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Lepidopteran caterpillars in the Cretaceous: were they a good food source for early birds?

Joshua Gauweiler, Carolin Haug, Patrick Müller & Joachim T. Haug

Abstract

Caterpillars are an omnipresent component in modern terrestrial faunas. Not surprisingly, they represent an important food source for larger animals. The oldest fossils of caterpillars are known from the Cretaceous. Yet, so far, only nine possible Cretaceous specimens have been reported. Here we expand the known record by four new specimens of caterpillars preserved in 99 million-year-old Kachin amber from Myanmar. The specimens cannot easily be interpreted in a taxonomic or phylogenetic frame. A simple morphometric comparison reveals that the new specimens differ in their relative body dimensions from those of the previously known specimens, expanding the morphological diversity of Cretaceous caterpillars. All caterpillars from the Cretaceous of which sizes are known are rather small, the largest definite one being only about 5 mm. Comparison to younger ambers reveals no clear directed preservation bias towards preserving only small caterpillars. In addition, the sizes of known adult lepidopterans from the Cretaceous are compatible with rather small caterpillars, although possibly slightly larger than the known ones. While small, the observed size range appears still to be within the size range of food items known to be consumed by modern birds. It therefore seems likely that also in the Cretaceous caterpillars were adequate food items for early birds.

Keywords: Burmese amber; Lepidoptera; larva; diversity; predator-prey interaction.

1. Introduction

The group Insecta with its myriads of representatives has been widely recognised as an important component especially of terrestrial ecosystems. Among the many lineages of Insecta, four have often been emphasized as being especially species-rich: Hymenoptera (wasps), Coleoptera (beetles), Diptera (flies), and Lepidoptera (moths). A major factor of the success of these lineages has been attributed to the distinct ecological and, coupled to this, morphological differentiation between early post-embryonic stages (larvae, see Haug 2020 for challenges of the term) and their corresponding adults.

In lepidopterans, this differentiation may be easily recognised, not least due to the famous children's book "The very hungry caterpillar" (Carle 1969). The larvae, caterpillars, are highly specialised feeding machines (as many other larvae, see discussion in Badano et al. 2021) and with this, some of them represent severe pests, destroying enormous amounts of plants. The adults are beautiful entities praised for their importance as pollinators.

All four lineages, including Lepidoptera, strongly diversified back in the Mesozoic. Yet, while caterpillars are an almost ubiquitous faunal element today, the fossil record of caterpillars in the Mesozoic is still very scarce. Only ambers have so far provided Mesozoic caterpillars, and so far only nine possible specimens: MacKay (1970) reported the first specimen, an isolated head from Canadian amber. Grimaldi & Engel (2005) reported a small leaf-mining caterpillar from Lebanese amber. Xia et al. (2015) provided images of two additional specimens, both from Myanmar amber. Haug & Haug (2021) reported a new caterpillar, also from Myanmar amber. Unlike the previously known Cretaceous caterpillars, the larva of Haug & Haug (2021) was armed with spines, most likely as a protection against predators. Very recently, additional four supposed specimens were reported by Fischer (2021) and Álvarez-Parra et al. (2021).

The low number of known caterpillars in Cretaceous ambers is unlikely to represent a preservational bias. In younger ambers, a larger number of caterpillars are known (Haug et al. in review), demonstrating that caterpillars can well be trapped and preserved in tree resins.

Here we report four additional specimens of caterpillars preserved in Cretaceous ambers. We compare these new specimens to the already known ones and discuss how far the new specimens expand our view on Cretaceous caterpillar diversity and if they might have represented an adequate food source for early birds.

2. Material and methods

2.1. Material

Four new fossil specimens are reported, all preserved in amber. They originate from Myanmar amber ("Burmese amber"), about 99 million-year-old deposits, Hukawng Valley, Kachin State (Cruickshank & Ko 2003; Shi et al. 2012; Yu et al. 2019).

Two specimens, BUB 3691 and BUB 3196, were legally exported from Myanmar prior to 2017 (see discussions in Haug et al. 2020a for this point). They are part of the collection of one of the authors (PM).

The other two specimens were legally purchased via the internet platform ebay.com, from the trader burmite-miner based in China. It is unclear when these specimens were exactly mined or exported from Myanmar. Especially for pieces of low monetary value, no export papers are usually available. The two specimens are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München, Germany, under the repository numbers PED 1390 and PED 1572.

2.2. Documentation methods

All specimens were documented on a VHX-6000 digital microscope, following standard procedures (e.g., Haug et al. 2013a; Haug & Haug 2019). This includes composite imaging in x-, y- and z-axis (Haug et al. 2011) as well as HDR (Haug et al. 2013b).

2.3. Measurements

In order to have a quantitative frame for comparisons, we measured certain dimensions of the specimens. As for some specimens no scales were available, we used relative lengths instead of absolute values (see Haug & Haug 2019; Herrera-Flórez et al. 2020). Dimensions measured were lengths of head, thorax, abdomen segments 1+2 (“free segments”), abdomen segments 3–6 (region with prolegs), remaining abdomen, thorax appendage (longest one), and abdomen appendage (longest one) (Fig. 1). For comparison, extant caterpillars of the group Gracillariidae depicted in the literature were also measured (Suppl. Table 1).

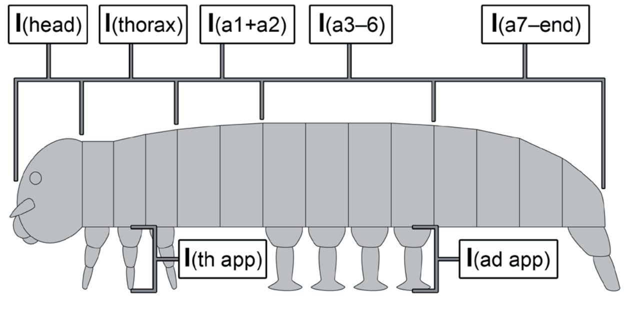

Fig. 1. Scheme of caterpillar in lateral view, highlighting the measured dimensions. Abbreviations: l(a1+a2) = length of abdomen segments 1+2; l(a3–6) = length of abdomen segments 3–6; l(a7–end) = length of posterior region of abdomen; l(ad app) = length of abdomen appendage (“proleg”); l(head) = length of head; l(th app) = length of thorax appendage (“leg”); l(thorax) = length of thorax.

3. Results

3.1. Description of specimen PED 1390

Body appears elongate, worm-shaped, with a distinct capsulate head and trunk (Figs. 2B, 3A–C) Trunk appears soft without distinct sclerotisations. Twelve distinct trunk units, separated by folds, are more or less apparent. The first two units likely form a single segment (thorax segment 1). The remaining units apart from the last one then likely represent a single segment each (thorax segments 2–3 and abdomen segments 1–7). The last unit, the trunk end, represents presumably a compound of several segments.

Not many details of the head accessible. The antenna is visible as well as an array of mouthparts (Fig. 2E). Mouthpart orientation seems to be prognathous. At least three short setae dorsally on the head capsule.

Trunk segments 1–3 (= thorax segments 1–3) each with a pair of appendages (“legs”, Fig. 2A, B). Exact subdivision of appendage elements unclear, several appendages with a distal claw (Fig. 2D). At least one pair (?) of short setae dorsally on trunk segment 1.

Trunk segments 4 and 5 (= abdomen segments 1 and 2) without appendages; each with at least two short setae dorsally. Segment 5 also with at least one short seta ventrally (Fig. 2A, B).

Trunk segments 6–8 (= abdomen segments 3–5) each with a pair of appendages (“prolegs”, Fig. 2A, B). Appendages of segments 6 and 7 proximally cone-shaped, distal area slightly widening (Figs. 2C, 3B). Appendage of segment 8 roughly rectangular; tapering distally. Appendages on segments 7 and 8 with a distal claw (?). Segments 6 and 7 each with at least two short setae dorsally.

Trunk segments 9–10 (= abdomen segments 6–7) without appendages; trunk end with short appendage. Segment 9 with at least one seta dorsally and another one ventrally. Segment 11 with at least six short setae dorsally (one visibly thicker than all others), at least one short seta posteriorly and two short setae ventrally. Trunk end also with short indistinct appendage ventrally (Fig. 2A, B).

3.2. Description of specimen BUB 3691

Body appears elongate, worm-shaped; head region appears to be missing (Fig. 4A, C). Trunk appears soft without distinct sclerotisations, but with numerous distinct folds. Not all folds representing segment boundaries, hence folds partly obscuring trunk segmentation, yet 13 distinct trunk units are more or less apparent (Fig. 4B). Anterior twelve units representing segments (thorax segments 1–3 and abdomen segments 1–9); last one, trunk end, most likely composite of two former segments (abdomen segments 10 and 11).

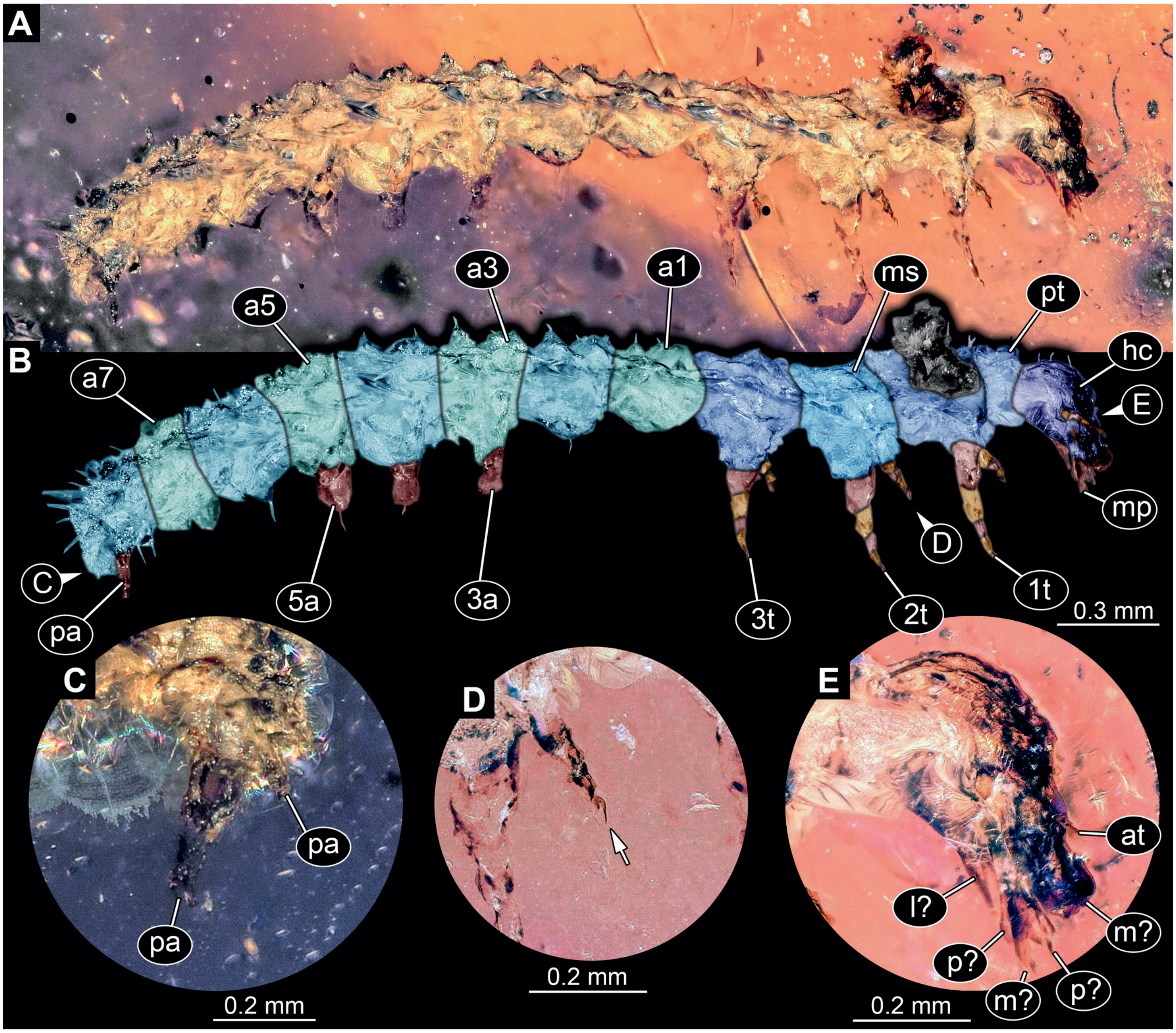

Fig. 2. New Cretaceous caterpillar specimen, PED 1390. **A** – Habitus in lateral right view. **B** – Colour-marked version of A. **C** – Close-up of posterior trunk appendages. **D** – Close-up of claws on thorax appendages (arrow). **E** – Close-up of the head capsule. Abbreviations: 3a–5a = appendage of posterior trunk (abdomen), "proleg" of abdomen segments 3–5; a1–7 = abdomen segments 1–7; at = antenna; hc = head capsule; l? = possible labium; m? = possible mandible; mp = mouthparts; ms = mesothorax; p? = possible palp; pa = appendage of posterior trunk (abdomen), "proleg" of abdomen segment 10; pt = prothorax; t1–t3 = trunk segment 1–3; ta3 = trunk/thorax appendage of trunk segment 3.

Trunk segments 1–3 (= thorax segments 1–3) each with a pair of appendages ("legs", Fig. 4B, D). Exact subdivision of appendage elements unclear, several legs with a distal claw (Fig. 4D). Trunk segment 1 with multiple setae (~36), distributed evenly over the segment, with dorsal setae being longer than the lateral and ventral setae. At least four setae on the appendages of trunk segment 1. Trunk segment 2 with at least three long and seven short setae dorsally; at least five short setae laterally. At least nine setae on the appendages of trunk segment 2; setae get shorter distally. Trunk segment 3 with at least three long and six short setae dorsally; at least five setae laterally. At least nine setae on the appendages of trunk segment 3; setae are all short.

Trunk segments 4 and 5 (= abdomen segments 1 and 2) without appendages (Fig. 4B, C). Trunk segment 4 with

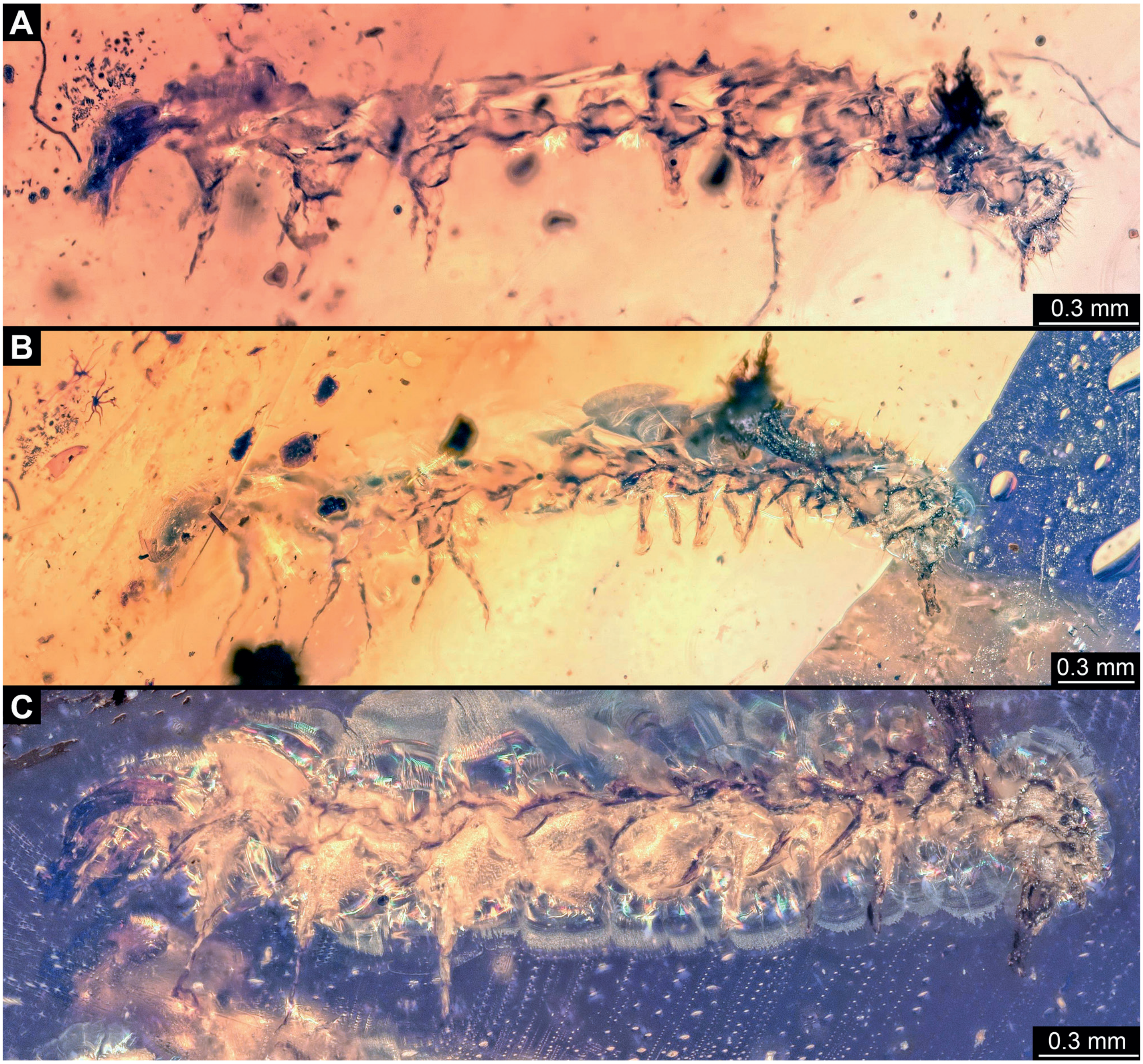

Fig. 3. New Cretaceous caterpillar specimen, PED 1390, continued. **A** – Lateral left view. **B** – Postero-lateral view, providing a better view on posterior appendages. **C** – Latero-ventral view.

at least one long and four short setae dorsally. Trunk segment 5 with at least one long and seven short setae dorsally; at least two long setae and one short seta ventrally.

Trunk segments 6–8 (= abdomen segments 3–5) each with a pair of appendages ("prolegs", Fig. 4B, E). Proximally cone-shaped, distal area widening slightly. Trunk segment 6 with at least two long and five short setae dorsally; at least one long seta and three short setae laterally. At least nine short setae on the appendages of trunk segment 6, two of them on the widened distal area. Trunk segment 7 with at least two long and five short setae dorsally; at least two long and two short setae laterally. At least nine short setae on the appendages of trunk segment 7, one of them on the widened distal area. Trunk segment 8 with at least one long seta and four short setae dorsally; one long seta and two short setae laterally. At least 13 short setae on the appendages of trunk segment 8, three of them on the widened distal area.

Trunk segments 9–12 (= abdomen segments 6–9) without appendages. Trunk segment 9 with at least five short setae dorsally; at least two long and four short setae laterally and two short setae ventrally. Trunk segment 10 with at least seen short setae dorsally; at least one long seta and four short setae laterally and five long setae ventrally. Trunk segment 11 with at least three long and three short setae dorsally; at least two long setae laterally and one short seta ventrally. Trunk end with multiple setae (~ 29); setae mostly laterally and posteriorly. Trunk end with at least four long setae and nine short setae; at least 13 shorter setae laterally and three short setae ventrally (Fig. 4B, C).

3.3. Description of specimen BUB 3196

Body appears elongate, worm shaped, with a distinct capsulate head and trunk region (Fig. 5A, B); air bubble obscuring the specimen partly. Trunk appears soft without sclerotisations. Twelve trunk units more or less apparent, each unit besides trunk end representing segments (thorax segments 1–3 and abdomen segments 1–8); trunk end representing compound of several segments. Trunk segments 4–9 all smaller than trunk segments 1–3, slightly tapering towards the trunk end.

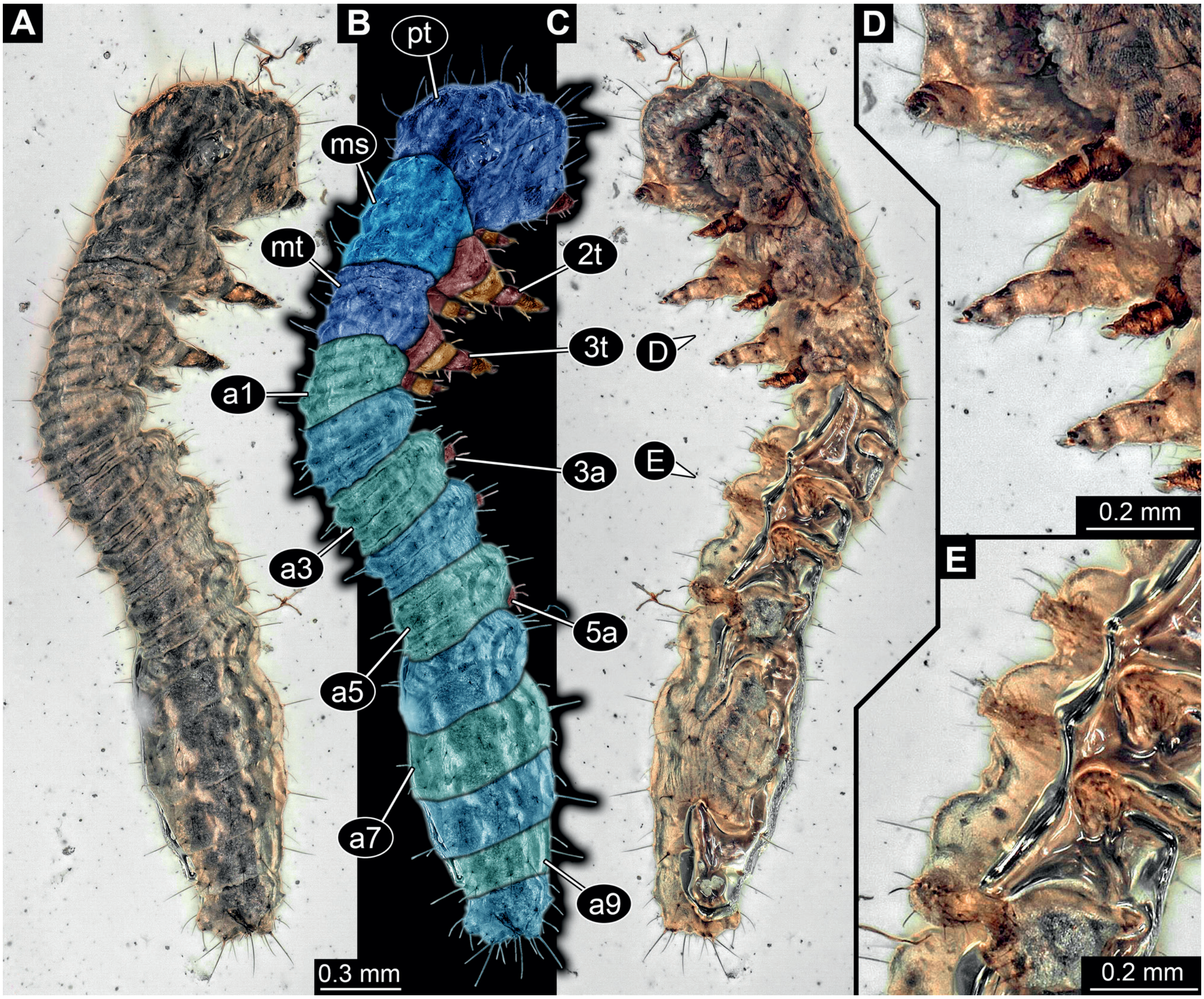

Fig. 4. New Cretaceous caterpillar specimen, BUB 3691. **A** – Habitus in dorso-lateral right view. **B** – Colour-marked version of Fig. 4A. **C.** – Habitus in ventro-lateral left view. **D** – Close-up of thorax appendages. **E** – Close-up of abdomen “prolegs”. Abbreviations: 3a–5a = appendage of posterior trunk (abdomen), “proleg” of abdomen segments 3–5; a1–9 = abdomen segments 1–9; ms = mesothorax; mt = metathorax; pt = prothorax; t1–t3 = trunk segment 1–3; ta3 = trunk/thorax appendage of trunk segment 3.

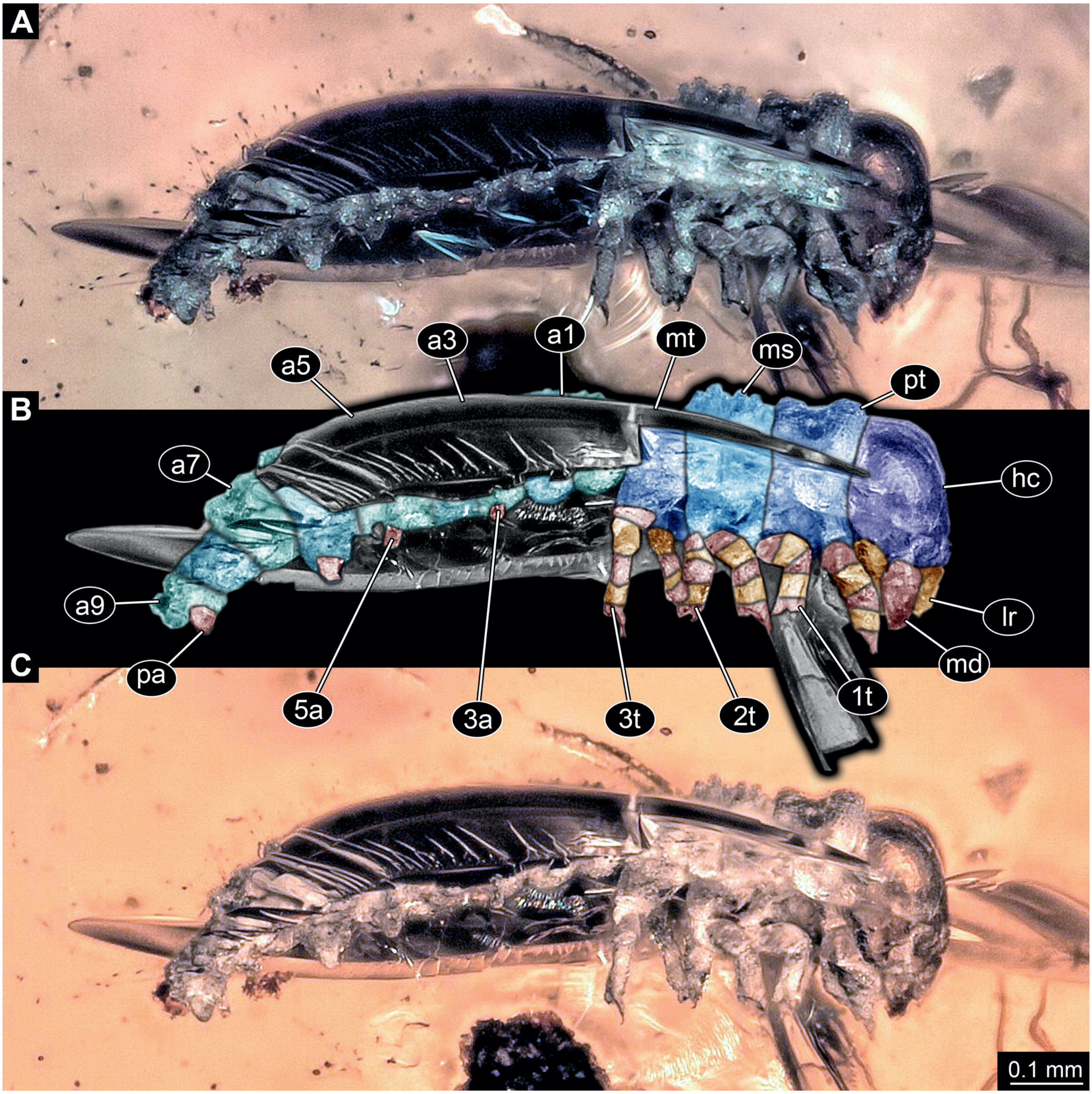

Fig. 5. New Cretaceous caterpillar specimen, BUB 3196. **A** – Habitus in lateral right view under cross-polarised coaxial illumination. **B** – Colour-marked version of Fig. 5A. **C** – Habitus in lateral right view under unpolarised low-angle ring light. Abbreviations: 3a–5a = appendage of posterior trunk (abdomen), "proleg" of abdomen segments 3–5; a1–9 = abdomen segments 1–9; hc = head capsule; lr = labrum; md = possible mandible; ms = mesothorax; mt = metathorax; pa = appendage of posterior trunk (abdomen), "proleg" of abdomen segment 10; pt = prothorax; t1–t3 = trunk segment 1–3; ta3 = trunk/thorax appendage of trunk segment 3.

Not many details of the head accessible (Fig. 5A, B). Labrum and mandible visible. Mouthpart orientation seems to be prognathous.

Trunk segments 1–3 (= thorax segments 1–3) each with a pair of appendages ("legs", Fig. 5B). Exact subdivision of appendage elements unclear; three appendages with a distal claw.

Trunk segments 4–5 (= abdomen segments 1–2) without appendages and almost entirely covered by the air bubble (Fig. 5A, B).

Trunk segments 6–9 (= abdomen segments 3–6) largely covered by the air bubble. Abdomen segments 3, 5 and 6 each with an indistinct appendage (most likely an appendage pair); abdomen segment 4 with no visible appendage (Fig. 5B), not clear if absent.

Trunk segments 10–12 (= abdomen segments 7–9) with no appendage on trunk segment 10 and 11. Strong tapering from trunk segment 10 to 11; 11 and 12 similar in size. Trunk end with short indistinct appendage (most likely appendage pair) ventrally (Fig. 5B). No details of setation recognisable.

3.4. Description of specimen PED 1572

Body appears elongate, worm-shaped, with a distinct capsulate head and trunk region (Fig. 6A, B). Trunk appears soft without sclerotisations. Thirteen distinct trunk units are more or less apparent (Fig. 6B). Anterior twelve units representing segments (thorax segments 1–3 and abdomen segments 1–9); last one, trunk end, most likely composite of two segments (abdomen segments 10 and 11).

Not many details of the head accessible (Fig. 6A, B). Mandible and labium apparent, although mostly the palp. Mouthpart orientation seems to be prognathous. At least five long and two short setae dorsally; at least five long setae ventrally. Also at least two setae on the mandibles.

Trunk segments 1–3 (= thorax segments 1–3) each with a pair of appendages (“legs”, Fig. 6A, B). Exact subdivision of appendage elements unclear, several legs with a distal claw (Fig. 6A). Trunk segment 1 with at least three long and three short setae dorsally; one long and one short seta ventrally. At least 14 setae on one of the appendages

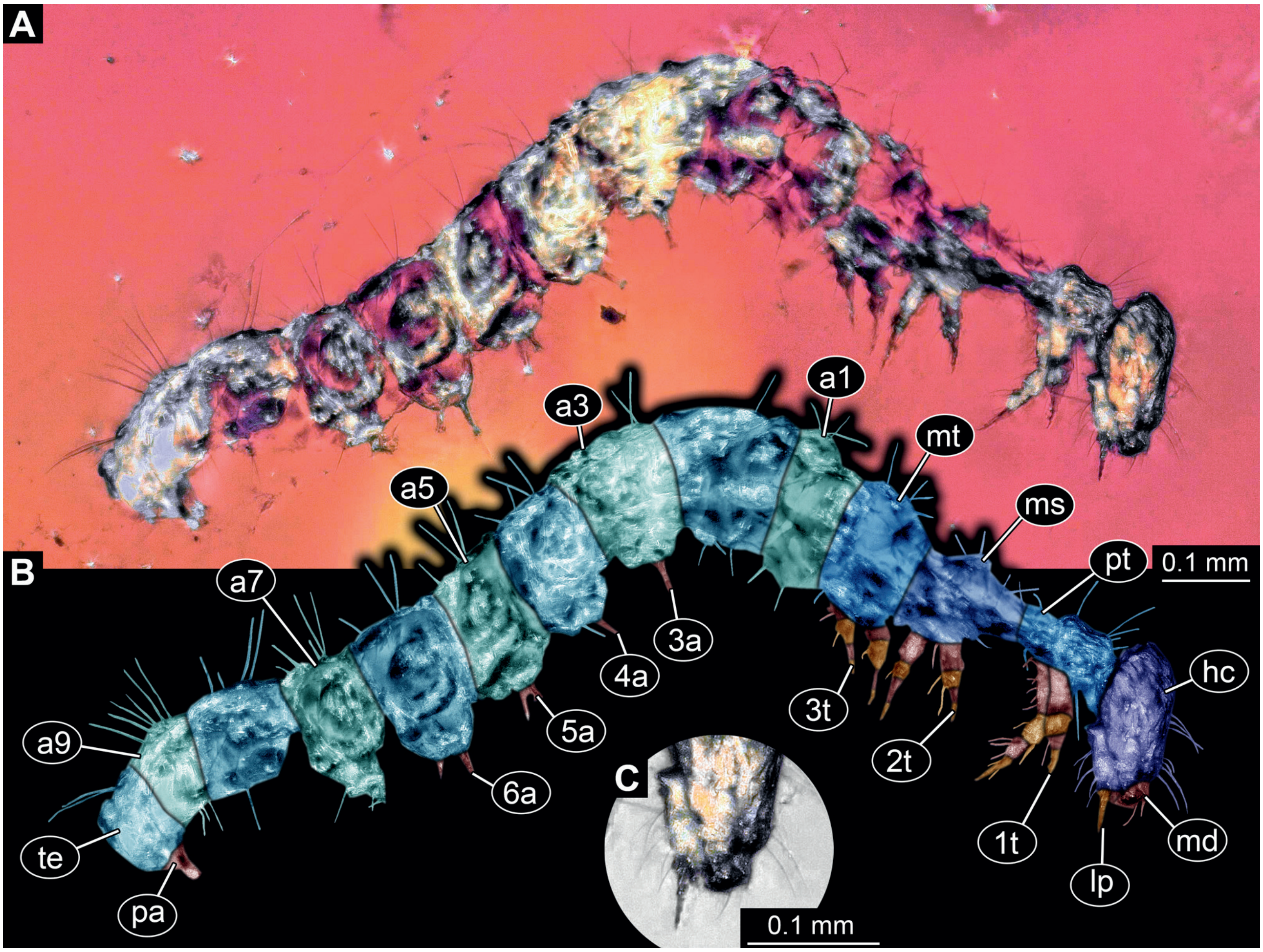

Fig. 6. New Cretaceous caterpillar specimen, PED 1572. **A** – Habitus in lateral right view. **B** – Colour-marked version of Fig. 6A. **C** – Close-up on possible mouthparts. Abbreviations: 3a–6a = appendage of posterior trunk (abdomen), “proleg” of abdomen segments 3–6; a1–9 = abdomen segments 1–9; hc = head capsule; lp = labial palp; md = possible mandibles; ms = mesothorax; mt = metathorax; pt = prothorax; t1–t3 = trunk segment 1–3; ta3 = trunk/thorax appendage of trunk segment 3; te = trunk end.

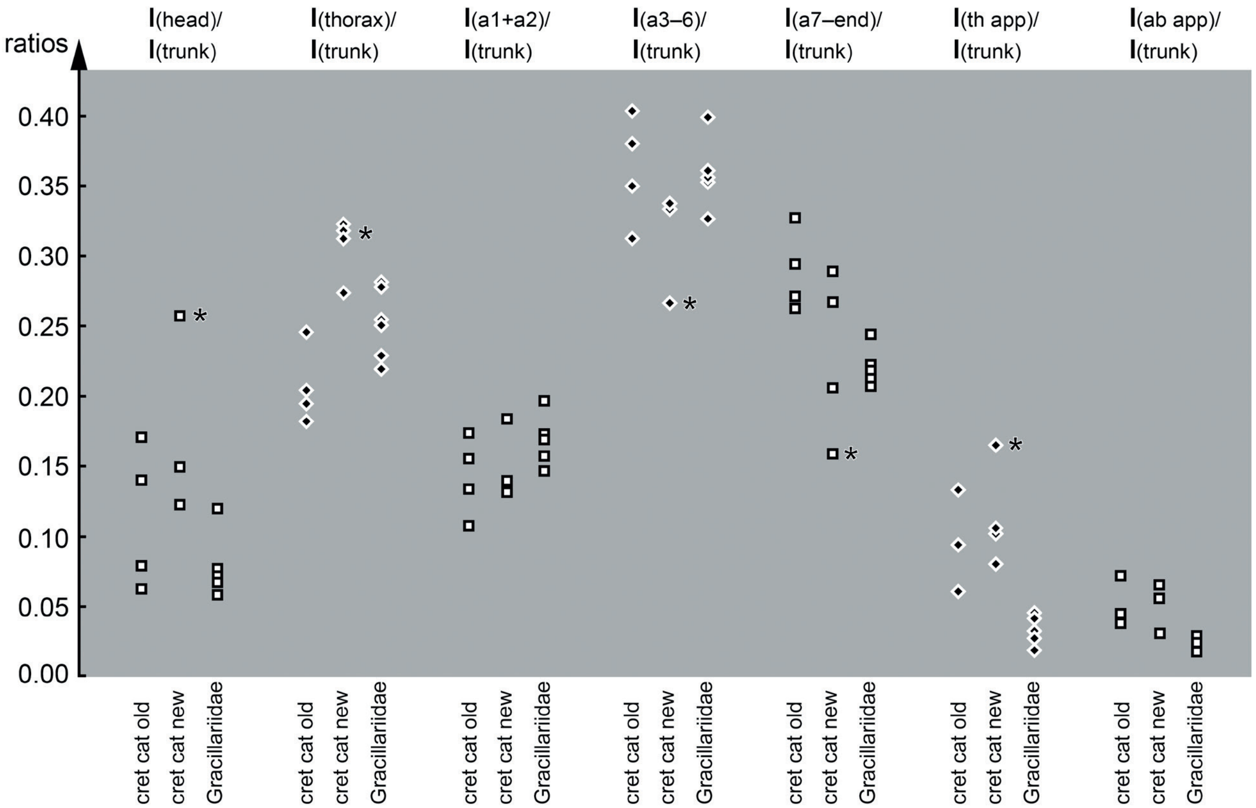

Fig. 7. Scatterplots of measured ratios of the Cretaceous caterpillars known before this study, those described in this study, and of extant caterpillars of Gracillariidae. Asterisks next to the symbols mark where the new fossils plot outside the range of the other groups. Abbreviations: cret cat old = previously known Cretaceous caterpillars; cret cat new = here reported new specimens; l(a1+a2) = length of abdomen segments 1+2; l(a3–6) = length of abdomen segments 3–6; l(a7–end) = length of posterior region of abdomen; l(ad app) = length of abdomen appendage ("proleg"); l(head) = length of head; l(th app) = length of thorax appendage ("leg"); l(thorax) = length of thorax; l(trunk) = length of trunk

of segment 1 (likely on the other one as well). Trunk segment 2 with at least five short setae dorsally; at least one short seta ventrally. At least three setae on the appendages of trunk segment 2. Trunk segment 3 with at least one long seta and three short setae dorsally; at least one short seta ventrally. At least two setae on the appendages of trunk segment 3.

Trunk segments 4 and 5 (= abdomen segments 1 and 2) without appendages (Fig. 6A, B). Trunk segment 4 with at least three long setae dorsally; at least two short setae ventrally. Trunk segment 5 with at least one long seta dorsally; at least three short setae ventrally.

Trunk segments 6–9 (= abdomen segments 3–6) each with appendages ("prolegs", likely always paired structures; Fig. 6B). Appendages short and roughly rectangular in lateral view. Trunk segment 6 with at least two long setae dorsally. Trunk segment 7 with at least two long and two short setae dorsally; at least one short seta ventrally. Trunk segment 8 with at least two long setae and one short seta dorsally. Trunk segment 9 with at least two long setae and one short seta dorsally.

Trunk segments 10–12 (= abdomen segments 7–9) without appendages; trunk segment 13 (= abdomen segment 10) with at least two long and three short setae dorsally; at least one long seta and two short setae ventrally. Trunk segment 14 (= abdomen segment 11) with at least two long and two short setae dorsally; at least one long seta ventrally. Trunk segment 15 (= abdomen segment 12) with at least six long setae dorsally; at least three short setae ventrally. Trunk end with at least two long setae dorsally and short indistinct appendage (most likely appendage pair) ventrally (Fig. 6B).

3.5. Description of plot

When plotting the different measured ratios for the already known Cretaceous caterpillars, the new caterpillars, and extant larvae of Gracillariidae, recognisable differences are revealed (Fig. 7). At least some of the new fossils plot pronouncedly outside the range of the other groups for relative lengths of head, thorax, abdomen segments 3–6, posterior region of abdomen, and thorax appendages.

4. Discussion

4.1. Identity of the new caterpillars

Two of the new caterpillars have only three pairs of anterior abdomen appendages, on abdomen segments 3–5, but not on 6. A similar condition appears in the specimen reported by Haug & Haug (2021). In the modern fauna, only a few caterpillars show this condition, most prominently caterpillars of Gracillariidae. Kumata (1985) reported also caterpillars of the group with prolegs on abdomen segment 6; these were not considered here for comparison with the fossils.

The larvae of Gracillariidae are well known as leaf miners. None of the definite caterpillars known from the Cretaceous shows specialisations that would be expected for leaf miners. Hence, it might be possible that the larvae with only three pairs of anterior abdomen appendages are closely related to Gracillariidae, but it is unlikely that they represent ingroups (see also discussion in Haug & Haug 2021).

Fischer (2021) described three larvae that he interpreted as larvae of Gracillariidae. Indeed these specimens show clear specialisations for leafmining. Yet, as already Fischer (2021: 141–142) pointed out, these are in certain aspects unusual. He showed that similar morphologies also occur (due to convergent evolution) in certain larvae of jewel beetles (e.g., Grebennikov 2013: 167, fig. 1) which are known from few fossils (Haug et al. 2021a), but also traces (Ding et al. 2014). Yet, in fact there is a third lineage of Holometabola with very similar-appearing larvae, Tenthredinidae, more specifically several species of birch-leafmining hymenopterans (e.g., Frost 1925, pl. 29, fig. 6; Digweed et al. 2009: 219, fig. 6a). It seems difficult to exclude that the fossils by Fischer (2021) could represent larvae of this group; at least some of the peculiarities (e.g., absence of leglets, large size) would be easier to understand in this frame.

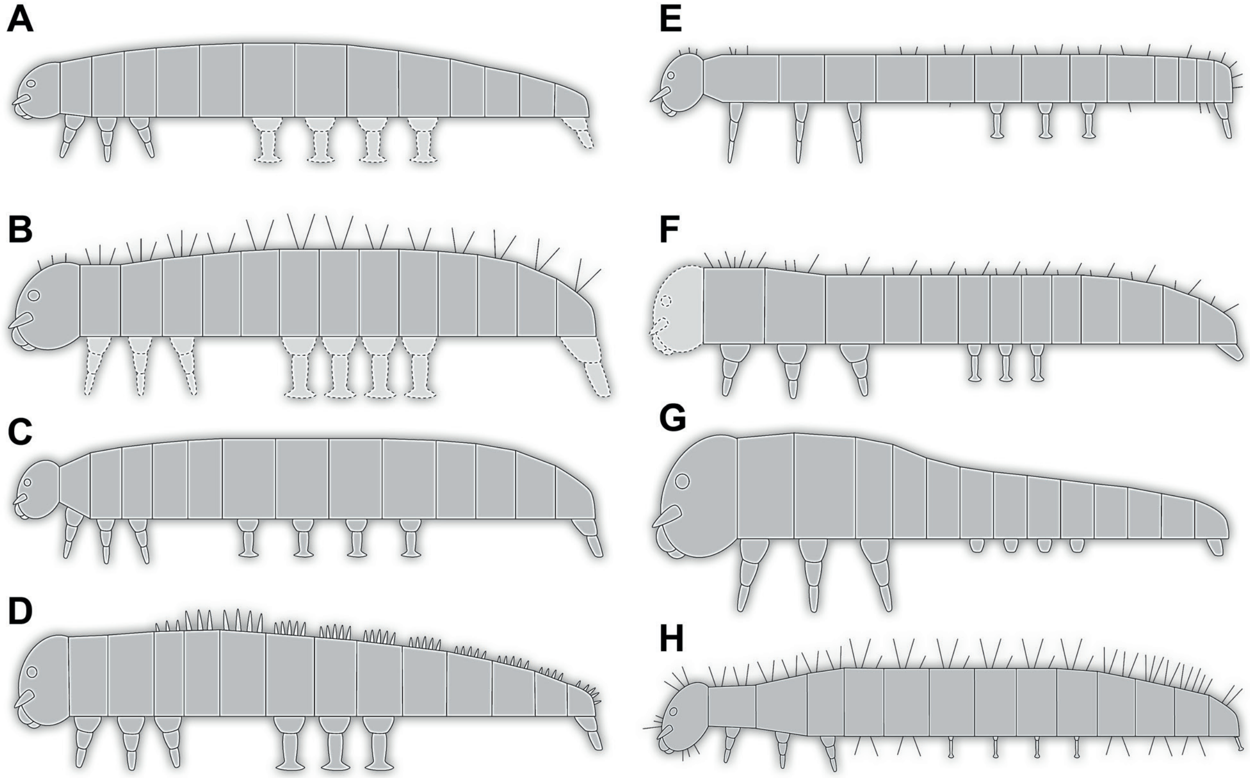

Fig. 8. Schematic representations of Cretaceous caterpillars. **A** – From Grimaldi & Engel (2005). **B**, **C** – From Xia et al. (2015). **D** – From Haug & Haug (2021). **E** – Specimen PED 1390. **F** – Specimen BUB 3691. **G** – Specimen BUB 3196. **H** – Specimen PED 1572. Stippled lines indicate structures either not preserved or not accessible.

For the other specimens, it remains very difficult to provide an educated guess concerning their relationships. Many important characters for further narrowing down a possible relationship are simply not preserved or accessible. Despite the fact that the more exact relationships of the caterpillars within Lepidoptera remains largely unclear, the new fossils provide some interesting signals concerning the diversity of Cretaceous caterpillars, as well as their possible role in the Cretaceous food web.

4.2. Expanding the diversity of Cretaceous caterpillars

As the plot of measured ratios reveals (Fig. 7), the new fossils have a body organisation so far not known from the Cretaceous concerning lengths of certain body regions or structures (Fig. 8). If taxonomic or phylogenetic interpretations of fossil specimens are challenging, these are often difficult to be included into measures of diversity over time. Morphological aspects of such animals offer an alternative objective measure of diversity, independent from a taxonomic frame (see Haug et al. 2020b, 2021a, 2021b, 2021c, 2021d, 2021e).

Although the new larvae cannot be easily treated in a taxonomic frame, we can recognise that they differ in some cases markedly from the already known ones. Given the low overall number of previously known caterpillars from the Cretaceous (not considering those of Fischer 2021 and Álvarez-Parra et al. 2021 due to uncertainties and inaccessibility of some details), it should not be surprising that the new ones expand the known morphologies. Still, the morphological frame provides a more independent frame here. This frame also further emphasises the difference of most of the fossils to modern larvae of Gracillariidae; especially the thorax appendages (legs) are shorter in modern leaf-mining larvae of Gracillariidae.

4.3. Caterpillars and the Cretaceous food web

In the modern fauna, caterpillars are an important food source for many birds. Around 80% of all non-tropical birds are at least partially insectivorous (Nyffeler et al. 2018, based on Lopes et al. 2016), which means that the availability of insects as a food source is tightly connected to birds in the same ecosystem. A lack of caterpillars as a food source in an environment, for example, can have influence on the breeding biology of some birds (Visser et al. 2006).

This aspect is further supported by the fact that not only birds but also almost all diapsidan reptiles that are herbivorous as adults have to consume animal protein in their early life to support their rapid growth (White 1985). This fact has led to a complicated relationship with caterpillars having developed a multitude of defensive strategies in the modern fauna to defend themselves against birds, including, but not being limited to, indicating indigestibility (aposematism), physical armour, or spines and long setae to avoid being consumed (Heinrich & Collins 1983).

So far, only a few caterpillars have been reported from the Cretaceous (Haug & Haug 2021); the four new specimens reported significantly expand the amount of known specimens. Yet, one aspect is quite apparent: all specimens of which the size is known are quite small (1 mm to 3.4 mm, around 5 mm for the specimen in Álvarez-Parra et al. 2021; only the specimens in Fischer 2021 are larger, up to 7 mm). Of course, this could be a preservational bias, with larger caterpillars having been present, but only small-sized individuals (for example earlier stages) becoming preserved in amber. This might also be due to a bias towards favouring describing adult insects over larvae. Yet, it cannot be excluded either that there were simply no larger caterpillars in the Cretaceous.

Given the so far low number of caterpillars at that time, an estimation of their position in the food web in the Cretaceous is challenging. Yet, their size might indeed be an indicator, as we could expect that caterpillars of a certain size will simply be too small to be interesting food items for early birds. For such an interpretation, we need to evaluate the possible sizes of caterpillars in the Cretaceous and the minimum sizes of modern-day caterpillars that are consumed by birds.

4.4. Caterpillar sizes in other ambers: indication of a preservation bias?

For evaluating a possible preservation bias of amber or resins in general selecting for smaller specimens, we can simply check the sizes of caterpillars preserved in other, hence younger types of amber. In Eocene Baltic amber, many caterpillars seem to be small, around the same size as the ones in Cretaceous amber, with lengths between 2–5 mm (Janzen 2002; Gröhn et al. 2015; Fischer et al. 2019). Yet, there are a few larger ones in the range of 7–8.5 mm in length (Ross 2010; Gröhn et al. 2015).

In Miocene ambers (recently reviewed in Haug et al. in review and references therein), also small specimens are known, yet in fact the larvae tend to be larger than the ones in the Cretaceous or even the Eocene. The larger specimens measure up to 11 mm (Poinar & Hammond 1998).

Even younger resins have so far rarely preserved caterpillars. A single specimen has been reported from Madagascar copal (or defaunation resin; Haug & Haug in review and references therein). It is not fully preserved inside the resin, but largely, possibly missing only minor parts of the head. The preserved part of the body measures more than 12 mm. Moreover, the larva has prominent long setae increasing its overall size.

The findings of caterpillars in younger resins clearly show that there is no principal preservation bias or restriction to the size range of caterpillars observed in Cretaceous amber. Instead, we could expect even specimens reaching into the centimetre range to be preserved in resins.

We should therefore expect that, if much larger caterpillars would have been around in the Cretaceous, that they could potentially be preserved in amber, up to at least 10 mm. Hence, the small size range of the known caterpillars may well reflect the fact that these were still smaller in the Cretaceous.

4.5. Sizes of adult lepidopterans in the Cretaceous

As pointed out, caterpillars may be small due to them representing earlier larval stages. We can look at adult size to get an impression of the maximum size of caterpillars that could have been around. Unfortunately, not much unlike caterpillars, also adult lepidopterans are rather rare in Cretaceous ambers. While the lineage of Lepidoptera seems to have diversified to a certain degree (SOHN et al. 2015; KAWAHARA et al. 2019; HAUG & HAUG 2021), we can expect that earlier sub-lineages were still quite dominating. Many representatives of these were in former times often referred to as “microlepidopterans”, already indicating a smaller size.

Looking at the few available fossils, WHALLEY (1987) mentioned a few Cretaceous specimens of Micropterigidae (WHALLEY 1977, 1978), but did not compare sizes to modern representatives, referring to the fossils as “small moths”. Their wingspans are around 10 mm and are apparently similar in size to modern representatives of Micropterigidae.

MARTINS-NETO & VULCANO (1989) and MARTINS-NETO (1999, 2001) mentioned three specimens: a representative of Micropterigidae with a body length of around 3.5 mm, a specimen of *Gracilepterix pulchra* with a body length of about 3 mm, and a representative of Undopterygidae with a hind wing length of around 3.1 mm.

GRIMALDI & NASCIMBENE (2010) mentioned that there are multiple adult lepidopteran specimens from New Jersey amber that have so far not been further described. The sizes of these therefore remain unknown.

POINAR (2017) described a representative of Gracillarioidea. No direct comparison to modern representatives was provided, but the body size was stated to be small (2.1 mm).

ZHANG et al. (2017) reported two representatives of Micropterigidae with body lengths of 2.5 and 3.5 mm. ZHANG et al. (2020a) reported three further fossils of Micropterigidae. These are of similar length to some modern representatives of the group (body length around 1.5 mm). ZHANG et al. (2020b) described a rather “large” moth of the group Geometridae with a body length of 5.7 mm and a wingspan of around 20 mm.

The majority of adult lepidopterans in the Cretaceous were apparently small. This is well compatible with the rather small size of the caterpillars. Yet, at least the example of the representative of Geometridae should have had larval stages that were indeed a bit larger than the ones so far found in amber.

4.6. Sizes of prey items of modern birds

The size range of the caterpillars preserved in Cretaceous ambers seems to reflect the sizes of the actually available caterpillars at the time, although slightly larger sizes can be expected. Now the question is, in how far this size range overlaps with the size ranges known to be preyed on in the modern fauna.

Unfortunately, the literature is astonishingly scarce about exact statements concerning the size of caterpillars that are consumed by birds. Generally, analyses focus on the relative prey-predator size relationships, not on absolute minimum sizes of prey that is consumed. We also consider birds as the most likely predators of these caterpillars, as most other insectivorous vertebrates (especially mammals and squamate reptiles) in the Cretaceous were cursorial or arboreal. Looking at our modern fauna, we can observe that caterpillars are mostly eaten by birds as they can most easily access leaves at any height.

Typically, if different birds are compared, there is a strong correlation between bird size and prey size (SAM et al. 2017): smaller birds eat smaller prey. MOHD-AZLAN (2014) showed that mangrove birds in Australia eat a wide array of different representatives of Euarthropoda concerning their size. Most important for our discussion, the smallest size category used by MOHD-AZLAN (2014) was < 5 mm, but was still widely preyed on by multiple different species of birds. TURNER (1982) suggested that birds, in his case swallows, do actively select prey by size, but that birds also eat small prey when it is very abundant. So if the foraging cost is low, because multiple small food items can be caught with little foraging as they are very abundant, birds will include small representatives of Euarthropoda (also Insecta) into their diet. It still appears that birds prefer larger prey by default, as it is easier to spot. Still, they are well able to recognise also small animals (at least around 1–2 mm) and will eat them, if convenient.

This suggests that the Cretaceous caterpillars, although at the lower range, would have been large enough to be eaten by birds (or other smaller reptiles) when taking modern ranges as a basis. Especially the larger specimens PED 1390 with 3 mm in length (Figs. 2A, B, 3) and BUB 3691 with 3.4 mm in length (Fig. 4A, B) would likely be in the visible range for such predators. The spines in the caterpillar reported by Haug & Haug (2021) may therefore have been a specialisation to increase handling times by a possible bird predator.

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Supplementary Table 1. Ratios of measurements used for Fig. 7. Abbreviations: l(a1+a2) = length of abdomen segments 1+2; l(a3–6) = length of abdomen segments 3–6; l(a7–end) = length of posterior region of abdomen; l(ad app) = length of abdomen appendage (“proleg”); l(head) = length of head; l(th app) = length of thorax appendage (“leg”); l(thorax) = length of thorax; l(trunk) = length of trunk

source	source year	source fig.	source p.	l(head) / l(trunk)	l(thorax) / l(trunk)	l(a1+a2) / l(trunk)	l(a3–a6) / l(trunk)	l(a7–end) / l(trunk)	l(th app) / l(trunk)	l(ad app) / l(trunk)
Grimaldi & Engel	2005	fig. 13.21	p. 566	0.08	0.18	0.17	0.38	0.26	0.09	0.04
Xia et al.	2015	–	p. 132	0.06	0.19	0.11	0.40	0.29	0.06	0.05
Xia et al.	2015	–	p. 133	0.17	0.25	0.13	0.35	0.27	–	–
Haug & Haug	2021	fig. 2	p. 103	0.14	0.20	0.16	0.31	0.33	0.13	0.07
PED 1390	this paper	Fig. 2	p. 47	0.12	0.32	0.18	0.33	0.16	0.10	0.06
BUB 3691	this paper	Fig. 4	p. 49	–	0.31	0.13	0.27	0.29	0.08	0.06
BUB 3196	this paper	Fig. 5	p. 50	0.26	0.32	0.14	0.34	0.21	0.17	0.07
PED 1572	this paper	Fig. 6	p. 51	0.15	0.27	0.14	0.33	0.27	0.11	0.03
Kumata	1985	fig. 10A	p. 131	0.08	0.23	0.20	0.36	0.21	0.03	0.03
Dekle	2007	fig. 6	p. 3	0.07	0.25	0.17	0.36	0.22	0.04	0.03
Davis & De Prins	2011	fig. 66	p. 69	0.07	0.25	0.15	0.35	0.24	0.04	0.03
Grebennikov	2013	figs. 2E–G	p. 168	0.12	0.28	0.17	0.33	0.22	0.02	0.02
Moreira et al.	2018	fig. 6b	p. 69	0.07	0.22	0.17	0.40	0.21	0.03	0.02
Davis et al.	2020	fig. 5d	p. 43	0.06	0.28	0.16	0.36	0.21	0.03	0.02