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Campodorus paradiesensis sp. nov. (Hymenoptera: Ichneumonidae: Ctenopelmatinae), a new species with a remarkable colour pattern from Northern Germany

Campodorus paradiesensis sp. nov. (Hymenoptera: Ichneumonidae: Ctenopelmatinae), eine neue Art mit außergewöhnlicher Färbung aus Norddeutschland

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Schlüsselwörter:
Ctenopelmatinae, Mesoleiini, *Campodorus*, neue Art, *Acer campestre*, *Pristiphora depressa*-Gruppe, Knospenschuppenmimese

Zusammenfassung
Campodorus paradiesensis sp. nov., eine neue Ctenopelmatine (Hymenoptera: Ichneumonidae) aus Schleswig-Holstein mit einer innerhalb ihrer Gattung einzigartigen Färbung, wird beschrieben und Einzelheiten zu ihrer Biologie werden dargestellt.

Keywords:
Ctenopelmatinae, Mesoleiini, *Campodorus*, new species, *Acer campestre*, *Pristiphora depressa* group, bud scale mimesis

Abstract
Campodorus paradiesensis sp. nov., a new ctenopelmatine species (Hymenoptera: Ichneumonidae) with a unique colour pattern within its genus, is described from Schleswig-Holstein, Germany, and information on its biology is given.

1. Introduction

Campodorus Förster, 1869 (Hymenoptera Linnaeus, 1758: Ichneumonidae Latreille, 1802: Ctenopelmatinae Förster, 1869: Mesoleiini Thomson, 1883), with 143 described species worldwide (Yu et al. 2016; Sun et al. 2020), is the largest genus within the Ctenopelmatinae (Kasparyan 2003). There are 99 species occurring in the Western Palaearctic (Sun et al. 2020), 45 of which are known from Germany (Riedel et al. 2021). A selection of 75 Palaearctic species, almost all with black metasoma, were included in a partial revision by Kasparyan. These include species with pectinate claws (Kasparyan 2003), species with yellow face or red mesothorax (Kasparyan 2005) and species with long-haired ovipositor sheath, entirely rufous hind tibia or white-banded tibiae (Kasparyan 2006). All *Campodorus* species with reliable host data are koinobiont endoparasitoids of tenthredinid sawflies mostly in the subfamily Nematinae (Hymenoptera: Tenthredinidae: Nematinae) (e. g. Zinnert 1969, Thirion et al. 1993, Shaw & Kasparyan 2003, Kasparyan & Kopelke 2009, Zwakhals et al. 2021) with some known exceptions of parasitoids of Blennocampinae and Selandriinae (e. g. Hinz 1961, Weiffenbach 1988, Horstmann 2008, Zwakhals & Blommers 2021). However, for the great majority of species no reliable host data exists.

From the 16th to the 25th of May 2020, two females and two males of a conspicuously bright coloured ctenopelmatine were observed on *Acer campestre* (Field Maple) in the author's garden in Mohrkirch, Schleswig-Holstein, Germany. The trees are located on top of a 3 m high earth bank. The wasps were found only on the wind-

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Fig. 1: *Campodorus paradiesensis* (females and males) in 2020.

Fig. 2: Habitat: East side of two *Acer campestre* trees on top of an earth bank in Mohrkirch, Schleswig-Holstein, Northern Germany.

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protected east side (Fig. 2), which is shaded in late afternoon. They were keyed to *Campodorus* with Townes (1969) and appeared to be an undescribed species. In 2021, another female was photographed and then collected on the 23rd of May at the same site and a further female was photographed on the 1st and 3rd of June.

2. Materials and Methods

Abbreviations

LIB = Leibniz Institute for the Analysis of Biodiversity Change, Hamburg
Lund = Lund University, Lund
NHMR = Natural History Museum, Rotterdam

Examined material and literature

One female specimen was examined, supplemented by field photographs of three more female and two male specimens. Original descriptions of all 143 valid *Campodorus* species worldwide were studied (Ashmead 1890, Ashmead 1902, Davis 1897, Fourcroy 1785, Gravenhorst 1829, Habermehl 1923, Heinrich 1950, Heinrich 1952, Hinz 1969, Holmgren 1856, Holmgren 1857, Holmgren 1876, Holmgren 1880, Jurine 1807, Jussila 1965, Jussila 1996, Jussila 2006, Kasparyan 1998, Kasparyan 2003, Kasparyan 2005, Kasparyan 2006, Parfitt 1882, Ratzeburg 1852, Roman 1909, Schmiedeknecht 1924, Schmiedeknecht 1925, Stephens 1835, Sun et al. 2020, Teunissen 1945, Teunissen 1953, Thomson 1883, Thomson 1894, Uchida 1935, Uchida 1942, Woldstedt 1874, Woldstedt 1877). Photographs of the C. G. Thomson collection (Lund) and of the type specimen of *Campodorus rubens* (Teunissen, 1953) (NHMR) were consulted. Additionally, specimens of several *Campodorus* species deposited in LIB, Hamburg were studied. The type specimen is deposited in LIB, Hamburg (catalogue Nr. ZMH 824700).
Morphological terminology largely follows Broad et al. (2018).

Molecular analysis

Genomic DNA extraction was made from the right midleg. PCR amplification and sequencing were done by Timo Wehrt at LIB, Hamburg, using the LCO1490 and HCO2198 primers (Folmer et al. 1994) to amplify the barcode region of the mitochondrial cytochrome oxidase subunit I (COI) using a standard DNA barcoding protocol. Sequence id and sample id referring to the BOLD database are presented in the results section.

Photographs

Field photographs were taken by the author with a Panasonic Lumix FZ1000 combined with a Raynox M-250 achromat and a Yongnuo YN14EX electronic flash. In order not to affect their natural behaviour, the wasps (except the type specimen) were not caught at any time for the photographs. The type specimen was examined using a WILD M5A stereomicroscope. Photographs of the type specimen were taken by Thure Dalsgaard at LIB, Hamburg, using a Canon EOS 5DS R with an MP-E 65mm objective and a Canon EOS 7D Mark II with a custom-made objective with Mitutoyo Plan Apo lenses, respectively, and stacked with Zerene Stacker.

3. Results

Holotype: Female. Germany, Schleswig-Holstein, Mohrkirch, hand-caught with a polystyrene tube from *Acer campestre* foliage, 23 V 2021 (Fig. 3).

Diagnosis

All coxae yellow and metasomal tergites 2-8 orange; head and mesosoma usually predominantly yellow.

Differential diagnosis

No other female *Campodorus* species with a reddish metasoma is known to have a predominantly yellow head, a predominantly yellow mesosoma or a predominantly yellow hind coxa. Thus, within the genus, the described species is easily recognised by its bright colouration. Field photographs of one very dark specimen with more extensive black on head and mesosoma show the hind coxa still predominantly yellow with only the very base darkened. Other *Campodorus* females with hind coxa predominantly yellow belong to *C. albilineatus* Sheng, Sun & Li, 2020 (hind coxa yellow dorsally, reddish ventrally; tergites black) and *C. flavomaculatus* Kasparyan, 2005 (hind coxa mainly yellow, remainder black; tergites black).
Etymology: *Campodorus paradiesensis* after the type locality, Paradies, Mohrkirch

Description of the female

Measurements: Body length 6.4 mm, fore wing length 5.3 mm, ovipositor sheath 0.4 mm.
Head: Face matt, finely granulate; upper margin with median small tubercle. Clypeus 2.8 as wide as high, shiny, swollen apicomedially, apical margin blunt me-

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Fig. 3: Holotype (photos: 3a-d LIB, Thure Dalsgaard; 3e Gavin Broad).

dially, lateral margins projecting as thin lobes; silvery setae longer than minimum height of mandible. Mandible finely and densely punctate centrally, smooth apically; upper mandibular tooth slightly wider and longer than lower tooth. Frons punctate. Antennal flagellum 33- to 36-segmented; first flagellomere 1.6 x longer than second flagellomere. Vertex and temple finely granulate. Occipital carina complete, slightly raised centrally, lower end reaching hypostomal carina distinctly behind mandibular base.

Mesosoma: Pronotum shagreened. Mesoscutum and scutellum shallowly punctate, finely granulate in between; notauli very shallowly impressed, not reaching middle of mesoscutum. Mesopleuron matt with shallow punctures, with silvery setae mostly restricted to the lower part; speculum shiny, almost smooth; upper end of epicnemial carina fading out before reaching subtegular ridge. Tarsal claws simple. Wings hyaline. Fore wing vein 3rs-m absent; vein 1cu-a postfurcal to M&RS, distal by 0.2; postnervulus intercepted at middle. Hind wing nervellus inclivious, intercepted below middle. Propodeum with median longitudinal and posterior transverse carinae complete; propodeal spiracle circular.

Metasoma: tergites finely shagreened. Dorsal median carinae of tergite 1 poorly defined, reaching beyond spiracle.

Colouration: yellow, except the following body parts:

Orange are: flagellum basally (not always), femora, tibiae, tarsomeres 1-4 of fore and mid tarsus, metasomal tergites 2-8 except laterotergites.

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Fig. 4: Variation in female colouration.

Dark brown to black are: thin to broad dorsolateral mark on scapus and pedicellus, flagellum except basally (not always), apices of mandibular teeth, mark covering stemmaticum and reaching occipital carina and temple, central and lateral marks on occiput (melanisation of head can be extended to entire frons, vertex, temple and gena); mesoscutal front margin centrally (can be absent), two parallel oval marks in anterior half of mesoscutum bordered by a stylised W-mark that reaches mesoscutal hind margin (W-mark can be separated into two longitudinal lateral marks and a posterior triangular mark; melanisation can be extended to almost entire mesoscutum except lateral margins and central patch), central mark on upper margin of mesopleuron (can be absent or extended to a large C-mark), most part of front margin of metapleuron, axillary troughs of mesonotum and metanotum, groove between metanotum and area basalis, apical part of area petiolaris (melanisation can be extended to entire propodeum), tarsal claws, tarsomere 5 of fore and mid tarsus, complete hind tarsus; metasomal tergite 1 anteriorly and medially (central melanisation can be absent or confluent with basal patch), ovipositor sheath.

The DNA barcode sequence of the type specimen is available at the BOLD systems database: sample & sequence id. CPACLB20210523

Male: Because no male specimen has been caught, it is not formally described here. Photos of living males (Fig. 1b, 1d, 8-9) show the same colour pattern as found in females with only the scapus and pedicellus remarkably differing in being almost entirely yellow. Apart from the reproductive organs, males can further be distinguished from females by a slenderer metasoma, as is usually the case with ichneumonids. Despite the lack of a male specimen, the sexes were associated by their behaviour, spatial-temporal cooccurrence and colouration.

4. Discussion

Barcoding and determination

Because the colouration is unusual for the genus, the specimen was barcoded to prove its relationship. The result shows a high genetic similarity to other *Campodorus* species, namely *C. commotus* (Holmgren, 1876) and *C. haematodes* (Gravenhorst, 1829) (each 97,5 % similar).

Although colouration is often variable and thus often not useful in distinguishing ctenopelmatine species, certain colour characters of the described species are unique within the genus, which makes colour-based identification feasible.

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Fig. 5: Field photographs of female 1.

Fig. 6: Field photographs of female 2.

Variability

Field photographs of three more females (Fig. 1a, 1c, 4-7) show a wide range of variation in melanisation of the head and mesosoma (Table 1). While in ♀2 the amount of black is even smaller than in the type specimen, ♀4 shows a strong melanisation, with the head, mesoscutum and mesopleuron largely and the propodeum almost completely black. However, the colour of the prothorax, scutellum, postscutellum and all coxae remains yellow and is thus considered a stable character.

In males (Fig. 1b, 1d, 8-9), the observed variability is less marked but only two were seen and none in the cold spring of 2021.

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Fig. 7: Field photographs of female 4.

Fig. 8: Variation in male colouration.

Biology

Adult feeding

♀1, ♀2, ♀4 and ♂1 were seen feeding on the flowers of *Acer campestre* (Fig. 10). This nectar source is used by a wide range of ichneumonid species in May and early June (pers. obs.). During the time the author spent at the site, 27 ichneumonid species representing 14 subfamilies were observed feeding on *A. campestre* flowers. There were no other nectar sources nearby at the time so it was not possible to investigate feeding preferences of the described species. No aphid colonies were present on the *A. campestre* at that time, *Aegopodium podagrari*a only started to bloom as the flight time was ending and no plants with extrafloral nectaries were around. It is unclear if the females host-feed, but at least destructive host feeding seems rather unlikely because host larvae are rather rare in general.

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Fig. 9: Field photographs of male 1 and male 2.

Fig. 10: Field maple flowers are used as nectar source by both sexes, 3rd of June 2021 (a) and 18th of May 2020 (b, c).

Temporal activity

In 2020, the first female and male were discovered on the same day, on the 16th of May. Because ichneumonid males hatch earlier than females, it is assumed that the flight period would have begun in early May or even earlier. The last female was seen on the 20th of May, the last male on the 25th of May.

In 2021, due to the very cold early spring, several common ichneumonid species appeared about two to three weeks later than in 2020. The two adjacent *Acer campestre* were monitored almost daily for up to several hours from late April onwards. The first individual was finally observed on the 23rd of May, but, because only two females were found in 2021, this says little about the actual flight period.

In 2020, females were mostly active before midday, while male activity frequently started at about midday. The females were not seen on the leaves during the afternoon but reappeared in the evening. On the 18th of May 2020, both sexes were still active at 8:40 p.m., at 13° C. ♂2 was found at 9:07 a.m. between *Acer campestre* leaves and was still there at 9:49 a.m. Presumably he was heating up before starting daytime activities.

On the 17th of May 2020, at about 6 p.m., ♀1 entered a place of concealment between *Acer campestre* leaves, presumably to stay there for the night.

♀1 survived a heavy shower on the underside of an *Acer campestre* twig, which was itself sheltered by leaves (Fig. 11).

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Tab. 1: Variable characters visible in field photographs

Character	Female 2 (light)	Female 3 (medium, type specimen)	Female 1 (medium dark)	Female 4 (dark)	Male 1 (light)	Male 2 (medium dark)
flagellar segments	36/36	35/35	33/33	35/35	36/36	34/34
dark stripe on scapus	thin	medium	broad	very broad	very thin	very thin
frons	yellow	yellow	black: 2 longitudinal stripes	black	yellow	yellow
temple	yellow	yellow	mostly yellow	black	yellow	yellow
mesoscutum: longitudinal stripes on anterior half	separated, very small	separated	confluent	confluent, also with lateral stripes	separated	confluent
mesoscutum: lateral stripes and median posterior mark	separated, posterior mark triangular	confluent	confluent	confluent, extended	separated, posterior mark triangular	confluent
mesopleuron	yellow	yellow	yellow	yellow with large black C-mark	yellow	yellow
propodeum	yellow	yellow	yellow	black	yellow	yellow
tergite 1: black colouration in dorsal view	only anterior patch	anterior and central patch separated	anterior and central patch confluent, extended	anterior and central patch confluent, extended	anterior and central patch separated	anterior and central patch separated

Inter- and intrasexual interactions

On the 18th of May 2020, ♀2 was observed approaching ♀1 and then moving towards her, although apparently unable to see her. Finally, she held her wings up and walked straight to her (Fig. 12), to finally jump on her and fly off. This happened very fast, so more detailed observations were not possible. It is assumed that chemical communication was responsible for the observed behaviour.

When apparently searching for mates, males were noticed to land on *A. campestre* leaves and take off after one to a few seconds, depending on temperature. At a relatively high temperature, about 18° C, they hardly landed at all. When a male arrived at a place where a female had stayed recently, the region was searched more intensively. On the 18th of May 2020, ♀1 and ♂2 were found in the morning, only 10 cm away from each other, on *Urtica dioica* leaves amongst the lowest *A. campestre* leaves, where they are thought to have spent the night. ♀1 spent almost the whole day on these *Urtica dioica* plants. A few *A. campestre* leaves which she had visited for a short time were intensively searched by the male, and even the surrounding *Urtica* leaves were investigated. Again, although the male was only 10 cm away from the female for some time, he seemed unable to detect her. Perhaps the female had already been fertilised and thus her olfactory attraction was rather low, suggesting that chemicals also play a role in mate finding.

Additionally, ♂1 was observed flying directly onto the fallen bud scales (Fig. 13 c-d), which were frequently lying on the leaves in May. These somewhat resem-

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Fig. 11: Female hiding from heavy rain, 18th of May 2020.

ble the wasps in shape, size and colour. It is unclear whether he was mistaking the bud scale for a potential competitor or a female, but it suggests that vision plays a role in intraspecific interaction. Additionally, also ♀1 was seen sitting on a bud scale in one case (Fig. 13 a-b).

Mimesis theory

Males and females were observed sitting for hours on the *A. campestre* leaves during the morning, completely exposed, but not reacting to any close movements of the author's hand. One female showed this behaviour also in the afternoon. The rough resemblance of the bud scales' colour (Fig. 13, 14) suggests mimesis, which is a plausible explanation for the unusual colouration of the species.

Interspecific interactions

Apart from host searching, only a few interspecific interactions were observed.

♂1 was seen flying into the web of *Metellina mengei* (Araneae: Tetragnathidae) but was able to free himself in time.

♂2 (once) and ♀1 (twice) were seen fleeing from a *Myrmica* (Hymenoptera: Formicidae) worker that was foraging on the same leaf, after being contacted.

♀1 was seen fleeing from *Anthocoris nemorum* (Hemiptera: Anthocoridae) (after being contacted) but not reacting significantly to either a hybotid or a micropezid fly that were both foraging on the same leaf (but not making contact).

Host searching behaviour

On the 20th of May 2020, before midday, the host searching behaviour of one female was monitored: A group of about 20 leaves was intensively searched for several minutes, before switching to another group. It seemed that the female was not able to remember which group she had investigated, because she frequently returned to groups that had already been searched. Hence, the same leaves were frequently searched several times. Other regions of the branches, on the other hand, were completely ignored, including some containing host larvae. It seemed that the larvae had to be detected by direct contact, because they were not found when the female was searching on a neighbouring twig. In the evening, searching was less thorough – the female was flying from twig to twig quickly and searching on foot for only a short time.

In 2021, the searching behaviour of another female was monitored: On the 1st of June, from 4.33 to 6.21 p.m.

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Fig. 12: Female 2 right before attacking female 1, 18th of May 2020.

(21° C, dull), a female was flying from leaf to leaf, running around for a few seconds and then taking off again. In that manner, she searched a large part of the tree. After investigating several neighbouring leaves, she sometimes flew a larger sweep, presumably in order to avoid searching the same leaves repeatedly. She flew very fast and thus was not easy to track. Rests for grooming lasted only a few seconds.

On several occasions, a searching female was seen to leave the *A. campestre* area southwards or northwards, following a hedgerow, or eastwards, down the earth bank. They continued to land on leaves but almost always came back to the *A. campestre* after a short time, whichever direction they had flown off. The neighbouring plants in the hedgerow were *Carpinus betulae* and *Quercus robur* southwards and *Corylus avellana* northwards. The herbs to the east were mainly *Urtica dioica* and *Aegopodium podagraria*. The females were apparently not interested in the other nearby plants.

Oviposition and host

On the 19th of May 2020, oviposition of ♀1 was observed. Having detected a host, a solitary free-living early instar sawfly larva, the female immediately attacked it from above, with her metasoma downcurved in typical ctenopelmatine manner. This took only a few seconds, then the female withdrew, rested for another few seconds on an adjacent leaf and flew off. The attacked larva was examined by torchlight in situ and an egg was visible inside, reaching from the apical part of the third thoracical segment to the end of the second abdominal segment (Fig. 16 a). There was a drop of leaked haemolymph dorsally on the second thoracical segment (Fig. 16 b), showing the oviposition site.

On the 3rd of June 2021, another attack was observed, by ♀4. After having found a host larva, the female contacted it with her ovipositor for only a very short time (Fig. 15) and then left the scene. As in 2020, the attacked larva was examined by torchlight in situ and, again, an egg was visible inside, reaching from the base of the fifth abdominal segment to the second quarter of the sixth abdominal segment (Fig. 16 d). There was a drop of haemolymph lateroventrally on the fifth abdominal segment (Fig. 16 c).

The host larvae belong to the *Pristiphora depressa* group (Hymenoptera: Tenthredinidae: Nematinae) which is restricted to *Acer* (Liston & Prous 2020). Two species are known or believed to feed on *A. campestre*: *P. depressa* (Hartig, 1840), which was seen ovipositing into a leaf of the very same tree on the 28th of May 2021

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Fig. 13: Female (c, d) and male (a, b) on fallen bud scales, 18th–19th of May 2020.

Fig. 14: Female resembling the fallen bud scales, 18th–19th of May 2020.

(Fig. 17), and *P. subbifida* (Thomson, 1871). Both species are thought to be univoltine and probably reproduce parthenogenetically because males are unknown (Prous et al. 2017). Whether the present *Campodorus* species attacks both species has yet to be proven through rearing or barcoding parasitised larvae. Neither species is reported as a host to any ichneumonoid or chalcidoid wasp so far (Yu et al. 2016).

Potential Distribution

It is unlikely that the present species is restricted to the north of Central Europe and it is probably fairly widespread, possibly as widespread as its host(s).

Pristiphora depressa has a Western Palaearctic distribution. It is widespread across Europe but currently known only from seven countries (Taeger et al. 2018) due to its confusion with *P. subbifida* in the past (Liston et al.

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Fig. 15: Female ovipositing into early instar larva of *Pristiphora depressa* group, 3rd of June 2021.

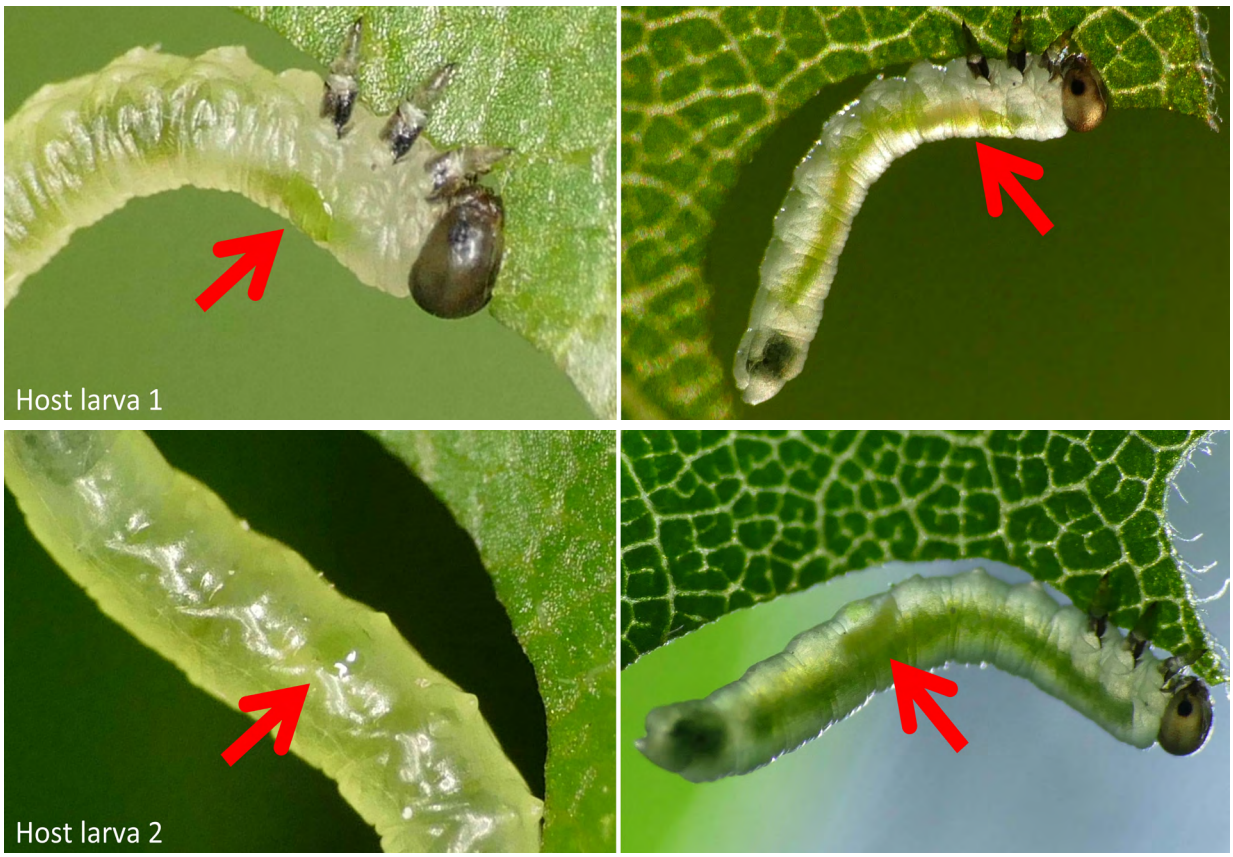

Fig. 16: Larvae of *Pristiphora depressa* group with leaked haemolymph (a, c) and eggs visible inside (b, d), 19th of May 2020 (a, b) and 3rd of June 2021 (c, d).

2019). It is thought to feed on *A. campestre* (Liston et al. 2019), although this has not yet been proven, nor is it known if it uses any other *Acer* species.

Pristiphora subbifida is known to be even more widespread, covering most of Europe and occurring also in the northeastern part of Asian Russia (Popov 2011). It is reported to be adventive in the USA and Canada (Smith 2016; Smith et al. 2018), thus being practically Holarctic. In Europe, *P. subbifida* was thought to feed monophagously on *A. campestre* (Liston & Späth 2008) until Stankevičienė and Šabūnaitė (2016) reported the larvae feeding on *A. mono*, *A. negundo* and surprisingly also on *A. pseudoplatanus*, *A. pseudoplatanus* 'Afropurpureum' and *A. platanoides* 'Globosum' in the Kaunas Botanical Garden of Vytautas Magnus University, Lithuania.

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Fig. 17: *Pristiphora depressa* (Hartig, 1840) (Tenthedinidae) ovipositing into *Acer campestre* leaf, 28th of May 2021.

5. Conclusions and prospects

The reason for the late description of this conspicuous *Campodorus* species is believed to lie in its presumed temporal and ecological restriction. Presumably, and despite the plant's attractiveness to ichneumonids, there have simply been no ichneumonidologists collecting extensively on or around *A. campestre* in May. This suggests that there may be more highly specialised tree-dwelling ctenopelmatine species awaiting discovery in Europe.

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