



## Description of *Enicotaenia*, a new genus of Archipini from Bolivia, with comments of male-female coupling adaptation (Lepidoptera: Tortricidae)

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### Abstract

*Enicotaenia interandina*, a new genus and species of the tribe Archipini (Tortricidae), is described from the Neotropics (Bolivia). The wing patterns and genitalia of both sexes are illustrated. This species is characterized by two unusually strong serrated lateral processes in the transtilla of the male genitalia and two subconical lateral pockets in the antrum of the female genitalia. These structures are presumably involved in the male-female coupling mechanism. The new combination *Enicotaenia marabana* (Razowski & Becker, 2000) is proposed.

**Key words:** *Enicotaenia interandina*, Neotropics, Archipini, genitalia characters, coupling mechanism

### Introduction

Pierce & Metcalfe (1922) erected Archipini through the observation of an elongated dagger-shaped signum bearing a capitulum in the bursa copulatrix of the female genitalia. Although this is a common feature of the tribe, it is far from universal (Common 1956; Horak 1984, 1999). Horak (1984) suggested the presence of a well-developed uncus brush as the true synapomorphy of the group, but this can be lost secondarily or can occur in other tribes such as Ceracini and Epitymbiini. Anyway, the monophyly of Archipini is well supported molecularly (Regier *et al.* 2012) and the group is taxonomically well established in the literature. The conflictive *Mictopsichia* Hübner, 1825 and several genera superficially similar as *Chamaepsichia*, Razowski, 2009, *Mictocommosis*, Diakonoff, 1977 and *Rubropsichia* Razowski, 2009 may belong to multiple different tribes (Brown 2005). The tribe Archipini is worldwide in distribution, with most of its diversity concentrated in the Oriental and Australian regions (Gilligan *et al.* 2018). Two genera represent a major radiation in the New World: *Argyrotaenia* Stephens, 1852 and *Clepsis* Guenée, 1845. Most of the sparse Neotropical representatives of the tribe either belong to these two genera or to closely related genera, namely *Ceritaenia* Razowski & Becker, 2000, *Claduncaria* Razowski & Becker, 2000, *Cornuclepsis* Razowski & Becker, 2000, *Cununcus* Razowski & Becker, 2000, *Exorstaenia* Razowski & Becker, 2000, *Farragona* Austin & Dombroskie, 2020, *Furcataenia* Razowski & Becker, 2000, *Idolatteria* Walsingham, 1914, *Ochrotaenia* Razowski & Becker, 2000, *Raisapoana* Austin & Dombroskie, 2020, *Saetotaenia* Razowski & Becker, 2000, *Spinotaenia* Razowski & Becker, 2000, *Sychnovalva* Razowski, 1997 and *Tacertaenia* Razowski, 1997 (Austin & Dombroskie 2020a, Obraztsov 1966, Razowski 1997, Razowski & Becker 2000, 2010). Assigning

new species in this taxonomic scenario is a complex matter. Many of these genera are based on sparse, often bizarre, or incomplete material (e.g.: a single sex). The morphological information is not exhaustive in many cases (e.g., no wing pattern or venation), and the basic molecular information available is still poor. In this article, we propose a new genus and species of Archipini from Bolivia that does not fit with any of the known genera, revealing, once again, an unstable taxonomic situation.

## Material and methods

The specimens were obtained by light trapping in Bolivia. Genitalia dissection procedure follows Robinson (1976). Dissections were performed using a Leica MZ8 stereomicroscope. Adults and genitalia were photographed using a Leica Z16 microscope, equipped with a CF500 camera and LAS 5.0 (Leica) image capture software. Depth of field was increased by z-stacking techniques. Images were edited using Photoshop 2024 (Adobe). Terminology of the genitalia structure follows Horak (1984); terminology of forewing pattern follows Brown & Powell (1991) as modified by Baixeras (2002). Forewing measurements were taken along a straight line from the base of the wing to the apex (including fringe).

DNA extraction was performed from the abdomen according to Monarch® PCR & DNA Clean-up Kit, following Patzold *et al.* (2020) protocol. COI amplification by PCR was attempted using the following primer combinations: LepF1/MLepR1, MLepF1/LepR1 (Hajibabaei *et al.* 2006) and C\_TypeF1/C\_TypeR1 (Hebert *et al.* 2013). The PCR products were purified following High Pure PCR Product Roche® Purification protocol. DNA labeling was performed with BigDye Terminator v3.1 Cycle Sequencing Ready Reaction ABI PRISM® (Applied Biosystems™). Amplicons were sequenced by Sanger method (Sanger & Coulson 1975) in an ABI 3730® DNA sequencing equipment (Applied Biosystems™) by the Genomic Services of the University of Valencia. Reading and assembly of the sequences were assisted by STADEN software Package® (Staden 1999) for two amplicons: LepF1-MLepR1 (307 bp) and CTypeF1-CTypeR1 (164 bp). Finally, the sequences were tested against the GenBank database by BLAST.

Phylogenetic tree species-level were resolved by using COI sequences available in BOLD (Ratnasingham & Hebert 2007). The genus-level multigene phylogeny of Archipini proposed by Dombroskie & Sperling (2013) was used here as a backbone. A sequence of the genus *Cerace* (sister tribe Ceracini) was added as outgroup. Sequences of selected representatives of the genera *Aphelia* Hübner, 1825, *Archips* Hübner, 1822, *Argyrotaenia*, *Claduncaria*, *Clepsis*, *Isotenes* Meyrick, 1938, and *Mictopsichia* were added. To simplify the analysis, the representatives of *Argyrotaenia* and *Clepsis* were restricted to Neotropical species. Sequences were aligned using MEGAX (Kumar *et al.* 2018). Phylogenetic distance trees were created using Neighbor-joining (NJ) (Saitou & Nei 1987) and Maximum Likelihood (ML)(Aldrich 1997) tests, changing the correction parameters to Kimura2 (K2P) (Kimura 1980). The statistical confidence of the clusters and distances was assessed using a bootstrap analysis with 1000 replications.

## Abbreviations

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**ICBiBE**, Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, España.

## Results

### Taxonomy

#### ***Enicotaenia* Pérez Santa-Rita, Dombroskie, Ledezma & Baixeras, new genus**

(Figs 1, 2A–F, SM1)

Type species.—*Enicotaenia interandina* Pérez Santa-Rita, Dombroskie, Ledezma & Baixeras, new species

**Diagnosis.** The forewing pattern is superficially similar to many other Neotropical Archipini, especially in the genera *Argyrotaenia* and *Furcataenia*, but is not as sexually dimorphic. The venation shows similarities with *Exorstaenia*, *Ochrotaenia*, *Saetotaenia* and *Argyrotaenia*, but the combination of  $R_4$  approximated to  $R_5$  at base (but not stalked) in forewing, with  $R_s$  and  $M_1$  connate, and  $M_3$  and  $CuA_1$  stalked in hindwing is unique.

Overall morphology of the male genitalia shows affinities with *Furcataenia* and *Aphelia* (s.s.), but the combination of characters delimits this genus as distinctive. Uncus is bifid in many *Claduncaria*, *Cornuclepsis*, some *Exorstaenia*, *Farragona*, *Tacertaenia* and *Aphelia* (s.s.), but entire in *Enicotaenia*. A continuous undivided transtilla is only known in *Argyrotaenia* group. However, the transtilla is relatively simple in most of these genera (*Argyrotaenia*, *Ceritaenia*, *Exorstaenia*, *Farragona*, *Ochrotaenia*, *Raisapoana* and *Tacertaenia*). A complex transtilla with a medial process is only known in *Furcataenia*. Variably developed lateral processes from the transtilla are found in some species of *Claduncaria*, *Spinotaenia* and *Aphelia* (s.s.); *Enicotaenia* has two dorso-lateral horn-shaped processes, which are strongly developed and serrated. Well-defined processes of the sacculus are only reported in *Furcataenia* and *Aphelia* (s.s.), but in *Enicotaenia* the process is smooth, single, and ventrally extended, not serrated.

The female genitalia of *Enicotaenia* are less informative, and no character except the presence of two lateral subconical pockets on the 8<sup>th</sup> sternite is autapomorphic. The two depressions present in the sclerotized antrum of *Aphelia* (see Fig. SM1) may resemble these pockets but lack apodem-like projections. *Enicotaenia* does not present a cestum in the ductus bursae, as in other genera such as *Clepsis*, *Sychnovalva*, *Saetotaenia* or *Spinotaenia*. The antrum of *Enicotaenia* is rather simple without vestiture, similar to some species of *Argyrotaenia*, while it is strongly spinulated in other genera such as *Furcataenia* or *Aphelia* (s.s.). *Enicotaenia* has a well-developed signum with capitulum, typically Archipini, as in other related genera such as *Argyrotaenia*, *Farragona*, *Furcataenia*, *Idolatteria* and *Raisapoana*. Some genera present a signum as a microthorny sclerite (*Chamaepsichia*, *Rubropsichia* or *Aphelia* (s.s.)), or directly the signum is absent (*Claduncaria*, *Ochrotaenia* or *Tacertaenia*).

**Description.** *Head:* Typically tortricoid. Vertex with long scales. Frons slightly convex and covered by scales in upper part. Antennae length ca. 0.5 as long as forewing costa, dorsally scaled, ventrally ciliated, cilia less 0.5 times width of flagellomere, males with more numerous cilia than females, two rows of scales per flagellomere. Maxillary palpus undetectable. Labial palpus porrect, length (all three segments combined) same as diameter of compound eye, uniformly scaled. Proboscis well developed, naked. Ocelli and chaetosemata well developed, evident.

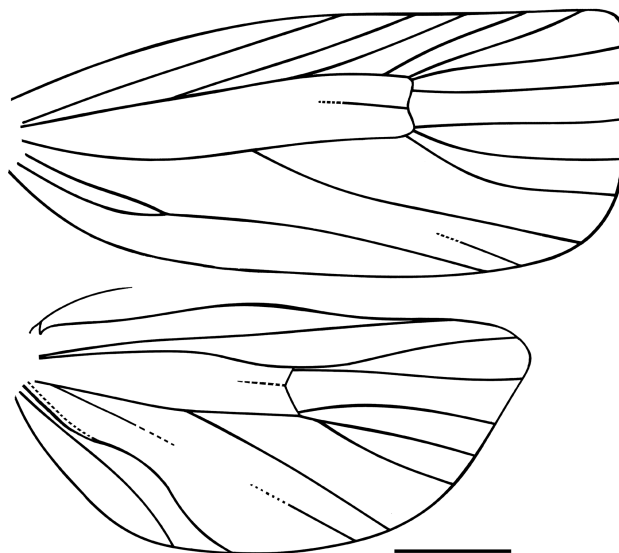
*Thorax:* Smooth-scaled including tegulae, with no tufts. Legs unmodified, male foreleg hairpencil absent. Wings with a venation typically for Archipini (Fig. 1). Forewing with a complete venation (based on one slide); M-stem absent, chorda and discal cross-vein obsolescent; discal cell ca. 0.7 times length of wing; all veins present and well defined except  $CuP$  reduced, retained only in terminal part;  $R_4$  to costa near apex,  $R_5$  to termen; distance between pairs of veins on termen between  $R_5$  and  $CuA_1$  relatively constant but distance between  $CuA_1$  and  $CuA_2$  slightly larger; anal veins bifurcate in basal area of wing, anal loop ca. 0.4 times length of  $1A+2A$ ; costal fold absent. Hindwing with no tubular M-stem in discal cell; vein  $Sc+R_1$  somewhat parallel to  $R_s$  basally, length ca. 0.7 times length of wing;  $R_s$  and  $M_1$  stalked, parallel basally, ca. 0.4 times length of wing;  $M_3$  and  $CuA_1$  connate;  $CuA_2$  well developed;  $CuP$  reduced, present only in distal portion;  $1A+2A$  sinuous, anal loop ca. 0.2 times length of  $1A+2A$ ;  $3A$  developed. Frenulum in females with three bristles and males with one.

*Male Abdomen:* Segment 8 in males with lateral long brush of scales projected caudad covering genitalia. Male genitalia (Fig. 2C–D) (based on three preparations) with tegumen strongly sclerotized and developed; uncus long (length ca. 0.5 as long as valva) simple clearly differentiated from tegumen; socii weakly developed, sclerotized, with some few long seta on each lobe; arms of gnathos sclerotized, mesally fused, with short dorsal serrations; transtilla continuous, well sclerotized, ventrolaterally with paired elongate serrated processes projecting caudad; valva regular, slightly sclerotized except for the sacculus, costa concave, cucullus rounded, hairy; sacculus well sclerotized, with presence of a fine ventral tooth (digitus) ca.  $2/3$  length of costa; juxta fused with caulis forming a subrectangular plate; phallus with coecum penis straight, distal portion strongly curved down, dorsally minutely serrated; vesica simple, globous, with no cornuti (no cornuti sockets; no deciduous cornuti detected in female genitalia corpus bursae).

*Female Abdomen:* Segment 7 in females without modified scaling (corethrogyne); Female genitalia (Fig. 2E–F) (based on two preparations) typically Archipini; ostium ringlike; subrectangular sterigma, concave in middle anteriorly, slightly sclerotized on posterior edge, lamella antevaginalis with two differentiated ventral pockets and two lateral depressions (sternite 8) each internally projected in a short apodeme. Antrum short; ductus bursae approximately the length of the corpus bursae, with distinct junction between corpus bursae and ductus bursae;

ductus seminalis postmedial; bulla seminalis well-defined; corpus bursae ovoid; signum well developed, elongated with the presence of interior dagger-shaped spine, length more than 0.5 width of the corpus bursae, an external capitulum well developed (one or two globular spermatophores were extracted from the corpus bursae). Anal papillae large, well developed, mesally constricted and covered by sparse long setae, posterior apophysis shorter than anterior apophysis.

**Etymology.** The genus name combines the related genus name *Argyrotaenia* with the classic Greek adjective *enikós* (ενικός), meaning “singular”, in reference to the unusual combination of characters present in the new genus. It is to be considered as feminine in gender.



**FIGURE 1.** Venation of *Enicotaenia interandina* new genus and species. Based on slide 21006. Dashed lines indicate obsolete veins. Scale bar: 1 mm.

***Enicotaenia interandina* Pérez Santa-Rita, Dombroskie, Ledezma & Baixeras, new species**

urn:lsid:zoobank.org:pub:0EB9272D-4A57-48DA-AD47-972D519B9876

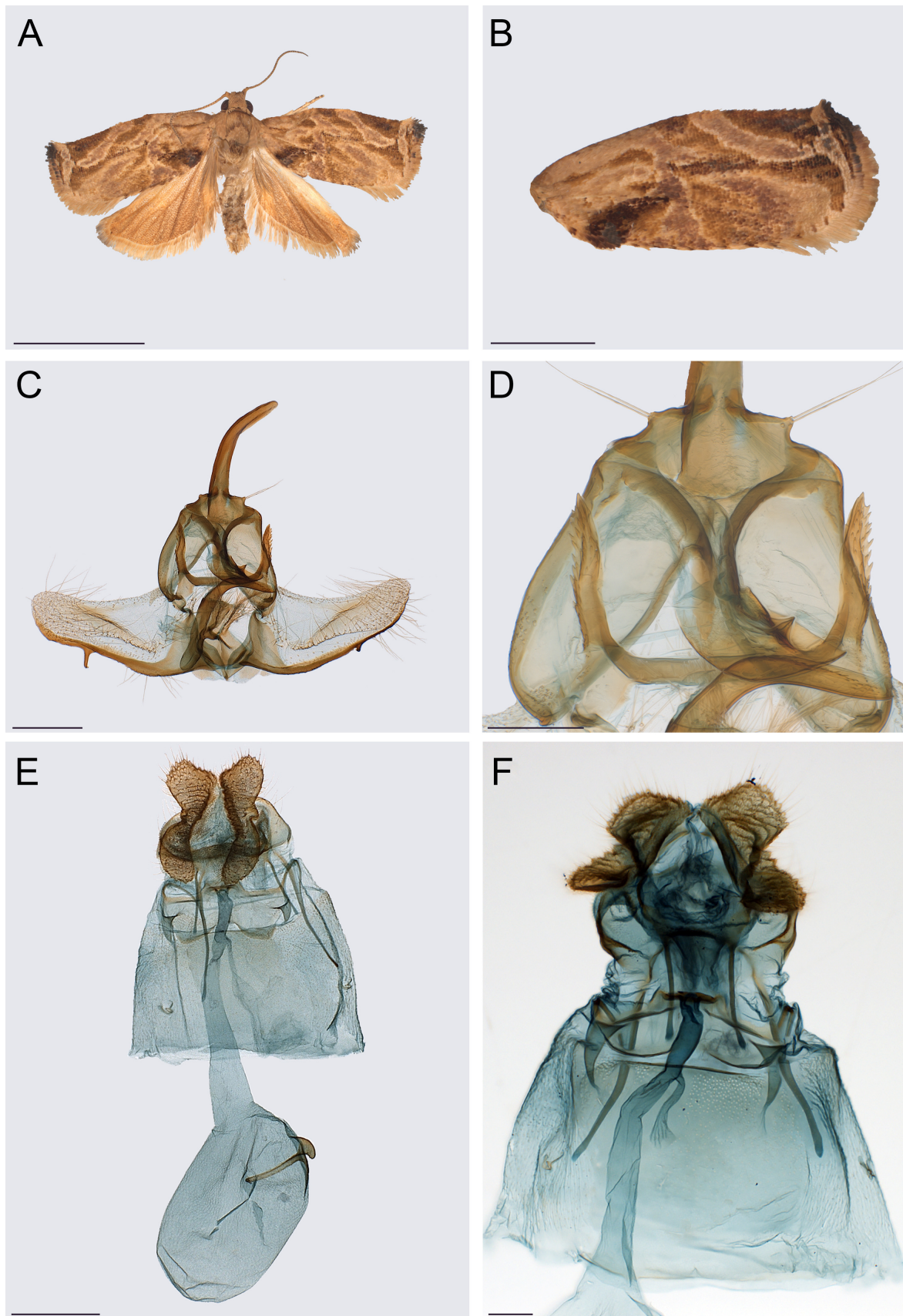
(Fig 2A–F)

**Type material.** Holotype. [BOLIVIA] ♂, Santa Cruz Department, Florida Province, Pampa Grande Municipality, locality of El Millu, 1534 m, S17°59'21.6"; W64°03'14.5", 28 Jan 2011, J. Baixeras, A. Valdivia and G. Fernández (GS 20681)-coll. MNKM. Paratypes. [BOLIVIA] 3♂, 2♀, Santa Cruz Department, Florida Province, Pampa Grande Municipality, locality of El Millu, 1534 m, S17°59'21.6"; W64°03'14.5", 28 Jan 2011, J. Baixeras, A. Valdivia and G. Fernández (GS 20680, 20717, 20720) (DNA collection codes: DNA2023006, DNA2023033, DNA2023038). 1 male and 1 female deposited in MNKM, 2 males and 1 female deposited in ICBiBE.

**Diagnosis.** This species may be distinguished from other Archipini by the characters discussed in the diagnosis of the genus. Only two species are known in the genus *Enicotaenia*, *Enicotaenia marabana* (Razowski & Becker, 2000) comb. n. and *E. interandina* here described, both extremely similar. The male of *E. marabana* is unknown, and the female is only known from the holotype, a single worn specimen from Brazil. The ductus bursae is rather broad in *E. interandina* and appears narrower in *E. marabana*. The anterior hypophysis is twice as long in *E. interandina* compared to *E. marabana*.

**Description.** *Head:* Frons, vertex, labial palpus and antenna orangish; presence of dark scales dorsally on labial palpus and antenna.

*Thorax:* Dorsum orangish with the presence of groups of dark scales mixed; forewing length 5.7–6.6 mm ( $\bar{x}$  =6.2; n= 4) in males, 7.0–7.4 mm ( $\bar{x}$  =7.2; n=2) in females. Forewing pattern (Fig. 2A–B) not sexually dimorphic. Forewing upperside general background colour from ochreous to orangish with scattered dark brown marks, without distinct system of strigulae; system of fasciae incomplete; basal and subbasal fasciae only expressed on dorsum as a dark brown transverse suffused area; median fascia brown, broader on costa, confluent to termen, narrowly fragmented across the wing; postmedian and preterminal fasciae fused as a preapical triangular spot; fringe dark in



**FIGURE 2.** Habitus and genitalia of *Enicotaenia interandina* new genus and species. A, Adult male Holotype; B, Upperside forewing pattern; C, Male genitalia (GS.: 20720); D, Gnathos and transtilla of male genitalia (GS.: 20681); E, Female genitalia (GS.: 20680); F, Detail of female genitalia (GS.: 21005). Scale bars: 2 mm (A); 1 mm (B, E); 500  $\mu$ m (C); 100  $\mu$ m (D); 200  $\mu$ m (F).

apical area, lighter in termen and tornus; interfascial areas light brown. Forewing underside uniformly creme, no system of strigulae. Hindwing upperside and underside fairly concolorous, uniformly light orangish brown. Female wing pattern similar to male, no obvious dimorphism.

*Abdomen:* Dorsad orangish, brownish cephalad, paler toward the caudal segments. Male and female genitalia as described for the genus.

**Molecular characterization.** We were able to obtain sequences for small fragments of COI from three specimens. Two identical small fragments of 164 bp were obtained from one male and one female specimens using the primer pair combination C\_TypeF1 and C\_TypeR1. Another small fragment of 307 bp was obtained from one female specimen using the pair combination LepF1 and MLepR1 primers.

The sequences are publicly available through GenBank accession numbers PV105885, PV241496 and PV241497.

**Biology and Distribution.** Early stages are unknown; adults have been collected in January (n=5). Adults were collected at middle elevation (1534 m) in Bolivia, Santa Cruz Department, Florida Province, in municipality of Pampa Grande, and locality of El Millu. The collecting sites include transitions between Bolivian montane dry forest and the slopes of the northern cloud forests of Yungas ecoregion.

**Etymology.** The specific epithet refers to the location of the collecting place, an area between inter-Andean dry valleys of the Bolivian montane dry forest and the slopes of the northern Bolivian Andes, a northern Yungas forest. This location has enormous interest from a conservation perspective.

### ***Enicotaenia marabana* (Razowski & Becker, 2000)—comb. n.**

*Furcataenia marabana* Razowski & Becker, 2000. Acta Zoologica Cracoviensia 43: 201.

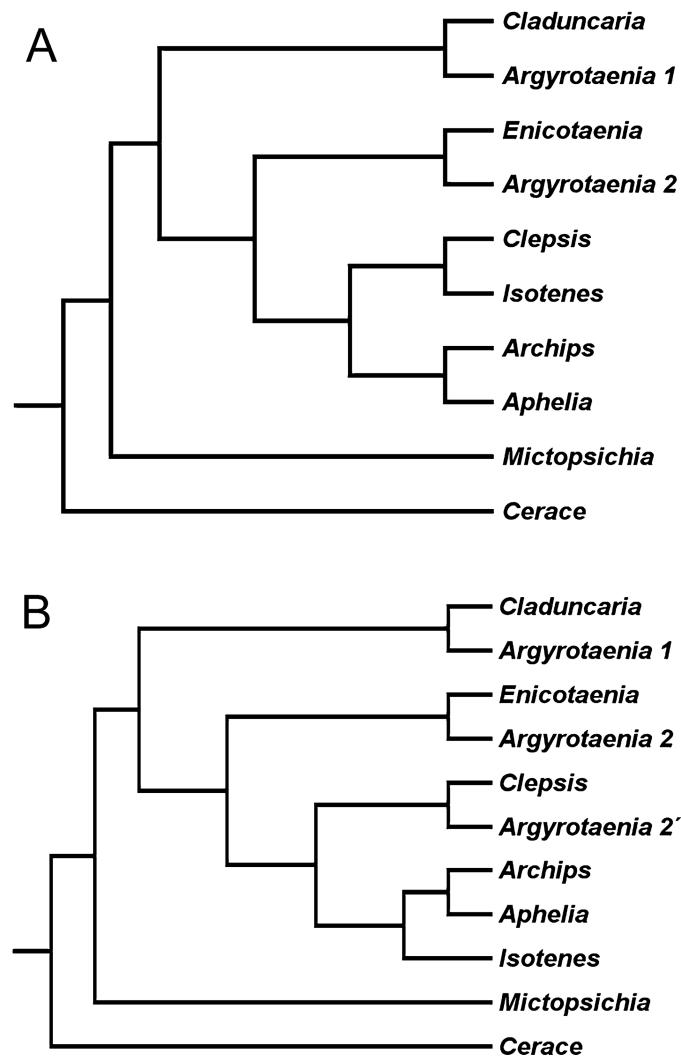
Razowski & Becker (2000) described the genus *Furcataenia* to include a series of species from Brazil with bizarre male genitalia. They also described *F. marabana*, a species based on a single worn female. In the female genitalia drawing by Razowski & Becker (2000) the ductus bursae is presumably rotated. The signum appears on the left part of the corpus bursae and should be on the right side. Anyway, the female genitalia are similar in both species, and they both appear to have the A8 pockets. It seems reasonable to assume that such a structure is an apomorphy of the genus, suggesting monophyly.

The discovery of *E. interandina* relates both species through the female genitalia, but the male of *E. interandina* is not assignable to *Furcataenia*. We propose the description of a separate genus, *Enicotaenia*, to include the new species together with *E. marabana*, closely related species. Because the information on *E. interandina* is more complete, we propose it as the type species for the genus.

## **Discussion**

Most of the specific diversity of Neotropical Archipini is contained in *Argyrotaenia* (90 spp.) and *Clepsia* (76 spp.). However, a group of Brazilian genera gather a poorly speciose, but morphologically diverse number of species not assignable to either of these two genera (Razowski & Becker 2000). The description of *Enicotaenia* from Bolivia suggests that the geographic range of this group of genera may have been underestimated, which may rather represent a lack of collecting effort in other areas. The type localities of the two species known so far of the genus *Enicotaenia* are not only more than 2,000 km apart but are also located in different biogeographic provinces (Navarro & Maldonado 2005, Morrone 2006).

Molecular barcoding evidence is known only from *Argyrotaenia*, *Clepsia* and *Claduncaria*, and now from *Enicotaenia*. The comparison of DNA barcode of *E. interandina* against databases did not provide any robust information. Sequence analyses using Maximum Likelihood (ML) and Neighbor Joining (NJ) methods (Figs SM2, SM3) placed *E. interandina* within a Neotropical group of *Argyrotaenia* (Fig. 3), rather than with representatives of *Aphelia* or *Archips*.



**FIGURE 3.** Clustering of *E. interandina* with other representatives of Archipini based on molecular analysis of COI sequence. A, ML analysis; B, NJ analysis.

Generic characters in Tortricidae usually include the venation, but it is unknown in many of the genera treated in this paper and may be of questionable taxonomic value due to its variability. Based solely on male genitalia, three major radiations may be distinguished among Neotropical archipines. The most distinctive group includes *Clepsis*, *Cornuclepsis*, and *Sychnovalva*. A second, morphologically more diverse group would be organized around *Argyrotaenia*, including at most *Ceritaenia*, *Claduncaria*, *Exorstaenia*, *Idolatteria*, *Ochrotaenia*, *Raisapoana*, *Saetotaenia* and *Tacertaenia*. Finally, there would be a group around *Aphelia*, including *Cununcus*, *Farragona*, *Furcataenia* and *Spinotaenia*. Overall, *Enicotaenia* fits in the last group. Genital characters among the representatives of this group include a proliferation of exaggerated male genital morphologies, including complex unci and transtillar processes (Austin & Dombroskie 2020b). These striking morphologies suggest rapid evolution. *Enicotaenia* presents a unique configuration in a continuous transtilla with pointed lateral serrated processes. Several genera included here present some degree of complexity in the transtilla. This is the case of *Furcataenia*, the genus with which *E. marabana* was originally combined. The presence of well-developed sclerotized processes in the sacculus is rare in the Neotropical genera of Archipini. However, some genera, such as *Ceritaenia*, *Raisapoana*, *Spinotaenia*, and *Saetotaenia* present some saccular projections, often serrated. Unfortunately, the female configuration is unknown in many of these cases, making the interpretation of these structures difficult.

Coupling mechanisms are poorly known in Tortricidae. There are several examples of intraspecific variation that question the lock-and-key hypothesis (Mutaten *et al.* 2007, Gilligan & Wenzel 2008, Rentel *et al.* 2017). Nonetheless, only few studies have hypothesized about male-female interactions (Ferro & Akre 1975, Pérez Santa-

Rita & Baixeras 2017, Austin & Dombroskie 2020b) or about functional morphology (Zlatkov *et al.* 2023) in Tortricidae. An analysis of the male and female genitalia allows for some conjectures about the coupling mechanism in *Enicotaenia*. The two serrated lateral processes of the transtilla of the male genitalia are separated by the same distance as the two lateral subconical invaginations situated in the 8<sup>th</sup> sternite of the female. The presence of apodemes connected to these invaginations suggests some active control by the female. Putative muscles for these apodemes could be some a specialized branch of muscles ms 7-8 (Kuznetsov & Stekolnikov 2001, Zlatkov *et al.* 2023). This suggests a peculiar copulation mechanism. Both the female sterigma and the male vinculum must be strongly bent. It also requires a deflection of the postvaginal female elements (including ovipositor) by the male uncus and gnathos. This coupling involves a rather forced abdominal position for male and female. The sigmoid-like curvature of the phallus and the tilted ostium seem to facilitate that position. Interestingly, the Palearctic *Aphelia viburnana* (Denis & Schiffermüller, 1775), although less conspicuously, also shows some structural similarities that may suggest a similar coupling mechanism (Fig. SM1). Future descriptions of females of related genera should look for similar structures, adding fresh material to uncover the mating process.

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**Supplementary Materials.** The following supporting information can be downloaded at the DOI landing page of this paper:

**FIGURE SM1.** Male and female genitalia of *Aphelia viburniana* (Denis and Schiffermüller, 1775). A, Male genitalia (GS: 862); B and C, Female genitalia (GS.: 4168). Scale bars: 1 mm (A, B); 500 µm (C).

**FIGURE SM2.** ML analysis of COI sequences of Archipini species.

**FIGURE SM3.** NJ analysis of COI sequences of Archipini species.