

## Article

# Systematics and Biogeography of the New World Genus *Plumolepilius* (Coleoptera: Curculionidae)

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**Abstract:** *Plumolepilius* Barrios-Izás & Anderson, 2016 is a leaf litter weevil genus that inhabits montane broadleaf forests from southern Mexico to northern Panama. The genus consists of 27 species, 22 distributed in the Chiapas Highlands province (Mexican Transition Zone) and 5 found in the Pacific dominion (Neotropical region) in Costa Rica and Panamá. Here, we analyze the phylogenetic relationships of the species of *Plumolepilius* based on 20 external body characters and 9 characters from the genitalia. The first dichotomy of the cladogram separates two species from the Pacific dominion from the remaining species of *Plumolepilius* from the Chiapas Highlands province and three species restricted to the Pacific dominion. We hypothesize that redundant distributions in the taxon-area cladogram of the genus may be due to dispersal events, probably during the Pleistocene glaciations.

**Keywords:** Mesoamerica; weevils; diversification



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## 1. Introduction

*Plumolepilius* Barrios-Izás & Anderson, 2016 (Curculionidae: Molytinae: Conotrachelini) is a leaf litter weevil genus from southern Mexico and Central America. It comprises at least 27 known species and a preliminary phylogenetic analysis has shown that it is monophyletic [1,2]. The distribution of the species of *Plumolepilius* ranges from southern Mexico through Central America reaching northern Panama, within the Mexican Transition Zone (Chiapas Highlands province) and the Pacific dominion of the Neotropical region (Puntarenas-Chiriquí province) [3], through a range of about 8° latitude. Species of *Plumolepilius* are mostly found in montane broadleaf humid forests, approximately between 1400 and 2800 m.a.s.l. All species have low dispersal capacities and show troglomorphic adaptations, such as the absence of hind wings and scutellum, fused elytra and reduced metasternum.

The dispersal–vicariance model has been proposed as one of the main hypotheses for explaining the evolution of the montane biota of Central America [4,5]. Pleistocene glaciations have played an important role in the distribution of biodiversity by expanding and contracting species' and ecosystems' distribution range. It has been demonstrated that during glacial periods, humid montane forest migrated to lower altitudes allowing the migration of species, while in warmer periods, humid forests contracted to upper altitudes, leaving species isolated.

Our aims are to analyze the phylogenetic relationships of the species of *Plumolepilius* and to propose a biogeographic hypothesis to help explain its diversification.

## 2. Materials and Methods

The phylogenetic analysis included all known species of *Plumolepilius*. Specimens were obtained on loan from the Insect Collection of the Canadian Museum of Nature

(CMNC). As outgroups, we used *Lepilius pulchellus* Champion, 1905 (Charlie W. O'Brien Collection), *L. chisosensis* Anderson 2010 (Museo de Zoología "Alfonso L. Herrera") and two undescribed species of *Lepilius* from Honduras and El Salvador (CMNC).

Specimens were relaxed by immersion in hot water with a solution of soap for 15–20 min. Abdominal ventrites were removed from the abdomen together with the alimentary canal, genitalia and fat and muscular tissues. The body was washed with water, then in a solution of ethanol (95%), air dried and double pin mounted. Fat and muscular tissues from abdominal content were cleared by immersion in a warm solution of KOH (10%) for 15–30 min. After clearing, abdominal structures were washed in water and ethanol (95%) to remove the KOH. Ventrites were mounted in a card and pin mounted together with the specimen. Male and female genitalia and associated sternites were mounted in slides using 5,5-dimethyl hydantoin formaldehyde (DMHF) [6].

For constructing the data matrix (Table 1), we used 20 external body characters and 9 characters from male and female genitalia. Multistate characters 10, 11, 19, and 26–28 were treated as additive. Characters and character states are described as follows (0 = plesiomorphic; 1–7 = apomorphic):

1. Apex of elytra shape: 0. rounded, 1. straight.
2. Femora with single spine on inner margin: 0. absent, 1. present.
3. Lateral expansions of pronotum contiguous with humeri: 0. absent, 1. present.
4. Pronotum: 0. subquadrate (width: length 1:0.8), 1. transverse (width: length 1:0.65).
5. Prosternal channel with plumose scales: 0. absent, 1. present.
6. Shape of elytral declivity: 0. rounded, 1. angulate.
7. Shape of elytral humeri in males: 0. rounded, 1. prominent.
8. Shape of elytral humeri in females: 0. rounded, 1. acutangulate.
9. Elytral tubercles: 0. absent, 1. present.
10. Shape of tubercle on interstice 5 at elytral declivity: 0. absent, 1. moderately developed, 2. well-developed.
11. Shape of interstice 4 at elytral declivity: 0. rounded, 1. angulate, 2. small tubercle present, 3. large tubercle present.
12. Elytral tubercle in females: 0. absent, 1. several small, 2. two large tubercles on 4th interstice, 3. two large tubercles on 4th interstice but convergent.
13. Elytral striae: 0. well-defined, 1. seriate-punctate.
14. Shape of apex of ventrite 5: 0. flat, 1. with two protuberances, 2. depressed.
15. Number of distinguishable genital sclerites: 0. two, 1. one.
16. Shape of genital sclerites: 0. symmetric, 1. asymmetric.
17. Shape of posterior genital sclerite: 0. hook-like, 1. flagellate, 2. sting-like, 3. enlarged-straight, 4. single plate, 5. not distinguishable, 6. karabiner-like.
18. Shape of anterior genital sclerite: 0. hook-like, 1. capsule, 2. sting-like, 3. enlarged-straight, 4. single plate, 5. folded plate, 6. flagellate, 7. absent.
19. Length of temones: 0. subequal to pedon, 1. between 1.5 and 2.0X length of pedon, 2. between 2.0 and 2.9X length of pedon, 3. more than 3.0X length of pedon.
20. Shape of pedon: 0. rectangular, 1. other shapes.
21. Bifurcation distance of spiculum ventrale: 0. first quarter, 1. half.
22. Shape of border of female tergite VII: 0. straight, 1. sinuated.
23. Spermatheca shape: 0. wide (twice width of gonocoxites), 1. thin (as wide as gonocoxites).
24. Appressed scales at mesanepisternum and mesepimeron: 0. present, 1. absent.
25. Erect scales at elytra: 0. absent, 1. present.
26. Elytral scales shape: 0. rounded, 1. slightly elongate, 2. clavate, 3. lanceolate.
27. Angle of elytral scales: 0. appressed, 1. almost erect, 2. suberect.
28. Density of erect or suberect scales: 0. absent, 1. sparse, 2. dense.
29. Tuft of setae on apex of abdominal ventrite 5: 0. absent, 1. present.

**Table 1.** Data matrix of morphological characters used in the cladistic analysis of *Plumolepilius*. '?' = unknown data.

Taxa						
<i>Lepilius</i> spp.	00000	00000	00000	00000	00000	0000
<i>Lepilius pulchellus</i>	00000	00000	00000	00000	00001	2110
<i>P. andersoni</i>	11011	11011	21100	14511	00111	2210
<i>P. antonioi</i>	11011	11010	22110	12231	01111	2211
<i>P. branstetteri</i>	11011	11111	32100	14251	00101	2211
<i>P. camuna</i>	11011	10?11	2?100	00021	???11	2210
<i>P. canoi</i>	11011	11010	30111	15511	00101	1220
<i>P. cortesi</i>	11011	11012	32100	14521	01101	3220
<i>P. daryi</i>	11011	10012	21100	16221	10111	2220
<i>P. genieri</i>	10011	11011	32101	15321	00101	2221
<i>P. guaimacaensis</i>	10011	10011	33110	14511	00101	2221
<i>P. hectori</i>	11011	10011	21001	15211	00111	2210
<i>P. linaresi</i>	11011	11010	32121	15321	10101	2221
<i>P. longinoi</i>	10011	11011	32110	12521	01101	2220
<i>P. macalajauensis</i>	10011	10011	33101	15521	01101	3221
<i>P. maesi</i>	11011	00000	00001	15521	00101	2221
<i>P. molinai</i>	10011	11011	21000	11621	01111	2210
<i>P. morronei</i>	11111	11010	31100	12221	00111	2221
<i>P. nelsoni</i>	10011	10?10	2?000	14421	???01	2220
<i>P. nicaraguensis</i>	11011	11011	20100	12631	01101	2221
<i>P. obrienorum</i>	11011	01000	00001	15531	00111	2221
<i>P. schusteri</i>	11111	11010	30101	?5511	00001	1220
<i>P. solisi</i>	10011	11110	32100	11331	01100	1001
<i>P. trifiniensis</i>	10011	11000	10000	12521	01101	3220
<i>P. velizi</i>	11011	11011	32121	11731	00101	1220
<i>P. yolnabajensis</i>	11011	10011	22100	12421	00101	2211
<i>P. zarazagai</i>	10011	11111	32100	14421	00111	2221

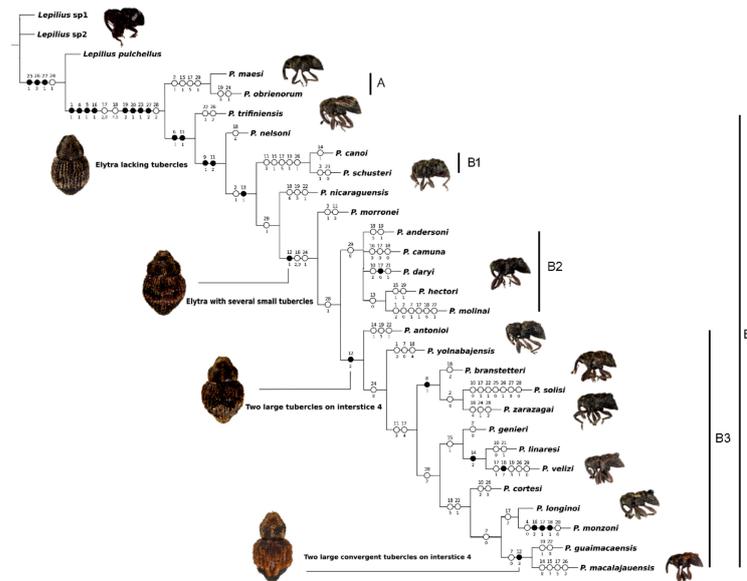
The cladograms were constructed using TNT software [7]. We conducted an implied weights analysis [8], with the constant of concavity (k) set to 6.48, selecting this value with the script setk [9].

### 3. Results

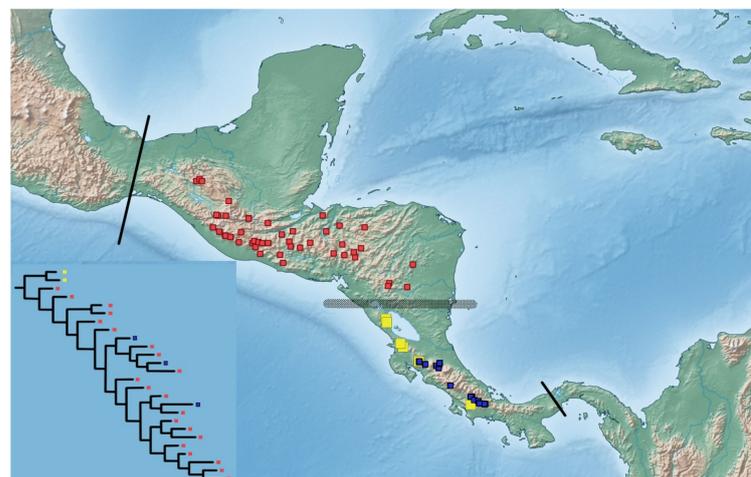
The analysis under implied weights with a concavity of 6.48 led to three cladograms (Figure 1), with 177 steps, a consistency index of 0.31 and a retention index of 0.57. Barrios-Izás et al. (2016) identified as synapomorphies of *Plumolepilius* the presence of plumose setae in the prosternal channel, the tubercle at the beginning of the elytral declivity on interval 4 and the swollen basal area of pronotum. *Lepilius* Champion was identified as the sister genus of *Plumolepilius*; here, we identified 12 morphological characters in *Plumolepilius* that support its separation from *Lepilius*. Some of these characters are the transverse pronotum, the presence of plumose scales, asymmetry of the genital and thinner spermatheca in *Plumolepilius*; and the ovate shape of the body, absence of tubercles or protuberances and absence of erect or suberect elytral scales in *Lepilius*.

Within *Plumolepilius*, we recovered two main clades. The first clade (clade A) is constituted by *P. maesi* and *P. obrienorum*, and the second clade (clade B) contains the remaining 25 species (Figure 1). Species in clade A inhabit the Pacific dominion, whereas those of clade B inhabit both the Pacific dominion and the Chiapas Highlands province (Mexican Transition Zone). Within clade B, *P. canoi* and *P. schusteri* are recovered as sister taxa (clade B1); and *P. andersoni*, *P. daryi*, *P. camuna*, *P. hectori* and *P. molinai* constitute a monophyletic group (clade B2). *Plumolepilius antonioi*, *P. yolnabajensis*, *P. branstetteri*, *P. solisi*, *P. zarazagai*, *P. genieri*, *P. linaresi*, *P. velizi*, *P. cortesi*, *P. longinoi*, *P. monzoni*, *P. guaimacaensis* and *P. macalajauensis* also constitute a monophyletic group (clade B3). The rounded shape of the elytral declivity supports clade A, whereas clade B has an oblique shape. Species within

clade B3 are characterized by the females having a well-developed tubercle on interstice 4 at the beginning of the elytral declivity. Within clade B3, females of *P. branstetteri*, *P. solisi* and *P. zarazagai* have an acute angulate shape of the humeral region. We were unable to find synapomorphies for clades B1 and B2. The presence of elytral tubercles in the females shows a nested distribution along the branches of the cladogram, from the absence of tubercles to the presence of small tubercles, two large tubercles on interstice 4 and two large convergent tubercle on interstice 4.



**Figure 1.** Strict consensus of the three cladograms of the species of *Plumolepilius* recovered under implied weights, with some of the characters represented.



**Figure 2.** Geographical distribution and taxon-area cladogram of *Plumolepilius* species corresponding to main clades A (yellow squares) and B (red and blue squares). Biogeographic barriers: Isthmus of Tehuantepec and lowlands of Panama-Colombia (black solid bars), and Nicaraguan lowlands (gray bar).

Based on the cladogram of *Plumolepilius* species, it is possible to obtain a taxon-area cladogram (Figure 2). We hypothesize that the redundant distributions of species of both main clades in the Pacific dominion are due to dispersal events, likely during the Pleistocene glaciations.

#### 4. Discussion

The species of *Plumolepilius* show patterns of endemism similar to other weevil genera that inhabit leaf litter (e.g., *Theognete* [10], *Tylodinus* [11], *Lepilius* [12]) or soil (e.g., *Neoubychia* [13]). With some exceptions, most of the species are allopatric and restricted to one or few localities. Species with a wider range of distribution are found on the Quaternary volcanic terranes of the northern side of the Central American Volcanic Arc, such as *P. trifiniensis*, recorded from the Atitlan Volcano in Guatemala to the east up to Santa Ana volcano in El Salvador; and *P. canoi*, recorded from four localities ranging from the cloud forest of La Union in Guatemala south to El Güisayote in Honduras [1,2]. All other species of *Plumolepilius* have very narrow distributional ranges; some of them are known only from the type locality.

Species distribution is constrained by a combination of species tolerance to physical variables, biotic interactions, historical processes and the dispersal abilities of the species. The species of *Plumolepilius* are associated with montane broad leaf forest, mainly oak and cloud forests between 1200 m and 2500 m. The main characters that might limit the dispersal abilities of *Plumolepilius* species are the lack of flight, which is associated with troglobiomorphic characters such as the reduced size of the metasternum, the absence of hind wings, the fused elytra and the absence of scutellum. It is well known for species inhabiting caves or soil that the development of characters (e.g., longer appendices and overdevelopment of some brain areas) for life in the darkness selects against traits that are not useful in these types of habitats (e.g., cuticle pigmentation, eyes and brain associated areas). Troglbiomorphism, either intermediate or extreme, is common in several subfamilies of the Curculionidae, namely, Brachycerinae, Molytinae and Cossoninae [14].

The high number of endemic species in the Mexican Transition Zones and other montane provinces of Central America has been explained under dispersal–vicariance models [4,5] during the Pleistocene climatic oscillations. Lower elevation ecosystems during warmer periods function as biogeographic barriers and montane ecosystems function as land islands where populations remain isolated for several thousands of years that may cause speciation processes; during colder periods, montane habitats descend and expand their distribution in lowlands, allowing the migration of species. We assume, based on the genetic time calibration of the diversification of other montane taxa, that the same processes might have acted in the speciation of *Plumolepilius*.

Along the Mexican Transition Zone, the Isthmus of Tehuantepec and the Lake Nicaragua depression have been recognized as important biogeographic barriers for species inhabiting montane ecosystems [15,16]; however, these are not universal barriers for species that have similar dispersal abilities, such as those of the genera *Lepilius* Champion, *Plumolepilius*, *Theognete* Champion, *Tylodinus* Champion as well as other leaf litter weevil genera. *Lepilius* has been recorded from samples collected from Texas to Costa Rica (Robert Anderson, pers. comm.), *Plumolepilius* has been recorded from southern Mexico to Panama, and *Tylodinus* has been recorded from northern Mexico to Panama [11].

The main barriers constraining the distribution of *Plumolepilius* species distribution are the Isthmus of Tehuantepec and the Chocó lowland forests; specimens of *Plumolepilius* have not been found beyond these limits until now. This area is considered to be within the Mesoamerican biodiversity hotspot [15,17]. The high number of endemisms and diversification of *Plumolepilius* within this area show the importance of conservation of the montane forests of Mexico and Central America, most of which have been legally protected since the 1950s. With some exceptions, most of these protected areas, especially in northern Central America, lack proper management to ensure their long-term conservation. The loss of montane habitats at the current rates of deforestation will drive to an accelerated rate of extinction of diverse groups of arthropods that remain unknown at species and molecular levels.

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