



**FRANCISCO ERIBERTO DE
LIMA NASCIMENTO**

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

**Análises cladística e biogeográfica de Aerenicini Lacordaire,
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Single Volume

SÃO PAULO

2022

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Original Version

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

Co-advisor: José Ricardo Miras Mermudes

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2022

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 mariaehelenae* (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 bistrinata* (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.

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; Nearn, 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 received due attention in his classification. Later, Thomsom (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 *Bifidunglenea* to Asian species in which the claws of all the tarsi in both sexes are bifid. According to Lin & Ge (2021), in *Tsounkranaglenea hefferi* 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 (36° 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 Amphionychides 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), Ærénicides are characterized especially 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 *Rumacoon 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 Lamiinae”. 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 Gilmour'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 *Recchia*) 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. spitzii* 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 acuminate 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	<i>Aerenomera</i> Gilmour, 1962 <i>Calliphaula</i> Lane, 1973 <i>Heterophaula</i> Lane, 1973 <i>Holoaerenica</i> Lane, 1973 <i>Paraphaula</i> Fuchs, 1963 <i>Phaula</i> Thomson, 1857 <i>Pseudophaula</i> Lane, 1973 <i>Hoplistonychus</i> Melzer, 1930
Group II: genera with short lower eyes lobes a) Elytral apex without two spines	<i>Eulachnesia</i> Bates, 1872 <i>Apagomera</i> Bates, 1881 <i>Apagomerella</i> Gilmour, 1962 <i>Pretilia</i> Bates, 1866 <i>Apagomerina</i> Gilmour, 1962 <i>Mariliana</i> Lane, 1970
b) Elytral apex with two spines	<i>Melzerelia</i> Lima, 1931
Group III: Genera with subcontiguous upper eyes lobes and acuminate elytral apex	<i>Hydraschema</i> Thomson, 1864 <i>Aerenicopsis</i> Bates, 1885 <i>Falsohippopsoides</i> Breuning, 1974 <i>Corupa</i> Lane, 1966 <i>Hydraschemopsis</i> Lane, 1966
Group IV: Genera with subcontiguous upper eyes lobes (or very close) and rounded elytral apices	<i>Aphilesthes</i> Bates, 1881 <i>Antodilanea</i> Gilmour, 1962 <i>Antodice</i> Thomson, 1864 <i>Cacsius</i> Lane, 1973 <i>Propantodice</i> Franz, 1954
Group V: genera with separated upper eye lobes	<i>Aerenica</i> Dejean, 1835 <i>Apophaula</i> Lane, 1973 <i>Apoaerenica</i> Martins & Galileo, 1985 <i>Rumacon</i> Blackwelder, 1946 <i>Dolaerenica</i> Martins & Galileo, 1985 <i>Pseudomecas</i> Aurivillius, 1920 <i>Montesia</i> Lane, 1938 <i>Vianopolisia</i> Lane, 1966 <i>Melzaerenica</i> Lane, 1976 <i>Aerenicella</i> Gilmour, 1962 <i>Coruparana</i> Lane, 1966 <i>Recchia</i> Lane, 1966 <i>Eponina</i> 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 ferruginous... Proeustemum 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 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 *Pithecolobium 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.

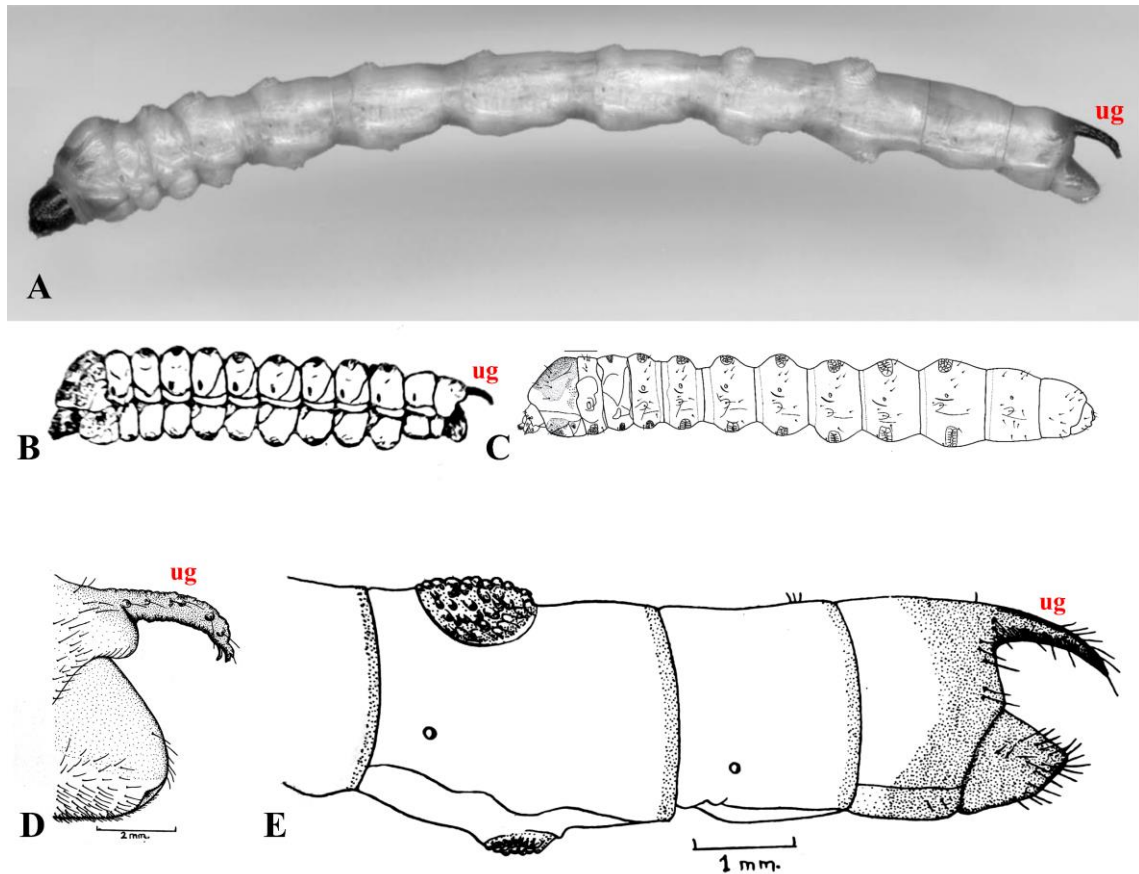


Figure 1. Larvae of Lamiinae in lateral view: A–B, Aerenicini species; A, *Aerenicopsis mendosa* Martins & Galileo, 1998 (from Svacha & Lawrence, 2014); B, *Hoplistonychus bondari* Melzer, 1930 (from Bondar, 1937); C, Hemilophini specie; C, *Phoebemima ensifera* Tippmann, 1960 (from Casari & Martins,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

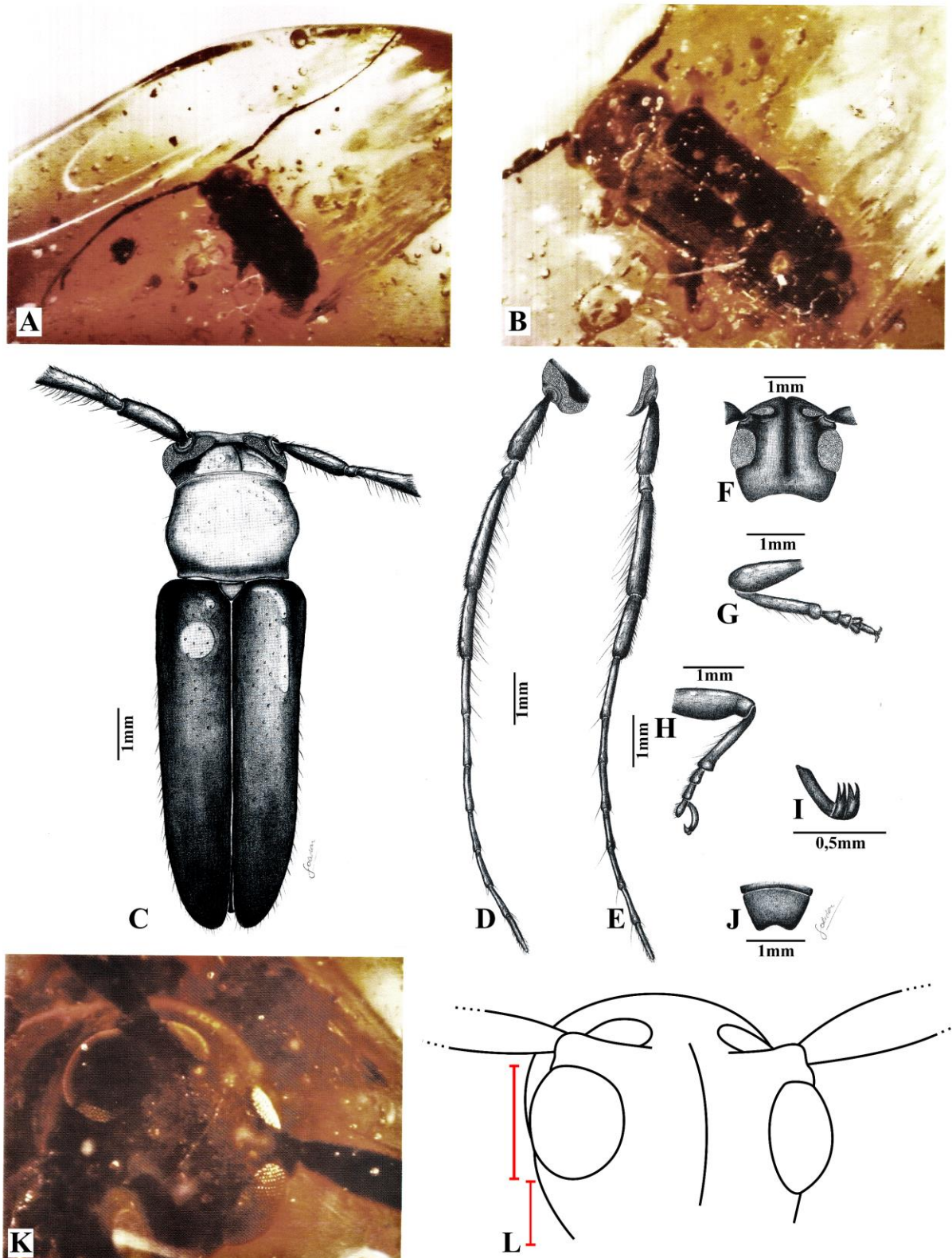


Figure 2. Fossil of *Paleohemilophus dominicanus* Martins & Galileo, 1999 holotype (adapted from Martins & Galileo, 1999): A, habitus in dorsal view, in amber; B, dorsal view amplified; C, habitus dorsal, drawing; D, left antenna; E, right antenna; F, head in frontal view; G, front leg; H, middle leg; 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 synonymized 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.

3. 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 mariahenae* (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 bistrinata* (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 15° and 30° 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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