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Review

Mesoamerican genera of Anomalini (Coleoptera: Melolonthidae: Rutelinae): A brief review

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ABSTRACT

Shiny chafers of the tribe Anomalini are represented in Mesoamerica by 14 genera and 240 species, but revisions, keys to species and biological information are scarce, despite the fact that a number of species have been cited as pests of diverse cultures, mainly as part of the white grub guilds. Past studies on the taxonomy of these species offer many problems, because the genera were not adequately defined, the species usually offer character variability, genitalia were rarely described, and many authors do not agree with the status of the names. After phylogenetic studies with a generic sample of Anomalini from the world, Ramírez-Ponce and Morón proposed the revalidation of the genera *Pachystethus* Blanchard and *Paranomala* Casey, as well as the redefinition of the genera *Anomala* Samouelle and *Callistethus* Blanchard, because the representatives of these lineages have unique combinations of morphological characters and some synapomorphies are supporting adequately the nodes in the strict concensus tree obtained during such analysis. After the publication of the cited work, new evidences were found suggesting that other groups of species need to be separate in distinct genera from *Paranomala* while other taxa are part of the *Paranomala* clade. In the present review we provide brief nomenclatural history for each genus and synopsis of the phylogenetic hypothesis that support a new proposal for the classification of the genera represented in Mesoamerica. Diagnosis and comments on the distribution of the 14 genera are provided. Color photographs, illustrations of diagnostic characters and a key to genera are also included.

KEYWORDS: shiny chafers, taxonomy, distribution, Mexico, Central America, importance, white grubs

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INTRODUCTION

Members of the tribe Anomalini are a nearly cosmopolitan scarab group, widely diverse, but easy to recognize because of its nine segmented antennae, elytra with membranous border and transverse labrum. We had world wide records for near 2000 species and 34 - 44 genera [1, 2] but taking account of recent studies on American fauna, these numbers have increased to 53 genera, including new taxa and changes in the nomenclature and tribal classification [3, 4, 5].

Aside from its ecological importance derived from the great specific richness, wide distribution and diversity of wild food preferences, larvae of many species of Anomalini are included as members of the white grub complex, sometimes as debris consumers that aid to increase the fertility of soils used for agriculture or, on the

other hand, are cited as pest for the root system of many cultivate plants [6, 7].

Notwithstanding, the taxonomic knowledge of the group is limited. Most of the collections lack correct specific determination for most part of the specimens. Other problems including vague generic limits, distinct criteria for use of morphological characters and diverse drafts on the systematics of the genera that supported the lists of species represented in each geographical region. Really, diverse facts do not aid to obtain taxonomical consensus. Many species show wide variation in color patterns, body size, and tegumentary sculpture. A large number of species were described with one of few specimens, lacking information on the specific variation, mouth parts, genital structures and precise distribution. Original descriptions are much brief, including uninformative details. Some type series are formed by representatives of two or more species [8, 4, 9].

One of the main problems is the heterogeneous composition of the hyperdiverse genus *Anomala* Samouelle. During two centuries many new species from Old and New Worlds were included in such genus, using vague criteria and delaying deep comparative studies on external morphology, with the result of numerous characters repeated in distinct taxa, or species included in the genus by the absence of some other characters [10]. Wide discordances in the generic limits of *Anomala* arbitrarily applied to a great number of species offer a large list of names without true relations or supposed paraphyly [4]. In recent years the comparative study of all described species is nearly impossible, so that we need to use representative samples for the preliminary phylogenetic analysis.

Definitions of other less diverse American genera of Anomalini with recent taxonomic reviews as of *Strigoderma* (40 species) and *Epectinaspis* (nine species) show some phyletic problems. *Strigoderma* includes some species with intermediate characters in reference to *Epectinaspis*, and the phylogenetic evidence shows that the latter genus is paraphyletic [5]. Strongly supported limits for each genus are not easy to obtain. According to our experience, intermediate or transitional forms between taxa are very frequent in Anomalini. These allowed arbitrary rules for the alpha taxonomy of the group [10] tacitly applied by most of the authors [11, 12, 13]. During the past 200 years the advancement on the general classification of Anomalini is scarce [14], and the acceptance of the generic names were according to the criteria of each author (Table 1).

Historically, the first works dealing with American species of Anomalini were written in accordance with the species groups previously known in the Old World. So that, some subgenera, divisions or sections was small parts of groups largely represented in Eurasia [15, 16]. Other works were focused on the species found in a well-limited geographical region [13, 17]. Recently, a number of descriptions of new American genera and species of Anomalini were published, including some brief reviews; proposals for adjustments, and for a new classification was supported based on comparative morphology and phylogenetic analysis [3, 4, 5, 8, 9].

Arrow said that one problem with the classifications supported on species from some geographical region is that many characters are not useful when applied to other faunal assemblages or to groups larger or shorter than those originally studied [18]. Some of the characters used in this kind of studies were frequently used with much flexibility by distinct authors who offered speculations on the affinities of the genera and species. Proposals based on integral comparative morphological evidences may be true, but others supported by adaptative characters may result in convergences or homoplasies included in artificial groups [4, 12].

Phylogenetical affinities for the American Anomalini are not easy to find, because the group is formed by some mixture of elements with different biogeographical origin. Apparently, a good number of taxa in the New World are closely related with taxa from the Old World, inclusively some Mesoamerican genera may represent relicts with Palearctic or Paleotropical origins. Some authors argued in favor of the above cited hypothesis, as an example: according to Lacordaire and Potts, *Strigoderma* is the American representative of Asiatic and African *Popillia*, because they share a good number of morphological characters and also present a strong gradation in some of these structures [10, 11]. On the other hand, Bates argued that *Phyllopertha tolucana* Bates is much distinct from the

Table 1. Synopsis of the history of the classification of the American genera of Anomalini.

Author's references / Genus name	[15, 19]	[16]	[11]	[12]	[13]	[1]	[2, 20]	[3]	[5]	[9]	Present work
Anomala	G	G	G	G	G	G	G	G	G	G	Valid genus OW*
Euchlora	SG					SG					Valid subgenus? OW
Spilota	SG		SG		G	SG					"*Xochicotlia*" mn NW
Strigoderma	G	G	G	G	G	G	G	G	G	G	Valid genus NW
Popillia	G	G	G			G	G		G	G	Valid genus OW**
Callistethus		G	G			G	G	G	G	G	Valid genus O-NW
Pachystethus		G	G		SG					G	Valid genus NW
Phyllopertha		G	G	G			G		G		Valid genus O-NW
Epectinaspis		G	G	G	G	G	G	G	G	G	Valid genus NW
Callirhinus		G	G	G	G	G	G	G	G	G	Valid genus NW
Dilophochila				G		G		G	G	G	Valid genus NW
Alamona					G						Syn *Strigoderma*
Anomalepta					G						Syn *Strigoderma*
Lamoana					G						Syn *Strigoderma*
Rhombonalia					G						Syn *Strigoderma*
Strigodermella					G						Syn *Strigoderma*
Anomalacra					G			G	G		Syn *Paranomala*
Paranomala					SG					G	Valid genus NW
Oliganomala					SG						Syn *Anomala*
Anomalopus					SG						Syn *Anomala*
Rugopertha							G		G		Valid genus NW
Mazahuapertha								G	G	G	Valid genus NW
Nayarita								G	G	G	Valid genus NW
Yaaxkumukia								G	G	G	Valid genus NW
Chelilabia								G	G	G	Subgenus *Paranomala*
Leptohoplia									G	G	Subgenus *Paranomala*
Anomalorhina									G	G	Valid genus NW
Balanogonia									G	G	Valid genus NW

Abbreviations: G - genus, mn - manuscript name, NW - New World, OW - Old World, SG - subgenus.
**A. orientalis* introduced in NW, ***P. japonica* introduced in NW.

European species of such genus, but is clearly related to it [12]. More than a century later *P. tolucana* was transferred to the monotypic new genus *Mazahuapertha*, and proposed as relict element with Eurasiatic affinities [3].

Motivated to enface this problem, Ramírez-Ponce and Morón carried an exercise of phylogenetic inference based on one sample of diverse genera of American, European and Asiatic Anomalini, obtaining evidence to support the separation of the species of *Anomala* from the Old and New World as distinct genera, *Anomala* and *Paranomala* respectively [9]. These results corroborate the opinions of Ohaus and Casey about some morphological differences between both groups of species [1, 13]. The new generic definitions for *Paranomala* and *Anomala* also aid to separate other genera with taxonomic problems, as *Callistethus* and *Pachystethus*, offering new diagnostic characters useful for updating the classification of the tribe, and some tools for the advancement in the study on the phylogeny of Anomalini and related groups.

According to the above cited ideas and conscious of that we need to obtain a complex classificatory scheme supported with good phylogenetic data, including both American and Old World lineages, the present work represent an updated synthesis on the history of classification and the systematics of the American Anomalini, previous to the formal discussion of the phylogenetic analysis and the new proposal for the supraspecific classification of the genus *Paranomala* Casey currently in progress. Such study will include comments on the affinities between diverse lineages, supported by phylogenetic evidences obtained by means of the analysis of a number of representative samples, larger than that in preceding studies conducted by us. Also, we made detailed comparative studies of many morphological characters used in old works, rejected by some past authors, that reveal useful values at different taxonomic ranks of the Anomalini applied to our results.

Brief analysis of the taxonomic history of the tribe anomalini

The publications of Burmeister, Blanchard, Lacordaire, Bates, Casey, Ohaus and Machatschke are the main extensive references for the shiny chafers of America [1, 2, 11, 12, 13, 15, 16, 20]. Comparative study of the classifications proposed by each of the above cited authors is not easy (Table 1), because each author used distinct taxonomic criteria, and the purposes of each work frequently were different.

Burmeister

For the first time, a classification for the tribe as part of other groups of "Rutelids" was proposed by Burmeister. In the book of 1844, a detailed assembly for each one of the six genera then recognized is included [15]. The genus *Anomala* Samouelle was formed with nine subgenera and 74 species. Subgenus *Anomala s.str.* was formed with 25 species separated into three groups, nine species from Java, China, Japan and Europe, and 16 species from America. Subgenus *Spilota* Dejean was formed by three species from Asia and eight new world species. The genus *Strigoderma* Dejean only included six American species. Main characters used for the genus rank classification are the form of the clypeus and protibia, form of pronotal basal margin, punctuation of pronotum and structure of mesosternum; for the subgenus rank the characters were shape of tarsal claws, form of mentum, pronotal, and elytral margin, and prominence of mesosternum. In the book of 1855, a new species from Brazil is described as *A. chromicolor*, and is included in the subgenus *Euchlora* Macleay with other three species from Asia [19].

Blanchard

As part of the catalogus of the beetles deposited in the collection of the Museum of Natural History in Paris, this author listed 14 genera of Anomalini for the world, seven of which were described as new. *Callistethus* Blanchard is represented in America as well as in Asia. *Epectinaspis* Blanchard and *Pachystethus* Blanchard are restricted to Mesoamerica. *Callirhinus* is endemic of western Mexico. The genus *Anomala* is divided in "divisions" some of them without name and others with the names used by Burmeister. His division VII includes only one Mexican species *A. rhizotrogoides*; divisions VIII and IX are formed by American taxa, 29 and 11 species respectively. The classification of the tribe is more complex

because it includes a large number of species and more morphological characters. Main characters used for the genus rank are: the form of tarsomeres and shape of tarsal claws, form of labium and palpomeres, body shape and size, structures of mesosternum and details of elytral striae. Proposals of Burmeister and Blanchard are much similar, because divisions VIII and IX correspond to the subgenera *Anomala* and *Spilota*. The differences are that Blanchard did not recognize the subgenus *Euchlora*, and separate the division VII [16].

Lacordaire

A total of 13 genera of Anomalini from the world were described in detail and placed in an old style taxonomic key. No new classification is included in his work, but useful morphological characters were discussed and comments on the affinities of each genus were included. Main characters used for genus rank were exposition of mesepimera and basal width of elytra. Genera from Old and New World were mixed, and did not find strong characters for the separation of *Spilota*, *Callistethus* and *Pachystethus* from *Anomala* [11].

Bates

This big work dealt only with the species of Mexico and Central America, but increased much knowledge on the Anomalini. The new genus *Dilophochila* and the first American species of *Phyllopertha* were described. Into the genus *Anomala* 65 new species were described to complete 108 species recorded in the study area. Proposed classification is much distinct from the preceding authors; the Mexican and Central American species were divided into three groups according to the shape of tarsal claws. The first group was divided into five sections attending to the form and extension of the meso-metasternum. Sections II and III of *Anomala* proposed by Burmeister, and division VIII of *Anomala* in the classification of Blanchard, were similar to the sections I and II in the book of Bates. The species included in the subgenus *Spilota* by Burmeister and in the division IX of Blanchard, characterized by the long mesosternal projection, are grouped in the sections 4 and 5 of the first group of *Anomala* proposed by Bates. *Anomala rhizotrogoides* remain isolated in a separate group supported by the simple tarsal claws [12].

Casey

The results of this author may represent the most detailed and contrasting classificatory system for American shiny chafers. Such a system was developed using the personal collection of the author with specimens mainly obtained in North American localities. Many new genera were proposed in this work as well as three new subgenera for *Anomala*. The subgenus *Paranomala* was the most diverse, some species were grouped in similar manner to that of Burmeister's sections or to division VII of Blanchard, but is not easy to correlate the classification of Casey with the old authors. Like Bates, *Anomala rizotrogoides* is placed apart, as the type species of the new genus *Anomalopus* that also included *A. tibialis* Schaeffer. On the other hand, *Spilota* was recognized in the genus rank, divided into four subgenera. All other genera of Anomalini proposed previously were recognized as valid. The main advantage of the work of Casey is that the morphological criteria used by the division of genera, subgenera and sections, were described in detail. The characters used included general body shape and size, surface sculpture, color, details of tarsal claws, legs, mesosternum, mouth parts, as well as geographical distribution [13].

Many authors after Casey said that such classification was much complex and excessive, including many over valuated importance of characters included in the definition of supraspecific categories. As a result, many genera and subgenera were placed in synonymy.

Ohaus

Volume 20 of *Coleopterorum Catalogus* included 3073 species of Rutelinae [21], an impressive difference from previous 818 known species listed in previous works [22]. As part of such catalogue the Anomalini were grouped in subgenera using the names previously assigned in the groups of species of Burmeister. Near 700 species of *Anomala* were divided into four subgenera (*Aprosterna* Hope, *Anomala* Samouelle, *Euchlora* MacLeay and *Spilota* Burmeister). Species in each subgenus were subdivided according to geographical regions. The American species were included in three subgenera. Ohaus synonymized nearly all the genera proposed by Casey (*Strigodermella*, *Alamona*, *Anomaleopta*, *Rhombonalia*, etc.) and

do not accept the genus *Phyllopertha* as part of the fauna in America [1].

An interesting point is the inclusion of seven species from tropical America as members of the subgenus *Aprosterna*. Previously, Burmeister and Blanchard recorded the genus only for Asia. On the other hand, the species of the subgenus *Spilota*, previously cited only for America and Asia, were also registered for Australia and Africa. But the main problem with this work is dealing with the absence of comments or data that explain the taxonomic changes, as is common in the catalogues or checklists. So, that classification needs to be used with caution in the absence of supports.

Machatschke

In his works this author proposed synonymies for 30 genera and subgenera described during the past 100 years simplifying excessively the classification of the Anomalini [23]. However, as the last worldwide catalogue published was used as obligate reference of authority, but as is common in other similar lists, due to the lack of details on the criteria, do not have real taxonomic value. Some taxa were revalidated in recent studies given precise diagnostic characters for the identification and comparative studies, as with *Callistethus* and *Pachystethus* [9]. In his catalogues Machatschke listed *Spilota* as synonym of *Callistethus* but grouped the species not as preceding authors did. Placed *Dilophochila* as synonym of *Anomala*, and listed *Phyllopertha* as valid for New World fauna, including the new monotypic genus *Rugopertha* for Honduras in Central America. Into the genus *Anomala* was proposed an elaborate scheme with 15 groups of species, but without explicit criteria [2, 20].

Diagnostic characters in Anomalini

Despite the changes of criteria among distinct authors cited above, it is possible to find a number of common characters typical of the Anomalini, that aid to support the taxonomic ranks and to propose classificatory hypothesis. Main morphological characters used by various authors are:

1) presence-absence and extension of the pronotal basal margin [13] of great taxonomic value also in other groups of Rutelinae [18, 24]. Casey proposed that complete pronotal margin is the primitive condition. Genera that do not present such character are *Callistethus*, *Yaaxkumukia*, *Nayarita*, *Pachystethus* and *"Xochicotlia";* incomplete margin is found in species of *Strigoderma*; and margin completely formed is always present in *Paranomala*, *Anomalorhina*, *Epectinaspis*, *Mazahuapertha*, *Callirhinus* and *Dilophochila*.

2) Form and extension of the meso-metasternal process, or a wide intercoxal prominent space at the middle of mesosternum, also has been frequently used as character for separation of genus or subgenus. The degree of development of such structures is widely variable but in some genera is easy to recognize some patterns, as in *Callistethus* and *Yaaxkumukia* the process is usually curved, much long and acutely pointed; in *Pachystethus*, *Callirhinus*, *"Xochicotlia"* and *Strigoderma* is short, rounded and stout; in *Nayarita* is long but narrowed from it base; in *Epectinaspis* is brief, weakly formed; meanwhile in *Dilophochila*, *Anomalorhina* and *Paranomala* is not developed.

3) Shape, position and extension of the mesepimera is another frequently used character all through the history of the group. In some genera, as *Strigoderma*, is directed upwards; in other genera as *Epectinaspis* and *Callirhinus* is easily visible from above.

Other characters has been used with less frequency by authors, some times weak changes not confirmed in posterior works, such as modifications in mouth parts [13], or in the form of tarsal claws [12], without other combined characters, favored artificial grouping. According to our phylogenetic analysis a great number of new characters have a strong phyletic mark, as the mesothoracic wings, genitalia of two sexes, as well as other meristic characters; the taxonomic value of some abandoned characters has been reinterpreted, such as form and details in tarsal claws and mouth parts.

All the new information used in diverse and variable combinations allows to recognize four main lineages in the American fauna of Anomalini, and gives us elements for proposing limits in diagnosis of each genus (Table 2). Many characters are strongly correlated, as has been

Table 2. Distinctive characters in the Anomalini genera.

Genera	Basal margin pronotum	Apical margin pronotum	Mesosternal projection	Parameres	Parame res-ventral plate	Mesepimeron	Apex elitral suture	Basal width pronotum	Scutellum	Sexual dimorphism
Nayarita	Absent	Absent	Small	Parallel	Free	Hidden	Rounded	Broad	Triangular	Present
"Xochicotlia"	Absent	Complete	Prominent, broad	Parallel	Partially fused	Slightly exposed	Spine-like	Broad	Triangular	Present
Callirhinus	Present	Complete	Prominent, broad	Perpendicular	Free	Exposed	Spine-like	Little narrow	Triangular	Present
Strigoderma	Present	Complete	Notable, broad	Some perpendicular	Free	Exposed, ascending	Spine-like	Narrow	Triangular	Present
Rugopertha	Present	Complete	Developed	n.a.	n.a.	Exposed	n.a.	Slight narrow	n.a.	n.a.
Epectinaspis	Present	Complete	Slightly broad	Some slightly perpendicular	Free	Exposed	Spine-like	Broad	Triangular	Present
Balanogonia	Present	Complete	Slightly broad	Perpendicular	Free	Slightly exposed	n.a.	Broad	n.a.	n.a.
Pachystethus	Absent	Incomplete	Prominent, broad	Parallel	Fused	Hidden	Spine-like	Broad	Triangular	Present
Callistethus	Absent	Incomplete, some complete	Very long, acute	Parallel	Fused	Hidden	Spine-like	Broad	Triangular	Scarce
Yaaxkumukia	Absent	Incomplete	Very long, acute	Parallel	Free	Hidden	Rounded	Broad	Parabolic	Scarce
Anomalorhina	Present	Complete	Narrow	Parallel	Free	Slightly exposed	n.a.	Broad	Parabolic	Absent
Dilophochila	Present	Complete	Absent	Perpendicular	Free	Hidden	Rounded	Narrow	Parabolic	Present
Mazahuapertha	Present	Complete	Brief	Perpendicular	Free	Slightly exposed	Rounded	Narrow	Triangular	Present
Paranomala	Present	Complete	Absent	Parallel	Free	Hidden	Rounded	Broad	Parabolic	Scarce

Data not available indicated as n.a.

observed by previous authors, facts that facilitate the assembly of packages of character states to recognize groups with different taxonomic rank (as the ascendant mesepimera associate with the expansion of the epipleura [11] or the ascendant mesepimera related with the protuberat mesosternum [13]).

Other useful characters for supraspecific diagnosis are: the sexual dimorphism (expressed as enlargement of fore legs and antennae, expansion of epipleura); form of fore tarsal claws; form of the distal part of elytra; shape of the apex of elytral suture; basal width of pronotum; form of the scutellum; exposition of prepygidium; length of metatarsomeres; and shape of clypeus. Within male genital capsule main useful supraspecific characters are: position of the parameres in reference to basal piece; tubular or flattened form of the parameres; and degree of fusion of the ventral plate with parameres.

Comments on each American genus of Anomalini

The following information is based on the original descriptions and in some regional brief reviews [3, 4, 5, 9]. The genus *Popillia* Dejean is represented in America only by one introduced species, and the genus *Phyllopertha* Stephens was considered as *incertae sedis* because the type specimen was not found and no specimen similar to the description is available at present; both genera were commented in such reference and are not included in this section [4].

Genus *Nayarita* Morón and Nogueira, 1998

(Figures 1, 13, 26, 30)

Type species: *Nayarita viridinota* Morón and Nogueira, 1998: 16.

Diagnosis. Body size big; body weakly convex, depressed, stout; clypeus with anterior border widened; five maxillary teeth; pronotum without anterior or posterior margins; pronotum with deep and dense punctuation; sutural apex of elytron rounded; epipleural fold much wide; meso-metaesternum projected; simple claws on middle and hind tarsi; dorsal coloration contrasted golden yellow with metallic green. Male genitalia: parameres distally curved; ventral plate long, bilobed, separated from parameres.

Distribution. Restricted. Slopes of Tepetliltic volcano, Santa María del Oro, Nayarit, and sierra de Mascota, Jalisco, Mexico.

Comments. Originally it was related with *Callistethus* and *Anomala*, but its position in the recent cladogram and some conspicuous characters shared with *Mimela* and *Anomala* is clear that have Palearctic affinities.

Genus *Callistethus* Blanchard, 1851

(Figures 2, 28, 32)

Type species: *Mimela auronitens* Hope, 1835: 114

Diagnosis. Body size big to medium; body convex, weakly depressed, stout; six maxillary teeth; pronotum without posterior margin, with incomplete anterior margin; pronotum usually with discrete fine punctuation; sutural apex of elytron spiniform; epipleural fold wide; meso-metaesternum much projected reaching procoxae; dorsal coloration variable, but usually intense green. Male genitalia: genital capsule much curved, parameres and ventral plate completely fused.

Distribution. Wide. Asia and America.

Comments. This genus is mainly found in southeast of Asia and some authors do not accept its representation in America, but we found phylogenetic evidences to support at least few species of Central and northern South America as members of this genus [9]. Recent study of the type specimens of *C. chrysanthe* (Bates), *C. phospora* (Bates), *C. specularis* (Bates), *C. xipostetha* (Bates), *C. pseudolepida* Morón and Nogueira, and *C. tlapanecus* Ramírez-Ponce and Morón confirm the existence of *Callistethus* in tropical or subtropical areas of the New World [25].

Genus *Yaaxkumukia* Morón and Nogueira, 1998

(Figures 3, 29)

Type species: *Yaaxkumukia ephemera* Morón and Nogueira, 1998: 27

Diagnosis. Body size medium; body much convex, stout; six maxillary rounded teeth; pronotum without posterior margin and with incomplete anterior margin; pronotum with discrete, much fine punctures; sutural apex of elytron rounded; epipleural fold narrowed; meso-metasternum clearly projected until procoxae; males with last pair of respiratory stigma placed

on conspicuous tubercles; coloration dorsally intense green, easy to lost by degradation, ventrally with submetallic shine. Male genitalia: parameres distally expanded and curved, aligned with basal piece; ventral plate short, separate from parameres. Distribution. Limited. Southeast of Mexico (Chiapas), Guatemala and Honduras.

Comments. After the description of this genus, the study of large series of specimens and the description of two new species, point out the impact of deforestation in the mountains of Central America on the populations of these limitedly distributed shiny chafers [26]. Genus *Yaaxkumukia* is closely related to the species of *Callistethus*; one of the shared characters is the tuberculiform last pair of respiratory stigma, but in the former is bigger than in the latter, mainly in males.

Genus *Paranomala* Casey 1915

(Figures 4, 10, 14, 19, 24, 31)

Type species: *Melolontha marginata* Fabricius, 1792: 164

Diagnosis. Body size small to large, ovate or elongate, convex; fronto-clypeal suture complete; pronotum with anterior and posterior borders complete; epipleural fold narrowed; sutural apex of elytron rounded; meso-metasternum with intercoxal space narrow or moderately wide but without projection; mesepimera not exposed dorsally. Coloration diverse, dark to shiny. Male genitalia: parameres tubiform, aligned with basal piece.

Distribution. Wide. America (southern Canada to Northern Argentina), Africa, India and southeastern Asia.

Comments. This genus was validated with support on phylogenetic inferences to accommodate most of the American species previously included in *Anomala* Samoulle [9]. Such classification reflects part of the scheme of Casey [13], who explained the differences between European and American species proposed the name *Paranomala* for a number of species in the New World. Current unpublished results obtained by Ramírez-Ponce and Morón with phylogenetic analysis of 81 taxa show topologies for well supported clades that will be ranked as four subgenera and 12 groups of species in America. Most interesting aspects deal with the new position of *Leptohoplia* Saylor and *Chelilabia* Morón and Nogueira as subgenera of *Paranomala*, and additions to renew the group of species "*capito*" *sensu* Machatschke [2] as the new subgenus *Bucaphallanus* Ramírez-Ponce and Morón [41].

Genus *Pachystethus* Blanchard, 1851

(Figures 5, 25)

Type species: *Popillia vidua* Newman, 1838 by monotypy.

Diagnosis. Body size small, body stout, depressed; six maxillary teeth; pronotum without posterior margin and anterior margin incomplete; pronotal surface with moderate punctuation; sutural apex of elytron spiniform; epipleural fold wide; meso-metasternum wide with projection; contrasting coloration or completely black. Male genitalia: parameres separated medially; ventral plate completely fused with the parameres.

Distribution. Limited. East and southeast of Mexico to Guatemala.

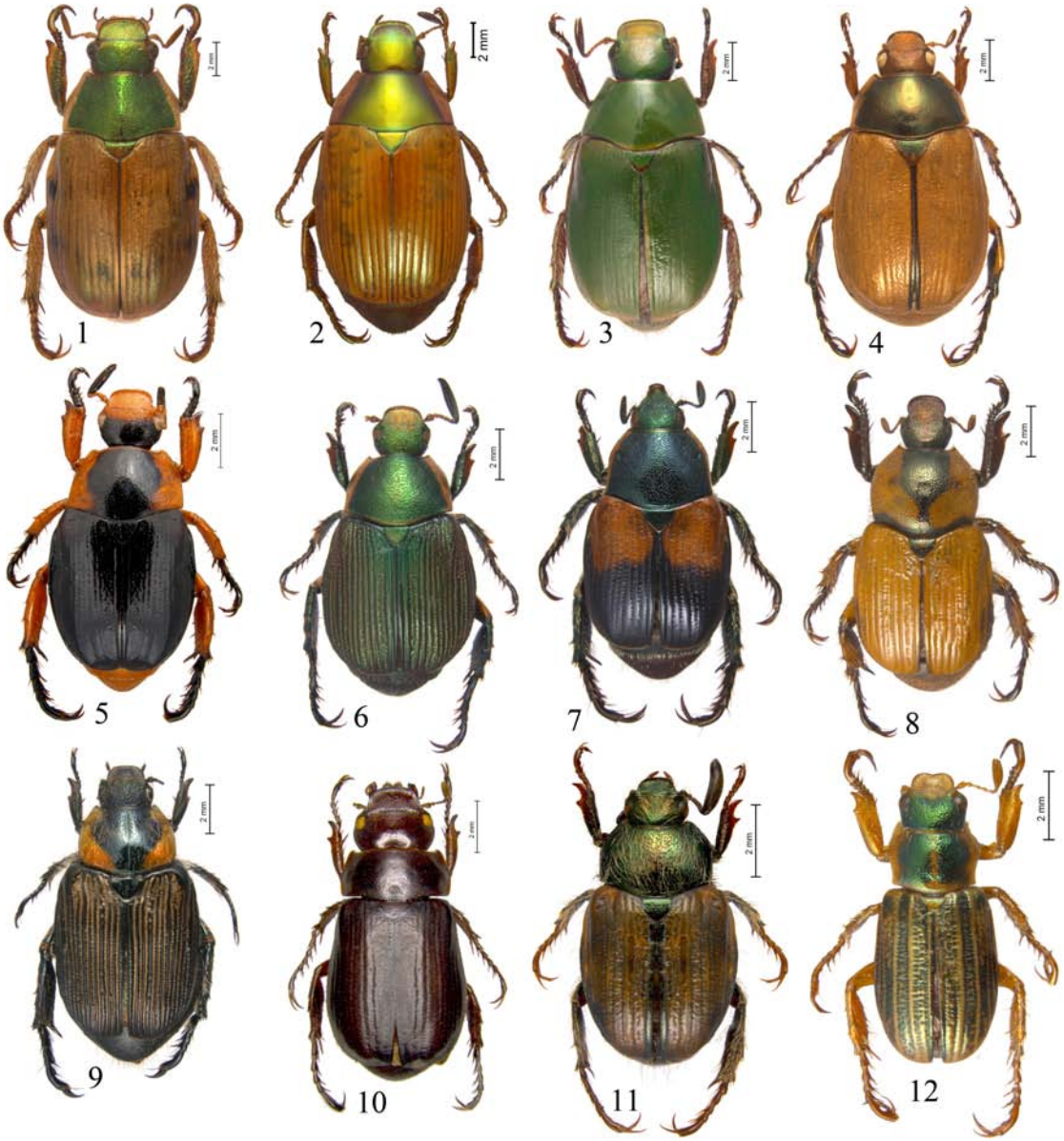
Comments. This genus was revalidated by Ramírez-Ponce and Morón [9], and the recent revision included three new species [27]. According to the phylogenetic analysis *Pachystethus* share characters with *Callistethus*, *Strigoderma*, *Balanogonia*, *Epectinaspis*, *Popillia* and *Callirhinus*, as the increased and wide meso-metasternal projection, depressed body, elytra narrowed towards the apex, protarsi and protibiae widened, and sutural apex of each elytron spiniform.

Genus *"Xochicotlia"* Ramírez-Ponce and Morón (unpublished)

(Figures 6, 16, 27)

"Type species" *Spilota micans* Burmeister, 1844: 269

Diagnosis. Body size small to moderate; body stout, depressed; fourth antennomere much elongate, five times longer than fifth antennomere; posterior width of pronotum briefly shorter than basal width of elytra; mesepimera weakly exposed dorsally; elytra clearly reduced in width towards the apex, flattened, with deep striae; sutural apex of elytron spiniform; meso-metasternal space

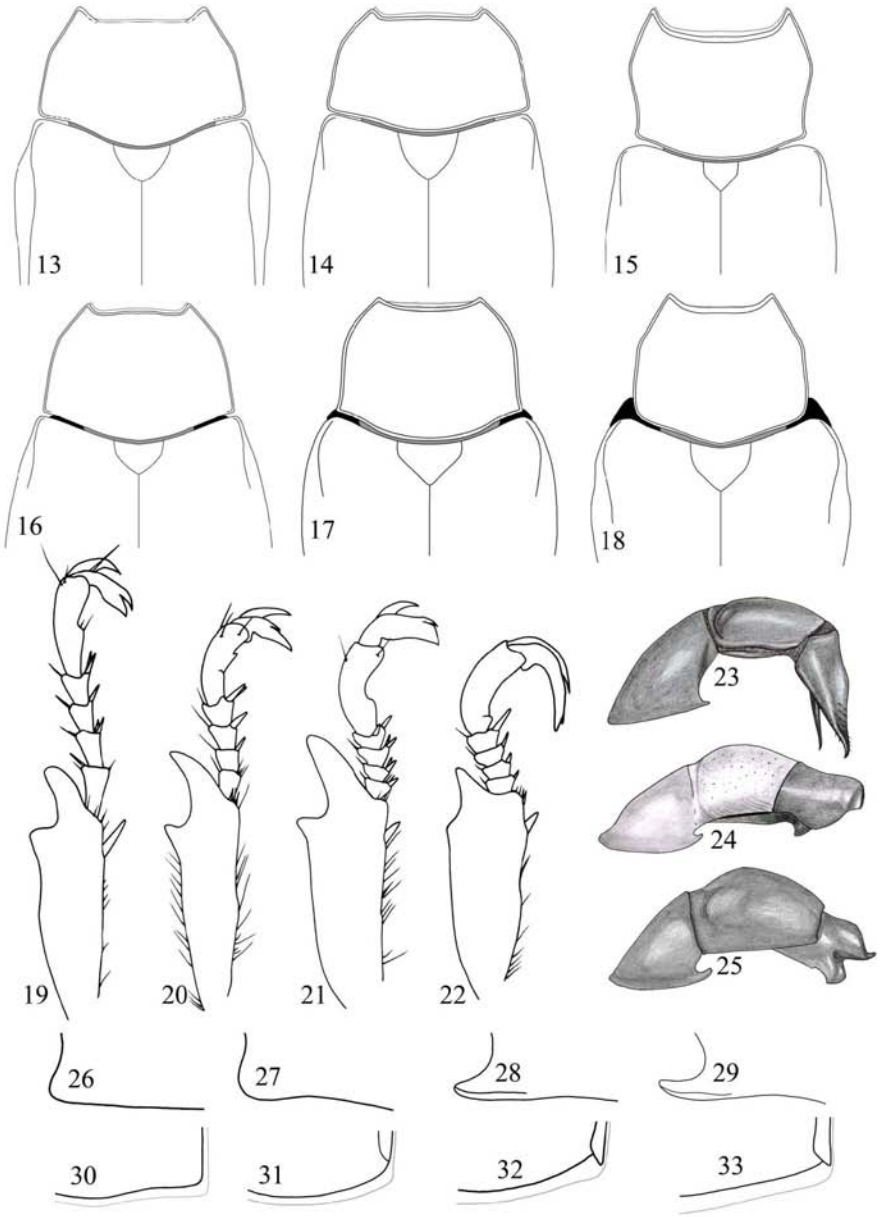


Figures 1-12. Dorsal view of some American genera of Anomalini. 1. *Nayarita* Morón and Nogueira, 2. *Callistethus* Blanchard, 3. *Yaaxkumukia* Morón and Nogueira, 4. *Paranomala* Casey, 5. *Pachystethus* Blanchard, 6. "*Xochicotlia*" Ramírez-Ponce and Morón, 7. *Callirhinus* Blanchard, 8. *Epectinaspis* Blanchard, 9. *Strigoderma* Burmeister, 10. *Paranomala* (*Bucaphallanus*) Ramírez-Ponce and Morón, 11. *Mazahuapertha* Morón and Nogueira, 12. *Dilophochila* Bates.

wide and prominent; prepygidium exposed in part. Male genitalia: parameres nearly cylindrical, longer than half of the length of tectum, partially fused with basal piece.

Distribution. Limited. Central and southern Mexico, with some records in Panama and Nicaragua.

Comments. Some of the species presently grouped in this new genus were associated with the old name *Spilota* Dejean. Burmeister used *Spilota* as subgenus including Asiatic and American species [15, 19]. In the same usage Blanchard and Casey only listed American species, but Ohaus also added species from Australia and Africa [16, 13, 1].



Figures 13-33. Diagnostic characters of genera of American Anomalini. 13-18. Dorsal view of pronotum and elytra in: 13. *Nayarita*, 14. *Paranomala*, 15. *Dilophochila*, 16. "*Xochicotlia*", 17. *Callirhinus*, 18. *Strigoderma*: 19-22. Dorsal view of tibia and tarsus of left fore leg in: 19. *Paranomala*, 20. *Mazahuapertha*, 21. *Epectinaspis*, 22. *Dilophochila*. 23-25. Lateral view of male genital capsule in: 23. *Callirhinus*, 24. *Paranomala*, 25. *Pachystethus*. 26-29. Lateral view of meso-metaesternal projection in: 26. *Nayarita*, 27. "*Xochicotlia*", 28. *Callistethus*, 29. *Yaaxkumukia*. 30-33. Dorsal detail of the apex of left elytron in: 30. *Nayarita*, 31. *Paranomala*. 32. *Callistethus* y 33. *Strigoderma*.

Machatschke synonimized *Spilota* under *Anomala*, but Frey take it again for a large number of American species [2, 20, 28]. The combination of characters is different from other groups of Anomalini, and phylogenetic analysis offer good support for such clade, but is better not to use the name *Spilota* in this genus-group because the name of Dejean is in homonymy with *Spilota* Billberg, 1820 (Coccinelidae) and with *Spilota* Huebner, 1822 (Lepidoptera). "*Xochicotlia*"

share characters with *Pachystethus*, *Strigoderma* and *Callistethus*.

Genus *Callirhinus* Blanchard, 1851

(Figures 7, 17, 23)

Type species: *Callirhinus metallescens* Blanchard, 1851: 176

Diagnosis. Body size medium; body stout, depressed; clypeus narrowed and distally curved as laminar projection; six maxillary teeth; pronotum with anterior and posterior margins complete; epipleural fold widened; sutural apex of elytron spiniform; meso-metasternal space wide and prominent; coloration diverse, contrasting dark and brilliant. Male genitalia: parameres depressed, plate-like, setose and perpendicular to basal piece; ventral plate long, separated from parameres.

Distribution. Limited. Western Mexico.

Comments. Wide variation in the color patterns of *C. metallescens*, and one interesting feeding habit on sugarcane leaves were described and illustrated [29]. Machatschke placed *Callirhinus* close to other species of "Anisoplina" [2]. The possible relictual condition of the genus in western Mexico was hypothesized [14], but the results of the phylogenetic analysis conduced by do not offer good support for the relation of *Callirhinus* with *Anisoplia*. According with our recent studies *Callirhinus* is part of the second lineage, related with *Strigoderma, Pachystethus* and "*Xochicotlia*".

Genus *Epectinaspis* Blanchard, 1851

(Figures 8, 21)

Type species: *Anomala* (*Phyllopertha*) *mexicana* Burmeister, 1844: 241

Diagnosis. Body size medium; body stout, weakly depressed; six maxillary teeth; clypeus of male briefly elevated; pronotum with anterior and posterior margins complete; anterior angles of pronotum acute, prominent; sutural apex of elytron spiniform; epipleural fold wide; meso-metasternal area without projection; mesepimera briefly seen from above. Male genitalia: parameres and ventral plate separate.

Distribution. Limited. Southern Mexico to northern Venezuela.

Comments. Paucar-Cabrera reviewed the taxonomy of the genus and made phylogenetic analysis, at the side detected paraphylic topology that support the related genus *Balanogonia* [5]. Both genera and *Strigoderma* share a number of characters, such as the form of pronotum, extension of mesepimera and elytral sculpture, but is easy to separate with the diagnostic characters cited above.

Genus *Strigoderma* Burmeister, 1844

(Figures 9, 18, 33)

Type species: *Strigoderma sulcipennis* Burmeister, 1844: 316

Diagnosis. Body size medium; body narrowed, with dorsal surface weakly flattened; six maxillary teeth; pronotum usually with complete anterior and posterior margins; posterior width of pronotum shorter than basal width of elytra; mesepimera usually ascendant and prominent; sutural apex of elytron spiniform; epipleural fold wide; meso-metaesternal area wide, protuberant; coloration variable. Male genital: parameres and ventral plate not fused.

Distribution. Wide. From United States to Argentina.

Comments. Historically, the taxonomic limits of this genus have been unclear. Casey accept the utility of the typical body shape, but Potts remarks that such character in some atypical species, induced to grouping these into erroneous groups, inclusive from the Old World [13, 10]. Bader made the alpha taxonomic revision of the genus, and also found evidences about the group not being a natural genus, and is in need of phylogenetic analysis [30]. At first hand, some species appear to be best situated in the genus *Paranomala*, but other species may form a new genus.

Genus *Rugopertha* Machatschke, 1957

Type species: *Phyllopertha sericeomicans* Nonfriend, 1891: 233 by monotypy.

Diagnosis. Body size small; body elongated; mesepimera exposed; mesosternal process briefly developed; coloration bright green to coopery green.

Distribution. Restricted. Central Honduras.

Comments. Blanchard described *Phyllopertha villosella* and *P. moreletiana* from Mexico [16],

and Bates argued that the genus *Phyllopertha* was badly defined, and placed such species as members of *Anomala* and *Epectinaspis*, respectively, but with reluctance described one new species in *Phyllopertha* (*P. tolucana*) [12]. Some years later Nonfried described *P. sericeomicans*, that Machatschke change to his newly proposed genus *Rugopertha* [2]. Such species looks like *Strigoderma* by the elongate body and the exposition of mesepimera, and particularly resemble species of the group *costulipennis* by the dorsal surface finely rugo-punctate [4].

Genus *Balanogonia* Paucar-Cabrera, 2003

Type species: *Epectinaspis freudei* Frey, 1968:14

Diagnosis. Body size small; body slightly elongated; six maxillary teeth; pronotum with complete anterior and posterior margins; anterior angles of pronotum obtuse, not prominent; epipleural fold poorly developed; meso-metaesternal area small, not produced; base of mesepimera briefly exposed near base of each elytron. Male genitalia: parameres setose, perpendicular to basal piece; ventral plate not fused with parameres.

Distribution. Restricted. Western Mexico (unique precise record is from Colima volcano, Jalisco, Mexico).

Comments. The two species presently described agree with the combination of characters originally proposed, as the setose parameres are perpendicular to basal piece [5]. This character is also found in species of *Strigoderma*, *Mazahuapertha*, *Callirhinus*, some species of *Paranomala* and other Old World taxa such as *Popillia* and *Anomala*. A new phylogenetic analysis including representatives of all American genera of Anomalini is necessary to obtain a better hypothesis on the relationships of *Balanogonia*, *Epectinaspis*, *Strigoderma* and *Paranomala*.

Genus *Mazahuapertha* Morón y Nogueira, 1999

(Figures 11, 20)

Type species: *Phyllopertha tolucana* Bates, 1888: 216

Diagnosis. Body size small; body form stout, shortened; maxillary lacinia reduced to three teeth; fifth antennomere with angulate keel; pronotum with both margins complete; pronotal basal width as the width of the base of elytra; mesepimera hidden; sutural apex of elytron rounded; epipleural fold narrow; meso-metasternal area narrowed, briefly projected; protibial spur absent; coloration contrasting, dark metallic green on head, pronotum, and scutellum, and dark yellow on elytra. Male genitalia: parameres plate-like, perpendicular to basal piece; ventral plate elongated, not fused with parameres.

Distribution. Restricted. Only known by type series from Toluca, state of Mexico, Mexico.

Comments. Original description detailed a number of characters of *Phyllopertha tolucana* not shared by species of *Phyllopertha* in the Old World, that support their proposal for the genus *Mazahuapertha* [3]. Our recent comparative studies offer shared characters of *Mazahuapertha* with *Epectinaspis*, *Strigoderma*, *Rugopertha*, *Callirhinus* and *Balanogonia*, as exposed mesepimera, narrowed base of pronotum, and meso-metasternal process briefly developed. Other characters are shared with *Strigoderma*, *Callirhinus*, *Balanogonia* and *Dilophochila*, such as depressed, plate-like parameres, perpendicular to basal piece, covered with short setae, as well as the free, elongated ventral plate.

Genus *Dilophochila* Bates, 1888

(Figures 12, 15, 22)

Type species: *Dilopochila bolacoides* Bates 1888: 261

Diagnosis. Body size small; body elongated, moderately convex; clypeus bilobated; three maxillary teeth; pronotum with both margins complete; sutural apex of elytron rounded; epipleural fold narrow, discrete; meso-metasternal area small, not produced; mesepimera hidden under humeral calla. Male genitalia: parameres plate-like, perpendicular to basal piece; ventral plate elongated, not fused with parameres.

Distribution. Limited. Southern Mexico (Chiapas, Oaxaca, Veracruz), Guatemala and Honduras.

Comments. This genus was listed as unique member of the subtribe Dilophochilina [31]. Later, the genus-name was placed as synonym of *Anomala* without listing *D. bolacoides* in any

group of species [20]. Posteriorly the type species was redescribed, revalidating the genus-name and describing five new species from Mexico, Guatemala and Honduras, including a key for the six species in the genus [3, 32]. As was discussed, no much characters are shared between *Dilophochila* and other American genera, as pronotal base narrower than the elytral base (also present in *Strigoderma* and *Mazahuapertha*), notably protibial widening (also in *Strigoderma*, *Epectinaspis* and *Pachystethus*), and depressed, plate-like parameres perpendicular to basal piece (shared with *Callirhinus*, *Strigoderma*, *Balanogonia* and *Mazahuapertha*) [3].

Genus *Anomalorhina* Jameson, Paucar-Cabrera and Solís, 2003

Type species: *Anomala turrialbana* Ohaus, 1928: 393

Diagnosis. Body size small; body ovate elongated; clypeus notably upturned; frons of male with basal tubercles; frontoclypeal suture erased at middle; six maxillary teeth; pronotum with complete anterior and posterior margins; pronotum of male with shallow depression on anterior middle; epipleural fold narrow, discrete; meso-metasternum with narrow process; base of mesepimera briefly exposed near humeral calla. Male genitalia: parameres aligned with basal piece.

Distribution. Limited. Costa Rica and Nicaragua.

Comments. Ohaus originally described only one female. The peculiar form of body, labrum, hind tibiae and coloration, offer an isolated position for this species between the Anomalini, but the addition of male dimorphic characters complete the diagnosis for another genus, much distinct from other American shiny chafers. Without a detailed comparative study of the morphology of *A. turrialbana* is not easy to hypothesized about its relationships within the Anomalini, but at first hand look more related to the lineage of *Paranomala*.

Key to the genera of Anomalini from America. Modified from [3, 4, 5, 9].

1 Clypeus with anterior border much wide (near half the length of clypeus in dorsal view). Maxilla with 5 teeth. Anterior pronotal margin absent. Middle third of lateral border of each elytron notably thickened in both sexes. Middle and hind tarsal claws simple. Western México (Nayarit) ……. ***Nayarita*** Morón and Nogueira

1´ Clypeus with anterior border narrow (near a quarter of the length of clypeus in dorsal view). Maxilla with 2, 3, 4, 6 teeth. Anterior pronotal margin present. Middle third of lateral border of each elytron some times thickened in females. Only hind tarsal claws simple. ……..…… …… 2

2 Posterior margin of pronotum absent. …… ...…… 3

2´ Posterior margin of pronotum present. ….…… ...……..……..... 6

3 Meso-metasternal projection long, with apex acute and/or curved, reaching posterior side of procoxae. Body size medium to large (14 - 22 mm). ……..……..... 4

3´ Meso-metasternal projection short, prominent and widely rounded, reaching at apex of mesocoxae. Body size small (10 - 13 mm) … ….……..……..……..... 5

4 Dorsal coloration bright emerald green. Last abdominal spiracle tuberculiform. Male genital capsule with parameres distally widened, ventrally not fused one with the other or with ventral plate. …….…… …..……. ***Yaaxkumukia*** Morón and Nogueira

4´ Dorsal coloration reddish brown, yellowish, green or bluish, with metallic or semimetallic luster. Last abdominal spiracle swollen or annular. Male genital capsule with parameres not widened distally, ventrally fused between it and with ventral plate. Mexico, Central America and Colombia. ….……..… ***Callistethus*** Blanchard

5 Male protarsi notably shortened and widened. Punctures on elytral striae small, simple. Parameres completely fused between it and with ventral plate. Coloration variable, bright black, reddish brown, dark brown, orange yellow or bright yellow without metallic luster. Central and southern Mexico. …..……. ..…… ***Pachystethus*** Blanchard

5´ Male protarsi briefly shortened. Punctures on elytral striae large, umbiliform or annulated. Parameres nearly fused to ventral plate but not fused one with the other. Coloration greenish

yellow or yellowish brown with intense metallic luster. Central and southern Mexico, Panamá and Nicaragua. …… ……..……. "***Xochicotlia***" Ramírez-Ponce and Morón (unpublished)

6 Clypeus with anterior border bilobed. Apex of protibia ventrally with mesial proyection. Maxillary lacinia with 4 teeth. Protarsal inner claw narrow, nearly as long as distal protarsomere. Southern Mexico, Guatemala and Honduras. ……. ***Dilophochila*** Bates

6´ Clypeus with anterior border straight, rounded o projected. Apex of protibia ventrally without mesial projection.Maxillary lacinia with 2, 3 or 6 teeth. Protarsal inner claw wide, notably shorter than distal protarsomere. ……..…… …….. 7

7 Dorsal part of mesepimere hidden under elytral humerus. Sexual dimorphism scarce. Southeastern Canada to Northern Argentina. ……..……. ***Paranomala*** Casey

7´ Dorsal part of mesepimere partially seen from above, not covered by elytral humerus. Sexual dimorphism notably in protibiae, protarsi and tarsal claws, elevation of clypeus and length of antennal club. …… ……..…. 8

8 Fronto-clypeal suture incomplete at middle. Lateral borders of clypeus clearly elevated over the base of ocular canthus. Male with antero-mesial pronotal depresión. Female with "V" shaped posterior pronotal border. Costa Rica and Nicaragua. ……..…… …..……. ***Anomalorhina*** Jameson, Paucar-Cabrera and Solís

8´ Fronto-clypeal suture complete. Lateral borders of clypeus nearly flat or scarcely, elevated over the base of ocular canthus. Males and females with completely convex pronotum, and posterior pronotal border straight or curved. ……..…. 9

9 Anterior border of clypeus elongate, plate-like, narrowed and curved towards apex. Central Western Mexico. ……..……..…… ……...…… ***Callirhinus*** Blanchard

9´ Form of clypeal border variable, but not narrowed to the apex. ……..……..… 10

10 Dorsal surface of pronotum and elytra finely rugo-punctate. Elytra without striae or longitudinal keels. Honduras. ……..... .....……. ***Rugopertha*** Machatschke

10´ Dorsal surface of pronotum and elytra with variable punctuation, but not finely rugo-punctate. Elytral surface with punctate striae, with longitudinal keels or nearly smooth. ……..... .....…11

11 Protibial spur absent. Fifth antennomere with notably angled ventral keel. Toluca, México. …….. ***Mazahuapertha*** Morón and Nogueira

11´ Protibial spur present. Fifth antennomere nearly cylindrical, without notably keel. … 12

12 Mesosternum with wide intercoxal area. Meso-metasternal projection more or less notably. Anterior border of clypeus semi-trapezoidal, nearly as the level of clypeal disk. USA. to Argentina. ……..…… …..……..… ***Strigoderma*** Burmeister

12´ Mesosternum with narrow intercoxal area. Meso-metasternal projection weak or absent. Anterior border of clypeus rounded or subquadrate, notably or moderately elevated. ……..…… ……..……. 13

13 Pronotum with posterior border rounded, anterior angles rounded, not reaching the posterior half of each eye. Anterior border of clypeus moderately elevate. Hind wings with anterior region to RA 3+4 without setae. Southwestern México. …… …..…….. ***Balanogonia*** Paucar-Cabrera

13´ Pronotum with posterior border sinuate, anterior angles acute, projected, covering more than 1/3 of posterior part of each eye. Anterior border of clypeus notably elevate. Hind Kings with anterior region to RA 3+4 setose. Southern Mexico to northern Venezuela. …… ……..…..……***Epectinaspis*** Blanchard

Synopsis on the phylogeny of American Anomalini

Using morphological characters of nearly all the genera of Anomalini known to the Americas and a representative sample of many groups of species of *Paranomala*, we conduct two series of phylogenetic analysis. The first series was made with the aid of traditional heuristic search in

NONA 2.0 [33], and the second series was developed with TNT technologies [34], with implicate and equal weights [35]. Results of both series of analysis offer few cladograms with congruent topologies, because at genus rank they correspond exactly, and allow to recognize four lineages of American genera (Figure 34): a) monotypic genus *Nayarita* appears as basal lineage, with supposed Palearctic affinity; b) a complex group formed by the genera *Strigoderma*, *Epectinaspis*, *Dilophochila*, *"Xochicotlia"* (and probably *Callirhinus*, *Balanogonia*, *Mazahuapertha* and *Rugopertha*) represent an heterogeneous clade with elements supposedly native of the New World or with Paleotropical affinities; c) another lineage formed by *Callistethus* and *Yaaxkumukia* probably with Oriental affinities; and d) the genus *Paranomala* formed by some complex and heterogeneous group of species, that need studies to support new subgenera and many new groups of species.

Results from the recent analysis using 81 terminals are not much different from the results obtained during our early studies, based on 46 terminals [9]. The work of many authors on the effects of the size of the samples into the phylogenetic inferences [36, 37, 38, 39, 40], demonstrate that the increase of terminals have a positive effect on the definition, stability of nodes and relations between taxa. Taking account of the increase of 10% to near 40% in our sample of terminals, and that the hypothesis obtained are much similar, we conclude that the results of the last analysis are better.

DISCUSSION

According to the preceding information it is evident that the classification of the American Anomalini remains as future subject of discussion, because much information to complete an optimal phylogenetic analysis is not easy to obtain. The better scheme will be obtained with the comparative study between representatives from all the world lineages. Also, an objective zoogeographical support will be added to obtain clear interpretations about the evolutionary hypothesis for each genus and distinct faunal assembles.

Studies on the immature stages, revision of type specimens, description of many new species,

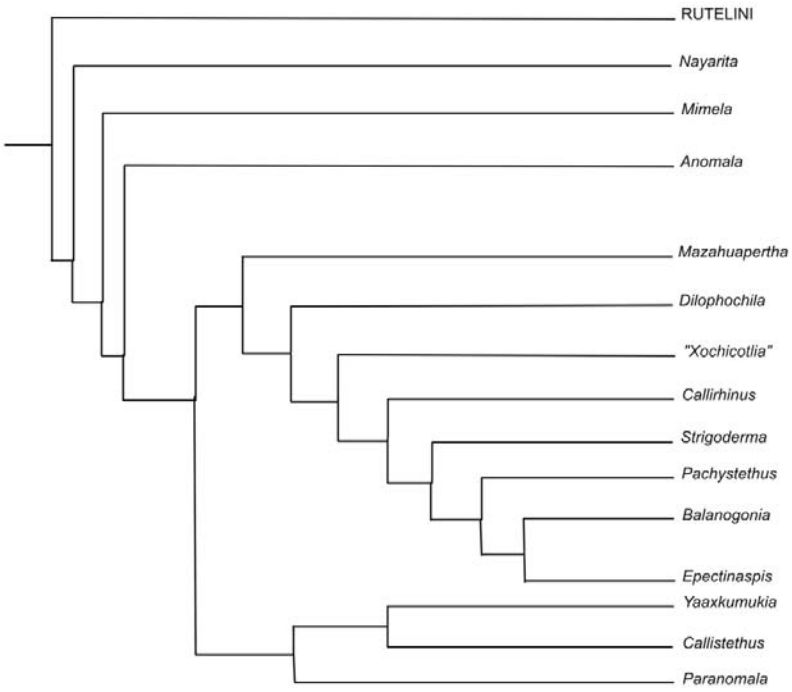


Figure 34. Dendrogram showing the hypothesis on the phylogenetic relationships between the American genera of Anomalini, including tentative position of the genera *Anomala* (s.*str*.) and *Mimela*.

molecular evidence and precise ecological information will be also important to complete the hypothesis of classification. We expect that in future new tests the approximations will be progressively refined and better supported than present proposals.

Exposed results also indicate significant advances in the description and definition of supraspecific taxa that aid to recognize particular problems. Some of these problems have been included in recent papers and others are nearly ready for publication. Other questions require more detailed studies, more specimens to review using fresh criteria and open mind. In our experience old ideas also will be useful with renewed points of view. Our results include a large number of characters never used before, as well as many characters continuously used since years back and other forgotten by some authors. Some old ideas about the structure of classification of shiny chafers were refreshed, gaining good support to the actual hypothesis.

One of the main problems dealing with the study of these beetles is in the collections. Nearly all the museums and institutions have large number of specimens mounted in the cabinets, but most part are poorly studied, not determined or provisionally identified. This fact reflects the reduced number of taxonomists interested in this abundant and diverse, but complex group. Unfortunately during our studies we had at hand very few correctly identified specimens from southeastern Asia or sub-Saharan Africa to make comparative descriptions, useful to confirm some problems with the genera *Anomala*, *Paranomala* and *Callistethus*.

Our main current objectives deal with the supraspecific classification of the large genus *Paranomala* in the Neotropical realm, including the definition, revision and phylogeny of each subgenus, the groups of species and the description of many new species.

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