Article

Bajacanthon, a New Subgenus for the Mexican Deltochilini (Coleoptera: Scarabaeidae: Scarabaeinae) Fauna [†]

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Abstract: In this study, data are presented for the designation of the new subgenus (*Bajacanthon*) for *Canthon obliquus* Horn, 1894 (Deltochilini). The new subgenus *Bajacanthon* is described based on a multiple evidence approach using morphological and molecular characters. This new subgenus has some unique characters, and is the remnant of an old South American migratory movement into the Mexican Transition Zone. This beetle species has survived in isolation in the south half of the peninsula of Baja California (Mexico). Results based on molecular clock inference showed that the split between the lineages leading to the subgenus *Bajacanthon* and *Boreocanthon* took place nearly 16 Mya, whereas the radiation within *Bajacanthon* was dated to 3.7 Mya.

1. Introduction

Deltochilini Lacordaire, 1856 (Coleoptera: Scarabaeidae: Scarabaeinae) (formerly Canthonini van Lansberge, 1875 in part) is one of the most diverse tribes of dung beetles in the Americas. It includes elements from three great migratory movements that summarize the Neotropical contribution to the Mexican Transition Zone: (1) a current migration, which continues expanding into Mexico in zones with tropical evergreen forest [1,2]; (2) a movement that occurred after the establishment of the Isthmus of Panama [1–3]; and (3) an ancient element that diversified in the present day Mexican Plateau along with widely distributed lineages in the current USA. [2,4,5].

Among these ancient Neotropical elements in Mexico, *Canthon obliquus* Horn, 1894 [6] has an exclusive set of characters that has led us to the hypothesis that this taxon could be classified as a new subgenus within *Canthon*. It is possible that the morphological novelties (e.g., novel paramers, distinctive elytra shape and apterism) observed in this taxon are the results of its long-term geographic isolation. The distribution of this beetle is limited to south of the Baja California Peninsula, mainly at Sierra de la Laguna Mountains and two more sites nearby at La Paz Bay (Figure 1).

Taxonomists traditionally have delimited taxonomic categories using specific diagnostic characters. For instance, wing modification in insects is diagnostic for order [7,8], tarsal formula is used for recognizing tribe [9], genitalia modifications for assigning species [10], etc. On the one hand, such diagnostic characters may evolve so slowly that successive

cladogenesis may pass unnoticed by the taxonomist, while on the other hand, the evolutionary rate of some of those characters may be so high that it leads to parallelisms and convergences that may mislead the taxonomist into establishing artificial taxa. Phylogenetic systematics mends those potential pitfalls by recognizing only monophyletic groups based on an exclusive set of synapomorphies. The advent of molecular data has allowed the use of discrete characters (e.g., segregated sites, sequence motives, etc.) and genetic distances as guidelines for assigning taxonomic ranks [11,12]. In phylogenetic systematics, a second rule to reduce subjectivity for assigning a taxonomic category is to give the same rank to sister clades.
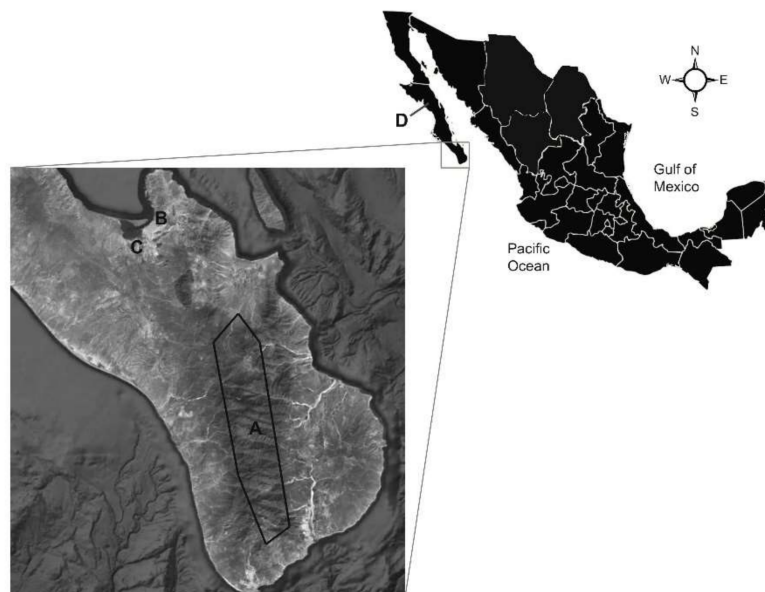

Figure 1. Collecting sites. *Canthon* (*Bajacanthon*) is distributed at the southernmost part of the Baja California Peninsula, Mexico. A, Sierra La Laguna mountain range; B, Cerro el Mesquitito; C, La Paz City; D, El Juncalito in the Sierra de la Giganta.

Canthon obliquus is perhaps one of the least understood species of Deltochilini. Here, we use a multiple evidence approach (i.e., morphology and DNA sequences) to investigate the phylogenetic relationships of *C. obliquus* with the other *Canthon* and test whether its placement in *Canthon* s. str. is phylogenetically sound. Specifically, the analyses are based on a detailed anatomical study of the endophallites, complemented with a phylogenetic and genetic distance analysis of a nucleotide data set. Additionally, a molecular clock model is applied to the phylogenetic data for inferring a temporal evolutionary scenario for this beetle species. We must stress that this study does not pretend in any way to be an extensive phylogenetic inference for the genus *Canthon*. This genus is highly heterogeneous and certainly not a monophyletic group. Thorough phylogenetic and taxonomic conclusions for this genus must require a wider taxa sampling than the one used here. The goal of this review is simply to present a well-supported taxonomic placement for *C. obliquus*.

2. Materials and Methods

2.1. Morphology Analyses

Morphological variation of the genitalia was examined in specimens collected from Sierra de la Laguna (Baja California Sur, Mexico), comparing them with five closely related *Canthon* taxa (i.e., *C. blumei*, *C. humectus humectus*, *C. humectus assimilis*, *C. humectus hidalgoensis*, and *C. (Boreocanthon) praticola*). The endophallus was dissected, and all of the components (i.e., endophallites) as well as the tegmen were photographed using a multifocal digital microscope Leica Z16 APOA. At least five specimens of each taxon were softened by immersion in hot water (i.e., 60 °C) for 60 min. Forceps were used for dissect-

ing the endophallus under a stereomicroscope. The aedeagus was removed through the pygidial opening and placed in an Eppendorf tube containing 10% KOH. The tubes were immersed in hot water (i.e., 65 to 70 °C) for 30 to 40 min or until the tissue was removed. The aedeagus was fixed in 70% ethanol after being rinsed under running. Male genitalia terminology follows Cristóvão and Vaz-de-Mello [13].

The material studied of *C. obliquus* was deposited in the in the Entomological Collection at Instituto de Ecología (IEXA), Xalapa, Veracruz, Mexico, and in the personal collection of Gonzalo Halffter (Coatepec, Veracruz, Mexico).

2.2. Molecular Analyses

2.2.1. Sampling, DNA Extraction, and Sequencing

For this study, four individuals were selected at random from the specimens collected at Sierra de la Laguna (Baja California) by Arriaga-Jimenez and Escobar during the fall of 2018. Specimens were collected with pitfall traps, euthanized and conserved in 100% ethanol before being transported to the laboratory. Once there, all specimens were frozen and stored at -20 °C. The data set encompassed sequences of two mitochondrial genes: Cytochrome Oxidase Subunit I (*COI*) and *16S rRNA*. Genomic DNA was recovered by grinding both hind legs of each beetle. Before this, the legs were observed under a microscope to remove any potential crude source of contamination (e.g., mites). Tissue samples were processed with the DNeasy Blood & Tissue kit (QIAGEN, Hilden, Germany) following the manufacturer protocol. The *COI* gene was amplified with primers M202 "Jerry" (5'-caacatttattttgattttttgg-3') and M70 "Pat" (5'-tccaatgcactaatctgccatatta-3') [14]. For *16S rRNA*, we used the primers M14 "16Sar" (5'-cgcctgtttaacaaaaacat-3') and M233 "ND1A" (5'-ggtcccttacgaatttgaatatatcct-3') [14]. PCR was performed using a general temperature program of 94 °C for denaturing, 50–53 °C for annealing and 72 °C for DNA extension. The program was repeated for 35 cycles. Successful PCR amplifications were purified using the QIAquick kit (QIAGEN, Hilden, Germany). Macrogen Inc. (Seoul, Korea) was responsible for the final sequence of the samples. Sequences were edited and aligned with the aid of the computer software Sequencher v5 (Gene Codes Corp, Ann Arbor, Michigan).

2.2.2. Phylogenetic Inference and Temporal Scenario

The data matrix for the combined data set encompassed a total of 1525 nucleotides (*COI*: 767 bp; *16S rRNA*: 758 bp). Homologous sequences for other Scarabaeinae taxa (viz., *Cryptocanthon lobatus*, *Canthon* (*Boreocanthon*) sp., *Pseudocanthon perplexus*, *Canthon blumei*, *C. humectus*, *C. occidentalis*, *C. riverai*, *C. indigaceus*, *C. imitator*, *C. cyanellus*, *C. lunatus*, *C. edentulus*, *C. lamprimus*, *C. luteicollis*, and *C. smargadulus*) were included in the analysis. Although limited, this species set includes taxa from North and South America. The geotrupid beetle *Frickius variolosus* Germain, 1897 was selected as outgroup for rooting the tree and character polarization. The phylogeny was recovered from a Bayesian inference analysis (BI) using the software MrBayes v3.2.3 [15]. The nucleotide substitution model for each locus was selected using the Akaike information criterion [16] in jMODELTEST v2.0.2 [17]. In all analyses, the partitions were declared as unlink, and no constraints in the topology were enforced. Analysis was set for 40 million generations for two independent parallel runs with one cold and three hot chains each. Trees and parameters were sampled every 1000 generations. The majority-rule consensus tree was obtained, with its respective posterior probabilities, after discarding the initial 25% of the accumulated trees [15]. The software MEGA v 6.0 [18] was used for computing corrected genetic distances. This correction was based on the Kimura two-parameter model of nucleotide substitution.

The Bayesian tree was used as the reference (i.e., tree prior) for inferring a temporal scenario for these taxa. The software BEAST v1.8.2 [19] was used for dating cladogenetic events. To estimate divergence times, the "uncorrelated relaxed clock" model was used. The genealogy was calibrated using the nucleotide substitution rates of 1.2% for *16S rRNA* and 2.0% for *COI* [20]. The nucleotide substitution models, as well as the parameters used as priors for each locus, were those indicated by jMODELTEST. The coalescence process

was used prior to the tree model. Monte Carlo Markovian Chains were run for 20 million generations, sampling trees and parameters every 1000 generations. The analysis was iterated until the combined results scored at least 200 for the Monte Carlo Markovian Chains effective sample size for all parameters, and posterior intervals spanning the 95% highest posterior density. The program TRACER v1.6 [21] was used for assessing the stationarity of all parameters. The resulting trees from each selected run were combined using LogCombiner v1.8.2 [19], applying a burn-in of 25%. The nodes evaluated were those that had a minimum posterior probability value of 0.9.

3. Results

Canthon (Bajacanthon) Halffter, New Subgenus

Type species: *Canthon obliquus* Horn, 1894, here designated (Figure 2).
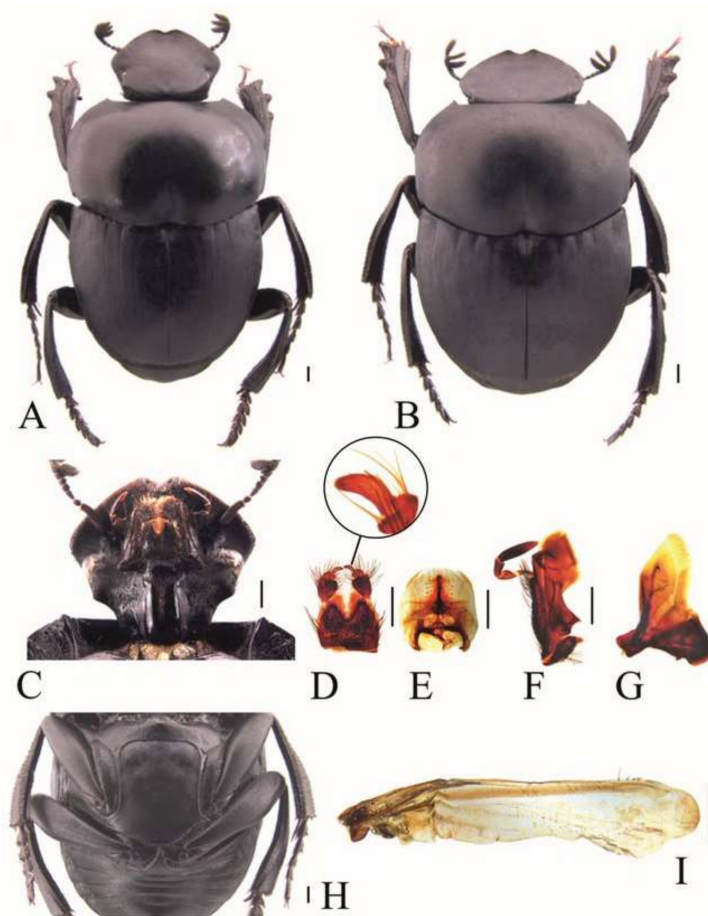
Figure 2. *Bajacanthon* subgen. nov. (**A**), dorsal habitus of *Canthon* (*Bajacanthon*) *obliquus* major male; (**B**), dorsal habitus of a minor male; (**C**), gula; (**D**), labium; (**E**), epipharynx; (**F**), right maxilla; (**G**), right mandible; (**H**), ventral view showing mesoventrites, metaventrites and mesocoxae; (**I**), reduced metathoracic wing. Scale = 0.5 mm.

Diagnosis. Dorsal surface of eyes narrow, barely visible; anterior edge of labium with deep triangular notch; separation between submentum and gula triangular, deeply elongated within gula; gula almost entirely divided in two parts longitudinally; pronotum wider than maximum elytral width, domed; brachypterous; metafemora ventrally with interrupted margin on the anterior edge, unmarginated posteriorly; meso- and metatarsomeres compressed; meso- and metatarsomeres I–IV triangular.

Description. Subgenus of *Canthon* (*sensu* Halffter and Martínez [22]). Maximum width on pronotum (Figure 2A,B). Head. Anterior edge slightly notched at center; anterior

and lateral edge not marginated; posterior edge of the frons with short and shallow groove at center. Head without tubercles or carinae. Dorsal surface of eyes narrow, barely visible. Clypeogenal sutures inconspicuous. Clypeal process keel-shaped, poorly defined. Separation between submentum and gula triangular, deeply elongated within gula; gula almost divided in two parts longitudinally (Figure 2C). Mouthparts (Figure 2D–G) as previously described for the subgenus *Canthon* [22,23], except for last labial palpomere reniform and glabrous (Figure 2D).

Thorax. Pronotum markedly transverse, domed, wide; posterior edge without margin; prescutelar depression well defined; mid-longitudinal line with shallow groove. Hypomeron almost flat anteriorly, without hypomeral carina. Metanepisternum with a well-marked keel parallel to the margin running across its the anterior 2/3. Mesoventrite long, equivalent to $2\frac{1}{2}$ times the distance between the internal margins of mesocoxae (Figure 2H). Mesocoxae longitudinal, parallel, separated by a rectangular metaventrite (Figure 2H).

Tergite 8. Exposed, as wide as long; almost flat, completely marginated, separated from tergite 7 by a complete margin. This is an important distinctive feature of many *Canthon* spp.

Wings. Elytra with nine striae; without humeral carina. Metathoracic wings reduced (Figure 2I), preventing flight.

Legs. Metafemora ventrally with marginal line not continuous on anterior edge (Figure 2H); posterior edge without margin. Protibiae tridentate. Second and third meso- and metatarsomeres laterally compressed, with external edge dilated, giving to each tarsomere a triangular appearance; apical metatarsomere rectangular. First metatarsomere equal or slightly smaller to second in length. Tarsal claws small, without teeth.

Tegmen. Parameres with globular and projecting apex; each paramere with a well-marked wing-shaped elongation (Figure 3A,B).
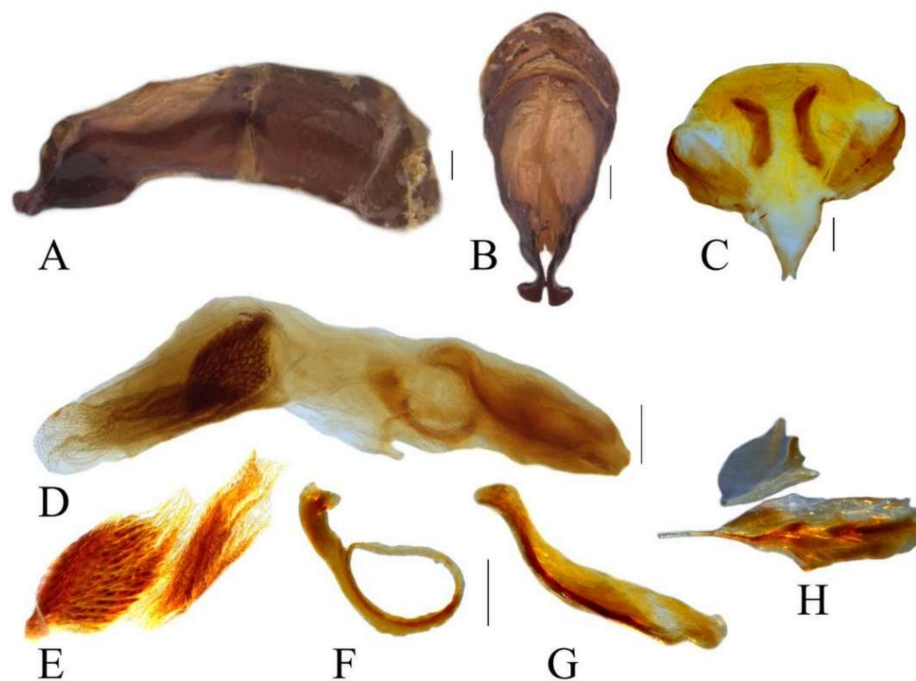
Figure 3. *Bajacanthon* subgen. nov. (**A**), aedeagus of *Canthon* (*Bajacanthon*) *obliquus*; (**B**), parameres; (**C**), genital segment; (**D**), internal sac of aedeagus; (**E**), raspules; (**F**), ring sclerite; (**G**), sigmoid sclerite; (**H**), flagellum. Scale = 0.2 mm.

Spiculum gastrale. Similar to the triangular type proposed by Medina et al. [24]; lateral sclerotized plates obliquely placed; medial sclerotized plate completely divided into two lateral chitinized plates, resembling two opposite half-moons (Figure 3C).

Endophallus. Tubular, elongated and membranous (Figure 3D). Apical area membranous, slender, semitransparent, covered by microscopic raspulae; with a darkened, oval and conspicuous area covered with large and sharp raspulae (Figure 3E) whose tips project inwards into the endophallus, and an elongated area parallel to the membrane, covered by very fine and dense raspulae.

Endophallites. (1) Circular part closed, thin, oval (Figure 3F); with an enlarged, sclerotized and sub-straight handle, (2) Elongated, sinuate (Figure 3G); apical border rounded and curved. (3) Transfer apparatus is irregular (Figure 3H); with a long filament at the apex; with a small free sclerite in the internal margin.

Secondary sexual characters. Male protibial spur elongated, bifurcated at the apex; female protibial spiniform, slightly curved, acute.

Taxonomy. Within *Canthon*, the subgenus *Bajacanthon* is characterized by a combination of characters that do not occur as such in any other species (see Diagnosis). In separating the subgenera of *Canthon* and its closely related taxa, the presence or absence of a parallel line on the anterior edge of the metafemora is a useful character. As an exception, in *Bajacanthon* the specimens can show a margin, though it is never complete, or it is totally absent. From the apical view, each one of the parameres has a wing-shaped expansion (Figure 3). Ventral structure of the clypeus with sensilla; with antescutelar impression. *Bajacanthon* differs from other North American *Canthon* by showing a parallel keel to the inner edge in the metaepisterna, and by the structure of the thoracic meta- and meso-tarsi.

To further explore the placement and affinities of *Bajacanthon* among the Deltochilini of the Mexican Transition Zone, the mouthparts have been compared with those of the species of *Canthon* found in Mexico [23]. The only clear character that differentiates *Bajacanthon* is the last labial palpomere reniform and glabrous.

DNA data. Our *COI* data set encompasses a fragment of 767 bp corresponding to the second half of the gene from position 740 to 1505. The *16S rRNA* data set encompasses a fragment of 758 bp that aligns to the middle section of the gene from position 484 to 1242. *Drosophila melanogaster* mitochondrial genome (GenBank accession number NC_024511) is used as a reference for the nucleotide position of both genes. The aligned matrix for the *COI* shows 291 segregated sites (262 polymorphic and 28 singletons), whereas the *16S rRNA* matrix shows 126 segregated sites (111 polymorphic and 15 singletons). In total, *Bajacanthon* has 12 fixed autapomorphies (Table 1). From these, six are found in the *COI* sequence (3 transitions, 2 transversions, and 1 mixed); whereas, the other six are in the *16S rRNA* sequence (4 transitions, 1 transversions, and 1 mixed). The average corrected genetic distance within individual taxa for the concatenated alignment is 0.8% (ranging from 0.0 to 3.6%; Table 2). In average *Bajacanthon* diverges from other taxa in 146.2 positions ($\pm$36). This is slightly smaller than the average difference between other groups (149.2 $\pm$ 48). Taking into account only the *COI* sequence data, the average corrected genetic distance within individual taxa is 1.1% (ranging from 0.0 to 5.5). On average, *Bajacanthon* diverges 12.7% ($\pm$1.5%) from other taxa. The average corrected distance between other taxa is 13.8% ($\pm$1.8%). A similar pattern is observed for the 16S rRNA data set. Although there is not a specific threshold, the BOLD initiative recommends a 2% distance for insects to differentiate and establish the species level [11,12]. Therefore, the average values obtained for these data sets (i.e., total evidence 11.2%, *COI* 12.7%, and *16S rRNA* 9.7%) certainly granted the assignation of the subgenus taxonomic rank.

Phylogenetic and temporal inference. The genera *Cryptocanthon* and *Pseudocanthon* are recovered in robust clades (Bayesian posterior probabilities = 1; Figure 4). However, even with the limited data set used here, the phylogeny shows that the genus *Canthon* is not a monophyletic group. The first split within the ingroup occurred around 35 Mya separating *Cryptocanthon* from the ancestor of the other genera. The radiation within *Canthon* started during the early Oligocene (31.5 Mya). *Pseudocanthon Canthon* diverged from a lineage within *Canthon* in the early Miocene (20 Mya). Another evolutionary lineage within the genus *Canthon* is that of the ancestor (22.8 Mya) of the subgenera *Boreocanthon* and *Bajacanthon*. These two subgenera split 16.4 Mya, and the radiation of *Bajacanthon* took

place during the Pliocene around 3.7 Mya. The molecular dating analysis suggests that the main radiation within each species sampled (including *C.* (*Bajacanthon*) *obliquus*) occurred mainly during the Pleistocene.

Table 1. Fixed segregated sites for *Canthon* (*Bajacanthon*) *obliquus*.

Position [1]	Cytochrome Oxidase Subunit I						16S rRNA					
	823	850	878	1007	1147	1198	636	694	1072	1073	1178	1239
C. (*Bajacanthon*) *obliquus*	C	C	A	C	T	T	G	G	G	C	C	A
C. (*Boreocanthon*) sp.	A	T	G	T	A	A	A	A	A	T	T	T
C. blumei	T	T	G	T	A	A	A	T	A	T	T	T
C. cyanellus	T	T	G	T	R	A	A	A	A	T	T	T
C. edentulus	A	T	G	T	A	A	A	A	A	T	T	T
C. humectus	T	T	G	T	G	A	A	T	A	T	T	T
C. imitator	T	T	G	T	A	A	A	T	A	T	T	T
C. indigaceceus	T	T	G	T	A	A	A	T	A	T	T	T
C. lamprimus	A	T	G	T	A	A	A	T	A	T	T	T
C. lunatus	T	T	G	T	A	A	A	A	A	T	T	T
C. luteicollis	T	T	G	T	G	A	A	T	A	T	T	T
C. occidentalis	T	T	G	T	A	A	A	T	A	T	T	T
C. riverai	T	T	G	T	R	A	A	T	A	T	T	T
C. smargadulus	A	T	G	T	A	A	A	A	A	T	T	T
Cryptocanthon lobatus	A	T	G	T	A	A	A	A	A	T	T	T
Frickius varilosus	T	T	G	T	A	A	A	T	A	T	T	T
Pseudocanthon perplexus	T	A	T	A	T	A	A	A	A	T	T	T

[1] Position number is referenced to the *Drosophila melanogaster* gene sequence (GenBank accession number NC_024511).

Table 2. Pairwise corrected genetic distances based on the Kimura two parameter model of nucleotide substitution. Diagonal line is the intra-taxon corrected distance.

	Cytochrome Oxidase I	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	*C.* (*Bajacanthon*) *obliquus*	1.8																
2	*C.* (*Boreocanthon*) sp.	9.7	5.5															
3	*C. blumei*	12.2	10.8	0.0														
4	*C. cyanellus*	12.9	13.3	12.5	4.0													
5	*C. edentulus*	10.4	11.3	11.2	11.8	0.0												
6	*C. humectus*	12.7	11.7	1.6	13.3	11.7	0.5											
7	*C. imitator*	13.7	12.3	9.1	14.8	11.4	10.1	1.1										
8	*C. indigaceus*	11.7	11.0	5.8	13.1	10.4	6.4	8.3	2.7									
9	*C. lamprimus*	11.1	11.8	12.6	10.3	11.5	13.4	16.7	14.4	0.5								
10	*C. lunatus*	12.6	11.7	11.1	12.0	8.3	12.2	12.3	12.8	14.2	0.0							
11	*C. luteicollis*	12.0	12.1	12.1	14.5	13.0	12.0	13.9	12.9	14.4	12.1	0.0						
12	*C. occidentalis*	13.5	13.4	6.2	14.2	12.2	7.3	11.0	8.0	13.1	13.5	13.4	0.7					
13	*C. riverai*	13.2	13.1	6.4	13.0	11.6	6.8	10.5	7.7	15.3	12.1	13.8	7.7	0.3				
14	*C. smargadulus*	15.2	13.6	13.7	15.2	15.1	14.3	15.5	13.5	17.3	15.4	16.2	15.5	14.5	0.0			
15	*Cryptocanthon lobatus*	14.2	14.6	15.3	15.3	13.7	16.4	16.4	14.5	15.8	15.8	15.6	14.8	14.6	16.1	1.0		
16	*Frickius varilosus*	15.2	16.8	17.1	15.9	15.0	17.7	16.4	16.1	16.4	15.8	15.8	16.3	16.4	17.9	16.7	0.0	
17	*Pseudocanthon perplexus*	12.4	12.6	11.5	12.4	11.6	11.5	13.5	12.1	12.8	12.0	10.7	12.6	12.8	16.5	14.9	16.6	0.3

	Cytochrome Oxidase I	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17

	16S rRNA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	*C.* (*Bajacanthon*) *obliquus*	0.3																
2	*C.* (*Boreocanthon*) sp.	4.5	1.7															
3	*C. blumei*	12.3	11.5	5.0														
4	*C. cyanellus*	8.9	7.7	14.9	1.3													
5	*C. edentulus*	8.1	7.8	15.4	9.5	0.0												
6	*C. humectus*	7.3	6.5	6.1	10.0	10.7	0.0											
7	*C. imitator*	7.2	6.4	7.1	9.7	11.1	2.2	0.1										
8	*C. indigaceus*	7.3	6.6	7.4	9.7	10.7	2.4	1.8	0.4									

Table 2. *Cont.*

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
9	*C. lamprimus*	6.9	6.2	9.9	7.1	7.6	6.0	5.6	5.8	0.0								
10	*C. lunatus*	8.5	7.5	15.1	9.1	5.7	9.9	10.5	9.5	8.4	0.0							
11	*C. luteicollis*	13.8	13.2	15.7	14.6	14.6	14.0	13.0	13.2	13.5	13.4	0.0						
12	*C. occidentalis*	6.7	6.6	7.2	10.3	10.9	2.5	2.7	2.8	5.5	10.1	13.6	0.3					
13	*C. riverai*	6.7	5.7	6.8	10.0	10.2	1.6	2.0	1.8	6.1	9.4	13.5	2.1	0.1				
14	*C. smargadulus*	11.4	11.1	12.2	11.8	11.7	10.9	10.8	11.5	11.8	13.2	14.3	10.7	11.5	0.0			
15	*Cryptocanthon lobatus*	20.1	18.0	23.5	21.2	20.0	18.9	17.7	17.6	16.4	21.4	20.1	17.6	18.0	18.8	0.8		
16	*Frickius varilosus*	15.2	14.6	19.8	16.2	15.5	15.2	14.3	14.2	16.4	16.7	18.8	15.1	14.8	17.6	15.2	0.0	
17	*Pseudocanthon perplexus*	10.8	8.9	14.8	10.7	11.9	10.0	9.6	9.8	8.8	11.6	12.9	9.8	9.9	11.9	16.5	13.4	0.1
	Combined Genes	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	*C. (Bajacanthon) obliquus*	1.1																
2	*C. (Boreocanthon) sp.*	7.1	3.6															
3	*C. blumei*	12.3	11.1	2.4														
4	*C. cyanellus*	10.9	10.5	13.6	2.6													
5	*C. edentulus*	9.3	9.5	13.3	10.6	0.0												
6	*C. humectus*	10.0	9.1	3.7	9.8	11.2	0.3											
7	*C. imitator*	10.5	9.3	8.1	12.3	11.2	6.1	0.6										
8	*C. indigaceus*	9.5	8.8	6.6	11.4	10.5	4.4	5.0	1.5									
9	*C. lamprimus*	9.5	9.6	11.6	9.0	10.0	10.5	12.2	11.0	0.3								
10	*C. lunatus*	10.5	9.6	13.0	10.5	7.0	11.1	11.4	11.2	12.0	0.0							
11	*C. luteicollis*	12.7	12.5	13.4	14.6	13.6	12.8	13.7	13.1	14.1	12.6	0.0						
12	*C. occidentalis*	10.0	10.0	6.7	12.3	11.5	4.9	6.8	5.4	10.1	11.8	13.5	0.5					
13	*C. riverai*	9.9	9.3	6.6	11.5	10.9	4.2	6.2	4.7	11.6	10.8	13.8	4.9	0.2				
14	*C. smargadulus*	13.9	12.7	13.2	14.0	14.0	13.1	13.2	12.8	15.4	14.7	15.6	13.8	13.5	0.0			
15	*Cryptocanthon lobatus*	17.0	16.2	19.2	18.1	16.7	17.6	17.0	16.0	16.0	18.5	17.0	16.2	16.3	17.0	0.9		
16	*Frickius varilosus*	15.2	15.9	18.3	16.0	15.3	16.7	15.5	15.4	16.4	16.3	16.9	15.8	15.8	17.8	16.0	0.0	
17	*Pseudocanthon perplexus*	11.6	10.8	13.1	11.6	11.7	10.8	11.6	11.0	11.2	11.8	11.5	11.3	11.4	14.9	15.6	15.2	0.2

Geographic distribution. The subgenus *Bajacanthon* has a single species: *C. obliquus* Horn, 1894, mainly distributed at Sierra de la Laguna, in the southernmost part of the Baja California Peninsula (Figure 1). In the original description, the species is reported from two localities: Pescadero and the Sierra El Chinche mountains. The latter is an alternative name for the Sierra de la Laguna, whereas Pescadero is a small town in the lowlands of Sierra de la Laguna. This Sierra is a mountain range, that represents a Neotropical sky island located in the far south of the Baja California Peninsula, is surrounded by the Sonoran Desert, the Pacific Ocean and the Gulf of California. This mountainous range is formed by steep mountains, made up of a series of canyons arranged mainly from east to west, which help to capture humidity from the ocean. The mountains span from 900 up to 2200 m a.s.l. During the early Paleogene there was a granite intrusion along the peninsula, which would form the base range of the Sierra de la Laguna [25]. Currently, these mountains have three well-defined vegetation types. So far, *Bajacanthon* is known from the deciduous subtropical mountain forest that is located above the 400 m line, and from a narrow band of oaks situated below the 1000 m line just prior to the pine-oak forest that covers the highest part of the sierra.

Outside of Sierra de la Laguna, only four specimens have been collected (Figure 1). The first is from Cerro El Mesquitito, southwest of La Paz City, Baja California Sur, 24°09′ N, 110°20′ W, elevation 70 m a.s.l., xerophilous vegetation, 26 October 1997, Armando Tejas leg. The second is from Cerro El Juncalito, Sierra de la Giganta, Baja California Sur, 26°45′ N, 112°46.5′ W, 28 August 2006, Guillermo Nogueira leg. The third specimen is from La Paz, Baja California Sur, 790 m a.s.l., no date nor collector. The fourth specimen from La Paz; Pedregal de La Paz, 58 m a.s.l., direct collection by Julian Blackaller, 19 February 2020.
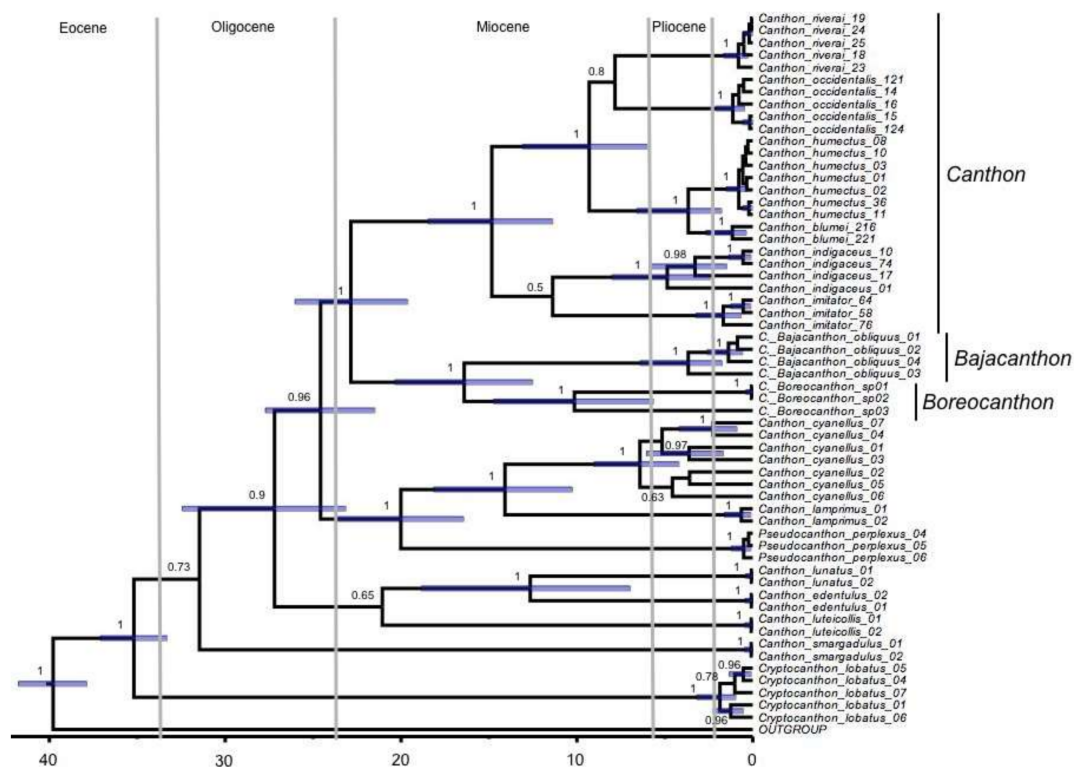
Figure 4. Chronogram for the phylogenetic history of *Canthon* (*Bajacanthon*) *obliquus* and closely related taxa. Numbers at nodes indicate Bayesian posterior probability values. Node bars indicate the 95% Highest Posterior Density for splitting age in nodes with a Bayesian posterior probability higher than 0.9. The temporal reconstruction supports Kohlmann and Halffter's conclusion that the origin of *Bajacanthon* took place during the Miocene (16.5 Mya) [5]. This subgenus is more closely related to the subgenus *Boreocanthon* than to other *Canthon* species from North or South America.

Ecology. *Bajacanthon* has been collected mainly in places between 450 and 700 m, and occasionally as high as 980 m, on the Pacific Ocean slope, the Gulf of California slope, and on the southern tip of Baja California. The vegetation in the collection sites is *selva baja caducifolia* (*sensu* Miranda and Hernández [26]) or *bosque tropical caducifolio* (*sensu* Rzedowsky [27]). This is a patch of isolated Neotropical vegetation located on the southern point of the peninsula and at the same time in the lower parts of the Madro-Tertiary forests. In the field, we have seen this species active between 8:30 am and 9:00 am, and between 3:30 pm and 4:00 pm. It has been observed moving over the soil, attracted to dung from animals such as foxes, large lizards (*Aspidoscelis maxima* (Cope 1864) and *Elgaria paucicarinata* (Fitch 1934)), bovine and human [28].

Dung beetles and man. These insects feed and developed not just on dung, but also in rotting fruit, fungus and carrion [29]. This particular behaviour of feeding and reproducing of the Scarabaeinae contributes to dung [30,31] and carrion removal [32]. This relocation of organic matter in decomposition makes them directly relevant to humans due to the ecosystem functions and services they provide, such as nutrient cycling, bioturbation, plant growth enhancement, parasite suppression, secondary seed dispersal among others [33–36]. Therefore, dung beetles play an important role to maintain ecosystem integrity. They can be very sensitive to human activities and habitat disturbance; hence, the conservation of vegetation islands, especially for a subgenus like *Bajacanthon*, is key to its conservation and the maintenance of the ecosystem services they provide.

Sierra La Laguna Biosphere Reserve is a natural protected area [37]. However, also, a sky island within an arid environment with a great level of endemisms, characterised by a special socio-ecological culture not found in other places in Mexico [38]. In this sense,

C. (Bajacanthon) obliquus an endemic dung beetle species from Sierra La Laguna [28,39] could be considered a good model for conservation and management [40] due to their reliability as indicators for environmental change, mainly disturbance. Although dung beetles are a well-known group, assessing the global threats to the conservation status of Mexican species by the IUCN Red Lists, is still a work in process. Therefore, the haste to protect endemic species, especially in protected areas, should be a priority.

Final considerations. In 2016, Tarasov and Dimitrov [41] proposed the revision of the taxonomic status of four tribes of Scarabaeinae, among them Deltochilini. With that study and that of Tarasov and Génier [42], a new organization into tribes of the Scarabaeinae genera with phylogenetic basis is partially established. The heterogeneous Deltochilini (former Canthonini) currently comprises 22 New World genera. Many of these include species representing important components of the Mexican Transition Zone.

The anatomical comparison of the structures of the endophallus of *C. obliquus* with those of five related taxa of Deltochilini (Figures 5 and 6) suggests that the changes in these structures depend on the particular lineage. For instance, the overall morphology of the internal sac of *Canthon humectus* (Say 1831) is similar to that of *Bajacanthon*. In contrast, *Canthon* (*Boreocanthon*) *praticola* LeConte, 1859 exhibits differences such as the absence of raspulaes and the shape of its sclerite 2 (Figure 6). The phylogenetic analysis, however, recovers a closer relationship between *Bajacanthon* and *Boreocanthon* (Figure 4). These evolutionary relationships are consistent with the biogeographic evidence by placing *C. obliquus* as the sister taxon of the *Boreocanthon*.
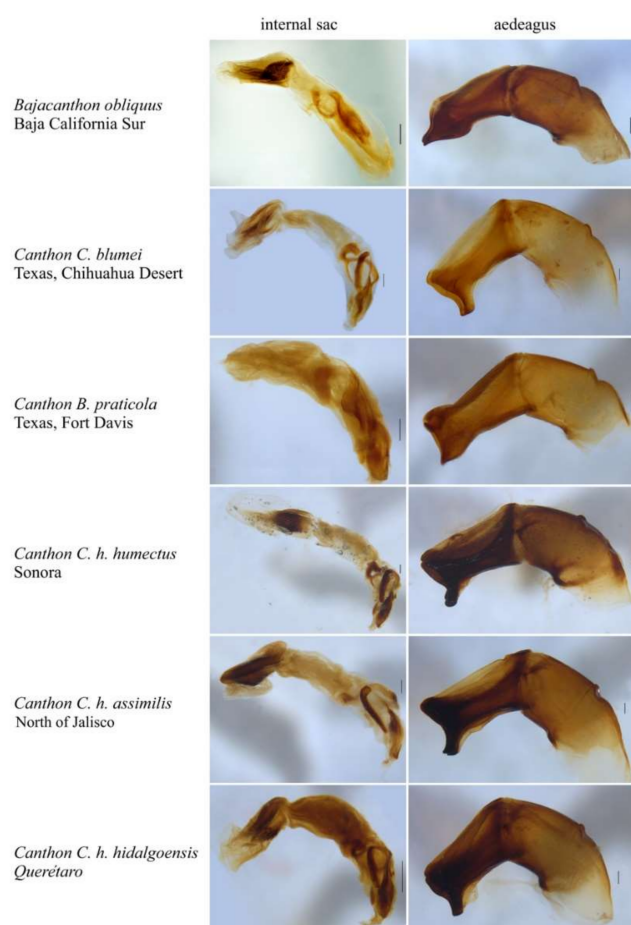
Figure 5. Comparison of the anatomy of the genital internal sac and aedeagus of *Canthon* (*Bajacanthon*) *obliquus* with related taxa of Deltochilini. Scale = 0.2 mm.
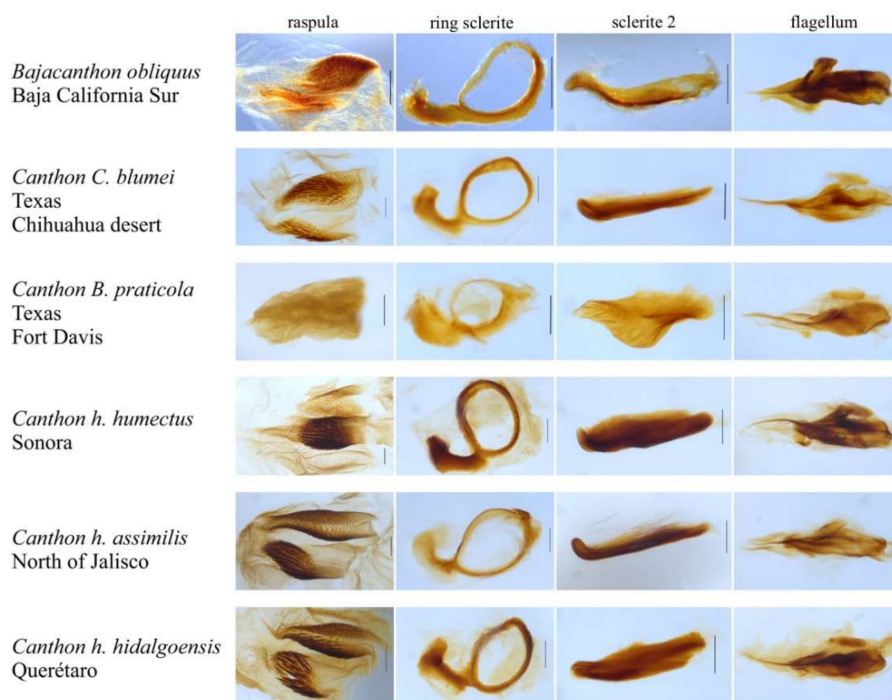
Figure 6. Comparative anatomy of the endophallus of Canthon (*Bajacanthon*) *obliquus* with related taxa of Deltochilini. Scale = 0.2 mm.

Certainly, Deltochilini is a group crowded of taxonomic problems [41,42]. *Canthon* is not an exception; in fact, it is possible that it is not a monophyletic genus (Figure 4). Perhaps, the decision of describing a new monotypic subgenus might seem an unnecessary complication. Based on an integrative approach, *Bajacanthon* is certainly an independent evolutionary lineage. Morphological characters (i.e., novel parameters, distinctive elytra shape and apterism), phylogenetic inference (i.e., monophyly), and genetic distances (i.e., total evidence 11.2%, *COI* 12.7%, and *16S rRNA* 9.7% from related taxa) support its recognition. Preliminary phylogenetic evidence suggests that *Bajacanthon* is more related to *Boreocanthon* than to other *Canthon* species. However, the precise phylogenetic placement of *C. (B.) obliquus* among other Deltochilini beetles cannot be accessed at this moment. We did not have access to key South American taxa (e.g., *C. pilularius*) that are essential for answering systematic questions regarding *Bajacanthon*. Assigning the subgenus rank to this lineage at this time will retain the uncertainty about its taxonomic position. It is important to emphasize that the present work is not in any way a thorough phylogenetic study for the genus *Canthon*. Thus, we do not pretend to draw robust taxonomic or systematic conclusions for *Canthon* and its species. The phylogenetic results presented here are framed within the view of a limited data set (both of taxa and characters). Therefore, their conclusions are no more than one hypothesis that may be used as a starting point for feature analyses. This study is part of an ongoing effort for understanding the complex biogeographic patterns at the Mexican Transition Zone as well as the evolutionary history of the scarabaeinae fauna that lives there.

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