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● 100-million-year history of caddisflies (Insecta: Trichoptera) as hosts of trematodes

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Abstract: This study explores the intricate parasitic relationship between a caddisfly larva and a trematode preserved in mid-Cretaceous Burmese amber. Through detailed morphological analysis, the caddisfly larva is classified within the suborder Integripalpia, closely resembling the family Calamoceratidae. Likewise, the parasite, exhibiting traits consistent with flatworms of the phylum Platyhelminthes, is tentatively identified as a digenean trematode. The discovery of ectoparasitism, where the trematode firmly attaches to the caddisfly larval exterior surface, challenges conventional understandings of trematode behavior, suggesting a departure from typical endobiotic lifestyles. The first finding of fossil flatworm parasitism on an aquatic insect sheds light on the evolutionary flexibility of trematodes and their ability to exploit diverse ecological niches. Moreover, the complex parasitic lifecycle, involving intricate stages from egg release to host transmission, underscores the complex interactions between organisms in ancient ecosystems.

Keywords: Aquatic insects, Burmese amber, Cretaceous ecosystem, paleoparasitology, taxonomy

● 毛翅目昆虫作为吸虫宿主的一亿年演化史（昆虫纲：毛翅目）

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摘要：本研究揭示了一种毛翅目幼虫与吸虫纲寄生虫在白垩纪中期缅甸琥珀中保存的复杂寄生关系。通过形态学分析，该毛翅目幼虫被归入完须亚目（Integripalpia），并与现生枝石蛾科（Calamoceratidae）形态高度相似。与其共生的寄生虫具有扁形动物门（Platyhelminthes）吸虫纲的典型特征，初步鉴定为复殖吸虫（Digenea）。该吸虫以体外寄生形式牢固附着于毛翅目幼虫体表，此发现挑战了传统认知——吸虫通常营体内寄生生活，表明其行为模式在早期演化中已呈现多样性。此为首例水生昆虫化石中吸虫寄生现象的记录，揭示了吸虫纲生物的演化可塑性及其对多样化生态位的利用能力。此外，从虫卵释放到宿主传播的复杂寄生生活史，进一步印证了古生态系统中生物间相互作用的精密性。

关键词：水生昆虫，缅甸琥珀，白垩纪生态系统，古寄生虫学，分类学

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Introduction

Trematoda, a class of flatworms commonly known as flukes or trematodes, comprises obligate internal parasites characterized by a complex life cycle necessitating one or more intermediate hosts, along with a definitive host for successful completion (Velázquez-Urrieta & Pérez-Ponce de León 2021). Typically, the initial intermediate hosts are molluscs, which become infected by the free-swimming larval forms, known as miracidia, either through penetration or ingestion of trematode eggs (Galaktionov & Dobrovolskij 2003; Koprivnikar *et al.* 2023). Within the tissues of molluscs, larval stages of trematodes undergo asexual reproduction (Yamaguti 1975). Subsequently, cercariae are released from molluscs into the environment and commonly seek out and infect the second intermediate host, where they encyst to form metacercariae (Faltynková *et al.* 2016). Upon ingestion by larger animals, metacercariae excyst and develop into adults, thus completing their life cycle. Adults primarily inhabit the digestive tracts or tissues of vertebrate hosts, where they engage in sexual reproduction. Notably, in definitive hosts, parasite eggs are frequently discharged along with host feces (Esch *et al.* 2002). Once shed in water, these eggs release free-living miracidia that are infective to intermediate hosts. Trematode infections have been documented to cause diseases in various vertebrates, including mammals, birds, amphibians, reptiles, and fishes (Bolek *et al.* 2019).

Caddisflies (Trichoptera) represent hosts for a diverse array of symbionts throughout their life cycle, including trematode metacercariae commonly found in their aquatic stage (Ilyushina 1990; Chae *et al.* 2000; Corallini & Marchetti 2016). The lifecycle continues as cercariae released from molluscs enter the case of a caddisfly larva, subsequently attaching to the caddisfly abdomen, penetrating through the integument, and ultimately reaching one of the silk glands, where metacercariae encyst and develop within the cyst (Caira 1981). Trematode parasitism in aquatic insects has been observed to induce behavioral and physiological alterations in hosts, including changes in feeding rates, stress responses, survival, and competitive abilities (Friesen & Detwiler 2021).

Despite Platyhelminthes being considered the most primitive divergent lineage of Bilateria (Hyman 1951; Littlewood 2008), credible fossil records are scarce (Wills 1993). The fossil record of various groups of Platyhelminthes was recently reviewed by various authors (Poinar 2015; Klompmaker & Boxshall 2015; Parry *et al.* 2019; De Baets & Huntley 2021). Recent fossil discoveries of Platyhelminthes have extended the record of parasitic flatworms further into the Paleozoic (Upeniece 2001; Dentzien-Dias *et al.* 2013). The oldest fossil evidence for trematodes is an egg recovered from an Early Cretaceous isolated terrestrial vertebrate coprolite in Belgium (Poinar & Boucot 2006), representing the earliest evidence for Trematoda in terrestrial predatory archosaurs (De Baets *et al.* 2015). However, these fossil records primarily consist of traces and eggs (Poinar 2003), and none of them is associated with aquatic insects.

In this study, a piece of mid-Cretaceous Burmese amber from northern Myanmar was examined, which contains a caddisfly larva parasitized by Trematoda. The aim was to describe the morphology of the caddisfly and trematode to confirm their identities and to uncover the first fossil record of flatworm parasitism in aquatic insects.

Material and methods

The amber was collected from well-established amber mines near Noije Bum Village (26°15'N, 96°33'E), Hukawng Valley, Kachin State, northern Myanmar. Subsequently, it was legally purchased from Tengchong, China, prior to 2017. The material is deposited in the Insect Collection of Jiangsu University of Science and Technology, China (CZT-TRI-MA2). The amber piece was trimmed with a small hand saw, ground with sand paper of different grit sizes, and polished with diamond grinding paste.

Observations of the material were performed with an SDPTOP SZM45 stereomicroscope, and the photographs were taken by a Canon EOS 6D digital camera, equipped with a Canon MP-E 65 mm macro lens. The raw images under incident light were combined using the focus-stacking software Zerene Stacker 1.04 (Zerene systems LLC, Richland, U.S.A.). All photographs were optimized using Adobe Photoshop 2021 (Adobe Inc., San Jose, CA, U.S.A.).

Results

Morphology of caddisfly larva

The body length is about 7 mm (Figs 1, 2). Head rugose, elongated, with length ca. two times longer than width (Fig. 3); dark brown, with yellowish spots located mostly on posterior part of head, ventrally mostly pale, with dark sclerites. Antennae short and hardly visible (Fig. 4A, B). Eyes small, surrounded with pale rings. Frontoclypeal apotome triangular, wider anteriorly. Mandibles darkly sclerotized, elongated, with one apical tooth. Labrum pale brown, dorsally with a transverse row of 14 setae. Labium wide basally, medially surrounded by a C-shaped sclerite, apically with several thin sclerites pointing to silk gland orifice. Ventral apotome unclear.

Pronotum pale in background, with brown lateral marks and long setae (Fig. 3A, C); anterolateral corners slightly projected. Mesonotum membranous, setal areas 3 (sa3) visible, each on prominent, separate anterolateral sclerite with about 6 long and 4 short setae. Metanotum membranous, setal areas 3 (sa3) each with 1 anterolateral sclerite, very weakly sclerotized, with about 4 short and 8 long setae (Figs 3, 4).

Legs mostly pale brown, with a dark median band on tibia of all legs (Figs 1, 2). Forelegs shortest (Fig. 5), tibia subequal in length to femur, inner margin with dense short setae, apex with a giant inner spine and a dorsal spine; tarsal claw with a stout basal seta. Midlegs (Fig. 6) and hind legs slender (Figs 6, 7), with one giant apical spine on inner margin of midlegs.

Abdomen membranous, pale yellow (Figs 9–11). Segment 1 with a pair of well-developed lateral humps (Fig. 9), the humps each rounded and covered with dense small spines. Abdominal gills present on ventrolateral areas of sterna 2–7 (Figs 9, 10), each gill with 1 or 2 slender filaments. Segments 3–8 setose along lateral line from anterior edge of segment 3 through anterior part of segment 8 (Fig. 9A, B). Posterior margin of tergum 9 elevated and with a rounded median process (Fig. 11), posterolaterally with two long setae. Anal prolegs well-developed (Fig. 11), each with a giant hook, an accessory hook located dorsally, and ca. 8 long setae.

Morphology of parasite

Body length ca. 5.7 mm, entirely membranous and glabrous (Fig. 12). Anterior half of body slender and near cylindrical, expanded posterolaterally; median part of body constricted, ventrally with an elevated rounded structure (ventral sucker) (Fig. 12C, D); posterior half of body near fusiform, with several ventral grooves.

Anterior half of body firmly attached to the caddisfly larval abdomen; posterior half of body detached from the caddisfly larval thorax; two long setae of the caddisfly larval thorax stretching out along the ventral grooves of the parasite.

Discussion

Taxonomy of caddisfly larva

The caddisfly larva's taxonomic classification aligns it with the suborder Integripalpia, due to the fully sclerotized pronotum and the presence of gills (Holzenthal *et al.* 2015). Further anatomical features, such as the shorter forelegs and longer mid- and hind legs, along with retractile lateral humps on abdominal segment one, closely resemble those of typical case-making families within Integripalpia (Holzenthal *et al.* 2015). Within Integripalpia, the presence of abdominal humps indicative of case making can exclude the larval affinity to the 'spicipalpian' cocoon-making families (Holzenthal *et al.* 2015). The absence of a prosternal horn further indicates the larva's placement within the infraorder Brevitentoria (Weaver 1984). Notably, the larva shares several key characteristics with the family Calamoceratidae, including inconspicuous antennae, a labrum with a median transverse row of 14 long setae, and a sclerotized pronotum with anterolateral extensions, as well as membranous meso- and metanotum (Wiggins 1996; Holzenthal *et al.* 2015). Despite these associations, further taxonomic assignment proves challenging due to the larva's immature status.

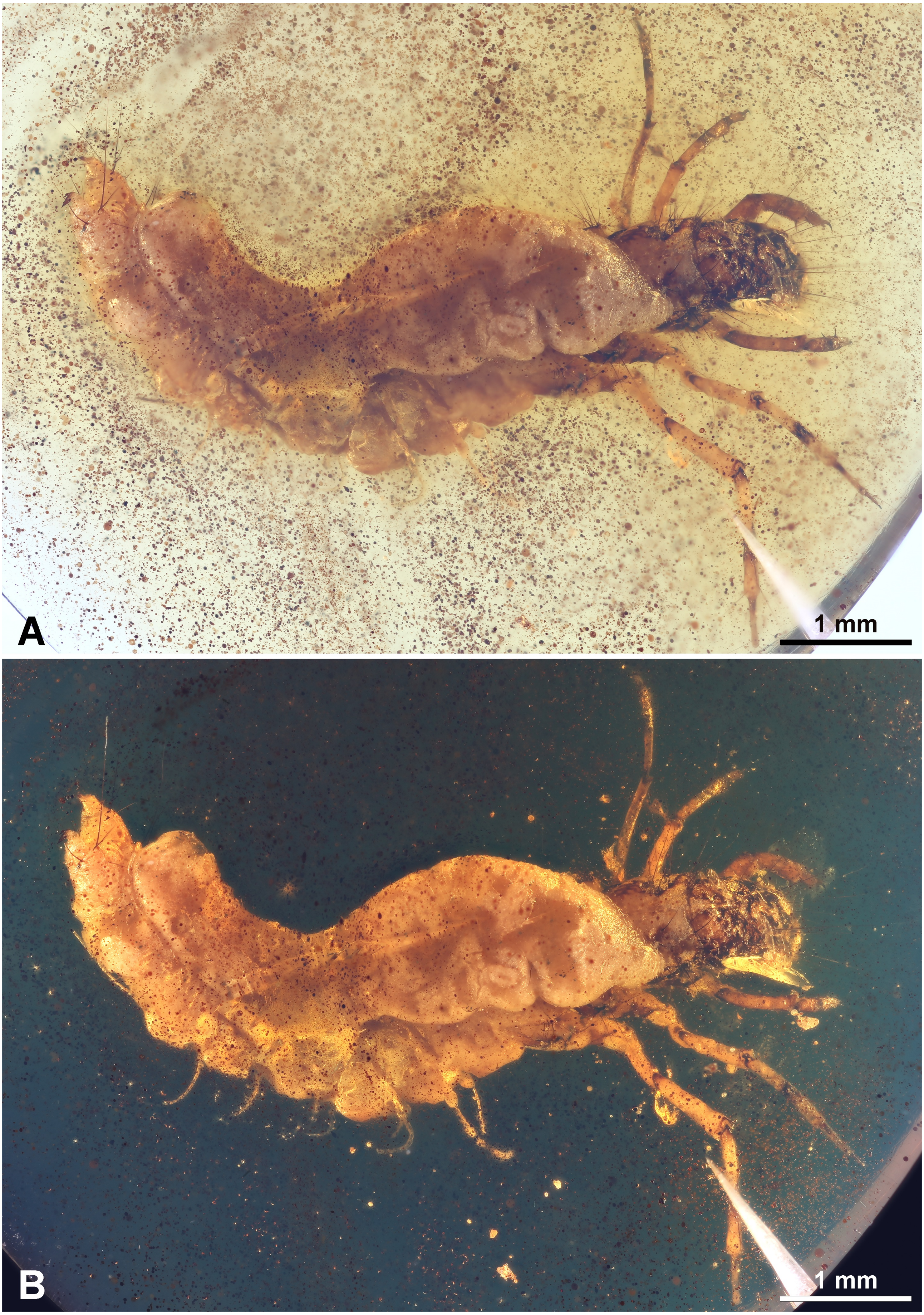

FIGURE 1. Dorsal habitus of caddisfly larva and trematode in amber: **A** white background **B** black background.

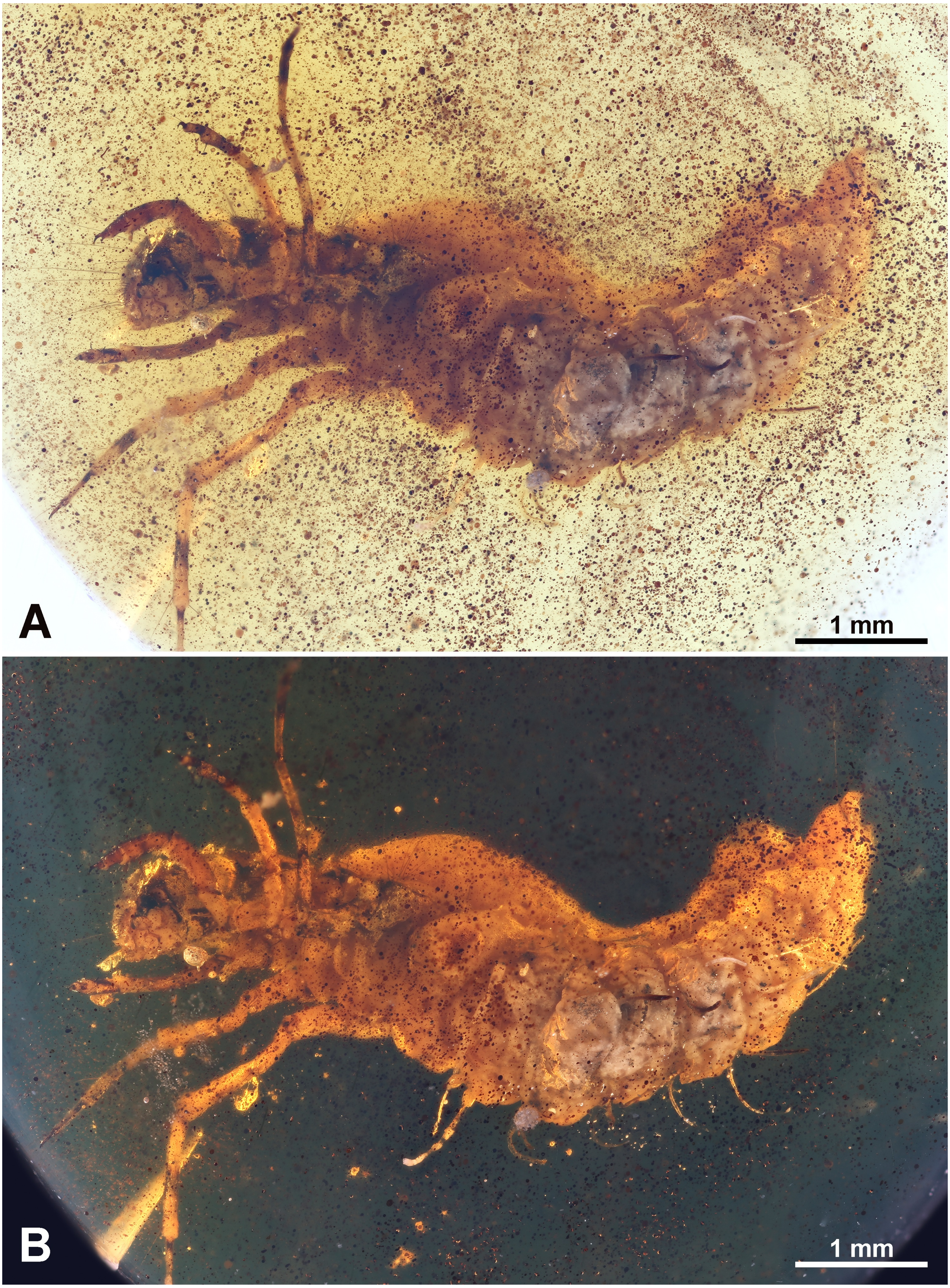

FIGURE 2. Ventral habitus of caddisfly larva and trematode in amber: **A** white background **B** black background.

FIGURE 3. Head and thorax of caddisfly larva in dorsal view: **A** white background **B** line drawing **C** black background.

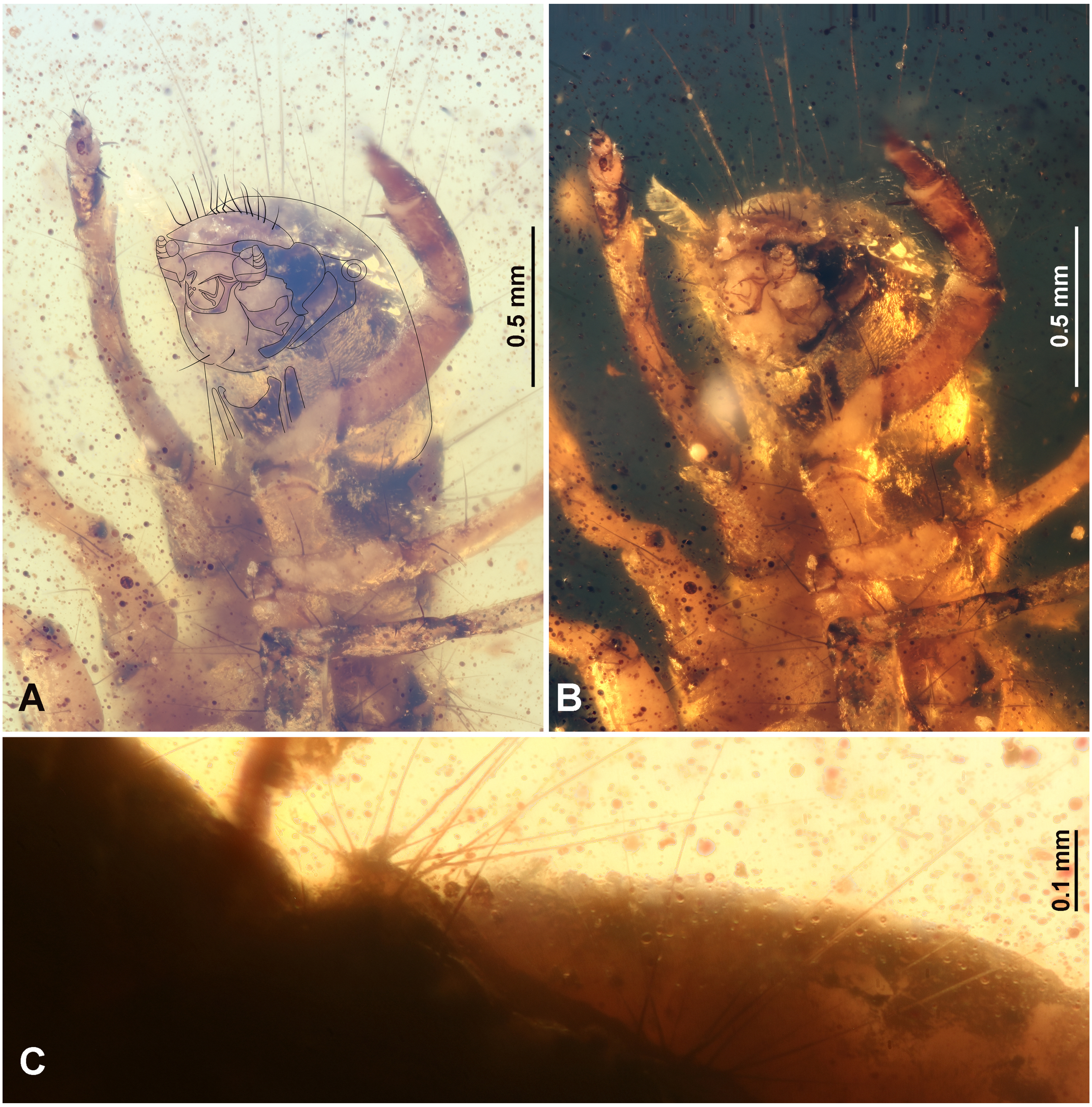

FIGURE 4. Head and thorax of caddisfly larva in ventral view: **A** white background **B** black background **C** detail of thoracic setae.

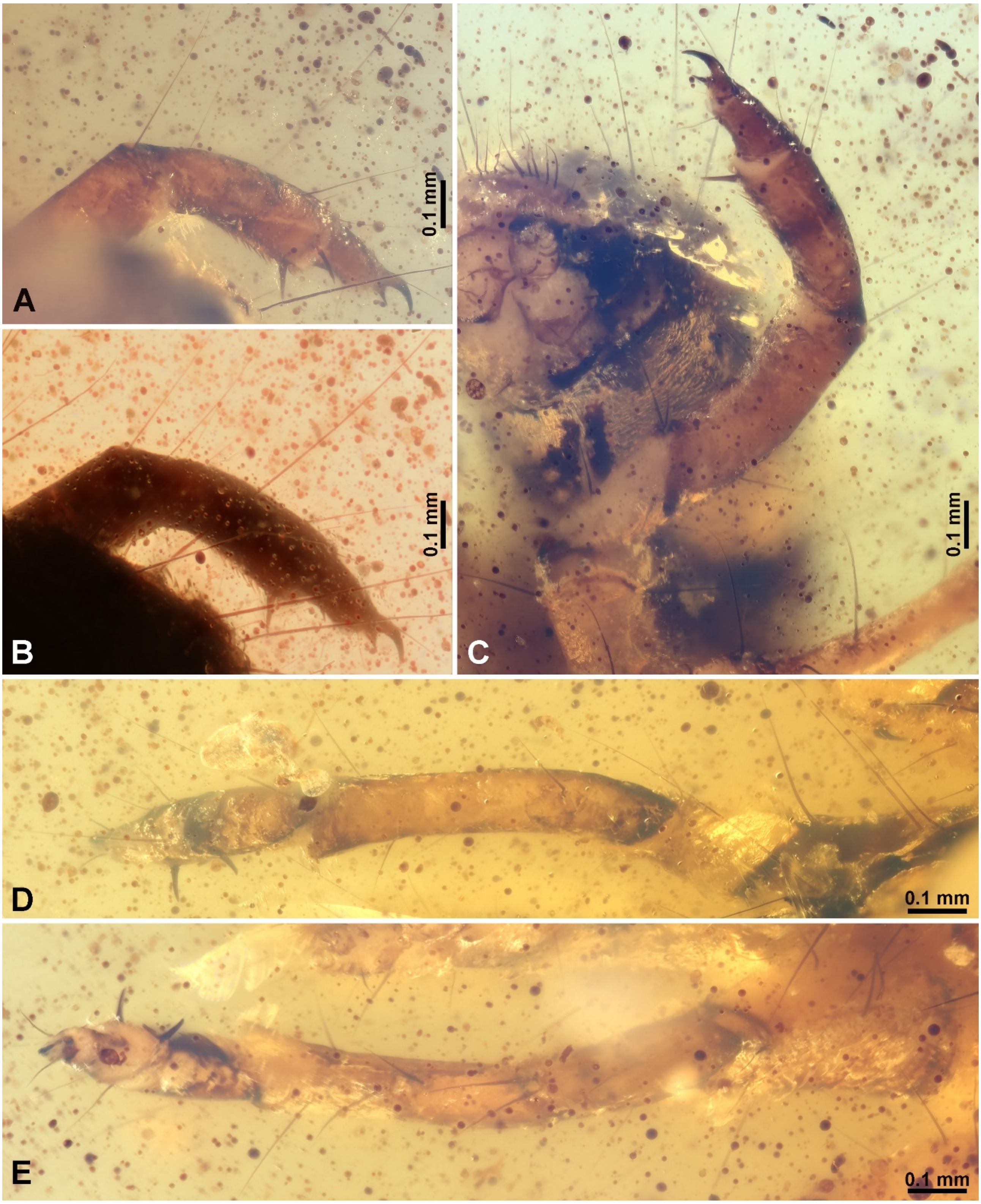

FIGURE 5. Forelegs of caddisfly larva: **A** left foreleg under reflected light, dorsal view **B** left foreleg under transmission light, dorsal view **C** left foreleg under reflected light, ventral view **D** right foreleg under reflected light, dorsal view **E** right foreleg under reflected light, ventral view.

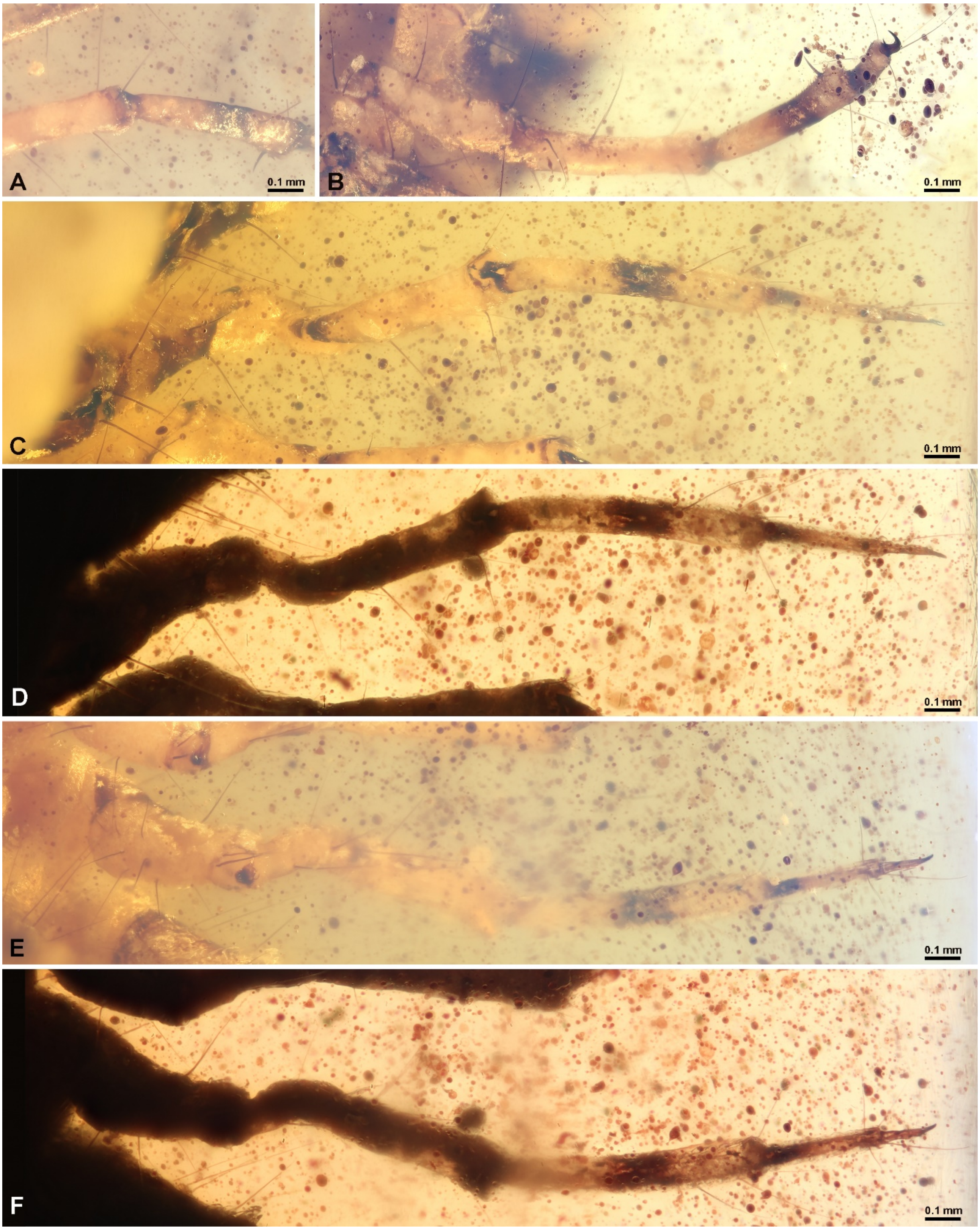

FIGURE 6. Midlegs of caddisfly larva: **A** left midleg under reflected light, dorsal view **B** left midleg under reflected light, ventral view **C** right midleg under reflected light, dorsal view **D** right midleg under transmission light, dorsal view **E** right midleg under reflected light, ventral view **F** right midleg under transmission light, ventral view.

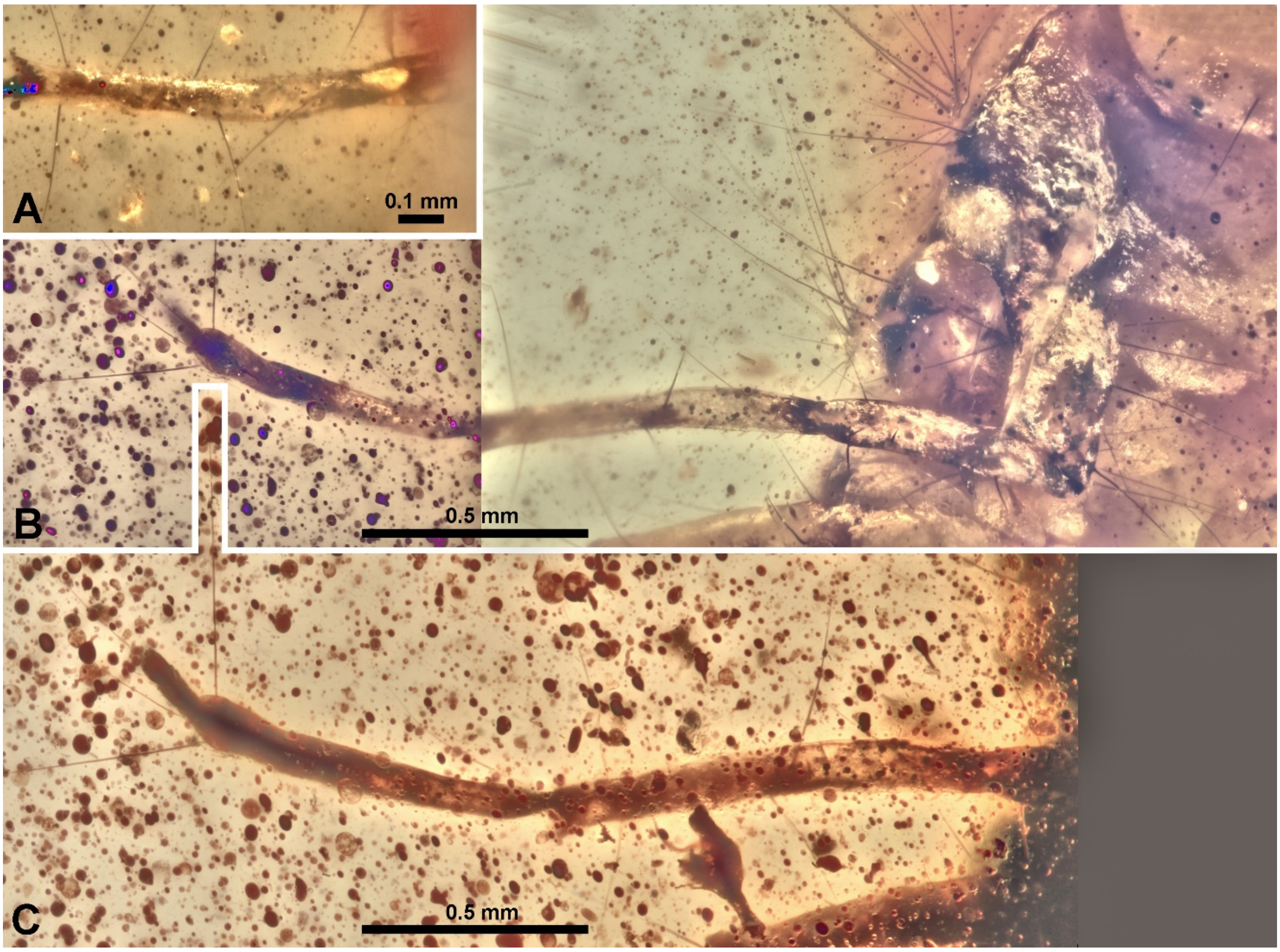

FIGURE 7. Left hind legs of caddisfly larva: **A** partial left hind leg under reflected light, dorsal view **B** under reflected light, ventral view **C** under transmission light, ventral view.

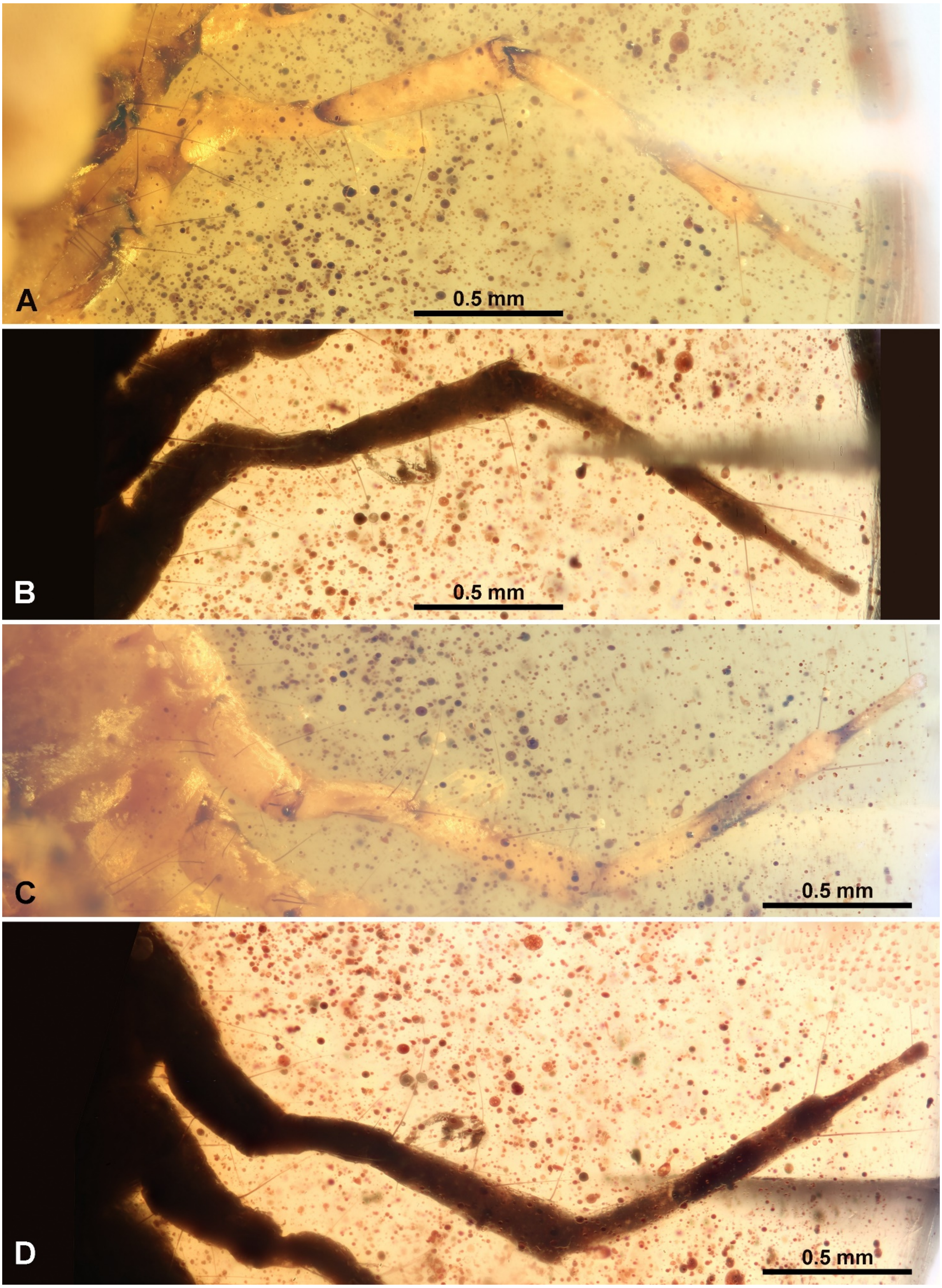

FIGURE 8. Right hind legs of caddisfly larva: **A** under reflected light, dorsal view **B** under transmission light, dorsal view **C** under reflected light, ventral view **D** under transmission light, ventral view.

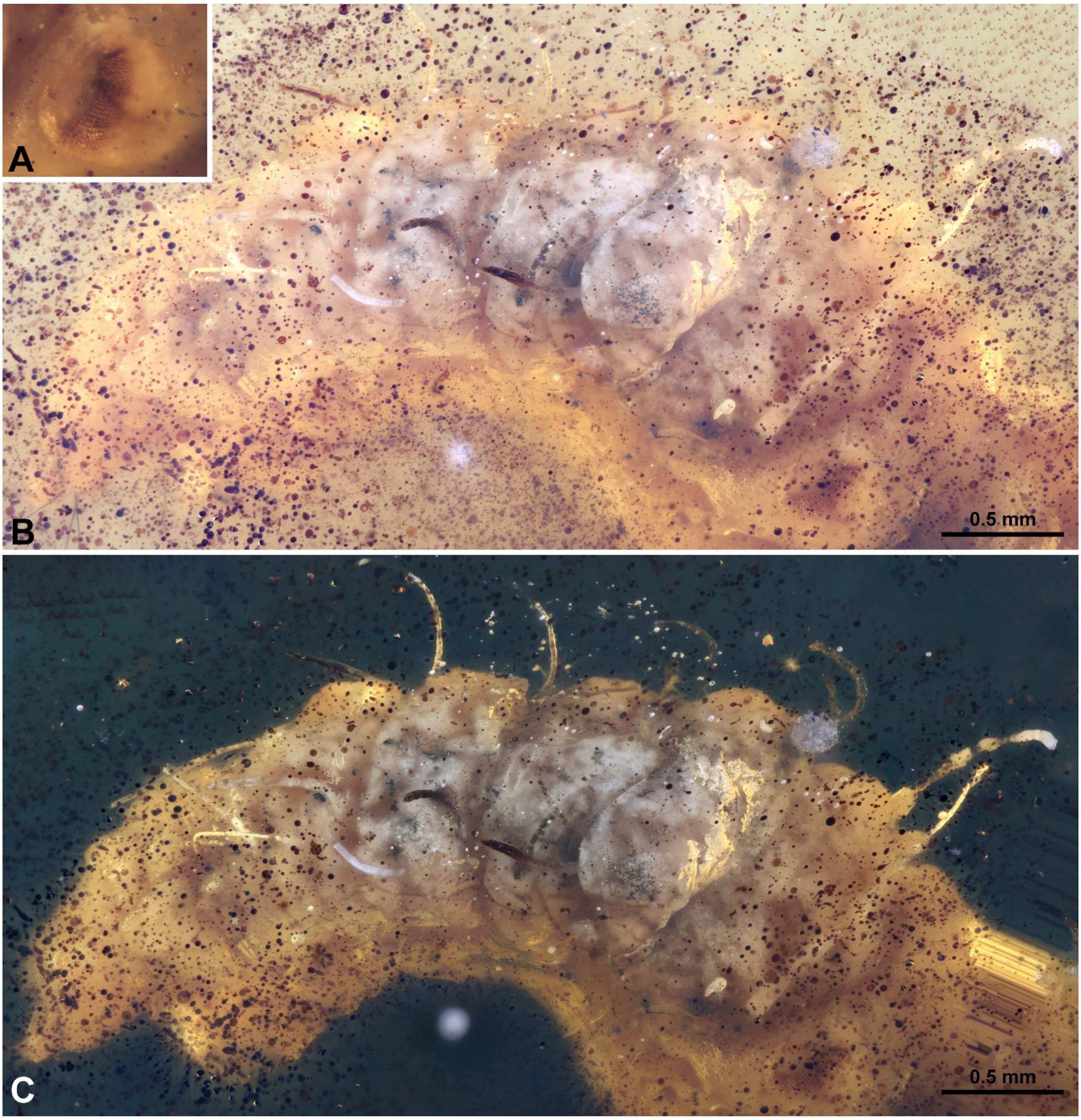

FIGURE 9. Abdomen of caddisfly larva in ventrolateral view: **A** detail of abdominal lateral hump **B** white background **C** black background.

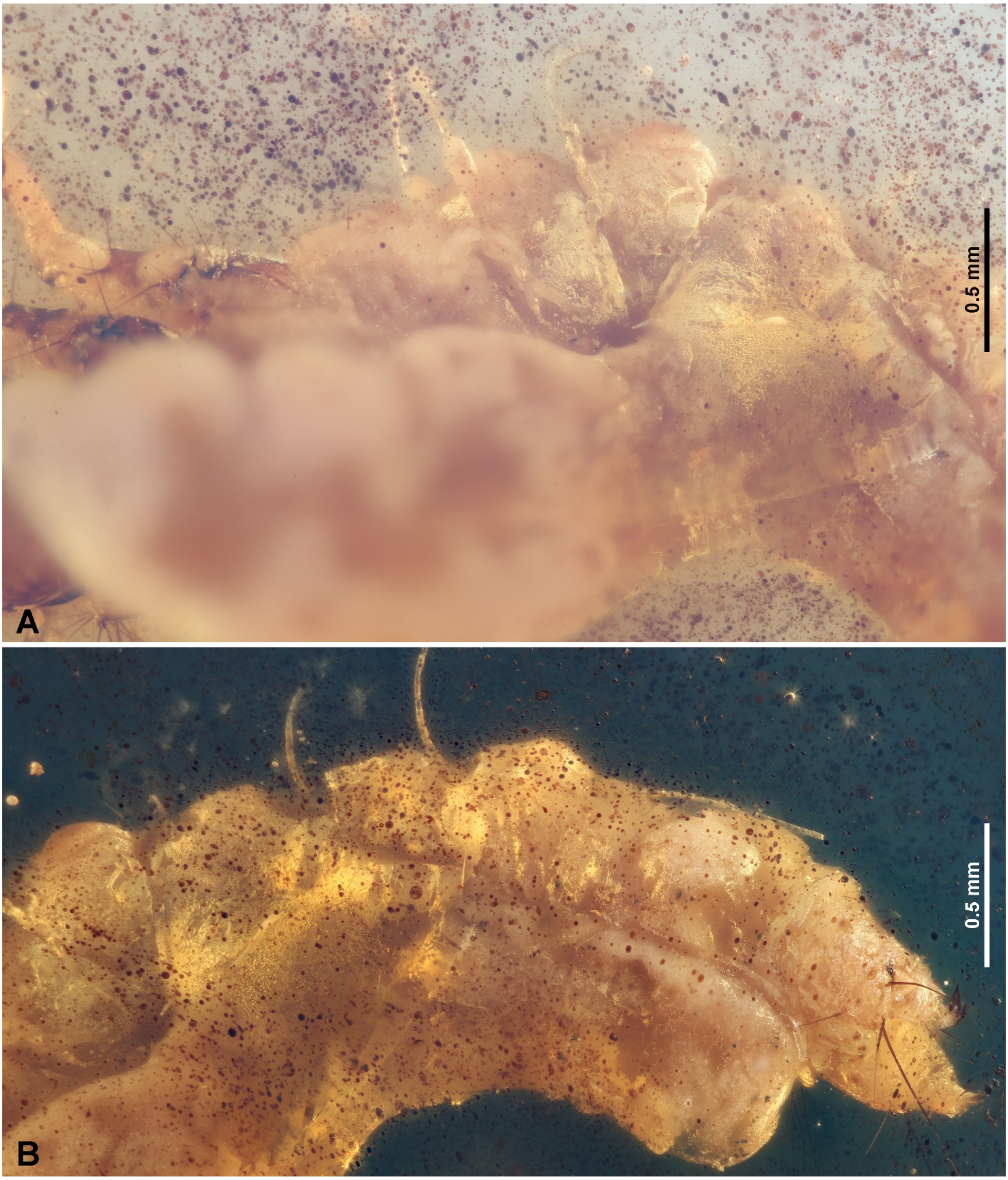

FIGURE 10. Abdomen of caddisfly larva in dorsolateral view: **A** white background **B** black background.

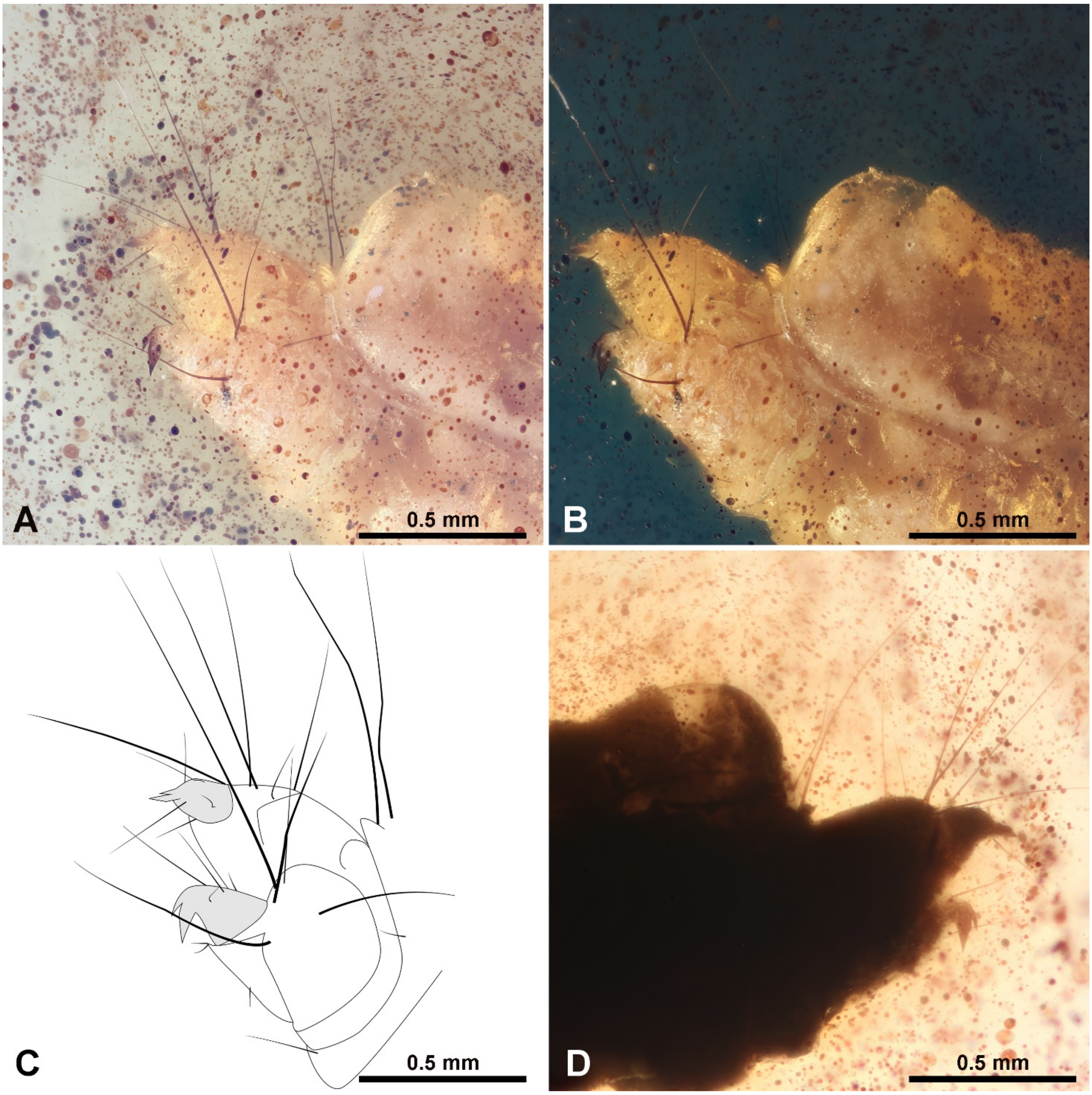

FIGURE 11. Abdominal tip of caddisfly larva: **A** under reflected light, white background, dorsolateral view **B** under reflected light, black background, dorsolateral view **C** line drawing, dorsolateral view **D** under transmission light, ventrolateral view.

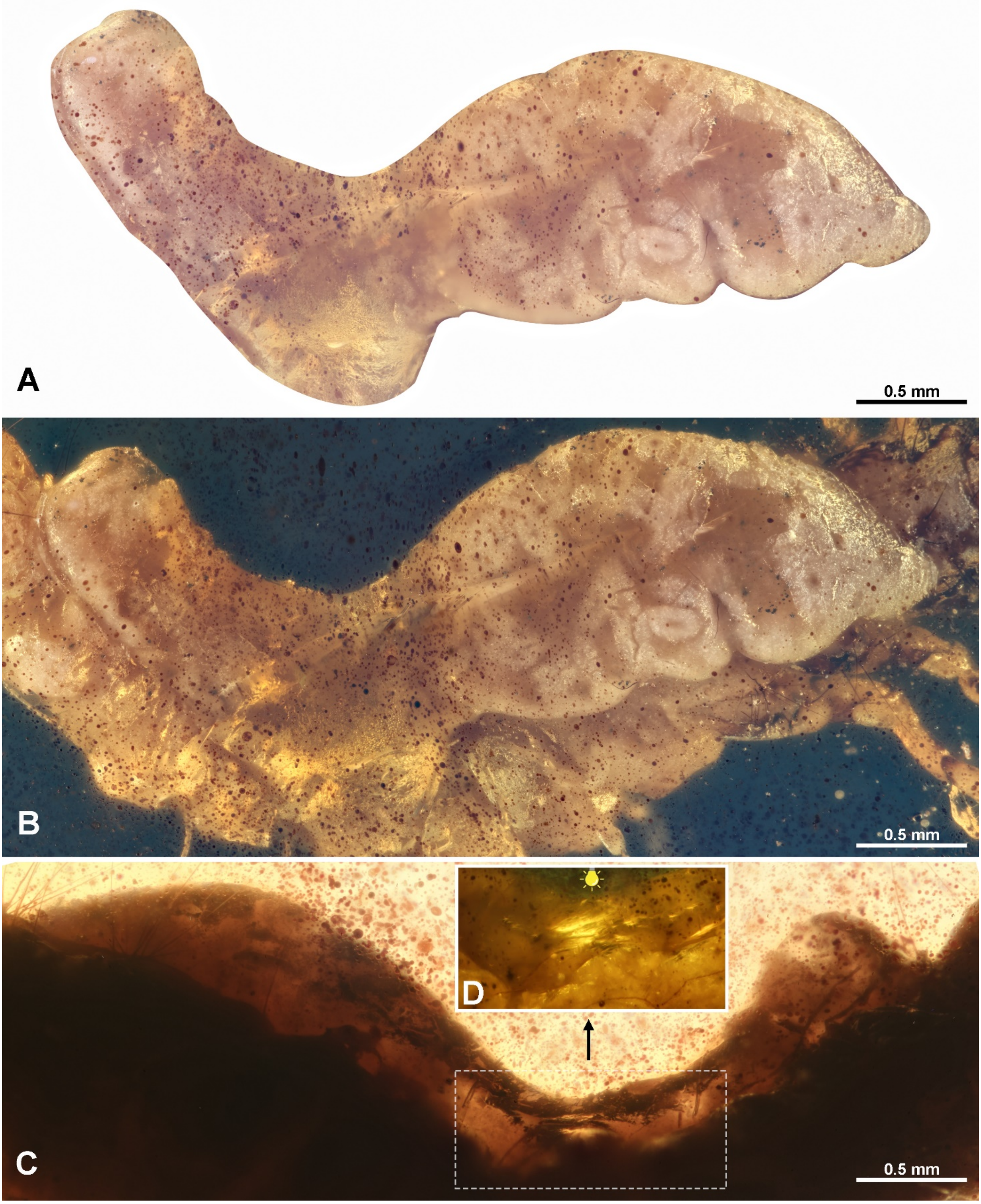

FIGURE 12. Habitus of the trematode: **A** under reflected light, white background, dorsolateral view **B** under reflected light, black background, dorsolateral view **C** under transmission light, ventrolateral view **D** lateral margin of the ventral sucker highlighted by lateral light source.

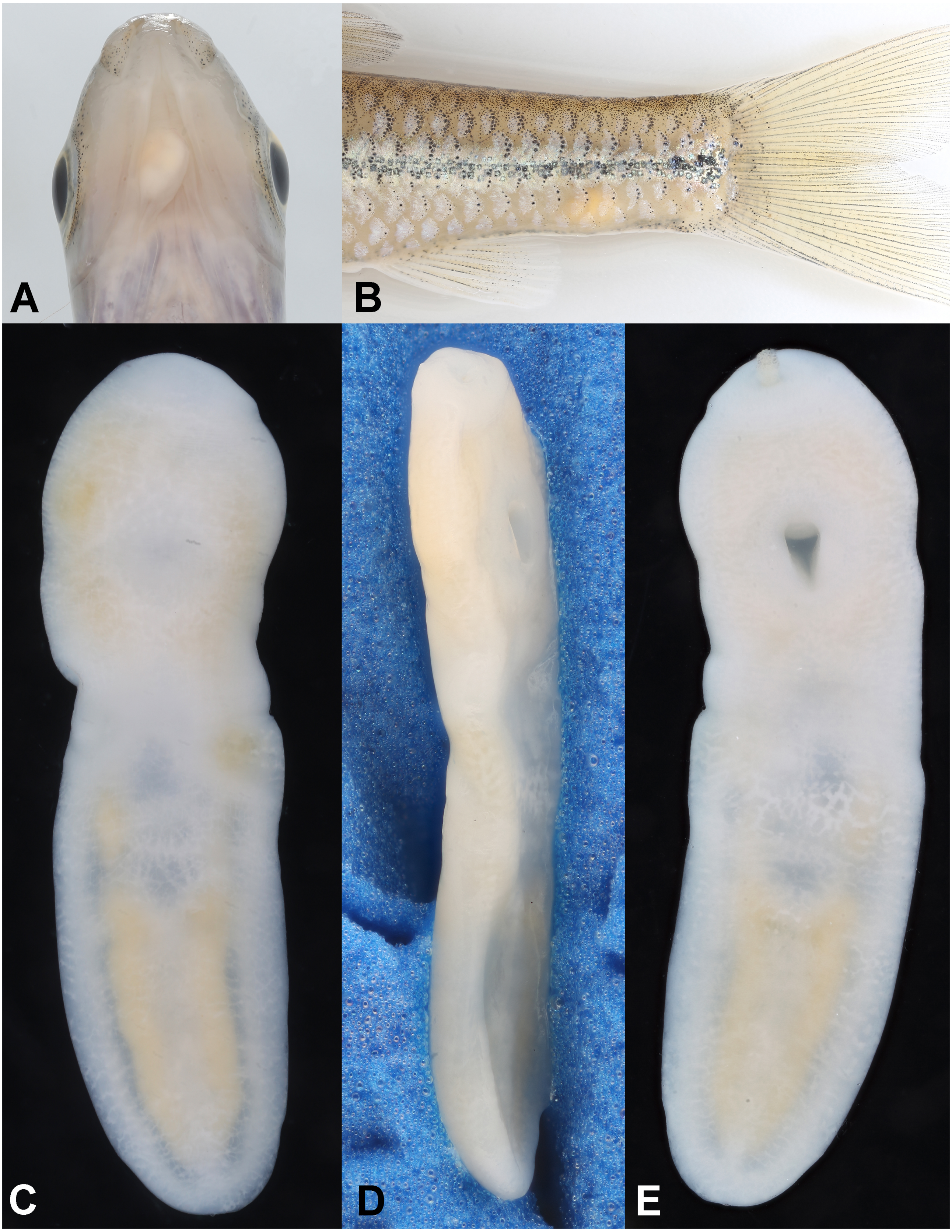

FIGURE 13. Habitus of *Clinostomum complanatum* (Rudolphi, 1814): **A** on the gills of a freshwater fish **B** under the skin of a freshwater fish **C** dorsal view **D** lateral view **E** ventral view.

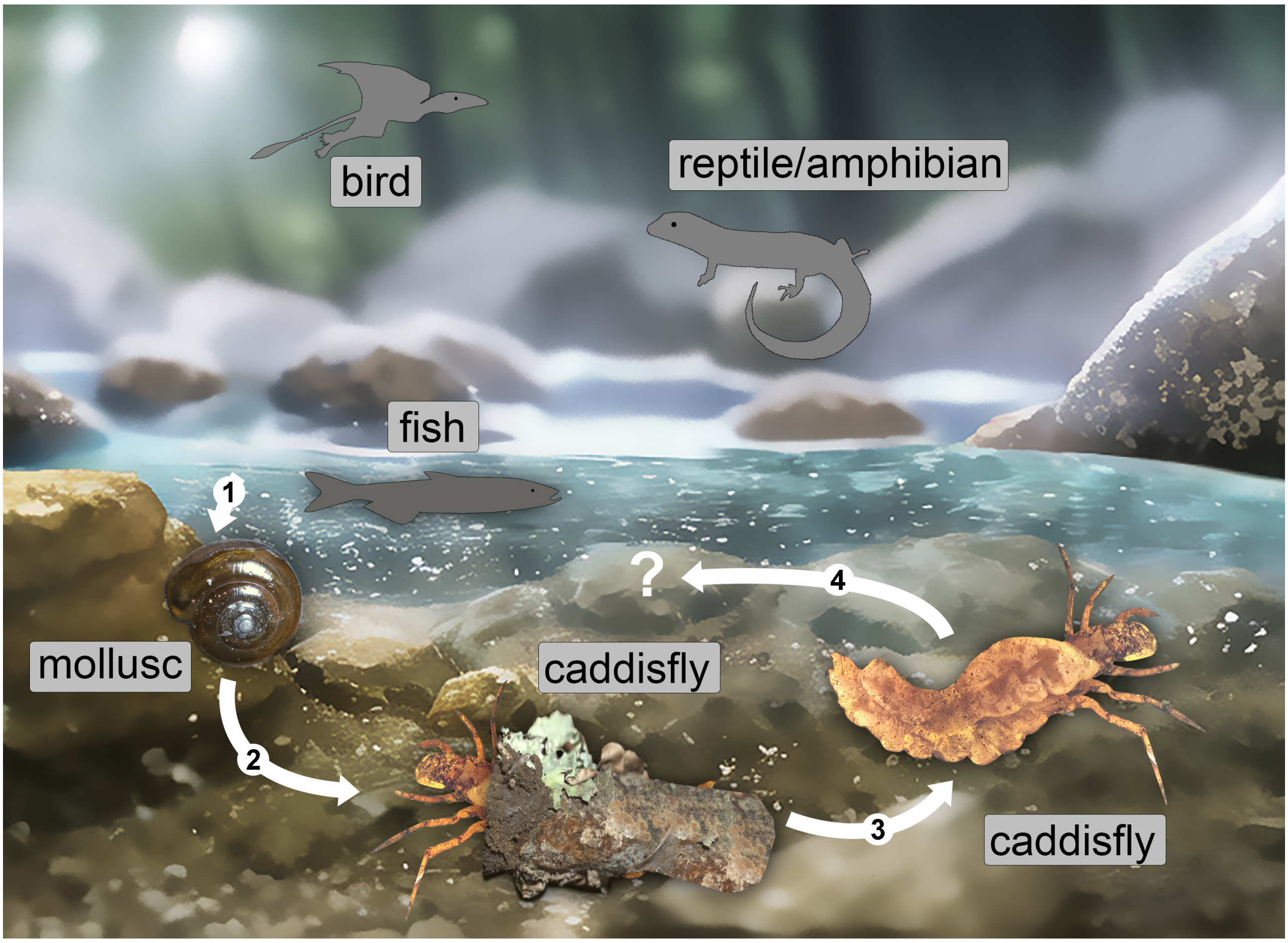

FIGURE 14. Reconstruction of the trematode life cycle. Numbers on arrows indicate steps of parasitism. Step 1: trematode eggs are released and miracidia penetrate a mollusc host. Step 2: miracidia develop into cercaria within the mollusc and then enter the case of the caddisfly larva. Step 3: the caddisfly larva exits its case due to discomfort caused by the attached cercaria. Step 4: trematode either reaches adulthood and produces eggs directly into the water, or it is ingested by larger animals along with the caddisfly larva as a metacercaria. Once inside the definitive host, the trematode reaches adulthood and releases eggs. Question mark indicates the uncertainty of the definitive host.

Taxonomy of parasite

The parasite exhibits morphological traits consistent with flatworms of the phylum Platyhelminthes, notably its bilateral symmetrical, nonsegmented body (Noreña *et al.* 2015). Features such as the presence of a developed ventral sucker, absence of opisthaptor, and unelongated body support its classification within the class Trematoda Rudolphi, 1808. The firmly attached anterior half of the parasite indicates the presence of another anterior attachment organ, very likely an oral sucker, a characteristic of Trematoda (Gibson *et al.* 2002). Moreover, the presence of a sucker rather than a broad holdfast assigns the parasite to the subclass Digenea Carus, 1863 (Gibson *et al.* 2002). However, detailed classification is hindered by limited visibility of ventral side and inner structures, with identification typically reliant on adult forms obtained from definitive hosts. The body form of the parasite is Distome, which contains an oral sucker and a ventral sucker. This digenean trematode is probably a metacercaria or adult due to its considerable body size and developed suckers. The pale, elliptical body and two suckers of the trematode is very similar to *Clinostomum complanatum* (Rudolphi, 1814), a digenean trematode of the family Clinostomidae (Fig. 13), known for its metacercariae frequently found under the skin, on the gills, and within muscle tissues of freshwater fishes (Aghlmandi *et al.* 2018). The body length of the trematode falls within the range of other reported digenean trematodes. For instance, species of *Clinostomum* Leidy, 1856 have body lengths ranging from

3–26 mm in similar stages (Gustinelli *et al.* 2010; Caffara *et al.* 2011; Rosser *et al.* 2017), and species of *Phyllodistomum* Braun, 1899 range from 1.7–13 mm (Cutmore & Cribb 2018).

The evolutionary implications

The intimate association between the caddisfly larva and the trematode is best interpreted as a form of ectoparasitism. This conclusion is supported by the anatomical and behavioral evidence preserved in the amber. The specialized suckers of the trematode are indicative of parasitic adaptations, designed for secure and sustained attachment to the host. Additionally, the case-building behavior of the caddisfly larva, which typically provides protection from external predators, would have allowed the gentle entrance of parasitic trematodes without disrupting the host's external defenses.

If the alternative predation hypothesis were accurate, one would expect to find the caddisfly larva within or near its protective case in the amber. However, the absence of the case in the fossil record refutes this hypothesis, further supporting the interpretation of the interaction as ectoparasitic rather than predatory or scavenging.

The discovery of a digenean trematode exhibiting ectoparasitism on a caddisfly larva in mid-Cretaceous Burmese amber provides insights into the evolutionary history of trematodes and their parasitic strategies. Such parasitism is contrary to the situation in extant caddisflies, where the cercariae released from molluscs penetrate the abdominal integument and develop within the caddisfly larvae (Caira 1981). The presence of ectoparasitism suggests that trematodes have evolved sophisticated mechanisms to exploit aquatic insects as intermediate hosts in their life cycles. Several factors may have contributed to the evolution of this unique parasitic strategy different from current ones. One possibility is that the caddisfly larva provided a convenient substrate for attachment and transmission of the trematode, offering access to resources necessary for the completion of its life cycle. Alternatively, environmental conditions or ecological pressures in the ancient stream ecosystem may have favored the evolution of ectoparasitism as an adaptive strategy for this trematode lineage.

Ectoparasitism in the mid-Cretaceous caddisfly-trematode association likely served several functions for the parasite. By attaching to the external surface of the case-making caddisfly larva, the trematode may have gained protection from predators or environmental stressors, such as water currents or fluctuations in temperature. Additionally, ectoparasitic attachment could have facilitated the dispersal and transmission of the trematode to other potential hosts within the aquatic ecosystem. Furthermore, the attachment may have provided the trematode with access to nutrients or metabolic resources derived from the caddisfly host.

Trematode parasites with their complex life cycles using several hosts could reflect the presence of other animals in an ecosystem and the diversity and abundance of animal communities (Faltýnková *et al.* 2020). The findings in this study imply the presence of symbiotic molluscs such as snails, fishes, near-water birds, reptiles, amphibians, and even mammals in the Cretaceous Burmese Forest (Ponomareva *et al.* 2022).

The possible scenario of parasitism involves a series of intricate steps (Fig. 14). First, trematode eggs are released from the adult; subsequently, miracidia emerge from each egg, penetrating a mollusc host. Within the mollusc, the miracidia develop into sporocysts, which further mature into rediae. Cercariae, the next larval stage, are then released from the rediae. Each cercaria exits the mollusc and is carried into the case of the caddisfly larva by the circulation of water generated by abdominal ventilation movements. Upon attachment to the caddisfly larval abdomen, the cercaria develops into a larger metacercaria or adult trematode. As a consequence of discomfort, the caddisfly larva exits its case, such case abandonment behavior due to environmental stressors has already been documented in another caddisfly larva from Burmese amber (Chen 2024). If the trematode reaches adulthood, it proceeds to produce eggs directly into the water. Alternatively, if the trematode remains in the metacercaria stage, it may be ingested by larger animals alongside the caddisfly larva, wherein it develops into an adult within the definitive host and subsequently releases eggs, which are expelled with the host's feces.

The unique parasitic lifestyle suggests that trematodes possess a degree of ecological flexibility and plasticity that allows them to adapt to diverse hosts and exploit novel ecological niches. Furthermore, the presence of ectoparasitism in ancient ecosystems highlights the importance of considering a broader range of parasitic associations in paleoecological reconstructions and evolutionary analyses. This discovery underscores the need for further exploration of parasitic diversity and ecological interactions across different geological time scales to fully comprehend the evolutionary history of parasitism in aquatic ecosystems.

Conclusions

The identification of ectoparasitism in the mid-Cretaceous caddisfly-trematode association provides valuable insights into the diversity of parasitic strategies employed by trematodes and their evolutionary implications. By investigating the evolutionary implications of this unique parasitic association, we enhance our understanding of the ecological dynamics and adaptive strategies that have shaped ancient aquatic ecosystems. This discovery highlights the complexity of host-parasite interactions and underscores the importance of interdisciplinary research in elucidating the evolutionary history of parasitism.

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