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RESEARCH ARTICLE

Description of the immature stages and natural history of the generalist seed feeder moth *Cydia tonosticha* (Lepidoptera: Tortricidae)

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ABSTRACT. The tortricid genus *Cydia* Hübner, 1825 is widely distributed and includes important pests of agriculture and forestry. Most of the research related to natural history and morphology of the immature stages of this genus involves species of economic importance. Thus, there is a lack of knowledge about non-pest species. Herein, we describe the morphology of the immature stages (eggs, larvae and pupae) and natural history of *Cydia tonosticha* (Meyrick, 1922), a widely distributed moth in the Neotropics and an important seed predator of *Cassia leptophylla* Vogel (Fabaceae). Scanning electron microscope images illustrating morphology of the immature stages are provided for the first time for a Neotropical *Cydia* species. This study contributes to our overall understanding of morphology, ecology, and consequently, evolutionary traits in Tortricidae.

KEY WORDS. *Cassia leptophylla*, electron microscopy, microlepidoptera, life cycles, life history, Neotropical Region.

INTRODUCTION

Comprised of over 11,000 species, Tortricoidea stands as one of the largest superfamilies among microlepidoptera, exclusively represented by Tortricidae (Gilligan et al. 2018). Most of these species inhabit tropical regions of the New World (Regier et al. 2012). Larvae of Tortricidae are well known for their feeding and shelter habits, where they burrow into roots, stems, seeds, fruits, or buds of their host plants. Additionally, gall-forming and mining behaviors have also been observed within this family (Mackay 1963, Daviault and Ducharme 1966, Stehr 1987, Brown and Nishida 2007). Some Tortricidae species can become agricultural pests, resulting in significant economic losses (Cepeda and Cubillos 2011).

Cydia Hübner, 1825 (Tortricidae: Olethreutinae: Grapholitini) is a widely distributed genus occurring in all biogeographical regions except for the Antarctic. More than 200 species have been described. Some of them are important pests of agricultural, horticultural and forestry crops, such as the codling moth, *C. pomonella* (Linnaeus, 1758) (Lacey and Unruh 2005, Salinas-Castro et al. 2014, San Martín-Romero et al. 2020). *Cydia tonosticha* (Meyrick, 1922) is distributed in the Neotropics, with records for Brazil, Panama, Peru, Venezuela and Chile. There it feeds on seeds of the Fabaceae genera *Cassia* and *Stryphnodendron* (Bobadilla and Vargas 2015). It is an important seed predator of *Cassia leptophylla* Vogel in South Brazil, a species employed for the rehabilitation of deteriorated landscapes and extensively utilized in urban tree planting due to its decorative qualities (Pereira et al. 2015).

The morphological study of the immature stages of Tortricidae species is important to better elucidate the evolutionary history and the systematics of the group, as in other microlepidopteran families (Kristensen et al. 2007, Vargas 2007). Although previous studies on *C. tonosticha* have contributed to the understanding of some aspects of its natural history (Penteado-Dias et al. 2008, Pereira et al. 2015), herein we provide a complete description of the immature stages (eggs, larvae, and pupae) and other information on the natural history of this tortricid feeding on *Cassia leptophylla* seeds.

MATERIAL AND METHODS

Specimens examined for the descriptions were obtained from fruits of *C. leptophylla*, all collected by the senior author in the municipality of Guarapuava, Paraná, Brazil. They were initially analyzed in the Laboratório de Morfologia e Comportamento de Insetos, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, and later in the Departamento de Zoologia, Universidade Federal do Paraná (UFPR), Curitiba, Paraná, Brazil. Part of the pod material was dissected to obtain the immature stages of *C. tonosticha* (eggs, larvae and pupae), and part was kept intact to obtain adults, which were pinned and dried.

Immature stages were fixed in 75% ethanol. For descriptions of the gross morphology, the specimens were cleared in a 10% potassium hydroxide (KOH) solution and slide-mounted in either glycerin jelly or Canada balsam. Observations were performed with the aid of a Leica® M125 stereomicroscope, and measurements were performed using an attached ocular micrometer (precision = 0.01 mm). Structures selected to be drawn were previously photographed using a photo stacking process associated with a Leica® Application Suite Version 4.12.0 stereomicroscope. These procedures were conducted at the Laboratório de Estudos de Lepidoptera Neotropical at Universidade Federal do Paraná, Curitiba, Paraná, Brazil. Vectorized line drawings were created using CorelDraw® software, with the corresponding digitized images serving as a reference. Six eggs and at least five specimens of the last instar larvae and pupae were used for the descriptions. Setal terminology follows Stehr (1987) for the larvae, Patocka and Turcani (2005) for the pupae.

For scanning electron microscope (SEM) analyses, additional specimens of the last instar larvae were dehydrated, mounted with double-sided tape on metal stubs, and coated with gold in a Bal-tec® SCD050 sputter coater. They were examined and photographed in SEM JEOL JSM 6360-LV scanning electron microscope at the Centro de Microscopia Eletrônica, UFPR. Vouchers of specimens, both immatures and adults, used in this study were deposited in the Coleção Entomológica Padre Jesus Santiago Moure (DZUP), UFPR. The voucher code of the immatures is DZUPIL 0175, and the vouchers of the adults are DZ 63.954; DZ 63.955; DZ 63.956; DZ 63.957 and DZ 63.958.

RESULTS

Morphology of the immatures

Egg: Flat and oval, firmly adhered to the leaf surface (Fig. 39), Average diameter ± standard deviation = 0.70 ± 0.001 mm, n = 5.

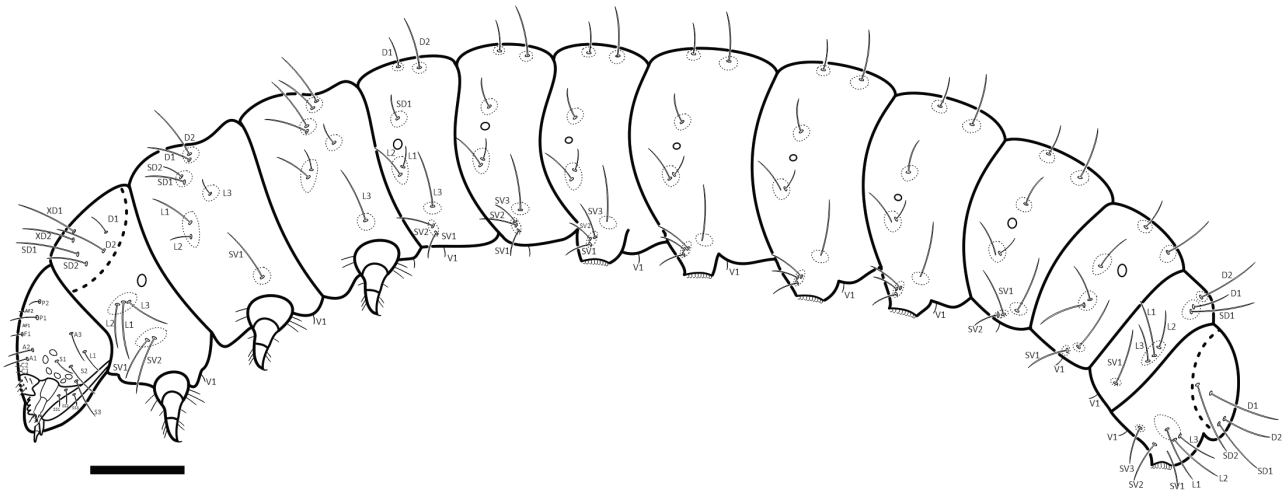
Larva: Semiprognathous; there is only one morphotype without hypermetamorphic development, buccal apparatus of chewing type. At least four instars were identified through head capsule measurements.

Last instar: Average total length ± standard deviation = 6.96 ± 0.16 mm; n = 5. Average head capsula length ± standard deviation = 1.6 ± 0.004 mm; n = 5. Head brown, slightly flattened dorsoventrally, with deep epicranial notch. Fronto-clypeus triangular. Labrum bilobated, with rounded edges and bearing five pair of short setae (Figs 7, 11). Mandibles with four well-developed cusps, having one pair of setae on proximal base. Maxilla three-segmented, with prominent basal segment bearing a pair of setae, and medium segment bearing one seta. Labial palpi short (Fig 8, 9). Labium with tubular spinneret having a pair of setae on proximal base (Figs 8, 9, 12). Antenna two-segmented, with eight apical sensilla, one of them distinctively filiform and longer (Figs 7, 10). Six circular stemmata, three proximal, one lateral, two at antenna base (Figs 6, 7, 13). Head chaetotaxy of the last instar exhibits the typical pattern described for Tortricidae (Patocka and Turcani 2005) (Fig. 1).

Thorax and abdomen cylindric, body creamy white in preserved material, bearing filiform setae, and integument sculptured with microtrichiae, except dorsally on T1 and A10. T1: bearing a light brown dorsal prothoracic shield, divided longitudinally (Figs 5, 6). A pair of lateral spiracles without elevated peritreme (Fig. 14). T1, T2, T3: legs present, with five well-developed setae on coxa, two on tibia, five on tarsus, all with a hook-shaped apical claw (Figs 8, 15); anterior base of coxae darker.

Thorax chaetotaxy of the last instar (Fig. 1): prothoracic shield with six pairs of setae. Dorsal group (D) bisetose; D1 short and D2 long. Extra dorsal group (XD) bisetose; both the same length. Subdorsal group (SD) bisetose; SD1 long and SD2 short. Lateral group (L) trisetose in pinnacle lateral to spiracle; L1 longer than others. Subventral group (SV) bisetose, inside the pinnacle; SV1 longer than SV2. Ventral group (V) unisetose, short, on the pinaculum. T2-3: Dorsal, subdorsal, lateral, subventral and ventral groups on pinacula. Dorsal group (D) bisetose; D2 longer than D1. Subdorsal group (SD) bisetose; SD1 longer than SD2. Lateral group (L) trisetose; L1 longer than others; L1 and L2 in a pinnacle, and L3 in other. Subventral group (SV) unisetose; SV1 long. Ventral group (V) unisetose, short, on pinacula.

Abdominal segments from A1 to A9 similar; A10 with a rounded anal shield (Figs 17, 21). Spiracles rounded, laterally present on A1-A8, without elevated peritreme; spiracle A8 similar in size to that of the prothorax and larger than those



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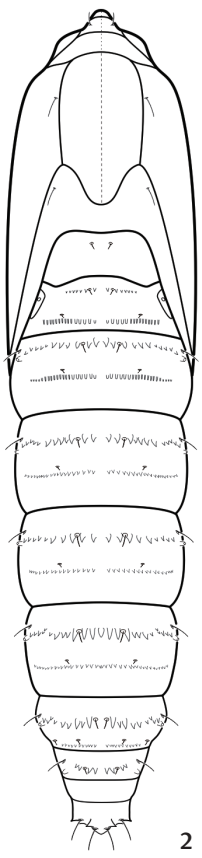

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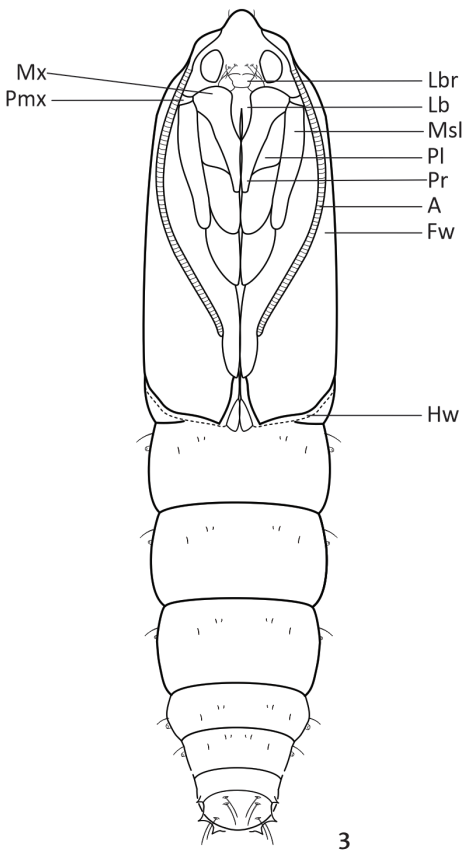

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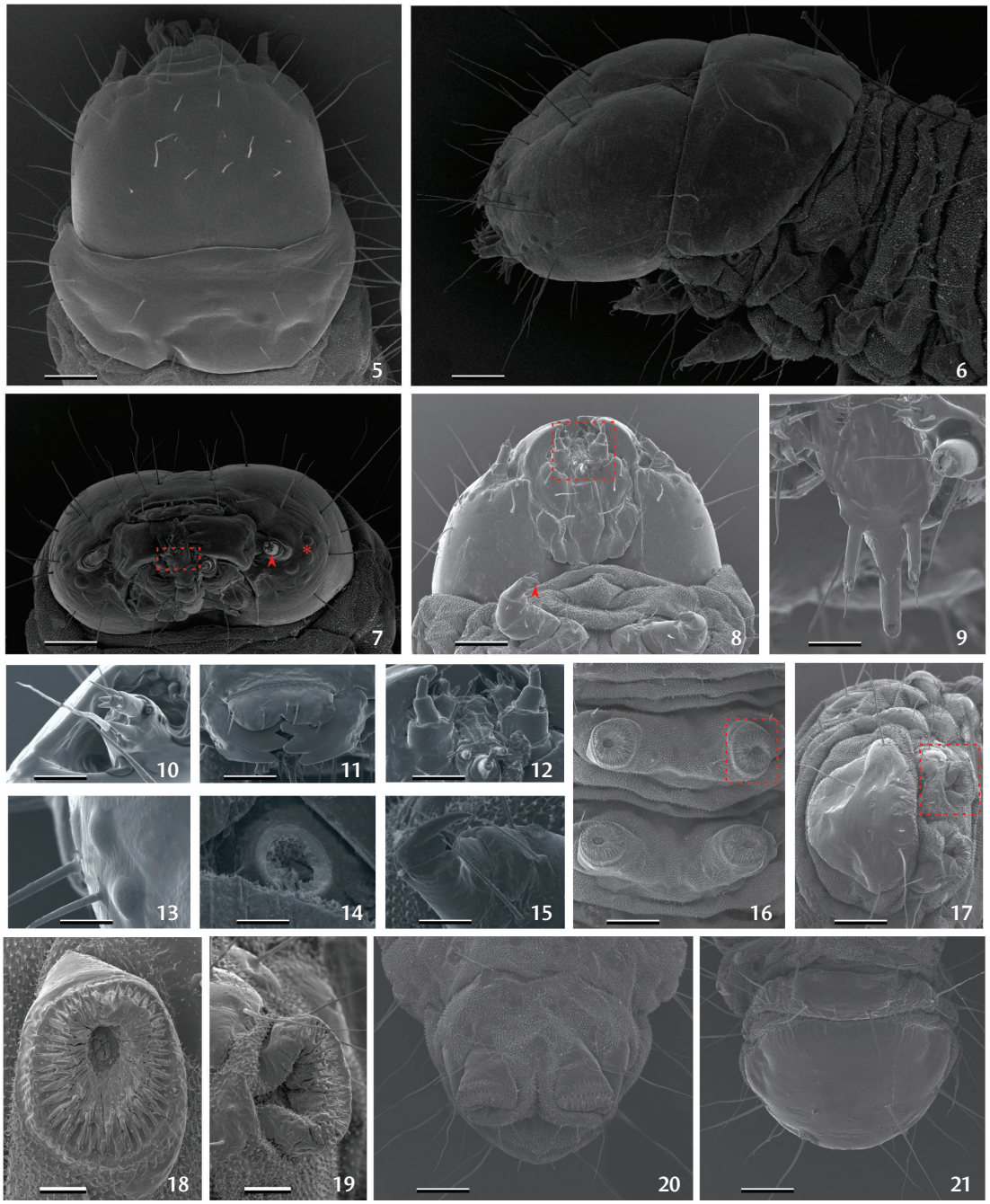
Figures 1–4. Last larval instar and pupal morphology of *Cydia tonosticha* under light microscopy: (1) larva chaetotaxy in lateral view; pupa, (2) dorsal, (3) ventral and (4) lateral views. Lbr: labrum; Mx: maxillae; Pmx: maxillary palpi; Lb: labium; Msl: mesothoracic legs; Pl: prothoracic legs; Pr: proboscis; A: antennae; Fw: forewings; Hw: hindwings. Scale bars: 1 = 1.0 mm, 2–4 = 0.5 mm.



Figures 5–21. Last larval instar of *Cydia tonosticha* under scanning electron microscopy; head and thorax: general morphology, (5) dorsal, (6) lateral, (7) frontal and (8) ventral views; (9) spinneret in detail, ventral, indicated by rectangular area marked in 7; (10) antenna in detail, anteroventral, indicated by arrow in 7; (11) labrum, anteroventral; (12) mouthparts, anteroventral, indicated by squared area marked in 8; (13) stemmata in detail, lateral, indicated by asterisk in 7; (14) spiracle on T1, lateral; (15) tarsal claw of first thoracic leg in detail, ventral, indicated by arrow in 8; (16) pseudopodium on A1-A2, ventral; (17) last abdominal segment, posterior, (18,19) pseudopodia in detail, indicated by rectangular area marked in 16 and 17 respectively; last abdominal segment, (20) ventral and (21) dorsal views. Scale bars: 5–8 = 200 µm, 9 = 100 µm, 10–15 = 25 µm, 16–17 = 200 µm, 18–19 = 50 µm, 20–21 = 200 µm.

of A1-7. Pseudopodia present on A3-6 and A10; A3-6 crochet arranged in uniordinal circles (Figs 16, 18); A10 crochet arranged in uniordinal transverse bands (Figs 17, 19, 20).

Abdominal chaetotaxy of the last instar (Fig. 1): A1-A8: Dorsal, subdorsal, lateral, subventral and ventral groups inside pinnacles. Dorsal group (D) bisetose; D1 dorsal and D2 dorsolateral, in different pinnacles, D2 longer than D1. Subdorsal group (SD) unisetose, near and above spiracle, except on A8 where it is located lateral to the spiracle. Lateral group (L) trisetose; L1 and L2 in one pinnacle under the spiracle, and L3 in other pinnacle more ventral; L1 shorter than others. Subventral group (SV) with all setae about the same length; A1 bisetose, A2-A6 trisetose, A7 bisetose, and A8 unisetose. Ventral group (V) A1-A8 unisetose; with all setae about the same length. A9: Pinnacles of both D2 of each side united dorsally. D1 on the same pinnacle of SD1; SD1 longer than other setae. Lateral group (L) trisetose; L1 longer than others. Subventral group (SV) unisetose, long. Ventral group (V) unisetose, short. A10: Dorsal group (D) and subdorsal group (SD) bisetose; all setae long inside a very conspicuous anal shield. Lateral group (L) trisetose, all setae inside a large pinnacle. Subventral group (SV) trisetose, at proleg base Subventral group (SV) trisetose, at proleg base. Ventral group (V) unisetose.

Pupa: Average length ± standard deviation = 6,74 ± 0.13 mm, n = 5. Obtect (Figs 2, 3, 4). Body brown and cylindrical (Fig. 4).

Head: front and clypeus smooth; cocoon cutter prominent and subtriangular (Figs 23, 24, 25, 26 27). Antennae not reaching the apex of the mesothoracic legs in length. Labrum subtriangular and narrow, with two pair of setae (Figs 23, 25, 26). Maxillae well developed. Maxillary palpi cuneiform. Labial palpi half the length of maxillae (Fig. 23).

Thorax: Pronotum as a narrow plate dorsally (Fig. 22). Forewings covering abdominal segments A1-A3 in ventral view (Fig. 3); hindwing concealed by the forewings; prothoracic and mesothoracic legs broad, visible ventrally (Fig. 3); metathoracic legs mostly covered by the forewings, except the apex that reaches the abdominal segment A4.

Abdomen: Abdominal segments from A2 to A7 with two transversal rows of spines dorsally, the anterior one with spines slightly bigger than the posterior, A2 with rows less prominent than others (Fig. 29); A8 with only one row of spines (Figs 30, 34). One dorsolateral pair seta in the segments T2-T3; one dorsal pair of setae from A1 to A7; A8 with two dorsal pairs of dorsal setae. Abdominal spiracles without elevated peritreme, well developed in A2-7 (Fig. 30), vestigial in A8 (Fig. 34), all of them bearing one supraspiracular seta (Fig. 30), two pairs of subspiracular setae present from A4 to A7; microsetae ventrally present from A5 to A8 (Figs 28, 31). Terminus bearing four spines dorsally, and one pair of spines lateroventrally (Figs 32, 33, 34); cremaster with one pair of dorsal setae, one pair of lateral setae and two pairs ventral setae.

Life history

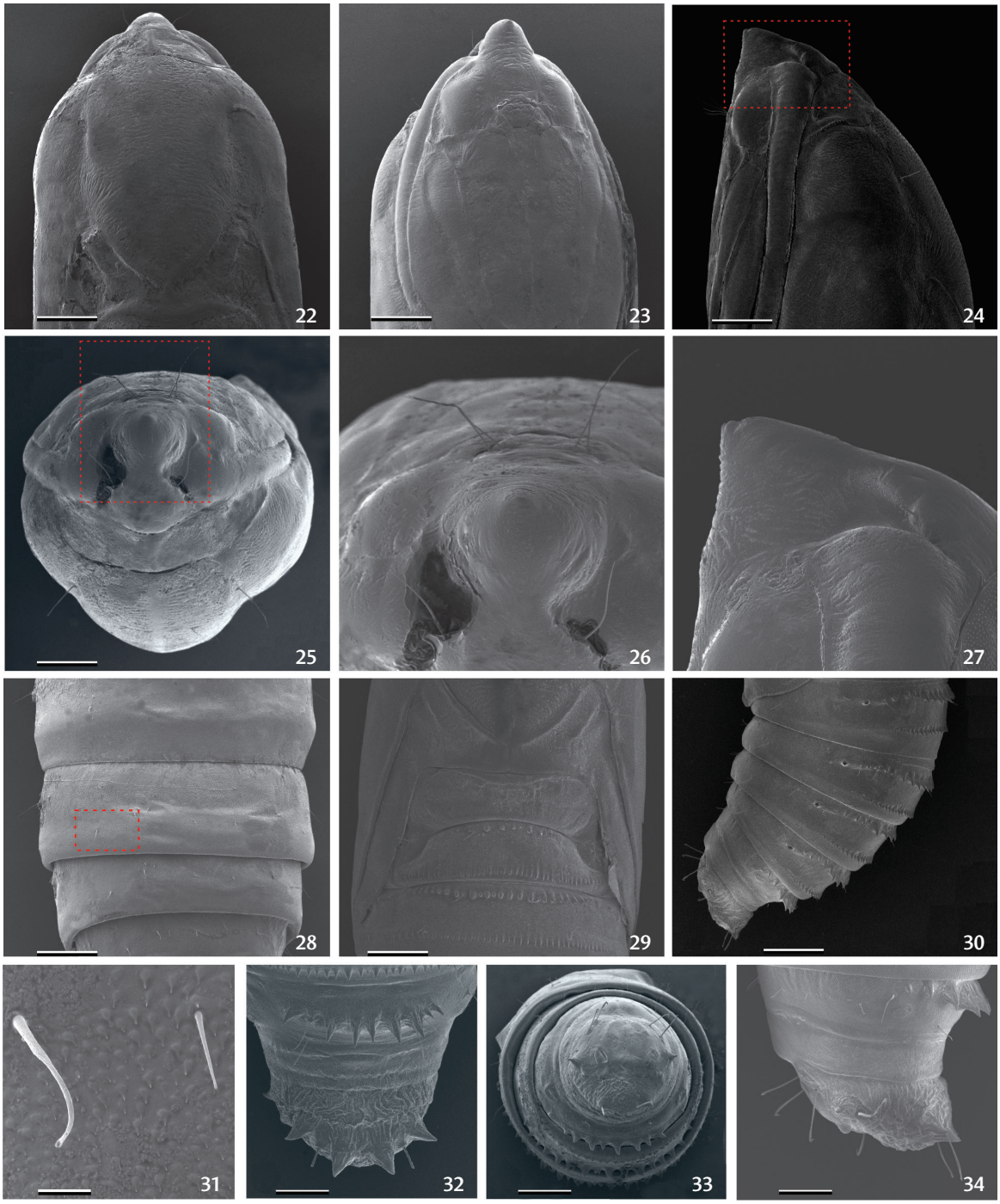
Native to the Atlantic Forest Biome, *C. leptophylla* is a widely spread species of Fabaceae. Mainly due to its ornamental appearance, it is commonly used in afforestation and urban decoration of streets and parks (Figs 35, 36). The species also has an ecological importance and is used to restore degraded areas. In natural environments, it occurs in secondary formations, mainly in mixed rainforest regions (Lorenzi 2002). The plant has indehiscent pods, which do not expose their seeds in both periods (pre and post dispersive) (Figs 36, 37); such pods are rigid and highly resistant, normally reaching more than 40 cm in length and harbor dozens of seeds (Fig. 37).

Adults of *C. tonosticha* (Fig. 38) oviposit on the pods of *C. leptophylla* (Fig. 39) in both dispersive periods. The larvae (Fig. 41) initially pierce and feed on the pod and its internal tissues and later pierce the seed coat, then accessing the endosperm and other structures (Figs 40, 41). Dissection of pods facilitate the observation of where seeds have been or not predated (Fig. 42).

In the last instar, the larva weaves the cocoon inside the pod, where it was previously occupied by the seed that was preyed upon (Fig. 42). The cocoon has a circular operculum (Fig. 42) which, before the emergence of the adult, is opened by the pupa (Fig. 43). In this process, the exuvia is partially protracted out of the opening in the pod (Fig. 44).

DISCUSSION

Though *C. tonosticha* is widely abundant and distributed in the Neotropics, this is the first time that their immatures are accurately described, and their natural history discussed. In fact, most of the studies concerned with biological aspects on species of *Cydia* are related to *C. pomonella*, due to its importance as a fruit and legume pest (Williams and McDonald 1982, Brown 1987, Ruberson et al. 1987, Timm et al. 2008, Pajač et al. 2011, San Martín-Romero et al. 2020). Such studies on immature morphology and natural history are important to better understand the morphological and ecological traits on microlepidoptera, providing basic information that can be used for more applied studies, such as the evolution and classification of Tortricidae (MacKay 1963).



Figures 22–34. Pupal characters of *Cydia tonosticha* under scanning electron microscopy: head and thorax general morphology, (22) dorsal, (23) ventral, (24) lateral and (25) anterior views; (26) head details, anterior, indicated by rectangular area marked in 25; (27) cocoon-cutter in detail, lateral, indicated by rectangular area marked in 24; abdominal segments, (28) ventral, (29) dorsal and (30) lateral views; (31) abdominal microsetae, ventral, indicated by rectangular area in 28; last abdominal segment in detail, (32) dorsal, (33) posterior and (34) lateral views. Scale bars: 22–25, 28–30 = 200 µm, 26–27, 32–34 = 100 µm, 31 = 25 µm.

Figures 35–44. Natural history aspects of *Cydia tonosticha* on *Cassia leptophylla* interaction: plant in (35) flowering and (36) fruiting periods; (37) detail of the indehiscent fruit (pod); (38) adult of *C. tonosticha*; (39) eggs placed on the pod; (40) detail of the entrance hole and excrement removed from the inside of the pod by the larva; (41) larva (final instar) feeding on pod and seed structures; (42) dissection of *C. leptophylla* pod showing non-predated seed (left) and predated seed with *C. tonosticha* pupal cocoon inside, arrow indicates operculum region; (43) pupa; (44) exuvia of *C. tonosticha* partially protracted. Scale bars: 37–38 = 50.0 mm, 39–44 = 5.0 mm.

Other *Cydia* species that had some aspects of their immature morphology and/or life history studied were the chestnut pests in North America: *Cydia splendana* (Hübner, 1799), *Cydia fagiglandana* (Zeller, 1841) and *Cydia glandicolana* (Danilevsky, 1968) (Brown and Komai 2008); the South American pest of *Araucaria angustifolia* (Bert.) O. Kuntze (Araucariaceae), *Cydia araucariae* (Pastrana, 1950) (Thomazini et al. 2011); the native Mexican Fabaceae pest, *Cydia deshaisiana* (Lucas, 1858) (San Martín-Romero et al 2020) and the mediterranean invasive pest, *Cydia interscindana* (Möschler, 1866) (Takács et al. 2022). In addition to those, Brown (1987) provided taxonomical keys to larvae of some other important pests, most of them from North America, including *Cydia strobilella* (Linnaeus, 1758), *Cydia ingens* (Heinrich, 1926), *Cydia piperana* Kearfott, 1907, *Cydia injectiva* (Heinrich, 1926) and *Cydia nigricana* (Fabricius, 1794). The new world species, *Cydia largo* Heppner, 1981 that feeds on *Acacia macracatnha* Humb. et Bonpl. ex Willd. (Fabaceae) is one of the few species without economic importance that had their immature stages aspects studied (Vargas and Parra 2006, Vargas, 2007).

Cydia tonosticha possess some traits generalized to Grapholitini, such as the semiprognathous head, head pigmented with six circular stemmata, body in a uniform creamy white color, dorsal prothoracic shield with a distinct medial sulcus, T1 with trisetose L group, T2-T3 with SV group unisetose, SD1 on A8 anterior from spiracle, A9 with D2's on same pinaculum, spiracles elliptical, prolegs with crochets arranged in uniordinal circles on A3-6, and in a uniordinal transverse band on A10 (Brown 1987).

One important character present on the larvae of *C. tonosticha* is the presence of an anal shield, that readily separates it from *C. ingens*, *C. injectiva*, *C. piperana*, *C. pomonella*, *C. stro-*

bilella, *C. splendana*, *C. fagiglandana* and *C. glandicolana* (Brown 1987, Vargas 2007, Brown and Komai 2008). The chaetotaxy of the larva also revealed some differences between *C. tonosticha* and other *Cydia* species. The SV group on A2 is trisetose in *C. largo* and bisetose on *C. nigrigana*, while the same group is unisetose in *C. tonosticha* (Brown 1987, Vargas 2007). The D group in A1 to A7 of *C. deshaisiana* is trisetose. On the same abdominal segments, the L group is unisetose in *C. deshaisiana* and trisetose in *C. tonosticha* (San Martín-Romero et al. 2020). Although very similar in pupal morphology, *C. tonosticha* presents the transversal rows of spines dorsally located more distant from the segment margins, while these rows are closer to the segment margins in *C. interscindana* (Takács et al. 2022).

The cocoon is woven inside the pod, where the consumed seed was located, allowing additional protection from external environmental variables, predators, and parasitoids (Hymenoptera, Braconidae). Unidirectional spines present on the pupa prevent displacement outside of the pod and facilitate pupal movements when the adult emerges.

Seed predation and the behavior of *C. tonosticha* described here occurs throughout the fruiting of *C. leptophylla* and lasts through the post-dispersal period, until the beginning of a new phenological cycle (Pereira et al. 2015). The characteristics of the pods and the way in which this interaction occurs provide constant and abundant sources of shelter and food to the species and continuity of this intricate insect-plant interaction.

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