FRANCISCO ERIBERTO DE LIMA NASCIMENTO

Cladistic analysis and biogeography of Aerenicini Lacordaire, 1872 (Insecta, Coleoptera, Cerambycidae, Lamiinae

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Single Volume

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Thesis submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Doctor of Science (Systematics, Animal Taxonomy and Biodiversity).

Advisor: Profa. Dra. Sônia Casari

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"*If karate used defend honor, defend life, karate mean something. If karate used defend plastic metal trophy, karate no mean nothing*"
Mr. Kesuke Miyagi

The Karate Kid Part III • 1989

RESUMO

O presente estudo buscou avaliar a monofilia de Aerenicini (Lamiinae, Cerambycidae) e seus gêneros, através de uma análise cladística baseada em dados fenotípicos. Adicionalmente, através de um estudo biogeográfico, buscamos entender os principais fenômenos que atuaram na evolução do grupo e as áreas de distribuição ancestral. Para termos uma ideia de quando esses eventos teriam ocorrido, realizamos uma filogenia datada de Lamiinae. Para a análise cladística, foi utilizada uma matriz morfológica de 110 caracteres contínuos e discretos, provenientes de estruturas internas e externas. Para a filogenia molecular calibrada, foram adotadas as sequências do Genbank, depositadas por autores anteriores. Foram utilizados fragmentos de dois marcadores mitocondriais (cox1 e rrnL) e três marcadores nucleares (Wg, CPS e LSU). As áreas de distribuição ancestrais de Aerenicini foram reconstruídas através da análise Bayesiana Binária MCMC (BBM), implementada na plataforma RASP 4.2. A filogenia molecular calibrada de Lamiinae estima a origem de vários grupos para o Cretáceo Superior com uma diversificação expressiva no período Cenozóico, consistente com o Máximo Termal Paleoceno-Eoceno e com sua consequente diversificação de angiospermas lenhosas. O tempo de divergência estimado para o clado Hemilophini+Aerenicini foi de cerca 40 Ma. O clado Hemilophini+Aerenicini foi corroborado com dados fenotípicos, no entanto, Aerenicini foi recuperado como parafilético, e os resultados indicam que alguns grupos atualmente em Aerenicini (*i.e. Phoebemima* Tippmann, 1960 e *Suipinima marginalis* Martins & Galileo 2004) estão mais relacionados evolutivamente à Hemilophini. O gênero *Hippopsis* (Agaphantini) foi recuperado como mais relacionado a Aerenicini. Para grupos não monofiléticos, são propostas as seguintes alterações taxonômicas: *Aerenica bandana* (Nascimento, Botero & Bravo, 2016) **comb. nov.**; *Antodice breyeri* (Prosen, 1954) **comb. nov.**; *Antodice eccentrica* Galileo & Martins, 1992 **stat. res.**; *Antodice flava* (Lane, 1939) **comb. nov.**; *Antodice flavumtuberculata* (Nascimento, Botero & Bravo, 2016) **comb. nov.**; *Antodice lanuginosa* (Martins & Galileo, 1985) **comb. nov.**; *Antodice metuia* (Martins & Galileo, 1998) **comb. nov.**; *Antodice modesta* Lane, 1939 **stat. res.**; *Antodice nigristernis* (Martins & Galileo, 1985) **comb. nov.**; *Antodice rustica* (Bates, 1881) **comb. nov.**; *Antodice mariahelenae* (Martins & Galileo, 2004) **comb. nov.**; *Hoplistonychus* Melzer, 1930, *Pseudophaula* Lane, 1973 and *Holoaerenica* Lane, 1973 = *Phaula* Thomson, 1857; *Phaula bondari* (Melzer, 1930) **comb. nov.**; *Phaula foersteri* Martins, 1984 **stat. res.**; *Phaula porosa* (Bates, 1881) **comb. nov**.; *Phaula pustulosa* (Lane, 1973) **comb. nov.**; *Phaula strigulata* (Lane, 1973) **comb. nov.**; *Phaula alveolata* (Martins, 1984) **comb. nov.**; *Phaula apleta* (Galileo & Martins, 1987) **comb. nov.**; *Phaula bistriata* (Lane, 1973) **comb. nov.**; *Phaula multipunctata* (Lepeletier & Audinet-Serville, 1825) **comb. nov.** and *Antonerella* **gen. nov**. para alocar *A. marginalis* (Martins & Galileo, 2004) **comb. nov.** A análise biogeográfica sugere que a evolução dos principais subgrupos de Aerenicini ocorreu nas regiões Sul e Sudeste do Brasil e em parte da região do Chaco. Vários grupos surgiram nesta região, por especiação simpátrica e, posteriormente, algumas linhagens teriam dispersado para outras áreas. Provavelmente, o padrão de distribuição atual teria sido resultado de fatores climáticos do Cenozoico. No geral, a diversidade de Aerenicini foi o produto de um balanço positivo de especiação-extinção por um longo período de tempo, especialmente ao longo da costa leste brasileira.

Palavras-chave: Evolução. Lamiinae. Morfologia. Neotropical. Taxonomia.

ABSTRACT

The present study aimed to evaluate the monophyly of Aerenicini (Lamiinae, Cerambycidae) and its genera, through a cladistic analysis based on phenotypic data. Additionally, through a biogeographic study, we seek to understand the main phenomena that acted in the evolution of Aerenicini and the areas of ancestral distribution. To estimate when these events would have occurred, we performed a dated phylogeny to Lamiinae. For the cladistic analysis, a morphological matrix of 110 continuous and discrete characters was proposed, based on internal and external morphological structures. For the calibrated molecular phylogeny, Genbank sequences fragments of two mitochondrial markers (cox1 and rrnL) and three nuclear markers (Wg, CPS and LSU). The ancestral distribution areas of Aerenicini were reconstructed using Bayesian binary MCMC (BBM) analysis, implemented in RASP 4.2 platform. The calibrated molecular phylogeny of Lamiinae estimates the origin of several groups for the Late Cretaceous with an expressive diversification in the Cenozoic period, consistent with the Paleocene-Eocene Thermal Maximum and its consequent diversification of woody angiosperms. The estimated divergence time for the Hemilophini+Aerenicini clade was *ca.* 40 Ma. The Hemilophini+Aerenicini clade was corroborated with phenotypic data, however, Aerenicini was retrivied as paraphyletic, and the results indicate that some groups currently in Aerenicini (*i.e. Phoebemima* Tippmann, 1960 and *Suipinima marginalis* Martins & Galileo 2004) are more evolutionarily related to Hemilophini. The genus *Hippopsis* (Agaphantini) was retrivied as related to Aerenicini. For non-monophyletic groups, the following taxonomic changes are proposed: *Aerenica bandana* (Nascimento, Botero & Bravo, 2016) **comb. nov.**; *Antodice breyeri* (Prosen, 1954) **comb. nov.**; *Antodice eccentrica* Galileo & Martins, 1992 **stat. res.** ; *Antodice flava* (Lane, 1939) **comb. nov.**; *Antodice flavumtuberculata* (Nascimento, Botero & Bravo, 2016) **comb. nov.**; *Antodice lanuginosa* (Martins & Galileo, 1985) **comb. nov.**; *Antodice metuia* (Martins & Galileo, 1998) **comb. nov.**; *Antodice modesta* Lane, 1939 **stat. res.** ; *Antodice nigristernis* (Martins & Galileo, 1985) **comb. nov.**; *Antodice rustica* (Bates, 1881) **comb. nov**.; *Antodice mariahelenae* (Martins & Galileo, 2004) **comb. nov.**; *Hoplistonychus* Melzer, 1930, *Pseudophaula* Lane, 1973 and *Holoaerenica* Lane, 1973 = *Phaula* Thomson, 1857; *Phaula bondari* (Melzer, 1930) **comb. nov.**; *Phaula foersteri* Martins, 1984 **stat. res.** ; *Phaula porosa* (Bates, 1881) **comb. nov**.; *Phaula pustulosa* (Lane, 1973) **comb. nov.**; *Phaula strigulata* (Lane, 1973) **comb. nov.**; *Phaula alveolata* (Martins, 1984) **comb. nov.**; *Phaula apleta* (Galileo & Martins, 1987) **comb. nov.**; *Phaula bistriata* (Lane, 1973) **comb. nov.**; *Phaula multipunctata* (Lepeletier & Audinet-Serville, 1825) **comb. nov.** and *Antonerella* **gen. nov**. to alocate *A. marginalis* (Martins & Galileo, 2004) **comb. nov**. The biogeographic analysis suggests that the evolution of the main subgroups of Aerenicini occurred in the South and Southeast regions of Brazil and in part of Chaco. Several groups arose in this region, by sympatric speciation and, later, some lineages would have dispersed. Probably, the current distribution pattern are the result of climatic factors of the Cenozoic. Overall, Aerenicini diversity was the product of a positive speciation-extinction balance over a long period of time, especially along the Brazilian east coast.

Keywords: Evolution. Lamiinae. Morphology. Neotropical. Taxonomy.

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1. INTRODUCTION

Cerambycidae Latreille is one of the most diverse families of Coleoptera (Insecta) whose species are usually characterized by the antennal length that can exceed body length for more than five times the body length (Svacha & Lawrence, 2014). Longhorn beetles, as they are commonly known, belong to the Phytophaga group (Chrysomeloidea and Curculionoidea), the largest and most successful lineage of animals associated with angiosperms (Farrell, 1998). The superfamily Chrysomeloidea includes Chrysomelidae Latreille and Cerambycidae *s.l.* (Cerambycidae, Disteniidae, Oxypeltidae, and Vesperidae) and among these, Cerambycidae is the most diverse (Svacha & Lawrence, 2014).

In many species with known life cycle, females oviposit in branches and trunks of trees, and after hatching, the larvae generate galleries by feeding the plant, which allow the entry of decomposing microorganisms that act in the cycling of many nutrients (Monne, 2001a, b, c; Cobb *et al*., 2010). Some species oviposit in plants with economic importance, damaging or even leading such plants to death, causing enormous economic damages (Martins, 1997).

The family currently comprises more than 35,000 described species and the America continent have the largest number of them, about 9,000 allocated in more than 1,600 genera (Monné & Bezark, 2009). Data on the number, distribution and taxonomic history of western species were treated by Monné (1993 –1995). These catalogs are constantly updated and available (Monne, 2021a, b, c).

This high diversity, according to Makino *et al*. (2007), is directly related to the presence and diversity of host plants. Because of this relationship, cerambycids can be used as bioindicators (Brown, 1997). The Neotropical species with their respective host plants were cataloged by Monné (2001a, b, c; 2002a, b; 2004).

Cladistic works in the group are scarce, and the hypotheses about evolutionary relationship of Cerambycidae with other families vary widely and even the hypotheses to support Cerambycidae as a clade are not consistent (Svacha & Lawrence, 2014). However, Lawrence *et al*. (2011) mention that Cerambycidae composes a clade (Cerambycoidea) together with Disteniidae, Oxypeltidae and Vesperidae.

Napp (1994), proposed for the first time a cladistic hypothesis of evolutionary relationship between subfamilies. In their study, 66 morphological characters of adults and 62 of larvae were analyzed and based on the results, Philinae as subfamily of Cerambycidae and Oxypeltidae and Disteniidae hitherto considered subfamilies, were elevated to families.

Currently the family is divided into eight subfamilies: Cerambycinae, Dorcasominae, Lamiinae, Lepturinae, Necydalinae, Parandrinae, Prioninae and Spondylidinae (Svacha & Lawrence, 2014). In recent years, some studies with molecular data, proposed phylogenies to comprehensive taxonomic levels of Cerambycidae (*e.g.* Haddad & McKenna, 2016; Haddad *et al.,* 2018; Nie *et al.*, 2021)

According to many studies, Prioninae and Parandrinae composing a clade, is the group with more plesiomorphic characters (*e.g.* Craighead, 1923; Saalas, 1936; Crowson, 1955; Svacha & Danilevsky, 1987; Napp, 1994; Biffi & Fuhrmann, 2013; Svacha & Lawrence, 2014; Nearns, 2013; Haddad *et al.*, 2017; Nie *et al.*, 2021). Some of these studies indicate that Prioninae have no synapomorphies (paraphyletic) and together with Parandrinae, compose a clade.

Prioninae is widely accepted as the most plesiomorphic group (Crowson, 1955; Linsley, 1961; Svacha & Danilevsky, 1987; Hanks, 1999; Svacha & Lawrence, 2014). This is corroborated by the discovery of the earliest fossil record *Cretoprionus liutiaogouensis* Wang *et al*., 2014 (Cerambycidae, Prioninae) dating from the lower Cretaceous (Wang *et al*., 2014). Liu *et al.* (2018) published the first complete mitogenome of a Prioninae [*Dorysthenes paradoxus* (Faldermann, 1833)], and based on 18 mitogenomes from 13 Cerambycidae, four Chrysomelidae and one Vesperidae species, a phylogenetic analysis was conducted through Bayesian inference and Maximum likelihood. In their results, a clade composed by Prioninae + Cerambycinae was retrieved. However, the authors did not use any species of Parandrinae in their analysis.

Molecular and biogeographic studies indicate that Prioninae originated in Gondwana and was the first lineage to diversify, while Lamiinae, the latter to diverge, would have arisen in Laurasia and migrated to the other regions later (Svacha & Lawrence, 2014). The subfamily Lamiinae (Flat-Faced Longhorns) is monophyletic, corroborated by morphological and molecular data (Liu *et al.* 2018; Napp, 1994; Haddad *et al.*, 2018; Souza *et al*., 2021; Ashman *et al*., 2022). However, its relationship with other subfamilies is controversial (Svacha & Lawrence, 2014).

In the cladistic analysis by Napp (1994), Cerambycinae is sister group of Lamiinae. However, for Svacha & Lawrence (2014), this hypothesis is not well supported and more recent studies, based on molecular data, indicate that Cerambycinae is closer to Prioninae and Dorcasominae whereas Lamiinae, together with Spondylidinae, Necydalinae and Lepturinae are more related. Currently, based on molecular phylogenies (Marvaldi *et al.*, 2009; Wang *et*

al., 2013; Haddad *et al.*, 2018; Nie *et al*., 2020), Lamiinae and Spondylinae are widely accepted as sister groups.

Lamiinae Latreille, 1825, with about 20,000 species is the most diverse among the subfamilies and represents 58% of the family's diversity (Rossa & Goczał, 2021). The group is subdivided into 86 tribes, that area characterized especially by the shapes of the tarsal claws, that can be: divaricate, appendiculate, bifid or simple (Martins & Galileo, 1990a; Galileo & Martins, 1998; 1999a, b;, 2003a, b).

1.1 On the tarsal claws

LeConte (1850) was the first who mentioned the shape of the tarsal claws to separate groups in Lamiinae. However, this feature did not recieved due attention in his classification. Later, Thonsom (1860), taking as base the work by LeConte, added some features and established some subdivisions in Lamiinae. This author also gave a secondary importance to the shape of the tarsal claws.

Lacordaire (1869) was the first who used such a feature to effectively separate Lamiinae into groups. This work was the most important for the classification of Lamiinae and their characters, are currently used to define subfamilies and tribes. Lacordaire (1869), thus, subdivided Lamiinae in two groups composed by four tribes. The first group has only one tribe, TMÉSISTERNIDES (Tmesisternini), characterized by the prognathous head and by having carinae in the lateral areas of pronotum. The second group is characterized by the pronotum without lateral carinae and by “normal head” (hypognathous), that was subdivided into two others groups, one composed by DORCADIONIDES and LAMIIDES VRAIES (simple tarsal claws), and another with PHYTOECIIDES, subdivided into 7 groups, characterized by the presence of not simple tarsal claws (*i.e.* appendiculate and bifid), which included AMPHIIONYCHIDES (Hemilophini), CALLIDES (Calliini), and AERENICIDES (Aerenicini). Important observations about Lacordaire's work were made by Fragoso *et al.* (1987), in which he links behavioral aspects to the morphological characters used in such classification: the relative size of ommatidia, finely faceted and vibrant integument color related to diurnal habits while ommatidia coarse faceted, and somber integument colors related to nocturnal habits.

Bates (1881) criticized the Lacordaire's classification, and questioned the importance of the system used by him: “Lacordaire’s elaborate classification of the Longicornia, in fact, fails

here, as it does elsewhere, from his too close adherence to technical system, by which he unconsciously sacrificed natural affinity in striving to secure absolute definitions." This comment by Bates was based on his pre-Darwinian evolutionary view. In fact, Henry Walter Bates (1825–1892) was crucial in consolidating the theory of evolution, generally attributed to Charles Darwin (1809–1882) and secondarily to Alfred Russel Wallace (1823 – 1913). It is notorious in his manuscripts that Bates, especially due to his long discussions with Wallace, during his survey in South America (Amazonas) had an evolutionary view on diversity (Ferreira, 1990, 2004). In an answer letter sent to Bates on November 22, 1860, Darwin (1860) wrote: "I am delighted to hear that you, with all your large practical knowledge of Nat. History, anticipated me in many respects & concur with me." Bates, therefore, tried (without a conventional phylogenetic method) to reflect the natural history in his classifications.

A discussion about the features used by Lacordaire was also made by Marinoni (1972), and about the shape of tarsal claws, the author comments (translated): "Although all species with non-simple claws appear to be effectively correlated, it does not mean that they cannot belong to this group of species with simple claws. It is even logical that if we consider a bifid or appendiculate claw as a derived character, it should be among the species of simple claws the origin of the same, and with which there must be closely related" Marinoni (1972) in his dissertation used numerical taxonomy methods, hitherto widely disseminated and accepted.

According to Martins & Galileo (1998), among the American tribe of Lamiinae, only Hemilophini and Aerenicini have bifid tarsal claws. However, it is not uncommon to find taxonomic problems and exceptions, as for example, the tribe Saperdini (Mulsant,1839) in which the American species have the claws simple or divaricate (Linsley & Chemsak, 1985; 1995). However, species from the Old World have the tarsal claws appendiculate in males (in most female all the claws are simple) and Lin & Tavakilian (2012) propose *Bifidunguiglenea* to Asian species in which the claws of all the tarsi in both sexes are bifid. According to Lin & Ge (2021), in *Tsounkranaglenea hefferni* Lin & Ge,2021, only the claws of mesotarsi are appendiculate with small lobe at inner side. Gahan (1897) studied and described in detail the forms of the tarsal claws found in Saperdini: "Here two conditions of the tarsal claws are indicated first, in which the claws are simple in both sexes; second, in which the claws of the female are simple, while those of the male are toothed or appendiculate at the base. Each of these two conditions is found with in a large number of species; but I find that a different structure of the claws prevails in almost as great a number." It is noteworthy that bifid tarsal claws occur in other groups, such as Galerucinae (Chrysomelidae), which mean an important

adaptation in phytophagous groups. Therefore, the shape of the tarsal claws in different groups of Lamiinae can be convergent and consecutively, their indiscriminate use can lead to artificial groupings. The function of composed claws in Cerambycidae was not studied. However, Mohamedsaid & Furth (2011) when studying this feature in groups of Gallerucinae (Chrysomelidae), infer that it is a secondary sexual characteristic (SSC) and when present in males, it serves to hold onto the surface of the female elytra during copulation.

1.2. On Aerenicini Lacordaire, 1872

Thomson (1860) proposed AMPHIONYCHITÆ (XIV Division) to group genera whose tarsal claws are bidentate (translated): "I have no hesitation in joining them into one same generic cut. These insects are remarkable in form… The claws of the tarsi are bidentate…". Subsequently, Thomson (1864) proposed AMPHIONYCHITÆ VERÆ (36º Division) to group the genera in AMPHIONYCHITÆ with the tarsal claws bifid, separating them from those with appendiculate claws (currently Caliini). Posteriorly, Thomson (1868) proposed the name HEMILOPHITÆ for the same family-group, and under the pre-requisites of article 23.9 ICZN (1999), it became a *nomen protectum* (Bousquet *et al*., 2009).

Finally, Lacordaire (1872) proposed Aerenicini (ÆRÉNICIDES) which was distinguished from AMPHIONYCHIDES (Hemilophini) by the elytra without lateral carinae; median legs without groove (except Antodice); bifid tarsal claws; abdominal ventrites II-IV shorter than the remaining; narrow metaventrite and very elongated body. The author also provided a key for the seven genera hitherto known.

Bates (1881) revised both groups, Amphionycha (Hemilophini) and Ærénicides (Aerenicini) and compared them with groups from the Old World. It is important to mention that this author was the first who noticed the similarity of such groups (New and Old World tribes) by the shape of the tarsal claws: "The Amphionyehides and Ærénicides are closely allied to the Phytoeciides of the Old World, having, like the typical species of that group, tarsal claws with very few exceptions bifid, *i.e.* their basal tooth pointed and as long or nearly as long as the stem of the claw" In fact, Bates (1881) did not establish a direct comparison and differentiation of these Aerenicini and Hemilophini, but compared both with groups in the Old World: "...These are distinguished from temperate and old-World forms of *Saperda* not by any constant peculiarity of structure, but a combination of characters..." According to Bates (1881), Aerénicides are caracterized especialy by the unretracted head and notched middle tibiae, while the species in Amphionychides (Hemilophini) by the head strongly retracted, the tibiae simple, and elytra with a distinct elevated carina, separating the dorsal surface from lateral.

Among the most important contributions in Aerenicini are those of the naturalist and entomologist Frederico Lane (1901–1979). Lane (1938a) began his studies with Aerenicini, describing *Hydraschema leptostylum*, *Aerenica parvula* [currently *Recchia parvula* (Lane, 1938)] and *Aerenica melanocera* [currently syn. of *Aerenicella spissicornis* (Bates, 1881)]. In the same year Lane (1938b) proposed the genus *Montesia*, to allocate his new species, *M. leucostigma*.

In 1958, Lane started to assemble a large number of species of Aerenicini in order to compare them with type-material deposited in American and European institutions and provide a detailed revision of the tribe, financed by the National Science Foundation grant (Washington), Conselho Nacional de Pesquisas (Rio de Janeiro) and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP). However, before Lane's publication, Gilmour (1962) published a synopsis of the tribe based especially on figures and descriptions, not in specimens. This work makes Lane deeply indignant forcing him to anticipate much of his studies, which until then would be published as a single work.

We can understand Lane's point of view, because of its extreme taxonomic zeal, demonstrated by his hard criticisms of illfounded taxonomic acts. Such zeal is demonstrated, for example, in Lane (1965a) (translated): “In these notes I wish to leave a vehement protest against the custom, which is becoming very frequent, of synonymizing species and genera in faith of mere speculation, without examining the types or any other detailed information about them, obtained in museums, where these are deposited.” In this study, the author also revalidated *Rumacon canescens* (Bruch, 1926). Lane (1965b) continues his contributions in the tribe, describing *Hydraschema villiersi*. Another good example can be found in Lane (1959), in which the author criticizes Breuning's classification, proposed in a series of works (Breuning, 1937, 1938, 1939, 1942, 1943, 1944) entitled "Études sur les Lamiaires". About the classification adopted by Breuning, Lane (1959) commented: "A lot of irresponsible naming is carried out on a pseudo-scientific basis that could be named "philatelic entomology"... Some modifications should be expected, of course, for Lacordaire's famous work is certainly outdated and deficient, but the task requires a responsible approach."

Gilmour's work was severely criticized by Lane (1974) in his work titled: “A Synopsis of Dr Gilmour's Synopsis of the tribe Aerenicini (Col., Cerambycidae: Lamiinae).” According to him: “What is disturbing is something like Dr. Gilmour’s “Synopsis of the tribe Aerenicini”, based on very limited amount of species, as well as a minimum knowledge on the tribe, and gamble on new genera raised by the differences or doubts honestly pointed out by other

entomologists.” In another passage, the author makes clear his frustration and the reason for not having continued his detailed review: “...after his “Synopsis” was published I did not continue my revision. I do not believe this type of competition advances Systematic Entomology.” One of the items criticized by Lane was Giulmour's identification key, which according to him: "This key is so full of characters that are incorrect, misleading, exaggerated, weak (in generic sense), and even forced, that it hardly useful for identifying purposes.” The characters used by Gilmour (1962) in his key were: “…Tarsal claws fissile. Intermediate tibiae with or without a dorsal sulcus. Head not retractile. Eyes emarginate. Elytra generally not costate, if present then not usually strong. Metathoracic episterna narrow. General form elongate and narrow, often strongly so.”

Lane (1966a) published a work exclusively composed by taxa of Aerenicini (it was the first anticipation of his review). He described, therefore, the genus *Melaerenica* (currently syn. of *Aerenicella* Lane 1966); *Recchia* for *R. ludibriosa*; *Coruparana* (currently syn. of *Recchi*a) for *C. veruta* and *C. fallaciosa*, both currently allocate in *Recchia*. In the same year, Lane (1966b) in his second anticipated work, described many taxa: *Hydraschema veruta* , and *H. cribripennis* ; the genus *Corupa* (currently syn. of *Hydraschema*) for *C. obliquevittata* (currently in *Hydraschema*); *Hydraschemopsis* (currently syn. of *Aerenicopsis* Lane 1966) for *H. pugnatrix* (currently in *Aerenicopsis*); *Aerenicopsis sublesta* and *A. malleri* ; and the genus *Vianopolisia* for *V. spitzi* Lane 1966.

Later, Lane (1970) described *Antodice inscripta*, *A. quinquemaculata* and *A. pudica*. In the same study, were described in Aerenicini: *Eulachnesia consobrina*; the genus *Mariliana* to allocate *M. ocularis* (Hope, 1846), *M.sumpta M. niveopicta* and *M. rupicola* (currently, both genera and its species are allocated in Hemilophini).

Lane (1973) described a series of taxa that was denominated by him as "Phaula complex": *Heterophaula* for *H. lichenigera* (Perty, 1832) (currently syn. of *Phaula* Lane 1973); *Calliphaula* for *C. leucippe* (Bates, 1881); *Apophaula* for *A. ocellata* Lane 1973; *Pseudophaula* for *P. porosa* (Bates, 188), *P. pustulosa* and *P. strigulata*. *Cryptophaula* for *C. microsticta* Lane, 1973 (currently the genus is a syn. of *Phaula*); *Holoaerenica* for *H. bistriata* Lane, 1973; *Cacsius* for *C. nobilis* Lane, 1973 and *Antodice venustula* Lane, 1973. In this same work, Lane also exhibits his disappointment with the work published by Gilmour (1962) (translated): “I contemplated a few years ago, among others, the revision of the Aerenicini tribe, supported by a grant from the National Science Foundation. As it turned out, when the work was in an advanced stage, the "Synopsis of the tribe Aerenicini" by Dr. E. Forrest Gilmour ... came to

light at the end of 1962, which led me to give up the review ... I do not see, however, how to avoid the adventurism of other possible "gilmoures", but by baptizing these various groups, leaving aside the discussion of their major and minor affinities" (Lane, 1973).

Since the 1980s, two Brazilian researchers, under Lane's own request, have continued to study Aerenicini's taxonomy. Dr. Ubirajara Martins (1932-2015), Lane's student, and Dr. Maria H. Galileo. Together, the authors have published dozens of articles about Aerenicini species. In the first of a series entitled (translated) "Contribution to the study of the Aerenicini Tribe", Martins (1984a) comments (translated): "The material of several institutions under Lane's responsibility came into my hands to be identified and returned, which made it possible to study a good number of specimens, many compared to the types by Dr. Lane during his stay at the British Museum and the Muséum National d' Histoire Naturelle." These contributions resulted in the subdivision of Aerenicini into five groups which are summarized in **Table 1**.

In this first contribution Martins (1984a) studied the genera with contrasting and glabrous punctures on elytra (Group I). This feature had not previously been used to define groups. Most of these genera were included in the "Phaula Complex" determined by Lane (1973).

In the second contribution, Martins (1984b) studied the genera with short lower eyes lobes (as long or slightly longer than genae length) named "Apagomerina group" (Group II) and genera with large upper eye lobes and acuminated elytral apex "Aerenicopsis group" (Group III).

Martins & Galileo (1985a) studied the genera with subcontiguous ocular lobes and rounded elytral apices (Group IV). In this work, the authors also provided a key to the *Antodice* species described so far. Martins & Galileo (1985a) separated the genus *Melzerella* Costa Lima 1931 by the elytral apex with two spines and later, Martins & Galileo (1985c) included it in the group II.

Martins & Galileo (1985b) also studied genera without contrasting punctures on elytra, with large lower eyes lobes and separated upper eye lobes (Group V). This is the most specious group with the highest number of genera (14 so far). In the last contribution of the series, Martins & Galileo (1985c) revised the genus *Recchia* which belongs to group V. Additionally, the authors listed the species and genera of the tribe. In addition to studying Aerenicini, Martins & Galileo (2014a, 2014b) also reviewed the taxonomy of the South American Hemilophini and divided the tribe into six groups.

Martins & Galileo (1996) made an important contribution, where they redefined Aerenicini by discriminating it from Hemilophini, by the lower eyes lobes occupying almost the entire side of the head and by the nocturnal habits. They propose the following key for Neotropical tribes with bifid claws (translated):

"**1.** Coarsely granulated eyes, well-developed lower eyes lobes, occupying almost entire side of head. Adults with nocturnal habits ..... Aerenicini

– Finely granulated eyes, short lower eye lobes, sometimes slightly longer than genae; adults of daily habits …….....……..... Hemilophini".

Therefore, the following genera were transferred from Aerenicini to Hemilophini: *Apagoerina* Gilmour, 1962; *Mariliana* Lane, 1970; *Eulachnesia* Bates, 1872 and *Columbicella* Galileo & Martins, 1990 (Martins & Galileo, 1996).

Table 1. Classification of Aerenicini according to Martins & Galileo 1985b

Group I: genera with contrasting elytral punctures	*Aerenomera* Gilmour, 1962 *Calliphaula* Lane, 1973 *Heterophaula* Lane, 1973 *Holoaerenica* Lane, 1973 *Paraphaula* Fuchs, 1963 *Phaula* Thomson, 1857 *Pseudophaula* Lane, 1973 *Hoplistonychus* Melzer, 1930
Group II: genera with short lower eyes lobes	
a) Elytral apex without two spines	*Eulachnesia* Bates, 1872 *Apagomera* Bates, 1881 *Apagomerella* Gilmour, 1962 *Pretilia* Bates, 1866 *Apagomerina* Gilmour, 1962 *Mariliana* Lane, 1970
b) Elytral apex with two spines	*Melzerelia* Lima, 1931
Group III: Genera with subcontiguous upper eyes lobes and acuminated elytral apex	*Hydraschema* Thomson, 1864 *Aerenicopsis* Bates, 1885 *Falsohippopsoide*s Breuning, 1974 *Corupa* Lane, 1966 *Hydraschemopsis* Lane, 1966
Group IV: Genera with subcontiguous upper eyes lobes (or very close) and rounded elytral apices	*Aphilesthes* Bates, 1881 *Antodilanea* Gilmour, 1962 *Antodice* Thomson, 1864 *Cacsius* Lane, 1973 *Propantodice* Franz, 1954
Group V: genera with separated upper eye lobes	*Aerenica* Dejean, 1835 *Apophaula* Lane, 1973 *Apoaerenica* Martins & Galileo, 1985 *Rumacon* Blackwelder, 1946 *Dolaerenica* Martins & Galileo, 1985 *Pseudomecas* Aurivillius, 1920 *Montesia* Lane, 1938 *Vianopolisia* Lane, 1966 *Melzaerenica* Lane, 1976 *Aerenicella* Gilmour, 1962 *Coruparana* Lane, 1966 *Recchia* Lane, 1966 *Eponina* Lane, 1939

1.3. Immature Stages of Aerenicini and Hemilophini

Martins & Galileo (1996) mentioned the peculiar morphology of the known Aerenicini larvae (two species), previously described by Duffy (1960). Related to one of the species described by Duffy (1960), there were some disagreements. Bondar (1915) reported the occurrence of a Cerambycidae species causing enormous damage to *Jacaranda mimosifolia* D. Don (Bignoniaceae) trees in the municipality of Piracicaba (state of São Paulo, Brazil). In a footnote, Bondar (1915) comments that a scientific name is not given because it is perhaps an undescribed species. Subsequently, Duffy (1960) described the larva collected by Bondar (1915) as an unknown species of the genus *Phaula*. This author, however, entitles its description as *Phaula thomsoni* Lacordaire, 1872 and indicated that Andrade (1928) reported *Jacaranda mimosifolia* as host plant for this species. The species mentioned by Bondar (1915) whose larva was described by Duffy (1960) in fact was a new species, described by Melzer (1930), who proposed a new genus to allocate it and named the species as *Hoplistonychus bondari* Melzer, 1930. Later, Bondar (1937) indicates that the species mentioned in his previous work is *H. bondari*.

Duffy (1960) also briefly described the larva of *Aerenicopsis mendosa* Martins & Galileo, 1998 as *Aerenicopsis championi* Bates, 1885, which a lateral view photograph was published by Svacha & Lawrence (2014). Both species, *H. bondari* and *A. mendosa* have in common a long thick, curved and strongly sclerotised process in IX abdominal segment (urogomphus) **(Fig 1).** In the key for immature Lamiinae, proposed by Duffy (1960), Aerenicini was inserted in the couplet of alternative "52" as follows: "Abdominal segment 9 bearing a very long, thick, rod-like process, which is strongly sclerotized and ferrugineous... Proeusteum sclerotised and ferruginous, contrasting with the distinct testaceous eustemum which is subtriangular. Dorsum of abdominal segment 10 sclerotized and ferruginous. [Spiracular peritreme with only a pair of subcontiguous, digitiform chambers.]".

Martins & Galileo (2014a) provided important comments on the larval stage in Aerenicini and related groups (translated): "In some species of Aerenicini, a tribe similar to Hemilophini, the pupal stage of some species occurs in the soil (Giacomel, personal communication who reared the larva, but did not publish his observations) and both tribes could have this behavior. In Hemilophini species, in the biology is different. In *A. versicolor*, the larvae, before the pupal stage (in instar VI?), dig an internal circular cut at the base of the branch, and that part of the plant usually falling. In *P. ensifera*, larval instars IV and V occur e inside the pupal chamber, two to four weeks before pupate. The pupal chamber is a section of the branch that falls on the

ground, but it was not explained whether the pupa was in the ground or not”

Until the work by Martins & Galileo (1996) no Hemilophini larva has been described and the authors commented (translated): "Unfortunately, this character cannot be comparatively evaluated because Hemilophini larvae are unknown". Recently, Casari & Martins (2013) described and illustrated the larva and pupa of *Phoebemima ensifera* Tippmann, 1960 the first description of immatures of Hemilophini. This allows us to make a brief comparison of the immature stages of some species of these two tribes. The authors compared the newly described Hemilophini larva with those of Aerenicini: “Spiracles with paired chambers are present, besides in Hemilophini (*Phoebemima ensifera*), only in Aerenicini…” However, there is no curved process in the IX abdominal segment of *P. ensifera* (Fig 1C). Clarke & Zamalloa (2009) described the life cycle of *P. ensifera* including larval and adult behavior and they found that *P. ensifera* oviposits its eggs in aerial branches of trees of *Pithecillobium scalare* Griseb. (Mimosaceae).

According to Zinovjev (1982), the caudal appendages can be found in several groups of insects, especially those with concealed feeding habits. These structures are associated with excavation, working as supporting locomotion. Recently, Tavakilian & Santos-Silva (2019), based on adult characters currently used to separate these tribes, transferred *Phoebemima* to Aerenicini. The main argument was the size of the lower eye lobes. In fact, Martins (2014) mentions that only *Phoebe* and *Phoebemima* have lower eyes as large as those in Aerenicini.

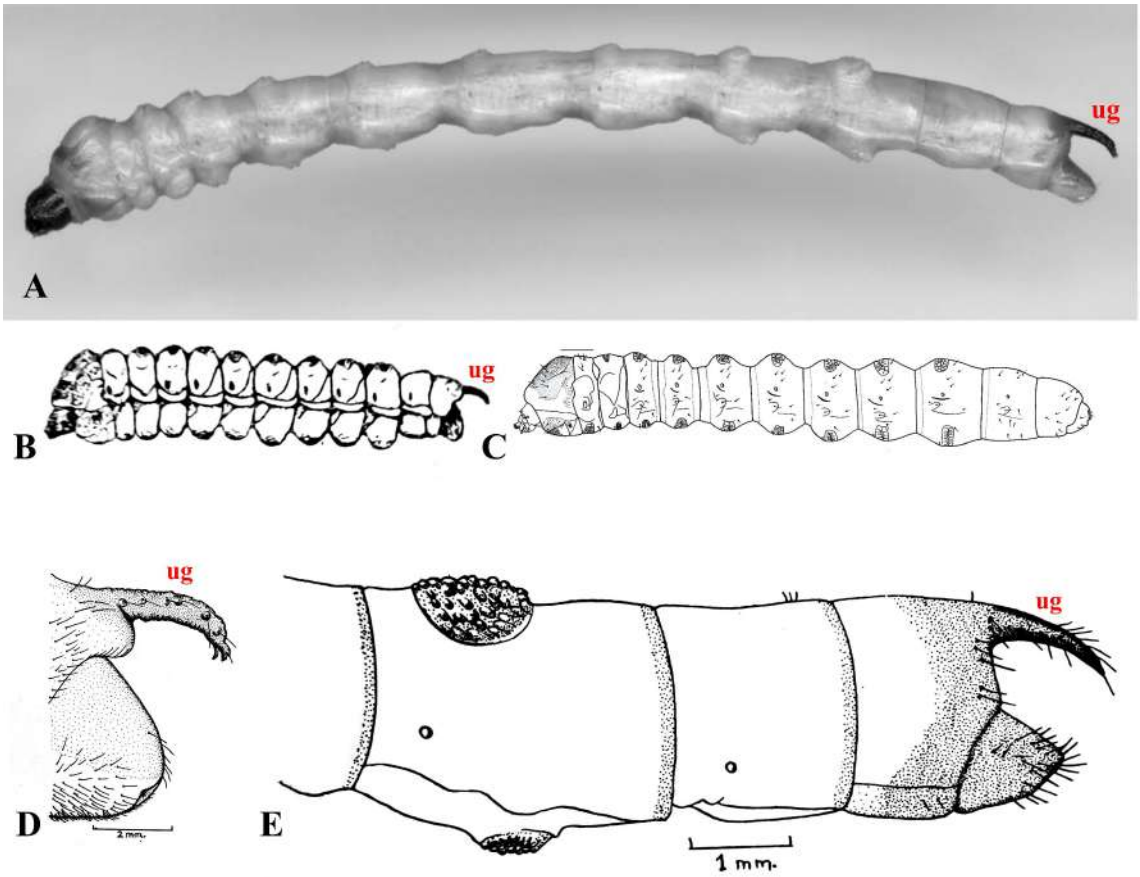

Figure 1. Larvae of Lamiinae in lateral view: A–B, Aerenicini species; A, *Aerenicopsis mendosa* Martins & Galileo, 1998 (from Svacha & Lawrence, 2014); B, *Hoplistonychus bondari* Melzer, 1930 (from Bondar, 1937); C, Hemilophini specie; C, *Phoebemima ensifera* Tippmann, 1960 (from Casari & Martins, 2013); D–E, Aerenicini species; D, abdominal segments VII–X of *A. mendosa*; E, distal segments of *Hoplistonichus bondari* (from Duffy, 1960). Abbreviation: ug=urogomphus.

1.4. Fossil Species

So far, Aerenicini fossils were not known, however, Martins & Galileo (1999) described *Paleohemilophus dominicanus* **(Fig. 2)**, an Oligocene fossil of Hemilophini. This species from Dominican Republic, was preserved in amber. According to these authors the fossil was collected in a mine, whose location was not provided. Martins (2014a) comments that Dominican Republic amber may have an age between 14 and 40 million years (Miocene to Eocene) depending on where they were found. According to this author, these mines are located in the Cordillera Septentrional and Cordillera Oriental, in which they are constantly exploited and traded by local population. It is not known for sure which mine the species comes from, which makes precise dating difficult. Amber fossils from the Dominican Republic have different ages, and to Iturralde-Vinent & MacPhee (1996), most originated in a single sedimentary basin during the lower Miocene and early Middle Miocene (15 to 20 million years ago), hypothesis reinforced by biostratigraphic and paleogeographic evidences.

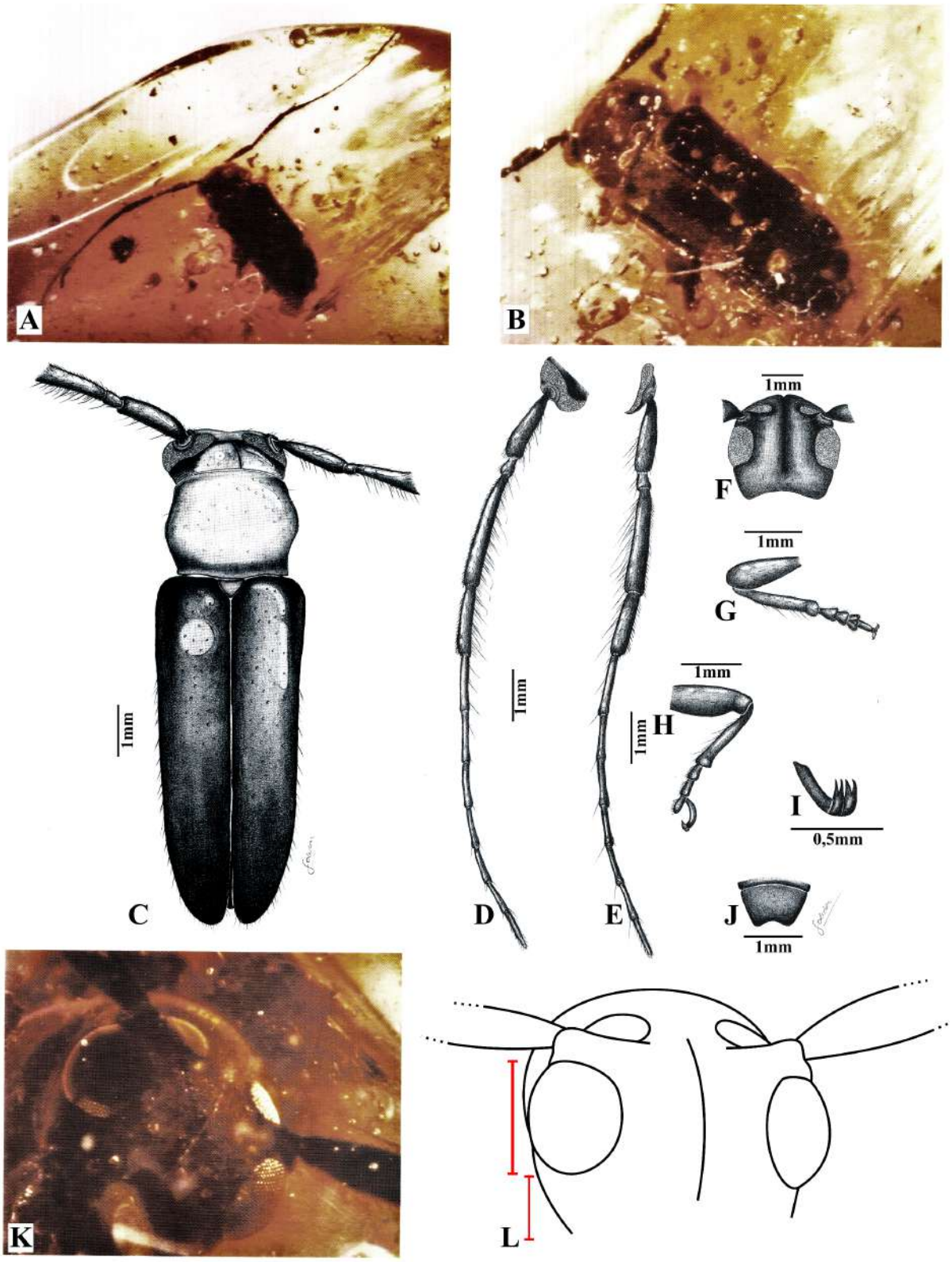

Figure 2. Fossil of *Paleohemilophus dominicanus* Martins & Galileo, 1999 holotype (adapted from Martins & Galileo, 1999): A, habitus in dorsal view, in amber; B, dorsal view amplified; C, habitus dorsal, drawing; D, left antenna; E, right antena; F, head in frontal view; G, front leg; H, middle leg; I, tarsal claw; J, abdominal ventrite V; K, head in frontal view, in amber; L, schematic drawing of the head in dorsal view, showing the ratio of the lower eye lobes and gena

1.5. Host Plants

Cerambycidae are highly specialized in consuming plant material and their larvae can be found on all parts of plants (stems, branches, roots and leaves), in a monophagy or polyphagy interaction (Haack, 2017). The efficiency in consuming plant material, composed of cells containing a resistant cell wall, is due to degrading enzymes, secreted by its digestive tract (Shin, *et al*., 2021). According to Cates (1980), monophagous-oligophagous herbivores exploit few and related plant species, especially in the early stages, while polyphagous species prefer the mature leaves of the various host plants. Some species of Aerenicini present a specificity interaction with the host plant, as is the case of *Aerenicopsis championi* Bates, which was introduced in Australia to control *Lantana camara* L. (Verbenaceae) (Palmer *et al.*, 2000). Monné (2001) compiled the host plant records of 11 species of Aerenicini which are summarized below.

List of host plant species

***Aerenica* Dejean, 1835**

***A. canescens* (Klug, 1825)**

Host plants - *Schizolobium excelsum* Vogel, *S. parahybum* (Vellozo) S.F. Blake (Caesalpiniaceae). Larva in living plant wood.

***Aerenicopsis* Bates, 1885**

***A. championi* Bates, 1885**

Host plants - *Lantana camara* Linnaeus, *L. hirsuta* Martius & Galeotti, *L. montevidensis* (K. Sprengel) Briquet, *L. urticaefolia* Miller (Verbenaceae).

***A. mendosa* Martins & Galileo, 1998**

Host plants - *Lantana camara* Linnaeus (Verbenaceae). Labels of types.

***Holoaerenica* Lane, 1973**

***H. multipunctata* (Lepeletier & Audinet-Serville, 1825)**

Host plants - *Aloysia gratissima* (Gillies & Hooker), *Lantana* sp. (Verbenaceae).

***Hoplistonychus* Melzer, 1930**

***H. bondari* Melzer, 1930**

Host plants - *Jacaranda mimosifolia* D. Don (Bignoniaceae). Larva in living plant wood.

***Phaula* Chevrolat, 1847**

***P. thomsoni* Lacordaire, 1872**

Host plants - *Jacaranda mimosifolia* D. Don (Bignoniaceae).

***Recchia* Lane, 1966**

***R. albicans* (Guérin-Méneville, 1831)**

Host plants - *Vernonia* sp. (Asteraceae).

***R. hirticornis* (Klug, 1825)**

Hosts plants - *Ambrosia scabra* Hooker & Arnott, *Chromolaena odorata* (Linnaeus) R.M. King & H. Robinson (Asteraceae).

***R. moema* Martins & Galileo, 1998**

Host plants - *Pterocaulon* sp. (Asteraceae).

***R. parvula* (Lane, 1938)**

Host plants - *Chromolaena odorata* (Linnaeus) R.M. King & H. Robinson (Asteraceae).

***Rumacon* Blackwelder, 1946**

***R. canescens* (Bruch, 1926)**

Host plants - *Alnus jorullensis* Kunth (Betulaceae). Larva under bark.

1.6. Current status of Aerenicini and objectives

All previous studies about Aerenicini, culminated in the complete revision of the tribe, and Martins & Galileo (1998) under the request of Dr. Lane, and based on the material from several institutions, gathered by him, fabulously complete the work of their master. In that work, six genera and five species were synonymyzed and 15 new species were described. In addition to the detailed revision, the authors compiled information about host plants, immature stages and propose keys for genera and species of each genus.

In the last phase of working, Dr. Ubirajara Martins (1932-2015) with his stereo microscope bring from the MZSP to home, and with the scientific and personal support of Antonio Santos-Silva (MZSP) (great friends since 1999) was working in the 15th volume of his series "Cerambycidae Sul-Americanos" that would deal with Aerenicini. Unfortunately, the author passed away before concluding his work.

Martins & Galileo (1998) provided important and unprecedented comments on the distribution of species. According to the authors, most species are distributed in South America between the 15° and 30° parallels, with no species recorded in Antilles and Chile. The authors questioned the fact that some Neotropical areas have poor diversity, as is the case of Amazon Region. Since Dr. Martins and Dr. Galileo have a deep knowledge of the Cerambycidae fauna of South America, these questions are extremely relevant and worthy of a detailed investigation.

The distribution of Aerenicini raises questions about the possible historical factors that influenced its evolution. Furthermore, the diagnostic characteristics, historically used to separate the groups, were never analyzed into the light of phylogenetic analyses. Therefore, the present study aims to: 1) verify whether Aerenicini is a natural group and what is its evolutionary relationship with other tribes of Lamiinae; 2) Test whether their genera are monophyletic and what is the evolutionary relationship between them; 3) Raise hypotheses about the possible areas inhabited by ancestral populations; 4) what were the biogeographic phenomena involved in its diversification; 5) why the group presents the current distribution and 6) when would the taxa have diverged. To answer such questions, we present a cladistic and biogeographic study of Aerenicini involving morphological, molecular and geological evidences.

2. MATERIAL AND METHODS

The photographs were taken at Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZSP) with a Canon EOS Rebel T3i DSLR camera (Taichung, Taiwan), Canon MP-E 65mm f/2.8 1–5X macro lens, controlled by Zerene Stacker software (http://zerenesystems.com/cms/stacker). The plates were edited with GIMP 2.10.6 (GNU Image Manipulation Program) and Inkscape 0.48.4. The characters and their states are respectively indicated in the figures, for example "50:2", where 50 is the character and 2 is its state. Measurements were taken in millimeters with an ocular Hensoldt/Wetzlar—Mess 10 (Taufkirchen, Germany) in the Leica MZ6 stereomicroscope (Wetzlar, Germany).

The acronyms used in the text are as follows:

C.W.T.—compared with types;

col.—collector;

col.—collector;

comb. nov. — combinatio nova

Figs/Fig—Figures/Figure

gen. nov. — genus novum

Hol. —Holotype;

id.— species identifier

Par. — Paratype

stat. res. — status resurrectus

Abbreviation of the depositary institutions of the examined material

INPA— Coleção Sistemática de Entomologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brasil

MZSP—Museu de Zoologia da Universidade de São Paulo, Brasil;

MZFS—Museu de Zoologia Universidade Estadual de Feira de Santana, Brasil;

MACN—Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina;

MLPA—Museo de La Plata, Universidad Nacional de La Plata, Argentina.

2.1. Comparative material

All material deposited at MZSP, which includes the specimens used in Martins & Galileo (1998) was examined. The data labels of the voucher specimens used in the cladistic analysis is listed below.

Spondylinae— *Spondylis buprestoides* (Linnaeus, 1758): Japan, Kagato,VII.1979, S. Delamutá (MZSP). **Agapanthiini**—*Agapanthia cardui* (Linnaeus 1767): Espanha, Cádiz (Alcalá de los Gazules), 31.III. 2001, Male, Pedro Coelho col, José Esteban id (MZSP); *Hippopsis pubiventris* Galileo & Martins 1988: **Hol.** Brazil, São Paulo (São Paulo, Saude), 15.XI.1980, Male, M.H.Galileo (MZSP); *Hippopsis truncatella* Bates 1866: Brazil, Pará, Santarem, VI.1919,S.M. Klages col. (MZSP). **Forsterini**— *Falsamblesthis ibiyara* Marinoni 1978: **Hol.**, Brazil, São Paulo (Itú, Faz. Pau D'alho), 20.VIII.1960, Female, U. Martins, R.C. Marinoni (MZSP); *Falsamblesthis seriepilosa* (Kirsch 1889) Ecuador, Imbabura, Chachimbiro, 18.XI.1984,Male, U. Martins 1985 (MZSP); *Falsamblesthis unguicularis* (Tippmann 1960), Bolivia, Sur Yungas (ChulumaniI) I.1948, Bridarolli col., R.C. Marinoni (MZSP). **Caliini**— *Callia azurea* Audinet-Serville 1835: Brazil, Paraná, Rolândia, X.1952, Male, Dirings (MZSP); *Drycothaea angustifrons* (Breuning 1943): Brazil, Amapá (Serra Lombarda), 4.IX.1961, Male (MZSP); *Gryllica picta* (Pascoe 1958): Brazil, Espirito Santo (Linhares), X.1972, Male, P.C. Elias (MZSP). **Phytoeciini**— *Mecas menthae* Chemsak & Linsley 1973: Mexico, Sinaloa, El Palmito, VIII.1983, Male, F. Hovore (MZSP); *Phytoecia* (*Pilemia*) *hirsutula* (Frölich 1793): România, 19.V.1969, Male, N. S Savulescu Frolich (MZSP). **Pteropliini**— *Ataxia luteifrons* (Bruch 1926): Sintype, Argentina, Catamarca BelénLa Ciénaga, XII. 1925, Weiser Wolters col, C. Bruch id (MZSP); *Ataxia obscura* (Fabricius 1801): Brazil, Amazonas, Pará, II.1963, Dirings (MZSP). **Sperdini—** *Glenea fasciata* (Fabricius 1781): Peru (introduced from Africa), Loreto, Meliton Carbajal (Ríoltaya); 4°14'S 73°44'W 11.VII.2013, Male, J.J.R. Hernandez, Santos-Silva & Nascimento 2019 (MZSP); *Saperda carcharias* (Linnaeus 1758): Noruega, Male, (MZSP). **Hemilophini—** *Adesmus borgmeieri* (Lane 1976): Brazil, Goiás, (Monte Alto, São Domingos) 13°46'S 46°37' W, 460m. 15-21.XI.2003, Male, Becker V. Ferro & E. Emery col. U. Martins id (MZSP); *Adesmus brunneiceps* (Aurivillius, 1920): Brazil, Espirito Santo (Linhares) 08.IX.1984, Male, Fiuza col, U. Martins (MZSP); *Apagomerella versicolor* (Boheman 1859): Brazil, Minas Gerais, (Pq. Es. Do Rio Doce), 27.X-14.XI.2013, Male, L. Migliore, Nascimento id (MZSP); *Apagomerella dissimilis* Galileo & Martins 2005:**Par.** Costa Rica, Guanacaste, (Agua Buena, Parque Nacional Guanacaste), VI.1992, III Curso Parataxon col. (MZSP); *Calocosmus nuptus* Chevrolat 1862: Jamaica, Male, F. Klages, F. Lane id

(MZSP); *Fredlanea velutina* (Lane 1966): **Par.**, Equador, Chimbo, 1891, Male, M. de Mathan col., F. Lane id.(MZSP); *Fredlanea viridipennis* (Bates 1881): Equador, Guayaquil-Cuenca, 4.III.1965, Female, (MZSP); *Ites plagiatus* Waterhouse 1880: Brazil, Amazonas, Benjamin Constant (Rio Javari), X.1960, Female, Dirings col. (MZSP); *Lycomimus ampliatus* (Klug 1825): Brazil, U. Martins 1982 (MZSP); *Mariliana cicadellida* Galileo & Martins 2004, **Par.**, Bolivia, Santa Cruz (Buena Vista 4-6K F&F Hotel), 17-19.X.2000, Female, Wappes & Morris col., U. Martins & Galileo 2003 id. (MZSP); *Phoebe concinna* White 1856: Brazil, Pará, Itaituba (Rio Tapajós), II.1961, Male, U. Martins (MZSP); *Phoebella phoebe* (Lepeletier & Audinet-Serville in Latreille, 1825): Brazil, Sta Catarina, Rio Vermelho, VIII.1963, Male, (MZSP); *Purusia acreana* Lane 1956, **Hol.**, Brazil, Acre, Alto Purus, XI.1950, Male, Dirings col, F. Lane id (MZSP); *Purusiella wappesi* (Martins & Galileo 2004): **Par.** Bolívia, Santa Cruz (Buena Vista 4-6K F&F Hotel), 1-8.XI.2002, Male, J.E. Wappes, U. Martins (MZSP); *Sphallonycha roseicollis* (Bates 1866): Brazil, Pará, Male, R. Dias col.,U. Martins 1990 id.(MZSP); *Tyrinthia paraba* Martins & Galileo 1991: **Par.**, Brazil, Amazonas, Benjamin Constant (Rio Javari), X.1952, Female, Dirings col., U. Martins id. (MZSP); *Tyrinthia scissifrons* Bates 1866: Brazil, Pará, Canindé (Rio Gurupi), 10.VI.1963, B. Malkin col., U. Martins id. (MZSP). **Aerenicini—** *Aerenica canescens* (Klug 1825), lect., Brazil, Rio de Janeiro (Rio de Janeiro, Instituto Osvaldo Cruz), 18-29.X.1938, Salobra col., F. Lane 1974 id. (MZSP); *Aerenicella spissicornis* (Bates 1881): **Hol.** of A. melanocera Lane, **C.W.T.**, Brazil, Paraná (Curitiba), 13.XI.1936, F.Lane 1937 (MZSP); *Aerenicopsis mendosa* Martins & Galileo 1998: **Par.**, Mexico, Veracruz (Mocambo), 10.VI.1958, Male, U. Martins id.(MZSP); *Aerenicopsis perforata* Lane 1939: Brazil, Minas Gerais, Mar de Espanha, 10.IX.1909, J.F. Zikan (MZSP); *Aerenicopsis pugnatrix* (Lane 1966), Bolivia, Santa Cruz (Boena Vista F&F. Hotel) 23-26.X.2000, Wappes & Morris col., J.E. Wappes id. (MZSP); *Aereniphaula bandana* Nascimento et al. 2017: **Par.**, Brazil, Bahia, Milagres (Faz. Salinas), 02.IX.2013, Male, Carvalho et al. col. Nascimento & Botero id. (MZSP); *Aereniphaula machadorum* Galileo & Martins 1990: **Hol.**, Brazil, Minas Gerais (Sta. Barbara, Peti-CEMIG), 21.XII.1987, Male, A.B. & A. Machado col., U. Martins & Galileo id. (MZSP); *Aerenomera boliviensis* Gilmour 1962: Bolivia??, Ponta Porrã, 1946, Male, F. Lane 1964 (MZSP); *Aerenomera spilas* Martins 1984: **Par.**, Brazil, Minas Gerais (B. Horizonte, Oscar Monte) Male, F. Lane id. (MZSP); *Antodice abstrusa* Lane 1940: **Hol.**, Brazil, Espirito Santo (Faz. Jerusalem), 20.XI.1914, Male, J.F. Zikan col., U. Martins id. (MZSP); *Antodice picta* (Klug 1825): Brazil, Santa Catarina, XII.1927, Male, A. Malle col., U. Martins id. (MZSP); *Antodice nympha* Bates 1881: Panama, La Cabima, Male, (MZSP); *Antodice lenticula* Martins & Galileo 1985, **Par.**, Brazil, Bahia, Sto Antonio da

Barra, 11.XII.1988, Female, Gounelle col., Martins id.(MZSP); *Antodice lenticula* Martins & Galileo 1986: Brazil, Piauí, Caracol (Serra das Confusões, Fonte dos Bois), 7-17.XII.2010, Female, Silva-Neto AM & Xavier M.col., U. Martins id. (MZFS*); Antodice tricolor* Martins & Galileo 1985: **Hol.**, Bolivia, Santa Cruz (Buena Vista pcia. Ichilo), II. 1950, Male, A. Martinez col., U. Martins id. (MZSP); *Antodilanea modesta* (Lane 1939): **Hol.**, Brazil, Mato Grosso (Salobra), 18-29.X.1938, Male, F. Lane (MZSP); *Aphilestes rustica* Bates 1881: Bolivia, Santa Cruz, 20.IX.1955, Female, Zischka F. Tippmann Wien (MZSP); *Apoaerenica martinsi* (Monné 1979): Bolivia, Santa Cruz (37Km SSE Buena Vista, Hotel Flora & Fauna), 5-15.XI.2001, Male, M.C. Thomas & B.K. Dozier (MZSP); *Apophaula ocellata* Lane 1973: **Hol.**, Brazil, Rio de Janeiro, Itatiaya, 16.I.1934, Female, J.F. Zikan col., F. Lane id. (MZSP); *Cacsius nobilis* Lane 1973: Brazil, Minas Gerais, Pedra Azul, XI. 1972, Female, Seabra & Oliveira col., M.A. Monné id. (MZSP); *Cacsius divus* (Melzer 1932): **Par.**, Brazil, Rio de Janeiro, Itatiaya, 1.XI.1928, Male, J.F. Zikan (MZSP); *Calliphaula filiola* Martins 1984: **Hol.**, Brazil, Minas Gerais (B. Horizonte), X.1950, Male, A.B. Machado col., U.R. Martins id. (MZSP); *Calliphaula leucippe* (Bates 1881), Brazil, Santa Catarina (Rio Vermelho), X.1955, Male, U.R. Martins (MZSP); *Eponina breyeri* (Prosen 1954): **Hol.**, Argentina, Formosa, Gran Guardia, II.1953, Male, Breyer col., A.F. Prosen id. (MZSP); *Eponina flava* Lane 1939: lect., Brazil, Mato Grosso, Salobra, 18-29.X.1938, Male, F. Lane (MZSP); *Holoarerenica bistriata* Lane 1973: **Par.**, Bolivia, Sta Cruz, Andrés Ibáñez (Sta Cruz de la Sierra), Male, J. Steinbach col., F. Lane id. (MZSP); *Holoarerenica apleta* Galileo & Martins 1987: **Hol.**, Guatemala, Verapaz, San Cristobal (Quixal), 3.V.1980, Female, H.L. Freude col., U. Martins & Galileo id. (MZSP); *Hoplistonychus bondari* Melzer 1930: **C.W.T.**, Brazil, São Paulo, Lindóia, 30.IX.1963, Male, J. Bick col., F. Lane id. (MZSP); *Hydraschema obliquevittata* (Lane 1956): Brazil, Minas Gerais, Pocinhos, 1850, Male, F. Halik col., F. Lane id. (MZSP); *Hydraschema leptostyla* Lane 1938: **Hol.**, Brazil, Goiás, Leop. Bulhões, XII.1935, Male, R. Spliz col., F. Lane id. (MZSP); *Melzerella lutzi* Costa Lima 1931: Brazil, Rio de Janeiro, Male, F. Lane id. (MZSP); *Melzerella huedepohli* Monné 1979: Bolivia, Santa Cruz (4-6K SSE Buena Vista, Hotel Flora & Fauna)1-8.IX.2002, Male, J.E. Wappes (MZSP); *Montesia leucostigma* Lane 1938: Bolivia, Santa Cruz, Prov. Andres, Ibanez (Potrerillos del Guenda) 17°40'S 63°27'W, 370m, 23-27.X.2007, Male, S.W. Lingafelter col., U.R.Martins & M.H. Galileo id.(MZSP); *Phaula lichenigera* (Perty 1832): Brazil, Santa Catarina, Rio Vermelho, X.1963, Male, Dirings(MZSP); *Phaula antiqua* Thomson 1857: Brazil, Minas Gerais, Aguas Vermelhas, XI.1970, Male, F.M. Oliveira col., M.A. Monné id. (MZSP); *Phaula thomsoni* Lacordaire 1872: C.W.T, Brazil, São Paulo, Dois Corregos, 11.III.1955, Male, U.R. Martins col., F.Lane id. (MZSP); *Phoebemima ensifera*

(Tippmann 1960): **C.W.T.,** Bolivia, Cochabamba (Chimore), Male, M.A. Monné id. (MZSP); *Phoebemima teteia* Martins & Galileo 1996: **Par.**, Brazil, Rondonia, Ouro Preto do Oeste, XI. 1983, Male, j. Becker & B. Silva col., U.R. Martins id. (MZSP); *Phoebemima theaphia* (Bates 1881): Brazil, Mato Grosso, Sinop (BR 163 Km 500 a 600), 12° 31'S 55° 37' W, 350m, X.1975, Female, Roppa & Alvarenga col., U.R. Martins 1994(MZSP); *Pseudomecas femoralis* Aurivillius 1920: Brazil, Mato Grosso, Chapada dos Guimarães, 24-29.X.1961, Male, F.M. Oliveira (MZSP); *Pseudomecas pickeli* (Melzer 1930): **Hol.**, Brazil, Pernambuco, Tapéra, 7.III.1929, Male, Don B. Pickel O.S.B. col., J. Melzer id. (MZSP); *Pseudophaula porosa* (Bates 1881): **C.W.T.**, Brazil, Paraiba, 1934, Male, Dr. P. Azevedo (MZSP); *Pseudophaula strigulata* Lane 1973: **Par.**, Bolivia, Prov. Del Sara, Male, Steinbach col., F. Lane id. (MZSP); *Recchia acutipennis* (Gahan 1889): **C.W.T.**, Argentina, Missiones, San Ignacio, XI.1945, Male, Prosen col., F. Lane id. (MZSP); *Recchia parvula* (Lane 1938): **Par.**, Brazil, Goiás, Leop. Bulhões, XII.1933, Male, R. Spliz col., F. Lane id. (MZSP); *Recchia hirticornis* (Klug 1825): Bolivia, Beni, Uyapi (Guanay), X-XI.1992, Male (MZSP); *Recchia albicans* (Guérin-Méneville 1831): Brazil, Santa Catarina, Rio Vermelho, III.1964, Male, Dirings(MZSP); *Recchia procera* Martins & Galileo 1985: **Hol.**, Brazil, São Paulo, Barueri, 17.XII.1960, Male, K. Lenko col., U.R. Martins id. (MZSP); *Rumacon annulicornis* (Melzer 1930): **C.W.T.**, Brazil, Minas Gerais, 13.X.1938, Male, F. Lane id. (MZSP); *Rumacon canescens* (Bruch 1926): Argentina, Jujuy (Huaico Hondo), I.1951, Male, Prosen col., F. Lane id.(MZSP); *Suipinima marginalis* Martins & Galileo 2004: **Par.**, Bolivia, Santa Cruz (4-6 Km SSE Buena Vista, Hotel Flora & Fauna), 17-19.X.2000, Male, Wappes & Morris col. U.R.Martins id. (MZSP); *Suipinima suturalis* Martins & Galileo 2004: **Par.**, Bolivia, Santa Cruz (4-6 Km SSE Buena Vista, Hotel Flora & Fauna), 16-31.X.2002, Male, Robin Clake col., U.Martin & Galileo id. (MZSP); *Suipinima flavumtuberculata* Nascimento Botero & Bravo 2016: **Par.**, Brazil, Bahia, Quixadá (Faz. Novos Horizontes), 5°3'38"S 39° 1'39"W, 205m, 25.IV.2014, Male, Bravo et. al. col., Nascimento & Botero id. (MZFS); *Vianopolisia spitzi* Lane 1966: **Hol.**, Brazil, Goiás, Vianópolis, XI.1931, Male, R. Spliz col., F. Lane id. (MZSP); *Vianopolisia captiosa* (Martins & Galileo 1985): **Par.**, Paraguai, Horqueta, 6.IX.1933, Male, Alberto Schultze col., U.R.Martins & M.H. id. (MZSP).

2.2. Taxon sampling

The choice of the terminal taxa was based on the criteria proposed by Prendini (2001): include the type species of supraspecific taxa and at least two species by non-monotypic supraspecific taxa; in the case of genera that have more than 10 species, species with wide

geographic distribution were added. This criterion was followed considering the availability of material and in order to better represent the morphological diversity of the group. The inclusion of these species is important to the identification and study of variable intraspecific features. All comparative material used to create characters, including photographed specimens, is deposited at MZSP.

The ingroup taxa is composed by 54 species, including representatives of the 26 genera currently composing Aerenicini **(table 1)**. The outgroup taxa are composed by 34 species with representatives of seven tribes of Lamiinae (**table 2**). The analysis was rooting in *Spondylis buprestoides* (Linnaeus, 1758), type species of Spondylinae which is sister group to Lamiinae. The taxon-character matrix was built through MorphoBank Version 3.0 web application (available at https://morphobank.org/index.php) then, exported to "TNT" (.tnt) format.

Table 2. Terminal taxa of ingroup (Aerenicini): list of genera (column 1) number of species in the genus (column 2) and species used in this work (column 3). (*) indicates the type species.

Aerenicini		
Aerenica Dejean, 1835	1	*A. canescens* (Klug, 1825)*
Aerenicella Gilmour, 1962	1	*A. spissicornis* (Bates, 1881)*
Aerenicopsis Bates, 1885	14	*A. mendosa* Martins & Galileo, 1998
		A. perforata Lane, 1939
		A. pugnatrix (Lane, 1966)
Aereniphaula Galileo & Martins, 1990	2	*A. bandana* Nascimento, Botero & Bravo, 2016
		A. machadorum Galileo & Martins, 1990*
Aerenomera Gilmour, 1962	2	*A. boliviensis* Gilmour, 1962*
		A. spilas Martins, 1984
Antodice Thomson, 1864	27	*A. abstrusa* Lane, 1940
		A. lenticula Martins & Galileo, 1985
		A. nympha Bates, 1881
		A. picta (Klug, 1825)*
		A. tricolor Martins & Galileo, 1985
Antodilanea Gilmour, 1962	2	*A. modesta* (Lane, 1939)*
Aphilesthes Bates, 1881	1	*A. rustica* Bates, 1881*
Apoaerenica Martins & Galileo, 1985	1	*A. martinsi* (Monné, 1979)*
Apophaula Lane, 1973	1	*A. ocellata* Lane, 1973*
Cacsius Lane, 1973	2	*C. divus* (Melzer, 1932)
		C. nobilis Lane, 1973*
Calliphaula Lane, 1973	2	*C. filiola* Martins, 1984

		C. leucippe (Bates, 1881)*
Eponina Lane, 1939	5	*E. breyeri* (Prosen, 1954)
		E. flava Lane, 1939*
Holoaerenica Lane, 1973	6	*H. apleta* Galileo & Martins, 1987
		H. bistriata Lane, 1973*
Hoplistonychus Melzer, 1930		*H. bondari* Melzer, 1930*
Hydraschema Thomson, 1864	8	*H. obliquevittataum* (Lane, 1966)
		H. leptostyla Lane, 1938
Melzerella Costa Lima, 1931	5	*M. huedepohli* Monné, 1979
		M. lutzi Costa Lima, 1931*
Montesia Lane, 1938	4	*M. leucostigma* Lane, 1938*
Phaula Thomson, 1857	7	*P. antiqua* Thomson, 1857*
		P. lichenigera (Perty, 1832)
		P. thomsonii Lacordaire, 1872
Phoebemima Tippmann, 1960	7	*P. ensifera* Tippmann, 1960*
		P. theaphia (Bates, 1881)
		P. teteia (Galileo & Martins, 1996)
Pseudomecas Aurivillius, 1920	6	*P. femoralis* Aurivillius, 1920*
		P. pickeli (Melzer, 1930)
Pseudophaula Lane, 1973	4	*P. porosa* (Bates, 1881)*
		P. strigulata Lane, 1973
Recchia Lane, 1966	25	*R. acutipennis* (Gahan, 1889)
		R. albicans (Guérin-Méneville, 1831)
		R. hirticornis (Klug, 1825)*
		R. parvula (Lane, 1938)
		R. procera Martins & Galileo, 1985
Rumacon Blackwelder, 1946	2	*R. annulicornis* (Melzer, 1930)
		R. canescens (Bruch, 1926)*
Suipinima Martins & Galileo, 2004	6	*S. flavumtuberculata* Nascimento, Botero & Bravo, 2016
		S. marginalis Martins & Galileo, 2004
		S. suturalis Martins & Galileo, 2004*
Vianopolisia Lane, 1966	2	*V. captiosa* (Martins & Galileo, 1985)
		V. spitzi Lane, 1966*

Table 3. Terminal taxa of the outgroup: list of genera (column 1) number of species in the genus (column 2) and species used in this work (column 3), (*) indicates the type species.

Spondylinae		
Spondylis Fabricius, 1775	1	*S.buprestoides* (Linnaeus, 1758)*
Agaphantini		
Agapanthia Audinet-Serville, 1835	3	*A. cardui* (Linnaeus, 1767)*
Hippopsis Lepeletier & Audinet-Serville 1825	45	*H.pubiventris* Galileo & Martins, 1988
		H. truncatella Bates, 1866
Forsteriini		
Falsamblesthis Breuning, 1959	10	*F. ibiyara* Marinoni, 1978
		F. seriepilosa (Kirsch, 1889)*
		F. unguicularis (Tippmann, 1960)
Caliini		
Callia Audinet-Serville, 1835	44	*C. azurea* Audinet-Serville 1835*
Drycothaea Thomson, 1868	30	*D. angustifrons* (Breuning, 1943)
Gryllica Thomson, 1860	6	*G. picta* (Pascoe, 1958)*
Pteropliini		
Ataxia Haldeman, 1847	41	*A. luteifrons* (Bruch, 1926)
		A. obscura (Fabricius, 1801)
Phytoeciini		
Phytoecia Dejean, 1835	62	*P.* (*Pilemia*) *hirsutula* (Frölich, 1793)
Saperdini		
Mecas LeConte, 1852	17	*M. menthae* Chemsak & Linsley, 1973
Glenea Newman, 1842	696	*G. fasciata* (Fabricius, 1781)
Saperda Fabricius, 1775	25	*S. carcharias* (Linnaeus, 1758)*
Hemilophini		
Adesmus Lepeletier & Audinet-Serville, 1825	68	*A. borgmeieri* (Lane, 1976)
		A. brunneiceps (Aurivillius, 1920)
Apagomerella Gilmour, 1962	2	*A. versicolor* (Boheman, 1859)
Calocosmus Chevrolat, 1862	17	*C. nuptus* Chevrolat, 1862*
Fredlanea Martins & Galileo, 1996	19	*F. velutina* (Lane, 1966)*
		F. viridipennis (Bates, 1881)
Hemilophus Audinet-Serville, 1835	4	*H. dimidiaticornis* Audinet-Serville, 1835*
Ites Waterhouse, 1880	2	*I. plagiatus* Waterhouse, 1880*
Lycomimus Melzer, 1931	3	*L. ampliatus* (Klug, 1825)
Mariliana Lane, 1970	8	*M. cicadellida* Galileo & Martins, 2004
Paleohemilophus Martins & Galileo, 1999	1	*P. dominicanus* Martins & Galileo, 1999 *+
Phoebe Audinet-Serville, 1835	22	*P. concinna* White, 1856

Phoebella Lane, 1966	3	*P. phoebe* (Lepeletier & Audinet-Serville, 1825)
Purusia Lane, 1956	1	*P. acreana* Lane, 1956*
Purusiella Dalens, Touroult & Tavakilian, 2010	2	*P. wappesi* (Martins & Galileo, 2004)
Sphallonycha Bates, 1881	1	*S. roseicollis* (Bates, 1866)*
Tyrinthia Bates, 1866	20	*T. paraba* Martins & Galileo, 1991
		T. scissifrons Bates, 1866*

2.3. Cladistic analysis

Proposals for primary homologies were made through direct observation of the specimens and literature. Neomorphical characters (presence and absence of a character) and transformational characters (character quality) in a reductive logic, were adapted from Sereno's proposal (2007). Morphological structures follow the terminologies proposed by Lawrence *et al.* (2010). Unobservable states are encoded as "?" and those not applicable as "-".

Here, we use the terms ambiguous (or unambiguous) synapomorphies instead of homoplastic synapomorphy. Ambiguous synapomorphy is a hypothesis of primary homologies, not corroborated as its initial proposal (primary homology), but retrieved as synapomorphy for a less inclusive clade, as explained by Pinna (1991).

The phylogenetic analysis was conducted using TNT software – Tree analysis using New Technology 1.5 in which the Maximum Parsimony method is implemented, choosing the shortest tree (in number of transformation steps) as the best hypothesis about the phylogenetic relationship of a given dataset (terminals + matrix) (Goloboff *et al.*, 2008). For the searches, we used the four new-technology algorithms (Goloboff, 1999; Nixon, 1999; Goloboff *et al.*, 2008b) of TNT, with the following parameters: 30 iterations of ratchet, 30 cycles of tree drifting, five rounds of tree-fusing. Parameters were used in driven searches set to reach 70 hits of the best score, with random seed equalling zero and collapsing of unsupported nodes (Goloboff *et al.*, 2008b).

Following (Goloboff, 1993), implied-weighting (IW) parsimony analysis was adopted to infer relationship between taxa. This approach tends to provide a better resolution than analysis with equal weights (EW) (Goloboff *et al.*, 2008a; Goloboff & Arias, 2019; Smith, 2019). However, arbitrary selection of the constant K value, tends to be an obstacle, since the results, based on their fit, can change drastically, as: smaller values tend to weigh more strongly homoplasies, while higher values tend to weigh less, being k∞ equivalent to EW; k=0. To reduce bias, an initial k value was obtained following the model proposed by Pastana (2021), in which an initial value of k, was obtained by calculating the average amount of homoplasy of

the matrix under equal-weights search. Three steps were followed: 1) number of steps/Minimum possible steps (number of characters) = average number of steps: 811,161/110 = 7,374.20; 2) minimum number of possible steps/number of characters = average of minimum number of steps: 131,000/110 = 1.20; and 3) average of homoplasies = observed - minimum: 7.374.20 - 1.20 = 7.373. Subsequently, the other K values were calculated for fits corresponding to 50, 51, 52, 53, 54, 55, 56, 57 and 58% of the fit of a homoplasy-free character by the following formula: k=fe/(1-f), where "k" is the constant, "f" is the fit value, and "e" is the average number of homoplasies. A sensitivity analysis was adopted to compare the result of different K values (Wheeler, 1995; Giribet, 2003). This approach compares common nodes under various weighting schemes, and choose the trees with nodes more stable and less sensitive to K values. Consecutively, a pairwise comparison of the topologies was performed in ViPhy v.1.3.1 (Bremm *et al*., 2011). The element-based score by Bremm *et al.* (2011) was adopted, since it takes into account similarities in terminal taxa and internal nodes of a given clade. The chosen tree therefore has the highest global average of element-based scores among all tested topologies.

The consistency (CI) and retention indices (RI) were calculated in TNT v.1.5 via wstats.run script. Relative Bremer supports (Goloboff & Farris, 2001) were also calculated in TNT v.1.5 by successive searches (via TBR) to test the stability of clades, in suboptimal trees with ≤ 10 extra steps. For each search, suboptimal trees equivalent to 2000 times the number of extra steps were retained (1/2000; 2/4000; 3/6000...10/20,000), totaling 110,000 unique suboptimal trees.

2.4. Biogeographic Analysis

Initially, a table with 1,358 geographic coordinates of all Aerenicini species and phylogenetically related species was created. Geographical distribution maps were generated in Esri ArcGIS 10.5 software (Environmental Systems Research Institute, 2017) based on the World Geodetic System 1984 (WGS 84). Data were obtained from the following catalogs: Monné (2021); Tavakilian & Chevillotte (2021) and Bezark (2021). The geographic distribution data will be submitted to the Global Biodiversity Information Facility (GBIF) platform (https://www.gbif.org/pt/). Additionally, data from species deposited at MZUSP, MZFS, MACN, MLPA and INPA were included in the analysis. Most records come from the southeast region of Brazil (Fig. 3B).

Since we wanted to know where the ancestral populations could have evolved, we needed to define the operational units for ancestral-area reconstruction (OUs). We chose to use Biogeographical regions (bioregions), which can be used as operational units in studies of conservation, historical biogeography, ecology, and evolution (Edler *et al.*, 2017). This method has several advantages, and among them: the OUs will not be chosen a priori and arbitrarily and there is no need to adjust the grids *a priori*, since the data are implemented with adaptive spatial resolution (Vilhena & Antonelli, 2015). The model generates a bipartite network between species and geographic grid, with adaptive resolution, which means, when the data is sparse, the grid size is large and vice versa, and there may be grids of different sizes in the same analysis. Each species is connected by an unweighted link. The bipartite network is then clustered with the Infomap algorithm to form the bioregions (Edler & Rosvall, 2015).

The geographic distribution data of Aerenicini were inserted into the WEB Infomap Bioregions application (https://www.mapequation.org/bioregions/) with the following resolution: Max cell size: 4; Min cell size 1; Max cell capacity 100; Min cell capacity 10. Eight bioregions were identified (Fig.3 C,D).

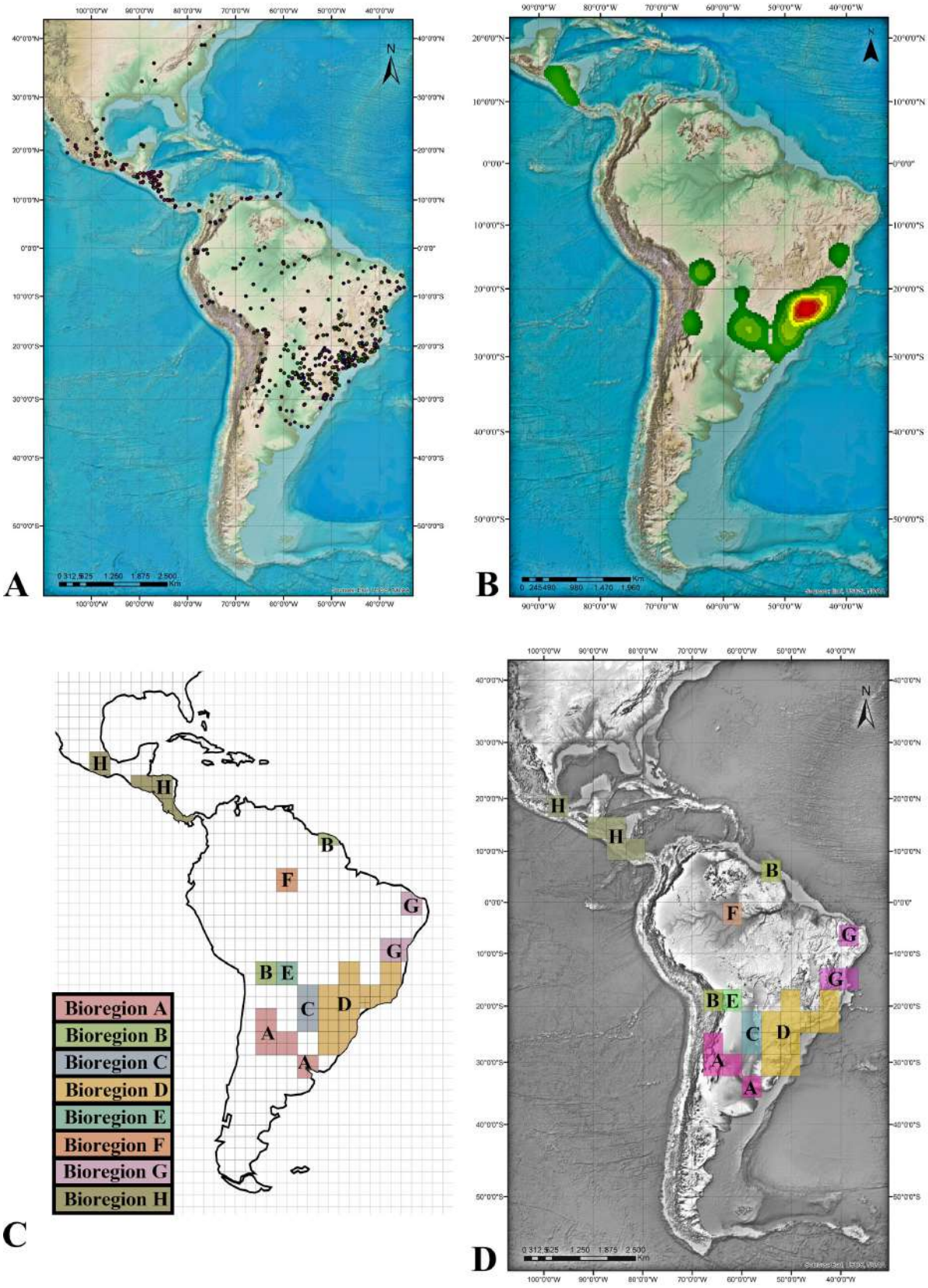

Figure 3. A, Geographical distribution map of Aerenicini (Coleoptera, Cerambycidae) species; B, density map of records, varying from green, yellow and red (red indicates the highest value); C, Bioregions retrieved through Infomap; D, relief map with Bioregions.

Subsequently, a BBM analysis was performed on the RASP 4.2 platform (Reconstruct Ancestral State in Phylogenies, Yu *et al.*, 2015). The analysis were performed with a maximum restriction of four areas, and for the ancestral distribution at the root of the tree, the "outgroup" option was chosen (Yu *et al*., 2015). BBM analysis reconstructs ancestral node distributions using probabilistic methods. We use this method this method because during its orogeny, the areas and their barriers can disappear and appear several times. The method therefore takes into account all possible scenarios and not just the most parsimonious. Also, unlike other methods, trees with polytomies can be implemented.

2.5. molecular analysis

In order to verify a minimum age for Aerenicini, we reanalyzed the phylogeny of Lamiinae, performed by Souza *et al.* (2020) whose sequences are available on GenBank. The five fragments provided by authors include: the mitochondrial markers cytochrome c oxidase subunit 1(cox1) and large ribosomal RNA subunit (rrnL), and the nuclear markers wingless (Wg), carbamoyl-phosphate synthase domain of the CAD locus (CPS), and large ribosomal rRNA subunit (LSU). To increase the representativeness of Aerenicini species, fragments of rrnL from the species *Recchia acutipennis* (Gahan, 1889) and *R. albicans* (Guérin-Méneville, 1831) were also included, as well as fragments of mitochondrial markers cox1 and rrnL of *Annamanum lunulatum* (Pic, 1934) (Lamiini), whose complete mitochondrial genome was published by Dai *et al.* (2020). This allowed us to perform and check the alignment quality. Laboratory methods, including extraction, using the DNeasy Blood & Tissue Kit (QIAGEN) and amplification also followed the protocol by Souza *et al*. (2020). The extractions and amplifications were performed at the Genomic Diversity Laboratory of the Biosciences Institute – IB-USP, São Paulo, Brazil. The sequencing was performed by Genome USP, São Paulo, Brazil.

To infer the divergence time of nodes, we performed dating analysis in the BEAST software v1.10.4 on CIPRES Science Gateway. All analysis were conducted on concatenated data under GTR + G + I model with four gamma categories. The following parameters were used: unlink site models; unlink clock models; uncorrelated relaxed clock with lognormal distribution and Speciation: birth-dead process. Six independent Markov chains Monte Carlo runs of 100,000,000 million generations with samples every 1000 generations. The results were checked using TRACER v1.648. Subsequently data were combined with LOGCOMBINER, to maintain the maximum clade credibility tree with 95% highest posterior density (HPD)

distributions around the estimated node ages using TREEANNOTATOR v1.8.2. The results were edited using FigTreev1.4.3 software.

Following the model by Ashman *et al.* (2022), we calibrated with the following fossil species: *Cretopionus liutiaogouensis* (Wang *et al.*, 2014) to constrain the most recent common ancestor (MRCA) of Cerambycidae, indicating a minimum age of 112 Ma; the species from Baltic amber *Apanopsimus balticus* Vitali, 2014 (Cerambycinae, Opsimini), and *Stenhomalus hoffeinsorum* Vitali, 2014 (Cerambycinae, Obriini) to constrain the MRCA of Cerambycinae and *Pogonocherus jaekeli* (Zang, 1905), to constrain the MRCA of Lamiinae, indicating a minimum age of 34Ma (the Oligocene–Eocene boundary) for Baltic amber fossils, as proposed by Ashman *et al.* (2022). We also include *Paleohemilophus dominicanus* Martins & Galileo, 1999, to constrain the MRCA of Hemilophini, indicating a minimum age of 20 Ma, as proposed by Iturralde-Vinent & MacPhee (1996).

3. RESULTS

The detailed study of both, specimens and bibliography, allowed us to list 110 morphological characters of 88 terminal taxa. Twenty-four quantitative characters were analyzed, with continuous data. Among the 86 qualitative characters, are included: 20 from the head; 15 from thorax; 17 from elytra; six from membranous wings; 12 from legs; eight from the abdomen and ten from genitalia. Below are listed the characters, their states and, when relevant, additional comments are provided. Character numbering follows TNT default, from 0 to 109. Both (discrete and continuous) matrices are also shown (Tables 4 and 5) .

Continuous characters with normalized values

0. **Scape length (x) in relation to prothorax length (1);** min= 0.17, max= 1.74 *Indices:* ci=0.189; ri=0.578

   Remarks: This is an important character used in the taxonomy of Cerambycidae. In Aerenicini, Martins & Galileo (1998) uses the length of scape as a reference to measure the length of the antennomere III, as in the alternative of couplet “8” (translated): Antennomere III shorter than the scape...Antennomere III as or longer than the scape". We used the length of prothorax as a reference to measure the length of all antennomeres, since the ratio of prothorax length and body length is relatively conserved.

1. **Pedicel length (x) in relation to prothorax length (1);** min= 0.07, max= 0.56. *Indices:* ci=0.230; ri=0.219
2. **Length of the antennomere III (x) in relation to prothorax length (1);** min= 0.17, max= 2.38. *Indices:* ci=0.198; ri=0.506
3. **Length of the antennomere IV (x) in relation to prothorax length (1);** min= 0.17, max= 1.70 *Indices:* ci=0.152; ri=0.431
4. **Length of the antennomere V (x) in relation to prothorax length (1);** min= 0.17, max= 1.74 *Indices:* ci=0.173; ri=0.569
5. **Length of the antennomere VI (x) in relation to prothorax length (1);** min= 0.15, max= 1.90 *Indices:* ci=0.201; ri=0.601
6. **Length of the antennomere VII (x) in relation to prothorax length (1);** min= 0.15, max= 1.90 *Indices:* ci=0.216; ri=0.614
7. **Length of the antennomere VIII (x) in relation to prothorax length (1);** min= 0.15,

max= 1.90 *Indices:* ci=0.223; ri=0.589

8. **Length of the antennomere IX (x) in relation to prothorax length (1);** min= 0.13, max= 1.90 *Indices:* ci=0.242; ri=0.602

9. **Length of the antennomere X (x) in relation to prothorax length (1);** min= 0.13, max= 1.94 *Indices:* ci=0.252; ri=0.582

10. **Length of the antennomere XI (x) in relation to prothorax length (1);** min= 0.18, max= 2.52 *Indices:* ci=0.292; ri=0.549

11. **Length of the antennomere XII (x) in relation to prothorax length (1);** min= 0.42, max= 0.84 *Indices:* ci=1.000; ri=1.000

12. **Length of abdominal ventrite II (x) in relation to abdominal ventrite I (1);** min= 0.33, max= 0.85. *Indices:* ci=0.133; ri=0.346

    Remarks: We considered the length in the anterior to posterior body axis. The length of the abdominal ventrites is not used in taxonomy, probably because it is conserved. We used the abdominal ventrite I as a reference for remaining. Generally, this ventrite is the longest, and specimens, who's abdominal ventrite V is notched, we considered the greatest length (excluding the notching).

13. **Length of abdominal ventrite III (x) in relation to abdominal ventrite I (1);** min= 0.33, max= 0.85. *Indices:* ci=0.133; ri=0.353

14. **Length of abdominal ventrite IV (x) in relation to abdominal ventrite I (1);** min= 0.31, max= 0.83. *Indices:* ci=0.125; ri=0.290

15. **Length of abdominal ventrite V (x) in relation to abdominal ventrite I (1);** min= 0.45, max= 0.89. *Indices:* ci=0.125; ri=0.370

16. **Humeral width (x) in relation to general body length (1);** min= 0.15, max= 0.65. *Indices:* ci=0.260; ri=0.611

    Remarks: With this character, we sought to quantitatively evaluate the general shape of the body, usually in the literature as "slenderer" or "more robust". Although it is evident a gradient among Aerenicini species, some groups have this characteristic very marked, as species of the genera *Aerenicopsis* and *Hydraschema*. This "slender" form probably co-evolved with the host plants, which are non-woody and shrubby. A good example is the species *Aerenicopsis championi* Bates, in which uses *Lantana camara* L. (Verbenaceae) as

host plant (Palmer *et al.,* 2000). Also, species of the genus *Hippopsis* (Agaphantini) have this form. In fact, these genera were retrieved as members of the clade 98.

17. **Prothorax length (x) in relation to elytral length (1);** min= 0.15,max= 0.37. *Indices:* ci=0.162; ri=0.537

18. **Distance between the antennal sockets (x) in relation to the length of prothorax (1);** min= 0.20, max= 0.88. *Indices:* ci=0.114; ri=0.485

19. **Median width of the prosternal process (x) in relation to the median width of the metaventrite (1)**; min= 0.01, max= 0.10. *Indices:* ci=0.120; ri=0.290

20. **Median width of the mesoventral process (except lateral expansion) in relation to the median width of the metaventrite (1);** min= 0.02, max= 0.24. I*ndices*: ci=0.163; ri=0.372

    Remarks: This character was used by Martins & Galileo (1998) diagnostic feature of Aerenicini (translated): "Mesosternal process narrow, with subparallel sides, truncated at the apex". Quantification, using the metathorax width as a reference, allowed us to objectively evaluate the evolution of this feature among terminals.

21. **Distance beteween upper eyes lobes (x) in relation to distance of antennal sockets (1);** min= 0.04, max= 0.44. *Indices:* ci=0.172; ri=0.495

    Remarks: In general, there is a great variation of this character among the groups of Aerenicini, as mentioned by Martins & Galileo (1998) (translated): “variable distance between lobes according to genera: more or so distant between them as the width of a lobe to very close or subcontiguous (separated by distance to a row of ommatidia)”. The distance between the eye lobes was used in the key proposed by these authors, in the alternative of couplet four and 11. As a reference, we used the distance between the antennal sockets.

22. **Length of the of the genae (x) in relation to lower eyes lobes (1);** min= 0.09, max= 2.12. *Indices:* ci=0.231; ri=0.600

    Remarks: The relation between the lower eye lobes and the gena length was used by Martins & Galileo (1996) as one of the characteristics to separate Aerenicini from Hemilophini. According to them, the lower eye lobes in Aerenicini are much longer than gena while, shorter or slightly longer in Hemilophini. Recently, Tavakilian & Santos-Silva (2019) transferred *Phoebemima* from Hemilophini to Aerenicini, based especially on this feature. These authors made some considerations about the differentiation between these tribes:

"Comparing the shape of lower eye lobes and also the shape of the ommatidia, it is not possible to understand the placement of *Phoebemima* in Hemilophini, since the eyes are not finely faceted and the lower eye lobes are much longer than gena... All these problems make the differentiation between Aerenicini and Hemilophini practically impossible, which suggests that they are a single tribe. However, for the time being, it is much more coherent to transfer *Phoebemima* to Aerenicini than maintain it in Hemilophini, following the concept of Martins & Galileo (1996)." Many species of Aerenicini have lower eye lobes occupying the entire side of the head and this is probably linked to the nocturnal habit. Although the quantification of this character is not as practical as the discretization made by previous authors, this character was retrieved as a synapomorphy of (clade 103) that groups Aerenicini species, except *Phoebemima* and *Suipinima marginalis*. We used the inferior ocular lobes length as a reference, to evaluate their relation with genae length. Our analysis indicates a range change from 0.227-0.276 to 0.044-0.054, evidencing, a marked increase in the lower eye lobes in this lineage. Obviously, the variation could be in the length of the genae rather than in eyes lobes. However, the general amount of ommatidia in the eyes lobes allows us to infer their increase in size.

23. **Prothorax width (x) in relation to prothorax length (1);** min= 0.70, max= 1.65.

Indices: ci=0.161; ri=0.503

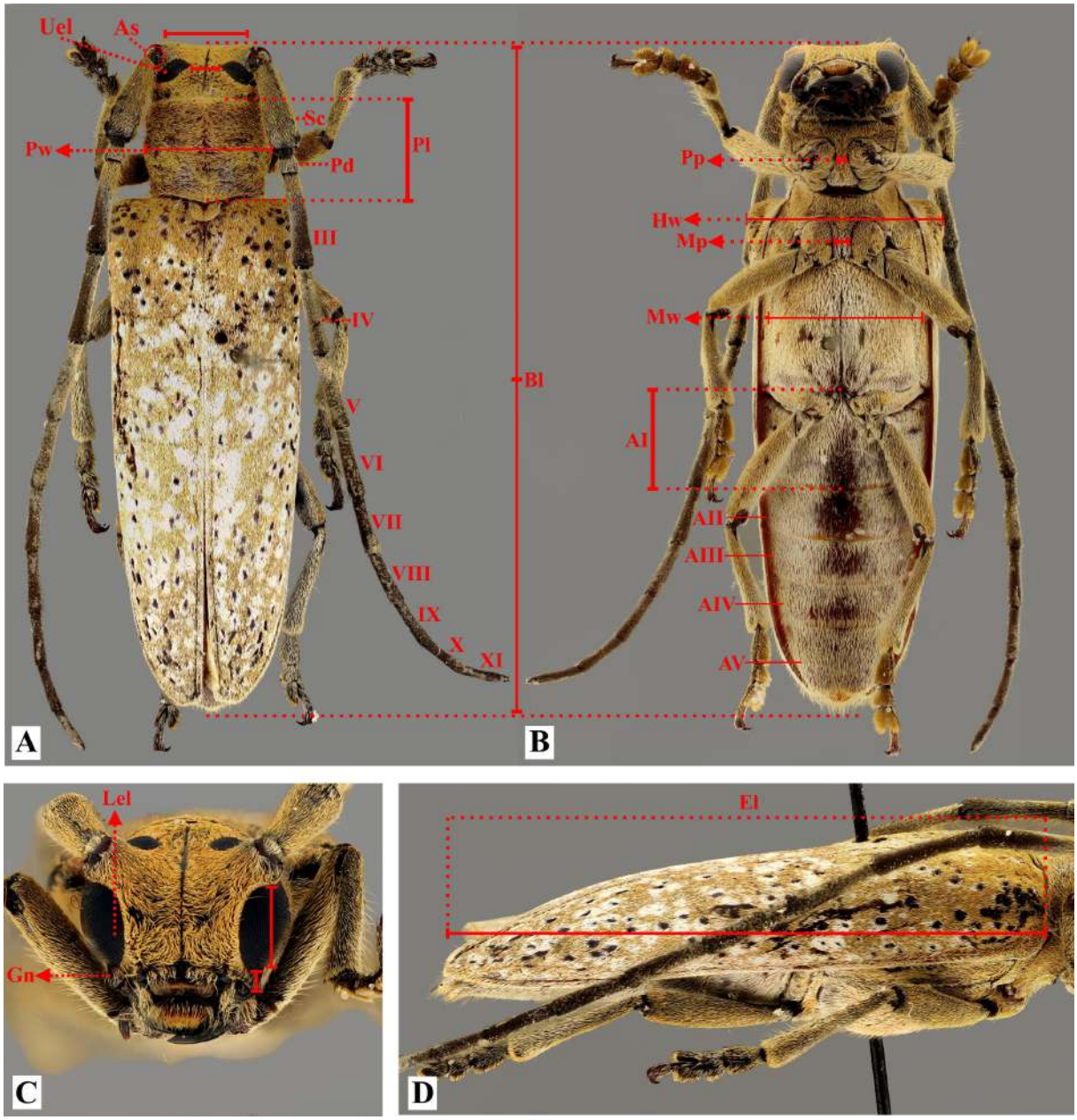

Figure 4. *Hoplistonychus bondari* Melzer, 1930. A–B, habitus: A, dorsal view; B, ventral view. C, head in front view; D, mesothorax and abdomen, lateral view. The lines represent the proportion of different body parts. Abbreviations: AI–AV, abdominal ventrites I–V; As, antennal socket; Bl, body length; El, elytral length; Gen, Gena; Hw, humeral width; III–XI, flagelomeres III–XI; Lel, lower eye lobe; Mp, mesoventral process; Mw, metaventrite width; pd, pedicel; Pl, prothorax length; Pp, Prosternal process; Pw, prothorax width; Sc, escape; Uel, upper eye lobe.

Discrete characters

24. **Mouthparts, palpi general color:** Yellowish (0), (Fig. 5A, B, C); Brownish (1), (Fig. 5D, E, F). *Indices*: ci=0.059; ri=0.568

Remarks: Quantifying characters that deal with colors is not an easy task. In an indirect way, color analysis deals with the adaptations of species in their ecological niche

(Hernández, 2002). According to Crowson (1981), beetles with dark colors have nocturnal habits, while those with more vibrant colors, are associated with daylight. There are some hypotheses about the role of colors and among them, it is worth mentioning the Thermal melanism hypothesis (thermal regulation) and Photoprotection hypothesis (protection against DNA degradation) (Lopez *et al*., 2021). Unlike the color of other parts of the body, the coloration of the mouth parts is relatively well preserved. It is possible to recognize two patterns (brown and yellowish) that may or may not correspond to the general color of the body. This character state (24:0) is an ambiguous synapomorphy of clade 111, which includes species of *Falsamblesthis* (Forsteriini) and clade 97, which includes several species of Aerenicini (+ *Hippopsis*) with brightly color patterns.

25. Mouthparts, maxillar distal palpomere, shape: Fusiform (0), (Fig. 5A, B, C; Fig.7 H) ; Cylindrical (1), (Fig. 5F; Fig. 7I); Clavate (2), (Fig. 5B; Fig. 7J). *Indices*: ci=0.286; ri=0.167

Remarks: The fusiform shape of the apical palpomere occurs in most Lamiinae (Svacha & Lawrence, 2014). According to Napp (1994), the aciculated apical palpomere of Lamiinae is a relatively constant character. Among the terminals, we were able to identify a cylindrical pattern (Fig 7I) in some species. In fact, this shape is an ambiguous synapomorphy for clade 136, which includes *Aerenica canescens* (type species of Aerenicini) and *Aereniphaula bandana*.

26. Mouthparts, maxillar palpomere IV, pubescence: Dense (0), (Fig. 5A, B, C); Sparse (1), (Fig. 5D, E, F). *Indices*: ci=0.100; ri=0.679

Remarks: Dense and sparse pubescence patterns evolved concomitantly in different groups. It is possible to recognize a pattern of dense pubescence in most Hemilophini species (clades 125 and 131) and in *Apophaula ocellata*, sister group of the remaining Aerenicini. Apparently, this is evidence of the evolution of the nocturnal habit in Aerenicini from a diurnal group, although there have been reversals.

27. Head, dorsal view, median sulcus, length: Short, does not cross the whole vertex area (0) (Fig. 7A); Long, it crosses the whole area of the vertex, obliterated by the prothorax. (1), (Fig. 7B). *Indices*: ci=0.125; ri=0.462

28. Head, dorsal view, vertex, punctures, size: Fine (0), (Fig. 6A); Coarse (Fig. 6A) (1). *Indices*: ci=0.125; ri=0.462

Remarks: Previous authors (*i.e.* Crowson, 1981) already mentioned the importance of the type of integumentary punctures for the Coleoptera systematics: "The relative sizes and density of such punctures provide very useful systematic characters at species level..." Head with dorsally fine punctures were retrieved as an ambiguous synapomorphy for clade 122 which is composed of Hemilophinni species, and for clades 167 and 162 which includes species of *Pseudomecas* and *Melzerella* species respectively. In addition, it also occurs in *Apoaerenica martinsi*. With the exception of *Pseudomecas*, the other groups have very showy elytral pubescence patterns.

29. **Head, frontal view, antennal tubercles, shape:** Abruptly elevated (0), (Fig. 5H); Gradually elevated (1), (Fig. 5I). *Indices*: ci=0.500; ri=0.667

Remarks: We consider tubercles abruptly elevated, when they rise from the median sulcus. Elevated tubercles occur in the genus *Hippopsis* (Agaphantini) (Fig. 5H) and *Tyrinthia* (Hemilophini).

30. **Head, frontal view, antennal tubercles, depression**: Absent (0); Present (1), (Fig 5 K). *Indices*: ci=0.500; ri=0.500

Remarks: As pointed out by Martins (2014b), the depression between the antennal tubercles (vertex) (Fig. 5K) is a characteristic of *Tyrinthia* species (Hemilophini) and this was retrieved as a synapomorphy for this genus.

31. **Head, lateral view, pubescent band obscuring integument:** Absent (0); Present (1), (Fig. 6D). I*ndices*: ci=0.111; ri=0.556

32. **Head, frons, shape:** Parallel sided (0); Converged downward (1); Converged upward (2). *Indices*: ci=0.143; ri=0.520

Remarks: The shape of frons was defined by the shape of the lower eye lobes in frontal view (Fig. 5G–L.). The parallel-sided pattern is the most common, occurring in both, outgroup and ingroup. The converged downward form is an ambiguous synapomorphy for several clades of Aerenicini (93; 136; 161 and 167).

33. **Head, frons, punctures, size:** Fine (0), (Fig. 8D); Coarse (1), (Fig. 8B). *Indices*: ci=0.200; ri=0.667

Remarks: Coarsely punctures in frons occurs in all Aerenicini (except *Suipinima marginalis* and *Phoebemima* species). Fine punctures occur in many groups of Hemilophini and, like other characters, may be associated with diurnal habit.

34. **Head, frons, pubescent pattern:** Sparse, not obscuring the integument (0), (Fig. 5I); Moderate, partially obscuring integument (1), (Fig. 5H); Dense, obscuring integument at least in some areas (2), (Fig. 5J). *Indices*: ci=0.091; ri=0.592

Remarks: The quantification of this feature is extremely difficult due its variation, sometimes even intraspecifically. We consider a moderate pattern when the integument is partially and evenly covered by pubescence. Although it rarely occurs, in these cases (intraspecific variation), a greater number of specimens was studied. In none of the observed specimen there is an extreme variation from sparse to densely distributed pubescence. In Aerenicini, dense pubescence on frons is an ambiguous synapomorphy for clade 157 which is part of what Lane (1973) called "Phaula complex". This pattern is also a synapomorphy of clade 173 that groups the two *Rumacon* species.

35. **Head, Frons, projections:** Absent (0); Present (1), (Fig. 6E, P). *Indices*: ci=0.500; ri=0.750

Remarks: Head with projections on frons only occurs in the outgroup (Hemilophini), in clade 134 which includes *Phoebe* and related genera, and also in *Tyrinthia scissifrons*.

36. **Head, Frons, median groove, perceptibility:** Conspicuous (0), (Fig. 5N); Inconspicuous (1), (Fig. 5O). *Indices*: ci=0.333; ri=0.000

Remarks: Frons with median groove inconspicuous was not observed in any New World specimens used in our analysis

37. **Head, ocular lobes, ommatidia, size:** Coarsely faceted (0), (Fig. 8A); Finely faceted (1), (Fig. 8C). *Indices*: ci=0.167; ri=0.828

Remarks: Lacordaire (1868) mentioned this character as an important taxonomic tool for Cerambycidae. The ommatidia size was also mentioned by Fragoso (1987) who associated it with the diurnal (Finely faceted) or nocturnal (Coarsely faceted) habit. Martins & Galileo (1996) differentiated Aerenicini from Hemilophini (among other characteristics) by coarsely faceted and finely faceted ommatidia respectively (Fig. 8A, C). Tavakilian & Santos-Silva (2019) transferred *Phoebemima* to Aerenicini based especially on features of the eye lobes. In fact, in some species, this differentiation is not so easy. We coded *Phoebemima* as having finely faceted eyes (Fig. 8C) aided also by probable diurnal habit (due to integumentary color pattern). It is noteworthy that some species of Aerenicini such as *Apophaula ocellata*, *Aphilestes rustica* and *Aerenicella spissicornes* were coded as having finely faceted eyes. This demonstrates

that, although many Aerenicini follow the pattern proposed by Martins & Galileo (1996), some species deviate from this rule. The species *Suipinima marginalis* also has coarsely faceted eyes, however, its position in Hemilophini is well supported. Another good evidence of the Aerenicini's nocturnal habit is that they are more easily collected with nocturnal light traps.

38. **Head, ocular lobes (upper and lower), connection:** Absent (0), (Fig. 7C); Present (1), (Fig. 7D, E). *Indices*: ci=0.500; ri=0.000

Remarks: According to Martins & Galileo (1998) in some species of *Aerenicopsis*, the eye lobes are divided. The connection or lack of this, between the lower and upper lobes must be related to the evolution of antennal tubercles, which according to Svacha & Lawrence (2014) provides better support for antennal movement. In fact, these species have very long antennae. In Aerenicini were verified separate eye lobes only in *Hydraschema obliquevittata* which is in the same clade (139) as *Aerenicopsis*.

39. **Head, ocular lobes, relation of rows of ommatidia that separates the lower and upper lobes in relation to Upper eye lobe width:** Subequal, with the same width as the upper eye lobe (0), (Fig. 7 D); Narrowed, narrower than the upper eye lobe (1), (Fig. 7 E). *Indices*: ci=0.071; ri=0.629

Contingent of 38: If character [38] is absent (0), [39] is inapplicable (-).

40. **Head, antennae, number of antennomeres:** Eleven (0); Twelve (1). *Indices*: ci=0.250; ri=0.400

Remarks: Antennae with twelve antenomeres is a synapomorphy of clade 134 (outgroup), which includes *Purusiella* and relatives. *Phoebe concina* which has eleven antennomeres is also inserted in this clade. Future phylogenetic studies, focused on Hemilophini, may better elucidate the evolution of this tribe. Our data only demonstrate that Hemilophini is a polyphyletic group.

41. **Antennae, flagelomeres, setae densely distributed:** Absent (0); Present (1), (Fig. 9 C). *Indices*: ci=0.333; ri=0.500

Remarks: In the ingroup, only *Aerenicella spissicornis* has flagellomeres with dense distributed setae. In Hemilophini, this pattern is an ambiguous synapomorphy of clade 129, which includes the type species of the tribe *Hemilophus dimitiaticornes* and the species of the genus *Tyrinthia*.

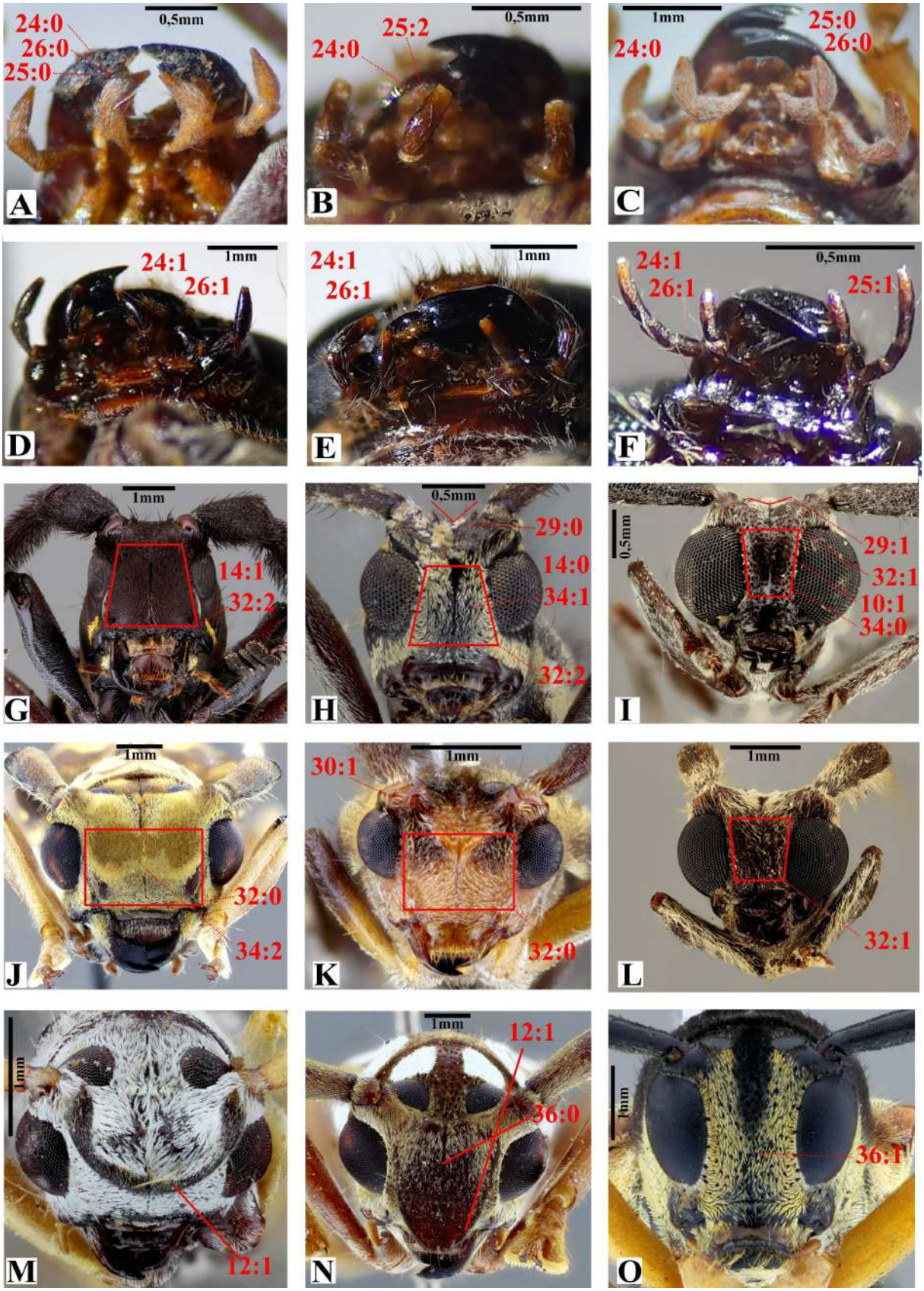

Figure 5. A–F, head ventral, mouthparts of Lamiinae species: A, *Adesmus borgmeieri* (Lane, 1976); B, *Eponina breyeri* (Prosen, 1954); C, *Purusiella wappesi* (Martins & Galileo, 2004); D, *Hoplistonychus bondari* Melzer, 1930; E, *Phaula lichenigera* (Perty 1832); F, *Aereniphaula bandana* Nascimento, Botero & Bravo, 2016. G–O, Head in frontal view: G, *Grylica picta* (Pascoe, 1958); H, *Hippopsis pubiventris* Galileo & Martins 1988; I, *Aerenicopsis mendosa* Martins & Galileo 1998; J,

Purusiella wappesi (Martins & Galileo, 2004); K, *Tyrinthia scissifrons* Bates, 1866; L, *Hydraschema obliquevittata* (Lane 1956); M, *Phoebe concinna* White, 1856; N, *Purusia acreana* Lane, 1956; O, *Glenea fasciata* (Fabricius 1781). Red numbers (*e.g.* 26:1) represent character and state respectively.

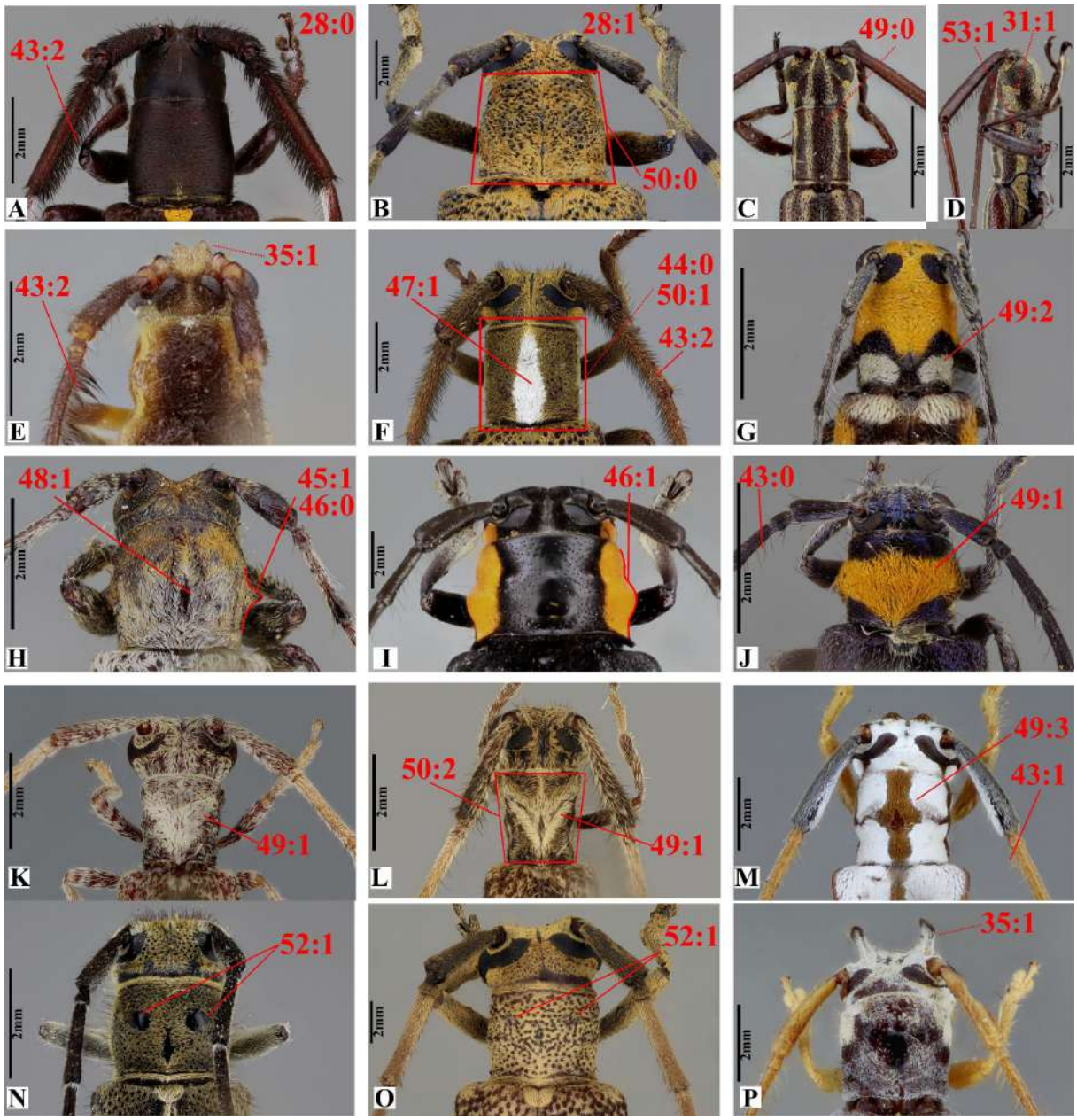

Figure 6. A–O, Head and prothorax of Lamiinae species in dorsal view (except D). A, *Grylica picta* (Pascoe 1958)**;** B, *Saperda carcharias* (Linnaeus, 1758); C–D, *Hippopsis truncatella* Bates, 1866; C, dorsal view; D, lateral view; E, *Tyrinthia scissifrons* Bates, 1866; F, *Calliphaula leucippe* (Bates, 1881); G, *Mariliana cicadellida* Galileo & Martins 2004; H, *Ataxia luteifrons* (Bruch, 1926); I, *Ites plagiatos* Waterhouse 1880; J, *Callia azurea* Audinet–Serville 1835; K, *Aerenica canescens* (Klug, 1825); L, *Aereniphaula bandana* Nascimento, Botero & Bravo, 2016; M, *Phoebella phoebe* (Lepeletier & Audinet–Serville, 1825); N, *Mecas menthae* Chemsak & Linsley 1973; O, *Phaula thomsoni* Lacordaire, 1872; P, *Phoebe concinna* White, 1856. Red numbers (*e.g.,* 47:1) represent character and state respectively.

42. **Head, antennae, scape, shape:** Narrowed basally, gradually widening towards apex (0), (Fig. 8F); Longitudinally subequal in diameter (1), (Fig. 8E); Fusiform, wider in the middle (2), (Fig. 8 G); Abruptly enlarged towards apex (3), (Fig. 8H). *Indices*: ci=0.600; ri=0.600

43. **Antennae, antennomere III, inner side, erect elongated setae density:** Scarce, few and sparse (0), (Fig. 6J); moderately dense (1), (Fig. 6M); Dense, abundant and close to each other (2), (Fig. 6A, E, F).

Remarks: While extreme character states (sparse and dense) are easily recognized, the moderate pattern is difficult to encode. We consider a distribution pattern of setae as moderately dense, when they do not form a brush pattern.

44. **Prothorax, sides, shape:** Subparallel (0), (Fig. 6F); non-parallel (1). *Indices*: ci=0.100; ri=0.438

Remarks: Considering the reductive method of coding, we separated, the pattern of prothorax subparallel-sided, from others that include both, prothorax with tubercles and prothorax without tubercles, with non-subparallel sides. Prothorax with subparallel sides is an ambiguous synapomorphy of clade 139, which includes species of *Hydraschema* and *Aerenicopsis*, clade 91 with *Calliphaula filiola*, species of *Hippopsis*, and clade 173 which groups *Rumacon* species.

45. **Prothorax, sides, tubercles:** Absent (0); Present (1), (Fig. 6H). *Indices*: ci=0.143; ri=0.739

Contingent of 44: If character [44] is subparallel (0), [45] is inapplicable (-).

46. **Prothorax, sides, tubercles, shape:** Culminated (0), (Fig. 6H); Rounded (1), (Fig. 6 I). *Indices*: ci=1.000; ri=1.000

Contingent of 45: If character [45] is absent (0), [46] is inapplicable (-).

47. **Prothorax, pronotum, contrasting dense pubescence:** Absent (0); Present (1), (Fig. 6F). *Indices*: ci=0.056; ri=0.541

Remarks: This character is quite difficult to encode due to its variable nature. However, dense pubescence forming defined areas is commonly found in diurnal species and is certainly related to camouflage or mimicry phenomena. Although it is possible to observe some pattern of pubescence in nocturnal species, the integument is partially exposed, which characterizes it as “non-dense”. Therefore, in this character and in

others which deal with "contrasting dense pubescence", we refer to pubescence that completely cover the integument, having its limits well defined (contrasting) in relation to the adjacent surface. Commonly, these areas have vibrant colors, especially white. This character was used by Martins & Galileo (1998).

48. Prothorax, pronotum, midline, occurrence of narrow longitudinal glabrous area: Absent (0); Present (1), (Fig. 6H). *Indices*: ci=0.143; ri=0.538

49. Prothorax, pronotum, contrasting dense pubescence, occurrence of the following patterns: Linear (0), (Fig. 6C); Triangular (1), (Fig. 6J, K, L); Rounded (2), (Fig. 6 G); Sinuous band (3), (Fig. 6M). *Indices*: ci=0.300; ri=0.500

Contingent of 47: If character [47] is absent (0), [49] is inapplicable (-).

Remarks: The occurrence of dense pubescent patterns does not exclude the presence of dense pubescence also in other areas.

50. Prothorax, relation of width between anterior and posterior margins: Narrower (0), (Fig. 6B); Subequal (1), (Fig. 6F); Wider (2), (Fig. 6L). *Indices*: ci=0.087; ri=0.543

Contingent of 44: If character [44] is subparallel (0), [50] is Subequal (1).

51. Prothorax, pronotum, tubercles: Absent (0); Present (1). *Indices*: ci=0.067; ri=0.576

52. Prothorax, pronotum, dorsolateral tubercles: Absent (0); Present (1), (Fig. 6N, O). *Indices*: ci=0.143; ri=0.625

Contingent of 51: If character [51] is absent (0), [52] is inapplicable (-).

53. Prothorax, pronotum, sides, occurrence of contrasting longitudinal dense pubescent bands: Absent (0); Present (1), (Fig. 6D; Fig. 10I). *Indices*: ci=0.091; ri=0.524

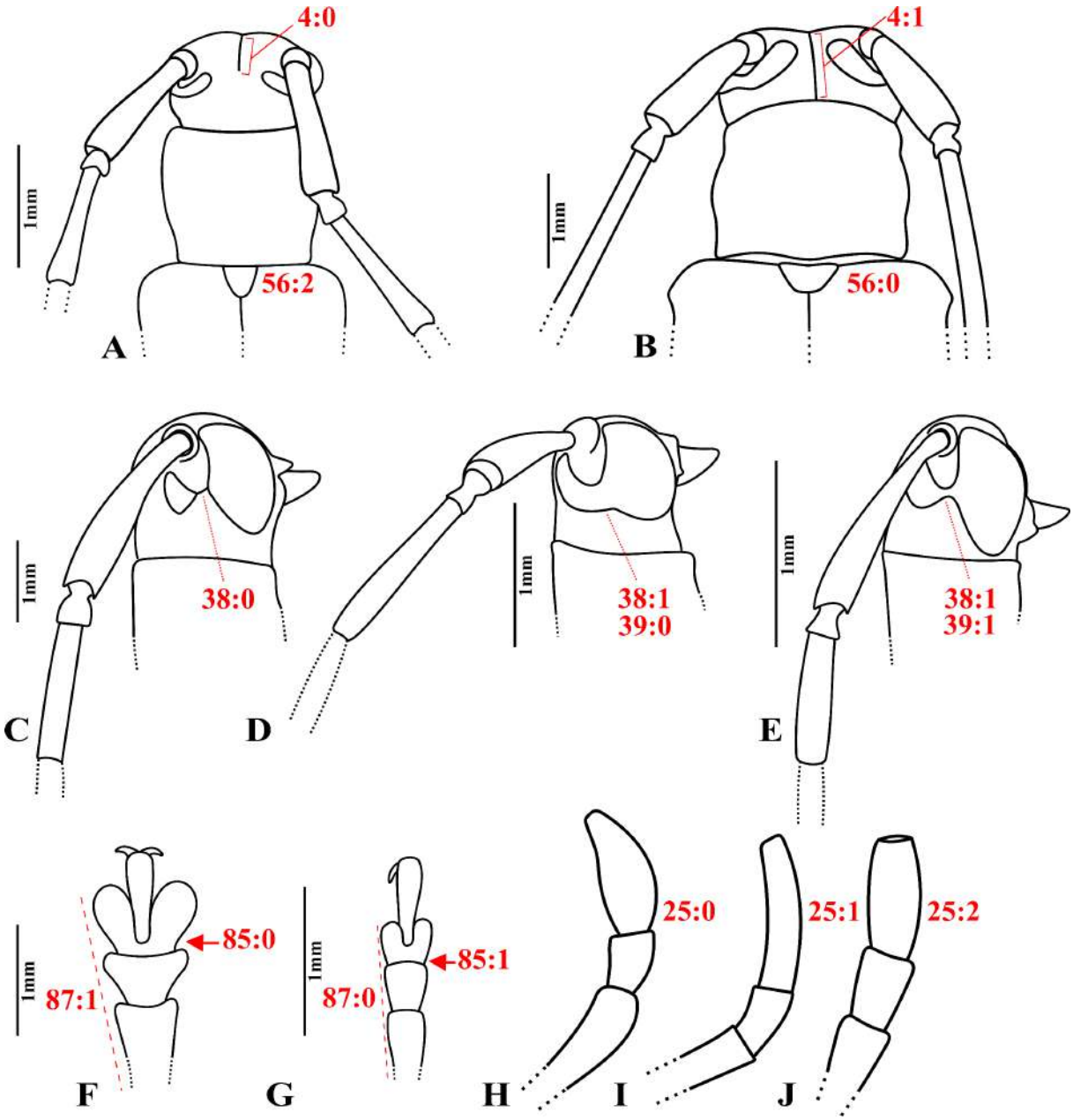

Figure 7. A–J, Schematic drawings of Lamiinae species: A–B, head, prothorax and basal region of elytra, dorsal view; A, *Apagomerella versicolor* (Boheman, 1859); B, *Calocosmus nuptus* Chevrolat 1862; C–E, prothorax and head detail in lateral view; C, *Hydraschema obliquevittata* (Lane 1956); D, *Antodice abstrusa* Lane, 1940; E *Aerenicopsis pugnatrix* (Lane 1966); F–G, tarsus; F, *Purusia acreana* Lane, 1956; G, *Agapanthia cardui* (Linnaeus, 1767); H–J, maxillar palpomeres; detail of distal palpomere: H, fusiform; I, cylindrical J, clavate. Red numbers (*e.g.* 38:0) represent character and state respectively.

54. **Mesothorax, mesepimeron, dense, contrasting pubescence:** Absent (0); Present (1).

Indices: ci=0.111; ri=0.636

55. **Mesothorax, mesoventral process, lateral expansion:** Absent (0), (Fig. 9B, C);

Present (1), (Fig. 9A). *Indices*: ci=1.000; ri=1.000

Remarks: When describing the general morphology of Hemilophini, Martins (2014a) comments that lateral articular processes may occur in the mesosternal process. In fact, we observed this character state in clade 125, which contains Hemilophini species (+*Suipinima marginalis* and *Phoebemima* species). The mesoventral process in Aerenicini does not have this expansion.

56. **Mesothorax, scutellum, width in relation to length:** Wider than long (0), (Fig. 7B); As wide as long (1); Longer than wide (2), (Fig. 7A). *Indices*: ci=0.091; ri=0.615

57. **Metathorax, metaventrite, lateral area, dense contrasting pubescence:** Absent (0), (Fig. 10); Present (1), (Fig. 10H). *Indices*: ci=0.500; ri=0.944

58. **Metathorax, metanepisternum, dense contrasting pubescence:** Absent (0), (Fig. 10F); Present (1), (Fig. 10I). *Indices*: ci=0.200; ri=0.810

59. **Elytra, lateral expansion:** Absent (0); Present (1), (Fig. 9A, B). *Indices*: ci=1.000; ri=1.000

Remarks: Martins (2014a) grouped the Hemilophini genera with elytral lateral expansions in "group C". This group included 18 genera and was retrieved as a synapomorphy of clade 131 that includes only two Hemilophini species. The clade 131 is sister group of others Hemilophini + Aerenicini and apparently this is a plesiomorphic feature. This may also indicate that the ancestor of this group (Aerenicini + Hemilophini) had diurnal habits since these cerambicids are mimetics of unpalatable species of Lycidae (Coleoptera) and they may even gregarious habits (Linsley, 1961).

60. **Elytra, contrasting dense pubescence: Absent (0); Present (1),** (Fig. 9D). *Indices*: ci=0.111; ri=0.714

Remarks: In Aerenicini, elytra with contrasting dense pubescence is an ambiguous synapomorphy of clade 94. Like other characters dealing with these contrasting dense pubescence, it can be a camouflage tool for the diurnal habit. This form is quite common in Cerambycidae and Martins & Galileo (1998) when characterizing Aerenicini, report as follows (translated): “Some genera with white elytral pubescence concentrated in patches or contrasting areas”.

61. **Elytra, punctures, relation with pubescence:** Obliterated, not contrasting (0); Not obliterated, contrasting (1), (Fig. 9G). *Indices*: ci=0.167; ri=0.722

Remarks: According to Martins & Galileo (1998) in many genera of Aerenicini, the elytral punctures are contrasted with the remain surface because they are glabrous or have a glabrous perimeter. Indeed, contrasting elytral punctures is an ambiguous synapomorphy of clade 137, which includes among others the "Phaula complex" and clade 136 with *Aerenica canescens*.

62. Elytra, humeral areas, contrasting integument color: Absent (0); Present (1), (Fig. 9 E). *Indices*: ci=1.000; ri=1.000

63. Elytra, occurrence of contrasting pattern of pubescence forming an "x": Absent (0); Present (1), (Fig. 9H). *Indices*: ci=1.000; ri=1.000

Contingent of 60: If character [60] is absent (0), [63] is inapplicable (-).

***Remarks*:** contrasting pattern of pubescence forming an "x" is a unambiguous synapomorphy of clade 162, which groups *Melzerella* species. This pattern is very rare and although we are using only two of the six species of *Melzerella*, this pattern occurs in almost all species of this genus (except *M. costalimai* Seabra, 1961). For this reason, we inserted it into our matrix, to test the hypothesis whether there would be any phylogenetic signals.

64. Elytra, apices, spiniform projection: Absent (0); Present (1), (Fig. 11D, E). *Indices*: ci=0.071; ri=0.581

Remarks: Martins & Galileo (1985b) defined some groups of genera based on the shape of the elytral apices. Elytra with spiniform projection occurs in clade 100, and is present in several species of this tribe. Following the logic of contingent coding, we separate the occurrence of these projections from the number of it, as proposed by Martins & Galileo (1985b).

65. Elytron, apex, number of spiniform projections: One (0), (Fig. 11D); Two (1), (Fig. 11E). *Indices*: ci=0.333; ri=0.500

Contingent of 64: If character [64] is absent (0), [65] is inapplicable (-).

66. Elytron, apex, shape: Transversally truncated (0), (Fig. 11E); Obliquely truncated (1), (Fig. 11I); Rounded (2), (Fig. 11F); Acuminate (3), (Fig. 11D, G). *Indices*: ci=0.200; ri=0.571

67. Elytra, apices, jointly rounded margins: Absent (0); Present (1), (Fig. 11H). *Indices*: ci=0.111; ri=0.429

68. **Elytra, humeral areas, contrasting concentrates punctures:** Absent (0); Present (1), (Fig. 9F, G). *Indices*: ci=1.000; ri=1.000

Remarks: In the alternative of couplet 6, from the key proposed by Martins & Galileo (1998), the presence of concentrated, contrasting punctures is mentioned as follows (translated): "...Basal region of the elytra (longer than twice the length of the scutellum) with concentrated punctures, juxtaposed, dense and on the rest of the elytral surface spaced apart…". This feature is a synapomorphy of clade 159, which includes *Phaula* and relatives.

69. **Elytra, area? concentrate punctures, length in relation to scutellum length:** Longer, exceeds three times the scutellum length (0), (Fig. 9F); Shorter, does not exceed three times the scutellum length (1), (Fig. 9G). *Indices*: ci=1.000; ri=1.000

Contingent of 68: If character [68] is absent (0), [69] is inapplicable (-).

70. **Elytra, presence of elongated erect setae:** Absent (0); Present (1), (Fig. 10F). *Indices*: ci=0.083; ri=0.389

71. **Elytra, dorsolateral areas, longitudinal carina:** Absent (0); Present (1), (Fig. 9C, D). *Indices*: ci=0.250; ri=0.727

Remarks: Lacordaire (1872) used the presence of humeral carina in Hemilophini to separate it from Aerenicini. However, since this characteristic is variable even in Hemilophini, Martins (2014a) grouped some genera that have humeral carina in "group F". In fact, elytra with humeral carina are only present in some groups of Hemilophini, as in clade 121 that includes the fossil *P. dominicanus*.

72. **Elytra, integument, orange longitudinal bands:** Absent (0); Present (1), (Fig. 9G, F). *Indices*: ci=0.500; ri=0.667

Remarks: As pointed out by Martins & Galileo (1998), these bands are present in the *Holoarenica* and *Phaula* genera of which they were grouped in clade 156.

73. **Elytra, sutural margins, delimited carina:** Absent (0); Present (1), (Fig. 9B). *Indices*: ci=0.100; ri=0.357

74. **Elytra, sutural margins, dense pubescence:** Absent (0); Present (1) (Fig. 9I, J, K, L). *Indices*: ci=0.125; ri=0.222

75. **Hindwing, veins, media posterior 3 + 4 (MP3 + 4), basal shape:** Angled upwards (0),

(Fig 12C); Slightly arched downwards (1), (Fig. 12E); Straight (2), (Fig. 12B). *Indices*: ci=0.200; ri=0.500

76. **Hindwing, veins, anal anterior:** Absent (0), (Fig. 12D); Present (1), (Fig. 12B, C, E). *Indices*: ci=0.500; ri=0.667

77. **Hindwing, veins, anal anterior 3 (AA3):** Absent (0), (Fig. 12B); Present (1), (Fig. 12E). *Indices*: ci=0.143; ri=0.250

Contingent of 76: If character [76] is absent (0), [77] is inapplicable (-).

78. **Hindwing, veins, anal anterior 3+4 (AA3+4) and AA4, shape:** Angled (0), (Fig. 12C); Arched (1), (Fig. 12E). *Indices*: ci=0.143; ri=0.143

Contingent of 77: If character [77] is absent (0), [78] is inapplicable (-).

79. **Hindwing, veins, anal Anterior 3+4 (AA3+4) and AA4, position in relation to Cu3+4:** Reaches Cu3+4 (0), (Fig. 12C); Does not reach Cu3+4 (1) (Fig. 12B). *Indices*: ci=0.250; ri=0.250

Contingent of 76: If character [76] is absent (0), [79] is inapplicable (-).

Contingent of 77: If character [77] is present (1), [79] Does not reach Cu3+4 (1) (-).

80. **Hindwing, veins, medial spur (MS), position:** Reaching the wing margin (0), (Fig. 12B, D); Does not reach the wing margin (1), (Fig. 12C, E). *Indices*: ci=0.077; ri=0.636

81. **Legs, yellowish integument:** Absent (0); Present (1) (Fig. 10B). *Indices*: ci=0.200; ri=0.500

Remarks: As mentioned by Crowson (1981), the integument in Coleoptera, although they can often be metallic and with vibrant in color, have a (perhaps plesiomorphic) tendency to be brownish. Similar to the color of the mouth parts, we observed a yellowish pattern, especially in diurnal groups, including species of the genus *Phoebemima*. Apparently, the color of the legs remains conserved (plesiomorphic) across some lineages.

82. **Legs, metafemora, length relative to mesofemoral lenght:** Subequal (0), (Fig. 13E); Longer (1), (Fig. 13A, B, C). *Indices*: ci=0.083; ri=0.711

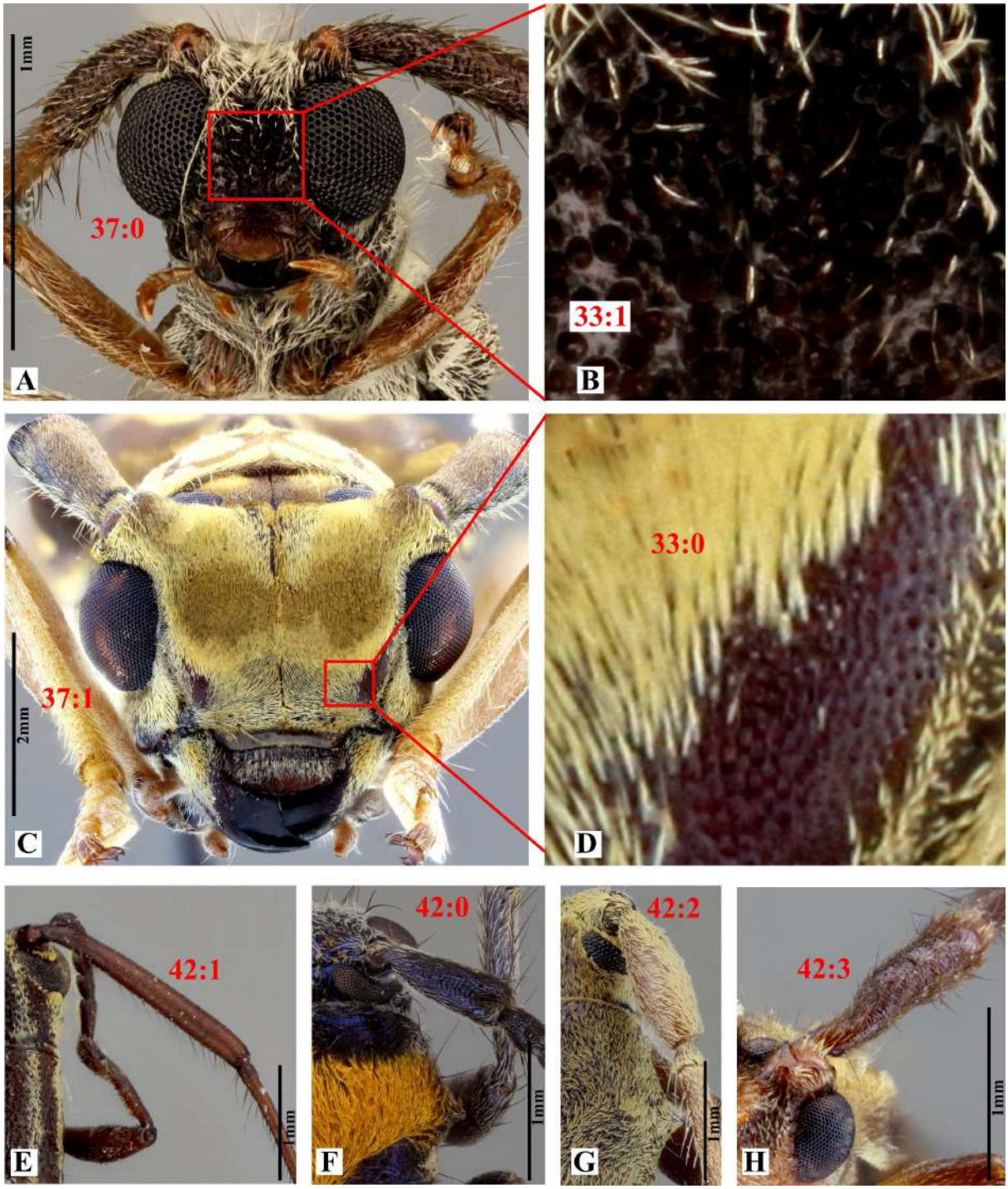

Figure 8. A–B *Antodice lenticula* Martins & Galileo, 1985: A, head in frontal view; B; detail of the frons integument. C–D, *Purusiella wappesi* (Martins & Galileo, 2004), C, head in frontal view; D, detail of the frons integument. E–H, lateral half of the head, prothorax and scape of Lamiinae species: E, *Hippopsis truncatella* Bates 1866; F, *Callia azurea* Audinet–Serville 1835; G, *Falsamblesthis seriepilosa* (Kirsch, 1889); H, *Tyrinthia scissifrons* Bates, 1866. Red numbers (*e.g.* 37:1) represent character and state respectively.

Remarks: Martins & Galileo (1998) used the metafemoral lenght in relation to the mesofemora in the alternative of couplet "23" of their key. Except for clade 148, which

includes *Antodices* and relatives, the others Aerenicini species have metafemora longer than the mesofemora.

83. **Legs, metafemora length, relative to abdomen length:** Shorter, less than a half the distance between the metacoxal cavity and the apex of abdomen (0), (Fig. 13B); Longer, more than a half the distance between the metacoxal cavity and the apex of abdomen (1), (Fig. 13D, F). *Indices*: ci=0.059; ri=0.600

84. **Legs, metatarsomeres, length relative to metatibia length:** Shorter, (0) (Fig. 11J); Subequal (1), (Fig. 11K); Longer (2), (Fig. 11L). *Indices*: ci=0.250; ri=0.600

85. **Legs, metatarsomeres, shape:** Abruptly widened (0), (Fig. 7F); Slightly widened (1) (Fig. 7G). *Indices*: ci=0.091; ri=0.697

86. **Legs, metatarsomere I, length relative to length of II + III:** Shorter (0), (Fig. 14A); Subequal (1), (Fig. 14B); Longer (2), (Fig. 14C). *Indices*: ci=0.125; ri=0.600

87. **Legs, metatarsomere III, lobes, width relative to width of I + II:** Subequal (0), (Fig. 7G); Wider (1), (Fig. 7F). *Indices*: ci0.083; ri=0.686

88. **Legs, claws, shape:** Not composed (without internal projection) (0), (Fig. 14E); Composed (with internal projection) (1), (Fig. 14F, G, H). *Indices*: ci=0.333; ri=0.600

89. **Legs, claws, shape of not composed claws**: Divaricate (0); Divergent (1).

Contingent of 88: If character [88] is composed (1), [89] is inapplicable (-).

90. **Legs, claws, shape of composed claws**: Appendiculate (0), (Fig. 14 F); Bifid (1), (Fig. 14 G, H). *Indices*: ci=0.333; ri=0.750

Contingent of 88: If character [88] is not composed (1), [90] is inapplicable (-).

91. **Legs, claws, bifid claws, inner projection, length relative to external projection:** Shorter (0), (Fig. 14G); Subequal (1), (Fig. 14H); Longer (2), (Fig. 14I). *Indices*: ci=0.286; ri=0.444

Contingent of 88: If character [88] is not composed (0), [91] is inapplicable (-) Contingent of 90: If character [90] is appendiculate (0), [91] is inapplicable (-).

Remarks: According to Martins (2014a) tarsal claws with wide internal projection and not acuminate, characterize the "A group" of Hemilophini. This form of tarsal claws is equivalent to "appendiculate" in which it characterizes tribes such as Caliini. In Aerenicini (except *Hippopsis*) the tarsal claws are bifid. According to Martins & Galileo

(1998), the length of the internal projections of the tarsal claws is always smaller than the external one (may or may not reach half of its length).

92. **Abdominal ventrites, contrasting, delimited, dense pubescent area**: Absent (0), (Fig. 14J); Present (1), (Fig. 14K, L). *Indices*: ci=0.077; ri=0.333

93. **Abdominal ventrites, pubescence forming longitudinal narrow bands:** Absent (0); Present (1), (Fig. 14M, N). *Indices*: ci=0.500; ri=0.800

Remarks: These longitudinal narrow bands are quite evident in *Recchia* species, and it is an ambiguous synapomorphy of the genus (clade 170). It is noteworthy that this genus was retrieved as monophyletic in our molecular analysis.

94. **Abdominal ventrite V, occurrence of notching at apex in males:** Absent (0) (Fig. 14J); Present (1), (Fig. 14L, Q). *Indices*: ci=0.100; ri=0.400

95. **Abdominal ventrite V, degree of notching in males:** Slightly notched (0), (Fig. 14P); Strongly notched (1), (Fig. 14Q). *Indices*: ci=0.143; ri=0.400

Contingent of 94: If character [94] is absent (0), [95] is inapplicable (-).

96. **Abdominal ventrite V, occurrence of notching at apex in females:** Absent (0); Present (1), (Fig. 14O, R). *Indices*: ci=0.111; ri=0.667

97. **Abdominal ventrite V, degree of notching in females:** Slightly notched (0), (Fig. 14O); Strongly notched (1), (Fig. 14R). *Indices*: ci=0.167; ri=0.167

Contingent of 96: If character [96] is absent (0), [97] is inapplicable (-).

98. **Abdominal ventrite V, median longitudinal sulcus in females:** Absent (0), (Fig. 14R); Present (1), (Fig. 14O). *Indices*: ci=0.111; ri=0.733

99. **Abdominal ventrite V of females, depression in the mid-apical region:** Absent (0); Present (1), (Fig. 14D). *Indices*: ci=0.143; ri=0.700

100. **Aedeagus, distal area in front of basal apophysis, lateral margin, shape:** Divergent forward (0), (Fig. 15A); Parallel sided (1), (Fig. 15B); Convergent forward (2), (Fig. 15C, D). *Indices*: ci=0.200; ri=0.636

Remarks: According to Wanat (2007), genitalia morphology have been used for at least the past 200 years and are important taxonomic tool for several groups of Coleoptera. During the taxonomic history of Cerambycidae, the morphology of the genitalia has been neglected, probably due to the species color pattern which it is usually specific

(Hubweber & Schmitt, 2009). Other reasons include scarcity of specimens (many species are only known by the holotype) or even too much "typological zeal" that seeks to keep the holotype intact at all costs. Regardless the reasons, some works have shown that the morphology of these structures has both taxonomic and phylogenetic relevance (*e.g.*, Ehara, 1954; Fragoso 1985a, b; Fragoso *et al.*, 1987; Hubweber & Schmitt, 2006). To Fragoso (1985a), it is possible to observe few patterns that allow grouping many species. This is probably due to the degree of convergence, as in other groups of Chrysomeloidea (Wanat, 2007). According to Hubweber & Schmitt (2009) the morphology of the genitalia can help us to understand the relationship of small groups of species (Hubweber & Schmitt, 2009). In our analysis, the convergent form of aedeagus (character state 2) is an ambiguous synapomorphy of clade 103, which includes all Aerenicini groups, as defined in this work. The other synapomorphies that support this clade are continuous, in other words, changes in the body proportions of species.

101. **Aedeagus, dorsal lobe, apical margin, shape:** Rounded (0), (Fig. 15B, C); Abruptly acuminate (1), (Fig. 15A); Gradually acuminate (2), (Fig. 15D). *Indices*: ci=0.182; ri=0.500

102. **Aedeagus, dorsal view, length of the dorsal lobe margin in relation to ventral lobe margin:** Subequal (0); Shorter (1); Longer (2). *Indices*: ci=0.222; ri=0.462

103. **Tegmen, parameres, dorsal view, shape of internal margin:** Convergent (0), (Fig. 15E); Parallel sided (1), (Fig. 15I); Divergent (2), (Fig. 15G). *Indices*: ci=0.111; ri=0.333

104. **Tegmen, parameres, lateral view, tubercle at base:** Absent (0), (Fig. 15N); Present (1), (Fig. 15P). *Indices*: ci=0.111; ri=0.200

105. **Tegmen, dorsal view, ring part, outer angles:** Absent (0), (Fig. 15I); Present (1), (Fig. 15K). *Indices*: ci=0.100; ri=0.400

106. **Tegmen, dorsal view, angled ring, shape:** Sharply angular (0), (Fig. 15O); Slightly angular (1), (Fig. 15E). *Indices*: ci=0.125; ri=0.462

Contingent of 105: If character [105] is absent (0), [106] is inapplicable (-).

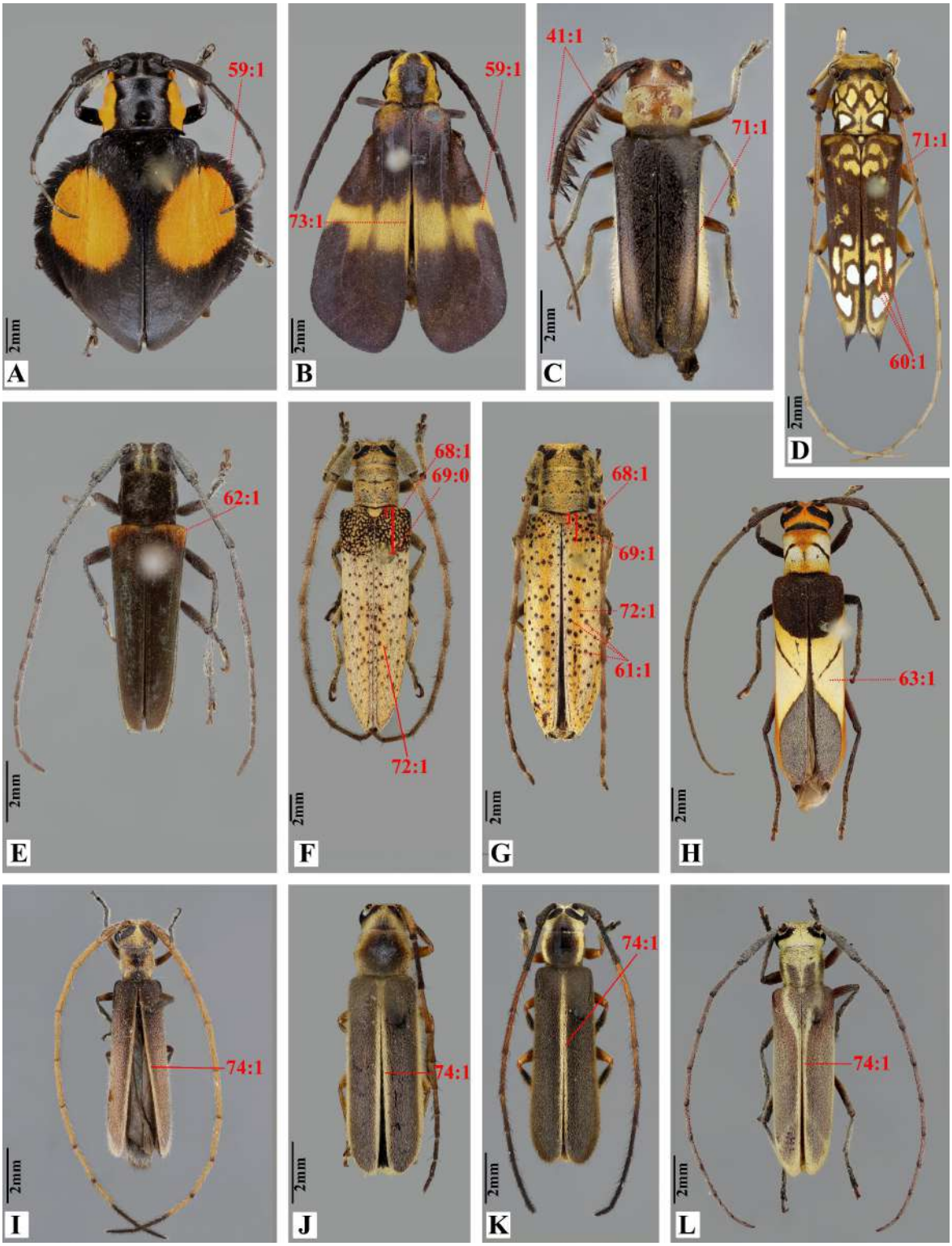

Figure 9. A–L, Habitus, dorsal. A–E, Hemilophini species: A, *Ites plagiatus* Waterhouse 1880; B, *Lycomimus ampliatus* (Klug 1825); C, *Hemilophus dimidiaticornis* Audinet–Serville, 1835; D, *Purusiella wappesi* (Martins & Galileo, 2004); E, *Fredlanea velutina* (Lane 1966). F–L, Aerenicini species: F, *Phaula lichenigera* (Perty 1832); G, *Holoarerenica apleta* Galileo & Martins, 1987; H, *Melzerella lutzi* Costa Lima, 1931; I, *Suipinima flavumtuberculata* Nascimento, Botero & Bravo, 2016; J, *Suipinima marginalis* Martins & Galileo, 2004; K, *Suipinima suturalis* Martins & Galileo, 2004; L, *Vianopolisia spitzi* Lane, 1966. Red numbers (*e.g.* 37:0) represent character and state respectively.

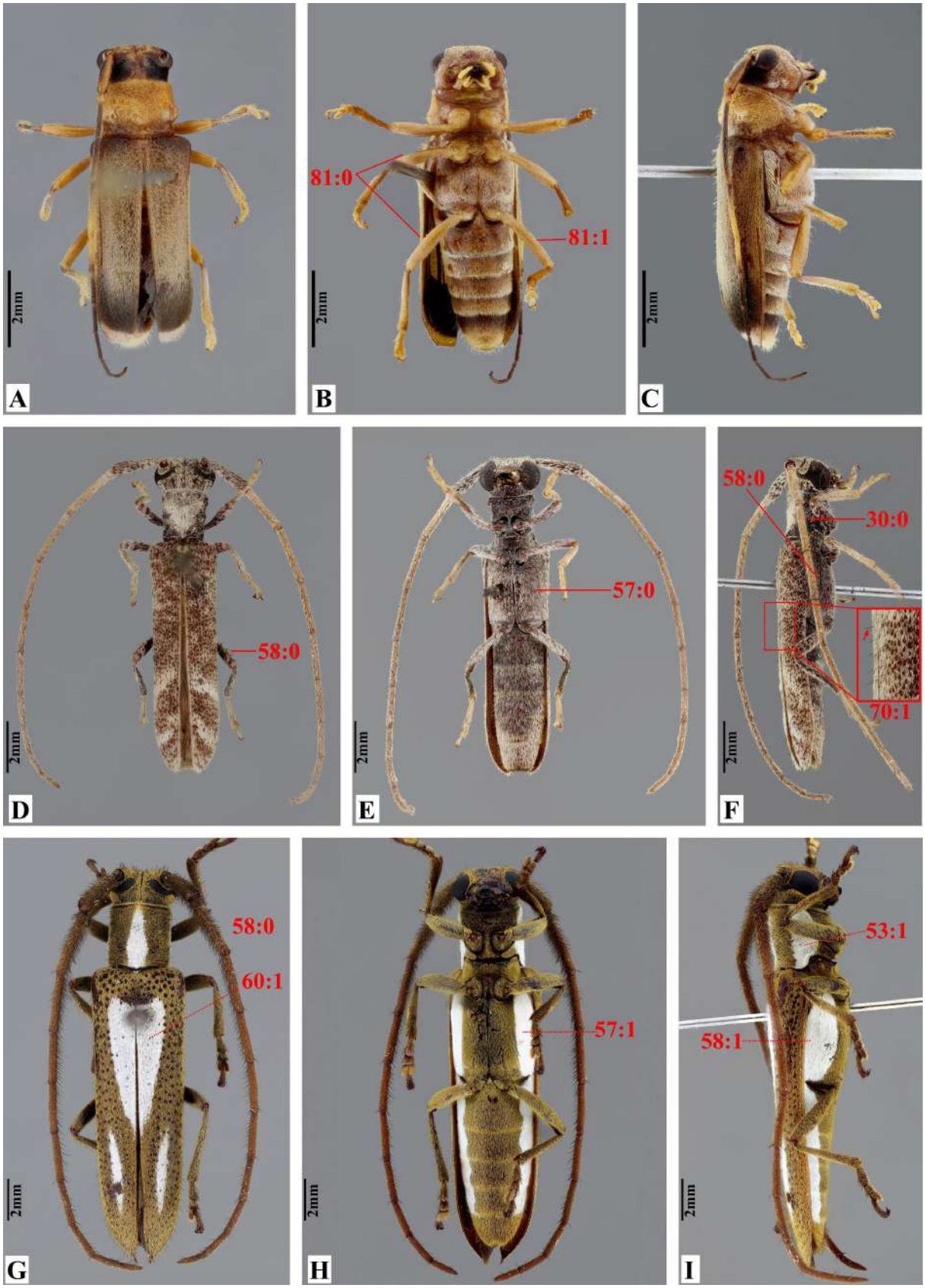

Figure 10. A–I, Lamiinae species, habitus dorsal, ventral, lateral: A–C, *Sphallonycha roseicollis* (Bates, 1866). D–F, *Aerenica canescens* (Klug, 1825) F, with elytral details. G–I, *Calliphaula leucippe* (Bates 1881). Red numbers (*e.g.* 62:1) represent character and state respectively.

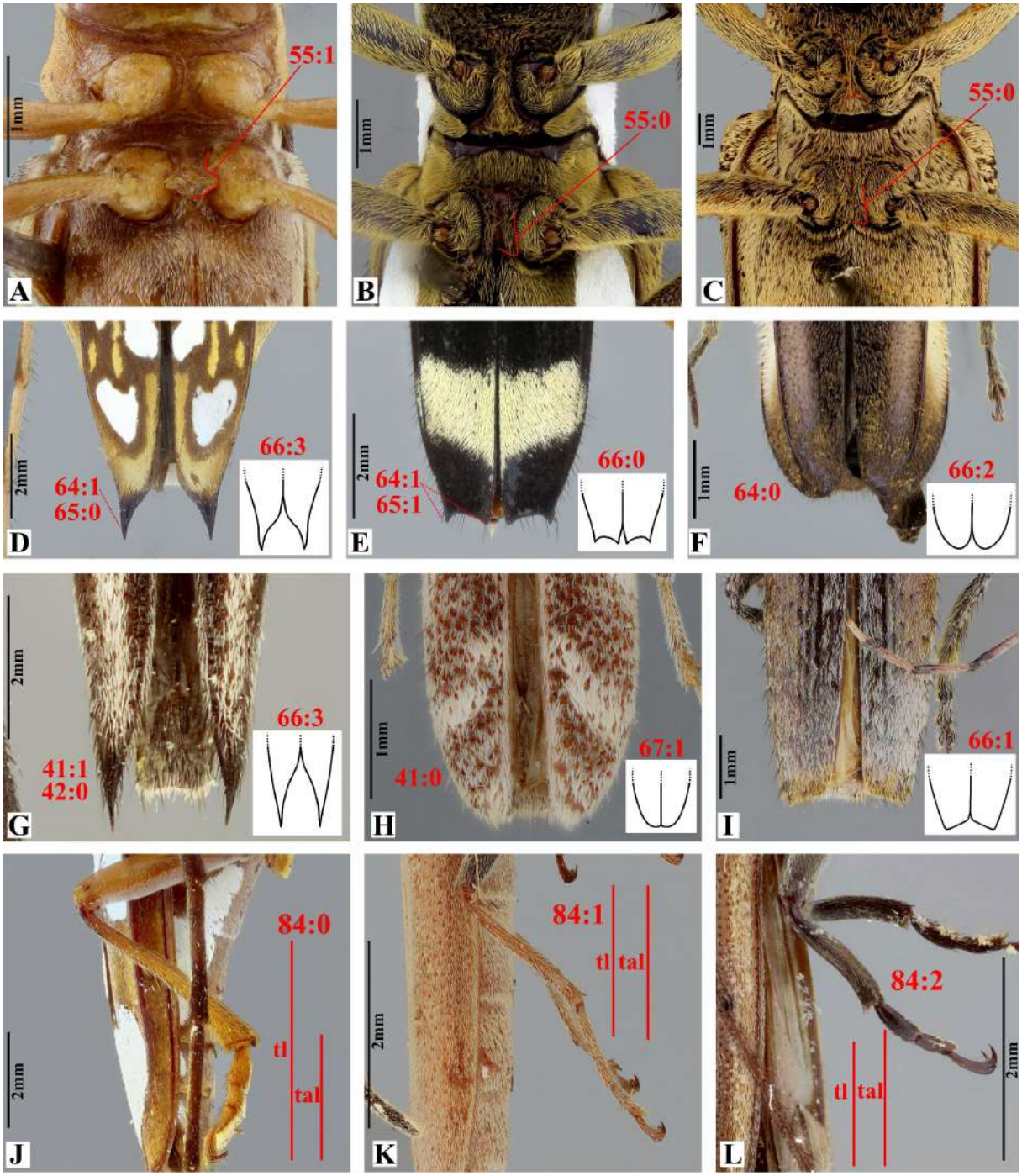

Figure 11. A–C, prosternum, mesoventrite and part of metaventrite of Lamiinae species: A, *Sphallonycha roseicollis* (Bates 1866); B, *Calliphaula leucippe* (Bates 1881); C, *Phaula thomsoni* Lacordaire 1872. D_I, elytral apices: D, *Purusiella wappesi* (Martins & Galileo, 2004); E, *Glenea fasciata* (Fabricius, 1781); F, *Hemilophus dimidiaticornis* Audinet–Serville, 1835; G, *Aerenicopsis pugnatrix* (Lane 1966); H, *Aerenica canescens* (Klug, 1825); I, *Ataxia luteifrons* (Bruch, 1926). J–L, parts of the elytra and hind legs in lateral view: J, *Purusia acreana* Lane, 1956; K, *Pseudomecas pickeli* (Melzer 1930); L, of *Hippopsis pubiventris* Galileo & Martins, 1988. Abbreviations: tl= length of tibia; tal= length of tarsomeres. Red numbers (*e.g.* 55:1) represent character and state respectively.

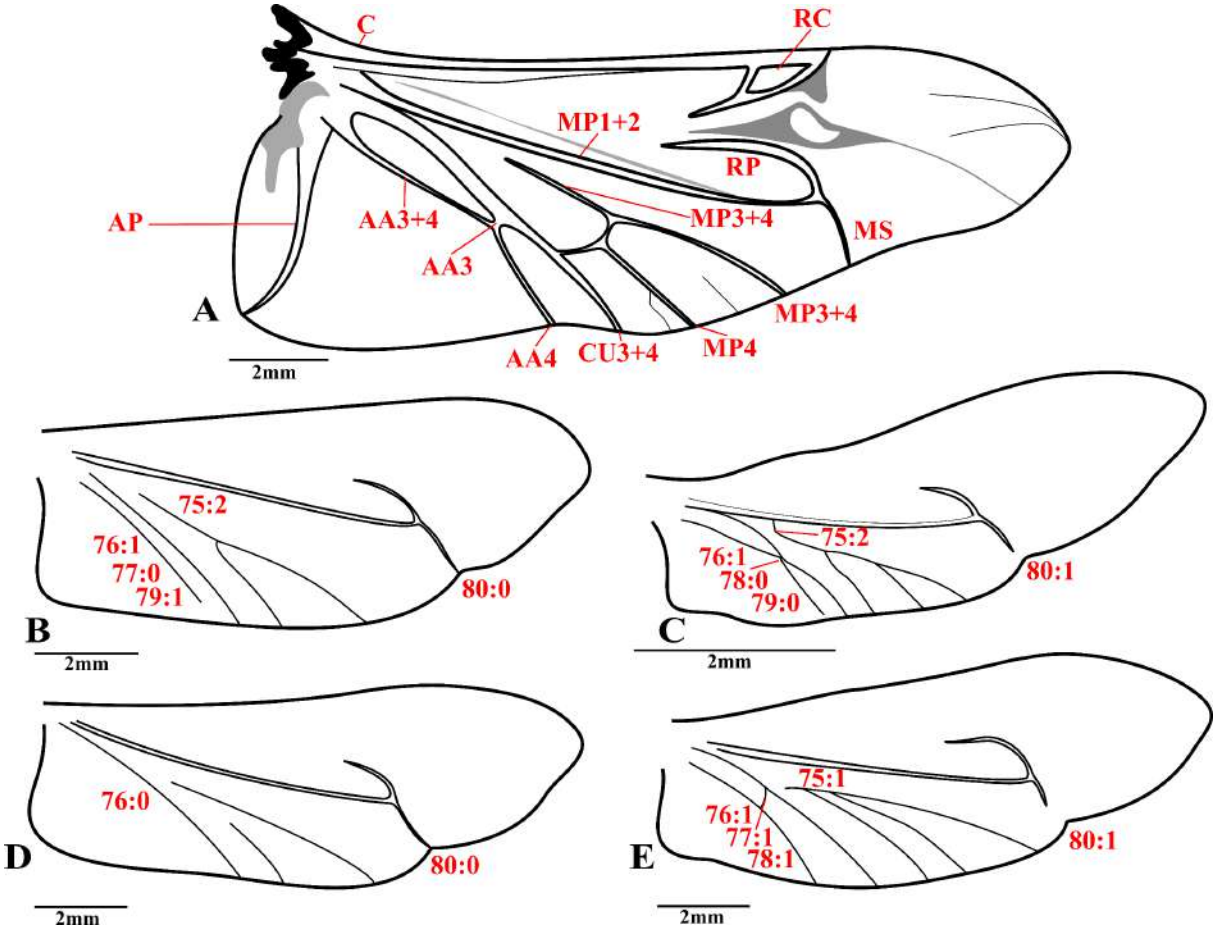

Figure 12. A–E, Left hindwing of Lamiinae species: A, *Spondylis buprestoides* (Linnaeus, 1758); B, *Antodice picta* (Klug, 1825); C, *Gryllica picta* (Pascoe 1958); D, *Phoebella phoebe* (Lepeletier & Audinet–Serville, 1825); E, *Aerenicella spissicornis* (Bates 1881). Abbreviations: AA= anal anterior; AP= anal posterior; C= costa; Cu= Cubitus; MP= medial posterior; MS= medial spur; RC= radial cell; RP= radius posterior; R= radius (details on vein numbering, see Svacha & Lawrence, 2014). Red numbers (*e.g.* 76:1) represent character and state respectively.

107. Tegmen, dorsal view, ring part, shape of unangulated ring part: Arched (0); Converging backwards (1), (Fig. 15O); Parallel sided (2), (Fig. 15I). *Indices*: ci=1.000; ri=1.000

Contingent of 105: If character [105] is present (1), [107] is inapplicable (-).

108. Tegmen, ring part, lateral view, shape: Arched (0), (Fig. 15J, N); Slightly sinuous (1), (Fig. 15L); Strongly sinuous (2), (Fig. 15H, P). *Indices*: ci=0.118; ri=0.571

109. Tegmen, struts: Absent (0); Present (1), (Fig. 15E, O). *Indices*: ci=0.071; ri=0.381

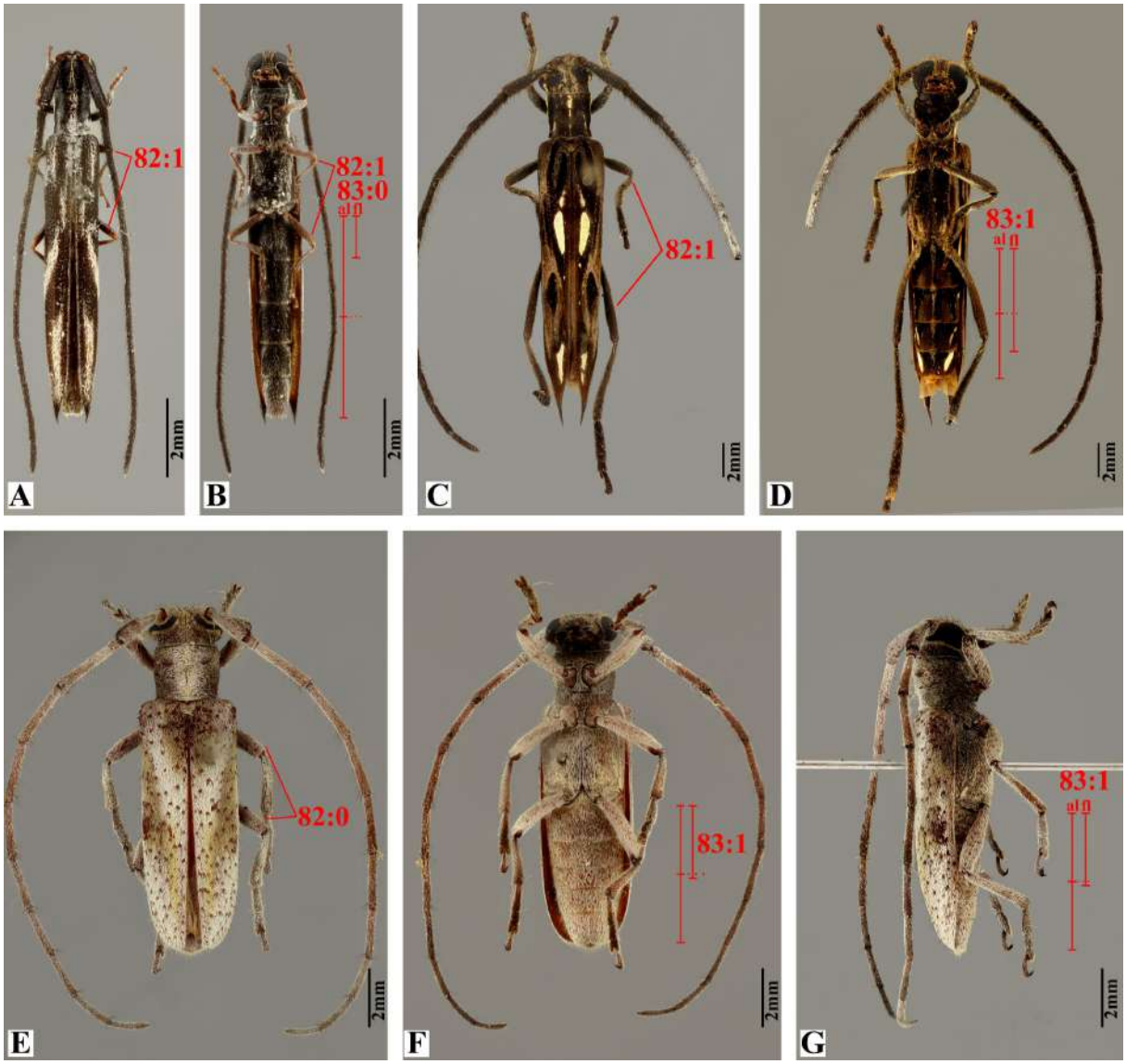

Figure 13. A–G, Habitus of Aerenicini species: A–B, *Aerenicopsis pugnatrix* (Lane 1966): A, dorsal view; B, ventral view; **C**–D, *Hydraschema leptostyla* Lane, 1938: C, dorsal view; D, ventral view; **E**–G, *Aerenomera boliviensis* Gilmour, 1962: E, dorsal view; F, ventral view; G, lateral view. Abbreviations: al= abdomen length; fl= metafemoral length. Red numbers (*e.g.* 83:1) represent character and state respectively.

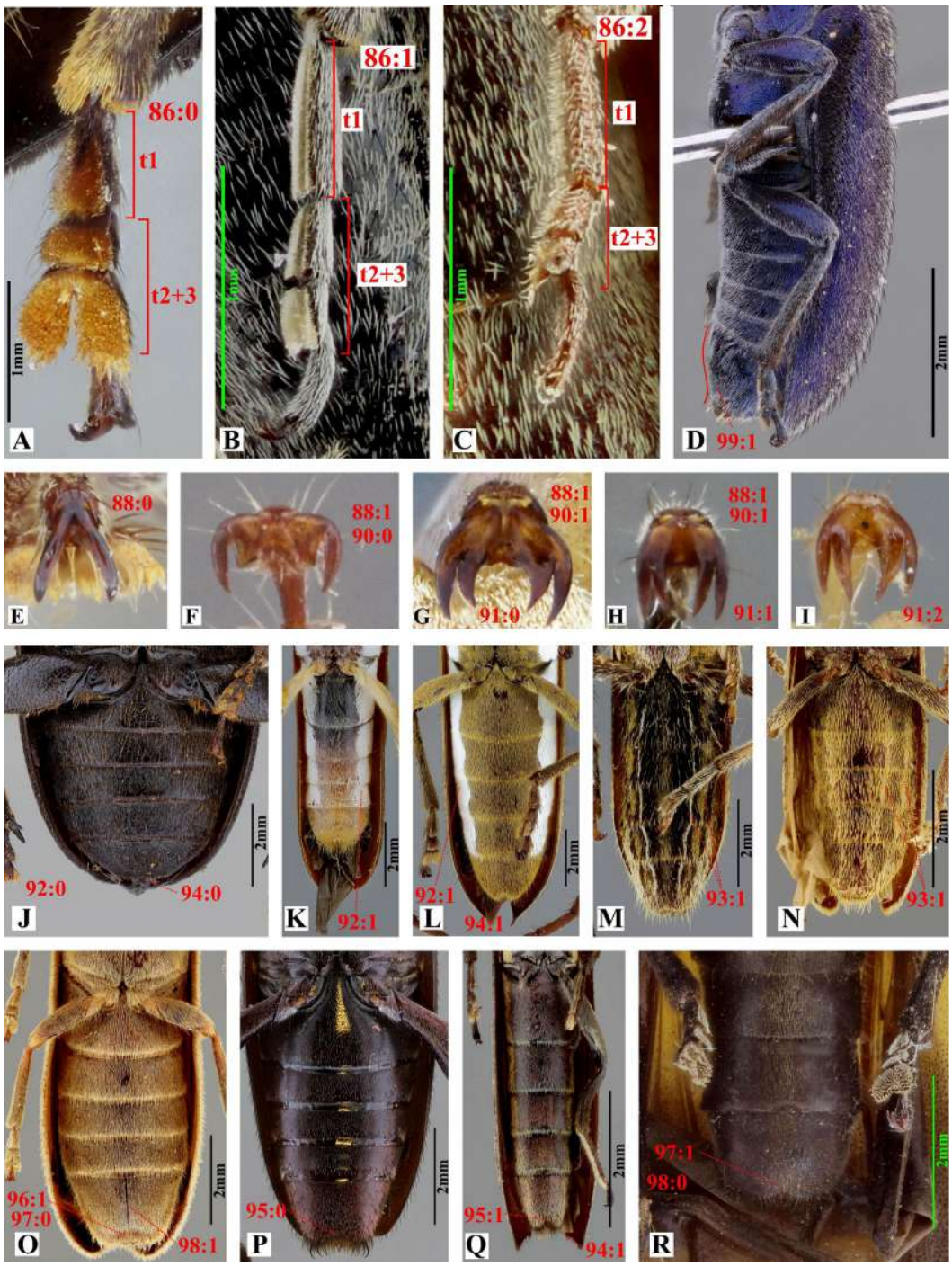

Figure 14. Lamiinae species: A–C, metatarsomeres; **A,** *Ites plagiatos* Waterhouse 1880; B, *Agapanthia cardui* (Linnaeus, 1767); C, *Aerenicopsis mendosa* Martins & Galileo 1998, lateral. D, meso, metathorax and abdomen, lateral view, *Callia azurea* Audinet–Serville 1835. E–I, tarsal claws in front view; E, *Ataxia obscura* (Fabricius 1801); F, *Falsamblesthis ibiyara* Marinoni 1978; G, *Purusiella wappesi* (Martins & Galileo, 2004); H, *Adesmus borgmeieri* (Lane, 1976); I, *Phoebe concinna* White, 1856. J–R, Abdominal ventrites: J, *Spondylis buprestoides* (Linnaeus, 1758); K, *Phoebella phoebe* (Lepeletier & Audinet–Serville, 1825); L, *Calliphaula leucippe* (Bates, 1881); M, *Recchia hirticornis* (Klug 1825); N, *Eponina breyeri* (Prosen, 1954); O, *Aphilestes rustica* Bates 1881; P, *Grylica picta* (Pascoe, 1958); Q, *Hippopsis truncatella* Bates, 1866; R, *Lycomimus ampliatus* (Klug 1825). Abreviations: tl=tarsomere length. Red numbers (*e.g.* 97:1) represent character and state respectively.

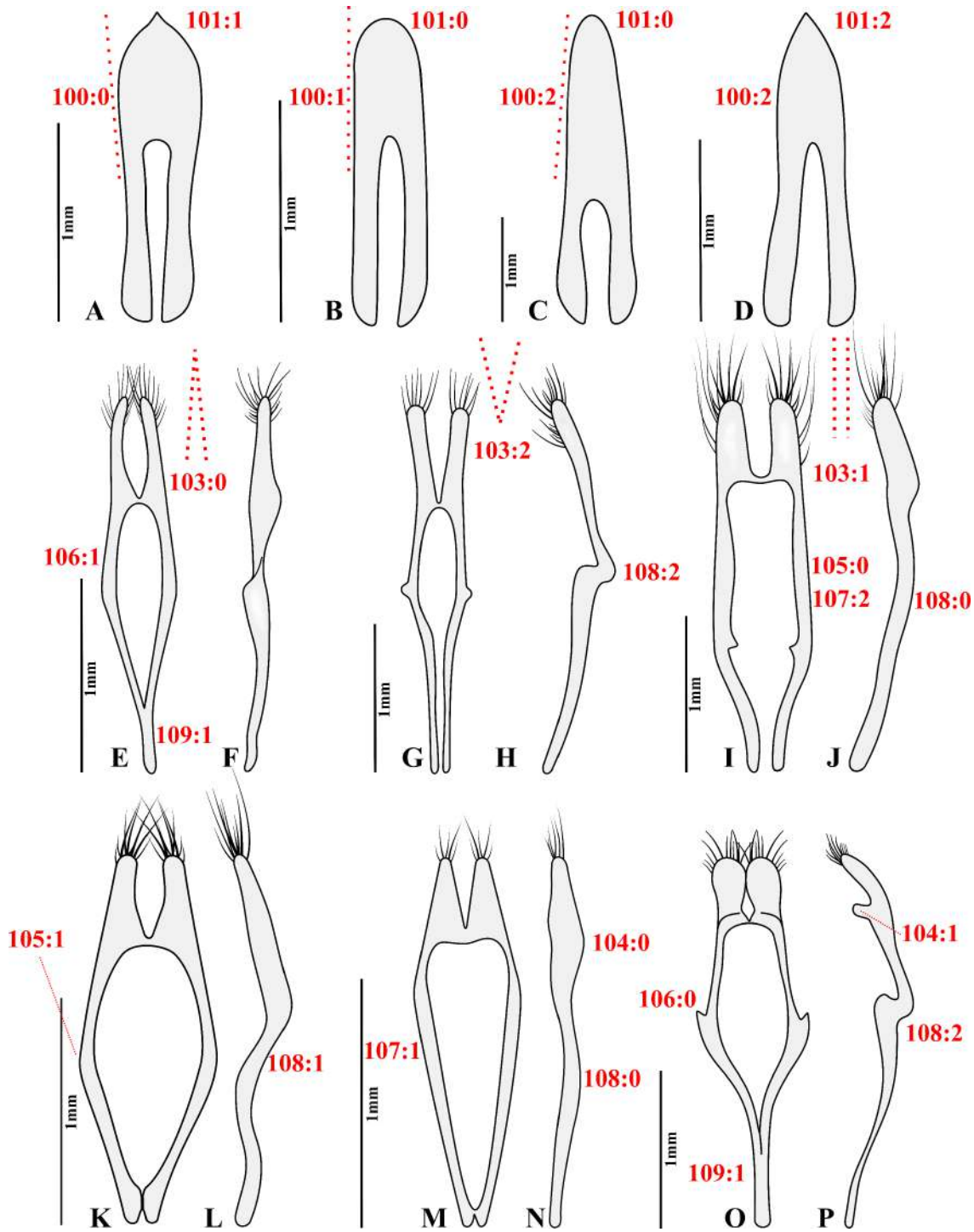

Figure 15. Male genitalia of Lamiinae species. A–D, Aedeagus in dorsal views: A, *Ataxia luteifrons* (Bruch, 1926); B, *Callia azurea* Audinet–Serville 1835; C, *Apophaula ocellata* Lane 1973; D, *Hemilophus dimidiaticornis* Audinet–Serville, 1835. E–P Tegmen: E–F, *Hippopsis pubiventris* Galileo & Martins 1988: E, dorsal view, F, lateral view; G–H, *Fredlanea velutina* (Lane 1966): G, dorsal view, H, lateral view; I–J, *Calliphaula leucippe* (Bates 1881): I, dorsal view, J, lateral view; K–L, *Calliphaula filiola* Martins, 1984: K, dorsal view, L, lateral view; M–N, *Aerenica canescens*; M, dorsal view, N, lateral view; O–P, *Mecas menthae* Chemsak & Linsley 1973: O, dorsal view; P, lateral view. Red numbers (*e.g.* 101:1) represent character and state respectively.

Table 4. Data matrix with 24 continuous quantitative characters for 88 taxa. "?" = not observed or inapplicable characters. The ingroup taxa are in bold.

	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
S. buprestoide	0	0	0	0	0	0	0	0	0	0	0	?	0,33	0,35	0,46	0,11	0,4	1	0,91	0,22	0,23	1	0,18	0,65
A. cardui	0,61	0,25	0,51	0,47	0,31	0,25	0,22	0,19	0,19	0,17	0,1	0	0,81	0,45	0,37	0,46	0,2	0,41	0,37	0,56	0,27	0,4	1	0,44
H. pubiventris	0,91	0,1	0,68	1	0,99	1	1	1	1	1	1	?	0,48	0,35	0,31	0,02	0	0,18	0	1	0,46	0,13	0,31	0
H. truncatella	1	0,1	0,75	0,94	1	0,83	0,85	0,85	0,84	0,83	0,99	?	0,42	0,35	0,31	?	0	0,27	0,03	0,89	0,36	0,17	0,32	0,05
F. ibiyara	0,35	0,14	0,31	0,79	0,59	0,43	0,31	0,32	0,25	0,22	0,17	?	0,64	0,45	0,42	?	0,2	0,36	0,47	0,56	0,41	0,3	0,3	0,47
F. seriepilosa	0,36	0,14	0,47	0,73	0,58	0,45	0,37	0,34	0,33	0,3	0,27	?	0,6	0,41	0,37	0,23	0,2	0,36	0,38	0,33	0,41	0,37	0,28	0,55
F. unguicularis	0,3	0,1	0,29	0,73	0,58	0,45	0,36	0,31	0,29	0,25	0,22	?	0,39	0,25	0,27	0,34	0,2	0,5	0,4	?	0,5	0,24	0,34	0,47
C. azurea	0,33	0,22	0,26	0,37	0,31	0,26	0,23	0,21	0,21	0,16	0,12	?	0,17	0,04	0,08	0,11	0,4	0,64	0,66	0,22	0,36	0,41	0,23	0,79
D. angustifrons	0,27	0,1	0,27	0,32	0,25	0,2	0,17	0,14	0,15	0,11	0,07	?	0,14	0,04	0,08	0,18	0,3	0,55	0,66	0,33	0,41	0,21	0,13	0,75
G. picta	0,26	0,22	0,44	0,32	0,22	0,17	0,12	0,1	0,1	0,08	0,04	?	0	0	0	0,16	0,3	0,55	0,15	0,56	0,68	0,2	0,57	0,4
A. luteifrons	0,29	0,39	0,21	0,45	0,38	0,3	0,28	0,22	0,21	0,19	0,12	?	0,44	0,25	0,27	?	0,2	0,5	0,46	0,78	0,73	0,33	0,18	0,54
A. obscura	0,27	0,06	0,19	0,45	0,34	0,28	0,25	0,22	0,21	0,17	0,13	?	0,39	0,2	0,17	?	0,3	0,46	0,62	1	1	0,41	0,18	0,74
M. menthae	0,34	0,22	0,33	0,45	0,3	0,25	0,22	0,21	0,2	0,17	0,15	?	0,94	1	0,98	0,61	0,2	0,36	0,9	0	0,05	0,64	0,3	0,58
P. hirsutula	0,27	0,14	0,23	0,32	0,21	0,17	0,17	0,15	0,15	0,14	0,09	?	0,46	0,49	0,42	0,71	0,3	0,46	0,94	0,44	0,23	0,8	0,47	0,56
G. fasciata	0,25	0,06	0,22	0,24	0,24	0,22	0,23	0,2	0,18	0,15	0,13	?	0,23	0,29	0,31	1	0,4	0,77	0,44	0,22	0,27	0,23	0,15	0,38
S. carcharias	0,27	0,14	0,31	0,37	0,31	0,26	0,22	0,19	0,19	0,17	0,19	?	0,52	0,37	0,5	0,75	0,3	0,32	0,59	0,22	0,23	0,3	0,15	0,45
A. borgmeieri	0,39	0,18	0,49	0,31	0,26	0,25	0,21	0,18	0,18	0,15	0,09	?	0,56	0,49	0,27	0,52	0,3	0,41	0,99	0,33	0,18	0,44	0,25	0,54
A. brunneiceps	0,49	0,18	0,59	0,49	0,36	0,33	0,27	0,25	0,23	0,2	0,14	?	0,42	0,39	0,37	0,46	0,3	0,5	0,96	0,22	0,36	0,23	0,1	0,5
A. versicolor	0,57	0,22	0,37	0,49	0,41	0,35	0,31	0,28	0,23	0,2	0,17	?	0,62	0,55	0,46	0,57	0,2	0,5	0,62	0,67	0,32	0,59	0,33	0,53
C. nuptus	0,48	0,22	0,68	0,56	0,4	0,3	0,27	0,22	0,21	0,2	0,15	?	0,33	0,14	0,17	?	0,4	0,5	0,69	0,56	0,46	0,23	0,14	0,56
F. velutina	0,36	0,14	0,55	0,4	0,29	0,23	0,19	0,17	0,14	0,14	0,11	?	0,33	0,35	0,29	0,46	0,2	0,55	0,62	0,33	0,59	0,37	0,35	0,42
F. viridipennis	0,45	0,22	0,66	0,6	0,4	0,31	0,28	0,25	0,22	0,18	0,12	?	0,33	0,14	0,27	?	0,3	0,5	0,66	?	?	0,37	0,41	0,48
H. dimidiat.	0,5	0,31	0,53	0,61	0,21	0,17	0,13	0,12	0,12	0,09	0,07	?	0,44	0,39	0,27	0,34	0,3	0,36	0,53	0,44	0,32	0,24	0,4	0,74
I. plagiatus	0,41	1	0,33	0,28	0,12	0,07	0,06	0,05	0,06	0,03	0	?	0,35	0,14	0,12	?	0,9	0,46	0,84	0,22	0,14	0,46	0,28	1
L. ampliatus	0,27	0,1	0,2	0,29	0,27	0,2	0,17	0,13	0,12	0,09	0,05	?	0,42	0,55	0,73	?	1	0,05	0,78	0,78	0,32	0,47	0,4	0,85
M. cicadellida	0,33	0,22	0,41	0,48	0,27	0,26	0,23	0,22	0,22	0,19	0,14	?	0,52	0,55	0,56	?	0,3	0,5	0,77	0,44	0,14	0,26	0,33	0,55

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
P. dominicanus	0,27	0,14	0,39	0,28	0,21	0,17	0,13	0,12	0,11	0,08	0,08	?	?	?	?	?	0,3	0,73	0,78	?	?	0,44	0,26	0,54
P. concinna	0,48	0,1	0,49	0,57	0,49	0,43	0,39	0,37	0,4	0,37	0,33	?	0,37	0,25	0,21	0,23	0,2	0,68	0,81	0,22	0,46	0,37	0,1	0,37
P. phoebe	0,59	0,22	0,71	0,91	0,71	0,6	0,5	0,47	0,46	0,45	0,32	1	0,39	0,14	0,15	0,11	0,2	0,32	0,9	0,33	0,36	0,2	0,13	0,32
P. acreana	0,45	0,06	0,62	0,6	0,52	0,42	0,33	0,29	0,28	0,27	0,19	0,43	0,33	0,25	0,21	0,16	0,2	0,55	0,81	0,67	0,55	0,23	0,15	0,4
P. wappesi	0,33	0,14	0,58	0,43	0,39	0,34	0,33	0,31	0,3	0,28	0,17	0,1	0,33	0,25	0,17	0,11	0,3	0,5	1	0,56	0,32	0,41	0,19	0,42
S. roseicollis	0,39	0,22	0,55	0,52	0,29	0,25	0,21	0,2	0,19	0,15	0,1	?	0,27	0,18	0,1	0,39	0,4	0,36	0,81	0,56	0,46	0,47	0,57	0,58
T. paraba	0,67	0,27	1	0,31	0,22	0,13	0,13	0,1	0,11	0,08	0,08	?	0,56	0,41	0,52	0,64	0,3	0,14	0,72	0,44	0,23	0,37	0,4	0,9
T. scissifrons	0,63	0,27	0,75	0,5	0,16	0,12	0,12	0,1	0,1	0,09	0,05	?	0,39	0,35	0,37	0,41	0,2	0,32	0,68	0,44	0,41	0,3	0,3	0,68
A. canescens	0,59	0,14	0,46	0,7	0,58	0,49	0,45	0,38	0,33	0,27	0,19	?	0,52	0,41	0,42	0,34	0,1	0,27	0,78	0,33	0,27	0,49	0,03	0,27
A. spissicornis	0,59	0,18	0,33	0,46	0,39	0,36	0,31	0,28	0,28	0,26	0,16	?	0,44	0,22	0,31	0,75	0,2	0,18	0,9	0,56	0,55	0,5	0,13	0,48
A. mendosa	0,58	0,1	0,3	0,58	0,55	0,45	0,43	0,38	0,36	0,32	0,21	?	0,81	0,55	0,37	0,34	0	0,09	0,18	0,56	0,36	0,09	0,01	0,3
A. perforata	0,67	0,22	0,29	0,67	0,62	0,51	0,47	0,41	0,37	0,34	0,23	?	0,6	0,51	0,46	0,46	0	0	0,16	0,89	0,41	0,06	0,01	0,24
A. pugnatrix	0,71	0,14	0,29	0,69	0,62	0,51	0,46	0,39	0,37	0,35	0,25	?	1	0,88	0,58	0,68	0	0	0,15	0,78	0,32	0,06	0,02	0,21
A. bandana	0,63	0,18	0,34	0,61	0,53	0,46	0,42	0,37	0,33	0,28	0,16	?	0,6	0,51	0,46	0,5	0,1	0,27	0,52	0,44	0,23	0,3	0,01	0,19
A. machadorum	0,67	0,14	0,34	0,61	0,54	0,47	0,45	0,41	0,38	0,34	0,25	?	0,54	0,51	0,42	0,43	0,1	0,09	0,47	0,67	0,41	0,19	0,01	0,19
A. boliviensis	0,47	0,27	0,46	0,66	0,59	0,51	0,47	0,42	0,4	0,37	0,27	?	0,23	0,25	0,27	0,27	0,3	0,36	0,71	0,56	0,36	0,36	0,08	0,53
A. spilas	0,4	0,27	0,41	0,57	0,52	0,45	0,43	0,37	0,35	0,3	0,19	?	0,33	0,14	0,14	0,11	0,3	0,41	0,56	0,44	0,36	0,39	0,08	0,4
A. abstrusa	0,47	0,06	0,57	1	0,98	0,89	0,73	0,46	0,4	0,36	0,27	?	0,37	0,55	0,42	0,41	0,1	0,14	0,49	0,22	0,05	0,03	0,08	0,34
A. lenticula	0,53	0,16	0,4	0,64	0,62	0,57	0,49	0,43	0,41	0,32	0,22	?	0,71	0,65	0,46	?	0,1	0,14	0,29	0,33	0,09	0	0,08	0,37
A. nympha	0,55	0,22	0,51	0,97	0,91	0,77	0,74	0,6	0,56	0,45	0,29	?	0,81	0,65	0,56	0,34	0,1	0,18	0,29	0,44	?	0,01	0,03	0,38
A. picta	0,53	0,14	0,51	0,88	0,86	0,78	0,75	0,74	0,67	0,59	0,39	?	0,56	0,59	0,42	0,68	0,1	0,23	0,29	0,44	0,14	0,01	0,03	0,34
A. tricolor	0,31	0,14	0,41	0,63	0,69	0,67	0,66	0,6	0,58	0,49	0,34	?	0,62	0,86	1	0,57	0,1	0,14	0,22	0,33	?	?	0,01	0,26
A. modesta	0,47	0,1	0,3	0,48	0,45	0,36	0,35	0,25	0,22	0,15	0,09	?	0,71	0,47	0,27	?	0,2	0,23	0,31	0,22	0,05	0,06	0,06	0,42
A. rustica	0,4	0,14	0,38	0,57	0,53	0,45	0,43	0,39	0,38	0,35	0,28	?	0,71	0,55	0,56	?	0,2	0,05	0,37	0	0	0,11	0,11	1
A. martinsi	0,5	0,14	0,39	0,54	0,47	0,37	0,39	0,31	0,31	0,26	0,15	?	0,71	0,55	0,27	0	0,1	0,14	0,37	0,44	0,18	0,19	0,1	0,48
A. ocellata	0,48	0,31	0,39	0,56	0,53	0,44	0,44	0,36	0,37	0,28	0,22	?	0,37	0,31	0,27	0,46	0,2	0,14	0,81	?	0,36	0,44	0,04	0,58
C. divus	0,72	0,22	0,38	0,56	0,48	?	?	?	?	?	?	?	0,42	0,35	0,37	0,34	0,1	0,23	0,78	0,33	0,32	0,27	0,13	0,38
C. nobilis	?	?	?	?	?	?	?	?	?	?	?	?	0,33	0,35	0,17	?	0,1	0,27	0,66	?	?	0,2	0,12	0,3
C. filiola	0,47	0,18	0,32	0,48	0,39	0,33	0,31	0,28	0,27	0,25	0,19	?	0,42	0,35	0,27	0,11	0,2	0,32	0,66	?	?	0,33	0,09	0,41

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
C. leucippe	0,35	0,22	0,36	0,49	0,39	0,35	0,3	0,27	0,23	0,22	0,15	?	0,39	0,35	0,31	0,23	0,2	0,32	0,52	0,78	0,46	0,27	0,08	0,28
E. breyeri	0,47	0,18	0,29	0,57	0,52	0,41	0,35	0,29	0,25	0,23	0,15	?	0,33	0,35	0,37	0,52	0,2	0,32	0,81	0,44	0,46	0,23	0,02	0,4
E. flava	0,39	0,22	0,28	0,37	0,29	0,22	0,19	0,18	0,18	0,15	0,14	?	0,23	0,25	0,23	0,34	0,1	0,36	0,81	0,56	0,32	0,44	0,03	0,47
H. apleta	?	?	?	?	?	?	?	?	?	?	?	?	0,42	0,35	0,37	?	0,1	0,23	0,88	0,33	0,27	0,34	0,06	0,45
H. bistriata	0,48	0,22	0,33	0,61	0,55	0,47	0,42	0,39	0,39	0,35	0,27	?	0,33	0,25	0,27	0,23	0,2	0,32	0,59	0,56	0,27	0,37	0,03	0,42
H. bondari	0,43	0,22	0,3	0,41	0,36	0,31	0,26	0,22	0,21	0,17	0,11	?	0,39	0,25	0,27	0,46	0,3	0,23	0,88	0,56	0,36	0,41	0,1	0,58
H. obliquevittata	0,62	0,18	0,3	0,56	0,49	0,43	0,41	0,35	0,35	0,28	0,23	?	0,52	0,35	0,17	0,23	0	0,05	0,66	0,44	0,18	0,27	0,03	0,17
H. letostyla	0,57	0,18	0,38	0,74	0,67	0,59	0,57	0,49	0,44	0,4	0,28	?	0,75	0,55	0,42	?	0,1	0	0,52	0,44	0,27	0,17	0,03	0,3
M. huedepohli	0,55	0,14	0,38	0,58	0,49	0,42	0,37	0,33	0,3	0,26	0,18	?	0,42	0,25	0,17	0,07	0,2	0,23	0,37	0,44	0,27	0,14	0,04	0,47
M. lutzi	0,55	0,18	0,38	0,57	0,47	0,39	0,35	0,31	0,29	0,26	0,18	?	0,42	0,43	0,44	0,23	0,2	0,23	0,37	0,44	0,36	0,1	0,04	0,45
M. leucostigma	0,66	0,1	0,29	0,48	0,43	0,37	0,34	0,29	0,27	0,24	0,19	?	0,42	0,25	0,17	0	0,1	0,27	0,52	0,44	0,36	0,26	0,05	0,32
P. antiqua	0,4	0,14	0,31	0,4	0,35	0,31	0,28	0,23	0,21	0,17	0,11	?	0,42	0,35	0,46	0,57	0,1	0,27	0,59	0,44	0,41	0,3	0,05	0,34
P. lichenigera	0,4	0,1	0,34	0,61	0,55	0,5	0,43	0,39	0,37	0,33	0,24	?	0,52	0,45	0,46	0,5	0,2	0,14	0,78	0,44	0,32	0,23	0,07	0,44
P. thomsoni	0,4	0,22	0,32	0,44	0,36	0,31	0,27	0,25	0,23	0,22	0,19	?	0,46	0,35	0,5	0,68	0,1	0,23	0,66	0,33	0,36	0,23	0,08	0,48
P. ensifera	0,34	0,1	0,6	0,45	0,36	0,31	0,28	0,26	?	?	?	?	0,33	0,14	0,17	0,23	0,3	0,32	0,88	0,56	0,46	0,39	0,18	0,48
P. teaphia	0,34	0,1	0,54	0,37	0,26	0,21	0,19	0,18	0,15	0,12	?	?	0,29	0,25	0,37	?	0,3	0,59	0,88	0,56	0,46	0,37	0,18	0,53
P. teteia	0,41	0,22	0,51	0,48	0,4	0,35	0,31	0,28	0,24	0,22	0,17	?	0,42	0,35	0,4	0,5	0,3	0,59	0,81	0,33	0,5	0,3	0,15	0,42
P. femoralis	0,67	0,27	0,34	0,58	0,52	0,45	0,41	0,37	0,33	0,28	0,23	?	0,62	0,45	0,46	0,23	0,1	0,27	0,52	0,44	0,32	0,33	0	0,13
P. pickeli	0,63	0,1	0,29	0,52	0,45	0,36	0,31	0,3	0,28	0,25	0,12	?	0,62	0,49	0,37	0,16	0	0,14	0,52	0,33	0,36	0,26	0,01	0,19
P. porosa	0,44	0,18	0,44	0,58	0,5	0,44	0,39	0,35	0,32	0,3	0,2	?	0,37	0,45	0,46	0,46	0,2	0,27	0,66	0,22	0,36	0,33	0,1	0,45
P. strigulata	0,4	0,22	0,39	0,53	0,47	0,42	0,38	0,36	0,33	0,32	0,21	?	0,42	0,35	0,37	0,34	0,3	0,27	0,81	0,22	0,32	0,41	0,1	0,47
R. acutipennis	0,71	0,18	0,33	0,48	0,44	0,41	0,37	0,34	0,32	0,27	0,21	?	0,52	0,45	0,37	0,34	0,2	0,27	0,59	0,22	0,23	0,3	0,1	0,37
R. albicans	0,73	0,14	0,39	0,53	0,47	0,43	0,39	0,37	0,32	0,28	0,21	?	0,52	0,35	0,17	0,23	0,2	0,27	0,59	0,33	0,36	0,3	0,1	0,37
R. hirticornis	0,72	0,14	0,38	0,49	0,44	0,41	0,36	0,33	0,31	0,26	0,18	?	0,42	0,35	0,31	0,27	0,2	0,32	0,81	0,44	0,41	0,4	0,08	0,37
R. parvula	0,71	0,18	0,38	0,48	0,44	0,41	0,37	0,34	0,31	0,26	0,19	?	0,37	0,2	0,23	0,34	0,2	0,36	0,66	0,44	0,46	0,44	0,07	0,4
R. procera	0,8	0,18	0,51	0,54	0,47	0,43	0,39	0,35	0,32	0,27	0,18	?	0,52	0,45	0,42	0,46	0,1	0,14	0,66	0,44	0,36	0,34	0,08	0,34
R. annulicornis	0,38	0,18	0,33	0,54	0,5	0,46	0,43	0,41	0,36	0,32	0,21	?	0,39	0,29	0,27	0,46	0,2	0,32	0,59	0,33	0,23	0,36	0,1	0,38
R. canescens	0,38	0,14	0,36	0,61	0,57	0,52	0,47	0,47	0,38	0,35	?	?	0,42	0,35	0,4	0,57	0,2	0,32	0,66	0,44	0,23	0,34	0,06	0,35
S. flavumt.	0,39	0,14	0,42	0,86	0,82	0,73	0,66	0,61	0,51	0,45	0,27	?	0,71	0,45	0,65	0,8	0,1	0,14	0,37	0,33	0,14	0,09	0,05	0,47

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
S. marginalis	0,4	0,27	0,44	0,56	0,33	0,27	0,25	0,22	0,21	0,19	0,14	?	0,52	0,65	0,65	0,57	0,2	0,36	0,52	0,33	0,14	0,13	0,23	0,63
S. suturalis	0,43	0,18	0,47	0,75	0,69	0,59	0,57	0,47	0,42	0,36	0,26	?	0,71	0,45	0,46	0,68	0,1	0,09	0,44	0,22	0,14	0,07	0,15	0,63
V. captiosa	0,66	0,1	0,4	0,52	0,44	0,41	0,34	0,35	0,32	0,28	0,18	?	0,52	0,45	0,37	0,34	0,2	0,27	0,59	?	0,32	0,4	0,05	0,4
V. spitzi	0,66	0,14	0,39	0,53	0,48	0,42	0,39	0,35	0,32	0,28	0,19	?	0,42	0,35	0,37	0,46	0,2	0,32	0,66	0,33	0,27	0,41	0,05	0

Table 5. Data matrix with 86 discrete morphological characters for 88 taxa. "?" = characters not observed; "–" = inapplicable characters. The ingroup taxa are in bold. Part I: 24-53; Part II 54-83; Part III 84-109

Part I

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Spondylis_buprestoides	1	-	1	0	1	1	0	0	2	1	0	0	1	0	1	1	1	0	1	0	0	0	-	0	0	-	1	0	-	0
Agapanthia_cardui	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	1	0	1	0	1	0	-	1	0	0	0	0	-	1
Hippopsis_pubiventris	0	0	1	1	1	0	0	1	2	1	1	0	0	0	1	0	0	0	1	0	0	0	-	1	0	0	1	0	-	1
Hippopsis_truncatella	1	0	1	1	1	0	0	1	2	1	1	0	0	0	1	0	0	0	1	0	0	0	-	1	0	0	1	0	-	1
Falsamblesthis_ibiyara	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	2	0	1	1	0	0	0	-	1	1	1	0
Falsamblesthis_seriepilosa	0	0	1	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	2	0	1	1	0	0	0	-	1	1	1	0
Falsamblesthis_unguicularis	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	2	0	1	1	0	0	0	-	1	1	1	0
Callia_azurea	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	-	0
Drycothaea_angustifrons	1	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	-	1	1	0	0
Gryllica_picta	1	0	1	1	0	1	0	1	2	0	0	0	0	1	1	1	0	1	0	2	0	0	-	0	0	-	0	0	-	0
Ataxia_luteifrons	1	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	-	0	1	1	0
Ataxia_obscura	1	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	-	0	1	1	0
Mecas_menthae	1	0	1	1	1	1	0	0	0	1	2	0	0	1	1	1	0	0	0	0	0	0	-	0	1	-	1	1	1	0
Phytoecia_Pilemia_hirsutula	1	0	1	0	1	1	0	0	0	1	2	0	1	1	1	1	0	0	0	0	1	0	-	0	0	-	1	0	-	0
Glenea_glenea_fasciata	0	0	1	1	1	1	0	0	0	1	2	0	1	1	1	1	0	0	1	0	1	0	-	0	0	-	0	0	-	0
Saperda_carcharias	1	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	0	-	0	1	-	0	0	-	0
Adesmus_borgmeieri	0	0	0	1	0	1	0	1	0	0	2	0	0	1	1	1	0	0	0	0	1	0	-	1	0	2	2	0	-	0

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Adesmus_brunneiceps	0	0	0	1	0	1	0	1	0	0	2	0	0	1	1	1	0	0	0	1	1	0	-	0	1	-	2	1	0	0
Apagomerella_versicolor	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	-	1	0	1	2	0	-	0
Calocosmus_nuptus	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1	0	0	-	0	1	0	0
Fredlanea_velutina	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	-	1	0	0	2	0	-	1
Fredlanea_viridipennis	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	0	-	1	0	0	2	0	-	1
Hemilophus_dimidiaticornis	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	0	1	0	2	1	1	1	0	0	-	1	1	0	0
Ites_plagiatus	1	0	0	1	1	1	0	1	0	1	1	0	0	1	0	-	1	0	0	0	1	1	1	1	0	0	1	1	0	0
Lycomimus_ampliatus	1	0	0	1	1	1	0	1	0	1	2	0	0	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	-	0
Mariliana_cicadellida	0	0	0	1	0	1	0	1	0	1	2	0	0	1	1	1	0	0	1	0	1	0	-	1	0	2	2	0	-	0
Paleohemilophus_dominicanus	?	?	?	1	?	1	0	0	0	0	?	0	0	1	1	1	0	0	0	0	1	0	-	0	0	-	1	0	-	0
Phoebe_concinna	0	0	0	1	1	1	0	0	0	0	2	1	0	1	1	1	0	0	0	1	1	0	-	0	0	-	2	1	1	0
Phoebe_phoebe	0	0	0	1	0	1	0	1	0	0	2	1	0	1	1	1	1	0	0	0	1	0	-	1	0	3	1	1	0	0
Purusia_acreana	0	0	0	1	1	1	1	1	0	1	2	1	0	1	1	1	1	0	0	1	1	0	-	1	0	3	2	1	0	0
Purusiella_wappesi	0	0	0	1	0	1	0	1	0	0	2	1	0	1	1	1	1	0	0	0	1	1	1	1	0	2	1	1	0	0
Sphallonycha_roseicollis	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	-	1	1	0	0
Tyrinthia_paraba	0	0	0	1	1	0	1	0	0	1	0	-	0	1	1	1	0	1	0	2	1	1	1	0	0	-	0	1	0	0
Tyrinthia_scissifrons	0	0	0	1	1	0	1	0	0	1	0	1	0	1	1	1	0	1	3	2	1	1	1	1	0	0	0	1	1	0
Aerenica_canescens	1	1	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	-	1	0	1	2	0	-	0
Aerenicella_spissicornis	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	1	0	1	0	2	1	0	-	1	0	0	2	0	-	0
Aerenicopsis_mendosa	1	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	-	1	1	0	1	0	-	1
Aerenicopsis_perforata	1	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	-	1	1	0	1	0	-	1
Aerenicopsis_pugnatrix	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	-	1	1	0	1	0	-	1
Aereniphaula_bandana	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	-	1	1	1	2	0	-	0
Aereniphaula_machadorum	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	-	0	0	-	1	0	-	1
Aerenomera_boliviensis	1	2	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	-	0	0	-	2	0	-	0
Aerenomera_spilas	1	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	-	0	0	-	1	0	-	0
Antodice_abstrusa	0	0	1	1	1	1	0	0	2	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0
Antodice_lenticula	0	0	1	1	1	1	0	0	2	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	-	2	1	0	0
Antodice_nympha	0	0	1	1	1	1	0	1	2	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	1	1	0	0

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Antodice_picta	0	0	1	1	1	1	0	1	2	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	1	0	-	0
Antodice_tricolor	0	0	1	1	1	1	0	0	2	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	-	2	1	1	0
Antodilanea_modesta	0	0	1	1	1	1	0	0	2	1	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	-	2	0	-	0
Aphilestes_rustica	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0
Apoaerenica_martinsi	0	2	1	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	-	1	0	1	2	1	0	0
Apophaula_ocellata	1	2	0	1	1	1	0	0	0	1	2	0	0	1	1	0	0	0	0	1	0	0	-	0	0	-	1	0	-	0
Cacsius_divus	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	-	1	0	0	2	0	-	0
Cacsius_nobilis	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	-	1	0	-	2	0	-	1
Calliphaula_filiola	0	0	1	1	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	-	1	0	0	1	0	-	1
Calliphaula_leucippe	1	0	1	1	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	2	1	0	-	1	0	0	1	0	-	1
Eponina_breyeri	0	2	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	-	0	0	-	2	0	-	0
Eponina_flava	0	2	1	1	1	1	0	0	0	1	2	0	0	0	1	1	0	0	0	1	1	1	1	0	0	-	2	0	-	0
Holoarerenica_apleta	1	0	1	1	1	1	0	0	0	1	2	0	0	0	1	1	0	0	0	0	0	0	-	1	0	1	1	1	1	0
Holoarerenica_bistriata	0	0	1	1	1	1	0	0	1	1	2	0	0	0	1	1	0	0	0	0	1	0	-	1	0	1	2	1	1	0
Hoplistonychus_bondari	1	0	1	1	1	1	0	0	0	1	2	0	0	0	1	1	0	0	0	1	1	0	-	0	0	-	2	0	-	0
Hydraschema_obliquevittata	1	0	1	1	1	1	0	1	1	1	0	0	0	0	0	-	0	0	0	1	0	0	-	1	0	0	1	0	-	1
Hysdraschema_letostyla	1	0	1	1	1	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	-	1	0	0	1	0	-	1
Melzerella_huedepohli	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	-	1	0	-	2	0	-	0
Melzerella_lutzi	0	0	1	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	-	1	0	-	2	1	0	0
Montesia_leucostigma	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	-	1	0	0	2	1	0	1
Phaula_antiqua	0	0	0	1	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	-	0	0	-	2	1	1	0
Phaula_lichenigera	1	0	1	1	1	1	0	0	1	1	2	0	0	0	1	1	0	0	0	0	0	0	-	0	0	-	1	1	1	0
Phaula_thomsoni	1	0	0	1	1	1	0	0	0	1	2	0	0	0	1	0	0	0	0	0	1	0	-	0	0	-	1	1	1	0
Phoebemima_ensifera	0	0	0	1	1	1	0	0	0	0	2	0	0	1	1	1	0	0	0	1	1	0	-	1	0	0	2	0	-	1
Phoebemima_teaphia	0	0	0	1	1	1	0	0	0	0	2	0	0	1	1	1	0	0	0	1	1	0	-	1	0	0	2	0	-	0
Phoebemima_teteia	0	0	1	1	1	1	0	0	0	0	2	0	0	1	1	1	0	0	0	0	1	0	-	1	0	2	2	0	-	1
Pseudomecas_femoralis	1	0	1	1	0	1	0	0	1	1	2	0	0	0	1	0	0	0	0	0	1	0	-	0	0	-	1	0	-	0
Pseudomecas_pickeli	0	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	-	0	0	-	1	0	-	0
Pseudophaula_porosa	1	0	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	-	0	0	-	2	1	1	0

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Pseudophaula_strigulata	1	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	-	0	0	-	2	1	1	0
Recchia_acutipennis	0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	-	1	1	0	2	0	-	0
Recchia_albicans	0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	-	1	1	0	2	0	-	1
Recchia_hirticornis	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	-	1	1	0	2	0	-	1
Recchia_parvula	1	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	-	1	1	0	2	0	-	1
Recchia_procera	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	-	1	1	0	2	0	-	1
Rumacon_annulicornis	1	0	0	1	1	1	0	0	0	1	2	0	0	0	1	0	0	0	0	0	0	0	-	1	0	1	1	0	-	0
Rumacon_canescens	1	0	0	1	1	1	0	0	0	1	2	0	0	0	1	0	0	0	0	0	0	0	-	0	0	-	1	0	-	0
Suipinima_flavumtuberculata	1	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	-	2	1	1	0
Suipinima_marginalis	0	0	0	1	1	1	0	0	0	0	2	0	0	0	1	1	0	0	0	0	1	0	-	1	0	1	0	0	-	0
Suipinima_suturalis	0	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	-	1	0	0	2	0	-	0
Vianopolisia_captiosa	0	0	1	1	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	-	1	0	0	2	0	-	1
Vianopolisia_spitzi	1	0	1	1	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	-	1	0	1	2	0	-	0

Part II

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
Spondylis_buprestoides	0	0	0	0	0	0	0	1	0	0	0	-	2	1	0	-	0	0	0	1	0	2	1	1	0	1	0	0	1	1
Agapanthia_cardui	0	0	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	0	1	0	1	1	1	1	0	0	0	1
Hippopsis_pubiventris	1	0	1	1	1	0	1	1	0	0	0	-	3	-	0	-	0	0	0	1	0	0	1	1	1	1	0	0	1	0
Hippopsis_truncatella	1	0	1	1	1	0	1	1	0	0	0	-	1	-	0	-	0	0	0	1	1	2	1	1	1	1	0	0	1	0
Falsamblesthis_ibiyara	0	0	1	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	0	1	0	1	0	0	0
Falsamblesthis_seriepilosa	0	0	1	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	0	1	1	1	0	0	0
Falsamblesthis_unguicularis	0	0	1	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	1	1	1	1	0	0	1
Callia_azurea	0	0	1	0	0	0	0	-	0	0	0	-	2	1	0	-	1	0	0	1	0	0	1	1	1	1	1	0	0	1
Drycothaea_angustifrons	0	0	0	0	0	0	0	-	0	0	0	-	2	1	0	-	1	0	0	1	0	0	1	1	1	1	1	0	0	1
Gryllica_picta	0	0	0	0	0	0	1	0	0	0	0	-	2	0	0	-	1	0	0	1	1	0	1	0	0	0	1	0	1	1
Ataxia_luteifrons	0	0	1	0	0	0	0	-	0	0	0	-	1	-	0	-	1	0	0	1	0	0	0	-	-	-	1	0	0	0
Ataxia_obscura	0	0	1	0	0	0	0	-	0	0	1	0	1	-	0	-	1	0	0	1	0	2	0	-	-	-	1	0	0	0

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
Mecas_menthae	1	0	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	1	1	1	1	1	1	0	0	0	0
Phytoecia_Pilemia_hirsutula	1	0	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	0	0	1	1	1	1	1	0	0	0	1
Glenea_glenea_fasciata	1	0	0	0	0	0	1	0	0	0	1	1	0	-	0	-	1	1	0	0	0	?	?	?	?	?	?	1	1	1
Saperda_carcharias	1	0	0	0	0	0	0	1	0	0	0	-	2	1	0	-	1	0	0	0	0	0	1	1	1	1	1	0	1	1
Adesmus_borgmeieri	1	1	0	1	1	0	1	0	0	0	0	-	2	0	0	-	1	1	0	1	0	0	1	1	1	1	1	0	0	0
Adesmus_brunneiceps	1	1	0	1	1	0	1	0	0	0	0	-	2	0	0	-	1	1	0	1	0	0	1	1	1	1	1	1	0	1
Apagomerella_versicolor	1	0	1	0	1	0	0	-	0	0	0	-	2	1	0	-	1	0	0	1	1	0	1	1	1	1	1	0	1	0
Calocosmus_nuptus	0	0	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	0	1	0	1	0	0	1
Fredlanea_velutina	0	1	0	0	0	0	1	0	1	0	1	1	0	-	0	-	1	1	0	0	0	0	1	1	1	1	0	0	1	1
Fredlanea_viridipennis	0	?	0	0	0	0	1	0	1	0	1	1	0	-	0	-	1	1	0	0	0	0	1	1	1	1	0	0	1	1
Hemilophus_dimidiaticornis	0	1	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	1	0	0	0	0	1	1	1	1	1	0	0	1
Ites_plagiatus	0	0	0	0	0	1	1	0	0	0	0	-	2	1	0	-	0	0	0	0	0	0	1	1	1	1	1	0	0	1
Lycomimus_ampliatus	0	0	0	0	0	1	1	0	0	0	0	-	2	0	0	-	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Mariliana_cicadellida	1	1	1	1	1	0	1	0	0	0	0	-	2	0	0	-	1	0	0	0	0	2	1	1	1	1	1	0	0	0
Paleohemilophus_dominicanus	?	?	0	?	?	0	0	?	0	0	0	-	2	0	0	-	1	1	0	1	?	?	?	?	?	?	?	0	?	?
Phoebe_concinna	1	1	0	1	1	0	1	0	0	0	0	-	0	-	0	-	1	1	0	0	0	2	0	-	-	-	0	1	0	1
Phoebe_phoebe	1	1	0	1	1	0	1	0	0	0	0	-	2	0	0	-	0	1	0	0	0	0	0	-	-	-	0	1	0	0
Purusia_acreana	1	1	0	1	1	0	1	0	0	0	1	0	3	-	0	-	0	1	0	0	0	0	1	1	1	1	0	0	1	1
Purusiella_wappesi	1	1	0	1	1	0	1	0	0	0	1	0	3	-	0	-	0	1	0	0	0	0	1	1	1	1	1	1	0	1
Sphallonycha_roseicollis	0	1	0	0	0	0	0	-	0	0	0	-	0	-	0	-	1	1	0	1	0	?	?	?	?	?	?	1	0	1
Tyrinthia_paraba	0	1	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	1	1	1	0	0	0	1
Tyrinthia_scissifrons	0	1	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	1	1	1	0	0	0	0
Aerenica_canescens	0	0	0	0	0	0	0	1	0	0	1	0	2	1	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	0
Aerenicella_spissicornis	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	0
Aerenicopsis_mendosa	0	0	1	0	0	0	0	0	0	0	1	0	3	-	0	-	0	0	0	1	0	?	?	?	?	?	?	0	1	0
Aerenicopsis_perforata	0	0	1	0	0	0	0	0	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	0
Aerenicopsis_pugnatrix	0	0	1	0	0	0	0	0	0	0	1	0	3	-	0	-	1	0	0	1	0	?	?	?	?	?	?	0	1	0
Aereniphaula_bandana	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	0
Aereniphaula_machadorum	0	0	1	0	0	0	0	1	0	0	1	0	3	-	0	-	0	0	0	1	0	0	1	1	1	1	0	0	1	0

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
Aerenomera_boliviensis	0	0	0	0	0	0	0	1	0	0	0	-	2	1	0	-	1	0	0	1	0	0	1	1	1	1	0	0	0	1
Aerenomera_spilas	0	0	0	0	0	0	0	1	0	0	0	-	2	1	0	-	1	0	0	1	0	0	1	1	1	1	0	0	0	1
Antodice_abstrusa	0	0	1	0	0	0	1	0	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	1	1	1	0	0	0	0
Antodice_lenticula	0	0	1	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	?	?	?	?	?	?	0	0	0
Antodice_nympha	1	0	1	0	0	0	1	0	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	1	1	1	1	0	0	0
Antodice_picta	1	0	1	0	0	0	1	0	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	0	1	1	0	0	0	0
Antodice_tricolor	0	0	1	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	1	1	1	0	0	0	0
Antodilanea_modesta	0	0	0	0	0	0	0	-	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	0	1	1	1	0	0	0
Aphilestes_rustica	0	0	0	0	0	0	0	-	0	0	0	-	2	0	0	-	0	0	0	0	1	2	1	0	1	1	0	0	0	0
Apoaerenica_martinsi	0	0	0	0	0	0	0	-	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	1
Apophaula_ocellata	0	0	0	0	0	0	0	-	0	0	1	0	3	-	0	-	0	0	0	1	0	0	1	1	0	1	1	0	1	0
Cacsius_divus	1	0	0	1	1	0	1	0	0	0	0	-	2	1	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	1
Cacsius_nobilis	1	0	0	1	1	0	1	0	0	0	0	-	2	1	0	-	1	0	0	1	0	?	?	?	?	?	?	0	1	1
Calliphaula_filiola	0	0	0	1	1	0	1	1	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	0
Calliphaula_leucippe	0	0	0	1	1	0	1	1	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	0
Eponina_breyeri	0	0	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Eponina_flava	0	0	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	0	2	1	1	1	1	1	0	0	0
Holoarerenica_apleta	0	0	0	0	0	0	0	1	0	0	1	0	2	0	1	1	1	0	1	1	0	?	?	?	?	?	?	0	0	0
Holoarerenica_bistriata	0	0	0	0	0	0	0	1	0	0	1	0	2	0	1	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0
Hoplistonychus_bondari	0	0	0	0	0	0	0	1	0	0	0	-	2	0	1	1	1	0	0	1	0	0	1	1	0	1	1	0	0	0
Hydraschema_obliquevittata	0	0	1	0	0	0	0	0	0	0	1	0	3	-	0	-	0	0	0	1	0	?	?	?	?	?	?	0	1	1
Hysdraschema_letostyla	0	0	1	0	0	0	1	0	0	0	1	0	3	-	0	-	0	0	0	1	0	0	1	1	1	1	0	0	1	1
Melzerella_huedepohli	0	0	0	1	1	0	1	0	0	1	1	1	2	0	0	-	0	0	0	1	0	0	1	1	1	1	1	0	1	1
Melzerella_lutzi	0	0	0	1	1	0	1	0	0	1	1	1	2	0	0	-	0	0	0	1	0	0	1	1	1	1	1	0	1	1
Montesia_leucostigma	0	0	0	1	1	0	1	0	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	1
Phaula_antiqua	0	0	0	0	0	0	0	1	0	0	1	0	3	-	1	0	1	0	1	1	0	0	1	1	0	1	1	0	1	0
Phaula_lichenigera	0	0	0	0	0	0	0	1	0	0	1	0	3	-	1	0	1	0	1	1	0	0	1	1	1	1	1	0	1	0
Phaula_thomsoni	0	0	0	0	0	0	0	1	0	0	1	0	3	-	1	0	1	0	0	1	0	0	1	1	0	1	1	0	1	0
Phoebemima_ensifera	1	1	0	1	1	0	1	0	0	0	0	-	2	-	0	-	0	0	0	1	0	0	1	1	1	1	1	1	1	1

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
Phoebemima_teaphia	1	1	0	1	1	0	1	0	0	0	0	-	2	-	0	-	0	0	0	1	0	0	1	0	0	0	1	1	1	1
Phoebemima_teteia	1	1	0	1	1	0	1	0	0	0	0	-	2	-	0	-	0	0	0	1	0	0	1	1	1	1	1	1	1	1
Pseudomecas_femoralis	0	0	0	0	0	0	0	0	0	0	0	-	3	-	0	-	1	0	0	1	0	2	1	1	1	1	0	0	1	0
Pseudomecas_pickeli	0	0	0	0	0	0	0	0	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	0
Pseudophaula_porosa	0	0	0	0	0	0	0	1	0	0	1	0	3	-	1	1	1	0	0	1	0	0	1	1	1	1	1	0	1	1
Pseudophaula_strigulata	0	0	1	0	0	0	0	1	0	0	0	-	2	1	1	1	1	0	0	1	0	0	1	1	1	1	1	0	1	0
Recchia_acutipennis	0	0	1	0	0	0	0	0	0	0	1	0	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	1
Recchia_albicans	0	0	1	0	0	0	0	0	0	0	0	-	3	-	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	1
Recchia_hirticornis	1	0	1	0	1	0	0	0	0	0	0	-	3	-	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	1
Recchia_parvula	0	0	1	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	1
Recchia_procera	0	0	1	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	1
Rumacon_annulicornis	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	0
Rumacon_canescens	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	-	1	0	0	1	0	0	1	1	1	1	1	0	1	0
Suipinima_flavumtuberculata	0	0	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	1	2	1	1	1	1	0	0	0	0
Suipinima_marginalis	0	1	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	0	1	?	?	?	?	?	?	0	1	0
Suipinima_suturalis	1	0	0	0	1	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	1	2	1	1	1	1	0	0	0	0
Vianopolisia_captiosa	0	0	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	0	0	1	1	1	1	0	0	1	1
Vianopolisia_spitzi	0	0	0	0	0	0	0	0	0	0	0	-	2	0	0	-	1	0	0	1	1	0	1	1	1	1	1	0	1	1

Part III

	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109
Spondylis_buprestoides	0	1	0	0	0	0	-	-	0	0	0	-	0	-	0	0	1	0	1	1	0	1	0	-	2	1
Agapanthia_cardui	1	1	1	0	0	1	-	-	0	0	0	-	0	-	0	0	2	2	0	1	0	1	0	-	1	0
Hippopsis_pubiventris	2	1	2	0	0	1	-	-	0	0	0	-	0	-	0	0	2	2	1	0	0	1	1	-	1	1
Hippopsis_truncatella	2	1	2	0	0	1	-	-	1	0	1	1	0	-	0	0	2	2	1	0	0	1	1	-	1	1
Falsamblesthis_ibiyara	0	0	1	1	1	-	0	-	0	0	0	-	0	-	1	1	1	1	1	0	0	1	0	-	0	1
Falsamblesthis_seriepilosa	0	0	1	1	1	-	0	-	0	0	0	-	?	?	?	?	1	1	1	1	0	1	0	-	0	1

	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109
Falsamblesthis_unguicularis	0	0	1	0	1	-	0	-	0	0	0	-	?	?	?	?	1	1	1	1	0	1	0	-	1	1
Callia_azurea	0	1	1	0	1	-	0	-	0	0	0	-	0	-	1	0	1	0	1	0	0	1	1	-	2	1
Drycothaea_angustifrons	0	0	1	0	1	-	0	-	0	0	0	-	0	-	1	0	1	2	1	1	0	1	0	-	1	1
Gryllica_picta	0	0	0	0	1	-	0	-	0	0	1	0	0	-	1	0	1	0	1	1	0	1	0	-	1	1
Ataxia_luteifrons	0	0	0	0	0	1	-	-	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	-	1	1
Ataxia_obscura	0	0	0	0	0	1	-	-	0	0	1	1	1	0	1	1	0	1	1	1	0	1	0	-	1	1
Mecas_menthae	0	0	1	0	1	-	1	0	0	0	1	1	0	-	1	0	1	0	0	1	1	1	1	-	2	1
Phytoecia_Pilemia_hirsutula	0	1	1	0	1	-	1	0	0	0	0	-	0	-	1	0	1	0	1	1	0	1	1	-	1	0
Glenea_glenea_fasciata	0	0	1	1	1	-	0	-	0	0	0	-	0	-	1	0	?	?	?	?	?	?	?	?	?	?
Saperda_carcharias	0	0	0	1	1	-	0	-	0	0	1	0	0	-	1	0	1	2	1	1	1	1	0	-	1	1
Adesmus_borgmeieri	0	0	1	1	1	-	1	1	1	0	1	0	?	?	?	?	1	0	1	1	1	1	1	-	2	1
Adesmus_brunneiceps	0	0	1	1	1	-	1	0	1	0	1	0	1	0	0	0	2	0	1	1	0	1	1	-	1	1
Apagomerella_versicolor	0	1	1	1	1	-	1	0	1	0	0	-	0	-	0	0	1	0	1	1	0	0	-	1	0	1
Calocosmus_nuptus	0	0	0	0	1	-	1	1	0	0	1	1	0	-	0	0	1	0	1	1	0	1	1	-	1	1
Fredlanea_velutina	0	1	1	0	1	-	1	0	0	0	1	1	?	?	?	?	2	0	0	2	0	1	1	-	2	1
Fredlanea_viridipennis	0	1	1	0	1	-	1	1	0	0	1	1	1	1	0	0	2	0	0	2	0	1	1	-	2	1
Hemilophus_dimidiaticornis	0	1	1	1	1	-	1	0	0	0	0	-	1	1	0	0	1	0	1	1	0	1	1	-	2	0
Ites_plagiatus	0	0	0	1	1	-	1	0	0	0	?	?	1	1	0	1	?	?	?	?	?	?	?	?	?	?
Lycomimus_ampliatus	0	0	0	1	1	-	1	0	0	0	?	?	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Mariliana_cicadellida	0	0	1	1	1	-	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	1	0	-	2	0
Paleohemilophus_dominicanus	?	?	?	?	1	-	1	1	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phoebe_concinna	0	0	0	1	1	-	1	2	0	0	1	1	1	1	0	0	2	0	1	1	0	1	1	-	1	0
Phoebe_phoebe	0	0	1	1	1	-	1	0	1	0	1	1	1	1	0	0	2	0	1	1	0	1	1	-	2	0
Purusia_acreana	0	0	0	1	1	-	1	0	1	0	0	-	1	1	0	0	2	0	1	0	1	1	1	-	1	0
Purusiella_wappesi	0	0	0	1	1	-	1	0	1	0	0	-	?	?	?	?	2	0	1	1	1	1	1	-	1	0
Sphallonycha_roseicollis	0	0	0	1	1	-	0	-	0	0	1	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Tyrinthia_paraba	0	0	0	1	1	-	1	0	0	0	0	-	0	-	0	0	2	0	1	1	0	1	1	-	2	0
Tyrinthia_scissifrons	0	0	0	1	1	-	1	0	0	0	1	0	0	-	0	0	1	0	1	1	0	1	1	-	2	0
Aerenica_canescens	2	1	2	0	1	-	1	0	0	0	1	1	1	1	0	0	2	0	1	1	0	0	-	1	0	0

	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109
Aerenicella_spissicornis	0	1	2	0	1	-	1	0	1	0	1	1	1	1	0	0	2	0	1	0	0	0	-	0	0	1
Aerenicopsis_mendosa	1	1	2	0	1	-	1	0	0	0	1	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Aerenicopsis_perforata	1	1	2	0	1	-	1	0	0	0	1	1	1	1	0	0	2	0	1	0	0	0	-	1	0	0
Aerenicopsis_pugnatrix	1	1	2	0	1	-	1	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aereniphaula_bandana	1	1	2	0	1	-	1	0	0	0	1	1	?	?	?	?	1	0	1	1	0	0	-	1	0	0
Aereniphaula_machadorum	1	1	2	0	1	-	1	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	-	2	1	0
Aerenomera_boliviensis	1	1	1	0	1	-	1	0	0	0	1	1	1	1	1	1	2	0	1	1	1	1	1	-	1	1
Aerenomera_spilas	1	1	1	0	1	-	1	0	0	0	1	1	1	1	1	1	2	0	1	1	1	1	1	-	1	1
Antodice_abstrusa	0	0	1	1	1	-	1	0	0	0	1	1	?	?	?	?	2	0	1	1	0	1	1	-	0	1
Antodice_lenticula	0	1	1	0	1	-	1	0	0	0	1	1	0	-	1	0	?	?	?	?	?	?	?	?	?	?
Antodice_nympha	0	0	1	1	1	-	1	0	1	0	1	1	?	?	?	?	2	0	0	1	0	0	-	1	0	0
Antodice_picta	0	0	1	1	1	-	1	0	0	0	1	1	0	-	1	0	2	0	1	1	0	1	1	-	0	0
Antodice_tricolor	0	0	1	1	1	-	1	0	0	0	1	1	?	?	?	?	2	0	1	0	0	1	1	-	0	0
Antodilanea_modesta	0	0	1	0	1	-	1	0	0	0	1	1	0	-	1	0	2	0	0	1	0	1	1	-	0	0
Aphilestes_rustica	0	0	1	1	1	-	1	1	0	0	1	1	1	0	1	1	2	0	1	1	0	1	1	-	1	1
Apoaerenica_martinsi	0	1	2	0	1	-	1	0	0	0	1	1	?	?	?	?	2	0	1	1	0	0	-	2	0	1
Apophaula_ocellata	0	0	1	1	1	-	1	0	1	0	1	1	1	1	0	0	2	0	1	0	0	1	0	-	2	1
Cacsius_divus	0	0	1	1	1	-	1	0	1	0	1	0	1	0	0	0	2	0	0	0	0	1	1	-	0	1
Cacsius_nobilis	0	0	1	1	1	-	1	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Calliphaula_filiola	0	0	1	1	1	-	1	1	0	0	1	1	?	?	?	?	2	2	1	0	0	1	0	-	1	1
Calliphaula_leucippe	0	0	1	1	1	-	1	0	1	0	1	1	1	1	0	0	2	0	1	1	0	0	-	2	0	1
Eponina_breyeri	0	0	1	0	1	-	1	0	0	1	1	1	1	0	0	0	2	0	0	1	0	0	-	1	0	1
Eponina_flava	0	0	1	0	1	-	1	0	0	0	1	0	0	-	0	0	2	0	0	1	0	0	-	1	0	1
Holoarerenica_apleta	1	0	1	0	1	-	1	0	0	0	?	?	1	1	1	1	?	?	?	?	?	?	?	?	?	?
Holoarerenica_bistriata	1	0	1	0	1	-	1	0	0	0	1	1	1	1	1	1	1	2	0	1	0	1	1	-	0	1
Hoplistonychus_bondari	0	0	0	1	1	-	1	0	0	0	1	1	1	1	1	1	2	0	0	0	0	1	1	-	0	1
Hydraschema_obliquevittata	0	1	2	0	1	-	1	0	0	0	1	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Hysdraschema_letostyla	0	1	2	0	1	-	1	0	1	0	1	1	?	?	?	?	2	0	1	1	1	1	1	-	0	1
Melzerella_huedepohli	0	0	2	1	1	-	1	0	1	0	1	1	?	?	?	?	2	0	1	1	0	0	-	2	0	0

	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109
Melzerella_lutzi	0	0	2	1	1	-	1	0	1	0	1	1	1	1	1	0	2	0	1	1	0	0	-	2	0	0
Montesia_leucostigma	0	0	1	1	1	-	1	0	1	0	1	1	1	0	0	1	2	0	1	1	0	0	-	2	0	1
Phaula_antiqua	0	0	1	1	1	-	1	0	0	0	1	1	1	1	1	1	2	0	0	0	0	1	1	-	0	1
Phaula_lichenigera	0	0	0	1	1	-	1	0	0	0	1	1	1	1	1	1	2	0	0	0	0	1	1	-	0	1
Phaula_thomsoni	0	0	1	1	1	-	1	0	0	0	1	1	0	-	1	1	2	0	0	1	0	1	1	-	0	1
Phoebemima_ensifera	0	1	1	1	1	-	1	1	0	0	0	-	1	1	1	1	1	0	2	1	0	1	1	-	1	0
Phoebemima_teaphia	0	1	1	1	1	-	1	1	0	0	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?
Phoebemima_teteia	0	1	1	1	1	-	1	1	1	0	1	1	?	?	?	?	1	2	1	1	0	1	0	-	2	1
Pseudomecas_femoralis	1	1	2	0	1	-	1	0	0	0	1	1	0	-	0	0	2	2	1	0	1	1	1	-	0	1
Pseudomecas_pickeli	1	1	2	0	1	-	1	0	0	0	1	1	0	-	0	0	1	0	1	1	1	0	-	2	0	1
Pseudophaula_porosa	0	1	1	1	1	-	1	0	0	0	1	1	1	1	1	1	2	0	1	1	0	1	1	-	0	1
Pseudophaula_strigulata	0	1	1	1	1	-	1	0	0	0	1	1	1	1	1	1	2	0	1	0	0	1	1	-	1	1
Recchia_acutipennis	0	0	2	1	1	-	1	0	0	1	1	1	1	1	0	0	2	0	1	1	0	1	1	-	0	1
Recchia_albicans	0	0	2	1	1	-	1	0	0	1	1	1	1	1	0	0	2	0	1	0	0	1	1	-	0	1
Recchia_hirticornis	0	0	2	1	1	-	1	0	1	1	1	1	1	1	0	0	2	2	1	0	0	1	1	-	0	1
Recchia_parvula	0	0	2	1	1	-	1	0	0	1	1	1	0	-	1	0	2	2	1	0	0	1	1	-	0	1
Recchia_procera	0	0	2	1	1	-	1	0	0	1	1	1	0	-	1	0	2	2	1	0	0	1	1	-	0	1
Rumacon_annulicornis	1	1	1	1	1	-	1	0	0	0	1	1	1	0	1	1	2	0	1	1	0	1	1	-	0	1
Rumacon_canescens	1	1	1	1	1	-	1	0	0	0	1	1	?	?	?	?	2	0	1	0	0	1	1	-	0	1
Suipinima_flavumtuberculata	0	0	1	1	1	-	1	0	0	0	1	1	1	1	0	0	2	0	1	1	0	1	1	-	0	1
Suipinima_marginalis	0	0	1	1	1	-	1	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suipinima_suturalis	0	0	1	1	1	-	1	0	0	0	1	1	1	1	1	1	2	0	1	1	1	0	-	1	1	1
Vianopolisia_captiosa	0	1	1	1	1	-	1	0	0	0	1	0	?	?	?	?	2	2	1	0	0	1	1	-	1	0
Vianopolisia_spitzi	0	1	1	0	1	-	1	0	0	0	1	0	1	1	0	1	2	2	1	0	0	1	1	-	0	1

3.1. Cladistic analysis results

The K values obtained through the method proposed by Pastana (2021) were: 7.37300; 7.67394; 7.98742; 8.31423; 8.65526; 9.01144; 9.38382; 9.77351 and 10.18176. In all implied weights searches, with different K values, only one most parsimonious tree was obtained. This is probably due to the inclusion of continuous characters, since these data provide better topological resolution (Goloboff *et al.*, 2006). The tree with K= 7.37300 was selected in the pairwise comparison (Fig. 16B). Calculations of nodal supports and character optimizations were performed based on this tree. Since our study focused on testing the monophyly and the relationship between Aerenicini groups, the relationship between outgroups is not taken into account, mainly due to low representativeness. The outgroup terminals were selected based on their morphological similarities, as indicated in previous taxonomic studies. Some considerations are made about Hemilophini, due to its close affinity to Aerenicini and for being better represented in our analysis.

A total of 62,972,667,078 rearrangements were examined, achieving a Best score hit of 70 after 5:45h. Aerenicini was retrieved as paraphyletic, since the genus *Hippopsis* (Agaphantini) is more related to Aerenicini groups (clade 103). The genus *Phoebemima* and *Suipinima marginalis* were retrieved in clade 124, which includes others genera of Hemilophini. The species of the monotypic genus *Apophaula ocellata* is the sister group of the remaining Aerenicini species (clade 102). A single discrete ambiguous synapomorphy was found in Aerenicini, which is the convergent shape of aedeagus (char. 100:2). The remaining synapomorphies are the following continuous quantitative characters: an increase in scape length (char. 0); general increase in the length of the flagelomeres (char. 4-10); decrease in humeral width (char. 16); decrease in prothorax length (char. 17) and decrease in genae length, which means an increase in the lower eye lobes (as previously discussed). *Apophaula ocellata* has eyes with finely faceted ommatidia, which may indicate that the ancestor of Aerenicini had diurnal habits.

The clade 102 (which excludes *Apophaula ocellata*) is characterized by the maxillary palpomere IV with sparse pubescence (char. 26:1); eye lobes coarsely faceted (char. 37:0) and tegmen arched in lateral view (char. 108:0). The clade 102, has two major lineages: clade 171, which comprises the genera *Vianopolisia* and *Recchia*, whose discrete synapomorphy is the apex of the aedeagus gradually acuminate towards apex (char. 102:2) as a sister group of clade 101, which includes the remaining Aerenicini groups

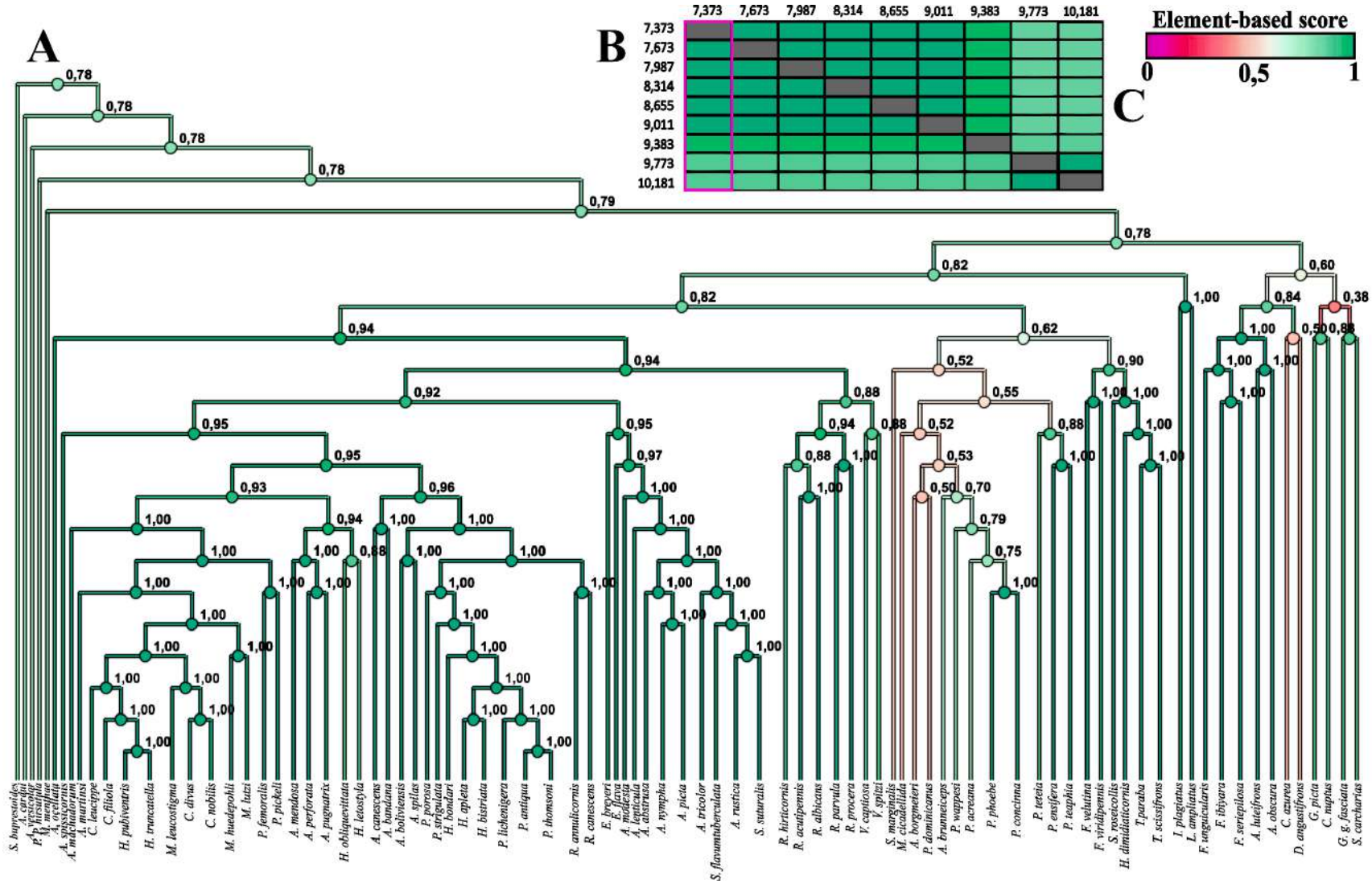

Figure 16. A, Reference tree of Aerenicini; B, pairwise comparison scheme of tested trees organized in descending order; C, color gradient representing the element-based score. The numbers at the nodes indicate the average similarity between the trees tested.

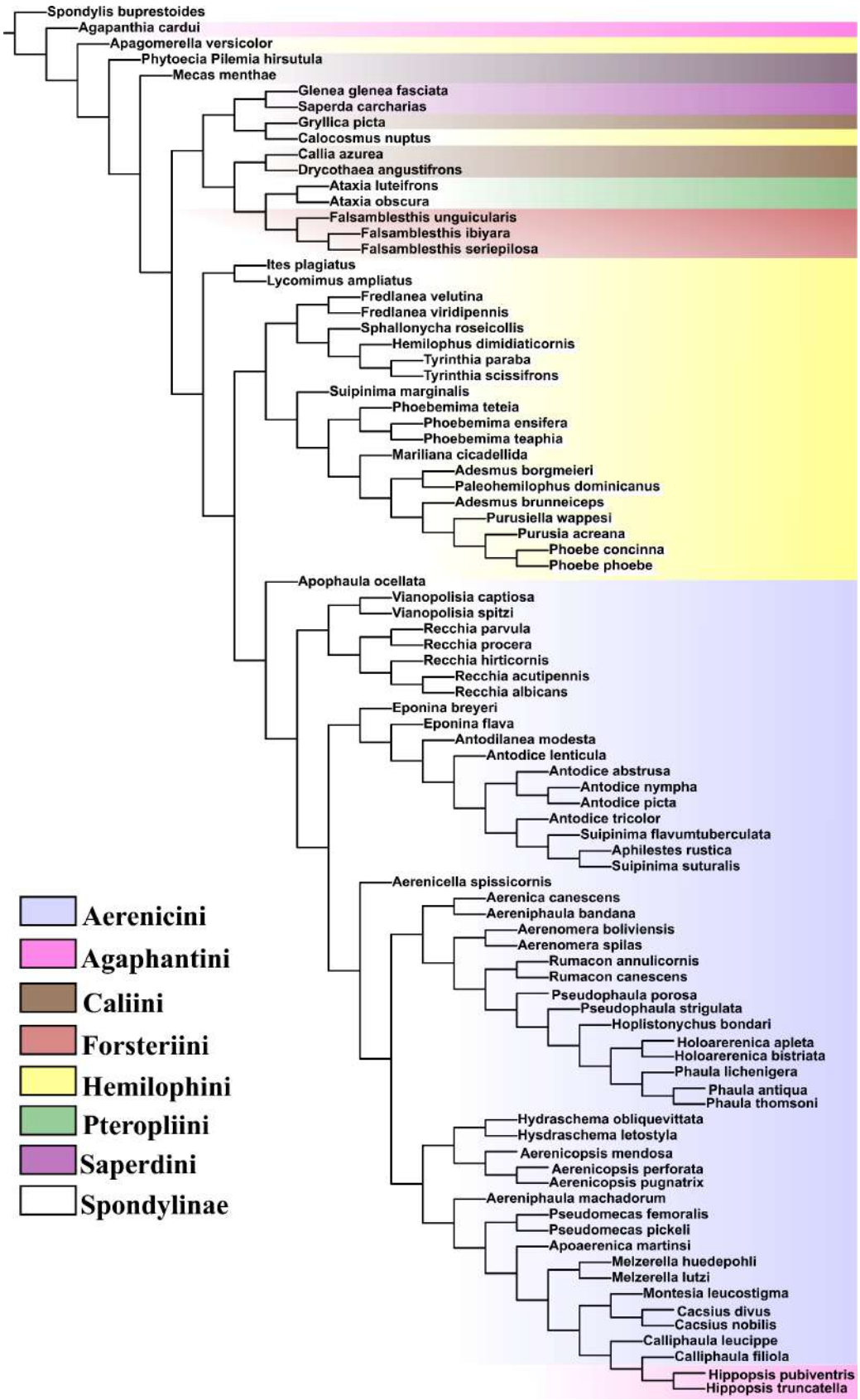

Figure 17. Simplified reference tree of Aerenicini obtained under parsimony optimality criterion and Implied weighting (k = 7,373) showing the relationship between the tribes of Lamiinae.

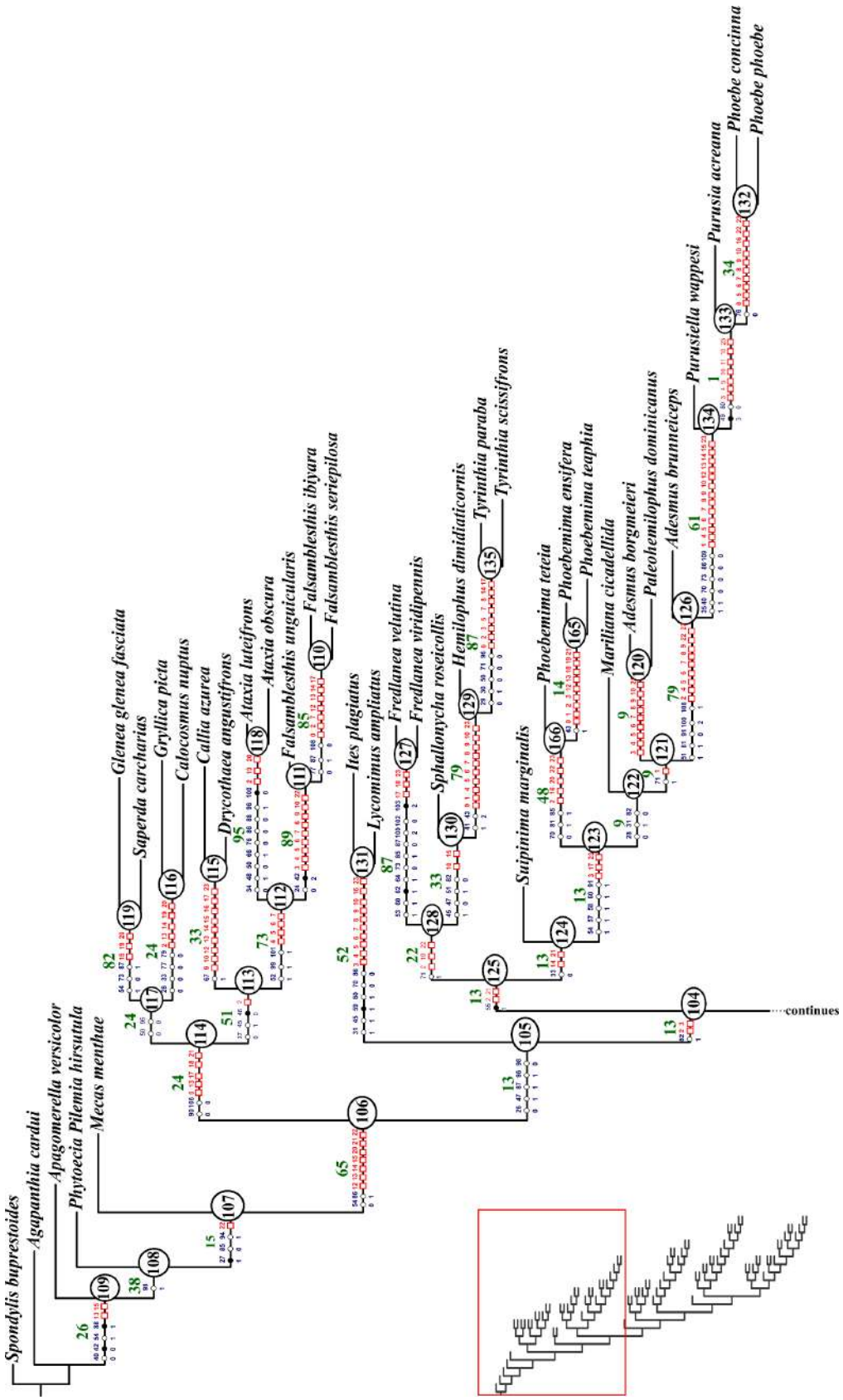

Figure 18. Part of the tree of Aerenicini. Blue numbers and circles, refer to discrete characters; numbers and red squares refer to continuous characters; numbers on the left of the branch are character and on the right, character state. Black circles are unambiguous synapomorphies. Green numbers are relative Bremer support. Node numbers referenced in the text displayed on each clade.

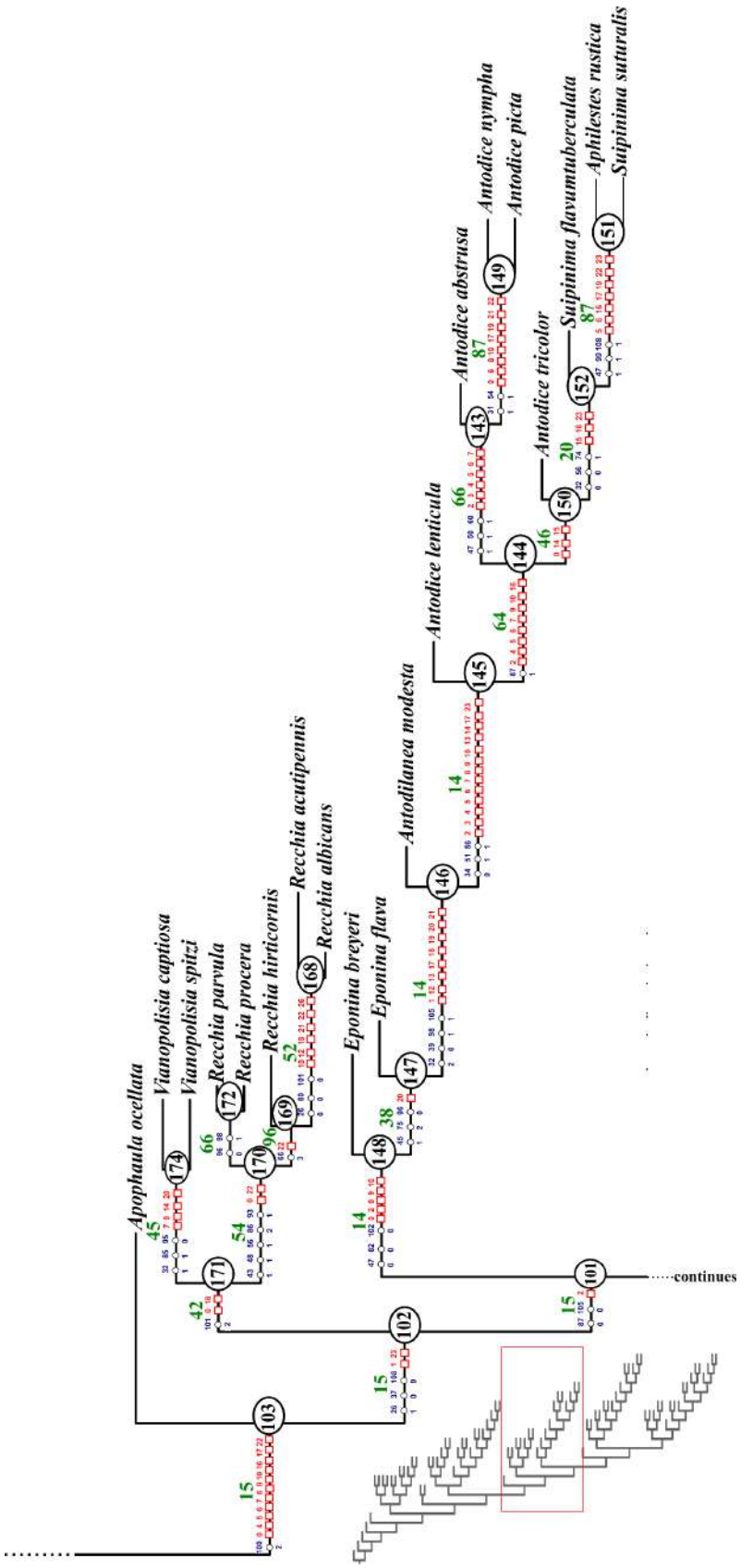

Figure 19. Part of the reference tree of Aerenicini. Blue numbers and circles, refer to discrete characters; numbers on the left side of the branch represent the character and on the right side the character state. Green numbers refer to relative Bremer support. Node numbers referenced in the text displayed above each clade.

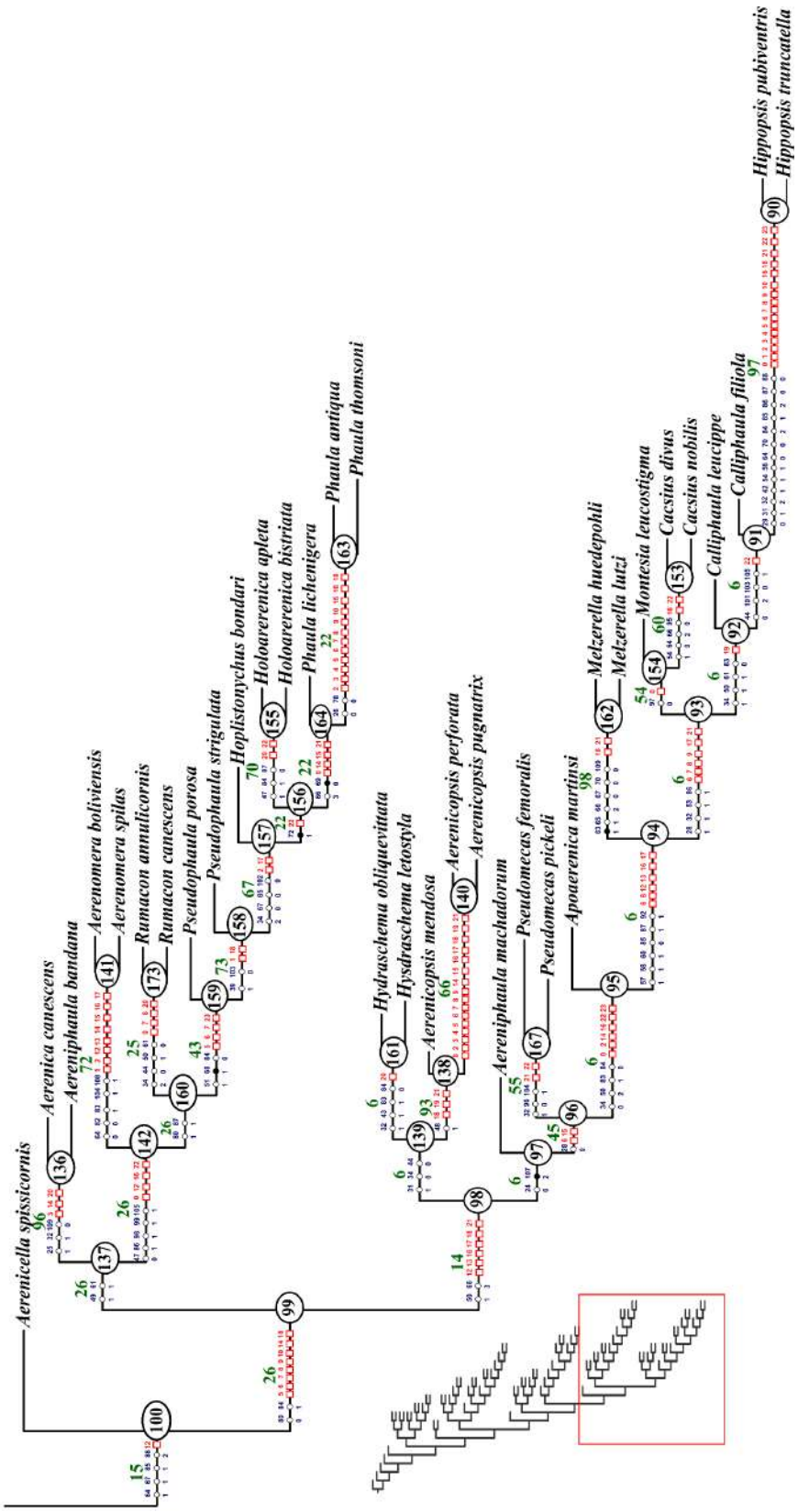

Figure 20. Part of the reference tree of Aerenicini. Blue numbers and circles, refer to discrete characters; numbers and red squares refer to continuous characters. Totally Black circles represent unambiguous synapomorphies. numbers on the left side of the branch represent the character and on the right side the character state. Green numbers refer to relative Bremer support. Node numbers referenced in the text displayed above each clade.

The species of the monotypic genus *Aerenicella spissicornes* is the sister group of clade 99, which includes the remaining Aerenicini groups. The clade 99 has two lineages, clade 137, which includes the type species *Aerenica canescens* and clade 98. It is noteworthy that in these clades are included species whose larvae were studied, *Hoplystonicus bondari* (clade 137) and *Aerenicopsis mendosa* (clade 98) and which larvae are equipped with urogomphus. Clade 98 is supported by species with the anterior margin of prothorax with the same width of posterior margin (char. 50:1) and by the elytral apices acuminate (char. 66:3) in addition to six continuous characters. This clade is composed by two groups, clade 139, which groups the genera *Hydraschema* and *Aerenicopsis* (both retrieved as monophyletic) and clade 97. *Aereniphaula machadorum* (which returns to its status as a monotypic genus) is a sister group to clade 96, which groups the monophyletic genus *Pseudomecas* (clado 167), sister group of genera whose species have vibrant colors.

The species *Apoaerenica martinsi* (Monné, 1979), the single representative of its genus, was retrieved as a sister group of clade 94, which is constituted by the genus *Melzerella* (clade 162). The clade 93 is composed by clade 154, which groups the species *Montesia leucostigma* as sister group of the monophyletic genus *Caccius* (clade 153). Finally, the enigmatic clade 92, which contains the paraphyletic genus *Calliphaula* as a sister group to *Hippopsis*.

The non-monotypic genera retrieved as monophyletic in our analysis are the following: *Aerenicopsis*; *Aeronomera*; *Cacsius*; *Holoaenica*; *Hydraschema*; *Melzerella*; *Phaula*; *Pseudomecas*; *Recchia*; *Rumacon* and *Vianopolisia*. For the remaining genera, new taxonomic rearrangements are proposed. A complete list of all node synapomorphies, including continuous data, as well as relative Bremmer support, is presented below.

List of Synapomorphies

Node 90:
Char. 0: 0.465-0.554 --> 0.911
Char. 1: 0.143-0.184 --> 0.102
Char. 2: 0.357-0.376 --> 0.683
Char. 3: 0.490-0.556 --> 0.935
Char. 4: 0.389-0.465 --> 0.987
Char. 5: 0.349-0.371 --> 0.829
Char. 6: 0.314-0.337 --> 0.851
Char. 7: 0.280-0.291 --> 0.851
Char. 8: 0.266 --> 0.842
Char. 9: 0.249 --> 0.834
Char. 10: 0.188 --> 0.991
Char. 16: 0.140-0.160 --> 0.040
Char. 18: 0.515 --> 0.029
Char. 21: 0.257-0.271 --> 0.171
Char. 22: 0.094 --> 0.310
Char. 23: 0.284-0.316 --> 0.053
Char. 29: 1 --> 0
Char. 31: 0 --> 1
Char. 32: 1 --> 2
Char. 54: 0 --> 1
Char. 56: 0 --> 1
Char. 64: 1 --> 0
Char. 70: 1 --> 0
Char. 84: 0 --> 2
Char. 85: 0 --> 1
Char. 86: 1 --> 2
Char. 87: 1 --> 0
Char. 88: 1 --> 0

Node 91:
Char. 22: 0.079 --> 0.094
Char. 44: 1 --> 0
Char. 101: 0 --> 2
Char. 103: 1 --> 0
Char. 105: 0 --> 1

Node 92:
Char. 19: 0.444 --> 0.778
Char. 34: 0 --> 1
Char. 50: 2 --> 1
Char. 61: 0 --> 1
Char. 83: 1 --> 0

Node 93:
Char. 6: 0.349-0.371 --> 0.337
Char. 7: 0.314 --> 0.291
Char. 8: 0.288-0.299 --> 0.266
Char. 9: 0.260 --> 0.238-0.249
Char. 17: 0.227 --> 0.273
Char. 21: 0.186 --> 0.257
Char. 28: 0 --> 1
Char. 32: 0 --> 1
Char. 53: 0 --> 1
Char. 86: 2 --> 1

Node 94:
Char. 6: 0.394 --> 0.349-0.371
Char. 8: 0.311 --> 0.288-0.299
Char. 12: 0.538-0.615 --> 0.423
Char. 13: 0.490-0.510 --> 0.347-0.429
Char. 16: 0.120 --> 0.140-0.160
Char. 17: 0.136 --> 0.227
Char. 57: 0 --> 1
Char. 58: 0 --> 1
Char. 60: 0 --> 1
Char. 85: 1 --> 0
Char. 87: 0 --> 1
Char. 92: 0 --> 1

Node 95:
Char. 0: 0.592-0.631 --> 0.554
Char. 2: 0.339-0.344 --> 0.357-0.376
Char. 14: 0.365 --> 0.269-0.308
Char. 16: 0.060-0.080 --> 0.120
Char. 22: 0.010-0.030 --> 0.044-0.079
Char. 23: 0.189-0.295 --> 0.316-0.453
Char. 34: 1 --> 0
Char. 50: 1 --> 2
Char. 83: 0 --> 1
Char. 84: 1 --> 0

Node 96:
Char. 6: 0.429 --> 0.394-0.406
Char. 15: 0.341-0.432 --> 0.159-0.227
Char. 28: 1 --> 0

Node 97:
Char. 24: 1 --> 0
Char. 107: 1 --> 2

Node 98:
Char. 12: 0.442-0.519 --> 0.538-0.615
Char. 13: 0.347-0.408 --> 0.490-0.510
Char. 16: 0.140-0.200 --> 0.060-0.080
Char. 17: 0.182-0.273 --> 0.091-0.136
Char. 18: 0.662 --> 0.471-0.515
Char. 21: 0.357 --> 0.186
Char. 50: 2 --> 1
Char. 66: 2 --> 3

Node 99:
Char. 3: 0.516 --> 0.582
Char. 4: 0.439-0.452 --> 0.516-0.529
Char. 5: 0.406 --> 0.451-0.463
Char. 6: 0.349-0.371 --> 0.429
Char. 7: 0.291-0.337 --> 0.371-0.383
Char. 8: 0.277-0.322 --> 0.333-0.345
Char. 9: 0.260-0.271 --> 0.282-0.315

Char. 10: 0.162-0.179 --> 0.188-0.214
Char. 14: 0.308 --> 0.365
Char. 18: 0.779-0.809 --> 0.662
Char. 80: 1 --> 0
Char. 84: 0 --> 1

Node 100:
Char. 12: 0.365-0.423 --> 0.442
Char. 64: 0 --> 1
Char. 67: 0 --> 1
Char. 85: 0 --> 1
Char. 86: 1 --> 2

Node 101:
Char. 2: 0.376-0.385 --> 0.330-0.339
Char. 87: 1 --> 0
Char. 105: 1 --> 0

Node 102:
Char. 1: 0.224 --> 0.184
Char. 23: 0.558-0.579 --> 0.400-0.421
Char. 26: 0 --> 1
Char. 37: 1 --> 0
Char. 108: 2 --> 0

Node 103:
Char. 0: 0.389-0.401 --> 0.478
Char. 4: 0.299-0.325 --> 0.439-0.452
Char. 5: 0.246-0.269 --> 0.406
Char. 6: 0.223-0.246 --> 0.349-0.371
Char. 7: 0.200-0.223 --> 0.291-0.337
Char. 8: 0.186-0.209 --> 0.277-0.322
Char. 9: 0.171-0.193 --> 0.260-0.271
Char. 10: 0.128-0.137 --> 0.162-0.179
Char. 16: 0.260-0.280 --> 0.200
Char. 17: 0.364-0.455 --> 0.273-0.318
Char. 22: 0.227-0.276 --> 0.044-0.054
Char. 100: 1 --> 2

Node 104:
Char. 2: 0.330 --> 0.376-0.394
Char. 3: 0.373-0.451 --> 0.516
Char. 82: 0 --> 1

Node 105:
Char. 26: 1 --> 0
Char. 47: 0 --> 1
Char. 87: 0 --> 1
Char. 96: 0 --> 1
Char. 98: 1 --> 0

Node 106:
Char. 12: 0.462-0.615 --> 0.365-0.423
Char. 13: 0.490 --> 0.347
Char. 14: 0.423-0.462 --> 0.269-0.308
Char. 15: 0.568-0.614 --> 0.455
Char. 20: 0.227-0.273 --> 0.318-0.364
Char. 21: 0.586-0.643 --> 0.400-0.457
Char. 22: 0.300 --> 0.227-0.276
Char. 54: 1 --> 0
Char. 80: 0 --> 1

Node 107:
Char. 22: 0.325 --> 0.300
Char. 27: 0 --> 1
Char. 85: 1 --> 0
Char. 94: 0 --> 1

Node 108:
Char. 98: 0 --> 1

Node 109:
Char. 13: 0.449 --> 0.490
Char. 15: 0.455 --> 0.568
Char. 40: 1 --> 0
Char. 42: 1 --> 0
Char. 54: 0 --> 1
Char. 88: 0 --> 1

Node 110:
Char. 0: 0.299 --> 0.350
Char. 2: 0.294 --> 0.312
Char. 7: 0.314 --> 0.320
Char. 12: 0.385 --> 0.596
Char. 13: 0.245 --> 0.408
Char. 14: 0.269 --> 0.365
Char. 17: 0.500 --> 0.364
Char. 77: 1 --> 0
Char. 87: 0 --> 1
Char. 108: 1 --> 0

Node 111:
Char. 3: 0.451 --> 0.725
Char. 4: 0.338-0.376 --> 0.580
Char. 5: 0.280-0.303 --> 0.429-0.451
Char. 6: 0.246-0.280 --> 0.314-0.360
Char. 7: 0.223 --> 0.314
Char. 8: 0.209 --> 0.254-0.288
Char. 9: 0.171-0.193 --> 0.215-0.249
Char. 10: 0.128 --> 0.171-0.222
Char. 22: 0.177-0.227 --> 0.276-0.300
Char. 24: 1 --> 0
Char. 42: 0 --> 2

Node 112:
Char. 4: 0.299-0.312 --> 0.338-0.376
Char. 5: 0.246-0.257 --> 0.280-0.303
Char. 6: 0.223-0.234 --> 0.246-0.280
Char. 7: 0.200-0.211 --> 0.223
Char. 52: 0 --> 1
Char. 99: 0 --> 1
Char. 101: 0 --> 1

Node 113:
Char. 2: 0.312-0.330 --> 0.267-0.294
Char. 37: 1 --> 0
Char. 45: 0 --> 1
Char. 46: 1 --> 0

Node 114:
Char. 0: 0.338 --> 0.287-0.299
Char. 13: 0.347 --> 0.245-0.286
Char. 17: 0.364-0.455 --> 0.500
Char. 18: 0.779-0.809 --> 0.588-0.662
Char. 21: 0.400-0.457 --> 0.300-0.329
Char. 90: 1 --> 0
Char. 106: 1 --> 0

Node 115:
Char. 9: 0.171 --> 0.160
Char. 10: 0.128 --> 0.120
Char. 12: 0.327-0.385 --> 0.173
Char. 13: 0.245 --> 0.041
Char. 14: 0.269 --> 0.077
Char. 15: 0.227-0.341 --> 0.182
Char. 16: 0.260-0.320 --> 0.340
Char. 17: 0.500 --> 0.545
Char. 23: 0.537-0.579 --> 0.747
Char. 67: 0 --> 1

Node 116:
Char. 2: 0.312-0.330 --> 0.439
Char. 13: 0.245-0.286 --> 0.143
Char. 14: 0.269-0.308 --> 0.173
Char. 19: 0.333-0.444 --> 0.556
Char. 20: 0.318-0.409 --> 0.455
Char. 28: 1 --> 0
Char. 33: 1 --> 0
Char. 77: 1 --> 0
Char. 79: 1 --> 0

Node 117:
Char. 50: 1 --> 0
Char. 95: 1 --> 0

Node 118:
Char. 2: 0.267-0.294 --> 0.213
Char. 19: 0.333-0.556 --> 0.778
Char. 20: 0.409-0.500 --> 0.727
Char. 34: 1 --> 0
Char. 48: 0 --> 1
Char. 50: 1 --> 0
Char. 66: 2 --> 1
Char. 76: 1 --> 0
Char. 86: 1 --> 0
Char. 88: 1 --> 0
Char. 96: 0 --> 1
Char. 100: 1 --> 0

Node 119:
Char. 15: 0.227-0.455 --> 0.750
Char. 19: 0.333-0.444 --> 0.222
Char. 20: 0.318-0.409 --> 0.273
Char. 54: 0 --> 1
Char. 73: 1 --> 0
Char. 87: 0 --> 1

Node 120:
Char. 3: 0.477 --> 0.307
Char. 4: 0.274-0.325 --> 0.261
Char. 5: 0.257-0.269 --> 0.246
Char. 6: 0.234-0.246 --> 0.211
Char. 7: 0.223 --> 0.177
Char. 8: 0.209-0.220 --> 0.175
Char. 9: 0.193 --> 0.149
Char. 10: 0.137 --> 0.094
Char. 21: 0.257-0.300 --> 0.443

Node 121:
Char. 1: 0.224 --> 0.184
Char. 71: 0 --> 1

Node 122:
Char. 28: 1 --> 0
Char. 31: 0 --> 1
Char. 82: 1 --> 0

Node 123:
Char. 3: 0.516 --> 0.477
Char. 17: 0.364-0.455 --> 0.500
Char. 23: 0.558-0.579 --> 0.537-0.547
Char. 54: 0 --> 1
Char. 57: 0 --> 1
Char. 58: 0 --> 1
Char. 60: 0 --> 1
Char. 91: 0 --> 1

Node 124:
Char. 14: 0.269-0.308 --> 0.365-0.404
Char. 21: 0.371 --> 0.257-0.300
Char. 33: 1 --> 0

Node 125:
Char. 2: 0.376-0.394 --> 0.439-0.493
Char. 21: 0.400-0.443 --> 0.371
Char. 55: 0 --> 1

Node 126:
Char. 2: 0.439-0.493 --> 0.575-0.593
Char. 4: 0.274-0.325 --> 0.363
Char. 5: 0.257-0.269 --> 0.326
Char. 6: 0.234-0.246 --> 0.269
Char. 7: 0.223 --> 0.246
Char. 8: 0.209-0.220 --> 0.232
Char. 9: 0.193 --> 0.204
Char. 22: 0.227-0.251 --> 0.153-0.187
Char. 23: 0.537 --> 0.495
Char. 51: 0 --> 1
Char. 81: 0 --> 1
Char. 91: 1 --> 0
Char. 100: 1 --> 2
Char. 108: 2 --> 1

Node 127:
Char. 17: 0.364-0.455 --> 0.500
Char. 18: 0.676-0.809 --> 0.662

Char. 23: 0.558-0.579 --> 0.484
Char. 53: 0 --> 1
Char. 60: 0 --> 1
Char. 62: 0 --> 1
Char. 64: 0 --> 1
Char. 73: 1 --> 0
Char. 85: 0 --> 1
Char. 87: 1 --> 0
Char. 100: 1 --> 2
Char. 102: 1 --> 0
Char. 103: 1 --> 2

Node 128:
Char. 2: 0.439-0.493 --> 0.548
Char. 10: 0.128-0.137 --> 0.111-0.120
Char. 22: 0.227-0.276 --> 0.350-0.399
Char. 71: 0 --> 1

Node 129:
Char. 0: 0.389-0.401 --> 0.503
Char. 1: 0.224 --> 0.265
Char. 4: 0.287 --> 0.210-0.223
Char. 5: 0.246 --> 0.166
Char. 6: 0.211 --> 0.131
Char. 7: 0.200 --> 0.120
Char. 8: 0.186 --> 0.119
Char. 9: 0.149 --> 0.094
Char. 10: 0.103 --> 0.068-0.077
Char. 23: 0.579 --> 0.684-0.737
Char. 41: 0 --> 1
Char. 43: 0 --> 2

Node 130:
Char. 10: 0.111-0.120 --> 0.103
Char. 15: 0.455 --> 0.386-0.409
Char. 45: 0 --> 1
Char. 47: 1 --> 0
Char. 51: 0 --> 1
Char. 82: 1 --> 0

Node 131:
Char. 3: 0.373-0.451 --> 0.294
Char. 4: 0.299-0.312 --> 0.274
Char. 5: 0.246-0.257 --> 0.200
Char. 6: 0.223-0.229 --> 0.166
Char. 7: 0.200-0.211 --> 0.131
Char. 8: 0.186-0.198 --> 0.119
Char. 9: 0.171 --> 0.094
Char. 10: 0.128 --> 0.051
Char. 16: 0.260-0.320 --> 0.940
Char. 23: 0.558-0.579 --> 0.853
Char. 31: 0 --> 1
Char. 45: 0 --> 1
Char. 59: 0 --> 1
Char. 60: 0 --> 1
Char. 70: 1 --> 0
Char. 86: 1 --> 0

Node 132:
Char. 0: 0.452 --> 0.478
Char. 5: 0.417 --> 0.429
Char. 6: 0.326 --> 0.394
Char. 7: 0.291-0.314 --> 0.371
Char. 8: 0.277-0.299 --> 0.401
Char. 9: 0.271-0.282 --> 0.370
Char. 10: 0.188 --> 0.316
Char. 16: 0.240 --> 0.220
Char. 22: 0.153 --> 0.128
Char. 23: 0.400 --> 0.368
Char. 76: 1 --> 0

Node 133:
Char. 3: 0.477-0.490 --> 0.569-0.595
Char. 4: 0.389 --> 0.490-0.516
Char. 5: 0.337 --> 0.417
Char. 10: 0.171 --> 0.188
Char. 11: 0.095 --> 0.429
Char. 16: 0.260 --> 0.240
Char. 23: 0.421 --> 0.400
Char. 49: 2 --> 3
Char. 80: 1 --> 0

Node 134:
Char. 1: 0.184 --> 0.143
Char. 4: 0.363 --> 0.389
Char. 5: 0.326 --> 0.337
Char. 6: 0.269 --> 0.326
Char. 7: 0.246 --> 0.291-0.314
Char. 8: 0.232 --> 0.277-0.299
Char. 9: 0.204 --> 0.271-0.282
Char. 10: 0.137 --> 0.171
Char. 12: 0.423 --> 0.327-0.365
Char. 13: 0.388 --> 0.245
Char. 14: 0.269-0.365 --> 0.212
Char. 15: 0.455 --> 0.159
Char. 23: 0.495 --> 0.421
Char. 35: 0 --> 1
Char. 40: 0 --> 1
Char. 70: 1 --> 0
Char. 73: 1 --> 0
Char. 86: 1 --> 0
Char. 109: 1 --> 0

Node 135:
Char. 0: 0.503 --> 0.631
Char. 2: 0.548 --> 0.747
Char. 3: 0.516 --> 0.503
Char. 5: 0.166 --> 0.131
Char. 7: 0.120 --> 0.097
Char. 8: 0.119 --> 0.107
Char. 14: 0.269-0.288 --> 0.365
Char. 17: 0.364 --> 0.318

Char. 29: 1 --> 0
Char. 30: 0 --> 1
Char. 50: 1 --> 0
Char. 71: 1 --> 0
Char. 96: 1 --> 0

Node 136:
Char. 3: 0.582 --> 0.608
Char. 14: 0.365 --> 0.423
Char. 20: 0.318-0.364 --> 0.273
Char. 25: 0 --> 1
Char. 32: 0 --> 1
Char. 109: 1 --> 0

Node 137:
Char. 49: 0 --> 1
Char. 61: 0 --> 1

Node 138:
Char. 18: 0.471-0.515 --> 0.176
Char. 19: 0.444 --> 0.556
Char. 21: 0.171-0.186 --> 0.086
Char. 48: 0 --> 1

Node 139:
Char. 31: 0 --> 1
Char. 34: 1 --> 0
Char. 44: 1 --> 0

Node 140:
Char. 0: 0.592-0.618 --> 0.669
Char. 2: 0.303 --> 0.285
Char. 3: 0.582 --> 0.673
Char. 4: 0.554 --> 0.618
Char. 5: 0.451-0.463 --> 0.509
Char. 6: 0.429 --> 0.463
Char. 7: 0.383 --> 0.394
Char. 8: 0.356 --> 0.367
Char. 9: 0.315 --> 0.337
Char. 14: 0.365 --> 0.462
Char. 15: 0.341-0.432 --> 0.455
Char. 16: 0.040 --> 0.000
Char. 17: 0.045-0.091 --> 0.000
Char. 18: 0.176 --> 0.162
Char. 19: 0.556 --> 0.778
Char. 21: 0.086 --> 0.057

Node 141:
Char. 1: 0.184 --> 0.265
Char. 2: 0.357-0.394 --> 0.412
Char. 12: 0.385-0.423 --> 0.327
Char. 13: 0.347 --> 0.245
Char. 14: 0.365 --> 0.269
Char. 15: 0.341-0.455 --> 0.273
Char. 16: 0.220-0.240 --> 0.260
Char. 17: 0.273-0.318 --> 0.364
Char. 64: 1 --> 0
Char. 82: 1 --> 0
Char. 83: 0 --> 1
Char. 104: 0 --> 1
Char. 108: 0 --> 1

Node 142:
Char. 0: 0.592 --> 0.427-0.465
Char. 12: 0.442-0.519 --> 0.385-0.423
Char. 16: 0.140-0.200 --> 0.220-0.240
Char. 22: 0.025-0.054 --> 0.079
Char. 47: 1 --> 0
Char. 86: 2 --> 1
Char. 98: 0 --> 1
Char. 99: 0 --> 1
Char. 105: 0 --> 1

Node 143:
Char. 2: 0.412-0.421 --> 0.511
Char. 3: 0.641-0.752 --> 0.882-0.974
Char. 4: 0.694 --> 0.860-0.911
Char. 5: 0.669 --> 0.771-0.783
Char. 6: 0.657 --> 0.726
Char. 47: 0 --> 1
Char. 50: 2 --> 1
Char. 60: 0 --> 1

Node 144:
Char. 2: 0.398 --> 0.412-0.421
Char. 4: 0.624 --> 0.694
Char. 5: 0.571 --> 0.669
Char. 6: 0.486 --> 0.657
Char. 7: 0.429 --> 0.463-0.600
Char. 9: 0.315 --> 0.359-0.448
Char. 10: 0.222 --> 0.265-0.274
Char. 16: 0.120 --> 0.100
Char. 87: 0 --> 1

Node 145:
Char. 2: 0.303 --> 0.398
Char. 3: 0.477-0.516 --> 0.641
Char. 4: 0.452 --> 0.624
Char. 5: 0.360-0.406 --> 0.571
Char. 6: 0.349 --> 0.486
Char. 7: 0.246-0.291 --> 0.429
Char. 8: 0.220-0.254 --> 0.407
Char. 9: 0.149-0.227 --> 0.315
Char. 10: 0.137-0.145 --> 0.222
Char. 13: 0.469 --> 0.551-0.592
Char. 14: 0.269-0.308 --> 0.423-0.462
Char. 17: 0.227 --> 0.136
Char. 23: 0.400-0.421 --> 0.368
Char. 34: 1 --> 0
Char. 51: 0 --> 1
Char. 56: 0 --> 1

Node 146:
Char. 1: 0.184 --> 0.143-0.163

Char. 12: 0.327-0.423 --> 0.615-0.712
Char. 13: 0.347 --> 0.469
Char. 17: 0.273-0.318 --> 0.227
Char. 18: 0.779-0.809 --> 0.309
Char. 19: 0.444 --> 0.333
Char. 20: 0.318 --> 0.091-0.136
Char. 21: 0.229-0.400 --> 0.057
Char. 32: 0 --> 2
Char. 39: 1 --> 0
Char. 98: 0 --> 1
Char. 105: 0 --> 1

Node 147:
Char. 20: 0.364 --> 0.318
Char. 45: 0 --> 1
Char. 75: 0 --> 2
Char. 96: 1 --> 0

Node 148:
Char. 0: 0.478-0.592 --> 0.465
Char. 2: 0.330-0.339 --> 0.294-0.303
Char. 8: 0.277-0.322 --> 0.254
Char. 9: 0.260-0.271 --> 0.227
Char. 10: 0.162-0.179 --> 0.145
Char. 47: 1 --> 0
Char. 82: 1 --> 0
Char. 102: 1 --> 0

Node 149:
Char. 0: 0.465 --> 0.529
Char. 6: 0.726 --> 0.737
Char. 8: 0.407-0.514 --> 0.559
Char. 10: 0.274 --> 0.291
Char. 17: 0.136 --> 0.182
Char. 19: 0.333 --> 0.444
Char. 21: 0.029 --> 0.014
Char. 22: 0.054-0.059 --> 0.030
Char. 31: 0 --> 1
Char. 54: 0 --> 1

Node 150:
Char. 0: 0.465 --> 0.389-0.401
Char. 14: 0.423-0.462 --> 0.558-0.654
Char. 15: 0.409-0.455 --> 0.568

Node 151:
Char. 5: 0.669 --> 0.589
Char. 6: 0.657 --> 0.566
Char. 16: 0.100 --> 0.140
Char. 17: 0.136 --> 0.091
Char. 19: 0.333 --> 0.222
Char. 22: 0.054-0.059 --> 0.113
Char. 23: 0.474 --> 0.632
Char. 47: 0 --> 1
Char. 99: 0 --> 1
Char. 108: 0 --> 1

Node 152:
Char. 15: 0.568 --> 0.682
Char. 18: 0.294-0.309 --> 0.368
Char. 23: 0.337-0.368 --> 0.474
Char. 32: 2 --> 0
Char. 56: 1 --> 0
Char. 74: 0 --> 1

Node 153:
Char. 18: 0.515 --> 0.662
Char. 22: 0.054-0.079 --> 0.123
Char. 54: 0 --> 1
Char. 64: 1 --> 0
Char. 66: 3 --> 2
Char. 95: 1 --> 0

Node 154:
Char. 0: 0.554 --> 0.656
Char. 97: 1 --> 0

Node 155:
Char. 20: 0.318-0.364 --> 0.273
Char. 22: 0.069 --> 0.064
Char. 47: 0 --> 1
Char. 84: 0 --> 1
Char. 87: 1 --> 0

Node 156:
Char. 22: 0.103 --> 0.069
Char. 72: 0 --> 1

Node 157:
Char. 2: 0.357-0.394 --> 0.330
Char. 17: 0.273 --> 0.227
Char. 34: 1 --> 2
Char. 67: 1 --> 0
Char. 85: 1 --> 0
Char. 102: 1 --> 0

Node 158:
Char. 1: 0.184 --> 0.224
Char. 18: 0.662 --> 0.779-0.809
Char. 39: 0 --> 1
Char. 103: 1 --> 0

Node 159:
Char. 5: 0.451-0.463 --> 0.440
Char. 6: 0.429 --> 0.394
Char. 7: 0.371-0.383 --> 0.360
Char. 23: 0.379-0.400 --> 0.453
Char. 51: 0 --> 1
Char. 68: 0 --> 1
Char. 84: 1 --> 0

Node 160:
Char. 80: 0 --> 1
Char. 87: 0 --> 1

Node 161:
Char. 20: 0.364 --> 0.273
Char. 32: 0 --> 1

Char. 43: 0 --> 1
Char. 83: 0 --> 1
Char. 84: 1 --> 0

Node 162:
Char. 16: 0.140-0.160 --> 0.180
Char. 21: 0.186 --> 0.143
Char. 63: 0 --> 1
Char. 65: 0 --> 1
Char. 66: 3 --> 2
Char. 67: 1 --> 0
Char. 70: 1 --> 0
Char. 109: 1 --> 0

Node 163:
Char. 2: 0.330 --> 0.321
Char. 3: 0.529-0.608 --> 0.438
Char. 4: 0.465-0.554 --> 0.363
Char. 5: 0.417-0.474 --> 0.314
Char. 6: 0.383-0.417 --> 0.280
Char. 7: 0.360-0.394 --> 0.246
Char. 8: 0.333-0.367 --> 0.232
Char. 9: 0.304-0.326 --> 0.215
Char. 10: 0.197-0.239 --> 0.188
Char. 15: 0.500 --> 0.568
Char. 16: 0.180 --> 0.120
Char. 18: 0.779 --> 0.662
Char. 26: 1 --> 0
Char. 78: 1 --> 0

Node 164:
Char. 0: 0.427 --> 0.401
Char. 14: 0.365 --> 0.462
Char. 15: 0.455 --> 0.500
Char. 21: 0.343-0.371 --> 0.229-0.300
Char. 66: 2 --> 3
Char. 69: 1 --> 0

Node 165:
Char. 0: 0.389-0.401 --> 0.338
Char. 1: 0.224 --> 0.102
Char. 2: 0.511 --> 0.538
Char. 3: 0.477 --> 0.451
Char. 12: 0.423 --> 0.327
Char. 13: 0.347 --> 0.245
Char. 18: 0.809 --> 0.882
Char. 19: 0.333-0.444 --> 0.556
Char. 21: 0.300 --> 0.371
Char. 43: 0 --> 1

Node 166:
Char. 2: 0.439-0.493 --> 0.511
Char. 16: 0.260-0.280 --> 0.300
Char. 20: 0.182-0.364 --> 0.455
Char. 22: 0.227-0.251 --> 0.177
Char. 23: 0.537-0.547 --> 0.484-0.526
Char. 70: 1 --> 0
Char. 81: 0 --> 1
Char. 85: 0 --> 1

Node 167:
Char. 21: 0.186 --> 0.257
Char. 22: 0.010-0.030 --> 0.005
Char. 32: 0 --> 1
Char. 96: 1 --> 0
Char. 104: 0 --> 1

Node 168:
Char. 10: 0.179 --> 0.205
Char. 12: 0.423 --> 0.519
Char. 18: 0.662 --> 0.588
Char. 21: 0.400 --> 0.300
Char. 22: 0.084 --> 0.103
Char. 26: 1 --> 0
Char. 80: 1 --> 0
Char. 101: 2 --> 0

Node 169:
Char. 22: 0.069-0.079 --> 0.084
Char. 66: 2 --> 3

Node 170:
Char. 0: 0.656 --> 0.707-0.720
Char. 22: 0.054 --> 0.069-0.079
Char. 43: 0 --> 1
Char. 48: 0 --> 1
Char. 56: 0 --> 1
Char. 86: 1 --> 2
Char. 93: 0 --> 1

Node 171:
Char. 0: 0.478-0.592 --> 0.656
Char. 18: 0.779-0.809 --> 0.662
Char. 101: 0 --> 2

Node 172:
Char. 96: 1 --> 0
Char. 98: 0 --> 1

Node 173:
Char. 0: 0.427-0.439 --> 0.376
Char. 7: 0.371-0.383 --> 0.406
Char. 8: 0.333-0.345 --> 0.356
Char. 20: 0.318-0.364 --> 0.227
Char. 34: 1 --> 2
Char. 44: 1 --> 0
Char. 50: 2 --> 1
Char. 61: 1 --> 0

Node 174:
Char. 7: 0.337 --> 0.349
Char. 9: 0.260-0.271 --> 0.282
Char. 14: 0.308 --> 0.365
Char. 20: 0.364 --> 0.318
Char. 32: 0 --> 1
Char. 85: 0 --> 1
Char. 95: 1 --> 0

3.2. Notes and taxonomic rearrangements

In this session we propose some taxonomic rearrangements, which aim to reflect the natural history of each group, agreeing with our results. For taxa whose representativeness was considered low (*i.e. Hippopsis*), we believe that an detailed future studies focused on these groups will be needed. For such groups, therefore, we prefer to keep the current classification.

AERENICINI Lacordaire, 1872

Aerenica Dejean, 1835

***Aerenica bandana* (Nascimento, Botero & Bravo, 2016) comb. nov.**

Aereniphaula bandana Nascimento, Botero & Bravo, 2016

Remarks: Although Nascimento *et al.* (2016) had not explained why they chose to insert their new species (*Aereniphaula bandana*) in this genus, it was because they were based on the key proposed by Martins & Galileo (1998), in which, in the alternative of couplet "5", include genera with strongly acuminate or spiny elytral apex. The difference between *Aerenica bandana* and *Aereniphaula machadorum* noted by the authors is notorious: "*Aereniphaula bandana* differs from *A. machadorum* by the upper eye lobes which are well separated, distance between them twice the width of each upper lobe...; the anterior margin of prothorax 1/3 wider than posterior margin; metatarsomere I 1/3 longer than II–III combined, and by the pattern of pubescence. In *A. machadorum*, the distance between the upper lobes is equal to the width of an upper lobe the prothorax has the same width at the anterior and posterior margins; and metatarsomere I twice the length of II–III combined". In fact, the pattern of elytral pubescence and the shape of prothorax are similar in *A. bandana* and *A. canescens*. These species differs, especially by the width of the upper eye lobes, which are wider in *A. bandana*. Clade 136, which comprises these two species, is supported by the cylindrical shape of the maxillary palpus (char. 25:1); frons, converged downward (char. 32:1) and by the absence of struts in the tegmen (char. 109:0), all ambiguous synapomorphy. The other synapomorphies are continuous characters.

Antodice Thomson, 1864

***Antodice breyeri* (Prosen, 1954) comb. nov.**

Aerenica breyeri Prosen, 1954

Aerenicoides breyeri; Gilmour, 1962

Eponina breyeri; Martins & Galileo, 1985

Eponina laetanda Lane, 1976

***Antodice eccentrica* Galileo & Martins, 1992 stat. res.**

Antodice eccentrica Galileo & Martins, 1992

Suipinima excentrica; Martins & Galileo, 2004

Remarks: Originally Galileo & Martins (1992) proposed the new species *Antodice eccentrica*, from Ecuador. Later, Martins & Galileo (2004) mentioned *S. eccentrica* (misspelled as "S. excentrica") in their taxonomic key without making a formal transference of this species. Nascimento *et al.* (2016) therefore formalized the new combination. Here, we propose the reinstatement of the species to its original combination. Our analysis retrieved *Suipinima* as a polyphyletic genus, with one of its species (*S. marginalis*) most closely related to Hemilophini. The remaining *Suipinima* species were retrieved within clade 148, which includes *Antodice* and relatives. Our results corroborate what Martins & Galileo (2004) already pointed, when proposing *Suipinima*, that it is an extremely heterogeneous group and closely related to *Antodice* (translated): "...*Suipinima* **gen. nov.** comprises species that differ in some characteristics. The shape of the prothorax is markedly rounded at sides, as in *S. eccentrica*, but can also have subparallel or slightly parallel sides wider anteriorly and with lateral tubercles, for example, in *S. una*. The tibias can be normal or thickened and with dense setae (*S. una*). The tarsal claws have a wide inner tooth (*S. suturalis*) or may be markedly bifid with the inner tooth subequal to the outer. *Suipinima* resembles *Antodice* by upper eyes lobes close or contiguous and differs by elytra without spots of white or yellowish pubescence." The main difference (elytral pubescence) that separates these genera is an intraspecific variation. The genus *Antodice* currently comprises 27 species and a detailed study will be necessary. Most likely this genus should be separated into subgroups. The metafemora, with length subequal to the mesofemora (char. 82:0) and the dorsal and ventral lobes of the aedeagus with subequal length (char. 102:0) are discrete synapomorphies to this group.

***Antodice flava* (Lane, 1939) comb. nov.**

Eponina flava Lane, 1939

***Antodice flavumtuberculata* (Nascimento, Botero & Bravo, 2016) comb. nov.**

Suipinima flavumtuberculata Nascimento, Botero & Bravo, 2016

***Antodice lanuginosa* (Martins & Galileo, 1985) comb. nov.**

Recchia lanuginosa Martins & Galileo, 1985

Eponina lanuginosa (Martins & Galileo, 1985)

Eponina lanuginosa; Martins & Galileo, 1998

***Antodice metuia* (Martins & Galileo, 1998) comb. nov.**

Eponina metuia Martins & Galileo, 1998

Remarks: When describing the genus *Eponina*, Lane (1939) mentions that its newly described genus is close to *Aerenica*. Until then, *Aerenica* was composed by several species that were transferred to *Recchia* [*i.e. Aerenica albicans* (Guérin-Méneville, 1831); *A. distincta* (Lane, 1939); *A. fonsecai* (Lane, 1939); *A.gemignanii* (Lane, 1939); and *A. hirsuta* (Bates, 1881)]. *Eponina*, therefore, would be closer to *Recchia*, according to this author. Martins & Galileo (1998), in his taxonomic key, separated these two genera (alternative of couplet 17) by metatarsomere I as long as the length of II + III, sides of the prothorax not forward divergent and antennae so long as the body. Our results indicate that *Eponina* is paraphyletic and closer to *Antodice* (including *Antodilanea*), especially by the metafemora length subequal to mesofemora (char. 82:0) and by the ventral and dorsal lobes of aedeagus with subequal length, additionally to five continuous characters (char. 0; 2; 8;9;10).

***Antodice modesta* Lane, 1939 stat. res.**

Antodilanea modesta (Lane, 1939)

Remarks: *Antodilanea* was proposed by Gilmour (1962) for *Antodice modesta* Lane, 1939. Currently the genus is composed of two species from South America (Brazil and Bolivia). The characters used by Gilmour (1962) to separate *Antodilaenea* from *Antodice* were the rounded elytral apices and the tarsal claws with the inner “tooth” short and laminiform. According to the same author: "This new genus is raised for the reception of the *Antodice*? *modesta* Lane, 1939..., which was doubtfully placed in the genus *Antodice* by Lane. It is obvious on the combination of characters that it cannot remain in *Antodice*”. Later, Lane (1974) mentioned that the characters used are dubious and come from a lack of knowledge of the group: "*Antodilanea* was a Gilmour gamble on a question mark, rather than an honest evaluation of a combination of characters". Martins & Galileo (1998) proves that the length of the inner tooth of claws is variable and the single character to separate these genera is the shorter antennae in

Antodilanea. Our results point to *Antodilaenea* as sister group of *Antodice* species (clade 146), supported especially by the frons shape, converged upward (char. 32:2); by rows of omatidia that separates the lower and upper lobe with the same width as the upper eye lobe (39:0); by the abdominal ventrite V of females, without longitudinal median sulcus (char. 98:0) and by the shape of tegmen ring, slightly angular (char. 106:1). However, due to the paraphyletic condition of *Eponina* (clade 148), we prefer to transfer *Antodilanea modesta* to its original genus, *Antodice*. Some species of *Eponina* have short antennae, which indicates that this is a plesiomorphic condition of this lineage.

***Antodice nigristernis* (Martins & Galileo, 1985) comb. nov.**

Recchia nigristernis Martins & Galileo, 1985

Eponina nigristernis (Martins & Galileo, 1985)

Eponina nigristernis; Martins & Galileo, 1998

***Antodice rustica* (Bates, 1881) comb. nov.**

Aphilesthes rustica Bates, 1881

***Remarks*:** *Aphilesthes* is a monotypic genus who's its representative, *Aphilesthes rustica* Bates, 1881, is distributed in South America. Since its original description, the genus is considered monotypic and according to Martins & Galileo (1998), the robust aspect of the species and the pubescence pattern, similar to a lampyrid (fireflies), differentiates *Aphilesthes* from all Aerenicini. In the taxonomic key of Martins & Galileo (1998), *Aphilesthes* is discriminate from *Antodilanea* and *Antodice* (alternative of couplet "12") by the flattened and projected sides of prothorax. In our analysis, *A. rustica* was retrieved in clade 152. This group is quite derived in relation to others species of *Antodice*. The closest relatives of *A. rustica* have a similar pubescent pattern. *Antodice flavumtuberculata*, like *A. rustica*, has lateral gibbosities on prothorax and probably, in a future revision of *Antodice*, this group will be separate.

***Antodice mariahelenae* (Martins & Galileo, 2004) comb. nov.**

Suipinima suturalis Martins & Galileo, 2004

***Remarks*:** The specific epithet is changed because the epithet "suturalis" is preoccupied by *A. suturalis* Galileo & Martins 1992. The epithet is in honor of Dr. Maria Helena M. Galileo for her contribution to the knowledge of Cerambycidae, especially for her numerous works with Aerenicini.

***Phaula* Thomson, 1857**

Hoplistonychus Melzer, 1930 **syn. nov.**

Pseudophaula Lane, 1973 **syn. nov.**

Holoaerenica Lane, 1973 **syn. nov.**

***Phaula bondari* (Melzer, 1930) comb. nov.;**

Hoplistonychus bondari Melzer, 1930

***Phaula* foersteri Martins, 1984 stat. res.**

Pseudophaula foersteri; Martins & Galileo, 1998

***Phaula* porosa (Bates, 1881) comb. nov.;**

Aerenica porosa Bates, 1881

Pseudophaula porosa; Lane, 1973a

***Phaula* pustulosa (Lane, 1973) comb. nov.;**

Pseudophaula pustulosa Lane, 1973

***Phaula* strigulata (Lane, 1973) comb. nov.;**

Pseudophaula strigulata Lane, 1973

***Phaula alveolata* (Martins, 1984) comb. nov.;**

Holoaerenica alveolata Martins, 1984

***Phaula apleta* (Galileo & Martins, 1987) comb. nov.**

Holoaerenica apleta Galileo & Martins, 1987

***Phaula bistriata* (Lane, 1973) comb. nov.**

Holoaerenica bistriata Lane, 1973

***Phaula multipunctata* (Lepeletier & Audinet-Serville, 1825) comb. nov.**

Saperda multipunctata Lepeletier & Audinet-Serville *in* Latreille, 1825

Holoaerenica multipunctata (Lepeletier & Audinet-Serville, 1825)

Aerenica multipunctata; Gemminger & Harold, 1872

Holoaerenica multipunctata; Martins, 1984

Aerenica albolateralis Fuchs, 1963

Holoaerenica albolateralis Martins, 1984

Remarks: The clade 159 includes many groups that Lane (1973) called the "Phaula complex". According to this author (translated): "... They have all the characteristics in common, but vary by the absence or presence of others, or by some more peculiar characters that could be tolerated until some future reviewer could study the tribe in detail..." Although Lane proposed several "small groups" with the intention of preventing superficial studies, such as that by Gilmour (1962), many of these groups (except *Pseudophaula*) were retrieved as monophyletic.

According to the taxonomic key by Martins & Galileo (1998), in the alternative of couplet “6” *Phaula* is separated from *Holoaerenica* and *Pseudophaula* by the width of the area with dense punctures at the base of elytra (longer than twice the length of the scutellum or only exceeding the length of scutellum). In our analysis, *Phaula*, is supported by the presence of tubercles on pronotum (char. 51:1) and metatarsomere shorter than metatibia length (char. 84:0), both ambiguous synapomorphies, and by the elytra with concentrate punctures at the base (char. 68:1), which is an unambiguous synapomorphy.

HEMILOPHINI Thomson, 1868

Antonerella gen. nov.

Type species: *Suipinima marginalis* Martins & Galileo, 2004 **(Fig. 21)**

Description: body elongate, general pubescence yellowish. Frons finely punctate; antennal tubercles widely separated, slightly elevated; lower eyes lobes emarginate; distance between upper eye lobes about width of one upper lobe; lower eye lobes distinctly longer than genae; antennae slender, with long, erect, moderately abundant setae ventrally. Prothorax slightly wider than long; sides rounded with anterior and posterior margins with subequal width; dense yellowish pubescence on sides. Elytra without lateral carina; with dense, erect setae, denser at margins; apex rounded.

Etymology: The Genus is named in honor of Antonio Santos-Silva (MZSP) for his friendship, and extreme dedication in the taxonomy of Cerambycidae.

Remarks: When proposing *Apagomerella* (to alocate *A. versicolor* (Boheman, 1859)], Gilmour (1962) differentiates it from *Apagomera* by the antennomere III shorter than scape and by the dorsally sucate mesotibia. According to Martins (2014a), *Apagomerella* fits into group D (species with convex elytra and without carina). According to the key proposed by the same author (alternative of couplet "5"), the genus is similar to *Columbicella* Galileo & Martins, 1990. *Apagomerella* differs from this genus especially by the anantennomere III shorter than IV; III—IX with sparse setae; antennae longer than body and upper eye lobes five times the width of an upper eye lobe width. Galileo & Martins (2005) described the second species of *Apagomerella* (*A. dissimilis*) and as the specific epithet suggests, it is very different from its congeneric. According to these authors, the upper eye lobes are closer to each other than the width of an upper lobe; prothorax with anterior and basal constrictions practically the same width. By going through the key proposed by Martins (2014a) and comparing *S. marginalis*

with *A. dissimilis*, we found that they are extremely similar species, including the pubescent pattern. Actually, we did not find any morphological expressive differences between these species, other than the disjunct distribution: while *A. dissimilis* was described from Costa Rica, *S. marginalis* occurs in Bolivia. The integument in *S. marginalis* appears darker while in *A. dissimilis* it is reddish. This variation may indicate a clinal variation rather than an interspecific difference. For this reason, we are synonymizing *A. dissimilis* with *S. marginalis*. Regarding *A. versicolor*, this species was originally described in Saperdini and is similar to some species of this tribe (*e.g. Mecas linsleyi* Knull 1974) Our cladistic analysis retrieved *A. versiculor* at the base of the tree, closer to Saperdini species. In the study by Souza et al. (2020), *A. versicolor* was retrieved closer to Aerenicini (*Recchia hirticornis*) than to Hemilophini. Based on this, the author suggested that these tribes should be synonymized. However, in addition to these two species, only *S. carcharias* (Linnaeus, 1758) and *Falsamblesthis ibiyara* Marinoni, 1978 are present in this study and in that of Souza *et al.* (2020). Although this work is not focused in Hemilophini, as well as the work by Souza *et. al.* (2021) was not, we think that a deeper and more detailed study of Hemilophini is necessary. For now, we propose the genus *Antonerella* to allocate *A. marginalis*. *Antonerella* differs from *Apagomerella* especially by the closer upper eye lobes, separated by about the width of an upper eye lobe, by the abruptly semicircular metanepisternum and by the prothorax with rounded sides. In *Apagomerella* the upper eye lobes are separated by about three times the width of an upper eye lobe, the prothorax has subparallel sides, strongly narrowed posteriorly, and the metanepisternum is elongated.

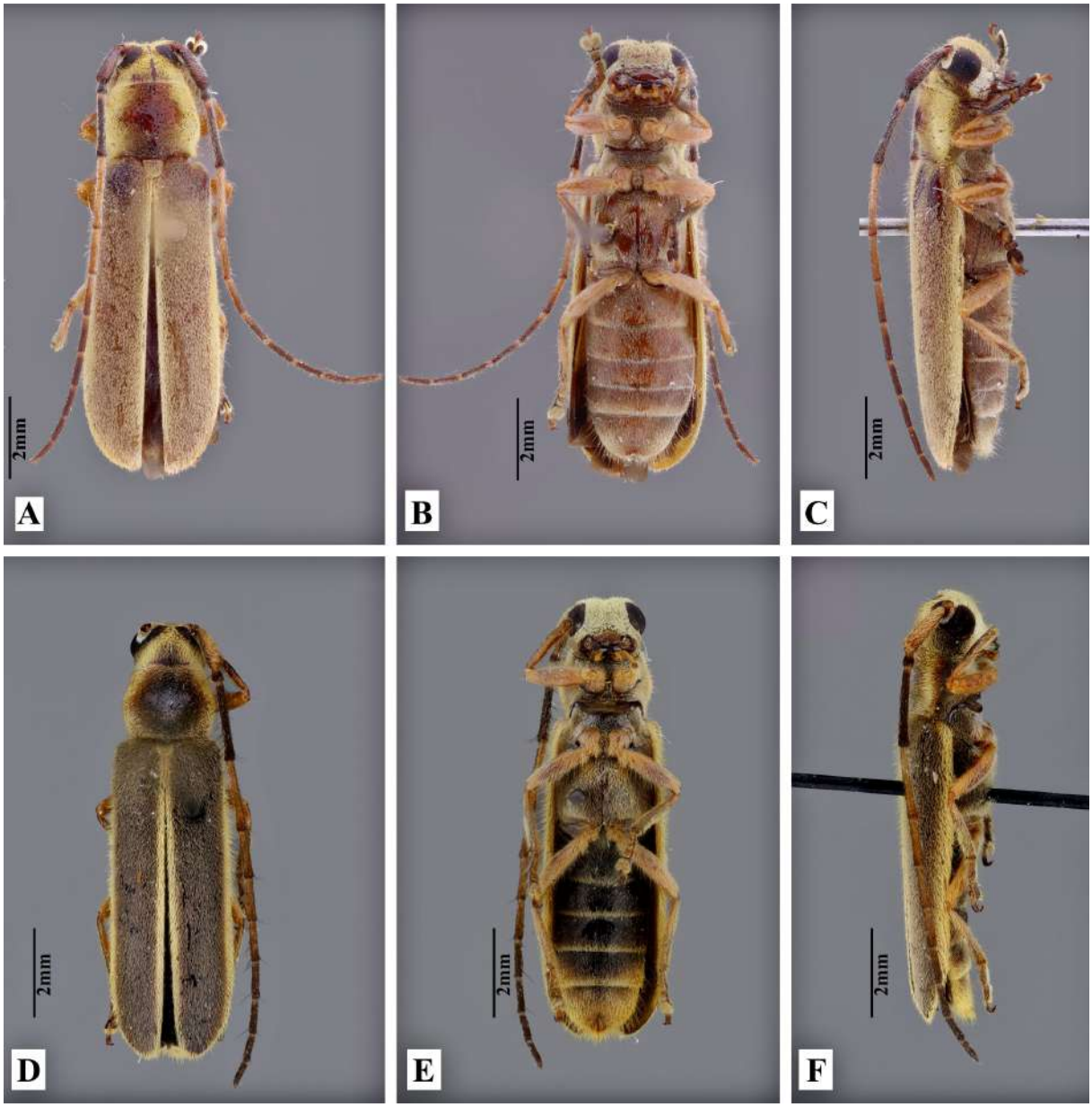

Figure 21. A–F, Habitus of Hemilophini species, dorsal, ventral and lateral: A–C, *Apagomerella dissimilis* Galileo & Martins 2005; D–F, *Suipinima marginalis* Martins & Galileo 2004.

***Antonerella marginalis* (Martins & Galileo, 2004) comb. nov.**

Suipinima marginalis Martins & Galileo, 2004

Apagomerella dissimilis Galileo & Martins, 2005 **syn. nov.**

***Columbicella* Galileo & Martins, 1990**

***Columbicella explanata* Galileo & Martins, 1990**

Remarks: When studying the original description and the images of *C. explanata*, available in Martins (2014a), the slender body pattern and the shape of the prothorax seemed similar to that found in *Antodice* species. In fact, this species was originally described in Aerenicini by Galileo & Martins (1990). The authors also mention that the lower eye lobes are moderately developed, but longer than the genae. We do not understand why Martins (2014a) inserted, without justifying, *C. explanata* among the Hemilophini groups. An ongoing study of this species will allow us to verify its phylogenetic position.

Molecular analys results

The final alignment resulted in 5,020 bp, of which the position of each marker is as follows: CPS= 1-1984; LSU = 1985-3195; rrnL= 3196-3738; Wg =3739-4222; cox1= 4223-5020. The large ribosomal RNA subunit (rrnL) amplified for the species *Recchia acutipennis* and *R. albicans* were deposited in GenBank under accession number: OM867660 and OM839759 respectively.

The aim of this work was not to test the evolutionary relationship of the tribes of Lamiinae, which was efficiently done by Souza et al. (2020). Instead, we propose a time estimation hypothesis for the groups used by Souza *et al.* (2020), both to have some temporal information about the Hemilophini+Aerenicini clade, and to know the divergence time for the Lamiinae lineages.

In general, the relationship among several clades proposed by Souza *et al.* (2020) was corroborated (*e.g.* Acanthocinini+Acrocinini and Acanthoderini; Agapantini and relatives; Lamiini and relatives and the relationship between Aerenicini and Hemilophini). Possible discrepancies may be due to missing data, from some markers, different search parameters or because the addition of some taxa (for details about the relationship of the tribes, see Souza *et al.,* 2020). Even with only one mitochondrial marker (16S), the genus *Recchia*, previously represented only by *R. hirticornis* in Souza et al. (2020), was retrieved as monophyletic and sister group of *A. versicolor* + others Hemilophini. The origin of *Recchia* was estimated at in 20 Ma ca., and the clade Aerenicini+Hemilophini would have appeared at about 40Ma in the Paleogene period.

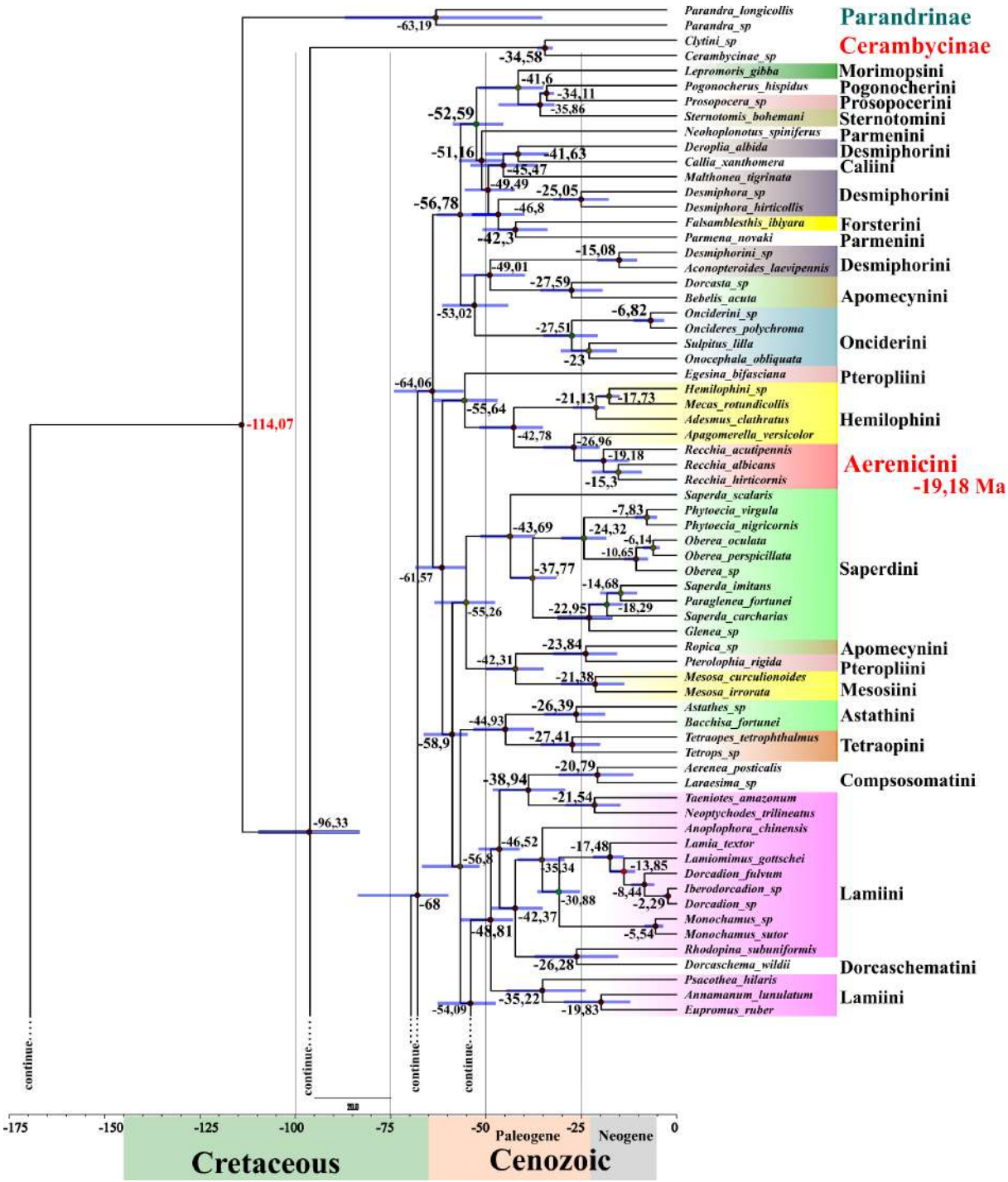

Figure 22. Part of fossil–calibrated Lamiinae timeline: MCMCTree estimates of lineage divergence times through Bayesian analysis and based on markers provided by Souza et al. (2020). The blue bars show 95% confidence intervals of the ages of the nodes and the scale bar is in millions of years (Ma).

Figure 23. Part of fossil–calibrated Lamiinae timeline: MCMCTree estimates of lineage divergence times through Bayesian analysis and based on markers provided by Souza et al. (2020). The blue bars show 95% confidence intervals of the ages of the nodes and the scale bar is in millions of years (Ma).

3.3. Biogeographic analysis results

The results of the BBM biogeographic analysis (Fig. 24) suggest 153 dispersal, 15 vicariance and 3 extinction events occurred in the evolution of Aerenicini. A scenario was recovered in which the CDG area would be the possible area of the ancestral population of Aerenicini (Fig. 27). This area is equivalent to the east coast of Brazil where today we have the Atlantic Forest. At node "103", in which the tribe is divided into two lineages, one of *Recchia* and relatives (node 59) and another with the other groups (node 102), in a scenario of diversification between the Amazon forest (Area E) and Atlantic Forest (CDE->CDE^C^D^E->CDE|CDE). This pattern of diversification would also have occurred in node "102", which separates the group of *Antodice* and relatives (node 69) and node 101, with the remaining groups. The dispersion of the lineages to Brazilian Northeast would have occurred from area D, which includes most of the Atlantic Forest (nodes 99; 98; 97). Lineages that occur in Central America (Area H) dispersed from two different routes: from area G, as in node 66, which includes *Antodice* and relatives, and another route from area D, as the group that includes the species of *Aerenicopsis* (Probable Route: D->BCDH->H|BCD Probability: 0.0255).

List of biogeographic events resulting from the Bayesian Binary Method (BBM)

NODE 54: Dispersal:0 Vicariance:0 Extinction:0 Event Route: D->D^D->D|D PROBABILITY: 0.8772

NODE 55: Dispersal:4 Vicariance:0 Extinction:0 Event Route: ADE->ADE^A^D^E->ACDE^A^D^E->ACDE|ADE PROBABILITY: 0.7512

NODE 56: Dispersal:2 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D->CDEG^D->CDG|DE PROBABILITY: 0.4950

NODE 57: Dispersal:5 Vicariance:0 Extinction:0 Event Route: CDE->CDE^C^D^E->ABCDE^C^D^E->ABCDE|CDE PROBABILITY: 0.3079

NODE 58: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D^E->ACDE^D^E->CDE|ADE PROBABILITY: 0.2797

NODE 59: Dispersal:1 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D->CDE|D PROBABILITY: 0.1614

NODE 60: Dispersal:5 Vicariance:1 Extinction:0 Event Route: D->ACDGH->AH|CDG PROBABILITY: 0.1996

NODE 61: Dispersal:2 Vicariance:0 Extinction:0 Event Route: DE->DE^D->BDE^D->BDE|D PROBABILITY: 0.0361

NODE 62: Dispersal:3 Vicariance:1 Extinction:0 Event Route: G->BEG->BG|E

PROBABILITY: 0.2754

NODE 63: Dispersal:4 Vicariance:2 Extinction:0 Event Route: G->G^G->BEG^G->G|BG|E PROBABILITY: 0.3335

NODE 64: Dispersal:3 Vicariance:1 Extinction:0 Event Route: E->BEG->EB|G PROBABILITY: 0.0643

NODE 65: Dispersal:3 Vicariance:2 Extinction:0 Event Route: DE->DE^E->BDEG^E->EB|G|DE PROBABILITY: 0.0078

NODE 66: Dispersal:4 Vicariance:1 Extinction:0 Event Route: G->DEGH->GH|DE PROBABILITY: 0.0173

NODE 67: Dispersal:1 Vicariance:1 Extinction:0 Event Route: DE->DEG->DE|G PROBABILITY: 0.0426

NODE 68: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CD->CD^D->CDEG^D->CDG|DE PROBABILITY: 0.1003

NODE 69: Dispersal:2 Vicariance:0 Extinction:0 Event Route: CDE->CDE^C->ACDE^C->ACE|CD PROBABILITY: 0.0957

NODE 70: Dispersal:3 Vicariance:1 Extinction:0 Event Route: CDE->ABCDEG->ABCDE|G PROBABILITY: 0.1347

NODE 71: Dispersal:2 Vicariance:0 Extinction:0 Event Route: CDG->CDG^D->CDEG^D->CDEG|D PROBABILITY: 0.3366

NODE 72: Dispersal:2 Vicariance:1 Extinction:0 Event Route: CDG->ACDEG->DG|ACE PROBABILITY: 0.2298

NODE 73: Dispersal:4 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D->ACDEGH^D->ACDGH|ED PROBABILITY: 0.2568

NODE 74: Dispersal:2 Vicariance:0 Extinction:0 Event Route: DEG->DEG^G->CDEG^G->G|CDEG PROBABILITY: 0.3261

NODE 75: Dispersal:2 Vicariance:0 Extinction:0 Event Route: DEG->DEG^D^E->DE|DEG PROBABILITY: 0.1419

NODE 76: Dispersal:3 Vicariance:0 Extinction:0 Event Route: DEG->DEG^D^E->CDEG^D^E->DEG|CDE PROBABILITY: 0.0487

NODE 77: Dispersal:5 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D^E^G->BCDEG^D^E^G->BCDEG|DEG PROBABILITY: 0.1519

NODE 78: Dispersal:3 Vicariance:0 Extinction:1 Event Route: DEG->DE->DE^E->ACDE^E->AE|CDE PROBABILITY: 0.1067

NODE 79: Dispersal:3 Vicariance:0 Extinction:1 Event Route: CDG->DG->DG^D^G-

>DEG^D^G->DG|DEG PROBABILITY: 0.1038

NODE 80: Dispersal:4 Vicariance:0 Extinction:1 Event Route: DEG->DG->DG^C^D^G->CDG^C^D^G->CDG|CDG PROBABILITY: 0.0254

NODE 81: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDG->CDG^D^G->CDEG^D^G->DEG|CDG PROBABILITY: 0.0381

NODE 82: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDG->CDG^C^D->CDEG^C^D->CDG|CDE PROBABILITY: 0.0104

NODE 83: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D^E->BCDE^D^E->BDE|CDE PROBABILITY: 0.4554

NODE 84: Dispersal:2 Vicariance:0 Extinction:0 Event Route: BCD->BCD^B->BCDE^B->BCD|BE PROBABILITY: 0.2482

NODE 85: Dispersal:4 Vicariance:1 Extinction:0 Event Route: D->BCDH->H|BCD PROBABILITY: 0.0255

NODE 86: Dispersal:1 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D->D|CDE PROBABILITY: 0.0126

NODE 87: Dispersal:4 Vicariance:0 Extinction:0 Event Route: CDG->CDG^G->ACDEGH^G->ACDEG|GH PROBABILITY: 0.2968

NODE 88: Dispersal:4 Vicariance:1 Extinction:0 Event Route: D->BDEG->EB|DG PROBABILITY: 0.4674

NODE 89: Dispersal:2 Vicariance:1 Extinction:0 Event Route: D->DG->D|G PROBABILITY: 0.6750

NODE 90: Dispersal:2 Vicariance:0 Extinction:0 Event Route: D->D^D->DEH^D->DEH|D PROBABILITY: 0.4296

NODE 91: Dispersal:1 Vicariance:0 Extinction:0 Event Route: BCD->BCD^A^B^C^D^E^F^G^H->ABCDEFGH^A^B^C^D^E^F^G^H->ABCDEFGH|ABCDEFGH PROBABILITY: 0.1035

NODE 92: Dispersal:2 Vicariance:0 Extinction:0 Event Route: D->D^D->BCD^D->D|BCD PROBABILITY: 0.0374

NODE 93: Dispersal:1 Vicariance:0 Extinction:0 Event Route: D->D^D->BD^D->BD|D PROBABILITY: 0.1607

NODE 94: Dispersal:0 Vicariance:0 Extinction:0 Event Route: D->D^D->D|D PROBABILITY: 0.1490

NODE 95: Dispersal:0 Vicariance:0 Extinction:0 Event Route: D->D^D->D|D PROBABILITY: 0.0959

NODE 96: Dispersal:2 Vicariance:1 Extinction:0 Event Route: D->BD->B|D PROBABILITY: 0.0988

NODE 97: Dispersal:2 Vicariance:0 Extinction:0 Event Route: DG->DG^D->CDG^D->D|CDG PROBABILITY: 0.0218

NODE 98: Dispersal:2 Vicariance:0 Extinction:0 Event Route: DG->DG^D^G->DG|DG PROBABILITY: 0.1081

NODE 99: Dispersal:2 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D->CDEG^D->DG|CDE PROBABILITY: 0.0160

NODE 100: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDE->CDE^C^D->CDEG^C^D->CDE|CDG PROBABILITY: 0.0085

NODE 101: Dispersal:2 Vicariance:0 Extinction:0 Event Route: CDE->CDE^D->ACDE^D->AD|CDE PROBABILITY: 0.0460

NODE 102: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDE->CDE^C^D^E->CDE|CDE PROBABILITY: 0.0174

NODE 103: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDE->CDE^C^D^E->CDE|CDE PROBABILITY: 0.0262

NODE 104: Dispersal:3 Vicariance:0 Extinction:0 Event Route: CDG->CDG^C^D->CDEG^C^D->CDG|CDE PROBABILITY: 0.1116

NODE 105: Dispersal:9 Vicariance:0 Extinction:0 Event Route: CD->CD^C^D^G->ABCDEFGH^C^D^G->ABCDEFGH|CDG PROBABILITY: 0.0498

Global Cost: Global Dispersal: 153; Global Vicariance: 15; Global Extinction: 3

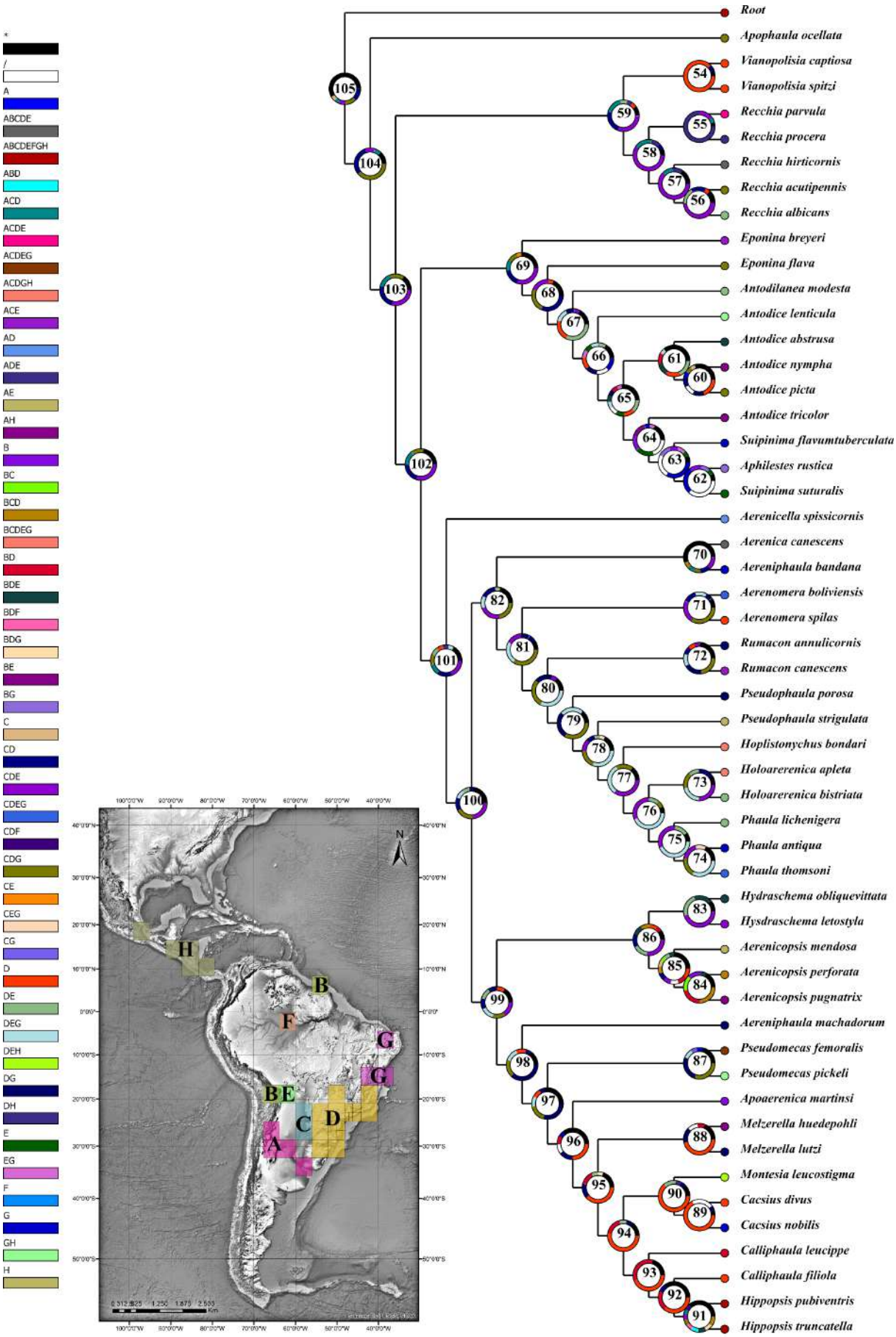

Figure 24. Result of biogeographic analysis representing ancestral distribution hypotheses based

on the Aerenicini phylogeny proposed here using the Bayesian binary MCMC (BBM) analysis. The numbers correspond to the cladogram nodes, and the colored circles correspond to the hypothetical ancestral area of each node. Circles with more than one color indicate more than one possibility of ancestral distribution. The letters before the terminal taxon names represent the current distribution according to bioregions.

4. DISCUSSION

4.1. On Aerenicini vs Hemilophini

Although, Aerenicini was retrieved as paraphyletic, with the current taxonomic changes (transference of *Phoebemima* and *Antonerella marginalis* gen. nov.), it is possible to distinguish Aerenicini from Hemilophini. Apparently, there were a series of changes in the body shape of the current Aerenicini species, which may be related to nocturnal habits and the type of host plant, which for many species is shrubby. The evolution of the body pattern of some groups (*i.e. Hyppopsis* and *Aerenicopsis*) may be linked to adaptations to they host plant.

Groups with non-composed tarsal claws (Pteropliini, Forsteriini) were retrieved as more related to groups with composed tarsal claws, whose species come from North, Central America and West Indies (Saperdini and Caliini). The Saperdini species analysed in this work, comes from the Old World and this indicates that Saperdini's bifid claws evolved separately from those of Aerenicini and Hemilophini. The results of the molecular analysis by Souza *et al.* (2020), also point to this scenario.

Regarding *Hippopsis*, Thomson (1860) proposed the group HIPPOPSITAE, whose type genus is *Hippopsis*, for several genera currently allocated in Agaphantini Mulsant (1839). Some authors (*i.e.* Lacordaire, 1872; Pascoe, 1866) separate Agapanthiini Mulsant (1839) from Hippopsini Thomson, 1860 by the antennae with 12 antennomeres, while in Hippopsini the antennae have 11 antennomeres. However, Breuning (1962) when revised the group, synonymized Hippopsini with Agapanthiini (which included groups with 12 antennomeres). The similarity of *Hippopsis* with some genera of Aerenicini is notorious. A good example is the genus *Aerenicopsis* Bates, 1885 (Aerenicini) which was described by Breuning (1940, 1974) based in two genera of Agapanthiini: *Falsohippopsis* Breuning, 1940 and *Falsohippopsoides* Breuning, 1974. According to Galileo & Martins (2010), this occurred with several groups revised by Breuning, because this author did not study the shape of tarsal claws of specimens (a feature so important for the taxonomy of the family). These convergences (similarity in body shape) are probably associated with the host plant, which in general are herbaceous in both groups, in other words, plants without woody stems and with small diameter.

The species *Aerenicopsis championi*, as already mentioned, is used to control *Lantana camara* (Verbenaceae). In *Hippopsis*, Giacomel (1989), described immatures of *Hippopsis quinquelineata* Aurivillius 1920, in which it attacks the fern species *Didymochlaena truncatula* (Sw.) J.Sm. (Didymochlaenaceae). When describing the life cycle of *Hippopsis lemniscata* (Fabricius), Piper (1977) comments that adults attack *Ambrosia artemisiifolia* L. (Asteraceae).

The genus *Hippopsis* has divergent tarsal claws, and is currently composed of 45 species distributed in Americas. The group has a troubled taxonomic history and is morphologically quite heterogeneous. *Hippopsis* was reviewed in detail by Galileo & Martins (1988a, b, c, d, e) who divided it into seven groups. According to the results by Souza et al. (2020), who used two specimens of *Hippopsis* identified only at generic level (*Hippopsis* sp.), Agaphantini was retrieved as monophyletic only in the bayesian analysis. Our results indicate that Agaphantini is a polyphyletic group. However, due to low representativeness, we prefer not to propose any taxonomic changes. A phylogenetic study focused on Agaphantini, could clarify the evolution of this group and help its classification. In summary, although our results group the species of *Hippopsis* and Aerenicini, we believe that this result is because *Hippopsis* is an extremely modified group with several convergences with Aerenicini. In this case, a study with molecular data, combined with morphology will be mandatory. As the results by Souza et al. (2020) and previous authors suggest, we also believe that Agaphantini needs to be separated.

As previous authors have already pointed out, there were profound changes in the ocular lobes (larger and coarsely faceted) in Aerenicini, but we also identified a change in the shape of genitalia. Regarding Hemilophini, although this tribe is not the focus of our work, it is worth making some comments about its current classification. When reviewing the South American species, Martins (2014a, 2014b) delimited six groups of genera defined as follows:

GROUP A - genera whose species have appendiculate and divaricate tarsal claws.

GROUPB - genera whose species have 12 antennomeres.

GROUP C - genera whose species have elytra widened to the sides:

GROUP D - genera whose species have convex elytra and without carina.

GROUP E - genera whose species have single carina on each elytron.

GROUP F - genera whose species have two carinae on each elytron.

Lacordaire (1868) in his memorable work "Genera des Coléoptères" indicated that a rigorous definition of Cerambycidae would hardly be possible in view of the morphological variation of the group (translated): “The only clear idea it brings to mind is that of an extreme variability of all the organs. Such is, in fact, the particular condition in which the Longicorns

find themselves and which makes their systematic arrangement the most arduous and thankless task". Several modern studies highlight the chaotic and deficient classification in Cerambycidae (Svacha & Lawrence, 2014; Haddad & McKenna, 2016). Currently, some molecular studiesalso demonstrate this chaos at tribal level (*i.e.* Souza *et al.*, 2020; Ashman *et al*.,2022). According to Souza *et al.* (2020) the convergent state for the characters currently used in tribal classification may indicate the non-monophily for the most specious groups, especially due to their disjunct distribution. Souza *et al*. (2020) also made some interesting considerations regarding the current tribal classification in Lamiinae: "The systematics of Cerambycidae still relies on typological criteria...The taxonomists working on this group have not fully embraced phylogenetic systematics yet, despite the early advice of authors like Lameere (1901) to incorporate the evolutionary history in the classification of these beetles..." However, in the same work, dealing with the clade Hemilophini+Aerenicini, the authors comment: "since our datasets do not include any representative of the type genera of Aerenicini and Hemilophini, we do not formalize their synonymy". While criticizing the "typological criteria", this comment also demonstrates that the authors approve it. As mentioned, both tribes (especially Hemilophini) are very specious and the simple synonymy between them could hide an entire evolutionary history of its lineages, as demonstrated in this work. From our perspective, this would be a mere adventure of current and "modern Gilmoures".

Instead of synonymizing groups with a large number of species, without a detailed study and with a good representativeness, we prefer to keep the current classification. The two main arguments that support our point of view are operational and theoretical. The first is related to the feasibility of studies, especially taxonomic revisions, since the creation of these large groups, can worsen the condition of a "taxonomic wastebasket". For Plotnick & Wagner (2006), systematic or taxonomic wastebaskets: "are the results of inadequate systematic research. In particular, they reflect a lack of adequate description and analysis of diagnostic characters and their distributions. They are often identified on the basis of plesiomorphies, homoplasies, or the lack of diagnostic characters found in related forms. Further research might break them down into multiple well-defined rates; however, incomplete redefinition of supraspecific taxa in taxonomic revisions can create wastebaskets if numerous taxa are not reclassified when establishing new, well-diagnosed rate". The second argument runs counter to the branching pattern of evolution. It makes no sense to artificially synonymize specious groups, since they probably contain several natural subgroups that should be further studied. Obviously, classifying and naming all clades in a phylogenetic analysis is an almost impossible task for the

current Linnaean classification system. However, synonymizing specious groups without a detailed study, makes this task even more difficult.

As noted by Bates (1881), the Aerenicini groups (with few exceptions) are not supported by unambiguous synapomorphies, instead by combinations of discrete and continuous characters. These ambiguous synapomorphies can only be better understood after a phylogenetic analysis, as a novelty revealed *a posteriori*. This phenomenon (ambiguous synapomorphies) may indicate some degree of convergence under the effect of natural selection in Aerenicini and may generate a background for future research (Sanderson & Hufford, 1996). Of course, the results of a cladistic analysis can be negatively influenced by "bad primary homology assumptions" and/or poor selection of OTUs. The evolutionary importance that we refer, is under a genuine and judicious research. Furthermore, we consider that a synapomorphy is also a historical event, since the conditions that led to that condition to appear or reappear (such as reversal) have caused a unique and exclusive effect for that clade at a certain point in its evolutionary history. Therefore, synapomorphy as an exclusive derivative character shared by two or more taxa does not mean that it is a unique and exclusive phenotypic or genotypic expression. However, the synapomorphies (discrete and continuous) retrieved in the present work, will help in the classification of new taxa and will support further studies.

4.2. Why are they distributed in this way?

Currently, the Atlantic Forest and Amazonian are separated by the dry diagonal area, that extends from Brazilian Northeast to Argentina (Vanzolini, 1963), which acts as a barrier for many groups of plants and animals (Ledo & Colli, 2017). However, several studies, based on taxa distribution, support the thesis of ancient connections between Amazonian (AM) and Atlantic Forest (AF) (Ledo & Colli, 2017). These connections were corroborated by Sobral *et al.* (2015) who conducted a study based on ecological niche modeling (ENM) for the Last Glacial Maximum. Among these routes, the oldest and most significant for the current diversity would be the south-eastern — north-western bridge (SE — NW) (Bigarella *et al.*,1975; Ledo & Colli, 2017). According to Sobral *et al.* (2015): "During Paleogene the Neotropical region was mainly covered by rainforests, and ancient AM and AF were continuous and interconnected. The Andean uplift and drastic climate changes along the Eocene/Miocene resulted in the formation of a drier area separating AM from AF. However, multiple evidences have indicated recurrent connections between Neotropical rainforests during Quaternary". The

ancestral area recovered for Aerenicini is consistent with the distribution commented by Martins & Galileo (1998), where most species would be distributed between the 15th and 30th parallels. It is also equivalent to the distribution of the Atlantic Forest 21 Ma ago, recovered by niche modeling (Fig. xxx). Probably these recurrent connections acted in the diversification of several groups of Aerenicini.

During the geological evolution of the Amazon region, a series of climatic changes would have occurred that affected the evolution of both aquatic and terrestrial biodiversity. According to (Hoorn, 2006) some studies suggest a series of recurrent and immense flooded (Figs. 25, 26) areas, with both river and marina origins (from the Caribbean region). These wetlands would have, through the vicariance effect, acted in the diversification of some groups and/or served as a barrier for others (Ayres & Clutton-Brock, 1992; Colwell, 2000). These scenarios may explain the low diversity of Aerenicini in the Amazon region. The marine incursions in Amazon region would be the result of the "Paleocene-Eocene thermal maximum" (PETM) in which a significant increase in global temperature occurred in a brief period (∼150 kyr), especially due to volcanic activities (Sluijs *et al.,* 2011)

According to the GAARlandia (Greater Antilles and Aves Ridge) hypothesis, between 35 and 33Ma during the transition Eocene-Oligocene, due to the elevation of the Greater Antilles, together with low sea levels, the Antilles would form a bridge between northern South America and the Greater Antilles (Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999). It is noteworthy that the occurrence of Aerenicini, as well as other Cerambycidae groups, is directly related to the presence of host plants (Makino *et al*. 2007). Therefore, the current distribution pattern and the consequent evolution of Aerenicini is also related to their host plants whose diversity was the result of orogeny and climatic factors in South America, since the Middle Cretaceous (Jaramillo *et al.*, 2010).

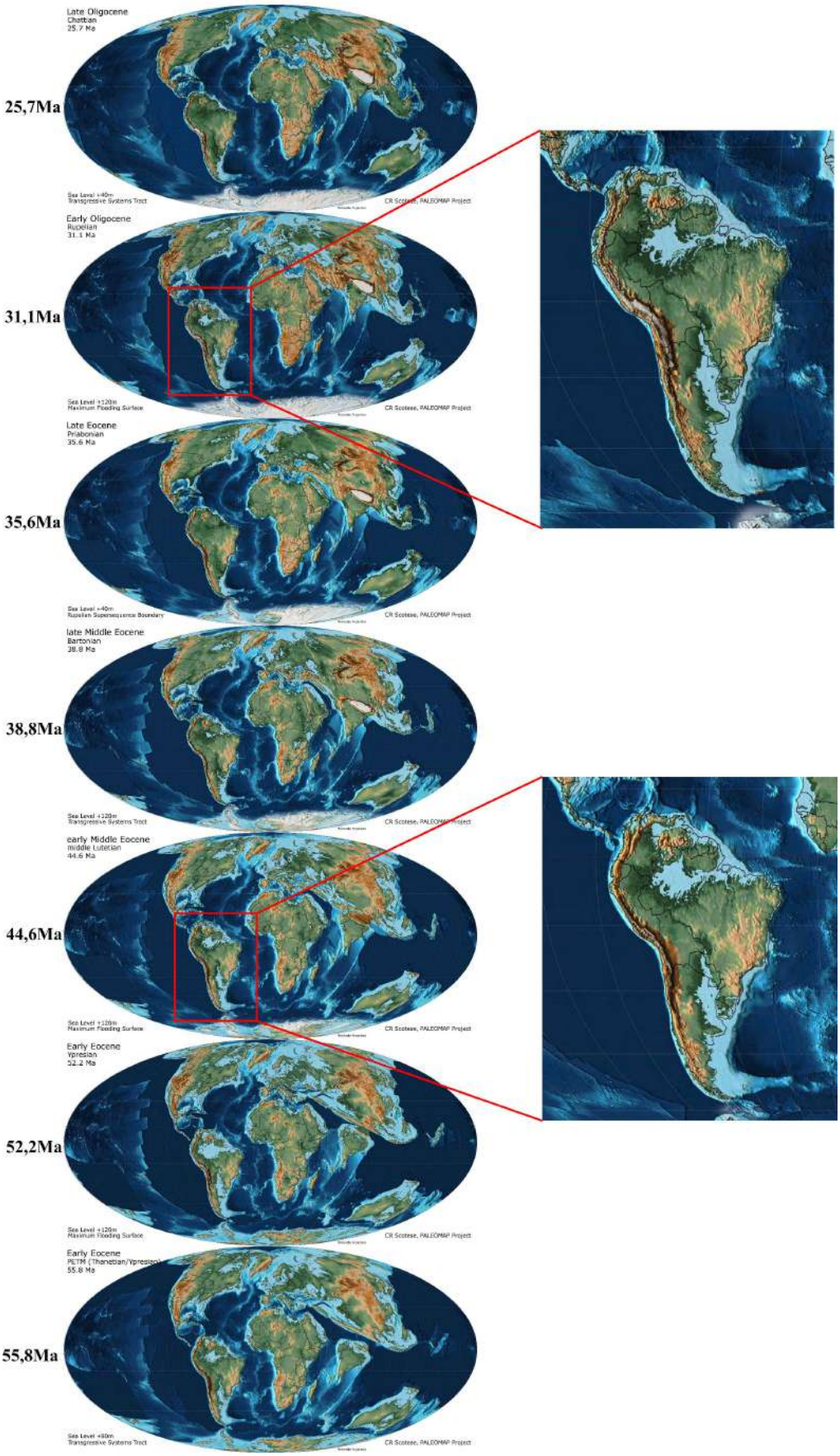

Figure 25. Cenozoic Plate Tectonic, Paleogeographic, and Paleoclimatic Reconstructions of Paleogene (from Scotese, 2014).

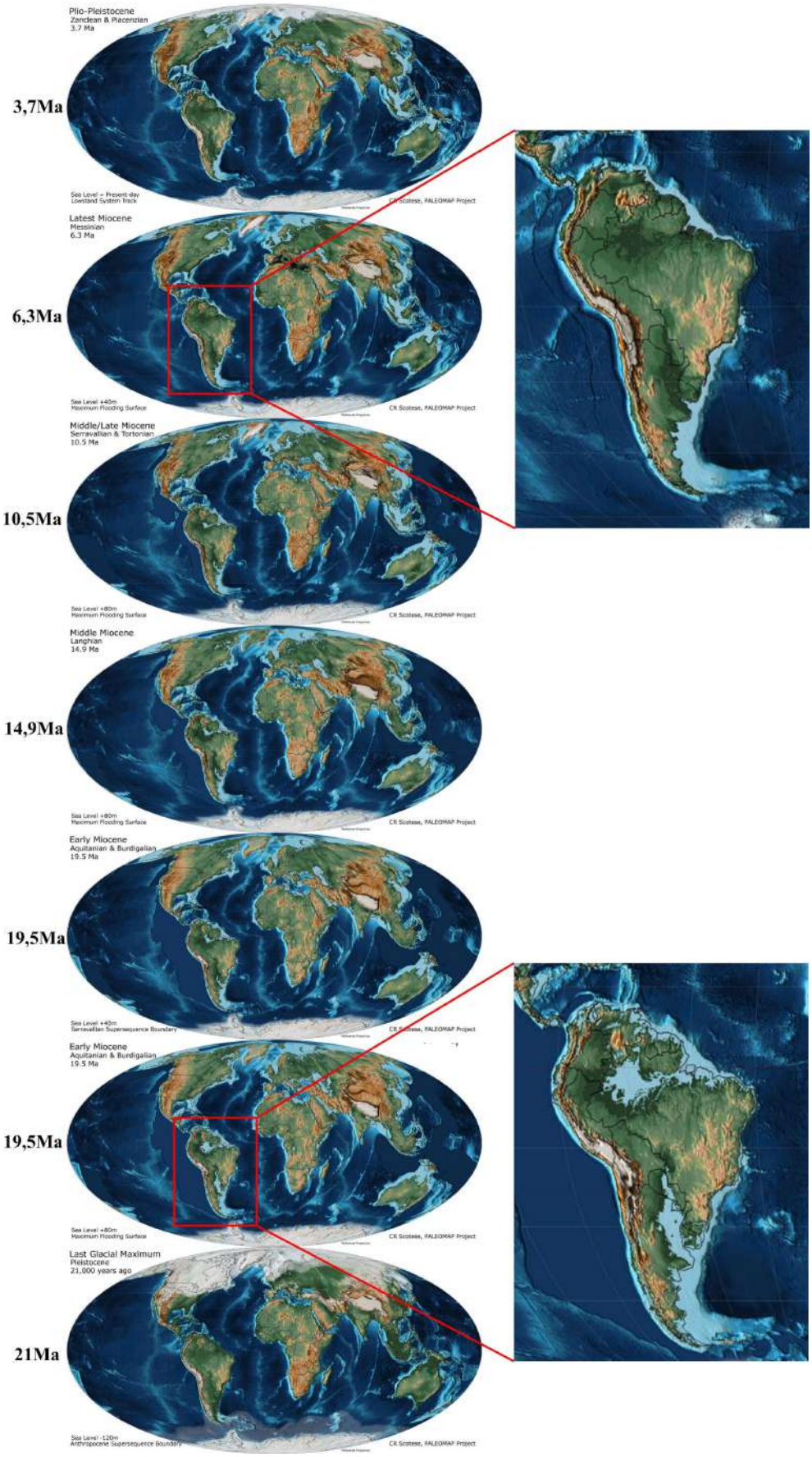

Figure 26. Cenozoic Plate Tectonic, Paleogeographic, and Paleoclimatic Reconstructions of Neogene (from Scotese, 2014).

Regarding the Central American groups, these probably had a more recent origin. According to O'Dea *et al.* (2016), the sea level dynamics and the consequent rise (acting as a bridge) or submersion (acting as a barrier) of the Panama isthmus affected the diversification of several terrestrial groups. Although with a lower diversity, the geomorphological dynamics of this area may have acted in the diversification of these groups. According to Halffter & Morrone (2017), elements from Neotropical and Nearctic biotas are mixed in a complex way in the Central America. When studying several taxa from the Western Hemisphere, especially from the Mexican Transition Zone (MTZ) fauna, Halffter (1974, 1978, 1987) proposed five faunal patterns. The distribution pattern of Aerenicini in this zone, has a "Typical Neotropical distributional pattern", which are groups with South America origin and with a distribution pattern influenced mainly by ecological factors (Halffter & Morrone, 2017). According to the classification presented by the same authors, Aerenicini groups would have a "Neotropical distributional pattern of wide penetration", in which the species colonized the lower lands reaching North America through the eastern coast (Fig.28 B).

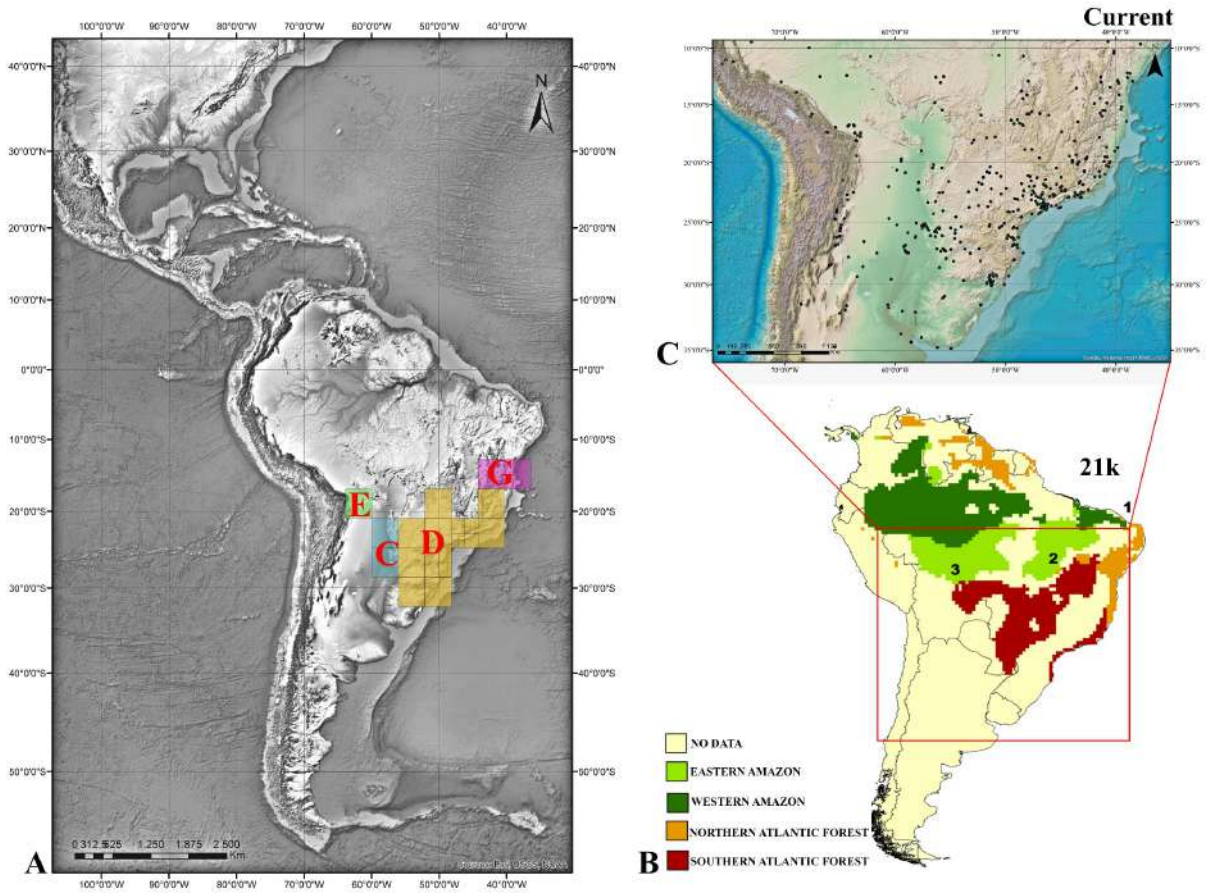

Figure 27. A, Bioregions of Aerenicini, retrieved through Infomap; B, 21 ka distribution models of Neotropical Rainforests proposed by Sobral *et al.* (2015); C, distribution map of Aerenicini species between the 10º and 35º parallels.

The dating result suggests a minimum age of at least 40 million years and we can infer that when populations reached the northern region of South America (previously impeded by the flooded Amazonian areas), the Antilles were already isolated by the ocean, preventing the dispersal of both plants and hosts. This would explain the absence of the group in the Antilles.

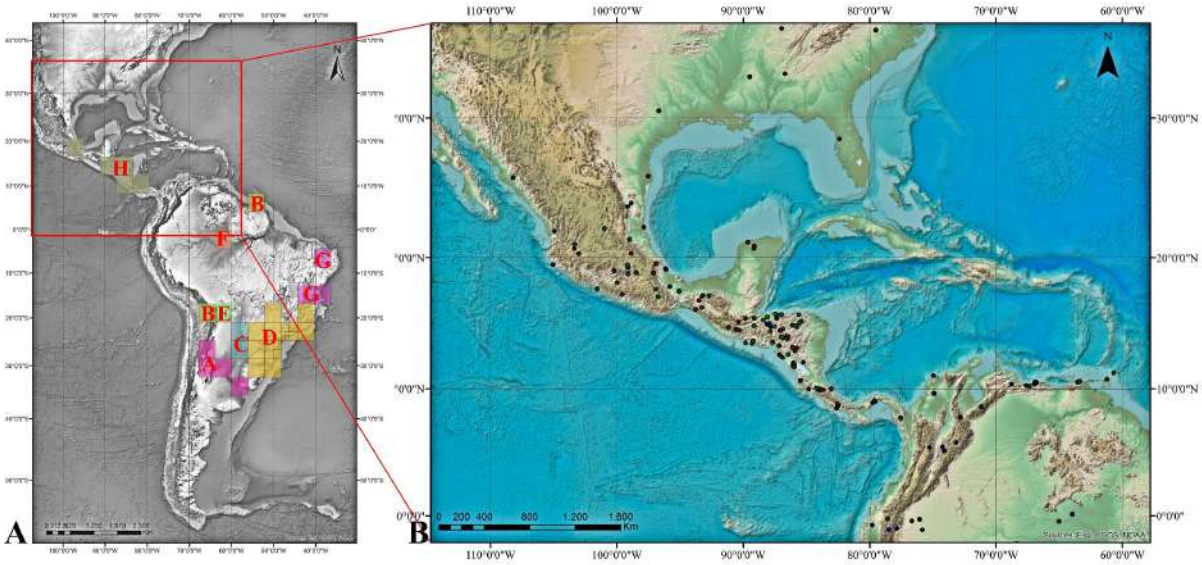

Figure 28. A, Bioregions of Aerenicini, retrieved through Infomap; B, geographic distribution map of Aerenicini species in Central America.

Ashman *et al.* (2022) carried out a study on the relationship of the Cerambycidae tribes of Australia. The authors presented a dated tree to Australian groups. Our dating result corroborate those of Ashman *et al.* (2022), in which several lineages of Lamiinae would have originated around 100Ma. According to Nie *et al.* (2021), who used full mitochondrial genomes to assess the evolution of Chrysomeloidea, Lamiinae would have its origin at about 130Ma. The diversification origin of several groups in our analysis occurred in the Upper Cretaceous (100.5 million to 66 million years ago). According to Jud *et al.* (2017), most known angiosperm wood fossils are dated to this period. In other words, the origin and diversification of Lamiinae groups from the Neotropical Region corresponds to the diversification of angiosperm wood. The study by Xing *et al.* (2015) suggests that in addition to a diversification of woody angiosperms in the Cenozoic, the distribution pattern of these groups was modeled especially by climatic factors.

Given their ancient origin and since they are the most diverse group of wood-feeding (xylophagous) known, it is not surprising that cerambycids have developed their plant cell wall degrading enzymes (PCWDEs) so effectively. For Shin *et al.* (2021), the evolution of the

PCWDEs of cerambycidae larvae evolved in a conservative way and have a strong phylogenetic signal. The host plants of several species of Aerenicini belong to the evolutionarily related Verbenaceae and Bignoniaceae families, both belonging to Lamiales order. These families diverged in the Late Cretaceous or early Tertiary and diversified especially in South America (Olmstead, 2013). Our data (estimation of divergence time and monophyly of several groups of Aerenicini) suggest that the diversification, as well as the distribution pattern of Aerenicini, may be directly associated with the evolution of their host plants.

Although we focused on understanding the evolution of Aerenicini and its subgroups, the results of this work could be a model for other groups, since the pattern of distribution and evolution of Aerenicini are congruent with other taxa, it is possible that this is one of the evolution patterns of the Neotropical Region. Overall, Aerenicini diversity was the product of a positive speciation–extinction balance over a long period of time, especially along the Brazilian east coast.

5. CONCLUSIONS

A study of Aerenicini species resulted in a matrix of 110 discrete and continuous characters and subsequent cladistic analysis revealed that the group is paraphyletic with the species of *Phoebemima* and *Antonerella marginalis* **gen. nov**. more closely related to Hemilophini. The genus *Hippopsis* (Agaphantini) was retrieved as more closely related to Aerenicini, however, we believe that this result is biased due to numerous evolutionary convergences. We conclude that a more detailed study of Agaphantini may clarify their classification. Our analysis also indicates that only discrete characters are not enough to understand the evolution of this group or separate it for taxonomic purposes. Aerenicini can be characterized by the convergent shape of aedeagus; an increase in scape length; general increase in the length of the antennomeres; decrease in humeral width; decrease in prothorax length and an increase in the lower eye lobes with a consequent reduction in genae. Many of these changes are probably linked to host plants and nocturnal habits adaptations. The following taxonomic changes are proposed: *Aerenica bandana* (Nascimento, Botero & Bravo, 2016) **comb. nov.**; *Antodice breyeri* (Prosen, 1954) **comb. nov.**; *Antodice eccentrica* Galileo & Martins, 1992 **stat. res.** ; *Antodice flava* (Lane, 1939) **comb. nov.**; *Antodice flavumtuberculata* (Nascimento, Botero & Bravo, 2016) **comb. nov.**; *Antodice lanuginosa* (Martins & Galileo, 1985) **comb. nov.**; *Antodice metuia* (Martins & Galileo, 1998) **comb. nov.**; *Antodice modesta* Lane, 1939 **stat. res.** ; *Antodice nigristernis* (Martins & Galileo, 1985) **comb. nov.**; *Antodice rustica* (Bates, 1881) comb. nov.; *Antodice mariahelenae* (Martins & Galileo, 2004) comb. nov.; *Hoplistonychus* Melzer, 1930, *Pseudophaula* Lane, 1973 and *Holoaerenica* Lane, 1973 = *Phaula* Thomson, 1857; *Phaula bondari* (Melzer, 1930) **comb. nov.**; *Phaula foersteri* Martins, 1984 **stat. res.**; *Phaula porosa* (Bates, 1881) **comb. nov**.; *Phaula pustulosa* (Lane, 1973) **comb.** nov.; Phaula strigulata (Lane, 1973) comb. nov.; Phaula alveolata (Martins, 1984) comb. nov.; *Phaula apleta* (Galileo & Martins, 1987) **comb. nov.**; *Phaula bistriata* (Lane, 1973) **comb. nov.**; *Phaula multipunctata* (Lepeletier & Audinet-Serville, 1825) **comb. nov.** and *Antonerella marginalis* (Martins & Galileo, 2004) **gen. nov.** The calibrated phylogeny of Lamiinae retrieved *Recchia* as monophyletic and sister group of *A. versicolor* + others Hemilophini. It was revealed that several groups arose during upper Cretaceous with an expressive diversification in the Cenozoic and that climatic changes that occurred in this period would have affected the evolution of both woody angiosperms and Lamiinae. The biogeographic analysis suggests that the evolution of the main subgroups of Aerenicini occurred in the South and Southeast regions of Brazil, in the area mentioned by Martins (1998) (between the 15º and 30º parallels) as the most specious, and in part of Chaco. The current diversity was the product of a positive speciation-extinction balance over a long period of time, especially along the Brazilian east coast.

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