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Chalcosicya maya n. sp, a new Mexican species (Coleoptera:
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and biogeography

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Chalcosicya maya n. sp, a new Mexican species (Coleoptera: Chrysomelidae: Eumolpinae) and its implications for morphology and biogeography

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Abstract. *Chalcosicya maya*, new species, (Coleoptera: Chrysomelidae: Eumolpinae) is described and the species key of Blake (1951) is modified to accommodate it. This is the first known mainland species of this previously Antillean genus. Sclerotized rods in the apical segment of the ovipositor of *Chalcosicya* Blake and related genera are shown to be useful systematic characters within the eumolpine tribe Adoxini. Relationships with other genera suggest that *Chalcosicya* belongs to a clade derived from ancestors with a western Tethyan distribution.

Resumen. Se describe *Chalcosicya maya* especie nueva (Coleoptera: Chrysomelidae: Eumolpinae). Esta es la primera especie conocida de tierra continente de este género previamente Antillano. La clave a las especies de Blake (1951) está modificado para acomodar esta especie nueva. Bielas esclerotizadas en el segmento apical del ovipositor en *Chalcosicya* y en géneros relacionados se ven como caracteres filogenéticos útiles dentro del tribo Adoxini. Relaciones con otros géneros sugieren que *Chalcosicya* pertenece a un clado derivado de ancestros con una distribución del Tethys oeste.

Key words. *Chalcosicya*, *Colaspina*, *Colaspidea*, Adoxini, ovipositor, Tethys Sea

Introduction

Blake (1930) erected the genus *Chalcosicya* for a eumolpine species from Cuba, and in subsequent publications (1938, 1951, 1966, 1971) added 24 more species and transferred three species of Suffrian, Bryant, and Blatchley to this genus, all from various islands of the West Indies. The genus is distinguished by small size (less than 4mm); robust, ovate body; black, dark bronze, green or blue color, and the dorsum usually covered with long hairs or scale-like setae. In this paper, I describe the first species of *Chalcosicya* known from the Central American mainland and revise the key to accommodate its identification. I also review Blake's (1951) discussion on the relations of *Chalcosicya* with other Eumolpinae genera, and propose a possible generic group and its biogeographical pattern.

Although *Chalcosicya* has been collected regularly in surveys of various Caribbean islands since Blake's studies, apparently no biological data have been published.

Materials and Methods

The description is based on two specimens collected in southern México. These were compared with specimens of the Antillean *Chalcosicya constanzae* Blake, *C. truncata* Blake and *C. grandis* Blake from the Florida State Collection of Arthropods (FSCA).

Results

Chalcosicya maya Flowers, new species

(Figures 1, 2, 5, 7-12, 25)

Diagnosis. Femoral teeth lacking, elytra rounded at apex in female, body evenly covered with stout, white, setae, without any trace of pattern.

Description (n=2). Length 2.9 mm, width 1.9 mm. Body color with head, pronotum, elytra, underside, and legs shining black, evenly covered with thick curved white setae, antennae, tarsi and apex of tibiae piceous (Fig. 1,2). Shape ovate, dorsally convex.



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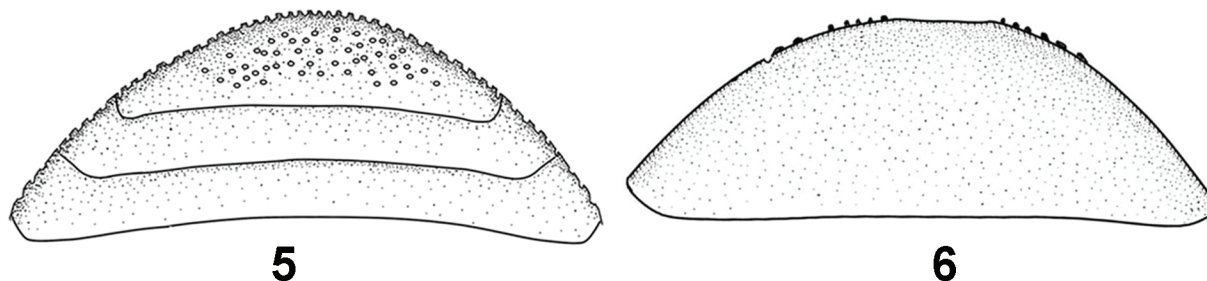


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Figures 1-4. Habitus and abdominal sternites of *Chalcosicya maya*, *Colaspina saportae*, and *Colaspidea oblonga* Blanchard. 1-2) *Chalcosicya maya*. 1) Lateral view; 2) dorsal view. 3) *Colaspina saportae*, dorsal view. 4) *Colaspidea oblonga*, dorsal view.

Head evenly punctate, punctures separated by distance greater than their diameters, apex of clypeus weakly emarginate. Frons strongly punctate with punctures separated by distance greater than their diameters, surface between punctures microreticulate; antennal calli smooth, delimited by a strong carina, surface within carina weakly concave. Eyes oval, shallowly and broadly emarginate at antennal insertion, with a deep sulcus along their upper margins. Mouthparts reddish brown, mandibles black, apex of labrum weakly emarginate.

Thorax: Prothorax distinctly wider than long, $L/W = 0.5$; pronotum convex, with posterior margin slightly wider than anterior margin; anterior angles acute, directed anteriorly; posterior angles ob-



Figures 5-6. Habitus and abdominal sternites of *Chalcosicya maya* and *Colaspidea oblonga* Blanchard. **5)** *C. maya*, abdominal sterna IV-VI, ventral view. **6)** *C. oblonga*, apical abdominal sternite.

tuse; all angles with a seta-bearing puncture; basal marginal bead present; lateral margins narrow, rounded, with widest part of pronotum behind middle; disc regularly, coarsely punctate, with punctures separated by a distance greater than their own diameters; surface between punctures microreticulate. Prosternum excavated for reception of gular area of head, subquadrate, wrinkled, sparsely punctate, with long, thick, whitish setae; posterior margin of intercoxal process truncate, width of intercoxal process 1.67× diameter of procoxa. Lateral arms of prosternum with anterior margin convex, surface setose. Proepimeron weakly concave, sparsely punctate, with punctures separated by distance greater than diameter of a puncture, with surface wrinkled. Mesosternum flat between coxae. Metasternum alutaceous; metepisternum with surface finely alutaceous.

Legs sparsely covered with long, thick, prostrate, whitish setae; all surfaces alutaceous. Femur strongly swollen in middle, lacking ventral teeth. Tibia with setae increasing in length toward apex of tibiae; all tibiae widened apically. Tarsi with claws bifid.

Elytra evenly punctate with punctures separated by distance less than their diameters; surface between punctures smooth with small punctulae; humeri prominent, subquadrate, width across humeri 1.2× width across pronotum; basal calli weakly developed; postbasal depression lacking. Sides of elytra subparallel in basal half, convergent in apical third; apices conjointly rounded.

Abdomen with segments subequal in length, with numerous long, thick, whitish setae; surface of segments alutaceous. Sterna VI and VII with lateral margins crenulate in female (Fig. 5). Pygidium lacking longitudinal median groove; pygidial surface finely alutaceous, apical margin crenulate.

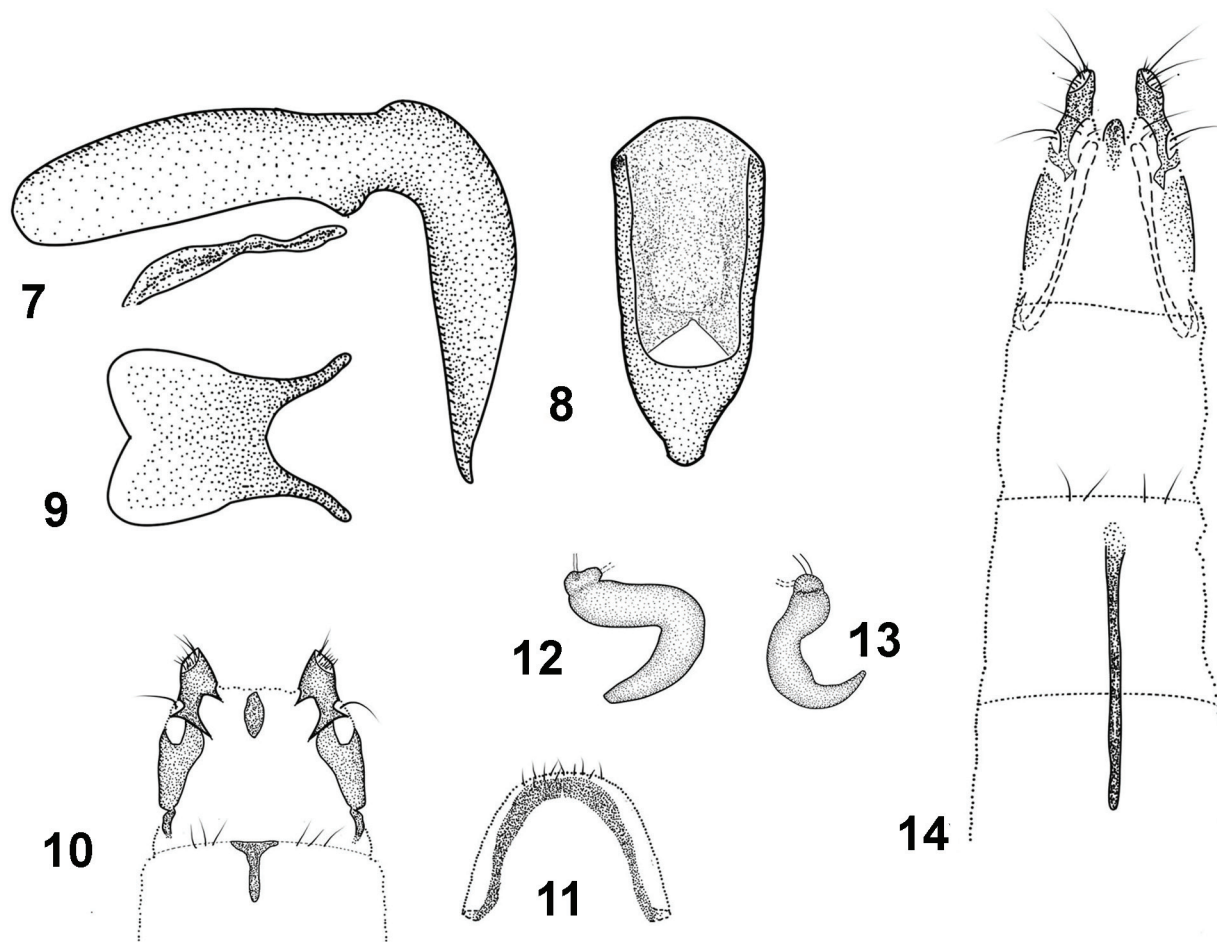
Genitalia: Aedeagus (Fig. 7-9) with basal hood broadly attached, basal spurs lacking, endophallus a membranous sac with numerous spicules. Ovipositor (Fig. 10, 11, 25) relatively short, sternum VIII short and T-shaped, hemisternites weakly sclerotized, narrowed basally; paraprocts relatively broad, curved inwardly at base to articulate with hemisternites; spermatheca (Fig. 12) with a small bulb-like receptacle and a larger inflated pump.

Material examined. Holotype ♂: MEXICO: Chiapas, 8.3 km S Narcisco Mendoza, 15 Sept. 1981, Clark & Coe [FSCA]. Allotype ♀: MEXICO: Chiapas, 11.2 km S Sumidero, 5 Sept. 1981, Clark & Coe [FSCA].

Etymology. *maya*, Spanish, named for the indigenous civilization in southern Mexico and Guatemala.

Key Placement. *Chalcosicya maya* presently keys to *Chalcosicya rotunda* Blake (couplet 8) in Blake’s (1951) key, as one of the group of species lacking teeth on the femora, but *C. maya* can be accommodated as follows:

- 8. Densely and evenly covered with short appressed scales, more or less concealing the integument beneath. ***C. nana* (Suffrian)**
- Scales or hairs not concealing the integument..... **8a**
- 8a(8). Irregularly covered with more or less erect scales; apex of median lobe of aedeagus forming an equilateral triangle (Fig. 13 in Blake 1951); Cuba. ***C. rotunda* Blake**
- Evenly covered with suberect hairs; apex of median lobe more elongate, with a low apical projection; southern Mexico. ***C. maya* Flowers**

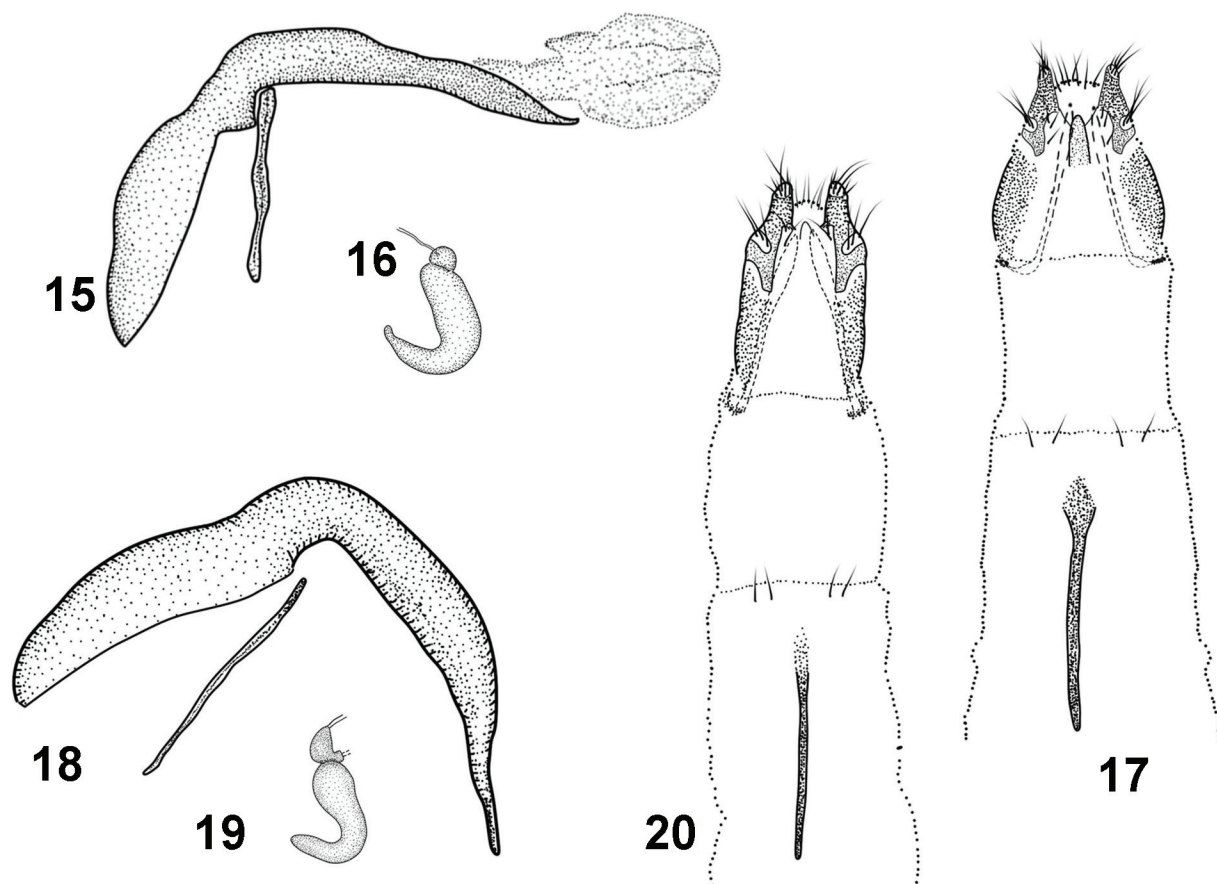


Figures 7-14. Structures of *Chalcosicya*. **7-12)** *Chalcosicya maya*. **7)** Median lobe, lateral view; **8)** median lobe, apical view; **9)** tegmen; **10)** ovipositor, ventral view; **11)** ovipositor, segment IX, dorsal view; **12)** spermatheca. **13-14)** Female genitalia of *Chalcosicya constanzae*. **13)** Spermatheca; **14)** ovipositor, ventral view.

Blake described three additional species of *Chalcosicya* in subsequent publications (Blake 1966, 1971). Two have toothed femora and the third is much larger than *C. maya*.

Discussion. *Chalcosicya maya* differs from the three Antillean species it was compared to in having a shorter ovipositor, and sternum VIII short and T-shaped (Fig. 10); in the Antillean species (as in Fig. 14) this sclerite is long and narrow. Variability in ovipositor length is found within other eumolpine genera such as *Prionodera* Chevrolat (Flowers 2004a) and *Beltia* Jacoby (Flowers, unpublished data). The ovipositor of *C. maya*, as well as those of the other species of *Chalcosicya* examined, differ from ovipositors in the Eumolpini illustrated in other publications (e.g., Askevold and Flowers 1994; Flowers 2004a, 2004b, 2009; Tanner 1927) in two important respects: the gonocoxi are single-segmented (the gonostyli are missing), and the paraprocts of the ninth segment of the ovipositor curve downward to meet the base of the hemisternites, which are relatively large, weakly sclerotized areas lacking basal rods (Fig. 24, 25).

This latter character appears in some, but not all, Adoxini: it is found in *Chalcosicya*, *Colaspina* Weise, and *Colaspidea* Laporte, *Macetes* Chapuis, *Demotina* Baly, and *Semmiona* Fairmaire, but not in *Graphops* LeConte or *Bromius* Chevrolat. In genera of Typophorini I have examined (*Typophorus* Chevrolat, *Metachroma* Chevrolat, *Paria* LeConte, *Afroeurymus* Selman) there is no connection between the elongate basal rods of the hemisternites and paraprocts. On the other hand, in all ovipositors of Eumolpini that I have seen, the hemisternites and paraprocts are prolonged into thin basal rods,

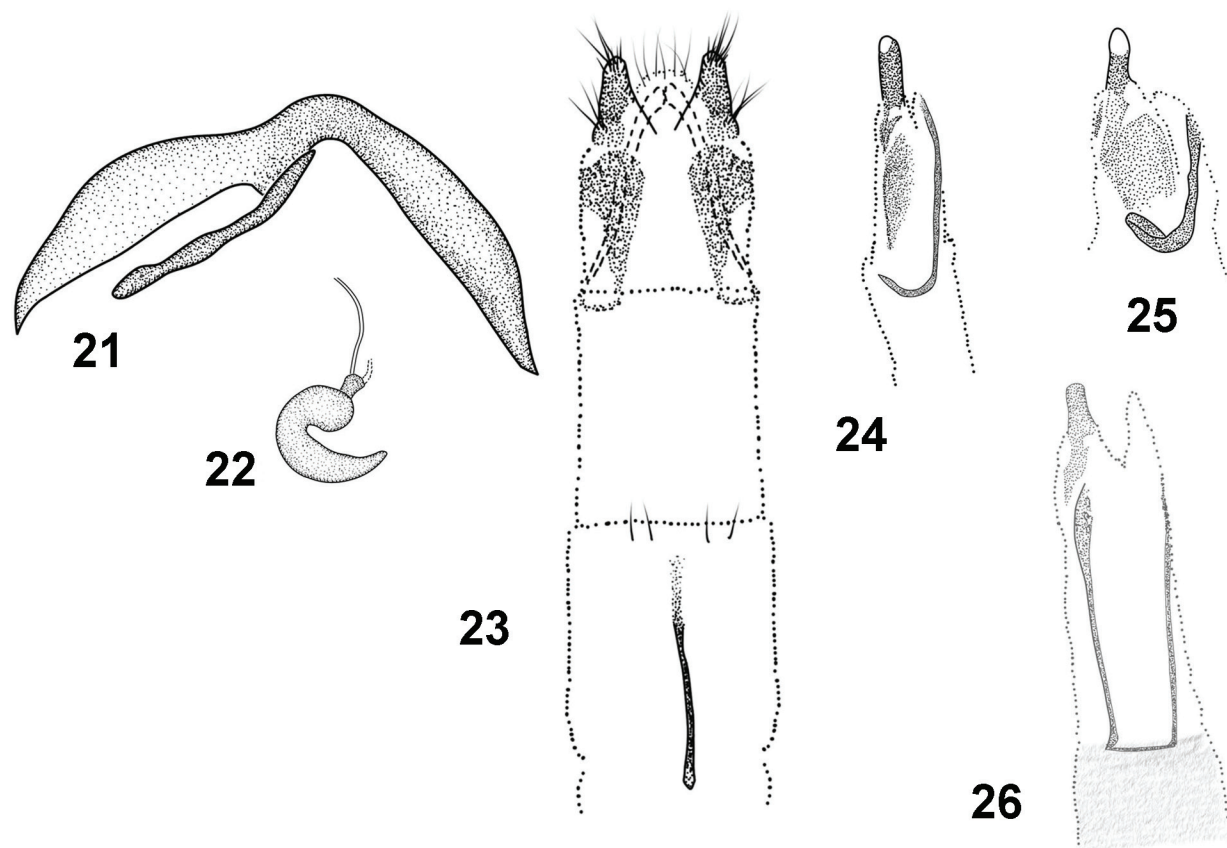


Figures 15-20. Structures of *Colaspina* and *Colaspidea*. **15-17)** *Colaspina saportae*. **15)** Median lobe, lateral view (endophallus partially everted); **16)** spermatheca; **17)** ovipositor, ventral view. **18-20)** *Colaspidea oblonga*. **18)** Median lobe, lateral view; **19)** spermatheca; **20)** ovipositor, ventral view.

and a separate transverse sclerite bridges them at the base of the apical segment (Fig. 26). This survey is very rudimentary but it offers some hope that characters exist that can define monophyletic groups within this large and confused tribe Adoxini.

In her revision of *Chalcosicya*, Blake (1951) noted similarities of this genus to *Colaspidea*. Both are small, have convex lateral wings of the prosternum, and are covered with hairs or hair-like setae. Blake felt that *Colaspidea* was clearly different from *Chalcosicya* because the dorsal setae in *Colaspidea* are hair-like, and those of *Chalcosicya* are scale-like (although even in that same publication Blake described both as pubescent and glabrous species). Blake also cited the lack of denticles on the femora of *Colaspidea* as a difference with *Chalcosicya*, although several species of *Chalcosicya* also lack denticles. Blake did not mention the monotypic European genus *Colaspina saportae* (Grenier) (Fig. 3), from Spain and southern France, which also strongly resembles *Chalcosicya* in the shape of the body and especially the pronotum have a much closer resemblance to *Chalcosicya* than does *Colaspidea*, and the single species, *C. saportae*, is dorsally clothed with the same type of scale-like setae as found in many *Chalcosicya*.

Chalcosicya, *Colaspina*, and *Colaspidea* share the following combination of characters: 1) pygidium lacking wing folding grooves; 2) lateral arms of the prosternum with convex anterior margins, and prosternum excavated for reception of the gula of the head; 3) dorsal surface (at least in most species) covered with hair-like or scale-like setae; 4) tarsal claws bifid; 5) pronotum with lateral margin distinct and smooth; 6) aedeagus with basal hood broadly attached and basal spurs lacking (Fig. 7, 15, 18, 21); and 7) ovipositor with paraprocts curved inwardly at the base and meeting the base of the hemisternites (Fig. 24, 25). *Colaspina*, *Colaspidea* and at least some *Chalcosicya* have elongate ovipositors with strap-

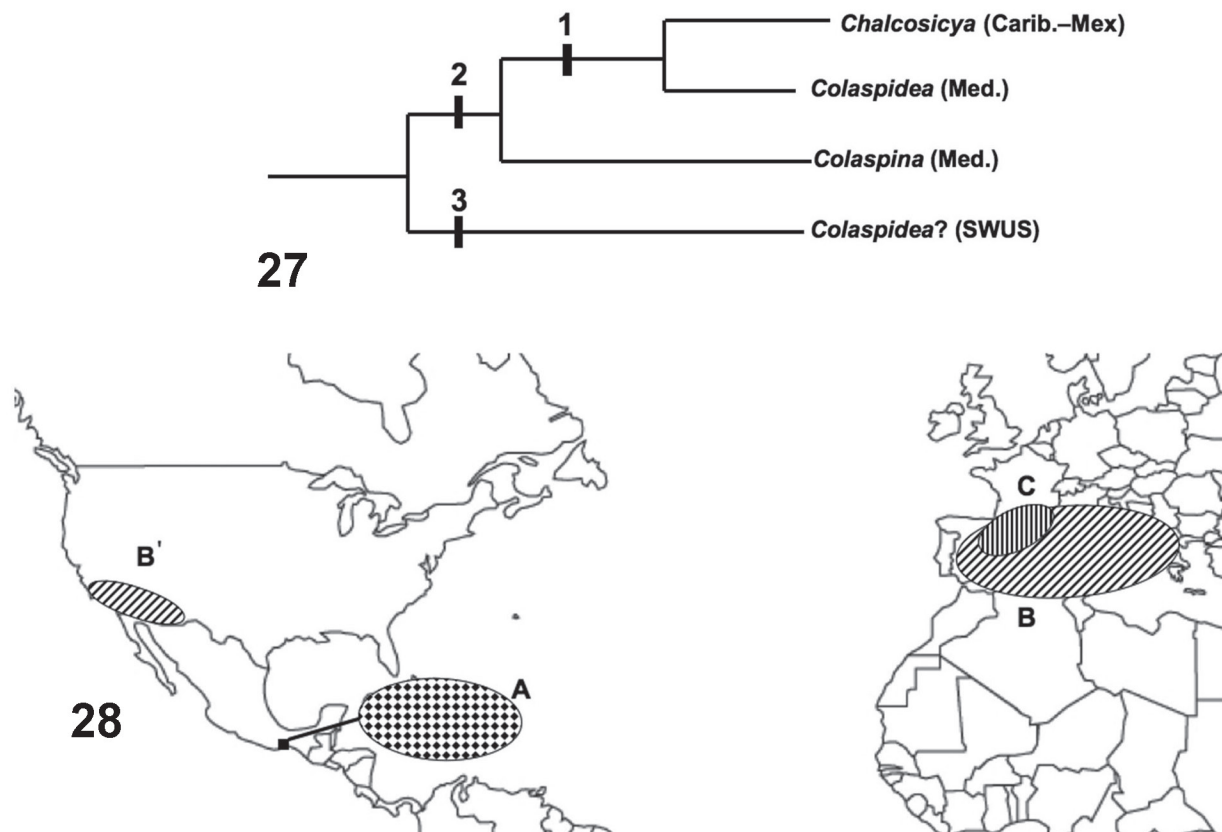


Figures 21-26. Structures of *Chalcosicya*, *Colaspina*, and *Colaspidea*. **21-23)** *Colaspidea smaragdulus* LeConte. **21)** Median lobe, lateral view; **22)** spermatheca; **23)** ovipositor, ventral view. **24-26)** Lateral view of apical segment of ovipositor. **24)** *Chalcosicya constanzae*; **25)** *Chalcosicya maya*; **26)** *Beltia* sp.

like VIII sternites and hemisternites lacking basal rods (Fig. 14, 17, 20, 23). Based on the combination of external and genitalic characters, I propose a hypothesis (Fig. 27) that *Chalcosicya* and Mediterranean *Colaspidea* (Fig. 4) are sister genera, with *Colaspina* forming a sister genus to the first two combined. A potential synapomorphy uniting *Chalcosicya* and *Colaspidea* may be the crenulate margin of the female apical abdominal sternite (Fig. 5, 6) which is much more developed in *Chalcosicya* (Fig. 5). The spermathecal shape is very similar in *Chalcosicya* and *Colaspina* (Fig. 12, 13, 16), but this shape of spermatheca is also found in unrelated genera (e.g., *Demotina* and *Graphops*). In the Mediterranean *Colaspidea* the spermatheca receptacle is somewhat larger (Fig. 19), and the body shape is different due to the wingless condition.

Colaspidea of California and the southwestern U.S.A. differs in two respects from their Mediterranean congeners: in the structure of the spermatheca (Fig. 22), which is very similar to the spermatheca of *Bromius obscurus* (L.), and in lacking crenulations on the apex of the last abdominal sternite. The difference in body form between the U.S. and Mediterranean species is due to the wingless condition of the latter; similar differences between winged and wingless forms can be seen within other genera, e.g., *Longitarsus* Latreille (Chrysomelidae: Galerucinae: Alticini). It may be that the U.S. *Colaspidea* represent a separate genus, but, as the group needs a general revision (Riley et al. 2002), its status is left as is for now. However, morphology suggests it to be otherwise closely related to the Mediterranean *Colaspidea*, and thus also to *Chalcosicya* and *Colaspina*.

Currently, *Chalcosicya* and *Colaspina* are classified in the Series Mychroites in the Adoxini (Bechyné 1953, Clavereau 1914); however, *Colaspidea* (or at least the New World part of this genus) has been placed in the Series Lepronites (Riley et al. 2003). Both these tribes are defined on the basis of widely distributed external characters (e.g. bodies covered with setae) that have little phylogenetic value above



Figures 27–28. Map and taxon–area cladogram of *Chalcosicya*, *Colaspina* and *Colaspidea*. **27)** Taxon–area cladogram. Synapomorphies: 1, crenulate margin of female abdomen; 2, spermatheca with small bulb-like receptacle; 3, Bromius–type spermatheca. Abbreviations: Carib, Caribbean; Mex, Mexican; Med, Mediterranean; SWUS, southwestern United States. **28)** Distribution map of genera. A (checkerboard), *Chalcosicya*, showing track to locality of *C. maya*; B (diagonal lines), Mediterranean *Colaspidea*; B' (same), United States *Colaspidea*; C (vertical lines), *Colaspina*.

genus level. This study suggests that all three genera belong in the same series, but correct placement of these genera must await much clearer definitions of subtribal groups in the Adoxini.

Biogeography. The discovery of a mainland species of *Chalcosicya* presents no particular biogeographic problem: there are numerous biogeographic connections between the greater Antilles and the Yucatán area of Mexico (Croizat 1958, 1976; Liebherr 1988; Morrone 2001). Biogeographic reconstructions, in particular GAARlandia (Greater Antilles-Aves Ridge-landia) (Iturralde-Vinent and MacPhee 1999), show no barriers up to the mid-Cenozoic that could not be overcome by a moderately mobile insect.

The sister-group relationship with Mediterranean *Colaspidea* and more distantly with South European *Colaspina*, then southwestern U.S. *Colaspidea*, raises somewhat more complicated issues (Fig. 28). These areas were connected up to at least the mid-Jurassic, forming the northern shore of the “Hispanic Corridor” (Rais et al. 2007) of the western Tethys Sea. Also, a fossil eumolpine identified as possibly an adoxine genus is known from the Crato Formation of the Cretaceous (Martill et al. 2007). The most parsimonious explanation is that ancestors of the *Chalcosicya-Colaspidea-Colaspina* clade were on both sides of the future Atlantic Ocean during this period. The fall of the Chicxulub bolide at the end of the Cretaceous would have been a severe disturbance, perhaps triggering mega-tsunamis that may have devastated all emergent islands and low-lying land masses over much of *Chalcosicya*’s present range (Iturralde-Vinent and MacPhee 1999). However, biogeographic literature abounds in cases of plant and animal groups that are older than the islands where they are endemic, or that have

survived in other places where geologic events have supposedly removed all terrestrial life (the “total inundation” theory for New Zealand and New Caledonia; see Heads (2010) for a review. While the affinities of *Chalcosicya-Colaspidea-Colaspina* with other eumolpine genera have yet to be determined, cladistic and biogeographical evidence points to two things: a Mesozoic age, and a Tethyan origin.

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Literature Cited

- Askeveld, I. S., and R. W. Flowers. 1994.** *Glyptosceloides dentatus*, a genus and species of Eumolpinae new to Chile (Coleoptera: Chrysomelidae). *Revista Chilena de Entomología* 21: 69-76.
- Blake, D. H. 1930.** Synonymies of Antillean Chrysomelidae, with descriptions of new species. *Bulletin of the Brooklyn Entomological Society* 25: 209-224.
- Blake, D. H. 1938.** Eight new species of West Indian Chrysomelidae. *Proceedings of the Entomological Society of Washington* 40: 44-52.
- Blake, D. H. 1951.** A revision of the beetles of the genus *Chalcosicya* Blake (Chrysomelidae) from the West Indies. *Bulletin of the Museum of Comparative Zoology* 106: 287-317.
- Blake, D. H. 1966.** Ten new chrysomelid beetles from the West Indies and Key West. *Proceedings of the Entomological Society of Washington* 68: 213-222.
- Blake, D. H. 1971.** Fifteen new West Indian chrysomelid beetles. *Proceedings of the Entomological Society of Washington* 73: 269-282.
- Bechyné, J. 1953.** Katalog der neotropischen Eumolpiden (Col. Phytoph. Chrysomeloidea). *Entomologische Arbeiten aus dem Museum G. Frey* 4:26-304.
- Clavereau, H. 1914.** Chrysomelidae 11: Eumolpinae. *In*: W. Junk and S. Schenkling, eds. *Coleopterorum Catalogus*. Berlin. 215 p.
- Croizat, L. 1958.** Panbiogeography, Vols. 1, 2a, and 2b. Published by the author; Caracas. 1731 p.
- Croizat, L. 1976.** Biogeografía analítica y sintética (“Panbiogeografía”) de las Américas. *Boletín de la Academia de Ciencias Físicas, Matemáticas y Naturales* 35: 1-890.
- Flowers, R. W. 1999.** Internal structure and phylogenetic importance of male genitalia in the Eumolpinae. p. 71-93. *In*: M. L. Cox (ed.). *Advances in Chrysomelidae biology* 1. Backhuys; Leiden. viii + 671 p.
- Flowers, R. W. 2004a.** A review of the Neotropical genus *Prionodera* Chevrolat (Coleoptera, Chrysomelidae, Eumolpinae) with description of a new genus. *Zootaxa* 631: 1-54.
- Flowers, R. W. 2004b.** New flightless Eumolpinae of the genera *Apterodina* Bechyné and *Brachypterodina* n. gen. (Coleoptera: Chrysomelidae) from the Neotropics. *Zootaxa* 549: 1-18.
- Flowers, R. W. 2009.** A new genus and species of Eumolpinae (Coleoptera: Chrysomelidae) from the western dry forest of Ecuador. *Zootaxa* 2132: 65-68.
- Heads, M. 2010.** Old taxa on young islands: a critique of the use of island age to date island-endemic clades and calibrate phylogenies. *Systematic Biology* 60: 1-15.
- Iturralde-Vinent, M. A., and R. D. E. MacPhee. 1999.** Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* No. 238: 1-95.
- Liebherr, J. K. (ed.). 1988.** Zoogeography of Caribbean insects. Cornell University Press; Ithaca, NY. ix + 285 p.
- Martill, D. M., B. Günter, and R. F. Loveridge. 2007.** The Crato fossil beds of Brazil, window into an ancient world. Cambridge University Press; Cambridge, U.K. xvi + 625 p.
- Morrone, J. J. 2001.** Biogeografía de América Latina y el Caribe. M&T-Manuales & Tesis SEA; Zaragoza. Vol. 3. 148 p.

- Rais, P., B. Louis-Schmid, S. M. Bernasconi, and H. Weissert. 2007.** Palaeoceanographic and palaeoclimatic reorganization around the Middle-Late Jurassic transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251: 527-546.
- Riley, E. J., S. M. Clark, R. W. Flowers, and A. J. Gilbert. 2002.** Family 124. Chrysomelidae. p. 627-691. *In*: R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds.). *American beetles*, Vol. 2. CRC Press; Boca Raton, FL. xiv + 861 p.
- Riley, E. G., S. M. Clark, and T. N. Seeno. 2003.** Catalog of the leaf beetles of America north of Mexico (Coleoptera: Megalopodidae, Orsodacnidae and Chrysomelidae, excluding Bruchinae). *Coleopterists Society, Special Publication no. 1*: 1-290.
- Tanner, V. M. 1927.** A preliminary study of the genitalia of the female Coleoptera. *Transactions of the American Entomological Society* 53: 5-50.

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