



KIMBERLY PAOLA
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**Cladistic analysis and taxonomic
revision of *Caciomorpha* Thomson,
1864 (Coleoptera, Cerambycidae,
Lamiinae, Anisocerini)**

Análise cladística e revisão taxonômica de
Caciomorpha Thomson, 1864 (Coleoptera,
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Dissertation 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 Master of Science (Systematics, Animal Taxonomy and Biodiversity).

Advisor: Prof. Dr. Sonia Casari

Co-Advisor: Dr. Juan Pablo Botero

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RESUMO

Uma análise filogenética e revisão taxonômica do gênero *Caciomorpha* Thomson, 1864 foi feita para provar a monofilia do grupo, corroborar a validade das espécies, criar uma chave taxonômica para sua identificação, e expandir o conhecimento atual da sua distribuição geográfica. Para lograr esses objetivos, uma análise cladística com pesagem igualitária e pesagem implícita foi feita, utilizando a parcimônia como critério de otimalidade. Após obter os resultados, o gênero e as espécies foram redescritos e uma chave taxonômica foi criada. *Caciomorpha* foi recuperado como parafiletico em relação aos gêneros *Parachalastinus* Galileo & Martins, 2001, *Phacellocera* Laporte, 1840 e *Chalastinus* Bates, 1862, sendo a espécie *Caciomorpha buquetii* (Guérin-Méneville, 1844) o grupo-irmão deles e das restantes espécies de *Caciomorpha*. Para recuperar a monofilia de *Caciomorpha* um novo gênero foi proposto, *Amazomorpha* **gen. nov.**, para incluir *C. buquetii*. Adicionalmente, toda a variabilidade observada nas espécies foi descrita e permitiu reconhecer que *C. palliata* (White, 1855) e *C. susua* (Martins & Galileo, 1996) são sinônimas, assim como descrever uma nova espécie da Colômbia, *C. colombiana* **sp. nov.** Mapas de distribuição para o gênero e suas espécies foram feitos, os quais demonstraram que todas as espécies do gênero ocorrem na região Andina, com *C. batesii* (Pascoe, 1858) e *C. robusta* Galileo & Martins, 1998 ocorrendo também na região amazônica, *C. palliata* na Mesoamerica e *C. plagiata* (Bates, 1875) ocorrendo também no Cerrado e Chaco. O levantamento das localidades do material examinado permitiu encontrar novos registros de distribuição geográfico para às espécies. Este estudo representa a primeira análise filogenética do gênero, usando características antes não usadas, como peças bucais, veação alar e terminalia feminina e masculina. Com os resultados do presente trabalho, *Caciomorpha* é confirmado como um gênero válido contendo seis espécies. Adicionalmente é fornecida uma chave para essas espécies, redesccrições, ilustrações e mapas de distribuição geográfica de todas as espécies.

Keywords: Serra-pau, Neotropical, filogenética, redesccrições, sinônimos.

ABSTRACT

A phylogenetic analysis and taxonomic revision of the genus *Caciomorpha* Thomson, 1864 was performed in order to prove the monophyly of the group, corroborate the validation of its species, provide a taxonomic key to the species of the genus, and to expand the current knowledge of its geographical distribution. To achieve these objectives, a cladistic analysis, with both equal weighting and implied weighting was performed, using parsimony as optimality criterion. After obtaining the results, the genus and its species were redescribed, and a taxonomic key was created. *Caciomorpha* was recuperated as paraphyletic in relation to the genera *Parachalastinus* Galileo & Martins, 2001, *Phacellocera* Laporte, 1840 and *Chalastinus* Bates, 1862, with *Caciomorpha buquetii* (Guérin-Méneville, 1844) as sister group of them, and all remaining *Caciomorpha* species. In order to recuperate the monophyly of *Caciomorpha*, a new genus was proposed, *Amazomorpha* **gen. nov.**, to include *C. buquetii*. Additionally, all variability observed in the species was described, and allowed to recognize that *C. palliata* (White, 1855) and *C. susua* (Martins & Galileo, 1996) are synonyms, and to describe a new species from Colombia, *C. colombiana* **sp. nov.** Distribution maps for the genus and its species were made, showing that all species occur in the Andean region, with *C. batesii* (Pascoe, 1858) and *C. robusta* Galileo & Martins, 1998 also occurring in the Amazon region, *C. palliata* in Mesoamerica and *C. plagiata* (Bates, 1875) also occurring in the Cerrado and Chaco. The gathering of localities from the examined material allowed to find new records of geographical distribution of the species. This study represents the first phylogenetic analysis for the genus, using novel features such as mouth pieces, wing venation and male and female terminalia. With the results of this work, *Caciomorpha* is confirmed as a valid genus containing six species. Additionally, it is provided a key to those species, redescrptions, illustrations, and geographical distribution maps for all the species.

Keywords: Longhorned beetle, Neotropical, phylogenetic, redescrptions, synonyms.

INTRODUCTION

Cerambycidae is one of the largest and most diverse families of Coleoptera, with about 40,000 described species around the world (Botero, 2018; Tavakilian & Chevillotte, 2021). According to Bezark (2022) there are over 11,000 species and 1,971 genera covering the western hemisphere, including the Caribbean arc.

The morphology of adults is extremely variable: the body length varies from 2 mm to 17 cm; the body form could be cylindrical, parallel sided, strongly dorsally flattened, or even circular shaped; the surface can be glabrous or pubescent, smooth or with punctures; the tegument can be of bright colors or very dark and cryptic (Švácha & Lawrence, 2014); the head exposed, hypognathous or prognathous (Hangay & Zborowski, 2010), with prominent mandibles. Although the great variability of body shapes, the family is mainly defined by well-developed antennae, from $\frac{1}{4}$ to three times the body length, hence their common names longhorned beetles, longicorns and capricorns. Other characteristics of the family commonly used are the antennae inserted in tubercle; eyes entire or divided, kidney-shaped; two apical spurs on tibiae (Triplehorn & Johnson, 2005); and pseudotetramerous tarsi. However, these characteristics have shown to be variable in some groups, and the last one is shared with Chrysomeloidea.

Regarding to the diet, most of the Cerambycidae larvae are xylophagous (Švácha & Lawrence, 2014), feeding on wood of plants which may be living or decayed (Hangay & Zborowski, 2010; Švácha & Lawrence, 2014). Therefore, there is an important ecological function associated to this family, such as degradation and decomposition of organic material, participating in the biological recycling of these materials (Švácha & Lawrence, 2014). Adults present variable and specific requirements, feeding on sap, leaves, blossoms, fruit, bark and fungi, and even sometimes only water (Švácha & Lawrence, 2014).

Cerambycidae feeding habits closely relate them to their host plants, bringing an economic importance to the family, because some of them are considered to be pest of forestry and horticulture (Hangay & Zborowski, 2010). Most of the species considered as pest attacks during the larval stage, mainly from the subfamilies Cerambycinae and Lamiinae (Švácha & Lawrence, 2014), but adults can also contribute to the damage, as they chew into bark and wood to feed and oviposit (Martinez, 2000).

Napp (1994) performed the first phylogenetic analysis using cladistic methodology for Cerambycoidea complex and considered nine subfamilies:

Anoplodermatinae, Parandrinae, Prioninae, Spondylidinae, Lepturinae, Aseminae, Cerambycinae, Lamiinae and Philinae. Also, that study allowed to identify Disteniidae as sister group of Cerambycidae. Later, Švácha *et al.* (1997) transferred Anoplodermatinae to Vesperidae, and mentioned a close relation between Vesperinae and Philinae. Bouchard *et al.* (2011) revised the family-group names in Coleoptera, and listed in Cerambycidae the following subfamilies: Apatophyseinae, Cerambycinae, Dorcasaminae, Lamiinae, Lepturinae, Necydalinae, Parandrinae, Prioninae and Spondylidinae. They listed Aseminae as a tribe in Spondylidinae. Currently, the most accepted classification is that presented by Švácha & Lawrence (2014), including eight subfamilies: Prioninae, Parandrinae, Dorcasominae, Cerambycinae, Spondylidinae, Necydalinae, Lepturinae and Lamiinae. Recently, Yan-Qun *et al.* (2018) in a molecular phylogeny of Chrysomeloidea (using mitochondrial DNA), established a well-supported relation between the subfamilies Cerambycinae and Prioninae, and the monophyly of Lamiinae.

Lamiinae Latreille, 1825 is the largest and most diverse subfamily in Cerambycidae, with 86 tribes, 3,009 genera and 21,461 species (Tavakilian & Chevillotte, 2021), containing more than half of the described Cerambycid species. Many Lamiinae species are considered to be of economic importance, especially in the tropics where they are particularly diverse.

The adults of Lamiinae have an extremely variable morphology, and some of their synapomorphies, according to Švácha & Lawrence (2014), are: “perpendicular frons, narrow and aciculate terminal palpal segment, presence of the antennal cleaner of the anterior tibiae, asymmetrical morphology of the mesoscutal stridulatory plate, obliquely sulcate anterior tibiae, and the unique protuberant bilobed basal sclerite of the tibial flexor apodeme”. Regarding the larval stage, they could be cylindrical or flattened (Švácha & Lawrence, 2014), and they could be apodes or have minute legs. They can be found in almost all biogeographic regions, except for Antarctica, and from sea level to 4,000 m (Monné *et al.*, 2017).

The monophyly of Lamiinae had been tested over the years using phylogenetic approaches such as the ones performed by Napp (1994), who used morphological characters; Raje *et al.* (2016), using partial sequences from two mitochondrial genes (*rrnS* and *cox1*); Haddad *et al.* (2018), using phylogenomic data from 522 single copy nuclear genes generated via anchored hybrid enrichment; Souza *et al.* (2020), using fragments of two mitochondrial and three nuclear markers (*cox1*, *rrnL*, *Wg*, *CPS* and *LSU*); and

Ashman *et al.* (2021), using phylogenomics. All of them corroborated the monophyly of Lamiinae.

According to Bouchard *et al.* (2011), Lamiinae is separated in 80 tribes, representing an extremely rich tribal subdivision. However, this classification is considered as artificial, and only based in arbitrary characters of adults (Ślipiński & Escalona, 2013). Therefore, tribal and even generic relationships remain largely unexplored (Souza *et al.*, 2020; Ashman *et al.*, 2021).

Currently, the tribe Anisocerini Thomson, 1860 contains 26 genera and 86 species, distributed in North, Central and South America (Tavakilian & Chevillotte, 2021; Bezark, 2022). Thomson (1860) characterized the tribe as follows (translated): “short body, sometimes rounded-shaped; wide head, frons long and flat; distant antennae, 1st article clavated, 3-4th articles dilated; prothorax usually with lateral spines; procoxal cavities entire, angulose laterally; femora clavated; tibiae sometimes flattened and expanded apically; tarsi short and robust”. Thomson (1864) briefly mentioned the tribe (divided into Anisoceritae and Onychoceritae), and provided a key for the genera. Later, Lacordaire (1872) reviewed the group (as Anisocérides), provided a new key to genera and described the tribe Platysternini (as Platysternides). Posteriorly, Lane (1973) proposed the synonymy of Platysternini Lacordaire, 1872 and Acanthomerosternoplioni Tippman, 1955 with Anisocerini.

After that, Linsley & Chemsak (1984) characterized the adults of Anisocerini by the following characters: “head not retractile, frons rectangular; eyes finely faceted, deeply emarginated; palpi unequal, slender; antennae slender, often ten-segmented in females, scape abruptly clavate, shorter than third segment. Pronotum transverse, strongly to feebly tuberculate laterally; disk shallowly tuberculate; prosternum narrow, intercoxal process usually broad, coxal cavities closed behind, angulate externally; mesosternum with intercoxal process variable, often broad, coxal cavities open to epimeron; metasternum rather short. Elytra strongly convex near apex; base often shallowly bigibbose; epipleura almost vertical; apices rounded. Legs robust; femora clavate; middle tibiae with an external sinus; front tarsi broad; claws divaricate; abdomen with sternites two to four narrow.” They also mentioned some species having prominent tubercles or spines on the pronotum, and antennae with clavated segments or setae.

More recently, Julio (2003a, unpublished paper), in his doctoral thesis, did the taxonomic revision and the only phylogenetic analysis of the tribe. As result of the phylogenetic analysis, he grouped the genera into five groups: “1. *Trygonoepelus*; 2.

Thryallis + *Anisocerus*; 3. *Caciomorpha*⁺ (*Caciomorpha*, *Phacellocera* + *Phacellocerina*, *Chalastinus*, *Parachalastinus*, *Gounella* + *Fredlanella*); 4. *Onychocerus*⁺ (*Onychocerus*, *Demophoo*, *Hoplistocerus*, *Cyclopeplus* + *Chapareia*); 5. *Acanthotritus*⁺ (*Acanthotritus* + *Satipoella*, *Xylotribus* + *Batesbeltia*, *Jurua*, *Badenella*, *Gymnocerina*, *Eusthenomus* + *Platysternus*)". He also published a few works on some genera of Anisocerini, such as *Demophoo* Thomson, 1864, *Satipoella* Lane, 1964, *Phacellocerina* Lane, 1964, *Gymnocerus* Audinet-Serville, 1835, and *Anisocerus* Lacordaire, 1830. In these works, he included synopsis, revisions and keys, and established differences with other similar genera (Julio 2003b, 2003c, 2003d, 2003e, 2003f).

The tribe was also mentioned in some works such as Bradley (1930), in the manual of genera of beetles of North America, where it was provided a key to tribes of Lamiinae; the catalogues of Aurivillius (1923), Gilmour (1965), and Monné (1994), and more recently, in Bouchard *et al.* (2011) taxonomic list. It is clear that studies of the tribe are rare and outdated, and there is not much information about the biology, ecology or phylogenetic relationships among the genera and the species.

1.1 On the genus *Caciomorpha* Thomson, 1864

The genus *Caciomorpha* Thomson, 1864 is one of the largest on the tribe, comprising seven species: *Caciomorpha batesii* (Pascoe, 1858); *C. buquetii* (Guérin-Méneville, 1844); *C. genalis* (Aurivillius, 1909); *C. palliata* (White, 1855); *C. plagiata* (Bates, 1875); *C. robusta* Galileo & Martins, 1998; *C. susua* (Martins & Galileo, 1996). The genus is distributed mainly in South America, with only one species reported to Central America, from Guatemala to Colombia (*C. palliata*).

Caciomorpha was described by Thomson (1864), for one species, *Phacellocera batesii* Pascoe, 1858, from Pará, Brazil, and was characterized by (translated): "having a parallel-sided body; elongate head; antennae of males very long; scape robust, long and clavate; antennomere III long, robust, and with dilated apex on internal margin; prothorax with lateral tubercles; apices of the elytra rounded; prosternal process laminiform; mesoventral process with apex bigibbose; and tarsi of the males dilated or setose."

Lacordaire (1872) synonymized *Caciomorpha* with *Phacellocera* Laporte, 1840. Later, Galileo & Martins (1998) revalidated *Caciomorpha* and proposed some characters to differentiate both genera. According to them, *Caciomorpha* differs from *Phacellocera* by the absence of dilation on apex of the antennomere IV, and the tubercle on the apical quarter of the elytra. In *Phacellocera*, the antennomere IV has a dilation on the apex, and

there is a tubercle on the apical quarter of the elytra. They also transferred five species to *Caciomorpha* (*Phacellocera buquetii*, *P. genalis*, *P. palliata*, *P. plagiata*, and *P. susua*), and described a new one (*C. robusta*). Moreover, Galileo & Martins (*op. cit.*) provided a taxonomic key to the species of the genus, mentioned a possible synonymy with *Phacellocerina* Lane, 1964, and redescribed *Caciomorpha*, adding the following characteristics (translated): “Frons with parallel or divergent sides toward the lower region, lower border in males with central notch. Lower eye lobes slightly shorter than genae; distance between upper eye lobes about as wide as one upper eye lobe. Antennae, in males, variable in size, usually twice the body length; in females, subequal or twice the body length. Scape robust, pyriform with dorsal face of the base flattened or slightly sulcate; pedicel unarmed; antennomere III, in females, as long as or longer than scape; in males, longer or twice the length of the scape. Apex of antennomere III distinctly dilation, usually with setae; antennomere IV without apical modifications (except in *C. genalis*); antennomere XI variable in size in relation to X. Prothorax wider than long; lateral sides with tubercles placed centrally, or slightly behind middle. Pronotum with three small tubercles: two anterior, well-projected, another centrally. Mesoventral process without tubercles. Elytra with centrobasal tubercle or gibbosity; anterior third asperate-punctate; apical half without tubercles or irregularities. Femora pedunculateclavate. Abdominal ventrite 5, in males, with rounded margin; in females, tumid and with semicircular centropical depression.”

Julio (2003d) differentiated *Caciomorpha* from *Phacellocerina* by the former “having the antennal tubercles close to each other; scape robust, pyriform, with dorsal face of the base flat; antennae long, in females almost twice the body length, in males, usually twice the body length; elytra with centrobasal gibbosity poorly elevated, anterior third with coarse punctation and apical half without irregularities; protibiae substraight.” This work was the last taxonomic study including the genus.

In this work we perform the first cladistic analysis of *Caciomorpha*, as well as the first taxonomic revision of the genus, including all seven species currently described in *Caciomorpha*.

1.2 Objectives

- 1) To establish hypothesis of phylogenetic relationships from the cladistic analysis of the genus and test the monophyly of the group;

- 2) To perform a taxonomic revision of *Caciomorpha* and verify the validity of the genus and species, and redescription of all taxa;
- 3) To make a key to all known species of *Caciomorpha*;
- 4) To design a geographic distribution map of the species.

CONCLUSIONS

The cladistic analysis indicated that, as currently known, *Caciomorpha* is not monophyletic, and *C. buquetii* appeared to belong to a new genus. With the description of a new genus to allocate *C. buquetii*, *Caciomorpha sensu novo* can be considered as a natural group. This was corroborated with the taxonomic revision, when the study of many specimens of those species allowed recognizing that *C. buquetii* does not match *Caciomorpha* features, and so a new genus was described to include it, *Amazomorpha gen. nov.* Also, during the taxonomic revision one new species and one synonym was identified. With those findings *Caciomorpha* now comprises six species. The geographic distribution of four species was expanded, two of them include new country records.

The sister group of *Caciomorpha sensu novo*, according to our analysis, is the clade formed by the genera *Phacellocera*, *Parachalastinus* and *Chalastinus*. The proximity between *Caciomorpha* with these genera was mentioned before by Julio (2003a), but never confirmed until now. During the taxonomic revision, these genera were compared and their differences were discussed (see page, 57-62). Also, *Amazomorpha gen. nov.* was found to be sister group of a clade formed by *Caciomorpha sensu novo* + *Phacellocera* + *Parachalastinus* + *Chalastinus*, the characteristics that differentiate these genera were also commented on the taxonomic revision.

Both, the equal weighting and implied weighting analysis gave the same result for the ingroup, corroborating once again the phylogenetic relations found on this work. However, many clades obtained in the cladistic analysis presented low support values. This is probably due to the high amount of homoplasies presented in the tribe, and in Cerambycidae in general. In order to strengthen these findings, other source of information should be explored, such as molecular tools and Scanning electron microscope (SEM).

Also, during the morphological study of many specimens from *Caciomorpha* and the type species of related genera (*Acanthotritus*, *Anisocerus*, *Chalastinus*, *Fredlanella*, *Gounellea*, *Jurua*, *Parachalastinus*, *Phacellocera* and *Phacellocerina*) some

characteristics never explored before in Anisocerini such as terminalia, hindwing and mouth pieces were used and found to be helpful in both the cladistic analysis and the taxonomic revision. The study of these kind of characteristics is then encourage for further studies, and the execution of tools, such as electronic microscopy, which allows to explore even more characteristics, is recommended.

Regarding the geographical distribution of the species, it was possible to identify that this genus is mainly Andean and Amazonian, with only one species occurring in Mesoamerica (*C. palliata*). Giving the wide distribution of *C. palliata*, is possible that the great variability of this species is due to its distribution. Such variability was not found in any other species of the genus, which have a more restricted distribution. When considering this variability, it was possible to establish the synonymy between *C. palliata* and *C. susua*, with priority to the name *C. palliata*. This finding was possible after the examination of many specimens from both nominal species, including photographs of type material.

Moreover, *Caciomorpha* was redescribed by Galileo & Martins (1998) in where they included some characteristics to differentiate the genus. However, some of those characters showed to be variable intraspecifically, and so, were not helpful taxonomically (see discussion of taxonomic revision, page 57-58). Also, Julio (2003d) indicated some features to separate *Caciomorpha* from *Phacellocerina*, some of those features were studied and showed not to be helpful either. Herein, new characteristics are proposed to separate those genera (see discussion of taxonomic revision, pages 60-61).

Lastly, the elytral pubescent pattern had been used to separate *Caciomorpha* species before (*e.g.* Galileo & Martins, 1998). This character showed to be helpful to separate *Caciomorpha* in two artificial groups, the first one with variegated pubescence, and the second one with a distinct sutural line of pubescence. This characteristic was constant across the specimens, and therefore used in the first step of the key to species.

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