012, flight interception trap, P. Grossi leg. (CEMT). – **Pernambuco**: 3 ♂♂, 2 ♀♀, Igarassu, Refúgio Ecológico Charles Darwin (“RECD”), 30 Oct. 2006, pitfall, Fernando A.B. Silva *et al.* leg. (CEMT); 2 ♀♀, Sirinhaém, Usina Trapiche, 08º39′27″ S, 35º10′21″ W, fragmento Xanguazinho, 24 Jul. 2010, pitfall with human faeces, R.P. Salomão leg. (UFPE).

No data: 1 ♀ (CEMT).

Description

Colouration. Dorsum slightly shiny and lustrous. Head and pronotum with colouration ranging from light green with yellowish reflections to dark purple without any trace of yellowish or greenish sheen; between these two extremes, head and pronotum with mixture of greenish, yellowish, and coppery sheen varying in dominance of some of those tonalities. Elytra usually very dark green or blue, or, more rarely, with strong purplish-blue sheen. Pygidium and metaventrite dark green or blue, without metallic sheen or with reduced sheen. Legs reddish-brown.

Head. Tegument with diffuse sheen, with strong alveolar microsculpture obliterating micropunctation. Clypeus with two small apical teeth obtuse and contiguous at base; with single transverse row of very short setae covering base of both teeth. Genae with distinct tooth immediately after clypeal-genal juncture. Posterior edge of head unmargined between eyes.

Thorax. Pronotum with shiny tegument, without microsculpture and with dense micropunctation at centre, punctures denser and with more marked than on head; on sides, micropunctation absent and tegument with diffuse shine due to alveolar microsculpture progressively more well marked towards outer edge. Posterior edge with fine transverse line at centre (usually extending only up to the second elytral stria). Hypomeral cavity with long yellowish setae; external edge with distinct tubercle. Metaventrite glabrous at centre; on the sides, with sparse setae close to anterior margin of metacoxae (Fig. 7B); anterior region of metaventrite with strong rivose microsculpture; centre and posterior region with dense micropunctation among strong alveolar microsculpture.

Legs. Ventral surface of all femora and tibiae bright. Protibiae narrow and with distinct expansion at internal edge; at apical third, with three small acute teeth on external edge, two most apical ones subequal in length and larger than basal (Fig. 11D). Mesofemora margined anteriorly only at basal third or half; unmargined portion of anterior edge with row of setae; posterior margin absent; tegument with micropunctation almost imperceptible. Metafemora margined only anteriorly, posterior margin absent; apical third or half of anterior edge covered by row of setae; tegument with well-marked micropunctation, denser at base than at apex; without coarse elongate punctation at base (Fig. 13B). Metatarsomeres II and V subequal in length and larger than the others; metatarsomere IV shorter than the others.

Elytra. With nine narrow striae: first six striae strongly marked, finely carinulate and widened at base; seventh stria present only after humerus and always very weak, without carinulae; eighth and ninth striae very tenuous, almost imperceptible; all striae lack carinulae before reaching apex of elytra; humeral carina present or absent. Interstriae with tegument at centre of disc bright, without microsculpture, and with dense micropunctation; on sides and apex, tegument with strong alveolar microsculpture and without distinct micropunctation.

Abdomen. Ventrite I–V with strong microsculpture throughout tegument; ventrite VI with microsculpture only slightly more diffuse than others. Pygidium covered by strong alveolar microsculpture obliterating indistinct micropunctation.

Aedeagus. Parameres almost as long as phallobase and symmetrical, with both faces flat. In lateral view, with apices widely bifurcate, with superior branch wider and more strongly projected than inferior one and bent upwards; inferior branch with acute apex and facing forwards; without ventral keel or notch (Fig. 19B).

Sexual dimorphism. **Males**: Protibial spur broad and bifid, with long, straight and acute external projection, and internal projection shorter, bent, and wider (Fig. 15M). Abdomen glabrous and without lateral foveae. Ventrite VI strongly narrowed at centre. Pygidium very short (length between 1.5 and 1.2 mm); apical margin of pygidium much wider than lateral margin. **Females**: Protibial spur fine and short, spiniform. Abdomen with three pairs of transverse foveae on the sutures between ventrites I–II, II–III, and III–IV, respectively; foveae margined anteriorly by row of long yellowish setae; row of setae present also on ventrites IV and V (Fig. 16C). Ventrite VI broad at centre, only very slightly narrowed by medial expansion of ventrite V. Pygidium shorter (between 1.2 and 1 mm); apical margin of pygidium only slightly wider than lateral margin.

Measurements

Males (N = 26). **TL:** AV: 8.5 ± 0.49; MX: 9.5; MN: 7.7. **EW:** AV: 5.9 ± 0.33; MX: 6.5; MN: 5.3. **PrL:** AV: 2.6 ± 0.23; MX: 3; MN: 2.1. **PrW:** AV: 5.1 ± 0.28; MX: 5.7; MN: 4.7. **PgL:** AV: 1.3 ± 0.09; MX: 1.5; MN: 1.2. **PgW:** AV: 2.6 ± 0.17; MX: 2.9; MN: 2.3.

Females (N = 23). **TL:** AV: 8.2 ± 0.47; MX: 9; MN: 7.1. **EW:** AV: 5.9 ± 0.36; MX: 6.4; MN: 5.2. **PrL:** AV: 2.6 ± 0.19; MX: 2.9; MN: 2. **PrW:** AV: 5.1 ± 0.35; MX: 5.8; MN: 4.5. **PgL:** AV: 1.1 ± 0.07; MX: 1.2; MN: 1. **PgW:** AV: 2.5 ± 0.12; MX: 2.7; MN: 2.3.

Geographical distribution

Northern Atlantic Forest from Alagoas to Espírito Santo (Brazil).

Ecoregions

Pernambuco Coastal Forests, Bahia Coastal Forests, Bahia Interior Forests.

Collecting sites (Fig. 41)

BRAZIL. **Pernambuco**: Igarassu (Refúgio Ecológico Charles Darwin), Sirinhaém. **Alagoas**: Ibateguara. **Bahia**: Encruzilhada, Santa Teresinha. **Minas Gerais**: Berizal (Serra do Anastácio). **Espírito Santo**: Marechal Floriano, Santa Teresa (Estação Biológica Augusto Ruschi, Estação Biológica de Santa Lúcia), Venda Nova do Imigrante.

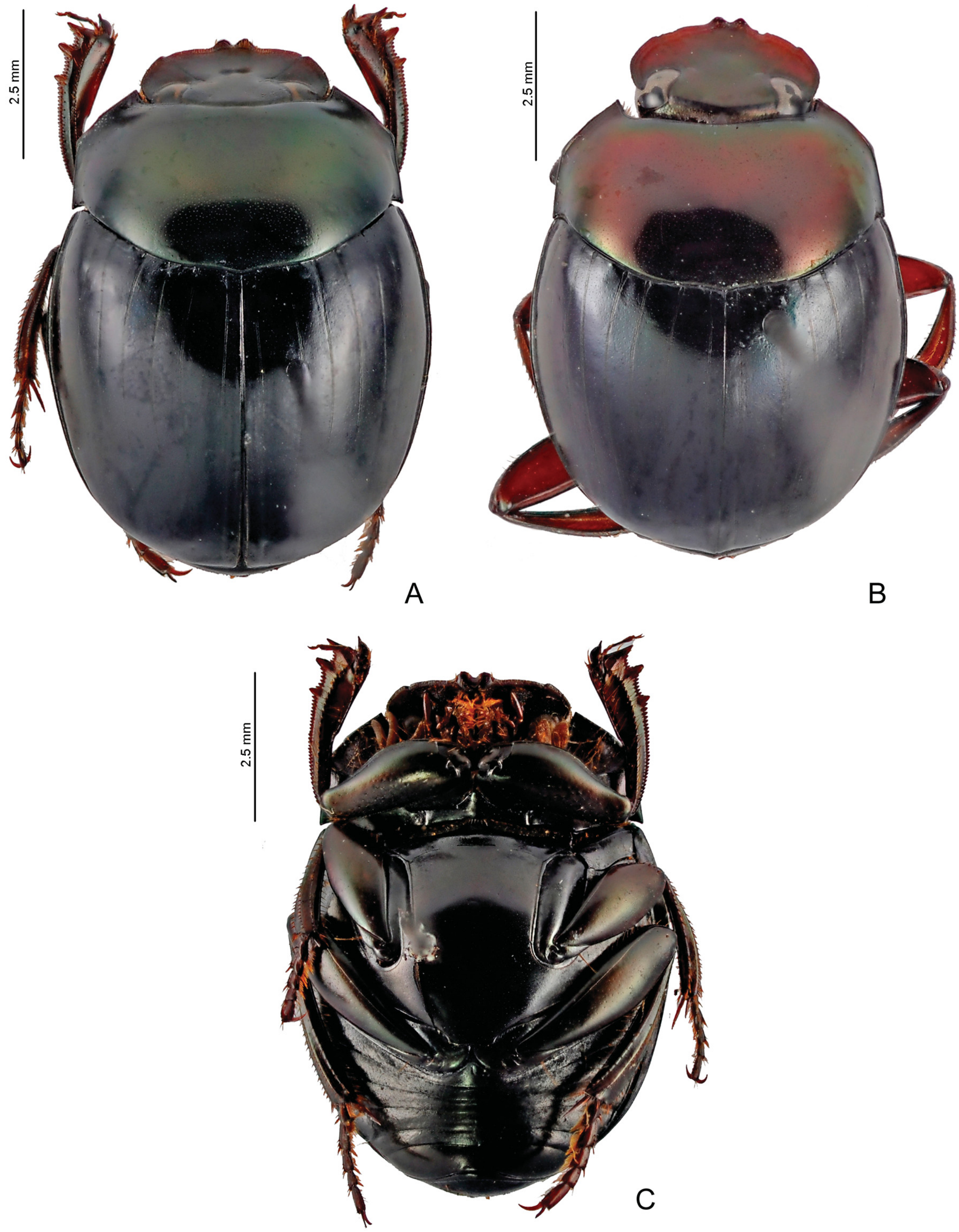

Fig. 42. *Sylvicanthon obscurus* (Schmidt, 1920). **A**. Dorsal view of the purplish form. **B**. Dorsal view of the yellowish form. **C**. Ventral view.

Intraspecific variation and taxonomic discussion

Sylvicanthon obscurus presents two important intraspecific variations, one intrapopulational and the other both geographical and intrapopulational. The former refers to the presence of a humeral carina at the eighth elytral stria (Fig. 12C): of the 267 specimens examined for this work, only 88 (46 ♂♂, 42 ♀♀) show some indication of this carina. Schmidt (1920, 1922) did not mention any variation on the presence of the humeral carina and considered it to be a characteristic differentiating *S. obscurus* from *S. candezei*, *S. foveiventris*, *S. furvus* and *S. securus* and that, at the same time, would approximate it to *S. aequinoctialis*, an opinion that was followed by Balthasar (1939), Pereira & Martínez (1956) and Martínez *et al.* (1964). Although it is a fact that the humeral carina is present only in *S. obscurus*, *S. aequicnotialis* and *S. proseni*, the first species distinguishes itself from the other two by being the only one in which this feature is not present in all the specimens examined. In *S. proseni*, and particularly in *S. aequinoctialis*, the carina may occasionally be only weakly marked, but it is never completely absent. Within a same population of *S. obscurus*, like the large series collected in Venda Nova do Imigrante (Espírito Santo, Brazil) (but also in other localities in the Brazilian northeast), there are specimens both with and without a humeral carina.

The second variation refers to colouration, of which two extreme forms can be observed: at one end of the spectrum, the head and pronotum colouration shows green and dark blue reflections (Fig. 42B); at the other end, head and pronotum are purple or dark purple, while the elytra are bright blue (Fig. 42A). Populations of *S. obscurus* in the Brazilian northeast (i.e., specimens collected in Alagoas, Pernambuco and Bahia) and in Minas Gerais have a colouration nearer to the latter extreme, with at most only some weak greenish or yellowish metallic reflections on the anterior region of the pronotum. The only specimen known from Bahia and those from Minas Gerais, in particular, show bright blue elytra; the other specimens from the Brazilian northeast have them as dark as in the green-yellowish specimens from Espírito Santo.

Differently, most of the individuals from Espírito Santo, including the lectotype (Fig. 40B), are more similar to the first end of the continuum described above. Nevertheless, there is a gradual intrapopulational variation in those specimens towards the other colour extreme, with individuals gradually showing a larger predominance of coppery sheen over greenish and yellowish tonalities up to a point where almost the totality of the pronotum and head have dark coppery or purple reflections. Therefore, while in the Brazilian northeast only the purple colouration is present, almost the entire variation spectrum is seen in Espírito Santo (although no specimens from this state are as close to the purple extreme as the darkest specimens from the northeast). The specimen from Encruzilhada (Bahia), which came from the former Antonio Martínez collection, bears a handwritten label "*Sp nov*", probably making reference to its peculiar colouration among the other *S. obscurus* (all the other known specimens with purple colouration were only recently collected, after 2006). However, after seeing that this characteristic varies intrapopulationally, we consider specimens from the Brazilian northeast and Minas Gerais conspecific with those from Espírito Santo under the name *S. obscurus*.

Despite sharing several characteristics with other members of the *furvus* subgroup, such as female abdominal foveae, protibiae expanded on their internal margin and parameres apically bifurcate, *S. obscurus* is the most distinguishable species in the group. It differs from all the others by the absence of coarse punctation at the base of the metafemora (Fig. 13B), the absence of a fine membrane connecting both branches of the apical bifurcation of the parameres, besides both branches being acuminate (Fig. 19B), and the presence of a row of long setae on the anterior margin of the female abdominal foveae (Fig. 16C). Furthermore, the elytral microsculpture pattern seen in *S. obscurus* is unique to this species among members of the *furvus* subgroup and its geographical distribution is completely disjunct, with *S. obscurus* occurring only in the northern portion of the Atlantic Forest, while the other three species are Amazonian. See Table 5 for more information on the differences between *S. obscurus* and closely related species; for differences with *S. foveiventris*, a species with which *S. obscurus* can be found in sympatry in Espírito Santo (and, perhaps, in Bahia), see the discussion under that species.

Comments

We found 11 specimens that, thanks to Adolf Schmidt's handwritten labels, we know are certainly part of the type series of *S. obscurus*: seven deposited in the SMTD (ex Bang-Hass collection) and four in the NHRS. Additionally, three other specimens deposited in the ZMHB bear modern labels indicating they would also be part of the original syntype series. According to Joachim Willers (personal communication to MC, 2015), curator at the ZMHB: "in our collection the species *Canthon obscurus* Schmidt, 1920 has a bottom label with an asterisc (*). This means that we should have type(s). Therefore I printed a syntype label for each specimen so that who is working on the species has an up-to-date information". One of those specimens also has a label handwritten by Schmidt and, hence, should indeed be a syntype of *S. obscurus* (Vaz-de-Mello & Cupello in press). That specimen also bears a green label handwritten "*S. Amerika* / *W. Meier* / *Hamburg*", information that probably makes reference to the collection of the German entomologist William Meier (1861–1940), from Hamburg, Germany (Joachim Willers, personal communication to MC, 2015; Weidner 1976). On the other hand, the other two specimens have labels indicating they were collected in Peru – therefore, different from the type locality cited by Schmidt (1920), the Brazilian state of Espírito Santo. Furthermore, after studying them, we could see that they are not actual *S. obscurus*, but rather two male *S. bridarollii*. It is, therefore, possible that someone other than Schmidt has positioned those two specimens bellow the label with the asterisk cited by Willers sometime after Schmidt's study of the ZMHB specimens and, consequently, they would not be part of the type series of *S. obscurus*. In light of all the evidence to the contrary, we decided not to include those two specimens in the *S. obscurus* type material listed above and not to consider them as true syntypes of this name.

Natural history

Label information reports collecting in October, November, December, January and July, which perhaps shows an annual activity pattern similar to that of *S. foveiventris*, species whose adults are active mainly during the hottest and rainiest months of the year. All the specimens with collecting method information were caught in pitfall traps baited with human faeces. Silva *et al.* (2010) collected *S. obscurus* (cited by them as "*Sylvicanthon* sp.") in Pernambuco only in areas of closed forest, although they have also set up traps in open habitats.

Sylvicanthon furvus (Schmidt, 1920)

Figs 6G, 11E, 13E, 15N, 16A, 19C, 20, 40C, 41, 43A–B

Canthon furvus Schmidt, 1920: 130–131, 133.

Canthon furvus – Schmidt 1922: 64, 75. — Balthasar 1939: 188; 1941: 341; 1951: 326. — Halffter & Martínez 1977: 63. — Krajcik 2012: 63.
Canthon furvum – Blackwelder 1944: 199.
Glaphyrocanthon (*Glaphyrocanthon*) *furvus* – Pereira & Martínez 1956: 126, 129. — Martínez *et al.* 1964: 5–6, 8, 10, 14, 20–21. — Vulcano & Pereira 1964: 662.
Sylvicanthon furvus – Halffter & Martínez 1977: 63. — Ratcliffe *et al.* 2015: 196.

Etymology

From the Latin '*furvus*', meaning 'black' or 'dark', probable reference to the consistently dark colouration of this species.

Material examined

Lectotype (here designated)
PERU: ♂**,** Cuzco, Quispicanchi, Marcapata. Former type locality cited by Schmidt (1920): "*Peru, Bolivien*", ("Typ.", "Marcapata / Peru", "Typus", "*furvus* / *Type m.*", "*furvus* / *A. Schm.*", "*Glaphyrocanthon* / *furvus* / *(Schm.)* / P. Pereira det. *60*", "9663 / E92 +", "NHRS-JLKB / 000021102", "LECTOTYPE ♂ / *Canthon* / *furvus Schm.* / des. F. Z. Vaz-de-Mello, 20*13*") (NHRS) (Fig. 40Ca–b).

Paralectotypes (4 ♂♂, 5 ♀♀)
BOLIVIA: 1 ♂, ("9662 / E92 +", "PARALECTOTYPE / ♂ / *Canthon* / *furvus Schm.* / des. F. Z. Vaz-de-Mello, 20*13*" "Bolivia", "*furvus*") (NHRS) (Fig. 40Cf); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *furvus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "*Canthon* / *furvus* / *A. Schmidt*", "Typus", "Coll. C. Felsche / Kauf 20, 1918", "Bolivia") (SMTD) (Fig. 40Cc); 1 ♂, ("PARALECTOTYPE / ♂ / *Canthon* / *furvus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Bolivia") (SMTD); 1 ♀**,** ("PARALECTOTYPE / ♀ / *Canthon* / *furvus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Bolivia") (SMTD); 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *furvus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Bolivia") (SMTD); 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *furvus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "Coll. C. Felsche / Kauf 20, 1918", "Bolivia") (SMTD).

PERU: 1 ♀, ("*furvus* / Schmidt", "Marcapata / Peru", "9664 / E92 +", "PARALECTOTYPE / ♀ / *Canthon* / *furvus Schm.* / des. F. Z. Vaz-de-Mello, 20*13*") (NHRS); 1 ♀, ("PARALECTOTYPE / ♀ / *Canthon* / *furvus Schm.* / des. F. Z. Vaz-de-Mello, 20*13*", "*Glaphyrocanthon* / *furvus* / *(Schm.)* / P. Pereira det. *60*", "Marcapata / Peru", "9661 / E92 +") (NHRS) (Fig. 40Ce); 1 ♂**,** ("PARALECTOTYPE / ♂ / *Canthon* / *furvus* / *Schmidt* / des. F. Z. Vaz-de-Mello, 20*14*", "*Canthon* / *furvus* / *A. Schmidt*", "Peru", "Gehr. W. Müller / Vermächt. 1909") (SMTD) (Fig. 40Cd).

Additional material (17 ♂♂, 8 ♀♀)
BOLIVIA: 1 ♂, no further data (MNHN); 1 ♂, no further data [labelled as homeotype of "*Canthon candezei*" by P. Pereira, 1942] (MZSP). – **La Paz**: 1 ♀, Larecaja, Guanay, 10 Nov. 2004, A.U. Peña leg. (CEMT); 2 ♂♂, Murillo, Farinas (MNHN); 2 ♂♂, Murillo, Zongo ("Songo") (MNHN); 1 ♂, same collecting data as for preceding (MZSP); 2 ♂♂, 3 ♀♀, Nor Yungas, Coroico (BMNH); 1 ♂, same collecting data as for preceding (MZSP); 1 ♀, same collecting data as for preceding (NMPC, ex. leg. Balthasar); 1 ♂, 1 ♀, Nor Yungas, Suapi (MNHN); 1 ♂, "Yungas de La Paz", 1000 m ("3,300 ft.") (BMNH).

PERU: **Cuzco**: 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º33′54.41″ S, 73º05′36.85″ W, 26–29 Jan. 2010, C. Carranza and C. Rossi leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º33′51.29″ S, 73º05′37.01″ W, 1457 m, 18–21 Sep. 2010, pitfall, M. Alvarado and J. Peralta leg. (MUSM); 1 ♂, La Convención, Echarate, Comunidad Campesina Santa Rosa, 12º34′14.23″ S, 73º05′41.87″ W, 1459 m, 14 Oct. 2009, C. Carranza and C. Rossi leg. (MUSM); 1 ♂, 1 ♀, Quispicanchi, Marcapata (NMPC, ex. coll. Balthasar). – **Junín**: 1 ♂, Chanchamayo, O. Schunke leg. (MNHN).

No data: 1 ♀ [small green label] (MNHN).

Description

Colouration. Very variable and iridescent. In general, head with greenish or bluish sheen. Pronotum usually purple; occasionally, with greenish sheen. Elytra purple or blue. Meso- and metafemora reddish-brown. Metaventrite with strong green shine. Pygidium of same colour as elytra.

Head. Tegument slightly shiny, with strong alveolar microsculpture obliterating dense surficial micropunctation; micropunctation almost imperceptible or even absent throughout outer edge of head. Clypeus with two apical teeth obtuse and only slightly separated from one another (Fig. 6F); with single transverse row of setae covering base of both teeth. Genae with weak denticle immediately behind clypeal-genal juncture. Posterior edge of head with fine incontinuous line between eyes, or completely unmargined.

Thorax. Pronotum with shiny tegument, and dense and well-marked micropunctation at centre; towards sides, micropunctation progressively less dense and well marked, sometimes absent on lateral edge; tegument among micropunctation completely smooth, microsculpture limited to very narrow strip of tegument on anterior edge of pronotum and anterolateral angles. Posterior edge with evident fine transverse line at centre (usually extending almost to third elytral striae). Hypomeral cavity with long yellowish setae at centre; external edge with weak tubercle. Metaventrite glabrous at centre; sides with few and sparse setae close to anterior margin of metacoxae; anterior region of metaventrite with distinct rivose microsculpture; centre and posterior region with dense micropunctation and very effaced, almost imperceptible microsculpture.

Legs. Ventral surface of all femora and tibiae shiny. Profemora with tegument with sparse micropunctation and without microsculpture at anterior half and with strong rivose microsculpture at posterior half and on anterior margin. Protibiae narrow and with distinct expansion on internal edge; at apical third, external edge with three small acute teeth; the two most apical ones subequal in length and larger than basal (Fig. 11E). Mesofemora margined anteriorly only at basal half; unmargined portion of anterior edge with row of short setae; posterior margin absent; tegument with strong rivose microsculpture. Metafemora margined only anteriorly, posterior margin absent; apical third of anterior edge covered by row of setae; with strong coarse elongate punctation at base and with sparse micropunctation on rest of tegument, which is covered by rivose microsculpture (Fig. 13E). Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than others.

Elytra. With only seven narrow visible striae: the first three or four striae well marked, finely carinulate, and widened at base; fifth to seventh striae progressively more effaced and interrupted; all striae lack carinulae before reaching apex of elytra, marked only by microsculpture or completely indistinct; humeral carina absent. Tegument of interstriae matte, with strong alveolar microsculpture throughout elytra surface; micropunctation totally oblitered by microsculpture and almost imperceptible.

Abdomen. Tegument of ventrites I–V with strong rivose microsculpture; ventrite VI smooth at centre and with weak rivose microsculpture on sides. Pygidium with shiny tegument; at centre, with diffuse microsculpture and dense micropunctation; on sides, with evident rivose microsculpture.

Aedeagus. Parameres longer than half-length of phallobase and with no noticeable asymmetry, both external faces flat. In lateral view, parameres with apices widely bifurcate, with inferior branch distinctly projected and divergent from superior branch; without ventral keel or notch (Fig. 19C).

Sexual dimorphism. **Males**: Protibial spur broad and bifid, with external projection spiniform and not much longer than internal projection, which is bent and widened (Fig. 15N). Abdomen without lateral foveae. Ventrite VI strongly narrowed at centre, with posterior posterior edge emarginate; anterior edge covered by weak medial flange of posterior edge of ventrite V. Pygidium very long (length between 1.4 and 1.1 mm) and convex; apical margin much wider than lateral margins. **Females**: Protibial spur simple, spiniform. Abdomen with three pairs of lateral transverse foveae between ventrites I–II, II–III, and III–IV, respectively; foveae not margined by row of long setae (Fig. 16A). Ventrite VI very broad at centre, posterior edge straight, without emargination; anterior edge subtly covered by weak medial flange of posterior edge of ventrite V. Pygidium shorter (between 1.1 and 0.9 mm) and flat; apical margin of pygidium only slightly wider than lateral margin.

Measurements

Males (N = 11). **TL:** AV: 7 ± 0.53; MX: 7.9; MN: 6.2. **EW:** AV: 5.2 ± 0.29; MX: 5.8; MN: 4.7. **PrL:** AV: 2.4 ± 0.13; MX: 2.6; MN: 2.2. **PrW:** AV: 4.4 ± 0.21; MX: 4.8; MN: 4.1. **PgL:** AV: 1.2 ± 0.07; MX: 1.4; MN: 1.1. **PgC:** AV: 2.2 ± 0.12; MX: 2.4; MN: 2.

Females (N = 6). **TL:** AV: 7.4 ± 0.40; MX: 8.1; MN: 7.0. **EW:** AV: 5.4 ± 0.15; MX: 5.5; MN: 5.1. **PrL:** AV: 2.4 ± 0.12; MX: 2.5; MN: 2.2. **PrW:** AV: 4.6 ± 0.12; MX: 4.8; MN: 4.5. **PgL:** AV: 1.0 ± 0.09; MX: 1.1; MN: 0.9. **PgW:** AV: 2.3 ± 0.15; MX: 2.4; MN: 2.0.

Geographical distribution

Eastern slopes of the Andes in Peru and Bolivia.

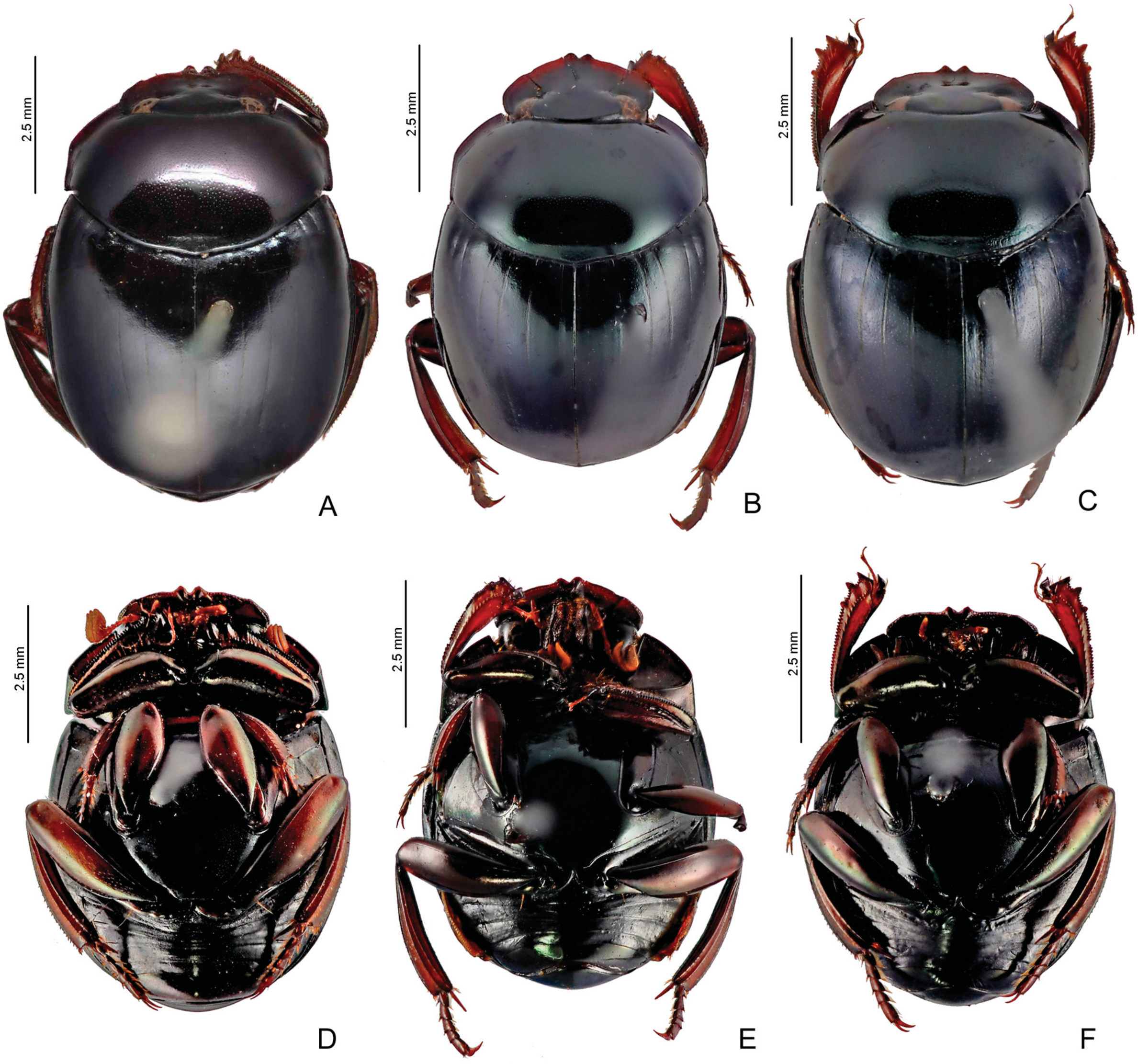

Fig. 43. The three Amazonian species of the *furvus* subgroup. **A, D**. *Sylvicanthon furvus* (Schmidt, 1920). **A**. Dorsal view. **D**. Ventral view. **B, E**. *S. monnei* sp. nov. **B**. Dorsal view. **E**. Ventral view. **C, F**. *S. mayri* sp. nov. **C**. Dorsal view. **F**. Ventral view.

Ecoregions

Peruvian Yungas, Bolivian Yungas. Eastern slopes of the Andes in Peru and Bolivia.

Collecting sites (Fig. 41)

PERU. **Junín**: Chanchamayo. **Cuzco**: La Convención (Echarate), Quispicanchi (Marcapata).

BOLIVIA. **La Paz**: Larecaja (Guanay), Murillo (Farinas, Zongo), Nor Yungas (Coroico, Suapi).

Intraspecific variation and taxonomic discussion

The *furvus* subgroup represents the assemblage with the most complex taxonomy in *Sylvicanthon*. One of the reasons for this is the small number of specimens found in collections: while we could examine 2060 specimens of the species of the *bridarollii* subgroup, the other subgroup with an intricate taxonomy, we had in front of us only 53 specimens of the three rarest species of the *furvus* subgroup (i.e., excluding *S. obscurus*). At least in part, this is a consequence of the small number of collections made in the species' occurrence area (the slopes of the Andes in Bolivia and Peru for *S. furvus*, southern Amazonia for *S. monnei* sp. nov. and western Amazonia for *S. mayri* sp. nov.). Nevertheless, it is probable that these species should have natural low population densities, since even modern collections made with pitfall traps baited with dung did not yield a large number of individuals (e.g., specimens of *S. monnei* sp. nov. collected in the northern region of Mato Grosso and the holotype of *S. mayri* sp. nov. in Rio Branco, Acre). A second reason for such a complex taxonomy in the *furvus* subgroup is the tenuous morphological differences found between *S. mayri* sp. nov., *S. furvus*, and *S. monnei* sp. nov. (distinctions between *S. obscurus* and these three species were discussed anteriorly; see more details on Table 5).

The differences between *S. furvus*, *S. mayri* sp. nov. and *S. monnei* sp. nov. may be classified into two groups: those referring to the microsculpture and those referring to the shape of the parameres. Regarding the former, we observe that *S. furvus* possesses a much stronger microsculpture than *S. mayri* sp. nov. and *S. monnei* sp. nov. over the body. The head of the first species is covered by a dense, strongly impressed alveolar microsculpture, which makes the tegument more opaque, while the other two species have the head largely microsculptured, but this microsculpture is much weaker and, in some areas of the head (especially on frons), it can be totally absent, which makes the tegument much brighter. The meso- and metafemora of *S. furvus* are entirely covered by a strong rivose microsculpture and have micropunctation almost imperceptible, while these structures are smooth in almost the entirety of their tegument (except for the anterior region of the apical area, which has a rivose microsculpture) and show an evident micropunctation in both *S. mayri* sp. nov. and *S. monnei* sp. nov.[22] (the profemora also have rivose microsculpture more strongly marked in *S. furvus* than in the other two species, but this difference is less noticeable). The pygidium of *S. furvus* has microsculpture ranging from having a clear alveolation to a completely diffuse one, while the microsculpture in both *S. mayri* sp. nov. and *S. monnei* sp. nov. is absent in almost the entire tegument and may be present only at the base (and, in this latter case, it is more evident in *S. monnei* sp. nov. than in *S. mayri* sp. nov.). Finally, on the elytra rest the major differences between the three species: in *S. furvus*, the entire elytral tegument is covered by a strongly-marked alveolar microsculpture so that the tegument has a very weak, diffuse silky shine. In *S. mayri* sp. nov., the tegument presents a very diffuse microsculpture, without an evident alveolar pattern, and, consequently, is more intense bright. Lastly, in *S. monnei* sp. nov., the microsculpture is completely absent on the elytra, which gives the tegument a smooth appearance with a strong, lustrous shine, and micropunctation is present.

The differences in the shape of the parameres are determinant for the separation of both *S. furvus* and *S. mayri* sp. nov. from *S. monnei* sp. nov. The paramere apex of the first two species, which do not show

Table 5. Summary of the morphological and distributional differences between the four species of the *furvus* subgroup.

	S. obscurus **(Schmidt, 1920)**	***S. furvus*** **(Schmidt, 1920)**	***S. monnei*** **sp. nov.**	***S. mayri*** **sp. nov.**
Tegument of head	With diffuse shine, with strong alveolar microsculpture present throughout the tegument	With diffuse shine, with strong alveolar microsculpture present throughout the tegument	Shiny, with weak alveolar microsculpture, which, in some areas, is completely absent	Shiny, with weak alveolar microsculpture, which, in some areas, is completely absent
Tegument of ventral face of meso- and metafemora	Entirely covered by rivose microsculpture, with no smooth area; micropunctation fine, almost imperceptible	Entirely covered by rivose microsculpture, with no smooth area; micropunctation fine, almost imperceptible	Smooth throughout most of tegument, excepting the anterior apical area of rivose microsculpture; micropunctation fine and evident in the smooth areas	Smooth throughout most of tegument, excepting the anterior apical area of rivose microsculpture; micropunctation fine and evident in the smooth areas
Coarse punctation at base of metafemora	Absent	Elongate punctures usually (but not always) well marked	Elongate punctures usually (but not always) well marked	Modified into simple fine punctures and always only slightly marked
Tegument of elytra	Smooth and with evident micropunctation at centre and with strong alveolar microsculpture on sides and apex	Matte, with strong alveolar microsculpture present throughout the tegument	Shiny and smooth, with almost no trace of microsculpture throughout the tegument	Shiny, with diffuse microsculpture, difficult to see and with ill-delimited alveoli
Female abdomen lateral foveae	Always strongly marked and deep; with row of long setae on anterior margin	Always strongly marked and deep; glabrous	Always strongly marked and deep; glabrous	Very shallow (particularly between ventrites III─IV) and poorly marked; glabrous
Tegument of pygidium	With strong alveolar microsculpture throughout the tegument	With diffuse alveolar microsculpture, at centre and apex, and strong rivose microsculpture at base	Completely smooth at centre with occasional microsculpture present only on sides	Completely smooth at centre with occasional microsculpture present only on sides
Apex of parameres (lateral view)	Strongly bifurcate; without a membrane connecting apical branches; superior branch very projected upwards, and inferior branch projected forwards	Strongly bifurcate; with fine membrane connecting apical branches; inferior branch well projected and widely divergent from superior branch	Only weakly bifurcate; with fine membrane connecting apical branches; inferior branch slightly indicated and parallel to superior branch	Strongly bifurcate; with fine membrane connecting apical branches; inferior branch well projected and widely divergent from superior branch
Distribution	Northern portion of the Brazilian Atlantic Forest, from Alagoas south to Espírito Santo	Eastern slopes of the Andes in Peru and Bolivia	Southern Amazonia, in the Brazilian states of Pará and Mato Grosso	Western Amazonia Colombia, Brazil (Amazonas and Acre) and Peru. Still little known

any differences from each other, has a strong bifurcation, with two widely divergent branches, being the inferior branch well developed and with a strong excavation posteriorly to it (Fig. 44A–B). In *S. monnei* sp. nov., in contrast, the apical bifurcation is much weaker, and the inferior branch is short and straight (Fig. 44C–D).

Distinctions related to the coarse punctation at the base of the metafemora and to the female abdominal foveae approach *S. furvus* to *S. monnei* sp. nov. on the one side, and separate them from *S. mayri* sp. nov. on the other. The coarse punctures of metafemora are usually longer and more well impressed in the first two species (Fig. 13C, E), while they are finer and much weaker in *S. mayri* sp. nov. (Fig. 13D). Nonetheless, there is a variation in the intensity on which these punctures are marked in different individuals of a same species (and also in *S. foveiventris* and *S. bridarollii*, the other two species in which these punctures are present). It is important to bear in mind, however, that it is only possible to see this distinction at the populational level, not at the individual one. The real difference should rest, therefore, when we see populations as a whole (in average, punctures are more profound in *S. monnei* sp. nov. and *S. furvus* than in *S. mayri* sp. nov.). When we have larger series of *S. furvus*, *S. monnei* sp. nov. and, especially, *S. mayri* sp. nov., we will be able to test more firmly whether this observation is correct or not. As for the abdominal foveae, they are as profound and clearly marked in *S. monnei* sp. nov. as in *S. furvus* (Fig. 16A), while they are very shallow (particularly the one between ventrites III–IV) in the only two known females of *S. mayri* sp. nov. (Fig. 16B).

Along with the morphological differences listed so far, these three species are totally allopatric, without any known overlapping zone between their distributions (Fig. 41). *Sylvicanthon furvus* is restricted to the cloud forests and the yungas on the eastern slopes of the Andes, in northern Bolivia and southern Peru. *Sylvicanthon monnei* sp. nov. is widely distributed in southern Amazonia, in the Brazilian states of Mato Grosso and Pará. Finally, *S. mayri* sp. nov. was recorded from four points very distant from one another in western Amazonia, in the Peruvian department of Madre de Díos, in the Brazilian states of Acre and Amazonas and in the Colombian state of Meta.

Comments

A male *S. furvus* collected in Bolivia and now housed at the MZSP is labelled "HOMEOTIPO" and "*Canthon* / *candezei* / *Har*. / P. Pereira det. *942*". Since the term homeotype refers to an ordinary specimen compared to a type specimen (Evenhuis 2008), it is curious to note that none of the known *S. candezei* syntypes bears any label by Padre Francisco Pereira, so indicating he did not have access to them. Besides, *S. candezei* and *S. furvus* are very distinct in terms of morphology and, therefore, it is improbable that such an experienced entomologist as Pe. Pereira could have confused them. On the other hand, he had access to the type specimens of *S. furvus* in 1960 (as stated by Pereira & Martínez 1960), and, hence, it might be possible that the homeotype label refers in fact to this latter name and has nothing to do with the 1942 identification label.

Natural history

Almost nothing is known on the biology of *S. furvus*. Most of the specimens examined, having likely been collected in the 19th and early 20th centuries, do not have bionomic data on their labels. The only information on the collecting methods comes from the label of a male collected in a pitfall trap (baited with human faeces?) in La Convención (Cuzco, Peru) in 2010. The only four specimens with data on the collecting month report January, September, October and November. Lastly, concerning the altitudinal range, specimens of *S. furvus* were found mostly between 1350 and 1850 m, being 450 m the lowest record (the female collected in Guanay, Bolivia). The type locality of *S. furvus*, Marcapata (Quispicanchi, Cuzco), is located around 3100 m a.s.l., which, if correct, would represent the highest altitudinal record for an American Deltochilini.

Sylvicanthon monnei sp. nov.

urn:lsid:zoobank.org:act:045BB71E-7DD7-4EE3-B7AE-E087F656F754

Figs 13C, 19D, 20, 41, 43B, E, 44C–D

Etymology

A tribute to the Uruguayan-Brazilian entomologist Miguel A. Monné, one of the leading specialists in the New World fauna of Cerambycidae and author of the main catalogue of the family's Neotropical species plus almost 200 papers dealing with longhorn beetle taxonomy. As the first author's supervisor throughout his entire undergraduation (2009–2013), it was prof. Monné who first opened doors so that he could work as a zoologist. Through his example and inspiration, MC's taste for taxonomy, zoological nomenclature and history of entomology, as well as his profound respect for all the great synthesizers of scientific knowledge, quickly flourished.

Material examined

Holotype

BRAZIL: ♂, Mato Grosso, Cotriguaçu, Fazenda São Nicolau, 09º51′18″ S, 58º13′22″ W, 200 m ("BRASIL: MatoGrosso.Cotriguaçu, / Faz. São Nicolau. flor.sec.200m / 9º51′18″ S, 58º13′22″ W. Fezes / hum. X-2009. Vaz-de-Mello") (CEMT).

Paratypes (8 ♂♂, 5 ♀♀)

BRAZIL: **Mato Grosso**: 2 ♂♂, Cotriguaçu, Fazenda São Nicolau, Prainha, 09º51′36″ S, 58º12′53″ W, Oct. 2009, pitfall, F.Z. Vaz-de-Mello leg. (CEMT); 2 ♂♂, 1 ♀, Diamantino, Fazenda São João, 14º14′10″ S, 56º08′11″ W, 400 m, 11 Jan. 2001, pitfall with dung, Génier & Vaz-de-Mello leg. (CMNC); 1 ♂, 2 ♀♀, Porto Estrela, ESEC Serra das Araras, Olho d'Água, 14 Oct. 2011, pitfall, M. Gigliotti leg. (CEMT); 1 ♂, Porto Estrela, ESEC Serra das Araras, Trilha Bocado do José, 15º38′50″ S, 57º12′27″ W, 238 m, 10 Oct. 2011, pitfall, F.Z. Vaz-de-Mello leg. (CEMT); 1 ♂, Querência, Fazenda São Luiz, 12º39.94′ S, 52º21.85′ W, 14 Jul. 2008, pitfall, R. Andrade leg. (CEMT); 1 ♂, 1 ♀, Querência, Fazenda São Luiz, 12º39.64′ S, 52º22.74′ W, 17 Jul. 2008, pitfall, R. Andrade leg. (CEMT). – **Pará**: 1 ♀, São Félix do Xingu, Pinkaití Reserve, 07º45′ S, 51º57′ W, 12 Nov. 1998, P.Y. Scheffler leg. (CEMT).

Description

COLOURATION. Head, pronotum, elytra and pygidium predominantly dark green. Metaventrite very dark, black with soft greenish reflections. Meso- and metafemora reddish-brown or dark brown.

HEAD. Tegument shiny, with well-marked micropunctation and weak alveolar microsculpture, in some specimens very effaced or even absent in some parts of head; micropunctation almost imperceptible or absent at apex of clypeus. Clypeus with two apical teeth obtuse and only slightly separated from one another; with single transverse row of short setae covering base of both teeth. Genae with weak denticle immediately behind clypeal-genal juncture. Posterior edge of head unmargined between eyes.

THORAX. Pronotum with shiny tegument with dense micropunctation at centre; towards the sides, micropunctation progressively less well marked, but always present and evident; alveolar microsculpture present only on anterolateral angles and in narrow strip on sides; at centre, tegument smooth. Posterior edge with fine transverse line at centre (usually extending up to second elytral stria) which, occasionally, can be difficult to see. Hypomeral cavity with some long yellowish setae at centre; external edge with weak tubercle. Metaventrite glabrous at centre; sides with few sparse setae near anterior margin of metacoxae (Fig. 7B); anterior region of metaventrite with tegument with strong rivose microsculpture; centre and posterior region with dense micropunctation and without microsculpture.

Legs. Ventral surface of all femora and tibiae bright. Profemora with tegument with sparse micropunctation and without microsculpture at anterior half and with strong rivose microsculpture at posterior half. Protibiae narrow and with distinct expansion on internal edge; at apical third, external edge with three small acute teeth, two most apical ones subequal in length and larger than basal (Fig. 11E). Mesofemora margined anteriorly only at basal half; unmargined portion of anterior edge with row of very short setae; posterior margin absent; tegument smooth and with sparse micropunctation, except apical anterior half, which has strong rivose microsculpture. Metafemora margined only anteriorly, posterior margin absent; apical third of anterior edge covered by row of setae; tegument with rivose microsculpture at anterior half and smooth with sparse micropunctation at posterior half; with strong coarse elongate punctation at base (Fig. 13C). Metatarsomeres II and V subequal in length and longer than others; metatarsomere IV shorter than others.

Elytra. With only seven narrow visible striae: first three or four well marked, finely carinulate, and widened at base; fifth to seventh progressively more effaced and interrupted; all striae lack carinulae before reaching apex of elytra, where they are marked only by microsculpture or completely indistinct; humeral carina absent. Tegument of interstriae shiny, without microsculpture, and with very dense micropunctation.

Abdomen. Tegument of ventrites I–IV with strong rivose microsculpture; ventrite VI smooth at centre and with weak rivose microsculpture on sides. Pygidium with bright tegument, without microsculpture, and with dense micropunctation (occasionally, weak microsculpture present on the sides of pygidium).

Aedeagus. Parameres longer than half-length of phallobase and without any noticeable asymmetry, with both external faces flat. In lateral view, parameres with apex slightly bifurcate, with inferior branch of bifurcation only very slightly projected and parallel to superior branch; without ventral keel or notch (Figs 19D, 44C–D).

Sexual dimorphism. **Males**: Protibial spur broad and bifid, with external projection spiniform and not much longer than internal projection, which is bent and widened (Fig. 15N). Abdomen without lateral foveae. Ventrite VI strongly narrowed at centre due to a distinct emargination on posterior edge; anterior edge slightly covered by weak medial flange of posterior edge of ventrite V. Pygidium very long (length between 1.2 and 1.0 mm) and convex; apical margin of pygidium much wider than lateral margins. **Females**: Protibial spur spiniform. Abdomen with three pairs of transverse foveae located between ventrites I–II, II–III, and III–IV, respectively; foveae not margined by row of long setae (Fig. 16A). Ventrite VI very broad at centre, posterior edge straight, without emargination; anterior edge subtly covered by weak medial flange of posterior edge of ventrite V. Pygidium shorter (about 0.9 mm) and flat; apical margin of pygidium only slightly wider than lateral margins.

Measurements

Males (N = 5). **TL:** AV: 6.6 ± 0.25; MX: 6.8; MN: 6.3. **EW:** AV: 4.9 ± 0.29; MX: 5.3; MN: 4.6. **PrL:** AV: 2.2 ± 0.13; MX: 2.4; MN: 2.1. **PrW:** AV: 4.4 ± 0.21; MX: 4.6; MN: 4.1. **PgL:** AV: 1.1 ± 0.09; MX: 1.2; MN: 1.0. **PgW:** AV: 2.2 ± 0.14; MX: 2.4; MN: 2.1.

Females (N = 3). **TL:** AV: 6.5 ± 0.20; MX: 6.7; MN: 6.3. **EW:** AV: 4.9 ± 0.28; MX: 5.1; MN: 4.7. **PrL:** AV: 2.1 ± 0.21; MX: 2.3; MN: 1.9. **PrW:** AV: 4.1 ± 0.3; MX: 4.4; MN: 3.8. **PgL:** AV: 0.9 ± 0.0; MX: 0.9; MN: 0.9. **PgW:** AV: 2.1 ± 0.0; MX: 2.1; MN: 2.1.

Geographical distribution

Southern Amazonia in Brazil.

Ecoregions

Xingu-Tocantins-Araguaia Moist Forests, Madeira-Tapajós Moist Forests, Mato Grosso Tropical Dry Forests, Chiquitano Dry Forests.

Collecting sites (Fig. 41)

BRAZIL. **Pará:** São Félix do Xingu. **Mato Grosso:** Cotriguaçu, Diamantino, Porto Estrela (Estação Ecológica Serra das Araras), Querência.

Intraspecific variation and taxonomic discussion

The two most closely related species to *S. monnei* sp. nov. are *S. mayri* sp. nov. and *S. furvus*, from which it can be differentiated by the following combination of characteristics: elytral tegument without any alveolar microsculpture among micropunctation (alveolar microsculpture strongly impressed in *S. furvus*, and diffuse, but still present in *S. mayri* sp. nov.), parameres with both branches of apical bifurcation only slightly divergent, the inferior branch being straight and little projected (Fig. 44C–D) (parameres strongly bifurcate at apex in *S. mayri* sp. nov. (Fig. 44A–B) and *S. furvus*, with the inferior branch well developed and widely divergent from the superior branch) and distribution in southern Amazonia (Fig. 41) (on the slopes of Andes in Peru and Bolivia for *S. furvus* and western Amazonia for *S. mayri* sp. nov.). A detailed comparison between these three species can be found in the discussion of *S. furvus* and on Table 5.

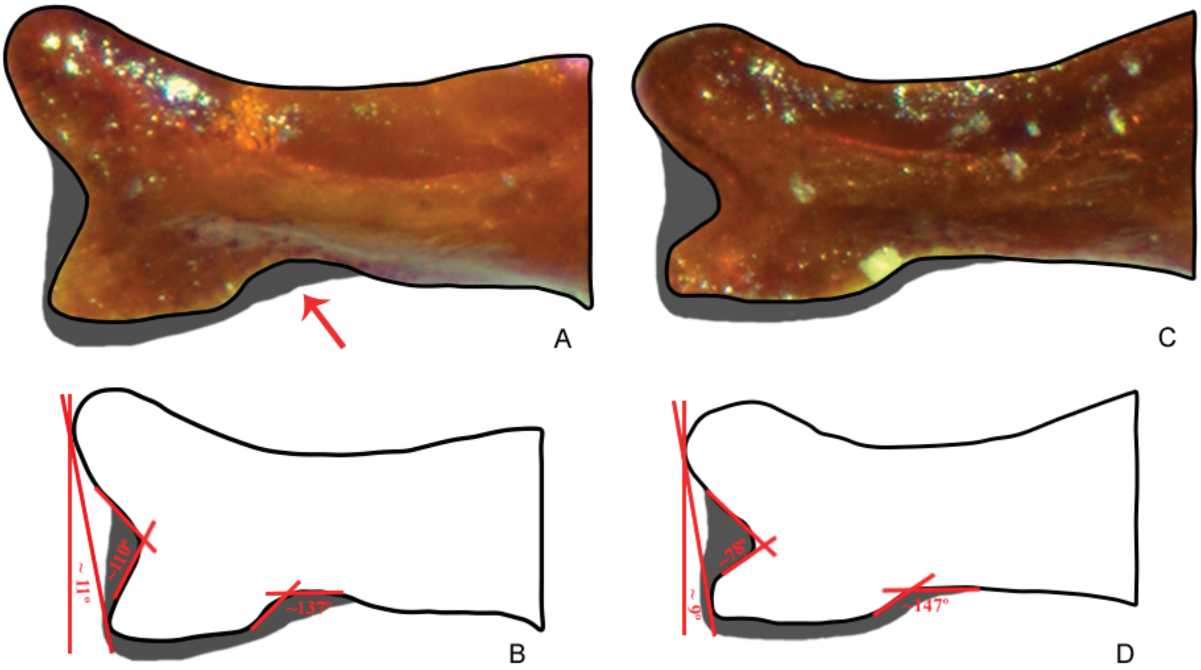

Fig. 44. Differences on the parameres of *Sylvicanthon mayri* sp. nov. and *S. monnei* sp. nov. (grayish zones represent original membraneous areas). **A–B**. *S. mayri* sp. nov. **C–D**. *S. monnei* sp. nov. Note that both branches of the apical bifurcation of the parameres of *S. mayri* sp. nov. are much more divergent than those of *S. monnei* sp. nov., which makes the internal angle between them more open in the first species (~110º) than in the second (~78º). In the same way, as the inferior branch is much more projected in *S. mayri* sp. nov. than in *S. monnei* sp. nov., the angle between the posterior region of that branch and the rest of the paramere is more open in *S. monnei* sp. nov. (~147º) than in *S. mayri* sp. nov. (~137º), species that seems to have a strong excavation at this point of the paramere (indicated by red arrow in A).

Two species of *Sylvicanthon* can be found in sympatry with *S. monnei* sp. nov.: *S. candezei* and *S. proseni*. From the first, *S. monnei* sp. nov. can be readily distinguished as follows: protibiae tridentate and with a distinct expansion on their internal margin (Fig. 11E) (bidentate and straight on its internal margin in *S. candezei*, Fig. 11J), females with three pairs of abdominal foveae (Fig. 16A) (without foveae in *S. candezei*) and parameres, in lateral view, without any notch on its inferior edge (Figs 19D, 44C) (with a profound notch on the middle of ventral edge in *S. candezei*, Fig. 17C). It is interesting to note that individuals from southern populations of *S. candezei*, i.e., those that can be in sympatry with *S. monnei* sp. nov., differ from northern specimens in having elytra without trace of microsculpture in the same way as seen in *S. monnei* sp. nov.

Comments

The holotype and two paratypes of *S. monnei* sp. nov. are part of a large series of dung beetles collected during a faunistic survey on the São Nicolau farm ("Fazenda São Nicolau"), in the municipality of Cotriguaçu (Mato Grosso, Brazil), done in two campaigns at the end of 2009; the three type specimens were caught during the first campaign, between the 5th and 16th of October. The survey was published by Vaz-de-Mello *et al.* (2011b), but, curiously, no *Sylvicanthon* (except *S. proseni*, then cited in *Canthon*) were included in the final list of 118 species present at the farm. Since 2009, three other new species were described from that material: *Lobidion punctatissimum* Génier, 2010 of Ateuchini (which was recently transferred to *Ateuchus* by Génier & Cupello 2018), and *Deltochilum* (*Aganhyboma*) *schefflerorum* Silva *et al.*, 2015 and *Hansreia peugeoti* Valois *et al.*, 2015 both in Deltochilini.

Natural history

The little we know on the biology of *S. monnei* sp. nov. is thanks to the information contained on specimen labels. Known specimens were collected in pitfall traps baited with human faeces in January, July, October and November. The species is found in altitudes between 230 and 400 m, in both primary and secondary semideciduous forests, but it is probably rare in both habitats.

Sylvicanthon mayri sp. nov.

urn:lsid:zoobank.org:act:260557DD-3E56-47DE-94AC-6F8DD638C039

Figs 13D, 16B, 19E, 20, 41, 43C, F, 44A–B

Etymology

A tribute to the German-American ornithologist, evolutionary theorist, philosopher and historian of biology Ernst Mayr (1904–2005), author of some of the major classics in evolutionary biology and, in the first author's view, one of the greatest and most versatile biologists of the 20th century. In special recognition of the immense intellectual influence he had (and continues to have) on MC's formation and in his choice to pursue a career as a systematist. Haffer (2007) presented the most complete biography of Ernst Mayr to date. The specific name is a noun in the genitive case.

Material examined

Holotype

BRAZIL: ♂, Acre, Senador Guiomard, Fazenda Experimental Catuaba, 10º04′ S, 67º37′ W (see comments below) ("BRASIL: AC. Rio Branco / Faz. Catuaba II - 1997 / F.Z. Vaz-de-Mello leg."), genital capsule extracted and glued to a point card (CEMT).

Paratypes (1 ♂, 2 ♀♀)

BRAZIL: **Amazonas**: 1 ♀, São Paulo de Olivença, Jun.– Jul. 1883, M. de Mathan leg. (CEMT).

COLOMBIA: **Meta**: 1 ♂ (dissected), “33 km E Villavicencio”, 2–4 Mar. 1972, dung trap, S. and J. Peck leg. (CMNC).

PERU: **Madre De Dios**: 1 ♀, Tambopata, Puerto Maldonado, 12º21′19″ S, 69º01′48″ W, 221 m, 26–27 Mar. 2009, L. Figueroa leg. (MUSM).

Description

COLOURATION. Head, pronotum, elytra, metaventrite, and pygidium dark green or dark blue. Meso- and metafemora reddish-brown; occasionally, with greenish reflections.

HEAD. Tegument shiny, with weak alveolar microsculpture and covered by dense well-marked micropunctation, which is almost imperceptible or even absent at apex of clypeus. Clypeus with two apical teeth obtuse only and only slightly separated from one another; with single transverse row of very short setae covering base of both teeth. Genae with small denticle immediately behind clypeal-genal juncture. Posterior edge of head unmargined between eyes or with very fine, almost imperceptible interrupted line at centre.

THORAX. Pronotoum with shiny tegument and with dense micropunctation at centre; towards the sides, micropunctation progressively less well-marked, but always present, although occasionally almost imperceptible; alveolar microsculpture between micropunctures present only on anterolateral angles and in narrow strip on lateral margins; at centre, tegument between micropunctures smooth or with very subtle microsculpture (as on elytra). Posterior edge with fine transverse line at centre (usually extending up to second elytral stria) which occasionally may be difficult to see. Hypomeral cavity with some long yellowish setae at centre; external margin with slight, almost inconspicuous tubercle. Metaventrite glabrous at centre; sides with few sparse setae near anterior margin of metacoxae (Fig. 7B); posterior region of metaventrite with narrow transverse strip of tegument with distinct rivose microsculpture; centre and posterior region with dense micropunctation and without microsculpture.

LEGS. Ventral surface of all femora and tibiae bright. Profemora with tegument with sparse micropunctation and without microsculpture at anterior half, and with strong rivose microsculpture at posterior half. Protibiae narrow and with distinct expansion on the internal edge; at their apical third, external edge with three small acute teeth, the two most apical ones subequal in length and larger than the basal (Fig. 11E). Mesofemora margined anteriorly only at their basal half; unmargined portion of anterior edge covered by row of very short setae; posterior margin absent; tegument smooth and with sparse micropunctation, except for anterior half, which has rivose microsculpture. Metafemora margined only anteriorly, posterior margin absent; apical third of anterior edge covered by row of setae; tegument with rivose microsculpture at anterior half, and smooth with sparse micropunctation at posterior half; base with very short, ill-delimitated or even almost totally absent coarse punctures (Fig. 13D). Metatarsomeres II and V subequal in length and longer than the others; metatarsomere IV shorter than the others.

ELYTRA. With only six or seven narrow visible striae: the first three striae well marked, finely carinulate, and widened at base; striae IV–VII progressively more effaced and interrupted; all striae lack carinulae before reaching apex of elytra, where they are marked only by microsculpture or are completely indistinct; humeral carina absent. Tegument of interstriae shiny, with very diffuse microsculpture (never in a well-delimitated alveolar pattern as in *S. furvus*) and with very dense micropunctation.

ABDOMEN. Tegument of ventrites I–V with strong rivose microsculpture; ventrite VI smooth at centre and with weaker rivose microsculpture on sides. Pygidium with shiny tegument, without microsculpture, and with dense micropunctation.

Aedeagus. Parameres much longer than half-length of phallobase, and without noticeable asymmetry, both external faces flat. In lateral view, parameres with apex widely bifurcate, with inferior branch of bifurcation distinctly projected and divergent from superior branch; without ventral keel or notch (Figs 19E, 44A–B).

Sexual dimorphism. **Males**: Protibial spur broad and bifid, with external projection spiniform and not much longer than internal projection, which is bent and widened (Fig. 15N). Abdomen without lateral foveae. Ventrite VI strongly narrowed at centre due to distinct emargination on posterior edge; anterior edge slightly covered by weak medial flange of posterior edge of ventrite V. Pygidium very long (length between 1.2 and 1.1 mm) and convex; apical margin of pygidium much wider than lateral margins. **Females**: Protibial spur spiniform. Abdomen with three pairs of very shallow transverse foveae located between ventrites I–II, II–III, and III–IV, respectively; foveae not margined by row of long setae (Fig. 16B). Ventrite VI wide at centre, posterior edge straight, without emargination; anterior edge subtly covered by medial flange of posterior edge of ventrite V. Pygidium shorter (between 0.9 and 0.8 mm) and flat; apical margin of pygidium only slightly wider than lateral margins.

Measurements

Males (N = 2). **TL:** AV: 7.0 ± 0.35; MX: 7.3; MN: 6.8. **EW:** AV: 5.0 ± 0.21; MX: 5.2; MN: 4.9. **PrL:** AV: 2.3 ± 0.07 MX: 2.4; MN: 2.3. **PrW:** AV: 4.4 ± 0.21; MX: 4.6; MN: 4.3. **PgL:** AV: 1.15 ± 0.07; MX: 1.2; MN: 1.1. **PgW:** AV: 2.2 ± 0.14; MX: 2.3; MN: 2.1.

Females (N = 2). **TL:** AV: 6.75 ± 0.07; MX: 6.8; MN: 6.7. **EW:** AV: 4.8 ± 0.35; MX: 5.1; MN: 4.6. **PrL:** AV: 2.05 ± 0.07; MX: 2.1; MN: 2.0. **PrW:** AV: 4.15 ± 0.21; MX: 4.3; MN: 4.0. **PgL:** AV: 0.85 ± 0.07; MX: 0.8; MN: 0.9. **PgW:** AV: 2.05 ± 0.07; MX: 2.1; MN: 2.0.

Geographical distribution

Western Amazonia, in Colombia, Brazil, and Peru.

Ecoregions

Guianan Moist Forests, Marajó Varzea, Japurá-Solimões-Negro Moist Forests.

Collecting sites (Fig. 41)

COLOMBIA. **Meta**: Villavicencio.

BRAZIL. **Acre**: Senador Guiomard. **Amazonas**: São Paulo de Olivença.

PERU. **Madre de Dios**: Tambopata (Puerto Maldonado).

Intraspecific variation and taxonomic discussion

Of all the species of *Sylvicanthon*, *S. mayri* sp. nov. is certainly the most enigmatic, with only four known individuals in collections, two males and two females. What we know about its distribution, for instance, is clearly fragmentary. The four known localities lie in western Amazonia and, together, they form a longitudinal arc with almost 2000 km from one end to the other (namely, Villavicencio, Colombia, in the north, and Puerto Maldonado, Peru, in the south) (Fig. 41). Some questions can be raised from this observation: does *S. mayri* sp. nov. also occur in the interior of Peru and in Ecuador or northern Bolivia? Is its distribution extended eastwards into the lowlands of the Brazilian Amazonia? Does this species also occur across the eastern slopes of the Andes in Peru and Ecuador as it does in Colombia? These questions will only be answered when a larger number of dung beetle collections are made throughout the Amazon Basin, especially in the state of Amazonas (Brazil), from where very little *Sylvicanthon* material is known (mostly from the capital, Manaus).

The morphological differences with the other two species of the *furvus* subgroup to which *S. mayri* sp. nov. is most similar (*S. furvus* and *S. monnei* sp. nov.) are very clear even from the small number of specimens we currently have on hand. *Sylvicanthon furvus*, in general, is distinguished from *S. mayri* sp. nov. in presenting a very strong microsculpture throughout the body tegument. This is very clear especially on the meso- and metafemora (which are almost entirely smooth, except in the apical areas of rivose microsculpture in *S. mayri* sp. nov., while they are totally covered by rivose microsculpture in *S. furvus*), and elytra (which have a diffuse microsculpture in *S. mayri* sp. nov., while they have a strong alveolar microsculpture obliterating the micropunctation in *S. furvus*). From *S. monnei* sp. nov., *S. mayri* sp. nov. is different mainly in the shape of parameres (with a strongly bifurcate apex, with its inferior branch distinctly divergent from the superior one, in *S. mayri* sp. nov. (Fig. 44A–B), and apical bifurcation branches only weakly divergent and with inferior branch only little projected and straight in *S. monnei* sp. nov. (Fig. 44C–D)). Lastly, the coarse punctation at the base of metafemora is distinct between *S. mayri* sp. nov., on the one side, and *S. furvus* and *S. monnei* sp. nov., on the other: in the two latter species, those punctures are clearly impressed and are elongated (Fig. 13C, E), while they are very fine and almost indistinguishable from the micropunctation in *S. mayri* sp. nov. (Fig. 13D). For a more detailed comparison between these three species and also with *S. obscurus*, see the discussions of *S. furvus*, *S. obscurus*, and Table 5.

Comments

The holotype of *Sylvicanthon mayri* sp. nov. is part of a large series of dung beetles collected in 1997 by the second author in the Brazilian state of Acre (some of the results of those collections were published in Vaz-de-Mello 1999). The Fazenda Experimental Catuaba, research base administered by the Federal University of Acre, contrary to what is said on the holotype's precedence label, is not located at the limits of the municipality of Rio Branco, but rather it is in the municipality of Senador Guiomard, about 25 km from the centre of Rio Branco. We revised for this work a great volume of envelopes with material collected by FZVM at Fazenda Catuaba and other nearby localities, but we failed to find any other specimens of *S. mayri* sp. nov. As argued earlier in this monograph, this fact should reflect the low population density the species of the *furvus* subgroup naturally have (see the discussion on *S. furvus*).

Natural history

The only specimen of *S. mayri* sp. nov. with known food habit data is the paratype from Villavicencio, which was collected in a pitfall trap baited with dung. The collecting months accurately reported were February and March, with the period June─July being the date reported for the São Paulo de Olivença specimen. Nothing more is known about the biology of *S. mayri* sp. nov.

Genus ***Canthon*** Hoffmannsegg, 1817

Canthon xanthopus Blanchard, 1846 restauration of original combination

Figs 7C, 45

Canthon xanthopum Blanchard, 1846: 166.

Canthon xanthopum – Blackwelder 1944: 202.
Canthon xanthopus – Lacordaire 1856: 78. — Harold 1868a: 140, 144; 1869b: 995. — Gillet 1911: 34. — Schmidt 1922: 72, 82. — Balthasar 1939: 226. — Martínez 1949b: 188; 1959: 45–46. — Vulcano & Pereira 1964: 636. — Halffter & Martínez 1977: 63. — Krajcik 2012: 64.

Glaphyrocanthon xanthopus – Martínez *et al.* 1964: 8.
Sylvicanthon xanthopus – Halffter & Martínez 1977: 63.

Etymology

From the Greek word '*xanthos*', meaning 'yellow'. Referring to the leg's yellowish colouration of this species, "Canthon *à pattes jaunes*" (Blanchard 1846).

Material examined

Lectotype (here designated)

BOLIVIA: ♂ , Santa Cruz, Vallegrande, cited by Blanchard (1846) as "*Province de Valle Graude*", ("LECTOTYPE ♂ / *Canthon* / *xanthopum* / *Blanch*. / des. F. Z. Vaz-de-Mello, 20*14*", "Type", "*Canthon* / *xanthopus* / *Blanch*", "Museum Paris / Santa-Cruz / (Valle Grande) / d'Orbigny 1834", "*6 B11* / *94*") (MNHN) (Fig. 45A).

Additional material (7 ♂♂, 12 ♀♀)

BOLIVIA: **Santa Cruz**: 1 ♀, Samaipata, Refugio Los Volcanes, 18º06.3′ S, 63º35.9′ W, 1050 m, 21–25 Feb. 2010, carrion, Edmonds and Vidaurre leg. (TAMU); 7 ♂♂, 11 ♀♀, Samaipata, Refugio Los Volcanes, 18º06.3′ S, 63º35.9′ W, 1050 m, 21–25 Feb. 2010, dead millipede, Edmonds and Vidaurre leg. (TAMU).

Collecting sites

BOLIVIA. **Santa Cruz**: Samaipata (Refugio Los Volcanes), Vallegrande.

Comments

The internal classification of the genus *Canthon*, as mentioned before, is extremely confusing and the genus is likely polyphyletic. Therefore, pointing out a clear relationship of *C. xanthopus* with any of the *Canthon* species groups could only be done in a tentative manner. By its overall morphology,

Fig. 45. *Canthon xanthopus* Blanchard, 1846. **A**. Lectotype and its labels. **B**. An ordinary specimen.

especially regarding the shape of protibiae and the presence of a long humeral carina reaching the apex of elytra, *C. xanthopus* seems to be close to the four species of the *maldonadoi* group, which is part of the *septemmaculatus* lineage as defined by Halffter & Martínez (1977). Nonetheless, the presence of a carina separating pygidium from propygidium in *C. xanthopus* is a feature that distinguishes this species from the members of that group – which do not possess any separation between pygidium and propygidium – and places *C. xanthopus* in the nominotypical subgenus. Therefore, a more careful analysis of the members of *Canthon* should be performed before a more confident decision is taken on the relationship between *C. xanthopus* and any particular species group. Hence, this species is put in *incertae sedis* within *Canthon* s. str.

As discussed earlier in this work, the name *Glaphyrocanthon cobosi* was considered a junior subjective synonym of *C. xanthopus* by Halffter & Martínez (1977) and has remained so up until now. It is interesting to revisit the taxonomic history of both names to understand the historical context that ultimately led Halftter & Martínez to propose that synonymy.

The true identity of *Canthon xanthopus*, described from "Province de Valle Graude", Santa Cruz, Bolivia, was a mystery to scarabaeidologists for more than a century since its description by Blanchard (1846), which was based on very vague and imprecize characters such as the shape of the clypeus and the colouration of the tegument. In his revision of *Canthon*, Harold (1868b) included *C. xanthopus* in a list of 23 species names he could not relate to any known species taxa, and that situation persisted even after his following year's study of the MNHN collection (Harold 1869c), where until today one of the syntypes of *C. xanthopus* is housed. The same is true for the revisions of Schmidt (1922) and Balthasar (1939), who did not include *C. xanthopus* in their identification keys.

The name, then, would not be mentioned again until Martínez *et al*. (1964). Those authors, in a footnote to their identification key to the species of *Glaphyrocanthon*, wrote that, judging only from its original description, it could be presumed that *C. xanthopus* was "very close" to *Glaphyrocanthon cobosi* Pereira & Martínez, 1960, a species also described from Santa Cruz, Bolivia. Nevertheless, *C. xanthopus* was not included in their key because they claimed they had never seen specimens of this species in person. Thirteen years later, Halffter & Martínez (1977) stated they had finally found "the type" of *C. xanthopus* in the MNHN. On examining it, they concluded that *C. xanthopus* and *G. cobosi* were synonyms and the species had to be transferred to *Sylvicanthon*.

During the preparation of this work, we found a specimen in the MNHN collected in 1834 by the French explorer and naturalist Alcide d'Orbigny (1802–1857) in the province of Vallegrande, Santa Cruz, Bolivia. That specimen fully agrees with Blanchard's description and collecting data, which led us to consider it one of the syntypes of *C. xanthopus*, the only one known to us. No specimens found at the MNHN bear any label by Gonzalo Halffter or Antonio Martínez; therefore, we do not know which specimen they were referring to when they wrote they had examined "the type" of *C. xanthopus*.

The study of that syntype (now lectotype) of *C. xanthopus* (Fig. 45A) and its comparison with the holotype of *G. cobosi* (Fig. 46A, deposited in the MACN) leave no doubt that the synonymy proposed by Halffter & Martínez (1977) is incorrect. Both species are easily distinguishable from one another by the shape of the eyes (with about ⅛ of the width of the interocular space in what is now known as *Canthon cobosi*, and ⅒, in *C. xanthopus*), the shape of the protibiae (with tiny teeth and truncate apex in *C. cobosi*, and with large teeth and an apex occupied by the apical tooth in *C. xanthopus*), the shape of the clypeal teeth (small, obtuse and separated from one another by a clypeal emargination in *C. cobosi*, and large, acute, without emargination in *C. xanthopus*), and the hypomeron (strongly excavated, with a tooth on the external edge, with a complete hipomeral carina in *C. cobosi*, only slightly depressed, without any teeth, and with a very short hipomeral carina in *C. xanthopus*). For a discussion on the transfer of both species to the genus *Canthon*, see the section 'Species composition' under *Sylvicanthon* above.

Canthon cobosi (Pereira & Martínez, 1960) revalidation and comb. nov.

Fig. 46A

Glaphyrocanthon (*Glaphyrocanthon*) *cobosi* Pereira & Martínez, 1960: 45–47

Glaphyrocanthon (*Glaphyrocanthon*) *cobosi* – Martínez *et al.* 1964: 5, 8, 11, 14. — Vulcano & Pereira 1964: 662; 1967: 561. — Halffter & Martínez 1977: 63 (as junior synonym of *Sylvicanthon xanthopus*).

Etymology

The specific name refers to the Spanish entomologist Antonio Cobos Sánchez (1922–1998) (Pereira & Martínez 1960).

Material examined

Holotype

BOLIVIA: ♀, Santa Cruz, Cordillera, Las Juntas, ("*BOLIVIA* / *Dº Sta. Cruz* / *Pcia. Cordillera* / *Las Juntas* / *Maldonado B: ! !* / *Coll. Martínez* / *Oct.-948*", "HOLOTYPUS", "*Glaphyrocanthon* / *(Glaph.)* / *cobosi sp.n.* / ♀ / A. Martínez det. 19*56*", "*FICHADO*", "MACN-En / 1009") (MACN) (Fig. 45B).

Additional material (22 ♂♂, 26 ♀♀)

ARGENTINA: **Jujuy**: 1 ♀, Parque Nacional Calilegua, Águas Negras, 500 m, 18 Dec. 1987, S. and J. Peck leg. (CMNC); 3 ♂♂ (1 dissected), 5 ♀♀, Santa Barbara, Yuto, Feb. 1982 (CMNC).

BOLIVIA: **Santa Cruz**: 1 ♂, Cordillera, Parabanó (CEMT); 1 ♀, Cordillera, Río Seco, Feb. 1961 (CMNC); 1 ♂, 4 ♀♀, Cordillera, Río Seco, Feb. 1962 (CMNC); 1 ♂, Santa Cruz de la Sierra, Río Piraí, Sep. 1964 (?) (CMNC); 2 ♂♂, 2 ♀♀, Tentarembei, 18º28′ S, 62º05′ W, 318 m, 6 Feb. 2010, human faeces, Vidaurre *et al.* leg. (CEMT); 3 ♂♂, Sara, Santa Rosa del Sara, Nov. 1969 (CMNC); 1 ♀, Santa Rosa del Sara, Nov. 1972 (CMNC).

BRAZIL: **Mato Grosso**: 5 ♀♀, Barra do Bugres, Rio Currupiras, 15º10′08.2″ S, 56º50′22.7″ W, 296 m, 28 Feb. 2010, pitfall with human faeces, J.G. Mota-Souza leg. (CEMT). – **Mato Grosso Do Sul**: 2 ♀♀, Aquidauana, Piraputanga, 17 Jun. 2000, V. Lopes leg. (CEMT); 1 ♂, Bodoquena, Fazenda Califórnia, 20º41′05″ S, 56º51′33″ W, Mar. 2011, human faeces, L.O. Bavutti leg. (CEMT); 1 ♂, Bodoquena, Fazenda Califórnia, 20º41′08″ S, 56º51′31″ W, Mar. 2011, human faeces, L.O. Bavutti leg. (CEMT); 1 ♀, Bonito, Fazenda Palmeirinhas, 21º11.269′ S, 56º33.701′ W, Nov. 2009, banana, F.O. Roque leg. (CEMT); 1 ♂, 2 ♀♀, Bonito, [Hotel] Cabanas, 21º10′15″ S, 56º26′22″ W, Dec. 2010, human faeces, L.O. Bavutti leg. (CEMT); 1 ♀, Bonito, Hotel Cabanas, 21º10′17″ S, 56º26′26″ W, Dec. 2010, human faeces, L.O. Bavutti leg. (CEMT); 1 ♀, Bonito, Hotel Cabanas, 21º10′20″ S, 56º26′37″ W, Dec. 2010, human faeces, L.O. Bavutti leg. (CEMT); 1 ♀, Bonito, Hotel Cabanas, 21º10′21″ S, 56º26′34″ W, Dec. 2010, human faeces, L.O. Bavutti leg. (CEMT); 1 ♂, Corguinho, Quinta do Sol, 19º49′57″ S, 54º49′45″ W, Feb. 2011, human faeces, L.O. Bavutti leg. (CEMT); 1 ♂, Corumbá, Dec. 2007, C. Aoki leg. (AMBC); 1 ♂, same collecting data as for preceding (CEMT); 1 ♂, 1 ♀, Corumbá, Passo do Lontra, Dec. 2005, J.N.C. Louzada leg. (CEMT); 1 ♂, Ivinhema, 22º31′41″ S, 53º53′38″ W, Mar. 2011, human faeces, L.O. Bavutti leg. (CEMT); 1 ♂, 1 ♀, Jardim, Jun. 2000, V. Lopes leg. (CEMT); 1 ♀, Jardim, Rio da Prata, 21º25′40″ S, 56º27′00″ W, Mar. 2011, human faeces, L.O. Bavutti leg. (CEMT).

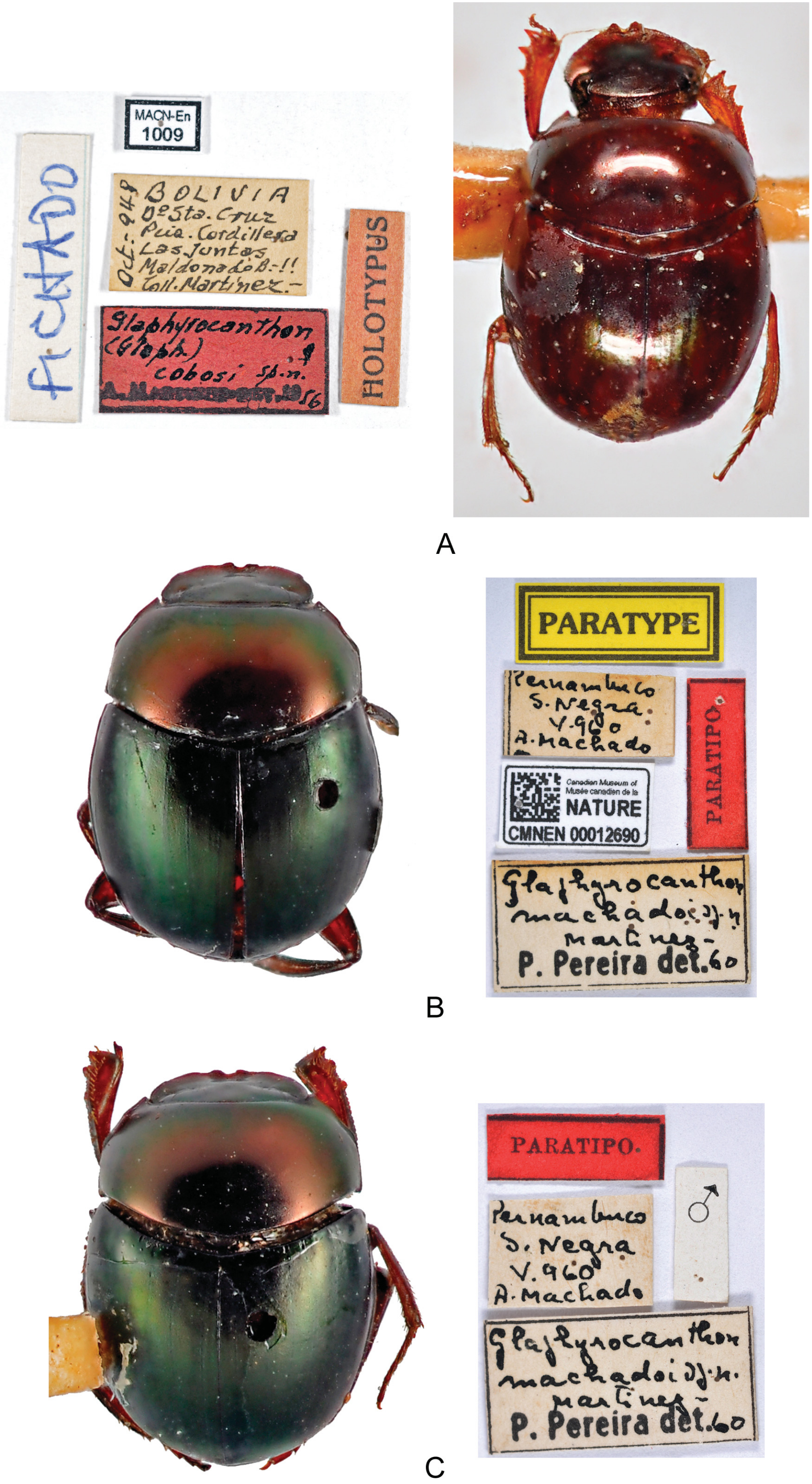

Fig. 46. A. *Canthon cobosi* (Pereira & Martínez, 1960) stat. et comb. nov., holotype. **B–C**. *Canthon machadoi* (Martínez & Pereira, 1967) comb. nov. **B**. Paratype 2. **C**. Paratype 4.

PARAGUAY: **Cordillera**: 1 ♀, 5 Jul. 2005, Naraujo leg. (CEMT); 2 ♂♂, Caacupé ("*Dº Capital* / *Caa Cupé*"), Oct. 1979 (CMNC).

Collecting sites

BRAZIL. **Mato Grosso**: Barra do Bugres. **Mato Grosso do Sul**: Aquidauana (Piraputanga), Bodoquena, Bonito, Corguinho, Corumbá, Ivinhema, Jardim.

BOLIVIA. **Santa Cruz**: Cordillera (Las Juntas, Río Seco), Santa Cruz de la Sierra, Sara (Santa Rosa del Sara).

PARAGUAY. **Cordillera**: Caacupé.

ARGENTINA. **Jujuy**: Parque Nacional Calilegua, Santa Barbara.

Comments

From the only geographical record ever published for *C. cobosi* – the locality of Las Juntas, in the province of Cordillera, Santa Cruz, Bolivia –, the known distribution of this species is widened to encompass areas also in Brazil (Mato Grosso and Mato Grosso do Sul), Paraguay and northern Argentina. There is, however, a noteworthy geographical variation that, when studied in more detail, may reveal that what we are considering to be a single species represents, in fact, two: specimens from Brazil, in general, are darker, with few coppery reflections, while individuals from Bolivia, Argentina and Paraguay show a coppery colouration with greenish reflections (Fig. 46A). As no other morphological variations were found and as there is chromatic variation even among individuals from Brazil (being some of them more coppery than others), we do not consider we have at this moment enough evidence for the existence of more than a single species. Nonetheless, we recognize that more research is needed in order to have a deeper understanding of the inter- and intrapopulational variation of *C. cobosi*. For details on the revalidation of this species from its synonymy with *C. xanthopus*, see the discussion under this latter species, while for details on its transference to *Canthon*, see section 'Species composition' under *Sylvicanthon* above.

Canthon machadoi (Martínez & Pereira, 1967) comb. nov.

Fig. 46B–C

Glaphyrocanthon machadoi Martínez & Pereira, 1967: 53–55

Glaphyrocanthon machadoi – Halffter & Martínez 1977: 63.
Sylvicanthon machadoi – Halffter & Martínez 1977: 63. — Vaz-de-Mello 2000: 195. — Silva *et al.* 2007: 230. — Costa *et al.* 2009: 91.
Canthon machadoi – Krajcik 2012: 64.

Etymology

The specific name refers to the Brazilian odonatologist Ângelo B.M. Machado, collector of the type series (Martínez & Pereira 1967). Pinto (2016) presented an interesting short biography of Ângelo Machado.

Material examined

Paratypes (4 ♂♂, 1 ♀)

BRAZIL: 1 ♂ ("*Glaphyrocanthon* / *machadoi sp. n* / *Martinez* - / P. Pereira det. *60*", "PARATIPO", "PARATYPE", "*Pernambuco* / *S. Negra* / *V.960* / *A. Machado*", "Canadian Museum of / Musée canadian de la / NATURE / CMNEN 0012690") (CMNC); 1 ♀ ("*Pernambuco* / *S. Negra* / *V.960* / *A. Machado*", "*Glaphyrocanthon* / *machadoi sp. n* / *Martinez* - / P. Pereira det. *60*", "PARATIPO", "PARATYPE", "♀", "H. & A. HOWDEN / COLLECTION / ex A. Martínez coll.", "Canadian Museum of / Musée canadian de la / NATURE / CMNEN 00019066") (CMNC); 1 ♂ ("*Pernambuco* / *S. Negra* / *V.960* / *A. Machado*", "*Glaphyrocanthon* / *machadoi sp. n* / *Martinez* - / P. Pereira det. *60*", "♂", "PARATIPO") (MZS); 1 ♂ ("*Pernambuco* / *S. Negra* / *V.960* / *A. Machado*", "*Glaphyrocanthon* / *machadoi sp. n* / *Martinez* - / P. Pereira det. *60*", "♂", "PARATIPO") (MZSP); 1 ♂ ("*Pernambuco* / *S. Negra* / *V.960* / *A. Machado*", "*Glaphyrocanthon* / *machadoi sp. n* / *Martinez* - / P. Pereira det. *60*", "♂", "PARATIPO") (MZSP).

Collecting sites

BRAZIL. **Pernambuco**: Reserva Biológica de Serra Negra.

Comments

The eight specimens of the type series of *C. machadoi* are the only known individuals of this species, which is apparently endemic to a '*brejo de altitude*' (Caatinga moist-forest enclave) in the Brazilian state of Pernambuco. However, only five of those specimens were found during this work: three male paratypes housed at the MZSP, and a male and a female paratype at the CMNC. Martínez & Pereira (1967) mentioned the holotype male and allotype female of *C. machadoi* were deposited at the "author's collection", without specifying which of the authors. As said earlier in this work, Martínez's holotypes and allotypes are nowadays housed at the MACN, while paratypes and ordinary specimens were incorporated to the CMNC via the Henry and Anne Howden collection. In none of them, however, either the holotype or the allotype of *C. machadoi* is preserved. Therefore, the whereabouts of those two specimens is unknown to us. As for the fifth male paratype, Martínez & Pereira (1967) stated it was deposited in the personal collection of its collector, Ângelo Machado (Belo Horizonte, Minas Gerais, Brazil), and it is probably still housed there.

Discussion

As discussed throughout this work, the taxonomy of *Sylvicanthon* – both the delimitation of its species and the limits of the genus itself – was in great chaos when we decided to undertake the project of revising it. With the findings presented by us in the previous pages, we propose solutions to many of the problems surrounding the systematics of *Sylvicanthon* and raise questions to be answered by future works. In the following paragraphs, we discuss some of our main proposals.

It was seen throughout this work that the set of taxonomically-informative characters is somewhat limited among *Sylvicanthon*. The main sources of evidence used for species delimitation and hypotheses of evolutionary relationships were the microsculpture of the tegument of head, pronotum, elytra, pygidium, metaventrite and the ventral surface of the metafemora, the shape of clypeus and protibiae, the pilosity of the hypomeral cavity and of the sides of the metaventrite, and some secondary sexual characteristics such as the shape of the protibial spur, the presence or absence of female abdominal foveae and the shape of the female ventrite V, as well as important characters related to the shape of the parameres. This set of characters, in fact, little differs from the ones used in other recent works dealing with the taxonomy of New World Deltochilini such as Rivera-Cervantes & Halffter (1999), González-Alvarado & Vaz-de-Mello (2014), Valois *et al.* (2015), Silva *et al.* (2015) and Nunes *et al*. (2018). The shape of the parameres and the microsculpture pattern, in particular, appear to bear good signal for very recent relationships (i.e., for species delimitation), showing that they are in a constant and profound evolutionary change. The role of sexual selection in the evolution of the parameres is evident, as discussed in detail in this paper, but the evolutionary forces acting on the microsculpture of the body's surface are not clear yet. One of the next frontiers to be explored by future studies on the morphology of *Sylvicanthon* is the anatomy of the pieces of the internal sac and the female genitalia which should provide some new interesting insights for the understanding of the group's diversity and evolution, especially concerning the role that sexual selection had in the genus' diversification.

Until the present work, very little was known about the distribution of the species of *Sylvicanthon*. In general, only the type locality or some very imprecize records from countries, states, or departments were known (and very often they were incorrect). With the results here obtained, it was seen that the inference of Halffter & Martínez (1977) that the *Sylvicanthon* species were essentially tropical forest dwellers was correct. With the exception of *S. enkerlini* which lives in dry forests between the Amazonia, Cerrado, Caatinga and the Atlantic Forest, all the other 14 species are found exclusively in the New World's four great areas of tropical rainforest: the Central American forests, the Chocó, the Amazonia, and the Atlantic Forest.

Martínez *et al.* (1964) hypothesized that the ancestral area of *Sylvicanthon* (cited as "grupo *aequinoctialis*" of *Glaphyrocanthon*) was the Amazon Basin. Given that the greatest diversity of the genus is indeed found there, with representatives of all subgroups present in that biome (including all members of the *bridarollii* and *securus* subgroups), this hypothesis seems to be correct. From that Amazonian ancestral area, at least three lineages independently dispersed towards the other tropical forest areas of the Americas. Firstly, the ancestors of *S. aequinoctilis* which probably invaded Central America during the Plio-Pleistocene as part of the Great American Biotic Interchange, at the same time as South American tropical forests spread northwards after the uplift of the Isthmus of Panama. Secondly, the ancestors of *S. foveiventris* and *S. obscurus* which independently arrived in the Atlantic Forest through the rich gallery forests and pockets of humid forests that flourished throughout the South American Dry Diagonal and connected the Amazonia to the Atlantic Forest during the Neogene. It is interesting to note that no species of *Sylvicanthon* are present in the Atlantic Forest south of the state of São Paulo, fact possibly explained by the lower average temperature in that southern region.

The major proposals for the relationships of *Sylvicanthon* with other Deltochilini groups are discussed in detail above. The first one – called by us "the *Glaphyrocanthon* clade hypothesis" and which is here championed as the most plausible explanation – states that the genus *Glaphyrocanthon* as defined today (i.e., based on Halffter & Martínez 1977) represents a large paraphylum from which several deltochiline lineages evolved, such as *Sylvicanthon*. This hypothesis finds some support in the only cladistics study that aimed at testing the phylogenetic relationship of the members of "*Canthon* sensu lato" (Medina *et al.* 2003). A second hypothesis – the Epilissini tribe – was championed by Montreuil (2010) and states that several telecoprid genera whose hypomeron is strongly excavated and protibiae are truncate at the apex would form a monophyletic group that arose in ancient Gondwana and that is nowadays scattered throughout the Americas, Africa, Madagascar, Southeast Asia and Australia. *Sylvicanthon*, although not cited by Montreuil (2010), would also be part of that clade judging from the characters listed by that author (Montreuil, personal communication to MC in June 2014, confirmed this observation). Finally, the third hypothesis, which is not incompatible with that of the Epilissini tribe, states that *Sylvicanthon* would be part of a putative clade formed by deltochiline genera with tarsal claws bearing a strong basal tooth, such as *Canthonella* and *Ipselissus*, from the New World, *Temnoplectron* and *Sauvagesinella*, from Australasia, and *Nesovinsonia*, from the island of Mauritius. Theorized by Halffter & Martínez (1967) and Matthews (1974), this group did not originally include *Sylvicanthon* possibly because those authors were unaware of the presence of a tiny tooth at the base of the claws of the species of *Sylvicanthon*, which is likely to be homologous to the larger tooth seen in *Pseudocanthon* and other groups studied by them. It is of great interest that future phylogenetic analyses test these three hypotheses.

In conclusion, therefore, this monograph revised the entire published knowledge, as well as a great volume of new data, on the species of the genus *Sylvicanthon* and proposed answers to some questions long posed by scarab beetle specialists. At the same time, we present new fascinating observations that we hope will instigate researchers to investigate the group's diversity through different perspectives, including the application of distinct morphological, molecular, ecological and evolutionary tools. These future studies, in turn, will shed light on the new questions raised by us throughout this monograph on the evolution of the *Sylvicanthon* and the rest of the New World dung beetle fauna.

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Appendix 1: Endnotes

[1] Throughout this monograph, the words systematics and taxonomy are treated as synonyms and, therefore, interchangeable. The following working definition is given: Systematics (= taxonomy) is the comparative study of the biological diversity, including the delimitation all of its hierarchical constituents (e.g., genes, populations, species and superior taxa), these constituents' evolutive (i.e., phylogenetic) relationships, and the ultimate (i.e., historical) causes that explain current and past states in terms of morphology, genetics, and distribution of Earth's biodiversity and each of its constituents.

[2] In fact, this and the other theoretical discussions present in this work (e.g., the definition of systematics, the critique of the 'extinction by speciation' idea, the use of the superspecies concept, and so on) were developed and written by the first author and are not necessarily endorsed either in full or in part by the second author. Therefore, for the sake of accuracy, they should be cited as 'Cupello in Cupello & Vaz-de-Mello'.

[3] According to Mayr (1982, 1985, 2004b), what is usually regarded by many authors as 'the' Darwinian Theory is, actually, a set of five major independent theories developed by Charles Darwin over several decades, namely the non-fixism ('evolution as such'), common descent, gradualism, populational speciation ('multiplication of species'), and natural selection. MC would also add the theory of sexual selection to this list due to the theory's key role both in Darwin's own view of the dynamics of the evolutionary process and in the modern evolutionary thinking.

[4] The case of new species originating from small, hybrid founder populations like the one described in Lamichhaney *et al.* (2018) clearly shows how problematic the procedure adopted by Hennig (1966) and the advocates of the so-called Hennigian species concept (e.g., Meier & Willmann 2000) – the so-called Hennigian Convention (Wilkins 2009; Zachos 2016) – of considering that an ancestral species always becomes extinct while giving origin to daughter species (i.e., when a speciation event involving some of its members occurs) can be. In the illustrative example in Lamichhaney *et al.*, a single male of the Darwin's finch *Geospiza conirostris* Ridgway, 1890 immigrated from its original endemic range on the small island of Española to the also small island of Daphne Major, both in the Galapagos Archipelago, but distant from one another by more than 100 km. On Daphne Major, that errant *G. conirostris* male bred with a resident *G. fortis* Gould, 1837 female, a crossing that gave origin to a new inbreeding lineage that, with just a single case of backcrossing between a F_1 male and a female of *G. fortis*, has remained isolated and both ecologically and morphologically distinct from the remainder populations of *Geospiza* Gould, 1937 on the island over the past 37 years. This fact led Lamichhaney *et al.* to infer that a rapid hybrid speciation event had occurred on Daphne Major. Consequently, should we apply the Hennigian procedure of considering the ancestral species extinct once a new daughter species arises, then both *G. fortis* and *G. conirostris* would now have to be considered extinct and new names would have to be established for them, even though no more than two individuals of each (only one of the latter) participated in that speciation event and their population structure as a whole was not affected by that event (in other words, it would have be indifferent for the population structure of *G. fortis* whether that errant male had died in the sea or given origin to a new hybrid species somewhere else). Besides, if we consider that the speciation process was fully completed as soon as the last backcrossing occurred, then individuals of *G. fortis* and *G. conirostris* living on their respective islands would have been born as part of one species and, in the course of their lives, would have changed to another species as soon as the hybrid species had been established. Finally, if we were to accept that an ancestral species must be automatically considered extinct as soon as a single errant individual forms a new hybrid species elsewhere, then we would never know whether the species we are dealing with today is the same as yesterday, since there will always be the possibility that some individual has interbred with a member of another species over the past night and potentially started the formation of a new hybrid species. The most reasonable

procedure, therefore, is to apply the concept of extinction by speciation only to populational processes and, especially, to events of dicopatric speciation, when the structure of the entire metapopulation is affected, not just a small subset of it or some few peripheral isolates as in the cases of peripatric and hybrid speciation.

[5] The difficulty in interpreting the populational nature of the Biological Concept is clear, for example, in Hausdorf (2011), who stated that it would make no difference in replacing the expression 'natural populations' with 'individuals' in the definition given by Mayr (1942). In fact, the difference between these terms becomes evident as soon as one realizes that 'natural populations' gives a probabilistic character to the concept, whereas 'individuals' makes it essentialist and deterministic. In the same way, the assertion of Cain (2009) that Mayr defended reproductive isolation as a "simple test for species rank" is a clear misunderstanding of the distinction between the species category and the species taxa (although it would be fair to say that some of Mayr's later writings (e.g., Mayr 2000) are indeed fairly confusing on this point).

[6] Authorship following Hegna *et al.* (2013).

[7] Subphylum's and class' authorship following Kluge (2010).

[8] Order's and suborder's authorship following Beutel & Leschen (2005).

[9] Family-group names' authorship following Bouchard *et al.* (2011).

[10] With the term '*Canthon* sensu lato', we intend neither to refer to a natural (i.e., monophyletic) group nor to propose a new formal classification. In fact, as we shall discuss, it is certain that this assemblage is rather artificial. When this term is employed, therefore, we only refer to a group of genera that were proposed based on species originally described in *Canthon* or which have had at some moment of their history been considered as close relatives to *Canthon* and with which they share great part of their taxonomic history. See Table 1 for more details.

[11] As well argued by Vaz-de-Mello (2008: 13), this was also the case for several other dung beetle genera that were highly heterogeneous in the 19th and early 20th centuries and were eventually split out into a myriad of new genera in the 20th and the early 21st centuries (e.g., *Panelus* Lewis, 1895, *Epilissus* Dejean, 1836, *Stiptopodius* Harold, 1871, *Trichillum* Harold, 1868 and *Pedaridium*, 1868). Although, as written by Vaz-de-Mello (2008), this was particularly true for genera poorly represented in collections, this has never been the case with *Canthon*, which is fairly common in any European natural history museum.

[12] Interestingly enough, Scholtz (2009) discussed that the same problem should possibly occur with the classification of the African genera formely placed in Deltochilini (i.e., prior to Tarasov & Génier 2015 and Tarasov & Dimitrov 2016).

[13] This identification is probably incorrect. Medina *et al.* (2003) observed that the hypomeral cavity of the specimens they studied (which are from Colombia) was glabrous. True *S. bridarollii*, as seen in the present revision, have a long pilosity on the hypomeral cavity. The species studied by Medina *et al.* (2003) should have been *S. edmondsi* sp. nov., a species that is found in sympatry with *S. bridarollii* and with which it is commonly mistaken.

[14] Halffter & Martínez (1977), for instance, stated that some "phyletic lineages" could be delimited within *Glaphyrocanthon*: the "*Coprocanthon*", "*variabilis*", "*rubrescens*", and "*pallidus*" species groups.

[15] Although some results of that analysis are indeed quite questionable, as the positioning of the genus *Gromphas* Brullé, 1838 at the base of the phylogeny and totally apart from the Phanaeini, tribe which it belongs to (Cupello & Vaz-de-Mello 2013, 2016).

[16] Although *Canthon* (*Glaphyrocanthon*) *ibarragrassoi* (Martínez, 1952), from South America, may be an exception, depending on the interpretation of the nature of the fine line that runs horizontally across the midline of the ventral surface of its hindfemora. Martínez (1952: 62) interpreted this possible margin as being a "thin, sinuous median sulcus" ("*fino surco medial sinuoso*"), while Pereira & Martínez (1956: 144) described it as a "Weak, irregular sulcus at the middle of the ventral surface [of metafemora]" ("*débil sulco irregular no meio da face ventral*"). Nevertheless, judging from our examination of specimens of *C. ibarragrassoi* (including the holotype deposited at the MACN), this structure does not seem to be an impression on the surface of the tegument, but rather a thin elevation. Hence, it would be better described as a margin instead of a sulcus, notwithstanding its central positioning on the metafemora. It is possible therefore that this margin may be homologous to the margin seen in *Canthon* s. str. and other groups. A scanning electron microscope examination can certainly give us more details as to the nature of this structure.

[17] Each of these polygons corresponds to an individual cell from the tegument that produced it (Krell 1994; Byers & Hinks 1973).

[18] Matthews (1966), who discussed in detail the dispersal of Scarabaeinae in the Antilles, had already noted that the dung beetle fauna of Central and North Americas was dominated by South American elements. See also the extensive discussion on the New World dung beetle biogeography presented by Halffter & Morrone (2017) and Halffter's numerous articles cited therein.

[19] After completion of the first draft of this work, Bert Kohlmann (EARTH University, Costa Rica) brought to our attention that populations from Osa Peninsula (e.g., Parque Nacional Corcovado), on the Pacific coast of Costa Rica, are different from others in Central America in both morphology (especially the elytral microsculpture) and genetics. According to Kohlmann, the Osa Peninsula had a rather particular geological history and many of its biotic elements seem to be endemic to it; in several cases, the sister species of Osa's species are distributed in other parts of Costa Rica and Central America, particularly along the Caribbean coast, so revealing a very intriguing vicariant pattern. Based on these observations, the Osa Peninsula populations of the *aequinoctialis* subgroup are currently under in-depth study by Bert Kohlmann, Ángel Solís (Museo Nacional de Costa Rica) and MC. In the meantime, we maintain our original identification of those specimens as *S. aequinoctialis* comb. nov.

[20] In Colombia, the Andes, in its northernmost portion, are divided into three independent mountain ranges: the Cordilleras Ocidental, Central, and Oriental. The latter, the longest one, extends northwards, from near the border of Ecuador and Colombia to close to the Caribbean Sea, branching south of Lake Maracaibo into the Cordillera de Mérida, which penetrates Venezuela and almost reaches the coast. This creates a group of long and high mountain ranges that acts as an important barrier largely preventing animal movements between regions east and west of the Andes.

[21] Michele Rossini (Instituto Tecnico per l'Agraria, l'Agroalimentare e l'Agroindustria "A. Cecchi", Italy; personal communication to MC, 2018), who revised the taxonomy of the *Onthophagus* belonging to the New World *hircus* species group for his PhD thesis (whose partial results were published in Rossini *et al.* 2018a, 2018b), informed us that in fact *O. haematopus* is not present in Colombia, but instead it is endemic to the Atlantic Forest. Therefore, this must be a misidentification.

[22] In general, an easy way to see the distinction on metafemora is as follows: in *S. furvus*, the coarse punctures at the base of metafemora are mingled among a strong rivose microsculpture, while in *S. mayri* sp. nov. and *S. monnei* sp. nov. the area covered by the rivose microsculpture usually does not reach those punctures, which, then, rest among a smooth tegument. However, in some specimens, the rivose microsculpture extends farther inferiorly on the metafemora and reaches some of the superior coarse punctures.

Appendix 2: Additional material examined

Between the acceptance of the manuscript of the monograph and the production of its first proofs, the senior author (MC) had the opportunity to visit three other natural history museums – CEAH, FSCA and MCZC – and was able to examine some additional specimens of *Sylvicanthon*, including some further paratypes of two of the new species. This new material examined is listed in the following sections:

Sylvicanthon aequinoctialis (Harold, 1868)

Material examined

COSTA RICA: **Heredia**: 12 ♂♂, 4 ♀♀, Sarapiquí, Puerto Viejo, Finca La Selva, Jun. 1979, trap with human faeces, T. Ray and C. Andrews leg. (MCZC). – **Limón**: 1 ♂, Guácimo, EARTH University, pitfall with human faeces, Oct. 2004, K. Beucke leg. (FSCA).

PANAMA: **Bocas del Toro**: 1 ♂, "12–15 km W Punta Peña", 21–22 Feb. 1999, pitfall with pig dung, Turnbow and Wappes leg. (FSCA). – **Chiriquí**: 2 ♂♂, 3 ♀♀, Gualaca, Hornito, Finca la Suzia, 9–15 May 1999, dung trap, Morris and Wappes leg. (FSCA). – **Colón**: 1 ♀, Fuerte Sherman, 15–24 Feb. 1999, pitfall with pig dung, R. Turnbow leg. (FSCA). – **Panama**: 3 ♂♂, "0.3 km W El Llano", 12 May 1996, dung trap, R. Turnbow leg. (FSCA); 4 ♂♂, 1 ♀, "10–15 km N El Llano", 425 m, 4–5 Jun. 1986, E. Giesbert, P.H. Sullivan and F.T. Hovore leg. (FSCA); 1 ♂, Barro Colorado Island, K.W. Cooper leg. (FSCA, ex R.E. Woodruff collection); 1 ♂, 2 ♀♀, same collecting data as for preceding (MCZC); 2 ♂♂, Barro Colorado Island, 22 Feb. 1955, C.R. Freund leg. (MCZC); 10 ♂♂, 7 ♀♀, Barro Colorado Island, Jul. 1969, J. Lawrence, B. Hlavac and T. Hlavac leg. (MCZC); 256 ♂♂, 97 ♀♀, Barro Colorado Island, Aug. 1969, J. Lawrence, B. Hlavac and T. Hlavac leg. (MCZC); 4 ♂♂, Barro Colorado Island, 30 Oct. 1973, E.J. Gerberg leg. (FSCA); 9 ♂♂, 8 ♀♀, Barro Colorado Island, 16–20 Feb. 1976, trap with human faeces, A. Newton leg. (MCZC); 1 ♂, 1 ♀, Barro Colorado Island, 31 Aug. 1978, trap with dung, A. Forsyth leg. (FSCA); 2 ♂♂, 1 ♀, Barro Colorado Island, "Shannon Trail", 15 Jun. 1961, leaf litter, E.O. Willis leg. (MCZC); 1 ♀, "Canal Zone, Madden Forest", 14 Dec. 1971, dung trap, H.P. Stockwell leg. (FSCA); 77 ♂♂, 55 ♀♀, "Canal Zone, Pipeline Road, Limbo Hunt Club", 26 May 1977, pitfall with human faeces, Lloyd R. Davis, Jr. leg. (FSCA); 6 ♂♂, 4 ♀♀, Cerro Azul, 12 May 1996, R. Turnbow leg. (FSCA); 2 ♂♂, 4 ♀♀, Cerro Azul, 12–13 May 1996, Wappes, Huether and Morris leg. (FSCA); 8 ♂♂, 3 ♀♀, Cerro Azul, 21 May 1996, R. Turnbow leg. (FSCA); 7 ♂♂, 5 ♀♀, Cerro Azul, 21–27 May 1996, Wappes, Huether and Morris leg. (FSCA); 3 ♂♂, Cerro Azul, 24 May 1996, pitfall with pig dung, R. Turnbow leg. (FSCA); 4 ♂♂, 3 ♀♀, Cerro Azul, 13–18 Feb. 1999, pitfall with pig dung, Turnbow and Wappes leg. (FSCA); 2 ♂♂, "El Llano-Carti Rd. km 7–9", 9 May 1996, pitfall with pig dung, R. Turnbow leg. (FSCA); 2 ♂♂, 1 ♀, "El Llano-Carti Rd. km 7–9", 24 May 1996, pitfall with pig dung, R. Turnbow leg. (FSCA); 1 ♂, "El Llano-Carti Rd. K 8–11", 1100 m, 24 May–2 Jun. 1992, J.E. Wappes leg. (FSCA); 3 ♂♂, "K 8–13 El Llano-Carti Rd", 21–24 May 1996, Wappes, Huether and Morris leg. (FSCA); 3 ♀♀, Parque Nacional Soberanía, 19–20 May 1999, Morris and Wappes leg. (FSCA); 3 ♂♂, 3 ♀♀, Parque Nacional Soberanía, 23–27 May 1996, Wappes, Huether and Morris leg. (FSCA); 1 ♂, 2 ♀♀, Parque Nacional Soberanía, 26 May 1996, pitfall with pig dung, R. Turnbow leg. (FSCA); 1 ♀, Parque Nacional Soberanía, 27 May 1996, dung trap, R. Turnbow leg. (FSCA); 4 ♂♂, "Pipeline Rd K 1–12", 26–30 Jun. 1997, Wappes and Morris leg. (FSCA); 4 ♀♀, "Pipeline Rd K 1–12", 30 Jun. 1997, dung trap, Morris and Wappes leg. (FSCA); 1 ♂, 4 ♀♀, "Pipeline Rd K 1–12", 8–9 Jul. 1997, dung trap, Morris and Wappes leg. (FSCA); 13 ♂♂, 5 ♀♀, "Pipeline Rd", 28 Jun.–9 Jul. 1997, R. Turnbow leg. (FSCA).

Sylvicanthon bridarollii (Martínez, 1948)

Material examined

BOLIVIA: **Cochabamba**: 1 ♀, Chapare (FSCA, ex E.N. Kellesvig–Waering collection); 1 ♀, Chapare, 15 May 1951, no collector (FSCA, ex E.N. Kellesvig–Waering collection); 2 ♀♀, Chapare, 400 m, 5 May 1951, no collector (FSCA, ex E.N. Kellesvig–Waering collection). – **Santa Cruz**: 1 ♀, Ichilo, "3.7 km SSE Buena Vista, Hotel Flora & Fauna", 430 m, 14–19 Oct. 2000, M.C. Thomas leg. (FSCA); 1 ♀, Ichilo, "3.7 km.SSE Buena Vista, Hotel Flora & Fauna", 430 m, 14–28 Oct. 2000, B.K. Dozier leg. (FSCA); 1 ♀, Ichilo, "4–6 km SSE Buena, Vista Fauna & Flora Hotel", 420–450 m, 2–12 Feb. 2000, pitfall with dung and carrion, J.E. Wappes leg. (FSCA); 2 ♂♂, Ichilo, "5km SSE Buena Vista, Hotel Fauna & Flora", 17º29.935′ S, 63º39.129′ W, 440 m, 24–31 Dec. 2003, S. and J. Peck leg. (FSCA).

ECUADOR: **Sucumbíos**: 6 ♂♂, 1 ♀, Limoncocha, Jul. 1979, trap with human faeces, T. Ray leg. (MCZC); 1 ♂, Limoncocha, 00º24′ S, 76º36′ W, 22 Jun. 1976, Peter L. Kazan leg. (FSCA).

PERU: **Huánuco**: 1 ♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva ("Tingo María Universidad"), Dec. 1974, Martínez leg. (FSCA).

Sylvicanthon foveiventris (Schmidt, 1920)

Material examined

BRAZIL: **Rio de Janeiro**: 1 ♂, Itatiaia, 700 m, Feb. 1959, W. Zikan leg. (CEAH).

Sylvicanthon genieri sp. nov.

Material examined

Paratypes

ECUADOR: **Pastaza**: 2 ♂♂, "38 km E of Baños", 1500 m, 9 Feb. 1990, dung bait, J. Watts and R. Beard leg. (FSCA).

PERU: **Huánuco**: 1 ♀, Leoncio Prado, Rupa-Rupa, Tingo María, Universidad Nacional Agraria de la Selva ("Tingo María Universidad"), Dec. 1974, Martínez leg. (FSCA).

Sylvicanthon seag sp. nov.

Material examined

Paratypes

BRAZIL: **Amazonas**: 6 ♂♂, 4 ♀♀, Manaus, 3 Jan. 1978, B.C. Ratcliffe leg. (FSCA); 1 ♂, 1 ♀, Manaus, BR 174, km 64, 20 Aug. 1984, Milan Hrabovsky leg. (FSCA).

FRENCH GUIANA: 1 ♀, Cayenne, Roura, Amazon Nature Lodge, "30 km SE Roura on Kaw Rd.", 04º33.570′ N, 52º12.433′ W, 300 m, 3–10 Jun. 2005, pitfall with human faeces, J.E. Eger leg. (FSCA); 1 ♂, "D-5 / 4k SE Tngmd Jct", 17–18 Aug. 1995, J.E. Wappes leg. (FSCA); 1 ♂, 2 ♀♀, "D-5 / 4k SE Tngmd Jct", 21–22 Aug. 1995, J.E. Wappes leg. (FSCA); 1 ♂, 4 ♀♀, "D-5 / 4k SE Tngmd Jct", 24–27 Aug. 1995, J.E. Wappes leg. (FSCA); 3 ♀♀, "D-5 / 4k SE Tngmd Jct", 25–27 Aug. 1995, J.E. Wappes leg. (FSCA).

TRINIDAD AND TOBAGO: 1 ♂, "1 mi. W. Morne / Bleu Trinidad", 23 Jun. 1968, Julius Boos leg. (FSCA).

Sylvicanthon proseni (Martínez, 1948)

Material examined

BOLIVIA: **Cochabamba**: 1 ♂, 1 ♀, Chapare, 400 m, 1 Oct. 1950, no collector (FSCA).

BRAZIL: **Rondônia**: 1 ♂, "62 km SW Ariquemes, near Fazenda Rancho Grande", 3–15 Dec. 1996, pitfall with fish carrion, J.E. Eger leg. (FSCA); 2 ♂♂, 1 ♀, "62 km SW Ariquemes, near Fazenda Rancho Grande", 4–16 Nov. 1997, pitfall with fish carrion, J.E. Eger leg. (FSCA).

ECUADOR: **Napo**: 4 ♂♂, 3 ♀♀, "20 km E Puerto Napo, Allinahui" 450 m, 9–12 Jan. 1994, P.H. Sullivan leg. (FSCA); 14 ♂♂, 4 ♀♀, Limoncocha, Jul. 1979, trap with human faeces, T. Ray leg. (MCZC); 1 ♀, Limoncocha, 00º24′ S, 76º36′ W, 29 Jun. 1972, Peter L. Kazan leg. (FSCA).

PERU: **Loreto**: 1 ♂, "80 km NE Iquitos, Explorama Lodge, 1 km from Amazon River on Rio Yanamono", 25–28 Aug. 1992, pitfall with human faeces, Castner and Skelley leg. (FSCA); 3 ♂♂, 2 ♀♀, "80 km NE Iquitos, Explorama Lodge, 1 km from Amazon River on Rio Yanamono", 1–5 Sep. 1992, pitfall with human faeces, Castner and Skelley leg. (FSCA); 14 ♂♂, 8 ♀♀, "160 km NE Iquitos, Explornapo Camp, 2 km from Rio Napo on Rio Sucusari", 27–31 Aug. 1992, pitfall with human faeces, J. Castner and Skelley leg. (FSCA); 1 ♀, "Explorama Lodge, 50 mi NE Iquitos on Amazon River", 12–19 Mar. 1988, J.E. Eger leg. (FSCA); 1 ♂, 1 ♀, Iquitos, Jungle Amazon Inn, 30 Dec. 1986–2 Jan. 1987, M.J. Halter leg. (FSCA); 2 ♂♂, 1 ♀, "near junction of Río Moranon and Río Ucayali", 4.8º S, 73.5º W, 6–20 Aug. 1994, P. Skelley leg. (FSCA).