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Caddisfly pupae (Trichoptera) from the Early Cretaceous of eastern China

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Abstract

Caddisfly adults and cases were relatively common fossils from the Mesozoic but the pupa is extremely rare. Here we described two well-preserved and uncased caddisfly pupae from the locality near the Shanghujia Village, Shouchang Township, Jiande City, Zhejiang Province, East China. New material including two pupal fossils with rather good detailed structures preserved such as mandible, abdominal hook plates, and anal processes. The new material provides new evidence for understanding development stage of Mesozoic trichopterans.

Key words: Caddisfly, pupa, Shouchang Formation, Barremian, "Jehol biota"

Introduction

Trichoptera, commonly known as caddisfly, is an important group of aquatic insects in nature, characterized by the hairs covering their wings as adults. As holometabolous insects, they undergo a distinct transitional developmental stage before the adult—the pupa. The pupae of trichopterans are of the exarate type, encased within a caddisfly case. They are characterized by wings closely appressed to the body and legs folded against the ventrolateral aspects.

The study of caddisfly fossils began in the early 19th century and numerous records have been documented from various geological periods worldwide. Among these, the Mesozoic is recognized as an important period in their evolutionary history, witnessing the emergence of significant groups such as Vitimotauliidae and Phryganeidae (Sukatsheva 2016; Sukatsheva & Aristov 2020). Caddisflies are mostly adults preserved in amber, while the immature stages inhabiting aquatic environments are less likely to be captured (Wichard 2021; Shi *et al*. 2024; Ross 2024a, b, 2025). In fossil compression, they are more likely to be preserved as adults and cases (Mouro *et al*. 2016; Robinson *et al*. 2018; Sukatsheva & Sinitshenkova 2023; Chao *et al*. 2024, 2025). Most previous research has focused on larval cases and adults, while pupal fossils received extremely little attention due to their scarcity (Gao *et al*. 2012). If pupae appear in the fossil record, they are usually preserved within their pupal cases (Frese *et al*. 2024). Research on uncased pupae is particularly scarce. To date, only two uncased pupal specimens have been found in the world: one from Australia and one from China (Davis *et al*. 2010; Frese *et al*. 2024).

Here, we report two newly discovered pupal specimens of Trichoptera from the Shouchang Formation in Zhejiang Province, East China, expanding the fossil sites of caddisfly pupae and providing significant new material for advancing understanding of their developmental biology.

Material and methods

Two specimens have been described in this study, both with parts and counterparts (NIGP209776 and NIGP209777). They were collected from the green-grayish shale of the middle-upper sections of Lower Cretaceous Shouchang

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Formation near Dongshan village, Shouchang Town, Jiande City, Zhejiang Province (see Huang *et al.* (2022) for locality map). Isotopic dating suggests an zircon U-Pb age (LA-ICM-MS) for the Shouchang Formation between 125 and 121 Ma (Li *et al*. 2011), corresponding to the middle Barremian age (according to the Internation Chronostratigraphic Chart, December, 2024). The age of the specimens is slightly younger than the *Confuciusornis*-rich fossil bed in Yixian Formation (125 Ma; Swisher *et al*. 2002) and closely related to Jehol biota. Previous investigations of the Shouchang Formation have also yielded rich fossils including insects, conchostracans, ostracods, shrimps, fishes, and plants (Lin 1994; Chen & Shen 1977; Wu & Yang 1980; Garassino *et al*. 2002; Zhang & Zhou 1974; Zhang 1978).

Specimens were prepared by using a sharp knife. Some photographs were taken under 70% ethanol to enhance contrast. Other photographs were taken using a Zeiss Discovery V16 stereomicroscope. Image stacks were processed using Helicon Focus 7.0.2 software. Line drawings were prepared in Adobe Illustrator 2025. The type specimens are deposited at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science (NIGPAS), Nanjing. Morphological terminology followed that of Holzenthal *et al*. (2007).

Systematic palaeontology

Order Trichoptera Kirby, 1813
Suborder Integripalpia Martynov, 1924
Family uncertain
(Figs 1–4)

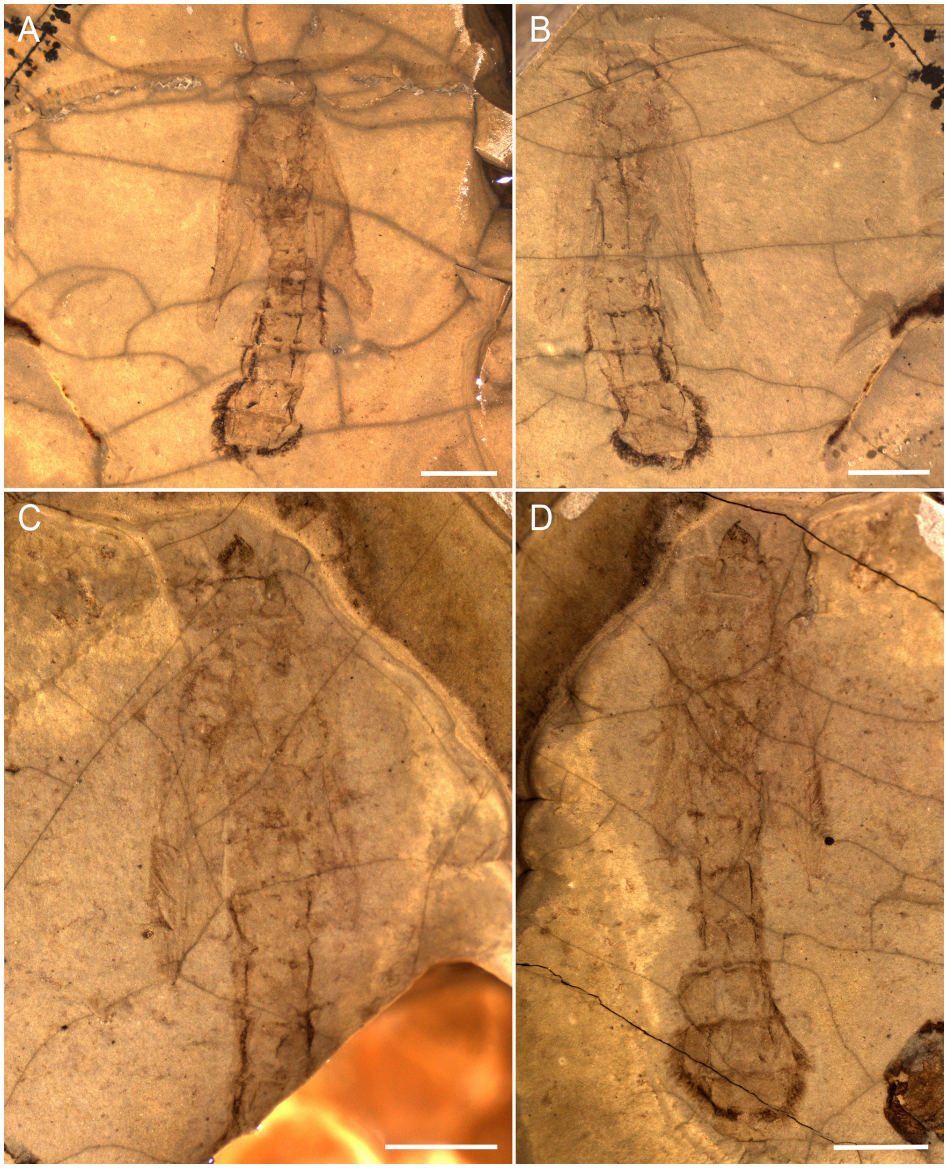

Figure 1. Photographs of two pupae. **A,** Part of NIGP209776. **B,** Counterpart of NIGP209776. **C,** Part of NIGP209777. **D,** Counterpart of NIGP209777. Scar bars = 2 mm.

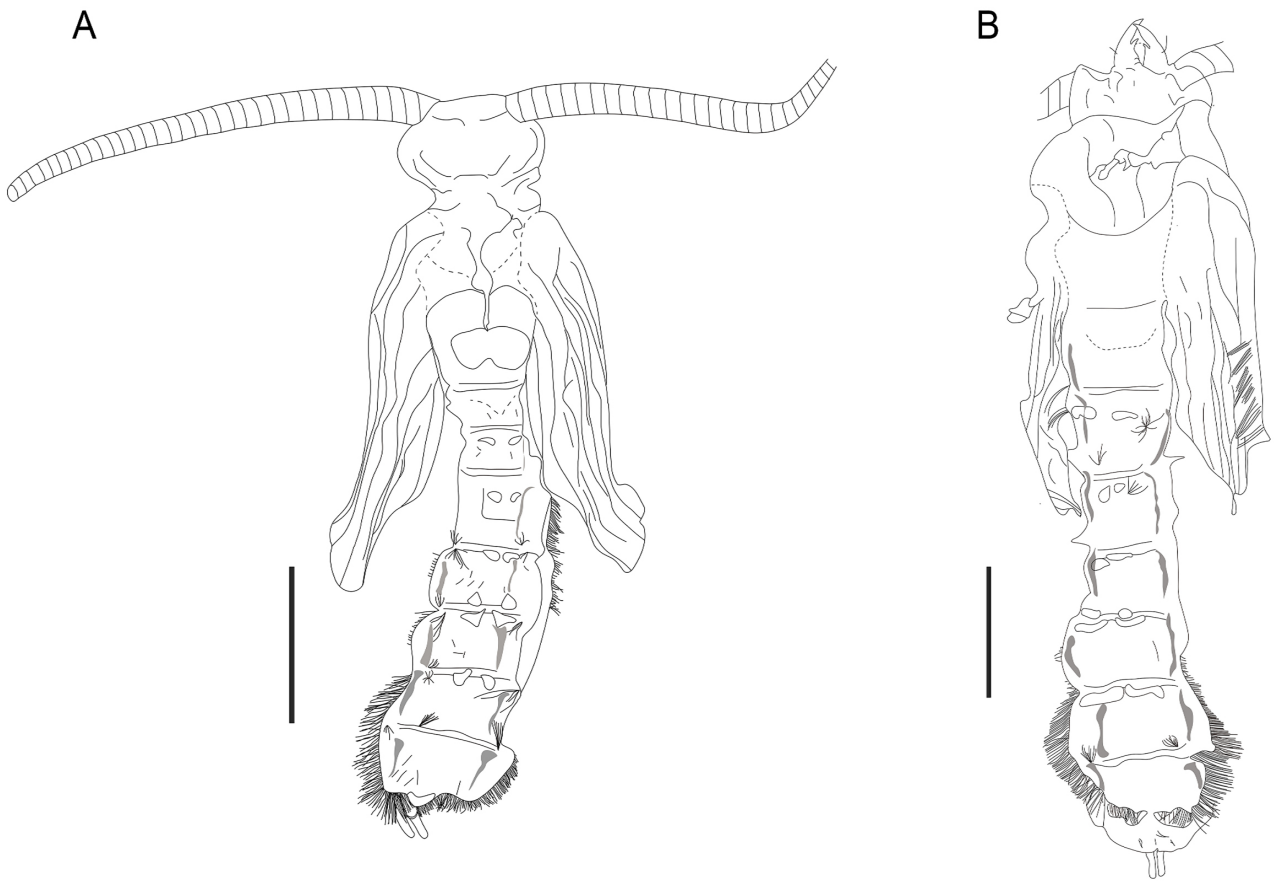

Figure 2. Line illustrations of two pupae. **A,** Part of NIGP209776. **B,** Counterpart of NIGP209777. Scar bars = 2 mm.

Material. Two nearly complete pupae (NIGP209776 and NIGP209777), at least one is an exuvium, both with parts and counterparts.

Locality and horizon. Dongshan village, Shouchang Township, Jiande City, Zhejiang Province; Shouchang Formation; middle Barremian, Early Cretaceous.

Diagnose. Antennae shorter than body length; mandibles each with a subapical tooth; abdominal segments III–VII bearing paired hook plates, with segment V possessing two pairs (anterior hook plates and posterior hook plates).

Remarks. The specimen can be excluded from all major families of Annulipalpia based on definitive morphological mismatches: Ecnomidae, Psychomyiidae, and Xiphocentronidae possess hook plates on segment II; Hydropsychidae have two pairs of hook plates on segments III and IV; Stenopsychidae are characterized by antennae longer than the body; and Polycentropodidae lack a subapical tooth on the mandibles. None of these character states occur in the present specimens. Their morphology instead shows closer affinity to Integripalpia, as supported by the presence of paired hook plates on abdominal segments III–VII and two pairs on segment V.

Description. NIGP209776 (Fig. 1A, 1B): Total length 11.0 mm. Posterior abdomen dilated, maximum width 2.4 mm. Head oval. Antennae filiform, at least 35 visible segments, total length 4.5 mm (preserved). Mandibles not preserved. Wings extending to median region of abdomen. Fissures from adult emergence on thoracic surface. Abdomen with scattered setae. Distinct dense and elongated lateral fringes surrounding segments VII and VIII. Abdominal segments III–VII each with paired hook plates; segment V with additional pair of post-segmental hook plates (Fig. 4A). Hook plates of the segments III, IV, and anterior pair of segment V (Va) composed of small hooks arranged in a circle (Fig. 3E–G). Paired anal processes at abdomen end (Fig. 3C).

NIGP209777 (Fig. 1C, 1D): Total length 13.3 mm. Posterior abdomen dilated, maximum width 2.9 mm. Head nearly square. Antennae incomplete, only basal portion remaining. Mandibles large, curved, crossing apically; with a prominent subapical tooth; outer edge base with single bristle (Fig. 3A, B). Wings extending to median region of abdomen. Thoracic surface without fissures. Lateral fringes, hook plates and anal processes as in NIGP209776.

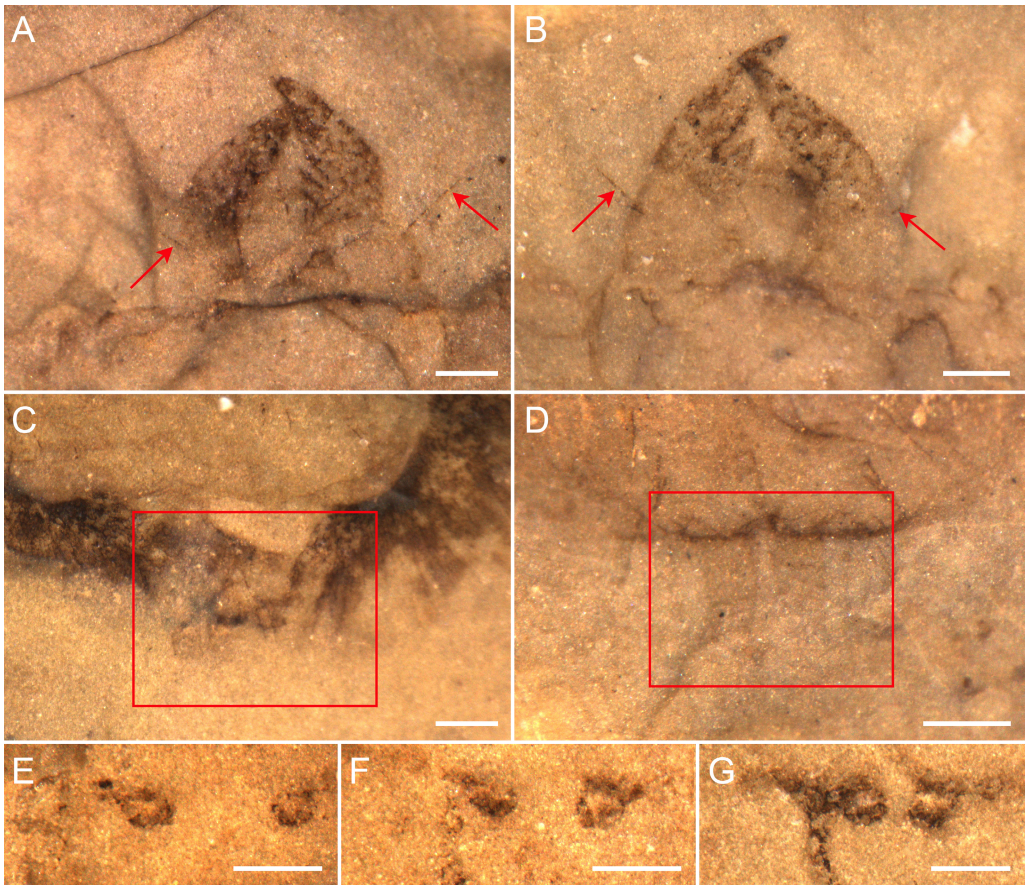

Figure 3. A, Mandible of NIGP209777 counterpart. **B,** Mandible of NIGP209777 part. **C,** Paired anal processes of NIGP209776 counterpart. **D,** Paired anal processes of NIGP209777 counterpart. **E–G,** hook plates of NIGP209776 (III, IV, Va). Scar bars = 0.2 mm.

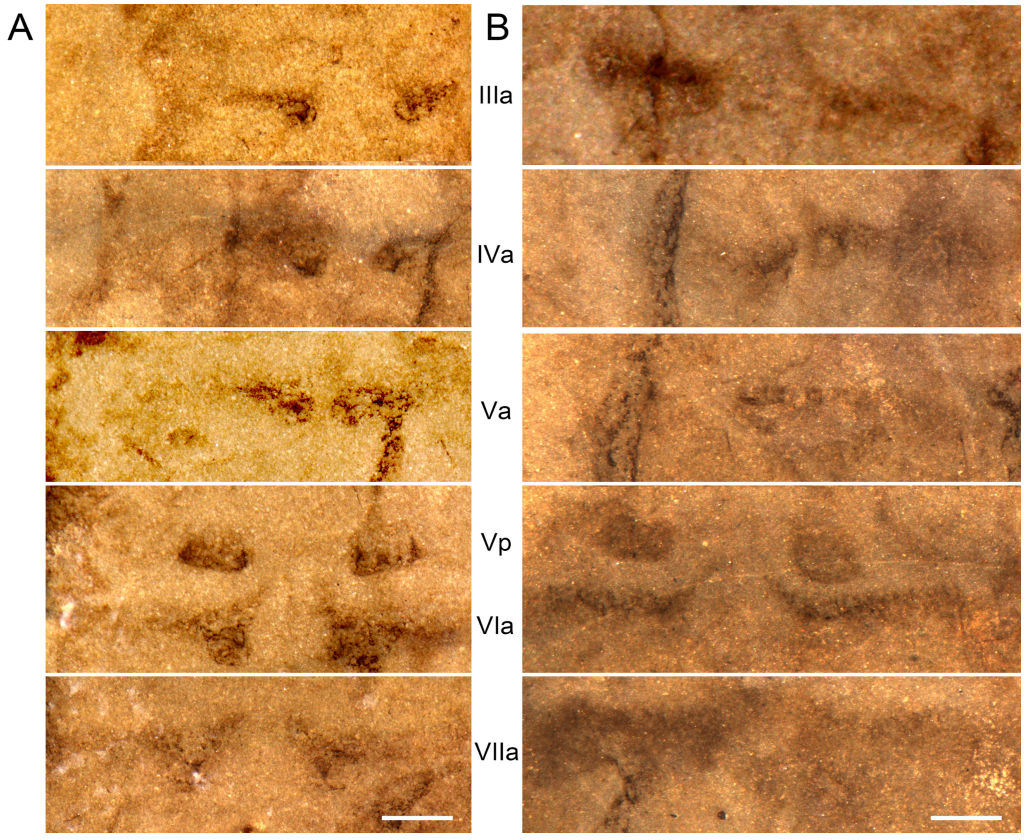

Figure 4. Photographs of hook plates. IIIa–VIIa = anterior hook plates of abdominal segment III–VII; Vp = posterior hook plates of segment V. **A,** NIGP209776 counterpart. **B,** NIGP209777 counterpart. Scar bars = 0.2 mm.

Discussion

The pupal stage, from when the pupae leave their cases until they emerge as adults, is very short, making buried pupae exceptionally rare in the fossil record. The specimens described here represent pupae preserved after leaving their cases or as an exuvium. The two pupal fossils described here are assigned to the same species based on the similar arrangement and characters of hook plates, distribution of lateral fringes. The current taxonomic work for Trichoptera pupae is relatively underdeveloped, with a scarcity of reliable diagnostic morphological characters (Wiggins & Currie 2019), which poses significant challenges for the accurate identification of pupal fossils.

Traditional taxonomy divides Trichoptera into Annulipalpia and Integripalpia (Martynov, 1924). Although Wiggins & Wichard (1989) proposed the monophyly of Spicipalpia (containing Rhyacophilidae, Hydrobiosidae, Hydroptilidae, and Glossosomatidae) based on pupation behavior, subsequent phylogenetic studies have not supported this view (Ivanov 1997). Recent phylogenetic research indicates that these families should be placed within Integripalpia. Based on transcriptome or targeted enrichment sequence data, Frandsen *et al*. (2024) found that Hydroptilidae and Ptilocolepidae form the sister group to the rest of Integripalpia, while a clade comprising Glossosomatidae, Hydrobiosidae, and Rhyacophilidae is sister to Phryganides. Based on genome data, Ge *et al*. (2024) demonstrated that Hydroptilidae represents a basal lineage within Integripalpia, and Glossosomatidae, Hydrobiosidae, and Rhyacophilidae constitute a monophyletic group serving as the sister lineage to Phryganides within Integripalpia.

Compared to the uncased pupal fossils from the Yixian Formation in China and McGraths Flat in Australia, the Shouchang specimens exhibit a distinct enlargement at the abdominal terminus (Davis *et al*. 2010; Frese *et al*. 2024). A detailed morphological comparison excludes placement within several families of Integripalpia: the hook plate arrangement (presence of paired hook plates on abdominal segments III–VII, with two pairs on segment V) differs from Molannidae and Atriplectididae; antennae length (shorter than body length) differs from Odontoceridae, Calamoceratidae and Leptoceridae; and the absence of abdominal setae or lateral fringes distinguishes it from Apataniidae, Beraeidae and Helicopsychidae. While the circular hook arrangement shows some similarity to Brachycentridae, Limnephilidae, and Phryganeidae within Integripalpia, several key morphological differences distinguish our specimens. Brachycentridae exhibits a sharply tapered abdomen, Limnephilidae has mandibles without subapical teeth, and Phryganeidae has two bristles on the outer edge of mandibles (Lepneva 1970; Ruiter & Robert 2019; Sukatsheva 2016). The expanded abdominal terminus of the Shouchang specimens aligns with the characteristic of Goeridae, but this family has no fossil record from the Mesozoic (Sukatsheva 2016).

Based on the extant pupae, we have been unable to identify any other pupal group that completely matches our specimens. Therefore, the taxonomic affiliation of these two pupal fossils remains undetermined.

Conclusion

The discovery of two new caddisfly pupae specimens enriches our understanding of Mesozoic caddisfly evolution. Compared to the fossil found in the Jehol biota, these new specimens exhibit distinct morphological characteristics, suggesting they belong to a different trichopteran group but cannot be assigned to extant family on the basis of current knowledge. While fossils from the Shouchang Formation are normally considered part of the general Jehol biota in southeastern coastal China, the study of these new caddisfly pupae fossils provide one case differences between the "Jehol biota" of southern China and the traditional Jehol biota of the Yanliao region.

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