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An interactive key to the European genera of Campopleginae (Hymenoptera, Ichneumonidae) and 20 new species for Sweden

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Darwin wasps of the subfamily Campopleginae are among the most poorly studied insect groups, which is to a large part due to inadequate identification tools. The currently 835 European species are classified into 42 genera, some of a somewhat unclear delimitation, and are very hard to identify using the incomplete, scattered and often poorly illustrated literature. We here assess different character systems for genus identification and provide an interactive, dynamic online key to the European genera. We apply this key to identify 3,500 specimens of the Swedish Malaise Trap Project to genus level. We then chose ten comparatively small genera for species-level identification, reporting a total of 37 species, 20 of which are new records for Sweden. The large number of species only found in a single trap location indicates that a lot remains to be discovered, even in an otherwise well-known fauna such as Sweden's.

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Our grasp of biodiversity is severely biased, to a point where the vast majority of our knowledge of ecology, behaviour, genetics, and conservation needs stems from just a tiny fraction of the tree of life (Zuk et al. 2014). Large biodiversity inventories in Sweden and Canada, based on morphological identification and on DNA barcoding, respectively, both found that the most severely understudied taxa are Diptera and parasitoid Hymenoptera (Hebert et al. 2016, Ronquist et al. 2020). Why are some taxonomic groups so much less studied than others? Some of the characteristics behind these biases are rather obvious: larger species are much better studied, as are more colourful ones, or those that live in close association with humans or that profit us economically.

Finally, the usefulness as model systems in ecological or evolutionary research can increase the popularity of a group, as exemplified by dung flies in sexual selection research (Parker 2001), ants as models for eusociality (Wilson & Hölldobler 2005), and flour beetles and *Drosophila* Fallén for genetics and developmental biology (Lynch et al. 2011).

None of these criteria can explain the scarcity of studies on Darwin wasps (Hymenoptera, Ichneumonidae) (Klopfstein et al. 2019). The members of this largest of all hymenopteran families are among the bigger hymenopterans and can be very colourful. They are abundant nearly everywhere, including in urban areas. And they deliver invaluable ecosystem services by regulating pest insects in agriculture and forestry. Nevertheless, the more than 25,000 described species (Yu et al. 2016) probably represent only a quarter of their true diversity, and with little more than two dozen researchers, the number of taxonomists working on this vast diversity is far from adequate (Klopfstein et al. 2019). A plethora of interesting questions pertaining to speciation (Feder & Forbes 2010), host-parasitoid co-evolution (Santos et al. 2022, Tschopp et al. 2013), and courtship behaviour and sexual selection (Steiner et al. 2010) thus remain virtually untapped. The main reasons for this neglect are probably historical and related to the continued low accessibility of the group. While recognition that a specimen is an ichneumonid is very easy due to the unique and rather uniform fore wing venation, sorting specimens into the 42 extant subfamilies can prove a formidable task (even though this was recently eased by a well-illustrated key for the Western Palaearctic: Broad et al. 2018). Once the correct subfamily has been identified, reliable keys to the genus or even species level can then be hard to come by even for well-known faunas such as the European one, and most keys that exist are incomplete or poorly illustrated (but see, e.g., Bennett 2015, Broad & Shaw 2016, Johansson 2021, Klopfstein 2014). Many entomologists, although starting to tackle this interesting group with great initial enthusiasm, later become discouraged by the sheer difficulty of the family.

Campopleginae are among the most difficult subfamilies of Darwin wasps, both in terms of genus and species identification, and are probably only surpassed in this respect by Phygadeuontinae (Broad et al. 2018). The main reason is their large diversity, combined with several vague and uncertain genus boundaries. There are currently 835 species known from Europe (Supplementary File S1) (Haraldseide 2021, Riedel 2017, 2018, Yu et al. 2016). Many additional species can be expected once all larger genera are subjected to a profound revision. The seminal work by Henry Townes, who provided genus-level keys for all subfamilies of Darwin wasps except Ichneumoninae and Hybrizontinae, is no exception there – it only features what he called "our best effort for the present" for Campopleginae, noting that "some of the genera themselves are somewhat arbitrary" (Townes 1970). Indeed, usage of his keys requires a lot of experience and the availability of a good reference collection, and several of his genus circumscriptions were later revised considerably. Nevertheless, his remains the only genus-level key currently available for the European fauna. Wahl (1991) suggested informal genus groups based on limited character evidence and on assumed character polarities, although he did not include any formal phylogenetic analysis and these concepts were never formally tested. The only molecular data currently available that includes at least a minimal taxon sampling consists of 28S rRNA and is rather inconclusive (Quicke et al. 2009). Jacques F. Aubert described 114 new species or subspecies in this subfamily, most of them still valid (e.g., Aubert 1960, 1964, 1972, Aubert 1974), but was also struggling to come up with robust generic limits. Klaus Horstmann around the same time made huge progress at sharpening generic definitions, partly by putting less emphasis on highly homoplastic characters such as ovipositor length, partly by erecting monotypic genera for some taxa that are isolated morphologically and thus previously obscured the limits of larger genera (Horstmann 1970, 1978, 1987a, 2004). However, he still perceived the generic classification as inadequate, stating that many genera as they are currently defined would likely turn out as para- or even polyphyletic, especially in the group including *Olesicampe* Förster, 1869, *Diadegma* Förster, 1869 and *Hyposoter* Förster, 1869 (Horstmann 2004). He went on to describe more than 240 species in this subfamily, 127 of them from Europe (Horstmann 1971, 1973b, 1980a, b, 1985, 1987b, 1993, 2008, Shaw et al. 2016). Besides most of the smaller genera, Horstmann also early on tackled one of the five largest genera, *Diadegma*, which currently includes 128 species in Europe, 39 of which were described by him (Horstmann 1969, 1973a, 1992, Horstmann & Shaw 1984, Shaw et al. 2016). And he picked up another one of the big five after Rudolf Hinz' death, completing a comprehensive revision of the Palaearctic *Dusona* Cameron, 1901 species (Hinz & Horstmann 2004, Horstmann 2009). His efforts now leave only *Campoplex* Gravenhorst, 1829, *Hyposoter* and *Olesicampe* as large, mostly unrevised genera. After Horstmanns untimely death, his well-sorted collection still harbours many unpublished insights in various genera and provided the basis for much recent and ongoing taxonomic work in the subfamily (di Giovanni et al. 2021, Riedel 2017, 2018).

The somewhat unstable genus-level taxonomy makes it difficult to start working on this subfamily, and species-level revisions especially of larger genera are only feasible if their circumscription is sufficiently stable, unless one would take over the immense task of revising all species of the subfamily in a particular region in one go. Given the often homoplastic morphology of the group, molecular data is essential to firmly delimit genera and put them on a scientific basis; however, coming up with an adequate taxon set for a phylogenetic study requires targeted sampling, which in turn is only facilitated by at least repeatable working hypotheses of the genera involved.

We here aim to alleviate these issues by embracing a digital tool for genus identification and allowing it to remain dynamic in order to incorporate future insights into the taxonomy and phylogeny of the group (Edwards & Morse 1995). The identification key proposed here is interactive, allowing the user to choose the order in which characters are addressed, which better accounts for the substantial intrageneric variability of most characters than any dichotomous key could (Kerner et al. 2021). Keeping the key online allows us to continuously update it when additional information becomes available, be it on the variability of certain morphological characters within one genus or on the generic limits altogether. We implement a feedback system to involve in its ongoing improvement the growing community of professional and amateur entomologists that use the key. This is especially important as the key currently is focused on species occurring in Sweden, but should in the future cover all the campoplegine diversity in Europe. All characters and their states in the key are illustrated by numerous photographs, and an online repository of species portraits shows the intergeneric diversity and allows checking of identification success. We hope that these tools help to speed up our ways of collecting taxonomic and faunistic information on this poorly known subfamily. We illustrate their application by identifying extensive material collected by the Swedish Malaise Trap Project (SMTP) (Karlsson et al. 2020) to genus and reporting 37 species of ten of the smaller genera, 20 of which are new records for the country.

Materials and methods

We obtained more than 50 vials with Campopleginae specimens kept in 95% ethanol from SMTP, which contained about 5,800 specimens. We dry-mounted all females and about a third of the males, resulting in roughly 3,500 specimens which were later sorted to genus (see below). In addition, we studied extensive reference material, mostly identified by Klaus Horstmann or Jacques F. Aubert, from the following institutions: Zoologische Staatssammlung München, Germany (ZSM); Musée cantonal de Zoologie, Lausanne, Switzerland (MZL); Naturhistoriska riksmuseet, Stockholm, Sweden (NHRS), Naturhistorisches Museum Bern and Basel, Switzerland (NMBE and NMBA, respectively). For the time being, we did not study any of the historical collections in Sweden in much detail, with the exception of some genera in Stockholm, as this was outside of the scope of this project. However, it would certainly be a worthwile undertaking, as it would allow comparing current and past diversity of the group.

We studied previously published keys and genus descriptions to extract useful characters and their states for genus identification (Horstmann 1970, 1978, 1987a, 2004, Townes 1970). Additionally, we tested characters used in two unpublished, draft dichotomous keys generated earlier by two of us (GRB and HH). We then used the Xper3 platform (Kerner et al. 2021) to set up an interactive key to genera, often treating species groups within some genera separately if they reflected significant morphological variation. The key and this publication follows the morphological terminology outlined in Broad et al. (2018), although we make reference to some often-used terms from Townes' system (Townes 1969).

Photographs of at least one female per genus were taken using the Keyence VHX 6000 photosystem, making use of both stacking and stitching techniques. We combined a habitus image with detailed views of the face, propodeum, mesopleuron, first tergite, wings, hind tibia and ovipositor into standard plates that allow checking identification success and deposited them under a Creative Commons 4.0 license on the Zenodo repository (https://zenodo.org), where they obtained a permanent Digital Object Identifier (DOI).

Ten genera from the SMTP material were subjected to species-level identification, two of which are monotypic, and the other eight were identified using published keys: *Callidora* Förster, 1869 (species identified using Tigner 1969), *Casinaria* Holmgren, 1859 (Riedel 2018), *Enytus* Cameron, 1905 (Horstmann 1973a), *Eriborus* Förster, 1869 (Horstmann 1987b), *Gonotypus* Förster, 1869, *Lemophagus* Townes, 1965 (Horstmann 2004), *Leptocampoplex* Horstmann,

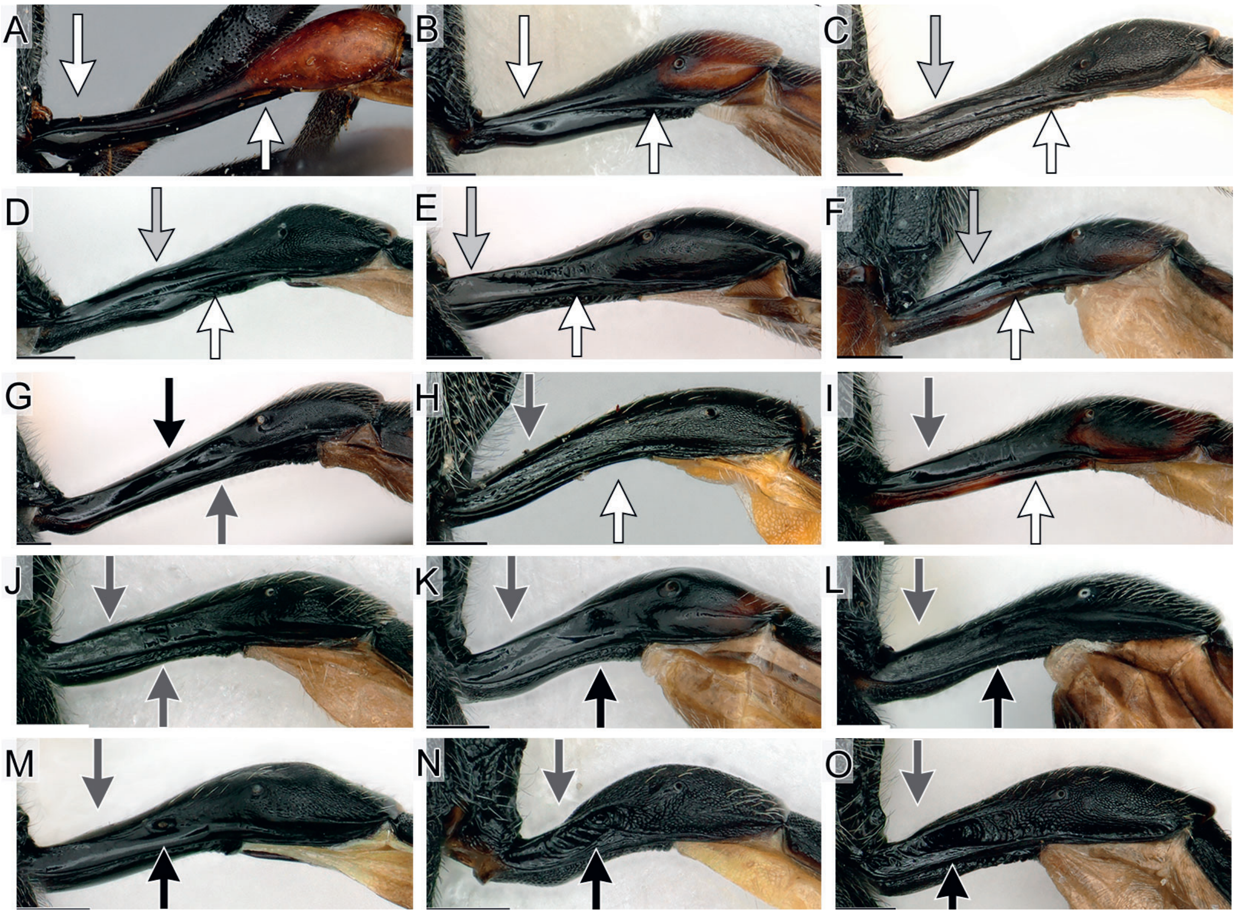


Figure 1. Variation in sternite height and glymma on first metasomal segment in 15 species; – A) *Charops cantator*; – B) *Casinaria petiolaris*; – C) *Campoplex* cf. *tibialis*; – D) *Callidora albovincta*; – E) *Sinophorus turionum*; – F) *Phobocampe bicingulata*; – G) *Dusona blanda*; – H) *Bathyplectes immolator*; – I) *Olesicampe patellana*; – J) *Hyposoter discedens*; – K) *Diadegma crassicorne*; – L) *Echthronomas quadrinotata*; – M) *Diadegma fenestrale*; – N) *Meloboris alternans*; – O) *Pyracmon sepiellus*. The arrows indicate the character states of the two characters; see main text for details. Scale bars indicate 0.2 mm.

Figur 1. Variation i sternithöjd och glymma på första bakkroppsegmentet hos 15 arter; – A) *Charops cantator*; – B) *Casinaria petiolaris*; – C) *Campoplex* cf. *tibialis*; – D) *Callidora albovincta*; – E) *Sinophorus turionum*; – F) *Phobocampe bicingulata*; – G) *Dusona blanda*; – H) *Bathyplectes immolator*; – I) *Olesicampe patellana*; – J) *Hyposoter discedens*; – K) *Diadegma crassicorne*; – L) *Echthronomas quadrinotata*; – M) *Diadegma fenestrale*; – N) *Meloboris alternans*; – O) *Pyracmon sepiellus*. Pilarna visar karaktärsalternativen till de två karaktärerna; se text för detaljer. Skalstreck 0.2 mm.

1970, *Meloboris* Holmgren, 1859 (*Nepiera* Förster, 1869) (Haraldseide 2021), and *Tranosemella* Horstmann, 1978 (Horstmann 1978). To obtain previously published faunistic data for these genera for Sweden, we queried Taxapad (Yu et al. 2016) and, especially for newer records for Sweden, the Artfakta database of Artportalen.

Results

Character assessment

Examining the diversity and distribution of characters regularly used in previous identification keys, we found that most of them are difficult to apply, both because some of their states overlap and thus are difficult to communicate properly and because of high intrageneric variability in part of the genera. Indeed, none of the characters used are constant within all of the genera, and any dichotomous keys thus need to key out multiple genera multiple times. Table 1 summarizes the distribution of some often-used characters in the European genera. The listed characters and their states are as follows (also see explanations in the following paragraphs): Position of suture between first sternite and tergite viewed from laterally (see also Fig. 1): below – at – above middle. Glymma on first tergite (see also Fig. 1): absent – shallow – deep. Fore wing areolet: open – closed, pentagonal – quadrate – petiolate. Hind wing vein 1Cu and cu-a (nervellus; see also Fig. 2): angled where 2Cu would intercept (often called “broken” in the literature) – weakly bowed – straight. Bow in vein M + Cu (see also Fig. 2): weak – moderately – strongly bowed, closer – more distant than length of nervellus from vein 1Cu. Ovipositor length: shorter than 0.4 times hind tibia – between 0.4 – 1.1 times hind tibia – longer than 1.1 times hind tibia. Width of clypeus and shape of its margin (see also Fig. 3): narrow – moderate – wide, straight – convex – triangular.

Despite the inconsistencies observed in many genera, we found several characters to be very useful for the delimitation at least some of the genera, and we discuss and illustrate them below. Examining the character variation also facilitates the use of the interactive key, which is introduced in a later section.

Height of first sternite and cross-section of petiole (Fig. 1). The height of the first sternite compared to its tergite in lateral view, combined with the shape of the cross-section of the petiole at about a third of its length, was used by Townes to split the subfamily as it is currently understood into the two tribes Campoplegini and Porizontini (Townes 1970), although these were later abandoned. In his interpretation, Campoplegini were defined by the suture between sternite and tergite lying at or above the middle, in combination with a circular or oval cross-section, with an exception being made for *Sinophorus* Förster, 1869 which, because of often pronounced lateral fields, rather shows a prismatic cross-section. We found that the position of the suture is consistently above the middle in lateral view in *Casinaria* and *Charops* Holmgren, 1859, but around the middle in most species of *Campoplex* and often even clearly below the middle in *Sinophorus* (Figs 1a–c, e). Furthermore, at least some species of several other genera not associated by Townes with Campoplegini, such as *Callidora* Förster, 1869 and *Phobocampe* Förster, 1869 (Figs 1d, f), are very similar to *Campoplex* in this respect. In other genera, such as *Diadegma*, *Hyposoter*, *Olesicampe* and related genera and even in *Bathyplectes* Förster, 1869 and *Nemeritis* Holmgren, 1860 (Figs 1h–o), it is again clearly below the middle and the cross-section clearly rectangular or trapezoidal. While useful when clear, these characters can be unreliable for genera with intermediate representatives. Figure 1 gives a detailed account of this character and its states, as follows: left arrow, white: sternite higher than tergite, suture above middle; light grey: sternite about as high as tergite, suture around middle; dark grey: sternite clearly lower than tergite, suture distinctly below middle; black: sternite fused to tergite, thus no suture visible except at base and sometimes apex.

Glymma and lateral fields on first tergite (Fig. 1). It remains to be demonstrated whether all the pit-like depressions laterally on tergite 1 in Campopleginae are indeed homologous with the glymma found in other ichneumonid subfamilies, but we here follow this assumption and thus the terminology in Broad et al. (2018). The presence or absence of a glymma is an often-used character to define and key genera in Campopleginae, even though intrageneric and rarely even intraspecific variation and the presence of intermediate forms has been noted repeatedly (Horstmann 1970, 2004, Townes 1970).

Table 1. Overview of character states found in the European genera of Campopleginae. The number of currently known European species is indicated, along with the preliminary assignment to a genus group. Characters and their state are explained in the main text, with dashes separating different states of one character and commas different characters. Character states given in brackets are especially rare within a genus. [1]This state only occurs in species of small body size.

Tabell 1. Översikt över karaktärsalternativen i europeiska släkten av Campopleginae. Antalet för närvarande kända europeiska arter anges, tillsammans med den preliminära tilldelningen till en släktgrupp. Karaktärer och deras tillstånd förklaras i huvudtexten, med streck som skiljer olika tillstånd av en karaktär och kommatecken olika karaktärer. Karaktärer som anges inom parentes är särskilt sällsynta inom ett släkte. [1]Denna karaktär förekommer endast hos arter med liten kroppsstorlek.

Genus	#species	Genus group	Sternite suture	Glymma	Areolet	Vein 1Cu and cu-a	Bow in vein M + Cu	Ovipositor	Clypeus
Alcima	1	*Diadegma*	below	absent – shallow	closed, petiolate	weakly bowed	weak, distant from 1Cu	short	narrow – moderate, convex
Bathyplectes	23	*Nemeritis*	below	absent	closed, pentagonal – quadrate – petiolate	angled	moderate, close to 1Cu	short – medium	wide, convex – triangular
Benjaminia	4	*Diadegma*	below	shallow – deep	open	straight – weakly bowed	weak, distant from 1Cu	short	narrow – moderate, convex
Callidora	2	unplaced	below – at middle	absent – shallow	closed, petiolate	weakly bowed – angled	weak, close to 1Cu	short	moderate – wide, convex
Campoletis	40	*Tranosema*	below	deep	closed, petiolate	angled	weak – moderate, close to 1Cu	medium – long	moderate – wide, with median tooth or lamella
Campoplex	122	*Campoplex*	(below) – at – above	absent	closed, quadrate –petiolate	angled	moderate, close to 1Cu	short – long	moderate – wide, straight – convex
Casinaria	31	*Campoplex*	above	absent	closed, quadrate –petiolate	straight – bowed – angled	weak – moderate, close to 1Cu	short	narrow – wide, straight – convex
Charops	1	*Campoplex*	above	absent	open	bowed – angled	weak, distant from 1Cu	short	moderate – wide, straight – convex
Chromoplex	1	*Diadegma*	below	shallow – deep	closed, quadrate –petiolate	straight (– bowed)	weak – moderate, distant from 1Cu	medium – long	moderate – wide, convex
Clypeoplex	1	*Nemeritis*	below	absent	closed, petiolate	straight – bowed – angled	moderate – strong, close to 1Cu	medium	narrow – moderate, convex
Cymodusa	16	*Nemeritis*	below	absent	open – closed, quadrate – petiolate	straight – bowed – angled	weak – moderate, close to 1Cu	medium	narrow – moderate, convex
Diadegma	128	*Diadegma*	below	shallow – deep	open[1] – closed, quadrate – petiolate	straight – bowed	weak – moderate, close[1] – distant from 1Cu	short – long	narrow – wide, straight – convex

Dolophron	2	*Tranosema*	below – at middle	shallow – deep	closed, quadrate	angled	moderate, close to 1Cu	medium	moderate – wide, straight
Dusona	120	unplaced	below (if visible)	absent – shallow	closed, quadrate –petiolate	bowed – angled	weak – moderate, close – distant from 1Cu	short – medium	moderate – wide, straight – convex
Echthronomas	4	*Diadegma*	below	deep	closed, quadrate –petiolate	straight	moderate, distant from 1Cu	short	narrow – moderate, convex
Enytus	8	*Diadegma*	below	shallow – deep	open	straight – bowed	moderate, distant from 1Cu	medium	wide, straight – convex
Eriborus	8	*Diadegma*	below	deep	open	straight – bowed	weak – moderate, distant from 1Cu	short	narrow – moderate, convex
Gonotypus	1	*Tranosema*	below – at middle	shallow – deep	open	angled	moderate – strong, close to 1Cu	short	narrow, straight
Hyposoter	62	*Diadegma*	below	shallow – deep	(open –) closed, quadrate – petiolate	straight – bowed	weak – moderate, distant from 1Cu	short	narrow – moderate, convex
Lathroplex	2	*Nemeritis*	below – at middle	absent	closed, pentagonal – quadrate	angled	moderate – strong, close to 1Cu	short - medium	narrow, straight – convex
Lathrostizus	13	*Diadegma*	below	deep	closed, petiolate	straight – bowed	weak – moderate, close to 1Cu	medium – long	wide, straight
Lemophagus	5	*Diadegma*	below	shallow – deep	closed, pentagonal – quadrate – petiolate	straight – bowed	weak – moderate, close to 1Cu	short	wide, straight
Leptocampoplex	1	unplaced	below – at middle	shallow – deep	open	straight – bowed – angled	moderate – strong, close to 1Cu	long	moderate – wide, straight – convex
Leptoperilissus	3	*Nemeritis*	below	absent	closed, pentagonal	straight – bowed – angled	moderate – strong, close to 1Cu	short	wide, straight – convex
Macrulus	1	unplaced	below – at middle	shallow – deep	closed, petiolate	angled	weak – moderate, close to – distant from 1Cu	long	moderate, convex
Macrus	2	unplaced	below	(shallow –) deep	closed, pentagonal – quadrate	straight – bowed – angled	weak – moderate, close to – distant from 1Cu	short - medium	moderate – wide, convex
Melanoplex	1	*Tranosema*	below – at middle	(shallow –) deep	closed, quadrate (– petiolate)	angled	moderate – strong, close to 1Cu	long	moderate – wide, convex
Meloboris (Meloboris)	5	unplaced	below	deep	closed, quadrate	straight	strong, close to 1Cu	short	narrow, straight
Meloboris (Nepiera)	7	unplaced	below – at middle	absent – shallow	closed, pentagonal – quadrate – petiolate	angled	strong, close to 1Cu	short	moderate, straight

Nemeritis	30	*Nemeritis*	below – at middle	absent	(open –) closed, quadrate – petiolate	angled	moderate – strong, close to 1Cu	medium – long	moderate – wide, straight – convex
Nepiesta	8	*Nemeritis*	below	absent	open	angled	moderate – strong, close to 1Cu	short	wide, convex – triangular
Olesicampe	87	*Diadegma*	below	absent – deep	closed, pentagonal – quadrate – petiolate	straight – bowed	weak – moderate, distant from 1Cu	short	wide, straight – weakly convex
Phobocampe	21	unplaced	below – at middle	absent – deep	closed, quadrate – petiolate	bowed – angled	moderate – strong, close to 1Cu	short	narrow – moderate, straight – weakly convex
Porizon	6	*Campoplex*	(below –) at middle	absent	open	angled	moderate – strong, close to 1Cu	medium – long	narrow – moderate, straight – weakly convex
Pyracmon	3	*Tranosema*	below	deep	closed, pentagonal – quadrate – petiolate	angled	moderate – strong, close to 1Cu	medium – long	moderate – wide, convex – triangular
Rhimphoctona	11	*Tranosema*	below	deep	closed, pentagonal	angled	moderate, close to or distant from 1Cu	medium – long	moderate – wide, convex – triangular
Scirtetes	1	*Tranosema*	below	shallow – deep	closed, quadrate – petiolate	angled	weak – mongderate, close to or distant from 1Cu	long	moderate – wide, straight
Sesioplex	3	*Campoplex*	(below –) at middle	absent	closed, petiolate	angled	moderate – strong, close to 1Cu	long	narrow – moderate, convex
Sinophorus	29	*Campoplex*	below – at middle	absent	closed, quadrate – petiolate	bowed – angled	weak – moderate, close to or distant from 1Cu	medium – long	moderate – wide, straight – convex
Synetaeris	2	*Tranosema*	below	shallow – deep	closed, petiolate	angled	moderate – strong, close to 1Cu	medium (– long)	moderate – wide, convex
Tranosema	10	*Tranosema*	below	shallow – deep	closed, quadrate – petiolate	straight – bowed – angled	weak – moderate – strong, close to 1Cu	medium – long	moderate, straight – weakly convex
Tranosemella	4	*Diadegma*	below	deep	closed, quadrate – petiolate	straight – bowed	weak – moderate, close to or distant from 1Cu	medium	moderate – wide, straight – weakly convex
Venturia	5	*Campoplex*	at middle	absent	closed, quadrate – petiolate	angled	weak – moderate, close to 1Cu	long	moderate – wide, weakly to strongly convex

The glymma can lie close to the spiracle (e.g., Fig. 1G) or closer to the base of the tergite (e.g., Fig. 1O), and it can consist of a vague and very shallow impression (Fig. 1J) or of a well-defined, moderately deep to deep pit (Figs 1K–O). While very useful in some genera where it is always present and that are otherwise quite variable, such as *Diadegma* and *Hyposoter*, the whole range of completely absent to weakly indicated to distinct and moderately deep can be observed in closely related genera, such as within *Olesicampe*. In some genera, especially the ones combined in the tribe Campoplegini by Townes (1970), there is never even a trace of a glymma; however, there can be longitudinal impressions or lateral, differently sculptured fields that might be confused with a shallow glymma (Fig. 1E). Figure 1 gives a detailed account of this character and its states, as follows: right arrow, white: without glymma, but often with a lateral field or longitudinal impression; grey: with weak indication of glymma in the form of a shallow and indistinct impression; black: with glymma developed as a shallow or deep, but always distinct cavity laterally on tergite 1.

Vein 1Cu and cu-a (nervellus) and shape of subbasal cell in hind wing (Fig. 2). This is one of the character complexes featuring very prominently in most Campopleginae keys, and it is likely that it has some phylogenetic meaning at least in some of the genera. However, it is also a character responsible for a lot of confusion in the novice to campoplegine identification, as its use is somewhat unusual in other ichneumonid subfamilies. In most Campopleginae, vein 2Cu (the "discoidella" in Townes' terminology, Townes 1970) is mostly reduced and even more so at its base instead of its apex (Fig. 2A–F), so that it is only rarely connected to veins 1Cu and cu-a (Fig. 2I–L), which together form the "nervellus" in Townes' terminology. 1Cu and cu-a can still be clearly angled at the place where 2Cu would intercept (Fig. 2I–J), which is called "nervellus broken" in earlier keys. In other cases, there is no trace of an angle in the nervellus to indicate where 2Cu would meet it, although in that case, the nervellus can be entirely straight but also weakly bowed. There are many intermediate cases, with a continuum between angled and bowed, and if 2Cu would attach very low (Fig. 2G), it is typically impossible to tell whether there is in fact a bow in the nervellus or not, as it would be just above the bulla in cu-a. This is especially the case in dried specimens, where the hind wing is regularly folded along that posterior flexion line, obscuring the view.

Nevertheless, the character can be very useful in some cases, especially if combined with the shape of the subbasal cell. In a group of genera that might prove monophyletic and that consists of *Diadegma*, *Hyposoter*, *Olesicampe*, *Echthronomas* Förster, 1869, *Enytus*, *Eriborus*, *Lathrostizus* Förster, 1869, *Lemophagus*, *Tranosemella* and several extralimital genera, the nervellus is never angled and vein M + Cu is bowed some distance from where it meets 1Cu, usually more than the length of 1Cu plus cu-a (Fig. 2A–D). M + Cu thus runs nearly parallel to 1A over its apical third or even half, leading to the subbasal cell appearing rather narrow and long and its apical portion nearly parallel-sided. In the opposite expression of this character, M + Cu is bowed very close to its interception with 1Cu (Figs 2f, h, i), which leads to the subbasal cell expanding continuously until very shortly before its apex. However, there are many intermediate forms in this character, and M + Cu is often so evenly curved that the state of this character is impossible to tell (in which case the character should be skipped in the interactive key to genera; see below). It also appears to be less reliable in smaller-bodied specimens, with some small *Diadegma* and many *Lathrostizus* and so on having the bow rather close to 1cu. It is thus a useful character complex if its expression is clear, but a confusing one in intermediate forms.

Figure 2 gives a detailed account of this character and its states, as follows: Bow in vein M + Cu – left arrow, white: bow at least as far away from 1Cu as the combined length of 1Cu and cu-a (nervellus), with vein 1Cu running nearly parallel to 1A, thus subbasal cell apically narrow and more or less parallel-sided; black: bow starts closer to 1Cu than the combined length of 1Cu and cu-a, bow moderate or strong; light red arrow with question mark: state cannot be decided on. Shape of vein 1Cu and cu-a (nervellus) – right arrow, white: straight or at most weakly bowed, not angled; grey: weakly to strongly angled at level where 2Cu would intercept, but not connecting to it; black: strongly angled and connected to the often pigmented 2Cu, light red arrow with question mark: state cannot be decided on.

Clypeus shape (Fig. 3). The shape of the clypeus has maybe received too little attention in previous genus-level treatments of the subfamily, except in terms of its general width and in the few very special cases such as *Campoletis* Förster, 1869, which have a strong tooth or at least distinct lamella medially on the apical margin (Fig. 3F). Wahl (1991) suggested that the wide clypeus state, which has the outer corner distinctly lateral of the tentorial pits (Figs 3a, b, d, e), should be interpreted as the plesiomorphic condition in the subfamily, and that the narrow clypeus with the tentorial pits directly above the outer corner of the clypeus (Figs 3g–i) was apomorphic for the more derived genera within Campopleginae. This seems like a reasonable assumption, even though detailed examination shows that the differences between these supposedly distinct character states are of a continuous nature (e.g., as in Figs 3c, f). In any case, the width of the clypeus and, associated with it, length of the mandibles provide valuable characters for genus delimitation, despite some overlap. Both the width, the convexity when viewed in profile (which is equivalent to a convexity in a longitudinal section), the convexity in a transverse direction (i.e., at or a bit below the tentorial pits), and the shape of the apical margin are useful to distinguish genera of different genus groups. The sharp median tooth on the apical margin of *Campoletis* represents a unique character for that

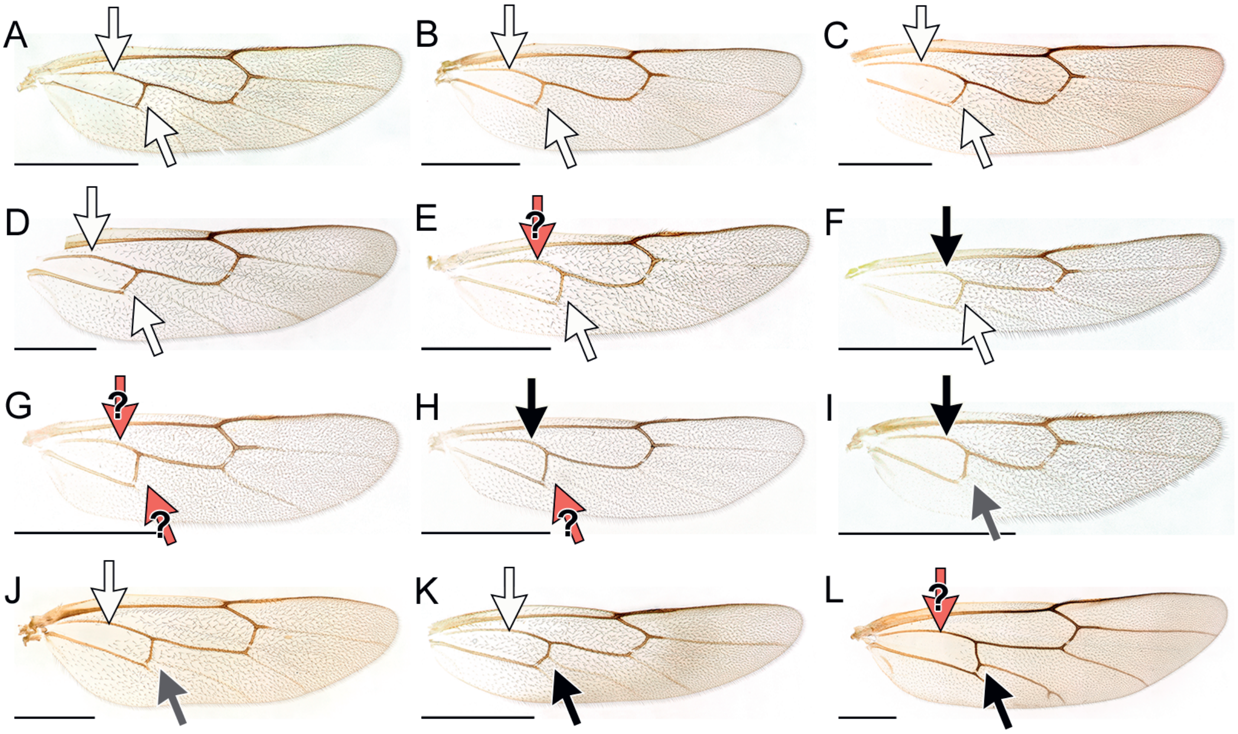


Figure 2. Variation in bow of vein M + Cu and shape of veins 1Cu and cu-a (nervellus) in 12 species; – A) *Hyposoter discedens*; – B) *Diadegma crassicorne*; – C) *Olesicampe patellana*; – D) *Echthronomas quadrinotata*; – E) *Phobocampe bicingulata*; – F) *Meloboris alternans*; – G) *Macrus parvulus*; – H) *Leptocampoplex cremastoides*; – I) *Bathyplectes anurus*; – J) *Dusona blanda*; – K) *Casinaria petiolaris*; – L) *Pyracmon sepiellus*. The arrows indicate the character states of the two characters; see main text for details. If a state cannot be determined with any certainty, as indicated here by light red arrows, then the character should be skipped in the interactive key and only picked up again if strictly necessary. Scale bars indicate 0.2 mm.

Figur 2. Variation i bågform hos vingribba M+Cu och form av vingribba 1Cu och cu-a (nervellus) hos 12 arter; – A) *Hyposoter discedens*; – B) *Diadegma crassicorne*; – C) *Olesicampe patellana*; – D) *Echthronomas quadrinotata*; – E) *Phobocampe bicingulata*; – F) *Meloboris alternans*; – G) *Macrus parvulus*; – H) *Leptocampoplex cremastoides*; – I) *Bathyplectes anurus*; – J) *Dusona blanda*; – K) *Casinaria petiolaris*; – L) *Pyracmon sepiellus*. Pilarna indikerar karaktärsalternativen för de två karaktärerna. Om ett karaktärsalternativ inte kan väljas med säkerhet, indikerad här med ljusröda pilar, så bör man bortse från karaktären i nyckeln och bara använda karaktären om det är helt nödvändigt. Skalstreck 0.2 mm.

genus, although some species have it reduced to a less distinct median lamella. The very narrow and in transverse transection strongly convex clypeus of *Lathroplex* Förster, 1869 (Fig. 3I) is the defining character of that genus. Most *Nemeritis* species have a very wide and short clypeus, different from any other genus, although this is not equally clear in all species. In the *Diadegma* group of genera (see below), the clypeus width is often the only character available to distinguish between some of the genera, with parasitoids of sawflies such as *Olesicampe* and *Lathrostizus* typically showing wider clypei.

Figure 3 shows representative examples of clypeus shapes: (a) wide, flat, with a nearly straight or slightly convex apical margin in *Nemeritis macrocentra* (Gravenhorst, 1829); (b). wide, rather flat, with a triangular apical margin in *Rhimphoctona rufocoxalis* (Clément, 1924); (c). wide, flat to a little convex in transverse section, with nearly straight to convex apical margin in *Olesicampe patellana*; (d).wide, flat, with straight to weakly convex apical margin and conspicuously smooth in *Leptoperilissus nitidus* Horstmann, 1981; (e). wide, convex in transverse section, with triangular to convex apical margin in *Bathyplectes curculionis* (Thomson, 1887); (f). moderately narrow, somewhat convex in transverse section, with apical margin with a strong median tooth in *Campoletis ensator* (Gravenhorst, 1829); (g). rather narrow, a little convex in both transverse and longitudinal section, with apical margin nearly straight in *Callidora albovincta*; (h). narrow, a little convex in transverse section and with apical margin convex in *Eriborus obscuripes* Horstmann, 1987; (i). very narrow, strongly convex in transverse section and with apical margin straight in *Lathroplex clypearis* Thomson, 1887.

Rare character states in Campopleginae (Fig. 4). Several genera or species can be recognized by a single or combination of two characters that show rare states. Colouration features prominently in this respect, as most European Campopleginae have an entirely black head, including the antennae, and metasoma, so that the few exceptions stick out. *Alcima orbitale* can easily be recognized by the yellow inner eye margins (Fig. 4A), although they might be reduced to just a short stretch around the height of the antenna; yellow inner orbits otherwise are only known from *Chromoplex picticollis* (Thomson, 1887), which has additional yellow markings on the clypeus and various parts of the mesosoma, which is also partly red-marked. The clypeus can be entirely yellow or orange with yellow markings (Figs 4b, c), which occurs in some species of *Echthronomas*, *Lathrostizus*, and *Olesicampe,* and in *Lathroplex clypearis* and *Hyposoter pallidirostris* (Schmiedeknecht, 1909). *Diadegma cinnabaritor* Aubert, 1970 has a largely orange clypeus in a dark face, but in that species, most of the mesosoma and metasoma is also entirely orange. An entirely yellow face (Fig. 4D) occurs in both sexes of *Echthronomas facialis* and in the males of some *Olesicampe* and *Rhimphoctona* Förster, 1869 and of *Tranosemella citrofrontalis* (Hedwig, 1939). White rings occur around the middle of the antennae of *Callidora albovincta* and *Casinaria affinis* Tschek, 1871, and close to the base in *Cymodusa declinator* (Gravenhorst, 1829) and *C. leucocera* (Fig. 4E).

Then there are unique characters that only occur in a single or very few genera. Most females of *Cymodusa* Holmgren, 1859 can easily be recognized by the eyes strongly converging ventrally and by the long setae on the compound eyes (Fig. 4E). The propodeal spiracle of nearly all Campopleginae is round or short-oval, at most 1.5 times higher than wide, while *Dusona* and *Charops* both have moderately to strongly elongate spiracles (Fig. 4F); the two genera can easily be told apart because the areolet is always closed in the former and open in the latter. *Charops cantator*, the only species of the genus occurring in Europe, also has the postpectal carina expanded medially into two lobes, a character otherwise only occurring in some *Lathrostizus* species (Fig. 4G). While the postpectal carina is complete in most species of Campopleginae, which is otherwise not very common in Ichneumonidae, it is broadly interrupted in front of each middle coxa in most species of the *Nepiera* subgenus of *Meloboris* (Fig. 4H), while it is interrupted medially in *Tranosema rostrale* (Brischke, 1880). *Phobocampe* is a genus that is intermediate or variable in many of the traditionally used characters and is thus notoriously difficult to cover in a dichotomous key; however, its stout body shape leads to an appearance that is rather easily memorized, although a bit difficult to pinpoint with individual measurements, which might overlap with other genera (Fig. 4I).

Figure 3. Variation in the shape of the clypeus in nine species, roughly sorted by their width; – A) *Nemeritis macrocentra*; – B) *Rhimphoctona rufocoxalis*; – C) *Olesicampe patellana*; – D) *Leptoperilissus nitidus*; – E) *Bathyplectes curculionis*; – F) *Campoletis ensator*; – G) *Callidora albovincta*; – H) *Eriborus obscuripes*; – I) *Lathroplex clypearis*. Scale bars indicate 0.2 mm.

Figure 3. Variation i formen på munskölden hos nio arter, grovt sorterade efter munsköldens bredd; – A) *Nemeritis macrocentra*; – B) *Rhimphoctona rufocoxalis*; – C) *Olesicampe patellana*; – D) *Leptoperilissus nitidus*; – E) *Bathyplectes curculionis*; – F) *Campoletis ensator*; – G) *Callidora albovincta*; – H) *Eriborus obscuripes*; – I) *Lathroplex clypearis* Skalstreck visar 0.2 mm.

It combines a very short head with strongly convergent temples and large eyes with a short pronotum, mesopleuron, propodeum, and second tergite, although the first tergite is often rather long. Also, its fore wing (Fig. 4J) has a very long 1Cu vein, typically more than 2.5 times as long as its diameter ("nervulus strongly postfurcal" in Townes's terminology, Townes 1970), and an angle between 2Cu and 1cu-a which is usually below 60°. However, there is some intrageneric and even intraspecific variability in these characters, and both aspects also occur in other genera, although rarely in combination (but see some *Casinara*, *Campoletis*, *Synetaeris heteropus* Thomson, 1887, etc.). *Rhimphoctona* is another easily recognized genus, having a nearly triangular clypeus (Fig. 3B) and a very thin ovipositor, which curves conspicuously in dried specimens (Fig. 4K). Such an ovipositor otherwise only occurs in *Nemeritis* species with a long ovipositor, from which *Rhimphoctona* species can easily be distinguished by their deep glymma, and in *Leptocampoplex cremastoides*, which has an open areolet. The ovipositor in general and especially its tip shows large variability, the functional morphology of which is in most cases not yet understood (Fig. 4L–O). *Gonotypus melanostomus* has a strongly enlarged dorsal valve (Fig. 4L), while the ovipositor of *Lathrostizus lugens* (Fig. 4M) is so strongly bowed upwards that it forms an angle with its base of about 70°. Other species never have such a strongly upcurved ovipositor, but they sometimes also show a second impression or second nodus in front of the notch common in Campopleginae, a character also seen in other genera, such as *Sesioplex* Viereck, 1912, *Tranosema hyperboreum* (Fig. 4N), *Diadegma latungulum* (Holmgren, 1887), *Porizon humili* (Horstmann, 1987), and so on. The genus *Macrus* Gravenhorst, 1829, on the other hand, shows a unique modification that is diagnostic, with the ovipositor tip abruptly becoming thin (Fig. 4O).

Genus circumscriptions

The last comprehensive genus-level revision of Campopleginae is now more than fifty years old (Townes 1970), and information about currently valid genus definitions are spread over several papers and often only available in German. We thus here outline the circumscription of each genus as it is currently understood and point to the relevant literature. We describe how its members can be diagnosed from other genera, focusing on as few characters as possible, instead of repeating all character states as listed in Table 1, and provide notes on potential confusions with or incomplete separation from other genera. A stable link is given to plates portraying one or several species of each genus that can be viewed online and are also available in Supplementary file S2. These portraits all follow the layout of the example in Figure 5, which shows *Leptocampoplex cremastoides*. If available, host data is summarized, mostly based on the extensive work by Shaw et al. (2016), and references are given to identification keys to European species.

There is currently no stable phylogeny available of the genera of Campopleginae. To nevertheless bring some order into the currently 42 genera recognized in Europe, we sort most of them into genus groups based on similarity; these might or might not turn out to be natural groups. These groups were partly taken from the literature (Townes 1970, Wahl 1991), partly based on our own assessments. Many genera remain unplaced in our ad-hoc system, and only a phylogenetic analysis with an extensive taxon sampling can finally validate some of these concepts.

Campoplex genus group

This group corresponds to the tribe Campoplegini sensu Townes (1970), with the addition of *Sesioplex*, which was only described or interpreted after its appearance. They can be differentiated from all the other genera by the shape of the first metasomal segment, where the sternite–tergite suture lies around or above the middle, the cross-section at about the basal third of the length of the tergite is circular of oval, and the postpetiole has a conspicuously roundish shape (Fig. 1A–C). There are exceptions though, especially in *Sesioplex* and *Sinophorus* (Fig. 1E), which often have the sternite–tergite suture clearly below the middle. They also tend to show distinct lateral fields on the tergite, which render the cross-section somewhat trapezoidal (Fig. 1E), although it usually becomes more rounded-oval when moving the cross-section closer to the front. And there are several extralimital genera that Townes placed in the second tribe he defined, Porizontini, which also have a high

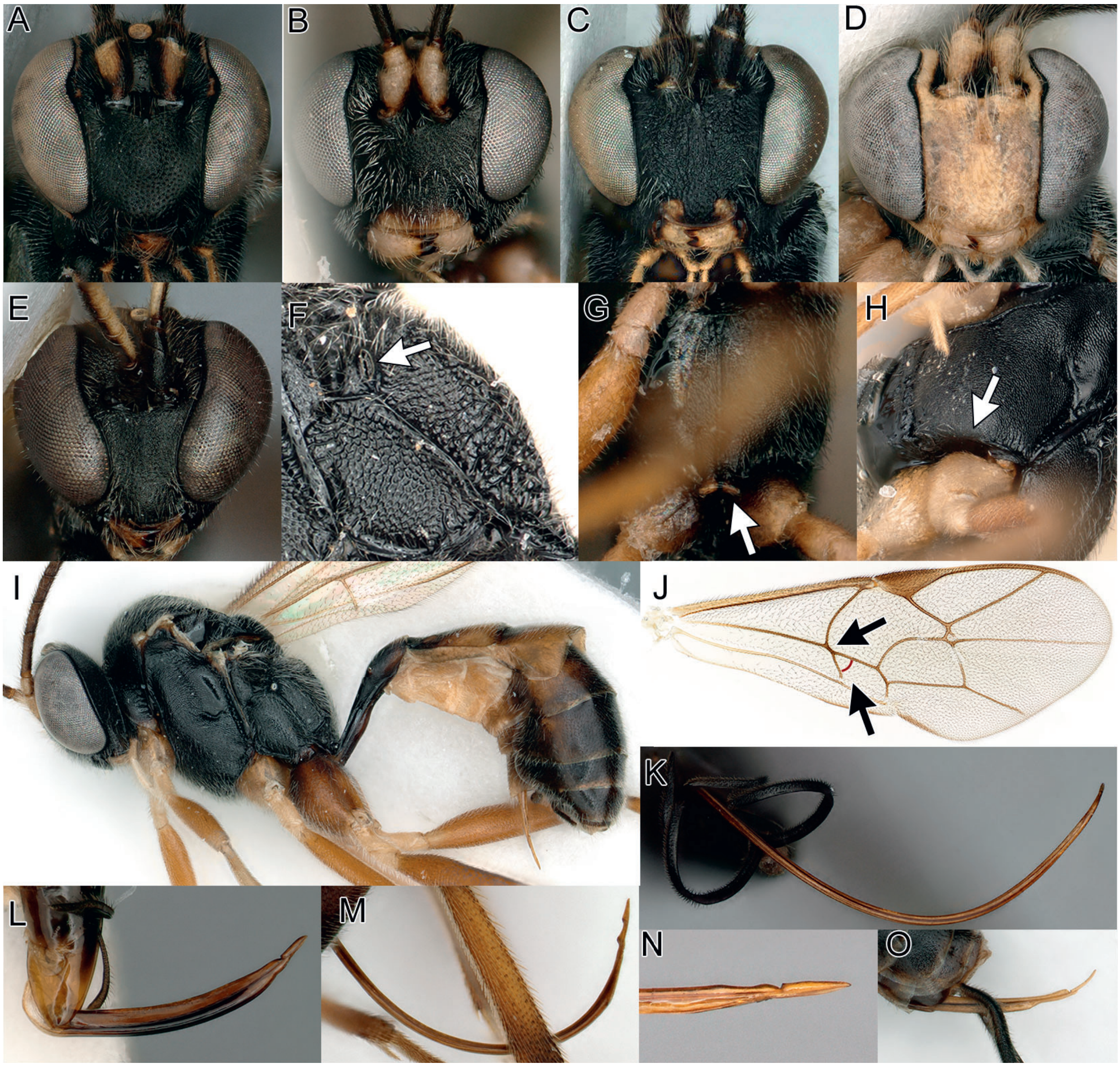


Figure 4. Character states rare among Campopleginae genera. Head colouration and facial features in; – A) *Alcima orbitale*; – B) *Lathrostizus forticanda*; – C) *Echthronomas quadrinotata*; – D) *Echthronomas facialis*; – E) *Cymodusa leucocera*; – F) propodeal spiracle of *Dusona notabilis*; – G) expanded lobes medially on postpectal carina in *Lathrostizus forticanda*; – H) postpectal carina interrupted in front of mid coxae in *Meloboris miae*; – I) sthout habitus of *Phobocampe bicingulata*; – J) forewing of *Phobocampe bicingulata*; ovipositors of; – K) *Rhimphoctona rufocoxalis*; – L) *Gonotypus melanostomus*; – M) *Lathrostizus lugens*; – N) *Tranosema hyperboreum*; – O) *Macrus parvulus*.

Figur 4. Ovanliga karaktärer hos Campopleginae-släkten. Ansiktsfärg hos; – A) *Alcima orbitale*; – B) *Lathrostizus forticanda*; – C) *Echthronomas quadrinotata*; – D) *Echthronomas facialis*; – E) *Cymodusa leucocera*; – F) spirakel på propodeum hos *Dusona notabilis*; – G) utvidgade lober medialt på postpectal carina hos *Lathrostizus forticanda*; – H) postpectal carina avbruten framför mellanhöften hos *Meloboris miae*; – I) habitus hos *Phobocampe bicingulata*; – J) framvinge hos *Phobocampe bicingulata*; ovipositor hos – K) *Rhimphoctona rufocoxalis*; – L) *Gonotypus melanostomus*; – M) *Lathrostizus lugens*; – N) *Tranosema hyperboreum*; – O) *Macrus* parvulus.

sternite–tergite suture and oval cross-section, such as *Callidora* (Fig. 1D) and some *Meloboris*. However, the sternite of these genera is expanded not close to the base as in the *Campoplex* genus group, but a bit further back. As these genera have a glymma at least in part of the species, Townes did not consider them as part of his Campoplegini. These characters are however often difficult to use when keying the group. Also, it remains to be shown whether the *Campopolex* group is indeed monophyletic, given that many *Nemeritis* species are very similar to some *Campoplex*, and *Casinaria* and *Charops* really appear rather peripheral in this assembly.

Campoplex Gravenhorst, 1829 – https://doi.org/10.5281/zenodo.6645995. This is the largest genus of the group, with 122 species known in Europe, and the most difficult one to define. Its sternite–tergite suture is around the middle (Fig. 1C) and sometimes a bit below, the cross-section nicely rounded in most species, and the ovipositor is always intermediate or long. The eyes are moderately emarginated opposite the antennal sockets and there is usually, but not always, an angle between vein 1Cu and cu-a of the hind wing. While *Casinaria* and *Charops* can easily be distinguished from *Campoplex* species by their high first sternite, strongly emarginated eyes and short ovipositors, the remaining genera show various transitions to species within *Campoplex*; see under these genera for distinguishing features. In fact, the genus might have served as a bit of a waste-basket for species that were otherwise difficult to place, and a revision is thus needed, ideally including a phylogenetic analysis, as some of the following genera, especially *Venturia* Schrottky, 1902, *Porizon* Fallén, 1813 and *Sesioplex*, might be nested within *Campoplex* and thus render it paraphyletic. *Campoplex* species attack various "Micro-" and "Macrolepidoptera", usually at a rather late stage of their development, although exceptions occur (Shaw et al. 2016). There is currently no modern revision of the genus. Horstmann split part of the genus, a group of 33 species in which the genal carina meets the mandible at almost a right angle, into species-groups, but mentioned the provisional nature of these (Horstmann 1985). It also remains unclear whether the genal carina character defines a monophyletic group or not, given how heterogeneous the included species are.

Casinaria Holmgren, 1859 – https://doi.org/10.5281/zenodo.6337052, https://doi.org/10.5281/zenodo.6337055. There are 31 species known from Europe, eight of which were described only recently (Riedel 2018). While the sternite–tergite suture is nearly straight in most genera, it is bowed in *Casinaria* and *Charops* (Figs 1a–b), starting clearly above the middle at some point close to the base and then slanting downwards before the spiracle. The eyes are strongly emarginated opposite the antennal sockets. As in the following genus, the ovipositor is rather short, the propodeum is often distinctly elongate between the hind coxae and with the carination partly or almost entirely reduced. In contrast to *Charops*, the areolet is closed in *Casinaria*. This seems to be a rather well-delimited genus, although there is a small species group around *C. stygia* which stand out through their rather wide clypeus and short second tergite. *Casinaria* uses Lepidoptera as hosts, mostly Noctuidae and Geometridae, although various other families are also attacked. Riedel (2018) provided a key to the European species.

Charops Holmgren, 1859 – https://doi.org/10.5281/zenodo.6646700. This genus is most diverse in the Afrotropical and Oriental regions and only represented by a single species in Europa, *Charops cantator*, although a probable undescribed species from France was mentioned by Shaw et al. (2016). *Charops* can be distinguished from all other genera by the high first sternite (Fig. 1A) in combination with an open areolet. The propodeal spiracle is very narrow, almost slit-like, which otherwise only occurs in *Dusona* (Fig. 4F), which has the sternite–tergite suture clearly below the middle, if it is not obliterated, and has a closed areolet. *Charops cantator* seems to be a specialist on Zygaenidae (Shaw et al. 2016).

Porizon Fallén, 1813 – https://doi.org/10.5281/zenodo.6337360. There are six European species known of this genus. They can be readily identified by their open areolet, which they only share with *Charops* in the current genus group. Except in *P. albistriae* (Horstmann, 1987), the propodeum is clearly elongate between the hind coxae, which is reminiscent of *Venturia* and some *Campoplex* species. *Porizon cleui* (Cleu, 1933) and *P. albistriae* have an ovipositor that is about as long as the first tergite and is rather abruptly curved upwards close to the end, while the remaining species

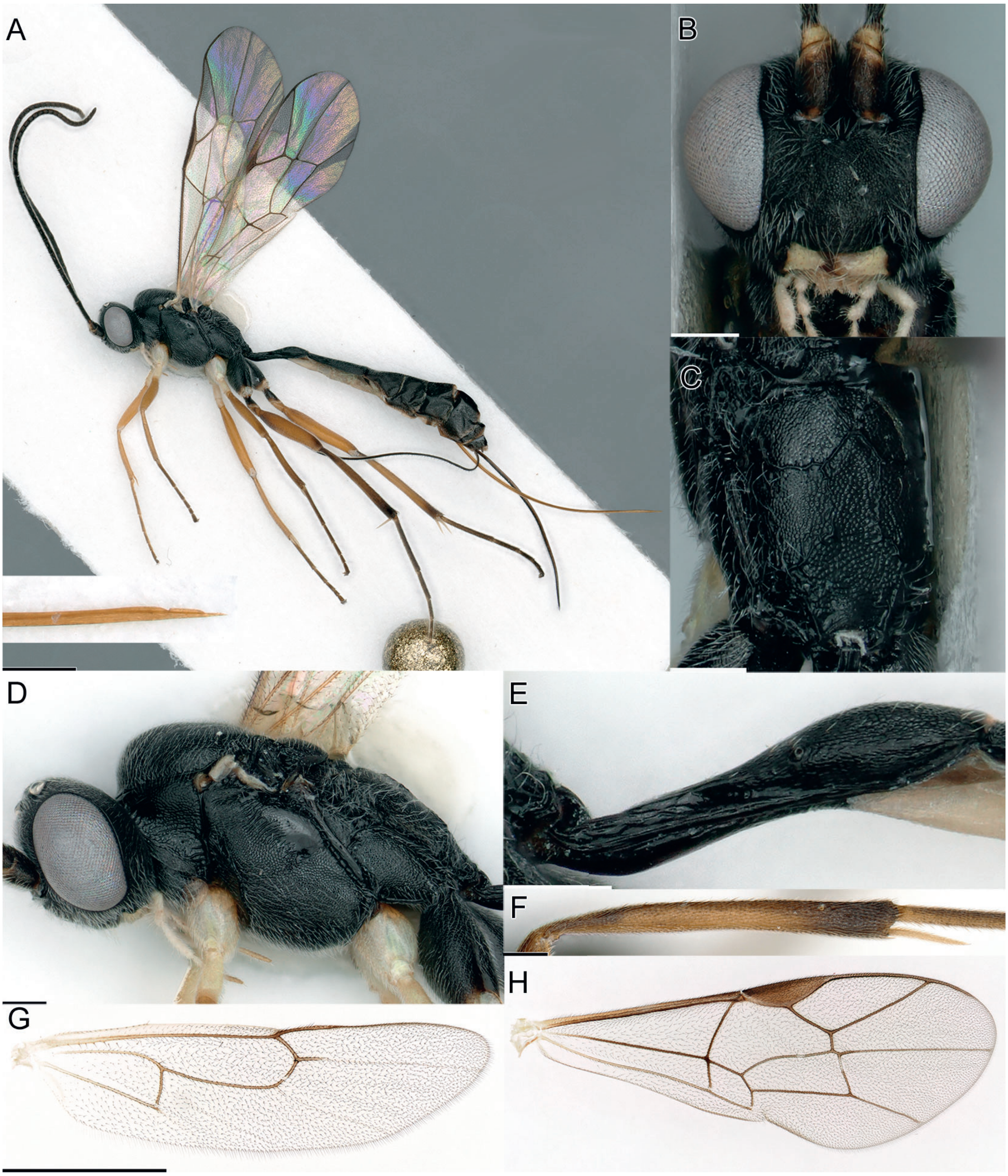


Figure 5. Species portrait of *Leptocampoplex cremastoides*; – A) habitus and ovipositor tip (inlay); – B) frontal view of head; – C) propodeum; – D) head and mesosoma from lateral view; – E) first segment of metasoma; – F) hind tibia; – G) hind wing; – H) front wing. The wings were photographed between two glass plates to ensure optimal flatness. Scale bars are 1 mm in A, G and H, and 0.2 mm in the remaining sections.

Figur. 5. Artporträtt av *Leptocampoplex cremastoides*; – A) habitus och äggläggningsrörets spets (infälld bild); – B) huvud framifrån; – C) propodeum; – D) huvud och mellankropp från sidan; – E) bakkroppens första segment; – F) bakskenben; – G) bakvinge; – H) framvinge. Vingarna är fotograferade mellan två glasplattor för att hålla dem plana. Skalstrecket är 1 mm i A, G och H och 0.2 mm i resterande bilder.

have a longer and more evenly curved ovipositor. *Porizon* species attack small Lepidoptera, such as Tortricidae and Yponomeutidae (Shaw et al. 2016). Horstmann (1987a) revised the known species.

Sesioplex Viereck, 1912 – https://doi.org/10.5281/zenodo.6337383. There are three species currently listed for Europe, two only from western Russia. The third, *Sesioplex punctulatus* Horstmann, 1978, is known from France. Like *Sinophorus* (Fig. 1E), *Sesioplex* has the sternite–tergite suture below the middle and a rather distinct dorsolateral carina, leading to a lateral field of the first tergite and a trapezoidal cross-section, although the postpetiole shows the typical roundish shape of the genus group. The ovipositor is of intermediate to long length and the propodeum only weakly elongate between the hind coxae. The area petiolaris of the propodeum is only very weakly impressed, which distinguishes it from *Sinophorus*. Also, most species of the genus have a distinct expansion of the upper valve in front of the notch, although this character is not very pronounced in *S. punctulatus* and also occurs in other genera. From *Nemeritis* and *Bathyplectes*, which also usually have a long ovipositor and no glymma, *Sesioplex* can be distinguished by the roundish postpetiole, which is flattened in the other two, and by the narrower clypeus. It remains to be shown whether *Sesioplex* indeed represents a separate entity to *Campoplex* or should rather be interpreted as a species group within that genus. The North American type species of the genus, *S. depressus* (Viereck, 1912), has been reared from a Gelechiidae moth, but otherwise host records are absent. Sanborne (1983) provided a key to the five species currently known in the genus.

Sinophorus Förster, 1869 – https://doi.org/10.5281/zenodo.6337396 . From Europe, 29 species are known in this genus. Nearly all of them have a very strongly impressed area petiolaris, and it is confluent with the very wide area superomedia anteriorly. Together, they can accommodate the petiole if it is bent upwards and forwards. However, this character complex is less pronounced in the *S. xanthostoma* (Gravenhorst, 1829) species group, and it also occurs in some *Campoplex*, from which most species can be distinguished by the shape of the petiole (Figs 1c, 1e). Sanborne (1984) lists additional characters to distinguish the two genera, such as the width of the area superomedia compared to the distance between the propodeal spiracles (usually >0.35 in *Sinophorus* and <0.3 in *Campoplex*) and a usually straight vein 2Cu in the hind wing of *Campoplex* but not *Sinophorus* (“discoidella” *sensu* Townes). However, there seem to be many intermediate forms in both genera, and molecular data might help clarify the best way of delimiting the two genera from each other. *Sinophorus* species attack various families of Lepidoptera, including small and large moths and even butterflies, and some species appear to be rather polyphagous (Shaw et al. 2016). Sanborne (1984) revised the world species and provided identification keys.

Venturia Schrottky, 1902 – https://doi.org/10.5281/zenodo.6337423. This genus is mostly Neotropical, Nearctic and Oriental in its distribution, and only five species occur in Europe. The propodeum is moderately to strongly elongate between the hind coxae in *Venturia*, but this character also occurs in some *Campoplex* and *Porizon*. Currently, the best character to distinguish *Venturia* from the other two genera are the male parameres, which show a distinct emargination dorsally in *Venturia*. They are closely related to *Campoplex*, and the delimitation between the two genera has changed repeatedly in the past (Horstmann 1973d, 1979, 2000). Indeed, it remains to be demonstrated whether that genus is paraphyletic with respect to *Venturia* – and potentially also to other genera in this group. The genus uses lepidopteran hosts, and *Venturia canescens* (Gravenhorst, 1829) is used extensively in biocontrol, as it attacks several pest species in storage facilities, and has been made a model organism for many parasitoid studies. It is nearly world-wide in its distribution and both parthenogenetic and sexually reproducing populations occur in Europe (Li et al. 2003). Horstmann (1973d, 1979) keyed the European species along with a number of species later moved to *Campoplex* and *Porizon* that are similar to *Venturia* species.

Diadegma genus group

This group is based on the presence of an elongate subbasal cell in the hind wing, with no angle between veins 1Cu and cu-a (“nervellus unbroken” in Townes 1970) and M + Cu running parallel to 1A over a length longer than the combined length of 1Cu and cu-a (Figs 2a–d). But beware that this character can be difficult to judge without some experience, and it seems to have been reversed in some small-bodied species. A distinct glymma on the first tergite (Figs 1j-m) is present in most members and most probably represents the plesiomorphic state in the group or even in the entire subfamily, but it is reduced in many species of several genera (Fig. 1I), such as nearly all *Lemophagus*, many *Olesicampe* and some *Hyposoter*. This group might well represent a natural entity.

Alcima Förster, 1869 – https://doi.org/10.5281/zenodo.6034964. This genus in Europe only includes *A. orbitale*, a species readily recognized by its yellow inner eye margins (Fig. 4A), which it only shares with *Chromoplex picticollis*, which has much more extensive colouration also on the mesosoma. The shape of the subbasal cell in the hind wing clearly places the genus in this group of genera, but it takes a rather isolated position judging from the unique shape of the first tergite and propodeum, although the strong spikes and long spurs of the hind tibia, as well as the strongly reclivous veins 1Cu and cu-a, are reminiscent of *Echthronomas* species, with which it might turn out to be closely related. The species has been reared from a variety of moth and butterfly families, although it appears to be entirely restricted to Zygaenidae in the United Kingdom, which indicates that there might be two taxa intermingled in this species (Shaw et al. 2016).

Benjaminia Viereck, 1929 – https://doi.org/10.5281/zenodo.6336822. The four European species of the genus are mostly Mediterranean in distribution, although there are probably large gaps in our faunistic knowledge of the genus. They can be readily recognized by the open areolet and the shape of the anterior section of the lateral longitudinal carina of the propodeum, which is expanded into a crest that covers the spiracle when the propodeum is viewed from above. We have only seen such an expansion in one other species, *Callidora analis* (Gravenhorst, 1829), which has a closed areolet and differs in the shape of the petiole. *Benjaminia* is probably monophyletic and all confirmed host records are from butterflies, more precisely, the nymphalid subfamily Melitaeinae. The world species of *Benjaminia* have been revised by Wahl (1989).

Chromoplex Horstmann, 1987 – type images provided by the Biological Museum in Lund: https://www.flickr.com/search/?tags=MZLUTYPE07174. This genus was erected by Horstmann (Horstmann 1987a) for *C. picticollis*, which still is the only species included in *Chromoplex* and which was formerly placed tentatively in *Diadegma*, where it might fit given its long ovipositor. The species is easily recognized by its colour pattern, with often extensive yellow inner eye margins and red colouration on the mesosoma. It also matches *Echthronomas* in the long spurs and strong spines on the hind tibia, the colour pattern, and short and strongly constricted temple. Indeed, it might turn out to be closely related to that genus. Two hosts have been recorded, the butterfly *Archon apollinus* Herbst, 1789 and the noctuid *Helicoverpa zea* Boddie, 1850 (Yu et al. 2016), a host range that seems very unlikely.

Diadegma Förster, 1869 – https://doi.org/10.5281/zenodo.6337085. This is a large genus with currently 128 species recognized in Europe. It contains most species with intermediate to long ovipositors that share the characteristics of the genus group, i.e., the distinct glymma (Fig. 1K), straight or weakly bowed 1Cu and cu-a, apically parallel-sided subbasal cell (Fig. 2B). However, smaller species often show a rather stout subbasal cell, which can lead to confusion with genera outside the group. Some species can be confused with *Tranosemella* or *Lathrostizus*, and species with an open areolet can be confused with *Enytus*; see under those genera for the discriminating features. There are also some species with short ovipositors, which can be confused with *Hyposoter* or even with the *Olesicampe* species formerly included in the genus *Holocremnus* Förster, 1869. In fact, the exact delimitation especially of the larger genera in the entire genus is in need of clarification, ideally with phylogenetic methods, and some species groups currently placed in *Diadegma* might turn out as mere *Hyposoter* species with long ovipositors. *Diadegma* species attack various “Micro-“ and “Macrolepidoptera”, often species feeding in leaf mines or that form communal webs, and many species have been reared from multiple families (Shaw et al. 2016). Although Klaus Horstmann worked extensively on this genus, the last published key is highly incomplete (Horstmann 1969). There is a more recent key to the species of the

Diadegma nanus (Gravenhorst, 1829) group (Shaw & Horstmann 1997), covering 30 species, including four formally undescribed ones.

Echthronomas Förster, 1869 – https://doi.org/10.5281/zenodo.6337116. This genus includes four species in Europe, all of which show at least some yellow colouration on the face or clypeus (Figs 4c–d). They are mostly rather rare, except for *Echthronomas quadrinotata*. Townes (1970) used a row of closely spaced setae ventrally along tarsomeres 1 and 2 and often the following to distinguish *Echthronomas*, *Eriborus* and several non-European genera from the remaining genera of the group. This row is indeed visible as a distinct structure that almost appears like a lamella on the tarsomeres of *Echthronomas* species; however, the tarsomeres are very setose all over, making judging this character rather difficult. And, as pointed out already earlier (Gauld 1984), this character shows a broad continuum also in other genera, including some *Hyposoter* species, and is thus rather unreliable. Vein 1Cu and cu-a in the hind wing (nervellus) is very strongly reclivous (Fig. 2D), meaning that the anterior corner of the subbasal cell is distinctly further from the wing base than the posterior corner. *Echthronomas* species furthermore also typically have very strong spines on the hind tibia and long hind tibial spurs, with the outer spur reaching to at least 0.75 times the length of the first tarsomere. However, both characters can also be found in *Hyposoter* species, but these rarely have any yellow colouration in the face, except for *Hyposoter pallidirostris*, and the ventral flange on the mandible is typically much more pronounced than in *Echthronomas*. From *Eriborus*, with which it might indeed be closely related, the genus can be distinguished by its closed areolet, which is always open in *Eriborus*. The genus is probably monophyletic and might be close to *Eriborus*, *Hyposoter*, *Alcima*, and some extralimital genera. *Echthronomas* species seems to be restricted to Arctiinae moths, although host records are from just two species (Yu et al. 2016). Horstmann (1987b) revised the European species.

Enytus Cameron, 1905 – https://doi.org/10.5281/zenodo.6337122. There are eight European species of this genus, most of which were formerly listed under *Diadegma*. All *Enytus* have an open areolet, which is rare in *Diadegma*, and vein 2rs-m in the fore wing (i.e., the inner vein of the open areolet) has about the same length as the 2+3M (the lower vein), while it is longer in *Diadegma* species with an open areolet, although there seems to be some overlap in this character (Horstmann 1970). *Enytus* species also have an entirely shagreened speculum, which is usually but not always at least partly smooth and shining in *Diadegma* species, and a rather short area superomedia, although that latter character is rather variable within *Diadegma*. It remains to be shown whether the genus will not just turn out as a species group within *Diadegma* or if it indeed constitutes a separate entity. *Enytus* attacks various lepidopteran families and its species are often very wide in their host ranges (Shaw et al. 2016). No key currently exists to these species, although some were revised under *Diadegma* (Horstmann 1969).

Eriborus Förster, 1869 – https://doi.org/10.5281/zenodo.6337132. The genus shows most of its diversity in the tropics and subtropics, but also occurs in Europe, with eight species known. As in *Echthronomas*, the species show a row of closely spaced setae on the ventral side of the first and second hind tarsomeres, but see under that genus for difficulties with this character. *Eriborus* has an open areolet and short ovipositor, a combination rare in the genus group. It can be distinguished from *Benjaminia* by the not expanded basal section of the lateral longitudinal carina of the propodeum. The few species of *Diadegma* with an open areolet either have a longer ovipositor or a very small body size of up to 3.8 mm, while most *Eriborus* are considerably larger (but see *E. braccatus* (Gmelin, 1790)). An open areolet is exceedingly rare in *Hyposoter*. *Eriborus* species parasitize various lepiopteran families, especially Noctuidae, Pyralidae and Tortricidae. The European species have been revised by Horstmann (1987b).

Hyposoter Förster, 1869 – https://doi.org/10.5281/zenodo.6337163. This is a large genus with currently 62 species recorded in Europe. Its members share a short ovipositor, short temple, a prominent flange along the ventral margin of the mandible, and a rather long hind tibial spur, which is usually more than 0.65 or even 0.75 times as long as the hind basitarsus. However, the genus is rather heterogeneous in many respects and might turn out not to be monophyletic as it is currently defined. Some species are very similar to species with longer ovipositors that are placed in *Diadegma*, and there might be some overlap or at least difficult delimitation with respect to some *Olesicampe* species that have a rather short temple and were for a while classified in *Holocremnus* (see *Olesicampe* section). Extensive sampling of all species groups of *Hyposoter* might thus be necessary to test its monophyly as it is currently defined. *Hyposoter* species attack a wide variety moths and butterflies, which they often kill before the host is fully grown, and some species form their cocoon within the remains of the host larva (Shaw et al. 2016). The genus includes many species with rather conspicuous colour patterns; a review of the European *Hyposoter* species is in the final stages of preparation (A.C. Galsworthy, pers. comm.).

Lathrostizus Förster, 1869 – https://doi.org/10.5281/zenodo.6337175. There are 13 European species currently described in this genus. They invariably have intermediate to long ovipositors and a closed areolet, and can thus be confused with *Diadegma* or *Tranosemella*. From both, they can be distinguished by their wide clypeus and comparatively long mandibles (Fig. 4B), and by their strongly upcurved ovipositor (Fig. 4M), even though there is some overlap in this latter character with many *Diadegma* species. *Lathrostizus* is very close to *Olesicampe* in both its morphology and biology (see below) and can often only be distinguished from species with a rather short gena (former genus *Holocremnus*) by the longer ovipositor, with males typically not identifiable. Some species have a yellow or orange clypeal margin (Fig. 4B), and some feature an additional impression or expansion in front of the notch of the upper valve of the ovipositor (Fig. 4M) or have the postpectal carina expanded into conspicuous flanges (Fig. 4G). Horstmann (2004) suggested that the genus might be polyphyletic within a wider definition of *Olesicampe*, and that the true species diversity of the genus in Europe might be higher than currently assumed. As with *Olesicampe*, *Lathrostizus* attacks sawflies, but groups that form galls or otherwise live inside their host plants (Horstmann 1971, Shaw et al. 2016). Horstmann revised the genus and provided identification keys (Horstmann 1971, 2004), and Kasparyan and Kopelke (2009) provided both a key and detailed rearing data.

Lemophagus Townes, 1970 – https://doi.org/10.5281/zenodo.6337275. There are five European species known in this genus, four of which seem rather uniform in their morphology and biology (Horstmann 2004), while the association of the fifth (*L. foersteri* (Tschek, 1871)) still requires confirmation. Within the genus group, they are very similar to some *Olesicampe* species that have a rather short gena, as the species formerly included in *Holocremnus*. *Lemophagus* species can be distinguished from them by the microsculpture of their face, which is covered by irregular rugae, some of which cross the entire face. This character can also readily be used to separate them from *Hyposoter*, from which they also differ by their broad clypeus. Their glymma is usually indistinct (cf. Fig. 1I) and the narrow subbasal cell in the hind wing less clearly developed than in most other species of the *Diadegma* group, which means that *Lemophagus* species might also be confused with genera outside the group that can have no angle between veins 1Cu and cu-a in the hind wing and a short ovipositor. This is especially true for some *Callidora* and *Phobocampe* species, but none of these has a rugulose sculpture of the face, and their temples are more strongly narrowed behind the eyes than in *Lemophagus*. The genus might turn out to be a species-group within *Olesicampe*, see also under that genus. The genus is unusual for attacking chrysomelid beetles (Shaw et al. 2016, Yu et al. 2016), although *L. foersteri* might have a different host range. Horstmann (2004) provided a key to the European species.

Olesicampe Förster, 1869 – https://doi.org/10.5281/zenodo.6337350, https://doi.org/10.5281/zenodo.6337340. This is a large genus with currently 87 species in Europe. Many species can readily be recognized as belonging to *Olesicampe* in both sexes by their wide temple, wide clypeus and elongate lower tooth of the mandible (Fig. 3C); however, there are numerous species with a rather short temple and equally long teeth, which were formerly included in *Holocremnus* (Schmiedeknecht 1909). They can be confused with *Hyposoter*, which has an even shorter temple and larger flange on the mandibles, or with *Lemophagus* (see under that genus). *Lathrostizus* is another genus of probably very close association, and while females can easily be told apart by their long ovipositor, the males are very difficult to distinguish from *Olesicampe* species with a rather short temple. The genus might turn out to be paraphyletic as currently defined with respect to these other genera. It attacks sawfly larvae that live exposed on their food plants, mostly Tenthredinidae. Some species are gregarious, using some of the larger sawfly species like Cimbicidae (Shaw et al. 2016). The genus is currently being revised (M. Riedel, pers. comm.).

Tranosemella Horstmann, 1978 – https://doi.org/10.5281/zenodo.6337415. Four species are currently listed for this genus, which Horstmann described mostly on the basis of the colour pattern of the hind tibia (Horstmann 1978), which is dark proximally and distally and light medially, while *Diadegma* either have a less contrasting colour pattern or, if there are dark bands, the base of the tibia has a light marking. This is in fact currently the only character that distinguishes them from *Diadegma*, although *Tranosemella* species tend to have a wider ventral flange on the mandible, rather long spurs of the hind tibia and a partly reduced carination of the propodeum, which might indicate an association with *Hyposoter*. From the latter, they can be distinguished by the longer ovipositor. A phylogenetic analysis is needed to clarify the status of this genus and that of its most common and rather variable species, *T. praerogator* (Linnaeus, 1758). *Tranosemella* species attack various groups of Lepidoptera. The key by Horstmann (1978) only includes two of the four species.

Tranosema genus group

This group can be recognized by their deep glymma, which in some genera lies closer to the base than to the apex (Fig. 1O), and the strong angle between veins 1Cu and cu-a in the hind wing. 1Cu is furthermore often inclivous, meaning that the posterior corner of the subbasal cell is distinctly further from the wing base than the anterior corner, and the subbasal cell is somewhat concave apically. Furthermore, the temple is moderately to very wide. It remains to be demonstrated whether this represents a monophyletic group or whether these characters rather represent symplesiomorphies. Indeed, there might be an association instead between the beetle-parasitising genera in this and in the next group, as suggested by Wahl (1991); see also comment under *Pyracmon*.

Campoletis Förster, 1869 – https://doi.org/10.5281/zenodo.6336937. Most of the 39 species recorded from Europe can readily be recognized by the clypeus being expanded medially as an acute tooth (Fig. 3F), although some only show a somewhat expanded lamella in its place. The areolet is usually very symmetrical, with 2m-cu attaching near or even proximal to the middle. The glymma is closer to the spiracle than to the base of the first tergite and the ovipositor is most often of moderate length but sometimes rather short or long. Species with a reduced tooth on the clypeus might be confused with *Synetaeris*, which also has a rather symmetrical areolet, but an apical margin of the clypeus that is nearly straight to very weakly convex and without a median expansion. *Campoletis* species attack various Lepidoptera, including many Noctuidae, and often kill the host before it is fully grown (Shaw et al. 2016). This seems like a well-defined genus, perhaps most closely related to *Synetaeris* Förster, 1869. Riedel (2017) revised the European species.

Dolophron Förster, 1868 – https://doi.org/10.5281/zenodo.6337089. This genus was only validly interpreted by Townes (1970), more than a hundred years after its original description, and equipped with *D. pedella* (Holmgren, 1860) as the type species. A second European species, *D. nemorati* Horstmann, 1978, was later added (Horstmann 1978). The deep glymma that lies closer to the base than the spiracle of the first tergite, together with a strongly angled 1Cu and cu-a and clearly inclivous 1Cu in the hind wing associates this genus with the current genus group. It can be confused with *Pyracmon* Holmgren, 1859 or *Synetaeris*, but the area superomedia is never so regularly pentagonal and closed apically by a complete carina in these genera. Outside the genus group, *Dolophron* is somewhat similar to *Phobocampe* which also has a rather stout body, and both often have a rather acute angle between veins 2Cu and 1cu-a. However, the two European *Dolophron* can be easily distinguished from *Phobocampe* by their much deeper glymma and shorter first tergite and by the area superomedia being separated by a strong apical carina from the area petiolaris. Both species have been reared from *Heterarthrus* Stephens, 1835, a genus of Tenthredinidae sawflies that live in blister mines in leaves of various trees (Horstmann 1978, Shaw et al. 2016). Horstmann (1978) keyed the two species.

Gonotypus Förster, 1869 – https://doi.org/10.5281/zenodo.6337143. This monotypic genus only contains *G. melanostoma*. Females of this species can readily be identified by the strongly expanded dorsal valve of the ovipositor, which is in part more than twice as high as the ventral valve in lateral view (Fig. 4L). The glymma is closer to the base than to the spiracle of the first tergite and the areolet is open, which is another unique character combination and underlines the somewhat isolated position of the species in the subfamily. Wahl (1991) placed *Gonotypus* in its own genus group. The closest relatives of *Gonotypus* thus remain unclear, but it attacks Coleophoridae (Shaw et al. 2016).

Melanoplex Horstmann, 1987 – https://doi.org/10.5281/zenodo.6337301. This monotypic genus was erected by Horstmann (1987a) to accommodate *M. bucculentus* (Holmgren, 1860), which formerly was included in various other genera. The first tergite of *Melanoplex* is rather long and slender compared to some other genera of the group and its glymma is situated about midway between the base and spiracle (cf. Fig. 1M), and the clypeus is conspicuously rounded and punctate. Otherwise, *Melanoplex* shows many similarities with *Pyracmon*, where it was at some point included, although the ovipositor of *Pyracmon* species is at least somewhat compressed. *Synetaeris* also has a rather slender first tergite and a clypeus that is rather convex in profile, although it is less strongly punctuate and the costula of the propodeum is less well developed than in *Melanoplex*. Some *Tranosema* Förster, 1869 species also have a similarly convex clypeus, but they differ by their shorter propodeum. It remains to be shown whether *Melanoplex* is sufficiently distinct to justify it being kept separate. Unfortunately, no host records are currently available for the species, which could shed further light on its evolutionary associations.

Pyracmon Holmgren, 1859 – https://doi.org/10.5281/zenodo.6337364. Three species of this genus are known from Europe. They share a rather short and stout first tergite with the deep glymma usually closer to the base than to the spiracle (Fig. 1O). In contrast to *Rhimphoctona*, with which they share the large head, wide temple and general habitus, the ovipositor is rather robust and rigid and somewhat laterally compressed, the apical margin of the clypeus is either evenly convex or at most weakly triangular, and the mandibular teeth are about equal in length. As in *Rhimphoctona*, there is a tooth apically on the outer side of the front tibia, a character otherwise known from Ctenopelmatinae and a few other unrelated Darwin wasp groups. This character is also shared with *Bathyplectes*, *Leptoperilissus* and *Nepiesta*, and Wahl used this character to suggest that these five genera belong to a natural group (Wahl 1991). We here put more emphasis on other characters, as the fore tibial tooth can be very difficult to interprete, especially in small specimens.

Differences between *Pyracmon* and *Melanoplex* and *Dolophron* are detailed under these genera. From *Synetaeris*, the genus can be the distinguished by its pentagonal or at least sessile quadrate areolet, while it is petiolate in *Synetaeris*, and by the clypeus which is rather flat in *Pyracmon* but conspicuously convex in profile in *Synetaeris*. However, it remains to be shown whether this distinction holds up, given that *S. brevicauda* Horstmann, 1987 (Horstmann 1987a) is somewhat intermediate between the two genera. Three of the seven *Pyracmon* species that are known in total have been reared from ground-dwelling beetles (Barron & Walley 1983), while there are no host records for the remaining species. Barron and Walley (1983) keyed the world species, while still including *Melanoplex bucculentus* and *Synetaeris heteropus* under this genus.

Rhimphoctona Förster, 1869 – https://doi.org/10.5281/zenodo.6337373. There are currently eleven European species known in this genus. They can be recognized by the rather short first tergite with the spiracle barely behind the middle and deep, rather basal glymma (cf. Fig. 1O), the nearly triangular clypeus (Fig. 3B), lower tooth longer than the upper, strongly expanded temples, and the thin and flexible ovipositor (Fig. 4K). They are most similar to *Pyracmon* species, from which they differ not only by the characters mentioned there, but also by the host range. *Rhimphoctona* parasitize beetles in wood, mostly Cerambycidae, with earlier mentions of Raphidioptera as hosts probably resulting from confusion with *Nemeritis* (Horstmann 1980b). The genus appears to be monophyletic, although *R. grandis* (Fonscolombe, 1852), the type species of the genus, takes on a somewhat isolated position. Horstmann (1980b) provided a key to the European species.

Scirtetes Hartig, 1838 – https://doi.org/10.5281/zenodo.6337375. This monotypic genus only includes *S. robustus* and can be readily recognized by its very short propodeum that drops down immediately behind the metanotum and is devoid of carinae, although the lateromedian longitudinal carinae can be weakly indicated among the rugae that cover it. The ovipositor is about as long as the hind tibia and evenly and strongly upcurved. The deep glymma is closer to the spiracle than the base of the first tergite. It remains unclear what the closest relatives are of this species. It has been reared from various Noctuidae (Shaw et al. 2016).

Synetaeris Förster, 1869 – https://doi.org/10.5281/zenodo.6646012. There are currently two species included in this genus, *S. heteropus* and *S. brevicauda*, and some new species await description in various collections. The distinction from some genera in this group, especially *Pyracmon* and *Tranosema*, is not entirely satisfying at present, see character evidence under these genera. As no host data is available for either of the two species, this also cannot be consulted to judge the level of differentiation. There is currently no key including both species, but merely a detailed description of *S. brevicauda* (Horstmann 1987a).

Tranosema Förster, 1869 – https://doi.org/10.5281/zenodo.6337400, https://doi.org/10.5281/zenodo.6337409. *Tranosema* is represented by ten species in Europe. It can be recognized by the rather short propodeum with a rather wide area superomedia, although this character is not equally distinct in all the species of the genus. *Tranosema* often has a quadrate, petiolate areolet, which it shares with *Synetaeris*, although it is nearly symmetrical in that genus, with vein 2m-cu meeting the areolet around its middle, while it is usually distinctly oblique in *Tranosema,* with 2m-cu meeting the areolet in its distal half. What complicates identification of *Tranosema* is that the most common species, *T. rostrale*, shows rather unique characteristics for the genus, including an often barely visible angle between 1Cu and cu-a in the hind wing (cf. Fig. 2H) and medially interrupted postpectal carina. The circumscription of the genus might have to be revised in the future. The only available key only includes five of the ten European species (Horstmann 1978).

***Nemeritis* genus group**

This is a rather vaguely defined assemblage of genera which have no glymma, a low sternite–tergite suture, and lateral fields on the first tergite which render its cross-section somewhat rectangular or trapezoidal. The mandibles are rather elongate and there is nearly always a clear angle between 1Cu and cu-a in the hind wing. The genera within the group can most easily be distinguished from each other by the shape of their clypeus, which is often rather distinct.

Bathyplectes Förster, 1869 – https://doi.org/10.5281/zenodo.6035106, https://doi.org/10.5281/zenodo.6330994. Five of the 23 European species of this genus were formerly known under *Biolysia* Schmiedeknecht, 1907, which was variously interpreted as a synonym of *Bathyplectes*, of *Nepiesta* Förster, 1869, or as an independent genus (Horstmann 1974). Most species have a very clear angle between veins 1Cu and cu-a of the hind wing (Fig. 2I), although this character is less clearly visible in some of the smaller species that have very weak venation. The clypeus is usually wider than the distance between the tentorial pits and both its margin and the cross-section between the tentorial pits is clearly convex (Fig. 3E). The temple is rather long and rounded and the propodeum conspicuously shortened, although usually not as much as in *Phobocampe* or *Scirtetes*. The ovipositor can be short to long. Species with a short ovipositor can be also be confused with *Callidora* species, which have a much narrower clypeus, with *Phobocampe*, which in contrast have a short and quickly converging temple, or with *Meloboris* (*Nepiera*), which usually have the postpectal carina interrupted behind the mid coxae. *Bathyplectes* species with a moderately to long ovipositor can be most easily mistaken for *Nemeritis* species, which also have a rather long and rounded temple, but an even wider and flatter clypeus, longer propodeum and often a thin and flexible ovipositor. *Nepiesta* species are very similar in the general habitus, shape of the clypeus and first tergite, but can be distinguished easily by their open areolet. The close association and potential synonymy of *Bathyplectes* and *Biolysia* appear justified not only on the grounds of species like *B. anurus* , which is somewhat intermediate, but also from the host range: all species with confirmed host records have been reared from curculionid beetles (Horstmann 1974, Shaw et al. 2016). After spinning their cocoon, the larvae of *Bathyplectes* are apparently capable of strong, jerking movements that cause the cocoon to jump up to several centimetres until it finds a safe spot to diapause (Shaw et al. 2016). Horstmann (1974) keyed the European species.

Clypeoplex Horstmann, 1987 – https://doi.org/10.5281/zenodo.6856942. This genus was erected by Horstmann (1987a) to accommodate *C. cerophagus* (Gravenhorst, 1829), a species previously placed in *Campoplex*, *Sesioplex* and even *Diadegma*. Its placement in the *Nemeritis* group is somewhat arbitrary at this point, and it might instead belong in the *Campoplex* group. It can be distinguished from *Campoplex* by its strong lateral fields on the first tergite, from *Sesioplex* by the shorter ovipositor without any modification in front of the notch, and from *Diadegma* by the complete lack of a glymma and the bowed vein M + Cu in the hind wing. Within the *Nemeritis* group, it can be confused with *Nemeritis* species that have rather short ovipositors, but these have a much wider face. The species has been reared from various "Microlepidoptera", often Gelechiidae and Ypsolophidae (Shaw et al. 2016).

Cymodusa Holmgren, 1859 – https://doi.org/10.5281/zenodo.6337067. There are 16 species in this genus known from Europe, and the females can readily be identified by their very strongly converging inner eye margins and hairy eyes (Fig. 4E). The males can be trickier to associate with this genus, as these characteristics are far less distinct. The sternite ends clearly beyond the spiracle (cf. Fig. 1C), which is unique in the genus group but occurs in genera of the *Campoplex* group and in *Dusona*, *Macrulus* Horstmann, 1987 and *Macrus*. The genus also bears some resemblance to *Callidora*, especially the *C. albovincta* group sensu Tigner (1969). *Cymodusa* species have been reared from various "microlepidoptera" families. Dbar (1984, 1985) keyed the European species.

Lathroplex Förster, 1869 – https://doi.org/10.5281/zenodo.6337171. The two species of this Western Palaearctic genus share the typical characteristics of this genus group, but are distinct by the conspicuously narrowed clypeus, which is very strongly convex in a transverse cross-section, both at the level of the tentorial pits and further down (Fig. 3I). This strong convexity is reminiscent of some *Bathyplectes* species, but these have the clypeus clearly wider than the distance between the tentorial pits (Fig. 3E). Nevertheless, they might turn out to be close relatives, which is also supported by them both attacking Coleoptera, although *Lathroplex* has been reared from Dermestidae rather than Curculionidae (Shaw et al. 2016, Vikberg 1999). The more recently described species, *L. anthreni* Vikberg, 1999, attacked large larvae of *Anthrenus museorum* (Linnaeus, 1761) under laboratory conditions (Vikberg 1999), but its rarity puts a potential effectiveness as a control agent in museum environments into question. Vikberg (1999) provides a differential diagnosis of the two species.

Leptoperilissus Schmiedeknecht, 1912 – https://doi.org/10.5281/zenodo.6337281. The three European species of this genus are known from Spain, Portugal and Bulgaria, while its centre of diversity seems to be the Mediterranean and Southwest Asia. The clypeus is very wide and conspicuously smooth and shining on a good portion of its surface (Fig. 3D), and the ocelli are enlarged in some of the species (Fig. 3D), which might point to a nocturnal habit. The angle between 1Cu and cu-a in the hind wing is not equally distinct in all the species. The short ovipositor associates the genus with *Nepiesta*, which also has a very wide clypeus and rather elongate area superomedia and might indeed be closely related. There is only one uncertain host record from a pyralid moth (Horstmann 1993). Horstmann (1993) keyed all known species of the genus but emphasized that too little is known about the species and intraspecific diversity in this taxon.

Nemeritis Holmgren, 1860 – https://doi.org/10.5281/zenodo.6337322, https://doi.org/10.5281/zenodo.6337330. The thirty European species are probably not yet covering the entire species richness in the region (Horstmann 1994). Females of those species with a relatively long ovipositor can readily be identified by it being rather thin and flexible (cf. Fig. 4K), a character only shared with *Rhimphoctona* and *Leptocampoplex*, see under these genera for distinguishing features. However, there are a number of species with an ovipositor only up to 1.2 times as long as the hind tibia, in which case it is robust and rigid, as in most Campopleginae genera. These and the males are more difficult to separate from similar genera. In all *Nemeritis*, the clypeus is rather flat and wide, as is the lower face (Fig. 3A), and the postpetiole is somewhat flattened (cf. Fig. 1C). The area superomedia is either rather long and narrow and in a different plane from the area petiolaris, or it is short, continuous with the area petiolaris and in the same plane. *Nemeritis* species can also be confused with some species of the *Campoplex* group that have a rather low first sternite, although the postpetiole is more rounded in that genus (Fig. 1C). As the areolet is sometimes open in *Nemeritis*, it might also be mistaken for *Nepiesta*, although only in the male sex, as *Nepiesta* always has a short ovipositor and its clypeus is never as flat and short. Many species of *Nemeritis* have been reared from Raphidioptera (Aspöck et al. 1991), but there is a species group with host records from Coleoptera and Lepidoptera living below bark (Horstmann 1994, Shaw et al. 2016), and confirmed records are still missing for the majority of species. Horstmann revised the genus repeatedly and provided identification keys (Horstmann 1973c, 1975, 1994), with the species diversity each time strongly increased. This indicates that many additional species can be expected, especially if various collection methods are combined (Horstmann 2008, Vas 2020).

Nepiesta Förster, 1869 – https://doi.org/10.5281/zenodo.6337338. Eight species of this genus are known from Europe, and they can readily be identified by their open areolet, although this also occurs in some *Nemeritis*, which have a longer ovipositor and flatter and wider clypeus (Fig. 3A). In most species, the thyridiae are reduced to invisibility and the area basalis is reduced, with the area superomedia thus reaching the base of the propodeum. The fore tibia has an apical tooth, like in *Rhimphoctona, Pyracmon, Leptoperilissus* and *Bathyplectes;* see under *Pyracmon* for a comments on the potential relatedness of these genera. Most species are strongly punctate, which is unusual in Campoplegine, and some species have a ventrally flattened hind trochantellus. The genus is also similar to *Leptoperilissus*, which has a closed areolet and mostly smooth clypeus (Fig. 3D). The only host records are from chrysomelid beetles (Cox & Broad 2020, Müller 1950). Horstmann (1973b) and more recently Vas (2019) keyed the known species.

Remaining genera

The remaining seven genera do not fit clearly in any of the previously listed genus groups, although future analyses might still reveal close associations. We here just list them alphabetically, together with notes on potential relationships.

Callidora Förster, 1869 – https://doi.org/10.5281/zenodo.6336856. The two European species were suggested to belong to distinct species groups by Tigner (1969). The female of the more common species, *C. albovincta*, is easily recognized by the median white band in the antenna, which it only shares with *Casinaria affinis*. The species has a weak or no angle between 1Cu and cu-a in the hind wing, the sternite–tergite suture of the elongate first metasomal segment only a little below the middle, and no glymma on the first tergite, but a longitudinal impression in its place (Fig. 1D). In the male sex, it can thus be confused with *Phobocampe*, from which it differs by the much longer propodeum, or *Meloboris* (*Nepiera*), which usually has the postpectal carina interrupted in front of the mid coxae (Fig. 4H). The males can even be confused with species of the *Campoplex* group, which have a much more rounded postpetiole. The shape of the areolet of *C. albovincta* is rather distinctive, it is petiolate, rather large and both the petiole above and 2m-cu below attach clearly before its middle. The second species, *C. analis*, shares with *C. albovincta* the elongate first tergite, but the sternite–tergite suture is clearly below the middle and there is a distinct glymma. The area basalis of the propodeum is nearly absent and only reflected by the thickened anterior transverse carina of the area superomedia, while the entire propodeum including the area basalis is elongate in *C. albovincta*. Furthermore, the male of *C. analis* has the last sternite elongate into a narrow median process not present in the other species. It remains to be shown whether the two species indeed form a monophyletic cluster. There is to our knowledge only one host record in the genus, of *C. analis* from an unidentified noctuid (Shaw et al. 2016). Tigner (1969) keyed the world species.

Dusona Cameron, 1901 – https://doi.org/10.5281/zenodo.6337098. With 120 European species, this is a rather large genus and one that is easily recognized by its elongate propodeal spiracle (Fig. 4F), which it only shares with *Charops cantator*, which has an open areolet. *Dusona* species have a closed, large, usually petiolate areolet and are often rather large. The sternite–tergite suture is clearly below the middle (Fig. 1G) if it is visible at all; it is often erased over most of its length and the tergite then entirely fused to its sternite. *Dusona* seems to be a rather early-branching genus in the subfamily, and a lot of its species diversity can be found in the tropics and subtropics (Santos et al. 2022). *Dusona* species have been reared from various lepidopteran families, and Geometridae seem particularly attractive (Shaw et al. 2016). Horstmann keyed the Western Palaearctic species (Horstmann 2009), and Meier et al. (2022) provide a photographic guide to the most important characters.

Leptocampoplex Horstmann, 1970 – Figure 5, https://doi.org/10.5281/zenodo.6337277. This monotypic genus was erected by Horstmann (1970) for *L. cremastoides*, a species formerly placed in *Nemeritis*, where it clearly does not fit given its small but distinct glymma. It can be readily identified by the thin and flexible ovipositor (cf. Fig. 4K) combined with an open areolet. It is hard to place this genus in a genus group as it combines a rather high sternite–tergite suture and rounded postpetiole with a deep glymma, which precludes it currently from being placed in the *Campoplex* group of genera, although it bears quite some similarities with certain *Porizon* species. It also resembles some *Nemeritis* with its rather narrow and long mandibles and thin and flexible ovipositor. Molecular data is needed to ascertain its placement. The species has been reared from various small lepidopteran hosts that either live under dead bark or among fungi or lichens (Shaw et al. 2016).

Macrulus Horstmann, 1987 – https://doi.org/10.5281/zenodo.6337287. This genus only includes *Macrulus areolaris* Horstmann (1987a). As with *Leptocampoplex cremastoides*, this species has a first tergite that is reminiscent of the *Campoplex* genus group, especially in the roundish shape of the postpetiole (cf. Fig. 1C), but it has a distinct glymma and the sternite–tergite suture is clearly below the middle. In contrast to *Leptocampoplex*, the areolet is closed, petiolate and obliquely quadrate and the propodeum has the connected area superomedia and area petiolaris distinctly impressed, as in some *Sinophorus* and *Campoplex* species, with which it also shares the long ovipositor. Its position in the phylogeny will need to be assessed with molecular methods. No host records exist that could shed light on its closest relatives.

Macrus Gravenhorst, 1829 – https://doi.org/10.5281/zenodo.6337295. The genus *Macrus* is represented in Europe by two species, *M. filiventris* Gravenhorst, 1829 and *M. parvulus*. It for a long time evaded interpretation (Townes 1970), until Aubert (1966) designated a lectotype for *Nemeritis angitiaeformis* Szépligeti, 1916 and synonymized it with *M. filiventris*. The distinguishing feature of the genus is the ovipositor (Fig. 4O), which has both the dorsal and ventral valves abruptly constricted preapically, its apex thus forming a very thin, needle-like tip. The deep glymma of the first tergite lies closer to the base than the spiracle or at most mid-way between them, which might indicate a close association with the *Tranosema* group. There is only a weak angle between 1Cu and the very short cu-a though (Fig. 2G), and it remains to be shown whether *Macrus* indeed is closely related to the *Tranosema* group. Several genera of Psychidae have been recorded as hosts (Shaw et al. 2016, Yu et al. 2016), and the special ovipositor might well represent an adaptation to the protective cases that the caterpillars build. Horstmann (1970) keyed and described the two European species.

Meloboris Holmgren, 1859 – https://doi.org/10.5281/zenodo.6337307, https://doi.org/10.5281/zenodo.6337316. This genus currently contains 12 species in Europe, five in the subgenus *Meloboris* and the remaining seven in *Nepiera*, two rather distinct subgenera that might merit generic status. Additional species can be expected in both groups, given that several new species were described in the last two revisions (Haraldseide 2021, Horstmann 2004). The genus is notoriously difficult to key out efficiently, as species exhibit a lot of variation in the traditionally used character complexes (Table 1). Except for *M. islandica* Hinz, 1969, the species of *Nepiera* have the postpectal carina interrupted behind the mid coxae (Fig. 4H), a unique character in the subfamily. The first tergite of the subgenus *Meloboris* is rather short and with a deep glymma that lies closer to the base than the apex (Fig. 1N), similar to some genera of the *Tranosema* group, while *Nepiera* species have an elongate first tergite with either no or a weak glymma. All species have a narrow and elongate area superomedia, which is in contrast to the *Tranosema* group of genera, which have a rather short and wide area superomedia. The first tergite of the *Nepiera* species reminds strongly of *Phobocampe* and *Callidora*, but these both always have a complete postpectal carina. *Meloboris* (*Nepiera*) species have been reared from various Lepidoptera, but mostly Noctuidae, while *Meloboris* (*Meloboris*) species are known mostly as parasitoids of Elachistidae, which form mines in grasses (Horstmann 2004, Shaw et al. 2016). Horstmann (2004) keyed the species of the subgenus *Meloboris*, while Haraldseide (2021) covered *Nepiera*.

Phobocampe Förster, 1869 – https://doi.org/10.5281/zenodo.6337354. There are 21 European *Phobocampe* species, although some species limits might either not have been fully appreciated yet or are still somewhat in flux (Shaw et al. 2016). The genus is somewhat difficult to key out, as the glymma can be distinct, weak or absent (Fig. 1F) and the angle between 1Cu and cu-a in the hind wing is present or absent (Fig. 2E). They are rather easy to recognize based on their body shape, once one has seen a few species of the genus: They are very stout, with a short head, mesosoma including propodeum and metasoma (Fig. 4I). The exception is the long first tergite (Fig. 1F), which is rather reminiscent of *Callidora*, *Meloboris* (*Nepiera*), with which it might be related, or of species in the *Campoplex* genus group. In fact, the sternite–tergite suture is often rather close to the middle, although the thickening of the sternite tends to be further back than in these and the petiole is trapezoidal or almost rectangular in cross-section. Other than its body shape, which is difficult to pinpoint on any single measurement, the best character to distinguish *Phobocampe* from the other genera is the small angle, usually below 60°, between 2Cu and 1cu-a in the fore wing and the long vein 1Cu, which is typically much longer than twice its diameter (Fig. 4J). However, there is some variation in this character complex within the genus, and there are other unrelated genera that also sometimes show these characteristics, for instance *Porizon transfuga* (Gravenhorst, 1829) or *Campoletis ensator*, but none of these have such a stout body shape. Many *Hyposoter* species have a similar appearance as they too are rather compact, but they typically have a much larger angle between 2Cu and 1cu-a. *Phobocampe* species attack various Lepidoptera, such as Geometridae and Erebidae, but also some butterfly families being popular hosts (Shaw et al. 2016). Several species seem to have rather broad host ranges, even though the species-level taxonomy might need to be revisited before we can draw sound conclusions on that (Shaw et al. 2016). The European species are keyed in Šedivy (2004), although the key is somewhat difficult to use due to heavy reliance on propodeal carination characters.

Interactive online key

An interactive key to campoplegine genera in Europe is provided under the following, permanent link: http://www.xper3.fr/xper3GeneratedFiles/publish/identification/-1175855634011042400/mkey.html. It includes all 42 genera currently known from Europe, each illustrated by at least one species, and singles out some easily recognized species. The key is dynamic in that future improvements of our knowledge of the intra- and inter-generic diversity will be continuously incorporated.

Figure 6 shows a screenshot of the online key as it currently appears before any character state is fixed. The left panel lists the available characters, while the taxa remaining is shown on the right. The characters appear ordered by information content, with the best characters at the top. One image represents the character, and hovering over it results in an enlarged view of the character. To see the character states, one needs to click on the arrow to open up the list, each of which is in turn illustrated. Ticking the box that fits the specimen at hand sets the character state. If the state has been set for at least one character, then a green button appears at the top that is used to “submit” the selection. The taxon list on the right then shows those taxa that still remain as potential results. The list of characters on the left is rearranged according to the most informative characters for the present candidate set of taxa. If a specific character is deemed by the user as informative given its apparent rarity, the magnifying glass at the bottom of the left panel can be used to search for the character name.

To make the most out of the information in the key, it can help to prioritize characters that seem rare or even unique in the specimen at hand, such as conspicuous colour patterns of the head or mesosoma. Each time the "Submit" button is pressed, the character list will be rearranged according to information content, and one might have to scroll up to the top again to see the most informative characters.

In the current version of the key, it is possible that one ends up with several taxa but no characters left to choose from. This might actually be the correct solution, as some specimens currently cannot be firmly attributed to one or the other genus, for instance in the genus group including *Hyposoter*, *Olesicampe*, *Diadegma* and related genera. It might also happen regularly for males, which sometimes cannot be clearly associated with a genus as long as the matching female is not known. Or one of the previous choices might turn out as incorrect; these can be viewed and revised in the "History" tab of the left panel. However, it might also be that a character is informative for your specimen that is in fact very variable in the genus and thus the program might erroneously judge it as uninformative. In such cases, it helps showing all the remaining characters by choosing "Settings" at the top right of the screen, then "Change options" and choosing "No" under "Show only discriminating characters". The same can be a good strategy if a character the user thinks should be informative does not show up in the list. The characters deemed non-discriminating by the program, often because they are polymorphic in one of the remaining taxa, are shown with whitish font and are arranged at the bottom of the list. Once the user has arrived at a solution, he or she can click on the taxon name in order to see images of representatives and a list of character states observed in the genus. This can be used to check the identification.

The key has been tested with around one hundred of the 835 species known in Europe and might thus not yet perfectly reflect the entire diversity. Feedback is thus very welcome in order to improve the key, also with respect to new characters and their state.

New Campopleginae for Sweden

Most of the about 3,500 specimens of the SMTP material that we sorted to genus were of the five largest genera *Campoplex*, *Diadegma*, *Dusona*, *Hyposoter*, and *Olesicampe*. No comprehensive keys exist currently for any of these, with the exception of *Dusona* (Horstmann 2009), which is reviewed elsewhere (Meier et al. 2022). But many of the smaller genera are amenable to identification, and we focussed on ten of them (Table 2), from which we identified 450 specimens (Supplementary File S3).

Table 2 provides an overview of the faunistic results. Of the 36 species recorded in the SMTP material, 19 represent new records for the country, while six additional species from these ten genera have earlier been recorded for Sweden, but were not found in our material. Ten of the 36 species were only recorded by one specimen or only in a single Malaise trap, indicating that further analysis of the SMTP material might reveal numerous additional species. In addition, we found another new species for Sweden in the collection of the Naturhistoriska Riksmuseet, *Casinaria stygia* Tschek, 1871.

Below we list the species of the ten genera present in the SMTP material, along with at least one detailed record of those species that are new for the country, which are marked with an asterisk. The remaining collection data of each specimen can be found in Supplementary File S2.

Callidora albovincta (Holmgren, 1860)

**Callidora analis* (Gravenhorst,1829) – Sweden: Go, Gotlands kommun, Roleks, 57.536783N, 18.337883E, border between mixed pine forest and open grazed calcareous pasture, Malaise trap. 5.vii.–17.vii.2005. leg. SMTP (3 males)

Casinaria affinis Tschek, 1871

Casinaria albipalpis (Gravenhorst, 1829)

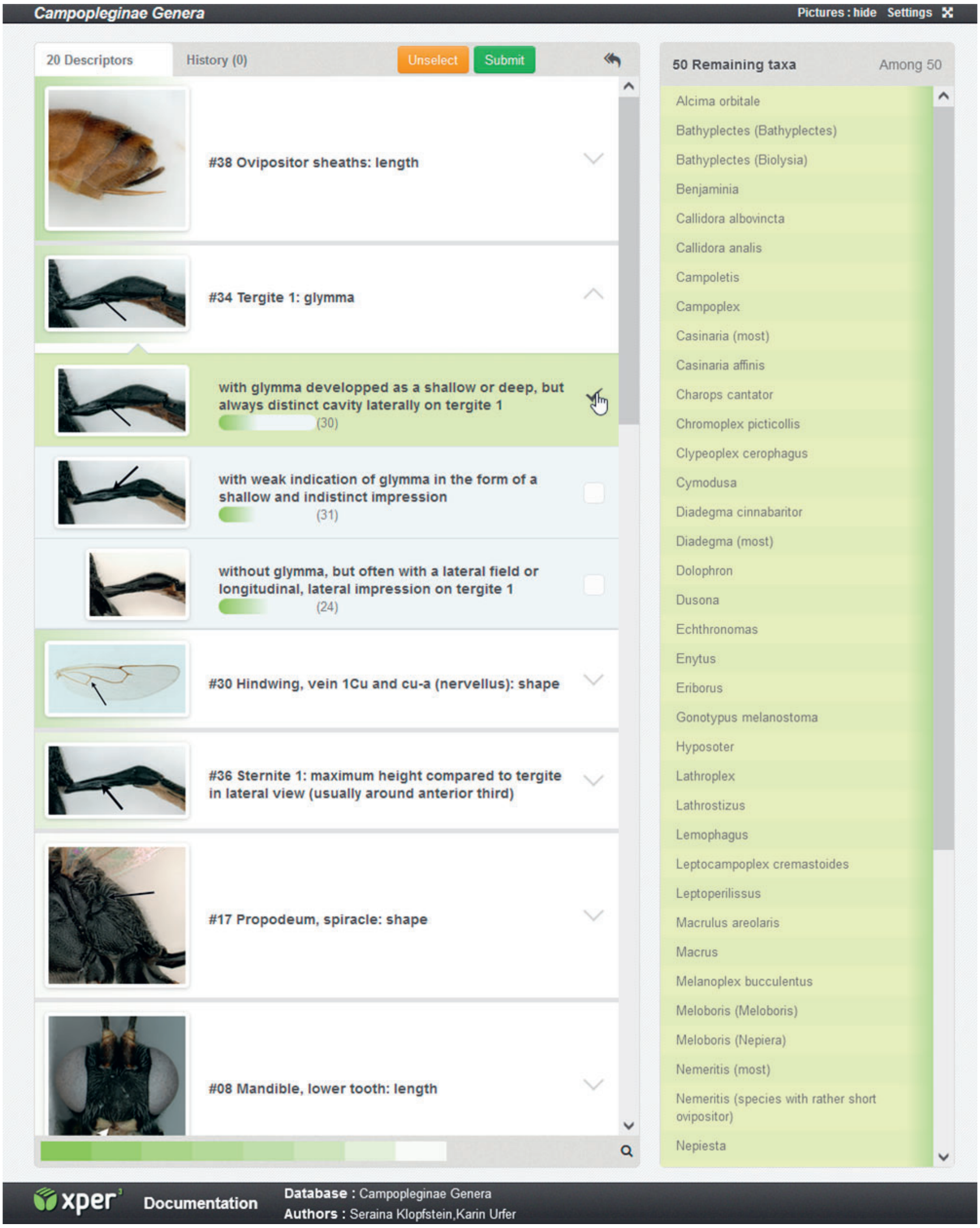
**Casinaria flagellator* Riedel, 2018 – Sweden: Up, Älvkarleby kommun, Båtfors, 60.46065N, 17.317817E, mixed pine forest with blue berry, Malaise trap. 17.vii. –16.viii.2005. leg. SMTP (1 female)

Casinaria ischnogaster Thomson, 1877

**Casinaria kriechbaumeri* (Costa, 1884) – Sweden: Go, Gotlands kommun, Roleks, 57.536783N, 18.337883E, border between mixed pine forest and open grazed calcareous pasture, Malaise trap. 6.vi. –5.vii.2005. leg. SMTP (1 female, 5 males.)

**Casinaria lamellata* Riedel, 2018 – Sweden: Öl, Mörbylånga kommun, Frösslunda alvar, 56.54745N, 16.57725E, alvar pasture, Malaise trap. 3.vi. –26.vi.2005. leg. SMTP (2 males)

Casinaria mesozosta (Gravenhorst, 1829)



#38 Ovipositor sheaths: length

#34 Tergite 1: glymma

with glymma developped as a shallow or deep, but always distinct cavity laterally on tergite 1 (30)

with weak indication of glymma in the form of a shallow and indistinct impression (31)

without glymma, but often with a lateral field or longitudinal, lateral impression on tergite 1 (24)

#30 Hindwing, vein 1Cu and cu-a (nervellus): shape

#36 Sternite 1: maximum height compared to tergite in lateral view (usually around anterior third)

#17 Propodeum, spiracle: shape

#08 Mandible, lower tooth: length

Alcima orbitale
Bathyplectes (Bathyplectes)
Bathyplectes (Biolysia)
Benjaminia
Callidora albovincta
Callidora analis
Campoletis
Campoplex
Casinaria (most)
Casinaria affinis
Charops cantator
Chromoplex picticollis
Clypeoplex cerophagus
Cymodusa
Diadegma cinnabaritor
Diadegma (most)
Dolophron
Dusona
Echthronomas
Enytus
Eriborus
Gonotypus melanostoma
Hyposoter
Lathroplex
Lathrostizus
Lemophagus
Leptocampoplex cremastoides
Leptoperilissus
Macrulus areolaris
Macrus
Melanoplex bucculentus
Meloboris (Meloboris)
Meloboris (Nepiera)
Nemeritis (most)
Nemeritis (species with rather short ovipositor)
Nepiesta

Database : Campopleginae Genera
Authors : Seraina Klopfstein,Karin Urfer

Figure 6. Screen shot showing the initial view of the interactive key, with characters in the left and taxa in the right panel. Clicking a downwards arrow opens the possible states of a character, along with the number of taxa for which a particular state has been coded. A choice can be submitted after specifying at least one character state, which removes taxa that do not match from the list on the right. Link to the key: http://www.xper3.fr/xper3GeneratedFiles/publish/identification/-1175855634011042400/mkey.html.

Figur 6. Skärmdump som visar första vyn i den interaktiva nyckeln, med karaktärer i den vänstra och taxa i den högra panelen. Genom att trycka på pilsymbolen i karaktärsrutan, öppnas möjliga karaktärsalternativ och antal möjliga antal taxa för de olika karaktärsalternativen anges. Allteftersom man väljer karaktärsalternativ, uppdateras taxalistan till vänster så att de taxa som inte passar med de valda alternativen försvinner. Länk till nyckeln: http://www.xper3.fr/xper3GeneratedFiles/publish/identification/-1175855634011042400/mkey.html.

Table 2. Number of recorded species of *Callidora*, *Casinaria*, *Echthronomas*, *Enytus*, *Eriborus*, *Gonotypus*, *Lemophagus*, *Leptocampoplex*, *Meloboris*, and *Tranosemella*. # SMTP – number of species found in the SMTP material; Singletons – number of species represented only by a single specimen in our material; Single trap – species found only in one trap; New for SE – species that represent new records for Sweden; Previous # – number of species previously known from Sweden; # not in SMTP – those among these that have not yet been found in the SMTP material; Total Europe – total number of species known in Europe. *including one species, *Casinaria stygia*, which was not found in the SMTP material, but in the collection of the Naturhistoriska riksmuseet.

Tabell 2. Antal noterade arter i *Callidora*, *Casinaria*, *Echthronomas*, *Enytus*, *Eriborus*, *Gonotypus*, *Lemophagus*, *Leptocampoplex*, *Meloboris*, and *Tranosemella*. # SMTP – antal arter noterade i Svenska Malaiseprojektets material; Singletons – antal arter representerade av ett enstaka exemplar i vårt material; Single trap – arter hittade i en enda fälla; New for SE – arter som representerar nya fynd för Sverige; Previous # – antal arter hittils kända från Sverige; # not in SMTP – de av dessa som hittils inte har hittats i SMTP-materialet; Total Europe – totalt antal arter kända i Europa. *inklusive en art, *Casinaria stygia*, som inte hittades i SMTP-materialet, utan i Naturhistoriska riksmuseets samling.

Genus	**# SMTP**	**Singletons**	**Single trap**	**New for SE**	**Previous #**	**# not in SMTP**	**Total Europe**
Callidora	2	0	1	1	1	0	2
Casinaria	14*	3	3	8*	7	1	31
Echthronomas	2	0	0	0	4	2	4
Enytus	4	1	2	3	3	2	8
Eriborus	2	0	0	2	1	1	8
Gonotypus	1	0	0	0	1	0	1
Lemophagus	4	1	3	3	1	0	5
Leptocampoplex	1	0	0	0	1	0	1
Meloboris (Nepiera)	4	0	0	2	2	0	7
Tranosemella	3	1	1	1	2	0	4
Total	37	6	10	20	23	6	71

**Casinaria moesta* (Gravenhorst, 1829) – Sweden: Öl, Mörbylånga kommun, Gamla Skogsby (Kalkstad), 56.6167N, 16.507617E, meadow with shrub vegetation, Malaise trap. 29.vi. –18.vii.2005. leg. SMTP (1 male)

Casinaria morionella Holmgren, 1860

**Casinaria nigripes* (Gravenhorst, 1829) – Sweden: Sö, Haninge kommun, Tyresta, Urskogsslingan, 59.1768N, 18.246933E, tall, flat-rock pine forest, Malaise trap. 20.vii.–11.viii.2004. leg. SMTP (1 male)

**Casinaria pallipes* Brischke, 1880 – Sweden: Go, Gotlands kommun, Roleks, 57.536783N, 18.337883E, border between mixed pine forest and open grazed calcareous pasture, Malaise trap. 2.ix. –8.xi.2005. leg. SMTP (1 female)

Casinaria petiolaris (Gravenhorst, 1829)

**Casinaria stygia* Tschek, 1871 – Sweden: Uppland [no precise locality information available], 12.vi.1912. leg. Abraham Roman (1 female) (NHRS-HEVA000016104)

**Casinaria trochanterator* Aubert, 1960 – Sweden: Öl, Mörbylånga kommun, Gamla Skogsby (Kalkstad), 56.6167N, 16.507617E, meadow with shrub vegetation, Malaise trap. 18.vii. –1.viii.2005. leg. SMTP (1 male)

Echthronomas facialis (Thomson, 1887)

Echthronomas quadrinotata (Thomson, 1887)

Enytus apostatus (Gravenhorst, 1829)

**Enytus appositor* (Aubert, 1970) – Sweden: Vr, Munkfors kommun, Ransäter, Rudstorp, 59.772956N, 13.473714E, sandy railway embankment through pasture-land, Malaise trap. 23.vii.–12.viii.2005. leg. SMTP (1 female)

**Enytus crataegellae* (Thomson, 1887) – Sweden: Öl, Mörbylånga kommun, Gamla Skogsby (Kalkstad), 56.6167N, 16.507617E, meadow with shrub vegetation, Malaise trap. 15.vi.–29.vi.2005. leg. SMTP (1 female)

**Enytus styriacus* (Horstmann, 1980) – Sweden: Lu, Jokkmokks kommun, Muddus nationalpark, 66.769533N, 20.111383E, blueberry spruce forest, Malaise trap. 15.vii.–16.viii.2005. leg. SMTP (1 female)

**Eriborus obscuripes* Horstmann, 1987 – Sweden: Up, Älvkarleby kommun, Båtfors, 60.46065N, 17.317817E, mixed pine forest with blue berry, Malaise trap. 17.vii.-16.viii.2005. leg. SMTP (4 females)

**Eriborus rufopictus* Horstmann, 1987 – Sweden: Vr, Munkfors kommun, Ransäter, Rudstorp, 59.772956N, 13.473714E, sandy railway embankment through pasture-land, Malaise trap. 7.vii.–15.vii.2005. leg. SMTP (1 female)

Gonotypus melanostoma (Thomson, 1887)

**Lemophagus crioceritor* Aubert, 1986 – Sweden: Sm, Torsås Kommun, Söderåkra, Påboda, 56.4347232N, 16.0708442E, private garden, Malaise trap. 1.viii.–16.viii.2008. leg. SMTP (1 female)

Lemophagus curtus Townes, 1965

**Lemophagus errabundus* (Gravenhorst, 1829) – Sweden: Up, Håbo kommun, Biskops-Arnö, 59.672133N, 17.50085E, elm grove, Malaise trap. 20.v.–20.vi.2005. leg. SMTP (1 female)

**Lemophagus pulcher* (Szépligeti,1916) – Sweden: Sm, Nybro kommun, Bäckebo, Grytsjöns naturreservat, Äng, 56.931407N, 16.085536E, old moisty haymaking meadow at edge of mixed forest, Malaise trap. 18.v.–15.vi.2006. leg. SMTP (1 female)

Leptocampoplex cremastoides (Holmgren, 1860)

Meloboris collector (Thunberg, 1824)

**Meloboris miae* Haraldseide, 2021 – Sweden: Sm, Nybro kommun, Bäckebo, Grytsjöns naturreservat, Äng, 56.931407N, 16.085536E, old moisty haymaking meadow at edge of mixed forest, Malaise trap. 10.x.–12.xi.2005. leg. SMTP (1 female)

Meloboris proxima (Perkins, 1942)

**Meloboris pseudocollector* Haraldseide, 2021 – Sweden: Sm, Torsås Kommun, Söderåkra, Påboda, 56.4347232N, 16.0708442E, private garden, Malaise trap. 3.x.–1.xi.2008. leg. SMTP (2 females)

**Tranosemella citrofrontalis* (Hedwig, 1939) – Sweden: Sm, Nybro kommun, Alsterbro/Alsterån, 56.936536N, 15.920167E, mixed forest, Malaise trap. 5.vi.–10.vi.2005. leg. SMTP (1 male)

Tranosemella coxalis (Brischke, 1880)

Tranosemella praerogator (Linnaeus, 1758)

Discussion

An interactive key to make Campopleginae genera more accessible

An interactive key as we introduce it here has many advantages. Identification is typically much faster than with dichotomous keys, as the character priorities are updated each time some character state has been set, in order to maximize the informativeness of the suggested characters. This is especially valuable in complex situations with a lot of variability of certain morphological characters within a genus. Furthermore, it is possible to search for characters that appear rare or even unique to a user who has already gained some experience with the group. Such characters might lead directly to the correct identification, while they might only appear late or not at all in a dichotomous key (Cerretti et al. 2012, Kerner et al. 2021, Klimmek & Baur 2018).

However, there are also some disadvantages, especially in the construction of the key. First of all, interactive keys require a comprehensive understanding of the variability of all the characters in every taxon, while this is not necessary for dichotomous keys. They are thus far more time-consuming to generate. Characters that are important for distinguishing some of the groups might not be relevant in others, but they still will appear in the list of an interactive key, which sorts characters strictly for their distinguishing potential. Furthermore, it is not possible to include multiple characters with different weights in a single couplet, for instance by using qualifiers such as “often” or “usually”. And finally, the software used might not be supported forever, and interactive keys thus are always in danger of losing their interface.

In the case of the European genera of Campopleginae, we consider these disadvantages being by far outweighed by the advantages. The database underlying the interactive key can regularly be exported in a format readable by other software packages, i.e., as an annotated XML file. And there is another strong argument for an online key, i.e., that it can remain dynamic and thus accommodate future insights. This is especially important in Campopleginae, where the coming years will certainly improve our understanding of the generic limits and intra-generic variability. The difficulty with current genus circumscriptions is caused in part by extensive homoplasy, but in part also by imperfect definitions (Horstmann 2004). Many genera will turn out as not monophyletic once molecular data has been consulted to construct a stable phylogeny.

In combination with the extensive illustrations and species portraits, the interactive key is an ideal tool also for students and laymen entomologists who dare tackle such a poorly known group. By setting up a form for feedback on the key, we hope to encourage the community to share their experience with the key and suggest ways to further improve it.

New Campopleginae for Sweden

Our analysis of ten genera of Campopleginae in about one third of the samples of the Swedish Malaise Trap Project demonstrate that there is still a lot to be discovered, even in countries as well-known as Sweden, the birth-place of modern classification. More than half of the 37 species found represent first records for the country. This proportion is rather high even for Darwin wasps, as Campopleginae are especially poorly studied, but even subfamilies that were considered rather well-known in the past yielded numerous new discoveries (Johansson 2020a, b, 2021, Johansson & Klopfstein 2020, Klopfstein 2014), and this is even more the case for taxonomically difficult genera and species groups (Johansson 2018, Johansson & Cederberg 2019). Among the remaining Campopleginae genera, there are still several large ones, especially *Hyposoter, Olesicampe,* and most of *Campoplex,* that have not yet been revised in modern times and from which not only new faunistic insights, but also new species for science are to be expected.

Together, these results confirm earlier suggestions of a high unknown diversity of parasitoid wasps even in well-studied faunas (Hebert et al. 2016, Ronquist et al. 2020). It is vital that such poorly known groups receive increased attention in future studies, in order to adequately reflect their diversity, ecological importance, and conservation needs.

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Supplementary material

Supplementary File S1: List of Campopleginae species from Europe with species author names.
Supplementary File S2: Plates of the European genera of Campopleginae.
Supplementary File S3: Specimen data.
Supplementary files are available for download at http://et-online.nu/.

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Sammanfattning

Klämbaksteklar (underfamilj Campopleginae i familjen Ichneumonidae) tillhör några av de minst kända insektsgrupperna i Sverige. Denna avsaknad på kunskap beror till stor del på bristfälliga identiferingsnycklar. De 835 europeiska arterna är fördelade på 42 släkten och artsavgränsningen för många arter är oklar, vilket gör dem mycket svåra att artbestämma med hjälp av den litteratur som finns att tillgå. Vi har granskat olika karaktärsystem för släktesidentifiering och presenterar här en interaktiv, dynamisk nätbaserad nyckel till de europeiska släktena. Vi använder nyckeln för att identifiera 3,500 exemplar insamlade i Svenska Malaisefälleprojektet till släktesnivå. Individer från tio relativt små släkten har sedan identiferas till artnivå och vi rapporterar här 37 arter, av vilka 20 är nya fynd för landet. I materialet finns ett stort antal arter som enbart hittats på en enda lokal, vilket tyder på att mycket återstår att upptäcka, även i den annars så välkända Svenska faunan.